

More, smaller bacteria in response to ocean's warming

X.A.G. Morán (1), L. Alonso-Sáez (2), E. Nogueira (1), H.W. Ducklow (3), N. González (4), Á. López-Urrutia (1), L. Díaz-Pérez (1), A. Calvo-Díaz (1), N. Arandia-Gorostidi (1), T.M. Huete-Stauffner (1)

(1) Instituto Español de Oceanografía, Centro Oceanográfico de Xixón, Spain; (2) AZTI-Tecnalia, Sukarrieta, Spain; (3) ; (4). Presenter contact details: xelu.moran@kaust.sa, Phone +966 12 8028581

Summary

Heterotrophic bacterioplankton are major players in organic matter cycling in the oceans. In spite of their high abundances and fast growth rates in surface waters, which make them suitable sentinels of global change, past analyses have largely overlooked this functional group. A time-series analysis of a decade of monthly observations in the upper mixed layer of the Southern Bay of Biscay continental shelf revealed strong seasonal patterns in the abundance, size and biomass of the universal groups of low (LNA) and high nucleic acid content (HNA) bacteria as distinguished by flow cytometry. Over this relatively short period we also found that bacterioplankton are already responding to the hypothesized temperature-driven decrease in body size. In particular, the variability of LNA bacteria was strongly coherent with ecological theories linking temperature, abundance and individual size. Concurrent with rising temperatures, significant interannual trends of increasing standing stocks (3% year⁻¹) accompanied by decreasing mean cell size (-1% year⁻¹) suggest a major shift in community structure, with a larger contribution of LNA cells to total biomass. Similarly to reports from other regions, LNA cells were likely dominated by members of the SAR11 clade at our site. We hypothesize that the increasing prevalence of these typically oligotrophic taxa may severely impact marine food webs and carbon fluxes in the future.

Introduction

The multiple effects of climate change in the oceans have largely neglected the smallest life forms, although heterotrophic bacteria represent the largest living biomass and are key players in marine biogeochemistry. Flow cytometric analyses of natural seawater consistently distinguish between two groups of cells according to their relative nucleic acid content, low (LNA) and high (HNA) (Gasol et al. 1999), with usually similar differences in relative cell size. LNA and HNA bacteria are generally affiliated to distinct phylogenetic groups, with the former including the widespread SAR11 clade. The relationships between abundance, cell size, biomass and temperature of LNA and HNA cells were explored in a decadal time-series. We specifically tested whether the universal decrease in body size as a consequence of global warming (Gardner et al. 2011) also applies to the tiniest planktonic organisms.

Materials and Methods

Bacterioplankton samples were taken monthly from April 2002 through March 2012 at a mid-shelf station (110 m depth) off Xixón, Spain, as part of the IEO programme Radiales. Flow cytometry and ancillary environmental samples were analyzed as described in detail

in Calvo-Díaz and Morán (2006). Upper mixed layer-averaged values of abundance, cell size, biomass and temperature were used for time-series analysis (Bode et al. 2011).

Results and Discussion

Temperature showed a expected, marked seasonality explaining 80% of total variance, while seasonal patterns were notably different for LNA and HNA bacteria. Abundance of LNA cells displayed a significant annual cycle (25% of variance explained), with March minima and summer-autumn maxima. Bacterial cell size ($0.03\text{-}0.10\ \mu\text{m}^3$) had also significant seasonal components for LNA and total bacteria. For LNA cells, abundance and size seasonal patterns were opposite and coherent with general ecological rules relating temperature, size and abundance (i.e. more abundant and smaller LNA bacteria were observed during warmer months). This consistent behaviour of LNA cells may be explained by the dominance within this group of the SAR11 clade. Long-term trends were also identified, with LNA cell abundance increasing significantly over the decade paralleling the increase in temperature observed for the April-July period. Negative decadal trends in bacterial cell size were consistently observed for both bacterial groups, with steeper slopes of HNA cells ($-0.007\ \log\ \mu\text{m}^3\ \text{year}^{-1}$) compared with LNA cells ($-0.004\ \log\ \mu\text{m}^3\ \text{year}^{-1}$). Consequently, total bacterioplankton cell size decreased consistently ($r = -0.95$) from 2002 to 2012, equivalent to shrinkage of $\sim 1\%$ per year⁻¹. Our analysis further shows that the mean contribution of LNA cells to total biomass has increased significantly by 7% over the decade and is now close to 50%. Residual correlation analyses gave additional support to temperature as the ultimate cause for the dominance of increasingly smaller LNA cells in our waters.

Adding to studies carried out with phytoplankton and zooplankton (Daufresne et al. 2009), this is the first documentation of a systematic long-term decline in the size of heterotrophic bacterioplankton, thus supporting the view that decreasing body size is a universal ecological response to global warming (Gardner et al. 2011). Gradual replacement of phylogenetic groups of heterotrophic bacteria typically better adapted to oligotrophic conditions such as LNA cells (Mary et al. 2006) will likely alter carbon fluxes and trophic relationships in the future ocean.

References

- Bode A., Anadón R., Morán X.A.G., Nogueira E., Teira E., Varela M. 2011 Decadal variability in chlorophyll and primary production off NW Spain. *Climate Research*, 48: 293-305.
- Calvo-Díaz A., Morán X.A.G. 2006 Seasonal dynamics of picoplankton in shelf waters of the southern Bay of Biscay. *Aquatic Microbial Ecology*, 42: 159-174.
- Daufresne M., Lengfellner K., Sommer U. 2009 Global warming benefits the small in aquatic ecosystems. *Proceedings of the National Academy of Sciences of the United States of America*, 106: 12788-12793.
- Gardner J.L., Peters A., Kearney M.R., Joseph L., Heinsohn R. 2011 Declining body size: a third universal response to warming? *Trends in Ecology & Evolution* 26: 285-291.
- Gasol J.M., Zweifel U.L., Peters F., Fuhrman J.A., Hagström Å. 1999 Significance of size and nucleic acid content heterogeneity as measured by flow cytometry in natural planktonic bacteria. *Applied Environmental Microbiology*, 65: 4475-4483.
- Mary I., Heywood J.L., Fuchs B.M., Amann R., Tarran G.A., Burkill P.H., Zubkov M.V. 2006 SAR11 dominance among metabolically active low nucleic acid bacterioplankton in surface waters along an Atlantic meridional transect. *Aquatic Microbial Ecology*, 45: 107-113.