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Carbon flows in the Westerschelde estuary (The Netherlands) evaluated by means of an ecosystem model (MOSES)

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Abstract

The autotrophic production and heterotrophic consumption of organic matter in the Westerschelde, a highly turbid and eutrophic estuary in the Southwest Netherlands is examined by means of a dynamic simulation model. The model describes the ecologically relevant processes in thirteen spatial compartments and adequately fits most observed data.

Three autotrophic processes are included in the model. Net pelagic photosynthetic production is relatively low (average 41 gC m^{-2} yr^{-1}) and three spatial compartments near the turbidity maximum zone are respiratory sinks of phytoplankton biomass. According to the model, net phytobenthic primary production is more important than pelagic primary production in the upstream half of the Westerschelde. On the scale of the entire estuary, benthic primary production amounts to about 60% of pelagic primary production. Water-column nitrification, which is very important in the nitrogen cycle, is most pronounced near the turbidity zone where it accounts for the major autotrophic fixation of carbon (up to 27 g C m^{-2} yr^{-1}). Viewed on the scale of the total estuary, however, the process is not very important.

Less than 20% of total organic carbon input to the estuary is primary produced, the remainder is imported from waste discharges and from the river.

The degree of heterotrophy of the Westerschelde estuary proved to be one of the highest yet reported. On average 380 g carbon per square metre is net lost per year (range 200–1200 gC m^{-2} yr^{-1}). The yearly community respiration (bacterial mineralization, respiration of higher trophic levels and sedimentation) is 4 to 35 times (estuarine mean of 6) higher than the net production. This degree of heterotrophy is highest near the turbidity maximum and generally decreases from the freshwater to the seaward boundary. About 75% of all carbon losses can be ascribed to pelagic heterotrophic processes; the sediment is only locally important.

Mineralisation rates are highest in the turbidity region, but as only a fraction of total carbon resides here, less than 20% of all organic carbon is lost in this part of the estuary. This result is in contradiction with a previous budget of the estuary, based on data of the early seventies, where more than 80% of all carbon was estimated to be lost in the turbidity zone. Part of this discrepancy is probably caused by changes that have occurred in the estuary since that time.

Due to the high heterotrophic activity, nearly all imported and *in situ* produced carbon is lost in the estuary itself and the Westerschelde is an insignificant source of organic matter to the coastal zone.

The model estuary acts as a trap for reactive organic matter, both from the land, from the sea or *in situ* produced. Internal cycling, mainly in the water column, results in the removal of most of the carbon while the more refractory part is exported to the sea.

Introduction

Estuaries are characterized by a strong diversity in carbon sources. This is because of the existence of an intertidal habitat, the supply of nutrients and organic material from the river and from the sea and the input of matter from human origin. If turbidity remains limited, estuaries can also support a high primary production as nutrients are abundant. Nevertheless, estuaries are usually heterotrophic ecosystems (Billen *et al.*, 1991; Smith & Hollibaugh, 1993) where respiratory processes exceed *in situ* production.

The Westerschelde estuary (260 km^2 in SAWES, 1991) drains about 21580 square kilometres of land in one of the most densely populated and highly industrialised regions of Europe (Wollast, 1988). This estuary is unusual due to the high degree of eutrophication which results from the discharge of untreated wastes (Heip, 1988) and due to the high residence time of the water masses (Soetaert & Herman, 1995a). A turbidity maximum resides in the upper estuarine part which increases the residence time of particulates in the estuary.

According to Wollast (1976, 1983) nearly all the degradable organic matter is mineralized in the upper estuarine region and less than 10% of total land-derived carbon reaches the sea. This clumping of bacterial activity in the turbidity zone seems in contradiction with results from Goosen *et al.* (1992) who found bacterial production in the marine part of the estuary to be substantial, even compared to microbial activity in the turbidity zone.

In what follows we present a tentative annual mass budget of the most important carbon sources and fluxes in the eutrophic Westerschelde estuary of the years 1980–1985. This budget is based on an estuarine ecosystem model that includes all major physical, ecological and biochemical processes. As the model formulations and goodnesses of fit were published elsewhere (Soetaert & Herman, 1995a, b; Soetaert *et al.*, 1994) we restrict ourselves to describing the major carbon fluxes. We illustrate the variability in time and space of the carbon dynamics as put forward by the model. Finally, we examine the degree of heterotrophy along the estuarine length axis and compare this with data from other coastal and estuarine areas.

Table 1. State variables modeled in MOSES.

State variable	Units
Fast-decay detritus	g C m^{-3}
Slow-decay detritus	g C m^{-3}
Freshwater diatoms	g C m^{-3}
Freshwater flagellates	g C m^{-3}
Brackish and marine diatoms	g C m^{-3}
Brackish and marine flagellates	C m^{-3}
Micro-zooplankton	g C m^{-3}
Brackish meso-zooplankton	g C m^{-3}
Marine meso-zooplankton	g C m^{-3}
Hyperbenthos	g C m^{-3}
Detrital silicate	g Si m^{-3}
Dissolved silicate	g Si m^{-3}
Nitrate and nitrite	g N m^{-3}
Ammonia	g N m^{-3}
Oxygen	g O m^{-3}
Chlorides	g Cl m^{-3}
Suspended matter	g m^{-3}
Benthic diatoms	g C m^{-3}
Benthic deposit feeders	g C m^{-3}
Benthic suspension feeders	g C m^{-3}

Material and methods

The MOdel of the Scheldt EStuary (hereafter referred to as MOSES) is a thirteen spatial compartment, tidally averaged model that describes carbon, nitrogen, oxygen and silicate fluxes in the pelagic, subtidal and intertidal area. The model is in essence a carbon model and coupling of all fluxes is done by means of stoichiometric equations. State variables included in MOSES are in Table 1. In the pelagic realm they comprize four phytoplankton and two mesozooplankton pools, the microzooplankton, the hyperbenthos, two detrital fractions (with different degradabilities), a dissolved and particulate silicate fraction, two nitrogen pools, oxygen, chlorides and suspended matter. Bacteria are not modeled separately but included in the detritus fraction. Benthic diatoms, suspension and deposit feeders are modeled in the intertidal bottom.

The spatial compartimentalisation of the pelagic and intertidal area is in Fig. 1. Subtidal areas are defined as that part of a pelagic compartment that is deeper than the intertidal and less deep than the channels. The channel bottom (depth >10 m) is assumed to be biologically and biochemically inert and is not modeled.

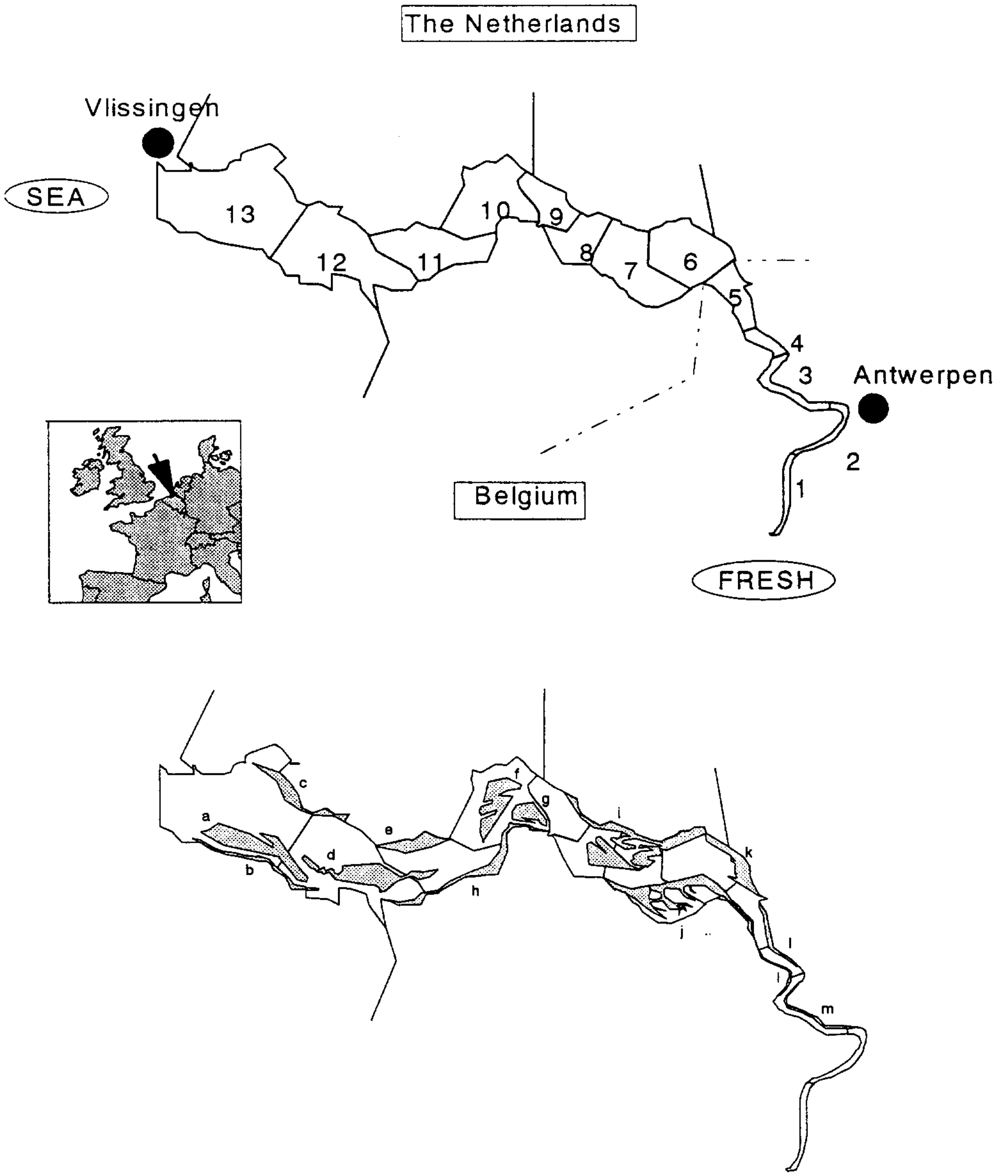


Fig. 1. Compartimentalisation of the pelagic (above) and the intertidal (below) in the Westerschelde model.

Pelagic constituents are moved by means of a tide-averaged, constant volume, advective-diffusive formulation (Soetaert & Herman, 1995a). Both a dissolved and a particulate (mud) transport are included. Resuspension and sedimentation of suspended matter is patterned according to Van Maldeghem *et al.* (1993). It is described as a fixed part of pelagic load that sediments to the bottom per day. The transport and sedimentation behavior of the pelagic detrital and living fractions is inbetween the behavior of dissolved and particulate matter. Organic carbon sedimentation is such that yearly values of benthic C fluxes obtained from Middelburg *et al.* (1995 and pers. comm.) are reproduced (Soetaert & Herman, 1993).

The biological processes described in MOSES are primary production (Soetaert *et al.*, 1994), feeding, respiration, excretion and physiological and predatory mortality. Biotic interactions are summarized in Fig. 2. In most cases the rate of change is expressed as first-rate kinetics with respect to the relevant state variable. Temperature dependence is modeled by means of a Q10 formulation, limitation functions are mostly described as a Monod equation.

Light-limited phytoplankton primary production is based on the model of Eilers & Peeters (1988). The description of algal primary production also includes nutrient limitation. Apart from grazing, dark respiration and salinity-stress mortality are the loss terms of phytoplankton standing stock (Soetaert *et al.*, 1994). Benthic algal production is modeled in much the same way as phytoplankton production, it is limited to the periods the intertidal flats are dry and a CO_2 limitation factor is included.

Higher trophic levels (micro- and mesozooplankton, hyperbenthos, benthic suspension and deposit feeders) are food-limited (threshold formulation). Part of ingested food is lost as faeces, another part is respired. Mortality includes an oxygen-dependent term (higher mortality when oxygen-depleted); the two mesozooplankton groups are also subjected to a salinity-stress mortality. An additional predatory mortality term allows for the inclusion of grazing by predators that are not explicitly modeled (e.g. fish). Benthic larvae (spawning) are included in the microzooplankton.

Aerobic organic matter degradation, denitrification and nitrification are the modeled biochemical processes in the water column (see Soetaert & Herman, 1995b). Oxygen is the limiting resource for aerobic mineralisation and nitrification; denitrification is inhibited at high oxygen concentrations. The availability of detritus is furthermore limiting the denitrification process, while ammonium is a limiting resource for the nitrification process.

Biochemical processes in the bottom are not modeled exhaustively but nutrient and oxygen exchange across the bottom-water interface is represented by means of the diagenetic model of Lancelot & Billen (1985). Organic carbon that sediments to the bottom is considered to be lost to the estuary (mineralized or buried).

Dissolution of particulate silicate and oxygen exchange across the water-air interface are also included in MOSES.

Forcing functions and boundary conditions were either kindly provided by Van Eck (SAWES, 1991) or were obtained from Klepper (1989).

For a detailed description of the model formulations, the obtained parameters and the goodnesses of fit the reader is referred to Soetaert & Herman (1993; 1995a, b) and Soetaert *et al.*, (1994). The model is able to reproduce most observed data that are available (see also Figs 3–4). Data on the benthos and microzooplankton were as yet insufficient to warrant a great calibration effort. Their role in the model is of minor importance compared to the mesozooplankton (Soetaert *et al.*, 1994).

Results

Spatio-temporal plots were produced by averaging the model output of the years 1980–1985 over a year and smoothing this by means of a double-weighted least squares regression (SYSTAT, 1992).

Description of spatial and temporal characteristics of the major organic carbon stocks in the model (Fig. 5)

Phytoplankton carbon in the model ranges from 0.02 gC m^{-3} in winter to 1.9 gC m^{-3} near the freshwater part in summer. Yearly averaged phytoplankton biomass drops from 1 gC m^{-3} near the freshwater part to 0.2 gC m^{-3} in the middle of the estuary after which biomass increases slightly (0.3 gC m^{-3}) towards the sea. The two peaks of phytoplankton biomass correspond with a freshwater and a brackish + marine community. For a detailed description of the factors that are responsible for this spatio-temporal pattern we refer to Soetaert *et al.* (1994).

Total organic carbon in the model ranges from 3 gC m^{-3} to 16 gC m^{-3}. In winter and autumn, organic matter peaks near the turbidity maximum (model spatial compartments 2 and 3). In summer, a maximum is observed very near to the freshwater boundary. This partly reflects the high phytoplankton standing stocks there. In general the organic load in the model decreases towards the sea.

Benthic diatom carbon in the intertidal increases from the seaward boundary (yearly average 4 gC m^{-2}) towards upstream (7 gC m^{-2}). Minimum biomass in the model is 2 gC m^{-2}, maximum biomass is 12 gC m^{-2}.

Description of spatial and temporal patterns of the various processes in the model (Fig. 6)

Aerobic mineralisation processes in the water column (Fig. 6a) are strongly patterned by the load of total organic carbon in the model (Fig. 5) but mineralisation is relatively more pronounced towards the sea

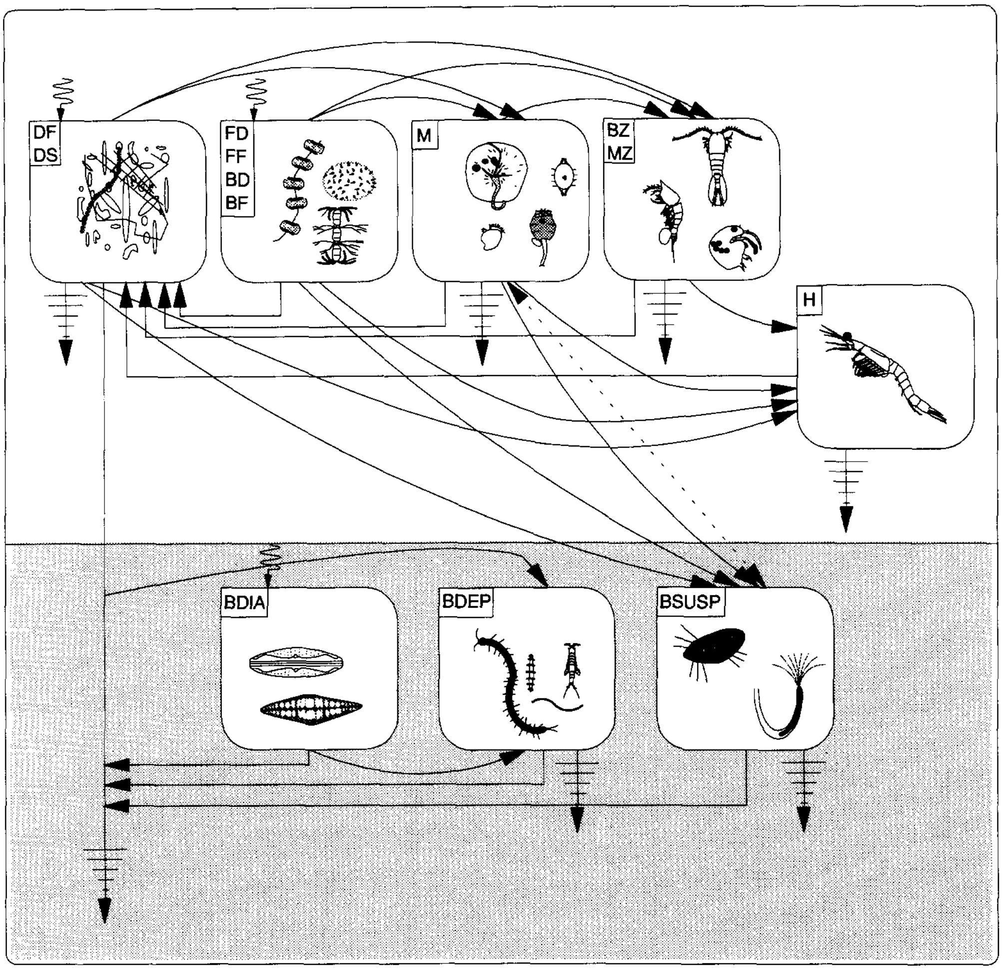


Fig. 2. Biotic interactions in MOSES. Curved arrows denote food relationships; undulated arrows denote primary production; the dotted arrow denotes spawning activity; the vertical arrows that are crossed with small lines indicate carbon loss to the system. DF = fast decaying detritus; DS = slow-decaying detritus; FD = freshwater diatoms; FF = freshwater flagellates; BD = brackish diatoms; BF = brackish flagellates; M = microzooplankton; BZ = brackish meso-zooplankton; MZ = marine meso-zooplankton; H = hyperbenthos; BDIA = benthic diatoms; BDEP = benthic depositfeeders; BSUSP = benthic suspension feeders.

and towards the freshwater boundary. This reflects the higher reactivity of organic matter imported from the river and the sea, compared to the resident organics in the mid-estuary.

Water-column denitrification rates in the model (Fig. 6b) clearly peak towards the fresh-water part of the estuary. They are substantially higher in summer when oxygen content of the water column is lower and temperature higher.

Pelagic carbon loss rates due to sedimentation (Fig. 6c) are most pronounced in the mid-estuary where tidal flats are relatively most abundant. Near the sea and near the river, the sedimentation surface is insignificant compared to total volume and sedimentation rates (expressed per volumetric units) are very small. The seasonality of sedimentation is not very pronounced and somewhat reflects carbon standing stock. When expressed per unit of intertidal surface (Fig. 6j) the amount of carbon lost to the intertidal flats (sedimentation + benthic uptake) decreases towards the sea. The slight increase at the three most downstream intertidal flats reflects the higher benthic biomass there.

The amount of carbon respired by the higher trophic levels (Fig. 6d) is most pronounced in summer in the marine part of the estuary. This reflects mesozooplankton standing stock (Soetaert & Van Rijswijk, 1993;

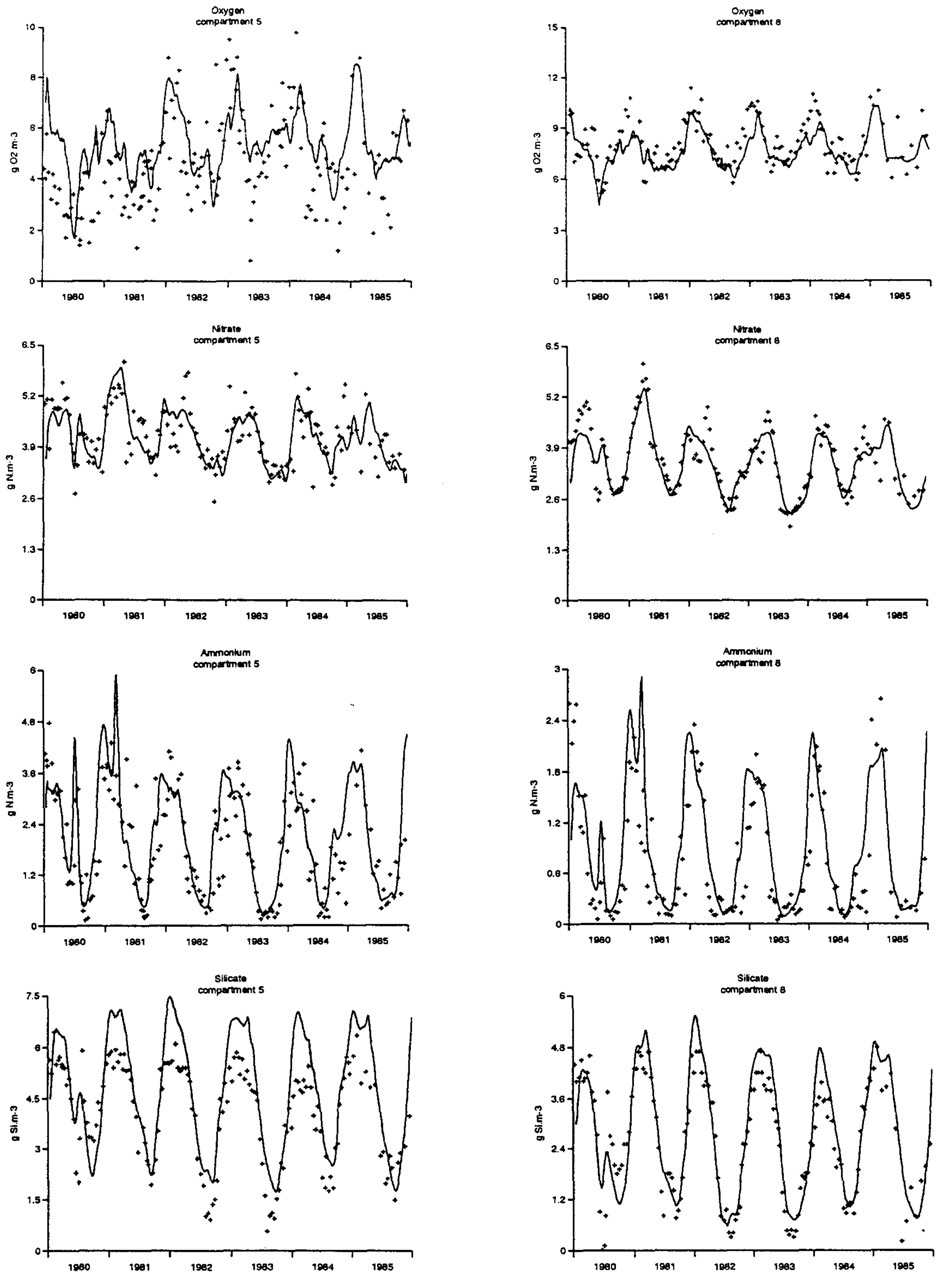


Fig. 3. Goodness of fit of modeled (full line) and observed ('+') variables for model spatial compartments 5 and 8. Variables are Oxygen, Nitrate, Ammonium and silicate.

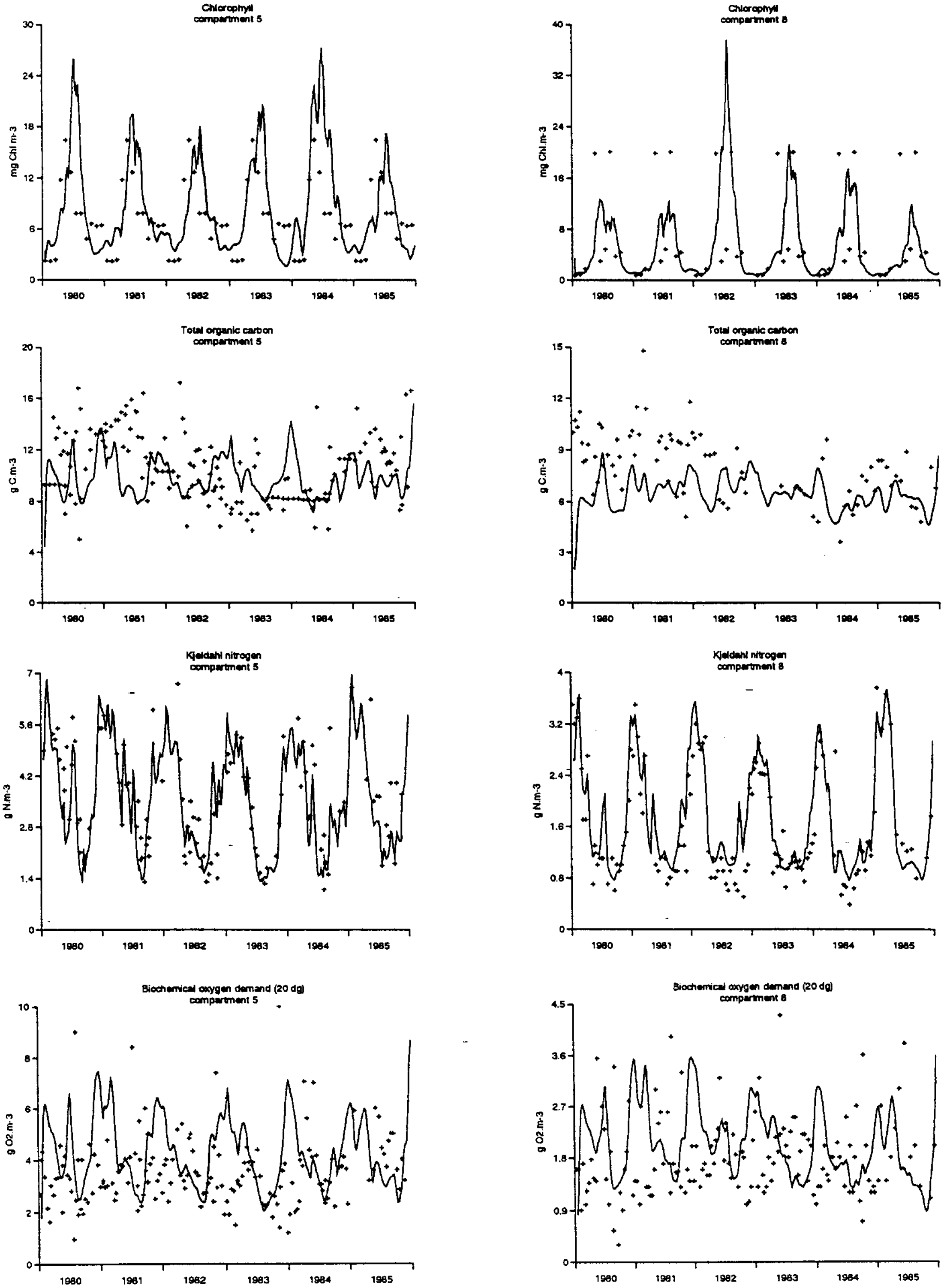
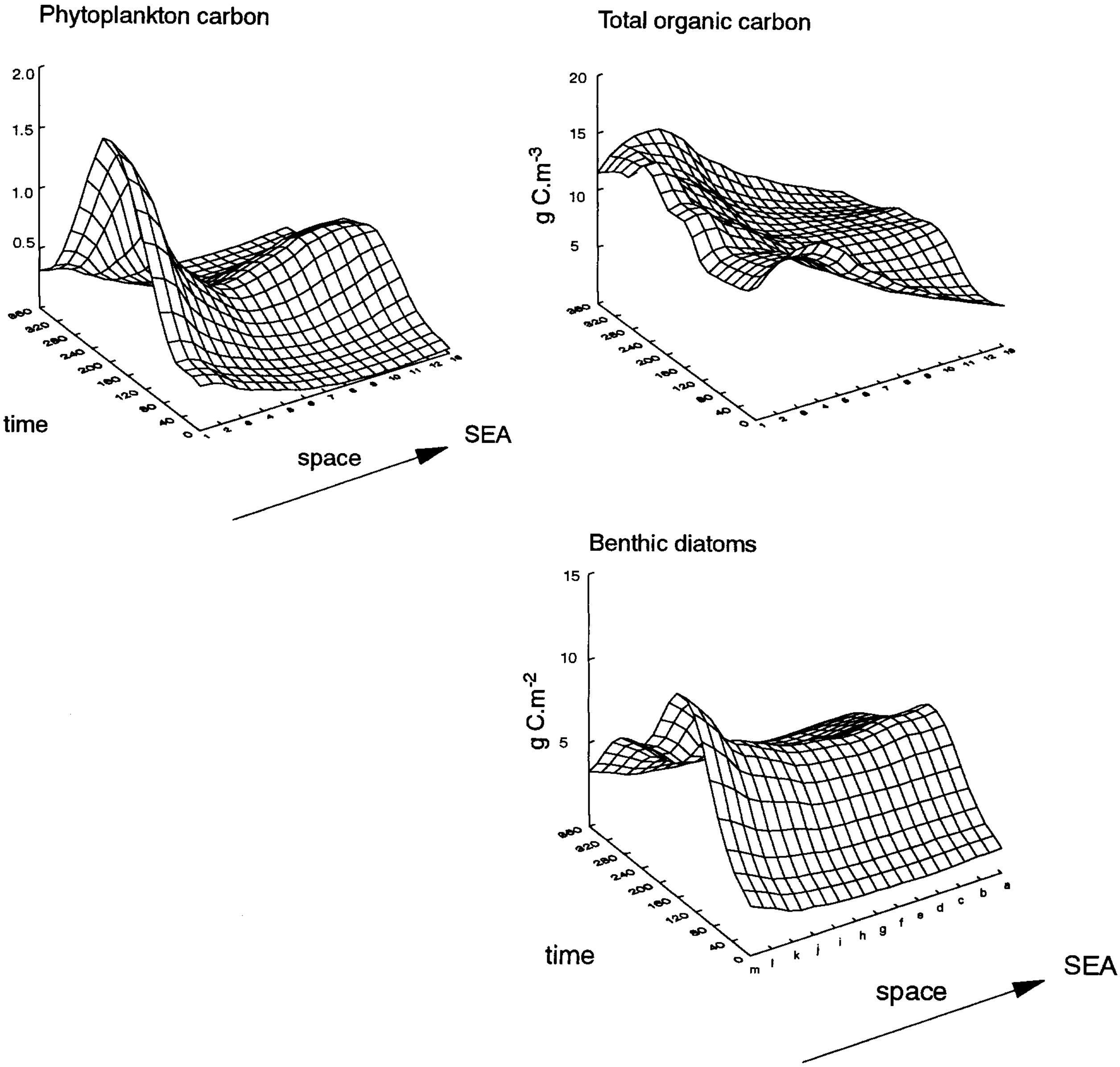


Fig. 4. Goodness of fit of modeled (full line) and observed ('+') variables for model spatial compartments 5 and 8. Variables are Chlorophyll, Total organic carbon, Kjeldahl nitrogen and biochemical oxygen demand.



Phytoplankton carbon

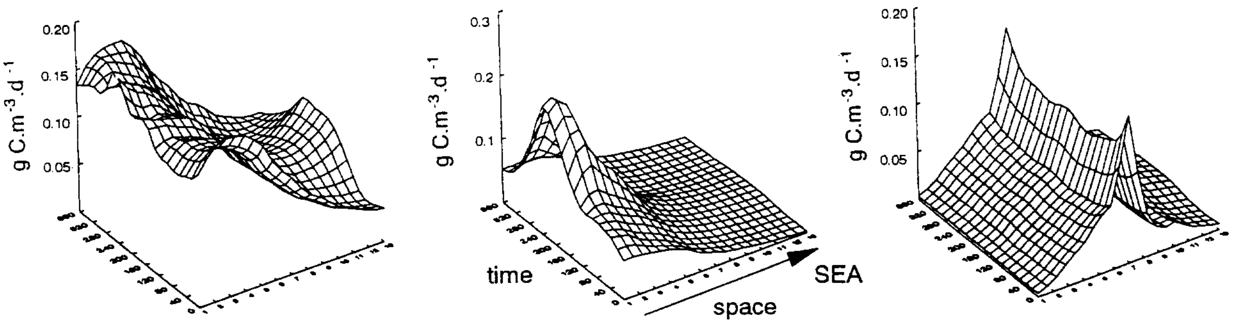
Total organic carbon

Benthic diatoms

Fig. 5. Temporal and spatial patterns of the major carbon stocks (six years average of model output). The X axis represents the space axis, Y gives the day number (starting on 01-jan, ending on 31-dec). Phytoplankton and total organic carbon are in pelagic compartments (1–13), benthic diatom carbon is in intertidal compartments (a–m).

Soetaert & Herman, 1994). In the brackish part of the estuary, carbon loss by the higher trophic levels is more evenly distributed throughout the year. Winter and spring consumption is mainly caused by mesozooplankton whose biomass peaks at that period (Soetaert & Van Rijswijk, 1993) while in summer microzooplankton consumption is more important in the model. Due to the different spatial and temporal characteristics of its constituents, the distribution of total carbon consumption in time and space (Fig. 6e) is complicated. The general trend reflects pelagic aerobic mineralisation rates, the denitrification has greatest impact upstream, sedimentation processes are most prominent in the mid-estuary and carbon lost by respiration of higher trophic levels is slightly obvious in total C consumption near the sea.

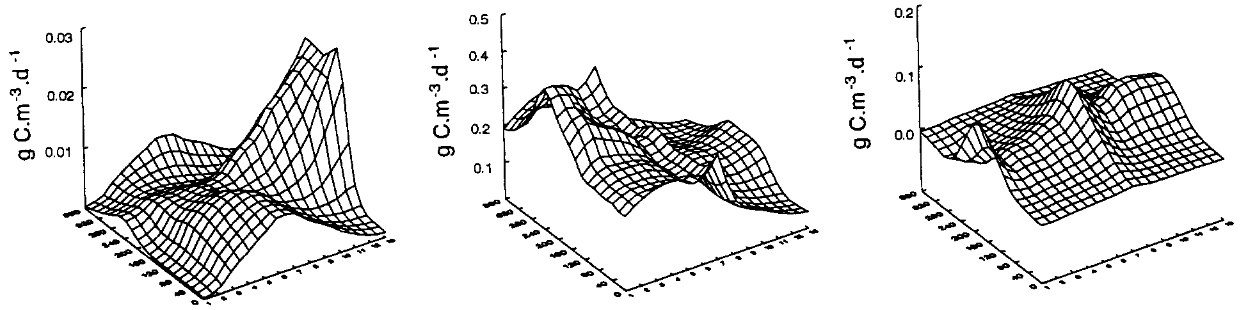
Among the primary production processes, nitrification rates (Fig. 6g) decline steadily towards the sea



(a) Aerobic mineralisation

(b) Pelagic denitrification

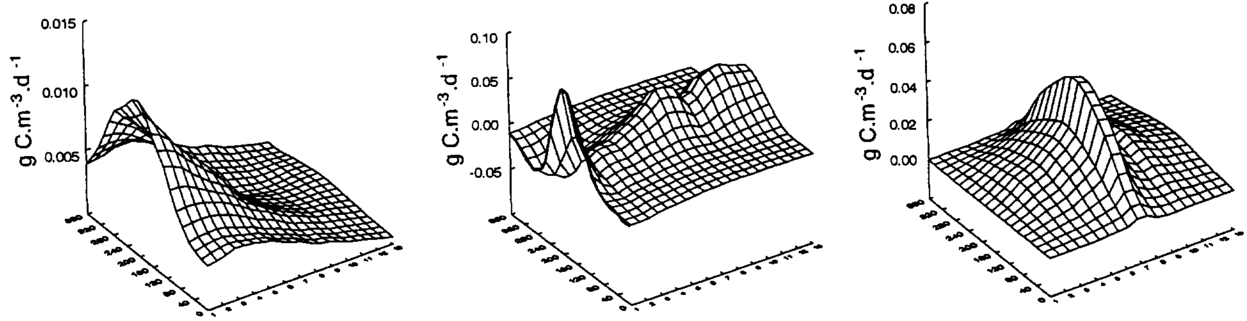
(c) Sedimentation



(d) Respiration higher trophic levels

(e) Total C consumption

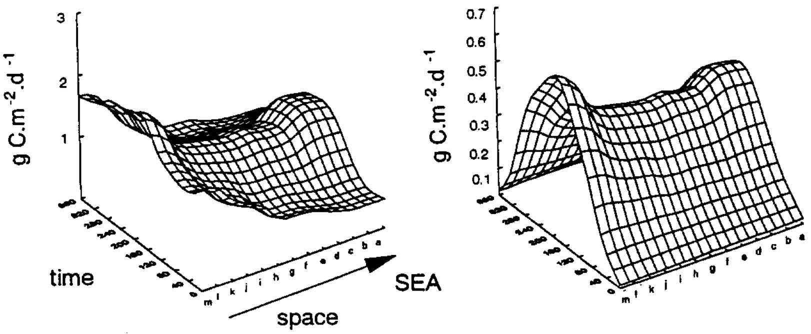
(f) Total autotrophic production



(g) Nitrification

(h) Net phytoplankton production

(i) Net benthic diatom production



(j) Carbon flux to the bottom

(k) Net benthic diatom production

Fig. 6. Temporal and spatial patterns of the various carbon consuming (6a...6e, 6j) and carbon producing processes (6f...6i, 6k) (six years average of model output). Carbon flux to the bottom (Fig. 6j) and benthic diatom production (Fig. 6k) are in the intertidal compartments, the other carbon processes are in the pelagic compartments.

Table 2. Comparison this model-Wollast (1976) in 1000 tonnes carbon per year. 'Upstream' = model compartments 1–4 'Downstream' = model compartments 5–13

10^3 ton C yr^{-1}		Model	Wollast
	Total import	+104	+102
Upstream			
	Degradation	− 13	− 40
	Sedimentation	− 1	− 46
	Production	+ 0.5	-
	Secondary prod.	− 0.3	-
	Other processes	− 0.2	-
	net C-loss	− 14	− 86
Downstream			
	Degradation	− 66	− 8
	Sedimentation	− 20	− 4
	Production	+ 18	+ 4
	Secondary prod.	− 9	-
	Other processes	− 7	-
	net C-loss	− 84	− 8
	Export to the sea	− 6	− 8

to very low levels. They peak in summer. Net phytoplankton production (Fig. 6h) is negative all over the estuary during the darker months, positive production values are attained in summer in all but model spatial compartment 2. Net production is lowest near the turbidity zone (spatial compartments 2–4) and increases both towards the freshwater and marine boundary.

Net benthic diatom production (Fig. 6i), expressed per unit volume is significant in the mid-estuarine region due to the presence of extensive tidal flats there. Benthic diatoms attain positive net production values all over the year. When expressed per unit of intertidal surface (Fig. 6k), net benthic diatom production reflects both the diatom standing stock (increase towards the freshwater zone) and the carbon flux towards the bottom (higher at the three most seaward compartments). The latter stems from the fact that diatom production is mainly CO_2 limited in the model. The sum of all autotrophic processes in the model (Fig. 6f) shows the predominance of benthic diatom production in the mid-estuarine region. The pattern up- and downstream corresponds more closely to phytoplankton primary production but the sharp seasonal gradients of phytoplankton productivity are moderated by the other autotrophic processes.

A yearly averaged carbon budget (Figs 7–9)

Mean net production and consumption rates expressed in pelagic units (g C m^{-3} d^{-1}) as put forward by the model are in Fig. 7. The most upstream part of the estuary (spatial compartment 2–4) is very turbid, causing yearly phytoplankton production to be negative (see Soetaert *et al.*, 1994). As there are almost no intertidal flats there, phytobenthos production is very small. Due to the high load of ammonium in the water column, nitrification is the most important primary production process in MOSES spatial compartments 2 and 3. Towards the middle of the estuary (spatial compartments 5–7), the turbidity of the water column decreases and phytoplankton net production becomes positive. As the intertidal surface/pelagic volume ratio is high in this part, phytobenthos primary production is the main autotrophic process here. Towards the sea, the pelagic gains in importance compared to the intertidal zone. Hence in the downstream part of the estuary (spatial compartments 8–13), phytoplankton production becomes the most important autotrophic process, phytobenthic production ranks second, while nitrification is unimportant here.

Net phytoplankton production in the model varies from −74 to 60 gC m^{-2} (total surface) per year. The phytobenthos produces some 80 to 120 gC m^{-2} (intertidal surface) per year. Total water-column nitrification varies from 4 to 27 gC m^{-2} yr^{-1} (total surface).

Except for model spatial compartment 7, pelagic aerobic mineralisation is the most important heterotrophic process in the estuary. Denitrification rates in the water column are high in the most upstream part of the estuary only. Sedimentation is most important in the mid-estuary. Net carbon consumption by the higher trophic levels is relatively unimportant, except at the most seaward compartments where it comprizes about 15% of all heterotrophic carbon loss.

Due to the funnel shape of the estuary, processes that occur at much lower rates near the sea can nevertheless be more important in absolute terms. The autotrophic and heterotrophic processes, expressed as the total amount of carbon gained or lost per spatial compartment per year are in Fig. 8. The total amount of carbon produced or consumed in the estuary increases almost exponentially with distance downstream. Processes that are linked to the intertidal area have greatest impact in pelagic compartments 6, 7 and 10.

Figure 9 gives the yearly integrated import, export, production and consumption processes for 1980–1985. All in all 104 000 tonnes C yr^{-1} is imported into the

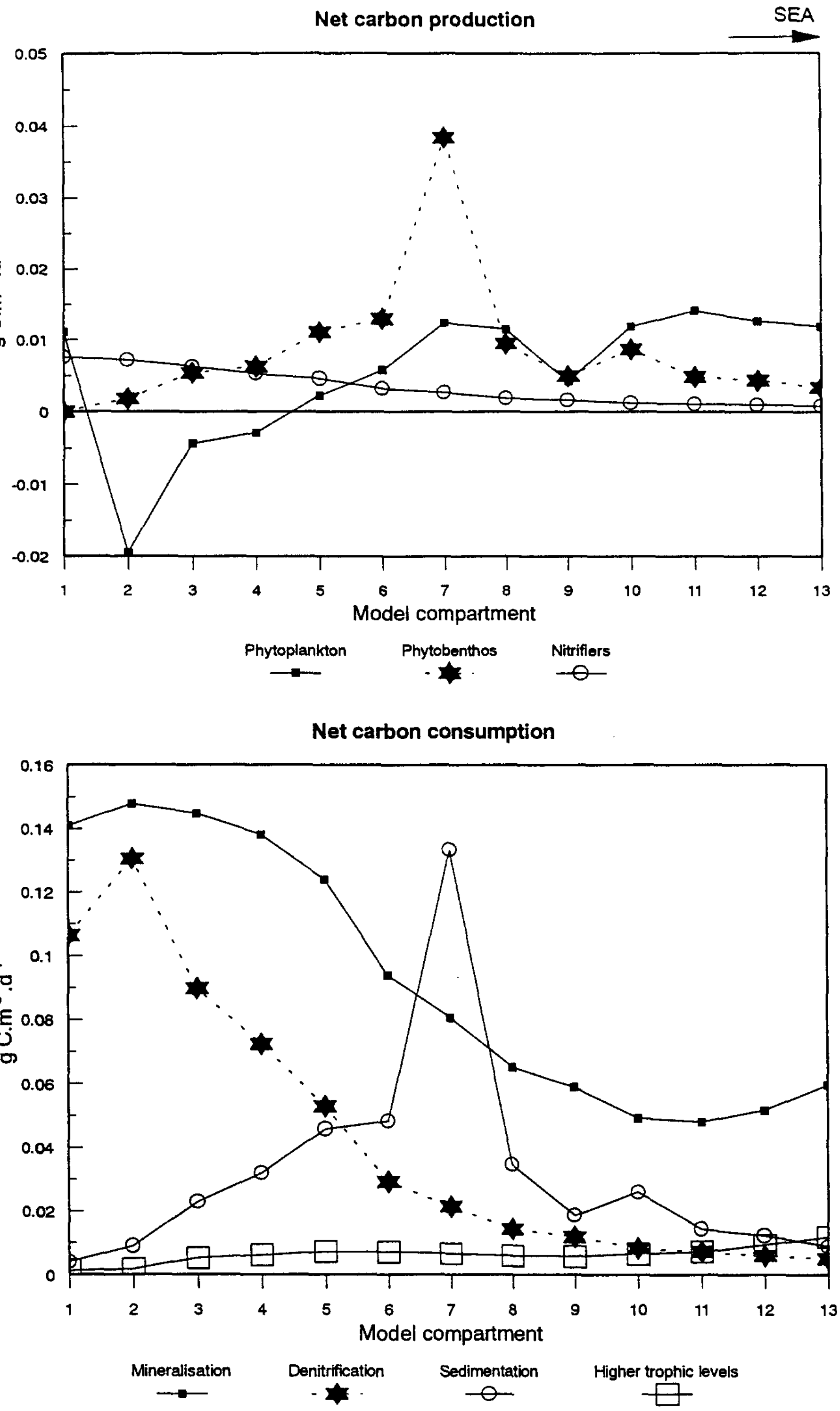


Fig. 7. Yearly averaged process rates (g C. m^{-3} d^{-1}) for the different (pelagic) model compartments.

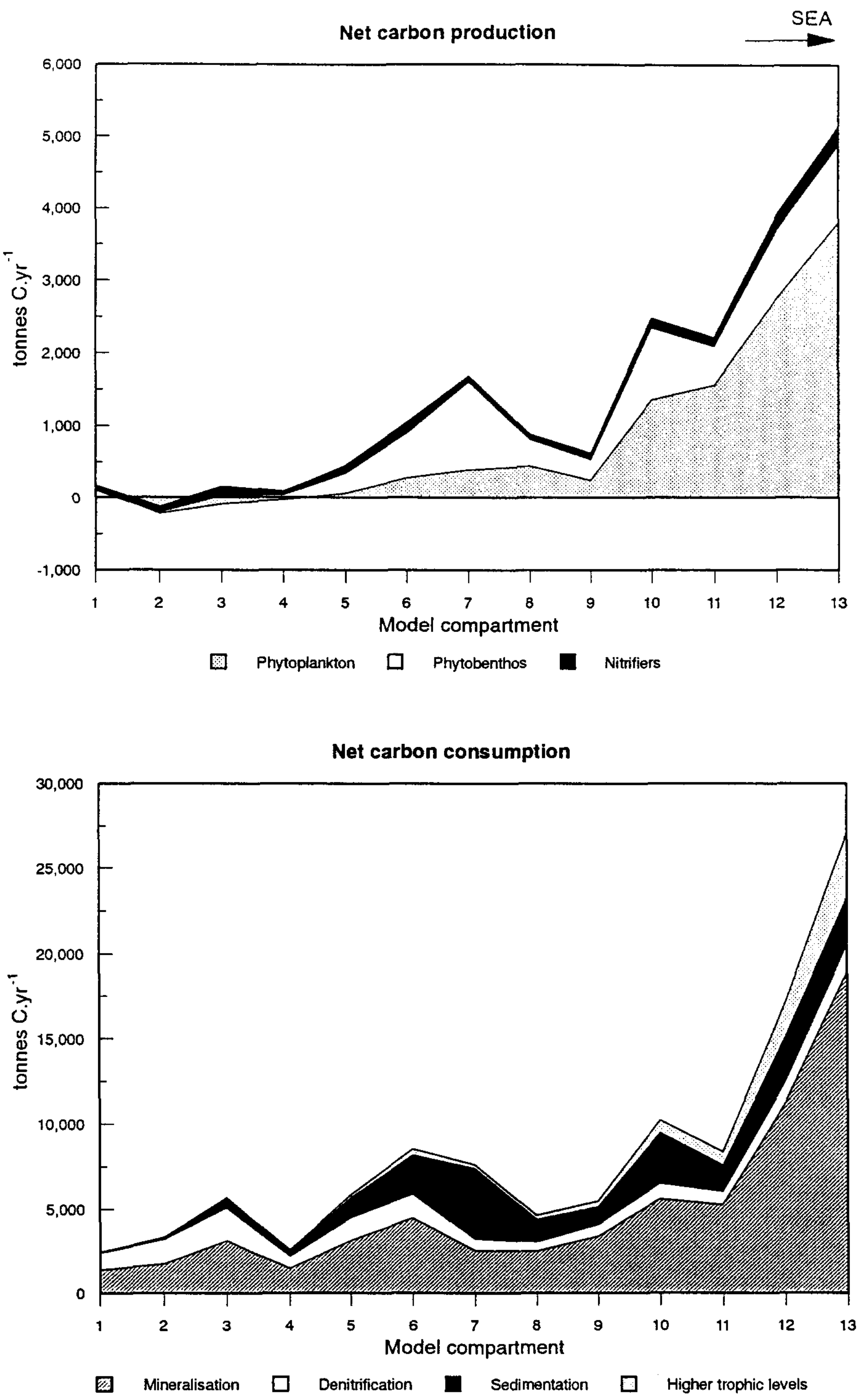


Fig. 8. Yearly carbon budget (tonnes C yr^{-1}) for the different pelagic compartments.

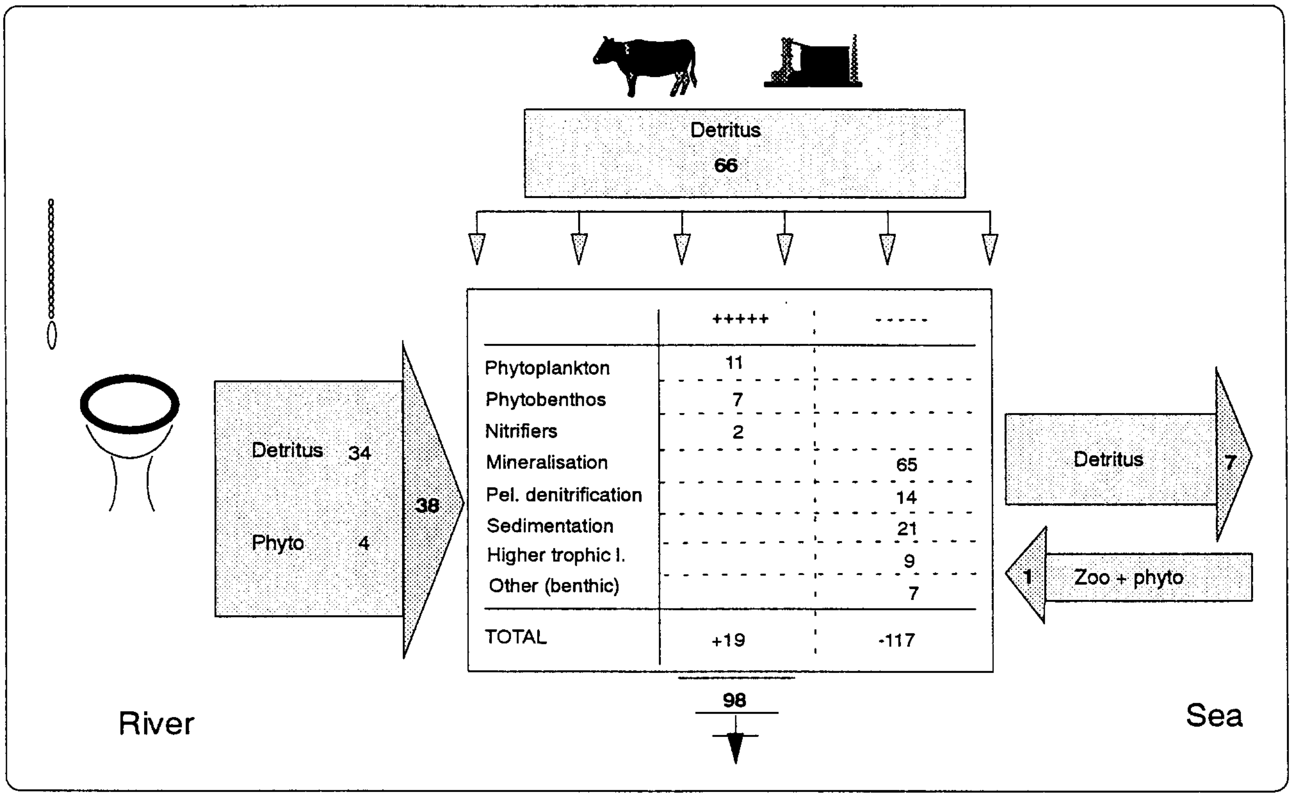


Fig. 9. Global carbon budget of the Westerschelde estuary, in 1000 tonnes C yr^{-1}. Positive values indicate (net) gain, negative values indicate (net) loss. The arrow to the left indicates exchange with the river; the arrows to the right indicate exchange with the sea. The small arrows on top are waste discharges. The bottom arrow indicates net carbon loss in the estuary.

estuary by means of waste discharges or from the river. By far the majority of this carbon consists of detritus. A small amount (1000 tonnes C yr^{-1}) of zoo- and phytoplankton is (net) imported from the sea. The amount of carbon primary produced in the estuary is much less (19 000 tonnes C yr^{-1}). Some sixty percent of this primary carbon is produced by the phytoplankton, thirty percent by phytobenthos, some 10% is formed by nitrifying activity. Amongst the decomposition processes, pelagic aerobic mineralisation is most important in the model (56%) followed by sedimentation (18%) and pelagic denitrification (12%). The higher trophic levels consume some 8% of all carbon in the estuary. Only 7000 tonnes of detrital carbon leaves the estuary at the sea side, while 98 000 tonnes C per year is net lost in the Westerschelde.

Autotrophic/heterotrophic balance (Fig. 10)

The net rate of carbon consumption (g C $m^{-2}yr^{-1}$) and the ratio of respiration versus autotrophic production in the model are in Fig. 10. The Westerschelde estuary is heterotrophic all over and the degree of heterotrophy is very high: carbon respiration is on average six times higher than net primary production and 0.06–0.31 gC m^{-3} is lost in the water column per day. This corresponds to a net carbon loss of 220–1200 gC m^{-2} per year (global estuarine average of 380 gC m^{-2} yr^{-1}). The heterotrophic nature of the estuary is highest near the turbidity maximum (spatial compartment 2) where community respiration is about 35 times higher than net production. The degree of heterotrophy decreases downstream, but respiration/production ratios are overall higher than 4. The slight rise from spatial compartment 11 towards downstream reflects the import of more reactive detritus from the sea, resulting in increased mineralisation rates.

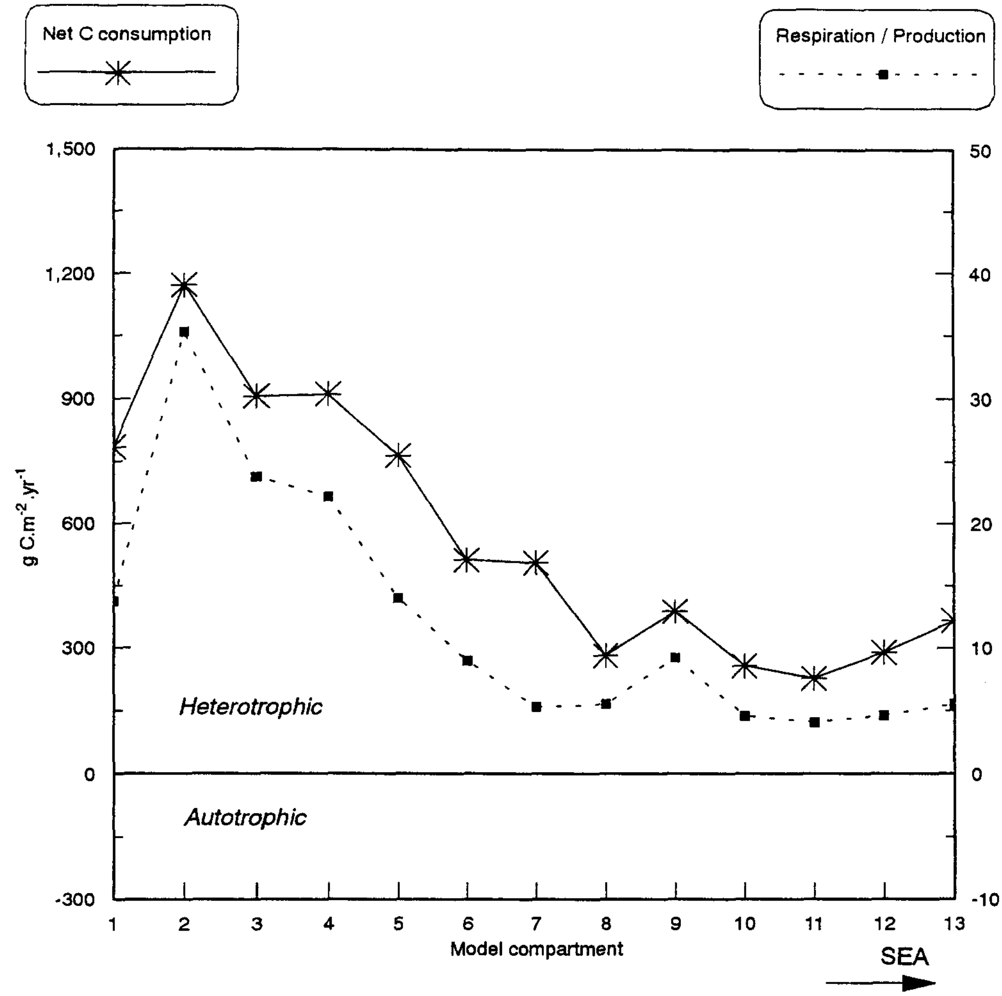


Fig. 10. Yearly net carbon consumption (Respiration – Production) and Respiration/production ratio for the different pelagic model compartments.

Discussion

The distribution of organic carbon in the Westerschelde is affected by physical processes such as residual estuarine circulation and mixing, as well as by a range of biochemical and biological reactions.

Sources of organic carbon

The river Schelde and waste discharges from point sources and tributaries are the main sources of organic matter to the estuary. Each year, they supply about 100 10^3 tonnes of carbon to the ecosystem. Compared to this allochtonous source of carbon, the primary formation of organic matter (in the model) is much less and amounts to 19 10^3 tonnes of carbon per year (some 72 gC m^{-2} yr^{-1}). Some sixty percent of this primary carbon comes from phytoplankton production, the benthic algae account for another 30%, while about 10% is due to pelagic nitrification.

Autotrophic processes

If turbidity remains restricted, the high nutrient load that is typical for many estuaries allows a high primary production at these sites. Hence estuaries are usually considered to be highly productive areas and in some cases they significantly add to coastal enrichment (Peterson *et al.*, 1988). The average phytoplankton production in estuaries was estimated to be about 190 gC m^{-2} yr^{-1} (Boynton *et al.*, 1982; Smith & Hollibaugh, 1993), which is much higher than the average of 41 gC

m^{-2} yr^{-1} that is modeled in the Westerschelde. Reasons for this low phytoplankton productivity are the high turbidity and relatively great depth of the Westerschelde estuary. This results in an adverse environment for the phytoplankton communities which have to spend a large amount of time in darkness (Soetaert *et al.*, 1994). Hence the production potential of the phytoplankton in the Westerschelde is far from being realised.

Due to the high turbidity of the water masses, we assume that benthic primary production is restricted to tidal flats when they are dry (Colijn & de Jonge, 1984). The mean annual phytobenthos biomass in the model of 4–7 gC m^{-2} falls well within ranges reported by de Jonge & Colijn (1992) for the Ems estuary. The model predicts benthic primary production values varying between 80 to 120 g C m^{-2} yr^{-1} (intertidal surface) and the seasonality in primary production is not very pronounced. Colijn & de Jonge (1984) found estuarine benthic primary production to vary between 47 and 314 g C m^{-2} yr^{-1}. Similarly, Jassby *et al.* (1993) found the overall mean productivity for 28 different sites to be 110 g C m^{-2} yr^{-1} and 50% of all values were within 66–180 g C m^{-2} yr^{-1}. Thus phytobenthos productivity in the model appears to be consistently estimated. In a set of preliminary experiments, Kromkamp *et al.* (1995) measured much lower phytobenthos production values in a central intertidal area (roughly estimated about 20 gC m^{-2} yr^{-1}). This could mean that our model estimates are too high. Nevertheless, in view of the difficulties inherent in the calculation of annual production of benthic microflora (Shaffer & Onuf, 1985), an estimate, consistent with literature data, seems to be most appropriate.

Because of the low primary production values in the pelagic, benthic algae are the major primary carbon source in model spatial compartments 4 to 7. Their contribution to total carbon fixation decreases towards the river and the sea as the ratio of intertidal surface versus water volume decreases and as the waters become less turbid towards the sea (allowing higher phytoplankton production). On average about one third of total primary production in the model is derived from phytobenthos. This is consistent with values cited in Smith & Hollibaugh (1993).

Bacterial autotrophy is usually considered to be of minor importance due to its inefficient energy generating system (Helder & de Vries, 1983) and they are mostly ignored in mass balance studies. We use a rather low carbon conversion efficiency of 0.033 gC $(gN)^{-1}$, which is near to efficiencies of 0.045 reported by Helder & de Vries (1983) and of 0.025 gC $(gN)^{-1}$ cited in Jassby *et al.* (1993). Other studies (Indrebø *et al.*, 1979) use higher efficiencies of 0.09 gC $(gN)^{-1}$.

Notwithstanding their low efficiency, in the Westerschelde model, the nitrifying activity in the upper estuarine stretch is so high (Soetaert & Herman, 1995b) that they are the most important carbon fixing organisms in this turbid part (about 25 g C m^{-2} yr^{-1}). On the scale of the entire estuary however, bacterial primary carbon fixation is not very important (about 10%).

High rates of carbon-fixation by nitrification were also observed at the oxic-anoxic interface in a permanently stratified estuary in western Norway (Indrebø *et al.*, 1979) and in a stratified saline lake (Cloern *et al.*, 1983). The latter authors found chemoautotrophic production to be 150 gC m^{-2} yr^{-1}, of which 45 to 80% was contributed by nitrifiers.

In the mid-estuarine region a large salt marsh is situated (Saeftinge), which is characterized by a high primary production (De Leeuw & Buth, 1991). This ecosystem is not included in our model, and according to Hemminga *et al.* (1993), export of vascular plant detritus from the Saeftinge salt marsh in the Westerschelde is insignificant. Hence, salt marshes are not considered to contribute to estuarine enrichment in the model.

Heterotrophic processes

In the model, the allochthonous and autochthonous particulate organic matter in the upstream estuarine part is temporarily retained in the region of high turbidity where it is degraded in an aerobic and anaerobic pathway before being flushed downstream. The more inert organic matter that reaches the middle region of the estuary then joins the carbon of marine origin. A substantial deposition on the extensive tidal flats occurs here in the model. All in all, sedimentation removes some 20% of total carbon in the estuary.

By far the major decomposition occurs by means of aerobic mineralisation (56% of all carbon loss). Water-column denitrification, which is a significant component in the nitrogen cycle (Soetaert & Herman, 1995b) is of less importance in carbon recycling, except in the most upstream compartments, where about 45 percent of total degradation is estimated to be anaerobic. The amount of carbon respired by organisms other than bacteria increases from about 1% in the most upstream compartments to about 14% near the sea; on average

8% of all carbon losses can be attributed to higher trophic levels in the model.

Decomposition rates in the model are most pronounced at the zone of maximal turbidity, where carbon concentrations are highest. As the carbon concentration and reactivity decreases towards the mid-estuary, decomposition rates become lower. With the input of reactive organic matter from the sea, aerobic decomposition rates increase from mid-estuary towards downstream but denitrification, which is inhibited by oxygen, further declines.

If we assume a growth yield of 0.5, our yearly-integrated values of bacterial production are close to production values measured *in situ* by Goosen *et al.* (1992), except for the most upstream compartment (Fig. 11). Bacterial production in spatial compartment 1 as given in Goosen *et al.* (1992) was measured at the freshwater boundary, irrespective of the phase of the tide (and hence some measurements were probably performed in the river rather than in the estuary). As bacterial production is higher in the river compared to the estuary (Goosen *et al.*, 1992) and as our estimates are compartment means, this could explain part of the differences of both estimates. A growth yield of 0.5 is not exceptionally high, although such efficiencies are only found in situations without nutrient limitation (Billen *et al.*, 1990). Thus, although independently derived, bacterial production measured in the field lends validity to our model estimates of bacterial activity.

The rates at which organic matter is formed or degraded are interesting for comparison with other areas, but concerning the estuarine ecosystem as a whole, total amounts are more instructive. The volume of the upstream estuarine compartments are only a fraction of the most seaward compartments. Hence, notwithstanding higher rates near the turbidity zone, by far the major production and consumption of carbon occurs in the most seaward part. Processes that are linked to the benthos are most pronounced in the mid-estuary where tidal flats are most abundant.

All in all, about 117 000 tonnes of carbon is consumed in the model estuary per year.

Impact of the turbidity zone on the estuarine carbon cycle (Fig. 12)

In the model, a small fraction of total carbon input is lost in the turbidity zone (model spatial compartments 1–4), mainly through bacterial degradation. Sedimentation and respiration by other organisms than bacteria are negligible in the turbidity zone. The primary formation of organic matter is almost nil there. Hence, of the 74 × 10^3 tonnes of carbon imported in this small stretch, some 60 × 10^3 (80%) is exported to the zone downstream. By far the largest amount of carbon is removed in the area downstream from the turbidity zone (spatial compartments 5–13) and pelagic bacteria are mainly responsible for this (65%). Sedimentation removes some 20% of primary produced and imported carbon, while secondary producers other than bacteria account for 9% of carbon loss in this estuarine stretch. Nearly all primary production occurs in this zone.

The predominance of carbon loss in the downstream zone in our model seems in contradiction with the lower degradation rates there. It is however the consequence of the larger volume residing in this part (95% of the entire Westerschelde volume) and the higher total standing stocks of carbon (85% of total Westerschelde carbon load in 1991, data from the JEEP data base).

Comparison with a previous budget

Another carbon budget of the Westerschelde, based on data of the early seventies was developed by Wollast (1976). He subdivided the Westerschelde into an upstream part near the turbidity maximum (our model spatial compartments 1 to 4) and a downstream part (compartments 5 to 13). There are some striking disagreements between the budget of Wollast and our budget that merit attention (Table 2).

A major difference is in the main centre of degradation. Wollast calculated that more than 80% of total carbon input was lost in the most upstream part of the estuary (compartments 1-4) and about half of this loss was due to sedimentation. Our budget reveals the opposite trend, with 80% of total loss occurring in the more downstream part of the estuary (compartments 5–13), mainly due to pelagic degradation.

Part of the discrepancy between both budgets could be methodological. Bacterial degradation in Wollast's budget was measured by means of dark bicarbonate ^{14}C intake (Billen *et al.*, 1976), which was taken indicative of heterotrophic respiration and the conversion into heterotrophic activity much depends on the use of fixed factors (Billen *et al.*, 1976). Pelagic degradation in the downstream part of the estuary was calculated such as to close the budget and it may have been underestimated: whereas our model and *in situ* measurements by Goosen *et al.* (1992) indicate that bacterial degradation rates are about 5 times lower in

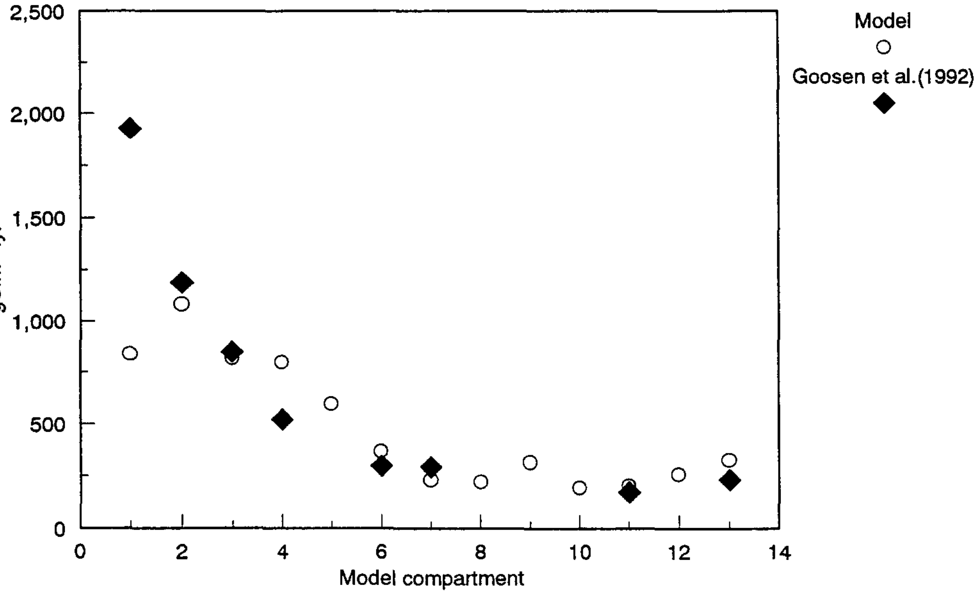


Fig. 11. Modeled versus *in situ* measured yearly bacterial production values (Goosen, 1992), assuming a growth yield of 50%.

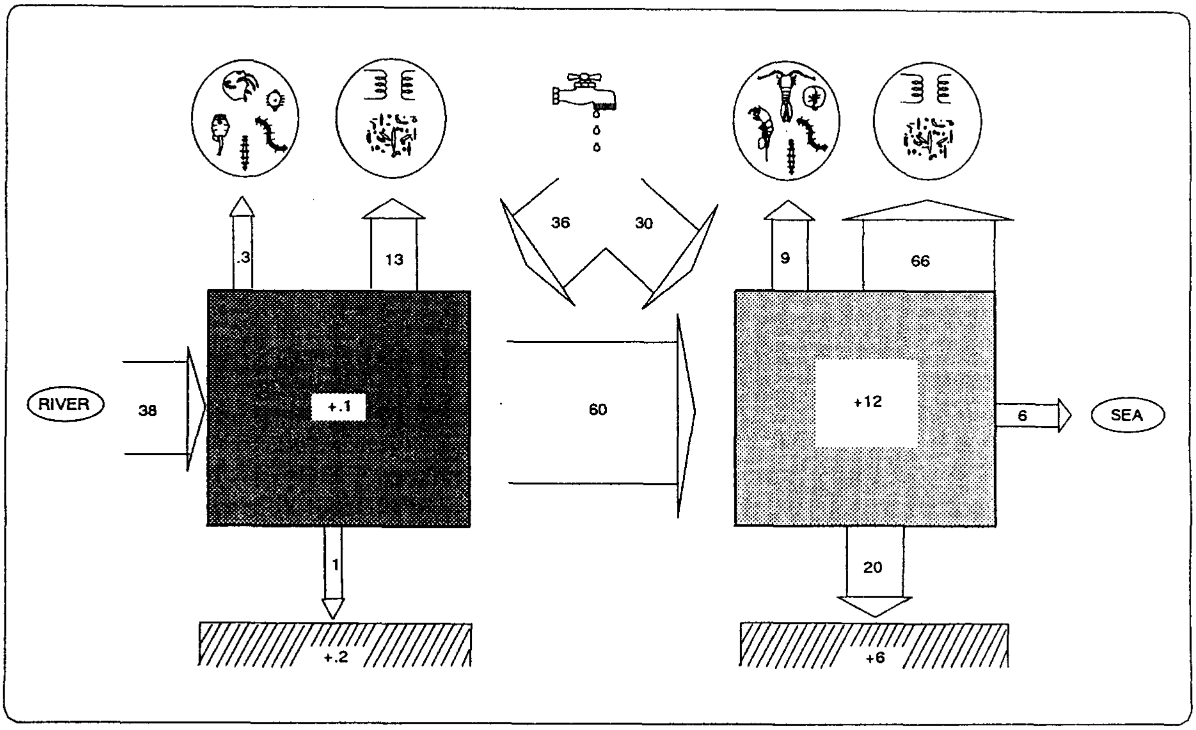


Fig. 12. Yearly carbon budget of the turbidity zone (pelagic compartments 1–4, darkly shaded) and of the zone downstream (compartments 5–13). Arrows directed to the boxes indicate import. The left icon above indicates higher trophic levels, the right icon denotes bacteria. Arrows directed towards the icons denote the amount of carbon respired by these groups. The tap in the middle of the graph denotes waste import.

the downstream part, Wollast (1976) assumed almost a 100-fold difference.

Furthermore, carbon sedimentation was calculated by Wollast by multiplying estimates of sediment accumulation rates with average carbon content in the sediments, while we patterned total organic matter sedimentation to recent estimates of sediment accumulation rates in Van Maldeghem *et al.* (1993) and to annual intertidal C fluxes measured by Middelburg *et al.* (1995, pers. comm.). The sedimentation estimates of Van Maldeghem *et al.* (1993) were based on data from the period 1975 to 1985 and they found net sedimentation to be largest in spatial compartments 6, 7 (Land of Saeftinghe) as well as in model compartment 10 (their compartments 7, 8 and 11). This was reproduced in our model. The upstream part of the estuary (where most sedimentation took place in the budget of Wollast) was even a net exporter of mud in Van Maldeghem *et al.*, (1993) but this is due to dredging activity. Nevertheless, there is evidence that the Westerschelde estuary itself has changed since the mid seventies (Soetaert & Herman, 1995b) and this too could account at least for some of the discrepancies. Based on a comparison of nutrient profiles from 1974 and 1991 and on a long-term series of oxygen, nitrate and ammonium concentrations, it was shown that the oxygen-deficient zone has moved upstream for at least 10 kilometres since 1975 (Soetaert & Herman, 1995b). Due to the larger extent of the anoxic zone in the early seventies, both the processes of denitrification (Soetaert & Herman, 1995b) and sulphate reduction in the water column (Wollast, pers. comm.) were much more important in the estuary then. *In situ* measurements performed in 1991 show that bacterial production immediately upstream from the estuary is some 25% higher than in the upper estuarine part (Goosen *et al.*, 1992). Assuming that the biochemical characteristics that now reside in the river were present in the upper estuarine part in the seventies, part of the budgettary discrepancy can be accounted for. Finally, sedimentation patterns in the estuary are continuously changing and shifts in the main deposition centres may have occurred as well (Wollast, pers. comm.).

Net heterotrophy in the Westerschelde

Many aquatic ecosystems are heterotrophic (respiration $\gg$ autotrophic production) and have food webs based on detritus. In a compilation of available literature, Smith & Hollibaugh (1993) showed most coastal marine communities to be net heterotrophic. With few exceptions, total respiration was between 1 to 2 times higher than autotrophic production, indicating that respiration and autotrophic production were closely linked. Net carbon consumption (respiration-autotrophic production) varied from −43 (net autotrophic) to +250 gC m^{-2} yr^{-1}. Compared to these values, the Westerschelde estuary is much more heterotrophic (average Resp/Prod ratio of 6, maximum of 35; average net C consumption of 380 gC m^{-2} yr^{-1}). Nevertheless, total respiration in the Westerschelde (300–1200, average of 450 gC m^{-2} yr^{-1}) is not so much larger than the estuarine mean of 356 gC m^{-2} yr^{-1} and falls well within estuarine ranges (Smith & Hollibaugh, 1993). Total primary production on the other hand is much lower (72 compared to 300 gC m^{-2} yr^{-1}) than the estuarine mean. Using the regression equation derived by Smith & Hollibaugh (1993), total autotrophic production should be as high as 370 gC m^{-2} yr^{-1} in the Westerschelde. That this is not the case merely stems from the fact that primary production is strongly limited by the high turbidity in the area. Thus, in contrast to the estuaries cited in Smith & Hollibaugh (1993), there is no close coupling of bacterial and primary production in the Westerschelde estuary and bacterial metabolism is mainly fuelled by exogenous organic matter. Similarly in the turbid Hudson River estuary, which receives a significant amount of allochthonous carbon, bacterioplankton production was shown to be about 4 times the value of depth-integrated phytoplankton production (Findlay *et al.*, 1991).

Contribution of the Westerschelde to coastal enrichment

Due to the high heterotrophic rates, the role of the Westerschelde estuary as a subsidizer of organic carbon to the North sea is only minor (a net export of 6000 tonnes of carbon per year in the model). Assuming the same heterotrophic and autotrophic characteristics at the sea boundary compared to the last model compartment, we calculated that if the estuary would be 3 to 4 kilometres longer, all imported and *in situ* produced carbon would be lost in the estuary itself. This probably reflects the scale at which coastal fertilisation by the estuary is tangible. Moreover, not all forms of organic carbon are exported to the sea in the model. Organic detritus is exchanged across the seaward boundary, with more refractory detritus leaving the estuary while more reactive matter (with a higher nitrogen content) enters the estuary. This explains the apparent paradox of our model estuary both exporting organic carbon and importing organic nitrogen (Soetaert & Herman, 1995b). In addition, some 500 tonnes carbon of marine zooplankton biomass is net imported into the estuary per year where they dy (Soetaert & Herman, 1994). A detailed budget of phytoplankton carbon shows that 4000 tonnes of carbon is imported from the river, while a small amount is brought in from the sea (Soetaert *et al.*, 1994). All this imported, relatively reactive organic carbon is incorporated into the estuarine web. Internal cycling, mainly in the watercolumn results in the removal of most organic matter that enters the estuary or is produced *in situ* and the more refractory part escapes to the sea. Because the estuary mineralizes nearly all allochthonous and *in situ* produced carbon, it is a large net nutrient exporter: despite the denitrification process that removes part of the nitrogen, the amount of dissolved nitrogen that is flushed to the sea is some 25% higher than the amount that enters from the river or from wastes (Soetaert & Herman, 1995b).

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The ecosystem model MOSES is available upon request from the authors. It can only be run under the model environment SENECA, which can be purchased from the same authors (price in 1994 US $100).

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