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4 **Increasing importance of small phytoplankton in a**
5 **warmer ocean**

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7 Xosé Anxelu G. Morán^{1,2*}, Ángel López-Urrutia¹, Alejandra Calvo-Díaz¹, William K. W.
8 Li³

9
10 ¹Instituto Español de Oceanografía, Centro Oceanográfico de Xixón, Camín de L' Arbeyal,
11 s/n, 33212 Xixón, Spain

12 ²The Ecosystems Center, Marine Biological Laboratory, 7 MBL Street, Woods Hole MA
13 02543, USA

14 ³Ecosystem Research Division, Bedford Institute of Oceanography, Dept. of Fisheries and
15 Oceans, Dartmouth, Nova Scotia B2Y 4A2, Canada

16 * Corresponding author: Tel +34 985308672

17 Fax +34 985326277

18 E-mail: xelu.moran@gi.ieo.es

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1 **Abstract**

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

16

1 INTRODUCTION

2 Picophytoplankton are photosynthetic unicellular organisms in the 0.2-2 μm size range that
3 are found throughout the world's oceans. They comprise cyanobacteria of the genera
4 *Synechococcus* and *Prochlorococcus* (Partensky *et al.* 1999) together with a diverse
5 ensemble of eukaryotic algae (Moon-van der Staay *et al.* 2001; Not *et al.* 2007).

6 Picophytoplankton cells have a ubiquitous distribution and contribute significant portions
7 of bulk phytoplankton biomass and production (Bell & Kalff 2001; Agawin *et al.* 2000).

8 The accepted view poses them as the dominant primary producers in vast areas of
9 oligotrophic oceans although they may also become important in coastal seas (Morán
10 2007). The structure and functioning of planktonic communities is strongly dependent on
11 the relative importance of picophytoplankton, directly impacting the ecosystem balance of
12 organic carbon produced in the upper ocean (Legendre & Le Fèvre 1991; Falkowski *et al.*
13 1998). A recent study has demonstrated that some of the carbon produced by
14 picophytoplankton may also be exported to the deep ocean (Richardson & Jackson 2007).

15 The effects of temperature on the biomass and production of phytoplankton
16 assemblages in the context of global ocean warming have been addressed in several studies
17 (Richardson & Schoeman 2004; Li *et al.* 2006a; Bopp *et al.* 2001; Behrenfeld *et al.* 2006),
18 but seldom focused specifically on the smallest size-class. In the review by Agawin *et al.*
19 (2000), temperature was positively related with the relative contribution of small cells to
20 total primary production but not to total chlorophyll, showing that chlorophyll may not be
21 as good a proxy for biomass in the picoplankton size class. A remarkably coherent pattern
22 of total phytoplankton cell density increase with temperature was found in the temperate
23 NW Atlantic by Li *et al.* (2006a). The overwhelmingly dominant contribution of

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

13

14 **METHODS**

15 Data were obtained in different cruises carried out from 1994 to 2005 in the NW Atlantic
16 ocean [48-60°W, see Fig. S1 in Li *et al.* (2006b)] and during a 5-year period (Apr 2002-
17 Mar 2007) within a long-term monitoring program with monthly samples in the NE [6°W,
18 see Fig. 1 in Calvo-Díaz *et al.*(2008)]. Latitude was 43°N in the NE and although most data
19 in the NW came from the same latitude, 39% of them were obtained at latitudes ranging
20 from 54° to 60°N. The seasonal cycle was well-covered by both datasets, with evenly
21 distributed data in the NW but fewer winter data in the NE (~5% of the total). No
22 significant differences could be detected in the amount of irradiance received in the two
23 regions. All data were obtained at the surface (NE, n=59) or the upper 10 m of the water

1 column (NW, n=97). Selected environmental variables are shown in Table S1. Spatial
2 autocorrelation was avoided by averaging results from 3 (NE) or more stations (NW)
3 sampled during the same day. Seawater samples were collected from Niskin bottles and
4 processed as detailed elsewhere (Li *et al.* 2006a; Morán 2007). Chlorophyll *a* concentration
5 was measured fluorometrically in acetone extracts. Nutrient concentrations were
6 determined with Technicon autoanalyzers. Picophytoplankton samples were fixed with
7 paraformaldehyde 1% + glutaraldehyde 0.05% (NE) or paraformaldehyde 1% (NW) and
8 stored frozen at -80°C until analysis. Thawed samples were counted by flow cytometry (Li
9 *et al.* 2006a; Morán 2007). The size of picophytoplankton cells was estimated from
10 cytometric light scatter signals calibrated with microspheres (NW) or through sequential
11 size fractionation of the community with Nuclepore polycarbonate filters (NE).
12 Picophytoplankton biomass was estimated from abundance and cell size data for each
13 dataset using a common conversion factor of 237 fg C μm^{-3} (Worden *et al.* 2004) and a
14 C:chlorophyll ratio (mg:mg) of 50 (Harris 1986) was used for estimating total
15 phytoplankton biomass from chlorophyll measurements. Although the C:chlorophyll ratio
16 is dependent on factors such as taxonomic composition or irradiance, it is unlikely that
17 these changes were different in both Atlantic sides so as to preclude the cross-regional
18 comparison of total phytoplankton biomass intended in this study. All linear regressions
19 were performed according to the ordinary least squares (OLS) method or Model I, since
20 measurement errors in temperature are much lower than those corresponding to
21 phytoplankton variables.

22

23 **RESULTS AND DISCUSSION**

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

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

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

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

18 A possible explanation for the relationship between temperature and the abundance
19 of the whole phytoplankton community (Li *et al.* 2006a) arises from a combination of the
20 temperature-size relationship referred commonly as the temperature-size rule (TSR,
21 (Atkinson *et al.* 2003) [that the average size of individuals is inversely related to
22 temperature, see Fig. S1 and accompanying text] and the cross-community scaling

1 relationship (CCSR) sensu White (White *et al.* 2007) [that total community abundance is
2 inversely related to average organism size].

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

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

20 For picophytoplankton our argument is a bit more complicated. If its contribution to
21 total phytoplankton remains constant with temperature, then picophytoplankton abundance
22 should increase with increasing temperature solely because total phytoplankton abundance
23 increases (i.e. the same percentage of a larger number). However, we argue that the relative

1 contribution of picophytoplankton to the total biomass of planktonic primary producers
2 should vary with temperature as a consequence of a combination of the TSR and the
3 within-community size scaling of abundance or individual size distribution (ISD) (White *et*
4 *al.* 2007), that is, the frequency distribution of individual body sizes in a community. Note
5 that the ISD is distinct from the CCSR mentioned above for total phytoplankton.

6 To explain the observed relationships between picophytoplankton abundance and
7 temperature shown in Fig. 1a we show the hypothetical distribution of the abundance of all
8 cells within the phytoplankton community versus size at two different temperatures (10°
9 and 20°C, Fig. 3). As discussed above an increase in temperature would shift the total
10 community to smaller sizes. The average size and abundance of picophytoplankton at a
11 given temperature for each station and sampling period would translate into a plot of
12 picophytoplankton abundance versus temperature equivalent to that shown in Fig. 1a for
13 data collected in the NW and NE Atlantic Ocean. Because the nominal upper size boundary
14 of picoplankton is fixed at 2 µm (Sieburth *et al.* 1978), the ISD would be shifted towards
15 smaller sizes as temperature rises (Fig. 3) and hence a larger proportion of the community
16 will be smaller than that size.

17 Based on the conceptual framework depicted in Fig. 3, we could make two
18 predictions. First, that there should exist a strong relationship between temperature and the
19 contribution of picophytoplankton to total phytoplankton abundance and biomass. Second,
20 that picophytoplankton abundance should be more related than total phytoplankton
21 abundance to temperature (steeper slope), because the former is determined not only by the
22 TSR – CCSR relationship but also by the TSR – ISD relationship. These predictions were
23 supported by our datasets: a significant increase in the proportion of biomass in the

1 picoplankton size-class with warmer conditions became evident for the entire temperature
2 range (Fig. 2), with a remarkably high percentage of its variance explained by this single
3 factor. Our results thus complement previous demonstrations of a significant increase in the
4 proportion of picophytoplankton primary production with temperature (Agawin *et al.*
5 2000). According to our analysis, picophytoplankton would dominate the biomass of
6 primary producers in the ocean's surface at a temperature of 19.7°C, although noticeable
7 fractions would already be present at lower temperatures. A rise in temperature of 3°C
8 would double picophytoplanktonic contribution at 15°C (32% vs 15%). Also as predicted,
9 the slope of the picophytoplankton abundance vs. temperature regression was 19% higher
10 than that corresponding to total phytoplankton in the NE region (Table S2).

11 Although total cell abundance is the “primary ecological currency” (Li *et al.* 2006a),
12 other variables such as biomass or production are equally important especially in a
13 biogeochemical context. The regional difference in the picophytoplankton abundance-
14 temperature relationships (Fig. 1a, Table S2), which was largely due to changes in the
15 respective size-temperature intercepts (Fig. 1b), collapsed when picophytoplankton was
16 expressed as biomass. Indeed, the biomasses of both picophytoplankton and total
17 autotrophs were strongly and inversely related to temperature in remarkably similar ways
18 for the two north Atlantic regions (Table S2, Fig. 4). A common response of temperate N
19 Atlantic picophytoplankton biomass to temperature, altogether explaining 66% of its
20 variance, became thus evident (Fig. 4a). The consistency of the variation along the -0.6 to
21 22°C temperature range is remarkable given site-specific differences in nutrient fluxes and
22 broad-group composition (Table S1). Indeed, the taxonomic structure of the assemblage
23 changed profoundly across this range: at low temperatures, *Prochlorococcus* were absent,

1 *Synechococcus* were sparse, and picoeukaryotes were abundant; at high temperatures,
2 *Prochlorococcus* became dominant despite higher concentrations of the other taxa. Thus it
3 was the ataxonomic size class of picophytoplankton that exhibited the strongest relationship
4 with temperature, not the component taxa (Doolittle *et al.* 2008).

5 Temperature covaries with several other factors in pelagic ecosystems, including
6 inorganic nutrient fluxes (Li 1998; Kamykowski *et al.* 2002)(Fig. 5), rendering it difficult
7 to disentangle the effects of each of them (Agawin *et al.* 2000). Possible changes in the
8 intercept or slope of the size-abundance relationships linked to factors other than
9 temperature were omitted from our argument and from Fig. 3 but they can be relevant
10 (Finkel *et al.* 2004). Typically for temperate waters, both regions were characterized by
11 maxima of inorganic nutrient concentrations in winter and minima in summer (Fig. 5).
12 However, significantly lower NO₃ and PO₄ concentrations were found in the NE region,
13 underlying an overall lower phytoplankton biomass (Table S1). Significant positive
14 correlations were found between pooled concentrations of both nutrients and chlorophyll,
15 higher in the case of PO₄ (r=0.43, p<0.0001, n=145). In an attempt to correct for these
16 regional differences, we estimated the biomass of picophytoplankton that could be
17 sustained by a PO₄ concentration of 1 μmol L⁻¹. The apparent temperature control of this
18 new variable (Fig. 4b) significantly improved that shown in Fig. 4a, with ~80% of the
19 variance explained (log Y = 3.57 + 7.19*X; r²=0.79, p<0.0001, n=145).

20 The entrainment of nutrients into the euphotic layer will likely decrease in future
21 scenarios due to enhanced stratification, especially in open-ocean lower latitude regions
22 (Sarmiento *et al.* 2004). A reduction in nutrient supply will additionally shift community
23 size structure to smaller species due to biophysical principles (Pasciak & Gavis 1974), as

1 empirically evidenced in the laboratory and the field (Jin *et al.* 2006) and shown in
2 modelling analysis (Bopp *et al.* 2005). Changes in nutrient supply at geological time scales,
3 driven by variations in latitudinal and vertical temperature gradients, seem to be responsible
4 for changing the average cell size of diatoms and dinoflagellates in the ocean (Finkel *et al.*
5 2007). In spite of these possible direct effects of nutrient concentrations, we believe that the
6 currently observed changes in phytoplankton were mainly related to temperature through
7 the mechanism depicted in Fig. 3. Nitrate and phosphate concentrations failed to
8 substantially explain changes in mean picophytoplankton cell size in any of the two
9 regions, with percentages of variance explained ranging from only 11 to 20%. At the
10 species level, correlation coefficients of *Prochlorococcus* and *Synechococcus* cell size with
11 temperature in the NE Atlantic were also consistently higher than with either nitrate or
12 phosphate, altogether rendering a lower role of inorganic nutrients in directly controlling
13 picophytoplankton cell size, as recently shown for tropical North Atlantic waters (Davey *et*
14 *al.* 2008).

15 The finding that picophytoplankton biomass increased with temperature (Fig. 4a)
16 seems, in principle, to be at odds with the extension of the energetic equivalence rule to
17 include temperature (Allen *et al.* 2002). This theory suggests that the “mass-corrected
18 abundance” ($N \cdot M^{3/4}$) should decrease with increasing temperature. However, this theory
19 would refer to total phytoplankton, not to the picoplankton size class. Phytoplankton
20 biomass, which can be considered a proxy to mass-corrected abundance, was in fact
21 inversely correlated with temperature in both regions (Fig. 4c) with remarkably similar
22 linear regressions (Table S2), in seeming support of an explanation based on biochemical
23 kinetics (Allen *et al.* 2002). This inverse covariation also emerges when global sea surface

1 chlorophyll concentration is examined in relation to sea surface temperature (Behrenfeld *et*
2 *al.* 2006) and in an analysis of annual anomalies of temperature and the biomass of larger
3 phytoplankton groups (Li & Harrison 2008). As for the opposite relationship between
4 picophytoplankton biomass and temperature, this could be partly explained by the TSR-ISD
5 relationship having a greater role than the energetic equivalence constraint. Again, if the
6 contribution of picophytoplankton to total phytoplankton remains constant with increasing
7 temperature, we would expect picophytoplankton biomass to also decrease with increasing
8 temperature. But because the percent contribution increases with temperature this effect
9 counteracts the decrease in total biomass resulting in a positive relationship between
10 picophytoplankton biomass and temperature. Furthermore, the inverse correlations of NO₃
11 and PO₄ concentrations with temperature both within and across regions (Fig. S2) suggest
12 that resource limitation can also contribute to the increase in the proportion of
13 picophytoplankton biomass with warmer conditions. Different nutrient requirements of
14 large and small phytoplankton cells are well-documented (Raven 1998; Chisholm 1992),
15 with low nutrient concentrations at high temperatures limiting the distribution of large cells
16 such as diatoms (Donald *et al.* 1997) but little effect on the smallest phytoplankters.

17 Several studies have predicted important consequences of climate change on
18 plankton communities (Richardson & Schoeman 2004; Hays *et al.* 2005; Beaugrand *et al.*
19 2008). The bottom-up effects that will be discussed below might be complicated by
20 simultaneous, and largely unknown changes to other components of pelagic food webs and
21 the complex community interactions (Strom 2008), which are not investigated here. An
22 implicit consequence of the consistent relationships found here between temperature, cell
23 size and picophytoplankton abundance is that the size of cells in phytoplankton

1 assemblages will gradually decrease with global warming. This prediction implicitly
2 assumes that the adjustment of phytoplankton would be the same over time (multiyear
3 change) as it is over space (cross ecosystem difference). If so, this relatively rapid change
4 might add to evolutionary pressures on phytoplankton communities towards picoplankton
5 sizes (Jiang *et al.* 2005). Size is a key property of phytoplankton, with far-reaching
6 influences in the structure and functioning of pelagic food webs (Cohen *et al.* 2003;
7 Legendre & Le Fèvre 1991) and ultimately the biogeochemical fate of photosynthesized
8 organic carbon (Falkowski *et al.* 1998). The observed decrease of total chlorophyll
9 concentration with increasing temperature in vast regions of the world oceans (Behrenfeld
10 *et al.* 2006) might be partly explained by the mechanisms proposed here and hence be
11 accompanied by a counterintuitive increase in the picophytoplankton component. The
12 strong relationship between temperature and the percent contribution of small cells to total
13 biomass of planktonic primary producers should allow the computation of global
14 picophytoplankton biomass distribution fields from remotely sensed chlorophyll
15 concentration and temperature.

16 Environmental selection towards smaller individual size in phytoplankton
17 assemblages, either phenotypic or genotypic (Falkowski & Oliver 2007), will have
18 profound implications for marine biogeochemistry (Bopp *et al.* 2005), especially when
19 jointly considered with other foreseen changes such as increased stratification and
20 expansion of low productivity areas (Sarmiento *et al.*, 2004, Behrenfeld *et al.*, 2006).
21 Smaller phytoplankters will likely encounter decreased inputs of nutrients from below
22 shallower, stronger pycnoclines, resulting in enhanced regeneration of nutrients in the
23 upper layers and lower carbon export (Bopp *et al.*, 2001). Since sinking velocity is heavily

1 dependent on cell size, the major alteration in the functioning of marine pelagic ecosystems
2 due to an increasing importance of small primary producers could be summarized in less
3 potential for carbon sequestration in the oceans interior.
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17

LEGENDS TO FIGURES

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 OLS linear regressions for log-transformed data of individual datasets detailed in Table 2S.

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 OLS linear regression for pooled log-transformed data (see Table S2 for details).

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. S_1 and S_2 are mean picophytoplankton cell sizes at 10°C and 20°C, respectively, with corresponding abundances A_1 and A_2 . $S_1 > S_2$, $A_1 < A_2$.

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 per $\mu\text{mol L}^{-1}$ 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 OLS linear regressions for log-transformed pooled data (see Table S2 for details and individual data set 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 $p < 0.001$.

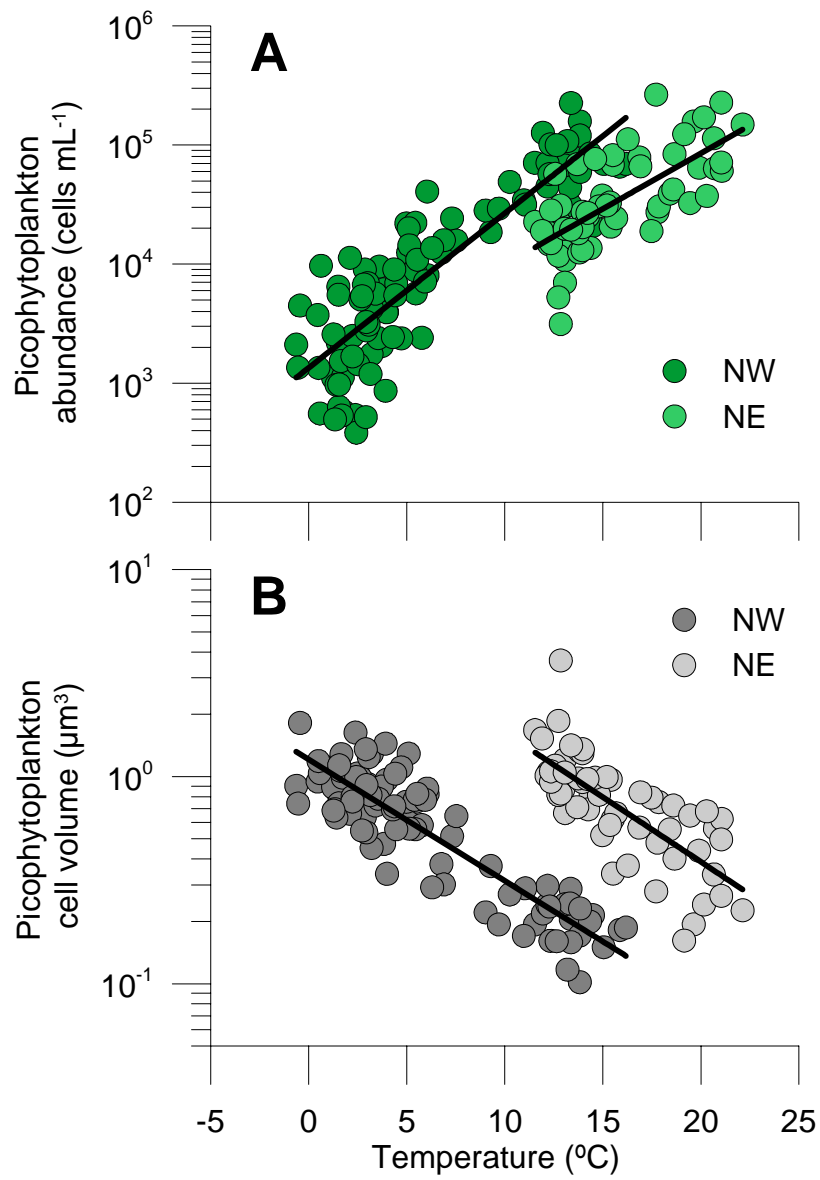


Fig. 1

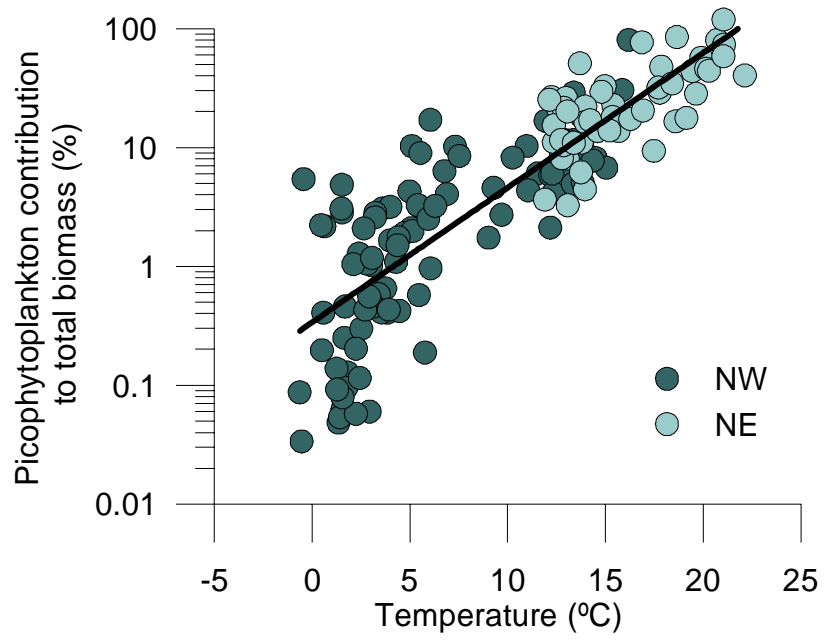


Fig. 2

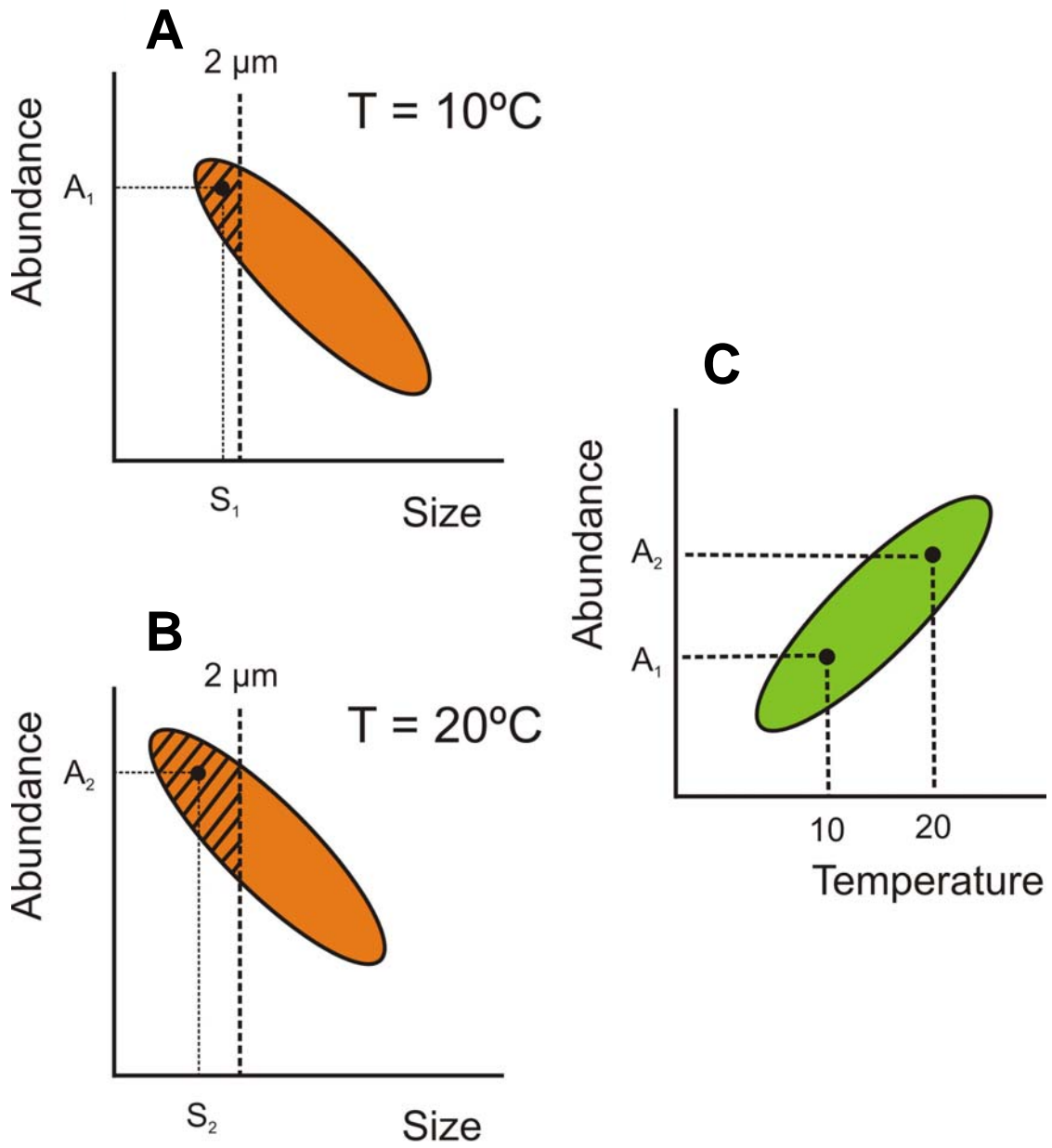


Fig. 3

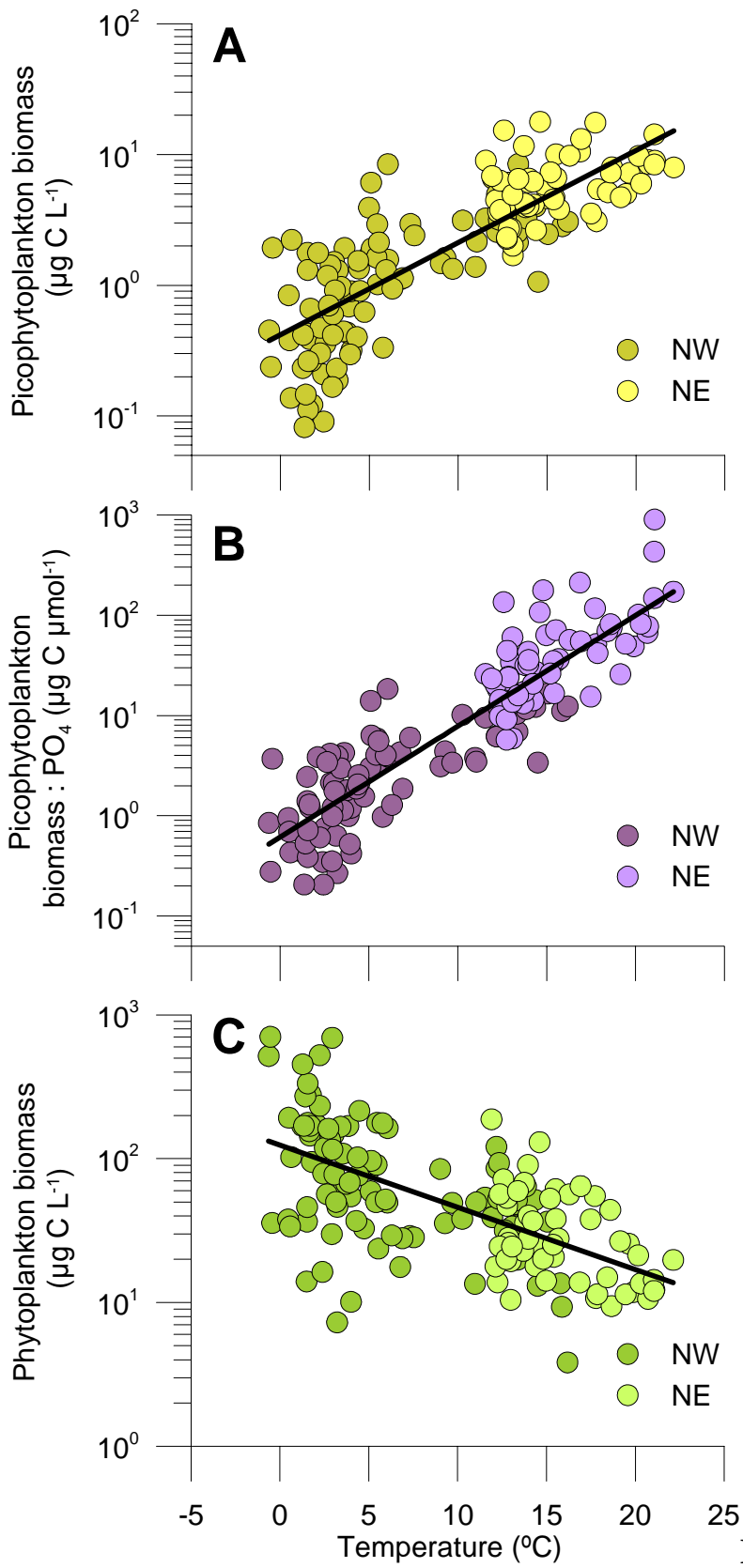


Fig. 4

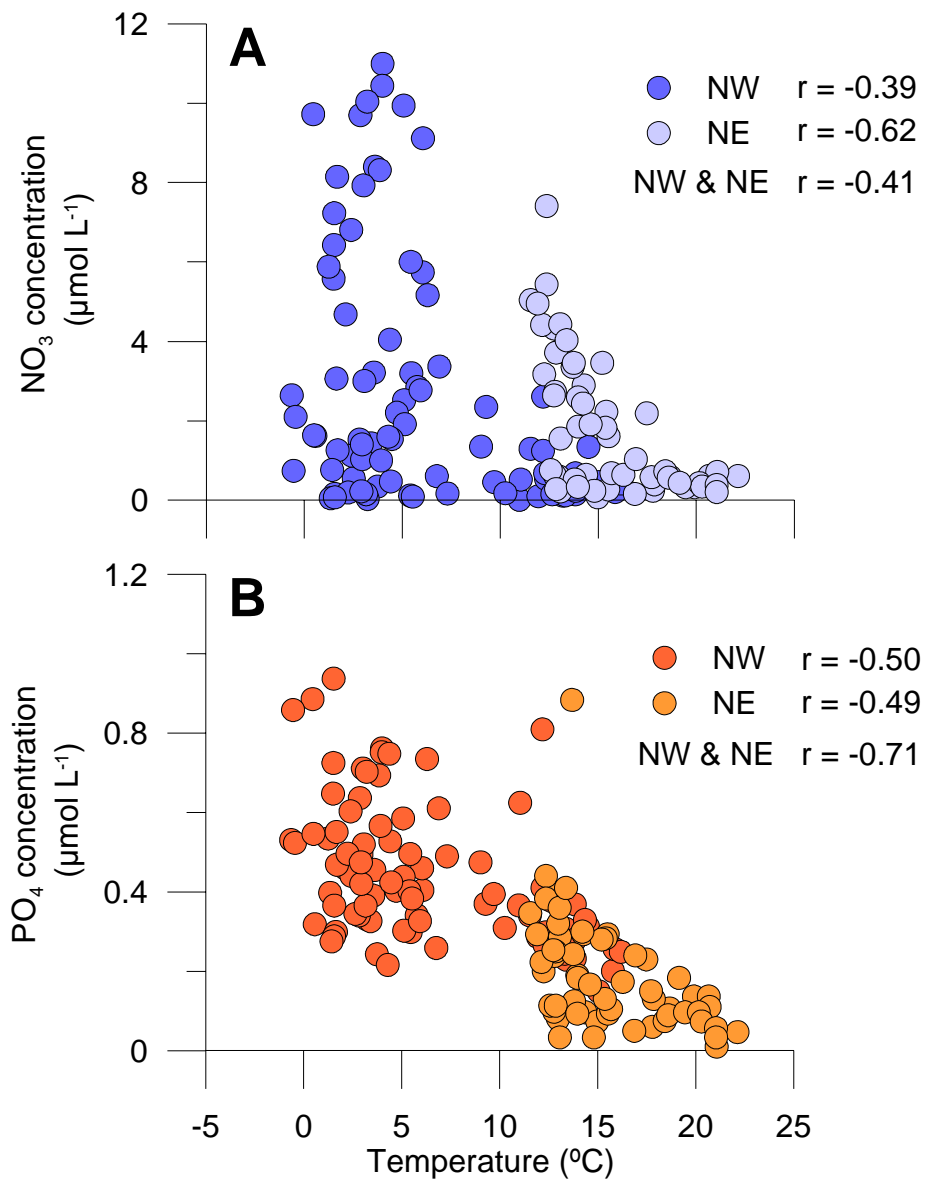


Fig. 5

SUPPORTING INFORMATION

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

Region	Temp (°C)	NO ₃ (µmol L ⁻¹)	PO ₄	Chl (µg L ⁻¹)	Pro	Syn (x 10 ⁴ cells mL ⁻¹)	Euk
NW	6.0 (-0.6-16.1)	2.67 (0.01-11.0)	0.44 (0.15-0.94)	2.13 (0.08-14.1)	0	1.99 (0.001-19.9)	0.95 (0.02-6.87)
NE	15.7 (11.6-22.1)	1.67 (0.07-7.4)	0.18 (0.01-0.88)	0.71 (0.19-3.76)	1.26 (0-12.1)	2.56 (0.03-13.9)	1.24 (0.25-5.44)
	***	*	***	***	***	ns	ns

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).

Region	Log-Y	X	Intercept	Slope	r^2	P-value	<i>n</i>
NE	Picophytoplankton abundance	Temperature	3.02 (0.20)	0.09 (0.01)	0.49	<0.0001	59
NW	Picophytoplankton abundance	Temperature	3.13 (0.05)	0.13 (0.01)	0.75	<0.0001	97
NE	Picophytoplankton cell-volume	Temperature	0.84 (0.12)	-0.06 (0.01)	0.56	<0.0001	59
NW	Picophytoplankton cell-volume	Temperature	0.08 (0.02)	-0.06 (0.01)	0.79	<0.0001	95
NE	Picophytoplankton abundance	Picophytoplankton cell-volume	4.31 (0.03)	-1.36 (0.12)	0.71	<0.0001	59
NW	Phytoplankton abundance	Picophytoplankton cell-volume	3.42 (0.06)	-1.90 (0.13)	0.68	<0.0001	98
NE	Picophytoplankton biomass	Temperature	0.28 (0.15)	0.03 (0.01)	0.16	0.0015	59
NW	Picophytoplankton biomass	Temperature	-0.40 (0.06)	0.07 (0.01)	0.48	<0.0001	95
NE & NW	Picophytoplankton biomass	Temperature	-0.38 (0.05)	0.07 (0.00)	0.66	<0.0001	154
NE	Phytoplankton biomass	Temperature	2.15 (0.19)	-0.05 (0.01)	0.20	0.0005	57
NW	Phytoplankton biomass	Temperature	2.11 (0.06)	-0.05 (0.01)	0.28	<0.0001	97
NE & NW	Phytoplankton biomass	Temperature	2.09 (0.05)	-0.04 (0.00)	0.39	<0.0001	154
NE	Picophytoplankton contribution	Temperature	0.08 (0.18)	0.09 (0.01)	0.47	<0.0001	57

NW	Picophytoplankton contribution	Temperature	-0.51 (0.09)	0.12 (0.01)	0.54	<0.0001	95
NE & NW	Picophytoplankton contribution	Temperature	-0.47 (0.06)	0.11 (0.01)	0.73	<0.0001	152

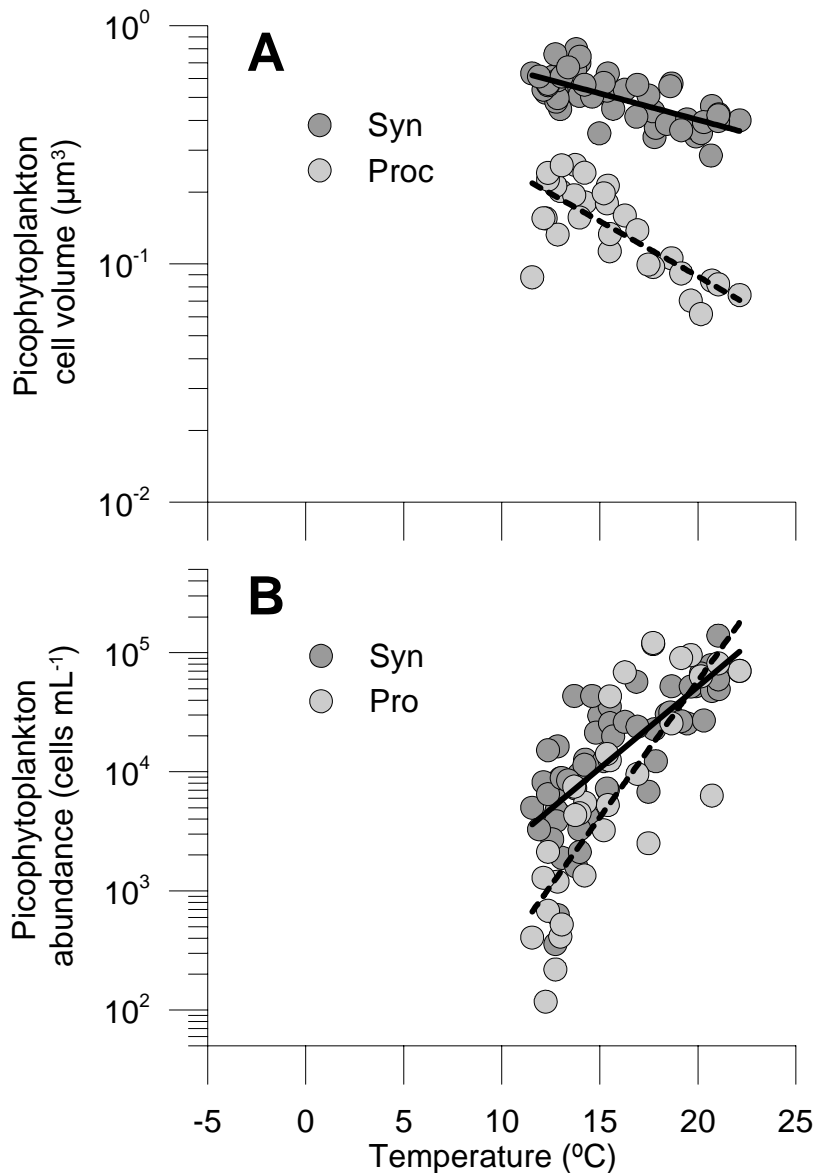


Fig. S1. The temperature-size and temperature-abundance rules for cyanobacteria. **(A)** Relationship between mean cell volume of *Synechococcus* (Syn) and *Prochlorococcus* (Proc) and temperature in the NE Atlantic region. **(B)** Relationship between *Synechococcus* and *Prochlorococcus* abundance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

The temperature size-rule and the average size of a community: The temperature size-rule (TSR) explains how the average size of individuals in a population decreases with increasing temperature but we extend it to the relationship between average community size and temperature. If community composition holds constant then the temperature-related decrease in size in each of the component populations will unequivocally result

in a smaller average size of the entire community. This is shown here for the two NE Atlantic picophytoplanktonic populations (*Synechococcus* and *Prochlorococcus*) for which we have size and abundance information. The average size of these two genera decreases with temperature as predicted by the TSR (Fig. S1A). Hence the change in average community size reported in Fig. 1B would likely result from the combination of these species-specific relationships into a community plot. The extension of the TSR from populations to communities is partially justified on the well known observation of latitudinal size variations. However shifts in phytoplankton community composition with temperature are well documented, driven by bottom-up processes associated with stratification, with warmer conditions favouring the predominance of smaller taxa within different functional groups (Karl *et al.* 2001; Finkel *et al.* 2005), thus enhancing the species-specific responses to temperature predicted by the TSR. An increase in temperature, stratification and nitrate limitation may also drive community composition to a relative increase in large sized nitrogen fixers such as *Trichodesmium*.

Fig. S1B above shows that population abundance increases with temperature for the two cyanobacteria. This is exactly the expected result from our argumentation detailed in the text for the temperature-picophytoplankton abundance relationship (Fig. 1). Interestingly, a stronger temperature-size relationship for *Prochlorococcus* than for *Synechococcus* (Fig. S1A) also results in a steeper slope of the abundance-temperature linear regression (0.23 vs 0.14, Figure S1B).

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