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**FEATURE ARTICLE**

# Optimal phytoplankton cell size in an allometric model

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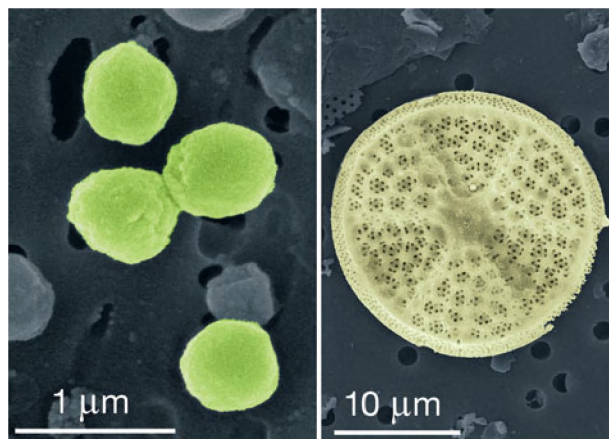
ABSTRACT : The competitive ability of phytoplankton cells is simulated in a model chemostat in which cell size is considered to be an adaptive trait. Parameters describing nutrient uptake kinetics are constrained by empirically derived allometric rules. With a steady input of a single nutrient, the evolutionarily stable cell size is selected through competition among phytoplankton. We find that large cells may be favored when (1) phytoplankton growth is limited by the rate at which internally stored inorganic nutrients can be converted into biomass, and (2) maximum quotas increase with size faster than minimum quotas. Increased internal quotas then accelerate the rate of biomass production in large cells, despite their enhanced requirements for resources. The evolutionarily stable strategy is set by the allometric relationships for nutrient uptake kinetics and by metabolism.

KEY WORDS: Phytoplankton · Allometry · Nutrient uptake · Nutrient storage · Evolution · Evolutionarily stable strategy · Mathematical model

False color SEM of cyanobacteria, *Prochlorococcus* spp. (left), and a fossil centric diatom, *Actinoptychus* spp. (right).

*Images: Anne W. Thompson (left); Jim Ehrman, Zoe Finkel, Mount Allison Digital Microscopy Lab (right)*

## INTRODUCTION

The size spectrum of phytoplankton is a defining characteristic of oceanic ecosystems. Cycling of carbon and other functional properties are strongly influenced by the relative abundance of small and large cells, which in turn appears to be dictated by local environmental conditions such as the water density profile (Li 2002) and mesoscale eddy activity (Rodriguez et al. 2001). Small phytoplankton species dominate the equatorial and subtropical oceans, where nutrient upwelling is low, while larger species are more abundant in subpolar regions, where nutrient supply is both large and highly variable in time (e.g. Uitz et al. 2006). The structure of phytoplankton communities thus presents large-scale geographical patterns that reflect circulation features and biogeochemical processes in the ocean.

The success of large phytoplankton remains somewhat poorly understood, especially when considered in terms of nutrient uptake kinetics. It is widely believed that small cells should dominate under steady-state conditions in the absence of predators. Simple scaling arguments suggest that the best evolutionary strategy is to minimize cell size in order to maximize the surface to volume ratio (Raven 1998, Jiang et al.

2005) and reduce sinking losses (Raven et al. 2005). More specifically, Laws (1975) showed analytically that the competitive advantage of large cells is determined by the size-dependence of the growth to loss ratio. Grover (1991) identified a trade-off between the rates of nutrient uptake and assimilation, but concluded that the potential benefit is not sufficient to compensate for the increased nutrient requirement in large cells.

Other studies suggest different mechanisms for the evolution of large phytoplankton. Thingstad et al. (2005) argued that the success of diatoms is due to their ability to use a non-limiting nutrient (silica) to increase their size without increasing their need for limiting nutrients. Yoshiyama & Klausmeier (2008) identified optimal cell sizes in a model of resource diffusion in fluids, and found that large cells can only outcompete smaller cells if the loss rate decreases with size. Among the studies addressing competition in non-equilibrium conditions, Grover (1990, 1991) found that trading-off competitive ability for high maximum growth rate, which might be achieved by increasing cell size, can be a successful strategy when nutrient supply is variable in time. An alternative hypothesis is that the appearance of predators triggers the evolution of large phytoplankton cells, which are less vulnerable to predation than small prey cells (Butterfield 1997). The theoretical study of Jiang et al. (2005), however, suggests that the evolutionarily stable cell size for phytoplankton co-evolving with zooplankton is still in the picoplankton range.

Here we use a simple theoretical framework (chemostat with a single nutrient) to demonstrate that, even in steady-state conditions and in the absence of predators, increasing cell size can be a successful strategy. The evolution of phytoplankton cell size is examined in the context of allometric scaling arguments derived empirically by Litchman et al. (2007) and grounded in theoretical predictions (Aksnes & Egge 1991, Armstrong 2008). The various parameters characterizing nutrient uptake kinetics can be expressed as power laws of cell volume. We refer to this scaling to constrain phytoplankton growth in a simple model, which we then use to identify evolutionarily stable cell sizes. The patterns emerging from our analysis are the result of the empirical allometric rules, without any artificial size-dependence that would *a priori* favor large cells in specific environmental conditions.

There are 3 principal results from our model. First, phytoplankton growth involves 2 processes: nutrient acquisition and assimilation of stored resources. If growth is limited by the rate of assimilation, increasing size can be an evolutionarily stable strategy that allows cells to produce more biomass by maintaining higher excess cell quota in steady state. Second, large cells are competitive when the storage capacity, defined as the difference between maximum and minimum quotas, increases with size. Third, the positive size-dependence of the storage capacity is traded-off with a higher surface to volume ratio. The evolutionarily stable cell size is set by the allometric relationships for nutrient uptake kinetics, which are empirically constrained, and by metabolic rates, which are not as well constrained.

The ecological model is presented in the next section. We derive size-dependent expressions for the maximum growth rate and half-saturation resource concentration, which together determine the shape of the Holling type II curve describing phytoplankton growth. This is followed by an analysis of the evolutionarily stable strategies (existence, sensitivity, and ecological significance), and a discussion of the limitations of the idealized framework. Finally, the implications of our main results are discussed in the context of modeling phytoplankton communities.

## ALLOMETRIC MODEL

To address the effect of size-dependence on phytoplankton growth, we use a mathematical model of nutrient storage with parameters constrained by empirical allometric relationships (Litchman et al. 2007). The model includes distinct mechanisms for nutrient uptake and assimilation (e.g. Droop 1973, Grenney et al. 1973, Collins 1980, Grover 1991, Flynn et al. 1997). We consider the size-dependence of the maximum uptake rate, half-saturation nutrient concentration, and cell quotas.

**The framework: a variable-internal-resources model.** We simulate phytoplankton growing on a single nutrient in a chemostat using the mathematical model formulated by Droop (1973). As the limiting resource we consider nitrogen, which is often the most limiting nutrient in the ocean. Let $N$ be the dissolved nutrient concentration ($\mu$mol m$^{-3}$), $Q$ the cell quota (internal concentration of nutrients, $\mu$mol cell$^{-1}$), and $B$ the density (cells m$^{-3}$). The model is written as a set of nonlinear ordinary differential equations:

$$\frac{dB}{dt} = \mu_{\infty}\left(1 - \frac{Q_{min}}{Q}\right)B - \delta B \tag{1}$$

$$\frac{dQ}{dt} = V - \mu_{\infty}(Q - Q_{min}) \tag{2}$$

$$\frac{dN}{dt} = d(N_0 - N) - VB \tag{3}$$

where $\mu_{\infty}$ is the growth rate at infinite quota, $Q_{min}$ the minimum quota required by each cell, $V = V(N, Q)$ is the nutrient uptake rate (a function of the dissolved nutrient concentration and cell quota), $d$ is the dilution

Table 1. Parameters of the variable-internal-resources model. See Table 2 for values

| Parameter | Definition | Unit |
|---|---|---|
| $V_{max}$ | Maximum nutrient uptake rate | µmol N cell$^{-1}$ d$^{-1}$ |
| $K_N$ | Half-saturation nutrient concentration (for uptake) | µmol N |
| $Q_{min}$ | Minimum quota ($N$ content) | µmol N cell$^{-1}$ |
| $Q_{max}$ | Maximum quota | µmol N cell$^{-1}$ |
| $\mu_\infty$ | Growth (cell multiplication) rate at infinite quota | d$^{-1}$ |
| $\delta$ | Loss rate | d$^{-1}$ |
| $m$ | Mortality rate | d$^{-1}$ |
| $d$ | Chemostat dilution rate | d$^{-1}$ |
| $N_0$ | Input nutrient concentration | µmol N |

rate, and $N_0$ is the input nutrient concentration. The parameter $\delta$ represents losses by the phytoplankton due to mortality and dilution, so that we write $\delta = m + d$. Parameters and corresponding units are listed in Table 1.

Phytoplankton growth as represented by Eqs. (1) to (3) includes 2 steps, nutrient uptake and assimilation (synthesis of biomass from inorganic nutrients), which are schematically illustrated in Fig. 1. The model effectively decouples these processes, and the growth rate is limited by the slower of the two. Diffusion rates of dissolved inorganic resources can also limit population growth (Yoshiyama & Klausmeier 2008), but this effect is not considered here.

New cells are produced at a rate proportional to the amount of internal resources in excess of the minimum quota ($Q$ includes both structural and stored nutrients; the excess quota is defined as $Q_{XS} \equiv Q - Q_{min}$, cf. Fig. 1). We define the quota-specific synthesis rate as

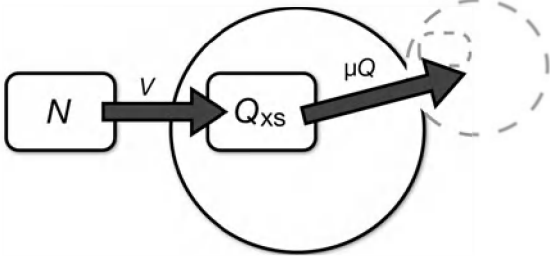$$\mu \equiv \mu_\infty \left( \frac{Q - Q_{min}}{Q} \right) \tag{4}$$



Fig. 1. Nutrient uptake and assimilation in the Droop model (adapted from Finkel et al. 2004, their Fig. 1). Nutrients are taken up through the cell membrane, and excess quota, defined here as $Q_{XS} \equiv Q - Q_{min}$, is used for the production of new biomass (new cells). The growth rate is determined by the minimum of nutrient uptake rate ($V$) and biomass production ($\mu Q$). At equilibrium, $V = \mu Q$ so that cell quotas are constant

In this model, µ can theoretically vary between 0 and $\mu_\infty$. The limit $Q \to Q_{min}$ corresponds to nutrient-starved cells, which do not have stored resources to be assimilated and thus cannot produce new biomass (hence µ = 0). In contrast, the rate of assimilation reaches its maximum, $\mu_\infty$, in the limit $Q \to \infty$, which corresponds to nutrient-replete cells. The yield is defined as $Q^{-1}$, the mass of nutrients needed to produce a new cell. The rate at which resources are assimilated is given by $\mu Q$.

If we form the equation for phytoplankton biomass, $P = QB$, we have

$$\frac{dP}{dt} = \frac{V}{Q} P - \delta P \tag{5}$$

and the equation for the resource is

$$\frac{dN}{dt} = d(N_0 - N) - \frac{V}{Q} P \tag{6}$$

From these equations we infer that the rate of phytoplankton growth is given by $VQ^{-1}$, the resource uptake divided by the amount of resources per new cell (Thingstad et al. 2005, Yoshiyama & Klausmeier 2008). If we assume that the cell quota $Q$ is in equilibrium (i.e. $dQ/dt = 0$, so that the value of $Q$ can be determined from the instantaneous nutrient concentration $N(t)$, then Eqs. (5) & (6) form a closed set of equations.

The phytoplankton per capita growth rate, a measure of fitness, is expressed as

$$G \equiv \frac{1}{P} \frac{dP}{dt} = \frac{V}{Q^*} - \delta \tag{7}$$

where the asterisk denotes an equilibrium value.

**Michaelis-Menten uptake and maximum quotas.** Uptake rate is often assumed to be limited by the external concentration of nutrients (but diffusion can also be important, cf. Yoshiyama & Klausmeier 2008). The Michaelis-Menten function is a common and mechanistically defendable choice to represent this limitation (Aksnes & Egge 1991, Armstrong 2008). We also take into account the upper bound on cell quota, which reflects the fact that cells have a finite storage capacity. Assuming that the uptake rate is a decreasing function of cell quota, the uptake function can be expressed as

$$V = V_{max} \left( \frac{Q_{max} - Q}{Q_{max} - Q_{min}} \right) \frac{N}{N + K_N} \tag{8}$$

where $V_{max}$ is the maximum uptake rate and $K_N$ the half-saturation nutrient concentration for uptake (Thingstad 1987). Uptake slows down as the quotas fill up, and stops when the maximum quota, $Q_{max}$, is reached. This prevents simulated cells from storing implausibly large amounts of nutrients when resources are abundant and assimilation is slow.

Given the uptake function (Eq. 8), we can find the equilibrium cell quota. This equilibrium is the value of $Q$ for which uptake is exactly balanced by assimilation, so that the cell is in steady state. Substituting Eq. (8) into Eq. (2), we solve for the cell quota and get

$$Q^* = \frac{V_{max}Q_{max}N + \mu_\infty Q_{min}\Delta Q(N + K_N)}{V_{max}N + \mu_\infty \Delta Q(N + K_N)} \qquad (9)$$

where we have defined $\Delta Q = Q_{max} - Q_{min}$, the storage capacity.

From Eq. (7) we then infer the per capita growth rate for cells whose uptake rate follows Eq. (8). After some algebraic manipulations we get

$$G = \frac{\mu_\infty V_{max}\Delta Q}{V_{max}Q_{max} + \mu_\infty Q_{min}\Delta Q} \cdot \frac{N}{N + \dfrac{K_N \mu_\infty Q_{min}\Delta Q}{V_{max}Q_{max} + \mu_\infty Q_{min}\Delta Q}} - \delta \qquad (10)$$

Eq. (10) has the form of the growth function proposed by Monod (1949) for bacterial cultures. It can conveniently be rewritten as

$$G = \mu_{max}\frac{N}{N + \kappa} - \delta \qquad (11)$$

where

$$\mu_{max} = \frac{\mu_\infty V_{max}\Delta Q}{V_{max}Q_{max} + \mu_\infty Q_{min}\Delta Q} \qquad (12)$$

$$\kappa = \frac{K_N \mu_\infty Q_{min}\Delta Q}{V_{max}Q_{max} + \mu_\infty Q_{min}\Delta Q} \qquad (13)$$

Here $\mu_{max}$ is the maximum specific growth rate and $\kappa$ is the half-saturation nutrient concentration for phytoplankton growth; these can be related to the empirical parameters in Monod's model. It should be emphasized that $\mu_{max}$ is different from $\mu_\infty$: the *maximum* growth rate $\mu_{max}$ is the actual (observable) fastest per capita growth rate when quotas are at equilibrium, as opposed to $\mu_\infty$, which is the rate of assimilation when quotas are infinite (i.e. not taking into account the coupling between uptake and assimilation). This distinction is subtle but important. Note also that $\mu_{max}$ approaches $\mu_\infty$ when the maximum quota is large compared to the minimum quota (Litchman et al. 2007) and when assimilation is slow compared to nutrient uptake (cf. Eq. 17 and discussion thereafter).

An interesting special case arises when cells have very large storage capacity. At the limit $Q_{max} \gg Q_{min}$, the expressions above reduce to

$$\lim_{\frac{Q_{max}}{Q_{min}} \gg 1} \mu_{max} = \frac{\mu_\infty V_{max}}{V_{max} + \mu_\infty Q_{min}} \qquad (14)$$

$$\lim_{\frac{Q_{max}}{Q_{min}} \gg 1} \kappa = \frac{K_N \mu_\infty Q_{min}}{V_{max} + \mu_\infty Q_{min}} \qquad (15)$$

which is also the result that one would obtain when assuming a Michaelis-Menten function for nutrient uptake, $V = V_{max}\dfrac{N}{N + K_N}$.

**Uptake- or assimilation-limited growth.** Two processes can limit phytoplankton growth in our model: resource uptake and resource assimilation. The slower of these two determines the rate at which the popula-

tion grows. When the maximum growth rate is given by Eq. (14), limiting processes can be identified by comparing the rates of uptake ($V$) and assimilation ($\mu Q$) under optimal conditions. If equilibrium quotas are assumed to be proportional to $Q_{min}$, then the uptake rate scales with $V_{max}$ and the assimilation rate scales with $\mu_\infty Q_{min}$.

Defining the ratio of uptake to assimilation rates as

$$\xi = \frac{V_{max}}{\mu_\infty Q_{min}} \qquad (16)$$

we identify 2 limits:

$$\mu_{max} \approx \mu_\infty \qquad \text{when } \xi \to \infty \qquad (17)$$

$$\mu_{max} \approx \frac{V_{max}}{Q_{min}} \qquad \text{when } \xi \to 0 \qquad (18)$$

The non-dimensional ratio $\xi$ determines the relative importance of assimilation-limitation and uptake-limitation in cell growth. Large values of $\xi$ indicate that growth is limited by the assimilation step. In that case, nutrients can be taken up faster than they can be used, and the maximum growth rate approaches the growth rate at infinite quota. When the ratio is small, nutrient uptake is the limiting step: resources are converted into organic matter nearly as fast as they are absorbed. Growth should then be proportional to the rate of nutrient uptake and inversely proportional to the amount of resources that are 'locked in' the minimum quota. Note that $\xi$ will be size-dependent if the uptake and assimilation rates are size-dependent.

**Size-dependent growth parameters.** We use allometric relationships for the 4 parameters $V_{max}$, $K_N$, $Q_{min}$, and $Q_{max}$ from the literature as detailed in Table 2. These have the form $as^b$, where $s$ is cell size (cell volume normalized by a reference volume), $b$ is the allometric exponent, and $a$ is a constant. We obtain expressions for the size-dependence of $\mu_{max}$ and $\kappa$ by substituting the allometric relationships into Eqs. (12)

Table 2. Scaling for size-dependent parameters ($x$) in the form $x = as^b$, where $s$ is the cell size normalized by 1 $\mu m^3$. Allometric relationships for $V_{max}$, $\mu_\infty$, and $Q_{min}$ are derived from a compilation of data from various phytoplankton groups (Litchman et al. 2007). Scaling for $Q_{max}$ is specific to diatom cells (Montagnes & Franklin 2001, their Table 3). Allometric coefficients and exponents for the growth and mortality rates are unspecified (–)

| Parameter | $a$ | $b$ (exponent) | Source |
|---|---|---|---|
| $V_{max}$ | $9.10 \times 10^{-9}$ | 0.67 | Litchman et al. (2007) |
| $K_N$ | 0.17 | 0.27 | Litchman et al. (2007) |
| $Q_{min}$ | $1.36 \times 10^{-9}$ | 0.77 | Litchman et al. (2007) |
| $Q_{max}$ | $4.64 \times 10^{-9}$ | 0.81 | Montagnes & Franklin (2001) |
| $\mu_\infty$ | $a_\mu$ | $\alpha$ | – |
| $m$ | $a_m$ | $\beta$ | – |

& (13) (see Appendix 1). The resulting expressions are specific to the choice of the uptake function $V(N,Q)$. Of the parameters in Eqs. (12) & (13), only $\mu_\infty$ is not constrained by an empirical power law; we have considerably reduced the number of parameters in the model by expressing phytoplankton growth in terms of cell size. If we assume that quotas are at equilibrium, we can use the consumer–resource model (Eqs. 5 & 6) with the expressions for $\mu_{max}(s)$ and $\kappa(s)$.

Note that we can consider either constant or size-dependent values for $\mu_\infty$. Because assimilation rate scales as $\mu_\infty Q_{min}$, the size-dependence of the assimilation rate follows that of the minimum quota when we assume a constant value for the growth rate at infinite quota. In our case this implies an allometric exponent of 0.77 (Table 2). This value happens to be remarkably similar to the $\frac{3}{4}$-power scaling of metabolic rates with body size (e.g. Kleiber 1947, West et al. 1997). It is consistent with the scaling of photosynthesis rate under optimal growth conditions assumed by Finkel et al. (2004). In our model, as in Finkel et al. (2004), actual growth rates depart from the rate of biomass synthesis because of resource limitation. The size-dependence of growth takes the form of a complex function of size, captured by the expressions for $\mu_{max}(s)$ and $\kappa(s)$ given in Appendix 1.

## RESULTS

With the model laid out, we can now use it to explore the evolutionary pressures on phytoplankton cell size. We proceed analytically to find evolutionarily stable strategies (ESS) in the model with constant nutrient supply.

### Evolutionarily stable size

ESS can be identified when considering cell size ($s$) as an adaptive trait. On ecological timescales, phytoplankton are competing for a single resource and only cells that are best adapted to their environment (i.e. that have the highest fitness, here defined by $G$) will survive. If we assume that (1) the environment is determined by the resident population; (2) the adaptive trait varies slowly compared to the ecological dynamics, so that on an evolutionary timescale the ecological model is always at equilibrium; and (3) invaders with slightly different trait values are introduced at low densities (e.g. Dercole & Rinaldi 2008), then invasibility is determined by the invasion fitness, i.e. the initial per capita growth rate of individuals with trait $s$ in the environment consisting of the resident population.

An ESS corresponds to a maximum of the invasion fitness function. When the resident strategy yields higher fitness than all nearby strategies, it is evolutionarily stable. The invasion fitness as defined by Eq. (7) vanishes when evaluated for the resident population. The resident can be replaced by invaders with positive fitness, so until it has reached the optimal value, evolution will move the resident cell size in the direction of the local fitness gradient. At the optimum cell size, $\bar{s}$, all invaders have a negative fitness. Mathematically, the conditions for $\bar{s}$ to be an ESS are

$$D(s) \equiv \left. \frac{\partial G}{\partial s} \right|_{s=\bar{s}} = 0 \tag{19}$$

and

$$\left. \frac{\partial^2 G}{\partial s^2} \right|_{s=\bar{s}} < 0 \tag{20}$$

where $G$, given by Eq. (11) and in which we have substituted the expressions for $\mu_{max}(s)$ and $\kappa(s)$, is evaluated at the equilibrium nutrient concentration ($N = N^*$). The function $G$ gives the fitness of a rare invader into the resident population.

In steady-state conditions, resource competition theory (Tilman 1980) applies, so that the ESS also corresponds to the minimum value of $N^*$ (cf. proof in Appendix 1): the phytoplankton that has the lowest threshold resource concentration wins the competition for a single limiting resource. The numerical simulations of Jiang et al. (2005) confirm that the nutrient–phytoplankton (NP) system evolves to a steady state where the concentration of dissolved nutrients is minimized and phytoplankton fitness is maximized. The ESS is globally stable; local stability or instability (evolution toward a fitness minimum) do not occur in these simulations. Thus, evolutionary dynamics drive cell size toward its optimal value, which can be either 0 (the smallest cells are favored) or some positive value.

The function $G$ is independent of the input nutrient concentration $N_0$, and depends on the dilution rate $d$ only through its contribution to phytoplankton loss. This implies that the optimal size is not affected by the resource supply. Since most parameters are constrained by empirical allometric relationships, the ESS is determined entirely by the values assigned to the loss rate ($\delta$) and growth rate at infinite quota ($\mu_\infty$). Note, however, that the existence of positive equilibrium solutions does depend on the rate of nutrient supply; a larger amount of resources must be supplied to sustain a population of large cells than a population of small cells.

Eqs. (19) & (20) are solved numerically for the evolutionarily stable size. Graphical solutions are useful for illustrating the concept of ESS. Fig. 3 shows an example of a pairwise invasibility plot (PIP). The approach consists of plotting the growth rate of an invader species (size $s' = s + \delta s$) in a resident population (size $s$) for
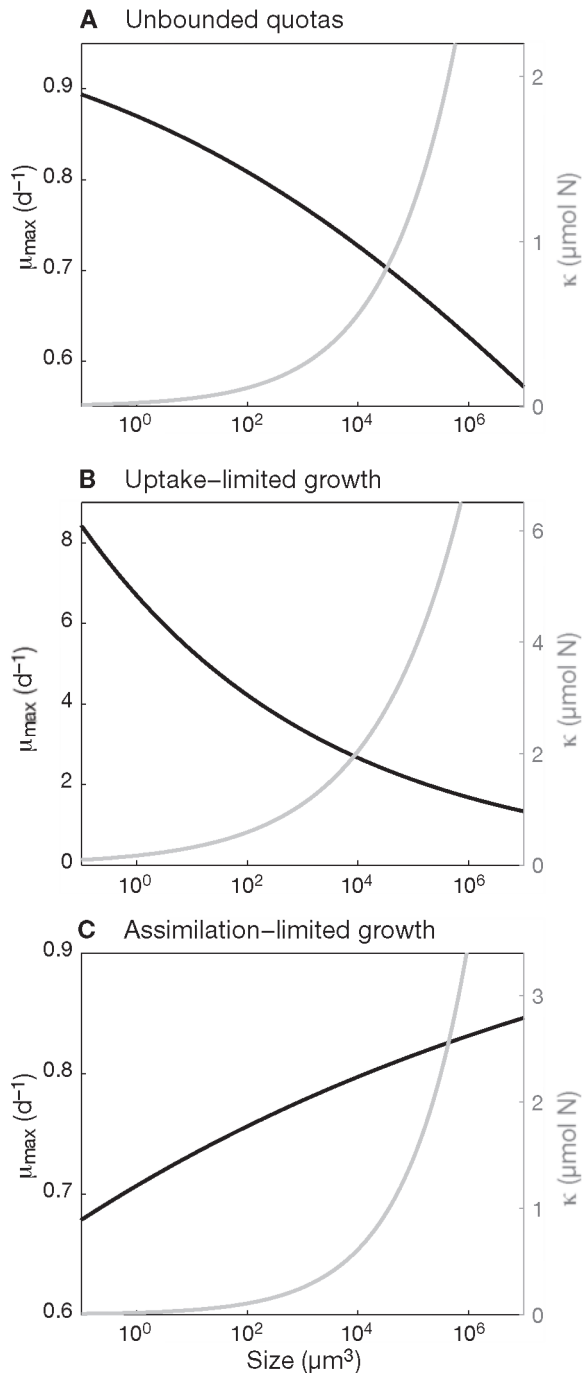
Fig. 2. Size-dependence of the maximum growth rate ($\mu_{max}$; ——) and half-saturation nutrient concentration ($\kappa$; ——), when it is assumed that (A) cell quotas are unbounded: $Q_{max} \gg Q_{min}$; (B) growth is limited by the rate of nutrient uptake: $\mu_\infty Q_{min} \gg V_{max}$; and (C) growth is limited by the rate of assimilation: $V_{max} \gg \mu_\infty Q_{min}$. Maximum quotas in (B) and (C) follow an allometric relationship (Table 2). We assume a constant value for the growth rate at infinite quota ($\mu_\infty = 1$, $\alpha = 0$). Since fast growth rates and low half-saturation values are advantageous, the smallest cells are favored in (A) and (B). Only the scenario shown in (C) provides a trade-off between $\mu_{max}$ and $\kappa$ as cell size increases, so that the optimal cell size can take intermediate or large values

all pairs $\{s,s'\}$. The growth rate is, by definition, zero for all $s = s'$ (the growth rate vanishes in steady-state). An ESS corresponds to a value of $s$ for which all nearby invaders ($|s - s'| \ll s$) have a negative growth rate. From the PIP we can see that $\bar{s}$ is an ESS in this particular example (Fig. 3). The stability of this point is not only local, since all invaders have a negative fitness, thus $\bar{s} = 56\ \mu m^3$ is a global ESS.

Some conclusions can be drawn from inspecting the form of the fitness gradient, $D$. Differentiating the expression for $G$ yields

$$D = \frac{N^*}{(N^* + \kappa)} \frac{\partial \mu_{max}}{\partial s} - \mu_{max} \frac{N^*}{(N^* + \kappa)^2} \frac{\partial \kappa}{\partial s} - \frac{\partial m}{\partial s} \quad (21)$$

The last term vanishes if we assume that losses are independent of size (i.e. $\beta = 0$, see Table 2). Solutions to Eq. (21) then require that the derivatives of $\mu_{max}$ and $\kappa$ have the same sign. This implies that there must be a trade-off between maximum growth rate and resource requirements in order to get a positive ESS. We will show that a trade-off is possible only when (1) the size-dependence of storage capacities is taken into account and (2) when growth is assimilation-limited as opposed to uptake-limited. These 2 aspects are examined separately.

### Assumption 1: no upper bound on internal quotas

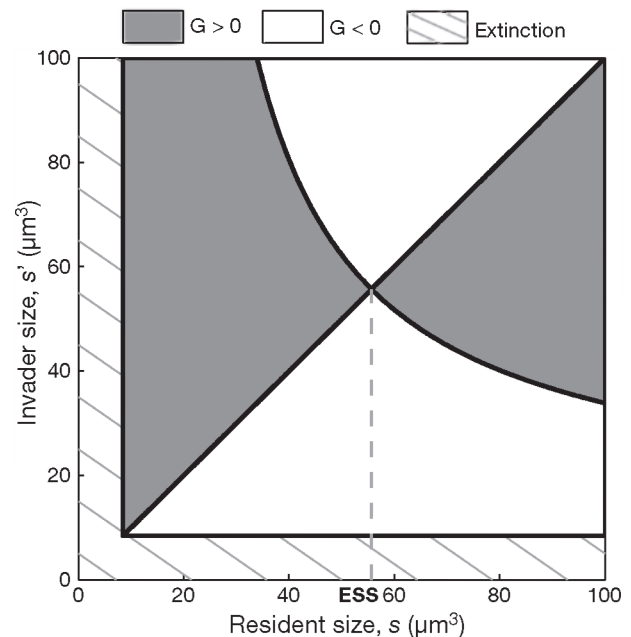If the maximum quota is very large compared to the minimum quota ($Q_{max} \gg Q_{min}$), then nutrient uptake is



Fig. 3. Pairwise invasibility plot. Parameters are $d = \delta = 0.34$, $N_0 = 25$, $\alpha = 0$, and $\mu_\infty = 0.5$. Here $\bar{s} = 56\ \mu m^3$ is an ESS: all invaders have a negative growth rate. There is no positive solution for $s < 7$

not restricted by the available space to store nutrients. This assumption effectively reduces the uptake rate $V$ to a Michaelis-Menten function, and the growth parameters are given by Eqs. (14) & (15). We examine how the maximum growth rate and half-saturation nutrient concentration depend on size to identify potential trade-offs.

The derivative of $\kappa$ is positive for all values of $s$ (Appendix 1). This implies that the half-saturation nutrient concentration strictly increases with size, thus favoring small cells. The derivative of $\mu_{max}$ is negative for all values of $s$ (Appendix 1), implying that the maximum growth rate decreases with size, so that again small cells are favored. These results (Fig. 2a) suggest that it is not possible to get an ESS (other than $\bar{s} = 0$) if maximum quotas are large for all cells. Small cells have the advantage of a larger surface to volume ratio—or, more precisely, surface to nutrient requirement ratio (Thingstad et al. 2005). To find a positive ESS, we must consider the size-dependence of the storage capacity.

### Assumption 2: assimilation-limited growth

Relaxing the first assumption, we now examine the case where nutrient uptake is fast compared to assimilation ($V_{max} \gg \mu_\infty Q_{min}$). This is a valid assumption for a wide range of cell sizes (Fig. 4A), and implies that assimilation of stored resources is the limiting step in phytoplankton growth. The maximum growth rate and half-saturation nutrient concentration from Eqs. (12) & (13) become

$$\mu_{max} \approx \mu_\infty \left(1 - \frac{Q_{min}}{Q_{max}}\right) \tag{22}$$

$$\kappa \approx \frac{K_N \mu_\infty Q_{min}}{V_{max}} \left(1 - \frac{Q_{min}}{Q_{max}}\right) \tag{23}$$

From the first expression we infer that, with $\mu_\infty$ constant, the derivative $\partial\mu_{max}/\partial s$ will be positive as long as $Q_{max}$ increases with size faster than $Q_{min}$. Indeed this appears to be the case (Table 2). The derivative of the half-saturation concentration is also positive (Appendix 1). Since $\kappa$ increases with size faster than $\mu_{max}$, the solution to Eq. (21) must be a maximum. Thus the conditions for the existence of an ESS (Eqs. 19 & 20) are satisfied. In contrast, when nutrient uptake is slow compared to assimilation ($V_{max} \ll \mu_\infty Q_{min}$), we find that $\mu_{max}$ is proportional to the ratio of $V_{max}$ and $Q_{min}$; thus it decreases with size, unlike $\kappa$ which still increases with size, being proportional to $K_N$. Hence a positive ESS is not possible in that case, and evolutionary pressure inevitably selects for the smallest cell size. The uptake-limited and assimilation-limited cases are illustrated in Fig. 2B,C.
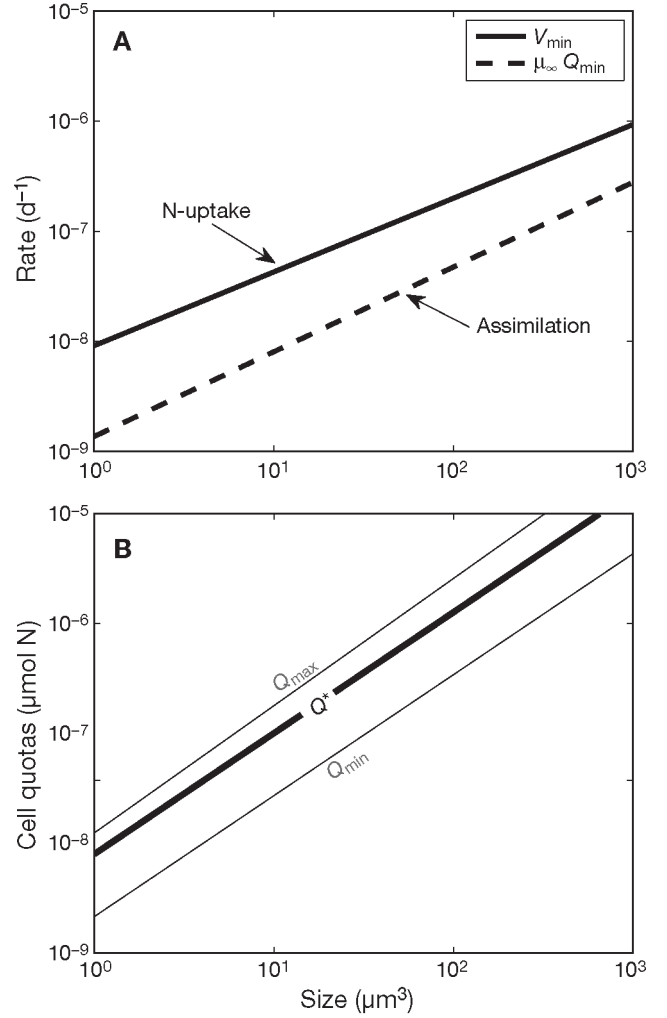


Fig. 4. (A) Scaling of nutrient uptake ($V_{max}$) and assimilation ($\mu_\infty Q_{min}$) when $\mu_\infty = 1$. Maximum uptake rate exceeds assimilation rate for in the range of observed phytoplankton cell sizes. (B) Cell quotas versus size. (——) $Q_{min}$ and $Q_{max}$ ; (▬▬▬) equilibrium quota when $N = \mu_\infty = 1$ and $\delta = 0.6$

Based on our analysis of the model under Assumptions 1 & 2, we conclude that size-dependence of the storage capacity is the key to evolving large cells in this model. Although empirical data suggest that the allometric exponent for maximum quota is larger than the allometric exponent for minimum quota, the difference between them is small and, given the paucity of data, there is likely a large uncertainty. We will keep that in mind as we carry out our analysis, but proceed on the assumption that $\Delta Q$ has a positive dependence on cell size. Another source of uncertainty is the size-dependence of the growth rate at infinite quota; if, as suggested by the metabolic theory of ecology, $\mu_\infty$ decreases with size, then the storage effect needs to be greater for the derivative of $\mu_{max}$ to be positive (see 'Discussion').

When storage capacity increases with size, the ability of large phytoplankton to store nutrients allows them to maintain a larger quota at equilibrium. Small cells fill up more quickly and thus see their uptake rate reduced because of quotas approaching the upper limit ($Q_{max}$) when the uptake rate is given by the function Eq. (8). The large equilibrium quota in large cells increases the rate at which biomass is produced; this is an advantage when growth is limited by the assimilation rate. The resulting trade-off between rapid maximum growth rate and high half-saturation concentration implies that there is an intermediate cell size for which growth is optimal.

## Sensitivity

The sensitivity of ESS values to the model parameters sheds light on the mechanisms of the evolution of large cells. We focus on the sensitivities to the growth rate at infinite quota and the loss rate, assumed here to be independent of size. Fig. 5 shows how the ESS varies with $\mu_\infty$ for different values of the loss rate $\delta$. The upper limit on ESS values is due to the collapse of the phytoplankton population when size increases past a threshold value; large cells require more nutrients than small ones and can only be supported by environments with high nutrient supply, at least when mortal-
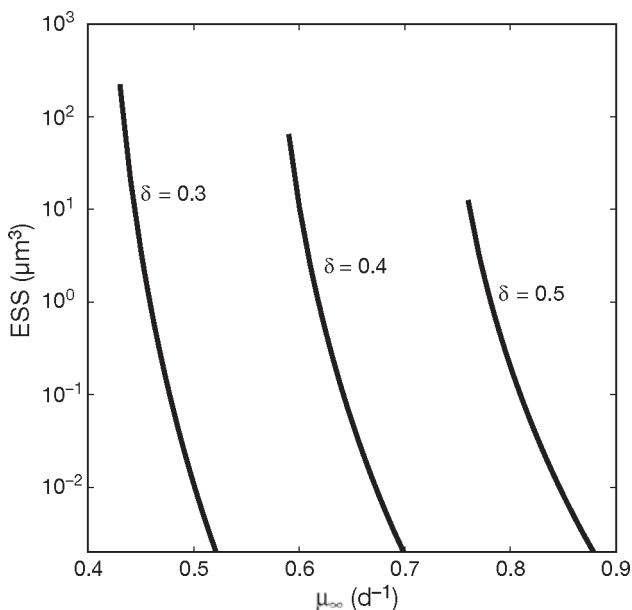


Fig. 5. Evolutionarily stable state ($\overline{s}$) versus the growth rate at infinite quota ($\mu_\infty$), for 3 different values of the loss rate ($\delta$). The model predicts ESS values up to $2 \times 10^2$ μm³. Note that the curves are interrupted at values of $\overline{s}$ for which the ecological model does not have a positive solution. There is no lower limit on evolutionarily stable size in the model, although real cells have a minimum sustainable volume. Parameters as in Fig. 3

ity is independent of size. No lower limit is imposed in the analysis, but it should be kept in mind that cell volumes of ~$10^{-1}$ μm³ are on the order of the smallest observed phytoplankton.

The evolutionarily stable size is negatively correlated with the growth rate at infinite quota (Fig. 5), assumed here to be the same for all species. In steady-state conditions, large cells have the advantage of maintaining a larger quota since $Q^*$ increases with size (Fig. 4B). Reducing the (size-independent) value of $\mu_\infty$ is one way to achieve assimilation-limited growth. The ESS does not depend on the input nutrient concentration $N_0$, which does not appear in the expression for $N^*$.

The ESS is positively correlated with the loss rate (Fig. 5). If we consider $m = 0$, this implies that the ESS increases with the dilution rate. If, however, we assume that dilution does not contribute to phytoplankton loss ($\delta = m$), then the ESS would be independent of the dilution rate $d$. This result was obtained by Jiang et al. (2005) for their NP model. The assumption is relevant under oceanic conditions, where nutrient supply is not necessarily correlated with phytoplankton loss. Regardless of the details of phytoplankton loss, the evolutionarily stable size always increases with $\delta$. The explanation lies in the fact that the equilibrium nutrient concentration ($N^*$) increases with the loss parameter (Appendix 1). Thus increasing $\delta$ benefits large cells which, having higher nutrient requirements, thrive when the ambient nutrient concentration is high.

The high sensitivity of the optimal cell size to the loss rate limits the range of parameter values for which the model predicts a positive ESS. Taking into account the size-dependence of mortality (e.g. due to increasing sinking rates with increasing weight) may expand the relevant range of parameter values, though this is not examined here.

## Size-dependence of the maximum growth rate

With size-dependent storage capacity, there is a range of cell sizes for which $\mu_{max}$ increases with size (Fig. 6). The ESS is always found in the region where $\partial\mu_{max}/\partial s > 0$. The value of cell size that optimizes maximum growth rate is a function of the growth and loss parameters (note that it is not an ESS); it is always positive and finite. The upper bound on the maximum growth rate is due to Assumption 2 failing as $s \to \infty$: uptake-limitation becomes increasingly important as cells get larger. This is evidenced by the non-dimensional ratio $\xi$ (Fig. 6).

Given the empirical allometric relationships (Table 2), the value of $\xi$ is always a decreasing function of cell size. Larger cells have an advantage when assimilation
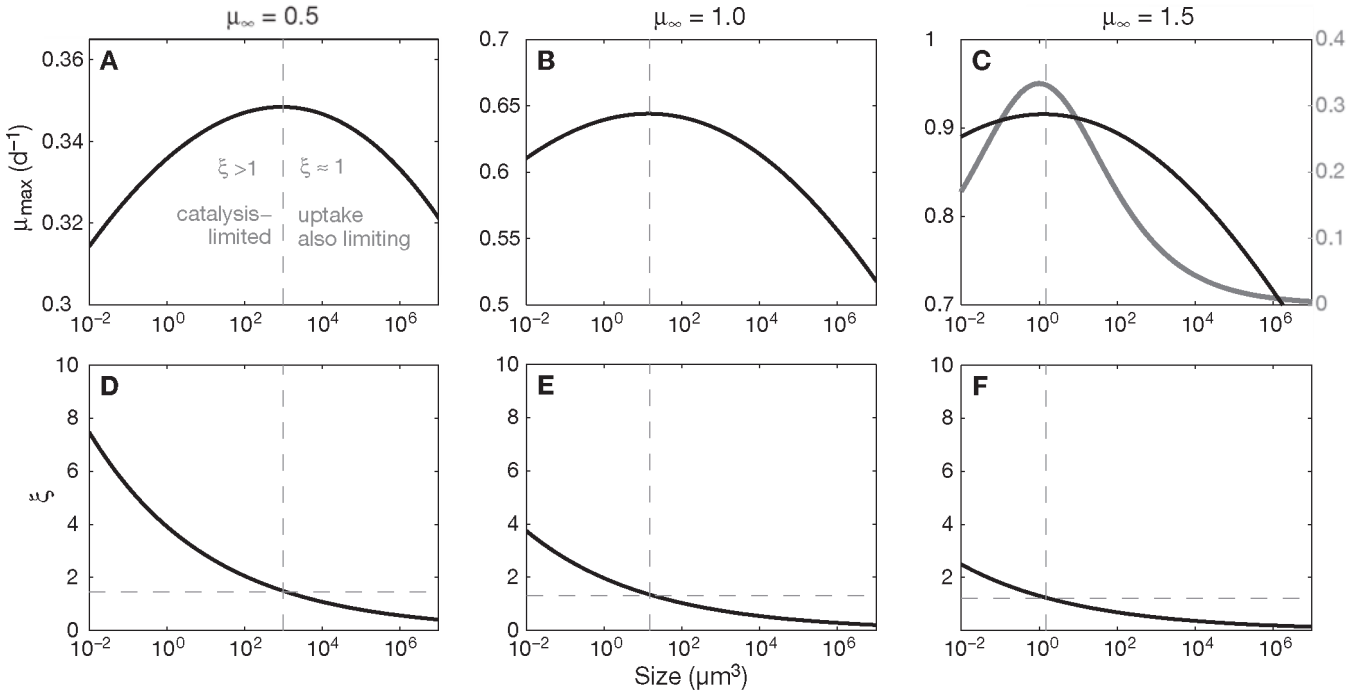
Fig. 6. (A–C) Maximum growth rate $\mu_{max}$ versus cell size, for (A) $\mu_\infty = 0.5$, (B) $\mu_\infty = 1.0$, and (C) $\mu_\infty = 1.5$. Cell size is expressed in $\mu m^3$. For reference, volumes of marine plankton range from roughly 0.5 $\mu m^3$ (*Prochlorococcus*) to more than $10^6$ $\mu m^3$ (diatoms). The maximum (– – – –) is highly sensitive to parameter values. In (C), the growth curve from the model by Jiang et al. (2005) is superimposed (——); the function has the form $\mu_{max} = x(x^2 + x + 1)^{-1}$, where $x$ is cell radius. (D–F) Ratio of the uptake rate and assimilation rate, $\xi$, for the same values of $\mu_\infty$. For small cells, assimilation is limiting phytoplankton growth ($\xi > 1$). (– – – –) the size optimizing $\mu_{max}$ corresponds to a value of $\xi \approx 1$

is limiting, because they have a higher cell quota at equilibrium, which allows them to produce biomass faster. When nutrient uptake is also limiting, smaller cells have an advantage due to their large surface to volume ratio. Indeed we find that the growth potential, $\mu_{max}$, increases with size when $\xi$ is large, but decreases with size when $\xi \approx 1$. We find that the positive relation between $\mu_{max}$ and size occurs in the range of cell sizes for which the non-dimensional ratio $\xi$ exceeds 1, confirming the importance of assimilation limitation.

The shape of the $\mu_{max}(s)$ function reflects the combined effects of size-dependent storage ability, nutrient limitation, and assimilation limitation (in contrast to the curves presented in Fig. 2, which highlight each of these effects when considered independently). It is qualitatively similar to the function assumed by Jiang et al. (2005) (Fig. 6C). However, unlike Jiang et al. (2005), we do not impose an arbitrary form to the size-dependence; our expression for the maximum growth rate is determined by the allometric relationships for nutrient uptake. Also in contrast to Jiang et al. (2005), the maximum of the curve is not constrained to the picophytoplankton size range. The maximum is very sensitive to the value of $\mu_\infty$, which is the only parameter appearing in the expression for $\mu_{max}(s)$ that is not empirically constrained.

## DISCUSSION

Using a simple ecosystem model, we have derived expressions for the resource-limited specific growth rate and half-saturation constant that, under 2 simple assumptions, depend only on the phytoplankton cell size. The first assumption is that nutrient uptake kinetics follow an exactly allometric relationship; in fact, these relationships are computed as the 'best fit' to large datasets that are typically noisy (e.g. Litchman et al. 2007), such that for a given phytoplankton species, excursions from the allometric rule can be significant. The second assumption is that cell quotas are always at equilibrium. This implies that nutrient uptake is fast compared to assimilation of stored nutrients and fluctuations in ambient nutrient concentration. While this assumption is consistent with our steady-state chemostat analysis, it becomes more restrictive if applied to time-varying systems. In the ocean, seasonal and diurnal cycles, as well as turbulent circulation features, influence the rate of nutrient supply to the euphotic zone, with consequences for phytoplankton dynamics. Assuming equilibrium quotas effectively prevents the simulated cells from accumulating nutrients during periods of abundance.

The proposed mechanism for the evolution of large cells relies strongly on the size-dependence of storage,

which implies that the allometric exponent of maximum quotas must be greater than that of minimum quotas. Although the allometric relationships used in the quantitative part of our analysis satisfy the necessary condition, the uncertainties in the measurements considerably exceed the difference between these exponents. Several published studies do assume size-dependent storage capacity (e.g. Grover 1989, Irwin et al. 2006), but more laboratory studies are needed in order to obtain a statistically significant relationship between storage capacity and cell size in phytoplankton.

The allometric model with constant (size-independent) storage capacity will also support an ESS if the mortality rate ($m$) decreases with size. Sinking is one mechanism which might produce size-dependent losses, but, at least for spherical cells, these losses would increase for larger organisms. Here we have neglected predation and other density-dependent effects on mortality. Because we assume a linear mortality rate, the evolutionarily stable size is independent of the input nutrient concentration. However, since the maximum cell size increases with the availability of resources, we expect to find only small cells in oligotrophic environments (even if they would be better competitors, populations of large cells are bound to collapse due to the lack of resources to support their growth). Evolutionary dynamics determine whether large or small (or intermediate) cells will dominate in eutrophic environments. Including a grazer population in the model leads to a dependence of the ESS on the nutrient supply and can destabilize the phytoplankton population dynamics (Jiang et al. 2005). Interestingly, the phytoplankton–zooplankton model can evolve to a fitness minimum (Jiang et al. 2005), opening up the door to evolutionary branching events and coexistence of multiple cell sizes. Even with grazers, however, ESS are constrained to the region where maximum growth rate increases with size (Jiang et al. 2005).

ESS values are highly sensitive to the value of the growth rate at infinite quota, $\mu_\infty$, which defines the maximum rate at which stored inorganic nutrients are converted into biomass. We have assumed $\mu_\infty$ to be independent of size, mainly because we do not have empirical evidence of an allometric relationship for this parameter across phytoplankton groups. If $\mu_\infty$ scales with body size as predicted by the metabolic theory of ecology (West et al. 1997), the analysis presented here should be revisited to account for the metabolic disadvantage of increasing cell size. A weak decrease of $\mu_\infty$ with size could reduce the magnitude of the storage effect without affecting the size-dependence of $\mu_{max}$. A strong decrease of $\mu_\infty$ with size, on the other hand, could qualitatively change the size-dependence of $\mu_{max}$ and $\kappa$. However, assuming a constant value for $\mu_\infty$ is not equivalent to assuming size-independent metabolism. The actual rate of biomass production in our model scales like $\mu_\infty Q_{min}$, which has an allometric exponent of $0.77$. The fact that this is so close to $\frac{3}{4}$ may not be meaningful, but it suggests that assuming a constant value for $\mu_\infty$ is not necessarily in conflict with metabolic theory.

The origin of allometry in biological systems is a fundamental question that is still widely debated. There are theories relating the scaling laws to basic physical and geometrical constraints (e.g. West et al. 1997). It is also plausible that allometric relationships themselves have evolved as a result of competition and adaptation processes. While some relationships are tied to biochemical or biomechanical principles, others probably are not, and might be considered as emergent properties of the ecological–evolutionary system. This question is, however, outside the scope of the present study.

Finally, we emphasize that our model is not formulated for a particular phytoplankton species, but rather as a framework describing phytoplankton ecological interactions in the most general sense possible. However, the framework may be more adequate for some phytoplankton taxonomic groups than others.

While diatoms are known to store nutrients and are well described by the Droop model, other taxa such as coccolithophorids and dinoflagellates may be more adequately represented by a classical Monod model. There is also a lack of empirical studies of the size-dependence of maximum quotas across taxa. Here we relied on diatom data for the size-dependence of the storage effect; other taxonomic groups may not follow similar allometric relationships.

## CONCLUSIONS

Phytoplankton can be studied using trait-based approaches (Litchman et al. 2007). Here we consider cell size as an adaptive trait and incorporate empirically derived allometric relationships (Litchman et al. 2007) into an ecological–evolutionary model to identify evolutionarily stable states. Using this framework, we revisit the paradigm of small-cell dominated phytoplankton communities in the absence of predation and time-variability of resource supply (Laws 1975, Raven 1998, Raven et al. 2005).

Results from our simulations suggest that the size-dependence of cellular quotas gives an advantage to large cells, which theoretically can evolve from small cells as a result of adaptation and competition processes. The mechanism selecting for large phytoplankton involves a trade-off between storage capacity and minimum nutrient requirement. Larger cells require more nutrients, but they have a higher cell quota at equilibrium, which allows them to produce biomass faster, thus giving them advantage under assimilation-limited conditions.

Smaller cells have an advantage under uptake-limited conditions due to their large surface to volume ratio. We find that, depending on the environmental conditions (dilution rate) and the metabolic rates (growth rate at infinite quota and respiration and/or mortality), the ESS can range from cyanobacteria-sized cells (0.1 to 1 $\mu m^3$) to diatom-sized cells ($\approx 10^2$ to $10^3$ $\mu m^3$).

Our analysis focuses on a single ecological mechanism, leaving out several potentially important factors affecting the evolution of cell size; perhaps most significant is the top-down control by zooplankton grazing preferentially on small phytoplankton cells. Here we purposely construct an idealized framework in order to gain a deeper understanding of its function. Despite its simplicity, the chemostat model, together with allometric scaling, provides a quantitative framework for studying evolutionary dynamics in phytoplankton. Results may be relevant to the interpretation of observed community structure in the global ocean. Moreover, the trait-based concepts developed in the present study may be implemented in more complex models, which can offer a more complete description of aquatic ecosystems by including competition and coexistence processes. The numerical model developed by Follows et al. (2007) is an ideal framework to simulate the assembly of phytoplankton communities in realistic oceanic conditions. The model operates on the principle that natural selection determines the geographical distribution of phytoplankton 'ecotypes' in the ocean. The size-dependent relations for specific growth and half-saturation nutrient concentration presented in the present study, incorporated into such a modeling framework, would provide a novel approach to simulating the assembly of size-structured communities.

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**Appendix 1.** Allometric model analysis

## EQUILIBRIUM SOLUTIONS

The equilibrium nutrient is obtained by solving the equation for $G = 0$. Then we can solve for the equilibrium phytoplankton concentration by substituting $V/Q = \mu = \delta$ into Eq. (6), which gives

$$P^\bullet = \frac{r(N_0 - N^\bullet)}{\delta} \tag{A1}$$

$$N^\bullet = \frac{\delta\kappa}{\mu_{max} - \delta} \tag{A2}$$

If the uptake function is given by Eq. (8) then the equilibrium nutrient concentration is

$$N^\bullet = K_N \left[ \frac{V_{max}}{\mu_\infty Q_{min}} \left( \frac{\mu_\infty}{\delta} - \frac{Q_{max}}{\Delta Q} \right) - 1 \right]^{-1} \tag{A3}$$

## SIZE-DEPENDENCE AND SENSITIVITY OF GROWTH PARAMETERS

The size-dependent growth parameters are

$$\mu_{max}(s) = \frac{9.10(4.64s^{1.48+\alpha} - 1.36s^{1.44+\alpha})}{(a_\mu)^{-1}42.22s^{1.48} + 6.31s^{1.58+\alpha} - 1.85s^{1.54+\alpha}} \tag{A4}$$

$$\kappa(s) = \frac{0.231(4.64s^{1.85+\alpha} - 1.36s^{1.81+\alpha})}{(a_\mu)^{-1}42.22s^{1.48} + 6.31s^{1.58+\alpha} - 1.85s^{1.54+\alpha}} \tag{A5}$$

where the allometric coefficient ($a_\mu$) and exponent ($\alpha$) for the growth rate at infinite quota have been left unspecified. Other empirical allometric relationships have been substituted (Table 2).

When $\alpha = 0$, the growth rate at infinite quota is equal to the constant $a_\mu$. We examine the size-dependence of $\mu_{max}$ and $\kappa$ under the assumption of constant $\mu_\infty$.

### Assumption 1: $Q_{max} \gg Q_{min}$

In the limit of unbounded quotas, the expressions for $\mu_{max}(s)$ and $\kappa(s)$ can be simplified to take the form of Eqs. (14) & (15). We differentiate the reduced expressions to examine the size-dependence of the growth parameters in the absence of the size-dependent storage effect.

Differentiating Eq. (14), we get

$$\frac{\partial}{\partial s}\mu_{max} = \frac{\partial}{\partial s}\left( \frac{9.10\mu_\infty s^{0.67}}{9.10s^{0.67} + 1.36\mu_\infty s^{0.77}} \right) \tag{A6}$$

$$= -1.23\frac{\mu_\infty^2 s^{0.44}}{(9.10s^{0.67} + 1.36\mu_\infty s^{0.77})^2}$$

which is negative for all values of $s$.

Differentiating Eq. (15) yields

$$\frac{\partial}{\partial s}\kappa = \frac{\partial}{\partial s}\left( \frac{0.231\mu_\infty s^{1.04}}{9.10s^{0.67} + 1.36\mu_\infty s^{0.77}} \right) \tag{A7}$$

$$= \frac{0.78\mu_\infty s^{0.71} + 0.08\mu_\infty^2 s^{0.81}}{(9.10s^{0.67} + 1.36\mu_\infty s^{0.77})^2}$$

which is positive for all values of $s$.

### Assumption 2: $V_{max} \gg \mu_\infty Q_{min}$

At the limit of assimilation-limited growth, the expressions for $\mu_{max}(s)$ and $\kappa(s)$ are given by Eqs. (22) & (23). The derivative of the maximum growth rate (Eq. 22) is

$$\frac{\partial}{\partial s}\mu_{max} = 0.012\mu_\infty s^{-1.04} \tag{A8}$$

which is positive for all values of $s$.

The derivative of the half-saturation nutrient concentration (Eq. 23) is

$$\tag{A9}$$

$$\frac{\partial}{\partial s}\kappa = \left( 1 - \frac{Q_{min}}{Q_{max}} \right)\frac{\partial}{\partial s}\frac{K_N\mu_\infty Q_{min}}{V_{max}} + \frac{K_N\mu_\infty Q_{min}}{V_{max}}\frac{\partial}{\partial s}\left( 1 - \frac{Q_{min}}{Q_{max}} \right)$$

From Eq. (A6) we know that the second term is positive. The first term is also positive:

$$\mu_{max}\frac{\partial}{\partial s}\frac{K_N\mu_\infty Q_{min}}{V_{max}} = 0.025\mu_{max}\mu_\infty s^{-0.63} \tag{A10}$$

Thus the derivative of $\kappa$ is positive for all values of $s$.

## EQUIVALENCE TO RESOURCE COMPETITION THEORY

Proof that under steady nutrient supply, the ESS always corresponds to the size that yields the lowest steady-state nutrient concentration (i.e. that has the competitive advantage*, cf. resource competition theory). We have

$$\frac{\partial G}{\partial s}\bigg|_{N=N^\bullet} = \frac{\delta}{\mu_{max}}\frac{\partial\mu_{max}}{\partial s} - \frac{\delta(\mu_{max} - \delta)}{\mu_{max}\kappa}\frac{\partial\kappa}{\partial s} - \frac{\partial m}{\partial s} \tag{B1}$$

and

$$\frac{\partial N^\bullet}{\partial s} = -\frac{\kappa\mu_{max}}{(\mu_{max} - \delta)^2}\left[ \frac{\delta}{\mu_{max}}\frac{\partial\mu_{max}}{\partial s} - \frac{\delta(\mu_{max} - \delta)}{\mu_{max}\kappa}\frac{\partial\kappa}{\partial s} - \frac{\partial m}{\partial s} \right] \tag{B2}$$

It is easy to see that if Eq. (B1) vanishes, then Eq. (B2) must vanish as well; thus $N^\bullet$ is an extremum. We can rewrite Eq. (B2) as

$$\frac{\partial N^\bullet}{\partial s} = -\gamma\frac{\partial G}{\partial s} \tag{B3}$$

where

$$\gamma \equiv \frac{\kappa\mu_{max}}{(\mu_{max} - \delta)^2} \tag{B4}$$

is always positive; then we have

$$\frac{\partial^2 N^\bullet}{\partial s^2} = -\frac{\partial\gamma}{\partial s}\frac{\partial G}{\partial s} - \gamma\frac{\partial^2 G}{\partial s^2} \tag{B5}$$

At the ESS, the first term vanishes, hence the second derivatives of $N^\bullet$ and $G$ have opposite signs. This implies that $N^\bullet$ is a minimum at the ESS if $G$ is a maximum.