Ecology Letters, (2001) **4**: 519–529

REPORT

Stoichiometric food quality and herbivore dynamics

Erik B. Muller[1]*, Roger M. Nisbet[1], Sebastiaan A. L. M. Kooijman[2], James J. Elser[3] and Edward McCauley[4]

[1]Department of Ecology, Evolution and Marine Biology, University of California, Santa Barbara CA 93106-9610, USA.
[2]Department of Theoretical Biology, Institute of Ecological Science, Vrije Universiteit, de Boelelaan 1087, 1081 HV Amsterdam, the Netherlands.
[3]Department of Biology, Arizona State University, Tempe AZ 85287, USA.
[4]Ecology Division, Department of Biological Sciences, University of Calgary, Calgary, Alberta, T2N 1N4 Canada.
**Correspondence: E-mail: muller@lifesci.ucsb.edu*

Abstract

Herbivores may grow with nutrient or energy limitation, depending on food abundance and the chemical composition of their food. We present a model that describes herbivore growth as a continuous function of two limiting factors. This function uses the synthesizing unit concept, has the hyperbolic Monod model as a limiting case, and has the same number of parameters as the Monod model coupled to Liebig's discontinuous minimum rule. We use the model to explore nutrient-limited herbivore growth in a closed system with algae, *Daphnia* and phosphorus as the limiting nutrient. Phosphorus in algae may substantially influence *Daphnia* growth. This influence changes over time and is most pronounced when algae and *Daphnia* populations fluctuate strongly. Relative to classic models that only consider food quantity as a determinant of *Daphnia* growth, our model shows richer dynamical behaviour. In addition to the standard positive equilibrium, which may be stable or unstable depending on nutrient availability, a new positive equilibrium may arise in our model when mortality rates are relatively high. This equilibrium is unstable and reduces the likelihood of long-term persistence of *Daphnia* in the system.

Keywords

Synthesizing unit, Droop model, Monod model, stoichiometric requirements, multiple limitation, growth model, food quality.

Ecology Letters (2001) 4: 519–529

INTRODUCTION

Plants and algae have highly variable nutrient contents. Because new herbivore biomass is produced with a tightly controlled elemental composition, a herbivore may experience energy or nutrient limitation depending on the abundance and composition of its food. Recently, this problem has attracted considerable attention from aquatic and terrestrial ecologists, as it is believed that the elemental composition of primary producers relative to the stoichiometric requirements of herbivores underlies major aspects of community organization and dynamics (Andersen 1997; Hessen 1997; Elser & Urabe 1999; Elser *et al.* 2001). We develop a new model describing herbivore growth with two potentially limiting compounds and illustrate model behaviour for a system with *Daphnia* and phosphorus-limited algae. Recent evidence shows that phosphorus-limited *Daphnia* growth can be induced in laboratory cultures (Urabe & Sterner 1996; Urabe *et al.* 1997; DeMott *et al.* 1998) and observed *in situ* (DeMott & Gulati 1999; Elser *et al.* 2001).

Traditionally, models describing the dynamics of plant and herbivore populations use a single currency, usually carbon, to describe the growth of herbivores (see, e.g. Nisbet *et al.* 1991, and references therein). An implicit assumption is that food quantity rather than its composition influences herbivore growth. When food composition becomes an issue, Liebig's minimum rule is usually invoked (Tilman 1982; Andersen 1997; Grover 1997; Loladze *et al.* 2000). The minimum rule asserts that only one compound can be truly limiting at any particular time, with the consequence that an organism may live in a borderline environment in which the limiting compound switches continually. Having a switch in a model is mathematically inconvenient and also implies that physiological regulation systems are unduly taxed in borderline environments. Near the switch, the minimum rule cannot describe growth realistically and thus it would be advantageous to have an equation describing growth as a continuous function of multiple limiting factors.

Drawing on recent advances in biochemistry (Kooijman 1998, 2000), we present a model of synthesizing units with which the effects of multiple limiting compounds can be described. Synthesizing units are "servers" that handle a potentially wide range of limiting compounds and form one or more products. We first discuss and illustrate the qualities

of a synthesizing unit by implementing the concept in the simple Monod model (Monod 1950), which is also the routine choice in previous models implementing the minimum rule (see, e.g. Grover 1997). We then incorporate the synthesizing unit concept in a model for aquatic producers (algae) and consumers (*Daphnia*), with producers growing according to Droop (1974) and consumers feeding with a type II functional response. We explore the dynamics of this system using a range of natural parameter values, and identify conditions under which phosphorus in food may strongly influence *Daphnia* growth.

SYNTHESIZING UNITS

A synthesizing unit converts substrates into products while meeting the stoichiometric requirements for product formation. An enzyme is an obvious example of a synthesizing unit, but we have also in mind an abstract representation of the biomass producing machinery in an organism, in which "substrates" are components in food and the "product" is biomass. It is this latter picture that we will use later in modelling the biomass synthesis rate of *Daphnia*. In this section we outline the theory of a synthesizing unit and compare its dynamics to the Monod model with a minimum rule.

A synthesizing unit can handle an arbitrarily large number of substrates and products, but here we restrict ourselves to two different substrates and one product, see Kooijman (1998, 2000) for a more exhaustive presentation. We consider a synthesizing unit with n_1 binding sites for substrate x_1 and n_2 binding sites for substrate x_2. The synthesizing unit is said to be in its binding stage if one or more of its binding sites are empty; the production stage starts with the occupation of all sites and ends with the release of products. We assume that substrate particles arrive at the binding sites of the synthesizing unit according to a Poisson process, and that the binding sites operate independently. The probability that an arriving substrate particle attaches to a binding site suitable for that substrate is constant, provided the site is empty (otherwise, the binding probability is zero). If binding and production are irreversible events, and the production period is exponentially distributed with mean $\dot{J}_m^{-1}$ it can be shown that the average rate at which the synthesizing units deliver product, $\dot{J}$, is approximately (Kooijman 1998, 2000)

$$\dot{J} = \frac{1}{\frac{1}{\dot{J}_m} + \frac{n_1}{\dot{J}_1} + \frac{n_2}{\dot{J}_2} - \left(\frac{\dot{J}_1}{n_1} + \frac{\dot{J}_2}{n_2}\right)^{-1}} \qquad (1)$$

in which $\dot{J}_1$ and $\dot{J}_2$ are the average rate at which the synthesizing unit binds x_1 and x_2, respectively. $\dot{J}_m$ is the maximum rate at which a synthesizing unit can deliver product.

When one of the substrate fluxes is very high, the reciprocal of this flux and the term in parentheses in the denominator is very small and consequently, Eq. (1) reduces to a simple hyperbolic expression. Thus, Monod's model (Monod 1950), which has the same functional form as the type II functional response, is a special case of the synthesizing unit concept. However, rates in the Monod model are usually expressed in terms of the substrate concentration rather than its flux. If concentrations are proportional to fluxes, the synthesizing unit concept provides a modelling framework that is more general than the Monod model. Later in this paper we use flux measures in describing assimilation rates.

Monod's model frequently serves as a framework for Liebig's minimum rule, which with two potentially limiting compounds can be written as (Grover 1997):

$$\dot{J} = \min\left(\frac{1}{\frac{1}{\dot{J}_m} + \frac{n_1}{\dot{J}_1}}, \frac{1}{\frac{1}{\dot{J}_m} + \frac{n_2}{\dot{J}_2}}\right), \qquad (2)$$

where 'min' specifies that the production rate is the lower value of the two ratios. In homogeneous environments, concentrations may be substituted for the flux measures in 2; then the conventional half saturation constants are proportional to $n_1\dot{J}_m$ and $n_2\dot{J}_m$.

Figure 1 illustrates that production with synthesizing units changes smoothly and continuously as the dominant limiting factor changes. The lines almost parallel to the axes in Figure la show convergence to classic Monod dynamics as the flux of one compound increases; this convergence is especially rapid when the flux of the most limiting factor is relatively low. Thus, the range of concentrations over which two compounds simultaneously and substantially limit the production rate may be narrow. Figure 1b shows that the synthesizing unit model nicely fits data generated by the Monod model with minimum rule. Thus, the credit that the minimum rule often gets due to its excellent fits of experimental data (see, e.g. Droop 1974) carries over to the synthesizing unit concept (however, parameter values do not carry over and require re-estimation).

In the context of synthesizing units, the previously unambiguous term "the limiting factor" requires redefinition, as any substrate, irrespective of its abundance, makes some contribution to the production rate. However, one substrate is likely to have a stronger limiting effect than the other, and it is convenient to define a dominant limiting substrate or most limiting compound. We say that substrate x_1 is the dominant limiting substrate when $n_1/\dot{J}_1 > n_2/\dot{J}_2$. Then, it takes more time for the synthesizing unit to bind the required number of copies of substrate x_1 than to bind the required number of copies substrate x_2.

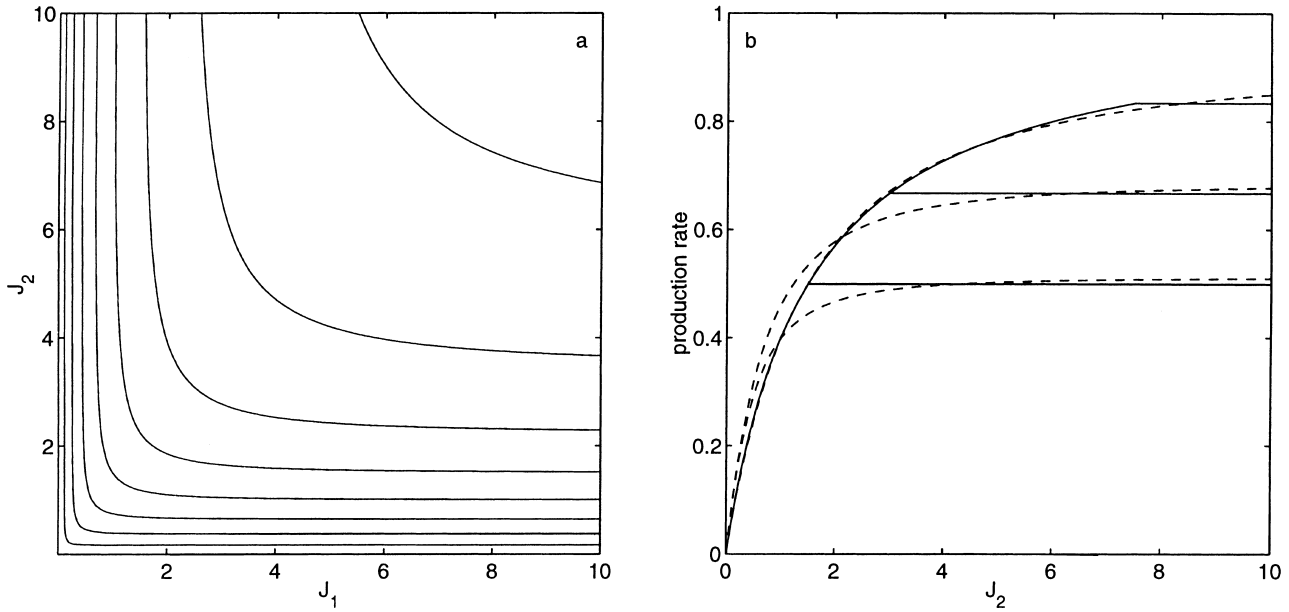

Figure 1 Synthesizing units describe the dynamics of growth at multiple limitations with smooth transitions between limiting compounds, while generally keeping a close match with Liebig's minimum rule. The left panel shows how the contour of the per capita rate of biomass synthesis changes as function of the assimilation flux of two growth limiting compounds: $n_1 = 1$, $n_2 = 1.5$, $\dot{J}_m = 1$ and the contour interval is 0.1. The right panel shows least squares fits of the synthesizing unit model (broken line) to artificial data generated by Liebig's minimum rule (solid line). Parameters used for the minimum rule are $n_2 = 1.5$ and $\dot{J}_m = 1$, and in sequential order from bottom to top, $n_1 = 1$, $n_1 = 2$ and $n_1 = 5$.

PRODUCER AND CONSUMER DYNAMICS

We now consider a system containing a producer and a consumer and assume that the system is closed for nutrients and biomass. We assume that one nutrient always limits producer growth and call this simply "the nutrient"; other nutrients and light energy are assumed to be abundant. We also assume that nutrient in dead biomass and faeces is instantaneously remineralized, and that any free nutrient is immediately taken up by the producer. Furthermore, we assume a constant carbon to nutrient ratio in consumers, although this ratio may vary slightly in practice (DeMott *et al.* 1998).

For producers, we follow the distinction that Kooijman makes between "structure" and "reserves" (Kooijman 1998) and assume that the mass of producer consists of nutrient reserves and structural biomass, each having a constant but different chemical composition (the biomass composition of producers may change as the amount of reserves relative to structure changes). Ideally, this assumption on the elemental ratios in reserves and structure should overlap substantially with what is usually understood as reserves and structure, but subtleties beyond the scope of this paper do exist, see Nisbet *et al.* (2000). Later we parameterize the model for a system with *Daphnia* as the consumer, alga as the producer, and phosphorus as the limiting nutrient. In this particular system, algal phosphorus reserves can be operationally defined as to be approximately equal to the phosphorus in compounds that are relatively soluble and that are associated with cytosol, whereas algal structure would contain the remainder of phosphorus (but see Nisbet *et al.* 2000, for the role of RNA, a compound relatively rich in phosphorus, in structure and reserves). Thus, the system has three state variables representing the structure of the producer, the nutrient reserves of the producer and the biomass of the consumer. Figure 2 illustrates this system with *Daphnia* as the consumer, alga as the producer and phosphorus as the limiting nutrient.

We assume that the producer grows according to Droop (Droop 1974; Kooijman 2000), and that the specific feeding rate of the consumer, j_p follows a type II functional response. The dynamics of the density of producer structure X_p (in C moles of biomass) are

$$\frac{dX_p}{dt} = \dot{r}_{pm} X_p \left(1 - \frac{n_p}{n_p + m}\right) - j_p X_c; \quad j_p \equiv \frac{j_{pm} X_p}{(X_p + K)}, \quad (3)$$

where j_{pm} is the maximum specific feeding rate, K the half saturation constant of the consumer, $\dot{r}_{pm}$, the maximum specific growth rate of producers, n_p the nutrient to carbon ratio in producer structure, and m the producer nutrient

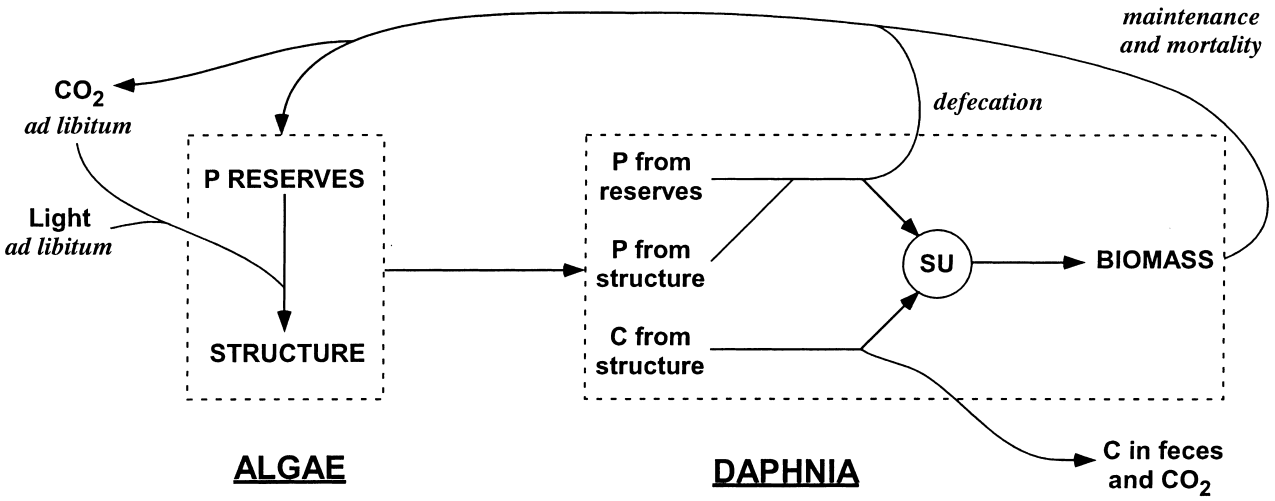

Figure 2 Diagram of system with algae and *Daphnia* in which algae experience a phosphorus limitation. Algae consist of structural biomass and phosphorus reserves, each having a constant elemental composition (the phosphorus content of algae changes as the amount of reserves relative to structure changes). *Daphnia* assimilates phosphorus and carbon from ingested algae to form biomass with constant elemental composition. Both elements influence the biomass synthesis rate of *Daphnia* through synthesizing units (SU). *Daphnia* excretes the phosphorus that is not assimilated and that is released during the respiration of biomass for maintenance purposes. This phosphorus, plus the phosphorus recycled instantaneously from *Daphnia* corpses, is immediately taken up by algae.

reserve density, defined as the total amount of nutrient in the reserves per unit of producer structure. The quantity $n_p + m$ is commonly referred to as the cell quota of the producer, and n_p as the minimum cell quota. We assume that all rates scale directly with biomass, and that consumers have a per capita mortality rate, $\dot{h}$, that is independent of their age. Then, $\dot{h}$ equals the specific rate at which biomass is lost due to mortality (Nisbet *et al.* 1997). If the specific consumer biomass synthesis rate $\dot{r}_c$, is some function of j_p and m to be specified later, then the dynamics of the consumer density is

$$\frac{dX_c}{dt} = (\dot{r}_c(j_p, m) - \dot{h})X_c \qquad (4)$$

Because the system is closed for nutrients and free nutrients are instantaneously taken up by producers, the nutrient reserve density follows from the balance equation:

$$m = \frac{(N_{tot} - n_c X_c)}{X_p} - n_p \qquad (5)$$

in which n_c is the nutrient to carbon ratio in consumer structure, and N_{tot} is the density of total nutrient in the system.

Consumers assimilate nutrients and carbon from producer structure and reserves, and we now assume that synthesizing units describe the rate at which consumers synthesize biomass. Nutrient reserves may contain little carbon, for instance, when polyphosphates are a major component of nutrient reserves. Thus, when phosphorus is being studied, we can make the simplifying assumption that algal phosphorus reserves do not contain carbon. However, if we want to model, for example, nitrogen-limited growth in herbivores, we cannot make this simplification. Producer structure, on the other hand, always contains both nutrients and carbon. We assume that the synthesizing unit does not discriminate between producer structure and reserves with regard to the origin of carbon and nutrients. We ignore subtle differences in energetic overheads involved in assimilating carbon or nutrients from producer structure and reserves, and assume that the consumer assimilates the two elements with a constant efficiency.

We have two choices for implementing maintenance. We can either debit this expenditure from the assimilation fluxes before biomass is formed, or add a loss term accounting for the respiration of biomass for maintenance purposes. Both options have conceptual problems, essentially due to the fact we do not consider energy reserves in consumers (if considered, energy reserves would allow for a variable carbon to nutrient ratio in consumers). We will address these issues in a future paper; for this paper we choose the second option, which is the simpler and commoner of the two. Then the maintenance and mortality rates add to a single loss term.

Using Eq. (1), we can now write the expression for the specific biomass synthesis rate of the consumers. The arrival flux of producer structure to the synthesizing unit is proportional to the feeding rate, and the arrival flux of nutrient reserves is proportional to the product of feeding rate and nutrient reserve density. Because producer structure

and nutrient reserves may both contain nutrients and carbon, the arrival fluxes of nutrients and carbon are weighted sums of j_p and m_{jp}, in which the weights consist of parameters representing stoichlometric requirements, assimilation efficiencies and growth overheads. To avoid the introduction of a large number of symbols, we combine those parameters in weighting factors and call them yield coefficients. A yield coefficient defines how much biomass (in moles of carbon) a consumer can make from a mole of carbon or nutrient in producer structure or nutrient reserves. The specific consumer biomass synthesis rate is

$$\dot{r}_c = \left(\dot{r}_{cm}^{-1} + \left((y_{p2} + y_{n2}m)j_p\right)^{-1} + \left(\left(y_{n1}m + y_{p1}\right)j_p\right)^{-1} - \left(\left(y_{p1} + y_{p2} + m(y_{n2} + y_{n1})\right)j_p\right)^{-1}\right)^{-1} - \dot{k} \qquad (6)$$

in which $\dot{k}$ is the maintenance rate, $\dot{r}_{cm}$ is the maximum specific consumer biomass synthesis rate, y_{p1} and y_{p2} are the yield coefficients for assimilating nutrients and carbon from producer structure, and y_{n1} and y_{n2} are the yield coefficients for assimilating nutrients and carbon from the nutrient reserves. All yields are non-negative and mass balance constraints dictate that $y_{p1} \leq n_p/n_c$ (when $y_{p1} = n_p/n_c$, all nutrients from producer structure can potentially be assimilated); $y_{p2} \leq 1$ (when $y_{p2} = 1$, all carbon from producer structure can be potentially assimilated and there is no growth overhead); $y_{n1} \leq 1/n_c$ (when $y_{n1} = 1/n_c$, all nutrients from producer nutrient reserves can potentially be assimilated); $y_{n2} \leq 1$ (when $y_{n2} = 1$, all carbon from producer nutrient reserves can be potentially assimilated and there is no growth overhead).

In order to visualize the limiting contribution of nutrients to the rate at which consumers synthesize biomass, we use the concept of the dominant limiting factor defined in the previous section. Nutrients are the dominant limiting factor for consumer biomass synthesis when

$$(y_{p2} + y_{n2}m)j_p > (y_{p1} + y_{n1}m)j_p.$$

We define the ratio of these two expressions as the limitation coefficient, L,

$$L = \frac{y_{p2} + y_{n2}m}{y_{p1} + y_{n1}m} \qquad (7)$$

when $L > 1$, nutrients are the dominant limiting factor for consumer biomass synthesis. This expression simplifies in our example with *Daphnia*, algae and phosphorus, as algal phosphorus reserves are assumed to contain no carbon; thus $y_{n2} = 0$.

DAPHNIDS AND ALGAE WITH LOW PHOSPHORUS

We illustrate the behaviour of the system with parameter values that are reasonable for a phosphorus-limited system with algae as producers and with daphnids as consumers (see Table 1). Some parameters show a large natural variability, notably the total phosphorus content of the system, the P to C ratio in algal structure, and the mortality rate in *Daphnia* populations, and for these parameters we examine the dynamics for a range of values. We keep the algal carrying capacity, which equals the total phosphorus density divided by the P to C ratio in algal structure, below 200 μM carbon (roughly equalling 2.4 mg C. L^{-1}) and thus explore a range that covers oligotrophic and eutrophic environments. For simplicity, we assume that algal phosphorus reserves lack carbon, and that daphnids can, if needed, assimilate all the phosphorus in their food with a 100% efficiency, implying that the yield coefficients for assimilating phosphorus are determined by the P to C ratios in algal structure and *Daphnia* biomass. We also assume that the maximum specific biomass synthesis rate in *Daphnia* is very large and set $1/\dot{r}_{cm}$ equal to zero. Thus, the growth potential of *Daphnia* is bounded through the feeding rather than the assimilation process.

A natural starting point for our analysis is to ignore the potential contribution of phosphorus to the *Daphnia* biomass synthesis rate. Then, Eq. (6) reduces to $\dot{r}_c = y_{p2}j_p$ and the system is similar to the classic Rosenzweig–MacArthur model (Rosenzweig & MacArthur 1963), except that it replaces the constant carrying capacity ((N_{tot}/n_p) in the logistic equation for algal growth with a variable factor that depends on consumer density (namely, $(N_{tot} - n_c X_c/n_p)$. Despite this difference, our model ignoring the contribution of food phosphorus content on *Daphnia* growth has the same qualitative behaviour as the Rosenzweig–MacArthur model. The phase plane plot in Fig. 3(a) shows a hump-shaped isocline for algae, and a straight vertical isocline for *Daphnia* (the isocline for algae shows the combinations of algal and *Daphnia* densities at which the algal density does not change; similarly, the isocline for *Daphnia* shows the non-growth combinations for *Daphnia*). The intercept of the two isoclines marks the viable or positive equilibrium, at which both populations coexist at constant densities (other equilibria are at (0,0) – no algae, no daphnids: and $((N_{tot}/n_p,0)$ – algae at carrying capacity, no daphnids). This viable equilibrium is stable at relatively low total phosphorus densities, and unstable at high total phosphorus densities. At these high total phosphorus densities, the densities of algae and *Daphnia* fluctuate in limit cycles with amplitudes that become progressively larger with increasing total phosphorus densities, a phenomenon called the "paradox of enrichment".

If we now add the possibility of phosphorus-limited *Daphnia* growth, hump-shaped isoclines for both algae and *Daphnia* arise. These isoclines may fail to cross, or may cross once or twice (see Fig. 3). With a single crossing, the model dynamics are qualitatively similar to the simplified model

Table 1 List of symbols and values; a # represents a number, and quantities representing rates contain a dot.

Symbol	Interpretation	Default value	Range	Dimension	Source
$\dot{h}$	Specific mortality rate	0. 15†	0–0.3†	d^{-1}	McCauley *et al.* 1988
$\dot{J}$	Production flux	–	–	# t^{-1}	
$\dot{J}_m$	Maximum production flux	–	–	# t^{-1}	
$\dot{J}_1$	Binding rate of substrate x_1	–	–	# t^{-1}	
$\dot{J}_2$	Binding rate of substrate x_2	–	–	# t^{-1}	
j_p	Specific feeding rate of consumer	–	–	d^{-1}	
j_{pm}	Maximum specific feeding rate of consumer	1.0	–	d^{-1}	Nisbet *et al.* 1991, 1997
K	Saturation constant of consumer feeding	12	–	µM C	Lampert 1977; McCauley *et al.* 1990
$\dot{k}$	Specific maintenance rate	0†	0–0.3†	d^{-1}	Bohrer & Lampert 1988; McCauley *et al.* 1990; Glazier 1991
L	Limitation coefficient	–	–	–	
m	Nutrient reserve density	–	–	µM P µM C^{-1}	
n_1	Number of binding sites for substrate x_1	–	–	#	
n_2	Number of binding sites for substrate x_2	–	–	#	
n_c	Nutrient to carbon ratio in consumer structure	0.0125	0.010–0.015	µM P µM C^{-1}	Elser *et al.* 2000
n_p	Nutrient to carbon ratio in producer structure	0.0033	0.0005–0.0050‡	µM P µM C^{-1}	Elser *et al.* 2000
N_{tot}	Density of total nutrient	0.45	0.1–0.5‡	µM	Watson *et al.* 1992
$\dot{r}_c$	Specific consumer biomass synthesis rate	–	–	d^{-1}	
$\dot{r}_{cm}$	Maximum specific consumer biomass synthesis rate	∞	–	d^{-1}	
$\dot{r}_{pm}$	Maximum specific growth rate of producers	1.0	–	d^{-1}	Smith & Kalff 1982
X_p	Producer density	–	–	µM C	
X_c	Consumer density	–	–	µM C	
y_{n1}	Yield coefficient for assimilating nutrients from producer nutrient reserves	80	70–100	µM P µM C^{-1}	Elser *et al.* 2000
y_{n2}	Yield coefficient for assimilating carbon from producer nutrient reserves	0.0	–	µM P µM C^{-1}	
y_{p1}	Yield coefficient for assimilating nutrients from producer structure	0.262	0.05–0.50	–	Elser *et al.* 2000
y_{p2}	Yield coefficient for assimilating carbon from producer structure	0.5	–	–	Nisbet *et al.* 1991, 1997

†The default value of the combined mortality and maintenance rates is 0.15 d^{-1}, and the range examined is 0–0.30 d^{-1}. ‡Values varied such that the algal carrying capacity N_{tot}/n_p is between 0 and 200 µM C.

version discussed above (see Fig. 3b). The viable equilibrium may be locally stable or unstable, depending on the total phosphorus density, and the model shows the paradox of enrichment. Furthermore, as in the simplified model, *Daphnia* can always persist in this system, provided that a viable equilibrium exists.

With a single viable equilibrium, the dynamics of algae and *Daphnia* may show population cycles like those in simple producer-consumer models (see Fig. 4). With similar parameter values to those in Fig. 3(b), population cycles are relatively large (see Fig. 4c). Relative to the simplified model ignoring the contribution of phosphorus to *Daphnia* growth, the limit cycles show somewhat smaller amplitudes for the *Daphnia* density and somewhat higher peaks in the algal density (results not shown). As *Daphnia* growth is restricted by algal phosphorus content, the control that *Daphnia* can exert on algal growth is less than in the simplified model and the so-called "prey escape cycles" are more pronounced. The amplitudes of the population cycles increase with increasing total phosphorus densities (see Figs 4a,c).

The relative contribution of phosphorus to the biomass synthesis rate of *Daphnia* changes during a cycle. With total phosphorus densities of 0.3 µM and 0.45 µM P, the limitation coefficient is periodically greater than 1 (see Figs 4b,d), implying that for part of the time phosphorus is the dominant limiting compound for *Daphnia* biomass synthesis. Phosphorus limitation is especially prevalent when the algal density is high (see Fig. 4), that is, when most of the phosphorus in the system is contained in algal structure. Because peak densities become progressively higher with increasing total phosphorus densities, high total phosphorus densities imply alternating periods of strong and weak phosphorus-limited *Daphnia* growth (see Figs 4 b,d). Phosphorus limitation may also be substantial (but

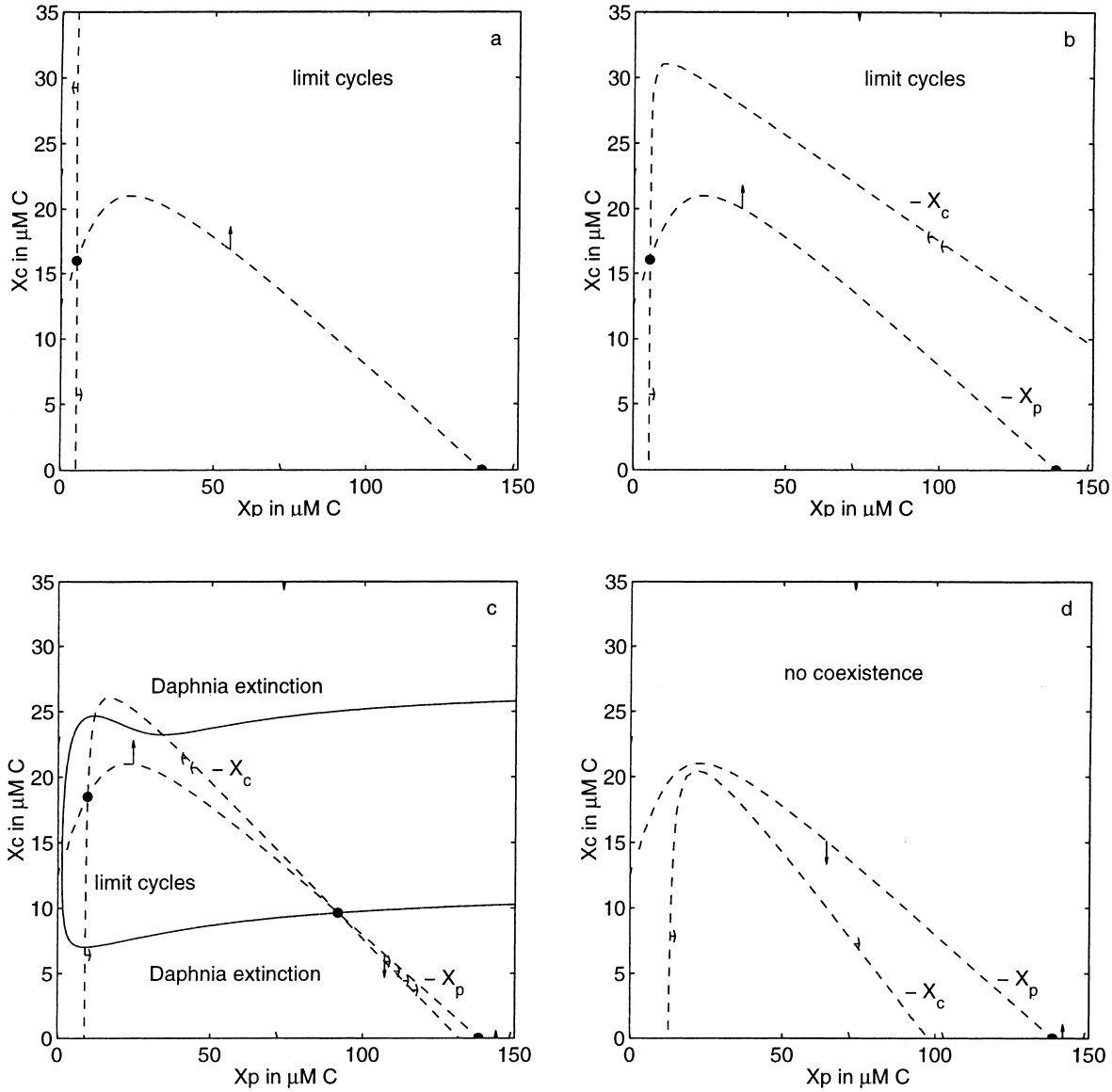

Figure 3 When phosphorus does not affect *Daphnia* growth (a), one positive equilibrium may exist (marked with the dot at (5,16); the stability of this equilibrium gives way to limit cycles with increasing total phosphorus densities. Inclusion of phosphorus as a determinant of the biomass synthesis rate of *Daphnia* causes the *Daphnia* isocline to bend. With a relatively low combined loss rate, the algal and *Daphnia* isoclines may cross once and both populations converge either to a stable equilibrium or limit cycles, depending on the total phosphorus density (b). With higher combined loss rates, two positive equilibria arise and the long-term dynamics of the system depend on initial concentrations (c). Inside the area enveloped by the solid line, the dynamics converge to limit cycles; outside this area, *Daphnia* will go extinct and algae grow to their carrying capacity. With yet higher mortality rates, the isoclines fail to cross (d), and *Daphnia* cannot persist. Parameter values are in Table 1, and the combined loss rates are 0.15 d^{-1} (a and b), 0.21 d^{-1} (c) and 0.25 d^{-1} (d). Phase plane plots are constructed with pplane 5 (Polking 1999).

never dominant) when the total phosphorus density is sufficiently low for a stable viable equilibrium. With a total phosphorus density of 0.2 µM and 0.25 µM P, the limitation coefficient approaches a steady state value of 0.92 and 0.51, respectively. The prevalence of phosphorus limitation for *Daphnia* is also affected by loss rates, as low maintenance and mortality rates lead to large amplitude cycles and hence favour periodical bouts of relatively strong phosphorus-limited *Daphnia* growth (results not shown). In general, factors that tend to destabilize the system also cause periods with strong phosphorus-limited conditions for *Daphnia*.

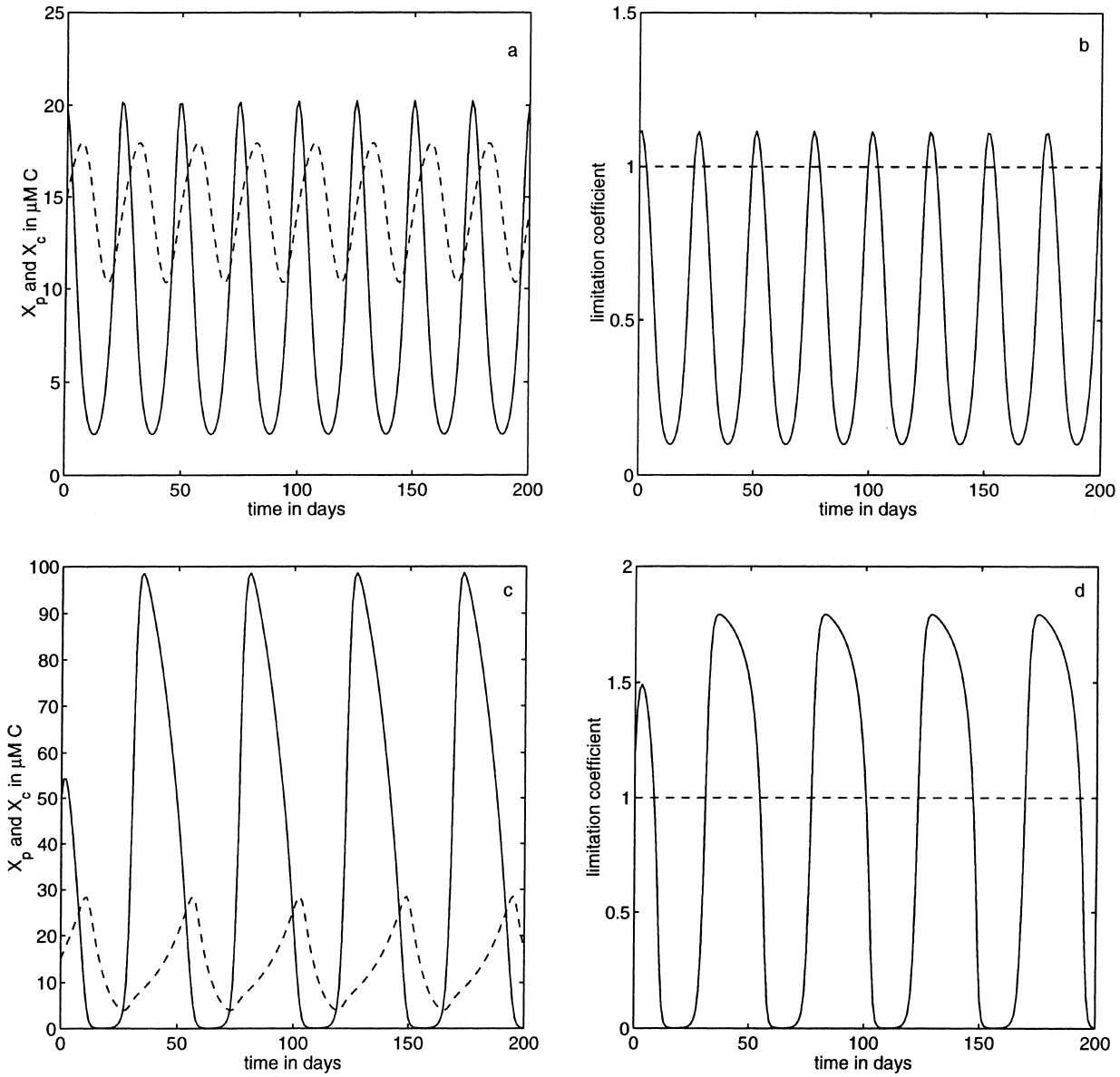

Figure 4 The impact that algal phosphorus can have on *Daphnia* growth depends on the stability of the system. With a low total phosphorus density of 0.3 µM, the densities of algae (solid line) and *Daphnia* (broken line) fluctuate with a relatively low amplitude (a), and algal phosphorus contributes little to the biomass synthesis rate of *Daphnia* (b). With a high total phosphorus density of 0.45 µM, algae (solid line) and *Daphnia* (broken line) show large amplitude cycles (c), and the limitation coefficient is periodically above 1 (d), implying that algal phosphorus is at times the dominant limiting factor for *Daphnia* growth. Parameter values are in Table 1.

The algae and *Daphnia* isoclines may also cross twice (see Fig. 3c), or they may fail to cross (see Fig. 3d). In the latter case, the *Daphnia* loss rates are too high for coexistence. *Daphnia* cannot persist and the algae grow to their carrying capacity. The former case is more interesting as it yields two viable equilibria (see Fig. 3c), and it arises when the combined mortality and maintenance rates are relatively high but not so high that the *Daphnia* isocline remains completely below the algal isocline. The equilibrium to the left has the same local properties as the one in Fig. 3(b); the novel equilibrium to the right is a saddle, implying that it is unstable and that the dynamics of the system depend on initial conditions. Combinations of algal and *Daphnia* densities inside the area enveloped by the solid line in Fig. 3(c) yield dynamics related to the equilibrium to the left, the algal and *Daphnia* densities are likely converge to limit cycles. In contrast, combinations of algal and *Daphnia* densities outside the area marked by the solid curve will

always lead to the extinction of *Daphnia*, whereas algae will increase to the carrying capacity. Thus, this system with the algal density at carrying capacity can not be invaded by *Daphnia* (unless the inoculum is very high). The potential dynamics with a second viable equilibrium are mathematically complex and it suffices to state here that the shape of the enveloped area may change considerably when parameters are altered, and that at high total nutrient densities, *Daphnia* may go extinct, regardless of initial conditions.

DISCUSSION

Liebig's rule of the minimum, which states that a process can only be limited by one factor at a time, is omnipresent in ecological thinking. Models routinely contain minimum functions with discrete switches between limiting factors (see, e.g. Andersen 1997; Loladze *et al.* 2000). However, this approach is mechanistically artificial and conceptually limiting. We have used a modelling framework that deals with multiple, simultaneously limiting factors. This mechanistically underpinned framework uses synthesizing units to describe smooth transitions between states with different dominant limiting factors. As a consequence, not one single factor determines completely the rate of a process at any time, although a factor may be dominant. The relative contribution of a factor to the rate of a process can be displayed with a simple mathematical expression defining the limitation coefficient. We have used the synthesizing unit concept in models describing the growth of herbivores subsisting on a producer made up of "reserves" and "structure" that differ in elemental composition, and parameterized our models for *Daphnia* subsisting on phosphorus-limited phytoplankton, but the formalism is general and could be equally well applied to any consumer feeding on a food source with variable nutrient content, for example, to herbivorous insects in terrestrial food webs where carbon to nutrient ratios in primary producers are much higher than in aquatic systems (Elser *et al.* 2000).

Our results confirm and generalize previous findings by Andersen (1997) and Loladze *et al.* (2000) that *Daphnia* may go extinct in circumstances where food composition strongly influences *Daphnia* growth. Long-term persistence of *Daphnia* depends on several parameters., notably the P to C ratio in algal structure, total phosphorus density, and the combined loss rates of *Daphnia*. Those parameters affect the shape of the isoclines and determine the number and nature of equilibria in our model. Fortunately, there is extensive empirical information for both the value of those parameters and their range in natural lakes (see Table 1), and we can therefore explore the effects of this variation in parameter values in natural systems. For example, an increase in the total phosphorus density increases the peaks of both isoclines and their intercepts with the x axis. An increase in combined *Daphnia* loss rates does not affect the shape of the algal isocline, but reduces the peak of the *Daphnia* isocline and its intercept with the x axis. Going from low to high *Daphnia* loss rates, the system has first one, then two and finally no viable equilibria (see Figs 3b–d). The range in loss rates over which two equilibria exist is very narrow for most parameter combinations.

An increase in the P to C ratio in algal structure does not directly affect the shape of the *Daphnia* isocline, but reduces the peak of the algal isocline and lowers the carrying capacity. Thus, the likelihood for *Daphnia* persistence increases and the odds for having two viable equilibria decreases. With a moderate P to C ratio in algal structure of 0.004 and a total phosphorus density of 0.4 μM (carrying capacity is 100 μM C), the combined loss rates have to be as high as 0.23 d^{-1} in order to have two viable equilibria, whereas with a marginal increase to 0.25 d^{-1}, the system does not support a viable *Daphnia* population. Those loss rates are high for *Daphnia*. With a very low P to C ratio in algal structure of 0.0005 and a total phosphorus density of 0.05 μM (carrying capacity is again 100 μM C), the combined loss rates must be smaller than 0.04 d^{-1} in order to have a viable *Daphnia* population: this loss rate is unrealistically low. Those examples show that, under constant growth conditions, most systems with *Daphnia* and algae will tend to have only one viable equilibrium.

Our results are consistent with experimental results and field observations that the phosphorus content of food can have a substantial effect on the growth of *Daphnia* (Urabe & Sterner, 1996; Urabe *et al.* 1997; DeMott *et al.* 1998; DeMott & Gulati 1999; Elser *et al.* 2001). We have shown that the magnitude of this effect is likely to change over time in real systems. The limitation coefficient, which displays the relative contribution of phosphorus to *Daphnia* growth closely follows the population cycles of algae (see Fig. 4). Phosphorus limitation is especially prevalent at high algal densities, and thus factors that destabilize the system also tend to bring about periods of strong phosphorus-limited *Daphnia* growth. Although the limitation coefficient is a dynamic quantity, it can be used to determine the potential of phosphorus to limit *Daphnia* growth. The limitation coefficient is highest when the phosphorus reserve density in algae is negligibly low. If we assume that *Daphnia* can, if needed, assimilate all the phosphorus in their food with a 100% efficiency, the limitation coefficient equals $y_{p2}n_c/n_p$, i.e. the ratio of the carbon to phosphorus ratio in *Daphnia* and the minimum cell quota times the assimilation efficiency for carbon. The range of values of these parameters for a system with algae and *Daphnia* are well known, and can be easily determined experimentally for other systems.

The relative contribution of phosphorus to the biomass synthesis rate of *Daphnia* changes during a cycle. With total phosphorus densities of 0.3 μM and 0.45 μM P, the

limitation coefficient is periodically greater than 1 (see Figs 4b,d), implying that for part of the time phosphorus is the dominant limiting compound for *Daphnia* biomass synthesis. Phosphorus limitation is especially prevalent when the algal density is high (see Fig. 4), that is, when most of the phosphorus in the system is contained in algal structure. Because peak densities become progressively higher with increasing total phosphorus densities, high total phosphorus densities imply alternating periods of strong and weak phosphorus limitation of *Daphnia* growth (see Figs 4b,d). Phosphorus limitation may also be substantial (but never dominant) when the total phosphorus density is sufficiently low for a stable viable equilibrium. With a total phosphorus density of 0.2 μM and 0.25 μM P, the limitation coefficient approaches a steady state value of 0.92 and 0.51, respectively. The prevalence of phosphorus limitation for *Daphnia* is also affected by loss rates, as low maintenance and mortality rates lead to large amplitude cycles and hence favour periodical bouts of relatively strong phosphorus-limited *Daphnia* growth (results not shown). In general, factors that tend to destabilize the system also lead to periods with strong phosphorus-limited conditions for *Daphnia*.

Consumers may play an important role in the recycling of nutrients in producers. Empirical information on nutrient recycling can be analysed with our model. Consumers necessarily excrete nutrients during maintenance processes at a rate $\dot{m}_c X_c$, in order to maintain a constant body composition. Additionally, consumers release the nutrients that they did not assimilate from their food: this release rate is $\left(j_p\left(n_p + m\right) - \dot{r}_c n_c\right)X_c$. Another source of nutrient recycling is the decomposition of dead consumers at a rate of $\dot{h} n_c X_c$. Commonly, the remineralization potential of consumers is expressed as the nutrient release rate as a fraction of the feeding rate (Elser & Urabe 1999). This remineralization potential equals $n_p + m + n_c\left(\dot{k} + \dot{h} + \dot{r}_c\right)/j_p$. Figure 5 shows a model fit of this remineralization potential to empirical data. These data, compiled by Elser & Urabe (1999), are from widely different sources and contain measurements on zooplankton from marine and aquatic systems. Despite the heterogeneity in source material, we obtain a good fit, even assuming that parameter values are similar in all systems. The C to P ratio in consumers is about 70, and the minimal C to P ratio in producers about 300, but the error bound on the latter is very high (see Fig. 5). The ratio of the combined loss rates and the feeding rate is 0.21. Those parameter values are reasonable for systems with *Daphnia* (see Table 1).

Finally, we note that it is possible to use synthesizing units to describe herbivore growth in many subtly different ways, all consistent with stoichiometric constraints. In this paper we have used arrival fluxes based on assimilation rates of elemental matter. With this assumption, the effect of food quality is simply to change the consumer's assimilation efficiency in response to the state of its food. Andersen (1997) notes that this assumption may overstate the effects of food composition, as the energy in large quantities of food is assumed unavailable to meet maintenance demands. Some authors (Andersen 1997; Hessen & Bjerkeng 1997) have proposed non-mechanistic, alternative representations of herbivore growth in response to this concern. We have work in progress on a family of models based on synthesizing units with different choices for the arrival fluxes, which will provide a mechanistic basis for these alternate models.

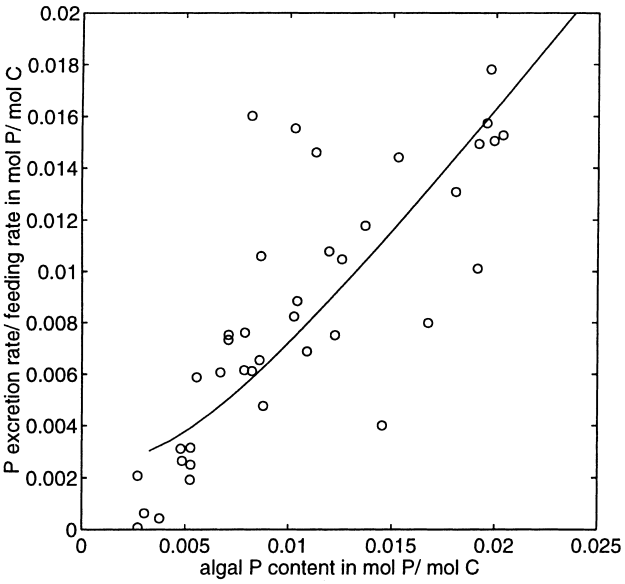

Figure 5 The model predicts the rate at which consumers excrete phosphorus relative to their feeding rate. This rate is a nonlinear function of algal phosphorus content, and also depends relatively strongly on the feeding rate. The line represents a model fit to empirical data compiled by Elser & Urabe (1999). Nonlinear least squares parameter estimates are (with standard error): $(\dot{k} + \dot{h})j_p = 0.2093$ (± 0.038), $n_c = 0.0147$ (± 0.0048), $n_p = 0.0032$ (± 1.9 10^5). The parameter y_{p2} can not be estimated and its value has been held at 0.5; it is assumed that, if needed, consumers can assimilate all phosphorus from algae, and therefore $y_{p1} = n_p/n_c$ and $y_{n1} = 1/n_c$.

ACKNOWLEDGEMENTS

This work is the fruit of a coincidental meeting between two working groups at the National Center for Ecological Analysis and Synthesis, Santa Barbara. We are indebted to Tom Andersen, Sebastian Diehl and Jotaro Urabe for stimulating discussions, and John Polking for numerically robust software to construct phase plane plots. E.B.M. and R.M.N. received support from the Office of Naval Research

(grant no. 00014-99-1-0024), and by the Minerals Management Service (MXIS agreement # 14-35-0001-30761 and # 14-35-0001-30758, Task #15117).

REFERENCES

Andersen, T. (1997). *Pelagic Nutrient Cycles*. Ecological Studies Vol. 129 . Springer Verlag, Berlin.

Bohrer, R.N. & Lampert, W. (1988). Simultaneous measurement of the effect of food concentration on assimilation and respiration in *Daphnia magna* Strauss. *Func. Ecol.*, 2, 463–471.

DeMott, W.R. & Gulati, R.D. (1999). Phosphorus limitation in *Daphnia*: evidence from a long term study of three hypereutrophic dutch lakes. *Limnol. Oceanogr.*, 44, 1557–1564.

DeMott, W.B., Gulati, R. & Siewertsen, K. (1998). Effects of phosphorus deficient diets on the carbon and phosphorus balance of *Daphnia magna*. *Limnol. Oceanogr.*, 43, 1147–1161.

Droop, M.R. (1974). The nutrient status of algal cells in continuous culture. *J. Mar. Biol. Assoc. UK*, 54, 825–855.

Elser, J.J., Fagan, W.Y., Denno, R.F., Dobberfuhl, D.R., Folarin, A., Huberdy, A., Inderkurdi, S., Kilham, S.S., McCauley, E., Schulz, K.L., Siemann, E.H. & Stexham, R. (2000). Nutritional constraints in terrestrial and freshwater food webs. *Nature*, 408, 578–580.

Elser, J., Hayakawa, K. & Urabe, J. (2001). Nutrient limitation reduces food quality for zooplankton: *Daphnia* response to seston phosphorus enrichment. *Ecology*, 82, 898–903.

Elser, J. & Urabe, J. (1999). The stoichiometry of consumer-driven nutrient recycling: theory, observations and consequences. *Ecology*, 80, 735–751.

Glazier, D.S. (1991). Separating the respiration rates of embryos and brooding females of *Daphnia magna*: implications for the costs of brooding and the allometry of metabolic rate. *Limnol. Oceanogr.*, 36, 354–362.

Grover, J.P. (1997). *Resource Competition*. Chapman & Hall, London.

Hessen, D.O. (1997). Stoichiometry in food webs – Lotka revisited. *Oikos*, 19, 195–200.

Hessen, D.O. & Bjerkeng, B. (1997). A model approach to planktonic stoichiometry and consumer-resource stability. *Freshwater Biol.*, 38, 447–471.

Kooijman, S.A.L.M. (1998). The synthesizing unit as model for the stoichiometric fusion and branching of metabolic fluxes. *Biophys. Chem.*, 73, 179–188. 360.

Kooijman, S.A.L.M. (2000). *Dynamic Energy Budgets and Mass Budgets in Biological Systems,* 2nd edn. Cambridge University Press, Cambridge.

Lampert, W. (1977). Studies on the carbon balance of *Daphnia pulex* de Geer as related to environmental conditions. ii. the dependence of carbon assimilation on animal size, temperature, food concentration and diet species. *Arch. Hydrobiologie, Suppl.*, 48, 310–335.

Loladze, Y. & Kuang & 1 Elser, J. (2000). Stoichiometry in producer-grazer systems: a Lotka–Volterra type model. *Bull. Mathemat. Biol.*, 62, 1137–1162.

McCauley, E., Murdoch, W.W. & Watson, S. (1988). Simple models and variation in plankton densities among lakes. *Am. Naturalist*, 132, 383–403.

McCauley, E., Murdoch, W.W., Nisbet , R.M. & Gurney, W.S.C. (1990). The physiological ecology of *Daphnia* – development of a model of growth and reproduction. *Ecology*, 71, 7103–7715.

Monod, J. (1950). La technique de culture continue; theory et applications. *Ann. l'Institute Pasteur*, 79, 390–410.

Nisbet, R.M., McCauley, E., De Roos, A.M., Murdoch, W.W. & Gurney, W.S.C. (1991). Population dynamics and element cycling in an aquatic plant-herbivore system. *J. Theoret. Pop. Biol.*, 40, 125–147.

Nisbet, R.M., McCauley, E., Gurney, W.S.C., Murdoch, W.W. & De Roos, A.M. (1997). Simple representations of biomass dynamics in structured populations (eds Othmer, H.G., Adler, F.R., Lewis, M.A. & Daloon, J.C.), pp. 61–79. *Case Studies in Mathematical Modeling – Ecology, Physiology, and Cell Biology*. Prentice Hall, N.J.

Nisbet, R., Muller, E.B., Lika, K. & Kooijman, S.A.L.M. (2000). From molecules to ecosystems through dynamics energy budget models. *J. Anim. Ecol.*, 69, 913–926.

Polking, J.C. (1999). Ode software for matlab. http://math.rice.edu/dfield/.

Rosenzweig, M.L. & MacArthur, R.H. (1963). Graphical representation and stability conditions for predator–prey interactions. *Am. Naturalist*, 97, 209–223.

Smith, R.E.H. & Kalff, J. (1982). Size-dependent phosphorus uptake kinetics and cell quota in phytoplankton. *J. Phycol.*, 18, 275–284.

Tilman, D. (1982). *Resource Competition and Community Structure*. Monographs in Population Biology, Vol. 17. Princeton University Press, Princeton.

Urabe, J., Clasen, J. & Sterner, R.W. (1997). Phosphorus limitation of *Daphnia* growth: is it real? *Limnol. Oceanogr.*, 42, 1436–14435.

Urabe, J. & Sterner, R.W. (1996). Regulation of herbivore growth by the balance of light and nutrients. *Proc. Natl. Acad. Sci., USA*, 93, 8465–8469.

Watson, S., McCauley, E. & Downing, J.A. (1992). Variation in algal community structure with enrichment. *Can. J. Fish. Aquat. Sciences*, 49, 2605–2610.

BIOSKETCH

Erik Muller studies the transduction of energy through biological systems ranging from individual organisms to ecosystems, and has a particular interest in the effects of toxic compounds on those systems.

Editor, J.P. Grover
Manuscript received 4 December 2000
First decision made 11 January 2001
Manuscript accepted 11 May 2001