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ARTICLE

The epibiotic life of the cosmopolitan diatom *Fragilariopsis doliolus* on heterotrophic ciliates in the open ocean

Flora J. Vincent[1] · Sébastien Colin[2] · Sarah Romac[2] · Eleonora Scalco[3] · Lucie Bittner[4] · Yonara Garcia[5] · Rubens M. Lopes[5] · John R. Dolan[6] · Adriana Zingone[3] · Colomban de Vargas[2] · Chris Bowler[1]

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Abstract

Diatoms are a diverse and ecologically important group of phytoplankton. Although most species are considered free living, several are known to interact with other organisms within the plankton. Detailed imaging and molecular characterization of any such partnership is, however, limited, and an appraisal of the large-scale distribution and ecology of such consortia was never attempted. Here, observation of *Tara* Oceans samples from the Benguela Current led to the detection of an epibiotic association between a pennate diatom and a tintinnid ciliate. We identified the diatom as *Fragilariopsis doliolus* that possesses a unique feature to form barrel-shaped chains, associated with seven different genera of tintinnids including five previously undescribed associations. The organisms were commonly found together in the Atlantic and Pacific Ocean basins, and live observations of the interaction have been recorded for the first time. By combining confocal and scanning electron microscopy of individual consortia with the sequencing of high-resolution molecular markers, we analyzed their distribution in the global ocean, revealing morpho-genetically distinct tintinnid haplotypes and biogeographically structured diatom haplotypes. The diatom was among the most abundant in the global ocean. We show that the consortia were particularly prevalent in nutrient-replete conditions, rich in potential predators. These observations support the hypothesis of a mutualistic symbiosis, wherein diatoms acquire increased motility and tintinnids benefit from silicification through increased protection, and highlight that such associations may be more prevalent than currently appreciated.

Introduction

Marine phytoplankton are photosynthetic microbes responsible for around half of Earth's net primary production [1]. Diatoms, a ubiquitous and predominant component of phytoplankton, are enveloped in a characteristic silica cell wall known as the frustule, and have been proposed to contribute around 40% of marine net primary productivity [2]. They serve as the basis of the marine food web and are significant players in global biogeochemical cycles [3, 4]. Diatoms are frequently reported to dominate phytoplankton communities in well-mixed coastal, as well as upwelling regions, where light and nutrients are available [5]. They are nonetheless frequent and diverse in open ocean oligotrophic systems [6] where their survival in such low-nutrient regions can

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✉ Colomban de Vargas
vargas@sb-roscoff.fr

✉ Chris Bowler
cbowler@biologie.ens.fr

[1] Institut de Biologie de l'École Normale Supérieure, École Normale Supérieure, Paris Sciences et Lettres Research University, CNRS UMR 8197, INSERM U1024, F-75005 Paris, France

[2] Station Biologique de Roscoff, Sorbonne Universités, UPMC Université Paris 06, CNRS, UMR7144, 29680 Roscoff, France

[3] Integrative Marine Ecology Department, Stazione Zoologica Anton Dohrn, Villa Comunale, 80121 Naples, Italy

[4] Sorbonne Universités, UPMC Univ Paris 06, Univ Antilles, Univ Nice Sophia Antipolis, CNRS, Evolution Paris Seine - Institut de Biologie Paris Seine (EPS - IBPS), 75005 Paris, France

[5] Department of Biological Oceanography, University of São Paulo, Praça do Oceanográfico 191, Cidade Universitária, São Paulo 05508-120, Brazil

[6] Sorbonne Universités, UPMC Univ. Paris 06, CNRS, Laboratoire d'Océanographie de Villefranche, CNRS UMR 7093, Villefranche-sur-mer, Paris 06230, France

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