

THE SIZE STRUCTURE OF MARINE PHYTOPLANKTON— WHAT ARE THE RULES?

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ABSTRACT

It has been suggested that the size structure of marine phytoplankton communities varies with concentrations of chlorophyll *a* (Chl *a*): When total biomass is low, biomass is added only to the smallest size class until an upper limit to Chl *a* in this size class—its biomass quota—has been reached. At this point biomass can only be added to the community by adding Chl *a* to the next larger size class until its quota too is reached, whereupon the next largest size class is filled up, etc. These rules predict a maximum biomass for all size classes, except for the largest one whose maximum biomass is set by the availability of inorganic nutrients, and abundance thresholds for all size classes except for the smallest one. Here these predictions were tested in a variety of environments, the California Current system, the Eastern Tropical North Pacific, and the Sargasso Sea. Even though the smallest and largest size classes followed the above rules, i.e., these had an upper biomass limit and an abundance threshold, respectively, biomass distributions of intermediate size classes did not support the simple set of rules. These results question the general validity of these rules.

INTRODUCTION

Marine phytoplankton communities often consist of hundreds of species. Describing and understanding these communities in terms of these species is either impractical due to the large number of species present or impossible due to the small size of many, which precludes their identification. Instead other parameters, such as size, gross taxonomic affiliation or functional group can be used to describe phytoplankton communities. Using size to describe these has many advantages. Size is easily determined (Malone 1980; Chisholm 1992) and rates of metabolic processes can often be estimated for different size classes using simple allometric relationships (Banse 1982; Peters 1983; Moloney and Field 1989; Finkel et al. 2010, hallo). These advantages have lead to the development of models of phytoplankton communities based on size (Moloney and Field 1991; Armstrong 1996; Thingstad 1998; Armstrong 1999; Irwin et al. 2006).

After reviewing field data, Chisholm (1992) suggested simple size-based rules for the assembly of marine phy-

toplankton communities; Thingstad (1998) presented a simple conceptual model that explains these rules. The rules are: 1. Phytoplankton communities are dominated by the smallest cells when total phytoplankton biomass is low, a rule for which ample empirical evidence exists (Chisholm 1992; Agawin et al. 2000). 2. As biomass increases it is added only to the smallest size class until an upper limit to total Chl *a* in this size class is reached, which will be called its biomass quota. For example, the quota for the $<1 \mu\text{m}$ size fraction is about $0.5 \mu\text{g-Chl } a \text{ L}^{-1}$ (Chisholm 1992). 3. Once this quota has been reached, biomass can be added to a system only by adding a larger size class of cells until its quota has been reached as well. This cycle continues, only limited by the maximum biomass that a system can attain (Thingstad 1998). This implies that for all size classes, except for the smallest one, there are thresholds of total phytoplankton biomass that have to be met before cells of these size classes are found in the system. Thus, phytoplankton pigment biomass of different size classes, when plotted against total Chl *a* (TChl *a*), are predicted to show successive waves of size classes, all eventually leveling out once they reached their biomass quota (fig. 1A). For example, Raimbault et al. (1988) observed that phytoplankton biomass in the <1 , <3 , and $<10 \mu\text{m}$ size classes had upper limits of 0.5, 1 and 2 Chl *a* L^{-1} in the Adriatic Sea. The following testable hypotheses are predicted by these rules: 1. The biomass of smaller size classes attains a constant value for large values of TChl *a*. 2. There exists an abundance threshold for all size classes except the smallest one, i.e., a threshold below which cells of any particular size class do not contribute significantly to phytoplankton biomass. 3. Relative contributions of intermediate size classes to TChl *a* will follow a characteristic sawtooth pattern when plotted against TChl *a* (fig. 1B).

The empirical rules above only refer to the average state of a system. In the case of Thingstad's (1998) model these refer to a system at steady state with a given level of total nutrients, which, when nitrogen is limiting phytoplankton biomass, would be the total nitrogen content of the system. Thingstad's (1998) model is based on the dependence of nutrient uptake rates on size and sim-

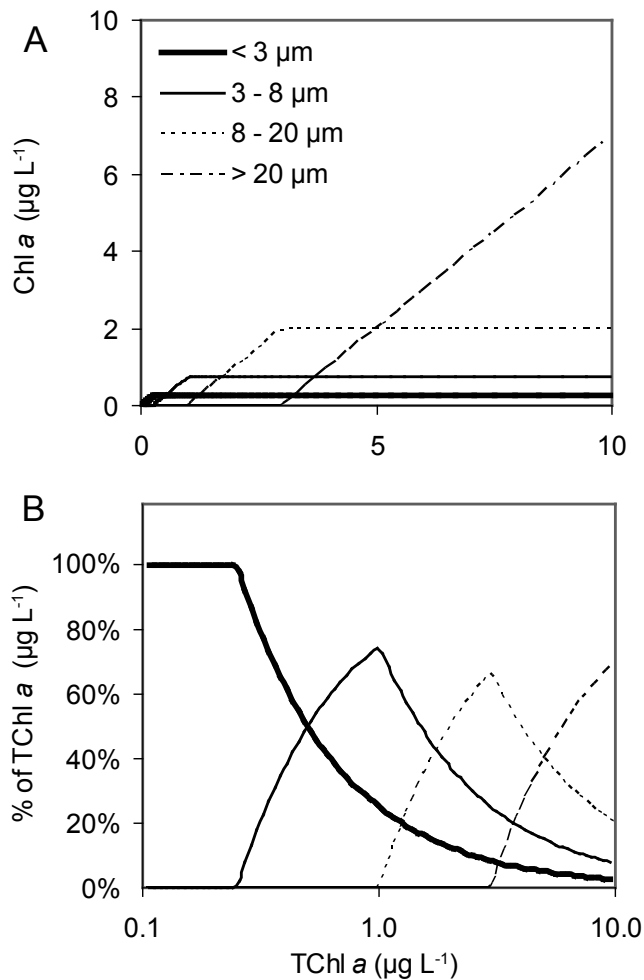


Figure 1. A graphical representation of the rules governing the contributions of different size classes to total phytoplankton biomass (TChl a). These graphs were derived from concepts in Thingstad (1998). A. The cumulative biomass of all size classes is plotted against TChl a. Note abundance thresholds for all size classes except for the smallest one and the attainment of class-characteristic upper biomass limits, i.e., quota, when TChl a is high. B. Using the data shown in panel A, the relative contribution of the size classes (% of total) was calculated and plotted against to log of TChl a.

ple predator-prey interactions that predict variations of phytoplankton size structure with total system biomass. The model implies that total phytoplankton biomass is controlled by the availability of resources but that community size-structure is controlled by grazers; i.e., by a balance of bottom-up and top-down forces.

The observations discussed above and Thingstad's model imply that simple rules exist that describe variations of phytoplankton size structure with total phytoplankton biomass. Their existence would suggest that phytoplankton community size structure can be predicted using simple rules and that phytoplankton community structure is primarily determined by size-dependent factors. However, these are only rules and we should expect that there are exceptions to these rules. For example, blooms of very small flagellates that

are at times observed in nearshore and coastal environments impacted by eutrophication (Gieskes and Krey 1983; Dahl et al. 1989) demonstrate that the patterns described above are not universally followed, i.e., these do not constitute laws. But are these patterns generally found in the marine environment, i.e., do these rules hold generally and has this been demonstrated? Demonstrating that these rules are generally valid would also lend further empirical support to Thingstad's model. The first step to test these rules will be made here using data from the California Current system as well as data from the Sargasso Sea and the Eastern Tropical North Pacific. The distributional patterns observed in these environments did not follow predicted patterns, suggesting that the rules described above may not be generally true.

METHODS

For this study size classes are operationally defined by the pore size of the filters used in the size fractionation experiment. Size fractionation experiments were carried out in the Southern California Bight and the California Current system during the April and July 2003 California Cooperative Oceanic Fisheries Investigations (CalCOFI) cruises (CC0304 and CC0307, respectively). Additional experiments, carried out as part of other studies, were carried out during two cruises to the Eastern Tropical North Pacific south and southwest of Baja California in February and November 2003 (MEX0302 and MEX0311) and during cruises to the Sargasso Sea off Bermuda during 1985 and 1986 (Goericke 1998). Water from the mixed layer, collected with hydrowire- or rosette-mounted Niskin bottles from a depth of 1 or 10 m, was used in all cases. The sum of chlorophyll a (Chl a_1) and divinyl-chlorophyll a (Chl a_2), was used as a proxy for total phytoplankton biomass and will be referred to as Chl a or TChl a. Samples were analyzed either using the fluorometric method (Holm-Hansen et al. 1965) to determine Chl a and "pheopigments" or by high-pressure liquid-chromatography (HPLC) to determine concentrations of chlorophylls and carotenoids. For fluorometric analysis, 250 or 500 ml seawater were filtered on 25 mm Whatman GF/F filters, 3 and 8 μm Nuclepore filters and 20 μm Nitex circles. Filtrations were carried in parallel. Each treatment was carried out in triplicate. During cruises CC0307 and MEX0311 1- μm filters were used as well. The filters were extracted for 24 hours in 90% acetone at -18°C . Concentrations of Chl a were determined on a Turner Designs 10AU fluorometer. For pigment analysis by HPLC, three samples, each from cruises CC0307 and MEX0311 were filtered onto 25 mm Whatman GF/F and 47 mm 3 and 8 μm Nuclepore filters. These filters were stored in liquid nitrogen for at least 24 hours and extracted in 100% acetone. Extracts were analyzed on a

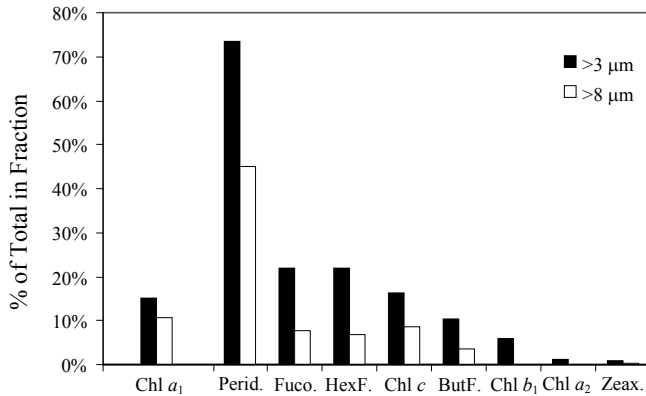


Figure 2. Size fractionation experiments in the California Current system (CalCOFI stations 93.100, 93.90, 90.80; i.e., n=3). For each pigment the contributions of the 3 to 8 and >8 μm size classes to the total concentration of that pigment are plotted. These pigments are representative of different groups of autotrophs, i.e., *Prochlorococcus* (Chl a₁; stdev = 1%), dinoflagellates (peridinin, Perid.; stdev = 31%), diatoms & haptophytes (fucoxanthin, Fuco.; stdev = 9%), haptophytes (19'-hexanoyloxyfucoxanthin, HexF.; stdev = 1%), chromophytes (chlorophyll c_{1,2}, Chl c; stdev = 2%), pelagophytes (19'-butanoyloxyfucoxanthin, ButF.; stdev = 3%), chlorophytes & *Prochlorococcus* (Chl b; stdev = 5%), *Prochlorococcus* (Chl a₂; stdev = 1%) and zeaxanthin (cyanobacteria, Zeax.; stdev = 0.6%).

C8-column based reverse-phase HPLC system as previously described (Goericke and Repeta 1993). Contributions of size fractions were calculated by subtraction, e.g., pigment biomass of the 3 to 8 μm size class was calculated by subtracting Chl a in the >8 μm treatment from Chl a in the >3 μm treatment. Chl a collected on Whatman GF/F filters was assumed to represent total Chl a present in the system and will be referred to as TChl a. In the California Current system the TChl a retention efficiency of these filters, relative to that of 0.2 μm Nuclepore filters, is 98 ± 2 % (n=24) (Goericke 2002). Statistical analysis of the data was carried out in Microsoft Excel.

RESULTS

In the California Current system size fractionation experiments were carried out in environments ranging from eutrophic coastal with TChl a larger than 10 μg

L⁻¹ to oligotrophic offshore, located at the edge of the central gyre of the North Pacific, with TChl a less than 0.1 μg L⁻¹. The Eastern Tropical North Pacific and the Sargasso Sea were typical of tropical and subtropical oligotrophic environments. Thus stations sampled for this study can be assumed to be representative of large areas of the world's ocean.

The effectiveness of filtration protocols used for size fractionation experiments was tested in the California Current system (CC0304) and the Eastern Tropical North Pacific (MEX0311) by combining size fractionations with the analysis of taxon-specific pigments by HPLC in samples from oligotrophic areas. In the California Current system, 17 and 9% of the chlorophyll a was retained by 3 and 8 μm Nuclepore filters, respectively (fig. 2). In contrast only 0 and 1% of divinylchlorophyll a and zeaxanthin were retained by these filters, respectively, i.e., pigments which in the open ocean are characteristic of the cyanobacteria *Prochlorococcus* sp. and *Synechococcus* sp. (Guillard et al. 1985; Goericke and Repeta 1992), the smallest known photoautotrophs. As expected, retention efficiencies of pigments associated with eukaryotes were higher. Highest values were observed for peridinin, the pigment characteristic of dinoflagellates. The relatively low retention efficiency of fucoxanthin by large pore-size filters (fig. 2) reflects the fact that fucoxanthin in these samples was primarily associated with haptophytes where it is a minor pigment (Jeffrey et al. 1997). Very similar results were obtained in the Eastern Tropical North Pacific where Chl a₂ and zeaxanthin in the >3 and >8 μm size fractions were only 0 to 1 % of the total (n = 3). These results show that the filtration procedures used effectively separated very small cells, such as *Prochlorococcus*, from larger cells and that small photoautotrophs were not significantly associated with larger particles or adhered to particles during sampling and filtration.

A large range of TChl a values was encountered in the California Current system. Thus results from that

TABLE 1

Size distribution of TChl a for open ocean stations where TChl a was less than 0.3 μg L⁻¹. Data are from cruises in April and July of 2003 in the California Current system (CC0304 and CC0307), the Sargasso Sea (Sargasso) during 1985 and 1986 (Goericke 1998) and the Eastern Tropical North Pacific (ETNP) during February and November 2003. Given are the average TChl a concentration (Average TChl a), the percent contribution of each size class to TChl a, and the number of samples used for the analysis (N). Significant regressions (type I, 95% significance level) of relative biomass (%) against TChl a (μg Chl a L⁻¹) are indicated with a '*'. The number of samples from each cruise or environment is given by 'N'.

	California Current system		Sargasso	ETNP	
	CC0304	CC0307	—	MEX0302	MEX0311
Average TChl a	0.16	0.16	0.11	0.17	0.17
<3 μm	75 ± 5 *	75 ± 5 * ¹	79 ± 4 *	86 ± 7 *	91 ± 6 * ¹
3 to 8 μm	16 ± 4 *	15 ± 5 *	12 ± 3 *	7 ± 1 *	4 ± 2
8 to 20 μm	6 ± 4	6 ± 2 *	5 ± 2 *	4 ± 2	3 ± 2
>20 μm	3 ± 1	4 ± 2	4 ± 2	3 ± 4	2 ± 1
N	20	12	7	9	18

¹Biomass in the 1 to 3 μm size class was determined as well and varied significantly with TChl a.

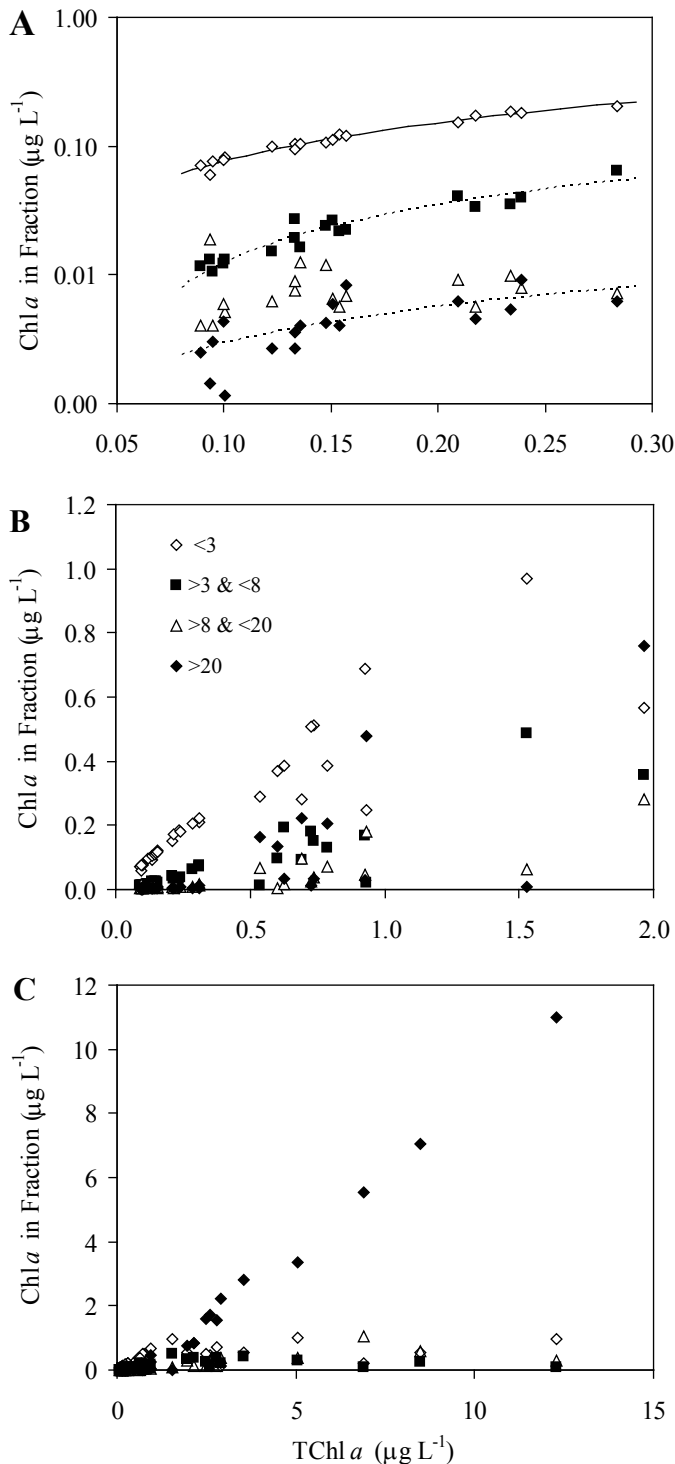


Figure 3. The pigment biomass ($\mu\text{g Chl } a \text{ L}^{-1}$) of the <3 , 3 to 8, 8 to 20 and >20 μm size classes plotted against TChl a for data collected on cruise CC0304 in the California Current system. A) the log of the size class pigment biomass is plotted against TChl a for values of TChl a ranging from 0 to $0.3 \mu\text{g Chl } a \text{ L}^{-1}$. B) The data plotted on a linear scale with TChl a ranging from 0 to $2 \mu\text{g Chl } a \text{ L}^{-1}$. C) The data plotted on a linear scale with TChl a ranging from 0 to $14 \mu\text{g Chl } a \text{ L}^{-1}$; the latter represents the largest TChl a concentration sampled for these experiments.

environment will be presented in detail. During April 2003 the $<3 \mu\text{m}$ size class dominated total pigment biomass (TChl a) in the California Current system when TChl a was low (i.e., TChl $a < 0.3 \mu\text{g L}^{-1}$). The $<3 \mu\text{m}$ size class contributed on the average 75% to TChl a (fig. 3a, table 1). The 3 to $8 \mu\text{m}$, 8 to $20 \mu\text{m}$ and $>20 \mu\text{m}$ size classes contributed on the average 16, 6 and 3% to TChl a , respectively (table 1, fig. 3a) in these sample. Biomass in the <3 and the 3 to $8 \mu\text{m}$ size class varied significantly with TChl a ($<3 \mu\text{m}$: $r^2 = 0.90$, $p(\text{slope} = 0) < 0.01$; 3 to $8 \mu\text{m}$: $r^2 = 0.99$, $p(\text{slope} = 0) < 0.01$). This observation implies that the $<3 \mu\text{m}$ and 3 to $8 \mu\text{m}$ size classes are “filled” simultaneously. Virtually identical results were obtained during July 2003 for low TChl a samples (CC0307, table 1) in regards to contributions to TChl a and variations of biomass in different size classes with TChl a ($<1 \mu\text{m}$: $r^2 = 0.92$, $p(\text{slope} = 0) < 0.01$; 1 to $3 \mu\text{m}$: $r^2 = 0.62$, $p(\text{slope} = 0) < 0.01$; 3 to $8 \mu\text{m}$: $r^2 = 0.28$, $p(\text{slope} = 0) < 0.05$). Data for TChl a values of up to $0.3 \mu\text{g L}^{-1}$, collected in other subtropical environments showed similar patterns (table 1); biomass in the 3 to $8 \mu\text{m}$ size class was a linear function of TChl a in both environments (Sargasso: $r^2 = 0.92$, $p(\text{slope} = 0) < 0.001$; ETNP: $r^2 = 0.68$, $p(\text{slope} = 0) < 0.05$). These patterns clearly do not follow the rule that stipulate that larger size classes are only filled up once smaller size classes have reached their biomass quota.

As TChl a increased above $0.3 \mu\text{g L}^{-1}$, contributions of different size classes to TChl a were much more variable (fig. 3b). In the California Current System the biomass of the <3 and 3 to $8 \mu\text{m}$ size classes reached apparent saturation values only once TChl a was larger than 1 to $2 \mu\text{g L}^{-1}$ (fig. 3c). However, the variability of the data and the absence of large numbers of data points in that range of TChl a precludes us to reach a firm conclusion. In contrast, biomass of the $>20 \mu\text{m}$ size classes did not reach saturation values (fig. 3c). Plots of relative contributions of different size classes to TChl a illustrate these patterns in more detail and allow a comparison of the field data from the cruises CC0304 and CC0307 in the California Current system (fig. 4) with predicted patterns (fig. 1b). Only the $<3 \mu\text{m}$ and $>20 \mu\text{m}$ size classes displayed the predicted patterns (fig. 4 a, d): the $<3 \mu\text{m}$ fraction had a constant relative biomass of about 75% when TChl a was low and started declining dramatically once TChl a was larger than $0.5 \mu\text{g L}^{-1}$. The $>20 \mu\text{m}$ fraction had, as predicted, an abundance threshold at about $0.5 \mu\text{g-Chl } a \text{ L}^{-1}$; below this threshold its relative biomass was constant and very low; once TChl a reached values larger than $0.5 \mu\text{g L}^{-1}$ its relative biomass increased dramatically, until it dominated TChl a for large values thereof. In contrast, the 3 to $8 \mu\text{m}$ fraction failed to attain small values of relative biomass for small values of TChl a as is predicted. The relative contribution of the 8 to $20 \mu\text{m}$

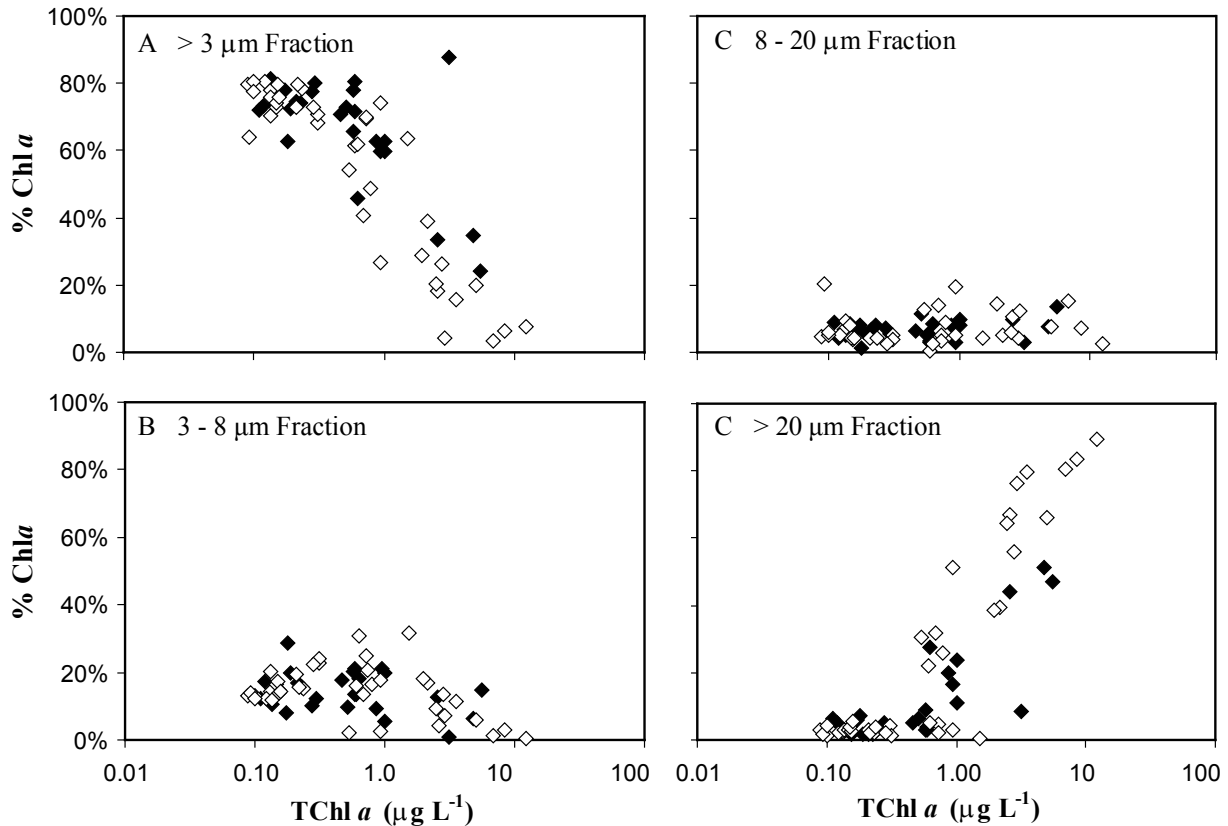


Figure 4. The relative pigment biomass (% of TChl *a*) of the <3 (A), 3 to 8 (B), 8 to 20 (C) and >20 (D) μm size classes plotted against log TChl *a* for data collected on cruises CC0304 (open symbols) and CC0307 (solid symbols) in the California Current system. Note that TChl *a* is plotted on a logarithmic scale for comparison with Figure 1b.

size class to TChl *a* varied from less than 5 % to 15% of the total but did not vary systematically with TChl *a* (fig. 4c) as is predicted (fig. 1 a,b). Overall the distributions of the 3 to 8 and 8 to 20 μm size classes do not display the expected sawtooth pattern (c.f. fig. 1b), i.e., do not follow the predicted patterns.

DISCUSSION

The objective of this study was to test a simple set of rules governing the size structure of phytoplankton communities (fig. 1), using data from the California Current system and other marine environments. Chl *a* was used as a proxy for phytoplankton carbon biomass in this study. Even though carbon to Chl *a* ratios are quite variable in algae (Geider 1987), ratios of Chl *a* in different size classes of algae reflect the corresponding carbon ratios well (Tremblay and Legendre 1994). This suggests that Chl *a* is an appropriate proxy for phytoplankton biomass for this study.

Results presented here suggest that the rules outlined in the introduction do not adequately describe contributions of different size classes to TChl *a*. In the California Current system small phytoplankters dominated phytoplankton biomass when TChl *a* was low, as predicted and

as expected based on empirical data from many studies (Chisholm 1992; Agawin et al. 2000). When phytoplankton biomass was high picoautotrophs were still present as predicted, contributing on the average $0.5 \mu\text{g Chl } a \text{ L}^{-1}$ to the total. Or, put differently, in the ocean there is a constant background of planktonic autotrophs, regardless of the waning and waxing of larger phytoplankters, such as diatoms or dinoflagellates (Chisholm 1992). The biomass of some size classes also attains maximum values, as predicted, even though these values were quite variable. For example, even though the <3 μm size class in the California Current system had an average biomass of $\sim 0.5 \mu\text{g Chl } a \text{ L}^{-1}$ for TChl *a* larger than 1 to 2 $\mu\text{g Chl } a \text{ L}^{-1}$, values as high as $2.7 \mu\text{g Chl } a \text{ L}^{-1}$ were observed for the <3 μm size class during cruise CC0307. Nonetheless, this study illustrates, similar to many others (see reviews by Malone 1980 and Chisholm 1992), that the variability of phytoplankton biomass in the ocean is generally due to the larger phytoplankters.

The most significant deviation of observed distributional patterns from those predicted is the absence of discrete abundance thresholds for some size classes. For example, it was not possible to unambiguously identify an abundance threshold for the 3 to 8 μm and 8 to 20

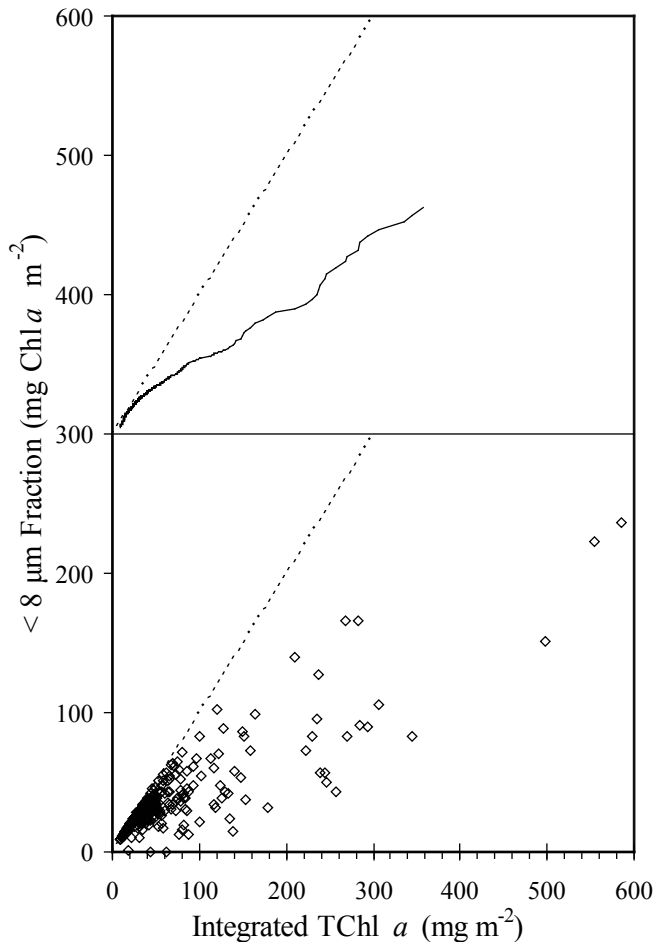


Figure 5. The contribution of the $<8 \mu\text{m}$ size class to euphotic zone integrated TChl a ($\text{mg Chl } a \text{ m}^{-2}$) in the California Current system from Mullin (1998). The data, $n = 557$, were collected by the CalCOFI technical group on cruises between 1994 and 1996. The lower panel shows the individual data points, the upper one shows the data smoothed using a loess function. The dotted line represents a 1:1 line for the data. In the California Current system stations with integrated TChl $a > 100 \text{ mg m}^{-2}$ have typically surface TChl a concentrations larger than $5 \mu\text{g L}^{-1}$.

μm size classes in data from three different environments, the California Current system, the Sargasso Sea and the Eastern Tropical North Pacific. It also appears that the biomass of the 8 to $20 \mu\text{m}$ size class does not reach an upper limit, i.e., its relative contribution to TChl a is constant, even when TChl a is large (fig. 3c). This point is also well illustrated by data published by Mullin (1998; 2000) that show convincingly ($n = 557$) that the biomass of the $<8 \mu\text{m}$ size class in the California Current system does not saturate as TChl a increases, even when TChl a reaches values larger than $10 \mu\text{g L}^{-1}$ (fig. 5, replotted from data in Mullin 1998 and 2000). Li (2002), using flow-cytometry data, observed patterns very similar to those described here. Whereas a decrease of the cellular abundance of picoautotrophs ($<2 \mu\text{m}$) with increasing Chl a standing stocks was mirrored by an increase in the cellular abundance of larger nanoautotrophs (10 to 20

μm), the cellular abundance of smaller nanoautotrophs did not vary with Chl a standing stock within the range of 10 to $1000 \text{ mg-Chl m}^{-2}$. The latter result confirms our observations for the intermediate size classes.

The data presented here illustrates that the variability of autotroph biomass in the California Current system is dominated by larger autotrophs. In contrast Marañón et al. (2001) reported that in the open North and South Atlantic variability of phytoplankton biomass was due to picoautotrophs only ($<2 \mu\text{m}$). It is interesting to note that Marañón et al. (2001) confined their analysis to stations with standing stocks of less than $40 \text{ mg TChl } a \text{ m}^{-2}$, i.e., stations where TChl a concentrations were mostly below $\sim 0.4 \mu\text{g L}^{-1}$ (Marañón et al. 2000). An analysis of the California Current system with stations confined to those with mixed layer TChl a less than $0.4 \mu\text{g L}^{-1}$ would result in a conclusion similar to that of Marañón et al. (c.f. fig. 3a), since larger taxa, such as diatoms, which are responsible for blooms in the California Current system (Venrick 2002; Goericke 2011), are virtually absent from the system when TChl a is less than $0.4 \mu\text{g L}^{-1}$. These results imply that the answer to the question “What dominates the variability of autotroph biomass in the ocean?” scales with the range of pigment concentrations observed in the study.

These results show that the rules that were suggested by Chisholm (1992) and given a theoretical justification by Thingstad (1998) cannot be applied without modifications to the California Current system. Some aspects of these rules—implied abundance thresholds for intermediate size classes and the postulated upper limits to total Chl a in some size classes—fail to adequately describe the size structure of phytoplankton communities in the California Current system and in other environments as well. Considering that the California Current system is a very heterogeneous system, likely representative of other temperate/subtropical marine systems (c.f. table 1), these results should caution us to use simple sets of rules to describe the size structure of phytoplankton communities in any marine environment without first testing these.

These results imply that size is just one of many important dimensions of phytoplankton community structure. These data suggest that size-based trophic interactions are insufficient to explain the different size distributions observed in the various environments, particularly distributions for intermediate-sized phytoplankters. For example, Irvin et al. (2006) have shown theoretically that phytoplankton size structure, among other factors, also depends on the maximum growth rate of the different groups of phytoplankters. This implies more consistent distributional patterns could emerge when taxon-specific biomass is used for such a study instead of size-class specific biomass since maximum

growth rates vary significantly among taxa, often independent of size (Chisholm 1992; Finkel et al. 2010). An analysis of taxon-specific biomass distributions from the California Current system confirms this (Goericke 2011); the biomass of different phytoplankton taxa followed patterns such as those shown in Figure 1.

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