

Carbon:phosphorus stoichiometry and food chain production

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Abstract

Incident light was manipulated in large plankton towers containing algae, microbes, and herbivores. Paradoxically, food chain production was lower with greater light energy input. This apparent paradox is resolved by recognizing stoichiometric constraints to food chain production. At high light, elevated algal biomass was achieved mainly by increases in cellular carbon. Consumers have a high phosphorus demand for growth, and thus a large excess of carbon inhibited, rather than stimulated, their growth. These experiments may help us predict the consequences of anthropogenic perturbations in nutrients, carbon, and solar energy. They also may help us to understand the wide range of consumer biomass and production at a given level of primary productivity in ecosystems.

Keywords

Bacteria, carbon, energy, nutrient limitation, phosphorus, phytoplankton, trophic level, zooplankton.

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INTRODUCTION

The rate at which a food chain provides energy and materials for upper trophic levels is a fundamental property for ecologists to study and a practical issue for management of systems where animals or their products are harvested. It is one of the major services provided by ecosystems, and it is a large part of the concern about global sustainability of the human population. Currently popular ecological theories predict either a positive or a neutral response of the biomass of upper trophic levels to increased primary production, depending on the number of trophic levels in an ecosystem (Oksanen *et al.* 1981; Power 1992). Empirical patterns between primary and secondary production are not yet so well defined. Secondary production is positively correlated with primary production when one looks over many orders of magnitude of these variables (e.g. McNaughton *et al.* 1989; Cyr & Pace 1993; Downing & Plante 1993), but the scatter is large, suggesting a wide range of possible relationships at more limited ranges.

Autotrophs in both terrestrial (Vitousek 1982) and aquatic (Hecky *et al.* 1993; Elser & Hassett 1994) habitats have wide variation in biomass nutrient (e.g. nitrogen or phosphorus) content. This variation arises because of the nutrient richness of the habitat (Bridgman *et al.* 1995; Vitousek 1997), the autotroph turnover rate (Sterner 1995), and the relative balance of light and nutrients

(Sterner *et al.* 1997). In contrast, the chemical make-up of consumers varies less, and consumers often have higher nutrient content than autotrophs (Sterner 1995). Plotted on a uniform scale with some rough indication of trophic level (Fig. 1), carbon:phosphorus ratios for aquatic food chains show similar but not identical minima for all trophic levels, but a greatly decreasing maximum with increased trophic level. Hence, those ecosystems with low algal carbon:phosphorus have well-balanced carbon and phosphorus, whereas those with high algal carbon:phosphorus ratios have carbon and phosphorus out of balance compared with the needs of the top consumers.

The contrast in nutrient content across trophic levels is potentially very large at the plant–animal interface, and it has been shown that algae with high carbon:phosphorus ratios are poor quality food for herbivores such as *Daphnia* with a high phosphorus demand (Sterner 1993), a result of a direct limitation of animal growth by phosphorus (Urabe *et al.* 1997). However, supply of carbon to the microbes such as heterotrophic bacteria might be enhanced when algae have surplus carbon (Sterner *et al.* 1997). For these reasons, one might expect greater importance of microbial carbon processing (a dissipative rather than a productive process) compared with grazing when the algal carbon:phosphorus ratio is high.

Global perturbations to solar insolation as well as to biogeochemical cycles will affect primary production in the future. Increased P(CO₂) might stimulate primary

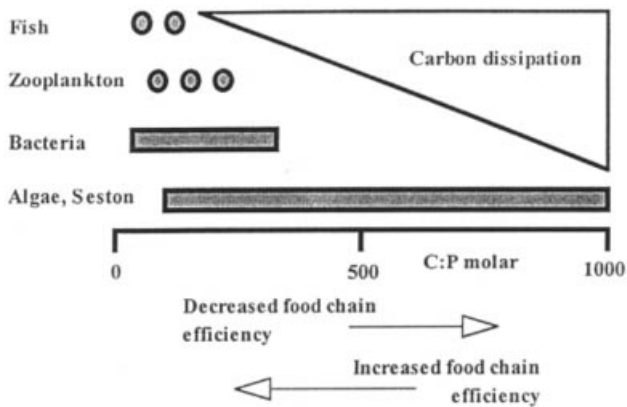


Figure 1 Diagrammatic representation of the carbon:phosphorus ratio in aquatic ecosystems. Individual species of algae in culture (Healey & Hendzel 1979), or mixed sestonic particles in lake samples (Elser & Hassett 1994), show a broad range of carbon:phosphorus ratios (all ratios are given as molar). The carbon:phosphorus ratio of heterotrophic bacteria seems to be more constrained, but again individual strains in culture (Kyle 1994) and collections of bacterial-sized particles from natural ecosystems (Vadstein *et al.* 1988) indicate considerable variability in carbon:phosphorus ratios within strains, though the range of that variation is less than that seen in algae. In contrast, metazoan zooplankton have been characterized as showing little intraspecific variability, and somewhat more interspecific variability (Hessen 1990; Andersen & Hessen 1991; Hessen & Lyche 1991). The total range of carbon:phosphorus ratios in metazoan zooplankton is considerably less than in bacteria or algae, and ranges from about 100 to about 200. Finally, the carbon:phosphorus ratios of fish are also constrained; fish carbon:phosphorus ratios also are low (Davis & Boyd 1978; Penczak 1985; George 1994).

production but have a detrimental effect on production of consumers by dilution of other essential elements by carbon (e.g. Lindroth *et al.* 1993). An understanding of carbon:nutrient balance across trophic levels, particularly in carbon-rich systems, might therefore help us predict changes in food chain production under different global change scenarios.

MATERIALS AND METHODS

We tested this set of hypotheses in two large (11.2 m high, 0.86 m diameter) indoor plankton towers (Lampert & Loose 1992). The towers were constructed from stainless steel and had temperature control. The temperature was 20°C in the upper 2.5 m and 10°C below that. Light was supplied by high wattage, near-daylight-spectrum lamps (Osram Powerstar HQIT-2000 W/D/I) with constant 24 h illumination.

In each of two runs, incident light was 60 $\mu\text{E m}^{-2} \text{s}^{-1}$ (low light) in one tower and 400 $\mu\text{E m}^{-2} \text{s}^{-1}$ (high light)

in the other. Experiments began by filling the towers with filtered (5 μm) water from a nearby lake. This water contained the natural microbial community present in the lake at the time of filling. Initial total phosphorus in the two runs was 0.72 and 0.50 μM . Nitrogen was amended by fertilization with NH_4NO_3 (nitrogen, 500 μM) to avoid nitrogen limitation. After 2–3 days for temperature stratification, phosphorus-limited, cultured algae (*Scenedesmus acutus*) were added. Measurements began on the day of algal addition. Zooplankton herbivores (*Daphnia hyalina*) were added 4 days later. The algae remained dominated by *Scenedesmus* throughout. Mean light in the upper stratified layer were ≈ 100 and 10 $\mu\text{E m}^{-2} \text{s}^{-1}$, respectively, in the two treatments, values lying within the range of daily integrated photon doses in mixed layers in natural lakes. Samples of algae and seston (GF/F filtration following 1 μm polycarbonate size fractionation) were mixed from five sampling ports located in the upper 2.5 m. Samples of zooplankton came from hauls of a zooplankton net from 3 m to the surface. Runs lasted 26 days. Assignment of treatments to towers was reversed for the second run.

Particulate carbon was analysed by a CHN analyser. Particulate phosphorus was analysed by persulphate digestion followed by a continuous-flow system utilizing the ammonium molybdate reaction. Algal biovolume came from a CASY particle counter, integrating over the range of particle size from 2.5 to 30 μm . Bacteria were enumerated by DAPI staining and epifluorescence microscopy (Porter & Feig 1980). Zooplankton biomass was measured by determination of dry mass on preweighed nylon screens. Zooplankton numbers were determined by microscopic enumeration of preserved samples. The carbon:phosphorus ratio of *Daphnia*, though not perfectly homeostatic, is constrained to a more limited range than the algae (Andersen & Hessen 1991); hence we did not measure zooplankton carbon:phosphorus during the experiment. For statistical analysis, results were analysed as an unreplicated, repeated measures Latin Square with run and tower as rows and columns of the Latin Square, and with light as a main effect. The interactions between day and each of light, tower, and run were also calculated. Together, these terms leave zero degrees of freedom (d.f.). The interaction between light and day was calculated from an F statistic calculated with the $L \times D$ (light by day) interaction in the numerator (d.f. = $t-1$, where t is the number of samples for that variable) and the pooled tower \times day and run \times day interactions in the denominator (d.f. = $2t-2$). A main effect of light was calculated from an F statistic calculated with the main effect of light in the numerator (d.f. = 1) and the pooled main effects of tower and run in the denominator (d.f. = 2). The main effect (L) is reported only if the interaction (L*D) was not

significant. Biomass variables but not element ratios were log-transformed prior to analysis.

RESULTS

The major statistically significant differences we observed were that high light yielded higher seston carbon (Fig. 3A) and lower zooplankton biomass (Fig. 2B). Algal biovolume was clearly higher in the high light towers than in the low light towers in both runs, though the statistical test for the effect of light somewhat exceeded the conventional level of 0.05 (biovolume, L, $F_{1,2} = 11.6$, $P = 0.08$). The interaction of light and day was significant for both zooplankton numbers (individuals per litre, not shown) ($F_{11,22} = 2.6$, $P = 0.03$) and biomass (Fig. 2B) ($F_{11,22} = 3.89$, $P = 0.003$). *Daphnia* biomass in the high light towers did not increase in either run (Fig. 2B, squares). Because we can safely assume low mortality to these herbivores (no predators were present), this lack of change of biomass indicates an essentially zero net secondary production. In contrast, and surprisingly given the other large changes we observed in the two kinds of food chains, heterotrophic bacterial numbers were very similar in the two treatments, generally within 10% of each other (L, L \times D, $P > 0.7$).

Seston chemistry showed that the major effect of higher light was to increase algal carbon. Total seston carbon (Fig. 3A) closely matched algal biovolume (L \times D, $F_{13,26} = 13.5$, $P < 0.001$). In contrast, seston carbon in the $< 1 \mu\text{m}$ fraction, our estimate of bacterial biomass, showed no significant relationships with light (Fig. 3B, L, L \times D, $P > 0.5$), and was less consistent across runs. Seston phosphorus in the total fraction decreased with

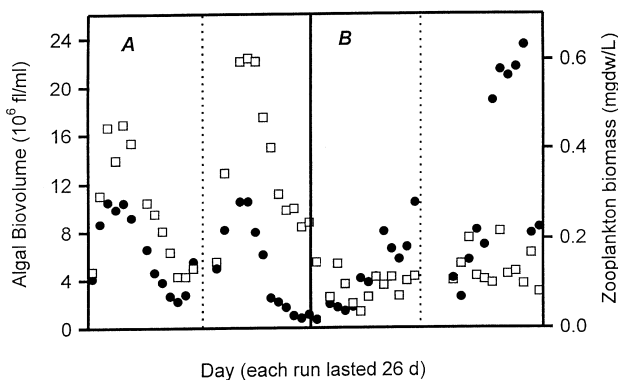


Figure 2 Dynamics of algae (A) and zooplankton (B) in plankton tower experiments manipulating incident light. The two experimental runs are shown sequentially (separated by dotted lines): \square , high light ($400 \mu\text{E m}^{-2} \text{s}^{-1}$); \bullet , low light ($60 \mu\text{E m}^{-2} \text{s}^{-1}$). Experimental runs lasted 26 days. Note that under high light, algal biovolume was greater, but zooplankton biomass was less compared with low light.

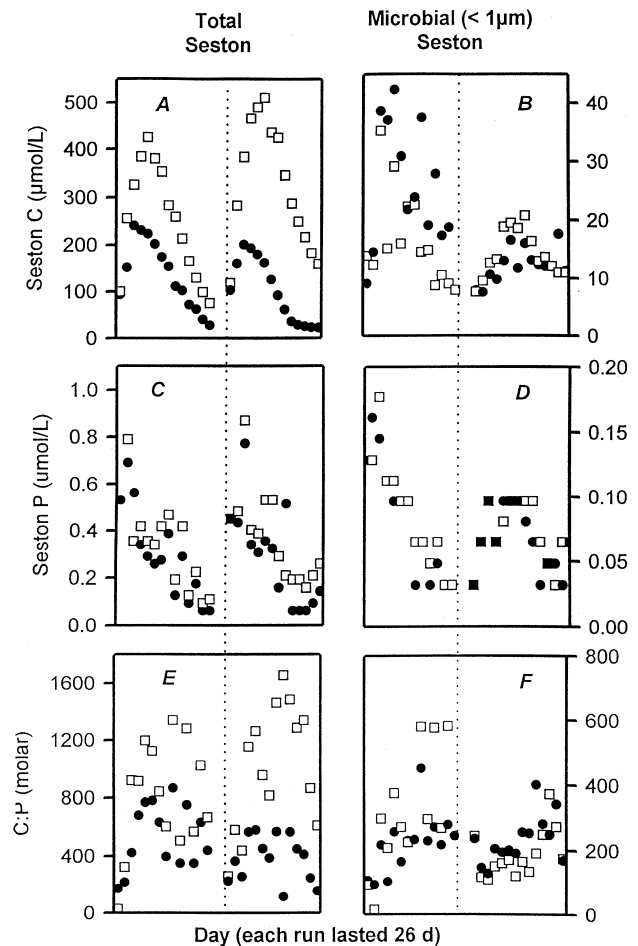


Figure 3 Dynamics of seston carbon, phosphorus, and their ratio in two size fractions. Dotted lines separate the two experimental runs. Left column, total seston ($0.7\text{--}80 \mu\text{m}$); right column, “microbial” seston ($0.7\text{--}1 \mu\text{m}$). Note differences in scales. \square , high light ($400 \mu\text{E m}^{-2} \text{s}^{-1}$); \bullet , low light ($60 \mu\text{E m}^{-2} \text{s}^{-1}$).

time during both runs due to sedimentation. The effect of light on total seston phosphorus was not as large as total seston carbon, but it was also highly significant (L, $F_{1,2} = 113$, $P = 0.009$, L \times D, $P = 0.96$) (Fig. 3C). Seston phosphorus in the $< 1 \mu\text{m}$ fraction did not vary significantly with light (Fig. 3D, L, L \times D, $P > 0.4$). The P value for the main effect of light on the total seston carbon:phosphorus ratio slightly exceeded the conventional 0.05 level ($F_{1,2} = 12.9$, $P = 0.07$); the interaction term was not significant ($P = 0.49$). This ratio is a composite of two variables and thus has larger variability than either alone. Based on the combined evidence of seston carbon, seston phosphorus, and seston carbon:phosphorus, we conclude that light had a positive effect on total seston carbon:phosphorus (Fig. 3E). In contrast, light had no significant effect on the carbon:phosphorus ratio of the $< 1 \mu\text{m}$ seston (L, L \times D, $P > 0.3$) (Fig. 3F).

DISCUSSION

Our experiments showed clear differences in the transfer of energy in the two kinds of food chains. In spite of the higher algal production at high light, zooplankton production was essentially zero. Under high light and high carbon conditions, excess carbon fixed by algae was not efficiently converted into zooplankton biomass. Earlier, similar trends were shown in short-term experiments conducted in beakers (Urabe & Sterner 1996). Factors that stimulate carbon fixation in excess of nutrients within autotroph biomass can be expected to have a negative impact on food chain production. Besides light, increases in inorganic carbon availability should have similar effects.

Two potentially confounding effects in our experiment are the depth distribution of zooplankton and direct effects of light on zooplankton feeding or growth. Daily observations of the distribution of the *Daphnia* were undertaken through observation windows on the tower sides. The great majority of *Daphnia* individuals was observed to occur above the thermocline, except in the low light towers at the very end of the two runs (about day 22). We surmised that the lack of food on these days caused the animals to move into the colder deep waters either to lower metabolic costs or to try to find food resources. Note that this difference in depth distribution runs counter to the observed trends in biomass, i.e. we observed high growth in towers where animals eventually moved into colder water. Regarding direct effects of light on the zooplankton, this experiment alone cannot separate direct and indirect effects of light. However, in the earlier small scale experiments (Urabe & Sterner 1996), algae grown at high light were fed to *Daphnia* under low light conditions, and direct light effects were categorically rejected. Others have found no direct effect of light on *Daphnia* grazing rates (Buikema 1973). Hence, we attribute the differences we observed in zooplankton populations at the different light levels to be an indirect result of the effects of light on algal chemical composition.

It has been hypothesized that excess carbon in high carbon:nutrient ratio ecosystems would be dissipated by bacteria (Sterner *et al.* 1997). However, we did not see a rerouting of production consistent with this hypothesis. Although the high light towers generated considerably higher organic carbon, microbial populations did not respond. We feel it is likely that phosphorus constrained the bacterial response. The carbon:phosphorus ratios in the microbial fraction (Fig. 3F) were relatively high compared with previous reports for bacteria, indicating strong phosphorus limitation of this trophic level. Under a strong phosphorus constraint, bacteria would not be able to process excess carbon produced by algae.

In pelagic ecosystems, a larger percentage of primary production is consumed by herbivores than in terrestrial ecosystems (Hairton & Hairton 1993). This difference has been ascribed to the presence of an additional trophic level, piscivorous fish, in pelagic food chains (Hairton & Hairton 1993). Here we wish to offer an alternative explanation. Plants in terrestrial ecosystems have generally larger carbon:nitrogen and carbon:phosphorus ratios than phytoplankton (Nielsen *et al.* 1996). As we have shown, food chain efficiency varies with the degree of mismatch between the carbon:phosphorus ratios of algae and consumers. The higher consumption of primary production in aquatic food chains may be because of a more favourable match between the chemical composition of the base of the ecosystem and the needs of the top consumers than occurs generally in terrestrial ecosystems, allowing for greater herbivore production. Note that when that match is made poor, aquatic food chains also show low efficiency of grazing food chains.

The relationship between biomass of upper trophic levels and primary production has attracted much attention. Though common sense suggests that greater energy input should yield higher productive capacities, food chain stoichiometry induced a surprising nonlinearity to ecosystem energetics. We observed a paradoxical decrease in food chain production (herbivores) with increased energy input. The constrained low carbon:phosphorus ratio of the herbivores in our experiments meant that high algal carbon:phosphorus ratios under high light were poor quality food (Sterner 1993; Urabe *et al.* 1997). The carbon fixed by the algae in excess of the phosphorus balance relative to the needs of the top consumers was a penalty, not a benefit, for food chain production. Understanding how top trophic levels respond to perturbations in biogeochemical cycles requires understanding stoichiometric constraints such as these.

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BIOSKETCH

Robert W. Sterner's research interests include nutrient dynamics, plankton physiology, limnology, and the interface between community and ecosystem ecology. Recent efforts have dealt with questions of zooplankton nutrition, and general questions of ecological stoichiometry in different ecosystems.

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