

Inter-specific scaling of phytoplankton production and cell size in the field

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This study tests the hypothesis that the interspecific scaling of phytoplankton production and cell size in the field follows the $\frac{3}{4}$ -power scaling law. Published data of cell size and in situ, cell-specific carbon production rates by single phytoplankton species, collected in surface waters of lakes, rivers, estuaries and oceans, are reviewed. Across more than nine orders of magnitude in cell volume, 98% of the variability in carbon production rates was explained by cell size. The slope (b) in the log–log relationship between carbon production rate and cell volume did not differ significantly from 1, either for diatoms ($b = 1.01$) or for dinoflagellates ($b = 0.89$). For all phytoplankton species considered together, which included also cyanobacteria and haptophytes, b took a value of 0.91, which is significantly higher than $\frac{3}{4}$. The observed nearly isometric scaling relationships between production rate and cell volume suggest that there is no relationship between phytoplankton growth rate and cell size. The present analysis confirms recent evidence showing that phytoplankton metabolism in natural conditions does not follow the $\frac{3}{4}$ -power scaling rule. It is argued that allometric models of plankton growth and metabolism should incorporate scaling parameters measured in situ on natural phytoplankton assemblages, rather than those obtained in the laboratory with monospecific cultures.

INTRODUCTION

General allometric models predict that, from microbes to the largest plants and animals, metabolic rate (R) scales with body mass or volume (M) according to the power equation:

$$R = aM^b$$

where a is a group-dependent coefficient and b , the size scaling exponent, tends to take a value of $\frac{3}{4}$ (the $\frac{3}{4}$ rule or Kleiber's rule) (Kleiber, 1947; Peters, 1983; West and Brown, 2005). If mass-specific metabolic rates or growth rates are considered, the corresponding scaling exponent, b' , is $b-1=-\frac{1}{4}$. Several models, based on the generic properties of transportation networks inside the organisms, have been proposed to explain the ubiquitous nature of these and other quarter-power allometric scaling laws (West *et al.*, 1997; Banavar *et al.*, 1999).

Regardless of the underlying mechanism, it is a solidly established observation that, within and across most taxonomic groups, larger organisms tend to have lower mass-specific metabolic rates than their smaller counterparts (Brown *et al.*, 2004; Savage *et al.*, 2004b).

In the case of phytoplankton metabolic rates, there is experimental evidence suggesting that departures from the general allometric rule are frequent. For instance, light limitation causes a reduction in the value of b for the rate of carbon fixation in diatoms (Finkel, 2001; Finkel *et al.*, 2004), because the pigment package effect has a stronger effect on larger species. Another type of deviation, frequently reported for phytoplankton, is that the size dependence of metabolism and growth is smaller than expected (e. g., $b > \frac{3}{4}$ or $b' > -\frac{1}{4}$), as shown for respiration rates (Tang and Peters, 1995) and growth rates (Banse, 1982; Sommer, 1989; Chisholm, 1992). As far as phytoplankton production is concerned, most evidence based on laboratory cultures does suggest that

Table I: Published values of the slope (b) in the log–log relationship between cell-specific carbon production and cell size in phytoplankton

Data origin	b	r ²	Technique	Reference
Laboratory cultures	0.53	0.86	¹⁴ C-uptake	Taguchi (1976)
Laboratory cultures	0.73	0.99	¹⁴ C-uptake	Blasco <i>et al.</i> (1982)
Laboratory cultures	0.57	0.92	¹⁴ C-uptake	Finkel (1998)
Laboratory cultures	0.75	0.99	Growth rates	Niklas and Enquist (2001)
Laboratory cultures	0.74	0.82	Growth rates	López-Urrutia <i>et al.</i> (2006)
Natural assemblages	1.03	0.91	¹⁴ C-uptake	Marañón <i>et al.</i> (2007)

b was calculated using reduced major-axis regression. In some studies, carbon production rate was determined as carbon fixation from ¹⁴C-uptake experiments, whereas in other cases it was determined from measured growth rates. All laboratory studies used cultures of single phytoplankton species. In the studies by Taguchi (1976), Blasco *et al.* (1982) and Finkel (1998), only diatoms were considered. In the other studies, species from different taxa were included.

b takes a value around $\frac{3}{4}$ or, at least, that it is significantly smaller than 1 (Table I). An extensive review of biomass production rates, including species spanning 20 orders of magnitude in body size from microalgae (cultured in the laboratory) to large trees, supports the universality of the $\frac{3}{4}$ -allometric rule for all photosynthetic organisms (Niklas and Enquist, 2001). In contrast, recent experimental work with natural phytoplankton assemblages indicates that carbon fixation scales approximately isometrically with cell size (Marañón *et al.*, 2007). The data shown in Table I suggest that the size scaling exponent for carbon production by natural phytoplankton assemblages in the field is significantly higher than that determined with laboratory cultures. This discrepancy can have important consequences, for both conceptual and practical reasons.

If the high *b* values measured in natural phytoplankton assemblages are confirmed, it would mean that a single size scaling rule cannot predict the metabolic rate of all photosynthetic organisms. The alleged universality of the $\frac{3}{4}$ -power rule would thus be seriously questioned, since phytoplankton account for nearly half of all primary production on Earth. In addition, the value of *b* is critical to understand the factors that control the size structure of planktonic communities. The implication of a *b* value well below 1 is that *b'* \ll 0 and, therefore, that smaller cells, on account of their much faster growth rates, should dominate all aquatic ecosystems. But nutrient-rich, productive waters are always characterized by a dominance of larger cells (Chisholm, 1992), which has been explained by the fact that smaller phytoplankton are more tightly controlled by grazing than larger cells (Kiørboe, 1993). However, the importance of this trophic factor may be smaller than

previously thought because, if *b* \sim 1 and *b'* \sim 0, large phytoplankton species may grow at least as fast as small ones. Finally, the choice of the size scaling exponent used may affect the predictions of size-based models of plankton structure and metabolic functioning, which so far have relied on parameters determined in laboratory cultures rather than in natural assemblages of phytoplankton.

Here, I review published data of cell size and carbon production rates by individual species in natural conditions, in order to test the hypothesis that the interspecific scaling of phytoplankton production and cell size in the field follows the $\frac{3}{4}$ -power law. The present analysis complements recent experimental measurements of the size scaling exponent of phytoplankton carbon fixation in oligotrophic and eutrophic marine waters (Marañón *et al.*, 2007). By using an independent data set of *in situ* carbon fixation and growth rates of individual species, I aim to determine if the previously observed deviation from the $\frac{3}{4}$ -power rule is confirmed, and to extend the analysis of the size scaling of phytoplankton metabolism to a wider range of aquatic ecosystems.

METHOD

The data used in the present analysis were all obtained from published reports on carbon fixation rates, growth rates and cell size of single phytoplankton species inhabiting surface waters of lakes, rivers, estuaries and oceans (see Appendices online at <http://plankt.oxford-journals.org>). Only data from samples collected in surface or near-surface waters (e.g. above the 50% PAR level) were considered, in order to minimize the effect of light limitation. In some studies, rates were measured under optimal light levels (e.g. under saturating irradiance during photosynthesis-irradiance experiments) or in nutrient-amended enclosures, in addition to ambient conditions. In these cases, only the maximum rates, measured at optimal light-levels and/or under increased nutrient conditions, were used. When several measurements of the same species were repeated over time at a particular location, the mean was calculated and used in subsequent analyses. However, if measurements of the same species were reported for different locations, data were handled separately. In this way, the original dataset, which included more than 200 measurements of *in situ* carbon fixation or growth rates, was reduced to 90 data points. The full dataset contains measurements of 51 species (see Appendix I online at <http://plankt.oxfordjournals.org>), including diatoms, dinoflagellates, haptophytes and cyanobacteria, and spans more than

nine orders of magnitude in cell volume and cell-specific carbon fixation rate.

In the studies used here, carbon fixation was determined with the ^{14}C -uptake technique during simulated *in situ* incubations or photosynthesis-irradiance experiments. Measuring the species-specific rate of carbon fixation requires that, after the incubation ends, cells of the species under study are isolated from the rest of the sample and assayed for ^{14}C activity using liquid scintillation counting. This separation can be performed under a dissecting microscope with a micropipette (Rivkin and Seliger, 1981) or, for smaller cells such as picophytoplankton, by using flow cytometric sorting (Li, 1994). When original carbon fixation data were given as hourly rates, daily rates were computed by multiplying by the duration of the photoperiod.

For the determination of *in situ* growth rates of individual phytoplankton species in natural assemblages, several techniques are available, including cell-cycle analysis (McDuff and Chisholm, 1982; Carpenter and Chang, 1988) and the monitoring of cell abundance during incubations in bottles or diffusion chambers under *in situ* temperature and irradiance conditions (Sommer, 1989; Furnas, 1990). While cell cycle analyses give an estimate of phytoplankton gross growth rate, not affected by mortality processes, incubations in containers yield estimates that approach net growth rates, to the extent that natural loss processes such as grazing may still occur during the experiments. However, in the only report of growth rates used here that was based on bottle experiments, dilution and pre-screening were used in order to minimize the presence of grazers in the experiments (Sommer, 1989). From the reported growth rates (μ , day^{-1}), carbon production rates (P , $\text{pg C cell}^{-1} \text{ day}^{-1}$) were calculated as follows:

$$P = (\text{base}^{\mu} - 1) \times C$$

where *base* is the logarithmic base used in the original calculations to compute growth rate and *C* is the cellular carbon content (pg C cell^{-1}) of the species. When, instead of *C*, cell volume (V , μm^3) was reported, the former was computed from the latter by using the relationship given by Montagnes *et al.* (Montagnes *et al.*, 1994):

$$C = 0.0109 \times V^{0.991}$$

Conversely, the same relationship was used to compute *V* when only *C* was reported. In the case of a few studies where neither *V* nor *C* was given (less than 10% of species), average cell dimensions were obtained

from other sources in the literature. Cell volume was then calculated from cell dimensions by taking into account the geometrical shape that most closely resembled that of the species in question (Sun and Liu, 2003).

Once all data had been collected, reduced major-axis regression was applied to \log_{10} -transformed variables in order to determine the parameters of the scaling relationship between carbon production and cell volume. The slope of the linear regression represents the size scaling exponent in the power equation relating carbon production rate to cell volume. Ninety-five percent confidence intervals for the regression parameters were calculated by bootstrapping over cases (2000 repetitions).

RESULTS

Cell size explained a high amount of variability in the carbon production rate of both diatoms and dinoflagellates, despite the fact that measurements were taken over a wide range of aquatic environments using varying experimental techniques (Fig. 1). For both groups, *b*, the exponent in the power relationship between carbon production and cell volume, was higher than the expected value of $\frac{3}{4}$. The value of *b* was not significantly different from 1, either for diatoms or for dinoflagellates (*t*-tests, $p > 0.2$) (Table II), indicating that

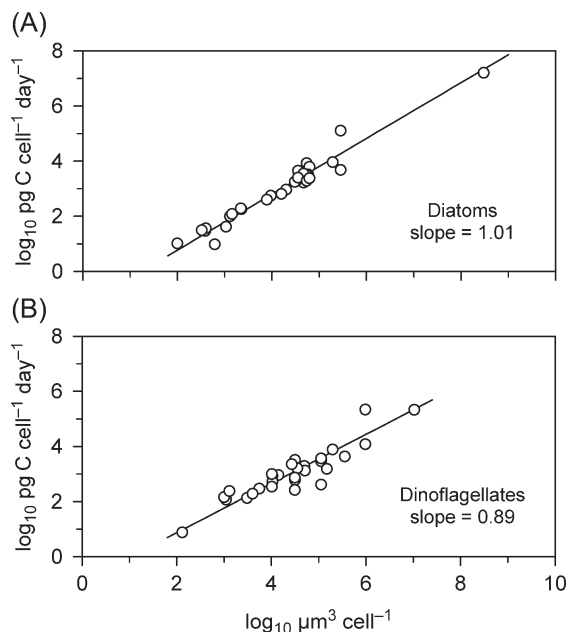


Fig. 1. Relationship between *in situ* cell-specific carbon production and cell volume for individual species of (A) diatoms and (B) dinoflagellates. See Table II for statistics.

Table II: Parameters of the reduced major-axis regression between \log_{10} cell volume (independent variable, $\mu\text{m}^3 \text{ cell}^{-1}$) and \log_{10} cell-specific carbon production (dependent variable, $\text{pg C cell}^{-1} \text{ day}^{-1}$) of single phytoplankton species in natural ecosystems

Data	<i>a</i>	<i>b</i>	r^2	<i>p</i>	<i>n</i>
Diatoms	-1.25 (-1.80, -0.88)	1.01 (0.91, 1.15)	0.93	<0.001	30
Dinoflagellates	-0.91 (-1.65, -0.23)	0.89 (0.73, 1.06)	0.83	<0.001	30
All species	-0.89 (-0.97, -0.81)	0.91 (0.88, 0.94)	0.98	<0.001	90

Limits of the 95% confidence intervals for the intercept (*a*) and the slope (*b*) are given in parentheses. *n* indicates that total number of cases in each analysis. Note that *n* is higher than the total number of species (see Appendix 1 online at <http://plankt.oxfordjournals.org>) because several measurements, conducted at different locations, were available for some species.

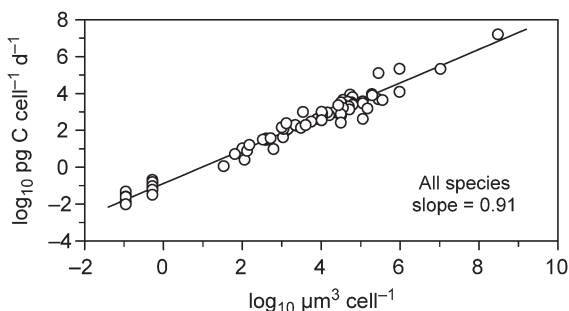


Fig. 2. Relationship between *in situ* cell-specific carbon production and cell volume for all individual species considered in this study. See Table II for statistics.

carbon production by these taxa in natural ecosystems scales isometrically with cell size. Diatoms showed a higher size scaling exponent (1.01) than dinoflagellates (0.89). However, comparison of the 95% confidence intervals revealed no significant differences in the scaling parameters between the two groups (Table II).

Considering all species together, 98% of the variability in individual production rates was explained by cell size (Fig. 2), which spanned more than nine orders of magnitude from *Prochlorococcus* ($0.11 \mu\text{m}^3 \text{ cell}^{-1}$) to *Ethmodiscus rex* ($3 \cdot 10^8 \mu\text{m}^3 \text{ cell}^{-1}$). The scarcity of data points in the cell size range $1\text{--}100 \mu\text{m}^3 \text{ cell}^{-1}$ reflects the experimental difficulties involved in identifying and measuring metabolic rates of single species of picoeukaryotes and small nanophytoplankton. The slope of the relationship between carbon production and cell size for the overall dataset was 0.91, which is significantly higher than $\frac{3}{4}$ and lower than 1 (*t*-tests, $p < 0.001$). Excluding the data for *Prochlorococcus* and *Synechococcus*, the overall slope became 0.97, which is significantly higher than $\frac{3}{4}$ (*t*-test, $p < 0.001$) and not significantly different from 1 (*t*-test, $p > 0.2$).

DISCUSSION

The present review shows that the cell size is a strong predictor of phytoplankton production rate across

widely contrasting environmental conditions and multiple taxonomic affiliations. From the smallest cyanobacteria to the largest diatoms, the species considered here differ in numerous properties, such as cellular ultrastructure, nutrient stoichiometry and pigment composition, and yet a single scaling model is able to predict their production rates across more than 9 orders of magnitude in cell volume. Phytoplankton cell size has been defined here as cell volume rather than cell biomass (e.g. carbon), in order to avoid the additional uncertainty involved in converting cell volume to cell carbon. Had cell size been expressed as carbon, the resulting scaling exponents would have taken a higher value. The magnitude of this effect would depend on the particular conversion equation used to compute cell carbon from cell volume. These equations take the form:

$$C = cV^d$$

where *C* is cell carbon, *V* is cell volume, *c* is a coefficient and *d* is the size scaling exponent for cell carbon content. In most empirical relationships between *C* and *V*, *d* takes a value below 1 (see review in Menden-Deuer and Lessard, 2000), which means that expressing cell size as cell carbon on Figs 1 and 2 would result in even steeper slopes. The observed isometric scaling relationship between production rate and cell volume suggests that the relationship between C-specific production rate and cell size will have a slope close to zero, indicating lack of size dependence in growth rates.

A potential problem of allometric analyses involving different taxonomical groups is that each group may be characterized by different scaling relationships (for instance, they may have different values of the coefficient *a* while having the same value of the exponent *b*). In this situation, fitting a single line through the overall dataset will yield a misleading value for the slope *b* (Martin *et al.*, 2005). In the present case, however, both diatoms and dinoflagellates, the best represented groups in the overall dataset, have high slopes—in both cases

not significantly different from 1. It can be concluded that the high value of the size scaling exponent for phytoplankton production rate, which deviates significantly from the $\frac{3}{4}$ -power rule, is not an artefactual result of data processing.

The high values of the size scaling exponent for production rate confirm recent measurements which indicated that the size scaling of phytoplankton photosynthesis in the ocean is approximately isometrical (Marañón *et al.*, 2007). A likely explanation for this departure from the $\frac{3}{4}$ -power rule lies in the existence of several strategies that allow larger phytoplankton to overcome the geometrical constraints imposed by cell size on resource acquisition (Chisholm, 1992; Raven, 1998). Elongated or prolate cell shapes, the presence of the vacuole, the ability to store nutrients intracellularly and the capacity to migrate vertically in the water column, among other characteristics, may allow large species to sustain comparatively high rates of resource use, biomass production and population growth. In this connection, it has recently been hypothesized that diatoms have increased their size partly by accumulating non-limiting cellular components while at the same time optimizing nutrient uptake (Thingstad *et al.*, 2005). Numerous *in situ* observations indicate that microphytoplankton in general, and diatoms in particular, can sustain higher biomass-specific production rates (Hashimoto and Shiomoto, 2002; Cermeño *et al.*, 2005a, 2005b; Claustre *et al.*, 2005) and growth rates (Strom and Welschmeyer, 1991; Latasa *et al.*, 2005) than pico- and nano-phytoplankton.

The question then arises as to what explains the discrepancy between laboratory and field studies regarding the size scaling of phytoplankton metabolism and growth. One factor that needs to be taken into account is that laboratory conditions are typically constant, while those in natural ecosystems change continuously, thus making balanced-growth unlikely (Berman-Frank and Dubinsky, 1999). It has been shown that larger phytoplankton can outcompete smaller species under conditions of variable nutrient supply (Stolte *et al.*, 1994) and fluctuating light availability (Mitrovic *et al.*, 2005), whereas the opposite occurs in more stable environments. Other strategies which may contribute to explain the metabolic performance of larger cells *in situ*, such as vertical migration, are obviously unlikely to represent an advantage in small-volume laboratory cultures. An additional reason for the discrepancy is that laboratory studies typically include a relatively small number of species belonging to a few divisions, and thus may not reflect the taxonomical diversity of natural phytoplankton assemblages. Whatever the causes for the different size scaling patterns found in laboratory cultures versus

natural phytoplankton assemblages, future efforts to construct size-based models of phytoplankton dynamics and metabolism should try to incorporate field measurements of the relevant scaling parameters, determined on natural assemblages, instead of relying on parameters obtained in the laboratory with monospecific cultures.

The observation of an isometric or near-isometric scaling relationship between phytoplankton metabolic rate and cell size has several implications for our understanding of the factors that control phytoplankton size structure in aquatic ecosystems. At the trophic ecology level, it suggests that size-dependent grazing pressure may not be such a relevant mechanism to explain the dominance of larger cells in eutrophic waters (Kjørboe, 1993). Recent modelling results also suggest that physiological responses alone may be sufficient to explain the dominance of picophytoplankton in oligotrophic environments and the increased abundance of larger cells as nutrient availability increases (Irwin *et al.*, 2006). The fact that large phytoplankton can sustain rates of production and growth as high as, or even higher than, those of small cells (Cermeño *et al.*, 2005a, 2005b; Claustre *et al.*, 2005; Marañón *et al.*, 2007) has also biogeochemical implications, because larger cells are responsible for most of the export of biogenic carbon towards the deep ocean and upper trophic levels (Legendre and Rassoulzadegan, 1996).

The interspecific scaling of population abundance in marine phytoplankton scales invariantly as the $-\frac{3}{4}$ -power of cell size, regardless of the environmental conditions (Cermeño *et al.*, 2006). Is it possible to reconcile the $-\frac{3}{4}$ size scaling of population abundance with the near-isometric size scaling of phytoplankton production reported here? The common $-\frac{3}{4}$ -scaling relationship between population abundance and body size has been suggested to arise from a $\frac{3}{4}$ -scaling relationship between metabolic rate and cell size (Enquist *et al.*, 1998). The argument can be summarized as follows: assuming that the rate of resource use (U) is proportional to metabolic rate (R), and given that the number of individuals (N) that can be sustained by a given amount of resources (S) is SU^{-1} , it follows that, if $R \propto M^{3/4}$, then $N \propto M^{-3/4}$. This argument, however, assumes that species live in separate environments with identical resource supply rates or that coexisting species use the same fraction of all available resources (Savage *et al.*, 2004a). These assumptions are not applicable to planktonic communities, where the species with higher mass-specific rates of resource use will sustain higher growth rates and therefore increase their abundance at the expense of other species. Therefore, the reciprocal size scaling pattern for metabolism (R) and abundance (N), whereby $R \propto M^b$ and $N \propto M^{-b}$, is unlikely to apply

to phytoplankton. In fact, it has been recently shown that the size scaling exponent for phytoplankton photosynthesis takes a higher value in eutrophic, coastal waters (1.14) than in the oligotrophic open ocean (0.96), while at the same time the size scaling exponent for phytoplankton abundance takes a *less* negative value in eutrophic ecosystems (-0.90) than in oligotrophic ones (-1.25) (Marañón *et al.*, 2007). This observation is the opposite of what is predicted by the reciprocal size scaling pattern for metabolism and abundance (Enquist *et al.*, 1998).

It thus seems that the size scaling of phytoplankton metabolism cannot be readily translated into a given relationship between abundance and cell size, and that additional processes must be considered. For instance, larger cells are likely to suffer comparatively higher loss rates through sedimentation, which could shift the abundance size spectrum towards more negative slopes. The opposite effect may result if smaller cells suffer higher relative loss rates through exudation or grazing. All these scaling relationships are likely to be regulated by additional factors such as temperature (Montagnes and Franklin, 2001 and references therein) and, particularly, resource availability (Finkel, 2001; Finkel *et al.*, 2004; Marañón *et al.*, 2007). Future studies should aim to determine the *in situ* scaling relationships between phytoplankton cell size and other relevant rates, such as nutrient uptake, light absorption, respiration, exudation, cell lysis, sedimentation and grazing, in order to build realistic allometric models based on ground-truth scaling parameters.

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SUPPLEMENTARY DATA

Supplementary data can be found online at <http://plankt.oxfordjournals.org>

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