

# Phytoplankton Size Structure<sup>☆</sup>

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## Introduction

Phytoplankton are unicellular organisms that drift with the currents, carry out oxygenic photosynthesis and live in the upper, illuminated waters of all aquatic ecosystems. There are approximately 25,000 known species of phytoplankton, including eubacterial and eukaryotic species belonging to 8 Phyla. This phylogenetically diverse group of organisms constitutes the base of the food chain in most marine ecosystems and, since their origin more than  $2.8 \times 10^9$  years ago, have exerted a profound influence on the biogeochemistry of Earth. Currently, phytoplankton are responsible for the photosynthetic fixation of around  $50 \times 10^{15}$  gC annually, which represents almost half of global net primary production on Earth. On average, 15% of phytoplankton net primary production is exported towards the ocean's interior, either in the form of sinking particles or as dissolved material. The mineralization of this organic matter gives way to an increase with depth in the concentration of dissolved inorganic carbon. The net effect of this phytoplankton-fuelled, biological pump is the transport of  $\text{CO}_2$  from the atmosphere to the deep ocean, where it is sequestered over the time scales of deep-ocean circulation ( $10^2$ – $10^3$  years). A small fraction (<1%) of the organic matter transported towards the deep ocean escapes mineralization and is buried in the ocean sediments, where it is retained over time scales of  $>10^6$  years. It has been calculated that thanks to the biological pump the atmospheric concentration of  $\text{CO}_2$  is maintained 300–400 ppm below the levels that would occur in the absence of marine primary production. Thus, phytoplankton play a role in the regulation of the atmospheric content of  $\text{CO}_2$  and therefore affect climate variability.

The cell size of phytoplankton ranges widely over at least 9 orders of magnitude, from a cell volume around  $0.1 \mu\text{m}^3$  (equivalent to approximately  $0.5 \mu\text{m}$  of equivalent spherical diameter, ESD) for the smallest cyanobacteria to more than  $10^8 \mu\text{m}^3$  (c.  $1000 \mu\text{m}$  in ESD) for the largest diatoms. Cell size is a master functional trait that affects many aspects of phytoplankton physiology and ecology over multiple levels of organization, including individuals, populations and communities. Phytoplankton size structure, the partitioning of biomass among species of different cell sizes, is a fundamental property of pelagic ecosystems that largely determines their food-web organization and biogeochemical functioning. This article is organized as follows: first, I describe the biogeography of phytoplankton size structure in the ocean and its importance for the trophic organization and biogeochemical functioning of planktonic communities, then I review the physiological and ecological implications of cell size and, finally, I discuss the role of different factors driving the variability in phytoplankton size structure.

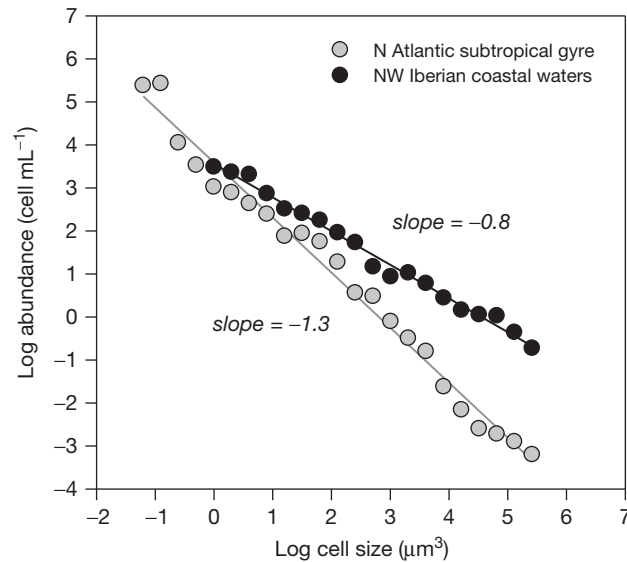
## Patterns of Phytoplankton Size Structure in the Ocean

A common approach to describe the size structure of phytoplankton communities is to construct size-abundance spectra, in which the abundance of all cells within logarithmic size classes is represented as a function of the nominal cell size of each class (Fig. 1). The slope of the size-abundance spectrum always takes negative values, because phytoplankton abundance tends to increase with decreasing cell size. This pattern results from the fact that the abundance of a population broadly depends on the ratio between resource supply and individual resource requirement. A given amount of resources, therefore, can support a large number of small individuals, or a small number of large organisms. The steepness (slope) of the size-abundance spectrum is a general indicator of the relative importance of cells of different size in terms of their contribution to total biomass. In waters with low phytoplankton biomass, such as the oligotrophic regions of the subtropical gyres, slope values range between  $-1.3$  and  $-0.9$ , whereas in productive, coastal waters slope values range between  $-0.6$  and  $-0.9$  (Fig. 1).

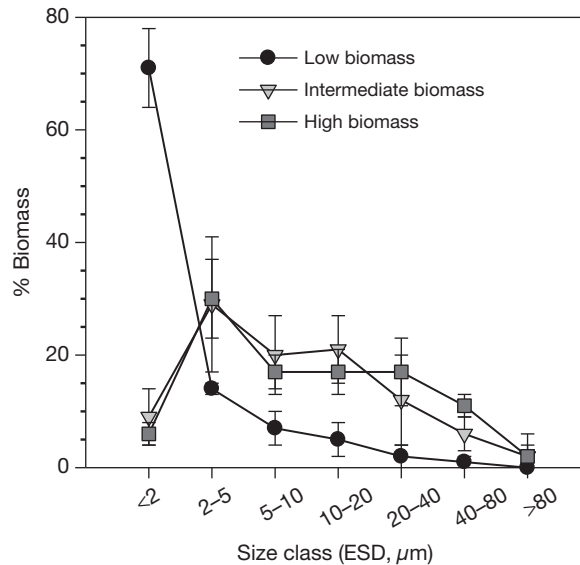
Using empirical volume to carbon conversion factors, it is possible to use the data shown in an abundance-size spectrum to construct a biomass-size spectrum, which gives the amount of biomass (in absolute or relative units) present in each size class (Fig. 2). While  $>60\%$ – $70\%$  of total biomass is contributed by picophytoplankton (cells with a diameter  $<2 \mu\text{m}$ ) in low-

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**Fig. 1** Size-abundance spectra in contrasting marine environments.



**Fig. 2** Biomass partitioning among size classes in samples from coastal and open-ocean waters with different amounts of total phytoplankton biomass (low:  $0.1\text{--}0.3\text{ mgChl } a\text{ m}^{-3}$ ; intermediate:  $1\text{--}2\text{ mgChl } a\text{ m}^{-3}$ ; high:  $>5\text{ mgChl } a\text{ m}^{-3}$ ). For each group of samples ( $n = 6$ ), the mean contribution of each size class to total carbon biomass is indicated. Bars represent the standard deviation.

productivity regions, the partitioning of biomass among the different size classes is more equitable in waters with intermediate and high standing stocks, which are characterized by a growing biomass contribution of cells in the size range  $5\text{--}40\text{ }\mu\text{m}$ . As a result, the mean cell size of the phytoplankton community tends to increase as total biomass increases. This variability in phytoplankton size structure has important implications for the food web structure and biogeochemical functioning of pelagic ecosystems (Table 1).

### Ecological and Biogeochemical Implications of Phytoplankton Size Structure

In communities dominated by picophytoplankton (cells  $<2\text{ }\mu\text{m}$  in diameter), where resource limitation leads to low phytoplankton biomass and production, the dominant trophic pathway is the microbial food web. Given that the growth rates of picophytoplankton and their protist microbial grazers are similar, trophic coupling between production and grazing is tight, most of phytoplankton daily primary production is consumed within the microbial community, and the standing stock of photosynthetic biomass is relatively constant over time. Phytoplankton exudation and microzooplankton excretion contribute to an important

**Table 1** General ecological and biogeochemical properties of plankton communities in which phytoplankton are dominated by small vs. large cells

Phytoplankton dominated by	Small cells (<2 $\mu\text{m}$ in diameter)	Large cells (5–40 $\mu\text{m}$ in diameter)
Total phytoplankton biomass	Low	High
Total primary production	Low	High
Dominant trophic pathway	Microbial food web	Classic food chain
Main loss process for phytoplankton	Grazing by protists	Sedimentation and grazing by metazoans
Photosynthesis to respiration ratio	$\sim 1$	$> 1$
Export ratio	5%–15%	$> 40\%$
Main fate of primary production	Recycling within the euphotic layer	Export towards deep waters

production of dissolved organic matter, which fuels bacterial production. In turn, bacteria are efficiently controlled by microbial protist grazers. The resulting complex food web is characterized by intense recycling of matter and low efficiency in the transfer of primary production towards larger organisms such as mesozooplankton or fish. Photosynthetic production of organic matter is nearly balanced by the respiratory losses with the microbial community. In addition, the small size of microbial plankton implies that losses through sedimentation are relatively unimportant. As a result, little newly produced organic matter escapes the euphotic layer.

In contrast, plankton communities dominated by larger phytoplankton, such as chain-forming diatoms, are characterized by enhanced sinking rates and simpler trophic pathways, where phytoplankton are grazed directly by mesozooplankton (the so-called classic food chain). Phytoplankton photosynthesis exceeds community respiration, leaving an excess of organic matter available for export. Thus, a major fraction of phytoplankton production is eventually transported towards deep waters, either directly through sinking of ungrazed cells, or indirectly through sedimentation of packaged materials such as aggregates and zooplankton fecal pellets. It must be noted that the microbial trophic pathway is always present in all planktonic communities, but its relative importance decreases in productive waters because of the addition of the classic food chain.

The ecological properties outlined above for phytoplankton assemblages dominated by small versus large cells dictate the biogeochemical functioning of the biological pump in contrasting marine environments. In stable, oligotrophic ecosystems, where small photoautotrophs dominate, primary production sustained by nutrients coming from outside the euphotic layer (new production) is small, and so is the ratio between new production and total production (the  $f$ -ratio), as well as the ratio between exported production and total production (the  $e$ -ratio). Typical values of the  $f$ - and  $e$ -ratios in these systems are in the range 5%–15%. Given that, in the long term, only new production has the potential to contribute to the transport of biogenic, organic carbon towards the deep ocean, the biological “soft-tissue” pump is weak and the net effect of the biota on the ocean-atmosphere  $\text{CO}_2$  exchange is small. By contrast, phytoplankton assemblages dominated by larger cells are typical of dynamic environments that are subject to intermittent perturbations leading to enhanced resource supply. In these systems, production and consumption of organic matter are decoupled, new and export production are relatively high ( $e$ - and  $f$ -ratios  $> 40\%$ ) and the biological pump effectively transports biogenic carbon towards the ocean’s interior. Given that large cells have fast sinking rates and are consumed by mesozooplankton, which produce fast-sinking fecal pellets, the fraction of the biogenic export flux that reaches the ocean floor and contributes to long-term carbon burial in the sediments increases with the mean cell size of the phytoplankton community.

### Cell Size and Phytoplankton Metabolism

Both nutrient uptake and light absorption are heavily dependent on cell size. The supply of nutrients to the cell may become diffusion-limited when nutrient concentrations are low, if the rate of nutrient uptake exceeds the rate of molecular diffusion and a nutrient-depleted area develops around the cell. Assuming a spherical cell shape and applying Fick’s first law of diffusion, the uptake rate ( $U$ ,  $\text{mol s}^{-1}$ ) can be expressed as:

$$U = 4\pi r D \Delta C \quad (1)$$

where  $r$  is the cell radius ( $\mu\text{m}$ ),  $D$  is the diffusion coefficient ( $\mu\text{m}^2 \text{s}^{-1}$ ) and  $\Delta C$  ( $\text{mol } \mu\text{m}^{-3}$ ) is the nutrient concentration gradient between the cell’s surface and the surrounding medium. The specific uptake rate (uptake per unit of cell volume) will then be:

$$U/V = 4\pi r D \Delta C (4/3\pi r^3)^{-1} = 3D \Delta C r^{-2} \quad (2)$$

Eq. (2) indicates that the specific uptake rate decreases with the square of cell radius. However, specific (i.e., normalized to mass or volume) metabolic rates in phytoplankton, and therefore specific resource requirements, decrease with cell size much more slowly. Typically, specific metabolic rates are proportional to cell volume elevated to a power between  $-1/3$  and 0 (see below), or to  $r$  elevated to a power between  $-1$  and 0. Therefore, large cell size is a major handicap when nutrient concentrations are low. Light

absorption per unit of photosynthetic pigment also decreases with increasing cell size because self-shading by pigment molecules (the so-called package effect) increases with cell size, especially under light limitation, when the intracellular pigment concentration is elevated. As a result of these biophysical constraints, small cell size is advantageous in environments where nutrients and/or light are in short supply.

Since Kleiber's pioneering studies with birds and mammals, it has been shown that the pace of metabolism (the rate at which individuals take up resources and process energy) slows down with increasing body size. From microbes to large animals and plants, individual metabolic rates ( $R$ ) scale as:

$$R = aW^b \quad (3)$$

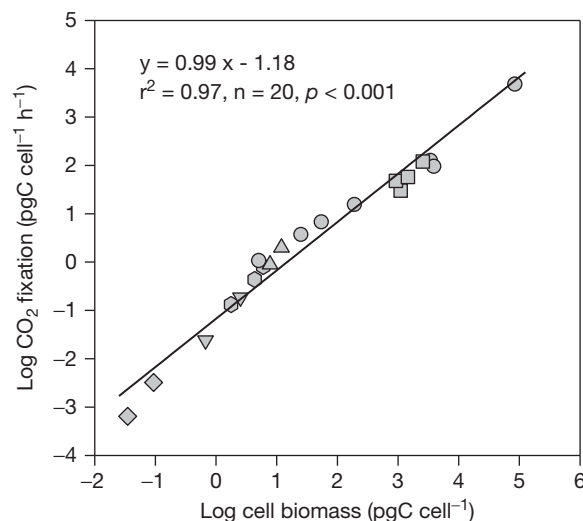
which is equivalent to:

$$\log R = \log a + b \log W \quad (4)$$

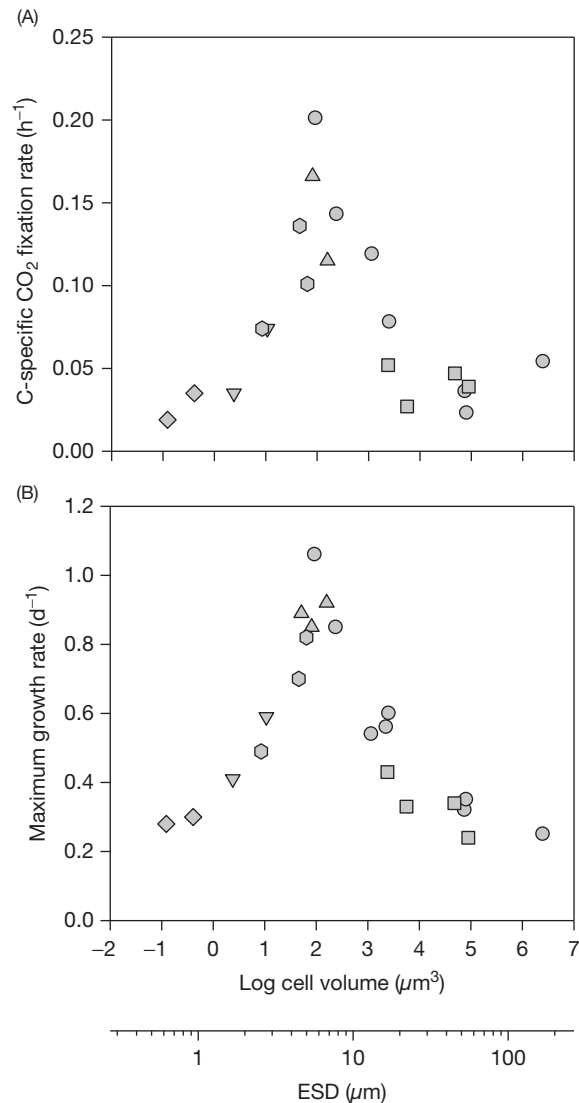
where  $b$ , the size scaling exponent, usually takes a value of  $3/4$  and  $a$ , the intercept of the log-log relationship, is a taxon-related constant. This  $3/4$ -power scaling relationship between body mass and individual metabolic rate, known as Kleiber's rule, has been confirmed in most multicellular organisms. When biomass-specific metabolism or growth rates are considered,  $b$  takes a value near  $-1/4$ . Eqs. (3), (4) mean that a 10-fold increase in cell size is associated with only a 5.6-fold increase in individual metabolic rate, which means that larger organisms have a slower pace of metabolism. Ascertaining whether phytoplankton metabolism and growth conforms to Kleiber's rule is relevant to understanding the mechanisms that control phytoplankton size structure in the ocean. Let us then examine the size scaling of individual metabolic rates, biomass-specific metabolic rate and maximum population growth rate.

Measurements of cell-specific metabolic rates, such as photosynthetic  $\text{CO}_2$  fixation and respiration, conducted both with laboratory cultures and natural populations, have revealed that Kleiber's rule does not apply to phytoplankton. The slope in the log-log relationship between cell size and cell-specific metabolic rate is near 1 (isometric scaling), in stark contrast to the predicted value of  $3/4$  (allometric scaling) (Fig. 3). If the cell-specific  $\text{CO}_2$  fixation rates of the different species shown on Fig. 3 are divided by their mean carbon biomass per cell, C-specific  $\text{CO}_2$  fixation rates ( $R^W$ , with units of  $\text{time}^{-1}$ ) are obtained. The size scaling of  $R^W$  in phytoplankton is unimodal:  $R^W$  decreases with increasing cell size, as predicted by Kleiber's rule, only for cells above approximately  $100 \mu\text{m}^3$  in cell volume, whereas it increases with size for cells in the range  $0.1$ – $100 \mu\text{m}^3$  (Fig. 4A).  $R^W$  takes similar values in cells around  $1 \mu\text{m}^3$  and  $10^5 \mu\text{m}^3$ , whereas the allometric scaling predicts that the smaller cells should have much higher (by a factor of c. 18) biomass-specific metabolic rates than their larger counterparts. Because reproduction and population growth require the acquisition of resources to produce new biomass, one would expect a linkage between the size scaling of  $R^W$  and that of maximum population growth rate ( $\mu_{\text{max}}$ ). This prediction is confirmed by the fact that the relationship between cell size and  $\mu_{\text{max}}$  is also unimodal (Fig. 4B).

Measurements of the cellular nutrient requirement and the maximum nutrient uptake rate ( $V_{\text{max}}$ ) in multiple species with cell sizes ranging from  $0.1$  to  $>10^6 \mu\text{m}^3$  have shed light on the potential mechanisms underlying the unimodal size scaling of phytoplankton growth.  $V_{\text{max}}$  scales isometrically with cell volume, which means that the ability to take up nutrients, when they



**Fig. 3** Size dependence of photosynthetic carbon fixation in laboratory cultures, growing under standardized conditions, of 20 phytoplankton species including diatoms (circles), dinoflagellates (squares), coccolithophores (upward triangles), chlorophytes, (downward triangles), cyanobacteria (diamonds) and others (hexagons). The line is the reduced major axis linear regression model.



**Fig. 4** Size dependence of (A) carbon-specific carbon fixation rate and (B) maximum growth rate in phytoplankton species maintained in the laboratory under standardized conditions. ESD: equivalent spherical diameter. Symbols as in Fig. 3.

are provided in high supply, is relatively constant across the entire size range. However, the size scaling of the cellular nutrient content is allometric, due to the fact that the amount of nutrient (nitrogen, phosphorus) per unit of cell volume decreases as cell size becomes larger. This means that, relative to their nutrient requirement, small cells have a lower uptake ability, compared with that of larger cells. Non-scalable components such as nucleic acids and membranes occupy an increasingly large fraction of cell volume as cells become smaller, which leaves less space for catalysts involved in biosynthesis. These limitations, which explain the relatively slow growth rates of very small cells, become less pronounced as cell size increases, which results in a positive size scaling of  $\mu_{\text{max}}$  in the  $0.1\text{--}100\ \mu\text{m}^3$  size range.

Increasing cell size gives enhanced ability to take up nutrients, when they are in high abundance, with respect to cellular requirements. However, increasingly large cell size also imposes constraints on the ability to convert nutrients into biomass. As cell size increases, intracellular distances from uptake to biosynthesis sites also increase, and the package effect becomes also more acute. These factors prevent the rapid conversion of nutrients into new biomass, leading to an uncoupling between nutrient uptake and nutrient assimilation.

In summary, small cells are limited by their comparatively small (relative to requirement) nutrient uptake ability and by their reduced biosynthetic ability due to the presence of non-scalable components. Large cells are limited by their ability to convert nutrients into biomass. As a result of a trade-off between these opposing effects of cell size, species with intermediate cell size are the ones that can sustain fastest growth rates under conditions of high resource supply.

## Cell Size and Phytoplankton Losses

Large size increases sinking velocity, which, for nonmotile cells, implies a reduction of their residence time in the euphotic layer. According to Stokes law, the sinking velocity of a spherical particle increases in proportion to the square of its radius. Assuming an excess cell density over medium density of  $50 \text{ g L}^{-1}$ , a picophytoplankton cell of  $r = 0.5 \text{ }\mu\text{m}$  will have a sinking velocity of only  $2\text{--}3 \text{ mm day}^{-1}$ , compared with  $20\text{--}30 \text{ m day}^{-1}$  for a microphytoplankton cell of  $r = 50 \text{ }\mu\text{m}$ . Although some large phytoplankton species have strategies to cope with sinking (such as motility, buoyancy control, departure from spherical shape, etc.), smaller species are at an advantage over their larger counterparts to remain within the euphotic zone. This advantage is particularly relevant in strongly stratified water columns, where the absence of upward water motion makes it unlikely for cells sinking below the pycnocline to return to the upper, well-illuminated waters.

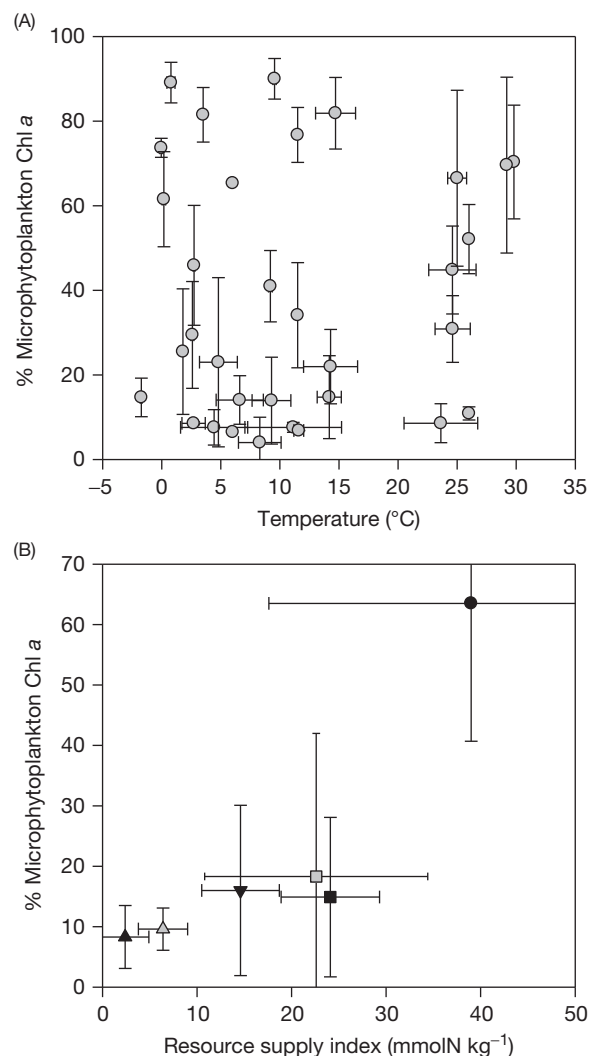
While small cell size is superior in terms of resource acquisition and avoidance of sedimentation, large cell size can provide a major competitive advantage because it offers a refuge from predation. The main reason is that the generation time of predators increases with body size more rapidly than the generation time of phytoplankton does. Small phytoplankton are typically consumed by unicellular protist herbivores, which have generation times similar to those of phytoplankton (in the order of hours to days). In contrast, larger phytoplankton, especially chain-forming diatoms, are mostly grazed by metazoan herbivores, such as copepods and euphausiids (krill), which have much longer generation times (weeks to months). When nutrients are injected into the euphotic layer, smaller phytoplankton are more tightly controlled by their predators and their abundance seldom increases substantially. On the contrary, larger phytoplankton, thanks to the time lag between their growth response and the numerical response of their predators, are better prepared to escape predation, which helps them to sustain positive net growth rates and thus form blooms.

## Drivers of Variability in Phytoplankton Size Structure

The superior ability of small cells to acquire resources (both light and nutrients) when they are in low supply explain that communities in waters with low phytoplankton biomass are dominated by pico- and small nano-phytoplankton. Examples of this pattern are the subtropical gyres, where permanently low nutrient supply leads to a marked dominance by picophytoplankton, and the temperate and polar regions in winter, when low light availability is associated with an enhanced contribution of pico- and small nano-phytoplankton to total biomass. Less immediate is the explanation for the increased dominance of larger cells in waters with high levels of phytoplankton biomass. Because the general allometric pattern predicts that growth rates increase with decreasing body size, the fact that small ( $<5 \text{ }\mu\text{m}$  in ESD) phytoplankton species rarely form blooms (defined as events of increased biomass in which total phytoplankton carbon is  $>200 \text{ mgC m}^{-3}$ ) has been often attributed to a stronger grazing pressure upon small cells, compared to that suffered by larger cells. However, the unimodal size scaling of phytoplankton metabolism (Fig. 4A) and growth (Fig. 4B) suggests that small cells are unlikely to form blooms simply because they produce biomass and grow more slowly than their larger counterparts. Cells with ESD  $> 30 \text{ }\mu\text{m}$  are also unlikely to form blooms because they have slow growth rates and fast sinking rates. As a result, intermediate-size species, in the range  $10\text{--}30 \text{ }\mu\text{m}$  in ESD, are the ones that contribute most of the biomass during phytoplankton blooms. Diatoms in particular tend to dominate blooms, thanks to their fast nutrient uptake rates and their ability to store nutrients in the vacuole, which allow them to effectively exploit intermittent nutrient pulses.

There is a broad association between sea surface temperature and phytoplankton size structure in the ocean, such that warm regions tend to be dominated by small cells, whereas cold regions show a higher contribution of larger cells. This association, however, may be due to an indirect rather than a direct effect, because temperature itself is also strongly correlated with resource availability. To separate the effects of the two driving factors, it is useful to examine size structure in waters with all combinations of resource supply and temperature. As shown in Fig. 5A, phytoplankton size structure is largely independent of temperature. Large cells dominate in nutrient-rich waters of the high-latitude seas, but also in warm, coastal areas that receive high nutrient loads through continental runoff, and in warm, tropical waters subjected to coastal upwelling. Conversely, small cells contribute most of the biomass not only in the warm, oligotrophic subtropical gyres, but also in polar and temperate waters during light-limiting conditions in winter as well as in the iron-limited regions of the Southern Ocean.

The large-scale biogeography of phytoplankton size structure is largely determined by resource supply (Fig. 5B). The subtropical gyres, characterized by persistent thermal stratification and slow nutrient supply from deep waters, show the lowest contribution of large cells to total chlorophyll *a* concentration. Temperate regions and open-ocean upwelling waters, which have an enhanced resource supply, show a higher contribution of large cells, while coastal productive waters, where resource supply is highest, show the largest dominance of large cells. The association between warm temperatures and small community mean cell size has led to the prediction that an enhanced dominance of small phytoplankton cells will be a general response of ocean ecosystems to climate warming. This is indeed likely to be the case for the low-latitude regions, where increased thermal stratification will result in more oligotrophic conditions. However, in high-latitude regions, where intense vertical mixing often leads to light limitation, ocean warming and freshening may result in shallower mixed layers, higher light availability, and consequently increased productivity and importance of large cells.



**Fig. 5** Relationship between (A) temperature and (B) resource supply and the contribution of the  $>20\ \mu\text{m}$  size class to total chlorophyll *a* concentration. The resource supply index was calculated as  $RSI = \frac{NO_3^{1\%PAR}}{\Delta\sigma_t} \times \frac{1\%PARz}{UMLZ}$  where  $NO_3^{1\%PAR}$  is the concentration of nitrate at the base of the euphotic layer,  $\Delta\sigma_t$  is the density difference between the surface and the base of the euphotic layer,  $1\%PARz$  is the depth of the euphotic layer, defined as the  $1\%$  PAR level, and UMLZ is the depth of the upper mixed layer, defined as the first depth at which  $\sigma_t$  is  $0.125$  units higher than the surface value. Mean and SD values are given for stations in the North Atlantic subtropical gyre (*gray upward triangle*), the South Atlantic subtropical gyre (*black upward triangle*), the North Atlantic temperate latitudes (*gray square*), the South Atlantic temperate latitudes (*black square*), the Equatorial and Mauritanian upwelling (*downward triangle*), and coastal waters of NW Iberian Peninsula (*circle*).

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