

ORIGINAL ARTICLE

Clonal expansion behind a marine diatom bloom

Maria Valeria Ruggiero¹, Domenico D'Alelio¹, Maria Immacolata Ferrante, Mariano Santoro, Laura Vitale, Gabriele Procaccini and Marina Montresor

Department of Integrative Marine Ecology, Stazione Zoologica Anton Dohrn, Villa Comunale, Napoli, Italy

Genetic diversity is what selection acts on, thus shaping the adaptive potential of populations. We studied micro-evolutionary patterns of the key planktonic diatom *Pseudo-nitzschia multistriata* at a long-term sampling site over 2 consecutive years by genotyping isolates with 22 microsatellite markers. We show that both sex and vegetative growth interplay in shaping intraspecific diversity. We document a brief but massive demographic and clonal expansion driven by strains of the same mating type. The analysis of an extended data set (6 years) indicates that the genetic fingerprint of *P. multistriata* changed over time with a nonlinear pattern, with intermittent periods of weak and strong diversification related to the temporary predominance of clonal expansions over sexual recombination. These dynamics, rarely documented for phytoplankton, contribute to the understanding of bloom formation and of the mechanisms that drive microevolution in diatoms.

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Introduction

Phytoplankton drive global biogeochemical cycles and regulate carbon fluxes in aquatic food-webs (Behrenfeld *et al.*, 2005; D'Alelio *et al.*, 2016). Eukaryotic microalgae reproduce asexually via mitosis and the sudden rise of cell division rates produces significant increases in the density of the population, called 'blooms' (Smayda, 1997; Wyatt, 2012).

Beside asexual reproduction, many unicellular eukaryotes include a sexual phase in their life cycle (Speijer *et al.*, 2015), which has important ecological and evolutionary implications (von Dassow and Montresor, 2010). Through recombination, sexual reproduction introduces new genetic variants in a population on which selection can act, thus allowing evolutionary adaptations and shaping the population's phenotypic profile. On the other hand, asexual reproduction allows the maintenance in the population of adapted genotypes in stable environmental conditions. However, genetic variation can arise in asexually reproducing species by means of mitotic mutations that can significantly contribute to the genetic standing variation in populations (Tibayrenc and Ayala, 2012).

Eukaryotic phytoplankton display a variety of life cycles, mating systems and ploidy levels; however, the role of these multifaceted life history architectures have in shaping genetic diversity is still poorly known

(Rengefors *et al.*, 2017). Theoretical models predict that even in predominantly asexual species, few recombination events per generation could be sufficient to give a population the same pattern of allelic variation as found in fully sexually reproducing organisms (Bengtsson, 2003). The rare occurrence of recombination has been invoked as the primary cause of the apparent dominance of clonal evolution, or clonality, in unicellular organisms, from bacteria to fungi and protozoans (Predominantly Clonal Evolution, PCE model (Tibayrenc and Ayala, 2012)). However, the PCE model mainly stems from observations carried out on non-free-living and pathogenic organisms. An alternative model of microevolution is the 'semi-clonal' or 'epidemic' model, in which recombination regularly occurs over long temporal scales but episodic clonal expansions can also occur (Smith *et al.*, 1993; Maiden, 2006). The latter are short-term periods of both fast population increase and remarkable genetic divergence only driven by mutations. The population genetic structure of free-living cyanobacteria (D'Alelio *et al.*, 2013), parasitic protozoa (Weedall and Hall, 2015) and fungi (MacLeod *et al.*, 2000) have been interpreted in the frame of this latter model.

We assessed the relative impact of clonality (genetic divergence) and sexual recombination (genetic reshuffling) on the population's genetic structure of the marine planktonic diatom *Pseudo-nitzschia multistriata*, a marine planktonic species recurrently blooming at the Long-Term Ecological Research station MareChiara (LTER-MC) in the Gulf of Naples (Ribera d'Alcalà *et al.*, 2004; D'Alelio *et al.*, 2010; Tesson *et al.*, 2014). Life history studies have revealed that *P. multistriata* has an heterothallic mating system: sexual reproduction can occur only when strains of

Correspondence: M Montresor, Department of Integrative Marine Ecology, Stazione Zoologica Anton Dohrn Naples, Villa Comunale, Naples 80121, Italy.

E-mail: marina.montresor@szn.it

¹These authors contributed equally to this work.

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