Aquat Ecol (2021) 55:1253–1271
https://doi.org/10.1007/s10452-021-09858-1

Shifts in zooplankton communities in high-mountain lakes induced by singular events (fish stocking, earthquakes): evidence from a 20-year survey in Slovenia (Central Europe)

Anton Brancelj

Received: 5 December 2020 / Accepted: 19 March 2021 / Published online: 8 April 2021

Abstract Thirteen mountain lakes, originally fishless, at 1325 and 2150 m a.s.l., with the maximum depths ranging from two to 15 m, and areas of 0.3 to 4.5 ha, were monitored between 1991 and 2012 in the Triglav National Park (Slovenia, Central Europe). The lakes are located on limestone bedrock, with no surface inflow or outflow. They range from ultra-oligotrophic to hypertrophic. They were stocked with fish between late 1920s and 1996. The zooplankton samples were collected as composites from the bottom to the surface at the deepest point of the lake, for both qualitative and quantitative analyses. In situ physical parameters in the water column were measured, and the samples for chemical analyses were collected in parallel with the zooplankton sampling. Thirty-two species, including Copepoda, Cladocera, Rotifera and Ciliata, were recorded. They belonged to three ecological groups: (1) constitutive, (2) scout and (3) benthic species. In some of the lakes, the species composition remained stable over the study period, but in lakes stocked with fish, significant changes occurred, in both species composition and biomass. Large-bodied species of Copepoda and Cladocera were eliminated by fish allowing small-bodied planktonic species of Copepoda, Cladocera and Rotifera to dominate the community, along with benthic species, associated with algal mats. The lake, stocked with fish in the 1920s, was hit by two strong consecutive earthquakes, in 1998 and 2004, after which a significant change in species composition and biomass was recorded.

Keywords Alpine lakes · Zooplankton · Biodiversity · Earthquake · Fish introduction · Human impact

Introduction

High-mountain lakes in the temperate zone are rather recent freshwater ecosystems. Deglaciation started about 10,000 years ago, and some lakes close to glaciers (*i.e.* above 2000–2500 m a.s.l.) have only recently lost their ice-cover (Rott et al. 1993; Bengtsson 2012). For this reason, most high-mountain lakes have a low biodiversity, including insects

Handling Editor: S.S.S. Sarma

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10452-021-09858-1.

A. Brancelj (✉)
Department of Organisms and Ecosystem Research,
National Institute of Biology, Večna pot 111,
1000 Ljubljana, Slovenia
e-mail: anton.brancelj@nib.si

A. Brancelj
University of Nova Gorica, Vipavska cesta 13,
5000 Nova Gorica, Slovenia

(aquatic larvae), most of which are tolerant of low temperatures, short ice-free periods and oligotrophic conditions. Fish have not colonized these lakes (Knapp and Sarnelle 2008; Ventura et al. 2017), as most lakes are connected to lowlands by rapids or even waterfalls, which enable up-stream colonization. Aquatic plants are usually present only in lower-altitude lakes (*i.e.* below the local tree line) (Urbanc-Berčič and Gaberščik 2002; Sienkiewicz and Gąsirovski 2016).

Colonization by zooplankton in the past was by natural vectors and only recently by humans. Transport of dormant eggs of Rotifera and Cladocera may have been by wind or birds, while Copepoda were probably transported only by migratory birds (*i.e.* waterfowl). Humans transported zooplankton within water containers, especially when trying to stock high-mountain lakes with fish (Ventura et al. 2017).

Research on high-mountain lakes around the world only began to attract attention recently, mostly related to climate change and airborn pollution (Anderson and Battarbee 1994; Batarbee et al. 2002, 2005, 2009; Catalan et al. 2002, 2017; Karst-Riddoch et al. 2005; Zhu et al. 2005; Williamson et al. 2008, 2016; Eskinazi-Sant'Anna et al. 2020). Most of these lakes are difficult to access, especially those above the tree line. However, in Europe they have been frequently visited or exploited by local people since the 15th century. In the Alps, as well as in other European mountain chains (the Pyrenees, and the Carpathian Mountains, including the Tatra Mountains), lakes close to or below the tree line were centers of economic activity, including seasonal farming, pasturing, mining, logging or charcoal production. The lakes above the tree line were visited only as resting points along trade routes or during seasonal migrations, crossing mountain ridges (Rejec Brancelj and Smrekar 2002).

Intensive studies on zooplankton community structure in high-mountain lakes were done so far only in the last two decades. They were carried out in rather short periods, usually within one or two years and focused on one/few lakes, but sampled with high frequency (*i.e.* several visits per year) (Schabetsberger et al. 2008; Ventura and Catalan 2008). On the other hand, most of the zooplankton surveys were done once or twice at the same lake and/or samples were collected over larger areas (Tonollli and Tonollli 1951; Löffler 1968, 1972; Cammarano and Manca 1997; Scabetsberger et al. 2006; Knapp and Sarnelle 2008; Kernan et al. 2009; Mis and Balik 2009; Burmistrova and Ermolaeva 2013; Ventura et al. 2017; Stoch et al. 2019). Only a small number of long-lasting studies, *i.e.* expanding over several consecutive years on the same lake or group of lakes, have been carried out. Evident reasons for this are logistical problems, as most high-mountain lakes are only accessible on foot (using horses or mules for transportation; more recently helicopters), with its concomitant limitations for carrying equipment (boats), while helicopter service is expensive. A few high-mountain lakes are accessible by car.

The Julian Alps (Slovenia; Central Europe) are the most south-eastern part of the Alps. Between 1991 and 2012, we performed regular national monitoring of these lakes in the late summer/early autumn for physical, chemical and biological parameters. At the same time, we performed research on the lakes within national (1995–1998: SLO-ALPE) and international projects (1994: AL-PE 2: Acidification of Mountain Lakes: Palaeolimnology and Ecology; 1995–1998: MOLAR: Mountain Lake Research; 2000–2003: EMERGE: European Mountain lake Ecosystems: Regionalization, diaGnostics & socio-economic Evaluation). Research activities ranged from present-day limnology (physical, chemical and biological parameters) to palaeolimnology (core-sample analysis), which focussed on airborne pollution, climate change, sedimentation and community structure/changes over time (Brancelj 2002; Batarbee et al. 2002, 2005; Baterbee and Bennion 2012). Environmental changes, as indicated by duration of ice-cover and occasional release of nutrients from the local permafrost, fish introductions and geological events (earthquakes, landslides) can impact these small but interesting habitats/ecosystems (Brancelj 2002; Brancelj et al. 2012).

The aim of this contribution is to present the distribution, dynamic and directions of changes in the zooplankton community structure in high-mountain lakes on limestone bedrock, related to the environmental changes and human impacts during 20-year-long period.

Material and methods

Description of the lakes

Within the Triglav National Park (TNP) in NW Slovenia (Central Europe; 46.20° N, 13.45° E, with an area of 880 km^2), there are 14 high-mountain lakes spanning an altitude gradient from 1325 to 2150 m a.s.l. (Fig. 1; Table 1; https://en.wikipedia.org/wiki/Triglav_National_Park). They are all on limestone bedrock with prevailing Triassic and local patches of Jurassic bedrock (Buser 1986). All of them were formed by the local glaciers and probably became ice-free *ca*. 5000 years ago at the lower altitudes and less than 1000 years ago at the highest altitudes. They are organized into three geographical/hydrological groups, namely Triglavska Jezera (eight lakes) (Jezero in Slovene = lake; Jezera in plural), Kriška Jezera (three lakes) and Krnska Jezera (three lakes; one of them not included in this study). There is no direct surface (*i.e.* river) connection between the lakes within each group, while the sub-surface hydrological connections are weak and occasional (Urbanc and Brancelj 2000; Brancelj 2002). An exception is Dvojno Jezero (Double Lake), which, during high water levels, forms for a short period (usually one or two weeks in late spring) one contiguous lake, but at low

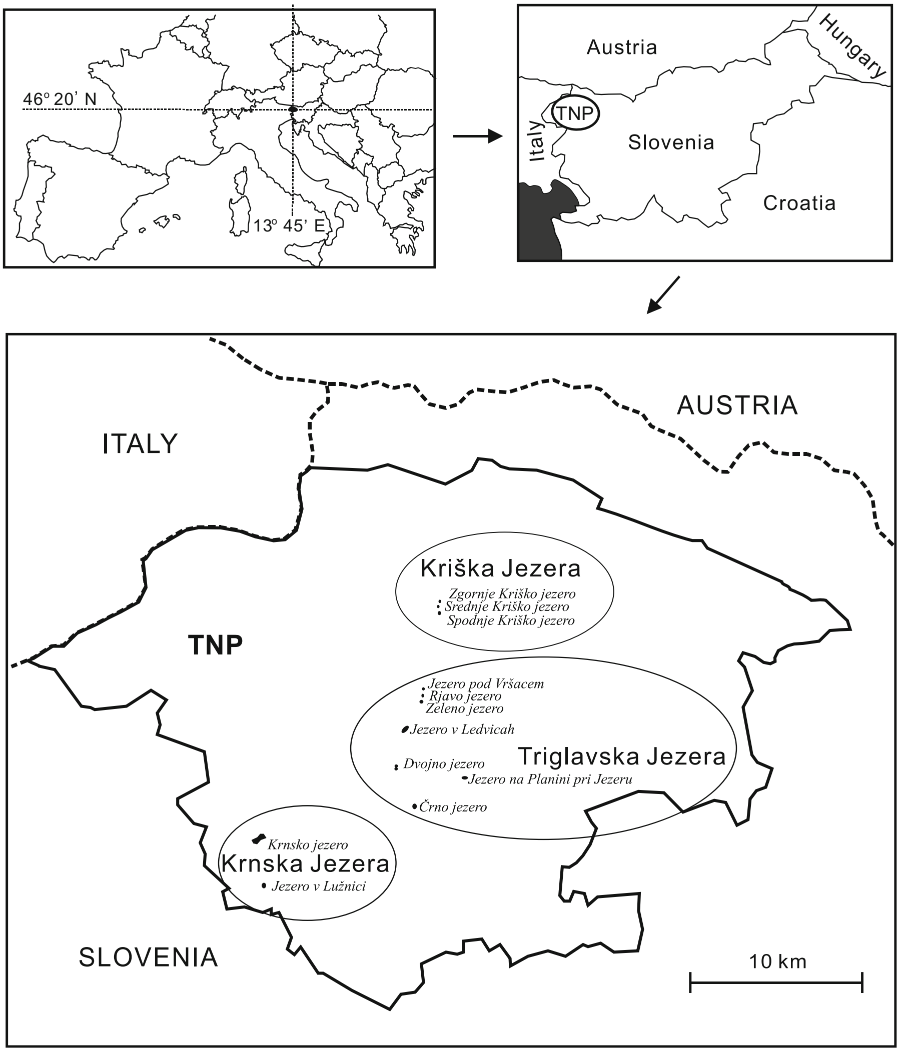


Fig. 1 Location of the Triglav National Park (TNP; Slovenia; Central Europe). Lake groups and the position of individual lake within each group are indicated in ovals

Table 1 The main characteristics of high-mountain lakes in the Triglav National Park (Slovenia; Central Europe)

Lake	Altitude (m a.s.l.)	Depth (m)	Area (ha)	Trophic state (1992)	Trophic state (2012)	Fish (stocked; year)	Macrophytes* (present; year)
(A) Rjavo Jezero (2)	2002	3	1.3	O	O	no	no
(A) Jezero pod Vršacem (3)	1993	6	0.6	O	O	no	no
(A) Zeleno Jezero (4)	1983	2	0.6	O	O	no	before 1900
(A) Jezero v Ledvicah (7)	1830	14	2.2	O	O	no	no
(A) Dvojno (5.) Jezero (9)	1669	8	1.0	O	M	1991	after 2000
(A) Dvojno (6.) Jezero (10)	1669	6	0.7	O	M	1991	after 2000
(A) Jezero na Planini pri Jezeru (11)	1430	10	1.6	E	E/H	1950s	before 1900
(A) Črno Jezero (13)	1325	6	0.9	O	M	1996	no
(B) Jezero v Lužnici (8)	1800	9	0.5	O	O	no	no
(B) Krnsko Jezero (12)	1383	15	4.5	M	M	1920s	before 1900
(C) Zgornje Kriško Jezero (1)	2150	8	0.7	UO	UO/O	no	no
(C) Srednje Kriško Jezero (5)	1950	8	0.3	O	O	no	no
(C) Spodnje Kriško Jezero (6)	1880	7	0.3	O	O	no	before 1900?

*Submerged macrophytes.

UO, ultra-oligotrophic; O, oligotrophic; M, mesotrophic; E, eutrophic; H, hypertrophic

(A)—Triglavska Jezera group; (B)—Krnska Jezera group; (C)—Kriška Jezera group. Jezero (*sing.*) / Jezera (*pl.*), lake/lakes. The numbers in brackets after the name of the lake refer to their position along a vertical distribution (highest/lowest) and are referred to in Fig. 4

levels (in summer and autumn) it separates into two lakes with slightly different physical and chemical characteristics (Brancelj 1999, 2002). When they are separate, they are designated as lake Dvojno 5th and Dvojno 6th Jezero due to their position within the Triglavska Jezera group.

The lakes' depths range from 2 to 15 m and are subject to water-level oscillations of one to two meters within a one-year hydrological cycle. Surface water temperature in August/September varied between 10–11 °C at the highest-altitude lake (Zgornje Kriško Jezero—hereafter ZKJ; 2150 m a.s.l.) to 20–21 °C at the lowest (Jezero na Planini pri Jezeru—hereafter Planina; 1430 m a.s.l.) (Brancelj 2002). Ice-cover period varies with altitude and between years. In 1992, the highest-altitude lakes were ice-free between the end of May and the end of November, while in 2012 they were ice-free from the mid-April until mid-December (Brancelj, personal observations and thermistor measurements—not published).

The lakes above the tree line (1670 m a.s.l. = higher-altitude lakes) are oligotrophic, with low nutrient levels (10–25 µg P_{tot}/L). Lakes below the tree line (= lower-altitude lakes) are mesotrophic or even hypertrophic, with P_{tot} concentration ranging from 25 µg/L on the surface to > 150 µg/L at the bottom. Elevated trophic levels are due to human activities such as pasturing and charcoal production in the past few hundred years (Rejec Brancelj and Smrekar 2002). Additional nutrient increases occurred after fish introductions (Brancelj et al. 2000; Brancelj 2002). pH is alkaline (7.5–8.1) due to the limestone bedrock, but near the surface it can decrease slightly after heavy rains or snow melt.

Oligotrophic lakes (Table 1) have high transparency, with Secchi-disk depth greater than lake depth. Before 2000, some lakes below the tree line had high transparency, which decreased after fish introduction. Before 1992, only two lakes (Krnsko Jezero—hereafter Krn; Planina) had Secchi-disk depth less than their actual depth. However, in late summer many lakes, including some oligotrophic ones, occasionally experience blooms of filamentous green algae (Zygnematales), which initially grew on the bottom in early summer and later floated to the surface, accompanied by some benthic Cladocera species.

Submerged macrophytes (genera *Batrachyum*, *Chara*, *Potamogeton*) are present in six lakes, two of them located above the local tree line (Zeleno Jezero; 1983 m a.s.l. and Spodnje Kriško Jezero; 1880 m a.s.l.). In two lakes (Dvojno 5th and Dvojno 6th Jezero; 1670 m a.s.l.), macrophytes were introduced recently, *i.e.* in 2000 (Table 1; Urbanc-Berčič and Gaberščik 2002).

In oligotrophic lakes, oxygen concentrations near the bottom were always well above hypoxia (*i.e.* $> 10\%$ saturation), while in mesotrophic or hypertrophic lakes anoxic conditions existed from a few months to the whole year (Brancelj 2002).

Fish introduction started in the lakes in the 1920s, when arctic char (*Salvelinus alpinus* (Linnaeus, 1758)), along with minnow (*Phoxinus phoxinus* (Linnaeus, 1758)), were introduced to lake Krn. Next was lake Planina, where chub (*Leuciscus cephalus* (Linnaeus, 1758)), crucian carp (*Carassius carassius* (Linnaeus, 1758)) and arctic char were introduced in the 1950s (probably in 1957), although the arctic char soon died out (Povž 1997). In lake Dvojno Jezero, about 20 specimens of arctic char were introduced in 1991 and started to reproduce in 1994 (Brancelj 1999, 2002). After 2012, specimens of minnow were recorded in the lake, too. In lake Črno Jezero, the first specimens of minnow were recorded in 1996 (Brancelj 2002).

In the past, lakes Planina and Črno Jezero were inhabited by native populations of Alpine newt (*Triturus alpestris* (Laurenti, 1768)) (Seliškar and Pehani 1935). The population in lake Planina disappeared after fish introduction in the 1950s, while a sharp decline was noted in lake Črno Jezero after 2000, *i.e.* soon after fish introduction (Brancelj, personal observation).

Field sampling and laboratory procedures

The zooplankton samples were collected in 13 lakes once per year between 1992 and 2012, from the second half of August to the first week of October, before the thermal mixing of the water column. The sampling visits were determined by weather conditions. 2006 was the only year when no sampling was performed. Occasionally certain lakes were not sampled due to logistic/safety problems related to weather conditions. Four lakes, Jezero v Ledvicah (hereafter Ledvica), Dvojno Jezero (5th and 6th lakes) and Planina, were re-sampled in 2019 using the same methods described below.

The zooplankton samples were collected by vertical tows of a plankton net at the deepest point of the lake, from bottom to surface. Two sets of samples were collected, each with three replicates (as amalgamated samples) to assess both zooplankton quantity (biomass) and quality (species composition). The plankton net had a mouth diameter of 20 cm, cone length of one meter, and mesh size of 100 µm (in the period 1992–1996), and 60 µm from 1997 onward.

Alongside the zooplankton samples, the physical measurements of water column parameters (transparency, temperature, pH, oxygen concentration) were made and the water samples for major ions were collected in a Van Dorn sampling bottle (Wildco, USA) from at least three depths within the water column (surface, middle, bottom).

In the laboratory, the zooplankton samples were identified to species level. Rotifera and large Ciliata were not collected specifically but were identified when present among the samples of the larger zooplankton, *i.e.* Copepoda and Cladocera, thus only abundant and larger-bodied Rotifera and Ciliata were collected. The relative abundance of each taxon in a sample was heuristically ranked from 1 to 5 (1—singleton, 2—rare, 3—occasional, 4—frequent, 5—abundant).

For total biomass evaluation, the samples were put on pre-weight cellulose filters, filtered, dried overnight at 106 °C, put in a desiccator for 24–48 h and then weighed to the nearest 0.1 mg (Sartorius, Germany). Biomass was evaluated as "an average biomass in a water column (g DW m^{-3})." Samples with very low biomass (below level-of-detection) but which contained fauna determined to species were labeled as "0.01 g DW m^{-3}," to distinguish them from years when samples were not collected at all (labeled with "ND"). In some samples, filamentous algae were not separated from the zooplankton, but algal contribution to overall biomass was low. During the study period, some lakes (ZKJ, Ledvica, Krn, Planina) were sampled more frequently (in one to three months' intervals) throughout the year, according to specific project requirements. These results are not presented in the results section but are included in the discussion.

Cluster analyses on similarity in zooplankton community composition between the lakes (species presence/absence) in the period between 1992 and 2012 and time series within the lakes for the same period were evaluated using the Bray–Curtis similarity index. A canonical correspondence analysis (CCA) was used to relate species distribution (species presence/absence) and eight environmental variables: altitude, lake depth and area, presence of fish and macrophytes, trophic state, transparency and near-bottom oxygen concentration.

The analyses on similarity indexes and CCA were made using Past3 statistical program (Hammer et al. 2001; https://www.bytesin.com/software/Download-PAST).

Results

Species composition

Over 20 years, 32 species were recorded: 11 species of Copepoda, 10 of Cladocera, 10 of Rotifera and one Ciliate species (Table 2; Online Resource). Three groups of zooplankton were present: (1) “constitutive species,” present in all/several consecutive years in abundant populations; (2) “scout species” (also called “emerging species”; Scabetsberger et al. 2008), which appeared only once or for a short period, usually present in the lower-altitude lakes affected by the recent fish introduction; and iii) “benthic species,” associated with suspended/floated mats of filamentous green algae.

Among the euplanktonic Copepoda, there were five species of Calanoida (belonging to the genera *Acanthodiaptomus*, *Arctodiaptomus*, *Eudiaptomus*) and four species of Cyclopoida (genera *Cyclops* and *Thermocyclops*). Among the six euplanktonic Cladocera species, there were four representatives of family Daphniidae (genera *Ceriodaphnia*, *Daphnia, Scapholeberis*), one species of Sididae (g. *Diaphanosoma*) and one of Bosminidae (g. *Bosmina*). There were nine genera of Rotifera, in the euplanktonic families Asplanchnidae (g. *Asplanchna*), Brachionidae (genera *Brachyonus*, *Keratella*, *Notholca*, *Platyias*), Conochilidae (g. *Conochilus*), Synchaetidae (g. *Polyarthra*), Trichocercidae (g. *Trichocerca*) and Trochosphaeridae (g. *Filinia*). Large-bodied Ciliates were represented by a single species in the family Spathiidae (g. *Spathidium*).

Benthic species occasionally present in the water column included Cyclopoida (genera *Eucyclops* and *Megacyclops*) and Cladocera (genera *Acroperus*, *Alona*, *Alonella*, *Chydorus*).

Ecological parameters determining zooplankton communities

The ordination based on canonical correspondence analysis (CCA) made a gradient distribution of zooplankton species for a period 1992–2012 between the highly eutrophic/hypertrophic lake Planina and a group of oligotrophic lakes, with ZKJ as an ultra-oligotrophic lake (Fig. 2). The percentage of the explained variance on the two major axes was 42.74% (axis 1: 27.08%; axis2: 15.65%) made on the whole species set and environmental parameters. Species *Cyclops vicinus, Diaphanosoma brachyurum*, *Heterocope saliens*, *Scapholeberis mucronata*, *Spathidium* sp. and *Thermocyclops dybowskii* were aligned along axis 1 as representatives of eutrophic/hypertrophic lakes, while *Arctodiaptomus alpinus* and *Asplanchna priodonta* as representatives of oligotrophic/ultra-oligotrophic lakes.

Among the eight ecological parameters for zooplankton composition, the most significant were trophic level, oxygen concentration and transparency, all arranged along axis 1. Less effective parameters included altitude, depth and lake area, along with fish and macrophyte presence, arranged along axis 2 (Fig. 2). Most of the lakes, *i.e.* 11 of them, were arranged in the central part of diagram, along axis 2. Exceptions were lakes Planina and Zeleno Jezero. Lake Planina is eutrophic lower-altitude lake, with low transparency, anoxic conditions near the bottom and stocked with fish and submerged macrophytes in the littoral zone. Lake Zeleno Jezero is higher-altitude lake, shallow, with its bottom covered with extensive mats of submersed macrophytes.

Total number of species decreased linearly with altitude ($R^2 = 0.729$) (Fig. 3). The lakes above the tree line had four to nine species each, which increased to 14–16 in lakes at lower altitudes.

The most common zooplankton species collected during the study period were: *Cyclops abyssorum tatricus,* recorded in 11 lakes (out of 13 surveyed); *A. alpinus* (nine lakes); *Bosmina longirostris* and *Polyarthra dolichoptera* (eight lakes each); and *Daphnia longispina* (six lakes). Lakes inhabited with *A. alpinus* decreased to seven lakes, as they were completely eliminated by fish from lake Dvojno Jezero after 2001.

Benthic species were frequently present in both higher- and lower-altitude lakes, but in low numbers/biomass (Table 2; Online Resource).

Table 2 List of zooplankton species recorded in the lakes of the Triglav National Park (Slovenia; Central Europe) in the period 1992–2012

Taxon	(A) Jezero pod Vršaci	(A) Rjavo Jezero	(A) Zeleno Jezero	(A) Jezero v Ledvicah	(A) Dvojno (5.) Jezero	(A) Dvojno (6.) Jezero	(A) Črno Jezero
COPEPODA							
Acanthodiaptomus denticornis (Wierzejski, 1887)							
Arctodiaptomus alpinus (Imhof, 1885)	X	X	X	X	X	X	
Arctodiaptomus laticeps (G.O. Sars, 1863)							
Cyclops abyssorum tatricus (Kozminski, 1927)	X			X	X	X	X
Cyclops strenuous Fischer, 1851					X	X	X
Cyclops vicinus Uljanin, 1875							
**Eucyclops serrulatus* (Fischer, 1851)	X	X			X	X	X
Eudiaptomus hadzici (Brehm, 1939)							
Heterocope saliens Lilljeborg, 1863							X
**Megacyclops viridis* (Jurine, 1820)					X		
Thermocyclops dybowskii (Landé, 1890							
CLADOCERA							
**Acroperus harpae* (Baird, 1836)	X				X	X	X
**Alona affinis* (Leydig, 1860)	X		X		X	X	
**Alonella nana* Baird, 1850							X
Bosmmina (Eubosmina) longirostris (O.F. Mueller, 1776)	X	X	X		X	X	X
Ceriodaphnia quadrangular (O.F. Mueller, 1785)							
**Chydorus sphaericus* (O.F. Mueller, 1785)	X	X	X	X	X	X	X
Daphnia (Daphnia) longispina O.F. Mueller, 1785	X			X			X
Daphnia (Daphnia) pulicaria Forbes, 1893							
Diaphanosoma brachyurum (Lievin, 1848)							
Scapholeberis mucronata (O.F. Mueller, 1776)							
ROTATORIA							
Asplancha priodonta Gosse, 1850							

Table 2 continued

Taxon	(A) Jezero pod Vršaci	(A) Rjavo Jezero	(A) Zeleno Jezero	(A) Jezero v Ledvicah	(A) Dvojno (5.) Jezero	(A) Dvojno (6.) Jezero	(A) Črno Jezero
Brachyonus angularis Gosse, 1851				X	X		X
Conchilus unicornis Rousselet, 1892							
Filinia longiseta (Ehrenberg, 1834)					X	X	X
Keratella hiemalis Carlin, 1943							X
Keratella quadrata (O.F. Mueller, 1786)				X	X	X	X
Notholca sp.							X
Platyias sp.			X				
Polyarthra dolichoptera Idelson, 1925	X			X	X	X	X
Trichocerca longiseta (Schrank, 1802)					X	X	X
CILIATA							
Spathidium sp.							
SUM OF TAXA	9	4	5	7	14	12	16

Taxon	(A) Jezero na Planini pri Jezeru	(B) Krnsko Jezero	(B) Jezero v Lužnici	(C) Zgornje Kriško Jezero	(C) Srednje Kriško Jezero	(C) Spodnje Kriško Jezero	SUM OF LOCATIONS
COPEPODA							
Acanthodiaptomus denticornis (Wierzejski, 1887)	X						1
Arctodiaptomus alpinus (Imhof, 1885)			X	X	X		9
Arctodiaptomus laticeps (G.O. Sars, 1863)	X						1
Cyclops abyssorum tatricus (Kozminski, 1927)	X	X	X	X	X	X	11
Cyclops strenuous Fischer, 1851	X						4
Cyclops vicinus Uljanin, 1875	X	X					2
*Eucyclops serrulatus (Fischer, 1851)		X	X		X		8
Eudiaptomus hadzici (Brehm, 1939)	X						1
Heterocope saliens Lilljeborg, 1863	X						2
*Megacyclops viridis (Jurine, 1820)							1
Thermocyclops dybowskii (Landé, 1890	X						1
CLADOCERA							

Table 2 continued

Taxon	(A) Jezero na Planini pri Jezeru	(B) Krnsko Jezero	(B) Jezero v Lužnici	(C) Zgornje Kriško Jezero	(C) Srednje Kriško Jezero	(C) Spodnje Kriško Jezero	SUM OF LOCATIONS
**Acroperus harpae* (Baird, 1836)			X				5
**Alona affinis* (Leydig, 1860)					X	X	6
**Alonella nana* Baird, 1850							1
Bosmmina (Eubosmina) longirostris (O.F. Mueller, 1776)	X	X					8
Ceriodaphnia quadrangular (O.F. Mueller, 1785)		X					1
**Chydorus sphaericus* (O.F. Mueller, 1785)		X	X	X	X	X	12
Daphnia (Daphnia) longispina O.F. Mueller, 1785	X	X				X	6
Daphnia (Daphnia) pulicaria Forbes, 1893		X		X	X		3
Diaphanosoma brachyurum (Lievin, 1848)	X						1
Scapholeberis mucronata (O.F. Mueller, 1776)	X						1
ROTATORIA							
Asplancha priodonta Gosse, 1850				X			1
Brachyonus angularis Gosse, 1851		X					4
Conchilus unicornis Rousselet, 1892		X					1
Filinia longiseta (Ehrenberg, 1834)		X		X			5
Keratella hiemalis Carlin, 1943	X	X					3
Keratella quadrata (O.F. Mueller, 1786)		X					5
Notholca sp.							1
Platyias sp.							1
Polyarthra dolichoptera Idelson, 1925	X	X		X			8
Trichocerca longiseta (Schrank, 1802)							3
CILIATA							
Spathidium sp.	X	X					2

Table 2 continued

Taxon	(A) Jezero na Planini pri Jezeru	(B) Krnsko Jezero	(B) Jezero v Lužnici	(C) Zgornje Kriško Jezero	(C) Srednje Kriško Jezero	(C) Spodnje Kriško Jezero	SUM OF LOCATIONS
SUM OF TAXA	14	15	5	7	6	4	

(A)—Triglavska Jezera group; (B)—Krnska Jezera group; (C)—Kriška Jezera group. * = benthic species randomly/frequently present in a water column. Jezero = lake

About 25% of the species, present during the sampling events, were restricted to one or two lower-altitude lakes with higher trophic state and stocked with fish (Table 2; Online Resource). Species exclusive to the lower-altitude eutrophic lake Planina were *Acanthodiaptomus denticornis* and *Arctodiaptomus laticeps* as constitutive species, while *Diaphanosoma brachyurum, Eudiaptomus hadzici, S. mucronata* and *T. dybowskii* belonged to scout species, but very common in lowland water bodies (except *E. hadzici*, which is a Balkan endemic) (Fig. 2). In two lakes, Planina and Krn (separated by 10 km), two species typical of mesotrophic/eutrophic conditions were recorded: *C. vicinus* and *Spathidium* sp. (Hansen and Jeppesen 1992), while *H. saliens* was found in lakes Planina and Črno Jezero, one km away.

About 10% of the species (= three) were restricted to cold oligotrophic lakes. *Arctodiaptomus alpinus* was present in all the lakes at or above the tree line as constitutive species. *Daphnia pulicaria* was constitutive species in two lakes in the Kriška Jezera group (> 2000 m a.s.l.), although it appeared once as scout species in lake Krn, too. *Platyias sp.* was recorded only once in lake Zeleno Jezero as scout species (Online Resource).

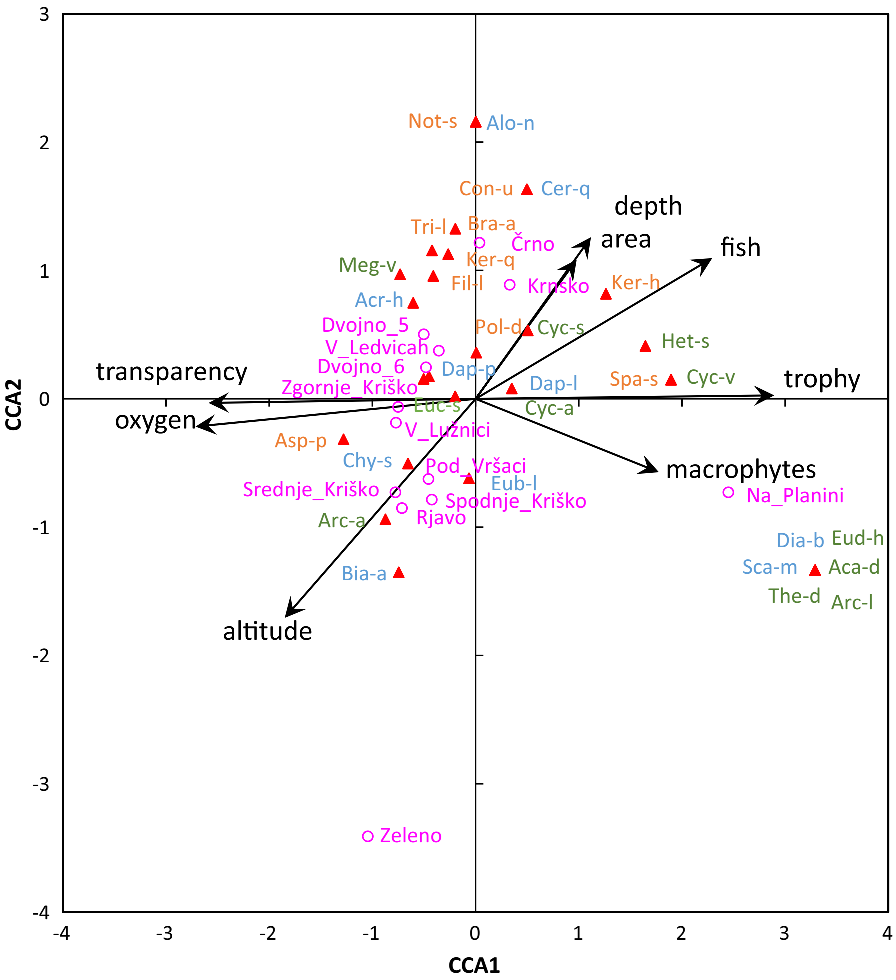
Based on the Bray–Curtis similarity index, the lakes were separated into two groups—the lakes with high trophic state (Planina, Dvojno (5th), Dvojno (6th), Črno Jezero and Krn = lower-altitude lakes) and the lakes with oligotrophic state (= higher-altitude lakes) (Fig. 4). The most distinct was lake Planina, at low altitude, highly eutrophic/hypertrophic lake, with a rich population of fish (carp and chub). Most similar to each other were lakes Dvojno (5th) and Dvojno (6th) Jezero, which merged when water level is high. They kept the same high-similarity status before and after fish introduction.

The changes in the zooplankton community (species presence/absence) occurring over the study period were compared for no-/low-impacted lakes (ZKJ and Ledvica), and heavily impacted lakes (Krn—earthquakes; Planina, Črno Jezero and Dvojno (5th) Jezero—stocked by fish) (Fig. 5; Online Resource). In non-/low-impacted lakes, the community structure remained relatively stable over several years, dominated by the representatives of genera *Arctodiaptomus* and *Daphnia*. Heavily impacted lakes had oscillations in community structure over short periods (*i.e.* even on a year-to-year basis). In the lakes with recently introduced fish (after 1990), there were changes in community as well as in size structure, *i.e.* shift from large-body zooplankton representatives of Copepoda and Cladocera to small-body representatives of Cladocera and Rotifera, usually accompanied with the representatives of benthic species (genera *Alona*, *Alonella, Chydorus, Eucyclops*). In lake Krn, effected by consecutive earthquakes in 1998 and 2004, the main change in community structure was among *C. vicinus*, exclusive large-body species before 1998 and *C. quadrangula*, a new inhabitant in 1998. In 2005, *C. vicinus* was no more present in the lake, and *C. quadrangula* become dominant until 2009, when the population of *C. vicinus* recovered. After 2010, both species co-existed as dominant zooplankton species along with certain representatives of Rotifera (genera *Brachyonus* and *Filinia*).

Biomass

Biomass varied between the lakes and years (Fig. 6). As the samples were collected in late summer/early autumn during different weather conditions, before and during sampling, they were not directly comparable and should be evaluated along with species composition, too. The values varied from 0.01 to about 0.5 g DW m^{-3}, but most of them were in a range between 0.1 and 0.2 g DW m^{-3}.

Fig. 2 Ordination diagram based on the canonical correspondence analyses (CCA) of planktonic species (present/absent) in the lakes of the Triglav National Park (Slovenia; Central Europe) in the groups Copepoda, Cladocera, Rotifera and Ciliata with respect to environmental variables for the period 1992–2012. Arrows—environmental parameters; circles—lakes; triangles—species. Each species is labeled with the first three letters of its genus name and the first letter of its species name as listed in Table 2



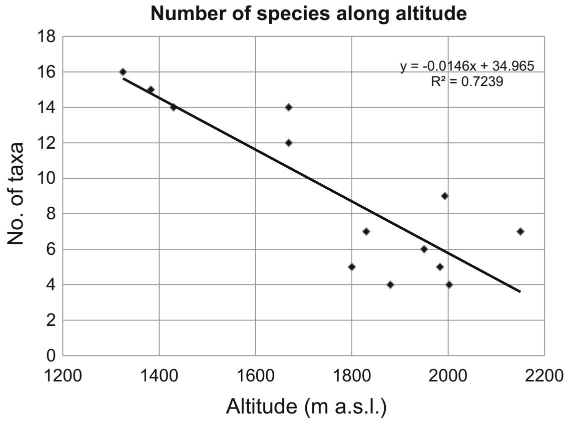


Fig. 3 Cumulative number of zooplankton taxa in relation to altitude in the lakes of the Triglav National Park (Slovenia; Central Europe) in the period 1992–2012

In oligotrophic and fishless lakes (ZKJ and Ledvica), or in the lakes with long-established fish population (Planina), variations in biomass were quite random and could be addressed either to sampling date/season or internal dynamics of the zooplankton. In these lakes, no significant changes in zooplankton community composition were recorded, although biomass oscillated on a year-to-year basis between 0.01 and 0.26 g DW m^{-3} in lake Ledvica, between 0.04 and 0.40 g DW m^{-3} in lake ZKJ, and between 0.02 and 0.51 g DW m^{-3}in lake Planina.

In lakes where fish had been recently introduced (in the 1990s; Dvojno (5th and 6th) and Črno Jezero), some years after introduction, significant long-lasting drops in biomass as well as shifts in species composition were observed. Biomass in all three lakes dropped from about 0.50 to < 0.01 g DW m^{-3}. Large-bodied zooplankton representatives (genera

Acanthodiaptomus, *Arctodiaptomus*, *Cyclops*, *Daphnia*, *Heterocope*) were completely expired within a few years, when the introduced fish started to reproduce and have established larger populations. Large-bodied species were replaced with small-bodied species belonging to the Rotatoria (genera *Brachyonus*, *Polyarthra*), planktonic Cladocera (g. *Bosmia*) or benthic Cyclopoida and Cladocera (genera *Alona*, *Chydorus*, *Eucyclops*,) (Fig. 6; Online Resource).

In lake Krn, the zooplankton community was affected by two consecutive earthquakes, the first in 1998 and the second in 2004, resulting in significantly reduced biomass, which only recovered in 2010, with some changes in species composition (Fig. 6). *Ceriodaphnia quadrangula,* absent before the first earthquake in 1998, become co-dominant after 2002 and remained until 2012 (Online Resource). Zooplankton biomass before the first earthquake was close to 0.20 g DW m^{-3} (exceptionally 0.34 g DW m^{-3}). After the earthquake, it dropped for several years and stayed at < 0.10 g DW m^{-3}, and after the second one was about 0.01 g DW m^{-3} rising to 0.15 g DW m^{-3} six years later (Fig. 6).

Comparison of communities in four lakes in the period 1991–2012 and 2019

Four lakes were resampled in 2019 (Ledvica, Dvojno Jezero (5th and 6th lake) and Planina). In the oligotrophic lake Ledvica there were no deviations from long-term observations, in both community structure and biomass (Online Resource). In both lakes of Dvojno Jezero, there was a clear absence of larger-bodied zooplankton species, previously common before the introduction of minnows. Only rare specimens of Rotifera and the benthic species *Chydorus sphaericus* were present in the 2019 samples. In lake Planina, there was a sharp decline in the biomass of zooplankton species in 2019. Most of the species previously recorded were present, but they were in low abundance. *Heterocope saliens* was absent in 2019, but it had previously been rare in the period 1991–2012, too. A new scout species was *P. dolychoptera*, which had not been recorded in the lake before.

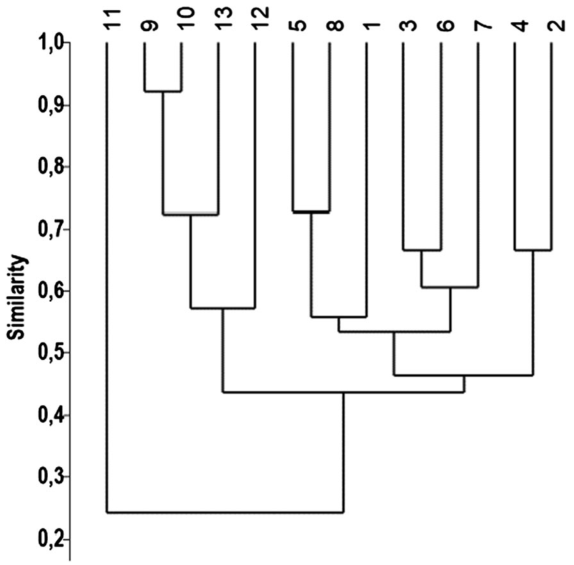


Fig. 4 Similarity among the lakes of the Triglav National Park (Slovenia; Central Europe) based on zooplankton species presence in the period (1992–2012). Full names of the lakes are listed in Table 1. Numbers in the top row indicate position of a lake along altitudinal gradient: highest (1) to the lowest located lake (13)

Discussion

Continuous long-term observations in high-mountain lakes are rare due to several problems, including logistics (*i.e.* transportation of equipment) and funding; thus, records of changes in zooplankton composition in high-mountain lakes are rather limited (Scabetsberger et al. 2006, 2008; Ventura et al. 2017). Most studies have been carried out as "flash-samplings," *i.e.* one/two surveys of the same lake within an interval of several years/decades (Catalan et al. 2009; Kernan et al. 2009; Stoch et al. 2019). Another method to assess zooplankton dynamics in high-mountain lakes is the analysis of sediment cores, but this is limited, as preserved morphological remains are restricted to one zooplankton group, the Cladocera (Brancelj et al. 2009; Kernan et al. 2009). Additional information on the presence of other groups (*e.g.*, Rotifera, Copepoda) has been achieved in the past few decades by recovery of specimens from "the sediment egg bank" by egg-hatch (Hairston 1996; Brendonck and De Meester 2003; Piscia et al. 2020).

Zooplankton species richness in the lakes of the Julian Alps follows the same pattern as observed elsewhere in the Alps and other temperate-zone

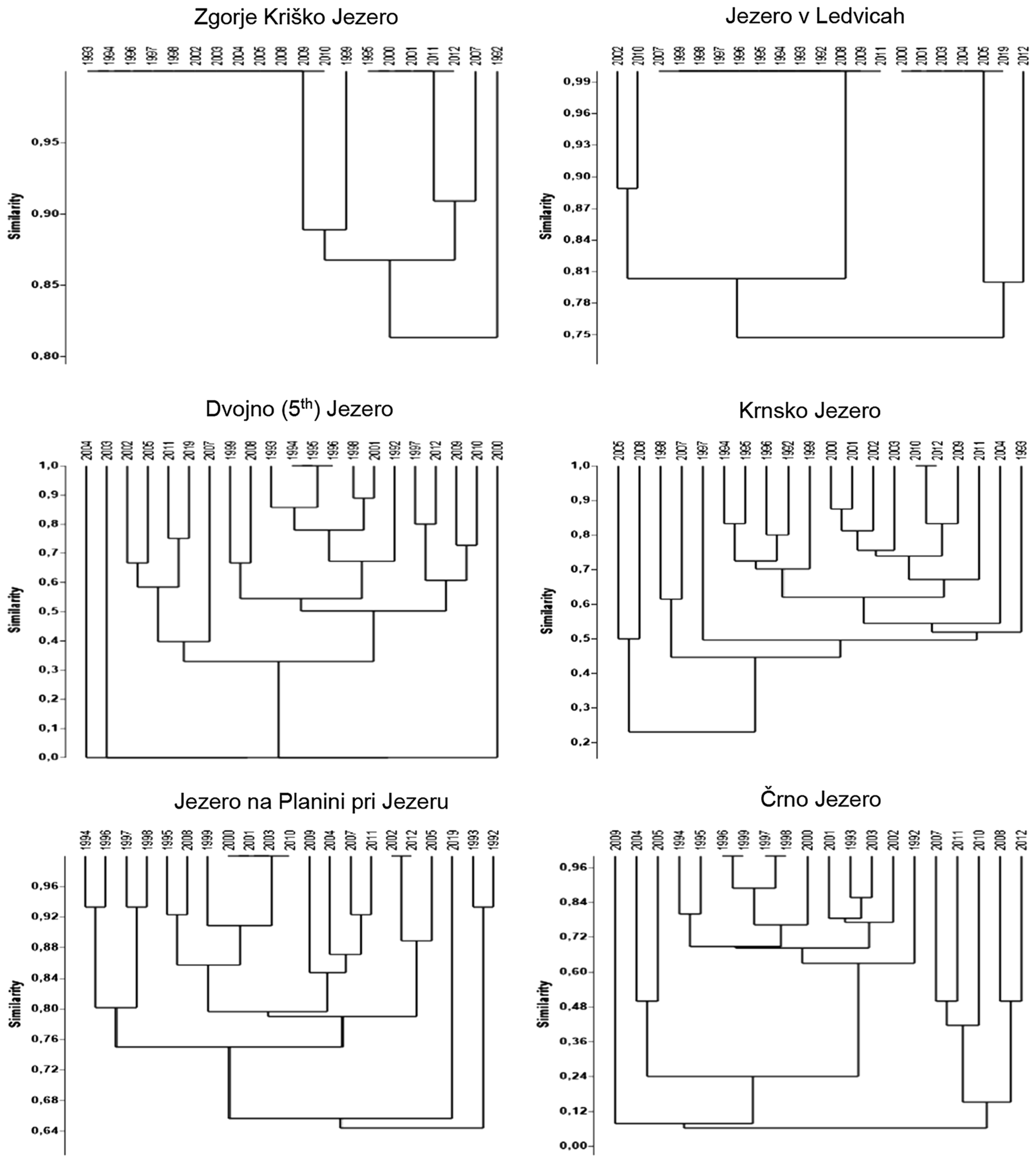


Fig. 5 Similarity in zooplankton communities in the period 1992–2012 in six lakes in the Triglav National Park (Central Slovenia). Top row: no-/low-impacted lakes; middle and bottom rows: heavily impacted lakes. Similarity values are not to the same scale

mountain ranges, *i.e.* it decreases with altitude. Altitude is actually a proxy for the temperature regime within the lakes, which seems to be the main factor determining their zooplankton communities (Jersabek et al. 2001; Winder et al. 2001; Catalan et al. 2009; Burmistrova and Ermoaeva 2013; Stoch et al. 2019). This pattern is different to that in tropical zone mountain ranges, where altitude is not a significant

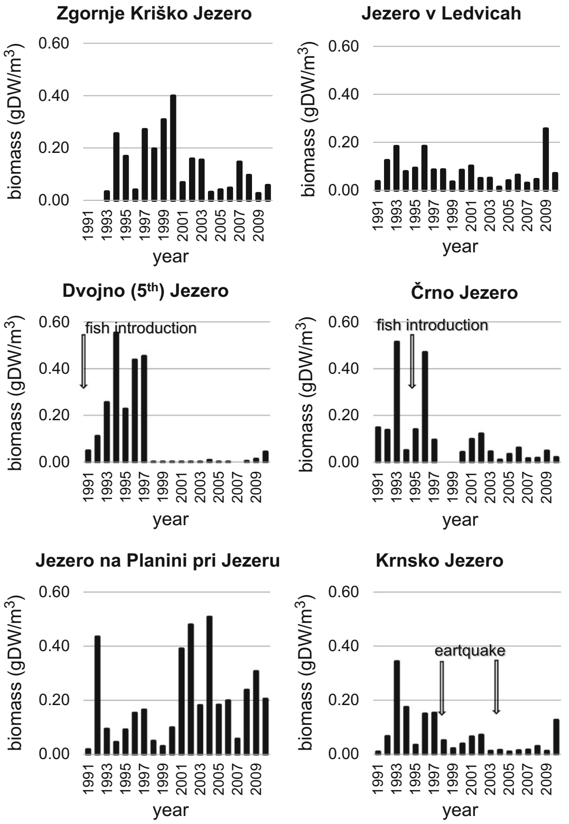


Fig. 6 Biomass of zooplankton in six lakes in the Triglav National Park (Slovenia; Central Europe) in the period 1991–2010. The events (fish introduction and earthquakes) which affected species composition and biomass are indicated with arrows

factor due to smaller temperature variation along the altitudinal gradient (Eskinazi-Sant'Anna et al. 2020).

Pan-European research projects on high-mountain lakes (AL:PE2, MOLAR, EMERGE) have shown that there are some differences in zooplankton communities in north–south and east–west directions on the continental scale, but there are no clear differences within individual lake districts, including the Alps (Kernan et al. 2009; Stoch et al. 2019). Most of the species studied in the TNP have relatively wide geographical distributions within the Alps but *E. hadzici* (endemic to lowland lakes in the Balkans) and *T. dybowskii* (common in lowland lakes across Europe), thus can be considered as scout species, which failed to establish stable and long-term populations in lake Planina. Two species, *A. alpinus* and *D. pulicaria*, only present in higher-altitude lakes in the TNP, are considered ice-age relicts. *Daphnia pulicaria* is common in northern lakes in Europe, while *A. alpinus* is restricted to the Alps (Jersabek et al. 2001).

As some lakes are shallow (depth < 10 m), some benthic species, especially *C. sphaericus*, regularly appeared in the water column. They were common in the lakes where filamentous green algae (genera *Mougeotia*, *Spirogyra*, *Zygnema*) were present during ice-free periods. These algae began to grow at the bottom of shallow lakes in late spring/early summer, eventually forming dense mats across the bottom, which then floated to the surface in late summer due to gases (O_2, CO_2) produced during photosynthesis or decomposition of organic material, carrying associated benthic taxa into the water column. The lakes within the TNP, in which filamentous green algae appeared, are divided into two groups: (a) lakes with no/low human impact, which are all located above the local tree line and algae were present only for short periods (few years) and (b) lakes with intensive human impact, located at or below the tree line, where algae are present regularly. Impacts on lake Planina (1430 m a.s.l.) began in the 18th century with forest exploitation (tree cutting and charcoal production) and farming (high-altitude pasturing) around the lake (Rejec Brancelj and Smrekar 2002). Next were fish introductions, to lake Krn (already heavily impacted during WW1 as part of the front-line) in the 1920s, lake Planina in the 1950s, and finally to Dvojno Jezero and Črno Jezero after 1990.

At the same time, all the lakes were impacted by climate change and long-distance air pollution. Lakes within the TNP are especially exposed to air-born pollution on a European scale, as prevailing SW-NE winds transport pollutants from the heavily industrialized and intensively farmed landscape of the Po valley (N Italy) (Battarbee et al. 2005). However, acid rain, resulting from combustion of fossil fuels before 1980 (coal and oil), had no significant impact on the pH of the lakes due to the neutralizing capacity of the limestone bedrock, and it remained close to neutral or slightly alkaline throughout the study period.

High resolution measurements of surface water temperature (in 6-h intervals) on four lakes (ZKJ, Ledvica, Krn, Planina) in the period 2000–2013 showed that the temperature increased for about 0.3 °C during the study period (data not published), in accordance with the general trend in the Alps (Battarbee et al. 2005; ARSO 2020). From 1994 to 2000, intensive snow melt of locally accumulated permanent snow was recorded in the catchments of the lakes ZKJ, Jezero pod Vršaci and Rjavo Jezero. Snow was partly covered by scree (local permafrost) in depressions above the lakes and protected from direct solar insolation. As a result of snow melt, there was an increase in filamentous green algae along the lake shores', but started to decrease after 2001. Increase in algal biomass could be attributed to the release of nutrients accumulated within the permafrost, although no increase in nutrients within the water column was recorded during routine sampling, as the nutrients had already been incorporated into the algal and zooplankton biomass.

In the lakes within the TNP, the number of zooplankton species decreases from 16–14 at low elevation (1300–1400 m a.s.l.) to 9–4 species at high elevation (> 1800 m a.s.l.). The rather low number of zooplankton species at higher elevations could be attributed to the fact that lakes close to and above 2000 m a.s.l. have only experienced prolonged ice-free periods in the last 50 years, *i.e.* after the 1970s, when the local climate became warmer and intensive permanent ice-melt, incl. permafrost, commenced (Gabrovec 1998; Frantar 2003/2004). For this reason, only a few cold-adapted (= cold-stenothermic) species, both phytoplankton and zooplankton, have established stable populations there, the zooplankton being characterized by univoltine populations that develop fast early in the year, from either ephippia (Cladocera), juvenile hibernating stages (= copepodites) or resting eggs (Copepoda) (Brancelj 2002). During several winter surveys on some lakes (Planina, Krn, Ledvica, ZKJ), over a meter of surface ice and snow was recorded, with very few zooplankton specimens in a water column. However, they emerged in significant numbers from hibernating stages soon after snow melt in late spring and early summer, along with a concomitant increase in biomass (Brancelj 2002).

Regardless of airborne pollution and the increases in the local temperatures, higher-altitude lakes in the TNP exhibited rather minor changes in zooplankton composition over two decades. In lake ZKJ, there were some sporadic attempts by Rotifera (scout species: *A. priodonta*, *Filinia longiseta* and *Polyarthra dolichoptera*) to establish populations alongside the large-bodied and highly competitive community of *A. alpinus*, *C. abyssorum tatricus* and *D. pulicaria*. Similar attempts were observed in lake Jezero pod Vršaci, dominated by *A. alpinus* and *C. abyssorum tatricus* (scout species: *P. dolichoptera*, *B. longirostris*), and in lake Ledvica, dominated by *A. alpinus*, *C. abyssorum tatricus* and *D. longispina* (scout species: *Brachyonus angularis*, *Keratella quadrata*, *Polyarthra dolicoptera*). In all these lakes the abundance of Rotifera in the past was low, with irregular inter-annual presence, but their presence indicates that the current communities will probably face some changes in structure in the future as a result of natural processes. At the same time, this also suggests the intensive passive transport of organisms by wind or birds.

More dynamic changes in zooplankton composition were recorded in lakes below the tree line to which fish had been introduced. For two lakes, Krn and Planina, there is no information on zooplankton composition before fish introductions, but some data from sediment-core analysis. The sediment-core analysis from lake Krn revealed intensive physical disturbance of sediments by torrents, avalanches and earthquakes, which had perturbated and blurred the sedimentary chronological record, although there were no records of planktonic Cladocera (*i.e.* ephippia) at all (Brancelj 2002). The sediment analysis from lake Planina revealed clear differences between pre- and post-fish introduction based on Cladocera remains (genus *Daphnia*) (Brancelj et al. 2000).

Community changes are well documented for lakes Dvojno Jezero and Črno Jezero (Brancelj 1999, 2002). In lake Dvojno Jezero, large-bodied species (*A. alpinus*, *C. abyssorum tartricus*), dominant before fish introduction (arctic char), were replaced by some benthic species, associated with filamentous green algae (*Acrperus harpae*, *C. sphaericus, Eucyclops serrulatus*), small-bodied euplanktonic Cladocera (*B. longirostris*) and some Rotifera, not recorded before fish introduction (*B. angularis*, *F. longiseta, K. quadrata*, *P. dolychoptera*, *Trichocerca longiseta*). The main change occurred after the first successful spawning of fish in 1994 (Brancelj 1999). There was a short time-lag (three years) before large-bodied zooplankton became rare, as some of them continued to recruit from the "sediment egg bank" after 1994. Similar observations have been made elsewhere in lakes subjected to fish introductions (Makarova et al. 2006; Piscia et al. 2020). After 1998 in lake Dvojno Jezero there was a clear change in zooplankton—in both species composition and biomass (Figs. 4 and 5;

Online Resource). Additional pressure on the zooplankton population was the introduction of minnow to the lake (after 2012); thus, only small-bodied species Cladocera and Rotifera (*C. spaericus*, *P. dolichoptera*, *T. longiseta*) were recorded in the 2019 survey.

Shifts from large-bodied to small-bodied zooplankton in high-alpine lakes have been recorded elsewhere (Brooks & Dodson 1965; Scabetsberger et al. 2006, 2008; Tiberti et al. 2014; Ventura et al. 2017), although only a few studies have monitored the shifts in zooplankton communities on fine time scales after fish introductions (Schindler & Parker 2002; Scabetsberger et al. 2006, 2008; Ventura et al. 2017).

The only native vertebrate top-predators in Alpine lakes are newts (*Triturus alpestris*). Across several hundred years in fishless lakes, zooplankton have adapted well to their comparatively weak predation pressure that has allowed large-bodied zooplankton species to co-exist (Schabetsberger et al. 2006, 2008). During their study on Alpine newts in lakes Črno Jezero and Planina, Seliškar and Pehani (1935) also compiled a short list of zooplankton species, two of which were large-bodied (*D. longispina, H. saliens*). We confirmed the presence of both these species in the same lakes during our studies up to 2003. In lake Planina, *H. saliens* managed to maintain a rather small population even in the presence of fish, as the water transparency is rather low and the fish (*C. carassius* and *L. cephalus*) are not specialized zooplankton consumers. In the transparent lake Črno Jezero, the situation was different. After the introduction of minnow in 1996, *D. longispina* and *H. saliens* soon disappeared, leaving only small-bodied Cladocera, most of them benthic, and Rotifers. At the same time, the population of *T. alpestris* in the lake declined significantly, with specimens showing evident signs of malnutrition (Brancelj, personal observations).

The lakes in the TNP are on a very active seismic zone, frequently affected by strong earthquakes (EMS = 4.0–5.6) (Vidrih 2008). As some of the lakes are surrounded by steep scree slopes, earthquakes are often accompanied by landslides plunging into the lakes, which could result in a pulse input of nutrients and resuspension of fine sediment impacting a lake's ecosystem. However, there is little published information on the impacts of earthquakes on aquatic fauna. In Lake Baikal (Russian Federation) in 1912, a massive release of methane resulting from an earthquake caused a mass kill of pelagic fish (Radziminovich et al. 2010). Another example is the exodus of common toads (*Bufo bufo* Linnaeus, 1758) from their breeding pools just before the strong earthquake in l'Aquila (Italy) in 2009 (Grant et al. 2011). An impact from this same earthquake was also documented on the microcrustacean community structure (Copepoda) in some karstic springs nearby (Galassi et al. 2014).

Impacts from earthquakes on zooplankton communities in lakes in the TNP have been recorded twice. The first became evident after the analysis of sediment cores from lake Ledvica, which indicated a significant increase in Cladocera remains, benthic (genera *Alona*, *Chydorus*) as well as planktonic (g. *Daphnia*) after an earthquake in 1895 and a landslide in 1912 (Brancelj et al. 2002).

The second was studied "in situ" after two consecutive earthquakes in 1998 and 2004 in the vicinity of lake Krn (Brancelj et al. 2012). Before 1998, no Cladocera were present in the water column, except for *C. sphaericus*, recorded in 1993. The timing of the earthquakes (April and June) significantly affected the resting stages of *C. vicinus* copepodites, which were presumably, partly or completely covered by fine sediment immediately after the earthquakes, thereby preventing most of them from entering the water column in late spring/early summer. After the 1998 earthquake, the first specimens of *C. quadrangula*, as a scout species, were recorded in the lake, although the *C. vicinus* population remained high (Online Resource). In 1998, some individuals of *D. pulicaria* and in 1999 *D. longispina* were present, although they were not recorded later. Over the next six years, *C. quadrangula* established a stable population. In autumn 2004, following the second earthquake, only a few specimens of *C. vicinus* were recorded, along with high populations of *C. quadrangula*, *K. quadrata* and *Spathidium* sp. Populations of both the latter two species also increased after the first earthquake. In 2005, only *C. quadrangula* was present in the lake, along with a few individuals of *B. longirostris*, another scout species. After 2007, *C. vicinus* gradually established a stable population, along with *C. quadrangula* and some Rotifera (*B. angularis*, *F. longiseta*), while some species, common before 2005, disappeared (*K. quadrata*, *P. dolichoptera*, *Spathidium* sp.).

In conclusion: although high-mountain lakes are remote, they are still subjected to evolution and change, including variations in the structure of their zooplankton communities. High-mountain lakes are actually dynamic habitats/ecosystems, vulnerable to natural and anthropogenic impacts. Events such as changes in climate, earthquakes and landslides or fish introduction can result in declines or extirpations of previously well-established species, and opportunistic influxes of pioneer/scout species taking advantage of changes in the community structure.

Acknowledgements The author would like to acknowledge all his colleagues at the National Institute of Biology for their assistance during heavy field work in the period 1992–2012, especially Olga Urbanc-Berčič†, Tina Leskošek, Nataša Gorjanc, Milijan Šiško, Davorin Tome, Gregor Muri, Tadej Mezek and Simon Lukančič. Andreja Jerebic carried out the analysis of the water samples in the laboratory and Milijan Šiško helped with some statistical analysis. The research was conducted with the financial support from European Union funded projects (AL:PE 2 (1993–1995)—EU contract EV5V-CT92-0205; MOLAR (1996–1999)—EU contract ENV4-CT95-0007; EMERGE: 2000–2003—EU contract EVKI-CT-1999-0003; as well as the national program P1-0255 (Communities, relations and communications in ecosystems), financed by the Slovenian Ministry of Science and Education (ARRS). The office of the Triglav National Park granted us the permission to sample the lakes and use their resorts during field work. Thanks to Henri Dumont, Lee Knight and three anonymous reviewers for the linguistic improvements and comments on the text.

Authors' contribution A. Brancelj organized and participate field work, work in the laboratory, made zooplankton analyses and write the paper. For contribution of participants during field and laboratory work, see Acknowledgements.

Funding This study was funded by national and international projects; European Union funded projects (AL:PE 2 (1993–1995)—EU contract EV5V-CT92-0205; MOLAR (1996–1999)—EU contract ENV4-CT95-0007; EMERGE: 2000–2003—EU contract EVKI-CT-1999–0003; the national program P1-0255 (Communities, relations and communications in ecosystems), financed by the Slovenian Ministry of Science and Education (ARRS).

Availability of data and materials All data generated or analyzed during this study are included in this published article and its supplementary information files.

Declarations

Conflict of interest The authors declared that they have no conflict of interest.

References

Anderson NJ, Battarbee RW (1994) Aquatic community persistence and variability: a paleolimnological perspective. In: Giller PS, Hildrew G, Rafaelli DG (eds) Aquatic ecology- scale, pattern and process. Blackwell Scientific Publications, Oxford, pp 233–259

ARSO (Slovenian Environmental Agency) (2020) Vse manj ledu tudi na Bohinjskem jezeru. https://www.arso.gov.si/vode/publikacije%20in%20poro%C4%8Dila/Led_Bohinj.pdf. Accessed 10 Oct 2020 (in Slovene)

Battarbee RW, Bennion H (2012) Using palaeolimnological and limnological data to reconstruct the recent history of European lake ecosystems: introduction. Freshw Biol 57:1979–1985. https://doi.org/10.1111/j.1365-2427.2012.02857.x

Battarbee RW, Grytnes JA, Thompson R, Appleby PG, Catalan J, Korhola A, Birks HJB, Heegaard E, Lami A (2002) Comparing palaeolimnological and instrumental evidence of climate change for remote mountain lakes over the last 200 years. J Paleolimnol 28:61–179

Battarbee RW, Patrick S, Kernan M, Psenner R, Thies H, Grimalt J, Rosseland BO, Wathne B, Catalan J, Mosello R, Lami A, Livingstone D, Stuchlik E, Straskrabova V, Raddum GO (2005) High mountain lakes and atmospherically transported pollutants. In: Huber UM et al (eds) Global change and mountain regions. Springer, Dordrecht

Battarbee RW, Kernan M, Rose NL (2009) Threatened and stressed mountain lakes of Europe: assessment and progress. Aquat Ecosyst Health Manag 12:118–128. https://doi.org/10.1080/14634980902905742

Bengtsson L (2012) Classification of lakes from origin processes. In: Bengtsson L, Herschy RW, Fairbridge RW (eds) Encyclopaedia of lakes and reservoirs. Springer, Dordrecht, pp 164–165

Brancelj A (1999) The extinction of *Arctodiaptomus alpinus* (Copepoda) following the introduction of char into a small alpine lake Dvojno Jezero (NW Slovenia). Aquat Ecol 33:355–361

Brancelj A (2002) Visokogorska jezera v Vzhodnem delu Julijskih Alp/High-mountain lakes in the Eastern part of the Julian Alps. Založba ZRC SAZU in Nacionalni Inštitut za Biologijo, Ljubljana. https://www.nib.si/aktualno/ponudba-strokovne-literature?view=details&id=16. Accessed 10 Oct 2020 (in English and Slovene)

Brancelj A, Šiško M, Rejec Brancelj I, Jeran Z, Jaćimović R (2000) Effect of land use and fish stocking on a mountain lake-evidence from the sediment. Period Biol 102:259–268

Brancelj A, Šiško M, Muri G, Appleby P, Lami A, Shilland E, Rose NL, Kamenik C, Brooks SJ, Dearing JA (2002) Lake Jezero v Ledvici (NW Slovenia) - changes in sediment records over the last two centuries. J Paleolimnol 28:47–58

Brancelj A, Kernan M, Jeppesen E, Rautio M, Manca M, Šiško M, Alonso M, Stuchlik E (2009) Cladocera remains from the sediments of remote cold lakes: a study of 294 lakes across Europe. Adv Limnol 62:269–294

Brancelj A, Žibrat U, Mezek T, Rejec Brancelj I, Dumont H (2012) Consecutive earthquakes temporarily restructured the zooplankton community in an Alpine Lake. Ann Limnol 48:113–123

Brendonck L, De Meester L (2003) Egg banks in freshwater zooplankton: evolutionary and ecological archives in the sediment. In: Van Donk E, Spaak P, Boersma M (eds) Recent developments in fundamental and applied plankton research. Kluwer Academic Publishers, Dordrecht, pp 65–84

Brooks JL, Dodson SI (1965) Predation, body size, and composition of plankton. Science 1:28–35. https://doi.org/10.1126/465science.150.3692.28

Burmistrova OS, Ermolaeva NI (2013) Zooplankton in high-mountain lakes of Altai. Inland Water Biol 6:194–202

Buser S (1986) Osnovna geološka karta – List Tolmin in Videm. Zvezni geološki zavod, Beograd (in Slovene)

Cammarano P, Manca M (1997) Studies on zooplankton in two acidified high mountain lakes in the Alps. Hydrobiologia 356:97–109

Catalan J, Ventura M, Brancelj A, Granados I, Thies H, Nickus U, Korhola A, Lotter AF, Barbieri A, Šiško M (2002) Seasonal ecosystem variability in remote mountain lakes: implications for detecting climatic signals in sediment records. J Paleolimnol 28:25–46

Catalan J, Barbieri MG, Bartumeus F, Bitušík P, Botev I, Brancelj A, Cogălniceanu D, Manca M, Marchetto A, Ognjanova-Rumenova N, Pla S, Rieradevall M, Sorvari S, Štefková E, Stuchlík E, Ventura M (2009) Ecological thresholds in European alpine lakes. Freshw Biol 54:2494–2517. https://doi.org/10.1111/j.1365-2427.2009.02286.x

Catalan J, Ninot JM, Aniz MM (2017) High mountain conservation in a changing world. In: Catalan J, Ninot JM, Aniz MM (eds) Advances in global change research. Springer, Basel

Eskinazi-Sant'Anna EM, de Souza Santos G, da Silva Alves NJ, Fortes Brito LA, Praça Leite MG (2020) The relative importance of regional and local factors in shaping zooplankton diversity in high-altitude tropical shallow lakes. J Freshw Ecol 35:203–221. https://doi.org/10.1080/02705060.2020.1770874

Frantar P (2004) Analiza temperaturnega režima in pojava ledu na Bohinjskem jezeru/analysis of temperature and appearance of ice on Bohinj Lake. Ujma 17:71–77 ((**in Slovene with English abstract**))

Gabrovec M (1998) The Triglav glacier between 1986 and 1998 / Triglavski ledenik med letoma 1986 in 1998. Geografski zbornik 38:89–110. http://giam.zrc-sazu.si/sites/default/files/zbornik/gabrovec38.pdf. Accessed 10 October 2020 (in Slovene with English abstract)

Galassi DMP, Lombardo P, Fiasca B, Di Cioccio A, Di Lorenzo T, Petitta M, Di Carlo P (2014) Earthquakes trigger the loss of groundwater biodiversity. Sci Rep 4:6273. https://doi.org/10.1038/srep06273

Grant RA, Halliday T, Balderer P, Leuenberger F, Newcomer M, Cyr G, Freund FT (2011) Ground water chemistry changes before major earthquakes and possible effects on animals. Int J Environ Res Public Health 9:2339–2342

Hairston NG (1996) Zooplankton egg banks as biotic reservoirs in changing environments. Limnol Oceanogr 41:1087–1092

Hammer Ø, Harper DAT, Ryan PD (2001) PAST: Paleontological statistics software package for education and data analysis. Palaeontol Electron. https://www.bytesin.com/software/Download-PAST. Accessed 15 Aug 2020

Hansen A-M, Jeppesen E (1992) Life cycle of *Cyclops vicinus* in relation to food availability, predation, diapause and temperature. J Plankt Res 14:591–605. https://doi.org/10.1093/plankt/14.4.591

https://en.wikipedia.org/wiki/Triglav_National_Park. Accessed 12 Aug 2020

Jersabek CD, Brancelj A, Stoch F, Schabetsberger R (2001) Distribution and ecology of copepods in mountainous regions of the Eastern Alps. Hydrobiologia 453(454):309–324

Karst-Riddoch T, Michael P, Smol J (2005) Diatom responses to 20th century climate-related environmental changes in high-elevation mountain lakes of the northern Canadian Cordillera. J Paleolimnol 33:265–282

Kernan M, Ventura M, Bitušík P, Brancelj A, Clarke G, Velle G, Raddum GG, Stuchlík E, Catalan J (2009) Regionalisation of remote European mountain lake ecosystems according to their biota: environmental versus geographical patterns. Freshw Biol 54:2470–2493

Knapp RA, Sarnelle O (2008) Recovery after local extinction: factors affecting re-establishment of alpine lake zooplankton. Ecol Appl 18:1850–1859

Löffler H (1968) Die Crustaceenfauna der Binnengewässerostafrikanischer Hochberge. Hochgebirgsforschung 1:107–170

Löffler H (1972) Contribution to the limnology of highmountain lakes in Central America. Int Rev Ges Hydrobiol 57:397–408

Makarová S, Černý M, Rees D, Stuschlik E (2006) Are they stil viable? Physical conditions and abundance of *Daphnia pulicaria* resting eggs in sediment cores from lakes in the Tatra Mountains. Biologia 61:135–146

Mis CADO, Balik MRUS (2009) Zooplankton composition and abundance in Lake Eğrigöl, a high mountain lake (Gündoğmuş, Antalya). Turkish J Zool 33:83–88

Piscia R, Bovio S, Manca M, Lami A, Guilizzoni P (2020) Evaluation of the egg bank of two samll Himalayan lakes. Water 12:491

Povž M (1997) Ribe v vodah Triglavskega narodnega parka / Fish in waters of the Triglav National Park. Ichthyos 14:40–44 ((**in Slovene with English abstract**))

Radziminovich YB, Shchetnikov AA, Vologina EG (2010) The "methane eruption" on Lake Baikal in 1912 as an effect of a strong earthquake. Doklady Earth Sci 432:583–586

Rejec Brancelj I, Smrekar A (2002) Človekovi vplivi na območju Triglavskega narodnega parka / Human impacts in the area of Triglav National Park. In: Brancelj A (ed) Visokogorska jezera v Vzhodnem delu Julijskih Alp/High-mountain lakes in the Eastern part of the Julian Alps. Založba ZRC SAZU in Nacionalni Inštitut za Biologijo, Ljubljana, pp 219–236

Rott H, Scherler KE, Reynaud L, Serandrei Barbero R, Zanon G (1993) Glaciers of the Alps. In: Williams RS and Ferrigno JG (Eds) Satelite image atlas of glaciers of the World. US Geological Survey Professional Paper 1386. US Governmental Printing Office, Washington, pp E1–E48

Scabetsberger R, Grill S, Hauser G, Wukits P (2006) Zooplankton successions in neighbouring lakes with contrasting impacts of amphibian and fish predators. Int Rev fuer

Hydrobiologie 91:197–221. https://doi.org/10.1002/iroh.200610867

Scabetsberger R, Luger MS, Drozdowski G, Jagsch A (2008) Only the small survive: monitoring long-term changes in the zooplankton community of an Alpine lake after fish introduction. Biol Invasions 11:1335–1345. https://doi.org/10.1007/s10530-008-9341-z

Schindler DW, Parker BR (2002) Biological pollutants: alien fishes in mountain lakes. Water Air Soil Pollut Focus 2:379–397. https://doi.org/10.1023/A:1020187532485

Seliškar A, Pehani H (1935) Limnologische Beiträge zum Problem der Amphibienneotenie. (Beobachtungen an Tritonen der Triglavssen). Verhandlungen der Internationalen Vereinigung für theoretische und ungewante Limnologie 7:263–294 ((**in German**))

Sienkiewicz E, Gąsiorowski M (2016) The effect of fish stocking on mountain lake plankton communities identified using palaeobiological analyses of bottom sediment cores. J Paleolimnol 55:129–150. https://doi.org/10.1007/s10933-015-9870-2

Stoch F, Vagaggini D, Margaritora FG (2019) Macroecological and spatial patterns in the distribution of cladocerans in Alpine lakes. Limnetica 38:119–136

Tiberti R, Brighenti S, Iacobuzio R, Pasquini G, Rolla M (2014) Behind the impact of introduced trout in high altitude lakes: adult, not juvenile fish are responsible of the selective predation on crustacean zooplankton. J Limnol 73:59–597. https://doi.org/10.4081/jlimnol.2014.969

Tonolli V, Tonolli L (1951) Osservazioni sulla biologia e ecologia di 170 popolamenti zooplanctonici di laghi Italiani di alta quota. Mem Istitit Italiano Idrobiol 16:21–25 ((**in Italian**))

Urbanc J, Brancelj A (2000) Sledilni poizkus v Jezeru v Ledvici, dolina Triglavskih jezer = Tracing experiment in the Ledvica Lake in the Triglav Lakes Valley. Geologija 42:207–214 ((**in Slovene with English abstract**))

Urbanc-Berčič O, Gaberščik A (2002) Vodni makrofiti / Aquatic macrophytes. In: Brancelj A (ed) Visokogorska jezera v Vzhodnem delu Julijskih Alp/High-mountain lakes in the Eastern part of the Julian Alps. Založba ZRC SAZU in Nacionalni Inštitut za Biologijo, Ljubljana, pp 129–136

Ventura M, Catalan J (2008) Incorporating life histories and diet quality in stable isotope interpretations of crustacean zooplankton. Freshw Biol 53:1453–1469

Ventura M, Tiberti R, Buchaca T, Buñay D, Sabás I, Miró A (2017) Why should we preserve fishless high mountain lakes? In: Catalan J et al (eds) High mountain conservation in a changing world, advances in global change research. Springer, Cham

Vidrih R (2008) Potresna dejavnost Zgornjega Posočja / Seizmic activity of the Upper Posočje area. Environmental Agency of the Republic of Slovenia, Seizmology and Geology office, Ljubljana

Williamson CE, Dodds W, Kratz TK, Palmer MA (2008) Lakes and streams as sentinels of environmental change in terrestrial and atmospheric processes. Front Ecol Environ 6:247–254

Winder M, Monaghan MT, Spaak P (2001) Have human impacts changed Alpine zooplankton diversity over the past 100 years? Arctic Antarctic Alpine Res 33:467–475

Zhu L, Wang J, Brancelj A (2005) A study on environmental changes based upon cladoceran assemblages from the core sediments in Chen Co, southern Tibet. Chinese Sci Bull 50:1386–1394