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Diatom assemblages in glacial-fed streams of Italian Western Alps

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Abstract

Glacier retreat in the Alps has been increasing in recent years, likely leading to the disappearance of most glaciers in coming decades. Glacier runoff affects river discharge and water physico-chemical parameters, creating specific environmental conditions for highly specialised organisms. We here investigated diatom communities in glacier-fed rivers of the Valle d'Aosta region (NW-Italy), analysing data collected between 2010 to 2019 for the WFD monitoring programs. The present paper provides a complete checklist of the species inhabiting this region, many of which are classified as endangered at different levels in the diatom Red List. We found significant differences between sites with different catchment glacier cover (CGC), in terms of taxonomic composition, ecological guilds and abundance of Red List taxa. In particular, we observed a significant increase in species richness with the decrease in CGC, as well as significant differences in terms of taxonomic composition in sites with different CGC. We highlighted the role of *Achnanthidium lineare* as an indicator species for streams with the highest glacial influence, together with *Hannaea arcus*, *Eucocconeis laevis* and other oligotrophic low profile species that are well adapted to physical stress induced by glacier runoff. On the other hand, streams with lower glacial influence were characterized by motile species mostly belonging to the genera *Navicula* and *Nitzschia*, due to the nutrient increase. The allochthonous invasive species *Didymosphenia geminata* was recorded in streams with marginal glacier cover; recently observed blooms indicate that conditions may become increasingly favorable for the spread of this species in Alpine environments, as glaciers retreat. The abundance of Red List diatoms increased significantly with increasing glacier cover suggesting that glacier-fed rivers are niches for the conservation of diatom biodiversity.

Keywords: diatom Red List, Valle d'Aosta, catchment glacier cover, climate change, mountain rivers, Bacillariophyceae

Introduction

Glacier retreat is now an established and globally recognised phenomenon (Zemp et al., 2019) with significant consequences on alpine rivers and the communities they host (Schneider et al., 2013; Daufresne & Boet, 2007). In their paper, Zekollari et al. (2019) projected a potential global ice mass loss by 2100 ranging from about 50 to 95% under different emission scenarios outlined by Meinshausen et al. (2011), RCP2.6 and RCP8.5, respectively. This phenomenon also affects the Alps, where glacier retreat has been increasing in recent years likely leading to the disappearance of most glaciers in the coming decades (Leclercq et al., 2014; Zemp et al., 2006). Glacier loss in the Alps involves ecological and environmental issues, such as biodiversity loss (Stibal et al., 2020), alteration of the hydrogeological cycle (Laurent et al., 2020) and increased geological hazards (Deline et al., 2021; Giardino et al., 2017), as well as socio-economic issues related to hydropower generation (Puspitarini et al., 2020) and tourism (Fischer et al., 2011).

Glaciers can play an important role in river discharge (Huss & Hock, 2018; Brunner et al., 2019). Glacial runoff causes physical and chemical changes in downstream waters, affecting parameters such as temperature, conductivity, turbidity, suspended solids, organic matter and nutrients (Brahney et al., 2021). Summer and seasonal mean discharge of glacially fed rivers has significantly increased in recent decades as a direct result of ice melt (Laurent et al., 2020). The coming decades are expected to be characterised by a marked decrease in summer discharge (about 50% under RCP8.5), while winter discharge is expected to double, due to an increasing ratio of rainfall to snowfall (Hanzer et al., 2018). As noted above, these shifts have significant downstream impacts on water quantity and quality (Laurent et al., 2020; Brahney et al., 2021; Robinson et al., 2016), but consequences on streams and biological communities are still poorly known. In this study, we investigated diatom communities in glacier-fed rivers of the Valle d'Aosta region (NW-Italy), analysing data sampled from 2010 to 2019.Valle d'Aosta glaciers are severely affected by global warming: in the last twenty years 32 glaciers disappeared, 22% of the glacier area has been lost and in 2022 the monitored glacier fronts retreated by an average of 46 metres (Diolaiuti et al., 2012; Cremonese, 2021; CRGV, 2023). The glacier runoff "peak water" has already occurred in this region, presumably in the last decades, and this has led to increased water scarcity in summer, which will be ever more pronounced in the coming years (Cremonese, 2021).

Among aquatic organisms, the ability of diatom communities to strictly respond to physico-chemical conditions makes them interesting for studying the impact of glacial retreat in glacial-fed rivers, which are affected by glacier retreat (Laurent et al., 2020; Brahney et al., 2021). Indeed, benthic diatoms are microalgae with excellent sensitivity to chemical parameters and physical disturbance (such as fluctuations in flow rate and suspended solids), making them an internationally adopted tool for assessing the river ecological status (Lobo et al., 2016; Passy, 2007). Benthic diatoms are crucial in alpine environments and above the tree line, as they are the main primary producers for the aquatic ecosystem, which receives minimal supply from the riparian vegetation (Battin et al. 2016; Zah & Uehlinger, 2001). Studies on diatoms of glacial-fed rivers are still scarce but have shown highly selected diatom communities near the glacier mouths, characterized by low diversity and seasonal community shifts (Cantonati et al., 2001; Gesierich & Rott, 2012; Fell et al., 2018; Bona et al., 2012). In this context, Brahney et al. (2021) showed how the alteration of glacial runoff can lead to a pronounced change of physico-chemical conditions favoring the reassembly of diatom communities and the blooming of the allochthonous invasive species *Didymosphenia geminata*. In general, these studies have focused on small area and communities living in a single or few rivers.

The present research aimed at analysing the diatom flora inhabiting 24 glacier-fed rivers flowing in the Valle d'Aosta region, over a basin area of 3000 km^2 with a special focus on species classified as endangered at different levels by the diatom Red List (Hofmann et al., 2018). Diatom communities were analysed from both taxonomical and functional point of views in relation to the catchment glacier cover and associated physico-chemical parameters, in order to assess the influence of glacier presence, at different extent, on diatom communities. Our results will be useful to better understand how diatom communities might evolve in the coming decades as glaciers continue to retreat.

Materials and methods

Study area

This study was conducted over the entire Valle d'Aosta region, in the western Italian Alps, using data coming from the monitoring network of the Italian Environmental Protection Agency (hereinafter ARPA) of Valle d'Aosta, composed of 24 glacier-fed streams and 174 sampling sites ranging from 400 m to 2280 m a.s.l. Valle d'Aosta is the region with the most extensive glacier cover in Italy; according to the GRGV inventories (www.catastoghiacciai.partout.it/ghiacciai), in 2020 the regional territory hosted 184 glaciers with a cumulative area of 120 km^2, which represents 36% of the whole Italian glacier area. The glaciers have an average altitude of nearly 3000 m a.s.l., ranging from 1400 m a.s.l. to 4800 m a.s.l. The largest glaciers are located in the Monte Rosa, Gran Paradiso and Mont Blanc massifs, areas of great importance for nature conservation (e.g. Gran Paradiso National Park) and alpine tourism.

Catchment glacier cover

To characterise the glacial run-off influence of each sampling site, catchment glacier cover (hereinafter, CGC) was calculated with QGIS as the percentage of the subtended catchment area covered by glacier, considering 2019 data (Regione Valle d'Aosta, 2019). The CGC index has been used in several works studying the glacial influence in rivers (e.g. Fell et al., 2018; Becquet et al., 2022). In the present study, the sampling sites covered the CGC range 0.4 – 51.1%, with the highest values found in the Valle di Gressoney, Val d'Ayas (Monte Rosa massif) and Val Ferret (Mont Blanc massif), and the lowest near the stream's confluence with the Dora Baltea river. Sampling points were then divided into 4 glaciological classes according to CGC values: GH1 > 11.5%, GH2 6.2 – 11.5%, GH3 4.5 – 6.2%, GH4 < 4.5% (Fig. 1). The thresholds used for class division are the first quartile, median and third quartile values, respectively, in order to have a good representative sample size for each class (GH1 = 107, GH2 = 102, GH3 = 114, GH4 = 102). GH1 sites have the maximum glacial influence, while GH4 samples have the lowest glacial influence.

Water quality data

Water samples for the physical and chemical analyses were collected together with diatom samples and analysed by ARPA Valle d'Aosta. In each sampling sites, the chemical and physical parameters required by the WFD, namely nitrate nitrogen ("$N\text{-}NO_3$"), Biological Oxygen Demand ("BOD_5"), total phosphorous ("TP"), conductivity ("EC"), percent dissolved oxygen ("%DO") and water temperature ("T"), were measured following Italian Standard method (APAT IRSA-CNR 29/2003).

Diatom sampling and identification

Epilithic diatoms were collected by ARPA Valle d'Aosta in the framework of the Water Framework Directive monitoring programs, from 2010 to 2019. 24 glacier- fed rivers and 174 sampling site were considered, for a total of 425 diatom samples. During the studied period, some sites were visited once (4) or twice (23), while the remaining 147 were visited at least three times. According to the European standard UNI EN 13946: 2014, in each reach five cobbles were chosen from the main flow and periphyton was collected by scraping their upper surface with a hard brush. Samples were then fixed with ethanol (70%) and transported to the laboratory, where they were treated with H_2O_2 (30%) and HCl. Permanent slides for the light microscope analysis were mounted using Naphrax®. Diatom identification and counting followed European Standard UNI EN 14407:2014. In all samples, a minimum of 400 valves were identified at species level and counted. Identification was based on several diatom floras and monographies (see Falasco et al., 2021), as well as recent taxonomic papers.

Diatom database preparation

For the biological data, the implementation of the database entailed a taxonomic alignment and update based on the most up-to-date sources, which was necessary since the systematic classification of diatoms has been constantly updated over the studied period. Diatom counts were then uploaded into Omnidia 6.1 (Leiconte et al., 1993) by which Shannon Index, richness (number of species), and diatom indices IPS (CEMAGREF, 1982), TI (Rott et al., 1999), ICMi (Mancini & Sollazzo, 2009; Kelly et al., 2009) were calculated. We computed the relative abundance of ecological guilds (namely low profile, high profile, motile, planktonic), based on the classification proposed by Passy (2007) and Rimet and Bouchez (2012). Each taxon identified was classified according to the German Red List for diatoms (Hofmann et al., 2018) which includes ten categories: "Extinct", "Threatened with extinction", "Strongly threatened", "Threatened", "Threat of unknown extent", "Extremely rare", "On the way to be threatened", "Data insufficient", "Not threatened" and "Not included in the list". For the statistical analyses, taking into account the significance of the categories for conservation and considering that the percentages in some of them were very low, we summed up the categories "strongly threatened", "threatened" and "on the way to be threatened" thus obtaining a unique "Sum of threatened" category. In our database, we did not find species classified as "extinct", "threatened with extinction", "extremely rare" and "Not included in the list".

Data analysis

To assess the possible influence of the glacier presence on diatoms, we considered indices and taxonomic composition. Possible differences in Shannon diversity index, richness, ecological guilds, Red list categories and diatom indices (IPS, Rott TI and ICMi) among the different CGC classes (i.e. GH1, GH2, GH3 and GH4) were tested with an analysis of variance (One-Way ANOVA) followed by Tukey's post-hoc test (or Mann-Whitney followed by Bonferroni correction if ANOVA assumptions were not met). To visually detect possible differences in terms of taxonomic composition among diatom samples collected in different CGC sites, we performed a Principal Coordinate Analysis (PCoA) basing on Bray-Curtis distance through PAST 4.12 software (Hammer et al., 2001). Possible statistically significant dissimilarities in taxonomical matrices of diatoms collected in different glaciological classes were tested through a One-Way PERMANOVA (Anderson, 2001). In R environment, we created a stacked chart of diatoms relative abundances using the function "geom_bar" in the package ggplot2 (Wickham, 2011). To check whether certain species were indicators of one particular glaciological class, we performed the Indicator Species Analysis (Dufrêne & Legendre 1997) with the function "multipatt" in the package indicspecies (Caceres & Legendre 2009).

Results

Environmental characterisation of glacial-fed streams

Concerning physical and chemical parameters, the low concentrations of nutrients and organic load, together with the high dissolved oxygen, indicate on average high-water quality in the whole study area. In detail, within the four glaciological classes, we observed differences in terms of environmental conditions, especially between the most upstream sites (belonging to GH1 and GH2) and the downstream sites (belonging to GH3 and GH4) (Fig. 2, Table I Supplementary material). Classes with the greatest glacial influence were characterized by lower nutrient concentrations (especially $N\text{-}NO_3$), lower temperatures, higher dissolved oxygen and increased suspended solids. In addition, GH1 differed from the other classes by a lower concentration of organic matter (BOD_5 median value = 1.0 mg/l) and lower conductivity (EC median value = 171 µS/cm).

Diatom assemblages and taxon biodiversity

The taxonomic richness of diatoms and Shannon diversity index increased with decreasing glacial influence, with significant differences between sites with major glacier runoff (GH1-GH2) and downstream sites (GH3-GH4) (Fig. 3). A total of 196 species from 63 genera were identified, with the lowest taxonomic richness recorded from a site belonging to GH1 (4 species) and the highest from a site classified as GH3 (34 species). A complete checklist of the identified diatom taxa is given in Table II (Supplementary materials).

In the whole studied area, the most abundant diatom species belong to the genus *Achnanthidium*: the species complex formed by *Achnanthidium pyrenaicum* and A*chnanthidium lineare*, with an average diatom presence of 26% per sample, was found in more than 95% of the samples. *Achnanthidium minutissimum* (Fig. 62) was present in more than 70% of the samples with a sample mean of 6%. Another common genus was *Encyonema*, present in about 85% of the samples, represented by the species *Encyonema silesiacum* and *Encyonema minutum* (7 and 4% sample average, respectively). Other frequent (> 50% samples) taxa were *Gomphonema elegantissimum* (65%*), Hannaea arcus* (62%), *Fragilaria vaucheriae (54%), Diatoma ehrenbergii* (52%) and *Reimeria sinuata* (51%), which together represented in mean 9% of the samples. Twelve taxa occurred between 50 and 20% of the samples, of which the most abundant species were *Nitzschia fonticola*, *Cocconeis lineata*, *Cocconeis euglypta* and *Gomphonella olivacea,* together representing in mean 6% of the diatom samples. The remaining diatoms belonged to almost 200 species, each contributing on average less than 0.5% to the diatom communities.

In terms of taxonomic composition, the PCoA analysis (Fig. 4) revealed the partial overlap of the four glaciological classes showing small difference according to Coordinate 2 (10.4% variance). Most of the explained variance in the ordination (21.5%) was explained by Coordinate 1, which from our results can be considered as a proxy for CGC. The One-way PERMANOVA confirmed significant differences in terms of taxonomic composition between each class (F= 17.33; *p-value* < 0.001) except between GH3-GH4 pair.

To better understand the differences among glaciological classes, we analysed the diatom assemblages. The relative abundances of diatom species are shown in Figure 5. *Achnanthidium* emerged as the most abundant genus, dominant in almost all samples. From GH1 to GH4 we found a turnover between *A. lineare*, the dominant species at higher CGC sites, and *A. pyrenaicum*, dominant in lower CGC classes, whereas *A. minutissimum* abundance did not seem to be influenced by the distance from the glacier. Quite rare *Achanthidium* species, such as *Achnanthidium cf. gracillimum* and *A. affine*, also characterised the GH1 class. *Encyonema* species (i.e. *E. minutum* and *E. silesiacum*) were the main co-dominant in all the glaciological classes. *Hannaea arcus*, abundant in GH1 class, decreased with CGC, until almost disappearing in GH4; *G. elegantissimum* and *N. fonticola* showed the opposite trend, becoming more abundant in lower CGC classes, characterised also by the presence of *Cocconeis* species (*C. euglypta* and *C. lineata*). The genus *Diatoma* was also found throughout the entire CGC gradient: *D. ehrenbergii* was constant in the different classes, while in the GH2 class there was an increase of *D. moniliformis* relative abundance.

Indicator species analysis (ISA; Table 1) highlighted *A. lineare* (Fig. 27 – 52, 60) as the main indicator species for sites with higher glacier cover (GH1 and GH2). *Hannaea arcus*, *Gomphonema tergestinum* and *A. affine* were among the indicator species that significantly characterized sites with the highest glacial influence (GH1). *Achnanthidium* species remain dominant also in GH3 and GH4 sites, although we noticed an increase of epiphytic (*Cocconeis spp.*) and mesotrophic species belonging to the genera *Navicula* (e.g. *N. cryptotenella*, *N. tripunctata*) and *Nitzschia (e.g. N. inconspicua, N. fonticola)*, which are indicator species for these sites. The presence of eutrophic species such as *Mayamaea permitis* and *Fistulifera saprophila* characterize GH4 sites while *D. geminata* (Fig. 63) resulted an indicator species for GH3 class.

Diatom communities structure, in terms of ecological guilds, showed some significant differences along the CGC gradient (Fig. 6). Low profile group (represented mainly by the genera *Achnanthidium*, *Hannaea* and *Fragilaria*) dominated in all sites; high profile species were stable and co-dominant in all sites while the motile group (mainly *Navicula* and *Nitzschia* species) was almost absent in GH1 and slightly replaced low profile species toward GH4 sampling sites.

The abundance of Red List diatoms increased significantly with reducing glacier cover (Fig. 7). Most of the endangered species were classified as "Threat of unknown extent" while "Strongly threatened", "Threatened" and "On the way to be threatened" diatoms are a tiny part. We found five "Strongly threatened" species, of which *Achnanthidium cf. gracillimum* was the most common one, sampled 8 times, with a peak of maximum relative abundance of 99% in one sample belonging to the GH1 class. Eleven "Threatened" species were counted: *Cymbella excisiformis* (Fig. 53 – 57) was the major representative species, sampled 66 times (15% of the samplings), 45 between GH1 and GH2 classes, and a maximum relative abundance of 20% recorded in GH1 class. *Fragilaria amphicephaloides* ("Threatened") was also present in eleven samples, reaching 14% of the community in GH1. Among the fifteen "Threat of unknown extent" recorded taxa, the most abundant was *A. lineare*, present in 95% of the samples and very common in all the glaciological classes. Belonging also to this Red List class, we found *Fragilaria austriaca* mostly collected in GH1 and GH3 classes. The class "On the way to be threatened" was the most abundant after the "Threat of unknown extent" and accounted for fourteen species: *H. arcus* and *Gomphonema calcifuga* were the most abundant. The first one was found in 60% of the samples, with a decrease of occurrence according to the distance from glacier (i.e. 93 records in GH1 vs 43 in GH4). *Gomphonema calcifuga* (Fig. 9 – 19) was sampled 21 times, exclusively in GH1 (15) and GH2 (6) sampling sites, reaching 24% of the diatom communities in GH1 class. Additionally, 141 "Not threatened" and twenty "Data insufficient" species were found.

Diatom indices (IPS, Rott TI and ICMi) are represented in Figure 8. As expected, water quality decreased with CGC, highlighting the increasing human presence downstream, although significant differences were only detected between classes GH1 and GH4. IPS values highlighted high quality status in all the monitored sites, while TI scores were for the most part belonging to the mesotrophic class. Sites belonging to the GH1 ranged from the ultra- to the meso-eutrophic quality classes while GH4 mainly described eutrophic conditions. ICMi revealed a decrease in quality status from "high" to "good" as we move towards lower CGC sites.

Discussion

This is the first research aiming at studying the benthic diatom flora inhabiting glacier-fed streams in NW-Italy. Through this study, we were able to provide a complete checklist of the species colonizing the glacier-fed streams of the Valle d'Aosta, many of which resulted classified as endangered at different levels by the most recent diatom Red List (Hofmann et al., 2018).

Environmental parameters

From the physico-chemical point of view, our results revealed disparities among rivers influenced by glacier cover at different extent. Indeed, the most notable differences can be seen in the downstream escalation of nutrients (N-NO_3 and TP) and organic matter, resulting in a slight reduction in dissolved oxygen percentage, attributable to heightened anthropogenic activities characterizing the GH4 downstream section. Conversely, the more glacially-influenced classes (i.e. GH1 and GH2) featured a greater total suspended solids load, originating from the melting of glacial masses (Slemmons et al., 2013; Geilhausen et al., 2013), and lower mean annual water temperatures. These results are in accordance with both the expected results and the indications in the literature (Brown, 2002; Milner et al., 2009; Robinson et al., 2016).

Diatoms diversity and richness

The increase in benthic diatom richness was significant as catchment glacier cover decreases. This observation is supported by earlier studies that focused on sampling distance from glacier margins in the Canadian Rockies (Gesierich & Rott, 2012), and on CGC evaluation in the Alps (Fell et al., 2018; Rott et al., 2006). Also Shannon diversity index significantly decreased from GH1 to GH4 CGC. This is easily explainable, since sites characterized by a high percentage of catchment glacier cover exhibit harsh physico-chemical conditions that have been identified as the responsible of a general decrease of richness and diversity in diatom communities (Fell et al., 2018; Thies et al, 2013), as well as other benthic organisms, such as macroinvertebrates (Jacobsen et al. 2014; Becquet et al. 2022). Our results confirm the conceptual model of lotic biomass and biodiversity as a function of glacial influence proposed by Milner and Petts (1994): harsh conditions of glacial streams (i.e. channel instability, low water temperature and high turbidity) limit the presence of benthic organisms as both biomass and diversity.

Diatom assemblages

Diatom community taxonomical composition differed significantly in the four CGC categories. *Achnanthidium* was by far the most common genus in all sites, with the three dominant species, *A. lineare, A. pyrenaicum*, and *A. minutissimum*. The high abundance of oligotrophic, rheobiontic, cold-adapted *Achnanthidium* spp. within mountains catchments was documented by previous research in the Alps (Gesierich & Rott, 2004), Himalaya (Cantonati et al., 2001), and North America (Gesierich & Rott, 2012). In various studies examining diatoms in biofilm near glacier mouths and high-altitude streams, *A. minutissimum* is described as a generalist dominant taxa in all mountainous areas of the planet (Thies et al., 2013; Fell et al., 2018; Cantonati et al., 2001; Gesierich & Rott, 2012; Rott et al., 2006). Its tolerance towards physical stress, as well as its pioneer character (Cantonati et al., 2001), explains this phenomenon. Our research confirms the widespread distribution of *A. minutissimum* in high-altitude streams and its generalist behavior. However, *A. minutissimum* still represent a species complex, difficult to be studied due to the small dimensions and the high intraspecific morphological variation characterizing the valves of this species. This still uncertain taxonomic identity is reflected in the broad ecological niche characterizing the species. Our study, also pointed out the role of *A. lineare* as indicator species for streams with the highest glacial influence. *Achnanthidium lineare* is an oligotrophic species (Van de Vijver et al., 2011); in literature, only one study (Fell et al.,2018) described this species as a glacier-fed stream specialist with high CGC. However, Falasco & Bona (2011) and Cantonati et al. (2012) found it in the Italian Alps, in sites characterized by high water velocity, even though not linked to glaciers. A recent work carried out by Bona et al. (2023) in the Gran Paradiso National Park showed a positive trend for *A. lineare* growth from 2005 to 2020 in Valle d'Aosta. *Achnanthidium lineare* is more sensitive to anthropogenic pressures (especially nutrient concentrations) compared to *A. minutissimum*, which however is common in mountain and mid-altitude streams with a wide tolerance range to water pollution and physical alterations (Brighenti et al., 2019). *A. pyrenaicum* also characterized the studied assemblages. This species is more sensitive to organic contamination, metals, and other pollutants than *A. minutissimum* (Cantonati et al., 2014). The different sensitivity of these three taxa could explain the shift from *A. lineare* being abundant upstream to *A. pyrenaicum* being dominant downstream and the generalist behavoiur showed by *A. minutissimum*.

Other indicator species for GH1 and GH2 classes, such as *H. arcus*, *E. minutum*, *G. calcifuga*, *Meridion circulare* were documented as typical flora of European (Cantonati et al., 2001; Rott et al., 2006), Himalaya (Cantonati et al., 2001) and North America (Gesierich & Rott, 2012) glacial stream. *H. arcus* was described as a resilient species, with a strong attachment to benthic substrates, able of withstanding high flow velocities and shear stress (Hieber et al., 2001). *Gomphonema* species (*G. tergestinum*, *G. olivaceoides* and *G. cymbelliclinum*), *A. affine* and *Eucocconeis laevis*, indicators for the highest CGC sites, are among the most sensitive diatom species collected in our study. Previously, Bona et al. (2008) identified *E. laevis* and *G. olivaceoides* (Fig. 20 – 26) in Valle d'Aosta, finding them as present in hydromorphologically disturbed sites influenced by human-induced physical alterations involving banks, riverbed substrate, and flow types. This highlights the suitability of these species for high glacial-influenced streams characterized by significant hydromorphological disturbance. GH1 glaciological classes is characterized by the presence of *Cymbella subhelvetica, Odontidium neomaximum* and *Fragilaria alpestris. Cymbella subhelvetica* is an oligotrophic species typical of high mountains lakes, springs and waterfalls in the temperate zone (Krammer, 2002; Le Cohu & Azémar, 2011). *Odontidium neomaximum* (Fig. 61) has been found in the European Alps in oligotrophic springs, lakes and rivers under a wide range of conductivities and calcium concentrations (Jüttner et al. 2015). The ecological data for *F. alpestris* is limited due to the challenges in its identification; however, from the analysis of the lectotype slide, the dominant species are indicators for good water quality, colonizing bryophyte vegetation and moistened rocks, a very common habitat in turbulent contexts near the glaciers mouth (Van De Vijver et al., 2020). *Nitzschia dissipata*, the only indicator species for GH2 glaciological class, was described by Cantonati & Spitale (2009) as a typical species colonizing bryophytes in streams of the Dolomiti Bellunesi. The indicator species for GH3 and GH4 classes are oligo-mesotrophic to eutrophic species, and this is attributed to an increase in anthropogenic pressure, resulting in a higher nutrient concentration. *Nitzschia fonticola, N. cryptotenella, Nitzschia archibaldii* and *N. tripunctata* are among the oligo-mesotrophic species

(Carayon et al. 2019), while *N. inconspicua*, *Cocconeis pediculus*, *M. permitis*, *F. saprophila* and N*avicula gregaria* are among the most tolerant species, adapted to impacted sites (Carayon et al., 2019; Jüttner et al., 2003; Cimarelli et al., 2015). All these changes in terms of taxonomic composition among CGC classes, were reflected in diatom indices, which showed a decrease in water quality status in the downstream sections.

Ecological guilds

Due to their resistance to elevated flow velocities, abrasion, and shear stress, low-profile diatoms (e.g. *Achnanthidium, Fragilaria, Hannaeae*) stand out as the most abundant guild in all the GH classes. This dominance is attributed to the selection favoring diatoms with streamlined forms, low motility, and strong attachment to benthic substrates which allow to overcome the shear stress induced by ice melting, hindering the high-profile diatoms development (Hieber et al., 2001, Bona et al., 2012; Wellnitz & Rader, 2003). The main differences in terms of ecological guilds between GH1-GH4 classes are among the motile guild. As explained by Passy (2007) and Rimet and Bouchez (2012), the motile guild includes species capable of free movement, exhibiting tolerance to high nutrient concentrations and low resistance to flow velocity (e.g. *Navicula, Nitzschia, Mayamaea*). The adaptability of motile groups to thrive and reproduce in impacted environments explains their predominance over other guilds toward sampling points characterized by heightened nutrient concentrations and, supposedly, lower flow velocity, particularly at GH4. This resistance to pollution is associated with the capacity of motile diatoms to optimize their position within the biofilm, thus avoiding disturbances (Lengyel et al., 2015).

Taxa of special interest

Forty-five taxa were defined on the Red List as “strongly threatened”, “threatened”, “Threat of unknown extent” and “on the way to be threatened” (Lange-Bertalot & Steindorf, 1996). The abundance of Red List diatoms increased significantly with reducing glacier cover, suggesting that Valle d’Aosta high altitude glacier-fed streams may act as a refuge for these species. This is linkable to the hydrochemistry and physical conditions present near the glaciers mouth which allow to host endangered oligotrophic and cold stenothermal species, as documented for Austrian Alps (Fell et al., 2018) and North America (Gesierich & Rott, 2012) but probably also because these environments have received limited research attention and these species appear as rare.

Achnanthidium cf. gracillimum and *C. excisiformis* were the most abundant species in “Strongly threatened” and “Threatened” classes, respectively. The real taxonomic identity of the *A.* cf. *gracillimum* found in the present paper is still uncertain, since this taxon morphologically does not perfectly fit into the criteria established to identify *Achnanthidium gracillimum* s.s. as illustrated and described in Jüttner et al. (2023) through the analysis of the type material. However, considering the spread of *A. cf gracillimum* in the whole investigated area, a deeper taxonomic analysis of this taxon will be necessary in future. *C. excisiformis* is widespread in the Nordic and Alpine region (Krammer, 2002) and it has been found in sites presenting high levels of pH, conductivity, dissolved oxygen, turbidity, nitrates, calcium and hardness (Falasco et al., 2012).

The observed trend in the red list abundance between GH1 and GH4 was primarily influenced by *A. lineare*, classified under the "Threat of unknown extent" category. This species is widely distributed throughout the entire Mediterranean basin, demonstrating a widespread presence in oligotrophic waters, not specific to glacier-related areas. For many years, *A. lineare* was included in the *A. minutissimum* s.l. complex, until in 2011, the analysis of the type material revealed the morphometric and morphological taxonomic features useful to separate these two taxa. For these reasons, further analyses of previous data are essential to gain a comprehensive understanding of its real distribution area and to better define its conservation status level. The large part of threatened species belongs to "Threat of unknown extent" and "On the way to be threatened" classes, underlying how much study these species need. Climate and glacier evolution could threaten or benefit these species.

Contrary to endangered species, glacier retreat may favor the habitat expansion for non-native species, colonizing river sites not affected by glacier cover, as observed for macroinvertebrate communities (Brown et al., 2007; Cauvy-Fraunié et al., 2015). Native to high latitude North American streams and known to frequent coldwater streams (Kilroy, 2004), *D. geminata* has seen a huge increase in the number of colonies in Europe acting like an allochthonous invasive species in many river network (Blanco & Ector, 2009). While this increase is commonly attributed to global warming, the specific cause of its expansion remains unclear, as noted by Taylor & Bothwell (2014). Field surveys in North and South America have shown that low phosphorus concentrations are among the environmental factors that favor the establishment of *D. geminata* blooms, together with ample light conditions (Kilroy & Bothwell, 2011; James et al., 2014). In high altitude montane streams under current climate warming, the documented declines in turbidity and subsequent increases in light penetration, coupled with lower levels of total phosphorus (TP), create conditions favorable to the formation of *D. geminata* colonies (Brahney et al., 2020). In this study *D. geminata* resulted present in GH3 class, as an indicator species, in agreement with Brahney et al. (2021) who showed that colony development primarily occurred in streams with marginal (2–5%) to no glacier cover. The glacier recession which is occurring in Valle d'Aosta could cause huge modifications in water quality characteristics in the future, facilitating *D. geminata* bloom formation at higher altitudes, as proposed by Brahney et al. (2020) for Canada glacier-fed streams. ARPA Valle d'Aosta (2022) recently discovered the first significant macroscopic bloom in the region in the Lys stream, specifically in two sampling points which were also examined in our study and classified as GH1 and GH2. This finding aligns with our hypothesis that, over time, with the ongoing recession of glaciers, favorable conditions for blooms may emerge at increasingly higher altitudes.

Conclusions

Overall this study has demonstrated the relation between alpine benthic diatom biodiversity and catchment glacier cover, describing glacial-fed streams as threatened diatoms niche. Glacier reduction is expected to continue in the European Alps throughout the 21st century (Leclercq et al., 2014; Zemp et al., 2006) and future changes in Alpine diatom communities should be considered. This community alteration could imply cascading effects for the higher trophic levels (Clitherow et al., 2013), given their role in the trophic networks of Alpine streams as the main primary producers (Battin et al., 2016).

In conclusion, this study sheds light on the influence of glaciers on diatom communities in glacier-fed streams. Future studies should focus on how quickly pioneer diatoms can colonise recently formed streams in areas of glacier retreat, and how the diatom community will adapt to the new scenario, which implies a change in the hydrological regime, with a possible increase in allochthonous diatom proliferation.

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Data availability statement

The data that support the findings of this study are openly available at ZENODO at https://doi.org/10.5281/zenodo.1089013.

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	Indicator species analysis		
	***	**	*
GH1	HARC, GTER, EULA, GCFU, GCBC	ACAF, MCIR, FALP, CSBH, GLOV	FSBH, GPDC, DTEN, ONMA, SVTL, ECPM
GH2	/	NDIS	/
GH3	/	DICG	DGEM, NPAD, CLCT
GH4	NINC, NCTE, COPL	NIAR, MPMI	NFOT, DVUL, GELG, FSAP
GH1 + GH2	ACLI, ENMI, GOLD	/	/

GH3 + GH4	NFON, NTPT, CLNT, CPED, NGRE, CEUG, RABB, APED	/	/

Table 1 - List of indicator species for different glaciological classes resituited by ISA (*** p-value < 0.001, ** p-value < 0.01, * p-value < 0.05).