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# Why Do Phytoplankton Evolve Large Size in Response to Grazing?

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**ABSTRACT:** Phytoplankton are among the smallest primary producers on Earth, yet they display a wide range of cell sizes. Typically, small phytoplankton species are stronger nutrient competitors than large phytoplankton species, but they are also more easily grazed. In contrast, evolution of large phytoplankton is often explained as a physical defense against grazing. Conceptually, this explanation is problematic, however, because zooplankton can coevolve larger size to counter this size-dependent escape from grazing. Here, we hypothesize that there is another advantage for the evolution of large phytoplankton size not so readily overcome: larger phytoplankton often provide lower nutritional quality for zooplankton. We investigate this hypothesis by analyzing an eco-evolutionary model that combines the ecological stoichiometry of phytoplankton-zooplankton interactions with coevolution of phytoplankton and zooplankton size. In our model, evolution of cell size modifies the nutrient uptake kinetics of phytoplankton according to known allometric relationships, which in turn affect the nutritional quality of phytoplankton. With this size-based mechanism, the model predicts that low grazing pressure or nonselective grazing by zooplankton favors evolution of small phytoplankton cells of high nutritional quality. In contrast, selective grazing for nutritious food favors evolution of large phytoplankton of low nutritional quality, which are preyed on by medium- to large-sized zooplankton. This size-dependent change in food quality may explain the commonly observed shift from dominance by small picophytoplankton in oligotrophic waters with low grazing pressure to large phytoplankton species in nutrient-rich waters with high grazing pressure.

**Keywords:** cell size, competition-predation trade-off, eco-evolutionary dynamics, ecological stoichiometry, nutritional quality, phytoplankton-zooplankton interactions.

## Introduction

Phytoplankton control almost half of the global primary production (Field et al. 1998; Falkowski and Raven 2007). Although small compared with terrestrial primary producers, phytoplankton display a wide variation in cell size spanning three orders of magnitude (Sieburth et al. 1978; Beardall et al. 2009). Presumably, such wide variation in cell size evolved because larger or smaller phytoplankton size maximizes fitness under different environmental conditions (Finkel et al. 2010). Typically, small phytoplankton are better competitors for nutrients (Litchman et al. 2007; Edwards et al. 2011; Burson et al. 2018), which is consistent with the common observation that small picophytoplankton dominate the oligotrophic waters of subtropical oceans (Agawin et al. 2000; Li 2002). The key question, then, is why should phytoplankton evolve large sizes?

Perhaps the most common answer centers on grazing. Specifically, cell size establishes a classic trade-off between competitive ability and vulnerability to grazing (Armstrong 1979, 1994; Holt et al. 1994; Leibold 1996; Chase et al. 2002). Small phytoplankton compete so well for nutrients because they have high surface area-to-volume ratios (maximizing nutrient uptake across the cell surface) and thin diffusion boundary layers (Grover 1989; Kjørboe 1993; Raven 1998). In contrast, large phytoplankton are weaker competitors for nutrients but may be less vulnerable to grazing (Berggreen et al. 1988; Reynolds 2006; Chen and Liu 2010). At least in ecological terms (i.e., without consideration of evolution), this trade-off implies that either small or large phytoplankton become dominant, depending on environmental conditions. In particular, small phytoplankton cells tend to dominate in oligotrophic waters with low zooplankton abundances, whereas large but less vulnerable phytoplankton dominate in nutrient-rich environments (Armstrong 1994; Li 2002; Irigoien et al. 2004; Marañón 2015).

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From an evolutionary perspective, however, the occurrence of large phytoplankton poses a challenging conundrum. While large phytoplankton can physically hinder grazing (Gliwicz and Lampert 1990; Irigoien et al. 2005), zooplankton can coevolve with phytoplankton size (Jiang et al. 2005; Sauterey et al. 2017). If zooplankton evolve larger body size, they may reduce or eliminate the size-dependent physical defense of their prey. Thus, coevolution of zooplankton size can enhance the vulnerability of large phytoplankton to grazing and potentially suppress their populations. Despite these caveats, large phytoplankton abound. Therefore, the question remains: How can phytoplankton take advantage of large cell size to reduce grazing pressure when zooplankton size coevolves?

We propose that the evolutionary advantage of large phytoplankton arises from a lower nutritional quality of large phytoplankton cells. Our proposition stems from two observations. First, large phytoplankton tend to have a lower nutrient content per unit biovolume (i.e., a lower nutritional quality) than small phytoplankton (Shuter 1978; Kiørboe 1993; Sunda and Hardison 2010). Second, zooplankton can graze selectively on nutritious phytoplankton (Cowles et al. 1988; Buskey 1997; Schatz and McCauley 2007; Meunier et al. 2016). Such selective grazing will favor dominance by phytoplankton of low nutritional quality (Grover 1995; Branco et al. 2010, 2018). Combining these two observations, large phytoplankton might evolve because their low nutritional quality reduces their palatability to selective zooplankton and thereby alleviates their grazing pressure. Yet large phytoplankton remain inferior competitors for nutrients. Thus, cell size may still enable a competition-predation trade-off between competitive ability and grazing risk but via low nutritional quality rather than enhanced physical defense of large cells. Is such defense based on low nutritional quality feasible and evolutionarily stable? Could it explain persistence of large phytoplankton over evolutionary time?

Here, we test this eco-evolutionary hypothesis with a model based on ecological stoichiometry. Our approach assumes that phytoplankton may vary plastically in their nutrient composition (Droop 1973; Sterner and Elser 2002; Branco et al. 2018) and that nutritional quality of phytoplankton decreases with cell size. With such an eco-evolutionary and stoichiometrically explicit model, we investigate the evolutionarily optimal cell size of phytoplankton in the absence versus presence of coevolving zooplankton along a gradient of nutrient enrichment. The model shows that phytoplankton evolve the largest cell size (but the poorest food quality) in nutrient-rich environments with coevolving zooplankton that strongly select for food of high nutritional quality. Thus, a size-based escape from grazing through low nutritional quality may indeed contribute to the evolution of large phytoplankton.

## The Model

### Model Overview

Our model considers a simple community, with one limiting nutrient and several phytoplankton and zooplankton species. Phytoplankton species compete for the limiting nutrient according to a variable-internal-stores model (Droop 1973; Grover 1991*b*), which has been widely tested in phytoplankton competition experiments (Grover 1991*a*; Ducobu et al. 1998; Passarge et al. 2006). Zooplankton species consume phytoplankton at a grazing rate that depends on both cell size and nutritional quality of phytoplankton.

The cell size of phytoplankton is a central trait that influences phytoplankton-zooplankton interactions. We assume that cell size evolves and determines the nutrient uptake kinetics (Litchman et al. 2007; Edwards et al. 2012), maximum specific growth rate (Banse 1976; Chisholm 1992; Savage et al. 2004), and susceptibility to grazing of phytoplankton (Kiørboe 2008). Cell size thus establishes a multi-dimensional trade-off, where small phytoplankton tend to grow and acquire nutrients faster than large phytoplankton but also offer more attractive food items for zooplankton. We assume that the body size of zooplankton also evolves. Their size is selected to maximize feeding rate on phytoplankton (i.e., to optimize size-based clearance rate and handling time). Hence, phytoplankton and zooplankton populations coevolve because they can adapt to changes in each other's body size.

We chose nitrogen as currency for the nutritional quality of phytoplankton. Nitrogen is an essential element in phytoplankton and zooplankton metabolism and an important limiting nutrient in many natural waters (Vitousek and Howarth 1991; Elser et al. 2007). The model is based on known allometric relationships for the nitrogen uptake kinetics of phytoplankton (Edwards et al. 2012) and nitrogen requirements of zooplankton (Andersen and Hessen 1991; Walve and Larsson 1999). Model variables, biological rates, and parameters are listed in table 1.

### Phytoplankton Dynamics

Our model assumes that the cellular nutrient content of phytoplankton species  $i$ ,  $Q_i$ , increases due to nutrient uptake and declines due to dilution by growth (Droop 1973):

$$\frac{dQ_i}{dt} = f_i - \mu_{P,i}Q_i, \quad (1)$$

where  $f_i$  is the specific nutrient uptake rate and  $\mu_{P,i}$  is the specific growth rate of phytoplankton species  $i$ .

The specific nutrient uptake rate of a phytoplankton species is a function of the available nutrient concentration,  $N$ , and of its cellular nutrient content  $Q_i$  (Morel 1987; Ducobu et al. 1998):

Table 1: Model variables, biological rates, and parameter values

Symbol	Definition	Value	Units	Source(s)
<b>Variables:</b>				
$N$	Nutrient concentration	...	$\mu\text{M}$	...
$P_i$	Population abundance of phytoplankton species $i$	...	cells $\text{L}^{-1}$	...
$Z_j$	Population abundance of zooplankton species $j$	...	ind $\text{L}^{-1}$	...
$Q_i$	Nutrient content of phytoplankton species $i$	...	fmol cell $^{-1}$	...
$q_j$	Nutrient content of zooplankton species $j$	...	$\mu\text{mol ind}^{-1}$	...
$x_i$	Cell size (diameter) of phytoplankton species $i$	...	$\mu\text{m}$	...
$y_j$	Body size (diameter) of zooplankton species $j$	...	$\mu\text{m}$	...
<b>Environmental parameter:</b>				
$T$	Total amount of nutrient in the ecosystem	1–200	$\mu\text{M}$	Wetzel 2001
<b>Biological rates of phytoplankton:</b>				
$f_i$	Specific nutrient uptake rate of phytoplankton species $i$	...	fmol cell $^{-1}$ day $^{-1}$	...
$\mu_{P,i}$	Specific growth rate of phytoplankton species $i$	...	day $^{-1}$	...
<b>Biological rates of zooplankton:</b>				
$e_j$	Clearance rate of zooplankton species $j$	...	$\text{L ind}^{-1}$ day $^{-1}$	...
$g_j$	Grazing rate of zooplankton species $j$ on phytoplankton species $i$	...	cells ind $^{-1}$ day $^{-1}$	...
$\mu_{Z,j}$	Specific growth rate of zooplankton species $j$	...	day $^{-1}$	...
<b>Phytoplankton parameters:</b>				
$f_{\text{max},i}$	Maximum nutrient uptake rate of phytoplankton species $i$	$5.88x_i^{2.46}$	fmol cell $^{-1}$ day $^{-1}$	Edwards et al. 2012 <sup>a</sup>
$K_{N,i}$	Half-saturation constant for nutrient uptake of phytoplankton species $i$	$.2x_i^{.99}$	$\mu\text{M}$	Edwards et al. 2012 <sup>a</sup>
$Q_{\text{min},i}$	Minimum nutrient content of phytoplankton species $i$	$.58x_i^{2.52}$	fmol cell $^{-1}$	Edwards et al. 2012 <sup>a</sup>
$Q_{\text{max},i}$	Maximum nutrient content of phytoplankton species $i$	$2.1x_i^{2.55}$	fmol cell $^{-1}$	Montagnes and Franklin 2001; Irwin et al. 2006
$\mu_{\text{max},i}$	Maximum specific growth rate of phytoplankton species $i$	$3x_i^{-.75}$	day $^{-1}$	Banase 1976; Savage et al. 2004
$d_i$	Specific mortality rate of phytoplankton species $i$	.1	day $^{-1}$	Sterner 1986
$V_p$	Additive genetic variance of phytoplankton size	.001	...	...

Zooplankton parameters:

$c_c$	Proportionality constant for clearance rate of zooplankton	$1.5 \times 10^{-11}$	$L \text{ ind}^{-1} \text{ day}^{-1} \mu\text{m}^{-3}$	Berggreen et al. 1988
$x_{\text{prey},j}$	Phytoplankton cell size preferred by zooplankton species $j$	$y_j/40$	$\mu\text{m}$	Berggreen et al. 1988 <sup>b</sup>
$\sigma_\alpha^2$	Variance of size preference of zooplankton	.5	...	...
$c_h$	Proportionality constant for handling time of phytoplankton prey by zooplankton	.005	$\text{ind day cell}^{-1}$	Turchin 2003; Saiz and Calbet 2007; Kjørboe 2008 <sup>c</sup>
$b_p$	Allometric increase of handling time with phytoplankton size	3	...	Kjørboe 2008 <sup>c</sup>
$b_z$	Allometric decrease of handling time with zooplankton size	2.11	...	Saiz and Calbet 2007 <sup>c</sup>
$q_{\text{min},j}$	Minimum nutrient content of zooplankton species $j$	$.05y_j^3$	$\text{fmol ind}^{-1}$	Andersen and Hessen 1991; Walve and Larsson 1999; Uye 1982
$q_{\text{max},j}$	Maximum nutrient content of zooplankton species $j$	$.075y_j^3$	$\text{fmol ind}^{-1}$	Andersen and Hessen 1991; Walve and Larsson 1999; Uye 1982
$\mu_{\text{max},Z,j}$	Maximum specific growth rate of zooplankton species $j$	.4	$\text{day}^{-1}$	Berggreen et al. 1988
$m_j$	Specific mortality rate of zooplankton species $j$	.1	$\text{day}^{-1}$	Hirst and Kjørboe 2002
$S_j$	Selectivity of zooplankton species $j$	0–40	$\mu\text{m}^3 \text{fmol}^{-1}$	...
$V_Z$	Additive genetic variance of zooplankton size	.01	...	...

Note: Unless otherwise stated, numerical simulations consider a community with the following initial conditions:  $N = T - PQ - Zq$ ,  $P = 10^7$  cells  $L^{-1}$ ,  $Q = Q_{\text{min}}$ ,  $Z = 10$  ind  $L^{-1}$ ,  $q = q_{\text{min}}$ ,  $x = 2 \mu\text{m}$ , and  $y = 80 \mu\text{m}$ . ind = individuals.

<sup>a</sup> Edwards et al. (2012) report allometric relationships on the basis of cell volume ( $V_j$ ), which we converted to cell size ( $x_j$ ) assuming cells had a spherical shape, i.e.,  $V_j = \pi x_j^3 / 6$ .

<sup>b</sup> We assume that the optimal cell size of phytoplankton prey is one-fortieth of the body size of zooplankton. This assumption is based on the food size spectra measured by Berggreen et al. (1988), where the cell size of phytoplankton experiencing the highest grazing rate is 0.025 times smaller than the body size of *Acartia tonsa* (Berggreen et al. 1988).

<sup>c</sup> Following Turchin (2003), we calculate the handling time of zooplankton as the inverse of their maximum grazing rate. We assume that maximum grazing rate increases allometrically with body weight of zooplankton (Saiz and Calbet 2007) and decreases linearly with phytoplankton biovolume (Kjørboe 2008). To obtain the proportionality constant  $c_h$ , we further assume that carbon contents of phytoplankton and zooplankton are 0.24 and 0.12  $\text{pg } \mu\text{m}^{-3}$ , respectively (Verity et al. 1992; Hansen et al. 1997).

$$f_i = f_{\max,i} \left( \frac{N}{N + K_{N,i}} \right) \left( \frac{Q_{\max,i} - Q_i}{Q_{\max,i} - Q_{\min,i}} \right), \quad (2)$$

where  $f_{\max,i}$  is the maximum nutrient uptake rate of phytoplankton species  $i$ ,  $K_{N,i}$  is its half-saturation constant, and  $Q_{\min,i}$  and  $Q_{\max,i}$  are its minimum and maximum cellular nutrient contents, respectively. Nutrient uptake increases with nutrient availability according to Michaelis-Menten kinetics (first term in parentheses). Furthermore, the nutrient uptake rate of phytoplankton decreases linearly with its cellular nutrient content (i.e.,  $Q_i$  is constrained between  $Q_{\min,i}$  and  $Q_{\max,i}$ ; second term in parentheses). Thus, the nutrient uptake rate is highest when phytoplankton is starved (i.e.,  $Q_i = Q_{\min,i}$ ) and zero when phytoplankton is satiated with nutrients (i.e.,  $Q_i = Q_{\max,i}$ ). These assumptions are well supported empirically (e.g., Morel 1987; Ducobu et al. 1998; Passarge et al. 2006).

The specific growth rate of phytoplankton,  $\mu_{P,i}$ , increases with its cellular nutrient content,  $Q_i$ , according to the Droop equation (Droop 1973; Grover 1991b):

$$\mu_{P,i} = \mu_{\max,i} \left( 1 - \frac{Q_{\min,i}}{Q_i} \right), \quad (3)$$

where  $\mu_{\max,i}$  is the maximum specific growth rate of phytoplankton species  $i$ . Hence, the specific growth rate of phytoplankton species  $i$  becomes zero if its cellular nutrient content has been exhausted to the minimum value  $Q_{\min,i}$  (Sterner and Elser 2002).

The population dynamics of phytoplankton depend on their specific growth rates, background mortality, and grazing rates:

$$\frac{dP_i}{dt} = (\mu_{P,i} - d_i)P_i - \sum_{j=1}^p g_{ij}[\mathbf{P}, \mathbf{X}, \mathbf{Q}, y_j]Z_j, \quad (4)$$

where  $P_i$  is the population abundance of phytoplankton species  $i$ ,  $d_i$  is its specific mortality rate, and  $Z_j$  is the population abundance of zooplankton species  $j$  (with  $p$  zooplankton species in total). The grazing rate of zooplankton species  $j$  on phytoplankton species  $i$ ,  $g_{ij}[\mathbf{P}, \mathbf{X}, \mathbf{Q}, y_j]$ , is a function of the population abundances ( $\mathbf{P}$ ), cell sizes ( $\mathbf{X}$ ), and cellular nutrient contents ( $\mathbf{Q}$ ) of all phytoplankton species in the community (where bold  $\mathbf{P}$ ,  $\mathbf{X}$ , and  $\mathbf{Q}$  represent typical vector notation) and of its own body size ( $y_j$ ).

The nutrient uptake parameters and maximum specific growth rate of phytoplankton all vary with cell size. Specifically, we assume that maximum nutrient uptake rate ( $f_{\max,i}$ ), half-saturation constant ( $K_{N,i}$ ), and minimum ( $Q_{\min,i}$ ) and maximum ( $Q_{\max,i}$ ) nutrient content increase with cell size (diameter)  $x_i$  according to known allometric relationships (Montagnes and Franklin 2001; Irwin et al. 2006; Edwards et al. 2012), with allometric exponents of  $\sim 1$  for  $K_{N,i}$  and  $\sim 2.5$  for  $f_{\max,i}$ ,  $Q_{\min,i}$ , and  $Q_{\max,i}$  (table 1; fig. 1A). Several studies

show that maximum specific growth rate ( $\mu_{\max,i}$ ) decreases with cell size, such that the smallest phytoplankton cells tend to grow fastest (Banse 1976; Savage et al. 2004). Therefore, we model  $\mu_{\max,i}$  as an allometrically decreasing function of cell size  $x_i$  (fig. 1B):

$$\mu_{\max,i} = 3x_i^{-0.75}. \quad (5)$$

### Zooplankton Dynamics

The grazing rate of zooplankton depends on the volume of water in which they search for prey (also known as the clearance rate), their size preference and selectivity for nutritional quality, and the handling time of their prey items.

First, zooplankton have to find their prey. We assume that the clearance rate of zooplankton species  $j$ ,  $\varepsilon_j$ , increases with its body size  $y_j$  (Berggreen et al. 1988):

$$\varepsilon_j = c_\varepsilon y_j^3, \quad (6)$$

where  $c_\varepsilon$  is a proportionality constant.

Second, we assume that zooplankton prefer phytoplankton cells of a suitable size, that is, that are neither too large nor too small in comparison to their own body size (Berggreen et al. 1988). We use a lognormal function to model the size preference  $\alpha_{ij}$  of zooplankton species  $j$  for phytoplankton species  $i$  of size  $x_i$  (fig. 1C):

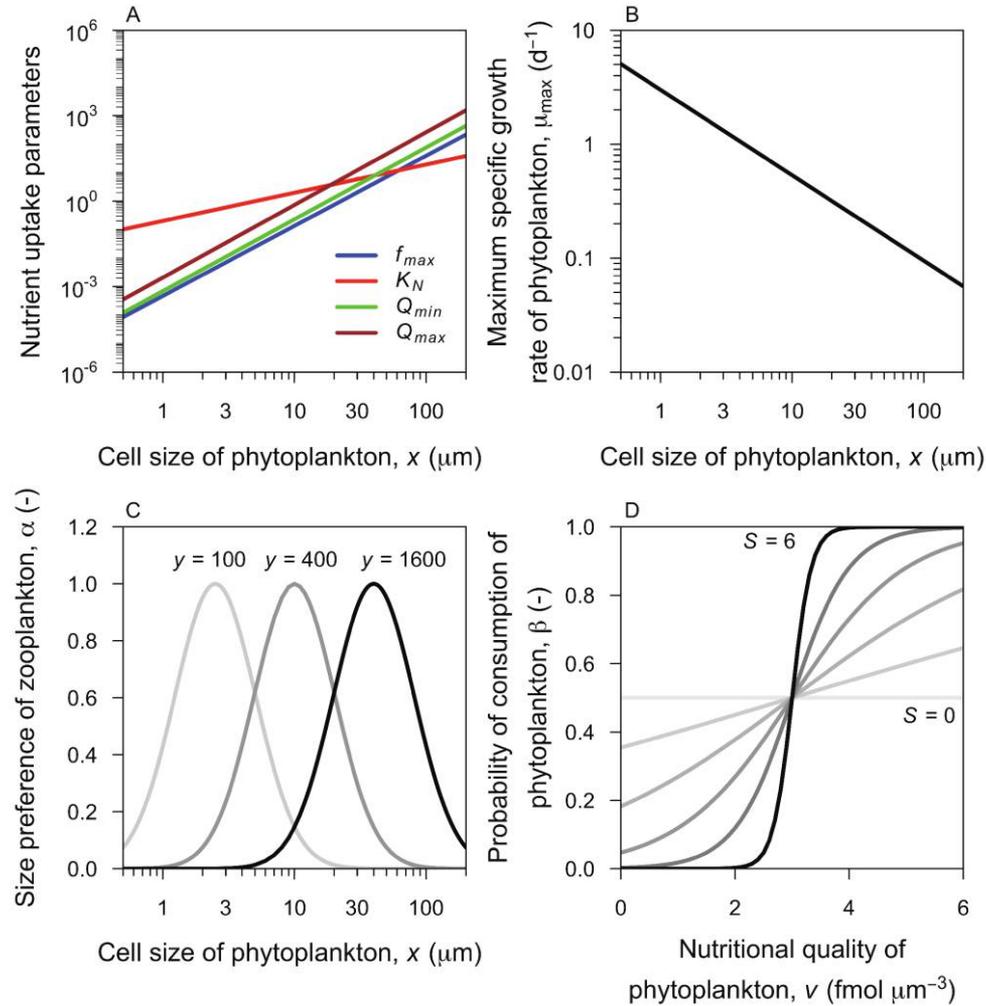
$$\alpha_{ij} = \exp \left( - \frac{(\ln(x_i/x_{\text{pref},j}))^2}{2\sigma_\alpha^2} \right), \quad (7)$$

where  $x_{\text{pref},j}$  is the phytoplankton cell size preferred by zooplankton species  $j$  and  $\sigma_\alpha^2$  represents the width of the lognormal relationship. Specifically, we assume that zooplankton prefer phytoplankton prey that are 40 times smaller than their own size, that is,  $x_{\text{pref},j} = y_j/40$  (based on data on the copepod *Acartia tonsa*; Berggreen et al. 1988).

Third, among the detected prey items of suitable size, zooplankton may select for the most nutritious prey. We define the nutritional quality of a phytoplankton species  $i$ ,  $v_i$ , as its nutrient content ( $Q_i$ ) per unit of biovolume ( $\pi x_i^3/6$ , given diameter  $x_i$ ). For spherical phytoplankton cells, this implies

$$v_i = \frac{Q_i}{\pi x_i^3/6}. \quad (8)$$

Since the minimum and maximum cellular nutrient contents ( $Q_{\min,i}$  and  $Q_{\max,i}$ , respectively) increase with cell size  $x_i$ , with an allometric exponent of  $\sim 2.5$  (table 1; fig. 1A), the nutritional quality of phytoplankton decreases with cell size. To model selective grazing, we assume that the probability  $\beta_{ij}$  that zooplankton species  $j$  will consume phytoplankton



**Figure 1:** Species traits assumed to depend on cell size and nutritional quality of phytoplankton. *A*, Allometric scaling of nutrient uptake parameters with phytoplankton cell size (table 1). The parameters include maximum nutrient uptake rate ( $f_{max}$ , pmol cell<sup>-1</sup> day<sup>-1</sup>), half-saturation constant ( $K_N$ ,  $\mu\text{M}$ ), minimum cellular nutrient content ( $Q_{min}$ , pmol cell<sup>-1</sup>), and maximum cellular nutrient content ( $Q_{max}$ , pmol cell<sup>-1</sup>). *B*, Maximum specific growth rate of phytoplankton,  $\mu_{max}$ , as function of phytoplankton cell size (eq. [5]). *C*, Size preference of zooplankton,  $\alpha$ , as a function of phytoplankton cell size. The curves are derived from equation (7), and each curve corresponds to a different zooplankton size ( $y = 100, 400, \text{ and } 1,600 \mu\text{m}$ ). *D*, Probability of consumption of phytoplankton,  $\beta$ , as function of their nutritional quality. The curves are derived from equation (9), and each curve corresponds to a different selectivity of zooplankton ( $S = 0, 0.2, 0.5, 1, 2, \text{ and } 6 \mu\text{m}^3 \text{ fmol}^{-1}$ ). For the purpose of illustration, this graph assumes that the average nutritional quality of phytoplankton in the community is  $v_{mean} = 3 \text{ fmol } \mu\text{m}^{-3}$ .

species  $i$  depends on the nutritional quality of this focal species  $i$  relative to the other species in the phytoplankton community (Egas et al. 2004; Rueffler et al. 2007; Branco et al. 2010):

$$\beta_{ij} = \frac{1}{1 + \exp(S_j(v_{mean} - v_i))}, \quad (9)$$

where  $S_j$  measures the selectivity of zooplankton species  $j$  (fig. 1D) and  $v_{mean}$  is the average nutritional quality in the phytoplankton community (weighted for the relative abun-

dances of the species). Hence, a low nutritional quality of phytoplankton may offer a defense against grazing provided that zooplankton indeed select nutritious food. Highly selective zooplankton ( $S_j \rightarrow \infty$ ) will switch abruptly to phytoplankton species exceeding average nutritional quality. Conversely, nonselective zooplankton ( $S_j = 0$ ) will consume each phytoplankton species with the same probability  $\beta_{ij} = 0.5$ .

Fourth, zooplankton require time to handle their selected prey. We assume that the handling time,  $h_{ij}$ , required by

zooplankton species  $j$  to consume phytoplankton species  $i$  depends on both phytoplankton size  $x_i$  and zooplankton size  $y_j$ :

$$h_{ij} = c_h \frac{x_i^{b_p}}{y_j^{b_z}}, \quad (10)$$

where  $c_h$  is a proportionality constant,  $b_p$  describes the allometric increase of handling time with phytoplankton size (Kiørboe 2008), and  $b_z$  describes the allometric decrease of handling time with zooplankton size (Hansen et al. 1997; Saiz and Calbet 2007). Hence, phytoplankton may defend themselves by increasing in size (increasing the numerator), but zooplankton may catch up by evolving a larger size as well (increasing the denominator).

The grazing rate of zooplankton species  $j$  on phytoplankton species  $i$ ,  $g_{ij}[\mathbf{P}, \mathbf{X}, \mathbf{Q}, y_j]$ , is modeled as a multispecies type II functional response. It combines the clearance rate ( $\varepsilon_j$ ), size preference ( $\alpha_{ij}$ ), selectivity ( $\beta_{ij}$ ), handling time ( $h_{ij}$ ), and abundance of the focal prey ( $P_i$ ) and other prey species ( $P_k$ ; Holling 1959; Krivan 1996; Branco et al. 2010):

$$g_{ij}[\mathbf{P}, \mathbf{X}, \mathbf{Q}, y_j] = \frac{\varepsilon_j \alpha_{ij} \beta_{ij} P_i}{1 + \sum_{k=1}^n \varepsilon_j \alpha_{kj} \beta_{kj} h_{kj} P_k}. \quad (11)$$

Zooplankton obtain nutrients from their prey. Specifically, the nutrient content of zooplankton individuals of species  $j$ ,  $q_j$ , increases due to nutrients contained in ingested prey and declines due to population growth (again via Droop kinetics; Grover 2003):

$$\frac{dq_j}{dt} = \sum_{i=1}^n g_{ij}[\mathbf{P}, \mathbf{X}, \mathbf{Q}, y_j] Q_i \left( \frac{q_{\max,j} - q}{q_{\max,j} - q_{\min,j}} \right) - \mu_{z,j} q_j, \quad (12)$$

where  $q_{\min,j}$  and  $q_{\max,j}$  are the minimum and maximum nutrient content and  $\mu_{z,j}$  is the specific growth rate of zooplankton species  $j$ . The first term on the right-hand side denotes nutrient intake by zooplankton, which increases with their grazing rate  $g_{ij}[\mathbf{P}, \mathbf{X}, \mathbf{Q}, y_j]$  and the cellular nutrient contents  $Q_i$  of ingested phytoplankton species. The term in parentheses constrains nutrient intake by zooplankton. That is, zooplankton extract all nutrients from ingested prey when they are nutrient starved (i.e.,  $q_j = q_{\min,j}$ ) but do not extract nutrients from ingested prey when they are satiated with nutrients (i.e.,  $q_j = q_{\max,j}$ ). Note that this formulation differs in a subtle way from how we modeled nutrient uptake of phytoplankton. According to equation (2), the nutrient uptake rate  $f_i$  declines when phytoplankton cells become satiated with nutrient. By contrast, zooplankton maintain high grazing rates  $g_{ij}[\mathbf{P}, \mathbf{X}, \mathbf{Q}, y_j]$  when they are satiated, but the surplus nutrient ingested by grazing zooplankton is excreted (see below). This assumption is supported by several empirical studies that show high nutrient excretion rates if zooplankton are satiated with nutrient (Sterner 1990; Elser and Hassett 1994; Elser

and Urabe 1999). We assume that the minimum and maximum nutrient content of zooplankton individuals vary isometrically with body volume (table 1).

The specific growth rate of zooplankton species  $j$  mirrors the Droop equation for phytoplankton (Droop 1973; Grover 1991b; Grover 2003):

$$\mu_{z,j} = \mu_{\max Z,j} \left( 1 - \frac{q_{\min,j}}{q_j} \right), \quad (13)$$

where  $\mu_{\max Z,j}$  is its maximum specific growth rate. This equation indicates that a high nutrient content of zooplankton supports a high specific growth rate, in line with the growth rate hypothesis (Main et al. 1997; Sterner and Elser 2002; Acharya et al. 2004).

The population dynamics of zooplankton species  $j$  is then given by

$$\frac{dZ_j}{dt} = (\mu_{z,j} - m_j) Z_j, \quad (14)$$

where  $m_j$  is its specific mortality rate.

#### Nutrient Dynamics

The nutrient (nitrogen) available in the environment is consumed by phytoplankton and recycled by phytoplankton and zooplankton (Grover 1995, 2003):

$$\begin{aligned} \frac{dN}{dt} = & - \sum_{i=1}^n f_i P_i + \sum_{i=1}^n d_i P_i Q_i + \sum_{j=1}^p m_j Z_j q_j \\ & + \sum_{j=1}^p \sum_{i=1}^n g_{ij}[\mathbf{P}, \mathbf{X}, \mathbf{Q}, y_j] \\ & \times Q_i \left( 1 - \frac{q_{\max,j} - q}{q_{\max,j} - q_{\min,j}} \right) Z_j, \end{aligned} \quad (15)$$

where the first term on the right-hand side describes nutrient uptake by phytoplankton and the second and third term describe nutrient recycling due to mortality of phytoplankton and zooplankton, respectively. The fourth and final term describes nutrient excretion by zooplankton (Grover 2003), which represents those nutrients that are not extracted from the ingested prey and are therefore released by zooplankton.

The total amount of nutrient in the ecosystem,  $T$ , includes the freely available nutrient,  $N$ , as well as the nutrient contained in phytoplankton and zooplankton:

$$T = N + \sum_{i=1}^n P_i Q_i + \sum_{j=1}^p Z_j q_j. \quad (16)$$

Differentiation of this equation shows that the total amount of nutrient remains constant (i.e.,  $dT/dt = 0$ ). Thus, our model ecosystem is a closed system with respect to nutrients.

### Coevolutionary Dynamics

To investigate coevolution of phytoplankton and zooplankton size, we consider a community consisting of one phytoplankton species ( $P$ ) and one zooplankton species ( $Z$ ). Fitness of phytoplankton ( $w_p$ ) and zooplankton ( $w_z$ ) is defined as their net specific (i.e., per capita) growth rate under the prevailing conditions (Lande 1982):

$$w_p = \frac{1}{P} \frac{dP}{dt}, \quad (17a)$$

$$w_z = \frac{1}{Z} \frac{dZ}{dt}. \quad (17b)$$

Evolutionary changes in phytoplankton and zooplankton size are modeled using a quantitative trait approach (Lande 1982; Cortez and Ellner 2010):

$$\frac{dx}{dt} = V_p x^2 \frac{\partial w_p}{\partial x}, \quad (18a)$$

$$\frac{dy}{dt} = V_z y^2 \frac{\partial w_z}{\partial y}, \quad (18b)$$

where  $V_p$  and  $V_z$  are additive genetic variances of phytoplankton and zooplankton size and the fitness gradients  $\partial w_p / \partial x$  and  $\partial w_z / \partial y$  measure how the fitness of phytoplankton and zooplankton varies with individual size. We impose a physiological minimum on phytoplankton size of  $x = 0.5 \mu\text{m}$ . This is about the size of *Prochlorococcus*, which is among the smallest phytoplankton of our planet (Chisholm et al. 1988; Biller et al. 2015).

Our formulation deviates slightly from the standard approach for quantitative trait evolution because of the additional terms  $x^2$  and  $y^2$  in equations (18a) and (18b). These terms convert evolutionary changes in absolute size to evolutionary changes in relative size. For bacteria an increase in size of  $1 \mu\text{m}$  will be a major evolutionary change, whereas for elephants the same increase in size will go unnoticed. Addition of these squared terms ensures that  $V_p$  and  $V_z$  are both dimensionless; hence, in relative terms organisms of different sizes will evolve at comparable rates. If body size is expressed on a logarithmic scale as  $X = \ln x$  and  $Y = \ln y$ , then equations (18a) and (18b) simplify to the standard form:

$$\frac{dX}{dt} = V_p \frac{\partial w_p}{\partial X}, \quad (19a)$$

$$\frac{dY}{dt} = V_z \frac{\partial w_z}{\partial Y}. \quad (19b)$$

We calculate the fitness gradients of phytoplankton and zooplankton numerically. At each time step, we generate two phytoplankton and two zooplankton mutant phenotypes with sizes slightly larger (+0.001%) and slightly

smaller (−0.001%) than the resident phenotypes. Subsequently, we calculate net specific growth rates of these mutant phenotypes in the environment set by the resident community to estimate the local fitness gradient and to assess whether changes in size were under directional or disruptive selection. We examined trait evolution with numerical simulations based on the NDSolve routine in Mathematica 10 (Wolfram Research, Champaign, IL).

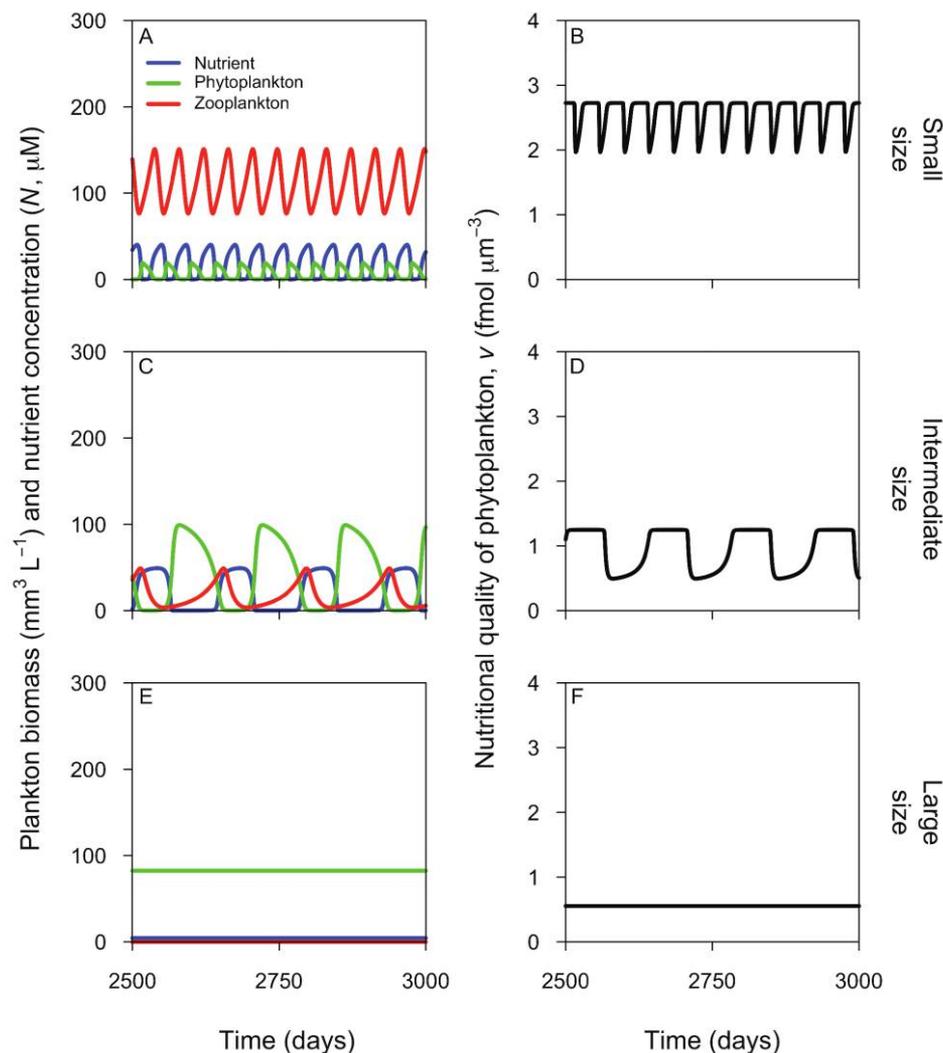
## Results

### Ecological Dynamics

To better understand the ecological context for the coevolution of phytoplankton and zooplankton size, we first investigate the underlying ecological dynamics of the model without evolution (fig. 2). We therefore compare ecological dynamics of small ( $x = 1 \mu\text{m}$ ,  $y = 40 \mu\text{m}$ ), intermediate (10, 400  $\mu\text{m}$ ), and large (60, 2,400  $\mu\text{m}$ ) phytoplankton and zooplankton, respectively, assuming that cell sizes of phytoplankton match the size preference of zooplankton (i.e.,  $x_i = x_{\text{pref},j}$ , so  $\alpha_{ij} = 1$ ; fig. 1C). In our model analysis, the amount of phytoplankton and zooplankton is expressed in terms of their total biovolume (a proxy of biomass), calculated as the product of individual biovolume and population abundance ( $(\pi x^3/6)P$  and  $(\pi y^3/6)Z$ , respectively). Calculation of plankton biomass enables comparison of results when individual sizes vary over orders of magnitude.

When phytoplankton and zooplankton are small, the clearance rate of zooplankton ( $\varepsilon$ ) is low (see eq. [6]). Due to their small cell size, phytoplankton have a low nutrient content per cell ( $Q$ ), yet they have a high nutritional quality ( $v$ ; i.e., they have a high nutrient content per unit biovolume). In this case, the predator-prey interaction leads to phytoplankton-zooplankton oscillations with low phytoplankton biomass and high zooplankton biomass (fig. 2A, 2B). When phytoplankton and zooplankton are of intermediate size, the phytoplankton-zooplankton oscillations produce higher phytoplankton biomass and lower zooplankton biomass (fig. 2C). Due to their intermediate cell size, phytoplankton display intermediate cellular nutrient content and nutritional quality (fig. 2D). When phytoplankton and zooplankton are large, the clearance rate is high but phytoplankton is of low nutritional quality. In this case, phytoplankton reaches a stable equilibrium with high biomass of low nutritional quality, whereas the zooplankton population becomes extinct (fig. 2E, 2F). Thus, the low nutritional quality of large phytoplankton can offer a very effective defense.

To confirm these results, we performed a bifurcation analysis along a gradient of phytoplankton cell size (fig. 3A, 3B). An increase in phytoplankton cell size enhances phytoplankton biomass and reduces zooplankton biomass (fig. 3A),



**Figure 2:** Impact of phytoplankton and zooplankton size on ecological dynamics without coevolution. *A, B*, Small phytoplankton ( $x = 1 \mu\text{m}$ ) and zooplankton ( $y = 40 \mu\text{m}$ ). *C, D*, Intermediate-sized phytoplankton ( $10 \mu\text{m}$ ) and zooplankton ( $400 \mu\text{m}$ ). *E, F*, Large phytoplankton ( $60 \mu\text{m}$ ) and zooplankton ( $2,400 \mu\text{m}$ ). Left panels show nutrient concentration, phytoplankton biomass, and zooplankton biomass (*A, C, E*); right panels show nutritional quality of phytoplankton ( $v$ ; *B, D, F*). Initial population abundances of phytoplankton and zooplankton are  $P = 10^7 \text{ cells L}^{-1}$  and  $Z = 10^6 \text{ ind L}^{-1}$  in *A* and *B*,  $P = 10^7 \text{ cells L}^{-1}$  and  $Z = 10^3 \text{ ind L}^{-1}$  in *C* and *D*, and  $P = 10^5 \text{ cells L}^{-1}$  and  $Z = 1 \text{ ind L}^{-1}$  in *E* and *F* (ind = individuals). Total nutrient in the ecosystem is  $T = 50 \mu\text{M}$ ; other parameters are as in table 1.

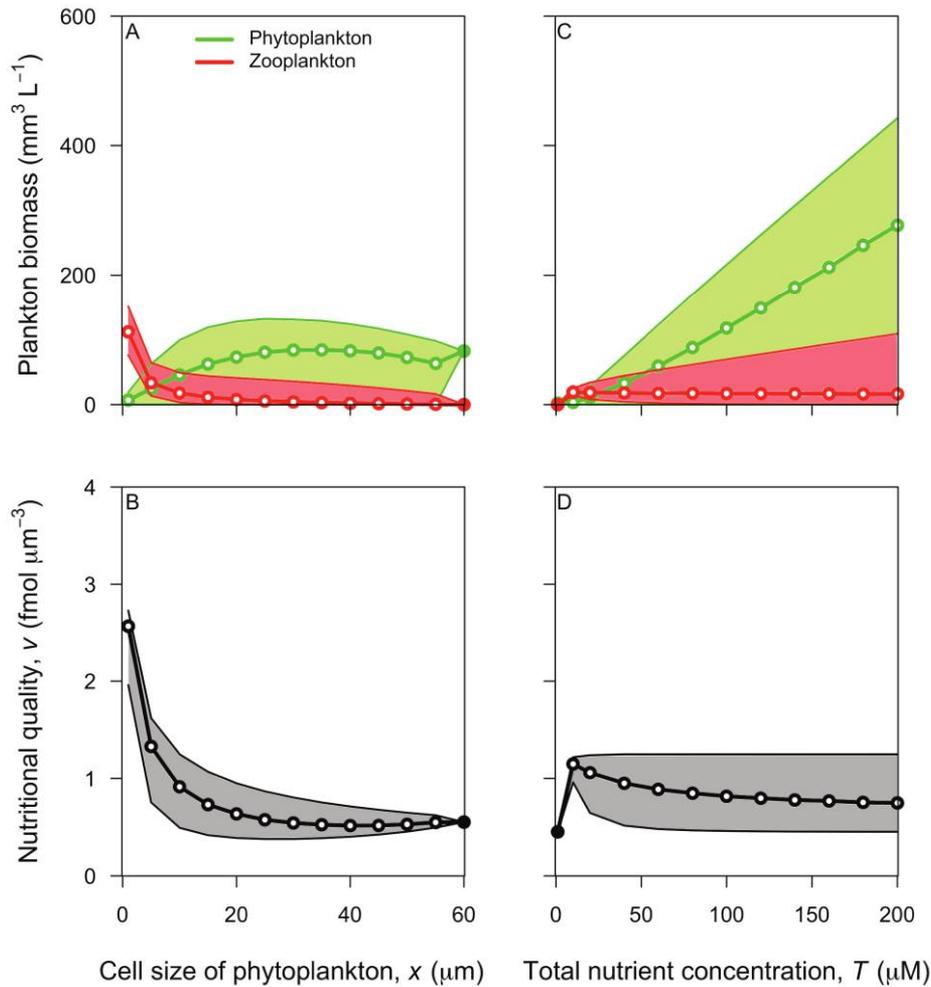
while the nutritional quality of phytoplankton decreases (fig. 3*B*). The low-quality food eventually drives the zooplankton population to extinction when phytoplankton cells become large (i.e., at  $x \geq 60 \mu\text{m}$  in fig. 3*A*).

The ecological dynamics of our model community is also affected by nutrient enrichment (fig. 3*C, 3D*). In very nutrient-poor environments, phytoplankton biomass (fig. 3*C*) and their nutritional quality (fig. 3*D*) are both low and therefore cannot sustain a zooplankton population. Nutrient enrichment stimulates phytoplankton biomass and nutritional quality, which enables establishment of the zooplankton population. With increasing nutrient enrichment, the ecological

dynamics are destabilized, which results in phytoplankton-zooplankton oscillations of increasing amplitude through a mechanism similar to that in the classical paradox of enrichment (Rosenzweig 1971).

#### *Eco-Evolutionary Dynamics*

To study the eco-evolutionary dynamics of phytoplankton cell size, we begin with a simple scenario where zooplankton are absent (fig. 4*A, 4B*). In this case, phytoplankton are not grazed and deplete the available nutrients. Nutrient depletion exerts strong selection on phytoplankton to increase

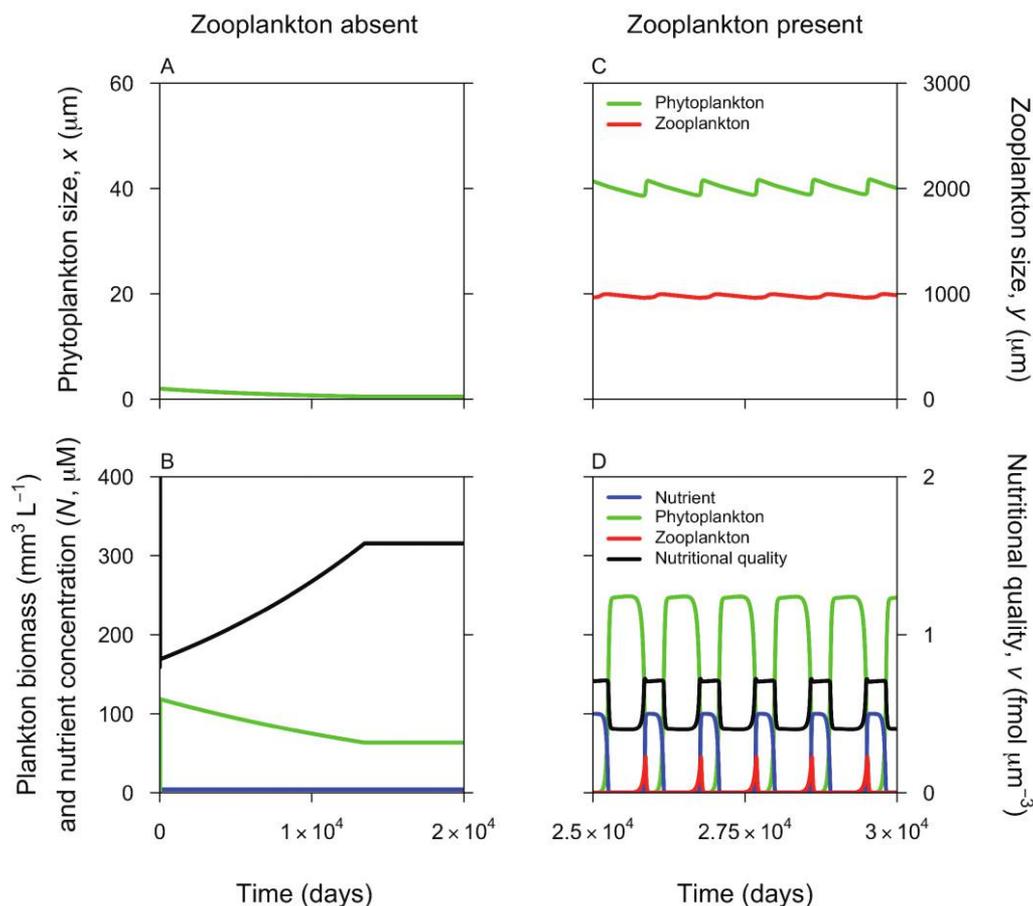


**Figure 3:** Bifurcation diagrams of the ecological dynamics along gradients of phytoplankton cell size and nutrient enrichment. *A, B*, Changes in phytoplankton and zooplankton biomass (*A*) and in nutritional quality of phytoplankton ( $v$ ; *B*) along a gradient of phytoplankton cell size. *C, D*, Changes in phytoplankton and zooplankton biomass (*C*) and in nutritional quality of phytoplankton (*D*) along a gradient of nutrient enrichment. Solid symbols denote stable equilibria, open symbols indicate average values, and shaded areas indicate the magnitude of phytoplankton-zooplankton oscillations. In *A* and *B*, total nutrient in the ecosystem is  $T = 50 \mu\text{M}$ , and the body size of zooplankton is assumed to be well adapted to the cell size of phytoplankton (i.e.,  $y = 40x$ , yielding  $\alpha = 1$ ). In *C* and *D*, phytoplankton and zooplankton size are  $x = 10 \mu\text{m}$  and  $y = 400 \mu\text{m}$ , respectively. Other parameters are as in table 1.

their competitive ability for nutrients (i.e., to develop a low  $R^*$ , sensu Tilman 1982). This can be achieved by the evolution of small cells because they have a high maximum nutrient uptake rate per unit biovolume,  $f_{\max}/x^3$ , and low half-saturation constant,  $K_N$  (see table 1). In the end, the phytoplankton population evolves toward a singular phenotype with small cells that cannot be invaded by any other phenotype (fig. 4A). Hence, the cell size of this singular phenotype represents an evolutionarily stable strategy (sensu Maynard Smith and Price 1973).

When selective zooplankton are added, selection for phytoplankton growth is opposed by selection against grazing.

In this case, phytoplankton evolve a much larger cell size than in the absence of zooplankton (fig. 4C), which reduces their nutritional quality (fig. 4D). The eco-evolutionary dynamics lead to oscillations of the phytoplankton and zooplankton populations (fig. 4D), where the low nutritional quality of the phytoplankton enables the development of strikingly high phytoplankton biomass at the peaks of the oscillations (compare fig. 4B with fig. 4D). The phytoplankton-zooplankton oscillations are accompanied by a mild trait cycle, with an increase in phytoplankton cell size when grazing rates are high and a decrease when grazing rates are low (fig. 4C). At each time point during this trait cycle, changes



**Figure 4:** Eco-evolutionary dynamics in the absence versus presence of zooplankton. *A, B*, Evolution of phytoplankton cell size (*A*) and population dynamics of phytoplankton (*B*) in the absence of zooplankton. *C, D*, Coevolution of phytoplankton and zooplankton sizes (*C*) and population dynamics of phytoplankton and zooplankton (*D*). Total nutrient in the ecosystem is  $T = 100 \mu\text{M}$ , and zooplankton are selective for nutritious prey ( $S = 40 \mu\text{m}^3 \text{fmol}^{-1}$ ). Other parameters are as in table 1.

in cell size were driven by directional selection rather than disruptive selection. Hence, we did not find indications for evolutionary branching in our model.

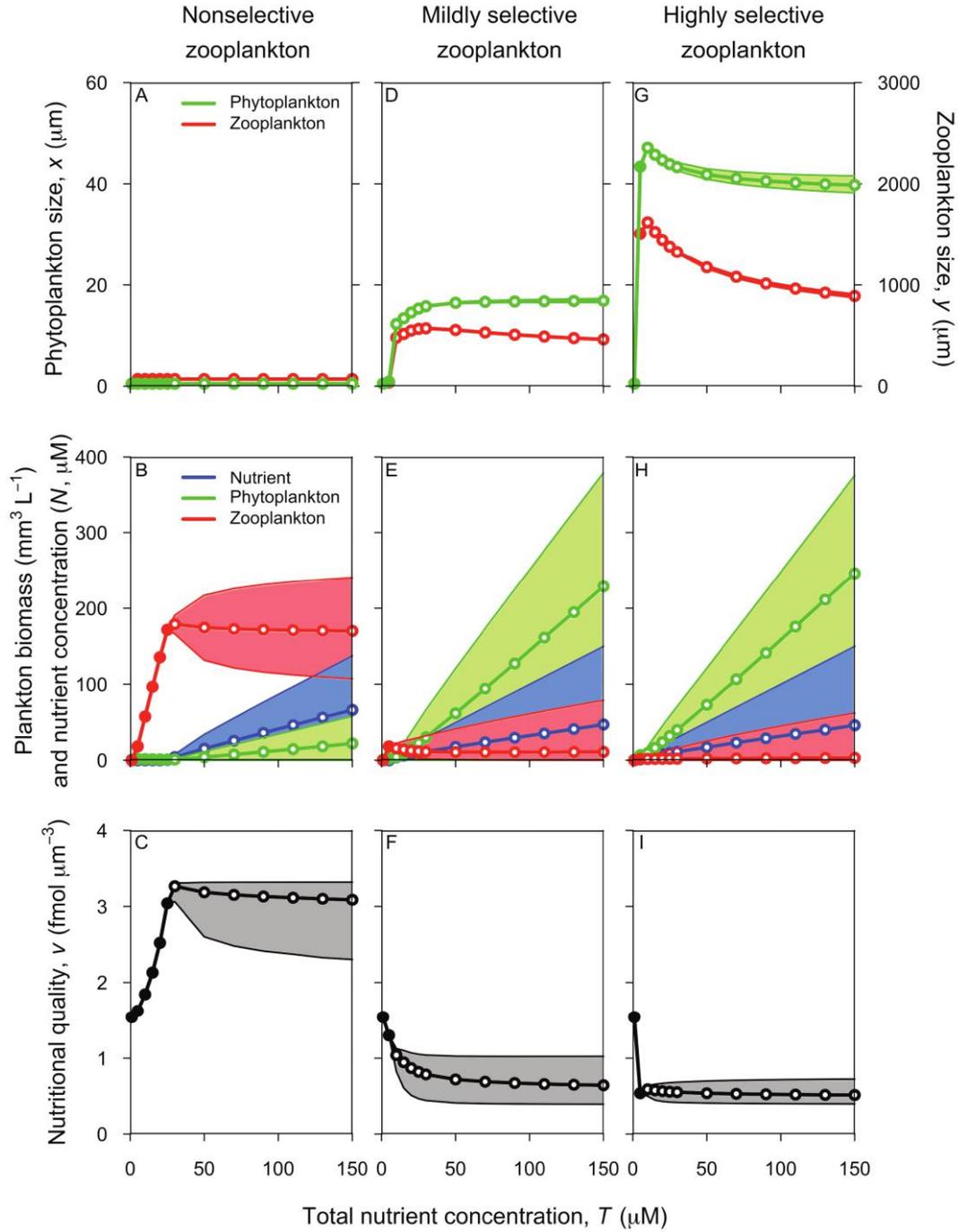
#### *Effects of Nutrient Enrichment and Zooplankton Selectivity*

We analyze the impact of nutrient enrichment on coevolution of phytoplankton and zooplankton size assuming that zooplankton are nonselective, mildly selective, or highly selective for the nutritional quality of their prey (fig. 5). When zooplankton are nonselective ( $S = 0$ ), the eco-evolutionary dynamics lead to small phytoplankton cells of only  $0.5 \mu\text{m}$  (fig. 5A). In nutrient-poor environments, low phytoplankton biomass (fig. 5B) and low nutritional quality (fig. 5C) support only a small zooplankton population. Nutrient enrichment enhances phytoplankton biomass and nutritional quality, which enables the development of a larger zooplank-

ton population. Further nutrient enrichment destabilizes the predator-prey interaction, resulting in pronounced fluctuations of phytoplankton and zooplankton biomass (fig. 5B) and the nutritional quality of phytoplankton (fig. 5C). Phytoplankton and zooplankton size remain small regardless of nutrient enrichment, however (fig. 5A).

When zooplankton are mildly selective, evolution produces medium-sized phytoplankton and zooplankton (fig. 5D). Nutrient enrichment results again in pronounced oscillations of phytoplankton and zooplankton biomass (fig. 5E) but with a much lower nutritional quality of phytoplankton than in the case of nonselective grazing (compare fig. 5F with fig. 5C).

When zooplankton are highly selective, evolution leads to large phytoplankton and zooplankton (fig. 5G). Their large sizes are again accompanied by pronounced phytoplankton-zooplankton oscillations (fig. 5H), a low nutritional quality



**Figure 5:** Bifurcation diagrams of eco-evolutionary dynamics along a gradient of nutrient enrichment. The graphs compare three communities, with nonselective zooplankton (A–C;  $S = 0 \mu\text{m}^3 \text{fmol}^{-1}$ ), mildly selective zooplankton (D–F;  $S = 4 \mu\text{m}^3 \text{fmol}^{-1}$ ), and highly selective zooplankton (G–I;  $S = 40 \mu\text{m}^3 \text{fmol}^{-1}$ ). A, D, G, Individual sizes of phytoplankton and zooplankton. B, E, H, Nutrient concentration, phytoplankton, and zooplankton biomass. C, F, I, Nutritional quality of phytoplankton. Solid symbols denote stable equilibria, open symbols indicate average values, and shaded areas indicate the magnitude of phytoplankton-zooplankton oscillations. In B, E, and H, part of the nutrient oscillations are hidden below the zooplankton oscillations. Parameter values are as in table 1.

of phytoplankton (fig. 5I), and a mild trait cycle in phytoplankton size (fig. 5G). It is noteworthy that nutrient enrichment in the presence of highly selective zooplankton induces a decrease in phytoplankton and zooplankton size. This size reduction is likely related to size-dependent nutrient demands of zooplankton. Specifically, smaller zooplankton individuals have lower minimum and maximum nutrient contents (table 1). Therefore, when the abundance of low-quality phytoplankton prey increases with nutrient enrichment, the specific growth rate of slightly smaller zooplankton may respond more strongly than that of large zooplankton. Hence, they may reach higher fitness than large zooplankton and natural selection favors a reduction in zooplankton size (fig. 5G).

#### *The Role of Size-Dependent Nutritional Quality*

To further evaluate our hypothesis linking large phytoplankton size to low nutritional quality, we also analyzed an alternative model in which the nutritional quality of phytoplankton is size independent. The model structure and parameter values are otherwise identical (see app. A for details; apps. A–C are available online).

When nutritional quality of phytoplankton is size independent, evolution favors small phytoplankton cells of  $\sim 0.5 \mu\text{m}$  in size and relatively high nutritional quality, almost regardless of zooplankton selectivity and the total amount of nutrient in the ecosystem (fig. 6A, 6B). The small phytoplankton cells are eaten by small zooplankton (fig. 6C) except in very nutrient-poor ecosystems where zooplankton become extinct (white region in fig. 6C).

In contrast, when nutritional quality decreases with phytoplankton size, selective grazing by zooplankton favors evolution of large phytoplankton cells of low nutritional quality (fig. 6D, 6E). Phytoplankton evolve the largest cells of up to  $\sim 50 \mu\text{m}$  when zooplankton is highly selective for nutritious food. Zooplankton adapt to the evolution of large phytoplankton cells and evolve larger body size than when nutritional quality is size independent (compare fig. 6C with fig. 6F). Hence, this model comparison illustrates that the size dependence of the nutritional quality of phytoplankton plays a key role in the evolution of large phytoplankton and zooplankton.

#### *Robustness of the Model Predictions*

Our model assumes that the maximum specific growth rate of phytoplankton ( $\mu_{\text{max},i}$ ) decreases allometrically with cell size (fig. 1B; e.g., Banse 1976; Savage et al. 2004). However, several other studies indicate that the growth rate of phytoplankton may be a unimodal function of cell size (Bec et al. 2008; Chen and Liu 2010; Marañón et al. 2013; Marañón 2015). To assess the robustness of the model predictions,

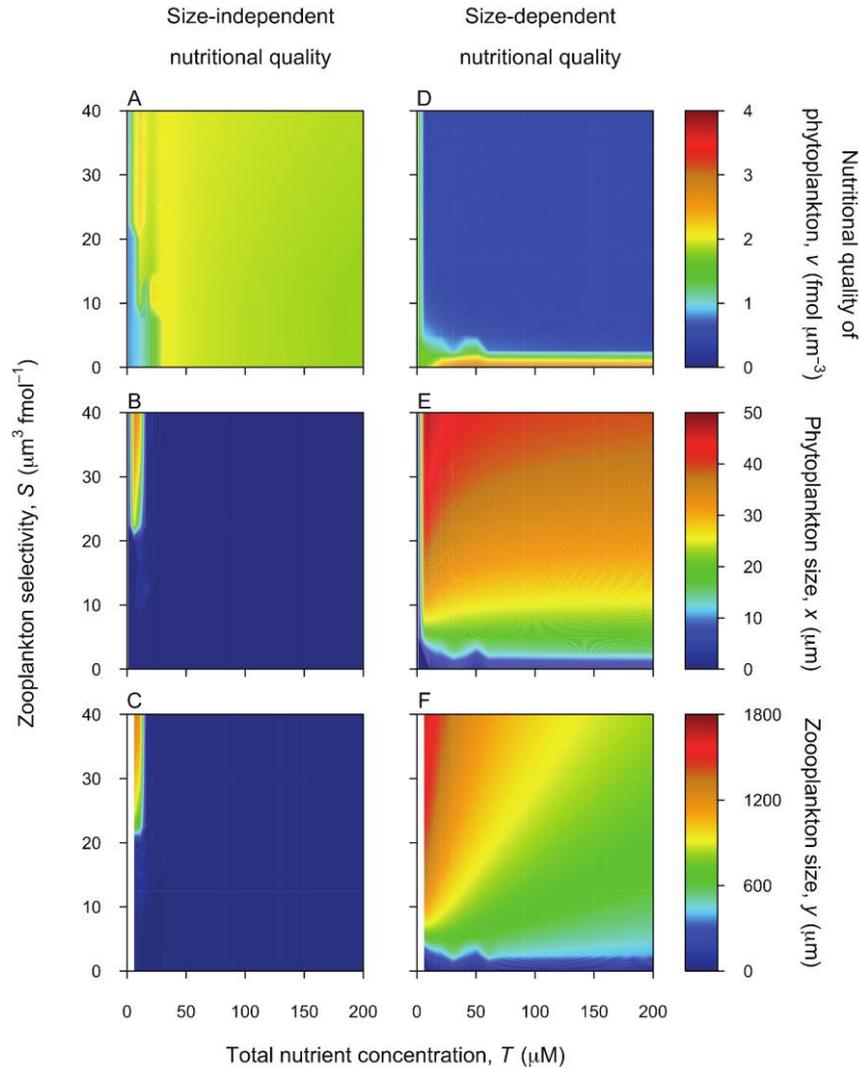
we therefore also analyzed a model version with  $\mu_{\text{max},i}$  as a unimodal function of phytoplankton size (app. B). This unimodal growth model predicts that even nonselective zooplankton can favor the evolution of large phytoplankton cells of low nutritional quality (compare fig. 5A–5C with fig. B1A–B1C; figs. B1, B2, C1 are available online). The other predictions of the allometric and unimodal growth model are very similar (compare fig. 6 with fig. B2). In particular, in both models the size-dependent change in nutritional quality of phytoplankton is key for the evolution of large phytoplankton cells.

Our model assumes that trait evolution proceeds through small mutational steps. However, a resident community resistant against small mutational changes might still be invaded by phenotypes with very different trait values. We therefore also investigated whether the resident community of figure 4C and 4D, consisting of large phytoplankton and zooplankton, can be invaded by phytoplankton of very different cell sizes. The invasion analysis shows that small phytoplankton species can indeed invade (fig. C1). Small phytoplankton have high specific growth rates (fig. 1B) and experience low grazing losses (fig. 1C) in a resident community dominated by large phytoplankton and zooplankton. Invasion of small phytoplankton might be followed by invasion of small zooplankton, which may lead to interesting patterns of evolutionary diversification in the size structure of plankton communities (e.g., Loeuille and Loreau 2005; Acevedo-Trejos et al. 2015). Further analysis of this diversification is beyond the scope of our study but certainly deserves attention in future work.

#### **Discussion**

Explanations for the evolution of phytoplankton size typically assume that large phytoplankton cells are less grazed because they are too big to be eaten or at least more difficult to consume than small phytoplankton. However, such physical defense against grazing can be readily countered when zooplankton coevolve to match the size of phytoplankton. Previous coevolutionary models have therefore found convergence to small phytoplankton cells (Jiang et al. 2005). Here, we propose that phytoplankton may evolve large size for a different reason. According to known allometric relationships, increasing cell size reduces the nutritional quality of phytoplankton. Our stoichiometrically explicit model shows that even if zooplankton coevolve in size, evolution of large but nutritionally poor phytoplankton cells offers a means to escape from high grazing pressure.

The key underlying assumption is that large phytoplankton species have lower nutritional quality than smaller ones. Several studies support this assumption (Shuter 1978; Kiørboe 1993; Sunda and Hardison 2010). For example, Shuter (1978) compiled the cell volume and minimum cellular nitrogen and

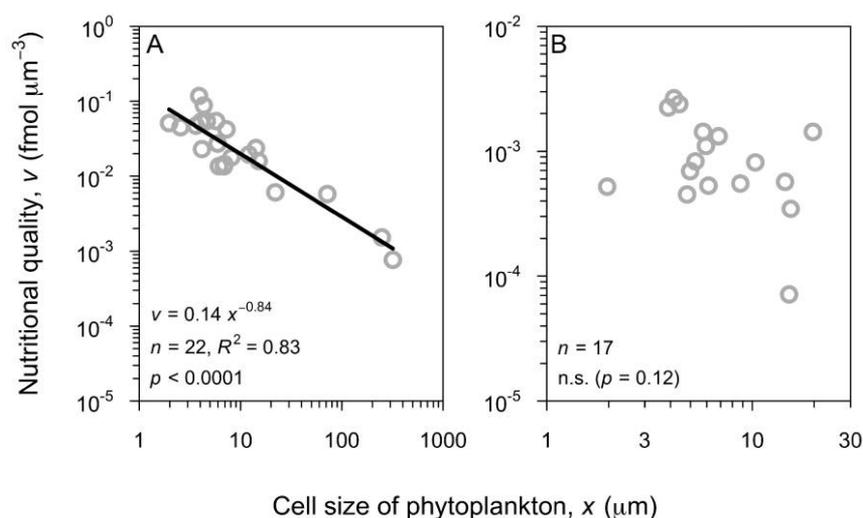


**Figure 6:** Phytoplankton-zooplankton coevolution along gradients of nutrient enrichment and zooplankton selectivity. The graphs compare two model scenarios where nutritional quality of phytoplankton is either independent of cell size (A–C) or decreases with cell size (D–F). A, D, Average nutritional quality of phytoplankton. B, E, Average cell size of phytoplankton. C, F, Average body size of zooplankton. The white regions in C and F indicate zooplankton extinction. Other parameters are as in table 1.

phosphorus contents of several phytoplankton species. We used these data to calculate nutritional quality of phytoplankton according to equation (8). The results show a significant decrease of nutritional quality with cell size for nitrogen (fig. 7A) but not for phosphorus (fig. 7B). This difference between nitrogen and phosphorus may just reflect limitations of the data set, however, as the phosphorus data of Shuter (1978) are based on a smaller number of species and span a smaller range of cell sizes than the nitrogen data.

Edwards et al. (2012) compiled a larger data set, with minimum cellular nutrient contents ( $Q_{\min}$ ) for nitrogen (~40 species) and phosphorus (~70 species). Analysis of their data also shows that nutritional quality ( $\nu$ , calculated from  $Q_{\min}$  and

cell volume) decreased with cell size for nitrogen but not for phosphorus. Why these patterns are different for nitrogen and phosphorus is not known (Edwards et al. 2012). It implies, though, that the model predictions for size-dependent nutritional quality (fig. 6D–6F) apply better to nitrogen, whereas the predictions for size-independent nutritional quality (fig. 6A–6C) apply better to phosphorus. In other words, phytoplankton are predicted to evolve larger cells in response to grazing in nitrogen-limited than in phosphorus-limited ecosystems. Intriguingly, marine diatoms are on average larger than freshwater diatoms (Litchman et al. 2009), which might be associated with the prevalence of nitrogen limitation in marine ecosystems. Future experiments



**Figure 7:** Data on the nutritional quality of phytoplankton as function of cell size. A, Nitrogen-based nutritional quality of 22 species as function of cell size. B, Phosphorus-based nutritional quality of 17 species as function of cell size. Nutritional quality was calculated from equation (8) using the cell volume and minimum cellular nitrogen and phosphorus contents of phytoplankton species reported by Shuter (1978). n.s. = not significant.

could test this hypothesis by exposing natural plankton communities to either nitrogen or phosphorus limitation and investigating whether the dominant phytoplankton species will indeed be larger under nitrogen-limited conditions.

Our model predicts that predator-prey oscillations can lead to coevolutionary trait cycles. During these cycles, phytoplankton size increased when grazing pressure was high and decreased when grazing pressure was low (fig. 4C). Similar trait cycles arise in other models of plant-herbivore coevolution (Loeuille et al. 2002; Mougi 2012; Tien and Ellner 2012). Trait cycles have even appeared in experimental studies (Yoshida et al. 2003; Meyer et al. 2006; Becks et al. 2012), where green algae became well defended when grazing pressure by rotifers was high but less defended and more competitive when grazing pressure was low. In these experiments, defense against grazing was not primarily related to cell size but to higher digestion resistance when algal cells passed through the zooplankton gut (Yoshida et al. 2003; Meyer et al. 2006) or to clumping of cells (Becks et al. 2012). In line with our model predictions, however, these experiments demonstrate that selective grazing may lead to interesting eco-evolutionary feedbacks between trait evolution and predator-prey oscillations.

The model predictions mirror size distributions of plankton in lakes and oceans. According to the model, in environments with low grazing pressure or nonselective grazing competition for nutrients will favor the evolution of small phytoplankton cells. Conversely, large phytoplankton are predicted to dominate in environments with high grazing pressure by nutritionally selective zooplankton (figs. 5, 6). This

size shift is supported by many empirical studies that show that small size confers a major competitive advantage under nutrient-limited conditions when grazing pressure is low (Grover 1989; Litchman et al. 2007; Edwards et al. 2011; Marañón 2015). For example, Burson et al. (2018, 2019) performed multispecies competition experiments with natural phytoplankton communities encompassing a wide range of cell sizes. Zooplankton was eliminated prior to their experiments. In all competition experiments, the two to four smallest phytoplankton taxa, ranging in size from 1.5 to 8.3  $\mu\text{m}$ , competitively displaced the larger phytoplankton species (Burson et al. 2018, 2019). Similarly, in the oceans small picocyanobacteria, such as *Prochlorococcus* and *Synechococcus*, dominate the oligotrophic subtropical gyres (Chisholm et al. 1988; Agawin et al. 2000; Li 2002). Conversely, large diatoms and dinoflagellates often become more prevalent in nutrient-rich coastal waters and upwelling regions, where competition for nutrients may be less intense but grazing for nutritious food often exerts a high selection pressure (Irigoien et al. 2004; Finkel et al. 2010; Marañón 2015).

Several other biological considerations could enrich our size-based stoichiometric model. For instance, addition of a predator on zooplankton can produce a three-level trophic cascade (Carpenter and Kitchell 1996; DeLong et al. 2015). Nutrient enrichment in tritrophic ecosystems may increase predator abundance rather than herbivore abundance, which may weaken selection against grazing in comparison to our two-trophic system. Furthermore, primary producers may develop other grazing defenses dependent on nutrient availability, such as tolerance by rapid compensatory growth

or the production of secondary metabolites (e.g., Coley et al. 1985; Stamp 2003; Agrawal and Weber 2015). For example, several phytoplankton species produce toxins that deter zooplankton (Wolfe et al. 1997; Mitra and Flynn 2006; Selander et al. 2019). Relaxation of grazing pressure through these alternative defense mechanisms will reduce the need to escape from grazing by the evolution of large size. Finally, phytoplankton size also affects other traits, such as the flotation or sinking velocity of cells (Reynolds 2006). For example, large buoyant cyanobacteria rapidly float upward and can develop dense blooms at the water surface, displacing smaller nonbuoyant species by shading them (Walsby et al. 1997; Huisman et al. 2004; 2018). Thus, other phytoplankton traits will also influence the evolution of phytoplankton size.

In conclusion, our results show that selective grazing on nutritious prey favors the evolution of large phytoplankton cells of low nutritional quality. Of course, this is not the only mechanism at play. Phytoplankton have also evolved other defense mechanisms (e.g., secondary metabolites, thick cell walls, long spines) and other size-dependent traits (e.g., buoyancy and sinking). Nonetheless, our study offers a novel solution to the classic question why phytoplankton evolve large size in response to grazing and thereby sheds new light on the eco-evolutionary forces shaping the size distribution and ecological stoichiometry of plankton communities.

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