Notes

TOO MUCH OF A GOOD THING: ON STOICHIOMETRICALLY BALANCED DIETS AND MAXIMAL GROWTH

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Abstract. Nutritional imbalances are of great interest in the ecological stoichiometry literature, in which researchers have focused almost exclusively on cases where nutrients are available in low amounts relative to energy (carbon), and animal growth is impaired due to insufficient nutrient intake. Little attention has been given to situations where food elemental content is higher than the level that satisfies animal requirements. However, most animals are strongly homeostatic with respect to the elemental composition of their body; hence they must excrete the excess of elements that are not in short supply. To date, stoichiometric theory has assumed that excretion of superfluous elements does not come with a cost and, thus, that consumption of food with surplus nutrients does not impair performance. Here we challenge this assumption, based on a compilation of several examples involving food phosphorus content that show that the performance of a wide variety of animals decreases when supplied with food containing high concentrations of (potentially) limiting nutrients. We discuss possible mechanisms for this phenomenon, and suggest that animals most vulnerable to effects of high food nutrient content are those that normally feed on low-quality (low-nutrient: C) food, and have a relatively low body nutrient content themselves, such as herbivores and detritivores.

Key words: high-P food; nutritional imbalance; stoichiometry theory; superfluous nutrients affect animal performance; threshold elemental ratio.

INTRODUCTION

Ecological stoichiometry, the study of the balance of energy and multiple chemical elements in ecological interactions (Sterner and Elser 2002), has flourished as a field of study in recent years. Whereas nitrogen (N) has been the main element of interest for terrestrial and marine ecologists (White 1993), most freshwater researchers have focused on phosphorus (P). Food with a low P:carbon (C) ratio can be a low-quality food for such diverse organisms as snails (Stelzer and Lamberti 2002), zooplankters (Boersma and Kreutzer 2002), insects (Perkins et al. 2004), fish (Borlongan and Satoh 2001), birds (Grone et al. 1995), and mammals (Riond et al. 2001), and it is relatively common that food P:C ratio for herbivores in nature is lower than expected thresholds for P limitation (Elser et al. 2000). However, it is also true that in many ecosystems food P:C ratios fall well above this threshold. For example, based on the study of Elser

et al. (2000) that considered possible P limitation for *Daphnia* (the most important crustacean zooplankter in lakes), around 22% of lake seston P:C ratios are higher than the proposed threshold elemental ratio (TER) for P limitation of ~0.0033 (or a P content of 0.43% P on a dry-mass basis, under the assumption that C is 50% of dry mass). To date, an implicit assumption of stoichiometric theory has been that variation in P:C ratio above the TER is irrelevant to animal performance. However, given that most animals actively maintain homeostasis with respect to the elemental composition of their body (Sterner and Elser 2002), stoichiometric theory predicts that they must excrete the excess of elements that are not in short supply, at the same time retaining the limiting nutrient with high efficiency. Indeed, increased P excretion under circumstances of high P availability has been observed in aquaculture settings (Rodehutscord et al. 2000) as well as for zooplankters (Olsen et al. 1986, Elser and Urabe 1999).

As noted, the implicit assumption that consuming food with excess nutrient content does not impair performance implies that dealing with superfluous elements does not come with a cost. Is this assumption valid? D.

Raubenheimer, S. J. Simpson, and co-workers (Raubenheimer and Simpson 1997, 2004, Simpson et al. 2004, Simpson and Raubenheimer 2005) developed a formal framework focusing on the macronutrients protein and carbohydrates in which they explicitly show that animals regulate their relative intakes of these nutrients when given the opportunity and that an excess of either protein or carbohydrates decreases fitness (Raubenheimer and Simpson 2004). Thus, animals perform best when the biochemical composition of the food is completely balanced with respect to the animal's requirements. Surprisingly, this approach has not really reached those studying chemical elements in a stoichiometric context, even though the theoretical approaches of ecological stoichiometry and the geometrical framework of Simpson and Raubenheimer have much in common.

Here, we contest the current "more is better (or at least never worse)" approach of ecological stoichiometry by presenting examples showing that, in a variety of taxa (fish, crayfish, cladocerans, molluscs, and insects), growth can decrease for food with high phosphorus content that would be generally be regarded as a "high-quality" food. We hope to show that such declines at high P content are real, are physiologically reasonable, and have potentially important evolutionary and ecological implications.

REDUCED GROWTH WITH A HIGH P:C DIET: WHEN IS P RICH TOO RICH?

Experiments with different levels of phosphorus in the food are fairly standard in aquaculture and agriculture settings (e.g., Skonberg et al 1997, Pimentel-Rodrigues and Oliva-Teles 2001). These studies are usually conducted to find the optimal balance between growth of the economically interesting species and the costs of feeds and waste removal. Benefits normally decrease with increasing phosphorus levels, and growth often reaches a plateau at 0.5–1.0% P (of dry mass) in the diet (Borlongan and Satoh 2001), which translates to a P:C ratio (atomic) in the food of 0.004–0.008, based on the assumption that ~50% of the dry mass is carbon. There are notable exceptions though, where overall performance decreases at higher levels of phosphorus (Fig. 1). These exceptions do not involve unreasonably high levels of food P content, and performance normally peaks at a food P content of ~1% P.

More ecologically oriented studies investigating the response of growth, survival, and reproduction to a range of different dietary P levels in the food are scarce. In most of these studies, investigators have used only two different P treatments, precluding the possibility of finding unimodal responses. There are, however, some examples of reduced growth on higher P levels. Dube and Culp (1997) observed that chironomids grew better on low levels of pulpmill effluent (with low levels of P) than on higher levels, which suggests that these detritivores are vulnerable to excess P, and several studies have indeed indicated unimodal responses of chironomid species presence to an increase in total P (Brooks et al. 2001). Frost and Elser (2002) observed a decrease in growth of mayflies feeding on exceptionally high food P content (~3.5% P) in comparison to food with 1% P, and Perkins et al. (2004) found similar results for caterpillars of *Manduca sexta* feeding on artificial diets. Plath and Boersma (2001) noted that growth in the cladoceran *Daphnia magna* was depressed when fed algae with more than ~1% P (Fig. 1). Building on these observations for *Daphnia*, Elser et al. (2005), in a study of snail–stromatolite interactions, invoked a unimodal animal response in which they observed increased animal performance after P enrichment from very low to moderate levels but decreased performance in a second experiment with stronger P enrichment that resulted in very low stromatolite P:C ratio. A subsequent experiment showed that, indeed, snail growth rate, survivorship, and overall production were maximal at intermediate stromatolite P:C ratio (Fig. 1d) (Elser et al. 2006).

From these physiological and ecological studies we conclude that decreases in consumer growth, reproduction, and survivorship due to high levels of P in the food are real. Thus, the assumption that consumption of stoichiometrically over-rich food does not incur a cost for the consumer is incorrect. It seems that stoichiometric imbalance, at least in terms of P:C ratio, can impair consumers whether that P:C ratio is higher or lower than the consumer's requirements. We now discuss possible mechanisms for these responses.

MECHANISMS

To our knowledge, no studies exist that have explicitly investigated the mechanisms involved in animal response to excess quantities of P, unlike the studies on protein vs. carbohydrates (e.g., Simpson et al. 2004). Many of the authors observing these phenomena have invoked methodological explanations. Shifts in pH, salinity, or potassium levels as a result of the addition of the P (added as KH_2PO_4), or potential interactions of P with other nutrients (magnesium, zinc, or manganese) were proposed as potential causes for decreased growth (Dy Peñaflorida 1999, Plath and Boersma 2001, Tan et al. 2001), but contested by others (Vielma et al. 2002, Perkins et al. 2004). Hence, while it is possible that experiments showing decreased animal performance under high dietary P are artefacts of the experimental execution, the relevant data are contradictory.

There are other possible explanations that are more ecologically and physiologically relevant. Perkins et al. (2004) suggested that supplying plants with high amounts of P might have changed other variables in the plants, such as carbohydrate availability, potentially causing decreased growth. Alternatively, behavioral
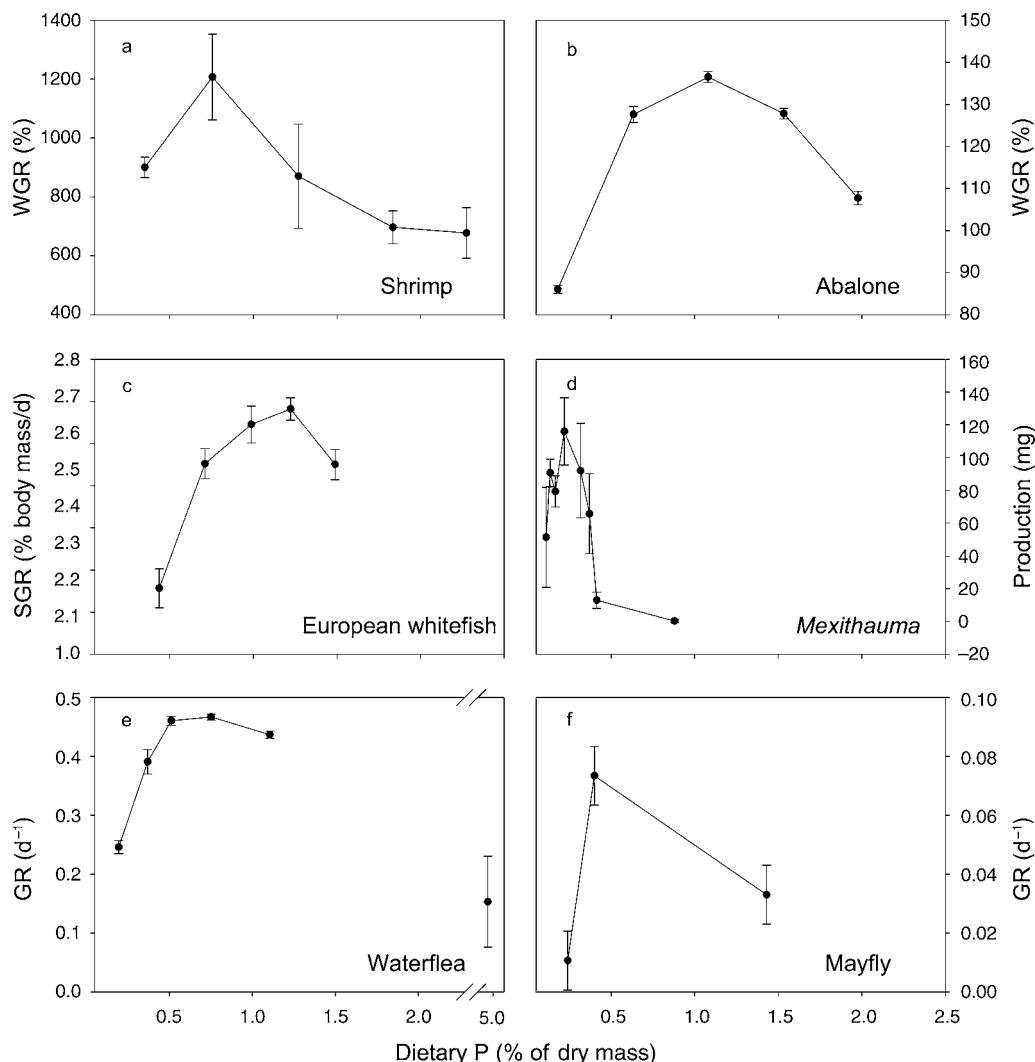
FIG. 1. Comparison of some published responses in a variety of taxa to dietary P content: (a) juvenile shrimp (*Penaeus monodon*) feeding on artificial diets (Dy Peñaflorida 1999); (b) abalone (*Haliotis discus hanni*) consuming artificial diets containing different amounts of phosphorus (Tan et al. 2001); (c) the European whitefish (*Coregonus lavaretus*) fed with graded levels of P in artificial food (Vielma et al. 2002); (d) stromatolite-grazing snail *Mexithauma quadripaludium* after P enrichment of stromatolite biomass in a field experiment (Elser et al. 2006); (e) waterfleas (*Daphnia magna*) cultured with laboratory grown algae, spiked with different amounts of K_2HPO_4 (Plath and Boersma 2001); (f) mayfly larvae (*Ephemerella* sp.) grown on natural periphyton spiked with dissolved K_3PO_4 (Frost and Elser 2002). Data are means ± SE; SGR = specific growth rate in percentage body mass per day, MGR = mass gain rate (increase in body mass) in percentage over the whole experimental period (16 weeks for Abalone, 90 days for shrimp), GR = instantaneous growth rate from $[\ln M_t - \ln M_0]/t$, in which M_t is mass at time t, and M_0 is mass at time 0, Production = the sum of mass increments (in milligrams) for all surviving snails after 39 days of experiment.

responses to food quality may be involved in producing a unimodal animal growth response to dietary P. Feeding at higher rates or for longer periods on food of inferior quality seems to be a common phenomenon (e.g., Slansky and Feeny 1977, Reynolds 1990, Wright et al. 2003). While increased intake rates potentially reduce the efficiency of extracting nutrients because not all of the food in the gut is fully digested, this is counteracted by passing more food through the gut in the same amount of time. Indeed, Plath and Boersma (2001) observed this

phenomenon for *Daphnia* feeding on P-depleted food and suggested that, in a persistently P-limited environment, adjusting the feeding effort directly to the P content of the food would be a fast and efficient way to optimize the uptake of a frequently limiting resource. Obviously, such a behavioral decision rule would fail if the normally limiting nutrient were to be present in excess. Consistent with this, Plath and Boersma's data indicate that *Daphnia*'s reduced growth rate at high food P:C ratio reflected an over-reduction in net C intake due

to reduced feeding effort. The animals were starving themselves for energy, despite a surfeit of available food (see also Simpson and Raubenheimer [2005]).

While Simpson et al. (2004) have explicitly considered fitness costs for both surpluses and deficits for protein and carbohydrates, ecological stoichiometry theory has thus far only been interested in the costs of excess C (insufficient nutrients), but not of excess P or N. This probably reflects the fact that most studies have been done in an ecological context where the goal was to evaluate the possible limiting effects caused by low nutrient availability in an ecosystem. Thus, food-quality effects on herbivores have been gauged in a range of autotroph nutrient:C ratios normally seen when that autotroph is limited by the nutrient in question. As a consequence, nutrients are almost never present in excess and nutrient-content gradients used in the studies were not broad enough for negative effects at high nutrient content to be observed. Moreover, many organisms have a capacity for storage of P and thus are able to buffer against temporary excesses of P (e.g., bones (Vielma and Lall 1998). This may be especially true for animals that have an evolutionary history of exposure to high dietary-P levels.

Hence, we conclude that, because nutrient excess incurs physiologically significant metabolic costs, decreased growth, survival, or reproduction of consumers will be exhibited whenever there is stoichiometric imbalance in the diet, even when the imbalance is in the direction of nutrient surplus. Incorporating such effects will likely improve the ability for stoichiometric theory to account for patterns in animal performance, trophic dynamics, and nutrient cycling in food webs. For example, had Anderson et al. (2005) included metabolic costs of excreting excess nutrients (not C) in their physiological model, growth efficiencies for C would have decreased again at very high P:C ratios of the food, and as a result predicted growth would have been maximal at the TER (threshold elemental ratio).

ECOLOGICAL AND EVOLUTIONARY CONTEXT

Given that reduced animal performance with P-rich food appears to be a real phenomenon and might manifest via several physiological and behavioral mechanisms, we might then wonder about the ecological relevance of such responses and their possible evolutionary implications. There seems to be a general trend, at least in aquatic systems but also likely to be the case in terrestrial systems, that as one ascends the food web from autotrophs to herbivores to higher predators that the nutrient (both P and N) content of organisms increases (Elser et al. 2000, Fagan et al. 2002, Sterner and Elser 2002). Thus, animals feeding at the base of the food web (on autotrophs or autotroph-derived detritus) should have developed sophisticated mechanisms for acquiring and retaining these potentially limiting nu-

trients. Consequently, as they live in this chronically nutrient-stressed environment, the likelihood that they will have developed mechanisms to deal with excess nutrients seems low. This is also the case for those animals that have very specialized feeding strategies on low nutrient:C food, such as phloem-feeders (Nevo and Coll 2001), or nectarivores (Nicolson and Fleming 2003). In contrast to the situation with basal consumers, animals higher in the food chain are generally confronted with lower concentrations of higher quality food (in terms of nutrient content) and thus would be less likely to experience nutrient deficiency. This also implies that they are more likely to have acquired physiological mechanisms to deal with high intake, including more sophisticated excretory pathways. So, we can suggest a general prediction that herbivores (especially those specialized on sources with low nutrient:C ratios) and detritivores would inherently be more sensitive to the effects of excess dietary-nutrient intake.

Other consumer traits might also be involved in mediating the susceptibility of particular taxa to excess dietary-P intake. For example, just as body P content is thought to be indicative of the sensitivity of consumers to effects of low dietary P:C ratio (all else being equal, P-rich consumers should more frequently experience P limitation due to low P:C food; Sterner and Elser 2002), body P content might also mediate sensitivity to effects of high dietary P:C. More specifically, low-P animals, which tend to have intrinsically lower growth rates and internal RNA levels (Elser et al. 2003), might be more frequently impacted by effects of high food-P content because, for them, P becomes "in excess" at an overall lower P content and because they are less able to dilute the incoming P into a rapidly expanding biomass and into significant P-rich internal sinks (e.g., RNA). Thus, we propose that the effects of excess dietary P on consumers will be most frequently observed for basal consumers (herbivores, detritivores) that have low biomass P content. In fact, the study of DeMott and Gulati (1999) suggests that indeed biomass of *Bosmina*, a species with a low P content relative to *Daphnia,* decreases at food P:C levels >0.013, whereas this was not the case with P-rich *Daphnia*. This scenario is also supported by the data of Elser et al. (2005, 2006), as the snail species they studied has a low body-P content (relative to the P content of crustacean and insect taxa for which data are available; Elser et al. 2000) and it seems to experience impaired performance due to "excess P" at a relatively low food P:C ratio compared to the other taxa in Fig. 1.

Under what circumstances might such consumers actually experience these negative effects, given that the actual P content of plant and detrital biomass in nature is generally low? Answering this question is difficult given the present data, but we offer several suggestions here. First, while plant and detrital P content is indeed

generally low, it is also variable in space and time. For example, while median P:C ratio of lake seston is relatively low (~0.01), lakes with seston P:C ratios as high as 0.05 (6% P on a dry-mass basis) exist (e.g., de Lange and Arts 1999). In such lakes, excessively P-rich seston may exclude certain members of the zooplankton community; no current studies consider such a possibility. Similarly, while terrestrial foliage is generally quite nutrient poor, considerable cross-taxon and cross-ecosystem variation exist that might contribute to unappreciated variations in the occurrence and success of different insect herbivores. It is also interesting to note that different plant parts differ considerably in nutrient content (Sterner and Elser 2002); for example, plant flowers are quite nutrient rich compared to plant leaves. Such differences might help in explaining why such obvious and apparently nutritious items are not consumed by at least some generalist herbivores that instead consume large amounts of relatively low-nutrient foliar biomass. Moreover, effects of excess nutrients might also explain the inconsistent results of studies on the effects of nutrient enrichments on fitness of insects that feed on phloem, a source of very low food quality in terms of nitrogen (Nevo and Coll 2001, Elberse et al. 2003).

Second, the existence of negative effects of high nutrient:C food might also help in understanding effects of local nutrient inputs on food webs. For example, it has been observed that consumer diversity in stream food webs declines significantly downstream in the immediate vicinity of point sources of nutrient pollution (Savage et al. 2002), or in lakes close to fish cages used in aquaculture (Guo and Li 2003). Perhaps effects of high dietary nutrient:C contribute at least partially to such responses. Moreover, the shift from benthic to pelagic production, which is often observed under intense eutrophication in aquatic systems and is normally explained by deteriorating light and oxygen availability close to the sediment, could also at least partially be caused by enrichment-induced increases in the nutrient content of food consumed by benthivores. In fact, low benthic light levels due to the high turbidity of eutrophied lakes should exacerbate this even further, as this implies less C fixation and a further increase in nutrient:C ratios of the available food (Sterner et al. 1997).

Ever since Hutchinson (1961) formulated his paradox of the plankton, and Tilman (1982) investigated the conditions necessary for the coexistence of species, many researchers have investigated competitive interactions between species. Tilman's original conclusion was that a certain system can only sustain as many species as there are limiting resources. This conclusion has now been modified in several ways. For example, poor food quality can induce reversals in the sign of interactions between potentially competing consumers (Loladze et al. 2004). Moreover, an increasing range of models has

been formulated that explicitly incorporate stoichiometric principles in studies of population dynamics (Loladze et al. 2000, Andersen et al. 2004, Kuijper et al. 2004), showing the consequences of variation in nutritional value for the dynamics and stability of predator–prey interactions. Without exception, these approaches have always assumed that more P is better (or at least never worse) for the consumer. Here, we have argued that this might not necessarily be the case, as has been shown for protein–carbohydrate balancing (Simpson et al. 2004). Most likely, unimodal responses of consumers to changes in food nutrient:C ratios will have major effects on the behavior of the models, just as introducing the effects of low food nutrient content did in the initial development of stoichiometric food-web models (Andersen et al. 2004). This additional nonlinearity in the response to limiting factors potentially opens up many more niches, and could be an additional factor explaining the coexistence of so many species in aquatic habitats and elsewhere.

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