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Ecological stoichiometry in freshwater benthic systems: recent progress and perspectives

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SUMMARY

1. Ecological stoichiometry deals with the mass balance of multiple key elements [e.g. carbon (C), nitrogen (N), phosphorus (P)] in ecological systems. This conceptual framework, largely developed in the pelagic zone of lakes, has been successfully applied to topics ranging from population dynamics to biogeochemical cycling. More recently, an explicit stoichiometric approach has also been used in many other environments, including freshwater benthic ecosystems.

2. Description of elemental patterns among benthic resources and consumers provides a useful starting point for understanding causes of variation and stoichiometric imbalance in feeding interactions. Although there is considerable overlap among categories, terrestrially-derived resources, such as wood, leaf litter and green leaves have substantially higher C : nutrient ratios than other resources of both terrestrial and aquatic origin, such as periphyton and fine particulate organic matter. The elemental composition of these resources for benthic consumers is modulated by a range of factors and processes, including nutrient availability and ratios, particle size and microbial colonisation.

3. Among consumers in benthic systems, bacteria are the most nutrient-rich, followed (in descending order) by fishes, invertebrate predators, invertebrate primary consumers, and fungi. Differences in consumer C : nutrient ratios appear to be related to broad-scale phylogenetic differences which determine body size, growth rate and resource allocation to structural body constituents (e.g. P-rich bone).

4. Benthic consumers can influence the stoichiometry of dissolved nutrients and basal resources in multiple ways. Direct consumption alters the stoichiometry of food resources by increasing nutrient availability (e.g. reduced boundary layer thickness on substrata) or through removal of nutrient-rich patches (e.g. selective feeding on fungal patches within leaf litter). In addition, consumers alter the stoichiometry of resources and dissolved nutrient pools through the return of egested or excreted nutrients. In some cases, consumer excretion supplies a large proportion of the nutrients required by algae and heterotrophic microbes and alters elemental ratios of dissolved nutrient pools.

5. Organic matter decomposition in benthic systems is accompanied by significant changes in the elemental composition of organic matter. Microbial colonisation of leaf litter influences C : nutrient ratios, and patterns of microbial succession (e.g. fungi followed by bacteria) may be under some degree of stoichiometric control. Large elemental imbalances

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exist between particulate organic matter and detritivores, which is likely to constrain growth rates and invertebrate secondary production. Such imbalances may therefore select for behavioural and other strategies for dealing with them. Comminution of large particles by benthic consumers alters detrital C : nutrient ratios and can influence the stoichiometry of elemental export from whole catchments.

6. A stoichiometric framework is likely to advance understanding of biogeochemical cycling in benthic ecosystems. A set of scenarios is developed that explores the influence of microbial elemental composition on nutrient spiralling parameters in streams, such as uptake length and uptake rate ratios. The presented hypothetical examples identify when the elemental composition of benthic stream organisms is likely to predict nutrient uptake ratios and conditions that would cause benthic stoichiometry and nutrient uptake from the water column to become uncoupled.

Keywords: biogeochemistry, detritus, ecological stoichiometry, food webs, rivers, streams

Introduction

Explicit consideration of the combined dynamics of key elements such as carbon (C), nitrogen (N) and phosphorus (P) has increased mechanistic understanding of diverse ecological topics, including trophic interactions (e.g. Elser *et al.*, 1998; Sterner *et al.*, 1998), nutrient cycling (e.g. Elser & Urabe, 1999; Vanni, 2002), population dynamics (e.g. Schade *et al.*, 2003; Andersen, Elser & Hessen, 2004; Moe *et al.*, 2005), and the role of species in ecosystems (e.g. Vanni *et al.*, 2002). Such progress stems, in part, from the elegance of ecological stoichiometric theory, which strives to crystallise complex dynamics into tractable mass balance relationships in ecological interactions. A major strength of the stoichiometric approach lies in its ability to transcend multiple levels of organisation by linking, for example, the biochemical makeup (and genetic structure) of individual organisms to ecosystem dynamics (e.g. Elser *et al.*, 1996, 2000b). As a consequence, ecological stoichiometry provides a framework facilitating integration across various levels of ecological organisation and of different ecological perspectives.

Although early development of stoichiometric theory can be traced to research conducted in many types of ecosystems (e.g. Lotka, 1925; Redfield, 1958; Tilman, 1982; Reiners, 1986, 1992), the most comprehensive studies of ecological stoichiometry have been conducted in freshwater pelagic ecosystems (Sterner & Elser, 2002). More recently, considerable progress has been made in understanding the causes and consequences of stoichiometric patterns in freshwater benthic systems (see Frost *et al.*, 2002b; this special issue). As these benthic studies begin to increase in number, synthesis of progress made and suggestions for future research will be helpful for focusing efforts on rewarding lines of ecological inquiry.

Freshwater benthic habitats (i.e. bottom surfaces of lakes, streams and wetlands) are an integral component of freshwater ecosystems and often form the basis for diverse and productive food webs (Covich, Palmer & Crowl, 1999; Vadeboncoeur, Vander Zanden & Lodge, 2002). Benthic environments can also be important sites for the uptake, transformation, and recycling of essential elements (i.e. C, N and P), and contribute significantly to ecosystem functions, such as nutrient cycling and whole-ecosystem metabolism (e.g. Stream Solute Workshop, 1990). As such, these systems offer a valuable context for testing, applying and expanding principles of ecological stoichiometry.

In this paper, our goal is to provide a brief synthesis of research dealing with ecological stoichiometry in freshwater benthic systems. Rather than reviewing all literature on this topic, our intent is to use current examples from the literature (including this special issue) to (i) highlight studies that have used a stoichiometric approach for understanding the ecological dynamics of benthic systems, (ii) elucidate the potential contributions of these studies to the general advancement of ecological stoichiometry, and (iii) offer suggestions for future lines of stoichiometric inquiry that may advance understanding of benthic populations, communities and ecosystems. We start by examining general patterns and likely causes of elemental variability among benthic resources and consumers. Next, we discuss how consumers may influence the stoichiometry of dissolved nutrients and basal resources, and then examine the stoichiometry of organic matter dynamics. Lastly, we explore ideas that relate ecological stoichiometry and biogeochemical cycling in streams.

Elemental patterns of resources and consumers

Ecological stoichiometry seeks to understand how differences (and similarities) between the elemental composition of food and the elemental requirements of consumers affect key processes in ecosystems (Sterner & Elser, 2002). A necessary first step is the description of variability in elemental composition at all levels of the food web and of the mineral resources. Also important are investigations that simultaneously examine the elemental composition of resources and the elemental requirements of consumers to assess the potential degree of elemental imbalance between the two (Elser *et al.*, 2000a; Frost *et al.*, 2002b). Severe consumer-resource imbalances may strongly affect the structure of food webs and constrain or alter key ecosystem processes.

Food resources

One primary food resource for many benthic consumers is organic matter attached to hard substrata. This resource may include varying amounts of algae, bacteria, fungi, the exopolymeric substances they exude, other non-living particulate organic matter, protozoa, and small metazoa. Hereafter, we will use the term 'periphyton' to refer to this organic matter on benthic surfaces. The C : N and C : P ratios of periphyton vary considerably in lakes (Fig. 1, Kahlert,

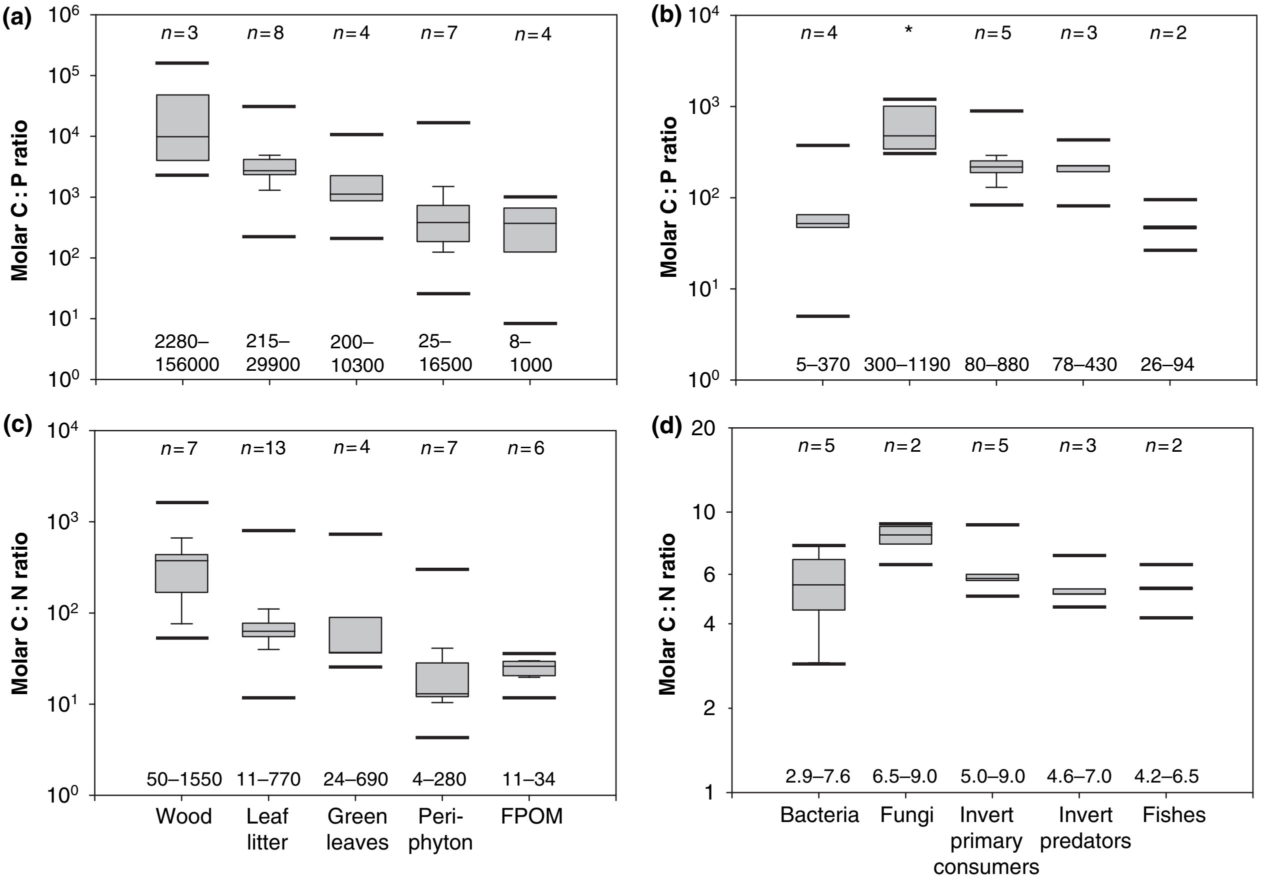

Fig. 1 Box plots of molar C : P (a,b) and C : N (c,d) ratios (median, 10th, 25th, 75th and 90th percentiles) for common freshwater benthic resources and consumers. Plots are based on multiple average values collected from 49 literature sources (sources and data are available from the lead author). Bold horizontal bars and numbers below each Box plot represent the total range of individual reported values (as opposed to mean values). *Based on ranges reported in Sterner & Elser (2002). Note difference in scale of panels.

1998, 2002; Frost & Elser, 2002a) and streams (e.g. Stelzer & Lamberti, 2001; Bowman, Chambers & Schindler, 2005). Two mechanisms may cause this variation: (i) differences in the composition of bulk periphtyon in terms of types and biomass of organisms present and amounts of non-living organic matter, and (ii) physiological processes of organisms residing in the periphyton. It appears that the first mechanism, proportional changes in type of organic material of differing elemental composition, can cause differences in periphyton C : N and C : P ratios (Frost, Elser & Turner, 2002a; Frost, Hillebrand & Kahlert 2005b). In fact, C : nutrient ratios of periphyton can be quite sensitive to changes in algal and/or bacterial biomass even if these constituents make up a relatively minor component of the periphyton (Frost *et al.*, 2005b). Empirical support for this hypothesis remains largely circumstantial due, in part, to the difficulty of quantifying the relative contributions and chemical composition of algae, bacteria, other microorganisms, and non-living organic matter in periphyton. Use of confocal laser scanning microscopy (e.g. Lawrence, Neu & Swerhone, 1998) and X-ray micro-analysis (e.g. Fagerbakke, Heldal & Norland, 1996) show promise for alleviating some of these methodological difficulties. Future efforts using such techniques will aid in quantifying the influence of periphyton composition on elemental content.

The second mechanism, changes to the nutrient content of periphytic algae, has been extensively examined in both lakes and streams by experimental manipulation of nutrient supply. Increasing supplies of inorganic N and P lowers C : N and C : P ratios in both stream and lake periphyton (Hillebrand & Kahlert, 2001, 2002; Stelzer & Lamberti, 2001; Frost & Elser, 2002a; Bowman *et al.*, 2005), including a modern stromatolitic community in a stream fed by thermal springs (Elser *et al.*, 2005a). While these studies implicate altered algal physiology as the reason for variable periphyton C : N : P ratios, other potential causes (i.e. nutrient adsorption and mineralisation during organic matter decomposition) cannot be precluded.

One key concept that invokes algal physiology to explain variation in periphyton C : N : P composition is the light : nutrient hypothesis (Sterner *et al.*, 1997). This hypothesis proposes that changes in the C : N and C : P ratios of primary producers reflects the balance of light and available nutrients. To date, little support has been found for this hypothesis in benthic ecosystems. For example, in littoral zones of lakes, experimentally reduced light intensities at set nutrient supply rates did not lower periphyton C : P ratios (Frost & Elser, 2002a; Huggins, Frenette & Arts, 2004) perhaps because these manipulations did not alter that balance of C and P acquisition by the benthic algae (but see Rosemond (1993) for an example of increased C : N ratios of periphyton in response to increased light). Given the current paucity of data, significant opportunity abounds for testing the light : nutrient hypothesis across a broad range of light and nutrient conditions in diverse benthic systems.

In addition to periphyton, many benthic consumers rely on allochthonous organic matter as a food source. In forested streams and wetlands, and in littoral zones of many lakes, a major proportion of this organic matter enters in the form of leaf litter (e.g. Webster *et al.*, 1999; Wetzel, 2001). C : nutrient ratios of leaf litter are usually high relative to those of benthic primary producers and bulk periphyton (Fig. 1; Enriquez, Duarte & Sand-Jensen, 1993; Findlay *et al.*, 2002; Cross *et al.*, 2003; Stelzer, Heffernan & Likens, 2003) and may confer strong growth and developmental constraints for leaf-eating detritivores (e.g. Iversen, 1974; Cross *et al.*, 2003). For example, growth rates and food conversion efficiencies of crane fly larvae were greatly reduced when fed leaf litter from trees exposed to a CO_2-enriched atmosphere, which resulted in a high C : N ratio of the litter (Tuchman *et al.*, 2002).

A substantial portion of the leaf litter that enters benthic systems is eventually broken down into fine organic particles (<1 mm in diameter). This fine particulate organic matter (FPOM), along with fine particles originating from autochthonous sources (i.e. periphyton, macrophytes), is an important food source for many benthic consumers in both lentic and lotic systems (e.g. Wallace & Webster, 1996). FPOM generally has higher nutrient content and lower C : nutrient ratios (Sinsabaugh & Linkins, 1990; Bonin, Griffiths & Caldwell, 2000; Cross *et al.*, 2003) in comparison with larger particles such as leaf litter or wood (Fig. 1; Findlay *et al.*, 2002; Cross *et al.*, 2003). In addition, C : nutrient ratios of particulate organic matter appears to decline consistently with decreasing particle size (Sinsabaugh & Linkins, 1990), which has been attributed to higher surface to volume ratios and thus a greater capacity for microbial nutrient immobilisation and adsorption (Sinsabaugh & Linkins, 1990). As an example, C : nutrient ratios of particulate organic matter in Appalachian headwater streams declined from approximately 4000 to 350 (C : P) and 70 to 25 (C : N) with a decline in particle size from >4 mm to <125 μm (Fig. 2). The magnitude of this decline was reduced under nutrient-enriched conditions (Fig. 2). Microbial mass-specific oxygen consumption has also been shown to increase with decreasing particle size (Sinsabaugh & Linkins, 1990; also see Peters, Benfield & Webster, 1989), suggesting that declines in C : nutrient ratios reflect increased microbial activity and potentially result in higher food quality for benthic consumers (e.g. Ward & Cummins, 1979). Because FPOM is a prominent component of most benthic systems (Ward *et al.*, 1994), additional research examining the causes and consequences of elemental and nutritional variation of FPOM should be a priority.

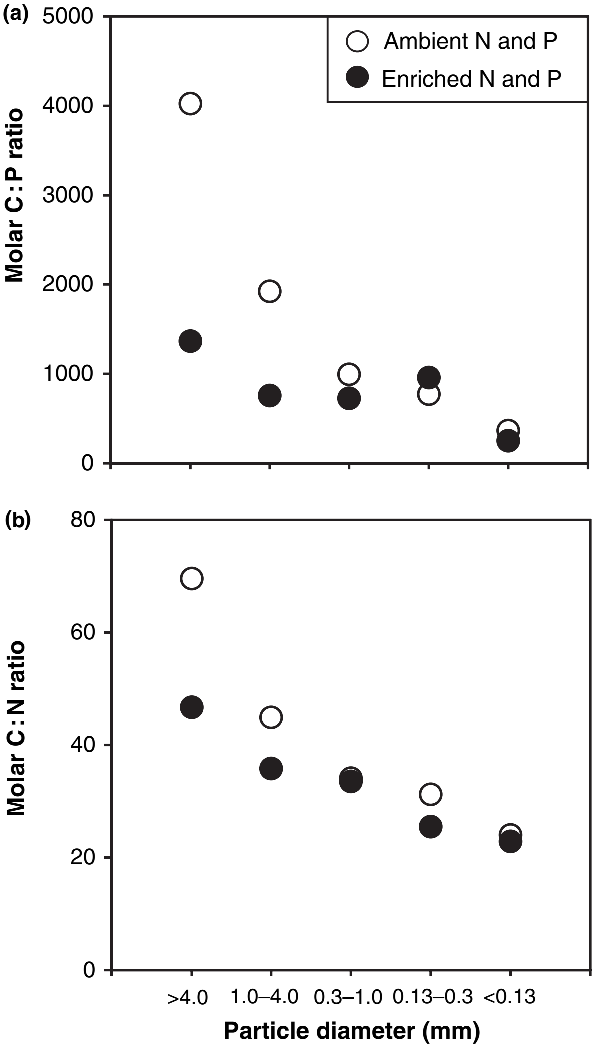

Fig. 2 Molar C : P (a) and C : N (b) ratios across a range of size classes of particulate organic matter (POM) in two Appalachian headwater streams at Coweeta Hydrologic Laboratory, NC, U.S.A. One stream had very low ambient N and P concentrations (average of 27 μg DIN L^{-1} and 4 μg SRP L^{-1}, respectively) and the other had been experimentally enriched with inorganic N and P (average of 414 μg DIN L^{-1} and 51 μg SRP L^{-1}, respectively) for 2 years (see Cross *et al.*, 2003). Composite bulk samples taken by hand and corer at multiple locations from the length of each stream were rinsed onto nested metal sieves. Each point represents a single subsample of these composites. Percent C, N, and P in each sample was quantified as in Cross *et al.* (2003).

Inputs of dissolved organic matter (DOM) can also be important (e.g. McDowell & Likens, 1988; Fiebig, 1995), and can strongly affect ecological processes in benthic ecosystems (Wetzel, 2001). Ratios of dissolved organic carbon (DOC) to total P or N can vary considerably among aquatic ecosystems and can influence the metabolism of heterotrophic microbial consumers (e.g. Cimbleris & Kalff, 1998; Wiegner & Seitzinger, 2004). Indeed, planktonic bacterial respiration (Smith & Prairie, 2004) and growth (Goldman & Dennett, 2000) has been linked to the DOC : nutrient ratios in the environment, suggesting that a stoichiometric perspective could also be useful to investigate the consequences of variable DOC : nutrient ratios on benthic microbes and their roles in ecosystems.

Consumers

Benthic consumers typically exhibit much less variation in elemental composition than the basal resources that they consume, such as periphyton or leaf litter (Fig. 1; Cross *et al.*, 2003; Frost *et al.*, 2003; Evans-White, Stelzer & Lamberti, 2005). In addition, benthic consumers often contain higher amounts of N and P (and consequently have lower C : P or C : N ratios) than their food resources (Fig. 1), suggesting that elemental imbalances between food resources and consumer requirements may be common in these systems (e.g. Liess & Hillebrand, 2005). The degree of elemental variability reported for freshwater benthic taxa is similar to that seen among pelagic zooplankton and terrestrial insects (Fagan *et al.*, 2002; Frost *et al.*, 2003; Evans-White *et al.*, 2005; Liess & Hillebrand, 2005). P content, as opposed to C or N content, is the dominant contributor to within- and among-taxon variability (Fig. 1; Cross *et al.*, 2003; Frost *et al.*, 2003; Evans-White *et al.*, 2005).

Based on the few studies examining community-wide patterns in benthic consumer elemental content, major differences among taxa appear to be related to broad-scale (i.e. class level or higher) phylogenetic patterns. For example, vertebrates contain much more P than invertebrates because of significant investment in P-rich bone tissue (Fig. 1; Sterner & George, 2000; Vanni *et al.*, 2002; Glaholt & Vanni, 2005). Among invertebrate taxa, crustaceans consistently exhibit higher P content (0.94%) and lower C (35%) and N (7.4%) content relative to both insects and mollusks (insects, P: 0.56%, C: 48%, N: 10%; mollusks, P: 0.81%, C: 42%, N: 9.6%, Evans-White *et al.*, 2005; also see Frost *et al.*, 2003). In addition, a number of studies have found that specific groups of aquatic insects (e.g. Coleoptera, Trichoptera) have particularly high C : P ratios relative to other groups (e.g. Cross *et al.*, 2003; Frost *et al.*, 2003; Evans-White *et al.*, 2005; Liess & Hillebrand, 2005). The causes of these differences are currently speculative, but it appears that phylogenetic constraints on the relative allocation of structural compounds (i.e. chitinous versus calcareous exoskeleton, bony skeleton) may play an important role in determining gross patterns of consumer elemental composition. Although not extensive, the studies available to date span relatively broad geographic regions and physicochemical conditions, suggesting that phylogeny, at least at the class level or higher, may be more important in determining consumer elemental composition than local environmental conditions or species composition within a higher taxonomic group.

When classifying benthic invertebrate consumers by functional characteristics, such as feeding mode (e.g. functional feeding groups; Cummins & Klug, 1979), predators have been shown to contain higher levels of N and P (Cross *et al.*, 2003; Evans-White *et al.*, 2005) than scrapers, shredders and collectors, which did not markedly differ form one another. For example, Cross *et al.* (2003) found that predators had 12–93% higher P contents and 7–16% higher N contents than other functional feeding groups. In addition, predatory dragonfly (Odonata) larvae in streams had significantly higher N content (11.2%) than their invertebrate prey (9.3%; Evans-White *et al.*, 2005). While reasons for this pattern are unclear, a number of alternative hypotheses prompted by similar observations in terrestrial food webs were presented by Fagan *et al.* (2002). These include the possibilities that predators have higher nutrient contents than their prey because (i) they have a nutrient-rich diet (i.e. prey) and their body nutrient contents are not strictly homeostatic or (ii) they have evolved a higher allocation to nutrient-rich body constituents (e.g. N-rich muscle tissue) because of greater supply of nutrients in their diet. Testing these hypotheses in benthic aquatic systems represents a fertile area for future investigation.

Evidence from a wide range of aquatic and terrestrial taxa indicates that P content changes predictably with growth rate because of the P-rich ribosomal RNA required for protein synthesis (Main, Dobberfuhl & Elser, 1997; Elser *et al.*, 2003b; but see DeMott & Pape, 2005). Such linkages among RNA, P content and growth rates form the basis of the 'growth rate hypothesis' (Elser *et al.*, 2000b), which posits that variation in organism C : P ratios is caused by differential allocation of P-rich RNA required for protein synthesis (Elser *et al.*, 1996; Sterner & Elser, 2002). In support of this hypothesis, growth rates were strongly correlated with the RNA content of snails that inhabit modern stromatolites in a stream fed by thermal springs (Elser *et al.*, 2005b). Interestingly, in this case, snail growth rates and body P content were uncoupled, and this discrepancy was attributed to the potentially toxic effects of extremely high P content of food resources when P supply was experimentally increased (also see Plath & Boersma, 2001). Other explicit tests of the growth rate hypothesis in benthic systems are lacking. However, several studies have reported negative correlations between consumer body size and P content, which could be related to differences in growth rate given that small-bodied animals tend to grow faster (Cross *et al.*, 2003; Evans-White *et al.*, 2005; Liess & Hillebrand, 2005). Because information abounds on the life histories and growth rates of benthic consumers (particularly stream invertebrates; Huryn & Wallace, 2000), quantifying P and RNA content and relating it to the growth of these same consumers could provide a straightforward and informative test of the growth rate hypothesis.

Bulk estimates of consumer and resource C : N : P ratios are a useful starting point to assess the relevance of consumer and resource C : N : P ratios, but efforts should now be made to identify if, when and where nutrient limitation of consumers may occur. Strict elemental composition of consumers may not be representative of their elemental requirements *per se*. Benthic consumers exhibit a large range of physiological and behavioural strategies for food acquisition and assimilation (Frost *et al.*, 2005a). For example, some benthic taxa may selectively consume or assimilate microbial cells from bulk leaf litter (e.g. Arsuffi & Suberkropp, 1985; Perlmutter & Meyer, 1991; Suberkropp, 1992), or periphyton (e.g. Mulholland *et al.*, 2000a), rendering stoichiometric comparisons of consumers and bulk resources potentially misleading. In addition, some taxa, such as tipulid crane fly larvae, harbour specific digestive enzymes or endosymbionts which may aid in nutrient or carbon balance (e.g. Klug & Kotarski, 1980; Sinsabaugh, Linkins & Benfield, 1985). Cognisance of these behavioural and physiological factors, and quantification of their importance, will aid in advancing our understanding of the origins and consequences of consumer-resource elemental imbalances.

Consumer homeostasis

Ecological stoichiometry is largely concerned with understanding how insufficient supplies of particular elements affect physiological processes and how this translates into altered ecological processes (Frost *et al.*, 2005a). A cornerstone of this approach is understanding the relative demands for multiple elements by organisms for maintenance, growth and reproduction. Often the demands of consumers vary little (i.e. they are homeostatic) as the organism grows and responds to changing food conditions. Benthic invertebrate consumers as a whole appear to be relatively homeostatic (Stelzer & Lamberti, 2002; Cross *et al.*, 2003; Frost *et al.*, 2003; Bowman *et al.*, 2005; Evans-White *et al.*, 2005) across a broad range of food qualities and physicochemical environmental conditions. However, an increasing number of studies suggest that the elemental composition of certain benthic taxa may be relatively plastic (i.e. less homeostatic) in comparison with the well-studied pelagic zooplankton. For example, Cross *et al.* (2003) reported up to fourfold differences in C : P and N : P ratios among stream insects (primarily Trichoptera), even when size and species identity was controlled for, in a nutrient-enriched stream compared with an adjacent reference stream. Others have found significant increases in P content of benthic insects (Frost & Elser, 2002b; Bowman *et al.*, 2005) and snails (Elser *et al.*, 2005b) with increased P content of food resources, and significant changes in C : N : P ratios of lentic snails and insects among seasons have been attributed to changes in nutrient content of periphyton (Liess & Hillebrand, 2005). It remains to be seen whether these changes can be attributed to increased consumer growth rates (and thus higher allocations of P-rich RNA) or the ability of some benthic taxa to store surplus P. Regardless of the mechanism, future progress aimed at predicting ecological consequences of elemental variation among benthic taxa will require (i) identification of when, where and for whom plasticity in nutrient content is common, and (ii) development of predictive mass balance models that relax the assumptions of strict homeostasis (e.g. Sterner & Elser, 2002). Moreover, experimental research utilising the homeostasis coefficient developed by Sterner & Elser (2002) will help focus efforts to compare quantitatively the degree of homeostasis among benthic consumers (see Bowman *et al.*, 2005; DeMott & Pape, 2005).

Effects of consumers on the stoichiometry of dissolved nutrients and basal resources

Productivity, behaviour, and population dynamics of benthic consumers are all affected, to some degree, by the quality of basal food resources. Consumers can in turn influence basal resource quality, and this influence may be mediated by consumer-driven changes in resource stoichiometry (e.g. Hillebrand, de Montpellier & Liess, 2004). One obvious mechanism by which benthic consumers can alter the stoichiometry of basal resources is through consumption. For example, the removal of periphyton by grazers can alter its physical structure and reduce the thickness of boundary layers, thereby increasing total and per capita supply of nutrients to algae and heterotrophic microbes within the periphyton (McCormick & Stevenson, 1989; Mulholland *et al.*, 1991; Rosemond, 1993; Rosemond, Mulholland & Elwood, 1993). Such effects should cause higher nutrient content of the periphyton and reduced C : nutrient ratios. Some benthic detritivores, such as peltoperlid stoneflies, primarily consume leaf mesophyll, and leave behind carbon-rich structural veins, potentially increasing C : nutrient ratios of leaf litter (e.g. Wallace, Woodall & Sherberg, 1970). Similarly, detritivores may feed selectively on nutrient-rich fungal patches (Arsuffi & Suberkropp, 1985) and thus are also expected to decrease litter C : nutrient ratios. Such direct consumptive effects are likely to influence the quality of food for other consumers.

Another way by which benthic invertebrates can alter the elemental composition of basal resources (e.g.

periphyton, leaf litter) and pools of dissolved nutrients (e.g. NH_4^+, PO_4^{3-}) is through the return of nutrients via egestion and excretion. The ratios at which elements are released by a consumer depend on the elemental composition of the food resource, the composition of the consumer's growing tissue, and the efficiency with which the consumer is able to utilise limiting and non-limiting nutrients (Sterner & Elser, 2002; Frost *et al.*, 2005a). Although carbon and nutrient assimilation efficiencies are known to vary widely across food types (Sterner & Elser, 2002), little is known about differences in efficiencies by consumers for utilising C, N and P and how such differences are affected by factors such as food composition or physiological condition.

Under what conditions is consumer-driven nutrient recycling likely to play a significant role in nutrient dynamics? In general, we might expect it to be important in ecosystems that support high consumer biomass and that have low nutrient concentrations and low external nutrient inputs (Vanni, 2002). The body-size distribution within a community is also likely to be important. Given the negative relationship between body size and mass-specific excretion rates (across large ranges in body size), a community composed of small consumers will be more important recyclers than a community of large consumers at the same biomass (Grimm, 1988; Vanni *et al.*, 2002; André, Hecky & Duthie, 2003; but see Conroy *et al.*, 2005).

There is evidence for stoichiometric control of nutrient recycling by consumers in pelagic systems (e.g. Elser & Urabe, 1999; Vanni, 2002), where it can control the identity of limiting nutrients (Elser *et al.*, 1988; Sterner, Elser & Hessen, 1992). Is nutrient recycling by benthic freshwater consumers as important? The few available data show some clear patterns that are in agreement with both stoichiometric theory and pelagic data. For example, insects and snails in a N-limited desert stream frequently disturbed by floods excreted 15–70% of the total ammonium supplied daily (based on 24-h N budgets) to primary producers (Grimm, 1988). An exotic snail population in a spring-fed stream excreted 65% of the ammonium demand of benthic plants and microbes (Hall, Tank & Dybdahl, 2003). Similarly, cichlid fishes in Lake Malawi's littoral zone supplied 46–48% of both the nitrogen and phosphorus required for production of epilithic algae (André *et al.*, 2003; also see Vanni *et al.*, 2002). Thus, although limited, the available evidence indicates that benthic consumers can be important in controlling nutrient delivery to primary producers, particularly when consumers are present at high biomass.

Consumers can also affect the *ratios* of dissolved nutrients available to primary producers and heterotrophic microbes (e.g. Elser & Urabe, 1999). In a study of nutrient recycling by tropical stream consumers, molar N : P ratios of nutrient excretions were negatively related to body N : P ratios and varied thirtyfold among 28 species of fish and amphibians (Vanni *et al.*, 2002). Similarly, crayfish grazers in a temperate stream had a significantly lower body N : P ratio and higher N : P ratio of excretions than co-occurring grazing snails (Evans-White & Lamberti, 2005). These two studies also point to the importance of structural characteristics (e.g. carapace and bone) in determining elemental body composition and, consequently, variation in excretion chemistry, as predicted by stoichiometric theory and data from pelagic studies (Reiners, 1986; Sterner & Elser, 2002).

In addition to excretion of soluble metabolic products, consumers also make nutrients available in egesta (e.g. faecal pellets; Wotton & Malmqvist, 2001), which clearly are an important fraction of nutrients released by consumers. Benthic insects in a desert stream egested 42–54% of ingested nitrogen, which was more than the 9–31% excreted as ammonia; equivalent data for snails were 26–39% for egestion compared with 9–13% for excretion (Grimm, 1988). N and P egested with the faeces of littoral cichlids in Lake Malawi represented approximately one third of the total N and P recycled by these fishes (André *et al.*, 2003). Moreover, nutrient ratios of egestion and excretion differed with a lower N : P ratio of faeces (12 : 1) than in excretions (21 : 1) (André *et al.*, 2003). Egestion by invertebrate consumers could directly affect the elemental composition of periphyton if faeces have a distinct elemental composition and significant quantities remain associated with the periphyton (Frost *et al.*, 2002a). In addition, faeces may leach P faster than N, which should lower the N : P ratio of periphyton (Hillebrand & Kahlert, 2001).

From the perspective of consumer-driven nutrient recycling, excretion products and faeces differ in other fundamental ways. First, excretion products are soluble and readily available for immediate uptake, while the nutrients bound in egesta must be leached and/or re-mineralised before they are available to autotrophs (coprophagous consumers, in contrast, may directly take them up; e.g. Wallace & Webster, 1996; Wotton *et al.*, 1998). Second, the physical transport of excretion and egestion products is likely to differ. In lakes, faeces may settle out of the water column, and in streams, the solubility of excretion products favours greater downstream transport relative to particulate egesta, depending on nutrient uptake kinetics and particle size (Stream Solute Workshop, 1990; Thomas *et al.*, 2001). Thus, the physical contrast between excretion and egestion products is likely to result in temporal and spatial differences in availability.

The stoichiometry of benthic detritus

Much recent research in the field of ecological stoichiometry has been directed toward food webs that are based on living primary producers. However, most plant material (50% to >80% depending on ecosystem type; Cebrian, 1999) is not grazed as live tissue but enters the detrital food web as dead material that is colonised by a diverse microbial and invertebrate community (Moore *et al.*, 2004). Although consideration of detritus has a rich history in ecology (Lindeman, 1942; Teal, 1962; Moore *et al.*, 2004), detrital food webs have rarely been approached from an explicitly stoichiometric perspective. This lack of focus is undoubtedly due in part to the complex nature of these food webs, exacerbated by the central importance of fungi, bacteria and other heterotrophic microorganisms (Meyer, 1994; Suberkropp, 1998).

Patterns that confirm a strongly stoichiometric component to litter decomposition have been apparent for some time. Immobilisation of nutrients by leaf litter can clearly influence nutrient availability in benthic ecosystems (e.g. Suberkropp, Godshalk & Klug, 1976; Gessner, 1991). Decomposition can be related both to C : N : P ratios of vegetation (Enriquez *et al.*, 1993; but see Gessner & Chauvet, 1994) and dissolved nutrient concentrations (e.g. Suberkropp & Chauvet, 1995; Gulis & Suberkropp, 2003). Both intra- and inter-specific variability in C : N ratio has been reported in fungi and large differences exist in C : nutrient ratios between fungi and bacteria (Fig. 1; Sterner & Elser, 2002). This has led to the hypothesis that the pattern of microbial succession on leaf litter that falls into streams (typically fungi first with a gradual increase in relative importance of bacteria; Suberkropp & Klug, 1976; Baldy, Gessner & Chauvet, 1995) is under some degree of stoichiometric control, as pointed out by Sterner & Elser (2002). Fungi have higher C : N ratios than bacteria (Fig. 1; Sterner & Elser, 2002). Consequently, stoichiometric imbalances between senescent leaf litter (high C : N and C : P ratios) and the nutritional requirements for fungal growth are lower than those for bacteria. In contrast, bacteria in general are the most nutrient-rich of all organisms, perhaps because of their high specific growth rates and consequent high RNA content. It seems possible that the high C : N and C : P ratios of freshly fallen leaf litter is a constraint to bacterial colonisation; a constraint that may eventually be relaxed by nutrient immobilisation and selective assimilation and respiratory losses of carbon by fungi.

Even after microbial conditioning, leaf litter often remains a low-quality (i.e. high C : nutrient ratio) food resource relative to living plant tissue (Fig. 1). This is particularly true in rivers and lakes where organic matter inputs are often dominated by terrestrial sources or emergent macrophytes and most *in situ* primary production is by relatively palatable, low C : nutrient micro-algae or submerged macrophytes with little sclerenchymatous tissue. Consequently, many invertebrate consumers of allochthonous organic matter, especially larger ones feeding on leaf litter, are likely to face similar imbalances to those experienced by microbes. Although C : N ratios of decomposing alder leaves can be as low as 12 (e.g. Gessner, 1991), C : nutrient imbalances are typically high (Fig. 1). For example, conditioned leaf litter from Appalachian (U.S.A.) headwater streams had average C : P and N : P ratios of 5360 : 1 and 75 : 1 (Cross *et al.*, 2003). Insects from these heterotrophic streams had correspondingly high C : P and N : P ratios compared with terrestrial and lake invertebrates (Cross *et al.*, 2003), especially among the shredders, a functional feeding group capable of consuming intact leaf litter (Cummins & Klug, 1979; Wallace & Webster, 1996). These differences may indicate some degree of adaptation of benthic invertebrates to the huge C : nutrient imbalances inherent in these strongly heterotrophic ecosystems. One mechanism to cope with such imbalances is, apart from possible physiological adaptations, the well-established preference of shredders for conditioned leaves (e.g. Bärlocher & Kendrick, 1975; Graça *et al.*, 2001), which involves selective feeding on nutrient-enriched fungal patches (Arsuffi & Suberkropp, 1985;

Suberkropp, 1992). An additional strategy may consist of fast gut passage time and consequent low carbon assimilation (Cebrian, 2004) coupled with efficient stripping of nutrients even during short resident times in the guts of freshwater detritivores.

Bacteria are among the most nutrient-rich of all organisms (Fig. 1; Sterner & Elser, 2002; Makino *et al.*, 2003) suggesting that bacteria are often nutrient-limited and probably play a minor role in consumer-driven nutrient recycling. Their high nutrient content, however, indicates that consumers of bacteria (e.g. flagellates, copepods), which all have *higher* C : nutrient contents than their food, will be important recyclers of nutrients, as pointed out by Sterner & Elser (2002). Consequently, although consideration of the 'microbial loop' has traditionally had an energetic focus, ecological stoichiometry suggests that consumption of N- and P-rich bacteria confers a central role for the microbial loop also in nutrient cycling (Elser *et al.*, 2003a).

An inevitable result of most detrital transformations is comminution of large particles into smaller ones (Ward *et al.*, 1994; Gessner, Chauvet & Dobson, 1999). In streams, this comminution promotes downstream movement of organic matter and eventual export from the ecosystem (Wallace *et al.*, 1991; Webster *et al.*, 1999). Given the evidence summarised above for increases in relative nutrient content of particulate organic matter that coincide with fragmentation, decreasing particle size (Fig. 2) and microbial colonisation, the size distribution of exported particles would be expected to affect not only total nutrient export from stream ecosystems but also the nutrient ratios of export. An analysis of long-term field and experimental data from Appalachian streams showed that removal of stream invertebrates (using insecticide) reduced the export of nutrients bound to FPOM by 33–42% compared with reference stream conditions (Cross *et al.*, in press). These changes were associated with average increases in the C : P (40%), C : N (14%) and N : P (16%) ratios of the total POM exported. Thus, it appears that the activity of detritivores can affect the stoichiometry of elements exported from whole catchments.

Ecological stoichiometry and the role of benthic communities in biogeochemistry

With its elemental focus, it is not surprising that some of the most influential early works in ecological stoichiometry were grounded in biogeochemistry. Biogeochemical cycles are an emergent ecosystem property consisting of a myriad of geochemical and biological reactions, many of which differ from the assimilatory and excretion processes most often addressed in ecological stoichiometry. Much biogeochemical research in streams has focused on single elements (e.g. Meyer & Likens, 1979; Triska *et al.*, 1984; Dodds *et al.*, 2000; Mulholland *et al.*, 2000b). When multiple elements have been addressed, relationships have largely been correlative (e.g. influence of C : N content on nitrogen uptake; sensu Dodds *et al.*, 2004) rather than mechanistic (but see Webster *et al.*, 2003).

The unidirectional flow of water in streams provides benthic organisms with a continuous supply of nutrients, in addition to oxygen, and removes metabolic wastes. From a stoichiometric viewpoint, this arrangement limits the ability of sessile, benthic organisms to alter the chemical environment to which they themselves are exposed, although downstream communities could be affected. Recognising this condition led to the concept of nutrient spiralling, and the spiralling framework has organised our thinking about stream biogeochemistry ever since (e.g. Webster & Patten, 1979; Stream Solute Workshop, 1990; Newbold, 1992; Grimm *et al.*, 2003). Despite the many advances that have been accomplished by studies of nutrient spiralling, lack of an explicit treatment of multiple elements and their relations constitutes a major shortcoming (but see Meyer, Likens & Sloane, 1981). Below, we explore how a stoichiometric viewpoint might help overcome this limitation.

Stoichiometry, resource limitation and nutrient spiralling

A logical starting point for relating ecological stoichiometry and nutrient spiralling is to explore the relationship between the N : P ratio of dissolved nutrients in the water column ($C_N : C_P$), the ratio of N and P uptake rates ($U_N : U_P$; where U is expressed as mass per unit area per unit time) and the mean N : P ratio of the benthic community responsible for assimilating nutrients ($B_N : B_P$). If the elemental composition of organisms (e.g. bacteria, algae, bryophytes, fungi) is constant within certain narrow limits, then $U_N : U_P$ (as measured using water column tracer techniques that quantify the removal of dissolved nutrients from the water column; see Stream Solute Workshop, 1990) will equal $B_N : B_P$ weighted for the growth rates of the various organisms assimilating these nutrients. Alternatively, if the stoichiometry of the benthic community as a whole is flexible to some extent, as might be expected based on the previous sections, then $C_N : C_P = B_N : B_P = U_N : U_P$ over the range of stoichiometric variability expressed by the benthos. It is not trivial that in either case, the summed composition of the benthic community ($B_N : B_P$) is expected to predict $U_N : U_P$. However, these predictions require several assumptions to be met, which may or may not hold in nature. These include:

- The water column is the primary source of nutrients to the benthos
- Turnover times of N and P within biotic compartments are similar
- The dominant fate of nutrients removed from the water column (U) is assimilation by organisms

Nutrient spiralling provides both a conceptual and methodological framework for quantifying nutrient cycling in streams (Newbold *et al.*, 1981, 1983). Simply put, a nutrient spiral (S) refers to the average distance a nutrient atom travels while completing one elemental cycle. Spiral length consists of two shorter lengths reflecting transport in inorganic and organic forms. The transport length of nutrients in inorganic form, referred to as the uptake length (S_W), also estimates the uptake rate of a nutrient according to:

$$U_i = \frac{QC_i}{\omega S_{W_i}} \tag{1}$$

where Q is stream discharge, ω is mean stream width, and i is the nutrient of interest (e.g. N or P).

The preceding paragraph describes how nutrient spiralling provides the means for estimating U and, therefore, the ability to test the predictions outlined above. Conversely, predictions of U based on stoichiometric mechanisms can be scaled to the ecosystem using eqn 1. Spiralling predicts that when organisms maintain a constant N : P ratio (i.e. show homeostasis), variation in the ratio of N and P uptake lengths ($S_{W\text{–}N} : S_{W\text{–}P}$) will be a linear function of external supply. For example, in a hypothetical stream reach with $B_N : B_P = U_N : U_P = 15$ and N and P concentrations (C_N and C_P) equal to 6.0 and 0.5 μM, respectively, the ratio of $S_{W\text{–}N}$ to $S_{W\text{–}P}$ will equal the ratio of relative supply to demand. That is:

$$\frac{S_{W-N}}{S_{W-P}} = \frac{C_N : C_P}{U_N : U_P} = \frac{12}{15} = 0.8 \tag{2}$$

In this case, $S_{W\text{–}N} : S_{W\text{–}P}$ is <1 indicating that, on average, nitrogen atoms are removed from the water column by benthic organisms over shorter stream lengths than phosphorus (Fig. 3, scenario I). This simple example results in a surprisingly formal argument for why uptake length is predicted to be shorter for a limiting nutrient. When benthic organisms are flexible in their stoichiometry and match the ratio of nutrients in the water column, $S_{W\text{–}N} : S_{W\text{–}P}$ will equal 1. Flecker *et al.* (2002) and Davis & Minshall (1999) report $S_{W\text{–}N} : S_{W\text{–}P}$ ratios of 0.6 and 1.5–4.9, respectively, suggesting that N was limiting in the former and P in the latter case. Likewise, Munn & Meyer (1990) found a shorter uptake length for P in a western North Carolina stream ($S_{W\text{–}N} : S_{W\text{–}P} = 8.1$; suggesting P was limiting) and for N in a stream in the Cascade range of Western Oregon ($S_{W\text{–}N} : S_{W\text{–}P} = 0.06$; suggesting N is limiting). In each of these cases, uptake length was shorter for the nutrient that was indicated to be limiting by molar ratios of ambient inorganic N and P concentrations.

The utility of beginning with this simplified case is that it helps identify several characteristics of stream ecosystems that can cause $U_N : U_P$ (and $S_{W\text{–}N} : S_{W\text{–}P}$) to vary from the value predicted by $B_N : B_P$. For example, the supply of N and P is rarely, if ever, fully provided by dissolved inorganic elements extracted from the water column, although uptake length calculations are almost exclusively determined from these forms. Alternate avenues of nutrient delivery to benthic organisms include local mineralisation of organic matter, perfusion of ground water through stream sediments, and direct use of nutrients in organic matter (Sheibley *et al.*, 2003; Brookshire *et al.*, 2005). Regardless of the mechanism, differential subsidies of N and P will cause $U_N : U_P$ to vary from $B_N : B_P$ (Fig. 3). Variable fractions of N and P demand met by flowing water supplies (F_N and F_P, respectively) will change relative uptake rates such that:

$$U_N : U_P = B_N : B_P\left(\frac{1 - F_N}{1 - F_P}\right) \tag{3}$$

For example, if 10% of N demand and 40% of P demand is supplied by non-water column sources, $U_N : U_P$ and $S_{W\text{–}N} : S_{W\text{–}P}$ would increase to approximately 23 and 1.9, respectively (Fig. 3, scenario II).

Ambient conditions: $C_{\mathrm{DIN}} = 6\ \mu\mathrm{M}$
$C_{\mathrm{SRP}} = 0.5\ \mu\mathrm{M}$
Biomass N : P ratio = 15

Assumptions: No net change in biomass
N and P have equal residence times within cells
Uptake compartments are homeostatic
(i.e. N : P ratio is constant)

Parameter or Compartment	Scenario I	Scenario II	Scenario III	Scenario IV
	- Inorganic nutrients from water column is sole nutrient source - No nutrient recycling	- Inorganic nutrients from water column supplies 90% of N and 60% of P - No nutrient recycling	- Inorganic nutrients from water column is sole nutrient source - N recycling is 4x more efficient than P recycling	- Inorganic nutrient from water column is sole nutrient source - Denitrification adds 20% to observed N uptake rate
$U_{\mathrm{N}} : U_{\mathrm{P}}$	15.0	22.5	3.8	18.0
$S_{\mathrm{W\text{-}N}} : S_{\mathrm{W\text{-}P}}$	0.8	1.9	0.3	0.7
Predicted limitation	Weak N-limitation	Strong P-limitation	Strong N-limitation	Moderate N-limitation

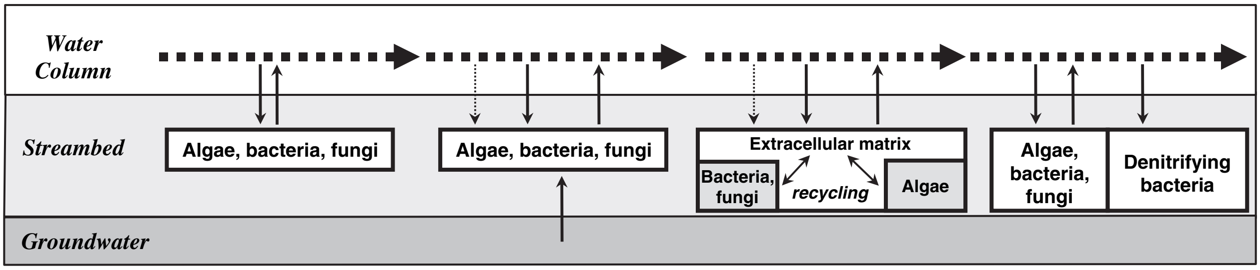

Fig. 3 Hypothetical relationship between stream water column N and P concentrations, uptake rates and uptake lengths (as determined by solute addition experiments) for various scenarios. In scenario I, the water column is the sole source of nutrients for benthic biomass production, assimilation by benthic organisms represents the only nutrient demand, and nutrients are not differentially recycled in the benthic compartment. In scenarios II–IV these assumptions are altered to assess how each affects nutrient spiralling ratios as determined by solute addition techniques. Dotted vertical arrows represent flows of inorganic N and P. Solid vertical arrows represent flows of dissolved and particulate organic N and P.

Note that gross $U_{\mathrm{N}} : U_{\mathrm{P}}$ (assimilation of N and P by organisms) has not changed and remains equivalent to $B_{\mathrm{N}} : B_{\mathrm{P}}$ (=15). However, differential use of N and P from non-water column sources has altered spiralling lengths, which now suggest P, rather than N, limitation ($S_{W\text{–}\mathrm{N}} : S_{W\text{–}\mathrm{P}} > 1$) despite water column concentrations that suggest otherwise ($C_{\mathrm{N}} : C_P < B_N : B_P$). Discrepancies between $U_N : U_P$ and $B_N : B_P$ could also arise from differential internal recycling of N and P (Fig. 3, scenario III) and non-assimilatory removal of nutrients from the water column (Fig. 3, scenario IV). Denitrification, nitrification, and sorption are a few processes that result in the loss of particular forms of nutrients from solution and are included in tracer-derived estimates of nutrient uptake in streams.

Stoichiometry, nutrient spiralling and longitudinal patterns in stream ecosystems

The examples in Fig. 3 illustrate how spiralling length is related to the elemental composition of benthic biomass. Unresolved to this point is how stoichiometric constraints and/or flexibility perpetuate longitudinally to influence the absolute and relative availability of N and P and the structure and function of downstream communities. Headwater streams are particularly important in the retention of nutrients (e.g. Alexander, Smith & Schwarz, 2000; Peterson *et al.*, 2001) because of their high ratios of benthic surface area to water volume and their spatial dominance in the landscape (Meyer & Wallace, 2001). Because discharging ground water passes benthic communities prior to entering the stream, headwater benthic communities are well positioned to influence the timing, form, and absolute and relative availability of N and P in streams. It is therefore reasonable to suspect that the stoichiometry of benthic organisms may exert its greatest influence on stream water nutrient concentrations in these reaches as well. Conversely, nutrients in larger streams tend to have had a longer residence time and to have experienced more 'turns of the spiral' than elements in headwater streams. With each successive spiral, the benthic stream community has an opportunity to influence the relative abundance of nutrients in the water and the form in which those nutrients are present.

A thorough assessment of the longitudinal implications of ecological stoichiometry in streams will require developing more sophisticated models, but common sense suggests that organism stoichiometry may influence longitudinal variation in N and P concentration through both uptake and recycling (R). Specifically, biotically induced changes in the relative availability of N and P requires that $(U_N - R_N) \neq (U_P - R_P)$. Examples of mechanisms that could cause such discrepancies include consumer-driven nutrient recycling, biomass accrual or loss, non-assimilatory pathways of nutrient loss from the water column (e.g. denitrification) and dissolved and particulate organic matter loss through downstream transport.

Conclusions

The application of ecological stoichiometry to benthic ecosystems has just begun (Frost *et al*., 2002b). At this stage, most studies have focused on (i) documenting stoichiometric variation in benthic consumers, periphyton, and detrital compartments, (ii) assessing how environmental factors influence this variation, and (iii) exploring the magnitude and importance of nutrient recycling by benthic consumers. Because rules of conservation of mass are universal, ecological stoichiometry should provide a useful and robust framework for addressing central ecological questions in benthic systems.

Although the implicit use of stoichiometric concepts has been evident in benthic studies for decades, recent interest in this topic, perhaps inspired by Sterner & Elser's (2002) comprehensive synthesis, has provoked a more explicit consideration of combined elemental dynamics in the benthos. This approach has already proven and will undoubtedly continue to be a rewarding path for gaining a mechanistic understanding of factors that influence benthic populations, communities and ecosystems.

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Corrigendum

There is an error in eqn 3, Fig. 3 and associated text in Cross *et al.* (2005). The corrected equation, figure and text are printed below. The corrected text begins with the last paragraph of page 1905 in Cross *et al.* (2005).

Correction (corrected text in italics):

The utility of beginning with this simplified case is that it helps identify several characteristics of stream ecosystems that can cause $\mathrm{U_N : U_P}$ (and $\mathrm{S_{W\text{–}N} : S_{W\text{–}P}}$) to vary from the value predicted by $\mathrm{B_N : B_P}$. For example, the supply of N and P is rarely, if ever, fully provided by dissolved inorganic elements extracted from the water column, although uptake length calculations are almost exclusively determined from these forms. Alternate avenues of nutrient delivery to benthic organisms include local mineralisation of organic matter, perfusion of ground water through stream sediments, and direct use of nutrients in organic matter (Sheibley *et al.*, 2003; Brookshire *et al.*, 2005). *Regardless of the mechanism, differential subsidies of N and P will cause* $U_N : U_P$ *to vary from* $B_N : B_P$ *(Fig. 3). Variable fractions of N and P demand met by flowing water*

***Ambient conditions**:* C_{DIN} = 6 μM
C_{SRP} = 0.5 μM
Biomass N : P ratio = 15

***Assumptions**:* No net change in biomass
N and P have equal residence times within cells
Uptake compartments are homeostatic
(i.e. N : P ratio is constant)

Parameter or compartment	Scenario I	Scenario II	Scenario III	Scenario IV
	- Inorganic nutrients from water column is sole nutrient source - No nutrient recycling	- Inorganic nutrients from water column supply 90% of N and 60% of P - No nutrient recycling	- Inorganic nutrients from water column is sole nutrient source - N recycling is 4*x* more efficient than P recycling	- Inorganic nutrient from water column is sole nutrient source - Denitrification adds 20% to observed N uptake rate
$U_N : U_P$	15.0	22.5	3.8	18.0
$S_{W\text{–}N} : S_{W\text{–}P}$	0.8	0.5	3.2	0.7
Predicted limitation	Weak N-limitation	Strong N-limitation	Strong P-limitation	Moderate N-limitation

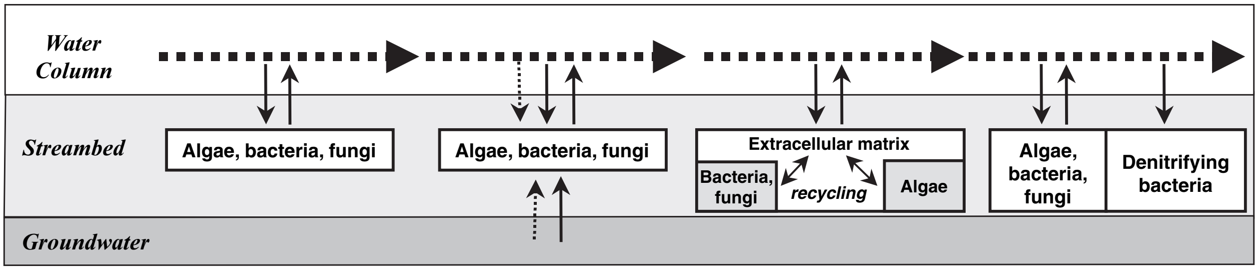

Fig. 3 Hypothetical relationship between stream water column N and P concentrations, uptake rates and uptake lengths (as determined by solute addition experiments) for various scenarios. In scenario I, the water column is the sole source of nutrients for benthic biomass production, assimilation by benthic organisms represents the only nutrient demand, and nutrients are not differentially recycled in the benthic compartment. In scenarios II–IV, these assumptions are altered to assess how each affects nutrient spiralling ratios as determined by solute addition techniques. Solid vertical arrows represent flows of dissolved inorganic N and P. Dotted vertical arrows represent flows of dissolved and/or particulate organic N and P.

supplies (F_N and F_P, respectively) will change relative uptake rates such that:

$$U_N : U_P = B_N : B_P \left(\frac{F_N}{F_P}\right) \tag{3}$$

For example, if 10% of N demand and 40% of P demand is supplied by non-water column sources (F_N and F_P equal 0.9 and 0.6, respectively), $U_N : U_P$ and $S_{W-N} : S_{W-P}$ would increase to about 22.5 and 0.5, respectively (Fig. 3, scenario II). In this scenario, gross $U_N : U_P$ (assimilation of N and P by organisms) has not changed and remains equivalent to $B_N : B_P$ (= 15). However, differential use of N and P from non-water column sources has exaggerated the degree of N limitation. Discrepancies between observed $U_N : U_P$ and $B_N : B_P$ could also arise from differential internal recycling of N and P (Fig. 3, scenario III) and non-assimilatory removal of nutrients from the water column (Fig. 3, scenario IV). Denitrification, nitrification, and sorption are a few processes that result in the loss of particular forms of nutrients from solution and are included in tracer-derived estimates of nutrient uptake in streams.

Reference

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