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Inter-Period and Inter-Season Variability of Zooplankton of a Mountain Lake With an Emphasis on Under-Ice Communities

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ABSTRACT

1. Only recently the under-ice period is recognised as a time of plankton activity. However, most studies on under-ice zooplankton focus on low-land lakes over relatively short temporal scales; long-term under-ice zooplankton dynamics in mountain lakes remain largely unknown.
2. We compared the under-ice zooplankton community (one sampling per year; $n=11$) to that of the ice-free seasons (monthly samplings) of mountain Lake Tovel. The considered timeframe (2001–2023) covered the period of an ecosystem change linked to intensified autumn mixing. To avoid confounding the effect of this ecosystem change with a seasonal effect, we first investigated the general patterns of abundance and biomass of rotifers and crustaceans for the years considered to determine the periods conforming to the ecosystem change (period 1: weak mixing; period 2: strong mixing).
3. Rotifers and crustaceans were sampled by a net (50 µm mesh size) from 35 m depth to the surface. Rotifer abundance and biomass were higher in period 1 (the years 2001, 2003, 2011, 2014 and 2016) than in period 2 (the years 2017, 2018, 2019, 2021, 2022 and 2023) conforming to the ecosystem change. We applied a taxonomic and functional perspective on zooplankton diversity as complementary approaches to investigate season and period differences.
4. With two-way ANOVA (period and season effect) considering temporal dependence and heterogeneity of data, taxonomic indices (abundance, biomass, species richness) and functional indices (effective number of functional groups, effective number of common functional groups, functional richness) of rotifers showed higher mean values during period 1 than period 2, while taxonomic indices of crustaceans (species richness, effective number of common species, effective number of dominant species) showed the opposite pattern. Thus, the ecosystem change linked to altered mixing patterns favoured crustaceans over rotifers. NMDS ordinations with taxonomic (species identity) and functional diversity (functional entities and community weighted mean trait values) of rotifers showed a splitting between periods but generally not between seasons. The prevailing absence of seasonal differences was linked to the lake's cold-water temperature year-round. The similarity of rotifer functional feeding preferences of the last 2 years of period 2 (2022 and 2023) to that of period 1 indicated that mixing intensity was declining again, a result not shown by taxonomy. From the last autumn to under-ice sampling, *Filinia terminalis*, *Kellicottia longispina*, *Keratella hiemalis*, *Polyarthra dolichoptera*, *Synchaeta kitina*, *S. lakowitziana*, *Bosmina longirostris* and nauplii

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and adults of *Cyclops strenuus* increased in abundance that we attributed to reproduction under ice. Under-ice indicator taxa were only found during period 2, namely *F. terminalis* and *S. lakowitziana*.

5. Our study showed that in mountain Lake Tovel the under-ice period is characterised by a similar high zooplankton diversity as during the ice-free period. Studies like ours, covering both taxonomic and functional diversity, are more needed to understand under-ice zooplankton communities.

1 | Introduction

Winter at high latitudes leads to an ice cover over freshwater lakes, and this is an important but poorly understood period for lake ecosystems. Historically, winter has been considered a period of stasis (Hampton et al. 2017) even though the successful growth of under-ice zooplankton, mainly *Diaptomus graciloides* and *Daphnia longispina*, has been observed in subarctic lakes (Rodhe 1953). Cross-seasonal effects are known as summer and autumn zooplankton influence winter community composition (six shallow polymictic lakes; Dokulil et al. 2014), and winter conditions influence plankton dynamics in the following seasons (101 lakes across wide gradients of latitudes, production and trophic status; Hampton et al. 2017). The interest in winter limnology and under-ice zooplankton has recently increased because lake ice formation in Northern Hemisphere lakes is delayed by 11 days, ice melts earlier by 7 days, and the period of ice cover is shorter by 17 days over the past 150 years (Sharma et al. 2021). Despite the recognition of these important changes, the influence of changing winter conditions on lake biota is still not fully understood (Hampton et al. 2017; Cotner et al. 2022).

Zooplankton, composed of ciliates, rotifers, cladocerans and copepods, are a key component in lake food webs as taxa transfer energy from lower to higher trophic levels. All these zooplanktic groups exhibit different life history strategies, food requirements and predation resistance (Brooks and Dodson 1965; Walz 1995; Saksgård and Hesthagen 2004; Brandl 2005), and thus, different environmental factors may determine their seasonal patterns, especially under ice. Evidence of under-ice zooplankton is relatively few and site-specific, hampering generalisations. Ciliates have a high biomass under ice when crustaceans show very low abundances (Masurian Lakeland; Kalinowska and Karpowicz 2020). *Cyclops* spp. (oligo-mesotrophic Lake Onego; Perga et al. 2021) and *D. mendotae* (eutrophic Shelburne Pond; Chiapella et al. 2021) migrate under ice. *Bosmina* spp. and *Daphnia* spp. show a higher abundance under snow-covered ice than under clear ice (eutrophic East 81 Slough pond; DeBates et al. 2003). In a meta-analysis, *D. hyalina* and *D. galeata* have a high probability of actively overwintering under ice in a free-swimming stage in deep lakes (de Senerpont Domis et al. 2007). Actively overwintering *Daphnia* species have a higher fatty acid concentration than those that overwinter inactively by entering diapause (comparison of six lakes; Mariash et al. 2017). It has been experimentally shown that later ice-in promotes zooplankton overwintering, which can diminish spring food availability for other consumers, potentially disrupting trophic linkages and energy flow pathways over the subsequent open-water season (mesotrophic Lac Hertel; Hébert et al. 2021). Different rotifer species dominate under ice (Dokulil and Herzig 2009: Neusiedler See: *Rhinoglena fertöensis*; Virro et al. 2009: Lake Vortsjärv: *Polyarthra dolichoptera*; Glazunova and Polunina 2013: lagoons in the Baltic Sea: *Keratella quadrata*, *Brachionus angularis*; Kalinowska and Karpowicz 2020: Masurian Lakeland: *Notholca squamula*; Kalinowska et al. 2021: dystrophic lakes in the Wigry National Park: *Keratella hiemalis*), and the rotifer under-ice community composition changes through time (Kalinowska and Grabowska 2016; Kalinowska and Karpowicz 2020). Considering seasonal differences, rotifers and crustaceans show a lower abundance and biomass under ice than during the ice-free period (Glazunova and Polunina 2013; Jensen 2019; Kalinowska and Karpowicz 2020; Ventelä et al. 1998) or show similar or higher abundance (Kalinowska et al. 2019). Thus, there is evidence that zooplankton can overwinter actively under ice.

Survival and reproduction of zooplankton depends on food quantity and quality (Peltomaa et al. 2017). The amount of fatty acids, especially unsaturated ones, determines food quality (Grosbois et al. 2017; Wacker and Weithoff 2009) with polyunsaturated fatty acids (PUFAs) deficits impairing zooplankton growth and survival (Taipale et al. 2012). For example, the calanoids *Eudiaptomus graciloides* (subarctic, oligotrophic lake Takvatn; Kers et al. 2024) and *Leptodiaptomus minutus* (mesotrophic Lake Simoncouche; Schneider et al. 2017) use fatty acids acquired before winter for egg production under ice. PUFAs in zooplankton are of dietary origin from phytoplankton (Brett and Müller-Navarra 1997), both from current supplies as well as from energy stored as lipid reserves (Perga et al. 2021). Under-ice growth and reproduction of phytoplankton depend on under-ice light availability that is higher with transparent (a.k.a. black ice; Weyhenmeyer et al. 2022) and less thick ice (Bertilsson et al. 2013; Bolsenga and Vanderploeg 1992). With thick ice, mobile phytoplankton taxa are more abundant, while non-mobile taxa are more abundant with thin ice (Özkundakci et al. 2016). The ability of phytoplankton to use organic carbon sources (mixotrophy) when photosynthesis is reduced or halted under ice is also important (Søgaard et al. 2021). These changes and adaptations in under-ice phytoplankton driven by light characteristics finally influence zooplankton abundance (Bramm et al. 2009).

Plankton communities are made up of coexisting species that fulfil different functions in an ecosystem (Kneitel and Chase 2004). By using functional traits that are any morphological, physiological, or phenological characteristics that define a species' niche and competitive ability (Geber and Griffen 2003; Violle et al. 2007), we can identify general rules for community assembly and link community ecology to ecosystem ecology (McGill et al. 2006). While the application of functional ecology in zooplankton studies is gaining interest in recent years (crustaceans: Hébert et al. 2016; copepods: Benedetti et al. 2022; rotifers: Obertegger and Wallace 2023), most studies on under-ice zooplankton are species-specific, reporting under which circumstances species dominate. However, Virro et al. (2009) and Shchapov et al. (2021) by using functional feeding traits, show that rotifer and crustacean predators, respectively, prevail under ice.

Most studies on under-ice zooplankton consider low-land lakes over relatively short temporal scales (days: DeBates et al. 2003; Perga et al. 2021; 1–2 years: Glazunova and Polunina 2013; Jensen 2019; Kalinowska and Karpowicz 2020; Kalinowska et al. 2019, 2021; Ventelä et al. 1998) because of the difficulty of under-ice sampling (Block et al. 2019). This temporal restriction limits our understanding of the temporal variability of zooplankton (Dokulil and Herzig 2009; Jensen 2019). Only a few studies cover several years (4 years: Hrycik et al. 2021; 10 years: Blank et al. 2009; 18 years: Virro et al. 2009; 27 years: Dokulil and Herzig 2009) of sampling of low-land and/or eutrophic lakes. Furthermore, little is known about under-ice zooplankton of mountain lakes (Jensen 2019), and this constitutes a major knowledge gap considering that mountain lakes are found globally and are important sentinels of global change (Moser et al. 2019).

Here, we assessed the under-ice zooplankton community of mountain Lake Tovel over a time span of 23 years and compared the under-ice community to that of the ice-free seasons. Lake Tovel is traditionally considered a cold-water lake (Cellamare et al. 2016), and the dinoflagellates of Lake Tovel show a variety of highly unsaturated lipids (galactolipids, betaine lipids, phospholipids, triacylglycerols) and mycosporine-like amino acids important for cold adaptation (Flaim et al. 2010, 2012, 2014). In fact, dinoflagellates generally dominate under ice in Lake Tovel, and chlorophyll-*a* (chl-*a*) as well as phytoplankton richness are similar between summer and under ice (Obertegger et al. 2022). While the upper lake layer shows higher water temperature during summer, Lake Tovel is impacted by harmful ultraviolet radiation leading to the persistence of only a few zooplankton species in the upper layer, and most taxa remain in colder lower layers (Obertegger et al. 2008). Thus, we suggest that most organisms thriving in this lake are adapted to low water temperatures. Furthermore, ice formation in Lake Tovel is delayed by ca. 5.1 days per decade (Flaim et al. 2020), and the lake shifted from a period of low autumn mixing intensity to a period of high mixing during the years 2010–2014 leading to an oxygenated hypolimnion (Flaim et al. 2020). Furthermore, reduced spring snowmelt results in whole-lake warming and increased stability of the water column in Lake Tovel (Flaim et al. 2019). We suggest that all these changes also influence zooplankton temporal patterns. We applied a taxonomic and functional perspective on zooplankton diversity as complementary approaches to investigate season differences and differences between periods of different mixing intensity (i.e., high vs. low). We hypothesised that: (i) zooplankton responded to the ecosystem change occurring during the years 2010–2014 and (ii) differences in zooplankton metrics (taxonomic and functional diversity) between the ice-free seasons and the under-ice period are minimal because Lake Tovel remains a cold-water habitat year-round.

2 | Materials and Methods

2.1 | Study Site

Lake Tovel (46.26137 N, 10.94934 E; 1177 m above sea level; area: 0.4 km^2; maximum depth: 39 m) is an Italian long-term ecological research site (LTER_EU_IT_090) in the Brenta Dolomites and belongs to international networks (LTER-Europe and ILTER). Lake Tovel is usually frozen from late December to mid-April with a mean ice thickness of 35 cm (range: 17–65 cm; $n = 15$; 2002–2024). The lake is oligotrophic (mean annual values for the whole water column: total dissolved phosphorus $< 10\,\mu g\,L^{-1}$, dissolved organic carbon $< 1\,mg\,L^{-1}$, conductivity $180\,\mu S\,cm^{-1}$; water transparency > 10 m; depth layer 0–20 m: chl-*a* $< 3\,\mu g\,L^{-1}$; Cellamare et al. 2016).

2.2 | Sampling

Sampling was done around midday over the deepest part of the lake. Under-ice sampling (January, February or March) was only once per year, and sampling during the ice-free seasons (spring: April to June; summer: July to September; autumn: October to December) was monthly. When referring to years, under-ice data were merged with seasons of the preceding year (i.e., under-ice sampling of the year 2002 was related to the ice-free samplings of the year 2001) like in Obertegger et al. (2022), because we accordingly reasoned that seasons of the preceding year are the starting conditions for under-ice conditions of the following year. We considered the years 2001, 2003, 2011, 2014 and 2016–2023 when under-ice data of the following year were available (under ice 2002, 2004, 2012, 2015 and 2017–2024), covering thus a time span of 23 years. When referring to an under-ice sampling, we reported the considered year, and to get the calendar year of the under-ice sampling, one must add 1 year.

Sampling under-ice occurred at different time points and temporal distances from the last autumnal sampling (Table 1) because of sampling constraints related to site access and safety reasons, an issue typical to under-ice sampling (Block et al. 2019). During all under-ice samplings, except for the years 2001 (calendar under-ice year 2002) and 2016 (calendar under-ice year 2017), a snow cover was present (Table 1) that can greatly reduce under-ice light (Leppäranta 2010).

Vertical profiles of water temperature and dissolved oxygen (DO % saturation) were taken with a multiparametric probe (Hydrolab Surveyor for 2001 and 2003 and Idronaut Ocean 316 from 2011 onwards). Zooplankton samples were taken by vertical tows (mesh size = 50 μm) from a depth of 35 m to the surface. Water samples for chl-*a* were taken with a 20-m long tube (weighted at the bottom), and chl-*a* was extracted (Whatman GF/C and GF/F filters) from 1 L with 90% acetone and determined spectroscopically according to the trichromatic method (Rice et al. 2017).

2.3 | Species Identification

Zooplankton composition and biomass were determined as described in Obertegger et al. (2007). Bdelloidea were only occasionally found and were not identified beyond group level because proper identification requires live specimens. We deliberately attributed bdelloid specimens to *Rotaria* because the only planktic or semi-planktic Bdelloidea belong to the genera *Rotaria* and *Philodinavus* and these genera only differ by their corona type (Obertegger and Wallace 2023).

TABLE 1 | Information on the temporal distance in days from sampling to sampling and ice in, snow presence and zooplankton abundance parameters.

	2001	2003	2011	2014	2016	2017	2018	2019	2021	2022	2023
Days from last autumn sampling to ice-in	28	33	8	24	12	2	3	38	4	34	84
Days from ice-in to under-ice sampling	104	90	84	57	35	56	41	78	67	63	40
Total days	132	123	92	81	47	58	44	116	71	97	124
Snow on ice	No	Yes	Yes	Yes	No	Yes	Yes	Yes	Yes	Yes	Yes
Asplanchna priodonta				1.9 (0.008)							
Brachionus angularis				2.0 (0.008)				4.9 (0.01)			
Filinia terminalis	2.4 (0.006)			**6.2** (0.02)						**6.2** (0.02)	1.9 (0.005)
Kellicottia longispina							**7.4** (0.05)	1.8 (0.005)		**12.6** (0.03)	**24.0** (0.03)
Keratella cochlearis					1.2 (0.003)			1.1 (0.0004)	1.3 (0.003)	4.3 (0.02)	4.5 (0.01)
K. hiemalis							2.3 (0.02)			3.3 (0.01)	**22.2** (0.03)
Polyarthra dolichoptera		2.1 (0.006)		1.5 (0.005)		**6.0** (0.03)	**6.0** (0.04)			3.0 (0.01)	
Synchaeta kitina		**7.1** (0.02)		4.1 (0.02)	2.3 (0.02)		**6.9** (0.04)			**10.3** (0.02)	
S. lakowitziana			**15.7** (0.03)	**292** (0.07)	4.3 (0.03)			**6.2** (0.02)	**8.1** (0.03)		
Bosmina longirostris				1.3 (0.003)							
Daphnia gr. *longispina*					1.3 (0.006)						
Nauplii		**13.6** (0.02)			4.1 (0.03)	**5.1** (0.03)	1.2 (0.005)	**25.3** (0.03)		1.8 (0.008)	
Cyclops strenuus							**5.5** (0.04)				

Note: As zooplankton abundance parameters, we report the *x*-fold increase from the last autumnal sampling to the under-ice sampling and growth rates (in parentheses; rotifers day^{-1}). Only increasing taxa are reported; in bold, the taxa showing a more than five times population increase.

The lower limit of species abundance was in the range of 15 individuals (ind) m^{-3}, thus very low. Consequently, we did not transform ind m^{-3} to ind L^{-1} (division by 1000) to avoid reporting abundance values less than 1 ind L^{-1}.

2.4 | Determination of Ecosystem Change

Lake Tovel shifted from meromixis to dimixis because of delayed ice-in that increased autumn mixing, leading to deepwater oxygenation (Flaim et al. 2020). To avoid confounding the effect of this ecosystem change with a seasonal effect, we first investigated the general patterns of abundance and biomass of rotifers and crustaceans for the years considered to determine the periods conforming to the ecosystem change (period 1: low mixing intensity; period 2: high mixing intensity).

2.5 | Population Growth Rate

We calculated the population growth rate using the exponential formula: $r = (\ln N_t - \ln N_0)/t$, where N_0 is the population abundance of the last autumn sampling and N_t is the abundance at the under-ice sampling after time t in days.

2.6 | Functional Diversity

We applied the functional approach only to rotifers because: (1) traits available for crustaceans (Barnett et al. 2007) do only partially conform to those of rotifers (Obertegger and Wallace 2023) and (2) the crustacean community of Lake Tovel showed a low diversity (only three truly planktic taxa: *Bosmina longirostris*, *D. longispina*, *Cyclops strenuus*). Other occasionally found crustacean taxa were two littoral taxa (*Alona* sp, *Chydorus* sp; found 13 and 4 times, respectively) and one of order Harpacticoida (found once) in the considered samples (total number of samples is 103).

Rotifer traits used (trophi type, corona type, lorica type, defence mechanism, biomass, feeding category) relate to morphological characteristics and rotifer diet (Obertegger and Wallace 2023). We used these traits (i) to calculate multidimensional, space-based indices of alpha functional diversity (functional richness, functional dispersion, functional divergence, functional evenness, functional originality, functional mean pairwise distance, functional originality and functional mean nearest neighbour distance; library mFD; Magneville et al. 2022) to investigate period and season differences; (ii) to calculate weighted mean trait values (CWMs; library BAT; Cardoso et al. 2024) of all traits to use in multivariate ordination as a complementary approach to using species identity; (iii) to cluster rotifers into functional entities to use in multivariate ordination as a second complementary approach to using species identity. Functional entities share the same trait combinations (details in Magneville et al. 2022), and biomass was transformed into a category (smaller or larger than the median biomass of rotifer taxa in Lake Tovel) because otherwise the continuous parameter biomass would have prevented the formation of entities. Of the 23 rotifer species, 15 functional entities were found (Table S1). Functional entities corresponded mostly to genera except for one functional entity where *Keratella*, *Brachionus* and *Kellicottia* were grouped. Furthermore, we specifically investigated seasonal differences in feeding categories sensu Gilbert (Gilbert 2022; i.e., microphagous rotifers, polyphagous rotifers, macrophagous algivores, macrophagous algivores/predators) that can reflect altered environmental conditions and community composition. The abundance of rotifers belonging to the same feeding category was summed; we reported feeding categories in percent of rotifer total abundance per sample.

2.7 | Alpha Diversity

We calculated taxonomic alpha diversity as Hill numbers according to Chao et al. (2024) to investigate the importance of infrequent, abundant and dominant species. Specifically, the Hill number with $q = 0$ is species richness, which is sensitive to infrequent species. The two Hill numbers with $q > 0$ consider abundance. The Hill number with $q = 1$ is Shannon diversity, which can be interpreted as the effective number of common or abundant species. The Hill number with $q = 2$ is Simpson diversity, which can be interpreted as the effective number of dominant or highly abundant species.

Similarly, we calculated functional alpha diversity applied to distances between species following the framework of Chao et al. (2019) using Hill numbers. Functional Hill numbers refer to the number of equally distinct functional groups (Chao et al. 2019) and can thus be directly compared to taxonomic Hill numbers. The terminology 'equally distinct' means that the pairwise distance between any two different species pairs is at least the distance tau, set here to the mean functional distance over all species. Trophi type, corona type, lorica type, defence mechanism, biomass and feeding categories of rotifers were the functional traits to assess functional distance.

2.8 | Beta-Diversity

We calculated taxonomic (Baselga 2010) and functional beta-diversity (Villéger et al. 2013; functional traits: trophi type, corona type, lorica type, defence, biomass and feeding categories of rotifers) based on incidence using library mFD (Magneville et al. 2022; Sørensen index of total dissimilarity). When the community dissimilarity between periods is different from that of within periods, then this indicates that periods are different; and the discriminating period is sensible (Figure S1). Contrarily, when the community dissimilarity between periods is similar to within a period, then this indicates that the discriminating period does not make sense.

Beta-diversity was partitioned into the two antithetic processes, nestedness (i.e., richness difference) and turnover (i.e., species replacement) sensu Baselga (2010) to investigate the processes driving community assembly using library betapart (Baselga et al. 2023). We determined how often a process (nestedness or turnover) dominated (> 50% portion of total community dissimilarity) in community comparisons at different levels of temporal resolution and finally reported in percent the dominance of each process. Dissimilarity was zero in few instances ($n=16$ of 1399 comparisons), and these zero dissimilarity community comparisons were not considered to calculate the dominance of processes. The different levels of temporal resolutions were (i) comparisons within periods specific for seasons, (ii) comparisons between consecutive seasons specific for periods and (iii) comparisons specific for seasons across periods (Figure S2).

For alpha and beta-diversity functional indices, the inclusion of abundance should convey the aspect of fitness and survival.

2.9 | Statistical Analyses

We used two-way ANOVA (season and period effect) to test for significant differences in abundance, biomass, alpha-diversity, beta-diversity and environmental parameters relevant to zooplankton (chl-*a*, mean of DO % and temperature over the whole water column). In two-way ANOVA, we checked for homogeneity of residuals (boxplots) and independence of residuals (autocorrelation function). In case of violation, we used generalised linear modelling allowing for larger spread and temporal dependence of residuals (library nlme; Pinheiro et al. 2023 as shown in Zuur et al. 2009). We log-transformed species richness and used library emmeans (Lenth 2024) to perform post hoc testing with Tukey correction. We further calculated Cohen's d as an effect size metric that indicates in standard deviations how far apart two group means are (d between 0.2 and 0.5 indicates a small effect, between 0.5 and 0.8 a medium effect, and >0.8 a large effect). We generally neglected small effects even though statistically significant.

We performed an indicator species analysis with package indicspecies (Cáceres and Legendre 2009) to find taxa specific for seasons within periods (e.g., spring of period 1). The indicator value index is the product of two conditional probabilities, called 'A' and 'B' (Dufrene and Legendre 1997; Cáceres and Legendre 2009): 'A' (i.e., *specificity* or *positive predictive value* of the indicator species) is the sample estimate of the probability that the surveyed community belongs to the target community given the fact that the taxon has been found. 'B' (i.e., *fidelity* or *sensitivity* of the species as indicator) is the sample estimate of the probability of finding the species in communities belonging to the specific group. We only considered taxa with a high (>0.75) A or B value.

We performed non-metric multidimensional scaling (NMDS) with abundance data at different resolution levels: (i) taxonomy (i.e., species identity), (ii) functional diversity (i.e., functional entities and CWMs of all traits). We reported stress as a goodness of fit statistic and performed Procrustes analysis to determine the similarity between ordinations using the library vegan (Oksanen et al. 2022). In environmental fitting of NMDS, we used environmental parameters relevant for zooplankton.

In all plots, we used colourblind friendly colours (library viridis; Garnier et al. 2024; https://medialab.github.io/iwanthue/).

3 | Results

3.1 | Period Effect on Zooplankton Abundance and Biomass

For the years considered, rotifer abundance varied between 237 (spring 2021) and 341,189 (summer 2001) ind m^{-3}. While in the year 2016 rotifer abundance generally was higher than 30,000 ind m^{-3} in spring and summer, after 2016 abundance dropped below 30,000 ind m^{-3} with only a few samplings showing a higher abundance (two of nine monthly samples in 2017, one of eight monthly samples in 2021; Figure 1). Crustacean abundance varied between 1 (spring 2001) and 5449 (summer 2003) ind m^{-3} and did not show a similar change as rotifers with the year 2016.

Rotifer biomass varied between 1.4 (spring 2021) and 11,771 (summer 2003) $\mu g\,m^{-3}$, and the crustacean biomass varied between 6.6 (spring 2001) and 24,697 (summer 2003) $\mu g\,m^{-3}$. While rotifer biomass was often higher than that of crustaceans until 2016, it was consistently lower than crustacean biomass after 2016 (Figure 1).

Based on the marked changes in rotifer abundance and biomass, we considered in addition to a seasonal effect also a period effect (i.e., period 1: the years 2001, 2003, 2011, 2014, 2016 vs. period 2: the years 2017, 2018, 2019, 2021, 2022, 2023) in the following considerations on zooplankton diversity and environmental parameters.

With two-way ANOVA (period and season effect), rotifer abundance and biomass were higher during period 1 than period 2 ($p<0.001$; Cohen's $d=1.15$; large effect) but did not show a season effect. Crustacean abundance and biomass neither showed a period nor a season effect.

Highest under-ice abundance of rotifers was found in the years 2001 (107,901 ind m^{-3}) and 2014 (93,427 ind m^{-3}) of period 1, where the ice cover consisted entirely of black, transparent ice and was snow covered, respectively. Other under-ice samplings with a snow cover in the years 2003 (period 1; 59,710 ind m^{-3}), 2017 (period 2; 14,903 ind m^{-3}) and 2022 (period 2; 14,424 ind m^{-3}) had similar high abundance, while other years of period 1 (2011, 2014, 2016) and period 2 (2018, 2019, 2021, 2023) had an under-ice abundance smaller than 10,000 ind m^{-3} (Figure 1A). Remarkably, the under-ice rotifer abundance in 2014 was the highest compared to other samplings of the same year (Figure 1A). Highest under-ice biomass of rotifers was found in the years of period 1 (2001: 3001 $\mu g\,m^{-3}$; 2014: 2414 $\mu g\,m^{-3}$; 2003: 1087 $\mu g\,m^{-3}$; Figure 1B) like abundance. Highest under-ice crustacean abundance (2022: 4295 ind m^{-3}; 2016: 3049 ind m^{-3}; Figure 1A) and biomass (2022: 9329 $\mu g\,m^{-3}$; 2016: 6659 $\mu g\,m^{-3}$; Figure 1B) were all found in years with and without a snow cover (Table 1).

3.2 | Alpha Diversity

The rotifer community was composed of 23 species of 15 genera and 15 species of them occurred under ice. The species *Filinia terminalis*, *Synchaeta lakowitzina*, *S. kitina*, *Keratella cochlearis* and *Kellicottia longispina* attained the highest under-ice abundance or were among the three species with the highest

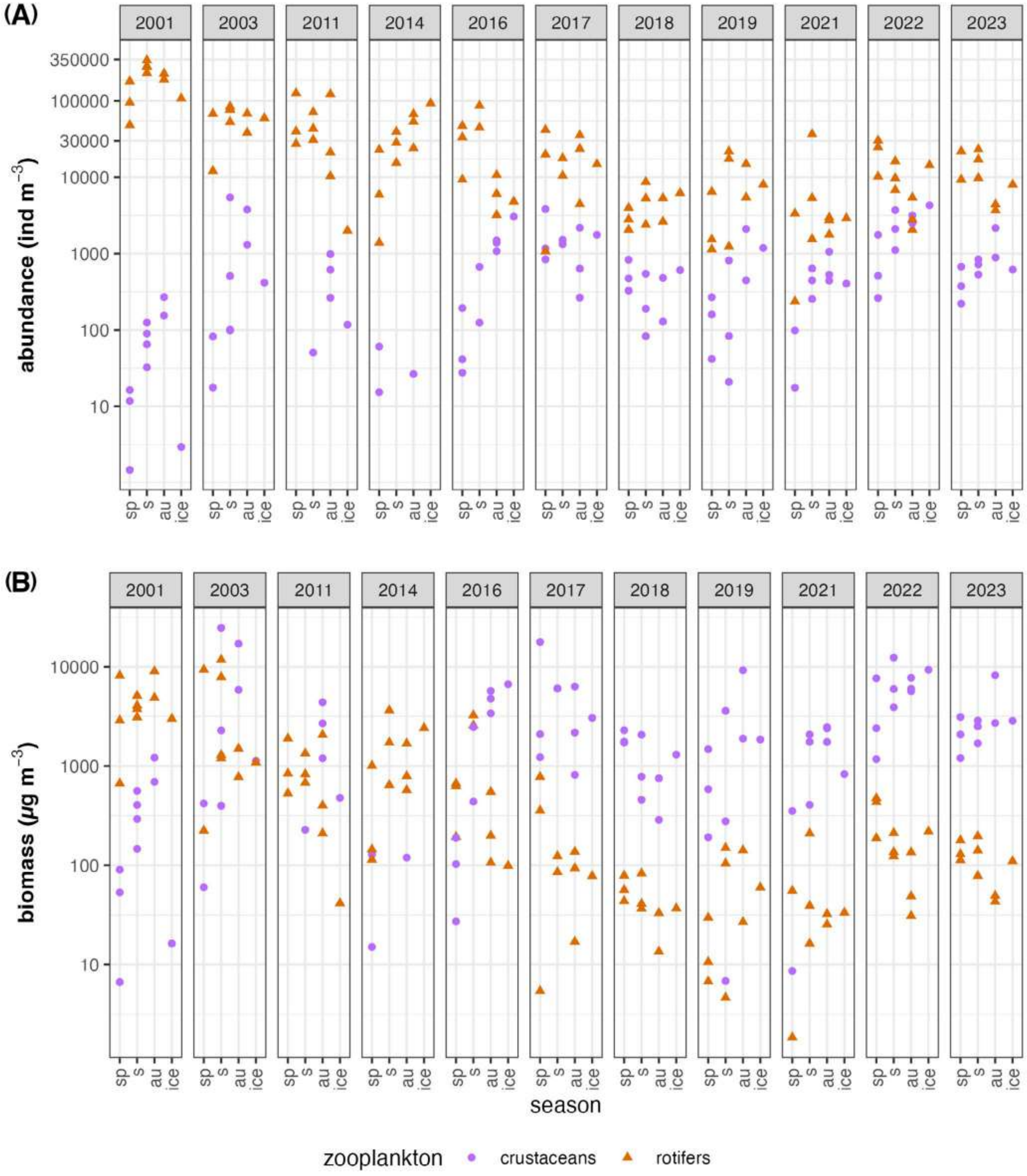

FIGURE 1 | Abundance (A) and biomass (B) of crustaceans and rotifers split by seasons (spring—sp; summer—s; autumn—au; under ice—ice) of the considered years; *y*-scales are logarithmic.

under-ice abundance (Figure 2). The species *K. hiemalis* and *P. dolichoptera* never dominated but also were among the first three species with the highest under-ice abundance.

The crustacean communities consisted of infrequent taxa (*Alona* sp, *Chydorus* sp, Harpactocoida) and taxa that were almost always found (*B. longirostris*, *D.* gr. *longispina*, *C. strenuus*). Copepods were always present under ice, either as nauplii or as adults except for under ice 2014. Cladocerans were also present under ice ($n = 7$) except for 2017, 2018, 2022 and 2023.

Most rotifer and crustacean taxa attained similar high abundance under ice than during other seasons (17 taxa; Figure 2). Of them, nine rotifer and three crustacean taxa showed an increase from the last autumn sampling to the under-ice sampling (Table 1). Among rotifers, *F. terminalis*, *K. longispina*,

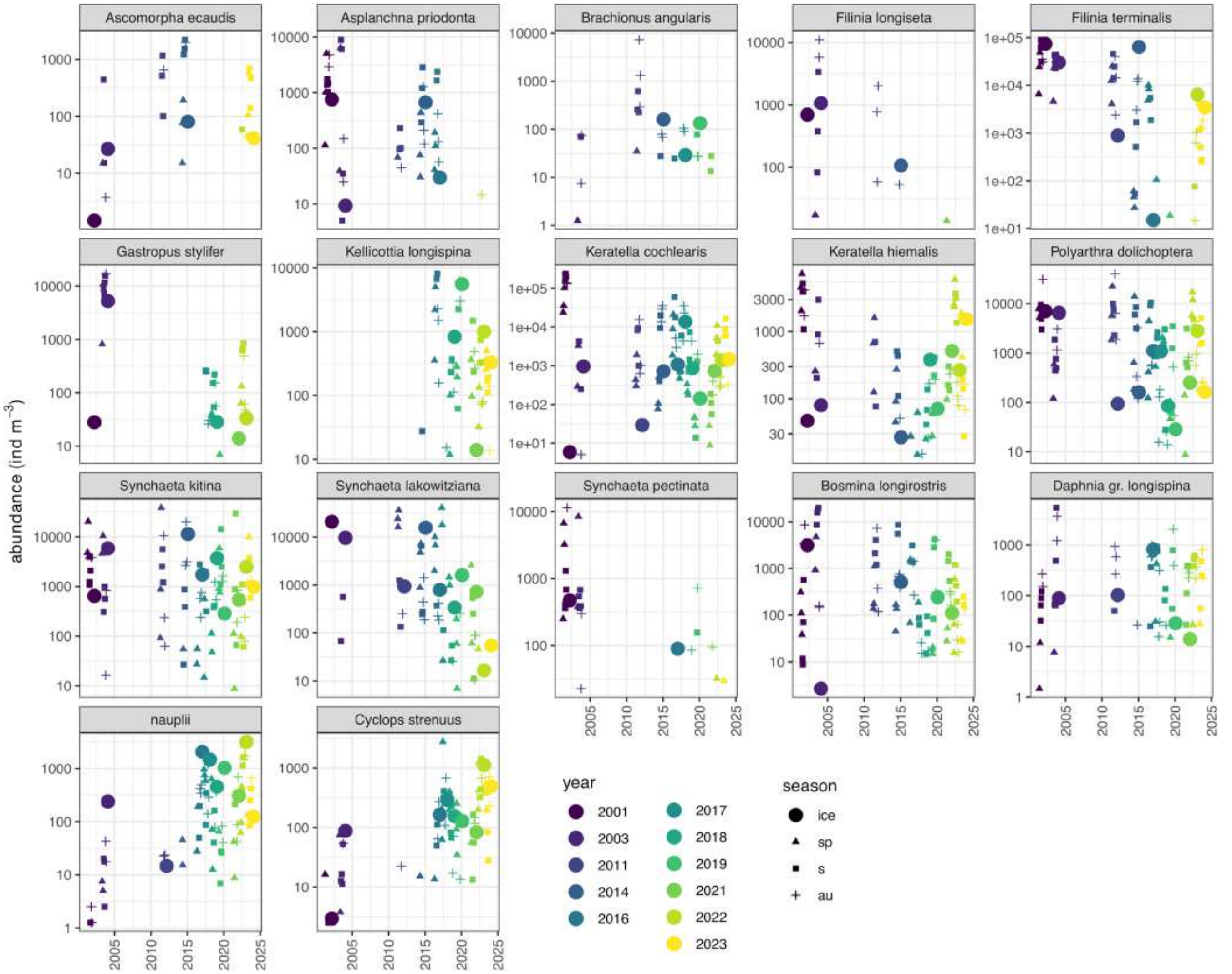

FIGURE 2 | Abundance (logarithmic scale) of taxa occurring under ice for the years considered. The symbol for under ice is larger for easier comparison to other seasons. The extremely infrequent taxa *S. tremula*/*oblonga* and Bdelloidea (only four times found) are not shown despite occurring under ice.

K. hiemalis, *P. dolichoptera*, *S. kitina* and *S. lakowitziana* showed a more than five times increase, while among crustaceans, nauplii and adults of *C. strenuus* showed such a marked increase (Table 1). Especially, *S. lakowitziana* stood out with its more than 250 times increase under ice in the year 2015. Furthermore, different taxa increased their abundance from the last autumnal sampling to the under-ice sampling. Specifically, the year 2001 (only black ice) and the years 2011, 2017 and 2021 (snow on ice) only one or two taxa with increasing abundance. Adults of *C. strenuus* showed a marked abundance increase only in 2018 when also *P. dolichoptera*, *S. kitina* and *K. longispina* showed a more than 5 times increase (Table 1).

From the last autumn to under-ice sampling, rotifer growth rates were low, varying between 0.0004 rotifers days^{-1} for a population that just kept its abundance to 0.07 rotifers days^{-1} for a population that showed an over 200-fold increase (Table 1).

Rotifers feeding on large algae (macrophagous algivores sensu Gilbert 2022) were present during all seasons and periods (Figure 3). In all seasons, the % abundance of microphagous rotifers sensu Gilbert (2022) was high from 2001 to 2014; then this functional feeding guild was almost absent from 2016 to 2021, and attained high values again in 2022 and 2023, especially during autumn and under ice (Figure 3).

3.3 | Taxonomic Hill Numbers

Rotifer species richness was higher during period 1 than period 2 (Table 2; Figure 4) with no seasonal differences. The effective number of common rotifer species (Shannon diversity) and the effective number of dominant rotifer species (inverse Simpson) did not show any season or period effect (two-way ANOVA; $p > 0.05$).

Crustacean species richness, effective number of common species (Shannon diversity), and effective number of dominant species (inverse Simpson) were higher during period 2 than period 1 for all seasons, except for under ice (Table 2; Figure 4). Seasonal differences were mainly found for period 2 (Table 2; Figure 4)

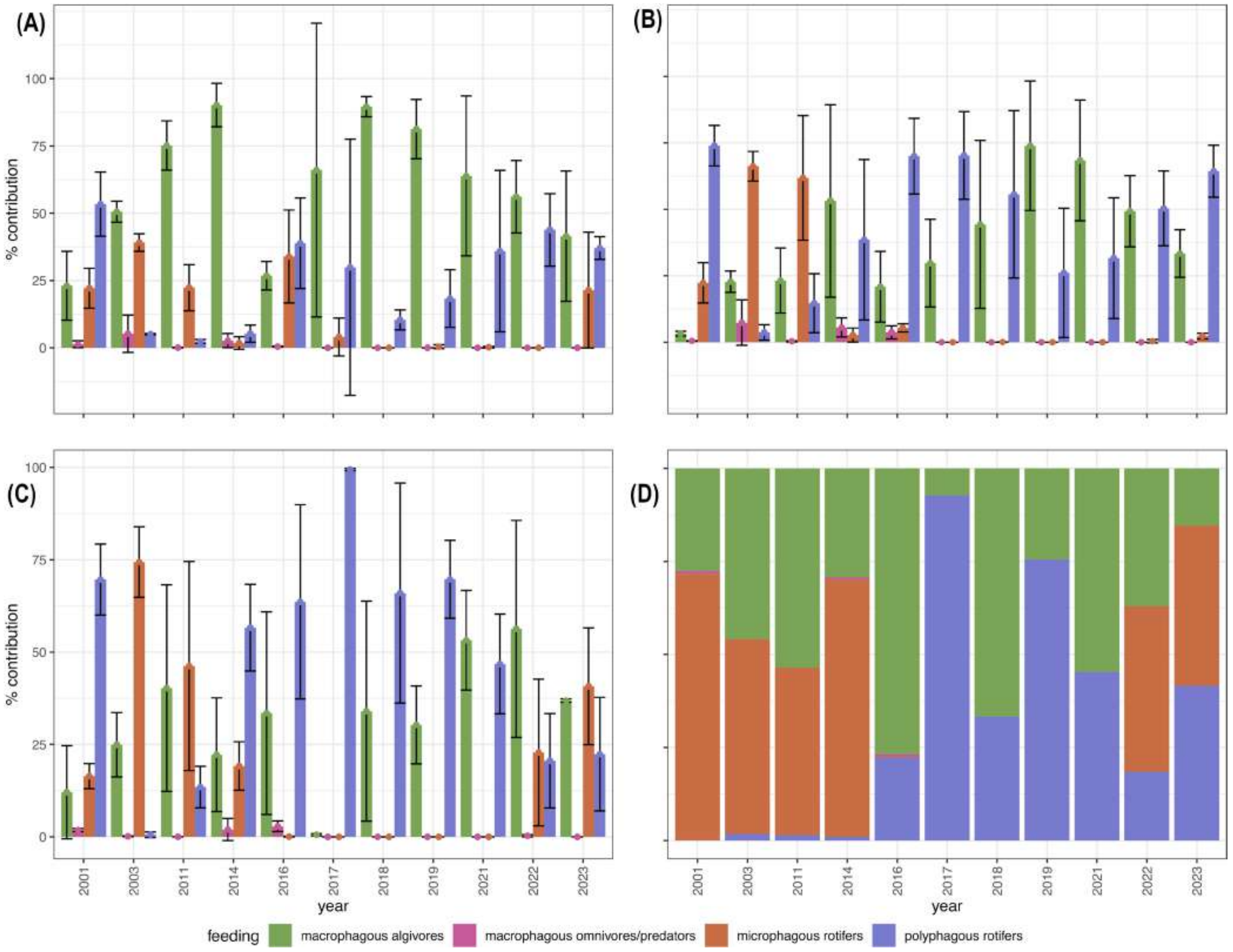

FIGURE 3 | Mean values of percent contribution of feeding categories of rotifers sensu Gilbert (2022) to rotifer total abundance for (A) spring, (B) summer, (C) autumn and (D) under ice. Error bars of one standard deviation are only shown for spring to autumn that have more than one sampling.

with only the effective number of dominant species having lower values under ice than during autumn.

3.4 | Functional Hill Numbers of Rotifers

Functional Hill numbers were higher for period 1 than period 2 for the effective number of equally distinct functional groups ($p < 0.001$; Cohen's $d = 3.21$; large effect) and the effective number of equally distinct common functional groups ($p < 0.05$; Cohen's $d = 0.61$; medium effect); while not for the effective number of equally distinct dominant functional groups. No season effects were found.

3.5 | Multidimensional Functional Space-Based Indices of Rotifers

Among the different multidimensional, space-based indices of alpha functional diversity, only functional mean pairwise distance showed higher values during spring and summer than under ice independent of periods ($p < 0.05$; Cohen's $d = 1.22$ and 0.84; large effect), and functional richness showed higher values during period 1 than period 2 ($p < 0.001$; Cohen's $d = 0.97$; large effect).

3.6 | Rotifer Taxonomic and Functional Beta-Diversity

Within periods, the mean incidence-based taxonomic dissimilarity of rotifer communities showed no statistically significant seasonal differences except for period 1 having a negligible seasonal effect (Table 3). Within seasons, the mean incidence-based taxonomic dissimilarity of communities between periods was higher than within periods, indicating that the splitting in periods was sensible. Furthermore, the mean community dissimilarities within seasons were not different between periods (e.g., spring of p1 not different from spring of p2; Table 3).

For the incidence-based functional dissimilarity, summer communities of period 1 had a higher mean dissimilarity than spring ones (Table 3). Remarkably, for period 2, under-ice communities had a higher mean dissimilarity than spring, summer and autumn communities. Within seasons, the

TABLE 2 | Summary of two-way ANOVA (season and period as main effects and their interaction) for the different taxonomic Hill numbers (Hill nrs.) of rotifers (rot) and crustaceans (crust).

	Hill nrs.	Period effect	Cohen's *d*	Season effect	Cohen's *d*
Rot	S	p1 > p2 ***, all seasons	1.18; large	ns	
	SH	ns		ns	
	inv Simp	ns		ns	
Crust	S	p2 > p1: sp, s, au: ***	sp = 0.64; medium	p1: sp < s*	0.32; small
			s = 1.13; large	p1: sp < au**	0.74; medium
			au = 0.99; large	p2: sp < s*	1.32; large
				p2: sp < au**	1.60; large
	SH	p2 > p1: sp: *; s, au: ***	sp = 1.01; large	p2: sp < s*	0.97; large
			s = 1.84; large	p2: sp < au**	1.49; large
			au = 1.56; large		
	inv Simp	p2 > p1: s, au: ***	s = 1.62; large	p2: sp < s*	0.89; large
			au = 1.48; large	p2: sp < au**	1.41; large

Note: Column period effect indicates for which seasons a difference between periods was found (e.g., spring of p1 vs. spring of p2); in the case of interaction, not all seasons are different between periods. Column season effect indicates for which season comparisons a difference within periods was found (e.g., spring of p1 vs. summer of p1). Species richness (S), Shannon diversity (SH), invers Simpson diversity (inv Simp), spring (sp), summer (s), autumn (au), under-ice (ice), period 1 (p1; years 2001, 2003, 2011, 2014 and 2016), period 2 (p2; years 2017, 2018, 2019, 2021, 2022 and 2023), not significant (ns). Cohen's *d* is reported only for significant results; *d* between 0.2 and 0.5 indicates a small effect, between 0.5 and 0.8 a medium effect and > 0.8 a large effect. Asterisks indicate statistical significance (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$).

mean incidence-based functional dissimilarity of communities between periods was higher than within periods only for summer and autumn, corroborating the splitting in periods. Contrarily, the mean dissimilarity within spring and under-ice communities of period 2 was not different from the mean dissimilarity between periods, and this indicated that splitting in periods did not reflect dissimilarities (Table 3). In addition, within seasons, a period effect was found with the mean functional dissimilarity of spring, summer and under-ice communities having higher values during period 2 than period 1 (Table 3).

3.7 | Decomposing Rotifer Beta-Diversity Into Turnover and Nestedness

Turnover dominated (i.e., turnover prevailed over nestedness in more than 50% of comparisons) in incidence-based taxonomic dissimilarity of communities at all comparison levels (within seasons specific for periods, between consecutive seasons within periods, within seasons across periods) except for two exceptions. Specifically, turnover and nestedness contributed equally to dissimilarity of under-ice communities of period 1, and turnover dominated in only 42% of comparisons between autumn and under-ice comparisons of period 1 (Table S2).

Nestedness dominated (i.e., nestedness prevailed over turnover in more than 50% of comparisons) the functional dissimilarity of communities at all comparison levels (within seasons specific for periods, between consecutive seasons within periods, within seasons across periods; Table S3).

3.8 | Indicator Species

Less rotifer taxa were indicators for seasons of period 2 than period 1, while crustacean taxa and nauplii were indicators for both periods (Table 4). Only for period 2, two rotifer taxa and one crustacean taxon were indicators for under-ice communities. Specifically, *S. lakowitziana*, which was an indicator for spring in general, also was an indicator for under ice of period 2. *F. terminalis*, which was an indicator for spring, summer and autumn of period 1, was an indicator of under ice of period 2. Nauplii and adults of *C. strenuus* were indicators for all seasons of period 2.

3.9 | NMDS

In NMDS, stress was lowest with CWMs (stress = 0.07), followed by functional entities (stress = 0.15) and taxonomy (stress = 0.16). In all NMDS ordinations (Figure 5), communities from period 1 and period 2 were mostly separated, and under-ice communities were mixed with those from other seasons. Specifically, with taxonomic NMDS, under-ice communities of period 1 were like spring communities of period 1 that formed a cluster with respect to summer and autumn communities. For period 2, no clustering of seasons as for period 1 was found. With NMDS based on functional entities and CWMs, no clustering of seasons was found. In environmental fitting (Table 5), temperature was the variable related to all three ordinations, with DO % and chl-*a* specific for NMDS ordinations. In NMDS with taxonomy, temperature was positively related to communities of period 2 but not in NMDS with functional entities and CWMs where temperature was

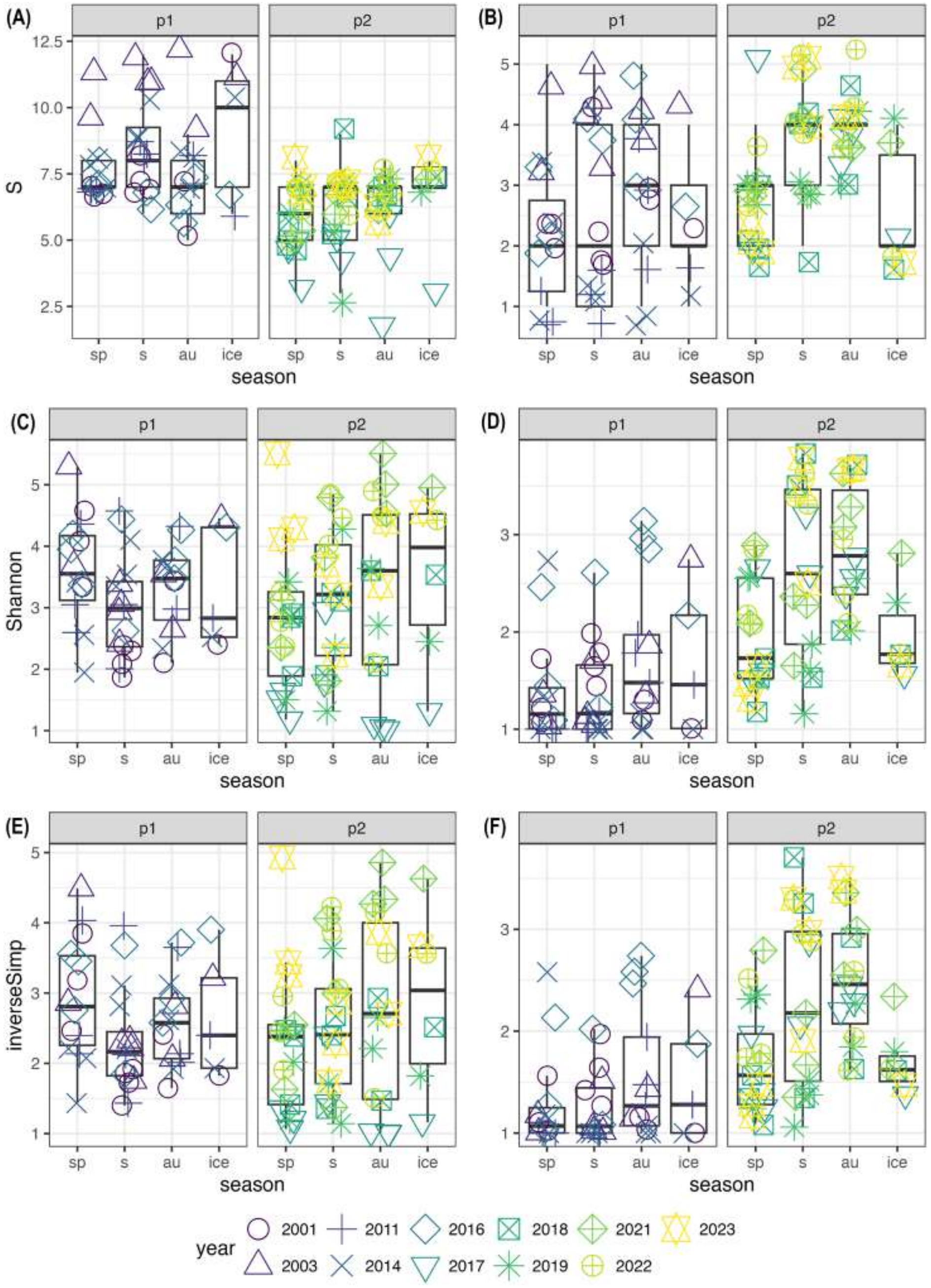

FIGURE 4 | Boxplots of taxonomic Hill numbers of rotifers (A, C, E) and crustaceans (B, D, F) split by periods (period 1; p1: Years 2001, 2003, 2011, 2014 and 2016; period 2; p2: Years 2017, 2018, 2019, 2021, 2022 and 2023) and seasons (spring—sp; summer—s; autumn—au; under ice—ice).

related both to communities of period 1 and period 2 and to communities from all seasons.

Comparing the NMDS ordinations (Table 6), taxonomy- and CWM-based NMDSs were highly correlated as indicated by their correlation in a symmetric Procrustes rotation.

3.10 | Environmental Variables

The mean water temperature and mean DO % were not different between periods but were different between seasons. Specifically, all seasons showed different values, with under-ice water temperature and dissolved oxygen showing lowest values with respect to other seasons (Figure 6). Contrarily, chl-*a* was not different between seasons but showed a period effect (Figure 6). Specifically, summer chl-*a* of period 1 was higher ($p < 0.05$) than that of period 2 (Cohen's $d = 0.96$; large effect).

4 | Discussion

This study assessed diverse facets of under-ice zooplankton with respect to the ice-free seasons of a mountain lake over a time span of 23 years. Under-ice communities are not static and species show a temporal succession (Kalinowska and Grabowska 2016; Kalinowska and Karpowicz 2020; Jensen 2019). While rotifer abundance shows low variability under ice, copepod abundance

TABLE 3 | Summary of two-way ANOVA (season and period as main effects and their interaction) based on incidence and abundance of rotifers and for functional beta-diversity (dissimilarity—diss.) of rotifers based on incidence.

Dissimilarity	Period effect	Cohen's *d*	Season effect	Cohen's *d*
Incidence-based taxonomic	p1 < p1p2***	0.99; large	ns	
	p2 < p1p2***	1.00; large		
Incidence-based functional	p1 < p1p2: sp***, s***, au***, ice**	1.42; large 1.21; large 0.66; medium 0.99; large	p1: sp < s**, sp < au ***	0.61; medium 0.1; negligible
	p1 < p2: sp***, s*, ice**	1.24; large 0.74; medium 1.32; large		

Note: Column period effect indicates for which seasons a difference between periods was found (e.g., spring of p1 vs. spring of p2); in the case of interaction, not all seasons are different between periods. Column season effect indicates for which season comparisons a difference within periods was found (e.g., spring of p1 vs. summer of p1). Spring (sp), summer (s), autumn (au), under-ice (ice); dissimilarity within period 1 (p1; years 2001, 2003, 2011, 2014 and 2016); dissimilarity within period 2 (p2; years 2017, 2018, 2019, 2021, 2022 and 2023); dissimilarity between periods (p1p2); not significant (ns); inverse Simpson (inv Simp); Shannon diversity (SH). Cohen's *d* is reported only for significant results; *d* between 0.2 and 0.5 indicates a small effect, between 0.5 and 0.8 a medium effect, and > 0.8 a large effect. Asterisks indicate statistical significance ($^{*}p<0.05$, $^{**}p<0.01$, $^{***}p<0.001$).

TABLE 4 | Indicator values for taxa specific for different seasons (spring—sp; summer—s; autumn—au; under ice—ice) of period 1 (years 2001, 2003, 2011, 2014 and 2016) and period 2 (years 2017, 2018, 2019, 2021, 2022 and 2023).

	Period 1				**Period 2**							
Taxon	**sp**	**s**	**au**	**ice**	**sp**	**s**	**au**	**ice**	**A**	**B**	**Stat**	***p***
Notholca squamula	■								1.00	0.14	0.378	0.044
Brachionus angularis			■						0.84	0.54	0.673	0.005
Filinia longiseta			■						0.79	0.46	0.602	0.003
Asplanchna priodonta	■	■	■						0.96	0.91	0.935	0.001
Synchaeta pectinata	■	■	■						0.95	0.37	0.596	0.023
S. lakowitziana	■				■			■	0.95	0.71	0.822	0.001
Filinia terminalis	■	■	■					■	0.99	0.89	0.938	0.001
Daphnia gr. *longispina*		■	■			■	■		0.94	0.84	0.884	0.001
Bosmina longirostris	■	■	■			■	■		0.96	0.96	0.958	0.001
Nauplii			■		■	■	■	■	0.98	0.84	0.905	0.001
Cyclops strenuus					■	■	■	■	0.94	0.88	0.911	0.001

Note: The indicator value is split into 'A' (sample estimate of the probability that the surveyed community belongs to the target community given the fact that the taxon has been found) and 'B' (sample estimate of the probability of finding the species in communities belonging to the specific group). The shading indicates for which season and period the taxon is an indicator.

increases towards ice-out in an oligotrophic lake (Jensen 2019). In contrast, in a eutrophic lake, under-ice rotifer abundance increases with time (Kalinowska and Grabowska 2016). These two studies indicate differences in zooplankton temporal development under ice linked to trophic state as suggested by Dokulil et al. (2014) and/or increased light availability (Obertegger et al. 2017) and thus potentially more phytoplankton food versus the end of winter. Our study is a snapshot study regarding under-ice sampling, and we can only speculate on the temporal variability of zooplankton under ice.

Here, taxonomic indices (abundance, biomass, species richness) and functional indices (the effective number of functional groups, the effective number of common functional groups, functional richness) of rotifers showed higher mean values in period 1 (the years 2001, 2003, 2011, 2014 and 2016) than in period 2 (the years 2017, 2018, 2019, 2021, 2022 and 2023). Especially, species richness, the effective number of functional groups, and functional richness are influenced by the number of infrequent species and infrequent functional traits, respectively, and thus mostly infrequent species with infrequent functional traits were lost from period 1 to period 2. However, the taxonomic indices of crustaceans (species richness, effective number of common species and effective number of dominant species) showed the opposite pattern, indicating that mostly already established species increased in abundance from period 1 to period 2. Similarly, multivariate ordinations indicated a separation of periods, mostly with taxonomy and functional entities. Thus,

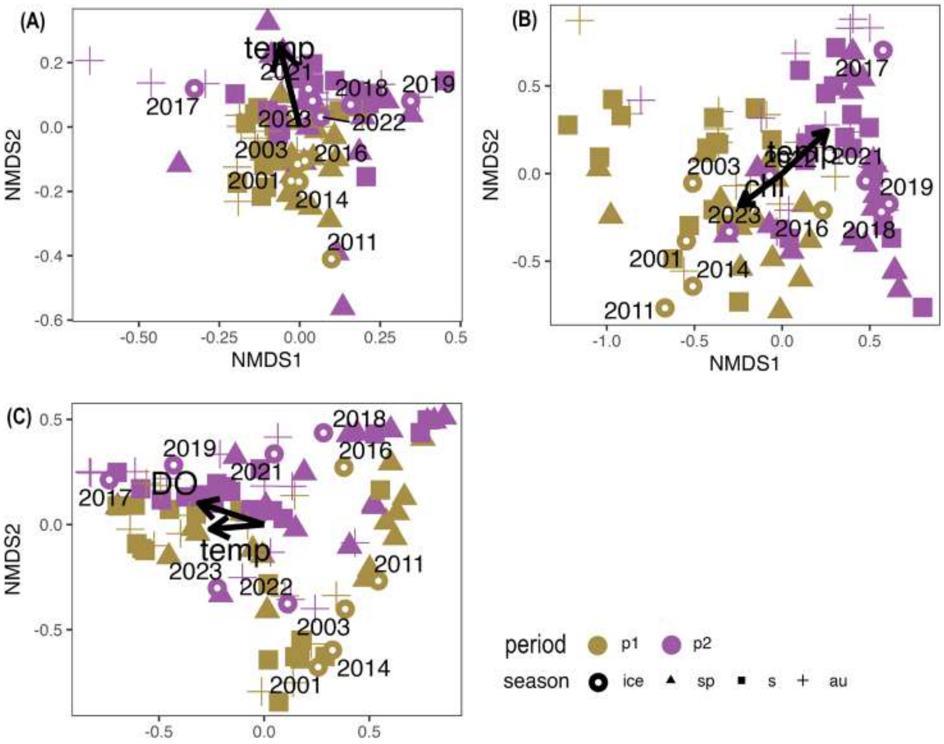

FIGURE 5 | NMDS with (A) rotifer taxa, (B) functional entities, (C) community weighted mean (CWM) of all rotifer functional traits. Arrows refer to environmental parameters related to the ordinations and different colours of communities to the two periods. Colours refer to periods (period 1; p1: Years 2001, 2003, 2011, 2014 and 2016; period 2; p2: Years 2017, 2018, 2019, 2021, 2022 and 2023) and seasons (spring—sp; summer—s; autumn—au; under ice—ice). The year is only shown for under-ice communities; mean water column temperature—temp; chl-*a*—chl; mean dissolved oxygen (% saturation)—DO.

TABLE 5 | Results of environmental fitting of variables (percent saturation of dissolved oxygen—DO; chl-*a*) on the NMDS ordinations; community weighted mean (CWM) of all rotifer functional traits.

	Variable	R^2	*p*
Taxonomy	Temperature	0.07	0.034
Functional entities	Temperature	0.13	0.005
	Chl-*a*	0.09	0.016
CWM	Temperature	0.06	0.034
	DO (%)	0.11	0.007

TABLE 6 | Procrustes statistic (*r*; correlation in a symmetric Procrustes rotation) and its significance for the comparison of NMDS ordinations based on taxonomy and functional approaches (functional differences based on functional entities; community weighted mean values of rotifer traits—CWM).

	Taxonomy	Functional entities
Functional entities	$r=0.25$; $p<0.01$	
CWM	$r=0.50$; $p<0.001$	$r=0.27$; $p<0.001$

the ecosystem change linked to altered mixing patterns (Flaim et al. 2020) favoured crustaceans over rotifers and had implications for zooplankton according to our first hypothesis.

The seasonality of zooplankton is generally driven by a combination of changes in temperature, food availability, predation and competition (Sommer et al. 2012). Under ice, zooplankton overwinter actively and can reproduce or overwinter inactively as resting stages (Socha et al. 2023). In a 2-year study in three eutrophic lakes, zooplankton reached similar or even higher abundance under ice than during the ice-free period (Kalinowska et al. 2019). Similarly, zooplankton abundance increases by removing snow on the ice cover in a dystrophic bog lake (Socha et al. 2023). However, in oligotrophic lake Tovel, the link between snow presence and under-ice zooplankton abundance and their biomass was not that tightly linked, as high abundance and biomass occurred with and without a snow cover. Furthermore, some zooplankton taxa (*Ascomorpha ecaudis*, *F. longiseta*, *G. stylifer* and *S. pectinata*) declined from autumn to under ice even though showing similar or higher abundances under ice than during other seasons. Contrarily, other taxa (*F. terminalis*, *K. longispina*, *K. hiemalis*, *P. dolichoptera*, *S. kitina*, *S. lakowitziana*, *B. longirostris* and nauplii and adults of *C. strenuus*) showed an increased population. Zooplankton in general (Gillooly 2000) and rotifers specifically (Sanoamuang 1993) have a longer life span (*F. terminalis* at 5°C: 23 days; Sanoamuang 1993) and a longer generation time (time from egg to maturity at 5°C; *F. terminalis*: 20 days; Sanoamuang 1993; *K. cochlearis*: 27 days; Walz 1983) at low than at high temperature. Furthermore, rotifers reproduce mostly parthenogenetically at low water temperature (Gilbert 2020). Considering a mean rotifer life span of 25 days at 5°C, the period from ice-in to sampling covered 1.7 generations for the year 2018 to 5.2 generations for the year 2001. Thus, we suggest that under-ice asexual reproduction of rotifers took place

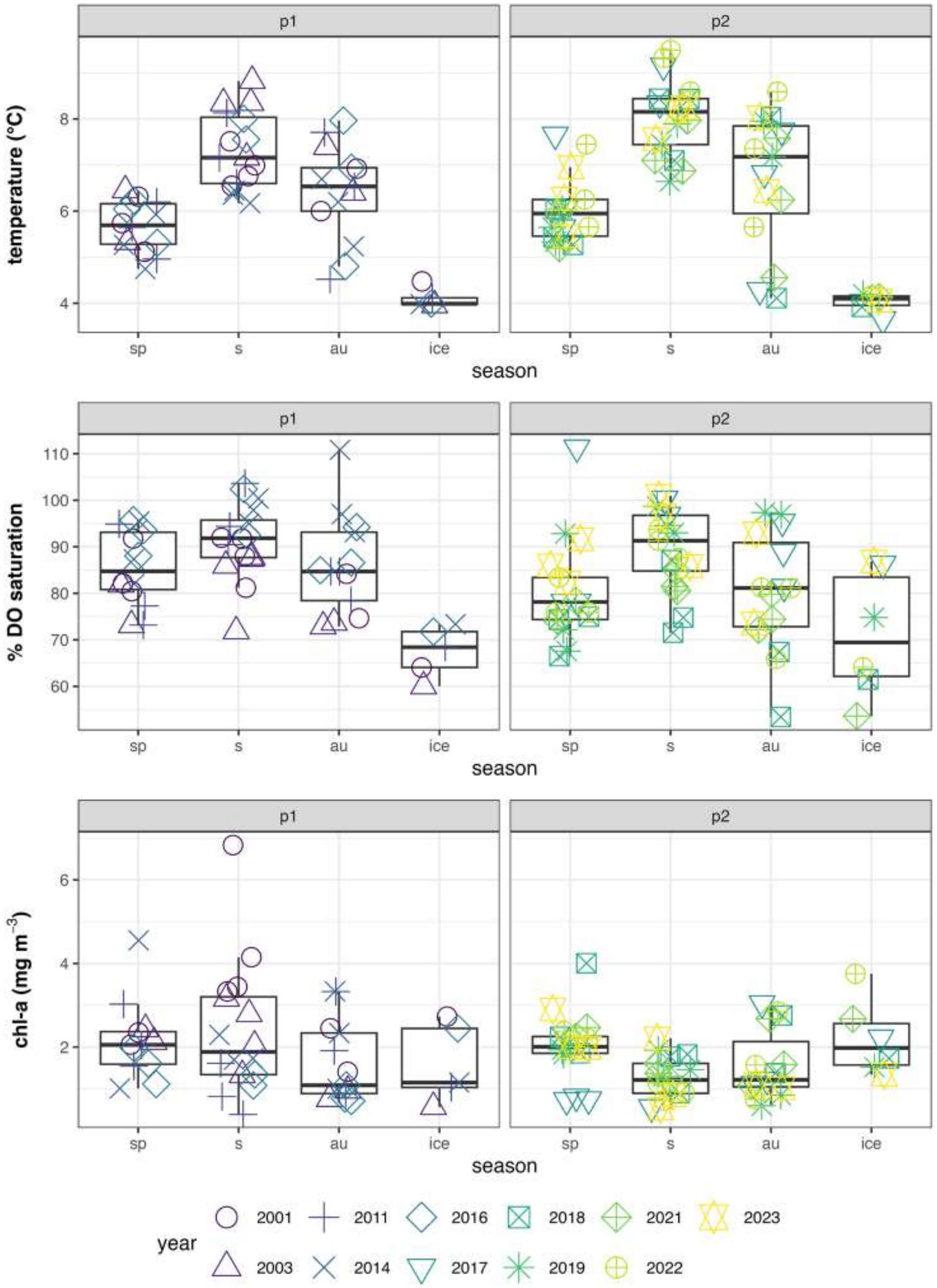

FIGURE 6 | Boxplots of mean water column temperature, % DO saturation and chl-*a* split by periods (period 1; p1: Years 2001, 2003, 2011, 2014 and 2016; period 2; p2: Years 2017, 2018, 2019, 2021, 2022 and 2023) and seasons (spring—sp; summer—s; autumn—au; under ice—ice).

to observe increasing abundance. In Lake Tovel, three cryptic species of *P. dolichoptera* exist, with two of them occurring from spring to autumn and one being a perennial species (Obertegger et al. 2014). We cannot exclude that the marked population increase of *P. dolichoptera* from the last autumn sampling to under-ice sampling was related to the succession of different cryptic species of *Polyarthra*, but this does not invalidate our conclusion on under-ice reproduction of rotifers. Because the effective number of common and dominant rotifer species was not different between seasons, we hypothesise that rotifer competition for food was not different under ice than during other seasons.

Some crustacean taxa actively overwinter under ice. In subalpine oligotrophic Lake Atnsjøen, nauplii of *C. scutifer* and *Arctodiaptomus laticeps* show a peak under ice in late winter (Jensen 2019); *C. scutifer* copepodites actively overwinter in subarctic lake Takvatn (Kers et al. 2024); reproduction of *C. scutifer* continues into winter in lake Tryvann (Elgmork 1981); and nauplii of *C. strenuus* hatch under ice in oligotrophic Lake Vormelitjenn (Naess and Nilssen 1991). Here, a five times increase in adults and even larger increase in nauplii of *C. strenuus* was observed from the last autumnal sampling to the under-ice sampling in the years 2003, 2017, 2018 and 2019. Considering that the time from ice-in to under-ice sampling was in 2003, 2017 and 2019 longer than the naupliar phase of *C. strenuus* lasting 45 days at 5°C (Elbourn 1966) and that 1–2 generations could occur from autumn to under ice, assuming a generation time of *C. strenuus* of 119 days at

5°C (Gillooly 2000), also copepod reproduction seemed possible under ice in Lake Tovel. Among cladocerans, *Bosmina longirostris* overwinters actively under ice in several lakes (Jensen 2019; Kalinowska and Karpowicz 2020) but shows a tendency to be absent during late winter in mesotrophic Lac Hertel (Hébert et al. 2021). Also, *D. hyalina* and *D. galeata* actively overwinter in deep lakes (de Senerpont Domis et al. 2007). Here, *B. longirostris* and *D.* gr. *longispina* were found after 57 and 35 days of ice-in, respectively, and we suggest that both cladocerans were actively overwintering in Lake Tovel, at least during the years 2014 and 2016, respectively. Thus, we suggest that also crustaceans actively overwintered and especially *C. strenuus* showed growth under ice. Adults of *C. strenuus* showed a marked abundance increase only in 2018 when also *P. dolichoptera*, *S. kitina* and *K. longispina* showed a marked increase. *Cyclops* spp. predate on these rotifers (Brandl 2005), and this overlap of three rotifer preys and their predator might have allowed *C. strenuus* to overwinter. In summary, we have evidence that zooplankton of Lake Tovel not only actively overwintered but also reproduced under ice, thus sustaining a diverse community as during the ice-free period according to our second hypothesis.

A substantial zooplankton community was present under ice despite low under-ice temperatures. Only two taxa were indicator taxa for under ice, namely *F. terminalis* and *S. lakowitziana*, and that only for period 2. *F. terminalis* is a species typical of low oxygen and cold water and feeds on decaying phytoplankton and associated bacteria (Ruttner-Kolisko 1980). Under-ice oxygen concentrations generally decline as winter progresses (Obertegger et al. 2017), and period 1 is characterised by hypoxic hypolimnetic waters and period 2 by well oxygenated waters (Flaim et al. 2020). Furthermore, *F. terminalis* is found at a depth of 15 m in August 2003 (corresponding to period 1) during midday in Lake Tovel (Obertegger et al. 2008). Thus, *F. terminalis* might find its specific niche during period 1 during most of the year in the lower layer or close to the hypolimnion, while during period 2 only under-ice conditions might fulfil the specific environmental needs of *F. terminalis*. Similarly, *S. lakowitziana* is a cold stenotherm planktic rotifer (Hollowday 2002) and is considered a winter species (Herzig 1987). In Lake Tovel, *S. lakowitziana* was an indicator for spring in both periods and for under ice of period 2. According to our first hypothesis that the ecosystem change influenced zooplankton, this might further indicate that the ecosystem change altered the seasonal preference of species such as *F. terminalis* and *S. lakowitziana*.

Taxonomic beta-diversity also reflected the splitting in periods ($p1 < p1p2$; $p2 < p1p2$). However, with functional beta-diversity, the splitting in periods did not reflect dissimilarities for period 2 and indicated a discrepancy. The functional NMDS ordination with CWMs also indicated that the under-ice community of 2023 belonging to period 2 was like communities of period 1. Similarly, feeding niches of the last 2 years of period 2 were like period 1. Indeed, Flaim et al. (2020) already stated that the period of enhanced mixing (here corresponding to period 2) will not continue unrestrictedly, and Obertegger et al. (2024) note a return to less mixed conditions based on reduced CO_2 emissions during the years 2022 and 2023. Small motile forms are favoured in nutrient-depleted and less mixed waters as they sink more slowly (Sommer et al. 2017). Thus, the increase in abundance of microphagous rotifers that primarily filter feed on fine detritus/organic aggregates, picoplankton, and small (2–10 µm) nanoplankton (Gilbert 2022) during the last 2 years of period 2 might indicate the return to less mixed conditions. Remarkably, this change in mixing was mainly indicated by functional approaches and not by taxonomic ones. In fact, functional diversity is a more effective tool to investigate ecosystem changes and disturbances than taxonomy (Mouillot et al. 2013). While rotifer predators dominate under ice in eutrophic Lake Vortsjärv over almost two decades (Virro et al. 2009), here microphagous (period 1) as well as macrophagous and polyphagous rotifers (both period 2) dominated under ice. Species of macrophagous rotifers sensu Gilbert (2022) translate to predators in Virro et al. (2009). Thus, this study showed a higher temporal variability in feeding strategies in oligotrophic Lake Tovel than eutrophic Lake Vortsjärv. Since little information on rotifer feeding strategies under ice exists, we can only speculate on possible links to trophic state.

Apart from period differences that were evident in most analyses, seasonal differences were not found with all analyses and not between all seasons. Therefore, our hypothesis of small seasonal differences was partly sustained. However, seasonal differences are apparent for bacteria when considering discrete layers in Lake Tovel (Obertegger 2022), while we considered the whole water column. Furthermore, lake bacterioplankton show more pronounced patterns than phytoplankton and zooplankton (Soininen and Köngäs 2012). Thus, here the reduced seasonality might be linked to considering the whole water column, to different planktic groups showing different seasonal patterns, and/or to the year-round cold-water temperatures in Lake Tovel according to our hypothesis. In any case, only in multivariate ordination with rotifer taxonomy was a clustering of spring and under-ice communities versus summer and autumn communities found during period 1, while communities of different seasons of period 2 were mixed. The crustacean number of dominant species was lower under ice than during autumn of period 2. Thus, different periods showed different seasonality. Remarkably, the functional mean pairwise distance between rotifers was smaller under ice than during summer, both for period 1 and 2, while functional beta-diversity of under-ice rotifer communities was higher than that of other seasons during period 2. While functional beta-diversity includes both shared and unique proportions of the trait space of the whole community (Villéger et al. 2013), the mean pairwise functional distance considers single species pairs, and small distances indicate that species are clumped in one section of the trait space and do not take up a large fraction of the available volume (Weiher et al. 1998). Thus, we suggest that the high functional beta-diversity was related to the fact that this index includes all species. Concomitantly, the low mean pairwise functional distance values under ice were related to the fact that some rotifer taxa were under-ice indicator taxa and thus species pairs were less different. These results indicated that different functional indices are needed to fully comprehend the different facets of diversity, as pointed out by Legras et al. (2018).

Decomposing beta-diversity into the two antithetic processes, we found that turnover dominated mainly taxonomic beta-diversity, while nestedness dominated functional beta-diversity at the three temporal scales considered. Similarly, in spatial studies, taxonomic turnover and functional nestedness determine community assembly of diatoms in a river (Hu et al. 2024) and of rotifers in a hypereutrophic river (Gadelha et al. 2023). Nestedness can reflect the diversity of available niches at different locations (Legendre 2014) or stochastic dispersal and/or extinction processes (Si et al. 2016; Lima et al. 2020), and turnover implies replacement of species due to environmental filtering, competition, and/or historical events (Legendre 2014; Nunes et al. 2016). Dispersal limitation typically increases with increasing spatial distance between communities (Heino et al. 2015). Soininen et al. (2018) report a dominance of turnover in taxonomic beta-diversity of freshwater organisms and relate it to strong environmental filtering by large environmental gradients. We assessed zooplankton diversity of the whole water column that encompasses large environmental gradients linked to parameters such as light, oxygen and food availability. Thus, here, turnover might be influenced by the large spatial extent of our sampling and functional nestedness by temporal dispersal limitation leading to the loss of traits. Specifically, infrequent species with infrequent traits might not endure temporal scales considered that spanned within seasons at least 1 month and across periods more than 10 years. While we can only speculate about the ultimate reasons for the patterns found, almost no period and seasonal effects were found, further corroborating our hypothesis of limited seasonality in a cold-water lake. However, periods did not have any influence on community assembly mechanisms in contrast to our first hypothesis.

Though zooplankton grazing rates decrease with temperature (Armengol et al. 2001), zooplankton grazing decreases specific phytoplankton groups such as diatoms and cryptophytes in a mesocosm experiment in a hypereutrophic pond (Hrycik and Stockwell 2021). In Lake Tovel, algal richness and chl-*a* are not different between summer and under ice, while algal biomass is higher during summer (Obertegger et al. 2022; chl-*a*: this study) and algal taxa such as dinoflagellates and Cryptophyceae show a higher abundance under ice than during summer (Obertegger et al. 2022). Furthermore, rotifer growth rates from the last autumn to the under-ice sampling were low, like values found at cold water temperature (Sanoamuang 1993). Thus, we suggest little grazing pressure on phytoplankton in Lake Tovel because of its oligotrophic state, the low zooplankton abundance and growth rate, and the low water temperature. Consequently, we suggest that since phytoplankton abundance might not be substantially reduced by zooplankton grazing, zooplankton reproduction was not compromised by low algal food sources.

Lake Tovel is a cold-water lake (Cellamare et al. 2016) with mean water temperature never exceeding 10°C all year round (this study). Remarkably, temperature was positively related to communities of period 2 only in NMDS ordinations with rotifer taxonomy. Acknowledging that no period effect was found for mean water temperature and that this temperature effect showed a low correlation and was not evident in NMDS ordinations with functional entities and CWMs, we suggest that this effect was negligible. In fact, all environmental parameters related to ordinations had a low correlation. This might be related to the fact that we analysed patterns across the whole water column, and this might dampen any environmental effect.

In summary, our study showed that in a cold-water mountain lake, some zooplankton taxa showed a population increase under ice; seasonal differences were not that important, and under-ice communities responded to altered mixing patterns. Especially, trait-based approaches indicated that the ecosystem change linked to longer mixing was mitigated versus the last years of period 2, as already shown for CO_2 emissions (Obertegger et al. 2024). Studies like ours are more needed to close the knowledge gap on under-ice zooplankton and to set the baseline in under-ice zooplankton community composition in mountain lakes, especially considering that ice cover is vanishing with climate change (Sharma et al. 2021).

Author Contributions

Conceptualisation: Ulrike Obertegger. Data analysis: Ulrike Obertegger, Stefano Corradini and Leonardo Cerasino. Preparation of figures and tables: Ulrike Obertegger, Stefano Corradini and Leonardo Cerasino. Conducting the research, data interpretation, writing: Ulrike Obertegger, Stefano Corradini and Leonardo Cerasino.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data are available from the corresponding author on reasonable request.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** fwb70085-sup-0001-DataS1.docx.