

Contemporary community composition, spatial distribution patterns, and biodiversity characteristics of zooplankton in large alpine Lake Sevan, Armenia

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ABSTRACT

We studied the quantitative composition, spatial distribution, and temporal dynamics of the zooplankton community of the alpine Lake Sevan, Armenia, the largest surface water in the Caucasus region. This article is providing a long-term information and fills the research gap of multiyear data on zooplankton, as the previous research on zooplankton provided only snapshots of the community, and a consistent assessment over multiple years was missing. However, an initial mini-review of historical studies indicated that zooplankton biomass and fish abundance were undergoing large fluctuations, indicating the importance of top-down control. We analysed 239 samples from the period 2016-2019 from 32 sampling sites in Lake Sevan and recorded 37 species of meso- and macrozooplankton (Rotifers, Copepods, Cladocera). Biomass fluctuations were high with peaking biomasses in 2016 and lowest biomasses in 2018, yearly averaged biomass varied about one order of magnitude. Variability over time was hence much higher than spatial variability. The pelagic habitat at the deepest part of the lake showed the highest diversity and biomasses but contrasts between sampling sites remained smaller than changes from year to year or seasonally. Many samples were dominated by a single species, and these key species explain observed biomass dynamics to a wide

extent. We applied hierarchical clustering in order to identify phenological groups that appear to show similar patterns of occurrence. This clustering resulted in 6 groups whereof 5 groups just consisting of one single species and these 5 key species were the Cladocerans *Daphnia magna*, *Daphnia hyalina*, *Diaphanosoma* sp. as well as the calanoids *Arctodiaptomus bacillifer* and *Acanthodiaptomus denticornis*. The most important species in Lake Sevan's zooplankton during the observation period was *D. magna*, which reached high biomasses in 2016 and 2017 but then suddenly almost disappeared in 2018 and 2019. When there were more *D. magna* present, the water became clearer, which was measured using Secchi depth. This shows that these large water fleas effectively controlled the amount of phytoplankton in the water. *Daphnia magna*, in turn, managed to dominate zooplankton community only during times of extremely low fish biomass indicating strong top-down control of this large Cladoceran by fish. Both observations together imply a strong trophic linkage between fish, zooplankton, and phytoplankton and provide evidence for trophic cascades in Lake Sevan. Besides the novel insights into zooplankton community dynamics of this unique lake of high socio-economical, cultural, and ecological importance, our study also points to potential management opportunities for eutrophication control by biomanipulation, as well as our investigation allows us to conclude that probably biotic factors were more important than abiotic factors in explaining the observed changes and dynamics within the plankton community.

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INTRODUCTION

Zooplankton plays an important role in the functioning of lentic freshwater and marine ecosystems (Sommer and Stibor, 2002). Filter-feeding zooplankters like Cladocerans, Calanoid copepods, and most rotifers, as well as raptorial cyclopoid copepods and specialized predatory species, are the main consumers of phytoplankton and,

therefore at a critical position in the food web. The zooplankton community composition is a major structuring force on phytoplankton communities (Sommer *et al.*, 2001), the major trophic channel between phytoplankton and fish (Sommer *et al.*, 2002), and zooplankton biomass dynamics are key players in trophic cascades (Carpenter *et al.*, 2001). This makes zooplankton also relevant for water quality management, *e.g.*, in lake-wide biomanipulation applications (Shapiro and Wright, 1974; Scharf 2008; Ha *et al.*, 2013). Moreover, numerous studies have proved that zooplankton taxa are sensitive and sometimes rapidly respond to environmental stressors, such as hydrological changes, climate changes, and anthropogenic water pollution (Duggan *et al.*, 2001; Wang *et al.*, 2010; Yang *et al.*, 2017; Berta *et al.*, 2019; Krylov *et al.*, 2019). The functional characteristics or taxonomic composition of zooplankton can therefore be used as a bioindicator as documented by a study on zooplankton communities along a gradient of urbanization (Shen *et al.*, 2021). Accordingly, changes in zooplankton communities can be seen as a warning sign of ecological distortion and can be critical to the whole lake ecosystem functioning given their central food web position (Xiong *et al.*, 2020). In summary, proper monitoring of zooplankton communities is key for understanding pelagic ecosystem dynamics and, hence a widely accepted and indispensable aspect in ecological conservation and management of lentic aquatic ecosystems. At the same time, zooplankton communities are complex and not easy to assess as they comprise different taxonomic groups (Rotifers, Copepods, Cladocerans) that display a wide range of physiological, ecological, and functional properties (Krzton and Kosiba, 2020). The interpretation of freshwater lake's community dynamics, particularly with respect to the major biotic and abiotic drivers or potential bioindication applications, is difficult and may even be lake-specific to some extent. It is, therefore, important to characterize the basal, lake-specific zooplankton community before their corresponding dynamics can be interpreted meaningfully. For many prominent water bodies such a basal characterization is missing, which is also the case for the large, alpine Lake Sevan in Armenia.

Lake Sevan is the biggest freshwater water body of Caucasus Region and one of the greatest freshwater high mountain lakes of Eurasia. It is a deep alpine lake in Gegharkunik Province in the eastern part of Armenia with a high level of endemism. Several aspects make the lake outstanding and special. First, the lake is located at high-altitude (1900 m asl) in a semi-arid climate, with cold winters and hot summers (Babayan *et al.*, 2006). And the biogeographical location of Lake Sevan (*i.e.*, Caucasus region, the contact zone between major European, Asian, and Mediterranean regions) within a biodiversity hot spot. Second, its large size (approximately 1250 km²) and specific morphometry with a separation into two subbasins: Small and Big Sevan, which are separated by a sill at the interconnection of both subbasins (Tab. 1; Fig. 1). While most of the tributaries enter the basin of Big Sevan, the outlet is in Small Sevan so that there is, on average, a continuous water transfer from Big towards Small Sevan. Accordingly, direct external loading is more strongly affecting Big Sevan than Small

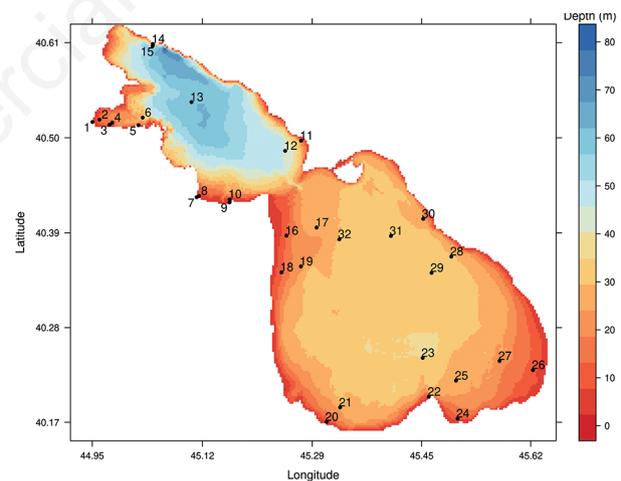


Fig. 1. Map of Lake Sevan including sampling points and depth information in meters as colour scale. Coordinates are given in degree north (latitude) and degree east (longitude).

Tab. 1. Morphometric characteristics of Lake Sevan (for water level on December 31, 2017 at the middle of the sampling period; data provided by the Hydrometeorology and Monitoring Center SNCO of the Ministry of Environment of the Republic of Armenia).

	Small Sevan	Big Sevan	Total
Water level	1900.46 m asl	1900.46 m asl	1900.46 m asl
Water volume	14.075 km ³	24.051 km ³	38.126 km ³
Surface area	338.42 km ²	939.71 km ²	1278.13 km ²
Max depth	81 m	32 m	81 m
Mean depth	41.6 m	25.6 m	29.8
Residence time*			180 years

*Calculated based on outflow from Lake Sevan.

Sevan so that the trophic state in Big Sevan is notably higher than in Small Sevan (Hovhannisyan, 1994).

The basic limnological features of the lake are summarized in Tab. 1 and further documented in the literature (Babayan *et al.*, 2006; Hovhannisyan, 1994; Krylov *et al.*, 2013; Shikhani *et al.*, 2021). On top of these eco-geographical settings, the lake has high economic importance as it provides energy, irrigation water and food to humans as well as a high cultural value for the Armenian nation. However, Lake Sevan also suffered from wide-reaching anthropogenic disturbance (Gabrielyan *et al.*, 2022) by eutrophication, water loss, and invasive species. The most important stressors for the lake are fluctuation of the lake water level, overfishing, species extinction and increase of nutrient loading (Gabrielyan *et al.*, 2022). Specifically, Lake Sevan experienced considerable changes since the 1980s and before. Water level dropped by almost 20 meters for hydropower and irrigation purposes and the lowest water level of the last two centuries was reached in 2001 (Danielyan *et al.*, 2011). Then, a water level re-rise of ca. 3.5 m was implemented from 2002 to 2010. Also, the fish community experienced changes due to ongoing overfishing and attempts to avoid the full extinction of Sevan trout (*Salmo ischchan*). Nutrient loading increased because formerly existing wastewater treatment facilities in the catchment went widely out of operation due to missing maintenance. Finally, climate change went on with consequences on temperature (increase of average temperature) conditions and local hydrology (decrease of annual precipitation) (Gabrielyan *et al.*, 2022; Ministry of Environment of the Republic of Armenia, 2020). Nevertheless, the scientific assessment within the plankton community of this lacustrine ecosystem is still limited particularly with respect to its quantitative ecology and dynamics.

Recent studies on Lake Sevan have focused on the physical conditions (Shikhani *et al.*, 2021), phytoplankton dynamics and algal blooms (Gevorgyan *et al.*, 2020).

The zooplankton compartment is well characterised with respect to species composition (Krylov *et al.*, 2010; 2016a, 2016b) but a wider assessment of community changes over seasonal and multiannual time scales including the statistical analysis of emerging patterns is missing. The existing, limited observations of the zooplankton community showed huge changes over time culminating in a remarkable and unexpected dominance of the large Cladocera *Daphnia magna* in the lake during the middle of the last decade. Having a size of up to 3-5 mm, *Daphnia magna* is a large-bodied species that usually dominates only in fish-free habitats where planktivory is low, which was conceptualised in the size-efficiency hypothesis (Brooks and Dodson, 1965; Hall *et al.*, 1976; Hülsmann *et al.*, 2005), stating that large-bodied species are the superior competitors for food

in comparison to other filter feeders (Kreutzer and Lampert 1999) but are extremely sensitive to fish predation. The specific role of *Daphnia magna* is therefore of special interest for Lake Sevan, not only concerning the competition with other zooplankters but also to water transparency (as a proxy for phytoplankton abundance) as *Daphnia magna* usually induces long-lasting clear water phases due to their high grazing pressure on phytoplankton. This paper seeks to fill this gap based on a 4-year sampling program that also included spatial differences, seasonal effects, as well as patterns in species occurrences within the community and potential functional implications.

The research focus of this publication is on the characterization of the zooplankton of Lake Sevan. For this target, we designed a sampling program, which included far more than 200 samples that were analysed for community composition, species abundance and biomass. We grouped taxa with similar patterns of occurrences by cluster analysis and evaluated the dynamics of these zooplankton groups. To our knowledge, our sampling program and its evaluation was the first time since the 1980s that data from spring, summer and autumn were collected in multiple years and comprehensively evaluated. We focused our sampling on the years 2016-2019 because the lake experienced major changes in the proceeding years, namely the lake level stabilised at a 3 m higher level and the population of fish increased substantially (see Gabrielyan *et al.*, 2022). We therefore hypothesized that changes in the zooplankton community can be expected. While designing our sampling program, we also reviewed existing knowledge on zooplankton from past literature in order to summarise available data sets and to put our results into the long-term context of the development of Lake Sevan.

Mini review: previous research on zooplankton

The studies on zooplankton of Lake Sevan were started in the end of 30s of the last century (Meshkova, 1968, 1975; Simonyan, 1991) and meanwhile stopped in the early 1990s, when the economic problems of Armenia did not allow for continuation of the research on Lake Sevan. The next stage of the investigations on the zooplankton community of the lake was in 2005, when the Russian-Armenian Biological Expedition for Hydrological Survey of Lake Sevan began and produced valuable results (Krylov *et al.*, 2010, 2013, 2015, 2016a, 2016b, 2018, 2019, 2021a, 2021b). However, even this Russian-Armenian research program had only limited intensity. Samplings were done with a quite high spatial resolution but irregularly and at low frequency.

Fig. 2 summarises the biomass of the zooplankton as published for the pelagic zone in Krylov *et al.* (2010, 2013, 2015, 2016a, 2016b, 2018, 2019, 2021a, 2021b). The

pelagic zone was selected since considerably more results on the pelagic zone have been published than on the littoral. Furthermore, Krylov *et al.* (2010) demonstrated that the biomass of zooplankton was higher in the pelagic zone compared to the littoral in recent years while it was opposite in the 1970s and 1980s. The comparison between zooplankton biomass of the periods 1937-72 (July)/1957-69 (October), 1975-80, 1981-85, and 2005-09 (Krylov *et al.*, 2010) with the more recent results shown in Fig. 2 suggests that considerably higher biomass values were reached in the last decade. For the periods before 2010, less than 10 g m^{-3} (fresh weight) were reported while single samplings resulted in zooplankton biomass well above 10 g m^{-3} after 2010. However, since the data presented by Krylov *et al.* (2010) on older periods are average values, it remains open, if such high zooplankton biomasses ($>10 \text{ g m}^{-3}$) occurred also before 2010. Maximal reported biomasses of more than 15 g m^{-3} are exceptionally high for an alpine lake and coincide with a period of rather low or slowly recovering, respectively, fish biomasses (Fig. 2).

Since 2005, Copepods and Cladocerans dominated in zooplankton based on biomass. Rotifers reached only a very small biomass (too small to be visible in Fig. 2). A particular feature of the period 2011-2017 was the occurrence of *Daphnia magna* in considerable to high abundances. Although not detected in water samples, it was present in Lake Sevan already in the first half of the 20th century as confirmed by the found specimen in the stomach of whitefish (Krylov *et al.*, 2013) pointing to high preference of the large-bodied *Daphnia magna* as prey for zooplankton-feeding fish. The occurrence or even dominance of *Daphnia magna* as observed from 2011-2017 was attributed to the very low abundance of fish in those years (compare Fig. 2). *Daphnia hyalina*, *Daphnia*

longispina and *Diaphanosoma brachyurum/lacustris* were further Cladocerans that occurred in parallel to *Daphnia magna*. Also, these species, particularly the *Daphnia* species, are rather large or intermediate in body size supporting the hypothesis that planktivory was very low at these times due to low fish biomass. It is also worth to be mentioned that *Diaphanosoma brachyurum/lacustris* was recorded in the lake from 2005 onwards (Krylov *et al.*, 2010). According to Krylov *et al.* (2021a, 2021b) the changes in fish density were affecting the composition of the zooplankton in general and go beyond the arrival of large-bodied *Daphnia*. Furthermore, the presence of *Daphnia magna* was accompanied by increased Secchi depth and changes in the abundance and composition of bacterioplankton, heterotrophic nanoflagellates, and phytoplankton (Krylov *et al.*, 2018, 2019, 2021a, b) indicating cascading effects along the food chain. Unfortunately, the literature does not provide complete data sets for all above mentioned zooplankton species for all years. Therefore and because of the low frequency of sampling, a comprehensive evaluation of the ecological interactions is impossible based on the available literature. Our study is adding data from a more coherent sampling strategy and therefore provides new insights into the dynamics within the zooplankton guild.

METHODS

Study area and field sampling

Given the large size of the lake and its separation into subbasins, the planktonic community was expected to display some degree of spatial heterogeneity and we therefore had a spatially resolving sampling design. We had 32

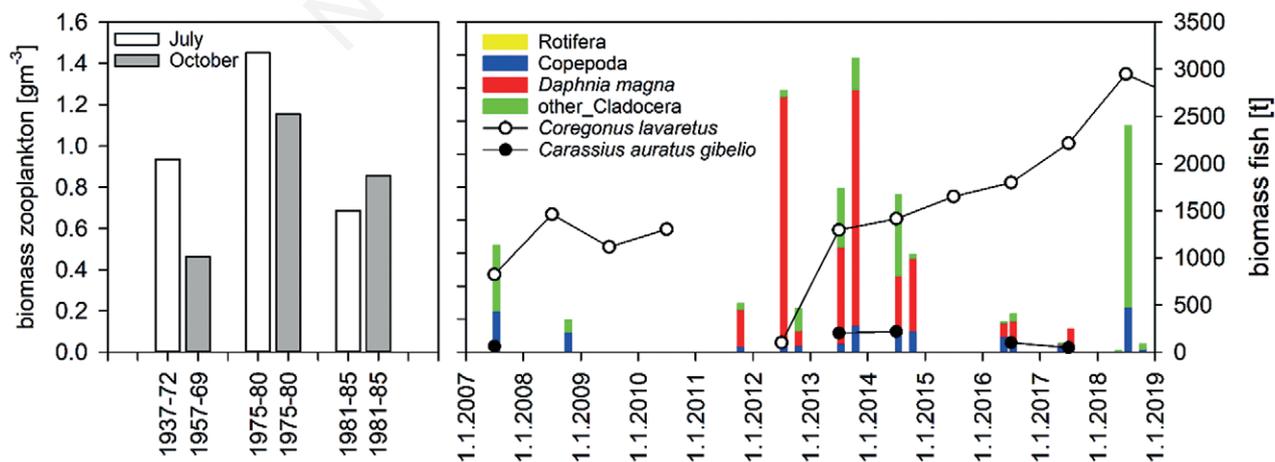


Fig. 2. Biomass of zooplankton in pelagic zone of Lake Sevan (columns, data from Krylov *et al.*, 2010, 2013, 2015, 2016a, 2016b, 2018, 2019, 2021a, 2021b) and estimated biomasses of the two dominant fish species *Coregonus* and *Carassius* (lines, data from Gabrielyan *et al.*, 2022).

sampling stations for zooplankton investigation: 15 observation points in Small Sevan and 17 observation points in Big Sevan. The depths at the sampling sites were different in order to cover potential gradients between littoral and pelagic habitats and were at 7, 20, 25, 30 and 60 m depth (the latter only in Small Sevan, see Tab. 2 and map in Fig. 1).

The study period covered the years from 2016 to 2019

and zooplankton was collected once a season in spring (May), summer (July) and autumn (October) in 2016-2018, and in spring and summer in 2019. This sampling design did obviously not allow for assessing population dynamics but is well suited for providing insights into spatial distributions and general biodiversity patterns within the zooplankton community.

Integral zooplankton samples at stations having a

Tab. 2. Overview for species-specific total biomass (expressed as mg wet weight m⁻³) calculated as the sum over all samples (n=239) including cumulative biomass and relative cumulative biomass. Note that for a deeper statistical analysis we later excluded rarely occurring species from the analysis (species found in less than 20 samples, see also Fig. 4).

Species/taxon	Total biomass (sum over all samples)	Cumulative total biomass	Relative cumulative biomass	Phenological group
<i>Daphnia magna</i>	80,241.8	80,241.8	0.329	1
<i>Arctodiaptomus bacillifer</i>	47,384.9	127,626.7	0.523	4
<i>Acanthodiaptomus denticornis</i>	36,814.4	164,441.1	0.674	3
<i>Daphnia hyalina</i>	21,211.4	185,652.5	0.761	6
<i>Diaphanosoma</i> sp.	19,412.9	205,065.4	0.840	2
<i>Nauplius</i> larvae	6871.2	211,936.6	0.869	5
<i>Cyclops strenuus</i>	6538.6	218,475.2	0.895	5
<i>Cyclops abyssorum</i>	6487.5	224,962.7	0.922	5
<i>Thermocyclops crassus</i>	4908.4	229,871.1	0.942	5
<i>Daphnia longispina</i>	4716.7	234,587.8	0.961	5
Calanoida	3261.8	237,849.6	0.975	5
<i>Cyclops</i> sp.	2374.1	240,223.8	0.984	5
<i>Cyclops vicinus</i>	2103.5	242,327.3	0.993	5
<i>Keratella quadrata</i>	474.3	242,801.5	0.995	5
<i>Polyarthra vulgaris</i>	202.3	243,003.8	0.996	5
<i>Euchlanis dilatata</i>	194.7	243,198.5	0.997	5
<i>Macrocyclus</i> sp.	178.1	243,376.6	0.997	Excluded
<i>Eucyclops serrulatus</i>	111.8	243,488.4	0.998	Excluded
<i>Megacyclus gigas</i>	105.6	243,594.0	0.998	Excluded
<i>Chydorus sphaericus</i>	89.0	243,682.9	0.999	5
<i>Filinia terminalis</i>	79.9	243,762.9	0.999	5
<i>Arctodiaptomus osmanus</i>	74.8	243,837.7	0.999	Excluded
<i>Asplanchna girodi</i>	49.6	243,887.3	0.999	5
<i>Synchaeta pectinata</i>	41.1	243,928.4	1.000	5
<i>Conochilus unicornis</i>	24.4	243,952.8	1.000	5
<i>Polyarthra dolichoptera</i>	21.4	243,974.2	1.000	Excluded
<i>Alona</i> sp.	12.0	243,986.2	1.000	Excluded
<i>Hexarthra mira</i>	8.0	243,994.1	1.000	5
<i>Cyclops lacustris</i>	5.3	244,007.0	1.000	Excluded
<i>Brachionus caliciflorus</i>	0.8	244,007.8	1.000	Excluded
<i>Brachionus quadridentatus</i>	0.6	244,008.5	1.000	Excluded
<i>Bdelloida</i> sp.	0.4	244,008.9	1.000	Excluded
<i>Notholca acuminata</i>	0.4	244,009.3	1.000	Excluded
<i>Lecane luna</i>	0.2	244,009.4	1.000	Excluded
<i>Bosmina longirostris</i>	0.2	244,009.6	1.000	Excluded
<i>Trichotria poccilum</i>	0.03	244,009.6	1	Excluded

depth of 7, 20, 25, 30 or 30 m were collected using an Apstein net with a 50 μm mesh size. And only at the deepest sampling point N 13 (60 m) in Small Sevan, a water sampler (volume: 4 liter) was used to collect separate samples from different depths (60 m; 50 m; 30 m; 25 m; 20 m, 15 m, 10 m, 5 m, 0 m), the water was immediately filtered through the above-mentioned Apstein plankton net on board of the vessel so that all zooplankters from the distinct depth samples were merged into one integral sample. The sampled volume at this station corresponded to 36 liters (9 depths times 4 L sampler volume). This different sampling strategy for the deepest point was applied because clogging of the net by filamentous algae (Genus *Melosira*) had occurred occasionally in the past. This problem, however, only occurred at the deepest point and therefore only for this station a distinct depth-sampling instead of directly taken integral net hauls was realized. The samples were preserved with 40% formaldehyde solution (4% final concentration). We measured the water temperature (thermometer) and water transparency (Secchi disk depth) during the field trips in each site.

Sample preparation and analyses

The fixed zooplankton samples were subsequently identified to the lowest taxonomic level and counted in a Bogorov counting chamber under the AmScope SE306R-PZ-P binocular stereo microscope. Rotifers, cladocerans and copepods were identified to species level by XSZ-107BN biological microscope using specialized species identification keys (Borutskiy *et al.*, 1991; Korovchinskiy, 2004; Alekseev and Tsalolikhin, 2010).

The counting data were converted to in-situ abundances and then converted to biomass of Copepods and Cladocerans on basis of length-weight-relationships on a taxon-specific level as outlined by Balushkina and Vinberg (1979). For this conversion, 25-35 (depending on their number) specimens of each taxon were measured with respect to body length. The volume of integral sample was calculated by multiplying the depth of sampling by the surface of Apstein net inlet.

The biomass of Rotifers was calculated by using tables with average individual weights (Mordukhaya-Boltovskoy, 1954). The abundance and biomass were provided per m^3 .

Data analyses and statistics

We analysed biomass distribution, community compositions and diversity by using taxon-specific biomasses. Similar analyses based on taxon abundances were mostly biased by the extraordinarily high abundances of the small-bodied organisms (*e.g.*, rotifers and nauplii larvae of copepods) or resulted in similar results

as the biomass data (if scaled data were used). It is therefore recommended to use biomass instead of abundance because biomass is a more robust indicator of functional characteristics or ecosystem metabolism (Saint-Germain *et al.*, 2007). In order to identify changes in the most present species, we firstly calculated species dominance defined as the biomass proportion of each species on total biomass. For a deeper statistical analysis based on Spearman correlation analysis we excluded rarely occurring species from the analysis. In our case, species that were found in less than 20 samples (out of 239 samples analysed) or only in single individuals were defined as rare and excluded in order to avoid zero-inflated data structures or calculation of linear model from low sample sizes. All rare species had only very low contribution to community biomass and therefore never changed overall biomass dynamics. This subset of frequent species contained 22 species out of 37 species, making up 99.8% of the overall biomass, identified in the whole data set. For a further complexity reduction, we grouped these 22 species into statistically derived phenological subgroups that were identified by a hierarchical clustering using proportional biomass data (*i.e.*, species-specific biomass proportion on total biomass within the respective sample) and the R-method *hclust()* with Euclidean distances and Ward's clustering method. We used Dunn's index (Dunn, 1974) to identify the most suitable number of subgroups by applying the R-method *cValid()* (Brock *et al.*, 2008). Maximising Dunn's index resulted into 6 groups (see results) that enabled an aggregated analysis and the identification of major patterns of their dynamics and occurrences. We used the Shannon index as a measure of biodiversity in our samples, calculated according to Oksanen *et al.* (2022) using the *vegan*-package (package version 2.6-4) in R.

Variance partitioning of the biomass distributions over space (*i.e.*, sampling station) and time (*i.e.*, year and season) was analysed by linear models and the method *calc.relimp()* from the package *relaimpo* (Grömping, 2006). All calculations, analyses, and visualisations were done in R version 4.2.2 (R Core Team, 2022), scripts are available on demand.

RESULTS

General patterns

The zooplankton observations in Lake Sevan covered 32 sampling sites and yielded 239 zooplankton samples, in total 37 different taxa were identified including Cladocera, Copepoda and Rotifer species. Biomass per sample, expressed as mg wet weight per m^{-3} , varied considerably among samples (Fig. 3) and followed a negative exponential distribution. Single species dominance in the sam-

ples, *i.e.*, the biomass proportion of most dominant species over total biomass in the respective sample, ranged between 0.23 and 0.94 with a mean of 0.53. Accordingly, many samples were dominated by just one species, *e.g.*, in 119 out of 239 samples, the single dominating species contributed more than 50% to total biomass. In 34 samples (*i.e.*, about 15%), the dominant species even contributed more than 75% to total biomass. Half of our samples showed a species dominance between 0.4 and 0.64. These biomass-dominating species in Lake Sevan's zooplankton were represented by abundant, large-sized crustaceans, such as *Daphnia magna*, *Diaphanosoma* sp., *Arctodiaptomus bacilifer* and *Acanthodiaptomus denticornis* (Fig. 4). However, although *Diaphanosoma* sp. achieved a relatively high biomass when it was occurring, it was only present in approximately half of the samples because it was mostly occurring in late summer. Therefore, when analysing total summed biomass over all samples, the three most dominating species were *Daphnia magna*, *Arctodiaptomus bacilifer* and *Acanthodiaptomus denticornis*, which together constituted already two thirds of the entire analysed zooplankton biomass in Lake Sevan (Tab. 2). Along the 10

most biomass-contributing species made up already more than 96% of the overall total biomass. In terms of abundance, of course, patterns became reversed and small bodied species dominated (rotifers) without contributing substantial biomass (Fig. S1).

While zooplankton biomasses in the two major sub-basins of Lake Sevan (Small and Big), were relatively similar to each other, biomass showed a contrasting pattern along depth with highest biomasses in the deeper pelagic habitats (depth of 60 m, see Fig. 5). This pattern was originating from higher abundances of *Daphnia magna*, which preferred pelagic over littoral habitats, at the sampling point of 60m depth. Aside of this deepest sampling point in the central area of Small Sevan, biomass decreased with increasing depth resulting in the highest biomasses at the shallowest (*i.e.*, 7 m) and deepest depth (*i.e.*, 60 m, Fig. 5) and lowest biomasses at stations having 30 m depth. Summer biomasses were higher than during spring and autumn reflecting the superior growing conditions during this season. Within the sampled period from 2016-2019, zooplankton biomass reached a remarkable minimum in 2018 being roughly one order of magnitude lower than in 2016 – the year

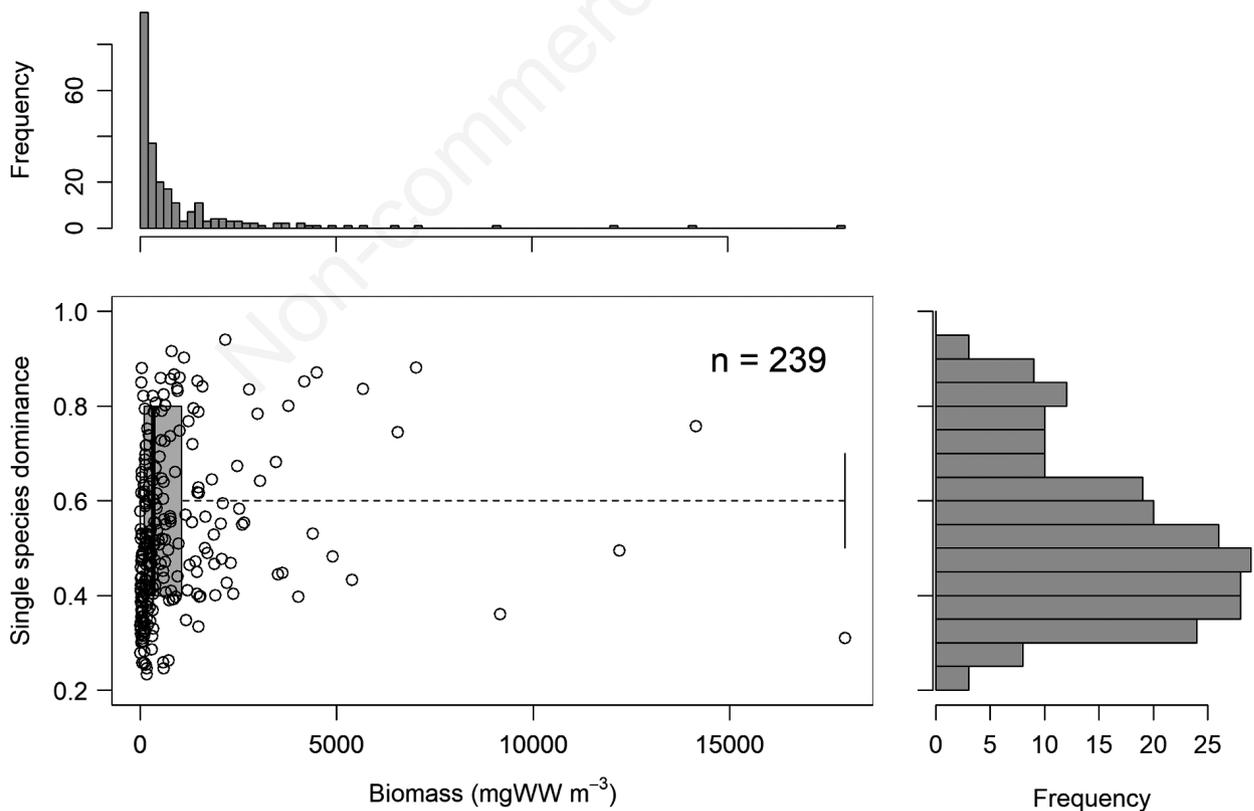


Fig. 3. Biomass distribution among all 239 zooplankton samples analysed (x-axis) plotted against species dominance (y-axis) defined as the biomass proportion of the single dominant species on total biomass. Histograms above and right of the central plot show the histogram of the respective axis variable. The boxplot in the background of the central plot shows median, Q25-Q75 interquartile, and range.

with the highest recorded biomasses (Fig. 5). Also, these patterns were mostly driven by the dynamics of *Daphnia magna*, which was not recorded in 2018 (see below).

Biodiversity of the zooplankton community in Lake Sevan, measured by the Shannon index, varied between 0.6 and 2.4 but showed only little contrast among habitats (Fig. 6), subbasins, years, and depths. It was only slightly higher during summer and in pelagic habitats (depth of 60 m). We noted a tendency towards higher diversity in samples with higher biomass resulting in a weak but significant positive relationship between Shannon diversity

and log-transformed biomass ($\text{Shannon}=1.3+0.06*\log[\text{biomass}]$, $R^2=0.12$, $F_{1,237}=33.1$, $p<0.001$).

Community composition

Astonishingly, taxon-specific biomasses were mostly non-correlated or positively correlated but showed far less negative correlations (Fig. 7). An exception from that was the pattern in *Diaphanosoma*, which had many negative spearman correlations indicating that the occurrence of this species is very distinct and often in situations

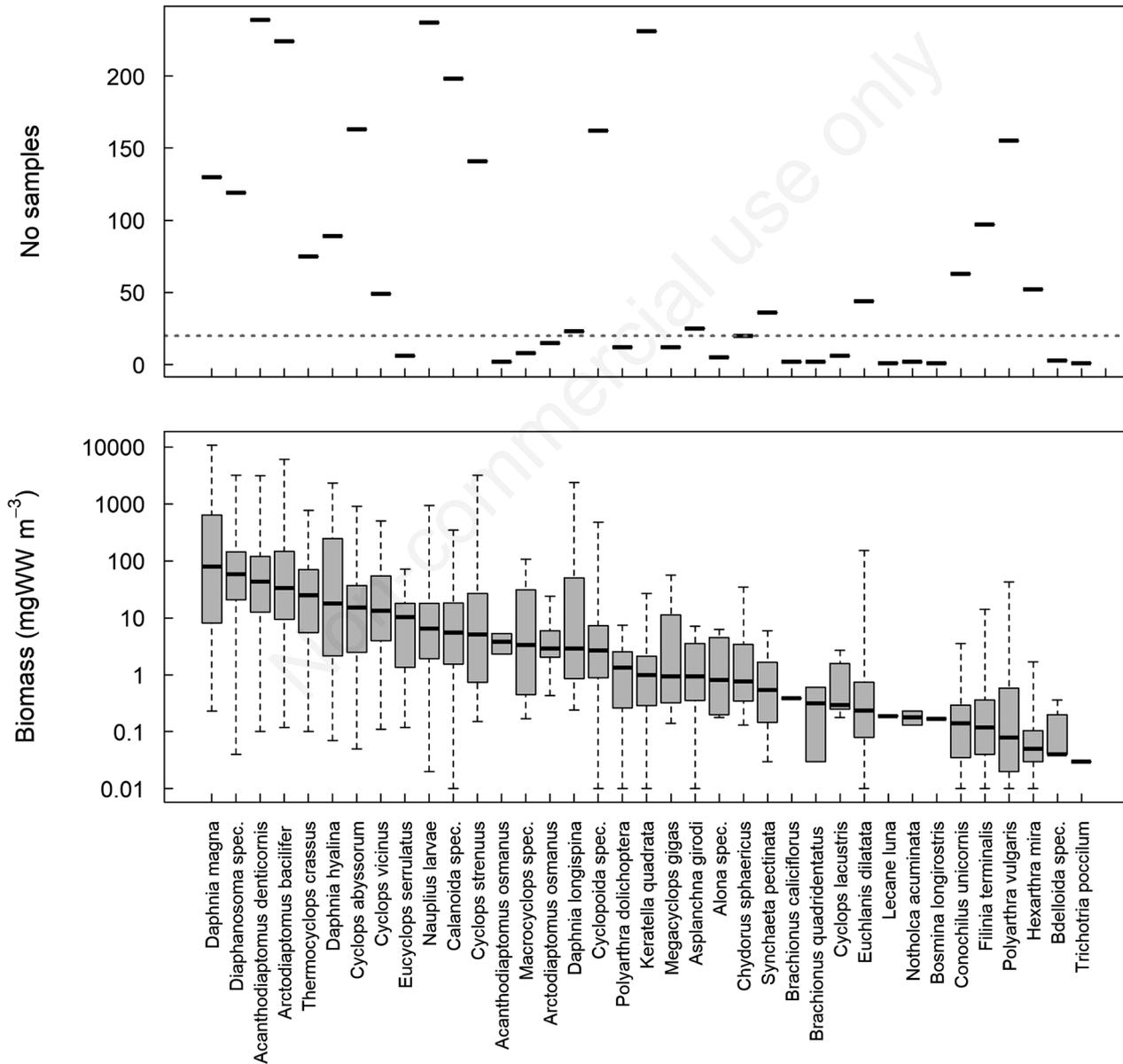


Fig. 4. Frequency of occurrence (top) of zooplankton species detected in Lake Sevan in the overall samples (n=239 samples) and median biomass per occurrence (bottom). The dotted line in the upper panel marks the threshold for defining rare species, which had been found in less than 20 samples (see text).

where other species are hardly present. Note, that we excluded rare species from this analysis by removing those taxa that occurred in less than 20 samples in order to avoid calculating correlation coefficients from small sample sizes with a high risk of spurious significances (see methods). Notably, this subset still contained 99.8% of total biomass sampled. The fact that not too many negative correlations could be found was a clear indicator that species occurrence is simply determined by the total biomass in the sample. That is, species reached higher biomasses in those samples that contained a high total biomass anyway (e.g., *Arctodiaptomus bacilifer* together with *Acanthodiaptomus denticornis* or *Cyclopoida* sp., see Fig. 7A). This pattern changed when biomass proportions were analysed (instead of total biomass), i.e., scaling the biomass of each species by the total biomass in the respective sample (i.e., values between 0 and 1). In this case, many negative correlations became visible (Fig. 7B), in particular in association with the two cladocerans *Daphnia magna* and *Diaphanosoma* sp., as well as *Arctodiaptomus bacilifer*. These species not only replaced each other (i.e., hardly occurred together in terms of biomass contributions) but also often excluded many other species when becoming dominant. Note, however, that many copepod and rotifer taxa still showed significant positive associations among each other in biomass pro-

portions (Fig. 7B), e.g., *Calanoida* with *Euchlanis* or *nauplia* with several rotifer species.

We explored these community patterns further by identifying phenological subgroups of species by hierarchical clustering. Interestingly, irrespective of whether absolute biomasses or biomass proportions were analysed, the definition of 6 subgroups were statistically meaningful and even the composition of these six groups was similar (though not exactly the same, see Fig. 7 C,D). Given the fact that the biomass fractions gave a better representation of antagonistic/synergistic interactions among species, we further concentrated on the hierarchical clustering based on biomass fractions. By defining these six derived subgroups (see also Tab. 2 for their taxonomic composition), a complexity-reduced picture of the Lake Sevan zooplankton community emerged (Fig. 8). Group 1, i.e., *Daphnia magna*, showed strongly negative, statistically significant relationships with the biomass proportions from the other groups (exception: Group 6, i.e., *Daphnia hyalina*). A similar statement could be made for Group 6 (*Daphnia hyalina*) indicating that the large-bodied Cladocerans tended to show antagonistic relationships to the other members of the community. In general, the groups 4, 5, and 6 were significantly negatively correlated and appeared to co-occur more rarely than expected by chance.

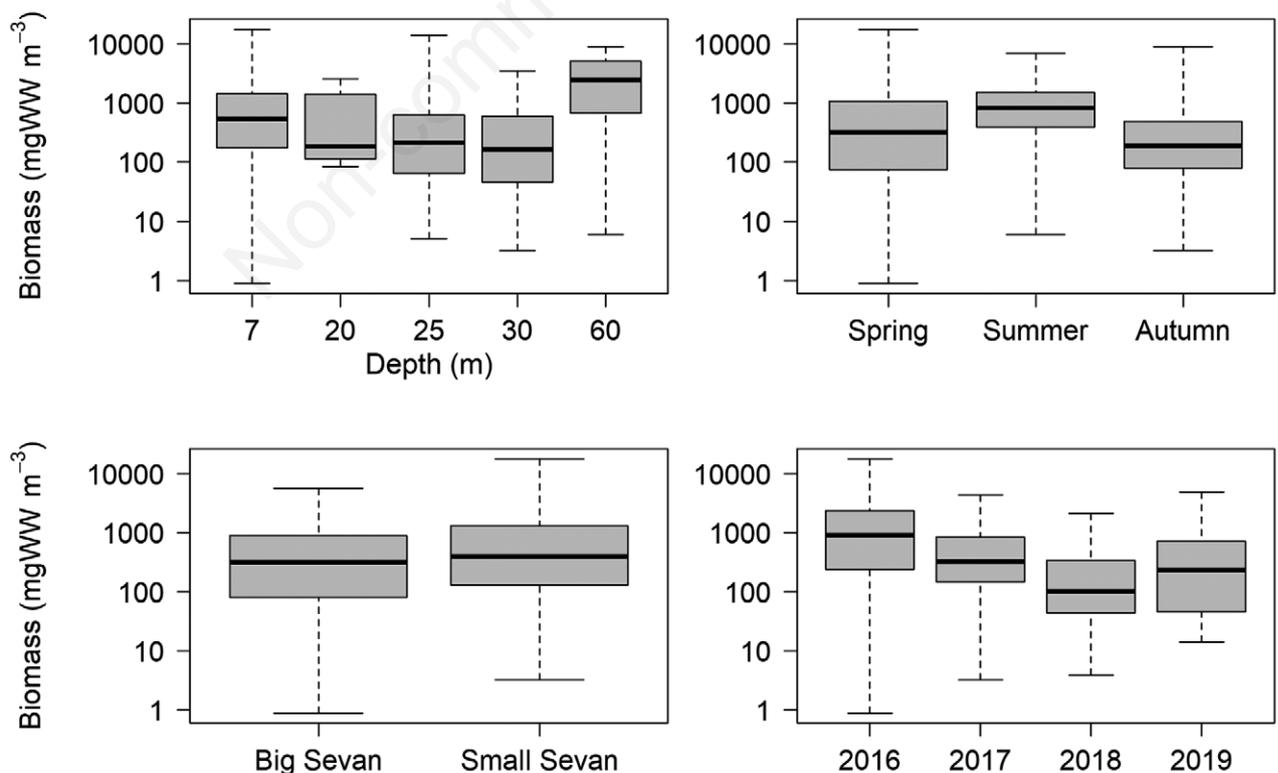


Fig. 5. Zooplankton biomass in Lake Sevan for specific habitats and times, total sample size is n=239.

These antagonistic interactions (Fig. 8) represented replacement-patterns among these groups that operated not only at the seasonal scale (*e.g.* spring species vs. summer/autumn species) but also interannually (Fig. 9). *Daphnia magna* (Group 1) and *Acanthodiptomus denticornis* (Group 3), for example, did separate along seasons with *Daphnia magna* dominating in summer while *Acanthodiptomus denticornis* mostly occurred during colder seasons. At the same time, *Daphnia magna* almost disappeared from Lake Sevan from 2018 onwards (Fig. 9) and opened a niche for the other groups. Such changes in the zooplankton community composition also came along with changes in the phytoplankton compartment as indicated by Secchi Disk depth (Fig. 9), which appeared to be higher during times of *Daphnia magna* dominance. A linear regression between mean proportion of *Daphnia magna* as explanatory variable and mean Secchi depth as response variable in fact showed a positive significant relationship ($y = 12x + 4$, $R^2=0.54$, $F_{1,9}=10.8$, $p=0.009$, see also Fig. S2).

Variance partitioning

Our study allowed to quantify the contribution of spatial and temporal dimensions to observed variability in

total zooplankton biomass and a linear model showed that sampling station, year and season (all as categorical variables) significantly influenced log-transformed sampled biomass and explained about 50% of total variance ($R^2=0.49$, Tab. 3). The two predictors from the temporal dimension, *i.e.*, season and year together, contributed approximately two-thirds to this overall R^2 while the spatial dimension, reflected by the different stations, explained only one third (Tab. 3). The most influential predictor was year indicating that interannual dynamics are more variable than seasonal dynamics. In summary, the spatial variability of zooplankton biomass in Lake Sevan was lower than the variability emerging at the time dimension, at least over the spatiotemporal scales assessed in our sampling (compare Figs. 10 and 11). Having said that, we at the same time emphasize that the various sampling sites were clearly different from each other, and the station number was still a highly significant predictor in our model (Fig. 10). There was no gradient or systematic pattern in these station-specific biomasses detectable but it turned out that the central station in Small Lake Sevan (station 13) yielded the highest biomasses indicating that the pelagic zone supports high zooplankton biomass.

When adding also phenological information to the

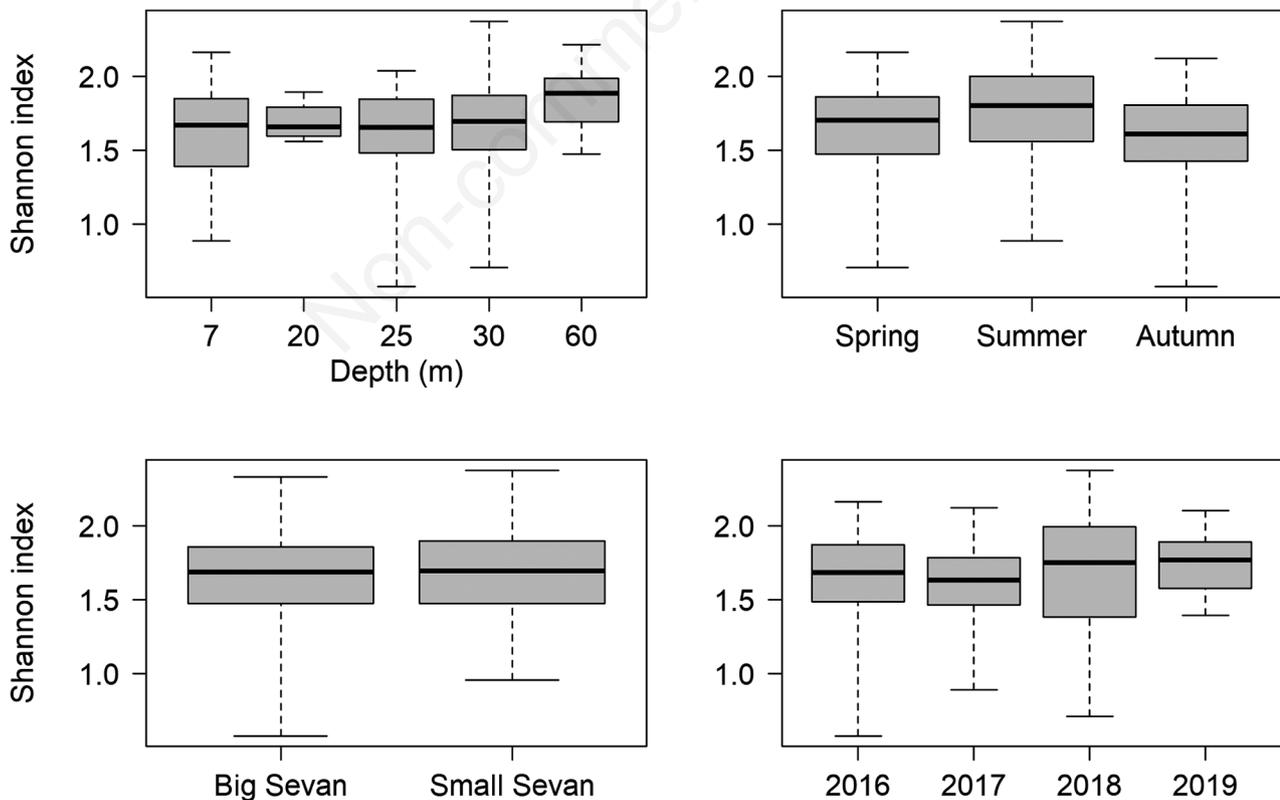


Fig. 6. Diversity (Shannon index, calculated based on biomasses) of zooplankton community for different habitats and times. Total sample size $n=239$.

model, as reflected by the 6 phenological groups defined above (Tab. 2, Figs. 7 and 8), the predictability of log-transformed biomass further increased and yielded an

overall $R^2=0.55$ (Tab. 4). In this model, station became most influential (partially explaining 18% of total variance) followed by the phenological groups (partially ex-

Tab. 3. ANOVA results (upper part) for a linear model on log-transformed total biomass as a function of sampling station, year, and season (all as categorical variables, $R^2=0.49$). Although all predictors were highly significant, their partial contribution to explained variance (lower part) is different with year contributing most to the explained variance. Both temporal factors combined together (year and season) explained a larger share of explained variance compared to the spatial factor (sampling station).

Analysis of variance					
	df	SQ	mean SQ	F	p-value
Station	31	120.91	3.90	2.20	0.0006
Year	3	122.48	40.83	23.06	<0.0001
Season	2	105.54	52.77	29.81	<0.0001
Residuals	202	357.65	1.77		
Relative importance estimates (partial contribution to R^2)					
Station	0.172				
Year	0.199				
Season	0.123				
Overall R^2	0.494				

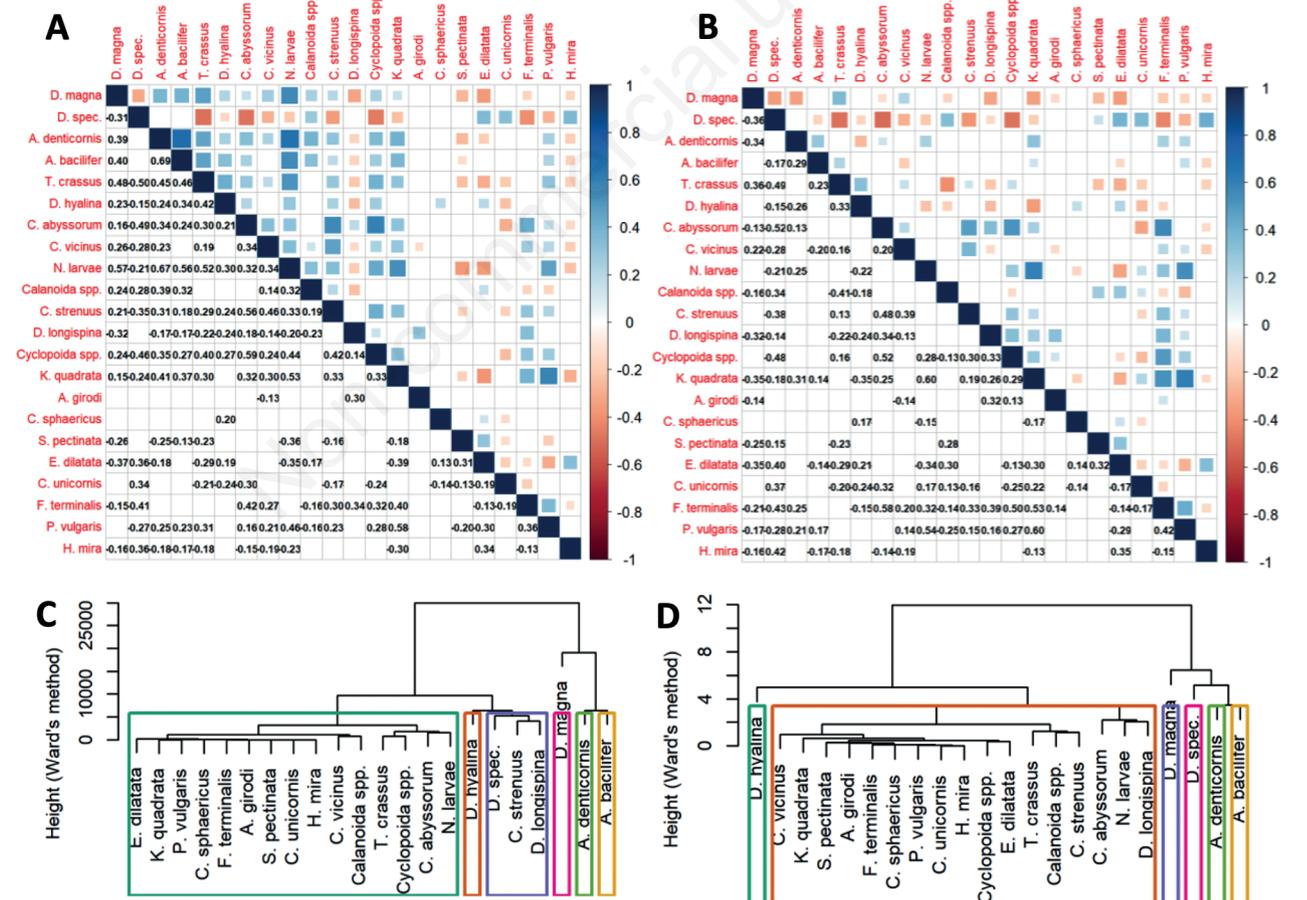


Fig. 7. Correlation plot of the most frequent species (being present in at least 20 samples) for species-specific absolute biomass (A) and biomass proportions (B). Only significant correlations are shown ($\alpha = 0.05$), the numbers below the diagonal show Spearman correlation coefficients. Clusters of similarly behaving species with respect to absolute biomass (C) or biomass proportions (D), respectively, had been identified by hierarchical clustering.

plaining 15% of total variance). However, if the two temporal predictors year and season were combined (together explaining 22% of total variance), the temporal dimension remained the most influential and more important than space or taxonomy as reflected by the biomass dynamics shown in Fig. 11.

DISCUSSION

Our study provided previously not available data on the long-term dynamics of zooplankton community of Lake Sevan. We presented not only an assessment of the species repertoire at a high spatial coverage and reasonable temporal resolution but also showed biomass dynamics over several years. These dynamics were unusually high and sharply fluctuating with major changes in community composition, namely the disappearance of the large-bodied *Daphnia magna* in the last sampling time points. These changes pointed to considerable changes in the biotic and/or abiotic conditions in this large, alpine lake.

A key instrument of our statistical analysis was the hierarchical grouping of phenological species groups. Interestingly, many of these phenological groups were just consisting of single species indicating the biomass dynamics were mostly driven by a few species. In terms of biomass contribution to the zooplankton community, these species were partly replacing each other at seasonal or annual scales. This required more analysis and interpretation, which follows below.

According to our results we assume that biotic factors were more important than abiotic factors given the major changes that are associated with the dynamics of *Daphnia magna* and the underlying changes in the fish com-

munity. For example, water level dynamics – a previously identified major factor for Lake Sevan ecosystem dynamics – remained low and the water level was almost stable during our observation period (Gabrielyan *et al.*, 2022). Also, meteorological conditions were not exceptional and no extreme events stood out during this period. A closer analysis of relevant biological factors was therefore required. In conclusion, while the species found in the lake were mostly typical species for large, stratified lakes with a dominating pelagic component, their occurrence and biomass dynamics showed larger dominance shifts and by that a partly unique pattern.

Biomass dynamics, species dominance, and ecosystem stability

Many zooplankton samples showed a high species dominance (Fig. 3). About half of the samples showed a single species dominance of 50% or more, this was also reflected in our phenological grouping. Comparative studies suggested that more diverse communities often show smaller compositional changes, *i.e.*, more stable dynamics, over time (Shurin *et al.*, 2007). The observed diversity characteristics of Lake Sevan zooplankton indicated on the one hand a relatively common species richness but, on the other hand, a rather low species evenness so that the resulting Shannon-Indices were rather low (*e.g.*, compare to Ramirez Garcia 2002; Thakur *et al.*, 2013; Bockwoldt *et al.*, 2017). In that respect, our observations in Lake Sevan fitted into this picture as the large fluctuations among a few dominating species came along with relatively low Shannon diversity. Rising temperatures in future due to global warming may act as an additional factor interfering with ecosystem stability (Zhao *et al.*, 2023). Given the fact that Lake Sevan is al-

Tab. 4. The same as for Tab. 3 but with extending the underlying linear model by the dominant phenological group (Group 1 to Group 6). This taxonomically based variable was given as categorical variable describing which of the 6 phenological groups are dominating in the respective sample (*i.e.*, having the highest biomass proportion).

Analysis of variance						
	df	SQ	Mean SQ	F	p-value	
Station	31	120.91	3.90	2.20	0.0002	
Year	3	122.48	40.83	23.06	<0.0001	
Season	2	105.54	52.77	29.81	<0.0001	
Dominant group	5	37.46	7.49	4.61	0.0005	
Residuals	197	320.19	1.63			
Relative importance estimates (partial contribution to R ²)						
Station	0.176					
Year	0.135					
Season	0.088					
Dominant group	0.148					
Overall R ²	0.547					

ready experiencing warming (Shikhani *et al.*, 2021), while further warming is expected in Armenia (Gevorgyan *et al.*, 2016; Aslanyan, 2020), we do not expect a more stable community assembly in Lake Sevan zooplankton in future.

Biodiversity can be seen as a structural component of communities and ecologists documented that not only structural, but also functional characteristics of communities play a role for ecosystem stability. A more food web-oriented analysis of Rooney *et al.* (2006) differenti-

ated between fast and slow trophic channels and their interplay. While fast channels show the highest energy flows in the food web, the slow channels can buffer fluctuations in these fast channels. Interestingly, the coupling of both channels is realised by top-predators (Rooney *et al.*, 2006). In case of Lake Sevan, the major top predator in the original food web, the endemic Lake Sevan trout (*Salmo ischchan*) suffered a severe population crash in the 70ies and 80ies of the last century and has still not recovered from this crash (Gabrielyan *et al.*, 2022). There

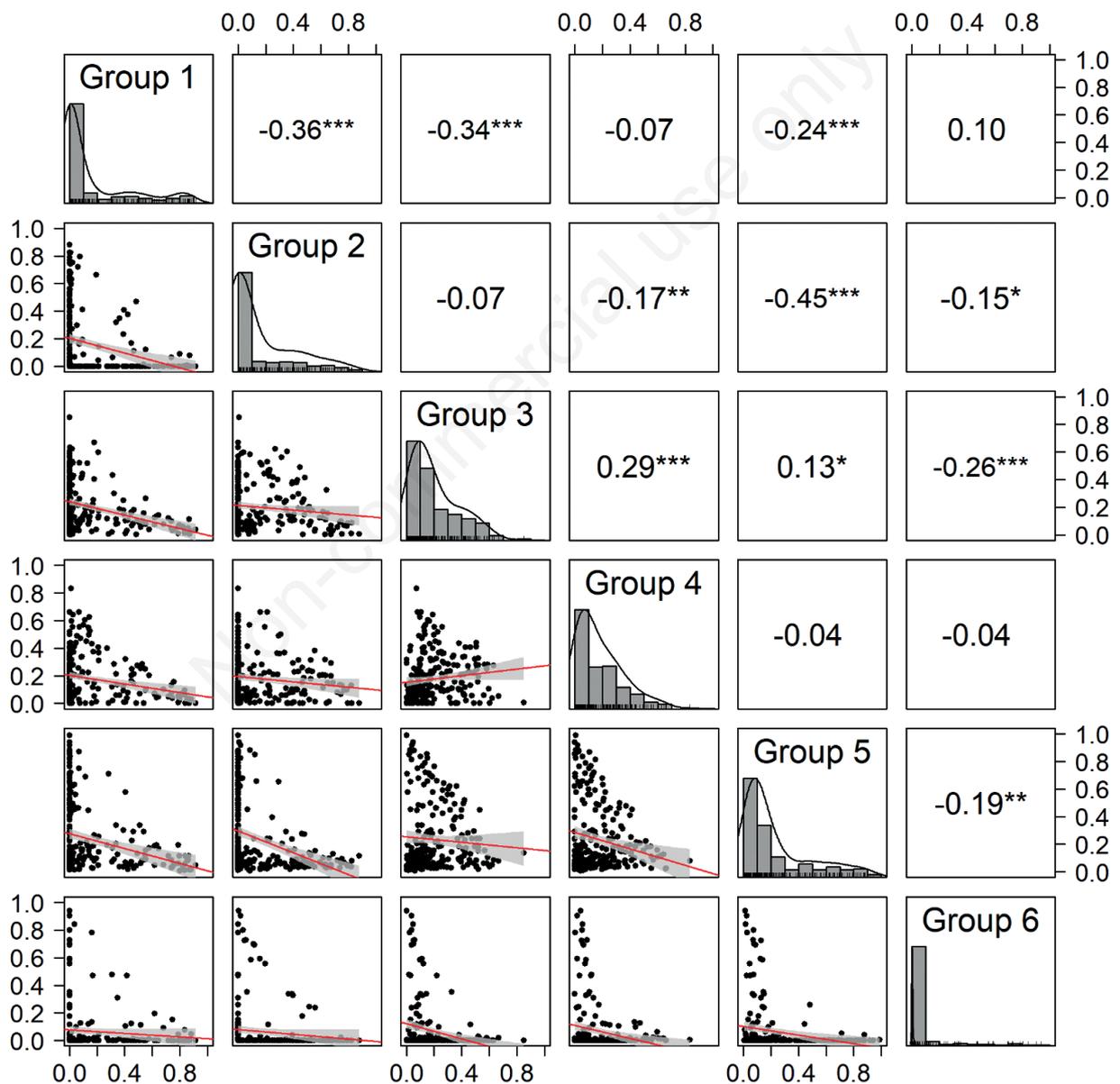


Fig. 8. Correlation plot using Spearman rank correlation for the biomass proportions of the 6 dominant subgroups defined by the hierarchical clustering in Fig. 7. The stars indicate statistical significance with: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Note that some groups consisted of single species as outlined in Tab. 2.

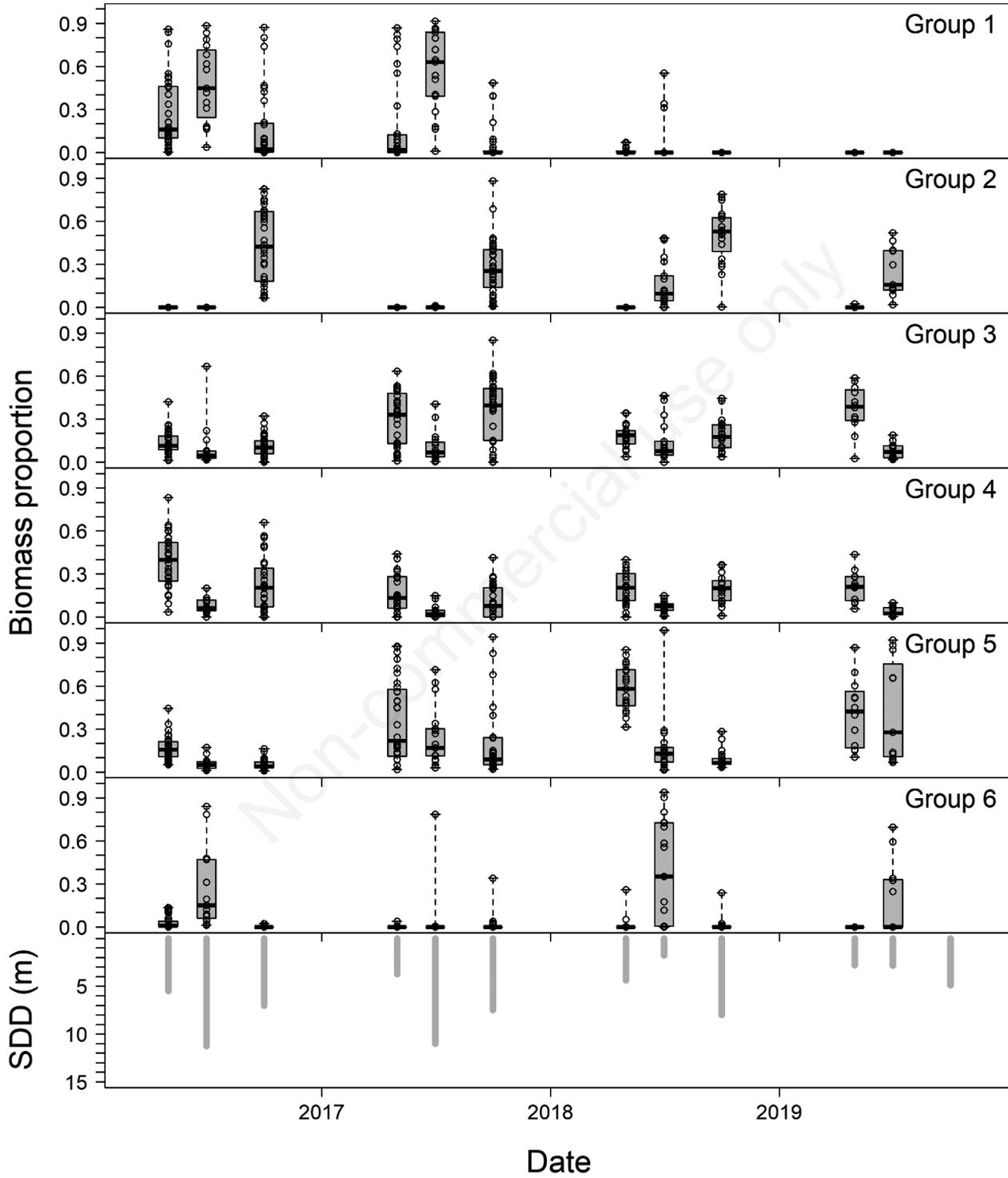


Fig. 9. The upper six panels show the dynamics of biomass proportions of the 6 phenological zooplankton groups (see text and Tab. 2) over the study period. The bottom panel shows the Secchi disk depths (m) from the sampling trips. Note that some groups consisted of single species as outlined in Tab. 2.

were hence good reasons to assume that Lake Sevan pelagic food web was susceptible to instabilities and large fluctuations given the loss of the top predator. This was at least reflected in our analysis of zooplankton community dynamics and was also matching with perturbations in the phytoplankton community with occasional outbursts of cyanobacterial blooms (Gevorgyan *et al.*, 2020; Hambaryan *et al.*, 2020). In that respect, a restoration of an abundant and viable top predator population could be a major stabilising influence on Lake Sevan ecosystem.

This can also be understood as a measure of “provident resilience management” (Weise *et al.*, 2020) in the frame of climate adaptation and stressor resistance.

Trophic cascades and biotic interactions

Plankton food-webs have been intensively studied for trophic interactions and in many lakes cascading effects along the major food chain have been documented. Such trophic cascades (Carpenter and Kitchell, 1993) emerge when biomass shifts propagate through the food web by

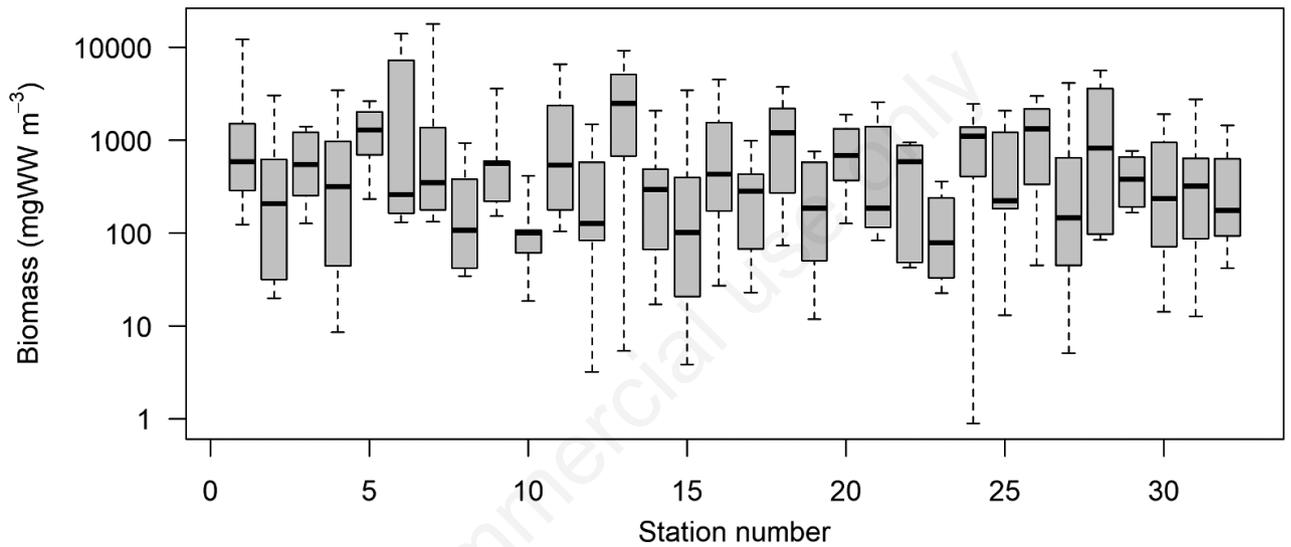


Fig. 10. Distribution of total zooplankton biomass among the 32 sampling sites over all 239 samples analysed. Note the logarithmic scale on the y-axis.

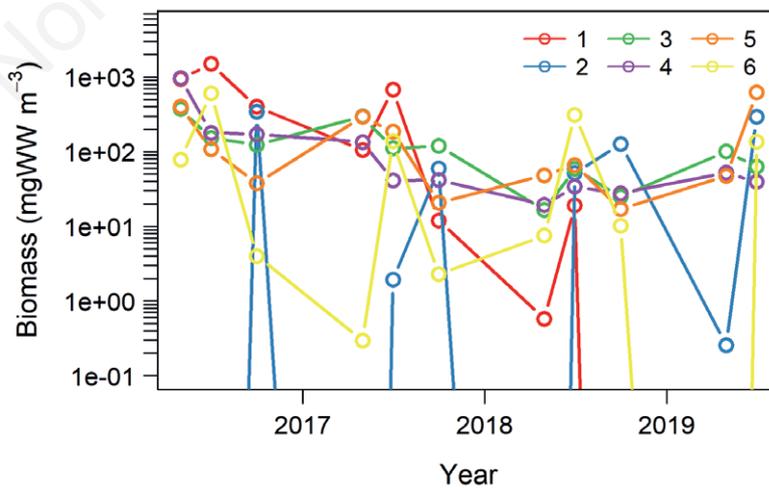


Fig. 11. Biomass dynamics of the 6 functional groups over the whole sampling period. Note the logarithmic scale of the y-axis. Lines crossing with the x-axis denote periods where the group was absent. This appeared for the groups 1,2 and 6, the single-species phenological groups with cladocerans. The ticks of the x-axis indicate 1st of January of the given year. Note that some groups consisted of single species as outlined in Tab. 2.

trophic interactions, *e.g.*, that high levels of predator abundance induce population declines in their prey and it affects the overall community structure. Such trophic cascades have been documented for lakes (Benndorf *et al.*, 1984) as well as for marine (Casini *et al.*, 2009) and terrestrial habitats (Ripple and Beschta, 2012) and played an important role in theory development of modern ecology as they highlighted the importance of predation and top-down effects on community and population dynamics. The influence of cascading effects may vary with time. Casini *et al.* (2009), for example, documented for the pelagic zone of the Baltic Sea that ecosystem functioning depended on the biomass level of planktivorous fish. When planktivores were highly abundant zooplankton was top-regulated, but when planktivores were reduced, *e.g.*, by high predation from cod, the major piscivore in the system, zooplankton was rather controlled by hydroclimatic conditions acting bottom-up. In Lake Sevan we observed similar patterns and hence empirical evidence for a trophic cascade in Lake Sevan where the development of high standing stocks of *Daphnia magna* coincided with increasing transparency (see section Results, significant negative correlation) and low fish biomass. We lack a detailed analysis of the phytoplankton community but samplings at seasonal scales showed relatively low algal biomass from 2013 until 2017 and a strong rise of phytoplankton biomass from 2017 to 2018 by a six-fold increase (Sakharova *et al.*, 2020). This strong biomass increase came exactly in time with the extirpation of *Daphnia magna*. Interestingly, the highly grazing-resistant gelatinous green algae (Porter, 1973) like *Sphaerocystis*, *Oocystis* or *Coelastrum* were abundant during *Daphnia magna* dominance but almost disappeared in 2018 (Asatryan *et al.*, 2022) when zooplankton grazing must have been much lower than before due to the extirpation of *Daphnia magna*. Finally, the period of *Daphnia magna* dominance co-occurred with low fish biomass (Fig. 2), though this link was weaker than the link between *Daphnia magna* and Secchi-depth. A correlation analysis showed, however, that the biomass of *Coregonus lavaretus* explained 31% of the variance in *Daphnia magna* biomass ($R^2 = 0.31$, $p = 0.03$, *Daphnia magna* biomass was $\log(n+1)$ -transformed). The trophic link between *Coregonus lavaretus* and *Daphnia magna* seemed to be strong as fish gut analyses showed in 2013 that all analysed specimens of *Coregonus lavaretus* contained *Daphnia magna* in their guts and in 90% of specimens *Daphnia magna* dominated as prey. In 2018, only 28% of whitefish exclusively fed on planktonic organisms and 44% on benthic organisms (mostly gammarids), while 21% of specimens had both groups of animals in their intestines. The fraction of planktonic prey in fish guts was in that year dominated by Calanoid copepods (Krylov *et al.*, 2021b).

Already in the 80s of the last century, limnologists contemplated about using trophic cascades as a management tool in order to influence productivity and control eutrophication (Carpenter *et al.*, 1985). Since then, there have been a number of positive examples how this biomanipulation can be used in lake management (Kasprzak *et al.*, 2007; Scharf, 2008) and its applicability as well as limitations have been reviewed (Benndorf, 1995; Benndorf *et al.*, 2002). It has been convincingly shown that biomanipulation can be a very useful tool if certain supporting circumstances are present in the given lake. A key factor in this respect seems to be the nutrient loading of the lake (Benndorf *et al.*, 2002, Mehner *et al.*, 2002). Whenever nutrients are above a certain level, biomanipulation effects weaken because of internal feedback mechanisms like the emergence of grazing-resistant algae like colonial or filamentous algae. It remains unclear whether the current nutrient conditions in Lake Sevan are above or below this critical level as the lake is undergoing eutrophication and recently suffered from mass developments of cyanobacteria and massive harmful algal blooms (Gevorgyan *et al.*, 2020; Hambaryan *et al.*, 2020). Nevertheless, based on our study we can conclude that probably the lake was susceptible to biomanipulation in the years before 2018 when the above-described trophic cascade was at play. In that respect, further research is needed to clarify the role of trophic interactions on the productivity and trophic state of this important, sensitive, and beautiful alpine lake.

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REFERENCES

- Alekseev V, Tsalolikhin S, 2010. [Key for determination of zooplankton and zoobenthos of freshwater European Russia]. [Book in Russian]. Moscow-St. Petersburg: 495 pp.
- Asatryan V, Stepanyan L, Hovsepian A, Khachikyan T, Mamyan A, Hambaryan L, 2022. The dynamics of phytoplankton seasonal development and its horizontal distribution in Lake Sevan (Armenia). *Environ. Monit. Assess.* 194:757.

- Babayan A, Hakobyan S, Jenderedjian K, Muradyan S, Voskanov M, 2006. Lake Sevan: experience and lessons learned brief (Lake basin management initiative). International Lake Environment Committee Foundation, Kusatsu, Japan. Available from: http://worldlakes.org/uploads/sevan_01oct2004.pdf
- Balushkina E, Vinberg G, 1979. [Relation between length and mass of body of plankton Crustaceous], p. 58-79. In: [Experimental and field investigations of biological basis of productivity of lakes]. [Book in Russian]. Leningrad.
- Benndorf J, 1995. Possibilities and limits for controlling eutrophication by biomanipulation. *Internationale Revue der gesamten Hydrobiologie* 80:519-534.
- Benndorf J, Kneschke H, Kossatz K, Penz E, 1984. Manipulation of the pelagic food web by stocking with predacious fishes. *Int. Rev. Gesamten Hydrobiol.* 69:407-428.
- Benndorf J, Böing W, Koop J, Neubauer I, 2022. Top-down control of phytoplankton: the role of time scale, lake depth and trophic state. *Freshwater Biology* 47:2282-2295.
- Berta C, Tóthmérész B, Wojewódka M, Augustyniuk O, Korponai J, Bertalan-Balázs B, Nagy AS, Grigorszky I, Gyulai I, 2019. Community response of Cladocera to trophic stress by biomanipulation in a shallow oxbow lake. *Water* 11:929.
- Bockwoldt KA, Nodine ER, Mihuc TB, Shambaugh AD, Stockwell JD, 2017. Reduced phytoplankton and zooplankton diversity associated with increased cyanobacteria in Lake Champlain, USA. *J. Contemp. Water. Res. Educ.* 160:100-118.
- Borutskiy E, Stepanova L, Kos M, 1991. [Calanoida of freshwaters]. [Book in Russian]. St. Petersburg: 500 pp.
- Brock G, Pihur V, Datta S, 2008. clValid: An R Package for Cluster Validation. *J. Stat. Softw.* 25:1-22.
- Brooks J, Dodson S, 1965. Predation, body size, and composition of plankton. *Science* 150:28-35.
- Carpenter SR, Kitchell JF, Hodgson JR, 1985. Cascading trophic interactions and lake productivity. *Bioscience* 35:634-639.
- Carpenter S, Kitchell J, 1993. *The trophic cascade in lakes*. Cambridge University Press, Cambridge: 400 pp.
- Casini M, Hjelm J, Molinero J-C, Lövgren J, Cardinale M, Bartolino V, Belgrano A, Kornilovs G, 2009. Trophic cascades promote threshold-like shifts in pelagic marine ecosystems. *P. Natl. Acad. Sci.-Biol* 106:197-202.
- Danielyan K, Gabrielyan B, Minasyan S, Chilingaryan L, Melkonyan H, Karakhanyan A, et al., 2011. Integrated Assessment of the Lake Sevan Environmental Conditions (GEO - Lake Sevan). Association "For Sustainable Human Development"/UNEP National Committee, Yerevan: 100 pp.
- Duggan IC, Green JD, Shiel RJ, 2001. Distribution of rotifers in North Island, New Zealand, and their potential use as bioindicators of lake trophic state. *Hydrobiologia* 446/447:155-164.
- Dunn JC, 1974. Well separated clusters and fuzzy partitions. *J. Cybernetics* 4:95:104.
- Friedman GM, 1950. [Bottom fauna of Lake Sevan]. [Article in Russian]. *Protocols of the Sevan Hydrobiological Station Tr. SGBS* 11:7-92.
- Gabrielyan B, Khosrovyan A, Schultze M, 2022. A review of anthropogenic stressors on Lake Sevan, Armenia. *J. Limnol.* 81:2061.
- Gevorgyan A, Melkonyan H, Aleksanyan T, Iritsyan A, Khalatyan Y, 2016. An assessment of observed and projected temperature changes in Armenia. *Arab. J. Geosci.* 9:27.
- Gevorgyan G, Rinke K, Schultze M, Mamyán A, Kuzmin A, et al., 2020. First report about toxic cyanobacterial bloom occurrence in Lake Sevan, Armenia. *Int. Rev. Hydrobiol.* 105:131-142.
- Grömping U, 2006. Relative Importance for Linear Regression in R: The Package relaimpo. *J. Stat. Softw.* 17:1-27.
- Ha JY, Saneyoshi M, Park HD, Toda H, Kitano S, Homma T, et al., 2013. Lake restoration by biomanipulation using piscivore and *Daphnia* stocking; results of the biomanipulation in Japan. *Limnology* 14:19-30.
- Hall D, Threlkeld S, Burns C, Crowley P, 1976. The size-efficiency hypothesis and the size structure of zooplankton communities. *Ann. Rev. Ecol. System.* 7:177-208.
- Hambaryan LR, Stepanyan LG, Mikaelyan MV, Gyurjyan QG, 2020. The bloom and toxicity of cyanobacteria in Lake Sevan. *Proceedings of the Yerevan State University - Chemistry and Biology* 54:168-176.
- Hovhanissian RH, 1994. [Lake Sevan Yesterday, today]. [Book in Russian]. Gitutyun Publishing House of the NAS RA, Yerevan: 478 pp.
- Hülsmann S, Rinke K, Mooij W, 2005. A quantitative test of the size efficiency hypothesis by means of a physiologically structured model. *Oikos* 110:43-54.
- Kasprzak P, Benndorf J, Gonsiorczyk T, Koschel R, Krienitz L, Mehner T, et al, 2007. Reduction of nutrient loading and biomanipulation as tools in water quality management: Long-term observations on Bautzen Reservoir and Feldberger Haussee (Germany). *Lake Reserv. Manage.* 23: 410-427.
- Korovchinskiy N, 2004. [Ctenopoda order of Cladoceras of the world fauna]. [Book in Russian]. Moscow: 410 pp.
- Kreutzer C, Lampert W, 1999. Exploitative competition in differently sized *Daphnia* species: a mechanistic explanation. *Ecology* 80:2348-2357.
- Krylov AV, Hakobyan SA, Nikogosyan AA, Hayrapetyan AH, 2010. [Zooplankton of Lake Sevan and its inflows], p. 168-200. In: Pavlov DS, Poddubny SA, Gabrielyan BK, Krylov AV (eds.), [Ecology of Lake Sevan during the period of water level rise. The results of Russian-Armenian biological expedition for hydrological survey of Lake Sevan (Armenia) (2005-2009)]. [Book in Russian]. "Nauka DNC" Publishing House.
- Krylov AV, Gerasimov YuV, Gabrielyan BK, Borisenko ES, Hakobyan SA, Nikogosyan AA, Ovsepyan AA, 2013. Zooplankton in Lake Sevan during the period of high-water level and low fish density. *Inland Water Biol.* 6:203-210.
- Krylov AV, Romanenko AV, Gerasimov YuV, Borisenko ES, Hayrapetyan AH, Ovsepyan AA, Gabrielyan BK, 2015. Distribution of plankton and fish in Lake Sevan (Armenia) during the process of mass growth of Cladocera. *Inland Water Biol.* 8:54-64.
- Krylov A, Hayrapetyan A, Bolotov S, Gerasimov Yu, Malin B, Kosolapov D, Hovsepyan A, 2016a. Changes in autumn zooplankton on the pelagic zone of Lake Sevan (Armenia) during the increase in fish abundance. *Inland Water Biol.* 9:142-149.
- Krylov AV, Hayrapetyan AH, Nikogosyan AA, Bolotov SE,

- 2016b. [Zooplankton], p. 109-159. In: Krylov AV (ed.), [Lake Sevan. Ecological state during the period of water level change]. [Book in Russian]. Filigran Publishing House: Yaroslavl.
- Krylov A, Kosolapov D, Kosolapova N, Hovsepyan A, Gerasimov Yu, 2018. The plankton community of Sevan Lake (Armenia) after invasion of *Daphnia* (Ctenodaphnia) magna Straus, 1820. *Biol. Bull.* 45:505-511.
- Krylov A, Hayrapetyan A, Tsvetkov A, Gerasimov Yu, Malin I, Gabrielyan B, 2019a. Interannual changes in the quantitative parameters and structure of invertebrates in the littoral and pelagic zones of Lake Sevan (Armenia) with fluctuations in meteorological conditions and fish biomass. I. Summer zooplankton. *Inland Water Biol.* 12:298-305.
- Krylov A, Hayrapetyan A, Tsvetkov A, Gerasimov Yu, Malin B, Gabrielyan B, 2019b. Interannual changes in the quantitative parameters and structure of invertebrates in the littoral and pelagic zones of Lake Sevan (Armenia) with fluctuations in meteorological conditions and fish biomass. II. Autumn Zooplankton. *Inland Water Biol.* 12:409-417.
- Krylov A, Hayrapetyan A, Kosolapov D, Sakharova E, Kosolapova N, Sabitova R, et al., 2021a. Features of structural changes in the plankton community of an alpine lake with increasing fish density in summer and autumn. *Biol. Bull.* 48:1272-1283.
- Krylov A, Hayrapetyan A, Ovsepyan A, Sabitova R, Gabrielyan B, 2021b. Interannual changes in the spring zooplankton of the pelagic zone of Lake Sevan (Armenia) in the course of increasing fish biomass. *Inland Water Biol.* 14:113-116.
- Krztoń W, Kosiba J, 2020. Variations in zooplankton functional groups density in freshwater ecosystems exposed to cyanobacterial blooms. *Sci. Total Environ.* 730:139044.
- Mehner T, Benndorf J, Kasprzak P, Koschel R, 2002. Biomani- pulation of lake ecosystems: successful applications and expanding complexity in the underlying science. *Freshwater Biol.* 47:2453-2465.
- Meshkova TM, 1968. [The zooplankton of lakes, ponds, and reservoirs of Armenia]. [Book in Russian]. Yerevan: 108pp.
- Meshkova TM, 1975. [Patterns of zooplankton development in Lake Sevan]. [Book in Russian]. Yerevan: 275 pp.
- Ministry of Environment of the Republic of Armenia, 2020. Fourth National Communication on Climate Change. Available from: https://unfccc.int/sites/default/files/resource/NC4_Armenia_.pdf
- Mordukhay-Boltovskoy FD, 1954. [Materials on the average weight of aquatic invertebrates of Don River basin]. [Article in Russian]. In: [Problems of Hydrobiology of inland waters: Proceedings of problematic and thematic meeting]. Zoological Institute AS USSR Moscow 2:223-241.
- Oksanen J, Simpson G, Blanchet F, Kindt R, Legendre P, Minchin P, et al., 2022. `vegan`: Community Ecology Package. R package version 2.6-4. Available from: <https://CRAN.R-project.org/package=vegan>
- Porter K, 1973. Selective grazing and differential digestion of algae by zooplankton. *Nature* 244:179-180.
- R Core Team, 2022. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. Available from: <https://www.R-project.org/>
- Ramírez García P, Nandini S, Sarma SSS, Robles Valderrama E, Cuesta I, Hurtado MD, 2002. Seasonal variations of zooplankton abundance in the freshwater reservoir Valle de Bravo (Mexico). *Hydrobiologia* 467:99-108.
- Ripple WJ, Beschta RL, 2012. Trophic cascades in Yellowstone: the first 15 years after wolf reintroduction. *Biol. Conserv.* 145:205-213.
- Saint-Germain M, Buddle CM, Larrivée M, Mercado A, Motchula T, Reichert E, et al., 2007. Should biomass be considered more frequently as a currency in terrestrial arthropod community analyses? *J. Appl. Ecol.* 44: 330-339.
- Sakharova E, Krylov A, Sabitova R, Tsvetkov A, Gambaryan L, Mamyán A, et al., 2020. Horizontal and vertical distribution of phytoplankton in the alpine Lake Sevan (Armenia) during the summer cyanoprokaryota bloom. *Contemp. Probl. Ecol.* 13:60-70.
- Scharf W, 2008. The use of nutrient reduction and food-web management to improve water quality in the deep stratifying Wupper Reservoir, Germany. *Hydrobiologia* 603:105-115.
- Shapiro J, Wright DI, 1974. Lake restoration by biomanipulation. Round Lake, Minnesota, the first two years. *Freshwater Biol.* 14:371-83.
- Shen J, Qin G, Yu R, Zhao Y, Yang J, An S, et al, 2021. Urbanization has changed the distribution pattern of zooplankton species diversity and the structure of functional groups. *Ecol. Indic.* 120:106944.
- Shikhani M, Gevorgyan A, Gevorgyan G, Misakyan A, Azizyan L, Barfus K, et al., 2021. Simulating thermal dynamics of the largest lake in the Caucasus region: The mountain Lake Sevan. *J. Limnol.* 81:2024.
- Shurin JB, Arnott SE, Hillebrand H, Longmuir A, Pinel-Alloul B, Winder M, Yan ND, 2007. Diversity-stability relationship varies with latitude in zooplankton. *Ecol. Lett.* 10:127-134.
- Simonyan A, 1991. [Zooplankton of Lake Sevan]. [Book in Russian]. Yerevan: 298 pp.
- Sommer U, Stibor H, 2002. Copepoda - Cladocera - Tunicata: The role of three major mesozooplankton groups in pelagic food webs. *Ecol. Res.* 17:161-174.
- Sommer U, Sommer F, Santer B, Jamieson C, Boersma M, Becker C, Hansen T, 2001. Complementary impact of copepods and cladocerans on phytoplankton. *Ecol. Lett.* 4: 545-550.
- Sommer U, Stibor H, Katechakis A, Sommer F, Hansen T, 2002. Pelagic food web configurations at different levels of nutrient richness and their implications for the ratio fish production: primary production. *Hydrobiologia* 484: 11-20.
- Thakur RK, Jindal R, Singh UB, Ahluwalia AS, 2013. Plankton diversity and water quality assessment of three freshwater lakes of Mandi (Himachal Pradesh, India) with special reference to planktonic indicators. *Environ. Monit. Assess.* 185:8355-8373.
- Trew BT, Maclean IMD, 2021. Vulnerability of global biodiversity hotspots to climate change. *Global Ecol. Biogeogr.* 30:768-783.
- Wang S, Xie P, Geng H, 2010. The relative importance of physicochemical factors and crustacean zooplankton as determinants of rotifer density and species distribution in lakes adjacent to the Yangtze River, China. *Limnologica* 40:1-7.

- Weise H, Auge H, Baessler C, Bärlund I, Bennett EM, Berger U, et al., 2020. Resilience trinity: safeguarding ecosystem functioning and services across three different time horizons and decision contexts. *Oikos* 129:445-456.
- Xiong W, Huang X, Chen Y, Fu R, Du X, Chen X, Zhan A, 2020. Zooplankton biodiversity monitoring in polluted freshwater ecosystems: A technical review. *Environ. Sci. Ecotechnol.* 1:100008.
- Yang J, Zhang X, Xie Y, Song C, Sun J, Zhang Y, 2017. Ecogenomics of zooplankton community reveals ecological threshold of ammonia nitrogen. *Environ. Sci. Technol.* 51:3057-3064.
- Zhao Q, Van den Brink PJ, Xu C, Wang S, Clark AT, Karakoç C, et al., 2023. Relationships of temperature and biodiversity with stability of natural aquatic food webs. *Nat. Commun.* 14:3507.

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Online supplementary material:

Tab. S1. Station list of the samplings in Lake Sevan.

Fig. S1. Heatmap of species abundance.

Fig. S2. Spatially averaged values of Secchi depth for all sampling times.