Ecology Letters, (2006) **9**: 1210–1215 doi: 10.1111/j.1461-0248.2006.00973.x

LETTER

Invariant scaling of phytoplankton abundance and cell size in contrasting marine environments

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Abstract

Scaling relationships such as the variation of population abundance with body size provide links between individual organisms and ecosystem functioning. Previous work, in marine pelagic ecosystems, has focused on the relationship between total phytoplankton abundance and the assemblage mean cell size. However, the relationship between specific population abundance and cell size in marine phytoplankton has received little attention. Here, we show that cell size accounts for a significant amount of variability in the population abundance of phytoplankton species across a cell volume range spanning seven orders of magnitude. The interspecific scaling of population abundance and cell size takes a power exponent near −3/4. Unexpectedly, despite the constraints imposed on large phytoplankton by limited resource acquisition, the size scaling exponent does not differ between contrasting marine environments such as coastal and subtropical regions. These findings highlight the adaptive abilities of individual species to cope with different environmental conditions and suggest that a general rule such as the 'energetic equivalence' constrains the abundance of phytoplankton populations in marine pelagic ecosystems.

Keywords

Cell size, ecological invariant, energy equivalence, macroecology, phytoplankton, population abundance, resource acquisition.

Ecology Letters (2006) 9: 1210–1215

INTRODUCTION

There exists an inverse relationship between population abundance (N) and organism size (M), such that

$$N = aM^b, \tag{1}$$

where a is a proportionality factor and b takes a value near −3/4 (Damuth 1981; Marquet *et al.* 1990; Brown 1995; Enquist *et al.* 1998). This relationship has been explained in terms of how individual organisms acquire and use resources as a function of their size (Enquist *et al.* 1998). Typically, individual resource requirements scale to the 3/4 power of organism size (Peters 1983). Consequently, larger organisms, on account of their higher resource requirements, attain lower population abundances than their smaller relatives. Previous work, in marine pelagic ecosystems, has focused on the relationship between total phytoplankton abundance and the assemblage mean cell size (Belgrano *et al.* 2002; Li 2002). However, this relationship reflects not only the variations in population abundance, but also the changes in species richness along the size spectrum. Given that species richness is often a skewed log-normal function of body size (May 1988; Fenchel 1993), the size scaling of population abundance and that of bulk phytoplankton abundance are not directly comparable.

Phytoplankton cells rely exclusively on their surface area and cell cross-section to take up nutrients and absorb light respectively. Assuming the simplest case of a spherical cell, an increase in radius decreases: (i) solute exchange on a volume basis due to a thicker diffusion boundary layer and a lower number of plasma membrane transporters per volume unit (Raven 1998); and (ii) the optical absorption cross-section, an estimate of light absorption efficiency per unit pigment content (Morel & Bricaud 1981; Kirk 1994).

A well-established biophysical theory, based on the geometrical features of phytoplankton cells, describes the size dependence of resource acquisition under nutrient- and light-limiting conditions. Nutrient uptake (U) per unit cell volume (V) depends on nutrient diffusion to the cell surface (Fick's first law):

$$\frac{U}{V} = 4\pi r D\,\Delta C\left(\tfrac{4}{3}\pi r^3\right)^{-1} = 3D\,\Delta C\,r^{-2}, \tag{2}$$

where r is cell radius, D is the substrate diffusion coefficient and ΔC is the concentration gradient of nutrient from the cell surface to the concentration in the bulk media (Pasciak & Gavis 1974). Given that mass-specific resource requirements necessary to sustain vital rates are roughly proportional to the inverse of cell radius, large-sized species must be seriously constrained at low nutrient concentrations such as those characteristic of the subtropical gyres (Chisholm 1992; Kiørboe 1993; Raven 1998).

Likewise, theoretical predictions supported by a number of experimental reports suggest that larger phytoplankton are at a disadvantage over smaller cells under light-limiting conditions. Light absorption for a spherical cell can be expressed as:

$$a = a^* c_i V, \tag{3}$$

where a^* is the pigment-specific absorption cross-section (m^2 mg pigment^{-1}) and c_i is the intracellular pigment concentration. On theoretical grounds,

$$a^* = \frac{3}{2} a_s^* \frac{Q(\rho)}{\rho}, \tag{4}$$

where a_s^* is the optical absorption cross-section for photosynthetic pigments in solution, $Q(\rho) = 1 + [2 \exp(-\rho)]/\rho + 2[\exp(-\rho) - 1]/\rho^2$, and $\rho = 2a_s^* c_i r$ (see Morel & Bricaud 1981; Kirk 1994). It arises from these equations that the ratio a^*/a_s^* decreases with cell size giving rise to a reduction in the light absorption efficiency per unit pigment content (the so-called package effect), and consequently in the size scaling exponent of phytoplankton photosynthesis (Finkel *et al.* 2004).

Thus, in keeping with the assumption that the population abundance of a phytoplankton species is primarily controlled by nutrient uptake and light absorption, the theoretical basis above leads to the hypothesis that the size scaling exponent of population abundance becomes more negative under resource limitation. In the present study, we test this hypothesis by analysing the relationship between population abundance and cell size of phytoplankton in a variety of marine environments characterized by highly contrasting resource conditions. Additionally, we also discuss the possibility that differences in resource levels between ecosystems may be accompanied by concomitant shifts in the cell size of phytoplankton species.

METHODS

We used data of species composition, abundance and cell size in the range of nano- and microphytoplankton from samples collected in marine pelagic ecosystems. Four Atlantic Meridional Transects (AMTs 1–4) from 48° N to 50° S ($n = 221$ samples) were representative of open ocean environments. The AMTs were sampled during September to October 1995 (AMT-1), April to May 1996 (AMT-2), September to October 1996 (AMT-3) and April to May 1997 (AMT-4). The courses of these cruises crossed the same regions of the Atlantic ocean by a similar route. An extensive data set (11-years weekly sampling, 1992–2002) from a coastal station (L4-Plymouth) in the English Channel was also used ($n = 448$ samples). Previous works have reported nutrient concentrations and other hydrographic variables in these contrasting environments. For instance, whereas in the Plymouth L4 station nitrate concentrations are in the range 0.5 to > 10 μM (Irigoien *et al.* 2005), in the Atlantic subtropical gyres nitrate concentrations are usually < 0.5 μM (Marañón *et al.* 2000). These differences in nutrient concentrations are consistent with a higher chlorophyll *a* concentration in the coastal station (0.5–9 mg Chl *a* m^{-3}) than in the Atlantic subtropical gyres (<0.5 mg Chl *a* m^{-3}). To further constrain variability in environmental conditions, the AMT data set was partitioned into different regions according to their physical, chemical and biological features (Marañón *et al.* 2000). We differentiated five oceanographic regions, namely, North Temperate (35–48° N), North Subtropical gyre (25–35° N), Upwelling (25° N–10° S), South Subtropical gyre (10–35° S) and South Temperate (35–50° S). A total of 11, 14, 30, 23 and 29 sites were sampled for North Temperate, North Subtropical gyre, Upwelling, South Subtropical gyre and South Temperate respectively. Water samples were collected from 7-m depth and from the bottom of the euphotic layer along the AMTs, whereas only samples from surface were obtained in the case of the L4 station. 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 at the species level with an inverted microscope at × 187, × 375 and × 750 magnifications in order to cover the whole photoautotrophic community encompassing the nano- and microphytoplankton size ranges. The volume of water samples used for sedimentation varied between 50 and 256 mL, according to the overall abundance of phytoplankton as shown by the fluorometer. At least 100 cells of each of the more abundant species were enumerated. 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.

Mean population abundance for each species was calculated for each data set in order to limit the variability associated with particular situations (e.g. blooms) and thus to obtain population abundance estimates with macroecological meaning. Moreover, our purpose in this study was to verify the effect of resource levels on the slope and intercept of the size scaling of population abundance for 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. These maximum population abundances conform to the upper limit of the abundance–body size constraint space defined in macroecology (Lawton 1990; Brown 1995). The upper limit of the population abundance-body size constraint space is, by definition, made up by the most abundant species along the size spectrum, and presumably, those species limited by their rates of resources (or energy) use. Below this upper boundary, there exists a number of rare (less abundant) species that, ultimately, conform to the lower boundary of the population abundance–body size constraint space, and whose occurrence is poorly understood.

RESULTS

Figure 1 shows the population abundance of the most abundant phytoplankton species on each size class plotted against cell size for station L4 in the English Channel and for the entire AMT data set. In both cases, phytoplankton cell size explained a significant amount of variability in population abundance [$F(\mathrm{L4})_{1,53} = 258.67$, $F(\mathrm{AMT})_{1,51} = 218.21$, $P < 0.0001$, see Table 1]. Reduced major axis regression analyses gave slopes of −0.71 and −0.75 for the English Channel and the AMTs respectively. We were particularly interested in determining if there were differences in the numerical value of the slopes between contrasting resource environments. Statistical analysis indicated that the slopes were not significantly different [test for the homogeneity of regression slopes, $F_{1,103} = 0.25$; $P = 0.615$], suggesting that the size scaling of population abundance was not particularly affected by environmental resource conditions. On the contrary, the regression intercept obtained from the English Channel data set was significantly higher than that obtained from the AMTs [analysis of covariance, $F_{1,103} = 45.01$; $P < 0.0001$], which, in agreement with previous works in lakes (Cyr *et al.* 1997), indicates that, overall higher population abundances occurred in the coastal ecosystem, most likely as a result of a higher resource supply. It is also noteworthy that the size range of observed species reached larger cell sizes in the coastal ecosystem, which again is likely to reflect differences in resource availability.

To further constrain variability in environmental conditions and focus our analysis on particular marine ecosystems, we analysed the interspecific scaling of population abundance and cell size from different oceanographic regions along the AMTs. In this case, only surface samples were used in the analysis in order to test the effect of nutrient availability. Additionally, light limitation was assessed using population abundances from samples collected at the bottom of the euphotic layer (*c.* 1% optical depth) throughout the AMTs. Figure 2 shows the relationship between population abundance and cell size for a variety of ocean regions, covering temperate to equatorial latitudes. The size scaling exponent of population abundance ranged from −0.77 to −0.81, and in every case this regression slope was not significantly different from −0.75 (two-tailed *t*-test, $P > 0.3$, $\alpha = 0.05$; see Table 1). The regression intercept showed higher values in more productive, temperate and upwelling regions, whereas lower values were obtained at the bottom of the euphotic layer and in the oligotrophic gyres. In general, most of the residual variation around the linear model can be attributed to variation in resource levels, and thus productivity, within each particular environment.

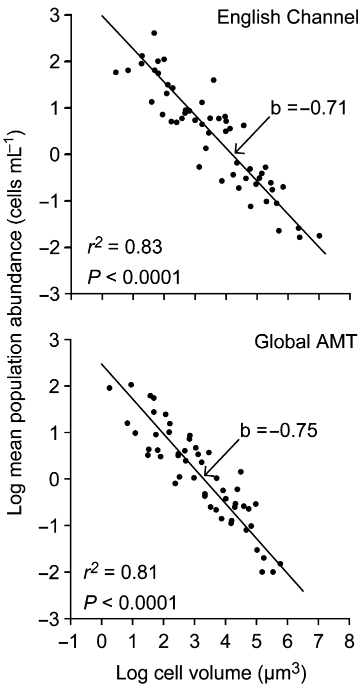

Figure 1 Relationship between log mean population abundance and log cell volume of phytoplankton species from the English Channel and the Atlantic Meridional Transects. Each data point represents the most abundant species in each size class of width 0.1 log cell volume.

DISCUSSION

Low nutrient concentrations and light-limited conditions are regarded as important evolutionary forces that select against large phytoplankton species in marine pelagic ecosystems (Chisholm 1992; Kiørboe 1993). This probably accounts for the paucity of large phytoplankton in unproductive regions of the ocean, where the bulk of biomass and primary production is mainly accounted for by smaller cells (Chisholm 1992; Li 2002). Nevertheless, large-sized phytoplankton

Table 1 Statistical parameters for the relationship between log population abundance and log cell volume from different marine environments

Data set	*n*	r^2	Intercept	Slope	*P*-value
English Channel	54	0.83	2.97 (2.66 to 3.31)	−0.71 (−0.79 to −0.64)	0.33
Global AMT	52	0.81	2.47 (2.16 to 2.78)	−0.75 (−0.83 to −0.67)	0.99
North Temperate	37	0.80	2.45 (2.03 to 2.87)	−0.77 (−0.89 to −0,65)	0.73
North Oligotrophic	35	0.79	2.20 (1.75 to 2.58)	−0.81 (−0.91 to −0.69)	0.35
Upwelling	40	0.71	2.53 (2.03 to 3.03)	−0.81 (−0.96 to −0.69)	0.36
South Oligotrophic	37	0.80	1.92 (1.49 to 2.34)	−0.80 (−0.92 to −0.67)	0.41
South Temperate	39	0.76	2.44 (2.01 to 2.92)	−0.79 (−0.93 to −0.67)	0.48
Bottom waters	48	0.86	2.42 (1.89 to 2.66)	−0.78 (−0.85 to −0.69)	0.55

AMT, Atlantic Meridional Transect; *n* is number of species included in the regression; r^2 is the determination coefficient of the regression of population abundance on cell size. Intercept and slope were obtained using reduced major axis regression analysis, as population abundance and cell size were both measured with error. Bootstrap confidence limits (95%) for the intercept and slope are given in parentheses. *P*-values from *t*-test indicate differences of the experimental slope relative to the −0.75 expected value at the 0.05 significant level.

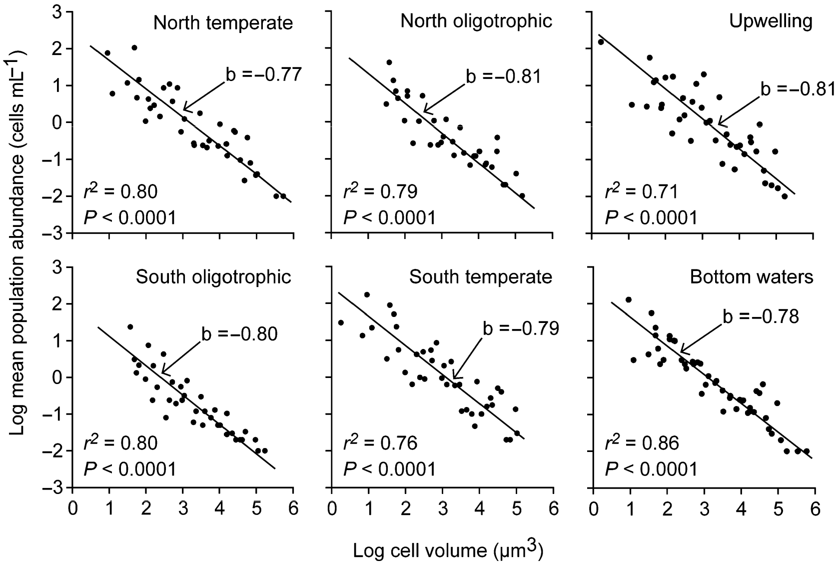

Figure 2 Relationship between log mean population abundance and log cell volume of phytoplankton species from different ocean regions along the Atlantic Meridional Transects. Each data point represents the most abundant species in each size class of width 0.1 log cell volume.

constitute a ubiquitous and persistent component of the autotrophic biota in these ecosystems, playing a key role in their ecological and biogeochemical functioning (Falkowski *et al.* 2004).

In her review on phytoplankton size, Chisholm (1992) wonders: 'Why are there any larger cells in the oligotrophic oceans at all?' However, a major question arises: are larger species inhabiting resource-limited environments at a disadvantage compared with smaller species? According to changes in the surface-to-volume ratio with varying cell size and its implications for resource acquisition, different size scalings of population abundance would be expected in contrasting resource environments. Our results, however, show a consistent −3/4-power size scaling exponent in all analysed environments (Figs 1 and 2). Remarkably, these results agree with an invariant size scaling exponent of population abundance by Chlorophyte species cultured in contrasting light conditions (Agustí & Kalff 1989). A number of adaptive strategies, previously reported in the literature, may play a role in satisfying the individual resource requirements by larger cells. These include variability in intracellular quotas and cell shape (Niklas 1994; Raven 1998; Thinsgtad *et al.* 2005), cell motility (Kiørboe 1993), nutrient storage (Raven 1998), alternative metabolic pathways such as N_2 fixation (Capone & Carpenter 1982), tradeoffs between pigment concentration and light absorption (Agustí 1991) and low photosystem I requirements (iron-rich complexes responsible for the transfer of photosynthetic electrons) in iron-poor environments (Strzepek & Harrison 2004). On this basis, our results suggest that large-sized phytoplankton species may have acquired a series of adaptive strategies that compensate for the competitive disadvantages arising from their larger cell size.

Biological species may allocate resources into many small-sized organisms or a few larger ones through tradeoffs between population abundance and body size. According to this, we considered the possibility that changes in the environmental resource conditions may have induced shifts not only in population abundances but also in the cell size of phytoplankton species. In this regard, we compared the relationship between population abundance and cell size obtained from the English Channel data set with that resulting from the AMTs. Our results indicated that the size range of observed species reached larger cell sizes in the coastal ecosystem. In principle, this may reflect the effect of resource levels on the species' cell size (i.e. an increase in the cell size of each particular species from open ocean to coastal ecosystems). However, a closer inspection of our data revealed that, in fact, differences in the size range covered by the phytoplankton assemblages were associated with variations in the taxonomic composition, which makes difficult to assess any shift in the species' cell size under different limiting conditions. In any event, we expect that shifts in cell size induced by differences in resource availability would affect the elevation rather than the slope of the relationship between population abundance and cell size.

Previous research indicates that carbon fixation or nitrogen and phosphorus subsistence quotas in phytoplankton relate to cell volume according to a power function with an exponent near 3/4 (Banse 1976; Shuter 1978; Blasco *et al.* 1982). Assuming that metabolic rates scale to the 3/4 power of organism size, a size scaling exponent of $-3/4$ for maximum population abundance implies that the upper limit to the amount of energy that each species can extract from the environment is not dependent on body size. This ecological invariant, previously reported in the literature for animals and vascular plants, is referred to as 'energetic equivalence rule' (Damuth 1981; Enquist *et al.* 1998) and suggests that similar evolutionary forces operate to determine the population abundance and cell size of phytoplankton species along the size spectrum.

Our starting hypothesis, based on the size dependence of resource acquisition, predicts a decrease in the size scaling exponent of population abundance under resource limitation. Other factors such as grazing pressure or hydrodynamics may also affect phytoplankton size structure within local plankton communities. For instance, grazing pressure is likely to affect larger species less severely. Large phytoplankton are grazed by mesozooplankters with larval stages, and thus, longer generation times than those of phytoplankton. Consequently, the temporal uncoupling between large-sized phytoplankton and mesozooplankton allows larger cells to proliferate whenever nutrient concentrations and light intensities keep high (Banse 1992; Kiørboe 1993). On the other hand, the upward water flow associated with mesoscale events can counterbalance the sinking of larger and heavier cells, thus increasing their residence time in the euphotic layer (Rodríguez *et al.* 2001). Strikingly, despite the fact that different factors may be in operation, our macroecological approach reveals an invariant size scaling pattern underlying the population abundance of dominant phytoplankton species across very different marine pelagic ecosystems.

According to our empirical model an increase in the supply of nutrients to the ecosystem gives rise to an increase in the elevation of the relationship between population abundance and cell size rather than to changes in the regression slope. This variability in the abundance–body size relationship, and therefore, in the energy flow along the size spectrum is likely to propagate toward upper trophic levels (Brown & Gillooly 2003; Ernest *et al.* 2003). Ultimately, incorporating macroecological analyses into nutrient–phytoplankton–zooplankton models may provide interesting insights into the ecological and biogeochemical functioning of marine pelagic ecosystems.

In summary, the results presented in this work indicate that large-sized phytoplankton species have evolved alternative strategies that compensate for the disadvantage of being larger, and allow them to meet their resource requirements. In addition, our findings suggest that, on ecological scales, a general rule such as that of 'energetic equivalence' may constrain the abundance of phytoplankton populations in the marine pelagial.

ACKNOWLEDGEMENTS

We thank all people who contributed to the collection of data. We also thank Susana Costas, Francisco G. Figueiras, John Marra, John A. Raven and Jaime Rodríguez for comments on the manuscript. P.C. was supported by postgraduate research fellowship from the Spanish Ministry of Science and Technology (MCYT). The research of R.P.H. is a contribution to the Plymouth Marine Laboratory Core Strategic Research Programme. AMT data collection was supported by the UK Natural Environmental Research Council through the Atlantic Meridional Transect consortium (NER/O/S/2001/00680). This is contribution number 143 of the AMT programme.

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Editor, Jim Elser
Manuscript received 14 August 2006
Manuscript accepted 17 August 2006