Original Articles

Long-term response of diatoms in high-elevation streams influenced by rock glaciers

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A B S T R A C T

In this study, we monitored diatom assemblages at various sites along a stream-lake network draining a glaciated alpine cirque landscape (2600 m asl) in the Swiss National Park over 19 years (2001–2020). The primary goal of this study was to examine the long-term changes in diatom assemblages in the running waters at high-elevation influenced by rock glaciers, and particularly the use of diatoms as indicators of environmental change. Because streams in the catchment are interconnected with lakes, another objective was to compare diatom assemblages between lake inlets and lake outlets as well as along the chain of lakes. The Macun cirque comprises two main drainage basins with one influenced by waters from rock glaciers. Lakes are interconnected by stream segments in both basins before merging at an outflow lake. We expected changes in diatom assemblages would reflect changes in long-term physico-chemistry of surface waters between basins, between lake inlets and outlets, and along lake chains. The novelty of this work is that covers a unique heterogeneous aquatic environment in the Alps affected by climate change, an area where the temperature has increased over twofold more than other regions in the northern hemisphere. This long-term study provides the opportunity of forecasting how other alpine freshwater ecosystems globally may change in the future. We combined a classical taxonomic approach and scanning electron microscopy (SEM) along with physico-chemical data across a broad spatio-temporal scale. Diatom assemblages showed distinct spatial differences between basins, reflecting basin-wide differences in water physico-chemistry. Diatoms in both basins displayed a major temporal shift in composition between samples collected pre-2010 with those collected post-2010 that also followed temporal changes in physico-chemistry, suggesting a tipping point occurred in the system. There were subtle differences in diatom assemblages between lake inlets and outlets, most evident in the precipitation/groundwater fed north basin. Lastly, a clear lake order effect was detected in both basins with upper basin sites differing from lower basin sites at similar altitude. We conclude that diatoms were effective in documenting the environmental changes that occurred in these alpine waters, specifically reflecting the abrupt change in physico-chemistry (concurrent tipping point in diatom assemblages) and the concomitant increase in surface water homogeneity and similarity of diatom assemblages over the study period.

1. Introduction

Freshwaters are sentinels of climate-related changes to landscapes, especially in glaciated alpine environments (The Intergovernmental Panel on Climate Change – IPCC, 2021). Glaciers are retreating at an accelerated rate worldwide, resulting in a reduced contribution of ice melt and increasing contributions of snow melt, groundwater and precipitation to running waters. In Switzerland, recent studies document an absence of snow accumulation over glaciers, while melt rates have substantially increased over the last 30 years (Geibel et al., 2022). In the Swiss Alps, the temperature increase trend is ca 5.7 °C per 100 years, which is more than twofold higher than the northern hemisphere in general (Rebetez and Reinhard, 2007; Schädler and Weingartner, 2010). This landscape transformation has consequently lead to quantitative and qualitative changes of alpine flowing waters with ramifications for flora and fauna (Milner et al., 2017; Huss and Hock, 2018). For example,

recent research suggests an increase in autotrophy of streams fed by glacial meltwaters over the next decades (Canadell et al., 2021). This greater instream production could lead to major changes in ecosystem functioning and metabolism of alpine waters and alterations in the composition of primary producers as well as microbial assemblages associated with biofilms.

Alpine waters are high elevation environments that host a diversity of organisms with many being endemic due to the relatively harsh conditions (short growth periods, low temperature, nutrient limitation) compared to lower elevation waters (Bundi, 2010; Milner et al., 2017). Earlier research described the kinds of running waters found in alpine environments in relation to water source; e.g., glacier-melt, snowmelt, groundwater-fed waters (Milner and Petts, 1994; Ward, 1994). Paillex et al. (2020) determined different types of intermittent alpine waters depending on the degree (timing, frequency, duration) of surface flow and the role of different water sources of streams. Another important feature of alpine landscapes is the presence of standing waters, ranging from small temporary ponds to permanent lakes (Oertli et al., 2008). Often these alpine lakes are connected by running waters, comprising both inlet and outlet biotypes. Lake outlets, in particular, are rather special aquatic habitats due to the influence of upstream lakes on physical–chemical properties of outlet streams (Soranno et al., 1999; Hieber et al., 2001). The interconnection of lakes and streams provide a diversity of habitats that contribute to the overall biodiversity of alpine waters (Bundi, 2010).

Most alpine waters are above tree line and autochthonous in nature (Füreder et al., 2003), thus primary producers dominate basal resources in energy flows through food webs (Zah et al., 2001; Sertic Peric et al., 2015). Diatoms are the main primary producer in alpine running waters (e.g., Rott et al., 2006; Kireta et al., 2012), although some filamentous algae, such as the gold alga *Hydrurus foetidus* (Villars) Trevisan or red alga *Lemanea* spp. Bory can be abundant. Further, oxygenic cyanobacteria and the chrysophyte *Phaeodermatium rivulare* Hansgirg often are present (Uehlinger, 1991; Rott et al., 2006). Diatoms can survive under extreme and harsh conditions; for instance, research of cryoconite holes revealed that 27 diatom genera could be cultured from samples frozen at −20 °C for over one year (Yallop and Anesio 2010). Diatoms respond directly to major physical, chemical, and biological properties in fluvial ecosystems, and their environmental preferences are well documented (Kelly et al., 1998; Stevenson, 2014). The wide variety of diatoms makes them excellent organisms for understanding environmental change in freshwaters, and therefore they are often used in the bioassessment of streams and lakes (Besse-Lototskaya et al., 2011; Charles et al., 2020; Falasco et al., 2021). Further, many diatoms are habitat specific, and thus can be used to examine spatial-scale patterns within and along streams or the role of lakes embedded in stream networks. Consequently, diatom assessments can provide mechanistic understanding of changes over time as well as spatial relations across environmental scales.

Monitoring is essential for effective long-term management of our natural resources. The understanding and forecasting of ecosystem dynamics over time is limited without environmental monitoring. For instance, monitoring has been the corner stone of understanding environmental change under today's rapid and ongoing climate scenarios. Monitoring also provides mechanistic information regarding ecological surprises that appear in datasets when summarizing temporal patterns (Dodds et al., 2012). For aquatic resources such as lakes and running waters, effective monitoring includes measures of water quality and quantity, as well as biotic resources such as primary producers, macroinvertebrates, and fish. Historical landscapes also have been elucidated through analysis of, e.g., ice cores and biotic remnants (diatoms, ephippia, chironomid mouthparts) from core samples of lake sediments. Studies analyzing diatom assemblages in the Alps cover mainly Italian waters, springs, and waters with high nutrient content (e.g., Cantonati, 1998; Cantonati et al., 2001, 2012; Falasco and Bona, 2011; Mogna et al., 2015). Long-term monitoring data are extremely sparse, and

mostly cover just a few years (Cantonati and Ortler, 1998; Gerecke et al., 2011; Cantonati et al., 2022). Previous studies of the Macun surface waters covered a shorter timeframe and were focused on spatial patterns in diatom diversity or strictly water chemistry (Robinson and Kawecka 2005; Kawecka and Robinson, 2008; Robinson et al., 2010, 2022). In this study, we focused on the diminishing influence of rock glaciers over time and the concomitant changes in water physico-chemistry on diatom assemblages as important bioindicators. For this paper, measures of water quality and diatoms have been recorded annually since 2001, encompassing a 19-year period from a high elevation landscape. The primary goal of this study was to examine the long-term changes in diatom assemblages in the running waters of the high-elevation Macun cirque, and particularly the use of diatoms as indicators of environmental change. Specifically, long-term changes in diatoms were compared between the two drainage basins in the cirque in relation to documented differences in physico-chemistry of the surface waters. Because streams in the catchment are interconnected with lakes, another objective was to compare diatom assemblages between lake inlets and lake outlets as well as along the chain of lakes. Lake chains can influence the physico-chemistry of waters flowing between lakes as well as waters along the lake chain continuum, a so-called lake order relationship (Soranno et al., 1999) as similarly described for running waters along the river continuum (Vannote et al., 1980). We expected changes in diatom assemblages would reflect changes in long-term physico-chemistry of surface waters between basins, between lake inlets and outlets, and along lake chains. The novelty of this work is that covers a unique heterogeneous freshwater environment in the Alps, an area where temperatures have increased over twofold more than other regions of northern hemisphere. This long-term study provides the opportunity of forecasting how other alpine freshwater ecosystems globally may change in the future. We combined a classical taxonomic approach along with physico-chemical data across a broad spatio-temporal scale in the evaluation, demonstrating that diatoms are sensitive and useful in assessing environmental changes in alpine waters. One major difficulty was to combine all the taxonomic data collected during the 19 year study period for nomenclature changes. Here, the authors re-examined all diatom samples, staring from 2001, using modern taxonomical concept literature to obtain reliable and precise results, including the use of scanning electron microscopy (SEM) for cell verification. In this paper, we used complete chemical data from whole study period (2001–2020) to determine the main factors shaping diatom assemblages, allowing the prediction of changes in alpine ecosystems globally in the future.

2. Materials and methods

2.1. Site description

The Macun Lakes (46°44′ N, 10°08′ E) is an alpine cirque (>2600 m asl) in Canton Graubunden, Switzerland (Fig. 1). The 3.6 km² region, annexed to the Swiss National Park in 2000, is an area designated for long-term monitoring of Alpine surface waters. The surrounding peaks have elevations between 2800 and 3000 m asl. The drainage network of Macun consists of a north and south basin (Fig. 1), including 26 small lakes and 10 temporary ponds. The four largest lakes, excluding lake Dragun, are interconnected by streams, each <500 m in length. These large lakes are ca 0.12 km² each and <10 m deep. The outlet stream (Zeznina) drains north to the Inn River near the town of Lavin, Switzerland, in the lower Engadine. Elevations of study sites were between 2610 and 2650 m asl. Water sources in the catchment originate from precipitation (mostly as snow in winter) and seven rock glaciers (Barsch, 1969) associated with the south basin. For instance, inputs from a large rock glacier (Macun1 in Barsch 1969; Fehr and Reich, 2015; Derungs and Tischhauser, 2017) influenced surface waters at Zeznina (site 10), although six other small rock glaciers add meltwaters to south basin streams.
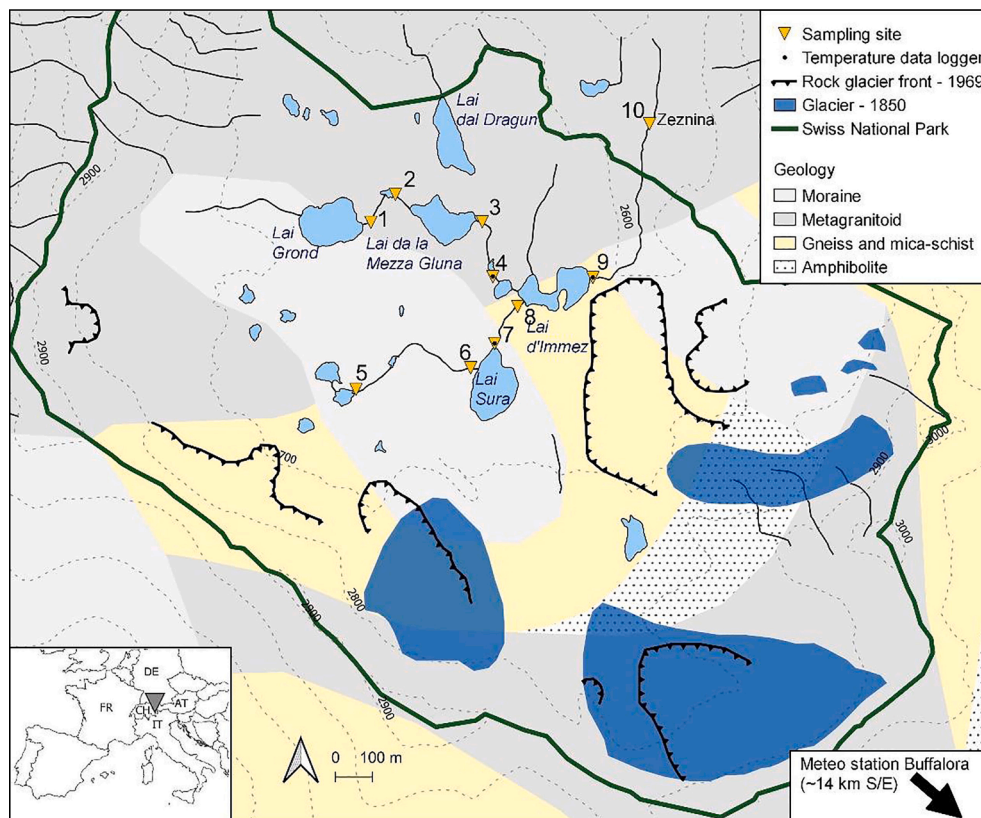
Fig. 1. Map of the Macun cirque in the Swiss National Park with locations of the 10 study sites shown as triangles: 1–Grond (G), 2–Mezza Gluna inlet (MIL), 3–Mezza Gluna outlet (MOL), 4–Immez north inlet (ILN), 5–Sura OB (SOB), 6–Sura inlet (SIL), 7–Sura outlet (SOL), 8–Immez south inlet (ILS), 9–Immez outlet (IOL), 10–Zeznina (Z). Note the rock glaciers influencing waters of the south basin as well as the large rock glacier that flows into site Zeznina. Map modified from Robinson et al. (2022).

Briefly, four sites are located in north basin: Grond (G), Mezza Gluna inlet (MIL), Mezza Gluna outlet (MOL), and Immez north inlet (ILN). In the south basin, another four sites include Sura OB (SOB), Sura inlet (SIL), Sura outlet (SOL), and Immez south inlet (ILS). The mainstem stream in the north basin originates from lake Grond outlet (site 1), followed by Mezza Gluna inlet (site 2) and then Mezza Gluna outlet (site 3) (Fig. 1). Site 4 in this chain is located at Immez lake inlet north. In the south basin, the mainstem stream originates upstream of two small nearby lakes and site 5 is located at the outlet of the lower lake. Site 6 is then located downstream at the inlet of Lai Sura lake, site 7 at the outlet of Lai Sura, and site 8 at the south inlet of lake Immez. Site 9 is located at the outlet of lake Immez where waters of both basins converge. The last site (10) is located ca 500 m downstream on this outlet stream (Zeznina) and is the lowest site monitored in the network (see Fig. 1).

Precipitation is low, around 850 mm y^{-1}, and air temperature ranges from >20 °C in summer to <–25 °C in winter (Buffalora climate station ~ 14 km southeast of Macun). A newly installed meteorological station at Macun (site 9 in Fig. 1) recorded a temperature maximum of 18.7 °C in July 2019 and a minimum of –23.2 °C in January 2019. The annual growth period ranges from 4 to 6 months (late spring to early autumn) depending on annual weather conditions with no long-term trends evident in mean water temperature (Robinson et al. 2022). Bedrock geology is slow-weathering crystalline (ortho-gneiss, meta-granitoid) rock. The area is above treeline, and terrestrial vegetation is typical alpine grasses and low-lying herbs with areas of bare rock. The area is remote and, being in the national park, is accessible only by foot. Aquatic vegetation is present in some lakes, predominantly Bryophyta (7 taxa) (Oertli et al., 2008). Helophytes also were noted, comprising *Eleocharis* sp., *Eriophorum scheuchzeri* Hoppe, *Glyceria* sp., and *Saxifraga stellaris* L. No other assessment of aquatic vegetation was made to date. The large lakes have fish (*Salmo trutta fario* L., *Salvelinus namaycush* Walbaum, *Phoxinus phoxinus* L.), and were last stocked in 1993 (P. Rey, personal communication).

2.2. Data collection

Field monitoring was conducted once each year in mid-summer between 27 July and 1 August since 2001. Various types of samples were collected from the 10 long-term monitoring sites used for the overall study (Fig. 1). As part of the present study, water samples were collected in 0.5 L pre-rinsed plastic bottles and returned to the Aua laboratory at Eawag for analysis of nitrogen and phosphorus constituents, dissolved organic carbon (DOC), particulate organic carbon (POC), total inorganic carbon (TIC), pH, and silicate following methods in Tockner et al. (1997). Further, spot measures of electrical conductivity and temperature (WTW LF 323), and turbidity (Cosmos, Züllig AG, Switzerland) were recorded directly in the field using portable meters. Robinson et al. (2022) document the long-term changes in physico-chemistry of flowing waters of the Macun Lakes region.

Periphyton was collected at each site each year (except 2006, 2014) by scraping the surface area from 5 haphazardly selected stones (n = 5 per year and site). Stones were scraped with a metal brush and sub-samples (10–15 ml) of the slurry filtered through Whatman GFF glass fiber filters. Scraped areas were ca 30 cm^2 per stone and a total of 180 samples were collected during the study. Filters were returned to laboratory and frozen (–25 °C) until analysis. For analysis, each filter was dried at 60 °C, weighed, combusted at 550 °C for 4 h, and then reweighed for estimates of ash-free dry mass (AFDM).

Diatoms were collected in 2001, 2002, 2004–2010, and then again in 2015, 2016, 2018–2020. Diatoms were sampled from the surface of submerged stones at each site (n = 5), ranging in size between 5 and 15 cm (b-axis). A total of 120 diatom samples were collected during the study. Sampling was conducted according to standard methods used in diatom monitoring studies and meets the requirements of the European Framework Directive (Directive 2000/60/EC). Specifically, diatoms were collected by brushing stones with a metal brush and storing the slurry in a 50-ml Eppendorf tube, preserved with 2 % formalin, and returned to the laboratory for analysis.

In laboratory, diatoms were cleaned by boiling with 30 % hydrogen peroxide (H_2O_2) for a few hours. Cleaned diatom material was pipetted on to coverslips and dried, then mounted on glass slides using Naphrax mounting medium (Brunel Microscopes ltd, Wiltshire, UK). Light microscopy (LM) observations were made with a Zeiss Axio Imager A2 (Carl Zeiss, Jena, Germany) using a ×100 Plan Apochromatic oil immersion objective (NA 1.46) equipped with Differential Interference Contrast (DIC). For proper identification of small-celled species, a scanning electron microscope (SEM) examination was performed. A few drops of cleaned material were put onto Whatman Nuclepore polycarbonate membrane filters (Fisher Scientific, Schwerte, Germany). Once dried, the membranes were mounted onto aluminum stubs and coated with 20 nm of gold using a turbo-pumped Quorum Q 150 T ES coater. SEM observations were performed using a Hitachi SU8010 microscope. A total of 300 to 400 valves were counted on each slide under LM and identified to species. The main identification literature included Krammer and Lange-Bertalot (1986), Krammer and Lange-Bertalot (1988), Krammer and Lange-Bertalot (1991a), Krammer and Lange-Bertalot (1991b), Lange-Bertalot (1993), Lange-Bertalot (2001), Lange-Bertalot and Metzeltin (1996), Reichardt (1999), Krammer (2002), Krammer (2003), Werum and Lange-Bertalot (2004), Hofmann et al. 2011, Levkov et al. (2016), Lange-Bertalot et al. (2011), and Lange-Bertalot et al. (2017).

2.3. Data analysis

Surface water physico-chemistry was compared among basins and over time, and summarized in tabular form in this paper. Further, a Principal Components Analysis (PCA) was completed to examine for water quality differences between basins over time using measures of temperature, turbidity, electrical conductivity (EC), dissolved nitrogen (DN), total phosphorous (TP), particulate phosphorous (PP), dissolved organic carbon (DOC), total inorganic carbon (TIC), and particulate organic carbon (POC). Differences in periphyton biomass (as AFDM) among basins and time were tested using two-way Analysis of Variance (ANOVA) on $\log(x + 1)$ transformed data, followed by Tukey's posthoc test when significant differences were found (Zar, 1984).

The complete diatom species list (370 species identified) was used to calculate taxonomic richness (number of species), Shannon's diversity (H') and Pielou's evenness (J') for each site and date in PRIMER v.7 software. Differences in each index among basins and time were tested using two-way ANOVA on $\log(x + 1)$ transformed data, followed by Tukey's posthoc test when significant differences were found (Zar, 1984).

Spatio-temporal patterns in diatom assemblages over time, among basins, and inlet and outlets was analyzed using relative abundance data with non-metric dimensional scaling analysis (nMDS) in PRIMER software. Species with at least 2 % relative abundance in a sample were used in the analysis, resulting in 78 different diatoms in the dataset. Diatom data were square-root transformed for the nMDS. Permutation analysis of variance (PERMANOVA) was used on the Bray-Curtis similarity matrix with 999 permutations to test whether diatom assemblages differed over time, between basins, and between lake inlets and outlets. Lastly, a distance-based redundancy analysis (dbRDA) was used to analyze the influence of environmental factors on diatom assemblages in PRIMER v.7 software (Anderson et al., 2008). To select which of the studied water parameters had an important influence on diatoms, a sequential test as a part of the dbRDA analysis was performed. Diatoms with at least a 5 % relative abundance in a sample were included in the analysis.

3. Results

3.1. Spatio-temporal patterns in physico-chemistry

The two basins showed different physico-chemical properties, mostly related to the influence of rock glaciers on surface waters in the south basin. In general, nitrogen levels were twice as high (on average ca 190 μg/L versus 80 μg/L, respectively) and particulate phosphorus levels twice as low (on average 5.0 versus 9.5 μg/L, respectively) in the south basin relative to the north basin (Table 1). Further, north basin streams were 3 °C warmer than south basin streams with annual fluctuations in temperature strongly reflecting local weather conditions of a particular year. Lying mostly on gneiss and granite geology, conductivities of surface waters were low (typically less than 10 μS/cm), although a large rock glacier resulted in higher values of ca. 19 μS/cm at Zeznina. The pH of waters was ca. 6.5–6.6 at all sites and water clarity was high (typically <2.5 NTUs). Silicate levels were suitable for algal growth and development, averaging 2.5 mg/L.

A principal components analysis (PCA) clearly separated the two main basins along PCA axis 2 with Immez OL and Zeznina placed intermediate to both basins (Fig. 2). Data were plotted to illustrate the temporal changes that occurred in Macun; here showing clear separation of years pre-2010 and years post-2010 along PCA axis 1. The most significant temporal change was a decrease in DN and DOC from pre-2010 with post-2010 data in the catchment. Further, levels of PP, TP and POC increased in south basin sites between the two periods to be more near north basin sites. Also notable was that both basins were still somewhat separated post-2010, although clearly becoming more similar in physico-chemistry. Robinson et al. (2022) provide a detailed assessment of the physico-chemistry of flowing waters in Macun during the 19-year study period, indicating that surface waters in both basin are becoming more similar due to a decrease in the influence of rock glaciers in the south basin, especially after 2009.

3.2. Spatio-temporal patterns in periphyton biomass

The biomass of periphyton fluctuated widely over the study period but showed a decrease in levels from 2010 onward at most sites (Fig. 3). Highest values before 2010 mostly were evident in the north and south basin (mean values 16.1 and 13.9 g/m^2 AFDM, respectively). Mean values at sites after 2010 (2010–2021) ranged from 5.1 to 7.5 g/m^2 AFDM and differed from pre-2010 values for all basins (p < 0.001 for all) except Zeznina (p = 0.249) (Fig. 3 insert). Immez outlet showed peaks in 2005–2007 (>20 g/m^2 AFDM), but with generally low values in other years (range in means 1.8–9.3 g/m^2 AFDM). In contrast, Zeznina had relatively low values each year (range in means 0.5–7.5 g/m^2) with higher values in 2005 (mean 12.8 g/m^2 AFDM) and 2019 (mean 14.0 g/m^2 AFDM)(Fig. 2).

3.3. Diatom assemblage structure

Of the 370 taxa identified, 34 taxa comprised at least 5 % of the relative abundance in diatom assemblages among sites (Fig. S1 in Supplementary Material). The most abundant diatoms with relative abundances reaching over 30 % included *Achnanthidium nanum* (F. Meister) Novais & Jüttner (maximum 89.4 %), *Achnanthidium minutissimum* (Kützing) Czarnecki (maximum 86.8 %), *Gomphonema exilissimum* (Grunow) Lange-Bertalot (maximum 68.1 %), *Odontidium mesodon* (Kützing) Kützing (maximum 68.8 %), *Psammothidium helveticum* (Hustedt) Bukhtiyarova & Round (maximum 68.0 %), *Psammothidium subatomoides* (Hustedt) Bukhtiyarova & Round (maximum 50.9 %), *Tabellaria flocculosa* (Roth) Kützing (maximum 48.8 %) and *Aulacoseira alpigena* (Grunow) Krammer (maximum 37.0 %). *A. nanum* was the most frequent species in all samples with an average abundance of 20.6 % over the study period. Both *Achnanthidium* species (*A. nanum* and *A. minutissimum*) had relatively high abundances each year of the study.

Other notable spatial patterns included *Odontidium mesodon* (Kützing) Kützing being the most frequent diatom at Zeznina and Sura inlet (SIL). *Gomphonema exilissimum* occurred at high abundances (mean 12.2 % per sample) at sites in the north basin (Grond, Mezza OL, Immez ILN) as well as Immez OL and Zeznina. It had lower abundances following 2010 at Immez OL and Zeznina. Species of *Psammothidium* usually

Table 1
Summary of water quality measures for sites from the north basin, south basin, Immez outlet and Zeznina over the 19-year period of study (see Map, Fig. 1). *median given for pH. Table modified from Robinson et al. (2022).

|		Conductivity μs/cm	Turbidity NTU	Temperature °C	pH*	NO₃-N μg/L	DN μg/L	PO₄-P μg/L	TP μg P/L	DOC mg/L	TIC mg/L	SiO₂ mg/L	Alkalinity mmol/L
North Basin	Mean	6.5	1.9	12.2	6.5	69.1	179.5	2.0	10.5	0.9	0.9	2.2	0.11
	SD	0.9	2.6	3.3	NA	20.3	91.6	1.3	6.5	0.5	0.4	0.6	0.03
	CV	13	134	27	NA	29	51	65	61	53	48	28	30
	Max	9.5	18.2	19.5	8.0	108.0	614.0	4.9	44.6	2.5	2.5	4.0	0.21
	Min	4.9	0.2	3.9	5.3	45.0	100.0	0.4	6.7	0.5	0.2	1.4	0.08
South Basin	Mean	10.3	2.0	9.3	6.4	177.6	260.3	2.3	7.0	0.7	0.8	2.4	0.09
	SD	3.1	2.2	3.2	NA	83.2	108.7	0.7	2.9	0.6	0.4	0.8	0.02
	CV	30	108	35	NA	47	42	32	42	88	47	33	21
	Max	24.0	10.7	14.6	7.7	470.0	520.0	3.6	17.2	3.6	1.6	4.1	0.1
	Min	5.3	0.1	2.1	5.2	53.4	101.0	1.0	3.8	0.2	0.2	1.3	0.1
Immez outlet	Mean	9.6	2.6	10.4	6.6	113.1	200.9	4.5	6.7	0.8	0.8	2.3	0.10
	SD	1.5	3.5	2.9	NA	38.2	89.6	5.8	1.5	0.4	0.5	0.7	0.02
	CV	15	132	28	NA	34	45	131	23	52	56	31	18
	Max	12.6	12.3	15.4	7.7	184.0	360.0	13.2	9.4	1.8	1.5	3.7	0.13
	Min	6.9	0.3	3.6	5.4	69.0	100.0	1.3	4.5	0.3	0.0	1.4	0.08
Zeznina	Mean	19.8	7.9	7.7	6.5	198.1	302.7	1.9	8.9	0.6	1.2	2.7	0.12
	SD	13.9	7.9	2.5	NA	68.0	100.8	0.7	5.3	0.3	0.4	0.8	0.01
	CV	71	99	32	NA	34	33	37	59	52	35	29	12
	Max	26.5	27.9	12.5	7.3	399.0	470.0	2.9	21.6	1.3	2.0	4.1	0.15
	Min	10.5	0.8	2.8	5.5	124.0	155.0	1.1	5.1	0.2	0.5	1.6	0.11
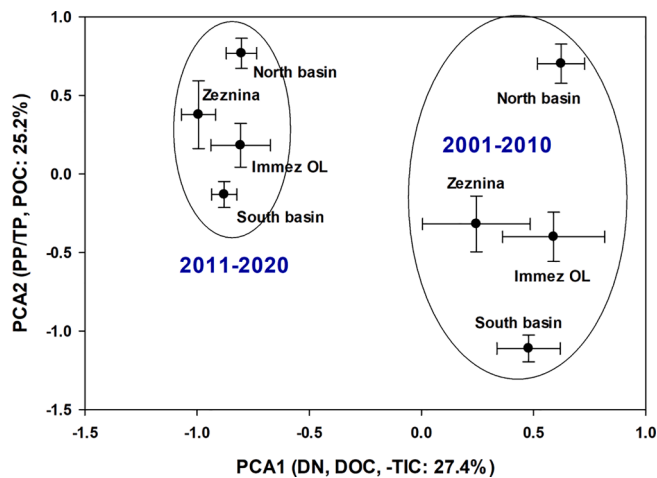
Fig. 2. Scatterplot of principal components analysis (PCA) of the measured physico-chemical parameters over the study period. Data are summarized by basin (north, south), Immez outlet, and Zeznina for year's pre-2010 (2001–2010) and year's post-2010 (2011–2020). Data presented as means and standard errors (SE) for the different groups.

occurred together with highest abundances at Immez ILN and Sura OL. *Tabellaria flocculosa* and *Aulacoseira alpigena* had highest abundances at Mezza OL and Immez ILN, as well as Grond in 2001 (*A. alpigena*) and 2002 (*T. flocculosa*: 45.8 %).

There appeared to be a clear temporal change in diatom assemblage structure before and after 2010. For instance, diatoms with high relative abundance pre-2010 decreased post-2010, whereas some diatoms with low relative abundances pre-2010 increased post-2010. Specifically, the proportion of *A. minutissimum* was low (0.8 % per sample) pre-2010 then increased to ca. 14.8 % post-2010. The highest share of *A. minutissimum* occurred at sites in the south basin and Immez OL, ranging from 18.0 % (ILS in 2020) to 86.8 % (IOL in 2018). The highest contribution of *A. minutissimum* pre-2010 was recorded at Mezza OL (2001), Sura OL (2002, 2005), and Sura OB (2004), but it was always<17.9 %. Further, *Psammothidium* spp. were generally lower in abundance before 2010 and gradually increased after 2010.

3.4. Spatio-temporal patterns in diatom diversity indices

The mean number of taxa ranged widely from a low of 12 taxa at Zeznina in 2001 to a high of 88 taxa at Immez OL in 2010 (Fig. 4). For individual basins, taxa number ranged from 22 (2020) to 61 (2010) in the north basin, from 29 to 62 taxa in the south basin, from 15 (2018) to 57 (2019) at Immez OL, and from 12 (2001) to 58 (2004) at Zeznina. In general, taxa numbers increased from 2001 to 2002–2004, and then decreased from 2005 to 2008, increasing again in 2010 followed by a decrease post-2010. Pre-2010 and post-2010 richness values differed for both basins (north basin, p = 0.027; south basin; p = 0.065) but not Immez OL or Zeznina (p > 0.05). The Shannon's diversity index increased from 2001 to 2002–2004, followed by a decrease in 2005–2008, a major increase in 2010, and then a decrease post-2010. A high value over 3.5 was observed in Immez OL in 2010 and the lowest value of 0.5 occurred at Immez OL in 2018. Temporal patterns in Shannon's index were similar across basins over the study period (range in p = 0.366 to 0.709). Pielou's index ranged from 0.5 to 0.8, demonstrating a relatively high degree of evenness in diatom assemblages at most sites and over time (range in p = 0.155 to 0.903). An exception was in 2018 where Pielou's index decreased to 0.2 at Immez OL, indicating the dominance by a few abundant taxa (Fig. 4).

3.5. Spatio-temporal patterns in diatom assemblages (basins, lake order, inlets/outlets)

Results of the non-metric multidimensional scaling analysis (nMDS) based on the top 78 diatoms clearly showed some distinctive spatio-temporal patterns among assemblages (Fig. 5). The stress value for the nMDS was 0.24. There were significant differences in diatom assemblages between the north and south basins (PERMANOVA, p = 0.001). Further, Immez OL samples were found intermediate of both basins, whereas Zeznina samples were mostly associated with samples from the south basin. Another important trend was the significant shift between pre-2010 samples and post-2010 observed at both basins, reflecting a major temporal change in diatom assemblages post-2010. These spatial–temporal patterns reflected those found in the PCA in physico-chemistry among sites (see Fig. 2).

There appeared to be subtle diatom assemblage differences between inlets and outlets grouped by basin and by study period (pre-2010, post-2010) in the catchment (PERMANOVA, p = 0.029; Fig. 6a). Inlet and outlet assemblages were mostly similar in the south basin (overlapping
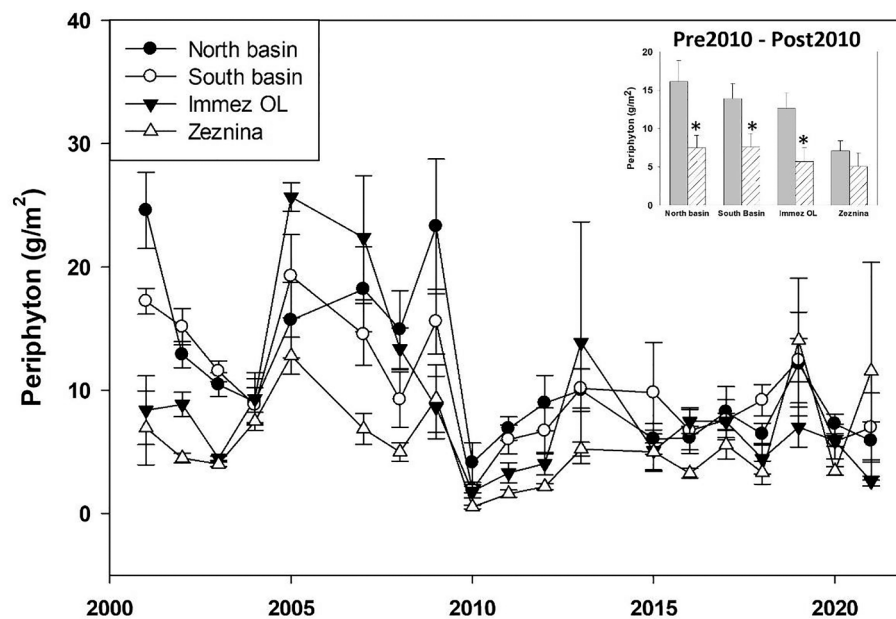
Fig. 3. Mean (±SE) periphyton biomass (g/m² as AFDM) of sites draining the north basin, south basin, Immez outlet (OL) and Zeznina over the 19-year study period. Insert shows data summarizing the different basins, Immez OL and Zeznina with pre-2010 (gray bars) with post-2010 (white, crosshatched bars) values (mean + SE). * = significantly different, p < 0.05.

ellipses of data), although differing between pre-2010 and post-2010 samples. Inlet assemblages clearly differed from outlet assemblages in the north basin, as well as between pre-2010 and post-2010 sample collections.

There was a clear lake order effect among sites grouped by basin and pre-2010 and post-2010 sample collections (Fig. 6b). Time periods of collections mostly differed along axis-1 with south basin sites situated on the right side of the plot and north basin sites on the left side. South basin lake order differences mostly followed along axis-2 in a negative relationship (increase in lake order with decrease axis-2 values, whereas the north basin lake sequence was more positive along axis-2 (increase in lake order with an increase in axis-2 values). Within a sample collection period (pre-2010, post-2010), south basin sites also shifted to the left side along axis-1 with the increase in lake order.

3.6. Influence of environmental variables on diatoms

The dbRDA results showed that diatom assemblages were associated with all measured environmental variables, except pH (Fig. 7). The first two axes of the dbRDA explained 76.3 % of the fitted variation. A sequential test showed that electrical conductivity (EC: 10.4 %), particulate organic carbon (POC: 5.2 %), turbidity (3.0 %), dissolved nitrogen (DN: 2.9 %) and temperature (4.3 %) should be included to final analysis and explain 23.1 % of the total variation among assemblages. Axis-1 of dbRDA was best explained by EC (r = –0.94), temperature (r = 0.54), POC (r = 0.50) and dissolved organic matter (DOC: r = 0.50), whereas axis-2 was associated with DN (r = 0.82), POC (r = –0.74) and total inorganic carbon (TIC: r = –0.57).

The two most frequent species (*A. minutissimum* and *A. nanum*) were not strongly associated with any environmental parameter, although *A. nanum* was positively correlated with axis-1 (r = 0.20) and negatively correlated with axis-2 (r = –0.08) (Table S2). In contrast, *A. minutissimum* was negatively correlated with axis-1 (r = –0.26) and axis-2 (r = –0.29) as well as *Adlafia minuscula* (Grunow) Lange-Bertalot (r = –0.37, –0.26, respectively).

For other common diatoms, *Aulacoseira* spp., especially *Aulacosira alpigena*, were positively correlated with axis-1 (r = 0.38–0.48) as well as *Gomphoenam exilissimum* (r = 0.24) and *Tabellaria flocculosa* (r = 0.48)(Table S2). In contrast, *Encyonema silesiacum* (Bleisch) D.G. Mann

and *Odontidium mesodon* were negatively correlated with axis-1 (r = –0.51, –0.66, respectively) and *E. silesiacum* also with axis-2 (r = –0.27). Along axis-2, positive associations were found for *Pinnularia subcapitata* W. Gregory (r = 0.42), *Pinnularia microstauron* (r = 0.37), *Eunotia praerupta* (r = 0.44), *Encyonema minutum* (Hilse) D.G. Mann (r = 0.43) and *Fragilaria capucina* Desmazières (r = 0.41). The common *Psammothidium helveticum* and *Psammothidium subatomoides* were positively correlated with axis-2 (r = 0.26, 0.26, respectively), whereas *Psammothidium scoticum* (R.J. Flower & V.J.Jones) Bukhtiyarova & Round was negatively associated with axis-2 (r = –0.33) as well as *Aulacoseira nivalis* (W. Smith) J. English & Potapova (r = –0.31). Lastly, *Fragilaria vaucheriae* (Kützing) J.B. Petersen (r = 0.026), *Staurosirella pinnata* (Ehrenberg) D.M. Williams & Round (r = 0.26) and *Surirella roba* (r = 0.24) were positively correlated with axis-2 (see Table S1 and S2 in Supplementary material).

4. Discussion

The physico-chemistry of the Macun lakes network showed strong basin differences with the north basin being warmer (ca. 3 °C) than the south basin. Differences between basins were also evident in contrasting nutrient levels of nitrogen and phosphorus as well as organic carbon. Robinson et al. (2022) suggested the main factor causing the differences between basins was the presence of rock glacier inputs in the south basin that were lacking in the north basin.

Rock glaciers were situated near the local boundary of permafrost, and annual surface temperature is close to melting conditions (Haeberli et al., 2006), which underlines their sensitivity to climate warming. These geological differences are reflected in the physico-chemistry of surface waters, providing distinct habitat templates that likely influenced the distribution and abundance diatoms. Zeznina, the lowermost site in the network, comprised waters from both basins as well as meltwaters from a large rock glacier; it represented yet another physico-chemical template in the system. These habitat templates act as spatial filters dictating the presence and absence of diatoms at respective sites in the Macun fluvial network (Southwood, 1977, 1988). For instance, periphyton biomass was substantially lower at Zeznina than at sites in both basins, which had similar biomass levels. The low periphyton biomass at Zeznina was probably caused higher shear stress and channel
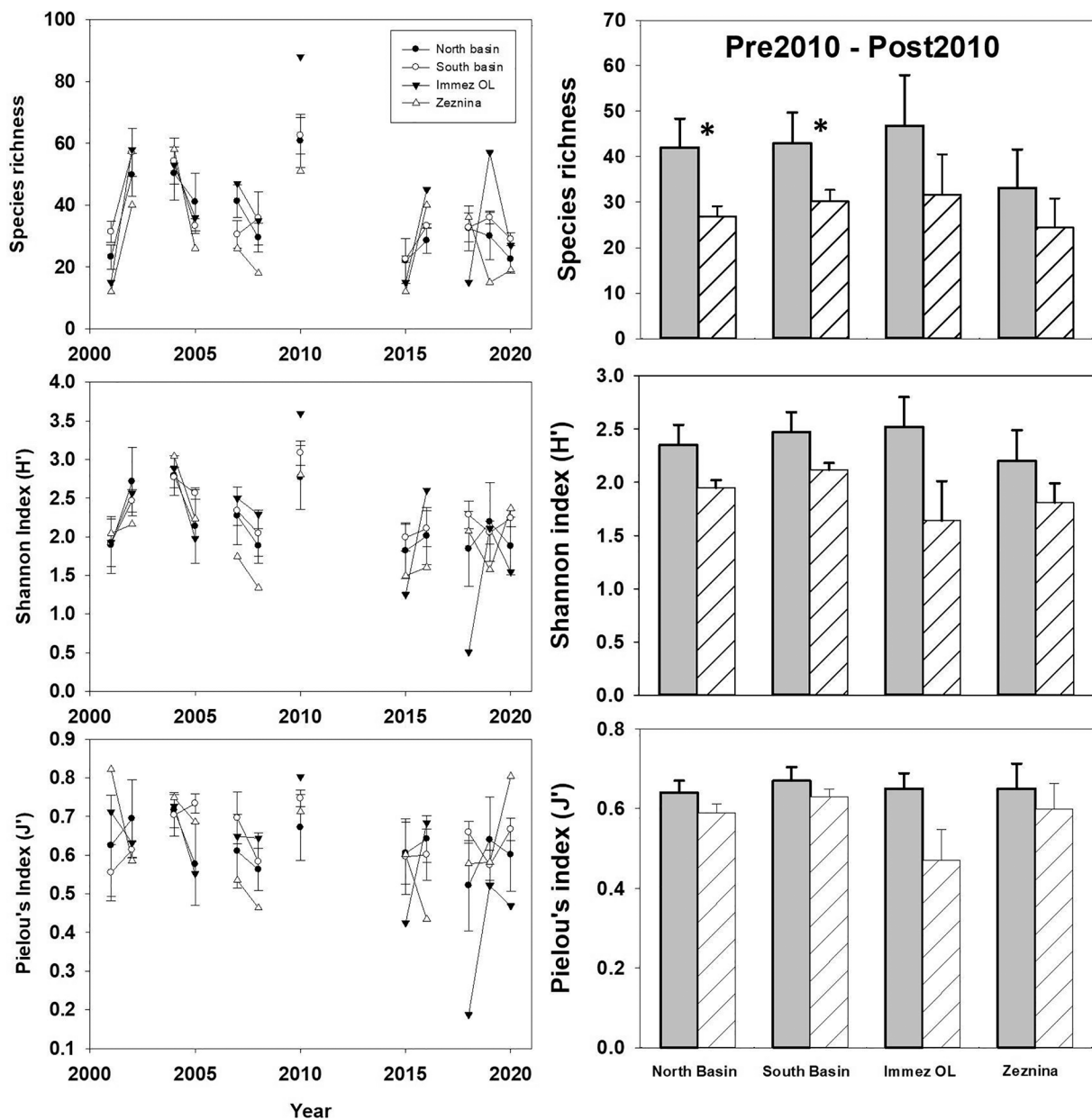
Fig. 4. Left side: Mean (±SE) number of taxa, Shannon Index, and Pielou's Index for sites in the north basin, south basin, Immez outlet and Zeznina. Right side: Graph summarizing the different metrics (mean + SE) for data collected pre-2010 (gray bars) and post-2010 (white, crosshatched bars) for north basin, south basin, Immez OL, and Zeznina.* = significantly different, p < 0.05.

destabilization than observed at the other sites (Bona et al., 2012; Wellnitz and Rader, 2003), as discussed further below.

The physico-chemistry of Macun has changed over time, becoming quite evident before and after 2010. Temporal changes were mostly related to decreases in nitrogen and dissolved organic carbon overall, and increases in phosphorus constituents and particulate organic matter in the south basin. The reduction in rock glacier inputs partially explains the large changes in south basin waters, also in terms of reduced nitrogen levels (see Fig. 2). Higher nitrate levels in glacial networks is an indicator of melting glacial ice, which flushes nitrogen from microbially active sediments (Baron et al., 2009). The reduction of rock glacier inputs in Macun, together with less atmospheric deposition, could explain the reduced nitrogen levels in south basin waters, (Rogora et al., 2006). One clear pattern developing was the homogenization of surface waters in the Macun catchment; this pattern likely will continue as meltwaters from the rock glaciers decrease over time in the south basin. Similarly,

diatom assemblages should reflect these temporal physico-chemical changes in the habitat template. For example, periphyton biomass decreased almost twofold in both basins post-2010 with a lesser decrease observed at Zeznina. In general, site Zeznina had relatively low AFDM values each year, but much higher values were noted in 2005 and 2019. These temporal phenomena are difficult to interpret, but at these dates a slightly higher nutrient concentration and temperature was noted. How this decrease in periphyton biomass post-2010 translates to diatom assemblages among sites is discussed below.

Diatom assemblages were dominated by small-celled taxa, primarily *Achnanthidium minutissimum* and *A. nanum*; the first species increased in abundance after 2010, especially in the south basin and Immez OL. Taxa belonging to the *Achnanthidium minutissium* complex are difficult to separate and thus may be grouped as a common taxon. For instance, *A. nanum* was not recorded in earlier studies of Macun diatoms and was likely grouped with *A. minutissium* (Kawecka and Robinson, 2008),
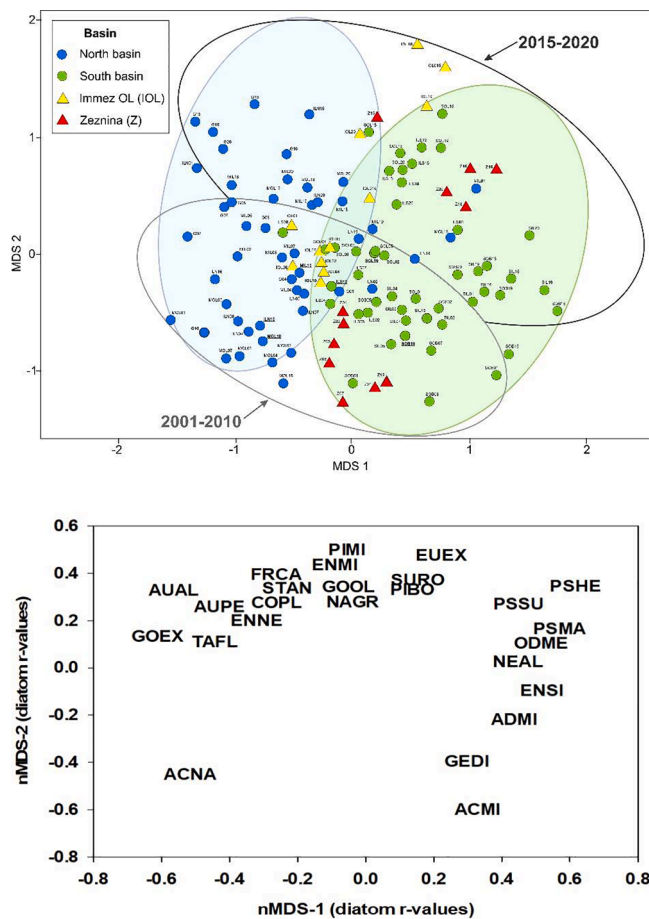
Fig. 5. (Top) Scatterplot of the non-metric dimensional scaling (nMDS) results based on 78 diatoms with a relative abundance of 2% or more. Numbers denote year of sample collection (2001–2020) for notated sites (Grond (G), Mezza Gluna inlet (MIL), Mezza Gluna outlet (MOL), Immez north inlet (ILN), Sura OB (SOB), Sura inlet (SIL), Sura outlet (SOL), Immez south inlet (ILS), Immez outlet (IOL), Zeznina (Z). Ellipses represent the two main group of diatom assemblages associated with the north and south basins as well as samples collected pre-2010 with those post-2010 (see methods for details). (Bottom) Scatterplot of diatoms highly associated with axis-1 and axis-2 of the nMDS plot (correlations of 0.30 or higher). See supplement Fig. 2 legend for notations of diatoms.

Fig. 6. Scatterplot of the nMDS results based on 78 diatoms with relative abundances of 2 % or more grouped by (A) lake inlets (IL) and lake outlets (OL) in the south basin (SB) and north basin (NB) for samples collected pre-2010 and post-2010, and (B) along the lake order sequence represented in both basins for the same time periods. All data are plotted as means ± SE. Red symbols are north basin and blue symbols are south basin sites. The increase in color darkness (light to dark) corresponds to the longitudinal sequence in lake order. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

however the nomenclature was rectified in the current study. In fact, *A. minutissimum* is a widespread diatom found in all types of waters except highly acidic or extremely electrolyte-poor systems (Lange-Bertalot et al., 2017). *Achnanthidium minutissimum* is considered a pioneer species and early colonizer, often colonizing substrata just after a disturbance event (Passy, 2007; Berthon et al., 2011). This species also is indicative of unpolluted or pristine waters (Kelly et al., 2008; Stubbington et al., 2019). The species was noted in the Southern Alps (Italy), being frequently associated with diatom assemblages of high elevation springs along with *Odontidium mesodon* (Cantonati, 1998; Cantonati et al., 2001, 2006). Studies of Fell et al. (2018) suggest that *A. minutissimum* is a primary colonizer in Alpine waters with low channel stability. This taxon often predominates in diatom assemblages in glacial streams (see Gesierich and Rott, 2012). Lastly, González-Paz et al. (2022) indicated *A. minutissimum* as a criteria of "reference conditions" and undisturbed streams of mountain areas in Spain.

The other frequent occurring taxa, *Achnanthidium nanum*, is relatively poorly known ecologically but often associated with lentic waters. Previously described as *Achnanthes nana* in a high altitude Swiss lake, it was renamed in 2015 to the genus *Achnanthidium* as *A. nanum* (Novais et al., 2015). *Achnanthidium nanum* usually co-occurs with other taxa in various freshwater habitats, even ponds, with low conductivity and
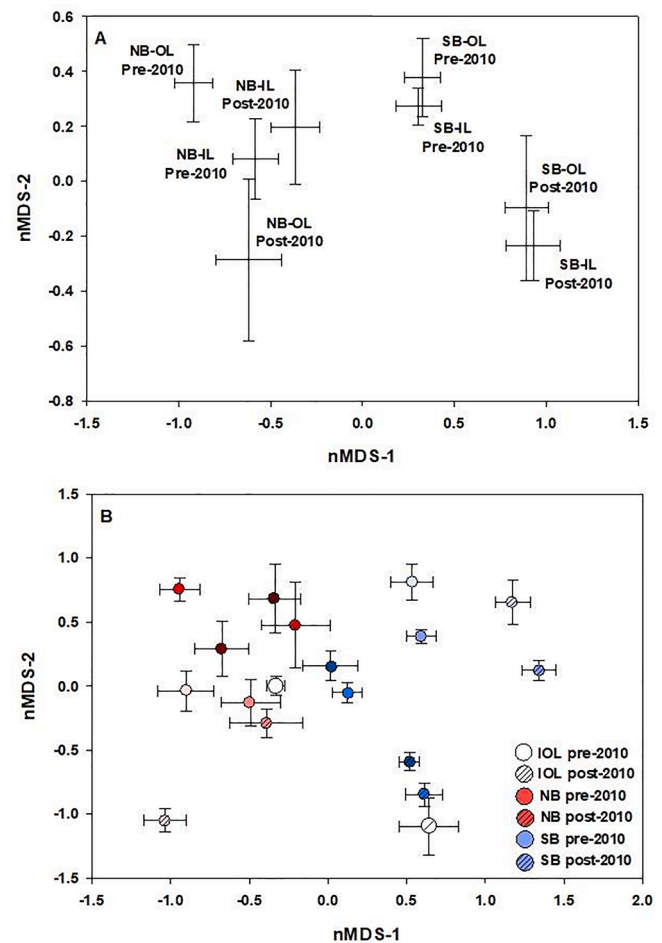
nutrients, such as *Achnanthidium caravelense, A. minutissimum, Odontidium mesodon* (syn. *Diatoma mesodon (Ehrenberg) Kützing),* and *Hannaea arcus (Ehrenberg) R.M.Patrick*. The species has been documented from various stations in Portugal, Scotland and Nepal. In Portugal, it occurred in well-oxygenated waters with pH 6.1–7.7 and low calcium concentrations (2–18 mg/L), low conductivity (39–94 μS/cm) and low nutrient levels. In Scotland, it occurred in waters with circumneutral to slightly alkaline pH and low to medium conductivity, and in Nepal, it was most abundant in streams with calcium levels below 15 mg/L (Novais et al., 2015). In Macun cirque, *A. nanum* was most frequent at Lai Grond (site 1), a lake outlet in the north basin.

Our results showed that *A. nanum* was negatively correlated, whereas *A. minutissimum* was positively correlated, with electrical conductivity. The abundance of both species and correlations with other environmental variables (e.g., nutrients) corresponded with the temporal (post- and pre-2010) physico-chemical changes observed in waters of the basins; i.e., general increase in EC, and the increase of PP, TP and POC at south basin sites (Robinson et al., 2022). Although the basins became more similar in physico-chemistry over the study period, each still showed differences in physico-chemistry as indicated in diatom assemblages post-2010. In particular, *A. nanum* seems to prefer nutrient-poor
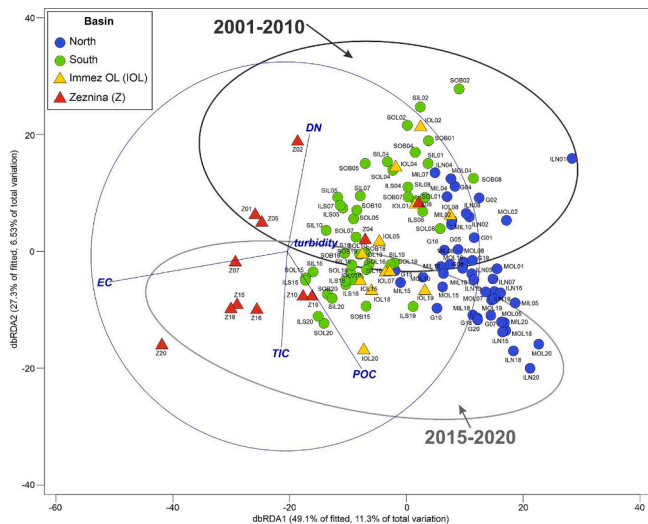
Fig. 7. Graphical presentation of relationship between environmental variables and diatom assemblages based on distance-based redundancy analysis (dbRDA) with ellipses representing samples collected pre-2010 and post-2010 in the north basin, south basin, Immez outlet and Zeznina. For site abbreviation see Fig. 5 legend.

waters with extremely low conductivity compared to *A. minutissimum*. As mentioned, *A. nanum* often is associated with lentic habitats, thus the interconnection of lakes and streams in Macun may favor its occurrence. These results support the use of diatoms for unraveling the heterogeneous nature of alpine surface waters, especially the juxta-positioning of lake and streams in such landscapes.

Another abundant diatom was *Gomphonema exilissimum*, a species considered a morphodeme or ecodeme of *G. parvulum* (Abarca et al., 2014). This diatom was probably identified as *G. parvulum* in earlier studies of alpine streams (e.g., Robinson and Kawecka, 2005), but naming was rectified in the current study on the same system. *Gomphonema exilissimum* typically occurs in unpolluted oligotrophic waters, but often in waters that are slightly acidic with low conductivity and nutrients, and on silica bedrock (Jütter et al., 2013; Abarca et al., 2014; Lange-Bertalot et al., 2017). In Macun, this diatom showed similar physico-chemistry relations as *A. nanum*, and at sites with higher turbidity such as Zeznina (note that turbidity of waters in Macun are low regardless, <10 NTUs on average, see Table 1). After 2010, the abundance of *G. exilissimum* decreased as did *A. nanum*.

Frequently occurring diatoms in the genus *Psammothidium* have similar ecology, occurring mainly in low conductivity waters (Rott et al., 2006; Lange-Bertalot et al., 2017). *Psammothidium helveticum* and *P. marginulatum* were reported as common species in assemblages from cryoconite holes on glaciers from Spitsbergen and Greenland (Yallop and Anesio, 2010) and other rock-glacier fed streams in the Alps (Thies et al., 2013). *Psammothidium helveticum* is characterized as preferring more acidic waters of a lentic character. It is also noted in small streams that are weakly acidic to circumneutral running waters but at relatively low abundances (Lange-Bertalot et al., 2017). In Macun, *P. helveticum* occurred mostly at south basin sites; south basin sites had lower pH than north basin sites pre-2010 with values increasing post-2010 (Robinson et al., 2022). It showed a low abundance in 2008, a year with relatively high turbidity in Macun waters. Based on this study, *P. helveticum* prefers undisturbed, oligotrophic waters, but can tolerate more circumneutral waters. The influence of rock glacier inputs to south basin physico-chemistry is noted for this diatom, as reported in various studies in the Alps with waters affected by rock glaciers (Thies et al., 2013; Fell et al., 2018).

Various planktonic diatoms also were recorded in diatom samples. This result is not surprising with sites being located above and below

lakes in the stream-lake network. Abundant planktonic diatoms were represented by *Aulacoseira* spp (*A. alpigena* and *A. nivalis* in particular) and *Tabellaria flocculosa*, indicating a lake influence on stream assemblages (see Schanz, 1984). Both diatoms were most frequent at Mezza Gluna outlet (site 3) and Immez inlet north (site 4). The stream between these two sites is low gradient (slope ca 1 %) and slow flowing (transient flow between sites ca 1 h for 150 m). *Tabellaria flocculosa* also was frequently noted in lake outlets of glacial headwaters in Canada (Gesierich and Rott, 2012). Both diatoms are cosmopolitan species, preferring oligotrophic lakes with low conductivity (Schanz, 1984; Buczkó et al., 2010). *Aulacoseira nivalis* is characteristic of alpine and northern waters (Krammer and Lange-Bertalot, 1991a), and frequently recorded in Carpathian lakes (Buczkó et al., 2010). *Tabellaria flocculosa* is an abundant diatom throughout Europe, preferring low conductivity streams on siliceous substrate; it is often found in high abundances in lakes of the Alps and Alpine foothills (Lange-Bertalot et al., 2017).

Achnanthidium spp., *Gomphonema* spp. and *Cocconeis* spp. are referred to as "pioneer" taxa and were frequently noted on debris in cryoconite holes as a representatives of (reservoirs/refugia of cold-loving algae) early successional processes (Yallop and Anesio, 2010), and also found in mature biofilms in lentic and lotic environments (Yallop and Kelly, 2006) and arctic waters with low conductivity (Remias, et al, 2009; Antoniades, et al. 2005; Michelutti, et al. 2006). It is likely that glaciers in many Alpine areas play a similar role of influencing diatom assemblages in outflow waters.

Most diatoms recorded in the Macun stream-lake network are taxa found in oligotrophic waters, whose abundances were negatively correlated with conductivity in this study. This is not surprising considering the nutrient-poor bedrock (local geology is predominantly orthogneiss and granite) reflected in the water physico-chemistry of studied streams. Although glacial melt results in strong fluctuations in water flow and turbidity in proglacial streams (Milner and Petts, 1994), glacial flour is essentially non-existent in our streams (turbidity is low) affected by rock glaciers so light availability does not limit algal growth.

A diatom of waters with relatively higher conductivity in the Macun plateau was *Odontidium mesodon*, which was quite abundant at Zeznina (site 10). Zeznina waters are influenced by inputs from a large rock glacier that increased conductivities twofold over upper basin sites (Robinson et al. 2022). This diatom is widely distributed in oligo-mesotrophic waters (Lange-Bertalot et al., 2017) and have high abundances in cold, oligotrophic waters in the Alps (Gesierich and Rott, 2004) and Himalaya (Cantonati et al., 2001). Its presence at Zeznina separated this site from other sites in the catchment in concert with the physico-chemical differences of Zeznina and the other waters of Macun.

Besides water chemistry and potential lake influence, other local factors affecting diatom distribution and abundance are channel slope and associated water current (Virtanen and Soininen, 2012). Sites belonging to the north and south basins have relatively low and similar slopes (<1%, personal observation) because they lie on the Macun plateau. Site Zeznina had the highest slope (>1%) and consequently water current. Current velocity is a driver of diatom assemblages; at high velocities, diatom assemblages appear to be highly specialized and assemblages are mostly dominated by those possessing streamlined forms, low motility and strong attachment to benthic substrates (Hieber et al., 2001). In these conditions with high shear stress, abrasion and scouring induced by channel destabilization, species richness (Soininen, 2004) and cell density tend to be low (Bona et al., 2012; Wellnitz and Rader, 2003). Its notable that Zeznina had the lowest number of diatom species recorded in this study.

Lake outlets generally buffer temporal changes in environmental conditions leading to more stable habitats throughout the year. We did not analyze seasonal patterns in diatom assemblages in this study, but Hieber et al. (2001) showed that algal assemblages of various alpine lake outlets reflected this stability displaying no significant seasonal changes in composition. We found little difference between lake inlet and lake outlet diatom assemblages in the south basin, but differences between

inlets and outlets were apparent in the north basin. The north basin lacks the rock glacier inputs associated with waters of the south basin. North basin waters were also warmer (ca 3 °C) than south basin waters, suggesting a lake warming affect that may have influenced outlet assemblages to some degree. During heatwaves, the temperatures of glacial-fed streams can be buffered by glacier melt that keep streams cool (Lisi et al. 2015). For Macun, this suggests that north basin streams with no glacial inputs were probably more sensitive to heating than south basin streams with rock glacial inputs. South basin streams are likely to become more sensitive to heatwaves as rock glacial inputs diminish in the relatively near future (Woodward et al., 2016). Lastly, the north basin has two large lakes embedded in the network, whereas only one large lake occurs in the south basin and is the final lake in that basin. The upper lakes in the south basin are small and probably had little influence on outlet stream physico-chemistry. A lake order effect is often noted in physico-chemical differences along lake chains (Soranno et al., 1999), and this was evident in diatom assemblages, especially composition differences of upper sites relative to lower sites in each basin.

Diatom diversity indices (richness, H') decreased post-2010 concomitantly with the decrease in periphyton biomass. In similar studies conducted in mountain streams (2650 m asl) in Spain, González-Paz et al. (2022) comparing diatom assemblages in periods 2003–2008 and 2016–2020 obtained similar trends of decreasing diversity indices. These authors interpreted this pattern as the result of ecosystem restoration and a decrease in pollution tolerant species. In our case, it seems that the main reason can be environmental homogenization and the predominance of *A. minutissimum*.

Similarly, dominance increased post-2010, suggesting fewer taxa with high abundances in samples. These changes in diatoms mirrored the changes in physico-chemistry, suggesting a tipping point occurred in the surface waters of Macun that clearly affected algal communities. Robinson et al. (2022) and this study indicate a loss in the inputs of rock glaciers in the catchment over time caused waters to become more similar between basins. Nitrogen concentrations have declined substantially and water pH has increased a unit (from <6 to 7) since the 1970s (see Schanz, 1984, for early records of water chemistry). Other studies in the Alps have also documented shifts in physico-chemistry and changes in biota in the same time period (e.g., Sertic Peric et al., 2015). These changes in alpine surface waters alter other biotic processes (competition, predation) that could influence primary producer abundances and distribution (Khamis et al., 2016). Reductions in rock glacial inputs in the catchment may cause subsequent increases in channel stability due to lower discharge variability and riverbed movement (Carrivick and Heckmann 2017), whereas spatiotemporal mixing of water sources creates more diverse habitat conditions (Fell et al., 2017). More homogeneous habitat properties among alpine streams may also cause reductions in diversity as evident in this study and other glacial streams with decreasing glacier water inputs (Fell et al., 2018).

Our results show that spatio-temporal changes, such as in physico-chemistry, in surface water environments can directly influence diatom assemblages. Environmental changes, e.g. reductions in glacial cover and inputs, are predicted to be ongoing across alpine landscapes globally, and especially in the Alps (IPCC 2021). Alpine streams are sentinels of these environmental changes due to strong atmospheric-cryospheric links, and as indicated through the biomonitoring of diatoms, and thus are excellent models for investigating climate-related changes on freshwater ecosystems (Fell et al., 2017). Our studies show that high elevation habitats are indeed sensitive, making them highly valuable for long-term studies of which diatoms are notable indicators of such sensitivity. Indeed, benthic primary producer (especially diatoms) response to glacier retreat can be a general feature of glacial-fed aquatic ecosystems globally.

5. Conclusions

The present study was conducted in a high alpine cirque comprising two distinct basins (north and south) that differed in physico-chemistry of surface waters. The presence of rock glaciers was an important factor affecting waters and associated diatom assemblages. The study involved two distinct periods (Pre-2010 and Post-2010), resulting from a reduced glacier-melt from rock glaciers that caused basin waters to become more similar. Homogenization in water chemistry was reflected in the diatoms (distribution and abundance) of surface waters. Periphyton biomass decreased almost twofold in both basins post-2010 with a lesser decrease observed at Zeznina stream. Diatom diversity indices decreased post-2010 concomitantly with the decrease in periphyton biomass. Diatom assemblages were dominated by small-celled taxa, primarily *Achnanthidium minutissimum* and *A. nanum*; the first species increased dramatically in abundance after 2010 in response to environmental changes in the catchment. Throughout the study period there were still significant differences in diatom assemblages between the north and south basins but one clear pattern developing was the homogenization of surface waters in the Macun catchment. This trend in physico-chemistry likely will continue as meltwaters from the rock glaciers decrease over time. More homogeneous waters among alpine streams may also cause reductions in diversity as evident in this study and other glacial streams with decreasing glacier water inputs.

CRediT authorship contribution statement

Łukasz Peszek: Investigation, Methodology, Writing – original draft. **Barbara Kawecka:** Investigation, Writing – review & editing. **Christopher T. Robinson:** Conceptualization, Methodology, Investigation, Writing – original draft.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

Acknowledgments

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2022.109515.

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