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Zooplankton biodiversity in the lakes of South Tyrol (Italy)

Abstract

The results of a survey on the planktic rotifers and crustaceans in 70 South Tyrolean lakes at altitudes ranging from 215–2892 m a.s.l., carried out between 1979 and 2015, are presented. The samples were collected both as part of lake monitoring efforts and in support of various scientific projects. The composition of zooplankton communities in different lakes is compared and the influence of environmental factors on biodiversity is examined. The total number of taxa amounted to 99, with 57 rotifers, 26 cladocerans and 16 copepods. The spectrum of taxa and their frequency of occurrence differed between lakes located above and below the treeline. *Polyarthra dolichoptera* was the most frequent species in all lakes, followed by *Kellicottia longispina*, *Keratella cochlearis* and *Synchaeta* spp. in the lakes below tree line and *Keratella cochlearis* and *Keratella* gr. *quadrata* in the lakes above tree line (alpine lakes). The cladocerans were mainly represented by species of *Daphnia*, *Bosmina* and *Ceriodaphnia* in the lakes below treeline and by *Chydorus sphaericus* above it. Among the copepods, *Cyclops abyssorum tatricus* played a prominent role in the alpine lakes. The rotifers *Anuraeopsis fissa*, *Brachionus calyciflorus*, *Collotheca pelagica*, *Pompholyx sulcata*, as well as the cladocerans *Daphnia ambigua* and *Daphnia pulex* found in this study of South Tyrolean lakes are presently not recorded in the national species lists. The analysis of the taxonomic composition of the zooplankton communities identified three groups of lakes, mainly differing in terms of altitude and trophic level. In the natural lakes below the treeline, the number of taxa per lake was significantly higher than in the alpine lakes and higher than in reservoirs. The number of taxa decreased significantly with increasing altitude but also correlated with the area of the lake and with parameters related to lake primary production and to the geology of the catchment area. The differences in the Shannon index values of the individual lakes were small, and the index correlated significantly only with altitude.

Keywords: checklist, rotifers, crustaceans, richness, altitudinal distribution, community composition

1. Introduction

Zooplankton consists of mostly microscopic animals floating in open water (pelagic zone) and includes protozoans and metazoans. Among the planktic metazoans, rotifers and crustaceans have the greatest biodiversity. Due to its central position in the food web, zooplankton contributes significantly to ecosystem functioning and not only establishes an important link between primary producers (algae) and end consumers (fish) but also plays an important role in the biochemical nutrient cycle. Zooplankton reacts quickly to changes in the ecosystem (Anton-Pardo et al. 2013; Gürbüzer et al. 2017; Garcia-Chicote et al. 2018) and is therefore well suited as bioindicator in monitoring programs (Ejsmont-Karabin 2012; Haberman & Haldna 2014).
The first studies of zooplankton in South Tyrolean lakes date back to the beginning of the 20th century (e.g., Brehm & Zederbauer 1905; Huber 1906), in the following decades, planktic crustaceans in particular were repeatedly the subject of surveys (e.g., Pesta 1923;

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Stella 1931; Tonolli & Tonolli 1951). With the establishment of the Biological Laboratory of the Provincial Agency for Environment and Climate Protection of the province of Bolzano in 1976, the analysis of zooplankton became an integral part of lake monitoring efforts and was later also performed within the framework of different scientific projects. The main objective of this work was to obtain an overview of the biodiversity of these animal groups in South Tyrolean lakes and to provide a previously not available check-list of zooplankton species (rotifers and crustaceans), based on the data collected from 1979 to 2015. Biodiversity data are particularly important as a basis for future long-term studies and for assessing the effects of climate and land use, especially in high alpine regions.
Furthermore, the communities of lakes at different altitudes were compared, both in terms of species richness and Shannon index, as well as community composition. Finally, the influence of various ecological factors on biodiversity was examined.

2. Materials and Methods

2.1 Study sites

The investigated area (Fig. 1) is the province of Bolzano (South Tyrol) in the Eastern Alps, a region with relatively few lakes, just over 300 with an area of more than 0.5 ha. Most of the lakes are small and shallow and must therefore be classified as ponds – in the following, however, all sampled standing water bodies are referred to as lakes. Almost 80 % of the lakes are alpine lakes (above the treeline), only few are in the valley floor (Fig. 2). Most lakes have an area of less than 1 ha and a maximum depth of less than 5 m. The catchment areas consist mainly of metamorphic and igneous bedrock (e.g., granite, gneiss, schists, porphyry) while a small fraction of the lakes lies in the limestone area.
We present the results of zooplankton surveys conducted in 70 lakes, including 47 lakes located above the treeline – alpine lakes – (2043 m a.s.l. to 2892 m a.s.l.), in the following referred to as above 2000 m, and 23 below the treeline (215 m a.s.l. to 1881 m a.s.l.) referred to as below 2000 m, 6 of which were reservoirs (Fig. 3). Quantitative zooplankton data are available for 61 lakes. The main characteristics of the sampled lakes are presented in Table 1, a list of the sampled lakes with information on altitude, morphometry and size of the catchment area can be found in the appendix (Table A).

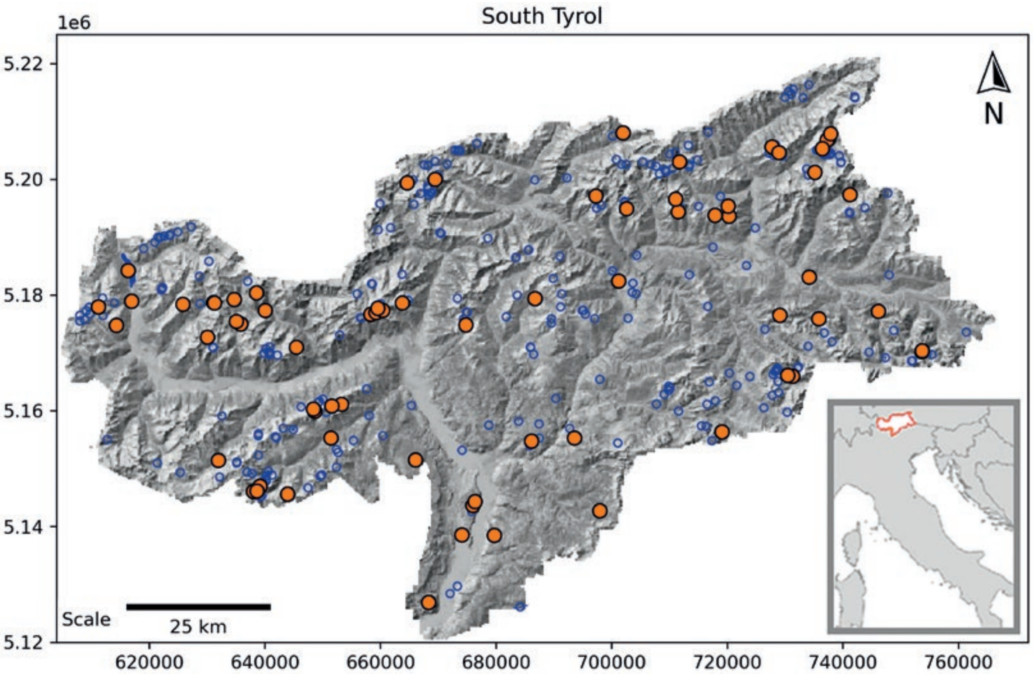

Fig. 1: Geographic distribution of the South Tyrolean lakes sampled within this study. The blue circles represent mapped lakes, the lakes sampled within this study are highlighted in red. Background map: Autonome Provinz Bozen Südtirol – Geo-Browser MapView.

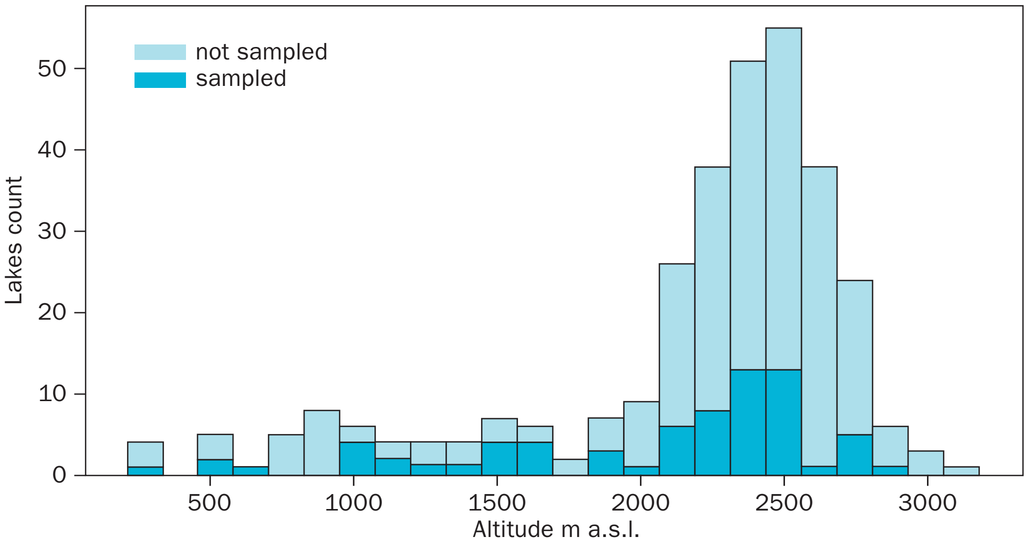

Fig. 2: Altitudinal distribution of all mapped lakes (316) and of lakes sampled (70) for zooplankton in South Tyrol.

Table 1: Characteristics of the lakes surveyed for zooplankton.

Parameter	Lakes < 2000 m	Lakes > 2000 m	Reservoirs
Number of lakes	23	47	6
Altitude (m a.s.l.)	215–1881	2043–2892	1498–1856
Average lake area (ha)	22.5	2.6	181.8
Maximum depth (m)	38	52	87
Conductivity (μS cm^{-1})	40–506	8–494	30–224
Total phosphorus (mg m^{-3})*	15	6	8
Calcium (g m^{-3})	4.81–56.08	0.86–44.51	5.50–25.30
Chlorophyll a (mg m^{-3})	0.4–17.1	0.1–19.8**	0.4–2.1
Minimum pH	6.30	6.87	6.68

* average total phosphorus of the euphotic zone
** Kratzbergersee 2000-10-04

Fig. 3: Some of the lakes sampled for zooplankton (clockwise: Montiggler Seen, Wilder See, Kratzbergersee, Hungerschartensee) (Photos: B. Thaler).

2.2 Sampling and analysis

All the data presented were collected during the years 1979–2015, either as part of the monitoring of the South Tyrolean lakes carried out by the Biological Laboratory (Provincial Agency for Environment and Climate Protection of the Province of Bolzano) or within the framework of EU-funded projects (AL:PE 1 and 2, Wathne et al. 1995; MOLAR, Wathne et al. 2000; EMERGE, Tolotti et al. 2006; permaqua, Thaler et al. 2015) and a master thesis (Vorhauser 2016).

The lakes below the treeline were sampled several times, including all seasons, as were two of the alpine lakes, the remaining lakes were sampled one to three times in total, in summer or autumn. The zooplankton samples were generally taken from the deepest point of the lake, as was the case with the samples for chemical water analysis, using a water sampler, initially a 2 L Ruttner sampler or a 5 L Schindler sampler, later a 5 L "Uwitec" sampler. Samples were taken at 1–5 m intervals, and then the samples from several depth levels were combined into a composite sample and filtered. The mesh size was 47 µm and 90 % ethyl alcohol was used for fixation. The rotifers were counted in sedimentation chambers under an inverted microscope (Zeiss Axiovert 35) at 100x magnification; the crustaceans were counted under a stereomicroscope (Zeiss Stemi SV 11) at 60x magnification, excluding cyclopoid and calanoid nauplii. Each zooplankton taxon was identified with an 8-character code. The rotifers were identified using Ruttner-Kolisko (1972) and Braioni & Gelmini (1983), while the crustaceans were determined using Flössner (1972), Margaritora (1983), Kiefer (1978) and Einsle (1993).

The storage, retrieval and sorting of data were accomplished using an SQLite database (Hipp et al. 2015), graphing and data presentation were performed in Jupyter (Kluyver et al. 2016).

To verify the similarity of the taxonomic composition between lakes, a cluster analysis based on the species presence-absence by means of the Ward's method and the "agnes" agglomerative coefficient was performed.

3. Results and Discussion

3.1 Species occurrence and frequency

We recorded a total of 99 taxa, of which 57 were rotifers and 42 crustaceans; the crustaceans included 26 cladoceran and 16 copepod taxa (Table 2). These numbers may seem relatively low compared to the rotifer and crustacean fauna of the littoral zone, but the biodiversity of zooplankton is naturally low, as the pelagic zone is almost an extreme habitat, with partly suboptimal oxygen and light conditions, and the absence of differentiated habitats and of structures providing refuge from predators (Thaler 2008; Ejsmont-Karabin et al. 2016).

Table 2: List of the zooplankton taxa.

CLASS MONOGONONTA (rotifers)	**code**
ORDER COLLOTHECACEA	
Family Collothecidae	
Collotheca pelagica (Rousselet, 1893)	Collpela
ORDER FLOSCULARIACEA	
Family Conochilidae	
Conochilus gr. *unicornis-hippocrepis*	Conounhi
Conochilus gr. *natans-dossuarius*	Cononado
Family Hexarthridae	
Hexarthra mira (Hudson, 1871)	Hexamira
Family Trochosphaeridae	
Filinia longiseta (Ehrenberg, 1834)	Fililong
Filinia terminalis (Plate, 1886	Filiterm

CLASS MONOGONONTA (rotifers)	code
ORDER PLOIMA	
Family Asplanchnidae	
Asplanchna priodonta Gosse, 1850	Asplprio
Asplanchnopus multiceps (Schrank, 1793)	Asplmult
Family Brachionidae	
Anuraeopsis fissa (Gosse, 1851)	Anurfiss
Brachionus angularis angularis Gosse, 1851	Bracangu
Brachionus calyciflorus s.l. Pallas, 1766	Braccaly
Brachionus sp.	Bracsp
Kellicottia longispina (Kellicott, 1879)	Kelllong
Keratella cochlearis (Gosse, 1851)	Keracoch
Keratella gr. *quadrata*	Keragrqu
*Keratella quadrata (*O. F. Müller, 1786*)*	Keraquad
Notholca gr. *labis-acuminata*	Nothlaac
Notholca labis Gosse, 1887	Nothlabi
Notholca squamula (Muller, 1786)	Nothsqua
Family Euchlanidae	
Euchlanis dilatata Ehrenberg, 1832	Euchdila
Euchlanis sp.	Euchsp
Family Gastropodidae	
Ascomorpha ecaudis Perty, 1850	Ascoecau
Ascomorpha ovalis (Bergendal, 1892)	Ascooval
Ascomorpha saltans Bartsch, 1870	Ascosalt
Gastropus stylifer Imhof, 1891	Gaststyl
Family Lecanidae	
Lecane gr. *lunaris*	Lecaluri
Lecane luna (Muller, 1776)	Lecaluna
Lecane mira (Murray, 1913)	Lecamira
Lecane subtilis Harring & Myers, 1926	Lecasubt
Family Lepadellidae	
Colurella sp.	Colusp
Lepadella sp.	Lepasp
Family Mytilinidae	
Mytilina ventralis (Ehrenberg, 1830)	Mytivent
Family Notommatidae	
Cephalodella forficula (Ehrenberg, 1838)	Cephforf
Cephalodella gibba (Ehrenberg, 1838)	Cephgibb
Cephalodella ventripes Dixon-Nuttal, 1901	Cephvent
Notommata glyphura Wulfert, 1935	Notoglyp
Family Proalidae	
Proales sp.	Proasp
Family Synchaetidae	
Ploesoma hudsoni (Imhof, 1891)	Ploehuds
Polyarthra dolichoptera Idelson, 1925	Polydoli
Polyarthra gr. *major-euryptera*	Polymaeu
Polyarthra gr. *vulgaris-dolichoptera*	Polyvuldo
Synchaeta gr. *stylata-pectinata*	Syncstpe
Synchaeta gr. *tremula-oblonga*	Synctrob
Synchaeta grandis Zacharias, 1893	Syncgran
Synchaeta kitina Rousselet, 1902	Synckiti
Synchaeta lakowitziana Lucks, 1938	Synclako
Synchaeta pectinata Ehrenberg, 1832	Syncpect

CLASS MONOGONONTA (rotifers)	**code**
Family Testudinellidae	
Pompholyx sulcata (Hudson, 1885)	Pompsulc
Family Trichocercidae	
Trichocerca capucina Wierzejski & Zacharias, 1893	Triccapu
Trichocerca cylindrica (Imhof, 1851)	Triccyli
Trichocerca elongata Gosse, 1884	Tricelon
Trichocerca longiseta (Schrank, 1802)	Triclong
Trichocerca pusilla (Lauterborn, 1898)	Tricpusi
Trichocerca similis (Wierzejski, 1893)	Tricsimi
Trichocerca sp.	Tricsp
Family Trichotriidae	
Trichotria pocillum (Muller, 1776)	Tricpoci
Trichotria tetractis (Ehrenberg, 1830)	Trittetr

CLASS BRANCHIOPODA (cladocerans)	**code**
ORDER ANOMOPODA	
Family Bosminidae	
Bosmina (Eubosmina) coregoni (Baird, 1857)	Bosmcore
Bosmina (Bosmina) longirostris (O. F. Müller, 1785)	Bosmloro
Bosmina (Eubosmina) longispina (Leydig, 1860)	Bosmlosp
Family Chydoridae	
Acroperus harpae (Baird, 1835)	Acroharp
Alona affinis (Leydig, 1860)	Alonaffi
Alona quadrangularis (O. F. Müller, 1776)	Alonquad
Alonella (Alonella) excisa (Fischer, 1854)	Alelexci
Alonella (Nanoalonella) nana (Baird, 1843)	Alelnana
Chydoridae gen.sp.	Chydgen
Chydorus sphaericus (O. F. Müller, 1776)	Chydspha
Leydigia (Neoleydigia) acanthocercoides (Fischer, 1854)	Leydacan
Leydigia (Leydigia) leydigi (Schödler, 1863)	Leydleyd
Family Daphniidae	
Ceriodaphnia pulchella Sars, 1862	Ceripulc
Ceriodaphnia quadrangula (O. F. Müller, 1785)	Ceriquad
Daphnia (Daphnia) ambigua Scourfield, 1947	Daphambi
Daphnia (Daphnia) cucullata Sars, 1862	Daphcucu
Daphnia (Daphnia) longispina (O. F. Müller, 1776)	Daphlong
Daphnia (Daphnia) pulicaria Forbes, 1893	Daphpuli
Daphnia (Daphnia) rosea Sars, 1862	Daphrose
Daphnia (Daphnia) pulex Leydig, 1860	Daphsp
Simocephalus (Simocephalus) vetulus (O. F. Müller, 1776)	Simovetu
Family Macrothricidae	
Macrothricidae gen.sp.	Macrgen
Macrothrix sp.	
ORDER CTENOPODA	
Family Sididae	
Diaphanosoma brachyurum (Liévin, 1848)	Diapbrac
Sida crystallina (O. F. Müller, 1776)	Sidacrys
ORDER HAPLOPODA	
Family Leptodoridae	
Leptodora kindtii (Focke, 1844)	Leptkind

CLASS MAXILLOPODA (copepods)	**code**
ORDER CYCLOPOIDA	
Family Cyclopidae	
Cyclops abyssorum Sars G. O., 1863	Cyclabys
Cyclops abyssorum subsp. *tatricus* (Kozminski, 1927)	Cyclabta
Cyclops strenuus Fischer, 1851	Cyclstre
Cyclops vicinus Uljanin, 1875	Cyclvici
Eucyclops serratulus (Fischer, 1851)	Eucyserr
Macrocyclops albidus (Jurine, 1820)	Macralbi
Mesocyclops (Mesocyclops) leuckarti (Claus, 1857)	Mesoleuc
Paracyclops fimbriatus (Fischer, 1853)	Parafimb
Thermocyclops crassus (Fischer, 1853)	Thercras
Thermocyclops dybowskii (Landé, 1890)	Therdybo
ORDER CALANOIDA	
Family Diaptomidae	
Acanthodiaptomus denticornis (Wierzejski, 1887)	Acandent
Arctodiaptomus alpinus (Imhof, 1885)	Arctalpi
Eudiaptomus gracilis (Sars G. O., 1863)	Eudigrac
Eudiaptomus vulgaris (Schmeil, 1896)	Eudivulg
ORDER HARPACTICOIDA	
Family Canthocamptidae	
Canthocamptus staphylinus (Jurine, 1820)	Cantstap
Family Harpacticidae	
Harpacticidae gen.sp.	Harpgen

Rotifers (Monogononta) were represented by 17 families with 27 genera and cladocerans (Branchiopoda) by 6 families with 13 genera. Among the copepods, 4 families with 11 genera were found, of which one family belonged to the order Cyclopoida, one to the order Calanoida, and two to the order Harpacticoida. The relative frequency of the various zooplankton families is shown in Figure 4.

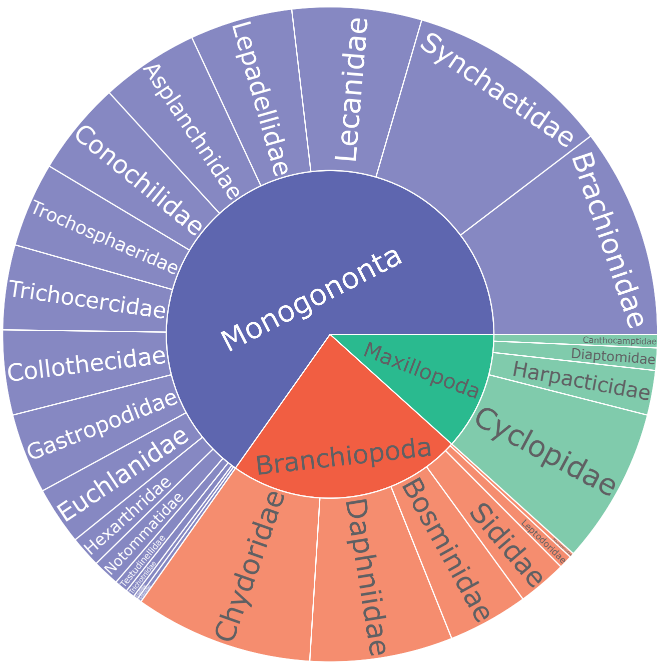

Fig. 4: Frequency of zooplankton families found.

Among the rotifers, the most diversified genera were *Trichocerca* from the family of Trichocercidae (7 species) and *Synchaeta* (6 species, Synchaetidae; see also Obertegger 2007). In the checklist of Italian fauna (Fontaneto et al. 2022), 67 species of rotifers – littoral species included – are reported for the Trentino-South Tyrol region. A large part of the listed pelagic species was encountered in our survey. A few taxa were new for the region, namely *Anuraeopsis fissa*, *Asplanchnopus multiceps*, *Brachionus calyciflorus*, *Collotheca pelagica* and *Pompholyx sulcata*. The total number of pelagic rotifers in the South Tyrolean lakes is comparable to the results reported for other regions (Karpovicz & Ejsmont-Karabin 2021).
Among the cladocerans, *Daphnia* (family Daphniidae) showed a relatively large diversity with 6 species. The observed number of planktic cladocerans – 26 taxa – is also consistent with data in the literature (Karpovicz & Ejsmont-Karabin 2021). Margaritora et al. (2021) listed 55 species of planktic and littoral cladocerans for the Trentino-South Tyrol region, but the majority of the list are littoral species, which were found only sporadically in the zooplankton samples taken within this survey. Two planktic species – *Daphnia ambigua* and *Daphnia pulex* – are new for the region. Also, two littoral species – *Leydigia acanthocercoides* and *Leydigia leydigi* – were not reported for this region in previous studies.
Among copepods, *Cyclops* (family Cyclopidae) showed the highest diversity with 4 species. The number of cyclopoid copepods (Cyclopoida) is rather low with 10 taxa, but similar results were also found in Polish lakes (Ejsmont-Karabin et al. 2020; Karpovicz & Ejsmont-Karabin 2021). Of the four species of calanoid copepods (Calanoida) reported for

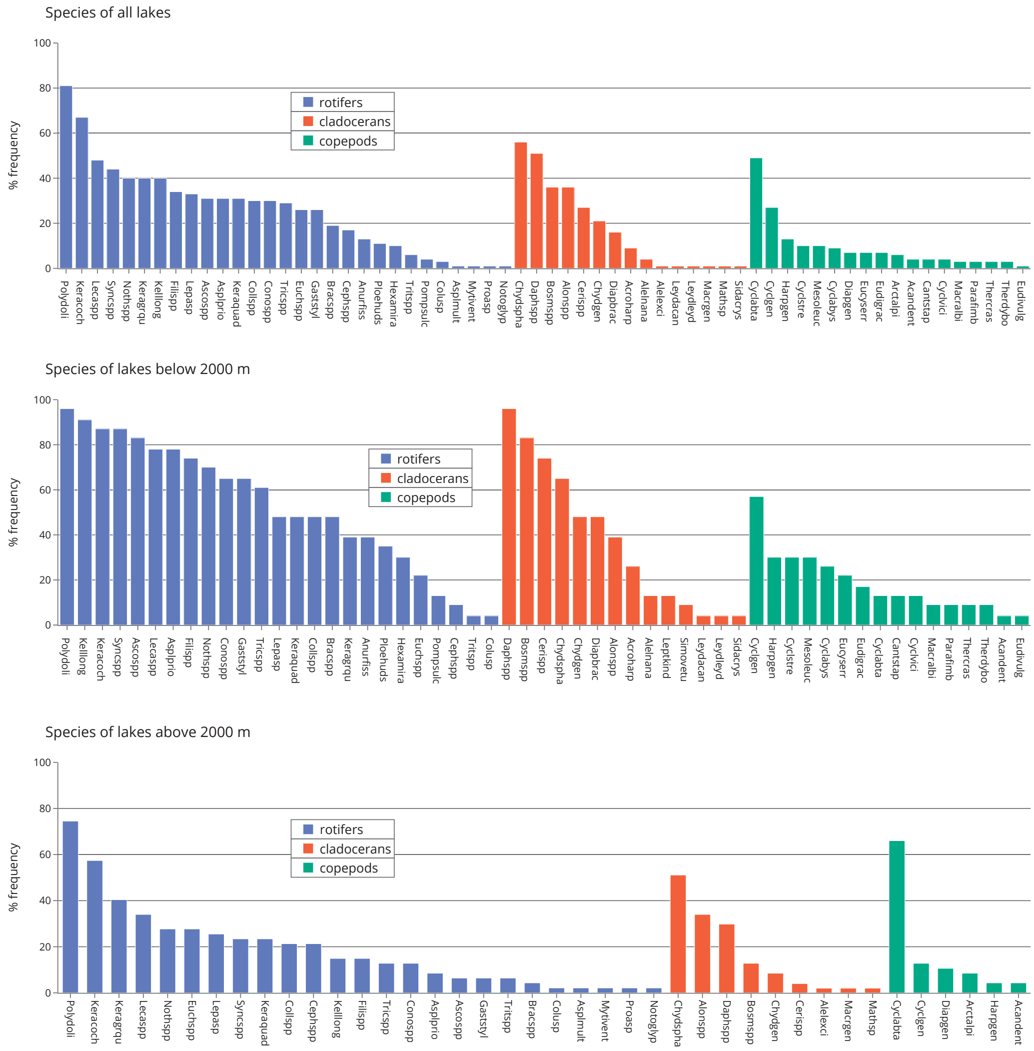

Fig. 5: Relative frequency of rotifer, cladoceran and copepod taxa; in some cases, the species of a genus were grouped together (e.g., *Synchaeta* species – Syncspp). Taxon codes as in Table 2.

the area Eastern Alps (Alfonso et al. 2021), two were present in our samples, furthermore, two species of *Eudiaptomus* – *E. gracilis* and *E. vulgaris* – were observed, for the latter, there is only an unpublished observation for South Tyrol (Alfonso et al. 2021).

Figure 5 shows the relative frequency of the most common rotifer, cladoceran and copepod taxa in all lakes, and the separate contributions for lakes below 2000 m and lakes above 2000 m. The most frequent rotifer taxa in the whole set of lakes were *Polyarthra dolichoptera* (81 %) and *Keratella cochlearis* (67 %). Also widely distributed were typical planktic species like *Synchaeta* spp., *Notholca* spp., *Keratella* gr. *quadrata* and *Kellicottia longispina* (approx. 40 %). *Polyarthra dolichoptera* is present in nearly all of lakes located below 2000 m and *Kellicottia longispina*, *Keratella cochlearis* and *Synchaeta* spp. reach a relative frequency of about 90 %. In the lakes above 2000 m, *Polyarthra dolichoptera* had the highest relative frequency (74 %), followed by *Keratella cochlearis* (57 %) and *Keratella* gr. *quadrata* (40 %); *Asplanchna priodonta* only played a minor role.

When considering the relative frequencies of the single species calculated for all lakes, it should be noted that the number of sampled lakes above 2000 m, the alpine lakes, is twice that of the lakes below 2000 m, however the alpine lakes were mostly sampled only once. Therefore, the data reflect the situation in one moment and the species spectrum may not be fully recorded. It has been observed that the composition of rotifer communities in particular can fluctuate greatly over time (Walsh et al. 2007).

As far as the cladocerans are concerned, considering all sampled lakes, *Chydorus sphaericus*, a both planktic and littoral species, was the most common (56 %), with typical planktic genera *Daphnia* and *Bosmina* also well represented (51 % and 36 %, respectively). In the lakes below 2000 m, the genera *Daphnia*, *Bosmina* and *Ceriodaphnia* showed the highest frequency (74 %–96 %). In the alpine lakes, *Chydorus sphaericus* was the most widespread cladoceran (51 %), and *Daphnia* species were also well represented.

With regard to the relative frequency of copepods, the following picture emerged: while representatives of planktic cyclopoid copepods were found in almost all lakes, calanoid copepods only occurred in about a quarter of the whole set of lakes, and always only with one species. The most frequent planktic copepods in all 70 lakes were the cyclopoid *Cyclops abyssorum tatricus* (49 %) and juvenile stages of Cyclopidae gen.sp. (27 %), the other taxa being present only in one to seven lakes each. *Cyclops abyssorum tatricus* was found in 66 % of alpine lakes and was the only copepod species in many of these lakes. In the lakes below 2000 m, the copepod variability was relatively high, with a total of 16 taxa observed, including *Cyclops strenuus*, *Mesocyclops leuckarti*, *Cyclops abyssorum* and *Cyclops vicinus*.

3.2 Composition of the zooplankton communities

To verify the similarity of the taxonomic composition between the lakes, a dendrogram analysis was performed based on the species presence-absence using the Euclidean distance algorithm.

The cluster diagram (Fig. 6) shows three main groups of lakes. Group one consists almost exclusively of alpine lakes; however, these lakes were sampled only once, so probably not all species were recorded. The lakes located in limestone are clustered close together (Fig. 6, cluster 1, blue asterisk), as is a group of lakes influenced by melting permafrost (rock glaciers) (Fig. 6, cluster 1, green asterisk). In this context, it can be noted that Jersabek et al. (2001) observed a marked change in species composition and a decline in species richness from hardwater habitats in the Limestone Alps to softwater sites in the Central Alps. Also, Tolotti et al. (2006) found differences in the zooplankton composition of lakes in silicate and lakes in limestone areas which they explain with the higher mineralisation and thus buffer capacity of hardwater lakes. A study on the influence of melting permafrost on the ecology of high mountain lakes showed that zooplankton reacts to the resulting chemical changes – including increased ion content, in particular high concentrations of sulphate, magnesium and calcium – with a reduction in species diversity, as only the most resistant species survive (Thaler et al. 2015).

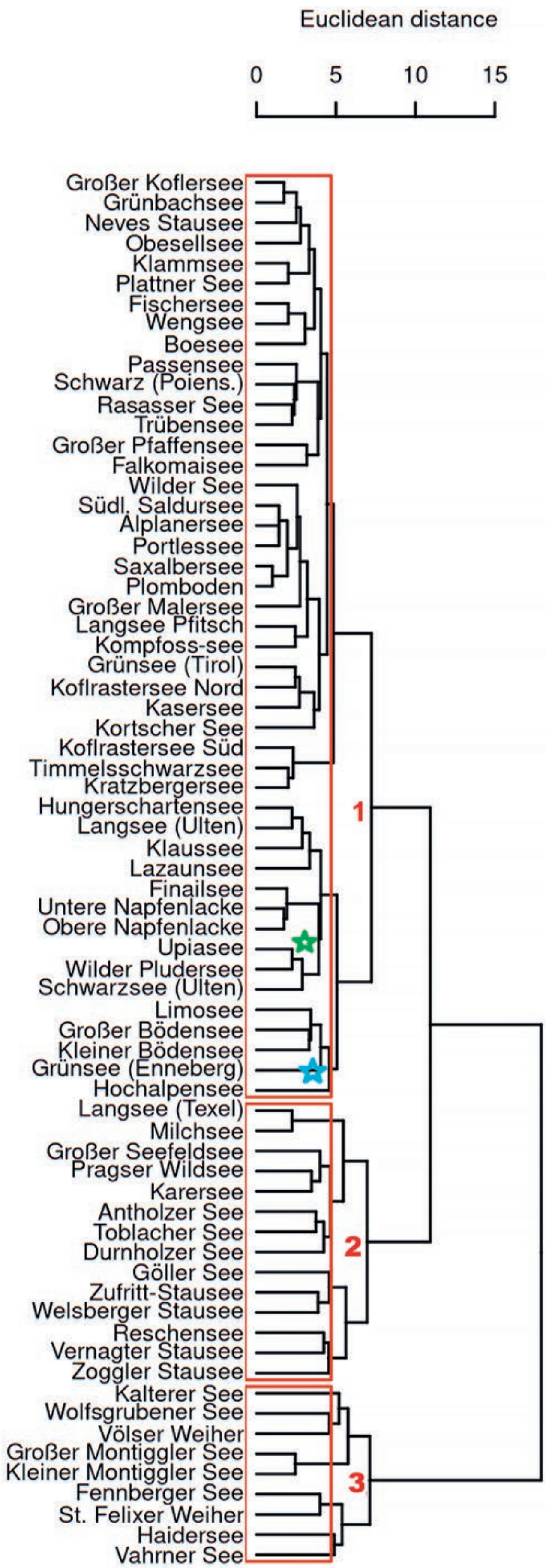

Fig. 6: Dendrogram based on the zooplankton taxa presence-absence (Euclidean distance, method "ward", function to compute agglomerative coefficient: agnes). Red lines mark the clusters; blue asterisk: lakes in limestone area; green asterisk: lakes influenced by permafrost.

Group two includes oligotrophic lakes situated below 2000 m, reservoirs and some of the frequently sampled alpine lakes. Group three consists of the meso- to eutrophic lakes situated below 2000 m.
The zooplankton communities of the first group showed a low taxa richness and were characterized by the rotifers *Polyarthra dolichoptera*, *Keratella cochlearis* and *Keratella* gr. *quadrata* and the crustaceans *Cyclops abyssorum tatricus* and *Chydorus sphaericus*. The communities of the second group were richer, with the rotifers *Kellicottia longispina*, *Keratella cochlearis*, *Polyarthra dolichoptera* and *Filinia terminalis* and the crustaceans *Daphnia longispina* and *Chydorus sphaericus* as the main representatives. The lakes of group three had quite diversified communities with the same main rotifer species as found in group two but also with species from the genera *Trichocerca* and *Synchaeta*. In these lakes, among the crustaceans, next to *Daphnia longispina* and *Chydorus sphaericus*, *Diaphanosoma brachyurum*, *Ceriodaphnia pulchella* and *Mesocyclops leuckarti* also played an important role.
As expected, despite the limitations of the single sampling, a visible difference can be identified in the community composition of alpine lakes and lower-lying meso- to eutrophic lakes. The oligotrophic lakes below the treeline and three frequently sampled alpine lakes lie in between.
The zooplankton was quantitatively recorded in 61 of the 70 lakes. In the lakes below 2000 m the abundances reached values ranging from 1 to 4878 ind. L^{-1} for rotifers, 0 to 115 ind. L^{-1} for copepods and from 0 to 401 ind. L^{-1} for cladocerans. In the lakes above 2000 m, the population densities were usually low, however, relatively high abundances of rotifers and copepods were also observed. Figure 7 shows the mean percentage of each zooplankton group, considering only lakes sampled more than once. All lakes but two alpine lakes present a high percentage of rotifers accounting for 59 to 99 % of total zooplankton. The predominance of rotifers indicates an increased trophic level (Gannon & Stemberger 1978) but is also related to high fish populations in all of these lakes (unpublished data), which leads to a depletion of crustacean plankton (Hessen et al. 2006; Tiberti et al. 2025). In the lower-lying lakes, the crustaceans are mainly represented by small cladocerans, which is primarily due to high fish pressure (Thaler & Tait 2021). The copepods are predominantly represented by cyclopoids, while calanoids are rare. The crustacean plankton of alpine lakes consists mainly of cyclopoid copepods.

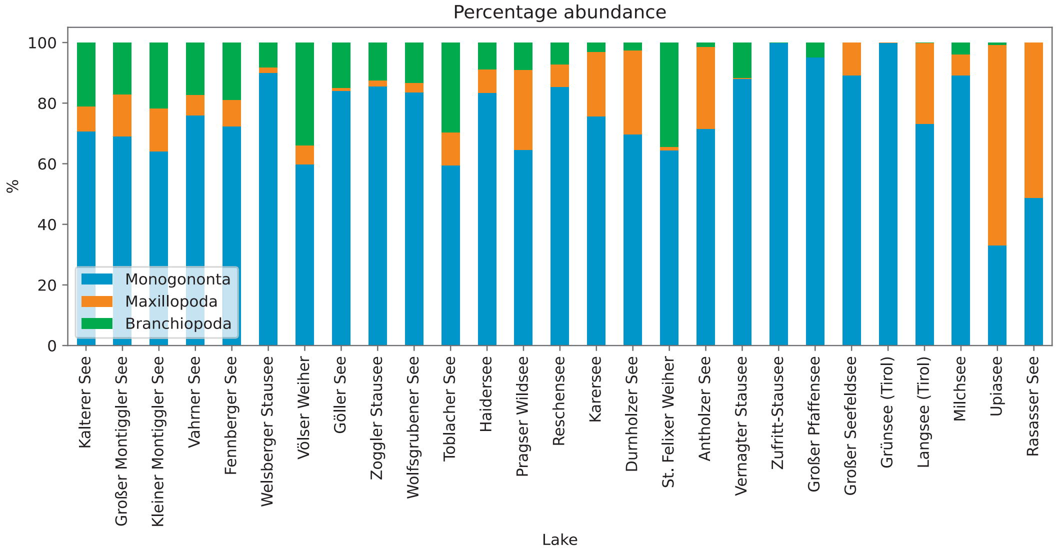

Fig. 7: Percentage composition of zooplankton by group (only lakes with more than one sampling). The last five on the right are reservoirs, the next seven to the left are alpine lakes.

3.3 Diversity and ecological factors

Zooplankton biodiversity was calculated with two commonly used indicators: species richness and Shannon index (Shannon 1948). Species richness represents the count of the total number of species, the Shannon index considers the number of species and their relative abundance, indicating how evenly the individuals are distributed among the different species. The number of taxa per lake was calculated from the sum of all taxa found during the entire study period. Since most of the high mountain lakes were sampled only once, in summer or autumn, it is likely that not the entire taxonomic spectrum could be recorded, not least due to the seasonality of population development (Jersabek et al. 2001). The Shannon index was calculated as the average of all values available for the survey period; the Shannon index of the repeatedly sampled lakes did not change significantly during the entire study period (Thaler & Tait 2021; unpublished data).

Total zooplankton taxa richness (Fig. 8) ranged from 5 to 58 taxa with an average of 31 taxa in lakes below 2000 m, and from 2 to 19 taxa with an average of 8 taxa in lakes above 2000 m. The values for the reservoirs (all located below 2000 m) were between 3 and 28 taxa with an average of 18.

The number of rotifer taxa varied from 9 to 31 (mean 19) in the lakes below 2000 m and from 1 to 12 (mean 5) in the lakes above 2000 m. Ejsmont-Karabin et al. (2020) provide comparable values for lowland lakes in Poland, and Tiberti et al. (2025) report similar values for high altitude lakes in the Western Alps.

The individual lakes hosted 1 to 16 species (mean 6) of cladocerans in lakes below 2000 m and 0 to 5 species (mean 2) above 2000 m. These relatively low numbers compared to data from the literature (e.g., Walseng et al. 2006; Ejsmont-Karabin et al. 2020) may be partly due the inclusion of almost exclusively planktic species in our study.

Concerning the copepods, the number of cyclopoid taxa amounted to 1 to 5 taxa in the lakes below 2000 m and 0 to 1 species in the alpine lakes. Calanoid copepods, however, were only found in a small number of lakes at each altitude and even then were represented by a single species (*Eudiaptomus gracilis* or *Eudiaptomus vulgaris* in lakes < 2000 m; *Arctodiaptomus alpinus* or *Acanthodiaptomus denticornis* in lakes > 2000 m, the latter also in one lake < 2000 m). The literature also states that calanoid copepods occur in a relatively small percentage of inland waters (Belmonte 2018). As with the cladocerans, the low number of copepods is due to the restriction to mainly planktic species. The higher species numbers for cladocerans than for copepods was also found by other authors (e.g., Heuschele et al. 2024). Heuschele et al. (2024) does not rule out differences in reproductive mode, feeding behaviour or other functional characteristics as possible reasons for this observation.

The taxa richness of the lakes at different altitudes differed significantly (Fig. 8), and while there was no difference between the reservoirs and the other lower-lying lakes, the number of species in the reservoirs and the alpine lakes differed significantly, too. Since reservoirs are artificial bodies of water whose ecosystems function differently from those of natural lakes and therefore differ in terms of the composition, abundance and diversity of zooplankton (Umi et al. 2024), they are listed separately here, even though they are also located below 2000 m.

The Shannon index (Fig. 8) varied from 0.47 to 1.72 (average 1.08) in lakes below 2000 m, from 0.47 to 1.19 (average 0.91) in reservoirs and from 0.0 (only 1 species) to 1.44 (average 0.73) in the alpine lakes. The differences in Shannon index values of the various groups of lakes (above 2000 m, below 2000 m and reservoirs) were small; only the values for lakes below 2000 m were significantly higher than those for alpine lakes.

All Shannon index values are relatively low, partly because of the dominance of a few taxa, due to an increased trophic state (Slugocki & Czerniawski 2018) in the lakes below 2000 m and partly due to the extreme conditions in the alpine lakes, where only the best adapted species can thrive (Lamouille-Hébert et al. 2024; Sommaruga 2025). However, even in alpine lakes, mass developments of individual species can occur (e.g., *Keratella cochlearis* 1074 ind. L^{-1}, Großer Pfaffensee, 1989-09-12).

The values of the lakes and reservoirs located below 2000 m are lower than those found in other lakes (e.g., lowland lakes in Polen; Slugocki & Czerniawski 2018). The low values

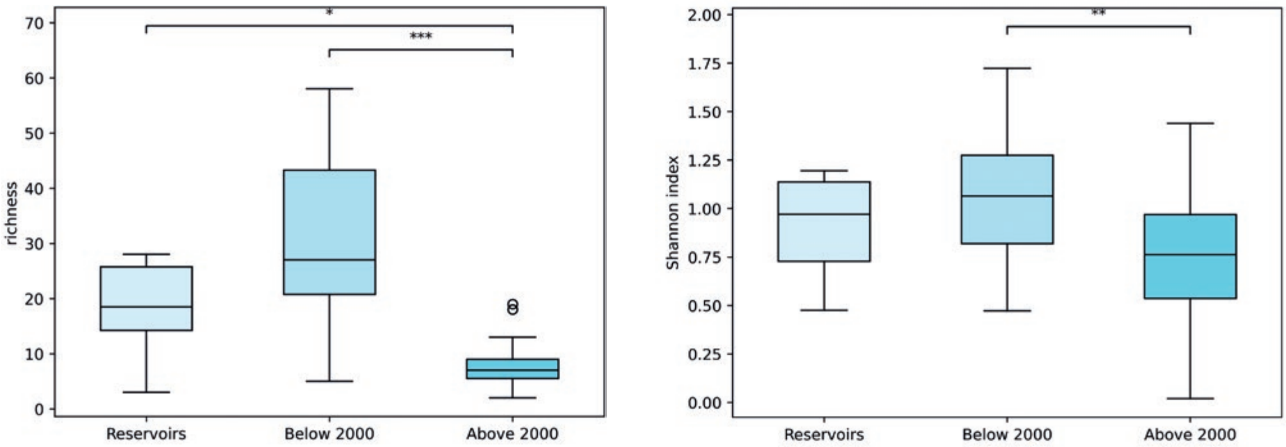

Fig. 8: Box plot of zooplankton species richness (6 reservoirs, 17 lakes < 2000 m, 47 lakes > 2000 m) and Shannon index (6 reservoirs, 17 lakes < 2000 m, 38 lakes > 2000 m). The stars indicate the level of significance (* $p < .05$, ** $p < .01$, *** $p < .001$).

of Shannon index of the alpine lakes agree with the values calculated by Tiberti et al. (2025) for alpine lakes in the Western Alps.

Diversity, measured in this study as species richness and Shannon index, is influenced by various environmental factors. Species richness generally decreases with increasing altitude (Hessen et al. 2007; Shurin et al. 2007), which is due in part to the decrease in temperature with altitude, leading to physiological limitations and reduced energy availability, but also influenced by other factors such as lake morphology, geology of the catchment area and parameters relevant to lake primary production (Obertegger et al. 2010). Obertegger et al. (2010) found that the size of a lake has the strongest influence on species richness of rotifers, and they attributed this to the greater variety of habitats in larger lakes and the lower extinction rate and higher immigration rate compared to smaller lakes. Furthermore, the influence of environmental factors on the number of species varies depending on the zooplankton group. In their study of predominantly shallow lakes, Jeppesen et al. (2000) found, for example, that lake depth correlated significantly and positively with the species diversity of rotifers, but not with the species diversity of cladocerans and copepods. Felifova et al. (2020) observed a positive correlation of copepod richness with waterbody area in Arctic lakes and ponds, while the cladocerans were positively correlated only with temperature.

To verify whether taxa richness and Shannon index correlate with ecologically important environmental factors, the non-parametric Spearman test was applied. The environmental factors examined were altitude, lake area, conductivity, alkalinity and the content of calcium, total phosphorus and chlorophyll a. Conductivity, alkalinity and calcium content provide an indication of the geology of the catchment areas, while total phosphorus content and chlorophyll a concentration are related to primary production.

The taxa richness of total zooplankton (Fig. 9) decreases significantly with altitude, showing a strong negative correlation ($p < .001$), moderate positive correlations were found between richness and lake area as well as with parameters related to primary production (total phosphorus, Chlorophyll a) and geology (conductivity, alkalinity and calcium) ($p < .001$).
When considering the three main groups rotifers, cladocerans and copepods separately (Fig. 9), a slightly different picture emerges. Rotifers show a strong negative correlation ($p < .001$) with altitude, while the other two groups are only moderately correlated with this parameter. The lake area appears to play a role only for rotifers, with a moderate positive correlation. Furthermore, there is a moderate correlation between rotifers and cladocerans and productivity-related parameters, which does not apply to copepods.

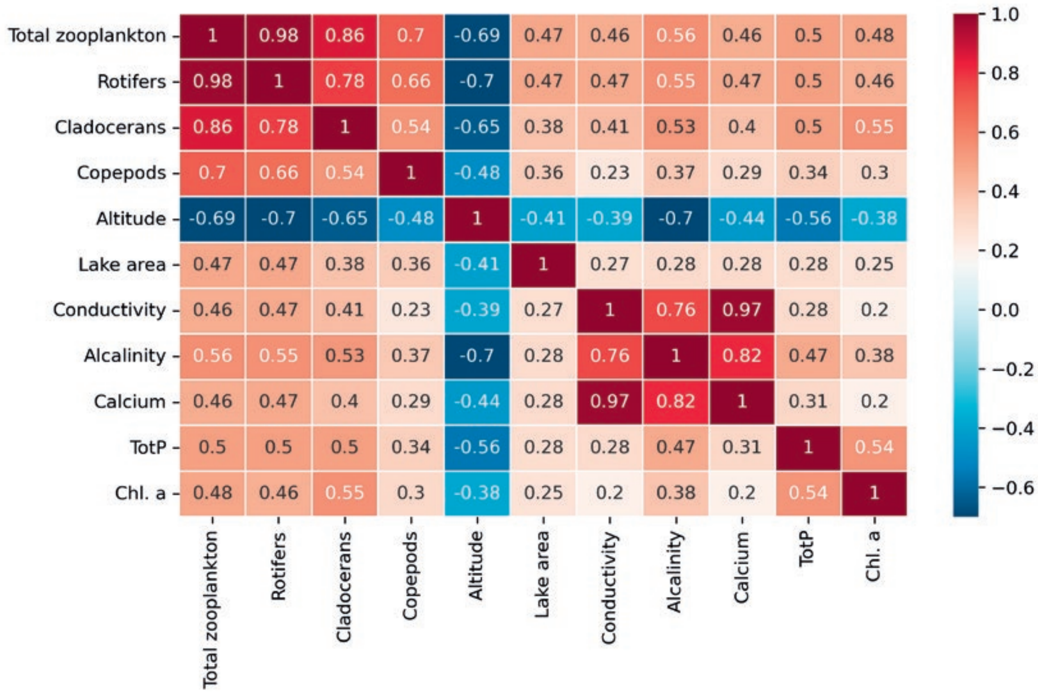

Fig. 9: Spearman correlation matrix (all lakes, n = 70) of taxa richness of total zooplankton, rotifers, cladocerans and copepods, as well as altitude, lake area, conductivity, alkalinity and the content of calcium, total phosphorus (TotP) and chlorophyll a (Chl. a). Physical and chemical values are averages of all available data for the period of survey. The colour intensity reflects the strength of the correlation. Absolute values from 0.20 to 0.39 indicate weak correlation, 0.40 to 0.69 moderate correlation, and 0.70 to 0.89 strong correlation (according to Fowler et al. 2009).

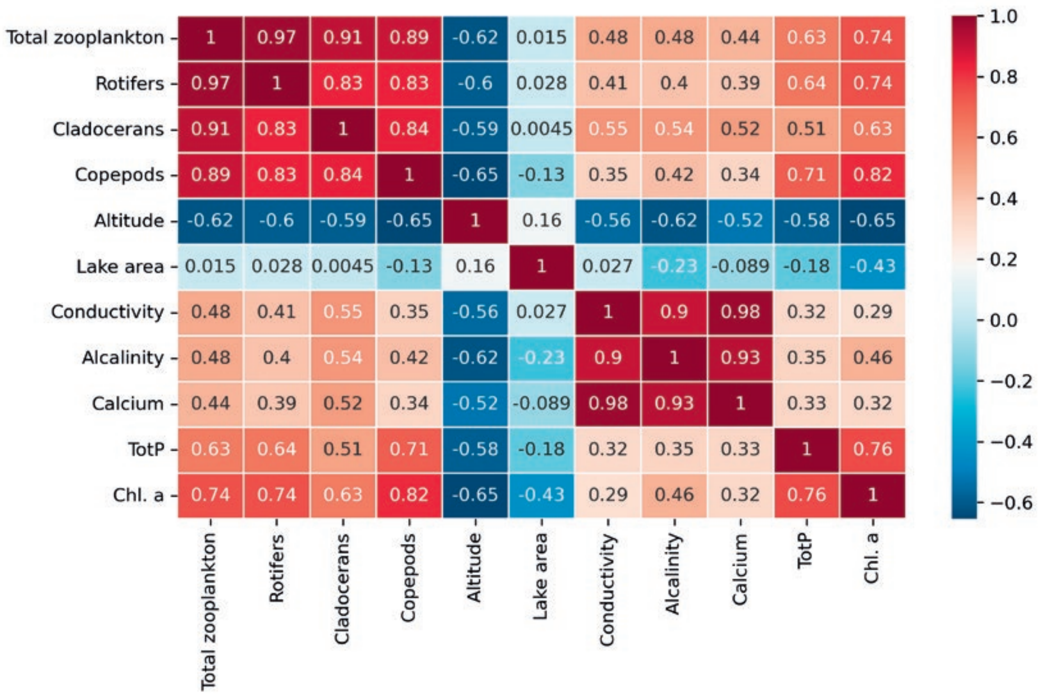

Fig. 10: Spearman correlation matrix (lakes below 2000 m, n = 23) of taxa richness of total zooplankton, rotifers, cladocerans and copepods, as well as altitude, lake area, conductivity, alkalinity and the content of calcium, total phosphorus and chlorophyll a (for explanation see previous caption).

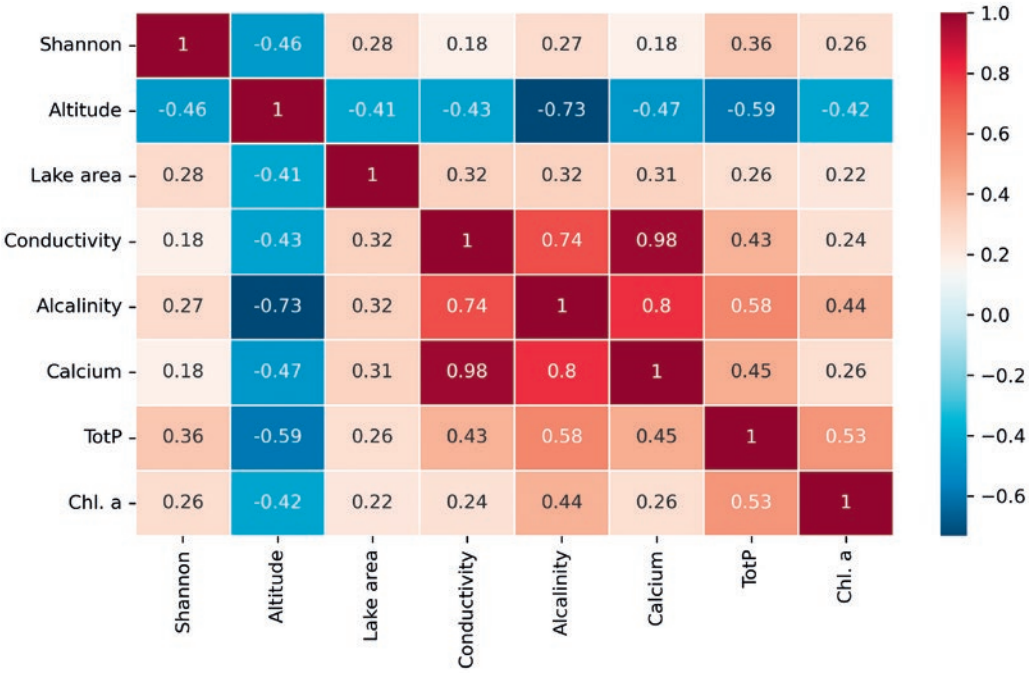

Fig. 11: Spearman correlation matrix of Shannon index (n = 61), altitude, lake area, conductivity, alkalinity and the content of calcium, total phosphorus and chlorophyll a (for explanation see previous captions).

The parameters related to geology show a moderate positive correlation with rotifers and cladocerans ($p < .001$), but no significant correlation with copepods.
Considering only the lakes located below 2000 m (Fig. 10), it can be observed that the richness of the total zooplankton and of the three zooplankton groups are positively correlated with the factors related to primary production (moderate to strong correlation; $p < .001$). However, no correlation between richness and lake size can be established.
In summary, across all of the lakes included in this study, altitude emerged as the most influential environmental factor for both overall taxa richness and richness of individual groups. Lake area showed a moderate positive correlation with total zooplankton and rotifer richness, in agreement with Obertegger et al. (2010), but only a weak correlation for cladocerans and copepods. Parameters related to geology and primary production correlated with total zooplankton, rotifer and cladoceran richness, but did not influence copepod richness. In lakes below 2000 m, productivity-related parameters strongly influenced the overall taxa richness and the richness of individual groups, while no correlation with lake area was identified.

The influence of environmental factors on species richness has been intensively studied previously (Jersabek et al. 2001; Hessen et al. 2006; Mis & Ustaoğlu 2017; Slugocki & Czerniawski 2018; Fefilova et al. 2020; Karpovic & Ejsmont 2021; Umi et al. 2024), with some of the reported results consistent with our findings, however, the results of these studies are not always in agreement. Jeppesen et al. (2000) found a decrease of all zooplankton taxa with increase of total phosphorus in studies of mainly shallow Danish lakes, however, these were eutrophic lakes with a high phosphorus content, whereas the lakes we studied were almost all classified as oligotrophic to mesotrophic. Studies of copepods by Jersabek et al. (2001) in lakes from the mountain to the alpine zone of the Eastern Alps showed that the size of the water body, trophic conditions, temperature, altitude, pH value and conductivity were the most important variables in terms of species distribution. These findings partially apply to our results: altitude showed a moderate correlation with copepod taxa richness, lake area and the parameters related to geology and to primary production a weak correlation. For Hessen et al. (2006), who studied the pelagic crustacean zooplankton of a large number of Norwegian lakes, the level of primary production was the major control of copepod and cladoceran richness,

whereas lake size only had a minor influence on species richness. We recorded similar patterns in our lakes, especially in those located below the treeline, where a relatively strong influence of primary production on taxa richness of cladocerans and copepods could be observed. When assessing the composition of rotifer and crustacean plankton in Malaysian lakes, Umi et al. (2024) also noted that the composition, abundance and diversity of species correlated significantly with environmental variables related to the trophic status of the lakes.
In contrast to the taxa richness, which correlated with all environmental parameters considered, albeit to varying degrees, the Shannon index (Fig. 11) correlates only with altitude (moderately negative, $p < .001$).

4. Conclusions

This study summarized the results of zooplankton surveys (rotifers and crustaceans) conducted in South Tyrolean lakes between 1979 and 2015, thus providing the first comprehensive zooplankton checklist of South Tyrol. A total of 70 lakes located at altitudes ranging from 215 to 2892 m a.s.l. were sampled, about 20 % of all lakes in South Tyrol. The total number of taxa amounted to 99: 57 rotifers, 26 cladocerans and 16 copepods. Some of the taxa identified are new records for the region and currently not present in the Italian species checklists for Trentino-South Tyrol (Fontaneto et al. 2022; Margaritora et al. 2021): the rotifers *Anuraeopsis fissa*, *Brachionus calyciflorus*, *Collotheca pelagica*, *Pompholyx sulcata* and the typical planktic cladocerans *Daphnia ambigua* and *Daphnia pulex*.
Analysis of the overall taxa richness and the richness of rotifers, cladocerans and copepods identified altitude as the most influential environmental factor, with the number of taxa decreasing significantly with increasing altitude. Taxa richness also correlated with lake size and with parameters related to lake primary production and catchment geology, with some differences depending on the zooplankton group.
The characterisation of zooplankton biodiversity in South Tyrol's lakes, the compiled checklist of zooplankton taxa and the ecological analysis presented in this study, form the basis for further investigations providing additional insights, particularly for high mountain lakes, especially in limestone areas, where, according to the literature (e.g., Jersabek et al. 2001), a greater species diversity than encountered in our work would be expected.
Comparison of these results with future studies also including lakes being created by melting glaciers could provide insight into the elsewhere observed impact of climate change on zooplankton richness and community composition (e.g., Tiberti et al. 2025).

5. Zusammenfassung

In der vorliegenden Studie werden die Ergebnisse der in den Jahren 1979 bis 2015 in 70 zwischen 215 und 2892 m ü.d.M. gelegenen Südtiroler Seen durchgeführten Untersuchungen des Rädertier- und Crustaceenplanktons vorgestellt. Die Probenentnahme erfolgte sowohl im Rahmen der Seenüberwachung als auch verschiedener wissenschaftlicher Projekte. Die Zusammensetzung des Zooplanktons in den verschiedenen Seen wird verglichen und der Einfluss von Umweltfaktoren auf die Biodiversität untersucht. Die Gesamtanzahl der Taxa belief sich auf 99, davon waren 57 Rädertiere, 26 Cladoceren und 16 Copepoden. Das Artenspektrum und die relative Häufigkeit der einzelnen Arten zeigten Unterschiede zwischen den Seen oberhalb und unterhalb der Baumgrenze. *Polyarthra dolichoptera* war die häufigste Art in allen Seen, gefolgt von *Kellicottia longispina*, *Keratella cochlearis* und *Synchaeta* spp. in den Seen unterhalb der Baumgrenze und *Keratella cochlearis* und *Keratella* gr. *quadrata* in den Seen oberhalb der Baumgrenze (alpine Seen). Die Cladoceren waren in den Seen unterhalb der Baumgrenze hauptsächlich durch *Daphnia*-, *Bosmina*- und *Ceriodaphnia*-Arten vertreten, in den alpinen Seen durch *Chydorus sphaericus*. Unter den Copepoden spielte *Cyclops* *abyssorum tatricus* in den alpinen Seen eine herausragende Rolle. Die in dieser Studie über Südtiroler Seen nachgewiesenen Rädertiere *Anuraeopsis fissa*, *Brachionus calyciflorus*, *Collotheca pelagica, Pompholyx sulcata* sowie die Cladoceren *Daphnia ambigua* und *Daphnia pulex* sind derzeit nicht in den nationalen Artenlisten enthalten. Die Untersuchung der taxonomischen Zusammensetzung der Zooplanktongemeinschaften ergab drei Gruppen von Seen, die sich hauptsächlich hinsichtlich ihrer Höhenlage und ihres Trophiegrads unterscheiden. In den natürlichen Seen unterhalb der Baumgrenze war die Anzahl der Taxa pro See deutlich höher als in den alpinen Seen und höher als in den Stauseen. Die Anzahl der Taxa nahm mit zunehmender Höhe deutlich ab, korrelierte aber auch mit der Fläche des Sees und mit Parametern, die mit der Primärproduktion des Sees und der Geologie des Einzugsgebiets zusammenhängen. Die Unterschiede zwischen den Shannon-Index-Werten der einzelnen Seen waren gering, und der Index korrelierte nur signifikant mit der Höhe.

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Appendix

Table A: Lakes sampled for zooplankton.

German name	Italian name	altitude (m a.s.l)	lake area (ha)	depth (m)	watershed (Kmq)	lake type
Kalterer See	Lago di Caldaro	215	131.1	5.6	47.27	<2000
Naturbad Gargazon*	Biopiscina Gargazzone	265				<2000
Großer Montiggler See	Lago di Monticolo Grande	492	17.8	12.5	2.27	<2000
Kleiner Montiggler See	Lago di Monticolo Piccolo	519	5.2	14.8	1.25	<2000
Vahrner See	Lago di Varna	678	1.5	3.5	1.78	<2000
Fennberger See	Lago di Favogna	1034	1.3	4.0	1.07	<2000
Welsberger Stausee**	Bacino di Monguelfo	1055	45	25.0		<2000
Völser Weiher	Lago di Fiè	1056	1.6	3.5	0.14	<2000
Göller See	Lago del Colle	1081	0.6	5.0	0.13	<2000
Zoggler Stausee**	Bacino di Zoccolo	1141	143.0	34.0	181.20	<2000
Wolfsgrubener See	Lago di Costalovara	1176	3.3	4.0		<2000
Toblacher See	Lago di Dobbiaco	1251	14.3	3.5	108.23	<2000
Haidersee	Lago di S. Valentino alla Muta	1449	89.0	15.0	33.97	<2000
Pragser Wildsee	Lago di Braies	1489	31.0	36.0	26.64	<2000
Reschensee**	Bacino di Resia	1498	660.0	25.0	176.00	<2000
Karersee	Lago di Carezza	1519	3.5	17.0	5.81	<2000
Durnholzer See	Lago di Valdurna	1560	11.6	12.8	27.87	<2000
St. Felixer Weiher	Lago di S.Maria (Tret)	1604	3.8	3.0	1.51	<2000
Antholzer See	Lago di Anterselva	1640	43.3	38.0	19.06	<2000
Vernagter Stausee**	Bacino di Vernago	1690	125.0	56.0	69.00	<2000
Zufritt-Stausee**	Bacino di Gioveretto	1850	70.0	50.0	77.00	<2000
Neves-Stausee**	Bacino di Neves	1856	48.0	86.0		<2000
Wengsee	Lago di Venga	1881	1.4	5.5		<2000
Grünsee (Enneberg)	Lago Verde (Marebbe)	2043	1.1	2.5	2.09	>2000
Kasersee	Lago della Casera	2117	2.9	5.2	5.27	>2000
Kratzbergersee	Lago di S.Pancrazio	2119	2.4	12.0	0.63	>2000
Obesellsee	Lago di Saltusio	2151	0.9	3.5		>2000
Limosee	Lago di Limo	2159	2.6	9.0	0.55	>2000
Klaussee	Lago della Chiusetta	2162	1.3	2.5		>2000
Falkomaisee	Lago Valcomai	2180	0.7	2.8	0.34	>2000
Großer Pfaffensee	Lago Grande del Prete	2222	1.7	5.6	0.39	>2000
Langsee (Pfitsch)	Lago Lungo del Passo (Vizze)	2231	0.6	17.2	0.04	>2000
Boèsee	Lago Boè	2250	0.6	16.0	0.59	>2000
Hochalpensee	Lago dei Colli Alti	2252	1.8	4.0	0.17	>2000
Grünbachsee	Lago Verde	2257	1.4	0.5	0.27	>2000
Klammsee	Lago di Gola	2258	1.1	2.7	0.67	>2000
Plattner See	Lago di Plat	2258	0.1	0.5	0.37	>2000
Großer Seefeldsee	Lago Grande di Maranza	2271	5.6	23.9	1.83	>2000

German name	Italian name	altitude (m a.s.l)	lake area (ha)	depth (m)	watershed (Kmq)	lake type
Großer Bödensee	Lago Grande dei Piani	2335	3.1	5.0		>2000
Kleiner Bödensee	Lago Piccolo dei Piani	2335	1.4	4.0		>2000
Grünsee (Spronser Seen)	Lago Verde di Tessa	2338	4.0	29.0	3.07	>2000
Langsee (Ulten)	Lago Lungo (Ultimo)	2340	3.7	3.0	4.87	>2000
Trübensee	Lago Torbo	2344	5.4	14.0	5.66	>2000
Langsee (Spronser Seen)	Lago Lungo di Tessa	2384	20.1	45.0	2.07	>2000
Alplanersee	Lago Trenta	2387	3.0	20.0	0.49	>2000
Koflrastersee Süd	Lago del Covolo Sud	2405	3.1	9.0	0.30	>2000
Koflrastersee Nord	Lago del Covolo Nord	2407	3.2	21.0	0.65	>2000
Passensee	Lago del Passo	2409	1.5	5.0	0.07	>2000
Lazaunsee	Lago di Lazaun	2429	1.8	2.0		>2000
Großer Koflersee	Lago Grande dei Covoli	2434	1.1	4.0	0.87	>2000
Kompfoss-See	Lago Campofosso	2442	1.2	8.2	0.10	>2000
Saxalbersee	Lago di Sassalbo	2460	2.1	13.8	0.54	>2000
Untere Napfenlacke	Lago Napfen inferiore	2478	0.3	2.0	0.02	>2000
Wilder Pludersee	Lago di Collecchio	2483	1.0	4.0	0.26	>2000
Plombodensee	Lago Plomboden	2486	3.0	6.7	0.37	>2000
Großer Malersee	Lago Maler Grande	2501	1.1	4.5	0.19	>2000
Kortscher See	Lago di Corces	2510	3.6	13.1	0.18	>2000
Obere Napfenlacke	Lago Napfen superiore	2514	0.2	2.0	0.01	>2000
Timmelsschwarzsee	Lago Nero del Tumolo	2514	6.4	27.0	1.05	>2000
Wilder See	Lago Selvaggio	2532	10.2	52.0	1.78	>2000
Milchsee	Lago di Latte (Tessa)	2540	2.3	12.3	0.65	>2000
Schwarzsee (Ulten)	Lago Nero (Val d'Ultimo)	2544	0.7	4.0	0.67	>2000
Schwarzsee (Poienseen)	Lago Nero (Campo Tures)	2551	1.1	6.7	0.19	>2000
Upiasee	Lago di Upia	2552	3.5	11.0	3.71	>2000
Rasasser See	Lago di Rasass	2682	1.5	9.3	0.15	>2000
Finailsee	Lago di Finale	2709	1.7	4.5	0.54	>2000
Südl. Saldursee	Lago di Saldura Sud	2747	1.6	8.5	3.06	>2000
Fischersee (Mals)	Lago di Saldura Ovest	2754	0.6	8.2	0.03	>2000
Hungerschartensee	Lago Tasca	2778	1.7	14.0	1.31	>2000
Portlessee	Lago di Portles	2892	0.6	10.0	0.14	>2000

*biopool
** reservoir