Ecology, 98(12), 2017, pp. 3044–3055

Drivers of nitrogen transfer in stream food webs across continents

Beth C. Norman,[1,26] Matt R. Whiles,[2] Sarah M. Collins,[3] Alexander S. Flecker,[4] Steve K. Hamilton,[5] Sherri L. Johnson,[6] Emma J. Rosi,[7] Linda R. Ashkenas,[8] William B. Bowden,[9] Chelsea L. Crenshaw,[10] Todd Crowl,[11] Walter K. Dodds,[12] Robert O. Hall,[13] Rana El-Sabaawi,[14] Natalie A. Griffiths,[15] Eugènia Marti,[16] William H. McDowell,[17] Scot D. Peterson,[18] Heidi M. Rantala,[19] Tenna Riis,[20] Kevin S. Simon,[21] Jennifer L. Tank,[22] Steven A. Thomas,[23] Daniel von Schiller,[24] and Jackson R. Webster[25]

[1]*Department of Microbiology and Molecular Genetics, Michigan State University, East Lansing, Michigan 48824 USA*
[2]*Department of Zoology, Cooperative Wildlife Research Laboratory, and Center for Ecology, Southern Illinois University, Carbondale, Illinois 62901 USA*
[3]*Center for Limnology, University of Wisconsin, Madison, Wisconsin 53706 USA*
[4]*Department of Ecology & Evolutionary Biology, Cornell University, Ithaca, New York 14853 USA*
[5]*Kellogg Biological Station, Michigan State University, Hickory Corners, Michigan 49060 USA*
[6]*USDA Forest Service, Pacific Northwest Research Station, Corvallis, Oregon 97331 USA*
[7]*Cary Institute of Ecosystem Studies, Millbrook, New York 12545 USA*
[8]*Department of Fisheries & Wildlife, Oregon State University, Corvallis, Oregon 97331 USA*
[9]*Rubenstein School of Environment and Natural Resources, University of Vermont, 303D Aiken Center, Burlington, Vermont 05405 USA*
[10]*Department of Biology, University of New Mexico, Albuquerque, New Mexico 87131 USA*
[11]*Southeast Environmental Research Center and Department of Biology, Florida International University, Miami, Florida 33199 USA*
[12]*Division of Biology, Kansas State University, Manhattan, Kansas 66506 USA*
[13]*Department of Zoology and Physiology, University of Wyoming, Laramie, Wyoming 82071 USA*
[14]*Department of Biology, University of Victoria, Victoria, Canada*
[15]*Climate Change Science Institute & Environmental Sciences Division, Oak Ridge National Laboratory, Oak Ridge, Tennessee 37831 USA*
[16]*Freshwater Integrative Ecology Group, Centre d'Estudis Avançats de Blanes (CEAB-CSIC), Blanes, Spain*
[17]*Natural Resources and the Environment, University of New Hampshire, Durham, New Hampshire 03824 USA*
[18]*Watershed Studies Institute, Murray State University, Murray, Kentucky 42071 USA*
[19]*Minnesota Department of Natural Resources, Division of Fish & Wildlife, St. Paul, Minnesota 55155 USA*
[20]*Department of Bioscience, Aarhus University, Aarhus 8000 Denmark*
[21]*School of Environment, University of Auckland, Auckland 1142 New Zealand*
[22]*Department of Biological Sciences, University of Notre Dame, Notre Dame, Indiana 46656 USA*
[23]*School of Natural Resources, University of Nebraska, Lincoln, Nebraska 68583 USA*
[24]*Faculty of Science and Technology, University of the Basque Country, Bilbao 48080 Spain*
[25]*Department of Biological Sciences, Virginia Polytechnic Institute and State University, Blacksburg, Virginia 24061 USA*

Abstract. Studies of trophic-level material and energy transfers are central to ecology. The use of isotopic tracers has now made it possible to measure trophic transfer efficiencies of important nutrients and to better understand how these materials move through food webs. We analyzed data from thirteen ^{15}N-ammonium tracer addition experiments to quantify N transfer from basal resources to animals in headwater streams with varying physical, chemical, and biological features. N transfer efficiencies from primary uptake compartments (PUCs; heterotrophic microorganisms and primary producers) to primary consumers was lower (mean 11.5%, range <1% to 43%) than N transfer efficiencies from primary consumers to predators (mean 80%, range 5% to >100%). Total N transferred (as a rate) was greater in streams with open compared to closed canopies and overall N transfer efficiency generally followed a similar pattern, although was not statistically significant. We used principal component analysis to condense a suite of site characteristics into two environmental components. Total N uptake rates among trophic levels were best predicted by the component that was correlated with latitude, DIN:SRP, GPP:ER, and percent canopy cover. N transfer efficiency did not respond consistently to environmental variables. Our results suggest that canopy cover influences N movement through stream food webs because light availability and primary production facilitate N transfer to higher trophic levels.

Key words: *^{15}N; food chain efficiency; food webs; isotope tracer experiment; nitrogen; stream.*

Introduction

Food web studies provide a framework for identifying the trophic positions of species in a community and their potential roles in ecosystem dynamics. Most studies that quantify biomass and energy transfer among food web components use carbon (C) as their currency for comparison. In C-based food webs, environmental variables such as light and nutrient availability (i.e., nitrogen, phosphorus) influence food chain efficiency (FCE), or the transfer of energy from basal resources to higher trophic levels, presumably by influencing basal resource

Manuscript received 27 May 2017; revised 8 August 2017; accepted 29 August 2017. Corresponding Editor: Sara Vicca.
[26] E-mail: bcheever@msu.edu

quality (Dickman et al. 2008, Peace 2015). However, an increasing awareness of the importance of nutrient stoichiometry in driving ecological processes (Sterner and Elser 2002) suggests that insights might emerge from investigating fluxes of other elements through food webs. In particular, nitrogen (N) and phosphorus (P) are most likely to limit consumer nutrition and thus affect food web interactions. For example, imbalances in C:N:P stoichiometry can predict whether animals will be energy or nutrient limited (Sterner and Elser 2002), and multi-element-based food webs provide a means of testing these predictions. In addition, food webs based on nutrients should provide information on when and where animals exert top-down influences on biogeochemical cycles. Whole-system measurements of N flux through food webs can provide useful information of trophic dynamics and how they vary across large spatial scales.

Streams are useful systems for comparative food web studies because they are amenable to whole-system approaches for quantifying nutrient fluxes using isotope tracers such as radioactive P (Newbold et al. 1983) and the stable isotope ^{15}N (Peterson et al. 2001). Tracer studies of nitrogen dynamics in streams have traditionally focused on nutrient fluxes to organisms or groups of organisms that assimilate dissolved inorganic nitrogen (DIN) directly from the water column (e.g., epilithon, microorganisms associated with detritus, etc.), which have been referred to previously as primary uptake compartments (PUCs; Mulholland et al. 2000). Isotope tracer studies have made fundamental contributions to a cross-biome perspective of stream ecosystem function and our understanding of element cycling (Mulholland et al. 2001, 2008, Peterson et al. 2001, Webster et al. 2003, Hall et al. 2009*a*, *b*). In this study, we used ^{15}N data to examine drivers of N transfers from PUCs to higher trophic levels and the influence of animals on assimilatory N uptake and storage in biomass across biomes.

We used data from 13 ^{15}N-labelled NH_4^+ ($^{15}NH_4^+$) tracer experiments that used similar methods to examine patterns of N transfer through stream food webs in different biomes. Our objective was to identify factors that influenced efficiency of N transfer through stream food webs, specifically from PUCs to primary consumers to predators, by comparing tropical, temperate, arid, and arctic streams with a range of physicochemical and metabolic characteristics. Using a rationale similar to that developed for energy transfer (Dickman et al. 2008), we predicted that (1) N transfer would be more efficient between upper trophic levels because stoichiometric differences between primary consumers and their basal food resources are larger than those between predators and prey (Sterner and Elser 2002), (2) this stoichiometric imbalance would also cause food chain efficiency of N (FCE_N) to respond more strongly to N transfer from PUCs to primary consumers than from primary consumers to predators, and (3) N transfer efficiency would increase with basal resource production and quality, leading to the prediction that environmental variables related to PUC quality, such as nutrient availability, canopy cover (i.e., light availability) and PUC C:N, would influence N transfer efficiency.

Methods

The 12 streams (13 studies, because one stream was investigated twice) included in this analysis were a subset of the $^{15}NH_4^+$ release experiments analyzed by Dodds et al. (2014*a*) and Tank et al. (*in press*) and were selected because they had both ^{15}N enrichment and biomass data for animals (Table 1). All studies used a similar design where $^{15}NH_4Cl$ was continuously added to each stream for 5–42 d to increase the $\delta^{15}N$ of the NH_4^+ pool by at least 100‰ without substantially increasing ambient NH_4^+ concentration (detailed methods for most sites have been published, references in Table 1). Biotic compartments were qualitatively sampled at several locations downstream of the isotope addition site periodically during and after the $^{15}NH_4^+$ release, including the dominant PUCs and up to three representative animal taxa from each dominant functional feeding group (consumer groupings based on feeding mechanism, sensu Cummins and Klug 1979) present at each site. PUCs sampled included epilithon, bryophytes, filamentous algae, macrophytes, epiphytes, coarse and fine particulate organic matter (CPOM and FPOM, respectively) with associated microorganisms, wood, and suspended fine particles (i.e., seston). Functional feeding groups sampled included scrapers, shredders, collector/gatherers, filterers, predators, and others (a group including decapods and vertebrate primary consumers). Biotic components were also sampled quantitatively at each site at least twice, at the beginning and end of the release periods, using standard procedures to estimate masses of food web components (Dodds et al. 2000, Hall et al. 2009*b*). Not all PUCs and functional feeding groups were present at all stream sites, thus the specific consumer taxa sampled at each site are given in Appendix S1: Table S1. The C and N content and $\delta^{15}N$ signature of PUC and animal biomass were quantified using CHN analysis and isotope ratio mass spectrometry, respectively (Dodds et al. 2004).

Water temperature, discharge (Q), stream pH, dissolved inorganic nitrogen (DIN; NH_4-N + NO_3-N) concentration, soluble reactive phosphorus (SRP) concentration, and percent canopy cover were measured at each site (Table 1). Dissolved oxygen concentration was measured continuously at stations upstream and downstream of the study reach for 24–48 h and diel changes in dissolved oxygen within the reach were used to calculate ecosystem respiration (ER) and gross primary production (GPP) after correcting for gas exchange (Mulholland et al. 2001). Specific collection and analysis methods are described by the original publications for each site (Table 1).

We used a dynamic compartment model to estimate first-order N turnover rate (d^{-1}) for each animal taxon,

TABLE 1. Environmental variables measured during the $^{15}NH_4^+$ release experiments.

Stream ID	Stream name	Reference	Latitude	Canopy cover (%)	Q (L/s)	Temp (°C)	DIN (μg/L)	SRP (μg/L)	DIN:SRP (molar)	GPP ($g\ O_2 \cdot m^{-2} \cdot d^{-1}$)	ER ($g\ O_2 \cdot m^{-2} \cdot d^{-1}$)	GPP:ER	pH
BCNC	Ball Creek, North Carolina	Tank et al. (2000)	35.1° N	93	130	7.2	6	3	4	0.06	29	0.002	6.5
ECMI	Eagle Creek, Michigan	Hamilton et al. (2001)	42.3N	89	202	23	33	3	21	0.8	6.4	0.125	7.54
UPTD†	Upper La Laja, Trinidad and Tobago	Collins et al. (2016)	10.5N	81	14	24.8	216	28	17	2.5	19.8	0.126	8.8
WBTN	Walker Brook, Tennessee	Mulholland et al. (2000)	36.0N	80	18	12.4	23	3	15	1.2	5.4	0.222	8.05
EVWT‡	Rio Maria, Panama	Whiles et al. (2013)	8.6N	80	22	20	126	4	65	0.001	0.71	0.001	7
EVNT‡	Rio Maria, Panama	Whiles et al. (2013)	8.6N	80	23	20	126	4	65	0.012	0.32	0.038	7
MCOR	Mack Creek, Oregon	Ashkenas et al. (2004)	44.2N	75	57	13.1	61	13	22	1.9	11	0.173	7.5
KCKS	Kings Creek, Kansas	Dodds et al. (2000)	39.1N	7	16	15.5	5	3	4	1.8	2.4	0.75	7.3
LIDK	Lilleaa, Denmark	Riis et al. (2012, 2014)	56.3N	6	63	12.4	1497	63	15	1.65	5.29	0.312	7.9
KTNZ§	Kyeburn, New Zealand	Simon et al. (2004)	45.0S	0	35	6.2	8	1	15	1.29	1.31	0.98	7.5
KGNZ§	Kyeburn, New Zealand	Simon et al. (2004)	45.0S	0	22	5.9	8	1	18	1.11	0.63	1.77	7.5
SBIC	Steinbogalaekur, Iceland	unpublished	66.0N	0	156	6.9	24	10	5	1.91	2.02	0.946	nc
SCAZ	Sycamore Creek, Arizona	unpublished	33.8N	0	43	23	15	14	2	15	8.3	1.807	8.45

Notes: Sites are listed in order of decreasing canopy cover with those classified as closed canopy in boldface type and open canopy in lightface type. References are original citations. DIN, dissolved inorganic nitrogen; SRP, soluble reactive phosphorus; GPP, gross primary production; ER, ecosystem respiration; nc, data not collected.

†UPTD canopy was modified by removing trees <30 cm in diameter within 5 m of stream. Canopy cover value reflects canopy at time of isotope addition.

‡EVWT and EVNT are the same stream sampled before and after the loss of amphibians due to chytridiomycosis outbreak, respectively.

§KTNZ and KGNZ are two tributaries of the same stream network with invasive brown trout and native *Galaxias*, respectively.

as described by Dodds et al. (2014*a*) and summarized in a conceptual figure (Appendix S1: Fig. S1). Briefly, the model used the change in $\delta^{15}N$ signatures of animals and up to three food resources, to estimate animal N uptake and loss. Temporal patterns were fit using the Solver function in Microsoft Excel to minimize the sum of square of errors (SSE) between observed and modeled $\delta^{15}N$. Potential food sources were identified by previous knowledge of the animal's feeding behavior and are published for some sites (e.g., Ball Creek, Rio Maria, Mack Creek, LaLaja, and Kings Creek; citations in Table 1). Many of the taxa were common and well-studied, allowing outside sources to inform diets (e.g., Merritt et al. 2008). Animals commonly had isotope tracer labels that exceeded their putative food, likely resulting from N pools with slow turnover rates in food or selective feeding and/or assimilation that could not be captured by standard sampling techniques. This required modeling a factor that accounted for mismatches between the peak food and animal ^{15}N enrichment (Dodds et al. 2014*a*). Error estimates were not created for individual fits, but most compartments had several sampling stations that were used to make multiple model fits of each animal taxon in each stream. Nitrogen turnover rates (d^{-1}) for individual animal taxa were calculated as the modeled uptake ($mmol\ N \cdot m^{-2} \cdot d^{-1}$) divided by the total N mass of each animal ($mmol\ N/m^2$), while PUC-specific N turnover rates were calculated from the exponential decline in ^{15}N content of the PUC biomass over time after cessation of the $^{15}NH_4$ addition.

We used PUC and animal turnover rates to calculate total N uptake rate ($mg\ N \cdot m^{-2} \cdot d^{-1}$) through each PUC and functional feeding group sampled at each site. We calculated total N uptake as the areal N mass ($mg\ N/m^2$) multiplied by the turnover rate (d^{-1}) for PUCs and for functional feeding groups with a single taxon. We used relative masses to determine a weighted average turnover rate for functional feeding groups with multiple representative animal taxa. Note that the total N uptake rates presented here are calculated from biomass N (areal N mass), making them distinct from the PUC-specific NH_4-N uptake quantified by Tank et al. (*in press*), as they include all forms of N assimilated into biomass, not just NH_4-N.

PUC total N uptake at each site was the sum of the total N uptake by all PUCs sampled. Similarly, primary consumer total N uptake was the sum of N uptake by

scrapers, shredders, collector/gatherers, filterers, and others at a given site. Note that we use the term "consumer" to refer to macroscopic animals; heterotrophic microorganisms associated with epilithon or detritus are part of the microbial biofilm community associated with PUCs. Predator total N uptake was the sum of total N uptake by invertebrate and vertebrate predators, representing a conservative estimate since, in most cases, there was not enough time for larger predators to approach isotopic equilibrium with their diets given the duration of the tracer additions (Hamilton et al. 2004). Consumer total N uptake was the sum of primary consumer and predator total N uptake rates. Total N uptake through all consumer groups are likely underestimates as only biomass-dominant taxa were collected. Transfer efficiency between trophic levels (i.e., from PUCs to primary consumers, from primary consumers to predators) was calculated as the total N uptake of the target consumer level divided by the total uptake of its food and multiplied by 100, while FCE_N was calculated as total predator uptake divided by total PUC uptake, multiplied by 100.

We calculated stream-specific composite PUC C:N ratios in order to estimate the influence of PUC quality on N transfer efficiency. We considered the relative biomass of each primary consumer, the relative importance of each PUC to the diet of these primary consumers, and the C:N of the PUCs. The adjusted C:N of a single consumer–PUC combination was then calculated as

$$\text{Adjusted C:N} = (\text{relative abundance of consumer biomass} \times \text{relative proportion of PUC in diet} \times \text{PUC C:N}) \quad (1)$$

where relative abundance of consumer biomass was calculated from dry mass measurements of qualitative samples, the relative proportion of PUC in animal diet was based on taxa-specific knowledge, and PUC C:N was measured empirically. The stream-specific composite PUC C:N was calculated as the sum of the adjusted C:N values for each consumer–PUC combination in a site.

Data analyses

Total N uptake rates and N transfer efficiencies in closed and open canopy sites were compared using *t* tests or Mann-Whitney rank sum tests when the data were not normally distributed. We defined open-canopy streams as those with <10% cover and closed as >70% cover (Table 1). Transfer efficiencies were compared among primary consumer functional feeding groups using a Kruskal-Wallis one-way analysis of variance (ANOVA) test with Dunn's pairwise comparisons.

We used principal components analysis (PCA) using the vegan R package (Oksanen et al. 2015, R Core Team 2015) to condense multiple potentially co-linear environmental variables (latitude, *Q*, stream temperature, DIN, SRP, DIN:SRP, GPP, ER, GPP:ER, weighted PUC C:N, and percent canopy cover) into two composite variables. The components from the PCA were then used as explanatory variables.

We used linear regression to estimate which environmental composite variable, or principal component, explained patterns of total N uptake and N transfer efficiency among trophic levels. In addition to this multivariate approach, we used simple linear regression to determine how N transfer was related to individual environmental variables. Total N uptake and N transfer efficiencies (as proportions) were natural logarithm transformed before regression analysis. We considered P values <0.05 to be significant and those between 0.05 and 0.1 to be marginally significant. Linear regressions, ANOVA, and *t* tests were performed using SigmaPlot (v. 13.0 Systat Software Inc., San Jose, California, USA).

Results

N movement from PUCs to primary consumers

N moved from PUCs to primary consumers differently among streams and between canopy cover types. PUC total N uptake rate ranged from 18 to 506 mg $N{\cdot}m^{-2}{\cdot}d^{-1}$ (mean 168.5; Fig. 1A) and did not differ among closed and open canopy sites (*t* test, $P = 0.11$). Primary consumer total N uptake rate ranged from 0.68 to 42 mg $N{\cdot}m^{-2}{\cdot}d^{-1}$ (mean = 11; Fig. 1B) across all sites and was four times greater in open canopy sites than closed canopy sites (*t* test, $P = 0.04$). N transfer efficiency from PUCs to primary consumers ranged from 0.39% to 43% (mean 11.5%) across all sites (Fig. 1C) and was similar in open and closed canopy sites (Mann-Whitney rank sum test, $P = 0.63$). Mean N transfer efficiency from PUCs to scrapers was five times greater than other functional feeding groups and significantly greater compared to the "other" group (Kruskal-Wallis ANOVA, $P < 0.001$; Fig. 2).

Principal components analysis condensed the environmental variables into two axes that explained 49% of the variance among sites (Fig. 3). The first principal component explained 30% of the variation in environmental variables among sites and was positively correlated with latitude and GPP:ER and negatively correlated with DIN:SRP, canopy cover and temperature (marginally; Table 2). The second principal component explained 19% of the variation among sites and was negatively correlated with DIN and SRP (Table 2).

Several environmental variables influenced total N uptake by primary consumers across our sites. PC 1 explained 54% of the variance in primary consumer total N uptake (linear regression, $r^2 = 0.54$, $P = 0.004$; Fig. 4A). This positive relationship suggests higher total N uptake by primary consumers with higher latitude and GPP:ER and with lower temperature, DIN:SRP, and percent canopy cover. Considering environmental variables correlated with PC 1 individually (Table 3), GPP:ER,

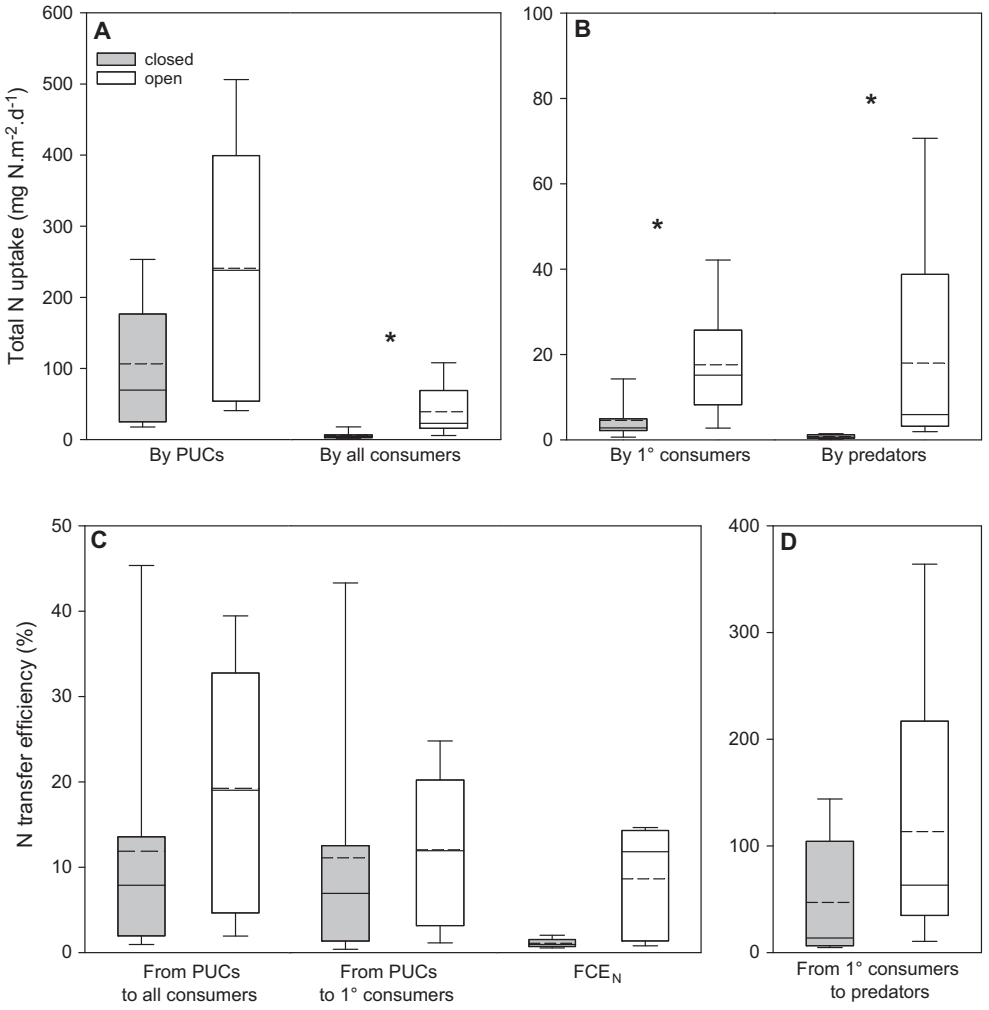

FIG. 1. (A, B) Total N uptake and (C, D) transfer efficiency in sites according to canopy cover type. Solid and dashed lines in boxes are medians and means, respectively, and whiskers show the 10th and 90th percentiles with outliers (dots). Asterisks indicate significant ($P < 0.05$) differences between open and closed canopy sites. PUC, primary uptake compartment; FCE_N, food chain efficiency of N.

DIN:SRP, and canopy cover explained 39%, 45%, and 40% of the variance in total primary consumer N uptake among sites, respectively, while relationships with latitude and stream temperature were not significant (Table 3).

Environmental variables did not strongly influence N transfer efficiency to primary consumers. N transfer efficiency from PUCs to primary consumers generally increased with PC 1 (Fig. 5A), although this relationship was not significant and only explained 16% of the variance among sites (linear regression, $r^2 = 0.16$, $P = 0.18$). There was no relationship between PC 2 and total N uptake by primary consumers (Fig. 4B) or N transfer efficiency from PUCs to primary consumers (Fig. 5B).

N movement from primary consumers to predators

N moved between consumer trophic levels more efficiently than from PUCs. Predator total N uptake ranged from 0.18 to 71 mg $N \cdot m^{-2} \cdot d^{-1}$ (mean 9 mg $N \cdot m^{-2} \cdot d^{-1}$; Fig. 1B). N transfer efficiency from primary consumers to predators averaged 80% (range 5–364%; Fig. 1D), more than seven times more efficient than transfer between PUCs and primary consumers (Mann-Whitney rank sum test, $P = 0.01$; Fig. 1C, D). Efficiencies measured in EVNT and LIDK were over 100% (144% and 364%, respectively; Appendix S1: Fig. S2C), suggesting intra-guild predation or predator subsidies (see *Discussion*). Canopy cover influenced N movement from primary consumers to predators. Predators took up ~17× more N in open sites than closed sites (Mann-Whitney rank sum test, $P = 0.008$). Mean transfer efficiency in open canopy streams was almost double that of closed canopy streams, although this difference was not significant (Mann-Whitney rank sum test, $P = 0.42$; Fig. 1D).

Environmental variables also influenced the rate of N movement from primary consumers to predators. Total

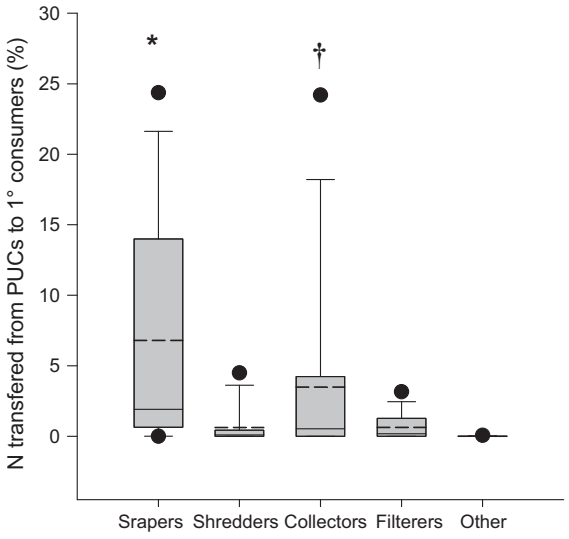

FIG. 2. Comparison of N transfer efficiency from PUCs to primary consumers by functional feeding group. Solid and dashed lines in boxes are medians and means, respectively, and whiskers show the 10th and 90th percentiles with outliers (dots). The number of sites included in each category is given in Appendix S1: Table S1. Asterisks indicate significant ($P < 0.05$) and daggers indicate marginally significant ($P < 0.1$) difference between a functional feeding group and the "other" group.

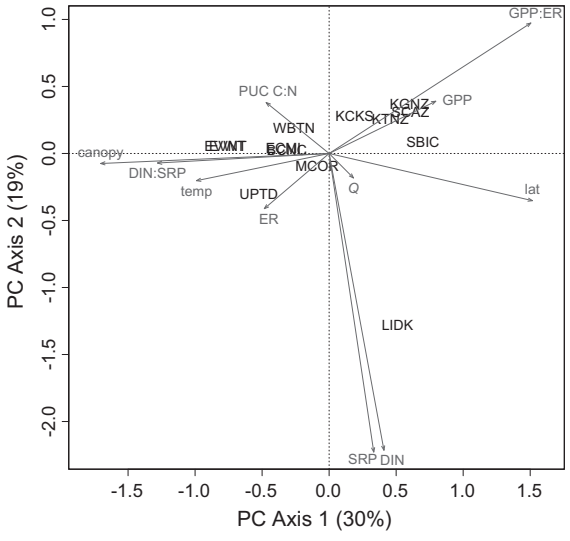

FIG. 3. Principal components ordination of environmental variables measured at each site including latitude (lat), stream discharge (Q), stream temperature (temp), dissolved inorganic nitrogen (DIN), soluble reactive phosphorus (SRP), DIN:SRP, gross primary production (GPP), ecosystem respiration (ER), GPP:ER, weighted PUC C:N, and percent canopy cover (canopy). Site names are given in Table 1.

N uptake by predators was positively related to PC 1 (linear regression, $r^2 = 0.43$, $P = 0.04$; Fig. 4C). This relationship was strongly driven by percent canopy cover, which explained 58% of the variance in predator total N uptake across sites when analyzed alone (linear regression, $r^2 = 0.58$, $P = 0.01$; Table 3). None of the other variables correlated with PC 1 were significantly related to predator total N uptake (Table 3).

In contrast, N transfer efficiency from primary consumers to predators did not vary systematically. There was no significant relationship between N transfer efficiency from primary consumers to predators and either principal component identified by PCA (linear regression; PC 1, $r^2 = 0.03$, $P = 0.66$; PC 2, $r^2 = 0.11$, $P = 0.36$; Fig. 5C, D).

N movement from PUCs to all consumers and N food chain efficiency

Consumer (primary consumers + predators) total N uptake was less than PUC total N uptake, ranging from 1.7 to 90 mg $N \cdot m^{-2} \cdot d^{-1}$ (mean 18 mg $N \cdot m^{-2} \cdot d^{-1}$; Fig. 1A) across all sites. N transfer efficiency from PUCs to all consumers ranged from 0.94% to 45% (mean 15%) across all sites (Fig. 1C). Consumer total N uptake was greater in open canopy streams than closed canopy

TABLE 2. Variable loading and correlations between variables and PC 1 and PC 2.

	PC 1			PC 2		
Variable	Loading	r	P	Loading	r	P
Latitude	0.45	0.82	**<0.001**	−0.10	−0.145	0.63
Q	0.05	0.10	0.75	−0.05	−0.08	0.80
Temperature	−0.29	−0.53	0.06	−0.06	−0.09	0.78
DIN	0.10	0.18	0.56	−0.66	−0.95	**<0.001**
SRP	0.12	0.22	0.47	−0.65	−0.94	**<0.001**
DIN:SRP	−0.38	−0.69	**0.009**	−0.02	−0.03	0.92
GPP	0.23	0.43	0.15	0.12	0.17	0.59
ER	−0.14	−0.26	0.39	−0.12	−0.18	0.57
GPP:ER	0.44	0.81	**<0.001**	0.29	0.41	0.16
%Canopy cover	−0.50	−0.92	**<0.001**	−0.02	−0.03	0.92
Weighted PUC C:N	−0.14	−0.25	0.41	0.11	0.16	0.60

Notes: Significant P values (≤0.05) are bolded. Ordination is shown in Fig. 1. PUC, primary uptake compartment.

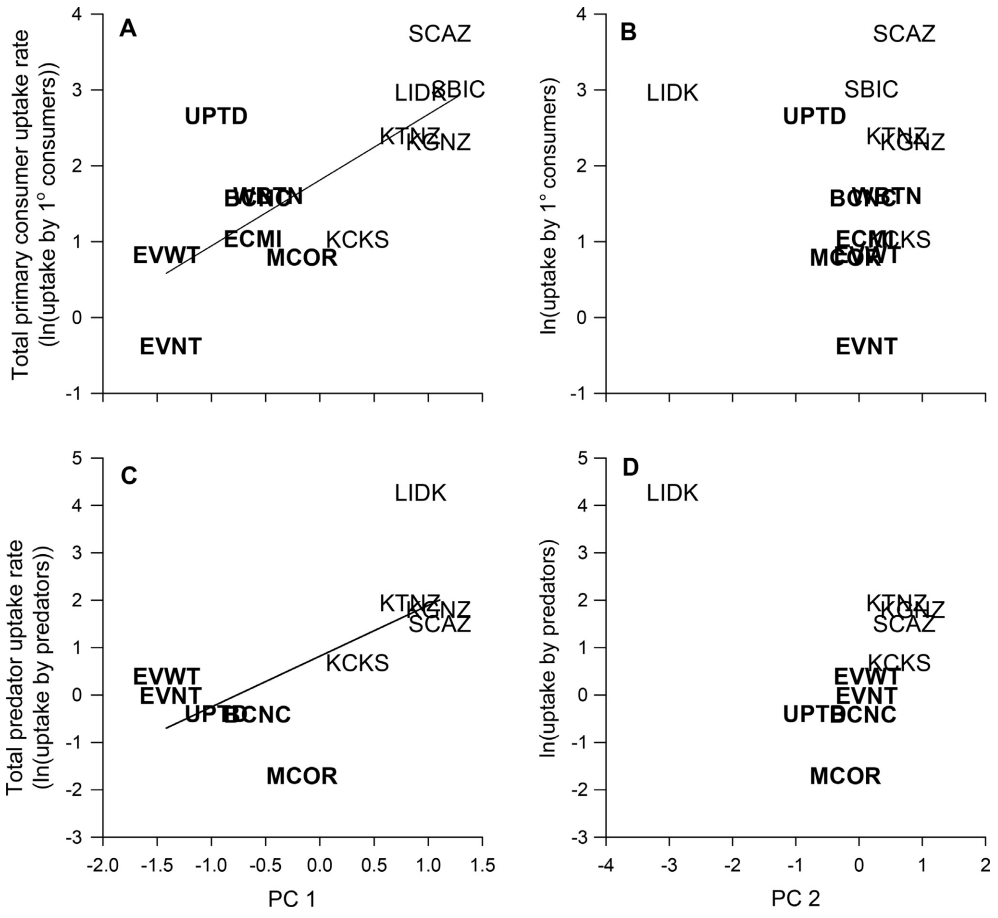

FIG. 4. Patterns of total N uptake by (A, B) primary consumers and (C, D) predators with PC 1 (A, C) and PC 2 (B, D). Closed and open canopy sites are in boldface and lightface type, respectively. Significant relationships are shown with regression lines.

streams (Mann-Whitney rank sum test, $P = 0.008$) while mean N transfer efficiency was similar between canopy types (t test, $P = 0.40$).

Transfer efficiency of N from the basal trophic level (PUCs) to the highest trophic level (predators), expressed as N food chain efficiency (FCE_N), also varied among sites. FCE_N ranged from 0.6% to 15% (mean 5%; Fig. 1C). Mean FCE_N was eight times greater in open than closed canopy streams, although this difference was not significant (Mann-Whitney rank sum test, $P = 0.15$). FCE_N increased with PC 1 (linear regression, $r^2 = 0.53$, $P = 0.02$; Fig. 5E). Of the environmental variables correlated with PC 1, latitude and percent canopy cover explained 40% and 47% of the variance in FCE_N among sites, respectively (Table 3). FCE_N was not related to PC 2 (linear regression, $r^2 = 0.08$, $P = 0.43$; Fig. 5F).

DISCUSSION

Our synthesis demonstrates that both physical and biological factors contribute to variability in total nitrogen uptake and nitrogen transfer efficiencies across regions and among trophic levels within food webs. As we predicted, N movement within food webs generally followed patterns of energy flow, with more efficient transfers among higher trophic levels than between basal resources and primary consumers. As a result, the movement of N from PUCs to primary consumers largely drove overall FCE_N. We also found general support for our prediction that environmental variables relating to PUC quality and production would influence N transfer efficiency, although the total amount of N transferred between trophic levels responded more consistently to environmental cues. The strong influences of canopy cover and GPP:ER suggest that primary production is an important driver of N movement through stream food webs.

N movement within stream food webs

We found that less than half of the pool of N in PUCs was taken up by primary consumers, which was surprising given that stream primary consumers can be nutrient limited (Rosemond et al. 1993, Cross et al. 2007). This suggests that animals may not be accessing a large portion of basal resource N, perhaps due to behavioral, life history, or physiological constraints. Dodds et al.

TABLE 3. Linear regressions of environmental variables with total N uptake by primary consumers and predators, and FCE_N.

	Total N uptake								FCE_N			
	Primary consumers				Predators							
Variable	Slope	Intercept	r^2	P	Slope	Intercept	r^2	P	Slope	Intercept	r^2	P
Latitude	0.031	0.71	0.22	0.11	0.049	−0.80	0.26	0.13	0.047	−5.33	0.40	0.05
Temperature	−0.029	2.24	0.03	0.57	−0.059	1.68	0.06	0.49	−0.097	−2.36	0.28	0.12
DIN:SRP	−0.037	2.58	0.45	**0.01**	−0.015	1.14	0.04	0.56	−0.020	−3.34	0.12	0.32
GPP:ER	0.111	1.19	0.39	**0.02**	0.991	0.21	0.18	0.22	0.933	−4.34	0.26	0.13
Canopy cover (%)	−0.017	2.60	0.40	**0.02**	−0.030	2.06	0.558	**0.01**	−0.021	−2.90	0.47	**0.03**

Notes: These environmental variables were all significantly correlated with PC 1. FCE_N, food chain efficiency of N. Significant P values (≤0.05) are bolded.

(2014*a*) demonstrated that "over labeled" animals (i.e., animal biomass more enriched than their resources) were common in this same data set, suggesting that animals access rapidly cycling N pools through selective feeding or assimilation. While such selection suggests that individuals use their resources efficiently, the mass of remaining slowly cycling N pools lead to decreased transfer efficiency within whole food webs. Inefficient N transfer may also indicate that factors other than or in addition to N, such as the availability of other nutrients (e.g., P; Cross et al. 2006) are limiting secondary production in these streams.

N moved from primary consumers to predators more efficiently than from PUCs to consumers in all of the streams, even though total N uptake was similar for primary consumers and predators. Higher transfer efficiency from primary consumers to predators is consistent with findings that predators consume nearly all of the secondary production in streams (Wallace et al. 1997). Higher transfer efficiencies at the top of the food web are also expected because predators have higher assimilation efficiencies than primary consumers and the degree of stoichiometric imbalance between predators and prey is generally less than that between primary consumers and their resources (Cross et al. 2003). This was true across our sites as the average C:N of PUCs, primary consumers, and predatory invertebrates was ~18 (range 8–31), 6 (5–11), and 5 (4–9), respectively. Predator efficiencies exceeding 100% suggest that predators were accessing N not accounted for in our estimates of total primary consumer N flux, perhaps due to intra-guild predation (Polis and Holt 1992) or mobile predators subsidizing their diets from outside the study reaches.

Patterns of nitrogen food chain efficiency in this study were generally similar to those based on carbon. FCE_N in these food webs were <20%, which is in the range of modeled carbon food chain efficiency in planktonic food webs (10–30%; Kemp et al. 2001). The efficiency with which primary consumers utilize basal resources is an important driver of carbon-based food chain efficiency (Dickman et al. 2008). This was true for our study as well, as evidenced by similar patterns of FCE_N and transfer efficiency from PUCs to primary consumers with environmental variables. However, FCE_N and transfer efficiency from PUCs to primary consumers were not always correlated, indicating that N transfer among animals played a role in FCE_N in some sites. This was particularly evident in the Denmark stream, LIDK. FCE_N in LIDK was highest among all sites, while transfer efficiency from PUCs to primary consumers was relatively low. N transfer efficiency between primary consumers and predators was unusually high in this site, over 300%. Highly mobile predatory vertebrates, including sticklebacks (*Gasterosteus aculeatus*) and brown trout (*Salmo trutta*), accounted for a significant proportion of predator total N uptake at LIDK and were likely obtaining N from outside the study reach. LIDK also had high DIN concentrations, an order of magnitude higher than other sites. However, as DIN was not a significant component of PC 1, we think the presence of mobile predators is a more likely explanation for the high FCE_N in this site. Other streams with high FCE_N, including KTNZ, KGNZ, and SCAZ also contained relatively mobile predators (brown trout, galaxiids, and longfin dace, respectively).

There are limitations to our approach for quantifying N movement through food webs. Only the dominant taxa were sampled, so our animal N uptake rates are underestimates, particularly if we missed taxa with fast turnover rates. More comprehensive sampling of predators compared to other invertebrates may have also contributed to overestimates of transfer efficiencies from primary consumers to predators. FCE_N and transfer efficiencies from primary consumers to predators may be underestimates in streams with large-bodied predators that likely did not achieve isotopic equilibrium during the $^{15}NH_4$-N addition (Hamilton et al. 2004) or in streams where emigration and immigration were significant.

Drivers of N trophic dynamics across streams

We predicted that variables related to PUC quality and system productivity would influence patterns of N movement among sites. We found that both total N uptake and N uptake efficiency were highly variable among sites but only total N uptake was consistently related to the environmental variables that we measured. Patterns of total N uptake generally followed our predictions regarding system productivity, responding to

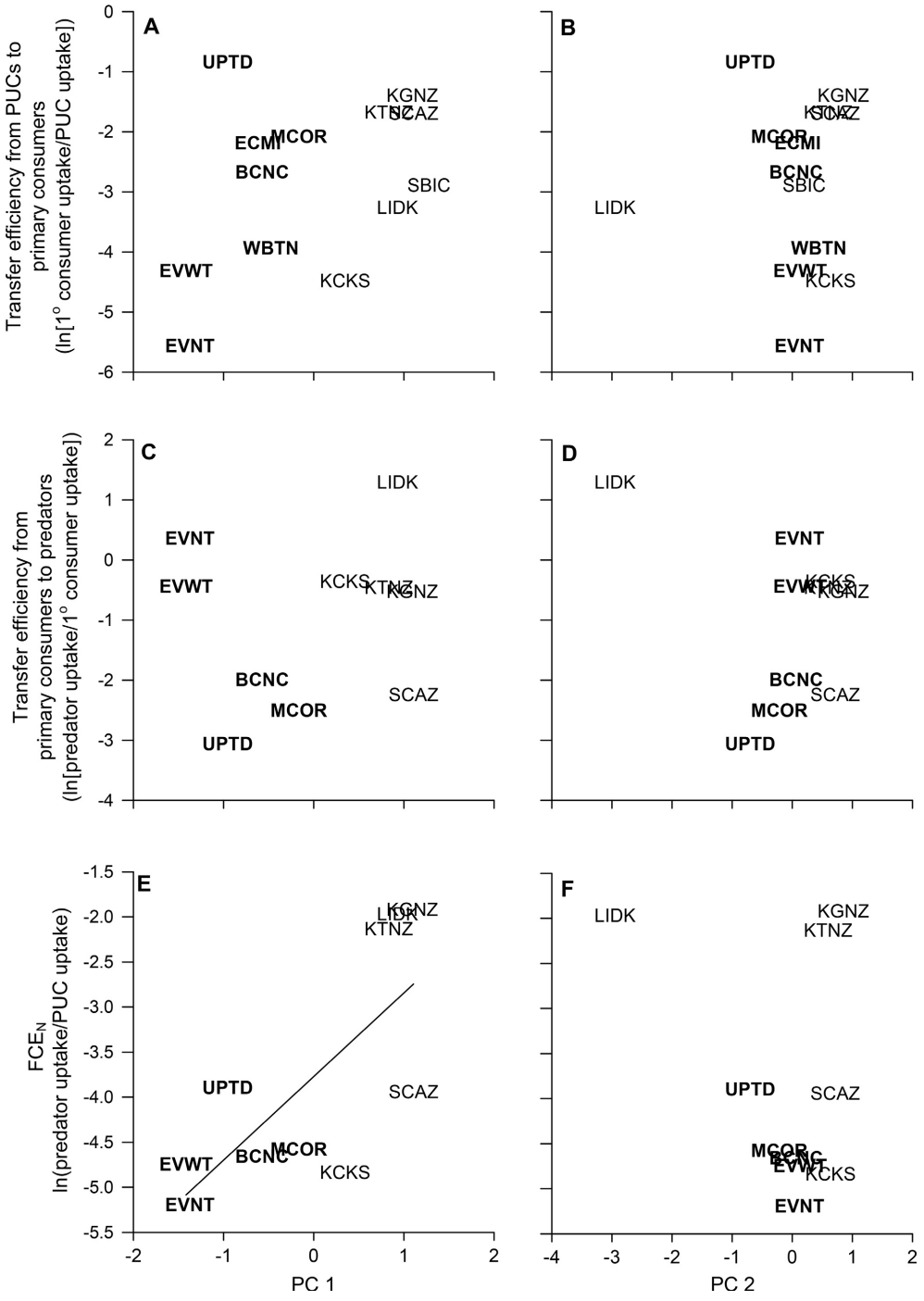

FIG. 5. Patterns of N transfer efficiency (A, B) from PUCs to primary consumers, (C, D) from primary consumers to predators, and (E, F) from PUCs to predators with PC 1 (A, C, E) and PC 2 (B, D, F). Closed and open sites are in bold and regular type, respectively. Significant relationships are shown with regression lines.

nutrient and metabolic variables. N transfer efficiency was less sensitive to the measured environmental variables and is presumably driven by other factors, perhaps including the efficiency of the specific taxa present.

We expected that N availability would be a strong driver of N food web dynamics as N limits algae or fungi in some of these sites (WBTN, SCAZ, KCKS; Tank and Dodds 2003). However, the availability of N relative to P was more important to total N uptake than DIN concentration alone. P availability has been shown to influence algal growth in several of our sites (SCAZ and KCKS; Tank and Dodds 2003), and the trend of

decreasing transfer efficiencies with increasing DIN:SRP (as a component of PC 1 and alone), while not significant, suggests a role for P in N trophic dynamics. In SCAZ, for example, the relatively low water N:P and abundance of filamentous algae capable of storing excess P (Siderius et al. 1996, Sterner and Elser 2002) may have caused a shift from P to N limitation, contributing to the high total N uptake observed at this site. It is possible that we underestimated the importance of N availability due to the low representation of high N streams in our data set. While stream DIN (μg/L) spanned four orders of magnitude across our sites, the high end of this gradient (>100 μg/L) was underrepresented. LIDK was the only site with DIN concentrations >1,000 μg/L and may be considered an outlier in the PCA (Jackson and Chen 2004). The influence of N availability on N food web dynamics remains an area for future research.

Several of our results indicate that primary production facilitates N movement within stream food webs. First, total N uptake from PUCs to primary consumers increased with PC 1, a composite variable positively correlated with GPP:ER, suggesting a positive relationship between N uptake and primary production. Second, light availability, or canopy cover, was an important driver of N movement across the study sites. Total N uptake rates by consumers were consistently greater in streams with open compared to closed canopies. The most total N uptake by primary consumers occurred in Sycamore Creek (SCAZ), Upper LaLaja (UPTD), LIDK, and SBIC; all except UPTD were open canopy systems. The dominant PUCs in terms of NH_4-N uptake in SCAZ, LIDK, and SBIC were primary producers (filamentous algae, epilithon, and bryophytes; Tank et al., *in press*). Although N transfer efficiency from PUCs to primary consumers was not significantly different between open and closed canopy sites, the most efficient transfers occurred in SCAZ, UPTD, LIDK, and the two New Zealand sites (KTNZ and KGNZ); again all open canopy systems except UPTD. Interestingly, modelled and experimental studies show a decrease in carbon transfer efficiencies with increased light availability in planktonic food webs (Dickman et al. 2008, Peace 2015). In these cases, increased light decreased phytoplankton quality; therefore element transfers appear to be responding to the same driver in these and our study.

There are several reasons why primary production may facilitate N movement within food webs. First, autochthonous biomass is a higher quality food source compared to allochthonous detritus. In addition, the stoichiometry of primary producers more closely resembles that of scrapers than the stoichiometry of detritus resembles detritivores (Cross et al. 2003, Bowman et al. 2005). Scraping as a feeding mechanism may also contribute to N movement by maintaining highly productive and actively cycling primary producer assemblages (Lamberti and Resh 1983, Wallace and Webster 1996) and by indirectly influencing primary producer nutrient content via nutrient recycling (Evans-White and Lamberti 2005, Hillebrand et al. 2008, Kohler et al. 2011). Such feedbacks may be weaker in detrital pathways (Cheever and Webster 2014). N transfer from PUCs to scrapers was more efficient than to shredders across our sites, and a comparison of N transfer in the Panama stream included in our dataset supports the hypothesis that scrapers enhance N transfer efficiencies. Data from EVWT and EVNT were generated from two tracer studies conducted in the same stream reach before and after the sudden, disease-driven loss of anuran larvae (tadpoles), most of which were scrapers (Whiles et al. 2013). The proportion of PUC N transferred to primary consumers decreased nearly fivefold after the loss of these dominant primary consumers.

We included the pre- and post-tadpole-decline release studies as separate data points because the decline significantly changed the food web and associated ecosystem processes in this stream (Whiles et al. 2013). The most apparent difference between pre and post decline conditions was GPP:ER (0.001 pre and 0.038 post), and this difference was greater than the post decline Panama site compared to Ball Creek. Also, GPP:ER was one of the variables that was significantly correlated with PC 1 and was an important driver when analyzed as a single variable.

Contrary to our expectations, composite PUC C:N was not a significant component of PC 1 or 2 and was not an important driver of N movement into primary consumers across our sites. The composite PUC C:N variable was an attempt to scale a PUC-specific measure to an entire stream reach. The calculation of this variable depended on several assumptions, including the relative abundance of PUCs in primary consumer diets. These proportions were determined from published diet descriptions of well-studied taxa and from site-specific knowledge, but likely vary among individuals, making composite PUC C:N somewhat of a subjective approximation.

The role of environmental variables in determining N movement to predators was less clear. Canopy cover was an important driver of total N uptake by predators and of FCE_N. This suggests that the legacy of PUC and primary consumer N dynamics affect N flow to predators. This has been observed in carbon-based aquatic food webs. Dickman et al. (2008) found increased carnivore efficiency in response to nutrient enrichment of a phytoplankton-zooplankton-shad food web. However, the differences in predatory physiology may be confounding the pattern we observed among our sites. Specifically, the sites with most predator N uptake and highest FCE_N (LIDK, KTNZ, KGNZ) are also open canopy sites. As previously discussed, we attribute the high FCE_N values in these sites to the presence of mobile predatory fishes, not environmental factors. Stream primary consumers are generally considered to be more stoichiometrically homeostatic compared to PUCs (but see Cross et al. 2003, Persson et al. 2010) and therefore less responsive to environmental factors. Traits such as physiology and behavior, rather than PUC quality or stoichiometric imbalances may influence N

dynamics among higher trophic levels (Leroux et al. 2012, Tanaka and Mano 2012).

Conclusions

Nutrient processing is a critical ecosystem service provided by streams, and its importance is increasing as humans continue to increase the amount of actively cycling N on the planet (Vitousek et al. 1997). Here, we show that environmental variables that affect basal resource quality and productivity, including canopy cover, nutrient availability, and primary production have strong effects on N trophic dynamics. Our results suggest that autochthony and herbivory enhance N transfer efficiency from basal resources to primary consumers and that this effect is attenuated for transfers between higher trophic levels. Based on patterns we observed, human activities that alter the amount of aquatic primary production (e.g., changes in watershed land cover and riparian habitats, sedimentation) may have strong influences on N movement through stream food webs, with implications for N storage and export. Further study is needed to determine the effects of specific anthropogenic alterations on stream food web N dynamics. Ecosystem-level tracer studies are powerful tools for testing these and related hypotheses, either in manipulative experiments or in "natural" experiments such as the comparison of pre- and post- amphibian decline N cycling in Panama (Whiles et al. 2013). Similar studies focusing on human-altered rivers will provide further insight into the degree to which human activities are altering these efficiencies and the underlying mechanisms. In addition, coordinated, cross-biome efforts such as the LINX I project in other ecosystems (Dodds et al. 2014*b*) would allow for cross-system comparisons and greatly enhance our understanding of nutrient movement through food webs.

Acknowledgments

We thank everyone who participated in the individual tracer experiments used in this analysis. We are grateful for the leadership and friendship of the late Pat Mulholland, whose legacy continues to inspire. This manuscript is the product of a workshop funded by a National Science Foundation grant (NSF-DEB 1052399) to M. R. Whiles and W. K. Dodds. Partial support during manuscript preparation to N. A. Griffiths was from the Department of Energy's Office of Science, Biological and Environmental Research. Oak Ridge National Laboratory is managed by UT-Battelle, LLC, for the U.S. DOE under contract DE-AC05-00OR22725. This manuscript has been authored by UT-Battelle, LLC under Contract No. DE-AC05-00OR22725 with the U.S. Department of Energy. The United States Government retains and the publisher, by accepting the article for publication, acknowledges that the United States Government retains a non-exclusive, paid-up, irrevocable, world-wide license to publish or reproduce the published form of this manuscript, or allow others to do so, for United States Government purposes. S. M. Collins was supported by a National Science Foundation Postdoctoral Research Fellowship in Biology (DBI-1401954).

Literature Cited

Ashkenas, L. R., S. L. Johnson, S. V. Gregory, J. L. Tank, and W. M. Wollheim. 2004. A stable isotope tracer study of nitrogen uptake and transformation in an old-growth forest stream. Ecology 85:1725–1739.

Bowman, M. F., P. A. Chambers, and D. W. Schindler. 2005. Changes in stoichiometric constraints on epilithon and benthic macroinvertebrates in response to slight nutrient enrichment of mountain rivers. Freshwater Biology 50:1836–1852.

Cheever, B. M., and J. R. Webster. 2014. Effects of consumers and nitrogen availability on heterotrophic microbial activity during leaf decomposition in headwater streams. Freshwater Biology 59:1768–1780.

Collins, S. M., et al. 2016. Fish introductions and light modulate food web fluxes in tropical streams: a whole-ecosystem experimental approach. Ecology 97:3154–3166.

Cross, W. F., J. P. Benstead, A. D. Rosemond, and J. B. Wallace. 2003. Consumer-resource stoichiometry in detritus-based streams. Ecology Letters 6:721–732.

Cross, W. F., J. B. Wallace, A. D. Rosemond, and S. L. Eggert. 2006. Whole-system nutrient enrichment increases secondary production in a detritus-based ecosystem. Ecology 87:1556–1565.

Cross, W. F., J. B. Wallace, and A. D. Rosemond. 2007. Nutrient enrichment reduces constraints on material flows in a detritus-based food web. Ecology 88:2563–2575.

Cummins, K. W., and M. J. Klug. 1979. Feeding ecology of stream invertebrates. Annual Review of Ecology and Systematics 10:147–172.

Dickman, E. M., J. M. Newell, M. J. Gonzalez, and M. J. Vanni. 2008. Light, nutrients, and food-chain length constrain planktonic energy transfer efficiency across multiple trophic levels. Proceedings of the National Academy of Sciences of the United States of America 105:18408–18412.

Dodds, W. K., et al. 2000. Quantification of the nitrogen cycle in a prairie stream. Ecosystems 3:574–589.

Dodds, W. K., et al. 2004. Carbon and nitrogen stoichiometry and nitrogen cycling rates in streams. Oecologia 140:458–467.

Dodds, W. K., et al. 2014*a*. You are not always what we think you eat: selective assimilation across multiple whole-stream isotopic tracer studies. Ecology 95:2757–2767.

Dodds, W. K., et al. 2014*b*. The Lotic Intersite Nitrogen Experiments: an example of successful ecological research collaboration. Freshwater Science 33:700–710.

Evans-White, M. A., and G. A. Lamberti. 2005. Grazer species effects on epilithon nutrient composition. Freshwater Biology 50:1853–1863.

Hall, R. O., et al. 2009*a*. Nitrate removal in stream ecosystems measured by ^{15}N addition experiments: total uptake. Limnology and Oceanography 54:653–665.

Hall, R. O., M. A. Baker, C. D. Arp, and B. J. Koch. 2009*b*. Hydrologic control of nitrogen removal, storage, and export in a mountain stream. Limnology and Oceanography 54:2128–2142.

Hamilton, S. K., J. L. Tank, D. F. Raikow, W. M. Wollheim, B. J. Peterson, and J. R. Webster. 2001. Nitrogen uptake and transformation in a midwestern U.S. stream: a stable isotope enrichment study. Biogeochemistry 54:297–340.

Hamilton, S. K., J. L. Tank, D. E. Raikow, E. R. Siler, N. J. Dorn, and N. E. Leonard. 2004. The role of instream vs allochthonous N in stream food webs: modeling the results of an isotope addition experiment. Journal of the North American Benthological Society 23:429–448.

Hillebrand, H., P. Frost, and A. Liess. 2008. Ecological stoichiometry of indirect grazer effects on periphyton nutrient content. Oecologia 155:619–630.

Jackson, D. A., and Y. Chen. 2004. Robust principal component analysis and outlier detection with ecological data. Environmetrics 15:129–139.

Kemp, W. M., M. T. Brooks, and R. R. Hood. 2001. Nutrient enrichment, habitat variability and trophic transfer efficiency in simple models of pelagic ecosystems. Marine Ecology Progress Series 223:73–87.

Kohler, T. J., J. N. Murdock, K. B. Gido, and W. K. Dodds. 2011. Nutrient loading and grazing by the minnow *Phoxinus erythrogaster* shift periphyton abundance and stoichiometry in mesocosms. Freshwater Biology 56:1133–1146.

Lamberti, G. A., and V. H. Resh. 1983. Stream periphyton and insect herbivores: an experimental study of grazing by a caddisfly population. Ecology 64:1124–1135.

Leroux, S. J., D. Hawlena, and O. J. Schmitz. 2012. Predation risk, stoichiometric plasticity and ecosystem elemental cycling. Proceedings of the Royal Society B 279:4183–4191.

Merritt, R. W., K. W. Cummins, and M. B. Berg. 2008. An introduction to the aquatic insects of North America. 4th edition. Kendall Hunt Publishing, Dubuque, Iowa.

Mulholland, P. J., 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. Ecological Monographs 70:471–493.

Mulholland, P. J., et al. 2001. Inter-biome comparison of factors controlling stream metabolism. Freshwater Biology 46:1503–1517.

Mulholland, P. J., et al. 2008. Stream denitrification across biomes and its response to anthropogenic nitrate loading. Nature 452:202–206.

Newbold, J. D., J. W. Elwood, R. V. O'Neill, and A. L. Sheldon. 1983. Phosphorus dynamics in a woodland stream ecosystem: a study of nutrient spiralling. Ecology 64:1249–1265.

Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, and H. Wagner. 2015. vegan: Community ecology package.

Peace, A. 2015. Effects of light, nutrients, and food chain length on trophic efficiencies in simple stoichiometric aquatic food chain models. Ecological Modelling 312:125–135.

Persson, J., P. Fink, A. Goto, J. M. Hood, J. Jonas, and S. Kato. 2010. To be or not to be what you eat: regulation of stoichiometric homeostasis among autotrophs and heterotrophs. Oikos 119:741–751.

Peterson, B. J., et al. 2001. Control of nitrogen export from watersheds by headwater streams. Science 292:86–90.

Polis, G. A., and R. D. Holt. 1992. Intraguild predation—the dynamics of complex trophic interactions. Trends in Ecology & Evolution 7:151–154.

R Core Team. 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/

Riis, T., W. K. Dodds, P. B. Kristensen, and A. J. Baisner. 2012. Nitrogen cycling and dynamics in a macrophyte-rich stream as determined by a ^{15}N-NH_4^+ release. Freshwater Biology 57: 1579–1591.

Riis, T., W. K. Dodds, P. B. Kristensen, and A. J. Baisner. 2014. Corringendum: nitrogen cycling and dynamics in a macrophyte-rich stream as determined by a ^{15}N-NH_4^+ release. Freshwater Biology 59:886–887.

Rosemond, A. D., P. J. Mulholland, and J. W. Elwood. 1993. Top-down and bottom-up control of stream periphyton: effects of nutrients and herbivores. Ecology 74:1264–1280.

Siderius, M., A. Musgrave, H. vandenEnde, H. Koerten, P. Cambier, and P. vanderMeer. 1996. *Chlamydomonas eugametos* (Chlorophyta) stores phosphate in polyphosphate bodies together with calcium. Journal of Phycology 32:402–409.

Simon, K. S., C. R. Townsend, B. J. F. Biggs, W. B. Bowden, and R. D. Frew. 2004. Habitat-specific nitrogen dynamics in New Zealand streams containing native or invasive fish. Ecosystems 7:777–792.

Sterner, R. W., and J. J. Elser. 2002. Ecological stoichiometry: the biology of elements from molecules to the biosphere. First edition. Princeton University Press, Princeton, New Jersey, USA.

Tanaka, Y., and H. Mano. 2012. Functional traits of herbivores and food chain efficiency in a simple aquatic community model. Ecological Modelling 237:88–100.

Tank, J. L., and W. K. Dodds. 2003. Nutrient limitation of epilithic and epixylic biofilms in ten North American streams. Freshwater Biology 48:1031–1049.

Tank, J. L., J. L. Meyer, D. M. Sanzone, P. J. Mulholland, J. R. Webster, B. J. Peterson, W. M. Wollheim, and N. E. Leonard. 2000. Analysis of nitrogen cycling in a forest stream during autumn using a ^{15}N-tracer addition. Limnology and Oceanography 45:1013–1029.

Tank, T. J., et al. Partitioning assimilatory nitrogen uptake in streams: an analysis of stable isotope tracer additions across continents. Ecological Monographs, 10.1002/ecm.1280.

Vitousek, P. M., J. D. Aber, R. W. Howarth, G. E. Likens, P. A. Matson, D. W. Schindler, W. H. Schlesinger, and G. D. Tilman. 1997. Human alteration of the global nitrogen cycle: sources and consequences. Ecological Applications 7:737–750.

Wallace, J. B., and J. R. Webster. 1996. The role of macroinvertebrates in stream ecosystem function. Annual Review of Entomology 41:115–139.

Wallace, J. B., S. L. Eggert, J. L. Meyer, and J. R. Webster. 1997. Multiple trophic levels of a forest stream linked to terrestrial litter inputs. Science 277:102–104.

Webster, J. R., et al. 2003. Factors affecting ammonium uptake in streams—an inter-biome perspective. Freshwater Biology 48:1329–1352.

Whiles, M. R., et al. 2013. Disease-driven amphibian declines alter ecosystem processes in a tropical stream. Ecosystems 16:146–157.

Supporting Information

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/ecy.2009/suppinfo