

Finding a partner in the ocean: molecular and evolutionary bases of the response to sexual cues in a planktonic diatom

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Summary

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- Microalgae play a major role as primary producers in aquatic ecosystems. Cell signalling regulates their interactions with the environment and other organisms, yet this process in phytoplankton is poorly defined. Using the marine planktonic diatom *Pseudo-nitzschia multistriata*, we investigated the cell response to cues released during sexual reproduction, an event that demands strong regulatory mechanisms and impacts on population dynamics.
- We sequenced the genome of *P. multistriata* and performed phylogenomic and transcriptomic analyses, which allowed the definition of gene gains and losses, horizontal gene transfers, conservation and evolutionary rate of sex-related genes. We also identified a small number of conserved noncoding elements.
- Sexual reproduction impacted on cell cycle progression and induced an asymmetric response of the opposite mating types. G protein-coupled receptors and cyclic guanosine monophosphate (cGMP) are implicated in the response to sexual cues, which overall entails a modulation of cell cycle, meiosis-related and nutrient transporter genes, suggesting a fine control of nutrient uptake even under nutrient-replete conditions.
- The controllable life cycle and the genome sequence of *P. multistriata* allow the reconstruction of changes occurring in diatoms in a key phase of their life cycle, providing hints on the evolution and putative function of their genes and empowering studies on sexual reproduction.

Introduction

Phytoplankton feature prominently in aquatic ecosystems, showing striking morphological and functional diversity and accounting for one-half of the Earth's primary productivity (Falkowski & Knoll, 2011). Diatoms are a major component of phytoplankton with over 100 000 species (Mann & Vanormelingen, 2013) and contribute substantially to primary production and major biogeochemical cycles (Armbrust, 2009). A high rate of DNA turnover, horizontal gene transfer (HGT) from bacteria and endosymbiotic events are responsible for the chimeric nature of diatom genomes, which have probably contributed to the heterogeneity of their physiological and ecological traits (Bowler *et al.*, 2010).

The first assembled genomes of a centric (*Thalassiosira pseudonana*, Armbrust *et al.*, 2004) and a pennate (*Phaeodactylum tricorutum*, Bowler *et al.*, 2008) diatom were small in size (27–32 Mb) with 10 000–14 000 genes. They contained only one-half of the genes with an annotated function, and *c.* 35% of the genes were reported to be species specific. Further, *c.* 5% of *P. tricorutum* genes were predicted to be acquired by HGT from

bacteria. These genomes contributed towards an understanding of the genes and pathways involved in nutrient assimilation and metabolism of diatoms. To improve our understanding of the evolution and adaptation of this highly diverse group of organisms, additional diatom genomes were sequenced, such as those of the open-ocean centric diatom *Thalassiosira oceanica* (Lommer *et al.*, 2012), the oleaginous *Fistulifera solaris* (Tanaka *et al.*, 2015) and the polar diatom *Fragilariopsis cylindrus* (Mock *et al.*, 2017), instrumental for the study of iron physiology, lipid metabolism and adaptation to cold, respectively.

The dynamics of planktonic communities are strongly dependent on the life cycle traits of the individual species. Diatoms have a unique life cycle characterized by progressive cell size reduction in the population, imposed by a rigid silica wall. A few exceptions apart, sexual reproduction is an obligate phase in diatom life cycles, important not only to generate genetic diversity, but also to escape the miniaturization process, thus allowing the persistence of populations by restoring the original cell size (Montresor *et al.*, 2016). It has been proposed that some of the unique features of the diatom genomes may reflect the unusual