

## REVIEW

## Stoichiometry and population dynamics

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**Abstract**

Population dynamics theory forms the quantitative core from which most ecologists have developed their intuition about how species interactions, heterogeneity, and biodiversity play out in time. Throughout its development, theoretical population biology has built on variants of the Lotka–Volterra equations and in nearly all cases has taken a single-currency approach to understanding population change, abstracting populations as aggregations of individuals or biomass. In this review, we explore how depicting organisms as built of more than one thing (for example, C and an important nutrient, such as P) in stoichiometrically explicit models results in qualitatively different predictions about the resulting dynamics. Fundamentally, stoichiometric models incorporate both food quantity and food quality effects in a single framework, allow key feedbacks such as consumer-driven nutrient recycling to occur, and generally appear to stabilize predator–prey systems while simultaneously producing rich dynamics with alternative domains of attraction and occasionally counterintuitive outcomes, such as coexistence of more than one predator species on a single-prey item and decreased herbivore performance in response to increased light intensity experienced by the autotrophs. In addition to the theoretical background, we also review recent laboratory and field studies considering stoichiometric effects on autotroph–herbivore systems, emphasizing algae–*Daphnia* interactions. These studies support the predictions of stoichiometric theory, providing empirical evidence for alternative stable states under stoichiometric constraints, for negative effects of solar radiation on herbivores via stoichiometric food quality, and for diversity-enhancing effects of poor food quality. Stoichiometric theory has strong potential for both quantitative and qualitative improvements in the predictive power of population ecology, a major priority in light of the multivariate anthropogenic and natural perturbations experienced by populations. However, full development and testing of stoichiometric population dynamics theory will require greater intellectual tolerance and exchange between researchers working in ecosystem and population ecology.

**Keywords**

Competition, facilitation, food quality, food web, herbivore, population dynamics, stoichiometry, trophic efficiency.

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**INTRODUCTION**

Few aspects of ecology – if any – have gained more attention than population dynamics. A vast range of empirical and theoretical studies have searched for general patterns in a field of oscillations and chaos. Appropriately, a number of reviews on the topic have recently appeared (cf. Murdoch *et al.* 2003; Turchin 2003) and thus a rehash of the general aspects that are normally covered under the heading of population dynamics would be redundant. Instead, in this

paper we will emphasize how aspects of food quality and cycling of key elements may have major, but under-appreciated, theoretical and practical implications for population dynamics, thus requiring a closer integration of population and ecosystem perspectives than is commonly employed. This falls within an emerging branch of ecology, now labeled ‘ecological stoichiometry’ (Sterner & Elser 2002), dealing with the balance of energy and chemical elements in ecological interactions and especially in trophic relationships.

While a number of elements are of potential interest, in general nitrogen (N) or phosphorus (P) are commonly invoked as limiting for autotrophic production (Hecky & Kilham 1988; Vitousek & Howarth 1991), and also likely to be important for heterotrophs. Based on an expanding range of studies in ecological stoichiometry, it has become increasingly clear that there is often a mismatch in the elemental composition of food and consumers (Reiners 1986; Hessen 1992; White 1993), and that this mismatch has large effects on the performance of individual consumers and on the transfer efficiency of carbon (C). Indeed, the reduced need for C-rich structural matter like cellulose and lignin in aquatic plants appears to be closely associated with higher trophic efficiency in aquatic food webs, in particular planktonic ones, compared with terrestrial systems (Hairton & Hairston 1993; Cebrian 1999). However, despite the likely importance of food quality impacts on consumers, the large literature on cyclic fluctuations in herbivore populations, such as those commonly seen in small mammals, has almost entirely focused on bottom-up effects in terms of food quantity and top-down effects from predators (Stenseth & Ims 1993; Gilg *et al.* 2003; Turchin 2003).

Nevertheless, a number of studies on terrestrial grazers have demonstrated a preference for high quality food in terms of high element : carbon ratios (White 1993; Sterner & Elser 2002). Several studies (e.g. McNaughton 1976; Grasman & Hellgren 1993; Moen *et al.* 1999) have addressed the high demands for dietary N and P for terrestrial grazers such as ungulates, and also to rodents (Eskelinen 2002) and insects (Fagan *et al.* 2002; Schade *et al.* 2003; Perkins *et al.* 2004). Transplant experiments with voles also suggest that environmental conditions like food quality rather than intrinsic mechanisms may explain the conspicuous variation in fluctuations and life-history traits between populations (Ergon *et al.* 2001). Some of these works also point to food quality effects on spatial population dynamics, since grazers ultimately will search for high quality food that may have an uneven spatial distribution (McNaughton 1976; Moran & Hamilton 1980; White 1993; Schade *et al.* 2003). However, this research has generally not addressed stoichiometric effects from a dynamic perspective, which is our emphasis in this review.

### THE BIOLOGICAL BASIS OF STOICHIOMETRIC IMBALANCE AND ITS ECOLOGICAL CONSEQUENCES

The high nutrient content of consumers and the highly variable but often low nutrient content of autotroph biomass raise fundamental questions about what causes such variation. It is clear from recent work with both heterotrophs and autotrophs that the answer resides in the major roles of N and P in proteins and RNA, respectively,

and the fact that the relative abundances of N and P in biomass are closely associated with growth rate in both autotrophs and heterotrophs (Elser *et al.* 2003a; Ågren 2004; Vrede *et al.* 2004). In autotrophs this variation has both inter- and intra-specific components, but it is generally recognized (Ågren 1988; Marschner 1995; Sterner & Elser 2002) that most variation is because of physiological plasticity of plant biomass in relation to growth conditions (light, CO<sub>2</sub>, nutrient supply and temperature). While heterotrophs can also show some physiological variation in C : N : P ratios (DeMott 2003; Makino *et al.* 2003), this variation is typically an order of magnitude less than what is encountered in autotrophs (Elser *et al.* 2000a).

Early on, several authors (Andersen & Hessen 1991; Sterner & Hessen 1994) speculated that zooplankton species with high body P-content, such as *Daphnia*, might have increased body allocation to P-rich compounds such as nucleic acids. Building on this idea, Elser *et al.* (1996) proposed the *growth rate hypothesis*, suggesting that high biomass P-content reflects increased allocation to P-rich ribosomal RNA needed to meet the protein synthesis demands of increased growth rates. Thus, any process of direct or indirect natural selection affecting growth and development capabilities, or physiological adjustment leading to changes in growth rate, could contribute to differences in the C : N : P ratios of the biomass being formed by a given organism. Preliminary calculations (Elser *et al.* 1996) and subsequent empirical investigations of increasing sophistication (Main *et al.* 1997; Vrede *et al.* 1998, 2002; Elser *et al.* 2000a; Gorokhova *et al.* 2002; Elser *et al.* 2003a; Acharya *et al.* 2004) have provided strong support for the growth rate hypothesis in a variety of contexts, including cross-species comparisons, ontogenetic shifts, physiological responses, and ecological comparisons (summarized in Elser *et al.* 2003a). Indeed, these associations may even hold when the ideas are transferred to the study of tumor dynamics (Elser *et al.* 2003b; Kuang *et al.* 2004). A genetic basis for these differences has also been hypothesized (Elser *et al.* 2000b), implicating the structure of the genes coding for the ribosomal RNA (the rDNA). Initial studies providing intriguing support for the hypothesized role of rDNA-based variations in causing differences in growth-RNA-P coupling have begun to appear (Gorokhova *et al.* 2002; Weider *et al.* 2004).

From this work one should expect that nutrient-rich herbivores will commonly encounter autotroph biomass with a chemical composition very different from their own. There are two sides of this stoichiometric coin. On one side, individual growth and population dynamics may be directly constrained by food quality in terms of nutrient element content. The other side implies that release and recycling of elements will be determined by the difference between ingested nutrients and those incorporated into new

consumer biomass. A consumer will most likely extract a maximum amount of whatever biochemical compounds and elements that are in short supply relative to its own demands, while any surplus will be released (Olsen *et al.* 1986). Thus, element deficiency in consumers will reduce the overall recycling rates and also change the proportions between recycled elements, with potentially strong effects on the autotroph community (Elser & Urabe 1999) and ultimately on consumer population dynamics.

Stoichiometric theory has quantified such constraints via the threshold elemental ratio (TER), the critical C : element ratio where limitation shifts from energy (C) to mineral nutrient (Urabe & Watanabe 1992). If prey biomass always is below the TER then the consumer will never suffer stoichiometric quality limitations, and there will be less deviation between a strictly quantity-based model and the stoichiometric equivalent. When food composition exceeds the TER animals will need to dispose ingested carbon that is in excess relative to their somatic needs. The transfer efficiency of C decreases, which again implies that the population growth rate at a given food quantity will also decrease. Reduced transfer efficiency can be due to reduced C assimilation (DeMott 1998), increased release of organic C compounds (Darchambeau *et al.* 2003), or increased respiration decoupled from mechanical or biosynthetic demands (Zanotto *et al.* 1997; Darchambeau *et al.* 2003; Trier & Mattson 2003). Maintaining a stationary population with low mortality losses is still possible above the TER, since maintenance metabolism primarily depends on the C supply (Sterner & Robinson 1994).

It should also be noted that nutrient deficiency likely has differential effects on growth during different stages of development (especially early stages characterized by high growth rates), and that nutrient limitation may have especially acute effects on reproductive output. Indeed, ontogenetic shifts in stoichiometric constraints are commonly observed (DeMott *et al.* 1998; Villar-Argaiz & Sterner 2002). Thus, fast-growing juveniles could represent a 'stoichiometric bottleneck' in response to poor food quality. It also appears that allocation to reproductive tissue has high costs in terms of N and P (Færøvig & Hessen 2003), suggesting strong effects of stoichiometric imbalance on reproductive output. Clearly such stage-specific effects will affect population structure and dynamics.

#### STOICHIOMETRY, DENSITY DEPENDENCE, AND FACILITATION

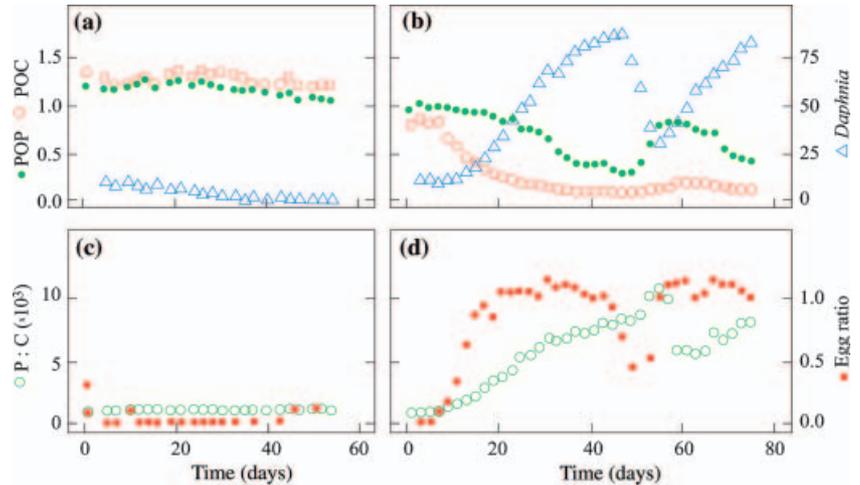
Grazing not only affects plant quantity, it may also affect plant quality in two essentially different ways. First, increased grazing could cause decreased food quality because the most nutritious plant material is removed, leaving the low-quality vegetation behind (cf. Turchin 2003).

Alternatively, grazing could trigger inducible defenses (Karban & Baldwin 1997; Tollrian & Harvell 1999) that would lower grazer performance. This would again reinforce negative density dependence, since grazers would face the double challenge of both reduced quantity and quality of food.

However, is negative density dependence likely to be the only rule for herbivores? Indeed, quite the opposite effect may also occur: increased grazing can cause improved food quality in a form of facilitation in which net growth rate increases with population density up to a certain level. Feedback related to food quality and nutrient release has a strong potential for positive density dependence in autotroph–herbivore systems under nutrient limitation. In such a stoichiometric facilitation scenario, grazers crop the autotroph biomass, thus reducing overall demand for nutrients and leaving less biomass in which a given amount of nutrients can be diluted. Simultaneously, nutrients recycled from the grazers can be acquired by the remaining autotroph biomass. This will be beneficial for the grazers, from the perspectives of both plant quantity (released nutrients stimulate more plant production) and plant quality (plant biomass has higher nutrient content). The initial stoichiometric conditions are important, since such effects will only be seen if herbivores are initially constrained by low nutrient content in the autotrophs. To the extent that there are ontogenetic shifts in metabolic and stoichiometric requirements, stoichiometric facilitation could thus also have strong bearings for age-structure in populations. The positive density dependence resulting from stoichiometric facilitation will be similar to the classical Allee effect, albeit without invoking the classical explanations such as reduced chance of mating at very low population density, lack of kin selection benefits within small groups, etc.

An illuminating example of stoichiometric facilitation was provided by Sommer (1992). Grazers (*Daphnia galeata*) were introduced in continuous, large-volume (10 L) algal cultures, with *Scenedesmus acutus* grown to steady state under P limitation at different dilution rates. Algal P-content increased hyperbolically with dilution rate, as predicted by the Droop model of nutrient limited autotroph growth (Droop 1974). In the low dilution cultures (below  $0.5 \text{ day}^{-1}$ , Fig. 1a) *Daphnia* failed to establish, but they showed positive population growth in *Scenedesmus* cultures grown at slightly higher dilution rates (Fig. 1b). Sommer (1992) showed convincingly that this outcome was caused by different food P-content rather than differences in food quantity between cultures. The increasing *Daphnia* population reduced both particulate P and C (Fig. 1b), but to different extents, such that the P : C ratio of particulate matter actually increased (Fig. 1d). As *Daphnia* biomass slowly accumulated in this initial, poor quality scenario, both somatic growth rates and egg production rates increased, resulting in a positive

**Figure 1** Development of *Daphnia galeata* introduced in P-limited continuous *Scenedesmus acutus* cultures with dilution rates of  $0.5 \text{ day}^{-1}$  (a, c) and  $0.6 \text{ day}^{-1}$  (b, d). Upper panels (a, b): development of particulate organic P and C [POP ( $\mu\text{g-atom L}^{-1}$ ): filled green circles; POC ( $\text{mg-atom L}^{-1}$ ): open red circles] and *Daphnia* biomass (blue triangles, left axis). Lower panels (c, d): development of P : C ratio (atom : atom; open green circles) and *Daphnia* egg ratio (filled red circles, left axis). Redrawn, with permission, from Sommer (1992).



relationship between net growth rate and *Daphnia* abundance. This is a transient situation, however, as further build-up of grazer biomass eventually reduces the food C : P ratio to levels below the TER, returning the system to energy limitation and ‘normal’ negative density dependence. A corresponding scenario has been documented over longer time scales by Urabe et al. (2002b) and will be discussed later. In these examples we see that stoichiometric mechanisms generate qualitatively different interactions among individuals and populations occupying the same trophic level; such effects are not generally represented in the core of ecological theory used to model population dynamics.

### MAKING THE LOTKA–VOLTERRA MODEL STOICHIOMETRICALLY EXPLICIT

How can stoichiometric effects be incorporated into ecological theory? The Lotka–Volterra prey–predator model has been a point of departure for much theoretical analysis on population dynamics. Interestingly, Lotka (1925) devoted much attention to stoichiometry in his seminal writings, yet the fact that consumers need a balanced diet has since been overshadowed in the core of ecological theory by a focus on overall food supply, emphasizing energy demands in the Lindeman (1942) tradition. Not until recently have the consequences of food quality and stoichiometric principles for population dynamics been explored. Our intention is not to argue that food quality is more important than food quantity for consumers. Rather, we will examine how these factors work in concert on population responses, and how *both* food quantity and quality aspects can be handled within a single theoretical framework using stoichiometric principles.

We consider a generic, open two-compartment autotroph–herbivore system with constant dilution at a specific rate  $D$  (Tables 1 and 2). Total nutrient ( $N_T$ ) is supplied at a constant rate  $DN_T$ , whereas autotroph ( $x$ ) and herbivore ( $y$ )

biomasses are lost at rates  $Dx$  and  $Dy$ . The model contains three functional relationships  $\kappa$ ,  $I$ , and  $g$ , representing the specific growth rate of the autotroph and the functional and numerical responses of the herbivore, respectively. The simplest possible alternatives in Table 1, i.e. density-independent specific growth rate and unsaturated functional response ( $\kappa_1$ ,  $I_1$  and  $g_1$ ); give the classical Lotka–Volterra model (Fig. 2a). The well-known neutral stability of the Lotka–Volterra model is changed to unconditional asymptotic instability or stability by adding either a saturating functional response (Fig. 2b:  $\kappa_1$ ,  $I_2$  and  $g_1$ ) or a density-dependent autotroph growth rate (Fig. 1c:  $\kappa_2$ ,  $I_1$  and  $g_1$ ). If both of these elements are included, we get the Rosenzweig & MacArthur (1963) model (Fig. 2d:  $\kappa_2$ ,  $I_2$  and  $g_1$ ), where the autotroph nullcline develops a characteristic hump shape when the carrying capacity ( $N_T/Q'$ ) is sufficiently high. The hump shape can be seen as resulting from the contrasting

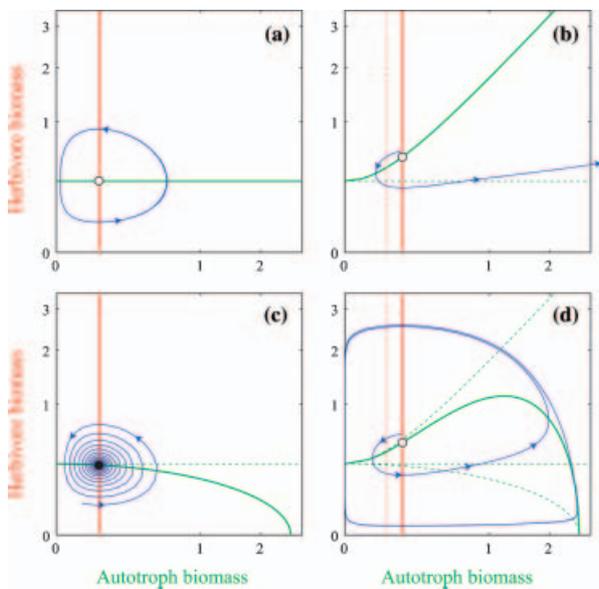
**Table 1** Model equations and functional dependencies used in Figs 2–4

Generic two-species autotroph–herbivore system with through-flow	
$x$ – Autotroph biomass	$\dot{x} = (\kappa - D)x - Iy$
$y$ – Herbivore biomass	$\dot{y} = [g - (m + D)]y$
Autotroph's specific growth rate	
$\kappa_1$ – Density independent	$\kappa_1 = \kappa'$
$\kappa_2$ – Logistic density dependence	$\kappa_2 = \kappa' \left(1 - \frac{Q'x}{N_T}\right)$
$\kappa_3$ – Stoichiometric density dependence	$\kappa_3 = \kappa' \left(1 - \frac{Q'x}{N_T - q}\right)$
Herbivore's functional response	
$I_1$ – Holling's type 1	$I_1 = I' \frac{x}{x'}$
$I_2$ – Holling's type 2	$I_2 = I' \frac{x}{x' + x}$
Herbivore's numerical response	
$g_1$ – Energetic constraints	$g_1 = \varepsilon I - r$
$g_2$ – Stoichiometric and energetic constraints	$g_2 = (\varepsilon I - r) \min\left(1, \frac{N_T - q}{qx}\right)$

**Table 2** Parameters used in Table 1. Typical values refer to a P limited lake plankton system with a *Daphnia*-type herbivore, as studied in Andersen (1997)

$\kappa'$	Autotroph: maximum specific growth rate	1.2 day <sup>-1</sup>
$Q'$	Autotroph: minimum nutrient content	3.8 µg P (mg C) <sup>-1</sup>
$I'$	Herbivore: maximum specific ingestion rate	0.8 day <sup>-1</sup>
$x'$	Herbivore: ingestion half-saturation parameter	0.2 mg C L <sup>-1</sup>
$\epsilon$	Herbivore: assimilation efficiency	0.8
$r$	Herbivore: specific respiration rate	0.2 day <sup>-1</sup>
$q$	Herbivore: nutrient content	30 µg P (mg C) <sup>-1</sup>
$m$	Herbivore: specific mortality rate	0.02 day <sup>-1</sup>
$N_T$	Total nutrient (=input concentration)	10, 50* µg P L <sup>-1</sup>
$D$	Dilution rate	0.01, 0.05** day <sup>-1</sup>

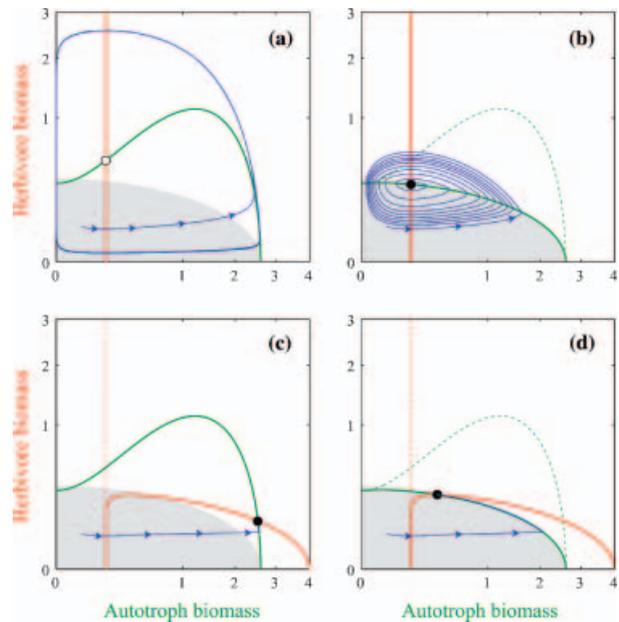
\*Fig. 3c, d only.  
 \*\*Fig. 3b, d only.



**Figure 2** Four non-stoichiometric autotroph–herbivore models: Classical Lotka–Volterra model (a: constant autotroph growth rate and herbivore clearance rate, as in Table 1 with functions  $\kappa_1$ ,  $I_1$ , and  $g_1$ ), with saturating functional response (b:  $\kappa_1$ ,  $I_2$ , and  $g_1$ ), with logistic density dependence (c:  $\kappa_2$ ,  $I_1$ , and  $g_1$ ), and the Rosenzweig–MacArthur model with logistic density dependence and saturating functional response (d:  $\kappa_2$ ,  $I_2$ ,  $g_1$ ). Green lines: autotroph nullclines, red lines: herbivore nullclines, open circles: locally unstable stationary points, filled circles: locally stable stationary points, blue curves with arrows: solution trajectories. All models with parameter values as in Table 2 and boundary conditions  $N_T = 10 \mu\text{g P L}^{-1}$ ,  $D = 0.01 \text{ day}^{-1}$ . Notice square-root scaled axes.

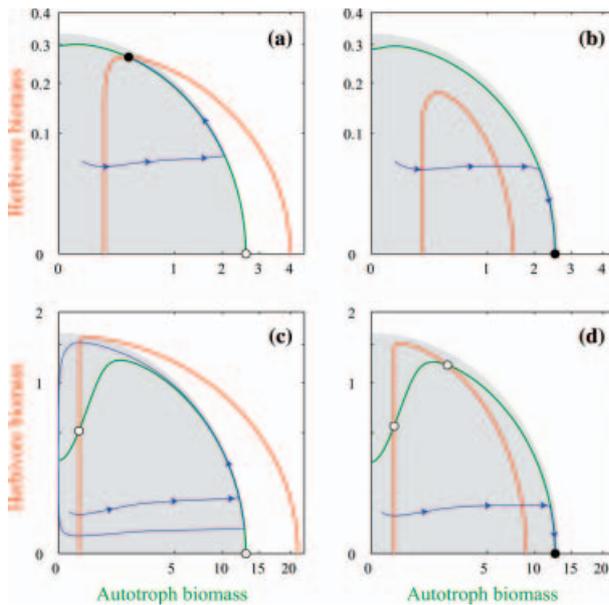
stabilizing effect of autotroph density dependence and destabilizing effect of herbivore feeding saturation (May 1976). The herbivore nullcline will be just a vertical line in all models in Fig. 2, although the inclusion of a saturating functional response will displace it to the right (cf. Fig. 2a,c vs. Fig. 2b,d). The Rosenzweig–MacArthur model is known to be asymptotically stable as long as the carrying capacity is below a critical level, above which the system exhibits a Hopf bifurcation from a stable focus to a limit cycle. When started from positive initial conditions, non-zero autotroph and herbivore biomasses will persist as long as the carrying capacity is higher than the herbivore nullcline level, and the dilution rate is below the washout conditions for autotrophs ( $D < \kappa'$ ) and herbivores ( $D < \epsilon I' - r - m$ ).

As stoichiometric considerations modify this system through both the density dependence of autotroph growth rate and the growth efficiency of herbivores, it is instructive to look at these effects separately (Fig. 3). Since plants and animals are made of basically the same building materials, it



**Figure 3** Step-by-step introduction of stoichiometric constraints to the Rosenzweig–MacArthur model (a:  $\kappa_2$ ,  $I_2$ , and  $g_1$ ), with stoichiometric density dependence (b:  $\kappa_3$ ,  $I_2$ , and  $g_1$ ), with stoichiometric numerical response (c:  $\kappa_2$ ,  $I_2$ , and  $g_2$ ), and with stoichiometric constraints on both autotroph carrying capacity and herbivore growth efficiency (d:  $\kappa_3$ ,  $I_2$ , and  $g_2$ ). Green lines: autotroph nullclines, red lines: herbivore nullclines, open circles: locally unstable stationary points, filled circles: locally stable stationary points, blue curves with arrows: solution trajectories. Shaded area bounds the total nutrient constraint on biomasses ( $Q'x + qy \leq N_T$ ). All models with parameter values as in Table 2 and external forcing  $N_T = 10 \mu\text{g P L}^{-1}$ ,  $D = 0.01 \text{ day}^{-1}$ . Notice square-root scaled axes.

is reasonable that their population sizes both should be constrained by the total nutrient of the system. If the herbivores have a constant nutrient content ( $q$ ) and the autotrophs have a minimum nutrient content  $Q'$ , then the system must be confined to the triangle bounded below by the positive cone (i.e.  $x \geq 0$  and  $y \geq 0$ ) and above by  $Q'x + qy \leq N_T$  (notice that straight lines become curved in the square root transformed coordinates of Figs 2–4). Notice that by this we implicitly assume that the concentration of dissolved inorganic nutrient is negligible, so that nutrient in autotrophs is given as the difference between the total and what is contained in herbivores. This simplifying assumption, which is very convenient for maintaining a planar phase space directly comparable to the Lotka–Volterra model, must be relaxed if the model is to be extended to representing several autotroph populations engaged in exploitative nutrient competition. Within this triangle the autotroph nutrient content ( $Q$ ) will be



**Figure 4** Dynamical properties of the stoichiometric autotroph–herbivore model (Fig. 3d) depends on external forcing (dilution rate and total nutrient). (a) Persistent, stable, over-damped system with low nutrient, low dilution ( $N_T = 10 \mu\text{g P L}^{-1}$ ,  $D = 0.01 \text{ day}^{-1}$ ); (b) Non-persistent, stable, over-damped system with low nutrient, high dilution ( $N_T = 10 \mu\text{g P L}^{-1}$ ,  $D = 0.05 \text{ day}^{-1}$ ); (c) Persistent, unstable, oscillating system with high nutrient, low dilution ( $N_T = 50 \mu\text{g P L}^{-1}$ ,  $D = 0.01 \text{ day}^{-1}$ ); (d) Non-persistent, stable, over-damped system with high nutrient, high dilution ( $N_T = 50 \mu\text{g P L}^{-1}$ ,  $D = 0.05 \text{ day}^{-1}$ ). Green lines: autotroph nullclines, red lines: herbivore nullclines, open circles: locally unstable stationary points, filled circles: locally stable stationary points, blue curves with arrows: solution trajectories. Shaded area bounds the total nutrient constraint on biomasses ( $Q'x + qy \leq N_T$ ). Notice square-root scaled axes.

constrained so that  $Q \geq Q'$  everywhere. Instead of defining the carrying capacity of autotrophs as the maximum biomass yield attainable from the total nutrient in the system ( $k_2$  in Table 1), mass conservation dictates that it should be based only on the part of the total nutrient that is available to autotrophs ( $k_3$ ). When herbivores have constant stoichiometry ( $q$ ), the quantity of nutrient available to autotroph growth will be  $N_T - qy$ . In contrast to logistic density dependence ( $k_2$ ), stoichiometric density dependence ( $k_3$ ) implies that autotroph growth rate becomes a decreasing function of both autotroph ( $x$ ) and herbivore ( $y$ ) biomasses. Comparing Fig. 3a,b makes it apparent that introducing stoichiometric density dependence has a strong effect on the shape of the autotroph nullcline, and thus also on the dynamical stability properties of the system: the limit cycle of the Rosenzweig–MacArthur model is turned into an asymptotically stable, under-damped focus. Fig. 3b also reveals a flaw of introducing stoichiometric density dependence alone: while the autotroph nullcline is constrained within the nutrient conservation region  $Q'x + qy \leq N_T$ , the dynamics are not – simply because the numerical response  $g_1$  does not involve any stoichiometric constraint on herbivore growth.

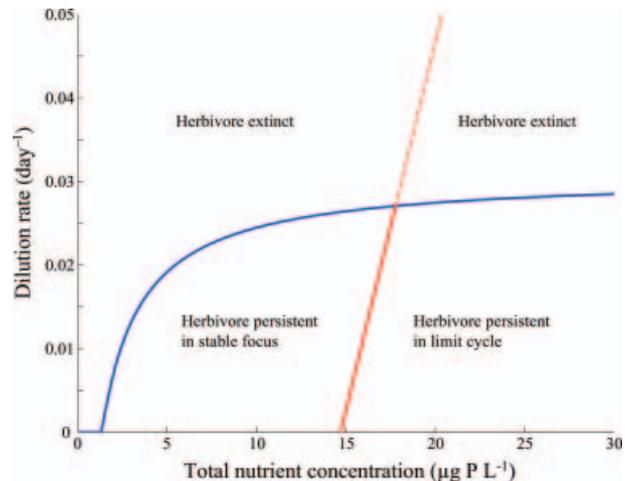
If herbivores maintain homeostatic control of body tissue while autotrophs do not, then stoichiometric constraints on herbivore growth yield are implied: herbivores cannot maintain constant nutrient content unless growth efficiency is scaled to the element least in supply in their food (Liebig's minimum principle translated to consumers). There are many ways to represent this constraint mathematically, but for the sake for illustration we will at present only consider the piecewise linear model ( $g_2$  in Table 1) suggested by Andersen (1997). Introducing stoichiometric effects on herbivore growth rate has dramatic effects on the shape of the herbivore nullcline, which now becomes hump-shaped, similar to the autotroph nullcline in the Rosenzweig & MacArthur (1963) model (Fig. 3c). The herbivore nullcline consists of two branches, corresponding to herbivores being limited by either food quantity or quality (as represented by the nutrient content of the food source). The quantity-limited branch will be superimposed on part of the vertical nullcline of the non-stoichiometric model (Fig. 3a), while the quality-limited branch will bend downward to the right and eventually intersect the  $x$ -axis (Fig. 3c). This intersection will be at a point where food quality is so poor that the herbivores are unable to maintain sufficient growth to balance the losses resulting from maintenance, mortality, and washout. The change in herbivore nullcline shape also entails a change in stability properties: the limit cycle of the Rosenzweig–MacArthur model turns into an asymptotically stable, under-damped focus, but lack of stoichiometric constraints on autotroph growth places the equilibrium

point outside the nutrient conservation region, just as in the previous case (Fig. 3b).

Combining the stoichiometric constraints on autotroph growth rate and herbivore growth efficiency is necessary to have a model where the dynamics are confined to the nutrient conservation region ( $Q'x + qy \leq N_T$ ). Fig. 3a,d show the strongly stabilizing effects of making a model stoichiometrically explicit compared to a non-stoichiometric one with identical parameter values. Nevertheless, the stoichiometric model exhibits the same 'paradox of enrichment' bifurcation as the Rosenzweig–MacArthur model (Rosenzweig 1971), although the stability change happens at a much higher total nutrient level compared to the non-stoichiometric case. This is illustrated in the high nutrient, low dilution case in Fig. 4c. Moreover, stoichiometry introduces an additional dynamical property not present in the other models: persistence becomes critically dependent on the dilution rate of the system. Increasing the dilution rate makes the rightmost branch of both the autotroph and herbivore nullclines move to the left. But the effect is stronger on the herbivore nullcline, so it moves further to the left with a given increase in dilution rate. When the nullcline intersections change places (Fig. 4c,d), a new internal stationary point may appear (Fig. 4d). The new nullcline intersection will always be a saddle point – attracting from some directions, repelling from others. Whether the saddle point appears or not is less important than the accompanying stability change at the grazer extinction equilibrium (where herbivore biomass is zero and autotroph biomass is at its carrying capacity). In this situation, a system with autotrophs at their carrying capacity cannot be invaded by herbivores.

The stability properties of the stoichiometrically explicit autotroph–herbivore model can be summed up as a two-dimensional bifurcation diagram with respect to total nutrient and dilution rate (Fig. 5). Two lines split the plane into four quadrants: the 'persistence boundary' (Andersen 1997) representing the deterministic extinction of herbivores, and the 'paradox of enrichment' boundary (Rosenzweig 1971) representing the stability change from focus to limit cycle. Above the persistence boundary, a scenario with autotrophs at their carrying capacity and no herbivores becomes the only stable equilibrium. At very low total nutrient, herbivore persistence is impossible at any dilution rate. With increasing total nutrient, herbivores can withstand higher washout losses, expanding the range of herbivore persistence up to an asymptotic level. The stability change boundary is, by comparison, mainly a function of total nutrient, with the critical level of enrichment increasing only slightly with through-flow.

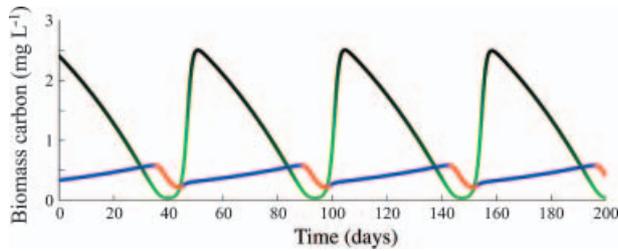
Non-stoichiometric models with through-flow will also have a boundary for herbivore persistence, but this boundary will typically be in effect only when dilution is



**Figure 5** Two-dimensional bifurcation diagram showing local stability properties of the model in Fig. 3d as function of total nutrient and dilution rate. Blue curve: herbivore persistence boundary; above this curve herbivores will go extinct. Red curve: boundary between locally stable and unstable internal equilibria (Hopf bifurcation); the unstable stationary point will lead to a limit cycle when the system is below the persistence boundary.

higher than the maximal net growth rate of the herbivore. For example, the parameters given in Table 2 correspond to a maximal, net herbivore growth rate of  $0.42 \text{ day}^{-1}$ , which implies non-stoichiometric extinction due to washout more than an order of magnitude above the boundary in Fig. 5. Both stoichiometric and non-stoichiometric models predict autotrophs to grow towards their carrying capacity in the absence of herbivores. But the stoichiometric point of view also has the qualification that this abundance of uncropped food may still not have necessary quality to sustain the proliferation of an invading herbivore population. The existence of plant communities uninvadable by herbivores is strongly suggested by the experiments of Sommer (1992) and Urabe *et al.* (2002a), as shown in Figs 1 and 8.

Both stoichiometric and non-stoichiometric prey–predator models can exhibit 'paradox of enrichment'-type bifurcations, but there are notable differences in what enrichment levels are needed to produce destabilization. With identical parameter sets (Table 2) the model in Fig. 3d destabilizes at an almost tenfold higher total nutrient level ( $15.7 \mu\text{g P L}^{-1}$ ) than the non-stoichiometric model in Fig. 3a ( $1.8 \mu\text{g P L}^{-1}$ ). The stabilizing effect of stoichiometry is shown in closer detail in Fig. 6: nutrient limitation reduces herbivore growth in periods of high autotroph biomass, thus preventing accumulation of herbivore biomass that will lead to overgrazing in the next turn of the positive feedback loop. Figure 6 illustrates how the constraints of energy and nutrient limitation on herbivore growth work together to reduce the amplitude of oscillations



**Figure 6** Detail of a solution time course of the system in Fig. 3d. Autotroph trajectory (black to green) is color coded so that black corresponds to severe nutrient limitation while green is growth under nutrient sufficient conditions. Herbivore trajectory (blue to red) is color coded so that blue corresponds to mineral nutrient (P) limitation, while red is growth under energy (C) limitation.

in a stoichiometrically explicit model. Herbivore growth efficiency is positively related to growth rate and nutrient content in the autotroph. Thus, herbivores will be nutrient limited for most of the cycle period, and only energy limited when algal biomass is low, but with high growth rates and high quality, as displayed in Fig. 6. One should also notice the contrast between the slow dynamics under periods with low food quality and low transfer efficiency, and the fast changes when the system becomes overgrazed and the nutrient content of autotrophs increases.

#### VARIATIONS ON THE STOICHIOMETRICALLY EXPLICIT THEME

Much of the theory outlined through Figs 2–4 is based on Andersen (1997), but the basic predictions on how stoichiometric principles will affect autotroph–herbivore dynamics have been supported and extended in a number of works over the past decade. For example, the model by Hessen & Bjerkeng (1997) was built on similar assumptions, such as fixed consumer stoichiometry, P recycling in proportion to the difference in P-content between resource and consumer, and a facilitation scenario via a combination of the Droop model and Michaelis–Menten kinetics. This analysis predicted cyclic events (amplitudes and periods) very much dependent on grazer stoichiometry in relation to the lower bound of the autotroph P-content (Droop’s ‘subsistence quota’). Low minimum P-content in autotrophs relative to that on the grazer implied longer time for grazer recovery via facilitation and prolonged amplitudes of the overall system. Loladze *et al.* (2000) also built on the basic framework of Andersen (1997), modifying the approach to include potential effects of light intensity by proposing that increasing light intensity has the effect of raising the maximum autotroph carrying capacity (in terms of C) for a given amount of nutrients in the system. Thus, in their approach, increased light intensity operates primarily by

lowering the value of  $Q'$  (minimal P : C ratio of the autotroph) and thus increasing overall autotroph biomass. Their analysis showed a whole family of dynamic consequences of increased light intensity, including a shift from stable equilibria at low-light intensity in which grazer biomass is positively related to light intensity to limit cycles (via a Hopf bifurcation) to a new equilibrium (via a saddle-node bifurcation) in which grazer biomass is negatively related to light (they called this ‘the paradox of energy enrichment’) and finally, via exchange of stability, to a new equilibrium in which the grazer is extinct. Thus, this model predicts negative effects on herbivores in response to increased light intensity under nutrient limitation, including possible herbivore extinction. Empirical data relevant to these predictions is considered in the following section.

Along the same lines of reasoning, Muller *et al.* (2001) found a ‘richer dynamic behavior’ by applying stoichiometric principles to classic food quantity models. In contrast to the piecewise linear relation between food nutrient content and consumer growth used by Andersen (1997) and Hessen & Bjerkeng (1997), they based their analysis on the more sophisticated concept of synthesizing units (see below). Nevertheless, their analysis predicted dynamical behaviors very similar to those presented in Figs 2–4. In absence of P-limitation, they predicted stable coexistence (as in Fig. 2a or lower left area of Fig. 5) that gives way to limit cycles with increased enrichment (lower, right area of Fig. 5). The inclusion of potential herbivore P-limitation first of all impacts both periods and amplitudes and predicts P-limitation for long periods of a cycle as illustrated in Fig. 6, and depending on dilution (death rate), the isoclines will fail to cross and the grazer will go extinct. This bifurcation sequence is also analyzed in greater detail in Kooijman *et al.* (2004).

The principle of only one resource being limiting at the time, often called the threshold model of resource limitation, has been known since at least the days of Justus Liebig. While conceptually attractive, and, at least to some extent, supported by empirical evidence, the kind of non-smoothness introduced by switches and thresholds also have potentially serious consequences. On the theoretical side, global stability properties can only be inferred from local stability analysis when all dynamical equations are continuously differentiable (Guckenheimer & Holmes 1988). Thus, the presence of functions with discontinuous first-order derivatives, such as min/max functions, weakens the inferences that can be made from local stability analysis. Secondly, all numerical methods for solving differential equations are based on extrapolation in time, which again depends on a certain level of smoothness in the underlying functions. Unless special precautions are taken, numerical solutions will be less efficient and less precise when the differential equations contain non-continuous functions

(e.g. Hairer *et al.* 1987). Thus, it is desirable both from theoretical and practical considerations to formulate differential equation models in terms of continuous functions whenever possible.

Most stoichiometric models of consumer metabolism contain at least one switch or threshold (Andersen 1997; Hessen & Bjerkeng 1997; Loladze *et al.* 2000, 2004). This also goes for consumer models where the requirements of strict homeostasis are relaxed (e.g. Thingstad 1987; Grover 2003). An important alternative is offered by the Dynamic Energy Budget (DEB) theory (Kooijman 2000), where biosynthetic processes are modeled by the generalized enzyme kinetics of synthesizing units. Just as the Michaelis–Menten model of enzyme kinetics, the kinetics of the synthesizing unit is derived from queuing theory. But, in contrast to threshold kinetics, synthesizing unit kinetics are continuously differentiable everywhere. DEB theory also has a consistent way of handling the fate of non-limiting nutrients, which is essential for dealing with nutrient balances. DEB theory is perhaps more conceptually difficult to grasp than threshold theory, and may also involve more parameters, some of which may also be less known, such as those involving internal turnover rates and feedback flows (in DEB theory called  $\kappa$  rules) of the abstract pools of structure and reserve. Still, there is little doubt that DEB theory is a more consistent framework for constructing stoichiometrically explicit models than the threshold principle, both from a physiological and a mathematical point of view.

Since early empirical findings of Andersen & Hessen (1991) showing that body elemental composition (%C, %N, %P as a function of dry mass) of some zooplankton species was insensitive to food abundance and quality, it has been customary to assume that consumers have strict homeostasis, i.e. the elemental composition of the consumer's biomass is fixed despite differences in the elemental composition of the diet. The implication of this assumption is that the consumer biomass may be represented in terms of a single element such as carbon or dry mass, since conversion to other elements is implicit by rigid stoichiometry. For theoretical development this has the desirable effect that the consumer population may be represented by a single-state variable, thus reducing the dimensionality of the system. It should nevertheless be noticed that this assumption is at best an approximation, as elemental composition of consumers does change both ontogenetically and in response to food composition (DeMott 2003). Still, what makes this approximation defensible is that, while not perfect, stoichiometric homeostasis is quite tight: consumer composition typically changes < 50%, even when food composition changes by more than an order of magnitude (Sterner & Elser 2002). Furthermore, the assumption appears not to have major impacts on

theoretical outcomes: in a model of a protist food chain with flexible consumer stoichiometry, Grover (2003) found qualitatively the same types of dynamics as in models with consumers exhibiting strict homeostasis, although he also found some situations where stoichiometry caused decreased stability compared to similar single-currency models.

The theory of physiologically structured populations (e.g. Metz & Diekmann 1986) can in principle handle the time evolution of the distribution of any set of physiological traits, including individual elemental composition. But nevertheless, although there appear to be no theoretical reasons for it to be so, practically all stoichiometric prey–predator models have so far neglected the effects of age or stage structure. An unstructured model will normally be a sufficient representation of unicellular organisms reproducing by binary fission, but may severely over-simplify size or age-dependent development, maturation, and mortality in metazoan consumers. The effects of ontogenesis will primarily appear as time lags in the numerical response of consumers (assimilated food will not be immediately transformed to new biomass capable of capturing new prey), but the relationships between development, growth rate, and body stoichiometry need also to be considered. The effects of food elemental composition and growth/reproduction have been comparatively well studied in a range of organisms, while the corresponding relationship with mortality has been largely unexplored. The recent study by Nelson *et al.* (2001) is a notable exception: by using a method of constrained population surface fitting (Wood 1994), they showed a significant positive relationship between food abundance (as chlorophyll *a*) and *Daphnia* mortality rate. This could be interpreted as the negative effects of food stoichiometry at high autotroph biomass being manifested not only as reduced growth and reproduction, but also as increased mortality. One would expect that any effects of stoichiometric mismatch on consumer mortality would tend to amplify the food quality driven extinction dynamics, already seen in unstructured models (e.g. Fig. 4b,d).

## ADDING COMPLEXITY

In situations with combined low food quality and high loss rates, several of the cited models predict that the grazer may go extinct. In a multi-species situation, one could expect a sequential loss of species according to their P-demands. Even without invoking the possibility of extinction, the competitive arena between species or stages will be influenced by their ability to cope with mineral limited food. As an analogue to the possibility of autotroph coexistence on multiple nutrients (Tilman 1980), several studies conclude that different stoichiometry of grazers may

have strong bearings on competition and also promote coexistence of herbivores in homogenous environments (Sterner & Hessen 1994; Kooi & Hanegraaf 2001; Hall 2004; Loladze *et al.* 2004). Competing pelagic grazers may occupy different 'stoichiometric niches' (e.g. P-rich *Daphnia* which seems quite sensitive to food P-contents vs. low P *Bosmina* which appears to be insensitive to food P-content; Sterner & Schulz 1998). Stoichiometric habitat heterogeneity or shifts in autotroph quality may thus promote coexistence of species.

In line with these *a priori* assumptions, a simulation with two grazers with different P-demands (Hall 2004) predicted coexistence at a stable equilibrium at intermediate nutrient supply, while the superior carbon competitor would dominate under food quantity limitation and the superior nutrient competitor (low P-demands) should dominate low nutrient environments. When including recycling scenarios, alternative stable states were predicted. Loladze *et al.* (2004) also analyzed a stoichiometric system containing one autotroph species and two consumers, showing that two species of herbivore can co-exist on a single prey species in a stoichiometric model. In their analysis, not only can the two herbivores coexist in a situation in which one is limited by food abundance (insufficient C) and the other by food quality (insufficient P), they can also coexist at a poor food quality equilibrium under which *both* of them are limited by P. It appears that stoichiometric mechanisms open considerable opportunities for coexistence of herbivore species.

Along the same lines of reasoning, stoichiometric constraints can promote omnivory, allowing for increased biodiversity and trophic articulation within food webs. This possibility was explored by Diehl (2003) who concluded that, in line with the arguments above, stable coexistence of two consumer taxa becomes possible if both are limited by the nutrient content of their prey resource. Omnivory might then evolve because competitor biomass is of higher quality than resource biomass. Coexistence of an omnivore and an intermediate consumer will depend both on food quantity and quality, and in line with the basic argument visualized in Fig. 6; when resource biomass approaches carrying capacity, the food quality decreases and omnivory will become an alternative from a food quality point of view. Additional theoretical and empirical evidence supporting the idea that stoichiometric food quality favors the evolution of omnivory has been provided recently by Eubanks *et al.* (2003) and Denno & Fagan (2004).

In an evolutionary context, excess carbohydrates that are built up in the autotroph can be traded for nutrients released by heterotrophs, and this exchange forms the basis of symbiosis (Kooijman *et al.* 2004). Building on a stoichiometric prey–predator model where the conversion efficiency from resource to consumer is variable and dependent on the stoichiometric balance between supply and demand, they

argued that such an exchange of goods in excess can form stable consortia that eventually integrate into a single entity of mixotrophic properties.

## EMPIRICAL EVIDENCE FOR THE EXISTENCE OF ALTERNATIVE STOICHIOMETRIC DOMAINS

In the previous sections we have described how stoichiometric mechanisms engender rich and complex autotroph–herbivore dynamics that in many cases differ qualitatively from the dynamics predicted by non-stoichiometric models. Stoichiometric models often involve bi-stability and a tendency for stabilizing dynamics within distinct alternative domains of attraction. In some cases novel mechanisms underpin the dynamics, such as the operation of intra-specific (and potentially inter-specific) facilitation instead of competition among consumers. Furthermore, models integrating the effects of both nutrients and light intensity as key resources for autotrophs have yielded novel predictions about effects on herbivore dynamics, including the 'paradox of energy enrichment' (Loladze *et al.* 2000) in which increased light intensity is seen to have negative impacts on herbivore abundance and production. In this section we synthesize empirical findings from the laboratory and field experiments that bear on these predictions.

Because of the hump-shaped herbivore nullcline under stoichiometric constraints, the multiple nullcline intersections make it possible to have bi-stable stationary states and alternate basins of attraction, as described above. A recent study by Nelson *et al.* (2001) was designed to experimentally test the predictions of Andersen (1997) with respect to the actual existence of such alternative domains. Details of this and the other experiments we will discuss are summarized in Table 3. This study involved three clones of *Daphnia pulex* grown separately, while a fourth treatment combined all three clones (all treatments in triplicate). Despite identical starting conditions, Nelson *et al.* observed two distinct types of dynamics, shown in Fig. 7a (left). In eight of the 12 mesocosms *Daphnia* rapidly achieved a high biomass, while simultaneously algal biomass (indicated by chlorophyll concentration) was reduced to low levels (termed high herbivore biomass dynamics, or 'high HBD,' by the authors). All eight of these mesocosms were from the single-clone treatment. In contrast, in the remaining four mesocosms, 'low HBD' results were obtained (Fig. 7a right), in which algal biomass remained high and *Daphnia* biomass low for much of the study period (in one of the four mesocosms, *Daphnia* never achieved high biomass and eventually dwindled to extinction). Interestingly, all three of the three-clone replicates exhibited this result. Demographic analysis indicated that high HBD result reflected an equilibrium in which the *Daphnia* were C-limited due to low algal abundance, while the authors inferred that algal

**Table 3** Overview of experimental setup, growth conditions, and biota in the studies shown in Figs 7–9 (Nelson *et al.* 2001, Sterner *et al.* 1998 and Urabe *et al.* 2002a, b)

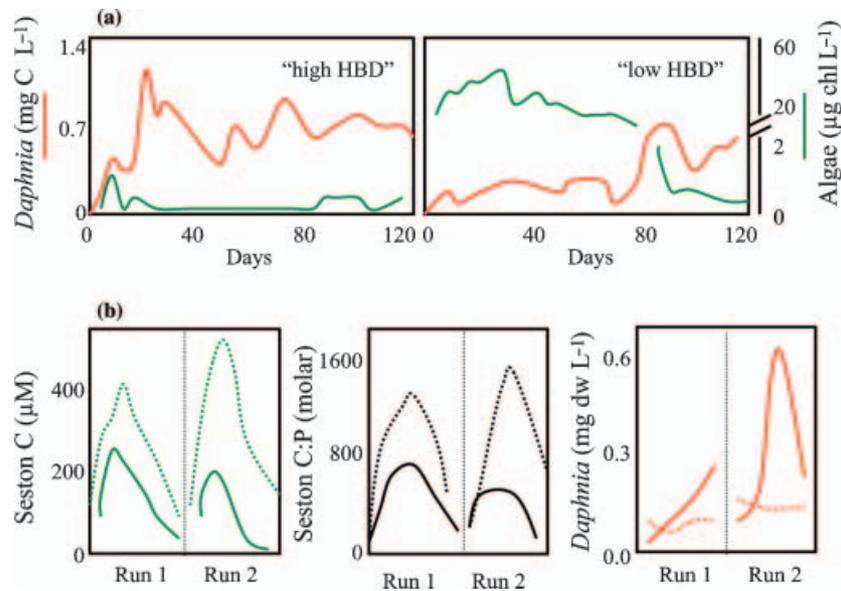
Study	Containers		Growth Conditions				Biota		Sampling		
	Volume (L)	Dimensions	P ( $\mu\text{M}$ )	N ( $\mu\text{M}$ )	N:P (atomic)	Light intensity ( $\mu\text{E m}^{-2} \text{s}^{-1}$ )	Temperature ( $^{\circ}\text{C}$ )	Autotroph(s)	Herbivore(s)	Duration (days)	Frequency
Nelson <i>et al.</i> (2001)	80	NA	0.32	28	90	75	15	Mixed green algae	<i>Daphnia pulex</i> (3 clones)	120	2 week <sup>-1</sup>
Sterner <i>et al.</i> (1998)	6300	11-m depth 0.86-m diameter	0.6	500	833	60 vs. 400 (24D : 0N)	20 (upper layer) 10 (lower layer)	<i>Scenedesmus acutus</i>	<i>Daphnia hyalina</i>	26	Every 2 day
Urabe <i>et al.</i> (2002a)	60	NA	0.5	40	80	40 vs. 320 (14D : 10N)	20	<i>S. acutus</i>	<i>Daphnia pulex</i> <i>Daphnia magna</i>	90	Every 5 day
Urabe <i>et al.</i> (2002b)	3140	4-m depth 1.0-m diameter	0–0.39	0–11.6	30	Ambient vs. 7% ambient	Ambient (18–20)	Mixed natural community	Mixed natural community	45	Every 5 day

P-content in the low HBD examples was in the range found to cause P-limitation in *Daphnia* by Sommer (1992).

Next we consider external factors and how they might alter autotroph–herbivore dynamics as predicted by stoichiometric theory. Both conceptual (Sterner *et al.* 1997) and quantitative (Loladze *et al.* 2000) work in ecological stoichiometry has come to emphasize the interplay of both light and nutrients in driving variation in herbivore dynamics in plankton systems. In this ‘light : nutrient hypothesis,’ it is proposed that high light in combination with low nutrient supply results in more severe phytoplankton nutrient limitation and thus generation of biomass with high C : nutrient content, with subsequent impacts on herbivore growth, population dynamics, and nutrient recycling feedbacks. This hypothesis has inspired a variety of empirical tests of its various aspects (Urabe & Sterner 1996; Sterner *et al.* 1997; Gurung *et al.* 1999; Chrzanowski & Grover 2001; Diehl *et al.* 2002; Hessen *et al.* 2002; Urabe *et al.* 2002a,b), of which we highlight three experiments that show effects of manipulations of light or light and nutrients on herbivore population dynamics.

First, we consider the plankton tower experiments of Sterner *et al.* (1998); experimental details in Table 3). Under low light, seston concentration (suspended biomass which includes phytoplankton but also some bacteria) and C : P peaked rapidly at relatively modest levels, then declined quickly as *Daphnia* increased (Fig. 7b), although the extent of the herbivore increase differed in the two runs. Under high light, seston reached very high levels as did its C : P ratio (> 1200) before declining due to sedimentation in the deep towers. In contrast to the low-light treatment, *Daphnia* populations did not increase at all during the 26-day period, staying at low levels similar to the inoculum size throughout. Thus, high-light intensity seems to have generated poor quality, high C : P autotroph production and thus an extensive ‘low HBD’ domain (*sensu* Nelson *et al.* 2001), as predicted by stoichiometric theory (Loladze *et al.* 2000).

A second laboratory example comes from a Japanese artificial ecosystem facility, the ‘Aquatron’ (Urabe *et al.* 2002a); an important aspect of this study was that it involved two species of *Daphnia*, *D. magna* and *D. pulex*, grown together. In all four of the low-light mesocosms (Fig. 8a left), algae showed a brief initial peak but were maintained at low levels throughout and had consistently high P : C (low C : P) in their biomass. *Daphnia* biomass increased rapidly, peaking within the first 45 days and then cycling somewhat erratically for the remaining period. In contrast, in three of the replicate high-light mesocosms (Fig. 8a middle), algae exhibited a very rapid increase and produced biomass with low P : C (high C : P). As a result, *Daphnia*’s increase was much delayed but did gradually reach a peak level comparable to that achieved under low light, followed by similar erratic fluctuations. As they reached this

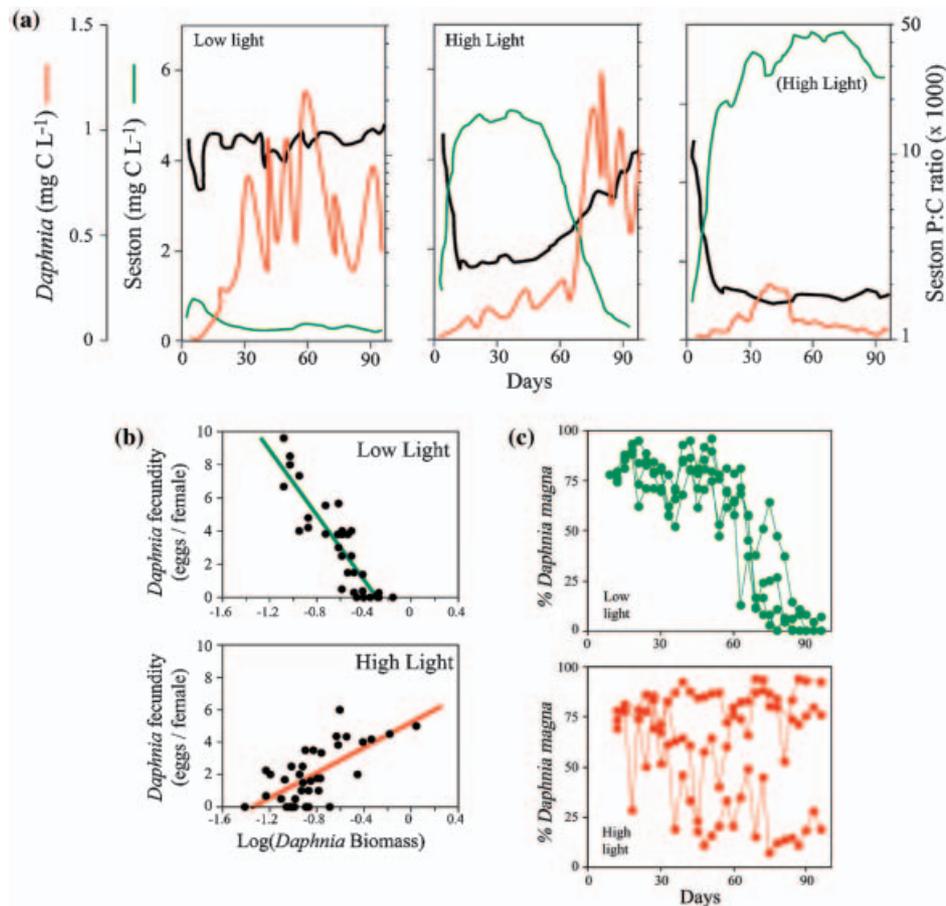


**Figure 7** (a) Examples of two types of herbivore dynamics in the study of Nelson *et al.* (2001). In this study, eight of the 12 mesocosms studied exhibited 'high herbivore biomass dynamics,' in which *Daphnia* populations increased rapidly during the first 20 days and maintained high but variable levels while algal biomass was low (left hand panel). However, four of the mesocosms exhibited 'low herbivore biomass dynamics' (right panel), in which algal biomass reached high levels and *Daphnia* populations remained at low levels for extended periods (in one case, for the entire observation period). Compare these dynamics to those observed under low and high light in the study of Urabe *et al.* (2002a) in Fig. 8. (b) Effects of elevated light intensity on algal biomass and C : P ratio and *Daphnia* dynamics in experimental 'plankton towers' (Sterner *et al.* 1998). The experiment was replicated in time and thus two 26-day runs are shown. Note that elevated irradiance (dashed lines) intensified the algal bloom, increased its C : P ratio, and completely inhibited the development of the *Daphnia* population compared to the normal light treatments (solid lines).

peak, algal biomass declined and P : C ratio increased. The fourth high-light replicate had somewhat higher light intensity than the others and showed somewhat different dynamics that included near extinction of the grazer (Fig. 8a right); interpretation of this replicate are discussed in Urabe *et al.* (2002a)). Under low light, conventional density dependence was observed in which increased *Daphnia* abundance was associated with reduced reproductive performance of individuals (Fig. 8b left). However, under high light during the early period of dynamics prior to *Daphnia* achieving its eventual population peak, the fecundity data show positive density dependence or facilitation; reproduction of individual herbivores was high when total herbivore abundance was high. The mechanism of this effect is clear: when algal C : P ratio was high under high light, increased cropping by higher biomass of grazers lowered algal biomass (and thus demand for nutrient), while excretion of P by the *Daphnia* (albeit limited due to its P-limitation) allowed the remaining algae to acquire P, thus reducing their overall C : P ratio and making them more nutritious. Furthermore, the sign reversal (from negative to positive) of the herbivore interaction strongly affected coexistence of the two *Daphnia* species (Fig. 8c). Under low light, the relative abundance of *D. pulicaria* increased to

nearly 100% in all four mesocosms (exclusion was achieved in three of the four), while in all four high-light enclosures, the two species coexisted at varying proportions throughout. Poor stoichiometric food quality, driven by increased light intensity that accentuated autotroph nutrient limitation, reduced the strength of competitive interactions between the grazers and thus favored coexistence, as predicted by stoichiometric theory (Loladze *et al.* 2004).

Our final example considers the effects of both nutrients and light in a field setting (Urabe *et al.* 2002b), leaving stainless steel, glass, and monospecific interactors behind and more completely involving the full complexity of natural systems. This experiment was performed in a highly P-limited lake (Lake 239), at the Experimental Lakes Area (Canada), a region where lakes are known to have seston with particularly high C : P ratio (Hassett *et al.* 1997; Elser *et al.* 1998) and where *Daphnia* growth has been demonstrated to be P-limited (Elser *et al.* 2001). Enclosures were allocated to two series of increasing nutrient enrichment, with one series receiving ambient light intensity and the other strongly shaded. Adding P to the enclosures had no impact on overall seston biomass at the end of the study period but produced strong declines in C : P ratios under both shaded and unshaded conditions (Fig. 9a,b). Shading reduced seston

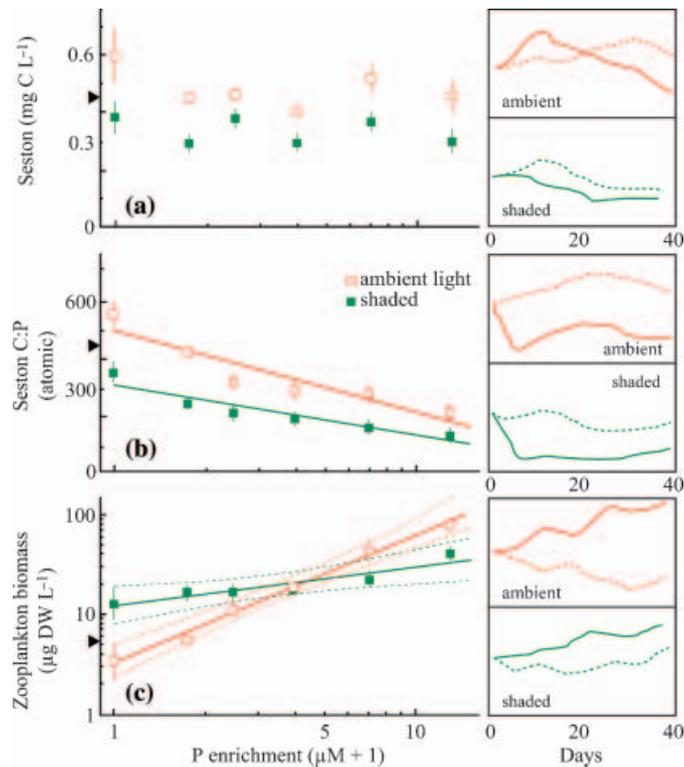


**Figure 8** Experimental results from a manipulation of light intensity under algal P-limitation in the ‘Aquatron’ experimental ecosystem facility (Urabe *et al.* 2002a). (a) Dynamics of seston biomass, P : C ratio, and *Daphnia* biomass under low light (left panel; four replicates showed dynamics like this), high light (middle panel; three replicates showed dynamics like this); and higher light (right panel; this high-light replicate inadvertently received *c.* 20% higher incident radiation). Note that P : C ratio (right axis, log scale) is by mass; that is, P : C ratios of 1, 5, 10, and 50 correspond to atomic C : P ratios of *c.* 2500, 500, 250, and 50, respectively. (b) Reversal of density dependence as a function of stoichiometric food quality. In the top panel, data from the low-light treatment during the period prior to the population reaching its first major peak are shown and illustrate a ‘normal,’ negative density dependence of fecundity (negative slope;  $P < 0.05$  for all data combined; data for each *Daphnia* species were also significant when analyzed separately). Under high light (bottom), density dependence is reversed (positive slope;  $P < 0.05$  for all data combined and for each species analyzed separately). (c) Reversal of density dependence under poor food quality favored coexistence of *D. magna* and *D. pulex* in the high-light treatment (bottom) but *D. pulex* was able to competitively exclude (or nearly so) *D. magna* under low light (top).

concentration at all levels of P-enrichment, simultaneously reducing seston C : P (Fig. 9a,b). Thus, both P-enrichment and shading improved stoichiometric food quality for the herbivores with only modest effects on overall food quantity. Responses of total zooplankton biomass were intriguing (Fig. 9c): in both shaded and control treatments, adding P resulted in increased zooplankton biomass at the end of the experiment. However, the effect of shading depended on P-enrichment: at high levels of P-enrichment (when seston C : P was low), shaded enclosures had lower zooplankton biomass, consistent with lower overall algal production under low light. In contrast, at low levels of P-enrichment,

shading produced a strong (*c.* 5-fold) increase in zooplankton biomass relative to fully illuminated enclosures.

In sum, these findings illustrate that stoichiometric impacts exist not only in mathematical models but are operating to drive the dynamics of real herbivores and autotrophs, both in the laboratory and in the field. While the studies to date have been of somewhat modest duration (at least compared to model outputs, not relative to the logistical demands of actually doing such experiments), they nevertheless support several key predictions of stoichiometric theory: alternative dynamical domains, novel population-interaction mechanisms (positive density-



**Figure 9** Effects of nutrient addition and shading on seston biomass and C : P ratio and zooplankton biomass in a field experiment in a P-limited lake (Urabe *et al.* 2002b). In each of (a), (b), and (c), the left hand panel shows mean values as a function of P-fertilization and shading treatment while the right hand panels depict temporal dynamics during the 40-day experiment with data for unfertilized (dashed lines) and  $+12 \mu\text{g P L}^{-1}$  ( $0.38 \mu\text{M}$ ) fertilization treatments shown for ambient (top) and shaded (bottom) treatments. (a) P-fertilization had no effect on overall seston biomass but shading consistently lowered seston biomass. (b) Fertilization strongly lowered seston C : P ratio in both light treatments, while shading significantly reduced C : P ratio at all P-fertilization levels. (c) Fertilization led to increased zooplankton biomass at the end of the experiment (mean data for the final 10 days of the study are shown) under both light treatments but the effect of shading depended on P-fertilization. At high levels of P input, shading decreased zooplankton production, as expected in conventional ecological theory. However, at low levels of P input similar to conditions in the lake itself, heavy shading led to a major increase in zooplankton biomass (note the log scale for zooplankton biomass). In each panel, the level of P-fertilization is indicated (the scale is log + 1 transformed, so unfertilized enclosures with no added P are plotted at a value of 1). In panels (a) and (b), error bars indicate  $\pm 1$  SE. of observations for each enclosure over all sampling dates. In panel (c), the dotted lines indicate 95% confidence limits on the regression. On each panel the black triangle on the y-axis indicates mean conditions in Lake 239 itself during the study period.

dependence), the ‘paradox of energy enrichment,’ and enhancement of species coexistence.

## CONCLUSIONS AND PROSPECTS

Papers reviewed in this article show that stoichiometric constraints have profound effects not only on organisms but also on models. However, it is fair to point out that the role of stoichiometry for population dynamics will surely be relevant mostly for nutrient-limited systems and mostly for the autotrophs and herbivorous animals within them, suggesting a limited domain for stoichiometric theory. On the other hand, most autotrophs are indeed limited by nutrient availability, as judged from their low nutrient quotas (Elser *et al.* 2000a), and herbivores are generally more nutrient-rich

than their food, arguing for frequent food quality constraints. Furthermore, autotrophic and herbivorous taxa dominate the world’s biodiversity. It is also important to note that the ‘bottom-up’ effects of stoichiometric constraints on consumer dynamics will also depend on the relative impact of ‘top-down’ forces (predation), but this holds also for strictly quantity-based models. Finally, we acknowledge that, to date, most work on stoichiometry in food webs has been devoted to planktonic systems, though we have mentioned several studies focusing on the potential impact of poor food quality in terrestrial food webs. Indeed, stoichiometric constraints have not yet been widely implemented into resource-consumer dynamic theory in the terrestrial realm. However, it is terrestrial systems where such impacts might be strongest, since terrestrial consumers face a diet that is far more deficient

in key nutrients compared with that experienced by their aquatic counterparts.

It seems that there is much to be gained by adding stoichiometric dimensions to population dynamics theory, accounting for not only the effects of food quantity but also for important aspects of food quality and the nutrient-recycling feedbacks generated from them. These gains are not merely incremental. Instead, stoichiometric models make qualitatively different predictions about stability, coexistence, and the effects of environmental perturbations on population dynamics. In the face of accelerating and multi-dimensional impacts of anthropogenic perturbations on ecosystems, ecology very much needs greater predictive power. We suggest that stoichiometric theory, even in its current imperfect form, is better suited to meet these challenges than existing population dynamic theory with its monotonic approach. However, introducing stoichiometric constraints into theoretical and empirical studies of population dynamics will require a far more comprehensive and explicit integration of population and ecosystem perspectives than has previously been achieved.

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