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# Biogeochemical shifts in a coastal upwelling area (NE Atlantic) do not lead to downsizing in phytoplankton species despite altering the structure of the community

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Theoretical studies, long-term surveys and experimental data predict a reduction in body size across taxa under the current warming context. However, this rule might not be ubiquitous. Here we present time series analyses of the biogeochemical and phytoplankton trends that occurred in station E2 off A Coruña (NE Atlantic) since the late 1980s. Upwelling strength and sea surface temperature remained stable during the last decades. However, while nitrate fertilization showed a slight increase, phosphate concentration has strongly risen leading to a negative trend in N:P. Phytoplankton abundance responded differently to these shifts, with dinoflagellates showing an increase in abundance. Quantile regression indicated a negative relationship between species exhibiting decreasing trends in abundance and cell size. A heterogeneous model was also apparent for the relationship between size and species being less susceptible to changes in both N:P and upwelling strength. By contrast, larger species tended to show positive changes with temperature. These results suggest that cell size is a limiting factor given that larger cells were hardly ever associated with species-specific increases in abundance with time, changes in N:P or upwelling. However, other factors would be responsible of the different responses to temperature changes though not interacting with size.

## Introduction

Body size is a fundamental trait in determining organism physiology and individual evolution, and is involved in many ecological processes such as food web structure or energy flux. Theoretical studies, long-term surveys and experimental data predict a reduction in body size across taxa under the current warming context according to the temperature–size relationships. This general trend towards smaller sizes at warmer temperatures would be especially apparent in aquatic ecosystems (Gardner *et al*. 2011). However, this rule might not be ubiquitous and important exceptions may exist (e.g. benthic diatoms, Adams *et al*. 2013). Phytoplankton is at the base of the aquatic food webs and changes in body size might have important and unpredicted effects for primary production, biogeochemical cycles and fishery yields. Hydro-climatic variation influence the structure of phytoplankton communities (e.g. Pérez *et al*. 2010), and these shifts would ultimately depend on species-specific functional traits and cell size (Edwards *et al*. 2011). Here we modeled the variability of a set of phytoplankton species in relation to changes in the environmental conditions occurring off A Coruña (NW Spain) since the late 1980s. We further analyzed the influence of cell size in determining and limiting the trends in abundance with time and the individual responses to changes in nutrient concentration, temperature and physical forcing.

## Material and Methods

Phytoplankton and biogeochemical sampling: Data were obtained from the time series project RADIALES conducted by the Instituto Español de Oceanografía off A Coruña (NW Spain) in operation since 1987. Specifically, water samples were collected monthly with 5 L Niskin bottles or a rosette sampler from depths of 0, 5, 10, 20, 30, 40 and 70 m at station 2 (depth = 80 m; 43º25'30''N, 08º26'20''W) during the period January 1989–December 2010 (n = 261 days sampled). For each sampling depth, samples were collected for the determination of phytoplankton abundance and nutrient and chlorophyll *a* concentration following the methods described in Casas *et al*. (1997). Phytoplankton was always counted by the same person (M.V.) following the technique described by Utermöhl, and whenever possible, organisms were classified at the species or genus level. For the purposes of the present work we used a set of 54 species. Cell biomass for each species was estimated in some samples from measurements of cell dimensions under the microscope and assigning a certain geometric shape to each species (see Huete-Ortega *et al*. 2010). A daily upwelling index was computed in a 2º × 2º grid centered at 43ºN–11ºW (González-Nuevo *et al*. 2014).

Statistical analyses: Seasonal and long-term trends in biogeochemical variables and upwelling index were evaluated using generalized additive mixed models (GAMMs, Wood 2006). Trends in species abundance were analyzed using GAMs with a Gaussian error structure as follows:

$$\ln(N_{i,t}) = \alpha + f_i(\mathrm{DoY}_t) + \beta_{i,1}\,\mathrm{Days}_t + \beta_{i,2}\,\mathrm{NUT}_t + \beta_{i,3}\,\mathrm{Temp}_t + \beta_{i,4}\,\mathrm{UI}_{\mathrm{X}t} + \epsilon_{i,t}$$

where $\ln(N_{i,t})$ is the natural log-transformed abundance (water column-averaged cells ml$^{-1}$) of species $i$ at a time $t$. $f$ is a one-dimensional non-parametric smoothing function fit by a penalized cyclic cubic regression spline with a maximum of 6 knots describing the effect of DoY (day of the year), and $\beta_s$ are parametric terms describing the effects of Days (consecutive days from 1989 to 2010), NUT (bottom N:P), Temp (surface temperature) and $\mathrm{UI}_\mathrm{X}$ (coastal upwelling averaged over the fifteen days preceding the sampling). In order to assess the association between cell size and the species' trends in abundance and species' responses to nutrient concentration, temperature and upwelling strength, parametric coefficients from the above equation were related to species' cell biomass by means of fitting quantile regression models (Cade and Noon 2003).

## Results and Discussion

Seasonality was the main pattern of variability of the environmental variables as typically shown at these latitudes (e.g. Huete-Ortega *et al*. 2010). However, long-term trends were also apparent. While the upwelling index, temperature and chl *a* concentration did not show significant changes from 1989 to 2010, bottom nitrate and phosphate concentration showed significant non-linear changes with a marked increase in concentration, slightly steeper for phosphate, starting in 1999. This resulted in a decreasing N:P trend from late 1990s onwards. Similar biogeochemical patterns were found at southern latitudes off the Galician coast (Pérez *et al*. 2010). The set of 54 species analyzed comprised six phytoplankton groups including thirty-five diatom taxa and thirteen dinoflagellate taxa. In general, all species showed patterns of seasonal change with peaks in spring and summer months. Long-term changes in abundance were variable across species with a slight proportion of the taxa (33 of 54) tending to increase. Within the main phytoplankton groups almost half of the diatoms (19 of 35) tended to increase their abundances, while all dinoflagellates (13 species) rose over the same years as found in neighboring areas (Hernández-Fariñas *et al*. 2014). Higher values of the N:P ratio and upwelling index favored increases in abundance for almost the majority of the taxa. However, warmer temperatures resulted in general decreases in abundance. Quantile regression showed a negative relationship between species exhibiting decreasing trends in abundance and cell size with slopes tending to be steeper for higher quantiles. Similarly, a heterogeneous model was also apparent for the relationships between cell size and species being less susceptible to changes in both N:P and upwelling strength. Slopes of the regression quantiles were steeper for higher quantiles in the case of the changes in abundance with nutrient concentration, and less variable regarding the relationship with the upwelling index. All these variations in the slope values suggest that cell size is a limiting factor in the sense that larger cells were hardly ever associated with species-specific increases in abundance with time, changes in N:P or upwelling. Limiting factors are common in ecological relationships (Cade and Noon 2003). By contrast, larger species tended to show positive changes with temperature for almost all quantiles pointing to a homogeneous model where other factors would be responsible of the different responses to temperature changes but not interacting with cell size.

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