## **PROJECT 2.10**

Most investigations on planktonic predators, prey, and their interactions ignore variation within populations, as establishing and measuring variation in these relatively small organisms is not easy. Recently, it has become clear that neither predator populations nor prey populations can be considered homogenous entities, as both in algae as well as in herbivorous zooplankton a lot of physiological and behavioural variation exists that has the potential to affect the outcome of predator-prey interactions. Especially within-species variation in nutrient stoichiometry, cell quota and nutritional demands has the potential to shape community structure. Thus, in this project, we focused on nutrient stoichiometry as the variable trait within populations, as 1) the processes that drive variation in this trait within populations are different in primary and secondary producers thus potentially leading to mismatch phenomena; and 2) the theoretical considerations are possible.

In phytoplankton, as the availability of light and nutrients fluctuate, there is variation in the nutrient stoichiometry of the alga. This variation is further influenced by growth rates, which culminates in most cases in the fact that fast growth is linked with a certain optimal nutrient content of the algae (less variation at higher growth rate), whereas slow growing algae can have a large array of different nutrient compositions (Hillebrand et al. 2013). These patterns were identified between populations of algae by averaging the individual responses of many different cells, but up until now, it was unclear whether this also holds within single species and even within populations, between single algal cells. Thus, we carried out several experiments investigating this. For example, we tested this hypothesis with a laboratory experiment performed with a monoculture of the ubiquitous diatom *Phaeodactylum tricornutum*. With a gradient in growth rate obtained using 10 chemostats, we were able to determine the effect of growth rate on this diatom's selected traits, such as cellular stoichiometry and cell size, besides the hypothesized change in the coefficient of variation. Our results showed indeed changing stoichiometry as well as less intercellular variability in the faster growing microalgal populations.



Fig 1. Reaction of the different traits of the diatom *Phaeodactylum tricornutum* to changes in growth rates of the cultures. Left, bulk C/P ratios shows that faster growing cells have indeed more phosphorus relative to carbon, so even within species the predictions made by Hillebrand et al (2013) hold. The right graph shows the variation in cell size within cultures, indicating that even between cells within one culture the variation in traits declines with growth rate: there are many ways to grow slow, but only very few to grow fast.

Zooplankton typically has a more constant nutrient stoichiometry, and a stronger degree of homeostasis. Here, we investigated variation in population growth rate in microalgae, linked this to intra-population variation in nutrient stoichiometry, and investigated the effect of these

growth rate-induced variations in cell nutrient quota on growth and dynamics of predators. If intra-population variation in nutrient stoichiometry increases with slower algal growth rates, we predicted that this will potentially lead a gradient of different food sources (with different stoichiometry) being available. Hence, we carried out different experiments to test this. At the moment of writing this report these are all still in the process of being analysed. Based on our findings that the growth rate of the algae affects their stoichiometry, and that this has consequences for heterotrophs, we investigated the impact of changing growth rates on the population growth rate of the dinoflagellate *Oxyrrhis marina* feeding on differently grown algae (*Rhodomonas salina*). As expected, we observed a gradient of C/P ratios in the algae with growth rate; this gradient was mirrored in the grazers. The growth rates of the grazers were not affected by the growing conditions of the algae, potentially because they were fed ad libitum, and as a result even at the low growth rates there were enough high quality particles available, as variation within the cultures was much higher here. In fact, we did observe selective feeding towards the faster growing algae.

Further, we fed differently grown algae to natural microzooplankton populations taken from the Helgoland Roads LTER. We hypothesized that depending on the growth rates of the algal cultures, their variation should be different and as a result, the diversity of grazers being able to survive on the slower growing algae should be higher. No data are available from these studies yet.

Finally, we analysed the changes in the phytoplankton community off Helgoland using a trait based approach, i.e. instead of studying the way and wane of different plankton species we investigated the changes in traits over the years. Using a trait-based approach, we examined changes in the functional structure of the southern North Sea phytoplankton over the past five decades in relation to environmental conditions. We identified a sudden shift in functional structure between 1998 and 2004. Early in the 2000's, the phytoplankton functional structure shifted from slow growing, autumn blooming, mixotrophic organisms, towards earlier blooming and faster-growing microalgae. Warming and decreasing dissolved phosphorus concentrations were linked to this rapid reorganization of the functional structure. We identified a potential link between this shift and dissolved nutrient concentration, and we hypothesise that organisms blooming early and displaying high growth rates efficiently take up nutrients which are depleted for late bloomers. Moreover, we identified that the above-mentioned functional change may have bottom-up consequences, through a food quality-driven negative influence on copepod abundances.

In short, using several different approaches we were able to show how strongly a large range of characteristics of primary producers is affected by growth rate, and that these changes in the algae can have potential repercussions for their grazers, ultimately with the potential of changing functional composition, impacting both food-web structure and biogeochemical cycles.

- Di Pane, J., Wiltshire, K.H., McLean, M.J., Boersma, M. & Meunier, C.L. Environmentally induced functional shifts in phytoplankton and their potential consequences for ecosystem functioning. Submitted to Global Change Biology. Aug, 2021.
- Groß, E., Boersma, M. & Meunier, C.L. **2021**. Environmental impacts on single-cell variation within a ubiquitous diatom: The role of growth rate. PLoS ONE 16: e0251213. DOI: 10.1371/journal.pone.0251213.
- Herstoff, E.M., Baines, S.B., Boersma, M. & Meunier, C.L. Does prey elemental stoichiometry influence copepod swimming and behavior over ontogeny? **2019.** Limnol Oceanogr 64:2467-2477. DOI: 10.1002/Ino.11198

- Herstoff, E.M., Meunier, C.L., Boersma, M. & Baines, S.B. **2021**. Leveraging differences in multiple prey traits allows selective copepods to meet their threshold elemental ratios. Limnology and Oceanography 66:2914-2922. DOI: 10.1002/Ino.11800
- Klip, H.L.C., Meunier, C.L. & Boersma, M. Less variability when growing faster? Experimental assessment of the effects of growth rate on functional traits of the marine diatom *Phaeodactylum tricornutum*. To be submitted to Limnology and Oceanography, Dec 2021.
- Meunier, C.L., Herstoff, E.M, Geisen, C. & Boersma, M. **2020**. A matter of time and proportion: The availability of phosphorus-rich phytoplankton influences growth and behaviour of copepod nauplii. J. Plankton Res. 42:530-538. DOI: 10.1093/plankt/fbaa037