Resource supply alone explains the variability of marine phytoplankton size structure

Emilio Marañón,[*1] **Pedro Cermeño,**[2] **Mikel Latasa,**[3] **Rémy D. Tadonléké**[†4]

[1]Departamento de Ecología y Biología Animal, Universidade de Vigo, Vigo, Spain
[2]Institut de Ciéncies del Mar, Departament de Biologia Marina i Oceanografia, CSIC, Passeig Marítim de la Barceloneta, 37-49 E-08003, Barcelona, Spain
[3]Instituto Español de Oceanografía, Centro Oceanográfico de Gijón, Gijón, Spain
[4]INRA UMR CARRTEL, Thonon-Les-Bains, France

Abstract

Due to the covariation between temperature and resource availability in the surface ocean, a correct assessment of resource supply is crucial to determine if temperature has a direct effect on phytoplankton size structure. To remove the effect of resources, López-Urrutia and Morán analyzed data subsets with narrow ranges of variation in Chlorophyll a (Chl a) concentration and found that temperature is correlated with Chl *a* partitioning among size classes, from which they concluded that temperature is an important variable to explain the variability of phytoplankton size structure. Our analysis, however, shows that resource supply varies widely also within these subsets and, importantly, that it is inversely correlated with temperature. Therefore, the relationship between temperature and size structure reflects instead the effect of resources. When groups of samples with similar resource supply conditions are considered, no correlation between temperature and phytoplankton size structure is observed, which invalidates the conclusion of López-Urrutia and Morán. Even within restricted ranges of variation for phytoplankton biomass and production, changes in resource supply alone are sufficient to explain the variability of phytoplankton size structure in the sea.

Assessing the relative importance of temperature vs. resources in the control of phytoplankton size structure is difficult due to the covariation of temperature and nutrient supply in the sea. Unlike previous studies (Agawin et al. 2000; Morán et al. 2010; Hilligsøe et al. 2011), the dataset used by Marañón et al. (2012) included observations from all combinations of temperature and resource availability conditions. This allowed us to show that small and large cells dominate under conditions of low and high resource availability, respectively, and that this pattern occurs regardless of seawater temperature. We, therefore, concluded that temperature plays no direct role in the control of marine phytoplankton size structure. In their comment, López-Urrutia and Morán (2015) reanalyse our dataset after partitioning it into subsets and argue that temperature is an important explanatory variable to understand the variability of phytoplankton size structure, particularly in oligotrophic waters. Here, we show that this conclusion is unwarranted, due to

an inadequate assessment of resource availability by López-Urrutia and Morán (2015).

The approach used by López-Urrutia and Morán (2015) (their Figs. 2, 3) has major shortcomings. First, they reduce the variability in Chlorophyll *a* concentration (Chl *a*) and primary production to a small fraction ($< 3\%$) of its natural range, but then they use these variables in the regression against the percentage of Chl *a* in different size classes. Not surprisingly, they find that the amount of variability in size structure that is explained by total Chl *a* or primary production is very small. Second, and more importantly, they assume that samples within a given range of Chl *a* or primary production correspond to assemblages that were all experiencing the same degree of resource availability. But, if we consider the location where samples were obtained (Fig. 1), it is unlikely that they correspond to environments with the same resource availability, notwithstanding the fact that Chl *a* levels were similarly low (Fig. 1A) or high (Fig. 1B). For instance, surface Chl *a* or primary production values in a highly productive system such as Ría de Vigo (NW Iberian peninsula) (Cermeño et al. 2006) can be on occasion as low as those measured in the oligotrophic waters of the tropical Atlantic (Marañón et al. 2001), yet it would be unjustified to

*Correspondence: em@uvigo.es

†Present address: Département des Sciences Biologiques, Université du Québec à Montréal, Canada
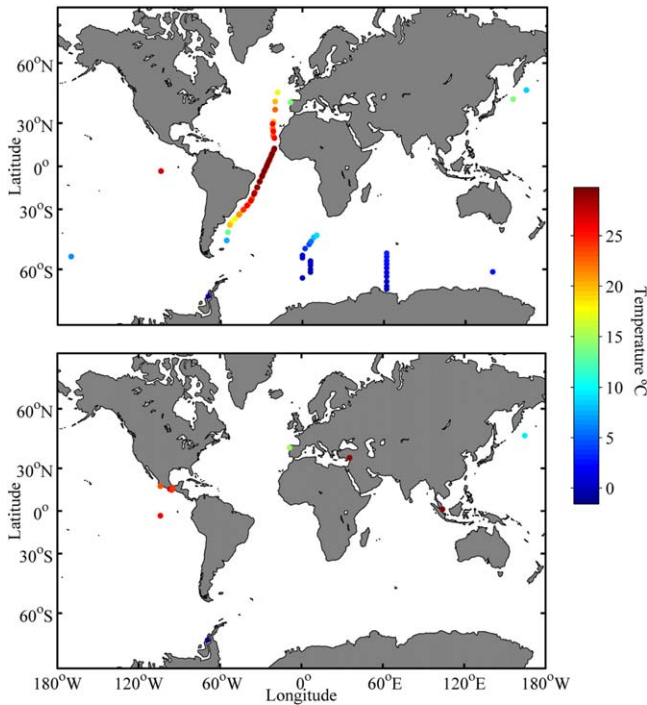
Fig. 1. Location and seawater temperature for surface samples with (A) low (<1 μg L^{-1}) and (B) high (>2 μg L^{-1}) Chl *a* concentration. When repeated measurements were available for the same location, mean temperature values were calculated. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

assume that resource supply conditions in the two systems are the same at any time. Chl *a* and primary production are valid indicators of resource supply and use when applied over a wide range of variability (in our analysis, approximately three orders of magnitude), but not necessarily when small ranges of variation are considered. For instance, the large variability (>20-fold) in the carbon to Chl *a* ratio means that Chl *a* concentration can be an unreliable indicator of phytoplankton biomass (Kruskopf and Flynn 2005). Similarly, at the local scale and over restricted ranges of variation, primary production may be only loosely related to resource supply conditions, due to the uncoupling between phytoplankton production and loss processes.

The key question is, thus, to ascertain whether sampling sites with different temperatures differ only in temperature or if in fact they differ also in resource supply. López-Urrutia and Morán (2015) acknowledge that some of the effects of temperature on size structure could be the result of covariation between temperature and nutrient supply, but they do not attempt to quantify this effect.

To assess if samples with different temperatures but similarly low (Fig. 1A) or high (Fig. 1B) Chl *a* concentrations have the same resource supply conditions, we used the resource supply index (RSI) described by Marañón et al. (2014). RSI is calculated as:
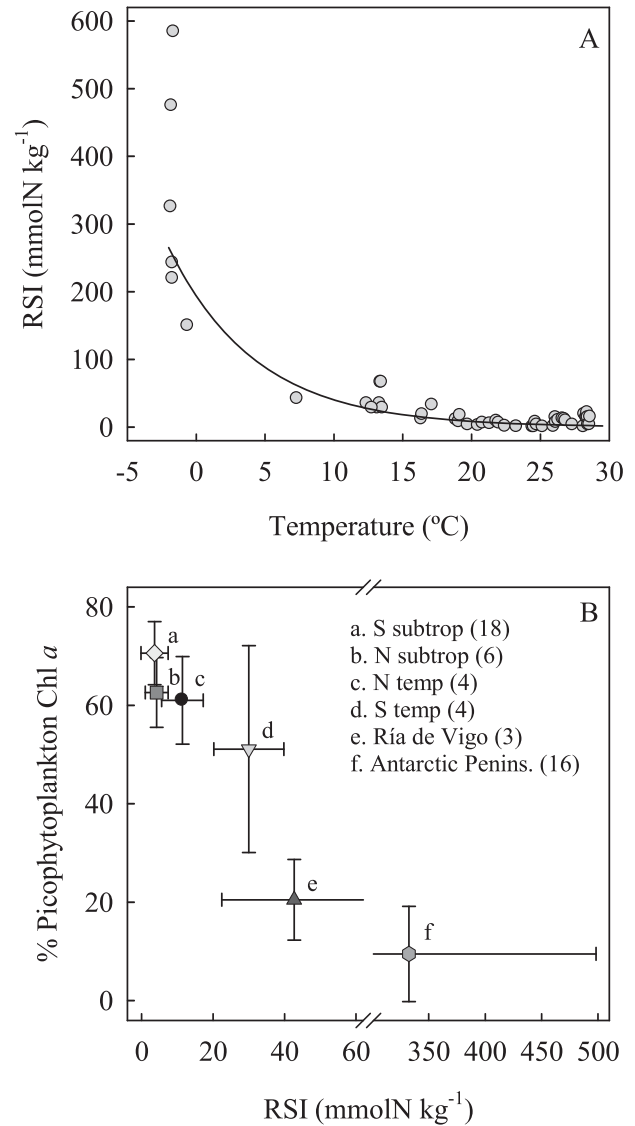

Fig. 2. (A) Relationship between temperature and the resource supply index (RSI) in locations with low surface Chl *a* concentration. The exponential fit is $y = 188.1 \ e^{-0.156x}$ ($r^2 = 0.45$, $p < 0.001$, $n = 50$). For the Rothera Time Series (RaTS) station in west Antarctic Peninsula, RSI was calculated only when the daily mean incident irradiance (PAR) was above the saturation irradiance for photosynthesis (I_k), which for the Antarctic Peninsula shelf takes an average value of 78 μmol photon m^{-2} s^{-1} (Moline et al. 1998). (B) Mean values ($\pm$ standard deviation) of RSI and picophytoplankton contribution to total Chl *a* concentration in the north (35–50°N) and south (35–50°S) temperate Atlantic ocean, the north (20–35°N) and south (6–35°S) Atlantic subtropical gyres, and coastal waters of Ría de Vigo (NW Iberian Peninsula) and the RaTS site (west Antarctic Peninsula). Number of samples for each region are indicated in parentheses.

$$RSI = \frac{NO_{3[1\%PAR]}}{\Delta\sigma_t} \times \frac{1\%PARz}{UMLz}$$

where $NO_{3[1\%PAR]}$ is the nitrate concentration at the base of the euphotic zone, $\Delta\sigma_t$ is the seawater density difference
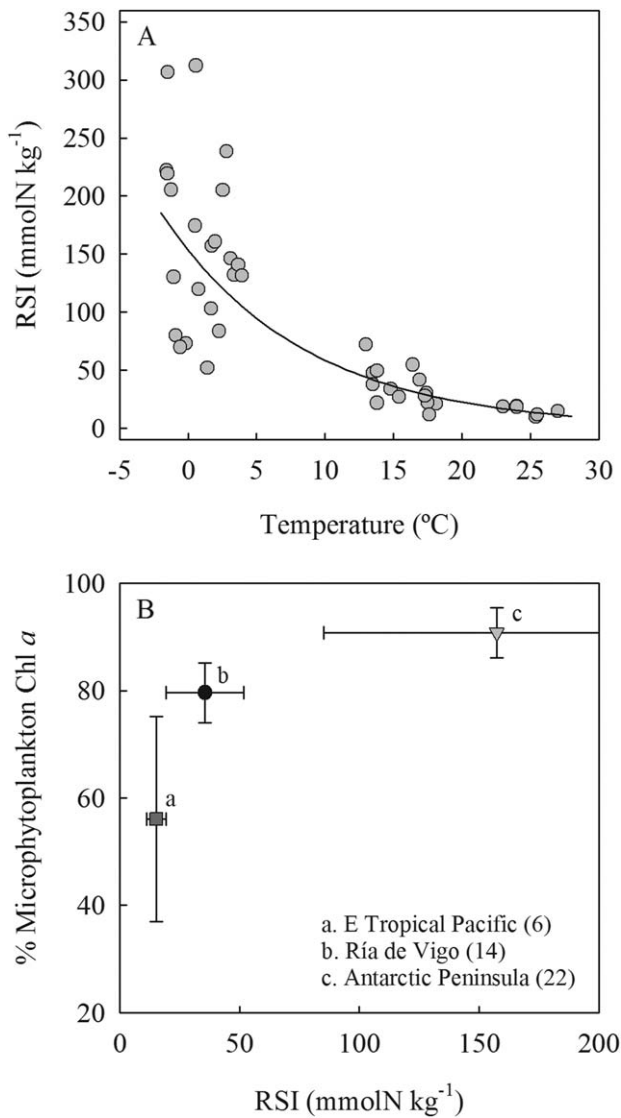
Fig. 3. (A) Relationship between temperature and RSI in locations with high surface Chl *a* concentration. The exponential fit is $y = 153.2 \, e^{-0.096x}$ ($r^2 = 0.82$, $p < 0.001$, $n = 42$). (B) Mean values ($\pm$ standard deviation) of RSI and microphytoplankton contribution to total Chl *a* concentration in west Antarctic Peninsula, Ría de Vigo, and the eastern tropical Pacific ocean.

between the surface and the base of the euphotic zone, 1%PARz is the depth of the euphotic zone, and UMLz is the depth of the upper mixed layer, defined as the first depth at which σ_t is 0.125 units higher than the surface value. Thus, RSI is based on nutrient concentration but also takes into account the degree of vertical stratification, which modulates upward nutrient transport, and the relationship between mixed layer depth and euphotic depth, which is a proxy for light limitation. López-Urrutia and Morán (2015) question the validity of this index because it is based on a single macronutrient. However, excluding denitrification areas, the concentrations of major macronutrients (nitrate, phosphate,

silicate) below the surface layer tend to covary through Redfield stoichiometry (Tyrrell 2001) and, therefore, using other nutrients would only affect the absolute values of RSI, not its patterns of variability. The rationale for using nitrate concentration is that nitrogen is the primary limiting nutrient for phytoplankton growth and production in the tropical and subtropical regions of the open ocean, as well as in temperate and polar seas during periods of seasonal stratification (Moore et al. 2013). RSI is explicitly not applied (Marañón et al. 2014) to high-nutrient, low-chlorophyll (HNLC) regions, where iron can be limiting for phytoplankton (Boyd et al. 2007; Moore et al. 2013). While acknowledging that RSI provides only a rough approximation to local-scale resource availability, we maintain that it represents a significant improvement over previous assessments based solely on the use of nutrient concentrations (Morán et al. 2010; Hilligsøe et al. 2011; Mousing et al. 2014). In this regard, we have recently shown that RSI captures the variability in resource supply between different coastal and open-ocean regions over broad latitudinal ranges, and that this variability leads to a resource-driven, biogeographic pattern in phytoplankton growth rates (Marañón et al. 2014) and size structure (Marañón 2015).

We found a significant, inverse relationship between temperature and RSI in low-Chl *a* samples from the tropical, subtropical, and temperate Atlantic Ocean, as well as from the coastal waters of Ría de Vigo and west Antarctic peninsula (Fig. 2A). Within open-ocean regions, the lowest RSI values were determined for the strongly stratified subtropical gyres, whereas higher RSI values were found in temperate waters. Even higher RSI values were calculated for Ría de Vigo, a coastal embayment where high nutrient concentrations coincide with a modest degree of vertical stratification, and upper mixed layers are typically shallow in relation to the depth of the euphotic zone. The highest RSI values occurred at the Rothera Time Series (RaTS) site in Marguerite Bay (west Antarctic Peninsula) (Clarke et al. 2008), as a result of the presence of very high nutrient concentrations at the base of the euphotic layer (e.g., $> 20 \ \mu mol \ L^{-1}$ of nitrate) and small vertical density gradients. The pattern of increasing resource availability from the subtropical gyres to temperate, open-ocean waters and then coastal waters was associated with a marked decrease in the relative Chl *a* contribution of picophytoplankton, from $>60\%$ in the subtropical gyres to 20% in Ría de Vigo and 10% in west Antarctic Peninsula (Fig. 2B). We also found a strong, inverse relationship between temperature and RSI in high-Chl *a* samples from the western Antarctic peninsula, the eastern tropical Pacific, and Ría de Vigo (Fig. 3A). As was the case in low-Chl *a* samples, phytoplankton size structure changed with resource availability also in these high-Chl *a* samples: the microphytoplankton contribution to total Chl *a* increased with increasing RSI (Fig. 3B). These observations indicate that the correlation between temperature and phytoplankton size

Table 1. Mean (± standard deviation) temperature, Chl *a* concentration, and contribution (%) to total Chl *a* by picophytoplankton in nonfertilized waters (Out; dissolved iron concentration < 0.1 nmol L^{-1}) during in situ iron release experiments. *n* is the number of measurements in each region.

Region	*n*	Temperature (°C)	[Chl *a*] (*µ*g L^{-1})	% Picophytoplankton Chl *a*	Source
Southern Ocean (*SOIREE*, Out)	14	2.6 ± 0.1	0.2 ± 0.1	39 ± 11	Gall et al. (2001)
W Subarctic Pacific (*SEEDS* I, Out)	10	8.9 ± 0.4	0.8 ± 0.1	27 ± 9	Tsuda et al. (2003)
E Subarctic Pacific (*SERIES*, Out)	5	11.5	0.4 ± 0.2	16 ± 6	Marchetti et al. (2006)

SOIREE, Southern Ocean Iron Release Experiment; *SEEDS*, Subarctic Pacific Iron Experiment for Ecosystem Dynamics Study; *SERIES*, Sub-Arctic Ecosystem Response to Iron Enrichment Study.

Table 2. Mean (± standard deviation) temperature, Chl *a* concentration, and contribution (%) to total Chl *a* by microphytoplankton in different regions which, at the time of sampling, had low (< 1 *µ*g L^{-1}) Chl *a* concentrations. *n* is the number of measurements in each region.

Region	*n*	Temperature (°C)	[Chl *a*] (*µ*g L^{-1})	% Microphytoplankton Chl *a*	Reference
Antarctic Polar Front	8	4.4 ± 2.8	0.2 ± 0.1	7 ± 4	Froneman et al. (2001)
Okhotsk Sea (NW Pacific Ocean)	9	6.3 ± 2.9	0.7 ± 0.2	11 ± 11	Shiomoto (1997)
W subarctic Pacific (summer and autumn)	7	11.3 ± 3.2	0.6 ± 0.2	7 ± 1	Imai et al. (2002)
Atlantic subtropical gyres	23	23.6 ± 3.1	0.1 ± 0.1	9 ± 5	Marañón et al. (2001)

structure shown by López-Urrutia and Morán (2015) is in fact the result of a correlation between temperature and resource availability, which, in turn, due to size-related differences in resource uptake and use (Litchman et al. 2007; Marañón 2009; Marañón et al. 2013; Marañón 2015), controls phytoplankton size structure.

López-Urrutia and Morán (2015) interpret their temperature-dependent functions (Fig. 2B,D) as a direct effect of temperature on phytoplankton size structure. Thus, the linear fit in their Fig. 2B predicts that the contribution of picophytoplankton to total Chl *a* increases by 16% for each 10°C of warming. To check if this relationship is in fact reflecting a causality link between temperature and size structure, we examined data from nonfertilized waters in HNLC regions, where low iron availability (< 0.1 nmol L^{-1} dissolved Fe concentrations) limits phytoplankton production and growth (Boyd et al. 2007), and standing stocks are low (i.e., Chl *a* < 1 *µ*g L^{-1}). Nonfertilized waters in the *SERIES* and *SEEDS* I experiments had a much lower picophytoplankton contribution than in the *SOIREE* experiment (Table 1), despite the fact that their temperature was considerably warmer – in direct contradiction with the predictions of López-Urrutia and Morán (2015). Similarly, the prediction that microphytoplankton contribution should decrease with increasing temperature (their Figs. 2D, 3D) is not verified when one compares low-Chl *a* waters from polar, subpolar, and tropical regions (Table 2): the percentage of Chl *a* in the microphytoplankton fraction remains constant across a 20°C temperature range.

The relationship between RSI and temperature indicates that, for temperatures above approximately 18°C in our data-set, resource supply conditions are relatively invariant both in low-Chl *a* (Fig. 2A) and high-Chl *a* (Fig. 3A) samples. To explore further if temperature alone (i.e., without being associated with changes in resource supply) is associated with changes in phytoplankton size structure, we examined the relationship between temperature and the contribution of picophytoplankton and microphytoplankton to total Chl *a* over the temperature range 18–30°C (Fig. 4). We found that temperature is not correlated to the contribution to total Chl *a* by picophytoplankton (Fig. 4A) and microphytoplankton (Fig. 4B). The lack of correlation between temperature and Chl *a* contribution by size classes over a substantial range of temperature (>12°C), in samples that had similar resource supply conditions, invalidates the claim by López-Urrutia and Morán (2015) that temperature is an important explaining variable of phytoplankton size structure at the global scale.

We think we have correctly appraised the importance given by Morán et al. (2010) to the temperature-size rule (TSR) as a mechanism to explain the pattern of increasing picophytoplankton dominance with temperature. The TSR rule is mentioned profusely throughout their article, illustrated in their Fig. 3, and used to make predictions which are then confirmed by the data. The following passages in Morán et al. (2010) show that the TSR rule is presented as the main mechanism responsible for the relationship between temperature and size structure: *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* (Abstract); *the relative contribution of*
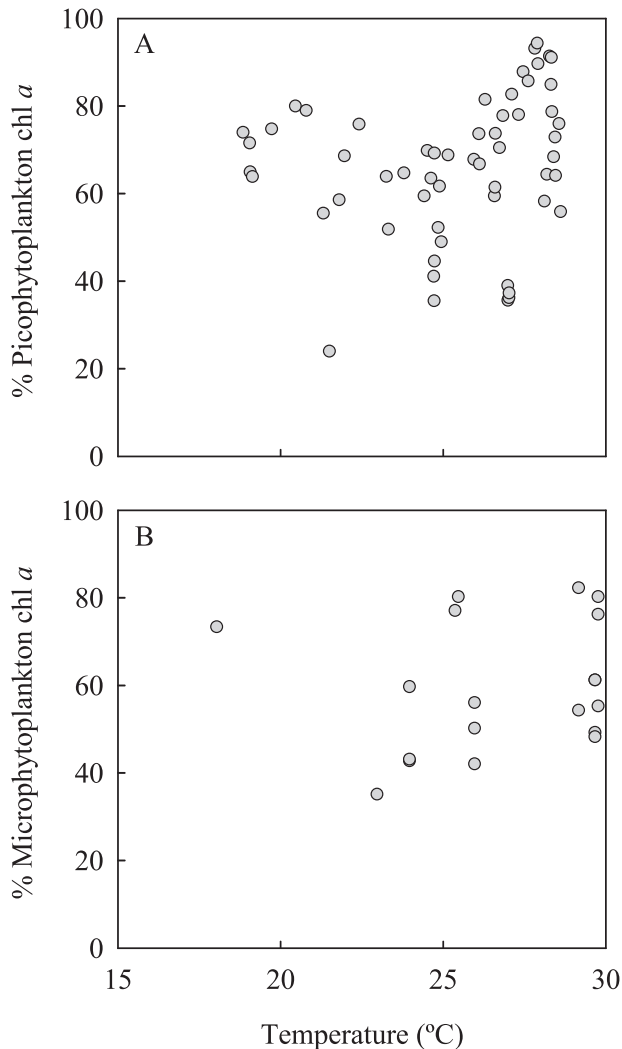
Fig. 4. Relationship between temperature and the percentage contribution by (A) picophytoplankton and (B) microphytoplankton to total Chl *a* concentration in samples with (A) low (<1 μg L^{-1}) and (B) high (>2 μg L^{-1}) Chl *a* concentration. Pearson's *r* values are 0.18 ($p = 0.17$, $n = 57$) in (A) and 0.14 ($p = 0.55$, $n = 19$) in (B).

picophytoplankton (…) should vary with temperature as a consequence of a combination of the TSR and the within-community size scaling of abundance (p. 1139); *the currently observed changes in phytoplankton were mainly related to temperature through the mechanism depicted in Fig. 3* (p. 1142).

López-Urrutia and Morán (2015) point out, referring to the study of Peter and Sommer (2012), that the TSR rule has now been shown to have a much stronger effect than the average of 2.5% shrinkage per °C reported by Atkinson et al. (2003). However, Peter and Sommer (2012) obtained a mean value of −0.60 for the slope of the log–log relationship between temperature and cell volume, which corresponds to a 3.6% decrease in cell size per °C of warming. When we repeat our simulations in Marañón et al. (2012), using this new value for the TSR, we find that a 10°C warming leads to

an increase in picophytoplankton contribution from 2.6% to 3.3%. If we compare this with the results of Morán et al. (2010), who observed an increase in picophytoplankton contribution from 4% to 70% with a 10°C increase in temperature (from 10°C to 20°C, their Fig. 2), then we must conclude that the TSR rule plays a very minor role in explaining the observed relationships between temperature and phytoplankton size structure in the ocean.

In Marañón et al. (2012), we used multiple regression to quantify the relative importance of temperature and resources (as reflected in the rate of primary production) in the control of phytoplankton size structure. We found that temperature and primary production explained 2% and 62%, respectively, of the variability in the contribution of microphytoplankton to total biomass. López-Urrutia and Morán (2015) argue that our analyses suffer from the so-called spurious correlation problem, because the dependent variable, percentage of Chl *a* in a given size class, carries in the denominator the total Chl *a* concentration, which is itself highly correlated with primary production, the independent variable. In their review of the spurious correlation problem in ecology, Prairie and Bird (1989) concluded that the fact that the same term appears in both the dependent and the independent variable does not invalidate the resulting relationship, provided that the measurement error in the independent variable is small relative to the population variance. The coefficient of variation of replicated Chl *a* measurements is <10%, a very small value considering that the total range of variability in Chl *a* concentration in our dataset is >800-fold. Other well-established relationships in ecology are also based on relationships between variables sharing a common term, such as the self-thinning law in plants or the allometry of metabolic rates in animals (Prairie and Bird 1989). In the latter case, metabolic rate (*R*) scales as the $3/4$-power of body mass (*M*), such that $R \propto M^{3/4}$. If mass-specific metabolic rate is calculated, this new variable scales as $M^{-1/4}$. The two relationships are equally valid expressions of a fundamental biological pattern, namely that the pace of metabolism in animals tends to slow down as body size increases. In a similar way, the Chl *a* concentration in picophytoplankton and microphytoplankton show fundamentally different patterns of variability in their relationship to total Chl *a* concentration (Fig. 5), and, therefore, the relationship between percentage Chl *a* and total Chl *a* concentration is also different for each size class. Picophytoplankton and microphytoplankton Chl *a* scale as total Chl *a* concentration to the power of 0.15 and 1.66, respectively (Fig. 5). As a result, the Chl *a* contribution of picophytoplankton and microphytoplankton scales as total Chl *a* concentration to the power of −0.85 and 0.66, respectively. Thus, the fast increase in the Chl *a* contribution of picophytoplankton as total Chl *a* concentration decreases below 1 μg L^{-1} is a genuine biological pattern that does not arise from data treatment.
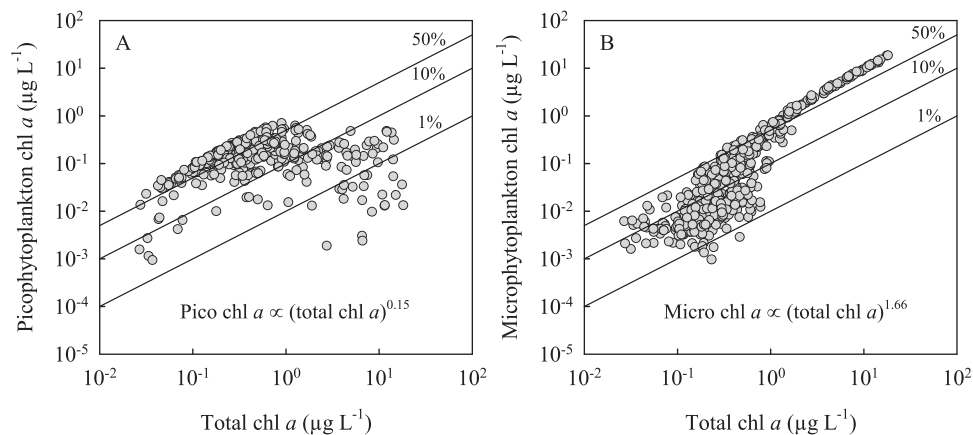
Fig. 5. Relationship between total Chl *a* concentration and Chl *a* concentration in the (A) picophytoplankton and (B) microphytoplankton size classes in coastal and open-ocean waters of polar, temperate, and tropical regions ($n = 496$). The linear fits between log-transformed variables were (A) $y = 0.15\,x - 0.83$, $r^2 = 0.035$, $p < 0.005$, and (B) $y = 1.66\,x - 0.63$, $r^2 = 0.82$, $p < 0.001$.

López-Urrutia and Morán (2015) claim that we neglected the consideration of the role of nutrients by Morán et al. (2010). However, in Marañón et al. (2012), we did discuss in detail the validity of nutrient concentration as a proxy for resource availability and use, but pointed out that it has serious limitations and concluded that *simply taking into account nutrient distribution does not allow evaluation of the relative role of temperature vs. resources in controlling phytoplankton size structure* (p. 1275, 1st para). The main reason is that dissolved nutrient concentrations are often disconnected from nutrient supply and utilization rates and, thus, phytoplankton size structure. Examples include (i) low nutrient concentration at the peak of blooms (typically dominated by large cells) (Cermeño et al. 2006), (ii) high nutrient concentrations during conditions of intense vertical mixing and/or low incident irradiance, which lead to light limitation and a dominance of small cells (Clarke et al. 2008), and (iii) constantly low nutrient concentrations in the upper layer in spite of large changes in nutrient diffusive fluxes into the euphotic layer (Mouriño-Carballido et al. 2011). As a result, the studies of Morán et al. (2010) and López-Urrutia and Morán (2015), as well as those of Hilligsøe et al. (2011) and Mousing et al. (2014), suffer from an inadequate assessment of resource supply, which leads to their conclusion that temperature has a direct effect on phytoplankton size structure. Our analysis, however, shows that, even within restricted ranges of variation for phytoplankton biomass and production, changes in resource supply alone are sufficient to explain the variability of phytoplankton size structure in the sea.

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