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

Zeynep Ersoy[1] | Erik Jeppesen[2,3,4,5] | Serena Sgarzi[1] | Ignasi Arranz[1] | Miguel Cañedo-Argüelles[1,6] | Xavier D. Quintana[7] | Frank Landkildehus[2] | Torben L. Lauridsen[2,3,4,5] | Mireia Bartrons[1] | Sandra Brucet[1,2,8]

[1]Aquatic Ecology Group, University of Vic – Central University of Catalonia, Vic, Catalonia, Spain
[2]Department of Bioscience, Aarhus University, Silkeborg, Denmark
[3]Sino-Danish Centre for Education and Research (SDC), University of Chinese Academy of Sciences, Beijing, China
[4]Greenland Climate Research Centre (GCRC), Greenland Institute of Natural Resources, Nuuk, Greenland
[5]Arctic Research Centre, Aarhus University, Aarhus, Denmark
[6]Freshwater Ecology and Management (FEM) Research Group, Departament de Biologia Evolutiva, Ecologia i Ciències Ambientals, Institut de Recerca de l'Aigua (IdRA), Universitat de Barcelona (UB), Barcelona, Catalonia, Spain
[7]GRECO, Institute of Aquatic Ecology, University of Girona, Girona, Spain
[8]ICREA, Catalan Institution for Research and Advanced Studies, Barcelona, Spain

Correspondence
Zeynep Ersoy and Sandra Brucet, Aquatic Ecology Group, University of Vic – Central University of Catalonia, Vic, Catalonia, Spain.
Emails: zeynep.ersoy@uvic.cat and sandra.brucet@uvic.cat

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Abstract

1. 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.
2. 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.
3. 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.
4. 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.
5. 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

1 | INTRODUCTION

Cascading trophic interactions have long been a field in aquatic ecosystem studies (Carpenter, Kitchell, & Hodgson, 1985; Jeppesen, Jensen, & Søndergaard, 2002; Polis, Sears, Huxel, Strong, & Maron, 2000). Most studies have focused on the abundance, biomass, or average size of predators and prey (Knight, McCoy, Chase, McCoy, & Holt, 2005; Pace, Cole, Carpenter, & Kitchell, 1999). Size-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 et al., 2006; Brown, Gillooly, Allen, Savage, & West, 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; 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, Beisner, Patoine, & Pinel-Alloul, 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, Chang, García-Comas, Gong, & Hsieh, 2013; Yvon-Durocher, Montoya, Trimmer, & Woodward, 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 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, Ismar, & Sommer, 2015; Marañón, Cermeño, Latasa, & Tadonléké, 2012; Sommer, Peter, Genitsaris, & Moustaka-Gouni, 2016). For example, high resource availability may promote growth of large-sized bloom-forming phytoplankton (Downing, Watson, & McCauley, 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, Faassen, Pennino, & Lurling, 2016; Ger, Urrutia-Cordero, et al., 2016; Jeppesen 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 size-based competition (Arranz et al., 2016; Brucet, Boix, López-Flores, Badosa, & Quintana, 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, Baum, Salomon, & Dulvy, 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, Maxwell, Reuman, & Jennings, 2010; Jennings, Warr, & Mackinson, 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, Hauptfleisch, Leavitt, & Ives, 2016; Einarsson, Gardarsson, Gislason & Ives, 2002). 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 & Örnólfsdottir, 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 & Örnólfsdottir, 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 (Jonasson & 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 defences of bloom-forming phytoplankton (Ger, Urrutia-Cordero, et al., 2016; Muller-Navarra, Brett, Liston, & Goldman, 2000; Steiner, 2003).

2 | METHODS

2.1 | 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 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, 0.14, 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).

2.2 | Experimental setup

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 setup, 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 setup, 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.

2.3 | 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 (μS/cm), and dissolved oxygen (mg/L) were measured in situ using a Hanna multiparameter meter (Hanna Instruments, U.S.A.). Water transparency (cm) was measured with a Secchi disc. 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, μg/L), soluble reactive phosphorus (μg/L), total nitrogen (μg/L), ammonium (NH_4^+, μg/L), and chlorophyll-*a* (chl-*a*, μg/L). Detailed information about chemical analysis can be found in Cañedo-Argüelles et al. (2017).

From the mixed water sample (10–12 L), 7 L was 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, Duncan, Gliwicz, Grygierek, & Herzig, 1976; Dumont, Van de Velde, & Dumont, 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.

2.4 | 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. Nonparametric 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 centred 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, Brucet, Ritterbusch, & Mehner, 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 and Buccianti (2011) that the proxy prevents spurious correlations that may appear when proportions and ratios are used in statistical analysis.

2.5 | Data analysis

All data were analysed using the "nlme" (Pinheiro, Bates, DebRoy, & Sarkar, 2017) and "car" (Fox & Weisberg, 2011) packages in R version 3.3.0 (R Core Team, 2016).

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 three 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 Fig. S1), 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 S1). 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, 2014). All graphs were produced with the "ggplot2" package (Wickham, 2009).

For all models, all predictor variables were scaled and centred prior to analysis in order to better compare and interpret predictors with different scales. Normality was checked by Shapiro–Wilk's test before analysis ($p > .05$) and variables were ln-transformed, when necessary. The correlation structure of the predictor variables was checked, and highly correlated variables ($r > .6$) (Emmrich et al., 2011) were removed before the analysis (see Table S1 in the supplementary material). As a random effect, the intercept was allowed to change with each enclosure to account for the temporal pseudoreplication. 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 values. Residual plots of the most parsimonious models were checked for normality.

3 | 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 figs 2 and 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 1), causing a decline in TTE (Figure 2). Although the differences in zooplankton, phytoplankton size diversity, and TTE between fish treatments were not significant in any sampling day (*t* test, $p > .05$, Benjamini–Hochberg correction), some differences were observed between fish treatments for zooplankton size diversity and TTE (Figures 2 and 3).

According to LMMs, zooplankton size diversity was negatively related to fish treatment and *Anabaena* occurrence ($p < .05$ and $p < .01$, respectively, Table 1). We did not include phytoplankton total biomass in the final model for zooplankton size diversity because it was correlated with phytoplankton size diversity (Table S1) and the most parsimonious model while using phytoplankton total biomass was the same as the one with phytoplankton size diversity (Table 1).

Phytoplankton size diversity was significantly higher after *Anabaena* bloom (factor *Anabaena* occurrence $p < .01$, Table 1) and slightly positively (but not significantly) related to productivity (using ln TP as a proxy, see Fig. S1) ($p = .07$, Table 1). In fact, productivity, *Anabaena* biomass and phytoplankton size diversity were highly correlated ($r > .6$, Table S1). TTE was significantly lower after *Anabaena* bloom (factor *Anabaena* occurrence $p < .001$, Table 1) and related positively to zooplankton size diversity ($p < .01$, Table 1 and Figure 3).

4 | 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)

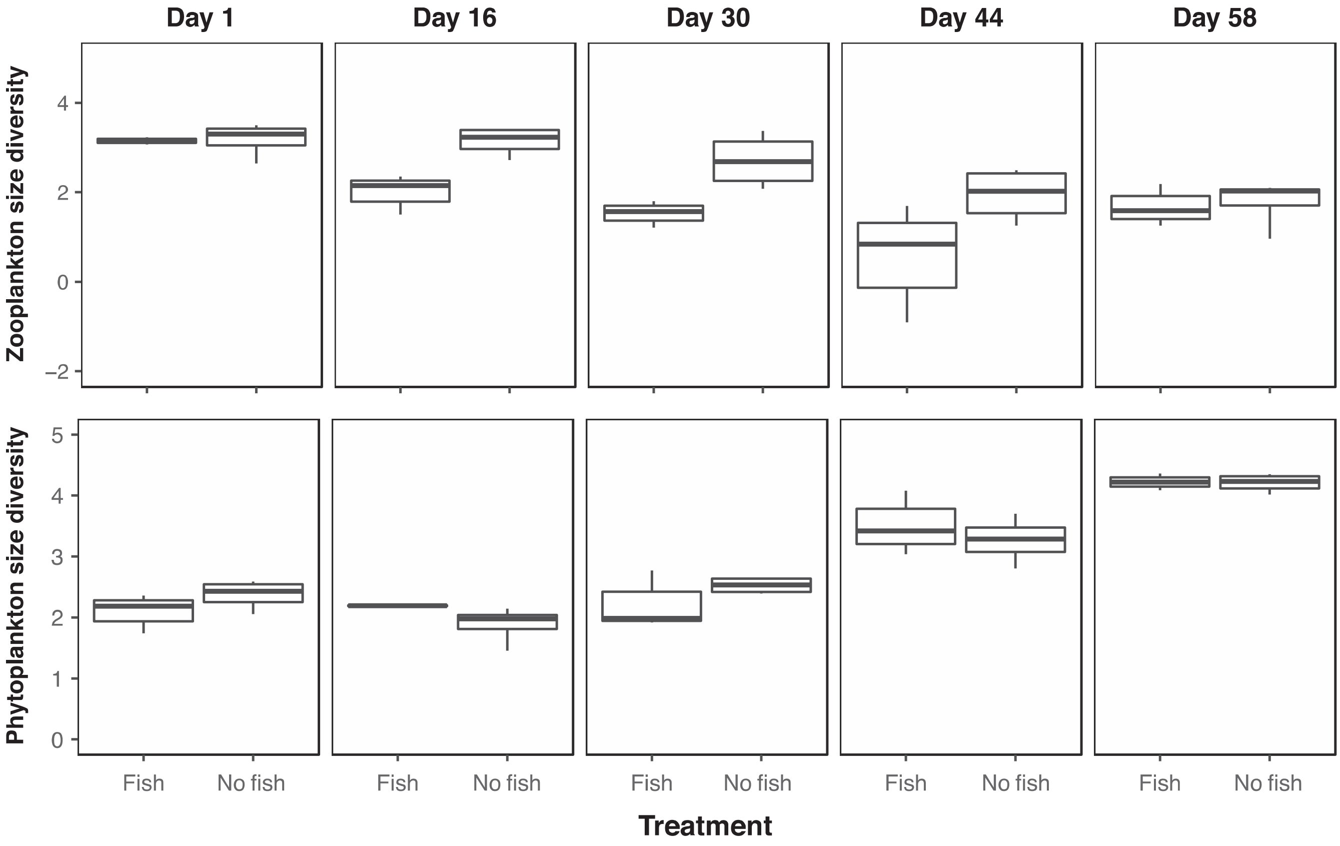

FIGURE 1 Zooplankton and phytoplankton size diversity for different treatments (fish, no fish) on each sampling day. Fish treatment and *Anabaena* occurrence were significant for zooplankton size diversity, while only *Anabaena* occurrence was significant for phytoplankton size diversity

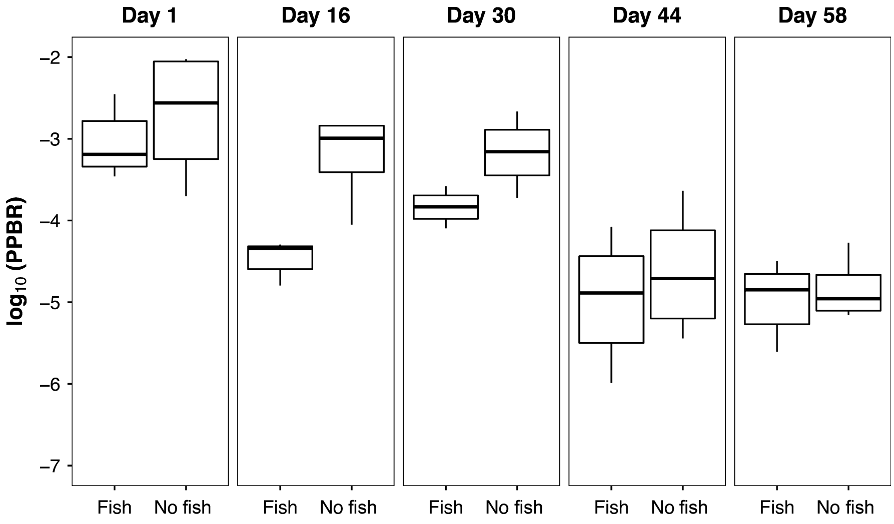

FIGURE 2 Log_{10} (PPBR) (=TTE) for different treatments (fish, no fish) on each sampling day. Zooplankton size diversity and *Anabaena* occurrence were significant for TTE

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

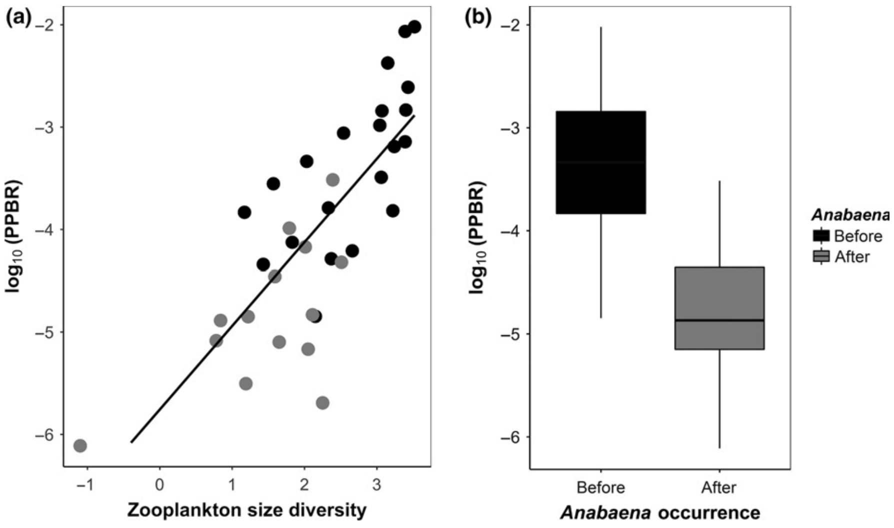

FIGURE 3 Effect of (a) predator (zooplankton) size diversity on biomass transfer efficiency (from phytoplankton to zooplankton) ($\log_{10}$ [PPBR]) (n = 35, Marginal R^2 = 0.69, Table 1). (b) Effect of *Anabaena* occurrence (before/after) on biomass transfer efficiency ($\log_{10}$ [PPBR]) (Table 1, $p < 0.01$). Different colours represent before and after *Anabaena* across all sampling dates

TABLE 1 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	**.03**	.47	.47
	Anabaena (after)		−0.81	0.18	27	−4.55	**<.01**		
Phytoplankton size diversity	ln TP	54.83	0.19	0.10	26	1.89	.07	.78	.78
	Anabaena (after)		0.91	0.15	26	6.24	**<.01**		
TTE	Zooplankton size diversity	75.19	0.58	0.12	26	4.76	**<.001**	.69	.69
	Anabaena (after)		−0.56	0.17	26	−3.25	**<.01**		

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 inhibition (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 S1). 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 (Jonasson & 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., 2016). 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; 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 the 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, Persson, De Roos, Jones, & Tranvik, 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, Compte, Boix, López-Flores, & Quintana, 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, 2004, 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 et al., 2017; Zhang et al., 2013).

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ORCID

Zeynep Ersoy http://orcid.org/0000-0003-2344-9874
Ignasi Arranz http://orcid.org/0000-0002-1517-1713
Miguel Cañedo-Argüelles http://orcid.org/0000-0003-3864-7451
Mireia Bartrons http://orcid.org/0000-0003-0617-9577
Sandra Brucet http://orcid.org/0000-0002-0494-1161

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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