

Stoichiometric relationships among producers, consumers and nutrient cycling in pelagic ecosystems

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Abstract. Most ecosystem models consolidate members of food-webs, e.g. species, into a small number of functional components. Each of these is then described by a single state variable such as biomass. When a multivariate approach incorporating multiple substances within components is substituted for this univariate one, a 'stoichiometric' model is formed. Here we show that the Nitrogen:Phosphorus ratio within zooplankton herbivores varies substantially interspecifically but not intraspecifically. By using stoichiometric theory and recent measurements of the N:P ratio within different zooplankton taxa, we calculate large differences in ratios of nutrients recycled by different zooplankton species. Finally, we demonstrate that N:P stoichiometry can successfully account for shifts in N- and P-limitation previously observed in whole-lake experiments. Species stoichiometry merges food-web dynamics with biogeochemical cycles to yield new insights.

Abbreviations: b — N:P in zooplankton biomass, f — N:P in algal biomass, L — maximum accumulation efficiency, N:P — ratio of nitrogen to phosphorus (moles:moles), s — N:P supply ratio from grazers, TN : Total nitrogen = seston N + dissolved N (μ moles/liter), TP — Total phosphorus = seston P + dissolved P (μ moles/liter).

Introduction

For the drama of life is like a puppet show in which stage, scenery, actors and all are made of the same stuff. The players, indeed, 'have their exits and their entrances,' but the exit is by way of translation into the substance of the stage; and each entrance is a transformation scene. So stage and players are bound together in the close partnership of an intimate comedy; and if we would catch the spirit of the piece, our attention must not all be absorbed in the characters alone, but must be extended also to the scene, of which they are born, on which they play their part, and with which, in a little while, they merge again (Lotka 1925).

So was imbedded a lengthy discussion of elemental cycling into a book best known today as a landmark of population theory. That Lotka's writings in biogeochemistry are infrequently cited while his contributions to population theory are widely recognized attests to the fact that population theory and biogeochemistry have seldom been blended. Biogeochemical studies often (for whatever reason) pay little attention to interspecific variations in constituent species and in their individual dynamics, concentrating instead on courser categories such as trophic levels. At the same time, population-level studies often neglect biogeochemistry. However, when this blend has been made, interesting findings have emerged (e.g. DeAngelis et al. 1989). With a reference to Lotka, here we will attempt to catch a portion of the 'spirit of the piece' in the pelagic food web which has been overlooked.

Nutrient cycling in pelagic ecosystems

The ratio of supply rates of two chemical resources can have a great influence on community structure (Tilman 1982). In aquatic environments, the N:P supply ratio is a key axis along which community structures varies (Hecky & Kilham 1988). 'Supply' in this context means the total flux of nutrient into the dissolved pool; thus, there are many different sources of supply. Allochthonous loading from runoff, groundwater, and rainfall is one source of nutrient into pelagic pools, including the dissolved pool. Autochthonous sources, sinks and transformations include N-fixation (Howarth et al. 1988), nitrification and denitrification (Seitzinger 1988). These fluxes together with transport processes, including sedimentation and resuspension (Dillon, Evans & Molot 1990) and eddy diffusivity (Stauffer 1987), modify the N and P concentrations in the surface layer from those based solely on loading. Each of the above contributes either directly or indirectly to the dissolved pools of nutrients.

Watershed inputs and physical mixing processes may dominate supply early in the growing season in temperate zone lakes. Many of the biogeochemical controls on the rates of supply from the watershed and from sediments are well understood. These fluxes are mediated by watershed morphometry, redox potential, pH, and physical turbulence. However, as density stratification becomes increasingly strong, nutrients recycled by consumers within the upper layer should make larger and larger contributions to the dissolved pool in this stratum. Organisms recycling nutrients *in situ* include microbes (Goldman 1984), zooplankton (Lehman 1984; Sterner 1989), and fish (Vanni & Findlay 1990). The relative importance of each of these is hotly contested; it may be that dominant recyclers vary from time to time and from place to place. Here, we will concentrate on the herbivorous zooplankton. Internal resupply by consumers is controlled

by factors such as consumption, respiration, excretion and migration, and is mediated by the structure of the food web. Enough has been learned about external nutrient inputs for the development of successful predictive models (Schindler 1971; Dillon & Rigler 1974; Fee 1979), and knowledge of controls on most other biogeochemical processes is growing. However, comparatively little is known about factors controlling internal resupply. Most studies of nutrient regeneration go no further than to measure this source of nutrient relative to others, with few attempts at cross-system comparisons, and little regard for determining the controlling mechanisms. Thus, we currently are ignorant of the controls of a major portion of N and P supply rates.

The gaps in our understanding of internal recycling processes are made more obvious by recent evidence indicating that the structure of a lake's food web exerts considerable influence on nutrient dynamics. Shifts in fish community composition, which have been repeatedly demonstrated to alter the intensity of zooplanktivory, can now be seen to have a clear and perhaps repeatable connection to nutrient budgets. A number of recent studies have measured P following fish manipulation. In some, increasing planktivory resulted in increases in TP (Drenner et al. 1990; Mazumder et al. 1990) and in others, reduction in planktivory resulted in decreased TP (Shapiro & Wright 1984; Reinertsen et al. 1990). One study measured both P and N, and reduction in planktivory decreased both TP and TN (Sanni & Wærvågen 1990). These studies suggest that the intensity of zooplanktivory is positively correlated with nutrients in the combined seston and dissolved pools. Under high planktivory, zooplankton biomass is generally lowered and zooplankton size structure is reduced (Persson et al. 1988), indicating that there is a lowered amount of nutrient within zooplankton biomass. Under these conditions, nutrients may be shifted into the seston and dissolved pools. In the opposite case, under low planktivory, nutrients shift out of the seston and dissolved pools; these may then appear in the zooplankton biomass. Such redistributions have not yet been measured, but are consistent with available evidence. Nutrient redistribution is not limited to this simple scheme; manipulation of zooplankton has also been shown to alter P sedimentation (Bloesch & Bürgi 1989) and reduction of zooplanktivory has been shown to shift P from seston into the dissolved pool (Faafeng & Brabrand 1990). If different food web structures induce such changes in the distribution of nutrients within pools, they also must induce changes in the fluxes of nutrients between pools. The interactions between food web dynamics and biogeochemistry thus appear to be strong, but at the present are poorly understood. There are many potential facets of this general problem which will require examination. Here, we will discuss a combination of theoretical and empirical studies which seeks to describe and predict how food

web structure and the N:P ratio are interrelated. By combining theory with single-species data on different zooplankton taxa we can successfully account for previously-described shifts in N and P limitation in whole ecosystem studies.

A stoichiometric model

Most food-web models treat species as univariate parameters characterized either by numbers, biomass, carbon content, or energy. A multivariate, stoichiometric approach of multiple elements within each species is an alternative approach. Such an approach requires linking phenomena on many scales, from elemental cycling in ecosystems to species structure in food webs to physiological budgeting of elements within constituent species.

A key relationship that must be part of this approach is the chemical content of different species. When organisms feed on resources having chemical composition similar to their own needs for growth and metabolism, little ingested food need be discarded as waste. However, when the chemical constitution of the food is imbalanced from the standpoint of the consumer, much ingested food is superfluous, and whatever essential material that is most deficient can become growth-limiting. At the plant-animal interface such imbalances in chemical content are severe since the composition of plant matter is very different from animal tissue. Furthermore, plants and animals demonstrate considerable interspecific variation in biochemical composition. Thus, the elemental stoichiometry of individual species at the plant-animal interface may have considerable, but yet underscribed, biogeochemical significance.

Recently, several models based on stoichiometry have been advanced to explain rates of nutrient resupply by grazing herbivores. These models are meant to describe how stoichiometry influences N and P recycling rates. Two such models (Olsen et al. 1986; Hessen & Anderson 1991) predict rates of P release given the C:P ratio in the animal's food together with its P requirements. By conservation of mass it is possible to calculate the P partitioned into growth vs. the P released back into the dissolved pool. A third model (Sterner 1990) predicts the ratio of N:P recycled, using mass balance to calculate the N:P supply ratio (s) given the N:P ratio in the animal's food (f) together with the N:P ratio in the animal's own body tissues (b). A critical feature of the third model is in the degree of homeostasis of the N:P ratio of zooplankton (b). When b is constant, s has a linear relationship with f in the range of $f > b$:

$$s = \frac{f - bL}{(1 - L)}$$

where L = the maximum accumulation efficiency for that element. An accumulation efficiency is defined (Sterner 1990) as a fractional number between zero and one given by the ratio of the rate of material leaving the food pool divided by the rate of material going into growth and reproduction. In the absence of sloppy feeding, the accumulation efficiency is the same as a gross growth efficiency (i.e. production over ingestion). The maximum accumulation efficiency for a given element, L , should occur when the food is deficient in that element. Most estimates of gross growth efficiency probably underestimate L because they have not specifically dealt with foods low in content of whichever element was being measured. One study by Olsen et al. (1986) showed that the release rate of P by *Daphnia* becomes essentially zero when the C:P ratio in the food exceeds a critical value in the range 320–430. These results indicate that L is near one in this case. The relationship becomes curvilinear in the range $f < b$:

$$s = \frac{f(1 - L)}{1 - \frac{Lf}{b}}$$

Finally, where $f = b$, the model predicts $s = f$.

Species stoichiometry coupled to grazer homeostasis makes two major predictions. First, the homeostatic herbivore should assimilate with higher efficiency any element in short supply in its food compared to elements appearing in surplus. Thus, feeding on N-limited algae, which have low N:P ratios, should result in low rates of N recycling relative to P. In contrast, feeding on P-limited algae, which have high N:P ratios, should result in low rates of P recycling relative to N. The effect of the homeostatic herbivore on algal growth limitation can be analyzed by a plot of s vs. f (Fig. 1A). When $s > f$, the grazer should influence algae to become P-, rather than N-limited, and when $s < f$, it should influence them to become N-, rather than P-limited. Note that when $f > b$, a shift toward P-limitation is predicted while when $f < b$, a shift toward N-limitation is predicted. The greater the value of L , the greater the predicted shift. The tendency for a homeostatic grazer to deflect the N:P supply ratio away from the N:P ratio in its food is an instability in the herbivore-plant interaction which would be overlooked without explicit consideration of multiple nutrient cycling.

The second major prediction made by stoichiometry and homeostasis is that the N:P resupply ratio should depend upon the N:P in the bodies of the herbivores. Herbivore species with a high ratio of N:P in their tissues should resupply nutrients at a relatively low N:P ratio compared to herbivore species with low body N:P (Fig. 1B). Consider a situation with two herbivore species of contrasting b . When f is between the lower b and

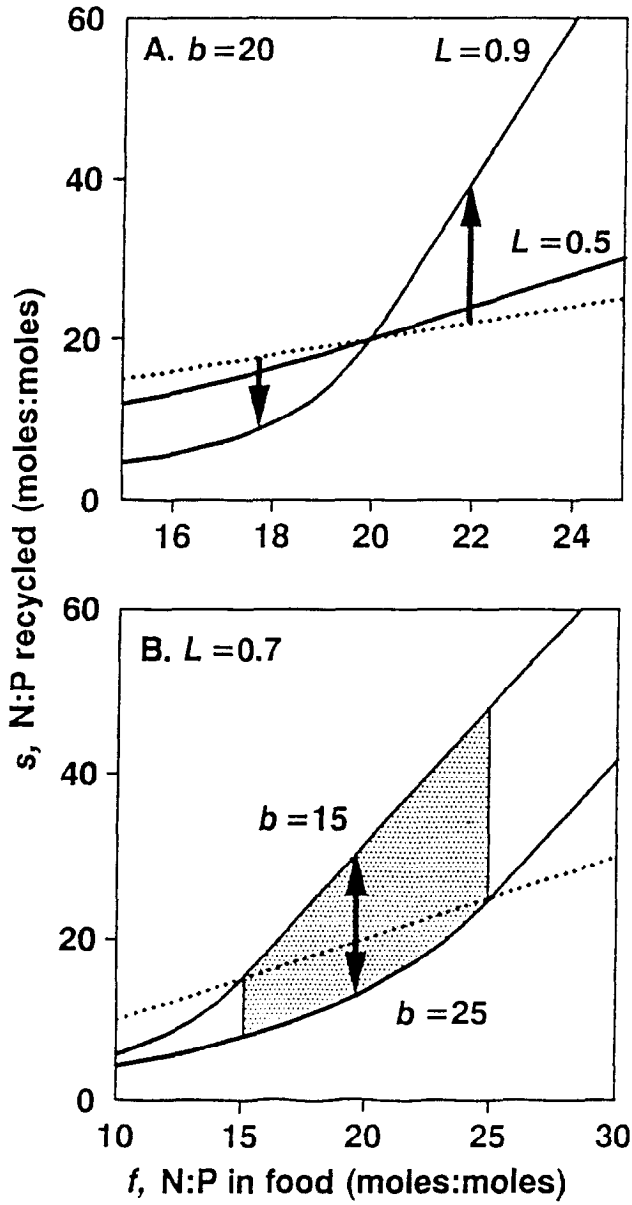


Fig. 1. N:P recycled (s) as a function of N:P in the grazers' food (f) as calculated from the recycling model (Sternner 1990) using values of zooplankton body N:P (b) and accumulation efficiency (L) as indicated. Dotted lines indicate $s = f$. A. The N:P supply ratios for one value of b and two different values of L . Up arrow: shift toward P-limitation; down arrow: shift toward N-limitation. B. The N:P supply ratios recycled by two herbivores differing in b (species 1, $b = 15$; species 2, $b = 25$). In the range $15 < f < 25$ the two grazer species skew the N:P ratio in opposite directions.

the higher b (Fig. 1B, stippled area), shifts in dominance from one grazer species to the other will skew N:P supply in opposite directions. Thus, community shifts between these two grazer species could induce different limiting resources for algal growth. Divorcing the food web structure from nutrient cycling or vice versa could easily lead one to miss some important interactions.

The validity of this model hinges on two points. First, the N:P ratio of individual herbivore species must be relatively homeostatic compared to the ratio in their food. Second, the N:P ratio of different herbivore species must differ from each other. Recent evidence indicates that both of these points are satisfied. In marine environments, where metazoan zooplankton herbivores are highly diverse (multiple phyla), the N:P ratio of individual herbivore species has long been known to be taxon-specific (Corner & Davies 1971). In freshwaters, metazoan zooplankton come from just two phyla (Rotifera and Arthropoda); nevertheless, recent study has shown that the zooplankton N:P ratio in freshwaters also is strongly taxon-specific.

Ratios of N:P of freshwater Crustacea vary between at least 12 and 52 (Table 1). Although additional measurements, especially of prominent groups not included here (e.g. copepod nauplii and rotifers) must still be made, certain important patterns have emerged. First, copepods have higher N:P ratios than cladocerans. The genus *Daphnia* has an especially low N:P compared to all other zooplankton so far measured. Second, P content — which is higher in *Daphnia* than in any of the other species studied — varies more than N content. There is a smaller analytical error in the method used for N than for P, but the standard deviations within zooplankton groups are fairly small relative to inter-taxon differences for P, but not for N. Thus, differences in analytical techniques does not explain why zooplankton were found to differ more in P content than in N content. We conclude that taxon-specific differences in the N:P ratio in these species are mostly attributable to differences in P content. Third, despite a known wide variation in the elemental ratios in their food, the N- and P-content of individual zooplankton species show a remarkably stable N:P ratio. In Table 1, the N:P ratios of individual taxa are similar across experiments, which represent wide ranges of nutritional conditions and life stages. Note too that the variation in N and P contents reported in Table 1 includes that associated with chemical analysis as well as true biological variation. Thus, rearing populations of individual zooplankton taxa on defined foods differing in biochemical composition offers the greatest power in determining the degree of homeostasis of the zooplankton N:P ratio. Such a study (Sterner et al. 1992) found that the N:P of zooplankton biomass varied only 10% when exposed to foods differing by > 700% in

Table 1. Elemental composition of freshwater zooplankton.

Taxon (Co = copepod, Cl = cladoceran)	n	%N	sd	n	%P	sd	N:P
Exp 1							
<i>Acanthodiaptomus denticornis</i> (Co)	13	11.0	1.7	22	0.63	0.20	38.7
<i>Bosmina longispina</i> (Cl)	18	9.5	1.0	15	0.87	0.15	24.2
<i>Diaphanosoma brachyurum</i> (Cl)	13	9.3	0.6	13	1.05	0.19	19.6
<i>Holopedium gibberum</i> (Cl)	13	9.3	0.8	14	1.08	0.07	19.1
<i>Daphnia longispina</i> (Cl)	47	9.2	0.8	35	1.42	0.26	14.3
Exp. 2							
<i>Eudiaptomus gracilis</i> (Co)	7	10.0	0.8	5	0.41	0.08	52.1
<i>Bosmina longispina</i> (Cl)	5	9.3	1.3	5	0.68	0.19	29.3
<i>Diaphanosoma brachyurum</i> (Cl)	2	10.5	—	2	0.95	—	23.4
<i>Daphnia longispina</i> (Cl)	4	9.5	0.6	5	1.58	0.26	12.9
<i>Daphnia cucullata</i> (Cl)	5	8.9	0.7	7	1.55	0.34	12.3
Exp. 3							
<i>Daphnia magna</i> (Cl)	43	8.2	1.0	29	1.36	0.3	12.7

Exp. 1: a series of measurements of C, N, and P in natural populations from a humic lake through a summer season (Andersen & Hessen 1991). Exp. 2: measurements of C, N, and P in a number of zooplankton species in spring, summer and autumn from five lakes with varying trophic and sestonic elemental composition (Hessen & Lyche 1991). Exp. 3: a laboratory study of *Daphnia magna* fed varying quantity and quality of phytoplankton in laboratory culture (Hessen 1990). N determined by CHN analysis and P determined with the ascorbic acid technique following H_2O_2 treatment and persulfate digestion. Separate measurements (number = n) consisted of 2–30 individuals. Percent N and percent P are by mass and the N:P ratio is by atoms.

the N:P ratio. Berberovic (1990) has argued that the elemental content of *Daphnia* in Lake Constance (in terms of C, H, and N; P was not measured) does not differ for different *Daphnia* spp., but shows some small variation within the life cycle. Behrendt (1990) noted large seasonal differences in the C:N:P of the phytoplankton of the Größer Müggelsee but relative constancy within the zooplankton. Zooplankton, in contrast to their food, do not store P or N; elements present in the food in excess of current requirements are recycled. Zooplankton do store energy as lipids, but these are either neutral fats or wax esters, neither of which contain much P or N. Thus, the two conditions required by the recycling model are met: the herbivore N:P ratio differs interspecifically, but not intra-specifically.

When the elemental composition of different zooplankton (Table 1) is

incorporated into the recycling model, we can begin to predict how the N:P supply ratio should respond to shifts in zooplankton species composition (Fig. 2). It is clear from Fig. 2 that the identity of the dominant herbivore species should have pronounced effects on the N:P supply ratio, particularly under P-limitation (f high) and when L is high. Species stoichiometry predicts that herbivore assemblages dominated by cladocerans, especially *Daphnia*, should be characterized by high N:P supply ratios, and thus lead algae toward P limitation. In contrast, herbivore assemblages dominated by copepods should be characterized by low N:P supply ratios, and thus lead algae toward N-limitation.

Field evidence for stoichiometric shifts

A very compelling demonstration of the influence of food web structure on the N:P supply ratio comes from a study of experimentally-induced shifts in herbivore species composition where N and P limitation of algal growth were simultaneously measured (Elser et al. 1988). N-limitation of algal growth was assessed by determining the enhancement of dark ^{14}C uptake upon NH_4^+ enrichment (Yentsch et al. 1977). P-limitation was assessed by the activity of alkaline phosphatase (Pettersson 1980). In whole-lake experiments, the food webs of two lakes were reciprocally manipulated during late spring: in Peter Lake, piscivorous bass were removed and zooplanktivorous cyprinids were enhanced, while in Tuesday Lake, bass were introduced and cyprinids were removed. N and P limitation were found to be inversely correlated and *in situ* transitions between N and P limitation were rapid (< 1 week). N limitation prevailed when the zooplankton were dominated by small-bodied species and P limitation prevailed when the community was dominated by large-bodied species, especially *Daphnia*. In supporting experiments in mesocosms, shifts in N vs. P limitation occurred within 3 d after manipulations of zooplankton. This study indicated that the structure of the herbivore guild was highly influential on the N:P supply ratio.

We have now calculated the N:P ratio of recycled nutrients (s) in Peter and Tuesday Lakes *a posteriori* for periods in the summer following fish manipulation when the zooplankton species and the relative degrees of N and P limitation in the algae were distinctly changing. To calculate the N:P supply ratio s for a given gross growth efficiency, it is necessary to know both the N:P in the seston food (f) and the N:P in the zooplankton biomass (b). As seston N:P ratio was not measured, we used the mean epilimnetic total N:total P (TN:TP) ratios during the study period (Peter = 13.3, Tuesday = 11.2). This number served only to allow us to calculate seasonal shifts; we do not expect that the TN:TP ratio is a good proxy for

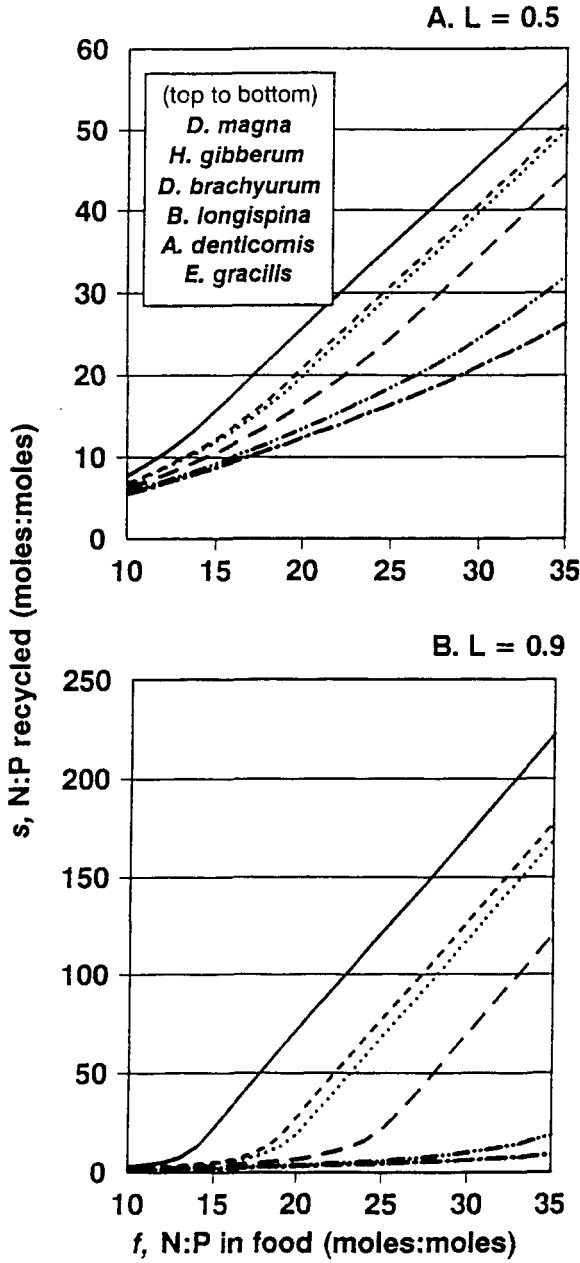


Fig. 2. The N:P ratio recycled (s) as a function of the N:P ratio in the grazers' food (f) using values for zooplankton body N:P (b) from Table 1. Where species were measured in > 1 Exp., means were weighted by sample size. For clarity, only one *Daphnia* sp. is indicated as all three *Daphnia* spp. were very similar. A. $L = 0.5$. B. $L = 0.9$.

seston N:P, especially because of the usual large amount of DON present in natural waters. Zooplankton b also was not measured. Thus, we estimated b for each date on the basis of the percentage of total biomass contributed by copepods vs. cladocerans (mostly *Daphnia*), assuming that copepods had an N:P of 39:1 (similar to *Acanthodiaptomus*, Table 1) and that *Daphnia* had an N:P of 13:1 (mean of *Daphnia* spp., Table 1). Because of the uncertainties in our estimates of f and b as well as a lack of information about background nutrient supply from sediments, fish, microbes, etc., we are concerned here only with qualitative outcomes.

In both lakes, alterations in the abundance of zooplanktivorous fish caused shifts in the composition of the zooplankton as the dominance shifted between copepods and cladocerans (Fig. 3). In Peter Lake (bass removed), cladocerans decreased and copepods became increasingly dominant, and in Tuesday Lake (bass added), copepods decreased and cladocerans became more dominant. Shifts in Tuesday Lake were particularly large: from 100% to almost 0% copepods. Thus, shifts in b also were large (39 to 13) in this lake. Our calculations indicate that substantial changes in the ratio of N:P recycled (s) also occurred during these time periods (Fig. 4). The timing of shifts in N- vs. P-limitation recorded by physiological assays corresponded well with the timing of shifts in s (Fig. 4). For both lakes, periods when s was high were periods of P-, rather than N-limitation, and periods when s was low were periods of N-, rather than P-limitation (Fig. 4). In applying stoichiometric theory *a posteriori* to this study, the qualitative shifts from one limiting element to another were correctly accounted for.

Conclusions

Nutrients in food webs

Results of several decades of repeated experimentation on lake food webs have shown that changes in the biomass or species composition of top trophic levels (fish) often propagate through the food web, sometimes reaching the primary producers at the very base (Hrbáček et al. 1961; Lynch & Shapiro 1981; Carpenter et al. 1985; McQueen et al. 1986). In the 'biomanipulation' of lakes, fish communities are modified so as to shift zooplankton grazers from small-bodied species to large-bodied ones, especially *Daphnia*; frequently a reduction in the standing stock of phytoplankton can be achieved. The conventional interpretation has been that lowered algal abundance is caused by increased grazing rates by the

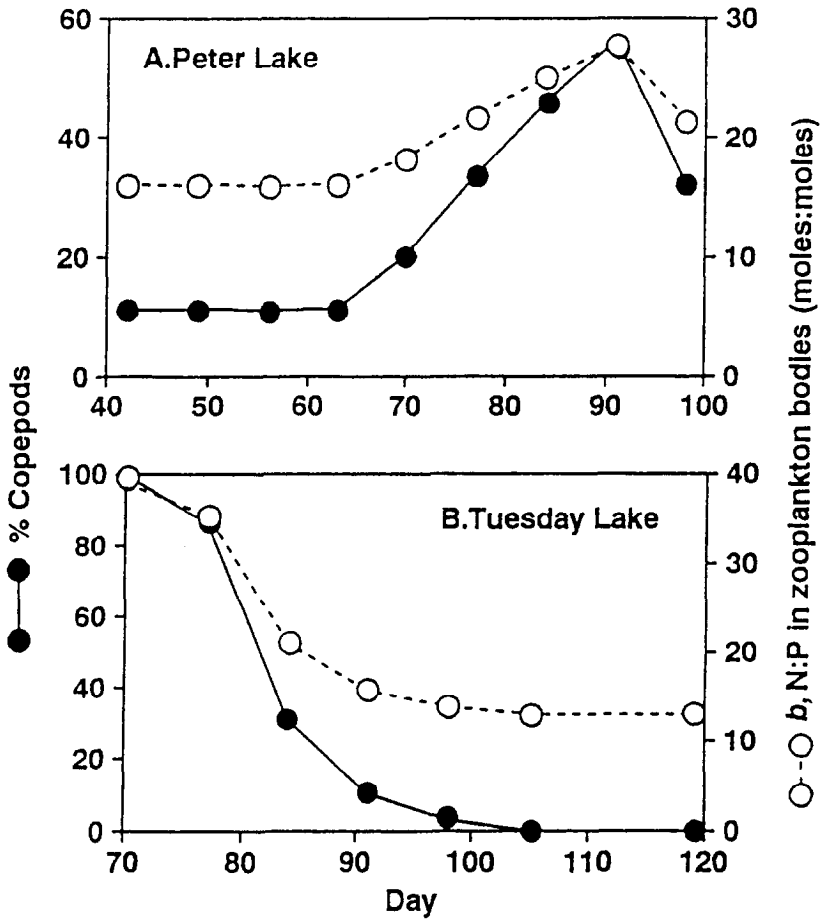


Fig. 3. Seasonal shifts in herbivore species composition and the calculated N:P ratio of the zooplankton pool (*b*) in Peter and Tuesday lakes in response to manipulated fish assemblages. Day 1 = 20 May 1985.

larger herbivores. A viable alternative interpretation involves biogeochemical functioning. Herbivore-species shifts change not only grazing pressure, they also cause rearrangements of N and P among biological and chemical pools. Specifically, the high P content of *Daphnia* means that shifting zooplankton to *Daphnia* dominance, even while keeping zooplankton biomass constant, funnels P out of the algal pool, which would decrease the algal standing stock if P were limiting. P may be accumulated in *Daphnia* biomass or may be lost from epilimnetic waters through post-mortem sedimentation or predatory losses. Note that field evidence already discussed (Shapiro & Wright 1984; Drenner et al. 1990; Mazumder

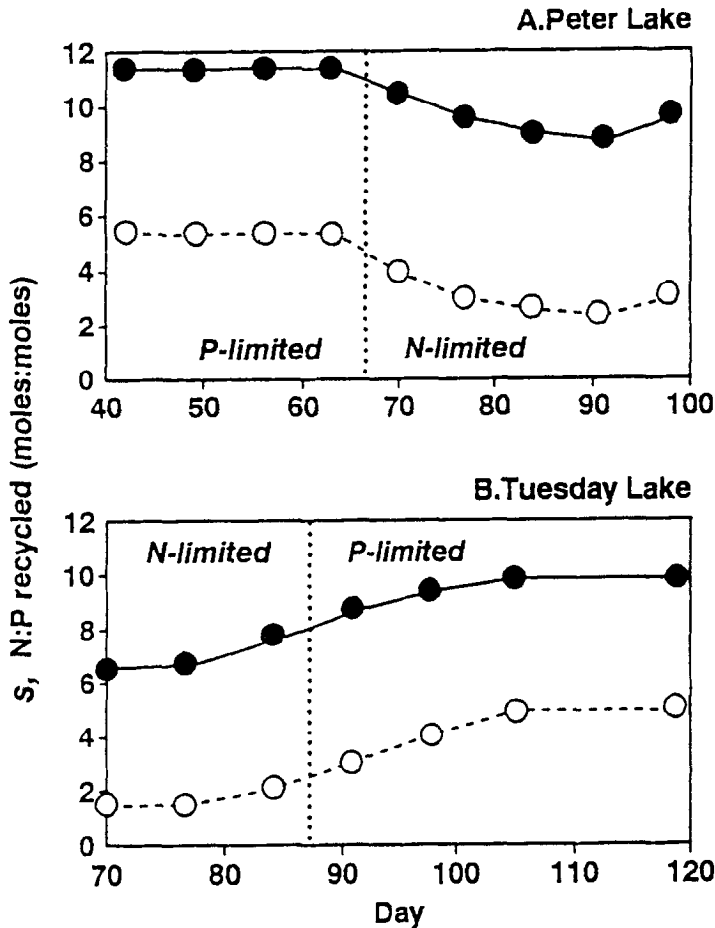


Fig. 4. Calculated seasonal shifts in the N:P supply ratio from herbivore nutrient regeneration (s) in Peter and Tuesday lakes. Solid: $L = 0.5$, dashed $L = 0.9$. Vertical dotted lines indicate shifts in algal nutrient limitation as measured by independent assays. Day 1 = 20 May, 1985.

et al. 1990; Reinertsen et al. 1990; Sanni & Wærvågen 1990) is consistent with this scenario. The situation under N-limitation is different. N content is less variable across zooplankton taxa than is P content. Thus, in an N-limited lake, shifts between herbivore species need not have a large impact on the algal N pool. Species stoichiometry predicts that functional linkages among species are qualitatively different when limiting elements differ. Such stoichiometric relationships may help explain the variable outcome of top-trophic-level manipulations on algal biomass (McQueen et al. 1986). There is a clear need for a greater integration of biogeochemistry

with trophic-based models to achieve a more comprehensive understanding of food web dynamics.

A food web is a complex network of individual organisms interacting in a dynamic environment. To study them, ecologists have created several abstractions of food webs, each of which has contributed to ecological theory. For example, when species are represented as accumulations of energy, trophic pyramids (Elton 1927) and perhaps food chain lengths (Schoener 1989) can be explained. Alternatively, interspecific interactions may be represented as either stimulatory, neutral, or inhibitory. Representative pluses, zeroes and minuses can then be arranged into a community matrix (Cohen 1978). Structural constraints on the numbers of predator species compared to prey species and the numbers of trophic links then emerge. A stoichiometric abstraction should identify patterns and processes not identified by extant theories.

It is likely that the stoichiometric aspect of trophic interactions is important in many different habitats. Stoichiometric imbalances between the elemental composition of leaf litter and the requirements of fungi, bacteria, and soil invertebrates influence nutrient release patterns and, thus, plant resource limitation (Wedin & Tilman 1990). In large mammals, nutrient imbalances in forage plants are known to influence rates of consumption as well as excretion (McNaughton 1990). Two aspects of ecosystem structure which likely magnify the importance of the stoichiometry of herbivore species are 1) the quantitative importance of herbivores in nutrient supply relative to all other potential sources, and 2) a high herbivore biomass relative to plant biomass. In temperate forests, summertime nutrient cycling can be dominated by frass fall from insect herbivores (Reichle et al. 1973). Given that herbivorous arthropods disproportionately accumulate certain elements relative to others (Weiss & Berenbaum 1989), we speculate that insect herbivores might also induce qualitative changes in resource supply ratios similar to those described here for zooplankton.

Feedbacks to the zooplankton

Homeostasis in herbivores relative to their food implies adjustments of net assimilation or excretion of elements to match metabolic and somatic requirements. Zooplankton, like other herbivores, normally exhibit lower C:P or C:N ratios than their food. When the C:P or C:N ratio of ingested food exceeds the animal's requirements, it must either assimilate less C relative to P or dispose of the excess C through respiration. In either case, growth efficiency in terms of C must be reduced when feeding on food

rich in C. The response of zooplankton exposed to food low in mineral content is to greatly lower the rate of clearance and ingestion, which also lowers both N and P release rates (Sterner & Smith 1993). The fact that zooplankton species differ in their elemental content means that relative success of different herbivore species might be influenced not just by food quantity, measured by units such as carbon, but also by food quality, in terms of N or P. *Daphnia*, for example, should be at a disadvantage to copepods when competing for P-limited food, as a larger biomass of copepods than *Daphnia* can be produced per unit P. Other herbivores are known to experience such nutritional challenges. N plays an important role in the nutrition of herbivores in terrestrial systems (Mattson 1980). Studies of insects (Dale 1988) and sea urchins (Renaud et al. 1990) in addition to zooplankton (Scott 1980; Checkley 1985; Kiørboe 1989; Sterner et al. 1992; Urabe & Watanabe 1992) have indicated that plant mineral nutrition influences food quality for herbivores. In mammals, mineral nutrient deficiency may be widespread (McNaughton 1988) even if it may play a small role in foraging decisions (Belovsky 1990). Stoichiometry presents a framework for studying such interactions within the herbivore guild and linking them to rates of nutrient cycling in the food web as a whole.

Conclusions

Stoichiometry in ecological interactions is hardly a new subject. One of the earliest and best-studied of all ecological principles, Liebig's Law of the Minimum, is stoichiometric. Lotka (1925) used the term in an ecological context. A. C. Redfield (1958) used stoichiometry to show how important organisms were to oceanic nutrient cycles. Morowitz (1968) wrote of the importance of biochemical content in constraining ecological interactions. More recently, Reiners (1986) has called stoichiometric models 'complementary' models of ecosystem dynamics. In this paper, we have discussed a stoichiometric model and have shown how it can potentially shed light on interactions that would otherwise appear mysterious.

In spite of a long period of awareness, the study of the stoichiometric properties of organisms in ecosystems has been limited. Much remains to be learned. A more complete understanding of the role of organisms in ecosystem functioning requires knowledge of not just biomass or numbers, but also the amounts and ratios of biologically critical substances at each point in the food web. Progress in the study of nutrient cycling processes may proceed more rapidly by recognizing that many regenerative pro-

cesses reflect the physiological properties of individual species seeking to maximize their success. Greater blending of biogeochemistry and trophic-based ecology is required.

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