

Abstract P2.03: The relevance of consumer competition and feeding traits, as well as their trade-offs, in determining multispecies trophic interactions

In the second funding period of DynaTrait, we studied the effect of inter- and intraspecific consumer trait variation on the consumer trade-off between starvation resistance and grazing rate in response to altered regimes of resource supply, again using a combination of laboratory experiments (continuous and semi-continuous culture techniques) and modelling approaches. We focussed on two types of starvation resistance: 1) the ability to reduce basal metabolism at the expense of reproduction, and 2) the ability of photosynthetic carbon fixation in addition to phagotrophy (mixotrophy). Furthermore, we investigated how inducible offense (formation of giant morphotypes capable of intraguild predation) and inducible defense (decreasing grazing susceptibility) interact with this trade-off by altering species interactions. Unfortunately, we were not able to develop a molecular assay to distinguish between different strains of *Euplotes octocarinatus*, which was planned as a continuation of our successful cooperation with Prof. Dr Thorsten Brinkhoff (AG Aquatic Microbial Ecology, ICBM, Oldenburg). This was in part due to restrictions regarding laboratory access and consumables related to the Covid-19 pandemic. However, we have successfully conducted a series of experiments investigating both mechanisms of starvation resistance under resource fluctuations as well as the interplay of inducible defenses and offenses.

The relevance of adaptive trait variation in nutritional strategies (heterotrophy, mixotrophy) for determining ciliate – microalgae trophic interactions

In the first part of the second phase, we studied performance and competition of purely heterotrophic and algal symbiont-bearing mixotrophic ciliates of the genera *Euplotes* (E) and *Coleps* (C) under different light and prey regimes to evaluate the effect of starvation resistance via mixotrophy on food web dynamics under homogenous and heterogeneous resource supply. We used a heterotrophic and a mixotrophic form of *Euplotes* and *Coleps*, respectively (E_{mix} , C_{mix} , E_{het} , C_{het}), all feeding on the microalgae *Cryptomonas* sp.. Starting with a short-term (9 days) experiment to estimate the parameter range and the extent of trait variation, we set up ciliate monocultures and two-genus mixtures ($E_{\text{mix}} + C_{\text{mix}}$, $E_{\text{het}} + C_{\text{mix}}$, $E_{\text{mix}} + C_{\text{het}}$, $E_{\text{het}} + C_{\text{het}}$) and exposed them to low and high prey concentrations and light intensities in a fully factorial design. Ciliate growth rates and total biovolume production were significantly and interactively determined by species combination, light intensity and prey concentration, the latter being the most important factor. Results indicated that genus-specific effects were as strong as trait variation in nutritional mode (mixotrophy versus heterotrophy). This aspect was therefore further investigated in a 48 day chemostat experiment focusing on the relevance of the consumer's starvation resistance via mixotrophic nutrition for species coexistence under constant and fluctuating regimes of resource supply. Using the same ciliate species as before, we set up all possible combinations of heterotrophs and mixotrophs ($E_{\text{mix}} + E_{\text{het}}$, $E_{\text{mix}} + C_{\text{het}}$, $C_{\text{mix}} + C_{\text{het}}$, $C_{\text{mix}} + E_{\text{het}}$), respectively, providing prey either continuously or in pulses under constant or fluctuating light conditions. Treatments entailed periods of resource depletion in fluctuating environments, but overall provided the same amount of prey and light as under constant conditions. To facilitate handling and sample processing, this experiment was split into two runs of 48 days, each comprising two species combinations, respectively. Competition between mixotrophic and heterotrophic ciliates in our experiment was significantly affected by prey supply, while the effect of light supply depended on species combination. Whether mixotrophs or heterotrophs dominated in competition thus strongly depended on the genera of the competing species, driven by species-specific differences in

the minimum resource requirements that are associated with feeding on shared prey, nutrient uptake, light harvesting and access to additional resources such as bacteria. All treatment effect depended on time, reflected in varied population dynamics of heterotrophs and mixotrophs in different treatments in the first 16 days of the experiment, while irrespective of light and prey supply, *Euplotes* dominated both mixed genus combinations by the end of the experiment, the heterotroph the same-genus *Coleps* mixture, whereas it was the mixotroph in the *Euplotes* mixture. Overall, genus-specific differences in response to resource supply mode led to faster competitive exclusion in mixed-genus combinations than in more similar species of the same genus. Fluctuations in resource supply did not alter the qualitative outcome of species competition, but influenced the shape of the population dynamics throughout the experiment and promoted species coexistence in some species combinations. Overall, our study demonstrated that genus- or species-specific traits other than related to nutritional mode may override the relevance of acquired phototrophy by heterotrophs in competitive interactions. Furthermore, it revealed that the potential advantage of photosynthetic carbon fixation of symbiont-bearing mixotrophs in competition with pure heterotrophs may differ greatly among different mixotrophs, playing out under different environmental conditions and depending on the specific requirements of the species. Complex trophic interactions determine the outcome of competition, which can only be understood by taking on a multidimensional trait perspective (Flöder *et al.*, revised manuscript under review).

The results of our competition experiment exemplify the potentially important role of externally generated resource fluctuations for the coexistence of different consumer species. However, species coexistence may also be enabled through internally generated resource fluctuations when associated with a gleaner-opportunist at the consumer level (Klauschies & Gaedke, 2020). While high abundances of the resources are giving fast-growing opportunist species a growth advantage, low abundances of the resources are promoting the survival of starvation resistant gleaner species instead. Nevertheless, this mechanism may only weakly stabilize species coexistence in systems exhibiting top-heavy biomass distributions across trophic levels as nutrient retention by consumers is likely to stabilize any internally generated consumer-resource fluctuations and thereby preventing temporal niche differentiation among the consumers (Klauschies & Gaedke, 2020).

In line with our experimental work, we also developed and analyzed a trait-based model comprising a mixotrophic consumer (e.g. a ciliate or mixotrophic algae) and an autotrophic (algae) or heterotrophic resource (bacteria) competing for inorganic nutrients. The model involves trade-offs between autotrophic and heterotrophic growth for the mixotroph, and between defense capacity against predation and maximum growth rate for the resource. We investigated the population and trait dynamics for different scenarios, in which none, one or both species were able to adapt their traits in response to selection. Under specific combinations of fixed traits, either species could dominate. However, the mixotroph often gained dominance when it could adapt its trait to exert both strong predation and competition pressure on the resource. Trait adaptation in the resource promoted its dominance only when the mixotrophy trait was fixed, whereas it played a minor role under coadaptation. Moreover, antiphase cycles often emerged when both species adapted their traits independently or interactively, with the species dominating that was able to adapt to the current selection pressure. Overall, our findings demonstrate that trait adaptation in mixotrophs substantially affects species composition and the shape and stability of population dynamics in food webs (Li *et al.*, submitted manuscript under review).

Effects of resource supply mode and food quality on the interplay of inducible defence and offence and resulting predator-prey interactions – relevance of inter- and intraspecific consumer trait variation

Focusing on the dynamics of reciprocal phenotypic plasticity, we investigated the intraspecific extent of the inducible defense in *Euplotes octocarinatus* and the relevance of this trait variation for trophic dynamics with the intraguild predator (IGP) *Stylonychia mytilus*, which is capable of an inducible offense, under different regimes of resource supply (homogenous versus heterogenous). At first, we determined the extent of phenotypic plasticity in ten different *Euplotes* strains in short-term experiments, testing for defense-related cell size changes in response to exposure to the chemical cue released by *Stylonychia* (using freeze-dried *Stylonychia* to prevent feeding). The strains revealed significant differences in their width and length development. In a subsequent semi-continuous 30-day experiment, four of these strains were incubated in monoculture and mixture with *Stylonychia*, providing prey either continuously or in pulses (*Cryptomonas*, fed in equal amounts every 2nd day or every 10th day). The polyclonal *Euplotes* population outperformed monoclonal populations, except for the strongest one, which developed the most pronounced inducible defense, especially under pulsed prey supply, and retained the highest biovolume. Although *Stylonychia* did not exhibit size changes, it dominated all communities irrespective of clonal composition. Pulsed resource supply promoted biovolume production of both species. However, periods of resource depletion resulted in more *Stylonychia* resting cysts, allowing *Euplotes* to resume its growth. Overall, this study demonstrated that intraspecific consumer trait variation strongly determines predator-prey dynamics and enhances coexistence among consumers, in particular under variable environmental conditions (Fenja-Marie Möller, Bachelor Thesis, Möller *et al.*, under review).

We further investigated the relevance of intraspecific consumer trait variation for food web dynamics in a similar set-up with *Euplotes* and *Stylonychia*, but this time including an additional intraguild prey, i. e. the non-defended heterotrophic ciliate *Coleps hirtus*. Here, we increased food web complexity and intraspecific diversity even more by including mono- and polyclonal cultures of both *Euplotes* and *Coleps* that were set up alone and in two-genus mixtures under continuous (fed three times a week) and pulsed (fed every fortnight) prey supply with or without the IGP *Stylonychia*. Community development in this experiment was strongly affected by prey supply mode, with prey pulses supporting biovolume production of *Coleps* and *Stylonychia* and coexistence in some species combinations, while *Euplotes* didn't grow well in any of the treatments. Intraspecific consumer trait variation affected *Euplotes* more than *Coleps*; however, in contrast to prior experiments, none of the polyclonal populations were clearly promoted in comparison to monoclonal ones in different treatments (Miriam Christa Schedl, Master Thesis, Schedl *et al.*, in prep.).

In order to further elucidate the role of resource supply for the extent of inducible defense in *Euplotes* and inducible offense in *Stylonychia*, we conducted a series of experiments testing the effects of *Cryptomonas* concentration (microalgal prey) and the presence of another ciliate, i. e. *Coleps hirtus* (competitor for *Cryptomonas*, intraguild prey for *Stylonychia*) on the reciprocal phenotypic plasticity of the target species and their population dynamics. First results show that microalgal prey concentration strongly determines the extent of expressed induced defense in *Euplotes* and that both, increasing *Cryptomonas* and increasing *Euplotes* concentrations have a positive effect on *Stylonychia* cell size (Lena Loh, Master Thesis, Loh *et al.*, in prep.).

Inspired by our experimental findings, we also developed a model to investigate the impact of trait adaptation on species coexistence in an IGP module, in which each of the species, i. e. basal prey, intraguild prey and intraguild predator can adapt in response to the prevailing selection pressure (Li et al. 2023). The adaptive IGP model accounts for both width and speed of trait adaptation within each species, allowing prey and predator species to mutually adjust their species-specific defensive and offensive strategies to each other interactively. We compared species persistence, community dynamics, and the occurrence of bistability between different versions of our IGP model where species were either able or unable to adapt their traits in response to selection along a gradient of enrichment represented by carrying capacity of the basal prey. We found that trait adaptation within multiple species greatly enhanced the coexistence of all three species in the module. A larger width of trait adaptation facilitated species coexistence independent of the speed of trait adaptation at lower enrichment levels, while a sufficiently large and fast trait adaptation promoted species coexistence at higher enrichment levels. Increasing the speed of trait adaptation buffered the detrimental effects of enrichment on the temporal variability of biomasses of all species. Finally, the bistability encountered in the non-adaptive IGP model was strongly reduced when allowing trait adaptation (Li et al. 2023). These findings resolve the contradiction between the empirical evidence of the widespread occurrence of IGP and the theoretical predictions that IGP should only occur under restricted conditions and lead to unstable community dynamics, which broaden the mechanisms underlying the maintenance of IGP modules in nature. Generally, by revealing the eco-evolutionary feedbacks among complex trophic interactions, this study demonstrates that intraspecific diversity may enhance interspecific diversity and stabilize food web dynamics.

Synthesis

In the synthesis phase of DynaTrait, we contributed to a review on flexibility in aquatic food web interactions by linking different scales and approaches in aquatic ecology. Trophic interactions are highly flexible, changing on temporal scales from diurnal to evolutionary times due to phenotypic plasticity, rapid evolution and species sorting. Small-scale experimental and theoretical approaches have demonstrated a high relevance of this flexibility for community dynamics and ecosystem processes; but the extent to which they drive dynamics, functioning and responses to global change in more complex communities is still poorly understood. Differences in methodology, focus and communication between research disciplines limit our ability to project effects of flexible trophic interactions onto larger spatial and temporal scales. To bridge this gap, we proposed a general framework for upscaling our knowledge on flexible interactions from small-scale research to large-scale model projections. Building on examples from aquatic communities, we used this framework to show how mechanisms demonstrated on the small scale may be linked to ecosystem functions relevant in large-scale (e.g. global ocean) models. We argue for incorporating flexibility in large-scale process-based models in order to improve their realism and predictive power, and discuss challenges and promising ways forward for achieving this (Van Velzen et al., in prep.).

References

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