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Review Paper

Nutritional Limitation Travels up the Food Chain

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Abstract

It is a well accepted fact that nutrient limitation of plants affects the growth and survival of herbivores, generally leading to lower performance of herbivores feeding on nutrient stressed plants. The effect of plants' growing conditions on predatory organisms, feeding one trophic level up, has been much less studied, and there is a general consensus that such effects would be small as herbivores often show relatively strong homeostasis with respect to their nutrient content. Here, we challenge this view, and show from several examples that despite the fact that herbivores buffer much of the variance in nutrient stoichiometry of their food, effects of growing conditions of the primary producers can travel up the food chain. We discuss the implications of these findings, and argue that phosphorus limitation of secondary consumers might be more common in marine than in freshwater systems.

Ohne Phosphor kein Gedanke
Jacob Moleschott, 1822–1893

1. Introduction

A search in the ASFA (Aquatic Sciences and Fisheries Abstracts) database (1971–2007) using the words phosphorus and fish as search strings results in over 3000 hits. Many of these relate to eutrophication and the related changes in fish communities (*e.g.*, Jeppesen *et al.*, 2000), the manipulation of fish stocks to improve water quality (*e.g.*, Shapiro, 1990), or the recycling of nutrients via fish excretion (Schindler and Eby, 1997; Vanni and Layne, 1997; Attayde and Hansson, 1999). On the other hand, a substantial amount of these 3000 papers deal with exactly the opposite subject, namely, the uptake of nutrients by fish in aquaculture settings, and the response of these fish to different amounts of phosphorus (P) in the food in terms of growth and reproduction (Sugiura *et al.*, 2000; Vielma *et al.*, 2002; Roy and Lall, 2003). These aquaculture studies typically use different levels of phosphorus in the food (*e.g.*, Skonberg *et al.*, 1997; Pimentel-Rodrigues and Oliva-Teles, 2001), and aim to find the optimal balance between growth of the economically interesting species and the costs of

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feed and waste removal. Benefits to fish typically decrease with increasing phosphorus levels, and growth often reaches a plateau at 0.5–1.0% P of dietary dry mass (BORLONGAN and SATOH, 2001). This translates as an atomic P:C (carbon) ratio in the food of 0.004–0.008, (C:P 125–250) based on the assumption that ~50% of the dry weight is carbon (BOERSMA and ELSER, 2006). Unfortunately, even though these citations mentioned above are found in the same databases, there seems to be very little cross-linking between disciplines. Moreover, especially ecologists show fairly little interest in the aquaculture literature, even though much can be learned from the experimental results collected in the highly standardized settings of aquaculture research.

In the aquatic ecological literature nutritional deficiencies are almost exclusively considered to be a problem of primary consumers. STERNER and ELSER (2002) in their book on ecological stoichiometry mainly consider herbivores. Also, the majority of papers before and since their influential book, deal with grazers. Food with a high C:P ratio (*i.e.*, low phosphorus content) can be a low quality food for such diverse organisms as snails (STELZER and LAMBERTI, 2002), zooplankters (BOERSMA and KREUTZER, 2002), and aquatic insects (PERKINS *et al.*, 2004). This is a relevant finding as the C:P ratio of many plants is both higher and much more variable than the C:P ratio of zooplankters and fish (Fig. 1). More specifically, in the relationship between plants and herbivores, nutrients such as nitrogen and phosphorus are often limiting, as there is a surplus of carbon in plants (WHITE, 1993). Obviously, this carbon is needed as an energy source, and hence it will disappear from the food chain as CO_2, but it implies that many consumers will have more problems meeting their nutrient requirements than their energy requirements. Moreover, the variation in the specific nutrient content of autotrophs, both between species and within species is generally larger than the variation in herbivores (*e.g.*, STERNER *et al.*, 1998), a variation arising from differences in the relative balance between light and nutrients (STERNER *et al.*, 1997), or the nutrient richness of the habitat (VITOUSEK, 1982). This implies that herbivorous zooplankters are regularly confronted with different quality food (C:P of algae ranges from 100–1000 in Fig. 1), in contrast to zooplanktivorous fish, which only have to deal with a range of around 70–200 (Fig. 1), which has led to the general emphasis on herbivorous zooplankton in the aquatic community when it comes to the effects of food quality on the food chain. Implicitly, this means that despite the enormous body of evidence from aquaculture settings, most aquatic ecologists assume that growth and production of secondary consumers is not affected by food quality, but by quantity only (*e.g.*, BRETT, 1993), although recent studies are finding more and more signs of phosphorus effects of fish under natural or semi-natural conditions (HOOD *et al.*, 2005; HIGGINS *et al.*, 2006).

Up until recently, most researchers asserted that herbivorous zooplankton showed near-to-perfect homeostasis, except perhaps for those high-latitude species that accumulate large stores of lipid. Almost nothing in life is for free, and neither is homeostasis. The process of handling excess carbon or nutrients invokes costs, and these are usually paid by a reduction in growth and reproduction. Homoeostasis means that the food quality effects in terms of nutrient ratios experienced by the primary consumers are buffered in these consumers and not transferred to higher trophic levels (BRETT, 1993). This automatically leads to the prediction that changes in nutrient stoichiometry in primary producers should not result in changes in nutrient stoichiometry on the consumer level, and hence such a food quality effect should not be transferred up the food chain as a quality effect. This would explain the modelling results by SCHINDLER and EBY (1997) who stated that P-limitation was likely in only a small subset of the fish they investigated. Obviously, nutrient stoichiometry of the algae influences the growth and reproduction of the herbivores dramatically (BOERSMA, 2000; ELSER *et al.*, 2001; AUGUSTIN and BOERSMA, 2006), leading to lower densities under phosphorus-limited conditions (SEIDENDORF *et al.*, 2007). Thus, a quality effect at the algal-zooplankton interface should be translated into a quantity effect on the zooplankton to higher consumer interface, which means that secondary consumers such as fish should not be affected by the trophic
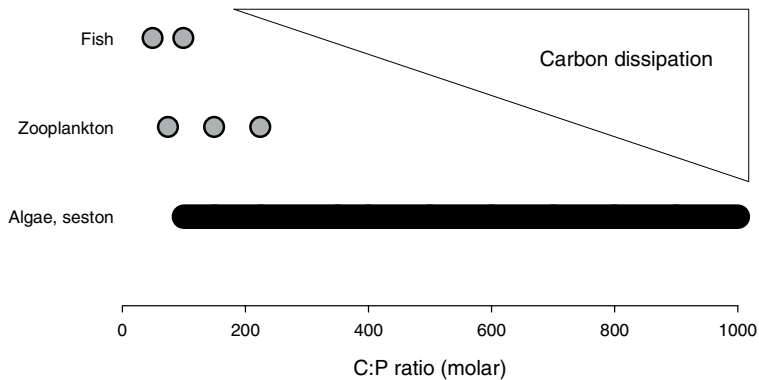
Figure 1.   Diagrammatic representation of the carbon:phosphorus ratio in aquatic ecosystems. Redrawn from STERNER *et al.* (1998). Carbon to phosphorus ratios in algae are highly variable between environments, species and growing conditions. Metazoan zooplankton has been shown to show very little intraspecific variability (indicated as the size of the symbols, and some variation between species. The carbon to phosphorus ratios of fish are also more or less constant within species, and lower than zooplankton. The carbon that disappears through the food chain dissipates as heterotrophs need C to cover their metabolic costs.

status of the system which changes the nutrient stoichiometry of algae, other than through quantitative responses on the zooplankton biomass available as a result of changes in food quality of the algae for the herbivores.

Recently, however, it has become more and more clear that nutrient homeostasis is less strict in herbivorous zooplankton than was previously believed, and differences in C : P ratio of a factor two are easily reached under different growing conditions of the animals (PLATH and BOERSMA, 2001; DEMOTT and PAPE, 2005). This implies that the quality of differently fed zooplankters as food for higher trophic levels will vary depending on the growing conditions of the animals. Here, we will show that these effects are indeed visible, and argue that a shift in our general thinking with regard to the effects of nutrient stoichiometry variability and its transfer to higher trophic levels is necessary.

2. Food Quality Travelling up the Food Chain: What Can We Learn from Different Systems?

In terrestrial ecosystems it is well established that host plant quality influences the response of predators feeding on the insect herbivores of these plants. In the majority of cases host plant quality has been expressed in terms of contents of secondary chemicals sequestered by the herbivores as a defence against their predators (*e.g.*, HARVEY *et al.*, 2003), and palatability or toxicity determines nutritional quality of the herbivore as food for higher predators. This phenomenon has also been described for the chemical defence of many marine organisms (MCCLINTOCK and BAKER, 2001; IANORA *et al.*, 2006), but seems much rarer in freshwater environments. Many authors have also shown that nutritional effects can travel up the food chain as essential fatty acids and other biomolecules (MAYNTZ and TOFT, 2001; ST. JOHN *et al.*, 2001; BOERSMA *et al.*, pers. comm.). In a way, these quality effects are not unexpected, as most organisms are far from homeostatic when it comes to fatty acid- or amino acid composition. Seasonal changes or species specific variation in biochemical composition of primary producers are transferred via the herbivorous zooplankters to higher

trophic levels. This makes essential fatty acids and amino acids ideally suitable as biomarkers and tracers for trophic pathways (*e.g.*, DALSGAARD and ST. JOHN, 2004), and is also the reason why many marine fish species are so good for human health. Fish contain so many polyunsaturated ω-3 fatty acids because they feed on zooplankters which also fed on the fatty acid producing microalgae.

Direct effects of nutrient additions propagating through to higher trophic levels have been addressed in terrestrial systems (WHITE, 1993), although this increased predator density after the addition of nutrients to plants was explained by the response of the predators to an increase in biomass of the herbivores (HUNTER and PRICE, 1992), and only the herbivores were thought to respond directly to higher plant nitrogen content. Given the fact that the homeostasis for nutrients in herbivores is not as strict as previously believed, the logical next step to take is now the investigation of direct nutrient (stoichiometric effects) on higher trophic levels in aquatic systems.

3. Nutrient Stoichiometry up the Food Chain

As a result of the perceived strict homeostasis in primary consumers mentioned above, the interest in the effects of nutrient imbalances on higher trophic levels has been fairly small. However this seems to be changing and almost concurrently with our first experiments on tri-trophic systems in an aquatic context (MALZAHN *et al.*, 2007; BOERSMA *et al.*, unpubl.), the same shift in interest is occurring in terrestrial ecology. FAGAN and DENNO (2004) state that it should be a research goal to establish these nutrient effects on predatory organisms, and KAGATA and OHGUSHI (2007) investigated the effect of different C:N ratios in willows (*Salix eriocarpa*) on leaf beetles (*Plagiodera versicolora*) and predatory ladybird beetles (*Aiolocaria hexaspilota*). They observed that ladybirds grew significantly better on leaf beetles that had consumed low C:N willow leaves, even though the differences in the C:N ratios of the leaf beetles were not significant. In a very recent paper FROST *et al.* (2008) investigated the responses of bacterial pathogens of the cladoceran *Daphnia* to phosphorus limitation, they observed that high C:P food of the zooplankter causes a significantly lower infection rate of the parasite, which is possibly caused by a different nutrient stoichiometry of the primary consumer.

In a series of experiments, we set out to investigate the reactions of a variety of secondary consumers where we knew that there was a change in the C:nutrient ratio in the primary consumers dependent on their food. We chose to investigate carbon to phosphorus ratios. This was for two reasons 1) phosphorus is often a limiting nutrient in lakes and coastal seas; and 2) the differences in C:P ratios between nutrient limited and nutrient replete algae are much larger than C:N ratios of the same algae under nitrogen limitation. Figure 2 shows the results of the different experiments, using different food chains each starting with nutrient-replete and phosphorus limited algae, that is: a) algae to daphnids to larval rainbow trout (BOERSMA, unpubl.); b) algae to copepod to ctenophore (SCHOO, pers. communication); c) algae to copepod to larval herring (MALZAHN *et al.*, 2007); and d) algae to dinoflagellate to copepod (HANTZSCHE, pers. communication). It becomes clear from Figure 2 that there is no general pattern. Freshwater fish (Fig. 2a, *Oncorhynchus mykiss*, rainbow trout) feeding on *Daphnia* react differently from marine fish (Fig. 2c, *Clupea harengus*, Baltic herring) feeding on copepods, even though in both cases the C:P ratio of the zooplankters varied considerably between nutrient limited and nutrient replete conditions. The difference between these two experiments is that *Daphnia* changed its C:P ratio from 130 to 230 when feeding on P-limited algae, *A. tonsa* as food for Baltic herring changed from 210 to 350. Given the fact that in many fish species (VIELMA and LALL, 1998; BORLONGAN and SATOH, 2001; VIELMA *et al.*, 2002) condition and growth saturate at around 0.5–1% phosphorus (C:P ~125–250) levels of their food, this means that even phosphorus limited *Daphnia* are

not expected to affect growth as they contain enough P to stay above the saturation point. In contrast, P-limited copepods clearly contain much less phosphorus than is required for optimal fish growth, which explains the lower condition of herring larvae feeding on P-limited *A. tonsa*. Interestingly, the cases in the study of SCHINDLER and EBY (1997) where growth appeared to be limited by the availability of phosphorus were of freshwater species whose diets were dominated by copepod prey (*i.e.*, vendace and sockeye salmon). We do not know much about the differences in P-demand between marine and freshwater fish, but based on the studies cited above we do not expect large differences. If the demands are indeed similar, the implication is that, despite the general consensus that primary production in lakes is more
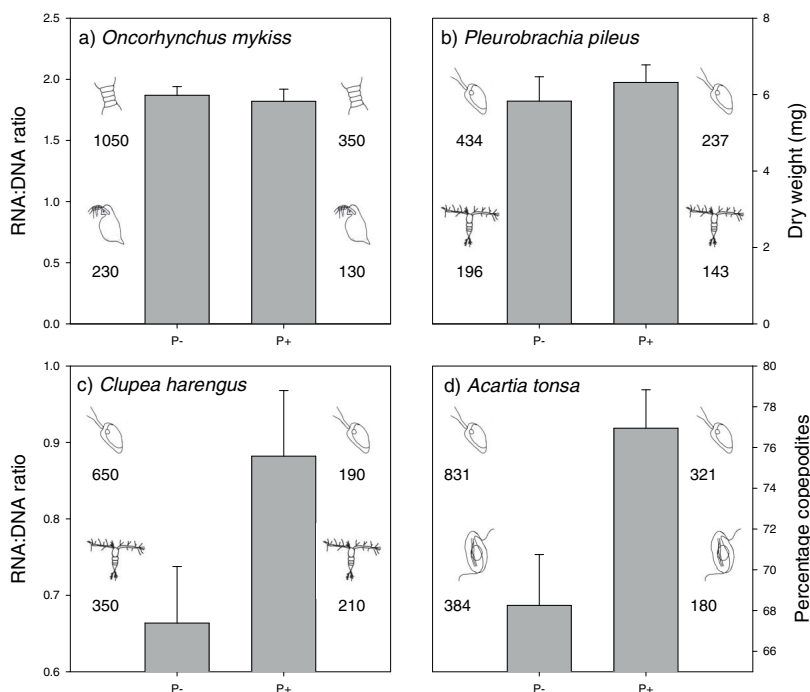

Figure 2.   Response of different secondary producers to different nutrient conditions in algae. In all cases, numbers under the drawings of the organisms give C:P ratios of primary producers above, and C:P ratios of the primary consumers below. The P-limited food chain is on the left, the phosphorus-replete food chain on the right. Error bars indicate standard errors in all cases. a) RNA:DNA ratio as a measure of condition of rainbow trout feeding on *Daphnia* which were grown under P-limited and P-replete conditions (BOERSMA *et al.*, unpubl.). Differences are not significant; b) Dry weight of the ctenophore *Pleurobrachia pileus* feeding on *Acartia tonsa* grown on *Rhodomonas salina* under low phosphorus and high phosphorus conditions. The difference in dry weight after five experimental days were not significant (SCHOO, pers. communication); c) Herring larvae which were kept on *Acartia tonsa* fed on high P and low P *Rhodomonas salina*. Larvae fed high P copepods had a significantly higher condition than those feeding on copepods which had low P food (MALZAHN *et al.*, 2007); d) *Acartia tonsa* stage distribution, expressed as the percentage of animals that were in a copepodite stage after the experimental duration in contrast to the naupliar stage, feeding on *Oxyrrhis marina*, which received low P and high P *Rhodomonas salina* as food (HANTZSCHE, pers. communication). *A. tonsa* feeding on the high P food chain were significantly further developed than those feeding on the low P food chain.
     In all cases the quantity of the food available to the top predators was identical.

often P-limited and in marine systems more often N- limited (but see ELSER *et al.*, 2007), and C : P ratios of seston in lakes are generally higher than in marine environments (ELSER and HASSETT, 1994), the likelihood that predators are limited by phosphorus is higher in marine environments than in lakes, as the main crustacean prey in marine systems (copepods) has a much lower P-content than cladocerans in lakes (HESSEN and LYCHE, 1991).

The ctenophore *Pleurobrachia pileus* (Fig. 2b) did not react to the different feeding conditions of their food. This can be explained on the one hand by the fact that in the experiment C : P ratios of the copepods did not differ significantly between high P and low P food. C : P ratios of *Pleurobrachia* are not available from the literature, but our own preliminary data suggest that they are fairly high. Hence, it could well be that even P-limited copepods do not contain low enough amounts of P to depress growth in *Pleurobrachia*. This might be one of the factors favouring gelatinous zooplankton growth over fish growth in high C : P situations.

Copepods themselves, in this case *Acartia tonsa* (Fig. 2d), as secondary consumers, feeding on the dinoflagellate *Oxyrrhis marina* are influenced by the growing conditions of these prey. The C : P ratio of *Oxyrrhis* is highly dependent on its feeding conditions (HANTZSCHE, pers. communication), as is predicted for many other micrograzers (GROVER and CHRZANOWSKI, 2006). These differences in the C : P conditions of the dinoflagellate lead to differences in the development of *A. tonsa*, which was significantly reduced under high C : P food.

From these examples it becomes clear that the C: nutrient of the primary producers can very well influence the performance of predators feeding on the herbivores. These can be direct effects of nutrient limitation, as was shown by MALZAHN *et al.* (2007), as well as indirect ones through changes in the biochemical composition of the algae. These observations mean that we have to re-evaluate the way we look at secondary consumers: they are not necessarily the phosphorus recyclers in every lake under every circumstance, they may well be sinks of phosphorus (KRAFT, 1992), retaining as much of the limiting nutrient as possible (VANNI *et al.*, 2006).

4. Relevance and Implications

It is difficult to completely assess the implications of our findings and how relevant these are to our understanding of natural systems, since almost no research in this context has been carried out. As stated above, in many cases the most obvious reaction of herbivore populations to nutrient limitation of their food is a decrease in population densities, which will influence the prey availability for higher predators. The effects of quality difference of the prey in comparison with the effects of quantity changes may be different from system to system. We expect that in such cases where prey availability is usually high, coupled with high phosphorus demand by the predators such quality bottom-up effects may be strongest. Direct quantity effects should not occur with high prey densities, and could at the same time lead to scarcity of the limiting resource in the prey. P-demand is usually high in organisms that have high growth rates (ELSER, 2002), such as larval fish. Larval fish growth typically follows the population increase of herbivorous zooplankton, which succeeds the spring bloom of phytoplankton. We expect that, if for some reason the tight coupling of these dynamics becomes less, perhaps through different changes in temporal dynamics of the three trophic levels as a result of changing temperatures, it could well be that the larval fish is faced with herbivorous zooplankton that is feeding on late-bloom phytoplankters rather than on early bloom ones. Feeding on late-bloom algae automatically implies that the nutrient conditions of these algae are more depleted with respect to phosphorus and nitrogen and thus these zooplankters are a food source of suboptimal quality for larval fish. Hence, we might have to consider much smaller ''match'' windows between predators and suitable prey if additionally to the solely biomass based match-mismatch hypothesis of CUSHING (1974), food quality

has to be considered as well. This narrowing of the match windows might help improve our understanding of year class variation in fish, which for many species cannot be explained using prey availability alone. Furthermore, different fish species have different nutrient stoichiometry (VANNI et al., 2002; HENDRIXSON et al., 2007), and we expect those species with the highest P-demand to suffer first. Interestingly, the study by HENDRIXSON et al. (2007) showed that the fish with the lowest P-demand were the planktivorous ones, which might be understood as an adaptation to fluctuating prey quality, as these fish will be the first to face the consequences of P-limited phytoplankton growth.

Phosphorus concentrations have shown dramatic decreases in many systems in the last decades, both in marine as well as freshwater systems (MÜLLER, 2002; WILTSHIRE et al., 2008), and are expected to decline even further. Concurrently, fisheries yields have also dropped (JEPPESEN et al., 2005), but it is unclear how much of that is related to over-fishing and how much to declining productivity of the system. It is to be expected that these decreases in phosphorus concentrations will also directly affect fish growth through increased C:P ratios of the plankton, and hence we expect fish production to decrease more than is expected on the basis of decreasing primary production alone. Furthermore, the increasing CO_2 concentrations in lakes and seas should cause a further increase of the C:nutrient ratios of the primary producers (e.g., LOLADZE, 2002) with consequences for the primary producers (URABE et al., 2003) and potentially also for the higher trophic levels.

Most likely, however, fish are not the first to suffer from phosphorus depletion, as they can use bones and scales, which contain large amounts of P, as storage for phosphorus. High P invertebrate predators may be much more vulnerable to the effects of P-depletion in herbivorous zooplankton. Examples might be early life stages of molluscs, such as squids and cuttlefish (VILLANUEVA and BUSTAMANTE, 2006), which have very high growth rates. Experiments with young Sepia officinalis (MELZNER et al., 2005) and Loligo opalescens (VIDAL et al., 2006) paralarvae have shown that growth rates are tightly coupled to RNA:DNA ratios and P-demand (GILLOOLY et al., 2005), and that RNA concentrations are exceptionally high in fast growing individuals. The combination of living in marine, copepod dominated systems, their high growth potential and their high RNA concentrations makes them susceptible candidates for P limitation. Squids' ability to withstand P limitation has not been tested yet, as most other secondary consumers (e.g., predatory cladocerans, aquatic insect predators) have not been tested for their homeostatic ability, even though they are ideal candidates for experimental feeding trials, bearing a huge potential to increase our knowledge on the flow of energy and matter.

The first steps into this new room of the large building of ecological stoichiometry have been made, and the results suggest that we have to rethink our views on the mechanisms of bottom-up effects propagating up the food chain. We believe that this is an exciting new direction in this field, and look forward to seeing future studies on this subject.

5. Acknowledgements

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