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Ecological stoichiometry in freshwater benthic ecosystems: an introduction

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SUMMARY

1. Ecological stoichiometry is a conceptual framework that considers how the balance of energy and elements affects and is affected by organisms in the environment. This perspective has seen recent development primarily in marine and freshwater pelagic ecosystems but its widescale application to freshwater benthic ecosystems remains limited.
2. This paper briefly introduces the concept of ecological stoichiometry, its potential application to freshwater benthic ecosystems, and it provides an overview of a series of papers that use a stoichiometric approach to illustrate the utility of this concept for studying a range of central questions about benthic ecosystems.
3. Papers in this issue include a detailed description of the elemental composition of stream benthic invertebrates, an analysis of the algal content of and its effects on C : P stoichiometry of periphyton, two reports exploring the stoichiometry of stromatolites and their snail consumers in a stream fed by thermal springs, an examination of the stoichiometric effects on stream periphyton and macroinvertebrates of slight nutrient enrichment resulting from treated sewage effluents, a study of nutrient release ratios and their control from crayfish and snails, a paper addressing the stoichiometric effects on fish and plankton that result from benthic food subsidies to fish, a study of the stoichiometry of tree leaves and litter and floodplain arthropods in the riparian zone of the Rio Grande, and a synthesis examining the current state and future potential of benthic stoichiometry.
4. The insights from these and other studies suggest that ecological stoichiometry has great potential to guide scientific thought and resolve long-standing problems in ecology. Increasing use of this stoichiometric perspective should thus lead to a deeper understanding of important ecological processes in freshwater benthic ecosystems.

Keywords: benthos, detritus, ecological stoichiometry, macroinvertebrates, periphyton.

Introduction

Ecological stoichiometry is based on the idea that the ratios of elements available to organisms affect their transformations in ecosystems (Frost *et al*., 2002; Sterner & Elser, 2002). Using this rationale, ecological stoichiometry is primarily focused on two questions: (i) what are the causes of variable ratios of carbon (C) to nutrients within and among organisms, and (ii) what are the consequences of mismatches between C : nutrient ratios of consumers and their food resources? The application of this framework to ecological questions is growing rapidly, with studies emerging from an array of ecosystems and a diverse assemblage of organisms (Sterner & Elser, 2002).

Given its apparent wide applicability and ability to generate novel explanations of observed ecological patterns, there have been calls to apply ecological stoichiometry to studies of ecological processes in benthic ecosystems (Steinman, 1996; Elser & Urabe,

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1999; Frost *et al.*, 2002; Sterner & Elser, 2002). Therefore, a special session on this topic was organised at the annual meeting of the North American Benthological Society in June 2003 in Athens, Georgia, U.S.A. It brought together research on ecological stoichiometry in a variety of lake and river ecosystems and was the impetus for the compilation of this special issue on benthic stoichiometry. What follows is a brief summary of key results from the papers selected for publication in this issue.

Overview of the papers in this special issue

Information on the elemental composition of consumers is a prerequisite for identifying elemental imbalances in food webs and for predicting their effects on key ecosystem processes (e.g. processes involved in nutrient cycling). Evans-White, Stelzer & Lamberti (2005) report on broad taxonomic and regional patterns in elemental composition of benthic macroinvertebrates and food resources in 35 Midwestern US streams. Results from this study underscore the importance of phylogeny (as opposed to stream location or trophic status) in determining stream invertebrate elemental content. Consistent differences were found in the carbon : nitrogen (C : N) and carbon : phosphorus (C : P) ratios among insects, molluscs, and crustaceans, regardless of stream identity. These data suggest that the relative dominance of broad taxonomic groups (e.g. crustaceans versus insects) may have a prominent influence on stream nutrient dynamics and trophic interactions.

Many studies of periphyton implicitly assume a relatively large contribution of algae to the complex mixture of organic matter that periphyton constitutes (Lock, 1993). In contrast to this assumption, Frost, Hillebrand & Kahlert (2005) report data suggesting relatively small contributions of algal biomass to periphyton and the resulting effects on periphyton C : P stoichiometry. Algae constituted, on average, only 8% of total organic C in samples collected from artificial substrates exposed in lakes and coastal areas in Canada, Hungary and Sweden. In addition, the average C : chlorophyll *a* ratio of natural periphyton was 450, which is well above values typically seen in pure algal cultures (20–200; Healey & Hendzel, 1979). A simple model delineated the effects of changing algal prevalence and elemental composition on the C : P stoichiometry of the periphyton. Even under conditions of low algal prevalence (5–10%), increasing algal C : P ratios could result in higher periphyton C : P ratios. Consequently, low prevalence does not preclude algae from altering the C : P ratios in periphyton.

Imbalanced consumer-resource nutrient ratios are likely to impose constraints on the growth and reproduction of heterotrophic organisms such as benthic invertebrates (Frost *et al.*, 2002). Benthic communities that are characterised by extremely low nutrient supply rates can provide the clearest examples of elemental constraints. The stromatolitic oncolites (i.e. mineralised microbial mats) and snails that graze on them in the Cuatro Ciénagas basin in north-eastern Mexico are one such community. Elser and colleagues report on this fascinating ecosystem in two papers in this issue. In the first paper, Elser *et al.* (2005a) describe the results of a factorial enclosure experiment in which P concentration and grazing by snails were manipulated and responses of the oncolites (organic matter content, nutrient ratios, metabolism, and microbial community structure) determined after an incubation period of 7 weeks. Grazing by snails had no effect on any response variable. Phosphorus enrichment, however, had strong effects on the nutrient ratios of surface layers, metabolic activity and algal community structure of the oncolites.

In a companion study, Elser *et al.* (2005b) examined the response of grazing snails to P-enrichment of the stromatolitic microbial communities. Results from two separate field experiments provide key insights into the optimal resource conditions (i.e. C : P ratio) for snail growth and survivorship. C : P ratios at the extremes (high and low) caused slower growth and higher mortality of snails. These results led Elser *et al.* (2005b) to suggest that snails exist on a 'stoichiometric knife edge', whereby intermediate C : P ratios of food are optimal and nutritional shifts in either direction reduce the growth and survivorship of snails. This concept of stoichiometric resource optima predicts that primary consumers may respond positively or negatively to low C : nutrient ratios in food resources depending upon the elemental requirements of the consumers and their physiological responses (e.g. ingestion and assimilation) to increases in food nutrient concentrations.

Human alteration of the landscape is influencing the amounts and ratios of essential elements available in freshwater ecosystems. Such changes may have profound consequences on stoichiometry of benthic communities. Bowman, Chambers & Schindler (2005) examine how elemental imbalances between consumer and food are altered by slightly elevated P inputs from treated municipal sewage effluents to rivers in the Canadian Rocky Mountains. Upstream of sewage treatment plants, food resources were found to have very high C : N and C : P ratios compared with their primary consumer, mayflies. These imbalances were reduced below sewage treatment plants, which discharge significant quantities of N and P into these rivers. As a result of the reduced elemental imbalances, a different assemblage of primary consumers was present at significantly higher biomass downstream (Bowman *et al.*, 2005). In addition, mayfly N : P recycling ratios calculated with a mass balance model were higher than periphyton N : P ratios only at sites upstream of sewage treatment plants, suggesting a reduction in P-limitation of consumers downstream. These results indicate that human modification of nutrient inputs into aquatic ecosystems can alter the stoichiometric relationships between consumer and food with consequent effects on food-web structure and function.

Consumer-driven nutrient recycling has been a fruitful field of research in pelagic freshwater systems (e.g. Elser & Urabe, 1999), but the role of excretion by consumers has not been widely studied in the benthos. While some data on nutrient content and ratios of excretion products have recently become available (Vanni, 2002), research on the consequences of consumer-driven nutrient recycling for benthic ecosystems is rare. In this issue, Evans-White & Lamberti (2005) report results from a laboratory study of two grazing consumers (a crayfish and a pleurocerid snail) that differ in body nutrient composition. Excretion N : P ratios, soluble reactive P concentrations and epilithon N concentration were related to body N : P ratio of the consumers, as predicted by ecological stoichiometry theory. These results indicate a potential role for consumer-driven nutrient recycling in the modification of dissolved nutrient concentrations and ratios in natural streams. Consequently, excretion may influence benthic algal nutrient content and ratios, as well as the type and degree of nutrient limitation of primary production. Clearly, these types of relationships can precipitate feedback interactions between algal resources and consumers. Further investigations into the role of consumer-driven nutrient recycling, including the potential importance of these feedbacks, represent a rich avenue for future benthic research.

Consumer-driven nutrient recycling also provides a framework for studying one aspect of benthic-pelagic coupling in lakes: the movement of nutrients from benthic to pelagic habitats mediated by fish excretion. Glaholt & Vanni (2005) describe laboratory and mesocosm experiments in which the consumption rate of a benthic fish species was manipulated in order to assess effects on body nutrient composition, excretion rates and ratios, plankton community dynamics, and nutrient flux between pelagic and benthic habitats. They found that the body nutrient composition of fish was not homeostatic: N : P ratio of fish bodies increased with consumption rate and was positively related to the excretion N : P ratio. In general, excretion rates (especially those of N) increased with consumption rate. Only weak effects of consumption rate on phytoplankton biomass and community structure were observed, although total algal biomass and nutrient fluxes to sediments responded positively. These data show that excretion can affect benthic-pelagic nutrient fluxes and pose important questions about the role of variable consumption in controlling body nutrient composition and excretion nutrient ratios.

The flooding of rivers and streams as well as subsurface hydrological connections can be important pathways of riverine nutrient inputs into riparian zones and river flood plains. The effects of these nutrient subsidies on the stoichiometry of food webs in the periodically inundated zones have received little previous attention. Tibbetts & Molles (2005) present a stoichiometric study of the riparian zone of the Rio Grande. In particular, they examine the elemental composition of live vegetation, plant litter and detritivore consumers at sites along the Middle Rio Grande that are characterised by the presence or absence of recent flooding. They found significant between-site differences in the elemental composition of vegetation, which were partly attributed to flooding history. One non-flooded site had an elevated N concentration in cottonwood leaves that was likely to be because of wastewater effluent upstream. Non-native vegetation, saltcedar (*Tamarix chinensis* Lour.) and Russian olive (*Elaeagnus angustifolia* L.), had higher mean leaf N concentrations and lower C : N ratios compared with native cottonwood [*Populus deltoides* ssp. *wislizenii* (S.Wats.) Eckenwalder]. Detritivores were much richer in N and P than litter at all sites, indicating that elemental imbalances may be a common feature of detritus-based food webs in riparian zones. Differences in the elemental composition of riparian plant litter and its consumers are likely to have strong effects on rates of litter decomposition, ratios of nutrients recycled by consumers and trophic interactions in these food webs.

In the final contribution of this issue, Cross *et al.* (2005) provide a brief synthesis of ecological stoichiometry as it has been applied to freshwater benthic ecosystems. Four primary questions are addressed: (i) what are the patterns and likely causes of variation in elemental content among benthic resources and consumers, (ii) how can benthic consumers influence the stoichiometry of dissolved nutrients and basal resources, (iii) how has ecological stoichiometry aided our understanding of organic matter transformations, and (iv) how can ecological stoichiometry be incorporated into studies of stream biogeochemistry? The synthesis shows that benthic ecology has been enriched by the application of stoichiometric perspectives to a number of important topics including grazer-periphyton interactions, consumer-driven nutrient recycling, leaf litter breakdown, and multi-element nutrient spiralling in streams. Exciting questions are generated by recent stoichiometric studies, which should lead to future tests of hypotheses relating to ecological stoichiometry in a range of benthic ecosystems.

All of the studies presented in this special issue use a stoichiometric perspective to examine key aspects of the dynamics in benthic food webs. In many cases, the insights generated by these stoichiometric investigations would not have resulted from a single-element focus. It is our hope that bringing these studies together will initiate future research aimed at increasing our mechanistic understanding of the elemental dynamics of food webs in freshwater benthic ecosystems.

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