A theoretical investigation of the diatom cell size reduction–restitution cycle

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ABSTRACT

An individual based model for the life cycle of diatoms (DiaLCM) has been developed to investigate the combined effects of the cell cycle and the cell size reduction–restitution cycle (SRRC) of this important marine phytoplankton group. Growth, grazing mortality and sinking are considered as size-dependent processes. The model is tested against laboratory results and reproduces the typical saw tooth pattern of mean population size as the result of the SRRC. The development of cell-size distribution patterns, their dependence on the environment and their influence on the ecosystem is investigated in a one-dimensional water column setting, where the diatoms face competition by a bulk phytoplankton species. Using a perpetual-year forcing, we find that the SRRC introduces interannual variability with periods of diatoms dominance interrupted by dominance of other phytoplankton. We find that inter- and intraspecific competition explains several of the observed characteristics in size frequency distributions, in particular the relatively narrow cell size spectra. In agreement with observations modeled auxosporulation events are rare with low numbers of auxospores.

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1. Introduction

The cell size of diatoms is relevant in many different research fields. For example, the size of diatom "shells" (frustules) from a geological era are utilized to determine climate change induced macroevolutionary shifts (e.g. Finkel et al., 2005). The cell size also determines the flow of energy to higher trophic levels, because grazing is to a large extent size-dependent (e.g. Hansen et al., 1997). Furthermore, the sinking speed as well as aggregate formation of cells depend on their size (e.g. Waite et al., 1997; Guidi et al., 2009). Hence size plays an important role in how fast matter, e.g. organic carbon or biogenic silica, is exported from the surface to the deep ocean.

The average cell size of a diatom population, however, does not remain constant over time. This is because diatoms undergo a so-called *cell size reduction–restitution cycle* (SRRC) with a gradual decrease of the frustules' size followed by a relatively rapid restoration to a size maximum. Minimum and maximum values differ typically by a factor of 2–5 (see e.g. Mann, 1988; Jewson, 1992b; Sarno et al., 2010; Nishikawa et al., 2013). The temporal variation of mean cell size shows a typical saw tooth pattern (e.g. Armbrust and

Chisholm, 1992; Nishikawa et al., 2013) with a diminution phase that takes several tens to hundreds of generations (e.g. Mann, 1988; Armbrust and Chisholm, 1992). Depending on the environmental conditions, the elapsed time for such a cycle varies considerably and may last several years (Mann, 1988; Jewson, 1992a,b; D'Alelio et al., 2010). While the decrease in size is a result of vegetative reproduction, the size restitution that follows after reaching a critical minimum cell size usually involves sexual reproduction.

Although sexual reproduction is obligatory for most diatom species to restore their cell size, there are only few direct observations of sexual events in nature, particularly in marine systems (see Crawford, 1995; Assmy et al., 2006; Holtermann et al., 2010; Sarno et al., 2010). The reasons why sex is so rarely observed have been discussed extensively. Possible explanations are very large generation numbers and thus a duration of the life cycle of several decades, so that sex occurs very infrequently (e.g. Mann, 1988), a short appearance of few hours or days (e.g. Mann, 2011) or very low abundance of sexual stages (e.g. Assmy et al., 2006), asexual size restitution strategies (e.g. Chepurnov et al., 2004), a bias originating from standard sampling strategies or problems in identification of sexual stages (as discussed in Koester et al., 2007).

Signatures of saw tooth patterns are, however, frequently found in diatom data sets, not only from laboratory studies (e.g. Armbrust and Chisholm, 1992; Amato et al., 2005; von Dassow et al., 2006) but also from marine monitoring stations (e.g. D'Alelio et al., 2010;

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Sarno et al., 2010; Nishikawa et al., 2013) and from sediments (Mann, 1988; Jewson, 1992b, and references therein). A closer look at size frequency distributions show that the occupied range of size classes is narrow compared to the potential range (e.g. Jewson, 1992b; Mann, 1988). The mechanisms behind are unclear but several processes are assumed to be involved, for example (see, e.g. Jewson, 1992b): increasing senescence of older (larger) cells selects for younger (smaller) cells; high grazing pressure on smaller cells favors larger cells; parasitism affecting mostly larger cells selects for smaller cells.

Size frequency distribution patterns are often unimodal, but bimodal or even multimodal distributions are also found (e.g. Mann, 1988; Jewson, 1992b). Again, the underlying reasons are unknown. It is conceivable that seasonal stratification and/or differential sinking speeds may lead to a separation of sub-populations which grow under different conditions; when re-entrained into the surface mixed layer, an assembly of different cell size classes will be the result. Resuspension of viable resting stages with different cell size from sediment may also affect size frequency distributions of a diatom population (Jewson, 1992b).

Little is also known about the ecological consequences of an SRRC. Direct observations point toward an increased export of biogenic silica after a mass sexual event of a polar diatom species (Crawford, 1995). Even less is known about the interaction with other species during the (multi-year long) period of cell size reduction. Finally, on the most fundamental level, the question of the evolutionary significance of an SRRC has been subject to speculation: the SRRC may act as a "sex clock", an internal clock for sexual reproduction (Lewis, 1984), as a "seeding strategy" (Smetacek, 1985) to spread the biomass to a wider range of cell sizes, or as a defense mechanism to minimize the losses through size-selective grazing pressure (Edlund and Stoermer, 1997).

Overall, although diatoms and their life cycle have been studied for more than a century, many open questions related to the SRRC remain. Some of them cannot easily be tackled by observations alone. Numerical modeling represents an underutilized tool to address some of the mentioned issues. Models can sharpen our senses for where to look next in the laboratory or in the field. More specifically, they can give us an idea which processes or mechanisms are most important under which circumstances.

Today's marine ecosystem models include diatoms either indirectly in a bulk phytoplankton compartment or directly as a functional group. None of these models, however, takes the SRRC into account. But what are we missing if we do not consider one of the most prominent features, one of the most ubiquitous, fundamental processes of one of the most dominant and widespread phytoplankton groups?

Our ultimate goal is to shed light on how cell size distribution patterns in nature emerge and develop, how they are influenced by the environment and which consequences the SRRC has on the ecosystem. We address these questions by developing a diatom life cycle model built on an individual based model approach and conducting a series of targeted model experiments. We will also analyze the differences between the traditional "compartment diatom" approach and our new one. We deliberately do not consider other aspects that regulate diatom dynamics like different nutrient limitations of growth, changes in stoichiometry or cell aggregation. They are all important in nature under certain circumstances but to describe these dynamics would superimpose the signal of the SRRC and would complicate the interpretation of the model results.

The paper is structured as follows. We first describe the main features of a diatom life cycle which are important from a modeler's point of view (Section 2). The concept of the life cycle model (DiaLCM) is then introduced in Section 3. We concentrate on a centric diatom, for which essential parameters are available. The model

description is followed by the evaluation of the model based on observations from a laboratory experiment (Section 4). Section 5 presents the results of model experiments with a seasonally forced water column model, that provides the environment for the diatom IBM. A number of sensitivity experiments are described. The results are discussed in Section 6 and the paper closes with conclusions and outlook (Section 7). Details of the model itself and the parameter settings are provided in the Appendices.

2. General description of the diatom life cycle

The life cycle of diatoms is characterized by changes in cell size on two different time scales. On diurnal time scales the *mitotic cell cycle* takes place: individual cells grow to approximately twice their minimum size and divide, resulting in two daughter cells. On longer, monthly to (multi-)annual time scales diatoms undergo a *cell size reduction–restitution cycle* (SRRC). To clearly discriminate these two modes of size changes, the generic term *size* needs further specification. While size may refer to volume or biomass, it may also be a particular linear dimension (length, height or diameter) of the cell, depending on its specific shape. For diatoms, mitotic cell size changes are a result of the increase in their pervalvar length (see Fig. 1, inset for cell morphology and terminology), while their apical radius remains constant. The SRRC, however, involves a diminution of the apical radius (see inset Fig. 1) from one generation to the next. As a consequence, cell volume and cell biomass increase during the cell cycle but decrease for successive generations.

The cell cycle consists of distinct phases involving different biochemical processes like DNA replication, chromosome segregation and cell division. Nevertheless, the biomass increase of each cell is approximately linear until the cell divides (see Olson et al., 1986). After cell division, the parental epivalve serves as the epivalve of one daughter cell while the parental hypovalve becomes the epivalve of the other daughter cell. As a result of this specific cell division process, the mean cell size of the population shrinks (MacDonald–Pfitzer Rule; MacDonald, 1869; Pfitzer, 1869), because after each cell division the daughter cell with the parental hypovalve has a smaller maximum apical radius (Fig. 1) and thus
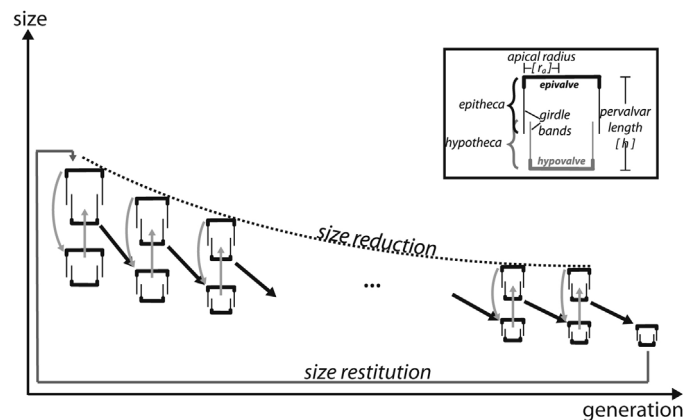

Fig. 1. Schematic representation of cell growth and division (light gray arrows), cell size reduction (black arrows) and cell size restitution (dark gray arrow) for diatoms. During the cell cycle diatom cells grow to about twice their original size. Two new hypovalves are formed followed by a cell division during which the parental epivalve remains the epivalve of one daughter cell; the parental hypovalve forms the new epivalve of the other daughter cell. Thus, from one generation to the next the apical radius shrinks (cell size reduction) but cell volumes between cells in different cell cycle phases and generations overlap. The reduction in size decreases with cell size: differences are larger for large cells than for smaller ones (indicated by the dotted line). Once a critical cell size is reached, the maximum cell size is restored. Note that the size differences between epitheca and hypotheca and from one generation to the next are not to scale. The inset schematically shows the morphology of a diatom cell and the pertinent terminology.