Nutrient Stoichiometry in Aquatic Ecosystems

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Introduction

In chemistry, the term 'stoichiometry' refers to the number of atoms of elements on both sides of a reaction. Stoichiometry tells you how many different molecules of each type of reactant you need to generate a specific product or set of products. Ecologists and limnologists can use these same principles of stoichiometry to understand aquatic ecosystems because individual species, like molecules, have defined chemical composition. The elemental formula of an individual species is normally not as strictly defined as the kinds of molecules we are most accustomed to thinking about, those with specific, unvarying composition. However, stoichiometry can still be a very useful approximation. Stoichiometry has much to say about the linkage of cycling of different elements and about patterns of nutrient limitation in primary producers and other parts of food webs. It bridges studies on individual species with studies dealing with the flow of matter and energy in ecosystems.

In this article, we first consider some of the patterns in elemental content of particular aquatic organisms and then we consider the ecological consequences of those patterns.

Stoichiometric Homeostasis

Homeostasis is one of the hallmarks of life. Homeostasis is a resistance to change. For example, homeothermic organisms maintain a constant body temperature in spite of fluctuating environmental temperature. There are many other examples of homeostasis in biology, like the pH of blood and the concentration of ATP in a cell. Homeostasis results from negative feedbacks. In ecological stoichiometry, we use this same term to refer to the tendency of an organism to maintain its chemical content in spite of variation in the chemical content of its resources (**Figure 1**). The figure illustrates the general principle. Mathematically, stoichiometric homeostasis (H) is defined as

$$y = cx^{1/H}$$

where $y =$ organismal elemental content (e.g., moles P per dry mass of animal), $c =$ a constant, $x =$ elemental content of resources (measured in the same units as 'y'), and H (the Greek letter 'eta') is the measure of homeostasis. If homeostasis is so strong that organismal content is constant no matter what the chemical content of the organism's food is, the stoichiometric coefficient H approaches infinity and we refer to that as a 'strict homeostasis'.
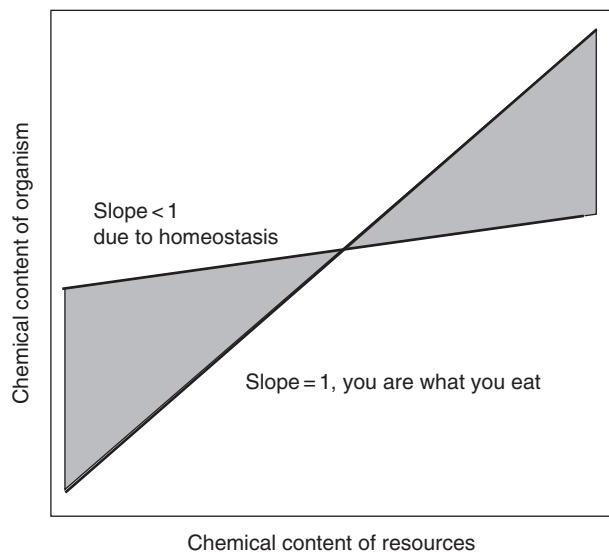
Not all species maintain stoichiometric homeostasis to the same degree, and within any given species not all resources are regulated equally. These differences will be elaborated upon later, but in terms of nutrients such as nitrogen and phosphorus, primary producers generally have more variable chemical content than animals. Algae and macrophytes, like other 'plants' and many microorganisms, can store nutrients by assimilating them at rates much larger than immediate requirements. Later, these organisms can then tap into these reserves for future growth. Animals have more limited capacity for nutrient storage. Differences in mean chemical content between plants and animals have also been suggested recently by analysis of selected proteomes (all of the proteins produced by a species) of these groups; animals had about 7% higher number of N atoms per amino acid side chain than did plants.

Within an animal taxon, variation in element content is lowest for macronutrients, intermediate for essential micronutrients, and highest in nonessential metals (**Table 1**). Animals apparently regulate macroelements most strictly and they regulate elements with definite biological function more than those elements that are incorporated into cells even though they are not essential for growth or survival.

There has been progress recently in defining patterns of homeostasis across elements and across organisms, but we are still a long way from a comprehensive understanding of all the potentially important patterns and contrasts. Homeostasis is an important concept in ecological stoichiometry because the stricter the homeostasis the closer the more an organism's chemical composition resembles a molecule with defined composition. Maintaining a given chemical content in spite of the composition of resources has some detrimental effects on fitness. As we will see later, homeostasis makes organism growth sensitive to the composition of the food that is eaten. Without homeostasis, organisms would 'be what they eat' and there would be no slowing of growth when an individual element becomes scarce. There must be substantial benefits to homeostasis to make up for the easily observed costs, but much less is known about the nature of these benefits.

Stoichiometry at the Organism Level

Let us now examine some of the stoichiometric patterns for particular aquatic organisms. Organisms vary in nutrient content for many reasons because there are many functions of different elements in biology. Several fundamental causes for organism-level variation in stoichiometry are phylogeny (closely related species are more likely to resemble each other in terms of stoichiometry as well as many other phenotypic traits), structure (especially for large organisms or those with major investments in support or defense), allometry (effects of body size), and life histories (high rates of growth have a unique stoichiometric signature). In considering these factors, we will start at the base of the food chain, the primary producers.

Primary Producers

As is apparent from many examples given throughout this article, stoichiometric variability is the hallmark of primary producers. This variability arises because nutrient uptake and biomass gain can be decoupled. For example, if one exposes a nutrient-limited algal cell suddenly to high concentrations of nutrients, within minutes it can replenish cellular nutrient stores. It then puts those stores to work over time scales of hours to days as the cell gains organic carbon via photosynthesis and eventually divides by fission or mitosis. Cells also may take up nutrients for more than any immediate growth needs, resulting in higher nutrient content than seen in long-term, high growth-rate situations. These cellular nutrient stores sometimes are in the form of specialized storage compounds such as poly phosphate (for P) or cyanophycin (for N). The autotroph cell can also divert resources among different functional pools, for example photosynthetic pigments are N-rich and often cells growing under low light and excess N will be very rich in these pigments. If that cell moves to a high light but low N environment, those pigments can be broken down and the N moved into different pools. In this way, photosynthetic pigments serve as an N reservoir, even though they are not storage compounds per se.

The general model used to describe the linkage between cellular stores and cell growth was proposed years ago by M.R. Droop. Droop's model applies

Figure 1 Stoichiometric homeostasis deals with the question of whether organisms 'are what they eat'. Organisms have varying strengths of regulating their own content of different elements. If the chemical content of organisms passively reflects the resources they take in, their own chemistry would match the chemistry of their resources, and observations would lie along the 1:1 line marked 'you are what you eat'. This would be an absence of stoichiometric homeostasis. Stoichiometric homeostasis reduces the slope of the relationship below the 1:1 line (shaded regions). Different organisms and different chemical resources produce different degrees of homeostasis (see for example Table 1).

Table 1 Coefficients of variation (CV) of content of different elements (log₁₀-transformed) measured over a season in a single pond

| Organism	Content of elements									
Amphipod	C 0.004	N 0.005	P 0.007	Cu 0.009	Zn 0.018	Se 0.019	As 0.021	Pb 0.059	Hg 0.079	Cd 0.124
Damselflies	C 0.004	N 0.004	P 0.016	Cu 0.024	Se 0.025	Zn 0.030	As 0.035	Hb 0.05	Cd 0.053	Pb 0.074
Snails	C 0.002	N 0.005	P 0.007	Se 0.018	Zn 0.018	As 0.018	Cu 0.019	Cd 0.040	Hb 0.045	Pb 0.085
Zooplankton	C 0.003	P 0.003	N 0.006	Zn 0.007	Se 0.017	Pb 0.02	As 0.026	Cu 0.035	Cd 0.041	Hg 0.059

The higher the CV, the more variable is the element in the given organism relative to the element's mean concentration. Elements are arranged left to right by increasing CV. Macronutrients are unshaded. Essential micronutrients are lightly shaded. Non-essential trace elements are darkly shaded.
Adapted from Figure 2 in Karimi R and Folt CL (2006) Beyond macronutrients: Element variability and multielement stoichiometry in freshwater invertebrates. *Ecology Letters* 9: 1273–1283. and [permission being sought].

under conditions of a single limiting chemical resource. Droop performed experiments with algae in continuous culture and suggested that growth rate was negatively and linearly related to ratio of biomass to nutrients within the cells (**Figure 2**). The Droop relationship ties a stoichiometric quantity (C:P) to a dynamic variable (growth rate).

Aquatic primary producers come from deeply branched evolutionary lineages. Some of the stoichiometric variability across diverse algal forms was recently described. Two of the major lineages, the 'red superfamily' and the 'green superfamily' can be separated on the basis of their patterns in trace metal composition. Members of the red superfamily (e.g., diatoms) tend to be higher in Cd, Co, and Mn whereas members of the green superfamily (e.g., green algae) tend to be higher in Cu, Zn, and Fe. Quite possibly these differences reflect major geological events such as the relative concentration of ocean oxygen during the evolutionarily origin of these groups.
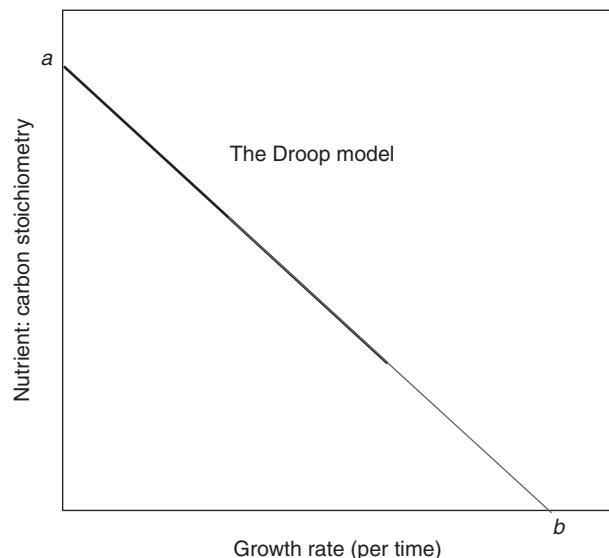
Figure 2 The functional coupling between organismal stoichiometry (e.g., C:P or C:N, vertical axis) and growth (per capita rate, time^{-1}) is often linear when one resource is limiting. This straight-line model is normally written algebraically as

$$\mu = \mu'(1 - (Q_{min}/Q))$$

where μ = cellular growth rate (time^{-1}), Q_{min} = the cell quota at zero growth, and Q is cell quota (in this case, P:C or N:C). The term 'quota' refers to the nutrients per cell or per biomass in the cell, e.g., P:C or N:C. In the Figure, a is $1/Q_{min}$ and b is μ'. The parameter μ' is a theoretical (high) growth rate that would be reached at infinite quota. The thick part of the line represents a range where one would expect to see actual observations. The narrow part of the line would be growth rates that were never observed.

Freshwater algae attached to substrates include microscopic forms ('periphyton') living in close association with other microbes and nonliving organic materials, all collectively forming a biofilm. These biofilms are the main source of autochthonous production in streams and sometimes in nearshore lake habitats as well. Living algae are often a minor contributor to the total carbon within such biofilms. Especially in streams, the stoichiometry of the entire biofilm is made up by living and nonliving components. In order of decreasing N and P content, those include wood, leaf litter, green leaves, and both periphyton and fine particulate organic matter (**Figure 3**). Stoichiometric variability at the base of stream food webs is probably more dependent on the relative contributions of these different components than it is on variation within any one component.

Zooplankton

Moving up the food chain from primary producers, we encounter a variety of herbivores. In water columns, these herbivores are members of the zooplankton. The freshwater zooplankton is not a particularly taxonomically diverse group; protozoans, rotifers, cladocerans and copepods as well as juvenile insects are common members. Cladocerans and copepods both belong to the Crustacea, and they plus the insects are all Arthropods. Though species from any number of these several major taxonomic groups may coexist, may have overlapping diets, and may share many other aspects of their ecology such as predators, they nevertheless can have divergent stoichiometries. In particular, some species, such as *Bosmina*, have low P content, whereas others, such as *Scapholeberis* or *Daphnia* have P content several times higher. All of these species, diverse from the standpoint of their elemental content, are members of the same taxonomic order. Homeostatic regulation of element content is highly variable, even within members of a single genus of zooplankton. Thus, stoichiometric patterns include not just average nutrient content but also the degree of variation within the taxon. We have made much progress in understanding the importance of average nutrient content, which will be apparent later in this article, but we have a very poor understanding of the ecological relevance of differences in homeostatic regulatory ability. Why some species are very homeostatic in element content and others are less tightly regulated is not at all understood yet.

Cross-species variability in average phosphorus content has been linked to life-history differences because biochemicals responsible for growth have a
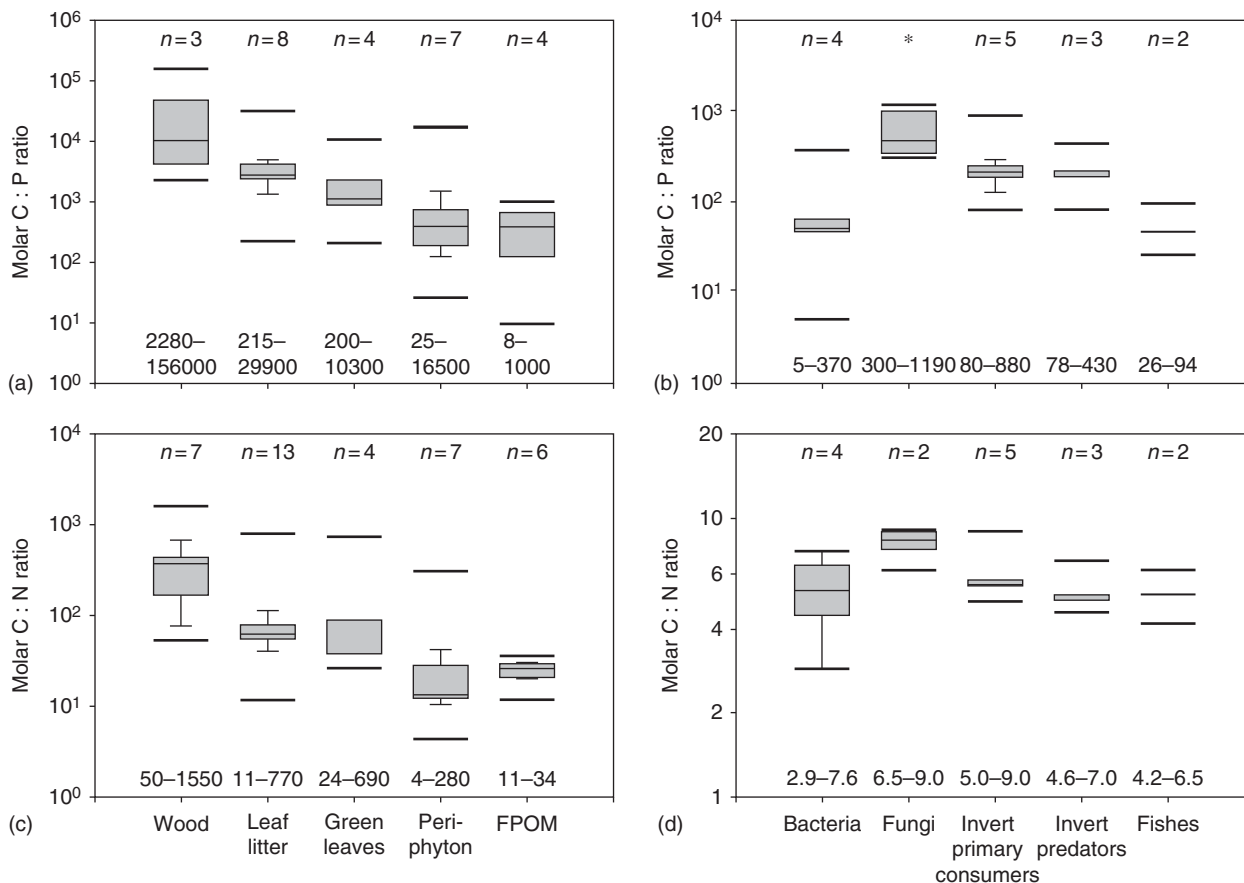
Figure 3 Means and variability of C:N:P stoichiometry in common freshwater benthic resources and consumers. FPOM: fine particulate organic matter. Boxes and whiskers give the median, 10th, 25th, 7th, and 90th percentiles of the data within each category. Original sources of data include 49 literature studies. Ranges are given in text below the boxes. Reproduced from **Figure 1** in, Cross WF, Benstead JP, Frost PC, and Thomas SA (2005) Ecological stoichiometry in freshwater benthic systems: Recent progress and perspectives. *Freshwater Biology* 50: 1895–1912, with permission from Blackwell Publishing.

distinct elemental signature. Species with a potential for rapid biomass growth rates must contain large complements of P-rich biosynthetic machinery. This machinery is dominated by ribosomes, subcellular organelles involved in protein synthesis and which have distinctly high P content. The Growth Rate Hypothesis (GRH) proposes that elevated P demands caused by increased allocation to P-rich ribosomal RNA under rapid growth drives variation in whole-organism P content and thus whole-organism C:P and N:P ratios. Through the GRH, there may be very strong couplings between life histories and stoichiometry and therefore nutrient and energy flow. One example of couplings between growth and P content is given in **Figure 4**. Note that the GRH coupling exists when overall food concentration is high. When food concentration is low, animals are likely mainly energy limited and couplings to nutrient content are muted or absent. Linkages among growth rate and

stoichiometry seem to depend upon the nature of growth limitation, what resource is limiting at any given time.
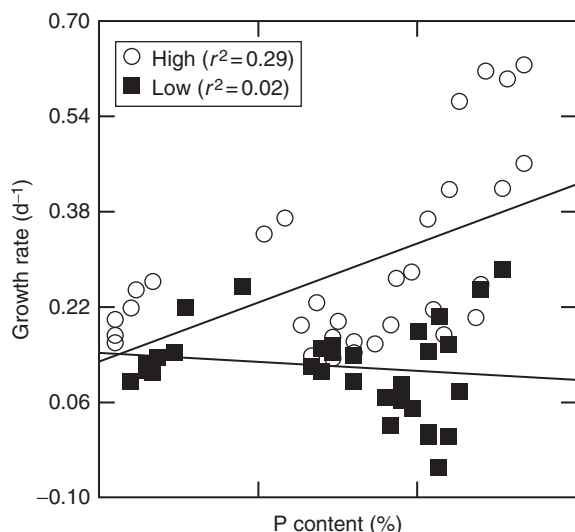
Other Aquatic Invertebrates

The stoichiometry of stream and lake benthic invertebrates has been explored, and wide chemical variation among the diverse members of this group has been observed. In one such study, %P ranged from ~0.2% to 1.5% and the N:P ratio ranged from <20 to >100. Trichoptera and Ephermeroptera were lower in %P and %N than Diptera, Odonata, and Plectoptera. When examined as a function of feeding group, predators were found to have higher P and N than other feeding groups. This is an impressive amount of stoichiometric variation. Not many studies have examined the consequences of this stoichiometric variation in streams, but perhaps some of the

same processes we describe later relative to planktonic systems hold as well in streams.

Bacteria and Protozoa

Heterotrophic microorgansms include bacteria and Protozoa. Not much work has been done yet on the stoichiometry of freshwater Protozoa. Freshwater bacteria are often found to have relatively high N and P content (low C:N and C:P) compared with other aquatic organisms. Studies suggest that bacterial N content is very homeostatic but P content varies with the availability of P for uptake as well as the growth rate of the bacteria. One study on *E. coli* that varied the chemistry of the growth substrate and the growth rate itself found a range in C:P from 40 to 75, a range in N:P from 11 to 18 and a very constant C:N of 4. At high growth rate, bacteria had low C:P and elevated RNA content. In comparing the results for *E. coli* with literature findings, this same study suggested that individual bacterial strains were strongly homeostatic whereas in nature bulk bacterial communities varied much more widely, suggesting that varying dominance of individual strains may be

responsible for much of the variation in bacterial C:N:P composition in the field. In this respect, stoichiometric patterns in the bacteria have a resemblance to other organisms, including freshwater zooplankton.

Fish

Fish are often the ecologically dominant vertebrates in aquatic ecosystems. Fish can be herbivores as well as carnivores or even detritivores or omnivores. Fish have numerous effects on aquatic ecosystems and at times they can be so abundant that they channel great quantities of nutrients in and out of their own biomass through feeding, excreting, etc.

This group too is characterized by wide stoichiometric variation and the ecological consequences of such a wide stoichiometric variability are just beginning to be understood. Phosphorus content of fish ranges from less than one to over four percent. Low-P fish include minnows in the Cyprinidae family. High-P fish occur in both temperate and tropical ecosystems; they are bony and are typical of the Percidae, Centrachidae and Loricariidae families. In fish, evolutionary patterns associated with structure (boniness) account for most of the stoichiometric variation. We see this in a very strong correlation between fish Ca and fish P (**Figure 5**). Fish skeletons can account for from one to more than five percent of body mass. Bony skeletal material is made of a calcium phosphorus mineral called apatite with chemical formula $Ca_5F(PO_4)_3$ where other anions may replace F. This large
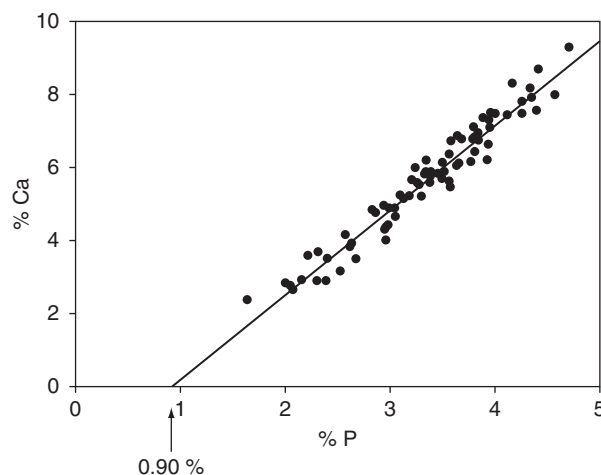

Figure 4 In a laboratory bioassay study involving four species from three genera of cladocerans, growth rate and P content were positively related when food concentration was high (open circles) but not when it was low (closed squares). At low food concentration, animals were energy limited, but at high food concentration they were likely P limited so that growth was linked to P levels in the animals. Reproduced from **Figure 2** in Ferrão-Filho AS, Tessier AJ, and DeMott WR (2007) Sensitivity of herbivorous zooplankton to phosphorus-deficient diets: Testing stoichiometric theory and the growth rate hypothesis. *Limnnology and Oceanography* 52: 407–415, with permission from American Society of Limnology and Oceanography.

Figure 5 Ca vs. P for 18 species of fish. The line has equation $y = 2.31x - 2.09$ ($r^2 = 0.95$). Reproduced from **Figure 4** in Hendrixson HA, Sterner RW, and Kay AD (2007) Elemental stoichiometry of freshwater fish in relation to phylogeny, allometry and ecology. *Journal of Fish Biology* 70: 121–140, with permission from Blackwell Publishing.

quantity of mineral has a great effect on the stoichiometry of individual species of fish – the slope of the line in **Figure 5** is almost exactly as predicted from the stoichiometry of apatite mineral.

We will now consider the ecological ramifications on these stoichiometric properties of species.

Food Quality

Consumers rely on organic food resources that may or may not closely match their own chemical requirements for survival and growth. The idea of a 'balanced' diet is familiar to everyone from the standpoint of human nutrition – it means that the chemical composition of food matches closely an ideal composition. Stoichiometry helps us understand how balanced vs. imbalanced a particular diet may be for any given aquatic consumer. Natural ecosystems often present highly imbalanced diets to consumers. Effects of many different nutritive substances such as vitamins, amino acids and fatty acids are known. Here, we will focus solely on individual chemical elements.

To help understand how different elements may limit consumer growth, we use a tool called a 'Threshold Element Ratio' (TER). A TER is the ratio of elements in an organism's resources where that organism is equally limited by both elements. When the ratio of elements (e.g., C:P) in the food exceeds the TER, the element in the denominator (P) limits consumer growth. Likewise, when the ratio is lower than the TER, the element in the numerator (C) limits growth. TERs are determined by two main things: the nutrient content of the consumer organism, which we considered earlier, and growth efficiency, which we will consider next.

Growth efficiency is defined as the amount an organism gains divided by the mass it ingests. Growth efficiencies based on carbon for aquatic consumers average around 0.3 with large variation around that average. Stoichiometry helps explain some of that variation. The growth efficiency of a strongly homeostatic organism must adjust to the composition of the food, otherwise the consumer would not be able to maintain its homeostasis. There are many well studied examples where decreased growth efficiency on poor quality (low nutrient) foods has been observed in aquatic systems. A good example is heterotrophic bacteria where growth efficiency is typically well above 50% for growth on substrates with C:N < 5, but declines to 10% or less on substrates with C:N ratios > 30. Because bacterial processing of organic carbon is often a very big part of the organic carbon cycle in lakes, these stoichiometric modulations of C shunted into cell growth versus loss as CO_2 or

organic C can play a very large role in the biogeochemical cycling of carbon.

TERs have been calculated for many aquatic organisms (**Figure 6(a)**). Fish have low C:P TERs (typically about 100–200), a reflection of their P-rich skeleton. The highest C:P TERs (about 500) are found for aquatic insects, which of course do not have bony skeletons but still require P for making RNA and other biomolecules. In fact, within the invertebrates, there is a statistically significant negative relationship between maximal potential growth rate and the C:P TER (**Figure 6(b)**, open symbols). Here we see the elemental requirements for the machinery for growth affecting whole-organism ecology, consistent with the Growth Rate Hypothesis described earlier.
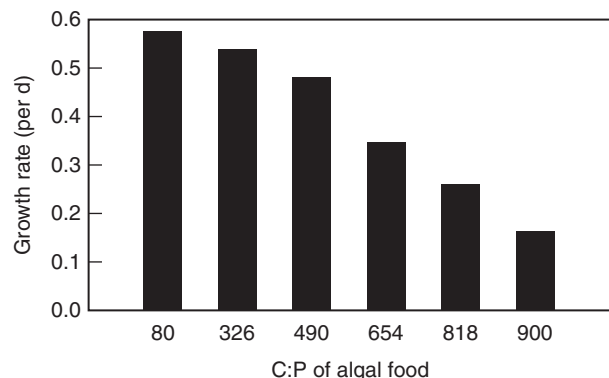
There have been numerous studies on stoichiometric dimensions to food quality in zooplankton.
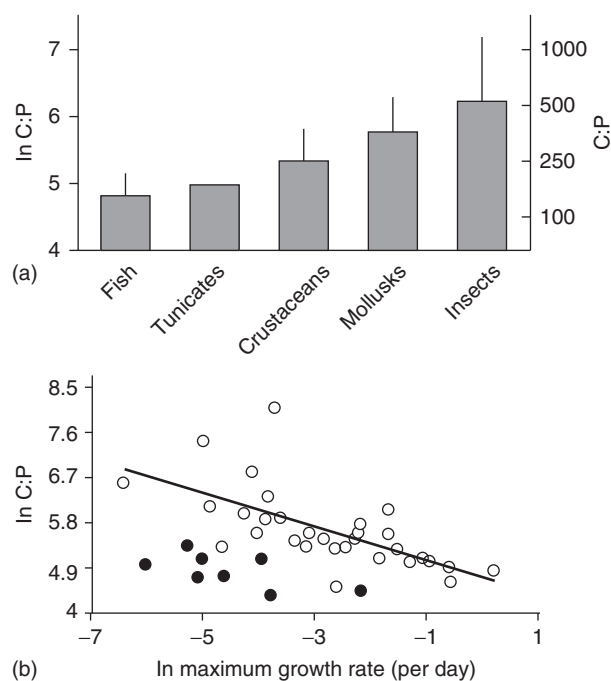
Figure 6 Ratios of C:P (moles C per moles P), where different kinds of aquatic animals switch between growth limitation by carbon vs. growth limitation by phosphorus. When food C:P exceeds an animal's TER, the animal is limited by P and when food C:P is less than an animals's TER, carbon limits growth. (a) Their higher TERs (mean ± SD) indicate that less food P is required per unit food carbon for mollusks and insects relative to fish, tunicates, and crustaceans. (b) A higher growth rate depresses the C:P TER in invertebrates (open circles), a signal consistent with the growth rate hypothesis. Further, at any given growth rate, high P content depresses fish C:P TER (closed circles) below that observed for invertebrates. Adapted from **Figures 2** and **4** in Frost PC, Benstead JP, Cross WF, Hillebrand H, Larson GL, Xenopoulos MA, and Yoshida T (2006) Threshold elemental ratios of carbon and phosphorus in aquatic consumers. *Ecology Letters* 9: 774–779, with permission from Blackwell Publishing.

One example comes from the study of a model organism in ecological stoichiometry, *Daphnia*, the water-flea. *Daphnia* are keystone herbivores in planktonic systems; they merit special attention because of the role they can play in decreasing algal biomass. Above, we discussed how *Daphnia* are generally high in P content. As one would therefore expect, *Daphnia* growth is sensitive to the P content of their food (Figure 7). Algae with high C:P ratio (and thus low P content) dramatically lowers *Daphnia* growth rate, in this case lengthening by three-fold the time to double biomass. Other studies on zooplankton stoichiometry have shown: (a) low P zooplankton such as *Bosmina* are much less affected by the C:P of algal food than are high P zooplankton like *Daphnia*; and (b) particular life stages of some zooplankton may be particularly sensitive to C:P of food; thus, an overall effect on the animal may be determined most at specific points in its life cycle One recent study showed that hybrids of two *Daphnia* species performed better on high C:P food than the two parental species, suggesting that success in stoichiometrically imbalanced systems might be responsible for maintenance of hybrids in the ecosystem.

Stoichiometry predicts that consumers of high element content should be rare in environments where that element is scarce. A large Norwegian study showed a strong relationship between the abundance of *Daphnia* and seston C:P ratios (Figure 8). In this study, all sites with high *Daphnia* abundance had seston C:P well below this organism's C:P TER. Seston C:P ratios were the most important variable in explaining the abundance of *Daphnia*. In general, physiological studies of TERs, laboratory growth studies, and field studies all point to a consistent conclusion, that high P herbivores like *Daphnia* are affected by stoichiometric imbalances between food and consumer.

There are some other very high imbalances between consumer and resource stoichiometry in streams and lake benthos. Certain consumers in those habitats subsist largely on nutrient-poor detritus. An example of stoichiometry affecting a stream invertebrate is given in Figure 9. In this study, snails were given two quantities of periphyton food that had been grown under different nutrient treatments. Periphyton grown with added P (treatments +P and +N +P) had C:P of about 200 whereas C:P was 400 or more when P was not added (treatments Ambient and +N). The snails were strongly homeostatic and they showed pronounced stoichiometric effects on growth at low but not high periphyton quantity.
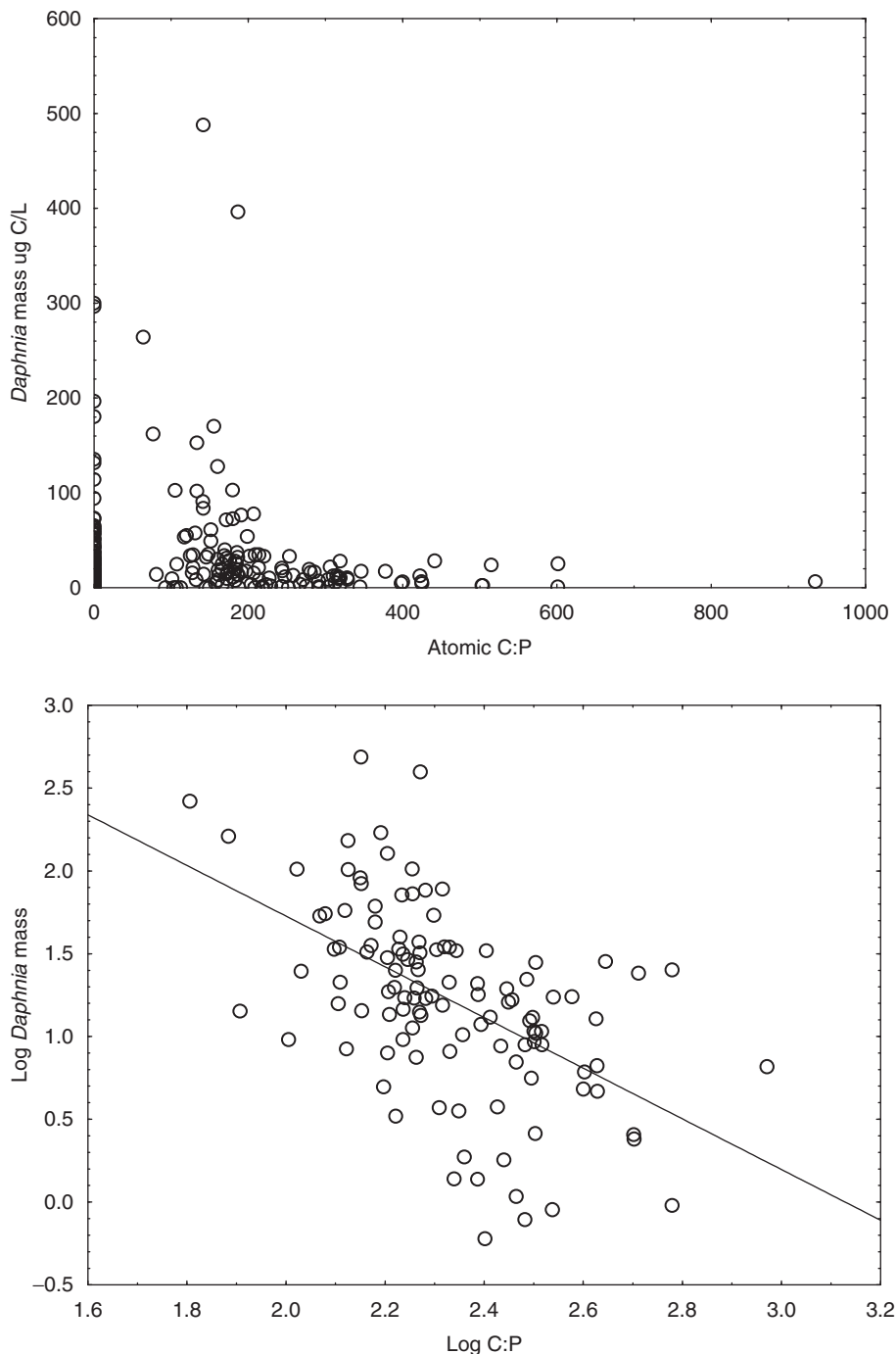
Although most studies of food quality have emphasized what happens when food is deficient in some element, recent studies have also shown that food may be imbalanced when it is too high in a particular element. Whether reduced food quality at high nutrient content is due to overt toxicity or because very high content of some element indicates some other chemical imbalance is not yet understood.

Nutrient Recycling

Next we consider stoichiometric aspects of nutrient cycling. In particular, we consider processes that deliver nutrients to the dissolved pool. Nutrients enter the dissolved pool in inland ecosystems from the air, the surrounding land, the sediments or substrate, and also from the organisms living in the water, which release nutrients as waste products. There are stoichiometric aspects to all of the above, but here we will focus on biological resupply, or nutrient recycling by consumers. Consumers here can range from Protozoa to fish.

The stoichiometry of nutrient recycling is related to food quantity, considered above. When an organism's food is deficient enough in a particular element for it to be limited by that element, a great premium is placed on not wasting that element. In order to maintain a stoichiometric homeostasis, organisms must efficiently retain elements in short supply in their food relative to stoichiometric requirements. For the same reason, they must either not assimilate or they must release upon assimilation, elements that are in

Figure 7 The planktonic herbivore, *Daphnia magna*, has much reduced growth rate when it feeds on algae of high C:P ratio (low P content). All algal food treatments in this study were the same species of algae, *Scenedesmus acutus*, grown under different conditions to get a stoichiometric range from 80 to 900. Converting from growth rate units one can find that at low C:P, these *Daphnia* double their biomass in 1.2 days, whereas at high C:P it takes 3.8 days, or more than three times as long. Adapted from DeMott WR, Gulati RD, and Siewertsen K (1998) Effects of phosphorus-deficient diets on the carbon and phosphorus balance of *Daphnia magna*. *Limnology and Oceanography* 43: 1147–1161, with permission from American Society of Limnology and Oceanography.

Figure 8 Consistent with predictions of stoichiometric theory, lakes with high C:P in their seston have lower abundance of the high-P, keystone genus, *Daphnia*. Data are from a survey of 400 Norwegian lakes. The upper panel shows the data plotted on linear axes and emphasizes how large populations build up only at C:P below the *Daphnia* TER, which typically is about 300. The lower panel shows the same data plotted on logarithmic axes and shows a strong consistently negative slope. Replotted from data published in Hessen DO (2006) Determinants of seston C:P ratio in lakes. *Freshwater Biology* 51:1560–1569. [permission being sought].

surplus to their own requirements. Stoichiometric homeostasis thus has a highly constraining effect on patterns of nutrient recycling by consumers.
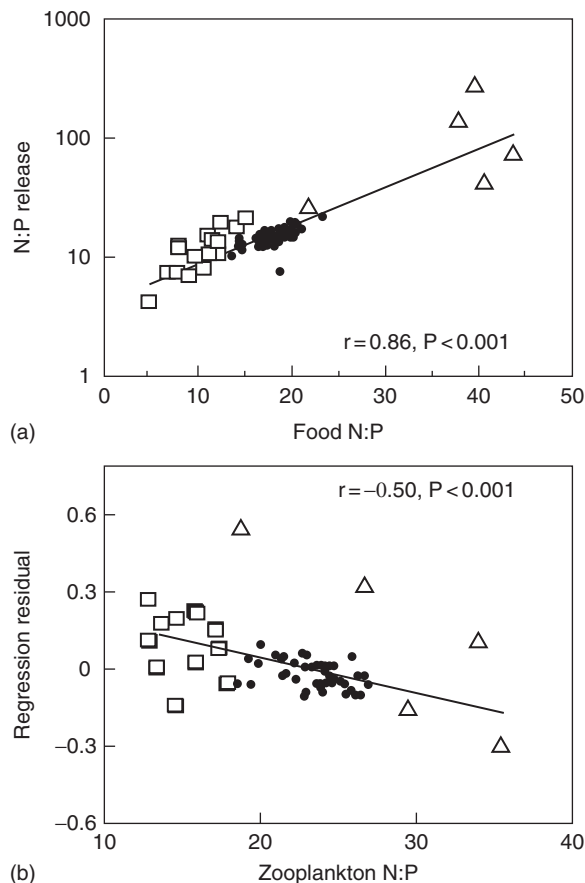
Many studies on many organisms have considered the N:P ratio of release by individual aquatic organisms. In Figure 10 we see data gathered from freshwater and marine zooplankton. Other studies with similar results have been conducted on bacteria, Protozoa, and vertebrates including fish. Figure 10 illustrates the two principal stoichiometric effects on
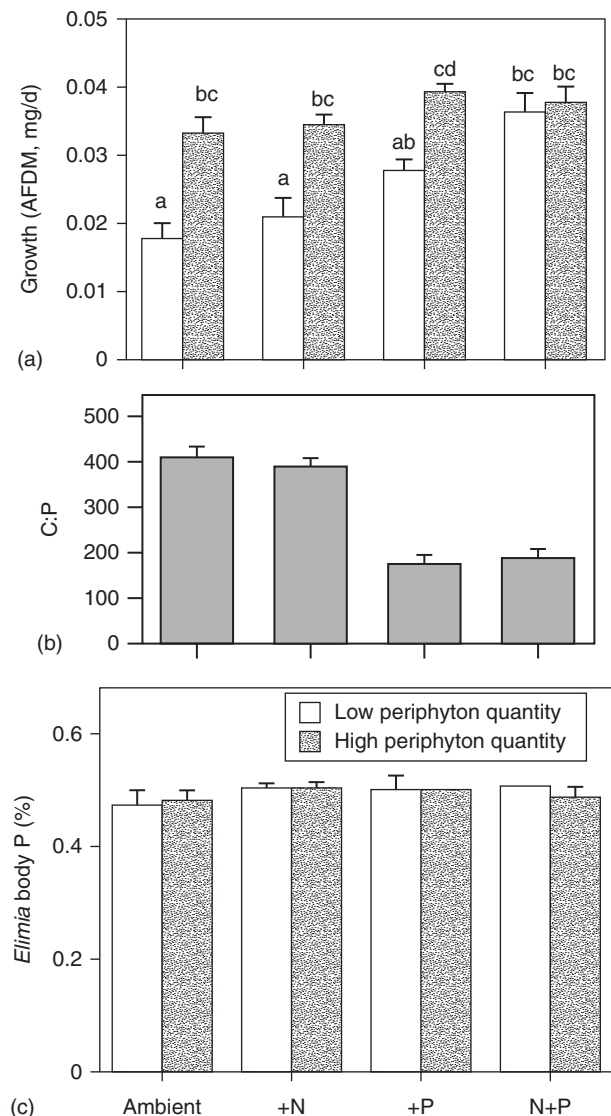
Figure 9 Effect of nutrient addition on periphyton and snail stoichiometry. Snails (*Elimia livescens*) were reared in experimental streams (flumes) and fed periphyton on clay tiles. An approximately similar periphyton biomass (low or high) was given to snails in all treatments. The experiment lasted 34 days. (a) Snails growth varied with nutrient treatments at low periphyton quantity but not high periphyton quantity. At low periphyton quantity, additions of P stimulated snail growth. (b) The C:P of the periphyton under different nutrient treatments. (c) The %P of the snails under different nutrient treatments. Note that the periphyton have more flexible nutrient content than the snails. Adapted from Stelzer RS and Lamberti GA (2002) Ecological stoichiometry in running waters: Periphyton chemical composition and snail growth. *Ecology* 83:1039–1051, with permission from Ecological Society of America (ESA).

Figure 10 Two aspects of stoichiometry altering nutrient fluxes through organisms. (a) The N:P released by zooplankton is positively related to the N:P of the food they are eating. (b) After accounting for the trend in (a), the consumers' own N:P ratio is negatively related to their N:P release (b). Reproduced from **Figure 4** in Elser JJ and Urabe J (1999) The stoichiometry of consumer-driven nutrient recycling: Theory, observations, and consequences. *Ecology* 80:735–751, with permission from Ecological Society of America (ESA).

nutrient recycling. First, the N:P recycled is positively related to the N:P in the food ingested. Note that because of the log scale in this Figure, the N:P released is not directly proportional to the N:P eaten. Instead, as N:P in the food increases slowly, N:P released increases very quickly. This upward trajectory was predicted mathematically, and it has been shown repeatedly in different nutrient cycling studies. When feeding on food of low N:P, a homeostatic consumer must keep the N for itself but recycle excess P, so that N:P released is very low. Likewise, when feeding on food of high N:P a homeostatic consumer must release excess N but keep relatively scarce P, making N:P recycled high. The second principle stoichiometric effect on nutrient recycling comes about because of the chemical variability among consumers. Consumers that are low in N:P will recycle at high N:P ratios and organisms that are high in N:P will recycle at low N:P. Given that many studies point to the critical importance of N:P loading as determining algal community structure, this example illustrates how ecological stoichiometry integrates species-level

information with ecosystem-level processes. It is remarkable that something as potentially complicated as the rates of nutrient release by living animals relates so strongly to simple measures such as nutrient content.

Community Dynamics

The separate effects of stoichiometry on animal growth and nutrient cycling considered above combine to influence community dynamics. One long-term culture study found two markedly different outcomes. In one, cultures had high abundance of algae but low abundance of grazers (a 'green' world). This first outcome was seen in the cultures with high algal C:P ratio. In the other outcome, cultures had low abundance of algae but high abundance of grazers (a 'clear' world). This second outcome was seen where algal C:P ratios were low. There was a sharp threshold between the two outcomes near the threshold, small differences in growth conditions promoting different stoichiometric ratios had large effect on community dynamics. Stoichiometry played a role in separating the green and the clear world. A second interesting aspect of this study was that high grazing promoted high food quality so that zooplankton had a positive demographic effect on their own populations – more zooplankton meant better food and therefore higher zooplankton growth. This kind of positive feedback between population size and population growth contrasts markedly with classical ideas about population regulation.

Mathematical, theoretical analyses have uncovered other surprising aspects of community dynamics associated with stoichiometry. Stoichiometrically explicit models of grazers, algae and nutrients suggest the existence of complex dynamics, including steady population changes through time, irregular, even chaotic, nonrepeating cycling of populations, and, in some versions of models, deterministic grazer extinction.

These different community dynamics emerge quite easily and naturally from models that explicitly incorporate stoichiometry. They suggest that classical, nonstoichiometric, ideas about population regulation, dynamics, and competition may be far off base when stoichiometric effects are important.

Whole-System Scale

These many stoichiometric patterns and processes that we have considered so far operate simultaneously to form aggregate stoichiometric properties of entire ecosystems. A touchstone for understanding ecosystem-level stoichiometry is the Redfield Ratio, a concept put forward by the oceanographer A.C. Redfield in the 1930s–1950s. Redfield noticed a correspondence between the C:N:P ratio in particulate matter of the surface ocean and dissolved nutrients in the deep ocean. The atomic ratio he observed was C_{106}:N_{16}:P_1, which is now called the Redfield Ratio. From this similarity he deduced that the entire global ocean had its nutrient content determined mainly by the biota. His argument was that both C and N come into stoichiometric balance with P, as set mainly by the demands of the oceanic biota. If either C or N are in short supply, the biogeochemical processes of primary production or N fixation can tap into atmospheric sources of these elements. Likewise, excesses of C or N can be vented to the atmosphere by respiration or denitrification. Phosphorus lacks an important gaseous phase, and its supply to the oceans is set by geological (or, now, human) action on the continents, which controls the rate of runoff from major river systems. The Redfield Ratio is similar to the ratios that many phytoplankton obtain when growing at either high growth rate or light limitation. The variation among species is such that if one takes an average of many different species, a C:N:P of 106:16:1 emerges. The Redfield ratio thus describes an overall mean of many species growing without strong single-element nutrient limitation.

The same kinds of measurements can be made for inland waters, but lakes, ponds, streams and rivers exhibit a greater degree of variability in their stoichiometric C:N:P ratios than do the oceans. This variability across sites can be due to many factors. Inland ecosystems are subject to widely varying inputs of elements from the atmosphere and from their watershed. They flush relatively rapidly compared with the time scales necessary for Redfield balancing mechanisms. Individual lakes, ponds, streams or rivers may be more homogeneous in terms of the many variable factors that determine biogeochemical potentials than the entire world's oceans; for example, highly unproductive lakes may lack anoxic zones that would support high levels of denitrification. They may be dominated by a small number of species during bloom conditions. There is a potentially large but variable detrital pool, poor in N or P, which may be found. Finally, they may be strongly limited by a single element, whether it be P or N or perhaps even some other nutrient. Given this large number of factors that can perturb C:N:P ratios away from Redfieldian balance, it is not surprising to see that freshwater systems are generally more stoichiometrically variable at the ecosystem level than are oceans ([Figure 11](#)). This great stoichiometric variability is the primary force that sets into motion many of the processes already described in this article, such as food quality constraints or stoichiometric determination of nutrient recycling
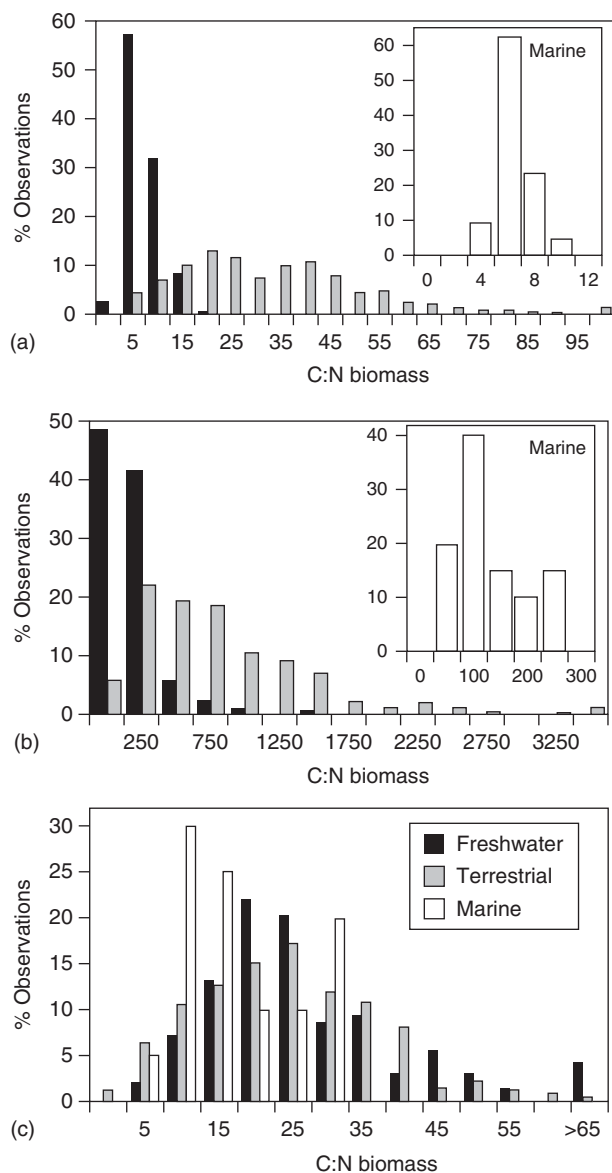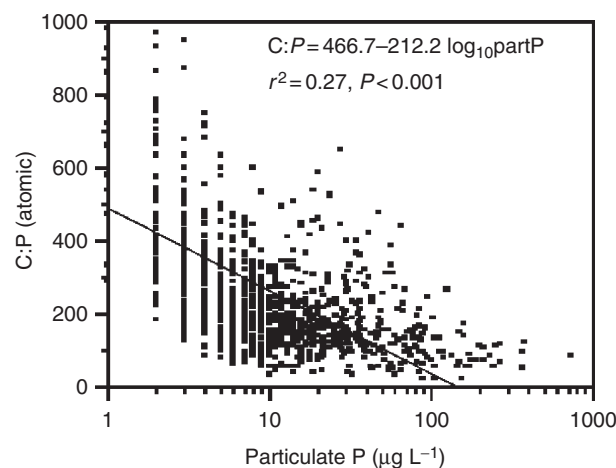
Figure 11 Variations in C:N:P stoichiometry at the base of marine (white), freshwater (black), and (for reference) terrestrial (gray) food webs. Data for lakes and oceans represent values of seston, including all particles living and dead, whereas data for terrestrial habitats reflect values for individual leaves. Note that freshwater systems have more variable C:N, C:P, and N:P ratios than do marine systems. This means the 'raw material' for stoichiometric determination of growth rate, nutrient cycling, etc. is greater in freshwater than marine systems. Though outside the scope of this article, this Figure also shows that terrestrial systems too have great stoichiometric variability at the base of their food chains. Reproduced from Figure 3.13 in Sterner RW and Elser JJ (2002) *Ecological Stoichiometry: The Biology of Elements from Molecules to the Biosphere*. Princeton, NJ: Princeton University Press. [permission being sought]

and thus is related to the input of carbon into particulate matter in inland ecosystems. As we discussed earlier, rates of carbon and nutrient acquisition in autotrophs are not tightly linked. When light is plentiful but nutrients are scarce, photosynthesis can be high compared to nutrient uptake and thus there develops a high C:P or C:N ratio in autotroph biomass. Characteristics of high light environments are clear water, shallow mixing or, in the case of benthos, shallow depth. The Light:Nutrient hypothesis suggests that stoichiometric variation a the base of food chains results from the relative balance of energy (light) and nutrients (N and P) available for primary producers.

Support for the Light:Nutrient hypothesis is accumulating. C:P ratios in 65 European lakes generally declined with increasing mixing depth (and zooplankton biomass correspondingly increased, as one would predict from food quality constraints). An elegant mathematical model of how mixing depth should affect lakes by way of stoichiometric shifts corresponded to the same patterns in the data. In another study, experimentally incubating phytoplankton from three Ohio lakes at different light levels and different nutrient levels caused seston C:N:P to shift in ways predicted by the Light:Nutrient hypothesis. C:P and C:N went up at higher light and down with increased nutrients. Third, seston in 112 Norwegian lakes covering a C:P from 24 to 1842 was related to measures of nutrient availability and it showed several different effects of decreased light owing to shading by algae in more productive water columns. Seston C:P in these Norwegian lakes declined strongly with increasing phosphorus (Figure 12). No effects of lake area,

patterns. Let us therefore now further analyze some of this great stoichiometric variability.

One explanation for this variation is the Light: Nutrient hypothesis. Light stimulates photosynthesis

Figure 12 Seston C:P ratios decline with increasing particulate P and therefore with overall productivity. Reproduced from Figure Hessen DO (2006) Determinants of seston C:P ratio in lakes. *Freshwater Biology* 51:1560–1569. [permission being sought]

season or latitude on C:P were detected. Particulate C did not correlate with C:P. The highest C:P ratios occurred in low P, therefore unproductive, lakes. C:P increased with increased values of the ratio of Secchi depth:total P and similarly C:P increased with the POC:chlorophyll ratio (representing the relative proportion of particulate detritus; Figure 5). As we saw earlier (Figure 8), high P *Daphnia* in these lakes were less abundant when seston C:P was high. There is mounting evidence that inland aquatic ecosystems do respond to relative availability of light vs. nutrients and thus these abiotic factors influence ecosystem dynamics in a way that is strongly mediated by stoichiometry.

One final stoichiometric aspect at the whole ecosystem scale relates to carbon fluxes in ecosystems. The fate and cycling of carbon in ecosystems is a topic of increasing concern in today's world. The human economy is run in part on cycling of carbon and nutrients for energy production, transportation, agriculture, etc. Fossil fuel combustion combined with land use changes have resulted in excess CO_2 building up in the atmosphere. Lakes often are carbon sources (not sinks) relative to global carbon cycling due to decomposition of terrestrially derived organic matter. However, lakes, and especially reservoirs, do build up significant reservoirs of carbon in their sediments. One early study suggested that lakes and reservoirs globally accumulated organic carbon at a rate of about 200 Tg year^{-1}, more even than the world's oceans even though the oceans cover a much greater fraction of Earth's surface. The fate of carbon cycling through ecosystems is closely related to stoichiometric ratios. It has been noted that ecosystems that are high in C:P or C:N show more carbon cycled through detrital food chain pathways, whereas those ecosystems with lower C:P or C:N ratios show more carbon channelized through herbivore/grazing pathways. We can expect that lakes and reservoirs that are higher in C:P and C:N likely bury a larger fraction of their organic carbon than do lakes at the opposite end of the stoichiometric gradient. Thus, ecological stoichiometry can be an important aspect of how inland ecosystems fit into global carbon cycles.

Further Reading

Andersen T, Elser JJ, and Hesson DO (2004) Stoichiometry and population dynamics. *Ecology Letters* 7: 884–900.

Boersma M and Elser JJ (2006) Too much of a good thing: On stoichiometrically balanced diets and maximal growth. *Ecology* 87: 1325–1330.

Cross WF, Benstead JP, Rosemond AD, and Wallace JB (2003) Consumer-resource stoichiometry in detritus-based streams. *Ecology Letters* 6: 721–732.

Elser JJ, Acharya K, Kyle M, et al. (2003) Growth rate–stoichiometry couplings in diverse biota. *Ecology Letters* 6: 936–943.

Frost PC, Benstead JP, Cross WF, et al. (2006) Threshold elemental ratios of carbon and phosphorus in aquatic consumers. *Ecology Letters* 9: 774–779.

Frost PC, Hillebrand H, and Kahlert M (2005) Low algal carbon content and its effect on the C:P stoichiometry of periphyton. *Freshwater Biology* 50: 1800–1807.

Hecky RE, Campbell P, and Hendzel LL (1993) The stoichiometry of carbon, nitrogen, and phosphorus in particulate matter of lakes and oceans. *Limnology and Oceanography* 38: 709–724.

Hendrixson HA, Sterner RW, and Kay AD (2007) Elemental stoichiometry of freshwater fish in relation to phylogeny, allometry, and ecology. *Journal of Fish Biology* 70: 121–140.

Hessen DO (2006) Determinants of seston C:P ratio in lakes. *Freshwater Biology* 51: 1560–1569.

Karimi R and Folt CL (2006) Beyond macronutrients: Element variability and multielement stoichiometry in freshwater invertebrates. *Ecology Letters* 9: 1273–1283.

Quigg A, Finkel ZV, Irwin AJ, et al. (2003) The evolutionary inheritance of elemental stoichiometry in marine phytoplankton. *Nature* 425: 291–294.

Sterner RW (1995) Elemental stoichiometry of species in ecosystems. In: Jones C and Lawton J (eds.) *Linking Species and Ecosystems*, pp. 240–252. New York: Chapman and Hall.

Sterner RW and Elser JJ (2002) *Ecological Stoichiometry: The Biology of Elements from Molecules to the Biosphere*. Princeton, NJ: Princeton University Press.

Sterner RW and Hessen DO (1994) Algal nutrient limitation and the nutrition of aquatic herbivores. *Annual Review of Ecology and Systematics* 25(1–29).

Vanni MJ, Flecker AS, et al. (2002) Stoichiometry of nutrient recycling by vertebrates in a tropical stream: Linking species identity and ecosystem processes. *Ecology Letters* 5(2): 285–293.

Relevant Website

www.wikipedia.com.