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Scaling-up from nutrient physiology to the size-structure of phytoplankton communities

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In many community assemblages, the abundance of organisms is a power-law function of organism size. In phytoplankton communities, changes in size structure associated with increases in resource availability and total biomass have often been interpreted as a release from grazer control. A metapopulation-like approach is used to scale up from the individual physiological responses to environmental conditions to community size structure assuming the community taxonomic composition reflects the species pool. We show that the size scaling of cellular nutrient requirements and growth can cause (1) the power-law relationship between cell size and abundance, (2) dominance of small phytoplankton cells under oligotrophic conditions, and (3) relative increase in abundance of larger phytoplankton cells under eutrophic conditions. If physiological differences associated with the taxonomic composition of different community size fractions are considered, then the model can replicate detailed field observations such as the absence of small, slow-growing Prochlorococcus spp. and the relative dominance of large diatom species in nutrient-rich, upwelling regions of the ocean.

INTRODUCTION

The size structure of phytoplankton communities strongly influences the function of aquatic ecosystems. Large phytoplankton cells are tend to be grazed by large zooplankton, resulting in shorter, simpler food webs resulting in more efficient matter and energy transfer to larger consumers (Ryther, 1969). Large and dense phytoplankton cells are responsible for the majority of exported production (Tremblay *et al.*, 1997; Laws *et al.*, 2000; Brown and Landry, 2001; Le Borgne *et al.*, 2002). This flux of fixed carbon and nutrients from the surface into the deep ocean sequesters carbon from the ocean-atmosphere system for hundreds to thousands of years (Eppley and Peterson, 1979; Falkowski *et al.*, 2000). Therefore, understanding the mechanisms controlling the size structure of the phytoplankton community in response to environmental forcing is essential to understanding temporal and spatial fluctuations in food web structure, the regulation of the biological pump, and the ability of the ocean to act as a long-term sink for atmospheric carbon dioxide.

Be it bacteria or large mammals, organism size is a predictor of metabolic rate:

$$M = c_1 V^b \tag{1}$$

where c_1 is a group-specific coefficient and b is the size scaling exponent of the relationship between the metabolic rate, M (for example growth rate) and a dimensionless measure of organism size, V (for example biovolume, normalized by a reference size). While c_1 is variable, b is commonly $^3/_4$ for organism-specific metabolic rates due to fundamental geometric constraints (West *et al.*, 1999; Banavar *et al.*, 2002). Assuming organism mass is linearly related to organism volume, the size-scaling exponent of mass-specific metabolic rates is

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$^3/_4 - 1 = -^1/_4$. Deviations in the $^3/_4$ size-scaling exponent have been associated with sub-optimal environmental conditions, such as extremes in temperature and irradiance (Banse, 1976; Peters, 1983a; Sommer, 1989; Finkel, 2001; Gillooly *et al.*, 2001). Resource limitation by light or nutrient availability can alter the size scaling of metabolic rates, resulting in a decrease in the size-scaling exponent (Finkel, 2001). A change in the size scaling of growth rate arising as a physiological response to resource availability will not in general be immediately balanced by a corresponding change in community loss terms and thus will lead to a change in phytoplankton community size structure.

The size-dependence of resource acquisition can have a large effect on phytoplankton physiology and growth rates and thus can potentially alter phytoplankton abundance and community-size structure. Experimental and theoretical evidence demonstrates that smaller cells have higher rates of nutrient uptake per unit biomass and lower half-saturation constants due to their higher surface area to volume (SA/V) ratios (Eppley and Thomas, 1969; Aksnes and Egge, 1991; Hein *et al.*, 1995). Additional size-dependent factors include metabolite leakage rates, nutrient storage, interactions with irradiance, and surge uptake. Furthermore, small cells have a lower minimum cellular metabolic requirement that selectively allows them to survive at much lower resource concentrations than larger cells (Shuter, 1978; Grover, 1991). For example, if we consider that nutrient flux to a phytoplankton cell depends on diffusion and that growth is a function of uptake and cell quota, then the resource concentration required to maintain a specific percentage of the maximum growth rate (if maximum growth rate is proportional to $V^{-0.25}$) will scale as $V^{1/3}$ (Pasciak and Gavis, 1974; Hudson and Morel, 1993; Finkel *et al.*, 2004). Lower resource requirement per individual supports higher population densities, decreasing the likelihood of genetic bottlenecks and chance stochastic extinction events (Fenchel, 1993). Small phytoplankton cells appear to have significant advantages over larger phytoplankton cells under nutrient-limited steady-state environmental conditions (Grover, 1989; Grover, 1991), giving them an apparent benefit over larger cells and could be expected to affect the community-size distribution.

Despite all the advantages of small size, phytoplankton cells span over ten orders of magnitude in cell volume. Taxonomic classes of phytoplankton have characteristic size ranges, resulting in a covariation between cell size and taxonomic structure and indicating a suite of adaptations for each range of cell sizes. Initially, we treat all phytoplankton as being physiologically identical, except for their cell size; later in the paper we consider the additional effects of taxonomic variation on maximum intrinsic growth rate and thus the relationship between organism size and abundance. Organism abundance per unit volume (A) is inversely related to organism size:

$$A = c_2 V^{\xi} \tag{2}$$

where the size-scaling exponent (ξ) is often -1 (Sheldon and Parsons, 1967; Sheldon and Kerr, 1972; Sheldon *et al.*, 1972) and c_2 is the concentration of cells of the reference size (1 μm^3). Subsequent studies have found considerable variability in ξ, which often ranges from $-5/3$ to $-2/3$ (Peters, 1983b; Sprules and Munawar, 1986; Boss *et al.*, 2001). The majority of field data suggest that small phytoplankton cells dominate in stable, oligotrophic environments such as the open ocean while larger cells can dominate biomass in variable, eutrophic environments such as coastal areas (Sprules and Munawar, 1986; Ahrens and Peters, 1991; Chisholm, 1992; Li, 2002). In some local studies, predominantly from terrestrial systems, the relationship between abundance and organism size more closely resembles a filled-in triangle where minimum abundance is fairly uniform across organism size and maximum abundance occurs for intermediate-sized species (Lawton, 1990; Blackburn and Gaston, 1996; Gaston and Blackburn, 2000) or multiple peaks are present (Griffiths, 1986).

Hypotheses for the relationship between abundance and organism size in the literature, such as size-dependent differences in energy use (Damuth, 1981), competitive interactions (Grover, 1989; Nee *et al.*, 1991), or the scale-free self-organization of complex adaptive systems (Rinaldo *et al.*, 2002), do not explain why variation in nutrient availability is associated with changes in the size structure of phytoplankton communities, although Sprules and Munawar (Sprules and Munawar, 1986) have hypothesized that variations in c_2 and ξ indicate a deviation from steady state. Food web models that include several trophic levels (often autotrophs, herbivores, and detritivores) and many size-dependent processes (uptake, respiration, sinking rate, grazing rate) have successfully simulated a large number of population- and community-level patterns, but due to a large number of parameters it can be difficult to attribute any particular pattern to any specific mechanism (Moloney and Field, 1991; Moloney *et al.*, 1991; Kerr and Dickie, 2001). These models have contributed to the conclusion that grazing regulates phytoplankton community size structure (Armstrong, 2003; Irigoien *et al.*, 2004; Morin and Fox, 2004), but the physical constraints that cell size places on phytoplankton metabolic rate and resource acquisition ability are often under-emphasized in the study of the relationship between abundance and

organism size. Brown *et al.*, 2004) have hypothesized that biomass-size distributions result from the size and temperature dependence of metabolic rates, but have not accounted for the effects of size on resource acquisition and nutrient requirements. Here we employ a size-resolved physiological model to construct a bottom-up steady-state numerical abundance distribution that incorporates the size-dependence of nutrient acquisition and use, allowing us to predict the size structure of phytoplankton communities as a function of physiological constraints and resource availability. The model's predictions should be most accurate in areas where bottom-up processes determine biomass, such as upwelling regions; where size-dependent grazing is not important, such as where salps that graze all sizes dominate; and deviations from the model could be useful for the identification of regions where size-dependent grazing is important.

METHOD

The size-constrained physiological model

To model the size structure of phytoplankton communities, biomass, and numerical abundance, we use an internal stores (Droop) formulation to describe the growth rate of phytoplankton as a function of the internal nutrient content in response to a continuous inflow of nutrient and outflow of both nutrient and cells (Grover, 1991). The three state variables are concentration of cells (X, cells l^{-1}), cellular nutrient content (Q, μmol of nutrient $cell^{-1}$), and the nutrient concentration in the environment (R, μmol l^{-1}), and their time derivatives are defined by:

$$dX/dt = X(\mu - D) \tag{3a}$$

$$dQ/dt = \rho - \mu Q \tag{3b}$$

$$dR/dt = D(R_0 - R) - \rho X \tag{3c}$$

where D is the dilution rate (h^{-1}), and R_0 is the concentration of nutrient introduced into the system (μmol l^{-1}). Growth rate (μ, h^{-1}) and uptake (ρ, μmol h^{-1} $cell^{-1}$) are defined as:

$$\mu = \mu'_{\max}(1 - Q_{\min}/Q) \tag{4a}$$

$$\rho = \rho_{\max} R/(K_m + R) \tag{4b}$$

where $\mu'_{\max}$ is the maximum potential growth rate obtained at infinite nutrient quota, $Q_{\min}$ is the cell quota at $\mu = 0$, $\rho_{\max}$ is the maximum uptake rate constrained by diffusion in the boundary layer outside the cell, and K_m is the nutrient concentration where $\rho = \rho_{\max}/2$. The definition of uptake (4b) includes the size-dependence of both active uptake into the cell and diffusion through the boundary layer outside the cell (Pasciak and Gavis, 1974; Berg and Purcell, 1977; Aksnes and Egge, 1991). Many other formulations are possible, but as our intent is to describe size-dependence of nutrient acquisition and utilization at equilibrium, in which nutrient limitation is determined by the maximum diffusive flux possible and active uptake considerations are ignored. We favour this simple set of equations over more sophisticated descriptions that are important for the simulation of time-series (Flynn, 2003), or multiple limiting nutrients (Flynn, 2002).

The dilution rate can be interpreted as a scaled volume flux into a patch of the surface ocean that is balanced by an equal flux out of the patch. If the volume flux is predominantly vertical then the in-flowing water will be nutrient rich and the out-flowing water will be relatively depleted of inorganic nutrient and rich with cells that will be eventually transported into the deep ocean and recycled back into inorganic nutrients. The vertical extent of the surface patch is set by physical mixing and will determine the dilution of the upwelling flux of nutrient and the average irradiance. High dilution rates describe upwelling zones and low dilution rates represent shallow stratified open ocean environments. In this model, dilution rate is an analog of Margalef's concept of energy (turbulence) as a driving factor controlling phytoplankton community composition (Margalef, 1978). Loss of cells at a rate XD can be used to describe grazing, sinking, and cell death to the extent these processes depend on the abundance of cells but are excluded here in order to focus on the influence of size-dependent physiological responses to a limiting nutrient on phytoplankton community-size spectra. Phytoplankton physiological processes respond relatively rapidly compared to many environmental fluctuations, so we employ a steady-state approximation to study the size-distribution of phytoplankton communities. At steady state, the following equilibria are predicted:

$$Q^* = Q_{\min}/(1 - D/\mu'_{\max}) \tag{5a}$$

$$R^* = K_m/(\rho_{\max}/(DQ^*) - 1) \tag{5b}$$

$$X^* = (R_0 - R^*)/Q^* \tag{5c}$$

Often the Droop model is used to simulate and predict the growth rate of phytoplankton in response to changes

in external nutrient concentration and to calculate the relative competitive ability, R^*, of organisms under equilibrium conditions (Tilman, 1977; Grover, 1991; Ducobu *et al.*, 1998) although many other considerations including surge uptake can be important (Flynn, 2003). With the exception of D and R_0, all other parameters in the Droop model depend on cell size,. Based on extensive experimental observations we express the size-dependence of $Q_{\min}$, $Q_{\max}$, $\mu'_{\max}$, K_m, and $\rho_{\max}$ by a power-law dependence on cell volume (Table I). The size scaling of $\rho_{\max}$ is estimated from the product of the maximum growth rate and the internal nutrient requirement $Q_{\max}$ at maximum growth rate. We solve for X^*, a measure of the ability of a species to convert nutrients into cells and biomass.

Scaling-up from physiological rates to the size scaling of abundance and biomass

Computing the density of cells for species of different sizes in a community requires knowledge of the abundance of a single species, X^*, the relationship between cell size and species diversity, and the controls on the distribution of the species in habitable space. We adopt a metapopulation framework to describe phytoplankton communities as the sum of discrete sub-populations (Hanski and Simberloff, 1997; Nee *et al.*, 1997). Species occupying a sub-population are drawn from a global species pool. Migrations among sub-populations and outside the metacommunity ensure that competition within sub-populations will not result in species extinction at the community level. Thus, the surface ocean is divided into a very large number of patches, there is no competition for resources among cells in different patches, and a patch is occupied by a single species selected by lottery from the potential species pool, which determines the potential appearance but not abundance of phytoplankton in the habitat. This approach is supported by observed characteristics of phytoplankton communities. Phytoplankton communities exhibit characteristic species–area relationships (Smith *et al.*, 2005) indicating that to some extent neutral theory of biodiversity regulates phytoplankton populations and dominates the effects of competition. In addition, phytoplankton cells are commonly small enough and at low enough abundance that interactions among neighbours are too slow to be primary determinants of competitive exclusion (Richerson *et al.*, 1970; Siegel, 1998). Within an interaction region, many factors including the extant species pool and nutrient competition determine the locally most-fit species. Beyond an interaction region, the winning species are determined independently and the existence of a large number of such independent regions means that average population sizes can be estimated by averaging over the potential species pool. The effects of cell size and complex competition processes will affect evolutionary success and are encoded in global species diversity. On longer time-scales, global species diversity may be influenced by physiology, competition, and selection, but we do not examine that dynamic process.

Species diversity (S, number of species/l) is often a skewed log-normal function of organism size (cell diameter, d), mean cell diameter, $\bar{d}$, and the standard deviation on a log scale, σ, (Van Valen, 1973; May, 1978; Fenchel, 1993; Brown, 1995; Gaston and Blackburn, 2000),

$$S(d) \propto 2 f_{LN}(d; \bar{d}, \sigma) \int_0^{d^\alpha} f_{LN}(x; \alpha\bar{d}, \sigma) dx \qquad (6a)$$

Table I: Volume (μm^3) scaling of physiological parameters, aVb, used in the physiological null model

Physiological parameter	Symbol	Units	B	a
[a]Maximum growth rate	μ_{max}'	Day^{-1}	−0.25	5.37
[b]Maximum uptake rate	ρ_{max}	μmol N (cell day)$^{-1}$	0.66	set by growth rate
[c]Half saturation constant	k_m	μmol N	0.33	1.00
Minimum cell quota	Q_{min}	μmol N (cell)$^{-1}$	0.72 ± 0.06[d]	$1.50 \cdot 10^{-9}$[d]
Maximum cell quota	Q_{max}	μmol N (cell)$^{-1}$	0.85[e]	$3.60 \cdot 10^{-9}$[e]

[a]Maximum growth rate, size-scaling exponent based on theoretical considerations (see text), the intercept is determined from a regression using data compiled by Tang (1995) and using b = 0.25,and represents the predicted maximum growth rate of a 1 μm^3 cell.
[b]Uptake rate, size-scaling exponent set based on theoretical considerations of diffusion (Aksnes and Egge, 1991), the intercept is set by the model.
[c]The half saturation constant, size-scaling exponent based on theoretical considerations of diffusion and size-dependent nutrient requirements (Aksnes and Egge, 1991), the intercept is from nitrogen uptake measured by Eppley and Thomas (1969) as interpreted by Stolte *et al.* (1994).
[d]Shuter, 1978.
[e]Montagnes and Franklin, 2001.

where α is the shape parameter and f_{LN} is the log-normal distribution

$$f_{LN}(d;\bar{d},\sigma) = \frac{1}{\sqrt{2\pi}\sigma d} e^{-(\log d-\bar{d})^2/2\sigma^2} \tag{6b}$$

Most observations of species diversity–size relationships are in terrestrial systems, but Fenchel (1993) demonstrated that this relationship can be extended to aquatic organisms, including plankton. Here we have assumed that this relationship holds for phytoplankton. Maximum species diversity for the log-normal distribution occurs at an intermediate cell size of $\exp(\bar{d} + \sigma^2/2)$, with variance $\exp(2d + \sigma^2)(e^{\sigma 2} - 1)$ around the intermediate cell size (Azzalini and Dalla Valle, 1996; Azzalini *et al.*, 2003). We constrain the range of cell sizes from a minimum diameter of 0.6 μm to the maximum size that can survive in a given habitat. Note that the relationship between species diversity and organism size is not always skewed log-normal, but can have multiple peaks or can be independent of cell size (Gaston and Blackburn, 2000), and size distribution data for phytoplankton species are difficult to obtain and are often biased by sampling effort and technology. Evidence of the diversity of picoeukaryotes has increased dramatically recently and we expect increased resolution of cryptic diversity across all size classes as our knowledge of molecular diversity increases. Given the little information available for the relationship between phytoplankton species diversity and cell size at different spatial and temporal scales we also consider the case where species diversity is independent of cell size, $S(d) = 1$.

Species diversity and cell abundance (X^*) are functions of d defined on a continuum, which is convenient mathematically but awkward for comparison to empirical measurements which measure quantities over discrete size classes. We define N as the number of cells in the community of diameter less than d,

$$N(d) = \int_{d_{\min}}^{d} X^*(x)\, S(x)\, dx \Big/ \int_{d_{\min}}^{d_{\max}} S(x)\, dx. \tag{7}$$

The abundance (A, cells/l) of cells in the community of diameter $d \pm \Delta d/2$ is

$$A(d) = \mathrm{d}N/\mathrm{d}d\, \Delta d = X^*(d)S(d)\Delta d \Big/ \int_{d_{\min}}^{d_{\max}} S(x)dx, \tag{7a}$$

which we computed for $\Delta d = 1$ μm. The biomass (B) of cells less than diameter d is defined as

$$B(d) = \int_{d_{\min}}^{d} X^*(x)\, V(x)\, S(x)\, dx \Big/ \int_{d_{\min}}^{d_{\max}} S(x)\, dx \tag{8}$$

where $V(d)$ is the volume of a cell of diameter d. Often, cellular carbon content is a power function of cell volume with an exponent between 0.75 and 1 (Menden-Deuer and Lessard, 2000). Our a priori assumption is that the carbon content per cell is proportional to cell volume, but if cellular carbon is $\propto V^{3/4}$ then there will be less biomass in the larger size fractions and a lower size-scaling exponent on biomass than predicted.

Our model predicts the relative number of cells of different sizes in phytoplankton communities and the size ranges present. The diameter of the largest cell present is $d_{\max} = \max\{d|\min(\mathrm{X}^*, \mathrm{Q}^*, \mathrm{R}^*) > 0\}$, the biggest diameter for which the equilibrium values of X, Q, and R are all physically reasonable. For simplicity it is assumed that all cells are spherical, although large cells are often highly prolate in shape (Grover, 1989). Although taxonomic differences in nutrient requirements and acquisition are well documented, for example *Prochlorococcus* has lost the ability to take up nitrate and depends on ammonium and organic nitrogen to fulfill its nitrogen requirements (Garcia-Fernandez et al., 2004), we assume all cells have the same type of nutrient uptake systems and use an unspecified form of nitrogen as the limiting nutrient to decrease model complexity and because it is often the proximate limiting nutrient for marine phytoplankton growth (Falkowski, 1997).

RESULTS

Environmental regulation determines maximum cell size in the community

Our model predicts an increase in the abundance of large cells relative to smaller cells with increasing nutrient availability, resulting in an increase in the maximum size of the cells present and average cell size of the phytoplankton community (Fig. 1). As a result, as total phytoplankton biomass increases with increasing nutrient availability, the fraction of the biomass contributed by the ≤ 2 μm size fraction, the picoplankton, decreases, in qualitative agreement with field observations from marine (Fig. 2) and aquatic ecosystems (Sprules and Munawar, 1986; Ahrens and Peters, 1991). For any

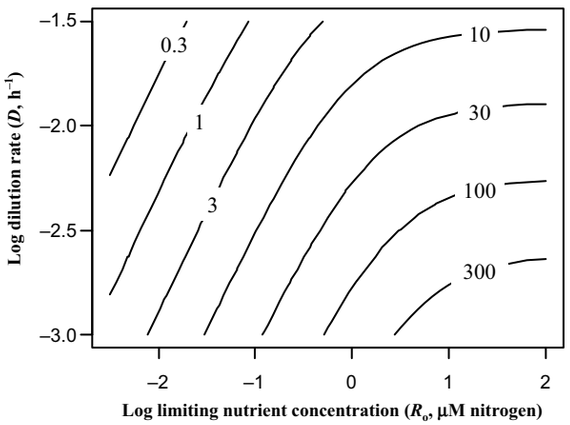

Fig. 1. Maximum cell diameter (μm) present in the community as a function of $\log_{10}$ limiting nutrient availability (μM nitrogen) and $\log_{10}$ dilution rate (h^{-1}).

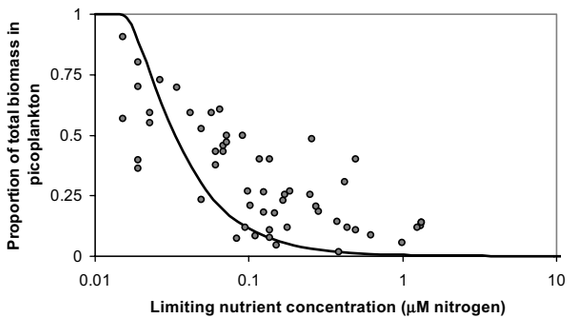

Fig. 2. Percentage of total biomass in the picoplankton size fraction (<2 μm in diameter) as a function of nutrient availability (μM nitrogen) for a dilution rate (D, h^{-1}) of 10^{-2} predicted by physiological null model and compared with field data of microbial size spectra compiled by Chisholm (1992). Total biomass is calculated assuming total biovolume is linearly proportional to carbon. Field data compiled by Chisholm (1992) was compared with the model predictions by converting μg Chl-*a* l^{-1} to μM nitrogen using C Chl^{-1} (wt/wt) = 10 and assuming C:N in biomass is in Redfield proportions.

given nutrient concentration, an increase in dilution rate decreases the size of the largest cell present in the community. This result depends on the assumption that maximum growth rate depends on cell size and not taxonomic affiliation; this assumption is relaxed in later results.

Consequences of the species diversity-organism size relationship for the size scaling of abundance

The relationship between organism size and species richness has a strong influence on the size scaling of abundance. When species richness is a skewed log-normal function of V then cell density is concave down with respect to V (Fig. 3a), but when species richness is independent of V then cell density is approximately a power-law function of V (Fig. 3b). If species diversity is a skewed log-normal function of cell size, then ξ can be quite variable and much flatter compared with the size-independent distribution $S(d) = 1$, depending on resource concentration, dilution rate, the size of the species with maximum abundance, and the range of cell sizes sampled. As nutrient concentration decreases, overall cell density (cells l^{-1}) decreases, until a threshold is reached (0.1 μM N). Further decreases in nutrient concentration result in an overall increase in abundance of any single species remaining due to the decrease in the number of species in the community. If species diversity

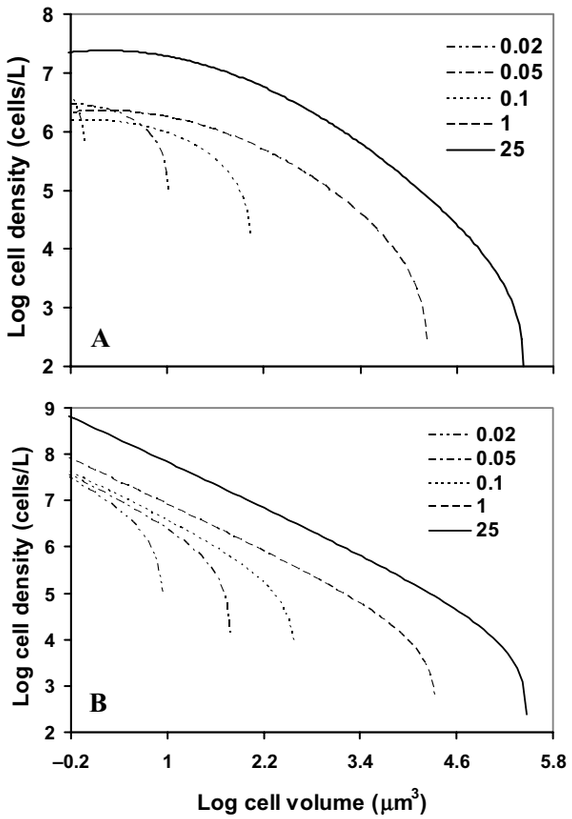

Fig. 3. Predicted relative abundance (A, Eq. 7a) of cells (l^{-1}) of different sizes (volume, μm^3) at a dilution rate of 1 week^{-1} for (**a**) a skewed log-normal relationship between species richness and cell size for five limiting nutrient concentrations (μM nitrogen): 0.02 (dotted-dotted dash), 0.05 (dotted-dash), 0.1 (small dash), 1 (large dash), and 25 (solid line). The skewed log-normal distribution is defined in Equation 6, with $\sigma = -3.5$, $\alpha = 4$ and $\bar{d} = -11.4$, for a community with cells ranging from 0.6 to 1000 μm diameter with maximum diversity at $d = 10$ μm, and (**b**) a uniform relationship between species richness and cell size for five limiting nutrient concentrations (μM nitrogen) as labelled above.

is independent of cell size ($S(d) = 1$), then the model predicts a power-law decrease in relative abundance of small versus larger cells that is uniform except at the largest sizes supported by the community, which exhibit a rapid decrease in cell density as they approach washout. Subsequent calculations assume $S(d) = 1$ because $A(d)$, then, more closely matches field observations, although these deviations may be due to historical difficulties in accurately sampling very small and very large phytoplankton cells. A balance between origination and extinction rates determines species diversity and both rates depend on cell size partly because of nutrient competition and physiological strategies available to cells of different sizes. Our approach recognizes these effects through the assumed species diversity function but does not model them.

Relative abundance of large versus small cells (ξ)

The size-scaling exponent (ξ) of abundance $A(d) \propto V^{\xi}$ is estimated by fitting predictions of relative abundance from cells 0.6 μm in diameter to the largest cell supported. We find $\xi = -1.6$ to -0.74, depending on the supplied nutrient concentration and the size scaling of Q_{min} (Fig. 4); note that this is in agreement with observations from phosphorus-limited lakes (see Fig. 4 in (Sprules and Munawar, 1986)). At high nutrient supply concentrations (R_0), $R^* << R_0$ so ξ is approximately the size-scaling exponent of $1/Q^*$, and as a result if $Q_{min} \propto V^{0.72}$ then $\xi \rightarrow -0.72$ under high R_0, and if $Q_{min} \propto V^1$ then $\xi \rightarrow -1$ under high nutrient concentrations (Fig. 4a). As R_0 decreases this simplification becomes increasingly inaccurate and ξ decreases. When R_0 is very close to R^*, the cells approach washout and X^* drops rapidly. Sampling cellular abundance for size fractions that are close to washout is difficult because as abundances drop ever increasing effort is required to observe the larger cells. As a consequence, we expect that several of the phenomena plotted here will be difficult to observe empirically. As dilution rate increases ξ decreases, except at extremely low R_0 where only small cells have viable population abundances (Fig. 4b).

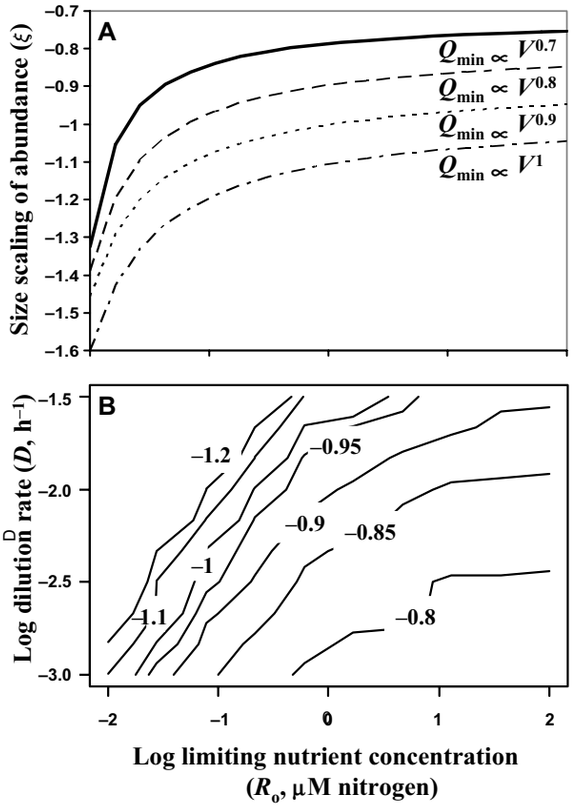

Fig. 4. Size scaling of abundance (cells l^{-1}) as a function of nutrient concentration (μM nitrogen) for (a) a range of size-scaling exponents for minimum cell quota for nitrogen: $Q_{min} \propto V^{0.7}$ (dotted lines), $Q_{min} \propto V^{0.8}$ (dashed line), $Q_{min} \propto V^{0.9}$ (dashed-dotted line), $Q_{min} \propto V^1$ (solid line), and (b) dilution rate (D, h^{-1}).

DISCUSSION

The pioneering work of R.W. Sheldon and others on particle distributions in the surface waters across the Atlantic and Pacific Oceans in the 1960–70s led to the general conclusion that there is roughly equal biomass for all particle sizes (Sheldon and Parsons, 1967; Sheldon *et al.*, 1972; Kerr and Dickie, 2001). This work was followed by the discovery that ubiquitous, abundant, and extremely small photosynthetic picoplankton (<2 μm in diameter), *Prochlorococcus* spp., contributes significantly to primary production and biomass in many oligotrophic regions of the world's oceans (Chisholm *et al.*, 1988; Li and Wood, 1988; Zubkov *et al.*, 1998) and the increasing awareness of pervasive populations of picoeukaryotes from a wide variety of taxonomic groups (Moon-Van Der Staay *et al.*, 2001). These observations have contributed to the paradigm that the euphotic zone of the ocean is often inhabited by a background of very abundant small phytoplankton cells that are accompanied by larger cells as nutrient availability increases (Sprules and Munawar, 1986; Ahrens and Peters, 1991; Chisholm, 1992).

Many factors affect the size structure of phytoplankton communities, including competitive interactions among phytoplankton taxa (Tilman, 1977; Grover, 1989), grazing (Gonzalez *et al.*, 1990; Kiorboe, 1993; Armstrong, 1994; Kerr and Dickie, 2001; Irigoien *et al.*, 2005),

sinking (Munk and Riley, 1952; Gavis, 1976; Kiorboe, 1993), and physical aggregation (Jackson, 1990; Burd and Jackson, 2002; Stemmann *et al.*, 2004). Observations of community-size structure can be difficult and can be distorted by sampling or analysis bias (Sheldon *et al.*, 1972; Griffiths, 1992; Blackburn and Gaston, 1996). Regardless of the degree to which these or any other factors contribute to the observed size structure of phytoplankton communities, the aggregate behaviour of the individual phytoplankton cells and the growth rate of the populations shape the size structure of phytoplankton communities. Considering the size-dependence of nutrient requirements, uptake, and growth, we have constructed a series of predictions for how phytoplankton community-size structure will change as a function of nutrient availability and dilution rate under steady state:

1. A population of large cells requires a minimum concentration of supplied nutrient. An increase in the concentration of the limiting nutrient results in an increase in the maximum cell size present, the range of cell sizes present in the community, and an increase in the proportion of total biomass present in the larger size fractions, in agreement with field observations (Chisholm, 1992; Li, 2002).
2. Communities are predicted to be characterized by a logarithmic decrease in cell density with increasing cell size and the relative numbers of large and small cells change with the concentration of limiting nutrient (*R*o) such that ξ is low (small-celled organisms dominate) under low nutrient concentration and highest under high nutrient concentration. The actual value of ξ depends on D and the size scaling of $Q_{\min}$.
3. Dilution rate determines the size scaling of $\mu/\mu_{\max}$ and therefore the size scaling of abundance under any given nutrient concentration. Fast dilution rates will tend to wash out large, slow growing cells ($D > \mu_{\max}$), while under slow dilution rates cells of all sizes will be supported.

Most of these predictions, in particular the logarithmic decrease in cell density with the logarithmic increase in cell size with a slope of -1.6 to -0.75 are in agreement with the range of values observed in field observations for phytoplankton and other autotrophs as well as range of heterotrophs (Damuth, 1981; Bonner, 1988; Tittel *et al.*, 1998; Boss *et al.*, 2001; Cavender-Bares *et al.*, 2001; Damuth, 2001; Belgrano *et al.*, 2002). The model predicts that the size scaling of biomass in the water column (bulk phytoplankton carbon l^{-1}) ranges from $V^{-0.85}$ to $V^{0.25}$ if the size scaling of carbon quota ranges between $V^{3/4}$ to V^{1}, also in agreement with many field observations (Rodriguez and Mullin, 1986; Sprules and Munawar, 1986; Ahrens and Peters, 1991). The trended change in ξ in response to R_o and D are in accord with observed changes in size structure with bulk chlorophyll concentrations (Tremblay and Legendre, 1994; Li, 2002) and phosphorus concentrations (Sprules and Munawar, 1986; Ahrens and Peters, 1991), but the trended change with nutrient concentration has not always been observed in marine systems (Cavender-Bares *et al.*, 2001), and in the English Channel average cell size was inversely related to nitrate and silicate concentration (Irigoien *et al.*, 2005). Size-dependence of light acquisition can be expected to interact with growth allometry (Finkel *et al.*, 2004), producing contrary relationships between cell size and nutrient concentration when light is the limiting or co-limiting resource and may be responsible for changes in the size distribution observed by Irigoien *et al.* (2005). Application of this general theoretical framework can replicate a range of patterns in the size structure of phytoplankton that have been previously explained by a number of different theories including deviations from steady state (Sprules and Munawar, 1986), size-dependent grazing (Armstrong, 1994; Kerr and Dickie, 2001; Armstrong, 2003; Irigoien *et al.*, 2005), size-dependent storage ability (Stolte *et al.*, 1994), and the intermediate disturbance hypothesis (Li, 2002). Armstrong's (2003) 'control rod' model predicts large cells can escape grazer control when nutrients are added; we show that similar phenomena can occur as a consequence of phytoplankton physiology and without invoking slow-growing size-specific grazers. Our model will be most accurate in biogeographic regions where phytoplankton biomass is determined primarily from the bottom-up such as upwelling regions. In grazer-controlled regions, the model provides relative growth rates in response to environmental variables that are needed to formulate a predictive top-down model.

Large cells can dominate under steady state conditions

It has often been noted that larger phytoplankton cells are at a competitive disadvantage because of their slower growth rates (Grover, 1989). Our model permits the coexistence of species covering a wide range of sizes and predicts abundance proportional to values ranging from $V^{-1.6}$ to $^{-0.75}$ depending on R_o, D and the size scaling of minimum quota. A number of field observations suggest that under certain environmental conditions, small phytoplankton cells can be relatively rare and large cells dominate the biomass spectrum (Furnas, 1991; Zubkov *et al.*, 1998; Partensky *et al.*, 1999; Li, 2002). For example, small *Prochlorococcus* spp. are geographically limited

between 50°N and 50°S (Zubkov *et al.*, 1998), and large diatoms often dominate in upwelling regions characterized by high nutrient, and high bulk chlorophyll concentrations (Margalef, 1978; Li, 2002). Deviations from steady state, nutrient pulsing, nutrient storage, and surge uptake abilities have been proposed to explain the dominance of large phytoplankton species (Sprules and Munawar, 1986; Stolte *et al.*, 1994; Stolte and Riegman, 1995; Tozzi *et al.*, 2004). Repeated observations of extraordinarily high growth rates and chlorophyll-*a* normalized primary production in the large phytoplankton size fraction under high nutrient, and high flow rates, such as upwelling conditions (Furnas, 1991; Tremblay and Legendre, 1994; Froneman *et al.*, 2001; Li, 2002) hint at an alternate, steady-state explanation. Phylogenetic differences in $\mu'_{\max}$, which are associated with changes in cell size, could explain the observations of high chlorophyll biomass and high rates of chlorophyll-*a* normalized primary production in the larger phytoplankton size fractions.

The effect of taxonomic variation in growth rates

Size is only one factor affecting physiological behaviour among phytoplankton species. Different taxonomic groups of phytoplankton are characterized by fundamental physiological differences. A compilation of maximum growth rates for a number of ecologically important taxonomic groups at a reference volume of 1 μm^3 (Table II) indicates that except for dinoflagellates, many of which are mixotrophs, larger phytoplankton taxa generally have inherently larger maximum growth rates per unit volume (Raven *et al.*, 2006). Many of the taxonomic groups have characteristic size ranges (Table II). The covariation in growth rate, phytoplankton size, and taxonomic structure is consistent with the high chlorophyll-normalized photosynthetic rates that have been reported for diatom-enriched macroplankton size fractions versus smaller size fractions from tropical (Furnas, 1991; Malone *et al.*, 1993; Maranon *et al.*, 2001), temperate (Tamigneaux *et al.*, 1999; Cermeño *et al.*, 2005a, 2005b), and polar regions (Legendre *et al.*, 1993). The combination of size and taxonomic variation can be incorporated into our model by varying maximum growth rate as a function of size and size-linked taxonomic variation.

For example, comparing a phytoplankton community with one taxonomic group (with constant $\mu'_{\max}$) with a community composed of slow-growing *Prochlorococcus* and *Synechococcus* spp., *E. huxleyi*, and fast-growing diatoms ($\mu'_{\max}$ from Table II) results in a decrease in the slope (ξ) and increase in the intercept (c_2) as one taxonomic group displaces another (Fig. 5). Gaps in the size spectra can arise as a result of allometric changes in growth rate within a taxonomic group causing major deviations from the power-law form of size distributions, especially over small-size ranges. The hydrographic regime (D and R_0) has a large impact on community-size structure leading to increased abundance of large cells under medium to high nutrient supply concentration (R_0) and decreased abundance of small cells under high nutrient supply concentration and high dilution rates, consistent with the lack of small cells and dominance of large cells observed in many upwelling regions (Tremblay and Legendre, 1994; Li, 2002). Higher rates of metabolite

Table II: Inherent taxonomic differences in growth rate estimated for a 1 μm^3 cell and assuming the size scaling of growth follows the 3/4 rule ($b = -0.25$)

	Relative μ_{max}	Size range diameter (μm)[f]	Observed μ_{max} g day^{-1}
Prochlorococcus spp.	1.00[a]	0.6–1	1–1.42[b]
Synechococcus spp.	2.89	1–2	1.97[c]
Emiliania huxleyi	6.38	2–10	1.3[d]
Dinoflagellate spp.	7.93	5–10^3 ($x = 20$)	1.41[e]
Diatom spp.	16.39	5–10^3 ($x = 15$)	2.92[e]

[a]The predicted maximum growth rate (divisions/day) for a *Prochlorococcus* cell with a cell volume of 1 μm^3 is 0.58 when $b = -0.25$.
[b]Shalapyonok *et al.*, 1998; Partensky *et al.*, 1999.
[c]Kana and Glibert, 1987.
[d]van Bleijswijk *et al.*, 1994.
[e]The maximum growth rate for the dinoflagellates and diatoms was estimated from Tang (1995), using an estimate of average cell volume of the phytoplankton data from Fig. 2 (Tang, 1995), and then calculating the maximum growth rate of the diatoms and dinoflagellates with $b = -0.25$ and a cell volume of 1 μm^3.
[f]The diameters of the different groups are estimates based on an examination of the size of species in the CCMP culture collection and reports in the literature.
[g]Observed μ_{max} is a measured growth rate of a particular species from the taxonomic group.

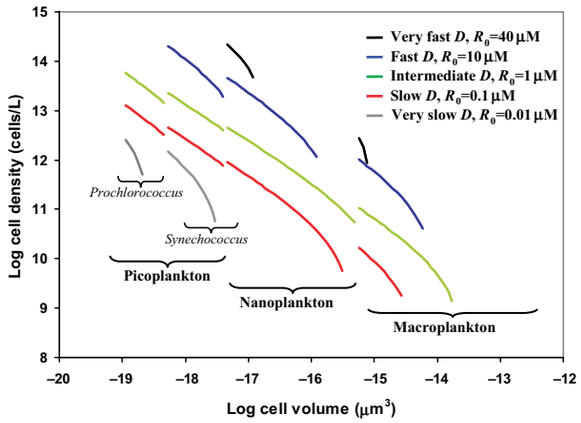

Fig. 5. Predicted cell densities in pico-, nano-, and microphytoplankton size fractions as a function of limiting nutrient concentration (μM nitrogen) where nutrient concentration covaries with dilution rate {log D = [(log R + 2)/2] −3}, and assuming that picoplankton are dominated by *Prochlorococcus* and *Synechococcus* spp., the nanoplankton are dominated by the coccolithophorid *Emiliania huxleyi*, and the microplankton are dominated by fast-growing diatoms with growth rates and size ranges as provided in Table II.

leakage in smaller cells due to their higher surface area to volume ratios may also contribute to the often lower-than-expected abundance of the picoplankton, *Synechococcus* and *Prochlorococcus* spp., relative to the abundance of the larger size fractions (Li, 2002).

Concluding remarks

Field observations indicate phytoplankton community-size structure often varies with resource availability and hydrographic conditions (Sprules and Munawar, 1986; Ahrens and Peters, 1991; Chisholm, 1992; Tremblay and Legendre, 1994; Li, 2002). Hypotheses that have been proposed to account for the size structure of phytoplankton communities include size- and density-dependent grazing (Armstrong, 1999; Armstrong, 2003), particle sinking and coagulation dynamics (Burd and Jackson, 2002; Stemmann *et al.*, 2004), size-dependent niche breadth (La Brecque, 1992; Brown, 1995), and size-dependent physiological strategies such as surge uptake or storage abilities (Stolte *et al.*, 1994; Stolte and Riegman, 1995; Tozzi *et al.*, 2004). We have shown that a size-resolved physiological model that describes growth rate as a function of the supply of nutrient with no competitive interactions can replicate the characteristic inverse power-law relationship between the abundance of phytoplankton cells and cell size, and the relative dominance of small phytoplankton cells observed under stratified, oligotrophic conditions, and the increase in the abundance of larger phytoplankton cells under well-mixed, eutrophic conditions. The ability of this physiological model to replicate commonly observed trends in community-size structure indicates that resource availability and volume flux may, at times, be the primary control on the size structure of phytoplankton communities although it is commonly believed that predation is required to explain the dominance of large phytoplankton in nutrient-rich environments (Armstrong, 2003; Irigoien *et al.*, 2004; Morin and Fox, 2004). Including a consideration of changes in the size-normalized maximum growth rate of different taxonomic groups of phytoplankton predicts the absence of small cells and dominance of large cells in areas of high nutrient input and high flow rates. The size scaling of phytoplankton physiology, growth and photosynthetic rate, nutrient quotas, and rates of resource acquisition always have the potential to shape the size structure of the phytoplankton community and are worth considering in conjunction with models employing grazing, coagulation, and sinking. Further refinements of this approach should investigate the effect of temporally varying nutrient environments on phytoplankton community-size structure by exploring alternate nutrient kinetic models, particularly the effects of surge uptake and nutrient storage.

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