UvA-DARE (Digital Academic Repository)

Eco-Evolutionary Dynamics of Ecological Stoichiometry in Plankton Communities

Branco, P.; Egas, M.; Elser, J.J.; Huisman, J.

Eco-Evolutionary Dynamics of Ecological Stoichiometry in Plankton Communities

Pedro Branco,[1] Martijn Egas,[2] James J. Elser,[3] and Jef Huisman[1,*]

1. Department of Freshwater and Marine Ecology, Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, PO Box 94248, 1090 GE Amsterdam, The Netherlands;   2. Department of Evolutionary and Population Biology, Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, PO Box 94248, 1090 GE Amsterdam, The Netherlands;   3. Flathead Lake Biological Station, University of Montana, 32125 Bio Station Lane, Polson, Montana 59860; and School of Life Sciences, Arizona State University, Tempe, Arizona 85119

ABSTRACT: Nitrogen (N) and phosphorus (P) limit primary production in many aquatic ecosystems, with major implications for ecological interactions in plankton communities. Yet it remains unclear how evolution may affect the N : P stoichiometry of phytoplankton-zooplankton interactions. Here, we address this issue by analyzing an eco-evolutionary model of phytoplankton-zooplankton interactions with explicit nitrogen and phosphorus dynamics. In our model, investment of phytoplankton in nitrogen versus phosphorus uptake is an evolving trait, and zooplankton display selectivity for phytoplankton with N : P ratios matching their nutritional requirements. We use this model to explore implications of the contrasting N : P requirements of copepods versus cladocerans. The model predicts that selective zooplankton strongly affect the N : P ratio of phytoplankton, resulting in deviations from their optimum N : P ratio. Specifically, selective grazing by nitrogen-demanding copepods favors dominance of phytoplankton with low N : P ratios, whereas phosphorus-demanding cladocerans favor dominance of phytoplankton with high N : P ratios. Interestingly, selective grazing by nutritionally balanced zooplankton leads to the occurrence of alternative stable states, where phytoplankton may evolve either low, optimum, or high N : P ratios, depending on the initial conditions. These results offer a new perspective on commonly observed differences in N : P stoichiometry between plankton of freshwater and those of marine ecosystems and indicate that selective grazing by zooplankton can have a major impact on the stoichiometric composition of phytoplankton.

Keywords: N : P ratio, phytoplankton, Redfield ratio, zooplankton, cladocerans, copepods.

* Corresponding author; email: j.huisman@uva.nl.

Introduction

Advances in our understanding of nutrient limitation in aquatic ecosystems benefited greatly from the pioneering work of Alfred C. Redfield, who noted that the ratio of dissolved inorganic nitrogen to phosphorus in the deep ocean is remarkably similar to the average cellular N : P ratio of phytoplankton in surface waters (Redfield 1958). The establishment of the Redfield ratio ($C : N : P = 106 : 16 : 1$) led to a plethora of studies on the ecological and evolutionary significance of the N : P stoichiometry of freshwater and marine phytoplankton (e.g., Falkowski 2000; Flynn 2002; Sterner and Elser 2002; Loladze and Elser 2011). Although the canonical Redfield ratio has long been a benchmark for the average N : P ratio of phytoplankton, these studies provided ample theoretical and experimental evidence of substantial variation in N : P stoichiometry within and among different species (Geider and La Roche 2002; Quigg et al. 2003; Klausmeier 2004*a*). This variation in N : P ratio suggests that natural selection favors phytoplankton with different N : P ratios in different environments.

On the one hand, nutrient availability in the environment may exert a bottom-up control on the N : P ratio of phytoplankton (Bergström and Jansson 2006; Elser et al. 2009). For example, Burson et al. (2016) studied how reduced phosphorus loads from European rivers have affected nutrient limitation of marine phytoplankton in the North Sea. Their bioassays revealed a spatial gradient from phosphorus limitation in coastal waters to nitrogen limitation farther offshore, accompanied by a strong decline of the N : P ratio of phytoplankton from nearshore to offshore waters. Thus, as demonstrated by numerous studies, changes in nutrient availability can alter the N : P stoichiometry of phytoplankton.

On the other hand, zooplankton may exert a top-down control on the N : P ratio of phytoplankton. The elemental com-

position of zooplankton is usually more homeostatic than that of primary producers, and zooplankton therefore recycle surplus nutrients back into the environment when faced with nutritionally imbalanced food (Sterner and Elser 2002). Such zooplankton-mediated nutrient recycling may change the environmental N:P ratio (Elser et al. 1988; Sterner et al. 1992; Elser and Urabe 1999). Furthermore, several zooplankton species are able to graze selectively on food that meets their nutrient requirements (Buskey 1997; John and Davidson 2001; Boersma and Elser 2006; Elser et al. 2016; Meunier et al. 2016). In particular, copepods tend to have a relatively high body N:P ratio and prefer nitrogen-rich phytoplankton (Cowles et al. 1988; Walve and Larsson 1999), whereas cladocerans have a relatively low body N:P ratio and perform best when consuming phosphorus-rich phytoplankton (Andersen and Hessen 1991; Schatz and McCauley 2007). Yet the extent to which selective zooplankton grazing may affect the N:P ratio of phytoplankton remains elusive.

An improved understanding of how these bottom-up and top-down processes shape the N:P stoichiometry of phytoplankton may be obtained by integrating eco-evolutionary dynamics into the field of ecological stoichiometry (Matthews et al. 2011). It has long been assumed that evolutionary processes occur on a much slower timescale than ecological processes and therefore have little impact on ecological interactions. However, in recent years it has been realized that ecological and evolutionary processes can take place at similar timescales (Hairston et al. 2005; Carroll et al. 2007; Schoener 2011) and hence that evolutionary changes can be fast enough to affect ecological interactions (Thompson 1998; Fussmann et al. 2007; Pelletier et al. 2009). One of the first demonstrations of eco-evolutionary dynamics came from laboratory experiments, where natural selection among phytoplankton varying in defense against grazing affected phytoplankton-zooplankton oscillations (Yoshida et al. 2003, 2004). Similar eco-evolutionary dynamics might play a role in the ecological stoichiometry of phytoplankton-zooplankton systems, although this possibility has not yet been extensively evaluated.

To explore these ideas, here we develop an eco-evolutionary model to investigate dynamic changes in the N:P stoichiometry of phytoplankton in response to phytoplankton-zooplankton interactions. We aim to address two interrelated questions: (1) How do eco-evolutionary changes in N:P stoichiometry of phytoplankton affect phytoplankton-zooplankton interactions? (2) How do differences in nutrient requirements and selectivity of zooplankton affect the N:P stoichiometry of phytoplankton? The model assumes that phytoplankton adapt their investment in nitrogen versus phosphorus uptake and that zooplankton display selectivity for phytoplankton with N:P ratios matching their nutritional requirements. Our analysis considers two contrasting scenarios: one where phytoplankton are grazed by nitrogen-demanding zooplankton ("copepods") and another where phytoplankton are grazed by phosphorus-demanding zooplankton ("cladocerans").

The Model

We consider a plankton community with two limiting nutrients (nitrogen and phosphorus), a phytoplankton species, and a zooplankton species. The growth rate of phytoplankton depends on their nitrogen and phosphorus contents, according to a variable-internal-stores model (Droop 1973; Grover 1991; Sterner and Elser 2002). Zooplankton grazing depends on the nutritional quality of phytoplankton (Sterner and Hessen 1994; Elser et al. 2000a), where zooplankton tend to have a preference for phytoplankton that match their nutritional demands (Boersma and Elser 2006; Elser et al. 2016; Meunier et al. 2016). We assume that investment of phytoplankton in the uptake of nitrogen versus phosphorus is an evolving trait. Specifically, phytoplankton face a trade-off whereby an increase in nitrogen uptake comes at the cost of a decrease in phosphorus uptake.

Phytoplankton Dynamics

It is well known that the cellular nitrogen and phosphorus contents of phytoplankton can change dynamically. Specifically, the cellular content of nutrient i of phytoplankton, Q_i, increases as a result of nutrient uptake and declines as a result of growth (Droop 1973):

$$\frac{dQ_i}{dt} = f_i(R_i, Q_i) - \mu(Q_N, Q_P)Q_i, \tag{1}$$

where $i = N, P, f_i(R_i, Q_i)$ is the uptake rate of nutrient i by phytoplankton as a function of the environmental nutrient concentration (R_i) and their cellular nutrient content (Q_i), and $\mu(Q_N, Q_P)$ is the specific growth rate of phytoplankton.

We assume that the nutrient uptake rate of phytoplankton increases with nutrient availability according to Michaelis-Menten kinetics but is suppressed by high cellular nutrient contents (Morel 1987; Ducobu et al. 1998):

$$f_i(R_i, Q_i) = f_{\max,i}\left(\frac{R_i}{R_i + K_i}\right)\left(\frac{Q_{\max,i} - Q_i}{Q_{\max,i} - Q_{\min,i}}\right), \tag{2}$$

where $f_{\max,i}$ is the maximum uptake rate of nutrient i by phytoplankton, K_i is their half-saturation constant, and $Q_{\min,i}$ and $Q_{\max,i}$ are their minimum and maximum cellular nutrient content, respectively. That is, the nutrient uptake rate is highest when phytoplankton are starved (i.e., $Q_i = Q_{\min,i}$) and reduces to 0 when phytoplankton are satiated with nutrients (i.e., $Q_i = Q_{\max,i}$). These assumptions are supported by studies of the nutrient uptake kinetics of phytoplankton

species (e.g., Morel 1987; Ducobu et al. 1998; Passarge et al. 2006).

The specific growth rate of phytoplankton follows a multinutrient extension of the Droop equation (Droop 1973; Klausmeier et al. 2004*b*) and is determined by the cellular content of the most limiting nutrient, according to the Law of the Minimum (von Liebig 1840):

$$\mu(Q_N, Q_P) = \mu_{max} \min\left(1 - \frac{Q_{min,N}}{Q_N}, 1 - \frac{Q_{min,P}}{Q_P}\right), \quad (3)$$

where μ_{max} is the maximum specific growth rate of phytoplankton. Which nutrient limits the growth rate of phytoplankton depends on the magnitude of the two terms in the minimum function. Equating the two terms in the minimum function shows that phytoplankton are colimited by nitrogen and phosphorus when their cellular N : P ratio equals a critical value $Q_N/Q_P = Q_{min,N}/Q_{min,P}$. We refer to this value hereafter as the optimum N : P ratio of phytoplankton (Rhee and Gotham 1980; Flynn 2002), denoted as $(N/P)^*_{phyto}$. When their cellular N : P ratio is lower than this optimum N : P ratio, phytoplankton growth is nitrogen limited. When it is higher, phytoplankton growth is phosphorus limited.

The population dynamics of phytoplankton are driven by their growth rate, mortality rate, and the grazing rate by zooplankton:

$$\frac{dA}{dt} = \mu(Q_N, Q_P)A - dA - g(A, Q_N, Q_P)Z, \quad (4)$$

where A is the population abundance of phytoplankton, d is their specific mortality rate, and Z is the population abundance of zooplankton. The grazing rate, $g(A, Q_N, Q_P)$, is a function of the population abundance and nutritional quality of phytoplankton (see below).

Zooplankton Dynamics

We incorporate the common observation that zooplankton tend to have a more homeostatic nutrient composition than phytoplankton (Sterner and Elser 2002) by assuming that their nitrogen and phosphorus contents, q_N and q_P, are fixed. Hence, the body N : P ratio of zooplankton is constant (i.e., $(N/P)_{zoo} = q_N/q_P$).

Several experimental studies show that grazing by zooplankton depends on the nutritional quality of phytoplankton (Cowles et al. 1988; DeMott 1989; Buskey 1997; John and Davidson 2001; Schatz and McCauley 2007; Martel 2009; Meunier et al. 2016). The grazing rate of zooplankton on phytoplankton may thus be modeled as a type II functional response (Holling 1959; Křivan 1996), which takes the nutrient contents of phytoplankton into account (Branco et al. 2010):

$$g(A, Q_N, Q_P) = \frac{a\alpha(Q_N, Q_P)A}{1 + ah\alpha(Q_N, Q_P)A}, \quad (5)$$

where a is the search rate of zooplankton, $\alpha(Q_N, Q_P)$ is the probability that zooplankton will consume encountered individuals of phytoplankton, given their nutritional quality, and h is the handling time of zooplankton per prey item.

We assume that zooplankton preferentially feed on phytoplankton with an N : P ratio neither much higher nor much lower than their own N : P requirements. This phenomenon has become known as the "stoichiometric knife edge" (Boersma and Elser 2006; Elser et al. 2016) and is incorporated in our model by a simple Gaussian relationship (fig. 1):

$$\alpha(Q_N, Q_P) = \exp\left\{-[(Q_N/Q_P) - (q_N/q_P)]^2/2(1/S)^2\right\}, \quad (6)$$

where S measures the selectivity of zooplankton for nutritionally balanced prey (i.e., the width of the Gaussian curve). If zooplankton are nonselective ($S \to 0$), then phytoplankton are consumed with the same probability, $\alpha = 1$, irrespective of their N : P ratio. Conversely, if zooplankton are highly selective ($S \to \infty$), then they consume only phytoplankton with N : P ratios matching their own body N : P ratio.

We assume that zooplankton assimilate the ingested phytoplankton with efficiency e (Loladze et al. 2000; Branco et al. 2010):

$$e(Q_N, Q_P) = \min\left(\frac{Q_N}{q_N}, \frac{Q_P}{q_P}\right), \quad (7)$$

which is defined as the lowest ratio of nutrient content of phytoplankton to nutrient content of zooplankton. Accordingly, high nutrient contents of phytoplankton or low nutrient contents of zooplankton will result in high assimilation efficiencies. Zooplankton usually have a higher nutrient content per unit carbon than phytoplankton (Elser et al. 2000*a*).
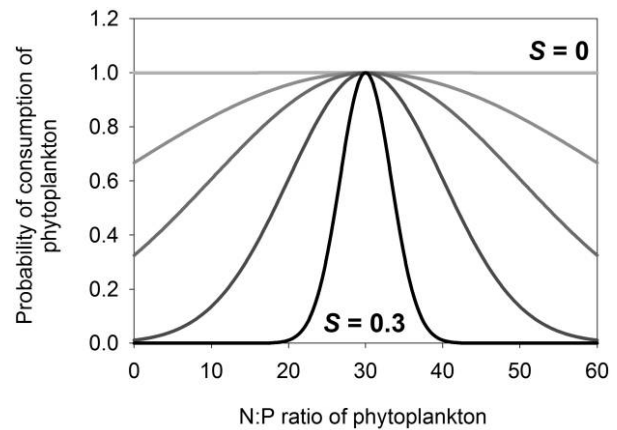

Figure 1: Diet of zooplankton as function of the N : P ratio of phytoplankton. The curves are derived from equation (6), and each curve corresponds to a different grazing selectivity of zooplankton ($S = 0$, 0.03, 0.05, 0.1 and 0.3). For the purpose of illustration, the N : P ratio of zooplankton is here assumed to be $(N/P)_{zoo} = 30$.

When expressed on a per-unit-carbon basis, this precludes assimilation efficiencies greater than 1.

The population dynamics of zooplankton are given by

$$\frac{dZ}{dt} = (e(Q_N, Q_P)g(A, Q_N, Q_P) - m)Z, \qquad (8)$$

where m is the specific mortality rate of zooplankton.

Nutrient Dynamics

Our model assumes that the nutrients available in the environment are consumed by phytoplankton and brought back into the system by degradation of dead organisms and nutrient excretion by zooplankton (Grover 1997):

$$\frac{dR_i}{dt} = -f_i(R_i, Q_i)A + dAQ_i + mZq_i \qquad (9)$$
$$+ g(A, Q_N, Q_P)Z(Q_i - e(Q_N, Q_P)q_i),$$

where the first term on the right-hand side describes nutrient uptake by phytoplankton and the second and third terms describe nutrient recycling due to the mortality of phytoplankton and zooplankton, respectively. The fourth term describes recycling through excretion of nutrients not utilized by the zooplankton population. Specifically, inserting equation (7) shows that this fourth term assumes that zooplankton retain the nutrient that limits their growth and excrete the surplus of the nonlimiting nutrient. We assume that food egestion by zooplankton is negligible.

The total amount of nutrient i in the ecosystem, T_i, includes the freely available nutrient in the environment as well as the nutrient contained in phytoplankton and zooplankton:

$$T_i = R_i + AQ_i + Zq_i. \qquad (10)$$

Differentiation of this equation shows that the total amount of nutrient i remains constant over time (i.e., $dT_i/dt = 0$; see app. A for the derivation; apps. A–C are available online). Thus, our model ecosystem is a closed system with respect to nutrients. We note that our model predictions remain qualitatively similar when this model assumption is relaxed to consider an open ecosystem with respect to nutrients (see app. B; figs. B1, B2; figs. B1, B2, C1, and C2 are available online).

Evolutionary Dynamics

In our evolutionary scenario, we assume that investment of phytoplankton in nitrogen versus phosphorus assimilation is an evolving trait. The reasoning for this assumption is that the enzymatic machinery involved in the uptake and subsequent assimilation of nitrogen and phosphorus into biomolecules is encoded in the genomes of organisms, and the expression level of these enzymes can therefore be modified by evolution. Nitrogen and phosphorus are both major constituents of cells, where nitrogen is mainly used in protein synthesis, whereas phosphorus is mainly used in RNA and DNA synthesis (Elser et al. 2000b; Loladze and Elser 2011). Following Klausmeier et al. (2007), in our model the trade-off between nitrogen and phosphorus assimilation is represented by a simple linear constraint between the maximum uptake rates of the two nutrients:

$$f_{max,N} = p_N F_{max,N},$$
$$f_{max,P} = p_P F_{max,P}, \qquad (11)$$

with $p_N + p_P = 1$, where p_i is the investment of phytoplankton in the uptake of nutrient i and $F_{max,i}$ is the maximum uptake rate of nutrient i when phytoplankton would invest exclusively in nutrient i (i.e., when $p_i = 1$). Hence, increasing investment in the maximum uptake rate of nitrogen comes at the cost of a reduction of the maximum uptake rate of phosphorus, and vice versa. In our analysis, we focus on the investment in nitrogen uptake, p_N and calculate the investment in phosphorus uptake simply as $p_P = 1 - p_N$.

Evolutionary changes in nitrogen and phosphorus uptake of phytoplankton affect their fitness in multiple ways, for example, by changing their competitive ability for these nutrients and their nutritional quality as food for zooplankton. In our model, phytoplankton fitness, w, is defined as their net specific growth rate under the prevailing conditions (Lande 1982):

$$w = \frac{1}{A}\frac{dA}{dt}. \qquad (12)$$

We study the evolutionary dynamics of phytoplankton by using a quantitative-trait approach and the theory of fast-slow dynamical systems (Cortez and Ellner 2010; Cortez 2011):

$$\varepsilon\frac{dp_N}{dt} = BV\frac{\partial w}{\partial p_N}, \qquad (13)$$

where ε measures the relative difference between timescales of ecological and evolutionary processes. Evolutionary processes occur at a rate slower than that of ecological processes when $\varepsilon > 1$, at the same rate when $\varepsilon = 1$, and at a faster rate when $\varepsilon < 1$. In our study, we assume that evolutionary processes are slower than ecological processes (i.e., $\varepsilon = 10$). The bounding function B takes the form $B = (p_N - p_{min})(p_{max} - p_N)$, where p_{min} and p_{max} are the minimum and maximum investment of phytoplankton in nitrogen uptake, respectively (Cortez and Ellner 2010). The parameter V is the additive genetic variance of the evolving trait. The fitness gradient on the right-hand side of equation (13) measures the direction and strength of natural selection exerted on the evolving trait. Hence, if the fitness gradient is positive (negative), then investment in nitrogen uptake will increase (decrease) over time.

We calculate the fitness gradient of phytoplankton numerically. At each time step, we generate two phytoplankton mutants with a phenotype slightly different from the resident phenotype ($\pm 0.001\%$) and calculate their net specific growth rates in the environment set by the resident community to estimate the local fitness gradient. We examined trait evolution with numerical simulations based on the NDSolve routine in Mathematica 10 (Wolfram Research, Champaign, IL).

Parameterization of the Model

We parameterize our model using nitrogen- and phosphorus-related parameter values of plankton communities. This allows realistic choices of parameter values, because many of the process descriptions in the model have been verified and measured for plankton species. Parameter values for phytoplankton were obtained from the green alga *Chlorella*, a genus of common phytoplankton species living in both freshwater and marine environments (Tischner and Lorenzen 1979; Passarge et al. 2006). The optimum N:P ratio of *Chlorella* predicted by our model is slightly above the Redfield ratio $((N/P)^*_{phyto} = Q_{min,N}/Q_{min,P} = 25.2$; see table 1). Since zooplankton may differ substantially in their elemental composition, we analyze two versions of our model representing two distinct zooplankton taxa. Cladocerans such as *Daphnia* dominate the zooplankton in many freshwater environments. They tend to have relatively high phosphorus demands and hence low body N:P ratios $((N/P)_{zoo} = 12$; Andersen and Hessen 1991; Matveev et al. 1994; Acharya et al. 2004). Conversely, calanoid copepods such as *Acartia* dominate the zooplankton in many marine environments and have much higher body N:P ratios $((N/P)_{zoo} = 34.3$; Berggreen et al. 1988; Walve and Larsson 1999; Sommer and Stibor 2002). The optimum N:P ratio of phytoplankton in our model thus lies between those of cladocerans and copepods:

$$\left(\frac{N}{P}\right)_{cladocerans} < \left(\frac{N}{P}\right)^*_{phyto} < \left(\frac{N}{P}\right)_{copepods}. \quad (14)$$

Model variables and parameters are listed in table 1, and we refer to appendix A for a complete list of model equations.

Model Analysis

The model is used to investigate the two research questions posed in the "Introduction." To investigate how eco-evolutionary changes in N:P stoichiometry of phytoplankton affect phytoplankton-zooplankton interactions, we first set the stage by assuming that zooplankton are absent and analyze the impact of nutrient enrichment on both ecological and eco-evolutionary dynamics of phytoplankton. Subsequently, we add zooplankton and analyze the ensuing phytoplankton-zooplankton interactions. To address how differences in nutrient requirements of zooplankton affect the N:P stoichiometry of phytoplankton, we explore the eco-evolutionary dynamics when phytoplankton are grazed by either phosphorus-demanding "cladocerans" or nitrogen-demanding "copepods." Finally, we investigate evolution of the N:P ratio of phytoplankton in response to variation in both grazing selectivity and body N:P ratio of these two contrasting zooplankton groups.

Results

Ecological versus Eco-Evolutionary Dynamics of Phytoplankton

First, we benchmark our model analysis of the N:P stoichiometry of phytoplankton in the absence of zooplankton. To understand the impact of evolution on the N:P stoichiometry of phytoplankton in the absence of zooplankton, we investigate two model versions: an ecological model where investment in nitrogen uptake is fixed and an eco-evolutionary model where investment in nitrogen uptake evolves. We assume that investment in nitrogen versus phosphorus uptake is balanced in the ecological model (i.e., $p_N = 0.5$), whereas it may evolve a wide range of values in the eco-evolutionary model (i.e., from $p_{min} = 0$ to $p_{max} = 1$). The ecological model predicts that low nitrogen availability in the ecosystem yields a low population abundance of phytoplankton, which deplete the dissolved nitrogen (fig. 2*A*). The cellular N:P ratio of phytoplankton stabilizes at a low value, and their growth is severely nitrogen limited (fig. 2*B*). In ecosystems with intermediate nitrogen availability, phytoplankton reach a high population abundance and deplete both dissolved nitrogen and dissolved phosphorus (fig. 2*C*). The cellular N:P ratio of phytoplankton stabilizes at an intermediate value, and their growth is colimited by both nutrients (fig. 2*D*). In nitrogen-rich systems, phytoplankton also reach a high population abundance (fig. 2*E*), but their cellular N:P ratio stabilizes at a high value and their growth is severely phosphorus limited (fig. 2*F*).

The eco-evolutionary model predicts that low nitrogen availability in the ecosystem again causes phytoplankton to reach a low population abundance and rapidly deplete the dissolved nitrogen (fig. 3*A*). Their investment in nitrogen uptake gradually evolves toward a high value (fig. 3*B*), and it follows from the trade-off built into the model that their investment in phosphorus uptake gradually declines. Initially, phytoplankton have a low cellular N:P ratio and their growth rate is nitrogen limited, but evolutionary adaptation of their nitrogen and phosphorus uptake capacities eventually leads to colimitation by nitrogen and phosphorus (fig. 3*C*). In ecosystems with intermediate nitrogen availability, phytoplankton reach a higher population abundance (fig. 3*D*). A balanced investment

Table 1: Model variables and parameter values

Symbol	Definition	Unit	Value	Source
Variables:				
R_i	Environmental concentration of nutrient i	μM	...	...
A	Population abundance of phytoplankton	cells L^{-1}	...	...
Q_i	Nutrient i contained in phytoplankton	fmol cell^{-1}	...	...
Z	Population abundance of zooplankton	ind L^{-1}	...	...
p_i	Investment of phytoplankton in uptake of nutrient i	...	...	...
Environmental parameters:				
T_i	Total concentration of nutrient i	μM	$T_N = 10$–200; $T_P = 1.2$–4	Wetzel 2001
Phytoplankton parameters:				
$F_{\max,i}$	Maximum uptake rate of nutrient i by phytoplankton investing exclusively in nutrient i	pmol cell^{-1} day^{-1}	$F_{\max,N} = .051$; $F_{\max,P} = .087$	Caperon and Meyer 1972; Passarge et al. 2006
K_i	Half-saturation constant of nutrient i for phytoplankton	μM	$K_N = 4.3$; $K_P = 9.32$	Tischner and Lorenzen 1979; Passarge et al. 2006
$Q_{\min,i}$	Minimum content of nutrient i in phytoplankton	fmol cell^{-1}	$Q_{\min,N} = 31$; $Q_{\min,P} = 1.23$	Irwin et al. 2006;[a] Passarge et al. 2006
$Q_{\max,i}$	Maximum content of nutrient i in phytoplankton	fmol cell^{-1}	$Q_{\max,N} = 126$; $Q_{\max,P} = 7.7$	Irwin et al. 2006;[a] Passarge et al. 2006
$\mu_{\max}$	Maximum specific growth rate of phytoplankton	day^{-1}	1.9	Passarge et al. 2006
d	Specific mortality rate of phytoplankton	day^{-1}	.1	Sterner 1986
$p_{\min}$	Minimum investment of phytoplankton in nitrogen uptake	...	0–.1	Klausmeier et al. 2007

p_{max}	Maximum investment of phytoplankton in nitrogen uptake	...	.9–1	Klausmeier et al. 2007
ε	Pace of evolution of phytoplankton	...	10	...
V	Additive genetic variance of evolving trait	...	0–.1	...
Zooplankton parameters:				
h	Handling time per prey item by zooplankton	ind day cell^{-1}	Copepod: 3.6×10^{-7}; cladoceran: 1.4×10^{-7}	Dumont et al. 1975; Kiørboe et al. 1985;[b] Matveev et al. 1994
a	Search rate of zooplankton	L ind^{-1} d^{-1}	Copepod: .001; cladoceran: .072	Matveev et al. 1994
q_i	Content of nutrient i in zooplankton	μmol ind^{-1}	Copepod: $q_N = .024$; $q_P = 7 \times 10^{-4}$; cladoceran: $q_N = .3$; $q_P = .025$	Dumont et al. 1975; Andersen and Hessen 1991; Walve and Larsson 1999[c]
m	Specific mortality rate of zooplankton	day^{-1}	.1	Hirst and Kiørboe 2002
S	Selectivity of zooplankton	...	0–.3	...

Note: Numerical simulations considered a community with the following initial conditions: $R_i = T_i - AQ_i - Zq_i$, $A = 10^7$ cells L^{-1}, $Q_i = Q_{min,i}$, $Z = 10$ individuals (ind) L^{-1}, and $p_N = p_P = 0.5$. Where available, parameter values for phytoplankton were obtained from *Chlorella* species (*Chlorella sorokiniana* in Tischner and Lorenzen 1979; *Chlorella vulgaris* in Passarge et al. 2006). In case parameter values were not available for *Chlorella* species, we refer to either empirical studies on other phytoplankton species (*Dunaliella tertiolecta* in Caperon and Meyer 1972; a mixture of several phytoplankton species in Sterner 1986; diatoms in Irwin et al. 2006) or theoretical studies (Klausmeier et al. 2007). Parameter values for the copepod were obtained from *Acartia* species (*Acartia tonsa* in Kiørboe et al. 1985 and *Acartia* sp. in Walve and Larsson 1999), whereas parameter values for the cladoceran were obtained from *Daphnia* species (*Daphnia magna* Straus in Dumont et al. 1975; *Daphnia longispina* in Andersen and Hessen 1991; *Daphnia carinata* in Matveev et al. 1994). Some parameter values were not available for *Acartia* species, in which case we refer to empirical studies on other copepod species (calanoid copepods in Dumont et al. 1975; marine epipelagic copepods in Hirst and Kiørboe 2002).

ᵃ The minimum and maximum contents of nitrogen in phytoplankton were calculated with the allometric scaling proposed by Irwin et al. (2006) in their table 1 and assuming that *Chlorella* typically has a cell diameter of 5 μm.

ᵇ We assumed that the cell volume of *Chlorella* is 1/20 that of *Rhodomonas baltica*, studied by Kiørboe et al. (1985), and that the handling time is primarily determined by the passage time through the gut of *Acartia* (i.e., handling time per prey item is inversely proportional to the number of prey that fit in the gut; Kiørboe 2008, p. 105).

ᶜ The nutrient contents of copepods and cladocerans were based on the range of nitrogen and phosphorus percentages of total dry weight observed by Walve and Larsson (1999) and Andersen and Hessen (1991), respectively. Dry weights of copepods and cladocerans were obtained from Dumont et al.'s (1975) measurements of various species of calanoid copepods and *Daphnia magna* Straus, respectively.
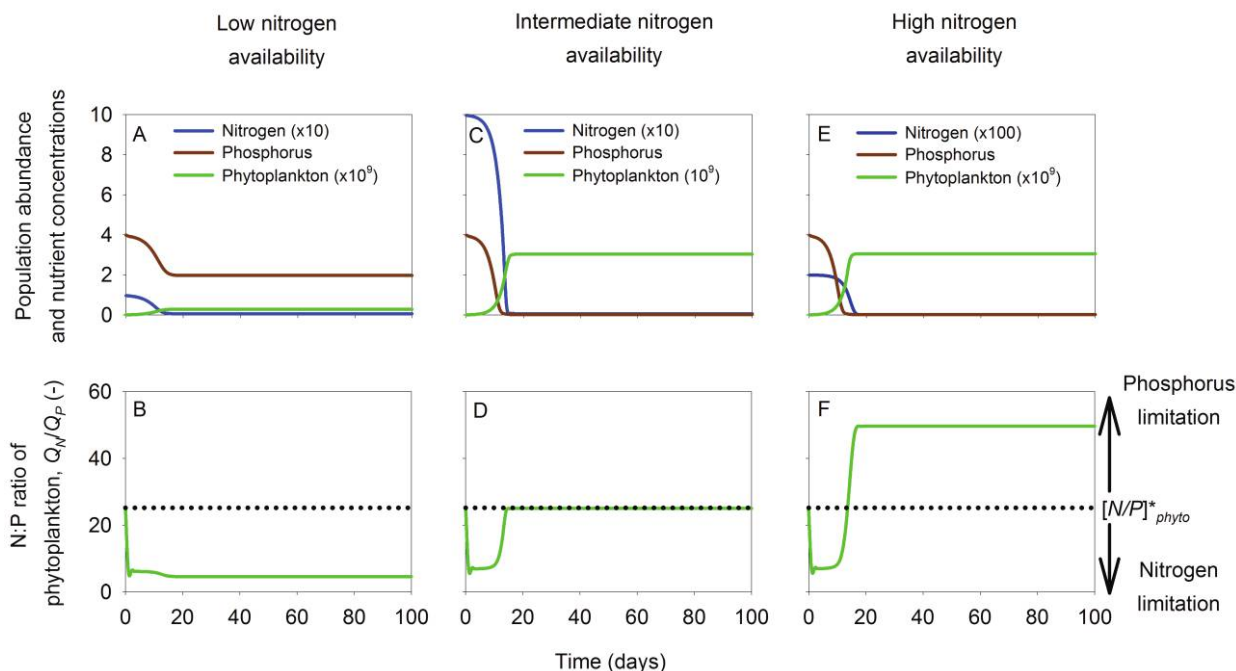
E7

Figure 2: Ecological dynamics of phytoplankton in the absence of zooplankton. The graphs compare three ecosystems, with low (*A*, *B*), intermediate (*C*, *D*), and high (*E*, *F*) nitrogen availability. *A*, *C*, *E*, Dynamics of phytoplankton and dissolved nitrogen and phosphorus concentrations. *B*, *D*, *F*, Cellular N:P ratio of phytoplankton (green line); the dotted horizontal line indicates the cellular N:P ratio at which phytoplankton are colimited by nitrogen and phosphorus. Parameter values are given in table 1, with a total nitrogen concentration of $T_N = 10 \mu M$ (*A*, *B*), $T_N = 100 \mu M$ (*C*, *D*), and $T_N = 200 \mu M$ (*E*, *F*), a total phosphorus concentration of $T_P = 4 \mu M$, and nonevolving phytoplankton ($V = 0$) with a constant investment in nitrogen uptake ($p_N = 0.5$).

in nitrogen and phosphorus uptake (fig. 3*E*) enables rapid convergence to colimitation by nitrogen and phosphorus (fig. 3*F*). In nitrogen-rich systems, dissolved phosphorus is rapidly depleted (fig. 3*G*). At an evolutionary timescale, phytoplankton reduce their investment in nitrogen uptake while increasing their phosphorus uptake capacity (fig. 3*H*), which gradually shifts their growth again from severe phosphorus limitation to colimitation by nitrogen and phosphorus (fig. 3*I*).

Eco-Evolutionary Dynamics of Phytoplankton-Zooplankton Interactions

As a next step, we introduce mildly selective zooplankton in our model and analyze the ensuing phytoplankton-zooplankton interactions, assuming either ecological dynamics (see app. C) or eco-evolutionary dynamics (figs. 4, 5). We contrast below the model results for two different zooplankton types: phosphorus-demanding "cladocerans" with a low N:P ratio (figs. 4, C1) and nitrogen-demanding "copepods" with a high N:P ratio (figs. 5, C2).

Phosphorus-Demanding Zooplankton ("Cladocerans"). In nitrogen-poor ecosystems, phytoplankton abundance is low,

and in both the ecological and eco-evolutionary models zooplankton cannot find sufficient food to survive (figs. 4*A*, C1). As a consequence, the phytoplankton dynamics are similar to those in the absence of zooplankton. In the eco-evolutionary model, investment of phytoplankton in nitrogen uptake increases during evolution, such that phytoplankton growth becomes colimited by nitrogen and phosphorus (fig. 4*B*, 4*C*).

For ecosystems with intermediate nitrogen levels, the model predicts a stable equilibrium with high phytoplankton and low zooplankton abundances in both the ecological and the eco-evolutionary models (figs. 4*D*, C1). In the eco-evolutionary model, phytoplankton shift their investment from nitrogen uptake to phosphorus uptake because of the high nitrogen and low phosphorus availability in the environment (fig. 4*E*). Phosphorus-demanding zooplankton prefer to graze on prey with low cellular N:P ratios, however, and therefore a too-high investment in phosphorus uptake may lead to negative fitness consequences for phytoplankton. To avoid being eaten, phytoplankton thus adjust their investment in nitrogen versus phosphorus uptake such that they still maintain a relatively high cellular N:P ratio, at which their growth rate remains phosphorus limited (fig. 4*F*).

Further nitrogen enrichment leads to a further increase of the phytoplankton N:P ratio in the ecological model and there-
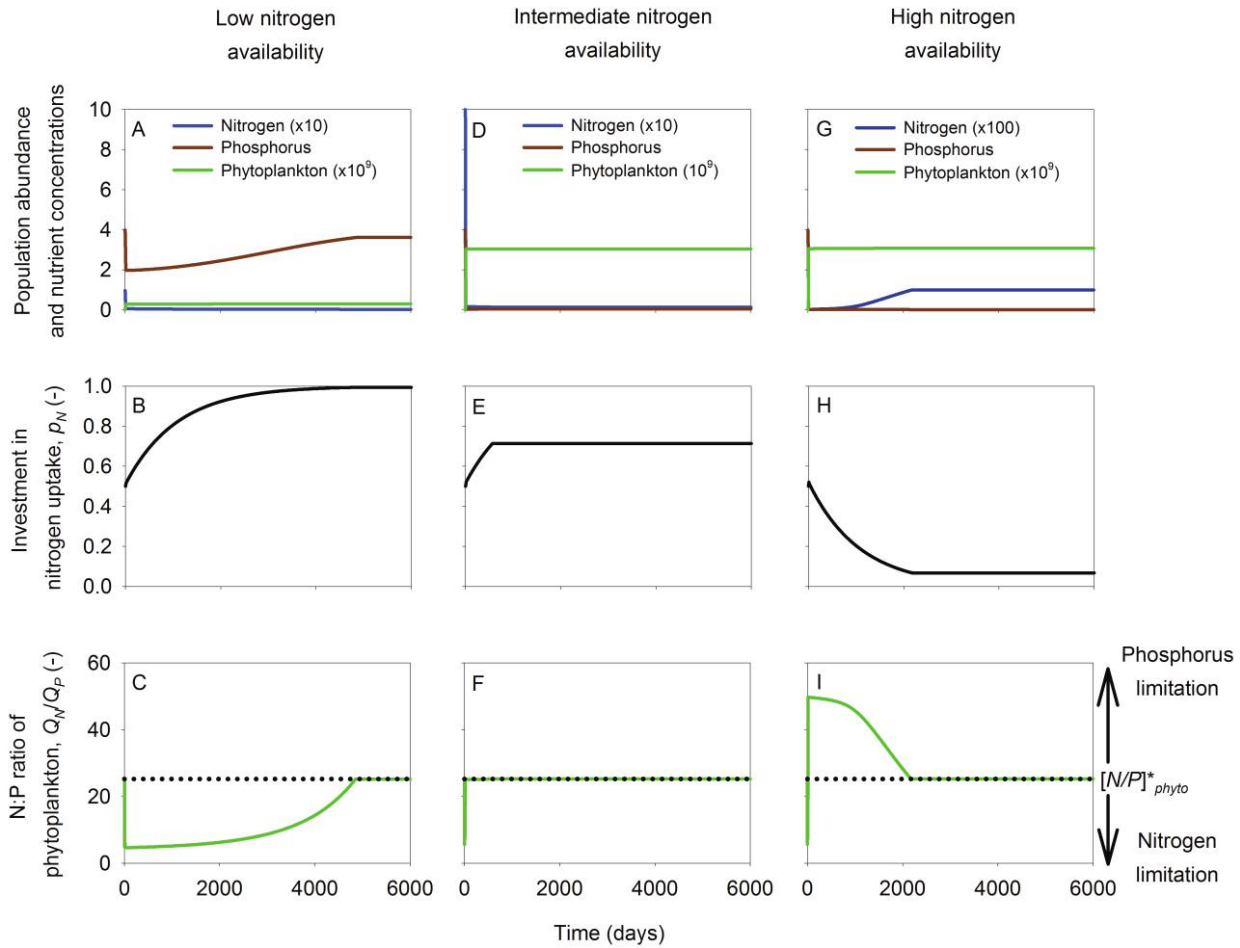
Figure 3: Eco-evolutionary dynamics of phytoplankton in the absence of zooplankton. The graphs compare three ecosystems, with low (*A–C*), intermediate (*D–F*), and high (*G–I*) nitrogen availability. *A, D, G,* Dynamics of phytoplankton and dissolved nitrogen and phosphorus concentrations. *B, E, H,* Investment of phytoplankton in nitrogen uptake. *C, F, I,* Cellular N : P ratio of phytoplankton (green line); the dotted horizontal line indicates the cellular N : P ratio at which phytoplankton are colimited by nitrogen and phosphorus. Parameter values are the same as in figure 2, but with evolving phytoplankton ($V = 0.1$) capable of investing in nitrogen uptake from $p_{min} = 0$ to $p_{max} = 1$.

fore to extinction of the phosphorus-demanding zooplankton, because the phosphorus content of its food becomes too low (fig. C1). In the eco-evolutionary model, however, the zooplankton population does not become extinct, but nitrogen enrichment leads to oscillations of the phytoplankton and zooplankton abundances (fig. 4*G*). We note that these predator-prey oscillations are sustained even if nitrogen availability is increased further (i.e., even at $T_N = 2{,}000$ μM and $T_P = 4$ μM, yielding $T_N : T_P = 500$; results not shown). Interestingly, the eco-evolutionary investment in nutrient uptake oscillates in phase with these predator-prey oscillations, thus displaying a small-amplitude trait cycle (fig. 4*H*). The cellular N : P ratio of the phytoplankton also fluctuates in sync, but it remains in the phosphorus-limited region (fig. 4*I*).

The period of the oscillations is much longer than the generation times of the organisms (fig. 4*G*–4*I*), indicating that evolutionary dynamics play a role. In essence, what happens is that, when zooplankton become rare, phytoplankton investment in nitrogen uptake declines and the N : P ratio of the phytoplankton moves toward a balanced colimitation by nitrogen and phosphorus. The declining N : P ratio of the phytoplankton raises their nutritional value, and the zooplankton population recovers. The increased grazing rate by phosphorus-demanding zooplankton, in turn, selects for an evolutionary increase of the nitrogen uptake rate, so that the phytoplankton population develops a higher N : P ratio to suppress grazing losses. Owing to the reduced nutritional value of the phytoplankton, the zooplankton population declines again, and the cycle starts anew.
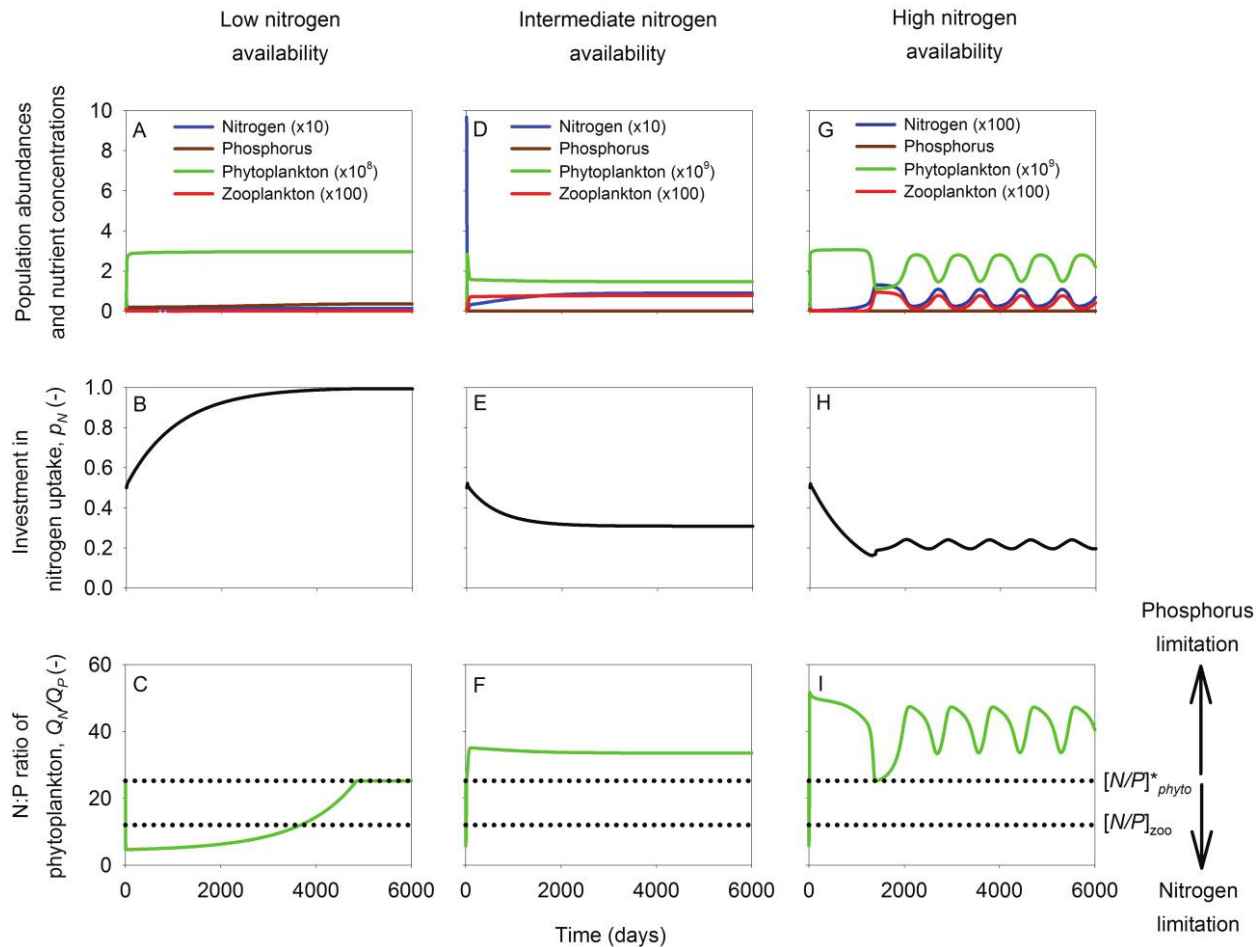
Figure 4: Eco-evolutionary dynamics of phytoplankton-zooplankton interactions with phosphorus-demanding zooplankton ("cladocerans"). The graphs compare three ecosystems, with low (*A–C*), intermediate (*D–F*), and high (*G–I*) nitrogen availability. *A, D, G,* Dynamics of phytoplankton, zooplankton, and dissolved nitrogen and phosphorus concentrations. *B, E, H,* Investment of phytoplankton in nitrogen uptake. *C, F, I,* Cellular N : P ratio of phytoplankton (green line); the dotted horizontal lines indicate the body N : P ratios at which phytoplankton and zooplankton are colimited by nitrogen and phosphorus. Parameter values are the same as in figure 3, with a mildly selective cladoceran as zooplankton ($S = 0.04$).

Nitrogen-Demanding Zooplankton ("Copepods"). The dynamics of a community with nitrogen-demanding zooplankton are strikingly different from those with phosphorus-demanding zooplankton. In both the ecological and eco-evolutionary models, grazing by nitrogen-demanding copepods leads to pronounced phytoplankton-zooplankton oscillations with nitrogen enrichment on ecological timescales (figs. 5, C2). In the ecological model, nitrogen-demanding zooplankton do not become extinct with nitrogen enrichment (not even when T_N is further increased to 2,000 μM; results not shown), because food quality remains sufficiently high (fig. C2). In the eco-evolutionary model, investment of phytoplankton in nitrogen uptake declines slightly with nitrogen enrichment and again shows small-amplitude trait cycles (fig. 5B, 5E, 5H). The

phytoplankton population develops a low cellular N : P ratio, which fluctuates in sync with the phytoplankton-zooplankton oscillations but remains in the nitrogen-limited region most of the time (fig. 5C, 5F, 5I).

Thus, the evolution of N : P stoichiometry in phytoplankton crucially depends on the type of zooplankton present in the community. With phosphorus-demanding cladocerans, evolution selects for phytoplankton with an N : P ratio higher than that of zooplankton (fig. 4F, 4I). In contrast, with nitrogen-demanding copepods, evolution selects for phytoplankton with an N : P ratio lower than that of zooplankton (fig. 5C, 5F, 5I). In both cases, phytoplankton attain a cellular N : P ratio that deviates from the N : P requirements of zooplankton, thus enhancing their fitness through reduction of grazing pressure.
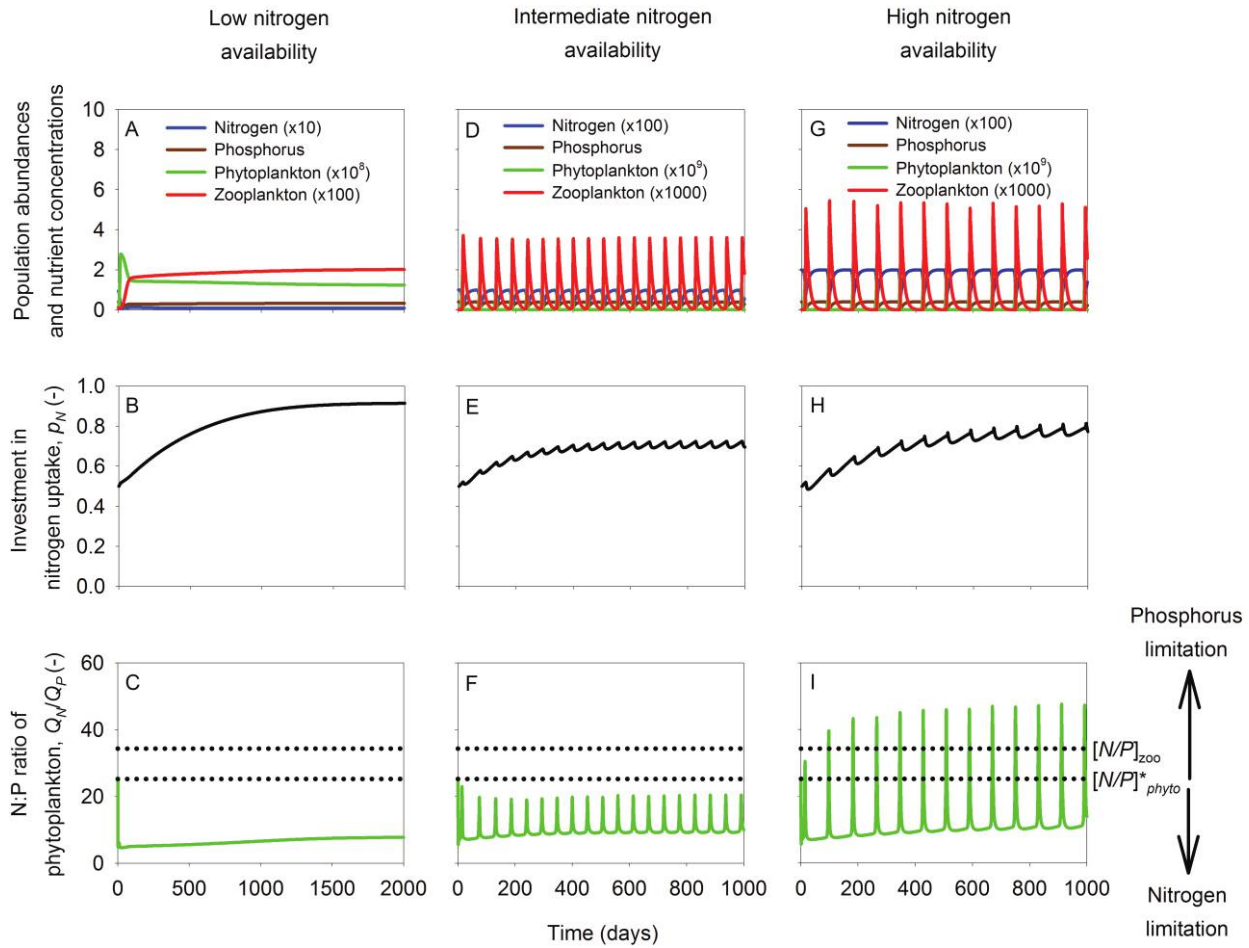
Figure 5: Eco-evolutionary dynamics of phytoplankton-zooplankton interactions with nitrogen-demanding zooplankton ("copepods"). The graphs compare three ecosystems, with low (*A–C*), intermediate (*D–F*), and high (*G–I*) nitrogen availability. *A, D, G*, Dynamics of phytoplankton, zooplankton, and dissolved nitrogen and phosphorus concentrations. *B, E, H*, Investment of phytoplankton in nitrogen uptake. *C, F, I*, Cellular N : P ratio of phytoplankton (green line); the dotted horizontal lines indicate the body N : P ratios at which phytoplankton and zooplankton are colimited by nitrogen and phosphorus. Parameter values are the same as in figure 3, with a mildly selective copepod as zooplankton (*S* = 0.04).

Effects of Zooplankton Selectivity

For our analysis of zooplankton selectivity, we apply bifurcation analysis to investigate three model scenarios: one where zooplankton are phosphorus demanding, with low body N : P ratio ("cladocerans"), another where zooplankton are nutritionally balanced, with intermediate body N : P ratio, and a third one where zooplankton are nitrogen demanding, with high body N : P ratio ("copepods"). For consistency, we parameterize all other aspects of the model for copepod zooplankton, such that the three model scenarios differ only in selectivity and body N : P ratio of zooplankton. To limit the number of possible model scenarios, we focus on ecosystems with relatively low total nitrogen and total phosphorus concen-

trations (thereby avoiding oscillations) at a balanced $T_N : T_P$ ratio of 25 : 1.

When zooplankton are phosphorus demanding, low zooplankton selectivity yields an equilibrium with low phytoplankton abundance (fig. 6*A*) and high zooplankton abundance (fig. 6*B*). Phytoplankton evolve a relatively high investment in nitrogen uptake (fig. 6*C*), and because grazing by zooplankton is hardly selective, the phytoplankton N : P ratio converges to its optimum value (fig. 6*D*). Increasing zooplankton selectivity at first results in a slight increase in zooplankton abundance. However, a further increase in selectivity of the phosphorus-demanding zooplankton enables phytoplankton to avoid being grazed by evolving a high N : P ratio, which causes a decreasing zooplankton and an increasing phytoplankton
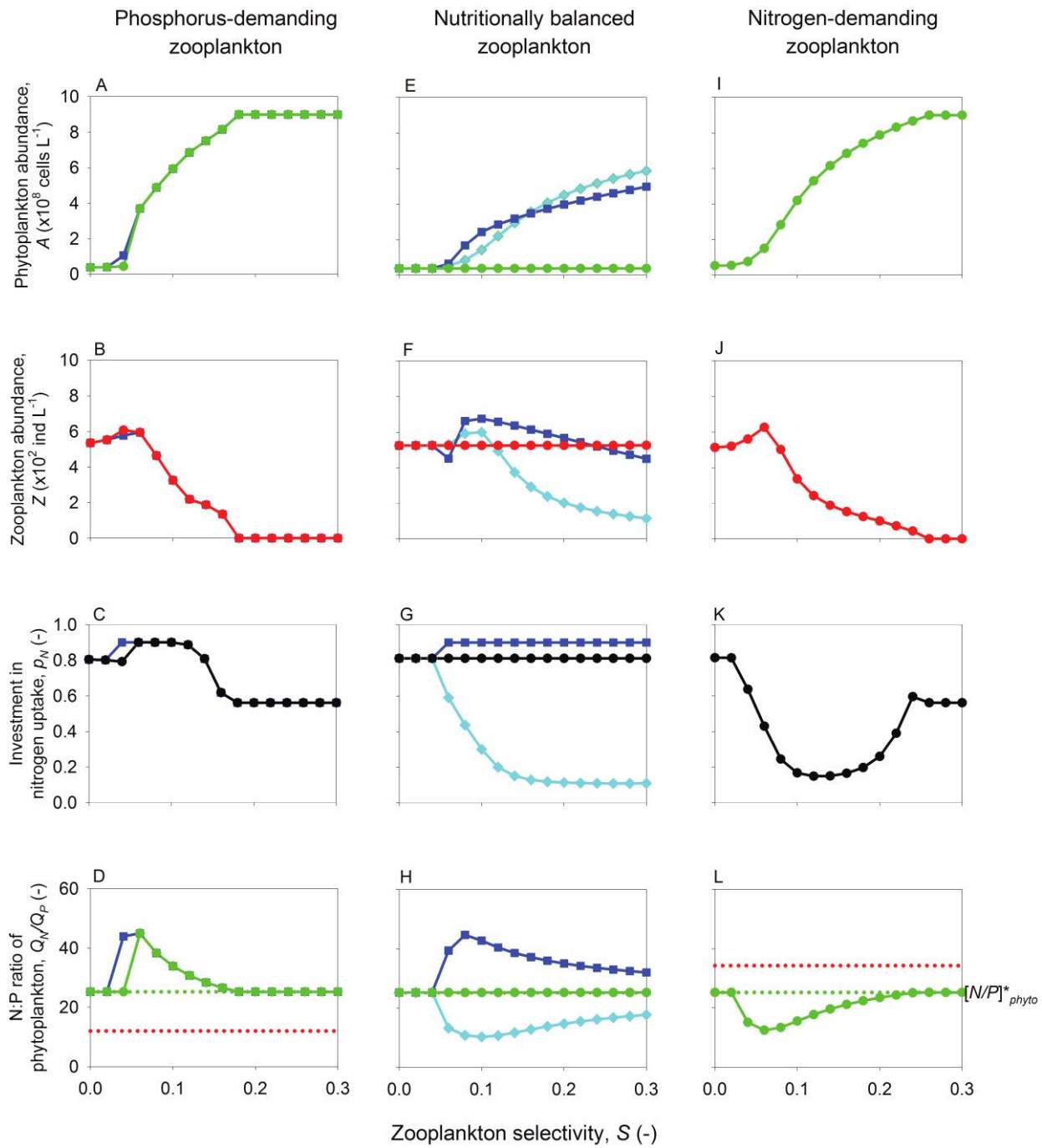
Figure 6: Bifurcation analysis along a gradient of zooplankton selectivity. Bifurcation diagrams are shown for a community with phosphorus-demanding (*A–D*), nutritionally balanced (*E–H*), and nitrogen-demanding (*I–L*) zooplankton. *A, E, I,* Population abundance of phytoplankton. *B, F, J,* Population abundance of zooplankton. *C, G, K,* Investment of phytoplankton in nitrogen uptake. *D, H, L,* Cellular N∶P ratio of phytoplankton (solid lines), as functions of zooplankton selectivity. Multiple solid lines within the same panel represent alternative stable states. The dotted green and red horizontal lines in *D, H,* and *L* indicate the body N∶P ratios at which phytoplankton and zooplankton, respectively, are colimited by nitrogen and phosphorus. Parameter values are given in table 1, with total nitrogen and total phosphorus concentrations of $T_N = 30\ \mu\text{M}$ and $T_P = 1.2\ \mu\text{M}$, respectively, and evolving phytoplankton ($V = 0.1$) investing in nitrogen uptake from $p_{\min} = 0.1$ to $p_{\max} = 0.9$.

E12

abundance. Investment of phytoplankton in nitrogen uptake and their N:P ratio are both highest in the presence of mildly selective zooplankton. Strongly selective zooplankton cannot find sufficient food matching their nutritional requirements, which leads to zooplankton extinction and subsequently allows phytoplankton to evolve to their optimum N:P ratio because they are no longer grazed. For a narrow range of zooplankton selectivities, our model predicts the occurrence of two alternative stable states (ASSs), depending on initial conditions: one ASS characterized by an optimum N:P ratio of phytoplankton and the other ASS characterized by a high N:P ratio of phytoplankton (green and blue lines, respectively, in fig. 6D).

When zooplankton are nutritionally balanced, the scope for occurrence of ASSs is considerably larger (fig. 6E–6H). In particular, the presence of mildly to strongly selective zooplankton yields three ASSs: one characterized by a low N:P ratio of phytoplankton, another by a high N:P ratio, and a third one by the optimum N:P ratio for balanced growth (fig. 6H). A phytoplankton N:P ratio that is either below or above the N:P requirements of zooplankton allows phytoplankton to escape from grazing. The phytoplankton N:P ratio of these two outer equilibria deviates most from the N:P requirements of the zooplankton at an intermediate grazing selectivity. At a higher grazing selectivity, a smaller deviation from the N:P requirements of zooplankton suffices to suppress the rate of grazing upon the phytoplankton population (compare figs. 1 and 6H). Phytoplankton with an optimum N:P ratio are heavily grazed, yet this equilibrium is also locally stable because small deviations in phytoplankton stoichiometry lead to only marginal reductions in grazing rate that do not compensate for the larger reduction of the growth rate.

When zooplankton are nitrogen demanding, increasing zooplankton selectivity again drives an increase in phytoplankton abundance (fig. 6I) and a decrease in zooplankton abundance that eventually leads to zooplankton extinction (fig. 6J). Investment of phytoplankton in nitrogen uptake (fig. 6K) and their N:P ratio (fig. 6L) are both lowest in the presence of mildly selective zooplankton and increase as zooplankton become strongly selective.

Synthesis

Zooplankton species differ in grazing selectivity and nutritional demands. Figure 7A illustrates published data on the body N:P ratio and grazing selectivity of four ecologically relevant zooplankton taxa, where grazing selectivity is estimated qualitatively. Of these four taxa, the freshwater cladoceran *Daphnia* is the least selective, with the lowest body N:P ratio (DeMott 1982; Andersen and Hessen 1991). Conversely, the marine copepod *Acartia* is the most selective, with the highest body N:P ratio (Walve and Larsson 1999;

Rollwagen Bollens and Penry 2003). The cladoceran *Bosmina* and the copepod *Eurytemora* have intermediate nutritional demands (Walve and Larsson 1999), with *Eurytemora* grazing more selectively than *Bosmina* (DeMott 1982; Tackx et al. 2003).

We used our eco-evolutionary model to investigate how the grazing selectivities and body N:P ratios of these zooplankton taxa might affect phytoplankton nutrient limitation and N:P ratios. For this purpose, we calculated the average N:P ratio of phytoplankton as function of the body N:P ratio and grazing selectivity of zooplankton. The results show that the eco-evolutionary dynamics can lead to three ASSs: one characterized by a low N:P ratio of phytoplankton (fig. 7B), another characterized by an optimum N:P ratio of phytoplankton (fig. 7C), and a third one characterized by a high N:P ratio of phytoplankton (fig. 7D). We note the consistency of these three ASSs with the earlier results in figure 6D, 6H, 6L.

Zooplankton that do not select for the nutritional quality of their food do not have a strong effect on the N:P ratio of phytoplankton. Hence, when zooplankton selectivity is low (e.g., *Daphnia*), the model predicts that only one of the ASSs exists, at which the N:P ratio of phytoplankton evolves toward an intermediate value close to their optimum N:P ratio regardless of the body N:P ratio of zooplankton (fig. 7C). When zooplankton are mildly selective and their body N:P ratio is relatively low (e.g., the cladoceran *Bosmina*), the model predicts evolution of phytoplankton with high N:P ratios (fig. 7D). Highly selective zooplankton with an intermediate body N:P ratio (e.g., the copepod *Eurytemora*) may favor a diverse community in which phytoplankton evolve either low, intermediate, or high N:P ratios (fig. 7B–7D). Finally, our model predicts that highly selective zooplankton with a high body N:P ratio, such as the copepod *Acartia*, will favor the evolution of phytoplankton with low N:P ratios (fig. 7B).

Discussion

Our model results generate four basic insights into the eco-evolutionary dynamics of N:P stoichiometry in phytoplankton-zooplankton interactions. First, evolution of the nutrient uptake kinetics of phytoplankton favors convergence to an optimum N:P ratio at which phytoplankton growth becomes colimited by nitrogen and phosphorus if zooplankton are absent, but it can lead to substantial deviations from this optimum N:P ratio when zooplankton are present in the environment. Second, nitrogen enrichment may cause a collapse of phosphorus-demanding zooplankton, but they can be rescued from extinction through eco-evolutionary adaptation of their phytoplankton prey. Third, interspecific variation in nutritional demands of zooplankton has major effects on the N:P ratio of phytoplankton. Fourth, our model predicts the occurrence of ASSs in the N:P stoichiometry of phytoplank-
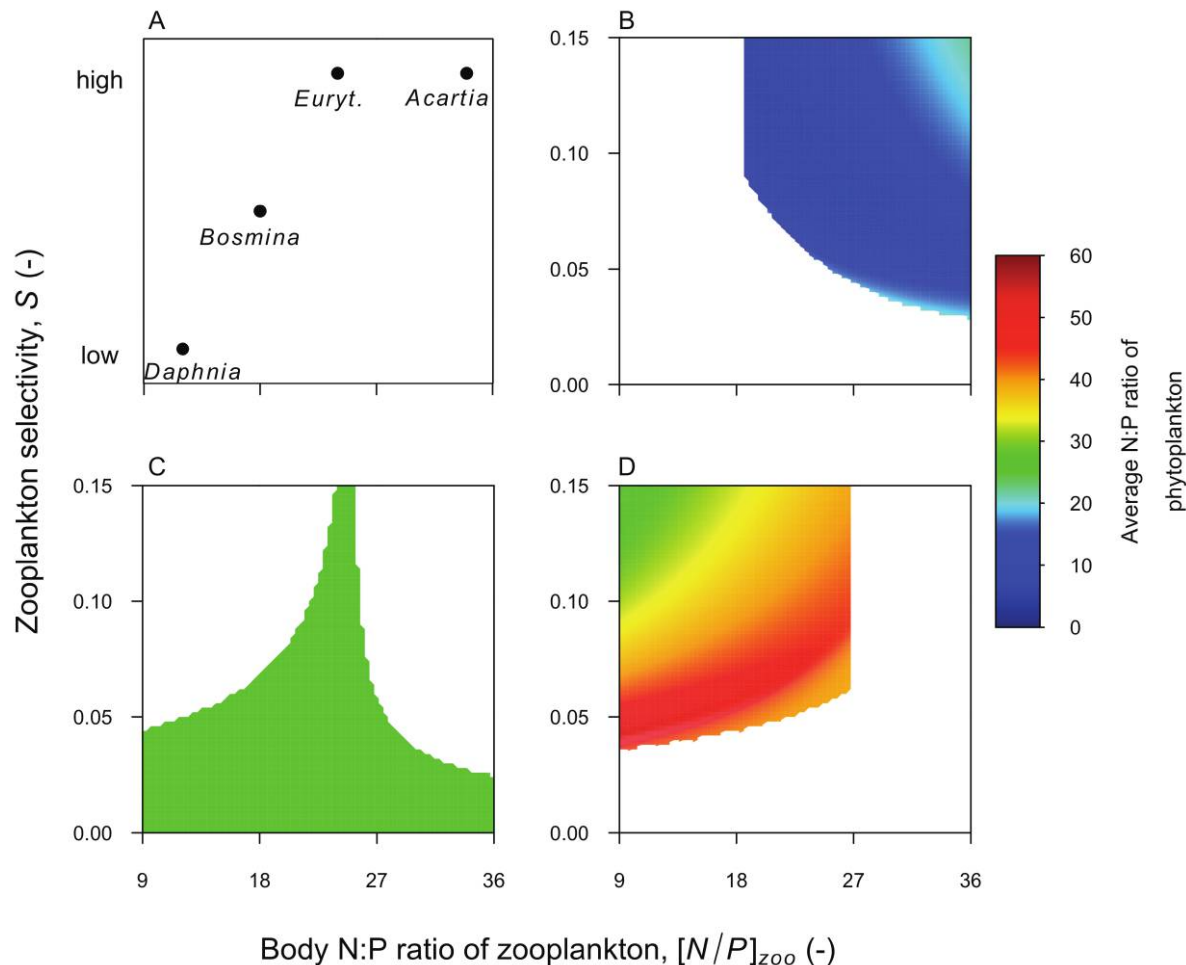
Figure 7: Effect of body N : P ratio and grazing selectivity of zooplankton on the N : P ratio of phytoplankton. *A*, Body N : P ratio and grazing selectivity of four ecologically relevant zooplankton taxa; Euryt. = *Eurytemora*. *B–D*, Alternative stable states with low (*B*), optimum (*C*), and high (*D*) N : P ratios of phytoplankton predicted as functions of the body N : P ratio and grazing selectivity of zooplankton. Parameter values used in *B–D* are the same as in figure 6.

ton if they are grazed by nutritionally balanced zooplankton. Below we discuss these four insights.

Is Colimitation by Nitrogen and Phosphorus an Evolutionarily Stable Strategy?

In the absence of zooplankton, our model predicts that evolution of nutrient uptake kinetics drives the elemental stoichiometry of phytoplankton toward an optimum N : P ratio at which their specific growth rate is equally limited by nitrogen and phosphorus (fig. 3*C*, 3*F*, 3*I*). Thus, in the absence of zooplankton, colimitation of phytoplankton by nitrogen and phosphorus is an evolutionarily stable strategy (sensu Maynard Smith and Price 1973). This is a classic result, in agreement with earlier model analyses of optimal uptake of two essential nutrients (Tilman 1982; Klausmeier et al. 2007).

When zooplankton are present, however, evolution of nutrient uptake may steer the N : P ratio of phytoplankton away from this optimum value (figs. 4–7). The largest deviations from the optimum N : P ratio of phytoplankton occur when zooplankton are mildly selective (fig. 6*D*, 6*L*). Specifically, phosphorus-demanding zooplankton favor the evolution of phytoplankton with a higher N : P ratio, which leads to severe phosphorus limitation (fig. 4). Conversely, nitrogen-demanding zooplankton favor the evolution of phytoplankton with a lower N : P ratio, which leads to severe nitrogen limitation (fig. 5). Both evolutionary strategies result from selection against grazing, which acts to minimize the grazing pressure on phytoplankton. These findings can be interpreted as an example of a competition-predation trade-off (Armstrong 1979; Holt et al. 1994; Leibold 1996; Chase et al. 2002; Křivan 2003; Yoshida et al. 2003), emerging from the

balance between selection for growth and selection against grazing.

Our eco-evolutionary model assumes that phytoplankton adapt their traits to increase their fitness (see eqq. [12] and [13]), which can potentially lead to divergence and coexistence of phenotypes on evolutionary timescales by a process called evolutionary branching (Geritz et al. 1998). We used pairwise invasibility plots to evaluate whether our model can produce evolutionary branching and found that investment in nitrogen uptake converges to evolutionarily stable equilibria (results not shown). Hence, these findings rule out the possibility of evolutionary branching from a single phytoplankton phenotype toward multiple phenotypes with different N:P stoichiometries.

Zooplankton Collapse and Their Eco-Evolutionary Rescue

An interesting observation is that phosphorus-demanding zooplankton populations may disappear with nitrogen enrichment in our ecological model (fig. C1) but not in our eco-evolutionary model (fig. 4).

In our ecological model, nitrogen enrichment leads to phytoplankton with high N:P ratios, which are of too-low food quality for phosphorus-demanding zooplankton. Hence, phosphorus-demanding zooplankton are predicted to disappear. This model prediction is akin to the "paradox of energy enrichment" in the model of Loladze et al. (2000), where enrichment with light energy increases the C:P ratio of phytoplankton and thereby reduces the food quality for phosphorus-demanding zooplankton to such an extent that they become extinct. The predictions of Loladze et al. (2000) are supported by experiments of Urabe and Sterner (1996), where increasing light levels enhanced primary production of the green alga *Scenedesmus* but also increased their C:P ratio, which led to strongly reduced growth of *Daphnia* because of the low quality of their algal food. Our results imply that nitrogen enrichment may lead to a similar collapse of phosphorus-demanding zooplankton, which may have considerable practical consequences in view of the current rise in N:P ratios in many lakes and coastal waters due to effective measures to reduce phosphorus loads but a global increase of nitrogen fertilizers (Grizzetti et al. 2012; Glibert et al. 2014; Burson et al. 2016).

In our eco-evolutionary model, phytoplankton in nitrogen-rich environments also increase their N:P ratio when grazed by phosphorus-demanding zooplankton, which leads to a decline of the zooplankton population. However, the selective pressure upon phytoplankton to develop a high N:P ratio relaxes when zooplankton become rare and the evolutionary dynamics shift from selection against grazing to selection for growth. As a consequence, the nutritional quality of phytoplankton gradually improves as its N:P ratio develops toward a more balanced colimitation by nitrogen and phosphorus. This improved food quality, in turn, enables recovery of the zooplankton population. Hence, our model results provide an interesting example where eco-evolutionary adaptation of the nutritional value of the prey rescues the predator population.

The Contrasting N:P Stoichiometry of Freshwater versus Marine Plankton

Our model predicts that phosphorus-demanding cladocerans select for phytoplankton with intermediate to high N:P ratios, whereas nitrogen-demanding copepods select for phytoplankton with low N:P ratios. Interestingly, cladocerans are particularly widespread in freshwater environments, whereas copepods dominate the zooplankton communities of marine environments. Hence, on the basis of our model findings, we expect that freshwater phytoplankton will tend to have a higher N:P ratio than marine phytoplankton.

These model predictions are consistent with field data. Elser and Hassett (1994) and Sterner et al. (2008) reported that, on average, the N:P ratio of phytoplankton is indeed higher in lakes than in marine sites. Traditionally, it was thought that lakes are more phosphorus limited (Vollenweider 1976; Schindler 1977), whereas marine ecosystems are more nitrogen limited (Blomqvist et al. 2004; Howarth and Marino 2006), which might explain this difference in phytoplankton N:P ratio. However, field data are somewhat contradictory here. Indeed, several reports of phosphorus limitation in various marine ecosystems (Thingstad et al. 1998; Wu et al. 2000; Burson et al. 2016) and widespread colimitation by nitrogen and phosphorus in freshwater ecosystems (Dzialowski et al. 2005; Elser et al. 2007) indicate that differences in nutrient limitation between freshwater and marine ecosystems are less pronounced than previously thought and are strongly site dependent. Moreover, in agreement with our model predictions, field data show that the N:P ratio of freshwater phytoplankton is higher than the body N:P ratio of freshwater zooplankton, whereas the N:P ratio of marine phytoplankton is lower than that of marine zooplankton (Elser and Hassett 1994). Hence, our model results indicate that key differences in the N:P requirements of freshwater cladocerans versus marine copepods may offer an interesting alternative explanation for these large-scale differences in phytoplankton N:P stoichiometry between freshwater and marine ecosystems.

Nutrient recycling by zooplankton is a mechanism that may also affect the N:P ratio of phytoplankton (Elser et al. 1988; Sterner et al. 1992; Elser and Urabe 1999). For example, Elser et al. (1988) and Sterner et al. (1992) reported a whole-lake experiment where cladocerans with a low body N:P ratio were replaced by copepods with a high body N:P ratio. Because copepods retained nitrogen while they recycled excess phosphorus, the environmental N:P ratio decreased, phytoplankton growth shifted from phosphorus to nitro-

gen limitation, and the N : P ratio of phytoplankton declined. Our model results predict that selective grazing by nitrogen-demanding copepods will also favor phytoplankton with low N : P ratios. Hence, nutrient recycling and selective grazing reinforce each other, as they have qualitatively similar effects on the N : P stoichiometry of phytoplankton. An interesting follow-up to our study will be to investigate the relative impact of nutrient recycling and selective grazing on the N : P ratio of phytoplankton, by explicitly quantifying both processes.

Alternative Stable States (ASSs)

In ecological systems, ASSs occur when ecosystems can settle in two or more stable equilibria, depending on the initial conditions (Scheffer et al. 2001; Beisner et al. 2003). Our eco-evolutionary model predicts the occurrence of up to three ASSs, with low, optimum, or high N : P ratio of phytoplankton, depending on the body N : P ratio and grazing selectivity of zooplankton (figs. 6, 7). The divergence of phytoplankton to either a low N : P ratio or a high N : P ratio can be understood as two alternative ways for phytoplankton to avoid grazing by selective zooplankton. The third ASS, with an intermediate phytoplankton N : P ratio, is predicted only when the N : P requirements of zooplankton approach the optimum N : P ratio of the phytoplankton. In this case, the reduction in grazing losses of phytoplankton by slightly evolving away from their optimum N : P ratio is small and does not outweigh the disadvantage of a lower growth rate due to stronger nutrient limitation.

The presence of ASSs implies that phytoplankton can evolve very different N : P ratios, depending on the initial conditions, and that environmental perturbations (e.g., nutrient enrichment) might shift the N : P ratio of phytoplankton from one stable equilibrium to a completely different one. Such catastrophic shifts in N : P stoichiometry of phytoplankton can have a profound impact on aquatic ecosystems, for example, by changing their species composition or altering biogeochemical cycles.

Further Development of Theory and Experiments

Our model is firmly based on previous work on the ecological stoichiometry of plant-herbivore interactions and is parameterized for a well-known system composed of phytoplankton (the green alga *Chlorella*) and two alternative zooplankton types with contrasting nutritional demands (copepods and cladocerans). Thus, the model predictions can be readily tested with a range of experimental approaches. Selection experiments among closely related phytoplankton strains that differ in the traits of interest have proven insightful in earlier studies (Yoshida et al. 2003; Stomp et al. 2004; Kasada et al. 2014; Sandrini et al. 2016) and can also provide a powerful framework to investigate the eco-evolutionary dynamics of variation in N : P stoichiometry during phytoplankton-zooplankton interactions. Furthermore, long-term experiments adopting an experimental evolution approach (Lenski et al. 1991; Collins and Bell 2004; Kawecki et al. 2012) could reveal the potential for evolution to steer the N : P ratio of phytoplankton into different directions. For example, one may perform lab experiments by growing phytoplankton with either copepods with high body N : P or cladocerans with low body N : P and testing whether these different herbivores indeed select for contrasting N : P in phytoplankton.

Yet some model assumptions and predictions need further investigation before the model can be fully embraced. One of the key assumptions of the model is that phytoplankton evolve their investment in nitrogen versus phosphorus uptake, whereas the N : P stoichiometry of zooplankton does not evolve. Although this simplifying assumption facilitates our model analysis, empirical studies show that zooplankton can evolve rapidly in response to the prevailing environmental conditions (Hairston et al. 1999; Carius et al. 2001; Gorokhova et al. 2002) and can adapt to changes in the nutritional quality of phytoplankton (Weider et al. 2005; Lemaire et al. 2012; Declerck et al. 2015). Therefore, an important next step in our model framework would be to consider phytoplankton-zooplankton coevolution, for example, by assuming that zooplankton evolve their N : P ratio in response to changes in phytoplankton N : P ratio.

A further theoretical challenge would be investigation of the implications of mixed diets. Our model assumes that selective zooplankton feed preferentially upon phytoplankton whose N : P ratio aligns closely with their own nutritional requirements. It is conceivable, however, that zooplankton will also meet their nutritional requirements if they graze on a mixture of high-N : P phytoplankton and low-N : P phytoplankton in a balanced way. This might lead to selective pressures on phytoplankton stoichiometry in mixed communities that deviate from our approach.

A key model assumption underlying all this work is that zooplankton can select among phytoplankton with different N : P ratios, either by direct detection of the nutritional quality of their prey or else indirectly by phytoplankton traits that correlate with their N : P stoichiometry. If this assumption does not hold, the model does not apply. Several studies have shown that herbivorous zooplankton species can indeed feed selectively on phytoplankton that match their nutritional requirements. Cowles et al. (1988) measured ingestion rates of nitrogen-demanding adults of the copepod *Acartia tonsa* on mixtures of two types of the marine diatom *Thallassiosira weissflogii* with different C : N ratios and found that they fed more heavily on diatoms with lower C : N ratio. Meunier et al. (2016) added a further layer of complexity to these studies by showing that the body N : P ratio of *A. tonsa* varies among life stages. They found that

young nauplii have a relatively low body N : P ratio and select for phosphorus-rich algae, whereas older copepodite stages with a higher body N : P ratio select for nitrogen-rich algae. Schatz and McCauley (2007) investigated the foraging behavior of the phosphorus-demanding cladoceran *Daphnia pulex* on the freshwater green alga *Chlamydomonas reinhardtii* along a spatial gradient of food quality and found that it preferentially fed in locations where the C : P ratio of its algal prey was lowest.

Although these empirical demonstrations of zooplankton selectivity are compelling, there is also a counterexample. Isari et al. (2013) reported that the copepod *Acartia grani* did not display selective feeding when offered mixtures of phytoplankton prey with different nutrient contents. As pointed out by Meunier et al. (2016), however, the study of Isari et al. (2013) measured selectivity among algae with fairly similar N : P ratios (9.5 vs. 7) but not among algae with divergent N : P ratios, such as nitrogen- and phosphorus-limited algae. Hence, further experimental tests of this critical model assumption with a wider variety of zooplankton and sufficient variation in the N : P stoichiometry of phytoplankton are warranted. Such experimental tests will help to test our key prediction that differences in grazing selectivity and nutritional demands of zooplankton may have a major impact on the N : P stoichiometry of phytoplankton-zooplankton interactions.

Acknowledgments

Literature Cited

Acharya, K., M. Kyle, and J. J. Elser. 2004. Biological stoichiometry of *Daphnia* growth: an ecophysiological test of the growth rate hypothesis. Limnology and Oceanography 49:656–665.

Andersen, T., and D. O. Hessen. 1991. Carbon, nitrogen, and phosphorus content of freshwater zooplankton. Limnology and Oceanography 36:807–814.

Armstrong, R. A. 1979. Prey species replacement along a gradient of nutrient enrichment: a graphical approach. Ecology 60:76–84.

Beisner, B. E., D. T. Haydon, and K. Cuddington. 2003. Alternative stable states in ecology. Frontiers in Ecology and the Environment 1:376–382.

Berggreen, U., B. Hansen, and T. Kiørboe. 1988. Food size spectra, ingestion and growth of the copepod *Acartia tonsa* during development: implications for determination of copepod production. Marine Biology 99:341–352.

Bergström, A., and M. Jansson. 2006. Atmospheric nitrogen deposition has caused nitrogen enrichment and eutrophication of lakes in the Northern Hemisphere. Global Change Biology 12:635–643.

Blomqvist, S., A. Gunnars, and R. Elmgren. 2004. Why the limiting nutrient differs between temperate coastal seas and freshwater lakes: a matter of salt. Limnology and Oceanography 49:2236–2241.

Boersma, M., and J. J. Elser. 2006. Too much of a good thing: on stoichiometrically balanced diets and maximal growth. Ecology 87:1325–1330.

Branco, P., M. Stomp, M. Egas, and J. Huisman. 2010. Evolution of nutrient uptake reveals a trade-off in the ecological stoichiometry of plant-herbivore interactions. American Naturalist 176:E162–E176.

Burson, A., M. Stomp, L. Akil, C. P. D. Brussaard, and J. Huisman. 2016. Unbalanced reduction of nutrient loads has created an offshore gradient from phosphorus to nitrogen limitation in the North Sea. Limnology and Oceanography 61:869–888.

Buskey, E. J. 1997. Behavioral components of feeding selectivity of the heterotrophic dinoflagellate *Protoperidinium pellucidum*. Marine Ecology Progress Series 153:77–89.

Caperon, J., and J. Meyer. 1972. Nitrogen-limited growth of marine phytoplankton—II. Uptake kinetics and their role in nutrient limited growth of phytoplankton. Deep Sea Research 19:619–632.

Carius, H. J., T. J. Little, and D. Ebert. 2001. Genetic variation in a host-parasite association: potential for coevolution and frequency-dependent selection. Evolution 55:1136–1145.

Carroll, S. P., A. P. Hendry, D. N. Reznick, and C. W. Fox. 2007. Evolution on ecological time-scales. Functional Ecology 21:387–393.

Chase, J. M., P. A. Abrams, J. P. Grover, S. Diehl, P. Chesson, R. D. Holt, S. A. Richards, R. Nisbet, and T. J. Case. 2002. The interaction between predation and competition: a review and synthesis. Ecology Letters 5:302–315.

Collins, S., and G. Bell. 2004. Phenotypic consequences of 1,000 generations of selection at elevated CO_2 in a green alga. Nature 431:566–569.

Cortez, M. H. 2011. Comparing the qualitatively different effects rapidly evolving and rapidly induced defences have on predator-prey interactions. Ecology Letters 14:202–209.

Cortez, M. H., and S. P. Ellner. 2010. Understanding rapid evolution in predator-prey interactions using the theory of fast-slow dynamical systems. American Naturalist 176:E109–E127.

Cowles, T. J., R. J. Olson, and S. W. Chisholm. 1988. Food selection by copepods: discrimination on the basis of food quality. Marine Biology 100:41–49.

Declerck, S. A. J., A. R. Malo, S. Diehl, D. Waasdorp, K. D. Lemmen, K. Proios, and S. Papakostas. 2015. Rapid adaptation of herbivore consumers to nutrient limitation: eco-evolutionary feedbacks to population demography and resource control. Ecology Letters 18:553–562.

DeMott, W. R. 1982. Feeding selectivities and relative ingestion rates of *Daphnia* and *Bosmina*. Limnology and Oceanography 27:518–527.

———. 1989. Optimal foraging theory as a predictor of chemically mediated food selection by suspension-feeding copepods. Limnology and Oceanography 34:140–154.

Droop, M. R. 1973. Some thoughts on nutrient limitation in algae. Journal of Phycology 9:264–272.

Ducobu, H., J. Huisman, R. R. Jonker, and L. R. Mur. 1998. Competition between a prochlorophyte and a cyanobacterium under var-

ious phosphorus regimes: comparison with the Droop model. Journal of Phycology 34:467–476.

Dumont, H. J., I. Van de Velde, and S. Dumont. 1975. The dry weight estimate of biomass in a selection of cladocera, copepods and rotifera from the plankton, periphyton and benthos of continental waters. Oecologia 19:75–97.

Dzialowski, A. R., S. Wang, N. Lim, W. W. Spotts, and D. G. Huggins. 2005. Nutrient limitation of phytoplankton growth in central plains reservoirs, USA. Journal of Plankton Research 27:587–595.

Elser, J. J., T. Andersen, J. S. Baron, A. K. Bergström, M. Jansson, M. Kyle, K. R. Nydick, L. Steger, and D. O. Hessen. 2009. Shifts in lake N:P stoichiometry and nutrient limitation driven by atmospheric nitrogen deposition. Science 326:835–837.

Elser, J. J., M. E. S. Bracken, E. E. Cleland, D. S. Gruner, W. S. Harpole, H. Hillebrand, J. T. Ngai, E. W. Seabloom, J. B. Shurin, and J. E. Smith. 2007. Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. Ecology Letters 10:1135–1142.

Elser, J. J., M. M. Elser, N. A. MacKay, and S. R. Carpenter. 1988. Zooplankton-mediated transitions between N- and P-limited algal growth. Limnology and Oceanography 33:1–14.

Elser, J. J., W. F. Fagan, R. F. Denno, D. R. Dobberfuhl, A. Folarin, A. Huberty, S. Interlandi, et al. 2000a. Nutrient constraints in terrestrial and freshwater food webs. Nature 408:578–580.

Elser, J. J., and R. P. Hassett. 1994. A stoichiometric analysis of the zooplankton-phytoplankton interaction in marine and freshwater ecosystems. Nature 370:211–213.

Elser, J. J., M. Kyle, J. Learned, M. L. McCrackin, A. Peace, and L. Steger. 2016. Life on the stoichiometric knife-edge: effects of high and low food C:P ratio on growth, feeding, and respiration in three *Daphnia* species. Inland Waters 6:136–146.

Elser, J. J., R. W. Sterner, E. Gorokhova, W. F. Fagan, T. A. Markow, J. B. Cotner, J. F. Harrison, S. E. Hobbie, G. M. Odell, and L. W. Weider. 2000b. Biological stoichiometry from genes to ecosystems. Ecology Letters 3:540–550.

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

Falkowski, P. G. 2000. Rationalizing elemental ratios in unicellular algae. Journal of Phycology 36:3–6.

Flynn, K. J. 2002. How critical is the critical N:P ratio? Journal of Phycology 38:961–970.

Fussmann, G. F., M. Loreau, and P. A. Abrams. 2007. Eco-evolutionary dynamics of communities and ecosystems. Functional Ecology 21: 465–477.

Geider, R. J., and J. La Roche. 2002. Redfield revisited: variability of C:N:P in marine microalgae and its biochemical basis. European Journal of Phycology 37:1–17.

Geritz, S. A. H., É. Kisdi, G. Meszéna, and J. A. J. Metz. 1998. Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. Evolutionary Ecology 12:35–57.

Glibert, P. M., R. Maranger, D. J. Sobota, and L. Bouwman. 2014. The Haber Bosch–harmful algal bloom (HB-HAB) link. Environmental Research Letters 9:105001. doi:10.1088/1748-9326/9/10/105001.

Gorokhova, E., T. E. Dowling, L. J. Weider, T. J. Crease, and J. J. Elser. 2002. Functional and ecological significance of rDNA intergenic spacer variation in a clonal organism under divergent selection for production rate. Proceedings of the Royal Society B 269:2373–2379.

Grizzetti, B., F. Bouraoui, F., and A. Aloe. 2012. Changes of nitrogen and phosphorus loads to European seas. Global Change Biology 18:769–782.

Grover, J. P. 1991. Resource competition in a variable environment: phytoplankton growing according to the variable-internal-stores model. American Naturalist 138:811–835.

———. 1997. Resource competition. Chapman & Hall, London.

Hairston, N. G., Jr., S. P. Ellner, M. A. Geber, T. Yoshida, and J. A. Fox. 2005. Rapid evolution and the convergence of ecological and evolutionary time. Ecology Letters 8:1114–1127.

Hairston, N. G., Jr., W. Lampert, C. E. Cáceres, C. L. Holtmeier, L. J. Weider, U. Gaedke, J. M. Fischer, J. A. Fox, and D. M. Post. 1999. Rapid evolution revealed by dormant eggs. Nature 401:446.

Hirst, A. G., and T. Kiørboe. 2002. Mortality of marine planktonic copepods: global rates and patterns. Marine Ecology Progress Series 230:195–209.

Holling, C. S. 1959. The components of predation as revealed by a study of small mammal predation of the European pine sawfly. Canadian Entomologist 91:293–320.

Holt, R. D., J. Grover, and D. Tilman. 1994. Simple rules of interspecific dominance in systems with exploitative and apparent competition. American Naturalist 144:741–771.

Howarth, R. W., and R. Marino. 2006. Nitrogen as the limiting nutrient for eutrophication in coastal marine ecosystems: evolving views over three decades. Limnology and Oceanography 51:364–376.

Irwin, A. J., Z. V. Finkel, O. M. E. Schofield, and P. G. Falkowski. 2006. Scaling-up from nutrient physiology to the size-structure of phytoplankton communities. Journal of Plankton Research 28: 459–471.

Isari, S., M. Antó, and E. Saiz. 2013. Copepod foraging on the basis of food nutritional quality: can copepods really choose? PLoS ONE 8(12):e84742. doi:10.1371/journal.pone.0084742.

John, E. H., and K. Davidson. 2001. Prey selectivity and the influence of prey carbon:nitrogen ratio on microflagellate grazing. Journal of Experimental Marine Biology and Ecology 260:93–111.

Kasada, M., M. Yamamichi, and T. Yoshida. 2014. Form of an evolutionary tradeoff affects eco-evolutionary dynamics in a predator-prey system. Proceedings of the National Academy of Sciences of the USA 111:16035–16040.

Kawecki, T. J., R. E. Lenski, D. Ebert, B. Hollis, I. Olivieri, and M. C. Whitlock. 2012. Experimental evolution. Trends in Ecology and Evolution 27:547–560.

Kiørboe, T. 2008. A mechanistic approach to plankton ecology. Princeton University Press, Princeton, NJ.

Kiørboe, T., F. Møhlenberg, and K. Hamburger. 1985. Bioenergetics of the planktonic copepod *Acartia tonsa*: relation between feeding, egg production and respiration, and composition of specific dynamic action. Marine Ecology Progress Series 26:85–97.

Klausmeier, C. A., E. Litchman, T. Daufresne, and S. A. Levin. 2004a. Optimal nitrogen-to-phosphorus stoichiometry of phytoplankton. Nature 429:171–174.

Klausmeier, C. A., E. Litchman, and S. A. Levin. 2004b. Phytoplankton growth and stoichiometry under multiple nutrient limitation. Limnology and Oceanography 49:1463–1470.

———. 2007. A model of flexible uptake of two essential resources. Journal of Theoretical Biology 246:278–289.

Křivan, V. 1996. Optimal foraging and predator-prey dynamics. Theoretical Population Biology 49:265–290.

———. 2003. Competitive co-existence caused by adaptive predators. Evolutionary Ecology Research 5:1163–1182.

Lande, R. 1982. A quantitative genetic theory of life history evolution. Ecology 63:607–615.

Leibold, M. A. 1996. A graphical model of keystone predators in food webs: trophic regulation of abundance, incidence, and diversity patterns in communities. American Naturalist 147:784–812.

Lemaire, V., S. Brusciotti, I. van Gremberghe, W. Vyverman, J. Vanoverbeke, and L. De Meester. 2012. Genotype × genotype interactions between the toxic cyanobacterium *Microcystis* and its grazer, the waterflea *Daphnia*. Evolutionary Applications 5:168–182.

Lenski, R. E., M. R. Rose, S. C. Simpson, and S. C. Tadler. 1991. Long-term experimental evolution in *Escherichia coli*. I. Adaptation and divergence during 2,000 generations. American Naturalist 138:1315–1341.

Loladze, I., and J. J. Elser. 2011. The origins of the Redfield nitrogen-to-phosphorus ratio are in a homoeostatic protein-to-rRNA ratio. Ecology Letters 14:244–250.

Loladze, I., Y. Kuang, and J. J. Elser. 2000. Stoichiometry in producer-grazer systems: linking energy flow with element cycling. Bulletin of Mathematical Biology 62:1137–1162.

Martel, C. M. 2009. Conceptual bases for prey biorecognition and feeding selectivity in the microplanktonic marine phagotroph *Oxyrrhis marina*. Microbial Ecology 57:589–597.

Matthews, B., A. Narwani, S. Hausch, E. Nonaka, H. Peter, M. Yamamichi, K. E. Sullam, et al. 2011. Toward an integration of evolutionary biology and ecosystem science. Ecology Letters 14:690–701.

Matveev, V., L. Matveeva, and G. J. Jones. 1994. Study of the ability of *Daphnia carinata* King to control phytoplankton and resist cyanobacterial toxicity: implications for biomanipulation in Australia. Australian Journal of Marine and Freshwater Research 45:889–904.

Maynard Smith, J., and G. R. Price. 1973. The logic of animal conflict. Nature 246:15–18.

Meunier, C. L., M. Boersma, K. H. Wiltshire, and A. M. Malzahn. 2016. Zooplankton eat what they need: copepod selective feeding and potential consequences for marine systems. Oikos 125:50–58.

Morel, F. M. M. 1987. Kinetics of nutrient uptake and growth in phytoplankton. Journal of Phycology 23:137–150.

Passarge, J., S. Hol, M. Escher, and J. Huisman. 2006. Competition for nutrients and light: stable coexistence, alternative stable states, or competitive exclusion? Ecological Monographs 76:57–72.

Pelletier, F., D. Garant, and A. P. Hendry. 2009. Eco-evolutionary dynamics. Philosophical Transactions of the Royal Society B 364:1483–1489.

Quigg, A., Z. V. Finkel, A. J. Irwin, Y. Rosenthal, T. Ho, J. R. Reinfelder, O. Schofield, F. M. M. Morel, and P. G. Falkowski. 2003. The evolutionary inheritance of elemental stoichiometry in marine phytoplankton. Nature 425:291–294.

Redfield, A. C. 1958. The biological control of chemical factors in the environment. American Scientist 46:205–221.

Rhee, G. Y., and I. J. Gotham. 1980. Optimum N : P ratios and coexistence of planktonic algae. Journal of Phycology 16:486–489.

Rollwagen Bollens, G. C., and D. L. Penry. 2003. Feeding dynamics of *Acartia* spp. copepods in a large, temperate estuary (San Francisco Bay, CA). Marine Ecology Progress Series 257:139–158.

Sandrini, G., X. Ji, J. M. H. Verspagen, R. P. Tann, P. C. Slot, V. M. Luimstra, J. M. Schuurmans, H. C. P. Matthijs, and J. Huisman. 2016. Rapid adaptation of harmful cyanobacteria to rising CO_2. Proceedings of the National Academy of Sciences of the USA 113:9315–9320.

Schatz, G. S., and E. McCauley. 2007. Foraging behavior by *Daphnia* in stoichiometric gradients of food quality. Oecologia 153:1021–1030.

Scheffer, M., S. Carpenter, J. A. Foley, C. Folke, and B. Walker. 2001. Catastrophic shifts in ecosystems. Nature 413:591–596.

Schindler, D. W. 1977. Evolution of phosphorus limitation in lakes. Science 195:260–262.

Schoener, T. W. 2011. The newest synthesis: understanding the interplay of evolutionary and ecological dynamics. Science 331:426–429.

Sommer, U., and H. Stibor. 2002. Copepoda-Cladocera-Tunicata: the role of three major mesozooplankton groups in pelagic food webs. Ecological Research 17:161–174.

Sterner, R. W. 1986. Herbivores' direct and indirect effects on algal populations. Science 231:605–607.

Sterner, R. W., T. Andersen, J. J. Elser, D. O. Hessen, J. M. Wood, E. McCauley, and J. Urabe. 2008. Scale-dependent carbon : nitrogen : phosphorus seston stoichiometry in marine and freshwaters. Limnology and Oceanography 53:1169–1180.

Sterner, R. W., and J. J. Elser. 2002. Ecological stoichiometry. Princeton University Press, Princeton, NJ.

Sterner, R. W., J. J. Elser, and D. O. Hessen. 1992. Stoichiometric relationships among producers, consumers and nutrient cycling in pelagic ecosystems. Biogeochemistry 17:49–67.

Sterner, R. W., and D. O. Hessen. 1994. Algal nutrient limitation and the nutrition of aquatic herbivores. Annual Review of Ecology and Systematics 25:1–29.

Stomp, M., J. Huisman, F. de Jongh, A. J. Veraart, D. Gerla, M. Rijkeboer, B. W. Ibelings, U. I. A. Wollenzien, and L. J. Stal. 2004. Adaptive divergence in pigment composition promotes phytoplankton biodiversity. Nature 432:104–107.

Tackx, M. L. M., P. J. M. Herman, S. Gasparini, X. Irigoien, R. Billiones, and M. H. Daro. 2003. Selective feeding of *Eurytemora affinis* (Copepoda, Calanoida) in temperate estuaries: model and field observations. Estuarine, Coastal and Shelf Science 56:305–311.

Thingstad, T. F., U. L. Zweifel, and F. Rassoulzadegan. 1998. P limitation of heterotrophic bacteria and phytoplankton in the northwest Mediterranean. Limnology and Oceanography 43:88–94.

Thompson, J. N. 1998. Rapid evolution as an ecological process. Trends in Ecology and Evolution 13:329–332.

Tilman, D. 1982. Resource competition and community structure. Princeton University Press, Princeton, NJ.

Tischner, R., and H. Lorenzen. 1979. Nitrate uptake and nitrate reduction in synchronous *Chlorella*. Planta 146:287–292.

Urabe, J., and R. W. Sterner. 1996. Regulation of herbivore growth by the balance of light and nutrients. Proceedings of the National Academy of Sciences of the USA 93:8465–8469.

Vollenweider, R. A. 1976. Advances in defining critical loading levels for phosphorus in lake eutrophication. Memorie dell'Istituto Italiano di Idrobiologia 33:53–83.

von Liebig, J. 1840. Die organische chemie in ihrer anwendung auf agrikultur und physiologie. Friedrich Vieweg, Braunschweig.

Walve, J., and U. Larsson. 1999. Carbon, nitrogen and phosphorus stoichiometry of crustacean zooplankton in the Baltic Sea: implications for nutrient recycling. Journal of Plankton Research 21:2309–2321.

Weider, L. J., W. Makino, K. Acharya, K. L. Glenn, M. Kyle, J. Urabe, and J. J. Elser. 2005. Genotype × environment interactions, stoichiometric food quality effects, and clonal coexistence in *Daphnia pulex*. Oecologia 143:537–547.

Wetzel, R. G. 2001. Limnology. 3rd ed. Academic Press, San Diego, CA.

Wu, J., W. Sunda, E. A. Boyle, and D. M. Karl. 2000. Phosphate depletion in the western North Atlantic Ocean. Science 289:759–762.

Yoshida, T., N. G. Hairston Jr., and S. P. Ellner. 2004. Evolutionary trade-off between defence against grazing and competitive ability in a simple unicellular alga, *Chlorella vulgaris*. Proceedings of the Royal Society B 271:1947–1953.

Yoshida, T., L. E. Jones, S. P. Ellner, G. F. Fussmann, and N. G. Hairston Jr. 2003. Rapid evolution drives ecological dynamics in a predator-prey system. Nature 424:303–306.
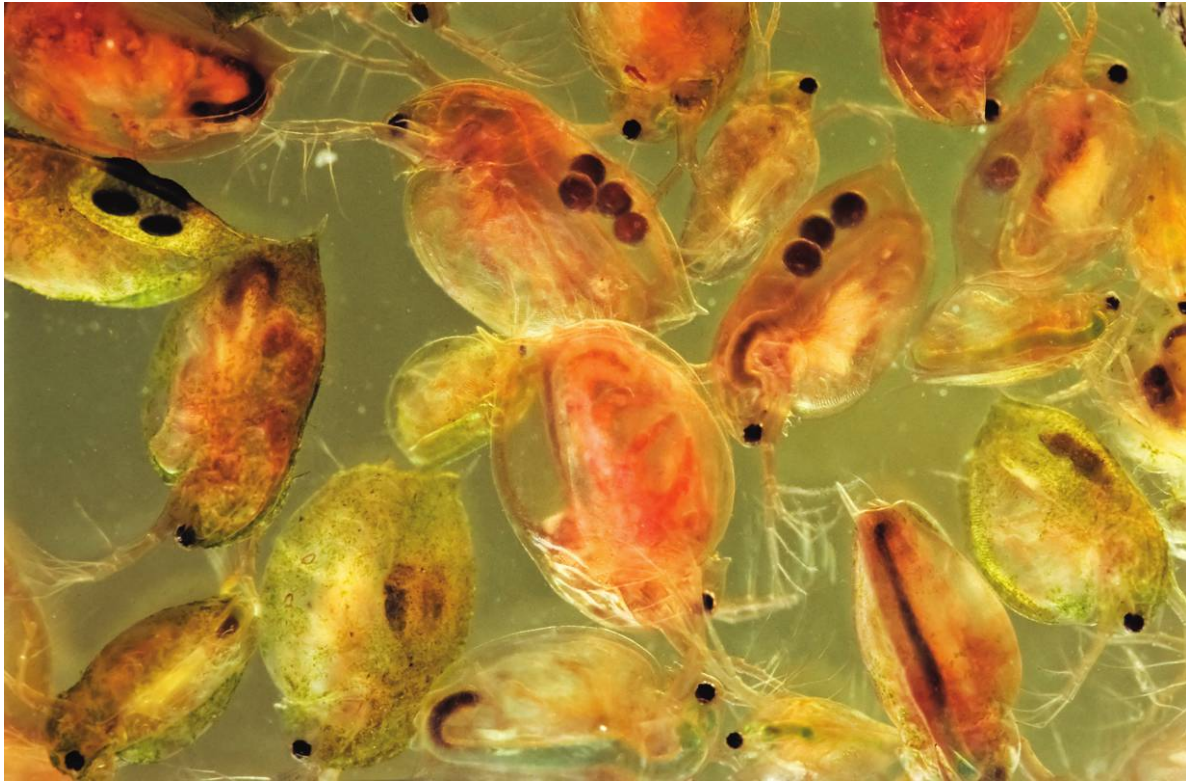
Daphnia sp. feeding on freshwater phytoplankton. Our model predicts that selective grazing by these phosphorus-demanding cladocerans will favor dominance of phytoplankton with high N : P ratios. Image © Jan van Arkel, IBED/University of Amsterdam.