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ROSEMARY MACKAY FUND ARTICLE

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In this 6th article of the series, G. E. Small, A. M. Helton, and C. Kazanci propose that homeostatic benthic consumers might play important roles in stream nutrient dynamics by preferentially recycling nonlimiting nutrients. Gaston E. Small is a graduate student at the University of Georgia where he studies ecosystem ecology. His research focuses on the effects of nutrient loading on stoichiometric relationships in stream food webs. Ashley M. Helton is a graduate student at the University of Georgia where she studies biogeochemistry and hydrology. Her research focuses on spatiotemporal patterns of metabolic processes in river-floodplain systems. Caner Kazanci is Assistant Professor in the Department of Mathematics and Faculty of Engineering at the University of Georgia. His research focuses on simulation and analysis of biological and ecological networks.

Can consumer stoichiometric regulation control nutrient spiraling in streams?

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Abstract. Homeostatic organisms regulate their elemental composition by retaining nutrients that are limiting and eliminating those in excess. We argue that this type of homeostatic regulation by consumers might decouple the downstream movement of limiting and nonlimiting nutrients in streams. To illustrate the influence of consumers on nutrient spiraling, we developed a longitudinal model of stream nutrient dynamics that explicitly incorporates stoichiometry and recycling. First, we simulated N- and P-tracer addition experiments in a P-limited stream with a particle-tracking algorithm that allowed us to follow the pathways of N and P atoms in the model ecosystem. Then, we varied the biomass, N:P ratio, and strength of stoichiometric regulation of consumers to quantify how these parameters affected modeled spiraling metrics. The particle-tracking simulation showed that the average time for a nutrient atom to complete a spiral increased with the fraction of atoms that entered the consumer compartment in each spiral, which in turn, increased with increasing consumer biomass. Increasing the consumer N:P ratio to exacerbate consumer stoichiometric imbalance with food resources changed the residence times of nutrients in the food web by increasing the downstream velocity of the nonlimiting nutrient and delaying downstream transport of the limiting nutrient. Decreasing the strength of stoichiometric regulation of consumers dampened the observed effects of increased consumer biomass and N:P ratios on nutrient spiraling. Our model results illustrate that consumers have the potential to influence stream nutrient dynamics through differential excretion of limiting and nonlimiting nutrients, but only at relatively high biomass. Stream biogeochemistry has largely focused on factors controlling the uptake of dissolved nutrients, but understanding how these nutrients are retained and recycled once they enter the stream food web will lead to a more complete understanding of nutrient dynamics in streams.

Key words: nutrient spiraling, ecological stoichiometry, excretion, nitrogen, phosphorus.

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Understanding the functional role of organisms in ecosystems is a central focus of much ecological research (Lawton 1994, Covich et al. 1999). In stream

ecosystems, benthic consumers affect ecosystem functioning by retaining, processing, and transporting organic matter and nutrients (Newbold et al. 1982, Merritt et al. 1984, Wallace and Hutchens 2000). Because consumers represent a relatively small standing stock of nutrients in stream ecosystems, they are thought to influence nutrient cycles primarily by altering the composition and turnover rates of the algal and microbial populations on which they feed (Merritt et al. 1984). However, consumers also can play a direct role in steam nutrient cycling by excreting dissolved nutrients previously bound within the stream food web. Evidence from diverse stream ecosystems has shown that consumer-driven nutrient recycling (sensu Elser and Urabe 1999) can supply a significant portion of dissolved nutrients to streams (e.g., Grimm 1988, Vanni et al. 2002, Hall et al. 2003, McIntyre et al. 2008).

The difference between the elemental composition of consumers and their food resources is one of the important factors that can control rates of nutrient recycling (Elser and Urabe 1999). Nutrient recycling by consumers can alter ecosystem nutrient availability (Elser et al. 1988) and the elemental composition of basal food resources (Evans-White and Lamberti 2006). We explored the interactions between the stoichiometric regulation of nutrient recycling by consumers and whole-stream nutrient dynamics and focused on the potential for consumers to affect traditional nutrient spiraling metrics.

Consumers and the temporal dimension of the nutrient spiraling concept

Coupled transformation and transport of materials in stream ecosystems traditionally has been described by the nutrient spiraling concept (Webster and Patten 1979, Newbold et al. 1981, Elwood et al. 1983, Stream Solute Workshop 1990). The spiraling framework considers downstream transport of nutrient atoms in dissolved and particulate (e.g., entrained within the stream food web) forms (Fig. 1A). In a single spiral, the average distance traveled downstream by a nutrient atom while it is incorporated into biomass (turnover length [S_B]) is typically small relative to the average distance traveled downstream by a nutrient in dissolved form (uptake length [S_w]). S_B is considered in some studies of stream nutrient dynamics (e.g., Newbold et al. 1983), but S_w is the dominant longitudinal process and is relatively straightforward to measure. Therefore, S_w has become the typical metric (along with related calculations, e.g., the mass-transfer coefficient [V_f], and areal uptake [U]) in understanding stream nutrient dynamics (e.g., Mulholland et al. 1997, 2008, Peterson et al. 2001, Hall et al. 2002, Valett et al. 2002). Many studies have quantified the uptake rate of dissolved nutrients to represent a stream's capacity to remove nutrients (e.g., Martí and Sabater 1996, Dodds et al. 2002, Mulholland et al. 2008) without reporting the fate of these nutrients once they enter particulate form. A fraction of

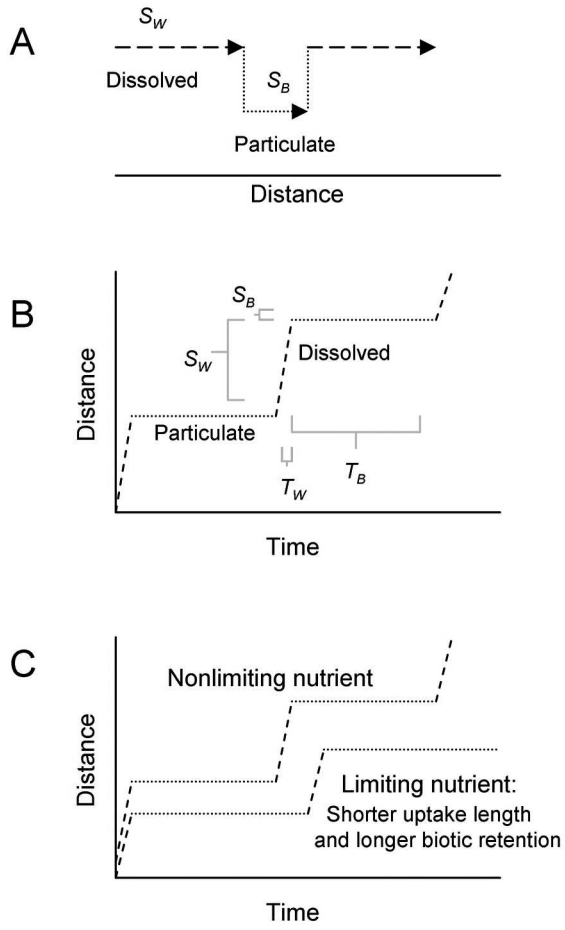

FIG. 1. A.—Nutrient spiraling in streams traditionally has been conceptualized as the transport and processing of nutrients in dissolved and particulate matter along a longitudinal gradient, where the length of a single spiral is the distance traveled downstream by the average nutrient particle in dissolved form (uptake length [S_W]) and particulate form (turnover length [S_B]). B.—Adding a temporal dimension to this spiraling diagram shows the analogs uptake time (T_W) and turnover time (T_B). Nutrients travel greater distances downstream in dissolved form, but they spend more time locked in the food web in particulate form. Mineralization rates are controlled by homeostatic biota, which release excess nutrients and retain limiting nutrients. C.—When the downstream paths of limiting and nonlimiting nutrients added to a stream simultaneously in dissolved and particulate forms are compared, limiting nutrients should have a slower average downstream velocity because of a combination of shorter S_W and longer T_B.

dissolved nutrients taken up (i.e., immobilized) will be lost through processes, such as denitrification (Seitzinger et al. 2006) or insect emergence (Jackson and Fisher 1986), but most will eventually be recycled (i.e., mineralized) and reenter the water column (Mulholland et al. 2000, Peterson et al. 2001) or be exported downstream in particulate form (Webster et al. 2003).

Therefore, the fate of stream nutrients might depend on both longitudinal spiraling and temporal dynamics, specifically the amount of time the nutrient is entrained within the food web before being released back into the water column. Some studies have reported turnover times of nutrients in various ecosystem components (e.g., Newbold et al. 1983, Mulholland et al. 2000, Tank et al. 2000), and time is implicit in the 1-dimensional transport equations that describe nutrient spiraling (Newbold et al. 1982), but the temporal dimension has received considerably less attention than has the longitudinal dimension in spiraling studies (but see Doyle and Ensign 2009).

Nutrients might travel a minimal distance downstream as biomass, but individual nutrient atoms spend much more time in the food web than in dissolved form. For example, a $^{32}PO_4$ tracer addition in Walker Branch, Tennessee, showed that although dissolved P traveled an average of 6.5× further than P in biomass, P remained in the food web >5000× longer than in dissolved form. In a single spiral, <3% of this P entered consumer biomass (which was dominated by the snail, *Goniobasis*), but these labeled P atoms remained essentially stationary for 153 d, on average (>10× as long as P in algae or detritus; Newbold et al. 1983). A ^{15}N-NH_4 tracer experiment at Walker Branch showed that ^{15}N entering consumers remained immobilized for >5× as long as in algae or detritus (Mulholland et al. 2000).

Visualizing a nutrient spiral along both time and distance reveals that the average nutrient atom remains relatively stationary for long amounts of time while in biomass, and then rapidly travels downstream during a short period of time while in dissolved form (Fig. 1B). The average downstream velocity for atoms of a given nutrient equals the distance of an average complete spiral (i.e., $S_w + S_B$) divided by the time to complete that spiral. Thus, increasing S_w or decreasing time retained in the food web can increase the rate of nutrient transport downstream. Therefore, the rate at which these nutrient atoms are mineralized to dissolved form has important consequences for the overall spiraling of nutrients in streams. However, compared to uptake processes, very little explicit attention has been given to nutrient mineralization in streams. Given that nutrients are retained in consumers on average 10× longer than in microbes, and 10^3 to 10^4× times longer than in the water column (e.g., Newbold et al. 1983, Mulholland et al. 2000), considering spiraling over time as well as distance probably will underscore the role that consumers play in stream nutrient dynamics.

Stoichiometric control of nutrient spiraling by consumers

Many consumers feed on food resources that are out of balance with their body elemental composition. Therefore, to maintain homeostatic body elemental composition, consumers retain nutrients that limit biomass production while preferentially excreting those in excess (Sterner and Elser 2002). Different species might vary in their strength of homeostatic regulation, but any individual consumer that regulates its elemental composition through postabsorptive processes (e.g., excretion) should retain limiting nutrients longer than nonlimiting nutrients. Assuming most consumers within a given stream are limited by the same nutrient, the sum of differential nutrient retention in individuals will increase the average amount of time that a limiting nutrient spends in the food web relative to a nonlimiting nutrient. Comparison of the paths of average hypothetical limiting and nonlimiting nutrient atoms over distance and time illustrates how increased turnover time of a limiting nutrient in the food web decreases the average downstream velocity of that limiting nutrient over multiple spirals (Fig. 1C). The result is that limiting and nonlimiting nutrients that enter the stream simultaneously will become separated over distance and time by the differential recycling of limiting and nonlimiting nutrients by consumers, according to their stoichiometric constraints. We posit that by emphasizing the temporal aspects of nutrient spiraling theory, these effects of stoichiometrically regulated consumer-driven nutrient recycling on stream nutrient dynamics will become evident.

A Stoichiometrically Explicit Model of Nutrient Spiraling

Model description

The importance of stoichiometric mechanisms in consumer-driven nutrient cycling in streams might depend, in part, on the biomass of consumers (and therefore, the flux of a nutrient released by consumers relative to the total flux of nutrients in a stream) and whether N:P ratios released from consumers strongly differ from those in food resources or in the water column (e.g., as hypothesized by Frost et al. 2002). To illustrate potential effects of consumer dynamics on

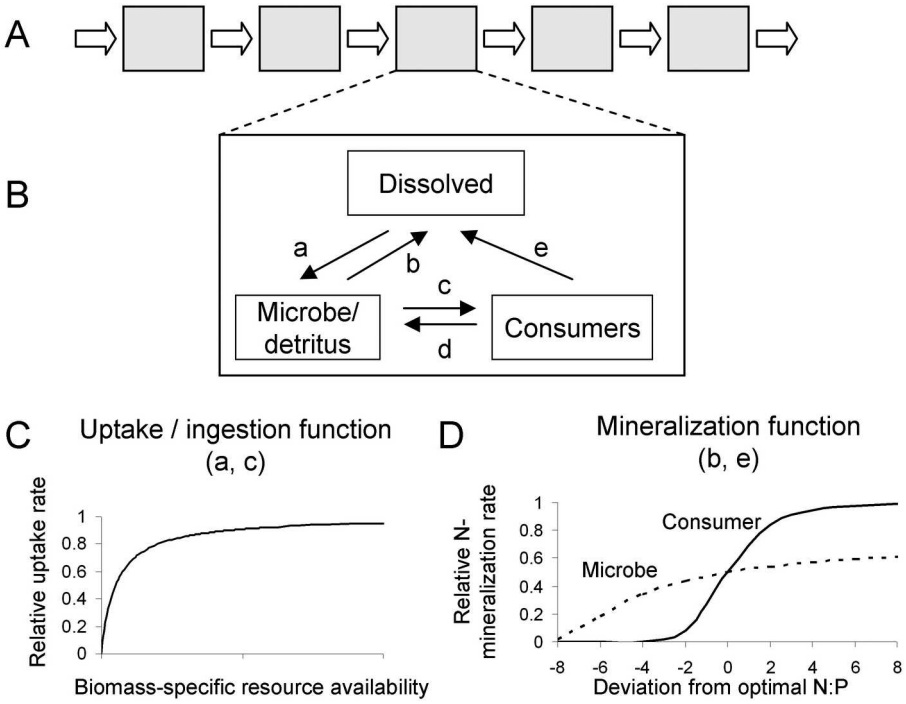

FIG. 2. A.—We created a longitudinally and stoichiometrically explicit stream model based on a series of nodes, each representing a 5-m stream reach (gray boxes). Nutrients move between nodes in the downstream direction. B.—Within each node, N and P atoms move between dissolved, microbe/detritus, and consumer compartments. Uptake of dissolved nutrients by microbes (a) and ingestion by consumers (c) are both represented with a Monod function (C) (a general example is shown here, but these 2 fluxes are parameterized differently in our model), where biomass-specific uptake increases to a maximum rate based on relative resource availability. Microbe/detritus (b) and consumer (e) compartments regulate their N:P ratios according to a sigmoidal mineralization function based on the deviation from a defined optimal biomass N:P (D). The steepness of this curve corresponds to the strength of homeostatic regulation. Consumer mortality (d) was represent by a first-order, donor-controlled term in the model.

nutrient spiraling, we developed a longitudinally and stoichiometrically explicit heuristic model for a heterotrophic, detritus-based stream and implemented the model under scenarios that spanned a range of consumer biomass and factors that control consumer elemental composition.

The 1-dimensional simulation model of N and P dynamics for a stream ecosystem (Fig. 2A) includes dissolved, microbe/detritus, and consumer nutrient compartments and fluxes between them (Fig. 2B). Nutrients in dissolved and microbe/detritus compartments can move downstream and between compartments within each stream reach. To illustrate how stoichiometric constraints can affect nutrient spiraling, we made several simplifying assumptions: 1) microbes and consumers regulate their elemental composition (N:P ratio) through postabsorptive processes and preferentially excrete the nonlimiting nutrient (Anderson et al. 2005), 2) all atoms of a given nutrient within a given model compartment are equally labile, 3) lateral inputs of nutrients are negligible (all inputs come from upstream), and 4) consumers are stationary (no drift).

Homeostatic organisms maintain a relatively fixed body elemental composition because they consist of biomolecules (proteins, nucleic acids, lipids, etc.) that have relatively fixed elemental ratios. However, changes in the relative amounts of specific biomolecules can alter an organism's elemental ratio (Sterner and Elser 2002). For example, in bacteria (e.g., Makino et al. 2003) and invertebrate consumers (e.g., Elser et al. 2005), ribonucleic acid (RNA) constitutes a large portion of the body P content. In these organisms, RNA (and therefore, total body P content) increases with elevated P availability. To represent this stoichiometric flexibility, we defined optimal N:P values for microbe and consumer compartments based on literature values (Appendix 1), representing the N:P ratio at which growth is maximized. In our model, the microbe/detritus and consumer compartments regulate their N:P ratios through excretion based on differences between the defined optimal N:P ratio

for that compartment and the actual N:P ratio at a given time in the simulation. One of the strengths of our model is this ability to reflect variable elemental composition of consumers in response to food nutrient content, consistent with empirical observations (e.g., Frost and Elser 2002, Cross et al. 2003, Elser et al. 2005).

Our model differs in key ways from previously published stoichiometrically explicit stream ecosystem models. Our model differs from the model proposed by Cross et al. (2005) by allowing differences in turnover time to affect spiraling. The model by Cross et al. (2005) is based on the assumptions that N:P of stream biota (B_N:B_P) equals the uptake ratio of N:P (U_N:U_P) and that turnover times for N and P in biota are equal. In their model, biotic elemental ratios were explicitly regulated by uptake and not mineralization (although the authors explored a scenario in which one element was recycled within biofilm more efficiently than the other). Thus, the model does not allow differences in turnover time to affect spiraling. A longitudinal stream model by Newbold et al. (1982) explored the roles of different consumer functional feeding groups in regulating the transport of organic material. Here, we take a similar approach to the Newbold et al. (1982) model except that we simultaneously consider 2 elements (N and P) in a maximally simplified, hypothetical stream food web. The purpose of our heuristic model is to explore how relatively simple assumptions about stoichiometrically controlled nutrient recycling by consumers can affect whole-stream nutrient dynamics.

Initially, we parameterized our model for Walker Branch (see *Model parameterization* below). In Part I, we used a particle tracking algorithm to follow individual N and P atoms across multiple spirals to create distributions of spiraling lengths and times. We then simulated a whole-stream N- and P-tracer experiment and measured the retention of labeled atoms in the stream. In Part II, we varied consumer biomass, consumer optimal N:P, and consumer stoichiometric regulation coefficients to measure the effects of these parameters on spiraling velocity.

Model structure

We used a series of differential equations to model N and P fluxes within and between 100 nodes (Appendix 2). Each node represented a 5-m stream reach with homogeneous compartments (dissolved, microbe/detritus, and consumer). We modeled transport of dissolved N and P by a 1st-order rate constant that moved N and P between nodes in the downstream direction, consistent with a stream discharge of 5 L/s. Diffusion was implicit because of assumed mixing within each node.

Microbial uptake of dissolved N and P from the water column was represented as a Monod function (Fig. 2C) that depended on the availability of dissolved nutrients relative to the microbial/detrital biomass (Blanch 1981, Riber and Wetzel 1987). Microbial mineralization was modeled as a sigmoidal function (Fig. 2D), where deviation from the defined optimal microbial biomass N:P ratio controlled rates of N and P mineralization by microbes according to the steepness of the sigmoidal curve (controlled by the homeostatic regulation coefficient, k_5; Appendix 1). In our model, when microbial N:P is equal to its defined optimal value, N and P are mineralized by microbes at ½ the maximum rate. As microbial N:P exceeds the optimal value (i.e., microbes are P deficient), N mineralization approaches the maximum rate, and P mineralization approaches 0. As N:P becomes lower than the optimal value, N is retained and P mineralization increases. Gross uptake of dissolved nutrients by microbes was not stoichometrically controlled, but stoichiometrically regulated microbial mineralization constrained the elemental ratios of the microbe/detritus compartment. As a result, net uptake of dissolved N and P (i.e., uptake – remineralization) was controlled by N:P ratios of dissolved and microbe/detritus compartments, consistent with the model by Cross et al. (2005).

Consumer ingestion was also modeled as a Monod function that depended on availability of food resources (microbe/detritus biomass) relative to consumer biomass. In our model, ingestion represents only nutrients that are ingested and assimilated across the consumers' digestive tracts. We assumed that consumers regulate their elemental composition through postabsorbtive nutrient processing (Sterner and George 2000, Anderson et al. 2005, Hood et al. 2005) rather than through selective assimilation of limiting nutrients. Thus, in our model, limiting and nonlimiting nutrients are assimilated in proportion to N:P of the microbe/detritus pool. We did not explicitly model consumer egestion (i.e., feces, which are produced with unassimilated nutrients), even though this process might be a significant nutrient flux (e.g., Grimm 1988). Explicitly including egestion in our model would not have affected the results qualitatively because we assumed that consumers regulated their elemental composition postabsorbtion. We did include a flow from consumers to detritus. This flow represented consumer mortality. A small fraction of consumer biomass dies and enters the detritus pool. Unlike egestion, which would occur at

the N:P ratio of the food resource, consumer mortality flux occurs at the N:P ratio of consumer biomass.

Consumers regulate their elemental composition by controlling N and P excretion rates according to the same sigmoidal function (with different parameters used to model microbial mineralization; Fig. 2D). They are less flexible than the microbe/detritus compartment in their elemental ratios, so they must maintain a body elemental composition closer to their optimum N:P and excrete more of the nonlimiting nutrient. Therefore, we used a higher homeostatic regulation coefficient (100 vs 10; Appendix 1), so that consumer excretion N:P responded rapidly to changes in food N:P and led to more immediate excretion of excess nutrients and retention of limiting nutrients as consumer N:P diverged from the defined optimum (Fig. 2D).

Model parameterization

We estimated reasonable ranges for parameter values from the literature where available (Appendix 1) and modified these values until model output (standing stocks, fluxes, S_Ws, and turnover times of compartments) was similar (Appendix 3) to values reported for Walker Branch (N dynamics: Mulholland et al. 2000, P dynamics: Newbold et al. 1983). We set the optimal N:P (mass ratio) for the microbe/detritus compartment at 10 (molar N:P = 22.1), based on the average N:P observed in fine particulate organic matter in a detritus-based headwater stream enriched in N and P (Cross et al. 2003). Initially, we set consumer optimal N:P (mass ratio) at 8 (molar N:P = 17.7), which was lower than the mean value but within the range of benthic consumers reported by Cross et al. (2003), because we wanted to simulate a P-limited food web. We set the N:P mass ratio of dissolved nutrients in the stream at 20.1, which is higher than dissolved N:P ratios reported for Walker Branch (mass ratio of 4.5; Appendix 3) because we selected optimal N:P values for microbe/detritus and consumer pools to create P-limitation. In addition, our model underestimates S_B compared to measured values from Walker Branch (2 m vs 25 m for P atoms), in part because we did not include the effects of consumers suspending detritus particles in the water column (e.g., through bioturbation). We varied selected parameters from these baseline conditions under different model scenarios (described in more detail below; Table 1).

We solved the equations numerically using the ode45 function in MATLAB (version 6.5; MathWorks, Natick, Massachusetts), which implements a Runge–Kutta method with adaptive time steps. Nutrient spiraling metrics have the most straightforward interpretation in a stream that is both temporally and longitudinally uniform (although real streams are both temporally and spatially variable). Our model automatically goes to temporal steady state. We forced our model to longitudinal steady state by setting upstream inputs of dissolved and detrital N and P equal to outputs at the downstream end of the model over successive model runs.

We calculated average spiraling metrics from these steady-state stocks and flows, as described in Newbold (1996). S_W (m) was calculated as the downstream flux / m width of dissolved nutrients divided by the uptake rate per unit area of dissolved nutrients by microbes. S_B (m) was calculated as the downstream flux of nutrients in particulate form divided by the total mineralization rate (microbial mineralization + consumer excretion)/m^2. Total spiraling length (S) is the sum of S_W and S_B. Downstream velocity (V_T; m/d) was calculated as the total downstream flux divided by the total standing stock (of all 3 compartments)/m^2. Total spiraling time (the average time for an N or P atom to complete 1 spiral) was calculated as S/V_T. In addition, turnover times of each of the 3 model compartments (the average time that an N or P atom is retained in a single model compartment) and turnover time in the entire food web (pooled microbe/detritus and consumer compartments) were calculated as the standing stock of the compartment(s) divided by total flux into the compartment(s). We also calculated the fraction of N and P atoms that entered the consumer compartment in a single spiral (b_C) as consumer ingestion divided by the sum of ingestion and microbial mineralization. This term can be interpreted as a measure of consumer ingestion efficiency, in that once a dissolved nutrient atom is taken up by the microbe/detritus compartment, b_C gives the probability of this atom entering consumer biomass before being mineralized back into dissolved form.

Part I: Simulation of tracer additions

We simulated tracer experiments with a new numerical simulation method, the particle tracking algorithm (Kazanci 2007, Tollner and Kazanci 2007), which is an individual-based method where discrete packets of material (N or P atoms) are labeled and tracked in time as they flow through the model compartments. In addition to tracking the storage values of model compartments over time (as occurs in a differential equation model), the particle tracking simulation (PTS) identifies which individual particles represent the storage values of each compartment. The method is particularly useful at steady state, where differential equation simulations give constant

TABLE 1. Spiraling metrics calculated from steady-state model output. t_C = turnover time in the consumer compartment, b_C = percentage of N or P atoms that enter consumers in a given spiral, S = average spiraling length, T = average time to complete 1 spiral, V = the average downstream velocity of a nutrient atom. N:P is reported as mass ratios.

	Model scenario					
Metric	No consumers	Low consumer biomass	Medium consumer biomass	High consumer biomass	High consumer N:P	Nonhomeostatic consumer
Parameters						
Consumer biomass (g AFDM/m^2)	0.0	1.1	11.1	43.7	11.1	11.1
Homeostatic regulation coefficient		100.0	100.0	100.0	100.0	10.0
Optimal consumer N:P		8.0	8.0	8.0	30.0	30.0
Actual consumer N:P		8.0	8.0	8.0	25.0	19.7
Model output						
N spiraling						
t_{CN} (d)		104.9	104.2	104.7	143.2	113.7
b_{CN} (%)	0.0	0.4	3.9	17.3	5.1	4.2
S_N (m)	245.7	246.5	253.7	293.3	255.5	254.0
T_N (d)	11.9	12.3	15.6	28.8	18.9	16.3
V_N (m/d)	20.7	20.1	16.2	10.2	13.6	15.6
P spiraling						
t_{CP} (d)		131.9	131.9	131.9	57.9	57.9
b_{CP} (%)	0.0	0.6	5.8	23.3	7.5	6.2
S_P (m)	186.9	187.4	191.1	214.5	192.6	191.0
T_P (d)	18.0	18.7	25.0	46.7	21.1	20.5
V_P (m/d)	10.4	10.0	7.7	4.6	9.1	9.3
N:P						
t_{CN}:t_{CP}		0.8	0.8	0.8	2.5	2.0
b_{CN}:b_{CP}		0.7	0.7	0.7	0.7	0.7
S_N:S_P	1.3	1.3	1.3	1.4	1.3	1.3
T_N:T_P	0.7	0.7	0.6	0.6	0.9	0.8
V_N:V_P	2.0	2.0	2.1	2.2	1.5	1.7

values for storage values over time, giving the illusion that the system has stopped, whereas PTS will show continuous movement of particles.

Two characteristics set PTS apart from other similar algorithms. 1) PTS deduces its rules on how an individual particle will move directly from the differential equation representation of the model. This feature eliminates the need for extra parameters or decisions that are required to build most individual-based models. Therefore, causality is preserved. 2) PTS is a stochastic method that is compatible with the master equation (Gillespie 1977, 1992, 2000). In other words, the mean of many PTS results agrees with the differential equation solution, and PTS provides accurate information on inherent fluctuations, such as diffusion processes, in the system.

PTS enabled us to observe the dynamics of individual particles in the stream network, whether the system was at steady state or was changing. Theoretically, this algorithm could track every individual atom in an ecosystem, but available computing power constrains our resolution to a coarser level. In our simulation, an N particle represents 1 mg of N atoms and a P particle represents 1 mg of P atoms. PTS simultaneously tracked >19 million individual particles, and this resolution is fine enough that the dynamics are consistent with the differential equation representation of the system. Therefore, the results of the simulation can be interpreted as the fate of individual atoms in our simulated stream ecosystem. We programmed the PTS model in C++ and used the steady-state solution described above for the initial condition.

We ran 2 sets of experiments with particle tracking under the medium consumer biomass scenario (Appendix 1). First, we followed 500 individual N and P atoms across a single spiral in a P-limited stream to create a distribution of spiraling lengths and times. Then we simulated N- and P-tracer addition experiments by labeling dissolved N- and P-atoms that entered the stream in 1 d and measured retention of these particles in a 500-m downstream reach for the next 200 d.

Part II: Consumer effects on nutrient spiraling under steady-state conditions

To explore how consumer biomass, N:P ratios, and stoichiometric regulation affect nutrient spiraling, we implemented the model under different scenarios by varying selected model parameters (Table 1). First, we implemented the model at 4 levels of consumer biomass: 0 g ash-free dry mass (AFDM)/m^2 (no consumers), 1.1 g AFDM/m^2 (low consumer biomass), 11.1 g AFDM/m^2 (medium consumer biomass), and 43.7 g AFDM/m^2 (high consumer biomass). These biomass values reflect the range of consumer biomass values reported in the literature (Fig. 3). Consumer biomass was varied by changing the ½-saturation constant for consumer ingestion (k_{12}) and was converted from mg N/m^2 to g AFDM/m^2 by assuming that the N content of consumer AFDM is 10% (Cross et al. 2003). Next, to simulate a greater imbalance between the stoichiometry of consumers and their food resource, we used parameters from the medium consumer biomass scenario, but changed the optimal consumer N:P mass ratio to 30 while keeping optimal microbial N:P at 10 (high consumer N:P scenario; Table 1). This optimal N:P ratio for consumers is within the range of benthic consumer N:P reported by Cross et al. (2003). Last, to explore how the strength of consumer homeostasis can affect nutrient spiraling, we decreased the strength of consumer stoichiometric regulation (k_8) from 100 to 10 (nonhomeostatic consumer scenario; Table 1), so that consumers had a diminished capacity for regulating their N:P ratios (i.e., as consumer biomass diverges from the defined optimal N:P, consumers are less able to retain the limiting nutrient and excrete the excess nutrient). We ran models for these 6 scenarios run to temporal and longitudinal steady state and calculated spiraling metrics directly from flows as described above (Table 1).

Results and Discussion

Part I: Simulation of tracer additions

The stochastic particle-tracking simulations yielded spiraling metrics (mean spiraling times and distances) nearly identical to those calculated using steady-state stocks and flows. However, the particle-tracking method elucidates the effect of variation in time and distance required for individual atoms to complete a spiral on the average times and distances typically calculated (Fig. 4A, B). Most simulated nutrient atoms had relatively short turnover times (i.e., positively skewed distributions in Fig. 4A). However, the small fraction of atoms that became entrained within the food web (those atoms in the tail of the distributions in Fig. 4A) had a large effect on mean nutrient spiraling metrics. For example, mean spiraling times for both N and P atoms (N: 15.6 d, P: 25.0 d) were nearly 2× the median values (N: 8.4 d, P: 14.0 d). Differential excretion of N and P by microbes and consumers contributed to the longer mean spiraling time for P in this simulation. The positively skewed distribution of spiraling lengths (Fig. 4B) was a result of the constant fraction of labeled dissolved nutrient atoms immobilized in each node under the steady-state conditions in the simulation. Longer spiraling distance for the nonlimiting nutrient (N: 253.7 m, P: 191.1 m) was an emergent effect of stoichiometric regulation by consumers and microbes based on differences in the supply of dissolved nutrients at equilibrium.

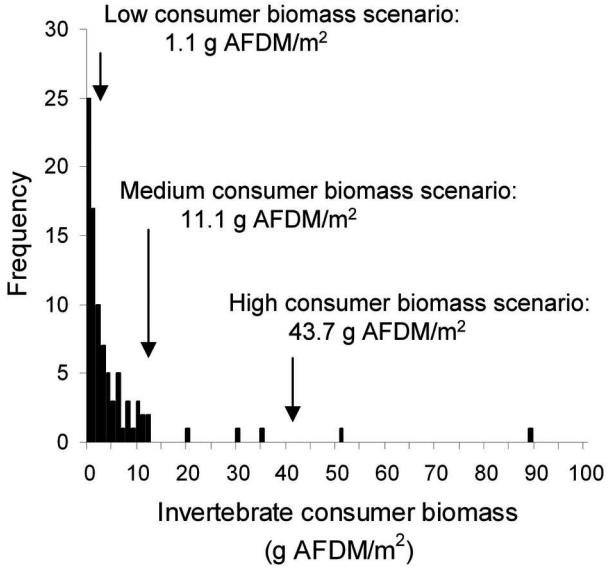

FIG. 3. Frequency histogram of 90 reported values of invertebrate consumer biomass in streams. Values were taken from reviews by Benke (1993) and Huryn et al. (2005) and from Marsh (1985), Grimm (1988), Caraco et al. (1997), Mulholland et al. (2000), Dodds et al. (2000), Tank et al. (2000), Hall et al. (2003), and Kelly et al. (2003). Our model scenario values for low, medium, and high consumer biomass are indicated, based on the assumption that consumer N-content was 10% of ash-free dry mass (AFDM).

Our simulated tracer experiment illustrates how N and P were retained in the stream food web over time (Fig. 5A, B). The maximum number of labeled atoms in the stream ecosystem occurred at 24 h when the tracer addition stopped. Highest concentrations of labeled atoms occurred at the uppermost stream nodes, with ~1300 mg labeled N/stream node and ~100 mg labeled P/stream node in the microbe/detritus compartment. Over time, the amount of

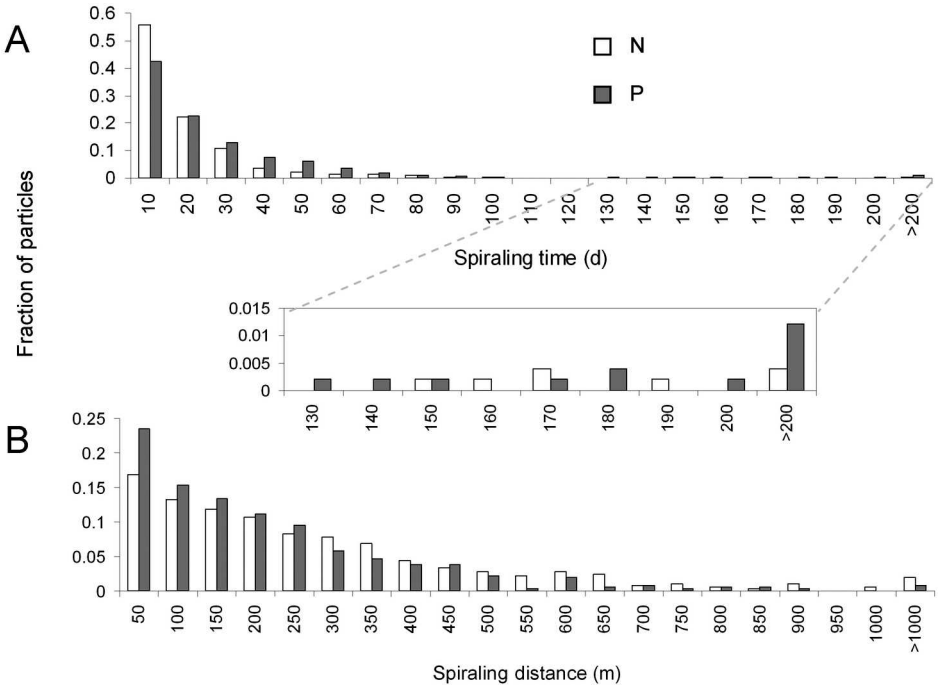

FIG. 4. Distribution of spiraling times (A) and distances (B) for 500 N and P atoms in a P-limited stream. Average spiraling time is strongly influenced by the small fraction of nutrient atoms that enter the slow-turnover consumer pool (shown in inset). Stoichiometric regulation by microbes and consumers causes longer average spiraling time for P (T_P) relative to N (T_N). Microbes and consumers also affect the supply of dissolved nutrients, creating a longer spiraling length for N (S_N) relative to P (S_P).

labeled atoms in the microbe/detritus compartment decayed because of mineralization and downstream transport of detritus. By 40 d, more labeled detritus occurred in downstream reaches, and a substantial amount of N and P had entered the consumer compartment. By 100 d, most of the labeled atoms remaining in the stream were in consumers. By 200 d, almost no labeled nutrient atoms remained in the microbe/detritus compartment, and consumers were the only long-term reservoir of these nutrients. Our simulated tracer experiment illustrated how consumer biomass contributes to long-term retention of labeled nutrients in a stream, and was consistent with results from field tracer experiments (Newbold et al. 1983, Peterson et al. 1997, Mulholland et al. 2000).

The overall importance of the differential recycling of limiting and nonlimiting nutrients in this simulation is most apparent when plotting the total amount of tracer N and P in the entire stream over time (Fig. 6). P had a higher maximum value than did N, indicating that labeled P was retained more efficiently than was N (i.e., more traced N had left the stream in the first 24 h). Half of the traced N had exited the stream by 18 d, whereas 37 d were required for ½ of the P to exit. Labeled N and P remaining in the stream at 200 d were almost exclusively in consumer biomass and represented 2% of total N tracer and 6% of total P tracer. These results illustrate our hypothesis that, in a P-limited stream, lower rates of P excretion by consumers will result in a slower downstream velocity for P atoms and increased P retention in the stream ecosystem.

Part II: Consumer effects on nutrient spiraling under steady-state conditions

Consumers at medium and high biomass substantially decreased the average downstream velocity of N and P atoms. In the medium and high consumer biomass scenarios, the average N and P atoms travelled downstream at ~¾ and ½ of the velocity of N and P atoms in the no consumers scenario (Table 1), respectively. In contrast, the effects of consumers on nutrient spiraling in the low consumer biomass scenario were negligible. The magnitude of the decrease in average downstream velocity of nutrient atoms depended on the probability of an atom entering consumers in a given spiral. In the low consumer biomass scenario, only 0.4% of N and 0.6% of P atoms entered the slow-turnover consumer compartment in a given spiral (i.e., N atoms entered a consumer once every 250 spirals and P atoms entered a consumer once every 167 spirals, on

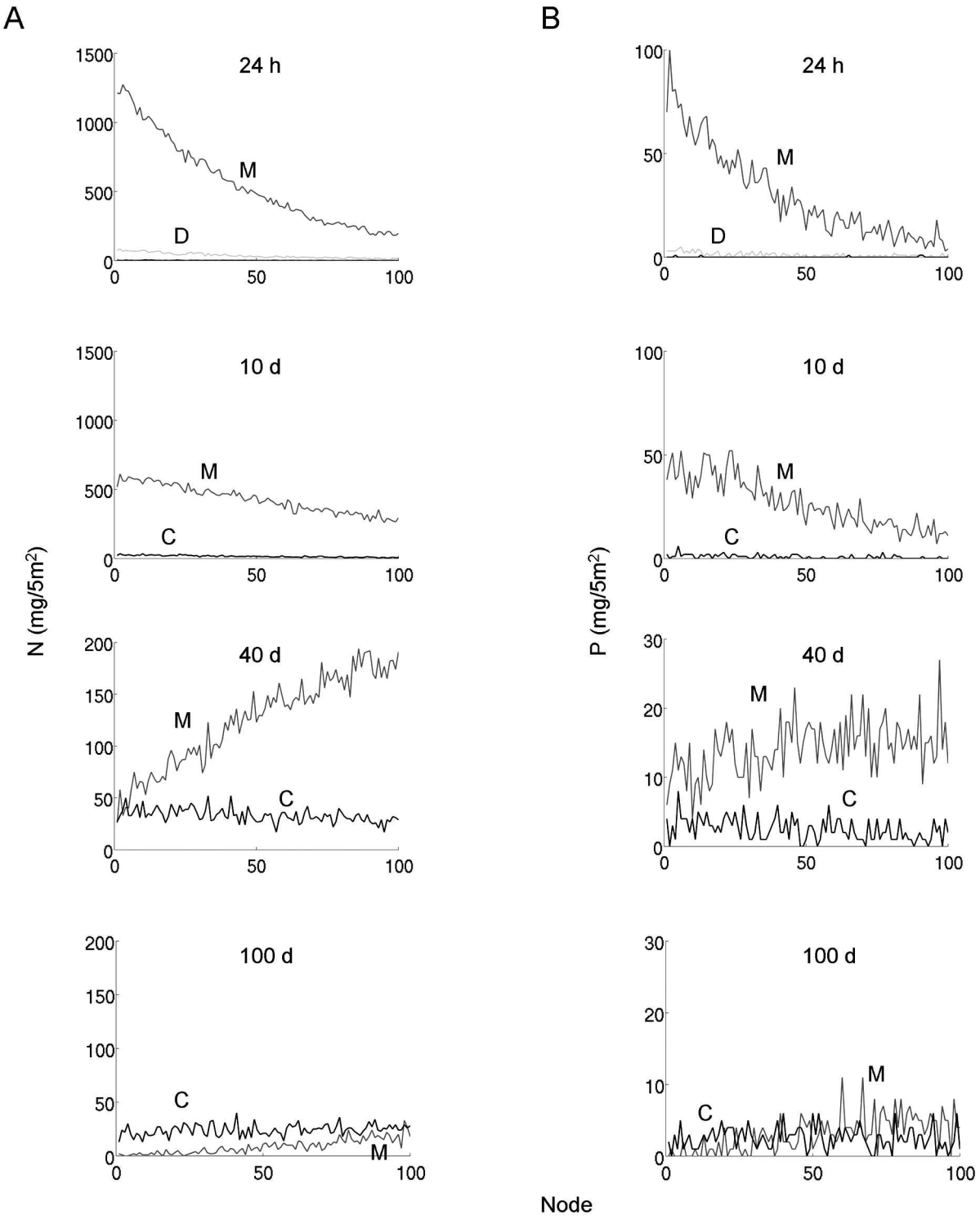

FIG. 5. Results of a simulated N (A) and P (B) tracer addition experiment. We labeled all dissolved N and P particles that entered the stream over a 24-h period and followed the fate of these particles over 500 m of stream for 200 d. Values for N and P are reported /stream node (= 5 m^2). Note rescaled *y*-axis between top and bottom panels. D = dissolved N or P atoms, M = N or P atoms in microbe/detritus, C = atoms in consumer biomass.

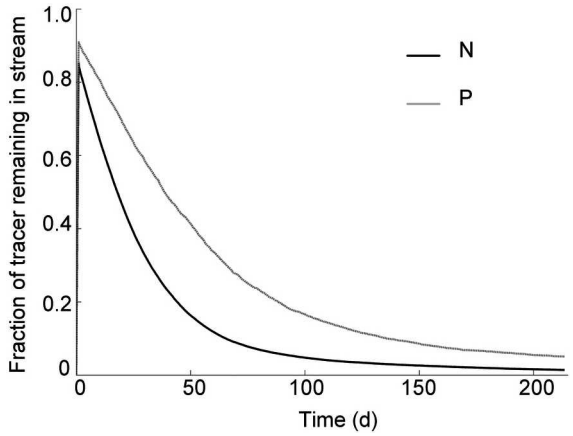

FIG. 6. Fraction remaining of total N and P tracer added to stream over time. Maximum values are <1 because some particles had exited the 500 m stream reach before the end of the 24-h tracer addition. In this P-limited stream, P atoms were taken up more efficiently and retained longer than were N atoms.

average). In contrast, in the high consumer biomass scenario, N and P atoms had a 17.3% and 23.3% probability, respectively, of entering consumers in a given spiral (i.e., N atoms entered a consumer every 6 spirals and P atoms entered consumers every 4 spirals, on average). Therefore, the manifested effect of consumers on ecosystem-level nutrient spiraling

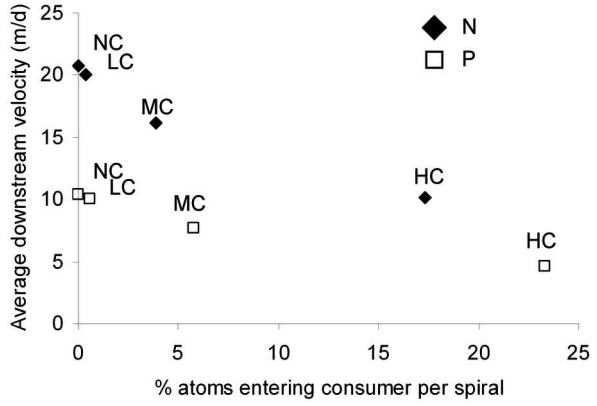

FIG. 7. Effects of consumer biomass and stoichiometric regulation on average downstream velocity of limiting (P) and nonlimiting nutrient (N). Consumer biomass determines the proportion of nutrient atoms that enter the slow-turnover consumer compartment in a given spiral. The higher average downstream velocity of N in these simulations is the result of a shorter average retention time in the microbe/detritus and consumer compartments. NC = no consumers, LC = low consumer biomass, MC = medium consumer biomass, HC = high consumer biomass.

parameters was directly proportional to the fraction of nutrient atoms that entered the consumers where they were then subject to homeostatic regulation (Fig. 7).

Consumers exerted their control on downstream velocity through their influence on turnover time rather than on spiraling length. Comparing the high consumer biomass and no consumers scenarios, consumers in the high consumer biomass scenario increased spiraling lengths relative to the no consumer scenario (N: 19%, P: 15%) because consumers decreased the microbe/detritus standing stock (which removes nutrients from the water column) consistent with empirical results (Mulholland et al. 1983, 1985). However, the presence of consumers increased the average N spiraling time 142% and P spiraling time 159%, and outweighed the propensity for spiraling length to increase downstream velocity. Therefore, the average downstream velocity decreased 51% for N and 56% for P (Table 1, Fig. 7).

The nonlimiting nutrient (N) had a greater spiraling length (S_N:$S_P > 1$) and a shorter spiraling time (T_N:$T_P < 1$) than did the limiting nutrient (P) in all scenarios (Table 1). Even in the absence of consumers, microbes differentially retained the limiting vs nonlimiting nutrient and controlled the relative magnitudes of N and P spiraling metrics. Consumers also affected nutrient spiraling by differential retention of the limiting nutrient. However, consumer turnover time was much longer than microbe/detritus turnover time, so even though only a small fraction of nutrient atoms enter consumers in a given spiral, consumers can have a significant effect on spiraling metrics. In fact, differences in average downstream velocity between limiting and nonlimiting nutrients were mainly driven by longer turnover times of limiting nutrients in consumer compartments (~105 d for N vs ~132 d for P; Table 1). Microbes might exacerbate the consumer effect directly via uptake (i.e., spiraling length is shorter for limiting nutrient; S_N:$S_P > 1$; Table 1) and indirectly via differential retention (i.e., microbial retention of the limiting nutrient increases the propensity for that limiting nutrient to enter the consumer biomass, b_{CN}:$b_{CP} < 1$; Table 1).

In the high consumer N:P scenario, optimal N:P was raised to 30, and therefore, consumers were attempting to maintain an N:P ratio that was much different than that of their food resource (microbe/detritus N:P = 10). Because consumers in this scenario were highly N limited, the turnover time was nearly 2.5× longer for N than for P in consumers. As a result, the average downstream velocity of N decreased (from 16.2 m/d to 13.6 m/d) and P increased (from 7.7 m/d to 9.1 m/d) relative to the medium consumer biomass scenario (Table 1). However, microbes were

still P-limited, resulting in slower average downstream velocity for P than N.

In the nonhomeostatic consumer scenario, the strength of homeostatic regulation by consumers decreased, and consumer N:P shifted closer to that of their food, the microbe/detritus compartment (19.7; Table 1). With greatly diminished homeostatic control on their N:P ratio, the effect of consumers on spiraling metrics was dampened. For example, consumers were still highly N-limited, but the difference between turnover times for N and P in consumer biomass was not as great as for consumers with stronger homeostatic regulation (nonhomeostatic consumers, N: 113.7 d, P: 57.9 d; homeostatic consumers; N: 143.2 d, P: 57.9; Table 1).

Our model results support the hypothesis of Frost et al. (2002) that the importance of stoichiometric mechanisms in consumer-driven nutrient recycling in streams depends on both consumer biomass and on the elemental imbalance between consumers and their food resources. Our model illustrates that consumer biomass controls nutrient spiraling rates by determining the propensity for a nutrient atom to enter the slow-turnover consumer compartment in a given spiral. For both limiting and nonlimiting nutrients, as consumer biomass increased, the fraction of N and P atoms entering the consumer compartment in a given spiral increased, resulting in decreased average downstream velocity for both N and P (Fig. 7). At every level of consumer biomass, average downstream velocity was slower for the limiting nutrient. Once a nutrient atom entered consumer biomass, how long it stayed in this compartment was controlled by the homeostatic regulation of the consumer, which resulted in longer turnover times for limiting nutrients and, ultimately, lead to a slower average downstream velocity. The effect of homeostatic regulation by consumers on nutrient spiraling was greatest for consumers that tightly regulated their body elemental composition (i.e., strict homeostasis) and fed on resources that had N:P ratios substantially different from their body elemental composition.

Empirical tests of model hypotheses

The most straightforward empirical test of hypotheses stemming from our model would be to add N- and P-tracers simultaneously to an experimental stream and to vary factors, such as N:P loading rates, consumer biomass, and consumer N:P ratios. Radioisotope tracer studies (^{32}P tracer additions) are logistically difficult, but one prediction from our model that could be tested with only a ^{15}N tracer addition is how changes in P-availability affect N-retention by consumers. Homeostatic consumers in high-P streams (feeding on P-rich basal food resources) should retain N more efficiently (i.e., more N ingested can be converted into consumer biomass) compared to P-limited consumers in low-P streams, where more excess N must be excreted. Even if consumers in high-P streams are not N-limited, as long as food resource N:P is less than consumers' optimal food resource N:P, N should have a longer retention time in homeostatic consumers. The result should be a slower average downstream velocity for N in high-P streams, driven by longer turnover times in consumer biomass.

Indirect effects of consumers: organic matter breakdown and functional feeding groups

Our model consisted of a single consumer compartment and a single microbe/detritus compartment, which was the only food resource for consumers. However, processing by invertebrate consumers alters the size and shape of organic matter, and different functional feeding groups contribute to the retention and mobilization of this organic matter in different ways (Wallace and Hutchens 2000). Feeding and egestion by benthic consumers in most functional feeding groups converts organic matter into smaller sized particles, which are more easily suspended and transported downstream. Incorporation of this dynamic into our model would have resulted in longer S_Bs (and therefore, longer spiraling lengths) for both N and P. This change would not have altered our results qualitatively, and therefore, would not have changed our interpretation of the direct effects of consumers on nutrient spiraling.

Other stream models have incorporated differential effects of invertebrate consumer functional feeding groups on the dynamics of individual nutrients in streams (e.g., Newbold et al. 1982). Here, we used a more simplified food web but incorporated 2 nutrients to explore the direct effects of consumer homeostatic regulation on nutrient spiraling in streams. An important next step will be to incorporate how different consumers might differentially regulate their stoichiometry. In our model, the elemental composition of consumers was controlled by 2 parameters: an optimal N:P ratio and coefficient for strength of homeostatic regulation. Both of these parameters potentially could differ among consumer groups. For example, fish have higher body P content than do invertebrate consumers (e.g., Vanni et al. 2002), invertebrate predators might have higher N content compared to other functional feeding groups (Cross et al. 2003), and some invertebrate consumer

taxa (e.g., Trichoptera) might have greater flexibility for body P content (Cross et al. 2003). Incorporating multiple types of consumers with different stoichiometric parameters would allow exploration of how ecological processes, such as competition and invasion, might alter stream nutrient dynamics and would be a step toward understanding ecosystem-scale nutrient dynamics as an emergent property of nutrient regulation by individual organisms.

What controls the magnitude of consumer effects on nutrient spiraling across stream ecosystems?

The standing stock of consumers in a stream ecosystem influences the likelihood of a nutrient atom entering consumer biomass in a given spiral (where it is then subject to consumer homeostatic regulation). Thus, it is not surprising that some of the empirical studies demonstrating consumer excretion as a significant component of nutrient dynamics have occurred in systems with consumer biomass similar to our high consumer biomass scenario (43.7 g AFDM/ m^2) (e.g., Hall et al. 2003: 35 g AFDM/m^2, Caraco et al. 1997: 51 g AFDM/ m^2, McIntryre et al. 2008: up to ~46 g dry mass/m^2). Several of the highest reported values of consumer biomass in streams are the result of invasive species (e.g., Caraco et al. 1997, Hall et al. 2003). Thus, species invasions might lead to increased potential for control of stream nutrient dynamics by consumer stoichiometry. However, consumer biomass in most streams for which data are available is less than in our medium consumer biomass scenario (11.1 g AFDM/ m^2; Fig. 3), and might be too low to alter nutrient dynamics significantly in many streams.

Our model simulations occurred in low-nutrient conditions (dissolved N = 159 μg/L, dissolved P = 8 μg/L). The effects of consumer-driven nutrient recycling are greatest under low-nutrient conditions (Evans-White and Lamberti 2006). However, differential consumer recycling of limiting and nonlimiting nutrients has the potential to affect nutrient spiraling in nutrient-enriched streams. Increased nutrient loading in streams can stimulate microbial and consumer production (e.g., Cross et al. 2006), increase the flow of nutrients through the food web, and potentially, increase their influence on nutrient spiraling. In general, increasing dissolved nutrient loading increases S_W (and therefore, spiraling lengths) through saturation of microbial uptake at elevated concentrations (Payn et al. 2005). If nutrient loading were balanced (proportional high inputs of dissolved N and P) in our model, turnover times in biotic compartments would not change substantially (standing stocks would increase, but inputs and outputs from these compartments would increase correspondingly). In this case, average downstream velocity would increase for both N and P because of increased S_W, and the importance of consumers in retaining nutrients would depend on how much of the elevated nutrient load in the stream ecosystem actually entered consumer biomass.

If nutrient loading were imbalanced (e.g., high dissolved N and low dissolved P inputs), turnover time for the nonlimiting nutrient in the microbe/detritus and consumer compartments would decrease markedly as homeostatic organisms attempted to maintain optimal N:P ratios. The combination of increased spiraling length and shorter turnover time for the excess nutrient would result in a much higher average downstream velocity for the nonlimiting nutrient. Anthropogenic nutrient loading might cause imbalanced inputs of different nutrients into streams (e.g., decline in P loading following ban of P detergents; Stow et al. 2001) and might increase the differential effects of biotic stoichiometric regulation on nutrient spiraling for limiting and nonlimiting nutrients. Exploration of the complex interactions between nutrient loading rates and consumer control of stream nutrient dynamics will be a fruitful area for further research.

Consumers did not affect absolute nutrient fluxes in our simulations because our model assumed a biogeochemical steady state. Instead, regulation of elemental ratios by microbes and consumers controlled the amount of N and P in these respective compartments, and affected turnover time and downstream velocity. In a stream that is not at steady state (either temporal or longitudinal), consumers potentially could exert stoichiometric effects on nutrient fluxes. If instream consumer biomass were increasing over time, the downstream flux of limiting nutrients would be depleted to a greater extent compared to the flux of nonlimiting nutrients. Similarly, if insect emergence were included in our model as a nutrient sink, limiting nutrients would be removed from the stream ecosystem at a relatively greater rate compared to nonlimiting nutrients. In our model, all nutrients entered a given stream reach from upstream, and a stoichiometrically regulated nutrient sink, such as insect emergence, would result in a longitudinal gradient in nutrient availability. Deviations from steady state create the potential for consumers to alter downstream nutrient fluxes, and this topic merits further exploration.

Conclusions

Time always has been an implicit component of nutrient spiraling, but we argue that time must be

considered explicitly if we are to understand fully the role of stoichiometric regulation by consumers. Our heuristic model results illustrate that sufficiently high levels of consumers can regulate whole-stream nutrient dynamics (i.e., the downstream velocity of individual nutrient atoms) by controlling the amount of time nutrients are entrained within the food web. By following individual particles across multiple spirals, we illustrated how the average downstream velocity of these atoms was delayed substantially by the small fraction that entered the slow-turnover pool of consumer biomass and remained there for a long time. Consumers that regulate their body elemental composition inevitably have longer turnover times for limiting nutrients than for nonlimiting nutrients, with the emergent effect of increased retention for limiting nutrients on an ecosystem scale. As consumer biomass increases, this emergent effect might lead to a decoupling of limiting and nonlimiting nutrient spirals in stream ecosystems. Empirical research focused on measuring nutrient uptake in streams has advanced our understanding of stream biogeochemistry, but extending this research to explore what factors control the fate of these nutrients once they enter the stream food web will lead to a more complete understanding of how nutrients are processed and transported in stream ecosystems.

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APPENDIX 1. State variables and parameters under the 6 model scenarios. Parameters were derived from target values for storage, fluxes, and elemental ratios reported in Cross et al. (2003), Mulholland et al. (1985, 2000), and Newbold et al. (1983).

		Model scenario						
Symbol	Explanation	No consumers	Low consumer biomass	Medium consumer biomass	High consumer biomass	High consumer N:P	Nonhomeostatic consumer	Units
i	Stream node (volume): 5 m long × 1 m wide × 0.1 m deep	500	500	500	500	500	500	L
	Stream node (area)	5	5	5	5	5	5	m^2
x_1	Dissolved N	79.3	79.3	79.4	79.4	80.4	81	mg/500 L
x_2	Microbe/detritus N	16565	16468	15529	11854	15515	15771	mg/5 m^2
x_3	Consumer N	0	557	5581	21887	10144	6681	mg/5 m^2
x_4	Dissolved P	3.9	3.9	3.9	4.1	4.1	4.1	mg/500 L
x_5	Microbe/detritus P	1645	1635	1542	1178	1541	1566	mg/5 m^2
x_6	Consumer P	0	70	697	2734	407	339	mg/5 m^2
k_1	Rate of water movment downstream	0.1	0.1	0.1	0.1	0.1	0.1	1/10 s
k_2	Maximum rate of N uptake/microbial N or P uptake/microbial P	2×10^{-5}	2×10^{-5}	2×10^{-5}	2×10^{-5}	2×10^{-5}	2×10^{-5}	mg dissolved N/mg microbial N/10 s mg dissolved P/mg microbial P/10 s
k_3	½-saturation constant for microbial N or P uptake (based on relative availability)	5×10^{-3}	5×10^{-3}	5×10^{-3}	5×10^{-3}	5×10^{-3}	5×10^{-3}	mg dissolved N/mg microbial N mg dissolved P/mg microbial P
k_4	Maximum rate of microbial N or P mineralization (biomass-specific)	1.95×10^{-5}	1.95×10^{-5}	1.95×10^{-5}	1.95×10^{-5}	1.95×10^{-5}	1.95×10^{-5}	mg dissolved N/mg microbial N/10 s mg dissolved P/mg microbial P/10 s
k_5	Homeostatic regulation coefficient for microbes	10	10	10	10	10	10	
k_6	Optimal N:P (mass) for microbe/detritus compartment	10	10	10	10	10	10	
k_7	Maximum rate of consumer N or P excretion (biomass-specific)		1.8×10^{-6}	1.8×10^{-6}	1.8×10^{-6}	1.8×10^{-6}	1.8×10^{-6}	mg dissolved N/mg consumer N/10 s mg dissolved P/mg consumer P/10 s
k_8	Homeostatic regulation coefficient for consumers		100	100	100	100	10	
k_9	Optimal N:P (mass) for consumers		8	8	8	30	30	
k_{10}	Rate of microbe/detritus movement downstream	2×10^{-6}	2×10^{-6}	2×10^{-6}	2×10^{-6}	2×10^{-6}	2×10^{-6}	1/10 s
k_{11}	Maximum rate of consumer ingestion (biomass-specific)		2×10^{-6}	2×10^{-6}	2×10^{-6}	2×10^{-6}	2×10^{-6}	mg microbial N/ mg consumer N/10 s
k_{12}	½-saturation constant for consumer ingestion (based on relative availability)		24	2.26	0.44	2.26	2.26	mg microbial N/mg consumer N
k_{13}	Decomposition rate of consumers		2×10^{-7}	2×10^{-7}	2×10^{-7}	2×10^{-7}	2×10^{-7}	1/10 s

APPENDIX 2. Model equations. x_1 is dissolved N, x_2 is microbial N, x_3 is consumer N, x_4 is dissolved P, x_5 is microbial P, and x_6 is consumer P. Terms *i* and *ii* represent the downstream movement of dissolved N and P between stream nodes, and *iii* and *iv* represent the downstream movement of microbial N and P. Terms *a*–*e* represent movement of N or P within a given stream node (corresponding to flows in Fig. 2B): *a* represents uptake of dissolved nutrients by microbes, *b* represents microbial mineralization, *c* represents consumer feeding, *d* represents consumer mortality, and *e* represents consumer mineralization. See Appendix 1 for parameter descriptions and values.

$$\frac{dx_{1i}}{dt} = \underbrace{k_1 x_{1(i-1)}}_{i} - \underbrace{k_1 x_{1i}}_{ii} - \underbrace{k_1 x_{2i}\left(\frac{(x_{1i}/x_{2i})}{k_3+(x_{1i}/x_{2i})}\right)}_{iii} + \underbrace{k_4 x_{2i}\left(\frac{1}{1+e^{k_5((x_{5i}/x_{2i})-(1/k_6))}}\right)}_{iv} + \underbrace{k_7 x_{3i}\left(\frac{1}{1+e^{k_8((x_{6i}/x_{3i})-(1/k_9))}}\right)}_{v}$$

$$\frac{dx_{2i}}{dt} = \underbrace{k_{10} x_{2(i-1)}}_{vi} - \underbrace{k_{10} x_{2i}}_{vii} + \underbrace{k_2 x_{2i}\left(\frac{(x_{1i}/x_{2i})}{k_3+(x_{1i}/x_{2i})}\right)}_{iii} - \underbrace{k_4 x_{2i}\left(\frac{1}{1+e^{k_5((x_{5i}/x_{2i})-(1/k_6))}}\right)}_{iv} - \underbrace{k_{11} x_{3i}\left(\frac{(x_{2i}/x_{3i})}{k_{12}+(x_{2i}/x_{3i})}\right)}_{viii} + \underbrace{k_{13} x_{3i}}_{ix}$$

$$\frac{dx_{3i}}{dt} = \underbrace{k_{11} x_{3i}\left(\frac{(x_{2i}/x_{3i})}{k_{12}+(x_{2i}/x_{3i})}\right)}_{viii} - \underbrace{k_{13} x_{3i}}_{ix} - \underbrace{k_7 x_{3i}\left(\frac{1}{1+e^{k_8((x_{6i}/x_{3i})-(1/k_9))}}\right)}_{v}$$

$$\frac{dx_{4i}}{dt} = \underbrace{k_1 x_{4(i-1)}}_{i} - \underbrace{k_1 x_{4i}}_{ii} - \underbrace{k_2 x_{5i}\left(\frac{(x_{4i}/x_{5i})}{k_3+(x_{4i}/x_{5i})}\right)}_{iii} + \underbrace{k_4 x_{5i}\left(\frac{1}{1+e^{k_5((x_{2i}/x_{5i})-k_6)}}\right)}_{iv} + \underbrace{k_7 x_{6i}\left(\frac{1}{1+e^{k_8((x_{3i}/x_{6i})-k_9)}}\right)}_{v}$$

$$\frac{dx_{5i}}{dt} = \underbrace{k_{10} x_{5(i-1)}}_{vi} - \underbrace{k_{10} x_{5i}}_{vii} + k_2 x_{5i}\left(\frac{(x_{4i}/x_{5i})}{k_3+(x_{4i}/x_{5i})}\right)_{iii} - \underbrace{k_4 x_{5i}\left(\frac{1}{1+e^{k_5((x_{2i}/x_{5i})-k_6)}}\right)}_{iv} - \underbrace{k_{11} x_{3i}\left(\frac{(x_{2i}/x_{3i})}{k_{12}+(x_{2i}/x_{3i})}\right)\left(\frac{x_{6i}}{x_{3i}}\right)}_{viii} + \underbrace{k_{13} x_{6i}}_{ix}$$

$$\frac{dx_{6i}}{dt} = \underbrace{k_{11} x_{3i}\left(\frac{(x_{2i}/x_{3i})}{k_{12}+(x_{2i}/x_{3i})}\right)\left(\frac{x_{6i}}{x_{3i}}\right)}_{viii} - \underbrace{k_{13} x_{6i}}_{ix} - \underbrace{k_7 x_{6i}\left(\frac{1}{1+e^{k_8((x_{3i}/x_{6i})-k_9)}}\right)}_{v}$$

APPENDIX 3. Comparison of physical characteristics and N and P standing stocks, spiraling lengths, and turnover times reported for Walker Branch, Tennessee, and in our low consumer biomass model scenario. N values for Walker Branch were taken from Mulholland et al. (2000), and P values were taken from Newbold et al. (1983). S_W = uptake length, S_B = turnover length, S_T = total spiraling length.

Variable	Walker Branch	Our model
Physical		
Discharge (L/s)	9.6	5.0
Width (m)	3.1	1.0
Depth (cm)	4.6	10.0
Water velocity (cm/s)	6.8	5.0
Stocks		
N		
Dissolved (μg DIN/L)	18.3	158.7
Microbe/detritus (mg N/m^2)	2406	3294
Consumer (mg N/m^2)	200	111
P		
Dissolved (μg PO_4-P/L)	4.1	7.9
Microbe/detritus (mg P/m^2)	244	327
Consumer (mg P/m^2)	22.8	13.9
N:P (molar)		
Dissolved	9.9	44.4
Microbe/detritus	21.8	22.3
Consumer	19.4	17.7
Spiraling metrics (m)		
N		
S_W	23–31 (NH_4^+) 101–∞ (NO_3^-)	246
S_B		1
S_T		247
P		
S_W	165	186
S_B	25	2
S_T	190	188
Turnover times (d)		
N		
Water	0.0035 (NH_4^+)	0.057
Microbe/detritus	12.5–24.7	11.8
Consumer	~115	105
P		
Water	0.052	0.043
Microbe/detritus	14.1	17.8
Consumer	153	132