

Adaptive Evolution of Phytoplankton Cell Size

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ABSTRACT: We present a simple nutrient-phytoplankton-zooplankton (NPZ) model that incorporates adaptive evolution and allometric relations to examine the patterns and consequences of adaptive changes in plankton body size. Assuming stable environmental conditions, the model makes the following predictions. First, phytoplankton should evolve toward small sizes typical of picoplankton. Second, in the absence of grazers, nutrient concentration is minimized as phytoplankton reach their fitness maximum. Third, increasing nutrient flux tends to increase phytoplankton cell size in the presence of phytoplankton-zooplankton coevolution but has no effect in the absence of zooplankton. Fourth, phytoplankton reach their fitness maximum in the absence of grazers, and the evolutionary nutrient-phytoplankton system has a stable equilibrium. In contrast, phytoplankton may approach their fitness minimum in the evolutionary NPZ system where phytoplankton and zooplankton are allowed to coevolve, which may result in oscillatory (unstable) dynamics of the evolutionary NPZ system, compared with the otherwise stable nonevolutionary NPZ system. These results suggest that evolutionary interactions between phytoplankton and zooplankton may have contributed to observed changes in phytoplankton sizes and associated biogeochemical cycles over geological time scales.

Keywords: adaptive evolution, body size, nutrient-phytoplankton-zooplankton (NPZ) model, phytoplankton, zooplankton

Phytoplankton are a polyphyletic group of single-celled primary producers that are ubiquitous in aquatic ecosystems. The range in size of these organisms is unprecedented, compared to that of any other eukaryotic group of organisms, spanning more than four orders of mag-

nitude in linear dimensions (from ~ 0.6 to $>1,000 \mu\text{m}$ equivalent spherical diameter; Sheldon et al. 1972; Margalef 1978; Falkowski et al. 2004). This range in phytoplankton size carries important biological consequences. The cell size of phytoplankton not only defines their metabolic activity, growth rates, and numerical abundance (Malone 1980; Peters 1983; Reynolds 1984; Chisholm 1992; Tang 1995; Tang and Peters 1995; Belgrano et al. 2002), it also strongly influences their contributions to biogeochemical cycles via size-dependent sinking (Falkowski et al. 1998) and affects community structure and dynamics via size-dependent species interactions (Brooks and Dodson 1965; Porter 1973, 1977; Reynolds 1984; Banse 1992; Cohen et al. 2003).

A diverse phytoplankton assemblage composed of species with different sizes has existed in the ocean for hundreds of millions of years. The fossil record indicates that major changes in species diversity within several marine phytoplankton groups have occurred, including such events as a rapid evolutionary radiation in the early Cambrian (Butterfield 1997) and a significant reduction in diversity at the Cretaceous/Tertiary (K/T) boundary (Falkowski et al. 2004). Associated with changes in species diversity are changes in phytoplankton size structure. Recent analyses indicate that the mean area of marine diatom frustules has decreased by more than twofold over the last half of the Cenozoic (Finkel et al. 2005). There is also some evidence that the cell size of individual phytoplankton species might have declined over time (Burckle and McLaughlin 1977). These patterns point to the intriguing question of whether there is an evolutionary tendency of these photosynthetic unicellular organisms toward smaller sizes, in contrast with the general increase in body sizes observed for some heterotrophic organisms (Alroy 1998; Schmidt et al. 2004b).

Small phytoplankton cells appear to have some advantages over larger cells, because the small-package effect associated with light harvesting and small diffusion boundary layers associated with nutrient uptake may allow small cells to utilize resources more efficiently (Raven 1994, 1998). These advantages may be partly behind the numerical dominance of picophytoplankton (phytoplankton between 0.6 and 2 μm in diameter) in contemporary

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oceans, which account for a major portion of ocean primary productivity (Raven 1998). Molecular phylogeny analyses suggest that picophytoplankton organisms arise independently within several major phytoplankton groups and are derived from ancestors with larger cell sizes (Raven 1998), again suggestive of the evolutionary tendency of phytoplankton toward small sizes.

Here we present and analyze an evolutionary nutrient-phytoplankton-zooplankton (NPZ) model to explore the patterns and consequences of the evolution of phytoplankton cell size. The evolutionary NPZ (ENPZ) model incorporates adaptive evolution of body size into a simple NPZ model. NPZ models have been commonly used to explore interactions between components of pelagic ecosystems (e.g., Riley 1946; Steele 1974; Fasham et al. 1990). These models can range from relatively simple forms with few state variables (e.g., Riley 1946) to more complex ones, such as those including microbial loops (e.g., Fasham et al. 1990; Steele 1998) or coupling to physical models (e.g., Hofmann 1988). Although numerous NPZ models have been developed since the original work of Riley (1946), to our knowledge, none of them have specifically considered evolutionary change. As one of the first models considering adaptive changes in planktonic systems (also see Stomp et al. 2004 for a study modeling adaptive changes in pigment composition of phytoplankton), the ENPZ model bridges the gap between selection on evolutionary time scales and interactions on ecological scales, allowing us to answer several important questions: Does natural selection drive phytoplankton cells toward a certain size? Do environmental nutrient status and zooplankton grazing affect phytoplankton size? What is the dynamical consequence of phytoplankton evolution? We first consider phytoplankton evolution in a nutrient-phytoplankton (NP) system when zooplankton are absent and then consider the case of phytoplankton-zooplankton coevolution in a nutrient-phytoplankton-zooplankton (NPZ) system.

The Model

The ENPZ model is built on a simple NPZ ecological model comprising three compartments: a single limiting nutrient, phytoplankton, and zooplankton. For simplicity, the model does not consider physical processes in the water column and assumes a calm, relatively stratified system. The model also does not explicitly consider the microbial loop but rather incorporates it implicitly in the form of nutrient recycling. Both phytoplankton and zooplankton may represent either a single species or an ensemble of species. Hence, evolutionary changes in their sizes may represent changes in the size of single species or changes in the average size of a species assemblage.

To incorporate adaptive evolution of body size into the

NPZ model, we assume that the rate of adaptive change is approximately proportional to the individual fitness gradient (i.e., the rate of change of individual fitness with respect to the trait value). Previous work has shown that this approximation can describe evolutionary change for quantitative phenotypic traits such as body size (Abrams et al. 1993; Dieckmann and Law 1996; Abrams 2001), regardless of whether evolutionary change is caused by changes in the relative frequency of different phenotypes within populations or is generated by mutation.

The Evolutionary NP (ENP) Model

In the absence of zooplankton grazing, the dynamical relationships between a limiting nutrient and phytoplankton populations can be described by

$$\frac{dN}{dt} = I + \gamma m P Q(\bar{x}) - \mu(\bar{x}) g(N) P Q(\bar{x}), \quad (1a)$$

$$\frac{dP}{dt} = P[\mu(\bar{x}) g(N) - m - s(\bar{x})], \quad (1b)$$

where N and P represent nutrient concentration and phytoplankton population density, respectively; $\mu(\bar{x})$ is phytoplankton maximum specific growth rate as a function of mean cell diameter \bar{x} (we assume that all algal cells are spherical and use cell diameter to represent algal size); $g(N)$ represents nutrient limitation experienced by phytoplankton; m is phytoplankton size-independent specific mortality rate; and $s(\bar{x})$ represents size-dependent phytoplankton sinking loss. Phytoplankton nutrient quota $Q(\bar{x})$ (the amount of nutrient in an individual cell) is also size dependent. A fraction (γ) of dead phytoplankton material is recycled to the nutrient pool, and nutrient is also replenished by allochthonous nutrient input (I).

We define the fitness of an individual phytoplankter with cell size x as its per capita growth rate under the prevailing conditions. We assume that the rate of change of the mean cell size of the phytoplankton population is proportional to the fitness gradient (Abrams et al. 1993; Dieckmann and Law 1996):

$$\frac{d\bar{x}}{dt} = V_x [\mu' g(N) - s']_{x=\bar{x}}, \quad (1c)$$

where V_x is the genetic variance of phytoplankton cell size and is assumed to be constant, μ' and s' represent the derivatives of $\mu(x)$ and $s(x)$ with respect to individual size x , respectively, which are to be evaluated at the mean cell size \bar{x} .

We must determine how size-dependent terms in equations (1) change with size before we proceed. Phytoplankton maximum specific growth rate, μ , does not bear a simple relationship with size over the possible range of phytoplankton cells. For species with relatively large cell sizes, maximum specific growth rate tends to decline with a decelerating rate as cell size increases (Banse 1976; Malone 1980; Chisholm 1992; Tang 1995), presumably because of the more efficient acquisition and use of resources by smaller cells (Raven 1994, 1998). In contrast, examinations of picophytoplankton show that their maximum specific growth rate tends to increase with size, possibly because of the limited supply of the cellular catalysts (e.g., enzymes) in extremely small cells (Raven 1986, 1994, 1998). These patterns imply that $\mu' > 0$ and $\mu'' < 0$ for very small x , and $\mu' < 0$ and $\mu'' > 0$ for relatively large x , which can be characterized by a single equation:

$$\mu(x) = \frac{x}{a_1x^2 + a_2x + a_3}, \quad (2)$$

where a_1 , a_2 , and a_3 are constants that take positive values. We use equation (2) in our model simulations, but we would like to point out that our general results rely on the qualitative behavior of $\mu(x)$ (the signs of μ' and μ'') and are not affected by the particular growth forms we choose to use. For example, equation (2) implicitly assumes that growth rate scales as the $-1/3$ power of individual volume ($\mu \approx 1/a_1x$) when the diameter x is relatively large. It has been suggested that metabolic rates (including growth rate) may scale as the $-1/4$ power of body volume (Brown et al. 2004); the qualitative results would remain the same if such a relation were used. Note that equation (2) effectively defines an optimal cell size ($x_{opt} = [a_3/a_1]^{1/2}$) associated with the largest growth rate (where $\mu' = 0$, $\mu'' < 0$), which bridges the region of $\mu' > 0$ and the region of $\mu' < 0$.

Assuming that phytoplankton cells are spherical, the sinking rate (s) of a cell with a diameter (x) increases in proportion to the square of its diameter, as given by the well-known Stokes equation,

$$s(x) = \alpha x^2, \quad (3)$$

where α is a constant whose value is affected by the density of the water and the algal cell as well as the viscosity of the water. Note that equation (3) implies $s' > 0$ and $s'' > 0$.

We assume that the nutrient quota of a cell is directly proportional to its volume:

$$Q(x) = \beta x^3, \quad (4)$$

where β is the quota for $x = 1$. The exact form of $Q(x)$ does not affect our results as long as $Q' > 0$.

The phytoplankton nutrient limitation term $g(N)$ is generally an increasing function of N ($dg/dN = g' > 0$) and is given by the familiar Michaelis-Menten-type equation:

$$g(N) = \frac{N}{K + N}, \quad (5)$$

where K is the half-saturation constant for nutrient uptake. Results remain qualitatively unchanged when equation (5) is replaced with other forms of $g(N)$ satisfying $g' > 0$.

The Evolutionary NPZ (ENPZ) Model

The equations for nutrient-phytoplankton-zooplankton ecological interactions are

$$\begin{aligned} \frac{dN}{dt} = & I + \gamma mPQ(\bar{x}) + \gamma dZq(\bar{y}) + \gamma [Q(\bar{x}) \\ & - \text{eq}(\bar{y})]C(\bar{x}, \bar{y})PZ - \mu(\bar{x})g(N)PQ(\bar{x}), \end{aligned} \quad (6a)$$

$$\frac{dP}{dt} = P[\mu(\bar{x})g(N) - m - s(\bar{x}) - C(\bar{x}, \bar{y})Z], \quad (6b)$$

$$\frac{dZ}{dt} = Z[eC(\bar{x}, \bar{y})P - d]. \quad (6c)$$

Here, $C(\bar{x}, \bar{y})$ represents the consumption rate of zooplankton (Z) on phytoplankton (P), which is a function of phytoplankton average cell size (\bar{x}) and zooplankton average body size (\bar{y}), $q(\bar{y})$ is zooplankton nutrient quota as a function of zooplankton body size, e is the conversion efficiency of zooplankton, and d is the specific mortality rate of zooplankton. The third and fourth terms in equation (6a) represent nutrient recycling from the zooplankton compartment and from the grazing process, respectively.

In the NPZ system, it is possible that both phytoplankton and zooplankton undergo evolutionary change such that coevolution between the two can occur. In such a case, the rates of adaptive change in body sizes of phytoplankton and zooplankton can be described by

$$\frac{d\bar{x}}{dt} = V_x[\mu'g(N) - s' - C'_xZ]_{x=\bar{x}, y=\bar{y}}, \quad (6d)$$

$$\frac{d\bar{y}}{dt} = V_y(eC'_yP)_{x=\bar{x}, y=\bar{y}} \quad (6e)$$

where V_x and V_y are genetic variance of body size in the phytoplankton and zooplankton populations, respectively,

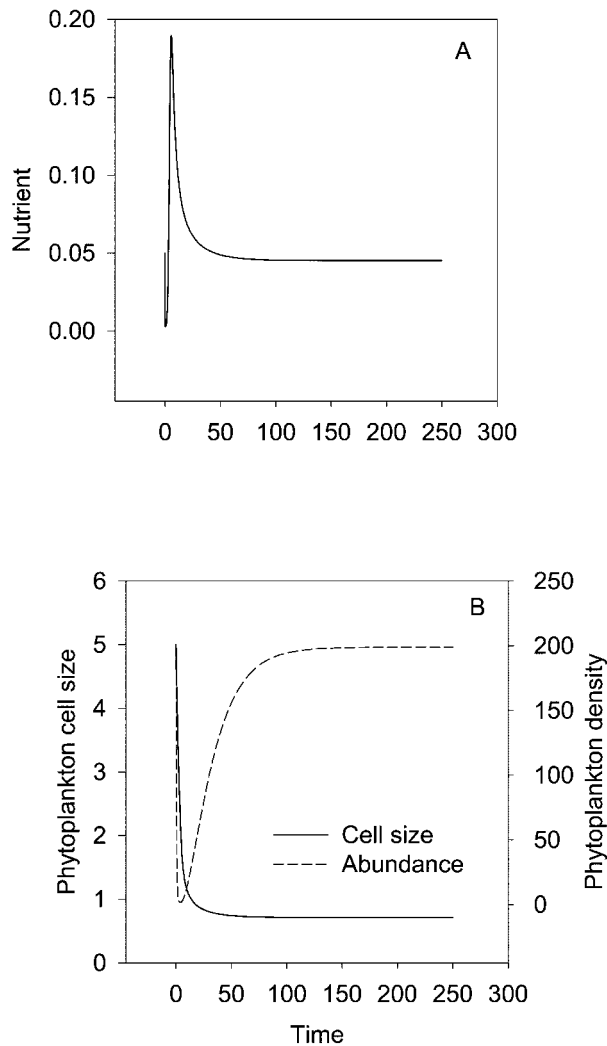


Figure 1: An example of the stable dynamics of the ENP system. *A*, Nutrient dynamics. *B*, Phytoplankton cell size and population dynamics. Parameter values are $I = 100$, $a_1 = 0.02$, $a_2 = 0.02$, $a_3 = 0.08$, $k = 2$, $m = 0.1$, $\alpha = 0.1$, $\beta = 10$, $\gamma = 0.1$, $V_x = 1$. Note that for the chosen parameters, there is a positive relationship between phytoplankton specific growth rate and cell size when size falls below 2, the optimal size for the highest maximum specific growth rate. The equilibrium phytoplankton cell size is always less than this optimal size.

and C'_x and C'_y are the derivatives of $C(x, y)$ with respect to x and y , respectively. All the derivatives are evaluated at the means \bar{x} and \bar{y} .

It is clear that zooplankton consumption rate $C(x, y)$ depends on both zooplankton and phytoplankton size. In general, zooplankton grazers are larger than their phytoplankton prey, and large grazers can potentially feed on a wider size range of phytoplankton cells than small ones (Reynolds 1984; Banse 1992). More importantly, zooplankton grazers do not just eat indiscriminately but se-

lectively feed on phytoplankton cells that are of certain size (relative to their own size; Mullin 1963; Frost 1972; Runge 1980; Parsons et al. 1984; Banse 1992), presumably as a way to maximize energy gains. Zooplankton selective feeding can be characterized by the following equation:

$$C(x, y) = \frac{C_m}{v + (x - \theta y)^2}, \quad (7)$$

where θ is a constant that defines zooplankton selectivity (C reaches its maximum value C_m/v with $x = \theta y$) and v is a constant depicting how rapidly C deviates from its maximum value as zooplankton size deviates from its preferred phytoplankton prey size.

Similar to phytoplankton nutrient quota $Q(x)$, zooplankton nutrient quota $q(y)$ is also assumed to be directly proportional to zooplankton body volume:

$$q(y) = \delta y^3, \quad (8)$$

where δ is the nutrient quota at $y = 1$.

Results of the ENP Model

Evolution of Phytoplankton Cell Size

Let us first consider evolution of phytoplankton cell size in the absence of grazers. Without solving for equations (1), important insight can be obtained by noting that at equilibrium, the right-hand side of equation (1c) equals 0, resulting in

$$\mu' = \frac{s'}{g} > 0. \quad (9)$$

Equation (9) indicates that at equilibrium, phytoplankton cell size should fall in the range where $\mu(x)$ increases with x . Because this only occurs within the size range of picophytoplankton, the model thus predicts that, absent grazers, phytoplankton should evolve toward extremely small size (i.e., picoplankton size; fig. 1). The rationale for large phytoplankton cells to evolve toward small size is simple: above the optimal size (x_{opt} where $\mu' = 0$), large phytoplankton cells are at a fitness disadvantage compared with smaller cells, owing to their lower growth rates and higher sinking rates. The reason that phytoplankton evolution does not end at the optimal size but declines further is because at the optimal size the fitness advantage afforded by the high growth rate is outweighed by the fitness disadvantage imposed by the relatively high sinking rate.

Stability of the ENP System

We first note that, because $\mu'' < 0$ and $s'' > 0$, phytoplankton fitness is always maximized ($\mu''g - s'' < 0$) at equilibrium in the ENP system. It can be readily shown that the nonevolutionary NP system as described by equations (1a) and (1b) always has a stable equilibrium. The question is whether the system can be destabilized by adaptive change in phytoplankton size. "Stability Analysis of the ENP System" in the appendix in the online edition of the *American Naturalist* describes the local stability analysis of the ENP system, which demonstrates that the ENP system is always stable with phytoplankton at fitness maximum. Thus, adaptive change of phytoplankton cell size alone cannot destabilize the ecological dynamics of the nutrient-phytoplankton interactions.

Effect of Evolution of Phytoplankton Cell Size on Standing Nutrient Concentration

It follows directly from equations (1b) and (1c) that both equilibrium phytoplankton size and standing nutrient concentration are independent of phytoplankton population density, as long as phytoplankton are able to exist. This allows us to address the important question of how phytoplankton evolution affects nutrient concentration. To answer this question, we implicitly differentiate equation (1b) at equilibrium, giving

$$\frac{dN}{d\bar{x}} = -\frac{\partial(dP/dt)/\partial\bar{x}}{\partial(dP/dt)/\partial N} = -\frac{\mu'g - s'}{\mu g'} = 0, \quad (10)$$

where $g' = \partial g/\partial N$. Note that this equation uses the equilibrium condition of equation (1c), $\mu'g - s' = 0$. Equation (10) suggests that N will approach either its maximum or its minimum as phytoplankton approaches their fitness maximum. "Derivation of Equation (11)" in the online appendix shows the derivation of the second-order differentiation, which is always positive:

$$\frac{d^2N}{d\bar{x}^2} = -\frac{\mu''g - s''}{\mu g'} > 0. \quad (11)$$

Together, equations (10) and (11) indicate that standing nutrient concentration will be minimized as phytoplankton reach their fitness maximum.

Effect of Increasing Nutrient Inflow on Phytoplankton Cell Size

Equations (1b) and (1c) imply that any effect of change in nutrient inflow on phytoplankton cell size depends solely on how it affects standing nutrient concentration.

To determine how changing nutrient flow affects standing nutrient concentration at equilibrium, we solve equations (1a) and (1b) for N and differentiate N with respect to I , yielding

$$\frac{\partial N}{\partial I} = 0. \quad (12)$$

Equation (12) suggests that changing nutrient inflow rate should not affect standing nutrient concentration. Together, equations (1c) and (12) suggest that phytoplankton equilibrium cell size will not respond to changes in nutrient inflow rate in the ENP system (Fig. 2A).

Results of the ENPZ Model

Phytoplankton Cell Size in the Presence of Zooplankton-Phytoplankton Coevolution

After substituting equation (7) into equations (6d) and (6e), we obtain the following equations for phytoplankton and zooplankton body size dynamics:

$$\frac{d\bar{x}}{dt} = V_x \left\{ \mu'g - s' + 2(x - \theta y) \frac{C_m Z}{[v + (x - \theta y)^2]^2} \right\}_{x=\bar{x}, y=\bar{y}}, \quad (13a)$$

$$\frac{d\bar{y}}{dt} = V_y \left\{ 2(x - \theta y) \frac{eC_m P}{[v + (x - \theta y)^2]^2} \right\}_{x=\bar{x}, y=\bar{y}}. \quad (13b)$$

Equation (13b) indicates that zooplankton size matches with their preferred phytoplankton prey size ($\bar{x} = \theta\bar{y}$) at equilibrium. This result reduces the equilibrium condition of equation (13a) to

$$\mu'g(N) - s' = 0, \quad (14)$$

a form that appears identical to the equilibrium conditions of equation (1c) for phytoplankton size dynamics in the ENP system. Equation (14) requires $\mu' > 0$ at equilibrium, suggesting that phytoplankton should still evolve toward picoplankton size.

One interesting question is how zooplankton grazing affects phytoplankton cell size. Equation (14) implies that, as in the ENP system, any change in phytoplankton equilibrium cell size is brought about solely by the change in standing nutrient concentration N ; grazing would not affect cell size if it did not change nutrient concentration. Thus, we can determine the grazer effect if we know, first, how cell size responds to changes in nutrient concentration

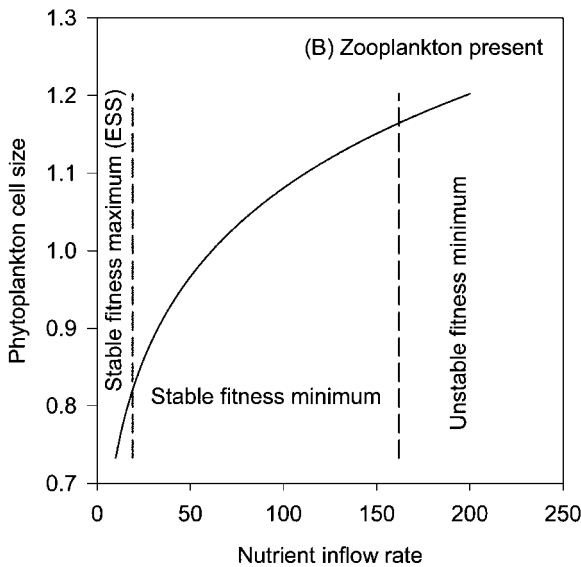
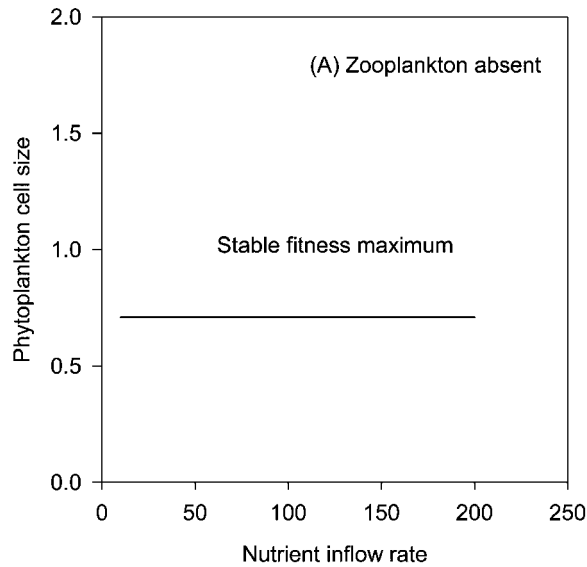


Figure 2: Effects of increasing nutrient flux on phytoplankton equilibrium cell size for (A) the evolutionary nutrient-phytoplankton system, which is always stable, and (B) the evolutionary nutrient-phytoplankton-zooplankton (ENPZ) system, which may become unstable with phytoplankton at fitness minimum. The two vertical dashed lines in B mark three regions: stable equilibrium with phytoplankton fitness maximum (ESS), stable equilibrium with phytoplankton fitness minimum, and unstable equilibrium with phytoplankton fitness minimum. Increasing nutrient flux tends to destabilize the ENPZ system. Parameter values are $d = 1$, $e = 0.3$, $C_m = 0.2$, $v = 1$, $\theta = 0.5$, $\delta = 20$, $V_y = 1$; other values are as in figure 1.

and, second, how nutrient concentration responds to grazing. Implicit differentiation of equation (14) yields

$$\frac{\partial x}{\partial N} = -\frac{\mu'g'}{\mu''g - s''} > 0, \quad (15)$$

which utilizes the fact that $\mu''g - s'' < 0$ at equilibrium. Equation (15) suggests that at equilibrium, any increase in standing nutrient concentration will lead to an increase in phytoplankton cell size. Implicit differentiation of equilibrium conditions of equation (6b) gives

$$\frac{dN}{dZ} = \frac{C}{\mu'g'} > 0, \quad (16)$$

suggesting that grazing has a positive effect on ambient nutrient concentration. Together, equations (15) and (16) suggest that zooplankton grazing should cause an increase in phytoplankton cell size (still within the range of picophytoplankton, as suggested by eq. [14]).

Effect of Increasing Nutrient Inflow on Phytoplankton Cell Size

In the ENPZ system, increasing nutrient inflow has a positive effect on standing nutrient concentration ($\partial N/\partial I > 0$; “The Effect of Changes in I on N in the ENPZ System” in the online appendix). This result, along with equation (15), indicates that higher nutrient inflow would cause phytoplankton equilibrium cell size to increase (fig. 2B).

Stability of the ENPZ System

Local stability analysis indicates that the nonevolutionary NPZ system in the form of equations (6a)–(6c) is always stable (results not shown). Here we are interested in whether phytoplankton-zooplankton coevolution can destabilize the system. As the local stability analysis is too complex for the full ENPZ system, here we use numerical simulations to explore the possibility of unstable dynamics.

Whether phytoplankton have a fitness maximum or minimum at equilibrium can have an important bearing on the stability of the ENPZ system. In contrast with the ENP system, where phytoplankton always evolves toward their fitness maximum ($\mu''g - s'' < 0$), phytoplankton may reach either their fitness maximum ($\mu''g - s'' - c_y''Z < 0$) or their fitness minimum ($\mu''g - s'' - c_y''Z > 0$) at equilibrium in the ENPZ system (zooplankton are always at their fitness maximum). Numerical simulations reveal many instances of unstable dynamics for the full ENPZ system (see fig. 3 for an example). Generally, unstable dynamics are associated with phytoplankton fitness minimum ($\mu''g - s'' - c_y''Z > 0$), although phytoplankton fitness minimum does not neces-

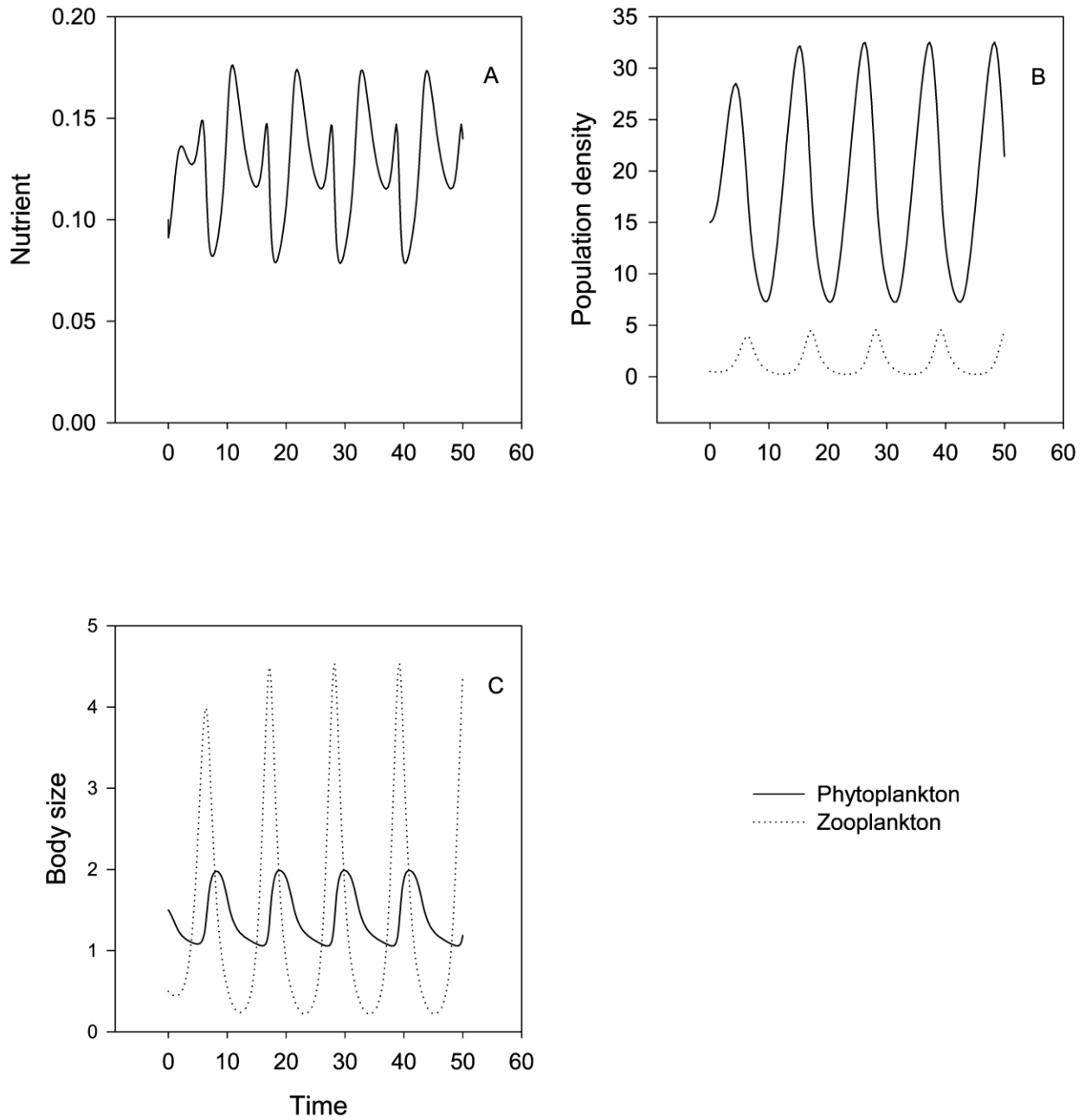


Figure 3: Example of the unstable dynamics of the evolutionary nutrient-phytoplankton-zooplankton system. *A*, Nutrient dynamics. *B*, Phytoplankton and zooplankton population dynamics. *C*, Phytoplankton and zooplankton body size dynamics. $I = 200$; other parameter values are as in figure 2.

sarily make the ENPZ system unstable (i.e., stable phytoplankton fitness minimum exists; fig. 2*B*). An unstable ENPZ system associated with phytoplankton fitness minimum can arise when the genetic variance of phytoplank-

ton is sufficiently large compared to that of zooplankton or when zooplankton are sufficiently abundant. As a result, increasing nutrient inflow, which tends to increase zooplankton abundance, can have a destabilizing effect (fig.

2B), in a way reminiscent of the phenomenon of paradox of enrichment for ecological systems without evolutionary components (Rosenzweig 1971).

Discussion

Our major findings can be summarized as follows. First, phytoplankton should evolve toward picoplankton size, regardless of the presence/absence of zooplankton (although zooplankton grazing has a positive effect on phytoplankton size). Second, in the absence of grazers, phytoplankton evolution tends to reduce standing nutrient concentration, which reaches a minimum as phytoplankton reach their fitness maximum. Third, increasing nutrient loading will lead to an increase in phytoplankton size in the presence of phytoplankton-zooplankton coevolution but will have no effect on phytoplankton size when zooplankton are absent. Fourth, phytoplankton evolution cannot destabilize a stable NP system in the absence of zooplankton, but phytoplankton-zooplankton coevolution can translate a stable nonevolutionary NPZ system into an unstable system, resulting in fluctuating dynamics of the entire system.

Directly testing most of these predictions is difficult at the current stage, given the lack of data on both phytoplankton cell size and environmental variables over evolutionary time scales. For example, no data are currently available to evaluate the possibility of fluctuating dynamics in phytoplankton size caused by phytoplankton-zooplankton coevolution, although one recent study indicates that cyclic changes in cell size of marine planktonic foraminifera, which can feed on diatoms, have commonly occurred in the Cenozoic (Schmidt et al. 2004a). Our model suggests, however, that cyclic changes in phytoplankton and zooplankton sizes due to coevolution are mostly likely to be found in regions with high nutrient influx (e.g., coastal waters).

One prediction, that phytoplankton tend to evolve toward small size, is consistent with secular changes in phytoplankton size structure on geological time scales (Finkel et al. 2005) and the polyphyletic origin of picophytoplankton (Raven 1998). This prediction, however, appears at odds with the fact that phytoplankton cell size in fact varies considerably among species, some of which can reach more than 1 mm in diameter (Sheldon et al. 1972; Margalef 1978; Falkowski et al. 2004). Several explanations could account for this discrepancy. First, while our model assumes stable environmental conditions, which lead to the presence of one single size class at equilibrium, a continuously changing environment may permit many species (of differing size) to coexist (Hutchinson 1961; Chesson 2000), particularly if larger cells have larger storage vacuoles that can store nutrients in excess of immediate cell

growth needs (Tozzi et al. 2004). Second, phytoplankton sinking rates are not simply determined by cell size, as assumed in the model, but are also influenced by some additional factors, such as cell morphology, cell physiology, and environmental physical conditions (Smayda 1970). These factors make it possible for phytoplankton cells that otherwise would sink rapidly, as determined by their size, to have a relatively long residence time in the euphotic zone. Indeed, it has been demonstrated theoretically that appropriate levels of turbulent diffusion could allow sinking phytoplankton populations to persist (Huisman et al. 2002). Third, our model does not consider the possibility that zooplankton themselves are subject to size-selective predation from planktivorous fish, which tend to feed upon large zooplankton individuals (Brooks and Dodson 1965). This selective pressure for small-bodied zooplankton may disrupt the coupled coevolution between phytoplankton and zooplankton, which may potentially lead to an increase in phytoplankton cell size.

Our model did not consider these complicating factors, but it nevertheless made predictions that are largely consistent with general ecological phenomena and established ecological principles. For example, the predominance of picophytoplankton in the open oceans (where disturbance is infrequent and planktivory is relatively unimportant, which probably best fits with our model assumptions) supports the evolutionary tendency of phytoplankton toward picoplankton size. The prediction that increasing nutrient flux should promote phytoplankton size in the ENPZ system is also in line with the well-known phenomenon that small phytoplankton species tend to dominate in nutrient-poor waters and that larger phytoplankton species are more abundant in nutrient-rich waters (Malone 1980; Chisholm 1992; Agawin et al. 2000; Li 2002; Irigoien et al. 2004). Current evidence also suggests that zooplankton grazing affects the size structure of phytoplankton community and often leads to an increase in the average size of phytoplankton assemblage (Porter 1973, 1977; Malone 1980; Sterner 1989; Carpenter and Kitchell 1993), which is again predicted by our model. Further, the minimization of standing nutrient concentration with maximizing phytoplankton fitness in the ENP system is directly comparable to the ecological R^* rule that a species that reduces ambient resource to the lowest level (lowest R^*) will displace all other competitors (Tilman 1982).

Our results on stability are qualitatively similar to those of previous adaptive evolution models. For instance, we found that phytoplankton evolution alone cannot destabilize phytoplankton-nutrient interactions in the absence of zooplankton. Similarly, Abrams (1992) found that predator evolution is unlikely to cause predator-prey cycles except under restricted conditions (lower predator consumption associated with higher prey abundance), al-

though the prey is a biological species, not inorganic nutrient, in his model. The present model also showed that zooplankton-phytoplankton coevolution can lead to oscillatory body size and ecosystem dynamics, which is consistent with the general notion that predator-prey coevolution is more likely to cause trait and population cycles (Abrams 2000). Despite these similar findings, the ENPZ model differs from most predator-prey coevolution models in two fundamental ways. First, while other models often make assumptions (frequently in the form of trade-offs associated with the evolving trait) that need to be substantiated empirically, our model is based on well-established allometric relationships. Second, while most other models do not consider nutrient dynamics (but see Loeuille et al. 2002 and Loeuille and Loreau 2004), our model explicitly considers the nutrient component, which allowed us to examine the interrelationship between phytoplankton size evolution and ambient nutrient conditions.

In summary, we constructed an evolutionary nutrient-phytoplankton-zooplankton model by incorporating adaptive change of phytoplankton and zooplankton body size into a simple nonevolutionary nutrient-phytoplankton-zooplankton model. The model makes several important predictions regarding phytoplankton size evolution under stable environmental conditions. Testing these predictions is hampered by the lack of long-term data on the evolution of phytoplankton cell size, zooplankton body size, and other environmental variables. As researchers have just begun to investigate changes in plankton size over microevolutionary and macroevolutionary scales (Schmidt et al. 2004a, 2004b; Finkel et al. 2005), we expect critical evaluations of our model predictions to be possible in the near future.

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Literature Cited

- Abrams, P. A. 1992. Adaptive foraging by predators as a cause of predator-prey cycles. *Evolutionary Ecology* 6:56–72.
- . 2000. The evolution of predator-prey interactions: theory and evidence. *Annual Review of Ecology and Systematics* 31:79–105.
- . 2001. Modelling the adaptive dynamics of traits involved in inter- and intraspecific interactions: an assessment of three methods. *Ecology Letters* 4:166–175.
- Abrams, P. A., H. Matsuda, and Y. Harada. 1993. Evolutionarily unstable fitness maxima and stable fitness minima in the evolution of continuous traits. *Evolutionary Ecology* 7:465–487.
- Agawin, N. S. R., C. M. Duarte, and S. Agusti. 2000. Nutrient and temperature control of the contribution of picoplankton to phytoplankton biomass and production. *Limnology and Oceanography* 45:591–600 (erratum 45:1891).
- Alroy, J. 1998. Cope's rule and the dynamics of body mass evolution in North American fossil mammals. *Science* 280:731–734.
- Banse, K. 1976. Rates of growth, respiration and photosynthesis of unicellular algae as related to cell size: a review. *Journal of Phycology* 12:135–140.
- . 1992. Grazing, temporal changes of phytoplankton concentrations, and the microbial loop in the open sea. Pages 409–440 in P. G. Falkowski and A. D. Woodhead, eds. *Primary productivity and biogeochemical cycles in the sea*. Plenum, New York.
- Belgrano, A., A. P. Allen, B. J. Enquist, and J. F. Gillooly. 2002. Allometric scaling of maximum population density: a common rule for marine phytoplankton and terrestrial plants. *Ecology Letters* 5:611–613.
- Brooks, J. L., and S. I. Dodson. 1965. Predation, body size and composition of plankton. *Science* 150:28–35.
- Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage, and G. B. West. 2004. Toward a metabolic theory of ecology. *Ecology* 85:1771–1789.
- Burckle, L., and R. B. McLaughlin. 1977. Size change in the marine diatom *Coscinodiscus nodulifer* A. Schmidt in the equatorial Pacific. *Micropaleontology* 23:216–222.
- Butterfield, N. J. 1997. Plankton ecology and the Proterozoic-Phanerozoic transition. *Paleobiology* 23:247–262.
- Carpenter, S. R., and J. F. Kitchell. 1993. *The trophic cascade in lakes*. Cambridge University Press, Cambridge.
- Chesson, P. 2000. Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics* 31:343–366.
- Chisholm, S. W. 1992. Phytoplankton size. Pages 213–237 in P. G. Falkowski and A. D. Woodhead, eds. *Primary productivity and biogeochemical cycles in the sea*. Plenum, New York.
- Cohen, J. E., T. Jonsson, and S. R. Carpenter. 2003. Ecological community description using the food web, species abundance, and body size. *Proceedings of the National Academy of Sciences of the USA* 100:1781–1786.
- Dieckmann, U., and R. Law. 1996. The dynamical theory of coevolution: a derivation from stochastic ecological processes. *Journal of Mathematical Biology* 34:579–612.
- Falkowski, P. G., R. T. Barber, and V. Smetacek. 1998. Biogeochemical controls and feedbacks on ocean primary production. *Science* 281:200–206.
- Falkowski, P. G., M. E. Katz, A. H. Knoll, A. Quigg, J. A. Raven, O. Schofield, and F. J. R. Taylor. 2004. The evolution of modern eukaryotic phytoplankton. *Science* 305:354–360.
- Fasham, M. J. R., H. W. Ducklow, and S. M. McKelvie. 1990. A nitrogen-based model of plankton dynamics in the oceanic mixed layer. *Journal of Marine Research* 48:591–639.
- Finkel, Z. V., M. E. Katz, J. D. Wright, O. M. E. Schofield, and P. G. Falkowski. 2005. Climatically driven macroevolutionary patterns in the size of marine diatoms over the Cenozoic. *Proceedings of the National Academy of Sciences of the USA* 102:8927–8932.
- Frost, B. W. 1972. Effects of size and concentration of food particles on the feeding behavior of the marine planktonic copepod *Calanus pacificus*. *Limnology and Oceanography* 17:805–815.

- Hofmann, E. E. 1988. Plankton dynamics on the outer southeastern U.S. continental shelf. III. A coupled physical-biological model. *Journal of Marine Research* 46:919–946.
- Huisman, J., M. Arrayás, U. Ebert, and B. Sommeijer. 2002. How do sinking phytoplankton species manage to persist? *American Naturalist* 159:245–254.
- Hutchinson, G. E. 1961. The paradox of the plankton. *American Naturalist* 95:137–145.
- Irigoien, X., J. Huisman, and R. P. Harris. 2004. Global biodiversity patterns of marine phytoplankton and zooplankton. *Nature* 429:863–867.
- Li, W. K. W. 2002. Macroecological patterns of phytoplankton in the northwestern North Atlantic Ocean. *Nature* 419:154–157.
- Loeuille, N., and M. Loreau. 2004. Nutrient enrichment and food chains: can evolution buffer top-down control? *Theoretical Population Biology* 65:285–298.
- Loeuille, N., M. Loreau, and R. Ferriere. 2002. Consequences of plant-herbivore coevolution on the dynamics and functioning of ecosystems. *Journal of Theoretical Biology* 217:369–381.
- Malone, T. C. 1980. Algal size. Pages 433–463 in I. Morris, ed. *The physiological ecology of phytoplankton*. University of California Press, Berkeley.
- Margalef, R. 1978. Life-forms of phytoplankton as survival alternatives in an unstable environment. *Oceanologica Acta* 1:493–509.
- Mullin, M. M. 1963. Some factors affecting the feeding of marine copepods of the genus *Calanus*. *Limnology and Oceanography* 8:239–250.
- Parsons, T. R., M. Takahashi, and B. Hargrave. 1984. *Biological oceanographic processes*. Pergamon, Oxford.
- Peters, R. H. 1983. *The ecological implications of body size*. Cambridge University Press, Cambridge.
- Porter, K. G. 1973. Selective grazing and differential digestion of algae by zooplankton. *Nature* 244:179–180.
- . 1977. The plant-animal interface in freshwater ecosystems. *American Scientist* 65:159–170.
- Raven, J. A. 1986. Physiological consequences of extremely small size for autotrophic organisms on the sea. *Canadian Bulletin of Fisheries and Aquatic Sciences* 214:1–70.
- . 1994. Why are there no picoplanktonic O₂-evolvers with volumes less than 10⁻¹⁸ m³? *Journal of Plankton Research* 16:565–580.
- . 1998. Small is beautiful: the picophytoplankton. *Functional Ecology* 12:503–513.
- Reynolds, C. S. 1984. *The ecology of freshwater phytoplankton*. Cambridge University Press, Cambridge.
- Riley, G. A. 1946. Factors controlling phytoplankton populations on Georges Bank. *Journal of Marine Research* 6:54–73.
- Rosenzweig, M. L. 1971. The paradox of enrichment: destabilization of exploitation ecosystems in ecological time. *Science* 171:385–387.
- Runge, J. A. 1980. Effects of hunger and season on the feeding behavior of *Calanus pacificus*. *Limnology and Oceanography* 25:134–145.
- Schmidt, D. N., H. R. Thierstein, and J. Bollmann. 2004a. The evolutionary history of size variation of planktic foraminiferal assemblages in the Cenozoic. *Palaeogeography Palaeoclimatology Palaeoecology* 212:159–180.
- Schmidt, D. N., H. R. Thierstein, J. Bollmann, and R. Schiebel. 2004b. Abiotic forcing of plankton evolution in the Cenozoic. *Science* 303:207–210.
- Sheldon, R. W., A. Prakash, and W. H. Sutcliffe. 1972. The size distribution of particles in the ocean. *Limnology and Oceanography* 17:327–340.
- Smayda, T. J. 1970. The suspension and sinking of phytoplankton in the sea. *Oceanography and Marine Biology Annual Review* 8:353–414.
- Steele, J. H. 1974. *The structure of marine ecosystems*. Harvard University Press, Cambridge, MA.
- . 1998. Incorporating the microbial loop in a simple plankton model. *Proceedings of the Royal Society of London B* 265:1771–1777.
- Sterner, R. W. 1989. The role of grazers in phytoplankton succession. Pages 107–170 in U. Sommer, ed. *Plankton ecology: succession in plankton communities*. Springer, Berlin.
- Stomp, M., J. Huisman, F. de Jongh, A. J. Veraart, D. Gerla, M. Rijkeboer, B. W. Ibelings, et al. 2004. Adaptive divergence in pigment composition promotes phytoplankton biodiversity. *Nature* 432:104–107.
- Tang, E. P. Y. 1995. The allometry of algal growth-rates. *Journal of Plankton Research* 17:1325–1335.
- Tang, E. P. Y., and R. H. Peters. 1995. The allometry of algal respiration. *Journal of Plankton Research* 17:303–315.
- Tilman, D. 1982. *Resource competition and community structure*. Princeton University Press, Princeton, NJ.
- Tozzi, S., O. Schofield, and P. Falkowski. 2004. Historical climate change and ocean turbulence as selective agents for two key phytoplankton functional groups. *Marine Ecology Progress Series* 274:123–132.

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