

Increasing importance of small phytoplankton in a warmer ocean

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Abstract

The macroecological relationships among marine phytoplankton total cell density, community size structure and temperature have lacked a theoretical explanation. The tiniest members of this planktonic group comprise cyanobacteria and eukaryotic algae smaller than 2 µm in diameter, collectively known as picophytoplankton. We combine here two ecological rules, the temperature–size relationship with the allometric size-scaling of population abundance to explain a remarkably consistent pattern of increasing picophytoplankton biomass with temperature over the –0.6 to 22 °C range in a merged dataset obtained in the eastern and western temperate North Atlantic Ocean across a diverse range of environmental conditions. Our results show that temperature alone was able to explain 73% of the variance in the relative contribution of small cells to total phytoplankton biomass regardless of differences in trophic status or inorganic nutrient loading. Our analysis predicts a gradual shift toward smaller primary producers in a warmer ocean. Because the fate of photosynthesized organic carbon largely depends on phytoplankton size, we anticipate future alterations in the functioning of oceanic ecosystems.

Keywords: allometric relationships, cell abundance, cell size, North Atlantic, ocean warming, phytoplankton, picophytoplankton, temperature

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Introduction

Picophytoplankton are photosynthetic unicellular organisms in the 0.2–2 µm size range that are found throughout the world's oceans. They comprise cyanobacteria of the genera *Synechococcus* and *Prochlorococcus* (Partensky *et al.*, 1999) together with a diverse ensemble of eukaryotic algae (Moon-van der Staay *et al.*, 2001; Not *et al.*, 2007). Picophytoplankton cells have a ubiquitous distribution and contribute significant portions of bulk phytoplankton biomass and production (Agawin *et al.*, 2000; Bell & Kalff, 2001). The accepted view poses them as the dominant primary producers in vast areas of oligotrophic oceans although they may also become important in coastal seas (Morán, 2007). The structure and functioning of planktonic communities is strongly dependent on the relative importance of picophyto-

plankton, directly impacting the ecosystem balance of organic carbon produced in the upper ocean (Legendre & Le Fèvre, 1991; Falkowski *et al.*, 1998). A recent study has demonstrated that some of the carbon produced by picophytoplankton may also be exported to the deep ocean (Richardson & Jackson, 2007).

The effects of temperature on the biomass and production of phytoplankton assemblages in the context of global ocean warming have been addressed in several studies (Bopp *et al.*, 2001; Richardson & Schoeman, 2004; Behrenfeld *et al.*, 2006; Li *et al.*, 2006a), but seldom focused specifically on the smallest size class. In the review by Agawin *et al.* (2000), temperature was positively related to the relative contribution of small cells to total primary production but not to total chlorophyll, showing that chlorophyll may not be as good a proxy for biomass in the picoplankton size class. A remarkably coherent pattern of total phytoplankton cell density increase with temperature was found in the temperate NW Atlantic by Li *et al.* (2006a). The

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overwhelmingly dominant contribution of picophytoplankton to total cell abundance (Li, 2002) implicitly suggests that some universal underlying mechanism may apply for both large and small phytoplankton. Although ongoing climate warming has been shown to result in a decline of total phytoplankton biomass, especially in subtropical oligotrophic regions (Richardson & Schoeman, 2004; Behrenfeld *et al.*, 2006), we lack a theoretical explanation for the unexpected parallel increase in absolute cell abundance (Li *et al.*, 2006a). We combine here two large time-series datasets of picophytoplankton abundance, cell size and biomass collected in mostly temperate North Atlantic waters, and apply current theories of temperature–size relationships and the allometric size-scaling of population abundance to explain remarkably consistent relationships between temperature and the biomass of primary producers across the eastern and western shores. This analysis provides a theoretical framework for assessing how marine phytoplankton communities might change in the near future.

Methods

Data were obtained in different cruises carried out from 1994 to 2005 in the NW Atlantic ocean (48–60°W, see Fig. S1 in Li *et al.*, 2006b) and during a 5-year period (April 2002 to March 2007) within a long-term monitoring program with monthly samples in the NE (6°W, see Fig. 1 in Calvo-Díaz *et al.*, 2008). Latitude was 43°N in the NE and although most data in the NW came from the same latitude, 39% of them were obtained at latitudes ranging from 54° to 60°N. The seasonal cycle was well covered by both datasets, with evenly distributed data in the NW but fewer winter data in the NE (5% of the total). No significant differences could be detected in the amount of irradiance received in the two regions. All data were obtained at the surface (NE, $n = 59$) or the upper 10 m of the water column (NW, $n = 97$). Selected environmental variables are shown in Table S1. Spatial autocorrelation was avoided by averaging results from three (NE) or more stations (NW) sampled during the same day. Seawater samples were collected from Niskin bottles and processed as detailed elsewhere (Li *et al.*, 2006a; Morán, 2007). Chlorophyll *a* concentration was measured fluorometrically in acetone extracts. Nutrient concentrations were determined with Technicon auto-analyzers. Picophytoplankton samples were fixed with paraformaldehyde 1% + glutaraldehyde 0.05% (NE) or paraformaldehyde 1% (NW) and stored frozen at –80 °C until analysis. Thawed samples were counted by flow cytometry (Li *et al.*, 2006a; Morán, 2007). The size of picophytoplankton cells was estimated from cytometric light scatter signals calibrated with micro-

spheres (NW) or through sequential size fractionation of the community with Nuclepore polycarbonate filters (NE). Picophytoplankton biomass was estimated from abundance and cell size data for each dataset using a common conversion factor of $237 \text{ fg C } \mu\text{m}^{-3}$ (Worden *et al.*, 2004) and a C:chlorophyll ratio (mg:mg) of 50 (Harris, 1986) was used for estimating total phytoplankton biomass from chlorophyll measurements. Although the C:chlorophyll ratio is dependent on factors such as taxonomic composition or irradiance, it is unlikely that these changes were different in both Atlantic sides so as to preclude the cross-regional comparison of total phytoplankton biomass intended in this study. All linear regressions were performed according to the ordinary least-squares (OLS) method or Model I, because measurement errors in temperature are much lower than those corresponding to phytoplankton variables.

Results and discussion

There are three main macroecological patterns that emerge from our data analyses, which are interrelated by the theoretical framework proposed below.

First, picophytoplankton abundance increased with temperature in a similar manner to that previously reported for total phytoplankton. By plotting only data in the picoplankton size class from Li and colleagues' original dataset ($n = 97$) in the NW Atlantic and comparing them with monthly data ($n = 59$) collected at roughly the same latitude on the NE coast (43°N, 6°W, Table S1), remarkably similar positive relationships with temperature arose (Fig. 1a, Table S2).

Second, temperature and picophytoplankton cell size were inversely related. Highly significant and similarly negative relationships between temperature and cell size was observed in both north Atlantic regions, although the intercepts differed by an order of magnitude (Fig. 1b). Details of the slopes and intercepts of these and all other OLS linear regressions are presented in Table S2.

Third, the proportion of biomass in the picoplankton size class significantly increased with warmer conditions along the merged temperature range (Fig. 2), with temperature alone explaining 73% of the variance in data pooled from both Atlantic regions (Table S2).

A possible explanation for the relationship between temperature and the abundance of the whole phytoplankton community (Li *et al.*, 2006a) arises from a combination of the temperature–size relationship commonly referred as the temperature–size rule (TSR; Atkinson *et al.*, 2003) (that the average size of individuals is inversely related to temperature, see Fig. S1 and accompanying text) and the cross-community scaling relationship (CCSR) *sensu* White (White *et al.*, 2007)

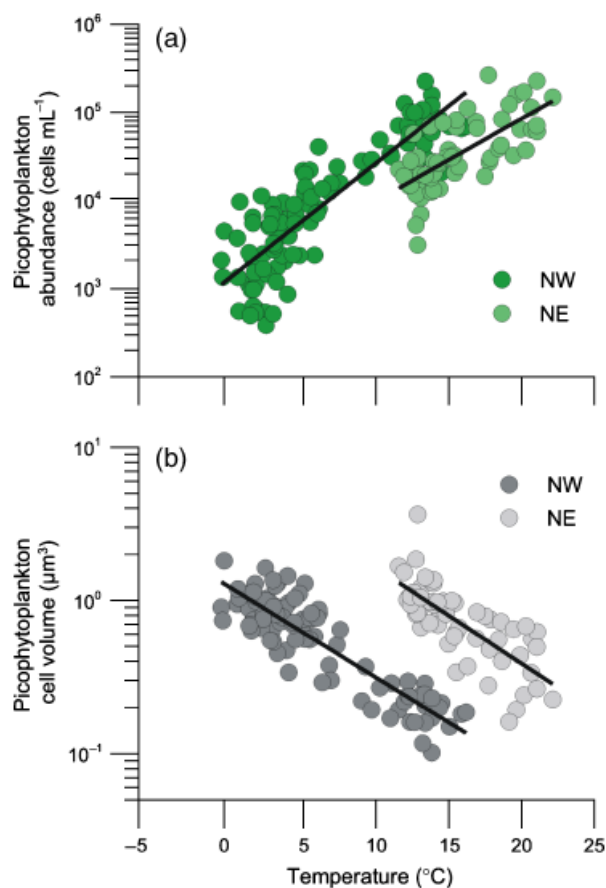


Fig. 1 The temperature–abundance and temperature–size rules. (a) Relationship between picophytoplankton abundance and temperature in the two north Atlantic regions (NW and NE). (b) Relationship between picophytoplankton mean cell volume and temperature in the two regions. Fitted lines are ordinary least-squares (OLS) linear regressions for log-transformed data of individual datasets detailed in Table S2.

(that total community abundance is inversely related to average organism size).

Although we will use the term TSR, the relationships between organism size and temperature within and across taxa can be of various types, of which the TSR is just one possibility. Changes in the average size in a population can arise both through phenotypic plasticity (the TSR) and from selection against particular-sized genotypes. Bergmann's rule is another well-known temperature–size relationship, loosely applied to endotherms and ectotherms, used to describe an increase in the body size of a species as latitude increases or environmental temperature decreases. Exceptions to the TSR rule are actively debated and out of the object of this analysis, but sometimes the same mechanism may be used to explain a reduction in maximum (and potentially mean) size in aquatic ectotherm taxa with reduced latitude (Makarieva *et al.*, 2005).

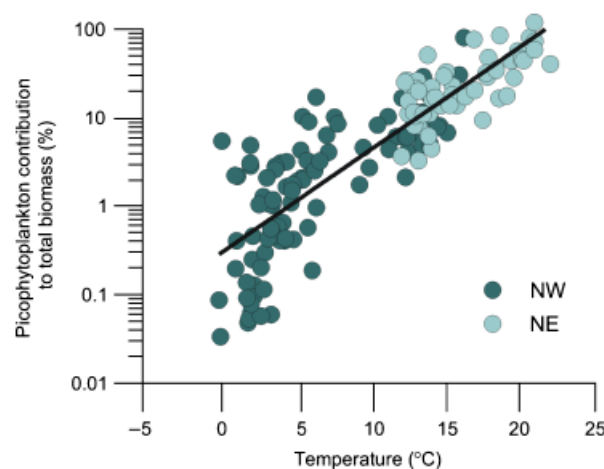


Fig. 2 Increasing dominance of picophytoplankton biomass with temperature. Relationship between the percent contribution of picophytoplankton to total phytoplankton biomass and temperature in the two regions. Fitted line is ordinary least-squares (OLS) linear regression for pooled log-transformed data (see Table S2 for details).

As a corollary of the TSR and CCSR theories, and under an energetic equivalence scenario (i.e. the same amount of resources utilized by all size classes), temperature should affect community abundance but indirectly through its effects on body size. In warmer conditions the average size of the organisms in a community would decrease as a consequence of the TSR (as shown in Fig. 1b for picophytoplankton) and because smaller organisms have lower absolute energy requirements (Gillooly *et al.*, 2001) the number of phytoplankton cells that can be sustained will be higher as shown by Li *et al.* (2006a).

For picophytoplankton our argument is a bit more complicated. If its contribution to total phytoplankton remains constant with temperature, then picophytoplankton abundance should increase with increasing temperature solely because total phytoplankton abundance increases (i.e. the same percentage of a larger number). However, we argue that the relative contribution of picophytoplankton to the total biomass of planktonic primary producers should vary with temperature as a consequence of a combination of the TSR and the within-community size scaling of abundance or individual size distribution (ISD) (White *et al.*, 2007), that is, the frequency distribution of individual body sizes in a community. Note that the ISD is distinct from the CCSR mentioned above for total phytoplankton.

To explain the observed relationships between picophytoplankton abundance and temperature shown in Fig. 1a, we show the hypothetical distribution of the abundance of all cells within the phytoplankton community vs. size at two different temperatures (10 and

20 °C; Fig. 3). As discussed above an increase in temperature would shift the total community to smaller sizes. The average size and abundance of picophytoplankton at a given temperature for each station and sampling period would translate into a plot of picophytoplankton abundance vs. temperature equivalent to that shown in Fig. 1a for data collected in the NW and NE Atlantic Ocean. Because the nominal upper size boundary of picoplankton is fixed at 2 µm (Sieburth *et al.*, 1978), the ISD would be shifted toward smaller sizes as temperature increases (Fig. 3) and hence a larger proportion of the community will be smaller than that size.

Based on the conceptual framework depicted in Fig. 3, we could make two predictions. First, that there should exist a strong relationship between temperature and the contribution of picophytoplankton to total phytoplankton abundance and biomass. Second, that

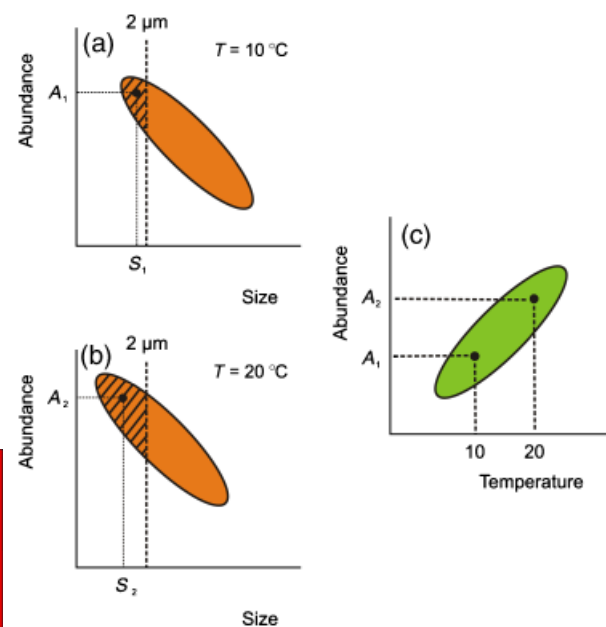


Fig. 3 Schematic representation of the effects of temperature on the size-scaling of phytoplankton abundance. (a) and (b) represent idealized individual size distributions (ISD) of two different phytoplankton communities at 10 and 20 °C, respectively. At high temperatures (b) the mean cell size of the phytoplankton community is lower than at low temperatures (a) so the ISD is shifted upwards to the left. Hence, a higher proportion of total cell abundance falls into the picoplankton (<2 µm) size class under warmer conditions (hatched area). (c) The abundance-temperature relationship emerges when the picophytoplankton abundances from different communities such as those represented in (a) and (b) are plotted in a cross-community chart against temperature. S₁ and S₂ are mean picophytoplankton cell sizes at 10 and 20 °C, respectively, with corresponding abundances A₁ and A₂. S₁ > S₂, A₁ < A₂.

picophytoplankton abundance should be more related than total phytoplankton abundance to temperature (steeper slope), because the former is determined not only by the TSR–CCSR relationship but also by the TSR–ISD relationship. These predictions were supported by our datasets: a significant increase in the proportion of biomass in the picoplankton size class with warmer conditions became evident for the entire temperature range (Fig. 2), with a remarkably high percentage of its variance explained by this single factor. Our results thus complement previous demonstrations of a significant increase in the proportion of picophytoplankton primary production with temperature (Agawin *et al.*, 2000). According to our analysis, picophytoplankton would dominate the biomass of primary producers in the ocean's surface at a temperature of 19.7 °C, although noticeable fractions would already be present at lower temperatures. An increase in temperature of 3 °C would double picophytoplanktonic contribution at 15 °C (32% vs. 15%). Also as predicted, the slope of the picophytoplankton abundance vs. temperature regression was 19% higher than that corresponding to total phytoplankton in the NE region (Table S2).

Although total cell abundance is the 'primary ecological currency' (Li *et al.*, 2006a), other variables such as biomass or production are equally important especially in a biogeochemical context. The regional difference in the picophytoplankton abundance–temperature relationships (Fig. 1a, Table S2), which was largely due to changes in the respective size–temperature intercepts (Fig. 1b), collapsed when picophytoplankton was expressed as biomass. Indeed, the biomasses of both picophytoplankton and total autotrophs were strongly and inversely related to temperature in remarkably similar ways for the two north Atlantic regions (Table S2, Fig. 4). A common response of temperate N Atlantic picophytoplankton biomass to temperature, altogether explaining 66% of its variance, became thus evident (Fig. 4a). The consistency of the variation along the –0.6 to 22 °C temperature range is remarkable given site-specific differences in nutrient fluxes and broad-group composition (Table S1). Indeed, the taxonomic structure of the assemblage changed profoundly across this range: at low temperatures, *Prochlorococcus* were absent, *Synechococcus* were sparse and picoeukaryotes were abundant; at high temperatures, *Prochlorococcus* became dominant despite higher concentrations of the other taxa. Thus it was the ataxonomic size class of picophytoplankton that exhibited the strongest relationship with temperature, not the component taxa (Doolittle *et al.*, 2008).

Temperature covaries with several other factors in pelagic ecosystems, including inorganic nutrient fluxes

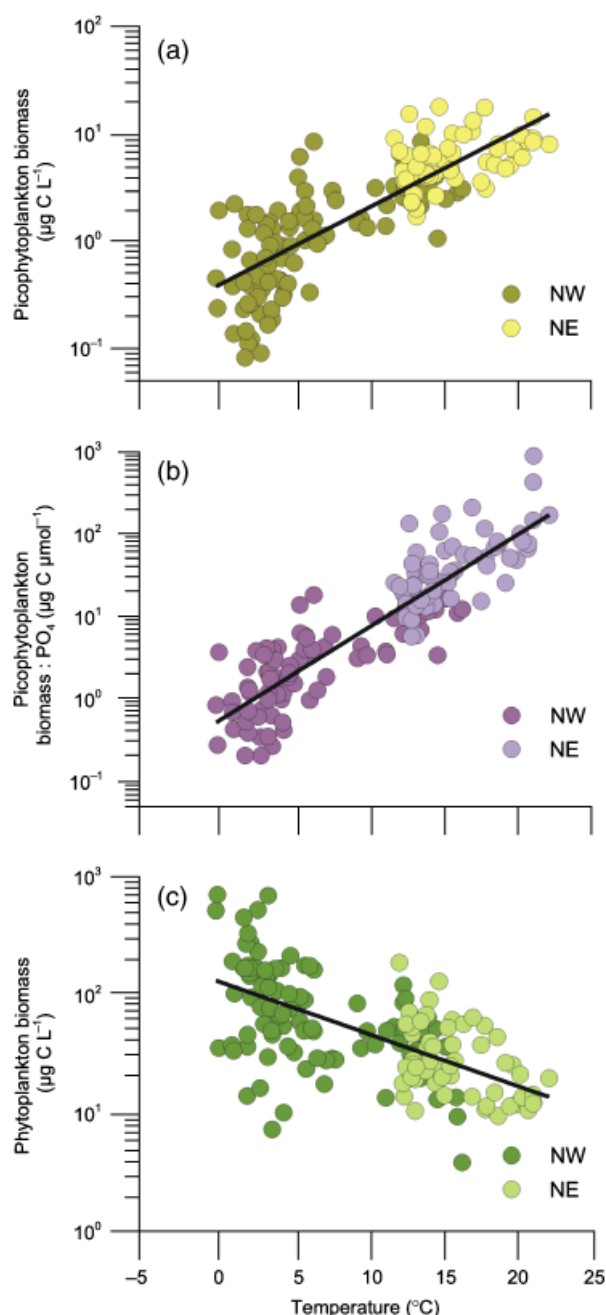


Fig. 4 Opposite relationships of picophytoplankton and total phytoplankton biomass with temperature. (a) Relationship between picophytoplankton biomass and temperature in the two regions. (b) Relationship between picophytoplankton biomass $\mu\text{mol}^{-1} \text{L}^{-1}$ of phosphate (picophytoplankton biomass: PO_4 ratio) and temperature in the two regions. (c) Relationship between total phytoplankton biomass and temperature in the two regions. Fitted lines are ordinary least-squares (OLS) linear regressions for log-transformed pooled data (see Table S2 for details and individual dataset regressions).

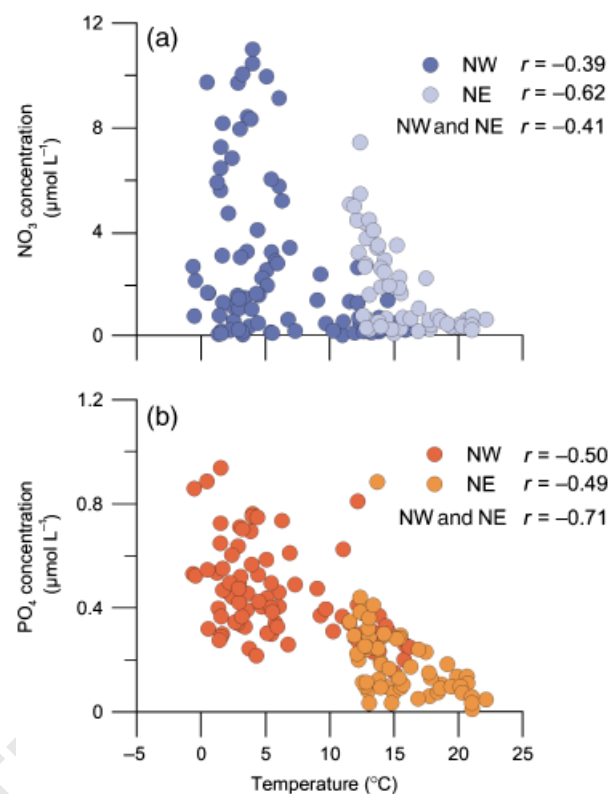


Fig. 5 Inorganic nutrient distributions. Relationships of nitrate (a) and phosphate (b) concentrations to temperature in the two north Atlantic regions. Pearson correlation coefficients within regions and for pooled data are also shown. All correlations were significant at $P < 0.001$.

(Li, 1998; Kamykowski *et al.*, 2002) (Fig. 5), rendering it difficult to disentangle the effects of each of them (Agawin *et al.*, 2000). Possible changes in the intercept or slope of the size–abundance relationships linked to factors other than temperature were omitted from our argument and from Fig. 3 but they can be relevant (Finkel *et al.*, 2004). Typically for temperate waters, both regions were characterized by maxima of inorganic nutrient concentrations in winter and minima in summer (Fig. 5). However, significantly lower NO_3 and PO_4 concentrations were found in the NE region, underlying an overall lower phytoplankton biomass (Table S1). Significant positive correlations were found between pooled concentrations of both nutrients and chlorophyll, higher in the case of PO_4 ($r = 0.43$, $P < 0.0001$, $n = 145$). In an attempt to correct for these regional differences, we estimated the biomass of picophytoplankton that could be sustained by a PO_4 concentration of $1 \mu\text{mol L}^{-1}$. The apparent temperature control of this new variable (Fig. 4b) significantly improved that shown in Fig. 4a, with $\sim 80\%$ of the variance explained ($\log Y = 3.57 + 7.19X$; $r^2 = 0.79$, $P < 0.0001$, $n = 145$).

The entrainment of nutrients into the euphotic layer will likely decrease in future scenarios due to enhanced stratification, especially in open-ocean lower latitude regions (Sarmiento *et al.*, 2004). A reduction in nutrient supply will additionally shift community size structure to smaller species due to biophysical principles (Pasciak & Gavis, 1974), as empirically evidenced in the laboratory and the field (Jin *et al.*, 2006) and shown in modeling analysis (Bopp *et al.*, 2005). Changes in nutrient supply at geological time scales, driven by variations in latitudinal and vertical temperature gradients, seem to be responsible for changing the average cell size of diatoms and dinoflagellates in the ocean (Finkel *et al.*, 2007). In spite of these possible direct effects of nutrient concentrations, we believe that the currently observed changes in phytoplankton were mainly related to temperature through the mechanism depicted in Fig. 3. Nitrate and phosphate concentrations failed to substantially explain changes in mean picophytoplankton cell size in any of the two regions, with percentages of variance explained ranging from only 11% to 20%. At the species level, correlation coefficients of *Prochlorococcus* and *Synechococcus* cell size with temperature in the NE Atlantic were also consistently higher than with either nitrate or phosphate, altogether rendering a lower role of inorganic nutrients in directly controlling picophytoplankton cell size, as recently shown for tropical North Atlantic waters (Davey *et al.*, 2008).

The finding that picophytoplankton biomass increased with temperature (Fig. 4a) seems, in principle, to be at odds with the extension of the energetic equivalence rule to include temperature (Allen *et al.*, 2002). This theory suggests that the 'mass-corrected abundance' ($N \times M^{3/4}$) should decrease with increasing temperature. However, this theory would refer to total phytoplankton, not to the picoplankton size class. Phytoplankton biomass, which can be considered a proxy to mass-corrected abundance, was in fact inversely correlated with temperature in both regions (Fig. 4c) with remarkably similar linear regressions (Table S2), in seeming support of an explanation based on biochemical kinetics (Allen *et al.*, 2002). This inverse covariation also emerges when global sea surface chlorophyll concentration is examined in relation to sea surface temperature (Behrenfeld *et al.*, 2006) and in an analysis of annual anomalies of temperature and the biomass of larger phytoplankton groups (Li & Harrison, 2008). As for the opposite relationship between picophytoplankton biomass and temperature, this could be partly explained by the TSR-ISD relationship having a greater role than the energetic equivalence constraint. Again, if the contribution of picophytoplankton to total phytoplankton remains constant with increasing temperature, we would expect picophytoplankton biomass to also

decrease with increasing temperature. But because the percent contribution increases with temperature this effect counteracts the decrease in total biomass resulting in a positive relationship between picophytoplankton biomass and temperature. Furthermore, the inverse correlations of NO_3 and PO_4 concentrations with temperature both within and across regions (Fig. S2) suggest that resource limitation can also contribute to the increase in the proportion of picophytoplankton biomass with warmer conditions. Different nutrient requirements of large and small phytoplankton cells are well documented (Chisholm, 1992; Raven, 1998), with low nutrient concentrations at high temperatures limiting the distribution of large cells such as diatoms (Donald *et al.*, 1997) but little effect on the smallest phytoplankters.

Several studies have predicted important consequences of climate change on plankton communities (Richardson & Schoeman, 2004; Hays *et al.*, 2005; Beaugrand *et al.*, 2008). The bottom-up effects that will be discussed below might be complicated by simultaneous, and largely unknown changes to other components of pelagic food webs and the complex community interactions (Strom, 2008), which are not investigated here. An implicit consequence of the consistent relationships found here among temperature, cell size and picophytoplankton abundance is that the size of cells in phytoplankton assemblages will gradually decrease with global warming. This prediction implicitly assumes that the adjustment of phytoplankton would be the same over time (multiyear change) as it is over space (cross-ecosystem difference). If so, this relatively rapid change might add to evolutionary pressures on phytoplankton communities toward picoplankton sizes (Jiang *et al.*, 2005). Size is a key property of phytoplankton, with far-reaching influences in the structure and functioning of pelagic food webs (Legendre & Le Fèvre, 1991; Cohen *et al.*, 2003) and ultimately the biogeochemical fate of photosynthesized organic carbon (Falkowski *et al.*, 1998). The observed decrease of total chlorophyll concentration with increasing temperature in vast regions of the world oceans (Behrenfeld *et al.*, 2006) might be partly explained by the mechanisms proposed here and hence be accompanied by a counterintuitive increase in the picophytoplankton component. The strong relationship between temperature and the percent contribution of small cells to total biomass of planktonic primary producers should allow the computation of global picophytoplankton biomass distribution fields from remotely sensed chlorophyll concentration and temperature.

Environmental selection toward smaller individual size in phytoplankton assemblages, either phenotypic or genotypic (Falkowski & Oliver, 2007), will have

profound implications for marine biogeochemistry (Bopp *et al.*, 2005), especially when jointly considered with other foreseen changes such as increased stratification and expansion of low productivity areas (Sarmiento *et al.*, 2004; Behrenfeld *et al.*, 2006). Smaller phytoplankters will likely encounter decreased inputs of nutrients from below shallower, stronger pycnoclines, resulting in enhanced regeneration of nutrients in the upper layers and lower carbon export (Bopp *et al.*, 2001). Because sinking velocity is heavily dependent on cell size, the major alteration in the functioning of marine pelagic ecosystems due to an increasing importance of small primary producers could be summarized in less potential for carbon sequestration in the oceans interior.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Summary of environmental characteristics in the two Atlantic regions. Mean values and ranges (among parentheses) of temperature, total chlorophyll (Chl), nitrate and phosphate concentrations and the abundance of *Prochlorococcus* (Pro), *Synechococcus* (Syn) and picoeukaryotes (Euk). Significant differences are indicated with asterisk notation: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ns, not significant.

Table S2. Linear regressions between phytoplankton variables and temperature. Statistical parameters for the OLS linear regressions between total phytoplankton and picophytoplankton abundance, cell-size and biomass and temperature for the two north Atlantic regions (NW and NE) and the whole data set (NE & NW).

Fig. S1. The temperature-size and temperature-abundance rules for cyanobacteria. (A) Relationship between mean cell volume of *Synechococcus* (Syn) and *Prochlorococcus* (Proc) and temperature in the NE Atlantic region. (B) Relationship between *Synechococcus* and *Prochlorococcus* abundance and temperature in the NE Atlantic region. Fitted lines are OLS linear regressions for log-transformed data (continuous for *Synechococcus* and dashed for *Prochlorococcus*).

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