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Stoichiometry in food webs – Lotka revisited

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Food web diagrams in the tradition of Elton (1927) and Lindeman (1942) focussed on interactions at the species level based on an upward flow of energy from photosynthesis to the top predator above which there is insufficient energy to sustain further levels. Nutrients entered this arena only at the end-point, where heterotrophic bacteria decomposed the dead corpses to resupply the primary producers. This simplified concept of energy flow has over the past 30 years been thoroughly criticized and reformulated (Pimm 1982, Polis and Winemiller 1994). Yet, the common currency in food web studies (for good reasons) still is dry-weight or carbon, and while the feedback effect of recycled detrital carbon has been thoroughly addressed (Patten 1985, Gaedke et al. 1994), the effects of other recycled elements has been less explored. In his pioneering work, Lotka (1925) recognized the vital importance of the flow of nutrient elements in food webs, and the importance of their relative proportions. This may be seen as the first attempt to link biogeochemical cycling to more classical ecology, an attempt that was largely ignored until recently, when there has been a new surge on the role of nutrient cycling as a structuring component to ecosystems and food webs (McNaughton 1988, DeAngelis 1992, Raubenheimer and Simpson 1994) and also to view aquatic food web regulation and stability in relation to these principles (Sterner and Hessen 1994).

Much of this recent effort has been devoted to lake ecosystems, in which phosphorus is a key element not only for the entire ecosystem productivity, but also for community composition and food web organization. Pioneering studies on food web regulation and structure in terms of “top-down” and “bottom-up” regulation has also been extensively examined in a vast number of lake ecosystems. Promoted by the trophic cascade theory (Carpenter et al. 1985, Carpenter and Kitchell 1988, McQueen et al. 1986) food web manipulation as a tool for eutrophication control has been extensively explored in lake ecosystems (Gulati et al. 1990). The lake food web thus offers both theoretical exercises and empirical examples to judge principles

and the ecological relevance of nutrient feedbacks relative to the more familiar direct interactions. A simplified aquatic food chain is commonly viewed as composed of four major levels: phytoplankton – zooplankton – zooplanktivore – piscivore, with a strict upward flow of energy, but with simultaneous producer-to-consumer and consumer-to-producer control. There exist numerous observations both for natural and manipulated ecosystems (see papers in Gulati et al. 1990), and the large majority of these confirm the strong effect of planktivorous fish on zooplankton size and species composition. The link from fish to phytoplankton biomass and composition is less clear cut, although there is evidence that at least large species of the grazer *Daphnia* may exert efficient control on most phytoplankton species when released from predation by planktivores. One of the things that really stands up after 20 years’ study on food web effects related to eutrophication, is in fact the key role of *Daphnia* in lake ecosystems. Yet there is a great unexplained variance in the phytoplankton response on biomanipulations, in particular on the possible control of toxic and filamentous cyanobacteria (“blue-greens”), which are among the most undesirable effects of severe eutrophication. There is reason to doubt the general ability of zooplankton grazers, even *Daphnia*, to control blue-greens by direct grazing, yet there is circumstantial evidence that *Daphnia* negatively affects the proportion of blue-greens (see Gulati et al. 1990). There have been a number of enclosure and whole-lake experiments demonstrating how reduced stocks of planktivorous fish may cause rapid and dramatic decreases in both biomass and share of blue-greens, but where these incidents cannot be explained by grazing control alone (Reinertsen et al. 1989, Sanni and Wærvågen 1990). Recent reviews on aquatic, biotic interactions and “biomanipulation” theory underline the complex nature of various interactions, and emphasize that empiricism frequently does not support predictions from conventional food web diagrams and cascading theory (Harris 1994, Reynolds 1994).

The intention is here to reiterate some aspects of biological nutrient cycling in lakes, and then examine the potential effects of these alternative indirect mechanisms relative to common, "direct" food web interactions. Such stoichiometric aspects have been especially elaborated for freshwater zooplankton, where major members are nearly homeostatic in their element proportions (C:N:P), making them particularly suitable for modelling purposes (Andersen and Hessen 1991, Hessen and Andersen 1992). Sterner et al. (1992), focussing on zooplankton, demonstrated how elemental ratios in producers and consumers may be of general importance for the structure of food webs, and how a stoichiometric view may offer a viable alternative to the direct interactions. By linking these recent ideas to some aspects of productivity and trophic cascading models in lakes, it may be demonstrated how these indirect interactions may work in parallel to the direct ones, and probably may explain some of the unexplained responses in food web manipulation experiments. I here explore aspects of stoichiometric theory at three levels of organization.

Stoichiometry and individual energetics

Herbivores face the challenge that they depend on a food resource that normally is qualitatively deficient relative to somatic needs. Grazers are commonly sub-saturated with regards to proteins, amino acid composition, fatty acids or other essential macromolecules relative to carbohydrates, and this may even be seen as an active plant strategy to keep grazer growth rates at a minimum or even below maintenance levels (White 1993). A similar view may be held for essential minerals like phosphorus (P). When comparing plant and grazer stoichiometry, there is a common mismatch between the somatic need for N or P relative to carbon in the grazer, and that offered by the plant (McNaughton 1988, Hessen 1992, Sterner and Hessen 1994). In pelagic systems, the C:N or C:P ratio of phytoplankton, and particularly of nutrient limited phytoplankton, by far exceed that of most pelagic grazers. Even when accounting for low assimilation rates for much of the algal cell carbon (e.g. cellulose or cellulose derivatives), there is commonly a N and P deficiency in net accumulated food relative to the grazers' stoichiometry (Sterner and Hessen 1994), leading to the assumption that zooplankton grazers may be directly mineral limited by their growth (Hessen 1992, Urabe and Watanabe 1992). This view is supported by the common observation that zooplankton, notably *Daphnia*, feeding on P-deficient algae, experience reduced growth rates and depressed fecundity, while high C:P algae are sufficient for maintenance (Sterner and Hessen 1994). These predictions and observations hinge to a great extent on the observation that freshwater crustacean zooplankters

have a fairly rigid intraspecific stoichiometry (C:N:P ratio), while having a variable intraspecific stoichiometry (Andersen and Hessen 1991). A most striking pattern is that most herbivorous cladocera, and notably the daphniids have a low N:P ratio (~12–15 by atoms) while copepods have a consistently higher N:P ratio (~40–50). This implies a relatively higher demand for P in *Daphnia* and a higher demand for N in the copepods.

The effects of elemental limitation on carbon household in the grazer may be profound (Hessen 1992). Using the freshwater crustacean *Daphnia* as an example, phosphorus-dependent regulation of growth efficiency in terms of carbon (γ_c) may simply be expressed as a piecewise linear function

$$\gamma_c = \gamma_L \cdot \min(1, Q_a/Q_z) \quad (1)$$

(Hessen and Andersen 1992), where γ_L is the assimilation efficiency for the limiting component (in this case either C or P), Q_a is the P:C ratio of food (algae) and Q_z is the P:C ratio of the grazer (zooplankton, *Daphnia*). γ_c is assumed constant at a maximum of 0.6 (60% of ingested C is utilized for growth, reproduction or maintenance). At some level of Q_a the net incorporation of P:C will reach a threshold below which the grazer must adjust its net intake of C, reduce the γ_c simply to maintain its elemental homeostasis. In nature, daphniids will most commonly face a situation with quantitative food limitation, and would thus suffer a competitive drawback relative to less P-demanding species. At all levels of food quantity, food quality (here in terms of a too low P:C ratio) may provide additional constraints on growth. It is thus important to notice that C- and P-limitation may occur simultaneously, apparently violating the Liebig minimum principle. The multiplicative effect of quantitative and qualitative food limitation is not straightforward however, as the relative importance of P-limitation (at a given Q_a) will decrease with decreasing food quantity (Sterner 1997). The baseline of this argument is that for a homeostatic grazer, the portion of C in food that is in excess relative to the availability of P (or whatever limiting element) will be wasted. That is, under nutrient deficiency, the efficiency of energy transfer in food webs will decrease and more carbon be wasted due to reduced carbon assimilation efficiency or increased respiratory losses.

Stoichiometry in two-compartment systems

Alfred J. Lotka not only pioneered the incorporation of stoichiometry in food webs, he later became more renowned for his contribution to dynamic modelling of competitors and predator-prey interactions (Lotka 1932). Yet at that time (and ever since) the stoichiometric thoughts never merged into these interactions, which in their various forms have been modelled almost en-

tirely based on quantitative interactions. In the classical Lotka-Volterra prey-predator (or algae-grazer) model, the stability or oscillations depend on food quantity solely and the predator isocline in the original model is simply the straight line extending vertically from the minimum biomass for net positive population growth without taking saturation effects into account. This well-known scenario for zero growth is thus when assimilated carbon balances maintenance. One important aspect of the stoichiometric principles is that there is a pronounced feedback from nutrient cycling, an interactive system in the terminology of Caughley (1976), and a more unexplored aspect relates to the possible P-limitation of the grazer as discussed above. When Q_a becomes depleted (most often at high algal biomass and low growth rate) the growth efficiency declines, and may finally reach a critical level that is too low to sustain positive population growth. Thus as Q_a decreases, the grazer isocline for zero net growth is shifted upwards, i.e. the required algal biomass for positive growth increases. In cases with low minimum Q_a and a P-demanding grazer, this may cause the system to enter an irreversible stage with high biomass of P-deficient phytoplankton which do not support zooplankton growth. It follows from these principles that grazers with high P requirements will be the most susceptible to low Q_a 's. The incorporation of these stoichiometric principles has been further explored in a three-compartment, chemostat model (Hessen and Bjerkeng 1997), demonstrating that a fluctuating and frequently low P:C in the algae indeed offers a protection from grazers with high P requirements, increasing the system stability. While White (1993) argues that high carbon-to-element ratios may be seen as an active strategy to suppress grazers, the costs will be reduced growth rates. At least for algae exposed to unselective grazers like *Daphnia*, a low P-low growth rate scenario would invoke a group defence argument (cf. Andersen 1997), suggesting that high C:P is not an active strategy. Yet it may create a "quality-starvation" in *Daphnia*, even at high food quantities.

Stoichiometry in freshwater food webs

At all levels of the food web, these stoichiometric limitations and stoichiometric footprints may be expected to be seen. General aspects of food web stoichiometry may also be predicted, and these may parallel the more conventional direct interactions of food webs as outlined in Fig. 1. The other side of the element limitation argument relates to the release (recycling) of excess nutrients. When there is surplus N or P in the diet, more of these elements will also be recycled to support primary production. The community structure will have strong bearings on this process, since different taxa or species have different nutrient requirements.

In Fig. 1, the direct top-down (piscivores to phytoplankton; TD 1–3) and bottom-up (nutrients to piscivores, BU 1–4) cascade-effects are supplemented with a set of indirect stoichiometric effects. The commonly reported direct effects of zooplanktivore fish are reduced average zooplankton size, reduced share of daphnids, increased share of copepods and rotifers (McQueen et al. 1986, Carpenter and Kitchell 1988, Gulati et al. 1990). Conversely a decrease in zooplanktivores would produce the opposite effect. These effects are summarized as TD 2 in Fig. 1. The stoichiometric counterpart is twofold, as both the fish and the zooplankton affect their milieu by their release products (labelled S1 and S2, respectively). While the role of zooplankton releases has gained considerable interest, less is known about the quantitative and qualitative role of fish releases. Consumers like fish may have profound effects on primary producers (cf. Carpenter et al. 1985, Persson et al. 1988, Carpenter 1988), not necessarily via zooplankton, but rather by quantitative and qualitative nutrient cycling. Lamarra (1975) suggested that release of N and P from cyprinids could be a major contributor to N and P in lakes. It is quite evident that presence or absence of fish may induce changes in the phytoplankton community which should be attributed to their release product rather than changed zooplankton grazing pressure (Reinertsen et al. 1989, Vanni 1994). In particular, the possible stimulatory effect of fish excreta on the development of blue-greens has attracted interest, and a number of mechanisms may be involved. Brabrand et al. (1990) demonstrated how release of iron from cyprinids stimulate phytoplankton growth and particularly the blue-greens. The pulsed release from fish contrary to zooplankton may favour the uptake-kinetics of blue-greens (Reinertsen et al. 1989). Detritivorous roach may feed in littoral sediments during day and excrete considerable amounts of P in the epilimnion during night, supporting the maintenance of blue-green blooms (Brabrand et al. 1990). Finally, the stoichiometry of the release products may in itself affect algal production and competition. While a N:P ratio of 12 (by weight) was found for detritivorous roach (*Rutilus rutilus*) (Brabrand et al. 1990), Dahl (1991) found a consistently low N:P ratio for zooplanktivorous cyprinids over the season, with an average of 3.9 ± 0.75 (SD) for roach and 4.4 ± 0.63 for bleak (*Alburnus alburnus*). With a sufficiently skewed N:P ratio towards N-limitation, blue-greens have a strong competitive advantage (Smith 1983) and such low N:P ratios may indeed add to the well recognized predation effects assuming that fish releases have a quantitative importance relative to other sources.

The subsequent effects of increased density of planktivorous fish on the zooplankton community are smaller sized species and reduced grazing pressure on phytoplankton and changes in phytoplankton community (TD 3). Herbivorous zooplankton do however also

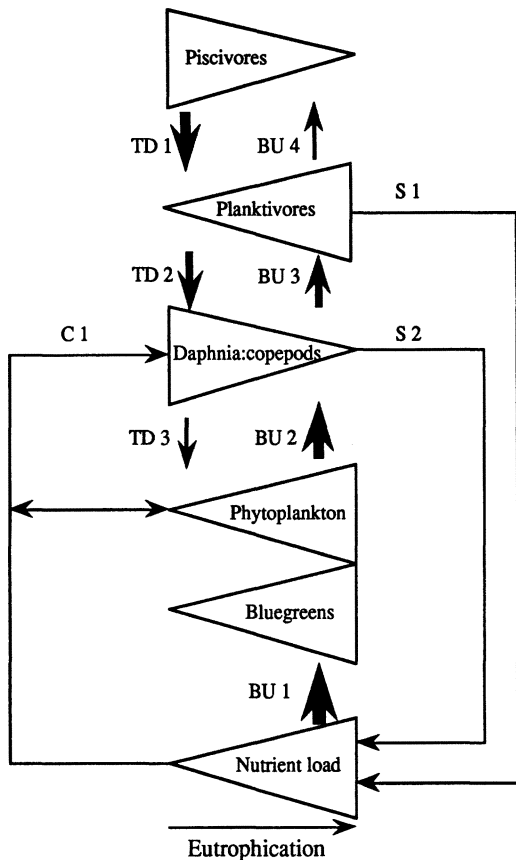


Fig. 1. Generalized trophic cascade diagram for a pelagic food chain. Direct top-down effects from piscivores to phytoplankton are labelled TD 1–TD 3, and direct bottom-up effects are labelled BU 1–BU 4. Arrow width indicates successively decreasing effect. The cascade effect at each major trophic level along a eutrophication axis is indicated by height of boxes, i.e. increasing nutrient load and decreased piscivore biomass from left to right. Indirect supports to the trophic cascade include nutrient release from fish and zooplankton (S 1 and S 2), while constraints in terms of low food quality is labelled C 1. For further explanation, see text.

regulate their food by their release products (S 2), and this again depends heavily on zooplankton community composition. The higher demand for P in *Daphnia* and the higher relative demand for N in the copepods implies a higher N:P-ratio in the release products would be expected from a *Daphnia* relative to a copepod. These considerations have been pursued in models (Hessen and Andersen 1992, Sterner et al. 1992), leading up to a suggestion that a reduced cladocera:copepod ratio would be beneficial for the blue-greens in terms of stoichiometry of the release products. As planktivorous fish selectively prefer cladocera to copepods, this would also imply that they promote a community with low

N:P release ratios. A study of the effect of food web manipulations in two lakes by altering density of zooplanktivorous fish demonstrated that concomitant shifts in zooplankton communities shifted the lake from P to N-limitation and vice versa (Sterner et al. 1992). A high abundance of daphnids relative to copepods could further increase sestonic N:P ratios, simply because *Daphnia* remove more P by sedimentation.

In principle the same mechanisms would work for the microbial components in the food web, which adjust their intake and release rates of ingested elements to match their bodily demands (Goldman et al. 1987a, b). Tezuka (1990) demonstrated how bacteria became net consumers (no release) of P at low substrate C:P ratios. The functional role of bacteria will thus be determined by the stoichiometry of the medium. When supply of P or N is sufficient, they are important mineralizers of nutrients, while during situations with nutrient deficiency they become net consumers of nutrients and thus important phytoplankton competitors. The ecological relevance of these processes hinge on the assumption that the biologically driven, internal nutrient fluxes are of a significant magnitude relative to external or internal abiotic loading. There is indeed evidence for this with regard to both zooplankton (Elser et al. 1988) and planktivorous fish (Brabrand et al. 1990, Vanni 1994).

Most of the “indirect” or stoichiometric regulation mechanisms are linked to the direct interactions like grazing or predation, and these may work in the same directions. Cyprinides may promote blue-greens by eliminating large *Daphnia* and thus reduce grazing pressure, but also by shifting the zooplankton community from cladocera to copepods and thus lower N:P ratios in the zooplankton release as well as by their own release products.

These indirect top-down effects are, however, accompanied by a set of bottom-up feed-back mechanisms pooled in the label C 1 in Fig. 1. Total supply of nutrient will determine the nutrient status of phytoplankton. During summer, recycling from biotic compartments constitute a major contribution. When phytoplankton is deprived of P this will create a negative feedback to zooplankton, in particular the daphnids, for reasons given above.

As the various grazers alter the availability of N and P in their food, they do not only alter the growth rate, but also the biochemical and nutritional quality of their food. Nutrient deficient phytoplankton and bacteria may serve as poor food for their grazers. A reduced food quality would be expected to primarily affect non-selective grazers like *Daphnia*, which also would be the first to approach P-limitation. This again would be unfavourable to many fish species. There are strong ties between first-order effects and feed-back effects, and in fact they cannot be easily separated. This is a further argument against a strict top-down or bottom-up view of aquatic food webs.

Conclusions

The outcome of these stoichiometric effects will depend on nutrient-quality of algae, food-web structure, community and species composition of the various trophic levels. They may be highly important in some lakes, less so in others. Yet they shed some light on the fact that biomanipulation may yield unexpected replies. In line with empyry, it is also reasonable that the strong link between piscivores and planktivores or planktivores and zooplankton is not followed up by correspondingly strong effects at the phytoplankton or microbial level, since the role of such stoichiometric linkages increase in importance towards the base of the food web. A most important implication of these indirect effects would be increased system stability. This holds in particular for the feed-back effects linked to food quality constraints of grazer success, where low quality food (high C:N or C:P ratios) would dampen the prey-predator oscillations predicted from simple quantity dependent Lotka-Volterra type models. Also stoichiometric models link the energy transfer in food webs to food quality, and thus merges fundamental principles of element household in organisms and ecosystems into "efficiency" of energy transfer.

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