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# Changes in phytoplankton size-structure with warming in the temperate North Atlantic

Xosé Anxelu G. Morán<sup>1</sup>, Ángel López-Urrutia<sup>1</sup>, William K.W. Li<sup>2</sup> and Alejandra Calvo-Díaz<sup>1, 3</sup>

<sup>1</sup> Instituto Español de Oceanografía, Centro Oceanográfico de Xixón, Camín de L'Arbeyal, s/n, 33212 Xixón, Spain, Tel: +34 985308672, Fax: +34 985326277, e-mail <u>xelu.moran@gi.ieo.es</u>

<sup>2</sup> Department of Fisheries and Oceans,Ecosystem Research Division, Bedford Institute of Oceanography, Dartmouth, Nova Scotia, Canada B2Y 4A2

<sup>3</sup> Department of Biological Oceanography, Royal Netherlands Institute for Sea Research (NIOZ), PO Box 59, 1790 AB Den Burg, The Netherlands

## Abstract

In the context of strong warming trends in the world oceans, we have lacked theoretical explanations for the macroecological relationships between phytoplankton total abundance, size-structure and temperature. Picophytoplankton - Prochlorococcus and Synechococcus cyanobacteria and eukaryotic algae smaller than 2 µm in equivalent spherical diameter- were long considered to be major contributors to photosynthetic carbon fixation only in oligotrophic regions. By merging two datasets collected mostly at 43°N on both the east and west sides of the temperate North Atlantic across a diverse range of environmental conditions, we show that the importance of picophytoplankton might increase with global warming. 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. Our results show that temperature alone explained 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 towards smaller primary producers in a warmer ocean in parallel to a decline in total phytoplankton stocks. Since the fate of photosynthesized organic carbon largely depends on phytoplankton size-structure we anticipate future alterations in the functioning of the pelagic ecosystem in the temperate North Atlantic.

Keywords: Temperature, phytoplankton, cell size, picophytoplankton, ocean warming, North Atlantic

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#### Introduction

The effects of temperature on marine phytoplankton standing stocks and primary productivity have been recently investigated in experimental and modelling studies in different basins (Bopp et al. 2001, Richardson and Schoeman 2004, Li et al. 2006, Behrenfeld et al. 2006) in connection with current ocean warming. However, few studies to date have directly focused on the relationships between temperature and the size-structure of planktonic primary producers. A convenient way of summarizing phytoplankton size-structure is the assessment of the relative contribution of its smallest component, Synechococcus and Prochlorococcus cyanobacteria (Partensky et al. 1999) and a diverse ensemble of tiny eukaryotes (Worden et al. 2004) included in the picoplankton [0.2-2 µm of equivalent spherical diameter (ESD)] size-class, collectively known as "picophytoplankton". Picophytoplankton are ubiquitously distributed in the world oceans, with the exception of polar seas where cyanobacteria are absent, and they are significant but variable contributors to total phytoplankton biomass and production (Bell and Kalff 2001, Agawin et al. 2000, Morán 2007), especially in oligotrophic regions. The ultimate fate of organic carbon photosynthesized in the upper ocean largely depends on the relative importance of picophytoplankton (Legendre and Le Fèvre 1991, Falkowski et al. 1998). Although previous work has demonstrated positive relations between picophytoplanktonic contribution to primary production and temperature (Agawin et al. 2000), we have lacked comprehensive, mechanistic explanations for the macroecological relationships between phytoplankton total abundance, size-structure and temperature.

A recent study in the temperate NW Atlantic has shown (Li et al. 2006) that the abundance of total phytoplankton cells increase in a highly coherent mode with increasing temperature from -0.5 to 16°C. Since picophytoplankton are the dominant contributors to total cell density (Li 2002), we looked in this study for some universal mechanism underlying this observation that could possibly apply for both small large and phytoplankton cells. We did so by combining here two extensive time-series data sets of picophytoplankton abundance, cell size and biomass collected in mostly temperate shelf and offshore waters on both sides of the North Atlantic ocean. We subsequently applied current ecological theories of temperature-size relationships and

the allometric size-scaling of population abundance to explain the observed patterns. More details of this study can be found in Morán et al. (2009).

# Material and methods

We merged two datasets of temperature, total chlorophyll *a* (chl *a*) and picophytoplankton abundance, mean ESD and biomass collected mostly at ca. 43°N on both sides, east and west, of the North Atlantic (Fig. 1). NW data were obtained in different cruises carried out from 1994 to 2005 and NE were obtained monthly, during a 5-year period (2002- 2007) within the Spanish Institute of Oceanography (IEO) RADIALES long-term monitoring program.



**Fig. 1**. Location of the stations sampled in (A) the northwestern and (B) the northeastern Atlantic Ocean for building up the dataset used in this study.

The seasonal cycle was reasonably well-resolved by both datasets, with only relatively fewer winter data in the NW. All data were obtained at the surface (NE, n=59) or the upper 10 m of the water column (NW, n=97). Spatial autocorrelation was avoided by averaging results from nearby stations sampled during the same day. Seawater samples were collected from Niskin bottles and processed as detailed in Li et al. (2006) and Morán (2007). Chl *a* concentration was measured fluorometrically in acetone extracts. Nutrient concentrations were determined with Technicon autoanalyzers. 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. 2006, Morán 2007). Size is expressed as biovolume ( $\mu$ m<sup>-3</sup>) after estimating the ESD of picophytoplankton cells (*Synechococcus*, *Prochlorococcus* and picoeukaryotes) from cytometric light scatter signals calibrated either with microspheres (NW) or through sequential size fractionation of the community with Nuclepore polycarbonate filters (NE). Picophytoplankton biomass was estimated from abundance and biovolume using a common conversion factor of 237 fg C  $\mu$ m<sup>-3</sup> for both datasets (Worden et al. 2004). A carbon to chl *a* ratio of 50 (mg:mg) was used for estimating total phytoplankton biomass from chl *a* measurements. All linear regressions were performed according to the ordinary least squares (OLS) method.

### **Results and discussion**

Selected environmental variables of the two N Atlantic regions are shown in Table 1. Total phytoplankton biomass, expressed as chl *a* measurements, was generally higher in the NW Atlantic, in correspondence with the overall higher concentrations of inorganic nutrients. Although there was some overlap at 12-15°C, temperatures were much colder on the NW side.

**Table 1.** Mean values (minimum-maximum) of temperature, chlorophyll a (chl), nitrate and phosphate concentrations and the abundance of *Prochlorococcus* (Pro), *Synechococcus* (Syn) and picoeukaryotes (Euk). Significant differences between regions are indicated with asterisk notation: \*, p<0.05; \*\*, p<0.01; \*\*\*, p<0.001; ns, not significant

Region	Temp	NO <sub>3</sub>	$PO_4$	Chl a	Pro	Syn	Euk
	(°C)	$(\mu mol L^{-1})$		$(\mu g L^{-1})$	$(x \ 10^4 \text{ cells mL}^{-1})$		
NW	6.0	2.67	0.44	2.13	0	1.99	0.95
	(-0.6-16.1)	(0.01-11.0)	(0.15-0.94)	(0.08-14.1)		(0.001-19.9)	(0.02-6.87)
NE	15.7	1.67	0.18	0.71	1.26	2.56	1.24
	(11.6-22.1)	(0.07-7.4)	(0.01-0.88)	(0.19-3.76)	(0-12.1)	(0.03-13.9)	(0.25-5.44)
	***	*	***	***	***	ns	ns

By redrawing only picophytoplanktonic data from the NW Atlantic dataset collected by Li et al. (2006), similar temperature-associated increases in the mean abundance of picophytoplankton cells were observed on both Atlantic regions (Fig. 2A). In turn, temperature and picophytoplankton cell volume were inversely related through highly significant and similarly negative relationships, although the intercepts differed by an order of magnitude (Fig. 2B).



**Fig. 2**. (A) Relationship between picophytoplankton abundance and temperature in the two N Atlantic regions. (B) Relationship between picophytoplankton mean cell volume and temperature in the two regions. Fitted lines are individual OLS linear regressions included in the plots. p<0.0001, n=59 (NE) and n=97 (NE, panel A) and 95 (NW, panel B).

A combination of two ecological rules provides an explanation for the relationship between temperature and the total abundance of autotrophic cells described in Li et al. (2006). These two theories are the so-called temperature-size rule (TSR, (Atkinson et al. 2003) [i.e. the average size of individuals is inversely related to temperature] and the cross-community scaling relationship (CCSR) as termed by (White et al. 2007) [i.e. total community abundance is inversely related to average organism size]. Under an energetic equivalence scenario, temperature would affect community abundance 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. 2B for picophyplankton) and because smaller organisms have lower absolute energy requirements the number of phytoplankton cells that can be hosted will be higher as shown by Li et al. (2006). If picophytoplankton contribution to total phytoplankton remains constant with temperature, then picophytoplankton cell abundance would increase with higher temperatures only because total phytoplankton abundance increases. However, we argue that the relative contribution of picophytoplankton to the total biomass of planktonic primary producers should vary with temperature as a result of combining 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. Because the nominal upper size boundary of picoplankton is fixed at 2 µm, a consequence of the ISD being shifted towards smaller sizes as temperature rises is that a larger proportion of the community will be smaller than that size. As a consequence, there should be a strong relationship between temperature and the contribution of picophytoplankton to both total phytoplankton abundance and biomass. Indeed, as shown in Fig. 3, a significant increase in the proportion of phytoplankton biomass within the smallest size-class with warmer conditions was observed for our dataset, both within and across regions. With pooled data, a notably high percentage (73%) of the variance in picophytoplankton contribution to total algal biomass was thus explained by a single factor. Following this analysis, picophytoplankton would dominate (>50%) the biomass of planktonic primary producers in the North Atlantic at a temperature of 19.7°C. However, its importance would become evident also at lower temperatures. For instance, a rise in sea surface mean temperature from 15°C to 18°C would double picophytoplanktonic contribution from 15% to 32%.



**Fig. 3.** 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 data. p<0.0001, n=152.

Focusing on the respective biomasses of picophytoplankton and total phytoplankton, they were strongly and inversely related to temperature in remarkably similar ways for the two regions (Fig. 4). The consistency of these variations along the merged -0.6 to 22°C temperature range is remarkable given cross-site differences in environmental properties and taxonomic composition (Table 1). The inverse covariation of total phytoplankton biomass with temperature had been previously observed in global (Behrenfeld et al. 2006) and basin-scale studies (Li and Harrison 2008).



**Fig. 4.** (A) Relationship between picophytoplankton biomass and temperature in the two regions. (B) Relationship between total phytoplankton biomass and temperature in the two regions. Fitted lines are OLS linear for the regional and pooled datasets..p<0.001, n=57-59 (NE), n=95-97 (NW) and n=154 (NE and NW).

It is well known that temperature covaries with quite a few other factors in the ocean, including inorganic nutrient concentrations (Li 1998), rendering it difficult to disentangle individual effects (Agawin et al. 2000). Typically, both temperate regions had nutrient maxima in winter and minima in summer, with overall significantly lower NO<sub>3</sub> and PO<sub>4</sub> concentrations in the NE (Table 1). Nutrients fluxes into the upper, well-lit layers of the ocean will likely decrease in the future due to enhanced stratification, especially in oligotrophic low latitude regions (Sarmiento et al. 2004), additionally shifting the community to smaller sizes due to biophysical principles (Pasciak and Gavis 1974, Jin et al. 2006, Bopp et al. 2005). Without dismissing these possible direct effects of nutrients, we consider that the observed distributions were mainly caused by temperature by means of the aforementioned mechanism. Neither NO<sub>3</sub> nor PO<sub>4</sub>

concentrations were able to substantially describe the changes in picophytoplankton cell size in the NE or the NW, either community mean values or populations distinguished by flow cytometry, with percentages of variance explained uniformly below 20%.

Important bottom-up effects of climate change on plankton communities have been predicted (Richardson and Schoeman 2004, Hays et al. 2005, Beaugrand et al. 2008). From the consistent relationships found here between temperature, cell size and picophytoplankton abundance, we predict that the size of cells in phytoplankton communities will gradually decrease with global warming, with the implicit assumption that the change would be the same over time as over space. Some indications that this might be so are stemming from 7 years of monthly observations in the NW Atlantic (Morán X.A.G. and Díaz-Pérez L, unpublished results). This relatively rapid change might add to evolutionary pressures acting on geological time scales (Jiang et al. 2005).

The gradual shift towards smaller primary producers in parallel to a decline in total phytoplankton biomass will probably have profound implications for marine biogeochemistry (Bopp et al. 2005), especially if we consider it together with other predicted alterations such as stronger stratification and expansion of oligotrophic regions (Sarmiento et al. 2004, Behrenfeld et al. 2006). Since the size of particles largely affects their sinking velocity, the major biogeochemical alteration we anticipate is a decrease in the potential of the North Atlantic and other oceans for  $CO_2$  sequestration as a consequence of the increasing importance of small phytoplankters in a warmer world.

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