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Growth and Functioning of the Microbial Plankton Community: Effects of Temperature, Nutrients and Light

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Summary

Microbial plankton form the basis of the food web in aquatic habitats. Due to their vast abundances they influence the cycling of elements and the Earth's climate at a global scale. Planktonic microorganisms are highly diverse and form complex networks of interactions. The growth and functioning of microbial plankton communities is strongly influenced by environmental factors, in particular by temperature and the availability of nutrients and light. This thesis aims at a better understanding of how these factors affect microbial plankton communities, which is highly relevant in the context of global climate change and anthropogenic changes in nutrient cycling.

As a first step this thesis focuses on a single species, the marine N_2-fixing cyanobacterium *Cyanothece*. A series of batch culture experiments revealed interactive effects of temperature, light and nitrogen source on the physiology and growth of *Cyanothece*. The rates of N_2 fixation and growth generally increased with light intensity until they levelled off at high light. Addition of nitrate suppressed N_2 fixation and slightly stimulated the growth rate, which increased with temperature across the entire experimental range from 14 to 38°C. However, when grown on N_2 only, temperature increased the rates of N_2 fixation and growth only in the range from 18 to 30°C. Above 30°C, N_2 fixation became limited by the rate at which oxygen diffused into the cell, which prevented a further increase of N_2 fixation and growth with temperature. Interestingly, temperatures below 21°C also limited N_2 fixation and induced nitrogen deficiency in *Cyanothece* because of two reasons: low temperature (i) delayed the timing of N_2 fixation until late in the night, and (ii) sharply increased the respiratory cost of N_2 fixation. These results offer a physiological explanation for why free-living N_2-fixing cyanobacteria in the open ocean are generally restricted to the warm waters of the (sub)tropical oceans.

In a second step this thesis advances towards a plankton community consisting of the N_2-fixing *Cyanothece* and its associated free-living chemotrophic bacteria. A series of chemostat experiments revealed that temperature and nutrients had interactive effects on plankton community structure. At steady state, higher temperatures strongly increased the abundance of *Cyanothece* but only mildly influenced the abundance of chemotrophic bacteria, which led to a higher proportion of *Cyanothece* at higher temperatures. Conversely, a higher supply of nitrogen and organic carbon had minor effects on *Cyanothece* but large effects on the abundance and species composition of the chemotrophic community. *Cyanothece* appeared to influence the composition of its associated bacterial community through a combination of competition for nutrients and facilitation due to the release of fixed nitrogen and carbon. These results suggest that the composition of free-living bacteria associated with N_2-fixing cyanobacteria is mainly driven by ecological niche differentiation rather than by tight evolutionary relationships with the N_2-fixing 'host'.

In a third step this thesis turns its focus on phytoplankton communities. I present a theoretical model for the competition between multiple phytoplankton species for two nutrients and light. The model results are summarized by the nutrient-load hypothesis, which states the following. In oligotrophic ecosystems phytoplankton species compete for nutrients and the species composition of the community depends on the ratio at which the growth-limiting nutrients are supplied to the system, as predicted by the well-established resource-ratio hypothesis. In eutrophic ecosystems, however, phytoplankton species compete for light, because the high nutrient loads generate high biomasses that induce self-shading. In this situation the species composition of phytoplankton communities does not depend on nutrient ratios but is determined by the absolute nutrient loads and often dominated by a single species. The nutrient-load hypothesis predicts that highest phytoplankton diversity is found at intermediate nutrient loads, where phytoplankton species compete for both nutrients and light. The nutrient-load hypothesis offers a solution for several discrepancies between classical resource-ratio theory and field observations, explains why eutrophication often leads to diversity loss, and thereby provides a new conceptual framework for patterns of biodiversity and community structure observed in nature.

In a fourth step this thesis focuses on a natural plankton community that was sampled from the Dutch Wadden Sea. A series of batch culture experiments revealed that, in the absence of nutrient and light limitation, temperature increased the maximum specific growth rate of the entire plankton community in accordance with the Arrhenius equation. This supports the prediction of the Metabolic Theory of Ecology that metabolic processes provide the foundation for a universal temperature response of ecological processes.

The insights obtained from this thesis show that temperature, nutrients and light have interactive effects on the growth and functioning of microbial plankton communities. Under ideal growth conditions temperature strongly increases plankton growth rates, suggesting that global warming will have a strong direct effect on the growth and species composition of plankton communities in eutrophic systems. However, low nutrient concentrations and low light availability dampen the effect of temperature, suggesting that oligotrophic ecosystems are generally more constrained by nutrient limitation than by temperature. Furthermore, the temperature response varies among species depending on their physiological traits. In particular, our results suggest that global warming will favor marine N_2-fixing cyanobacteria more than other phytoplankton species.