Cell Size as a Key Determinant of Phytoplankton Metabolism and Community Structure

Emilio Marañón

Departamento de Ecología y Biología Animal, Universidade de Vigo, 36310 Vigo, Spain; email: em@uvigo.es

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abundance, allometry, biomass, growth, size structure

Abstract

Phytoplankton size structure controls the trophic organization of planktonic communities and their ability to export biogenic materials toward the ocean's interior. Our understanding of the mechanisms that drive the variability in phytoplankton size structure has been shaped by the assumption that the pace of metabolism decreases allometrically with increasing cell size. However, recent field and laboratory evidence indicates that biomass-specific production and growth rates are similar in both small and large cells but peak at intermediate cell sizes. The maximum nutrient uptake rate scales isometrically with cell volume and superisometrically with the minimum nutrient quota. The unimodal size scaling of phytoplankton growth arises from ataxonomic, size-dependent trade-off processes related to nutrient requirement, acquisition, and use. The superior ability of intermediate-size cells to exploit high nutrient concentrations explains their biomass dominance during blooms. Biogeographic patterns in phytoplankton size structure and growth rate are independent of temperature and driven mainly by changes in resource supply.

INTRODUCTION

Cell size is a master functional trait that affects virtually every aspect of phytoplankton biology at the cellular, population, and community levels (Chisholm 1992, Raven 1998, Litchman & Klausmeier 2008, Finkel et al. 2010). Phytoplankton cell volume spans more than nine orders of magnitude, from approximately 0.1 μm^3 in the smallest cyanobacteria to $>10^8$ μm^3 in the largest diatoms. Most phytoplankton communities have a continuum of species of different cell sizes that can be represented by size-abundance spectra, in which the abundances of all cells within logarithmic size intervals are plotted as a function of the nominal size of each interval (**Figure 1*a***). The slope of the size-abundance spectrum is a general descriptor of phytoplankton size structure that broadly reflects the relative importance of different size classes in terms of their contribution to total biomass (**Figure 1*b***). These slopes are usually between −1.3 and −0.9 in the stratified waters of low-latitude, open-ocean environments (Cavender-Bares et al. 2001, Huete-Ortega et al. 2012), where small cells account for most of the biomass, and between −0.9 and −0.5 in the more turbulent waters of coastal, productive regions, where larger cells generally form the bulk of the biomass (Reul et al. 2005, Huete-Ortega et al. 2010). Changes in the slope have also been related to mesoscale variability in vertical water motion (Rodríguez et al. 2001).

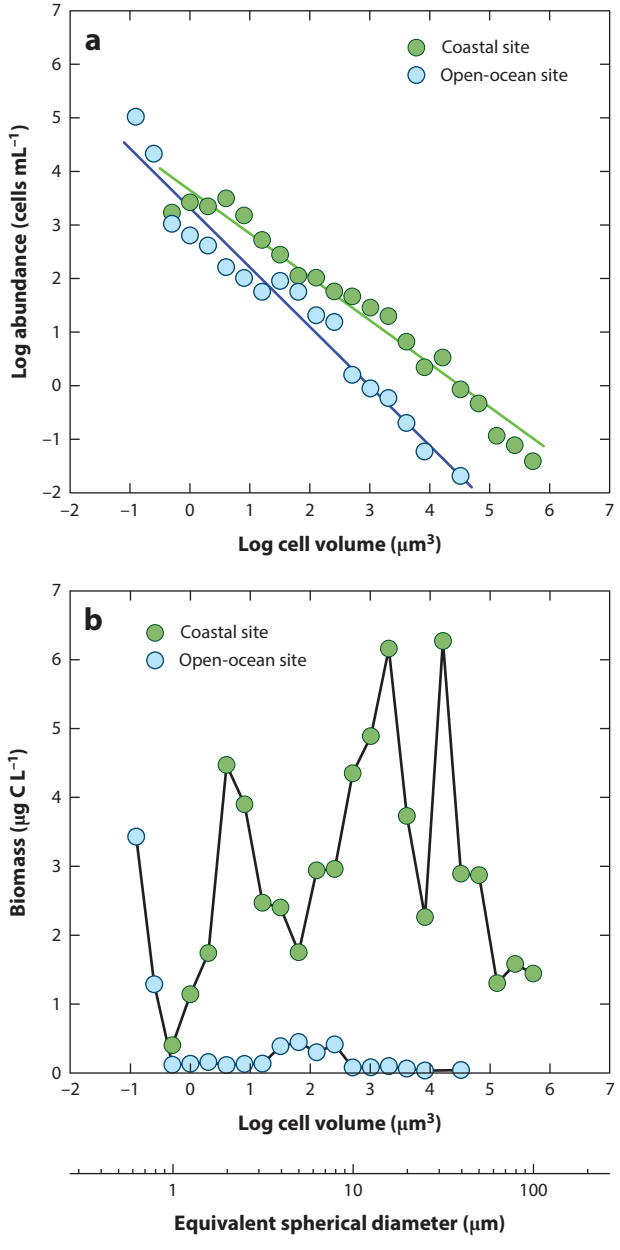
The size structure of phytoplankton, understood as the partitioning of biomass among species of different cell sizes, is a key property of pelagic ecosystems that controls their food-web organization and biogeochemical functioning (Legendre & Rassoulzadegan 1996, Falkowski et al. 1998). When picophytoplankton (cells <2 μm in diameter) dominate, as is typically the case in low-productivity waters, tight trophic coupling between photoautotrophs, heterotrophic bacteria, and their protist predators results in complex microbial food webs, which favor the recycling of matter rather than its efficient transfer toward upper trophic levels (Azam et al. 1983, Legendre & Le Fèvre 1995). In addition, the small cell size of the dominant autotrophic and heterotrophic components of the microbial plankton community means that their sedimentation is slow. As a result, most of the biogenic carbon is remineralized within the euphotic layer, and thus the biological pump in these systems has limited potential to contribute to net atmospheric CO_2 drawdown (Falkowski et al. 1998). In contrast, plankton communities of productive waters are dominated by larger phytoplankton, such as chain-forming diatoms, and are characterized by simpler trophic pathways and enhanced sinking rates. In these settings, a larger fraction of phytoplankton production is eventually exported from the euphotic zone, either directly through the sinking of ungrazed cells or indirectly through the sedimentation of aggregates and zooplankton fecal pellets, with the result that the biological pump is more efficient in transporting biogenic carbon toward the ocean's interior (Boyd & Trull 2007, Guidi et al. 2009). In view of its numerous ecological and

Figure 1

Size structure of phytoplankton at contrasting sites. (*a*) Log-log relationship between phytoplankton cell size and abundance in surface waters of a coastal site (Ría de Vigo, northwest Iberian peninsula; chlorophyll *a* concentration = 1.0 mg m^{-3}) and an open-ocean site (the subtropical North Atlantic gyre, 26°N, 34°W; chlorophyll *a* concentration = 0.1 mg m^{-3}). The reduced-major-axis (RMA) regression lines are $y = -0.81x + 3.65$ ($r^2 = 0.96$, $n = 21$, $p < 0.001$) for the coastal sample and $y = -1.11x + 3.32$ ($r^2 = 0.96$, $n = 18$, $p < 0.001$) for the open-ocean sample. (*b*) Relationship between log cell size and phytoplankton biomass for the same samples. Cell abundance and size were measured with flow cytometry and microscopy image analysis (Rodríguez et al. 1998). Note that individual cell size is used in all size-scaling relationships shown throughout this article, even though some species may form chains or colonies. Cell biovolume was converted to carbon biomass by using empirical conversion factors (Cermeño et al. 2005a, Huete-Ortega et al. 2012). The bottom *x* axis shows equivalent spherical diameters. Original data provided by José M. Blanco, Jaime Rodríguez, and María Huete-Ortega.

biogeochemical implications, obtaining a mechanistic understanding of the factors that control the variability of phytoplankton size structure remains a central goal in biological oceanography.

The study of the rate of metabolism—the biological transformation of energy and resources—offers a powerful unifying framework to link the biology of individual organisms to the ecology of populations, communities, and ecosystems (Brown et al. 2004). Temperature and body size are the main controlling factors of metabolic rate. From microbes to large animals and plants, the relationship between individual metabolic rate (R) and body mass (M) can be described by a power



function of the form $R = aM^b$, where a is a group-dependent coefficient and b is the size-scaling exponent. Since it was first shown that b takes a value of 3/4 in birds and mammals (Kleiber 1932), the so-called Kleiber's rule or 3/4-power rule has been confirmed in most multicellular organisms (Savage et al. 2004). If mass-specific metabolic rates are computed (in units of time^{-1}), the size-scaling exponent becomes −1/4, indicating that metabolism slows down with increasing body size: A 10,000-fold increase in body size results in a 10-fold decrease in mass-specific metabolic rate. Several models, based on the generic properties of resource transportation networks, have been proposed to explain the pervasiveness of quarter-power scaling in biology (West et al. 1997, Banavar et al. 1999), but their applicability to unicellular organisms is unclear. Establishing whether the size scaling of phytoplankton metabolism follows the general allometric theory is thus a major prerequisite for understanding the dynamics of phytoplankton size structure in the ocean.

CELL SIZE AND PHYTOPLANKTON METABOLISM

Phytoplankton cellular composition, metabolic rates, nutrient uptake kinetics, and growth rates all show various degrees of size dependence (Chisholm 1992, Kiørboe 1993, Raven 1998, Litchman et al. 2007, Marañón 2008b, Finkel et al. 2010). There is general agreement among studies that the cellular contents of carbon, nitrogen, and phosphorus scale with cell volume (V) with an exponent between 0.7 and 0.9, indicating that larger cells are less biomass-dense (Smith & Kalff 1982, Verity et al. 1992, Menden-Deuer & Lessard 2000, Montagnes & Franklin 2001, Marañón et al. 2013). Some evidence also suggests that the carbon-to-nitrogen ratio tends to be lower in the smallest phytoplankton (Raven 1994, Marañón et al. 2013). A major constraint imposed by increasing cell size is a reduction in nutrient diffusion per unit of cell volume and a thickening of the diffusion boundary layer around the cell (Pasciak & Gauis 1974, Kiørboe 1993, Raven 1998), with the result that the nutrient concentration threshold below which cells cannot sustain a given growth rate increases rapidly with cell size (Chisholm 1992). Light absorption per unit of chlorophyll *a* also decreases in larger cells because self-shading by the pigment molecules (the package effect) increases with size, especially under light limitation, when intracellular pigment concentrations are higher (Finkel 2001, Finkel et al. 2004). Owing to these fundamental biophysical constraints, small cell size is clearly advantageous in environments where light and/or nutrient availability is low. Even under nutrient-saturating conditions, it can be expected that small cells will still be superior competitors. If maximum nutrient uptake per cell (V_{max}) is proportional to cell surface area (Aksnes & Egge 1991), then V_{max} will scale as $V^{2/3}$, and the nutrient uptake per unit of cell volume will therefore scale as $V^{-1/3}$. Thus, as cell size increases, the ability to obtain nutrients decreases faster than volume-specific nutrient quotas (Smith & Kalff 1982, Litchman et al. 2007).

Experimental studies and literature reviews have confirmed the general allometric pattern of an inverse relationship between cell size and both growth and biomass-specific metabolic rates (Banse 1982; Blasco et al. 1982; Geider et al. 1986; Sommer 1989; Tang 1995; Tang & Peters 1995; Finkel et al. 2004, 2010; López-Urrutia et al. 2006), although it has often been noted that the overall size dependence of phytoplankton metabolism is weaker than that observed in macroorganisms (Banse 1982, Sommer 1989, Chisholm 1992). However, a limitation of most of these studies is that they have considered only species with $V > 100$ μm^3 [equivalent spherical diameter (ESD) of 6 μm], thus disregarding all picophytoplankton and a fraction of the nanophytoplankton. In any case, considering the benefits of small cell size in terms of resource acquisition, high biomass-specific metabolic rates, and fast division rates, combined with the much faster sinking rates of large cells and thus their loss from the euphotic zone (Smayda 1970), the obvious question is why phytoplankton blooms in the sea are virtually never dominated by small cells.

WHY ARE BLOOMS NOT DOMINATED BY SMALL CELLS?

The most accepted explanation for the fact that blooms (defined here as events of increased phytoplankton net growth leading to biomass concentrations above 100–200 mg C m^{-3}) are dominated by large rather than small cells is that the former are more likely to outgrow their predators during conditions of enhanced growth (Kiørboe 1993, 2008; Irigoien et al. 2005; Barton et al. 2013). The main reason is that the grazers of small phytoplankton are unicellular protists with generation times as short as those of their prey, whereas larger cells are consumed mainly by metazoan zooplankton whose generation times are orders of magnitude longer. The lagged response of metazoan herbivores to pulses of enhanced phytoplankton growth, compared with a faster numerical response by the heterotrophic protists, would allow larger cells to escape predation and dominate the bloom.

The reasoning above is only partially supported by in situ determinations of the size dependence of phytoplankton losses to grazing. First, it is now clear that heterotrophic protists (in particular dinoflagellates) are important consumers of large cells such as diatoms (Calbet 2008, Sherr & Sherr 2009). Second, although some studies have found that the smallest phytoplankton (picocyanobacteria and picoeukaryotes) do suffer higher grazing losses than larger cells (Latasa et al. 1997, Landry et al. 2000, Strom et al. 2007), others have reported similar grazing pressure on phytoplankton groups of markedly different mean cell size (Latasa et al. 2005, Gutiérrez-Rodríguez et al. 2011, Teixeira et al. 2011, Chang et al. 2013). In addition, global analyses of grazing rate by microzooplankton, which collectively consume most of the phytoplankton daily production, indicate that losses to predation are of the same magnitude (approximately 60–70% of daily primary production) in regions that are known to have widely contrasting phytoplankton size structure (Calbet & Landry 2004, Schmoker et al. 2013). This picture, suggesting a relatively low degree of size dependence in grazing pressure, does not change substantially when also considering the role of mesozooplankton, which contribute only a modest fraction of daily phytoplankton losses, particularly in high-productivity regions (Calbet 2001). It therefore seems justified to reexamine the size scaling of phytoplankton metabolism and growth in order to evaluate the relative roles of bottom-up and top-down processes in driving the variability of plankton size structure.

SIZE SCALING OF METABOLIC RATE AND GROWTH: ISOMETRY AND UNIMODALITY

Cell-Specific Metabolic Rates

Investigating the nature of the relationship between phytoplankton cell size and metabolic rate is relevant to understanding the mechanisms that control plankton community structure and to determining whether general allometric mechanisms that operate in multicellular macroorganisms are also valid for unicellular microorganisms (DeLong et al. 2010). It also has practical interest, because ecological models often rely on the use of size-scaling relationships for phytoplankton growth and metabolic rates (Armstrong 1994, Poulin & Franks 2010, Follows & Dutkiewicz 2011, Ward et al. 2012). Typically, these models use size-scaling parameters that have been determined from literature-based compilations of laboratory measurements (López-Urrutia et al. 2006, Litchman et al. 2007), which, owing to the lack of methodological consistency among studies, contain a large degree of uncertainty. However, determining size-scaling relationships for phytoplankton metabolism in situ is complicated by the fact that many different species, with widely contrasting cell sizes, abundances, and individual metabolic rates, co-occur in any given seawater sample.

One approach to determining the size scaling of metabolic rates in natural phytoplankton assemblages is to combine measurements of size-fractionated carbon uptake rate with size-abundance spectra obtained with flow cytometry (for cells with a diameter below 5–10 μm) and microscopy image analysis (for larger cells) (Marañón et al. 2007). The application of this approach has revealed that, in both coastal and open-ocean waters, the log-log relationship between cell volume and cell-specific photosynthetic rates has a slope significantly higher than 3/4 and not significantly different from 1 (Marañón et al. 2007, Huete-Ortega et al. 2012). A literature review of species-specific production rates in situ also concluded that the size-scaling slope for phytoplankton metabolic rate is significantly higher than 3/4 and, for both diatoms and dinoflagellates, not significantly different from 1 (Marañón 2008a). Finally, a recent study of the metabolic rates of 22 cultured species of phytoplankton from five phyla and spanning more than seven orders of magnitude in cell size confirmed that phytoplankton metabolism does not follow the 3/4-power rule (López-Sandoval et al. 2013, 2014). The slope in the log-log relationship between metabolic rate and cell volume (V) is 0.87 for photosynthesis (**Figure 2*a***) and 0.91 for respiration (**Figure 2*b***). Given that larger cells are less carbon dense, and carbon biomass in phytoplankton therefore scales with V with an exponent smaller than 1 (Menden-Deuer & Lessard 2000), expressing cell size as cell carbon increases the scaling exponents for photosynthesis and respiration to 0.99 and 1.04, respectively. Thus, irrespective of the metric used to describe cell size, phytoplankton metabolism scales isometrically or nearly isometrically, which implies that the pace of metabolism is broadly similar in both small and large cells, in stark contrast to the predictions of the 3/4-power rule.

Considering the strong biophysical constraints that increasing size imposes on photoautrophic unicellular organisms, particularly in terms of light acquisition and nutrient uptake (Chisholm 1992, Kiørboe 1993, Raven 1998), it is remarkable that large cells are able to sustain metabolic rates that are comparable (per unit of volume or biomass) to those of their smaller counterparts. However, large cells possess several traits that can help them to overcome size-related constraints, including changes in cell shape that increase the effective surface-to-volume ratio, an increased ability to store nutrients (Litchman et al. 2007), and a reduction in volume-specific nutrient requirements resulting from changes in their stoichiometry (Thingstad et al. 2005). However, as discussed below, small cells can also be subject to limitations related to nutrient uptake and use (Marañón et al. 2013).

Biomass-Specific Metabolic Rates and Growth

Even though cell size can explain a large amount of the variability in metabolic rate in log-log plots, indicating the broad validity of a power-law model, the assumption of linearity can mask the existence of curvature in metabolic scaling (Kolokotrones et al. 2010). This is the case for the photosynthesis data shown in **Figure 2*a***, which were better described by a quadratic model. The presence of curvature in metabolic scaling becomes much clearer when the same carbon fixation data are divided by cell biomass: When plotted against cell size (**Figure 2*c***), the resulting biomass-specific metabolic rate (in units of time^{-1}) displays a marked unimodal pattern. Because population growth is closely linked to metabolism (Fenchel 1974), the same unimodal pattern is observed when the abundance-based maximum growth rate is plotted against cell size (**Figure 2*d***). Thus, the highest biomass-specific metabolic rates and growth rates in phytoplankton are achieved by species of intermediate cell size, a conclusion that is also supported by field measurements (Bec et al. 2008, Chen & Liu 2011).

The unimodality in the size scaling of phytoplankton growth and metabolism mirrors the pattern described by DeLong et al. (2010), who found that biomass-specific respiration rates decrease with body size in metazoans, are roughly independent of cell size in protists, and increase

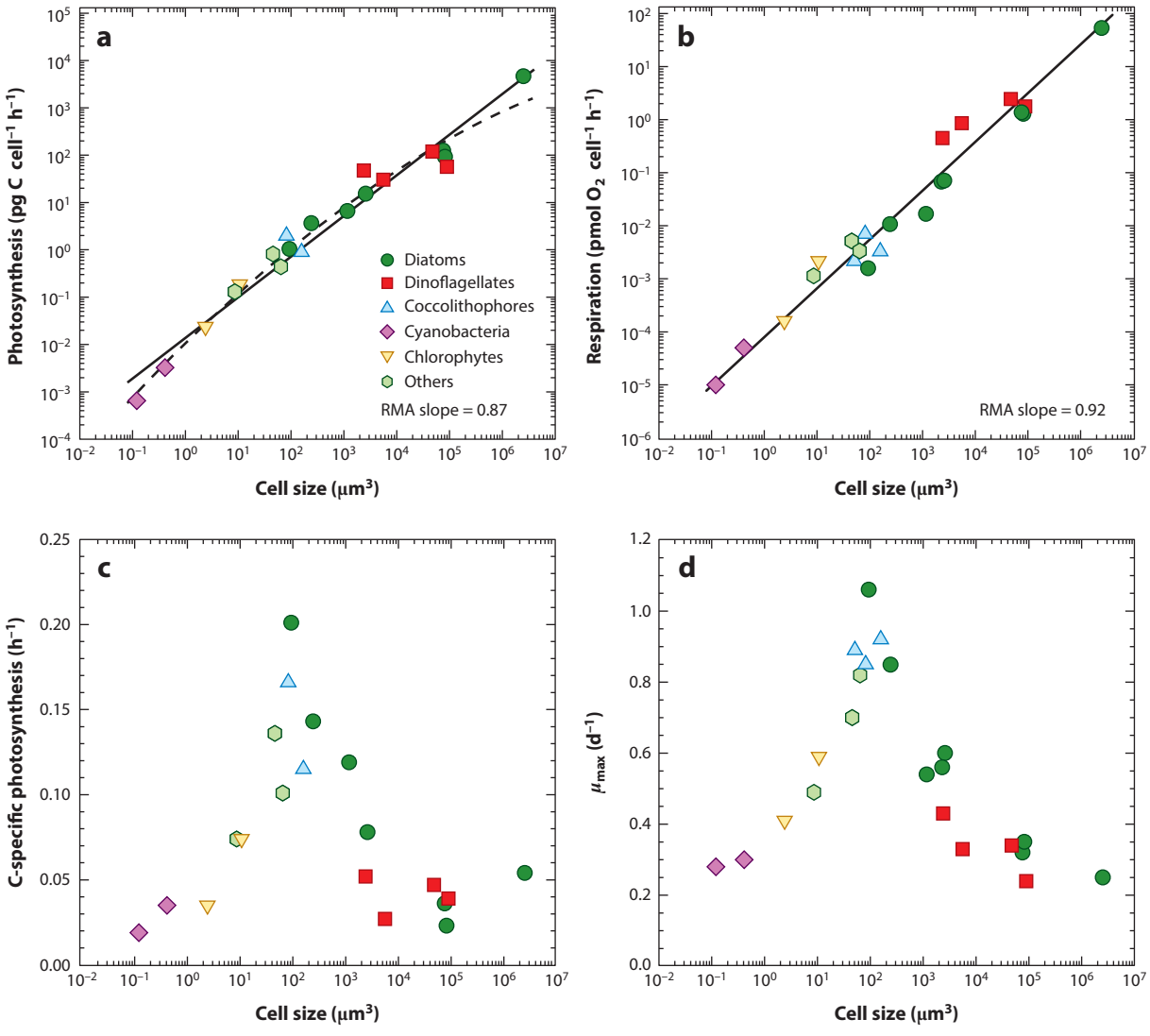


Figure 2

Size scaling of phytoplankton metabolism and growth. Plotted against cell size are (*a*) photosynthesis per cell, (*b*) dark respiration per cell, (*c*) carbon-specific photosynthesis, and (*d*) maximum population growth rate (μ_{max}) in a study of 22 species growing under the same conditions (Marañón et al. 2013, López-Sandoval et al. 2014). The studied species included diatoms, dinoflagellates, coccolithophores, cyanobacteria, and chlorophytes. Photosynthesis and respiration were measured with the ^{14}C-uptake and O_2-evolution techniques, respectively, and μ_{max} was computed from cell abundance. Reduced-major-axis (RMA) regression was applied to $\log_{10}$-transformed variables. The resulting linear fits are $y = 0.87x - 1.86$ ($r^2 = 0.96$, $n = 20$, $p < 0.001$) in panel *a* and $y = 0.92x - 4.10$ ($r^2 = 0.96$, $n = 22$, $p < 0.001$) in panel *b*. The quadratic regression in panel *a* is $y = -0.047 \times ^2 + 1.10x - 1.98$ ($r^2 = 0.96$, $n = 22$, $p < 0.001$). Panels *c* and *d* adapted from Marañón et al. (2013) with permission (© John Wiley & Sons Ltd/CNRS).

with cell size in prokaryotes. These changes reflect variations across the different domains of life in the constraints that operate on metabolism and growth. In the case of phytoplankton, however, unimodality does not seem to arise from changes in cell organization (e.g., a transition from prokaryotes to eukaryotes), because the decrease in growth rate with decreasing cell size is also observed in the smallest eukaryotic algae (Bec et al. 2008, Marañón et al. 2013) (**Figure 2*c,d***). Hence, unimodality seems to emerge as a direct consequence of changes in cell size, which impose stronger growth constraints on small and large cells compared with intermediate-size cells. Given that population growth ultimately depends on the uptake of nutrients and their conversion into new biomass, investigating how nutrient requirements, uptake, and assimilation change along the size spectrum can offer insight into the size dependence of phytoplankton growth and metabolic rates.

ISOMETRIC SIZE SCALING OF MAXIMUM NUTRIENT UPTAKE

Small cells are better prepared than larger cells to avoid the diffusion limitation of nutrient uptake, which explains why the former tend to dominate phytoplankton biomass in oligotrophic environments. However, understanding which cell sizes predominate during blooms, when nutrients are available in high concentrations, requires considering the size scaling of the cell-specific maximum nutrient uptake rate (V_{max}). Theoretically, assuming that ion handling time and transporter density are size independent, V_{max} is expected to be proportional to cell surface area (Aksnes & Egge 1991) and to scale as $V^{2/3}$, as found by Smith & Kalff (1982) in a study of eight species ranging in cell volume from 10^2 to 10^4 μm^3. Literature-based analyses of V_{max} data from a larger number of species spanning a broader range in cell size have given size-scaling exponents that range between 2/3 and 1 (Litchman et al. 2007, Finkel et al. 2010, Edwards et al. 2012). Two limitations of data compilations are that the observations originate from cultures experiencing different growth conditions and that the protocols to measure key physiological properties often vary, thus introducing uncertainty in the obtained relationships and parameters. In particular, estimates of V_{max} are highly sensitive to differences in methodological procedures, such as the length of time over which uptake rates are measured (Harrison et al. 1989).

The determination, following standardized protocols, of maximum nitrogen uptake (V_{maxN}) in 22 species spanning more than seven orders of magnitude in cell size (**Figure 3*a***) has revealed that nutrient uptake in phytoplankton scales isometrically with cell volume (Marañón et al. 2013). As the nitrogen density of cells decreases with increasing size (Menden-Deuer & Lessard 2000, Montagnes & Franklin 2001), the scaling exponent in the relationship between the minimum nitrogen quota (Q_{minN}) (Droop 1973) and V_{maxN} takes a value (1.15) that is significantly greater than 1 (**Figure 3*b***). This pattern implies that the nitrogen-specific maximum nitrogen uptake rate increases by a factor of >5 from the pico- to the microphytoplankton and hence that, when nutrients are in high supply, larger cells are able to obtain nutrients at a rate that greatly exceeds their minimum requirements. The mechanism whereby increasingly large cells are able to maintain the same volume-specific rate of nutrient uptake as smaller cells do is currently unknown. The fact that the slope of the relationship between V_{maxN} and both V and Q_{minN} does not change across the size spectrum suggests that the underlying mechanism must be general, rather than associated with particular traits such as the presence of the vacuole in diatoms or the departure from a spherical shape in intermediate-size and large cells. One testable hypothesis is that the density of nutrient uptake sites on the membrane increases with cell size as a result of an evolutionary pressure to ensure access to nutrients during transient episodes of enhanced nutrient supply.

There are large quantitative implications if the size-scaling exponent of V_{max} takes a value of 1 as opposed to 2/3. If $V_{max} \propto V^1$, a 1,000-fold increase in V results in a 1,000-fold increase in

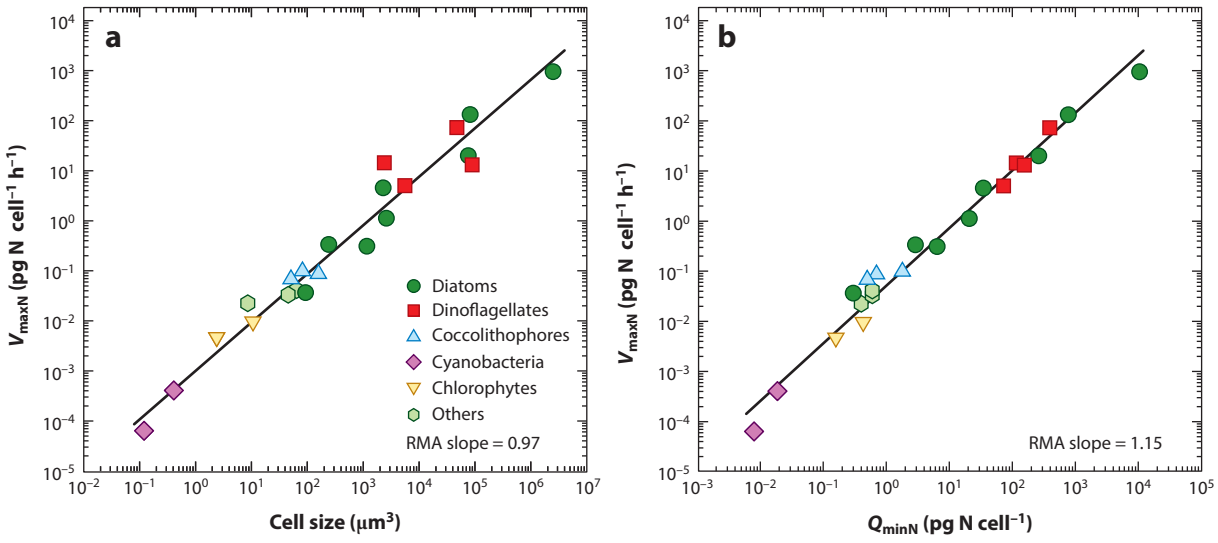


Figure 3

Size scaling of maximum nitrogen uptake rate (V_{maxN}). V_{maxN} is plotted against (*a*) cell size and (*b*) minimum nitrogen quota (Q_{minN}). V_{maxN} was determined in nitrogen-limited populations during the stationary growth phase, and Q_{minN} was calculated as the lowest nitrogen cell content measured throughout the growth cycle (Marañón et al. 2013). Log_{10}-transformed data were fitted to linear models using reduced-major-axis (RMA) regression: $y = 0.97\,x - 3.00$ ($r^2 = 0.96$, $n = 22$, $p < 0.001$) in panel *a*, and $y = 1.15\,x - 1.29$ ($r^2 = 0.98$, $n = 22$, $p < 0.001$) in panel *b*. Figure adapted from Marañón et al. (2013) with permission (© John Wiley & Sons Ltd/CNRS).

V_{max}, whereas if $V_{max} \propto V^{2/3}$, the same increase in V results in only a 100-fold increase in V_{max}. Thus, applying a 2/3 size-scaling exponent for V_{max} underestimates the nutrient uptake ability of large phytoplankton cells by approximately one order of magnitude and overestimates that of small cells by the same amount. Another way to put this is to consider that if $V_{max} \propto V^{2/3}$, the volume-specific V_{max} will scale as $V^{-1/3}$, implying that a population of a large species (e.g., with a cell volume of 10^5 μm^3) should take approximately 50 times longer to consume a given amount of nutrients than would a population of a small species (e.g., with a cell volume of 1 μm^3) with the same biovolume concentration. In contrast, the time required to consume all initial nutrients by equally dense batch cultures is relatively similar and varies only by a factor of 2–3 across a cell size range of 0.1–10^6 μm^3 (Marañón et al. 2013).

It can be concluded that large cells are not constrained, relative to their smaller counterparts, by their ability to obtain nutrients when they are in high supply. However, the fact that growth and metabolic rates do slow down with increasing cell size for cells with ESDs larger than 5 to 10 μm (**Figure 2*c*,*d***) indicates that some other limiting factor must be operating. The next section discusses the trade-off mechanisms that may explain why increasing cell size can have opposite effects on metabolism and growth in small to intermediate species (those with ESDs of approximately 0.6 to 10 μm) and intermediate to large species (those with ESDs of approximately 10 to >100 μm).

MECHANISMS UNDERLYING THE UNIMODAL SIZE SCALING OF PHYTOPLANKTON GROWTH

Variability in growth rate along the size spectrum can arise as a result of changes in metabolic processes of gain (nutrient uptake and assimilation, carbon fixation) and loss (exudation, respiration).

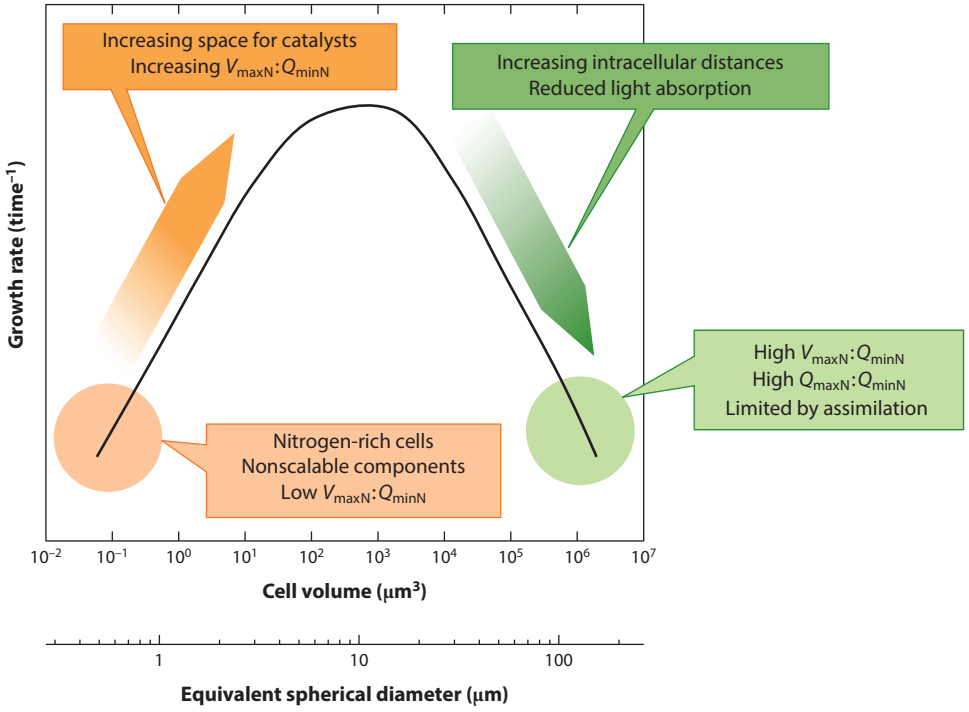


Figure 4

Potential mechanisms underlying the unimodal size scaling of phytoplankton growth. V_{maxN} is the maximum nitrogen uptake rate; Q_{maxN} and Q_{minN} are the maximum and minimum nitrogen quotas, respectively.

However, the extracellular release of dissolved organic carbon and respiration (both expressed as a fraction of photosynthetically fixed carbon) are relatively low (<5% for exudation and <15% for respiration) in exponentially growing algal cultures and, in addition, remain relatively constant across the whole cell size range (López-Sandoval et al. 2013, Marañón et al. 2013). The constancy of biomass-specific respiration across the size spectrum does not support the size dependence of respiratory losses as an important factor to explain the size scaling of phytoplankton growth (Laws 1975). Therefore, size-related changes in anabolic processes such as carbon fixation and nutrient uptake and assimilation must be the driving factors behind the unimodal size scaling of growth rate (**Figure 4**).

Small phytoplankton show volume-specific V_{max} values similar to those of larger cells (**Figure 3*a***), but they have lower carbon-to-nitrogen ratios and therefore are more nitrogen rich (Marañón et al. 2013), which reflects reduced storage of carbon-rich macromolecules and an increased contribution to total biomass of nonscalable, nitrogen-containing molecules such as nucleic acids and membrane proteins (Raven 1994). Nonscalable components occupy an increasing fraction of total volume as cell size decreases (Raven 1998), thus reducing the amount of space available for catalytic and biosynthetic units. These factors, combined with the fact that small cells have lower nitrogen-specific nitrogen uptake abilities than larger cells, can explain the relatively low growth rates of the former. These limitations become progressively less acute as cell size increases, more space becomes available for catalytic units, and nutrient uptake ability is enhanced, thus resulting in a positive relationship between cell size and both biomass-specific production and growth rate in the size range of 0.1–100 μm^3 (**Figure 4**).

Given that V_{max} increases with cell size faster than Q_{minN} does (**Figure 3*b***), the larger the cells are, the higher is their ability to obtain nutrients in excess of their requirements. If the V_{max}-to-Q_{minN} ratio alone were the key factor determining the potential for algal growth, one would expect the growth rate to increase continuously as the cell size becomes larger. In contrast, growth rates decrease with increasing cell size in the size range of 10^2–10^6 μm^3, which is probably related to the increasing intracellular distances for the transport of nutrients and CO_2 required for biosynthesis (Wirtz 2011) and also to the enhanced package effect, which reduces light absorption (Finkel 2001). These factors prevent the rapid conversion of nutrients to new biomass, which results in a progressive uncoupling between nutrient uptake and nutrient assimilation. Therefore, V_{max} is not necessarily a good predictor of growth potential in phytoplankton.

In summary, small cells are constrained mainly by their comparatively small (relative to requirements) nutrient uptake ability as well as their reduced biosynthetic ability as a result of the presence of nonscalable components, whereas large cells are limited mainly by the conversion of nutrients into biomass as a result of size-related constraints imposed on intracellular resource transport. The resulting trade-off between these opposing size-driven limiting processes would explain why cells of intermediate size achieve the fastest growth rates. The question now becomes, how do these size-dependent changes in metabolism and growth relate to the variability and patterns of phytoplankton size structure in the sea?

PHYTOPLANKTON SIZE STRUCTURE: PATTERNS AND DRIVERS OF CHANGE

From Size Scaling of Metabolism to Community Size Structure

The link between the size scaling of phytoplankton metabolism and growth and the size structure of natural assemblages is not straightforward, because changes in the abundance of a given species or size class depend not only on nutrient uptake or biomass production and growth but also on loss processes such as predation, sinking, and viral lysis, all of which can be subject to various degrees of size dependence (Raven 1998). The traditional assumption has been that, as with plants and metazoans (Savage et al. 2004), the maximum growth rate of phytoplankton decreases with increasing cell size. Given that sinking also increases with cell size, the fact that small cells fail to dominate blooms has been attributed mainly to their larger susceptibility to grazing. However, the novel size-scaling relationships discussed above suggest that small cells are unlikely to dominate blooms simply because they grow more slowly than some of their larger counterparts.

To test whether the unimodal size scaling of maximum growth rate observed in the laboratory is also reflected in real patterns at sea, we must consider the size distribution of bloom-forming species. An analysis of 70 bloom samples in coastal, highly productive waters of the northwest Iberian peninsula revealed that the dominant species during events of enhanced algal biomass belonged most frequently to intermediate size classes (**Figure 5*a***), which supports the connection between the size scaling of maximum growth rate and the actual size structure of phytoplankton. The size distribution of bloom-forming species is, however, shifted toward somewhat larger sizes compared with the unimodal pattern observed in the laboratory, which likely reflects the role of large cell size as a protection against predation. Very large cells (e.g., with an ESD of >80 μm), being subject to heavy losses through sinking, seldom form blooms in these locations.

Measurements of the amount of chlorophyll *a* collected by filters of different pore size suggest that, as total phytoplankton biomass increases, the biomass in each size class keeps growing until it reaches an upper limit, which is higher for progressively larger cell sizes (Marañón et al. 2001, 2012; Ward et al. 2014). This implies that, beyond a certain limit, more phytoplankton biomass

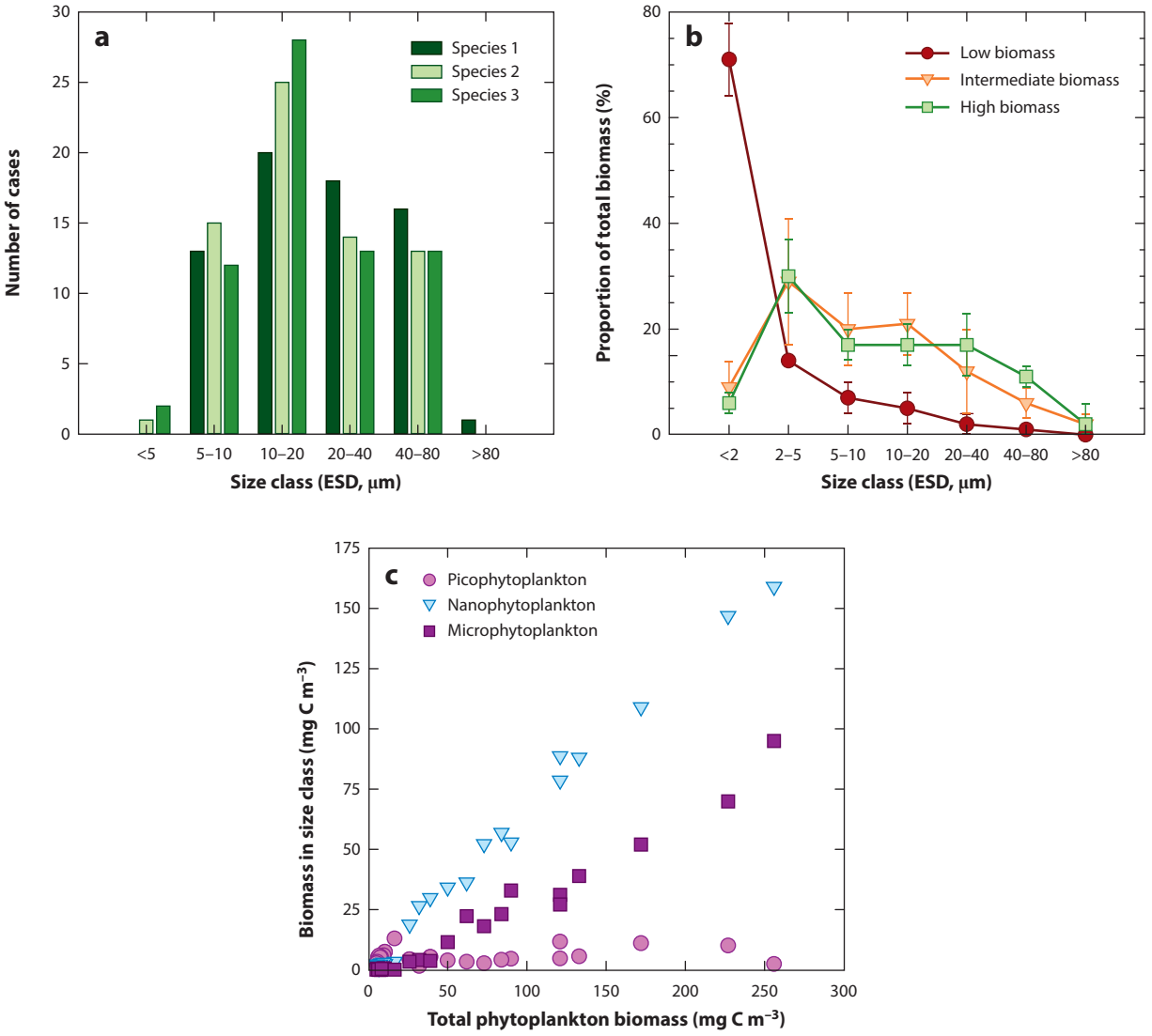


Figure 5

Patterns in phytoplankton size structure. (*a*) Size distribution of bloom-forming species in coastal waters of the northwest Iberian peninsula. For each sample obtained during a bloom (samples with total phytoplankton carbon of >200 mg C m^{-3}; $n = 70$), species were ranked according to their total population biomass. The frequency distribution shows the number of cases in which the three top-ranking species (whose identity varied among samples and which together accounted for, on average, 70% of total phytoplankton biomass) belonged to each size class. (*b*) Mean contributions of different size classes to total carbon biomass in samples with low ([chlorophyll *a*] < 0.3 mg m^{-3}), intermediate (1 < [chlorophyll *a*] < 2 mg m^{-3}), and high ([chlorophyll *a*] > 5 mg m^{-3}) phytoplankton biomass, obtained in coastal and open-ocean waters ($n = 6$ for each biomass level). Bars indicate standard deviations. (*c*) Relationship between biomass in different size classes (pico-, nano-, and microphytoplankton, referring to cells with diameters of <2 μm, 2–20 μm, and >20 μm, respectively) and total phytoplankton biomass. Species were assigned to size classes based on their individual cell sizes. Abbreviation: ESD, equivalent spherical diameter. Original data provided by Manuel Varela and Francisco G. Figueiras (panel *a*) and by José M. Blanco, Jaime Rodríguez, and María Huete-Ortega (panels *b* and *c*).

can be added only if larger and larger size classes are added (Chisholm 1992). This tenet is incorporated into size-structured ocean food-web models, in which the nutrient supply limits the number of coexisting size classes, and zooplankton grazing limits the amount of biomass within each size class (Armstrong 1994, Poulin & Franks 2010, Ward et al. 2014). However, a different perspective is given by the analysis of biomass size spectra, based on the measurement of cell abundance and biovolume using flow cytometry and microscopy. First, the range of cell sizes present is comparable in all regions, despite widely differing nutrient supply regimes (**Figures 1** and **5*b***): Relatively large cells (ESDs of 20–80 μm) are also present in ultraoligotrophic waters. Second, coastal waters containing very different amounts of phytoplankton (intermediate- and high-biomass samples in **Figure 5*b***) show a remarkably similar distribution of biomass along the size spectrum, with the 2–5-μm ESD size class accounting for the largest share of total biomass. As total phytoplankton biomass increases, the biomasses of both nano- and microphytoplankton increase monotonically, but nanophytoplankton dominate, typically contributing 60–80% of the total biomass (**Figure 5*c***).

These patterns are robust, because the broad partitioning of biomass among size classes does not change significantly when different empirical functions (Verity et al. 1992, Menden-Deuer & Lessard 2000, Montagnes & Franklin 2001) are used to convert cell biovolume into units of carbon (Cermeño et al. 2005a). Modeling work has also shown that the biomass contribution of nanophytoplankton increases with total biomass (Ward et al. 2012). Thus, there is a discrepancy between the size-fractionated chlorophyll *a* results and the size partitioning of carbon biomass based on flow cytometry and microscopy measurements of cell size and abundance. The size-fractionated chlorophyll *a* data likely overestimate the importance of microphytoplankton and underestimate that of nanophytoplankton, because chain-forming species are retained by the 20-μm filter even if their individual cell sizes are smaller and because filter clogging in rich waters leads to a reduction in the effective filter pore size. These results suggest that, in productive regions, nanophytoplankton rather than microphytoplankton are the dominant size class, which reflects the competitive advantage provided by intermediate cell size in terms of nutrient acquisition and conversion into new biomass.

The preceding arguments provide an ataxonomic view of the mechanisms that explain why most bloom-forming species are of intermediate cell size. However, it must be noted that not all intermediate-size species have the same probability of forming blooms (defined as events of high phytoplankton biomass): Diatoms in particular most often dominate when algal standing stocks and productivity are high (Karentz & Smayda 1984, Smetacek 1999, Sarthou et al. 2005). As an example, 80% of the 70 blooms examined in **Figure 5*a*** were dominated by diatoms. Of especial importance is the presence of the vacuole, which allows diatoms to increase the effective surface-to-cytoplasm ratio, maintain high nutrient uptake rates for longer, and exploit nutrient pulses more effectively than other taxa of the same size (Falkowski & Oliver 2007, Cermeño et al. 2011). Compared with other groups, diatoms are more capable of sustaining fast carbon fixation rates after nutrients have been exhausted from the external medium (López-Sandoval et al. 2014), which, together with luxury nutrient uptake (Stolte & Riegman 1995), allows them to decouple carbon and nitrogen acquisition, thus gaining a competitive advantage over other taxa during conditions of intermittent resource supply. From an ecological standpoint, it has been argued that diatoms are less susceptible to grazing on account of their large apparent size (due to their spines) and the presence of the frustule, among other defense mechanisms (Smetacek 1999, Irigoien et al. 2005). The reasons for the success of diatoms in high-productivity regions thus appear to be both physiological and ecological.

In open-ocean, oligotrophic waters, such as those of the subtropical gyres, the size distribution of biomass is heavily skewed toward the picophytoplankton (**Figures 1*b*** and **5*b***), as the

cyanobacterium *Prochlorococcus* accounts for a large share of the total biomass (Zubkov et al. 1998, Marañón et al. 2003). This is also reflected in the size-abundance spectrum, which typically exhibits very steep slopes (between −0.9 and −1.3). The subtropical gyres are near-steady-state ecosystems, with comparatively low variability in resource supply rates, and therefore it can be hypothesized that the size scaling of phytoplankton abundance in these regions is coupled to the size scaling of metabolic rate.

Let us assume that, in a resource-limited ecosystem, the abundance of a given species (or size class) depends on the ratio between the resource supply rate and the resource consumption rate, the latter of which is in turn controlled by the metabolic rate. Given that individual metabolic rates and thus resource consumption rates increase with cell or body size, a given amount of resources can sustain a large number of small organisms or a small number of large organisms. If we further assume that access to resources is size independent, the size-scaling exponent for cell abundance will be the same as that of the metabolic rate but with the opposite sign (Enquist et al. 1998), a condition known as reciprocal size scaling of abundance and metabolism. Huete-Ortega et al. (2012) tested this prediction in surface, light-saturated, nutrient-limited phytoplankton assemblages of the subtropical and tropical Atlantic; consistent with the hypothesis, they found that the size-scaling exponent of the log-log relationship between the individual metabolic rate and cell size averaged 1.16, whereas the size-scaling exponent for cell abundance was −1.15.

Thus, it appears that the regularity and slope value of the size-abundance spectrum, a pervasive property of phytoplankton assemblages in quiescent, low-productivity environments, can be traced back to the size scaling of metabolic rate. In coastal upwelling regions, however, the reciprocal size scaling of metabolism and abundance is not observed, because nutrients are delivered to the euphotic layer mostly through discontinuous pulses, which are preferentially utilized by intermediate-size and large cells on account of their high V_{max} and nutrient storage capacity (Stolte & Riegman 1995, Litchman et al. 2007, Marañón et al. 2013). The result is that, in these non-steady-state systems, phytoplankton size structure is shifted toward an enhanced biomass dominance of nano- and microphytoplankton (**Figure 5*b***), which is also reflected in less steep slopes of the size-abundance spectrum (**Figure 1*a***).

Drivers of Change in Phytoplankton Size Structure

Nutrient supply is regarded as the single most important factor controlling phytoplankton size structure, based on the well-known association between oligotrophic conditions and picophytoplankton dominance in the low latitudes and between higher nutrient availability and an enhanced contribution of larger cells in high latitudes and coastal waters. However, there are often exceptions to this pattern. In temperate seas during winter, nutrient concentrations are high, but small cells contribute a substantial fraction of total biomass (Irigoien et al. 2005, Cermeño et al. 2006b, Arbones et al. 2008). In coastal waters of the Antarctic Peninsula, phytoplankton in the <5-μm size class account for one-third of total chlorophyll *a* in winter, coinciding with very high nutrient concentrations throughout the water column (Clarke et al. 2008). Light availability thus appears to be an important factor for phytoplankton size structure: Small cells are less heavily affected by the package effect and cope better with reduced light conditions (Raven 1998, Finkel et al. 2004, Cermeño et al. 2005b), which explains their increased biomass contribution during winter.

Given that primary production requires the use of both light and nutrients, its rate can be used as a proxy for combined resource use. An analysis of phytoplankton size structure throughout the global ocean found that the rate of primary production is a good predictor of the dominance by different size classes: The importance of large cells increases rapidly with a growing rate of carbon fixation in a pattern that is independent of geographical location (Marañón et al. 2012).

Using in situ data of nutrient concentration, vertical density stratification, and light penetration, one can calculate a resource supply index (RSI) that captures broad differences in nutrient and light availability for phytoplankton in contrasting ocean regions (Marañón et al. 2014). The subtropical gyres have the lowest RSI values and show the smallest contribution of large cells to total chlorophyll *a* concentration (**Figure 6*a***) and biomass (**Figure 5*b***). Temperate regions and the open-ocean upwelling region (including waters affected by the equatorial and Mauritanian upwellings) have an enhanced resource supply and a higher contribution of large cells, whereas coastal productive waters, which have the highest RSI values, show the largest percentage of chlorophyll *a* in the >20-μm size fraction. Large-scale variability in phytoplankton size structure across coastal and open-ocean regions thus reflects the changes in resource supply.

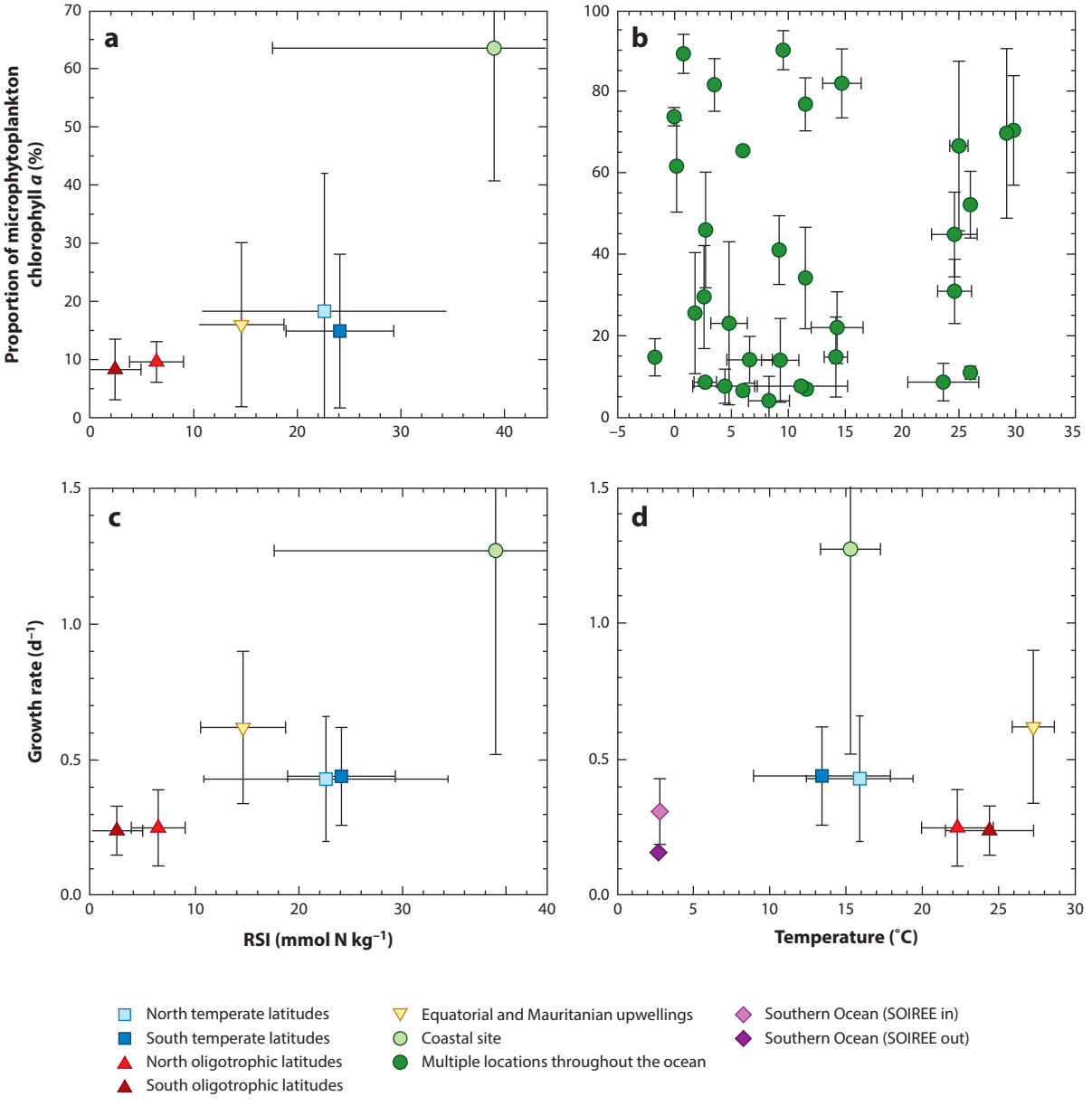
The analysis of population size-abundance spectra, in which the population abundances of individual species are plotted against their mean cell size, gives additional insight into the mechanisms that control phytoplankton size structure in contrasting environments (Cermeño et al. 2006a). In principle, given that small cell size confers a competitive advantage under conditions of limited resource supply, one might expect that the interspecific scaling of population abundance and cell size would show steeper (i.e., more negative) slopes in more oligotrophic environments, indicating that nutrient limitation causes a stronger reduction in the abundance of larger species. In contrast, similar slope values were found in coastal, temperate, and tropical waters with widely differing nutrient availabilities (Cermeño et al. 2006a), and the intercept values increased from oligotrophic to eutrophic waters (Cermeño & Figueiras 2008, Cermeño et al. 2008), reflecting the positive relationship between resource supply and algal standing stocks.

The invariant across-system size scaling of population abundance implies that large phytoplankton species living in oligotrophic waters are present in the abundances that correspond to their cell sizes and the available nutrient supply, which suggests that they are able to overcome the limitations arising from cell size (Cermeño et al. 2006a). The ability to migrate vertically in the water column (Villareal et al. 1996), the possession of vacuoles (Raven 1987), the presence of nitrogen-fixing endosymbionts (Villareal et al. 2012), and changes in cell shape (Niklas 1994) and nutrient stoichiometry (Thingstad et al. 2005) are some of the adaptive strategies that explain the presence, in normal abundances, of large cells in oligotrophic systems. However, nutrient-impoverished conditions do restrict the number (species richness) of large species that are able to survive in oligotrophic regions. In spite of the invariant size scaling of population abundance, the slope of the total size-abundance spectra is more negative in the subtropical gyres than in coastal waters, which indicates that species richness decreases more rapidly with increasing cell size in the oligotrophic regions (Cermeño et al. 2008). Hence, biogeographic differences in resource supply control phytoplankton size structure by imposing changes in the distribution of species richness across the size spectrum.

Temperature is an important controlling factor of body size in ectotherms (Forster et al. 2012). The mean intraspecific cell size in protists decreases by approximately 2.5% per degree Celsius of warming (Atkinson et al. 2003), which in principle could lead to an increased biomass contribution of picophytoplankton as the ocean warms. In addition, experimental warming in mesocosms can result in enhanced zooplankton grazing activity and a subsequent shift toward a smaller mean community cell size (Sommer & Lengfellner 2008, Yvon-Durocher et al. 2010). In fact, the decrease in body size with climate warming has been proposed as a universal ecological rule in aquatic ecosystems (Daufresne et al. 2009). In an analysis of picophytoplankton abundance and cell size in the North Atlantic, Morán et al. (2009) found that temperature alone explained most of the variability in the relative contribution of picophytoplankton to total biomass, regardless of the trophic status as inferred from nutrient concentration.

However, considering only nutrient concentration does not allow one to discern the effects of resources on phytoplankton size structure. For instance, equally low nutrient concentrations can

be the result of recent, intense consumption by phytoplankton in productive waters (associated with a dominance of large cells) or strong thermal stratification over seasonal or longer timescales (associated with a dominance of small cells). In addition, a full consideration of the role of resources must also include irradiance: Because of light limitation, high nutrient concentrations in winter typically coincide with a relatively small contribution of large cells. Given that resource availability in the ocean often covaries with temperature over multiple temporal and spatial scales, disentangling the effects of these two factors requires analyzing phytoplankton size structure in waters with all combinations of resource supply and temperature. An analysis by Marañón et al. (2012) revealed that phytoplankton size structure in the sea is largely independent of temperature



(**Figure 6*b***). Large cells dominate in the nutrient-rich, cold waters of the high-latitude seas but also in warm, coastal areas affected by continental runoff and in tropical waters subjected to coastal upwelling. Conversely, small cells contribute most of the biomass in the warm, oligotrophic gyres but also in polar waters during light-limiting conditions in winter as well as in the iron-limited regions of the Southern Ocean.

These resource-driven changes in phytoplankton size structure can be regarded as manifestations of community structure reorganization, which arises from the environmental selection of size- and taxon-related functional traits that control the acquisition and use of light and nutrients (Margalef 1978). Warming of the low-latitude regions is expected to enhance the dominance of small cells as a result of increased nutrient limitation (Peter & Sommer 2013), potentially leading to a reduction in the strength of the biological carbon pump (Bopp et al. 2005, Steinacher et al. 2010). By contrast, warming of the high-latitude seas, if conducive to higher rates of light utilization (Doney 2006) and productivity, will favor large cells and enhance biogenic carbon export. In some coastal regions, even if surface waters warm, increasingly frequent episodes of nutrient runoff from land will likely promote the occurrence of phytoplankton blooms (Beman et al. 2005) and thus a shift toward larger mean cell size. Consequently, there will be no single, universal response of phytoplankton size structure to global-change effects in the ocean.

The association between an increasing dominance of large cells and conditions that stimulate the metabolism of phytoplankton is confirmed when mean growth rates (carbon fixation rate divided by biomass, in units of time^{-1}) determined in contrasting regions are plotted against resource supply (**Figure 6*c***). There is a resource-driven, biogeographic pattern whereby not only standing stocks but also phytoplankton growth rates increase from the subtropical gyres to the open-ocean upwelling and temperate regions and then the coastal waters (Marañón et al. 2014). This pattern, which is paralleled by a growing contribution of large cells to total biomass (**Figures 5*b*,*c*** and **6*a***), argues against the suggestion that the variability in phytoplankton standing stocks is disconnected from their intrinsic growth rates (Behrenfeld & Boss 2014) and also challenges the view that phytoplankton sustain fast growth rates in the oligotrophic ocean (Laws 2013). The large-scale coupling between resource supply and phytoplankton growth rate and size structure (**Figure 6*a*,*c***) highlights the crucial role of environmental forcing in the control of phytoplankton dynamics. Temperature, however, seems to play a much smaller role than resources, because it shows no relationship with biomass-specific phytoplankton production rate across different oceanic and coastal regions (**Figure 6*d***).

Figure 6

Effects of resources and temperature on phytoplankton size structure and growth rate. (*a*) Contribution of microphytoplankton (cells with a diameter of >20 μm) to total chlorophyll *a* concentration as a function of the resource supply index (RSI) in coastal and open-ocean waters of the Atlantic. (*b*) Proportion of microphytoplankton chlorophyll *a* plotted against temperature in surface samples obtained throughout the world (see sampling locations in Marañón et al. 2012). (*c*,*d*) Total phytoplankton growth rate plotted against RSI (panel *c*) and temperature (panel *d*) in coastal and open-ocean waters at polar, temperate, and tropical latitudes. Bars indicate standard deviation. The growth rate was calculated as the daily carbon fixation rate divided by phytoplankton carbon biomass (Marañón 2005). The RSI (not to be confused with a nutrient concentration) was calculated as RSI = $[NO_{3(1\%PAR)}/\Delta\sigma_t] \times [1\%PARz/UMLz]$, where $NO_{3(1\%PAR)}$ is the nitrate concentration (mmol N m^{-3}) at the base of the euphotic zone, $\Delta\sigma_t$ is the density (σ_t) difference (kg m^{-3}) between the surface and the base of the euphotic zone, 1%PAR*z* is the depth (m) of the euphotic zone, and UML*z* is the depth (m) of the upper mixed layer (Marañón et al. 2014). The data in panels *a*, *c*, and *d* were obtained at a coastal site (Ría de Vigo, northwest Iberian peninsula) (Cermeño et al. 2006b), in the Southern Ocean during the Southern Ocean Iron Release Experiment (SOIREE) (Boyd et al. 2000), and at different points during the Atlantic Meridional Transect (AMT) (Marañón et al. 2000). The AMT data were partitioned based on sampling latitude: north temperate (35–49°N), south temperate (35–48°S), north oligotrophic (20–31°N), south oligotrophic (10–34°S), and equatorial and Mauritanian upwellings (5°S–20°N). Panel *b* adapted from Marañón et al. (2012) with permission (© American Association for the Sciences of Limnology and Oceanography).

It must be stressed that assessing the temperature dependence of phytoplankton metabolism requires standardizing the metabolic rates by biomass, not by chlorophyll *a*. The cellular content of chlorophyll *a* is highly variable and depends not only on irradiance and temperature (Geider 1987) but also on nutrient availability (Cullen et al. 1992, Kruskopf & Flynn 2005), which can lead to severely biased patterns if chlorophyll-specific metabolic rates are used.

The lack of relationship between temperature and phytoplankton biomass-specific production shown in **Figure 6*d*** may seem surprising because temperature governs the metabolism of all organisms (Gillooly et al. 2001), and the temperature dependence of algal growth, based on laboratory measurements under near-optimal conditions, is well established (Eppley 1972). However, as Eppley himself noted, we must distinguish between the temperature dependence of maximal growth rates and that of realized growth rates in the field. Experimental and observational evidence indicates that, under nutrient limitation, the sensitivity of phytoplankton metabolism to temperature is reduced or even disappears entirely (Eppley 1972, Staehr & Sand-Jensen 2006, O'Connor et al. 2009, Tadonléké 2010), which likely reflects the limited applicability of Arrhenius kinetics under conditions of low substrate concentration (Davidson & Janssens 2006, Davidson et al. 2006). Widespread nutrient limitation at the ocean's surface (Moore et al. 2013) thus may explain the lack of temperature dependence of realized phytoplankton metabolic rates, with potentially important consequences for the modeling and prediction of global-change effects on the marine biota.

SUMMARY POINTS

1. Combining the study of the size scaling of phytoplankton abundance, biomass, metabolism, and growth allows a mechanistic, integrative understanding of the structure and functioning of plankton communities and pelagic ecosystems.
2. Biomass-specific metabolic rates in phytoplankton do not decrease allometrically with increasing cell size, as predicted by Kleiber's rule. Both very small and very large cells can sustain similar biomass-specific metabolic rates, but the fastest growth is achieved by cells of intermediate size.
3. Maximum nutrient uptake rate (V_{max}) scales isometrically with cell volume and superisometrically with cell-specific nutrient requirement. Assuming that V_{max} scales as the 2/3 power of cell volume can lead to a 10-fold underestimation of the nutrient uptake ability of large cells in high-nutrient conditions.
4. The unimodal size scaling of phytoplankton maximum growth rate arises from size-dependent trade-off processes related to nutrient requirements, acquisition, and use. Small cells are constrained by their reduced biosynthetic ability as a result of the presence of nonscalable components, whereas large cells are limited by slow nutrient assimilation into biomass as a result of long intracellular distances for resource transport.
5. The superior ability of intermediate-size cells to convert nutrients into biomass explains why the size distribution of bloom-forming species is also unimodal. The size structures of moderately rich and very rich waters are similar and in both cases are dominated by nanophytoplankton.
6. The biogeography of phytoplankton size structure and growth rate, which is independent of temperature, is driven mainly by differences in resource availability. The most relevant global-change effects on phytoplankton size structure and growth are likely to be those causing changes in resource supply.

DISCLOSURE STATEMENT

The author is not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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Errata

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