A tracer investigation of nitrogen cycling in a pristine tundra river

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Abstract: The fate of nitrogen (N) in drainages depends in part on N storage and transformation within the river network. The addition of an [^{15}N]NH_4^+ isotopic tracer to a tundra river provided information on the uptake, food web transfer, and ecosystem retention of N. The fourth-order Kuparuk River ecosystem took up 60% of the NH_4^+ within 1 h and 1 km of the point of tracer addition. Long-lived biota and epilithon retained measurable amounts of the added ^{15}N for up to 2 years. These transformations and storages within rivers exert control over the timing of N export, the chemical form of exported N, and, consequently, its ecological impact on downstream aquatic ecosystems.

Résumé : Le sort de l'azote (N) dans les eaux de drainage dépend en partie de l'accumulation de N et de sa transformation dans le réseau hydrographique. L'ajout d'un traceur isotopique [^{15}N]NH_4^+ aux eaux d'une rivière coulant dans la toundra a permis d'amasser de l'information sur le N (absorption, transfert dans la chaîne alimentaire et rétention dans l'écosystème). L'écosystème de la rivière Kuparuk, un cours d'eau du quatrième ordre, avait absorbé 60 % de le NH_4^+ au bout de 1 h à 1 km du point d'injection. Les éléments du biote à longue durée de vie et l'épilithon ont conservé des quantités mesurables du ^{15}N jusqu'à 2 ans après l'injection. Ces transformations et cette accumulation dans les cours d'eau régissent le rythme d'exportation de N, la forme chimique sous laquelle il est exporté et, par conséquent, son impact écologique sur les systèmes aquatiques situés en aval.

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Introduction

Nitrogen (N) serves as an essential and often limiting nutrient for stream and river biota (Grimm and Fisher 1986; Perrin et al. 1987; Pringle 1987), and N cycles are subject to major disturbance by human activity (Biggar and Corey 1969; Tiedemann et al. 1978). As a consequence, the life processes of streams, rivers, lakes, and many estuaries are greatly altered by changes in the amount or form of N inputs (Edmondson 1969; Hynes 1969; Ketchum 1969). A major unresolved question in the study of N cycles of flowing waters is how to determine the fate of N entering rivers. Tracing N flow is difficult because nonconservative solutes such as ammonium (NH_4^+), nitrate (NO_3^-), and dissolved organic N (DON) are transported downstream while being taken up and recycled over varying and usually unknown distances. Phosphorus (P) also limits stream primary production, frequently as a colimiting element with N (Peterson et al. 1993*a*). Studies of P cycling using ^{32}P addition to streams have facilitated the formulation and testing of stream P spiraling models (Newbold et al. 1981, 1983*a*). However, the ability to define stream N dynamics at the ecosystem scale has been more limited because of the lack of a suitable radiotracer for N. Here, we report results of an N stable isotope tracer experiment designed to determine the fate of NH_4^+-N entering a tundra river on the North Slope of Alaska. One reason we chose to add ^{15}N rather than ^{32}P was because of a zero-release policy for radioisotopes at this site. However, since both elements circulate throughout the stream food web, there is great similarity between the information obtained with either tracer.

Site description

The Kuparuk River is a fourth-order meandering tundra river with a mean summer discharge of 1–3 m^3/s (Peterson et al. 1993*a*). The 5-km study reach consists of alternating pools and riffles with rock and cobble bottom colonized with bacteria and diatoms along with patchy and sparse cover of filamentous algae and aquatic mosses. The insect fauna is dominated by filter-feeding blackflies (*Prosimulium* sp.), but grazing mayflies (*Baetis* spp.) and chironomids (the tube-dwelling *Orthocladius* sp.) are also abundant. The largest abundant insect is the caddis fly, *Brachycentrus americanus*, which along with *Baetis* provides a major portion of the diet of the only species of fish in the study reach, Arctic grayling (*Thymallus arcticus*).

Primary production in the Kuparuk is limited by P and secondarily by N when P is added simultaneously (Peterson et al. 1983). N in the form of NH_4^+, NO_3^-, and DON enters the river naturally with seepage water from the soils along the river banks. Ammonium levels in river water are lower (0.1–0.5 μM) than in soil seepage water (1–20 μM) (M. Miller, Department of Biological Sciences, University of Cincinnati, unpublished) due to active uptake by microbes, algae, and mosses in the river and to nitrification. During this experiment, NH_4^+ and NO_3^- concentration averaged 0.2 and 1.0 μM, respectively. DON concentrations were not measured but are normally much greater than NH_4^+ and NO_3^- levels (Peterson et al. 1992).

More detailed descriptions of the site are available in Deegan and Peterson (1992) Peterson et al. (1993*a*), and Hershey et al. (1997).

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Methods

Experimental design

We simulated the constant seepage mode of NH_4^+ flux from land to water by continuous drip addition of ^{15}N-labeled ammonium chloride (10% ^{15}N) to achieve enrichment of the riverine dissolved ammonium pool by up to 1000‰ while elevating the background concentration of ammonium by less than 1%. Thus, the added $[^{15}N]NH_4^+$ served as a true tracer and was assumed to follow pathways identical to those followed by NH_4^+ from natural seepage entering the river. The enriched NH_4^+ solution held in a streamside carboy was pumped by a solar-powered dual-channel peristaltic pump into both sides of a turbulent riffle to achieve rapid mixing. We tested for mixing by sampling on both sides of the rivers at the first station (0.08 km) below the dripper. Results indicated incomplete mixing (~25% differences), and thus, data from the 0.08-km station must be viewed cautiously.

Sampling

Samples of algae, moss, epilithon, and insects were collected at stations along a transect from upstream (reference station at –0.5 km) to 5 km downstream of the dripper site. Locations relative to the tracer addition (0 km) were –0.5, 0.08, 0.18, 0.68, 0.85, 1.5, 3.0, 4.0, and 5.0 km. The three most downstream stations were within the reach that had been receiving P fertilization each summer since 1983. The remaining stations were in the unfertilized portion of the river and are thus suitable for travel distance and uptake rate calculations that apply to the unperturbed reference reach. The microbial film with associated detritus on rocks (epilithon) was removed by wire bristle brush and filtered onto precombusted glass fiber filters (Whatman GF/F). Samples of moss (active growing tips), filamentous algae, and insects were collected from riffle rocks with forceps. Insects were held in 0.2 μM filtered lake or river water in glass vials overnight to clear their guts. Samples were dried at 50°C and shipped to The Ecosystems Center Stable Isotope Laboratory in Woods Hole, Mass., for analysis. ^{15}N was determined by combustion of dried samples and the isotope ratio was measured on a Finnigan Delta S mass spectrometer. Results are expressed as $\delta^{15}N$ values where $\delta^{15}N = (R_{sample}/R_{standard} - 1) \times 1000$ where $R = {}^{15}N{:}{}^{14}N$ and the N isotope standard is air.

In this paper, all reported $\delta^{15}N$ values have been corrected by subtracting the natural abundance $\delta^{15}N$ value of similar samples from the reference reach from the measured δ unless otherwise noted. Thus the reported values are proportional to the tracer content rather than also reflecting the natural variations due to N sources and trophic level (Peterson et al. 1993*a*). The range in natural abundance $\delta^{15}N$ values in this river is typically from 1 to 9‰, and therefore, these adjustments are in most cases relatively minor due to the high enrichment. Note that the variation between replicate samples in enrichment studies is larger in absolute terms than in natural abundance studies. For example, an enriched sample of $\delta^{15}N$ value ~400‰ might vary by 20 or 30‰ in duplicate samples whereas a natural abundance value of 4.0‰ would be unlikely to vary by more than 1.0‰. While there are many possible reasons for the larger variation in enrichment studies, most are due to natural processes, not to analytical errors, which average less than 0.2‰.

We used two similar equations to estimate residence times of N in various compartments and NH_4^+ travel distances (Ball and Hooper 1961). The travel distance downstream (uptake distance) was estimated from the best fit to a similar relationship: $C_d = C_{origin}e^{-\phi d}$ where $C = \delta^{15}N$ value, d = distance, and mean travel distance = $1/\phi$. Travel distances reported here are not corrected for lateral seepage inputs of NH_4^+ or for recycling of NH_4^+. Thus, we view the calculated values as apparent travel distances. The travel distance for fine particulate N assimilated by blackflies was estimated by best fit of blackfly $\delta^{15}N$ value distribution with distance to a mixing equation for ^{15}N content of fine particulate organic N (FPON) that included upstream inputs, epilithic sloughing, FPON sedimentation and resuspension, and downstream transport through a series of 100-m stream segments.

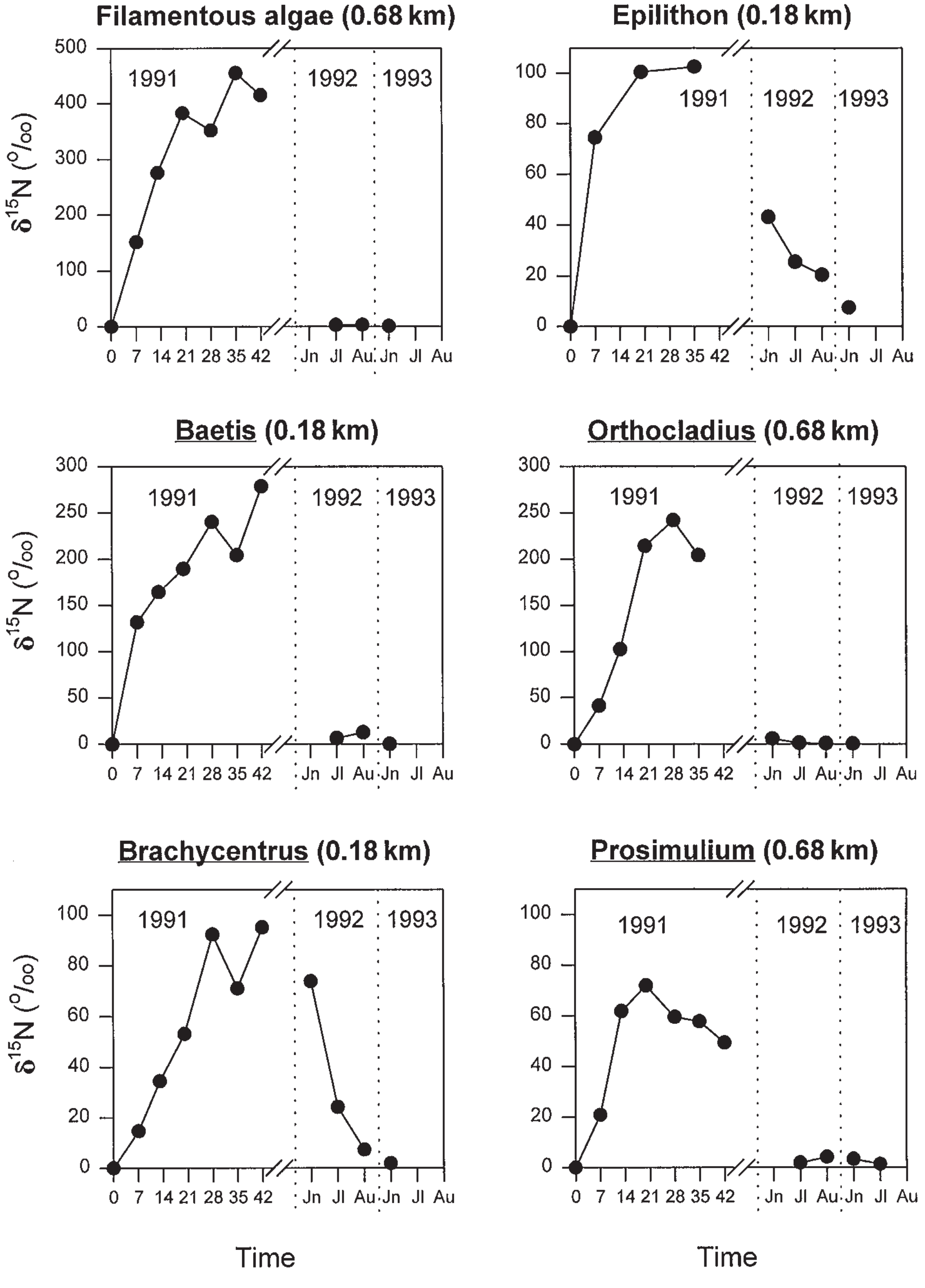
Results

The natural abundance distributions of $\delta^{15}N$ values from the river biota have been reported previously (Peterson et al. 1993*b*) and reflect the normal pattern of ^{15}N enrichment in consumers. During this study, we monitored the $\delta^{15}N$ values of samples from the reference station weekly to determine if variations during the experiment would complicate interpretation of the tracer information. There was little variation over the 7 weeks of intensive monitoring during summer 1991. The values (mean ± SD) were as follows: filamentous green algae, 2.18 ± 0.18; *Orthocladius*, 3.04 ± 0.23; *Baetis*, 2.55 ± 0.39; *Prosimulium*, 4.23 ± 0.23; *Brachycentrus*, 4.83 ± 0.29. As mentioned above, these values were subtracted from the measured values in the ^{15}N-enriched reach so that the values presented below would be directly proportional to the added ^{15}N tracer content.

The corrected $\delta^{15}N$ values of primary producers and consumers immediately downstream of the ^{15}N dripper increased at different rates and reached very different maximum values (Fig. 1; Table 1). After 4 to 6 weeks of continuous ^{15}N addition, most taxa reached relatively constant values, indicating that their N contents were uniformly labeled. The maximum observed $\delta^{15}N$ values were highest in filamentous algae and the grazing insects *Orthocladius* and *Baetis* and lower in epilithon (microbial film on rocks) and in the particle-filtering insects *Prosimulium* and *Brachycentrus*. The differing levels of ^{15}N enrichment achieved by the various taxa are an indication of their relative degree of dependence on the ^{15}N-enriched dissolved NH_4^+. For example, filamentous green algae achieved $\delta^{15}N$ values (Table 1) close to the calculated $\delta^{15}N$ value for the dissolved NH_4^+ pool (1000‰). We assume that this indicates a strong preference for NH_4+ as compared with NO_3^-. This occurred in spite of the fact that NO_3^- was present in higher concentrations than NH_4^+ throughout the experiment (mean concentrations 1 and 0.2 μM, respectively). Primary producers such as mosses and the diatoms that support the chironomid *Orthocladius* had lower ^{15}N contents reflecting uptake of dissolved NO_3^- in addition to NH_4^+. Note that we are inferring the $\delta^{15}N$ values of the diatoms on the *Orthocladius* tubes from the $\delta^{15}N$ values (maximum = 419‰) of *Orthocladius*, the consumer (Hershey et al. 1988).

The longitudinal distributions of tracer ^{15}N in primary producers and in grazers along the sampling transect were quite consistent throughout the study (Fig. 2). The unusually constant discharge of about 1 m^3/s and consistently low NH_4^+ concentration of about 0.2 μM during the experiment contributed to this consistency. The distribution of ^{15}N with distance in attached primary producers that assimilated NH_4^+ directly from the water was used to calculate an average travel distance of 1.0 km for dissolved NH_4^+, which corresponds to uptake of about 60% within 1.0 km of travel. The mayfly *Baetis*, which grazes on epilithon, and the tube-dwelling *Orthocladius* had a similar longitudinal ^{15}N distribution to epilithon and attached filamentous algae. Thus the calculated apparent NH_4^+ travel distance is similar if we use the data for consumers *Orthocladius* or *Baetis* rather than the primary producer data to perform the calculation. From this uptake information, the mean discharge and the volume of the reach, we calculate an average residence time of NH_4^+ in the river water of approximately 1 h during the 6 weeks of continuous ^{15}N addition. Note that these

Fig. 1. Time course of $\delta^{15}N$ values at a single station for selected components of the river ecosystem. The increase in 1991 during tracer addition is plotted versus day relative to the start of ^{15}N addition. Declines in subsequent years when $[^{15}N]NH_4^+$ was not added are indicated as June, July, or August samplings. The 1992 samples of *Orthocladius*, *Baetis*, and *Prosimulium* represent new cohorts whereas *Brachycentrus* has a multiyear life cycle and samples are of the same cohort.



are long-term averages and are not corrected for recycling or seepage of NH_4^+. These values are not directly comparable with values obtained from short-term solute release studies. However, we note that samples of *Orthocladius* collected at day 3 indicated an apparent travel distance for NH_4^+ that was similar to the distance calculated from week 5 samples, even though we expected recycling to increase the apparent travel distance over time.

Prosimulium, a filter-feeder, had a different downstream $\delta^{15}N$ distribution than algae or grazing insects. This insect had low $\delta^{15}N$ values at the first two stations downstream of the dripper but higher values at stations 0.68 and 0.85 km downstream (Fig. 2). Even farther downstream the values declined, and at 3 km the $\delta^{15}N$ values were similar to those at 0.08 km. This downstream location of the ^{15}N maximum in *Prosimulium* is due to their mode of feeding and might be explained as follows. Because blackfly larvae ingest fine particles carried by the current, much of their food at the stations near the dripper consisted of unlabeled particles imported from upstream of the ^{15}N addition site. Farther downstream, they ingested an increasing proportion of particles generated within the ^{15}N-enriched zone by sloughing of epilithon and resuspension of

Table 1. Corrected maximum $\delta^{15}N$ for Kuparuk River biota during the 1991 ^{15}N addition and the day and distance downstream at which the maximum occurred.

Sample type	Corrected maximum $\delta^{15}N$	Day	Distance (km)
Filamentous algae	871	13	0.08
Moss (*Schistidium* sp.)	185	35	0.18
Epilithon	108	35	0.08
Orthocladius sp.	419	20	0.18
Baetis sp.	279	42	0.08
Brachycentrus sp.	95	42	0.18
Prosimulium sp.	72	20	0.68
Rhyacophila sp.	92	42	0.08
Tipulid	7	42	0.18
Young-of-year Arctic grayling	91	47	0.80

Fig. 2. $\delta^{15}N$ values of Kuparuk River biota along downstream transects of sampling stations after 1 and 5 weeks of continuous enriched $[^{15}N]NH_4^+$ tracer addition at 0 km.

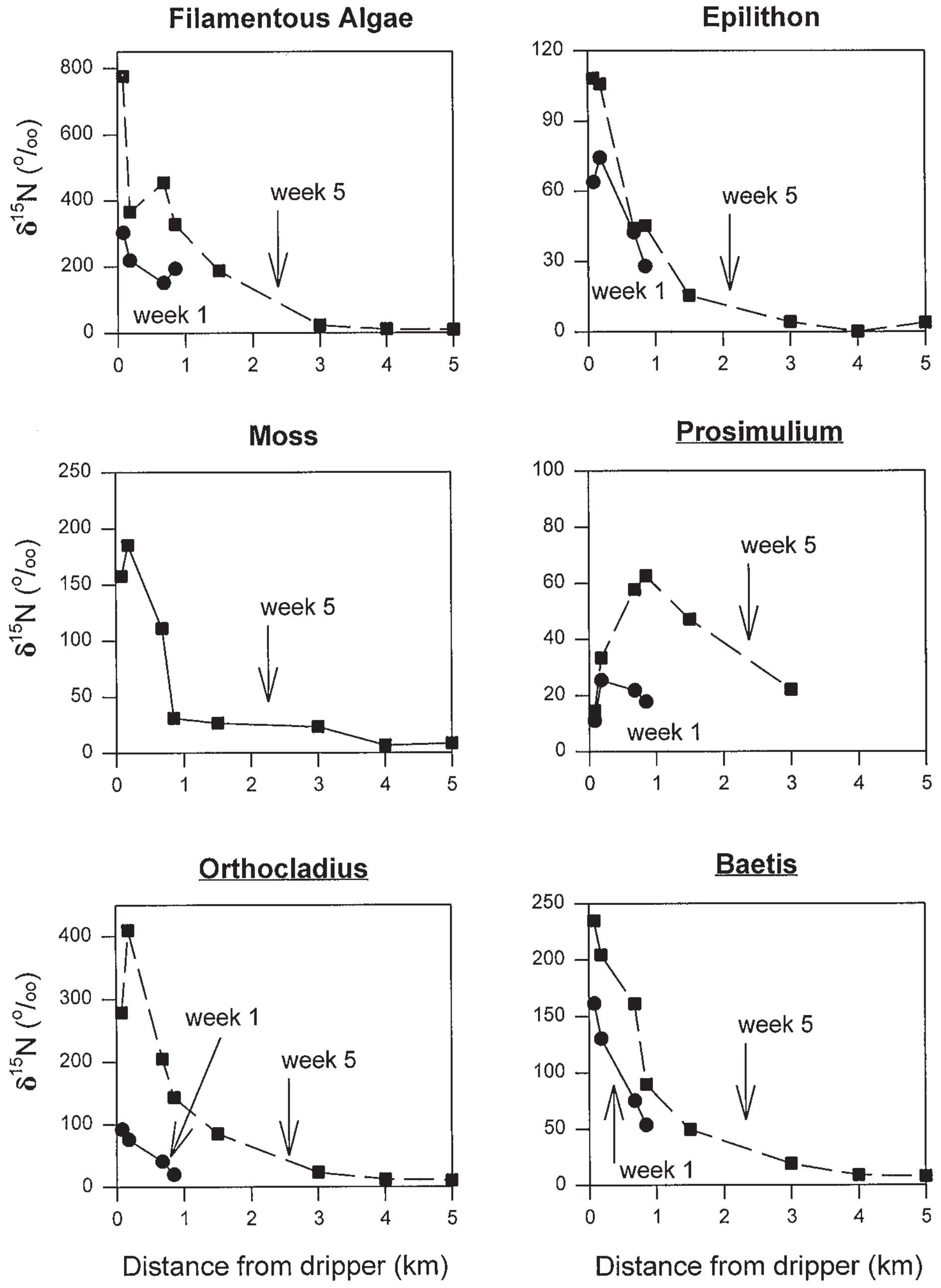
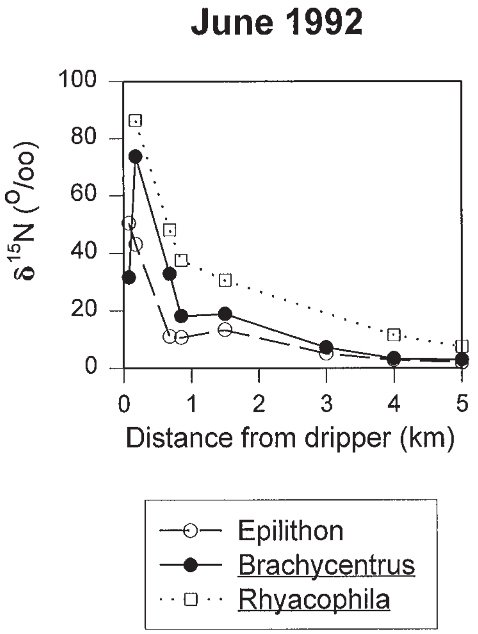


Fig. 3. $\delta^{15}N$ values of samples collected in late June 1992, the year after the ^{15}N addition.



fine particles, and thus assimilated higher amounts of tracer ^{15}N. The longitudinal distribution of the tracer ^{15}N values in *Prosimulium* indicated that the fine particles ingested and assimilated had an average travel distance of 1.0 km. Studies conducted with ^{14}C-labeled natural fine organic particles in temperate streams of similar size have given comparable estimates of travel distance (Cushing et al. 1993).

The ^{15}N tracer addition was stopped in mid-August 1991 after 6 weeks of continuous addition. By mid-August, water temperatures were falling, most insects had emerged, and fish were migrating to overwintering lakes and springs. The Kuparuk freezes solid with no flow from October until the following May when high runoff due to snowmelt typically occurs. After the snowmelt discharge, we sampled in late June 1992 to determine if the tracer N had been exported due to metabolic turnover of N, insect drift, scouring of rock surfaces, and organic sediment export. Some components such as filamentous algae and the diatom-feeding chironomid *Orthocladius* contained very low amounts of tracer the following summer (Fig. 1). These organisms presumably assimilated unlabeled NH_4^+ and NO_3^- coming from upstream. However, we found that the epilithon, mosses, and large insects such as *Brachycentrus* and the predaceous caddis *Rhyacophila* sp., which have multiyear life cycles, were still strongly labeled with ^{15}N (Figs. 1 and 3). There was no evidence that the ^{15}N distributions of these components had been displaced downstream, which illustrated the ability of the epilithic film, mosses, and insects to withstand scouring and displacement during high discharge (Fig. 3). Observations and aerial photographs of the stream bottom during snowmelt in other years have shown that a large fraction of the bottom is covered by anchored ice, which diminishes the potential scouring of a large proportion of the stream bottom (B.J. Peterson, personal observations). The slow rate of decline in $\delta^{15}N$ values of epilithon and *Brachycentrus* over the winter in comparison with the rapid labeling during a few weeks in the previous July is undoubtedly due to the slowing of metabolic processes during the long frozen period of October–May. Probably much of the ^{15}N loss that occurred was due to natural metabolic turnover of N before the fall freeze and during the interval between thaw and the June sampling rather than to physical removal and replacement of the epilithon. A small fraction of the tracer ^{15}N was still measurable in the epilithon and in *Brachycentrus* after 2 years in June 1993 (Fig. 1).

Discussion

No previous ^{15}N tracer studies of streams are available; hence the closest comparisons that can be made between this tracer study of the N cycle are with prior radiolabeled phosphate ($[^{32}P]PO_4^{3-}$) studies of the P cycle because in both tracer studies, it is possible to estimate travel distances and to trace the nutrients throughout the trophic structure. Comparisons between the current experiment and stream NH_4^+ and NO_3^- uptake and travel distance measurements based on enrichments (increases in concentration, not in isotopes) are biased by the overestimate of uptake distance associated with the enhanced concentrations required (Mulholland et al. 1990; Webster et al. 1991). Our uptake distance estimates are based on long-term average $\delta^{15}N$ values rather than one-time estimates obtained with short-term solute addition experiments designed to estimate uptake distances. N fertilization studies such as that of Newbold et al. (1983*b*) provide information on the impact of N enrichment on stream processes such as primary production and decomposition, but do not usually provide tracer information (however, see Peterson et al. 1993*b*). Given these caveats and the observation that NH_4^+ is not the primary limiting element in the Kuparuk, we offer a few cautious comparisons.

The cycling of N in streams bears many similar features to the P cycle as defined with ^{32}P additions. Mulholland et al. (1990) found that $[^{32}P]PO_4^{3-}$ had an uptake distance of from 29 to 164 m in Walker Branch, while Ball and Hooper (1961) found uptake distances of from 400 to 10 000 m in the West Branch of the Sturgeon River depending on reach and year. Uptake distances are a complex function of nutrient concentration, biotic and abiotic uptake activity, and physical characteristics of streams. In relatively small, shallow, and swift streams and rivers, most uptake is by benthic primary producers, detritus, and sediments. In this case, for a given nutrient concentration and uptake rate, the travel distance will increase as stream depth and water velocity increase. Thus, we would expect the Kuparuk to have a greater NH_4^+ uptake distance than Walker Branch on the basis of physics alone, as discharge in Walker Branch was between 2 and 10 L/s for these measurements. However, it is interesting that the average $[^{32}P]PO_4^{3-}$ uptake distance of about 1.3 km in the Sturgeon River is similar to the NH_4^+ uptake distance of about 1.0 km in the Kuparuk. The mean discharge in both rivers was about 1.0 m^3/s and both were infertile with relatively low summer temperatures. These comparisons between NH_4^+ and PO_4^{3-} uptake are deceptive because NO_3^- is not considered and in the Kuparuk, NO_3^- is usually in higher concentration and probably travels farther than either PO_4^{3-} or NH_4^+. It would be useful to determine the relationships between stream discharge (or dimensions) and nutrient travel distances in the field by performing stream-order comparisons within one type of stream. This could be done with stable N isotope ^{15}N for either NH_4^+ or NO_3^- in nutrient-poor waters up to a maximum discharge of about 100 m^3/s before the approach would become prohibitively expensive.

The Kuparuk is primarily P limited and we expected the ecosystem to be leaky with respect to N. Yet, NH_4^+ uptake was rapid. In fact, NO_3^- is the main form in which inorganic N is exported. NH_4^+ appears to be taken up almost as aggressively as PO_4^{3-}, and when excess NH_4^+ fertilizer is added, it is rapidly nitrified (Peterson et al. 1993*a*). However, in the study reach for this experiment, NH_4^+ concentrations were consistently low.

Tundra lakes and streams both have the ability to retain significant amounts of N for 2–3 years after addition. In a tundra lake, Kling (1994) found that added $[^{15}N]NH_4^+$ was mainly stored in sediments where remineralization returned available N to the water column each year. In the tundra stream, ^{15}N was stored in the epilithic biofilm plus benthic detritus as well as in longer-lived organisms. After 3 years, the ^{15}N levels in the lake and river were reduced to the limits of detection. Most of the loss from the river reach was probably due to flushing downstream, but undoubtedly, some label persisted in the larger benthic detrital pools.

In this study, we used samples of algae and insects to indirectly assess the dynamics of N pools that we could not measure. The algae, mosses, and epilithon samples provided time-integrated measures of NH_4^+ travel distance. The differences in $\delta^{15}N$ values of primary producers suggested different preferences for NH_4^+ versus NO_3^-. These tissue samples are relatively easy to collect and inexpensive to analyze. It would be difficult to process sufficient NH_4^+ grab samples to estimate mean travel distance over 6 weeks. In a similar manner, *Prosimulium* served as persistent collectors of fine particles in transport. These inferences about the NH_4^+ and fine sestonic N pools need to be checked with direct measurements, which we were unable to obtain due to the low NH_4^+ concentrations and lack of sufficiently large sestonic N samples. However, use of the biota as natural integrative samplers of ecosystem fluxes is appealing and efficient.

The ability to efficiently define the pathways and rates of N flow in the natural field setting is required to test and improve our conceptual and mathematical models of the N cycle of rivers. Parallel N isotope tracer experiments have proven useful in the analysis of lake and forest ecosystems (Kling 1994; Nadelhoffer and Fry 1994). Quantitative knowledge of the fate of N in both pristine and managed ecosystems is becoming increasingly important as humans continue to load the biosphere with excess anthropogenic N from fertilizer and fossil fuel combustion (Peterson and Melillo 1985; Schindler and Bayley 1993; Galloway et al. 1994). Tracer addition of stable N isotopes to natural ecosystems provides a powerful approach for obtaining critical information on how ecosystems assimilate, transform, store, and export N.

Acknowledgments

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