Mesopredator-mediated trophic cascade can break persistent phytoplankton blooms in coastal waters

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Abstract

Managing eutrophied systems only bottom-up (nutrient decreases) can be economical and ecological challenging. Top-down controls (grazing) were sometimes found to effectively control phytoplankton blooms. However, mechanistic insights, especially on possible trophic cascades, are missing in brackish, species-poor coastal waters, where large cladocera are absent. In this study, we set-up large mesocosms for three consecutive years during growth season. One set of mesocosms was controlled by mesopredator (gobies and shrimp), whereas the other mesocosms had no such mesopredator present. The results were standardized to monitoring data of the actual ecosystem to denote possible differences between treatments and the system. We found that fish mesocosm showed lower turbidity, phytoplankton biomass, and nutrients

compared to no-fish mesocosm and the actual ecosystem. This decrease allowed macrophytes to colonize water depths only sparsely colonized in the ecosystem. Rotifer biomass increased in fish mesocosms compared to the actual ecosystem and no-fish mesocosm. Likewise, copepod biomass that potentially grazes upon rotifers and other microzooplankton decreased in fish mesocosm. No-fish mesocosm were colonized by omnivorous mesograzer (*Gammarus tigrinus*), creating additional pressure on macrophytes and increasing grazing-mediated nutrient release. Zooplankton was not able to control the non-nutrient limited phytoplankton. We propose a new mechanism, where a higher mesopredator density will increase grazing on phytoplankton by promoting microzooplankton capable of grazing on picophytoplankton. This proposed mechanism would contrast with freshwater systems, where a decrease of zooplanktivorous fish would promote larger phytoplankton grazer like cladocera. Biomanipulation in such species-poor eutrophic coastal waters may be more successful, due to less trophic pathways that can cause complex top-down controls. We conclude that an improved fishing management on non-endangered top predator, like pike and sander may promote gobies and shrimp, which can cause a trophic cascade improving water quality.

Keywords

food web, mesocosm, top-down control, eutrophication, grazing, phytoplankton, goby

Introduction

One of the biggest challenges in ecosystem restoration is restoring deteriorated aquatic ecosystems back to an undisturbed state in the coming decades. One factor that still affects ecosystems until nowadays is eutrophication. There were different approaches developed to control eutrophication, mostly by decreasing inflow of elements, like Nitrogen, and Phosphorus (Schindler 1977, Vitousek et al. 1997, Schindler et al. 2016). These decreases worked mostly for

deep lakes, where pre-eutrophication Chlorophyll concentrations were reached after three decades, but with different plankton species compositions than before eutrophication (Jochimsen et al. 2013). Larger bodies of water, like the Baltic Sea would not reach pre-disturbed phosphate concentrations within the next 100 years, at the current rate of nutrient concentration decrease, due to insufficient inflow decrease in some areas (HELCOM 2014). Shallow aquatic ecosystems are even more affected, as they lack the water depth for long-term nutrient sequestration. Pre-disturbed ecosystem states in shallow waters were reached with large external measures, like increased water removal, within a little more than 30 years (Chorus et al. 2020). Such approaches aimed at bottom-up control can become unfeasible, especially, if management practices do not improve within the surrounding catchment area. For example, still increasing phosphorus stocks in soils (van Dijk et al. 2016), can cause ongoing phytoplankton growth in shallow coastal waters through nutrient flushing (Berthold et al. 2018a). However, shallow coastal systems are very important, globally, as they can make up to 10% of the global coastline (Dürr et al. 2011), and act locally as nutrient filter for the Baltic Sea (Asmala et al. 2017).

Biomanipulation was proposed as additional sustainable method to support restauration efforts (Jeppesen et al. 2007), as it acts top-down on phytoplankton biomass. There are a wide variety of biomanipulative studies published, either in mesocosms, or in whole lakes (Jeppesen et al. 1990, Søndergaard et al. 2007). Most studies described an effective decrease of phytoplankton biomass, depending on the ratio of zooplanktivorous to piscivorous fish, and the amount of large cladocera as unselective filter feeders. However, most of those experiments focus on shallow, limnic systems, but shallow coastal waters are somewhat understudied, yet similarly impacted by eutrophication. In addition, such brackish systems show rarely, if any large cladocera, removing one important zooplankton group as an effective grazer on phytoplankton. Coastal waters are

furthermore connected to limnic and marine systems and are hatching points for migratory fish species. A total removal of one fish species like in enclosed systems (lakes) is therefore not possible. Such prerequisites make biomanipulative approaches in shallow coastal waters challenging. Nonetheless, biomanipulative approaches need to be explored, if nutrient decreases by point sources cannot be lowered any further.

Furthermore, the Baltic Sea is already more impacted by increased sea surface temperature, compared to other areas in the world (Reusch et al. 2018). This temperature, and nutrient condition acts upon the functioning of the food web, by promoting a decrease in body size of every compartment of the food web (Peter and Sommer 2013, Liénart et al. 2021). If it is true that increasing temperatures decrease the cell size of phytoplankton (Sommer et al. 2017), than the food web would equally respond selecting smaller individuals (Liénart et al. 2021). Such small phytoplankton is problematic, as it may pass zooplankton grazing (Lürling 2020), therefore lowering food web efficiency. One such system with perennial dominance of picophytoplankton is the Darß-Zingst lagoon system (DZLS, Albrecht et al. 2017), which is located at the southern Baltic Sea coast of Germany. The DZLS is a typical lagoon system of the southern Baltic Sea and acts as a model ecosystem, due to its salinity and trophic gradient (Schiewer 2007). This system is dominated by up to 90% of cyanobacteria, showing simultaneously a high TN:TP of 35:1, and no available dissolved inorganic P during summer (Berthold 2016, Berthold et al. 2018b, Schumann et al. 2019). There is a fluctuating dominance of copepods over rotifers throughout the year (Feike et al. 2007), and grazing of zooplankton is assumed to be only around 3% of the gross primary production (Heerkloss et al. 1984). In theory, such low grazing rates would point to a missing top-down control within the ecosystem, where the amount of planktivorous fish is too high. However, there have been increasing amounts of reports, that such

food web interactions are too simple. For example, grazing on copepods can act as switch within trophic cascades, depending on pre-dominant phytoplankton size classes and nutrient availability (Stibor et al. 2004). Such trophic cascades can change the composition of micro- and mesozooplankton (Zöllner et al., 2009), ultimately affecting a zooplankton-mediated top-down control on phyto- and bacterioplankton (Zamora-Terol et al. 2020). In the case of the DZLS, such a trophic cascade may have been observed, with possible grazing of *Eurytemora affinis* on eggs and adults of the rotifer *Keratella cochlearis* (Feike and Heerkloss 2009). However, rotifers such as *K. cochlearis* are known to graze upon bacterioplankton (Haukka et al. 2006), but also on filamentous cyanobacteria (Novotny et al. 2021), which provide a large fraction of total biovolume in the DZLS (Albrecht et al. 2017, Berthold and Schumann 2020). The DZLS shows a relatively short food web, with a high redundancy (Paar et al. 2022), and a dominant energy- and matter flow within the microbial loop (Schiewer et al. 1990, Schiewer 2007). An increased grazing pressure by rotifers and ciliates may disrupt the microbial loop, by lowering the picoplankton compartments that otherwise turn over nutrient pools through enzymatic activity within hours (Berthold and Schumann 2020).

We therefore questioned if restoration measures focusing on nutrient decrease were not successful, because a trophic cascade prohibited an efficient grazing on phytoplankton, in combination with nutrient-efficient phytoplankton. We hypothesized that with the removal of piscivorous fish (large predator, trophic level 3), mesopredator grazing (gobies, shrimp, smaller predator of trophic level 3) upon mesograzer (herbi- and omnivorous amphipods, isopods, trophic level 2) and zooplankton (copepods, cladocera) would cause a disruption of the pelagic and benthic nutrient recycling, ultimately promoting a clear water state. If this trophic cascade did not exist, a complete exclusion of all mesopredator would lead to very high numbers of

zooplankton, promoting a clear water state. The exclusion of mesopredator would be equal to an efficient grazing control of top predators like pike. The actual ecosystem would be used as control for the annual development of all monitored variables (nutrients, phytoplankton, zooplankton) in mesocosms. The main contrasting hypotheses can be formulated as follows:

i) Mesopredator presence will disrupt the microbial loop in a eutrophic lagoon through an intra-zooplankton trophic cascade, causing a clear water state.

ii) Absent mesopredator will liberate zooplankton of grazing pressure, increasing grazing rates on phytoplankton, causing a clear water state.

We used large *ex-situ* mesocosms for this biomanipulation and replicated them three years in a row, to catch possible interannual effects. Monitoring of the actual ecosystem and the mesocosms allowed to follow the seasonal development of all pelagic compartments.

Material and Methods

Experimental Set-up

The mesocosms were set-up on the premises of the Biological Station Zingst near the DZLS on the southern Baltic Sea coast. A general experimental set-up can be found in Berthold (2018). Briefly, mesocosms were 2200-liter glass fiber containers embedded in the ground to allow for passive temperature control. Mesocosms stood on an unobstructed field without interference of any structure that would impact wind, precipitation, or sunlight. We followed design suggestions made by Raffaelli and Moller (1999) regarding replicates, independence and ecosystem comparability (see following points). The mesocosms were started in 2015, and were repeated in 2016, and 2017 for a total of five replicates per treatment over these three years. Each year, mesocosms were filled with new habitat sediment (5 cm total height) and habitat water in late

spring, and mesocosms with and without treatment were assigned randomly to avoid pseudo-replicates (Raffaelli and Moller 1999). Habitat water was pumped in from the near-by lagoon system (50 m). Sediment was collected from a nearby site (Grabow, Bodstedter Bodden) with known macrophyte colonization to allow macrophyte sprouting. The mesocosms ran for a whole growth season, starting in April, and ending in September of each year, to include the annual macrophyte growth season. After the end of each season, mesocosms were emptied and cleaned. All biomass (pelagic, benthic) was collected and quantified (see below). Mesocosms of the first year were equipped with two optodes at two depths (surface ~5 cm, and 70 cm) to test stability of primary production and effects of sediment respiration. Animals were collected with a beach seine right before experimental start. The beach seine was pulled along 100 m, and animal biomass per square meter was calculated. We used this areal biomass to calculate the amount of animals to be added to the fish mesocosms. Some further methodological remarks can be found in the Supplement.

Fish and shrimp were kept in aerated containers, and their length determined before setting in mesocosms. We used the gobiid species *Pomatoschistus microps* and *P. minutus*, as well as the shrimp species *Palaemon elegans*. These species are abundant within the DZLS, and graze as mesopredators on larger zooplankton and mesograzers (amphipods, isopods) (Gagnon et al., 2021; Pasquaud et al., 2010; Pihl et al., 2006). For simplicity, those mesocosm are labelled as fish mesocosm throughout, whereas mesocosms without added fish and shrimp are labelled as no-fish mesocosm.

Mesocosm monitoring

Mesocosms were sampled frequently (biweekly) for abiotic and biotic parameters. Abiotic parameters included turbidity (optical density at 720 nm, m^{-1}), dissolved inorganic phosphorus

(DIP, µmol L^{-1}), and dissolved inorganic nitrogen (DIN, sum of nitrate, nitrite, ammonium, µmol L^{-1}), total phosphorus (TP, µmol L^{-1}), and total nitrogen (TN, µmol L^{-1}), and oxygen saturation (%). DIN and DIP was analyzed according to Hansen and Koroleff (1999). TN and TP were analyzed with an adjusted protocol using a sub-boiling extraction with potassium persulphate (Berthold et al. 2015). Determination limits were 0.26 µmol L^{-1} for nitrate, 0.6 for ammonium, 0.05 µmol L^{-1} for DIP, 3 µmol L^{-1} for TN, and 0.22 µmol L^{-1} for TP.

Water samples were filtrated onto glass fiber filters to determine Chlorophyll *a* concentrations (Chl *a*). Chl *a* was determined with a cold EtOH extraction overnight (Strickland and Parsons 1972) and Chl content was calculated following the standard HELCOM procedure (HELCOM 2013).

Zooplankton was sampled at least four times over the course of each experiment fixating 1 L of a water sample with formaldehyde (4 % final concentration). The 1 L of full sample sedimented 24 h, 900 ml of supernatant were removed, and the sample was taken up in the remaining 100 ml. These were analyzed in total or in parts of at least 10 ml. An inverse microscope or Kolkwitz chambers were used for counting. Abundance numbers of occurring species were transformed to biomass (fresh mass µg L^{-1}) using average geometric equivalents of individual body volumes according to a list by Heerkloss et al. (1991). This list also accounts for different size stages in copepods based on their life stage.

Animal and plant biomass was collected at the end of each replicate run in September. Animals were counted and weighed. All animals were euthanized according to the regulations of the University of Rostock and the experiments were supervised by the animal welfare officer. Macrophyte biomass was harvested by hand, determined on genus level, blotted dry and wet-

weighed. Biomass was then dried at 90 °C for 24 hours and re-weighed. Water content (%) was calculated based on differences between wet and dry mass.

We further used the experimental and monitoring data to model seasonal dynamics of dissolved, and total nutrients, Chl *a*, turbidity, and zooplankton species. Prior to modelling, we log-transformed and standardized our data. We chose to standardize our experimental data with the respective ecosystem monitoring data (daily measurements from Julian day 120 to 270, years 2015 – 2017) to make our data directly comparable to ecosystem trends (see Supplement Figure 1 for ecosystem averages of years 2015 – 2017). Standardization was carried out with the *scale* function of R (R Core Team 2018), which calculates a z-score of the respective data set. Zooplankton monitoring data was only available until December 2013 (see Supplement Figure 2 for ecosystem average per zooplankton group) and was only sampled once per week. We therefore used data from a longer period up until the last available years (2003 – 2013) for standardization with our mesocosm data (2015 – 2017). We chose a generalized additive model (GAM, *gam* function, R package *"mcgv"*, Wood 2011, Gaussian distributional assumptions, variable knots depending on data availability, k = 4 – 20), as the best model to reflect the experimental data. We used the GAM to predict the seasonal development as function of sampling date in both mesocosm experiments and the ecosystem. The GAM allowed to depict seasonal dynamics and is used as an informative tool here.

Results

Pelagic elemental composition

Dissolved nitrogen (DIN) concentrations within mesocosms tended to increase above average in both treatments until June and would decrease below average in September (Figure 1A). Concentrations within the ecosystem were rather stable throughout this period, with only a small

decrease during August. This development points to a higher DIN availability in both mesocosm treatments compared to the actual ecosystem. On the contrary, DIP concentrations in both mesocosm treatments, dropped during the month of June, with fish mesocosms showing even lower concentrations compared to no-fish mesocosms (Figure 1B). Contrary to the mesocosms, DIP concentrations within the ecosystem did not show any trends throughout the observational period. However, DIP concentrations were mostly close to the determination limit, pointing to overall low DIP concentrations.

Total nitrogen (TN) concentrations within mesocosms developed differently in both treatments already from the start. TN concentrations in fish mesocosm remained around average. TN concentrations in no-fish mesocosms increased in all years, and throughout the observational period (Figure 2A). This development contrasts the DIN development and indicates free DIN was incorporated into other fractions instead. Ecosystem concentrations would decline from June onwards. The trends in both mesocosm treatments points to a higher (no-fish mesocosm), or stable (fish mesocosm) availability of N compared to the actual ecosystem. Comparable to TN, TP in both mesocosm treatments increased steadily, but fish mesocosms reached average concentrations only at the end compared to no-fish mesocosms (Figure 2B). Ecosystem concentration of TP would decrease from July onwards. The positive TP trend in both mesocosm treatments indicates a steady P accumulation and is consistent with the DIP increase starting in August. The DIP:TP remained around 5 – 10% in all mesocosms and the ecosystem (Supplement Figure 1A). The DIN:DIP ratio dropped after August in mesocosms, indicating that DIP was maybe growth limiting during May to June (Supplement Figure 1B). The peak of TN:TP ratio was highest in fish mesocosms (on average up to 120:1 TN:TP) during July, compared to no-fish

mesocosms (on average up to 90:1 TN:TP). Interestingly, the ecosystem showed lowest TN:TP ratios during summer (50:1 TN:TP, Supplement Figure 1C).

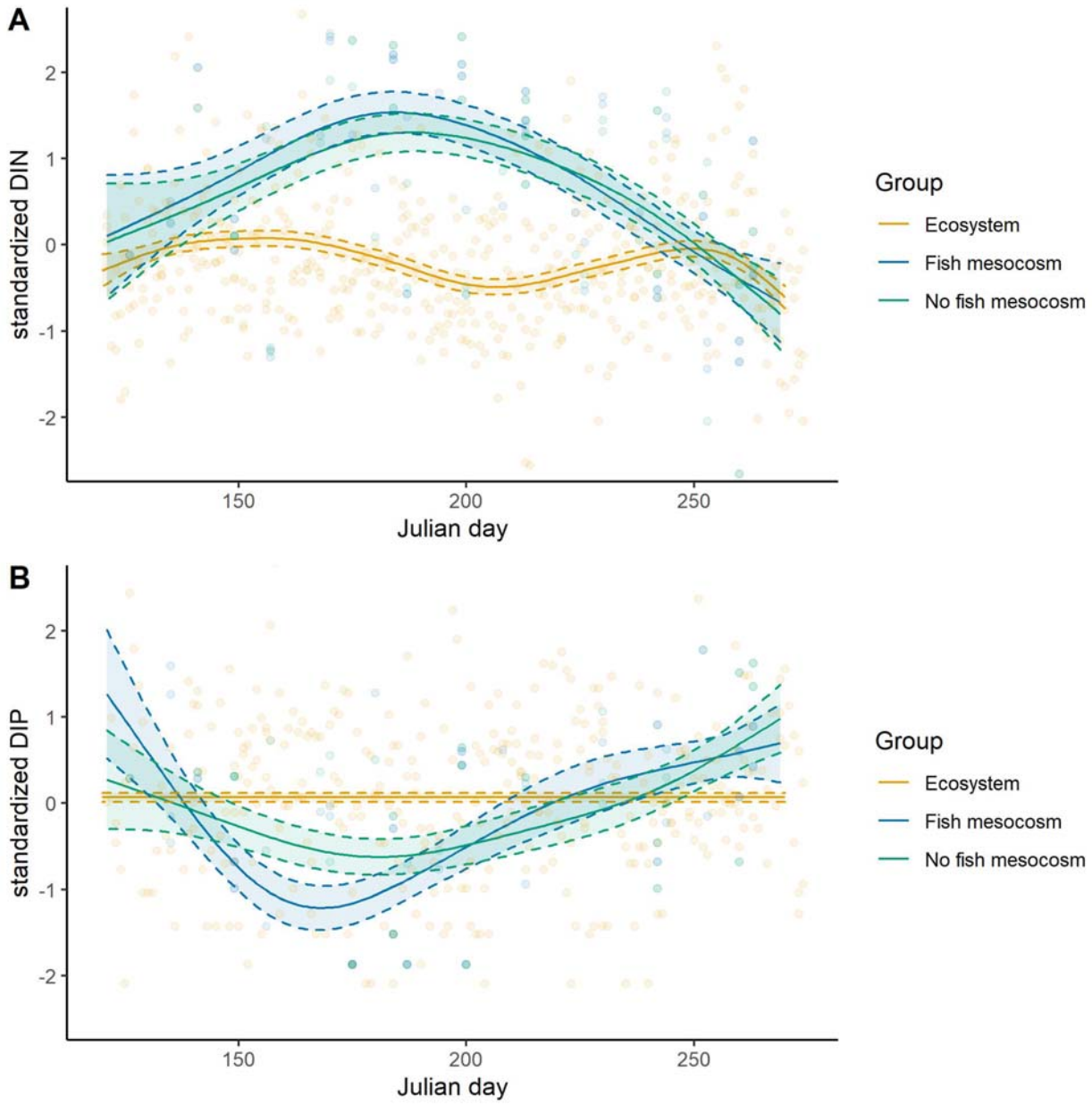

Figure 1 Seasonal development of standardized dissolved inorganic nitrogen (Panel A, sum of nitrate, nitrite, and ammonium = DIN), and standardized dissolved inorganic phosphorus (Panel

B, DIP) in fish (green) and no-fish (blue) mesocosm and the actual ecosystem (orange) over the years of 2015 to 2017. The development of both nutrient fractions (points) was modelled (generalized additive model) depending on day of the year (April – October, x-axis) with all replicates being pooled. The solid line represents the mean and the dotted line the 95 % confidence interval. Values of mesocosms and the ecosystem were log-transformed and standardized (z-score), to enable a direct comparison of ecosystem with mesocosms.

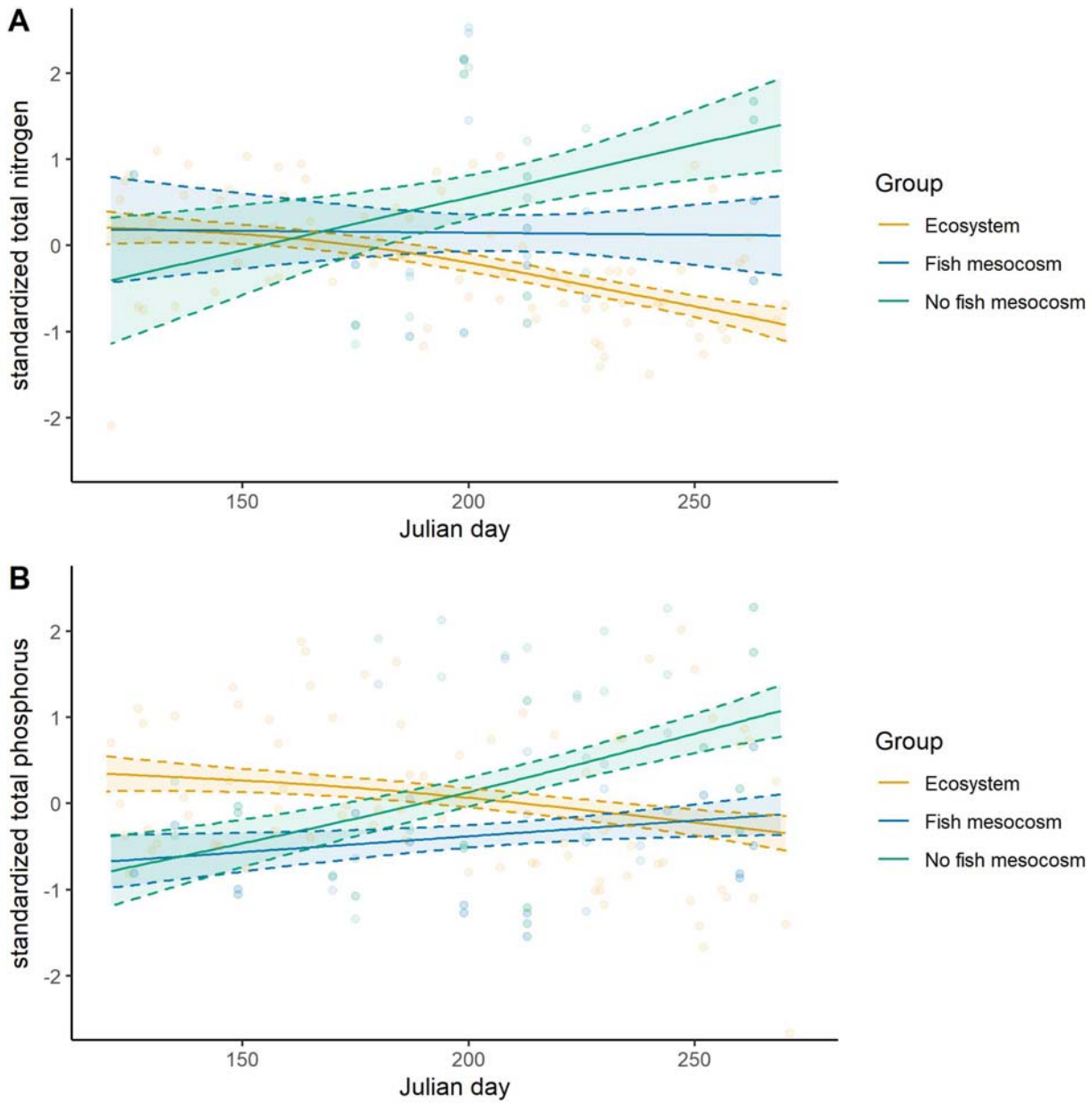

Figure 2 Seasonal development of standardized total nitrogen (Panel A, total N), and standardized total phosphorus (Panel B, total P) in fish (green) and no-fish (blue) mesocosm and the actual ecosystem (orange) over the years of 2015 to 2017. The development of both nutrient fractions (points) was modelled (generalized additive model) depending on day of the year (April – October, x-axis) with all replicates being pooled. The solid line represents the mean and the dotted line the 95 % confidence interval. Values of mesocosms and the ecosystem were log-

transformed and standardized (z-score), to enable a direct comparison of ecosystem with mesocosms.

Development of planktonic compartments

Chl *a* concentration decreased in both mesocosm treatments below ecosystem average until June, when both treatments started to develop independently from each other (Figure 3A). Fish mesocosms remained below average towards the end. Contrary, no-fish mesocosms showed a strong increase of Chl *a* until the end of the experiment. This pattern coincides with steady nutrient increases in no-fish mesocosms (Figure 3). The ecosystem showed decreasing Chl *a* concentration after the initial spring bloom, and possibly a small bloom in August.

Likewise, turbidity within both mesocosm treatments decreased initially, but split again after June (Figure 3B). Fish mesocosms continued to show below average turbidity. No-fish mesocosms increased their turbidity in a similar pattern as with Chl *a*. It was not possible to discriminate with the current data set if Chl *a* increased due to increased amounts of particles (abiotic and biotic), or if turbidity increased due to increased Chl *a* (attenuating phytoplankton biomass). Ecosystem turbidity was highest during May and steadily declined afterwards and was comparably to fish mesocosm turbidity in September.

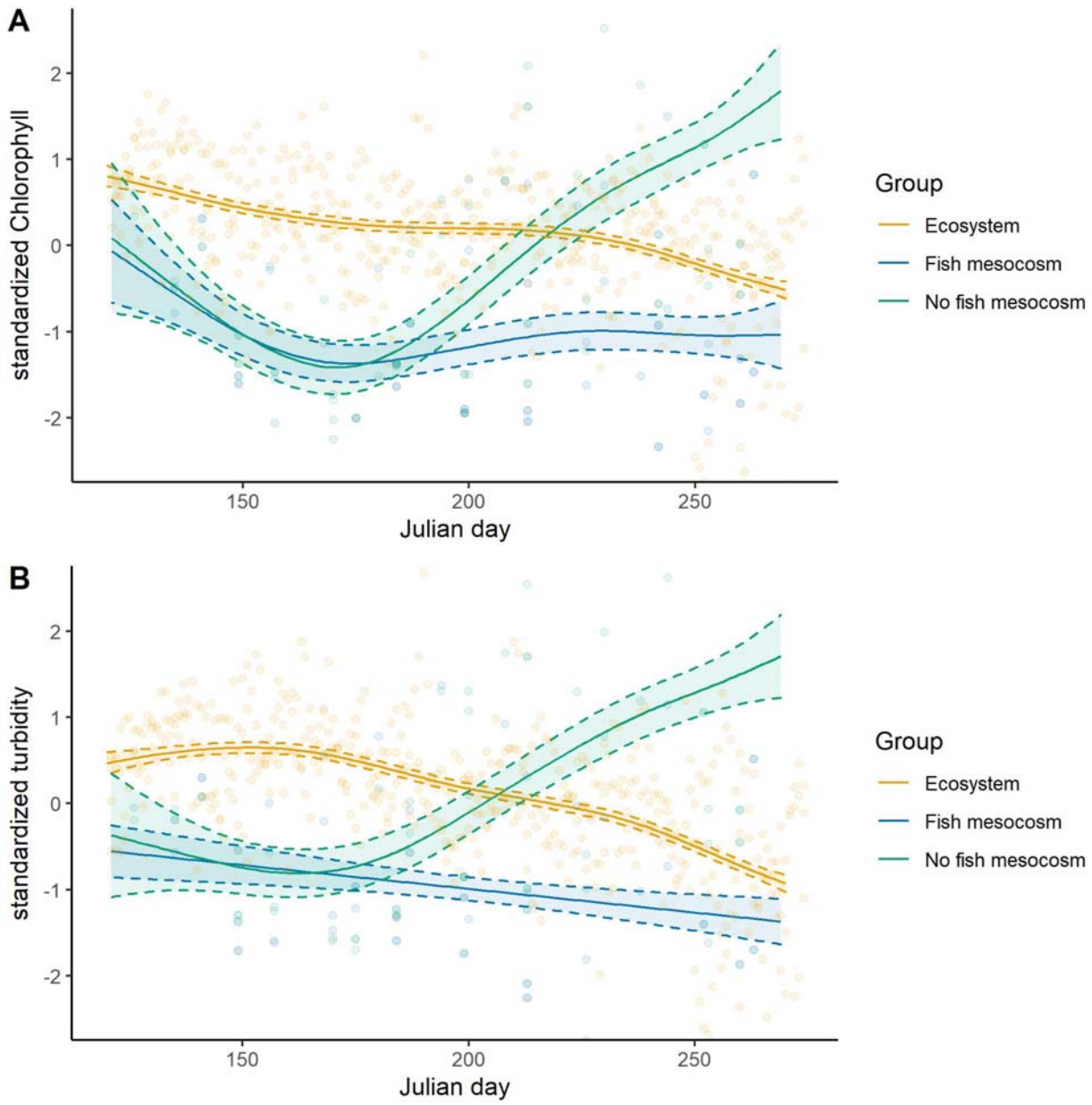

Figure 3 Seasonal development of standardized Chlorophyll *a* (Panel A, proxy for phytoplankton biomass), and standardized turbidity (Panel B, absorption at 720 nm, proxy for attenuation) in fish (green) and no-fish (blue) mesocosm and the actual ecosystem (orange) over the years of 2015 to 2017. The development of both particulate fractions (points) was modelled (generalized additive model) depending on day of the year (April – October, x-axis) with all replicates being pooled. The solid line represents the mean and the dotted line the 95 % confidence interval.

Values of mesocosms and the ecosystem were log-transformed and standardized (z-score), to enable a direct comparison of ecosystem with mesocosms.

Zooplankton biomass (as µg FM L^{-1}) per zooplankton class showed different developments within both mesocosm treatments and compared to the ecosystem (Figure 4). Cladocera biomass remained above average in both mesocosm treatments. However, cladocera (*Bosmina* and *Alona* spp.) were rarely detected in the actual ecosystem, indicating inconclusive trends. Copepod biomass in fish mesocosms declined steadily after May. Interestingly, the decline of copepod biomass from July on coincides with an increase of Monogononta biomass. Monogononta biomass was average from May until June, reaching above-average biomass during the end of the experiment, contrary to the ecosystem and no-fish mesocosm. No-fish mesocosm showed overall average copepod biomass throughout all experimental runs. Monogononta biomass in no-fish mesocosm showed a similar trend like fish mesocosms but with a lower overall biomass. There were no detectable differences in species composition between ecosystem and the mesocosms. Cladocera biomass was dominated by *Bosmina* and *Alona* spp., copepod biomass by *Eurytomora affinis* and *Acartia tonsa*, and monogononta biomass by *Keratella* spp., *Filinia* spp., *Brachionus* spp., and *Synachaeta* of various size classes.

Overall, these results point to an increased grazing pressure on copepods in fish mesocosms, whereas this pressure was less pronounced in no-fish mesocosms, compared to the ecosystem. Interestingly, fish occurrence caused above average Monogononta biomass in all three years and indicates possible indirect effects on their occurrence and abundance.

Zooplankton within the ecosystem showed again different dynamics. Cladocera density showed no trend, caused by a low number of overall observations, and total biomass. Copepods within the ecosystem declined after high initial numbers in April and showed a second peak later in the year. This development was contrary to both mesocosms, where copepod biomass was average or below average in the later months. Monogononta density was highest in June/July, but declined afterwards and remained then lower compared to biomass in fish mesocosms. In conclusion, both treatments had a different impact on abiotic (nutrients) parameters, phytoplankton (Chl *a*), zooplankton, macrophyte and animal biomass (Supplement Figure 4), compared to each other, but also to the actual ecosystem. These differences are indicative of altered regulating mechanisms caused by the biomanipulation.

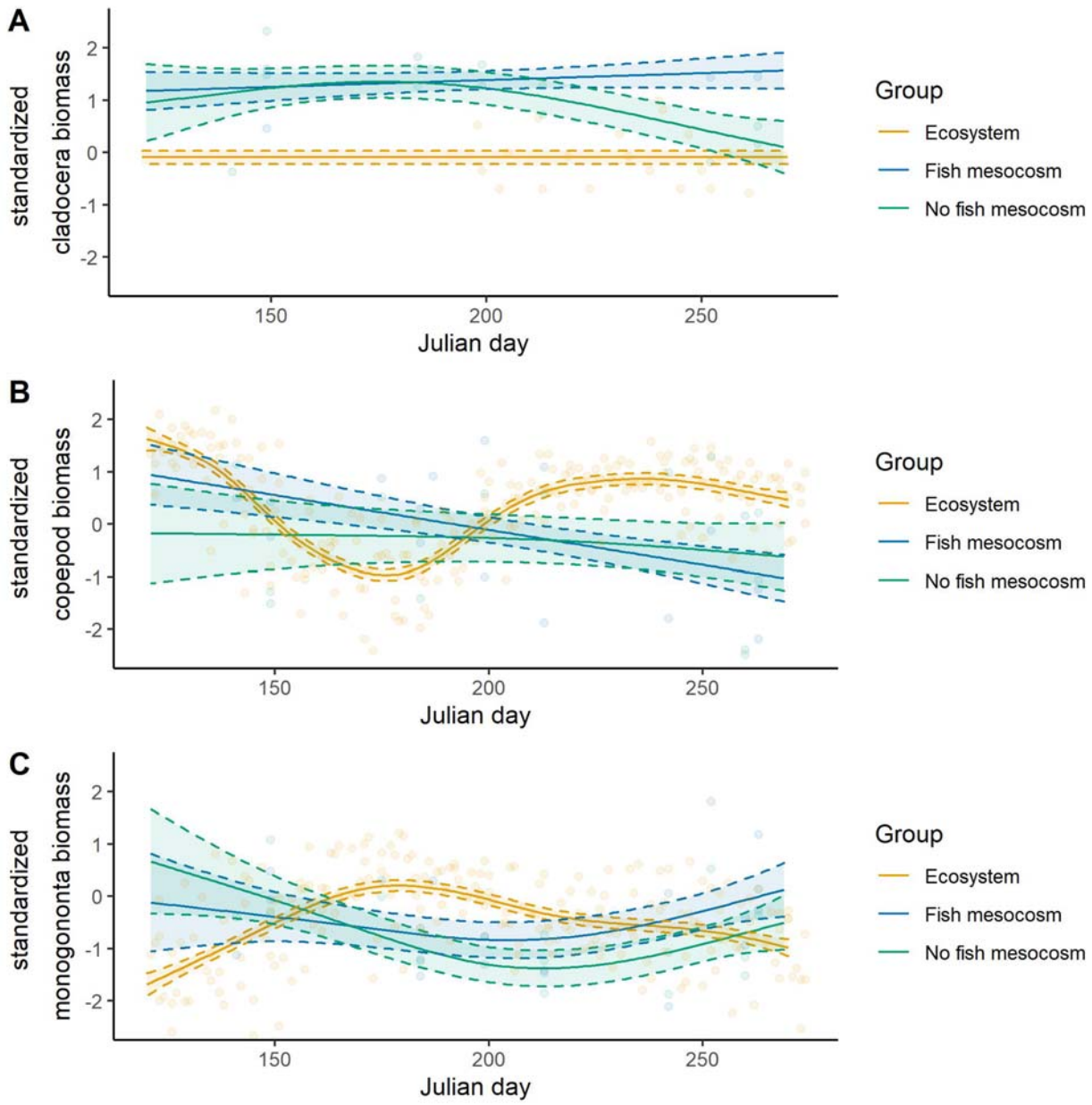

Figure 4 Seasonal development of standardized cladocera (Panel A), standardized copepods (Panel B), and standardized monogononta biomass (Panel C) as fresh mass (µg L^{-1}) in fish (green) and no-fish (blue) mesocosm over the years of 2015 to 2017 and the actual ecosystem (orange, 2011 – 2013). The development of all zooplankton fractions (points) was modelled (generalized additive model) depending on day of the year (April – October, x-axis) with all replicates being pooled. The solid line represents the mean and the dotted line the 95 %

confidence interval. Values of mesocosms and the ecosystem were log-transformed and standardized (z-score), to enable a direct comparison of ecosystem with mesocosms.

Discussion

Food web impact of biomanipulation

The results of this mesocosm approach needs to be analyzed regarding its number of available trophic levels. The no-fish mesocosms showed in all replicates a large biomass of gammarids (representative individuals identified as invasive *Gammarus tigrinus*), with similar or even higher animal biomass compared to fish mesocosms (Supplement Figure 4). The trophic position of gammarids depends on the presence of grazers present and can cause a trophic cascade in species-poor ecosystems (Compte et al., 2012). This cascade can result in macrophyte loss, increased turbidity and occurrence of other zooplankton grazers (Compte et al. 2012), similar to our results (see Figure 4). The removal of mesopredator will allow mesograzer to reach a biomass density which is determined by the overall primary production capacity within the ecosystem (Eriksson et al., 2012). However, it cannot be concluded that no-fish mesocosms were more productive based on higher animal biomass, as gammarids grazed most of the macrophyte biomass, and probably all the epiphyte biomasses. A recent study showed that gammarid grazing can cause up to 30% biomass loss of charophytes in the DZLS (Berthold et al., 2022) and that grazing pressure may increase with increasing temperatures (Pellan et al., 2016) or P-concentrations within the water column (Östman et al. 2016). A control of these mesograzer by increasing the presence of mesopredator like gobies and shrimp should, therefore, be considered

necessary. Gammarids as mesograzer release nutrients by grazing on epiphytes and macrophytes, which can favor phytoplankton. Furthermore, decreased macrophyte biomass lowers direct (nutrients, Kufel & Kufel 2002) and indirect competition (allelopathy, Vanderstukken et al. 2011) with phytoplankton, leading ultimately to a decreased habitat for phyto- and bacterioplankton grazers, like sessile rotifers (Miracle et al. 2007). An increased grazing pressure on gammarids would still allow growth control of epiphytic algae by gastropods (Gagnon et al. 2021), which are very abundant in the form of *Hydrobia* sp. in the coastal waters of the southern Baltic Sea (Paar et al. 2022). This epiphytic grazing is important especially in turbid coastal waters, where macrophytes are already under light limitation, and epiphytic biomass can increase rapidly during summer months (Paar et al., 2021), possibly causing additional stress on macrophytes (Lin et al., 1996; Özkan et al., 2010). The no-fish mesocosm seemed to have less capacities to buffer external nutrient inflows by bulk deposition (Supplement Table 1), because pelagic nutrient stocks increased for both N and P (Figure 2). This nutrient increase favored phytoplankton directly, as seen by increasing Chl *a* (Figure 3), as well as probably epiphytic biomass (Xie et al. 2013). Ultimately, this increasing phytoplankton biomass will result in lower primary production of all compartments (phytoplankton, macrophytes, epiphytes) as seen in lakes (Blindow et al., 2006) and mesocosms (Berthold and Paar 2021).

Fish mesocosm showed lowered turbidity and phytoplankton biomass compared to no-fish mesocosm and the actual ecosystem. These results are surprising at a first glance, as fish occurrence is linked to increased turbidity and phytoplankton biomass in mesocosms and the ecosystem (Stephen et al., 2004; Williams, Moss, & Eaton, 2002). However, the trophic position as well as function of the occurring fish species needs to be considered. Cyprinid fish forage mostly in sediments and thus negatively affect under water light climate (Williams et al. 2002).

Such cyprinids dominate in eutrophic coastal waters of the southern Baltic Sea contrary to similar freshwater systems (Winkler 2002). Sediment foraging has the detrimental effect, as it can possibly release large amounts of stored P in shallow areas of such coastal lagoons (Berthold et al. 2018c). Surprisingly, grazing on copepods and cladocera in our mesocosms decreased nutrient concentrations, phytoplankton biomass and turbidity nonetheless, which is in contrast to findings in freshwater systems (Feuchtmayr et al., 2009; Jakobsen et al., 2004; Stephen et al., 2004). However, there are also other works in freshwater systems, where planktivorous fish had only little effect on grazing control by zooplankton, as phytoplankton grew faster than being grazed upon (Van De Bund et al. 2004, Villena and Romo 2007). Such outcomes can mainly be explained by the additional experimental fertilization, which mainly supports fast-growing or grazing resistant phytoplankton. However, environmental daily nutrient depositional rates are lower than experimentally added nutrient pulses, and usually do not occur in the form of large, pulse-wise perturbations. Instead, the rate of perturbation is important for organisms and ecosystems to buffer press or pulse disturbances (Shade et al. 2012). In the context of our mesocosms, focusing solely on top-down control allowed to study the impact of altered trophic pathways. The stable TN levels in our fish mesocosms were important for macrophyte establishment, as macrophyte stands tend to decline above thresholds of ~100 µmol TN L^{-1} (Barker et al. 2008) or under prolonged eutrophic conditions (Coffin et al. 2018). Likewise, a meta-analysis showed that even though fish abundance can increase TP levels, TN is major driver on macrophyte occurrence in already eutrophic lakes (Feuchtmayr et al. 2009). These findings are in line with our results, as TP increased to ecosystem-levels within fish mesocosms but were not causing increased phytoplankton biomasses. Phytoplankton biomass in this lagoon is probably co-limited for N, as fertilization experiments with P did not yield any growth

response between spring to autumn (Berthold and Schumann 2020). The establishment of macrophytes due to altered nutrient budgets within the water column probably caused several feedback loops. It is assumed that macrophytes can act as particle traps, however these traits were not observed in these coastal waters (Meyer et al. 2019), or other shallow lakes (Vanderstukken et al. 2011). Nonetheless, submerged macrophytes can improve water chemistry by affecting the sediment microbiome (Ciurli et al. 2009, Zhao et al. 2013), which alters organic C decomposition (Sullivan et al. 2006, Gette-Bouvarot et al. 2015), ultimately lowering O_2 respiration in fish mesocosm (Compte et al. 2012). A similar development can also be seen in the areal O_2 production of our mesocosms, with fish mesocosm showing a higher net-production with macrophyte establishment in August (see Supplement Figure 1).

Contrary to the mesocosms, the ecosystem showed different dynamics for dissolved nutrients, and decreasing amounts of total nutrients throughout the growth season. The DZLS shows a residence time of 8 – 61 days (Schiewer, 2007), pointing to a steady loss of nutrients after winter nutrient peaks and spring blooms. Macrophytes tend to occur only in shallow regions of the lagoon system, where light is less limiting. However, those local sub-populations are probably especially adapted to low-light climate (Piepho 2017). Therefore, an increase in light penetration depth would allow submerged macrophytes to reach higher biomasses, creating some feedback loops as mentioned above. The question evolves, why phytoplankton biomass remains at a relatively high level within the ecosystem. One cause can be that grazing control on phytoplankton probably decreases, as phytoplankton biomass stabilizes after day 200. This timeframe is in line with the decrease of rotifers biomass (*Keratella* spp.), probably caused by increasing numbers of copepods (*Eurytemora affinis*, Feike & Heerkloss 2009). It is assumed that copepods can cause a grazing pressure on eggs and adult rotifers (Azémar et al. 2007, Feike

and Heerkloss 2009). Contrary, the increase in rotifers seems to coincide with the constant below average Chl *a* concentrations and turbidity within fish mesocosm, whereas there is an increase of both Chl *a* and turbidity in no-fish mesocosm. It is therefore possible that grazing pressure within the zooplankton group (intra-guild) caused an inefficient grazing pressure on phytoplankton. These complex trophic niches within zooplankton were recently described for the Baltic Sea, and point to an important impact of rotifers and ciliates on the food web (Zamora-Terol et al. 2020, Novotny et al. 2021).

Disrupting the microbial loop: A possible switch to treat eutrophic systems?

An increase of rotifer abundance and even diversity was described in top-down manipulated mesocosms (Hansson et al. 2004, Stephen et al. 2004, Miracle et al. 2007), but their impact on pelagic nutrient flows was never clearly established, probably due to simultaneous experimental overload of the nutrient background. Copepod grazing can cause a trophic cascade by grazing on ciliates, which favors heterotrophic nanoflagellates and lowers bacterioplankton. Bacterioplankton is an effective competitor for nutrients with phytoplankton, if organic C is abundant (Joint et al. 2002). The DZLS shows high levels of particulate (16 mg C L^{-1}) and dissolved (12 mg C L^{-1}) organic C, and bacterial activities (18 µg C h^{-1} L^{-1}, Schumann et al. 2003). Thus, efficient grazing on bacterioplankton may favor phytoplankton in otherwise nutrient-limited systems. Furthermore, rotifers and ciliates have been described to efficiently graze on small particles and filamentous phytoplankton (Zamora-Terol et al. 2020). Especially filamentous cyanobacteria and picocyanobacteria contribute up to 90% of the phytoplankton biovolume in the DZLS (Albrecht et al. 2017, Berthold and Schumann 2020) and the Baltic Sea (Celepli et al. 2017). Indeed, a variety of studies showed that rotifers and other microzooplankton tend to increase with mesopredator presence (Compte et al., 2011; Compte et

al., 2012; Šorf et al., 2015). Furthermore, rotifers seem to be more abundant when nutrients are lower, and temperatures increase (Jeppesen et al. 2007, Šorf et al. 2015). The presence of mesopredator which controlled mesograzer and mesozooplankton should have therefore allowed the microzooplankton to increase its abundance, creating further feedback loops by increasing light penetration depth. This increased light penetration favored macrophytes, which in turn favored even more sessile rotifers among others. A higher amount of macrophytes could potentially allow some biomass to overwinter and create further feedbacks earlier the next year. Contrary, having no grazing pressure on macro- and mesozooplankton did not cause a decrease of phytoplankton biomass, but in conjunction with mesograzer caused a bottom-up control of the ecosystem by releasing more internal nutrients and buffering less external nutrients.

To apply this food web cascade, a temporary change in fishing practices may be an option. For example, an increased fishing quote on top-predators like perch, pike and sander may increase the abundance of gobies and shrimp. Cyprinid fish should be taken into account, too, as their foraging behavior increases turbidity (Williams et al. 2002) and thus lowering macrophyte biomass (Körner and Dugdale 2003). Decreasing turbidity would also improve the sexual selection process of gobies, increasing mating success (Järvenpää and Lindström 2004). An increase of timed catch rates would have the side effect of increasing recreational use of coastal waters (Alberini et al. 2007). Even though recreational fishery only accounts for 3% of total fish catches in the Baltic Sea (Zeller et al. 2011), recreational fishery can catch up to 70% of top-predator like cod in German coastal waters (Strehlow et al. 2012). It is likely that a combination of management options need to be considered (size and catch limits, time slots) to limit the impact on endangered top-predators, like cod (Haase et al. 2022), and focus on other non-threatened top-predator.

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