Increasing periphyton biomass and cyanobacteria in alpine streams with retreating glaciers

Georg Niedrist[1], Maria Chiara Vulcano[1], Martin Kainz[2], and Leopold Füreder[1]

[1]Universität Innsbruck
[2]WasserCluster Lunz

October 17, 2023

Abstract

Deglaciation in mountain catchments changes water source contributions and associated habitat conditions in usually cold and dynamic mountain rivers. Although recent research has listed consequences of glacier retreat for aquatic biodiversity, specific invertebrate and algal groups, quantitative effects on the aquatic food web structure remain poorly understood. In this study we assessed abiotic habitat conditions together with the composition and the biomass of periphyton in 5 catchments in the Central European Alps over the snow-free period and reveal significant links to declining glacier cover. We found that reduced glaciation leads to decreasing sediment concentrations and also to lower runoff, which in combination affects the stability of benthic habitats. The reduced sediment load of the rivers dominates the consequences of glacial retreat in subsequent river habitats more than the decreasing nutrient supply. Periphyton biomass in glacier-fed rivers is expected to increase with ongoing deglaciation and warming, which subsequently favors particularly diatoms and cyanobacteria. This work thus illustrates clear links between decreasing glacier cover and the identity and relevance of aquatic producers in alpine river catchments, and provides evidence for shifting resource base in terms of biomass with potential consequences for its nutritional quality.

Introduction

Accelerated glacier retreat in alpine regions and the European Alps is reducing melt-water contributions to mountain rivers and is ultimately changing the habitat conditions for aquatic life in these high-altitude waters. The retreat of glaciers is linked to a reduced hydrological variability, a decrease in sediment load, or altered water chemistry (Milner *et al.* , 2017), but also rising water temperatures (Niedrist, 2023). Based on their preferences and traits, invertebrates seem to be differently prepared to such climate change effects (Niedrist & Füreder, 2023). While overall changes of specialized glacier-fed river communities (i.e., their community structure) and effects of glacier retreat on freshwater biodiversity are well studied (Jacobsen *et al.* , 2012; Füreder, 2012; Hotaling *et al.* , 2017; Cauvy-Fraunié & Dangles, 2019), the quantitative response of different biotic components is still poorly understood. In addition, effects of habitat ameliorations on population structures, as observed in other extreme ecosystems (Baum *et al.* , 2005; Bærum *et al.* , 2021), have not been examined yet.

Periphyton, or benthic biofilm, is the dominant food source for invertebrates in alpine streams (Niedrist & Füreder, 2017) and allochthonous input plays a minor role above the tree line (Vannote *et al.* , 1980). Given the dependency of first invertebrate consumers upon sufficient basal production, the dietary availability and quantity of periphyton may regulate grazing invertebrate abundance with subsequent cascading effects on predatory insects and cold-water fish populations in stream food webs. While the occurrence of diatoms, or chrysophytes in mountain and alpine streams (Hieber *et al.* , 2001; Rott *et al.* , 2006; Uehlinger *et al.* , 2010) and their response to deglaciation (Rott *et al.* , 2006; Fell *et al.* , 2018), but also the detailed composition of biofilms in glacier-fed streams (Brandani *et al.* , 2022), has been studied thoroughly, quantitative effects have not yet been estimated and consequences of glacier retreat on periphyton availability remain thus difficult to predict.

Different algal and bacterial groups that form periphyton (e.g., diatoms, green algae, brown algae, cyanobacteria) contain distinct lipids and fatty acids (i.e., highly nutritious polyunsaturated fatty acids) at different levels (Galloway & Winder, 2015; Twining *et al.* , 2016) that are highly nutritional and required by invertebrate grazers, so that the nutritional status of periphyton is largely linked to its lipid composition. Since deglaciation leads to tremendous abiotic habitat changes (Milner et al. 2017) and shifting niches for algal and bacterial groups (Uehlinger *et al.* , 2010), changes in periphyton biomass and lipid composition, thus in the provision of dietary nutrients are expected.

In this study we quantify and characterize benthic periphyton in mountain streams that drain glaciated catchments in the eastern European Alps. These high-altitude catchments vary in the extent of glaciation and form a gradient of catchment ice cover that served as a proxy for different stages of glacier retreat for this study.

The aim of this field study was to; a) quantify habitat-specific environmental changes relevant for the growth of primary producers (i.e., turbidity, water temperature, nutrients) that are linked to differences in catchments' glacier coverage; b) quantify the periphyton biomass along the gradient of glaciated catchment cover, and; c) identify group-specific responses to changing habitat conditions linked to glacier retreat. This study tested the hypothesis that reduced glaciation in mountain stream catchments is negatively linked with the harshness of physical habitat conditions for primary producers (i.e., water temperature, sediment load), resulting in higher periphyton biomass availability. Further, we hypothesized that the amelioration of physical habitat conditions might also provide opportunities for previously non-dominant primary producers to thrive and increase their abundance. By testing these assumptions, this research provides insight into the effects of glacier retreat on habitat conditions and the biomass and composition of primary producers in high-altitude rivers, thus contributing to a deeper understanding of the impacts of climate change-driven glacier retreat on primary producers in glacier-fed streams.

Material and Methods

Sampling design

This field study was conducted at five alpine streams in the Central Eastern Alps in the summer of 2022 (sampling in July, August, and September). The study design included sites at similar elevations (2127 m – 2363 m a.s.l.), with comparable topography and similar distance from the water source, but in catchments with differing glacier areas (Fig. 1) and different stages of glacier retreat.

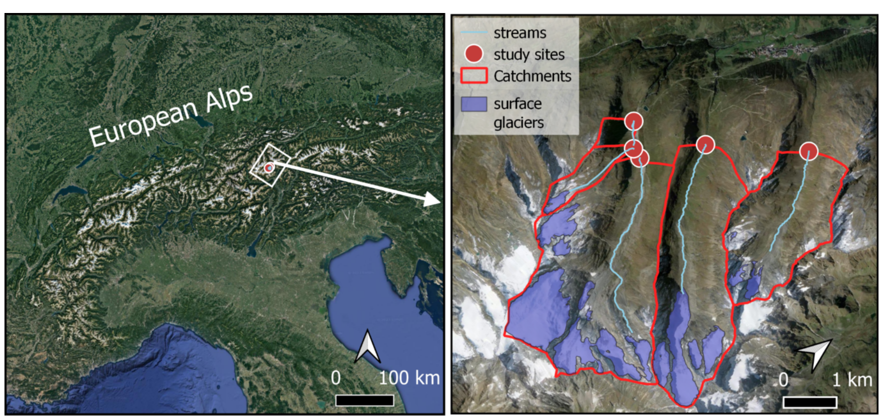


Fig. 1. Study sites and catchments in the European Alps with indicated glacier cover (right; CORINE land coverage 2018).

Characterization of habitat conditions and catchments

At each site, river water temperature was recorded continuously (hourly measurements) with digital loggers (Onset Tidbit2, MA, U.S.A.) and water was filtered through pre-combusted Whatman^{TM} GF/F filters (0.7 um) to quantify sediment concentrations (3x 0.5 L). Water discharge was estimated using depth/velocity transects and the Ott discharge probe (Ott MF Pro, Kempten, Germany), and water samples were taken to quantify nitrate (NH_3-N), dissolved nitrogen, and dissolved and total phosphorous concentrations. The concentration of suspended sediment (mg L^{-1}) was assessed by combusting filters at 450°C for 4 hours. We modelled the sediment load (mg s^{-1}) by combining discharge (L s^{-1}) and sediment concentrations (mg L^{-1}). Each catchment was delineated using QGIS (QGIS Development Team, 2009) using highly resolved digital elevation data retrieved from the Austrian data repository (www.data.gv.at). The ratios of glacial land-cover were calculated based on the freely available CORINE Land Cover data (https://land.copernicus.eu/pan-european/corine-land-cover) from 2018.

Periphyton screening

We used the BenthoTorch² (bbe Moldaenke, Germany) to differentiate among the main periphyton groups that estimates the composition of the following larger periphyton groups based on their *in vivo*fluorescence excitation spectra: cyanobacteria (pigment-group A), diatoms and chrysophytes (pigment-group B), and green algae (pigment-group III). The fast non-invasive measurements allowed spatially highly resolved assessments of total chlorophyll *a*concentrations and relative contributions of the different periphyton groups across a river. We analyzed 10-15 cobble surfaces (diameter >10 cm) in each of the 3 transects across each study stream on three occasions during summer 2022 (July, August, September), resulting in up to 45 sampled cobble surfaces per study river and month.

Periphyton sampling and biomass quantifications

Periphyton was sampled over the same three transects across each study reach with up to 7 sampled cobble surfaces per transect. All scraped surfaces per transect were pooled and divided into 50 mL fractions (3): two were transferred onto GF/C filters (1.2 µm; Whatman^{TM}) and one was kept frozen until fatty acid analyses. Ash-free dry mass (AFDM, expressed in mg cm^{-2}) was quantified by drying filters for 24 hours at 60°C followed by ashing at 450°C for 4 hours (loss on ignition (Heiri, Lotter & Lemcke, 2001)). The chlorophyll *a* content (µg cm^{-2}) was quantified using a U-3900H spectrophotometer (Hitachi, Tokyo, Japan) following the extraction protocol as described elsewhere (Lorenzen, 1967).

Fatty acid analysis

Lipids and their FA were analyzed as described by (Guo *et al.* , 2015). Briefly, total lipids from freeze-dried (i.e., all lipids and FA were reported as dry weight; DW) periphyton retained on filters (~5 mg) were dissolved in ice-cold chloroform (2 mL) and stored under N_2 atmosphere over night at -80°C to improve lipid extraction efficiency. Samples were then further extracted in chloroform-methanol (2:1) and NaCl (0.8 mL; salt wash), vortexed and sonicated, and subsequently analyzed gravimetrically in pre-weighed tin capsules (total lipid content determination). Fatty acids from total lipid extracts were derivatized to fatty acid methyl esters (FAME) in a H_2SO_4 methanol solution for 16 hours at 50°C. All FAME were stored at -80°C until being separated using gas chromatography (THERMO^{TM} Trace GC) and detected using flame ionization detection (FID). FAME were separated by a Supelco SP-2560 column (100 m, 25 mm i.d., 0.2 µm film thickness), identified by comparison to the retention times of known standards (37-component FAME Mix, Supelco 47885-U; Bacterial Acid Methyl Ester Mix, Supelco 47080-U). The FAME concentrations were quantified using calibration curves based on known standard concentrations. All FAME analyses were replicated within the study design (e.g., 3 periphyton samples per sampling at each transect).

Data analysis

Habitat conditions crucial for primary producers in alpine rivers (water temperature indices, sediment concentration and sediment load, concentrations of nutrients such as nitrate and dissolved phosphorous) were linked to glacier cover in the catchment (GCC, %) using general linear models (GLMs) or generalized additive models (GAMs), depending on the type of the relationship. The percentage of explained deviance (R^2) was used to evaluate model performance. As different water temperature indices we calculated the average of daily means, daily ranges, and daily maximum and minimum for two weeks after sampling (July 2022). For comparisons of sediment and nutrient concentrations, we also considered data from the previous year, 2021. This extended dataset allowed us to assess the variability for these parameters.

The relationships between glacier cover (and associated habitat conditions) and the biomass of periphyton groups were tested using GLMs/GAMs. Data manipulation and testing was done using *R* v.4.2.2 (R Core Team, 2021), GAMs were built using the *mgcv* package (Wood, 2011), graphics were produced using *ggplot2* (Wickham, 2016, 2) and *ggtern* (Hamilton & Ferry, 2018). Biotic data were assessed in the summer months (July, August, and September) in the year 2022 only.

Results

Habitat conditions

Water turbidity (i.e., sediment concentration) was mostly differing among sites and positively linked to glacier cover in the catchment (% GCC, Fig. 2A). Along the gradient of decreasing glaciation, sediment concentration and sediment load (product of concentration and runoff, in g s^{-1}) decreased exponentially from 30% to 0% glaciation (with an average rate of -12% and -21% per 1%-decrease in GCC, for sediment concentration and sediment load, respectively) (Fig. 2).

The concentration of nitrate, dissolved nitrogen and dissolved/total phosphorus was not related with the glacier cover in both years (p>0.05). Similarly, averaged water temperature metrics for July 2022 (daily means, daily ranges, daily maxima and minima) were not related to the glacier cover of the catchments (linear models, p>0.05, Fig. S1).

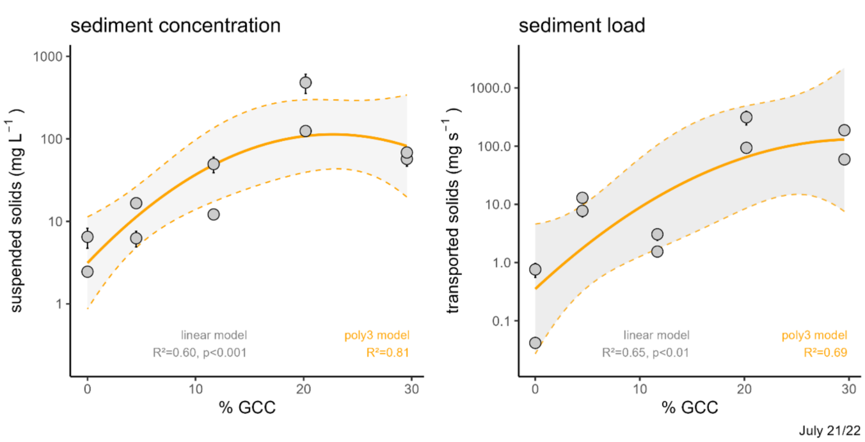


Fig. 2. Relationship between the suspended sediment concentration (left) and the sediment load (right)

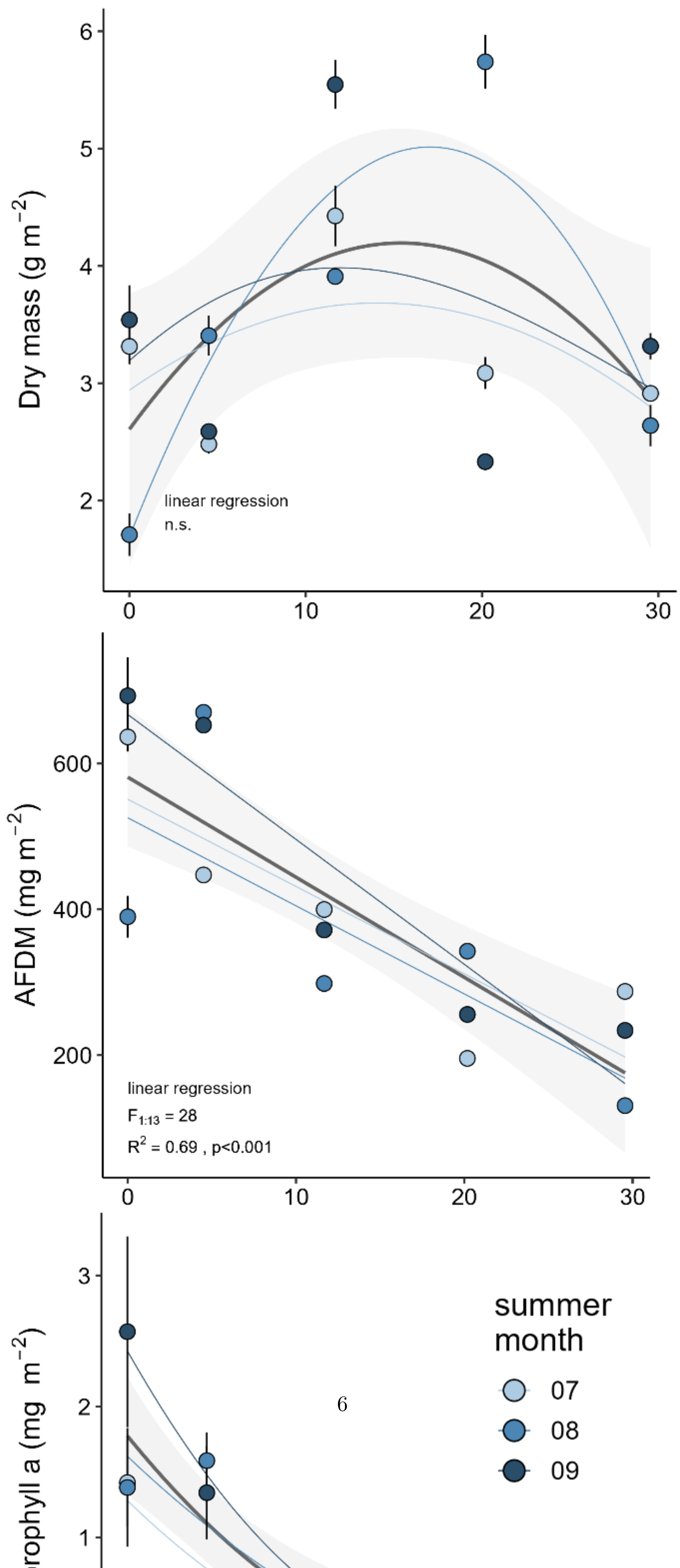
with the relative glacier cover in the catchment (% GCC) in the study streams during July 2021 and 2022 with indications of relationships (polynomial regressions in orange, linear model as grey text). Dashed lines indicate 95% confidence intervals, vertical dotted line indicates the breakpoint of the relationship. Y-axis has a log-scale.

Periphyton biomass in differently glaciated catchments

The mean dry mass of biofilm in the study streams ranged from 1710 to 5740 mg m^{-2}, whereas the mean organic fraction (ash-free dry mass, AFDM) was significantly lower (ranging from 130 to 693 mg m^{-2}; mean values). Single highest AFDM densities reached 1181 mg m^{-2} in the least glaciated catchments. The periphyton dry mass (g m^{-2}) was not related to the degree of glaciation in the studied catchments (no significant linear relationship, $p=0.78$, $R^2=0.01$, Fig. 3 A). Instead, AFDM was significantly negatively linked to glaciation in the catchment ($F_{1,13}=28$, $p<0.001$, $R^2=0.68$, Fig. 3 B) in all sampled months. In streams with larger glacial influence, the AFDM reached 300 mg m^{-2}, whereas the AFDM of riverbeds with little (10%) or no glacial input reached mean values of 500-600 mg m^{-2}. Compared to the potential link between nutrients (i.e., NO_3-N) and AFDM (no significant relationship, $p=0.062$), the effect size of the relative glacier cover in the catchment exceeded the one of nitrate concentration ($R^2_{partial}= 0.45$ vs. 0.10).

The biofilm dry mass per study stream varied among transects, with large deviations found for the total dry mass (estimates within same streams deviate between 29-48%, Fig. S2) and smaller variability for the AFDM (organic fraction; 14 – 35% (95% CI) (Fig. S2). Chlorophyll *a*

contents (µg cm^{-2}) were negatively related to glaciation (polynomial model, $R^2=0.63$, $p=0.002$, Fig. 3).



Dry mass (g m^{-2})
linear regression
n.s.
AFDM (mg m^{-2})
linear regression
$F_{1:13}$ = 28
R^2 = 0.69 , p<0.001
rophyll a (mg m^{-2})
summer
month
07
08
09

Fig. 3. Periphyton mass dynamics along glacier-fed rivers with different degrees of glaciated catchment (% GCC) with dry mass (top), ash-free dry mass (AFDM, center), and chlorophyll a concentration (bottom).

Periphyton community composition

The analysis of the community composition (relative abundance of the three groups) revealed the dominance of pigment-group B (diatoms and chrysophytes) over the other two groups, cyanobacteria and green algae (Fig. 4). While we found individual transects being dominated by green algae or cyanobacteria, all stream reaches and most sampled transects (87 %) were dominated by pigment-group B (diatoms and chrysophytes). Across all samples (n=45), diatoms made up between 62 % and 74 % (95% CI) of the producer communities.

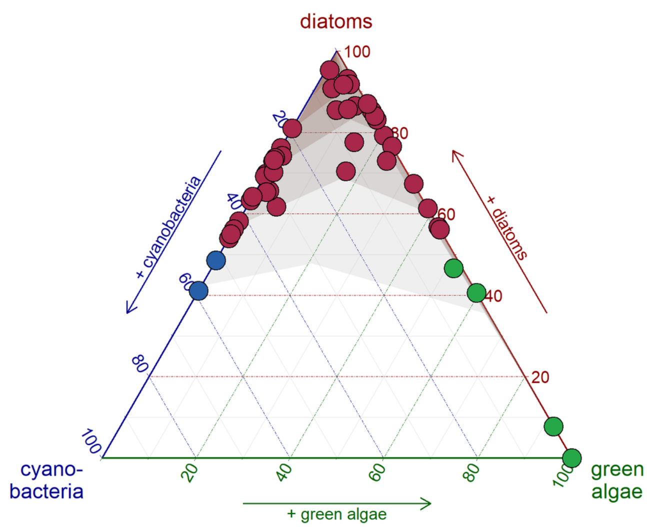


Fig. 4. Ternary plot of periphyton compositions illustrating that most sites and transects are dominated by diatoms and/or chrysophytes. Colors highlight the dominance in all subsamples (transects). Each circle corresponds to a composite transect sample (each consisting of 7 single measurements). Shades of grey illustrate sample density in the respective corner(s), most samples are dominated by diatoms/chrysophytes.

The biomass of diatoms and chrysophytes was significantly negatively linked with glaciation (2nd order polynomial model, R^2=42, p<0.001, Fig. 5 B), with biomass doubling when glacier-cover lowers from 30% to 0.5%. Pigment-group A was also negatively related to glacier-cover (R^2=0.25, p<0.001), but biomass remained low (<3.2 mg cm^{-2}; Fig. 5 A). In contrast, the biomass of pigment-group C was positively related to the glacier-cover in a catchment, but remained <2.5 mg cm^{-2} (=8 to 22% of total periphyton biomass, 95%-CI) across all study streams. The composition and the contribution of different groups did not differ significantly among different summer months (Fig. 5).

The estimated diatom biomass was related to the palmitoleic acid (16:1n-7) content, a diatom-related fatty acid (F=8.1, p=0.01, R^2=0.4, Fig. 6).

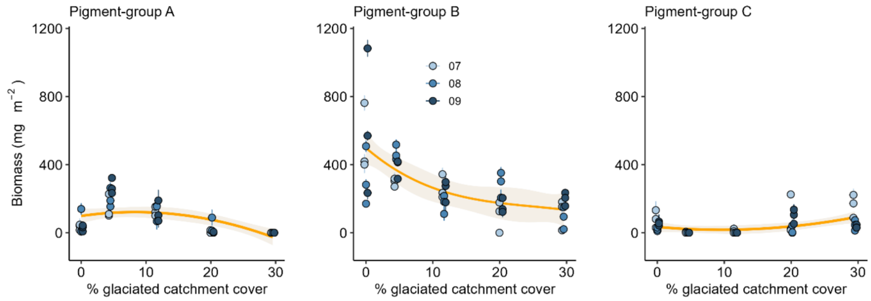


Fig. 5. Biomass of periphyton pigment groups along the gradient of glaciated catchment cover. Points represent means (n=3) and deviations limit standard errors of each transect. Lines are polynomial models (2[nd] order) best describing the relationships of mean biomass per stream (n=9). The colors indicate different sampling months (07 = July, 08 = August, 09 = September).

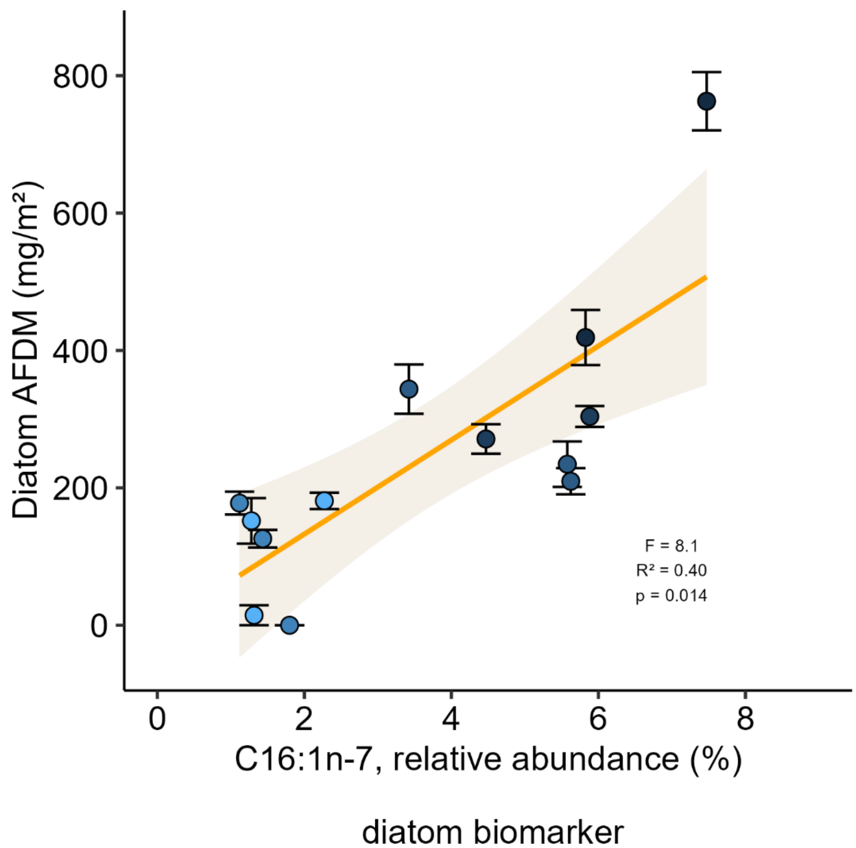


Fig. 6. Relationship of diatom biomass with the diatom-specific palmitoleic acid (16:1n-7). Points illustrate mean concentrations per measured transect in the different study sites. The solid orange line is a simple linear regression with 95% confidence interval (brown area), the fill color of points corresponds to the %glaciation in the catchment (with higher values indicated by brighter colors).

Discussion

Glacier-retreat in Alpine catchments is progressing fast with accelerating rates (Hugonnet *et al.* , 2021), altering the geomorphological and hydrological characteristics of downstream rivers (Milner *et al.* , 2017). While consequences for invertebrates (esp. cold-water specialists) have been extensively studied (e.g., Jacobsen*et al.* , 2012; Cauvy-Fraunié & Dangles, 2019) and are well predicted (Wilkes *et al.* , 2023), impacts on primary producers remain poorly understood (but see Fell *et al.* (2018) on expected decrease of diatom richness as glaciers retreat). In this study we quantified how glacial contribution regulates periphyton biomass in glacier-fed mountain streams, which expands our understanding of glacier loss effects on primary production in these fast transforming headwaters (Sudlow, Tremblay & Vinebrooke, 2023). Abiotic shifts appear to ameliorate habitat conditions that favor periphyton growth, as evidenced by higher biomass in less glaciated catchments. Also, a reduced glacial influence seems to promote the colonization and establishment of less nutritious basal resources, such as cyanobacteria, demonstrating that the provision of dietary primary producers to stream consumers is fundamentally linked with flow regimes of glacial streams.

Ameliorating habitat conditions

Contrary to the general assumption that stream water temperatures increase in catchments with lower glacial cover (Füreder & Niedrist, 2020), our findings revealed that waters from catchments with larger glaciers exhibited higher summer temperatures compared to those fed by smaller glaciers. Sites with higher glacial coverage also had the highest daily minimum temperatures. These temperature patterns suggest that glacier-fed river temperatures are not simply driven by the quantity of ice in the catchment, but indicate to a more complex relationship with glacier cover, discharge, and river morphology (Williamson, Entwistle & Collins, 2019). Flat and broad floodplains might lead to larger river surface areas and allow water to warm faster (Williamson *et al.* , 2019; O'Sullivan, Devito & Curry, 2019), as likely the case in this study. Since periphyton growth is generally enhanced by increasing temperatures through its direct influence on metabolic rates and nutrient uptake (Demars *et al.* , 2011), considering such antagonistic temperature dynamics is important to predict periphyton shifts as glaciers keep retreating. During summer, however, water temperature and nutrients may not be the limiting factor for periphyton growth in glacier-fed streams, but physical habitat conditions are. In particular, this study confirmed that the effects of physical limitation outcompetes a potential effect of nutrients on the periphyton growth in glacier-fed rivers (as hypothesized by (Sudlow*et al.* , 2023).

This field study across catchments with varying glacier coverage revealed an exponential decrease in meltwater turbidity and sediment load as glaciers recede. This milder physical habitat condition enables periphyton to thrive even during high flow conditions. The reduced sediment concentrations in the waters reduce drag forces, facilitating the colonization of habitats by species with outward growth forms (Rott*et al.* , 2006), rather than solely early colonizers with small cells (Biggs, Goring & Nikora, 1998). Furthermore, the study indicates that the consequences of glacier retreat for sediment load and water turbidity are significant. These effects can be partially predicted based on the degree of glaciation in the catchment, with sediment concentration and load decreasing exponentially when the degree of glaciation drops <30%. On average, sediment concentration and load decreased by 12% and 21% per 1% decrease in relative glacier cover, indicating a disproportionally higher decrease of sedimented substrates in glacial streams with respect to discharge (-8.9% per 1% decrease in relative glacier cover). However, it is important to note that sediment concentration in glacier-fed rivers can vary considerably and may be influenced by factors such as glacial activity, river slope, and flow velocity (Mao *et al.* , 2019).

Reduced sediment concentrations in less glaciated catchments generally improve the underwater photosynthetically active radiation (PAR) and can promote periphyton growth to certain extend (Boix Canadell *et al.* , 2021). In return, sediment transport can, depending on the flow velocity, abrade and scour periphyton biomass. Despite the potential photoinhibition by high UV-radiation in clear waters (Martyniuk, Modenutti & Balseiro, 2014; Jacobsen & Dangles, 2017; Elser *et al.* , 2020), we detected highest periphyton biomasses in rivers with no or little turbidity and less in waters with higher glacial contributions. We thus suggest that the light regime and the UV-stress in the studied sites was of minor importance for primary productivity than the physical abrasion by high discharge or transported sediment (Rinke, Robinson & Uehlinger, 2001; Hoyle *et al.* , 2017; Sudlow*et al.* , 2023).

Glacial water typically carries higher nutrient concentrations, particularly nitrogen and phosphorous, which can influence periphyton growth, as summarized by Sudlow *et al.* (2023). The nitrogen delivered by glacier melt originates from atmospheric deposition (Saros*et al.* , 2010). Unlike non-glaciated catchments, glacial streams still exhibit higher nitrogen concentrations (Hood & Scott, 2008; Slemmons *et al.* , 2013; Sudlow *et al.* , 2023), but with glacier retreat, a general decline in nutrient levels is anticipated to occur across the river network level. However, these assumptions were only partly confirmed in this study (i.e., we observed a weak negative link of nutrients with %glaciation in the catchments), assuming area-specific (and geology-based) differences. This potential interplay of factors during glacier retreat underscores the importance of understanding glacial stream nutrient dynamics to evaluate the (future) productivity of these ecosystems.

Increasing and diversifying periphyton biomass with declining glacial influence

Decreasing glacier-cover in the catchment has been linked to increasing biomass of benthic biofilms in glacial streams. Thus, warmer, slower, and less turbid waters seem to promote periphyton growth as suggested by (Sudlow *et al.* , 2023), suggesting that the suppression by physical disturbance in glacial streams appears to be greater than the inhibition by UV radiation in clear mountain waters (Hoyle *et al.* , 2017). Depending on how periphyton is quantified (dry weight vs. ash-free dry mass), our analysis reveals different biomass patterns across the rivers with different glacial influence. We attribute such difference to the accumulation of glacial flour in the biofilm because silt accumulation in epilithon that has been reported previously (Graham, 1990). Thus, this underscores the importance of quantifying periphyton biomass using ash-free dry mass, also in slightly turbid rivers.

Generally, the screened periphyton in all study streams was dominated by the pigment-group B (diatoms and chrysophytes). Although cyanobacteria and green algae were present at most sites, diatoms and chrysophytes contributed between 62 and 74% to the total chlorophyll a content, similar to the reported dominance of species in such ecosystems (Rott*et al.* , 2006; Fell *et al.* , 2018) or previous pigment screenings (Niedrist, Cantonati & Füreder, 2018). The quantifications of this pigment group correlated with the content of the diatom-specific palmitoleic acid in the same samples, which generally verified the quantifications based on fluorescence measurements. Along the gradient of glaciation, we found increases of diatoms and chrysophyte densities. We attribute this to the more benign habitat conditions in less glaciated catchments (i.e., decreased turbidity, calmed discharge, elevated temperature) that generally promotes and allows growth of present periphyton groups (Cauvy-Fraunié *et al.* , 2016; Sudlow*et al.* , 2023). The more favorable habitat conditions also support other periphyton groups, such as cyanobacteria. We observed an increasing cyanobacteria pigment content in the periphyton as glaciation decreased. Although densities remain below those of diatoms or chrysophytes even in unglaciated catchments, this confirms the general advance of cyanobacteria also in oligotrophic waters (e.g., Reinl*et al.* , 2023) and the known positive growth response of the cells to increasing temperatures (Lürling *et al.* , 2013). However, the share of immigrating species in this increase of biomass remains unknown. To estimate and compare the many species quantities at taxonomically higher level, methods such as qPCR will be necessary.

Conclusion

The rapid retreat of glaciers in mountain catchments (Sommer *et al.* , 2020; Hugonnet *et al.* , 2021) is causing significant changes in the hydrological and geomorphological characteristics of downstream rivers (Milner *et al.* , 2017). Besides the well-studied effects on invertebrates, especially cold-water specialists, the impacts on primary producers are only partly understood (e.g., Niedrist *et al.* , 2018; Fell *et al.* , 2018). This study focused on quantifying the regulation of periphyton biomass and the composition by glacial contribution, expanding our understanding of glacier loss on primary production in these rapidly transforming headwaters. We revealed that reduced glacial influence leads to ameliorated habitat conditions favoring periphyton growth, with higher biomass content observed in less glaciated catchments. Thereby, reductions in sediment load have been identified most beneficial for periphyton growth, whereas summer water temperature alone may not be the limiting factor for periphyton growth in these systems. Given the regulatory role of sediment for biota in glacier-fed rivers, predictions of sediment dynamics are crucial for understanding future habitat developments in mountain streams. However, developing such predictive models requires data from diverse glacial streams with varying topographical characteristics. Therefore, we recommend a collaborative approach that utilizes existing data from observed glacial streams to improve the accuracy of predictions.

Additionally, the colonization and establishment of groups previously underrepresented in highly glaciated catchments, such as cyanobacteria, are promoted by the reduced glacial influence. This study also highlights the importance of quantifying periphyton biomass using ash-free dry mass, even in slightly turbid rivers, since sediments might blur the estimations using dry mass only. Overall, this research contributes to our understanding of the complex interactions between glacier retreat, periphyton communities, and their habitats in mountain rivers, emphasizing the need for collaborative efforts and further investigation to predict future habitat developments in the face of ongoing glacier loss across the globe.

Acknowledgements

This research was funded by the Austrian Science Fund (FWF): P 34310.

Competing interests

There are no competing interests to declare that are relevant to the content of this article.

Data availability

The data used for this study is published in the KNB repository and can be accessed using this DOI: 10.5063/F1154FH3.

References

Bærum K.M., Finstad A.G., Ulvan E.M. & Haugen T.O. (2021). Population consequences of climate change through effects on functional traits of lentic brown trout in the sub-Arctic. *Scientific Reports* **11** , 15246. https://doi.org/10.1038/s41598-021-94350-x

Baum D., Laughton R., Armstrong J.D. & Metcalfe N.B. (2005). The effect of temperature on growth and early maturation in a wild population of Atlantic salmon parr. *Journal of Fish Biology* **67** , 1370–1380. https://doi.org/10.1111/j.0022-1112.2005.00832.x

Biggs B.J.F., Goring D.G. & Nikora V.I. (1998). Subsidy and Stress Responses of Stream Periphyton to Gradients in Water Velocity as a Function of Community Growth Form. *Journal of Phycology* **34** , 598–607. https://doi.org/10.1046/j.1529-8817.1998.340598.x

Boix Canadell M., Gómez-Gener L., Ulseth A.J., Clémençon M., Lane S.N. & Battin T.J. (2021). Regimes of primary production and their drivers in Alpine streams. *Freshwater Biology* **66** , 1449–1463. https://doi.org/10.1111/fwb.13730

Brandani J., Peter H., Busi S.B., Kohler T.J., Fodelianakis S., Ezzat L., *et al.* (2022). Spatial patterns of benthic biofilm diversity among streams draining proglacial floodplains. *Frontiers in Microbiology* **13**

Cauvy-Fraunié S., Andino P., Espinosa R., Calvez R., Jacobsen D. & Dangles O. (2016). Ecological responses to experimental glacier-runoff reduction in alpine rivers. *Nature Communications* **7** , 12025. https://doi.org/10.1038/ncomms12025

Cauvy-Fraunié S. & Dangles O. (2019). A global synthesis of biodiversity responses to glacier retreat. *Nature Ecology & Evolution* **3** , 1675–1685. https://doi.org/10.1038/s41559-019-1042-8

Demars B.O. l., Russell Manson J., Ólafsson J.S., Gíslason G.M., Gudmundsdóttir R., Woodward G., *et al.* (2011). Temperature and the metabolic balance of streams. *Freshwater Biology* **56** , 1106–1121. https://doi.org/10.1111/j.1365-2427.2010.02554.x

Elser J.J., Wu C., González A.L., Shain D.H., Smith H.J., Sommaruga R.,*et al.* (2020). Key rules of life and the fading cryosphere: impacts in alpine lakes and streams. *Global Change Biology* , gcb.15362. https://doi.org/10.1111/gcb.15362

Fell S.C., Carrivick J.L., Kelly M.G., Füreder L. & Brown L.E. (2018). Declining glacier cover threatens the biodiversity of alpine river diatom assemblages. *Global Change Biology* **24** , 5828–5840. https://doi.org/10.1111/gcb.14454

Füreder L. (2012). Freshwater ecology: Melting biodiversity.*Nature Climate Change* **2** , 318–319. https://doi.org/10.1038/nclimate1508

Füreder L. & Niedrist G.H. (2020). Glacial Stream Ecology: Structural and Functional Assets. *Water* **12** , 376. https://doi.org/10.3390/w12020376

Galloway A.W.E. & Winder M. (2015). Partitioning the Relative Importance of Phylogeny and Environmental Conditions on Phytoplankton Fatty Acids. *PLOS ONE* **10** , e0130053. https://doi.org/10.1371/journal.pone.0130053

Graham A.A. (1990). Siltation of stone-surface periphyton in rivers by clay-sized particles from low concentrations in suspention.*Hydrobiologia* **199** , 107–115. https://doi.org/10.1007/BF00005603

Guo F., Kainz M.J., Sheldon F. & Bunn S.E. (2015). Spatial variation in periphyton fatty acid composition in subtropical streams.*Freshwater Biology* **60** , 1411–1422. https://doi.org/10.1111/fwb.12578

Hamilton N.E. & Ferry M. (2018). Ternary diagrams using ggplot2.*Journal of Statistical Software, Code Snippets* **87** , 1–17. https://doi.org/10.18637/jss.v087.c03

Heiri O., Lotter A.F. & Lemcke G. (2001). Loss on ignition as a method for estimating organic and carbonate content in sediments: reproducibility and comparability of results. *Journal of Paleolimnology* **25** , 101–110. https://doi.org/10.1023/A:1008119611481

Hieber M.M., Robinson C.T., Rushforth S.R. & Uehlinger U. (2001). Algal communities associated with different alpine stream types. *Arctic, Antarctic, and Alpine Research* **33** , 447–456. https://doi.org/10.2307/1552555

Hood E. & Scott D. (2008). Riverine organic matter and nutrients in southeast Alaska affected by glacial coverage. *Nature Geoscience***1** , 583–587. https://doi.org/10.1038/ngeo280

Hotaling S., Finn D.S., Joseph Giersch J., Weisrock D.W. & Jacobsen D. (2017). Climate change and alpine stream biology: progress, challenges, and opportunities for the future. *Biological Reviews* **92** . https://doi.org/10.1111/brv.12319

Hoyle J.T., Kilroy C., Hicks D.M. & Brown L. (2017). The influence of sediment mobility and channel geomorphology on periphyton abundance. *Freshwater Biology* **62** , 258–273. https://doi.org/10.1111/fwb.12865

Hugonnet R., McNabb R., Berthier E., Menounos B., Nuth C., Girod L., *et al.* (2021). Accelerated global glacier mass loss in the early twenty-first century. *Nature* **592** , 726–731. https://doi.org/10.1038/s41586-021-03436-z

Jacobsen D. & Dangles O. (2017). *Ecology of High Altitude Waters* . Oxford University Press, Oxford.

Jacobsen D., Milner A.M., Brown L.E. & Dangles O. (2012). Biodiversity under threat in glacier-fed river systems. *Nature Climate Change* **2** , 361–364. https://doi.org/10.1038/nclimate1435

Lorenzen C.J. (1967). Determination of chlorophyll and pheo-pigments: Spectrophotometric equations. *Limnology and Oceanography* **12** , 343–346. https://doi.org/10.4319/lo.1967.12.2.0343

Lürling M., Eshetu F., Faassen E.J., Kosten S. & Huszar V.L.M. (2013). Comparison of cyanobacterial and green algal growth rates at different temperatures: *Temperature and phytoplankton growth rates* . *Freshwater Biology* **58** , 552–559. https://doi.org/10.1111/j.1365-2427.2012.02866.x

Mao L., Comiti F., Carrillo R. & Penna D. (2019). Sediment Transport in Proglacial Rivers. In: *Geomorphology of Proglacial Systems: Landform and Sediment Dynamics in Recently Deglaciated Alpine Landscapes* . Geography of the Physical Environment, (Eds T. Heckmann & D. Morche), pp. 199–217. Springer International Publishing, Cham.

Martyniuk N., Modenutti B. & Balseiro E.G. (2014). Can increased glacial melting resulting from global change provide attached algae with transient protection against high irradiance? *Freshwater Biology* **59** , 2290–2302. https://doi.org/10.1111/fwb.12431

Milner A.M., Khamis K., Battin T.J., Brittain J.E., Barrand N.E., Füreder L., *et al.* (2017). Glacier shrinkage driving global changes in downstream systems. *Proceedings of the National Academy of Sciences of the United States of America* **114** , 9770–9778. https://doi.org/10.1073/pnas.1619807114

Niedrist G.H. (2023). Substantial warming of Central European mountain rivers under climate change. *Regional Environmental Change* . https://doi.org/10.1007/s10113-023-02037-y

Niedrist G.H., Cantonati M. & Füreder L. (2018). Environmental harshness mediates the quality of periphyton and chironomid body mass in alpine streams. *Freshwater Science* **37** , 519–533. https://doi.org/10.1086/699480

Niedrist G.H. & Füreder L. (2023). Disproportional vulnerability of mountain aquatic invertebrates to climate change effects. *Arctic, Antarctic, and Alpine Research*

Niedrist G.H. & Füreder L. (2017). Trophic ecology of alpine stream invertebrates: Current status and future research needs. *Freshwater Science* **36** , 466–478. https://doi.org/10.1086/692831

O'Sullivan A.M., Devito K.J. & Curry R.A. (2019). The influence of landscape characteristics on the spatial variability of river temperatures. *CATENA* **177** , 70–83. https://doi.org/10.1016/j.catena.2019.02.006

QGIS Development Team (2009). QGIS Geographic Information System. Open Source Geospatial Foundation Project

R Core Team (2021). *R: A language and environment for statistical computing.* R Foundation for Statistical Computing, Vienna.

Reinl K.L., Harris T.D., North R.L., Almela P., Berger S.A., Bizic M., *et al.* (2023). Blooms also like it cold. *Limnology and Oceanography Letters* , lol2.10316. https://doi.org/10.1002/lol2.10316

Rinke K., Robinson C.T. & Uehlinger U. (2001). A Note on Abiotic Factors that Constrain Periphyton Growth in Alpine Glacier Streams. *International Review of Hydrobiology* **86** , 361–366. https://doi.org/10.1002/1522-2632(200106)86:3<361::AID-IROH361>3.0.CO;2-Z

Rott E., Cantonati M., Füreder L. & Pfister P. (2006). Benthic algae in high altitude streams of the Alps - A neglected component of the aquatic biota. *Hydrobiologia* **562** , 195–216. https://doi.org/10.1007/s10750-005-1811-z

Saros J.E., Rose K.C., Clow D.W., Stephens V.C., Nurse A.B., Arnett H.A., *et al.* (2010). Melting Alpine Glaciers Enrich High-Elevation Lakes with Reactive Nitrogen. *Environmental Science & Technology* **44** , 4891–4896. https://doi.org/10.1021/es100147j

Slemmons K.E.H., Saros J.E., Simon K., Ruggerone G.T., Bloomfield J., Dirzo R., *et al.* (2013). The influence of glacial meltwater on alpine aquatic ecosystems: a review. *Environmental Science: Processes & Impacts* **15** , 1794. https://doi.org/10.1039/c3em00243h

Sommer C., Malz P., Seehaus T.C., Lippl S., Zemp M. & Braun M.H. (2020). Rapid glacier retreat and downwasting throughout the European Alps in the early 21st century. *Nature Communications***11** , 3209. https://doi.org/10.1038/s41467-020-16818-0

Sudlow K., Tremblay S.S. & Vinebrooke R.D. (2023). Glacial stream ecosystems and epilithic algal communities under a warming climate.*Environmental Reviews* . https://doi.org/10.1139/er-2022-0114

Twining C.W., Brenna J.T., Hairston N.G. & Flecker A.S. (2016). Highly unsaturated fatty acids in nature: What we know and what we need to learn. *Oikos* **125** , 749–760. https://doi.org/10.1111/oik.02910

Uehlinger U., Robinson C.T., Hieber M. & Zah R. (2010). The physico-chemical habitat template for periphyton in alpine glacial streams under a changing climate. *Hydrobiologia* **657** , 107–121. https://doi.org/10.1007/s10750-009-9963-x

Vannote R.L., Minshall G.W., Cummins K.W., Sedell J.R. & Cushing C.E. (1980). The River Continuum Concept. *Canadian Journal of Fisheries and Aquatic Sciences* **37** , 130–137. https://doi.org/10.1139/f80-017

Wickham H. (2016). *ggplot2: Elegant Graphics for Data Analysis* . Springer-Verlag, New York.

Wilkes M.A., Carrivick J.L., Castella E., Ilg C., Cauvy-Fraunié S., Fell S.C., *et al.* (2023). Glacier retreat reorganizes river habitats leaving refugia for Alpine invertebrate biodiversity poorly protected.*Nature Ecology & Evolution* , 1–11. https://doi.org/10.1038/s41559-023-02061-5

Williamson R.J., Entwistle N.S. & Collins D.N. (2019). Meltwater temperature in streams draining Alpine glaciers. *Science of the Total Environment* **658** , 777–786. https://doi.org/10.1016/j.scitotenv.2018.12.215

Wood S.N. (2011). Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models.*Journal of the Royal Statistical Society. Series B (Statistical Methodology)* **73** , 3–36. https://doi.org/10.2307/41057423