

Temperature affects the size-structure of phytoplankton communities in the ocean

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Abstract

The strong inverse correlation between resource availability and temperature in the ocean poses a challenge to determine the relative effect of these two variables on the size-structure of natural phytoplankton communities. Marañón et al (2012) compiled a dataset of concurrent temperature and resource level proxies that they claim disentangled the effect of temperature from that of resource supply. They concluded that the hypothesis that temperature per se plays a direct role in controlling phytoplankton size structure should be rejected. But our reanalysis of their data reaches a very different conclusion and suggests that they failed to separate the effects of temperature from the effects of resources. Although we obviously concur with Marañón et al (2012) in the long-known predominance of small phytoplankton cells under oligotrophic conditions, from our point of view this should not deter us from considering temperature as an important explanatory variable at a global scale since we show that, for the vast oligotrophic areas of the world's oceans where chlorophyll concentrations are below $<1 \mu\text{g L}^{-1}$ temperature explains a high proportion of the variability in the size distribution of phytoplankton communities, a variability that can not be explained on the basis of the resource level proxies advocated by Marañón et al. (2012).

The size-structure of marine phytoplankton communities determines many of the community rates and biogeochemical fluxes in the ocean. Hence, there is a demand to understand the effects of temperature and resource availability on phytoplankton size composition as both environmental variables are expected to change under future climate scenarios. Morán et al. (2010) analyzed two picophytoplankton time series in the North Atlantic to show that temperature was able to explain a high percentage of variability in size-structure. This conclusion was challenged by Marañón et al. (2012) who compiled a dataset of 500 measurements of size-fractionated Chlorophyll *a* (Chl *a*) concentration in the euphotic layer of the oceans to study the effects of resources and temperature on the size-structure of phytoplankton communities. Marañón et al. (2012) found a strong correlation between the size-structure of the phytoplankton communities and productivity levels, a conclusion we concur with. The evidence supporting the predominance of small phytoplankton cells under oligotrophic conditions is overwhelming and was summarized by Chisholm (1992) in the sentence: “One thing that can be stated unequivocally about phytoplankton size is that the fractional contribution of small cells to the standing crop increases as total chlorophyll

decreases.” The reason for this pattern is probably the conjunction of several factors including resource acquisition strategies (Irwin et al. 2006), grazing (Irigoien et al. 2005), and sinking effects (Rodríguez et al. 2001).

Hence, we agree with Marañón et al. (2012) in that to determine the effect of temperature on phytoplankton size-structure it is necessary to study gradients in temperature that are not associated with changes in total phytoplankton biomass. Marañón et al. (2012) built a second dataset of 330 concurrent temperature and size-fractionated chlorophyll measurements that, supposedly, disentangled the effect of temperature from that of resource supply. They show that, for this new dataset, temperature explains very little variance in the percentage of total chlorophyll in the picophytoplankton size fraction. Based on this analysis Marañón et al. (2012) concluded that the hypothesis that temperature per se can affect phytoplankton size-structure should be rejected. But the effects of resource availability, as indicated by the correlation between percentage contribution of picophytoplankton and total chlorophyll concentration are still present in this second dataset (Fig. 1A), and hence, the analysis of Marañón et al. (2012) fails to fully separate the effects of temperature from the effects of resources. Most of the data at high temperatures where the percent contribution of picophytoplankton is low correspond to areas where the

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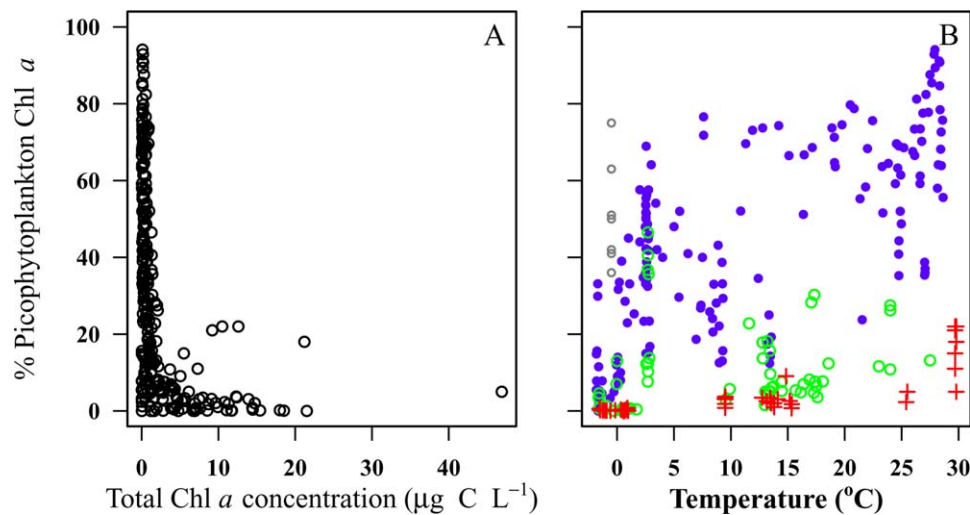


Fig. 1. Percent contribution of picophytoplankton to total Chl *a* concentration vs. (A) the total Chl *a* concentration and (B) temperature. Data was kindly provided by Marañón et al. (2012) and correspond to the references cited in their Table 2. In (B) blue filled circles represent conditions with total chlorophyll concentrations $< 1 \mu\text{g L}^{-1}$, green empty circles conditions between $1 \mu\text{g L}^{-1}$ and $2 \mu\text{g L}^{-1}$ and red crosses conditions where chlorophyll levels are $> 2 \mu\text{g L}^{-1}$. Grey circles represent data where total chlorophyll concentration was not available. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

total biomass is high (i.e., chlorophyll concentration $> 2 \mu\text{g L}^{-1}$, Fig. 1B).

A better way to disentangle the effects of temperature and resources is to build subsets of the data with sufficient variation in temperature but for which the effect of resources on phytoplankton size-structure is negligible. For example, if we consider only conditions where total chlorophyll concentration is $< 1 \mu\text{g L}^{-1}$, the effect of resource availability (using total chlorophyll as a proxy) is very low ($r^2 = 0.07$, $n = 164$, $p < 0.001$, Fig. 2A), but temperature explains a significant amount of variation of the percent contribution of picophytoplankton to total biomass ($r^2 = 0.49$, $n = 164$, $p < 0.001$, Fig. 2B). Marañón et al. (2012) stated in the abstract that “picophytoplankton contribution is substantial ($> 40\%$), at all temperatures, only when chlorophyll *a* (Chl *a*) concentration is $< 1 \mu\text{g L}^{-1}$.” However, using their data, we observe that when total chlorophyll is $< 1 \mu\text{g L}^{-1}$ the percent contribution of picophytoplankton varies widely from about 0% to 100% and the contribution of picophytoplankton increases with increasing temperature (Fig. 2B). Similarly, Marañón et al. (2012) asserted that “This contribution (the contribution of microphytoplankton to total biomass) increases rapidly with total biomass and productivity, reaching values $> 80\%$ when Chl *a* concentration is $> 2 \mu\text{g L}^{-1}$ irrespective of water temperature.” When we plot the percent contribution of microphytoplankton to total biomass at Chl *a* concentrations $> 2 \mu\text{g L}^{-1}$ (Fig. 2C, $r^2 = 0.07$, $n = 71$, $p = 0.02$) it varies from about 40% to 100%, decreasing with increasing temperature (Fig. 2D, $r^2 = 0.57$, $n = 75$, $p < 0.001$), values $> 80\%$ were only reached when water temperatures were below $17\text{--}18^{\circ}\text{C}$. Contrary to their general assertions temperature played a significant role within each subset, of high or

low productivity, of their data. Even if we make stronger restrictions on the range of chlorophyll concentrations considered (Table 1), the effect of temperature on the size-structure of phytoplankton communities is evident. In each of six different resource level classes the percentage contribution of picophytoplankton to total biomass increased with increasing temperature. Similarly, the percentage contribution of microphytoplankton decreased with increasing temperature (Table 1). Both for picophytoplankton and microphytoplankton, with the exception of the resource level class between $1 \mu\text{g L}^{-1}$ and $2 \mu\text{g L}^{-1}$, the relationships with temperature were significant. Furthermore, the pattern observed could not be explained by resource level proxies.

Chlorophyll concentration is a coarse proxy for primary productivity since both variables are highly correlated. The patterns shown in our Fig. 2 using chlorophyll as a proxy for resource supply are confirmed using instead primary productivity, albeit with a lower number of data (Fig. 3). Again, when resource supply (using primary production as a proxy) is low ($< 25 \mu\text{g C L}^{-1} \text{ d}^{-1}$) the effect of resource availability is very low ($r^2 = 0.12$, $n = 105$, $p < 0.001$, Fig. 3A), but temperature explains a significant amount of variation of the percent contribution of picophytoplankton to total biomass ($r^2 = 0.43$, $n = 105$, $p < 0.001$, Fig. 3B). Similarly, when primary production is high ($> 200 \mu\text{g C L}^{-1} \text{ d}^{-1}$) the effect of resource supply on the percent contribution of microplankton to total chlorophyll is not significant ($r^2 = 0.08$, $n = 17$, $p = 0.28$, Fig. 3C) but temperature explains a significant amount of the variance in microplankton contribution ($r^2 = 0.37$, $n = 17$, $p < 0.05$, Fig. 3B). In any case, primary productivity itself is also a coarse proxy for resource supply. It is fundamentally difficult to get a synoptic measure of resource

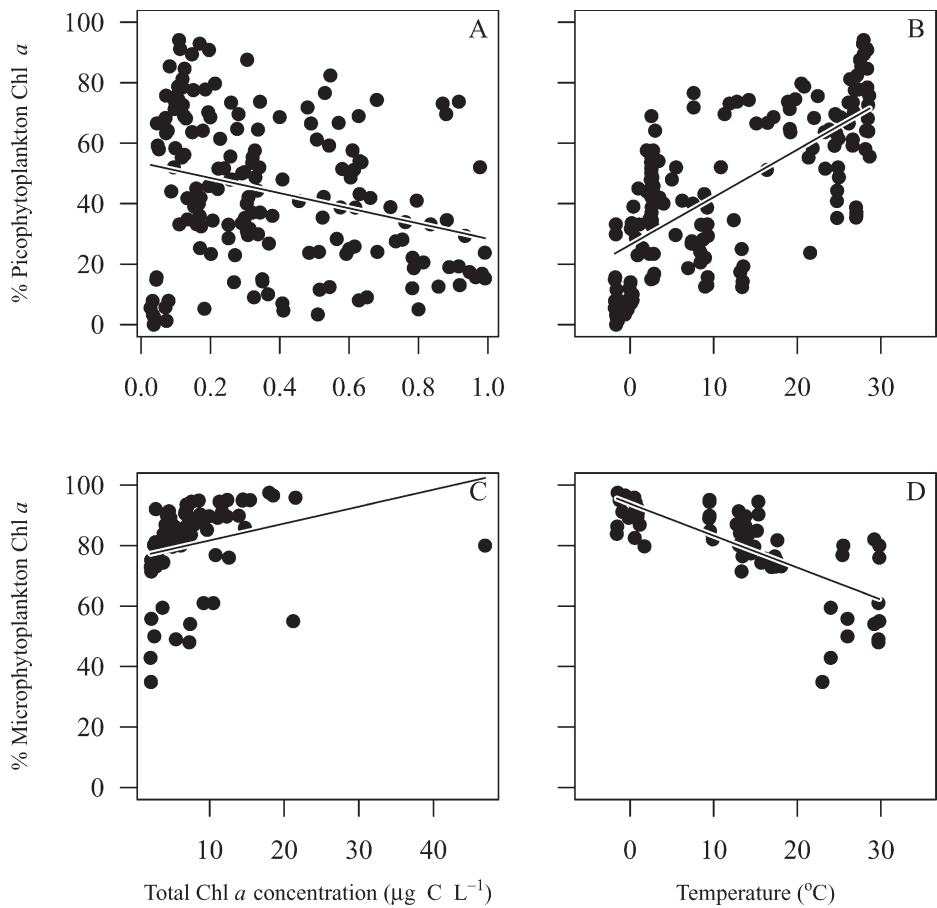


Fig. 2. Percent contribution of (A, B) picophytoplankton and (C, D) microphytoplankton to total Chl *a* concentration vs. (A, C) the total Chl *a* concentration and (B, D) temperature . Data are from Table 2 in Mara \acute{n} on et al. (2012). (A, B) present a subset of the dataset where total chlorophyll concentrations < 1 $\mu\text{g L}^{-1}$, while (C, D) present another subset where total chlorophyll concentrations > 2 $\mu\text{g L}^{-1}$. Similar to Mara \acute{n} on et al. (2012) Figs. 3 and 4 but with different data subsets and scales.

supply in the ocean where phytoplankton growth may be under the control of multiple factors, including inorganic nutrients, trace metals, or irradiance. The calculation of a valid resource supply index based on a single macronutrient which summarizes all these dependencies (Mara \acute{n} on et al. 2014) can be highly debatable too and the problem of separating resource supply from temperature dependence in the ocean remains elusive. The situation is even further complicated by the decoupling in space and time between accumulated biomass and the supply of resources and the growth of phytoplankton. It is difficult to resolve the effects of temperature from the effects of resources and we acknowledge that some of the effects of temperature on size structure could still be a result of correlations between temperature and stratification or nutrient supply not captured by the categorizations in primary productivity.

So, contrary to Mara \acute{n} on et al. (2012) views, our analysis shows that there is no reason to reject the hypothesis that temperature “per se” plays a direct role in controlling the variability of phytoplankton size-structure in the ocean. Our

reanalysis of Mara \acute{n} on et al. (2012) dataset is in agreement with the results by Mousing et al. (2014) using an independent dataset and with recent experimental results in

Table 1. Pearson correlations between temperature and the percentage of Chl *a* in each size fraction (pico < 2 μm , nano 2–20 μm , and micro > 20 μm) when the original dataset of Mara \acute{n} on et al. 2012 was divided into six productivity classes of increasing Chl *a* content. ns, not significant, * p < 0.05, ** p < 0.01, *** p < 0.001. *n*, number of data (note that *n* varies because sometimes one of the size fractions was not measured)

Resource level	%Pico	%Nano	%Micro	<i>n</i>
($\mu\text{g Chl L}^{-1}$)				
<0.1	0.89**	−0.8**	−0.55**	25
>= 0.1 and <0.5	0.72**	−0.57**	−0.45**	87–92
>= 0.5 and <1	0.4**	−0.25(ns)	−0.28*	51–52
>= 1 and <2	0.19(ns)	0.5**	−0.17(ns)	28–32
>= 2 and <5	0.73**	0.62**	−0.73**	29–33
>= 5	0.79**	0.63**	−0.81**	43–44

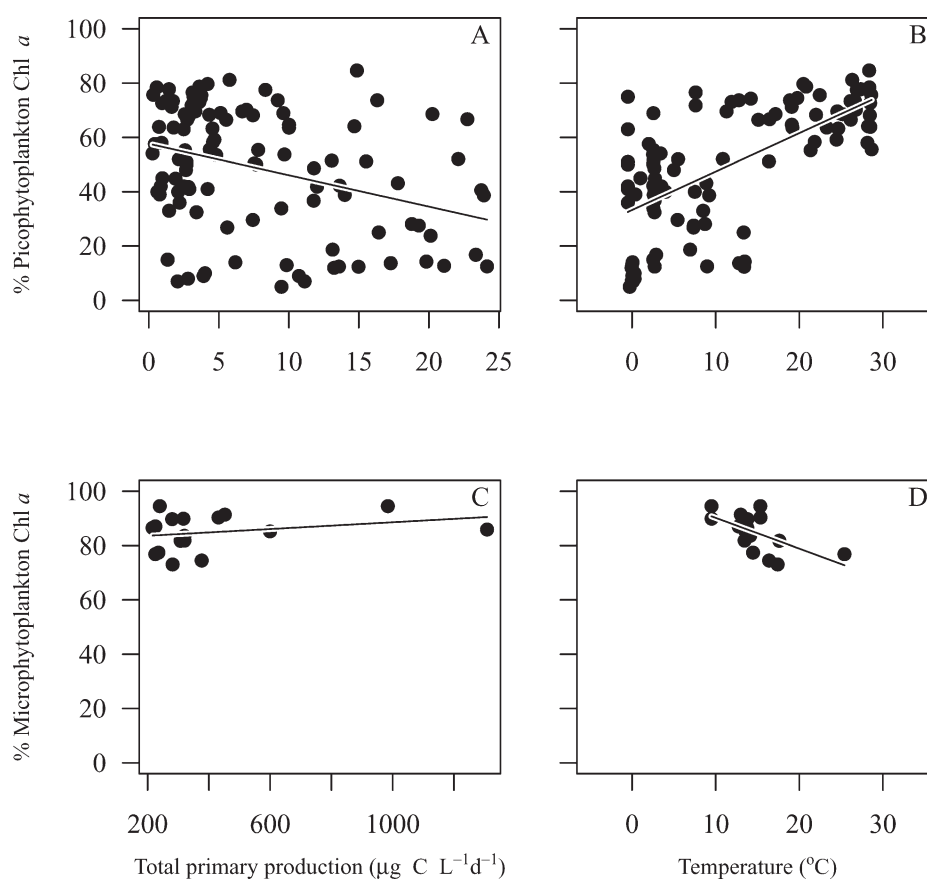


Fig. 3. Percent contribution of (A, B) picophytoplankton and (C, D) microphytoplankton to total Chl *a* concentration vs. (A, C) the total primary production and (B, D) temperature. Data are from Table 2 in Marañón et al. (2012). (A, B) present a subset of the dataset where primary production is $< 25 \mu\text{g C L}^{-1} \text{d}^{-1}$, while (C, D) present another subset where primary production is $> 200 \mu\text{g C L}^{-1} \text{d}^{-1}$.

mesocosms where the effect of temperature on size-structure was found significant (Peter and Sommer 2012). In their paper, Marañón et al. (2012) criticized our previous analysis

(Morán et al. 2010) reporting a relative increase in picophytoplankton abundance with increasing temperature. Marañón et al. (2012) argued that this relationship could be

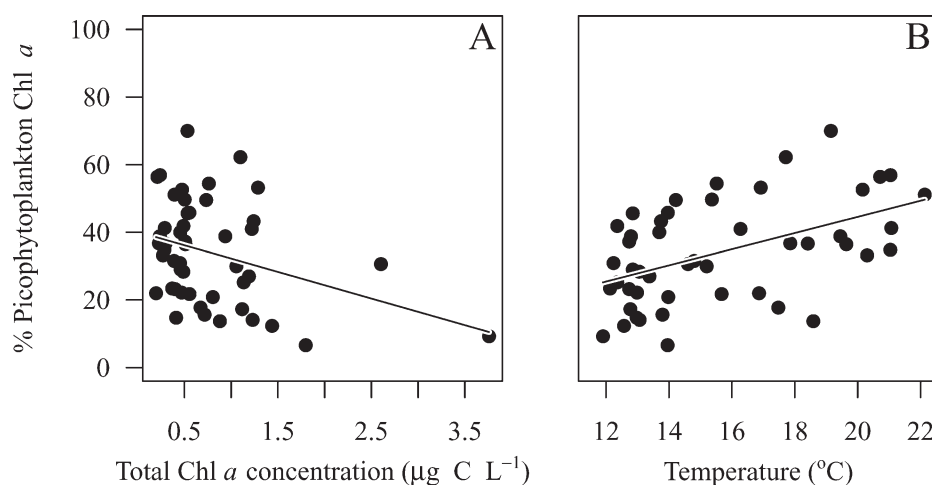


Fig. 4. Percent contribution of picophytoplankton to total Chl *a* concentration vs. (A) the total Chl *a* concentration and (B) temperature, data from (Morán et al. 2010).

explained virtually solely by nutrient limitation but they neglect the statement in our work (Morán et al. 2010) that nitrate and phosphate concentrations failed to substantially explain changes in mean picophytoplankton cell size in any of the two regions under study. If we repeat a similar analysis to the one performed by Marañón et al. (2012) with data from one of the North Atlantic regions where size fractionated chlorophyll data is available (the NE), temperature has a highly significant effect on the percent picophytoplankton contribution to total chlorophyll concentration ($r^2 = 0.24$, $p = 0.0004$, $n = 48$, Fig. 4B) while total chlorophyll concentration explained much lower variance in the data ($r^2 = 0.12$, $p = 0.019$, $n = 48$, Fig. 4A). Marañón et al. (2012) also incorrectly mention that temperature-driven changes in phytoplankton size-structure were explained by Morán et al. (2010) uniquely as a manifestation of the temperature-size rule (TSR) (Atkinson et al. 2003). Even though in natural assemblages the TSR has now been shown to have a much stronger effect [a ca. fourfold decrease at a one order of magnitude increase in temperature, (Peter and Sommer 2012)] than the average 2.5% shrinkage per °C reported by Atkinson et al. (2003) and used by Marañón et al. (2012), we agree that, solely, the TSR cannot explain the changes in the percent contribution of picophytoplankton to total phytoplankton. Morán et al. (2010) were explicit in explaining that “the relationships between organism size and temperature within and across taxa can be of various types, of which the TSR is just one possibility.” So we hypothesize that the reduction in picophytoplankton average cell size with increasing temperature observed by Morán et al. (2010) is likely the result of both a shift towards smaller sizes within species and a shift in picophytoplankton community composition towards a predominance of smaller-sized picophytoplankton species.

Temperature can also affect the size-structure of phytoplankton communities through a modification of the grazing interactions between phytoplankton and their predators (López-Urrutia 2008). The lower predatory control in cold waters would favor the opening of loopholes (sensu Irigoien et al. 2005) into which phytoplankton blooms develop, a phenomenon that would be more frequent in cold than in warmer waters (Rose and Caron 2007); although recent experiments in mesocosm suggest this cannot be the sole explanation for the effects of temperature on size-structure (Peter and Sommer 2012). But even if we follow a view where resource availability is the only factor controlling the functioning and size-structure of phytoplankton communities, temperature should still play a role. Temperature affects the rate at which nutrients are taken up by the cell through multiple mechanisms: through the temperature dependent metabolic processes controlling nutrient ion handling times, through the changes in the diffusion of nutrients with temperature following Stokes-Einstein equation and through changes in fluid viscosity with temperature (Aksnes and Egge 1991). Temperature also modifies the relative nitrogen to

phosphorus demands in phytoplankton and hence resource allocation (Toseland et al. 2013). Recent modeling studies also support the hypothesis that smaller plankton species have an accentuated competitive advantage at higher temperatures (Reuman et al. 2014). We might speculate that this interaction between the effects of temperature and resources could be responsible for the different correlation coefficients, and even a sign switch for nanoplankton, between temperature and the percentage chlorophyll concentration in each size fraction (Table 1).

The strong correlation between resource availability and temperature in the sea introduces some multicollinearity problems in the multiple regression approach as applied by Marañón et al. (2012) to evaluate the relative importance of each factor. But more importantly, because primary production is strongly related to total chlorophyll concentration, and the percentage contribution to total chlorophyll contains in the denominator the total chlorophyll concentration, the multiple regression approach in Marañón et al. (2012) suffers from a classical spurious correlation problem when plotting y/x vs. x what might inflate the proportion of variance explained by resource availability. This inflation of the explained variance effect would particularly affect those results in Marañón et al. (2012) analyses where the percentage contribution decreases with increasing resource availability as it is the case of picophytoplankton contribution. We agree, however, that in natural systems where both resource availability and temperature affect size-structure, the wide resource gradients and their correlation with temperature makes difficult the detection of the effects temperature. But, from our point of view this should not deter us from considering temperature as an important explanatory variable at a global scale since we have shown that, for the vast oligotrophic areas of the world's oceans where chlorophyll concentrations are below $<1 \mu\text{g L}^{-1}$ temperature explains a high proportion of the variability in the size distribution of phytoplankton communities, a variability that cannot be explained on the basis of the resource level proxies advocated by Marañón et al. (2012).

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