

Within-lake variability in predation risk shapes the spatio-temporal structure of the zooplankton community

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Abstract

1. While it is well-accepted that predation plays a key role in shaping both size structure and species composition in natural ecosystems, fine-scale variation in predation risk within ecosystems has been largely neglected. The objective of this study was to use normalised size spectra (NSS) to investigate whether small-scale spatial variation in predation risk (by fish) can modulate zooplankton community structure at the within-lake level in a small temperate lake.
2. We tested the difference in the NSS between two hydrologically well-connected basins of a lake exhibiting contrasting thermal regimes. The first is a well-mixed shallow basin (max. depth 2.5 m) that is inaccessible to brook charr (*Salvelinus fontinalis*) during summer because the temperature is too warm. The second is a deeper basin (max. depth 18 m) offering a thermal refuge during summer because of lake stratification. As a consequence of these differences in fish accessibility, the fishless basin should contain larger and more abundant zooplankters, inducing a change in NSS slope and height.
3. Our results showed that both the zooplankton size structure and taxonomic composition were distinct in the two basins, with a higher proportion of small individuals and a higher abundance of zooplankton in the shallow basin compared to the deep one. Furthermore, following cooling of the epilimnion in late summer, the zooplankton communities of both basins exhibited a clear shift in size structure and species composition: in autumn, there were smaller individuals and larger proportions of Bosminidae and Daphniidae compared to colonial rotifers than in summer. These results suggest a potential effect of the change in the spatial distribution of brook charr which feed preferentially on large individuals, reducing the average body size of the zooplankton community.
4. Our results show that predation risk by fish can induce a spatial and temporal variation in zooplankton community structure within small temperate lake ecosystems exhibiting contrasted thermal regimes. Other potential predators also influenced the zooplankton community structure, creating a complex interplay that has to be taken into account to disentangle ecological processes and predict their future changes.

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KEYWORDS

brook charr, normalised size spectra, size structure, spatial heterogeneity, underwater vision profiler

1 | INTRODUCTION

Variations in community size structure provide valuable information on ecosystem processes such as productivity and energy transfers within trophic networks (Gómez-Canchong, Blanco, & Quiñones, 2013; Petchey & Belgrano, 2010; Trebilco et al., 2013). Indeed, most ecological and physiological processes are size-dependent, and aquatic systems often exhibit size-structured trophic interactions (Brown et al., 2004; Dickie et al., 1987). Whereas it is clearly accepted that predation can explain differences in the size structure of prey populations among systems, fine-scale spatial heterogeneity in predator distribution could be critical in shaping the prey community structure even within a given system (Mehner et al., 2005; Pinel-Alloul, 1995). This phenomenon is probably more strongly linked to biotic than to abiotic processes, suggesting that it is essential to consider such a heterogeneity to understand the functioning of an ecosystem as a whole (Pinel-Alloul & Ghadouani, 2007; Potts et al., 2020). Furthermore, fine-scale heterogeneity in community size structure could possibly be of the same magnitude as broad-scale heterogeneity (Mehner et al., 2005).

During summer, deep and cold waters in stratified temperate zone lakes offer a thermal refuge to organisms that do not tolerate long exposure to warm temperatures (Littlefair et al., 2021). Shallow areas situated far from thermal refuges could thus become poorly accessible to cold-water stenothermic fish, resulting in a heterogeneous distribution of predation risk within lakes where warm-water fish are absent, with potential consequences for the trophic dynamics of the entire system. Such a spatial heterogeneity in the distribution of predation risk should be reduced at the end of the summer, when cooling surface waters allow cold-water stenothermic fish to access shallow areas that were too warm during summer (Guzzo et al., 2017). Such restored connectivity could enhance habitat coupling between littoral and pelagic areas (Schindler & Scheuerell, 2002; Vadeboncoeur et al., 2002) and dramatically change the distribution of predation risk within the lake, with potential consequences on the size-structure of the lower trophic levels.

A lot of research has shown that predation can strongly affect zooplankton community size structure, either through a reduction of body size in more abundant species or by shifting the dominance from larger to smaller taxa (Magnan, 1988; Quintana et al., 2015). However, while much research has focussed on how predation affects zooplankton community structure at the among-lake level (Lacasse & Magnan, 1992; Magnan, 1988; Rodríguez et al., 1993; Vanni, 1986), only a few studies have looked at within-lake differences in community structure (e.g., Lake Superior, 82,103 km²; Yurista et al., 2014).

The normalised size spectra (NSS) approach, proposed by Sprules and Munawar (1986), could help to address the comparison

of inter- and intra-system differences in community structure since it is not focussed on taxonomic differences that could exist at both levels. The conceptual framework behind NSS provides a tool to incorporate all community size-structure data (i.e., from different trophic levels) into a single metric to effectively analyse their patterns. More specifically, NSS is a representation of the biomass or biovolume of organisms found in log-spaced size classes forming a straight line (Sprules & Munawar, 1986). Since aquatic ecosystems organisms are smaller and more abundant at lower trophic levels, NSS can be used to explore community trophic structure and, potentially, its dynamics (Brown et al., 2004; Gómez-Canchong, Blanco, & Quiñones, 2013; Trebilco et al., 2013). On the one hand, NSS slopes can be interpreted simply as variations in the size structure of the community. On the other, NSS intercepts are linked to overall organism abundance and to system productivity, whether we consider one trophic level or the entire network (Sprules & Barth, 2016). A high NSS intercept is thus expected to be associated with a highly productive system with high biomass (Sprules & Barth, 2016; Yurista et al., 2014). NSS deviations from theoretical linearity (sometimes called “secondary structures”; e.g., Arranz et al., 2019) also could provide information on changes in productivity and trophic relationships (Sprules & Barth, 2016; Thiebaut & Dickie, 1992; Yurista et al., 2014). Predators tend to linearise NSS by controlling prey populations so that secondary structures in NSS could reflect predator avoidance or a trophic bottleneck (Arranz et al., 2019; Mehner et al., 2018).

In this study, we used the zooplankton community of a small temperate lake to analyse within-lake variation in prey size structure in relation to both among-basin differences in predation risk, as well as thermal regime and system productivity. In the absence of fish predation, thermal regime is expected to change the size of zooplankters by affecting growth rate and maturation, leading to an overall smaller average body size (Evans et al., 2020; Moore et al., 1996), with potential effects on NSS slope. Primary productivity could play a role in NSS intercept variations, with higher productivity leading to increased zooplankton biomass (McCauley & Kalf, 1981; Sprules & Barth, 2016; Yurista et al., 2014).

We used individual body size data to build NSS and taxonomic information to interpret any secondary structures in the data from zooplankton samples collected in the main (deep) and a shallow basin of the lake. The only fish species in the system is the brook charr (*Salvelinus fontinalis*), a cold stenothermic species. It has been shown that brook charr use two main sources of prey (i.e., zoobenthos and zooplankton) in these temperate lakes, and that it can have significant impacts on the abundance and size structure of zooplankton (Lacasse & Magnan, 1992; Magnan, 1988; Rodríguez et al., 1993). These conditions make this lake an ideal model to study the top-down effect on zooplankton within the same system. Furthermore,

previous radiotelemetry studies have suggested that the shallow basin is not accessible to brook charr during summer because of elevated temperatures (Bertolo et al., 2011; Goyer et al., 2014). More recent data from brook charr equipped with 3D acoustic tags confirmed that they spend more than 95% of their time in the deep basin of the study lake during the summer. Zooplankton are thus expected to be free of, or experience lower brook charr predation risk, in the shallow basin than in the deeper basin.

We tested whether (1) zooplankton community size structure differed spatially between the two lake basins and between the littoral and pelagic habitats of the deeper basin, where we expected less abundant and smaller zooplankters as a result of the presence of fish during summer (Bertolo et al., 2011; Burks et al., 2002; Goyer et al., 2014; Lacasse & Magnan, 1992; Magnan, 1988; Quintana et al., 2015; Rodríguez et al., 1993; Vanni, 1986). We also tested whether (2) zooplankton community size structure differed seasonally in relation to variation in fish access to shallow areas. In the latter, the zooplankton community should abruptly change in autumn, when fish can access shallow parts of the lake, reducing zooplankton abundance and their average body size. Finally, we tested whether (3) nonlinearities occurred in the NSS in relation to fish predation. We expected that organisms with predation defences (e.g., gelatinous *Holopedium* sp.; Detmer et al., 2017) should be more abundant in the deep basin where fish exert strong predation pressure and therefore create secondary structures in their size range.

This study aimed to address whether within-lake heterogeneity at fine spatial and temporal scales could be critical to the understanding of trophic relationships in heterogeneous ecosystems. Given that one of the main drivers in these systems is temperature, we anticipate that global warming will lead to dramatic changes in predator habitat use in temperate lakes, with potential consequences for the functioning of the whole ecosystem.

2 | METHODS

2.1 | Study site

We used Lake Ledoux (Mastigouche Wildlife Reserve, Quebec, Canada; 46.802381N, 73.277136W) as a model system. It is a small oligotrophic temperate lake with substantial background information on brook charr (e.g., Bertolo et al., 2011; Bourke et al., 1997; Goyer et al., 2014). The waters are relatively clear (Secchi depth of 7 m) and no hypoxia occurred during the study period. Lake Ledoux has a main deep basin (max. depth 18 m) and two shallower basins with mean depths of ~1.5 m and ~5 m at the west and east sides, respectively (Figure 1). The lake is typical of Canadian Shield lakes and is located in a protected area, where logging is limited and sport fishing is strictly controlled by the Quebec Government. During the whole study period, Lake Ledoux was closed to fishing.

The shallow basin is accessible to brook charr but is not widely used during summer because it is too warm (Bertolo et al., 2011; Goyer et al., 2014). The deep basin offers a thermal refuge in deep

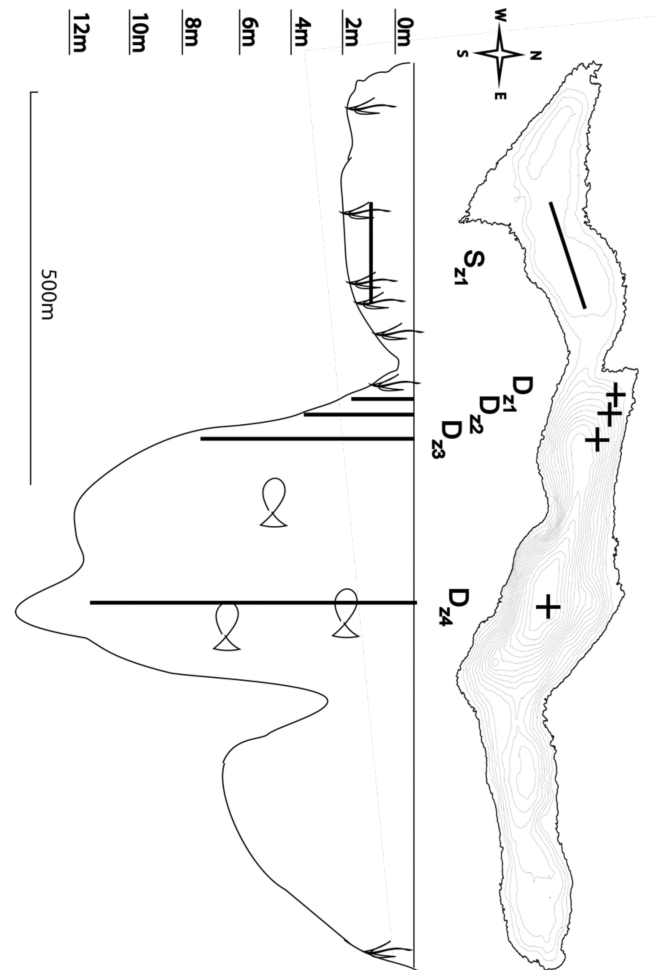


FIGURE 1 Schematic representation of Lake Ledoux (above: top view with 1 m isobaths; below: cross-section along its major axis). Vertical scale is exaggerated to better show depth differences. The four stations (D_{z1}, D_{z2}, D_{z3} and D_{z4}) where vertical sampling was done are represented by crosses (above) and vertical lines (below). Horizontal sampling in the shallow basin (S_{z1}) is represented by lines in both views.

cold waters, allowing fish to thermoregulate in the metalimnion (Bertolo et al., 2011; Goyer et al., 2014) and thus continue to feed on zooplankton during the whole year. The littoral area of the deep basin was included in the study to compare it to the shallow basin: this allowed us to compare two locations with similar depths but with sharp differences in connectivity with the thermal refuge in the central pelagic area. The eastern basin, which is intermediate in depth and thus with less contrasted thermal regimes, was not included owing to logistic constraints. We then focused our sampling effort on the most contrasted areas in terms of predation risk. Sampling occurred from 23 July to 8 October 2018. Submerged aquatic vegetation was relatively abundant in the shallow western basin (hereafter “shallow basin”) and only patchily distributed in the littoral areas of the deep basin. Brook charr individuals make excursions to the epilimnion but often stay in the 5–6 m depth layer, which corresponds to their preferred temperature in the metalimnion (Bertolo et al., 2011; Goyer et al., 2014). Brook charr avoid temperatures

above 22°C (Goyer et al., 2014), so individuals encounter strong thermal constraints to feeding in the shallow basin during the stratified period (May to September) (based on recent high-frequency hydroacoustic telemetry surveys, <3% of fish recorded position occurred in the shallow basin during August).

2.2 | Spatio-temporal distribution of zooplankton

We used weekly sampling with an *Underwater Vision Profiler* (UVP 5; Hydroptics, Villefranche sur mer, France) to obtain an appropriate spatio-temporal resolution of the zooplankton community. The UVP counts and measures particles with an equivalent spherical diameter (ESD) greater than 68 µm, but it also can take high-frequency pictures of larger particles (including living zooplankton) directly in the water (Picheral et al., 2010). Originally designed for sampling relatively large particles (>1 or 2 mm; e.g., zooplankton found in marine habitats), the UVP used here was calibrated by the manufacturer to optimise the capture of relatively small freshwater zooplankton (see below) by zooming the camera optics and reducing the focal length between the lens and the lit area (M. Picheral, LOV oceanographic observatory, Villefranche sur Mer, France, pers. comm.). The sampling volume of each image was 0.18L and the sampling frequency was 11 images/s (see Supplementary 1 in Appendix S1 for UVP processing configuration).

In order to minimise uncertainty related to image resolution, UVP pictures (hereafter called “vignettes”) were not identified at the lowest

taxonomic level possible but rather, grouped into the following coarse categories: copepods, Holopediidae (*Holopedium glacialis*), other cladocerans, Chaoboridae, rotifer colonies (*Conochilus* sp.), and several rarer categories that made up fewer than 0.8% of the particles (e.g., Volvocales, Arachnidae, Notonectidae; Figure 2). “Other cladocerans” included mainly Bosminidae and Daphniidae, the latter being largely dominant in large size classes. Non-living particles were classified into the “detritus” and “badfocus/artefact” categories. Submerged aquatic vegetation were placed into the “SAV” category whereas the “Others” category was created for living-particle vignettes that could not be identified (too small or blurry) (Figure 2). Details about the size distribution of the main zooplankton categories listed above are given in Figure S1.

2.3 | UVP sampling

Weekly UVP sampling took place from 23 July to 8 October. To account for potential diel variations in the vertical distribution of zooplankton and thus ensure that the whole zooplankton community was included in the NSS, UVP sampling was performed at noon and midnight (solar time). This reduced potential biases from zooplankton moving into the sediment during the day. Night sampling on 6 August and 1 October were not done because of weather constraints and thus were not considered in the analyses.

Vertical UVP profiles were performed at four different stations in the deep basin to assess both the vertical distribution of

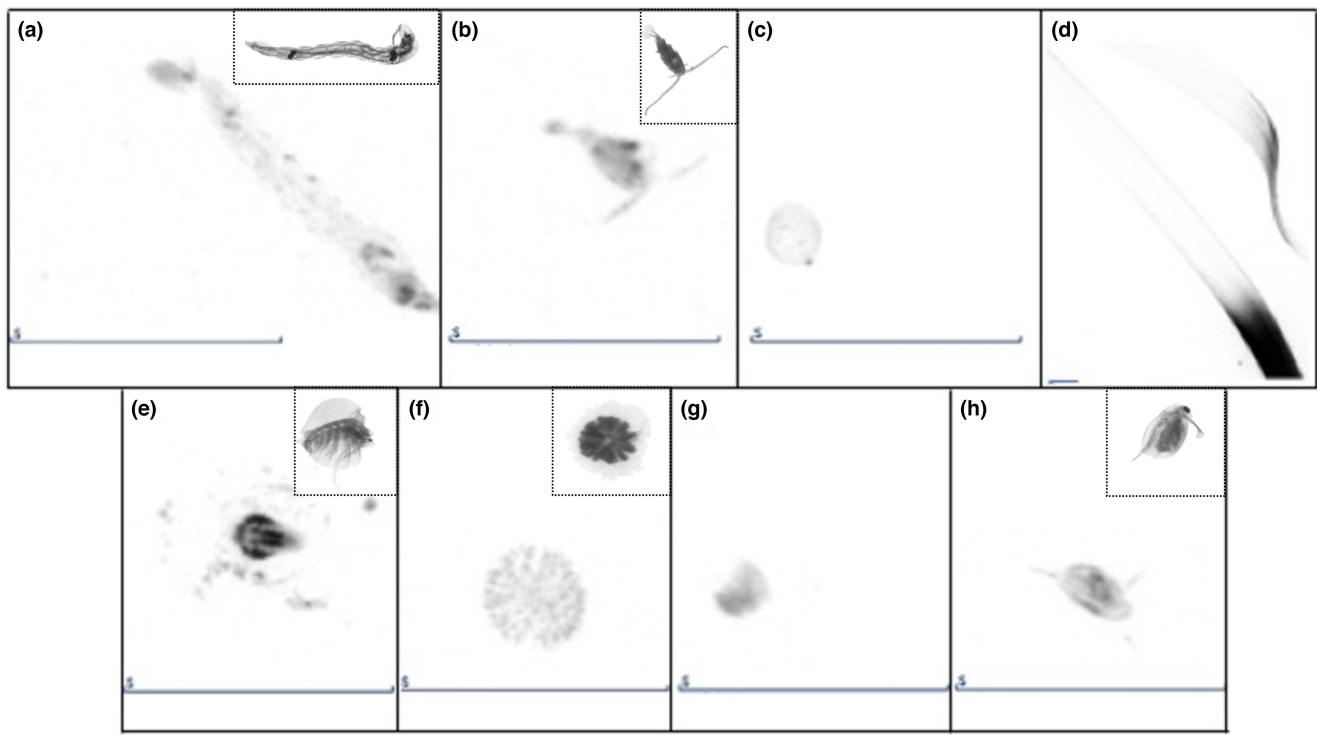


FIGURE 2 Examples of underwater vision profiler (UVP) pictures (vignettes) showing the main zooplankton categories found in Lake Ledoux during the sampling program: (a) Chaoboridae; (b) copepods; (c) Volvocales; (d) aquatic vegetation; (e) *Holopedium glacialis* (note the gelatinous capsule partially visible in the image); (f) colony of *Conochilus* sp.; (g) unidentified; and (h) daphnids. For some taxa, examples of zooscan vignettes in the top right corner. The scale bar is 5 mm.

the zooplankton community and the shore-to-centre gradient (D_{z1} – D_{z4} ; Figure 1). The uppermost 0.4 m of the water column was avoided owing to the height of the UVP, whereas the deepest 2 m was avoided to reduce the risk of interference by bottom substrate and/or sediment resuspension. Total zooplankton abundance did not show any day/night deficit (Doubek index [Doubek et al., 2020] was not different from 0 – Student test's p -value = 0.89), suggesting that this had no significant effect on our interpretation. Thus, the deep basin sampling extended from 0.4 m to 2 m (D_{z1}), 4 m (D_{z2}), 8 m (D_{z3}) and 11 m (D_{z4}). The vertical spatial resolution was given by the accuracy of the UVP depth sensor (0.1 m). Since zooplankton diel vertical migration generally occurs at dawn and dusk, the four stations were sampled within an hour to ensure that no zooplankton migration began during sampling (Lampert, 1989). Since the depth of the shallow basin did not allow vertical profiles with the UVP, we sampled a 150-m horizontal transect parallel to the shore at its centre (Figure 1). We cannot exclude the possibility that zooplankton could exhibit horizontal migration patterns within the shallow basin from the centre to the shore of the basin (Gonzalez Sagrario & Balseiro, 2010). It was not possible to test this hypothesis since the UVP could not be deployed too near to the shore because of a risk of collisions with the rocky bottom. However, noon and midnight sampling controlled for the nycthemeral variability in zooplankton distribution as a result of either horizontal and vertical diel migrations.

2.4 | Schindler–Patalas ground validation

On a few occasions (see zooplankton sampling section for details), UVP sampling was coupled with Schindler–Patalas sampling to get a qualitative validation of the UVP taxonomic information. The Schindler–Patalas box was used to sample a water volume of 30 L, filtered with 63- μ m sieve. Zooplankton was collected at both noon and midnight on three occasions during the season, on the day following UVP sampling (25 July, 15 August and 6 September). Sampling took place at the same first three stations of the vertical UVP sampling: at 1.5 m depth for D_{z1} and D_{z2} , and at 1.5, 3, 5 and 8 m depth for D_{z3} . There were no night samples on 6 September because of a storm event. Samples were stored in a glucose-formaldehyde solution (4%) before analysis (Prepas, 1978). Since our goal was to validate the UVP coarse classification rather than get a classification at the species level, zooplankters were identified with the Zooscan processing system (Gorsky et al., 2010), which allows a six-fold higher resolution of images and a much faster acquisition than microscopy. Zooscan uses platforms similar to our UVP (Zooproces and Ecotaxa; Picheral et al., 2017) and provides the same kind of measurements. All 64,359 Zooscan vignette predictions were checked manually. These data were compared to UVP taxonomy data to provide some clues about unidentified individuals in UVP vignettes that were sorted into the “Others” category. It was difficult to identify small zooplankters because UVP resolution was not sufficiently high to detect discriminating attributes such as appendages. This explains why half of the individuals smaller than 600 μ m and, to a lesser extent, individuals smaller than 900 μ m,

were classified into the “Others” category. However, the comparison with Zooscan data provided some insight on these undefined individuals, which are likely to be mostly copepods and to a lesser extent *Daphnia* spp. or Bosminidae (Figure S2). We noticed some bias from UVP classification (e.g., the “Others” category was better classified by Zooscan), but this bias was constant through time as was the methodology used. Thus, this did not influence the variation in zooplankton composition described in this study.

2.5 | Limnological variables

Vertical profiles of fluorescence and temperature (fluoroprobe; bbe Moldaenke) were recorded weekly at station D_{z4} during all sampling periods, and at station S_{z1} from 13 August to 08 October. The fluorescence profile reflected the vertical distribution of phytoplankton concentration. Fluorescence was converted into surface unit by multiplying the average value by the depth of the water column. The epilimnion temperature of the lake was considered to be homogeneous (both in the horizontal and vertical axes; Bertolo et al., 2011; Goyer et al., 2014) and was estimated by the temperature measured at 1 m depth at D_{z4} . Spatio-temporal variations of temperature and phytoplankton concentration were visualised graphically to interpret NSS differences. Spatial differences in fluorescence were assessed with Wilcoxon tests while temporal variations in fluorescence were tested for each station using generalised additive models (GAM).

2.6 | Size spectra metrics

Equivalent spherical diameter (ESD) was calculated from area measurements for each zooplankton picture and transformed into biovolume, assuming spherical volume (Supplementary 2 in Appendix S1). These biovolumes were integrated and normalised into log-spaced size classes to build the normalised biovolume size spectrum (NBSS) (Sprules & Barth, 2016; Sprules & Munawar, 1986; Supplementary 2 in Appendix S1). Size diversity indexes also were calculated for each sampling occasion based on Quintana et al. (2008) to get complementary information about zooplankton size structure.

2.7 | Data analyses

All analyses were performed with R software (R Core Team, 2021).

2.7.1 | Estimation of NBSS parameters

In order to analyse the relative contributions of location and seasonality on zooplankton size structure, NBSS values were calculated from zooplankton biovolumes sampled weekly at each station with the UVP. Noon and midnight samples also were distinguished to account

for sampling design. The NBSS is expected to follow a power law distribution whose slopes and intercepts can be estimated by linear regression on a log-log plot (Edwards et al., 2017; White et al., 2008). Since we sampled five stations for 11 weeks at two periods of the day (noon and midnight), we built a total of 110 NBSS for which we derived both the slope and the intercept. The intercept can be strongly correlated with the slope (Gómez-Canchong, Quiñones, & Brose, 2013). To avoid this correlation, and given the fact that the 0 value of the Log of the class volume is far to the right of the considered size spectrum (see Figure 3), the midpoint height was used instead of the intercept (Gómez-Canchong, Blanco, & Quiñones, 2013; Sprules & Barth, 2016). The ordinate of the point at the middle of the size spectrum (hereafter "height") was calculated from the corresponding linear regression equation. NBSS heights were strongly correlated with the total biovolume of zooplankton (Pearson $R^2=0.72$, $p<0.001$).

2.7.2 | Spatio-temporal variation in size structure parameters

The 110 estimates of NBSS parameters were used to build different linear models to analyse the effects of the station, week and period of the day to test the spatial and temporal hypotheses and verify that potential zooplankton vertical migration did not bias the results. The Akaike information criteria (AIC), the Δ_{AIC} ($AIC_{\text{model}} - AIC_{\text{min}}$), and degrees of freedom (as an index of the number of variables used in a model) were used to select the best and most parsimonious model

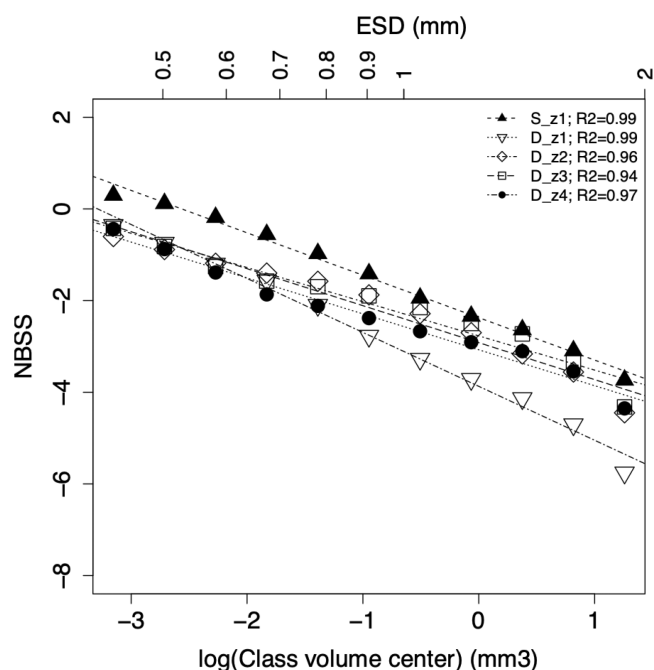


FIGURE 3 Normalised biovolume size spectra (NBSS) of the five sampled stations (S_{z1} in the shallow basin and D_{z1} – D_{z4} in the deep basin). As a reminder, NBSS is calculated with the sum of volumes of every organism within each size classes, divided by the extent of the size class.

(package *aod*; Lesnoff & Lancelot, 2012). Models were ranked using Δ_{AIC} —the difference in AIC between a candidate model and the model with the lowest (best) AIC (Burnham & Anderson, 2004). Once the best model was selected, Tukey's *post hoc* test was used to identify which groups were different in terms of slopes and heights. The same analytical workflow was used to assess the spatio-temporal variation of the size diversity index. Correlations between temperature and NBSS slopes or heights were tested using a Spearman rank correlation test to assess if there was a relationship between temperature and community structure. This could reflect an indirect effect of predation risk when fish are limited in their movements by temperature.

2.7.3 | Taxonomic composition and NBSS secondary structures

We analysed zooplankton community composition to examine whether variations in zooplankton size structure are linked to a shift in individual size distributions within a given taxon or to a change in community composition. Differences in zooplankton composition among weeks and stations also were investigated with NMDS (Bray–Curtis distances) and PERMANOVA analyses (package *vegan*; Oksanen et al., 2013), and explored graphically by visualising the biovolume of each category per week for each station. This information also was valuable to better understand the possible deviations from linearity in the NBSS. Nonlinearities of the NBSS line were determined visually on the log-log plot of each station. The linear model was compared to a second-order polynomial model to test for the presence of nonlinearity. Only NBSS size class ranges that clearly visually deviated from linearity were tested with this approach (Figure S3). When a polynomial model was retained based on its AIC, the NBSS was recalculated by removing zooplankton taxa one at a time to assess graphically whether linearity was restored (Figure S4). This allowed us to assess if the nonlinearity of the NBSS was caused by a particular taxon, thus pinpointing the position of this taxon that stood out in the trophic network.

3 | RESULTS

3.1 | Temperature and productivity variation

Temperatures profiles of both basins were similar for the first 2.5 m depth. Thermal stratification and the thermocline remained stable at station D_{z4} from the beginning of sampling period, 23 July, to 6 September, with a surface temperature above 20°C. The epilimnion temperature then gradually decreased, with the near disappearance of stratification in October (Figure 4).

Fluorescence differed between D_{z4} and S_{z1} ($p<0.001$), with the deep basin being more productive because of a deep chlorophyll maximum (Figure S5). However, S_{z1} had higher fluorescence values than D_{z4} when considering only the common 0–2 m layer of the two basins ($p<0.001$). We were able to graphically distinguish a decrease

in fluorescence in the final 2 weeks of sampling in the deep basin, but no temporal pattern was detected by the GAM for D_{z4} or S_{z1} ($p=0.12$ and 0.18 , respectively).

3.2 | NBSS standardisation

When all zooplankton data derived from the weekly UVP samplings were pooled into a single NBSS, a straight-line connected points from the fourth to the fourteenth class (0.4–2 mm), whereas the first three classes (0.25–0.4 mm) and the last two (2–2.7 mm) clearly deviated from the line (Figure S6). Comparing this NBSS with the Zooscan-derived size spectrum showed that these size classes were indeed underestimated relatively to the other classes, creating artefacts (Figure S6). Therefore, the three smallest size classes were removed from the analysis because they were probably underestimated as a consequence of the UVP's optical detection limit (Forest et al., 2012; Lombard et al., 2019). The two larger size classes also were removed because we considered these outliers to be artefacts (e.g., avoidance behaviour by large organisms).

3.3 | Model selection of explanatory variables

Based on AIC and the degrees of freedom, the best model to explain NBSS slope variations included both station and date, and both terms were significant ($p < 0.01$ and $p < 0.001$, respectively; Table 1). The best model to explain NBSS height variations included the effects of station and period of the day. While station had a significant effect ($p < 0.001$), period of the day did not ($p = 0.06$). Models with interaction terms between explanatory variables were not selected, meaning that differences among stations in NBSS height or slope were not influenced by time (Table 1).

3.4 | NBSS spatial variation

Based on *post hoc* tests, we graphically represented NBSS variations according to station and date variables to visualise them. The NBSS slope at station D_{z1} (NBSS slope median = -1.31) differed significantly from the other three stations in the deep basin (NBSS slope medians = -1.05 , -1.05 , and -1.00 at stations D_{z2} , D_{z3} and D_{z4} , respectively),

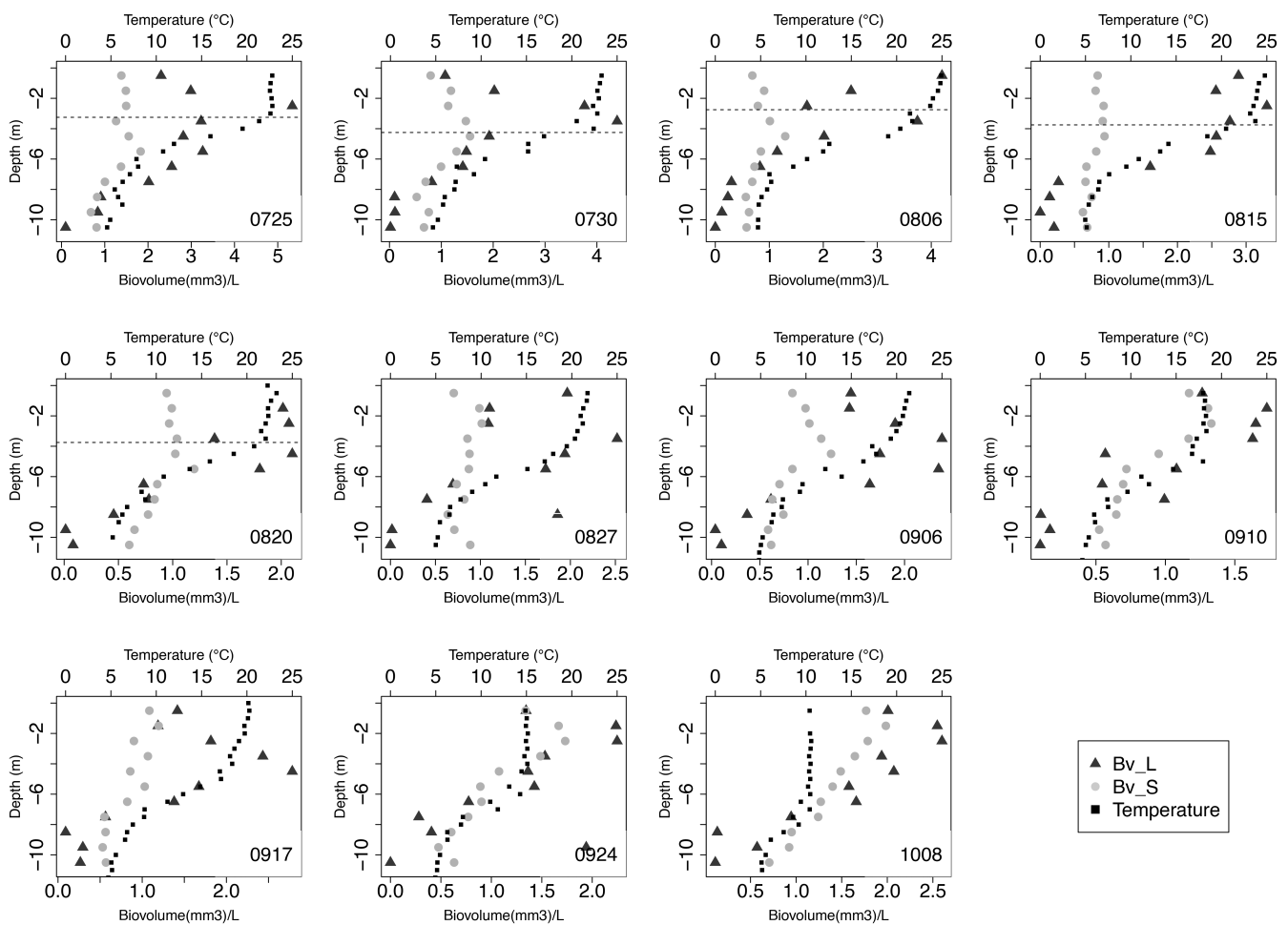


FIGURE 4 Vertical distribution of the biovolumes of large (ESD > 1 mm; light circles) and small (ESD < 1 mm; dark circles) zooplankton at the deepest station of Lake Ledoux (D_{z4}). Squares represent the temperature along the vertical profile and the horizontal dashed lines represent the depth where temperature drops below 22°C. Each panel represents 1 week. Date (MMDD) is mentioned at the bottom of each panel.

TABLE 1 Summary of model (glm) AIC values used to select the best models explaining NBSS (slope and height) and size diversity index variations in the dataset. The degrees of freedom (df) of the model gives the number of parameters in the model. Best models, combining a Δ AIC inferior to two and the lowest number of df, are highlighted with Δ AIC values in bold.

Model	df	Slope		Height		Size diversity index	
		AIC	Δ AIC	AIC	Δ AIC	AIC	Δ AIC
M0 = -1	2	42.5	53.3	219.3	40.0	22.7	54.1
M1 = -station	6	33.9	44.6	185.6	3.3	-18.8	12.6
M2 = -period	3	44.2	55.0	218.5	36.2	22.2	53.6
M3 = -week	3	6.5	17.2	219.3	37.0	17.6	49.0
M4 = -station + week	7	-10.7	0	184.6	2.2	-28.8	2.6
M5 = -week + period	4	7.6	18.3	218.3	35.9	16.5	47.9
M6 = -station + period	7	35.6	46.3	183.9	1.5	-20.3	11.1
M7 = -week + period + station	8	-9.8	1.0	182.4	0	-31.4	0
M8 = -week + station + station:week	11	-9.0	1.8	189.1	6.8	-28.5	2.9
M9 = -week + period + station + station:week + period: station	16	-8.4	2.4	194.0	11.7	-26.6	4.8

but not from the NBSS slope in the shallow basin (S_{z1} ; NBSS slope median = -1.18; Figures 3 and 5a). The slope at S_{z1} (shallow basin) also was significantly steeper than the three stations in the deep basin (D_{z2} , D_{z3} and D_{z4} ; Figures 3 and 5a), which were not significantly different. This result indicates that the shallow basin and to some extent the littoral zone of the deep basin (D_{z1}) exhibited significant higher proportions of small individuals than deep-basin stations D_{z2} , D_{z3} and D_{z4} .

While results for the NBSS slopes showed some similarities between the two shallow stations (S_{z1} and D_{z1} ; Figure 5a) and among the three deeper stations of the deep basin, the results of NBSS height showed a clear pattern separating the two basins (Figure 5b). *Post hoc* tests revealed that NBSS height was greater at station S_{z1} compared to all deep-basin stations (D_{z1-z4} ; Figure 5b), indicating that total zooplankton biovolume was significantly higher in the shallow basin (S_{z1}) compared to the four deep-basin samples (D_{z1-z4}). This difference was clear for the smaller half of the size classes but decreased for the larger half at stations D_{z2-z4} (Figure 3). Furthermore, NBSS height was lower at D_{z1} than at D_{z2} and D_{z3} but did not differ significantly from D_{z4} . Stations D_{z2-z4} did not differ significantly from each other. This means that there was a lower overall abundance of zooplankton (biovolume) with a higher proportion of small individuals in the littoral (D_{z1}) than in the pelagic (D_{z2-z4}) areas of the deep basin (Figures 3 and 5).

3.5 | NBSS temporal variation

NBSS slopes tended to flatten during the first 5 weeks (the median of NBSS slopes from 23 July to 20 August varied from -0.97 to -0.67, respectively) before dropping during the next 2 weeks and reaching a lower plateau during the last 4 weeks (late September and October; median of NBSS slopes between -1.22 and -1.28; Figure 6a). From this, we defined three groups: "summer" from 23 July to 20 August, "transition summer-autumn" from 27 August to 04 September,

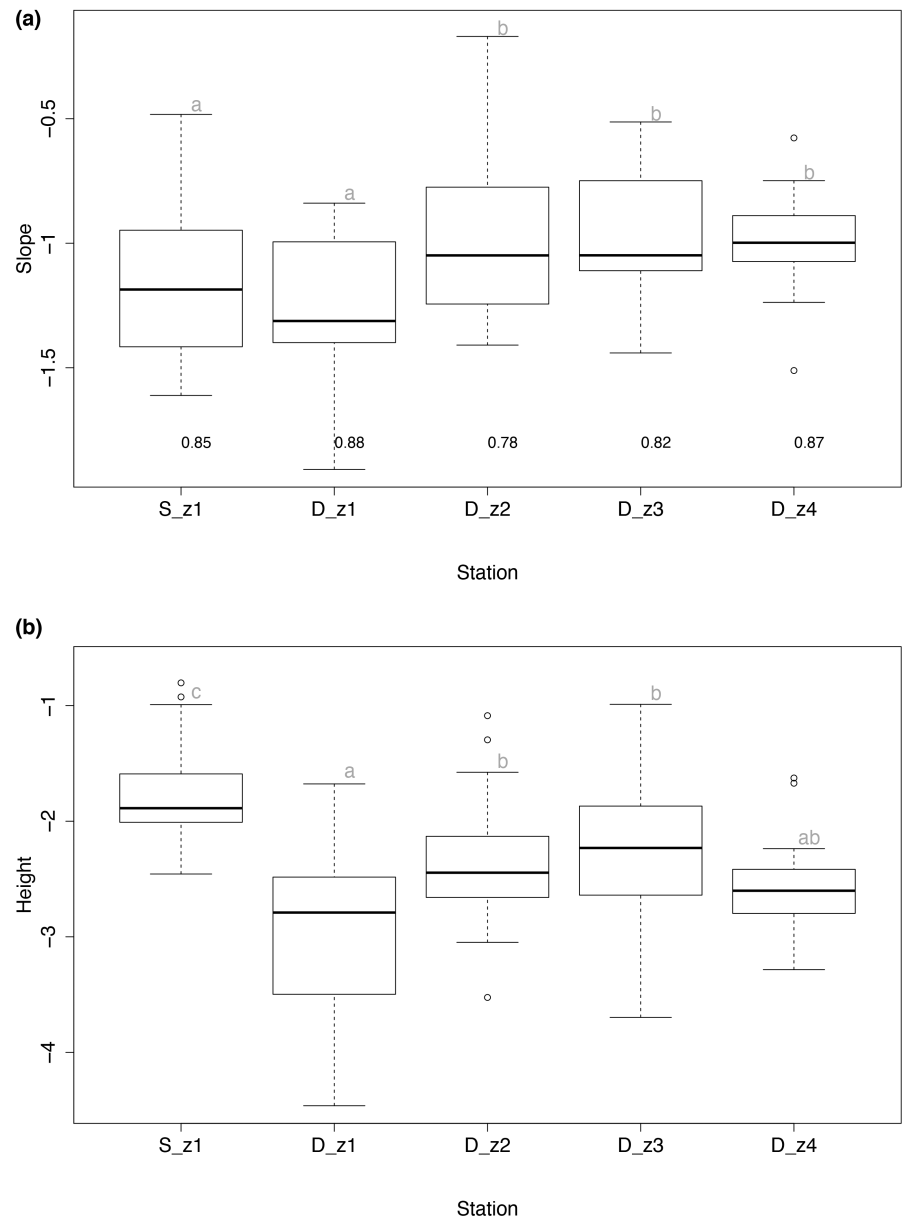
and "autumn" from 10 September to 08 October. Based on *post hoc* tests, NBSS slopes did not differ within the summer or the autumn periods; however, they were significantly different between summer and autumn except for 23 July, which did not differ significantly from three of the autumn weeks. The observed temporal patterns were apparently related to changes in temperature, since we found a positive relationship between the lake's epilimnion temperature and NBSS slopes ($p < 0.001$, $r = 0.63$). Temporal variations in NBSS slopes matched the weekly changes in epilimnion temperature (Figure 6a). NBSS slopes began to decline when the epilimnion temperature dropped below 22°C (i.e., in late August). Beyond this threshold, slopes remained stable even though the epilimnion temperature decreased further. These results indicate a shift from larger to smaller individuals through the sampling period (summer to autumn).

Since the variable "week" was retained in some plausible models to explain NBSS height, graphical representation revealed tendencies. As expected, NBSS heights did not show any temporal pattern, but tended to decrease until 9 September and then increased during the last 4 weeks of sampling (Figure 6b). However, *post hoc* tests did not show any significant differences between weeks, as expected with the previous model selection. Heights also were not correlated with temperature (p value = 0.36, $r = 0.09$).

3.6 | Size diversity index variations

Based on AIC and the degrees of freedom, the best model to explain the size diversity index variations included the effects of station, date and period of the day. All terms were significant; $p < 0.001$, $p < 0.001$ and $p < 0.05$, respectively; (Table 1). *Post hoc* tests showed that D_{z1} had the lowest size diversity while D_{z3} , D_{z4} and S_{z1} had the highest one (Figure S7). Furthermore, although *post hoc* tests did not show differences among the dates, there was a trend of a reducing size diversity from the beginning to the end of the study period

FIGURE 5 Boxplots showing the effect of station on the slope (a) and height (b) of the normalised biovolume size spectra (NBSS). Letters above boxplots represent groupings of Tukey's *post hoc* tests. In (a), black numbers below the boxplots are the averaged adjusted R^2 calculated for the slopes included in the corresponding station.



(Figure S7). Finally, the size diversity index was slightly lower during the day, compared to the night ($p=0.044$; Figure S7).

3.7 | Taxonomic composition and NBSS secondary structures

In addition to size structure differences, the composition of the zooplankton community clearly differed between the shallow and deep basins of the lake (Figure 7). NMDS and permanova analyses showed significant differences in community composition between S_{z1} and D_{z1} on one side, and D_{z2} , D_{z3} and D_{z4} on the other side (Figure S8). Firstly, the abundance of *H. glacialis* was more than six-fold higher in the deep basin (D_{z4}) than in the shallow one. Secondly, colonies of the rotifer *Conochilus* sp. were 2.1-fold more abundant at S_{z1} compared to D_{z4} . All stations of the deep basin had similar taxonomic

compositions, although D_{z1} and D_{z2} had fewer *H. glacialis*. D_{z1} also had low abundances of large-sized individuals, with individuals larger than 1 mm being completely absent in some samples. Finally, there were few Chaoboridae in the shallow basin whereas they were always abundant in the deep basin. One can clearly see the contrast in zooplankton community compositions before and after the late August threshold (July and September, respectively; Figure 7a,b), and the NMDS and PERMANOVA analysis brought statistical support for this observation, distinguishing different taxonomic composition among the two periods (Figure S8). While there were variations between these two sampling dates, *H. glacialis* remained more abundant in the deep basin whereas colonies of *Conochilus* sp. were more abundant in the shallow basin.

Populations of both copepods and "other cladocerans" had different size structures between the two basins, with the larger individuals of both groups being more abundant in the shallow basin

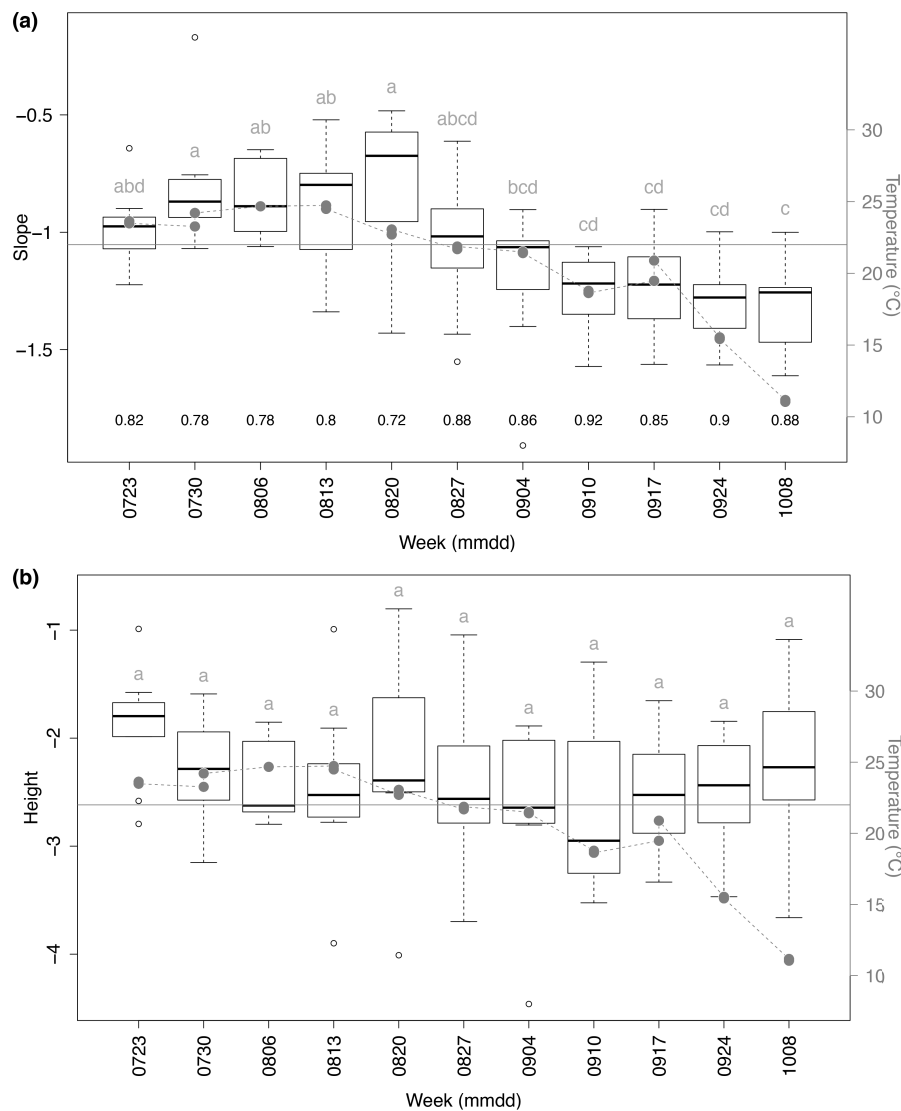


FIGURE 6 Boxplots showing the effect of time (weeks) on the slope (a) and height (b) of the normalised biovolume size spectra (NBSS). Temperature is represented for each week, with the horizontal line representing the 22°C upper limit threshold for brook charr. Letters above the boxplots represent groupings of Tukey's *post hoc* tests. In (a), black numbers below the boxplots are the averaged adjusted R^2 calculated for the slopes included in the corresponding week.

although we determined with NBSS slopes that the proportion of large versus small organisms is lower in the shallow basin, compared to the deep one. Later in the season, “other cladocerans” increased their proportions compared to *Conochilus* sp. colonies or *H. glacialis* (i.e., jelly taxa) in both the shallow and deep basins. Copepods showed no clear spatial or temporal patterns.

Visual inspection of the residuals of the different NBSS slopes showed a deviation from linearity for stations D_{22-24} (Figures 3 and S3). More specifically, we observed an overabundance of individuals with equivalent spherical diameters from 0.84 to 2.02 mm. Taxonomic data showed that the dome-shaped NBSS in the lake's deep basin was directly associated with the contribution of *H. glacialis*. If *H. glacialis* had been absent in the lake, the NBSS would have been linear (Figure S4).

4 | DISCUSSION

Our study revealed that the size structure of the zooplankton community can vary sharply even within a relatively small lake, with clear

differences observed not only between basins but also within small ranges (40m between D_{21} and D_{22}) of a given basin. Our results also suggest that the presence of a thermal barrier limiting movements of a top predator can shape key components of the trophic network, even though the effects of predation on zooplankton are not as straightforward as expected. The NBSS approach showed that the range of spatio-temporal variation in the size structure of the zooplankton community is similar to ranges observed among different systems (Dai et al., 2017). This approach also revealed the key role of seasonal temperature changes in shaping the trophic network by modulating the degree of functional coupling between habitats by the top predator. Moreover, linking NBSS with taxonomic data allowed us to demonstrate that the strong spatial pattern observed in zooplankton body size was associated with a clear pattern in community composition.

4.1 | Spatial pattern

Ecological theory predicts a slope of -1 for the NBSS of aquatic multi-trophic communities (Brown et al., 2004; Mehner

et al., 2018). Lake Ledoux, with an average NBSS slope of -0.81 , is within the range observed for freshwater ecosystems (-0.8 to -1.2 ; Dai et al., 2017; Mehner et al., 2018; Sprules & Barth, 2016; Yurista et al., 2014). However, on the one hand, the value observed in Lake Ledoux for zooplankton is closer to -0.75 , which is expected for communities composed of a single trophic level (Brown et al., 2004; Trebilco et al., 2013), suggesting that this trophic network is mainly composed of herbivorous organisms exposed to little predation and thus potentially forming secondary NBSS structures (Mehner et al., 2018). On the other hand, the within-lake differences in NBSS or size diversity index observed in this study were relatively large, showing that variations in zooplankton community structure can differ sharply at a very small spatial scale (c. 40 m between D_{z1} and D_{z2} , with median NBSS slopes of -1.31 and -1.05 , respectively), which is likely to be the result of differences at higher trophic levels.

The overall zooplankton biovolume concentration was higher in the shallow basin, and the higher absolute biovolume of small individuals increased the NBSS slope, suggesting higher community productivity (Sprules & Barth, 2016; Trebilco et al., 2013; Yurista et al., 2014). Shallow habitats are warmer and less light limited, leading to potentially stronger primary production per unit volume (Petersen et al., 1997). However, taking into account the deep chlorophyll maximum in the deep basin showed that it was more productive than the shallow one, suggesting that the absence of fish predation played a role in the higher height of NBSS in the shallow basin. In addition, the unexpectedly low proportion of large individuals and the large proportion of colonial rotifers in the zooplankton community of the shallow basin may suggest that invertebrate littoral predators (e.g., notonectid and odonates) were abundant, and potentially consumed large numbers of large-sized zooplankton. The steeper slope in the shallow basin compared to the deep one could reflect a more complex trophic network than expected (Brown et al., 2004; Mehner et al., 2016, 2018). This result is somewhat puzzling since a visual predator such as brook charr would have been expected to select large individuals in the zooplankton community in the deep basin, so the opposite pattern should have been observed (Blumenshine et al., 2000). One possible explanation could be that zooplankton face more predation risk by gape-limited *Chaoborus* sp., concentrated in the deep basin (Kurek et al., 2010) and relatively abundant in Lake Ledoux compared to other lakes in the same region (Drouin et al., 2009; Gignac-Brassard et al., 2022). Thus, the largest zooplankton could be in a size refuge (Braun et al., 2021; this has been shown by Arranz et al., 2019; Mehner et al., 2016 for prey fish). Thus, *Chaoborus* sp. most likely played an important role in the dynamics of small size classes of zooplankton (Lagergren et al., 2008), as confirmed by the significant negative correlation between *Chaoborus* sp. abundance and the abundance of both small and middle size classes ($ESD < 1$ mm; Spearman rank correlation test with $\rho = -0.38$; $p < 0.01$), but not of large zooplankters.

The flatter NBSS slope in the deep basin also might be a result of differences in zooplankton species composition (i.e., higher

abundances of *H. glacialis* in the deep basin). Even though Holopediidae have been shown to avoid the littoral zone when fish are present (Lauridsen et al., 2001), it is not clear why they did not proliferate in the shallow basin where another jelly organism, *Conochilus* sp., dominated. Their large abundance in the deep basin formed a bump in the NBSS that can be interpreted as a trophic bottleneck in the presence of gape-limited predators (here *Chaoborus* sp.). Brook charr also could feed on medium-sized zooplankton like *Daphnia* spp. and copepods rather than larger zooplankton, but their impact should be much lower (e.g., Magnan, 1988). This could explain the relatively smaller size of other cladocerans in the deep basin compared to the shallow one. The flatter NBSS slope in the deep basin also could reflect the observed high concentrations of large zooplankton in the epilimnion during summer, where warm temperature reduced fish predation risk.

4.2 | Temporal pattern

No temporal pattern was related to NBSS height (i.e., zooplankton overall biovolume) across stations, which is in accordance with the relative stability of phytoplankton concentration that we found during the sampling period. However, the size diversity index changed over time, with a less diverse community in autumn compared to summer. The analysis of NBSS slopes corroborated this pattern since their dramatic drop started in late August, a period corresponding to a decrease in epilimnion temperature below 22°C , suggesting an abrupt change in zooplankton size structure over time. Zooplankton size structure did not change further (i.e., NBSS slopes did not steepen further) after the temperature drop even though surface temperature continued to decrease from 22°C to 11°C . This suggests a threshold effect linked to the drop in the thermal barrier for fish (Goyer et al., 2014). Therefore, this result clearly does not support a physiological effect on zooplankton growth driven by temperature. Indeed, considering only the temperature, zooplankton average body size should be smaller in warm temperature (Evans et al., 2020; Moore et al., 1996) with a steeper NBSS slope in summer. Instead, the decrease of the proportion of large zooplankters in autumn (e.g., steeper NBSS slopes and lower size diversity index) suggests an increased effect of fish predation on the structure of the community, even in the deep basin. This could be the result of the exploitation of large-sized zooplankters present in epilimnion, inaccessible to the fish during summer. Complementarily, the increase of proportions of zooplankton biovolume in small size classes (i.e., same NBSS height but steeper slope) indicated a release in the predation pressure within these size classes. Thus, fish might feed on invertebrates when they are able to go into the littoral areas (Guzzo et al., 2017), thus releasing predation pressure by invertebrates on zooplankton.

A similar effect of the thermal barrier on the strength of the littoral–pelagic coupling was observed on lake trout (*Salvelinus namaycush*) by Guzzo et al. (2017). The earlier the onset of summer temperatures, the earlier the fish-related coupling between pelagic

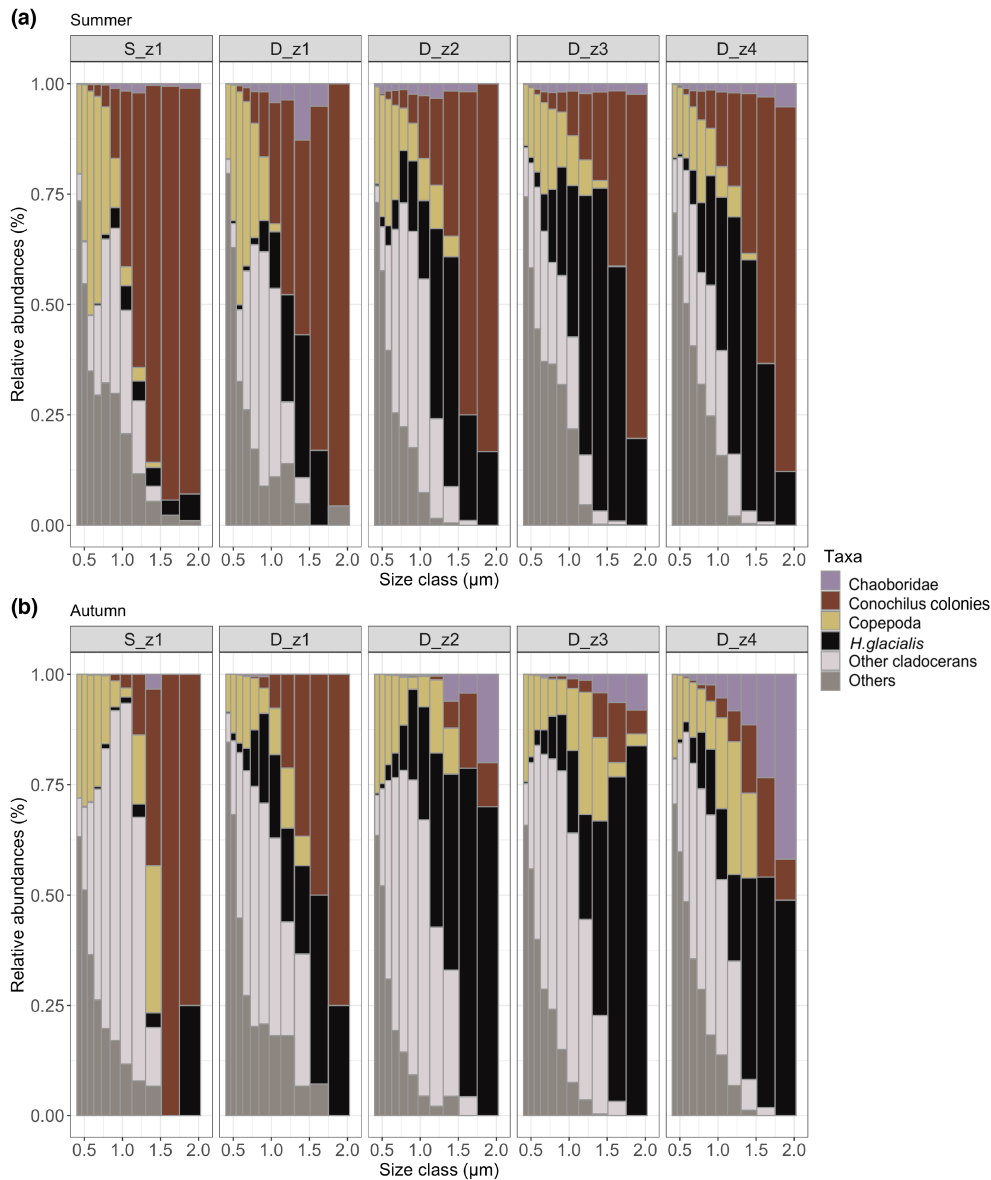


FIGURE 7 Histograms of relative zooplankton composition in two contrasting seasons: (a) summer and (b) autumn. From left to the right: shallow basin S_{z1} ; deep basins D_{z1} , D_{z2} , D_{z3} , D_{z4} .

and littoral habitats was interrupted, with potential cascading effects on both trophic networks (Schindler & Scheuerell, 2002) and fish condition (Guzzo et al., 2017). The average swimming speed of brook charr increased from summer to autumn, corroborating this interpretation (Figure S9), as did previous studies showing that juvenile brook charr decreased their feeding activity above 22°C in this system (e.g., Marchand et al., 2002). This suggests that brook charr has a lower influence on the prey community when surface temperatures exceed the 22°C threshold.

Among our different metrics, the size diversity index was the only one to show a slight difference between day and night, which may indicate less complete sampling of the community during the day. Although the integration of the water column allowed us to take into account the variations of the whole community, we recommend sampling at least at night to solve similar questioning.

4.3 | Seasonal variation of zooplankton species composition

While the NBSS and the size diversity index showed differences between basins in terms of size/trophic structure, the taxonomic data helped to determine the specificity of each trophic network and to interpret their secondary structures. Some taxa were clearly under-represented in the isolated shallow basin (e.g., *H. glacialis* and *Chaoborus* sp.), whereas others (e.g., *Conochilus* sp. and daphnids) were relatively more abundant than in the deep basin. When the thermal barrier of the top predator was lifted, zooplankton size structure and composition rapidly changed in both basins. Whereas brook charr is known to feed on *H. glacialis*, they also can efficiently suppress competitors of *H. glacialis* by eating large *Daphnia* spp. and copepods as well as the invertebrate predator

of *H. glacialis*—*Chaoborus* sp. during autumn, thus indirectly favouring the *H. glacialis* population (Detmer et al., 2017). Therefore, the zooplankton community shift is not only shaped directly by fish predation, but also by its indirect effects on invertebrate predators and competition dynamics, together with changes in environmental factors such as light period and temperature (Bürgi et al., 1985).

4.4 | Concluding remarks

Our results clearly show that fine-scale variations in zooplankton distribution can be of the same magnitude as reported inter-lake variations (Brucet et al., 2010; Dai et al., 2017). Coarse taxonomical data allowed us to better investigate the mechanisms behind these variations but it also demonstrates that it is necessary to develop more accurate *in situ* methods to combine fine-scale studies with fine taxonomy resolution. We also showed how habitat coupling can dramatically increase when thermal barriers for top predators become permeable. Global warming has an increasingly strong impact on lake temperature (Dokulil et al., 2021; O'Reilly et al., 2015) and should increase the spatial and seasonal differences of thermal regimes in the future, with potential consequences on the trophic coupling between the littoral and pelagic habitats. In this context, such habitat decoupling could last longer in the summer (Dokulil et al., 2021) and even occur in previously coupled ecosystems. Consequently, global warming could disrupt trophic dynamics and, in turn, the functioning of the whole ecosystem (Dokulil et al., 2021; Sharma et al., 2007).

AUTHOR CONTRIBUTIONS

Conceptualisation, developing methods, conducting research: RL, MP, PM, AB. Data analysis, preparation of figures and tables: RL. Data interpretation, writing: RL, MP, PM, AB.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

A common repository dedicated to RIVE studies is being built to gather database, metadata and R scripts from the research group. In the meantime, all data used to produce this article are available from the authors upon reasonable request.

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