PHYTOPLANKTON SIZE STRUCTURE

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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 eight phyla. This phylogenetically diverse group of organisms constitutes the base of the food chain in most marine ecosystems and, since their origin more than 2.8×10^9 years ago, have exerted a profound influence on the biogeochemistry of Earth. Currently, phytoplankton are responsible for the photosynthetic fixation of around 50×10^{15} g C annually, which represents almost half of global net primary production on Earth. Some 20% of phytoplankton net primary production is exported toward 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-fueled, biological pump is the transport of CO_2 from the atmosphere to the deep ocean, where it is sequestered over the timescales of deep-ocean circulation (10^2–10^3 years). A small fraction ($<1\%$) of the organic matter transported toward the deep ocean escapes mineralization and is buried in the ocean sediments, where it is retained over timescales of $>10^6$ years. It has been calculated that thanks to the biological pump the atmospheric concentration of 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 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 $0.1 \, \mu m^3$ for the smallest cyanobacteria to more than $10^8 \, \mu m^3$ for the largest diatoms. Cell size affects many aspects of phytoplankton physiology and ecology over several levels of organization, including individuals, populations, and communities. Phytoplankton assemblages are locally diverse: typically, several hundreds of species can be found in just a liter of seawater. Therefore, a full determination of

the biological properties of all species living in a given water body is not possible. The study of cell size represents an integrative approach to describe the structure and function of the phytoplankton community and to understand its role within the pelagic ecosystem and the marine biogeochemical cycles. This article starts with a review of the relationship between cell size and phytoplankton metabolism and growth. It follows with a description of the general patterns of variability in the size structure of phytoplankton in the ocean. Next, the different mechanisms involved in bringing about these patterns are examined. The article ends with a consideration of the ecological and biogeochemical implications of phytoplankton size structure.

Phytoplankton Cell Size, Metabolism, and Growth

Cell Size and Resource Acquisition

Like any other photoautotrophic organisms, phytoplankton must take up inorganic nutrients and absorb light in order to synthesize new organic matter. 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, $\mathrm{mol \, s^{-1}}$) can be expressed as

$$U = 4\pi r D \Delta C \qquad [1]$$

where r is the cell radius (μm), D is the diffusion coefficient ($\mu m^2 \, s^{-1}$), and ΔC ($\mathrm{mol} \, \mu m^3$) 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

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

Equation [2] indicates that 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 mass or 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. The nutrient concentration below which phytoplankton growth starts to be nutrient-limited can be calculated, for a range of cell sizes and growth rates, as follows. Nutrient limitation occurs when $U < \mu \times Q$, where μ is the specific growth rate (s^{-1}) and Q is the cell's quota for the particular nutrient (mol cell^{-1}). Q can be computed by applying an empirical relationship between cellular nitrogen content and V (pgN $= 0.017\,2\,V^{1.023}$) and D is assumed to be $1.5\,cm^2\,s^{-1}$. The threshold for nutrient limitation increases exponentially with cell radius (Figure 1). In this particular example, if the ambient nitrogen concentration is $10\,nM$, a cell of $r = 1\,\mu m$ could grow at growth rates well above $1\,d^{-1}$ without suffering diffusion limitation, whereas a cell of $r = 6\,\mu m$ would already experience diffusion limitation at $\mu = 0.1\,d^{-1}$. Processes such as turbulence, sinking, and swimming, which enhance the advective transport of nutrients toward the cell surface, partially compensate for the negative impact of large cell size on diffusive nutrient fluxes. The effect, however, is small and does not alter the fact that larger cells are at a disadvantage over smaller cells for nutrient uptake.

Light absorption in phytoplankton is a function of cell size and the composition and concentration of pigments. The amount of light absorbed per unit pigment decreases with cell size and with intracellular pigment concentration, because the degree of self-shading among the different pigment molecules (the so-called package effect) increases. The optical absorption cross-section of a phytoplankton cell is given by

$$a^* = (3/2)(a_s^* Q \rho) \qquad [3]$$

where

$$Q = 1 + 2(e^{-\rho}/\rho) + 2(e^{-\rho} - 1)/(\rho^2) \qquad [4]$$

and

$$\rho = a_s^* c_i d \qquad [5]$$

Units of a^* and a_s^* are m^2 (mg chl a)$^{-1}$, Q and ρ are coefficients without dimensions, c_i is the intracellular chlorophyll a concentration (mg chl a m^{-3}), and d is cell diameter (m).

The package effect can be quantified as the ratio between the actual absorption inside the cell (a^*) and the maximum absorption possible, determined for the pigment in solution (a_s^*). The higher the package effect, the lower the value of a^*/a_s^*. The data shown in Figure 2, calculated assuming $a_s^* = 0.04\,m^2$ (mg chl a)$^{-1}$ and a range of c_i values between 10^6 and 10^8 mg chl a m^{-3}, indicate that the package effect increases with cell size, which means that, other things being equal, larger phytoplankton are expected to be less efficient than smaller cells at absorbing light. This effect is much stronger under low
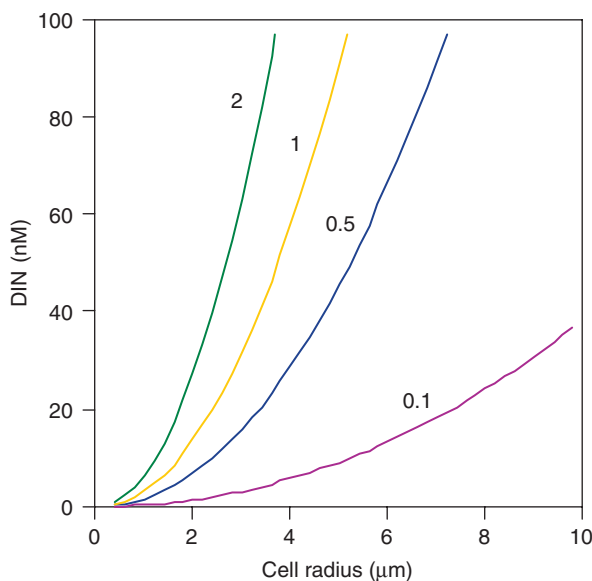
Figure 1 Relationship between cell radius and the concentration of dissolved inorganic nitrogen (DIN) below which phytoplankton growing at rates of 0.1, 0.5, 1, and 2 d^{-1} begin to suffer diffusion limitation of growth.
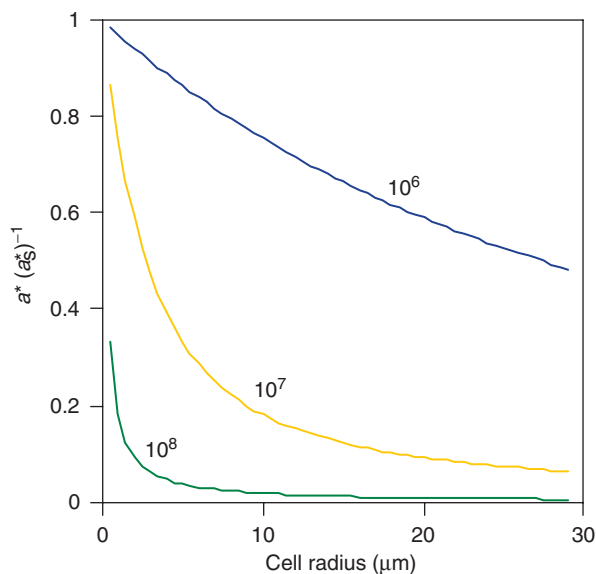
Figure 2 Relationship between cell radius and the package effect for intracellular chlorophyll a concentrations of 10^6, 10^7, and 10^8 mg m^{-3}.

light conditions, when c_i tends to be larger as a result of photoacclimation.

The general allometric theory predicts a reduction in metabolic rates (R) with body size (W, in units of biomass or volume). From unicells to large mammals, individual metabolic rates (R) scale as:

$$R = aW^b \qquad [6]$$

which is equivalent to

$$\log R = \log a + b \log W \qquad [7]$$

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. When biomass-specific metabolism or growth rates are considered, b takes a value near $-1/4$. Equations [6] and [7] mean that a 10-fold increase in cell size is associated with only a 7.5-fold increase in individual metabolic rate, and therefore larger organisms have a slower metabolism. In the case of phytoplankton, one would expect that the geometrical constraints on resource acquisition and use would result in a reduction in specific metabolism with cell size. However, several experimental studies with laboratory cultures and natural phytoplankton assemblages suggest that the relationship between photosynthesis and cell size cannot be predicted by a single scaling model and that phytoplankton metabolism often departs from the 3/4-power rule. For instance, the size scaling of photosynthesis in cultured diatoms has been shown to depend on light availability (Figure 3). Light limitation leads not only to low photosynthetic rates (irrespective of cell size) but also to a reduction in the size scaling exponent b, indicating a faster decrease in specific photosynthesis with cell size as a result of a stronger package effect in larger cells. In addition, changes in taxonomic affiliation of phytoplankton species along the size spectrum may interfere with the effects of cell size *per se*. If we consider natural phytoplankton assemblages, which include a mixture of species from diverse taxonomic groups, the scaling between phytoplankton photosynthesis is approximately isometric (Figure 3). This means that, under natural conditions at sea, the expected slowdown of metabolism as cell size increases does not seem to occur. This pattern results from the fact that larger species possess strategies that allow them to sustain higher metabolic rates than expected for their size (see below). Thus, both resource availability and taxonomic variation along the size spectrum help explain why the scaling of phytoplankton growth rates and cell size is quite variable. However, before turning our attention to the size scaling of
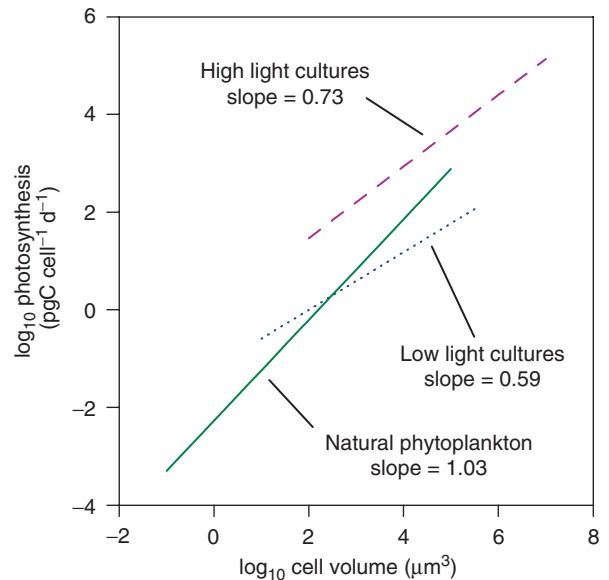
Figure 3 Scaling relationship between photosynthesis per cell and cell size in diatom cultures growing under high-light conditions, diatom cultures growing under light-limited conditions, and natural phytoplankton assemblages in the ocean.

phytoplankton growth rates, we need to look into the relationship between cell size and loss rates, because the net growth rate of any population ultimately depends on the balance between production and loss processes.

Cell Size and Loss Processes

Respiration and exudation are the main metabolic loss processes for phytoplankton. In most organisms, individual respiration rates increase as the 3/4-power of body size (e.g., $b = 3/4$). However, several studies of the size scaling of phytoplankton respiration in algal cultures show that, although taxon-related differences exist, b tends to be significantly higher than 3/4, indicating that respiration increases with cell size more steeply than predicted by the general allometric theory. This effect has been attributed to the fact that smaller algae seem to have lower respiration rates than expected for their size, perhaps as an energy-saving strategy in organisms with a comparatively small capacity for accumulation of reserves. As far as exudation is concerned, theory predicts that smaller cells, on account of their higher surface-to-volume ratios, should suffer a relatively greater loss of cellular compounds through the cell membrane. However, both laboratory work with cultures and experimental studies at sea have failed to provide conclusive evidence as to the existence of higher relative rates of exudation in smaller cells as compared to larger cells.

One of the most unquestionable effects of large cell size for phytoplankton is that it 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 $50 \, g \, l^{-1}$, a picophytoplankton cell of $r = 0.5 \, \mu m$ will have a sinking velocity of only $2–3 \, mm \, day^{-1}$, compared with $20–30 \, m \, day^{-1}$ for a microphytoplankton cell of $r = 50 \, \mu m$. Although many large phytoplankton species have acquired different strategies to cope with sinking (such as motility, buoyancy control, departure from spherical shape, etc.), smaller species are clearly 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. 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 are mostly grazed by metazoan herbivores, such as copepods and euphasiaceans, which have much longer generation times (in the order of weeks to months). When nutrients are injected into the euphotic layer, smaller phytoplankton are efficiently 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 able to form blooms and carry on growing until nutrients are exhausted. As discussed below, this trophic mechanism plays a role in determining the size structure of phytoplankton communities in contrasting marine environments.

Cell Size and Growth Rates

Experiments with cultured and natural phytoplankton species have yielded quite variable values for the scaling exponent in the equation relating growth rate (units of $time^{-1}$) to cell size. The most frequently reported values for b range between -0.1 and -0.3. It has been noted that the size scaling of phytoplankton growth rates is relatively weak (that is, b tends to take a less negative value than $-1/4$). Furthermore, although the slope of the growth versus size relationship may be similar in different taxonomic groups, the intercept frequently is not: for instance, diatoms consistently have higher growth rates than other species of the same cell size. Another feature in the size scaling of phytoplankton growth is that very small cells (less than $5 \, \mu m$ in diameter) depart from the inverse relationship between cell size and growth rate, showing slower rates than expected for their size. This pattern probably results from the influence of nonscalable components (such as the genome and the membranes), which progressively take up more space as cell size decreases, thus leaving less cell volume available for rate-limiting catalysts and the accumulation of reserves.

Although experimental determinations in natural conditions are still scarce, the available data suggest that phytoplankton populations in nature tend to exhibit less negative size scaling exponents in the power relation between growth rate and cell size. In fact, there is evidence to suggest that this size-scaling exponent may even become positive under favorable conditions for growth, such as high nutrient and light availability. This means that, when resources are plentiful, larger phytoplankton may grow faster than their smaller relatives. Several strategies allow larger species, and diatoms in particular, to achieve high growth rates (e.g., $> 1 \, day^{-1}$) in nature in spite of the geometrical constraints imposed by their size. These strategies include the increase in the effective surface-to-volume ratio, due to changes in cell shape and the presence of the vacuole; the accumulation of nonlimiting substrates to increase cell size and optimize nutrient uptake; and the ability to sustain high specific uptake rates and store large amounts of reserves under conditions of discontinuous nutrient supply.

Patterns of Phytoplankton Size Structure in the Ocean

Size-Fractionated Chlorophyll *a*

Given that chlorophyll *a* (chl *a*) serves as a proxy for phytoplankton biomass, a common approach to study the relative importance of phytoplankton with different cell sizes is to measure the amount of chl *a* in size classes, usually characterized in terms of equivalent spherical diameter (ESD) of particles. The most frequently considered classes are the picophytoplankton (cells smaller than $2 \, \mu m$ in ESD), the nanophytoplankton (cells with an ESD between 2 and $20 \, \mu m$), and the microphytoplankton (cells with an ESD larger than $20 \, \mu m$). When we plot together hundreds of
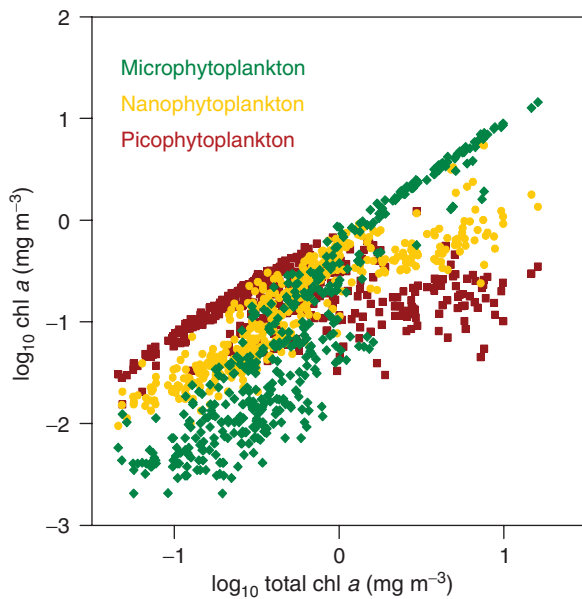
Figure 4 Chlorophyll *a* concentration in picophytoplankton, nanophytoplankton, and microphytoplankton vs. total chlorophyll *a* concentration in samples obtained throughout the euphotic layer in coastal and oceanic waters of widely varying productivity.

measurements of size-fractionated chl *a* concentration, obtained throughout the euphotic layer in coastal and oceanic waters of widely varying productivity, several consistent patterns emerge (Figure 4). In relatively poor waters, where total chl *a* concentrations are below 0.8–1 mg m^{-3}, picophytoplankton account for up to 80% of total chl *a*, while microphytoplankton typically contributes less than 10%. As total chl *a* increases, the concentration of picophytoplankton chl *a* reaches a plateau at around 0.5 mg m^{-3} and then decreases in very rich waters. Similarly, nanophytoplankton chl *a* rarely increases beyond 1 mg m^{-3}. By contrast, microphytoplankton chl *a* continues to increase, so that at total chl *a* levels above 2 mg m^{-3} this size class accounts for more than 80% of total chl *a*, while picophytoplankton contribute less than 10%. Compared to the other size fractions, nanophytoplankton show smaller variability in their relative contribution to total chl *a*, which normally falls within the range 20–30%. The patterns shown in Figure 4 reflect both temporal and spatial variability in total phytoplankton biomass and the relative importance of each size class. Thus, the oligotrophic waters of the subtropical gyres are typically dominated by picophytoplankton, whereas in upwelling areas and coastal, well-mixed waters microphytoplankton usually account for most of the photosynthetic biomass. Similarly, in ecosystems that experience marked seasonal variability, microphytoplankton dominate the episodes of intense algal growth and biomass, such as the spring bloom. Small nano- and picophytoplankton

become more important during periods of prolonged stratification and low nutrient availability, as well as during conditions of intense vertical mixing that lead to light limitation of growth.

Size–Abundance Spectra

Although the partition into discrete classes is useful to describe broadly the size structure of the community, the different phytoplankton species are in fact characterized by a continuum of cell sizes that is best represented with a size–abundance spectrum. In this approach, the abundance (N) and cell size (W) of all species present in a sample are determined, using flow cytometry for picophytoplankton and small nanoplankton and optical microscopy for large nanoplankton and microphytoplankton. Size–abundance spectra are constructed by distributing the abundance data along an octave scale of cell volume. The abundance of all cells within each size interval is summed and the resulting abundance is plotted on a log-log scale against the nominal size of the interval. When these spectra are constructed at the local scale, it is common that the relationship between abundance and cell size shows irregularities, for example, departures from linearity. This is the case of large blooms, when one or a few species make up a major fraction of total phytoplankton abundance, which translates into a bump in the size–abundance spectrum. However, when numerous observations, collected over longer spatial and temporal scales, are put together, good linear relationships are usually obtained. In these cases, the slope of the linear relationship between log N and log W (the size-scaling exponent in the power relationship between N and W) is a general descriptor of the relative importance of small versus large cells in the ecosystem. Figure 5 illustrates the differences in the phytoplankton size–abundance spectrum between two contrasting ecosystems such as the oligotrophic subtropical gyres of the Atlantic Ocean ($N \propto W^{-1.25}$) and the productive waters of the coastal upwelling region in the NW Iberian peninsula ($N \propto W^{-0.90}$). Typically, the slopes of the size–abundance spectrum in oligotrophic, open ocean waters are in the range -1.1 to -1.4, while values between -0.6 and -0.9 are measured in coastal productive environments. The size spectrum extends further to the left in oligotrophic ecosystems, reflecting the presence of the prochlorophyte *Prochlorococcus*. At 0.1–0.2 μm^3 in volume, this species is the smallest and most abundant photoautotrophic organism on Earth, and dominates picophytoplankton biomass in the oligotrophic open ocean. When combined with size-scaling relationships for biomass and metabolism, size–abundance spectra allow us to determine the variability in the flow of
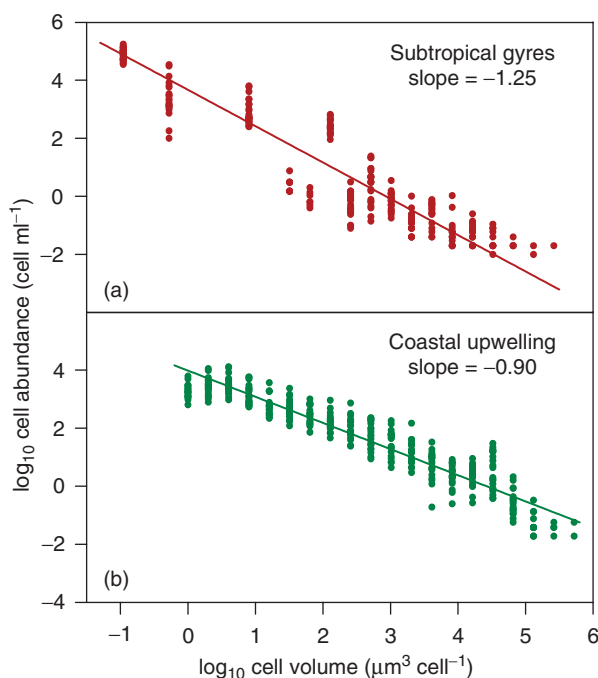
Figure 5 Size–abundance spectra in natural phytoplankton assemblages from (a) the Atlantic subtropical gyres and (b) coastal upwelling waters off NW Iberian peninsula. Spectra were constructed by combining measurements collected throughout the euphotic layer during different sampling surveys. Reprinted with permission from Marañón E, Cermeño P, Rodríguez J, Zubkov MV, and Harris RP (2007) Scaling of phytoplankton photosynthesis and cellsize in the ocean. *Limnology and oceanography* 54(5): 2194. Copyright (2008) by the Americal Society of Limnology and Ocenography, Inc.

materials and energy along the size spectrum. For instance, if phytoplankton photosynthesis per cell (P) in the ocean scales isometrically with cell size ($P \propto W^1$), the above-mentioned scaling exponents for phytoplankton abundance (between -0.6 and -0.9 for eutrophic waters and between -1.1 and -1.4 for oligotrophic ones) imply that total photosynthesis per unit volume ($N \times P$) must increase with cell size in productive ecosystems, while it decreases in unproductive ones.

Factors Controlling Phytoplankton Size Structure

Given their superior ability to avoid diffusion limitation of nutrient uptake, it is no surprise that picophytoplankton dominate in the oligotrophic waters of the open ocean. However, the competitive advantage of being small, although reduced, is not eliminated under resource sufficient conditions. One can therefore ask why is it that picophytoplankton do not dominate also in nutrient-rich environments. This is tantamount to asking what mechanisms are

responsible for the increased importance of larger cells under conditions of high nutrient availability, such as those found within upwelling regions, frontal regions, and cyclonic eddies. Hydrodynamic processes have been suggested to play a role, since upwelling water motion causes a retention of larger cells, counteracting their tendency to sink out of the euphotic layer. However, upwelling of subsurface waters also contributes to the injection of nutrients into surface waters and therefore the physical transport mechanism cannot be easily distinguished from a direct nutrient effect. These two processes, however, have been separated experimentally during iron addition experiments in high-nutrient, low-chlorophyll regions. Invariably, iron addition brings about an increase in phytoplankton biomass and a marked shift toward a dominance by larger species, usually chain-forming diatoms. Since hydrodynamics remain unaltered during these experiments, these observations highlight the role of the nutrient field in determining phytoplankton size structure. Two main, nonexclusive processes contribute to the selective growth and accumulation of larger cells in high-light and nutrient-rich environments. First, larger phytoplankton are capable of sustaining higher biomass-specific metabolic rates and growth rates than smaller cells when resources are abundant. Second, larger phytoplankton are less efficiently controlled by grazing, as a result of the difference between their generation time and that of their predators.

Ecological and Biogeochemical Implications of Phytoplankton Size Structure

Phytoplankton size structure affects significantly the trophic organization of the planktonic ecosystem and, therefore, the efficiency of the biological pump in transporting atmospheric CO_2 toward deep waters ([Table 1](#)). In communities dominated by picophytoplankton, 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 (dinoflagellates, ciliates, and heterotrophic nanoflagellates) 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. Phytoplankton exudation and microzooplankton excretion contribute to an important production of dissolved organic matter, which fuels bacterial production. In turn,

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	Large cells
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	~1	>1
f-ratio and e-ratio	5–15%	>40%
Main fate of primary production	Recycling within the euphotic layer	Export toward deep waters

bacteria are efficiently controlled by protist microbial grazers. The resulting, complex food web is characterized by intense recycling of matter and low efficiency in the transfer of primary production toward larger organisms such as mesozooplankton or fish. Photosynthetic production of organic matter is balanced by the respiratory losses with the microbial community. In addition, the small size of microbial plankton implies that losses through sedimentation are unimportant. As a result, little newly produced organic matter escapes the euphotic later. In contrast, plankton communities dominated by large 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 toward 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 carbon toward the deep ocean, the biological pump in these systems has a low efficiency and the net effect of the biota on the ocean–atmosphere CO_2 exchange is small. By contrast, phytoplankton assemblages dominated by larger cells are typical of dynamic environments that are subject to 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 toward the ocean's interior, thus contributing to CO_2 sequestration.

Nomenclature

a^*	absorption coefficient of pigments *in vivo*
a_s^*	absorption coefficient of pigments in solution
c_i	intracellular chlorophyll *a* concentration
d	cell diameter
D	nutrient diffusion coefficient
N	cell abundance
P	photosynthesis per cell
Q	cellular nutrient quota
r	cell radius
R	metabolic rate
U	nutrient uptake rate
V	cell volume
W	cell size (volume or weight)
μ	growth rate

See also

Carbon Cycle. Microbial Loops. Phytoplankton Blooms. Plankton. Primary Production Distribution. Primary Production Methods. Primary Production Processes.

Further Reading

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Biographical Sketch

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