

Charles University

Faculty of Science

Study programme: Ecological and evolutionary biology (B0511A030013)

Branch of study: B-EKOEVO (0511RA030013)



Julie Komárková

Food webs of glacier-fed streams.

Potravní sítě ledovcových toků.

Bachelor's thesis

Supervisor: Mgr. Kateřina Kopalová, Ph.D.

Prague, 2024

Acknowledgement:

I would like to thank my supervisor, Kateřina Kopalová, for professional guidance in writing my thesis. I would like to also thank Tyler Kohler for valuable ideas and help with source searching, together with language corrections. To both of them, my gratitude is for the introduction to this exciting topic.

Prohlášení:

Prohlašuji, že jsem práci napsala samostatně. Všechny použité zdroje a literatura jsou v práci řádně citovány a práce nebo její podstatná část nebyla využita jako závěrečná práce k získání jiného, nebo stejného akademického titulu. Dále prohlašuji, že technologie podporované AI byly v práci použity pouze ke zlepšení čitelnosti jazyka, nikoli k vyhledávání zdrojů, interpretaci dat či vyvozování vědeckých závěrů.

V Praze, 26.4. 2024

Julie Komárková

Abstract

This work focuses on glacier-fed stream ecosystems, with the centre of attention being on the community composition and characterization of their food web structure. Glacier-fed streams are harsh environments in terms of their physicochemical characteristics. These streams exhibit low temperatures and specific flow regimes, with the peak of meltwater generation, and thus discharge, in the summer. In turn, streamwater nutrient concentrations, light availability, and turbidity all vary seasonally according to the flow regime. Compositionally, glacier-fed stream habitats host chemolithotrophic bacteria along with photoautotrophic producers, such as diatoms, *Chrysophyceae*, and Cyanobacteria, which together serve at the bottom of food webs as primary producers. These streams also host some fungal taxa, that together with heterotrophic bacteria, represent the primary decomposers. Macroinvertebrates, including the water larvae of species *Diamesa* and *Pseudodiamesa*, or from the Ephemeroptera or Plecoptera groups, are important secondary producers with high feeding plasticity; that is, they are mainly grazing biofilm or collecting/filtering organic matter, with the possibility of predation. Other than that, in glacier-fed streams, there is usually no presence of higher trophic levels with large-bodied organisms. With global glacier retreat, glacier-fed streams are changing, with alterations to their flow regime and rising temperatures. Shifts in habitat conditions and composition structures will lead to more diverse food webs, with more trophic levels as colonisation of new species will occur. These alterations will be further elaborated in this thesis.

Keywords: ecology, glacier-fed streams, food webs, community structure, climate change

Abstrakt

Tématem této práce jsou ekosystémy ledovcem napájených toků se zaměřením na společenstva toků, spolu s identifikací struktur potravních sítí. Ledovcové toky představují drsné prostředí z hlediska fyzikálně-chemických vlastností, s proměnlivými vodními režimy, s největším průtokem v letních měsících, a specifickými světelnými a nutričními podmínkami. Základem potravních sítí jsou fotoautotrofní producenti, jako jsou rozsivky, *Chrysophyceae* a sinice, spolu s chemolithotrofními bakteriemi. V ledovcová voda hostí také některé taxony hub, které jsou s heterotrofními bakteriemi hlavními rozkladači. Ze skupiny bezobratlých jsou v ledovcových tocích vodní larvy druhů *Diamesa* a *Pseudodiamesa*, dále ze skupin Ephemeroptera či Plecoptera. Tyto všežravé druhy jsou charakterizovány vysokou potravní plasticitou. Larvy filtrují nebo spásají především epilimnické biofilmy, v některých případech se však mohou uchýlovat k predaci. Mimo bezobratlé, v ledovcových tocích obvykle nežijí zástupci s většími tělesnými rozměry, kteří by tvořili vyšší stupně trofických úrovní. Změna klimatu s ústupem ledovců ovlivňuje vlastnosti ledovcových toků, a to například v průtoku vody a teplotě, která se neustále zvyšuje. Posuny ve stanovištních podmínkách a struktuře společenstva v tocích povede ke složitějším potravním sítím, s více trofickými úrovněmi. Tyto změny budou více rozvedeny v práci.

Klíčová slova: ekologie, ledovcové toky, potravní sítě, struktura společenstva, změna klimatu

List of contents

1. Introduction	1
2. Glacier-fed streams	2
2.1. Characteristics of high mountain streams	2
2.2. Resource limitation in GFSs	6
3. Organismal communities in GFSs	7
3.1. Microbial community composition	7
3.2. Epilithic communities	9
3.3. Macroinvertebrate community structure	12
4. Food webs and trophic interactions in GFSs	14
4.1. Trophic levels and energy flow in GFSs	15
4.2. Primary producers	16
4.3. Consumers	18
4.4. Predators within GFSs.....	19
5. Impact of global warming on food webs in GFS	20
5.1. Changes in habitat conditions	20
5.2. Transformation of GFS community structure	23
6. Discussion	25
7. Conclusion	26
8. References	27

1. Introduction

Despite comprising only 10% of global land area, glaciers have a substantial influence on diverse aspects of life on Earth, from providing small microhabitats within the ice (Weisleitner et al., 2020), to influencing global carbon fluxes (Battin et al., 2023; NSIDC, 2024). Glaciers are a major part of the global cryosphere (which also includes snowfields, permafrost, and high mountain streams and lakes), creating a complex system in which a more profound understanding of habitat dynamics, and developing an integrated view of global trends, may help to predict the outcome of ongoing climate changes (Elser et al., 2020; IPCC, 2019). Mountain ranges serve as global ‘water towers’ and have an essential, or at least supportive, role in providing freshwater to many big rivers flowing through the most populated areas in the world, thereby ensuring half of the freshwater supply for billions of people and their agriculture (Immerzeel et al., 2020; Viviroli et al., 2007). Water from high mountains, specifically from glaciers, provides water reserves and constant flow during hot and dry seasons to downstream areas (Immerzeel et al., 2020).

Glacier-fed streams are a specific stream type found in alpine catchments, and which serve as headwaters to compounding river networks (Füreder & Niedrist, 2020). Besides their ecological function, glacier-fed streams are unique habitats with harsh ecological conditions, harbouring specialised organisms, and exhibiting specific trophic structures and feeding regimes. Studying these ecosystems can help us understand the ecological processes driving trait, functional, and biological diversity responses to climate change on a broader scale (Brown et al., 2018). Due to global higher mean temperatures, which predominantly affect high mountain areas with a rate of 0.3°C per decade, streamwater temperatures increase, and after a certain threshold in increased water discharge in time, meltwater from melting ice will ultimately decrease until completely melted, leading to habitat changes within those catchments (IPCC, 2019; Milner et al., 2017). The loss of glaciers will result in more stable flow regimes, changes in glacier-derived suspended sediment loads, and shift in streamwater biogeochemistry (e.g. elements such as C, N, P and Fe) (Ren et al., 2019). In glacier forelands, with newly exposed land created as glaciers recede, the colonisation of riparian vegetation together with the expected treeline upward migration, further impacting the quantity and quality of organic matter to the stream (Huss et al., 2017; McKernan et al., 2018).

With these points in mind, the goals and intentions of my thesis are as follows: First, I will characterise the physicochemical conditions of glacier-fed streams based on current

knowledge from literature. Second, I will describe the organismal communities in these streams and their interactions within food webs. Lastly, I will synthesise this general content and discuss it in light of climate change to investigate how ecosystem alterations may impact habitat conditions, and thereby stream communities and food web structure. My hypotheses resulting from my goals are: First, the main organismal groups dominating in glacier-fed streams might be the phototrophic diatoms together with representative species *Hydrurus foetidus* from *Chrysophyceae*. Secondly, hypothesis referring to global warming sounds: food webs will be altered by changes in their conditions also impacting their inhabitants.

2. Glacier-fed streams

2.1. Characteristics of high mountain streams

High mountain streams can be classified by the origin of their water (see Fig. 1), which leads to different yearly flow regimes and distinctive physical and chemical habitat conditions (Milner & Petts, 1994). In the traditional classification according to Ward (1994), between the permanent snowline and the treeline, streamwater sources can be either dominated by glacier ice melt (kryal), groundwater springs (krenal), or seasonal snowmelt/rainwater (rhithral) (Brown et al., 2003; Ward, 1994). All of them may eventually be influenced by glacier meltwater, because in the lower parts of the catchments (with increasing distance from the glacier), streams create a network of catchments representing various water sources (Füreder, 2007; McGregor et al., 1995). For that, the term “glacio-rhithral zone” is commonly used, reflecting the contributions from various water sources (Füreder, 1999). With shrinking glaciers and corresponding creation of new valley terrain, these various types of streams may also connect in the proglacial floodplain area. Floodplains typically have a mainstem, composed of a braided glacier-fed stream with multiple channels, with groundwater- or snowmelt-fed streams from the lateral hillslopes that serve as tributaries, creating heterogeneous environments (Brandani et al., 2023). With receding glaciers, the streams fed by groundwater and snowmelt are expected to dominate at the expense of the glacier-fed mainstem, reducing this heterogeneity (Milner et al., 2017).

Krenal streams have their origin mainly in groundwater, with developed hyporheic zones, where the groundwater meets the surface and creates streams (Sawyer et al., 2014). Krenal streams possess higher physicochemical stability, with streamwater temperatures which vary only 1-2°C, higher amounts of dissolved organic carbon concentration, higher electrical

conductivity, and consistent discharges with greater water clarity compared to glacier-fed streams (Brandani et al., 2022; Füreder, 2007; Ward, 1994). This higher stability is reflected by the organismal structure and ecological processes in these streams. Krenal streams, specifically those that are not connected to glacier-fed streams, are more productive and accumulate more biomass, compared to glacier-fed streams (Brandani et al., 2022).

Seasonal snowmelt streams (rhithral) have their peak discharge in spring and summer (at higher altitudes the peak can be delayed until July), and usually peak before the peak of glacier runoff. These streams are characterised by larger temperature ranges than in other stream types, with maximum temperatures reaching between 5° and 10°C. Usually, the water in rhithral streams is clear with small turbidity. However, in the peaks of their flow regime, turbidity may be higher due to the resuspension of fine sediments from the streambed. (Brown et al., 2003; Milner & Petts, 1994; Ward, 1994).

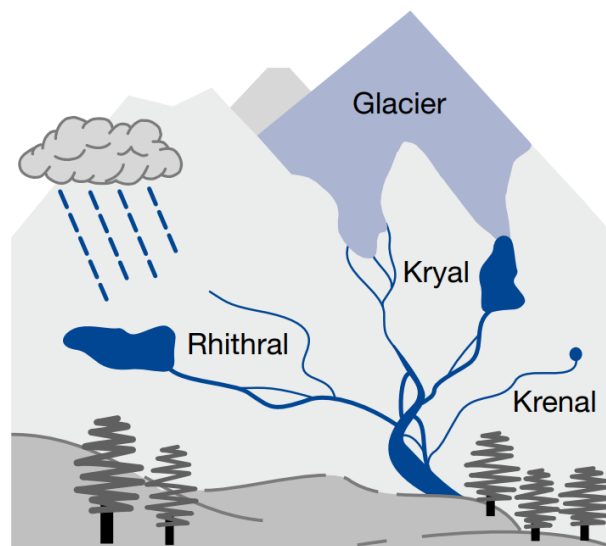


Figure 1: High mountain stream types with different sources of origin (Hieber et al., 2002)

Glacier-fed streams (i.e. the kryal streams; hereafter abbreviated to ‘GFSs’) are specific ecosystems at the interface between the cryosphere, hydrosphere, pedosphere, and biosphere (Füreder et al., 2001). Their water origin from the glacier, including the supraglacial (i.e. the top of a glacier), englacial (i.e. within the ice of a glacier), subglacial (i.e. under a glacier) flow paths (see Fig. 2), and thus water temperatures are maintained around 0°C, with small temperature fluctuations during the year (Brown et al., 2003; Milner & Petts, 1994). GFSs are characterised by their low conductivity, which also exhibits annual variations (Weijs et al.,

2013). In the winters with cold and snowy weather, the runoff can be reduced near to zero due to decreased water runoff through ice-filled intra-glacier spaces (Hotaling et al., 2017). Streams themselves may freeze or be covered with a layer of snow and ice that blocks the penetration of light to the water (Boix Canadell et al., 2021).

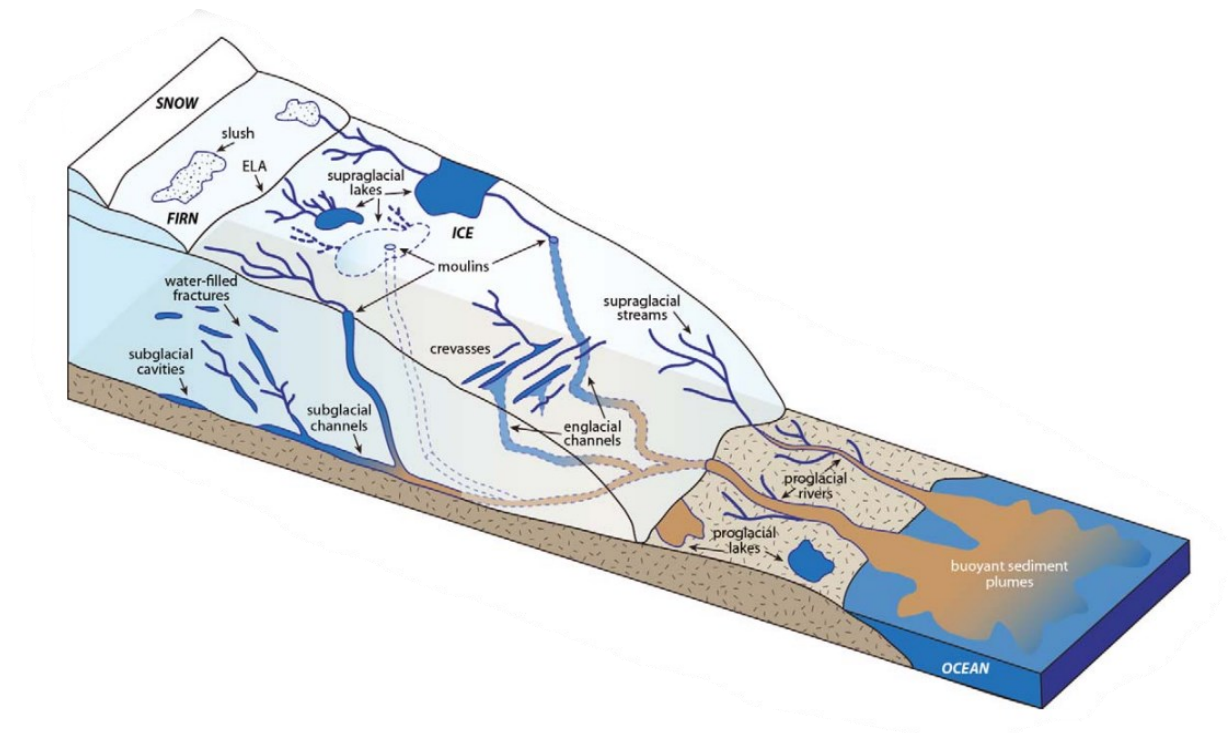


Figure 2: Illustration of Greenland's ice sheet hydrologic system; ELA means the equilibrium line altitude between the accumulation zone and ablation zone (Chu, 2014)

The seasonal light regime in GFS is very specific due to its connection with glacier melt. In summer months, there is a peak in water discharge, typically during July in the Northern Hemisphere, depending on day length and shift in solar angle, which may be even amplified by the steep-sided stream valleys, where those streams flow. With more solar radiation and higher temperatures, the meltwater may directly flow on the supraglacial surface into proglacial streams, or it may drain through the glacier mass through fractures, moulin, and crevasses within the ice (Hotaling et al., 2017). Those large diel (24-hour period) flow fluctuations peak in early to late afternoon, exaggerated as the summer goes on. Melting glacial ice adds to the whole set of key environmental conditions, which include low temperatures, high discharge dynamics, unstable channel morphology, and increased turbidity from suspended sediment

loads. Especially high turbidity in meltwater peaks limits the amount of photosynthetically active radiation (PAR) penetrating to streambeds, causing reduced photosynthetic primary production and extremely short growing seasons (Brown et al., 2003; Füreder, 1999; Füreder & Niedrist, 2020; Ward, 1994). As the peak in runoff passes, the water becomes slower flowing, shallower, and clearer with lower turbidity (Rott et al., 2006). These short time periods in the early stages of the summer melt peak, where optimal conditions are caused mainly by thawing snow after the winter, along with the period at the end of glacier melt in autumn before the winter comes, create advantages to enhance productivity of light-dependent primary producers. Thus, these periods are referred to as ‘windows of opportunity’ (Boix Canadell et al., 2021; Hotaling et al., 2017b; Uehlinger et al., 2010).

Physicochemical conditions, nutrients concentrations, and organismal communities within GFSs reflect processes occurring at both the catchment scale and along various flow paths, including glacial and non-glacial sources (Wilhelm et al., 2013). GFSs are usually subdivided into upper metakryal and lower hypokryal zones according to habitat conditions and faunal compositions (Ward, 1994).

Another type of alpine stream that is not yet well described and studied, may be icy seeps. Those very cold springs have summer temperatures below 2°C, as GFSs, and originate from the subterrain ice covered by thick layers of inorganic debris (from ‘rock glaciers’). These streams have more stable channels than most GFSs, and their specific microbial communities contain only a limited number of cyanobacteria, indicating that their food webs may be supported by different basal energy pathways. Their organismal structure partially overlaps with snowmelt- and glacier-fed streams (Hotaling et al., 2019). These streams may be interesting to study, especially considering climate change and melting glaciers, because the rock glaciers (with the insulating effect of debris) are predicted to melt at slower rates (Anderson et al., 2018; Rounce et al., 2023). Thus, icy seeps may possibly create refugia for freshwater cold-adapted organisms (Hotaling et al., 2019).

2.2. Resource limitation in GFSs

The ecosystem structure and function of organisms in GFSs are closely related to their limitation in specific nutrients, and thus a paragraph about it is inevitable (Kohler et al., 2024; Sterner & Elser, 2017). Streams with high alpine headwater sources above the treeline are typically nutrient-poor waters, lacking input of allochthonous (i.e. originating outside the streamwater) organic matter. In forested lower altitude running waters where the vascular plants can grow on the banksides, the carbon sources can include leaf litter or wood, for example (Rosemond et al., 2015; Zah et al., 2001). Ecosystems with an input of organic carbon (C) with a terrestrial origin are usually limited by other nutrients, such as nitrogen (N) and phosphorus (P). In contrast, ecosystems with poorly developed soil and no vegetation on banks may have their microbial metabolism limited by C (Rosemond et al., 2015; Kohler et al. 2024). Stream microbial activity is particularly connected to substrate biofilms (i.e. a microorganismal community living on the surface of streambeds) (Geesey et al., 1978). Due to the scarcity of organic C sources, limitations by physical abiotic disturbances, light conditions, and autochthonous energy sources lead to different autotrophic metabolic pathways, especially closer to the glacier terminus (see Fig. 3) (Zah & Uehlinger, 2001). With this in mind, it is important to mention chemolithotrophic pathways in cryospheric benthic ecosystems. Metabolically active chemolithoautotrophic organisms may have the uptake of manganese and iron, or metabolic pathways based on sulphur, nitrogen or hydrogen from the environment (Bourquin et al., 2022; Margesin & Collins, 2019). Understanding the mechanisms of metabolism and biogeochemical cycles in GFS biofilms is crucial for food web studies because, through nutrient uptake, nutrients are transferred to higher trophic levels (Ren et al., 2017; Schiller et al., 2007).

Rapid glacier shrinking, induced by climate, will alter the nutrient stoichiometry of GFSs. The rate of glacier melting will increase up to the maximum runoff (so-called ‘peak water’) when the water flow from melting glaciers steadily declines (Huss & Hock, 2018). After the peak water, a shift is predicted to take place in P supply, possible decrease in concentrations (although this depends upon the geology of the bedrock), and trends of increasing C concentrations. Shifts in nutrient supplies are affecting microbial energetics with unknown consequences on downstream habitats (Kohler et al., 2024). These aspects of global change will be discussed in other parts of my work.

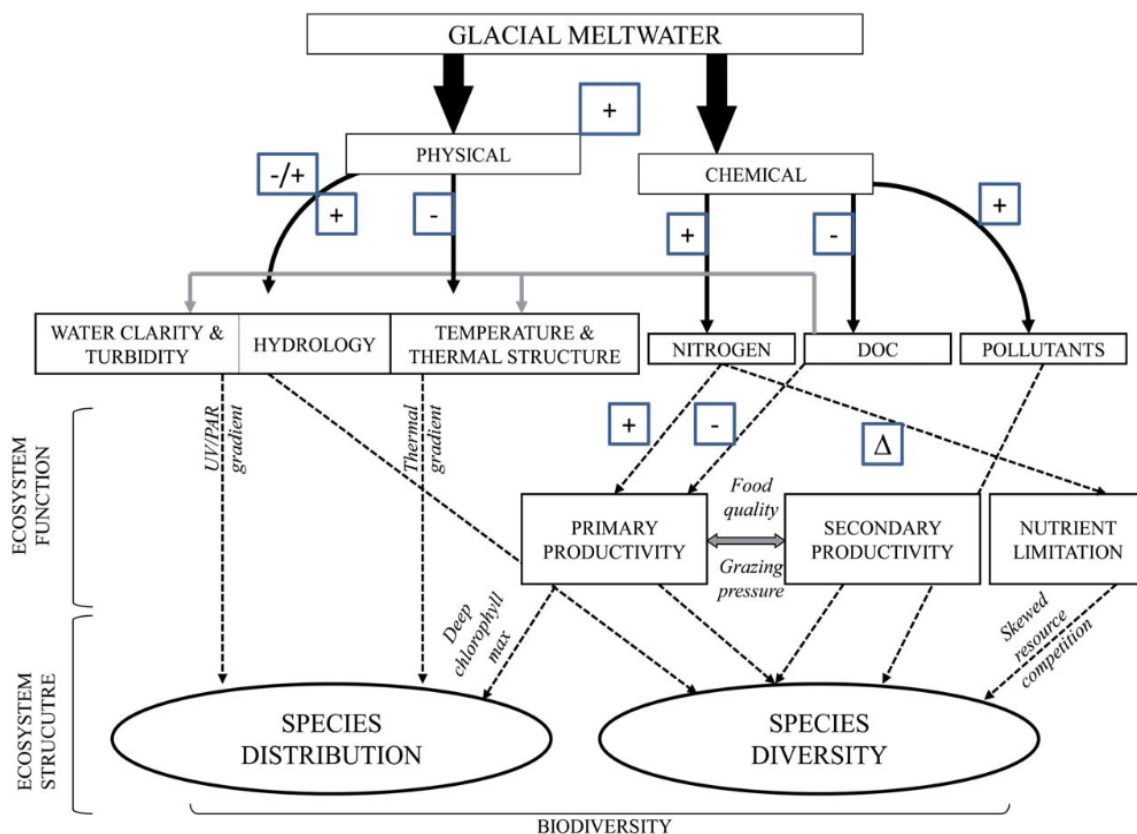


Figure 3: Schema from Slemmons et al. (2013) showing a conceptual model of glacier meltwater on physical or chemical aspects, with possible biological responses affecting ecosystem function and structure (signs indicate an increase or decrease, and the delta symbol a change in the metric).

3. Organismal communities in GFSs

3.1. Microbial community composition

Glacial ecological niches are embedded within very stressful conditions that microorganisms have to cope with and adapt to (Anesio et al., 2017). Glacier surfaces with wet snow provide active habitats with variable communities of organisms during the year, and in comparison, to highly dynamic GFSs, represent a harsh but more constant ecosystem (Hodson et al., 2008). Organisms such as snow algae, prokaryotic autotrophs, heterotrophs, viruses, and photosynthetic cyanobacteria are the main components of microbial biomass at the glacier surface (Anesio et al., 2017; Christmas et al., 2015). Cryoconite holes (structures that form around solar-heated debris) on the glacier surface harbour a greater diversity of life than snow on the surface, and are dominated by bacteria, cyanobacteria, diatoms, and even include tardigrades (Edwards et al., 2011; Hodson et al., 2008). The bacterial diversity and community

composition of glacier-fed streamwater and biofilms closely interact with these communities inhabiting the glacier ice and soil debris. Specifically, glacier meltwater runoff assemblages are composed of the same phyla as communities as those from ice or soil (though some phyla are more/less abundant in streams), and variation within the stream may stem from the different sources of microorganismal biodiversity in these glacier habitats (Besemer et al., 2012; Wilhelm et al., 2013).

The dominant bacterial phyla in ice, streamwater, and biofilms are generally similar, and include the phyla *Proteobacteria*, *Bacteroidetes*, and *Actinobacteria* (Wilhelm et al., 2013). Typically, the relative abundance of *Betaproteobacteria* specifically is higher in meltwater runoff. Genera such as *Pseudomonas*, *Bacillus*, *Geobacill*, *Staphylococcus* and *Acinetobacter* are predominant in both soil and water runoff (Liu et al., 2015; Sajjad et al., 2021). Only a few phyla were found only in streams, such as *Verrucomicrobia* and *Nitrospira* from a study from the Austrian Alps (Wilhelm et al., 2013). Furthermore, other GFS specialists are the bacteria from the family Exiguobacteriaceae (Hotaling et al., 2019). These specific biofilm taxa may have a critical role in the biogeochemistry of GFSs (such as *Nitrospira*) due to their metabolic pathways that impact the physicochemical shifts in streams (Wilhelm et al., 2013).

From the groups with a versatility of different metabolic pathways, bacteria *Bradyrhizobium*, *Rhizobium* or the previously mentioned *Nitrospira* genus with nitrogen-fixing abilities were also found in glacier habitats. Other types are, for instance, the obligate methylophs *Methylibium* and *Methylotenera*, and sulphur- and sulphate-reducing *Desulfococcus* or *Thiobacillus* (Fodelianakis et al., 2022; Kohler et al., 2020; Yang et al., 2016). Interestingly, when comparing GFSs metabolic activity with other high mountain stream types, the chemolithotrophic prokaryotic communities are more abundant in GFSs, in contrast with heterotrophic prokaryotes in non-GFSs (Michoud et al., 2023a).

Microbial α diversity (number of taxa within one site) decreases with higher elevation, which may be related to an increasing degree of environmental harshness closer to the glacier. The number of microorganisms delivered to the water from non-glacier sources forming the metacommunity size (the set of local communities and dispersal ability connecting these communities (Leibold et al., 2004)) in the stream network, is increasing with the other contributing sources to the stream getting stronger and determining the overall biodiversity downstream (Wilhelm et al., 2013). In the lower parts of streams, the microbial α diversity is also higher than closer to the glacial terminus. In contrast, the microbial β diversity (turnover of taxa between sites) decreased with increasing temperature, which means that community

structure gets more similar across sites (homogenisation) in the absence of glaciers (Hotaling et al., 2017; Wilhelm et al., 2013).

3.2. Epilithic communities

As described earlier, the light conditions for aquatic photoautotrophs are variable throughout the year. This is partly due to the extended period of snow cover over winter months, and partly because of the high water turbidity during the summer months (Milner & Petts, 1994). The specific hydrologic regimes of GFSs create ‘windows of opportunity’ for primary production in the spring before the summer peak in meltwater, and secondly, in the period at the end of the runoff peak, where conditions to develop are the most optimal (Boix Canadell et al., 2021). On top of reducing light availability, the presence of suspended sediments and glacier flour within the water leads to abrasion of streambed surfaces. The resulting substrate instability exacerbates conditions already unfavourable for the attachment of benthic organisms (Bürgi et al., 2003). As a result, primary production, and autochthonous organic matter fluxes in general, are low and seasonally variable in GFSs, creating organic carbon limitation (Uehlinger et al., 2010.; Bürgi et al., 2003).

Epilithic communities (i.e. organisms growing on the substrate) in GFSs are composed of the algal communities, that above the tree line gradually vary in the direction from the glacier, where there can be algae connected to glacier ice (Hieber et al., 2001). Zonation in photoautotroph composition also varies in the streambed (Rott et al., 2006). The spray zone of the stream can be occupied by the green alga *Trentepohlia*. Closer to the stream, where desiccation can occur, may be the cyanobacterial genus *Gleocapsa* or *Chlorogloea* (Rott et al., 2006).

The most common eukaryotic algae in GFSs are diatoms (Bacillariophyta), green algae, and the golden algae *Chrysophyceae*. Diatom communities vary along the stream continuum with a pattern of increasing richness with decreasing glacier influence. GFSs diatom diversity includes some rare and endangered species (such as *Navicula detenta*) (Fell et al., 2018). Examples of common diatoms that may be highly abundant are, for instance, taxa of the generalist genera *Achnantheidium* (such as *A. minutissimum* complex - Fig. 4), which has a cosmopolitan distribution (Fell et al., 2018). Secondly, *Encyonema* may also be common, as well as species from genera *Psammothidium*, *Pinnularia*, *Navicula*, *Eunotia*, *Cymbopleura*, *Brachysira*, and *Neidium* (Michoud et al., 2023a; Rott et al., 2006). Green algae groups in GFSs

may be represented by species from groups *Charophyta*, *Chlorophyta*, *Cercozoa*, *Klebsormidiophyceae* or *Trebouxiophyceae* (Michoud et al., 2023b).

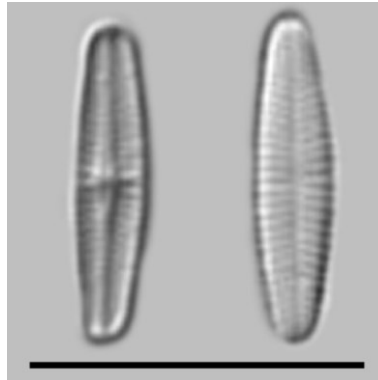


Figure 4: The diatom *Achnantheidium minutissimum*, Scale bar = 10 μm ;
(source: <https://diatoms.org/genera/achnantheidium>)

From *Chrysophyceae*, the most common representative is typically *Hydrurus foetidus* (Fig. 5) (Cantonati et al., 2001). *Hydrurus foetidus* is a primary producer species of high-altitude streams dominating in holarctic distribution (i.e. habitats found all around the Northern Hemisphere) (Bürge et al., 2003). In the biomass peak during favourable conditions, *Hydrurus foetidus* may rapidly grow only for a short duration (Uehlinger et al., 1998). However, *Hydrurus* is not common everywhere, and in a study of GFS in Africa, *Chrysophyceae* was not abundant, and their role in the stream was presumably taken over by the dominating cyanobacteria (Michoud et al., 2023b). In Antarctic regions, where the ice-free landscapes are full of ponds and lakes, microbial communities create dense cyanobacterial mats covering the substrates of streams. Those mats are a matrix that includes species of filamentous cyanobacteria such as *Leptolyngbya* or *Oscillatoriales*, together with various mat-inhabiting diatoms, such as *Navicula*, *Fragilaria*, *Stauroneis*, or *Nitzschia* (Fernández-Valiente et al., 2007).

From the prokaryotic microalgae cyanobacteria (they are not true algae but share a similar physiology and ecology as eukaryotic algae) may be the genera *Chamaesiphon* and *Lyngbya*, among others (Hieber et al., 2001; Rott et al., 2006).



Figure 5: The Chrysophyte alga *Hydrurus foetidus*

(source: https://www.algaebase.org/search/images/detail/?img_id=22873)

GFSs also host some fungal taxa, and together with bacteria serve as the main decomposers (Kohler et al., 2022). Glacier shrinkage will accelerate downstream decomposition of organic matter and alter microbiome structure and function. The majority of species in GFSs seem to be species from the group *Chytridiomycetes* (such as the parasitic *Rhizophydiales*), followed by Dikarya, which includes the hyphomycetes *Ascomycota* and *Basidiomycota*. However, the presence of fungi is notably lower when compared to the abundance of autotrophs (Kohler et al., 2024). Interestingly, given the lack of allochthonous organic carbon in GFSs, many of these fungi focus their efforts on the algae. For example, *Chytridiomycota* are recognized for their role as parasites of algae, penetrating the diatom's protoplast and digesting their organic components of the walls (Senga et al., 2018). The dominance of parasitic fungi in GFSs is related to the phenomenon called a “fungal shunt”, with the result being that they may modify microbial interactions and carbon flow within the system. Infected diatoms by the fungi are more vulnerable to heterotrophic bacteria, nanoflagellates or virus infections that accelerate the diatom decay and may provide the food for higher trophic levels (Klawonn et al., 2021; Kohler et al., 2022).

3.3. Macroinvertebrate community structure

The structure of macroinvertebrate communities in GFSs is closely linked to their hydrological regimes and physicochemical characteristics. Additionally, within GFSs, the composition of streambed substrates forms microhabitats with distinct features, such as mesolithal (cobbles), macrolithal (coarse cobbles), and megalithal (boulders) substrates (Füreder & Niedrist, 2020). The distance from the glacier also plays a significant role in shaping macroinvertebrate community structure. Various studies (Becquet et al., 2022; Cauvy-Fraunié et al., 2015; Füreder & Niedrist, 2020) suggest that as glacial influence increases, there is a decrease in both the total abundance and taxonomic richness of macroinvertebrates. Taxon richness and density seem to be lower in GFSs than in more environmentally favourable non-GFSs (Niedrist et al., 2018).

The most important taxa connected to the upper part of the stream are larvae of the dipteran family Chironomidae. Typically, macroinvertebrate glacial specialists are represented by the chironomid subfamilies Diamesinae (Fig. 6), Orthoclaudiinae, and Chironominae in the Palearctic regions (Cauvy-Fraunié et al., 2015; Füreder & Niedrist, 2020). In the tropical GFSs of Ecuador, the upper part of the stream is dominated by chironomid taxa from Podonominae (Jacobsen et al., 2010). These groups have characteristic traits that help them adapt to the challenging conditions found in GFSs. They have small body sizes with the ability to take refuge in the substrate. The absence of resistance forms (i.e. eggs, statoblasts, states of dormancy) makes them rely on other adaptations to survive in GFSs, which is connected to the univoltine or semivoltine life histories (i.e. one or two generations per year) in those groups. This can be advantageous because the environmental conditions can vary greatly from season to season (Ilg & Castella, 2006), and therefore multiple hatches per year can prevent populations from extinction. Individuals of these groups are also highly adapted to constant low temperatures. For instance, species from *Diamesa* and *Pseudodiamesa* can finish their annual life cycle even when water temperatures never exceed 2°C (Milner et al., 2001).

In a study from New Zealand, the dominant taxa in the upper part of a GFS are from the group Ephemeroptera, and the genera *Deleatidium* and *Nesameletus* (Cadbury et al., 2011). Individuals from Plecoptera and Trichoptera were also observed, though mostly in the lower parts of streams, where channel stability is higher. The macroinvertebrate composition in Antarctic regions may manifest through different patterns. In more extreme Antarctic conditions, the most abundant taxa are the nematodes, such as *Scottinema lindsayae*,

Eudorylaimus, and *Plectus*. Furthermore, in flowing streams, there may be rotifers and tardigrades residing in stream sediments (Treonis et al., 1999).

With increasing distance from glaciers, conditions in streams become more favourable for more diverse communities (Becquet et al., 2022; Khamis et al., 2016). In the lower parts of GFSs, typically around a distance of 1 km from the glacier snout, the Diptera Clinocerinae, *Corynoneura* spp., Simuliidae, Ceratopogoninae, and Tanypodinae are all notably more abundant (Becquet et al., 2022; Debiasi et al., 2022). Individuals from Nematoda can be parasites of *Diamesa* larvae and pupae in the upper part of GFSs, but also free-living species in the glacio-rhithral zone (Debiasi et al., 2022). There may also be larvae from other groups found, such as taxa from Ephemeroptera including *Baetis* sp. (Fig. 7), Plecoptera with the species *Nemoura* sp., or *Dictyogenus fontium* and Trichoptera. Further, there may be organisms from the non-insect group Oligochaeta, a subclass of phylum Annelida with species of aquatic worms (Debiasi et al., 2022; Liu et al., 2022).

High mountain streams commonly lack fish, especially those fed by glaciers. If fish are present, GFSs generally support a notably low diversity (Ward, 1994). In the upper part of the stream, no ichthyofauna species are generally observed. Fish in high-altitude waters are usually connected in streams closer to lakes, either upstream or downstream (Jacobsen et al., 2016).



Figure 6: Picture on left - overwintering frozen larvae of *Diamesa zernyi*; picture on right - same larvae recovered at 4°C (Lencioni, 2004)



Figure 7: Image of larvae *Baetis alpinus*, family Ephemeroptera
(source: <https://observations.be/species/718583/>)

4. Food webs and trophic interactions in GFSs

In understanding food web complexity and connectivity, it is crucial to connect studies of energy flow and nutrient cycling with studies of species composition in stream ecosystems. Generally, the energy and nutrient dynamics within food webs hinge upon two primary sources: autochthonous inputs originating internally from the stream environment, and allochthonous inputs derived from external sources (Füreder et al., 2003). In most alpine streams, it is commonly thought that the biomass of autochthonic primary producers is more important in the headwater streams, where the rock deserts are common, and allochthonous sources decrease at lower altitudes with the presence of subalpine forests (Sertić Perić et al., 2021). Those harsh upstream conditions lead to variations in community structure and function, such as decreased growth and production rates, along with food webs favouring alternative food sources (Füreder et al., 2003). However, it also depends on how different species react to a stream with different basal resources, community structure, density, and competition intensity (Clitherow et al., 2013; Sertić Perić et al., 2021).

To analyse food web structure in GFSs, stable isotope analysis is a favoured method. These studies use different naturally occurring stable isotopes of C and N (usually $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) in organisms (Füreder et al., 2003; Peterson & Fry, 1987). The isotopic signatures found in consumers typically reflect those of the organic matter they consume and assimilate. Thus, for example, nitrogen signatures may increase with each trophic level (at a rate $\delta^{15}\text{N}$ of 2.25‰ per trophic level in Zah et al. (2001)). Discrimination of isotopes in primary and secondary consumers can reveal the trophic connections between those organisms and allow researchers

to trace the flow of organic matter and nutrients through food webs (Peterson & Fry, 1987; Zah et al., 2001).

However, isotope analysis may be problematic in some streams. For example, ancient radiocarbon ^{14}C trapped in glaciers released together with meltwater can be incorporated into microbial and metazoan food webs by directly feeding on organic particles or grazing on biofilm that has previously assimilated old C (Fellman et al., 2015). Even the overlapping C sources with variability in local stream habitats, together with altered biogeochemical inputs of fast glacier retreat, may vary between sites. Analysing organisms at higher trophic levels based on radiocarbon dating may get confusing, because their age due to ancient carbon may be overestimated by up to 1100 years (Hågvar & Ohlson, 2013).

For better analysis of stable isotope data to estimate the contributions of different sources to a mixture based on the isotopic signatures, Bayesian mixing models are applied. Those statistical models incorporate prior information about the potential sources and their isotopic compositions, as well as variability in the data and its uncertainties, to generate posterior distributions of source contributions (Jackson et al., 2011). Using Bayesian inference techniques allows an improved understanding of trophic interactions, food web dynamics, and niche partitioning in ecological systems (Niedrist & Füreder, 2018).

Another method to characterise food webs in GFSs, where the webs are generally short, is to directly determine the gut contents of macroinvertebrates under the microscope (Clitherow et al., 2013). Instead of focusing on the quantity, these analyses can identify the presence or absence of links between consumers and primary producers (Parker & Huryn, 2006). However, this method is very time demanding.

4.1. Trophic levels and energy flow in GFSs

Trophic ecology synthesises interactions within the ecosystem, follows feeding relationships, and tries to trace the bottom-up and top-down forces in the system. Trophic levels are certain positions in food webs that energy flows through and is represented by each organism living in the ecosystem (see Fig.8). Those levels are shown in the trophic structure, therefore assimilating both biodiversity and ecosystem functioning. (Niedrist & Füreder, 2017; Thompson et al., 2012).

As previously discussed, food webs in high mountain streams are largely dependent on two main factors, which are organic carbon availability and water origin (Füreder et al., 2003) that latter of which especially has a significant impact on the primary producer trophic level. Identifying each trophic level in the food chain properly may be especially challenging due to various reasons. For example, problems that may arise may be connected to difficulty in determining the origin of the gut contents and the source of contained detritus. Furthermore, most stream animals are omnivores that change their feeding regime according to the dynamic nature of food availability, and their developmental stage which may have different requirements. Due to this, it may be uncertain if the found taxa in gut content were taken directly by feeding on them, or indirectly from their prey (Parker & Hury, 2006). Thus, different studies come with different assumptions and simplifications required for the specific study (Füreder et al., 2003).

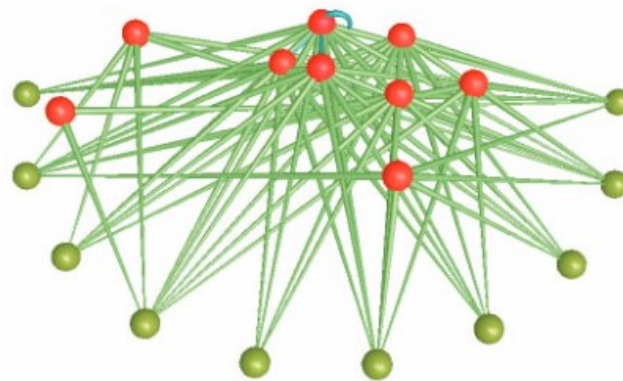


Figure 8: Diagram from Clitherow (2013) showing the simplified food web structure of the Ödenwinkelkees river in the Austrian Alps in 2011. Green nodes represent the primary producers, red nodes consumers and lines between them feeding links. The blue line represents cannibalistic links.

4.2. Primary producers

In GFSs, bioavailable dissolved organic matter (DOM) and detritus serve as important food sources for consumers and stimulate primary production. For examining the organic carbon values, stable isotope analyses can help identify the origin of dissolved organic carbon (DOC) present in the water. Available DOC in those environments is seasonally variable. DOM and DOC can get to the water from different ranges of sources, according to the ice and snow melting regimes and precipitation. In the transition periods on the early stage of melt peak and

at the end of it, there is observed higher variability of DOC values due to different origins, suggesting the additional sources of DOC, such as precipitation inputs (Spencer et al., 2014). The majority of glacially derived organic carbon is released with the summer peak of melting ice, possibly mainly sourcing from subglacial channels (Bhatia et al., 2013). Furthermore, some studies have shown that the sources of DOC gradually change with the distance from the glacier snout (Milner et al., 2017). Firstly, melted glacier water contains ancient bioavailable organic carbon from the glacier layers that can be metabolised by the heterotrophic bacteria in the streamwater of the upper parts of GFSs (Fellman et al., 2015; Niedrist & Füreder, 2017). Further downstream, the origin of DOC in the water shifts to autotrophic sources, such primary producers are cyanobacteria, epilithic algae - chrysophytes, diatoms and chlorophytes. The amount of algal biomass tends to increase with the distance from the glacier (Slemmons et al., 2013). Even lower, allochthonous inputs of DOC may increase until the stream reaches the treeline, where the character of in-stream dynamics changes (Fellman et al., 2015).

Furthermore, biofilms in GFSs are generally limited by both N and P (Ren et al., 2019). However, biofilms demonstrate stoichiometric flexibility, allowing them to create biomass with high carbon-to-phosphorus (C:P) and nitrogen-to-phosphorus (N:P) ratios. This, in turn, can lead to P limitation for consumers (Ren et al., 2019).

Diatoms, cyanobacteria, chrysophytes, and chlorophytes are globally distributed groups that form the epilithic biofilms in GFSs, and their composition varies spatially (Niedrist & Füreder, 2018). The most important source of organic matter in GFS is from senescing algae, which are decomposed in microbial biofilms to produce highly available exudates. The processes of primary producer decomposition by microorganisms may maintain critical nodes of C and other nutrients in GFS networks. (Kohler et al., 2022; Sudlow et al., 2023)

To illustrate the role of primary producers within the food web, Figure 9. in the text below from study by Brandani et al. (2022) may be convenient. Figure presents a co-occurrence network comparing GFS with non-GFS lateral tributaries. Co-occurrence networks do not explicitly mean the food web structure, clusters represent more functional groups within the stream biofilms. However, from this comparison study, there are clearly visible interactions between prokaryotic and eukaryotic (phototrophs + fungi) organisms, even though it is showing only the top 10% positive interactions between them. From network structures it is evident that the photoautotrophic nodes are in the centre of prokaryotic clusters, indicating close relationships between autotrophs and heterotrophs. Those several peripherally located prokaryotes at each node may suggest the metabolic connections between both groups. Those

autotrophs may be particularly important in the upper stream parts of GFSs, where the heterotrophs may use the organic matter from algae as a scarce food source. Furthermore, from clusters, it is also evident the important role of fungi within webs.

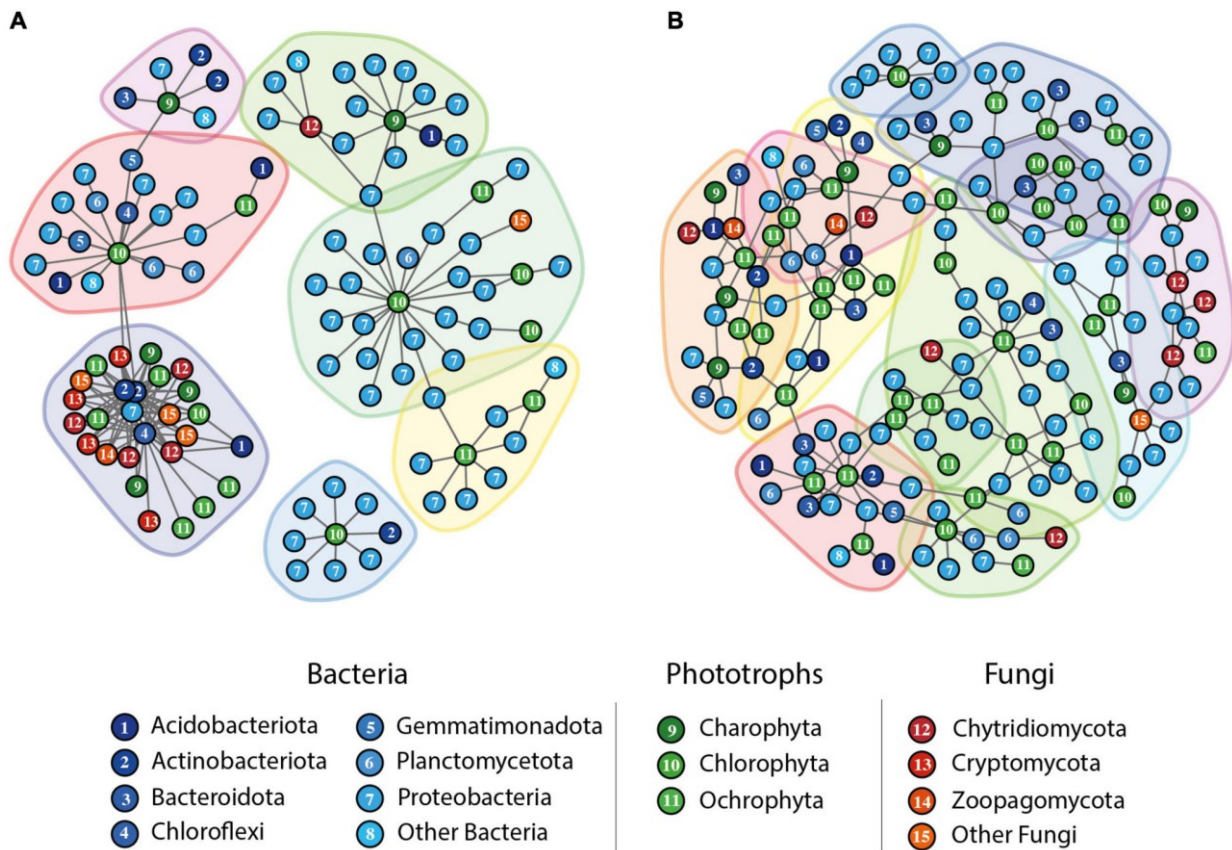


Figure 9: Representation from Brandani et al. (2022) showing a comparison of co-occurrence network structure in **A** - a GFS network, and **B** - non-GFS lateral tributaries (krenal, rhithral streams).

4.3. Consumers

GFS biofilms, composed of microorganisms along with detritus, have a direct influence on the composition of secondary producers/primary consumers, such as grazers, collectors, and filterers (Zah et al., 2001). Macroinvertebrates as GFS specialists have opportunistic omnivorous feeding behaviour and their distributions are highly patchy within the stream, as with biofilm distributions (Clitherow et al., 2013; Sertić Perić et al., 2021). Macroinvertebrates predominantly rely on biofilm as their primary food source (Sertić Perić et al., 2021). Of this, the main constituent is the common filamentous alga *Hydrurus foetidus* and epilithic diatoms. In calmer and more favourable environments, the detritus becomes the dominant food source

for macroinvertebrates and is indicated by a shift within the diet of chironomids to more autochthonous sources in harsher GFSs (Niedrist & Füreder, 2018).

Among macroinvertebrates, the main consumer is the previously mentioned Chironomidae family, which seems to have a wider feeding niche than species of Baetidae and Heptageniidae also occurring in GFSs. This suggests that group Chironomidae are opportunistic omnivores in GFSs (Clitherow et al., 2013; Sertić Perić et al., 2021).

4.4. Predators within GFSs

The major predators in alpine streams which can occur in glacier-fed streams are the predatory stoneflies (Plecoptera – Perlodidae family, such as *Dictyogenus* spp.), some caddisflies (Trichoptera family, such as *Rhyacophila* spp.), and certain chironomid species (Tanypodinae spp.). Due to the high feeding plasticity of invertebrates in GFSs, it has been observed that chironomid species that are commonly considered grazers or collectors exhibit higher than normal predator activity, likely due to harsh and variable conditions. In some cases, there have even been observed cannibalism between chironomid larvae (Clitherow et al., 2013).

In comparison to krenal streams, the ratio of invertebrate predator to prey biomass in GFSs, according to one study from an Alaskan river, was 26 times lower. This may indicate significant variations in material and energy flow within food web nodes. (Parker & Huryn, 2006)

To conclude, the GFS food web structure appears generally simple, with short food chain lengths, and a limited number of trophic levels. These levels include primary producers (diatoms, filamentous algae, heterotrophic bacteria, cyanobacteria, and mosses), primary consumers, omnivores and predators. Despite low taxonomic richness overall, there is high connectance in interactions between trophic levels (Clitherow et al., 2013; Niedrist & Füreder, 2017; Parker & Huryn, 2006). To compare GFSs with other stream types, krenal streams together with rhithral streams have more nodes within the food web structure, and longer feeding links between them (Brandani et al., 2022).

5. Impact of global warming on food webs in GFS

5.1. Changes in habitat conditions

Mountain regions are one of the most threatened areas by global warming, with rapid effects on the habitats above the permanent treeline. The disappearance of glaciers will profoundly transform the alpine landscapes (as in Fig. 10), with significant implications on local and even global biodiversity, from genes to whole community structures (Giersch et al., 2017). Globally, the area of land with glaciers is significantly decreasing due to higher temperatures (Zemp et al., 2015). It has consequences on the glacier runoff, which is variable during the year, with the peak in summer (Bliss et al., 2014). The most dramatic decrease in discharge, with an increased mean global temperature between 1.5°C and 3°C, will impact areas where there is already relatively low ice cover in high mountain areas, such as in the Central Europe Alps, Scandinavia, Caucasus, and the Middle East (Rounce et al., 2023). The summer peak in those areas will decrease the most in comparison with other regions with glaciers (Milner et al., 2017). Simulations of glacier mass balance show that by the end of the 21st century, approximately half of the world's glaciers are predicted to disappear, including the European Alps, western Canada, western USA, and New Zealand's glaciers (Rounce et al., 2023). Regionally, land glaciers in Alaska, the South Canadian Arctic, South Asia, and Southern Andes will drastically reduce in size, to about 11 to 23% of their size in 2015 (Huss, 2012; Rounce et al., 2023). Those worldwide changes in mass will affect summer discharge peaks and overall runoff and may have potential cascading impacts on downstream water resources (Bliss et al., 2014; Milner et al., 2017). GFSs will transform into streams with a more stable environment, with water sources fed by seasonally melting snowcover (McKernan et al., 2018). In the long term, when the peak of meltwater decreases, higher annual temperatures are expected within streams (Huss et al., 2017). In the future, deglaciated areas will create newly emerged ecosystems that may broadly vary from mild to extreme ecological conditions. In areas with steep slopes, cold temperatures, geomorphic activity, and limited available nutrients or water supply, the colonisation of new habitats will be low overall. However, in areas where post-glacial habitats are expected to have mainly mild ecological conditions, a boost of biogeochemical processes and primary productivity may emerge, together with the colonisation of new species (Bosson et al., 2023).

Glacier shrinkage has an effect on the physicochemical conditions in the ecosystem. It impacts the concentrations of C, N, and P within the catchment (Hood & Berner, 2009). The

highly bioavailable dissolved organic carbon (DOC) from glaciers has a big relevance for downstream catchment C cycling and sustaining aquatic food webs (Singer et al., 2012). It is expected that the DOC in the water will decrease with vanishing glaciers (Milner et al., 2017; Singer et al., 2012).

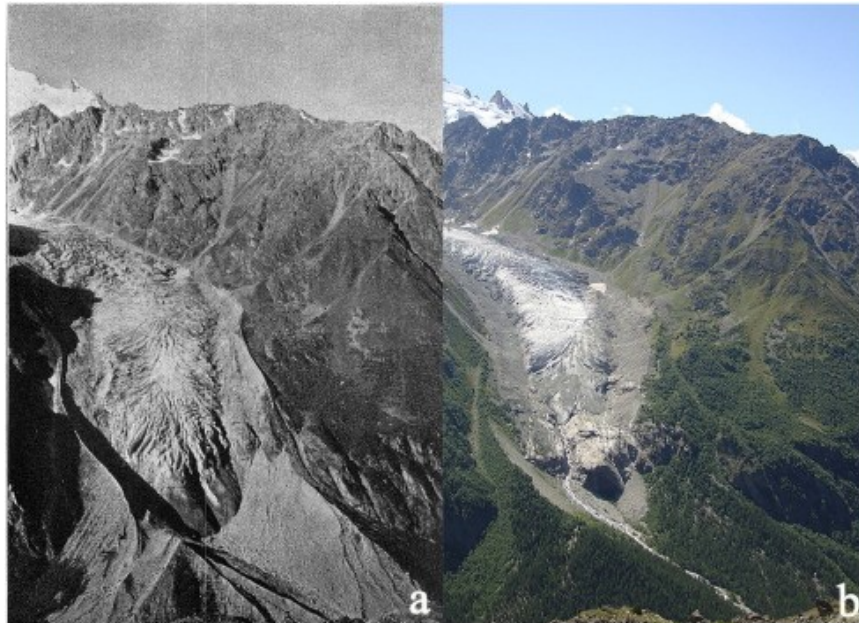


Figure 10: Illustration of the pace of melting glaciers - Kashkatash Glacier in the Northern Caucasus, photo **a**: by Burmester (1913) from 1911; photo **b**: by Bushueva (2009); (taken from Solomina et al., 2016)

The runoff also acts as a source of N, which possibly originates from microbial ecosystems on glacier ice, subglacial sediment, and nearby soils, and high concentrations may promote nitrification (Wadham et al., 2016). These transformations may contribute to the eventual N flux in glacier runoff, with impacts on downstream ecosystems (Milner et al., 2017). Concentrations of all forms of inorganic (nitrate, and ammonium; dissolved inorganic nitrogen; DIN) and organic (dissolved organic nitrogen; DON) N in the streamwater increase with the loss of glacier coverage (Hood & Berner, 2009; Hood & Scott, 2008). Furthermore, changes in P inputs to streamwater are expected to decrease. This is possible due to the reduced activity of the subglacial rock weathering (Hood & Berner, 2009) and subsequent microbial uptake (Kohler et al. 2024).

Altered nutritional inputs from deglaciation and their consequences on GFS community structure can be experimentally tested by manipulative experiments, with specific nutrient

additions to the stream. Studies have shown that N additions had stimulatory effects on the algal biomass, while P inputs increased biodiversity in streams and thus alter the food web structure (Kohler et al., 2016). The N and DOC amounts from glacier meltwater, in the short term, may initially increase, which may reduce the limitation by nitrogen and increase the total biomass of primary producers (Cauvy-Fraunié et al., 2016; Kohler et al., 2016). However, in the long term, after the peak water, the transition from ice-locked highly bioactive DOC to terrestrial DOC (which is a less labile form), will substitutionally decrease available DOC in the water affecting the heterotrophic production (Milner et al., 2017; Ren et al., 2019).

In GFSs, after peak water, it is expected that there will be a suspended sediment decline (Fleming & Clarke, 2005). Reduced suspended sediment in streamwater will decrease turbidity and increase light penetration in the water column, with expected increases in the primary producer base. Those changes in primary production, such as during the summer peak in discharge, may lead to changes in the feeding habits and phylogeny of primary consumers due to the different patterns of development and abundance of periphyton (Sertić Perić et al., 2021). There may also be a shift in the current productivity windows towards earlier days in spring and later to the winter (Boix Canadell et al., 2021). Studies also suggest that the associated shift in metabolic pathways will lead to a reduction in the “grey” food web (dominated by chemolithoautotrophs) corresponding with a rise in the “green” food web, which is sustained by photoautotrophy (Kohler et al., 2022).

The shifts in hydrogeomorphic processes within the stream (see Fig. 11), resulting in the stabilisation of hydrologic regimes and benthic sediments, will follow the patterns of riparian vegetation in its structural composition according to the succession stages (Klaar et al., 2015; McKernan et al., 2018). Also, changes in air temperature may shift the treeline to higher altitudes (Grigor’ev et al., 2013). With rising temperatures, the phenology of the growing season for riparian flora occurs earlier in the year (Huss et al., 2017). Those changes may result in largely herbaceous-dominated vegetation that also may influence aquatic macroinvertebrate structure in GFSs (McKernan et al., 2018). In addition to macroinvertebrates, plants with roots may cause biostabilization of the stream sediment, making biofilm communities less vulnerable to erosion. However, this effect will be spatially variable, because it depends on mature sediments and the scale of disturbance from the fast-flowing GFS channel, so it cannot be

implied generally (Roncoroni et al., 2019). Furthermore, with decreasing glacier influence, bryophytes may occur and thus compete with benthic algae (Milner et al., 2017).

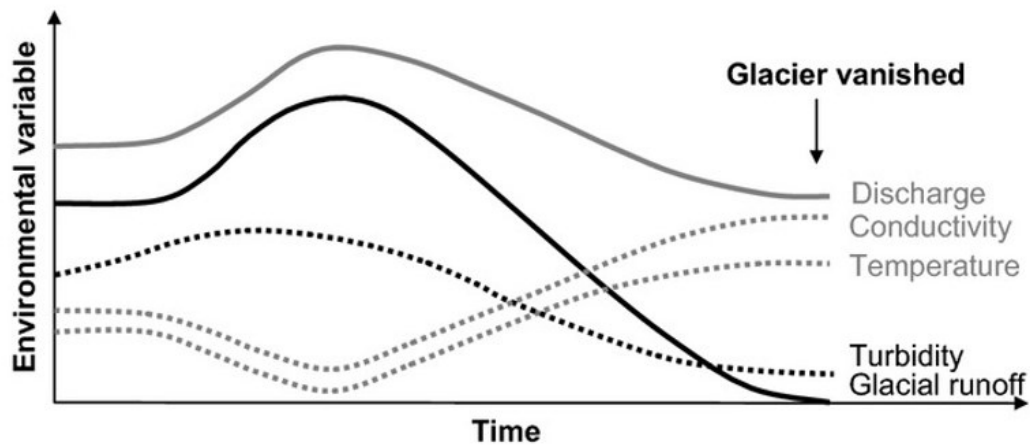


Figure 11: Conceptual diagram from Jacobsen et al. (2014) predicting potential variations over time in certain environmental parameters within GFSs, which could occur at any location along the stream as a result of glacier retreat.

5.2. Transformation of GFS community structure

High mountain ecosystems function like isolated islands, potentially limiting the movement of species. These habitats harbour a greater number of endemic species, particularly those adapted to cold-water environments (Giersch et al., 2017). However, the migration of rare species between alpine habitats remains unlikely due to the low biogeographical connectivity between mountain ranges. This limited connectivity can significantly impact metapopulation dynamics (Brown et al., 2011; Monaghan et al., 2005). As glaciers recede, and the geohydrology of GFSs undergo transformation, the unique and harsh habitats that support numerous range-restricted species are increasingly vulnerable to extinction (Brown et al., 2007).

During the initial phase of glacier retreat, leading up to peak water, we can expect greater contributions of meltwater and a shift toward a community dominated mainly by specialised chironomid species (Milner et al., 2009). Interestingly, after peak water, the α diversity and the total abundance of macroinvertebrates in GFSs should increase with a decrease in the contribution of meltwater to the stream (Brown et al., 2007). More secondary consumers residing in GFSs with more favourable conditions could be beneficial for fish colonisation, even

invasive species (Gallardo et al., 2016), or other freshwater insectivores from downstream regions of the catchment (Niedrist & Füreder, 2017). Thus, GFSs will colonise larger-sized predators which will influence the food web (Jacobsen et al., 2014).

High-altitude streams are furthermore expected to become more environmentally homogenous. With the upward community shift within the stream network, β diversity among streams will decline, as well as the γ diversity (diversity within a whole region) is expected (Brown et al., 2007; Wilhelm et al. 2013; Giersch et al., 2017). That is also connected to a decrease in biodiversity at the population-genetic level (Finn et al., 2013). Due to the small population sizes of rare taxa in GFSs, those communities are vulnerable to those described changes of regimes and more prone to stochastic extinctions (Brandani et al., 2022).

Changes in food web structure due to different inputs of glacier meltwater can be described as the bottom-up forces. It is related to the biofilm community structure changing with altered quality and quantity of DOC released from glaciers. On the other hand, top-down effects characterise the colonisation of larger taxa and their competition for resources with species already living in streams. (Milner et al., 2017) Thus, another impact on the food web within GFS is that it is expected that the intensity of species interactions could become more intense as meltwater contribution decreases (Milner et al., 2009).

An experimental study with flow manipulation from Cauvy-Fraunié (2016) tested the impact on community structure in a GFS from the Ecuadorian Andes. Over a 4-year period, they examined the effects of reduced meltwater discharge on community structure. Their results may illustrate the effects of rapid glacier retreat on GFSs. The study shows that the decrease of glacier runoff resulted in an increase in benthic algal biomass, with a consequence of enhanced herbivore densities. Change in flow reduction had not affected the taxon richness, only taxon replacement from downstream, such as Ceratopogonidae and Empididae, and the loss or overall lower abundance of specialised taxa, such as Simuliidae. Furthermore, reduced flow enhanced predation and competition pressures. In summary, the relationship between the amount of disturbance, species composition, and interactions within the food web, is crucial for understanding the effect of glacier retreat on GFSs (Cauvy-Fraunié et al., 2016).

6. Discussion

GFSs are characterised by their low temperatures, high turbidities, and fast flowing streams, due to their water originating from glaciers. GFS microorganisms are likely limited by C, due to a lack of allochthonous organic C inputs to the stream. However, the glacier still contributes some amounts of ancient carbon trapped in the subglacial sediments, as well as in surficial layers of snow. GFSs are not particularly limited by N, although they may be limited by P since its primary input is from glacier weathering. Those specific conditions lead to other metabolic pathways within resident biofilms, such as chemolithoautotrophy, that provide important links in the food web for transferring C to higher trophic levels. In accordance with my first hypothesis, the primary producers such as the diatoms, filamentous algae, heterotrophic bacteria, and cyanobacteria are an important part of the primary producers. Those compositions may spatially vary, with the most visible differences highlighted in this work. However, the influence of chemolithotrophs should not be neglected, most importantly because they might be replaced in the future by above stated primary producers.

Higher trophic levels, including filterers, scrapers, and collectors are composed mainly of aquatic macroinvertebrate larvae from groups including Chironomidae, Plecoptera, and Trichoptera. Those omnivorous groups characterise feeding flexibility according to the available food, with predator behaviours possible.

In my second defined hypothesis, I determined the alterations by global change impacting the GFSs physicochemical conditions together with organismal structure. Due to higher air temperatures in high mountain areas, glacier ecosystems are one of the most threatened habitats globally, with possible consequences for downstream areas. With rapid glacier retreat, glaciers in Europe, for instance, are predicted to almost completely disappear by the end of 2100. With increasing contributions from precipitation and groundwater replacing meltwater in these streams, N concentrations are predicted to decrease. Glacier recession, after the expected peak water, will furthermore impact turbidity, which may be lower, produce higher mean water temperatures and more stable channel flow. With more stable benthic substrates and stream margins, riparian vegetation may colonise, and the treeline may shift to higher elevations, with resulting inputs of terrestrially derived DOC. Colonisations of fast-growing organisms are expected to be more limited by P. Studies also propose more primary sources and more photoautotrophs. High mountain networks are further expected to become more

homogeneous and connected, and new large-bodied predators may colonise from downstream areas to higher altitudes, which may also impact food web structure.

Since the early years of the 21st century, the topic of GFSs started to be more studied, improving our understanding of habitat conditions and local biota. The articles on community structure, which started to come later, generally targeted one specific species or functional group of organisms, with just a few studies specifically about trophic structure. However, with better analytical techniques available in the past few years, the topic is better covered now. The pressure and impacts of global warming on these environments make this a hot topic, with many studies with new discoveries and specific implications. This research has covered the known information about GFSs with the focus on their food webs. To build upon these research findings, future studies, which will inevitably be connected to global warming, might further examine the altered interactions between organisms and changes in community structure.

7. Conclusion

Studying GFSs food webs offers a profound understanding of the ecological relationships found within high mountain ecosystems and their further impacts on downstream ecosystems. Patterns of nutrient limitation, light and temperature regimes, and stream discharge within the year, together with overall extreme habitat conditions, create organismal communities with specific characteristics. Due to patchy distributions, low population densities, and just a few locally variable dominant species living in them, food webs are generally short, with few trophic levels but with high connectivity between organisms. Climate change influencing habitat conditions in GFS will lead to a shift in primary producers, where photoautotrophs will be favoured creating “greener” food webs. Due to higher mean temperatures, the cold-adapted species will move into refuges or become extinct. With the colonisation of downstream species to upper parts of the stream food webs may have more trophic levels with larger-bodied organisms and predators

8. References:

- Anderson, R. S., Anderson, L. S., Armstrong, W. H., Rossi, M. W., & Crump, S. E. (2018). Glaciation of alpine valleys: The glacier – debris-covered glacier – rock glacier continuum. *Geomorphology*, *311*, 127–142. <https://doi.org/10.1016/j.geomorph.2018.03.015>
- Anesio, A. M., Lutz, S., Christmas, N. A. M., & Benning, L. G. (2017). The microbiome of glaciers and ice sheets. *Npj Biofilms and Microbiomes*, *3*(1), 1–11. <https://doi.org/10.1038/s41522-017-0019-0>
- Battin, T. J., Lauerwald, R., Bernhardt, E. S., Bertuzzo, E., Gener, L. G., Hall, R. O., Hotchkiss, E. R., Maavara, T., Pavelsky, T. M., Ran, L., Raymond, P., Rosentreter, J. A., & Regnier, P. (2023). River ecosystem metabolism and carbon biogeochemistry in a changing world. *Nature*, *613*(7944), 449–459. <https://doi.org/10.1038/s41586-022-05500-8>
- Becquet, J., Lamouroux, N., Condom, T., Gouttevin, I., Forcellini, M., Launay, B., Rabatel, A., & Cauvy-Fraunié, S. (2022). Macroinvertebrate distribution associated with environmental variables in alpine streams. *Freshwater Biology*, *67*(10), 1815–1831. <https://doi.org/10.1111/fwb.13977>
- Besemer, K., Peter, H., Logue, J. B., Langenheder, S., Lindström, E. S., Tranvik, L. J., & Battin, T. J. (2012). Unraveling assembly of stream biofilm communities. *The ISME Journal*, *6*(8), 1459–1468. <https://doi.org/10.1038/ismej.2011.205>
- Bhatia, M. P., Das, S. B., Xu, L., Charette, M. A., Wadham, J. L., & Kujawinski, E. B. (2013). Organic carbon export from the Greenland ice sheet. *Geochimica et Cosmochimica Acta*, *109*, 329–344. <https://doi.org/10.1016/j.gca.2013.02.006>
- Bliss, A., Hock, R., & Radić, V. (2014). Global response of glacier runoff to twenty-first century climate change. *Journal of Geophysical Research: Earth Surface*, *119*(4), 717–730. <https://doi.org/10.1002/2013JF002931>
- Boix Canadell, M., Gómez-Gener, L., Ulseth, A. J., Cléménçon, M., Lane, S. N., & Battin, T. J. (2021). Regimes of primary production and their drivers in Alpine streams. *Freshwater Biology*, *66*(8), 1449–1463. <https://doi.org/10.1111/fwb.13730>
- Bosson, J. B., Huss, M., Cauvy-Fraunié, S., Clément, J. C., Costes, G., Fischer, M., Poulenard, J., & Arthaud, F. (2023). Future emergence of new ecosystems caused by glacial retreat. *Nature*, *620*(7974), 562–569. <https://doi.org/10.1038/s41586-023-06302-2>
- Bourquin, M., Busi, S. B., Fodelianakis, S., Peter, H., Washburne, A., Kohler, T. J., Ezzat, L., Michoud, G., Wilmes, P., & Battin, T. J. (2022). The microbiome of cryospheric ecosystems. *Nature Communications*, *13*(1), 3087. <https://doi.org/10.1038/s41467-022-30816-4>
- Brandani, J., Peter, H., Busi, S. B., Kohler, T. J., Fodelianakis, S., Ezzat, L., Michoud, G., Bourquin, M., Pramateftaki, P., Roncoroni, M., Lane, S. N., & Battin, T. J. (2022). Spatial patterns of benthic biofilm diversity among streams draining proglacial floodplains. *Frontiers in Microbiology*, *13*. <https://doi.org/10.3389/fmicb.2022.948165>
- Brandani, J., Peter, H., Fodelianakis, S., Kohler, T. J., Bourquin, M., Michoud, G., Busi, S. B., Ezzat, L., Lane, S., & Battin, T. J. (2023). Homogeneous Environmental Selection Structures the Bacterial Communities of Benthic Biofilms in Proglacial Floodplain Streams. *Applied and Environmental Microbiology*, *89*(3), e02010-22. <https://doi.org/10.1128/aem.02010-22>
- Brown, L. E., Hannah, D. M., & Milner, A. M. (2003). Alpine Stream Habitat Classification: An Alternative Approach Incorporating the Role of Dynamic Water Source Contributions. *Arctic, Antarctic, and Alpine Research*, *35*(3), 313–322. [https://doi.org/10.1657/1523-0430\(2003\)035\[0313:ASHCAA\]2.0.CO;2](https://doi.org/10.1657/1523-0430(2003)035[0313:ASHCAA]2.0.CO;2)
- Brown, L. E., Hannah, D. M., & Milner, A. M. (2007). Vulnerability of alpine stream biodiversity to shrinking glaciers and snowpacks. *Global Change Biology*, *13*(5), 958–966. <https://doi.org/10.1111/j.1365-2486.2007.01341.x>
- Brown, B. L., Swan, C. M., Auerbach, D. A., Grant, E. H. C., Hitt, N. P., Maloney, K. O., & Patrick, C. (2011). Metacommunity theory as a multispecies, multiscale framework for studying the influence of river network structure on riverine communities and ecosystems. *Journal of the North American Benthological Society*. <https://doi.org/10.1899/10-129.1>

- Brown, L. E., Khamis, K., Wilkes, M., Blaen, P., Brittain, J. E., Carrivick, J. L., Fell, S., Friberg, N., Füreder, L., Gislason, G. M., Hainie, S., Hannah, D. M., James, W. H. M., Lencioni, V., Olafsson, J. S., Robinson, C. T., Saltveit, S. J., Thompson, C., & Milner, A. M. (2018). Functional diversity and community assembly of river invertebrates show globally consistent responses to decreasing glacier cover. *Nature Ecology & Evolution*, 2(2), 325–333. <https://doi.org/10.1038/s41559-017-0426-x>
- Bürgi, H. R., Burgherr, P., & Uehlinger, U. (2003). Aquatic Flora. In J. V. Ward & U. Uehlinger (Ed.), *Ecology of a Glacial Flood Plain* (s. 139–151). Springer Netherlands. https://doi.org/10.1007/978-94-017-0181-5_9
- Cadbury, S. L., Milner, A. M., & Hannah, D. M. (2011). Hydroecology of a New Zealand glacier-fed river: Linking longitudinal zonation of physical habitat and macroinvertebrate communities. *Ecohydrology*, 4(4), 520–531. <https://doi.org/10.1002/eco.185>
- Cantonati, M., G. C., Jüttner, I., & Cox, E. (2001). Diatom assemblages in high mountain streams of the Alps and the Himalaya. *Nova Hedwigia*, 123, 37–62.
- Cauvy-Fraunié, S., Espinosa, R., Andino, P., Jacobsen, D., & Dangles, O. (2015). Invertebrate Metacommunity Structure and Dynamics in an Andean Glacial Stream Network Facing Climate Change. *PLOS ONE*, 10(8), e0136793. <https://doi.org/10.1371/journal.pone.0136793>
- 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(1), 12025. <https://doi.org/10.1038/ncomms12025>
- Christmas, N. A. M., Anesio, A. M., & Sánchez-Baracaldo, P. (2015). Multiple adaptations to polar and alpine environments within cyanobacteria: A phylogenomic and Bayesian approach. *Frontiers in Microbiology*, 6. <https://doi.org/10.3389/fmicb.2015.01070>
- Chu, V. W. (2014). Greenland ice sheet hydrology: A review. *Progress in Physical Geography: Earth and Environment*, 38(1), 19–54. <https://doi.org/10.1177/0309133313507075>
- Clitherow, L. R., Carrivick, J. L., & Brown, L. E. (2013). Food Web Structure in a Harsh Glacier-Fed River. *PLOS ONE*, 8(4), e60899. <https://doi.org/10.1371/journal.pone.0060899>
- Debiasi, D., Franceschini, A., Paoli, F., & Lencioni, V. (2022). How do macroinvertebrate communities respond to declining glacial influence in the Southern Alps? *Limnetica*, 41(1), 121–137. <https://doi.org/10.23818/limn.41.10>
- Edwards, A., Anesio, A. M., Rassner, S. M., Sattler, B., Hubbard, B., Perkins, W. T., Young, M., & Griffith, G. W. (2011). Possible interactions between bacterial diversity, microbial activity and supraglacial hydrology of cryoconite holes in Svalbard. *The ISME Journal*, 5(1), 150–160. <https://doi.org/10.1038/ismej.2010.100>
- Elser, J. J., Wu, C., González, A. L., Shain, D. H., Smith, H. J., Sommaruga, R., Williamson, C. E., Brahney, J., Hotaling, S., Vanderwall, J., Yu, J., Aizen, V., Aizen, E., Battin, T. J., Camassa, R., Feng, X., Jiang, H., Lu, L., Qu, J. J., Saros, J. E. (2020). Key rules of life and the fading cryosphere: Impacts in alpine lakes and streams. *Global Change Biology*, 26(12), 6644–6656. <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(12), 5828–5840. <https://doi.org/10.1111/gcb.14454>
- Fellman, J. B., Hood, E., Raymond, P. A., Hudson, J., Bozeman, M., & Arimitsu, M. (2015). Evidence for the assimilation of ancient glacier organic carbon in a proglacial stream food web. *Limnology and Oceanography*, 60(4), 1118–1128. <https://doi.org/10.1002/lno.10088>
- Fernández-Valiente, E., Camacho, A., Rochera, C., Rico, E., Vincent, W. F., & Quesada, A. (2007). Community structure and physiological characterization of microbial mats in Byers Peninsula, Livingston Island (South Shetland Islands, Antarctica). *FEMS Microbiology Ecology*, 59(2), 377–385. <https://doi.org/10.1111/j.1574-6941.2006.00221.x>
- Finn, D. S., Khamis, K., & Milner, A. M. (2013). Loss of small glaciers will diminish beta diversity in Pyrenean streams at two levels of biological organization. *Global Ecology and Biogeography*, 22(1), 40–51. <https://doi.org/10.1111/j.1466-8238.2012.00766.x>
- Fleming, S. W., & Clarke, G. K. (2005). Attenuation of High-Frequency Interannual Streamflow Variability by Watershed Glacial Cover. *Journal of Hydraulic Engineering*, 131(7), 615–618. [https://doi.org/10.1061/\(ASCE\)0733-9429\(2005\)131:7\(615\)](https://doi.org/10.1061/(ASCE)0733-9429(2005)131:7(615))

- Fodelianakis, S., Washburne, A. D., Bourquin, M., Pramateftaki, P., Kohler, T. J., Styllas, M., Tolosano, M., De Staercke, V., Schön, M., Busi, S. B., Brandani, J., Wilmes, P., Peter, H., & Battin, T. J. (2022). Microdiversity characterizes prevalent phylogenetic clades in the glacier-fed stream microbiome. *The ISME Journal*, *16*(3), 666–675. <https://doi.org/10.1038/s41396-021-01106-6>
- Füreder, L. (1999). High alpine streams: Cold habitats for insect larvae. In R. Margesin & F. Schinner (Ed.), *Cold-Adapted Organisms: Ecology, Physiology, Enzymology and Molecular Biology* (s. 181–196). Springer. https://doi.org/10.1007/978-3-662-06285-2_10
- Füreder, L., Schütz, C., Wallinger, M., & Burger, R. (2001). Physico-chemistry and aquatic insects of a glacier-fed and a spring-fed alpine stream. *Freshwater Biology*, *46*(12), 1673–1690. <https://doi.org/10.1046/j.1365-2427.2001.00862.x>
- Füreder, L., Welter, C., & Jackson, J. K. (2003). Dietary and Stable Isotope ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) Analyses in Alpine Stream Insects. *International Review of Hydrobiology*, *88*(3–4), 314–331. <https://doi.org/10.1002/iroh.200390028>
- Füreder, L. (2007). Life at the Edge: Habitat Condition and Bottom Fauna of Alpine Running Waters. *International Review of Hydrobiology*, *92*(4–5), 491–513. <https://doi.org/10.1002/iroh.200610987>
- Füreder, L., & Niedrist, G. H. (2020). Glacial Stream Ecology: Structural and Functional Assets. *Water*, *12*(2), Article 2. <https://doi.org/10.3390/w12020376>
- Gallardo, B., Clavero, M., Sánchez, M. I., & Vilà, M. (2016). Global ecological impacts of invasive species in aquatic ecosystems. *Global Change Biology*, *22*(1), 151–163. <https://doi.org/10.1111/gcb.13004>
- Geesey, G. G., Mutch, R., Costerton, J. W., & Green, R. B. (1978). Sessile bacteria: An important component of the microbial population in small mountain streams 1. *Limnology and Oceanography*, *23*(6), 1214–1223. <https://doi.org/10.4319/lo.1978.23.6.1214>
- Giersch, J. J., Hotaling, S., Kovach, R. P., Jones, L. A., & Muhlfeld, C. C. (2017). Climate-induced glacier and snow loss imperils alpine stream insects. *Global Change Biology*, *23*(7), 2577–2589. <https://doi.org/10.1111/gcb.13565>
- Grigor'ev, A. A., Moiseev, P. A., & Nagimov, Z. Ya. (2013). Dynamics of the timberline in high mountain areas of the nether-polar Urals under the influence of current climate change. *Russian Journal of Ecology*, *44*(4), 312–323. <https://doi.org/10.1134/S1067413613040061>
- Hågar, S., & Ohlson, M. (2013). Ancient carbon from a melting glacier gives high ^{14}C age in living pioneer invertebrates. *Scientific Reports*, *3*(1), 2820. <https://doi.org/10.1038/srep02820>
- Hieber, M., Robinson, C. T., Rushforth, S. R., & Uehlinger, U. (2001). Algal Communities Associated with Different Alpine Stream Types. *Arctic, Antarctic, and Alpine Research*, *33*(4), 447–456. <https://doi.org/10.1080/15230430.2001.12003454>
- Hock, R., G. Rasul, C. Adler, B. Cáceres, S. Gruber, Y. Hirabayashi, M. Jackson, A. Kääb, S. Kang, S. Kutuzov, Al. Milner, U. Molau, S. Morin, B. Orlove, and H. Steltzer, 2019: High Mountain Areas. In: *IPCC Special Report on the Ocean and Cryosphere in a Changing Climate* [H.-O. Pörtner, D.C. Roberts, V. Masson-Delmotte, P. Zhai, M. Tignor, E. Poloczanska, K. Mintenbeck, A. Alegría, M. Nicolai, A. Okem, J. Petzold, B. Rama, N.M. Weyer (eds.)]. Cambridge University Press, Cambridge, UK and New York, NY, USA, pp. 131-202. <https://doi.org/10.1017/9781009157964.004>.
- Hodson, A., Anesio, A. M., Tranter, M., Fountain, A., Osborn, M., Priscu, J., Laybourn-Parry, J., & Sattler, B. (2008). Glacial Ecosystems. *Ecological Monographs*, *78*(1), 41–67. <https://doi.org/10.1890/07-0187.1>
- Hood, E., & Scott, D. (2008). Riverine organic matter and nutrients in southeast Alaska affected by glacial coverage. *Nature Geoscience*, *1*(9), 583–587. <https://doi.org/10.1038/ngeo280>
- Hood, E., & Berner, L. (2009). Effects of changing glacial coverage on the physical and biogeochemical properties of coastal streams in southeastern Alaska. *Journal of Geophysical Research: Biogeosciences*, *114*(G3). <https://doi.org/10.1029/2009JG000971>
- Hotaling, S., Hood, E., & Hamilton, T. L. (2017). Microbial ecology of mountain glacier ecosystems: Biodiversity, ecological connections and implications of a warming climate. *Environmental Microbiology*, *19*(8), 2935–2948. <https://doi.org/10.1111/1462-2920.13766>

- Hotaling, S., Foley, M. E., Zeglin, L. H., Finn, D. S., Tronstad, L. M., Giersch, J. J., Muhlfeld, C. C., & Weisrock, D. W. (2019). Microbial assemblages reflect environmental heterogeneity in alpine streams. *Global Change Biology*, 25(8), 2576–2590. <https://doi.org/10.1111/gcb.14683>
- Huss, M. (2012). Extrapolating glacier mass balance to the mountain-range scale: The European Alps 1900–2100. *The Cryosphere*, 6(4), 713–727. <https://doi.org/10.5194/tc-6-713-2012>
- Huss, M., Bookhagen, B., Huggel, C., Jacobsen, D., Bradley, R. s., Clague, J. j., Vuille, M., Buytaert, W., Cayán, D. r., Greenwood, G., Mark, B. g., Milner, A. m., Weingartner, R., & Winder, M. (2017). Toward mountains without permanent snow and ice. *Earth's Future*, 5(5), 418–435. <https://doi.org/10.1002/2016EF000514>
- Huss, M., & Hock, R. (2018). Global-scale hydrological response to future glacier mass loss. *Nature Climate Change*, 8(2), 135–140. <https://doi.org/10.1038/s41558-017-0049-x>
- Ilg, C., & Castella, E. (2006). Patterns of macroinvertebrate traits along three glacial stream continuums. *Freshwater Biology*, 51(5), 840–853. <https://doi.org/10.1111/j.1365-2427.2006.01533.x>
- Immerzeel, W. W., Lutz, A. F., Andrade, M., Bahl, A., Biemans, H., Bolch, T., Hyde, S., Brumby, S., Davies, B. J., Elmore, A. C., Emmer, A., Feng, M., Fernández, A., Haritashya, U., Kargel, J. S., Koppes, M., Kraaijenbrink, P. D. A., Kulkarni, A. V., Mayewski, P. A., Baillie, J. E. M. (2020). Importance and vulnerability of the world's water towers. *Nature*, 577(7790), 364–369. <https://doi.org/10.1038/s41586-019-1822-y>
- Jackson, A. L., Inger, R., Parnell, A. C., & Bearhop, S. (2011). Comparing isotopic niche widths among and within communities: SIBER – Stable Isotope Bayesian Ellipses in R. *Journal of Animal Ecology*, 80(3), 595–602. <https://doi.org/10.1111/j.1365-2656.2011.01806.x>
- Jacobsen, D., Dangles, O., Andino, P., Espinosa, R., Hamerlík, L., & Cadier, E. (2010). Longitudinal zonation of macroinvertebrates in an Ecuadorian glacier-fed stream: Do tropical glacial systems fit the temperate model? *Freshwater Biology*, 55(6), 1234–1248. <https://doi.org/10.1111/j.1365-2427.2009.02348.x>
- Jacobsen, D., Cauvy-Fraunie, S., Andino, P., Espinosa, R., Cueva, D., & Dangles, O. (2014). Runoff and the longitudinal distribution of macroinvertebrates in a glacier-fed stream: Implications for the effects of global warming. *Freshwater Biology*, 59(10), 2038–2050. <https://doi.org/10.1111/fwb.12405>
- Jacobsen, D., Laursen, S. K., Hamerlík, L., Moltesen, K., Michelsen, A., & Christoffersen, K. S. (2016). Fish on the roof of the world: Densities, habitats and trophic position of stone loaches (Triphlophysa) in Tibetan streams. *Marine and Freshwater Research*, 68(1), 53–64. <https://doi.org/10.1071/MF15225>
- Khamis, K., Brown, L. E., Hannah, D. M., & Milner, A. M. (2016). Glacier–groundwater stress gradients control alpine river biodiversity. *Ecohydrology*, 9(7), 1263–1275. <https://doi.org/10.1002/eco.1724>
- Klaar, M. J., Kidd, C., Malone, E., Bartlett, R., Pinay, G., Chapin, F. S., & Milner, A. (2015). Vegetation succession in deglaciated landscapes: Implications for sediment and landscape stability. *Earth Surface Processes and Landforms*, 40(8), 1088–1100. <https://doi.org/10.1002/esp.3691>
- Klawonn, I., Van den Wyngaert, S., Parada, A. E., Arandia-Gorostidi, N., Whitehouse, M. J., Grossart, H. P., et al. (2021). Characterizing the “fungal shunt”: Parasitic fungi on diatoms affect carbon flow and bacterial communities in aquatic microbial food webs. *Proc. Natl. Acad. Sci. U.S.A.* 118. doi: 10.1073/pnas.2102225118
- Kohler, T. J., Van Horn, D. J., Darling, J. P., Takacs-Vesbach, C. D., & McKnight, D. M. (2016). Nutrient treatments alter microbial mat colonization in two glacial meltwater streams from the McMurdo Dry Valleys, Antarctica. *FEMS Microbiology Ecology*, 92(4), fiw049. <https://doi.org/10.1093/femsec/fiw049>
- Kohler, T. J., Vinšová, P., Falteisek, L., Yde, J. C., Hatton, J. E., Hawkings, J. R., Lamarche-Gagnon, G., Hood, E., Cameron, K. A., & Stibal, M. (2020). Patterns in Microbial Assemblages Exported From the Meltwater of Arctic and Sub-Arctic Glaciers. *Frontiers in Microbiology*, 11. <https://doi.org/10.3389/fmicb.2020.00669>

- Kohler, T. J., Fodelianakis, S., Michoud, G., Ezzat, L., Bourquin, M., Peter, H., Busi, S. B., Pramateftaki, P., Deluigi, N., Styllas, M., Tolosano, M., de Staercke, V., Schön, M., Brandani, J., Marasco, R., Daffonchio, D., Wilmes, P., & Battin, T. J. (2022). Glacier shrinkage will accelerate downstream decomposition of organic matter and alters microbiome structure and function. *Global Change Biology*, 28(12), 3846–3859. <https://doi.org/10.1111/gcb.16169>
- Kohler, T. J., Bourquin, M., Peter, H., Yvon-Durocher, G., Sinsabaugh, R. L., Deluigi, N., Styllas, M., & Battin, T. J. (2024). Global emergent responses of stream microbial metabolism to glacier shrinkage. *Nature Geoscience*, 1–7. <https://doi.org/10.1038/s41561-024-01393-6>
- Leibold, M. A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J. M., Hoopes, M. F., Holt, R. D., Shurin, J. B., Law, R., Tilman, D., Loreau, M., & Gonzalez, A. (2004). The metacommunity concept: A framework for multi-scale community ecology. *Ecology Letters*, 7(7), 601–613. <https://doi.org/10.1111/j.1461-0248.2004.00608.x>
- Lencioni, V. (2004). Survival strategies of freshwater insects in cold environments. *Journal of limnology*, 63, 45–55. <https://doi.org/10.4081/jlimnol.2004.s1.45>
- Liu, Q., Zhou, Y.-G., & Xin, Y.-H. (2015). High diversity and distinctive community structure of bacteria on glaciers in China revealed by 454 pyrosequencing. *Systematic and Applied Microbiology*, 38(8), 578–585. <https://doi.org/10.1016/j.syapm.2015.09.005>
- Liu, Y., Tian, Y., Gao, Y., Cui, D., Zhang, W., Jiao, Z., Yao, F., Zhang, Z., & Yang, H. (2022). The Impacts of Different Anthropogenic Disturbances on Macroinvertebrate Community Structure and Functional Traits of Glacier-Fed Streams in the Tianshan Mountains. *Water*, 14(8), Article 8. <https://doi.org/10.3390/w14081298>
- Margesin, R., & Collins, T. (2019). Microbial ecology of the cryosphere (glacial and permafrost habitats): Current knowledge. *Applied Microbiology and Biotechnology*, 103(6), 2537–2549. <https://doi.org/10.1007/s00253-019-09631-3>
- McGregor, G., Petts, G. E., Gurnell, A. M., & Milner, A. M. (1995). Sensitivity of alpine stream ecosystems to climate change and human impacts. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 5(3), 233–247. <https://doi.org/10.1002/aqc.3270050306>
- McKernan, C., Cooper, D. J., & Schweiger, E. W. (2018). Glacial loss and its effect on riparian vegetation of alpine streams. *Freshwater Biology*, 63(6), 518–529. <https://doi.org/10.1111/fwb.13088>
- Michoud, G., Kohler, T. J., Peter, H., Brandani, J., Busi, S. B., & Battin, T. J. (2023a). Unexpected functional diversity of stream biofilms within and across proglacial floodplains despite close spatial proximity. *Limnology and Oceanography*, 68(9), 2183–2194. <https://doi.org/10.1002/lno.12415>
- Michoud, G., Kohler, T. J., Ezzat, L., Peter, H., Nattabi, J. K., Nalwanga, R., Pramateftaki, P., Styllas, M., Tolosano, M., De Staercke, V., Schön, M., Marasco, R., Daffonchio, D., Bourquin, M., Busi, S. B., & Battin, T. J. (2023b). The dark side of the moon: First insights into the microbiome structure and function of one of the last glacier-fed streams in Africa. *Royal Society Open Science*, 10(8), 230329. <https://doi.org/10.1098/rsos.230329>
- Milner, A. M., & Petts, G. E. (1994). Glacial rivers: Physical habitat and ecology. *Freshwater Biology*, 32(2), 295–307. <https://doi.org/10.1111/j.1365-2427.1994.tb01127.x>
- Milner, A. M., Brittain, J. E., Castella, E., & Petts, G. E. (2001). Trends of macroinvertebrate community structure in glacier-fed rivers in relation to environmental conditions: A synthesis. *Freshwater Biology*, 46(12), 1833–1847. <https://doi.org/10.1046/j.1365-2427.2001.00861.x>
- Milner, A. M., Brown, L. E., & Hannah, D. M. (2009). Hydroecological response of river systems to shrinking glaciers. *Hydrological Processes*, 23(1), 62–77. <https://doi.org/10.1002/hyp.7197>
- Milner, A. M., Khamis, K., Battin, T. J., Brittain, J. E., Barrand, N. E., Füreder, L., Cauvy-Fraunié, S., Gíslason, G. M., Jacobsen, D., Hannah, D. M., Hodson, A. J., Hood, E., Lencioni, V., Ólafsson, J. S., Robinson, C. T., Tranter, M., & Brown, L. E. (2017). Glacier shrinkage driving global changes in downstream systems. *Proceedings of the National Academy of Sciences*, 114(37), 9770–9778. <https://doi.org/10.1073/pnas.1619807114>
- Monaghan, M. T., Robinson, C. T., Spaak, P., & Ward, J. V. (2005). Macroinvertebrate diversity in fragmented Alpine streams: Implications for freshwater conservation. *Aquatic Sciences*, 67(4), 454–464. <https://doi.org/10.1007/s00027-005-0787-0>

- Morselli, M., Semplice, M., Villa, S., & Di Guardo, A. (2014). Evaluating the temporal variability of concentrations of POPs in a glacier-fed stream food chain using a combined modeling approach. *Science of The Total Environment*, 493, 571–579. <https://doi.org/10.1016/j.scitotenv.2014.05.150>
- National Snow and Ice Data Center. (2024). *Homepage*. <https://nsidc.org/home>
- Niedrist, G. H., & Füreder, L. (2017). Trophic ecology of alpine stream invertebrates: Current status and future research needs. *Freshwater Science*, 36(3), 466–478. <https://doi.org/10.1086/692831>
- Niedrist, G. H., & Füreder, L. (2018). When the going gets tough, the tough get going: The enigma of survival strategies in harsh glacial stream environments. *Freshwater Biology*, 63(10), 1260–1272. <https://doi.org/10.1111/fwb.13131>
- 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(3), 519–533. <https://doi.org/10.1086/699480>
- Parker, S. M., & Huryn, A. D. (2006). Food web structure and function in two arctic streams with contrasting disturbance regimes. *Freshwater Biology*, 51(7), 1249–1263. <https://doi.org/10.1111/j.1365-2427.2006.01567.x>
- Peterson, B. J., & Fry, B. (1987). Stable Isotopes in Ecosystem Studies. *Annual Review of Ecology and Systematics*, 18, 293–320.
- Ren, Z., Gao, H., Elser, J. J., & Zhao, Q. (2017). Microbial functional genes elucidate environmental drivers of biofilm metabolism in glacier-fed streams. *Scientific Reports*, 7(1), 12668. <https://doi.org/10.1038/s41598-017-13086-9>
- Ren, Z., Martyniuk, N., Oleksy, I. A., Swain, A., & Hotaling, S. (2019). Ecological Stoichiometry of the Mountain Cryosphere. *Frontiers in Ecology and Evolution*, 7. <https://doi.org/10.3389/fevo.2019.00360>
- Roncoroni, M., Brandani, J., Battin, T. I., & Lane, S. N. (2019). Ecosystem engineers: Biofilms and the ontogeny of glacier floodplain ecosystems. *WIREs Water*, 6(6), e1390. <https://doi.org/10.1002/wat2.1390>
- Rosemond, A. D., Benstead, J. P., Bumpers, P. M., Gulis, V., Kominoski, J. S., Manning, D. W. P., Suberkropp, K., & Wallace, J. B. (2015). Experimental nutrient additions accelerate terrestrial carbon loss from stream ecosystems. *Science*, 347(6226), 1142–1145. <https://doi.org/10.1126/science.aaa1958>
- 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(1), 195–216. <https://doi.org/10.1007/s10750-005-1811-z>
- Rounce, D. R., Hock, R., Maussion, F., Hugonnet, R., Kochtitzky, W., Huss, M., Berthier, E., Brinkerhoff, D., Compagno, L., Copland, L., Farinotti, D., Menounos, B., & McNabb, R. W. (2023). Global glacier change in the 21st century: Every increase in temperature matters. *Science*, 379(6627), 78–83. <https://doi.org/10.1126/science.abo1324>
- Sajjad, W., Ali, B., Bahadur, A., Ghimire, P. S., & Kang, S. (2021). Bacterial Diversity and Communities Structural Dynamics in Soil and Meltwater Runoff at the Frontier of Baishui Glacier No.1, China. *Microbial Ecology*, 81(2), 370–384. <https://doi.org/10.1007/s00248-020-01600-y>
- Sawyer, A. H., Kaplan, L. A., Lazareva, O., & Michael, H. A. (2014). Hydrologic dynamics and geochemical responses within a floodplain aquifer and hyporheic zone during Hurricane Sandy. *Water Resources Research*, 50(6), 4877–4892. <https://doi.org/10.1002/2013WR015101>
- Senga, Y., Yabe, S., Nakamura, T., & Kagami, M. (2018). Influence of parasitic chytrids on the quantity and quality of algal dissolved organic matter (AOM). *Water Research*, 145, 346–353. <https://doi.org/10.1016/j.watres.2018.08.037>
- Sertić Perić, M., Nielsen, J. M., Schubert, C. J., & Robinson, C. T. (2021). Does rapid glacial recession affect feeding habits of alpine stream insects? *Freshwater Biology*, 66(1), 114–129. <https://doi.org/10.1111/fwb.13621>
- Schiller, D. V., Martí, E., Riera, J. L., & Sabater, F. (2007). Effects of nutrients and light on periphyton biomass and nitrogen uptake in Mediterranean streams with contrasting land uses. *Freshwater Biology*, 52(5), 891–906. <https://doi.org/10.1111/j.1365-2427.2007.01742.x>

- Singer, G. A., Fasching, C., Wilhelm, L., Niggemann, J., Steier, P., Dittmar, T., & Battin, T. J. (2012). Biogeochemically diverse organic matter in Alpine glaciers and its downstream fate. *Nature Geoscience*, 5(10), 710–714. <https://doi.org/10.1038/ngeo1581>
- Slemmons, K. E. H., Saros, J. E., & Simon, K. (2013). The influence of glacial meltwater on alpine aquatic ecosystems: A review. *ENVIRONMENTAL SCIENCE-PROCESSES & IMPACTS*, 15(10), 1794–1806. <https://doi.org/10.1039/c3em00243h>
- Solomina, O., Bushueva, I., Dolgova, E., Jomelli, V., Alexandrin, M., Mikhaleiko, V., & Matskovsky, V. (2016). Glacier variations in the Northern Caucasus compared to climatic reconstructions over the past millennium. *Global and Planetary Change*, 140, 28–58. <https://doi.org/10.1016/j.gloplacha.2016.02.008>
- Spencer, R. G. M., Vermilyea, A., Fellman, J., Raymond, P., Stubbins, A., Scott, D., & Hood, E. (2014). Seasonal variability of organic matter composition in an Alaskan glacier outflow: Insights into glacier carbon sources. *Environmental Research Letters*, 9(5), 055005. <https://doi.org/10.1088/1748-9326/9/5/055005>
- Sterner, R. W., & Elser, J. J. (2017). Ecological Stoichiometry: The Biology of Elements from Molecules to the Biosphere. In *Ecological Stoichiometry*. Princeton University Press. <https://doi.org/10.1515/9781400885695>
- Sudlow, K., Tremblay, S. S., & Vinebrooke, R. D. (2023). Glacial stream ecosystems and epilithic algal communities under a warming climate. *Environmental Reviews*, 31(3), 471–483. <https://doi.org/10.1139/er-2022-0114>
- Thompson, R. M., Brose, U., Dunne, J. A., Hall, R. O., Hladysz, S., Kitching, R. L., Martinez, N. D., Rantala, H., Romanuk, T. N., Stouffer, D. B., & Tylianakis, J. M. (2012). Food webs: Reconciling the structure and function of biodiversity. *Trends in Ecology & Evolution*, 27(12), 689–697. <https://doi.org/10.1016/j.tree.2012.08.005>
- Treonis, A. M., Wall, D. H., & Virginia, R. A. (1999). Invertebrate Biodiversity in Antarctic Dry Valley Soils and Sediments. *Ecosystems*, 2(6), 482–492. <https://doi.org/10.1007/s100219900096>
- Uehlinger, U., Zah, R., & Bürgi, H. (1998). The Val Roseg project: temporal and spatial patterns of benthic algae in an Alpine stream ecosystem influenced by glacier runoff. *IAHS publ*, (248), 419–424.
- 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. In R. J. Stevenson & S. Sabater (Ed.), *Global Change and River Ecosystems—Implications for Structure, Function and Ecosystem Services* (s. 107–121). Springer Netherlands. https://doi.org/10.1007/978-94-007-0608-8_8
- Viviroli, D., Dürr, H. H., Messerli, B., Meybeck, M., & Weingartner, R. (2007). Mountains of the world, water towers for humanity: Typology, mapping, and global significance. *Water Resources Research*, 43(7). <https://doi.org/10.1029/2006WR005653>
- Wadham, J. L., Hawkings, J., Telling, J., Chandler, D., Alcock, J., O'Donnell, E., Kaur, P., Bagshaw, E., Tranter, M., Tedstone, A., & Nienow, P. (2016). Sources, cycling and export of nitrogen on the Greenland Ice Sheet. *Biogeosciences*, 13(22), 6339–6352. <https://doi.org/10.5194/bg-13-6339-2016>
- Ward, J. v. (1994). Ecology of alpine streams. *Freshwater Biology*, 32(2), 277–294. <https://doi.org/10.1111/j.1365-2427.1994.tb01126.x>
- Weijs, S. V., Mutzner, R., & Parlange, M. B. (2013). Could electrical conductivity replace water level in rating curves for alpine streams? *Water Resources Research*, 49(1), 343–351. <https://doi.org/10.1029/2012WR012181>
- Weisleitner, K., Perras, A. K., Unterberger, S. H., Moissl-Eichinger, C., Andersen, D. T., & Sattler, B. (2020). Cryoconite Hole Location in East-Antarctic Untersee Oasis Shapes Physical and Biological Diversity. *Frontiers in Microbiology*, 11. <https://doi.org/10.3389/fmicb.2020.01165>
- Wilhelm, L., Singer, G. A., Fasching, C., Battin, T. J., & Besemer, K. (2013). Microbial biodiversity in glacier-fed streams. *The ISME Journal*, 7(8), 1651–1660. <https://doi.org/10.1038/ismej.2013.44>
- Yang, G. L., Hou, S. G., Le Baoge, R., Li, Z. G., Xu, H., Liu, Y. P., Du, W. T., & Liu, Y. Q. (2016). Differences in Bacterial Diversity and Communities Between Glacial Snow and Glacial Soil on the Chongce Ice Cap, West Kunlun Mountains. *Scientific Reports*, 6(1), 36548. <https://doi.org/10.1038/srep36548>

- Zah, R., & Uehlinger, U. (2001). Particulate organic matter inputs to a glacial stream ecosystem in the Swiss Alps. *Freshwater Biology*, 46(12), 1597–1608. <https://doi.org/10.1046/j.1365-2427.2001.00847.x>
- Zah, R., Burgherr, P., Bernasconi, S. M., & Uehlinger, U. (2001). Stable isotope analysis of macroinvertebrates and their food sources in a glacier stream. *Freshwater Biology*, 46(7), 871–882. <https://doi.org/10.1046/j.1365-2427.2001.00720.x>
- Zemp, M., Frey, H., Gärtner-Roer, I., Nussbaumer, S. U., Hoelzle, M., Paul, F., Haeberli, W., Denzinger, F., Ahlstrøm, A. P., Anderson, B., Bajracharya, S., Baroni, C., Braun, L. N., Cáceres, B. E., Casassa, G., Cobos, G., Dávila, L. R., Granados, H. D., Demuth, M. N., Vincent, C. (2015). Historically unprecedented global glacier decline in the early 21st century. *Journal of Glaciology*, 61(228), 745–762. <https://doi.org/10.3189/2015JoG15J017>