P1.17 Adaptive trait dynamics of lake phytoplankton at short time scales PI Bernd Blasius

The analysis of trait distributions is one of the most advanced approaches in modern ecology, bridging the gap between monitoring data and ecological modeling. The success of this approach is based on a comprehensive representation of the entire ecological community as a continuous distribution of trait values. This allows, for example, to study the influence of environmental factors in terms of the resulting adaptive changes in the trait distribution. In DynaTrait project P1.17 we applied this approach to the case of lake phytoplankton. As traits we focused on geometric characteristics of phytoplankton cells (linear size, volume, surface area, and shape) as they are among the most easily measurable quantities in phytoplankton and can be readily obtained by flow cytometry and microscopy. Additionally, we could use a modelling approach to capture the geometric characteristics of cells of different species and thereby greatly simplify their parameterization. For example, the size of a cell size can serve as a parameter for allometric scaling of its metabolic rate, whereas cell shape can describe deviations from this scaling. Using this approach, the major aim in our project was to characterize the spectrum of cells' geometric traits in phytoplankton and its short-time adaptive response to changing environmental factors and thereby to improve our understanding of the relationship between geometric traits and the ecological success of species characterized by abundance and diversity patterns.

We started the project by analyzing seasonal and daily variation in the size spectrum of phytoplankton, obtained by flow cytometry at different depths of Lake Greifensee. To relate the measured linear size of cells to biomass we subsequently developed a framework for determining an averaged relationship between linear cell size and cell volume (Mittler *et al.* 2019). To our surprise, we found that this relationship strongly depends on the shape of phytoplankton cells, which inspired us to investigate the relation of cell geometry and diversity in phytoplankton (Ryabov *et al.* 2021). Below we briefly describe main results of this project.

Flow cytometry allows us to estimate the composition of phytoplankton communities with unprecedented temporal resolution. Here, we were interested in the distributions of length, biovolume and other characteristics of phytoplankton cells, as well as their dependence on environmental parameters such as temperature and light intensity. Therefore, during the first part of the project, we analyzed flow cytometry data sets of phytoplankton in Lake Greifensee at different time points, depth in the water column, and environmental conditions. This analysis revealed that the abundance of phytoplankton as a function of cell length, L, is characterized by a power law, $P(L) \sim L^a$, with an exponent a that ranges from 2.4 to 3.4 across samples. Monthly averaged cell spectra were rather constant during the seasons, revealing a stable characteristic of the phytoplankton community with small fluctuations from July to October. At the same time, cell size distributions showed diurnal oscillations and a dependence on depth, with the steepest slope of the distribution in samples obtained at night at the border of the euphotic zone.

Flow cytometry evaluates mainly the longest linear dimension of phytoplankton cells. Thus, to calculate the biovolume distribution or total biovolume, we were interested to find an average relationship between cell length and volume. This task is quite difficult because the shapes of phytoplankton cells and colonies are extremely diverse and there is no unambiguous relationship between their volume, V, and longest linear size, L. However, we could show that an approximate scaling law between these parameters can be found, likely because variation in shape within each size class is limited by cell physiology, predator pressure, and optimal resource acquisition. To determine this scaling and test its seasonal and interannual variation, we performed a weighted regression analysis of the relationship between cell length and volume for phytoplankton communities in Lake Constance from 1979 to 1999. After testing different approaches to the weighted fit, we found that the best prediction of total community biovolume based on measurements of cell length and abundance is obtained when the regression is weighted by squares of species abundance.

Despite the large variability in species composition, we found that the relationship between the cell volume and longest linear size can be approximated by a power law $V(L) \sim L^{\alpha}$. However, this dependence is isometric, $\alpha = 3$, only if we restrict the range to small cells ($L < 25$ µm). In contrast, if all cells and colonies are included, the averaged scaling law shows much slower growth of volume with linear cell size, characterized by an exponent of $\alpha = 1.7$. The best description is provided by a nonlinear power-law function, describing a change in the scaling exponent from 3 for small cells to about 0.4 for large cells. The developed approach (Mittler et al. 2019) can be applied to other systems and allows converting phytoplankton length distributions into distributions of biovolume and biovolume-related phytoplankton traits.

Further analysis revealed a surprisingly strong influence of cell shapes not only on cell biomass but also on phytoplankton diversity. While the influence of size on the ecophysiological characteristics of an organism is well understood, little was known about how the shape of individuals is related to taxonomic richness, especially in microorganisms such as phytoplankton. To better understand this relationship, we analyzed global datasets of unicellular marine phytoplankton (Ryabov et al. 2021). Using two measures of cell shape elongation, we quantified taxonomic diversity as a function of cell size and shape. We found that there is an interplay between different cell sizes and shapes, where the cells of intermediate volumes have the greatest variation in shape, ranging from oblate to extremely prolate forms, while cells of both large and small volumes are compact (e.g., spherical or cubic). At the same time, spherical shapes exhibit the largest variation of cell volumes. Finally, we showed that taxonomic diversity decreases exponentially with cell elongation for attenuated and flattened cells and follows a lognormal dependence on cell volume, peaking for compact cells of intermediate volume. This relationship explains up to 92% of the total biodiversity variance in our data. These previously unreported patterns in phytoplankton diversity reveal selective pressures and ecophysiological constraints on the geometry of phytoplankton cells, which may improve our understanding of marine ecology and the evolutionary rules of life.

Publications

Mittler, U., Blasius, B., Gaedke, U. & Ryabov, A.B. (2019) Length-volume relationship of lake phytoplankton. Limnol. Oceanogr. Methods, 17, 58–68.

Ryabov, A.B., Kerimoglu, O., Litchman, E., Olenina, I., Roselli, L., Basset, A., Stanca, E., Blasius, B. (2021) Shape matters: the relationship between cell geometry and diversity in phytoplankton. Ecology Letters, 24, 847–861.