

Influence of diatom diversity on the ocean biological carbon pump

Paul Tréguer^{1*}, Chris Bowler², Brivaela Moriceau¹, Stephanie Dutkiewicz³, Marion Gehlen⁴, Olivier Aumont⁵, Lucie Bittner⁶, Richard Dugdale⁷, Zoe Finkel⁸, Daniele Iudicone⁹, Oliver Jahn³, Lionel Guidi¹⁰, Marine Lasbleiz¹¹, Karine Leblanc¹¹, Marina Levy⁵ and Philippe Pondaven¹

Diatoms sustain the marine food web and contribute to the export of carbon from the surface ocean to depth. They account for about 40% of marine primary productivity and particulate carbon exported to depth as part of the biological pump. Diatoms have long been known to be abundant in turbulent, nutrient-rich waters, but observations and simulations indicate that they are dominant also in meso- and submesoscale structures such as fronts and filaments, and in the deep chlorophyll maximum. Diatoms vary widely in size, morphology and elemental composition, all of which control the quality, quantity and sinking speed of biogenic matter to depth. In particular, their silica shells provide ballast to marine snow and faecal pellets, and can help transport carbon to both the mesopelagic layer and deep ocean. Herein we show that the extent to which diatoms contribute to the export of carbon varies by diatom type, with carbon transfer modulated by the Si/C ratio of diatom cells, the thickness of the shells and their life strategies; for instance, the tendency to form aggregates or resting spores. Model simulations project a decline in the contribution of diatoms to primary production everywhere outside of the Southern Ocean. We argue that we need to understand changes in diatom diversity, life cycle and plankton interactions in a warmer and more acidic ocean in much more detail to fully assess any changes in their contribution to the biological pump.

Through photosynthesis, the primary producers build biomass by taking up CO₂ and thus influence its concentration in Earth's atmosphere¹. Among the microscale planktonic primary producers, diatoms are unique because of their silicified cell walls, which provide mechanical protection from grazers². Since the early Cenozoic, diatoms have become the most abundant and diverse siliceous marine microorganisms³, and have emerged as key drivers of the silicon cycle⁴. Their fast growth rates in high-nutrient environments^{5–7} (Supplementary Section 1) and comparatively large sizes also make them important contributors to organic carbon production in the euphotic zone⁸. They have been estimated to contribute as much as 20% of the total primary production on Earth, and up to 40% of the total marine primary production⁹ (Supplementary Section 1). The organic carbon synthesized by photosynthesis in the surface oceans is transferred to the trophic network, and may then be exported to depth, where most of it is remineralized to CO₂. This export is termed the biological carbon pump¹⁰. Diatoms are also believed to contribute ~40% of particulate organic carbon export¹¹, which can reach either the mesopelagic layer (the lower limit of which is ~1,000 m, coinciding with the nitrate maximum) or deeper, into the bathypelagic layer, which is also known as the 'CO₂ sequestration layer'. Carbon reaching bathypelagic depths is removed from the atmosphere for at least 100 years, and carbon will ultimately reach sediments at the seafloor and be buried.

An important concept in marine-plankton ecology is Margalef's mandala¹², which posits that diatoms characteristically thrive in nutrient-rich surface layers and turbulent conditions, and are thus typically found at high latitudes and in coastal upwelling regions (Fig. 1). Through remote sensing, new observation tools and models, abundant diatoms have also been identified in meso/submesoscale fronts^{13,14} (Fig. 1) and shown to contribute significantly to the 'shade flora' found at the deep chlorophyll maximum (DCM)¹⁵. The use of molecular biology techniques has further revealed that diatoms may be more relevant in oligotrophic systems than generally considered¹⁶. Herein we address the following questions: what factors control the distribution of diatoms in the ocean? What is the contribution of diatoms in carbon export from the photic layer? Are diatoms efficient transporters of organic carbon to the CO₂ sequestration layer? Can we predict the fate of diatoms in the future ocean impacted by climate change?

Controls of the distribution of diatoms in the ocean

Large-scale patterns of diatom distributions from ocean-colour remote sensing^{17,18} along with field observations^{19–21} reveal that they are an important component of phytoplankton biomass at high latitudes during spring (that is, in April–June in the Northern Hemisphere and October–December in the Southern Ocean) and in equatorial and coastal upwelling regions. They are present at lower

¹Marine Environmental Sciences Laboratory (LEMAR, UMR 6539) at the European Institute for Marine Studies, Université de Bretagne Occidentale, CNRS, Plouzané, France. ²Institut de biologie de l'École normale supérieure, École normale supérieure, CNRS, INSERM, PSL Research University, Paris, France.

³Department of Earth, Atmospheric and Planetary Sciences, Massachusetts Institute of Technology, Cambridge, MA, USA. ⁴Laboratoire des Sciences du Climat et de l'Environnement, Institut Pierre Simon Laplace, CEA-CNRS-UVSQ, Orme des Merisiers, Gif-sur-Yvette, Paris, France. ⁵Sorbonne Universités (UPMC Univ Paris 06)/CNRS/IRD/MNHN, Laboratoire d'Océanographie et du Climat, Institut Pierre Simon Laplace, Paris, France. ⁶Sorbonne Universités, UPMC Univ Paris 06, Univ Antilles Guyane, Univ Nice Sophia Antipolis, CNRS, Evolution Paris Seine, Institut de Biologie Paris Seine, Paris, France.

⁷Romberg Tiburon Center, San Francisco State University, Tiburon, CA 94920, USA. ⁸Environmental Science Program, Mount Allison University, Sackville, NB, Canada. ⁹Stazione Zoologica Anton Dohrn, Naples, Italy. ¹⁰Sorbonne Universités, UPMC Université Paris 06, CNRS, Laboratoire d'Océanographie de Villefranche, Observatoire Océanologique, Villefranche-sur-Mer, France. ¹¹Aix-Marseille Université, Université de Toulon, CNRS, IRD, MIO, UM110, Marseille, France. *e-mail: paul.treguer@univ-brest.fr