



## Recent and subfossil diatom assemblages as indicators of environmental change (including fish introduction) in a high-mountain lake

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### ABSTRACT

We investigated modern-littoral and subfossil sediment-core diatoms in the shallow (max depth 6.4 m) high-mountain Lake Balma in the Orsiera Rocciavè Nature Park (Italian Western Alps). Our study provided evidence that might be related to the response of diatom assemblages to fish introduction, in particular the decreasing of the nutrient-enrichment sensitive low-profile life-form/ecological guild and the increase in species known to react positively to the augmented nutrient availability due to fish excretions (e.g., *Fragilaria nanana*, *Pseudostaurosira brevistriata*, *Staurosirella neopinnata*). We are, however, aware that some of these effects could as well have been caused by pastures and cattle watering, and by increased temperatures due to global warming, and we acknowledge the typical complex-interaction pattern among different stressors. High-mountain lakes are “early warning systems” for the whole alpine system and can contribute valuable information also on the interactions between environmental global changes and anthropogenic impacts. Benthic diatoms, in particular, can provide useful indications on the deleterious effects of non-native fish introduction, cattle grazing, and global warming, and thus support an adaptive and sustainable management of high-mountain lakes for the sake of nature conservation.

### 1. Introduction

Alpine lakes are considered remote and pristine ecosystems, where harsh environmental conditions generally allow for the colonization by a few well-adapted species, resulting in low diversity communities with relatively simple structures, and simple trophic webs (e.g., Füreder et al., 2006; Cantonati et al., 2020). However, alpine lakes are very sensitive to anthropogenic impacts, both on a local (water abstraction, tourism, grazing, introduction of non-native species) and global scale (long-range pollutant transport, radioactive-nuclides transport, acid rain, global climatic changes) (Psenner and Schmidt, 1992; Psenner and Catalan, 1994; Camarero et al., 1995a, 1995b; Battarbee et al., 2002; Magnea et al., 2013). Alpine lakes are therefore of pivotal importance to study global changes in water quality and biodiversity (Rogora et al., 2018), and to assess the large-scale effects of anthropogenic activities (e.g., Battarbee et al., 2009). High altitude lakes are considered “early

warning systems” for the whole mountain environment (MOLAR Water Chemistry Group, 1999; Perilli et al., 2020).

Natural environmental changes and anthropogenic disturbances can interact, leading to combined effects on the freshwater communities. Williams et al. (2016) found that anthropogenic pressures, including fish introductions, could confound the role of climate change in shaping subfossil invertebrate assemblages. Tiberti et al. (2019) point out that introduced fish is a challenging conservation and management problem, even in nature preserves of the Alps, but that it also typically interacts in a complex way with other threats. Raposeiro et al. (2017) showed that predator introductions (fish) differently affected chironomid and diatom taxa in an Azorean lake, in addition to climate oscillations, volcanic eruptions, and other anthropogenic activities, while communities seemed to be more triggered by climatic fluctuations during the fishless lake period. Recently, Perilli et al. (2020) investigated the consequences of fish introduction on macrobenthic invertebrate communities of alpine

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lakes through paleolimnological analyses, focusing on brook trout stocking as a complementary factor, interacting with other features in shaping chironomid communities.

Introduction of non-native species is one of the major reasons for the worldwide decline in biodiversity (Raposeiro et al., 2017), being considered one of the main threats to global autochthonous biodiversity, especially in alpine lakes (Knapp et al., 2001; Schabetsberger et al., 2009; Tiberti et al., 2014; Tiberti et al., 2016). Effects of fish introductions on lake ecosystems have long been debated and it has been hypothesized that such effects should be strongest in oligotrophic lentic systems, where fish were not formerly present (e.g., Brancelj et al., 2000; Milardi et al., 2016). Although alpine lakes were generally fishless, due to the presence of natural migration barriers (e.g., Pechlaner, 1966; Fritts and Rodda, 1998; Sax et al., 2002; Gurevitch and Padilla, 2004), these environments have been often stocked with salmonids, such as *Salvelinus fontinalis* (brook trout) and *Salmo trutta* (brown trout), for recreational purposes (Tiberti et al., 2014; Sánchez-Hernández et al., 2015), causing consequences on food web structures and ecosystem functions. Moreover, fish introduction can interact with temperature increase due to global warming, amplifying the effect on freshwater communities, especially in alpine lakes, which are considered remote and undisturbed but extremely susceptible and vulnerable to both natural and anthropogenic impacts (Schabetsberger et al., 2009; Tiberti et al., 2014; 2016; Perilli et al., 2020).

Diatoms are single-celled eukaryotic organisms with the ability to photosynthesize and colonize almost every known moist or aquatic environment (Bulínova et al., 2010). They are very important in freshwater environments, due to primary production (Mann and Droop, 1996), and are useful indicators for several environmental alterations, such as acidification, nutrient enrichment, variation of water temperature, and conductivity (e.g., Rimet and Bouchez, 2012). Benthic littoral diatoms are an immensely powerful indicator of local pollution sources and are among the first tools to detect deterioration of lake environments (e.g., Rimet et al., 2016). Moreover, diatom assemblages are used in paleolimnological analyses to detect changes in pH and nutrient levels (e.g., Bennion et al., 2004). When the scope is to point out the effects of a disturbance event, a so called top & bottom paleolimnological approach is often used (e.g., Vermaire and Gregory-Eaves 2008), meaning that the ecological situation as reflected by recent sediments is compared to the one documented by pre-disturbance sediments). However, there is still a lack of knowledge about high-altitude lakes in many alpine environments (Robinson et al., 2010; Feret et al., 2017) and new studies are required.

In this context, it was deemed of interest to assess the temporal changes within the diatom assemblages in a high-altitude lake located in the Italian Alps (Lake Balma, Piedmont, Italy) in a nature preserve, and subject to brook trout introduction for recreational fishing at the end of the 20th century. The aims of the present study were (i) to characterize the modern diatom assemblages in Lake Balma in the littoral habitats, (ii) to characterize the diatom taphocoenoses through analyses on selected lake-sediment sections, and finally (iii) to assess changes in diatom community in relation to environmental change (including fish introduction). The present study also aims at deepening analyses formerly carried out in Lake Balma, including other proxies, at contributing to studies on the interactions between global change and non-native fish introductions, and at showing that diatoms, being able to reflect the effects of environmental change at local (including fish introduction) and global change, can provide useful indications for environmental management and nature conservation in high-mountain lakes.

## 2. Methods

### 2.1. Study area

Lake Balma is located above the tree line in the Cottian Alps

(Municipality of Coazze, Piedmont, northwestern Italy), at 2116 m a.s.l. (Fig. 1a, b). It represents a typical example of an alpine lentic environment (in the sense of Füreder et al., 2006), and is included in the Special Area of Conservation (SAC) and Special Protection Area (SPA) IT1110006 “Orsiera Rocciavère” and in the Orsiera Rocciavère Nature Park. The lake is of glacial origin, with a circular perimeter equal to 414 m, while the surface area is 1.21 ha and maximum depth is 6.42 m. These data were provided by GeoStudio RC (Giaveno, Italy), which performed a morphometric and bathymetric survey of the lake using drones. The main catchment core is composed of ophiolite metamorphic bedrock and the landscape is dominated by rocky outcrops, ridges, and mountain walls. The ice cover generally lasts from late October to late May/early June. A small inlet is located at the western shore, dividing into three small branches before entering the lake. Although a true outlet is not evident, at the eastern side, the Rio Balma originates by water filtration through the sediments delimiting the basin (Fig. 1b, c) (Perilli et al., 2020).

The main source of human impact for this area from the last four decades of the 20th century is represented by long-distance airborne transport of pollutants from the urban areas in the plain, grazing activities (with pastures reaching part of the shores of the lake which is periodically even used for cattle watering), and fishing (Pastorino et al., 2020; Perilli et al., 2020). Lake Balma was formerly fishless, but brook trout was introduced for recreational fishing during the last decades of the 20th century, since the 1970 s (Balma et al., 1992; Pastorino et al., 2020; Perilli et al., 2020). The brook trout population is well structured, with individuals in age classes from 0 + to 4 + and an average fish biomass equal to 17.89 g m<sup>-2</sup> (Pastorino et al., 2020).

### 2.2. Physical and chemical parameters

At each littoral sampling site, the main chemical and physical features were measured during both sampling campaigns. Water temperature (°C), dissolved oxygen (% and mg L<sup>-1</sup>), pH and conductivity (µS cm<sup>-1</sup>) were recorded using field meters (HI 9033 conductivity meter, HI 9125 pH/ORP meter, HI 9147 oximeter; all instruments were manufactured by Hanna Instruments Inc., Woonsocket, RI, USA). Water samples were collected at each site in sterile containers paying attention to avoid inclusion of sediment particles, and then brought to the laboratory. Here, NO<sub>3</sub> concentrations (mg L<sup>-1</sup>) were quantified measuring the absorbance at 525 nm, obtained by an adaptation of the cadmium-reduction method (APHA, AWWA, WEF, 1998); NH<sub>4</sub><sup>+</sup> concentrations (µg L<sup>-1</sup>) were measured by an adaptation of the Nessler method, measuring the absorbance at 420 nm (ASTM 2015); finally, the PO<sub>4</sub><sup>3-</sup> concentrations (µg L<sup>-1</sup>) were obtained with an adaptation of the ascorbic acid method (APHA, AWWA, WEF, 1998) measuring absorbance at 610 nm. Analyses were carried out using a multi-parameter spectrophotometer (HI83200-02, manufactured by Hanna Instruments Inc. Woonsocket, RI, USA) and three replicates were done for each parameter.

### 2.3. Lake sediment coring

A coring campaign was conducted in October 2018, using a 50-mm diameter, Kajak-type, gravity sediment corer (e.g., Renberg 1991). One, 40-cm long core was extracted from the deepest point of the lake (6.42 m) (Fig. 1c). The core was sealed in a coring tube, brought to the laboratory and stored at 4 °C until further analyses. Subsamples were obtained by cutting the core in 2-cm interval transverse sections, in agreement with previous core analyses performed by Perilli et al. (2020) for the same site. The age-depth model used for the present study (Fig. 2) was developed for Lake Balma by Perilli et al. (2020) using the RStudio Package *Clam* 2.3.2 (Blaauw 2010) through smooth interpolation function, analyzing <sup>14</sup>C AMS data and total Pb concentrations determined by Inductively Coupled Plasma-Mass Spectrometry (ICP-MS). These data were obtained from a core collected nearby the core sample site

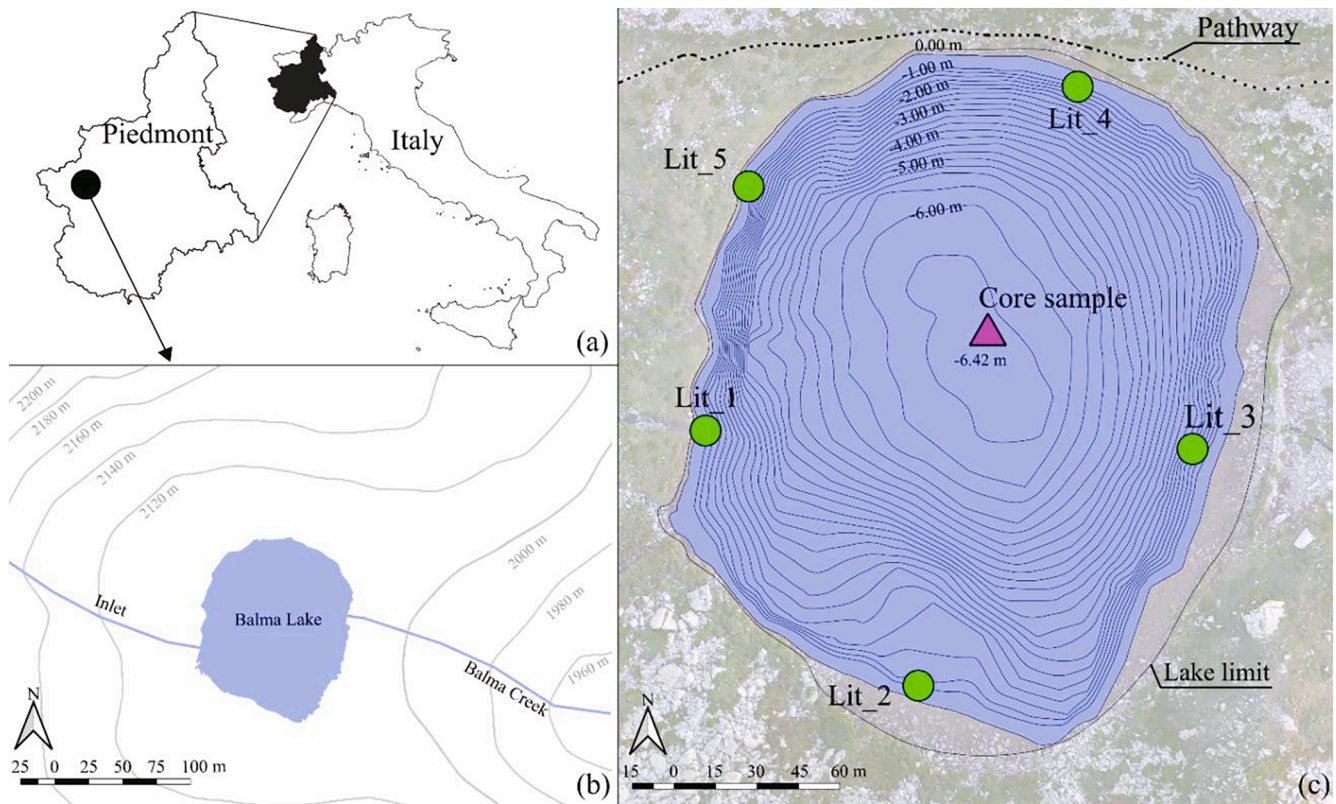


Fig. 1. Study area (a, b) and location of the sampling sites in Lake Balma (c).

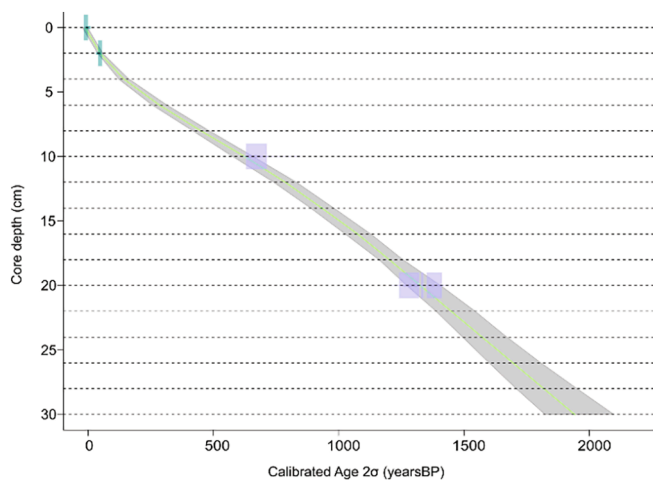


Fig. 2. Age-depth model based on smooth interpolation of best point calibration estimates from <sup>14</sup>C dates and non-carbon dates (Pb concentrations in core sections) obtained using the *Clam* 2.3.2 package for RStudio. Gray area shows the 95% confidence intervals based on 1000 interactions; green line represents the best-fitted age (mod. from: Perilli et al. 2020). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

considered in the present study. Average sediment accumulation rate for Lake Balma was 0.018 cm year<sup>-1</sup> (Perilli et al., 2020). For the present study, four representative sections were analyzed to compare communities in recent and ancient sediments. The top section (0–2 cm) was selected to represent the most recent sediment conditions; the 2–4 cm section was chosen because it corresponds to the fish-introduction period (1970 s) (Perilli et al., 2020); deep sections were chosen at 8–10 and 20–22 cm, corresponding to the <sup>14</sup>C AMS radiocarbon dates.

Chosen sections and relative calendar dates estimated from the age-depth model are reported in Table 1.

#### 2.4. Modern diatom assemblages

Two sampling campaigns were carried out in 2018 during the ice-free period, in summer (early August) and at the beginning of the fall season (October). To check modern diatom assemblages in Lake Balma, five sites were chosen in the littoral zone (Fig. 1c), acknowledging the occurrence of different microhabitats (presence of gravel, cobbles and small boulders) and in agreement with the results of the bathymetric surveys. These sites were the same considered by Perilli et al. (2020) in a macroinvertebrate community study, and descriptions are reported in Table 2. Diatom sampling was performed following CEN (2003) and King et al (2006). At each site, diatoms were removed with a toothbrush from cobbles and small boulders (size: class: 64–256 mm) collected from down to 60 cm water depth. Five replicates were collected at each site during each sampling event (*n* = 50). Samples were immediately fixed with formaldehyde solution (4% v/v) and brought to the laboratory for further analysis.

#### 2.5. Diatom sample analysis and slide preparation

Samples for morphotaxonomic diatom analysis (for both sediment

**Table 1**  
Lake Balma core sections and related calendar ages estimated from the age-depth model developed by Perilli et al. (2020) for the Lake Balma (Fig. 2).

Depth of core section (cm)	Age-range estimated from age-depth model
0 - 2	AD 2017–1995
2 - 4	AD 1995–1951
8 - 10	AD 1499–1404
20 - 22	AD 626–513



**Table 2**

Geographical coordinates and short description of the Lake Balma littoral sampling sites (mod. from: Perilli et al. 2020).

Sampling site	Longitude	Latitude	Site description
Lit_1	07°10'49.22"	45°02'13.39"	northwestern shore near the inlet; gravel and cobbles
Lit_2	07°10'51.26"	45°02'11.83"	southern shore; submerged boulders
Lit_3	07°10'53.78"	45°02'13.50"	eastern shore; boulders
Lit_4	07°10'52.46"	45°02'15.76"	northern shore; cobbles
Lit_5	07°10'49.63"	45°02'15.02"	northwestern shore; gravel and cobbles, with organic debris
Core sample	07°10'52.23"	45°02'14.28"	center of the lake; sand and mud. Depth: 6.42 m

cores and modern samples) were prepared eliminating the organic matter by oxidation on a heating plate using hydrogen peroxide (H<sub>2</sub>O<sub>2</sub>), and hydrochloric acid (HCl) was added to remove carbonates (e.g., Lai et al., 2019). After rinsing several times with distilled water, permanent slides were mounted using the Naphrax® (refractive index = 1.73) mounting medium. Diatom observations and counts (~400 valves for each slide) were performed using a light microscope equipped with phase contrast and micrometric scale at × 1000 magnification. Diatom species were identified according to Lange-Bertalot (2001), Krammer (2002), Krammer and Lange-Bertalot (2007a), Krammer and Lange-Bertalot (2007b), Blanco et al. (2010), Falasco and Bona (2013). Nomenclature and some taxonomic concepts were updated using AlgaeBase (Guiry and Guiry, 2020) and Cantonati et al. (2017).

## 2.6. Ecological factors inferred from lake-sediment diatom assemblages

To infer/reconstruct selected environmental variables from the diatom taphocoenoses of the lake-sediments' sections the following two training sets were composed: a) SWAP < 20 m & < 30 μScm<sup>-1</sup>: out of the > 170 lakes of the SWAP database (Surface Waters Acidification Program; Stevenson et al., 1991) only lakes with maximum depth < 20 m and conductivity < 30 μS cm<sup>-1</sup> were selected. b) 25\_Ita.Alps: out of the ca. 30 lakes included in the Marchetto and Schmidt (1993) dataset some were discarded because they were too deep and/or had a too high conductivity to be comparable with Lake Balma; the 22 retained lakes were integrated with three high-mountain lakes (Angeli and Rose 2006) selected from a database of the southeastern Italian Alps (Lagorai mountain range) including also several shallow lakes with low conductivity (Cantonati and Lazzara 2006).

To allow for direct comparison of the performance of the two training sets, three factors were reconstructed using both SWAP < 20 m & < 30 μScm<sup>-1</sup> and 25\_Ita.Alps: conductivity (Cond), pH, and nitrates (NO<sub>3</sub><sup>-</sup> mg L<sup>-1</sup>). Unfortunately, total phosphorus (TP, μg L<sup>-1</sup>) is not available in the SWAP database, and was therefore reconstructed, as well as ammonium (NH<sub>4</sub><sup>+</sup>, μg L<sup>-1</sup>), from the 25-lakes dataset of the Italian Alps. It was planned to reconstruct from the customized SWAP database also dissolved organic carbon (DOC) and total organic nitrogen (TON) but the inferred values for these two parameters turned out to be negative, and the regression models didn't fit as well as for the other factors.

Taking into due account changes in nomenclature and taxonomic concepts, exact correspondences between the two mentioned training sets and our species list (Supplementary material Table 1) were established whenever feasible. For both sets of inferred variables, we used all species for which the establishment of a correspondence was possible.

The calculation of the inferred ecological factors was done with the *rioja* R package (Juggins 2017).

## 2.7. Data processing and analysis

A threat status (a measure of rarity), according to current (Hofmann et al., 2018) and previous (Lange-Bertalot 1996) Red List data for Central Europe, was assigned for all diatom taxa (from both sediment cores and modern samples) in the present study. For the taxa present in both lists, it is thus possible to check whether conservation status was improving or declining. Further ecological attributes (trophic and mineralization preferences, aerial species) available in Hofmann et al. (2018) were used as well. To obtain a general ecological perspective of the communities studied, the observed taxa were assigned to and life-form/growth-form, guild and size classes provided by Rimet and Bouchez (2012) (Supplementary material Table 1).

All analyses were performed in the R statistical environment (R Core Team, 2019) accessed through its graphical interface RStudio version 3.4.3. Figures were produced with RStudio and processed with the software Inkscape version 0.92. All diatom data were converted to relative abundances which were visualized with dot plot diagrams organized by site and core samples using the *rioja* R package (Juggins 2017). In these plots, a point is generated for each taxon within its corresponding sample that is proportional in size to its relative abundance.

Potential indicator taxa of the different core sections and modern assemblages were identified using the Indicator Value (*IndVal*) (Dufrene and Legendre 1997) method, using the *duleg* function in the *labdsv* package in R (Roberts 2016).

To explore relationships between sites and core samples, a Non-metric Multidimensional Scaling (NMDS) was carried out using the taxa as variables. Data were log[*x* + 1] transformed prior to analysis, and NMDS were produced using the *vegan* package in the RStudio environment (Oksanen et al., 2018). To minimize the influence of rare species, only species with relative abundances > 2% or present in at least two samples were included.

## 3. Results

### 3.1. Chemical and physical features

Mean values of the chemical and physical parameters measured at Lake Balma during the study period are reported in Table 3. Temperatures are lower in fall (around 8 °C) than in summer (around 12 °C) in agreement with air-temperature seasonal trends, and no thermal stratification was observed in the water column. Conductivity was around 12 μS cm<sup>-1</sup> in summer and around 19 μS cm<sup>-1</sup> in fall. Generally, fair oxygenation levels were detected in summer, while values were lower in fall. pH values ranged between 7.14 in summer and 7.61 in fall. Regarding the nutrients, values observed in summer and autumn were similar for NH<sub>4</sub><sup>+</sup> (around 80 μg L<sup>-1</sup>) and for TP (10 μg L<sup>-1</sup>), while NO<sub>3</sub><sup>-</sup> (mg L<sup>-1</sup>) concentrations were higher in summer than in fall.

**Table 3**

Mean values and standard deviations of chemical and physical parameters measured at Lake Balma during the two sampling campaigns (summer and fall) in 2018.

	Summer		Fall	
	11.95	± 0.69	8.44	± 0.37
Temperature (°C)				
Dissolved oxygen conc. (mg L <sup>-1</sup> )	7.7	± 2.4	5.9	± 0.3
Oxygen saturation (%)	92	± 29	65	± 4
pH	7.14	± 0.44	7.61	± 0.10
Conductivity (μS cm <sup>-1</sup> )	13	± 1	19	± 1
NH <sub>4</sub> <sup>+</sup> (μg L <sup>-1</sup> )	80	± 50	70	± 40
NO <sub>3</sub> <sup>-</sup> (mg L <sup>-1</sup> )	9.26	± 2.40	7.34	± 2.06
TP (μg L <sup>-1</sup> )	10	± 10	10	± 10

3.2. Diatoms

Overall (recent and subfossil) 103 taxa were found. Red List information (Hofmann et al., 2018) was available for 84% of the 93 species identified at least at the species level. Of these, 55% were found to belong to one of the threat categories (1, 2, 3, G, R, V, D-oligotraphentic) (Supplementary Material Table 1). Overall (L = littoral zone; CT = core top, 0–2, 2–4 cm; CD = core deep, 8–10, 20–22 cm), 12 species are reported in the Red List (Hofmann et al., 2018) as “1 = threatened with

extinction”, “2 = strongly threatened” or “3 = threatened”: *Brachysira brebissonii* (L,CT), *Cavinula pseudoscutiformis* (L,CT,CD), *Encyonema gaeumannii* (L,CD), *Eunotia bigibba* (CT), *E. cisalpina* (CT), *Navicula exilis* (CT), *Neidium alpinum* (L), *N. bisulcatum* (L), *Nitzschia cf. alpina* (L), *Psammothidium cf. chlidanos* (CD), *Sellaphora ventraloconfusa* (L,CT,CD), *Stauriforma exiguiformis* (L,CT,CD).

3.2.1. Modern diatom assemblages

5794 valves belonging to 81 taxa (mostly species) and 32 genera

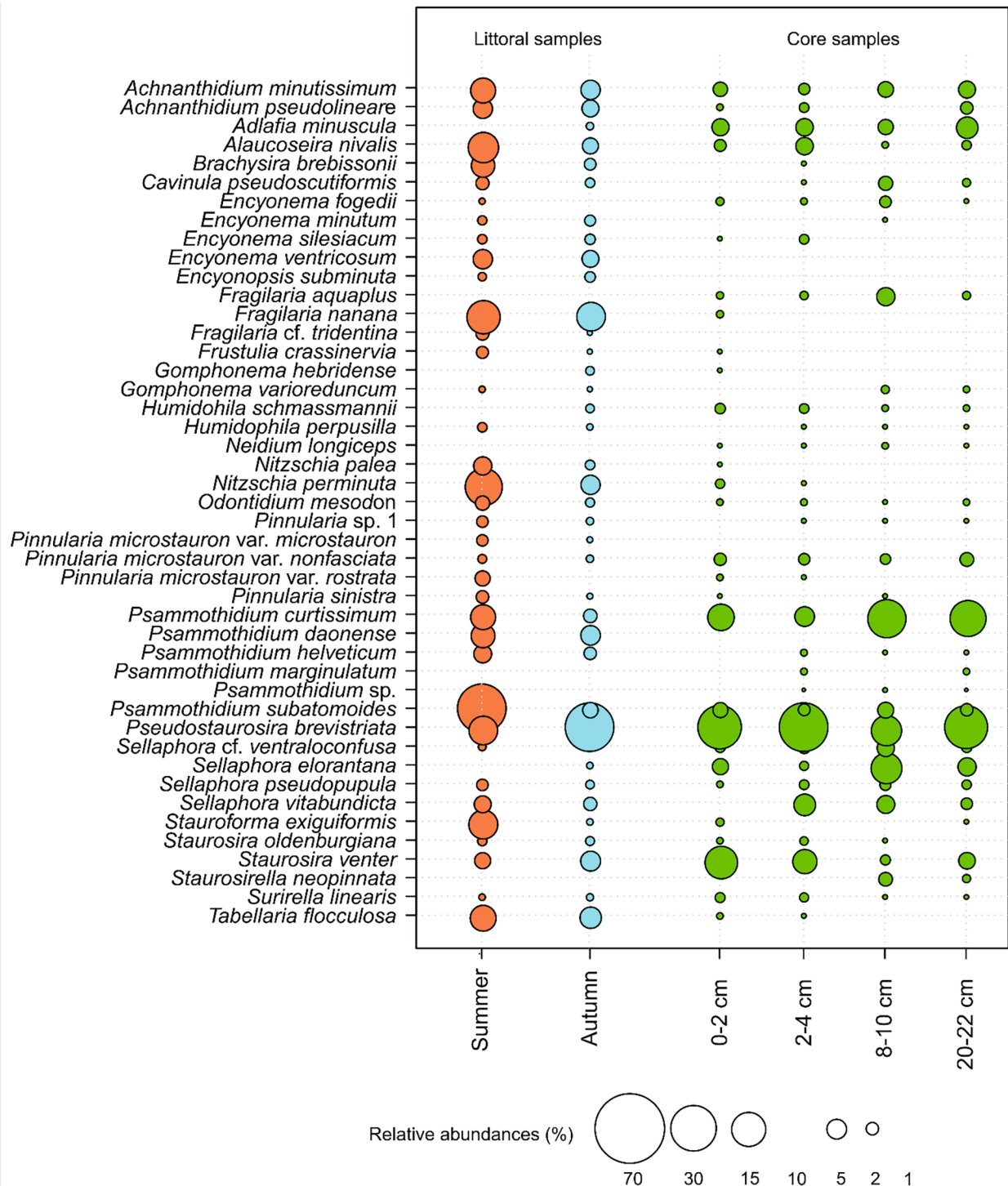


Fig. 3. Dot plot representation of relative abundances for littoral and core samples. The size of a dot is proportional to the relative abundance of each species in a given sample. Only diatoms with relative abundances > 2% or present at least in two samples are plotted.

were identified from littoral samples (Supplementary Material Table 1). Community composition and relative abundances of the main taxa observed in littoral samples are shown in Fig. 3.

The most abundant genera were *Psammothidium*, *Gomphonema*, *Pinularia*, and *Encyonema*, while the most abundant species was *Pseudostaurosira brevistriata* (3.0–14.0% in summer and 7.9–51.7% in fall). Other frequent species were *Psammothidium subatomoides* (0.32–68.1% in summer; 0.8–10.4% in fall); *Fragilaria nanana* (2.1–11.5% in summer; 8.5–12.9% in fall); *Nitzschia perminuta* (0.2–26.3% in summer and 2.1–8.5% in fall), *Achnanthyidium pseudolineare* (0.3–8.2% in summer and 1.6–8.1% in fall), *Achnanthyidium minutissimum* (0.2–13.2% in summer and 0.6–9.6% in fall), *Tabellaria flocculosa* (3.2–6.6% in summer and 1.5–16.1% in fall), and *Staurosira venter* (0.7–4.1% in summer and 0.4–13.9% in fall).

The most frequent ecological guilds in Lake Balma littoral samples were the high-profile and low-profile guilds (Fig. 4a). High-profile species were 24.3% in summer and 53.7% in fall, while low-profile were 43.1% in summer and 21.5% in fall. High-profile species were mainly represented by *Pseudostaurosira brevistriata*, which showed high relative abundances in fall (Fig. 3). Motile guild ranged between 17.2% in summer and 11.6% in fall. Among the planktonic guild species, *Fragilaria nanana* and *Aulacoseira nivalis* were the most abundant. The planktonic guild ranged between 14.8% in summer and between 13.1% in fall.

### 3.2.2. Subfossil diatom assemblages

2334 valves belonging to 62 taxa and 28 genera were identified from the Lake Balma sediment core. Relative abundances of the main taxa are shown in Fig. 3. As already observed for the littoral community, *Pseudostaurosira brevistriata* is the most abundant species, occurring in all analyzed sections with relative abundances between 14.1% (section 8–10 cm) and 40.9% (section 2–4 cm). The second taxon in terms of frequency was *Psammothidium curtissimum*, which was found in all sections and ranged between 5.9% (section 2–4 cm) and 22.4% (section 8–10 cm). *Staurosira venter* showed higher abundances in the top sections than in the deep ones (Fig. 3). *Sellaphora elorantana*, *S. pseudopupula*, and *S. ventraloconfusa* were found in all the core samples analyzed, while *Sellaphora vitabundicta* was absent in the top section (0–2 cm). Some species were found only in the top samples, such as *Achnanthyidium sublineare*, *Tabellaria flocculosa*, *Brachysira brebissonii*, and *Fragilaria nanana*.

Trends of life-forms / ecological guilds observed in the core samples are shown in Fig. 4b. The high-profile guild showed higher relative abundances in the top sections (53.4% in the 0–2 cm and 57.5% in the 2–4 cm) than in the deep ones (26.1% in the 8–10 cm and 40.0% in the 20–22 cm). Low-profile abundances were virtually constant in the deep sections (31.1–33.1%), with clearly decreasing values in the 0–2 cm and 2–4 cm samples (19.2% and 13.9% respectively). The most frequent

taxon of the planktonic guild in the littoral samples, *Aulacoseira nivalis*, showed higher relative abundances in the top core sections (2.2% in the 0–2 cm and 4.7% in the 2–4 cm) than in the deep ones (0.7% in the 8–10 cm and 1.3% in the 20–22 cm).

Non-metric Multidimensional Scaling is reported in Fig. 5. Littoral communities showed a discrete overlap between summer and fall samples, conditioned by the most abundant taxa collected in the littoral zone. Top core samples 0–2 cm and 2–4 cm were placed closer to the littoral than the 8–10 cm and 20–22 sections, which were slightly separated from littoral assemblages.

### 3.2.3. Indicator species of the different groups of littoral and sediment samples

The IndVal procedure allowed to identify statistically significant indicator species for the following groups: littoral: summer, fall; core top: 0–2, 2–4 cm; core deep: 8–10 (Table 4). The five indicators for the epilithic community in summer included *Psammothidium subatomoides* and *Aulacoseira nivalis* while the 4 indicators for the epilithic community in fall included *Fragilaria nanana*, *Pseudostaurosira brevistriata*, and *Tabellaria flocculosa*. The four indicators for the topmost sediment section include *Fragilaria aquaplus* and *Staurosira oldenburgiana* while only *Staurosirella neopinnata* was a significant indicator for the 2–4 cm section. The three significant indicators for the deep 8–10 cm section were *Humidophila perpusilla*, *Encyonopsis subminuta*, and *Stauroforma exiguiformis*.

### 3.2.4. Ecological factors inferred from lake-sediment diatom assemblages

As concerns the ecological factors and parameters inferred from the diatom taphocoenoses using two customized training sets (SWAP < 20 m < 30 μScm<sup>-1</sup> and 25 Ita.Alps; Table 5), the values obtained are consistent between the two databases. Nitrates showed a slight increase after fish introduction whilst pH, conductivity, and total phosphorus remained more or less stable throughout the four sediment sections considered. Ammonium apparently decreased in the two top sections.

## 4. Discussion

### 4.1. Subfossil diatom assemblages

The lake-sediment analyses suggest an increase in nutrients over time in Lake Balma. This is confirmed by diatom-inferred values for nitrates (not for total phosphorus and ammonium). Top sections are characterized by a decrease in abundance of low-profile species (Fig. 4b). The high/low profile ratios are mainly related to nutrient availability and to organic pollution, with high-profile species becoming more abundant than low-profile ones when nutrient levels increase (Rimet et al., 2009; Berthon et al., 2011; Béres et al., 2014; Hlúbíková et al., 2014; Marcel et al., 2017).

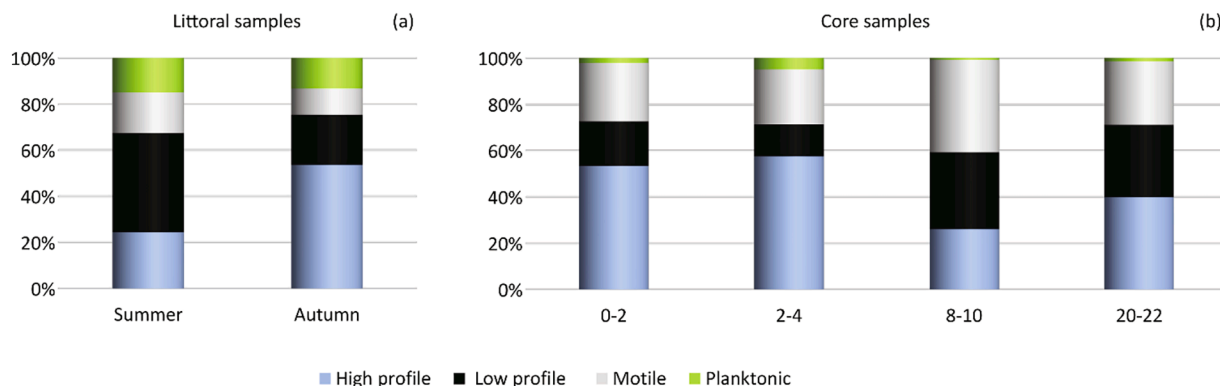
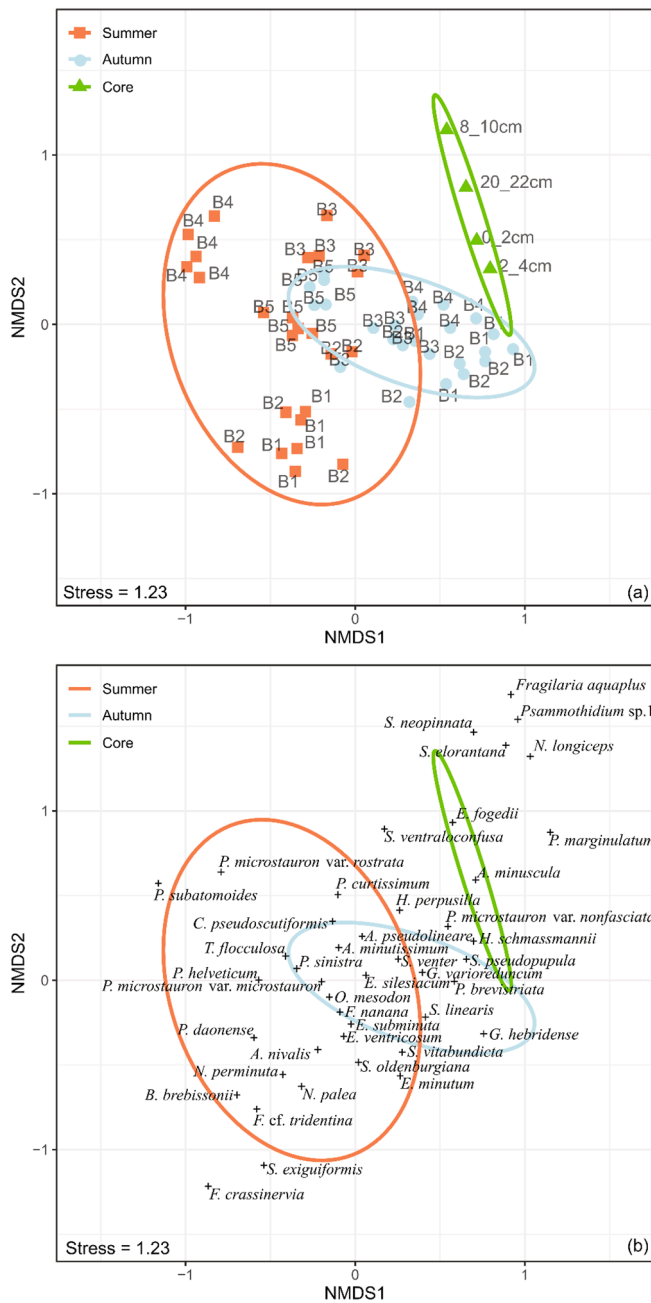


Fig. 4. Diatom community composition in terms of life-forms/growth-forms (Rimet and Bouchez 2012) observed in the littoral samples (a) and in the core samples (b) from Lake Balma.



**Fig. 5.** Non-Metric Multidimensional Scaling (NMDS) performed on the modern diatom community (littoral samples) and on the subfossil diatom community (core sections). Sites (a) and species (b) are shown. Only species with relative abundances > 2% or present at in least two samples are included. Species codes are provided in Table 4.

In the top sections (0–2 cm and 2–4 cm), *Staurosira venter* is more abundant than in the deep samples (8–10 cm, 20–22 cm). The species is mesotrophic (Van Dam et al., 1994) and high-profile (Rimet and Bouchez, 2012) and is also present in all the littoral sites. Some authors report that nutrient load might be associated to fish introduction, likely because fish excretions generate P and N in forms readily available for the algal community (Carpenter et al., 1992; Schindler et al., 1993; Schaus et al., 1997). Fish introductions can affect the trophic web with cascading effects, including a primary production increase (Du et al., 2015; Raposeiro et al., 2017).

A diatom species associated to fish introduction is *Fragilaria nanana*, as reported in a study performed in an alpine lake within the Tatra

**Table 4**

Indicator species identified with the *IndVal* procedure (Indicator Value Method). The species codes are those available in the software Omnidia (<https://omnidia.fr/en/>).

Species	Code	Sample	Group	Indval	p-value
<i>Psammothidium subatomoides</i>	PSAT	Recent	Summer	0.625	0.011
<i>Psammothidium curtissimum</i>	PMTC	Recent	Summer	0.595	0.001
<i>Psammothidium daonense</i>	PDAO	Recent	Summer	0.505	0.014
<i>Aulacoseira nivalis</i>	AUNI	Recent	Summer	0.492	0.044
<i>Nitzschia perminuta</i>	NIPM	Recent	Summer	0.476	0.011
<i>Encyonema ventricosum</i>	ENVE	Recent	Autumn	0.540	0.001
<i>Fragilaria nanana</i>	FNAN	Recent	Autumn	0.540	0.001
<i>Pseudostaurosira brevistriata</i>	PSBR	Recent	Autumn	0.539	0.001
<i>Tabellaria flocculosa</i>	TFLO	Recent	Autumn	0.393	0.049
<i>Fragilaria aquaplus</i>	FAQP	Core	0–2 cm	0.667	0.011
<i>Staurosira oldenburgiana</i>	SODB	Core	0–2 cm	0.600	0.012
<i>Sellaphora pseudopupula</i>	SPPU	Core	0–2 cm	0.533	0.035
<i>Sellaphora ventraloconfusa</i>	SVTC	Core	0–2 cm	0.429	0.045
<i>Staurosirella neopinnata</i>	SPIN	Core	2–4 cm	0.492	0.042
<i>Humidophila perpusilla</i>	DGPE	Core	8–10 cm	0.667	0.010
<i>Encyonopsis subminuta</i>	ESUM	Core	8–10 cm	0.591	0.010
<i>Stauroforma exiguiiformis</i>	SEXG	Core	8–10 cm	0.552	0.025

**Table 5**

Ecological factors reconstructed from the customized SWAP and from the 25 high-mountain lakes of the Italian Alps databases.

	SWAP < 20 m&<30µScm <sup>-1</sup>			25_Ita.Alps				
	NO <sub>3</sub>	pH	Cond	Cond	pH	TP	NO <sub>3</sub>	NH <sub>4</sub>
	mg L <sup>-1</sup>	unit	µS cm <sup>-1</sup>	µS cm <sup>-1</sup>	unit	µg L <sup>-1</sup>	mg L <sup>-1</sup>	µg L <sup>-1</sup>
0–2 cm	1.91	7.8	26	22	7.0	10	0.64	31
2–4 cm	1.94	7.8	27	20	7.0	7	0.70	24
8–10 cm	1.34	7.7	20	31	6.9	18	0.59	87
20–22 cm	1.90	7.8	26	27	7.0	12	0.58	59

Mountains (Poland) by Sochuliaková et al. (2018). The authors observed that *F. nanana* appeared with increasing water temperatures but also with increasing nutrient concentrations related to high salmonid densities. In fact, *F. nanana* prefers nutrient enriched waters (Cantonati et al., 2019), and might thus be favored by a well-structured fish population with high densities (Griffiths 2006). In the same way, Sienkiewicz and Gašiorowski (2014) observed the substitution of former species with *F. nanana* after brook and brown trout introductions for recreational purposes. In a recent paleolimnological, multiproxy study of a high mountain lake in the Southern Carpathians (Romania) to uncover responses to climatic and human pressure over the past 500 years, Szabó et al. (2020) report the dominance of *Asterionella formosa*, *Fragilaria tenera*, *F. nanana*, *F. nanoides*, and *Discostella pseudostelligera*, as an indication of eutrophic conditions. The planktonic *F. nanana* is one of the most abundant taxa in the littoral samples of Lake Balma, and was observed only in the top section (0–2 cm). It is likely possible that the species colonized the lake after brook trout introduction (which occurred in the 1970 s), in response to increasing nutrient concentrations favored by the well-structured brook trout population, which nowadays shows high densities in Lake Balma (17.89 g m<sup>-2</sup>) (Pastorino et al., 2020). Moreover, when the availability of P and N for phytoplankton increases due to fish excretion (Carpenter et al., 1992; Schindler et al., 1993; Schaus et al., 1997), the abundances of planktonic species increase (St. Jacques et al., 2005), as observed in Lake Balma (Fig. 4a, b). Spitale et al. (2015) noted that several *Fragilaria* species are particularly competitive in waters with higher N:P ratio generated by relatively high nitrate values in oligotrophic waters, a situation found also in Lake Balma.



On the other hand, Michelutti et al. (2015) associated *Fragilaria nanana* and *Tabellaria flocculosa* (the latter also present only in the top sections 0–2 cm and 2–4 cm) to increasing water temperature in alpine lakes, and Catalan et al. (2002, 2009) report *F. nanana* as an indicator of increasing water temperatures in alpine environments. *T. flocculosa* is favored by higher water temperature values (Hobaek et al., 2012), which allow blooming events in relation to a prolonged growing season (Hallstan et al., 2013).

In the deep core sections (8–10 cm and 20–22 cm), the low-profile life-form is mainly related to the genus *Psammothidium*, including typical cold stenothermic species, inhabiting both lentic and lotic environments (e.g., Potapova, 2012; Enache et al., 2013; Kopalová et al., 2016; Blanco et al., 2017). *Psammothidium curtissimum* is a cryophilic species (e.g., Pienitz 2018), which was more abundant in the deep core samples than in the top sections but that is still present in modern Lake Balma. Decreasing abundances of *P. curtissimum* are generally related to increasing water temperatures.

The IndVal indicator species identified for the 8–10 cm core section are the mire species *Stauriforma exiguiformis* and *Encyonopsis subminuta*, and the aerial species *Humidophila perpusilla* (e.g., Cantonati et al., 2017). This might point to a lake affected by important water-level fluctuations and with relevant portions of the shores evolving into a mire.

Our results agree with Perilli et al. (2020), who studied modern and subfossil midge assemblages within Lake Balma in relation to fish introductions: variations in the chironomid community observed in Lake Balma reflect the increasing trend of water temperatures from the end of the 19th to the beginning of the 20th century due to global warming, in particular for the Alps (Beniston, 2006; Auer et al., 2007; Ilyashuk et al., 2011; 2019). Cold stenothermic chironomids (*Corynocera oliveri*, *Micropsectra*, *Heterotrissocladius marcidus* type) disappeared in the recent sediment samples while species well adapted to warmer temperatures and shallow habitats (*Zavreliomyia*) appeared; on the other hand, the chironomid *Zavreliomyia* could be related to an increase in the lake productivity, especially in the shallow zone, which could be strongly influenced by warm summers (Perilli et al. 2020).

#### 4.2. Modern diatom assemblages

No thermal stratification was observed in the water column due to shallow depth (max 6.4 m) of the lake. This points to Lake Balma as a system in which shallowness does not allow for strong vertical gradients relevant for the microphytobenthos (e.g., important light attenuation, hypolimnion with increased nutrient concentrations etc.; Cantonati et al., 2009) but still of sufficient depth and size to allow an introduced brook-trout population to persist with relatively high densities.

In large and/or sufficiently-deep lakes, the development of important vertical gradients causes littoral communities to reflect the conditions of the shores (e.g., nutrient status) rather than the whole-lake or open-water trophic situation (e.g., Spitale et al., 2011), and the in-depth study of littoral diatom assemblages needs to take into account depth-distribution features (e.g., Cantonati et al., 2009). In high-mountain lakes with important vertical structure, littoral algae are known to reflect well only the impact of fishes that forage in shoals along the shores (e.g., minnows, Gacia et al., 2018), or of typical benthivorous fishes that re-suspend sediments.

Due to shallowness combined with relatively large size (for a high-mountain lake), this is not the case for Lake Balma where littoral epilithic diatoms (as well as subfossil sediment-core diatoms) react to changes in whole-lake trophic status and metabolism, and to the impacts affecting them.

The modern diatom community was found to be species rich and to include also Red List species (Hofmann et al., 2018). *Humidophila schmassmannii* is considered to be relatively rare by Genkal and Yarushina (2017), and is typical of freshwater alpine oligotrophic environments (Fallu et al., 2000; Antoniadis et al., 2008). *Sellaphora*

*ventraloconifusa* is classified as “2 = strongly threatened”, “oligotrophic dystrophic” species by Hofmann et al. (2018), in agreement with Camburn and Charles (2000) who considered it as a typical high-mountain lake species related to low conductivity. *Stauriforma exiguiformis* is sensitive to higher concentrations of suspended organic matter and high nutrient concentrations (Peeters and Ector 2017), and is considered as “3 = threatened” by Hofmann et al. (2018).

The most abundant taxon in the littoral samples was *Pseudostaurisira brevistriata*, a cosmopolitan species which prefers environments with high silica concentrations and pH levels around 7 (Schmidt et al., 2004; Milan et al., 2015). Under these environmental settings, *P. brevistriata* can be very abundant, as also observed in Lake Balma. Moreover, *P. brevistriata* and *Staurisirella neopinnata* could be favored by ice presence and permanence, as observed by some authors (Douglas and Smol, 1999; Schmidt et al., 2004). *P. brevistriata* and *S. neopinnata* prefer slightly higher trophic conditions than those typically observed in alpine lakes (Cantonati et al., 2009). In particular, *P. brevistriata* is a high-profile species (Rimet and Bouchez 2012), which tolerates a certain degree of environmental variation. This fact could explain the increasing relative abundances observed in fall in Lake Balma. Brancelj et al. (2000) noted an obvious increase in *S. neopinnata* (reported as *Fragilaria pinnata* in the cited paper) in the uppermost section of a sediment core documenting the deleterious effects of fish introduction in a mountain lake.

Leira et al. (2015) used the sediment record of two high-mountain lakes in the Adamello-Brenta Nature Park (Italian southeastern Alps), used as reservoirs for hydroelectric power generation, to assess the influence of water-level fluctuations due to water exploitation on these ecosystems as reflected by diatom ecological and life-form groups. Of the two study lakes, one was fishless whilst the other had been illegally stocked with brook trout. There are striking analogies between species composition and life-form/ecological guild proportions between the Lake Balma modern littoral and upper core sections and the lake affected by fish introduction (in particular the abundant occurrence in the sediment record of the latter of *P. brevistriata*, *S. neopinnata* -reported as *S. pinnata* in the cited paper-, and *Staurisira venter*), and between Lake Balma deep core sections and the fishless lake.

*Achnanthis pseudolineare* and *A. minutissimum*, found in all the littoral sites, are often associated (Feret et al., 2017). *A. minutissimum* is considered to be the most widespread species in freshwater alpine systems (Van et al., 1994; Feret et al., 2017), and is a low-profile taxon (Rimet and Bouchez, 2012) which prefers good quality waters but tolerates a certain degree of pollution.

Sampling campaigns allowed to collect a high number of taxa in Lake Balma (81 taxa, 32 genera). As reported by Robinson et al. (2010), in high mountain environments, number and abundances of benthic diatom species increase with anthropogenic activities (grazing, fish introductions), due to colonization and development of taxa which tolerate increasing nutrient concentrations. In Lake Balma this is the case for *Encyonema minutum* and *Nitzschia palea* which are an oligo-β-mesotrophic (Hoffmann 1994) and a eutrophic (Van Dam et al., 1994) species, respectively. Moreover, the planktonic *Fragilaria nanana* is associated to increasing trophic conditions (Sienkiewicz and Gąsiorowski, 2014; Cantonati et al., 2019), and *Staurisira venter* could indicate mesotrophic-eutrophic conditions (Van Dam et al., 1994). The presence and abundance of high-profile species (especially in fall) observed in the Lake Balma could also be related to an alteration of the trophic condition. Feret et al. (2017) report that low-profile taxa are expected as dominant in oligotrophic alpine lakes placed on siliceous substrates, due to the low tolerance to nutrient enrichment. On the other hand, high-profile species can tolerate changes in trophic conditions (Berthon et al., 2011; Rimet and Bouchez, 2012). Our results indicate that slight alterations in the trophic level of Lake Balma might have occurred or are still occurring. The absence of *Eunotia exigua* (an acidification indicator) and the presence of *Frustulia crassinervia* (sensitive to decreasing pH) suggest that there is no ongoing acidification in Lake Balma (Cantonati



et al., 2011), as also confirmed by the diatom-inferred pH values that remained fairly stable over time (Table 5).

#### 4.3. Environmental change and fish introduction

The lake was subject to fish introduction for recreational fishing at the beginning of the 1970s, and first investigations regarding macrobenthic invertebrates allowed to detect changes in chironomid communities likely related to the effect of both fish introductions and climate change. The effect of increasing water temperatures on the organisms inhabiting high-altitude lakes can be worsened by direct anthropogenic impacts (Milardi et al., 2016), such as fish introduction (Raposeiro et al., 2017; Perilli et al., 2020), which represents one of the main threats (Vitousek et al., 1996; Brancelj et al., 2000; Mooney and Cleland, 2001; Raposeiro et al., 2017; Tiberti et al., 2019), in particular for highly restricted, susceptible, and vulnerable environments such as alpine lakes (Fritts and Rodda, 1998; Sax et al., 2002; Gurevitch and Padilla, 2004). Consequences of non-native fish introductions include cascading effects on the trophic webs and ecosystem functions (Tiberti et al., 2014; Sánchez-Hernández et al., 2015).

#### 5. Conclusions

Our study investigated modern-community and subfossil benthic diatom assemblages within a high-mountain lake in the Italian Alps (Lake Balma, Piedmont, Italy), in order to check for temporal variations due to direct and indirect anthropogenic impacts, with special attention to the hitherto often neglected non-native fish introductions and environmental change (especially global warming).

Our study of modern-littoral and subfossil sediment-core diatoms provided evidence that might be related the response of diatom assemblages to fish introduction, in particular the decreasing of the nutrient-enrichment sensitive low-profile guild and the increase in species known to react positively to the increased nutrient availability due to fish excretions (*Fragilaria nanana*, *Pseudostaurosira brevistriata*, *Staurosirella neopinnata*). We are, however, aware that some of these effects could as well be caused by pastures and cattle watering, and by increased temperatures due to global warming, and we acknowledge the typical complex-interaction pattern among different stressors (e.g., Tiberti et al., 2019). Our results agree with those reported in previous studies carried out in Lake Balma, and could be the basis for further efforts to elucidate interactions between global changes and anthropogenic impacts.

High-mountain lakes are an important component of the alpine system, and host low-diversity assemblages and poorly-structured trophic networks that respond rapidly to environmental changes and anthropogenic disturbances. However, high-mountain lakes are also shelter to rare and endangered (Red List) species. The notably high proportion (55%) of diatom species belonging to threat categories of the Red List that we found appears to be typical of high ecological-integrity springs and lake of the Alps (ca. 50% according to Cantonati et al., 2012). Therefore, it is of pivotal importance to improve the knowledge about these environments, especially in previously uninvestigated alpine lakes. Moreover, alpine lakes are “early warning systems” for the whole alpine system (MOLAR Water Chemistry Group, 1999; Perilli et al., 2020), and can contribute valuable information also on the interactions between environmental global changes and anthropogenic impacts. Benthic diatoms, in particular, can provide useful indications on the deleterious effects of non-native fish introduction, grazing, and global warming, and thus support an adaptive and sustainable management of high-mountain lakes for the sake of nature conservation.

#### CRedit authorship contribution statement

**Marco Cantonati:** Conceptualization, Methodology, Data curation, Validation, Writing - original draft, Writing - review & editing,

Resources, Visualization, Supervision. **Raffaella Zorza:** Methodology, Data curation, Validation, Writing - original draft, Resources, Supervision. **Marco Bertoli:** Conceptualization, Investigation, Methodology, Data curation, Formal analysis, Validation, Writing - original draft, Writing - review & editing, Visualization, Supervision. **Paolo Pastorino:** Conceptualization, Investigation, Methodology, Data curation, Validation, Writing - original draft, Visualization, Supervision. **Gianguido Salvi:** Methodology, Formal analysis, Validation, Resources, Visualization. **Giulia Platania:** Investigation, Methodology, Data curation, Writing - original draft, Visualization. **Marino Prearo:** Investigation, Methodology, Data curation, Writing - original draft, Project administration, Resources, Funding acquisition. **Elisabetta Pizzul:** Conceptualization, Investigation, Methodology, Data curation, Validation, Writing - original draft, Writing - review & editing, Project administration, Resources, Visualization, Supervision, Funding acquisition.

#### 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.

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#### Appendix A. Supplementary data

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