TESI DOCTORAL

Biotic and environmental factors shaping body size distributions in freshwater planktonic food webs

Zeynep Ersoy

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Escola de Doctorat

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Programa de doctorat: **Experimental Sciences and Technology**

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Nobody said it was easy

No one ever said it would be this hard.

- Coldplay, The Scientist

~~Love~~ Thesis doesn't just sit there, like a stone,

it has to be made, like bread;

remade all the time, made new.

- Ursula K. Le Guin

To my family and Onur

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I met warm people with a welcoming culture and language, good friends and experienced field works, conferences, enjoyable meals, meetings and unforgettable moments.

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ABSTRACT

Individual size-based interactions play a significant role in the community dynamics and ecosystem processes of aquatic ecosystems, because body size is a key trait of organisms that is highly linked to metabolic rates. Climate change and disturbances influence freshwater planktonic food webs, weakening the strength of size-based interactions. Earlier studies mostly focused on alterations in body-size distributions in single trophic levels, but the understanding of size-based interactions among adjacent trophic levels is still limited. Moreover, only a few studies explored the short-term resilience of communities to disturbances. However, evaluation of body size structure of interacting trophic levels simultaneously while accounting for intraspecific variation and understanding resilience of communities would bring novel insights into strength of trophic interactions.

In this thesis, we conducted four related but independent studies to obtain a deeper understanding of the size-based trophic interactions. We aimed to demonstrate biotic and environmental factors influencing size-based interactions in planktonic food webs using different research approaches (e.g. observational and experimental approaches) at different locations: (1) snap-shot sampling of 30 shallow lakes in Turkey along a latitudinal gradient, assessing size-structured predation on prey size structures from fish to phytoplankton, accounting also for the effects of physical factors (e.g. temperature and resource availability); (2) mesocosm experiment in Lake Mývatn, Iceland, testing the effect of fish predation and cyanobacteria blooms on the size structure of lower trophic levels and the energy transfer along the food web; (3) mesocosm experiment in Lake Müggelsee, Berlin, evaluating the effect of fish removal on the resilience of planktonic communities and their cascading effects along the food web; and (4) microcosm experiment in ponds of Empordá Wetlands, Catalonia, assessing the effect of intraspecific variation in zooplankton predators on their prey size structure, and possible consequences for the community functioning.

Overall, our key findings from this thesis can be summarized as follows: 1) In Turkish shallow lakes, we observed positive correspondence between fish and zooplankton size structure in interacting trophic levels, after confounding for the environmental factors such as temperature and resource availability. While phytoplankton size structure was mainly driven by the physical factors such as nutrients and temperature, zooplankton size structure was related to the diversity in predators. 2) In the mesocosm experiment in Lake Mývatn, fish presence caused negative changes in zooplankton size and community structure. However, the increased phytoplankton size diversity due to occurrence of cyanobacteria blooms overrode the fish effects and weakened efficient energy transfer along the food web. 3) Our results from short-term fish predation experiment close to Lake Müggelsee (IGB, Berlin) indicated low resilience in zooplankton communities. Zooplankton community composition shifted, releasing grazing control on phytoplankton in enclosures with fish. 4) In the microcosm experiment in Mediterranean ponds, we found differences in prey (bacterioplankton and phytoplankton) size structure as a result of predation by different developmental stages of zooplankton, indicating possible implications on food web functioning such as energy transfer and food web capacity. This thesis suggests that integrating size-based relationships and resilience of communities together with intraspecific variation is important while studying trophic interactions. Understanding these interactions will allow us to better manage and restore aquatic ecosystems in the face of climate change and other human-induced disturbances.

RESUM (in Catalan)

Les interaccions basades en la mida individual dels organismes tenen un paper important en la dinàmica de la comunitat i en els processos dels ecosistemes aquàtics, ja que la mida d'un individu és un tret clau dels organismes molt vinculat a la seva taxa metabòlica. El canvi climàtic i les pertorbacions afecten a les xarxes tròfiques planctòniques d'aigua dolça, debilitant les interaccions basades en la mida dels individus. Estudis anteriors sobre el tema es centren principalment en l'estudi de les alteracions de les distribucions de mides en un nivell tròfic determinat, però la comprensió de les interaccions basades en la mida dels individus de nivells tròfics adjacents encara és limitada. A més, molt pocs estudis han explorat la resiliència a curt termini de les comunitats a les pertorbacions. Tanmateix, l'avaluació de l'estructura de mides simultània entre nivells tròfics adjacents tenint en compte la variació intraespecífica i entenent la resiliència d'aquestes comunitats portarà nou coneixement sobre la força de les interaccions tròfiques.

En aquesta tesi es van desenvolupar quatre estudis relacionats però independents per obtenir una comprensió més profunda de les interaccions tròfiques basades en la mida individual dels organismes. L'objectiu era demostrar com els factors biòtics i ambientals afecten les interaccions basades en la mida dels individus de xarxes tròfiques planctòniques utilitzant diferents aproximacions (observacionals i experimentals) en diferents localitats: (1) mostreig de 30 llacs poc profunds de Turquia distribuïts al voltant d'un gradient latitudinal per avaluar com l'estructura de mides dels depredadors afecta l'estructura de mides de les preses, tenint en compte els efectes de factors físics com la temperatura o la disponibilitat de recursos; (2) experiment de mesocosmos al Llac Mývatn, Islàndia, per testar l'efecte de la depredació (de peixos) i els blooms de cianofícies en l'estructura de mides de nivells tròfics més baixos i de la transferència d'energia al llarg de la xarxa tròfica; (3) experiment de mesocosmos al Llac Müggelsee, Berlin-Alemanya, per determinar l'efecte de l'eliminació de peixos en la resiliència de les comunitats planctòniques i els seus efectes en cascada a la resta de la xarxa tròfica; i (4) experiment de microcosmos a llacunes dels Aiguamolls de l'Empordà per avaluar l'efecte de la variació intraespecífica de depredadors de zooplàncton en l'estructura de

mides de les seves preses, i les possibles conseqüències per al funcionament de la comunitat.

Generalitzant, les nostres troballes clau d'aquesta tesi es poden resumir de la manera següent: 1) Vam observar una correspondència positiva entre l'estructura de mides de nivells tròfics interactuants com són els peixos i el zooplàncton en llacs somers turcs, després de considerar factors ambientals com la temperatura i la disponibilitat de recursos. Mentre que l'estructura de mides del fitoplàncton estava principalment impulsada per factors físics (nutrients i temperatura), l'estructura de mides del zooplàncton estava relacionada amb la diversitat de depredadors. 2) En els experiments de mesocosmos al Llac Mývatn, la presència de peixos va provocar canvis negatius en la mida del zooplàncton i l'estructura de la comunitat. Tanmateix, un augment posterior de la diversitat de fitoplàncton a causa de l'aparició d'un bloom de cianofícies va sobrepassar els efectes dels peixos i va afeblir la transferència d'energia al llarg de la xarxa tròfica. 3) Els experiments de depredació de peixos a curt termini al costat del Llac Müggelsee (IGB, Berlin) van mostrar la baixa resiliència de les comunitats de zooplàncton, amb canvis en la composició de la comunitat que van produir un alliberament en el control que exerceix el zooplàncton en el fitoplàncton. 4) Els experiments a les llacunes mediterrànies dels Aiguamolls de l'Empordà van mostrar diferències en l'estructura de mides de les preses (bacterioplàncton i fitoplàncton) com a resultat de la depredació per part de diferents estadis de desenvolupament del zooplàncton, indicant possibles implicacions en el funcionament de la xarxa tròfica (com transferència d'energia i capacitat de la xarxa tròfica). Aquesta tesi ressalta la importància d'integrar les relacions basades en la mida dels organismes i la resiliència de les comunitats amb la variació intraespecífica dels organismes a l'hora d'estudiar les interaccions tròfiques entre els organismes d'un ecosistema aquàtic. La comprensió d'aquestes interaccions ens permetrà gestionar i restaurar millor els ecosistemes aquàtics davant el canvi climàtic i altres pertorbacions induïdes per l'home.

LIST OF CHAPTERS

This thesis is composed of 4 chapters and each of them contributed to articles to be published in scientific journals:

Chapter 1

Brucet, S., Tavşanoğlu, U.N., Özen, A., Levi, E., Bezirci, G., Çakıroğlu, A.İ., Jeppesen, E., Svenning, J.C., **Ersoy, Z.**, Beklioğlu, M. 2017. Size-based interactions across trophic levels of food webs in shallow Mediterranean lakes, *Freshwater Biology*, 62, 1819-1830, doi: 10.1111/fwb.12997

SB and MB developed the idea. All other authors contributed to the sampling and laboratory work. SB, UNT and ZE did the statistical analyses. SB wrote the first draft. All authors contributed to the final version and revisions.

Chapter 2

Ersoy, Z., Jeppesen, E., Sgarzi, S., Arranz, I., Cañedo-Argüelles, M., Quintana, X.D., Landkildehus, F., Lauridsen, T.L., Bartrons, M., Brucet, S. Size-based interactions and trophic transfer efficiency are modified by fish predation and cyanobacteria blooms in Lake Mývatn, Iceland. 2017. *Freshwater Biology*, 62, 1942-1952*,* doi: 10.1111/fwb.13039

ZE, EJ and SB developed the idea. All other authors contributed to the conduction of the experiment, sampling and processing of the samples. ZE organized the dataset, calculated all metrics and conducted all statistical analyses. ZE wrote the first draft. All authors contributed to the final version and revisions.

Chapter 3

Ersoy, Z., Bartrons, M., Mehner, T., Brucet, S. Short-term fish predation destroys resilience of zooplankton communities and destroys recovery of phytoplankton control by zooplankton grazing. In review, PLoS ONE.

ZE, MB, TM and SB developed the idea. ZE and MB conducted the experiment. ZE processed all samples and conducted all statistical analyses. ZE wrote the first draft. All authors contributed to the final version.

Chapter 4

Ersoy, Z., Brucet, S. Intraspecific variation in zooplankton predation affects phytoplankton community size structure. Submitted to Hydrobiologia.

SB conducted the experiment. SB and ZE developed the idea. ZE conducted all statistical analyses and wrote the first draft. All authors contributed to the final version.

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GENERAL INTRODUCTION

Trophic interactions in aquatic food webs

Organisms interact with each other and the environment around them. They can compete for resources, predate on each other (i.e. cannibalism) or on other preys, altering the dynamics of aquatic ecosystems. The study of these trophic interactions has been an important topic in food web ecology since early 1940s (Lindeman, 1942). Later, several studies contributed to the knowledge on consumer-resource interactions in aquatic ecosystems (Carpenter, Kitchell, & Hodgson, 1985; Pace, Cole, Carpenter, & Kitchell, 1999; Polis, Sears, Huxel, Strong, & Maron, 2000). These interactions in the food web can be controlled through predation (top-down) and resource availability (bottom-up) (Jeppesen et al., 1997; Polis et al., 2000). However, the relative contribution of top-down and bottom-up controls has been still intensively debated. Trophic cascades illustrate top-down control properly. A trophic cascade can be defined as an indirect positive impact of a predator on the lower trophic level such as primary producers. For instance, planktivorous fish predation on zooplankton could release zooplankton grazing on phytoplankton and therefore favor phytoplankton growth (Pace et al., 1999). However, bottom-up controls imply the modification of interactions depending on nutrient availability in the system (Figure 1).

Several approaches exist to study trophic interactions, from taxon-based to trait-based approaches. Many studies examined interactions between organisms and their effects on community structure, abundance and biomass using taxon-based approach which considers species identity rather than their functional roles in the community (Carpenter, 1987; Jeppesen, Jensen, & Søndergaard, 2002; Polis et al., 2000). Nonetheless, not many studies have focused on community structure based on individual sizes, although individuals within communities differ in terms of body size, and ontogenetic stage, especially in aquatic ecosystems due to indeterminate growth (Brose, Jonsson, et al., 2006; Trebilco, Baum, Salomon, & Dulvy, 2013). This fact results in size-structured communities, that differ in their size-specific life history characteristics (e.g. feeding, growth, mortality). All these size-related differences could modify trophic interactions along the food web. Therefore, further research on size-based approaches is required for understanding of complex trophic interactions.

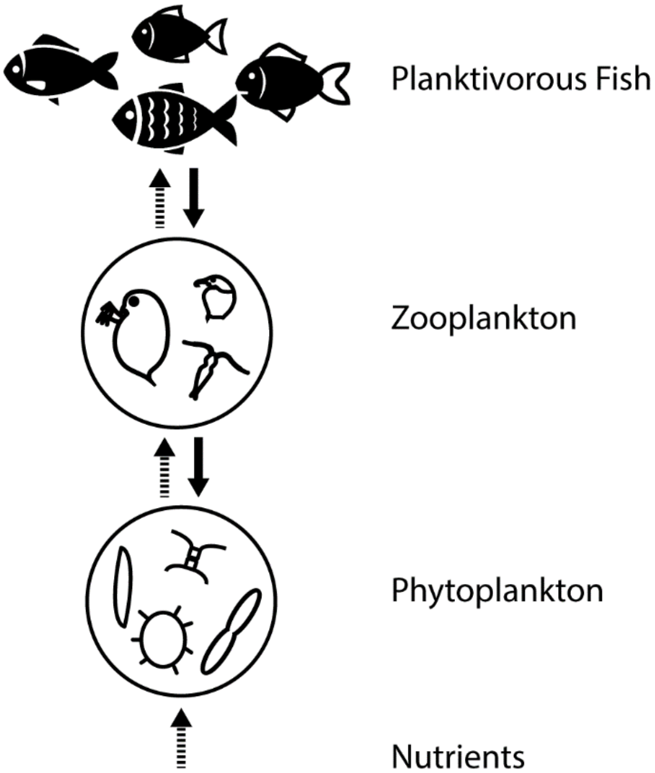


Figure 1. Example of a tri-trophic level food web. First trophic level: primary producers (i.e. phytoplankton), second trophic level: primary consumers (i.e. zooplankton), third trophic level: secondary consumers (i.e. planktivorous fish). Solid arrows indicate top-down control (e.g. predation, grazing) on the lower trophic level. Dashed arrows indicate bottom-up control (e.g. nutrient uptake). Change in abundance, biomass or size in one trophic level has an effect on the adjacent trophic level(s). For example, high fish predation can decrease zooplankton abundance and body size.

Role of body size in trophic interactions of aquatic ecosystems

Body size is one of the key traits of all organisms. It is highly linked to metabolic rates, such as growth, reproduction and population growth rates (Calder, 1984; Robert Henry Peters, 1983) and thus provides important biological and ecological information (White, Ernest, Kerkhoff, & Enquist, 2007). Changes in body size structure (Figure 2) could inform about predator-prey interactions, population dynamics, nutrient cycling, and trophic energy transfer in food webs (Brose, Jonsson, et al., 2006; Sommer, Peter, Genitsaris, & Moustaka-Gouni, 2017; Woodward et al., 2005). The underlying links between organisms' body size and these ecosystem processes can be quantitatively predicted by the Metabolic Theory of Ecology (MTE) (Brown, Gillooly, Allen, Savage, & West, 2004). According to MTE, metabolic rates of organisms and ecological processes scale with body size and temperature. Predator-prey interactions between the organisms link individual metabolism to communities and ecosystems through energy flow in the food web (Trebilco et al., 2013).

Earlier studies revealed the relationship between the size structure of prey and predators and trophic transfer efficiency (TTE) (Barnes, Maxwell, Reuman, & Jennings, 2010; Jennings, Warr, & Mackinson, 2002). Trophic transfer efficiency (TTE) reflects how efficient energy (i.e. biomass, production) is transferred from one trophic level to upper trophic levels. It was first explained by Lindeman (1942) as total production ratios between adjacent trophic levels. A recent study in a marine ecosystem has shown contrasting effects of prey (phytoplankton) and predator (zooplankton) size diversity on TTE, that is, high predator size diversity facilitated TTE, while high prey size diversity decreased it (García-Comas et al., 2016). This study is one of the first assessing the consequences for body size structure across interacting trophic levels (García-Comas et al., 2016). More work on such studies may be very promising to understand the strength of interactions across all trophic levels (Brose et al., 2016; Trebilco et al., 2013).

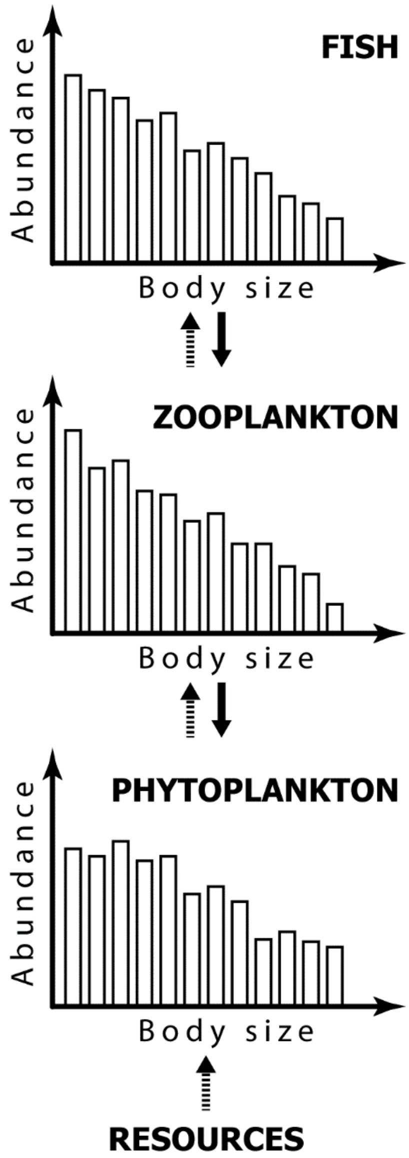


Figure 2. Conceptual scheme simplifying size-based interactions from fish to phytoplankton in tri-trophic level food web. Solid arrows indicate top-down control (e.g. predation, grazing) on the lower trophic level. Dashed arrows indicate bottom-up control (e.g. nutrient uptake). Graphs for each trophic level show body size distributions. Predators with a certain size in one trophic level can feed on a certain range of preys in the lower trophic level, affecting size structure of the food web.

The community size structure also responds to environmental changes such as flooding, climate warming and land use intensity (Brucet, Boix, López-Flores, Badosa, Moreno-Amich, et al., 2005; Emmrich, Brucet, Ritterbusch, & Mehner, 2011; Woodward, Perkins, & Brown, 2010), thus has several applications in terms of conservation and management (Trebilco et al., 2013). All these findings make body size as valuable and informative measure as species for understanding trophic interactions and ecosystem functioning (Woodward et al., 2005). Moreover, it could provide a good measure of biodiversity in aquatic ecosystems (Brucet et al., 2017; Brucet, Boix, López-Flores, Badosa, & Quintana, 2006). Taxonomic identification does not give much information about the organisms functions' in the ecosystems, whereas body size predicts well the functional relatedness in terms of niche, diet and growth. Because measurement of biodiversity indices is dependent on taxonomic expertise, sized-based approaches are good alternatives to traditional biodiversity indices and also can potentially complement the taxon-based approaches.

Size-based indices

Several size-based indices have been developed to understand the patterns in body size structure in aquatic ecosystems:

1. Mean body size

Mean body size is calculated as geometric or arithmetic mean of individuals of the same species. Mean body size is a simple and basic measure to understand body size structure. Several studies (Brucet et al., 2010; Emmrich et al., 2014; Gardner, Peters, Kearney, Joseph, & Heinsohn, 2011) have shown that it varies significantly with biotic and environmental changes. However, it does not have the ability to integrate the variability in the body size distributions.

2. Size spectrum

In 1972, Sheldon and his colleagues developed the idea of the biomass size spectrum, one of the first sized-based approaches where they related biomass with body sizes of microorganisms from oceans and explored underlying trophic interactions. Biomass size spectrum predicts a linear decrease in abundance with body size in log-log scale (mostly in $\log_2$ or $\log_{10}$)(Platt & Denman, 1978). This approach was initially used for plankton (Sprules & Munawar, 1986). Later on, similar relationships between organisms' biomass and size were observed for other groups such as fish and macroinvertebrates (Kerr & Dickie, 2001; Rochet & Trenkel, 2003; Sweeting, Badalamenti, D'Anna, Pipitone, & Polunin, 2009).

Normalized biomass spectra (NBS) was developed as an alternative to biomass size spectra (Platt & Denman, 1978). It is constructed by dividing biomass in each size class interval to the linear width of the interval. Normalization allows comparison of spectra from different studies which have different logarithmic scales, because the width of the logarithmic size class intervals increases as body size classes increase (Sprules & Barth, 2016 and references therein). The normalized abundance spectrum (i.e. individual size distribution) gives a linear relationship between normalized numerical abundance of individuals and size classes (White et al., 2007) (Figure 3). Linear slopes of -1 and -2 are very common for normalized biomass and abundance spectra, respectively (Sprules & Barth, 2016).

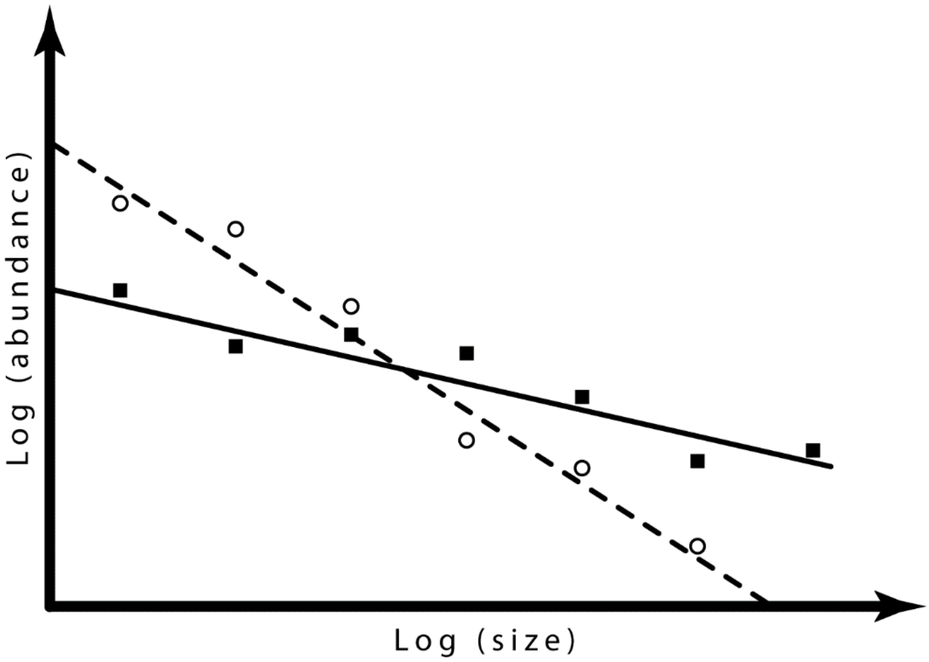


Figure 3. Size spectrum example from two different communities with different body size distributions. The solid line shows the community that is dominated by large-sized individuals (flatter slope); while the dashed line shows the one with higher abundance of small-sized individuals (steeper slope).

One of the most important parameters of the size spectrum is the slope. It represents the relative contribution of different sized individuals and thus provides an understanding of the patterns in body size distribution. It can be used to make an estimate of predation pressure or fishing intensity (Blanchard et al., 2005; Zimmer, Hanson, Butler, & Duffy, 2001). For instance, if the slope is steeper, it indicates high relative abundance of small-sized individuals in the community, where large-sized individuals were strongly predated (Emmrich et al., 2011). Moreover, it could inform about the food availability where steeper slopes indicate decreased food availability for large size classes (Zhou, 2006). The slope of the body size spectrum can also be an estimator of trophic transfer efficiency (Kerr & Dickie, 2001; Mehner et al., 2018). Steeper slope indicates lower efficiency in energy transfer through the food web to larger organisms (Benejam, Tobes, Brucet, & Miranda, 2018; Dossena et al., 2012).

Intercept of size spectra is used to estimate productivity potential and food web capacity (Gaedke, 1993; Sprules & Munawar, 1986). Thus, systems with high productivity are more likely to have higher intercepts and flatter slopes (Finlay, Beisner, Patoine, & Pinel-Alloul, 2007; Zhang et al., 2013). Another parameter of the spectrum is R^2 (coefficient of determination of the regression), which is a index of stability (García-Comas et al., 2014). Variations in the linearity may explain how much the observed spectrum deviates from the fitted spectrum under steady state conditions (Chang et al., 2014). These variations can result from the appearance of secondary structures that occur due to complex trophic links such as intraguild predation (Chang et al., 2014). Furthermore, a recent study by Arranz, Hsieh, Mehner, & Brucet (2018) has shown that these deviations from linearity may inform about alterations in predator-prey interactions due to environmental disturbances such as fishing pressure and eutrophication.

3. Size diversity (μ)

Size diversity is a single measure that is based on Shannon-Wiener diversity index for continuous variables (Pielou, 1969). It is calculated by using the individual size measurements of organisms with non-parametric kernel estimations as probability density functions (Quintana et al., 2008, 2016). It is calculated by following the equation:

$$\mu = -\int_{0}^{+\infty} p_X(x) log_2 p_X(x)\, dx$$

where $p_x(x)$ is the probability density function of size x.

It gives information about size range (i.e. variability) and evenness (i.e. regularity) of the body size distributions as Shannon-Wiener diversity index combines the number of individuals and relative abundance (Brucet et al., 2010, 2006; Quintana et al., 2008).

For instance, high size diversity indicates a wide size range and even representation of the different sizes along the size distribution (Emmrich et al., 2011). In highly dynamic systems with non-linear size spectrum, size diveristy is a better indicator than slope of the size spectrum (García-Comas et al., 2014). Size diversity also has the ability to capture information about intraspecific variability (Brucet et al., 2018), which is a highly important variable to be considered in eco-evolutionary studies.

4. Size evenness (J_e)

While size diversity index is about regularity and variability in the body size distributions, size evenness index represents regularity (Quintana et al., 2016). Size evenness index is practical to understand changes in size diversity irrespective of the size range. It is calculated by dividing the exponential of the size diversity by its possible maximum for a given size range following the formula:

$$J_e(\mathrm{X}) = \frac{\exp\big(\mu(X)\big)}{\exp\big(\mu(LN)\big)}, 0 \leq J_e(\mathrm{X}) \leq 1$$

where $\mu(LN)$ is size diversity of Log-Normal distribution.

Both size diversity and size evenness indices have many advantages over other size metrics. The use of diversity and evenness terms in ecology makes their interpretation very clear. They are easy to calculate and do not involve statistical fitting as body size spectrum. Moreover, they can be compared across organisms or studies because they are scale invariant (Quintana et al., 2008, 2016).

Factors affecting size-based interactions in planktonic food webs

So far, most studies explored modifications in size structure of each trophic level individually and their consequences in the ecosystem functioning. Nonetheless, distinct trophic levels can be influenced differently by a variety of biotic and environmental factors, which could influence overall patterns in the food web functioning. Consumer-resource relationships are central in shaping prey community and their size structure.

For instance, size-selective fish predation can have a negative effect on prey abundance, mean size and size diversity, resulting in community dominated by smaller individuals and few large individuals (Brooks & Dodson, 1965; Brucet et al., 2010; Quintana et al., 2015; Ye, Chang, García-Comas, Gong, & Hsieh, 2013). On the other hand, large-sized individuals can have advantages over small-sized individuals for avoiding predation due to their resistance to grazing (Arim, Abades, Laufer, Loureiro, & Marquet, 2010; Ger, Urrutia-Cordero, et al., 2016). High resource availability (i.e. productivity) is another cause of the increase in large-sized phytoplankton (Downing, Watson, & McCauley, 2001). In contrast, low resource availability favors small-sized algae which are better at nutrient uptake (Finkel et al., 2010). At the same time, low resource availability could increase size diversity in fish and zooplankton communities because of stronger competitive interactions (Arranz et al., 2016; Quintana et al., 2015). In this way, organisms can avoid competitive exclusion and better exploit low resources because they diversify into different sizes, thus feeding niches (i.e. niche partitioning).

Another factor affecting these predator-prey interactions is intraspecific trait variation. Darwin was one of the earliest ecologists recognizing individual differences in same species such as age, size, shape and behavior, which forms the foundation of natural selection and evolutionary biology (Bolnick et al., 2011). Most of this variation comes from changes in body size during the developmental stages of organisms (Miller & Rudolf, 2011). Several organisms in aquatic ecosystems experience ontogenetic shifts and change size and diet during their lifetime, which can modify competitive and predatory networks and consequences for trophic cascades (Bolnick et al., 2011; Violle et al., 2012). For example, Rudolf & Rasmussen (2013) showed that stage-specific roles of aquatic macroinvertebrates resulted in changes in community structure. Therefore, differences in ecosystem processes such as net ecosystem production and respiration were observed. Similar developmental changes can be observed in certain groups of zooplankton, which are located in a fundamental position in the food web (i.e. sandwiched in-between phytoplankton and fish) (Jeppesen et al., 2011) and thus have significant roles in cascading trophic interactions. Several studies have focused on these effects of intraspecific variation in zooplankton with different traits ranging from resource use, feeding and amino acid composition (Berggren, Bergström, & Karlsson, 2015; Brucet, Boix, López-Flores, Badosa, & Quintana, 2005; Brucet, Compte, Boix, López-Flores, & Quintana, 2008). However, to our knowledge changes in their prey size spectra due to intraspecific variation in predation of different developmental stages have not been explored yet. Considering that these effects on prey size spectra can allow us to understand the consequences of disregarding intraspecific variability while studying trophic interactions.

In addition to consumer-resource interactions and intraspecific variability, temperature could also influence the size structure because individual size is directly related to metabolic rates and growth of individuals (Brown et al., 2004). Evidence from field experiments and model predictions suggest that communities are altered and dominated by smaller individuals when temperature increases (Daufresne, Lengfellner, & Sommer, 2009; Gardner et al., 2011), following the temperature-size rule (Atkinson, 1994). For instance, in fish communities, the relative abundance of smaller fish is predicted to be higher with climate warming as a result of higher and earlier reproduction, and faster growth rate (Jeppesen et al., 2010). As a result, greater fish predation pressure with climate warming could cause stronger top-down controls, which cascades down the food web and changes ecosystem production (Jeppesen et al., 2010, 2014). Phytoplankton communities display a similar response to higher temperature, as smaller individuals increase at warmer temperatures (Morán, López-Urrutia, Calvo-Díaz, & Li, 2010; Sommer et al., 2017; Yvon-Durocher, Montoya, Trimmer, & Woodward, 2011). This change in size distribution is highly related to greater metabolic rates and nutrient uptake rates of small phytoplankton in warmer conditions (Litchman, Klausmeier, Schofield, & Falkowski, 2007) as predicted by the MTE (Brown et al., 2004). Consequently, with increased demand for resources, smaller sized individuals perform better and obtain a competitive advantage over larger ones (Winder, Reuter, & Schladow, 2009) due to their high surface area to volume ratio and high growth rates (Litchman, de Tezanos Pinto, Klausmeier, Thomas, & Yoshiyama, 2010). At the same time, occurrence of large inedible phytoplankton taxa with filaments or colonies (e.g. Cyanobacteria) are also related to higher temperatures (Paerl & Huisman, 2008).

Overall, size-based relations in the food web are complex and are controlled by several different factors at varying trophic levels. Deeper understanding of these factors and corresponding changes is necessary to identify the strength of size-based trophic interactions (Brose et al., 2016).

Resilience to environmental disturbances in size-based interactions of planktonic food webs

Aquatic ecosystems are facing anthropogenic disturbances, such as pollution, climate warming, invasive species intrusion, fish stocking and habitat disruption at an unprecedented level, which have consequences on community and size-based trophic interactions. Therefore, with several factors affecting size-based interactions across different trophic levels, the need for assessing their ability to return to pre-disturbance state (i.e. resilience, Pimm, 1991) arises.

Earlier studies found evidence of changes in size-based trophic interactions as a result of environmental disturbances such as changes in land-use, impacts of hydropower plants, fishing pressure, fish stocking and human-induced climate warming (Arranz et al., 2018; Benejam, Saura-Mas, et al., 2016; Brucet et al., 2013). In this thesis, we focus on the effects of high fish predation (i.e. disturbance) on resilience of zooplankton community and size structure. We expect to observe a high abundance of small-sized fish as temperatures increase (Brucet et al., 2013; Jeppesen et al., 2010, 2014), because of the metabolic constraints (explained above in MTE). Additionally, fish stocking can also cause high fish predation pressure. Fish stocking is a common problem in most of the naturally fishless mountain lakes, which could have severe consequences on the other food web components such as zooplankton, macroinvertebrates etc. (Knapp, Matthews, & Sarnelle, 2001; Schabetsberger, Luger, Drozdowski, & Jagsch, 2009). Thus, in warmer future, stronger fish predation could create decreased top-down control of phytoplankton with consequences on the quality of aquatic ecosystems (Brucet et al., 2013; Jeppesen et al., 2010). Identifying resilience in zooplankton communities and cascading size-based trophic interactions to fish predation disturbance is therefore necessary for management and restoration purposes.

OBJECTIVES

The main objective of this thesis was to evaluate biotic and environmental factors shaping body size distributions and thus community structures in planktonic food webs of shallow lakes and ponds. Here, we focused on tri-trophic food web, which is composed of primary producers (i.e. phytoplankton), primary (i.e. zooplankton) and secondary consumers (i.e. planktivorous fish). We aimed to determine the effects of consumer-resource dynamics, intraspecific variation and environmental factors on size-based trophic interactions. We further investigated the relationship between body size distributions and trophic energy transfer along the food web, and resilience of aquatic communities to disturbances of high fish predation. We wanted to answer these key questions in the following chapters using different study approaches:

- ✓ How does size-structured predation affect prey size structure across interacting trophic levels (fish, zooplankton, phytoplankton)? How do confounding factors such as resource availability and temperature influence body size distributions across trophic levels and interact with predation effects? (Chapter 1)

- ✓ How do size-based interactions among individuals affect top-down and bottom-up processes on the planktonic food web, and trophic transfer efficiency (TTE)? (Chapter 2)
- ✓ How resilient zooplankton community is to short-term fish predation from a taxonomical and size-based perspective? How does this effect of resilience cascade down to the food web? (Chapter 3)
- ✓ How does intraspecific variation in zooplankton predation affect their prey (bacterioplankton and phytoplankton) size structure in Mediterranean ponds? (Chapter 4)

STUDY APPROACH

Observational and experimental studies as tools in determining size-based interactions of planktonic food webs

There are different research approaches to study the ecology of aquatic ecosystems, from observational (e.g. snapshot sampling, monitoring), experimental (e.g. in-situ, laboratory) to modelling. While observational studies aim at identifying existing relationships without any manipulation, experimental ones focus on the responses of systems to previously defined manipulations. For example, snapshot sampling is sampling of several locations at the same period according to a standard protocol. When combined with space-for-time substitution (SFTS) approach, observational studies could allow high spatial resolution for investigating macroecological concepts. This approach has been used in many studies to compare similar ecosystems in different climatic regions (Gyllström et al., 2005; Jeppesen et al., 2014; Kosten et al., 2009). It strengthens the inference and predictive power of the studies, because it allows identifying long-term changes by using spatial gradients as a measure of time. Nonetheless, still local geology, biogeography and land use differences could be disregarded in this approach (Jeppesen et al., 2014; Meerhoff et al., 2012) .

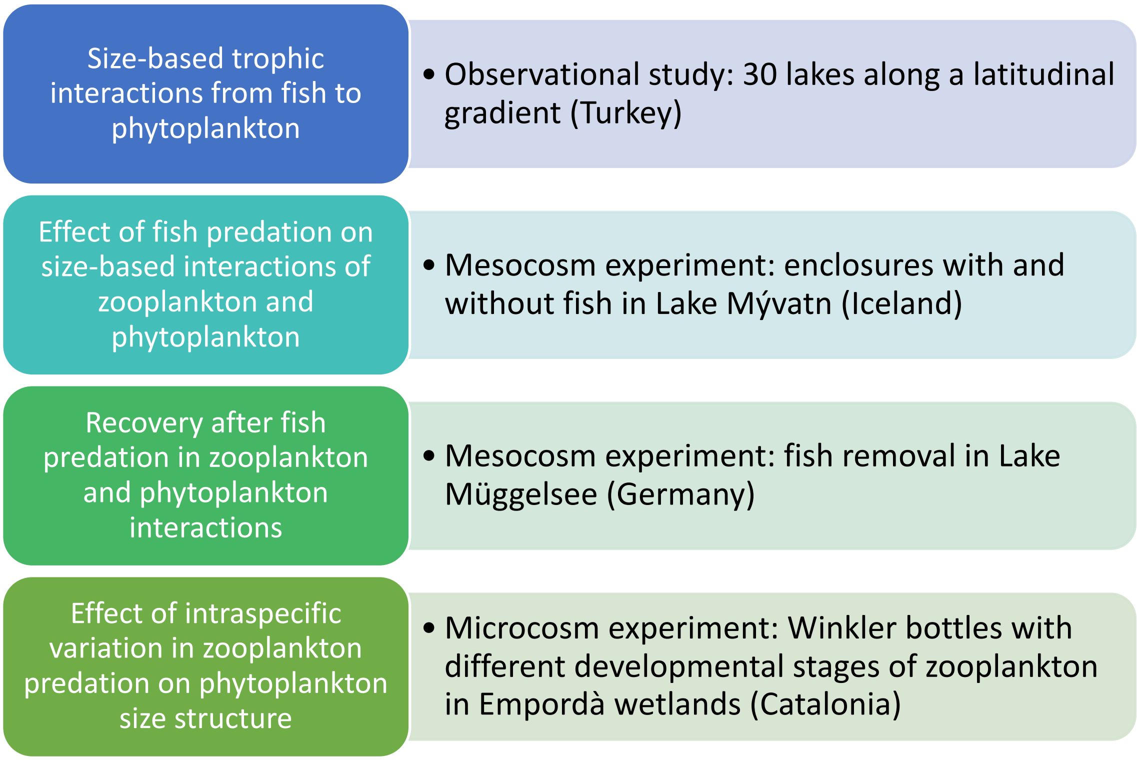
Experiments can vary in scale from micro to meso and also in location from in-situ (i.e. field) to laboratory. They allow us to manipulate controlled systems that mimic natural conditions and observe causal relationships (O’Gorman et al., 2012). They have many advantages, as they facilitate replication, investigate complex ecosystem mechanisms that otherwise would be difficult to observe in nature. Although some argue that experimental studies are reliable for studying short-term responses of ecosystems in small scale (Benincá et al., 2008; Stewart et al., 2013), there are some studies showing long-term responses ranging from 1 year up to 20 years (Olsen et al., 2015; Sistla et al., 2013). However, to what extent these experimental results represent real, natural ecosystems has been debated (Schindler, 1998; Yvon-Durocher, Jones, Trimmer, Woodward, & Montoya, 2010).

Each of these research approaches has their own advantages and weaknesses. Therefore, single approaches are not enough to identify fully the complex patterns in ecosystems. Data from experiments, observations and models should be combined for full comprehension of the complex relations of nature (Woodward et al., 2010). Different methods together could be more powerful and fill the deficiency in one another to predict better the ecological patterns.

In this thesis, to answer our key questions (explained above) we used a mix of observational and experimental approaches mostly in shallow lakes and ponds around the world (explained below).

STUDY AREA & EXPERIMENTAL SET-UP

This thesis is composed data from snapshot sampling of 30 lakes and field experiments in different parts of the world, involving different climates from polar, temperate to arid (Figure 4).



Size-based trophic interactions from fish to phytoplankton	• Observational study: 30 lakes along a latitudinal gradient (Turkey)
Effect of fish predation on size-based interactions of zooplankton and phytoplankton	• Mesocosm experiment: enclosures with and without fish in Lake Mývatn (Iceland)
Recovery after fish predation in zooplankton and phytoplankton interactions	• Mesocosm experiment: fish removal in Lake Müggelsee (Germany)
Effect of intraspecific variation in zooplankton predation on phytoplankton size structure	• Microcosm experiment: Winkler bottles with different developmental stages of zooplankton in Empordà wetlands (Catalonia)

Figure 4. Objectives and methodology of each chapter of the thesis.

In the first chapter, we focused on the size-based interactions in aquatic food webs of 30 shallow lakes from Turkey (41°520N, 27°580E- 37°060N, 29°360E). The lakes were sampled once during summer between 2007-2010 using standardized methods with snapshot sampling and using spatial gradient. Sampling sites spanned 5° latitudinal gradient, encompassing two different climate zones from the semiarid to warm temperate subhumid. They also had high variations in terms of physical and chemical parameters.

In the second chapter, we conducted a field mesocosm experiment in Lake Mývatn, north-east Iceland (65°400N, 17°000W, 277 m a.s.l.) to investigate the effect of fish predation on size-based interactions in the planktonic food web. Although most Arctic and sub-Arctic lakes are oligotrophic and have simple food webs (Hobson & Welch, 1995), Lake Mývatn is a naturally eutrophic sub-Arctic lake, with high loading of nutrients from past and present volcanic areas (Einarsson, 2004). Consumer-resource interactions of zoobenthos, fish and algae play an important role in the nutrient dynamics of the lake. We chose Lake Mývatn to observe how fish would influence trophic interactions in these cold and eutrophic lake with simple food web structures.

In the third chapter, we conducted a field mesocosm experiment consisting of 12 enclosures (8 with fish, 4 without fish) to assess recovery of zooplankton community after short-term fish predation. The experiment was established inside a small channel connected to Lake Müggelsee at the IGB's ground in Berlin, east Germany (52°26'53.1"N 13°38'52.7"E).

In the fourth chapter, we used a dataset from (Brucet et al., 2008), which is an in-situ feeding experiment of different developmental stages (i.e. nauplii, copepodite and adult) of a calanoid copepod. The experiment was composed of 20 Winker bottles with four treatments (3 for each developmental stage + control), each replicated five times. The experiment was conducted in the Mediterranean shallow lagoons of Empordà Wetlands Natural Park (NE Spain). The zooplankton communities of these wetlands are often dominated by single species. Therefore, intraspecific variation in predation could play an important role in determining trophic interactions. Using this dataset, we focused on the effect of intraspecific variations in predation of different developmental stages of a calanoid copepod on their prey (bacterioplankton and phytoplankton) size structure.

CHAPTER 1

Size-based interactions across trophic levels of the food web in shallow Mediterranean lakes

Brucet, S., Tavşanoğlu, U.N., Özen, A., Levi, E., Bezirci, G., Çakıroğlu, A.İ., Jeppesen, E., Svenning, J.C., **Ersoy, Z**., Beklioğlu, M. *Freshwater Biology* (2017), 62, 1819-1830.

Abstract

Body size is a key trait of an organism which determines the dynamics of predator–prey interactions. Most empirical studies on the individual size distribution of the aquatic community have focused on the variations in body size of a single trophic level as a response to certain environmental variables or biotic factors. Few studies, however, have evaluated how individual size structure is altered simultaneously across interacting trophic levels and locations. Such comparative examinations of the size distribution in predator and prey communities may bring insight into the strength of the interactions between adjacent trophic levels.

We assessed the potential predation effect of size-structured predators (i.e. predation by individuals of different sizes) on prey size structure using data from 30 shallow Turkish lakes spanning over five latitudinal degrees. We correlated size diversity and size evenness of predator and prey assemblages across the planktonic food web after accounting for the confounding effects of temperature and resource availability. We expected to find a negative relationship between size diversity of predators and prey due to the enhanced strength of top-down control with increasing predator size diversity. We also hypothesised that competitive interactions for resources in less productive systems would promote a higher size diversity. We further expected a shift towards reduced size diversity and evenness at high temperatures.

In contrast to our hypothesis, we found a positive correlation between size structures of two interacting trophic levels of the planktonic food web; thus, highly size-diverse fish assemblages were associated with highly size-diverse zooplankton assemblages. The size evenness of fish and phytoplankton assemblages were negatively and positively related to temperature, respectively. Phytoplankton size diversity was only weakly predicted by the resource availability.

Our results suggest that size structure within a trophic group may be controlled by the size structure at adjacent trophic levels, as well as by temperature and resource availability. The positive relationship between the size diversity of fish and zooplankton suggests that higher diversity of the resources drives a higher size diversity of consumers or vice versa, and these effects are beyond those mediated by taxonomic diversity. In contrast, the size diversity and size evenness of phytoplankton are mainly influenced by physical factors in this region and perhaps in warm shallow lakes in general.

Keywords: fish, phytoplankton, predator-prey interactions, size diversity, zooplankton

Introduction

Body size is one of the most important traits of an organism because it is related to biological rates, such as growth, respiration, mortality (Brown et al., 2004; Robert Henry Peters, 1983), and population abundance (Brown et al., 2004); and it also determines the dynamics of predator–prey interactions and the resilience of the food webs (Arim et al., 2010; Brose, Williams, & Martinez, 2006; De Roos & Persson, 2002). Accordingly, variations in size structure may affect ecosystem functioning (Brose et al., 2012; Petchey, McPhearson, Casey, & Morin, 1999; Rudolf, 2012).

It is well known that size-selective predation has strong effects on the size structure of prey communities (Brooks & Dodson, 1965; Brucet et al., 2010; Jonsson, Cohen, & Carpenter, 2005; Zimmer et al., 2001). However, empirical research including simultaneous evaluation of individual size structures across interacting trophic levels and locations (Brose, Jonsson, et al., 2006; García-Comas et al., 2016) is limited, probably because equally well-resolved size data comprising the entire food web are scarce (Woodward et al., 2005) and because the statistical fitting of the size distribution may be complicated by the appearance of non-linear relationships (e.g. Mehner et al., 2016; Vidondo, Prairie, Blanco, & Duarte, 1997). As a result, the effects of size-structured predation (i.e. predation by individuals of different sizes) on the individual size structure of prey are poorly understood (Brose, Jonsson, et al., 2006; García-Comas et al., 2016; Mehner et al., 2016; Rudolf, 2012). Comparative examination of the distribution of abundance among body sizes in predator and prey communities may bring insight into the strength of the interactions between adjacent trophic levels (Brose et al., 2016; Brose, Jonsson, et al., 2006; Mehner et al., 2016; Trebilco et al., 2013) and into the biomass transfer through the food web (García-Comas et al., 2016). For example, recent studies have shown that the altered size structure of predator populations induced by climate change can leave predators incapable of controlling prey size distribution, ultimately causing an allometrically induced trophic cascade, which affects ecosystem functioning (Brose et al., 2016; Jochum, Schneider, Crowe, Brose, & O'Gorman, 2012).

In this study, we provide a broad picture of the size distribution across interacting trophic levels of the planktonic food web (fish, zooplankton, and phytoplankton) in 30 warm water lakes by using two synthetic measures of size distribution: the size diversity and size evenness indices (Brucet et al., 2006; Quintana et al., 2008, 2016). Size diversity is based on the Shannon-Wiener diversity index (Pielou, 1969) and integrates the amplitude of the size (either weight or length) range and the relative abundance of the different sizes in the same way as Shannon species diversity integrates the number of species and their relative abundance. Both variability and regularity of the distribution of size data contribute to size diversity, and the size evenness index accounts for the regularity (i.e. shape of the size distribution; Quintana et al., 2016). In contrast to the traditional biomass size spectrum (Kerr & Dickie, 2001), size diversity and size evenness indices have the advantage that they do not require statistical fitting (thus, their estimates are insensitive to the strength of model fit). Furthermore, both indices are scale invariant and comparable for any type of distribution (Quintana et al., 2008, 2016), which may facilitate comparative inspection of the distribution of abundance among body sizes at interacting trophic levels. Previous studies showed that the size diversity index provides relevant information on the effects of predation on prey size distribution (Quintana et al., 2015; Šorf et al., 2015; Tavşanoğlu et al., 2015; Ye et al., 2013). Specifically, some studies have shown that predation normally accumulates prey within a narrow size range, leading to low size diversity (Badosa et al., 2007; Brucet et al., 2010; Compte, Gascón, Quintana, & Boix, 2011, 2012). Size diversity may, however, also be an indicator of resource niche partitioning (García-Comas et al., 2014; Ye et al., 2013) because in aquatic ecosystems body size is often a good proxy for ecological niche (Jennings, Pinnegar, Polunin, & Boon, 2001; Stouffer, Rezende, & Amaral, 2011; Woodward & Hildrew, 2002b). Recent investigations (García-Comas et al., 2016; Ye et al., 2013) provided evidence that in zooplankton communities, higher size diversity represents increased strength of top-down control on phytoplankton. The underlying mechanism is that each size group of predators has its own optimal prey size; thus, increasing size diversity of predators promotes diet niche partitioning in terms of prey sizes and elevates the strength of top-down control (García-Comas et al., 2016; Rudolf, 2012; Ye et al., 2013).

Shifts in temperature and resource availability may also affect the size structure of aquatic communities and may confound the potential effects of size-structured predation on prey (Binzer, Guill, Rall, & Brose, 2016; Emmrich et al., 2014; Garzke, Ismar, & Sommer, 2015; Marañón, Cermeño, Latasa, & Tadonléké, 2012; Sommer et al., 2017). In accordance with the temperature–size rule (Atkinson, 1994) and empirical evidence (e.g. Daufresne, Lengfellner, & Sommer, 2009; Gardner, Peters, Kearney, Joseph, & Heinsohn, 2011; Morán, López-Urrutia, Calvo-Díaz, & Li, 2010), higher temperatures should induce a shift towards reduced body size, which may be reflected in lower size diversity and evenness. The effect of resource availability is less clear. According to theoretical models (Kerr & Dickie, 2001), resource availability would increase the relative abundance of large organisms. However, a negative relationship between resource availability and zooplankton and fish size diversity was found in empirical studies and was explained by competitive interactions for resources in less productive systems, promoting diversification of communities by size (Brucet et al., 2006; Emmrich et al., 2011; Quintana et al., 2015) or an effect of population dynamics (i.e., pulses of reproduction due to increased food availability, resulting in dominance of small individuals and low size diversity) (García-Comas et al., 2014). Furthermore, resource availability may have a bigger effect on phytoplankton than in other trophic groups (Marañón, Cermeño, Latasa, & Tadonléké, 2015; Quintana et al., 2015).

Here, we assessed the potential predation effect by size-structured predators on prey size structure by searching for relationships between size diversity and size evenness of predator and prey across the planktonic food web (fish, zooplankton, and phytoplankton). We also accounted for the effects of temperature and resource availability in the models. We hypothesized that the enhanced strength of top-down control at increasing predator size diversity (García-Comas et al., 2016; Ye et al., 2013) will lead to a negative relationship between size diversity and size evenness of predators and prey (i.e. negative relationship between fish and zooplankton size diversity or between zooplankton and phytoplankton size diversity). A simultaneous comparison of size diversities of predators and prey communities across several lakes is not yet available, but a negative relationship has been found between zooplankton and phytoplankton size diversities in marine systems (García-Comas et al., 2016). We also hypothesised a negative relationship between productivity (i.e. resource availability) and size diversity and evenness, due to competitive interactions for resources in less productive systems. Concerning temperature, we expected a lower size diversity and evenness in warmer lakes.

In accordance with studies on species diversity, an alternative hypothesis in which predator and prey size diversity are positively correlated could also be plausible: predator diversity could reduce the strength of top-down control by promoting intra-guild interactions among predators and diminishing enemy impacts on preys (Finke & Denno, 2005), and prey size diversity could increase predator size diversity because the diversity of resources is expected to promote diversity of consumers (Fox, 2004; Ritchie, 2010).

We further evaluated the relationship between the size diversity of the prey and the log biomass ratio between adjacent trophic levels as a measure of classic top-down control (i.e. when assessing factors determining phytoplankton size diversity, we added the log zooplankton:phytoplankton biomass ratio as an additional predictor). We expected to find a negative relationship indicating that increased density of predators reduces prey size diversity as a result of the accumulation of organisms in the less predated sizes (Brucet et al., 2010; Quintana et al., 2015).

Methods

Site description

Thirty shallow (<18 m maximum depth) lakes spanning over almost five latitudes, from the warm temperate north (41°52´N, 27°58´E) to the semiarid south (37°06´N, 29°36´E) of the Western Anatolian Plateau of Turkey, and with an altitude range of 1-1328 m, were selected (Figure 5). The lakes included two distinct climates, the semiarid region located in mid to south-west Turkey and the warm temperate subhumid region located in north-west Turkey, exhibiting average annual (1980–2010) temperatures and precipitation of 14.5 and 12.0ºC and 545.4 and 632.3 mm, respectively, and net evaporation of 616.3 and 338.8 mm, respectively (Turkish State Meteorological Service; www.mgm.gov.tr). The lakes also covered wide gradients of nutrient concentrations, conductivity, and lake area (Table 1). Fishing and stocking is expected to be negligible in these lakes because in Turkey these activities are mainly conducted in large lakes or reservoirs that were not part of this study. Furthermore, inland fishing in Turkey constitutes only a low share of total fish production (Harlioğlu, 2011) and the recent increase in aquaculture production has led to a further decline in inland catches (Turkish Statistical Institute, http://www.tuik.gov.tr).

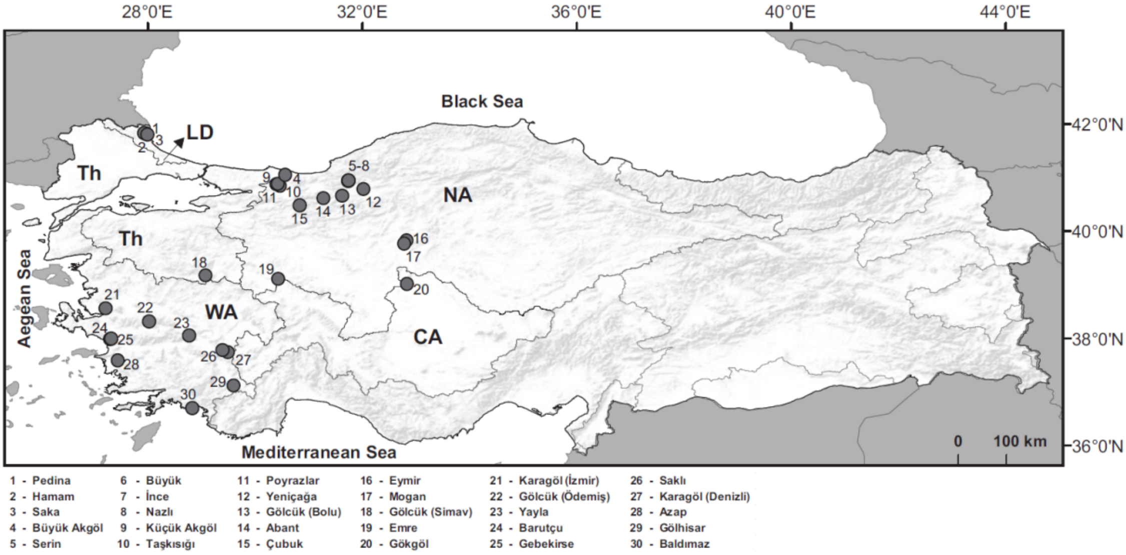


Figure 5. The location of the study lakes and their names. The Freshwater Ecoregions from Abell et al. (2008) are shown and the names of these freshwater ecoregions in the western part of Turkey are given as abbreviations: LD Dniester-Lower Danube, Th Thrace, NA Northern Anatolia, CA Central Anatolia, WA Western Anatolia. Figure modified from Boll et al. (2016)

Sampling and laboratory analysis

The 30 lakes were sampled once during the peak growing season (July to August) of 2007–2010, following largely the standardized sampling protocol described in detail by Moss et al. (2003) (for details of the sampling see Levi et al. (2014) and Çakıroğlu et al. (2014)). Mean annual temperatures interpolated for a 30 arc-second spatial resolution (1 km^2 resolution) grid were assembled from the WorldClim database using the sampling location coordinates of each study lake (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005). Dissolved oxygen (mg L^{-1}), conductivity (±1 µS cm^{-1}), pH, and Secchi disc transparency were measured *in situ* at the deepest part of the lake.

Water samples for chemical analysis (total phosphorus (TP), total nitrogen (TN), and chlorophyll *a* (chl-*a*) and determination of biological variables (zooplankton and phytoplankton) were taken from depth-integrated, mixed samples (40 L) at the deepest point in the pelagic zone. Water samples were kept frozen until analysis and the methods for analyses of TP, TN, and chl-*a* are given in (Özen, Karapinar, Kucuk, Jeppesen, & Beklioglu, 2010). Per-cent plant volume inhabited (PVI%) (plant coverage × average plant height/water depth *sensu* Canfield et al. (1984)) for each submerged and floating-leaved plant species was recorded at even intervals along each transect line.

From the 40 L mixed pelagic sample, 50 ml were taken and fixed using 2% Lugol solution for phytoplankton counting. Depending on the sample size, different phytoplankton volumes were settled for 16-24 hours and horizontal transects were counted until 100 individuals of the most abundant species had been enumerated. At least 10 individuals were measured from each species and biovolume was calculated according to Hillebrand, Dürselen, Kirschtel, Pollingher, & Zohary (1999) and Sun & Liu (2003).

Table 1. Physico-chemical, morphometric, and biotic characteristics of the study lakes. Standard deviation (SD) (n=30). Annual precipitation and net evaporation (estimated as evaporation minus precipitation) were assembled from the Turkish State Meteorological Service (www.mgm.gov.tr).

	Mean	**Minimum**	**Maximum**	**SD**
Latitude (°)	39.7	36.7	41.8	1.5
Altitude (m)	657.5	1.0	1328.0	504.1
Lake area (ha)	91.5	0.1	635.0	145.8
Maximum depth (m)	4.3	0.6	1.7	3.8
Mean temperature (°C)	24.4	18.3	32.4	3.5
Sum of precipitation (mm)	716	424	1044	146.1
Net evaporation	558.3	432.9	765.3	119.6
pH	8.31	6.92	9.64	0.6
Conductivity (µS cm^{-1})	1248	104.0	8583	2219
Total phosphorus (µg L^{-1})	128	15	633	141
Total nitrogen (µg L^{-1})	1081	239	2180	596
Secchi depth/maximum depth	0.32	0.05	1.00	0.20
Dissolved oxygen (mg L^{-1})	6.6	0.6	15.3	2.9
Chlorophyll-*a* (µg L^{-1})	19.8	2.4	95.1	21.9
NPUE (number of fish net^{-1} night^{-1})	162	0.3	1160	247
Plant Volume Inhabited (%)	14	0	78	20

For pelagic zooplankton, 20 L of the mixed pelagic sample were filtered through a 20 µm mesh size filter. Additionally, we sampled littoral zooplankton using a tube sampler, taking a 20 L composite water sample covering the whole water column and subsequently filtering it through a 20 µm filter. Pelagic and littoral zooplankton samples were analysed separately. Zooplankton was preserved in 4% Lugol solution. All zooplankton taxa were identified to genus or species level, whenever possible. In case of subsampling, we assured that at least 100 individuals of the most abundant taxa were counted. In order not to miss rare species, we examined the whole sample. For each lake, the body size of at least 25 individuals of each species was measured, when enough individuals were present in the sample. For copepods, 25 individuals were measured from each development stage (nauplii, copepodites and adults) to account for ontogenetic differences. Biomass dry weight (dry wt) estimations were obtained from the allometric relationship between the weight and the length of the body (Dumont, Van de Velde, & Dumont, 1975; McCauley, 1984). For Rotifera, biovolume was estimated from measurements of the principal diameters of the organisms, and biomass dry weight was calculated by converting biovolume into dry weight (Dumont et al., 1975; Malley, Lawrence, Mac Iver, & Findlay, 1989; Ruttner-Kolisko, 1977). Shannon–Wiener diversity (H) was calculated according to Shannon and Wiener in (Pielou (1969).

Composition and relative abundance of the fish were determined using Nordic benthic multimesh gill nets (CEN standard, 14757, 2005). Multimesh gill nets (12 mesh sizes between 5.0 and 55 mm in a geometric series) were set in a random-stratified sampling design in the pelagic and the littoral areas of the lakes. The smallest mesh size of 5 mm allowed 0+ fish to be included in the catches. The number of nets used per lake was proportional to the lake area, the maximum number being eight (Boll et al., 2016). Nets were set for a 12-h period from before dusk and lifted after dawn. The data represent the average net catch per lake, expressed as catch per unit effort (NPUE; number of fish net^{-1} night^{-1}). The fork length of all fish was measured.

Size metrics

We used two non-taxonomic size metrics: body size diversity and body size evenness. We calculated size diversity and size evenness (Brucet et al., 2006; Quintana et al., 2008, 2016) for each fish, zooplankton, and phytoplankton sample using individual size measurements as proposed by Quintana et al. (2008). For zooplankton and phytoplankton, we obtained the actual distribution of individual body sizes in each lake by multiplying the proportion of individuals of a given body size for a given species (or life stage in the case of copepods) by the total number of this species (or life stage in the case of copepods). For fish, this was not needed since all fish in the sample were measured. Thus, for all three trophic groups, size diversity and size evenness were estimated from the body sizes (weight for zooplankton and phytoplankton and length for fish) of individuals and not from the mean size of each species. Both size metrics were based on individual abundance (not on biomass).

Size diversity and size evenness were calculated according to Quintana et al. (2008, 2016). The proposed size diversity (μ) is computed based on the Shannon diversity expression adapted for a continuous variable, such as body size. This measure takes the form of an integral involving the probability density function of the size of the individuals described by the following equation:

$$\mu = - \int_{0}^{+\infty} p_X(x) log_2 p_X(x)\, dx$$

where $p_x(x)$ is the probability density function of size x. The non-parametric kernel estimation was used as a probability density function, which is applicable to any type of size distribution. Before computing size diversity, data are automatically standardized by division of each size value by the geometric mean of the size distribution. The size diversity index (μ) is the continuous analogue of the Shannon diversity index and it produces values in a similar range to those of the Shannon species diversity index (Brucet et al., 2010; Quintana et al., 2008). However, negative values of size diversity (extremely low size diversity) are feasible in that the method uses a continuous probability density function for the probability estimation, and probability densities over 1 are possible.

The use of size diversity for analysis of the shape of size distributions has several advantages: 1) its meaning is easy to interpret since the concept of diversity is well established – high size diversity means a wide size range and/or similar proportions of the different sizes along the size distribution (e.g. Emmrich et al., 2011); 2) after data standardization, samples measured with different units, such as length, weight, or volume, are comparable; 3) in contrast to the traditional biomass size spectrum, size diversity and size evenness indices do not require creation of arbitrary size classes and statistical fitting and their estimates are therefore insensitive to the strength of model fit (but see Edwards, Robinson, Plank, Baum, & Blanchard, 2017); 4) it is a single-value metric, which simplifies the comparison between samples (e.g. Brucet et al., 2010).

Size evenness (J_e) is calculated by dividing the exponential of the size diversity by its possible maximum for a given size range (Quintana et al., 2016). The size evenness ranges between 0 and 1 because of the division by the maximum exponential diversity. Based on the total number of individuals measured in each sample, we estimated that all samples from all trophic levels had a size diversity and size evenness error estimation lower than 10%.

It was not possible to analyze piscivorous fish as a separate trophic level since they had low abundances in most of the samples (on average just 5% of total fish NPUE), meaning that the number of individuals available to calculate size diversity with an error lower than 10% was too small. However, we ran additional models by including only non-piscivorous fish as a trophic group. Since juveniles of several piscivorous fish species are planktonic, we established a threshold size of 15 cm below which we considered them non-piscivorous (e.g. Mehner et al., 2016), and we re-calculated fish size diversity excluding the true piscivores. From here on, we refer to fish size diversity and fish size evenness when all fish were included in the calculations and non-piscivorous fish size diversity and non-piscivorous fish size evenness when piscivorous fish were excluded.

Predictor variables

As a measure of size-structured predation, we included size diversity and size evenness of potential predators (i.e. when assessing factors determining phytoplankton size diversity, we added size diversity of zooplankton as predictor). As a measure of resource availability, we included the size diversity and size evenness of potential prey. In each model, we also included mean temperature (log-transformed) and TP (log-transformed) as well. Moreover, we added the log biomass ratio between adjacent trophic levels as a more classic measure of potential predation impact (i.e. when assessing factors determining phytoplankton size diversity, we added the log zooplankton:phytoplankton biomass ratio as an additional predictor of grazing

pressure on phytoplankton). We could not evaluate the effect of fish size diversity/evenness on non-piscivorous fish size diversity/evenness because there were few lakes with piscivorous fish and the relationship would thus have been misleading (i.e. the two metrics had the same value for several lakes).

Data analysis

We ran general linear models (GLMs) for each phytoplankton, zooplankton, and fish size structure metric. In each model we used the previously mentioned predictor variables: size diversity (or size evenness) of potential predators, mean temperature, TP, the size diversity (or size evenness) of potential prey as a measure of resource availability and the log biomass ratio between adjacent trophic levels. We searched for the most parsimonious model by an automatic stepwise backward selection of one predictor variable at a time by minimizing the Akaike information criterion (AIC). The most parsimonious model was the combination of variables having the strongest impact on outcomes. To compare the relative strength of the significant predictors, we additionally calculated their standardised (beta) coefficients. In the model for zooplankton size diversity, we did not include phytoplankton size diversity because it was correlated with TP, and in the model for zooplankton size evenness, we did not include phytoplankton size evenness because it was correlated with temperature (both correlation coefficients higher than 0.4).

We additionally ran a second set of GLMs (see Table 7) to explore whether a relationship existed between size diversity and species diversity within each assemblage, as well as with environmental factors influencing community diversity other than temperature and resources (i.e. weakly correlated variables in Table 1). Thus, as predictor variables we included the taxonomic diversity of each organism group, temperature, TP, net evaporation, conductivity, lake area, and depth [temperature and altitude were highly correlated (correlation coefficient higher than 0.6), so altitude was not used as a predictor variable].

We further analyzed the relationship between fish and zooplankton trophic levels by calculating the average fish trophic level in a lake and searching for its relationship with zooplankton size diversity using GLM. We estimated the average trophic level of the fish species in a lake using the information in www.fishbase.org. The trophic level of a fish species defines its position within a food web, and it is estimated by considering both its diet composition and the trophic level of its food item(s). We calculated the average trophic level of the fish assemblage in a lake by weighting the trophic level index of each species by its abundance in a given lake. For young-of-the-year (YOY) and smallest fish (< 6 cm) that could not be identified, the trophic index was set to 2.5, which roughly represents a diet consisting of 50% phytoplankton and 50% zooplankton. We are aware that the diet of these fish depends on the fish species and may vary with climate, and we therefore re-ran the analysis using a trophic index of 3 (a higher percentage of zooplankton in the diet).

For all the analyses, we inspected residual plots to assure that there were no deviations from normality and homoscedasticity, and we checked that the assumption of no autocorrelation in residuals was not violated using Durbin-Watson tests. We inspected the variance inflation factor (VIF) and tolerance values to ensure that there was no multicollinarity among predictors in the final set used for the analyses. GLMs were performed in 'R' version 2.9.1 (Development Core Team 2009) using the BRODGAR v. 2.7.2 statistical package (Highland Statistics Ltd., Newburgh, U.K.).

Results

Size diversity (µ) ranged between a minimum of -0.81 for fish to a maximum of 4.0 for phytoplankton (Table 2). Negative values (extremely low size diversity) were rare (only 3 of the 120 samples analyzed). Size evenness (J_e) ranged between a minimum of 0.39 to a maximum of 0.90, both for fish. No significant differences were found for µ and J_e of zooplankton between the pelagic and littoral habitats (1.88 ± 0.49 and 1.99 ± 0.62 for µ in the pelagic and littoral and 0.70 ± 0.1 and 0.74 ± 0.1 for J_e in the pelagic and littoral, respectively; ANOVAs, $p>0.05$) and the predictors of both models were the same; thus, only the results for pelagic zooplankton are presented as from here.

Table 2. Size metrics (i.e. response variables) ($n=30$) of different assemblages, their minima, means, maxima, and standard deviation (SD).

	Mean	Minimum	Maximum	SD
Fish (all fish)				
Size diversity	1.32	-0.81	2.42	0.71
Size evenness	0.71	0.39	0.90	0.12
Non-piscivorous fish				
Size diversity	1.33	-0.81	2.42	0.68
Size evenness	0.72	0.44	0.91	0.11
Zooplankton				
Size diversity	1.88	0.80	2.50	0.49
Size evenness	0.70	0.49	0.83	0.09
Phytoplankton				
Size diversity	2.48	-0.03	4.00	0.94
Size evenness	0.68	0.45	0.86	0.11

Fish size diversity (μ_{fish}) was significantly positively related to zooplankton size diversity ($\mu_{zooplankton}$), explaining 35.5% of the variation in the data (Table 3, Figure 6). As judged from the significant positive relationship between μ_{fish} and $\mu_{zooplankton}$ (Table 3), fish size distributions with a wide size range and more similar proportions of the different sizes were associated with zooplankton size distributions with similar characteristics (Figure 7). High $\mu_{zooplankton}$ reflected the presence of large-sized Cladocera or Copepoda in similar proportions as small-sized rotifers and nauplii (Figure 7), causing a bimodal size distribution with a second dome (i.e. curved-shaped), corresponding to large sizes beginning around size class -0.7 ($\log_2$ µg dry weight). However, when only few sizes of fish dominated (low μ_{fish}, Figure 7), $\mu_{zooplankton}$ was low, and the zooplankton size distribution had a unimodal shape and a narrower size range, with dominance of small sizes mainly represented by rotifers. When only non-piscivorous fish were analyzed, their size diversity was also positively related only to $\mu_{zooplankton}$ but the relationship was slightly weaker (Table 3).

Table 3. Results of general linear models (GLMs) showing the variables significantly affecting the size structure of phytoplankton, zooplankton and fish assemblages. For zooplankton size diversity, we ran two models, one including fish size diversity (all fish) and another including non-piscivorous fish size diversity as predictors, and both models were significant. Only the most parsimonious model is presented. Coefficients (estimates and standard error, SE), beta (standardised) coefficients (Beta coeff.), t-value, significance (*p* value) and variability explained by the model (%). n.s., non-significant; log Fish:Zooplankton, fish:zooplankton biomass ratio; log Zoo:Phyto, zooplankton:phytoplankton biomass ratio.

Response variable	**Model**	**AIC**	**Predictors**	**Estimate**	**SE**	**Beta coeff.**	**t-value**	***p* value**	**%**
Fish (all fish)									
Size diversity	Full	-25.2	Zooplankton size diversity	0.865	0.235	0.596	3.69	.001	36.0
			Log temperature	0.623	1.370	0.074	0.45	.653	
			Log TP	-0.032	0.279	-0.019	-0.11	.910	
	Best	-29.0	Zooplankton size diversity	0.861	0.225	0.593	3.82	.001	35.5
Size evenness	Full	-133.0	Zooplankton size evenness	0.173	0.243	0.121	0.71	.483	29.7
			Log temperature	-0.566	0.244	-0.406	-2.31	.028	
			Log TP	-0.086	0.048	-0.302	-1.80	.082	
	Best	-136.1	Log temperature	-0.625	0.231	-0.448	-2.70	.011	20.1
Non-piscivorous fish									
Size diversity	Full	-23.1	Zooplankton size diversity	0.645	0.243	0.471	2.65	.014	22.3
			Log temperature	0.376	1.420	0.047	0.26	.793	
			Log TP	0.028	0.290	-0.018	-0.09	.923	
	Best	-27.1	Zooplankton size diversity	0.643	0.233	0.470	2.77	.010	22.1
Size evenness	Full	-128.6	Zooplankton size evenness	0.221	0.263	0.167	0.84	.408	4.2
			Log temperature	0.010	0.265	0.008	0.04	.969	
			Log TP	0.026	0.052	0.098	0.50	.621	
Zooplankton									
Size diversity	Full	-45.3	Fish size diversity	0.399	0.114	0.579	3.50	.002	36.7
			Log Fish:Zooplankton	-0.049	0.109	-0.086	-0.45	.655	
			Log temperature	0.388	0.961	-0.067	-0.40	.690	
			Log TP	-0.120	0.226	-0.101	-0.53	.601	
	Best	-50.6	Fish size diversity	0.408	0.107	0.593	3.82	.001	35.5
Size evenness	Full	-146.5	Fish size evenness	0.105	0.153	0.150	0.68	.500	11.7
			log Fish:Zooplankton	-0.002	0.021	-0.024	-0.11	.610	
			Log temperature	0.360	0.204	0.369	1.76	.090	
			Log TP	0.011	0.045	0.056	0.25	.805	
Phytoplankton									
Size diversity	Full	-7.60	Zooplankton size diversity	-0.338	0.302	-0.249	-1.12	.273	11.2
			Log Zoo:Phyto	-0.145	0.249	-0.121	-0.58	.566	
			Log temperature	0.040	2.306	0.004	0.02	.986	
			Log TP	0.505	0.357	0.267	1.41	.169	
	Best	-11.0	Log TP	0.615	0.339	0.325	1.82	.080	10.5
Size evenness	Full	-134.9	Zooplankton size evenness	-0.169	0.242	-0.132	-0.70	.491	22.1
			Log Zoo:Phyto	-0.031	0.032	-0.191	-0.98	.338	
			Log temperature	0.368	0.249	0.294	1.48	.152	
			Log TP	0.053	0.046	0.209	1.16	.255	
	Best	-138.2	Log temperature	0.480	0.214	0.385	2.25	.032	14.8

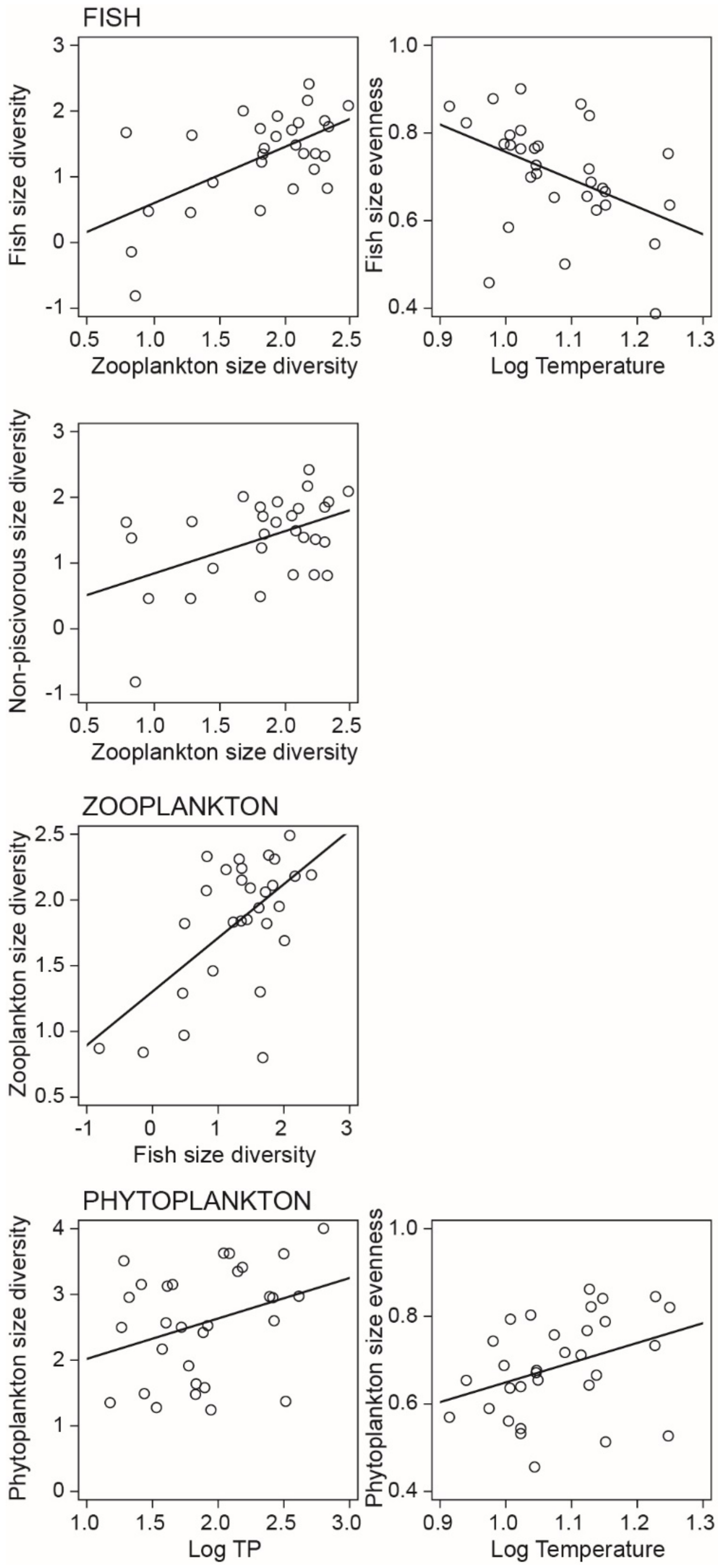


Figure 6. Relationship between size metrics of different organism groups (all fish, non-piscivorous fish, zooplankton, and phytoplankton) and the independent variables (see Table 3 for statistical results). TP, Total Phosphorus.

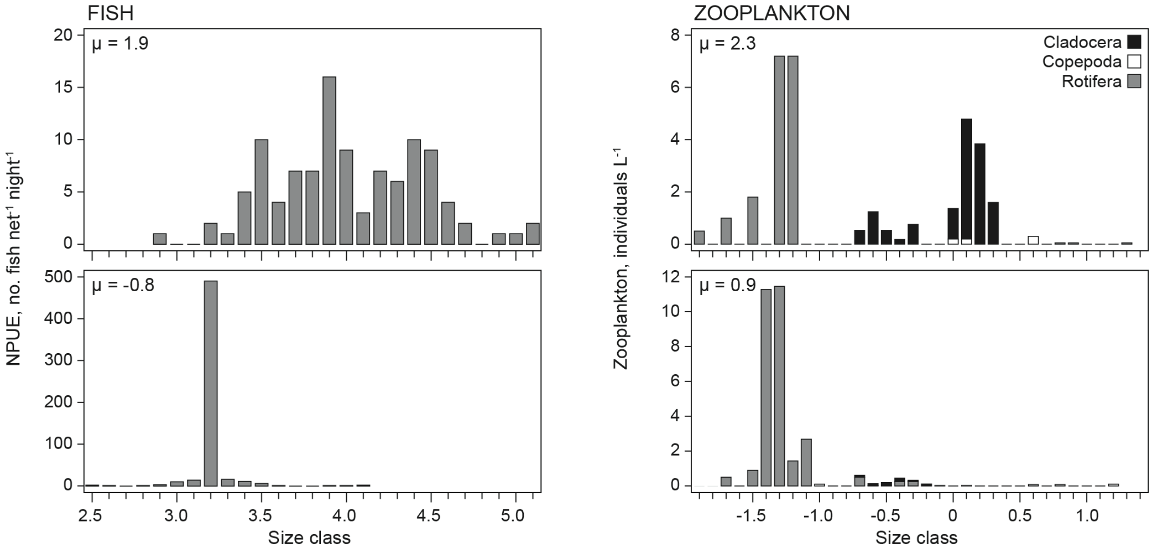


Figure 7. Example of a lake with a fish and zooplankton community of high size diversity (panels above) and a lake with a fish and zooplankton community of low size diversity (panels below). Size class represents $\log_2$ with size in micrograms dry weight for zooplankton and cm for fish. μ, size diversity. Note that the size classes were used in this figure only for better representation of the number of individuals of each size. However, the size diversity and size evenness index were not calculated using size classes but using individual size measurements.

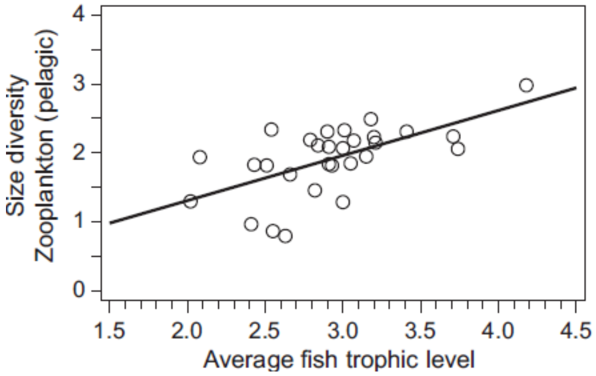


Figure 8. Relationship between average fish trophic level in a lake and zooplankton size diversity.

GLMs showed that temperature was related to $J_{e\ fish}$, while there were no links to the other trophic levels (Table 3, Figure 6). Fish size evenness was lower at higher temperatures. No variables were found to be significant for the size evenness of non-piscivorous fish and zooplankton models.

Phytoplankton size diversity ($\mu_{phytoplankton}$) was only weakly and positively predicted by TP (Table 3, Figure 6) and there were no links to the other trophic levels. $J_{e\ phytoplankton}$

was positively related to temperature. The log biomass ratio between adjacent trophic levels was not significant in any case.

The additional GMLs (Table 7) including as predictors species diversity within each assemblage and other environmental factors which may influence community diversity (Table 1) showed that size diversity of fish, non-piscivorous fish and zooplankton was positively related with species diversity of the trophic group. However, according to beta coefficients (i.e. which give information on the relative strength of the significant predictors), the size diversity of the interacting trophic level was still the strongest predictor in the model for fish, non-piscivorous fish and zooplankton size diversity, whereas no environmental variables were significant.

Average fish trophic level in the lakes explained 36.7% of the zooplankton size diversity variation (Figure 8). When using a trophic index of 3 for YOY, average fish trophic level in the lakes explained 24.5% of the zooplankton size diversity variation.

Discussion

In contrast to our first hypothesis, our results showed correspondence of size structures between interacting trophic levels of the planktonic food web. Thus, highly size diverse fish assemblages were associated with highly size diverse zooplankton assemblages, a relationship that was not violated by variation in temperature and resource availability (TP). The correspondence between fish and zooplankton size diversity agrees with the correspondence found in the size distributions of piscivorous and non-piscivorous fish in European lakes (Mehner et al., 2016). A potential explanation is that higher diversity of resources drives higher consumer size diversity. Albeit our focus is size diversity, the underlying mechanism would be similar to that proposed for the positive relationship between species diversity of adjacent trophic groups in terrestrial (e.g. Haddad et al., 2009) and model (Fox, 2004) systems: a prey community (zooplankton) highly diverse in sizes could promote size diversity at the higher trophic levels (fish) via productivity effects or by enabling niche partitioning (Currie, 1991; Tilman, 1982). In contrast, low zooplankton size diversity (e.g. lower abundance of large body sizes) could create energetic bottlenecks in fish, potentially explaining the low size diversity values. Evidence that a diversity of prey sizes may favour a size diverse predator community has previously been found in laboratory and field experiments, although the signal was weak (Rudolf, 2012).

An alternative explanation may also be possible: higher diversity of sizes in consumers could also promote diversification of resources by size. Thus, high size diversity in fish assemblages may create more chances for resource partitioning in terms of prey size (e.g. zooplankton, macroinvertebrates) (Woodward & Hildrew, 2002b), likely resulting in a reduced predation pressure on large-bodied zooplankton (Jansson, Persson, De Roos, Jones, & Tranvik, 2007; Persson et al., 2003) and thus an increase in zooplankton size diversity. This agrees with the correlation observed between the average trophic level of fish in the lakes and zooplankton size diversity (Figure 8) – the higher the average trophic level of fish in a lake (i.e. more fish and macroinvertebrates prey), the higher the size diversity of zooplankton. Hence, the mechanism would be similar to that observed in studies on species diversity in which predator diversity reduces the strength of top-down control by promoting intra-guild interactions among predators and diminishing enemy impacts on preys (Finke & Denno, 2005). Conversely, a community of predators with similar-sized individuals (e.g. dominance of small size fish) occupying similar niches may result in a prey community less diverse in size because some prey sizes would be disproportionally predated over the rest (Brucet et al., 2010).

One may argue that species diversity could be the main factor driving the correspondence between fish and zooplankton size diversity relationships. However, we did not find a significant relationship between fish and zooplankton species diversity ($p>0.05$). When we additionally explored whether a relationship existed between species and size diversity within each assemblage (Table 7) a significant percentage of the variability in size diversity of fish and zooplankton was explained by species diversity (i.e. the fish and zooplankton assemblages most diverse in species were also the most diverse in body size), but the size diversity of the interacting trophic level was still the variable contributing most in the two models. These results suggest that size diversity within a given organism group may have effects on other organism groups and that these are beyond those mediated by taxonomic diversity. Furthermore, size diversities of fish and zooplankton were not significantly related to any other environmental variable, suggesting that the effect of confounding factors in the observed patterns can be excluded.

Our results provide further evidence of the negative effect of temperature on fish body size (Emmrich et al., 2014; Jeppesen et al., 2010, 2012) since the size evenness of fish assemblages (including all fish) decreased in warmer lakes. The major temperature gradients in Turkish lakes are associated with altitudinal and, to a lesser extent, latitudinal gradients (Boll et al., 2016). Thus, high altitude and colder Turkish lakes exhibited fish size distributions where individual sizes were more evenly distributed than those in low altitude warm lakes. This is in agreement with studies conducted at European scale (Emmrich et al., 2014), showing that warmer lakes have monotonically decreasing size distributions dominated by small sizes, whereas large sizes are scarcer. The results from the size evenness index indicate that temperature has a greater influence on the relative distribution of fish sizes (i.e. the shape of the size distribution) than the amplitude of the size range. Yet, temperature did not influence the size evenness of non-piscivorous fish (Table 3), probably because large piscivorous fish are mainly found in colder lakes (Boll et al., 2016), and the effect of temperature weakens when piscivores are excluded from the analysis.

We did not find any relationship between zooplankton and phytoplankton size structures. Instead, phytoplankton size diversity was better predicted by TP though the relationship was weak (significance level of only 0.08). This may be due to the prevailing influence of physical factors in the phytoplankton nutrient uptake. Our results agree with previous studies in marine systems where changes in resource supply alone have been demonstrated as sufficient to explain the variability of phytoplankton size structure (Marañón et al., 2015). In phytoplankton assemblages, smaller sizes are favored at low nutrient availability due to the higher surface:volume ratio or lower resource requirements, whereas large algae are often (but see Jensen *et al*., 1994) better competitors at high concentrations (Guidi et al., 2009; Litchman & Klausmeier, 2008). This might explain the positive response of phytoplankton size diversity to TP. Our results partially contrast with the previous study on marine plankton (García-Comas et al., 2016) showing that nano-microplankton (prey) size diversity was negatively related to size diversity of mesozooplankton (predators), as well as to physical factors.

In contrast, the phytoplankton size evenness in our Turkish study lakes was related to temperature, with higher size evenness in warm lakes located in lowlands than those high altitude lakes.

We recognize that our study is based on correlational evidence, which does not necessarily imply causal relationships, and, thus, more investigations using, for example, size-based experiments will be needed to further elucidate the effect of size-based predator–prey interactions. Ideally, these experiments would need to compile data on stomach content and/or stable isotopes at the lowest level (i.e. species or life stages) and combine it with size-based metrics in order to provide better knowledge of the trophic link strengths that affect the size distributions (Boukal, 2014; Brose, 2010). Furthermore, we categorized phytoplankton, zooplankton, and fish as belonging to single trophic levels, but omnivory and intraguild predation may be relevant for shaping the patterns of size diversity. Nevertheless, when we ran the model for only non-piscivorous fish, the size diversity of zooplankton remained the only variable predicting non-piscivorous fish size diversity, and no relationship was found between non-piscivorous fish and the abundance of piscivorous fish (results no shown; $p > 0.1$), suggesting that piscivore predation had a weak impact on non-piscivorous fish size structure. This may be due to the low abundance of piscivorous species in these lakes or to the low predator–prey size ratios and the resulting size refuges for prey fish, as found for European lake fish communities (Mehner et al., 2016).

We also acknowledge that our design is based on the classical three-level food web since our methodology did not allow to test for the effects of the microbial loop or the predation of copepods. Studies in marine systems show that copepod grazing may have different effects on phytoplankton cell size depending on the number of food chain links within the microbial food web and that these grazing effects also interact with temperature and nutrient supply (Sommer et al., 2017 and references therein). Thus, we advocate for including the microbial loop in future studies exploring the relationship between zooplankton and phytoplankton size diversity.

In conclusion, our results suggest that, in Turkish lakes, size structure within a trophic group may be controlled by the size structure in other trophic groups, as well as by temperature, resource availability, and taxonomic diversity. The positive relationship between the size diversity of fish and zooplankton suggests that higher diversity of prey may drive a higher size diversity of predators, as earlier suggested in studies of species diversity, or vice versa, and these effects are beyond those mediated by taxonomic diversity. In contrast, the size diversity and size evenness of phytoplankton are mainly influenced by physical factors. Additionally, our results suggest that it is important to take variation in temperature and resource availability into account when studying trophic interactions in size-structured predator–prey systems.

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CHAPTER 2

Size-based interactions and trophic transfer efficiency are modified by fish predation and cyanobacteria blooms in Lake Mývatn, Iceland

Ersoy, Z., Jeppesen, E., Sgarzi, S., Arranz, I., Cañedo-Argüelles, M., Quintana, X.D., Landkildehus, F., Lauridsen, T.L., Bartrons, M., Brucet, S. *Freshwater Biology* (2017), 62, 1942-1952.

Abstract

Trophic cascade studies have so far mostly focused on changes in the abundance, biomass or average size of prey and predators. In contrast, individual size-based interactions, playing a key role in the trophic structure and functioning of aquatic ecosystems, have been less explored. We conducted a 3-month in situ experiment in Lake Mývatn, Iceland, with two fish treatments (with and without fish, *Gasterosteus aculeatus*). After the first month of the experiment, *Anabaena* blooms appeared in the lake. We studied the effects of fish predation and occurrence of cyanobacteria blooms on the individual size structure (i.e. the distribution of the number of organisms over a size range) of zooplankton and phytoplankton. We also assessed the potential consequences for trophic transfer efficiency (TTE) (measured as the predator to prey biomass ratio) in the planktonic food web. Our results showed that fish predation and cyanobacteria bloom had a negative relationship with size diversity of zooplankton, which became dominated by small-sized individuals in both cases. The phytoplankton size diversity changed over time particularly due to the blooming of large-sized *Anabaena*, and its increase was apparently mainly driven by changes in resources. Low zooplankton size diversity related to fish predation reduced TTE, particularly in the enclosures with fish. This may be because low zooplankton size diversity represents a lower partition of resources among consumers, thereby decreasing the trophic energy transfer. With the occurrence of *Anabaena* bloom, high phytoplankton size diversity coincided with a lower energy transfer in all enclosures likely due to reduced zooplankton grazing when large-sized colony-forming *Anabaena* dominated. In conclusion, our results indicate that both top-down and bottom-up forces significantly influence the size structure of planktonic communities. The changes in size structure were related to shifts in the energy transfer efficiency of the Lake Mývatn food web. Thus, our study underpins the importance of taking into account size-based interactions in the study of trophic cascades, particularly in a warming climate where strong planktivorous fish predation and frequent cyanobacteria blooms may occur.

Keywords: fish predation, phytoplankton, size structure, trophic interactions, zooplankton

Introduction

Cascading trophic interactions have long been a field in aquatic ecosystem studies (Carpenter et al., 1985; Jeppesen et al., 2002; Polis et al., 2000). Most studies have focused on the abundance, biomass or average size of predators and prey (Knight, McCoy, Chase, McCoy, & Holt, 2005; Pace et al., 1999). Sized-based interactions between predators and prey at adjacent trophic levels in the food web have often not been considered, despite that they play a key role in the trophic structure and functioning of aquatic ecosystems (Brose, Jonsson, et al., 2006; Brown et al., 2004; Brucet et al., 2017; Emmerson & Raffaelli, 2004).

Body size is a fundamental functional trait of organisms because it is linked with life- history patterns such as reproduction, growth and respiration (Brown et al., 2004; Calder, 1984; Robert Henry Peters, 1983). It also provides information about prey-predator interactions, top-down and bottom-up control and the energy transfer through aquatic food webs (De Roos & Persson, 2002; Finlay et al., 2007; Woodward et al., 2005; Yvon-Durocher & Allen, 2012). Several studies have shown that both biotic interactions (e.g. predation, competition) and environmental factors (e.g. temperature, productivity) can affect the individual body size structure (i.e. the distribution of the number of organisms over a size range) of aquatic communities (Ye et al., 2013; Yvon-Durocher et al., 2011; Zhang et al., 2013).

Many of these existing investigations have focused on variations in body size structure at a single trophic level, but the different trophic groups in a food web may respond differently to biotic and environmental factors (Brose, Jonsson, et al., 2006; Brucet et al., 2017; Quintana et al., 2015). Changes in resource availability are known to shape phytoplankton size structure in both freshwater (Brucet et al., 2017; Quintana et al., 2015) and marine ecosystems (Garzke et al., 2015; Marañón et al., 2012; Sommer et al., 2017). For example, high resource availability may promote growth of large-sized bloom-forming phytoplankton (Downing et al., 2001). Occurrence of blooms driven by bottom-up control is likely to alter size-based interactions in the food web, but so far, this has not been explored thoroughly. For example, blooms may cause toxicity and obstruct the feeding of zooplankton (Ger, Urrutia-Cordero, et al., 2016; Ger, Faassen, Pennino, & Lürling, 2016; Jeppesen, Søndergaard, et al., 2005; Ye et al., 2013), which may lead to weaker size-based trophic cascades. Low resource availability can result in higher size diversity in zooplankton and fish due to sized-based competition (Arranz et al., 2016; Brucet et al., 2006; García-Comas et al., 2016; Quintana et al., 2015). Because predation is size dependent (Brooks & Dodson, 1965), top-down control may also alter the size structure of prey communities (Iglesias et al., 2008; Jeppesen et al., 2003; Rettig, 2003). A high predation pressure has been shown to reduce size diversity at several trophic levels (e.g. zooplankton and phytoplankton) due to accumulation of individuals in the less predated size classes (Brucet et al., 2010; Quintana et al., 2015; Tavşanoğlu et al., 2015). However, how the size diversity of interacting trophic levels responds simultaneously to different environmental and biotic factors is less clear. The only study available (Brucet et al., 2017) showed that the size structure within a trophic group of the lake pelagic food web could be controlled by the size structure at adjacent trophic levels, as well as by temperature and resource availability.

Analysis of body size distribution across several trophic levels provides understanding of prey-predator interactions and stability in food webs as interactions among species and trophic levels are based on metabolic and size-related networks (Brose et al., 2016; Trebilco et al., 2013; Woodward et al., 2005). Moreover, relationships between the size structure of predators and prey could affect the trophic energy transfer in food webs (Barnes et al., 2010; Jennings et al., 2002) which is described as the ecological efficiency in transferring energy at one trophic level to upper levels (Hairston, & Hairston, 1993). A recent study in a marine system (García-Comas et al., 2016) revealed that high prey size diversity of phytoplankton prevents efficient biomass transfer to upper trophic levels via predation defence or slow population turnover times. That is, blooms formed due to large-sized and colony-forming phytoplankton species that are less vulnerable to grazing by zooplankton may cause high phytoplankton size diversity, and this suppresses the energy flux through the food web (Steiner, 2003; Ye et al., 2013). Furthermore, a high standing biomass of primary producers due to the slower population turnover rates of larger than smaller organisms may inhibit the energy transfer (Yvon-Durocher et al., 2011). However, in ecosystems with high size diversity of predators (e.g. zooplankton), the differently sized predators may benefit from being able to forage on prey items of several sizes, which consequently may facilitate biomass transfer because of diet niche partitioning (García-Comas et al., 2016; Ye et al., 2013).

We conducted a mesocosm experiment with two fish treatments (with and without fish) in Lake Mývatn in Iceland. Lake Mývatn is a naturally eutrophic sub-Arctic lake considered to be mainly driven by bottom-up forces (Einarsson, Gardarsson, Gíslason, & Ives, 2002; Einarsson, Hauptfleisch, Leavitt, & Ives, 2016). Zoobenthos mostly composed of chironomids, accounts for most of the secondary production of the lake (Lindegaard & Jónasson, 1979) and shows strong fluctuations depending on consumer-resource interactions with fish and algae/detritus (Ives, Einarsson, Jansen, & Gardarsson, 2008). However, some investigations have evidenced that top-down processes are also important in shaping the ecosystem processes in Lake Mývatn (Bartrons et al., 2015; Cañedo-Argüelles et al., 2017; Einarsson, 2010; Einarsson & Björk Örnólfsdóttir, 2004). Thus, three-spined stickleback (*Gasterosteus aculeatus*: Gasterosteidae), the most abundant fish species in the lake, demonstrates spatial and temporal variations that are affected by variations in the benthic community (Einarsson et al., 2004). At the same time, blooms of cyanobacteria (mostly *Anabaena*) occur frequently during summer. Although cyclic and semicyclic occurrences of *Anabaena* have been reported, occurrence is highly variable (Einarsson et al., 2004) and concurs with the cycles of zoobenthos. Blooms appear during years when the chironomid population collapses and trigger high internal loading of phosphorus from the sediment (Einarsson & Björk Örnólfsdóttir, 2004). Moreover, some studies have suggested that because *Anabaena* can grow under low N conditions, blooms are related to the naturally low N:P levels in the incoming spring water to the lake (Jónasson & Adalsteinsson, 1979). *Anabaena* blooms also appeared during our mesocosm experiment (Cañedo-Argüelles et al., 2017).

The aim of this study was to assess how cascading top-down effects of fish predation and occurrence of cyanobacteria blooms affect the size structure of interacting trophic levels (zooplankton and phytoplankton). We also explored how such size structure changes in different trophic levels were reflected into the trophic transfer efficiency through the food web. We had two hypotheses:

1) Size diversity (based on individual body sizes) of zooplankton and phytoplankton would respond differently to top-down and bottom-up processes and the intensity of the response would differ before and after the cyanobacteria bloom. We expected that zooplankton size diversity would mainly be driven by top-down effects, at least before the bloom, and that diversity would decrease due to size-selective fish predation, resulting in dominance by smaller sized zooplankton individuals. We also expected that the top-down effects would weaken after the bloom. In contrast, as mentioned above, we expected that the size structure of phytoplankton would be less affected by trophic cascades and be driven rather by changes in resource availability (i.e. productivity) than by predation, particularly during the blooms of the large-sized and colony-forming *Anabaena* (Brucet et al., 2017).

2) Trophic transfer efficiency would be lower in the fish enclosures due to lower zooplankton size diversity before the bloom (García-Comas et al., 2016). Moreover, the higher size diversity of phytoplankton during the *Anabaena* bloom would reduce energy transfer to higher trophic levels (Auer, Elzer, & Arndt, 2004) due to decreased edibility, low nutritional value and increased predation defenses of bloom-forming phytoplankton (Ger, Urrutia-Cordero, et al., 2016; Müller-Navarra, Brett, Liston, & Goldman, 2000; Steiner, 2003).

Methods

Study site

Lake Mývatn (37 km^2) is a shallow eutrophic crater lake, located in the north-eastern part of Iceland (65°40′ N, 17°00′ W, 277 m a.s.l.). The lake is divided into two major basins – the North Basin (8.5 km^2) and the South Basin (28.2 km^2). Maximum depth is nearly 4 m in the South Basin and around 5.5 m in the North Basin due to dredging in connection with diatomite mining. The mean depths of the South and the North Basin are around 2.5-4 m and 1-2.5 m, respectively (Einarsson et al., 2004). The water column is vertically mixed during summer, and thermal stratification starts in mid-winter when the thermocline develops under ice (Ólafsson, 1979a). Ice cover lasts about 190 days (Rist, 1979). The lake is mostly fed by artesian springs through groundwater supplies from its eastern shore. Springs from a nearby geothermal area feed the North Basin and their temperature may reach 30 °C. The springs entering the South Basin are colder (5 °C) (Ólafsson, 1979a). The estimated inputs of phosphorus, nitrogen and silica from the springs are 0.05 mol m^{-2} $year^{-1}$, 0.14 mol m^{-2} $year^{-1}$ and 12 mol m^{-2} $year^{-1}$, respectively (Ólafsson, 1979b). The spring water is very rich in phosphate (1.62 µM). The reactive basaltic bedrock and the low vegetation in the catchment of the lake, together with the high temperature and constant flow, create high nutrient concentrations and high pH in the incoming springs (Einarsson et al., 2004; Thorbergsdóttir & Gíslason, 2004). Internal nutrient loading and nitrogen fixation by cyanobacteria play a significant role in the nutrient dynamics of the lake (Einarsson et al., 2004; Ólafsson, 1979b).

Experimental set-up

The experiment included two fish treatments (with/without fish) and each treatment had four replicates. Eight circular enclosures (diameter: 1.2 m) were established in the western part of the South Basin of the lake. One of the fish enclosure replicates was omitted from the analyses because it was destabilised after a storm event, leading to entry of lake water and fish. The experiment lasted for 58 days, from 23 June to 20 August 2014, with five biweekly samplings (Day 1, 16, 30, 44 and 58)

The enclosures were made of a polyethylene tube folded around a metal cylinder, which was attached to a plastic hoop placed 30 cm above the surface and inserted 20 cm into the sediment. The enclosures were located randomly in the same area to avoid significant differences among benthic parameters, such as hatching of zooplankton. They were filled with lake water using a net with 1 mm mesh size to prevent fish entrance. The initial water level in all enclosures was 0.8 m and this did not change significantly during the experiment. Before the experiment, macrophytes were harvested from the bottom of the enclosures to establish similar starting conditions. One week after the establishment of the set-up, a mixture of plankton was sampled near the experimental site using a vertical plankton net from a moving boat. Of the plankton mixture, 1 L was added to each enclosure to create a natural aquatic food web with similar communities. Three-spined stickleback, a common and the most abundant planktivorous fish in the lake, was used in the fish treatment (Millet, Kristjánsson, Einarsson, & Räsänen, 2013). The species is an important top-down driver of the trophic cascade in Lake Mývatn (Adalsteinsson, 1979; Gislason, Gudmundsson, & Einarsson, 1998). Two weeks after the addition of plankton inoculum, four similar-sized three-spined sticklebacks (about 5.5 cm), caught with fyke nets close to the experimental set-up, were added to the enclosures with fish. In previous studies conducted in the South Basin and the North Basin, stickleback densities ranged between 0.3 and 2.5, and 100 and 200 individuals per m^2, respectively (Gislason et al., 1998), which also covers the stickleback density used in our experiment.

Sampling and laboratory analysis

Three days after the fish addition, biweekly samples were taken from all enclosures from 23 June until 20 August. Physical variables such as temperature (°C), pH, conductivity ($\mu S\ cm^{-1}$) and dissolved oxygen ($mg\ L^{-1}$) were measured in situ using a Hanna multiparameter meter (Hanna Instruments, USA). Water transparency (cm) was measured with a Secchi disk. Water samples (10-12 L) were taken with a 1-m long Plexiglas cylinder (diameter: 6 cm) (Ramberg, 1979) along the water column from three different points in each mesocosm and subsequently mixed for analysis of chemical and biological variables. The samples were analysed for total phosphorus (TP, $\mu g\ L^{-1}$), soluble reactive phosphorus (SRP, $\mu g\ L^{-1}$), total nitrogen (TN, $\mu g\ L^{-1}$), ammonium (NH_4^+, $\mu g\ L^{-1}$) and chlorophyll-a (chl-a, $\mu g\ L^{-1}$). Detailed information about chemical analysis can be found in Cañedo-Argüelles et al. (2017).

From the mixed water sample (10-12 L), 7 L were filtered through a filter with 50 µm mesh size and stored in 4% acid Lugol's solution for zooplankton identification and enumeration. Zooplankton samples were identified to species level except some Rotifera that were identified to genus level. All copepods were classified as adults, copepodites and nauplii. The size of at least 25 individuals (if possible) from each zooplankton taxon was measured. For copepods, size was measured independently for different life stages (adults, copepodites and nauplii) to represent ontogenetic shifts. For all zooplankton taxa, biomass dry weight was computed using allometric relationships between weight and body length in the literature (Bottrell et al., 1976;

Dumont et al., 1975; McCauley, 1984). For phytoplankton, unfiltered water samples were taken and stored in 4% acid Lugol's solution. Phytoplankton were identified to genus level and 5-10 individuals from each genus were measured.

Total length and width were measured for single cells, filaments and colonies.

Phytoplankton biovolume was calculated from body measurements using geometric formulae (Sun & Liu, 2003) and converted to biomass by multiplying with a factor of 0.29 (Reynolds, 1984). For both zooplankton and phytoplankton, at least 100 individuals of the most abundant taxa were counted.

Size diversity and estimation of trophic transfer efficiency

Size diversity was calculated from individual length measurements of zooplankton and phytoplankton taxa for each enclosure and each sampling date according to Quintana et al. (2008). It is a simple representation of the size structure of a community based on the Shannon diversity index, but for continuous variables (herein length) (Brucet et al., 2006; Quintana et al., 2008). The size diversity index (μ_2) was computed following the formula:

$$\mu_2(x) = -\int_0^\infty \rho_x\,(x)\log_2 \rho_x(x)dx$$

where p_x (x) is the probability density function of size x. Non-parametric kernel estimation approach was applied to find the probability density function, which gives reliable estimates of most size distributions. Dispersion of the function is regulated by a bandwidth parameter and the estimator is calculated as the sum of kernel functions centered at the sample points (Quintana et al., 2008). Size diversity is very useful and easy to interpret as it defines a single value that is comparable across studies and represents the size range and evenness of a size distribution. High size diversity indicates a broad size range with equal distribution of the different sizes within a size spectrum, whereas low size diversity specifies a narrow size range with high dominance of certain sizes (Emmrich et al., 2011; Hurlbert, 1971; Quintana et al., 2016). Since size diversity is calculated as the relative contribution of different sizes along the size distribution, the relationship between size diversity and total biomass is not a result of spurious correlation but of the ecosystem processes (García-Comas et al., 2016; Ye et al., 2013).

Although predator to prey biomass ratios have been used as a predictor of top-down control in several studies (Cañedo-Argüelles et al., 2017; Jeppesen et al., 2003; Ye et al., 2013), in our study we used predator (zooplankton) to prey (phytoplankton) biomass ratio (PPBR) in log scale ($\log_{10}$ [PPBR]) as a proxy of the trophic transfer efficiency (TTE) to reflect the efficiency in energy transfer between adjacent trophic levels through the trophic cascade. TTE was originally described by Lindeman (1942) as the total production ratio between adjacent trophic levels. Low TTE indicates low transfer of production (i.e. biomass) from a low trophic level to upper trophic levels, and high standing production at lower trophic levels whereas high TTE implies the opposite. However, because it is difficult and time consuming to measure the production rate in natural ecosystems, we did not evaluate it. Moreover, it has been shown that in planktonic systems TTE varies mostly with biomass ratios rather than with production ratios (Huntley & Lopez, 1992). The use of $\log_{10}$ (PPBR) is straightforward and has been validated by many studies (Gaedke & Straile, 1994; García-Comas et al., 2016; Jennings et al., 2002; Yvon-Durocher et al., 2011). It also agrees with the postulates of Pawlowsky-Glahn & Buccianti (2011) that the proxy prevents spurious correlations that may appear when proportions and ratios are used in statistical analysis.

Data analysis

All data were analysed using the “nlme” (Pinheiro, Bates, DebRoy, Sarkar, & Team, 2017) and “car” (Fox & Weisberg, 2011) packages in R version 3.3.0 (R Core Team, 2018).

Linear mixed models (LMMs) were run to test how fish predation and cyanobacteria blooms affected zooplankton and phytoplankton size diversity and TTE and, additionally, to assess the influence of other environmental and biotic factors (e.g. resource availability).

In total, we ran 3 models with phytoplankton size diversity, zooplankton size diversity and TTE as response variables. The models tested the influence of fish treatment (factor), *Anabaena* occurrence (factor), fish × *Anabaena* occurrence interaction and additional relevant biotic and environmental predictors on phytoplankton size diversity, zooplankton size diversity and TTE. As biotic and environmental predictors, in the model for zooplankton size diversity, we included phytoplankton size diversity (as a measure of resource availability). In the model for phytoplankton size diversity, we included TP (ln-transformed) (see Figure 18), zooplankton biomass (ln-transformed) and zooplankton size diversity as indicators of resource availability, predation pressure and size-structured predation, respectively. In the model for TTE, we included phytoplankton and zooplankton size diversity as predictor variables. We did not include sampling day as this was strongly correlated with the following predictors: phytoplankton size diversity, zooplankton size diversity and phytoplankton total biomass (Table 8). Thus, the general structure of the three models were:

RESPONSE VARIABLE ~ fish (fish/no fish) + *Anabaena* occurrence (before/after) + (fish × *Anabaena* occurrence) + specific biotic and environmental predictors.

Marginal R^2 (variance explained by fixed factors) and conditional R^2 (variance explained by fixed and random factors) values (Nakagawa & Schielzeth, 2013) of the LMMs were calculated by applying the r.squaredGLMM function in “MuMIn” package (Bartoń, 2016). All graphs were produced with the “ggplot2” package (Wickham, 2009).

For all models, all predictor variables were scaled and centered prior to analysis in order to better compare and interpret predictors with different scales. Normality was checked by Shapiro-Wilk’s test before analysis ($p>0.05$) and variables were ln-transformed, when necessary. The correlation structure of the predictor variables was checked, and highly correlated variables ($r>0.6$) (Emmrich et al., 2011) were removed before the analysis (see Table 8 in the appendix). As a random effect, the intercept was allowed to change with each enclosure to account for the temporal pseudo-replication. We then tested whether or not a random slope for sampling day (either correlated and/or independent) would improve the model and compared the models with different random effect structures using the maximum likelihood estimation method. Finally, we did not include sampling day as a random slope in the models because it did not improve the model parameters. The most parsimonious models were selected from the full models by automatic step-wise selection (function stepAIC from MASS package;

Venables & Ripley, 2002) based on Akaike information criteria (AIC) values. Residual plots of the most parsimonious models were checked for normality.

Results

The community composition and size structure of zooplankton and phytoplankton changed during the experiment and between treatments. Large and colony-forming cyanobacteria, *Anabaena* started to appear on day 30 and became dominant hereafter, and the biomass of Cladocera was lower in the enclosures with fish (see Figure 2 & 3 in Cañedo-Argüelles et al., 2017). Moreover, zooplankton size diversity started to decrease, while phytoplankton size diversity increased after the occurrence of *Anabaena* bloom on day 30 (Figure 9), causing a decline in TTE (Figure 10). Although the differences in zooplankton, phytoplankton size diversity and TTE between fish treatments were not significant in any sampling day (t-test, $p > 0.05$, Benjamini Hochberg correction), some differences were observed between fish treatments for zooplankton size diversity and TTE (Figure 10 & Figure 11).

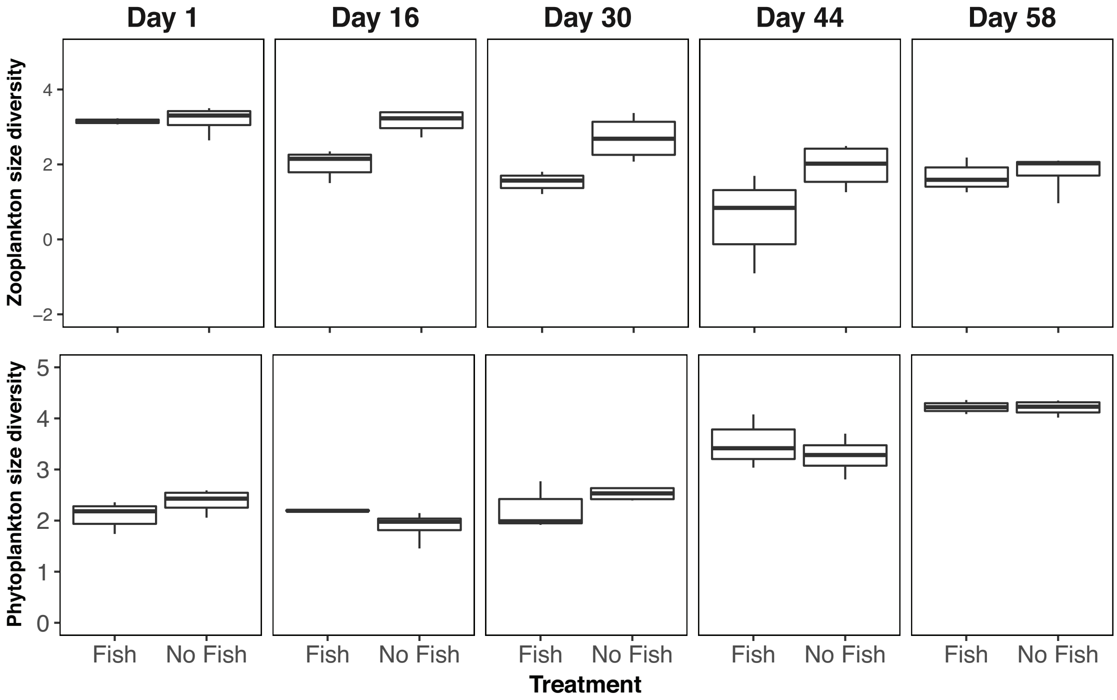

Figure 9. Zooplankton and phytoplankton size diversity for different treatments (fish, no fish) on each sampling day. Fish treatment and *Anabaena* occurrence were significant for zooplankton size diversity, while only *Anabaena* occurrence was significant for phytoplankton size diversity.

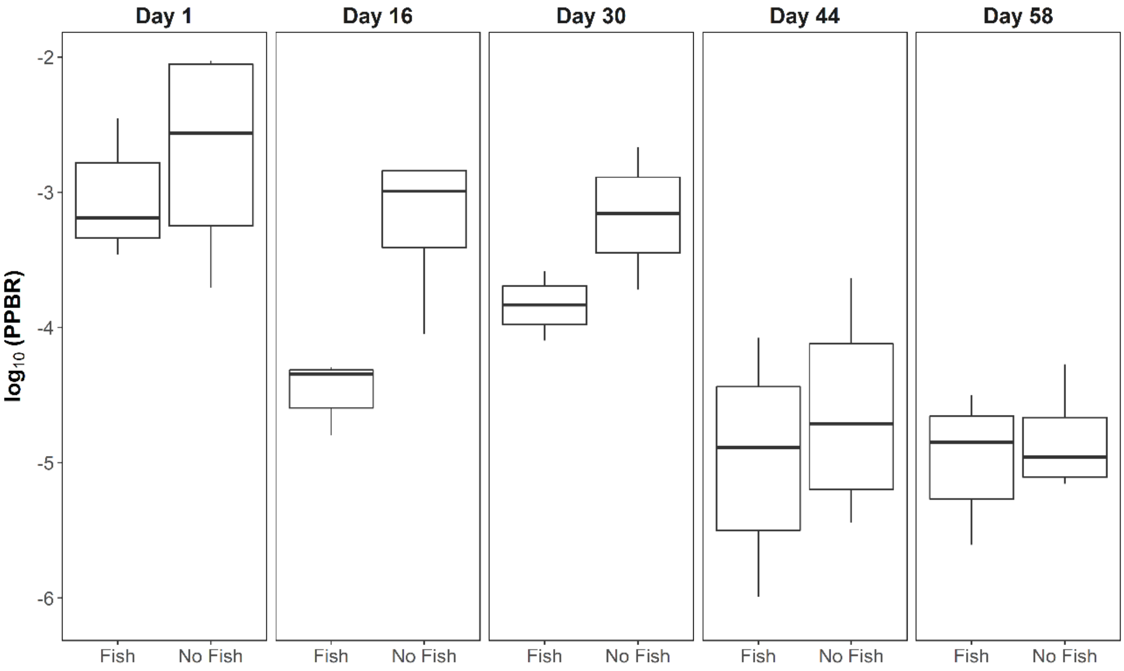

Figure 10. Log_{10} (PPBR) (=TTE) for different treatments (fish, no fish) on each sampling day. Zooplankton size diversity and *Anabaena* occurrence were significant for TTE.

According to LMMs, zooplankton size diversity was negatively related to fish treatment and *Anabaena* occurrence (p<0.05 and p<0.01, respectively, Table 4). We did not include phytoplankton total biomass in the final model for zooplankton size diversity because it was correlated with phytoplankton size diversity (Table 8) and the most parsimonious model while using phytoplankton total biomass was the same as the one with phytoplankton size diversity (Table 4).

Table 4. Results of linear mixed models showing environmental and biotic factors affecting zooplankton size diversity, phytoplankton size diversity, and TTE. Here, we show only best models with a random effect of the enclosures on the intercept. Significant p values are highlighted in bold. The initial models were as: RESPONSE VARIABLE ~ fish treatment (factor: fish/no fish) + *Anabaena* occurrence (factor: before/after) + (fish × *Anabaena* occurrence) + biotic and environmental predictors). The factor levels "before" (*Anabaena* occurrence) and "no fish" (fish treatment) were baselines for the models. TTE, trophic transfer efficiency; AIC, Akaike information criteria; TP, total phosphorus.

Response variable	Predictors	AIC	Estimate	SE	DF	t-value	*p* value	Conditional R^2	Marginal R^2
Zooplankton size diversity	Fish treatment (fish)	89.24	-0.76	0.25	5	-3.07	**0.03**	0.47	0.47
	Anabaena (after)		-0.81	0.18	27	-4.55	**<0.01**		
Phytoplankton size diversity	ln TP	54.83	0.19	0.10	26	1.89	0.07	0.78	0.78
	Anabaena (after)		0.91	0.15	26	6.24	**<0.01**		
TTE	Zooplankton size diversity	75.19	0.58	0.12	26	4.76	**<0.001**	0.69	0.69
	Anabaena (after)		-0.56	0.17	26	-3.25	**<0.01**		

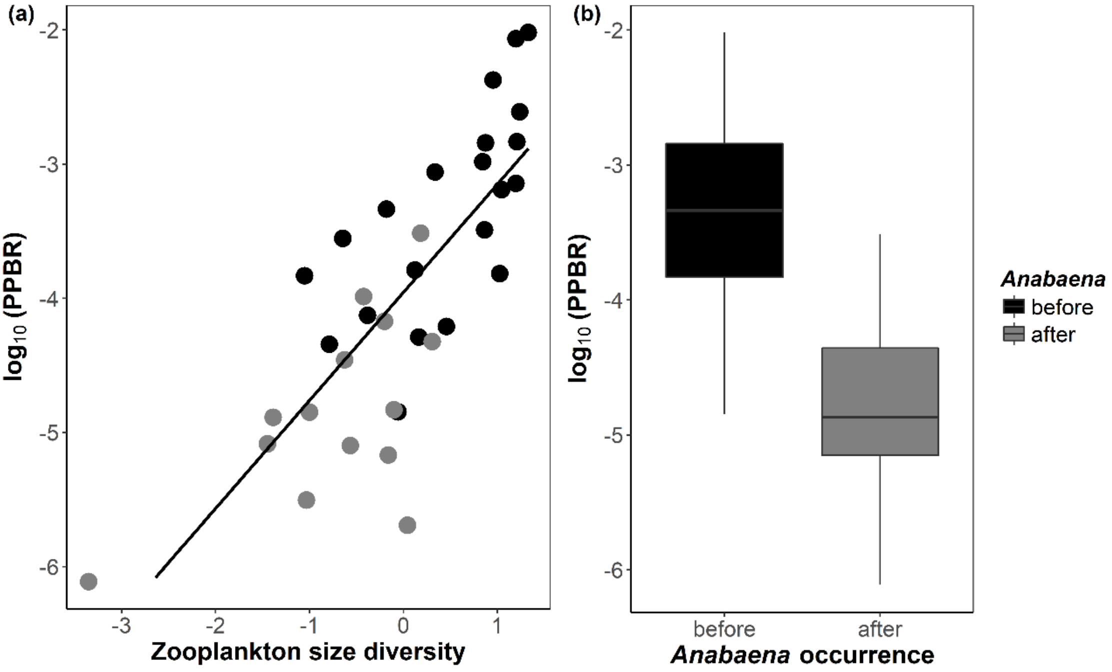

Figure 11. Effect of (a) predator (zooplankton) size diversity on biomass transfer efficiency (from phytoplankton to zooplankton) ($\log_{10}$ [PPBR]) (n=35, Marginal R^2=0.69, Table 4). (b) Effect of *Anabaena* occurrence (before/after) on biomass transfer efficiency ($\log_{10}$ [PPBR]) (Table 4, p<0.01). Different colours represent before and after *Anabaena* across all sampling dates.

Phytoplankton size diversity was significantly higher after *Anabaena* bloom (factor *Anabaena* occurrence $p<0.01$, Table 4) and slightly positively (but not significantly) related to productivity (using ln TP as a proxy, see Figure 18) ($p= 0.07$, Table 4). In fact, productivity, *Anabaena* biomass and phytoplankton size diversity were highly correlated (r> 0.6, Table 8). TTE was significantly lower after *Anabaena* bloom (factor *Anabaena* occurrence $p<0.001$, Table 4) and related positively to zooplankton size diversity ($p<0.01$, Table 4 and Figure 11).

Discussion

Our results suggest that both predation and resource availability influence zooplankton and phytoplankton size structure, but in different ways. While the zooplankton size structure was mainly shaped by fish predation and the cyanobacteria bloom, phytoplankton size structure responded mainly to the bloom, which was apparently driven by productivity. The results also suggest that the cyanobacteria blooms altered the energy transfer in the trophic cascade of Lake Mývatn. Concordantly, Cañedo-Argüelles et al. (2017) found a higher abundance of smaller zooplankton taxa (e.g. Rotifera) in the enclosures with fish. Several other experimental and field studies (Brucet et al., 2010; Iglesias et al., 2011; Jeppesen et al., 2003) have shown that the zooplankton community had a narrower size range and was dominated by smaller individuals along the size distribution in the presence of fish.

Occurrence of cyanobacteria blooms was related to low zooplankton size diversity. Comparable results were found in a spatial study of Lake Mývatn in which smaller zooplankton taxa were associated with *Anabaena* (Bartrons et al., 2015). Cyanobacteria are unpalatable to most zooplankton (particularly some of the large cladocerans), as the colonial and filamentous forms clog the feeding apparatus of the zooplankton, thereby reducing zooplankton grazing rates (DeMott, Gulati, & Van Donk, 2001; Paerl & Otten, 2013; Webster & Peters, 1978; Wilson, Sarnelle, & Tillmanns, 2006). This may also explain the negative correlation between the size diversity of zooplankton and the size diversity of phytoplankton (the latter mainly reflecting *Anabaena* abundance).

Another explanation of the reduced size diversity of zooplankton with the occurrence of *Anabaena* might be that cyanobacteria toxins such as polypeptide microcystins alter the feeding behaviour of large zooplankton through feeding inhibiton (DeMott, Zhang, & Carmichael, 1991) and prey avoidance (Ger, Faassen, et al., 2016). Our results indicating negative consequences of blooms on zooplankton size diversity agree with those of previous studies where similar adverse effects of toxicity on zooplankton size structure have been observed (Ghadouani, Pinel-Alloul, & Prepas, 2006; Zhang et al., 2013). In addition, they support the finding of Bell (2002) that the cascading effect of planktivorous fish did not extend from zooplankton to phytoplankton due to dominance of inedible phytoplankton.

Phytoplankton size diversity was not affected by fish predation throughout the experiment. In contrast, we found a strong relationship of *Anabaena* biomass and phytoplankton size diversity with resource availability in both fish treatments (Table 8). In Lake Mývatn, internal loading of nutrients commonly occurs with wind-induced sediment resuspension (Einarsson et al., 2004). Because tube-forming chironomids prevent resuspension by binding the sediment, in years with low abundance of chironomid larvae (midges), high resuspension, high phosphorus loading and thus extensive *Anabaena* blooms occur (Ólafsson & Paterson, 2004; Webert et al., 2017). Naturally low N:P levels in inflows due to the high P loading from the volcanic region could additionally enhance cyanobacteria blooms (Jónasson & Adalsteinsson, 1979). Similarly, studies undertaken in freshwater and marine ecosystems have shown that the size structure of phytoplankton responds primarily to the availability of nutrients in the system (Brucet et al., 2017; Garzke et al., 2015; Quintana et al., 2015; Sommer et al., 2017). While small-sized phytoplankton dominate under oligotrophic conditions due to a high surface area to volume ratio and higher growth rates, larger individuals are superior competitors under eutrophic conditions because they are better at nutrient storage (Litchman & Klausmeier, 2008; Robert H. Peters & Downing, 1984; Romo et al., 2004).

As expected, we found cascading effects of fish on TTE, TTE being lower when the zooplankton size diversity was controlled by fish. This supports earlier studies revealing a negative relationship between size-selective fish predation and the transfer of energy from primary to secondary producers (de Bernardi, Giussani, & Manca, 1987; Jansson et al., 2007). Additionally, throughout the experiment, high phytoplankton (prey) size diversity induced by the cyanobacteria bloom reduced TTE, while high zooplankton (predator) size diversity stimulated biomass transfer through the trophic cascade. This is in agreement with a study conducted in a marine system (García-Comas et al., 2016).

A possible explanation of the lower TTE with decreased predator size diversity is niche partitioning. Greater predator size diversity may create several different feeding niches as differently sized predators collectively can prey on a wider range of prey sizes (Brucet et al., 2008; García-Comas et al., 2016; Ye et al., 2013). When the predator community was dominated by zooplankton of less diverse sizes, as in the beginning of the experiment due to fish predation in some enclosures, predators occupied less feeding niches and the energy transfer in the trophic cascade was therefore lower. Similarly, after the bloom, zooplankton size diversity decreased in all enclosures in both the presence and absence of fish due to the high prey (phytoplankton) size diversity. This prevented effective transfer of energy across the trophic cascade, and *Anabaena* bloom drove the TTE. This may be due to decreased grazing of zooplankton on phytoplankton because of the inedibility of large-sized or colony-forming phytoplankton (Steiner, 2003) or decreased phytoplankton population turnover rates (Yvon-Durocher et al., 2011). A slower turnover rate of primary producers causes accumulation of biomass at lower trophic levels and decreases the energy transfer, thereby destabilising trophic cascades (Jones & Jeppesen, 2007).

We acknowledge that our investigation has certain limitations. We analysed a simple trophic food web with three interacting trophic levels – planktivorous fish, zooplankton and phytoplankton. In more complex systems, omnivory and intraguild predation could be important factors for trophic relationships (Chang et al., 2014; Finke & Denno, 2005; Post & Takimoto, 2007). We also recognise that our experimental design did not allow tests of other trophic components such as the microbial loop. The microbial loop may increase the nutrient cycling and energy transfer in food webs (Blanchard, Heneghan, Everett, Trebilco, & Richardson, 2017). Although the role of microorganisms is valuable in food web studies to elucidate complex networks, microbial loop interactions have not yet been thoroughly investigated in size-based ecosystem studies (Blanchard et al., 2017).

In conclusion, our results suggest that size-based interactions across trophic levels could be important determinants of trophic cascade relationships and should be considered to properly manage freshwater ecosystems in the future.

They also support the documented well-known negative effect of planktivorous fish predation on the size structure of zooplankton communities. However, the occurrence of large-sized cyanobacteria interfered with the cascading effect of fish predation on zooplankton size structure, reducing the energy transfer through the food web. In contrast, phytoplankton size diversity tended to be significantly controlled by resources and not by consumers. This indicates that productivity might overrule size-based cascading interactions and prevent proper energy transfer in freshwater food webs. Understanding size-based interactions in a warming climate is crucial since stronger predation from smaller fish (Jeppesen et al., 2012) and increased occurrence of cyanobacteria blooms (Jöhnk et al., 2008) are to be expected. This will create disturbance of natural aquatic zooplankton communities with potential implications for ecological state and ecosystem functioning (Velthuis, De Senerpont Domis, et al., 2017; Zhang et al., 2013).

Acknowledgments

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CHAPTER 3

Short-term fish predation destroys resilience of zooplankton communities and prevents recovery of phytoplankton control by zooplankton grazing

Ersoy, Z., Bartrons, M., Mehner, T., Brucet, S. Short-term fish predation destroys resilience of zooplankton communities and destroys recovery of phytoplankton control by zooplankton grazing. In review, PLoS ONE.

Abstract

Planktivorous fish predation directly affects zooplankton biomass, community and size structure, and may indirectly induce a trophic cascade to phytoplankton. However, it is not clear how quickly the zooplankton community structure and the cascading effects on phytoplankton recover to the unaffected state (i.e. resilience) once short-term predation by fish stops. The resilience has implications for the ecological quality and restoration measures in aquatic ecosystems. To assess the short-term zooplankton resilience against fish predation, we conducted a mesocosm experiment consisting of 12 enclosures, 8 with fish and 4 without fish. Plankton communities from a natural lake were used to establish phytoplankton and zooplankton in the mesocosms. High biomasses (about 20 g wet mass m^{-3}) of juvenile planktivorous fish (perch, *Perca fluviatilis*) were allowed to feed on zooplankton in fish enclosures for four days. Thereafter, we removed fish and observed the recovery of the zooplankton community and its cascading effect on trophic interactions in comparison with no fish enclosures for four weeks. Short-term fish predation impaired resilience in zooplankton community by modifying community composition, as large zooplankton, such as calanoids, decreased just after fish predation and did not re-appear afterwards, whereas small cladocerans and rotifers proliferated. Total zooplankton biomass increased quickly within two weeks after fish removal, and at the end even exceeded the biomass measured before fish addition. Despite high biomass, the dominance of small zooplankton released phytoplankton from grazer control in fish enclosures. In contrast, in no fish enclosures without predation disturbance, a high zooplankton:phytoplankton biomass ratio accompanied by low phytoplankton yield (Chlorophyll-a:Total phosphorus ratio) reflected phytoplankton control by zooplankton. Accordingly, the zooplankton community did not recover from the effect of fish predation, indicating low short-term resilience. Comprehensive views on short and long-term resilience of zooplankton communities are essential for restoration and management strategies of aquatic ecosystems to better predict responses to global warming, such as higher densities of planktivorous fish.

Keywords: resilience, zooplankton, fish predation, trophic interactions

Introduction

Predators play a crucial role in food webs, by shaping the structure of prey communities and affecting ecosystem functioning, for example through trophic cascades, modification of energy flow and altered biodiversity (Carpenter et al., 1985; Pace et al., 1999; Paine, 1966). In aquatic ecosystems, predation by planktivorous fish can strongly affect zooplankton biomass, community composition and size structure (Brooks & Dodson, 1965; Brucet et al., 2010; Jeppesen et al., 2003, 2004). Several enclosure experiments and field studies have demonstrated that planktivorous fish predation caused a decrease in abundance of big cladocerans (e.g *Daphnia*) while favoring small cladocerans (e.g *Bosmina, Chydorus*), copepods and rotifers (Beklioglu & Moss, 1996; Jakobsen, Hansen, Jeppesen, Grønkjær, & Søndergaard, 2003; Vanni, 1987). Fish predation can also have indirect effects on phytoplankton communities either through trophic cascades (Carpenter et al., 2001; Iglesias et al., 2011; Jeppesen et al., 2014) or nutrient recycling (Attayde & Hansson, 2001; Schindler, 1992; Schindler, Knapp, & Leavitt, 2001). Phytoplankton could benefit from controlled zooplankton grazing by fish and/or extra nutrients enhanced by fish resuspension (Matsuzaki, Usio, Takamura, & Washitani, 2007) or excretion (Brabrand, Faafeng, & Nilssen, 1990). For this reason, lake restoration measures like biomanipulation mostly focus on reducing fish predation on zooplankton by planktivorous fish removal. This favors the recovery of large-sized zooplankton, which are the most efficient phytoplankton grazers, and leads to improvement of water quality (Mehner, Benndorf, Kasprzak, & Koschel, 2002; Søndergaard, Lauridsen, Johansson, & Jeppesen, 2017; Søndergaard, Liboriussen, Pedersen, & Jeppesen, 2008).

With the increase of anthropogenic influences including climate change, habitat disturbance, overfishing and introduced species, the need to understand aquatic ecosystems' resilience to disturbance has become more urgent. Resilience is defined as the ability of a system to recover after a disturbance and return to pre-disturbance state (Ives & Carpenter, 2007; Pimm, 1991). An example of disturbance for aquatic ecosystems could be higher densities of planktivorous fish, for example caused by climate warming or fish stocking, whose higher predation may induce trophic cascades and impair ecosystem functioning in terms of biodiversity and energy flow (Ersoy et al., 2017; Jeppesen et al., 2014; Zhang et al., 2013). In this sense, the capacity to identify the time for recovery and re-organisation of the zooplankton community structure after planktivorous fish removal is crucial for application of management strategies aimed to restore lake ecological status, as well as to understand failures in management (Hilt, Brothers, Jeppesen, Veraart, & Kosten, 2017; Knapp & Sarnelle, 2008; Verdonschot et al., 2013).

Although there are many studies investigating the cascading effects of fish predation on zooplankton and phytoplankton communities (Bartrons et al., 2018; Brucet et al., 2017; Hansson et al., 2007; Nõges, Järvalt, Haberman, Zingel, & Nõges, 2016), there are only a few focusing on zooplankton communities' resilience to predation (Donald, Vinebrooke, Anderson, Syrgiannis, & Graham, 2001; Knapp, Hawkins, Ladau, & McClory, 2005; Knapp et al., 2001; Knapp & Sarnelle, 2008; Mcnaught et al., 1999). These former studies investigated the zooplankton communities in several lakes in North America, which had a history of fish stocking but experienced gradual fish removal or disappearance due to unsuitable spawning grounds. Subsequently, the zooplankton community returned within a few years to their previous conditions characterized by large-sized taxa, indicating long-term resilience. However, it remains unanswered how fast a zooplankton community recovers, once fish predation is completely stopped, in the temporal dimension of days or weeks. Answering this question could potentially improve our understanding about short-term resilience and stability of zooplankton communities and may help develop better management and conservation measures after sudden changes in freshwater ecosystems.

Here, we tested the short-term resilience of the zooplankton community to fish predation using a mesocosm experiment. We further assessed whether the potential recovery of zooplankton biomass after the stop of fish predation induced a comparably quick recovery of the top-down control by zooplankton on phytoplankton (expressed as zooplankton:phytoplankton biomass (zoo:phyto biomass) and chlorophyll-a:total phosphorus ratios (chla:TP)). We hypothesized that size-selective fish predation would affect the zooplankton biomass and community composition and would shift mean length towards smaller individuals (Brucet et al., 2010; Ersoy et al., 2017), hence reducing top-down control on phytoplankton and increasing phytoplankton yield (chla:TP) (Ersoy et al., 2017; Lemmens, Declerck, Tuytens, Vanderstukken, & de Meester, 2017). We further expected that the zooplankton community is highly resilient and hence would quickly return to the pre-disturbance attributes within a few days after stop of predation. However, cascading effects on phytoplankton were expected to show a time lag in the response because phytoplankton has short turnover rates and hence may profit from the temporally reduced zooplankton grazing.

Methods

Ethics statement

The specific experiment was not seperately approved by an animal research ethics committe. However, there is an ethics approval for experimental work with perch, issued to TM (Ernährung / Verhaltenstypen / Fische – G 0115 / 14, Landesamt für Gesundheit und Soziales Berlin, Germany). Animal procedures were conducted following German Animal Welfare Laboratory Regulations (Tierschutzversuchstier-verordnung, Anlage 2 TierSchVersV, https://www.gesetze-im-internet.de/tierschversv/BJNR312600013.html). Fish is euthanized with 9:1 95% EtOH:clove-oil solution (CarlRoth, Karlsruhe, Germany) and a subsequent hit on the head.

Experimental set-up

We established 12 circular and closed enclosures (diameter: 1.2 m) inside a small channel connected to Lake Müggelsee at the IGB's ground in Berlin (ca. 80-90 cm deep). The initial water level in all enclosures was 1 m (~1000 L) and this did not change substantially during the experiment. To avoid stratification and ensure homogeneity and mixing in the enclosures, small aquarium water pumps (Sera pond precision, pond pump SP 500, Heinsberg, Germany) were installed at the mid-bottom of each enclosure. Nets (5 x 5 cm) were placed above the enclosures to avoid impact from birds, falling leaves etc. Before the experiment started, plankton inoculum and nutrients were added on certain days (see day numbers with negative sign in Figure 12). The experiment lasted for 43 days, from 30 May to 11 July 2016 with five samplings (days 1, 8, 15, 29, 43).

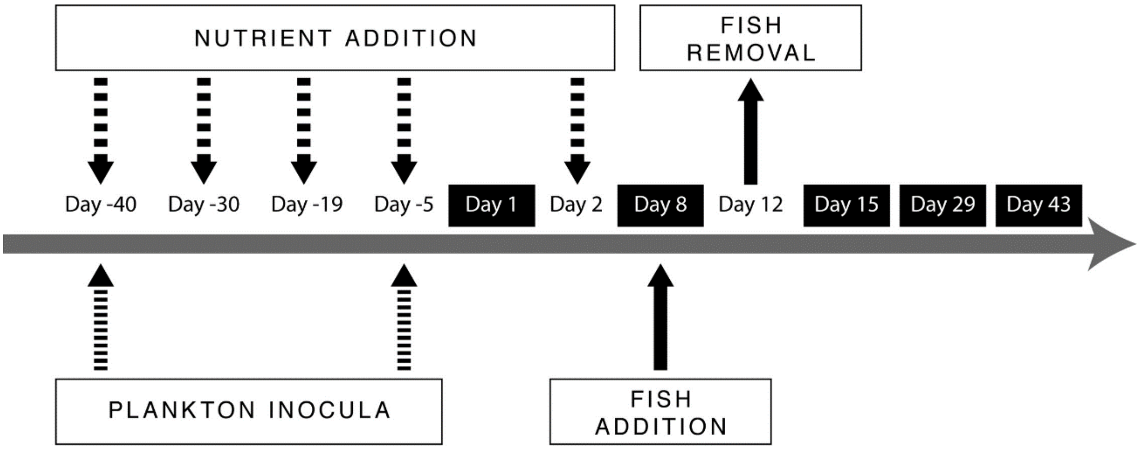

Figure 12. Experimental schedule showing plankton inoculation, fish addition, removal and sampling days. Days enframed with black show the sampling days.

Nutrient addition

Both N and P were added before the experiment started to counteract the concentration decrease from denitrification and sedimentation and to enable appropriate plankton development throughout the experiment.

Na_2HPO_4 (Sodium phosphate dibasic dehydrate) and $Ca(NO_3)_2$ (Calcium nitrate tetrahydrate) were used as a P and N-source, respectively. The target nutrient concentrations were 175 µg P L^{-1} and 1.5 mg N L^{-1} in each enclosure, and hence initially 180 mg P and 1545 mg of N were added per enclosure. In response to declining nutrient concentrations as measured in the enclosures, nutrients were added at days -40 (i.e. 40 days before the first sampling), -30, -19,-5 and 2 to facilitate phytoplankton growth (Figure 12).

Plankton inoculum

Zooplankton and phytoplankton inocula from Lake Müggelsee were used to establish plankton communities in the mesocosms. Before the experiment started, lake water (2000 L) was filtered through 30 µm mesh size and mixed to create a natural mix of phytoplankton and zooplankton (day -40). From the plankton mixture, 3.5 L was added to each enclosure. The water temperatures were low in spring 2016, and hence the zooplankton communities in Lake Müggelsee consisted of only a few larger crustaceans. Therefore, a second inoculum of natural zooplankton was prepared at day -5 by filtering nearly 2300 L of water from the lake through 100 µm mesh and adding the content of two horizontal net hauls (mesh size: 100 µm, about 5 minutes duration). The zooplankton inoculum was gently mixed, and 1.5 L of the mixture was added to each mesocosm.

Sampling and laboratory analysis

Sampling started at day 1 (Figure 12), about one week after the addition of nutrients and the second plankton inoculum which were conducted on day -5. Three water samples (about 7 L each) were taken with a water sampler at the surface, from the middle and the bottom layer of each enclosure and mixed thoroughly for analysis of chemical and biological variables. One part of mixed samples (about 1.5 L) was analysed for total phosphorus (TP, µg L^{-1}) and chlorophyll-a (chla, µg L^{-1}). TP was determined using ascorbic acid-molybdate complex following persulfate digestion [38]. For chla analyses, water samples (100-200 ml) were filtered through 25 mm diameter Sartorius MGF Glass-Microfiber Disc. The filters were placed into 2 ml reaction vessels, frozen at -80 ºC, freeze-dried and thereafter stored at -25 ºC in the dark until analysis. Chla was measured using high-performance liquid chromatography (HPLC) following the methodology from Shatwell, Nicklisch, & Köhler (2012). For calculating phytoplankton biomass, we converted chla to dry weight biomass (µg L^{-1}) by multiplying with 66 (Reynolds, 1984).

From the mixed water sample, another 5 L were filtered through a 30 µm mesh and stored in 4% formaldehyde solution for zooplankton quantification. Large zooplankton (cladocerans and copepods) were counted and their length measured under a stereomicroscope while rotifers and copepod nauplii were counted and measured under a light microscope. All organisms were identified to species level except some rotifers that were identified to genus level. We measured at least 20 individuals (if possible) from each taxon and counted at least 100 individuals of the most abundant taxa. We classified copepods as adults, copepodites and nauplii to account for differing abundances during ontogeny. For all zooplankton groups, we calculated biomass by using available allometric relationships between weight and body length (Bottrell et al., 1976; Dumont et al., 1975; McCauley, 1984).

Fish addition and removal

Juvenile European perch (*Perca fluviatilis*), which are typically planktivorous (Persson, 1990), were used as predators in the fish enclosures. Two to four weeks before the experiment, fish were caught by traps at the shoreline of Lake Müggelsee, held in aquaria and fed with red blood worms (*Tubifex* spp.) regularly. Fish were not fed during the two days before adding them to the enclosures to ensure that they were hungry enough to feed intensely on the zooplankton in the enclosures. Five perch of about 5 cm length and 4 g wet weight each were added to each fish enclosure (day 8). Fish were allowed to feed on zooplankton for four days. Average daily food consumption of a juvenile perch of 2-4 g is known to be around 4.5% of its biomass per day (Fiogbé & Kestemont, 2003). We estimated the daily food consumption by five perch (20 g) in one enclosure (~1000 L) to be about 900 µg L^{-1} day^{-1} (20 mg L^{-1} × 4.5 %). Therefore, the daily consumption of all fish was substantially higher than the initially available zooplankton biomass in fish enclosures (around 500 µg L^{-1} at day 1, Figure 13), indicating that strong predation effects were likely during four days of predation. Four days after fish stocking (day 12), we removed the fish by electrofishing, euthanized them with 9:1 95% EtOH:clove-oil solution (CarlRoth, Karlsruhe, Germany) and a subsequent hit on the head. We sampled the zooplankton and phytoplankton communities in both fish and no fish enclosures three times within the subsequent four weeks (days 15, 29, 43).

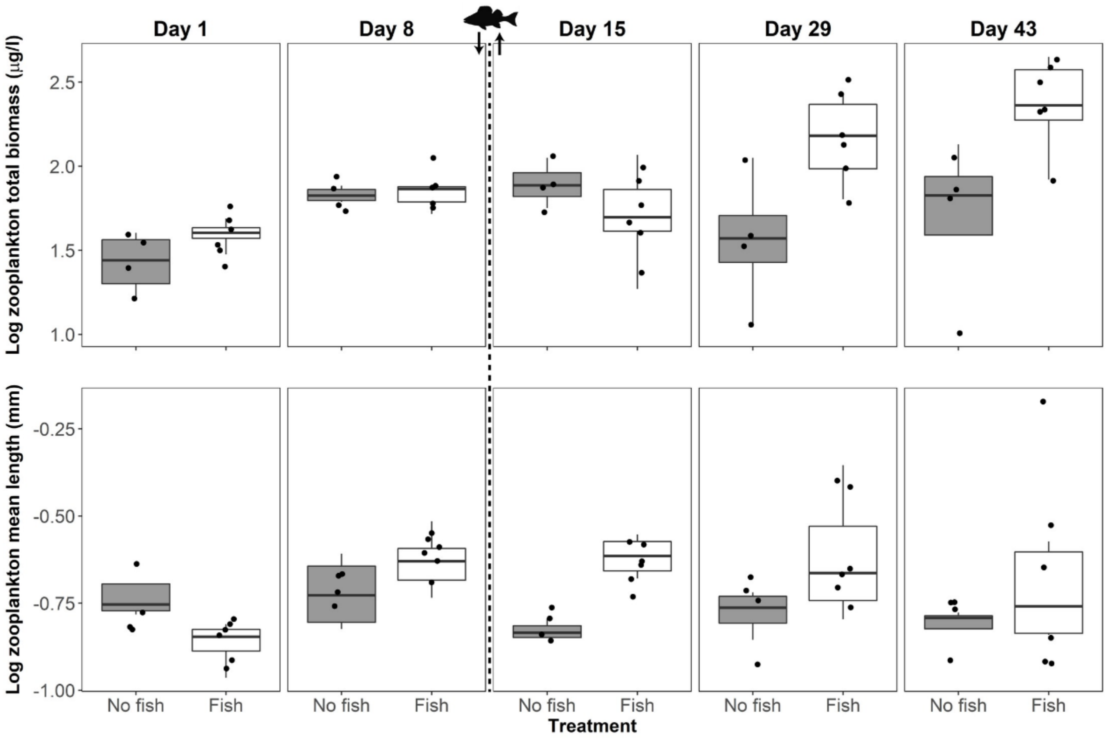

Figure 13. $\log_{10}$ (zooplankton total biomass) and $\log_{10}$ (zooplankton mean length) for different treatments (no fish, n=4; fish, n=6) on each sampling day. Fish image with arrows indicates addition and removal of fish.

Data analysis

We excluded two fish enclosures from the data analyses because throughout the experiment, there were dead fish in one enclosure because of pump malfunctioning, and one enclosure stocked with fish became an extreme outlier in terms of total zooplankton abundance because of a massive rotifer bloom (See E8 in Figure 20). Finally, we used four enclosures without fish and six enclosures stocked with fish in our data analyses. Moreover, we assumed that the chla:TP ratio measured on day 1 was similar to that on day 8 (both dates before fish stocking), because we did not measure chla and TP on day 8.

We calculated linear mixed models (LMMs) to assess changes in predation pressure on zooplankton and cascading effects on phytoplankton communities between fish and no fish enclosures during the experiment, by testing the following variables of zooplankton community and size structure: 1) zooplankton total biomass, 2) zooplankton mean length, 3) zooplankton:phytoplankton biomass ratio as an indicator of top-down control on zooplankton (Brucet et al., 2017; Ersoy et al., 2017; Jeppesen et al., 2003; Ye et al., 2013) and 4) chla:TP ratio as an indicator of phytoplankton yield (Beklioğlu et al., 2017; Jeppesen et al., 2003). Firstly, we checked for temporal correlation by adding first-order autocorrelation structure (correlation=corCAR1(form=~Sampling Day|Enclosure ID)) (Pinheiro & Bates, 2000) on the random-effects variance-covariance matrix of latent variables of the LMMs in "nlme" package (Pinheiro et al., 2017). Then, we compared the models (fitted with maximum likelihood estimation) with and without autocorrelation structure using likelihood ratio tests. There were no significant differences between these models ($p>0.05$), and hence we removed the temporal autocorrelation structure from the models. Accordingly, we used fish treatment and sampling day as fixed factors, and enclosure ID was modeled as a random factor. We checked the diagnostic plots of residuals of the models for the homogeneity of variance and tested the normality of residuals by Shapiro–Wilk's test ($p > 0.05$). Variables were log transformed to achieve normal distributions and match the requirements of the statistical test. A significant interaction between treatment (fish, no fish) and sampling day would indicate that stocking and removal of fish in the fish enclosures modified zooplankton community and strength of trophic interactions over time differently in the fish than in the no fish enclosures.

Additionally, we tested for the resilience of the plankton communities by comparing zooplankton biomass, zooplankton mean size, zooplankton:phytoplankton biomass and chla:TP ratios between the sampling day immediately before fish stocking (day 8) and at the end of the experiment (day 43), separately for fish and no fish enclosures. The plankton communities would be considered resilient if there were no differences in these variables between the two sampling days, indicating that the plankton communities have returned to their pre-disturbance state within five weeks. These planned contrasts were estimated by paired Student's and Welch's t-tests according to checks for normality with Shapiro–Wilk's test ($p > 0.05$) and the homogeneity of variances with F-tests. We corrected for multiple comparisons for each response variable for fish and no fish enclosures using Bonferroni method to avoid Type 1 error (adjusted p-value = α / number of tests). Then, the results of planned contrasts were considered significant for $p<0.025$ ($\alpha=0.05$).

All analyses were performed using “nlme” package (Pinheiro et al., 2017) and all graphs were plotted using “ggplot2” package (Wickham, 2009) in R version 3.4.3 (R Core Team, 2018).

Results

The interaction between fish treatment and sampling day in the LMMs was significant for zooplankton biomass, zooplankton mean length, zooplankton:phytoplankton ratio and chla:TP ratio (Table 5). These results suggest differing successions of the zooplankton and phytoplankton communities between fish and no fish enclosures. Because of the significant interactions between the main effects, we do not focus further on the main effects in isolation.

Table 5. Results of linear mixed models to test for differences in zooplankton total biomass, zooplankton mean length, zooplankton:phytoplankton biomass ratio and chla:TP ratio.

Response variable	Predictors	df	F value	p-value
$\log_{10}$(zooplankton total biomass)	Fish	1	12.5	**0.0077**
	Sampling day	4	7	**0.0004**
	Fish × Sampling day	4	5.11	**0.0027**
$\log_{10}$(zooplankton mean length)	Fish	1	3.46	0.1
	Sampling day	4	2.68	**0.0494**
	Fish × Sampling day	4	4.49	**0.0054**
$\log_{10}$ (zoo:phyto biomass)	Fish	1	3.55	0.0961
	Sampling day	4	6.89	**0.0004**
	Fish × Sampling day	4	2.71	**0.0473**
$\log_{10}$ (chla:TP)	Fish	1	13.64	**0.0061**
	Sampling day	4	2.65	0.0509
	Fish × Sampling day	4	2.69	**0.0486**

Significant p-values are highlighted in bold.

To evaluate the resilience of the plankton communities, planned contrasts between day 8 (before fish stocking) and day 43 (end of experiment) revealed that zooplankton biomass was significantly higher in fish enclosures at day 43 than at day 8. The median of total zooplankton biomass across the six enclosures increased from 73 to 232 µg L^{-1}. The median of zooplankton mean length across the six fish enclosures declined from 0.23 µm (day 8) to 0.18 µm (day 43) (Figure 13). However, zooplankton mean length was not significantly different between these days (Table 6), certainly caused by one strongly deviating enclosure in which the zooplankton length was high at day 43 (Figure 13). In the no fish enclosures, there were no differences in zooplankton biomass and mean length between days 8 and 43. In contrast, the zooplankton:phytoplankton biomass ratio was significantly higher at the end of the experiment compared to the sampling at day 8, whereas the chla:TP ratio was lower in the no fish enclosures (Figure 14). Both ratios did not differ between days 8 and 43 in the fish enclosures (Table 6).

Table 6. Results for contrasts between day 8 and day 43 for each response variable.

Response variable	Treatment	t value	p-value
$\log_{10}$ (zooplankton total biomass)	Fish	-3.50	**0.017**
	No fish	0.50	0.65
$\log_{10}$ (zooplankton mean length)	Fish	0.34	0.75
	No fish	2.16	0.12
$\log_{10}$ (zoo:phyto biomass)	Fish	-1.62	0.17
	No fish	-5.71	**0.01**
$\log_{10}$ (chla:TP)	Fish	0.55	0.60
	No fish	4.91	**0.016**

Significant p-values are highlighted in bold.

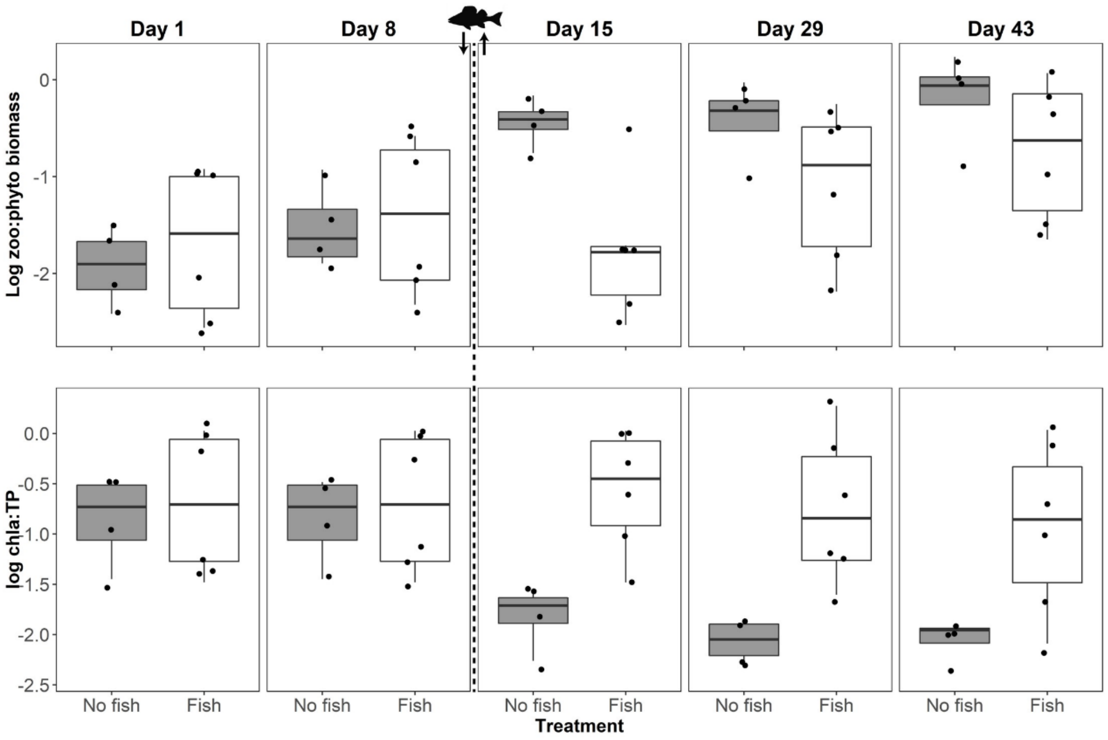

Figure 14. $\log_{10}$(zooplankton:phytoplankton biomass) and $\log_{10}$(chla:TP) and ratio for different treatments (no fish, n=4; fish, n=6) on each sampling day. Fish image with arrows indicates addition and removal of fish.

The zooplankton community composition was modified in response to fish predation. Relative biomasses of nauplii and Calanoida adults declined immediately after fish predation in fish enclosures. Calanoida adults did not re-appear afterwards. Before the fish addition, *Daphnia* had higher biomass relative to other Cladocera taxa. However, after fish removal, Cladocera consisted mostly of small-sized taxa (*Bosmina* and *Chydorus*) and their relative contributions increased strongly during the last four weeks of the experiment in the fish enclosures compared to the period before fish addition (Figure 21). In contrast, the community composition in the no fish enclosures remained relatively stable (Figure 21).

Discussion

Our results suggest that the predation on zooplankton by planktivorous fish in the few days between stocking and removal (i.e. short-term disturbance) caused significant changes of the zooplankton community in the fish relative to the no fish enclosures. Zooplankton biomass was higher at the end of the experiment than before fish predation in fish enclosures, whereas it did not change substantially in the no fish enclosures without disturbance. The indicators of trophic interactions (zooplankton:phytoplankton biomass and chla:TP ratios) reflected control of phytoplankton by grazing zooplankton only in the no fish enclosures, where high grazing pressure (i.e. high zoo:phyto biomass) decreased phytoplankton yield (i.e. low chla:TP). In contrast, phytoplankton was not under effective grazer control in the fish enclosures even after the stop of fish predation. Presumably, the shift in zooplankton community and size structure in response to fish predation prevented a trophic cascade down to phytoplankton, and hence phytoplankton proliferated despite high zooplankton biomasses in the fish enclosures. These effects were not transient, but persisted until the end of the experiment, indicating that the zooplankton communities were not resilient to strong, albeit short, fish predation effects.

Zooplankton biomass increased after stop of fish predation in fish enclosures, even reaching higher biomasses at the end than before fish addition. Furthermore, there was a slight trend that zooplankton mean length declined during this period in the fish enclosures. These results partly contrast with the results of other studies where fish predation caused a decline in biomass and mean length of the zooplankton community, because large-sized individuals decreased and small-sized ones dominated (Brucet et al., 2010; Christoffersen, Riemann, Klysner, & Sondergaard, 1993; Iglesias et al., 2011; Tavşanoğlu et al., 2015). However, the earlier studies reflect the effect of permanent fish predation. In contrast, we evaluated the changes in the zooplankton community immediately after the stop of fish predation. In this sense, we focus on the effect of a short-term disturbance on zooplankton-phytoplankton interactions, in comparison with otherwise similar, but non-disturbed systems.

Obviously, fish predation, which lasted four days only, has changed the zooplankton community composition more than the zooplankton biomass in the fish enclosures, as shown by the development of different zooplankton taxa after fish removal. The biomass of large-sized taxa such as calanoids declined after fish stocking and did not increase again during the experiment, even when fish were removed. This result is consistent with previous similar studies (Mcnaught et al., 1999; Sarnelle & Knapp, 2004), where the large calanoid copepod *Hesperodiaptomus* did not re-appear for several years even after fish disappearance. Together with their relatively low abundance, this delay of recovery may be attributed to the low metabolic rates and complex reproduction strategies of calanoid copepods (Sommer & Stibor, 2002). Because copepods are obligate dioecious, mate limitation could decrease biomass and delay improvement in sexually reproducing populations (Courchamp, Clutton-Brock, & Grenfell, 1999; Kramer, Sarnelle, & Knapp, 2008). Surprisingly, the biomass of similarly sized big Cladocera like *Daphnia* was less affected by predation, but the contribution of *Daphnia* to total zooplankton biomass was minor at the end of the experiment because the number of relatively small Cladocera taxa (e.g *Chydorus, Bosmina*) increased rapidly. These small taxa may have profited from the warm temperatures (between 20°C and 22°C from end of May until mid-July) and a quick maturation from their juvenile stages (Mcfeeters & Frost, 2011; Velthuis, van Deelen, van Donk, Zhang, & Bakker, 2017). Accordingly, the disturbance by fish predation provided a ‘window of opportunity’ for the small cladocerans, and hence the zooplankton community composition did not recover to the original state from before the disturbance. The changes in community composition in the fish enclosures observed between days 8 and 43 of our experiment cannot be attributed to seasonal effects, since zooplankton biomass and mean length were relatively constant in the no fish enclosures without disturbance.

Interestingly, the shifts in zooplankton community composition as induced by fish predation prevented an effective phytoplankton control even after the fish predation has stopped. It has been shown several times that small zooplankton taxa are less efficient than large species to suppress phytoplankton biomass, even if they occur in high biomasses (Bartrons et al., 2015; Carpenter et al., 2001; DeLong et al., 2015). Accordingly, we observed both a high zooplankton:phytoplankton biomass ratio and a high chla:TP ratio in the fish enclosures, indicating high phytoplankton biomasses and yield at high zooplankton biomasses. In contrast, the zooplankton community in the no fish enclosures remained relatively stable, but the control of phytoplankton by zooplankton grazers became stronger towards the end of the experiment, indicated by a high zooplankton:phytoplankton biomass ratio, but a low phytoplankton yield. Therefore, it is surprising to see that the enclosures strongly differed at the end of the experiment with respect to the strength of the zooplankton-phytoplankton interaction, although all enclosures had no fish at this time, and zooplankton was exposed to fish predation only for four out of 43 days in the fish enclosures. Therefore, the legacy of short-term predation and disturbance had long-lasting effects on trophic interactions, reflecting weak short-term resilience of zooplankton to fish predation. Monitoring studies in lakes suggest, however, that larger zooplankton species may recover after stop of fish predation in the long-term, suggesting that only short-term resilience of zooplankton may be impaired by massive disturbance (Balayla, Lauridsen, Søndergaard, & Jeppesen, 2010; Jeppesen, Jensen, Søndergaard, & Lauridsen, 2005). Seasonality and other environmental factors can also influence these resilience mechanisms by modifying population dynamics (Adrian, Wilhelm, & Gerten, 2006).

We recognize that our experimental design had certain limitations. Although mesocosms are helpful for mechanistic studies, their use has limitations when complex interactions and long-term responses have to be explored (Altermatt et al., 2015; Stewart et al., 2013). Moreover, in our experimental set-up we considered a simple three trophic level cascade and ignored the effects of omnivory, intraguild predation, ontogenetic changes, the contribution of the microbial loop to food web interactions (Blanchard et al., 2017; Chang et al., 2014; Polis & Strong, 1996) and the role of resting stage banks in natural communities (Donald et al., 2001). Subsequent studies may verify, for example, whether the resilience of zooplankton communities and the response of top-down control and phytoplankton yield depend on species or sizes of planktivorous fish feeding upon the zooplankton.

A recent study investigating multiple dimensions of stability of freshwater ecosystems to single perturbations has found that the recovery in the ecosystem functioning was highly related to the recovery in the community composition of plankton in mesocosms (Hillebrand et al., 2018). Within this context, our findings could be relevant for better restoration and management strategies in a rapidly changing world. Increased climate warming and invasive species could exacerbate resilience in large-sized zooplankton, which could have severe consequences for restoration measures (Florian, Lopez-Luque, Ospina-Alvarez, Hufnagel, & Green, 2016; Gutierrez et al., 2016). Understanding and identifying the mechanisms of short-term and long-term resilience of natural communities will be essential for conserving the ecosystem functions and predict community dynamics in response to future disturbances (Woodward et al., 2016).

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CHAPTER 4

Intraspecific variation in zooplankton predation affects phytoplankton community size structure

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Abstract

Intraspecific trait variation is very common in communities and mostly arise from differences in size and ontogenetic stage of individuals. While several studies in aquatic ecosystems investigated the role of intraspecific variation in different types of organisms on cascading trophic interactions, the effect of predation from different developmental stages on their prey size structure is not examined thoroughly. Our aim was to assess the effects of intraspecific variation in predation on the prey size structure. We conducted a microcosm experiment using zooplankton as a model organism. The experiment consisted of three different developmental stage (i.e. nauplii, copepodite and adult) of a calanoid copepod *Calanipeda aquaedulcis* grazing on their prey for 24 hours (i.e. bacterioplankton and phytoplankton) and controls, replicated 5 times (n=20). Our findings from prey size structure demonstrated that adult stages (i.e. largest sized stage) had the strongest effects on phytoplankton size spectrum, shifting prey assemblage towards smaller individuals. They also altered energy transfer and productivity potential of the food web. In contrast, we did not observe differences between prey spectrum of nauplii vs. copepodite and copepotide vs. adult stages possibly because of diverse prey choice of copepodites. Our results indicated the importance of intraspecific variation of predators and their possible implications while studying ecosystem functioning. Changes in the developmental patterns of organisms with human-induced disturbances and climate warming could influence underlying predator-prey mechanisms profoundly and modify trophic interactions.

Keywords: developmental stage, ontogeny, predation, zooplankton, phytoplankton, size spectrum

Introduction

It was first Darwin and Wallace who were fascinated by the differences among individuals within populations (Darwin & Wallace, 1858). Later, many studies have provided evidence that trait variation among individuals (i.e intraspecific variation) could affect strength of prey-predator interactions, and thus ecosystem functioning and processes (Litchman & Klausmeier, 2008; McGill, Enquist, Weiher, & Westoby, 2006; Post, Palkovacs, Schielke, & Dodson, 2008). However, still these variations have been overlooked in community ecology studies (Bolnick et al., 2011; Violle et al., 2012).

Most of the intraspecific variation among individuals arise from variance in size and ontogenetic stage of individuals in populations (Persson, 1999; Polis, 1984). Recent field and experimental research in aquatic ecosystems showed that seasonal changes in the body size structure and ontogeny of predators ranging from dragonflies to salamanders have high potential to alter predation and competition patterns in food webs, and ecosystem processes such as respiration and productivity (Krenek & Rudolf, 2014; Rudolf, 2012; Rudolf & Rasmussen, 2013; Rudolf & Van Allen, 2017). There are several studies investigating effects of intraspecific variation in life history characteristics of fish on trophic cascades (Fryxell & Palkovacs, 2017; Howeth, Weis, Brodersen, Hatton, & Post, 2013; Palkovacs & Post, 2009; Post et al., 2008). They explored changes in consumer-resource relationships depending on different foraging traits in same species of fish. Studies on intraspecific variation in zooplankton included differences in resource use between seasons (Berggren et al., 2015), stoichometric and isotopic variability (Carrillo, Reche, & Cruz-Pizarro, 1996; Main, Dobberfuhl, & Elser, 1997; Matthews & Mazumder, 2007), amino acid composition (Brucet, Boix, López-Flores, Badosa, & Quintana, 2005) and feeding (Brucet et al., 2008; Poulet, 1977). Nonetheless, the effects of intraspecific variation in zooplankton predation on their prey community and size structure are less clear (Calbet, Garrido, Saiz, Alcaraz, & Duarte, 2001).

Zooplankton are diverse group of organisms with different feeding strategies and have the potential to modify the relative abundances of phytoplankton and microbial species and their size structure. Thereby, they affect the trophic interactions between them, as well food web structure (e.g. Franks, 2001; He, Zhu, Song, Jeppesen, & Liu, 2015; López-Flores, Boix, Badosa, Brucet, & Quintana, 2006; Muylaert et al., 2003; Zöllner, Santer, Boersma, Hoppe, & Jürgens, 2003). Certain groups of zooplankton change their diet along ontogeny. For example, calanoid copepods may be predators or selective feeders (Allan, 1976; Kleppel, 1993) and they often display ontogenetic diet shifts to meet their energetic requirements of respiration, reproduction and growth (Schellekens, De Roos, & Persson, 2010). This includes changes in the type and size of the preys they consume as they grow (Bonnet & Carlotti, 2001; Brucet et al., 2008; Fernández, 1979). As a result, resource partitioning could decrease intraspecific competition between different stages (Brucet, Boix, López-Flores, Badosa, & Quintana, 2005; Meyer, Irigoien, Graeve, Head, & Harris, 2002).

There is evidence that grazing of the different developmental stages within a single zooplankton species could alter trophic interactions in distinct ways. High abundance of small copepods (e.g. copepodites or nauplii) may have a greater impact on phytoplankton community structure than the larger copepods (e.g. adults) (Calbet et al., 2001). Moreover, previous research demonstrated that different stages had varying grazing effect on their preys (Merrell & Stoecker, 1998; Meyer et al., 2002; Miller & Rudolf, 2011; Poulet, 1977). However, none of them focused on the effect on the prey size structure, which could give key information about ecosystem stability and trophic interactions (Brose, Jonsson, et al., 2006; Emmerson & Raffaelli, 2004; Woodward et al., 2005). Because body size is a very important trait of organisms that is related to life history features and biological rates (Brown et al., 2004), focusing on body size distributions of preys could inform about the possible alterations in the community. These changes in the community and size structure of phytoplankton communities can lead to shifts in the ecosystem processes and functioning (Trebilco et al., 2013). For example, a high size diversity in preys could decrease grazing efficiency due to predation avoidance strategies and weaken energy transfer in the food web (Ersoy et al., 2017; García-Comas et al., 2016). Furthermore, the small-sized phytoplankton are considered to compete more efficiently under nutrient-limiting conditions and have higher metabolism and reproduction rate (Litchman et al., 2010; Litchman & Klausmeier, 2008).

On the other hand, large-sized phytoplankton are better at storing nutrients, predation avoidance but have low metabolic activity (Finkel et al., 2010).

Understanding the interactions between different trophic levels and prey-predator relationships is crucial in a changing world where there may be strong shifts in trophic cascades. Smaller sized plankton are anticipated to increase with warmer climate (Daufresne et al., 2009; Morán et al., 2010; Yvon-Durocher et al., 2011). At the same time, small zooplankton individuals may increase due to higher fish predation at warmer temperatures (González-Bergonzoni et al., 2014; Jeppesen et al., 2010). Therefore, it is highly essential to understand how intraspecific variation in a predator affects the size structure of its prey in order to get more insight into the strength of biotic interactions in trophic cascades.

In this study, we use zooplankton as a model predator organism to assess the effect of intraspecific variation in grazing on its prey size structure. Thus, we conducted a field experiment in Mediterranean coastal lagoons by adding different developmental stages of the calanoid copepod *Calanipeda aquaedulcis* (Kritschagin, 1873) into small bottles and observed the grazing effect on bacterioplankton and phytoplankton size structure after 24h. In a previous study, Brucet et al. (2008) showed that the diet of the calanoid copepod *Calanipeda aquaedulcis* changed along ontogeny, with nauplii, copepodites and adults grazing on different prey types. Here, we hypothesized that the intraspecific variation among different developmental stages of predators would cause variations in the phytoplankton community size structure. Since the size of the selected prey increased with increasing size of the copepod stage (Brucet et al., 2008; Hansen, Bjornsen, & Hansen, 1994; Merrell & Stoecker, 1998), we expected that this would be reflected in a decrease in the slope of the prey size spectrum (i.e. size structure), as a result of the decrease of the relative abundance of large preys from smallest (i.e. nauplii) to largest developmental stage (i.e. adults). Thereafter, we discussed the potential consequences of the changes in phytoplankton size structure produced by the intraspecific differences in zooplankton predation on the phytoplankton community and the food web.

Methods

Experimental set-up

The experiment was conducted in May in the Empordà Wetlands Natural Park (NE Spain). These wetlands are made up of several Mediterranean shallow lagoons that are not subject to tidal effects, but prone to several disturbances such as floods, sea storms during autumn and winter, and desiccation in summer (Brucet et al., 2006; Brucet, Boix, López-Flores, Badosa, & Quintana, 2005). The zooplankton communities of these wetlands are often dominated by few species. Therefore, intraspecific variation in predation could play an important role in determining trophic interactions (Brucet, 2003). For the experimental microcosms, we took samples from lagoons in the La Pletera salt marshes, which are scarce in inorganic nutrients and dominated by heterotrophic nano- and microplankton due to their long confinement periods (López-Flores et al., 2006).

Zooplankton sampling and selection of developmental stages

Before the experiment, we collected copepods from the lagoons using a plankton net with a mesh size of 50 µm. 20 Winker-bottles of 250 ml were filled with filtered (through 50 µm) surface water from these lagoons. We added different stages of *Calanipeda aquaedulcis* selected under a stereomicroscope. The experimental set-up was composed of four treatments (3 for each developmental stage + control), each replicated five times (n=20). The treatments were nauplii (from NI to NVI – hereafter called Stage 1), copepodites (from CI to CV - Stage 2) and adults (Stage 3). After identified and selected under stereomicroscope, nauplii (30), copepodites (6) and adults (2) were pipetted into each bottle, in proportions similar to their natural densities at the time of the sampling. We did not add any zooplankton in controls, which only contained filtered pond water. All bottles were incubated in situ for 24 hours in depth of 10-15 cm (Brucet et al., 2008). At the end of the experiment, the samples were collected, fixed with Lugol's iodine solution for microscopic identification and enumeration. Although each developmental stage had different clearance rates for the different prey types, we observed a significant grazing of all stages (i.e. an average of 167, 166 and 176 ml d-1 in nauplii, copepodites and adult treatments, respectively; Brucet et al 2008).

Prey composition

We focused on different preys of zoooplankton including micro, nano, pico and bacterioplankton. While microplankton consisted of auto- (AD) and heterotrophic dinoflagellates (HD) and ciliates, autotrophic picoflagellates (APF) and haptophytes were included in nanoplankton. Picoplankton was composed of auto- (APF) and heterotrophic picoflagellates (HPF). Bacterioplankton and APF were the most abundant prey. APF and HPF were the highest in terms of biomass (Brucet et al., 2008).

Sample processing

Prey samples were counted and identified to genus level under inverted microscope for microplankton. We counted at least 100 individuals of the most abundant taxa and measured 5–10 individuals from each genus.

For bacterioplankton and autotrophic pico- and nanoplankton, samples were analyzed with FACSCalibur Flow Cytometer (BD Biosciences) using laser emitting at 488 nm. We filtered samples through 50 μm mesh and fixed with 1% paraformaldehyde and 0.05% glutaraldehyde (final concentration) and froze in liquid nitrogen and stored frozen at –20°C. More details of the procedure can be found in López-Flores et al. (2006).

For heterotrophic pico- and nanoplankton taxonomic identification and counting, we mixed 1 ml of the sample by inversion, stained for 10 minutes with fluorochrome 4’-6-diamidino-2- phenylindole (DAPI; final concentration of 0.5 μg ml^{-1}) and filtered through a 0.2 μm polycarbonate filter (Millipore, Isopore membrane filters). Then, we mounted the filters on a glass slide and check by epifluorescence microscopy with a UV excitation filter block and 1000X oil immersion. We counted at least 300 individuals. This method enabled us to distinguish the heterotrophic from the autotrophic pico- and nanoplankton by visualizing the DAPI-stained nuclei (blue) and the chlorophyll a autofluorescence (red) (Porter & Feig, 1980).

We calculated individual biovolumes of microplankton, nano- and picoplankton (μm^3) from body measurements from the microscope and cytometry following the geometric formulae by Hillebrand et al. (1999).

Prey size spectrum

Linear size spectrum of bacterioplankton and phytoplankton was constructed for each sample (controls and developmental stage treatments with replicates) to assess the effect of different developmental stages (i.e. different sized-grazing) on their prey size structure.

We followed the approach from Sheldon, Prakash, & Sutcliffe (1972) which is based on the linear log-log relationship between abundance (total number of individuals per ml per size class) and individual biovolumes (i.e. negative relationship between abundance and size). For size spectrum, we calculated nine size classes in $\log_2$ scale ranging from (1st class: < 8 μm^3, 2nd class: 8-16 μm^3 etc.). We combined few large size classes together because of their low abundance (Arranz et al., 2016; Benejam et al., 2018) and filled empty size classes with zeros. Although there is some discussion about this approach of zero filling (Gómez-Canchong, Blanco, & Quiñones, 2013; Loder, Blackburn, & Gaston, 1997), several studies followed the same methodology (Arranz et al., 2016; Benejam, Teixeira-de Mello, et al., 2016). The abundance per each size class was then divided by the linear distance between each size class to account for the differences in the width of the size classes (i.e. normalized abundance spectrum) (Sprules & Barth, 2016; White et al., 2007). We applied ordinary least -squares linear regression for $\log_2$ biovolume classes and $\log_2$ normalized abundance (normalized total number of individuals per ml per size class) to calculate the slope, intercept and coefficienct of determination (R^2) for each stage and replicate (n=20). For normalized abundance size spectrum consisting several trophic levels, slope is predicted to be nearly -2 (Sprules & Barth, 2016). The slope indicates the relative contribution of small- and large-sized individuals. For instance, steeper slopes reflect a high accumulation of small-sized individuals in the body size distribution, whereas flatter slopes indicate greater relative contribution of large-sized individuals (Emmrich et al., 2011). It has been also confirmed empirically that the slope is highly related to trophic transfer efficiency (Mehner et al., 2018). Another parameter that can be obtained from the size spectrum is the intercept which indicates food-web capacity or productivity potential (Gaedke, 1993). Thus, higher intercepts are expected with higher nutrients levels in the systems. The degree of linearity of size spectrum (e.g. coefficient of determination of the regression) may refer to what extent the observed values are far from the fitted model during steady state conditions (Chang et al., 2014) and also inform about prey-predator interactions (Arranz et al., 2018). These deviations from the linearity may be reflected by the appearance of secondary structures in the size spectrum (i.e. nonlinear dome shapes structures corresponding to certain size classes systematically deviating from slope of the linear spectrum) (Arranz et al., 2018; Chang et al., 2014; Mehner et al., 2018).

Data analysis

We used one-way analysis of variance (ANOVA) to compare the grazing effect of different developmental stages on their prey size spectrum metrics: slope, intercept and R^2. Before the analysis, we checked normality of the response variables by Shapiro Wilk's test ($p > 0.05$) and homogeneity of variance by Levene's test ($p > 0.05$). At first, we observed the boxplots, fitted vs residual values for each variable using Q-Q plots. In order to improve the normality of the residuals for slope and intercept, we removed three outliers for each of the 3 response variables (which corresponded to the same replicates). Subsequently, we ran TukeyHSD posthoc tests with p value adjustment for multiple comparisons. For R^2, we conducted non-parametric Kruskal-Wallis test.

We performed all statistical analyses in R version 3.4.3 (R Core Team, 2018) and all graphs were plotted using "ggplot2" package (Wickham, 2009).

Results

In total, 20 linear models were fitted for normalized abundance size spectra of control and each developmental stage with 5 replicates. Slopes ranged between -1.95 and -2.61, while intercepts ranged between 14.89 and 17.1. R^2 for ordinary least -squares linear regression between $\log_2$ size classes and $\log_2$ normalized abundance ranged between 0.51 and 0.67 and p-value was always significant (i.e. lower than 0.05). Average size spectra for control and each stage are shown in Figure 15.

Slope and intercept of the normalized abundance size spectra of preys significantly differed according to the predator ontogenetic stage (ANOVA: $F=6.06$, $p<0.01$ and $F=3.44$, $p=0.05$, respectively, Figure 16). According to posthoc tests, there was a significant difference between control and adults (Stage 3) (TukeyHSD, $p=0.01$), and nauplii (Stage 1) and adults (Stage 3) (TukeyHSD, $p=0.02$) for the slope of the size spectra (Figure 16). For intercept, significant differences appeared between nauplii (Stage 1) and adults (Stage 3) (TukeyHSD, $p=0.05$). However, we did not find any differences between stages for the coefficient of determination (R^2) (Figure 16).

Abundance of different prey groups revealed differences between treatments (Figure 17). While microplankton abundance was lowest in adult stage treatment, nanoplankton and picoplankton abundance were the highest in that treatment. Bacterioplankton abundance was highest in the controls. Copepotides (Stage 2) and adults (Stage 3) did not show substantial differences in terms of different prey abundances.

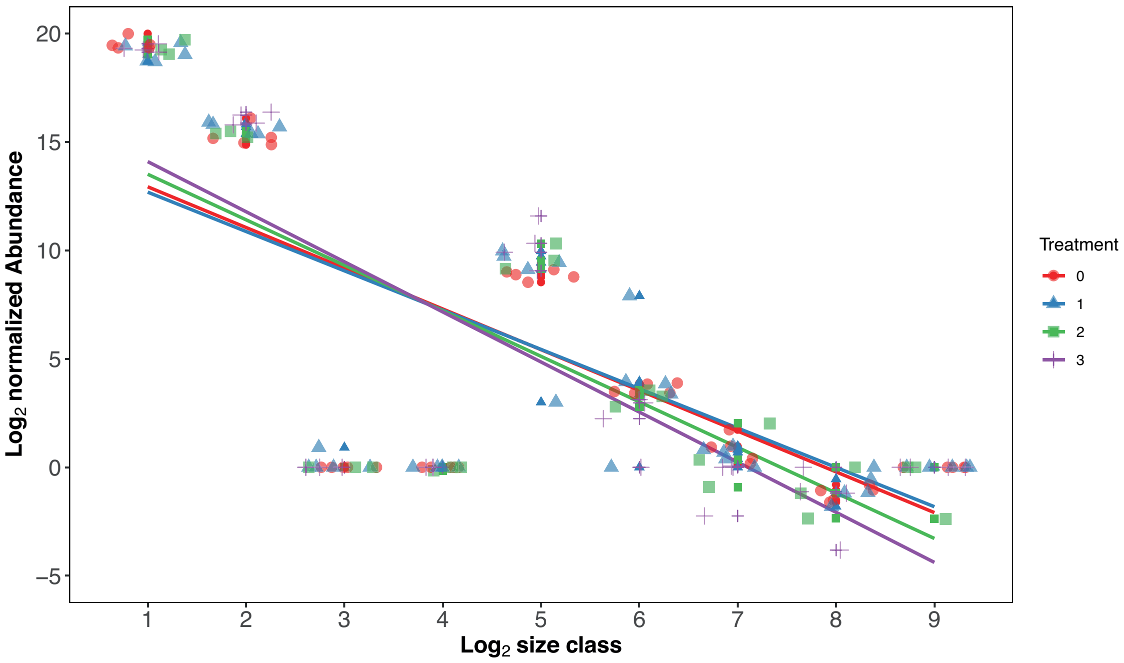

Figure 15. Normalized abundance size spectra of phytoplankton for each developmental stage and control treatments. The size classes range from bacterioplankton (<8 mm^3) to microplankton (> 1024 mm^3). Treatment 0: control, Treatment 1: Nauplii (Stage 1), Treatment 2: Copepodites (Stage 2), Treatment 3 (Stage 3),: Adults. Equations for Control: $y = 15.4 + -2.04x, R^2 = 0.54$; Treatment 1: $y = 15.3 + -2.03x, R^2 = 0.53$; Treatment 2: $y = 15.6 + -2.1x, R^2 = 0.55$; Treatment 3: $y = 15.8 + -2.15x, R^2 = 0.54$. Regression lines represent the average size spectrum for each treatment. geom_jitter function from ggplot2 package was applied to remove the overplotting of the points. Different sized and colored points represent these overplotted values of different developmental stages. The regression lines were separated slightly using image editing tools (Adobe Illustrator CC) for better visibility.

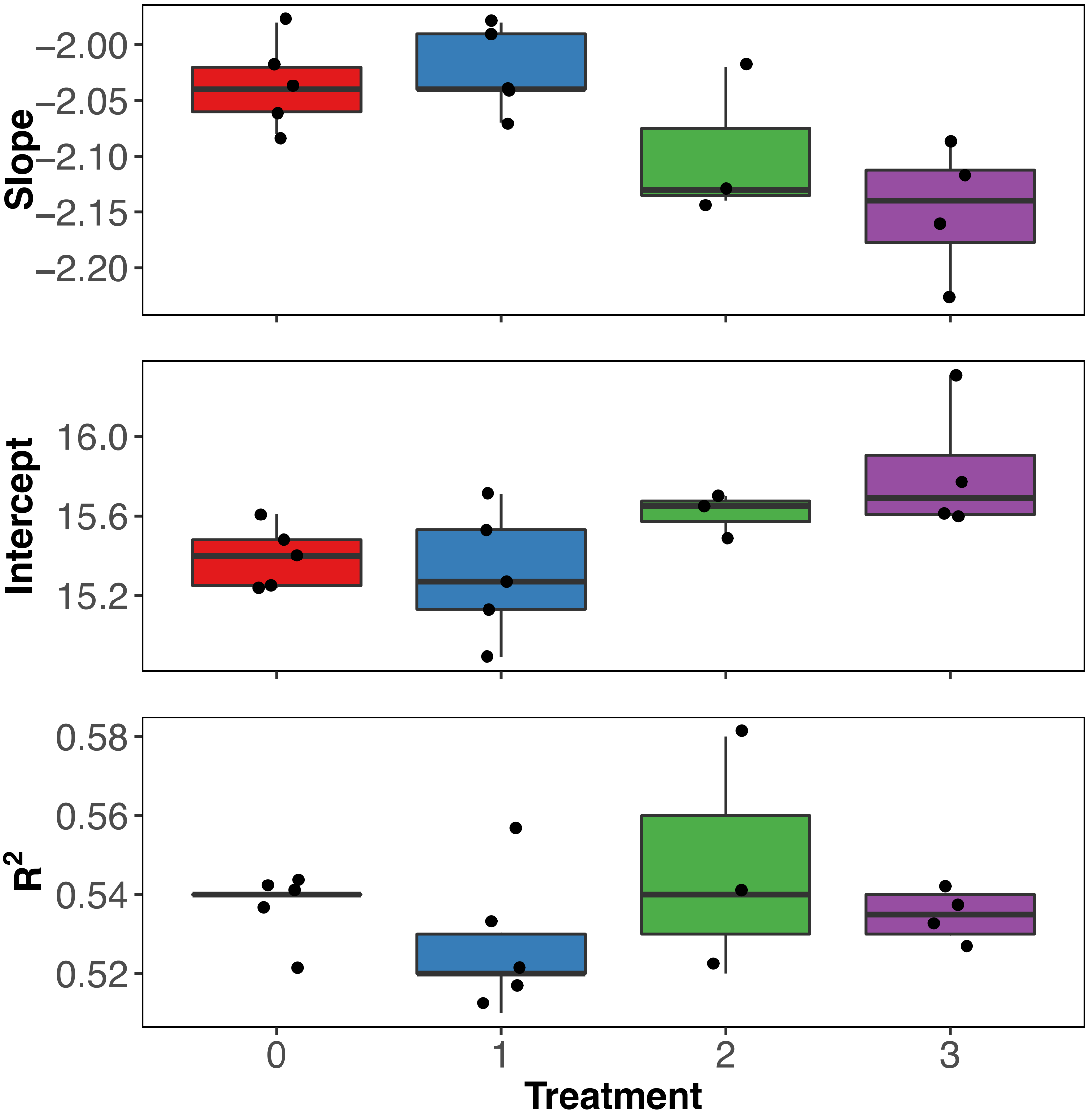

Figure 16. Slope, intercept and R^2 obtained from normalized abundance size spectra of phytoplankton for each developmental stage and control treatments. Treatment 0: control, Treatment 1: Nauplii (Stage 1), Treatment 2: Copepodites (Stage 2), Treatment 3: Adults (Stage 3).

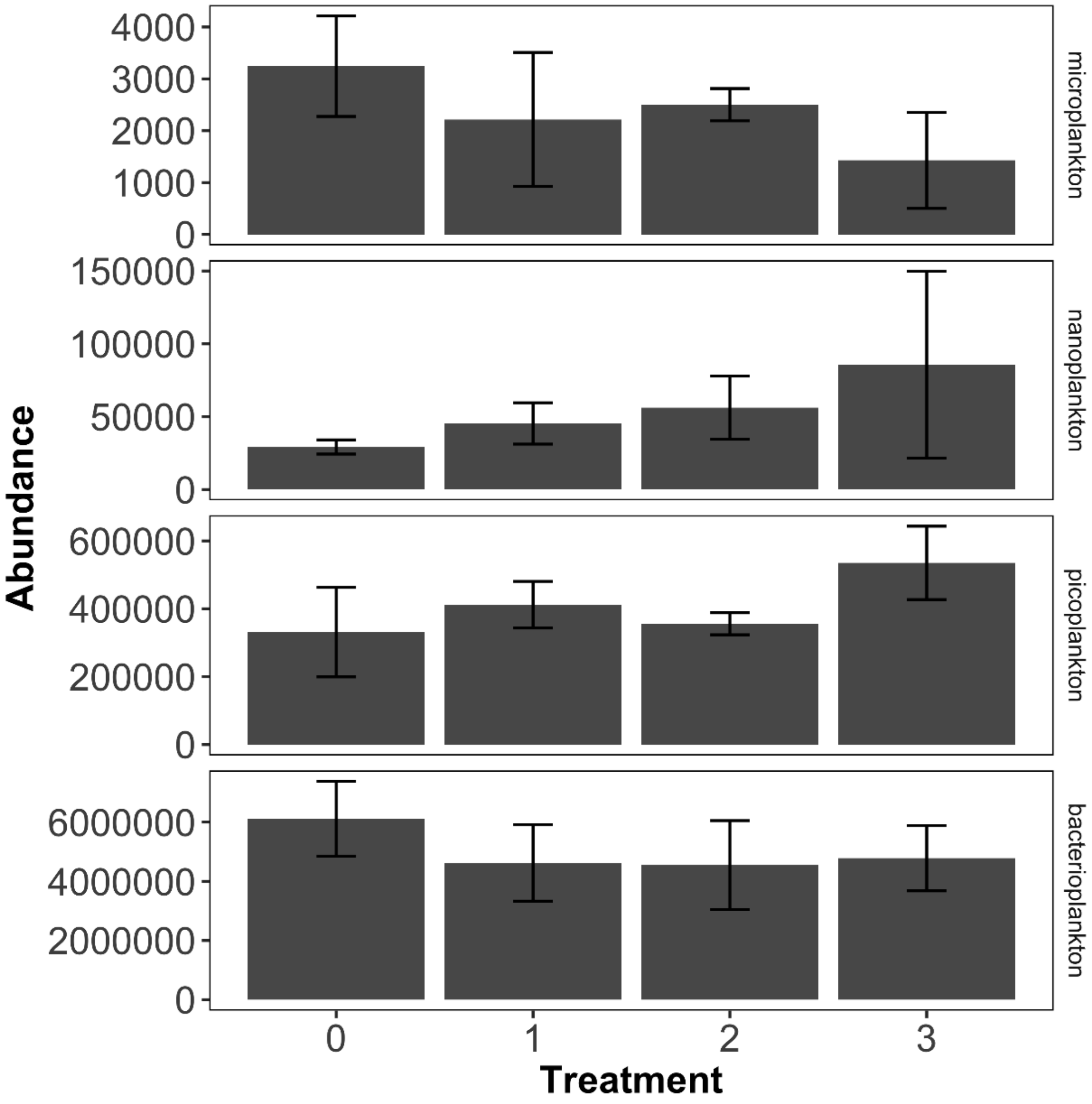

Figure 17. Total abundance of different groups of prey in each developmental stage and control treatments. Treatment 0: Control, Treatment 1: Nauplii (Stage 1), Treatment 2: Copepodites (Stage 2), Treatment 3: Adults (Stage 3). Error bars represent standard deviation.

Discussion

Ontogenetic shifts are very common in natural communities (Rudolf & Lafferty, 2011) with possible effects on ecosystem functioning (Rudolf & Van Allen, 2017). Our findings suggest that intraspecific variation in different developmental stages of a zooplankton predator leads to variations in the prey (i.e. phytoplankton and bacterioplankton) size structure. In line with the changes in diet along ontogeny found by Brucet et al. (2008), we observed differences in the resulting prey size spectrum slopes and intercepts, with steeper slopes and higher intercepts in phytoplankton size spectra of adults' experimental bottles. However, our results suggest that nauplii and copepodites stages had similar effects on phytoplankton size structure.

Although previous research has shown that adult stages of calanoids prefer larger sized preys than nauplii do (e.g microplankton, nanoplankton) (Berggreen, Hansen, & Kiørboe, 1988; Poulet, 1977), they did not analyze the possible effects on the resulting prey size structure. Our experimental study demonstrated the strongest changes in prey size spectra as a result of grazing by adult stage of the copepods when compared to nauplii stage. In the adult stage treatment, the resulting prey size spectra had steeper slopes and higher intercepts compared to nauplii stages, indicating higher relative abundance of smaller preys and higher productivity, respectively. As Woodward & Hildrew (2002a) suggested, niche overlap between nauplii and adult stages decreased as size differences between stages increased. This explanation is in accordance with our findings where abundance of microplankton was lowest in adult stage treatment, while pico- and nanoplankton had the highest abundance observed in that treatment. This is probably as a result of adults' higher ingestion rates (and selection) for larger preys (mostly ciliates) and also lower ingestion rates on smaller preys (e.g. picoplankton) (Brucet et al. 2008). Moreover, higher productivity as a result of dominance of smaller individuals could be explained by faster growing rate of small pytoplankton (Litchman et al., 2010).

Higher ingestion of ciliates is beneficial for copepods (Bonnet & Carlotti, 2001) and may have resulted in a trophic cascade in adult stage treatment in our experiment. Similar results were observed in a recent microcosm study, where top-down control of copepods on ciliates caused increase in picoplankton and modified phytoplankton community composition and thus size structure (Armengol, Franchy, Ojeda, Santana-del Pino, & Hernández-León, 2017). Nevertheless, we did not observe significant differences in the coefficient of determination of the size spectrum among stages (i.e. certain size classes systematically deviating from the linear spectrum). This could be related to variations in trophic cascades among different stages.

Theoretical models and empirical research indicate that the slope of the abundance size spectrum reflects energy transfer efficiency across the different trophic levels (Kerr & Dickie, 2001; Mehner et al., 2018). Ciliates, as mixotrophs (i.e acting both autotrophic and heterotrophic) could facilitate energy transfer in planktonic food webs (Ward & Follows, 2016). The steeper slopes and thus lower efficiency in trophic energy transfer (Dossena et al., 2012) in adult stage treatment may be due to high ingestion rates of ciliates and thus their low abundance. Accordingly, by altering slope and intercept of their prey size spectra, different developmental stages could change not only community size composition, but also trophic energy transfer and productivity potential of their prey communities.

Despite the divergence between nauplii and adult stages, there were similarities in phytoplankton size structure between control and nauplii treatment. In our experiment, nauplii consumed predominantly heterotrophic picoflagellates (HPF) (i.e. small picoplankton). Its niche also overlapped with the other stages, because all stages grazed on AD and HD (Brucet et al., 2008) and there was no substantial difference in abundance of different groups between nauplii and copepodite stages (Figure 17). However, nauplii did not graze on ciliates. There is evidence that nauplii stages are less selective than other stages (Allan, 1976; Swadling & Marcus, 1994). One possible reason for observing similar prey spectra in control and nauplii treatments could be that nauplii stages had narrow prey size range (Brucet et al., 2018; Woodward & Hildrew, 2002a), therefore this did not affect phytoplankton size structure notably. Earlier studies found that nauplii could not graze efficiently because they do not have required appendages during the early period of their growth (Mullin & Brooks, 1967; Paffenhöfer & Lewis, 1989). Hence, their grazing was constrained by physical limitations. This could explain the similarities on prey spectra in controls and nauplii stage treatment. Furthermore, we did not detect any difference between copepodite and adult stages on phytoplankton size spectra. Similar effects of adults and copepodites are possibly due to the highly diverse prey choice of the copepodites. They consume wide range of preys varying from HPF to ciliates (Brucet et al., 2008).

Our results should be interpreted cautiously because the populations in nature normally do not consist of only one of these developmental stages, but multiple stages coexist with each other. Additionally, since we collected zooplankton from natural communities, we could not account for other possible intraspecific variation (e.g.

foraging strategy, behaviour etc.) already present in these communities. Considering only one trait could not cover the other functional variation existing in the communities (Albert et al., 2010). However, still we can not disregard that body size incorporates many aspects of different trait variations in phytoplankton (Litchman, Ohman, & Kiørboe, 2013).

In conclusion, our results showed a significant role of the intraspecific variation in developmental stages of zooplankton on prey size spectra. Climate change scenarios predict temperature increase and alterations in phenology of aquatic microorganisms (Edwards & Richardson, 2004; Gerten & Adrian, 2000). These disturbances could affect the relative abundance or emergence of different developmental stages and cause mismatches within grazing interactions (Yang & Rudolf, 2010). For example, Sommer et al. (2006) have shown that the nauplii stages appeared earlier with water temperature increase, which affected feeding of fish larvae that are highly dependent on them as resource. Recent meta-analysis has shown that the indirect effects of intraspecific variation in traits ranging from foraging, life history and personality are more powerful to modify community composition than the species effects (Des Roches et al., 2018). Thus, understanding how intraspecific variation in predators could cascade down to the food web is critical for freshwater ecosystems.

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GENERAL DISCUSSION

This PhD thesis focused on the different links of the interacting trophic levels in the tri-trophic planktonic food webs (from fish to phytoplankton in Chapter 1, 2 and 3; from zooplankton to phytoplankton in Chapter 4). In general, our results clearly showed that body size and community structure of interacting trophic levels are important determinants of predator-prey interactions and energy transfer in planktonic food webs. Environmental factors such as temperature, resource availability and other disturbances such as fish stocking also influenced single trophic levels and therefore have profound cascading effects on the food webs and community resilience. Intraspecific variation in different developmental stages of predators also reinforced variations in trophic interactions by shaping prey size structure, due to the changes in resource use along the ontogeny.

Predator-prey size structure across interacting trophic levels

Earlier studies of trophic interactions focused mostly on effects of top-down and bottom-up controls on single trophic levels. However, identifying size-based interactions across interacting trophic levels is rare, but can give more insight into ecosystem functions and energy transfer (Brose, Jonsson, et al., 2006; García-Comas et al., 2016). This kind of approach is usually difficult to conduct, because it is challenging to find equally well resolved individual size data of several trophic levels. This PhD thesis is one of the first studies analyzing simultaneous evaluation of interacting trophic levels in different freshwater systems: Turkish Mediterranean shallow lakes (Chapter 1) and Lake Mývatn in Iceland (Chapter 2). Our results from Turkish lakes suggested positive correlations between size diversity of fish and zooplankton. Different sizes of fish with similar abundance led to highly size diverse zooplankton communities. At the same time, the opposite was also true: similar proportions of different sizes of zooplankton resulted in communities with high fish size diversity. However, we did not observe similar effects from zooplankton to phytoplankton, which contrasts with the previous findings in marine systems of García-Comas et al. (2016), where they revealed negative relationship between prey (nano-microplankton) and predator (mesozooplankton) size diversity. These variations could be caused by different predator-prey mechanisms or behavioral adaptation in these systems and in various climatic regions. Phytoplankton size structure was strongly driven by temperature and productivity, that is their size distribution was more diverse and even with high nutrient availability and warmer temperatures, respectively. Our findings support similar patterns observed in other freshwater and marine systems (Quintana et al., 2015; Sommer et al., 2017), where physical factors such as temperature and nutrients were the major drivers of phytoplankton size structure.

We showed positive influence of high fish size diversity on zooplankton as higher diversity of consumers enhanced diversification of resources by resource partitioning in 30 Turkish shallow lakes. In addition, in the mesocosm experiment in Lake Mývatn with presence and absence of similar-sized fish species, we showed that fish presence had negative effects on zooplankton size diversity and resulted in communities dominated by smaller individuals. Therefore, we can argue that although high diversity in fish has positive effects on zooplankton size structure in Turkish lakes, presence of similar-sized fish influences zooplankton negatively because of size selective fish predation. In the same experiment, zooplankton size diversity was also negatively affected by high phytoplankton size diversity caused by cyanobacteria blooms. Our results agree with previous studies where blooms interfered with zooplankton grazing and thus adversely affected zooplankton size structure (Ger, Urrutia-Cordero, et al., 2016; Ghadouani et al., 2006). These studies suggest that the major changes in zooplankton composition were related to feeding inhibition in zooplankton caused by filamentous and colonial large phytoplankton. Similarly in our experiment, this increase in phytoplankton size diversity hindered the efficient transfer of energy production to the upper trophic levels (from phytoplankton to zooplankton) in the food web, probably due to high standing biomass of large primary producers caused by inedibility and low nutritional value (García-Comas et al., 2016). In contrast, low zooplankton size diversity decreased energy transfer from phytoplankton to zooplankton due to reduced niche partitioning. Because less diverse sizes of zooplankton having less feeding niches were not able to take advantage of a variety of differently sized phytoplankton (Ye et al., 2013), energy is not transferred efficiently to the upper trophic (e.g. zooplankton) levels. Our results from this experiment are in accordance with observed patterns in marine systems, where trophic energy transfer decreases with high prey (phytoplankton) size diversity and increases with high predator (zooplankton) size diversity (García-Comas et al., 2016). Thus, we can propose general mechanisms for relationship between trophic transfer and predator-prey size structure both in marine and freshwater systems.

Overall, our results highlight the importance of using size-based metrics such as size diversity and size evenness in predicting communities' responses to environmental and biotic changes. We further suggest that inclusion of enviromental factors such as temperature and resource availability is essential while studying size-structured communities and making inferences about potential changes with global climate warming. In this thesis, we show that size-based approaches can help us grasp the prey-predator interactions and the whole ecosystem functioning in a better way.

Resilience in size-based interactions of planktonic food webs

Understanding resilience of size-based interactions is quite crucial regarding ecosystem restoration and management. With current rates of climate change and human related disturbances, studies focusing on resilience of communities to perturbations are increasing (Spears et al., 2017). However, not many studies investigate recovery and resilience in size-based interactions of communities, while studying effects of top-down control. Only few studies focused on the resilience in zooplankton communities to gradual fish removal or disappearance in North American mountain lakes and the cascading changes in trophic interactions, focusing on long-term period (Donald et al., 2001; Knapp et al., 2001; Knapp & Sarnelle, 2008). However, it is still not clear how resilient communities are to complete fish removal in short-term period. Deeper understanding of short-term resilience of communities would bring more insight when taking decisions for restoration and management measures. In this thesis, we explored beyond only instant effects of fish predation and tested for the first-time short-term resilience in zooplankton community and size structure after fish removal in an experimental set-up and explored the resulting outcomes in phytoplankton communities.

Even though they did not assess the ability of communities and related trophic interactions recover after fish predation, previous studies and part of this thesis have shown the negative effects of fish predation on zooplankton (Brucet et al., 2010; Cañedo-Argüelles et al., 2017). They revealed that fish predation alters zooplankton community composition and decreases zooplankton mean size, having cascading consequences in phytoplankton. Our results from the resilience experiment similarly showed adverse effects of fish predation. Our results indicated low resilience of zooplankton biomass and size to fish predation in short-term, that is the zooplankton community structure did not return back to its previous state (before fish addition) after 4 weeks. We found a shift in zooplankton species composition and size structure as a result of fish predation disturbance, causing small sized taxa (i.e small Cladocera, Rotifera) to take over some large-sized taxa. This cascading effect caused release of phytoplankton from control by zooplankton, increasing phytoplankton yield. In contrast, non-disturbed systems (i.e.controls) stayed relatively stable and had greater grazing control on phytoplankton. Related experimental studies investigating permanent fish predation (Iglesias et al., 2011; Tavşanoğlu et al., 2015) found similar results, which indicates negative relationship between fish and zooplankton size structure. Overall, our findings extend the knowledge in terms of short-term resilience. These results are novel and relevant for restoration ecology of shallow lakes and ponds. We show that the communities' resilience do not depend only on the removal of predators. Their recruitment after the perturbation could be affected by other factors such as seasonality, different reproduction strategies and reproduction rates of certain taxa. Resilience patterns in aquatic communities are expected to change with global climate change, thus predicting their responses to future disturbances are crucial. We suggest that these factors should be considered in restoration plans such as biomanipulation and for other perturbations.

Effect of intraspecific variation of predation in trophic interactions

Classical approach in community ecology regards different individuals of the same species as identical. Nonetheless, organisms change their characteristics such as feeding niche, foraging behaviour and life-history traits as they grow. One of the most obvious intraspecific variation appears from differences in body size and ontogenetic stage of individuals (Polis, 1984). However, this variability is disregarded in most food web studies where species mean effect is assumed to indicate underlying trophic interactions (Carpenter, 1987; Pace et al., 1999). Recently Rudolf & Van Allen (2017) studied the succession in developmental stages of predatory salamander and revealed the variations in ecosystem functions such as ecosystem rates and primary production of different stages. Nonetheless, as many other studies they did not evaluate the changes in prey size structure which could inform better about ecosystem stability and energy transfer (Trebilco et al., 2013). In this thesis, we focused on intraspecific variation in predators using zooplankton as a model organism and assessed effects of distinct developmental stages of zooplankton on their prey size spectra in a microcosm experiment. Our results revealed that the adults (largest sized stage) had the strongest effect on the prey size spectra. As in previous studies (Rudolf & Rasmussen, 2013), we observed the strongest functional effect on largest sizes on the trophic interactions. This could be explained by the highest trophic position of larger predators and wider prey selections of larger stages than the smaller ones (Woodward et al., 2005). Steeper slope and higher intercept of the prey size spectra in large stages of the predators indicated dominance of small sized preys (e.g. bacterioplankton) and higher productivity, respectively. In contrast, we did not observe differences between nauplii and copepodite stages, possibly because of diverse prey preference of copepodites, which could have coincided highly with diet of nauplii (Brucet et al., 2008). Thus, the change in the prey size spectra was consitent with the changes in the diet of the different developmental stages (Brucet et al., 2008).

When disturbances affect populations with human activities and climate change, understanding the stage specific responses will be essential. Our study underlines the significance of intraspecific variability in predators while determining the prey size structure and the possible consequences on community structure and functioning. We also extend the knowledge in intraspecific variation in predation by assessing changes in size spectra, which is a very powerful method to reveal also community dynamics.

Future work

In this thesis, we have used different research approaches in the study of freshwater trophic interactions from different regions so that each could complement the other's weaknesses. However, still each approach had their own caveats. In the majority of this thesis, we considered size-based trophic interactions in a simple way consisting of three trophic levels, without links of microbial loop or intraguild predation, because it was difficult to integrate equally resolved data for each trophic link. Inclusion of microbial loop is very limited in size-based studies, but would provide more clear understanding of the underlying complex networks if included (Blanchard et al., 2017). Due to similar reasons, temporal resolution was rather weak both in our observational and experimental studies. Exploration of the trophic interactions in longer time scales would allow more clear understanding of transitions between states before and after perturbations and stability in the communities. With recent advances in automated estimation of population abundance and size structure (Bruijning, Visser, Hallmann, & Jongejans, 2018), it is possible to have higher temporal and spatial scales in food web studies due to the fast and more efficient ways to analyze more samples.

For future studies, size based metrics could be complemented with other methods such as stomach content, stable isotope analysis and modelling, which could improve the conclusions drawn from sized-based approaches alone. Stable isotope analysis are effective for identifying trophic links and diet composition (Boecklen, Yarnes, Cook, & James, 2011) as well as energy flow. For example, they can be used to define trophic levels of different size and stage of organisms and create well defined size-based networks. Additionally, individual based models for predator-prey interactions could incorporate individual size-abundance relationships together with stage specific responses of different species. This way, it could be possible to make inferences about population and community responses to global climate change and extreme events. Thus, for future work we encourage inclusion of all trophic links in food web studies, exploration in wider temporal resolution and combination of modelling to make better predictons to environmental changes in dynamic systems.

Our research focused on freshwater ecosystems. How to extrapolate the size-based interactions to terrestrial ecosystems has not been well defined. Historically, size based metrics became more approved among aquatic scientists than among terrestrial ones. Terrestrial ecologists adopted more species niche concept and used rank-abundance relationships rather than the size spectrum as aquatic ecologists did. These variations in study approach could have arisen from the variations among the study organisms in these different ecosystems. Aquatic organisms mostly have indeterminate growth (i.e. body size changes as they grow), and their functions and diet in the ecosystem change (e.g ontogenetic niche shift) during their developmental process (Kerr & Dickie, 2001, Trebilco et al., 2013). Individual body size often determines predator- prey interactions in these ecosystems (Brooks & Dodson, 1965). Furthermore, in plankton food webs aquatic herbivores (i.e. zooplankton) are constrained by their gape. Gape-limitation often has an impact on size range of preys that they can ingest. However, for example terrestrial herbivores can ingest parts of plants, without affecting the whole individual (Shurin, Gruner, & Hillebrand, 2006). Hence, size-based approaches are more relevant in aquatic ecosystems (including marine systems) as body size and trophic level of organisms are highly linked. It is, therefore, crucial to assess study organisms and their niche and trophic levels before generalizing our results from this thesis into other ecosystems such as terrestrial systems.

This thesis assessed the size-based interactions and possible implications for ecosystem functioning in the aquatic planktonic food webs, using size-based metrics. Here, we show that use of size metrics could help to characterise the environmental and biotic disturbances that the aquatic communities and ecosystems are facing. We reveal that size-based approaches are as good as taxonomic approaches to determine biodiversity and ecosystem functioning. Furthermore, we argue that they can be used to help better monitor and restore aquatic ecosystems. For example, size diversity and slope of the size spectrum can provide valuable information about the recovery of the communities after the environmental perturbation is removed such as during invasive fish removal or biomanipulation in terms of removal of planktivorus fish. Beyond those uses, it is possible to integrate size measurements into normal monitoring schedule by complementing with other taxonomic metrics. Moreover, they can even contribute to the European Water Framework Directive implementation, in order to make clear inferences about the good ecological status of the freshwater ecosystems, as it has already been proposed (Reyjol et al., 2014).

GENERAL CONCLUSIONS

1. There is a positive correspondence between size structures of interacting trophic levels in 30 Turkish shallow lakes. Fish size diversity is related with zooplankton size diversity, suggesting that higher diversity in resources support higher diversity in consumers or vice versa.

2. Changes in fish size evenness in Turkish lakes are explained by the differences in temperature. In warmer lakes, fish tend to have irregular size distributions where small-sized fish dominate.

3. Phytoplankton size structure (i.e diversity and evenness) is more driven by temperature and resource availability, than by predation in Turkish lakes. This could be attributed to the significance of physical factors affecting nutrient uptake of phytoplankton.

4. It is essential to consider environmental factors such as temperature and resource availability while studying size-based trophic interactions.

5. Fish predation and cyanobacteria blooms are key factors modifying cascading trophic interactions in planktonic food webs of the naturally eutrophic Lake Mývatn.

6. While zooplankton size diversity is controlled by fish predation and the cyanobacteria blooms, phytoplankton size diversity is mainly driven by resources in Lake Mývatn as in Turkish shallow lakes.

7. Zooplankton experience negative changes in their grazing and foraging behavior after the bloom, due to increase in phytoplankton size diversity in Lake Mývatn. Because bloom forming cyanobacteria interfere with zooplankton grazing, effective energy transfer through the food web is lowered.

8. Zooplankton community are not resilient to short-term fish predation as shown in fish removal mesocosm experiment in close to Lake Müggelsee, Berlin.

9. Fish predation in enclosures with fish (in experiments close to Lake Müggelsee) alters zooplankton community composition and size structure. Some of the large sized zooplankton taxa disappear, as small sized taxa of Cladocera strongly increase as a result of fish predation.

10. A shift in the zooplankton community composition and size structure disturb the trophic cascade of the system (in experiments close to Lake Müggelsee). The resulting zooplankton community after fish predation are not able to graze efficiently on (and control) phytoplankton and thus increase phytoplankton yield.

11. Different taxa of zooplankton respond differently to fish predation (in experiments close to Lake Müggelsee). These differences could be related to other environmental factors such as seasonality and variations in reproduction and growth of different zooplankton groups.

12. Together with effects of fish predation on size-based trophic interactions, understanding resilience of zooplankton community structure can provide information for ecosystem functioning and freshwater management strategies to follow in the future where there will be many disturbances.

13. Although overlooked in many studies, size related intraspecific variability in different developmental stages of organisms is an important factor to be considered in food web studies. Grazing by different developmental stages of predators cause variations in prey size spectra, where larger sized predator (i.e adults) have stronger effects on their preys.

14. Our findings also reveal the importance of mixotrophy in shaping consumer-resource interactions. Large ciliates feeding from Mediterranean ponds on small phytoplankton cause variations in prey composition and thus size structure.

CONCLUSIONS GENERALS (in Catalan)

1. Hi ha una correspondència positiva entre les estructures de mides de nivells tròfics adjacents en 30 llacs poc profunds turcs. La diversitat de mides de peixos es relaciona amb la diversitat de mides de zooplàncton, fet que suggereix que una major diversitat de recursos pot suportar una major diversitat de consumidors, o viceversa.

2. Els canvis en la uniformitat de mides dels peixos de llacs turcs es poden explicar per les diferències de temperatura entre llacs. En els llacs més càlids, els peixos tendeixen a tenir distribucions de mida irregular on dominen els peixos de mida petita.

3. L'estructura de mides del fitoplàncton (en concret, la diversitat i la uniformitat) de llacs turcs està més influenciada per la temperatura i la disponibilitat de recursos que per la depredació. Aquest fet pot ser degut a la importància dels factors físics que afecten l'absorció de nutrients del fitoplàncton.

4. És fonamental considerar factors ambientals com la temperatura i la disponibilitat de recursos quan s’estudien les interaccions tròfiques basades en la mida dels individus.

5. La depredació de peixos i els blooms de cianofícies modifiquen les interaccions tròfiques en cascada de xarxes tròfiques planctòniques del Llac Mývatn.

6. Mentre que la diversitat de mides del zooplàncton està controlada per la depredació de peixos i els blooms de cianofícies en el Llac Mývatn , la diversitat de fitoplàncton és impulsada principalment pels recursos, tant al Llac Mývatn com als llacs turcs (tots poc profunds).

7. El zooplàncton experimenta canvis negatius en el seu comportament d’alimentació després del bloom, a causa de l'augment en la diversitat de mides del fitoplàncton en Llac Mývatn. Els blooms de cianofícies interfereixen en

l’alimentació del zooplàncton i, per tant, redueixen la transferència d'energia efectiva a través de la xarxa tròfica.

8. La comunitat de zooplàncton no és resilient a la depredació dels peixos a curt termini, segons l’experiment al costat del Llac Müggelsee.

9. La composició de la comunitat de zooplàncton i la seva estructura de mides es poden veure alterats per la depredació de peixos (experiments al costat del Llac Müggelsee). Alguns dels tàxons de zooplàncton de grans dimensions poden desaparèixer quan els tàxons de mida petita Cladocera (per exemple, Bosmina i Chydorus) augmenten significativament per la depredació dels peixos.

10. Un canvi en la comunitat de zooplàncton i en la seva estructura de mides provoca una alteració de la cascada tròfica del sistema (experiments al costat del Llac Müggelsee). El zooplàncton resultant després de la depredació de peixos no és prou eficient per controlar el fitoplàncton i la biomassa de fitoplàncton augmenta significativament.

11. Diferents tàxons de zooplàncton responen de manera diferent a la depredació dels peixos (experiments al costat del Llac Müggelsee). Aquestes diferències es podrien relacionar amb factors ambientals com l'estacionalitat, i les variacions en la reproducció i el creixement de diferents grups de zooplàncton.

12. Juntament amb els efectes de la depredació dels peixos en les interaccions tròfiques dependents de la mida dels individus, entendre la resiliència de l'estructura de la comunitat de zooplàncton pot proporcionar informació sobre el funcionament dels ecosistemes i sobre les estratègies de gestió de l'aigua dolça a seguir en un futur que es preveu amb moltes alteracions.

13. Encara que es passa per alt en molts estudis, la variabilitat intraespecífica de mides entre diferents etapes del desenvolupament dels organismes és un factor important a considerar en els estudis de xarxes tròfiques. Alimentació de les diferents etapes de desenvolupament dels depredadors causa variacions en els espectres de mida de les preses, on un depredador de major tamany (és a dir, els adults) té efectes més forts en les preses.

14. La mixotròfia és important a l’hora de configurar les interaccions entre els consumidors i els recursos. Els ciliats que s'alimenten de fitoplàncton petit fan variar la composició de les preses de llacunes mediterrànies i, per tant, la seva estructura de mides.

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APPENDICES

Chapter 1

Table 7. Additional general linear models (GLMs) including temperature, TP, altitude, net evaporation, conductivity, lake area, and depth as predictor variables for the size structure of phytoplankton, zooplankton, and fish assemblages (only the best model is shown). The taxonomic diversity of each organism group was also included as predictor variable. Temperature and altitude were highly correlated (correlation coefficient higher than 0.6), so altitude was removed as a predictor variable. For zooplankton size diversity, we ran two models, one including fish size diversity and another including non-piscivorous fish size diversity as predictors, and both models were significant. We only present the model explaining the highest percentage of variability. Coefficients (estimates and standard error, SE), beta (standardised) coefficients (Beta coeff.), t-value, significance (P value) and variability explained by each model (%). n.s., non-significant.

Response variable	Predictor	Estimate	SE	Beta coeff.	t-value	*p* value	%
Fish (all fish)							
Size diversity	Zooplankton size diversity	0.868	0.187	0.598	4,63	<0.01	56.7
	Fish species diversity	1.107	0,308	0,464	3,59	<0.01	
Size evenness	Log temperature	-0.624	0.231	-0.448	-2.70	<0.05	20.1
Non-piscivorous fish							
Size diversity	Zooplankton size diversity	0.649	0.207	0.474	3.14	<0.01	40.5
	Non-piscivorous fish species diversity	0.966	0.340	0.430	2.84	<0.01	
Size evenness	n.s						
Zooplankton							
Size diversity	Fish size diversity	0.316	0.097	0.459	3.27	<0.01	53.2
	Zooplankton species diversity	0.530	0.167	0.445	3.17	<0.01	
Size evenness	n.s.						
Phytoplankton							
Size diversity	Log TP	0.615	0.339	0.325	1.82	<0.1	10.5
Size evenness	Log temperature	0.480	0.214	0.385	2.25	<0.05	14.8

Chapter 2

Table 8. Pearson correlation coefficients of predictor variables. *p≤ 0.05, **p≤ 0.01.

	Phytoplankton size diversity	**Zooplankton size diversity**	**Phytoplankton total biomass**	***Anabaena* biomass**	**Ln zooplankton total biomass**	**Day**	**Ln TP**	**Phytoplankton species diversity**
Phytoplankton size diversity	1	-0.50**	0.85**	0.84**	-0.07	0.85**	0.73**	0.38*
Zooplankton size diversity		1	-0.34*	-0.35*	0.56**	-0.61**	-0.37*	-0.33
Phytoplankton total biomass			1	0.97**	0.05	0.74**	0.70**	0.12
***Anabaena* biomass**				1	0.07	0.72**	0.69**	0.07
Ln zooplankton total biomass					1	-0.12	0.01	-0.52**
Day						1	0.70**	0.39*
Ln TP							1	0.18
Phytoplankton species diversity								1

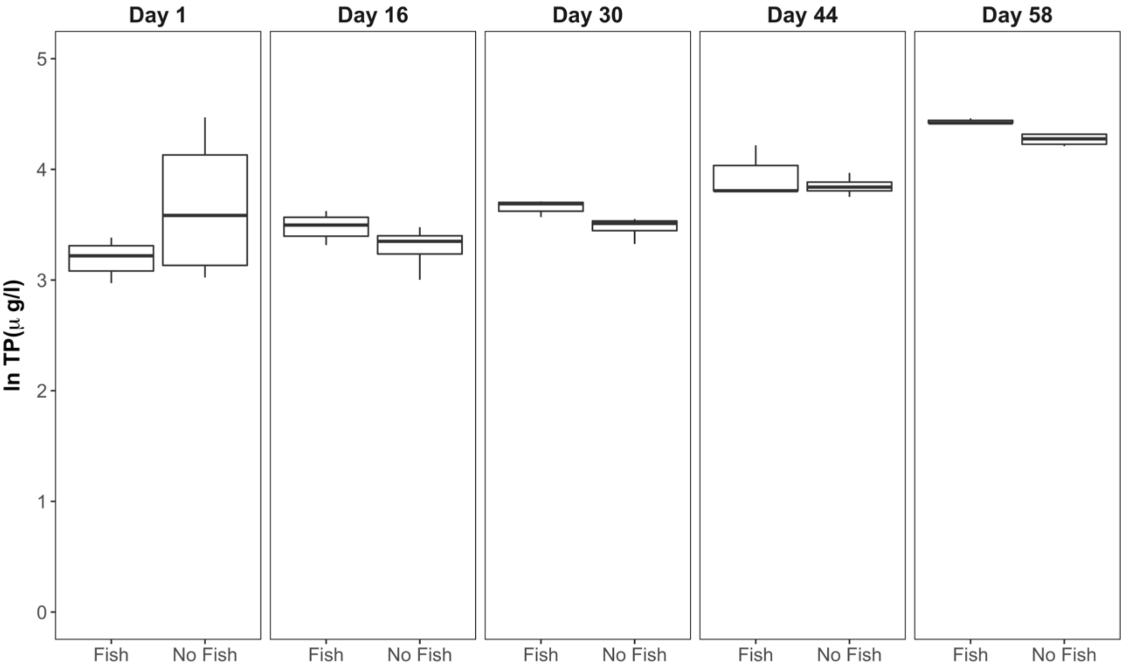

Figure 18. Ln TP (µg/L) for different treatments (Fish, No fish) on each sampling day.

Chapter 3

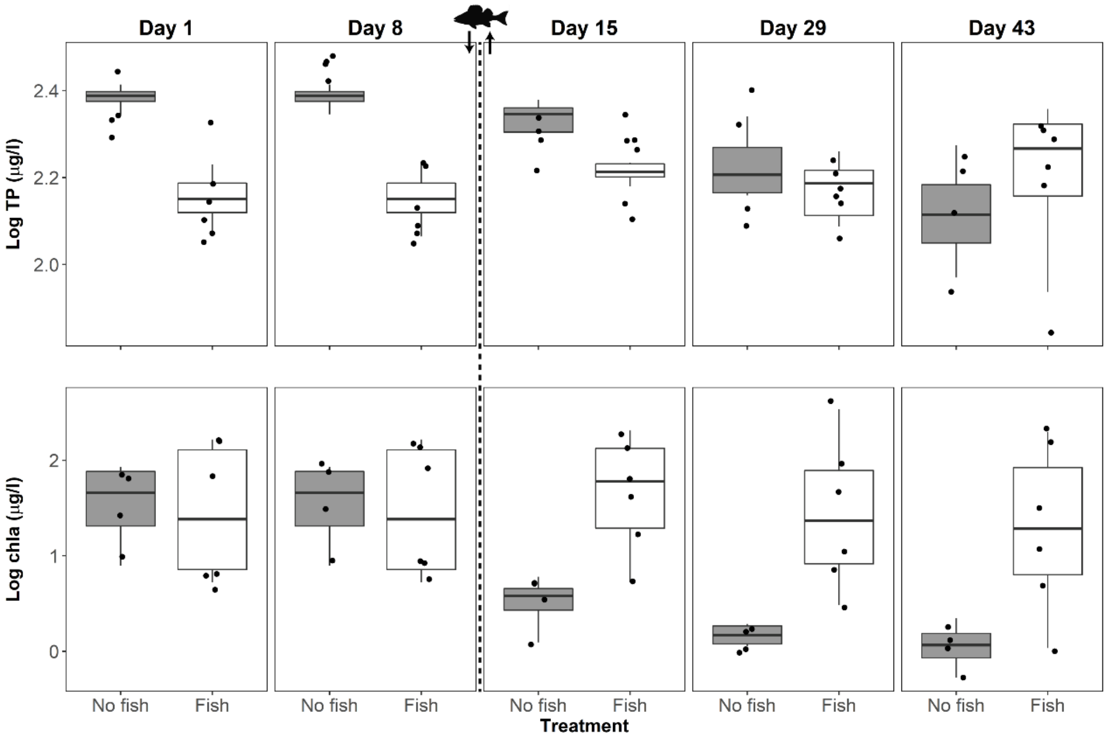

Figure 19. $\log_{10}$(TP) and $\log_{10}$(chla) for different treatments (no fish, n=4; fish, n=6) on each sampling day. Fish image with arrows indicates addition and removal of fish.

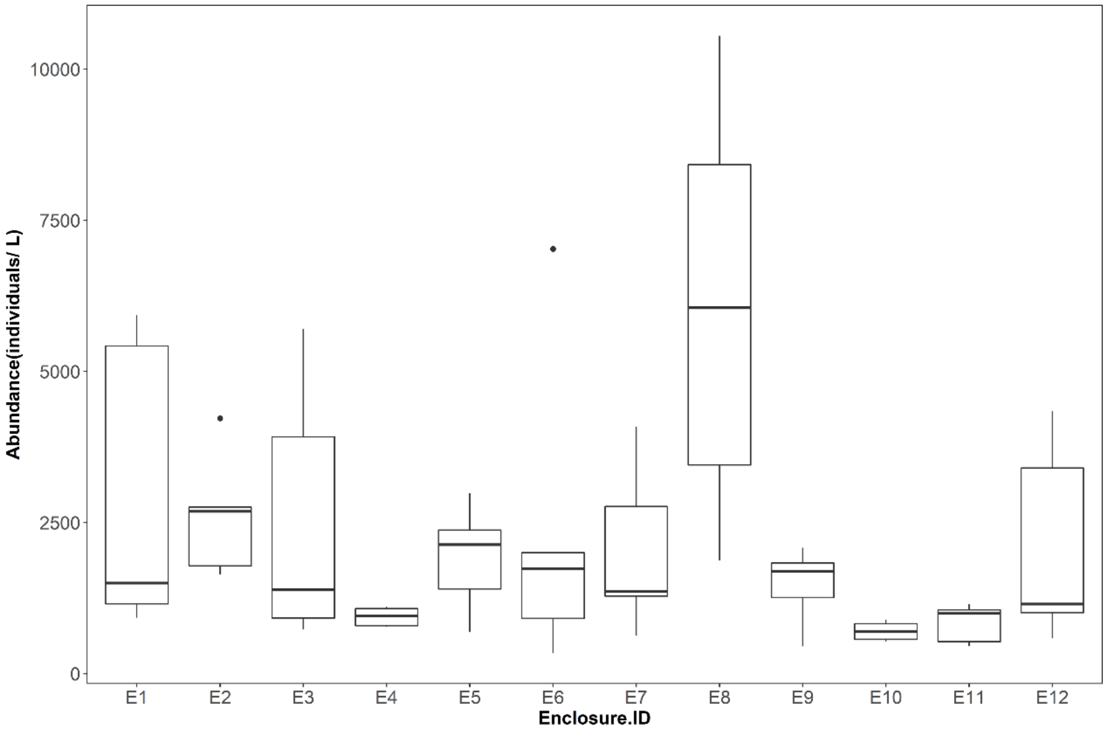

Figure 20. Total abundance of zooplankton in each enclosure. E1-8 are fish enclosures and E9-12 are no fish enclosures. Enclosures E5 and E8 were excluded because there was dead fish in one enclosure because of pump malfunctioning, and one enclosure stocked with fish became an extreme outlier in terms of total zooplankton abundance because of a massive rotifer bloom.

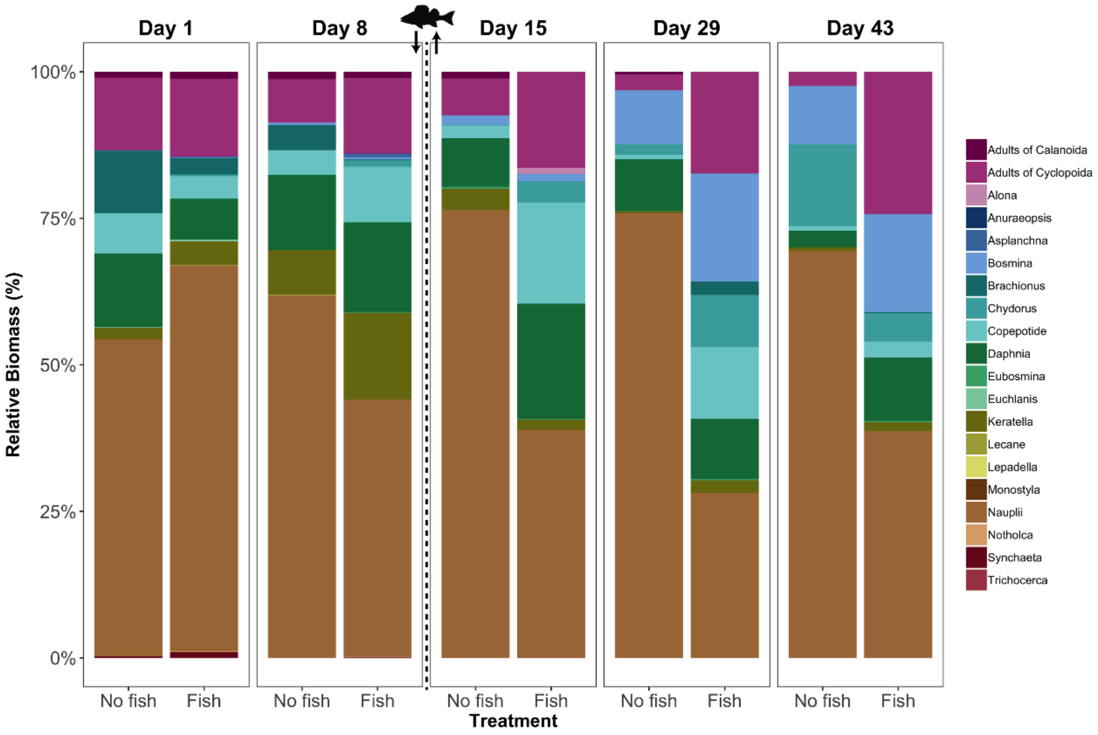

Figure 21. Relative average biomass of different zooplankton taxa for different treatments (no fish, n=4; fish, n=6) on each sampling day. Fish image with arrows indicates addition and removal of fish.

Other publications by the author

Cañedo-Argüelles, M., Sgarzi, S., Arranz, I., Quintana, X.D., **Ersoy, Z.**, Landkildehus, F., Lauridsen, T., Jeppesen, E., Brucet, S. Role of predation in biological communities in naturally eutrophic subarctic Lake Mývatn, Iceland, Hydrobiologia (2017), 790, 1, 213–223, doi:10.1007/s10750-016-3031-0

Oral participations in conferences

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