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Single cell carbon and nitrogen dynamics in chain forming diatoms, including their resting stage

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Abstract

The oceans are a fundamental part of all life on earth, accounting for more than half of Earth's oxygen production. The ocean is also key to long term carbon dioxide sequestration. Diatoms are a group of phytoplankton differentiated by their silica shell/frustule and account for ~20% of global primary production. Some of these diatoms form colonies/chains which are viewed as a way to reduce grazing pressure, but also effect aggregation, sedimentation, and nutrient assimilation. Exponential growth conditions during algae blooms have been well studied. Less is known about how they survive between blooms when conditions are no longer optimal. In nature, high nutrient availability in the photic zone and subsequent blooms only last a few weeks. Growth limited conditions persist for most of the year.

In **chapter I** and **II**, shifts in carbon and nitrogen assimilation dynamics were investigated in two chain forming diatoms: *Chaetoceros affinis* (**I**) and *Skeletonema marinoi* (**II**) at the beginning of nitrate limitation. *C. affinis* which are often larger than *S. marinoi* and are relatively more abundant during summer conditions with low nitrate availability. *Skeletonema* produce smaller cells and dominate at the beginning of blooms, where they thrive and assimilate excess nitrogen. *C. affinis* produced exudates of sugars and was colonized by attached bacteria that assimilated both carbon and nitrogen derived from their host. Later, diatoms were remineralised by bacteria, releasing ammonium. This ammonium could balance carbon assimilation for active diatoms. I speculate that cells in chains could benefit from remineralization of other cells in the chain and supply active cells with ammonium. *S. marinoi* showed no difference in carbon and nitrogen assimilation depending on chain length. The cells assimilated nitrate at a rate 25-65 times lower than the diffusive supply could provide, when compared to modelled diffusive supply from the ambient water. This indicated that cells were limited by biological uptake rates rather than diffusive supply. In **chapter I** and **II**, I demonstrated that *C. affinis* and *S. marinoi* had different ways of dealing with nitrate limitation, corresponding to the niches they fill. *C. affinis* recirculate the nitrogen with help of bacteria, which would allow them to keep a standing population in low nitrogen availability between blooms. *S. marinoi* on the other hand assimilated an excess of nitrogen during high availability, where they usually dominate.

In addition to playing a key role in primary production and nutrient turnover, diatoms also contribute to particle transport from the photic zone to the sediment. Diatoms form resting stages which can survive decades to centuries in dark and anoxic sediments. Mechanism of survival is unknown, and they have previously been considered as "dormant" in the sediment. Basic mechanisms for cell maintenance in resting stages of *S. marinoi* were investigated in **chapter III**. I showed that they were able to assimilate both nitrate and ammonium in dark and anoxic conditions. The nitrogen specific generation time varied between 23-500 years which may be enough to maintain viable cells, but not for growth. In **chapter IV**, I investigated if resting stages could use nitrate as an electron acceptor and assimilate organic molecules available in the sediment (acetate and urea). The resting stages performed dissimilatory nitrate reduction to ammonium (DNRA) and assimilated N from urea. They could not assimilate carbon from urea but assimilated carbon from acetate. Hence, the sediment provides resting stages with both carbon and nitrogen for assimilation and respiration. I have shown that diatom resting stages are not as dormant as previously assumed. I also showed that two common chain forming diatoms have different mechanisms of circumventing reliance on nitrate diffusion from the ambient water. The next step is to connect this to marine monitoring and prediction models taking chain formation into account. This thesis has only scratched the surface on chain forming diatoms responses to adverse conditions. Considering the large diversity of chain forming diatoms, the responses to such conditions may be equally diverse.