Influence of stream size on ammonium and suspended particulate nitrogen processing

Wilfred M. Wollheim,[1] *Bruce J. Peterson, Linda A. Deegan, John E. Hobbie, and Beth Hooker*
Ecosystems Center, Marine Biological Laboratory, Woods Hole, Massachusetts 02543

William B. Bowden,[2] *Kenneth J. Edwardson, and David B. Arscott*[3]
Department of Natural Resources, University of New Hampshire, Durham, New Hampshire 03820

Anne E. Hershey[4]
Department of Biology, University of Minnesota, Duluth, Duluth, Minnesota 55812

Jacques Finlay
Department of Integrative Biology, University of California, Berkeley, Berkeley, California 94720-3140

Abstract

We used $^{15}NH_4$ tracer additions to determine travel distances of ammonium (NH_4) and suspended particulate organic nitrogen (SPON) in six streams ranging from second to fifth order located within a single watershed on the North Slope of Alaska. Based on the distribution of ^{15}N stored in stream bottom compartments (primary producers or grazers), we estimated NH_4 travel lengths. We used a two-compartment model to estimate the travel length of SPON based on the distribution of source ^{15}N on the stream bottom and $SPO^{15}N$ in the water column. Both NH_4 and SPON travel lengths (S_w and S_p, respectively) increased with discharge primarily due to changes in depth and velocity. Variation in the vertical mass transfer coefficient (v_f) of both NH_4 and SPON did occur among the streams but was not related to stream size and was relatively small compared to the change in physical characteristics. Thus, in the Kuparuk watershed, physical gradients outweighed biological or chemical changes as controls on NH_4 and SPON travel length. The one exception was the Kuparuk fertilized reach, where phosphorus fertilization greatly increased biological activity and NH_4 processing compared to unaltered streams. Longitudinal gradients in major biological driving variables such as litter inputs, debris dams, and shading are absent in the Arctic, perhaps explaining the relatively uniform NH_4-v_f. Watersheds in other biomes may show differing degrees of physical versus biological/chemical controls. A conceptual model is presented for comparing the relative strength of these controls among different watersheds. Strong relationships between discharge and travel length should greatly aid development of watershed models of nutrient dynamics.

The ability of streams to process nutrient inputs from terrestrial systems can have important impacts on downstream ecosystems such as larger rivers, lakes, and estuaries (Hopkinson and Vallino 1995; Peterson et al. 1997). Although

nutrient transport is relatively rapid in streams, retention and transformation by stream biotic processes can significantly alter nutrient export (Meyer and Likens 1979; Meyer et al. 1981; Triska et al. 1984; Mulholland 1992). Smaller headwater streams, because of their high surface to volume ratios compared to larger streams, are locations of high processing relative to transport and may play a disproportionate role in controlling nutrient flux from large watersheds (Alexander et al. 2000).

Both physical and biological stream characteristics are influenced by stream size. Changes in physical characteristics are linked to increasing discharge, which can in turn influence biological characteristics (Vannote et al. 1980). As discharge increases downstream, water depth, velocity, and width increase predictably (Leopold and Maddock 1953). Although more variable, numerous biological characteristics can also change systematically with stream order (Vannote et al. 1980; Minshall et al. 1983; Naiman et al. 1987). As streams increase in size, physical changes (i.e., increased velocity and depth) are certain and lead to greater nutrient transport, whereas changes in nutrient processing by biota could potentially enhance or offset the effect of increased velocity and depth.

The interaction between physical, biological, and chemical characteristics is inherent in the spiraling concept of stream nutrient dynamics (Webster and Patten 1979; Newbold et al. 1981). A measure of the downstream movement of a nutrient molecule is the travel distance, the average distance a nutrient molecule travels before it is removed from the water (Newbold et al. 1981). Nutrient travel distance has been proposed as a useful parameter for modeling nutrient fluxes at the watershed scale (Vörösmarty and Peterson 2000). The interaction of physical, biological, and chemical characteristics in determining travel distance is formalized as follows (Stream Solute Workshop 1990):

$$S_w, S_p = \frac{v \times d \times C}{U} = \frac{v \times d}{v_f} \tag{1}$$

where S_w and S_p = travel distance (m) of dissolved or particulate form, respectively; v = water velocity (m s^{-1}); d = water depth (m); C = nutrient concentration (μg m^{-3}); and U = areal uptake (for dissolved nutrients) or settling (for particulates; μg m^{-2} s^{-1}; *see Table 1* for summary of variable abbreviations). U/C is also known as the depositional velocity for particulates (m s^{-1}) and is more generally known as the vertical mass transfer coefficient (v_f) when applied to dissolved nutrients (Stream Solute Workshop 1990). As discharge increases downstream, it has been shown that on average velocity and depth are proportional to $Q^{0.1}$ and $Q^{0.4}$, respectively (Leopold and Maddock 1953). Thus, if the ratio of concentration and uptake remains constant, we would expect the increase in S_w or S_p to be proportional to $Q^{0.5}$ (Stream Solute Workshop 1990). However, if areal uptake relative to nutrient concentration changes in the downstream direction, S_w or S_p will not necessarily increase predictably based on changing physical dimensions.

In this paper, we report the effect of stream size on travel lengths of ammonium and suspended particulate organic nitrogen (SPON) in a series of streams located in a single

Table 1. Summary of variables, symbols, and units used in the text.

Variable	Symbol	Units
Discharge	Q	m^{-3} s^{-1}
Water velocity	v	m s^{-1}
Water depth	d	m
Nutrient concentration (NH$_4$ or SPON)	C	μg m^{-3}
Distance	x	m
Areal uptake rate	U	μg m^{-2} s^{-1}
Mass transfer coefficient (or depositional velocity)	v_f	m s^{-1}
NH$_4$ travel distance	NH$_4$-S_w	m
SPON travel distance	SPON-S_p	m
Longitudinal decline of stream bottom ^{15}N	k_1	m^{-1}
^{15}N stored in the stream bottom	^{15}N$_{source}$	μg ^{15}N m^{-1}
Flux of ^{15}N in suspended organic matter	SPO^{15}N	μg ^{15}N s^{-1}
SPO^{15}N suspension rate	k_s	s^{-1}
Distance specific SPO^{15}N settling rate	k_2	m^{-1}
Stream bottom ^{15}N at $x = 0$ m	A_0	μg ^{15}N m^{-1}

watershed on the North Slope of Alaska. Using stable isotope tracer additions of ^{15}NH$_4$, we determined whether NH$_4$-S_w and SPON-S_p followed simple scaling relationships as stream size increased or whether variations in biological or chemical characteristics altered the relationship.

Materials and methods

Study sites—Ammonium dynamics were investigated during summers between 1991 and 1997 in six stream reaches. The streams ranged from second to fifth order with summer median discharges from 0.06 to 26.3 m^3 s^{-1} (Table 2). All streams are located in the Kuparuk River watershed on the North Slope of Alaska (Fig. 1). The Kuparuk River flows northward, draining a watershed area of 8,107 km^2. The Kuparuk River is roughly 250 km long from headwaters to mouth.

Vegetation in the watershed is predominately grasses and shrubs. Shading and litter inputs are minimal. Most allochthonous organic matter enters as peat (Harvey et al. 1997). Permafrost is present throughout the area, and streams are frozen solid between October and May. Discharge generally peaks in late May or early June during snowmelt and reaches baseflow during July. Days are 24 h long during July. Mean water temperature during the tracer addition periods ranged from 9.8 to 13.7°C (Table 2).

^{15}NH$_4$ was added in the Kuparuk reference reach in 1991, Blueberry Creek in 1994, the Kuparuk fertilized reach and Imnavait Creek in 1995, the Lower Kuparuk in 1996, and E-1 Creek in 1997 (Fig. 1). The stream reaches were considered pristine with the exception of the Kuparuk fertilized reach, which has had PO$_4$ added to it during July and August annually since 1983 (Peterson et al. 1993) and now contains thick mats of the bryophyte, *Hygrohypnum* spp. (Bowden et al. 1994; Finlay and Bowden 1994; Arscott et al. 1998).

Dominant bottom substrates are either gravel (Lower Ku-

Table 2. General stream characteristics. Temperatures are averages and discharges are medians for the entire ^{15}N addition period. Summer median discharge was higher in E-1 Creek than in Imnavait Creek, but discharge corresponding with NH_4-S_w measurement was less in E-1 than in Imnavait. The Kuparuk reference and fertilized reaches are adjacent to one another, but average discharge was higher in 1995 than in 1991.

Stream reach	Stream order	Addition year	Discharge (m^3 s^{-1})	Temperature (°C)	Substrate	Type of stream
E-1 Creek	second	1997	0.11	9.8	Cobble	Tundra
Imnavait Creek	second	1995	0.06	10.2	Root-bound peat	Beaded/peaty
Blueberry Creek	second	1994	0.40	13.7	Cobble	Lake outlet
Kuparuk reference	fourth	1991	0.70	10.3	Cobble	Meandering tundra
Kuparuk fertilized	fourth	1995	3.34	9.2	Cobble	Fertilized meandering tundra
Lower Kuparuk	fifth	1996	26.3	12.7	Gravel	Moderately braided

paruk), cobble (Kuparuk reference and fertilized, Blueberry, E-1), or root bound peat (Imnavait) (Table 2). Substrates in pools are covered by sediments during low flow periods. Imnavait Creek is a beaded stream with relatively deep pools (up to 2 m deep) that are connected by short, very shallow (<0.1 m) riffle segments. Beaded streams are common in the Arctic foothills and are formed by thermal erosion along the intersections of ice wedge polygons (Péwé 1966). All but the Lower Kuparuk are located near the Toolik Lake Long Term Ecological Research (LTER) site in the northern foothills of the Brooks Range (Fig. 1). The Lower Kuparuk site is located on the coastal plain about 20 km from the Arctic Ocean and 10 km west of Prudhoe Bay.

Tracer addition—^{15}N enriched NH_4Cl was added continuously to each stream from 3 to 6 weeks beginning between 28 June and 6 July. The $^{15}NH_4$ solution was added at a con-stant rate from a streamside carboy using a battery-powered peristaltic pump. The amount of $^{15}NH_4$ added was always less than 1% of ambient NH_4 concentrations, making this a true tracer that would follow ambient pathways for NH_4. The addition sites were located at the top of constricted riffles to ensure rapid mixing in the water column. The experimental design is described in more detail in Peterson et al. (1997).

Physical parameters—We determined discharge, water depth, water velocity, and lateral input rates in each reach for the time period corresponding with the S_w or S_p estimate. Because S_w was an integrated measure over several days (*see below*), average physical parameters were determined for the same time period. The S_p estimate was an instantaneous measure, so we used physical parameters estimated for the sample day.

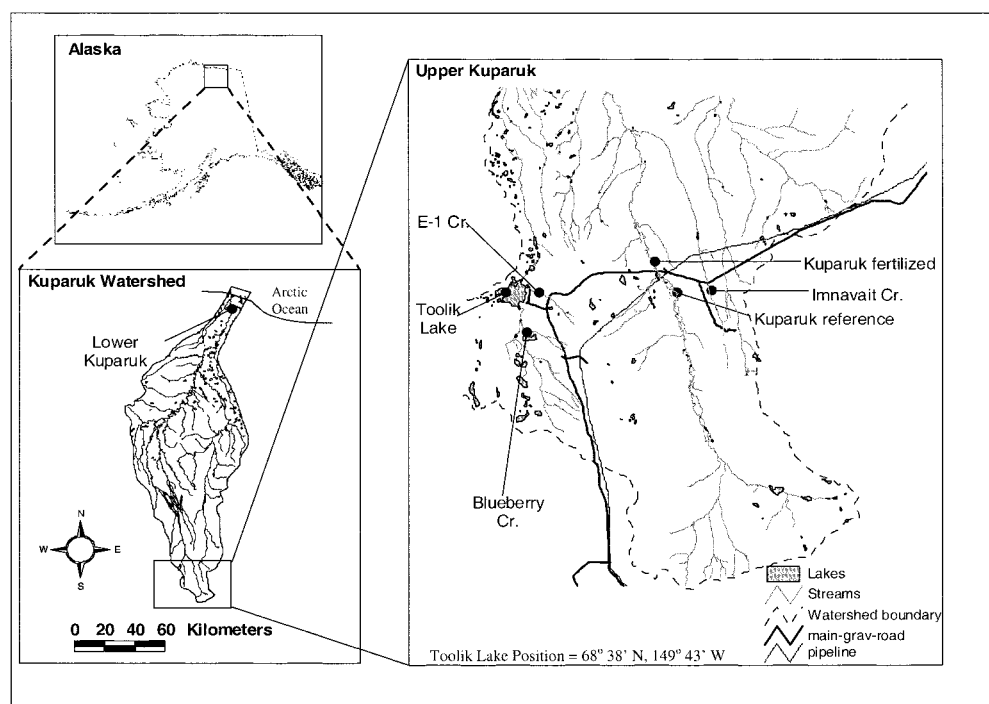Discharge was determined from stage height recorded by

Fig. 1. Study sites in the Kuparuk River watershed, North Slope, Alaska.

a data logger and stage versus discharge relationships developed for each stream. Discharge information for the Lower Kuparuk was obtained from the U.S. Geological Survey (USGS). Median discharge over the time period corresponding with the S_w measurement was used for comparisons with depth, velocity, and S_w. Mean depths were measured once for each stream from cross-sectional transects placed at regular intervals along the reach. Generally 10–20 depth measurements were made on each cross-sectional transect with the exception of pools in the Lower Kuparuk, where measurements were made 1/4, 1/2, and 3/4 of the way across the channel. Mean depth was weighted for frequency of pools and riffles. Daily mean depths were calculated using changes in stage height measured by the data logger. Depths measured in the Kuparuk reference and fertilized reach in 1995 were used to estimate depths for similar discharges during the 1991 Kuparuk reference addition.

Conservative solute injections, using either Bromine or rhodamine, were conducted in each stream to determine water velocity and lateral water input rates (Kilpatrick and Cobb 1985). Where several additions were conducted within a stream, discharge versus water velocity relationships were determined and used to estimate velocity corresponding with the S_w or S_p measurement; otherwise scaling relationships for changing velocity with discharge at a given location were used (Leopold and Maddock 1953). Four injections were conducted in E-1 Creek in 1997, two in Imnavait Creek in 1995, four in Blueberry Creek in 1994, five in the Kuparuk reference and fertilized reaches between 1994 and 1996, and one in the Lower Kuparuk in 1996 (Edwardson 1998). We assumed relationships developed for 1994–1996 in the Kuparuk fertilized and reference reaches were applicable to comparable discharges during the 1991 Kuparuk reference experiment. Lateral water inputs as a function of discharge (Q_{lat}, m^{-1}) did not vary predictably with discharge in each stream, so average Q_{lat} for each stream was used to make dilution corrections of $\delta^{15}N$ of the biota and SPON over distance.

Biological and chemical characteristics—NH_4, NO_3, and soluble reactive phosphorous (SRP) concentrations were determined from filtered samples using colorimetric techniques on an Alpkem® autoanalyzer. NH_4 was also determined using manual methods (Strickland and Parsons 1972) during 1994 and 1995. NH_4 concentrations were needed to calculate NH_4 uptake rates using Eq. 1. We used average NH_4 concentrations from longitudinal transects collected either on the date of the NH_4-S_w measurement (E-1), within several days of the NH_4-S_w measurement (Kuparuk fertilized reach, Imnavait), or over the entire summer (Kuparuk reference reach, Lower Kuparuk). We had particular difficulty with the NH_4 measurement during 1994, so the NH_4 estimate for Blueberry Creek is from the day nearest the S_w measurement where good analytical technique was achieved (drip day 29). We assume NH_4 was constant over time. Estimates of low-level NH_4 concentrations using the colorimetric technique are difficult (Aminot et al. 1997; Holmes et al. 1999), and we were often near the limit of detection. NH_4 concentrations and uptake rate estimates should be viewed cautiously, but note

that NH_4-S_w and NH_4-v_f estimates are independent of NH_4 concentration.

We collected SPON samples weekly by filtering a known volume of water through a pre-ashed GF/F filter. Nitrogen retained on the filter was determined using a Perkin-Elmer CHN analyzer. In Blueberry Creek and the Kuparuk fertilized reach, SPON concentrations varied with discharge, so SPON versus Q relationships were used to determine SPON concentration on the day of SPO^{15}N sampling. In Imnavait Creek, SPON was not related to discharge, so a summer average SPON concentration was used. In the Lower Kuparuk, an average SPON concentration was determined from samples collected at similar discharges during 1994 and 1995.

We determined a habitat-weighted gross primary production (GPP) for each stream using chamber measurements of O_2 change. Primary producers included epilithon in pools (Kuparuk reference, Kuparuk fertilized, and Lower Kuparuk) and riffles (all streams but Imnavait), and two species of mosses, *Hygrophypnum* spp. (Kuparuk fertilized only) and *Schistidium agassizii* (Kuparuk reference and fertilized). To determine epilithic primary production, representative rocks were placed in chambers, and changes in O_2 concentrations were measured in the light and dark to determine net primary production (NPP) and respiration (R), respectively (Arscott et al. 1998). Bryophyte production was measured by placing bryophytes, removed from rocks and rinsed of detritus, in chambers to determine O_2 change per gram dry mass. NPP and R were then converted to areal estimates using cover to biomass relationships developed in each stream (Arscott et al. 1998). GPP was the sum of NPP and R. Whole-reach average GPP was determined by weighting estimates by the area of each habitat (pool/riffle and epilithon/*S. agassizii*/ *Hygrohypnum* spp.). GPP was not measured in Imnavait.

NH$_4$ travel distance calculation—We determined NH_4-S_w at the beginning of the addition period using natural abundance corrected $\delta^{15}N$ values of biota over distance. $\delta^{15}N$ is defined as

$$\delta^{15}N = \left(\frac{R_{sample}}{R_{std}} - 1\right) \times 1000 \qquad (2)$$

where $R = {}^{15}N : {}^{14}N$ ratio, and the N isotope standard is air ($R_{std} = 0.003663$). The biota compartments used for the calculation were primary producers or their grazers (i.e., compartments tied to NH_4). In E-1 the decline of $^{15}NH_4$ in the water column was measured directly; prior to 1997 the technology did not exist to measure $\delta^{15}NH_4$ at low NH_4 concentrations. An estimate of S_w using biota is a time-integrated measure that incorporates temporal variation in solute dynamics.

We corrected for dilution of the $\delta^{15}NH_4$ signal resulting from lateral inputs of unlabelled NH_4 by scaling $\delta^{15}N$ values at each station using dilution rates and assuming NH_4 concentrations were constant over distance; these corrections had generally little impact on the S_w estimate. Natural-log transformed $\delta^{15}N$ values were regressed versus distance to determine k (distance-specific uptake rate, m^{-1}), the inverse

Table 3. Summary of chemical and biological features in each stream reach. GPP is a habitat-weighted mean for the whole stream reach from early July measurements. ND = no data.

Stream reach	NH_4 (μM)	NO_3 (μM)	PO_4 (μM)	DIN: SRP (molar)	GPP (μg O_2 m^2 h^{-1})
E-1 Creek	0.1	2.6	0.08	33.8	45.8
Imnavait Creek	0.35	0.2	0.08	7.4	ND
Blueberry Creek	0.3	0.3	0.20	3.0	126.1
Kuparuk reference	0.2	1.0	0.08	15.0	78.8
Kuparuk fertilized	0.15	0.5	0.14	4.9	123.5
Lower Kuparuk	0.25	1.2	0.08	18.1	31.7

of which is S_w (m). NH_4-v_f and NH_4-U were determined using Eq. 1.

Use of biota ^{15}N to estimate S_w required several assumptions, including (1) downstream movement of the biota used in the calculation did not occur, (2) regeneration of $^{15}NH_4$ was small, (3) ^{15}N content of NO_3 was small if compartment-specific NO_3 uptake rates were high. There was no indication that any of these compartments, including the grazing insects, moved downstream during the experiment. We minimized the likelihood of $^{15}NH_4$ regeneration by using isotope transects from early in the addition period, before much tracer regeneration was likely. The effect of nitrification and $^{15}NO_3$ uptake is similar to that of uptake of regenerated $^{15}NH_4$ but was assumed to be small.

Samples were collected at 4 to 8 stations extending downstream from the drip site and at one station above the drip site to determine natural abundance $\delta^{15}N$. Transect length depended on stream size (Table 4). Details on sampling biota for ^{15}N can be found in Peterson et al. (1997). Details on direct measurement of $^{15}NH_4$ used in E-1 can be found in Holmes et al. (1998) and Mulholland et al. (2000). All isotope samples were run at the Ecosystems Center of the Marine Biological Lab on a Finnegan Delta-S mass spectrometer.

SPON travel distance calculation—Travel distance of suspended particulate organic N ($SPO^{15}N$-S_p) formed from $^{15}NH_4$ via in-stream processes was estimated using a two-compartment model, with ^{15}N stored in the stream bottom as the source and $SPO^{15}N$ as the sink. The model is similar to that previously used for estimating nitrification rates (Mul-

holland et al. 2000). The equations governing the relationship between source and sink ^{15}N content are

$$\frac{d(^{15}N_{source})}{dx} = -k_1 \times (^{15}N_{source}) \qquad (3)$$

$$\frac{d(SPO^{15}N)}{dx} = k_s \times (^{15}N_{source}) - k_2 \times (SPO^{15}N) \qquad (4)$$

where $^{15}N_{source}$ is the stock of ^{15}N in the source compartment (μg ^{15}N m^{-1}), $SPO^{15}N$ is the ^{15}N flux of SPON (μg ^{15}N s^{-1}), k_1 is rate of decline in source ^{15}N over distance (m^{-1}), k_s is the rate of suspension (s^{-1}), k_2 is the distance-specific settling rate of $SPO^{15}N$ (m^{-1}), and x is distance (m) (Table 1). $^{15}N_{source}$ is the product of ($\delta^{15}N_{source}/1,000$), R_{std}, and source total N (μg N m^{-1}); $SPO^{15}N$ is the product of ($\delta^{15}N/1,000$), R_{std}, SPON concentration (μg m^{-3}), and discharge (m^3 s^{-1}). The ^{15}N content at any distance downstream of the addition site is predicted by the solutions to Eqs. 3 and 4:

$$^{15}N_{source} = A_0 \times e^{-k_1 \times x} \qquad (5)$$

$$SPO^{15}N = \frac{(k_s \times A_0)}{(k_2 - k_1)} \times (e^{-k_1 \times x} - e^{-k_2 \times x}) \qquad (6)$$

where A_0 is the ^{15}N content of the source at $x = 0$ m (μg ^{15}N m^{-1}). $SPO^{15}N$ could originate from a variety of compartments, including epilithic diatoms, epilithic detritus, and fine benthic organic nitrogen (FBON). Despite this uncertainty, we can solve for k_2 if k_1 is similar for all possible sources or if the assumed source compartment dominates $SPO^{15}N$ production. In each stream, we assumed k_1 estimated from epilithon on the day of the $SPO^{15}N$ measurement reflected source ^{15}N distribution. This assumes that the primary source of ^{15}N in the SPON compartment is via autotrophic assimilation and sloughing. Direct labeling of SPON from $^{15}NH_4$ was minimal because SPON remained labeled after completion of the tracer addition, suggesting a stream bottom source. The ($A_0 \times k_s$) and k_2 that provided the best fit of the $SPO^{15}N$ fluxes over distance were determined using the Marquardt-Levenberg algorithm in Sigma Plot (Jandel Scientific). SPON-S_p is the negative inverse of k_2.

Statistics—All relationships between discharge (Q) and depth, velocity, depth $\times$ velocity, S_w, and S_p were analyzed assuming a power equation ($Y = aQ^b$), where Y is the dependent variable and a and b are estimated coefficients. Re-

Table 4. NH_4-S_w estimates and related variables from early in the addition period for each stream. Discharge, depth, and velocity are estimates from the start of the addition to the day of S_w measurement. Sample day refers to days since start of $^{15}NH_4$ addition. r^2 and p level refer to regression of ^{15}N isotope data vs. distance used to determine NH_4-S_w.

Stream reach	Discharge (m^3 s^{-1})	Depth (m)	Velocity (m s^{-1})	Compartment sampled	Sample day	Transect length (m)	NH_4-S_w (95% C.I.) (m)	n	r^2	p
E-1 Creek	0.021	0.06	0.16	NH_4	1	128	40 (37.5–42.7)	4	0.99	<.001
Imnavait Creek	0.029	0.57	0.02	*Baetis*	3	175	70 (55–95)	4	0.99	.004
Blueberry Creek	0.287	0.20	0.28	*Orthocladius*	3	210	152 (101–303)	4	0.97	.013
Kuparuk reference	1.72	0.58	0.26	*Orthocladius*	3	1,600	454 (403–520)	7	0.98	<.001
Kuparuk fertilized	5.01	0.79	0.70	*Schistidium*	3	1,100	278 (226–344)	5	0.99	<.001
Lower Kuparuk	18.3	0.91	0.36	Epilithon	6	12,400	5,360 (3,040–22,800)	6	0.77	.022

Table 5. SPON-S_p estimates and related variables from stream and sample time where estimate was significant at $p = 0.10$. The conversion index is the percentage of the $^{15}NH_4$ drip rate that is suspended as SPO^{15}N on the given sample day. Day post 3 refers to 3 d after the $^{15}NH_4$ addition ended.

Stream	Sample day	Discharge ($m^3 \, s^{-1}$)	SPON ($\mu g \, L^{-1}$)	Source compartment	Source k_1 (m^{-1})	SPON-S_p (m)	p	SPON-v_f ($m \, s^{-1}$)	SPON-U ($\mu g \, m^2 \, s^{-1}$)	Conversion index (%)
Imnavait Creek	35	0.033	14.3	Mayflies*	0.0134	113	.032	1.08E−04	1.5	35
Blueberry Creek	17	0.26	16	Epilithon	0.0066	420	.076	1.18E−04	1.9	21
Blueberry Creek	31	0.30	16.7	Epilithon	0.01	320	.009	1.77E−04	2.9	31
Blueberry Creek	Post 3	0.15	13.2	Epilithon	0.01	670	.006	4.02E−05	0.5	12
Kuparuk fertilized	31	3.59	19.5	Epilithon	0.0010	1,262	.008	3.05E−04	5.9	29
Lower Kuparuk	13	28.60	11.3	Epilithon	0.000385	9,680	.001	0.73E−04	0.8	36

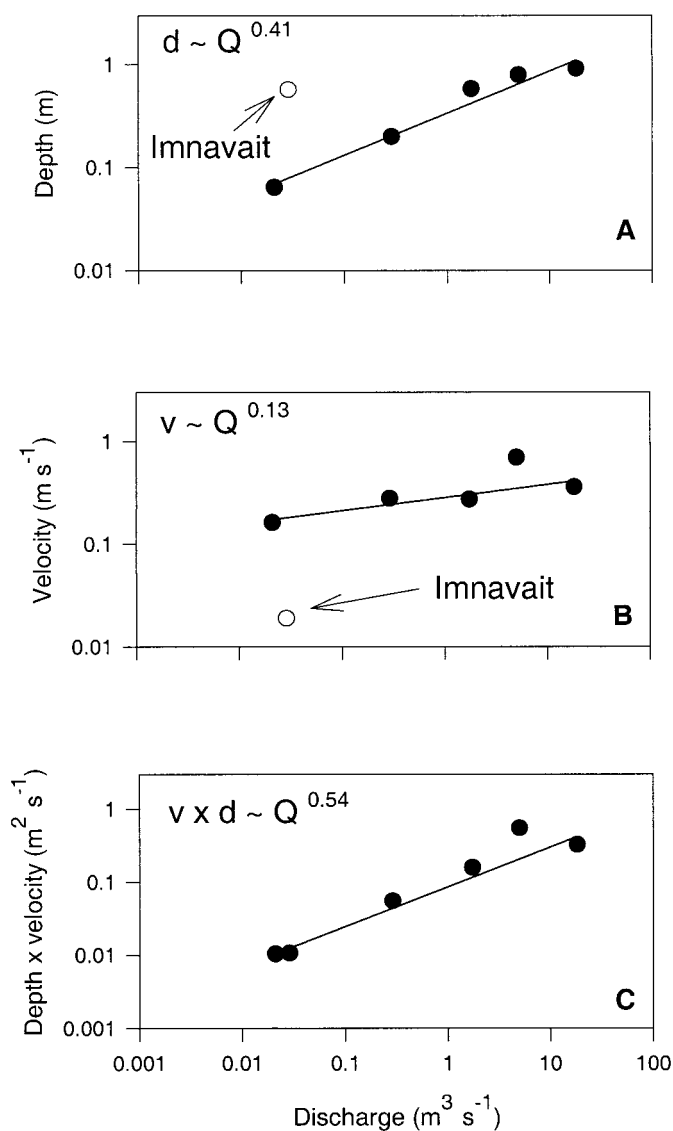* Epilithon distribution was inferred from grazers of epilithon.

Fig. 2. (A) Depth (d), (B) velocity (v), and (C) velocity × depth ($v \times d$) versus median discharge (Q) for the early addition period corresponding with the NH_4-S_w estimate. Imnavait is not included in the regression estimates for (A) and (B).

gression parameters were fitted using weighted least squares to correct for unequal variances assuming a weighting factor, $w = 1/Y^2$. All analyses were conducted in Sigma Plot (Jandel Scientific).

Results

Physical, chemical, and biological characteristics—Median discharge during the time period corresponding with the NH_4-S_w estimate ranged almost three orders of magnitude from 0.021 $m^3 \, s^{-1}$ in E-1 to 18.3 $m^3 \, s^{-1}$ in the Lower Kuparuk (Table 4). Discharge on the day of the SPON-S_p estimates ranged from 0.033 to 28.6 $m^3 \, s^{-1}$ (Table 5).

Mean velocities (v) and depths (d) increased with discharge (Table 4). If Imnavait is excluded, velocity increased by $Q^{0.13}$ ($r^2 = 0.62$, $p = 0.11$), and depth increased by $Q^{0.41}$ ($r^2 = 0.94$, $p = 0.002$) (Fig. 2A,B). Imnavait was exceptional because it is a beaded stream with numerous large deep pools connected by short, shallow riffles. When the product of depth and velocity ($v \times d$) was regressed against discharge, Imnavait was no longer an outlier ($v \times d \sim Q^{0.54}$, $r^2 = 0.82$, $p = 0.0001$) (Fig. 2C).

NH_4, NO_3, SRP, molar DIN : SRP, and GPP did not show any trends with increasing discharge (Table 3). NH_4 concentrations were always low. The highest SRP concentrations occurred in Blueberry Creek and the Kuparuk fertilized reach. NO_3 concentrations were variable (Table 3). DIN : SRP ranged from 3 in Blueberry Creek to 34 in E-1, driven primarily by variability in NO_3. Habitat-weighted GPP ranged from 31.7 mg $O_2 \, m^{-2} \, h^{-1}$ in the Lower Kuparuk to > 100 mg $O_2 \, m^{-2} \, h^{-1}$ in the Blueberry Creek and the Kuparuk fertilized reach (Table 3).

NH_4 dynamics—^{15}N content in primary producers and their consumers declined exponentially with distance in each stream (Fig. 3). NH_4-S_w ranged from 40 m in E-1 to 5,360 m in the Lower Kuparuk (Table 4). In E-1, NH_4-S_w determined from NH_4 and from biota was similar (40 m vs. 36 m), which suggests use of biota to determine NH_4-S_w early in the addition period is acceptable.

As expected, NH_4-S_w increased with discharge across the six stream reaches. Excluding the Kuparuk fertilized reach, NH_4-S_w was proportional to $Q^{0.60}$ ($r^2 = 0.77$, $p = 0.011$; Fig.
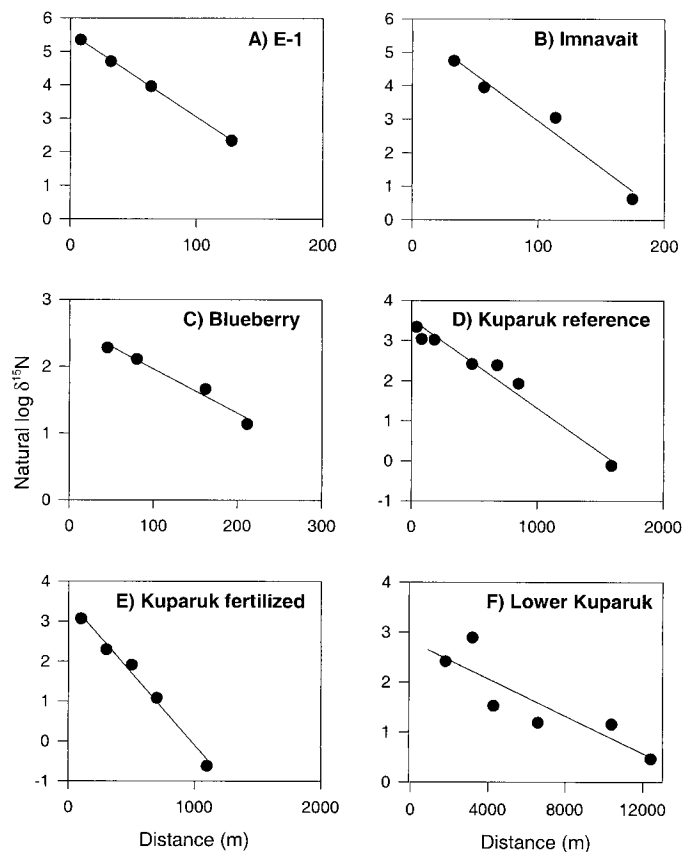
Fig. 3. Natural log of the natural abundance and dilution-corrected δ^{15}N versus distance as calculated from: (A) NH_4 in E-1 Creek in 1997 on day 1; (B) *Baetis* sp. in Imnavait Creek in 1995 on day 3; (C) *Orthocladius* sp. in Blueberry Creek in 1994 on day 3; (D) *Orthocladius* sp. in the Kuparuk reference reach in 1991 on day 3 of the addition; (E) the moss *Schistidium agassizii* in Kuparuk fertilized reach in 1995 on day 3, (F) epilithon in the Lower Kuparuk in 1996 on day 6. Lines are regression fits. The negative inverse of the slope is equal to S_w.

Fig. 4. NH_4 parameters versus discharge from early in the addition period for each stream. (A) NH_4-S_w. Error bars are 95% C.I. based on the regressions in Fig. 3. Regression slope and r^2 does not include the Kuparuk P-fertilized reach. (B) NH_4-v_f. Error bars are 95% C.I. based on S_w error bars only and (C) NH_4 uptake.

4A). S_w in the Kuparuk fertilized reach was shorter than in the Kuparuk reference reach despite higher discharge (Fig. 4A).

Because $v \times d$ was proportional to $Q^{0.54}$ (Fig. 2C) and S_w was proportional to $Q^{0.6}$ (excluding the Kuparuk fertilized reach), most of the increase in S_w was due to changes in depth and velocity. The transfer coefficient (NH_4-v_f) determined from S_w, v, and d (Eq. 1) was relatively constant in the four streams with the lowest discharge but was much higher in the Kuparuk fertilized reach and lower in the Lower Kuparuk (Fig. 4B). Variability in NH_4-v_f determined the variation around the S_w versus Q relationship (Fig. 4A).

NH_4-v_f is a function of both areal uptake rate and nutrient concentration ($v_f = U/C$). NH_4-U ranged from 0.21 μg m^{-2} s^{-1} in the Lower Kuparuk to 4.18 μg m^{-2} s^{-1} in the Kuparuk fertilized reach. There was no clear trend in uptake rate with increasing discharge, although highest rates occurred at intermediate discharges in the unmanipulated streams (Fig. 4C). Uptake rates should be viewed cautiously because of the difficulty measuring NH_4 concentrations at such low levels (Aminot et al. 1997; Holmes et al. 1999). Note that NH_4-

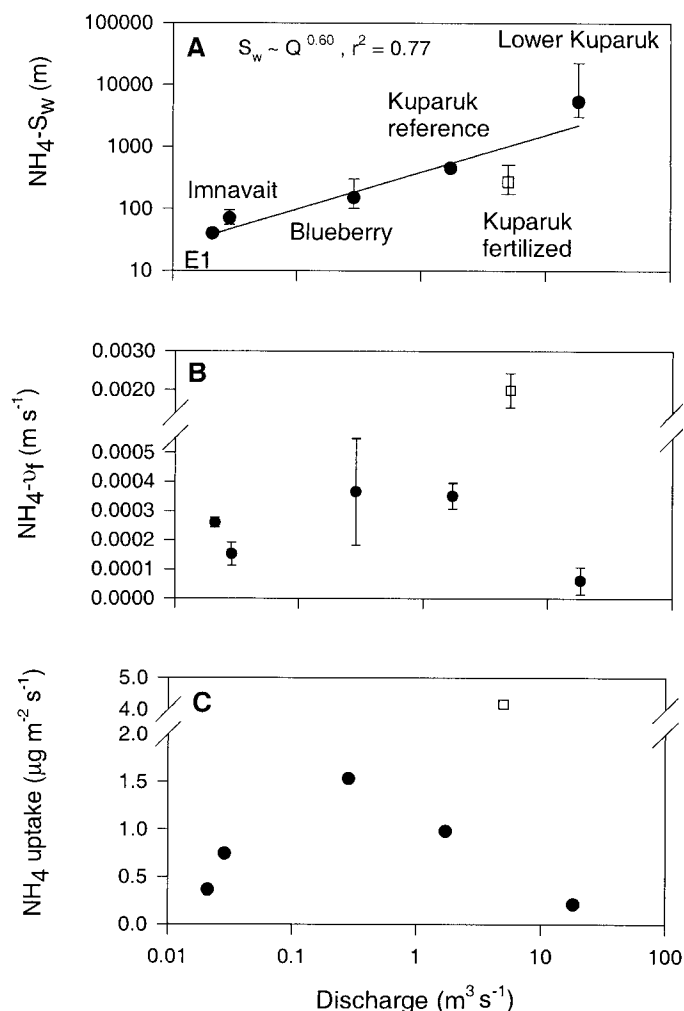S_w and v_f estimates were determined without use of NH_4 concentrations.

NH_4-v_f was positively correlated with GPP, with the Kuparuk fertilized reach much higher than the other streams (Fig. 5A). Primary production was a secondary factor explaining variation in NH_4-S_w. Excluding the Kuparuk fertilized reach, NH_4-v_f was not related to the DIN:SRP ratio (Fig. 5B). NH_4-U was also positively related to GPP and inversely related to DIN:SRP ratio (data not shown). The response of the Kuparuk fertilized reach in particular suggests that NH_4 uptake, DIN:SRP, and GPP are related.

SPON dynamics—SPON-S_p determined by fitting the two-compartment model ranged from 113 m in Imnavait at a discharge of 0.033 m^3 s^{-1} to 9,680 m in the Lower Kuparuk at a discharge of 28.6 m^3 s^{-1} (Table 5; *see Fig. 6* for an example of model fit). We included only estimates of S_p (= $-1/k_2$) when k_2 was significant at the $p = 0.10$ level.

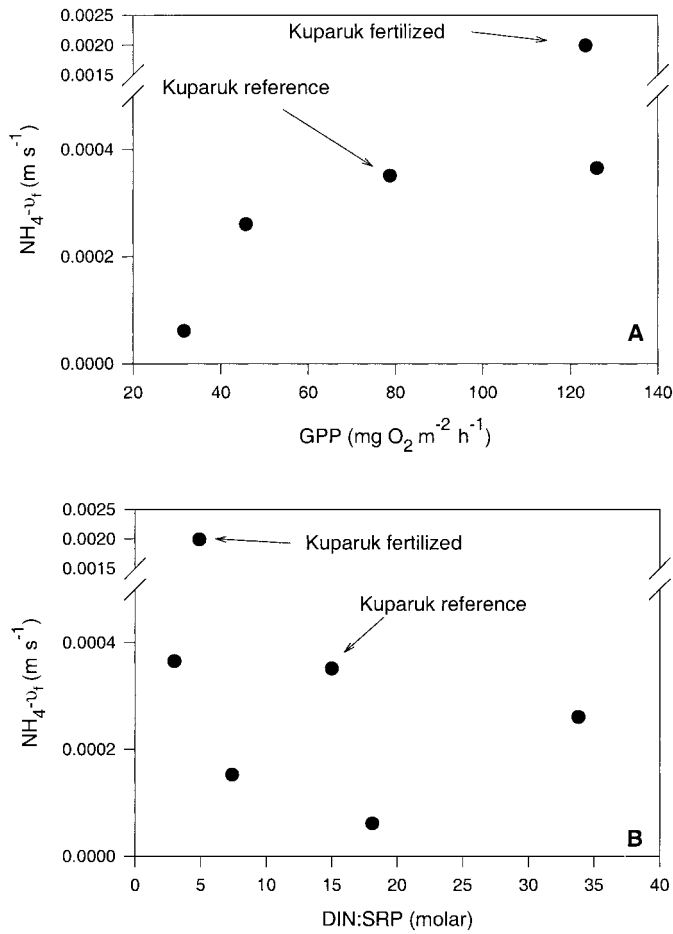SPON-S_p, including the Kuparuk fertilized reach, was

Fig. 5. (A) NH_4-v_f versus GPP as measured early in the addition period for each stream. (B) NH_4-v_f versus DIN:SRP molar ratio. Kuparuk fertilized and reference reaches are labeled for comparison.

Fig. 6. Example of observed and model-predicted $SPO^{15}N$ flux (μg ^{15}N s^{-1}) over distance. Predicted fluxes are based on fitting the two-compartment model assuming epilithon is an indicator of the source ^{15}N distribution. Data are for the Kuparuk fertilized reach on day 31.
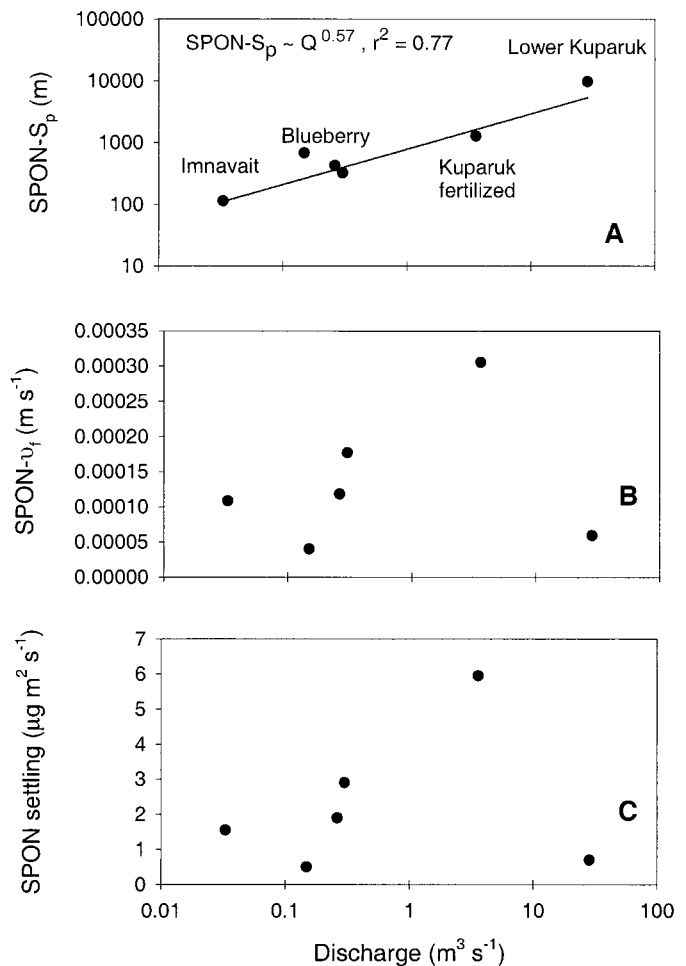
Fig. 7. SPON parameters versus discharge. (A) SPON-S_p, (B) SPON-v_f, and (C) SPON settling rate.

again strongly related to discharge ($S_p \sim Q^{0.57}$, $r^2 = 0.57$, $p = 0.004$; Fig. 8A). The rate of change was almost identical to the change in velocity and depth with discharge ($v \times d \sim Q^{0.58}$, $r^2 = 0.89$, $p = 0.003$). As with NH_4, changes in physical characteristics explained changes in SPON-S_p as discharge increased. However, within Blueberry Creek, S_p was anomalously high at the lowest discharge (Table 5, Fig. 7A).

SPON-v_f values varied sevenfold, the lowest occurring once in Blueberry Creek and the highest in the Kuparuk fertilized reach (Table 5, Fig. 7B). Areal deposition rates varied similarly, ranging from 0.5 μg N m^{-2} s^{-1} in Blueberry Creek to 5.9 μg N m^{-2} s^{-1} in the Kuparuk fertilized reach (Table 5, Fig. 7C).

The gross amount of $SPO^{15}N$ produced was estimated using the model-fitted parameters and setting SPON settling (k_2) to 0. Gross flux of $SPO^{15}N$ was compared to the $^{15}NH_4$ addition rate and can be viewed as an index of NH_4 conversion to SPON. This index will vary over time as more ^{15}N taken up by the biota is suspended in the water column. By late in the experiments, the amount of $SPO^{15}N$ produced represented a sizeable fraction of the $^{15}NH_4$ addition rate, with an average conversion index of 33% (Table 5). In Blue-
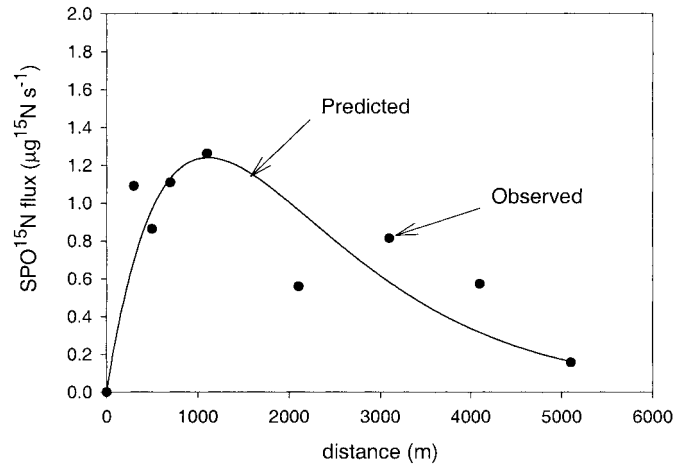
Fig. 8. Comparison of SPON-S_p (m) versus discharge (m³ s⁻¹) determined in this study with those reported in the literature.

berry Creek, the conversion index increased from 21% on day 17 to 31% on day 31 and declined to 12% 3 d after the end of the addition (Table 5).

Discussion

NH₄ travel length and discharge: physical versus biological/chemical control—In the Kuparuk River watershed, changing physical characteristics (depth and velocity) explained the increase in NH_4-S_w as stream size increased. Biological and chemical changes, reflected in v_f, were relatively small and not related to in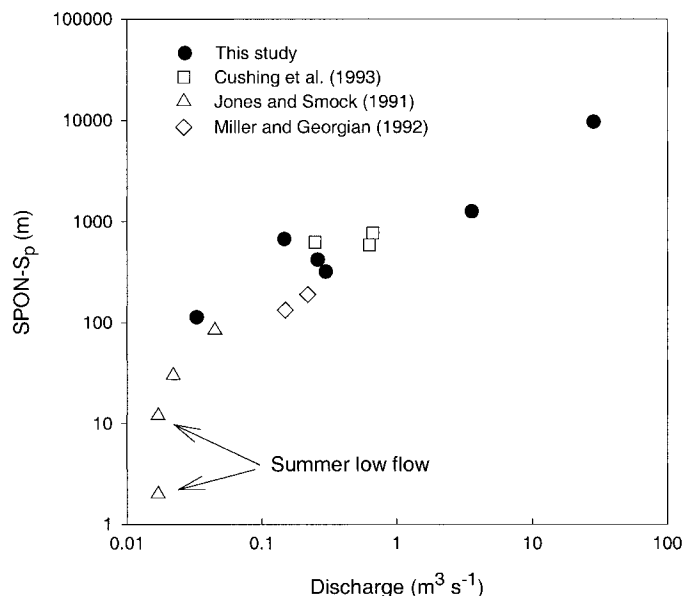creasing discharge. Only when P limitation was removed via P fertilization was biological activity strong enough to counter increased velocity and depth, leading to a lower NH_4-S_w in the Kuparuk fertilized reach than expected.

The importance of depth and velocity in determining travel lengths has been demonstrated for organic matter (Minshall et al. 1983; Naiman et al. 1987) as well as for dissolved nutrients (Davis and Minshall 1999). Davis and Minshall (1999) found that after accounting for different depths and velocities, streams with very different NO_3-S_w values had similar NO_3-v_f and suggest that v_f is a more useful measure for comparing nutrient dynamics among streams. NO_3-v_f summarized from several studies of non-Arctic streams ranged from 1.2×10^{-5} to 9.9×10^{-5} m s⁻¹ (Davis and Minshall 1999). NH_4-v_f values in our unfertilized Arctic streams were higher but of similar magnitude, ranging from 6.1×10^{-5} to 3.7×10^{-4} m s⁻¹ (Fig. 4B). The sixfold range in NH_4-v_f we found was smaller than the 33-fold range in depth × velocity. Because NH_4-v_f was independent of stream size, the S_w versus Q relationship was controlled primarily by changing physical dimensions, with scatter caused by variations in NH_4-v_f.

Although biological activity did not control changes in travel length with stream size, it did control the range of

NH_4-S_w observed (in addition to scatter) by maintaining a relatively constant v_f. For v_f to remain constant, both uptake and concentration must either stay constant or vary proportionally. In either case, stream bottom activity determined the average level of v_f throughout the watershed. Understanding the controls of v_f is critical for understanding S_w at the watershed scale.

Factors controlling NH_4-v_f—v_f is determined by the relative amounts of uptake and concentration. If nutrient uptake is already saturated, increasing concentrations will cause v_f to decline (Davis and Minshall 1999). Conversely, if concentrations remain constant but uptake increased because of recovery from disturbance or removal of some other limitation (e.g., carbon, light, other nutrients), v_f will increase. An example of the latter case is the Kuparuk fertilized reach, where P limitation has been experimentally removed. In response, GPP, NH_4 uptake, and NH_4-v_f have increased dramatically, resulting in NH_4-S_w shorter than in the Kuparuk reference reach, despite greater depth and velocity (Fig. 4A).

In general, higher GPP led to higher NH_4-v_f and U, with the Kuparuk fertilized reach showing an extreme response (Fig. 5A). This suggests that primary production is an important determinant of NH_4 dynamics in the Arctic during the growing season. However, variability in primary production was small compared to increases in depth and velocity and therefore did not control changes in S_w with increasing discharge. The order of magnitude greater NH_4-v_f in the Kuparuk fertilized reach, despite a GPP within the range observed in unfertilized streams, might be partly due to changes in community structure. One response to fertilization has been colonization by the bryophyte, *Hygrohypnum* spp., which showed strong preference for NH_4 over NO_3, unlike the dominant prefertilization bryophyte (J. C. Finlay and W. B. Bowden unpubl. data), or epilithon (Wollheim et al. 1999). Blueberry Creek also showed high GPP, but a much lower NH_4-v_f than the Kuparuk fertilized reach (Fig. 4B). A lower NH_4-v_f could result from preferential use of NO_3 or a greater use of internally recycled N. The low GPP in the Lower Kuparuk might result from frequent scouring of primary producers caused by unstable substrates in this stream (personal observation).

The demand for NH_4 might be expected to decrease as DIN : SRP increases because P limitation increases and NO_3 also becomes more available. In the unfertilized Arctic, we see little evidence that NH_4-v_f declines with increasing DIN : SRP (Fig. 5B). One possible explanation is as N becomes more abundant, dissimilatory uptake of NH_4 (i.e., nitrification) increases. We were able to measure nitrification rates only in E-1, the stream with the highest DIN : SRP, where 40% of NH_4 uptake was nitrification (B. J. Peterson unpubl. data). When NH_4 was added to two forested streams, nitrification increased considerably (Newbold et al. 1983; Richey et al. 1985), potentially keeping NH_4-v_f constant despite higher concentrations. The role of nitrification in the other Arctic streams remains unknown.

The River Continuum Concept (RCC) stressed the importance of indirect effects of increasing stream size on biological characteristics and processes, such as the amount of woody debris, leaf litter inputs, and shading (Vannote et al.

1980). For example, carbon retention was higher in smaller streams in part because of the greater amount of woody debris in headwater streams (Minshall et al. 1983; Naiman et al. 1987). Within single stream reaches, nutrient retention was influenced by biological factors related to stream size such as litter inputs (Mulholland et al. 1985) and shading (Mulholland et al. 2000). Other controls on solute dynamics that potentially vary with stream size include disturbance (Grimm 1987), substrate size (Marti and Sabater 1996), abundance of debris dams (Munn and Meyer 1990), and exchange with the hyporheic zone (Valett et al. 1996).

In this study, physical changes associated with increasing stream size directly changed travel lengths, but gradients in stream bottom processes were not observed. Variables driving the RCC in temperate systems are absent in the Kuparuk watershed. For example, low-order streams in the Arctic are rarely shaded by overhanging vegetation, and allochthonous leaf inputs are minimal (Harvey et al. 1997). In addition, the major allochthonous input is peat, which tends to be of poor quality (Peterson et al. 1986) and probably has limited influence on N cycling. The Kuparuk watershed therefore provides a baseline for understanding the effect of scale on solute dynamics where conditions are relatively uniform and unimpacted.

Conceptual model of watershed nutrient dynamics—The relative importance of physical (depth and velocity), biological (uptake), and chemical (concentration) changes as stream size increases will vary in different watersheds and across seasons. Whereas changes in physical characteristics (depth and velocity) are predictable with discharge, both downstream and at a location (Leopold and Maddock 1953), changes in biological and chemical characteristics can be more complex, especially with human impacts. Equation 1 [$S_w = (vdC)/U = (vd)/v_f$] can be used as a framework to explore the relative importance of physical versus biological/chemical changes (Fig. 9), with the vertical mass transfer coefficient v_f ($= U/C$) an indicator of the latter. If v_f of a nutrient shows no trend along a river transect, then physical changes dominate and the change in S_w with increasing discharge (i. e., slope in Fig. 9A, top panels) will be determined entirely by changes in depth and velocity. The degree of deviation from (or scatter around) this slope, caused by a continuum (or variability) in v_f, indicates the relative importance of biological and/or chemical changes with increasing stream size (Fig. 9A). Biological and chemical changes might be natural (e.g., the RCC) or the result of human influence. The effects of increased nutrient loading (chemical changes) as streams flow from relatively pristine headwaters to more human-dominated landscapes could potentially be evaluated in this context.

Along a river transect, v_f could on average stay constant (no trend) or show increasing or decreasing trends, depending on the interaction between nutrient loading rates, the degree of nutrient limitation, and biological characteristics. Constant v_f would occur if uptake rates and concentrations both showed no trends but would also occur if both increased proportionally (Fig. 9B, scenario 1 and 2, respectively). The former case is more or less what we observed for NH_4 in unfertilized streams in the Kuparuk watershed

(Fig. 9B, scenario 1). Scenario 2 would occur if concentration of a limiting nutrient increased and first-order kinetics controlled uptake at the scale of whole stream reaches (Fig. 9B, scenario 2). Changes in v_f would occur if uptake and concentration did not vary proportionally. For example, if concentration of a nonlimiting nutrient showed an increasing trend downstream, uptake would change little, and v_f would decline (Fig. 9B, scenario 3). Alternatively, v_f could increase if uptake increased more than concentration (e.g., if light or other nutrient limitation declines, or if disturbance declines; Fig. 9B scenario 4). Scenario 4 is the type of response shown by the Kuparuk fertilized reach, where P fertilization led to increased uptake of NH_4.

This conceptual model (Fig. 9) is a simplification in several ways. First, it assumes an idealized continuum that is unlikely for biological and chemical characteristics, as has been demonstrated for the River Continuum Concept (Minshall et al. 1985). For example, concentration would show a step function below nutrient point sources. Second, uptake across water–sediment boundaries can also be controlled by Michaelis-Menton kinetics (Sanford and Crawford 2000), which would tend to cause a decline in v_f with increasing concentration, whether or not the nutrient was limiting (Davis and Minshall 1999). Whether first-order or Michaelis-Menton kinetics better describe uptake at the stream reach scale is unclear. Finally, large rivers may exhibit completely different dynamics because of greater water column processing. Nevertheless, general patterns of v_f along river transects might be a valuable tool for comparing solute dynamics in different watersheds. Moreover, stream reaches that deviate from relationships within watersheds (e.g., the Kuparuk fertilized reach) can be useful for understanding the controls of solute dynamics.

SPON dynamics—SPON travel distance (SPON-S_p) was also influenced primarily by increased depth and velocity with stream size, suggesting that in the Kuparuk watershed, physical changes outweigh biological or chemical variations for N (though NO_3 travel distances were not measured). SPON-v_f was relatively constant, although among nonfertilized streams, variation in one stream (Blueberry Creek) was greater than across streams.

SPON-S_p values determined in this study correspond well with particulate travel lengths determined by others. Cushing et al. (1993) measured carbon travel distances similar to those determined for SPON in this study (Fig. 8). Depositional velocities derived from travel lengths ranged from 0.7 $\times 10^{-4}$ to 1.6 $\times 10^{-4}$ (Cushing et al. 1993), falling within our measured range of SPON-v_f (Fig. 7B). Estimates from two other studies also correspond well with our measurements (Fig. 8; Jones and Smock 1991; Miller and Georgian 1992). The correspondence between SPON-S_p and discharge across diverse sites suggests that changes in particulate travel lengths across scale are controlled primarily by changes in physical characteristics. Depositional velocities of particulate matter varied less than discharge across sites. However, this relationship apparently breaks down at small scales. Two small streams studied at low flow by Jones and Smock (1991) deviated from the overall relationship (Fig. 8), perhaps because of numerous debris dams that were absent from
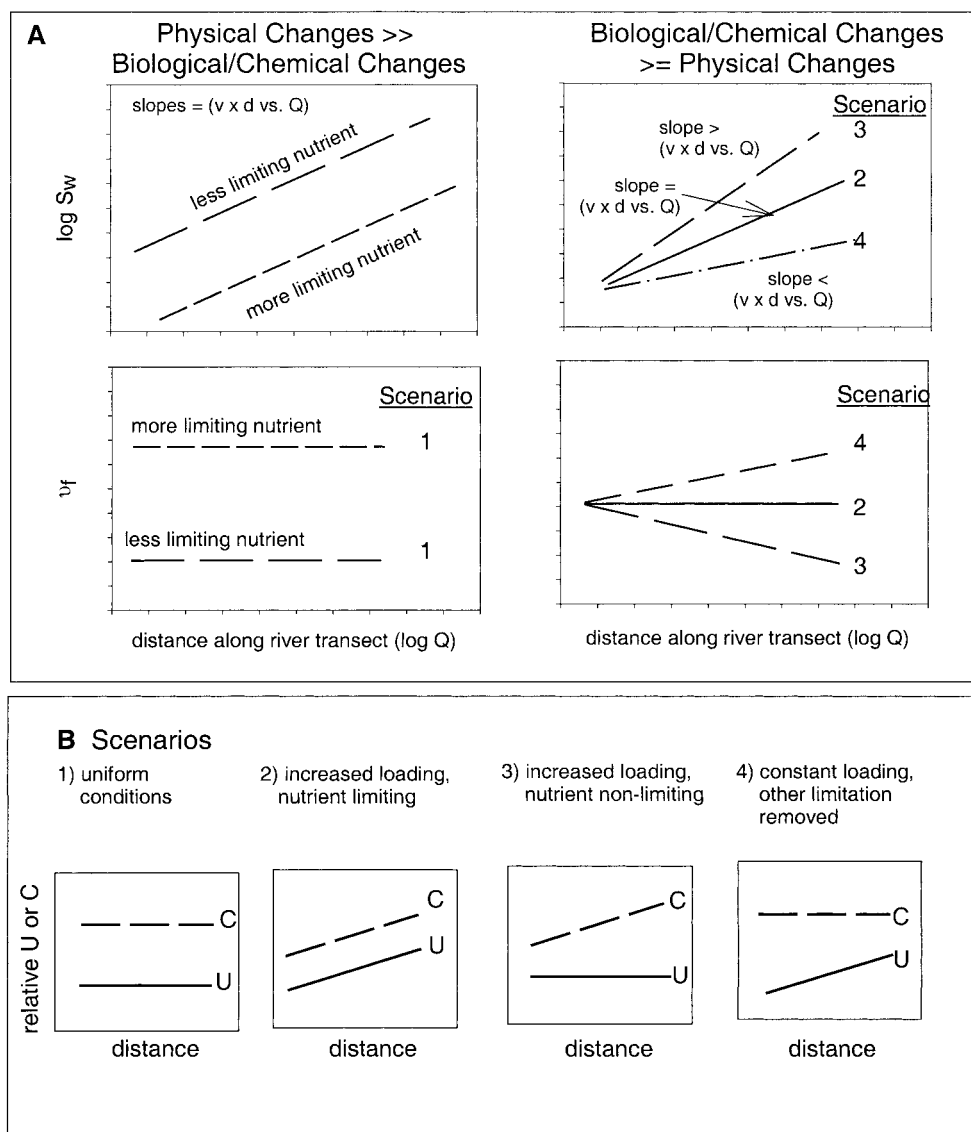
A

Physical Changes >>
Biological/Chemical Changes

Biological/Chemical Changes
>= Physical Changes

slopes = (v x d vs. Q)

less limiting nutrient

more limiting nutrient

log S_w

Scenario
3
2
4

slope >
(v x d vs. Q)

slope =
(v x d vs. Q)

slope <
(v x d vs. Q)

Scenario

more limiting nutrient — 1

less limiting nutrient — 1

v_f

Scenario
4
2
3

distance along river transect (log Q)

distance along river transect (log Q)

B Scenarios

1) uniform
   conditions

2) increased loading,
   nutrient limiting

3) increased loading,
   nutrient non-limiting

4) constant loading,
   other limitation
   removed

relative U or C

C
U

C
U

C
U

C
U

distance   distance   distance   distance

Fig. 9. Conceptual model of the interaction between uptake length (S_w), vertical mass transfer coefficient (v_f), areal uptake (U), and concentration (C) along a river transect (represented by the logarithm of discharge, Q, as a surrogate for distance) for several loading and nutrient limitation scenarios. (A) Expected patterns of changing S_w and v_f along a river transect based on the relative importance of physical versus biological/chemical changes. Top panels in (A) show expected S_w versus Q corresponding with the different v_f versus Q in the bottom panels of (A). Slopes for S_w versus Q are compared to those expected from changes in velocity and depth ($v \times d$ versus Q) only. Numbers refer to scenarios described in (B). (B) Possible scenarios of changing U and C with distance downstream that would apply to v_f relationships numbered in (A).

the other streams. Debris dams increase retention of particulates as well as inorganic nutrients (Bilby 1981; Minshall et al. 1983; Triska et al. 1984; Munn and Meyer 1990).

The ability of streams to process NH_4 and SPON in certain cases may be linked. For both NH_4 and SPON, the Lower Kuparuk had the lowest and the Kuparuk fertilized reach the highest v_f and U estimates. The extremely high biomass of the moss *Hygrohypnum* spp. in the Kuparuk fertilized reach (Arscott et al. 1998), which contributed to high NH_4 demand, can also act to filter particulates. FBON biomass was extremely high within the mats of *Hygrophypnum* spp. (un-

publ. data). Similarly, shifting substrates that might reduce primary productivity in the Lower Kuparuk may also slow the net settling of FBON.

There is considerable uncertainty in our estimate of SPON-S_p because the two-compartment model required several assumptions. First, we assumed that the source compartment had a longitudinal ^{15}N distribution similar to that measured in epilithon. If k_1 values are similar among different sources, SPON-S_p will not be affected. In the Kuparuk fertilized reach, epilithon and FBON had similar k_1 values, so SPON-S_p in this stream is robust despite uncertainty in

the actual source compartment. Unfortunately we did not measure FBO^{15}N in most of our other experiments. Second, we assumed little or no resuspension of labeled material. When we did measure FBO^{15}N, enrichments were low, but if surface material consisting of recently settled SPO^{15}N became quickly resuspended, SPON-S_p would be overestimated (labeled SPO^{15}N might have cycled between water and substrate several times). Cushing et al. (1993) found that retention of 99% of deposited material was only 1.5 to 3 h. The SPON-S_p estimates reported here are therefore maximums, and SPON-v_f and U are minimums. Despite these uncertainties, our results agree well with other published results.

A fairly significant proportion of the ^{15}NH$_4$ added to each stream returned to the water column as SPO^{15}N (conversion index, Table 5). Thus, an inorganic nitrogen molecule converted to organic form may be stored in the stream bottom for only short periods of time (on the order of weeks). Others have shown that inorganic nutrients taken up by the stream bottom are stored until high discharge events export them in an organic form (Meyer et al. 1981; Mulholland 1992). Discharge corresponding with the S_p estimate was significantly above baseflow in Imnavait and the Kuparuk fertilized reach and was slightly higher in the Lower Kuparuk. Relatively high rates of sloughing may in part explain the large percentage of ^{15}NH$_4$ conversion to SPO^{15}N in these streams. Transformation from inorganic to organic forms of nitrogen with subsequent transport downstream could have important implications for downstream processes.

Conclusion

Understanding how nutrient dynamics change with stream size is necessary for modeling nutrient fluxes from watersheds to the coastal zone. In the Arctic, NH$_4$-S_w and SPON-S_p could be fairly well predicted from discharge along the river network because during the growing season, uptake and settling velocities were relatively constant and did not vary systematically compared to changing physical characteristics. NH$_4$ entering large streams was likely to be transported farther than NH$_4$ entering small streams because physical changes outweighed the stream's ability to quickly process inputs. Because of this tendency and because most inputs from terrestrial systems enter into lower order streams (Vannote et al. 1980; Naiman et al. 1987) an understanding of headwater-stream processes is critical for determining watershed scale nutrient fluxes. Biological or chemical gradients were not evident in this Arctic watershed, but could occur in forested or human-influenced watersheds, potentially altering the relationship between nutrient travel distances and stream size. Further work is required to determine the relationships between nutrient processing and stream size in other biomes and seasons, as well as for other dissolved nutrients.

References

ALEXANDER, R. B., R. A. SMITH, AND G. E. SCHWARZ. 2000. Effect of stream channel size on the delivery of nitrogen to the Gulf of Mexico. Nature **403:** 758–761.

AMINOT, A., D. S. KIRKWOOD, AND R. KÉROUEL. 1997. Determination of ammonia in seawater by the indophenol-blue method: Evaluation of the ICES NUTS I/C5 questionnaire. Mar. Chem. **56:** 59–75.

ARSCOTT, D. B., W. B. BOWDEN, AND J. C. FINLAY. 1998. Comparison of epilithic algal and bryophyte metabolism in an arctic tundra stream, Alaska. J. N. Am. Benthol. Soc. **17:** 210–227.

BILBY, R. E. 1981. Role of organic debris dams in regulating the export of dissolved and particulate matter from a forested watershed. Ecology **62:** 1234–1243.

BOWDEN, W. B., J. C. FINLAY, AND P. E. MALONEY. 1994. Long-term effects of phosphate fertilization on the distribution of bryophytes in an arctic river. Freshw. Biol. **32:** 445–454.

CUSHING, C. E., G. W. MINSHALL, AND J. D. NEWBOLD. 1993. Transport dynamics of fine particulate organic matter in two Idaho streams. Limnol. Oceanogr. **38:** 1101–1115.

DAVIS, J. C., AND G. W. MINSHALL. 1999. Nitrogen and phosphorus uptake in two Idaho (USA) headwater wilderness streams. Oecologia **119:** 247–255.

EDWARDSON, K. J. 1998. M.S. thesis, Univ. New Hampshire.

FINLAY, J. C., AND W. B. BOWDEN. 1994. Controls on production of bryophytes in an arctic tundra stream. Freshw. Biol. **32:** 455–466.

GRIMM, N. B. 1987. Nitrogen dynamics during succession in a desert stream. Ecology **68:** 1157–1170.

HARVEY, C. J., B. J. PETERSON, W. B. BOWDEN, L. A. DEEGAN, J. C. FINLAY, A. E. HERSHEY, AND M. C. MILLER. 1997. Organic matter dynamics in the Kuparuk River, a tundra river in Alaska, USA. J. N. Am. Benthol. Soc. **16:** 18–23.

HOLMES, R. M., A. AMINOT, R. KÉROUEL, B. A. HOOKER, AND B. J. PETERSON. 1999. A simple and precise method for measuring ammonium in marine and fresh water ecosystems. Can. J. Fish. Aquat. Sci. **56:** 1801–1808.

————, J. W. MCCLELLAND, D. M. SIGMAN, B. FRY, AND B. J. PETERSON. 1998. Measuring ^{15}N-NH$_4^+$ in marine, estuarine, and fresh waters: An adaptation of the ammonia diffusion method for samples with low ammonium concentrations. Mar. Chem. **60:** 235–243.

HOPKINSON, C. S., AND J. J. VALLINO. 1995. The relationship among man's activities in watersheds and estuaries: A model of runoff effects on patterns of estuarine community metabolism. Estuaries **18:** 598–621.

JONES, J. B., AND L. A. SMOCK. 1991. Transport and retention of particulate organic matter in two low-gradient headwater streams. J. N. Am. Benthol. Soc. **10:** 115–126.

KILPATRICK, F. A., AND E. D. COBB. 1985. Measurement of discharge using tracers. Techniques of water-resources investigations of the United States Geological Survey, USGS.

LEOPOLD, L. B., AND T. MADDOCK, JR. 1953. The hydraulic geometry of stream channels and some physiographic implications. Geological Survey Professional Paper **252:** 1–56.

MARTI, E., AND F. SABATER. 1996. High variability in temporal and spatial nutrient retention in Mediterranean streams. Ecology **77:** 854–869.

MEYER, J. L., AND G. E. LIKENS. 1979. Transport and transformation of phosphorus in a forested stream ecosystem. Ecology **60:** 1255–1269.

————, ————, AND J. SLOANE. 1981. Phosphorous, nitrogen, and organic carbon flux in a headwater stream. Arch. Hydrobiol. **91:** 28–44.

MILLER, J., AND T. GEORGIAN. 1992. Estimation of fine particulate transport in streams using pollen as a seston analog. J. N. Am. Benthol. Soc. **11:** 172–180.

MINSHALL, G. W., K. W. CUMMINS, R. C. PETERSEN, C. E. CUSHING, D. A. BRUNS, J. R. SEDELL, AND R. L. VANNOTE. 1985. De-

velopments in stream ecosystem theory. Can. J. Fish. Aquat. Sci. **42:** 1045–1055.

———, R. C. PETERSON, K. CUMMINS, W. T. L. BOTT, J. R. SEDELL, C. E. CUSHING, AND R. L. VANNOTE. 1983. Interbiome comparison of stream ecosystem dynamics. Ecol. Monogr. **53:** 1–25.

MULHOLLAND, P. J. 1992. Regulation of nutrient concentrations in a temperate forest stream: Roles of upland, riparian, and instream processes. Limnol. Oceanogr. **37:** 1512–1526.

———, J. D. NEWBOLD, J. W. ELWOOD, L. A. FERREN, AND J. R. WEBSTER. 1985. Phosphorous spiralling in a woodland stream: Seasonal variation. Ecology **66:** 1012–1023.

———, J. L. TANK, D. M. SANZONE, W. M. WOLLHEIM, B. J. PETERSON, J. R. WEBSTER, AND J. L. MEYER. 2000. Nitrogen cycling in a forest stream determined by a ^{15}N tracer addition. Ecol. Monogr. **70(3):** 471–493.

MUNN, N. L., AND J. L. MEYER. 1990. Habitat-specific solute retention in two small streams: An intersite comparison. Ecology **71:** 2069–2082.

NAIMAN, R. J., J. M. MELILLO, M. A. LOCK, T. E. FORD, AND S. R. REICE. 1987. Longitudinal patterns of ecosystem processes and community structure in a sub-arctic river continuum. Ecology **68:** 1139–1156.

NEWBOLD, J. D., J. W. ELWOOD, R. V. O'NEILL, AND W. VAN WINKLE. 1981. Measuring nutrient spiralling in streams. Can. J. Fish. Aquat. Sci. **38:** 860–863.

———, ———, M. S. SCHULZE, R. W. STARK, AND J. C. BARMEIER. 1983. Continuous ammonium enrichment of a woodland stream: Uptake kinetics, leaf decomposition, and nitrification. Freshw. Biol. **13:** 193–204.

PETERSON, B. J., M. BAHR, AND G. W. KLING. 1997. A tracer investigation of nitrogen cycling in a pristine tundra river. Can. J. Fish. Aquat. Sci. **54:** 2361–2367.

———, J. E. HOBBIE, AND T. L. CORLISS. 1986. Carbon flow in a tundra stream ecosystem. Can. J. Fish. Aquat. Sci. **43:** 1259–1270.

———, AND OTHERS. 1993. Biological responses of a tundra river to fertilization. Ecology **74:** 653–672.

PÉWÉ, T. L. 1966. Ice-wedges in Alaska-classification, distribution, and climactic significance. *In* Permafrost international conference, Lafayette Ind. Proceedings of the national academy of science national resource council publication **1287:** 76–81.

RICHEY, J. S., W. H. MCDOWELL, AND G. E. LIKENS. 1985. Nitrogen tranformations in a small mountain stream. Hydrobiologia **124:** 129–139.

SANFORD, L. P., AND S. M. CRAWFORD. 2000. Mass transfer versus kinetic control of uptake across solid-water boundaries. Limnol. Oceanogr. **45:** 118–1186.

STREAM SOLUTE WORKSHOP. 1990. Concepts and methods for assessing solute dynamics in stream ecosystems. J. N. Am. Benthol. Soc. **9:** 95–119.

STRICKLAND, J. D. H., AND T. R. PARSONS. 1972. A practical handbook of seawater analysis. Ottawa, Canada, Fisheries Research Board of Canada.

TRISKA, F. J., J. R. SEDELL, K. CROMACK, JR., S. V. GREGORY, AND F. M. MCCORISON. 1984. Nitrogen budget for a small coniferous forest stream. Ecol. Monogr. **54:** 119–140.

VALETT, H. M., J. A. MORRICE, C. N. DAHM, AND M. E. CAMPANA. 1996. Parent lithology, surface-subsurface exchange, and nitrate retention in headwater streams. Limnol. Oceanogr. **41:** 333–345.

VANNOTE, R. L., G. W. MINSHALL, K. W. CUMMINS, J. R. SEDELL, AND C. E. CUSHING. 1980. The river continuum concept. Can. J. Fish. Aquat. Sci. **37:** 130–137.

VÖRÖSMARTY, C. J., AND B. J. PETERSON. 2000. Macro-scale models of water and nutrient flux to the coastal zone. *In* J. Hobbie [ed.], Estuarine science: A synthetic approach to research and practice. Island Press.

WEBSTER, J. R., AND B. C. PATTEN. 1979. Effects of watershed perturbation on stream potassium and calcium dynamics. Ecol. Monogr. **49:** 51–72.

WOLLHEIM, W. M., AND OTHERS. 1999. A coupled field and modeling approach for the analysis of nitrogen cycling in streams. J. N. Am. Benthol. Soc. **18:** 199–221.