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Article

Sex in marine planktonic diatoms: insights and challenges

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With 1 figure and 1 table

Abstract: Diatoms are diploid eukaryotic microalgae, key-players in the ocean and are responsible for a large fraction of the global primary production. These unicellular microalgae have a unique life cycle characterized by progressive cell size reduction; the restitution of the large cell size is accomplished within the sexual phase. Here we summarize the available evidence for the presence of sex in marine planktonic diatoms and results of more recent investigations aimed at defining environmental or endogenous cues for sexualisation. Genomic resources are now opening up new avenues for elucidating the molecular mechanisms involved in different aspects of the sexual phase, such as cell size control, mating type definition, meiosis, and gamete recognition systems. Understanding the regulatory mechanisms and signalling pathways underlying the onset of sex in diatoms will provide important information to comprehend their ecological and evolutionary success.

Keywords: auxosporulation; diatoms; genomics; life cycle; mating types; meiosis; sex

Introduction

Sex is a common feature of most eukaryotes. It involves the formation of gametes through meiosis, where genetic recombination occurs, and the conjugation of gametes, which leads to the combination of two parental genomes for the production of offspring with novel assortments of genetic material. Sex has many benefits, such as purifying deleterious mutations, promoting genetic variability, increasing the speed of evolution, but also considerable costs (e.g., breaking up associations of genes that have accumulated through selection) (Barton & Charlesworth 1998; Otto & Lenormand 2002; Meirmans et al. 2012).

While meiotic sex is almost ubiquitous across multicellular eukaryotic lineages, it is often difficult to assess its occurrence in unicellular organisms, where it can be facultative or only visible under specific conditions. Yet, sex has been reported in many protists (Speijer et al. 2015). Evidence is largely based on 'visual observations' from studies carried out with cultures in the laboratory under controlled experimental conditions, where sexual stages and their distinctive morphological and cytological features have been described (e.g., Pfiester & Anderson 1987; Chepurnov et al. 2004; Lahr et al. 2011). Information on the molecular mechanisms that regulate different aspects of the sexual phase in protists, i.e. mating systems, pheromone signalling and gamete conjugation, is limited to studies carried out on only a handful of model species (e.g., Umen 2011; Sekimoto et al. 2012; Goodenough & Heitman 2014). The availability of genomic resources for an increasing number of protists now allows the presence of sex to be inferred in unicellular microalgae for which experimental evidence is still lacking. This is the case of the small prasinophyte *Ostreococcus tauri*, where evidence of recombination and chromosomal segregation was detected by analysing eight loci on neutrally evolving intergenic regions (Grimsley et al. 2010). In addition, core meiotic genes have been detected in the genome of *O. tauri* (Derelle et al. 2006) and of the symbiontic dinoflagellate *Symbiodinium* (Chi et al. 2014), which argues for the existence of a sexual phase in these species.

Diatoms are one of the major lineages of photosynthetic eukaryotes and include planktonic and benthic species ubiquitous in marine and freshwater environments. They belong to the Stramenopila group and are a very diverse lineage that includes about 10^5 species (Mann & Vanormelingen 2013). Based on the morphology and ultrastructure of their siliceous frustule, diatoms can be divided into four major groups: radial centrics, at the base of the phylogenetic tree, multipolar centrics, araphid and raphid pennates, the latter representing the evolutionary most recent group (Kooistra et al. 2007). Diatoms are key-players in the ocean, being responsible for about 20% of the global primary production (Mann 1999). These microalgae have a unique life cycle characterized by progressive cell size reduction and the restitution of the large cell size is accomplished within the sexual phase, which thus has an additional fundamental role in the evolutionary history and ecology of diatoms. A number of review papers dealing with various aspects of the life cycles of marine

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