

## REPORT

# On the influence of food quality in consumer–resource interactions

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## Abstract

While nutrients are an important regulating factor in food webs, no theoretical studies have examined limits to consumer growth imposed by nutrient concentrations (i.e. food quality) of their prey. Empirical studies have suggested that nutrients may play a role in limiting assimilation efficiencies of herbivores. Using a simple food chain model, I find that prey nutrient concentration does directly influence the growth rate of consumers and potentially increase the stability of consumer–resource interactions. This suggests that the strength of trophic cascades and the relative importance of top–down versus bottom–up control in food webs is significantly influenced by nutrient availability in food resources of consumers. Additionally, the results imply that increases in resource input may cause a change in which resource is limiting and thereby negate any potential “paradox of enrichment”.

## Keywords

Consumer–resource, food quality, multiple limiting resources, paradox of enrichment, trophic cascade

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## INTRODUCTION

Recent theoretical studies have shown that pelagic food web structure can have strong effects on community stability and the strength of trophic cascades (Huxel & McCann 1998; McCann *et al.* 1998a, b). A number of factors have been cited as important in structuring food webs of pelagic systems, including intraguild predation and omnivory within the zooplankton guild, food quality and nutrient stoichiometry, allochthonous inputs, high diversity, and spatial heterogeneity (Strong 1992; Polis & Strong 1996; Huxel & McCann 1998; Mackay & Elser 1998; McCann *et al.* 1998a, b). Whereas other structures are possible, recent theoretical food web studies have focused on energy as the currency of choice (Huxel & McCann 1998; McCann *et al.* 1998a, b). While these studies have had some success in explaining food web dynamics, energetic models have been criticized on the basis that community dynamics often cannot be predicted from data on diet or energy flow (Reiners 1986; Polis 1991; White 1993). Recent studies of pelagic systems have found that organismal stoichiometry of key nutrients (nitrogen and phosphorus) and the recycling of these nutrients can constrain food web dynamics (Stern *et al.* 1992; Vanni & Layne *et al.* 1997; Vanni *et al.* 1997; Elser & Foster 1998; Elser *et al.* 1998). Thus in these systems, energy flow may not be an adequate predictor of food

web dynamics. Other studies (Stern & Hesson 1994; Elser *et al.* 1996) suggest that herbivores with high nutrient demands may be limited not by energetic demands but by the mineral elements of their food. Similarly, Brett & Müller-Navarra (1997) suggest that highly unsaturated fatty acid content of resource species may determine energetic efficiency across the consumer–resource interaction, thereby influencing the strength of trophic coupling and trophic cascades in aquatic pelagic food webs. Thus nutrient stoichiometry or concentrations may be an important factor missing in energetically based food chain models. Here I present a food web model in which population growth of both prey and consumers depend upon both nutrients and energetics.

Food chain models that incorporate nutrients typically focus only on the direct influence of nutrients on the growth of producers and have found that nutrient inputs tend to destabilize food webs (14). These models have found that the dynamics of the entire system may be limited by nutrient availability at the producer level (so that productivity of the system is limited) (DeAngelis 1992; Holt *et al.* 1994). However, recent empirical studies have demonstrated that organismal nutrient concentration can regulate population growth of phytoplankton and herbivorous zooplankton (Elser *et al.* 1988, 1996, 1998; Stern 1993; Stern & Hesson 1994; Stern *et al.* 1996; Brett & Müller-Navarra 1997; Vanni & Layne 1997;

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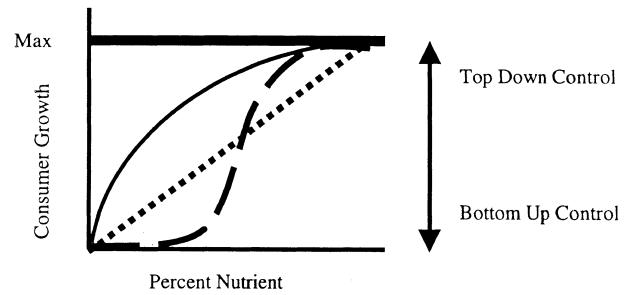
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Vanni *et al.* 1997; Mackay & Elser 1998). Among herbivorous zooplankton, *Daphnia* has high requirements for phosphorus. Over the course of a growing season, *Daphnia* can sequester P, thereby reducing the availability of this resource to the rest of the pelagic system, slowing the dynamics of the food web (Sterner *et al.* 1992, 1994; Elser *et al.* 1996; Vanni & Layne 1997; Vanni *et al.* 1997). McCann *et al.* (1998b) have found that food web processes that reduce interaction strengths and/or growth rates tend to stabilize community dynamics. Thus, one would expect that incorporating a nutrient-based growth limiting term for consumers in model food webs also would tend to stabilize food webs.

To examine the effects of nutrient limitation on consumer growth, one can begin with a two trophic level food web model based upon both nutrients and energetics. The realistic formulation of a food web model in which consumers are regulated by both nutrients and energetics represents a strong challenge. How might these two factors interact to regulate food web dynamics? Can one assume that the most limiting factor to consumers' growth regulates the consumer–resource interaction? Or is one factor just a scalar, with values between 0 and 1, of maximum potential growth based upon the other factor? Or alternatively, do nutrients and energetics interact in a nonlinear multiple resource fashion? Sterner & Hessen (1994) suggest that when the nutrient to carbon ratio in food is below the requirement of consumers, the nutrient becomes limiting in a linear fashion relative to the product of the concentration of the nutrient times the amount of food consumed. But at ratios above the requirement, the consumer will be satiated in terms of nutrients. However, this functional relationship need not be linear and any functional response that imposes a limit to growth due to the ratio of food consumed versus some limiting nutrient (e.g. minerals, vitamins, fatty acids) will give qualitatively similar results. Different functional responses will differ significantly as to where the shift from top–down to bottom–up control occurs (Fig. 1). Further experimental work is needed to establish a more general functional form.

For the present model, I hypothesized a saturating type II functional response of growth versus amount of nutrient consumed as a general model. This agreed with Sommer's suggestion that the relationship was analogous to Droop's model (which is similar to a type II functional response) (Sommer 1992). Thus, the function that relates the interaction between nutrient concentration of the prey ( $N_R$ ) and the nutrient requirements of the consumer ( $N_C$ ) has a general form of  $f(N_R, N_C)$ . In simulations with nutrient limitation, I use  $R/[k_3(k_4 + Ck_2)]$  as the specific form of this function, where  $R/k_3$  equals  $N_R$  and  $Ck_2$  equals  $N_C$ . In simulations without nutrient limitation,  $f(N_R, N_C)$  is set to 1. I incorporate nutrient dynamics into



**Figure 1** Hypothesized curves for consumer growth versus nutrient concentration of prey. The switch from top–down control to bottom–up control may be a gradual or a steep gradient depending upon the exact relationship between consumer growth and the nutrient content of their prey (solid line with arrows). The solid line is a type II functional response (such as the one used here and similar to the one suggested by Sommer 1992); the dotted line is a linear response (such as hypothesized by Sterner & Hessen 1994); and the dashed line is a type III functional response. Max is the maximum growth rate, i.e. no nutrient limitation. The type II functional response will more quickly move from bottom–up control at low nutrient concentration of the prey to top–down control compared with the other functional forms. Thus using a type II functional form may make the model results presented herein conservative.

a two trophic level model modified from the Yodzis & Innes (1992) consumer–resource energetic model. In order to focus on the consumer–resource interaction, the general model system does not include a nutrient recycling loop, instead nutrients enter into the system (from an allochthonous source) at a constant rate. This framework also allowed for examining the impact of varying the rate of supply of allochthonous nutrients into the system, which can significantly influence the dynamics of the system (DeAngelis 1992; Sommer 1992). This agrees with the finding of Sommer (1992) where increased rates of nutrient input resulted in higher algae P content and eventually increased densities of *Daphnia*. Thus, I used the following set of three equations:

$$\begin{aligned} \frac{dN}{dt} &= I - \frac{rRN}{k_1 + N} - eN \\ \frac{dR}{dt} &= \frac{k_3}{k_1 + N} \frac{rRN}{R + R_0} - \frac{x_c y_c CR}{R + R_0} \end{aligned} \quad (1)$$

$$\frac{dC}{dt} = -x_c C + \left[ \frac{R}{k_3 (k_4 + Ck_2)} \right] \left[ \frac{x_c y_c CR}{R + R_0} \right]$$

where  $N$  is the mass of nutrient in grams;  $R$  is the biomass of the prey or resource species in grams;  $C$  is the biomass of the consumer in grams;  $I$  is the amount of allochthonous nutrient input into the system ( $\text{gN day}^{-1}$ );  $r$  is the per

capita growth rate of  $R$  per day in terms of nutrient mass per biomass of  $R$  ( $\text{gN gR}^{-1} \text{day}^{-1}$ );  $e$  is the loss of nutrient in outflow ( $\text{gN day}^{-1}$ ),  $k_1$  is the half saturation point for the functional response between the nutrient and the prey;  $k_2$  is the mass of nutrient per unit of consumer biomass ( $\text{gN gC}^{-1}$ );  $k_3$  is the conversion of nutrient mass to prey biomass ( $\text{gR gN}^{-1}$ );  $k_4$  is the half saturation point of the functional response between the nutrient and the consumer;  $x_c$  is the mass-specific metabolic rate of the consumer measured relative to the production-to-biomass ratio of the prey density;  $y_c$  is a measure of the ingestion rate per unit metabolic rate of the consumer; and  $R_O$  is the half saturation point for the functional response between the prey and consumer.

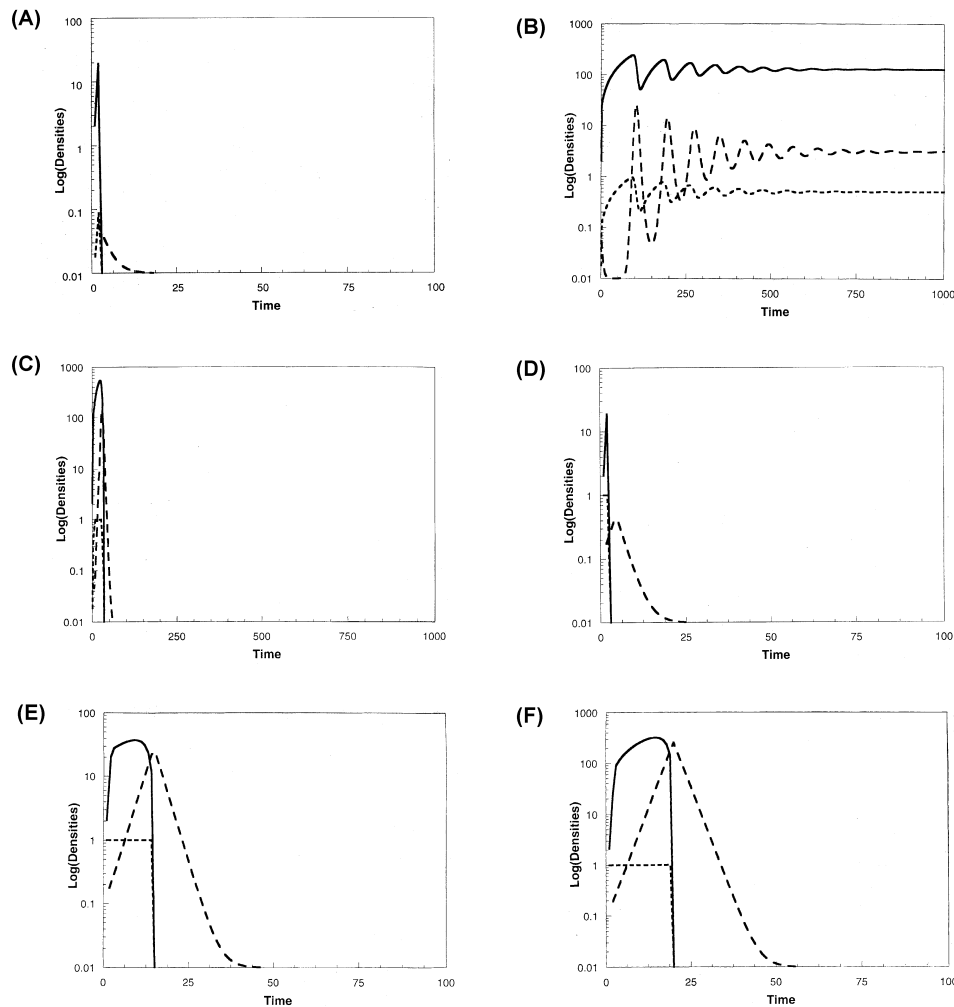
The consumer dynamics in system (1) result from a loss of biomass due to metabolic processes (e.g. starvation) and the consumer-prey type II functional response multiplied by the nutrient based limiting function. This function is dependent upon the ratio of the amount of nutrient in the prey biomass ( $N_R$ ) and the amount of nutrient in the consumer biomass ( $N_C$ ). This represents a measure of the potential for consumer growth based upon the available nutrient (for the consumers this is the amount of nutrient in the prey). While this function can theoretically exceed 1, it has a biological limit of 1: when it exceeds 1, the growth of the consumer then becomes limited by energetics (its maximal metabolic and consumption rates,  $x_c$  and  $y_c$ ). Studies of nitrogen and phosphorus composition have elucidated patterns that are instructive to understand the link between consumer's elemental composition, biochemistry, life history, and growth (Sterner 1993; Elser & Hassett 1994; Sterner *et al.* 1994; Elser *et al.* 1996, 1998). For example, *Daphnia*, a herbivorous cladoceran, has a relatively high specific P concentration (and therefore a low N:P ratio) while copepods have lower specific P concentrations (and therefore high N:P). These differences between the two taxa are partially the result of life history characteristics. Cladocerans experience greater growth rates and short life spans, while copepods are longer lived and have lower growth rates. Thus cladocerans, such as *Daphnia*, require higher levels of RNA for protein synthesis and therefore higher phosphorus contents and lower N:P ratios (Sterner *et al.* 1994; Elser *et al.* 1996). Furthermore, copepods undergo complete metamorphosis while cladocerans do not. During development from juvenile stages to adulthood, copepods increase in structural proteins as they grow in size, resulting in increases in the N:P (as protein:RNA) ratio. This is not restricted to aquatic systems; as *Drosophila* exhibit similar trends in elemental composition during metamorphosis (Sterner *et al.* 1994). However, in model system (1), consumer nutrient concentrations were assumed constant.

I examine the dynamics in terms of stability by comparing the results of system (1) with  $f(N_R, N_C)$  set to  $R/[k_3(k_4 + Ck_2)]$ , as opposed to setting this to 1. I also vary the input of allochthonous nutrient ( $I$ ) to examine whether these inputs are stabilizing or not. One would expect that low to moderate levels of allochthonous inputs should have a stabilizing effect, but higher levels will result in a collapse of the system.

Simulation results of three levels of input for  $f(N_R, N_C)$  set to  $R/[k_3(k_4 + Ck_2)]$  or to 1 are given in Fig. 2. When  $f(N_R, N_C)$  is set to 1, at all levels of nutrient input the consumer becomes extinct. In simulations with  $f(N_R, N_C)$  following from system (1), both the consumer and the prey persist for at least 1000 model days when  $I > 0$ . At no input ( $I = 0$ ), the time frame over which both species persisted depended upon the initial value of N. Low levels of allochthonous nutrients stabilized the system. Thus in all cases examined here, setting the function  $f(N_R, N_C)$  to  $R/[k_3(k_4 + Ck_2)]$  stabilizes the system by allowing increased persistence of the consumer and by increasing prey density. However, there may be levels of input that allow for persistence when  $f(N_R, N_C)$  is set to 1, but not when  $f(N_R, N_C)$  is less than 1.

Increased stability occurs because the function has a biological limit of 1 and usually is much less than this limit, thus weakening the strength of the consumer-prey interaction. In consumer-resource phase space, nutrient limitation [i.e.  $f(N_R, N_C)$  less than 1] pushes the zooplankton nullcline to the right, thereby increasing stability. When the consumer growth-prey nutrient content function equals one, then the system is only limited by the rate of consumption by the consumer; if the growth rate of the prey is great enough, then the system can exhibit large fluctuations in population size and perhaps crash. Thus, one can think of the system approaching the "paradox of enrichment" at high prey growth rates when nutrient concentration of the prey is not limiting for the consumer. If the nutrient concentration is limiting, the population growth of the consumer is reduced and the system becomes more stable. This may explain why the paradox of enrichment is readily found in model systems, in which only a single resource (currency) can be limiting, but not in natural systems where there are numerous potentially limiting resources. Furthermore, because I began with parameter values for which the system without nutrient dynamics is highly unstable, these results may be extrapolated to a wide range of parameter values for which the system is initially more stable (Fig. 3, Yodzis & Innes 1992).

One can then ask whether models of two currencies can result in a paradox of enrichment. In this model system, I found that input or allochthonous nutrients influence the dynamics in a manner similar to what Huxel & McCann

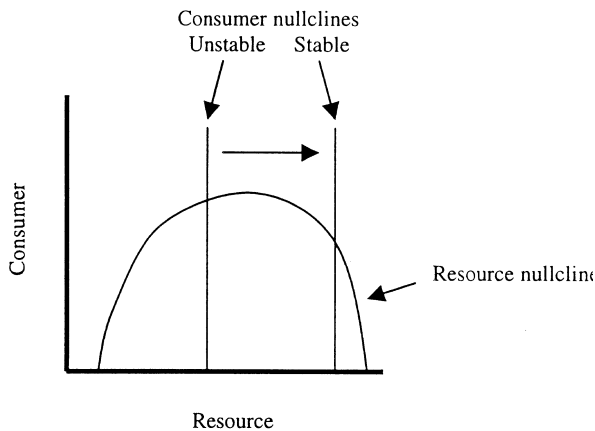


**Figure 2** In the model system, I used the following parameter values in the numerical simulations:  $x_C = 0.4$ ;  $y_C = 2.009$ ;  $R_O = 0.16129$ ;  $e = 0.1$ ;  $k_1 = 0.05$ ;  $k_2 = 0.10$ ;  $k_3 = 25.0$ ;  $k_4 = 10.0$ ;  $r = 0.10$  (2,3,18). Three different values for  $I$  (0.0, A and D; 0.1, B and E; 1.0, C and F) were used to represent no input, low input (oligotrophic conditions), and high input (eutrophic conditions). Numerical simulations are run for the course of a 100-day growing season following a water column turnover that creates an initial pool of nutrients. This time frame allows the effects of nutrient sequestration to become important. The system continued to run for 1000 model days to determine whether the system reaches equilibrium when persistence occurred (B). In numerical simulations, the functional form  $f(N_R, N_C)$  was set to either  $R/k_3(k_4 + Ck_2)$  (A–C) or to 1 (D–F). The solid line presents nutrient levels ( $N$ ), the dashed line represents the resource species ( $R$ ), and the dotted line represents the consumer ( $C$ ).

(1998) found, in that low levels of input stabilize while higher levels destabilize food web dynamics. Thus at high nutrient input, a paradox of enrichment occurs suggesting that in pelagic systems, in which the paradox of enrichment does not seem to occur, multiple resources ( $>2$ ) can be limiting (Tilman 1977, 1982; Leibold 1997). However, this result may not hold in systems where nutrient concentrations vary greatly across species, and lower food quality species increase in numbers due to lower attack rates compared with higher food quality

species (Hessen & Nilssen 1986). Thus, while I set the nutrient concentration of the prey constant, this probably does not hold in natural systems where heavy predation on high quality prey can result in favourable conditions for low quality prey.

These results have several important predictions. First, consumer nutrient requirements may limit their growth, which results in increased food chain stability. Empirical studies indicate that herbivores exhibit lower assimilation efficiencies than carnivores due to the large differences in



**Figure 3** This figure illustrates how nutrient limitation  $f(N_R, N_C) < 1$  can move the consumer nullcline to the right of the hump (peak) of the resource nullcline, thereby moving the system to a region of stability from a region of instability (DeAngelis 1992). The unstable situation occurs in the current model when  $f(N_R, N_C) = 1$  (see Fig. 2).

nutrient content of their respective resources (Sterner *et al.* 1994; Elser *et al.* 1996), and that herbivorous zooplankton in general may be limited by nutritionally inadequate phytoplankton (Brett & Müller-Navarra 1997). One could hypothesize that given very low food quality (in terms of nutrient contents) of producers, herbivores in these systems exhibit prey selection, intraguild predation (including cannibalism), or both. Second, any growth limitation may cause a shift from complete top-down control via consumption to a more mixed control wherein bottom-up control via food quality and nutrient supply can be important. This agrees with the findings of Brett & Goldman (1996, 1997) who performed meta-analyses on trophic cascade experiments in lake systems, and found that zooplankton biomass responded to both predation and nutrient treatments in some systems (see also McQueen *et al.* 1986). One would expect that this shift is gradual and the steepness of the gradient will depend upon the functional form of the consumer growth–nutrient concentration relationship (Fig. 1). Furthermore, the shift from top-down control to bottom-up control will weaken trophic cascades (Vanni 1996; Strong 1992; Brett & Goldman 1996, 1997; Brett & Müller-Navarra 1997).

Third, the amount of initial input into the system can significantly influence stability of the system, receiving little allochthonous inputs. While nutrient recycling was not included in model system (1), herbivores may provide a benefit to primary producers by accelerating the rate of recycling of limiting resources (DeAngelis 1992; Holt *et al.* 1994; Vanni 1996). Fourth, one can reason that nutrient additions (and similarly allochthonous inputs) that increase nutrient levels above the level of nutrient

limitation, will produce strong trophic cascades (e.g. increased consumer densities in two trophic level systems), but only up to a utilization saturation point. For example, *Daphnia* may experience growth limitations due to phosphorus only when its prey has carbon:phosphorus ratios of greater than 300:1 (Sterner *et al.* 1994).

Given these potential outcomes, consumer and resource community composition should be greatly influenced by elemental stoichiometry and nutritional content in general, which will have important consequences on the strength of trophic cascades (Elser *et al.* 1988, 1996, 1998; Sterner 1993; Sterner *et al.* 1994; Vanni 1996; Brett & Müller-Navarra 1997; Hassett *et al.* 1997). I suggest that more experiments need to approximate and parameterize the functional form of consumer–resource interactions as influenced by resource nutritional content. Most significantly, the parameters of the functional form, and perhaps the form itself, may differ among species and among nutrients (DeMott 1999). This will require experiments and hypotheses that incorporate consumer growth–nutrient concentration relationships to delineate conditions for strong trophic cascades and cautions against making ecosystem level predictions without accounting for differences among species.

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