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Pulling the Plug—Draining an Alpine Lake Failed to Eradicate Alien Minnows and Impacted Lower Trophic Levels

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Abstract: Fish introduction into fishless high-altitude lakes has detrimental effects on biodiversity. Removal of alien fish through intensive fishing is cost-intensive and difficult to achieve in productive lakes. Lake Sulzkarsee is the only lake in the National Park Gesäuse, Austria, and was an important breeding site for amphibians until the lake was stocked with fish in the late 1970s. Salmonids were eradicated in 2005, but the lake remained degraded by the introduced minnows (*Phoxinus* sp.). In 2018, the lake was drained through a siphon pipe and then by pumping out water with dirt water pumps. The deepest part was treated with slaked lime, but several hundred adult minnows survived in sediment crevices and reproduced in the following season. After drainage, the phytoplankton biomass increased. Indicator species, such as *Daphnia longispina* and amphibians, showed signs of recovery, but they went back to an impacted state when minnows recovered after the failed eradication attempt. Purse seines proved to be the most efficient gear to catch minnows. These results indicate that deep mountain lakes are difficult to drain efficiently. Sediment treatment is required to eliminate all fish.

Keywords: alien species; alpine lake; drainage; fish removal; lake drainage; plankton; resilience; top-down effects

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1. Introduction

The inadvertent or deliberate introduction of alien predators into natural ecosystems is among the major causes for species extinction. Stocking lakes with alien fish has led to some of the most devastating eradications of native species. For instance, the release of Nile Perch (*Lates niloticus*) into East Africa's Lake Victoria during the 1950s drove more than 200 of the 500+ endemic cichlid species to extinction [1]. The large-scale stocking campaigns of originally fishless high-altitude lakes caused less known, but nevertheless far-reaching, changes in these ecosystems [2,3].

Most alpine lakes develop after retreating glaciers leave behind basins and moraines. Downstream physical barriers, such as cascades and steep river stretches, prevent fish colonization; hence, most mountain lakes were originally fishless and contained specific amphibians and aquatic invertebrates. However, there is a long tradition of stocking these ecosystems with fish. In the Alps, the first records date back to the 15th century. The original purpose was the entertainment of feudal landowners, who wanted to fish during their hunting expeditions. Salmonid species, such as brown trout (*Salmo trutta* forma *fario*) or Arctic charr (*Salvelinus umbla*), were translocated and often persisted as stunted populations [4,5]. Later, salmonids were carried or airlifted to remote places, becoming a widespread threat for mountain lakes all over the globe [6,7]. European minnows (*Phoxinus* sp.) were sometimes introduced as prey for salmonids [7] or as live baitfish for anglers [3]. The fast reproduction, high densities, and the ability of minnows to tolerate low oxygen make them particularly effective predators [8].

Stocking fish into previously fishless high-altitude lakes affects planktonic and benthic invertebrates, as well as vertebrates, such as amphibians [9,10]. Large cladocerans and copepods often disappear due to the size-selective predation of fish, releasing smaller taxa, such as rotifers, from competition for food [2,11,12]. Cascading trophic interactions may subsequently change phytoplankton communities [13]. The richness and abundance of conspicuous benthic macro-invertebrates are reduced in the presence of fish [2,14]. Most native amphibians disappear after fish introduction [2,8,15–18], but unpalatable species, such as common toads (*Bufo bufo*), can survive [19]. Even macrophytes can be disturbed by stocking phytophagous fish [20,21].

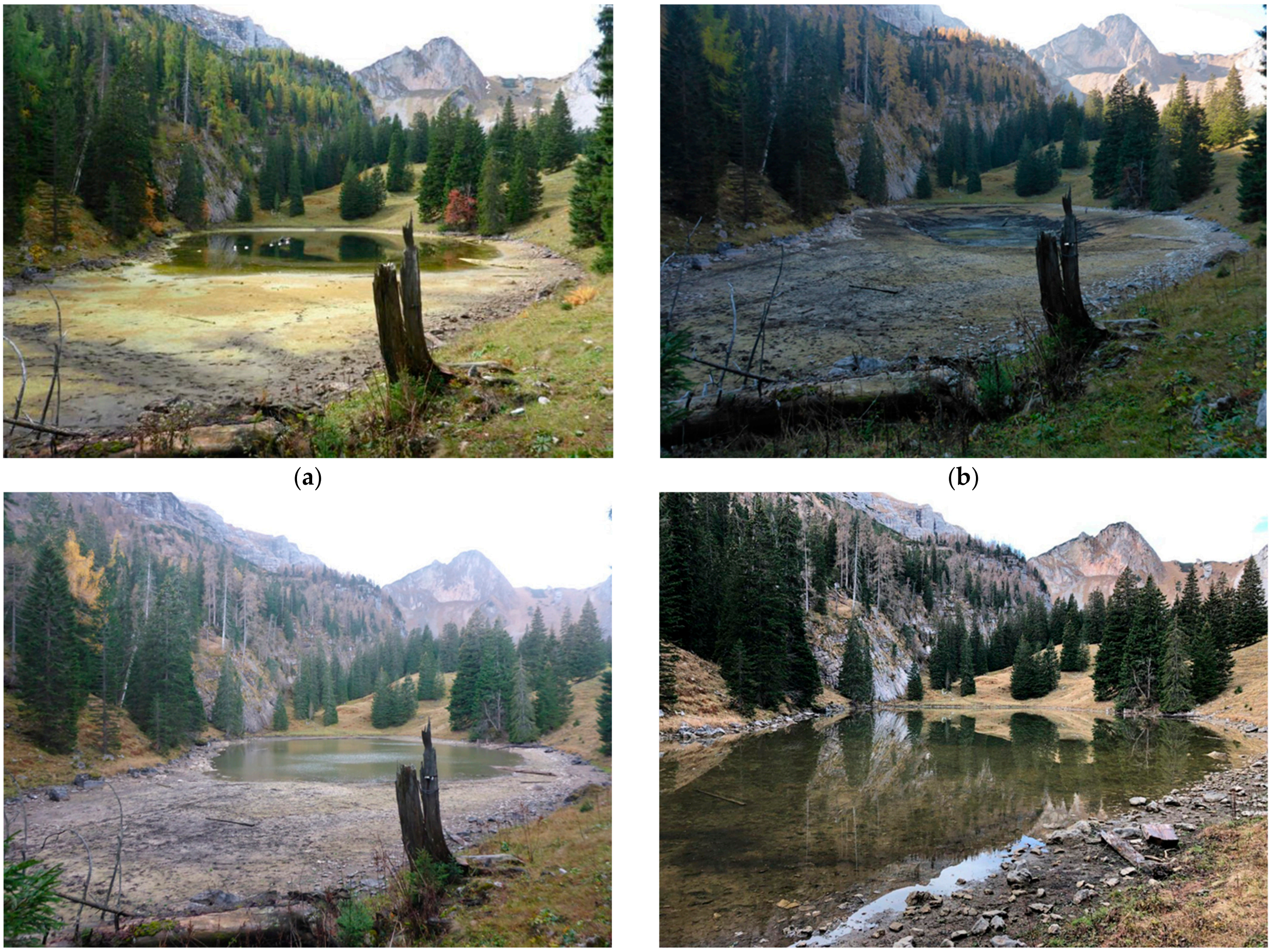
With the devastating impact of alien predators becoming obvious during the past decades, various methods have been proposed for fish eradication. Among them are intensive fishing with active (purse seines, electrofishing, and spear fishing) and passive methods (traps, fyke nets, and gill nets), drainage, liming, treatment with piscicides (e.g., rotenone, antimycin, saponins, and niclosamide), deoxygenation (e.g., dry ice, sugar, molasses, whole milk, and lactose), biological control through the introduction of predators, and explosives [22–25]. Currently, fish eradication programs are undertaken in various mountain ranges, such as in the Pyrenees, the Italian Alps, and in the Sierra Nevada, US [3].

When fish are eradicated, the mountain lakes can revert to conditions that resemble those found in lakes that remained fishless [26]. In the Sierra Nevada, US, communities converged on the configuration of unstocked lakes within 11–20 years after fish disappearance [2]. Crustaceans [27], macroinvertebrates [2,28,29], and amphibians return once fish are removed [29–33]. In this study, we set out to drain an entire alpine lake (Sulzkarsee; National Park Gesäuse, Austria). We describe the abiotic conditions, as well as the phyto- and zooplankton communities, before (2003 and 2013), during (2018), and after (2018–2022) drainage of the lake and tested the efficiency of different fishing gear to remove minnows. We recount the unsuccessful attempt to eliminate alien minnows and discuss the potential and risk of lake drainage for future eradication campaigns. Finally, we assessed anuran densities by counting egg masses and by mark-recapture experiments.

2. Materials and Methods

2.1. Study Area and Stocking History

The National Park Gesäuse (Styrian Calcareous Alps, Austria, established 2002) protects 12,000 ha of a pristine limestone massif, including steep rockfaces and ravines. Due to the unique topography, the park harbors the highest numbers of endemic species in any Austrian National Park [34]. Lake Sulzkarsee (1450 m a.s.l.) is the only alpine lake within the National Park Gesäuse (Figure 1). It is embedded into the moraines extending between the steep cliffs of the surrounding peaks (~2000 m altitude). Clayey silt material within the glacial deposits retains the water [35]. During snow melt and heavy rains, a small creek flows into the lake from the Southwest. Lake Sulzkarsee undergoes considerable changes in water level (app. 1.5 m), but never dries up completely. It has a maximum depth of 7 m, a surface area of 8540 m^2, and a volume of 19,890 m^3. After drainage and when the lake refilled, the maximum recorded depth was 6.5 m due to sediment sliding towards the center.



(**a**) (**b**) (**c**) (**d**)

Figure 1. The lake during the drainage operation: on 4 September 2017 (the buoys held the pipe afloat) (**a**); 16 October 2018 (after complete drainage) (**b**); 29 October 2018 (**c**); and 13 November 2018 (partially refilled after heavy autumn rains) (**d**).

At least since the 15th century, the surrounding pasture has been used for cattle grazing during the summer. The name "Sulzchar" is first mentioned in 1434 in connection with logging activities by the owner, the monastery "Admont". Since the 18th century, the alpine pasture has been used quite intensively (maximum 160 cattle and 200 sheep), and the lake was used as a watering place for the animals. Likely, this has increased the nutrient load in the lake. In 2007, a wooden fence was built along the crest of the moraine in the North, halfway around the basin, excluding cattle from access to the lake. According to locals, large populations of alpine newts (*Ichthyosaura alpestris*), common frogs (*Rana temporaria*), and common toads (*Bufo bufo*) used the lake for reproduction before the introduction of fish.

Sulzkarsee was stocked for the first time during the 1970s with alien rainbow trout (*Oncorhynchus mykiss*). After that, approximately 80 Arctic charr, together with some rainbow trout and brown trout, were introduced annually until 2002, when stocking was finally stopped after the establishment of the national park. No reproduction of salmonids was ever observed, as the lake has no suitable gravel substrate for oviposition. In 1979 and again in 1980, approximately 1000 minnows from Zeller See (Salzburg, Austria) were introduced and still thrive in the lake. The last salmonids from original stocking campaigns were removed in 2005. After minnow eradication through drainage failed, we stocked 500 brown trout (ca. 25 cm total length, 190 kg total) again as top predators in 2019, but they died out within 1 year after stocking. The salmonid presence and relative minnow abundance were evaluated qualitatively by visual inspection from the shore and while snorkeling (Figure 2).

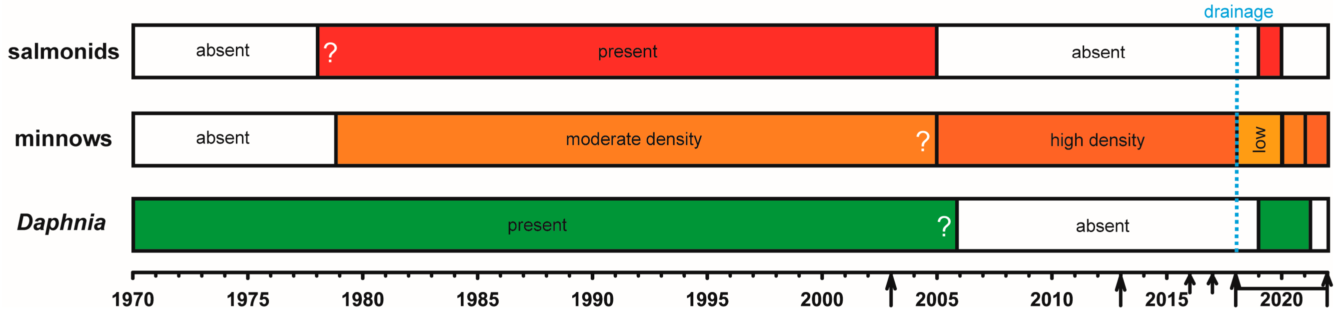


Figure 2. Timeline of events in Lake Sulzkarsee. Arrows indicate the main operations (long arrows representing the main measurements and samplings.details on fishing operations can be found in Table 1). Uncertain changes in presence or abundance are indicated by "?". Lake drainage occurred in 2018 (vertical blue interrupted line). Teleost fish taxa are shown in red (salmonids) and orange (minnows; darker colors mean higher densities).

2.2. Lake Drainage

Mid-October 2016, a 250 m long PVC pipe (inner diameter: 8 cm) was laid from the deepest area of the lake over a ridge (+4 m height), down to below a forest road (−42 m below lake surface; Figure 3). Eight buoys (Jetfloat) kept the angular intake socket afloat at circa 50 cm below the water surface (Figure 1a). Shutoff valves were inserted at the intake, at the highest point of the pipe (1450 m) and at the outlet (1404 m, Figure 3). The local fire brigade filled the pipe from below by pumping water into the pipe. Lake water was then siphoned down until the pressure difference exceeded the physical limit of raising the water column over the ridge (ca. 3–4 m). During the first trials in 2016 and 2017, the lake level was intermittently lowered for up to 2 m through the siphon (see Results). In 2018, a vacuum pump was installed at the crest to restart the pipe after the breakaway of the water column due to physical constraints. On 10 October 2018, the full lake drainage was launched: three dirt-water pumps (one with 2.6 m^3 min^{-1} and two with 1.3 m^3 min^{-1} maximum throughput) were installed in the center of the lake and started at 15:00 local time. A diesel aggregate (GSW50 Power Engineering) was placed at the forest road, and cables were laid to power the pumps. The stronger pump was fed into the existing pipe, while the hoses of the two others ended just below the crest of the ridge. The water was drained off to Sulzkar creek and the surrounding alpine pasture and woodland (Figure 3).

2.3. Liming

In a preliminary trial in the winter before the lake drainage (17 December 2017), 17 holes were cut into the ice cover with a chain saw, and a total of 1250 kg of burnt lime were dumped into the lake.

On 15 October 2018, after the lake drainage, the sediment was treated with 750 kg of burnt lime. The lime was mixed with lake water taken from one of the pumps within a 90 L container and hosed down through a pipe (diameter 10 cm) into the deepest part of the lake when the remaining puddle was about 15 cm deep (area ca. 300 m^2). The slaked lime was distributed above the puddle (area ca. 800 m^2) by dragging the mouth of the hose with a rope across the deepest 1 m of the lake basin.

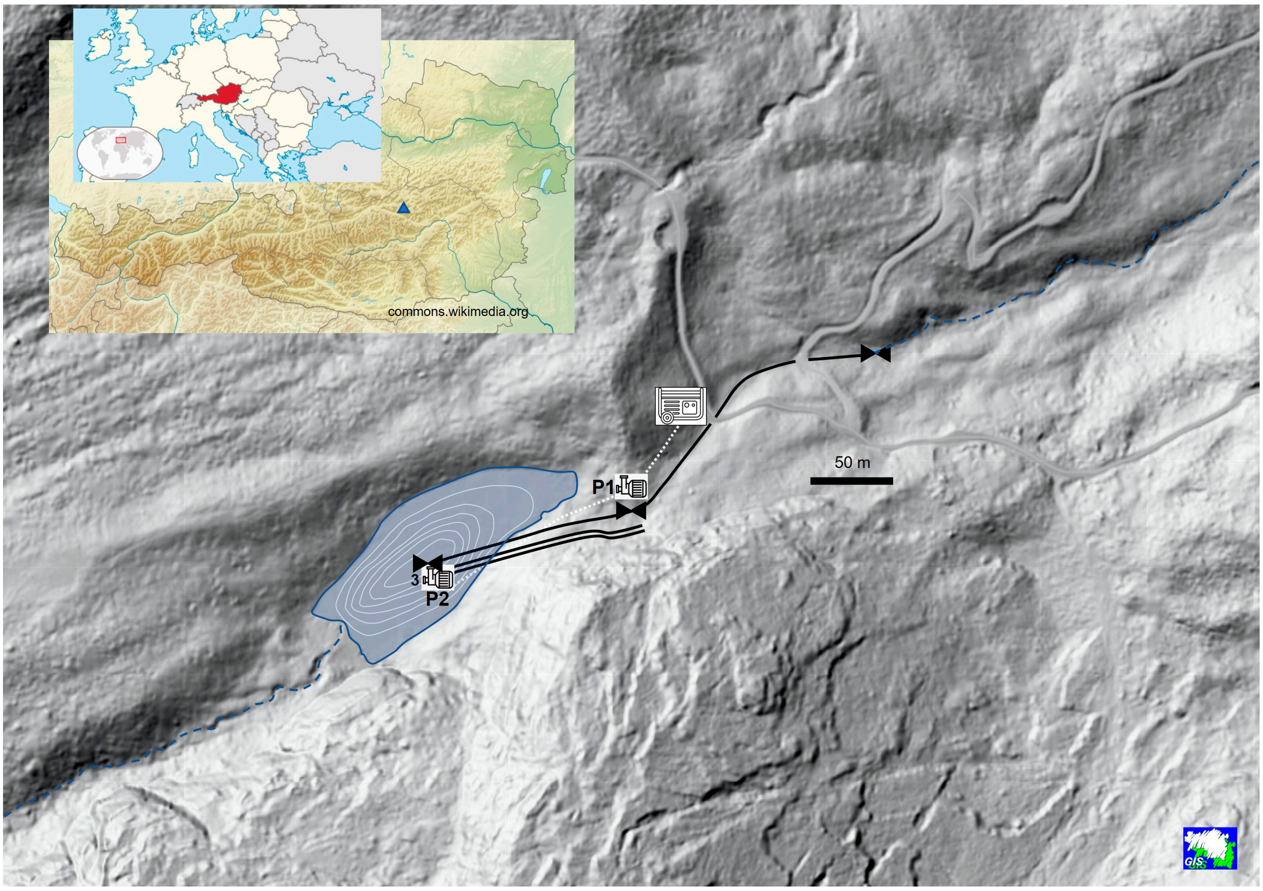


Figure 3. Shaded relief map of Lake Sulzkarsee (blue surface) and surrounding alpine environment. An intermittent creek (blue dashed line) flows into the lake and emerges below the forest road (grey lines). A PVC siphon pipe (black line on top) was operated from the lake surface over a ridge (pump P1 for filling syphon pipe) to below the forest road. It was equipped with three valves (black triangles). The residual volume was drained in 2018 with three (3) electric dirt water pumps (P2), with one ejected into the tube and the other two into hoses ending below the ridge (two short parallel black lines). Pumps were driven by power lines (white dotted line) from a diesel generator (symbol) placed at the forest road. Inserts show Austria and the position of Lake Sulzkarsee (blue triangle). Basemap and inserts taken from "Digitaler Atlas Steiermark" and "Wikimedia Commons", respectively.

2.4. Sample Collections

Lake Sulzkarsee was studied in 2003, 2013, and during 2018–2022. Water samples were collected 1–5 times per year during the ice-free period with a 5 L Schindler-Patalas trap in 1 m depth intervals at the deepest point of the lake down to 5–6 m depth, depending on the water level. No samples were taken below 6 m to avoid dragging sediment into the open water. The temperature was recorded with a thermometer mounted within the trap, and the oxygen, pH, and conductivity were measured with a HACH HQ 30d multimeter. Nutrients were measured according to DIN norms in a certified water laboratory in 2003, 2013, 2019, and 2020 (Hydrologische Untersuchungsstelle Salzburg). Samples for nutrient analyses were pooled from 1, 3, and 5 or 6 m depth.

Quantitative phytoplankton and zooplankton samples were collected with the Schindler trap at 2 to 4 depth intervals (see Results). For phytoplankton, samples of 100 mL unfiltered water were preserved with Lugol's solution [36] and kept in brown glass bottles. Zooplankton samples were filtered through a 30 µm mesh sieve and preserved in 4% formaldehyde. In 2003, plankton samples from 1, 3, and 6 m depth were pooled. To detect rare species, integrated plankton samples were collected by vertically towing a 30 µm plankton net (diameter 45 cm) from the bottom to the surface.

Algae were counted under an inverted microscope (Telaval 3, Jena; magnification 40–1000×) by applying the method of Utermöhl [37]. Biovolumes were calculated by fitting geometric bodies to cell dimensions [38]. Zooplankton samples were stained with Rose Bengal. Samples were counted under the inverted microscope (magnification 40–100×). Biovolumes and biomasses were calculated by approximating natural shapes with geometric formulae for rotifers [39] and from length–weight relationships for crustaceans [40], respectively.

2.5. Fishing

Over the study period, different fishing gear was used to fish for salmonids (2003/2013) and to reduce minnows in the lake (2016–2022; Table 1). Gill nets were usually exposed overnight in water up to 2 m depth, while traps baited with press cakes of pumpkinseeds remained in the lake during fishing operations (<2 m, Table 1). Electrofishing was performed with an ELT-62II (Grassl, 2.6 kW). The electrofishing equipment was placed in a dinghy and towed while 3 people were wading and fishing along the shoreline. Purse seines were put out in a circle from shore into ca. 1.5 m deep water and back and then retrieved (10 min per tow).

Minnows caught in 2016 were transported to the large Austrian lake (4.5 km^2) Zeller See, from where they originated and where they had disappeared meanwhile. Live fish from traps, purse seines, and electrofishing (2013–2020) were released in Sulzkar creek, emerging 500 m below the lake from its subterranean flow. They likely wandered down to the River Enns, where minnows occur naturally. From 2021 onwards, minnows were transported alive to a local hatchery. Over the years, the fishing efforts of different people and the gear used varied; hence, the catch per unit effort (CPUE) was only calculated for the most concerted operations in 2020. Effort was defined as the time needed for a team of 3 people to operate one piece of gear during the fishing operations and to count the catch. In 2021, Petr Pokorný developed purse seines specifically designed to catch minnows (Table 1, Figure S1).

Table 1. Fishing gear and duration of fishing operations (2003–2022) carried out before and after the drainage operation.

Year	Gear	Dimensions	Total Time of Fishing Operation
2003	1 multi-mesh gill net; deep lake	50 m long × 1.5 m wide, 6.5–70 mm mesh size	3 h
2013	2 multi-mesh gill nets; deep lake Electrofishing	30 m × 1.5 m, 5–55 mm ELT-62 Grassl 2.2 kW	26 h 3 h
2016	4 minnow traps	1.5 long × 0.5 wide × 0.3 m high, 5 mm	2 d
2017	bottle traps	1.5 l PET bottles	Several weeks
2018	4 rectangular minnow traps	0.54 m × 0.25 m × 0.25 m, 3 mm	13 d
2019	4 umbrella minnow traps 2 rectangular minnow traps 8 bottle traps	0.95 m × 0.95 m × 0.60 m, 5 mm as above as above	16 d
	4 multi-mesh gillnets	30 m × 1.5 m, 5–55 mm, effective mesh sizes 5, 6.25, 8, and 10 mm	3 d
2020	14 umbrella traps	as above	8 d
	2 small gill nets	40 m × 0.3 m, (alternating 10 m of 5 mm and 6.25 mm mesh sizes)	8 d
	2 large gill nets	50 m × 2 m, 6 mm	3 d
	purse seine	10 m (5 + 5 m wings) × 1.5 m, 7 mm	3 d
	electrofishing	as above	4 d
2021	purse seine	8 m × 0.5 m, 2 mm, cod-end 0.85 mm	4 d
2022	purse seine 1 purse seine 2 purse seine 3	8 m × 0.8 m, 2 mm, 0.85 mm 16 m × 1 m, 2 mm, 0.85 mm 12 m × 1 m, 2 mm, 0.85 mm	4 d

2.6. Amphibians

On 8 June 2019, 50 males and 50 females of the common toad from the lake were marked with 12 mm PIT-tags (passive integrated transponders; 134.2 Khz), and on 1 and 2 June 2021, 297 males and 104 females were marked. Each year, the toads were recaptured one day after tagging. The total number of adults in the lake were estimated with a "Petersen" estimate in 2019 and with "Baily's triple catch" estimate in 2021 [41]. The number of female common frogs spawning in the lake were estimated by counting the number of egg clutches. Alpine newts were searched for in shallow water by visual inspection during the day and night.

3. Results

3.1. Lake Drainage

In 2016, the suction pipe was filled on 13 October and ran with a discharge of ca. 10 L sec^{-1} before it stalled 3 weeks later. It was restarted on 24 November and operated until 30 November. The lake level dropped for a maximum of 2 m. In 2017, drainage started on 8 August, but four weeks later, the lake reached the maximum water level again due to heavy rains in the summer. The lake level dropped to −1.5 m from the maximum water level between 4 and 19 September (Figure 1a). Finally, in 2018, the pipe was activated on 18 July and ran until the beginning of August. When it stalled, it was reactivated again with a vacuum pump inserted at the pipe's turning point. At approximately −3 m water level from the maximum level, the physical limit was reached due to the constraints of the air pressure difference between the intake and outlet of the siphon and the friction loss in the pipe. A water column can only be raised for a maximum of 10.3 m at sea level (1013 mbar). Such a vacuum requires the atmospheric pressure to force the water up the pipe, and that fails at the point where the weight of the column equals the air pressure, which at 1446 m is only around 850 mbar (7–8.5 m height difference from water level to the crest of the ridge). Especially during periods of depression (low air pressure), the water column frequently broke off.

On 10 October 2018, the newly installed dirt water pumps were started running (Figure 1). Due to operating the siphon pipe before, the water level was already at −2.5 m under the maximum water level when the dirt water pumps were started, and more than 6300 m^3 of the residual lake volume were pumped out until the lake was almost dry. Due to the friction loss and vertical height of up to 11 m, the pumping capacity was below 2 m^3 min^{-1}. As soon as the pumps operated, cracks opened throughout the basin, and the sediment slid towards the center of the lake (Video S1). Two ponors (sink holes) occurred along the northeastern shore at ca. −3 m (diameter ca. 15 cm), and a small spring flowed into the lake along the southeastern shore (ca. −5.5 m depth, 0.5 L sec^{-1}). After 80 h of pumping, the lake was almost empty (Figure 1b). As water was slowly seeping into the lake basin, it was kept empty by the on-and-off operation of 1 pump for 24 h until 15 October, when liming started at 10:00. The residual water (ca. 20 cm water level) was then pumped into circulation, adding lime. The slaked lime was kept in the lake for about 2 h and drained again. Approximately 500–1500 minnows were killed. No fish were observed when the water had cleared up on 16 October. Heavy autumn rains filled the lake basin (−0.5 m from the maximum water level) within one month after drainage (Figure 1c,d).

3.2. Stratification

A distinct stratification persisted throughout the summer, with temperature gradients ranging from 18–10 °C from the surface to 6 m depth. Homeothermic conditions were reached in October when extended autumn rains and wind set in (Figure 4a, only the period 2019–2021 is shown; additional data shown in Table A1). In spring 2019 and 2021, oxygen depletion (<1 mg L^{-1}) was observed in the deepest sampled layer. A metalimnetic oxygen maximum of around 2 m depth developed during the summer (Figure 4b). Elevated conductivity and lower pH in the hypolimnion continued throughout the summer (Figure 4c,d). Biogenic decalcification led to a maximum pH of up to 9.2 in the epilimnion

(Figure 4d). Nutrients briefly increased in 2019 in the season after lake drainage, but were back to pretreatment mesotrophic conditions in 2021 (Table 2).

Table 2. Nutrients in Lake Sulzkarsee (mg L^{-1}) before (2003, 2013) and after drainage (2019, 2021). TP, Total phosphorous; TDP, Total dissolved phosphorous; n.a., not available.

	2003	**2013**	**2019**	**2021**
TP	0.015	0.01	0.136	0.012
TDP	0.0039	n.a.	0.003	0.004
PO_4^{3-}-P	n.a.	n.a.	0.0033	<0.0033
NH_4^+-N	<0.002	0.016	2.176	n.a.
NO_2^--N	<0.003	<0.015	0.003	n.a.
NO_3^--N	0.13	0.102	<0.25	<0.25

3.3. Plankton

A total of 135 phytoplankton (Table A2) and 52 zooplankton taxa were found (Table A3). Each year after ice break, fast-growing, small flagellate algae dominated the phytoplankton community, whereas larger taxa (e.g., Dinophyceae) and colonies (Chlorophyceae) took over later during the season (Figure 5). The lake drainage in 2018 caused major changes in the species assemblage. The original dominance of Chlorophyceae in 2003 and 2013 shifted towards a higher abundance of Chrysophyceae, Conjugatophyceae, and Dinophyceae after the lake drainage. In 2020 and 2022, the relative abundance of major algal families had reverted to a pre-drainage species assemblage. However, in 2021, it was different, showing a highly dynamic succession after this major impact on the ecosystem. Generally, the total algal biomass in autumn had about doubled from the 2000s to the 2020s. The algal biomass was generally higher in the epilimnion, except during early spring, when algal populations were building up in the meltwater.

Daphnia longispina dominated the zooplankton biomass in 2003, when minnows were kept down and ashore by piscivorous salmonids (Figures 2, 6 and 7). Once the salmonids were removed in 2005, *Daphnia* vanished from the plankton community and rotifers dominated. In 2019, the season after the lake drainage, *Daphnia* recovered from ephippia in the egg bank and persisted until 2021. When, in 2022, the minnows finally increased again in numbers and the salmonids restocked in 2019 were gone, *Daphnia* once again disappeared from the zooplankton. In 2018, *Ceriodaphnia pulchella* was recorded for the first time in low numbers. In August 2019, it dominated, but by September dropped to about 10% of the biomass of *Daphnia longispina*. It finally reappeared in September 2022 in low densities (2.6 mg m^{-3}). No clear patterns in depth distributions were observed in cladocerans. In contrast, rotifers frequently reached higher biomass in deeper layers.

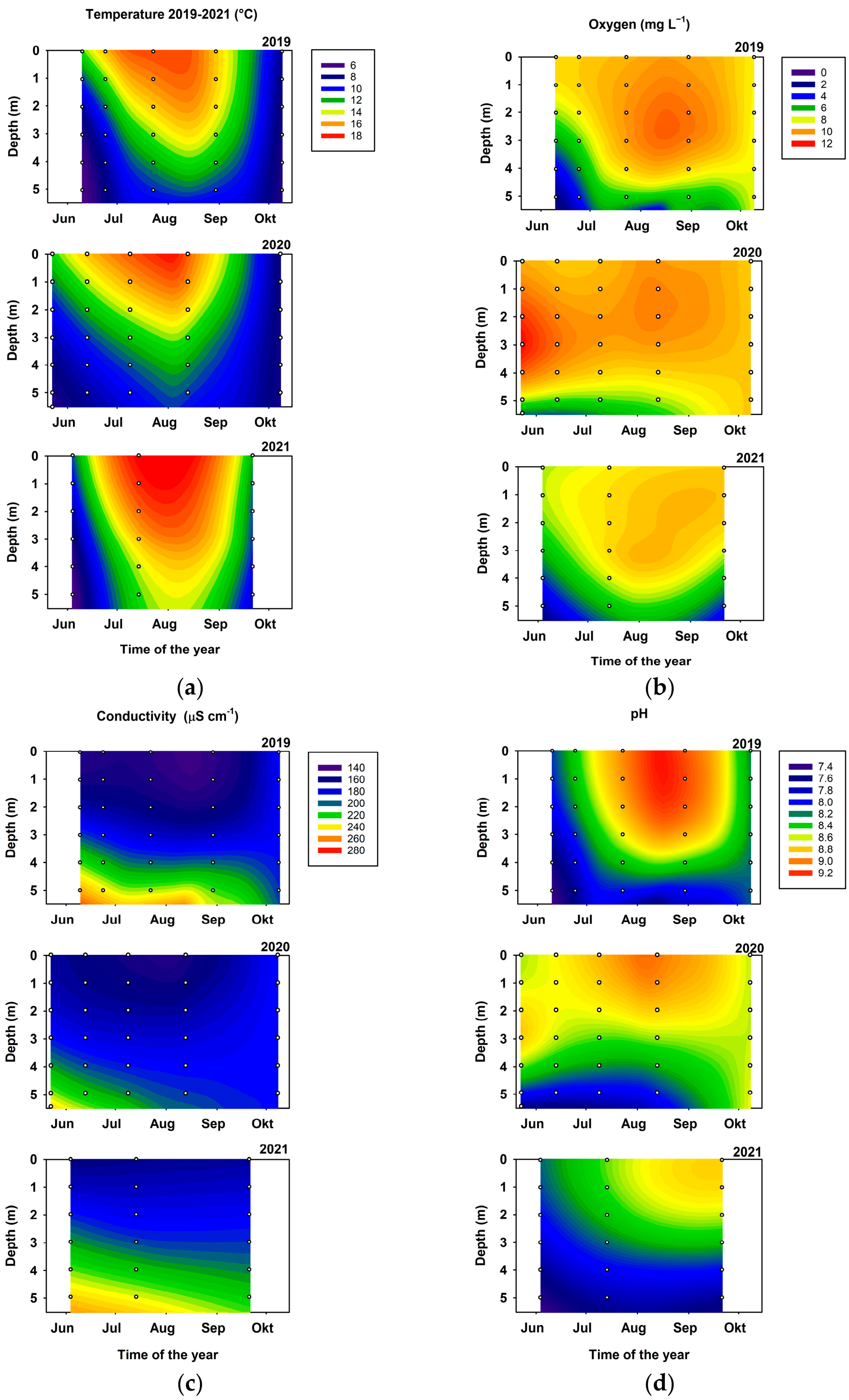


Figure 4. Temperature (**a**), oxygen (**b**), conductivity (**c**), and pH (**d**) in Lake Sulzkarsee (2019–2021) following the 2018 lake drainage.

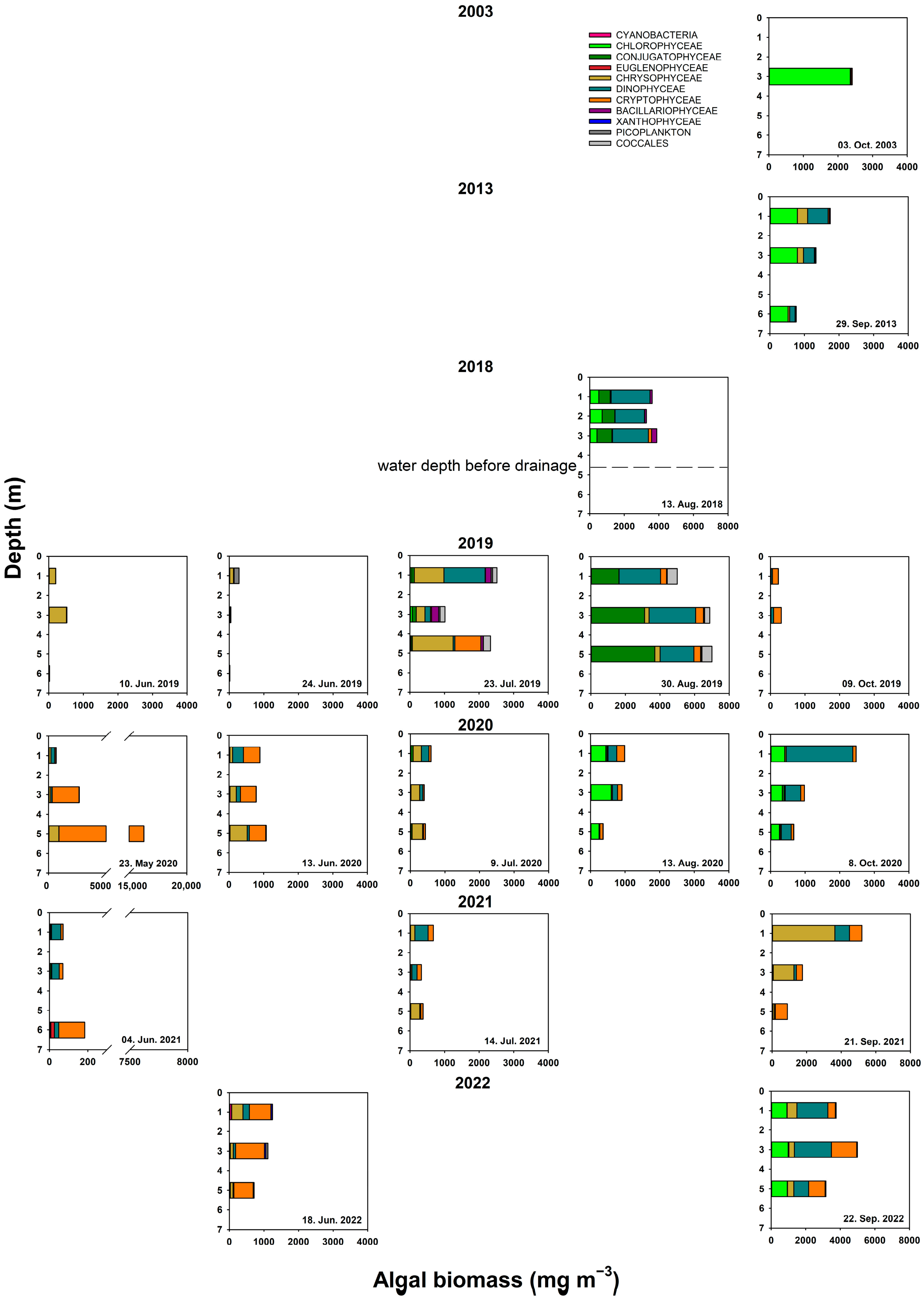


Figure 5. Phytoplankton biomass in Lake Sulzkarsee (2003–2022) before and after lake drainage (October 2018). Panels are lined up temporally from May to October. Water depth in August 2018 was 4.5 m during sampling.

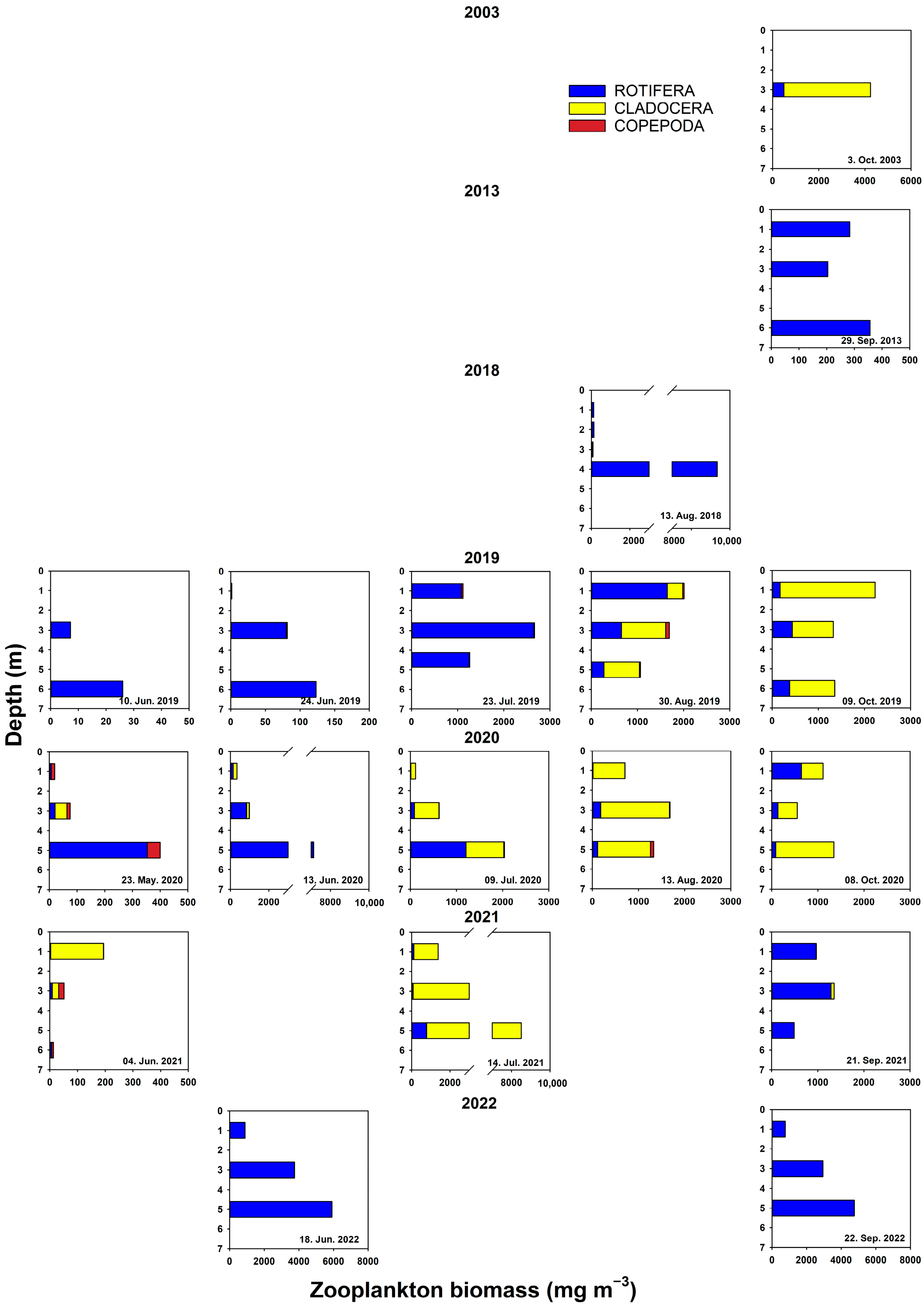


Figure 6. Zooplankton biomass in Lake Sulzkarsee (2003–2022) before and after lake drainage (October 2018). Panels are lined up temporally from May to October. Water depth in 2018 was 4 m during sampling.

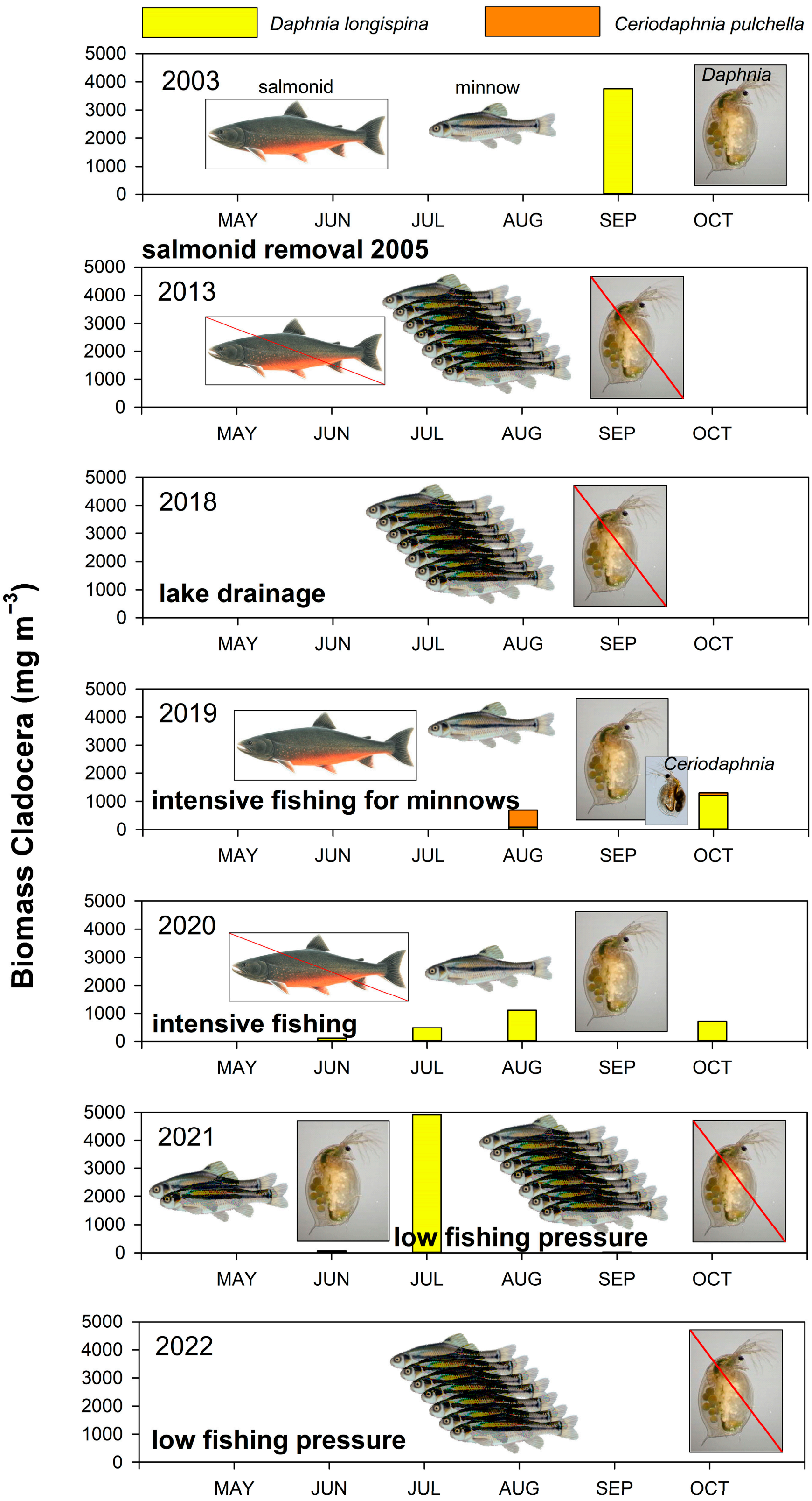


Figure 7. Biomass of Cladocera (average density of 3 different water depths) in relation to year, season, and relative fish abundance. The icons depict the presence or absence of cladocerans and salmonids and the relative abundance of minnows. The positions of the icons of organisms are not bound to the exact time of the year.

3.4. Fishing

During a first 3 h fishing operation in 2003, 8 Arctic charr and 1 rainbow trout were caught. In 2005, the last remaining salmonids were caught by the national park rangers (no data available). In 2013, no salmonids were caught in the gill nets anymore. A total of 1064 minnows were caught by electrofishing.

Over the study period of 7 years (2016–2022), a total of 75,100 minnows were caught (Figure 8a), of which 72,000 were released alive. After the lake drainage in 2018, the minnow population was massively reduced, but several hundred larger (>6 cm total length) individuals had survived and started to reproduce in June 2019, 3 weeks after ice break. Despite intensive fishing in 2019 and 2020, the population recovered and markedly increased in abundance in 2021, when fishing pressure was reduced.

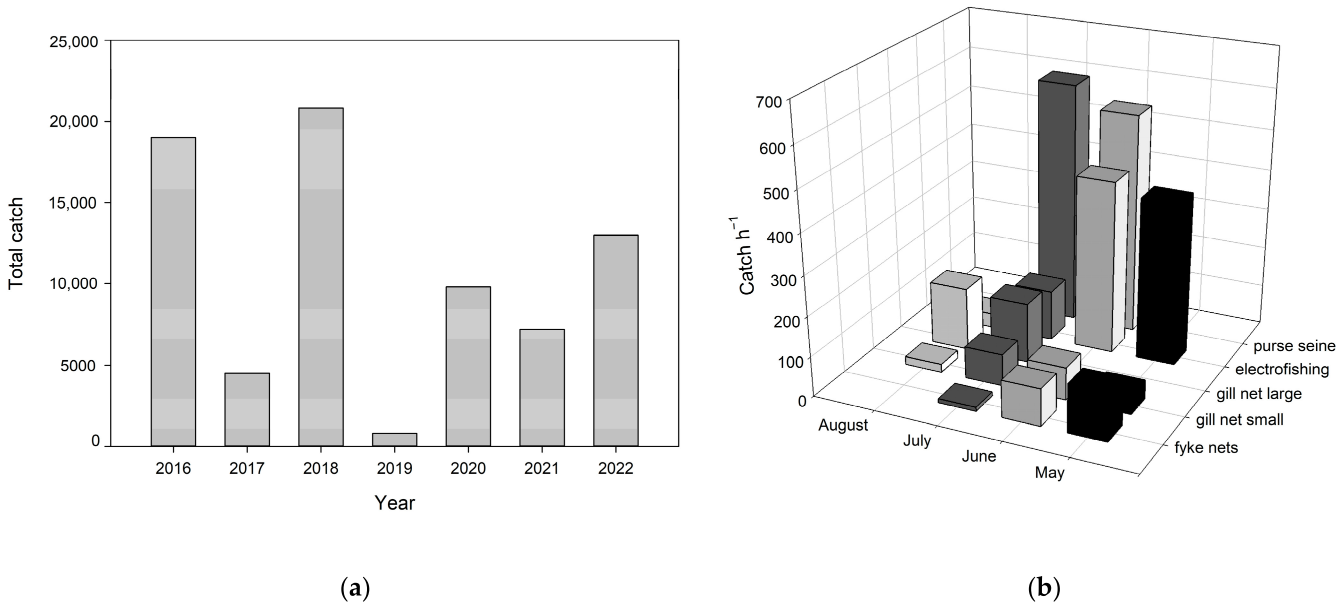


Figure 8. Total catch of minnows before and after lake drainage in 2018 (**a**) and catch per unit effort (CPUE) with different gear types used in 2020 (**b**). See Table 1 for description of fishing gear.

Fish were caught with all gear types, but purse seines were the most effective gear in terms of invested labor (Figure 8b). The purse seines used from 2021 onwards yielded maximum catches of 1500 individuals per tow, covering circa 10–30 m^2 of the lake bottom. Electrofishing was an effective tool to catch small yearlings in shallow shoreline regions. Trout introduced in 2019 did hunt for minnows, and some survived under ice, but they disappeared due to unknown reasons during summer 2020.

3.5. Amphibians

The mark-recapture experiments yielded mean numbers of 2817 (S.E. ±1400) male and 250 (±65) female toads in 2019, and 3194 (±1672) males and 359 (±326) females in 2021. The sex ratio was strongly biased towards males, with 9 to 11 times more males than females at the spawning site on the days of sampling. In 2019 and 2021, 99 and 184 egg clutches of common frogs, respectively, were recorded.

4. Discussion

4.1. Fish Removal

After long human interference, the restoration of natural communities in newly created protected areas is a protracted process. When the National Park Gesäuse was established in 2002, restoring the only natural lake, Lake Sulzkarsee, and the surrounding terrestrial forest communities became an important goal. The lake was degraded by the eutrophication of grazing cattle and by the introduction of alien fish. While alpine farming and forestry persisted over hundreds of years prior to our study [42], fish stocking only took place during the 1970s. Compared to the ongoing long-term efforts to let natural forest communities regrow in the national park, restoring the lake seemed a task that could have been accomplished within years rather than decades. While excluding cattle from the lake and removing introduced salmonid fish was an easy task, eliminating minnows proved impossible, up till now.

Eradicating small, fast-reproducing alien fish by intensive fishing is very labor- and cost-intensive, if at all possible. In oligotrophic Pyrenean alpine lakes, it took 4–6 years of electrofishing and gill and fyke netting throughout the ice-free period and in weekly intervals to eradicate minnows (Marc Ventura, personal communication [3]). With the budget available for the Sulzkarsee project, it was impossible to eradicate minnows by intensive fishing, as a broad belt of macrophytes offers plenty of hiding places and impairs fishing operations. Accordingly, it is unrealistic to fish out the countless alpine lakes containing cyprinids today. Draining a lake basin may, therefore, be tested as a comparatively cheap restoration tool.

To our knowledge, this was the first attempt to drain an entire alpine lake basin of this size, as previous attempts were made in pond environments [33]. Although we came close to success, fewer than 1000 2-years-and-older minnows survived, very likely within crevices in the untreated slope sediments (Video S1). While we managed to eradicate the fish concentrating in the residual water volume by liming, the pH shock was not delivered to the exposed slope sediments. This may have been achieved by pumping out the $Ca(OH)_2$-rich water and spraying it over the entire lake basin, but due to time constraints, it was logistically not possible to take this important last step. Prior to drainage, the dumping of burnt lime from the ice cover failed altogether, as we did not dissolve the lime and intermix it with the lake water (e.g., with an outboard engine).

Shallow Alpine lakes with nearly level access to downward slopes could be drained through a siphon. Fish will likely disappear when the lakes can be kept dry for longer periods during the summer or when low temperatures cause freezing of the sediment. Chances increase when the drainage is followed by long fair-weather periods in autumn. If subsurface springs appear during lake drainage, liming is essential, as the fish try to escape into untreated clean water and may hide in underground watercourses.

The piscicide rotenone has been one of the methods used for large-scale eradication programs, but environmental and health risks have limited its use in alpine lakes [24,43]. It will be particularly difficult to use this poison within protected areas and in karstic landscapes, where the treated water may resurface in springs or lowland aquifers. More research is needed to determine whether it could be used efficiently in alpine lakes and to eventually develop safe eradication protocols.

It is unlikely that the introduction of any alien piscivore (e.g., fertile or infertile triploid pike, *Esox Lucius*, or different salmonids) can drive minnows to extinction in a lake as productive and richly structured as Lake Sulzkarsee [44]. The introduced brook trout were observed hunting for minnows, keeping them shoaling near shore, but they showed no significant impact on the minnows' fast population growth in the fertilized lake. Additionally, there remains the risk of the successful reproduction of another alien fish species further reducing native amphibians.

Any combination of methods will increase the probability of success. Dense macrophyte belts provide shelter for juveniles and shoaling fish like minnows impeding fishing operations. Intensive fishing with different gear, draining the shallow macrophyte belt, and subsequent chemical treatment of the residual volume could lead to successful eradication of minnows within a reasonable amount of time. After ice brake in the following spring, intensive fishing is required to either confirm successful eradication or to catch fish that survived the treatment.

We aimed at catching as many fish as possible alive. However, live transport is only possible where forest roads reach close to the lakes. The minnows are now contained in a hatchery until their genetic lineage is determined. Since minnows comprise a species complex of at least four species in Austria [Anja Palandačić, pers. communication], care should be taken to determine the species and only use it for restocking where it occurred previously. Much care should be taken that fish are not used for reintroductions in environments where fish were naturally absent. Even though fish eradication is the ultimate goal in these restoration projects, minimizing pain for the individual fish is an ethical responsibility. We were catching minnows with all fishing gear, but the custom-built drag nets were the most effective and welfare-friendly fishing tool.

The species communities in shallow alpine lakes of the northern calcareous Alps are adapted to short-term desiccation events [45]. Imagines of insects (e.g., chironomids, trichopterans, and coleopterans) return for oviposition. Plankton organisms hatch from the egg bank, and worms (oligochaetes and nematodes) retreat to deeper sediment layers. Even superficial treatment with lime does not prevent recolonization within relatively short periods of time [46]. The macrophyte belt of Sulzkarsee had been dry for three consecutive seasons, but regrew during the first summer after drainage.

4.2. Physical Environment and Impact of Fish on Lower Trophic Levels

Throughout the study, the nutrient load of Lake Sulzkarsee was higher than expected for a small oligotrophic alpine lake at this altitude. The mesotrophic conditions likely result from century-long fertilization by livestock excreta and runoff from the surrounding alpine pasture. However, excluding cattle from the lake did not result in a noticeable reduction of nutrients in the lake between 2003 and 2013. During drainage, sliding sediments exposed precipitated nutrients and fertilized the lake during refilling. Phosphorous and nitrogen compounds were back to pretreatment conditions 3 years after drainage. However, flakes of superficial sediments and algae were observed floating on the lake surface for 4 years. The water retention time is unknown, but the inflow of meltwater and storm water runoff likely flushes the system within less than one year.

Abiotic conditions were favorable for the fast growth of minnows (summer temperatures of 10–18 °C, pH 7.4–9.2, oxygen 6–12 mg L^{-1}). Oxygen depletion occurred under the ice, but obviously never reached lethal levels for minnows. Only hatchery-reared, large brown trout did not seem capable of surviving under natural conditions for more than a year after lake drainage. Likely, some inflow of oxygenated water persists during the ice cover. Hence, induced deoxygenation was not considered as a management tool.

Daphnia longispina exemplarily reacted to fish abundance. It was present when minnows were kept away from the open water by salmonids. As soon as the piscivores were gone, minnows grew more abundant and spread throughout the lake, driving *Daphnia* to disappearance from the plankton. *Ceriodaphnia pulchella* occurred, which is known to coexist with planktivores in stocked alpine lakes. Additionally, rotifer abundance and biomass increased [7,12].

Lake drainage resulted in complex changes of the phytoplankton community. The original dominance of chlorophyceans gave way to chrysophyceans, conjugatophyceans, and dinophyceans. The species assemblage seemed to slowly revert to the original pretreatment state. Total algal biomass had increased, but the complex interactions of fertilization through drainage, cascading trophic interactions from the manipulation of fish communities, and potential effects of climate change resulted in a highly dynamic succession that had not yet reached a steady state again by the end of our study.

Fish eradication would certainly allow amphibian populations to increase in numbers. Newts (*Ichthyosaura alpestris*) were abundant in nearby ponds, but very few were observed in the lake. Alpine newts are highly threatened by fish introductions [18]. Previous research showed that alpine newts escape from waterbodies inhabited by alien fish [47], but recolonization is possible. Common frogs were comparatively scarce for a lake of this size (pers. obs. [48]), as minnows can prey on the small tadpoles [17]. Some adults were seen leaving the lake during drainage, confirming overwintering in the lake [48]. Only common toads were abundant, as they can cope with predatory fish [19].

5. Conclusions

Many species communities have been altered by species introductions and climate change. By removing fish, vast numbers of alpine lakes could still be restored. Although our study was not successful, lake drainage could be considered as a restoration tool for small, shallow lakes when limited budgets do not allow multi-year fishing operations. Further experiments—preferably in manmade water bodies—are needed to develop appropriate guidelines. Liming of the entire sediment increases the probability of killing all the fish. Concurrently, the detrimental effects of fish introductions need to be better communicated to stakeholders.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/w15071332/s1, Video S1: Time lapse of lake drainage; Figure S1: Purse seining in Lake Sulzkarsee.

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Appendix A

Table A1. Sampling date, depth, temperature, oxygen concentration and saturation, pH, and conductivity in Sulzkarsee. On 13 August 2018, the water depth was 4.5 m.

	Depth (m)	Temp. (°C)	O_2 (mg L^{-1})	O_2 (%Sat)	pH	Cond. (μS cm^{-1})
3 October 2003	0.3	10.4	12.3	127	8.3	183
	1	9.6	12.5	128	8.3	183
	2	9.3	12.6	127	8.4	183
	3	9.2	12.0	121	8.4	183
	4	9.1	12.0	121	8.4	184
	5	9.0	12.0	121	8.3	184
	6	9.0	11.9	120	8.3	184
29 September 2013	0	10.0	10.4	115	7.9	189
	1	9.4	10.5	112	8.0	190
	2	8.8	9.6	100	8.2	193
	3	8.3	9.0	93	8.2	196
	4	8.1	8.3	84	8.1	198
	5	7.9	8.0	81	8.1	198
	6	7.9	7.8	80	8.1	201
	7	7.8	7.4	75	8.1	204
13 August 2018	0	20.0	8.8	122	9.0	142
	1	18.7	9.2	122	9.0	145
	2	17.5	9.5	122	9.1	145
	3	14.0	12.6	156	9.0	180
	4	11.0	9.9	118	8.1	232
18 June 2022	0	17.7	8.4	106	8.7	155
	1	16.1	8.9	108	8.6	159
	2	12.9	10.1	114	8.6	171
	3	10.3	10.9	117	8.6	194
	4	8.4	10.1	102	8.2	211
	5	7.6	5.8	59	7.8	230
22 September 2022	0	7.5	7.8	77	7.9	204
	1	7.1	7.8	77	8.0	205
	2	7.0	7.8	76	8.0	206
	3	7.0	7.8	76	7.9	207
	4	6.9	7.7	75	7.9	208
	5	6.9	7.6	74	7.9	208

Table A2. Phytoplankton species in Lake Sulzkarsee (2003–2022).

Phytoplankton
Bacillariophyceae
Achnanthes sp. Bory, 1822
Achnanthidium minutissimum (Kützing) Czarnecki, 1994
Achnanthidium spp. Kützing, 1844
Amphora sp. Ehrenberg ex Kützing, 1844
Asterionella formosa Hassall, 1850
Aulacoseira islandica (O. Müller) Simonsen, 1979
Cyclotella spp. (Kützing) Brébisson, 1838, nom. et typ. cons.
Cymbella sp. C. Agardh, 1830, nom. et typ. cons.
Fragilaria spp. Lyngbye, 1819
Lyngbya sp. C. Agardh ex Gomont, 1892, nom. et typ. cons.
Meridion circulare (Greville) C. Agardh, 1831
Navicula sp. Bory, 1822
Nitzschia acicularis (Kützing) W. Smith, 1853
Nitzschia sp. Hassall, 1845, nom. cons.
Ulnaria acus (Kützing) Aboal, 2003
Ulnaria delicatissima var. *angustissima* (Grunow) Aboal & P.C. Silva, 2004
Chlorophyceae

Table A2. *Cont.*

Ankistrodesmus fusiformis Corda, 1838
Ankistrodesmus spiralis (W.B. Turner) Lemmermann, 1908
Botryococcus braunii Kützing, 1849
Chlamydomonas spp. Ehrenberg, 1833, nom. cons.
Chlorococcales
Chlorococcales indet.
Coenochloris fottii (Hindák) Tsarenko, 1990
Coenococcus planktonicus Korshikov, 1953
Desmodesmus brasiliensis (Bohlin) E. Hegewald, 2000
Dictyosphaerium subsolitarium Van Goor, 1924
Elakatothrix cf. *genevensis* (Reverdin) Hindák, 1962
Elakatothrix gelatinosa Wille, 1898
Eutetramorus globosus Walton, 1918
Koliella cf. *longiseta* (Vischer) Hindák, 1963
Lagerheimia ciliata (Lagerheim) Chodat, 1895
Monoraphidium griffithii (Berkeley) Komárková-Legnerová, 1969
Monoraphidium tortile (West & G.S. West) Komárková-Legnerová, 1969
Nephrocytium agardhianum Nägeli, 1849
Oedogonium sp. Link ex Hirn, 1900
Oocystis spp. Nägeli ex A. Braun, 1855
Pandorina morum (O.F. Müller) Bory, 1826
Pediastrum duplex Meyen, 1829
Planktosphaeria gelatinosa G.M. Smith, 1918
Pseudopediastrum boryanum (Turpin) E. Hegewald, 2005
Pseudopediastrum integrum (Nägeli) M. Jena & C. Bock, 2014
Pseudosphaerocystis lacustris (Lemmermann) Nováková, 1965
Pteromonas sp. Seligo, 1887
Raphidocelis danubiana (Hindák) Marvan, Komárek & Comas, 1984
Scenedesmus ecornis (Ehrenberg) Chodat, 1926
Scenedesmus obtusus Meyen, 1829
Scenedesmus spp. Meyen, 1829
Scenedesmus subspicatus Chodat, 1926
Scourfieldia sp. G.S. West, 1912
Sphaerocystis schroeteri Chodat, 1897
Stauridium tetras (Ehrenberg) E. Hegewald, 2005
Tetrabaena socialis (Dujardin) H. Nozaki & M. Itoh, 1994
Tetrachlorella alternans (G.M. Smith) Korshikov, 1939
Tetradesmus obliquus (Turpin) M.J. Wynne, 2016
Tetraedron sp. Kützing, 1845
Vitreochlamys fluviatilis (F. Stein) Batko, 1970
Chrysophyceae
Bitrichia chodatii (Reverdin) Chodat, 1926
Chromulina sp. Cienkowsky, 1870
Chrysochromulina parva Lackey, 1939
Chrysococcus sp. Klebs, 1892
Chrysolykos planctonicus B. Mack, 1951
Chrysophyceae spp. Pascher, 1914
Dinobryon cylindricum O.E. Imhof, 1887
Dinobryon cylindricum var. *alpinum* (O.E. Imhof) H. Bachmann, 1911
Dinobryon divergens O.E. Imhof, 1887
Dinobryon sociale (Ehrenberg) Ehrenberg, 1834
Mallomonas spp. Perty, 1852
Ochromonas sp. Vysotskii, 1887
Pseudokephyrion sp. Pascher, 1913
Pseudopedinella erkensis Skuja, 1948
Uroglena sp. Ehrenberg, 1834
Coccales

Table A2. *Cont.*

Coccales indetermined
Conjugatophyceae
Cosmarium bioculatum Brébisson ex Ralfs, 1848
Cosmarium neodepressum G.J.P. Ramos & C.W.N. Moura, 2020
Cosmarium pseudopyramidatum P. Lundell 1871
Cosmarium reniforme (Ralfs) W. Archer, 1874
Cosmarium spp. Corda ex Ralfs, 1848
Cosmarium tenue W. Archer, 1868
Gonatozygon brebissonii De Bary, 1858
Gonatozygon monotaenium De Bary, 1856
Hyalotheca dissiliens Brébisson ex Ralfs, 1848
Mougeotia sp. C. Agardh, 1824
Pleurotaenium sp. Nägeli, 1849
Spirogyra sp. Link, 1820
Spondylosium pygmaeum Cooke, 1880
Staurastrum acutum var. *varians* (Raciborski) Coesel & Meesters, 2013
Staurastrum cf. *paradoxum* Meyen ex Ralfs, 1848
Staurastrum cf. *polymorphum* Brébisson, 1848
Staurastrum muticum Brébisson ex Ralfs, 1848
Staurastrum sp. Meyen ex Ralfs, 1848
Staurodesmus cuspidatus (Brébisson) Teiling, 1967
Staurodesmus patens (Nordstedt) Croasdale, 1957
Staurodesmus sp. Teiling, 1948
Cryptophyceae
Cryptomonas curvata Ehrenberg, 1832
Cryptomonas erosa Ehrenberg, 1832
Cryptomonas marssonii Skuja, 1948
Cryptomonas ovata Ehrenberg, 1832
Cryptomonas pyrenoidifera Geitler, 1922
Cryptomonas spp. Ehrenberg, 1831
Plagioselmis nannoplanctica (Skuja) G. Novarino, I.A.N. Lucas & Morrall, 1994
Rhodomonas pusilla (Bachmann) Javornický, 1967
Cyanobacteria
Anabaena sp. Bory ex Bornet & Flahault, 1886
Anathece minutissima (West) Komárek, Kastovsky & Jezberová, 2011
Aphanocapsa delicatissima West & G.S. West, 1912
Aphanocapsa elachista West & G.S. West, 1894
Aphanothece sp. Nägeli, 1849
Chroococcus minutus (Kützing) Nägeli, 1849
Coelosphaerium kuetzingianum Nägeli, 1849
Dactylococcopsis fascicularis Lemmermann, 1898
Eucapsis aphanocapsoides (Skuja) Komárek & Hindák, 2016
Limnococcus limneticus (Lemmermann) Komárková, Jezberová, O. Komárek & Zapomelová, 2010
Merismopedia glauca (Ehrenberg) Kützing, 1845
Merismopedia sp. Meyen, 1839
Nostoc sp. Vaucher ex Bornet & Flahault, 1886
Oscillatoria limosa C. Agardh ex Gomont, 1892
Oscillatoria sp. Vaucher ex Gomont, 1892
Oscillatoriaceae Gen. sp.
Planktolyngbya limnetica (Lemmermann) Komárková-Legnerová & Cronberg, 1992
Pseudanabaena catenata Lauterborn, 1915
Pseudanabaena limnetica (Lemmermann) Komárek, 1974
Pseudanabaena sp. Lauterborn, 1915
Snowella lacustris (Chodat) Komárek & Hindák, 1988
Dinophyceae

Table A2. *Cont.*

Ceratium hirundinella (O.F. Müller) Dujardin, 1841 *Glenodinium* sp. Ehrenberg, 1836 *Gymnodinium lantzschii* Utermöhl, 1925 *Gymnodinium* spp. F. Stein, 1878 *Gymnodinium uberrimum* (G.J. Allman) Kofoid & Swezy, 1921 *Parvodinium* cf. *umbonatum* (F. Stein) Carty, 2008 *Peridinium cinctum* (O.F. Müller) Ehrenberg, 1832 *Peridinium* sp. Ehrenberg, 1830 *Peridinium volzii* Lemmermann, 1905 *Peridinium willei* Huitfeldt-Kaas, 1900 Euglenophyceae
Euglena spp. Ehrenberg, 1830 *Lepocinclis spirogyroides* B. Marin & Melkonian, 2003 *Menoidium* sp. Perty, 1852 *Trachelomonas* cf. *hispida* (Perty) F. Stein, 1878 *Trachelomonas* sp. Ehrenberg, 1834 *Trachelomonas volvocina* (Ehrenberg) Ehrenberg, 1834 Picoplankton
μ-Algen (Picoplankton excl. Bacteria) Flagellata indet. Xanthophyceae
Tetraëdriella jovetii (Bourrelly) Bourrelly, 1968 *Tribonema* sp. Derbès & Solier, 1851

Table A3. Zooplankton species in Lake Sulzkarsee (2003–2022).

Zooplankton
Rotifera
Anuraeopsis fissa (Gosse, 1851) *Ascomorpha ecaudis* Perty, 1850 *Asplanchna priodonta* Gosse, 1850 Bdelloidea Gen. sp. *Cephalodella* cf. *ventripes* (Dixon-Nuttall, 1901) *Cephalodella gibba* (Ehrenberg, 1830) *Cephalodella* sp. *Cephalodella sterea* (Gosse, 1887) *Collotheca* sp. *Colurella obtusa* (Gosse, 1886) *Colurella* sp. *Encentrum lutra* Wulfert, 1936 *Epiphanes brachionus* (Ehrenberg, 1837) *Filinia passa* (Müller, 1786) *Filinia terminalis* (Plate, 1886) *Keratella cochlearis* (Gosse, 1851) *Keratella cochlearis f. micracantha* (Lauterborn, 1900) *Keratella cochlearis* var. *hispida* (Lauterborn, 1898) *Keratella tecta* (Gosse, 1851) *Keratella testudo* (Ehrenberg, 1832) *Lecane closterocerca* (Schmarda, 1859) *Lecane luna* (Müller, 1776) *Lecane lunaris* (Ehrenberg, 1832) *Lecane* sp.

Table A3. *Cont.*

Lepadella patella (Müller, 1773)
Lepadella patella persimilis De Ridder, 1961
Lepadella quadricarinata (Stenroos, 1898)
Lepadella sp.
Lophocharis cf. *gracilis* Dvořáková, 1960
Monommata sp.
Mytilina mucronata (Müller, 1773)
Pleurotrocha petromyzon Ehrenberg, 1830
Polyarthra dolichoptera Idelson, 1925
Polyarthra sp.
Proales fallaciosa Wulfert, 1937
Synchaeta cf. *kitina* Rousselet, 1902
Synchaeta cf. *pectinata* Ehrenberg, 1832
Synchaeta cf. *tremula/kitina*
Synchaeta lakowitziana Lucks, 1930
Synchaeta pectinata Ehrenberg, 1832
Synchaeta spp.
Synchaeta tremula (Müller, 1786)
Trichocerca iernis (Gosse, 1887)
Trichocerca longiseta (Schrank, 1802)
Trichocerca porcellus (Gosse, 1851)
Trichotria pocillum (Müller, 1776)
Cladocera
Acroperus harpae (Baird, 1834)
Alona rectangula G.O. Sars, 1862
Alona sp.
Alona quadrangularis (O.F. Müller, 1776)
Ceriodaphnia pulchella G.O. Sars, 1862
Daphnia longispina (O.F. Müller, 1776)
Copepoda
Eucyclops serrulatus (Fischer, 1851)

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