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Resource levels, allometric scaling of population abundance, and marine phytoplankton diversity

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Abstract

We analyzed the relationship between population abundance and cell size in phytoplankton assemblages from coastal, shelf, and open-ocean environments. Our results show that across the entire size spectrum considered, population abundance increases over two orders of magnitude from subtropical to coastal regions. We find a highly significant linear relationship between nutrient concentration and the intercept of the log-log relationship between population abundance and cell size. In contrast to overall patterns reported mainly for vascular plants and animals, marine phytoplankton diversity does not show any consistent trend along either latitudinal or productivity gradients. These results imply that large-scale (biogeographic) variations in phytoplankton standing stocks are controlled by changes in population abundances rather than by systematic variations in species richness. These findings provide a mechanistic connection among nutrient availability, population dynamics, and phytoplankton diversity over macroecological scales.

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The metabolic theory of ecology, a synthetic and unifying theory derived from the analysis of macroecological patterns, has greatly expanded our ability to identify the overall principles and mechanistic bases that govern life on Earth (Brown et al. 2004). Built upon the assumption that metabolic constraints are reflected in many properties of the ecosystem, such as population abundance, energy use, and biodiversity, this ecological theory considers three main components, namely, body size, temperature, and resources, as major determinants of the metabolic rate. However, whereas body size and temperature have been widely incorporated into macroecological models of biochemical kinetics (Hemmingsen 1960; Calder 1984; West et al. 1999) and population abundance (Damuth 1981; Peters 1983; Enquist et al. 1998), resources have so far received little attention (but *see* Finkel et al. 2004; Irwin et al. 2006).

To a first approximation, the number of individuals, N, of a given species is predicted to vary as,

$$N \propto [R]M^b \quad (1)$$

where $[R]$ is the concentration of the limiting resource, M is the species body size, and b is the size scaling exponent (slope) that takes a value near –3/4. This is the theoretical framework of a resource-based model that assumes that a given amount of resources may satisfy the metabolic demands of many small-sized organisms or a few larger ones (Damuth 1981; Peters 1983; Enquist et al. 1998). Equation 1 thus assumes that (1) individual metabolism is fueled by resources available in the environment, (2) resources are partitioned equitatively among coexisting species, and (3) all organisms use a common source of resource (inorganic nutrients for phytoplankton). According to this, Eq. 1 predicts higher population abundances as resource availability increases, but the size scaling exponent of population abundance is expected to remain constant.

Previous works have investigated the relationship between total abundance or biomass and cell/body size, spanning from small picoplankton cells to large mesozooplankters (i.e., Li 2002; Irwin et al. 2006; San Martín et al. 2006). These studies point to a relatively consistent pattern with a size scaling exponent (b parameter) in the range –0.75 to –1.2. However, these analyses account not only for variations in population abundances but also for changes in species richness along the community size spectrum. Furthermore, in many cases, different trophic levels are included in the analysis. Given that there is a loss of energy across different trophic levels (i.e., from phytoplankton to zooplankton) (Lindeman 1942), these studies are not strictly comparable to those in which only population abundances and a single trophic level are approached.

Additionally, macroecological analyses offer clues to underlying mechanisms that constrain ecosystem complexity, and hence biodiversity (Blackburn et al. 1990; Brown 1995). Typically, the relationship between productivity and biodiversity is described by monotonic or unimodal functions (Ricklefs and Schluter 1993). In this regard, we would expect an increase in the number of biological species in environments characterized by high or intermediate levels of productivity, and thus resource supply. Here, we test these predictions by analyzing the relationship between population abundance and cell size, as well as the species richness of phytoplankton assemblages, across highly contrasting marine environments.

Material and methods

Data collection—We compiled data on nano- (2–20 μm of equivalent spherical diameter [ESD]) and microphytoplankton (>20 μm ESD) assemblages, in terms of species composition, abundance, and cell size, from a variety of marine environments covering subtropical to coastal waters. These environments were the Ría de Vigo, Spain (n = 150), the coast off Coruna, Spain (n = 932), the Atlantic Iberian shelf (n = 50), the English Channel (n = 451), the Baltic Sea (n = 957), the Bothnia Gulf (n = 211), Skagerrak/Kattegatt (n = 95), and four Atlantic meridional transects (AMT 1–4) from 48°N to 50°S in the Atlantic Ocean, which were partitioned into north temperate (35–48°N, n = 11), north subtropical (25–35°N, n = 14), upwelling systems (25°N–10°S, n = 30), south subtropical (10–35°S, n = 23), and south temperate (35–50°S, n = 29) according to their physical, chemical, and biological features. The combined data set spans approximately seven orders of magnitude in abundance and cell volume. Mean nitrate, chlorophyll *a* (Chl *a*) concentration, and primary production rate were in the range 0.05–>10 μmol L^{-1}, 0.5–>10 mg Chl *a* m^{-3}, and 1–>1,000 mg C m^{-3} d^{-1}, respectively. Additionally, we compared our results on the scaling of population abundance and cell size from natural phytoplankton assemblages with those obtained for chlorophytes and diatoms grown in nutrient-replete laboratory cultures.

Microscopic analyses—At each station, two replicate seawater samples were preserved, one with 1% buffered formalin (to preserve calcium carbonate structures) and the other with 1% final concentration Lugol's iodine solution. After sedimentation of a subsample for 24 h (Utermöhl's technique), cells were measured and counted with an inverted microscope. Cell volume was calculated by assigning different geometric shapes that were most similar to the real shape of each phytoplankton species. Finally, a mean cell volume was assigned for each phytoplankton species within each data set. Phytoplankton carbon biomass for each species was estimated from known relationships with cell volume (Strathmann 1967).

Data analyses—Mean population abundance for each individual species was calculated for each data set. Our purpose in this study was to investigate the effect of resource levels on the species limited by their rates of resource use. In this regard, we selected the most abundant species in each 0.1-log-cell-volume size class (referred to in the text as dominant species). These species conformed to the upper limit of the area defined by the relationship between population abundance and body size (Brown 1995) and, thus, were likely to be limited by the rate of resource supply. In every case, reduced major-axis regression analysis (regression model II) was applied to log-transformed values of abundance (y-axis, cells per mL) and cell volume (x-axis, μm^3). The resulting key parameters were the intercept (a) and slope (b) of the regression model, log [cell abundance (cells per mL)] = $a - b$ log [cell volume (μm^3)].

Photosynthesis rate—Photosynthesis was determined with the ^{14}C-uptake technique during simulated in situ incubations. After incubation, samples were filtered, using low-vacuum pressure (<100 mm Hg), through glass-fiber filters or polycarbonate filters (0.2 μm in pore size). Dark-bottle ^{14}C-activity was subtracted from light-bottle ^{14}C activity.

Diversity index—Species diversity was computed from the abundance and biomass data using the Shannon diversity index, $H' = -\sum_{i=1}^{k} \ln(p_i)p_i$, where p_i is the abundance or biomass of species i divided by the total abun-

dance or biomass of k species within each community (i.e., k includes all the species identified on each sample). This index reflects species richness S (number of species), evenness ($H'/\log[S]$), and their intercorrelations, and it is considered the best measure of their joint influence.

Results and discussion

Scaling patterns of population abundance and cell size—The population abundance of phytoplankton was a decreasing power function of cell volume (Fig. 1; *see also* Table 1). In all cases, cell volume accounted for a significant amount of variability in population abundance (Table 1). Although we focused our analysis on dominant phytoplankton species (i.e., those limited by the rates of resource supply; *see* Methods), the scaling of population abundance, including all identified species within each ecosystem, was also a decreasing power function of cell volume (Fig. 2). In this case, the relationship was best depicted by a polygonal area in which the upper limit was made up by the dominant species, whereas the lower limit was composed of a number of rare species, the abundances of which are not well understood yet. Because our main purpose was to investigate the allometric scaling of population abundance for species limited by the rates of resource supply, we further analyzed the statistical parameters (slope and intercept) derived from the relationship between population abundance and cell size (on a logarithmic scale) of dominant phytoplankton species. The slope of this relationship measures the change in population abundance expected from a unit change in log cell volume, and it can be used as an index of the relative abundance reached by species of different sizes. On the other hand, the intercept can be used to compare the average population abundance between different ecosystems whenever slopes are identical. Our statistical analyses indicated that, spanning highly contrasting marine environments, the slope was not significantly different from $-3/4$ (t-test, $\alpha = 0.05$, $p > 0.05$; Table 1) despite the well-known biophysical constraints of larger species under resource limited conditions (Chisholm 1992; Finkel et al. 2004; Irwin et al. 2006). In contrast, the regression intercept increased by more than two orders of magnitude from oligotrophic, open-ocean waters to eutrophic coastal waters (Fig. 1; Table 1). In this context, previous work in lakes has shown that the regression intercept increases in concert with lake productivity, which can be regarded as a surrogate of resource levels (Cyr et al. 1997). Consequently, we analyzed the relationship between the regression intercept and the average nutrient concentration (dissolved inorganic nitrogen [DIN]), plotting together all analyzed environments. As

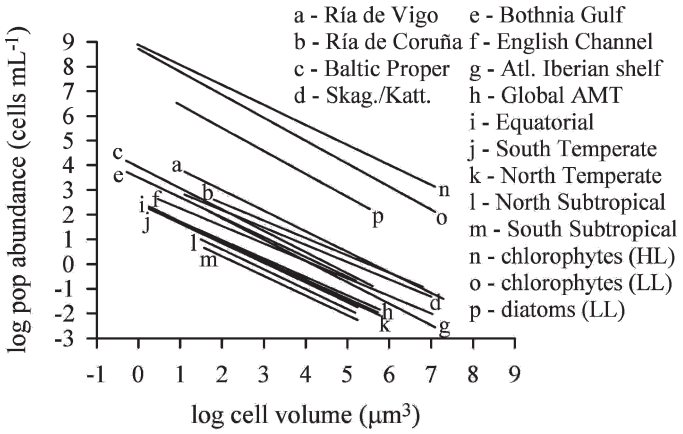

Fig. 1. Best fits to data for the relationship between log population abundance and log cell volume of dominant phytoplankton species from different marine environments and from species grown under nutrient-replete laboratory conditions. HL and LL are for laboratory-cultured populations grown under high-light and low-light conditions, respectively. Relationships for chlorophytes were taken from Agustí and Kalff (1989), and the relationship for diatoms was built up from data taken from Finkel (1998).

Table 1. Statistical parameters for the relationship between log population abundance and log cell volume of phytoplankton from different marine environments. Intercept and slope were obtained using reduced major-axis regression analysis since population abundance and cell size were both measured with error. Confidence limits (95%) for the intercept and slope are given in parentheses. Statistical differences among regression parameters can be assumed whenever confidence intervals do not overlap; n is number of species included in the regression; R^2 is the determination coefficient of the regression of population abundance on cell size; p values from two-tailed t-tests indicate differences of the experimental slope relative to the -0.75 expected value at the 0.05 significance level.

Data set	Intercept	Slope	R^2	n	p value
Ría de Vigo	4.65 (3.86, 5.44)	−0.83 (−1.01, −0.65)	0.53	42	0.379
Coast off Coruna	3.87 (3.35, 4.39)	−0.70 (−0.83, −0.58)	0.74	36	0.187
Baltic proper	3.93 (3.58, 4.27)	−0.86 (−0.97, −0.75)	0.82	46	0.054
Skagerrak/Kattegatt	3.56 (3.03, 4.09)	−0.70 (−0.83, −0.56)	0.62	43	0.461
Bothnia Gulf	3.50 (3.09, 3.92)	−0.80 (−0.94, −0.66)	0.67	45	0.484
English Channel	2.97 (2.65, 3.29)	−0.71 (−0.79, −0.63)	0.83	54	0.335
Atlantic Iberian shelf	3.59 (2.96, 4.22)	−0.87 (−1.02, −0.72)	0.73	40	0.103
AMT global	2.47 (2.15, 2.80)	−0.75 (−0.84, −0.66)	0.81	52	0.986
North temperate	2.45 (2.03, 2.87)	−0.77 (−0.88, −0.65)	0.80	37	0.734
North subtropical	2.20 (1.76, 2.64)	−0.81 (−0.93, −0.68)	0.80	35	0.349
Equatorial	2.53 (2.03, 3.03)	−0.81 (−0.96, −0.67)	0.70	40	0.411
South subtropical	1.92 (1.49, 2.34)	−0.80 (−0.92, −0.68)	0.80	37	0.410
South temperate	2.44 (2.01, 2.86)	−0.80 (−0.93, −0.67)	0.76	39	0.442

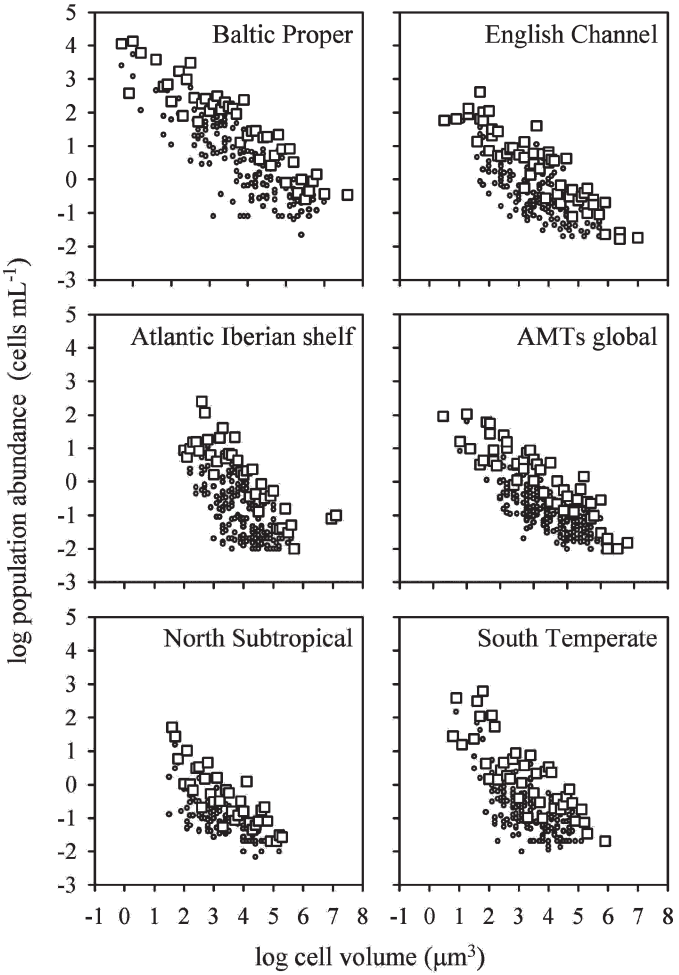

Fig. 2. Examples of the relationship between log population abundance and log cell volume for all identified species within each ecosystem. Each data point represents one species. Open squares highlight dominant species.

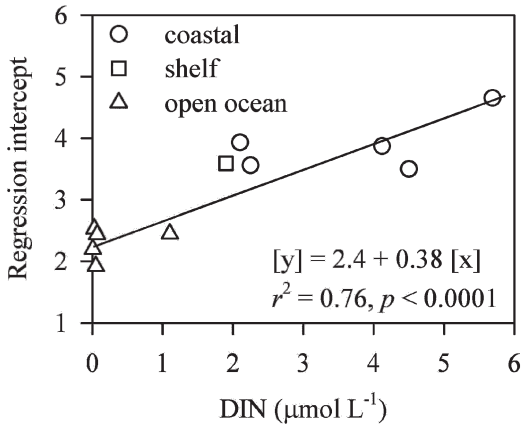

Fig. 3. Dissolved inorganic nitrogen concentration [DIN] versus the regression intercept of the relationship between log population abundance and log cell volume across coastal, shelf, and open-ocean environments.

expected, the regression intercept increased consistently with increasing DIN concentration, highlighting important changes in population dynamics in response to resource availability (Fig. 3). Our analysis assumes that nitrogen limits phytoplankton growth. However, other nutrients, including phosphate or iron, may limit phytoplankton growth over vast areas in the ocean. Further research must include the impacts of other limiting nutrients on macroecological patterns of marine phytoplankton abundance and growth.

The uppermost limit to the abundance of phytoplankton populations is attained using monospecific cultures under optimal resource conditions such as those simulated in the laboratory. Figure 1 shows the population abundance attained by phytoplankton species in natural samples and those cultured under nutrient-replete laboratory conditions. Again, we observed up to eight orders of magnitude of difference in the regression intercept from populations inhabiting subtropical environments to populations cultured under nutrient-replete laboratory conditions, but each had rather similar slopes. Typically, the relationship between population abundance and body size is explained in terms of the ways in which individual organisms acquire and use resources as a function of their body size. Previous works have reported striking variations in the relationship between metabolism and cell size in phytoplankton as a result of resource limitation or taxonomic differences in resource acquisition (Finkel et al. 2004; Cermeño et al. 2005; Marañón et al. 2007). For instance, it is well known that, despite their large volume, diatoms may grow faster than small cyanobacteria in unstable coastal environments. In contrast to this, the consistency of the −3/4-power exponent of population abundance reported in this study points to the operation of an overall −3/4-power rule for phytoplankton metabolism. Discrepancies between these results and previous metabolism-size spectra reported for natural phytoplankton assemblages could be related to size-dependent cell losses (respiration, sedimentation, grazing) or differences in net growth efficiencies associated with variations in taxonomic composition.

Scaling patterns and the diversity of marine phytoplankton—Assuming that resources are partitioned among coexisting species, for a given amount of resources, an increase in species richness should lead to lower population abundances (Blackburn et al. 1990). In this regard, any variability in species richness across ecosystems could bias the interpretation of the statistical parameters derived from the relationship between population abundance and cell size. However, the number of phytoplankton species across different marine ecosystems was largely indistinguishable despite different environmental resource conditions (Fig. 4A). Given that, on average, the population abundances increased over two orders of magnitude from subtropical to coastal regions, these results imply that large-scale (biogeographic) variations in phytoplankton standing stocks are largely controlled by changes in population abundances rather than by systematic variations in species richness.

Our analyses point to important findings concerning marine phytoplankton diversity. Diversity–productivity

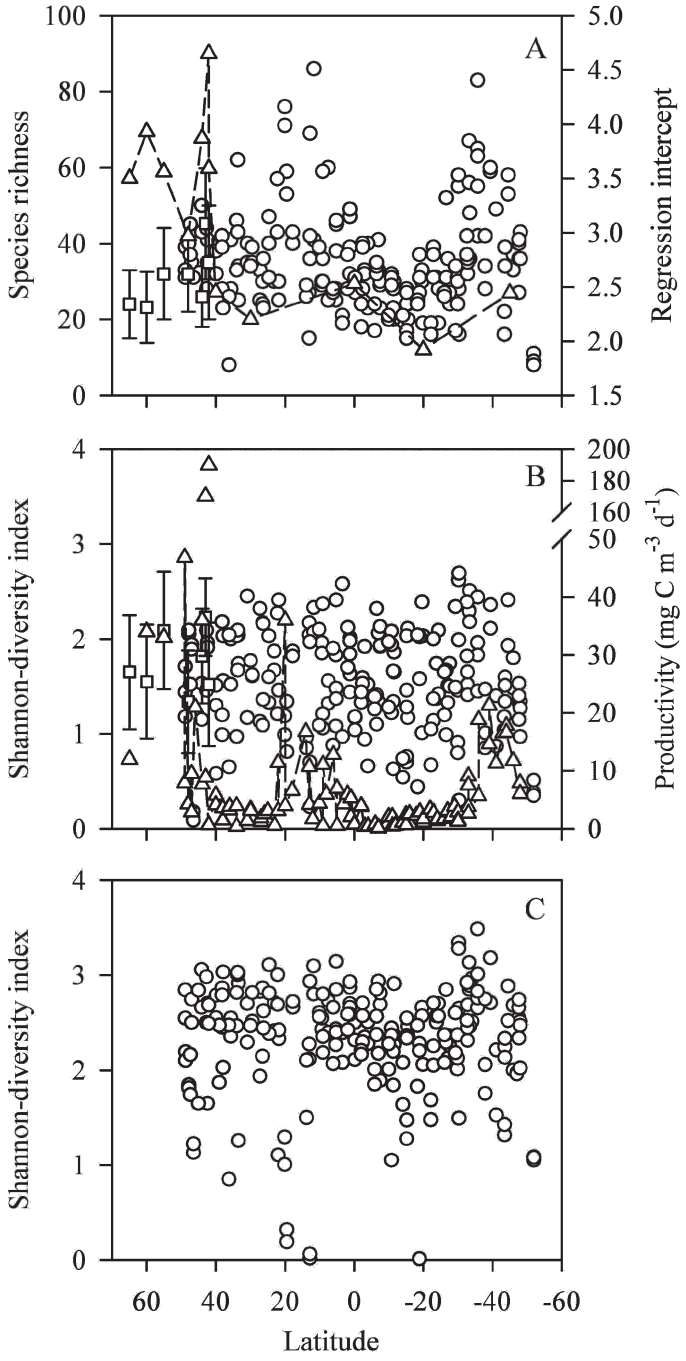

Fig. 4. Phytoplankton diversity from 65°N to 50°S expressed as (A) number of species, (B) Shannon diversity index obtained from abundance estimates for AMTs (circles), and the Ría de Vigo, the Atlantic Iberian shelf, coast off Coruña, the English Channel, Skagerrak/Kattegatt, the Baltic proper, and the Bothnia Gulf (squares), and (C) Shannon diversity index obtained from biomass estimates for the AMTs. Error bars indicate standard deviation. Shown superimposed on panels are (A) the regression intercept of the relationship between population abundance and cell volume for each data set (triangles), and (B) phytoplankton productivity at surface (in units of mg C m^{-3} d^{-1}) for the AMTs, the Ría de Vigo, the Atlantic Iberian shelf, coast off Coruña, the English Channel, Skagerrak/Kattegatt, the Baltic proper, and the Bothnia Gulf (triangles). Along the AMTs, the regression intercept for each defined biogeographic region is plotted at the middle latitude of that region. Productivity along the AMTs is binned in 1 degree of latitude.

relationships typically show monotonic or unimodal patterns with a higher number of species at high or intermediate levels of productivity, respectively (Ricklefs and Schluter 1993). When applied to marine phytoplankton, these patterns contrast with the classical view that biodiversity increases from poles to tropics (Gaston 2000), since at low latitudes in the ocean, where high temperatures induce strong and persistent water-column stratification, primary productivity is largely limited by nutrient supply (Falkowski et al. 1998). Our results, however, reveal that marine phytoplankton diversity does not show any consistent trend along either latitudinal or productivity gradients (Fig. 4B). Taking into account that smaller species attain much higher population abundances than their larger relatives, it is conceivable that the lack of diversity patterns may have resulted from the use of abundance estimates instead of biomass for the calculation of phytoplankton diversity. Our results, however, do not differ when diversity is calculated in terms of biomass (Fig. 4C). Thus, although phytoplankton diversity may respond to local variations in resource supply (Irigoien et al. 2004) (e.g., there are wide variations in phytoplankton diversity within our database; Fig. 4B), the lack of large-scale diversity patterns in marine phytoplankton suggests that these organisms are only minimally controlled by mechanisms operating over long temporal and spatial scales such as those that regulate the global biogeography of macroorganisms (Hillebrand and Azovsky 2001).

Our macroecological analyses are the result of integrating multiple ecological interactions and different hydrodynamical scenarios. However, our analysis is not able to capture time-resolving events (i.e., eddies, coastal upwelling, etc.), or particular short-term variability, which may play a critical role in controlling phytoplankton size structure within local plankton communities For instance, it is well known that due to their ability to store nutrients in large intracellular vacuoles and their high maximal uptake rates, episodic inputs of nutrients into the euphotic layer lead to the onset of massive diatom blooms, with comparatively small responses from small-sized phytoplankters, however. In this line, experimental work and modelling results indicate that, in nutrient-rich waters, larger cells may attain higher photosynthetic rates than those predicted by classical allometric models, which provide a physiology-driven mechanism to explain large cell dominance in eutrophic regions (Cermeño et al. 2005; Irwin et al. 2006; Marañón et al. in press).

Grazing or hydrodynamical forcing may also affect phytoplankton size structure within local plankton communities. Grazing is likely to affect larger species less severely. Whereas the biomass of small-sized species is tightly controlled by microzooplankton, large phytoplankton are grazed by mesozooplankters, which have longer

generation times than those of phytoplankton. Consequently, the temporal decoupling between large-sized phytoplankton and mesozooplankton allows larger cells to proliferate whenever nutrient concentrations and light intensities stay high (Kiørboe 1993). Likewise, the upward water flow associated with eddies or upwelling events can counterbalance the sinking of larger and heavier cells, thus increasing their residence time in the euphotic layer (Rodriguez et al. 2001). Strikingly, despite the fact that different factors may be in operation, our analysis reveals simple macroecological patterns underlying the structure and functioning of marine plankton communities over large spatial scales (*see also* Cermeño et al. 2006).

Emergent properties of marine pelagic ecosystems may provide new insights into the ecological functioning of microbial communities. Common biophysical rules that occur in virtually all taxa and kinds of environments dictate the way in which resources are partitioned among individuals (Peters 1983; Brown et al. 2004). Here, we have shown that over spatial and temporal scales relevant for macroecological processes, a simple linear relationship may describe the mechanistic connection between nutrient availability and population abundance. However, despite the fact that all life forms share common resource partitioning rules, our analyses reveal particular features underlying the (macro)ecological structure of marine phytoplankton assemblages. For instance, the lack of large-scale diversity patterns across latitudinal and productivity gradients contrasts strikingly with the overall trends reported mainly for vascular plants and animals. We speculate that these particular features might result from the special nature of microbial plankton communities characterized by great dispersal capabilities, high patch connectivity, chaotic biological interactions (Huisman and Weissing 1999), short generation times (Falkowski et al. 1998), and a high frequency of environmental reset (Sommer 1985; Dolan 2005). For instance, a bloom of a phytoplankton species can develop and disappear in a matter of days, compared to the decades needed for the dominance of a terrestrial woody plant (Dolan 2005). Thus, our findings suggest that the global-scale diversity patterns of microbial plankton communities are likely to be regulated by mechanisms different from those that affect macroorganisms.

Previous works have indicated that microbial plankton communities are controlled by nonequilibrium mechanisms, which prevent the system from reaching steady-state conditions (Hutchinson 1961; Richerson et al. 1970; Huisman and Weissing 1999). The wide variability range in phytoplankton diversity within any given location and the lack of large-scale diversity patterns across either latitudinal or productivity gradients observed in this study suggest that nonequilibrium dynamics are likely to override the operation of global-scale mechanisms that shape phytoplankton diversity in the ocean (Harris 1986). Our study highlights the overall patterns that underlie the structure and functioning of marine phytoplankton communities over large spatial scales. Future macroecological analyses should be focused on the linkages among nutrient availability, population dynamics, and community size structure, and their interrelation to marine biogeochemical cycles.

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