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ORIGINAL ARTICLE

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

Sandra Brucet^{1,2,3} | Ülkü Nihan Tavşanoğlu⁴ | Arda Özen^{4,5} | Eti Ester Levi⁴ | Gizem Bezirci⁴ | Ayşe İdil Çakıroğlu⁴ | Erik Jeppesen^{3,6,7,8} | Jens-Christian Svenning³ | Zeynep Ersoy^{1,4} | Meryem Beklioğlu^{4,9}

¹Aquatic Ecology Group, University of Vic – Central University of Catalonia, Vic, Spain

²Catalan Institution for Research and Advanced Studies, ICREA, Barcelona, Spain

³Department of Bioscience, Aarhus University, Aarhus, Denmark

⁴Department of Biology, Limnology Laboratory, Middle East Technical University, Ankara, Turkey

⁵Department of Forest Engineering, Cankiri Karatekin University, Çankırı, Turkey

⁶Sino-Danish Centre for Education and Research (SDC), Beijing, China

⁷Greenland Institute of Natural Resources, Greenland Climate Research Centre (GCRC), Nuuk, Greenland

⁸Arctic Centre, Aarhus University, Aarhus, Denmark

⁹Kemal Kurdaş Ecological Research and Training Stations, Middle East Technical University, Ankara, Turkey

Correspondence

Sandra Brucet, Aquatic Ecology Group, University of Vic – Central University of Catalonia, Vic, Spain. Email: sandra.brucet@uvic.cat

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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.
- 2. 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 which may also affect size structure. 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.
- **3.** 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 zoo-plankton assemblages. The size evenness of fish and phytoplankton assemblages was negatively and positively related to temperature, respectively. Phytoplankton size diversity was only weakly predicted by the resource availability.
- 4. 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

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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

1 | 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, Gillooly, Allen, Savage, & West, 2004; 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, Abades, Laufer, Loureiro, & Marquet, 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, Hanson, Butler, & Duffy, 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 wellresolved 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 nonlinear 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 in natural food webs are poorly understood (Brose, Jonsson et al., 2006; García-Comas et al., 2016; Mehner et al., 2016; Rudolf, 2012). Comparative examination of the size distribution in predator and prey communities may bring insight into the strength of the interactions between adjacent trophic levels (Brose, Jonsson et al., 2006, 2016; Mehner et al., 2016; Trebilco, Baum, Salomon, & Dulvy, 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 using two synthetic measures of size distribution: the size diversity and size evenness indices (Brucet, Boix, López-Flores, Badosa, & Quintana, 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; Sorf et al., 2015; Tavşanoğlu et al., 2015; Ye, Chang, García-Comas, Gong, & Hsieh, 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., 2013; 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, 2002). 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 (Emmrich et al., 2014; Garzke, Ismar, & Sommer, 2015; Marañón, Cermeño, Latasa, & Tadonléké, 2012; Sommer, Peter, Genitsaris, & Moustaka-Gouni, 2016). 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, Brucet, Ritterbusch, & Mehner, 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., 2013). 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 hypothesised 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 intraguild interactions among predators and diminishing enemy impacts on preys (Finke & Denno, 2004, 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).

2 | METHODS

Site description 2.1

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 1-1,328 m, were selected (Figure 1). 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 12.0°C 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 (Harlioglu, 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).

2.2 Sampling and analysis

The 30 lakes were sampled once during the peak growing season (July to August) of 2007-2010, following largely the standardised sampling protocol described in detail by Moss et al. (2003) (for details of the sampling, see Levi et al., 2014; Cakıroğlu et al., 2014). Mean annual air temperatures interpolated for a 30-arc-second-spatial resolution (1 km² 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), conductivity ($\pm 1 \mu$ S/cm), 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 and Beklioglu (2010). Per cent plant volume inhabited (PVI%: plant coverage \times average plant height/water depth sensu Canfield et al., 1984) for each submerged and floating-leaved plant species was recorded at even intervals along a transect line.

From the 40-L mixed pelagic sample, 50 ml was taken and fixed using 2% Lugol solution for phytoplankton counting. Depending on the sample size, different phytoplankton volumes were settled for 16-24 hr 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, Durselen, Kirschtel and Zahary (1999) and Sun and Liu (2003).



FIGURE 1 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)

TABLE 1 Physicochemical, 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	17.4	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
рН	8.31	6.92	9.64	0.6
Conductivity (µS/cm)	1248	104.0	8583	2219
Total phosphorus (µg/L)	128	15	633	141
Total nitrogen (µg/L)	1081	239	2180	596
Secchi depth/maximum depth	0.32	0.05	1.00	0.20
Dissolved oxygen (mg/L)	6.6	0.6	15.3	2.9
Chlorophyll a (µg/L)	19.8	2.4	95.1	21.9
NPUE (number of fish per net per night)	162	0.3	1160	247
Plant volume inhabited (%)	14	0	78	20

For pelagic zooplankton, 20 L of the mixed pelagic sample was 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- μ m filter. Pelagic and littoral zooplankton samples were analysed separately. Zooplankton was preserved in 4% Lugol's 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, Maclver, & 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

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2.3 | 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:

$$\mu = -\int_0^{+\infty} p_X(x) \text{log}_2 p_X(x) dx$$

where $p_x(x)$ is the probability density function of size x. The nonparametric kernel estimation was used as a probability density function, which is applicable to any type of size distribution. Before computing size diversity, data were automatically standardised 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 standardisation, 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); and (4) it is a single-value metric, which simplifies the comparison between samples (e.g. Brucet et al., 2010).

Size evenness ($J_{\rm e}$) was 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 ranged 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 analyse 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 planktivorous, we established a threshold size of 15 cm below which we considered them non-piscivorous (e.g. Mehner et al., 2016), and we recalculated 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.

2.4 | 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).

2.5 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 ⁶ WILEY Freshwater Biology

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 minimising 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 S1) 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 analysed 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 reran 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 multicollinearity among predictors in the final set used for the analyses. GLMs were performed in "R" version 2.9.1 (R Core Team 2009) using the BRODGAR v. 2.7.2 statistical package (Highland Statistics Ltd., Newburgh, U.K.).

3 RESULTS

Size diversity (μ) ranged from 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 three of the 120 samples analysed).

	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

Size evenness (J_e) ranged from 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 \pm 0.49 and 1.99 \pm 0.62 for μ in the pelagic and littoral and 0.70 \pm 0.1 and 0.74 \pm 0.1 for J_e in the pelagic and littoral, respectively; ANOVAs, p > .05), and the predictors of both models were the same; thus, only the results for pelagic zooplankton are presented as from here.

Fish size diversity (μ_{fish}) was significantly positively related to zooplankton size diversity (µzooplankton), explaining 35.5% of the variation in the data (Table 3, Figure 2). As judged from the significant positive relationship between μ_{fish} and $\mu_{\text{zooplankton}}$ (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 3). High $\mu_{zooplankton}$ reflected the presence of large-sized Cladocera or Copepoda in similar proportions as small-sized rotifers and nauplii (Figure 3), causing a bimodal size distribution with a second dome (i.e. curved-shaped), corresponding to large sizes beginning around size class -0.7 (log₂ µg dry weight). However, when only few sizes of fish dominated (low μ_{fish} ; Figure 3), µ_{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 analysed, their size diversity was also positively related only to $\mu_{zooplankton}$, but the relationship was slightly weaker (Table 3).

GLMs showed that temperature was related to $J_{e \text{ fish}}$, while there were no links to the other trophic levels (Table 3, Figure 2). 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 (µphytoplankton) was only weakly and positively predicted by TP (Table 3, Figure 2), and there were no links to the other trophic levels. Je phytoplankton was positively related to temperature. The log biomass ratio between adjacent trophic levels was not significant in any case.

The additional GLMs (Table S1) including species diversity as predictors within each assemblage and other environmental factors BRUCET ET AL.

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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	0.86	0.24	0.60	3.69	.001	36.0
			Log temperature	0.62	1.37	0.07	0.45	.653	
			Log TP	-0.03	0.28	-0.02	-0.11	.910	
	Best	-29.0	Zooplankton size diversity	0.86	0.23	0.59	3.82	.001	35.5
Size evenness	Full	-133.0	Zooplankton size evenness	0.17	0.24	0.12	0.71	.483	29.7
			Log temperature	-0.57	0.24	-0.41	-2.31	.028	
			Log TP	-0.09	0.05	-0.30	-1.80	.082	
	Best	-136.1	Log temperature	-0.63	0.23	-0.45	-2.70	.011	20.1
Non-piscivorous fish									
Size diversity	Full	-23.1	Zooplankton size diversity	0.65	0.24	0.47	2.65	.014	22.3
			Log temperature	0.38	1.42	0.05	0.26	.793	
			Log TP	0.03	0.29	-0.02	-0.09	.923	
	Best	-27.1	Zooplankton size diversity	0.64	0.23	0.47	2.77	.010	22.1
Size evenness	Full	-128.6	Zooplankton size evenness	0.22	0.26	0.17	0.84	.408	4.2
			Log temperature	0.01	0.27	0.01	0.04	.969	
			Log TP	0.03	0.05	0.10	0.50	.621	
Zooplankton									
Size diversity	Full	-45.3	Fish size diversity	0.40	0.11	0.58	3.50	.002	36.7
			Log Fish:Zooplankton	-0.05	0.11	-0.09	-0.45	.655	
			Log temperature	0.39	0.96	-0.07	-0.40	.690	
			Log TP	-0.12	0.23	-0.10	-0.53	.601	
	Best	-50.6	Fish size diversity	0.41	0.11	0.59	3.82	.001	35.5
Size evenness	Full	-146.5	Fish size evenness	0.11	0.15	0.15	0.68	.500	11.7
			Log Fish:Zooplankton	-0.01	0.02	-0.02	-0.11	.610	
			Log temperature	0.36	0.20	0.37	1.76	.090	
			Log TP	0.01	0.05	0.06	0.25	.805	
Phytoplankton									
Size diversity	Full	-7.60	Zooplankton size diversity	-0.34	0.30	-0.25	-1.12	.273	11.2
			Log Zoo:Phyto	-0.15	0.25	-0.12	-0.58	.566	
			Log temperature	0.04	2.31	0.01	0.02	.986	
			Log TP	0.51	0.35	0.27	1.41	.169	
	Best	-11.0	Log TP	0.62	0.34	0.33	1.82	.080	10.5
Size evenness	Full	-134.9	Zooplankton size evenness	-0.17	0.24	-0.13	-0.70	.491	22.1
			Log Zoo:Phyto	-0.03	0.03	-0.19	-0.98	.338	
			Log temperature	0.37	0.25	0.29	1.48	.152	
			Log TP	0.05	0.05	0.21	1.16	.255	
	Best	-138.2	Log temperature	0.48	0.21	0.39	2.25	.032	14.8

which may influence community diversity (Table 1) showed that size diversity of fish, non-piscivorous fish and zooplankton was positively related to 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 4). When using a trophic

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FIGURE 2 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

index of 3 for YOY, average fish trophic level in the lakes explained 24.5% of the zooplankton size diversity variation.

4 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 support a sizediverse 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, 2002), 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 4)-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 intraguild interactions among predators and diminishing enemy impacts on preys (Finke & Denno, 2004, 2005). Conversely, a community of predators with similar-sized individuals (e.g. dominance of small-sized 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 > .05). When we additionally explored whether a relationship existed between species and size diversity within each assemblage (Table S1), 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



FIGURE 3 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 4 Relationship between average fish trophic level in a lake and zooplankton size diversity

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 although 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 favoured at low nutrient availability due to the higher surface:volume ratio or lower resource requirements, whereas large algae are often (but see Jensen, Jeppesen, Olrik, & Kristensen, 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 nanomicroplankton (prey) size diversity was negatively related to size diversity of mesozooplankton (predators), as well as to physical WILEY Freshwater Biology

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 in high-altitude lakes.

We recognise 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 predatorprey 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 to provide better knowledge of the trophic link strengths that affect the size distributions (Boukal, 2014; Brose, 2010). Furthermore, we categorised 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 (Post & Takimoto, 2007; Quintana et al., 2015). 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 not shown; p > .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., 2016 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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ORCID

Sandra Brucet D http://orcid.org/0000-0002-0494-1161 Eti Ester Levi D http://orcid.org/0000-0001-9038-7285 Zeynep Ersoy D http://orcid.org/0000-0003-2344-9874

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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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