

Critical role of parasite-mediated trophic interactions for energy flow and community dynamics

Patch Thongthaisong¹, Minoru Kasada¹, Hans-Peter Grossart¹, and Sabine Wollrab¹

¹Leibniz-Institute of Freshwater Ecology and Inland Fisheries in the Forschungsverbund Berlin eV

May 13, 2022

Abstract

Parasites form an integral part of food webs, however, mechanistic insights into the role of parasites for energy flow and community dynamics is currently limited by a lack of conceptual studies investigating host-parasite interactions in a community context. In aquatic systems, chytrids constitute a major group of fungal parasites and their free-living infective stage (zoospores) forms a highly nutritional food source to zooplankton. Consumption of zoospores can create an energy pathway from otherwise inedible phytoplankton to zooplankton (“mycocoloop”). The impact of such parasite-mediated energy pathways on community dynamics and energy transfer to higher trophic levels is of high importance considering eutrophication and global warming induced shifts to dominance of unfavourable prey such as cyanobacteria. We theoretically investigated community dynamics and energy transfer in a food web consisting of an edible-nonhost and an inedible-host phytoplankton species, a fungal parasite, and a zooplankton species grazing on edible phytoplankton and fungi. Food web dynamics were investigated along a nutrient gradient for two cases: (1) non-adaptive zooplankton species representative for filter feeders like cladocerans and (2) zooplankton with the ability to actively adapt their feeding preferences like many copepod species. For both feeding strategies, the importance of the mycocoloop for zooplankton increases with nutrient availability. This increase is smooth for non-adaptive consumers. For a consumer with an adaptive feeding preference, we observe an abrupt shift from almost exclusive preference for edible phytoplankton (dominant prey) at low nutrient levels to a strong preference for parasitic fungi at high nutrient levels. The model predicts that parasitic fungi can contribute up to 50% of the zooplankton diet in nutrient rich environments, agreeing with empirical observations on zooplankton gut content from eutrophic systems during cyanobacterial blooms. Our findings highlight the role of parasite-mediated energy pathway for predictions on energy flow and community composition under environmental change.

Critical role of parasite-mediated trophic interactions for energy flow and community dynamics

Patch Thongthaisong^{1,2}, Minoru Kasada^{1,3}, Hans-Peter Grossart^{1,2,4}, Sabine Wollrab^{1,4}

¹Leibniz Institute of Freshwater Ecology and Inland Fisheries (IGB), Germany, ²Potsdam University, Institute for Biochemistry and Biology, Germany, ³Tohoku University, Graduate School of Life Sciences, Japan, ⁴Berlin-Brandenburg Institute of Advanced Biodiversity Research (BBIB), Germany

Contact information

PT: ipatchy80@gmail.com

Zur alten Fischerhütte 2 16775 Stechlin OT Neuglobsow, Germany

Abstract

Parasites form an integral part of food webs, however, mechanistic insights into the role of parasites for energy flow and community dynamics is currently limited by a lack of conceptual studies investigating host-parasite

interactions in a community context. In aquatic systems, chytrids constitute a major group of fungal parasites and their free-living infective stage (zoospores) forms a highly nutritional food source to zooplankton. Consumption of zoospores can create an energy pathway from otherwise inedible phytoplankton to zooplankton (“mycoloop”). The impact of such parasite-mediated energy pathways on community dynamics and energy transfer to higher trophic levels is of high importance considering eutrophication and global warming induced shifts to dominance of unfavourable prey such as cyanobacteria. We theoretically investigated community dynamics and energy transfer in a food web consisting of an edible-nonhost and an inedible-host phytoplankton species, a fungal parasite, and a zooplankton species grazing on edible phytoplankton and fungi. Food web dynamics were investigated along a nutrient gradient for two cases: (1) non-adaptive zooplankton species representative for filter feeders like cladocerans and (2) zooplankton with the ability to actively adapt their feeding preferences like many copepod species. For both feeding strategies, the importance of the mycoloop for zooplankton increases with nutrient availability. This increase is smooth for non-adaptive consumers. For a consumer with an adaptive feeding preference, we observe an abrupt shift from almost exclusive preference for edible phytoplankton (dominant prey) at low nutrient levels to a strong preference for parasitic fungi at high nutrient levels. The model predicts that parasitic fungi can contribute up to 50% of the zooplankton diet in nutrient rich environments, agreeing with empirical observations on zooplankton gut content from eutrophic systems during cyanobacterial blooms. Our findings highlight the role of parasite-mediated energy pathway for predictions on energy flow and community composition under environmental change.

Keywords : adaptive preference, energy flow, mycoloop, parasites, parasitic fungi, zooplankton.

Introduction

Parasites are an integral but often neglected part of food webs (Lafferty et al. 2008, Sukhdeo 2012). Taking parasites into account increases biodiversity and food web complexity. Currently mechanistic insights into the role of parasites on energy flow and community response patterns to environmental change is limited by a lack of conceptual studies investigating host-parasite dynamics in a community context (Buck et al. 2015). Thereby, existing theoretical and experimental studies support the importance of investigating parasitic interactions in a community context to assess the direct and indirect effects of parasites on non-host species (Miki et al. 2011, Banerji et al. 2015, Prosnier et al. 2018). One direct link between host-parasite and predator-prey interactions is the consumption of parasites by higher order predators (Johnson et al. 2010). For multi-host parasites this forms an important transmission pathway, however, parasites with free-living life stages or ectoparasites can be prone to direct consumption resulting in death and digestion of the parasite (Johnson et al. 2010). Consumption of parasites can substantially contribute to energy flow in food webs (Michalska-Smith et al. 2018), especially if it creates a link from an otherwise inedible prey (host) to a predator (Johnson et al. 2010). Examples for such parasite-mediated trophic interactions are known for a wide range of animals from terrestrial as well as aquatic systems (see review by Johnson et al. 2010), such as ticks on mammal skin that are eaten by birds (Ndlovu and Combrink 2015), or earthworms feeding on parasitic flatworms on snail skin (Hobart et al. 2021), and zooplankton consumption of zoospores, the free living stage of parasitic chytrids which might emerge from, for example, infection of (inedible or toxic) cyanobacteria (Kagami et al. 2014) or infections on the skin of amphibians (Buck et al. 2011).

In this study we use an example from the aquatic environment to investigate the consequences of such parasite-mediated trophic interactions for energy flow and community response along a nutrient gradient. Parasitic chytrids, form a dominant group of parasites in aquatic systems (Grossart et al. 2019). The zoospores - the free living stage of parasitic chytrids infecting phytoplankton - can form a highly nutritional food source for zooplankton, even increasing the supply of polyunsaturated fatty acids (PUFAs) compared to phytoplankton, which is the primary food source for zooplankton (Kagami et al. 2007, Agha et al. 2016, Rasconi et al. 2020). Of special interest is the case where zooplankton consumption of zoospores creates an additional trophic pathway from otherwise inedible phytoplankton to zooplankton, the so called ‘mycoloop’ (Kagami et al. 2007, Miki et al. 2011). While dominance of inedible phytoplankton would typically be assumed to limit zooplankton growth and energy flow to higher trophic levels, the presence of the mycoloop can enhance zooplankton growth, thus increasing food availability for higher trophic levels (Rasconi et al.

2014). Specifically, in temperate regions, the mycoloop might regularly form an important energy source for zooplankton during the late summer season, when phytoplankton communities are typically dominated by less edible algae (Sommer et al. 2012). Furthermore, its importance may be on the rise with world-wide eutrophication and global warming leading to increasing dominance of - often inedible or even toxic - cyanobacteria (Huisman et al. 2018, Bogard et al. 2020).

Due to multiple feedbacks within the plankton community, the net effects of parasitic fungi on primary production, community composition and energy transfer are difficult to predict. While chytrid infection of inedible phytoplankton species could indirectly support edible-insusceptible phytoplankton species via decreasing resource competition, zooplankton consumption of zoospores may at the same time lead to increasing top-down pressure on edible phytoplankton (Miki et al. 2011, Kagami et al. 2014). The net effect of chytrid infections on community composition and energy transport in planktonic food webs may depend on the specific environmental context. Furthermore, the importance of the mycoloop for zooplankton (i.e., the relative contribution of fungi to net energy gain of zooplankton) will depend on the feeding strategy of the zooplankton and differs between non-adaptive (passive) filter feeders like cladocerans (Uszko et al. 2015) vs. adaptive (active) hunters like copepods (Meunier et al. 2016). Especially for copepods experimental results indicate that they might actively choose fungi over other (less nutritious) prey (Ray et al. 2016).

We theoretically investigated the importance of parasite mediated trophic interactions for community dynamics and its consequences for energy flow along a nutrient gradient, by using a simplified food web model. The food web consists of two groups of phytoplankton, edible vs. non-edible, competing for a shared resource, parasitic fungi specialized on inedible phytoplankton and zooplankton feeding on edible phytoplankton and parasitic fungi. Extending on previous work by Miki et al. (2011), we accounted for (more realistic) nonlinear food/nutrient uptake terms and different feeding strategies representative for dominant zooplankton groups, i.e. non-adaptive (passive) filter feeders like cladocerans (Uszko et al. 2015) vs. adaptive (active) hunters like copepods (Meunier et al. 2016). Our results show that, under the assumption of saturating food/nutrient uptake rates, the increasing importance of the mycoloop with nutrient enrichment is much more pronounced compared to assuming linear food uptake terms. While the importance of the mycoloop increases smoothly for a non-adaptive consumer, we observed an abrupt shift towards strong preference for parasitic fungi from low to high nutrient levels for zooplankton with adaptive prey preference. Our theoretical results emphasize the importance of parasite-mediated trophic interactions on community dynamics and trophic transfer efficiency and how this is modulated by consumer feeding strategies.

Methods

Model system

We investigated the biomass distribution and dynamics of a planktonic food web consisting of two types of primary producers (phytoplankton) which share a limiting nutrient source N , assumed to be phosphorus [$\mu\text{g P}\cdot\text{L}^{-1}$], a zooplankton species Z , and parasitic fungi F . The food web is based on the following assumptions: one phytoplankton species P_E is well-edible for Z , while the other phytoplankton species P_I is inedible for Z . P_E is the superior resource competitor, while P_I is the inferior resource competitor. Furthermore, P_E is insusceptible to fungal infection, while P_I is susceptible to infection by F . F is edible for Z , thereby creating an alternative nutrient pathway from the otherwise inedible P_I to Z , i.e. the mycoloop.

The food web was translated into a corresponding differential equation system (Eqs 1-5). All biomasses are expressed in units of phosphorus [$\mu\text{g P}\cdot\text{L}^{-1}$]. Nutrient dynamics were assumed to follow chemostat dynamics with maximum nutrient availability $N_{\max}$ and dilution rate q (Eq. 1). In contrast to the basic model presented in Miki et al. (2011), we assumed a saturating functional response for the nutrient uptake of both phytoplankton species following Monod kinetics with maximum growth rate $\mu_{\max,i}$, $i \in \{E, I\}$, and half saturation constant K (Eqs. 2, 3). Similar to Miki et al. (2011) and in line with published dependencies of infection rate on host density (Gerla et al. 2013, Frenken et al. 2020), we assumed a linear dependency of the infection of F on host biomass P_I with infection rate β and conversion efficiency f_F (Eq. 4). We furthermore assumed a saturating functional response type III (Holling 1959) for the food uptake term of Z with food

uptake rate a_Z and handling time h_i , $i \in \{P_E, F\}$ (Eq. 5). A functional response type III has been shown to be representative for zooplankton species with a selective feeding behavior, like raptorial copepods, but also for filter feeders with the ability to down regulate their filtration rate if prey density is low, which has been reported for several daphnia species (Uszko et al. 2015, Kiørboe et al. 2018, Sandhu et al. 2019). Correspondingly, we assume a functional response type III to mimic the (disproportional) release of low abundant prey from predation pressure - not captured by a functional response type II (Wollrab and Diehl 2015). In addition to this density dependent food uptake term, we consider a prey preference parameter p_Z which defines the preference level of Z for F vs. P_E . For this, the food uptake rate a_Z is multiplied by the preference parameter $p_Z \in [0, 1]$, with p_Z indicating the preference for P_E , and $(1 - p_Z)$ indicating the preference for F , respectively. Correspondingly, a value of $p_Z = 0$ (1) indicates that Z feeds exclusively on F (P_E), where $p_Z = 0.5$ indicates no preference. Consumed prey biomass was converted to zooplankton biomass by conversion efficiencies e_P and e_F for edible phytoplankton and fungi, respectively.

$$\frac{dN}{dt} = q(N_{\max} - N) - \frac{\mu_{max,E} N}{K+N} P_E - \frac{\mu_{max,I} N}{K+N} P_I, \quad (1)$$

$$\frac{dP_E}{dt} = \frac{\mu_{max,E} N}{K+N} P_E - \frac{p_Z \cdot a_Z \cdot P_E^2}{1+h_{P_E} \cdot p_Z \cdot a_Z \cdot P_E^2 + h_F \cdot (1-p_Z) \cdot a_Z \cdot F^2} Z - q P_E, \quad (2)$$

$$\frac{dP_I}{dt} = \frac{\mu_{max,I} N}{K+N} P_I - \beta P_I F - q P_I, \quad (3)$$

$$\frac{dF}{dt} = f_F \beta P_I F - \frac{(1-p_Z) \cdot a_Z \cdot F^2}{1+h_{P_E} \cdot p_Z \cdot a_Z \cdot P_E^2 + h_F \cdot (1-p_Z) \cdot a_Z \cdot F^2} Z - q F, \quad (4)$$

$$\frac{dZ}{dt} = \frac{(e_P \cdot p_Z \cdot a_Z \cdot P_E^2 + e_F \cdot (1-p_Z) \cdot a_Z \cdot F^2)}{1+h_{P_E} \cdot p_Z \cdot a_Z \cdot P_E^2 + h_F \cdot (1-p_Z) \cdot a_Z \cdot F^2} Z - (q + m_Z) Z. \quad (5)$$

$$\frac{dp_Z}{dt} = V \frac{\partial W_Z}{\partial p_Z} + B(p_Z). \quad (6)$$

For the (non-adaptive) fixed preference case, representative for passive filter feeders like cladocerans, including species with the ability to actively egest unfavourable prey (Uszko et al. 2015), p_Z was assumed to be a constant parameter (Eqs. 1-5). For the adaptive preference case, representative for active hunters like copepods (Ray et al. 2016), p_Z is not fixed, but itself a function of time (Eq. 6). We used a fitness gradient approach to describe the adaptive preference dynamics (Abrams and Matsuda 2004, Mougi and Iwasa 2010, Yamamichi et al. 2019). For this case, the value of p_Z depends on the fitness gradient of Z , described by the effect of a change of p_Z on the net energy gain of zooplankton $\left(\frac{\partial W_Z}{\partial p_Z}\right)$, where $W_Z(t) = \frac{1}{Z} \cdot \frac{dZ}{dt}$ is the net-growth of zooplankton. This fitness gradient is multiplied by the speed of adaptation V . This first term of Eq. 6 describes the ability of Z to adapt its prey preference p_Z to optimize its own fitness (net energy gain). The second additive term of Eq. 6 is a boundary function $B(p_Z) = \frac{C}{p_Z^2} - \frac{C}{(1-p_Z)^2}$ with the scaling constant c , which keeps the value of $p_Z(t)$ within the range of $[0, 1]$ (Yamamichi et al. 2019).

Parameter values (Appendix S1: Table S1) and initial conditions (see section on model analysis) were taken from Miki et al. (2011), with the exception of the maximum growth rate of P_I ($\mu_{max,I}$), which was chosen to be higher than in the original parameterization. The latter was motivated by the fact that, dependent on species identity, the difference in maximum growth rate between edible and inedible phytoplankton species does not need to be very pronounced (Burson et al. 2018). Correspondingly, we decreased the difference in maximum growth rate between P_E and P_I , to reduce the effect of principle physiological differences between the two phytoplankton species on system dynamics.

Model analysis

For all simulations, we varied maximum nutrient availability $N_{\max}$ from 0.1 to 65 $\mu\text{g P}\cdot\text{L}^{-1}$ in steps of 0.1, ranging from oligotrophic to eutrophic conditions (Carlson and Simpson 1996). Equilibrium densities were examined along a grid of p_Z and $N_{\max}$ levels. We investigated the equilibrium dynamics of the study system for the case of (1) fixed food preference of Z for P_E vs. F , covering the full range of possible preference levels within the interval of $[0, 1]$, and (2) adaptive food preference of Z .

For the fixed preference case, we numerically solved the system of Eqs. 1-5 for transects along $N_{\max}$ for

fixed values of p_Z . Transects were calculated for p_Z values from 0 to 1 in steps of 0.01 using a standard Runge-Kutta solver (*ode45*) in MATLAB R2018b (MathWorks). For each run, we integrated the system for 20000 time units, starting from the initial conditions $N(0) = 8$, $P_E(0) = 0.472 \times 10^{-6}$, $P_I(0) = 8.68 \times 10^{-6}$, $F(0) = 2.4 \times 10^{-6}$, and $Z(0) = 0.21$. For the forward calculations, the transects started at $N_{\max} = 0.1$. The system dynamics were followed along increasing values of $N_{\max}$ by using the solution reached at the end of the previous run to be the initial condition for the next run with slightly increased $N_{\max}$ by 0.1. For each run, the mean biomass of each state variable was calculated using the last 20% of total time steps. In case the system exhibited oscillatory dynamics, we also calculated the standard deviation of the mean. A species was considered to be extinct if its mean biomass over the last 20% of time steps was less than $0.0001 \mu\text{g P}\cdot\text{L}^{-1}$. In case of extinction at the end of the previous run, 0.0001 was added to the initial biomass of the corresponding population in the following run, allowing for re-invasion. The continuation was performed until reaching $N_{\max} = 65 \mu\text{g P}\cdot\text{L}^{-1}$. Following the same procedure, system dynamics were also continued for fixed values of $N_{\max}$ along increasing values of p_Z . All transects were also followed in the opposite directions, i.e. along decreasing values of $N_{\max}$ and p_Z , results were identical to the forward calculations. Bifurcation analysis and specifically the detection of a Hopf bifurcation was performed using MatCont 7p2 (Dhooge et al. 2006), a software package usable within MATLAB.

For the adaptive preference case, system dynamics for Eqs. 1-6 were followed along increasing $N_{\max}$, using the same procedure as for the fixed preference case, with starting values $N_{\max} = 0.1$ and $p_Z(0) = 0.5$, increasing $N_{\max}$ by steps of 0.1. System dynamics of Eqs 1-6 tended to reach equilibrium dynamics faster than for the non-adaptive case (Eqs. 1-5), therefore, for the adaptive preference case, system dynamics were only followed for 10000 time units.

Furthermore, we calculated the **energy flow** for different prey preference and nutrient levels. The energy flow can be assumed to be equivalent to the flow of the limiting nutrient (Rooney et al. 2006). Given that the biomasses in our model system are expressed in terms of the limiting nutrient, energy flow corresponds to the biomass flow along each trophic link. We evaluated two measures of energy flow along each trophic link: (1) net-energy gain of the respective consumer biomass, and (2) gross energy flow. For example, the net energy gain of Z along the $P_E - Z$ link is given by $g_{P_E Z} = \frac{e_P \cdot p_Z \cdot \text{toc} \cdot P_E^2 \cdot Z}{1 + h_{P_E} \cdot p_Z \cdot \text{toc} \cdot P_E^2 + h_F \cdot (1 - p_Z) \cdot \text{toc} \cdot F^2}$, while the gross energy flow along the $P_E - Z$ link is given by $\frac{g_{P_E Z}}{e_P}$. In case of oscillatory dynamics, we used the mean biomass of all state variables for the calculation of energy flow. The relative contribution of fungi to net energy gain of zooplankton was calculated by $\frac{g_{FZ}}{g_{P_E Z} + g_{FZ}} \times 100$. We also calculated the transfer efficiency of the mycoloop by calculating the ratio between the net energy gain of zooplankton from fungi and the net energy gain of the inedible phytoplankton host from nutrient uptake $\frac{g_{FZ}}{g_{NP_I}} \times 100$.

Results

Community patterns for the fixed preference case

Along the enrichment gradient ($N_{\max}$), the superior resource competitor (edible phytoplankton) can establish at the lowest enrichment level ($N_{\max} > 0.055$), independent of the preference value. The invasion threshold for zooplankton depends on the available prey biomass and the preference value for edible phytoplankton, the enrichment level for successful invasion increasing with decreasing preference for the phytoplankton. For enrichment levels slightly above the invasion threshold for zooplankton, the inedible phytoplankton and finally the parasitic fungi can successfully invade. The invasion boundaries for zooplankton, inedible phytoplankton and fungi are very close to each other, nearly overlapping, therefore only the coexistence boundary is indicated in Fig. 1 (red curve). Coexistence is not possible for too low enrichment levels and too strong preferences for fungi.

Within the coexistence area, the mean biomass of all food web compartments along the mycoloop increase with nutrient enrichment (Fig. 1a,b,d,e), whereas it decreases for edible phytoplankton (Fig. 1c). The community is dominated by either edible phytoplankton (at low nutrient availability) or zooplankton (at high nutrient availability, apart from regions with an almost exclusive preference for fungi) (see Appendix S2, Fig.

S2.1).

The response of zooplankton along the preference gradient differs for low vs. high enrichment levels (Fig. 1a). For low enrichment levels, zooplankton increases with increasing preference for edible phytoplankton. For high enrichment levels, zooplankton shows a hump shaped relationship reaching the highest biomass at $p_Z \approx 0.3$. With increasing preference for edible phytoplankton, the phytoplankton decreases due to stronger top-down pressure through zooplankton (Fig. 1c), while the biomass of fungi increases (Fig. 1b). The abundance of the fungal host (inedible phytoplankton) shows a hump shaped relationship with respect to the preference, peaking at $p_Z \approx 0.3$, where its parasite is the preferred prey (Fig. 1d). For high enrichment levels, the area with highest inedible phytoplankton biomass overlaps with the region of maximum biomass of zooplankton (Fig. 1a,d), indicating a strong top down control on both prey species, releasing the phytoplankton host from infection through fungi and from nutrient competition with edible phytoplankton.

At preference values close to one (i.e. strong preference for edible phytoplankton), the system exhibits oscillatory dynamics. This region extends towards lower preference levels with nutrient enrichment (area to the right of the black dashed line in Fig. 1). The oscillatory dynamics are characterized by small amplitude cycles for low enrichment and a pronounced increase of cycle amplitudes at high enrichment levels (Fig. 1f).

In the area with stable point equilibria (area to the left of the black dashed line in Fig. 1), all compartments reach their maximum biomass at the highest investigated enrichment level (Fig. 1a-e). Only in the absence of zooplankton (edible phytoplankton-only state), for preference values close to zero, the edible phytoplankton increases with enrichment (area to the left of the red line in Fig. 1c). The maximum fungal biomass and freely available nutrient levels are observed at high preference values for edible phytoplankton ($p_Z \approx 0.8$) (Fig. 1b,e).

In comparison to the assumption of linear food uptake rates (Miki et al. 2011), there is no qualitative change in the biomass response pattern along the nutrient gradient under the assumption of nonlinear food uptake rates, as illustrated for $p_Z = 0.5$ (Fig. 2a,b). However, while the phytoplankton host is predicted to reach a higher biomass compared to its parasite throughout the nutrient gradient for the linear case, under the assumption of saturating food uptake terms the phytoplankton host only dominates at the highest nutrient levels (see Appendix S2, Fig. S2.2). Furthermore, zooplankton can invade at lower prey abundance (lower $N_{\max}$) compared to the linear case, so edible phytoplankton cannot reach as high biomass levels and decreases more steeply along the nutrient gradient compared to the linear case (Fig. 2a,b).

Community patterns for the adaptive preference case

Following the optimal preference values p_Z^* (average equilibrium value of $p_Z(t)$ in case of oscillatory dynamics) which are reached along nutrient enrichment for the adaptive preference case (Eqs. 1-6), two different regimes can be distinguished for low vs. high enrichment levels (Fig. 1, 2c). In Regime I ($N_{\max} < 40 \mu\text{gP}\cdot\text{L}^{-1}$), edible phytoplankton clearly dominates total available prey for zooplankton and correspondingly the optimal preference is almost exclusive for edible phytoplankton (p_Z close to 1) (Fig. 2c, 3c). In Regime II ($N_{\max} > 40 \mu\text{gP}\cdot\text{L}^{-1}$), with biomass of fungi and its relative contribution to total prey biomass reaching a critical threshold (Fig. 3d), optimal preference exhibits a pronounced shift towards preference for fungi with further enrichment, even though edible phytoplankton still dominates the total available prey (Fig. 2c). In Regime I, the qualitative pattern of the community response to nutrient enrichment is identical to the fixed preference case (Fig. 2b,c), even edible phytoplankton is only slightly decreasing. In Regime II, the freely available nutrient (N) and mean biomasses of both zooplankton prey remain constant (Fig. 1e, 2c, 3d), keeping relative contribution of fungi to total available prey biomass at 33% (Fig. 3c, 2d). Only zooplankton and inedible phytoplankton (host) increase with further nutrient enrichment (Fig. 2c). Zooplankton biomass increases more steeply with nutrient enrichment compared to Regime I (Fig. 2c) and reaches a higher maximum biomass compared to the case without prey preference ($p_Z = 0.5$) (Fig. 3a). The equilibrium dynamics exhibit the same stable vs. oscillatory behavior as the fixed preference case for the respective parameter combination on the $p_Z - N_{\max}$ plane.

It is notable that the adaptive preference values neither follow maximum zooplankton biomass (Fig. 3a) nor

values with highest top-down control and, therefore, lowest total prey biomass (Fig. 3b). They also do not follow the highest biomass values of fungi, albeit being the more profitable prey for zooplankton (greater conversion efficiency of fungi than edible phytoplankton) (Fig. 3c). So, what governs the optimal preference value along the enrichment gradient and how is this related to total and relative prey densities?

Analyzing the equilibrium condition for the fitness gradient term of Eq. 6 ($\frac{\partial W_Z}{\partial p_Z} = 0$), which optimizes zooplankton net-growth ($W_Z = \frac{1}{Z} \cdot \frac{dZ}{dt}$), reveals a negative correlation between the relative contribution of fungi to total prey biomass ($F/(P_E + F)$) and total prey biomass ($P_E + F$) (Fig. 3d). Comparing these optimal prey availabilities (black dash-dotted line in Fig 3d) with the simulated equilibrium values for the mycoloop food web (Eqs. 1-6) (black solid line in Fig. 3d) reveals that the optimal value of the fitness gradient term cannot be reached before prey composition along the enrichment gradient reaches the optimal prey availability (black dot in Fig. 3d). Once reached, total and relative prey values are preserved at these values with further enrichment, while the optimal preference value keeps decreasing (increasing preference for fungi) with further nutrient enrichment (for further details see Appendix S3).

Energetic role of the mycoloop

In the investigated mycoloop food web, there are two alternative energy pathways: one from edible phytoplankton directly to zooplankton and the other from inedible phytoplankton via parasitic fungi to zooplankton (mycoloop). A comparison between three sets of assumptions: (M1) linear food uptake rates for all species with zooplankton without prey preference ($p_Z = 0.5$), (M2) saturating food uptake rates for phytoplankton and zooplankton without prey preference, and (M2+) in addition to M2, zooplankton with adaptive prey preference (Fig. 2), shows that predictions on the dominance of energy flow between both pathways is independent of the zooplankton feeding strategy. A strong dominance of energy flow along the direct phytoplankton pathway is predicted at low nutrient availabilities. An increasing importance of energy flow along the mycoloop is predicted with nutrient enrichment (Fig. 2e,f). This reflects the increase in fungi biomass and the decrease in edible phytoplankton biomass along the nutrient gradient (Fig. 2a,b,c). For the adaptive preference case, the increasing importance of the mycoloop along the nutrient gradient is much more pronounced, with almost exclusive preference of zooplankton for edible phytoplankton in Regime I to an equal importance of energy flow between both energy pathways in Regime II (Fig. 2d,e,f). Energy flow along the mycoloop would even dominate for nutrient enrichment levels beyond the investigated values (see Appendix S4).

Comparing the shift in the distribution of energy flow between both pathways along the nutrient gradient, reveals significant differences between scenarios M1, M2 and M2+ (Fig. 2e,f). At low nutrient availability, predictions on net energy gain of zooplankton from fungi are highest under the assumption of linear food uptake terms (Fig. 2e). However, at high nutrients, under the assumption of saturating food uptake terms, zooplankton is predicted to gain up to 50-55% of its energy from fungi, while net energy gain stays well below 40% for the linear case (Fig. 2e). The difference in predictions is even more pronounced for the transfer efficiency along the mycoloop, which reaches 30% under the assumption of saturating functional responses while it remains below 5% under the assumption of linear food uptake rates (Fig. 2f). At lower nutrient availabilities, transfer efficiency is highest under the assumption of saturating food uptake rates and fixed preference ($p_Z = 0.5$), however, the adaptive preference case reaches similarly high values under high nutrient availabilities (Regime II) (Fig. 2f).

Discussion

Our model results highlight the critical role of parasite-mediated trophic interactions for community response and the importance of energy flow through the mycoloop pathway along a nutrient gradient, and how this is modulated by zooplankton feeding strategies. Our analysis extends on existing theory (Miki et al. 2011) by taking non-linear feeding interactions and different zooplankton feeding strategies into account, representative for major feeding guilds, i.e. non-adaptive filter feeders like cladocerans vs. adaptive active hunters like

raptorial copepods. While we observe a smooth increase in energy flow through the mycoloop pathway with nutrient enrichment for a non-adaptive zooplankton, for an adaptive zooplankton, our results suggest an abrupt shift from dominance of energy flow through the direct phytoplankton-zooplankton pathway at low nutrient levels (Regime I) to equal dominance of both pathways at high nutrient levels (Regime II). Our study specifically indicates that parasitic fungi can contribute 50% or more to the diet of zooplankton in nutrient rich environments with the dominance of inedible phytoplankton. This clearly exceeds predictions under the assumption of linear feeding interactions (Miki et al. 2011) and is supported by empirical observations showing that fungal zoospores can contribute 50-60% to the zooplankton diet during phytoplankton blooms dominated by inedible species (Rasconi et al. 2014).

A notable result is that the reachability of an optimal prey preference might be limited by the food web response, due to a trade-off between total prey biomass and relative contribution of the more profitable prey (fungi) to total prey. In contrast to indications from previous studies on optimal foraging on multiple prey (Visser and Fiksen 2013), our results show that optimality might not be reached before a critical threshold of relative and total prey availability is reached, which itself is constrained by the community response along the nutrient gradient. Furthermore, the comparison of biomass patterns for the fixed and the adaptive preference case shows that the optimization of net-energy gain does not necessarily maximize consumer biomass. Our results suggest that the co-dependence of relative and total prey availability and the negative correlation between alternative prey species effectively keeps the adaptive preference function from maximizing consumer biomass. It would be interesting to look at the general relevance of this finding for adaptive predation in natural, complex communities.

This study also adds new aspects to the importance of food web structure for food web dynamics (Drossel et al. 2001, O’Gorman et al. 2010) and how this is modulated by species specific rates (Gibert and DeLong 2017) and trait adaptation (Cattin et al. 2004). The community response pattern with an increase of all species along the mycoloop but a decrease of edible phytoplankton with increasing nutrient availability (non-adaptive case and Regime I) follows the dynamics predicted for food webs consisting of one chain of even and one chain of odd length, which are connected via a shared resource and a shared predator (Wollrab et al. 2012). Similar to predictions from classic food web theory on predator-mediated coexistence between competing prey species (Holt et al. 1994, Leibold 1996), we also observe a shift from dominance of exploitative to apparent competition for the mycoloop web, reflected by the initial dominance and successive decrease (increase) of the superior (inferior) resource competitor with nutrient enrichment. While inedible phytoplankton would profit from enrichment even in the absence of the mycoloop, in its presence, zooplankton gains additional energy which results in an increased predation pressure on edible phytoplankton. This highlights the relevance of general topological features also in the context of parasitic interactions.

Furthermore, a comparison between dynamic properties of the structurally equivalent plankton food web (Thingstad and Sakshaug 1990, Stibor et al. 2004, Wollrab and Diehl 2015), where ciliates are structurally at the same position as parasitic fungi in the mycoloop food web, provides new insight into the occurrence of abrupt shifts in community response along a nutrient gradient. For both webs, the occurrence of a regime shift in community response is critically related to the assumption of an adaptive feeding strategy of the consumer. The topologically constrained community response where ciliates/fungi increase with nutrient enrichment while the alternative prey decreases, leads to a disproportional (abrupt) shift in prey preference for ciliates/fungi along the nutrient gradient (Wollrab and Diehl 2015, Wollrab et al. 2020). Notably, in both cases this abrupt shift in prey preference creates a bottleneck in energy flow and leads to a drastic shift in community responses to further enrichment, which is absent if assuming a non-adaptive consumer (for further details see Appendix S5). This finding reveals the critical interplay of structural features, functional response type and production rates for occurrence of abrupt shifts in community composition along a nutrient gradient (see details in Appendix S5).

Our analysis of the mycoloop food web also supports the potentially stabilizing role of parasites for system dynamics (Lafferty et al. 2006, Rogawa et al. 2018), constituting weak links in comparison to classic predator-prey interactions due to differences in productivity (Johnson et al. 2010). The growth/infection rate of

phytoplankton vs. parasite prey determines the amount of energy (biomass) that can be produced per unit of time. Given the large difference in phytoplankton growth vs. fungal infectivity rate in our study system, the path from edible phytoplankton to zooplankton can be characterized as a fast energy pathway, while the path from fungi to zooplankton can be considered as a slow energy pathway. Hence, with increasing preference for parasitic fungi, the slow energy channel stabilizes the oscillatory dynamics of the fast energy channel (Rooney et al. 2006, Blanchard et al. 2011, Gellner and McCann 2016, see also Appendix S3, Fig. S3.3). We have to caution that the observed stabilizing role of the mycoloop might partly be due to the simplified representation of the host-parasite interaction, which ignores the time lag between parasite infection and zoospore emergence. A more detailed description of the parasite-host interactions, separating infected from susceptible host, might to some extent counteract the stabilizing features.

Given the empirical counter part of our modeled system, our results are of high relevance with global warming not only increasing the risk of cyanobacterial blooms (Davis et al. 2009), but also the prevalence of parasitic infections (Harvell et al. 2002, Ibelings et al. 2011, Gsell et al. 2013). Based on direct phyto-zooplankton interactions, a decline in zooplankton would be expected with increasing dominance of inedible phytoplankton (Lampert 1987). However, our results suggest that this might be counteracted if parasites form an alternative food source for zooplankton (Kagami et al. 2007, Frenken 2018, Agha et al. 2018). Extending on existing theory (Miki et al. 2011) by taking non-linear feeding interactions and different zooplankton feeding strategies into account, our model analysis provides a more realistic prediction on the importance of energy flow along the mycoloop for major feeding guilds, i.e. non-adaptive filter feeders like cladocerans vs. adaptive active hunters like raptorial copepods. Our study highlights that the dominant feeding guild might play a crucial role in the community response to environmental change. More generally our study suggests that taking parasitic interactions into account in a community context might be crucial to assess how environmental change will impact community response and trophic transfer efficiency. Additionally, the obtained limitations on optimal prey choice in the context of food web topology and corresponding community feedbacks have implications far beyond the investigated study system.

Data availability statement

No empirical data was used in this research.

Acknowledgement

PT thanks the Ecological Modelling group at IGB for helpful discussions, especially Lilla Kiss for help with illustrating the energy flow, and the Ecological Modeling group at the University of Potsdam and Kevin Lafferty for helpful comments on an earlier version of the manuscript. This project was funded by the German Research Foundation (DFG) Priority Program 1704: DynaTrait (WO 2273/1-1) and (GR 1540/30-1). MK received funding from the Grant-in-Aid for JSPS Fellows (MK 19J00864). The work was partly funded by the German Federal Ministry of Education and Research BMBF within the Collaborative Project "Bridging in Biodiversity Science - BIBS" (funding number 01LC1501). All responsibility for the content of this publication is assumed by the authors.

Author contributions

PT, SW and HPG designed the study; PT performed the modeling work; PT and SW analyzed the results; all authors were involved in interpreting the results; PT wrote the first draft of the manuscript. All authors contributed substantially to revisions.

Literature cited

Abrams, P. A., and H. Matsuda. 2004. Consequences of behavioral dynamics for the population dynamics of predator-prey systems with switching. *Population Ecology* 46:13-25.

- Agha, R., A. Gross, M. Gerphagnon, T. Rohrlack, and J. Wolinska. 2018. Fitness and eco-physiological response of a chytrid fungal parasite infecting planktonic cyanobacteria to thermal and host genotype variation. *Parasitology* 145:1279–1286.
- Agha, R., M. Saebelfeld, C. Manthey, T. Rohrlack, and J. Wolinska. 2016. Chytrid parasitism facilitates trophic transfer between bloom-forming cyanobacteria and zooplankton (*Daphnia*). *Scientific Reports* 6:35039.
- Banerji, A., A. B. Duncan, J. S. Griffin, S. Humphries, O. L. Petchey, and O. Kaltz. 2015. Density- and trait-mediated effects of a parasite and a predator in a tri-trophic food web. *Journal of Animal Ecology* 84:723–733.
- Blanchard, J. L., R. Law, M. D. Castle, and S. Jennings. 2011. Coupled energy pathways and the resilience of size-structured food webs. *Theoretical Ecology* 4:289–300.
- Bogard, M. J., R. J. Vogt, N. M. Hayes, and P. R. Leavitt. 2020. Unabated Nitrogen Pollution Favors Growth of Toxic Cyanobacteria over Chlorophytes in Most Hypereutrophic Lakes. *Environmental Science & Technology* 54:3219–3227.
- Buck, J. C., K. I. Scholz, J. R. Rohr, and A. R. Blaustein. 2015. Trophic dynamics in an aquatic community: interactions among primary producers, grazers, and a pathogenic fungus. *Oecologia* 178:239–248.
- Buck, J. C., L. Truong, and A. R. Blaustein. 2011. Predation by zooplankton on *Batrachochytrium dendrobatidis*: biological control of the deadly amphibian chytrid fungus? *Biodiversity and Conservation* 20:3549–3553.
- Burson, A., M. Stomp, E. Greenwell, J. Grosse, and J. Huisman. 2018. Competition for nutrients and light: testing advances in resource competition with a natural phytoplankton community. *Ecology* 99:1108–1118.
- Cattin, M.-F., L.-F. Bersier, C. Banašek-Richter, R. Baltensperger, and J.-P. Gabriel. 2004. Phylogenetic constraints and adaptation explain food-web structure. *Nature* 427:835–839.
- Davis, T. W., D. L. Berry, G. L. Boyer, and C. J. Gobler. 2009. The effects of temperature and nutrients on the growth and dynamics of toxic and non-toxic strains of *Microcystis* during cyanobacteria blooms. *Harmful Algae* 8:715–725.
- Dhooge, A., W. Govaerts, Y. A. Kuznetsov, W. Mestrom, A. M. Riet, and B. Sautois. 2006. MATCONT and CL MATCONT: Continuation toolboxes in matlab:100.
- Drossel, B., P. G. Higgs, and A. J. McKane. 2001. The Influence of Predator–Prey Population Dynamics on the Long-term Evolution of Food Web Structure. *Journal of Theoretical Biology* 208:91–107.
- Frenken, T. H. M. 2018, April 18. Live and Let die : How climate change affects bottom-up and top-down factors regulating phytoplankton disease. Dissertation, Utrecht University. <http://localhost/handle/1874/363352>.
- Frenken, T., T. Miki, M. Kagami, D. B. Van de Waal, E. Van Donk, T. Rohrlack, and A. S. Gsell. 2020. The potential of zooplankton in constraining chytrid epidemics in phytoplankton hosts. *Ecology* 101:e02900.
- Gellner, G., and K. S. McCann. 2016. Consistent role of weak and strong interactions in high- and low-diversity trophic food webs. *Nature Communications* 7:11180.
- Gerla, D. J., A. S. Gsell, B. W. Kooi, B. W. Ibelings, E. Van Donk, and W. M. Mooij. 2013. Alternative states and population crashes in a resource-susceptible-infected model for planktonic parasites and hosts: *Planktonic host-parasite dynamics*. *Freshwater Biology* 58:538–551.
- Gibert, J. P., and J. P. DeLong. 2017. Phenotypic variation explains food web structural patterns. *Proceedings of the National Academy of Sciences* 114:11187–11192.
- Grossart, H.-P., S. Van den Wyngaert, M. Kagami, C. Wurzbacher, M. Cunliffe, and K. Rojas-Jimenez. 2019. Fungi in aquatic ecosystems. *Nature Reviews Microbiology* 17:339–354.

- Gsell, A. S., L. N. de Senerpont Domis, K. J. Verhoeven, E. van Donk, and B. W. Ibelings. 2013. Chytrid epidemics may increase genetic diversity of a diatom spring-bloom. *The ISME Journal* 7:2057–2059.
- Hobart, B. K., W. E. Moss, T. McDevitt-Galles, T. E. Stewart Merrill, and P. T. J. Johnson. 2021. It's a worm-eat-worm world: Consumption of parasite free-living stages protects hosts and benefits predators. *Journal of Animal Ecology* n/a.
- Holling, C. S. 1959. Some Characteristics of Simple Types of Predation and Parasitism¹. *The Canadian Entomologist* 91:385–398.
- Huisman, J., G. A. Codd, H. W. Paerl, B. W. Ibelings, J. M. H. Verspagen, and P. M. Visser. 2018. Cyanobacterial blooms. *Nature Reviews Microbiology* 16:471–483.
- Ibelings, B. W., A. S. Gsell, W. M. Mooij, E. Van DONK, S. Van Den WYNGAERT, and L. N. De SENERPONT DOMIS. 2011. Chytrid infections and diatom spring blooms: paradoxical effects of climate warming on fungal epidemics in lakes. *Freshwater Biology* 56:754–766.
- Johnson, P. T. J., A. Dobson, K. D. Lafferty, D. J. Marcogliese, J. Memmott, S. A. Orlofske, R. Poulin, and D. W. Thieltges. 2010. When parasites become prey: ecological and epidemiological significance of eating parasites:10.
- Kagami, M., E. von Elert, B. W. Ibelings, A. de Bruin, and E. Van Donk. 2007. The parasitic chytrid, *Zygorhizidium*, facilitates the growth of the cladoceran zooplankter, *Daphnia*, in cultures of the inedible alga, *Asterionella*. *Proceedings of the Royal Society B: Biological Sciences* 274:1561–1566.
- Kagami, M., T. Miki, and G. Takimoto. 2014. Mycoloop: chytrids in aquatic food webs. *Frontiers in Microbiology* 5:166.
- Kjørboe, T., E. Saiz, P. Tiselius, and K. H. Andersen. 2018. Adaptive feeding behavior and functional responses in zooplankton. *Limnology and Oceanography* 63:308–321.
- Lafferty, K. D., S. Allesina, M. Arim, C. J. Briggs, G. D. Leo, A. P. Dobson, J. A. Dunne, P. T. J. Johnson, A. M. Kuris, D. J. Marcogliese, N. D. Martinez, J. Memmott, P. A. Marquet, J. P. McLaughlin, E. A. Mordecai, M. Pascual, R. Poulin, and D. W. Thieltges. 2008. Parasites in food webs: the ultimate missing links. *Ecology Letters* 11:533–546.
- Lafferty, K. D., A. P. Dobson, and A. M. Kuris. 2006. Parasites dominate food web links. *Proceedings of the National Academy of Sciences* 103:11211–11216.
- Meunier, C. L., M. Boersma, K. H. Wiltshire, and A. M. Malzahn. 2016. Zooplankton eat what they need: copepod selective feeding and potential consequences for marine systems. *Oikos* 125:50–58.
- Michalska-Smith, M. J., E. L. Sander, M. Pascual, and S. Allesina. 2018. Understanding the role of parasites in food webs using the group model. *Journal of Animal Ecology* 87:790–800.
- Miki, T., G. Takimoto, and M. Kagami. 2011. Roles of parasitic fungi in aquatic food webs: a theoretical approach. *Freshwater Biology* 56:1173–1183.
- Mougi, A., and Y. Iwasa. 2010. Evolution towards oscillation or stability in a predator–prey system. *Proceedings of the Royal Society B: Biological Sciences* 277:3163–3171.
- Ndlovu, M., and L. Combrink. 2015. Feeding preferences of Oxpeckers in Kruger National Park, South Africa : original research. *Koedoe : African Protected Area Conservation and Science* 57:1–6.
- O’Gorman, E. J., U. Jacob, T. Jonsson, and M. C. Emmerson. 2010. Interaction strength, food web topology and the relative importance of species in food webs. *Journal of Animal Ecology* 79:682–692.
- Prosnier, L., V. Medoc, and N. Loeuille. 2018. Parasitism effects on coexistence and stability within simple trophic modules. *Journal of Theoretical Biology* 458:68–77.

- Rasconi, S., B. Grami, N. Niquil, M. Jobard, and T. Sime-Ngando. 2014. Parasitic chytrids sustain zooplankton growth during inedible algal bloom. *Frontiers in Microbiology* 5:229.
- Rasconi, S., R. Ptacnik, S. Danner, S. Van den Wyngaert, T. Rohrlack, M. Pilecky, and M. J. Kainz. 2020. Parasitic Chytrids Upgrade and Convey Primary Produced Carbon During Inedible Algae Proliferation. *Protist* 171:125768.
- Ray, J. L., J. Althammer, K. S. Skaar, P. Simonelli, A. Larsen, D. Stoecker, A. Sazhin, U. Z. Ijaz, C. Quince, J. C. Nejstgaard, M. Frischer, G. Pohnert, and C. Troedsson. 2016. Metabarcoding and metabolome analyses of copepod grazing reveal feeding preference and linkage to metabolite classes in dynamic microbial plankton communities. *Molecular Ecology* 25:5585–5602.
- Rogawa, A., S. Ogata, and A. Mougi. 2018. Parasite transmission between trophic levels stabilizes predator–prey interaction. *Scientific Reports* 8:12246.
- Rooney, N., K. McCann, G. Gellner, and J. C. Moore. 2006. Structural asymmetry and the stability of diverse food webs. *Nature* 442:265–269.
- Salmaso, N., and M. Tolotti. 2021. Phytoplankton and anthropogenic changes in pelagic environments. *Hydrobiologia* 848:251–284.
- Sandhu, S. K., A. Yu. Morozov, A. Mitra, and K. Flynn. 2019. Exploring nonlinear functional responses of zooplankton grazers in dilution experiments via optimization techniques. *Limnology and Oceanography* 64:774–784.
- Sommer, U., N. Aberle, K. Lengfellner, and A. Lewandowska. 2012. The Baltic Sea spring phytoplankton bloom in a changing climate: an experimental approach. *Marine Biology* 159:2479–2490.
- Stibor, H., O. Vadstein, S. Diehl, A. Gelzleichter, T. Hansen, F. Hantzschke, A. Katechakis, B. Lippert, K. Loseth, C. Peters, W. Roederer, M. Sandow, L. Sundt-Hansen, and Y. Olsen. 2004. Copepods act as a switch between alternative trophic cascades in marine pelagic food webs. *Ecology Letters* 7:321–328.
- Sukhdeo, M. V. 2012. Where are the parasites in food webs? *Parasites & Vectors* 5:239.
- Thingstad, T. F., and E. Sakshaug. 1990. Control of phytoplankton growth in nutrient recycling ecosystems. Theory and terminology. *Marine Ecology Progress Series* 63:261–272.
- Uszko, W., S. Diehl, N. Pitsch, K. Lengfellner, and T. Muller. 2015. When is a type III functional response stabilizing? Theory and practice of predicting plankton dynamics under enrichment. *Ecology* 96:3243–3256.
- Visser, A., and O. Fiksen. 2013. Optimal foraging in marine ecosystem models: selectivity, profitability and switching. *Marine Ecology Progress Series* 473:91–101.
- Wollrab, S., and S. Diehl. 2015. Bottom-up responses of the lower oceanic food web are sensitive to copepod mortality and feeding behavior. *Limnology and Oceanography* 60:641–656.
- Wollrab, S., P. Pondaven, S. Behl, B. Beker, and H. Stibor. 2020. Differences in size distribution of marine phytoplankton in presence versus absence of jellyfish support theoretical predictions on top-down control patterns along alternative energy pathways. *Marine Biology* 167:9.
- Yamamichi, M., T. Klausches, B. E. Miner, and E. van Velzen. 2019. Modelling inducible defences in predator–prey interactions: assumptions and dynamical consequences of three distinct approaches. *Ecology Letters* 22:390–404.

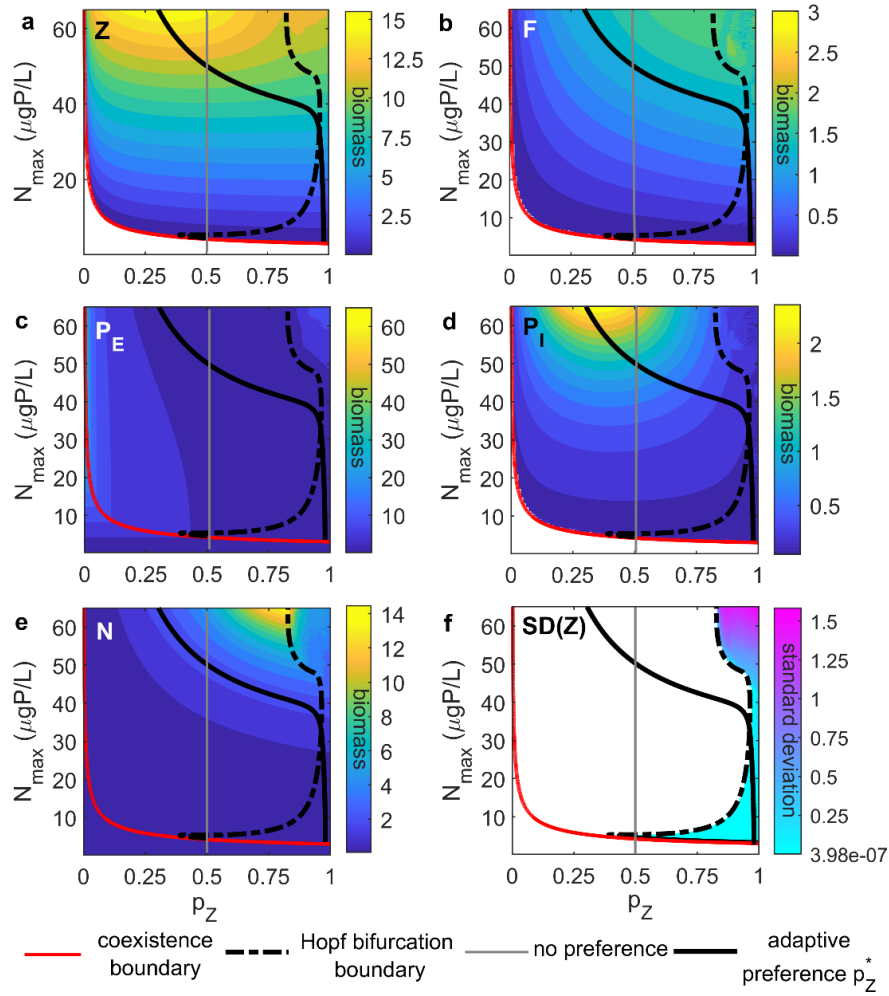


Figure 1 . Effect of nutrient enrichment ($N_{\max}$) and prey preference (p_Z) of zooplankton (Z) for edible phytoplankton (P_E) and parasitic fungi (F), on species biomass and stability. Panels (a-e) illustrate the mean equilibrium biomass [$\mu\text{gP}\cdot\text{L}^{-1}$] for (a) zooplankton Z , (b) parasitic fungi F , (c) edible phytoplankton P_E , (d) inedible phytoplankton P_I , and (e) freely available nutrient N , white areas indicate the extinction of the respective species. The dash-dotted line (Hopf bifurcation boundary) separates the area of stable point equilibria (on the left) from the area with oscillatory behaviour (on the right). The optimal preference (p_Z^*) is only illustrated within the area of coexistence ($N_{\max} > 2.7 \mu\text{gP}\cdot\text{L}^{-1}$). Panel (f) shows the standard deviation of the mean biomass of zooplankton for regions with oscillatory behaviour.

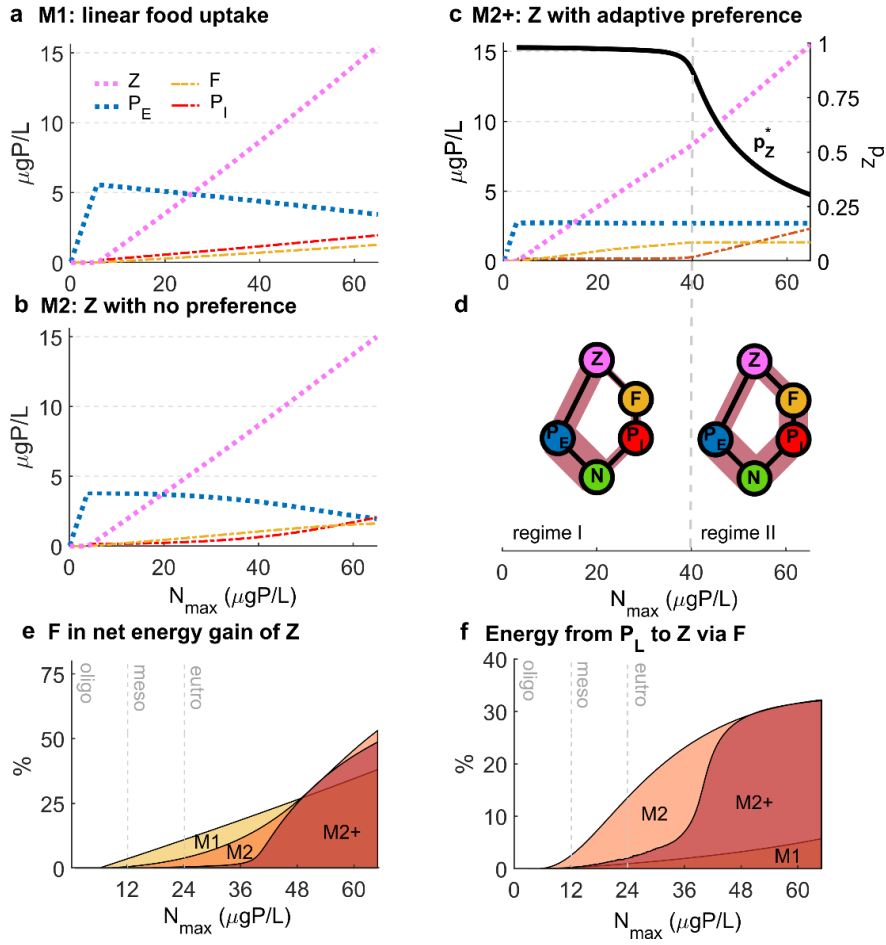


Figure 2. Changes in the mean equilibrium biomass of all food web compartments with increasing $N_{\max}$ under the assumption of (a) linear food uptake terms (Miki et al. 2011) (M1), (b-c) saturating food uptake terms for (b) non-adaptive zooplankton with no prey preference ($p_Z = 0.5$) (M2), (c) adaptive zooplankton with adaptive prey preference ($p_Z(t)$) (M2+). In panel (d) the distribution of energy flow in the food web is illustrated for Regime I and Regime II of M2+. The relative energy flow along each interaction link is illustrated by the width of the brown shaded area for Regime I (at $N_{\max} = 25 \mu\text{gP}\cdot\text{L}^{-1}$) and Regime II (at $N_{\max} = 65 \mu\text{gP}\cdot\text{L}^{-1}$ and $p_Z^* = 0.3034$). Panels (e-f) show a comparison of M1, M2 and M2+ for (e) relative contribution of fungi to net energy gain of zooplankton and (f) transfer efficiency along the mycocoop.

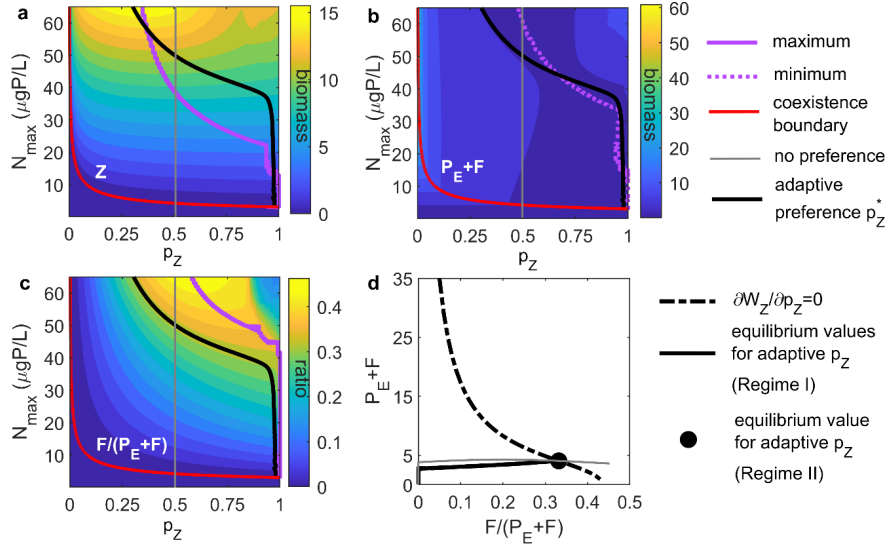


Figure 3. Illustration of optimal prey preference values (p_Z^*) for the case of adaptive zooplankton (black solid line) in comparison to maximum (a) zooplankton biomass, (c) relative contribution of parasite (F) to total prey, indicated by a pink solid line, and (b) minimum total prey biomass ($P_E + F$) indicated by a pink dotted line. Panel (d) illustrates the optimal prey availability following the optimal fitness strategy $\frac{\partial W_Z}{\partial p_Z} = 0$ (dash-dotted line) and its dependence on relative contribution of fungi to total prey biomass. Solid lines indicate the calculated values for the adaptive preference case with increasing $N_{\max}$ under Regime I. The intersection point of calculated and optimal values is indicated by a point and represents the equilibrium value reached under Regime II.