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TITLE: Do marine phytoplankton follow Bergmann's rule *sensu lato*?

AUTHOR: ['Ulrich Sommer', 'Kalista Higinia Peter', 'Savvas Genitsaris', 'Maria Moustaka-Gouni']

ABSTRACT:

**ABSTRACT** Global warming has revitalized interest in the relationship between body size and temperature, proposed by Bergmann's rule 150 years ago, one of the oldest manifestations of a biogeography of traits. We review biogeographic evidence, results from clonal cultures and recent micro- and mesocosm experiments with naturally mixed phytoplankton communities regarding the response of phytoplankton body size to temperature, either as a single factor or in combination with other factors such as grazing, nutrient limitation, and ocean acidification. Where possible, we also focus on the comparison between intraspecific size shifts and size shifts resulting from changes in species composition. Taken together, biogeographic evidence, community-level experiments and single-species experiments indicate that phytoplankton average cell sizes tend to become smaller in warmer waters, although temperature is not necessarily the proximate environmental factor driving size shifts. Indirect effects via nutrient supply and grazing are important and often dominate. In a substantial proportion of field studies, resource availability is seen as the only factor of relevance. Interspecific size effects are greater than intraspecific effects. Direct temperature effects tend to be exacerbated by indirect ones, if warming leads to intensified nutrient limitation or copepod grazing while ocean acidification tends to counteract the temperature effect on cell size in non-calcifying phytoplankton. We discuss the implications of the temperature-related size trends in a global warming context, based on known functional traits associated with phytoplankton size. These are a higher affinity for nutrients of smaller cells, highest maximal growth rates of moderately small phytoplankton (ca.  $10^2 \mu\text{m}^3$ ), size-related sensitivities for different types of grazers, and impacts on sinking rates. For a phytoplankton community increasingly dominated by smaller algae we predict that: (i) a higher proportion of primary production will be respired within the microbial food web; (ii) a smaller share of primary production will be channeled to the classic phytoplankton → crustacean zooplankton → fish food chain, thus leading to decreased ecological efficiency from a fish-production point of view; (iii) a smaller share of primary production will be exported through sedimentation, thus leading to decreased efficiency of the biological carbon pump.

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