

Modelling interactions of food quality and quantity in homeostatic consumers

ROBERT W. STERNER

Department of Ecology, Evolution and Behaviour, University of Minnesota, 100 Ecology, 1987 Upper Buford Circle, St Paul, MN 55108, U.S.A.

SUMMARY

1. Boundaries between growth limitation by carbon (C) and phosphorus (P) in homeostatic heterotrophic consumers such as zooplankton will vary as demands on these two elements vary, as they should at different food quantities. At very low food quantity when production is close to zero, metabolic requirements (for carbon) become more important than growth requirements (for carbon and phosphorus in fixed proportion). Thus, the boundary separating C- and P-limited growth should be at a higher C : P ratio at low food quantity than at high food quantity.
2. A model including both metabolism and growth indicates that consumer growth should differ between foods of high vs. low phosphorus concentration only when food quantity is above a certain level. Thus, two foods might give identical consumer growth rates at low food quantity but give different consumer growth at higher quantity.
3. Solution of the model using parameters based on 2 mm *Daphnia* compared with a survey of C and P in seston of marine and freshwater sites supports earlier conclusions of the potential importance of food quality constraints on *Daphnia* growth.

Introduction

The papers in this special issue signal a growing appreciation of the possibility that algal chemical composition affects the production, and hence population dynamics and fitness, of herbivorous zooplankton in nature. Food quality has long been a major feature of studies of terrestrial herbivores including insects (Dale, 1988), bison (Breman & de Wit, 1983), moose (Belovsky, 1981) and deer (Grasman & Hellren, 1993). Still, it may come as a surprise to see discussions of food quality constraints in pelagic herbivores. Compared to terrestrial plants, algae are less chemically defended and generally have much lower carbon contents compared to other essential elements than terrestrial plants, primarily because of their lack of support structures. It thus would seem that single-celled algae would be relatively high quality food for the animals that eat them. Nevertheless, recent work indicates that algae can, in fact, be poor in quality for zooplankton. The concentration of either certain polyunsaturated fatty acids (PUFA) (Müller-Navarra, 1995; Brett & Müller-Navarra, 1997; DeMott & Müller-

Navarra, 1997), or individual elements, such as phosphorus (Sterner & Hessen, 1994; Sundbom & Vrede, 1997), within the algal food base are related to zooplankton growth rates. In laboratory experiments, diet supplementation with P stimulates growth of *Daphnia* living on P-deficient food (Urabe *et al.*, 1997). Thus, the question of existence of food quality constraints in some places for some zooplankton is no longer the chief question. Attention now turns to the more sophisticated questions about when and where food quality constraints are important.

The purpose of this paper is to explore mathematically how food quality and quantity interact, with an ultimate goal of knowing more about when and where food quality is an important feature of zooplankton ecology. One form of this interaction is obvious: when food is very low in quantity, differences in qualities are unlikely to matter much since fitness will be low for all qualities, whether high or low. Thus, quality differences are more likely to matter when quantity is relatively high. The model introduced here, though,

examines a more complex aspect of quantity–quality interactions. Consider that heterotrophic organisms have two chief needs from their food: energy for metabolism and structural material for new biomass. This study adopts a simplified view that total energy available for metabolism is directly proportional to total food quantity. Such a simplification overlooks differences in digestibility as well as other features such as differences in energy content of different biochemicals. This simplification allows food quantity to be equated to total food carbon in this study, as in many others. The materials now being discussed relative to food quality in zooplankton [phosphorus and fatty acids (FA)] are used by the animals primarily for ‘structure’. Thus, individual FA are needed for cell membranes or as precursors for hormones, neither of which serves as a primary substrate for cellular energy. Phosphorus is necessary for a variety of things; quantitatively, the most important of these probably are nucleic acids (Elser *et al.*, 1996).

This model is based on two components of the algal food: carbon (C) and phosphorus (P). C is essential both for energy and for biomass, while P is considered only to have a structural role. By this, it is meant that P is not lost by the animal due to metabolism. C, on the other hand, is degraded to CO₂ and lost. P, of course, has essential involvement in respiration and other metabolic pathways, but we can think of a pool of P recycled within the animal during metabolism. As such, there is a ‘structural’ pool of P necessary for performing metabolism, but P is not used up during metabolism the way C is. The model would be just as valid for any other two parameters, providing that one has both uses and the other is used only for structure. In addition, the model is solved by assuming homeostasis between the two parameters in structural material. Specifically, this study assumes a constant C : P ratio in biomass of a species of zooplankton regardless of the food C : P ratio. The model would be valid for other substances which show similar degrees of homeostasis.

Two different thresholds will be important in analysing the model. The first of these is the individual food threshold (Lampert, 1977). The individual food threshold is the quantity of food necessary for there to be zero net change in animal mass. At this threshold, energy assimilated equals energy lost due to maintenance. The individual food threshold has units of food quantity, and for brevity it will be referred to as

the ‘quantity threshold’. The second threshold is the composition of the food, where there is a transition in limitation of animal growth between one substance (in this case either C or P) and another (Anderson, 1992; Hessen, 1992; Urabe & Watanabe, 1992). This threshold has been called the ‘elemental threshold’ or the ‘threshold element ratio’ (TER) (Urabe & Watanabe, 1992, 1993). In the present study, this threshold is referred to as the ‘quality’ threshold to contrast it succinctly with the quantity threshold. Food with C : P ratio above the quality threshold causes P limitation in animal growth, while food below that ratio has excess P compared to the animal’s needs.

Previous models of food quality in zooplankton have been based on an empirically determined net production efficiency in units of carbon (Anderson, 1992; Hessen, 1992; Urabe & Watanabe, 1992). This net production efficiency corresponds to the ratio of C put into new production by the animal (growth plus reproduction) divided by C ingested. However, net production efficiency need not be a constant; for example, for foods greatly above the quality threshold in C : P, net production efficiency (based, as is normally the case, on C) is predicted to be very low (Urabe & Watanabe, 1992). Thus, such models may be appropriate for certain situations, but it would be advantageous to have a model which dynamically predicts net production, rather than being based on empirically determined values.

Description of the model

The structure of the model is indicated in Fig. 1. The consumer ingests food, part of which is egested and part of which is assimilated across the gut wall. Some of the assimilated matter exits the consumer due to respiration (C) and excretion (P). The remainder goes towards production. Beyond this simple bioenergetics structure there are several features which make the model particularly appropriate for modelling food quantity and quality in zooplankton or other consumers. First, the flux of material into production will be treated as a homeostatically controlled parameter. The term ‘homeostasis’ is used in the same sense as used by Kooijman (1995); namely, the composition of the consumer organism is held constant regardless of the composition of the food the consumer ingests. In the particular instance of C and P in this model, the C : P ratio of production will be held constant and

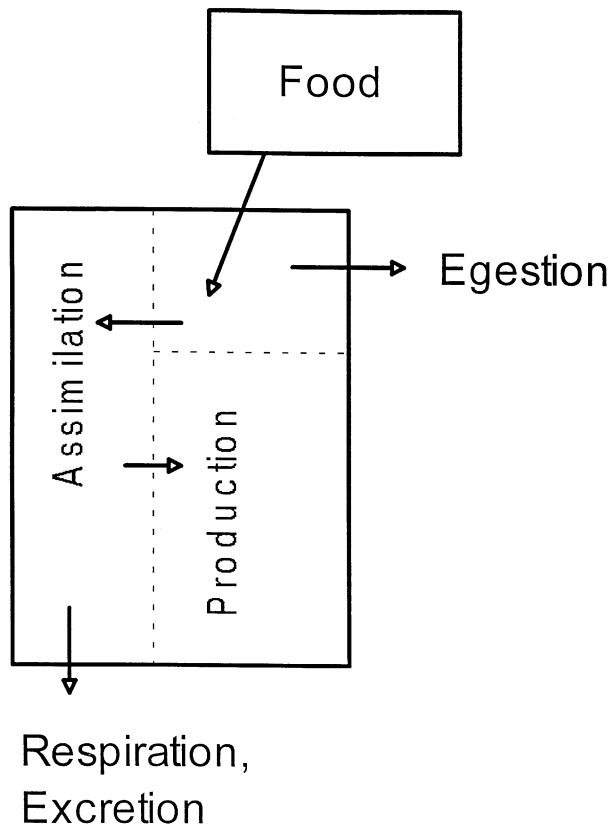


Fig. 1 Schematic of fluxes of C and P in the homeostatic consumer. The larger rectangle indicates the consumer. Food is ingested and subsequently either egested or assimilated. Material which is assimilated can go towards maintenance and therefore is excreted, or it can go towards production.

will equal the C : P ratio of consumer biomass (see Urabe, 1993; Urabe *et al.*, 1995).

Second, the model deals explicitly with two parameters in the food. C is used by consumers for maintenance and production. P is used only for growth. Both the fluxes of C and P in Fig. 1 are tied to the use of C for metabolism in the following way. The biomass of the consumer is used to determine the amount of carbon necessary for maintenance. Any assimilated carbon in excess of metabolic requirements is put towards production. Due to homeostasis, P is then put towards production in a constant ratio compared to the C put towards production. The consumer must therefore regulate the C and P going into production by adjusting respiration and excretion. Possible changes in assimilation efficiencies will be considered in the discussion.

First the mass transfers will be defined in a general way. Production of C can be written:

$$\frac{dC_Z}{dt} = [\text{ingestion} \cdot \text{assimilation} - \text{respiration}] C_Z$$

and phosphorus production is similar except for the terminology of soluble release:

$$\frac{dP_Z}{dt} = [\text{ingestion} \cdot \text{assimilation} - \text{excretion}] C_Z$$

Stoichiometric models differ from other models in the 'simplifying' constraints that they use. In many population models, a complex non-linear system of time derivatives is analysed by assuming equilibrium, and thus setting time derivatives to zero, creating a simpler set of equations than the original ones. The equilibria are then determined. Such a process takes a general non-linear system and creates a specialized case (equilibrium) because the special case is more mathematically tractable than the general system. Further simplifications then occur when the stabilities of equilibria are determined by linearization, creating a linear system of equations, which is analysed using matrix algebra and local stability is calculated (Yodzis, 1989). Stoichiometric models are mathematically similar in that they also take non-linear systems and create linear systems, but in an entirely different way. In stoichiometric models, it is homeostasis which introduces the linearity (Kooijman, 1995). Notably, in the case of homeostatic consumers, the linearity in the model is a statement of a true constraint; it is not a simplification of a more complex general system made just for mathematical tractability. This feature of stoichiometric models is one of the chief ways that they differ from other models in biology, and it means that they are not based on traditional assumptions of equilibrium of population sizes. In the case where elemental proportions in biomass are held constant, a boundary condition is input to a general system and analysis can proceed.

In the present example, homeostasis means:

$$\frac{C_Z}{P_Z} \cdot \frac{dP_Z}{dt} = \frac{dC_Z}{dt}$$

So, in general,

$$\frac{C_Z}{P_Z} = (\text{ingestion}_P) (\text{assimilation}_P) - \text{excretion} = (\text{ingestion}_C) (\text{assimilation}_C) - \text{respiration}$$

At the transition between the consumer being limited by C and being limited by P, two conditions are met. Under P limitation the consumer has very low or zero P release, and under C limitation there is no excess C to be disposed of. At the boundary between these two, both conditions are met. Thus, excretion is set equal to zero, and respiration equal to a single value, *m*. Now, the formula can be written:

$$\frac{C_Z}{P_Z} \cdot g P_F a_P - 0 = g C_F a_C - m.$$

To visualize this result, the equation can be rearranged so that the boundary between C and P limitation in the consumer is given as a relationship where food quantity (*C_F*) is a function of food quality (*f = C_F/P_F*):

$$C_F = \frac{m}{a_C g - \frac{C_Z a_P g}{P_Z f}}$$

Analysis of the model

The equation immediately above has the general form indicated in Fig. 2. It can be seen in the figure that the boundary between C and P limitation in the homeostatic consumer is not constant, instead it is predicted to vary with food quantity. Specifically, as the quantity becomes lower, such that the consumer gets closer and closer to starvation, the C : P ratio for transition between C-and P-limited growth in the consumer gets larger and larger. Fig. 2 emphasizes that a single ratio of transition between limiting factors should not be expected to apply for all situations, rather, the boundary between limitation by different dietary substances is a variable.

There are two asymptotes indicated in Fig. 2. Asymptote 'A' is the quality threshold, or the ratio of C : P for transition between C and P limitation in the consumer when food quantity is very high, where growth can be high if food is of sufficiently high quality. Such a ratio essentially corresponds to the thresholds that have been calculated by others before (Anderson, 1992; Hessen, 1992; Urabe & Watanabe, 1992). In the present terminology, asymptote A occurs at:

$$\frac{C_F}{P_F} = \frac{C_Z}{P_Z} \cdot \frac{a_P}{a_C} .$$

a result similar to those obtained by previous models. Asymptote 'B' is the quantity of food where the C : P

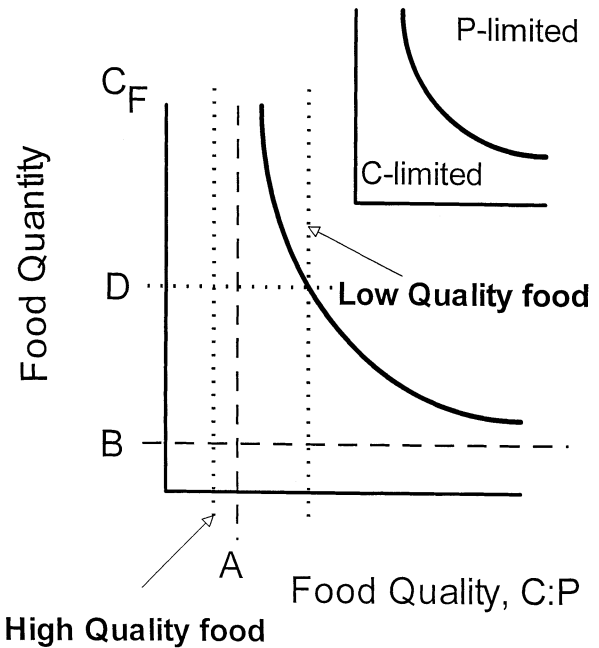


Fig. 2 Qualitative plot showing the major features of the boundary between carbon (C) and phosphorus (P) limitation in the homeostatic consumer. (Function is not plotted accurately for graphical clarity.) Inset shows the regions where the homeostatic consumer is limited by either C or P. In the larger plot it is seen that the boundary is a hyperbolic function which asymptotically approaches finite values near each of the x- and y-axes (points labelled A and B, respectively). Those asymptotes have well-defined meanings (see text). At low food quantity, the ratio of C : P in the food which makes the consumer P limited becomes large. At high food quantity, that ratio is smaller. Lines with short dashes indicate two foods of high food quality (low C : P ratio) and low food quality (high C : P ratio). The vertical line of low food quality intersects the boundary between C and P limitation (solid curve) at food density indicated by D. It is at this food quantity that differences in quality between the two food types should appear.

ratio of transition between C-and P-limited growth becomes infinite. Asymptote B occurs at:

$$m = a_C g C_F$$

which can be seen to be where C assimilated (right-hand side) is exactly equal to metabolic requirements (lefthand side). This is the quantity threshold. Thus, the present model formalizes in mathematical terms the prediction made on intuitive grounds by Urabe & Watanabe (1992) that the ratio for transition between C and P limitation becomes infinite at the quantity threshold. In other words, what happens is that as food quantity becomes lower and lower, demands for metabolism become larger and larger relative to

demands for growth (due to shrinkage in the latter, not growth in the former). Thus, more and more C relative to P is required, and the boundary for transition becomes higher and higher as food becomes scarcer and scarcer.

One more value indicated on Fig. 2 requires interpretation. The model predicts that for any C : P ratio greater than A (any food potentially poor in quality), there will be some food concentration D where the homeostatic consumer switches between limitation by C (at low food quantity) and limitation by P (at high food quantity). Thus, at food concentrations less than D, the consumer should show identical growth on both 'low' and 'high' quality foods because P is present in excess of growth requirements in both cases. However, at food concentrations higher than D, the consumer should show lower growth on low quality than high quality foods. Such an interaction between food quality and quantity was guessed at earlier from laboratory experiments (Sterner & Robinson, 1994), but it has not been demonstrated.

Data consistent with such an interaction between quality and quantity are also available from an experimental study of the rotifer *Brachionus rubens* (Rothhaupt, 1995). In Rothhaupt's study, the rotifer was reared on either high- or low-N foods. The present study assumes that the C : N ratio in the food will behave like the hypothesized trends for the C : P ratio, although it is recognized that protein catabolism for energy occurs and might complicate matters. The feature of the response of the rotifer to food quality and quantity most interesting in this context is that below a food quantity of about 1 mg C l^{-1} , the two foods yielded indistinguishable rotifer growth, but they clearly differed at higher concentrations (Fig. 3). It appears that the food quantity labelled D in Fig. 2 occurs at about 1 mg C l^{-1} in the rotifer data. If indeed the qualities of low-N algae are similar at low concentration but differ at high concentration, as implied in Fig. 3 and elsewhere (Sterner & Robinson, 1994), an interaction between quality and quantity based on a process similar to the model presented here is strongly indicated.

This model predicts combinations of food quantity and quality where transitions between C and P limitation in consumer growth can be expected. Most previous studies have used single values for this boundary, either from models or from empirical relationships between consumer growth and food composition, or

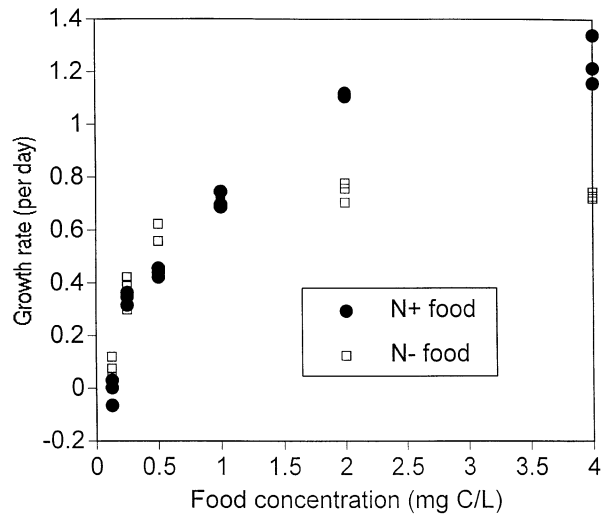


Fig. 3 Growth rates of the rotifer *Brachionus rubens* as a function of food quantity and quality (redrawn from original data provided by K.-O. Rothhaupt, published originally in Rothhaupt, 1995).

they have been based on individual measurements of carbon assimilation at a small number of food quantities. One study (Elser & Hassett, 1994) concluded that many freshwater lakes had seston composition that would lead to P limitation for *Daphnia* but few if any marine sites would be expected to have such nutritional constraints. This idea was further tested by comparing data from that study with the output of the present model. Basing the parameters on published values for *Daphnia* individuals of 2-mm body length ($\approx 4 \mu\text{mol C}$ per individual, Lynch, Weider & Lampert, 1986), the following values were utilized: $m = 0.002 \text{ h}^{-1}$ (based on basal respiration rate at very low food of $2 \mu\text{g C mg}^{-1} \text{ h}^{-1}$, Bohrer & Lampert, 1988); $g = 0.001$ (based on data in Lampert, 1994); $a_C = 0.5$; $a_P = 0.9$; and a molar ratio of C : P of 90 for *Daphnia* (based on Sterner & Hessen, 1994). Thresholds are then calculated to be at C : P in algae of 171 (quality) and $4 \mu\text{mol C l}^{-1}$ ($= 48 \mu\text{g C l}^{-1}$) (quantity). The calculated quality threshold is somewhat lower than empirical estimates, which have been reported to be at ≈ 300 (Sterner, 1993), but previous reports may refer to somewhat limiting food where the C : P boundary should be larger than this asymptotic threshold. Furthermore, earlier empirical reports refer to C : P ratios where animal growth is noticeably limited by quality, not to the exact position of transition between C and P limitation. Thus, these model calcula-

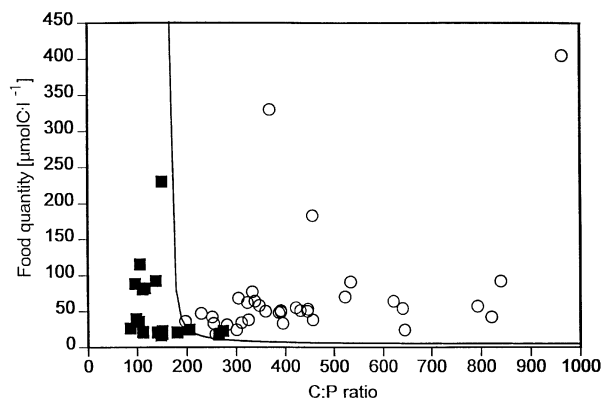


Fig. 4 Representation of the model calculated for parameters estimating a 2 mm *Daphnia* relative to the food quantity ($\mu\text{mol C}$) and quality (C:P, atomic) in a series of sites studied previously (Elser & Hassett, 1994). \circ = freshwater; \bullet = marine.

tions can be considered consistent with empirical measurements of the quality threshold. The calculated quantity threshold is $4 \mu\text{mol C l}^{-1}$, somewhat higher than empirical estimates, which are in the range of $1\text{--}2 \mu\text{mol C l}^{-1}$ (Gliwicz, 1990; Lampert, 1994). Nevertheless, given the overt simplicity of this model, agreement of calculated and empirical thresholds is adequate.

Plotting the model results along with the data from Elser & Hassett (1994) indicates that quantity-quality interactions do not alter previous conclusions based on single element ratios of food quality (Fig. 4). Although the bend in the model output is noticeable on the graph, it does not dramatically alter the predictions of individual lakes potentially with C-vs. P-limited *Daphnia*. Given the uncertainties of this approximate calculation, this author is unwilling to remark in great detail about exactly how many sites fall on each side of this boundary. A relatively conservative view of the results presented in Fig. 4 is that some freshwater sites fall close to the boundary of transition, and for these lakes, quantity-quality interactions, if they could be accurately determined, might be important in determining whether *Daphnia* should be P limited or not. Very surprisingly, calculations from this model suggest that essentially all freshwater sites studied by Elser & Hassett would be expected to show P-limitation in *Daphnia* growth. This view seems overly extreme, but nevertheless is the conclusion reached for this chosen parameter set.

Discussion

Understanding food quality constraints of substances held at homeostatic proportions by consumer herbivores (such as P for zooplankton) requires detailed bioenergetics information, particularly under near-starvation conditions where production is a small fraction of metabolism. Luckily, such information is available for the herbivore *Daphnia*, but unfortunately it is less precisely known for other herbivores. That information on *Daphnia* has been used to calculate the boundary between C and P limitation as a function of food quantity. The present model suggests that we should avoid thinking of a single food composition which creates poor quality food for any given consumer species. Instead, bioenergetics suggests that the food-consumer system is a highly dynamic one, with the precise boundary between limitation by different substances in the food depending upon many factors but with certain consistent trends. Because metabolism becomes more important relative to production at low food quantity, the boundary between C (need for both metabolism and production) and P (needed only for production) limitation becomes larger at low food quantity. That boundary is essentially infinite at the individual food threshold where assimilation equals metabolism, and production is zero. Environments with low food quantity would not be expected to show dramatic food quality constraints on consumer organisms.

A more quantitative analysis of the model, using parameters based on 2-mm *D. pulex*, in comparison with a survey of a variety of freshwater and marine sites, failed to find strong evidence that the elevation in the C:P boundary at low food quantity is a significant factor for most sites, although some sites were close to the boundary. The food quantities predicted to show elevated C:P boundaries by low food quantity were lower than the actual concentration of C measured in most sites (Fig. 4). However, it is not certain that all sestonic C in this data set should be considered assimilable. It is premature to accept that food quantity-quality interactions are unimportant in most habitats, but, for this set of parameters and this set of lakes, the interaction does not appear to be a major feature. The prediction of which habitats should exhibit P-limited *Daphnia* growth based on the asymptotic quality threshold is virtually identical to the more detailed model including both the quality and the quantity thresholds.

A subtler prediction of the model, which seems to be consistent with available data, is that a single type of food, deficient in one or more substances, might only become a poor food at high enough food quantity where production demands escalate until the availability of a single substance in the food can become rate-limiting to growth. Data for rotifers grown at low food quantity (Rothhaupt, 1995) are consistent with this prediction.

To construct this model, it was necessary to make certain assumptions about how the animal maintains its homeostasis. For the present study it was assumed that assimilation across the gut wall is essentially a passive process with a constant efficiency. Such a view is consistent with recent studies on assimilation of various elements by microcrustacea and other organisms (Reinfelder & Fisher, 1991, 1994a, b), which demonstrate a close correspondence between assimilation efficiency and the fraction of an element in the food which is found in soluble cytoplasmic pools. Although differential production of gut enzymes is well-described in microcrustacea (Harris *et al.*, 1986; Hassett & Landry, 1983, 1990a, b), indicating some ability to modify digestive processing of foods, it is not known whether differential assimilation of individual elements across the gut wall is under physiological control, and therefore contributes to maintenance of homeostasis. Pinocytotic uptake would preclude extensive sorting at this level of physiology. Nevertheless, some differences in assimilation caused by variable gut passage time at different food quantities can be expected.

The animals in this model maintain homeostasis by varying the proportion of assimilated element which is subsequently released as soluble material. In this model, homeostasis is maintained as a cellular process of differential release of material back to the environment after it has been assimilated. It is not very likely that excess C is removed by cellular respiration, as this generates ATP energy, conjuring up the humorous image of the animal doing extra work on its environment (swimming?) in order to maintain its homeostasis. Instead, excess C might be released by the animal as dissolved organic carbon (DOC), which has been measured to be $\pm 10\%$ of total C release in *Daphnia* feeding on high quality food (Lampert, 1978). However, DOC release of *Daphnia* on low quality, high C foods, has yet to be reported. It is an open question today where homeostasis is maintained. There are a

number of reasons why it is an interesting question. Release of DOC vs. CO₂ might have ecosystem consequences such as between dissolved organic nitrogen (DON) and dissolved inorganic nitrogen (DIN) (Bronk, Gilbert & Ward, 1994). Furthermore, it would be interesting to know exactly how the animal regulates homeostasis, as this would tell us more about the costs of homeostatic maintenance, which are very poorly understood (Sterner, 1995).

However, in spite of the importance of answering this open question for various reasons, the precise location of homeostatic maintenance is not critical to the conclusions from the model discussed here. If excess C were released by DOC rather than respiration, all the conclusions of the analysis presented here would be unaltered, although the exact structure of the model might need some adjustment.

This model also assumed that there was no effect of food concentration on assimilation or respiration. This assumption contradicts the known dependence of respiration on food quantity due to specific dynamic action (SDA) (Lampert & Bohrer, 1984; Bohrer & Lampert, 1988; Urabe & Watanabe, 1990). Qualitatively, SDA would be expected to increase C demands as food quantity goes up, thus acting in the opposite direction to the trends modelled here. *Daphnia* feeding on high food concentrations may have about a twofold greater metabolic rate than those near the quantity threshold (Lampert & Bohrer, 1984). Accurate modelling of SDA would require measurements of SDA on foods of differing qualities. Measurements of SDA on foods of different qualities might help resolve some of the above-mentioned issues about costs of homeostasis.

In summary, it can be expected that a homeostatic consumer living on the brink of starvation will probably not show detectable responses to changes in food quality, because growth is low anyway and because growth does not dominate metabolism in the element budgets. Calculations of food quantity and quality leading to C vs. P limitation in 2-mm *Daphnia* indicate, surprisingly, that nearly all freshwater sites in the data set of Elser & Hassett (1994) would potentially have P-limited *Daphnia*. We are a long way from understanding exactly when and where food quality is important to zooplankton, but we must strive toward answering this set of questions. We have achieved a deep appreciation of the ways that predation influences body size patterns in zooplankton communities, but predation

does not do a particularly good job of sorting out species within size ranges. Food quality, including C : P ratio, might be extremely important in resolving many unexplained patterns in zooplankton community structure.

Acknowledgments

I thank Shahid Naeem for pointing out that stoichiometric models are linear systems. This model on food quantity and quality was stimulated by conversations with Daniel Schindler. Karl-Otto Rothhaupt provided raw data from his published study. Jim Elser and Pat Hassett provided raw data from their published study, including previously unpublished portions. I thank Jotaro Urabe, Peder Yurista and Kim Schulz for comments on the model. Jim Elser and Jotaro Urabe read and commented on the manuscript. Financial support was given by NSF grants DEB-9119781 and DEB-9421925.

References

- Anderson T.R. (1992) Modeling the influence of food C : N ratio, and respiration on growth and nitrogen excretion in marine zooplankton and bacteria. *Journal of Plankton Research*, **14**, 1645–1671.
- Belovsky G. (1981) Food plant selection by a generalist herbivore: the moose. *Ecology*, **62**, 1020–1030.
- Bohrer R.N. & Lampert W. (1988) Simultaneous measurement of the effect of food concentration on assimilation and respiration in *Daphnia magna* Straus. *Functional Ecology*, **2**, 463–471.
- Breman H. & de Wit C.T. (1983) Rangeland productivity and exploitation in the Sahel. *Science*, **221**, 1341–1347.
- Brett M.T. & Müller-Navarra D.C. (1997) The role of essential fatty acids in aquatic foodweb processes. *Freshwater Biology*, **38**, 483–499.
- Bronk D.A., Gilbert P.M. & Ward B.B. (1994) Nitrogen uptake, dissolved organic nitrogen release, and new production. *Science*, **265**, 1843–1846.
- Dale D. (1988) Plant-mediated effects of soil mineral stresses on insects. *Plant Stress–Insect Interactions* (ed. E. A. Heinrichs), pp. 35–110. John Wiley and Sons, New York.
- DeMott W.R. & Müller-Navarra D.C. (1997) The importance of highly unsaturated fatty acids in zooplankton nutrition: evidence from experiments with *Daphnia*, a cyanobacterium and lipid emulsions. *Freshwater Biology*, **38**, 649–664.
- Elser J.J. & Hassett R.P. (1994) A stoichiometric analysis of the zooplankton-phytoplankton interaction in marine and freshwater ecosystems. *Nature*, **370**, 211–213.
- Elser J.J., Dobberfuhl D.R., MacKay N.A. & Schampel J.H. (1996) Organism size, life history, and N : P stoichiometry. Towards a unified view of cellular and ecosystem processes. *Bioscience*, **46**, 674–684.
- Gliwicz Z.M. (1990) Food thresholds and body size in cladocerans. *Nature*, **343**, 638–640.
- Grasman B.T. & Hellren E.C. (1993) Phosphorus nutrition in white-tailed deer: nutrient balance, physiological responses, and antler growth. *Ecology*, **74**, 2279–2296.
- Harris R.P., Samain J.F., Moal J., Martin-Jezequel V. & Poulet S.A. (1986) Effects of algal diet on digestive enzyme activity in *Calanus helgolandicus*. *Marine Biology*, **90**, 353–361.
- Hassett R.P. & Landry M.R. (1983) Effects of food-level acclimation on digestive enzyme activities and feeding behavior of *Calanus pacificus*. *Marine Biology*, **75**, 47–55.
- Hassett R.P. & Landry M.R. (1990a) Effects of diet and starvation on digestive enzyme activity and feeding behavior of the marine copepod *Calanus pacificus*. *Journal of Plankton Research*, **12**, 991–1010.
- Hassett R.P. & Landry M.R. (1990b) Seasonal change in feeding rate, digestive enzyme activity, and assimilation efficiency of *Calanus pacificus*. *Marine Ecology Progress Series*, **62**, 203–210.
- Hessen D.O. (1992) Nutrient element limitation of zooplankton production. *American Naturalist*, **140**, 799–814.
- Kooijman S.A.L.M. (1995) The stoichiometry of animal energetics. *Journal of Theoretical Biology*, **177**, 139–149.
- Lampert W. (1977) Studies on the carbon balance of *Daphnia pulex* de Geer as related to environmental conditions. IV. Determination of the ‘threshold’ concentration as a factor controlling the abundance of zooplankton species. *Archiv für Hydrobiologie. Supplement*, **48**, 361–368.
- Lampert W. (1978) Release of dissolved organic carbon by grazing zooplankton. *Limnology and Oceanography*, **23**, 831–834.
- Lampert W. (1994) Phenotypic plasticity of the filter screens in *Daphnia*: Adaptation to a low-food environment. *Limnology and Oceanography*, **39**, 997–1006.
- Lampert W. & Bohrer R. (1984) Effect of food availability on the respiratory quotient of *Daphnia magna*. *Comparative Biochemistry and Physiology*, **78A**, 221–223.
- Lynch M., Weider L.J. & Lampert W. (1986) Measurement of the carbon balance in *Daphnia*. *Limnology and Oceanography*, **31**, 17–33.
- Müller-Navarra D. (1995) Evidence that a highly unsaturated fatty acid limits *Daphnia* growth in nature. *Archiv für Hydrobiologie*, **132**, 297–307.

- Reinfelder J.R. & Fisher N.S. (1991) The assimilation of elements by marine copepods. *Science*, **251**, 794–796.
- Reinfelder J.R. & Fisher N.S. (1994a) The assimilation of elements ingested by marine planktonic bivalve larvae. *Limnology and Oceanography*, **39**, 12–20.
- Reinfelder J.R. & Fisher N.S. (1994b) Retention of elements absorbed by juvenile fish (*Menidia menidia*, *Menidia beryllina*) from zooplankton prey. *Limnology and Oceanography*, **39**, 1783–1789.
- Rothhaupt K.O. (1995) Algal nutrient limitation affects rotifer growth rate but not ingestion rate. *Limnology and Oceanography*, **40**, 1201–1208.
- Sterner R.W. (1993) *Daphnia* growth on varying quality of *Scenedesmus*: Mineral limitation of zooplankton. *Ecology*, **74**, 2351–2360.
- Sterner R.W. (1995) Elemental stoichiometry of species in ecosystems. *Linking Species and Ecosystems* (eds C. G. Jones and J. H. Lawton), pp. 240–252. Chapman and Hall, New York.
- Sterner R.W. & Hessen D.O. (1994) Algal nutrient limitation and the nutrition of aquatic herbivores. *Annual Review of Ecology and Systematics*, **25**, 1–29.
- Sterner R.W. & Robinson J. (1994) Thresholds for growth in *Daphnia magna* with high and low phosphorus diets. *Limnology and Oceanography*, **39**, 1229–1233.
- Sundbom M. & Vrede T. (1997) Effects of fatty acid and phosphorus content of food on the growth, survival and reproduction of *Daphnia*. *Freshwater Biology*, **38**, 665–674.
- Urabe J. (1993) N and P cycling coupled by grazers' activities: food quality and nutrient release by zooplankton. *Ecology*, **74**, 2337–2350.
- Urabe J. & Watanabe Y. (1990) Influence of food density on respiration rate of two crustacean plankters, *Daphnia galeata* and *Bosmina longirostris*. *Oecologia*, **82**, 362–368.
- Urabe J. & Watanabe Y. (1992) Possibility of N or P limitation for planktonic cladocerans: an experimental test. *Limnology and Oceanography*, **37**, 244–251.
- Urabe J. & Watanabe Y. (1993) Implications of sestonic elemental ratio in zooplankton ecology: reply to the comment by Brett. *Limnology and Oceanography*, **38**, 1337–1340.
- Urabe J., Nakanishi M. & Kawabata K. (1995) Contribution of mesozooplankton to the cycling of N and P in Lake Biwa. *Limnology and Oceanography*, **40**, 232–242.
- Urabe J., Clasen J. & Sterner R.W. (1997) Phosphorus-limitation of *Daphnia* growth: is it real? *Limnology and Oceanography*, **42**, 1436–1443.
- Yodzis P. (1989) *Introduction to Theoretical Ecology*. Harper and Row, New York.

(Manuscript accepted 20 March 1997)

Appendix 1 Definition of symbols used

Symbol	Definition	Dimensions
C_F	Food carbon	$\mu\text{mol l}^{-1}$
P_F	Food phosphorus	$\mu\text{mol l}^{-1}$
C_Z	Zooplankton carbon	μmol
P_Z	Zooplankton phosphorus	μmol
g	Clearance rate	$\text{l } \mu\text{mol}^{-1} \text{ C h}^{-1}$
a_C	Assimilation of C	Dimensionless fraction
a_P	Assimilation of P	Dimensionless fraction
m	Specific respiration rate	h^{-1}
f	C : P ratio in food (= C_F/P_F)	molar ratio