

## ROSEMARY MACKAY FUND ARTICLE

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*In this first article of the series, P. C. Frost, R. S. Stelzer, G. A. Lamberti, and J. J. Elser discuss ecological stoichiometry in the benthos of lentic littoral and lotic habitats. Paul Frost is a Postdoctoral Research Associate at the University of Notre Dame. He mainly examines the origins of mass balance constraints and their effects on ecological processes in benthic environments. Bob Stelzer is an Assistant Professor in the Biology and Microbiology Department at the University of Wisconsin-Oshkosh. He does research on ecosystem processes and trophic interactions in streams. Gary Lamberti is a Professor of Biological Sciences at the University of Notre Dame. His research interests are in benthic processes in streams, rivers, and lakes and in linkages among aquatic ecosystems. Jim Elser is a Professor of Biology at Arizona State University. His primary research interest is in the causes and consequences of the stoichiometric coupling of elements in living systems.*

### Ecological stoichiometry of trophic interactions in the benthos: understanding the role of C:N:P ratios in lentic and lotic habitats

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**Abstract.** This paper considers how the theory of ecological stoichiometry may be applied to issues of importance to benthic ecologists. Ecological stoichiometry considers both the causes of elemental (C:N:P) imbalances between trophic levels and their consequences on foodweb dynamics (e.g., predator-prey interactions) and ecosystem processes (e.g., nutrient cycling). Elemental imbalances are created between consumers and their food, in part, by the accumulation of C relative to other nutrients (N and P) in benthic organic matter as a result of the deposition of detritus and/or unbalanced growth in aquatic producers. High C:N and C:P ratios in food material can reduce growth and reproduction and alter related processes such as nutrient release in benthic consumers. By affecting consumer metabolism, elemental imbalances may affect population dynamics, trophic interactions, and gross transfer efficiencies in benthic systems. Future work is needed to quantify the frequency and magnitude of elemental imbalances, to determine why elemental ratios differ within and among trophic levels, and to examine how stoichiometric imbalances affect fundamental ecosystem processes (e.g., nutrient cycling and spiraling, consumer growth dynamics, and responses to environmental disturbance) in benthic systems.

**Key words:** ecological stoichiometry, benthos, C:N:P ratios, littoral, streams.

The idea that the relative abundance of elements in the environment can affect biological transformations of materials is not new. Lotka

(1925) anticipated ecological stoichiometry in his book, *The elements of physical biology* (p. 50; italics his): “. . . we may employ the term *Stoichiometry* to denote that branch of the science which concerns itself with the *material* transformations, with the relations between the *masses* of the components”. However, the realization that elemental requirements of organisms link the cycling of multiple elements in ecosystems

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was not widely recognized until the work of Redfield (1958, 1963), who showed that biogeochemical cycles of C, N, and P in the open oceans are strongly coupled because of the incorporation of C, N, and P at particular ratios in phytoplankton biomass. This work has come to imply that there is a relatively fixed elemental signature in organisms, the Redfield ratio (C:N:P ~106:15:1), which translates into a rigidly proportional cycling of those elements in the environment (Stumm and Morgan 1996, Falkowski 2000). However, C:N:P ratios can vary widely within and between species across ecosystems (Duarte 1992, Hecky et al. 1993, Elser and Hassett 1994, Elser et al. 2000a). This variation in the elemental composition of organisms has considerable biological meaning, and affects a wide range of ecological phenomena (Sterner and Hessen 1994, Sterner 1995, Cebrian 1999, Elser and Urabe 1999, Elser et al. 2000b, Sterner and Elser 2002). In this paper, we examine: 1) the causes of differences in the C:N:P composition of organisms within and between trophic levels, and 2) the consequences that these differences may have on a range of ecological processes (e.g., decomposition, nutrient cycling and spiraling, and consumer growth rates and efficiencies) in benthic systems.

Ecological stoichiometry considers how the relative proportions of chemical elements affects their biological transformations in ecological interactions. Particular emphasis has been placed on differences in elemental composition between producers and consumers because these differences can affect a number of patterns and processes in ecosystems, including nutrient cycling (Elser and Urabe 1999), trophic interactions (Sterner et al. 1997, Elser et al. 1998), population dynamics (Andersen 1997, Loladze et al. 2000), and community structure (DeMott and Gulati 1999). Elemental imbalances occur when consumers obtain elements from their food in proportions different from those required for their growth, reproduction, and maintenance (Fig. 1; Sterner and Hessen 1994, Sterner 1997, Frost and Elser 2002a). Although elemental imbalances between consumers and their food sources are common in lake planktonic and terrestrial ecosystems (Elser et al. 2000a), the extent and frequency of such imbalances in benthic systems is largely unknown.

Elemental imbalances at the base of food webs appear to be widespread and are created,

in part, by high atomic C:x (where x can be any other nutrient) ratios in food sources available to consumers (Fig. 1A, y-axis). The elemental composition of benthic particulate organic material (POM; mainly detritus, bacteria, fungi, algae, and meiofauna at the base of the food web) has not been extensively studied, but available data indicate that C:x ratios in this organic matter can vary substantially (Duarte 1992, Kahlert 1998, Hillebrand and Sommer 1999, Stelzer 1999, Frost and Elser 2002b). Elemental imbalances are also created by the elemental composition of consumers themselves (Fig. 1A, x-axis, Elser and Hassett 1994, Sterner and Hessen 1994, Sterner and Elser 2002). Currently, almost nothing is known about patterns of inter- and intraspecific variation in the C:N:P stoichiometry of benthic consumers (Elser and Urabe 1999, Frost 2001). Without these comprehensive data on consumer C:N:P stoichiometry, we can only assume that benthic consumers have similar C, N, and P requirements as other aquatic and terrestrial invertebrates because fundamental processes of growth and reproduction in animals appear to require particular amounts of N and P (Sterner 1995, Elser et al. 1996, Elser et al. 2000a).

Most of the work in ecological stoichiometry has examined food webs in pelagic ecosystems and so we are faced with questions about how to apply this conceptual framework to benthic systems. What factors affect stoichiometric relationships in food webs of benthic ecosystems? How may these factors differ among benthic systems? For example, detrital input from riparian vegetation dominates the biomass of organic material in small temperate streams (Fisher and Likens 1973) and, consequently, should control the C:N:P stoichiometry of benthic POM in these systems. On the other hand, autochthonous primary production may dominate the C:N:P content of benthic POM in streams of other geographic regions (Minshall 1978) or at different points in the river continuum (Vannote et al. 1980). In the following sections, we examine some causes of stoichiometric variation in the benthos and the consequences that elemental imbalances may have for benthic ecology.

### Ecological Stoichiometry in Stream and Lake Benthos

Lake littoral and stream benthic environments are structurally similar in ways that dis-

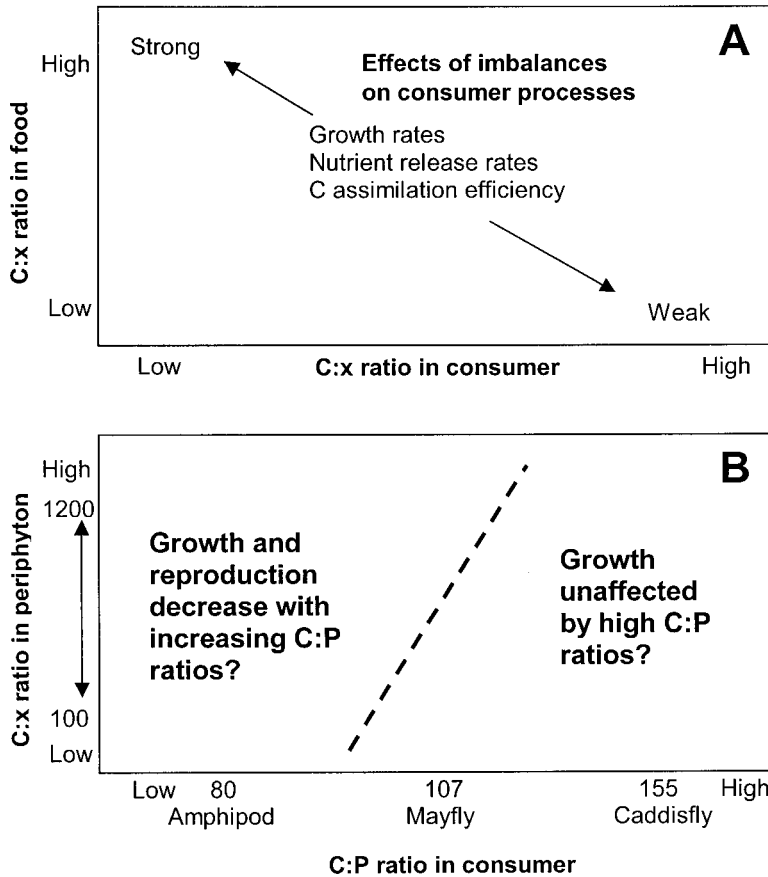


FIG. 1. How elemental imbalances develop between consumers and food. A.—Elemental imbalances occur when consumers of low C:x ratios eat food of high C:x ratios. Under such circumstances, consumer processes (e.g., growth) can be constrained and related ecological processes (e.g., nutrient recycling) strongly affected. B.—Benthic data from Canadian Shield lakes that show the range of C:P ratios in periphyton relative to benthic consumers (PCF, unpublished data). Similar to planktonic data (Andersen and Hessen 1991), benthic consumers can have relatively low C:P ratios compared to their food and differences can exist among consumer taxa. However, whether consumer processes are affected by changes in C:P ratios of their food remains largely unknown.

tinguish them from pelagic environments. For example, benthic autotrophs and heterotrophs are typically attached or closely associated with inorganic and organic substrates. Because of the intimate association of benthic biota and bottom substrates, these organisms rely on connections from below (organic substrates, mineral dissolution, groundwater) as well as from above (water column, settling material) for elements and energy. Although phytoplankton depend entirely on nutrients obtained from the water column during their growing season, benthic microbes, algae, and plants may obtain elements from surface water, substrates, and groundwater (Burk-

holder 1996, White and Hendricks 2000). Therefore, all of these nutrient supplies may affect nutrient supply ratios to benthic producers and microbes.

At a larger scale, watershed and airshed properties likely have fundamental influences on stoichiometric relationships in benthic habitats. Mineral composition of rocks and soils, land use, atmospheric deposition, and hydrology are among the factors that can affect the flux of nutrients supplied to lakes and streams (Allan 1995). Ecotones between terrestrial environments and aquatic environments can also modulate the rates and ratios of nutrients that enter

lakes and streams (Peterjohn and Correll 1984) because some elements are retained more efficiently than others (Lowrance et al. 1984). Regardless of whether this retention is primarily physical, chemical, or biological in nature, the altered elemental ratios supplied to benthic habitats could affect the magnitude of elemental imbalances among trophic levels.

The strength of lateral connections between terrestrial and aquatic environments will also affect POM C:x ratios by altering the balance of autotrophy versus heterotrophy in the ecosystem. In lakes and streams where allochthonous inputs of POM to the benthos are high (e.g., Findlay et al. 1997, Webster et al. 1997), the elemental composition of this material will largely determine the size of elemental imbalances at the consumer–food interface at the base of the food web. Under these circumstances, the stoichiometry of benthic POM will reflect the C:N:P ratios in the allochthonous material when it enters the benthos but with subsequent changes during its decomposition (Kaushik and Hynes 1971, Suberkropp et al. 1976, Melillo et al. 1984, Hecky et al. 1993).

Mismatches between the elemental composition of allochthonous POM and consumers likely have consequences on the growth and production of benthic heterotrophs and important ecosystem processes, such as nutrient mineralization. For example, decomposition rates of organic matter are fastest when its elemental composition is similar to that of microbes (Goldman et al. 1987, Tezuka 1990). In a broad survey, decomposition rates of plant detritus from terrestrial and aquatic habitats were strongly negatively correlated with tissue C:N and C:P ratios (Enriquez et al. 1993). Low rates of decomposition of terrestrially derived POM thus are not surprising given that its C:N ratios (i.e., >30, Gosz et al. 1973) are typically much higher than those of microbial and metazoan heterotrophs that process that organic matter (mean C:N ratios of 6–7) in aquatic systems (Andersen and Hessen 1991, Elser et al. 2000a, Goldman and Dennett 2000).

The potential for POM elemental composition to affect microbial growth and mineralization processes will depend in part on the plasticity of microbial C:N:P ratios. Heterotrophic bacteria that are growing rapidly tend to have lower C:x ratios than bacteria that are growing slowly (Chrzanowski et al. 1996). Bacterial C:P ratios

can vary twofold (Chrzanowski et al. 1996, Goldman and Dennett 2000) across a range of nutrient concentrations and ratios. Bacterial C:N ratios also vary but less so than C:P ratios (Kirchman 2000). The presence of plasticity in bacterial C:N:P ratios indicates that microbial heterotrophs can reduce the extent of elemental imbalances between themselves and their substrates (Chrzanowski et al. 1996). In addition, in environments with pulsed nutrient supply, bacterial plasticity provides a competitive strategy that allows growth demands to be met by storing elements (i.e., luxury P-uptake) and/or lowering cellular demands (Vadstein 2000).

The effects of POM elemental composition on microbial processes in the benthos will also depend on the supply of dissolved nutrients. In streams and lakes with high concentrations of nutrients, benthic bacteria may be able to meet much of their N and P demands from dissolved pools (e.g., Caraco et al. 1998, Suberkropp 1998). In fact, nutrient amendments can increase rates of decomposition in streams with low concentrations of dissolved N and P (e.g., Robinson and Gessner 2000). High C:x ratios in POM should thus most tightly constrain benthic microbial processes in oligotrophic systems, where the total supply of N, P, and other nutrients is low relative to bacterial growth demands.

Benthic algae and macrophytes may serve as an important pool of elements at the base of food webs in environments where allochthonous carbon supply to benthic habitats is low and light availability is high. In such systems, C:N:P ratios of benthic POM will be largely determined by the relative rates of net autotrophic production (i.e., C-fixation) and nutrient uptake in primary producers (Frost and Elser 2002b). In lakes, the balance between C-fixation and nutrient uptake should, in turn, be affected by epilimnetic dissolved inorganic carbon (DIC), photosynthetically active radiation, and dissolved nutrient pools (Sturner et al. 1997, Frost and Elser 2002b). Similarly, in streams, the elemental composition of new autotrophic production will largely be governed by the relative supply of light, N, and/or P. Because surface water in streams is generally at or near equilibrium with atmospheric CO<sub>2</sub>, DIC rarely limits autotrophic production in flowing waters (Peterson et al. 1993).

In lakes, the nutrient content of groundwater discharge can influence the elemental composi-

tion of biofilms found on soft sediments (Hagerty and Kerfoot 1998), and thus likely affects the growth rates of littoral algae and plants. In streams, there is also evidence that high nutrient concentrations in upwelling zones can increase algal growth and biomass (Valett et al. 1994). Furthermore, such variation in dissolved nutrient concentrations and ratios along stream flow paths is also likely to produce spatial variation in nutrient uptake and in elemental composition of algae, plants, and microbes (Mulholland et al. 1995). Consequently, benthic ecologists seeking to explain variation in algal and plant stoichiometry should explore linkages among multiple physicochemical factors in surface water, groundwater, and the elemental demands of new autotrophic production.

#### *Stoichiometry in lotic environments*

The defining characteristic of streams and rivers is unidirectional flow. Water, solutes, POM, organisms, and sediments move more or less down elevational gradients. Nutrient spiraling (Webster 1975, Newbold et al. 1982) describes the exchange of nutrients between dissolved inorganic pools in the flowing water column and particulate organic pools largely associated with the bottom along the length of a stream. Variation in the elemental composition of algae, microbes, macrophytes, and macroconsumers could influence nutrient spiraling properties of streams. For example, N remineralization lengths will tend to increase when consumers have much lower C:N ratios than that of their food because ingested N should be highly conserved in consumer biomass. Using a conceptual model, Fisher et al. (1998) described how nutrient retention increases during the early stages of succession in streams when net ecosystem production is positive. Similarly, as the C:x ratio of stream consumers decreases (they become more nutrient-rich), ecosystem retention of nutrient x should increase because there should be positive net incorporation of nutrient x by the consumer assemblage (i.e., when populations are growing). Clearly there are other factors that affect nutrient remineralization length and retention in streams, such as water velocity, movement of bedload, consumer drift rates, and vertical and lateral connectedness among subsystems. Given these many factors that affect nutrient remineralization and retention, what is the

relative influence of elemental imbalances in trophic interactions on remineralization length, retention, and other aspects of nutrient cycling? The answer to this question awaits future research. It would seem that the importance of stoichiometric mechanisms in consumer-driven nutrient cycling in streams will depend, in part, upon: 1) the biomass of consumers and, hence, the flux of a nutrient released by consumers compared to the total flux of the nutrient in a stream, and 2) whether N:P ratios (or other nutrients) released from consumers strongly differ from those ingested and/or in dissolved pools. For example, high N:P ratios in consumers relative to their food should yield low N:P ratios in released materials (Sterner 1990, Elser and Urabe 1999).

Consumers can sometimes represent a major source and sink for nutrients in streams. For example, Mulholland et al. (1991) found that P excretion by *Elimia* snails provided ~14% of the P uptake by algae in experimental streams. In a desert stream, Grimm (1988) found that 15 to 70% of the N taken up by algae was remineralized by invertebrates. In a tropical stream, the fish assemblage was estimated to supply up to 126% of the algal demand (Vanni et al. 2002). The effects of primary consumers on stream nutrient dynamics may extend beyond nutrient recycling. Consumers can affect many benthic properties (e.g., algal biomass and production, detritus processing) that affect the movement of chemical elements within stream ecosystems (e.g., Mulholland et al. 1991). Tracer additions of stable isotopes, which have been used to determine N cycling characteristics in streams (e.g., Mulholland et al. 2000), offer promise in integrating the influences of lotic consumer elemental composition on reach-scale fluxes and ratios of nutrients. Adding a thorough stoichiometric component to such studies might allow them to yield even greater insight.

In addition to nutrient remineralization, nutrient uptake lengths could also be influenced by stoichiometry in basal species (Fisher et al. 1998). Variation in C:N:P content among different autotrophs in streams could influence the relative uptake lengths of different nutrients. For example, algal species with high cellular N:P ratios would have a higher demand for N relative to P, and consequently decrease N and increase P uptake lengths compared to taxa with inherently lower N:P ratios. However, these interac-

tions may be complicated by nutrient effects on algal physiological status, which is known to vary widely within species (e.g., Healey and Hendzel 1979). In artificial streams, for example, manipulations of dissolved nutrient concentrations and ratios strongly altered C:N:P ratios of attached algae (Stelzer and Lamberti 2001).

Bulk nutrients in surface water or groundwater may not always be the most appropriate indicator of the nutrients available for biotic uptake by stream biota because of rapid nutrient cycling within biofilms (Riber and Wetzel 1987). In such cases, the concentration and ratio of elements resupplied by cell lysing and mineralization within the biofilm may be more relevant to algae and microbes, as shown in a system with low supply of P in stream water (Mulholland et al. 1991). In the artificial streams of Mulholland et al. (1991), P cycling within biofilms was a significant source of P taken up by the benthic algae.

The size of consumers and their proximity to biofilms may also affect the spatial scale at which consumers influence nutrient resupply rates and ratios in streams. For example, meiofauna (such as early instar chironomids) that forage within biofilms (below the boundary layer) will likely have different effects on dissolved N:P ratios in streams than larger consumers such as snails that forage in biofilms but excrete nutrients outside of the boundary layer. Nutrients released by an early instar chironomid in a thick biofilm will likely not travel far in the stream because of diffusional constraints in boundary layers (Riber and Wetzel 1987). Snails are large relative to the depth of an average biofilm, so nutrients released by these consumers may immediately be advectively transported in stream currents outside of the biofilm. Therefore, cycling of N and P by large primary consumers will likely operate at a much different spatial scale than cycling by small consumers in streams.

Elemental imbalances can also affect growth dynamics in benthic consumers. For example, differences in the elemental ratios of benthic food sources and primary consumers can affect consumer growth rates in streams. Söderström (1988) found that mayfly growth and development was sensitive to C:N ratios in their detrital food. Stelzer and Lamberti (2002) found that growth rates of *Elimia* snails were limited by P when snails were offered low quantities of pe-

riphyton. However, it remains unclear how widespread such effects on consumer growth and reproduction are in streams, and what environmental factors increase their likelihood and magnitude.

Changes in the elemental composition of allochthonous detritus in stream food webs could affect its decomposition rate and quality for macroconsumers. For example, Rier et al. (2002) found that senesced aspen leaves with increased C:N ratio and lignin content (grown on elevated CO<sub>2</sub>) placed in a forest stream were associated with decreased community respiration and microbial biomass but not lower rates of microbial production. Among leaves grown on elevated CO<sub>2</sub>, fungal biomass was negatively correlated with leaf C:N ratio. In a related study, Tuchman et al. (2002) found that *Tipula* larvae fed senesced microbially colonized leaves with increased C:N ratio and lignin had lower growth and consumption rates and reduced conversion efficiency than larvae offered higher-quality leaves. This work may have broad applicability for the metabolism and trophic transfer efficiency of POM entering aquatic systems in an era when atmospheric CO<sub>2</sub> is increasing globally. Stoichiometric models of trophic dynamics (e.g., Andersen 1997) incorporate such effects and, when modified to meet the particular situations found in the benthos, may help in predicting possible impacts of global change on stream food webs.

#### *Stoichiometry in lake littoral zones*

In this section, we apply ecological stoichiometry to a series of case studies relevant to littoral zones and their role in lake ecosystem function. First, we examine why C:x ratios vary in aquatic macrophytes and how such variation may affect the movement of nutrients into and out of littoral zones. We next consider how light and nutrients (DIC, P) may affect the elemental composition of littoral-zone biofilms. We then address how detritivorous fish and zebra mussels influence pelagic nutrient dynamics.

Aquatic plants are often the dominant component of organic matter pools in littoral zones of temperate lake ecosystems (Wetzel 1979). These aquatic producers transport large amounts of P from the sediments into their tissues during the summer growing season (Barko and Smart 1980, Rattray et al. 1991). It appears that little of this transported P is released from

living shoots (Graneli and Solander 1988), but rather most P-release from aquatic plants occurs during decomposition (Carpenter and Lodge 1986). Consequently, the role of macrophytes in lake nutrient dynamics appears controlled by factors that affect the transport of P from sediments into plant tissues and its subsequent release from dead plant matter.

From a stoichiometric perspective, plant C:P ratios should reflect the balance between demands by plant growth and P supply rates from sediments and surrounding water. When P supply is low (low-P sediments and/or water), growth demands for P are likely to exceed the amount that can be acquired by the plant. The results of high demand relative to supply are nutrient-limited growth rates and high C:P ratios in plant material (Sterner and Elser 2002). Conversely, when P supply increases (P-rich sediments or water) and/or growth demands slow, either from low light or limited C availability (Madsen and Sand-Jensen 1994), tissue C:P ratios decrease (Titus and Andorfer 1996). For submersed macrophytes, C:P ratios in biomass thus appear to vary as acquisition of C relative to P changes under different environmental conditions.

Variation in the C:x ratios in macrophytes likely affects the rate of bacterial release of CO<sub>2</sub> and dissolved nutrients from dead plant matter (Carpenter and Lodge 1986). As discussed above, when plant detritus is deficient in materials necessary for bacterial growth, rates of decomposition decrease (Graneli and Solander 1988, Enriquez et al. 1993). Reduced rates of bacterial degradation of plant detritus means that more plant matter will be buried in littoral sediments and that there is less net nutrient mineralization. In fact, nutrient-deficient plant detritus can act as a nutrient sink over time (Graneli and Solander 1988), presumably because of the uptake of dissolved nutrients by bacteria degrading C-rich and nutrient-poor plant material. Nutrient ratios released from lake sediments are thus controlled, in part, by a complex feedback involving factors that affect the ratio of nutrient uptake by aquatic plants and, in turn, the ratio of elements that are released from dead and decomposing plant matter.

C:N:P ratios in benthic algal communities in littoral zones may be controlled by low supply rates of DIC relative to other elements (Hecky

and Hesslein 1995). The frequent limitation of benthic algal photosynthesis by inorganic C in lakes (Fairchild and Everett 1988, Fairchild and Sherman 1992) may be caused by slow diffusion of CO<sub>2</sub> through excessively thick boundary layers (Turner et al. 1994, Hecky and Hesslein 1995). However, even in softwater lakes with low DIC concentrations, high ratios of DIC:P supply can lead to P-limited algal growth and high C:x ratios in benthic POM (Frost and Elser 2002b). Consequently, an understanding of how boundary layers affect C:x ratios in benthic algae requires knowledge of how the supply of DIC is changed by this physical barrier relative to multiple other elements.

Elemental imbalances between consumers and food can also affect the connections between benthic and pelagic habitats in lakes. Detritivorous fish, which feed on benthic organic material and excrete nutrients in pelagic areas (Vanni 1996, Schaus et al. 1997), represent one example of a link between these subsystems. Rates and elemental ratios of excretion by fish vary widely but the cause of such variation appears related to stoichiometric factors (Schaus et al. 1997, Vanni et al. 2002). For example, in a study of an Ohio reservoir, the N:P ratio in the body of gizzard shad was ~6 (but varied slightly with body size), whereas waste N:P ratios varied between 3.8 and 38 (Schaus et al. 1997). As for other consumers, variable excretion ratios by detritivorous fish should reflect the difference between the supply of elements in detrital food and the fish's requirements for growth and maintenance (Vanni 1996). A mass balance model (Vanni 1996) illustrated how nutrient excretion rates and ratios reflect the difference between the elements required for detritivorous fish maintenance and growth and those provided in their food. In this model, a change in detrital food N:P ratios from ~4 to ~30 would increase N:P ratios in the waste released by detritivores from <5 to >140. This amplification of N:P ratios because of consumer processing is one of the hallmarks of homeostatic nutrient regulation (Sterner 1990), and has been well-documented for zooplankton (Elser and Urabe 1999). Consequently, to understand patterns of nutrient excretion by fish in benthic food webs, it is necessary to simultaneously examine food N:P ratios along with fish elemental demands (Vanni 1996, Schindler and Eby 1997, Sterner and George 2000).

Ecological stoichiometry has also been used to understand the role of zebra mussels in nutrient cycling in the western basin of Lake Erie (Arnott and Vanni 1996). Arnott and Vanni (1996) observed a strong effect of seston N:P ratios and mussel nutrient content on excreted N:P ratios (explaining 51% of the variability in N:P ratios of excretion by small mussels). Zebra mussels could, thereby, strongly affect epilimnetic dissolved N and P availability by returning to the water column a large portion of the nutrients that otherwise would have settled onto the lake bottom and been removed from pelagic circulation (Heath et al. 1995, Arnott and Vanni 1996). Further, such return of nutrients is controlled by zebra mussels that appear to sequester N more rapidly than P. Given the relatively low N:P ratios (<15) excreted by zebra mussel (Arnott and Vanni 1996), grazing activities of zebra mussels may substantially alter pelagic N:P ratios and even promote increased prevalence of undesirable cyanobacteria that tend to dominate systems with low N:P supply ratios (<16; Smith 1983).

The use of ecological stoichiometry to study lake and stream benthos has only just begun. The first steps in this process are to recognize the potential value of this approach and to start obtaining the basic data on the elemental composition of important organisms and components of their benthic environment. For example, how much do benthic POM and aquatic plants vary in elemental composition? How does the C:N:P stoichiometry of these organic matter sources compare to the needs of consumers and microbes? These descriptive studies will provide a further basis for research aimed at understanding the causes and consequences of observed patterns in benthic C:N:P stoichiometry and thus improve our knowledge of benthic subsystems and their role in lotic and lentic environments.

### Conclusions and Future Research Directions

We have highlighted phenomena associated with food quality and consumer-driven nutrient cycling that have been the primary foci to date in ecological stoichiometry. However, all predator-prey interactions are governed by the law of mass conservation and can be examined with a stoichiometric framework (Elser et al. 1996). Predator and prey, under these circumstances,

could be any consumer (from viruses and bacteria to top predators) and any resource used by these heterotrophs. Thus, ecological stoichiometry holds great promise to improve our understanding of a variety of trophic interactions in benthic ecosystems. This promise will only be realized by increasing the number and types of stoichiometric studies of benthic environments.

The first research priority for benthic stoichiometric analysis is simply to determine the elemental composition of a wide variety of benthic organisms in diverse taxonomic and functional groups. Without such descriptive studies, research examining the causes and consequences of elemental imbalances would likely be misguided and poorly focused. Although it is clear that autotrophic C:N:P ratios vary considerably among and within ecosystems, the data for benthic autotrophic biomass in freshwater systems remain generally sparse (Kahlert 1998, Francoeur et al. 1999, Frost and Elser 2002b). Patterns of elemental composition in benthic consumers are also poorly described. How much inter- and intraspecific variation is found in benthic consumers? How does this variation change with respect to life-history stage or strategies? For example, how do aquatic insects vary in C:N:P content compared to other benthic consumers, such as fish, mollusks, and crustaceans? Algivorous and detritivorous fish, with P-rich bones, appear to have lower C:P and N:P ratios in their bodies compared to other benthic taxa (Schindler and Eby 1997, Vanni et al. 2002) and may experience acute elemental imbalances when feeding on P-limited algae or nutrient-poor detritus. Research is needed to assess patterns of elemental composition within and among benthic taxa found across a diverse array of environmental conditions.

Emerging from these descriptive studies of benthic autotrophs and consumers will be questions related to the causes of variation in the elemental composition of organisms. One approach follows the line of reasoning that an organism's biochemical makeup translates into its elemental composition (Vollenweider 1985, Elser et al. 1996, Kilham et al. 1997). For example, changes in the P content of zooplankton appear strongly linked to the amount of ribosomal RNA because other significant pools of P (DNA, phospholipids, ATP) are either relatively small or constant in animal body tissue (Elser et al. 1996, Dobberfuhl 1999). Benthic studies will

benefit by examining interactions among organismal genetics, biochemistry, and stoichiometric requirements because these interactions provide the basis for complementary physiological, ecological, and evolutionary hypotheses (Elser et al. 2000b).

Ecological hypotheses addressing patterns of variation in C:N:P ratios in food webs may be most productive if they center on the effects of diverse environmental factors on the relative rates of C and nutrient acquisition by producers and consumers. For example, several hypotheses for variable C:N:P ratios in benthic autotrophs could be examined: 1) the light:nutrient hypothesis, in which differences in C acquisition from photosynthesis and N or P uptake result under different light:nutrient conditions, and thus affect autotroph C:N:P stoichiometry (Sterner et al. 1997, Frost and Elser 2002b), 2) an ultraviolet (UV)-impact hypothesis, in which UV alters aspects of growth, nutrient uptake, and elemental ratios in autotrophic communities (Hessen et al. 1997, McNamara and Hill 2000, Xenopoulos et al. 2002), 3) a temperature hypothesis, in which water temperature affects the relative pool sizes of algal cellular constituents and alters C:N:P ratios of these autotrophs (Rhee and Gotham 1981), and 4) a grazer hypothesis, in which consumers alter the total supply and ratios of elements available for autotrophic uptake, and thereby change their C:N:P ratios (Hillebrand and Kahlert 2001, Frost et al. 2002).

Stoichiometric theory also provides a framework for hypothesis generation to guide future studies of benthic ecological processes such as secondary production and nutrient recycling. For example, does poor stoichiometric food quality (insufficient N or P content) constrain consumer growth rates in the benthos? Does variation in consumer nutrient content itself influence how different consumers perform on a given food? Does consumer-driven nutrient recycling feedback on stoichiometric food quality affect trophic dynamics? These questions have been addressed in planktonic studies with experiments that supplement food resources with particular elements (Rothaupt 1995, Urabe et al. 1997, 2002a, b, Elser et al. 2001) and similar designs could be used in benthic studies. Hypotheses invoking stoichiometric food quality to explain patterns of species composition in benthic invertebrate communities should also be tested. For example, previous work in pelagic systems

demonstrated a strong relationship between seston C:P ratios and the relative abundance of P-rich *Daphnia* and P-poor *Bosmina* (DeMott and Gulati 1999). Are there similar patterns of consumer community structure in benthic systems that are driven by stoichiometric food quality?

The benthic ecologist hoping to address such stoichiometric questions in streams and/or littoral zones will face considerable methodological challenges. Similar to the pelagic ecologist studying seston stoichiometry, one challenge for benthic ecologists will be to quantify elements in the different components of benthic POM. Improving techniques in advanced microscopy (Lawrence et al. 1998) and X-ray microanalysis (Heldal 1993, Norland et al. 1995) may allow better quantification of benthic algal, microbial, and detrital components and their C:N:P ratios. Centrifugation techniques have proved useful in separating algal and detrital fractions in bulk benthic POM (Hamilton and Lewis 1992). Use of multiple radioactive and stable isotope tracers simultaneously would also help elucidate the rates and ratios of elemental flows among POM components, their consumers, and surrounding waters. Regardless of our ability to characterize C:N:P ratios in the benthos, ecological stoichiometry is, in itself, a method of thinking that helps develop an integrative scientific approach based on first principles, and thus should prove to be a useful tool for benthic ecologists (Elser 2000).

Our paper has examined the basis for and potential applications of ecological stoichiometry to benthic ecosystems. We hope that this treatment will lead to more detailed stoichiometric analyses of benthic organisms relative to their lake and stream environments, and in turn a better understanding of benthic ecosystems. Single-factor frameworks (based on energetics or single elements alone) may have limited additional value in the quest to improve our understanding of Earth's ecosystems in general (Reiners 1986, Elser et al. 1996, Hessen 1997, Elser and Urabe 1999) and, we would argue, of benthic environments as well. Ecological stoichiometry permits a deeper integration of the activities of benthic organisms with multiple factors in their environment while connecting those ecological interactions to fundamental biological mechanisms. Ecological stoichiometry thereby offers an important new framework for theory and hypothesis generation as we seek

better explanations for patterns and processes in benthic ecosystems.

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