PHYTOPLANKTON SIZE

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INTRODUCTION

In reviewing this subject, it became clear to me that plankton ecologists fall out into two groups: Those who delight in finding the patterns in nature that can be explained by size, and those who delight in finding exceptions to the established size-dependent rules. I came to appreciate the degree to which the satisfaction of both groups is equally justified. The mechanisms underlying the size-dependent patterns have undoubtedly steered the general course of phytoplankton evolution, but the organisms that do not abide by the rules reveal the wonderful diversity of ways in which cells have managed to disobey the "laws" scripted for them. The simplicity of the general relationships serves as a stable backdrop against which the exceptions can shine. By understanding the forces that have driven the design of these exceptions, we can begin to understand the ecology that has shaped past and present planktonic ecosystems.

This is not a comprehensive review, since all aspects of the life of a phytoplankton cell are influenced, more or less, by its size. Instead, I have chosen to explore specific dimensions of the topic which I find to be particularly provocative, or which appear to be ripe for new advances and approaches.

ALLOMETRIC RELATIONSHIPS

Size-Dependence of Growth and Metabolism

Allometry is the study of the correlates of body size. Although its origins can be traced back to Elton (1927), the field has undergone a resurgence in the last decade (Peters, 1983; Calder, 1984). Plankton ecologists have participated in this resurgence, stimulated largely by the works of Fenchel (1974), Banse (1976; 1982), Peters (1978) and Platt and co-workers (e.g. Platt and Denman, 1977; 1978; Platt and Silvert, 1981; Silvert and Platt, 1978; 1980; Geider et al., 1986).

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According to allometric theory, a diverse set of characteristics of organisms scale with body size such that:

$$R = a W^b \tag{1}$$

i.e. $$\log R = \log a + b \log W \tag{2}$$

where R is a specific rate process (t^{-1}), e.g. respiration or growth rate, W is some measure of body mass, and a and b are constants. Indeed, this relationship seems to hold for a diversity of processes among unrelated organisms (Peters, 1983). The mass-specific value of the exponent, b, is relatively constant (-0.25) for large data sets covering broad size ranges. The value of a, on the other hand, is variable, differentiating major groups of organisms such as homeotherms, heterotherms, and unicells (Fenchel, 1974). The fact that b is dimensionless and relatively constant for a variety of physiological processes, has elevated it nearly to the status of a "natural law" in the biological sciences (Peters, 1978; Platt and Silvert, 1981).

How well does this relationship apply within the restricted realm of phytoplankton cells? The answer is not straightforward. Eppley and Sloan (1965) were among the first to reveal the dependency of respiration rate on cell size in marine phytoplankton. Applying allometric theory to Eppley and Sloan's data, Laws (1975) and Banse (1976) found that respiration rate scaled roughly as the -0.25 power of cell mass, supporting the universality of the "-0.25 rule." Subsequently, however, Falkowski and Owens (1978) and Langdon (1987; 1988) found no relationship whatsoever between mass and respiration. One is left with the impression that there simply is not enough data to say anything conclusive about this relationship.

Eppley and Sloan (1966) also were among the first to look at the relationship between cell size and maximum specific growth rate in phytoplankton. Here, a reasonably consistent picture has emerged (albeit, after several rounds of revision). For large data sets spanning broad size ranges (10^1 - 10^5 pg C cell-1), the allometric equation has been

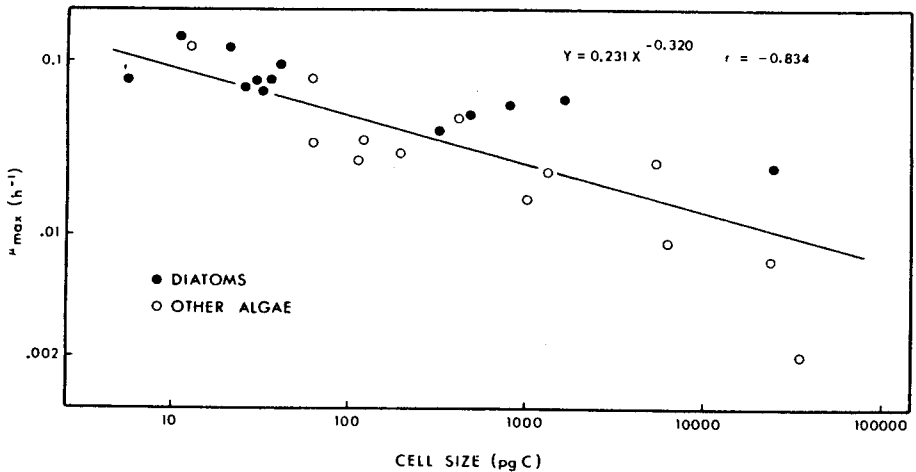$$Y = 0.231 X^{-0.320} \qquad r = -0.834$$

Fig. 1. Relationship between phytoplankton cell size and the maximum specific growth rate of species grown under optimal conditions of light and temperature. Growth rates were normalized to 20°C when necessary using a Q_{10} of 1.88. From Schlesinger et al., (1981). Note that the slope for diatoms is significantly less negative than that of the data set as a whole.

shown to apply for eukaryotic phytoplankton grown under optimum conditions (Fig. 1). The value of b is closer to -0.30 than -0.25, however, (Langdon, 1988; Schlesinger et al., 1981), as was predicted by Platt and Silvert (1981) for aquatic organisms on theoretical grounds.

The error associated with data sets such as that shown in Fig. 1 is large, however. When one systematically examines specific groups of phytoplankton under identical experimental conditions, one finds that the value of b is consistently less negative than -0.30, i.e. the mass-dependency of growth rate is weaker. For diatoms and dinoflagellates, for example, the value of b is -0.13 and -0.15, respectively (Blasco et al., 1982; Banse, 1982; Chan, 1978), and it decreases significantly (to -0.08) for low-temperature species (Sommer, 1989). More importantly, although b is roughly the same for diatoms and dinoflagellates, the value of a for these two groups is very different: 0.14 for dinoflagellates vs. 0.48 for diatoms. In other words, diatoms grow three times faster than dinoflagellates of equal size. Therefore, in many ways, it is the properties of the value of a rather than b that are of most interest to phytoplankton ecologists (Platt, 1985).

Thus, although the allometric equations derived by Schlesinger et al. (1981) and Langdon (1988) are valid for the particular data sets they collected, they are not of great use in predicting the growth rate of a given phytoplankton cell from its size (or carbon content). This is obvious from the discussion of diatoms and dinoflagellates above, and is also apparent if one tries to apply the relationship to prokaryotic picoplankton. For example, the use of the Schlesinger et al. (1981) equation:

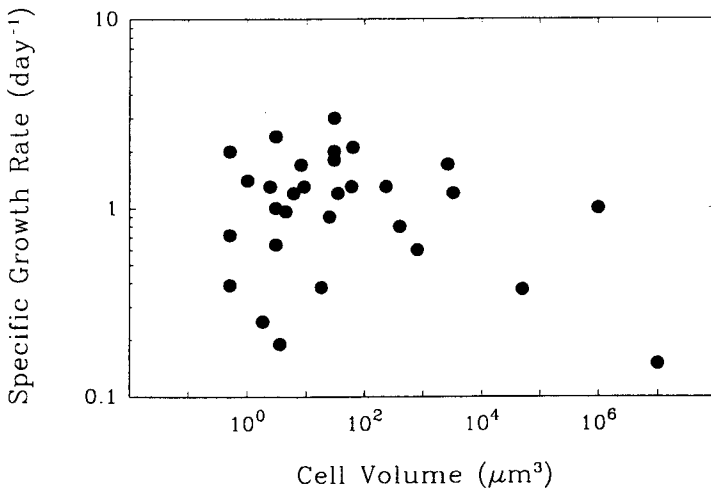$$\mu_{max} = 5.53 \ W^{-0.32} \tag{3}$$

Fig. 2.   Relationship between phytoplankton cell size and the maximum specific growth rate of species grown under optimal conditions of light and temperature. Data includes all of the autotrophic organisms in Table 4 from Raven (1986). Growth rates were normalized to 20°C using a Q_{10} of 2.0. Note, for comparison with (a), that a cell 75 μm^3 in volume (5 μm in diameter) has roughly 10 pg C. The organisms smaller than this deviate significantly from the general relationship.

(where μ is expressed in day^{-1}) to predict the maximum growth rates of *Synechococcus* (which have roughly 0.25 pg C cell^{-1}) yields a μ_{max} in excess of 8 day^{-1}, which is unrealistic. This result is not surprising considering that the maximum growth rates for diatoms are around 2.5 day^{-1} (Blasco et al., 1982) whereas those for *Synechococcus* are around 1.5 day^{-1} (Kana and Glibert, 1987), and that picoplankton were not considered in the derivation of the Schlesinger et al. (1981) relationship. The deviation of very small cells from the Schlesinger/Langdon relationships is revealed even more dramatically in a compilation of maximum growth rates presented by Raven (1986), which includes data points for prokaryotes and other small-sized species (Fig. 2).

To further complicate this picture, even within a given species of diatom, the maximum growth rate can vary by a factor of 2, *increasing* with size as cells are transformed from pre- to post-auxospore cells. Similarly, when mean cell size decreases in diatoms because of the reduction of frustule size over succeeding generations, growth rates decrease (Chisholm and Costello, 1980). This goes against all allometric reasoning, but is a central characteristic of diatoms, and speaks to the influence of individual species characteristics on intrinsic growth rates. To quote LaBarbera (1989), "Scaling studies paint nature with a very broad brush; they are more akin to the gas laws of physics than to Newton's laws. They do not afford much precision in their predictions for individuals or perhaps even species..."

To sum up, size-dependence of growth rate and metabolic processes in phytoplankton as a group is weak. The ecological differences between the taxonomic groups appear to override the influence of size on growth potential.

Size and Maximum Abundance

Anyone who has cultured organisms, or observed them in the field, has an intuitive sense of the inverse relationship between the size of an organism and its local abundance. This relationship formed the conceptual foundation for the "ecological pyramid" of Elton, and can have implications in the analysis of food web dynamics (Platt and Denman, 1977, 1978). In a rather provocative paper, Duarte et al. (1987) showed that the relationship is highly conserved for aquatic organisms in culture: the maximum density achievable in
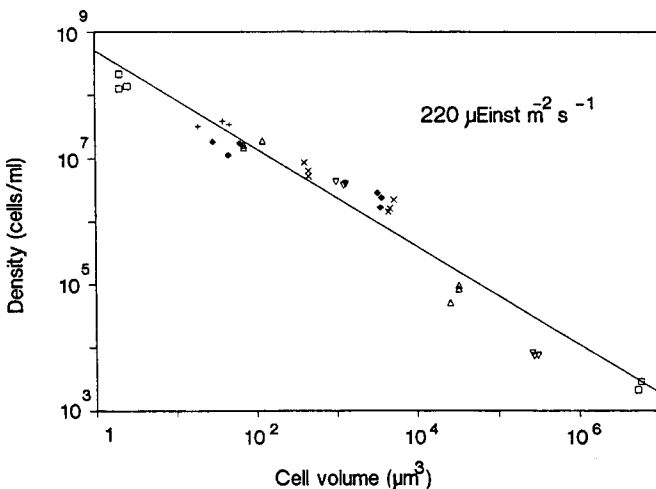

Fig. 3.   Relationship between maximal cell density (D_{max}) and cell volume (V) in phytoplankton cultures grown under identical conditions. Different symbols represent different species (from Agusti and Kalff, 1989).

culture (D_{max}), of organisms ranging in size from bacteria to fish, is inversely related to body size (V), according to the equation:

$$\log (D_{max}) = 8.53 - 0.95 \log (V) \qquad (4)$$

Because the slope of this line is close to unity, the maximum biomass ($V * D_{max}$) achievable in cultures of aquatic organisms is a constant (6 x 10^8 μm^3 ml^{-1}), regardless of the size of individual organisms. At these biomass levels, organisms are using 0.1 % of the volume available to them and are separated by 10-20 equivalent spherical diameters. It is probably not coincidental that the region around an organism defined by a radius of 10 spherical diameters is the region within which the cell can influence the concentration of nutrients relative to that of the bulk fluid. Under severe nutrient limitation, the transport of nutrients to the cell through this region can be limited by molecular diffusion (see below).

Again, the question is, do these relationships hold when phytoplankton alone are considered? By reviewing the literature, Agusti et al. (1987) found the relationship between the maximum density in phytoplankton cultures and cell size to be:

$$\log D_{max} = 9.04 - 1.27 \log V \qquad (5)$$

In subsequent work, Agusti and Kalff (1989) tested the size-density relationship directly by growing cells ranging from 2 to 5 x 10^6 μm^3 under identical conditions in culture (Fig. 3). They found that the relationship between maximum density and cell volume was:

$$\log D_{max} = 8.7 - 0.79 \log V \qquad (6)$$

In this case, the slope is significantly less than one, the opposite of the results from the literature survey (Eq. 5). If one "splits the difference", however, it is not difficult to be convinced that on average, phytoplankton reach a constant maximum biomass in culture, regardless of their size.
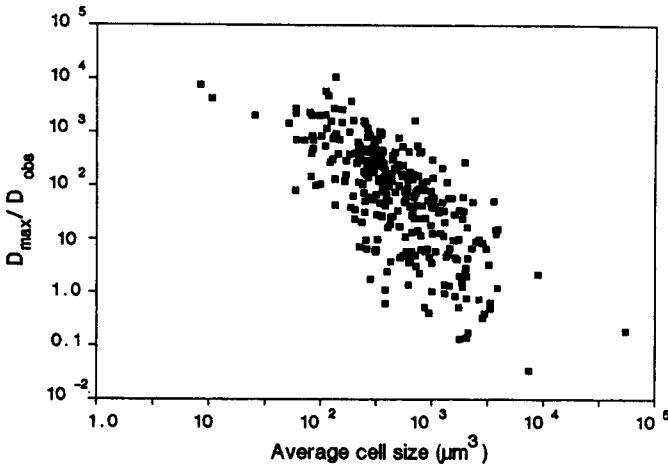

Fig. 4.   Relationship between the ratio of the predicted maximal cell densities (D_{max}) and the observed densities (D_{obs}) and the mean cell size of phytoplankton communities from 165 Florida lakes (from Augusti et al., 1990).

It appears that there is a "...fundamental regularity that determines how organisms use the available space..." (Duarte et al., 1987). No clear picture has emerged as to what this "regularity" is for organisms in general, nor phytoplankton in particular, but for the latter, light and nutrient supply would be the likely regulators. Agusti and Kalff (1989) showed that the size dependency of D_{max} (Eq. 6) is quantitatively conserved under light-limited conditions in cultures, however, and evidence from Florida lakes suggests that at D_{max}, the phytoplankton community is regulated by autogenic factors rather than nutrients (Agusti et al., 1990). Furthermore, there is an inverse relationship between density and average cell size in these lakes (Fig. 4), consistent with the culture work described above, and patterns observed in marine ecosystems (see below). Finally, Duarte et al. (1990) also showed that the range of population densities achievable by different phytoplankton genera in the Florida lakes is a function of the size plasticity in the genera, again pointing to a fundamental regulatory role of size in community dynamics.
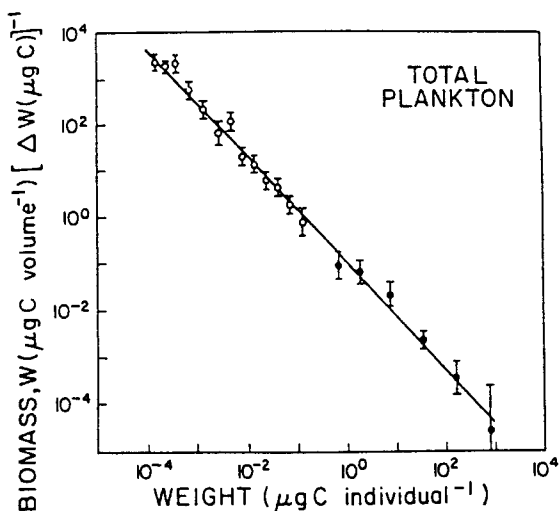

Fig. 5.   Normalized biomass spectrum of the data of Beers et al. (1982) for euphotic zone plankton in the North Pacific Central Gyre (from Rodriguez and Mullin, 1986; see also Platt et al., 1984).

Community Size Spectra

Particulate matter in seawater is distributed among size classes in a manner that is reminiscent of those described above. Small particles are numerically more abundant than large ones, such that there are roughly equal amounts of material in logarithmically equal size intervals (Sheldon and Parsons, 1967; Sheldon et al., 1972). The situation is more complex here, however, because the diversity of species and trophic levels are contributing to the biomass in each size class, and the flow of energy and matter through the food web leaves its imprint on the spectrum. In the face of all of this complexity, however, normalized biomass spectra (Platt and Denman, 1977; 1978) constructed with the living component of the particulate matter in pelagic ecosystems (e.g. Sprules and Munawar,

1986; Sprules et al., 1983; Platt et al., 1984; Rodriguez and Mullin, 1986) have surprisingly conservative properties which conform to the equation:

$$\log B_w = a + b \log W \qquad (7)$$

where B_w is the total biomass of organisms in weight class W, divided by W (Fig. 5). Since B_w is equal to the numerical abundance of organisms in a given size class, Eq 7 is identical in form to Eqs 4, 5, and 6, with weight substituted for volume. Although the shape of this spectrum can be predicted from simple assumptions about ecological efficiencies and food web structure (Kerr, 1974; Platt and Denman, 1977; 1978), random encounter models also are successful (Kiefer and Berwald, 1991), leaving mechanistic interpretations ambiguous. Much like the V/D_{max} spectrum, the slope of the normalized
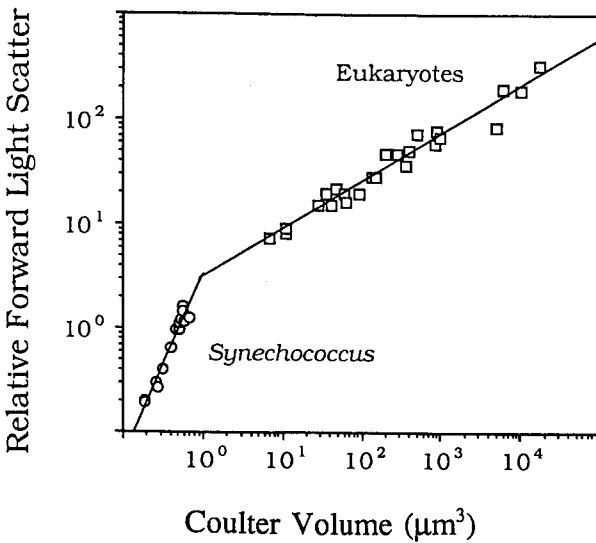

Fig. 6.   Relationship between Coulter volume and forward angle light scatter measured using flow cytometry. Several species of eukaryotic phytoplankton were used to construct the upper portion of the curve, and different strains of *Synechococcus* were used for the lower portion. (unpublished data of R. Olson, M. DuRand, and E. Zettler).

biomass spectrum is usually close to -1. It has been shown to vary with the productivity and size of ecosystems, however, decreasing with increasing eutrophy (Sprules and Munawar, 1986). As such, these spectra can be used with some success for the prediction of fish stocks (e.g. Sheldon et al., 1967; Maloney and Field, 1985; Borgmann, 1982). I believe that biomass spectra are underutilized as tools for understanding planktonic ecosystems, particularly in the oceans (cf. Agusti et al., 1990; 1991; Duarte et al., 1990). This is undoubtedly because of sampling problems, and the tedium involved in building the data sets required for the analyses.
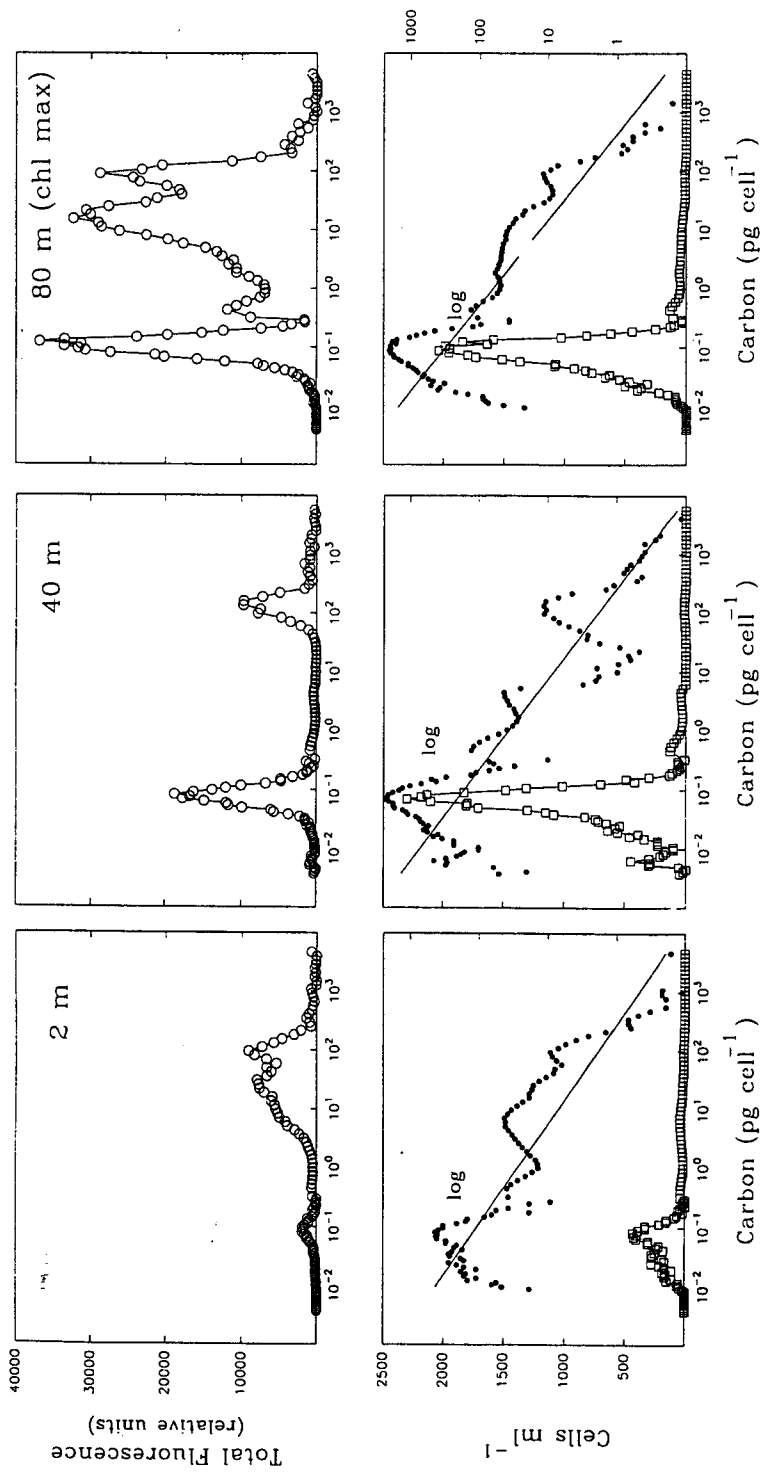
Fig. 7. Distributions of total fluorescence and cell concentration among size classes of fluorescent particles at three depths from the OFP station (31°50′N, 64°10′W) off Bermuda. The top graphs show the total fluorescence in a given size category, and the bottom shows the distribution of the numerical abundance of the cells on a log (solid dots) and linear (squares) scale. Numerically dominant cells in the small size classes are *Synechococcus* and *Prochlorococcus*.

Given the promise of size spectra as synoptic measures of the structure and function of planktonic ecosystems, we have begun to explore the utility of flow cytometric measurements for their automated construction (see also Yentsch and Phinney, 1989). Present technology limits us to particles no larger than 150 μm in diameter, but high sensitivity flow cytometry (Button and Robertson, 1989; Olson et al., 1990b) allows us to push the lower limits of spectra down to about 0.3 μm diameter, which is difficult to achieve using conventional techniques. Although flow cytometers measure light scatter rather than equivalent spherical diameter, the former can be converted to the latter using a reasonably simple calibration curve (Fig. 6), and volume can be converted to particulate carbon using appropriate equations (Strathmann, 1967; DuRand, unpublished).

Examples of flow cytometrically derived size spectra of particles from three depths in the Sargasso Sea are shown in Fig. 7. Although only the autofluorescent particles were analyzed in this particular example, it is technically feasible to collect data on all particles to construct a full spectrum analogous to that shown in Fig. 5. Our presumption, based on the theory above, is that in doing so the "valleys" in the log transformed data in Fig. 7 would disappear because of the contribution of heterotrophic organisms[1]. Besides highlighting the potential of flow cytometric analysis for the automated generation of pelagic size spectra, the examples in Fig. 7 illustrate an interesting point: Although the size distribution of phytoplankton appears to be unimodal and dramatically skewed toward the smaller size classes (cf. Yentsch and Phinney, 1989), the distribution of total fluorescence among size classes is bimodal, with a sizable fraction of the total fluorescence coming from the larger cells. This is not easily reconciled with the size-fractionated chlorophyll generalizations discussed below, but we cannot rule out the possibility that the picoplankton have a lower fluorescence yield than do the larger cells. Further work is needed, but the potential utility of these types of spectra for analyzing the planktonic community is clear.

Samples in Fig. 7 were analyzed using an Epics V flow cytometer, modified for high sensitivity (Olson et al., 1990) for the ultraplankton, and rapid sample throughput (Olson et al., 1991) for the larger cells. Cell volumes were calculated from light scatter according to the calibration curve in Fig. 6, and then converted to particulate carbon according to the Strathmann (1967) equations for the eukaryotic phytoplankton, and similar equations derived experimentally for the picoplankton (DuRand, unpublished).

SIZE-FRACTIONATED CHLOROPHYLL

One thing that can be stated unequivocally about phytoplankton size is that the fractional contribution of small cells to the standing crop increases as total chlorophyll decreases. If size-fractionated chlorophyll measurements are pooled from all over the oceans, regardless of climate or depth, we find that there is an envelope which defines the maximum fraction of the chlorophyll that will be found in cells less than 1 μm in diameter at a given total chlorophyll concentration (Fig. 8). The upper bound fraction amounts to roughly 0.50 μg l^{-1}, regardless of the total chlorophyll concentration. In extremely oligotrophic waters, the picoplankton chlorophyll is often much less than this, but usually comprises as much as 90% of the total chlorophyll biomass; in nutrient rich (high chlorophyll) areas they usually realize their maximum "potential biomass" (i.e. 0.50 μg l^{1}),

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[1]At present, we cannot distinguish between detritus and living non-fluorescent organisms, but this is theoretically possible through the use of fluorescent vital stains.

which under these conditions is a relatively small percentage of the total phytoplankton chlorophyll.

Using an extensive and coherent data set from the Mediterranean Sea, Raimbault et al. (1988) extended this general analysis to other size classes of cells, revealing a general pattern in the size structure of phytoplankton communities. The total amount of chlorophyll in each size fraction has an upper limit, corresponding to roughly 0.5, 1, and 2 μg l^{-1} for the <1, <3, and <10 μm size fractions, respectively (Fig. 9). Thus, beyond certain thresholds, chlorophyll can only be added to a system by adding a larger size class
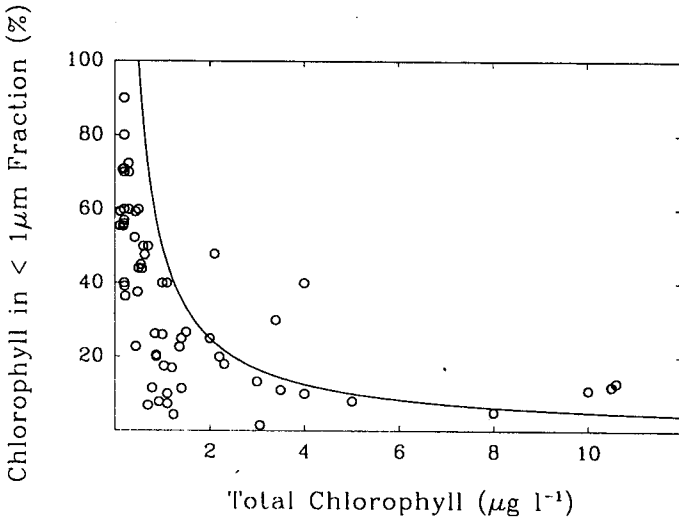

Fig. 8.   Fraction of total chlorophyll that will pass through a 1 μm pore size filter as a function of total chlorophyll for a variety of locations and depths throughout the world's oceans. The solid line describes the set of theoretical values where the concentration of chlorophyll in the less than 1 μm fraction is 0.50 μg l^{-1}. This appears to be the maximum amount found in this fraction, regardless of total chlorophyll concentration. Data were compiled from: Takahashi and Bienfang, 1983; Raimbault et al., 1988; Herbland et al., 1985; Chavez, 1989; Herbland and LeBouteiller, 1981; Smith et al., 1985; Harrison and Wood, 1988; Platt et al., 1983; Furnas and Mitchell, 1988; and Hopcroft and Roff, 1990. In cases where a single reference had too many data points to include in the figure, a random sample of points was selected.

of cells. Diatoms play a particularly important role in this "additional" chlorophyll. In a transect across the western north Pacific, Odate and Maita (1988) showed that diatoms were responsible for virtually all of the variation in the >10 μm fraction. Similarly, Chavez (1989) showed that variability in chlorophyll off the coast of Peru was directly related to numbers of diatoms present.

The patterns that emerge from studies of size fractionated chlorophyll biomass leave us with a fundamental question: Why are the oligotrophic oceans dominated by small

cells? The answer is not clear-cut, but we will explore some ideas in the next two sections.

SIZE, NITROGEN PREFERENCE, AND OLIGOTROPHY

In oligotrophic oceans, which are dominated by small cells, the majority of the primary production is believed to be driven by reduced (remineralized) nitrogen (NH_4^+ and urea). Conversely, large cells dominate in areas which have relatively high supply rates of NO_3^- ("new" nitrogen) and can support a relatively large phytoplankton biomass (Dugdale and Goering, 1967; Eppley and Peterson, 1979; Malone, 1980a,b). This rather universal trend has contributed to sustaining the hypothesis that large cells use primarily NO_3^- as their nitrogen source, and small cells use primarily NH_4^+. The origin of this hypothesis is usually attributed to Malone (1971,1980b); however, he was the first to insist that high levels of net plankton productivity in NO_3^- rich areas need not result from a causal relationship between size and NO_3^- assimilation (Malone, 1975), which is the case developed below.
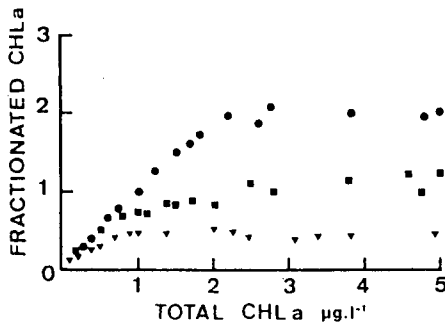

Fig. 9.   Relationships between total chlorophyll a and the maximum amount of chlorophyll a in the $< 1 \mu m$ (triangles), $< 3 \mu m$ (squares) and $< 10 \mu m$ (circles) fraction in the Mediterranean Sea (from Raimbault et al., 1988).

One should be able to test this hypothesis by examining the forms of nitrogen assimilated by different size classes using N^{15} tracer experiments. Indeed, much of the evidence in support of it (Nalewajko and Garside, 1983; Probyn, 1985; Probyn and Painting, 1985; Koike et al., 1986; Harrison and Wood, 1988; Bienfang and Takahashi, 1983) has emerged from such measurements. It is difficult to do these measurements without ambiguity, however, because the small size fraction contains heterotrophic bacteria, which can be responsible for a significant fraction of the total NH_4^+ assimilation in the euphotic zone (Eppley et al., 1977; Laws et al., 1984; 1985; and most notably Wheeler and Kirchman, 1986). Thus, measured nitrogen assimilation by the small size fraction is most likely biased in the direction of NH_4^+ preference.

Even with this bias, however, an overview of the literature does not lead to exclusive support for the hypothesis that small cells preferentially assimilate reduced nitrogen. Sherr et al. (1982) found, for example, that smaller cells had a greater affinity for both NH_4^+ and NO_3^- than did larger cells in Lake Kinneret. Similarly, Furnas (1983) found that ammonium uptake averaged between 50 and 67% of the total uptake for both

Table 1. Fraction of the Total Nitrogen Assimilated as Nitrate (f-ratio) for Different Size Fractions of Phytoplankton from Various Regions of the World's Oceans (courtesy of S. Carler, Bedford Institute).

Location and Water Type	Size (μm)	F-Ratio	Reference
Narragansett Bay (USA) "COASTAL"	TOTAL <10	0.29 0.27	Furnas (1983)
N.W. Atlantic "COASTAL" "OCEANIC"	TOTAL < 1 TOTAL < 1	0.48 0.34 0.02 0.02	Harrison & Wood (1988)
Antarctic "COASTAL"	TOTAL <15 < 1	0.58 0.53 0.57	Probyn & Painting (1985)
Antarctic "COASTAL"	TOTAL <20 <10	0.27 0.14 0.22	Koike et al. (1986)
Antarctic "COASTAL"	TOTAL <100 < 10	0.28 0.19 0.21	Koike et al. (1981)
South Benguela Upwelling (South Africa) "COASTAL" "OCEANIC"	TOTAL <10 < 1 TOTAL <10 < 1	0.71 0.58 0.44 0.17 0.13 0.33	Probyn (1985)
Sapelo Island (USA) "COASTAL"	< 1	0.03	Wheeler & Kirchman (1986)
Lake Kinneret (Israel)	TOTAL <10	0.18 0.16	Sherr et al. (1982)

the total plankton and $<10\mu$m fractions, even though the standing crop was distributed evenly between the large ($> 10~\mu$m) and small fractions. Ronner et al. (1983) found similar trends for the Scotia Sea. Although Harrison and Wood (1988) found that NH_4^+ was favored disproportionately by the picoplankton fraction in a variety of oceanographic regimes, the differences in the fractional uptake were not large. Finally, if one examines the f-ratio (i.e. the fraction of the total nitrogen uptake accounted for by NO_3^- uptake) of total and fractionated populations from a variety of locations, strong patterns are lacking (Table 1).

Thus, the dominance of larger cells in areas enriched with NO_3^- does not appear to be a result of a causal link between cell size and preference for either nitrate or ammonium. Indeed, Taylor and Joint (1990) showed through simulation that the relative biomass of picoplankton and larger phytoplankton is a function of the total nitrogen concentration below the mixed layer, and not whether the nitrogen is in the form of nitrate or ammonium. They showed further that intense mixing favors larger cells, and that the change to picoplankton dominance (and low f-ratios) under low mixing regimes occurs even when the physiology of the large and small size fractions is modelled identically. Chavez (1989) postulated a similar mechanism.

DIFFUSION LIMITATION OF NUTRIENT TRANSPORT

The dominance of picoplankton in oligotrophic oceans also might result from the fact that the acquisition of nutrients by large cells can be limited by molecular diffusion at the very low nutrient concentrations. Munk and Riley (1952) were the first to analyze the potential for phytoplankton to be limited by the rate at which molecular diffusion can supply nutrients to the surface of the cell. The problem was reconsidered by Pasciak and Gavis (1974), who concluded that diffusion limited transport could play a role in limiting the growth of very large cells in the sea. These studies pre-date the discovery of picoplankton, however, and also did not have the benefit of accurate measurements of the extremely low concentrations for both macro- and micronutrients in the oligotrophic oceans (Garside, 1982; Bruland, 1983).

We now know that typical concentrations of NO_3^- and NH_4^+ in the surface waters of oligotrophic oceans are about 10-20 nM (e.g. Eppley and Koeve, 1990). To appreciate exactly how dilute this environment is, it helps to create a mental picture: There are roughly 10^{16} molecules of NO_3^- in a liter of seawater at this concentration, and the molecules are roughly 1 μm apart. (To complete the image, in typical oligotrophic surface waters individual cyanobacteria are roughly 1 mm apart from one another, and large net plankton are 3 cm apart). Thus, a single *Synechococcus* cell, would have at most a few NO_3^- molecules near its surface membrane at any instant in time. Molecules of trace elements are even more rare on the horizon.

With this new picture in mind, at what values of cell size, nutrient concentration, and growth rate would diffusion limit the supply of nutrients to a cell? Using the approach of Hudson and Morel (1991) and Morel et al. (1991), consider the limiting case, i.e. a spherical cell which is a perfect sink for nutrients, such that the uptake rate is fast enough that the concentration of nutrients is zero at the cell surface. For a cell with a cell quota of limiting nutrient equal to Q (mole cell^{-1}), and a specific growth rate, μ (sec^{-1}), the supply of nutrients to the cell, J, must be greater than or equal to $\mu * Q$ if the cell is to survive. Using the formulation for steady diffusion to a sphere with zero boundary conditions, one can calculate the value of J as follows:

$$J = 4\pi r D S \qquad (8)$$

where r is the radius of the cell, D is the molecular diffusion coefficient ($=2 \times 10^{-5}$ cm^2 sec^{-1}), and S is the ambient concentration of the nutrient in question. One can calculate the carbon content of a cell of radius r using the equation of Strathmann (1967), and the value of Q using the Redfield ratio. Knowing Q, one can calculate, for a range of cell sizes and growth rates, the ambient concentration of nutrient at which diffusion limitation would limit the growth of phytoplankton cells of different sizes (Fig. 10).

The advantages of being small in low nutrient environments can be seen clearly in Fig. 10. At ambient nitrogen concentrations of 10 nM, a cell of radius 0.35 μm can grow at a rate of 1 day^{-1}, which is not uncommon for these regions (e.g., Iturriaga and Mitchell, 1986; Bienfang and Takahashi, 1983; Douglas, 1984; Iturriaga and Marra, 1988), without being near diffusion limitation. A cell of radius 1 μm, however, could not grow at this rate at 10 nM N, because diffusion could not supply it fast enough. In other words, in this environment a 10 μM radius cell would be at the threshold for diffusion limitation when growing at about 0.1 day^{-1}, whereas a 0.5 μm cell could grow at 20 times this rate and not exceed the diffusion limitation threshold. Hudson and Morel (1991) and Morel et al. (1991) did a similar analysis for iron and zinc availability in oligotrophic oceans, and conclude that diffusion limitation imposes constraints on cell size and/or cell quotas of these two trace elements in oligotrophic oceans. Indeed, Sunda et al. (1991) have shown that open ocean strains of diatoms have much smaller cell quotas for iron than do their coastal counterparts.
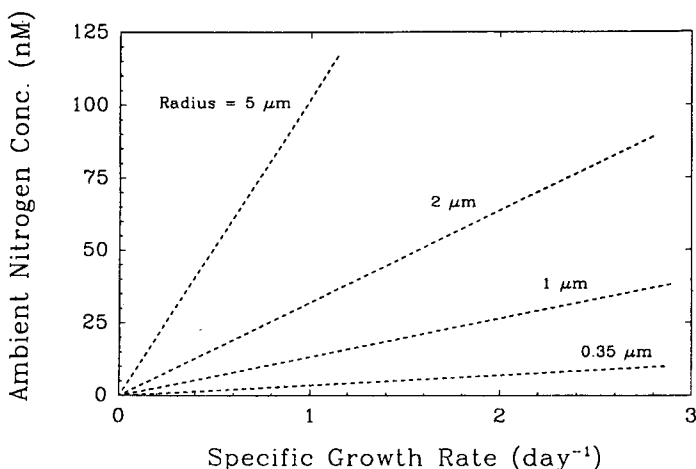

Fig. 10. Ambient concentration of nitrogen at which cells of different sizes would be diffusion limited as a function of growth rate. A cell of radius 5 μm growing at 1 day^{-1}, for example, would be diffusion limited at nitrogen concentrations less than 100 nM, whereas a cell of radius 0.35 μm growing the same rate would not be diffusion limited until concentrations dropped below 5 nM.

I have ignored sinking, swimming, and turbulent shear in this simple analysis, each of which can reduce the extent of diffusion limitation for larger cells to some extent (Pasciak and Gavis, 1975; Gavis, 1976). The influence is not large, however. To use an extreme case to illustrate the outer bound, a 200 μm diameter cell swimming at maximal swimming rates (300 μm sec^{-1}) can, at most, double its nutrient uptake rate over the diffusion limited rate; motions because of shear and sinking would less than double it (Gavis, 1976). Even large flocs of diatoms, which are centimeters in diameter, can, at most, double their nutrient uptake rate through rapid settling (Logan and Alldredge, 1989). Although these effects are not insignificant, they do not change the general message of Fig. 10. The size dependencies depicted here are logarithmic, thus, doubling does not

greatly change the results. I also am ignoring the fact that the cell quota, Q, decreases with growth rate in phytoplankton, thus the nutrient requirement would be lower for lower growth rates. Although I have not done a quantitative analysis of how Fig. 10 would change with a variable Q, the effect should not be dramatic.

According to the analysis shown in Fig. 10, at ambient nitrogen concentrations typical of oligotrophic oceans, a cell of radius 5 μm would be diffusion limited at growth rates greater than 0.1 day^{-1}. Since there is reasonable evidence that cells grow at rates significantly faster than this (e.g., Laws et al., 1984), one cannot help but wonder: Why are there any large cells in the oligotrophic oceans at all? How do they cope with this handicap? Although this is one of those "whys" that has no real answer, we can identify some mechanisms that have evolved in large cells which help them overcome their disadvantage. For example, shape can be very important. A spherical shape is not the optimum configuration for transport of nutrients (Munk and Riley, 1952). In fact, over certain size ranges, prolate spheroidal cells have a greater nutrient acquisition ability than spherical cells of equivalent volume (Grover, 1989). It is probably not coincidental, therefore, that pennate diatoms are found in great abundance in the equatorial Pacific (Chavez et al., 1991), where iron availability has been hypothesized to limit phytoplankton growth (Martin et al., 1991).

Nitrogen fixation, either autonomous or through symbioses, is another mechanism that allows large cells to thrive in nutrient poor waters. The colonial, nitrogen-fixing cyanobacterium, *Trichodesmium*, for example, plays a more significant role in the total productivity in oligotrophic oceans than previously thought, largely because of novel mechanisms for nutrient acquisition (e.g. Karl et al., 1991a,b). Analogously, large diatoms have enhanced nitrogen availability through symbioses with nitrogen-fixing cyanobacteria (Venrick, 1974; Mague et al., 1974; Heinbokel, 1986), which in some cases can supply 100% of the nitrogen requirement (Martinez et al., 1983). Diatoms may have other gimmicks: Goldman (1988) built a relatively strong theoretical case for a "two layer" model of oligotrophic systems, in which large diatoms occupy the deep euphotic zone and can grow at relatively rapid rates driven by periodic inputs of nitrate from below the mixed layer. Moreover, evidence suggests that large diatoms can regulate their buoyancy enough to facilitate daily excursions between the nitricline and the surface waters (Villareal, 1988; Villareal and Carpenter, 1989).

Therefore, extremely low nutrient concentrations are probably a powerful selective force against large cells in the oligotrophic oceans. The fact that small cells also dominate nutrient-rich areas of the open sea, such as the equatorial Pacific (Chavez, 1989), is not inconsistent with this hypothesis if we accept the evidence that iron limits production in these regions (Martin et al., 1991; Hudson and Morel, 1991; Morel et al., 1991). In fact, the dominance of small cells in these areas could be used as circumstantial support for the hypothesis that some form of trace nutrient limitation (most probably iron) plays a role in regulating the size of phytoplankton crops in nutrient rich oceanic zones.

SYNECHOCOCCUS AND *PROCHLOROCOCCUS*: SAME SIZE, COMPLEMENTARY NICHES

Up to this point we have examined the phytoplankton community as an assemblage of cells of different sizes and examined the properties of the community which can be explained on the basis of the size distribution. I would like now to examine the properties of two species belonging to one size class, such that, by definition, all differences between the species must be size-independent.

Table 2. The Pigment Composition of Typical Marine *Prochlorococcus* and *Synechococcus* (from Chisholm et al., 1988; 1991; Goericke and Repeta, 1991).

SYNECHOCOCCUS	*PROCHLOROCOCCUS*
Chlorophyll *a*	Divinyl Chlorophyll *a*
Phycoerythrin	Divinyl Chlorophyll *b*
ß-carotene	α-carotene
xeaxanthin	xeaxanthin
	Chlorophyll *c* - like pigment

In oligotrophic oceans the dominant species that pass through a 1 μm filter are *Synechococcus* and the marine prochlorophyte, *Prochlorococcus* (Chisholm et al., 1988; 1991). These cells are quite similar in size, although *Prochlorococcus* is almost always slightly smaller than *Synechococcus* (Olson et al., 1990b). Recent DNA sequence analyses (Urbach et al., 1991; Palenik and Haselkorn, 1991) suggest a relatively close taxonomic affinity between these two groups, yet they differ dramatically in their pigment composition (Table 2). Unlike typical cyanobacteria, *Prochlorococcus* lack phycobili-proteins and contain chlorophyll *b*, α-carotene, xeaxanthin, and a chlorophyll *c* - like pigment, possibly Mg 3,8-divinylpheoporphyrin a_5. Moreover, both their chlorophyll *a* and *b* are divinyl chlorophylls (Goericke and Repeta, 1991).

Although the two types of cells are nearly identical in size, are closely related, and almost always co-occur, their relative abundance in time and space is different (Olson et al., 1990b). For several years now, we have been following the two populations at monthly intervals at the OFP station off Bermuda. The numerical abundance of *Prochlorococcus* is always greater than that of *Synechococcus* (Fig. 11), and the median depth of these cells is always equal to or deeper than that of *Synechococcus*. When surface temperatures are high (Fig. 11) and the mixed layer is shallow, *Prochlorococcus* forms a sizeable sub-surface maximum layer (July in Fig. 12), and is an order of magnitude more abundant than *Synechococcus*. As the mixed layer deepens in the fall, and nutrients are entrained into the mixed layer from below the thermocline, *Prochlorococcus* "blooms" in the surface waters, where it greatly outnumbers *Synechococcus* (Nov. in Fig. 12). When surface temperatures are cold, however, and the water column is well mixed (Feb. in Fig. 12), the two types of cells have roughly the same abundance in the water column. The same dynamics depicted in Figs. 11 and 12 can be seen in the spatial dimension for various transects in the Atlantic and Pacific oceans (Olson et al., 1990b).

The general picture that emerges suggests that *Prochlorococcus* is more efficient than *Synechococcus* at using low light, as would be expected from their pigment compositions (Glover et al., 1986; Waterbury et al., 1986; Olson et al., 1988, 1990a,b). Evidence also suggests that *Prochlorococcus* may have a different temperature optimum than does *Synechococcus*, and may be less efficient at using the low nutrient concentrations characteristic of the surface waters of the Sargasso Sea in summer (Olson et al., 1990b).

An interesting outcome of the dynamics of these two populations is that the balance of the advantages and disadvantages for the two types of cells results in a fairly constant total cell biovolume when the two populations are considered as one (faint dotted line in Fig. 11). The two populations are complementary: They fill the space "allotted" to 1 μm cells in the euphotic zone throughout the year. Although our data are not as resolved for the larger cells (Olson et al., 1990b), their numerical abundance does not display this type of constancy through the seasons. This is consistent with the image created above, i.e. that the small cells are a lawn upon which larger cells can be found in varying amounts depending on the available light and nutrients.
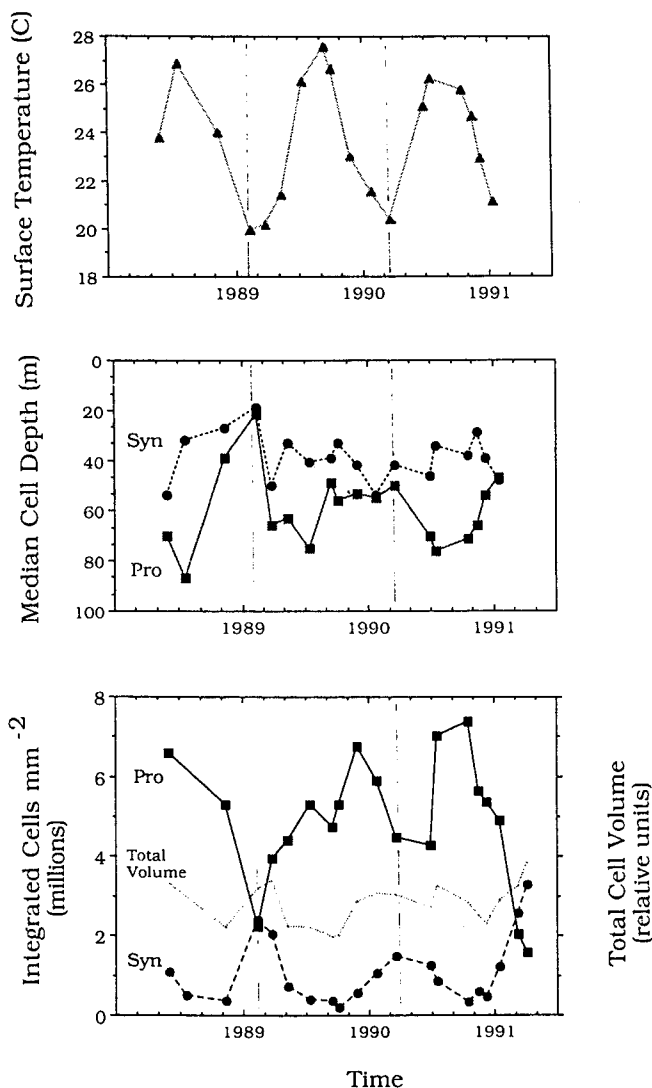

Fig. 11.   Seasonal dynamics of *Synechococcus* (Syn) and *Prochlorococcus* (Pro) in the Sargasso Sea off Bermuda ("OFP" 31°50'N, 64°10'W).   (A) Surface temperature, (B) Median depth occupied by the two populations, (C)Intergrated numerical abundance of the individual species, and the summed biovolume (faint dotted line) of the two species calculated using a diameter of 0.7 and 1.0 μm for Pro and Syn, respectively. (adapted from Olson et al., 1990, and unpublished data of Olson and Chisholm).

It is sobering to realize how much our picture of the size structure of phytoplankton communities has changed in the past decade. In the early years the community was separated into "large and small" categories (net- and nannoplankton) by a 20 μm mesh net. When marine *Synechococcus* were discovered a decade ago, followed by the discovery of *Prochlorococcus* and eukaryotic ultraplankton, our image of the median size category in phytoplankton communities gradually shifted such that the modal size is now around 2-3 μm. One cannot help but wonder if there is an even smaller group waiting to be discovered. We can take some comfort, however, in the fact that the size of *Prochlorococcus* is near the theoretical limit for the smallest possible autotroph (Raven, 1986).

I have not included some very important size-dependent properties of phytoplankton in this review, which should at least be noted. First, there is a pigment "package effect" in cells, which is an increasing function of cell size and influences the efficiency with which cells absorb light (e.g. Bricaud et al., 1988; Yentsch and Phinney, 1989). Second, I have ignored the influence of size-selective grazing, grazing thresholds, and differential
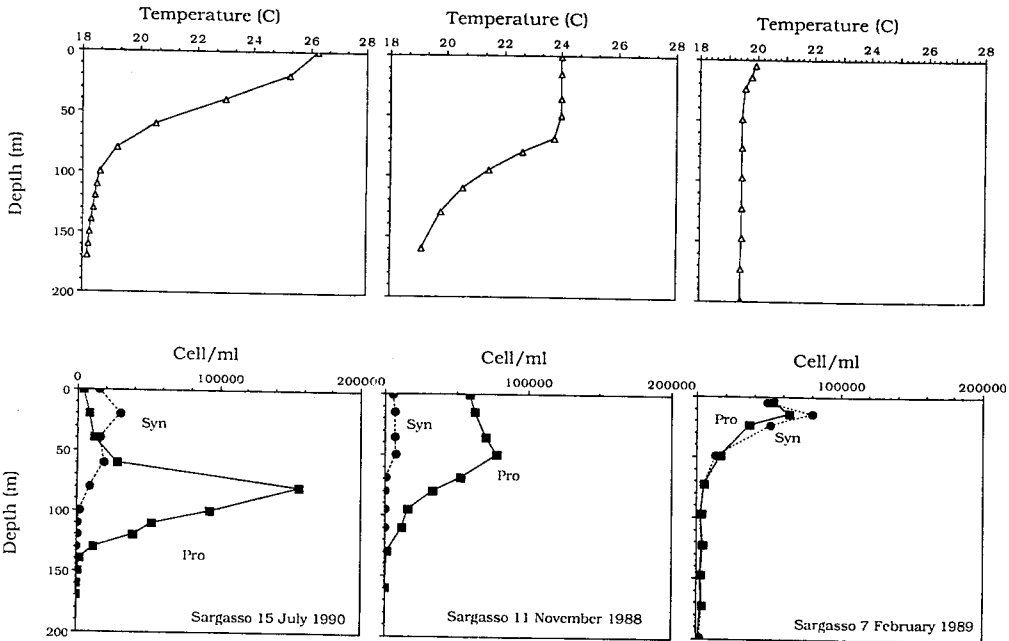

Fig. 12. Depth profiles of temperature, concentrations of *Synechococcus* (Syn) and *Prochlorococcus* (Pro) typical in the summer, winter, and fall in the Sargasso Sea. Under highly stratified summer conditions, *Synechococcus* dominates in the surface waters, and *Prochlorococcus* forms a large sub-surface maximum, which sits below the thermocline and just above the nitricline. As the mixed layer deepens and nutrients are entrained into the surface waters in the fall, *Prochlorococcus* "blooms" in the mixed layer, significantly outnumbering *Synechococcus*. Under the deep mixing conditions of winter, both organisms have similar distributions (adapted from Olson et al., 1990, and unpublished data of Olson and Chisholm).

settling rates on phytoplankton size distributions, which must influence the size distribution we measure in any snapshot of the pelagic community. Third, I have not addressed the puzzling dependence of DNA content on cell size in phytoplankton (Holm-Hansen, 1969), the adaptive significance of which has been the subject of much speculation over the years (e.g., Cavalier-Smith, 1978; 1980; Lewis, 1985). Each of these topics is worthy of a review in and of itself.

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