Alternative states of a simple predator-prey system induced by competition between small edible and large inedible algae and fungal parasitism (APPS)

Recently, the importance of fungi in aquatic systems as a source of "microbial dark matter" has been recognized, indicating that fungi can substantially affect aquatic ecosystems ranging from syntrophic to parasitic interactions with other organisms.
Chytrids constitute the dominant group of fungal parasites in aquatic systems and can be highly host specific. Furthermore zoospores - the free living infective stage of parasitic fungi – have been shown to form a highly nutritional food source to zooplankton. Recently attention has been drawn to the fact that ingestion of zoospores can create an energy pathway from otherwise inedible phytoplankton to zooplankton, the so called "mycoloop". In light of a globally rising dominance of cyanobacteria along with eutrophication and global warming, it is important to assess how the presence of the mycoloop will influence the stability and energy transfer in aquatic systems. In this project we combined experimental studies with theoretical investigations to assess how the mycoloop potentially affects community composition, population dynamics, and nutrient/energy transfer in aquatic ecosystems. While the experimental setup allowed to assess the importance of the isolated and combined effects of zooplankton and chytrids on phytoplankton dynamics and its effects on competition between small well edible and large non-edible (susceptible) phytoplankton species for two contrasting nutrient scenarios, the model analysis allowed to investigate the importance of the mycoloop for energy flow and system stability as well as its influence on community composition and along an environmental gradient (nutrient availability) for selective versus non-selective zooplankton species.
For the experiment we used a model system of large (inedible) phytoplankton (*Staurastrum* spp.) and its specialized parasitic chytrid (van den Wyngaert et al. 2017, *Protist*), small (edible) phytoplankton (*Cryptomonas* spp.) and a common zooplankton species (*Daphnia magna*). The selected zooplankton species can consume the edible phytoplankton as well as the free-living stage of chytrids, i.e. zoospores, but not the large phytoplankton. We investigated competition between both phytoplankton species in presence/absence of chytrids and/or zooplankton under low versus high nutrient cultivation conditions. As expected, the experimental results showed that the presence of chytrids decreased the abundance of large phytoplankton through infection, to the benefit of small phytoplankton. In contrast, the presence of zooplankton decreased the abundance of small phytoplankton through predation, positively affecting large phytoplankton. These results were independent of nutrient conditions. In the full system (both phytoplankton species, predator and parasite), at high nutrient levels, the phytoplankton densities developed similar to the case of

zooplankton predation only, resulting in a pronounced increase in large phytoplankton. At low nutrient levels, zooplankton showed a pronounced increase at the beginning of the experiment, correspondingly small phytoplankton dramatically decreased during this initial phase. However, at the end of the experiment, with decreasing zooplankton biomass, small phytoplankton increased again and dominated the phytoplankton community. Comparing differences in biomass accumulation of large vs. small phytoplankton between treatments, we observed an increased competitive advantage of large phytoplankton over small phytoplankton for the full system in comparison to in the presence of either zooplankton or chytrids. The increase of pronounced increase of zooplankton for the low nutrient case indicates that chytrids indeed represented a good food resource and led to strong top-down control on small phytoplankton, benefitting large phytoplankton. The results suggest that chytrids affect predator-prey interactions and phytoplankton competition and reveals a potentially synergistic effect of predator and parasite on the proliferation of inedible phytoplankton. This study suggests the presence of chytrids differently affects phytoplankton predator-prey and competition interactions depending on nutrient availability.

In the corresponding theoretical study, we used the same food web approximation: one inedible (susceptible), one edible (in-susceptible) phytoplankton species, a parasitic fungus species (chytrid) specialized on the inedible phytoplankton and zooplankton feeding on edible phytoplankton and fungi. We investigated system dynamics of a corresponding differential equation system along a nutrient gradient under the assumption of fixed versus flexible zooplankton prey preference for phytoplankton versus parasitic fungi. We furthermore compared model predictions to experimental observations on changes in community composition. For this we analyzed the transient dynamics of the model output contrasting predictions from the basic food web model with versions differentiating the host population into susceptible and infected. The model implications of the basic food web show an increasing importance of the mycoloop pathway for energy flow to zooplankton with increasing nutrient availability. Under the assumption of adaptive zooplankton prey preference we observe a regime shift from low to high nutrient availability, where community composition and energy flow is dominated by edible phytoplankton at low nutrient availability, whereas energy flow is more balanced between the direct phytoplankton and the fungi pathway at higher nutrient availability. Moreover, we observe that even a slight preference of zooplankton for fungi increases food web stability. The comparison of model output and experimental results revealed that the differentiation of susceptible and infected stages of the host population (large phytoplankton) is critical for a good match between model predictions and experimental results. It specifically enables to successfully reproduce the initial increase of zooplankton and the dynamics of small phytoplankton under both high and low nutrient conditions. In contrast the basic model (not discriminating between susceptible and infected host stage) could only reproduce the population dynamics for the high nutrient case. Investigating the influence of adaptation speed of zooplankton preference on system dynamics reveals that increasing speed of adaptation can increase the period of zooplankton dominance. The model results furthermore reveal that the short-term predictions, matching with the duration of the experiment of a month, might differ quite significantly from the long-term expectation. This illustrates the limited ability to extrapolate results from short term experiments to long-term expectations.

In an additional modeling study, we investigated how the isolated and combined presence of predators and parasites affects adaptation of prey resistance and how this influences community dynamics For this the food web was reduced to one phytoplankton species with the ability to adapt its size. We assumed that parasitic chytrids are more likely to infect larger cells of the phytoplankton population, while zooplankton can exclusively feed on the smaller cell sizes and is unable to prey on the large phytoplankton cells. Therefore phytoplankton can decrease/increase its size in order to escape parasite or zooplankton infection/predation, respectively. Correspondingly, phytoplankton faces a size tradeoff between their tolerance to predators or parasites. Zooplankton was also assumed to have the ability to adapt its size to optimize predator-prey size ratio, however, facing a trade-off between increasing energy demand and decreasing mortality rate with increasing body size. We observe that when combined, zooplankton and chytrids reach higher biomasses and strongly reduce phytoplankton biomass compared to the case where either predator or parasite is present, indicating an indirect facilitation between zooplankton and chytrids. Yet, for some parameter combinations competitive exclusion between zooplankton and parasitic chytrids can also occur. Especially, phytoplankton growth rate and chytrid mortality could be shown to have a large influence on the model predictions (i.e., facilitation or competition). Our study suggests that the interaction of predation and parasitic infection can strongly influence zooplankton–phytoplankton co-evolution, the outcome being dependent on viability parameters of phytoplankton and chytrids.

In conclusion, our studies support the strong influence of parasitic fungi and specifically the mycoloop pathway for community composition, energy flow and system stability. Furthermore, it reveals that the importance of the mycoloop and its net effects are dependent on the environmental context and species identity (phytoplankton growth, adaptation ability, feeding strategy). Results from this study show that parasitic fungi can influence species interactions with implications for energy availability to higher trophic levels. The findings underline the important role of parasitic fungi for ecosystem functioning of aquatic systems.