

Regulation of chain length in two diatoms as a growth-fragmentation process

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Chain formation in diatoms is relevant because of several aspects of their adaptation to the ecosystem. However, the tools to quantify the regulation of their assemblage and infer specific mechanisms in a laboratory setting are scarce. To address this problem, we define an approach based on a statistical physics model of chain growth and separation in combination with experimental evaluation of chain-length distributions. Applying this combined analysis to data from *Chaetoceros decipiens* and *Phaeodactylum tricornutum*, we find that cells of the first species control chain separation, likely through a cell-to-cell communication process, while the second species only modulates the separation rate. These results promote quantitative methods for characterizing chain formation in several chain-forming species and in diatoms in particular.

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I. INTRODUCTION

Diatoms are unicellular algae characterized by a rigid external cell wall (the frustule) composed of two siliceous and unequal halves (called the valves), with the bigger one fitting onto the smaller one like a lid fits onto its box. This ecologically key class of algae inhabits all the aquatic environments, from salty waters to brackish and fresh waters. They have a deep impact on oxygen production on Earth, fixing at least one fifth of the total carbon fixed per year on our planet [1]. Additionally, diatoms are the most diverse class of algae, numbering 12 000 described species to date and possibly 8000 unknown species [2].

One of the main features characterizing diatoms is their ability to form variably stiff [3] and differentially shaped chains [4]. Chains are produced only at mitotic division, when two daughter cells do not separate completely but stay together. Usually, intercellular junctions are not accompanied by cytological contact between sibling cells. In diatoms cell division is very peculiar (see Ref. [5] for an extensive review of mitosis and cytokinesis in diatoms), with the daughter cells “growing” within the mother, then separating via an animal-like cleavage furrow [5,6], followed by the synthesis of a new silica cell wall (similar to what happens to the cellulose cell wall in plants). Upon separation, in most species the two daughter cells keep physical contact and produce variably long chains. Chain formation is a species-specific (and possibly ecotype-specific) feature, and the junction modes known to date are quite diverse [7–10], with some species showing cells connecting to each other via frustule processes (e.g., *Skeletonema* [11], *Chaetoceros* [12], the extant genus *Trochosira* [13]), others producing mucus pads that keep the cells together from the apices (e.g., *Asterionellopsis* [14], *Tabellaria* [15]), the extant family Rutilariaceae [16]), and others synthesizing chitin threads between adjacent cells (*Thalassiosira* [9]).

The reasons and mechanisms for diatom chain formation are still being debated. Likely chains have ecological importance [17–20], which could range from buoyancy behavior, similar to flocculation in yeast [21,22], to increased resistance to predators. More generally, clustering is sometimes interpreted as a first step towards multicellularity [23], the second being division of labor with the evolution of specialized cells [24], as in the slime mold *Dictyostelium discoideum* [25]. Diatom ability to produce chains has never been interpreted as a sign of nascent multicellularity, although in some cases (*Licmophora*, *Encyonema*, or *Navicula ramosissima*) particularly complex colonies have been hypothesized to contain specialized and behaviorally differentiated cells [26]. In other phytoplankters [27] as well as in yeasts [28], multicellular-like behavior was invoked and experimentally induced.

One prominent question is the extent and mechanisms that different species and ecotypes use to control the range of chain lengths found in a population. A minimal mechanism purely controls the robustness of junctions, with more fragile junctions being more prone to separation (thereby reducing the average chain length of a population). The extent to which separation may be produced by environmental forcing, e.g., strain due to the fluid shear, is still unclear (see, e.g., Ref. [29]). For example, the physical separation rate may be increased in the presence of turbulent flows, while in these conditions it might be more advantageous for a species to maintain or even increase its average chain length. Alternatively, chain separation might be under more tight regulation, involving, e.g., communication between neighboring cells. Such mechanisms may allow chain formers to react to different environmental changes.

Despite the existing knowledge, the process of chain formation is still poorly understood. Most importantly, no widely accepted tools exist to quantify it in controlled settings. In this scenario, even the elementary statistical physics models to understand and quantify data are an open question. Here, we address these issues with a combination of experiments

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