

Summary Project 1.10

Within this project we established a new indoor mesocosm facility, 12 fully controlled “Planktotrons”, designed to conduct marine and freshwater experiments for biodiversity and food web approaches using natural or artificial, benthic or planktonic communities. The Planktotrons are a unique and custom-tailored facility allowing longterm experiments. Wall growth can be inhibited by a rotating gate paddle with silicone lips. Additionally, temperature and light intensity are individually controllable for each Planktotron and the large volume (600 L) enables high-frequency or volume-intense measurements. In a pilot freshwater experiment various trophic levels of a pelagic food web were maintained for up to 90 d. First, an artificially assembled phytoplankton community of 11 species was inoculated in all Planktotrons. After 22 d, two ciliates were added to all, and three *Daphnia* species were added to six Planktotrons. After 72 d, dissolved organic matter (DOM, an alkaline soil extract) was added as an external disturbance to six of the 12 Planktotrons, involving three Planktotrons stocked with *Daphnia* and three without, respectively. We demonstrate the suitability of the Planktotrons for food web and biodiversity research. Variation among replicated Planktotrons did not differ from other laboratory systems and field experiments. We investigated population dynamics and interactions among the different trophic levels, and found them affected by the sequence of ciliate and *Daphnia* addition and the disturbance caused by addition of DOM.

Effect of tDOM on bacteria and phytoplankton

Using flat, stackable culture flasks in a laboratory experiment we compared “combined” effects of directly added tDOM, which simultaneously acts as a resource subsidy, and through change of light conditions with “isolated” effects achieved purely through altered light. For the latter, a separate flask with tDOM stacked onto the actual culture flask created tDOM-shading without a resource subsidy. Potential effects by dissolved nutrients were compensated by phosphate addition to the shading and control treatments. As responses in a complex phytoplankton community may be mediated by shifts in composition, we conducted the experiment with nine phytoplankton species (Chlorophyta, Bacillariophyta, and Cryptophyta) in monoculture and with phytoplankton communities of two different diversity levels, that were assembled by mixing 3 and 9 species, respectively.

tDOM-shading had minor effects on phytoplankton and bacterial growth, while the tDOM-addition increased phytoplankton and bacterial growth, except for cryptophytes. Cryptophyte abundance responded negatively to tDOM-addition. Phytoplankton community composition and fatty acid composition were affected by tDOM-addition compared to the control. Positive diversity effects, thus higher phytoplankton or bacterial response in more diverse mixtures, compared to less diversity mixtures or monocultures, could not be observed. This may have been caused by a poor translation of taxonomic diversity into functional diversity in our experimental setup, or strong competition as

single species dominated the mixtures. Our results show that the responses of phytoplankton on abiotic changes, such as tDOM-addition or shading, are highly species-specific and can cause shifts in phytoplankton community composition, especially when such a complex substance with multiple effects, like tDOM, is involved.

Interactive effects of nutrients and temperature fluctuation on phytoplankton

To assess the interactive effects of nutrients and temperature on phytoplankton and the important role of temperature fluctuations, we grew a natural phytoplankton community under fluctuating and constant temperature regimes across 25 combinations of nitrogen (N) and phosphorus (P) supply in a laboratory experiment. Temperature fluctuations decreased phytoplankton growth rate (r_{max}), as predicted by nonlinear averaging along the temperature–growth relationship. r_{max} increased with increasing P supply, and a significant temperature \times P \times N interaction reflected that the shape of the thermal reaction norm depended on nutrients. By contrast, phytoplankton carrying capacity increased with N supply and in fluctuating rather than constant temperature. Higher phytoplankton N:P ratios under constant temperature showed that temperature regimes affected cellular nutrient incorporation. Minor differences in species diversity and composition existed. Our results suggest that temperature variability interacts with nutrient supply to affect phytoplankton physiology and stoichiometry at the community level.

Resource use efficiency in phytoplankton species and communities

Using four species of freshwater phytoplankton, and their mixture, we further asked how the RUE for nitrogen and phosphorus depends on the stoichiometry of resource supply and how this differs between single species and their mixture. We conducted a factorial laboratory experiment spanning 25 different nutrient supply treatments with differing absolute and relative nitrogen (N) and phosphorus (P) concentrations. N and P supply increased biomass production and decreased C:nutrient ratios and RUE for the respective nutrient, but always significantly affected by the supply of the respective other nutrient. Biomass peaked at molar N:P supply ratios above the Redfield ratio (18-22). Species tended to respond similarly to the resource gradients. Consequently, mixtures outperformed the component species only during early growth responses, but not regarding maximum biomass and RUE. Bioassays performed at the end of the main experiment revealed predominance of N-limitation, but again strongly depending on the interaction between both nutrient gradients. Our study suggests that stoichiometric constraints of resource incorporation and RUE need to be accounted for when studying the response of phytoplankton to natural and anthropogenic variation in resource availability.

Biodiversity as driver for ecosystem functioning under environmental change

To investigate the interactive effects of biodiversity as driver for ecosystem functioning, and environmental changes that can affect ecosystems by directly changing, e.g., light and resource supply but also by acting via disturbance events, such as an

increased perturbation and runoff of terrestrial dissolved organic matter (tDOM) into aquatic systems, we conducted another Planktotron experiment. We hypothesize that highly diverse communities are less affected by disturbance events than less diverse communities. We further hypothesize that the effects of these disturbance events depend on the disturbance history of the community. We tested these hypotheses in a long-term (78 days) experiment using indoor-mesocosms, which were inoculated by either low or high diverse artificial phytoplankton communities. All 12 mesocosms received a natural bacterial community, two different bacterivore ciliates, and three different *Daphnia* species. A first tDOM pulse was added to half (3 low and 3 high diversity) of the mesocosms at the beginning of the experiment, a second tDOM pulse was added to all 12 mesocosms after 41 days. Only the bacterial abundance increased with higher phytoplankton diversity, but neither phytoplankton nor zooplankton biomass. However, no significant interaction between diversity and disturbance was observed, indicating that higher phytoplankton diversity did not dampen the response to the pulse disturbance for any of the trophic levels. The first tDOM pulse resulted in an increase of phytoplankton biomass and bacterial abundance, which was marginal more expressed in the high diversity phytoplankton communities. The second tDOM pulse strengthened the positive effect on bacterial abundances and *Daphnia* dry weight, but had no effect on phytoplankton biomass, thereby the communities with one single or two tDOM pulses respond consistent. Thus, the disturbance history was in this experiment of minor importance and the positive effect of biodiversity was not significantly expressed. However, tDOM addition had a positive effect on the pelagic food web and no shift from a classical grazing chain towards a microbial loop food web occurred, regardless of the diversity level or the amount of tDOM disturbances.

To summarize, in this project we investigated the dynamics of trophic interactions as mediated by trait-based diversity at various trophic levels. We manipulated diversity at the base (phytoplankton) and top (zooplankton) of this food web, and study effects on trophic transfer, food web dynamics and ecosystem functioning. We included stoichiometry and fatty acid composition of the key trophic levels as potentially important qualitative controls, as well as trait-based assessments of bacterial metabolic capabilities and of the complex organic resources fuelling the microbial loop. We included high-resolution mass spectrometry in the context of an ecological experiment to describe chemical diversity of dissolved organic matter (DOM) as derived from biota differing in diversity and to uncover its potential effects along the microbial loop. Further, we exposed our food webs to (a) pulse(s) of coloured, terrigenous DOM as external forcing with disturbance-character, and studied its effect on food web dynamics (i.e. the grazing link as well as the microbial loop).

We demonstrated that phyto- and zooplankton diversity affected trophic transfer, zooplankton growth and dynamics, and the trophic linkage intensity as assessed by the dynamics of both trophic levels. Further, phytoplankton diversity increased the chemical

diversity of dissolved organic matter, and thereby affected bacterial resource use, and long-term functional diversity and biomass of bacterioplankton.

Publication list Project 1.10:

1. Gerhard, M., C. Mori, M. Striebel. 2021. Nonrandom species loss in phytoplankton communities and its effect on ecosystem functioning. *Limnology and Oceanography*. doi: 10.1002/lno.11642
2. Frank, F., M. Danger, H. Hillebrand, M. Striebel. 2020. Stoichiometric constraints on phytoplankton resource use efficiency in monocultures and mixtures. *Limnology and Oceanography*. doi: 10.1002/lno.11415
3. Gerhard, M., A. M. Koussoroplis, H. Hillebrand, M. Striebel. 2019. Phytoplankton community responses to temperature fluctuations under different nutrient concentrations and stoichiometry. *Ecology*. doi.org/10.1002/ecy.2834
4. Hodapp, D., H. Hillebrand, M. Striebel. 2019. "Unifying" the concept of resource use efficiency in ecology. *Frontiers in Ecology and Evolution*. doi.org/10.3389/fevo.2018.00233
5. Gall, A., U. Uebel, U. Ebensen, H. Hillebrand, S. Meier, G. Singer, A. Wacker, M. Striebel. 2017. Planktotrons: A novel indoor mesocosm facility for aquatic biodiversity and food web research. *Limnology and Oceanography Methods*. doi: 10.1002/lom3.10196