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and their Tidal System - SMART

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ECOLOGICAL SHIFTS OF STREAM ECOSYSTEMS IN A DEGLACIATING AREA OF THE EUROPEAN ALPS

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Abstract

This thesis provides a contribution to the knowledge on the effects of deglaciation on alpine stream ecosystems, taking into account also the hydroecological influence of thawing permafrost and paraglacial features. With a focus on the European Alps, a review is provided on the climate changes and shifts in the cryosphere (snow, glaciers, permafrost), the related changes in hydrology, geomorphic processes and the physical and chemical habitat of alpine river networks, and the consequent shifts in stream communities and food webs. A conceptual model is provided to summarize the complex interactions and the cascading effects triggered by deglaciation on hydrology, habitat and biota of alpine streams, that can be useful for educational purposes and to help the scientific community to contextualize these issues to other alpine areas. Deglaciation induces homogenisation of river networks, loss of biodiversity, and shifts in primary and secondary production, functional diversity and food webs. The scarce published studies on streams influenced by permafrost provide hints on the role of thawing rock glaciers (i.e. evident form of mountain permafrost) in shaping the ecology of freshwaters, and reveal important research gaps. To increase the knowledge on this topic, different alpine streams fed by waters of different origin were selected in two subcatchments (Zay, Solda) of a deglaciating area of the Central Italian Alps (Solda Valley), and their habitat conditions and benthic invertebrate communities were investigated over a two-year period. Rock glacier-fed streams could be distinguished from those fed by glaciers, groundwater and those of mixed origin because of their constantly clear and very cold waters, stable channels, and high concentrations of ions and trace elements that increased as summer progressed. Furthermore, the Zay rock glacier strongly influenced the glacier-fed stream through an intense export of solutes, which become progressively more relevant towards the end of summer. This influence was also due to the contribution of a proglacial lake and a moraine body, that both strongly decreased the glacial influence along the glacier-fed stream before its confluence with the rock glacier outflow. The wide range of habitat conditions revealed to strongly influence the benthic invertebrate communities in the study area. Channels with groundwater (*krenal*) and mixed (*glacio-rhithral*) exhibited a higher taxa richness and diversity. Peaks of abundance and biomass in the catchment were recorded just downstream the talus body, in the upper *glacio-rhithral* channel. Chironomidae from the cold-adapted genus *Diamesa* were dominant in the proglacial sections (*upper kryal*) of the glacier-fed streams. The proglacial lake, the moraine body and the rock glacial tributary at Zay contributed to the amelioration of the environmental features of the glacier-fed stream (*lower kryal*), boosting high invertebrate biomass and abundance and causing shifts in the community composition (e.g. increased Orthocladiinae and other Diamesinae chironomids, abundant Trichoptera). The two *rock glacial* communities differed considerably between each other. In fact, the community of the Zay rock glacial stream was partially influenced by the seepage of glacier waters, and resembled those of the surrounding *lower kryal*. On the

contrary, the Solda *rock glacial* stream, detached from any glacier influence, hosted a rich and diverse community which resembled those of *glacio-rhithral* and *krenal*, even though with a higher abundance of *Diamesa*. Overall, the results of this thesis showed that in the advanced phases of glacier retreat, paraglacial landforms and permafrost can increasingly contribute to the riverscape diversity and shape the ecology of river networks. Because of their unique environmental settings, r*ock glacial* streams should be considered a distinct alpine stream habitat, acting in deglaciating catchments as stepping stones that enhance the upstream colonisation of non-glacial communities following glacier retreat. At the same time, they might represent *cold refugia* for cold-stenothermal and/or typically glacial taxa when glaciers will be disappeared, because of the slower thawing rate of rock glacier ice. In this context, the presence of *Diamesa* kryal specialist species in *rock glacial* streams deserves further investigation, in order to understand the potential conservation value that these habitats may have in buffering the β-diversity reduction which is predicted in alpine areas as a consequence of glacier loss.

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INTRODUCTION

According to the last report from the Intergovernmental Panel on Climate Change [IPCC], anthropogenic radiative forcing is the main driver of the current, accelerated climate change, such that the "*Human influence has been detected in warming of the atmosphere and the ocean, in changes in the global water cycle, in reductions in snow and ice, in global mean sea level rise, and in changes in some climate extremes. […] It is extremely likely that human influence has been the dominant cause of the observed warming since the mid-20th century.*" (IPCC, 2013). The accelerated loss of cryosphere is among the most evident effects of the current climate change worldwide. In the Polar regions the ice sheets of Greenland and the Antarctic are shrinking, thus contributing to the sea level rising and to modifying the Gulf current with climatic positive feedbacks. The Arctic sea ice and the spring snow cover over the whole Northern hemisphere are decreasing in extent (IPCC, 2013). In the mountains, glaciers shrinkage is affecting several ecosystem services (e.g. climate regulation, hydropower production, tourism), including the provisioning of freshwater used in downstream areas for food production and other fundamental human needs (Milner et al., 2017). The degradation of permafrost is another outcome of climate change, and in Polar regions it provides positive feedbacks to the climate system by releasing carbon compounds in the atmosphere (IPCC, 2013). Other consequences of permafrost degradation include an increased geomorphologic risk with enhanced natural hazards (e.g. rockfalls, landslides, debris-flows; see Schoeneich et al., 2011) and water contamination (Beniston et al., 2018; Colombo et al., 2018a). Among the multiple, multifaceted and interconnected effects of the cryosphere loss, evidence is increasing of vast ecological shifts that are occurring worldwide and include loss/replacement of habitats and species, and changes in the biogeochemical cycles, ecological communities and ecosystem functioning (Fountain et al., 2012).

Among the areas where cryosphere is shrinking at increasing rates, the European Alps represent one of the most studied and monitored mountain ranges worldwide (see chapter I). Being among the most densely populated mountain areas in the world, they are particularly affected by local and regional-scale human pressures, also because of their vicinity to intensively urbanised and industrialised areas. Effects of snow cover changes, glacier retreat and permafrost thaw on the social, economic and ecological systems over the Alpine region are well documented and will increase in the near future (e.g. Beniston et al., 2018).

Aim of this thesis is to analyse the ecological shifts of stream ecosystems associated with deglaciation in the European Alps. The work investigates the combined role of shrinking glaciers and thawing permafrost in driving habitat conditions and biota of the Alpine river networks, with particular attention focused on the characterisation of streams fed by thawing rock glaciers. Among the most evident and common forms of mountain permafrost, rock glaciers are lobate or tongue-shaped assemblages of poorly sorted, angular rock-debris and ice that show evidence of present or past movement (Jones et al., 2019). While the debate on a clear definition and classification of rock glaciers is still open (e.g. an action group of the International Permafrost Association, launched during the 2018 European Conference on Permafrost in Chamonix, is working on agreed standard guidelines for rock glaciers inventorying), studies on their hydrological importance in deglaciating mountain catchments have been progressively increasing in the last years (Jones et al., 2019). Although only a fraction of rock glaciers have water outflow at their front (this proportion is unknown, but e.g. in our study area only 3/8 rock glaciers showed permanent water outlets), and only a (unknown) fraction of rock glaciers still contains ice, this work provides a contribution to the increasing body of knowledge on their ecological importance to freshwater ecosystems under thawing conditions.

The first chapter is a published literature review on the available knowledge on the effects of climate change and deglaciation on the alpine stream ecosystems in the European Alps. Because the shrinkage of permafrost ice is much slower than that of glacier ice (Jones et al., 2019), the geomorphology and hydrology of alpine catchments will be increasingly shaped by the influence of permafrost thaw and the processes and landforms occurring in terrains left uncovered by glaciers (e.g. proglacial lakes, moraine deposits, talus fans). This transition from glacial to periglacial/paraglacial influence (Haeberli et al., 2017) has the potential to substantially affect the hydrology and the physical and chemical features of alpine river networks, as well as their ecology.

Alpine stream ecosystems rely upon the contribution of a shifting water balance, which, at present, is being increasingly shaped by stochastic precipitation patterns and groundwater contribution. Thus, chapter I provides a summary on the available knowledge on the hydroecological implications of these shifts, on evidences of occurring changes in the prevalence of hydromorphological processes, and on shifts in the water quality and the overall habitat conditions. The review focuses on the biological implications of these changes, in particular on microbial communities, primary producers and invertebrate communities and their interactions within the food webs. To summarize the interactions between several macroscale, mesoscale and microscale drivers, and to identify the key ecological shifts of stream ecosystems associated with deglaciation in the European Alps, a conceptual model has been designed. Although developed in the context of the European Alps, this model may serve as a useful tool for science communication, and may be applied and contextualised to other deglaciating mountain areas. This is something already occurring, as a permission request for the utilisation of the model already came from Prof. Brian Whalley (University of Sheffield, UK) for conference presentation of a study located in Norway (2019 meeting of the British Society for Geomorphology). From the literature review, it emerged that the increasing role of permafrost thaw in shaping the hydroecology of alpine river networks represents an understudied topic, for the European Alps as well as at the global scale.

To help filling this knowledge gap, a deglaciating high-mountain area in the Ortles-Cevedale massif (Solda Valley, Eastern-Central Italian Alps) was investigated. Two sub-catchments, differing in terms of glacier coverage and abundance of paraglacial features, were identified, and monitored over a set of sampling stations that were characterised in terms of hydrology, hydrochemistry, physical conditions, and abundance of organic detritus, primary production, and benthic invertebrate communities. Field activities were undertaken for two consecutive years (2017/2018), in different key periods of the snow-free summer, i.e. snowmelt, glacier ablation, autumn recession. The second and third chapters report on this empirically-based field research and its findings.

The second chapter is a published characterization of the habitat conditions of streams fed by thawing rock glaciers, in comparison with the other stream habitats which have been well-investigated in the available literature. This chapter describes the influence of rock glacier streams on the hydrology and on the physical and chemical features of the alpine river networks and helps to further understanding. As such, the paper is the first to demonstrate the increasing and combined influence of rock glaciers and other features of the Alpine paraglacial landscape (i.e. proglacial lake, moraine and a talus slope) on the river habitat conditions in areas experiencing glacier retreat. In particular, this increasing influence is highlighted for catchments in the late phases of deglaciation, when the hydrological role of glaciers is fading and that of other geomorphological drivers can emerge. Furthermore, and with reference to limited studies elsewhere, it was possible to identify the key habitat features that distinguish *rock glacial* streams from the alpine stream types previously described in relation to water source: glacier-fed (*kryal*), groundwater-fed (*krenal*) and mixed-origin (*glacio-rhithral*) streams.

The third chapter describes the biological implications of the presence of thawing rock glaciers and the other paraglacial features in the catchment. With a focus on the benthic invertebrate communities, insights are provided on the biogeographical role of rock glacial streams, which may represent stepping stones favouring the colonisation of upstream reaches following glacier retreat and, after glaciers loss, may represent refugia for cold-adapted taxa. The research revealed that rock glaciers and other paraglacial features shaped the benthic communities by disrupting the linear gradients of abundance, biomass and taxa composition along the glacier-fed stream. The chapter also provides a first attempt of understanding the role of aquatic bryophytes, typically abundant in rock glacial channels, in modulating abundance, biomass and body size patterns in alpine streams under deglaciation. The analysis of such metrics is underrepresented in previous alpine stream studies, where the invertebrate density is the most common parameter assessed. Within this context, the adopted approach may contribute to the general improvement of knowledge on alpine stream invertebrates.

The reference chapter of the thesis provides the complete bibliography for the three chapters and this introduction, while the supplementary material includes the additional information, the used datasets and the records of participation to conferences and meetings.

This thesis includes only a part of the large amount of data produced during the three-year doctoral study, which are synthetically reported in Table A. The information not included here will be processed and is aimed to be published in the near future, as briefly illustrated in the conclusive part of this thesis.

Table A. *Activities undertaken during my PhD, and the corresponding outcomes/assessed parameters and place where activity was conducted (QMUL= Queen Mary University of London; IGB= Leibniz Institute of Freshwater Ecology and Inland Fisheries, Berlin; FEM= Edmund Mach Foundation, Trento, UniTN= University of Trento; UniBZ= University of Bolzano/Bozen; Solda= Solda Valley; Cevedale= Val de la Mare, MUSE= Museum of Natural Sciences, Trento). Where I was not directly involved in the activity/outcome, the person/laboratory is provided in brackets*

Activities	Location[1]	Date/Period	Outcomes/parameters
Attendance of lessons and exams (6 months); Fulfilment of the SMART programme credits requirement	QMUL	September 2016 - March 2017	Chapter I. First published paper
Improvement of English language skills	QMUL, IGB, FEM	September 2016 - March 2017	
Field activities	Solda, Cevedale	Summer 2017/2019	> 40 field campaigns; Chapters II, III. Second published paper
Recognition field trip	Solda, Cevedale	September 2016	Planning of the surveys
Collection of water samples	Solda, Cevedale	Summer 2017/2019	Base chemistry (FEM), DOC (Dolomiti Energia), water stable isotopes (UniBZ)
Collection, filtering and acidification of water samples	Solda, Cevedale	Summer 2017/2019	Trace elements concentration (EcoResearch Srl lab)
Collection of invertebrate samples	Solda, Cevedale	Summer 2017/2018	Benthic invertebrates and detritus
Assessment of stream physical parameters	Solda, Cevedale	Summer 2017/2019	Habitat conditions
Longitudinal surveys (12 days)	Solda	Summer 2018	See chapter II
Discharge measurements	Solda	Summer 2018/2019	Hydrology
Collection of pelagic sediment cores from the Lake Marmotte (2706 m a s.l)	Cevedale	September 2017	Long term deglaciation history (main: Monica Tolotti)
Laboratory activities and data analysis			
Sorting and identification of invertebrates	QMUL, IGB, FEM	2017/2019	Chapters II, III
Determination of: BOM, Suspended solids concentration, Epilithic production (Chl-*a*, AFDM), Body size of invertebrates	FEM	2017/2019	Assessment of the invertebrate communities - MSc thesis University of Parma (co-supervision with M.C. Bruno); BD thesis University of Padua (co-supervision with M.C. Bruno) Assessment of habitat features, abundance of organic detritus, primary production and invertebrate biomass

Other activities (>500 hrs)	Solda, Cevedale		Not included in the chapters
Collection and preparation of invertebrates, laboratory activities	Solda, FEM	2017/2019	Food web analysis with stable isotopes (FEM lab)
Collection, dissection and preparation of lake sediment cores	Cevedale, FEM	2018	Forecasted preparation of joint papers (first author: Monica Tolotti) Co -supervisor in the thesis of a MSc student of the University of Pavia (supervisor M. Tolotti)
Collection and identification of diatoms and Eubacteria/Archaea (my supervisor Monica Tolotti and students)	Cevedale, Solda, FEM	2018/2019	Forecasted preparation of joint papers (first author: Monica Tolotti)
Identification of copepoda (my supervisor Maria Cristina Bruno)	FEM	2019	Forecasted preparation of joint papers
Networking activities			
Collaboration with University of Bolzano/Bozen		2016/2019	Contribution for Chapter II
Collaboration with the Geological Office, Province of Bolzano/Bozen (W. Mair)		2018/2019	Contribution for Chapter II
Started a collaboration with the Museum of Science of Trento (Dr. Valeria Lencioni)	FEM/MUSE	2019	Identification of Chironomidae species, forecasted preparation of joint papers
Collaboration with the Institute of Geological Sciences, Polish Academy of Science (E. Zawisza), Warsaw, Poland	Cevedale	2019	Identification of sub-fossil Cladocera remains from lake sediments, forecasted preparation of joint papers

CHAPTER 1

Ecosystem shifts in Alpine streams under glacier retreat and rock glacier thaw

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1.1 INTRODUCTION

Glacier retreat and permafrost thaw are among the most evident effects of current climate change (Intergovernmental Panel on Climate Change [IPCC], 2013). The global character and the speed of present deglaciation are unprecedented in the Holocene (Solomina et al., 2015), and reflect a dominant anthropogenic component (Marzeion et al., 2014). The consequences of deglaciation are a global issue, since the cryosphere provides important ecosystem services such as water provisioning, especially during hot and dry periods, climate regulation, and the global cycling and sequestration of carbon (Anesio et al., 2009; Milner et al., 2017). Mountains are acknowledged as early warning areas of global warming because of their high sensitivity to temperature changes and limited direct human impacts (Beniston, 2005; Körner et al., 2005). As they store and supply freshwater to rivers and lowland areas, with a vital importance for human societies and ecosystems (Meyer et al., 2007), mountains are considered as “water towers” of the world (see Viviroli et al., 2007). In the European Alps (hereafter referred to as “the Alps”), climate change and the accelerated reduction of the cryosphere (Vincent et al., 2017; Beniston et al., 2018) have many consequences, including summer water shortages at the whole basin scale (European Environment Agency [EEA], 2009; Huss, 2011), increased geomorphologic risk (e.g. Haeberli and Beniston, 1998; Haeberli et al., 2010; Kellerer-Pirklbauer et al., 2011; Mair et al., 2015; Haeberli et al. 2016), depletion of drinking water quality (Bogataj, 2007, Mair et al., 2015), and decline of tourism (Smiraglia et al., 2008). Long term changes also pertain to the overall Alpine mountain ecology, with a reported decrease and in places the extinction of sensitive habitats, species, and populations (e.g. Walther, 2004; Schröter et al., 2005; EEA, 2009; Dirnböck et al., 2011). Furthermore, changes in climate and deglaciation interact with local pressures, potentially multiplying the consequences. For example, water exploitation for hydropower production (e.g. Permanent Secretariat of the Alpine Convention, 2009) and drinking water supply (e.g. Klug et al., 2012), intensification of transhumance (Tiberti et al., 2014), stocking with allochthonous fish (e.g. Tiberti et al., 2013), and touristic activities and infrastructures (e.g. Rixen et al., 2011) currently represent major local stressors for freshwaters in the Alps.

Several reviews have been published to date on the effects of deglaciation on alpine freshwaters, especially during the last years. While McGregor et al. (1995) focus on the effects of hydropower generation and glacier loss specifically in the Alps, most reviews have a global perspective as they focus on the relationship between habitat changes and biotic shifts associated to glacier shrinkage at high latitudes and altitudes. Some focus on single ecosystem drivers (i.e., the importance of the ice melt: Slemmons et al., 2013); others provide different frameworks of analysis (i.e., hydroecology: Milner et al., 2009; the “multitrophic” approach: Fell et al., 2017); or focus on the organism-based research by emphasizing methods and approaches (i.e., Hotaling et al., 2017). Milner et al. (2017) provide a wider context by considering the implications of glacier loss to physical and chemical fluxes, biodiversity, and ecosystem services to lowland areas along the river continuum. However, although these reviews have been important in highlighting the significance of glacier retreat for freshwater ecosystems, they pay little attention to the thawing of permafrost. With a focus on mountain areas, only Huss et al. (2017) consider the combined loss of snow, permafrost, and glaciers, analysing the resulting changes in the overall ecology, geomorphology, and socio-economy. Our review builds on this holistic approach to cryosphere and provides a synthesis of the consequences of both glacier retreat and permafrost thaw (hereafter referred to as “deglaciation”) on stream ecosystems in the Alps which, to the best of our knowledge, is the first synthesis for a specific mountain range. Mountain ranges around the world differ in terms of climate, topography, average elevation, geology, distribution and prevalence of glacial and periglacial forms and phenomena, sensitivity to climate change, and local and regional human pressures (e.g. Huss et al., 2017). These peculiarities likely drive unique and mountain range specific patterns of responses to deglaciation. Likewise, as the most studied mountain range in the world (Figure 1.1), research on the Alps has the potential to provide insights into the effects of deglaciation elsewhere.

To synthesize the complex effects of climate change and deglaciation on stream ecosystems in the Alps, we developed a conceptual model (Figure 1.2), which provides a framework for our review. Herein, stream ecosystems located above the treeline are referred to as “alpine streams”, whereas “Alpine streams” are alpine streams located in the Alps.

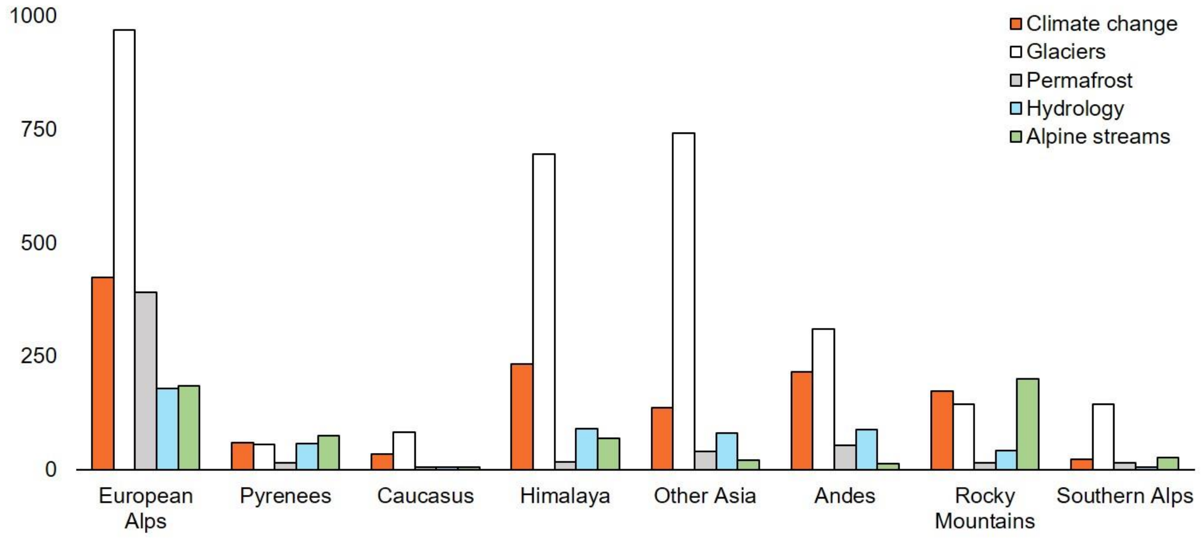
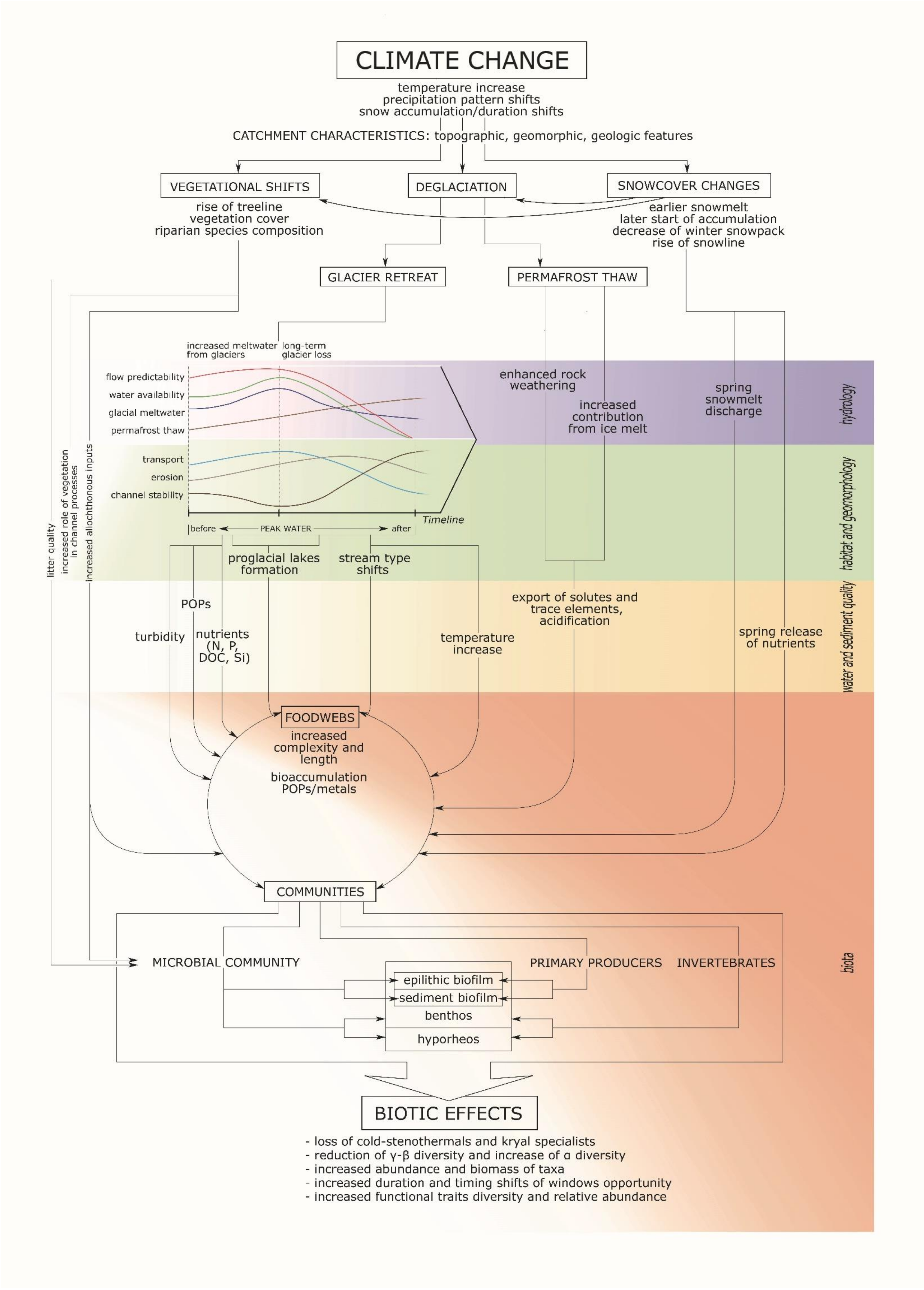


Figure 1.1. *Number of scientific studies published on the topics of climate change, glaciers, permafrost, alpine hydrology and alpine streams for the major world mountain regions at temperate latitudes (30-60°) and with an appreciable cryosphere extent (UNEP, 2008).*
NOTE: We selected in Web of Science (www.webofknowledge.com, last access 25/01/2019) searches on each region (keywords: "Alps" NOT "New Zealand", "Pyrenees", "Caucasus", "Himalaya", "Karakoram", "Tienshan" OR "Tien Shan" OR "Tian Shan" OR "Tianshan", "Kunlun Shan" OR "Kunlun mountains" OR "Kunlunshan", "Andes", "Rocky Mountains" OR "Rockies", "New Zealand" AND "Alps") as TOPIC (word included at least in title, abstract, or keywords), and crossed with each subject (keywords: "climate change" OR "global warming", "glacier" OR "glaciers" NOT "rock glacier" NOT "rock glaciers", "permafrost" OR "rock glacier" OR "rock glaciers", "hydrology" OR "hydrological", "stream" OR "streams") as TITLE (only included in the title). In the graphic "Other Asia" = Kunlunshan, Tienshan, Karakoram.

Figure 1.2 *(NEXT PAGE). Conceptual model of the effects of climate change and deglaciation on Alpine stream ecosystems. Lines with arrows: direct influence. Climate change interacts with catchment-specific features in determining deglaciation and shifts in snow cover and vegetation. These key catchment changes and their interactions have distinct consequences on the hydrology, geomorphology and habitat, and on the quality of water and sediment (different layers). Different time scale impacts of glacier retreat are summarized in the specific chart, showing the trend of key hydrological and geomorphological parameters over the two identified phases, i.e. before and after the "peak water" period governed by glaciers. All the specified abiotic changes have different consequences for the stream biota, i.e. the different interacting communities resulting in an altered food webs (cycle). "Microbial community" is meant here as Archaea, Eubacterial heterotrophs and Fungi, and "Primary producers" include Algae, Cyanobacteria and Bryophytes. The resulting key biotic effects of deglaciation on Alpine streams are summarized in bullet points.*


CLIMATE CHANGE
temperature increase
precipitation pattern shifts
snow accumulation/duration shifts
CATCHMENT CHARACTERISTICS: topographic, geomorphic, geologic features
VEGETATIONAL SHIFTS
rise of treeline
vegetation cover
riparian species composition
DEGLACIATION
SNOWCOVER CHANGES
earlier snowmelt
later start of accumulation
decrease of winter snowpack
rise of snowline
GLACIER RETREAT
PERMAFROST THAW
increased meltwater from glaciers
long-term glacier loss
flow predictability
water availability
glacial meltwater
permafrost thaw
transport
erosion
channel stability
Timeline
before
PEAK WATER
after
enhanced rock weathering
increased contribution from ice melt
spring snowmelt discharge
hydrology
habitat and geomorphology
water and sediment quality
biota
litter quality
increased role of vegetation in channel processes
increased allochthonous inputs
proglacial lakes formation
stream type shifts
POPs
turbidity
nutrients (N, P, DOC, Si)
temperature increase
export of solutes and trace elements, acidification
spring release of nutrients
FOODWEBS
increased complexity and length
bioaccumulation POPs/metals
COMMUNITIES
MICROBIAL COMMUNITY
PRIMARY PRODUCERS
INVERTEBRATES
epilithic biofilm
sediment biofilm
benthos
hyporheos
BIOTIC EFFECTS
- loss of cold-stenothermals and kryal specialists
- reduction of γ-β diversity and increase of α diversity
- increased abundance and biomass of taxa
- increased duration and timing shifts of windows opportunity
- increased functional traits diversity and relative abundance

1.2. SETTING THE SCENE: THE WARMING ALPS AND THEIR DEGRADING CRYOSPHERE

The Alps (43-48°latitude, 5-17°longitude) are the highest (4,810 m a.s.l.) and largest (190,000 km^2) mountain system entirely located in Europe, covering 11% of the continental area (Treccani Enciclopedia, 2018) in one of the most densely populated areas worldwide (Huss et al., 2017). Because of their geographical location, the large-scale influences of different climate regimes (Atlantic, Mediterranean, Polar, Continental and African) interact with local features (e.g. topography, aspect, proximity to the sea), producing a large climatic variability (Beniston, 2006) that enhances biodiversity (Nagy et al., 2003; Alpine Ecological Network, 2018).

The Alps have experienced an increase in average annual temperature of 2°C between the late 19th and the early 21st Century, corresponding to more than twice the global and European averages (Auer et al., 2007; EEA, 2009). This trend is predicted to continue, as reviewed under different IPCC scenarios by Gobiet et al. (2014). On average, temperature is estimated to rise by 1.5°C during the first half of the 21st Century, and by 3.3°C during the second half, with more pronounced changes predicted at higher elevations (Gobiet et al., 2014; Kotlarski et al., 2015). Although slight average precipitation shifts were recorded during the second half of the past century depending on the Alpine sector (Auer et al., 2007), future trends are uncertain. Recent estimates support the hypothesis that, despite an overall decrease in summer precipitation in the area, high elevations may face an increased rainfall during the same season because of convective phenomena (Giorgi et al., 2016), and the seasonality and intensity of extreme precipitation events may change (Brönnimann et al., 2018).

Reductions in snow, glacier and permafrost extent are all features of the changing Alpine cryosphere (Beniston et al., 2018). The ongoing rise of the snowline is expected to continue during the 21st Century, with a decline of the snow cover and an earlier snowmelt onset during spring (Huss et al., 2017; Beniston et al., 2018,). Alpine glaciers have been receding at increasing rates during recent decades (Zemp et al., 2006; Haeberli et al., 2007; EEA, 2017). Around 75% of the Alpine glaciated surface recorded during the period 1971-1990 is predicted to vanish by 2050 (Haeberli and Hohman, 2008), while 80 to 100% of the glaciers in the Alps are expected to disappear by the end of the 21th Century (Zemp et al., 2006), with very small glaciers (< 0.5 km^2 area), representing the vast majority, vanishing over the next two decades (Huss and Fischer, 2016).

Glacier retreat is paralleled by permafrost loss. Permafrost is defined as “ground (soil or rock, including ice and organic material) that remains at or below 0 °C for at least two consecutive years” (Dobinski, 2011). Rock glaciers, defined by van Everingden (2005) as “masses of rock fragments and finer material that contains either interstitial ice or an ice core and show evidence of past or present movement”, are an evident and common form of mountain permafrost (Schoeneich et al., 2011). As for glaciers, a large proportion of Alpine permafrost is located close to the melting point, and is therefore particularly sensitive to increases in atmospheric temperature. Responses to warming comprise thermal and geomorphic alterations, such as the thinning of the active layer (i.e. the upper part, seasonally freezing and thawing) and the melting of internal ice (i.e. permafrost thaw) with associated destabilization of slopes, increased frequency and magnitude of mass movements such as debris flows, rockfalls and rockslides (Schoeneich et al., 2011), and increased creeping velocity of active rock glaciers (Kääb et al., 2007; Harris et al., 2009; Kellerer-Pirklbauer et al., 2011).

Permafrost thaw triggered by increasing air temperature is much slower than glacier retreat (Beniston et al., 2018), since the active layer acts as a thermal buffer (Harris et al., 2008). Rock glaciers are thermally decoupled from external climate and are therefore less climatically sensitive than glaciers (Jones et al., 2018). For the same reason, debris covered glaciers have been reported to retreat at a slower rate than uncovered glaciers (Scherler et al., 2011), at least in the initial phases of glacial shrinkage (Banerjee, 2017). Although the present volume of the Alpine permanent cryosphere is difficult to quantify, Boeckli et al. (2012) estimated that permafrost has a larger extent (ca. 2,000-11,600 km^2) with respect to glaciers (ca. 2,000 km^2), and the shrinkage rates of the permafrost ice are estimated to be roughly 10-100-times lower than melting rates of the surface glacier ice (Haeberli et al., 2016). As a result, the relative importance of permafrost will increase during the 21st century with a shift from glacial/periglacial to paraglacial/periglacial dominated processes, and here we summarize the significant effects anticipated on the hydrology, water quality and biodiversity of Alpine freshwaters.

1.3. DEGLACIATION AND SHIFTING STREAM HABITAT CONDITIONS

In this section we discuss the observed and predicted shifts in hydrology, geomorphology, habitat type, and water quality of Alpine streams as a consequence of deglaciation.

1.3.1. Hydrology

Glaciers and snow currently represent major drivers of the Alpine hydrology, as their seasonal melting is strongly associated with surface and groundwater flows. Driven by thawing-freezing cycles, discharge can be highly variable, with seasonal maxima during summer and minima during winter, and large diel fluctuations in summer (e.g. Malard et al., 1999; Ward, 1999; Smith et al., 2001; Jansson et al., 2003). Mountain rock glaciers store large amounts of water, trapped in the form of ice, which makes them significant water reservoirs in arid regions (Rangecroft et al., 2015; Jones et al., 2018). However, rock glaciers currently contribute only little to water flow in Alpine stream networks (Geiger et al., 2014, Krainer et al., 2007). For example, Krainer et al. (2011) found that only 1.4% of the annual outflow from the Lazaun rock glacier watershed to have a permafrost ice origin, and that rock glaciers contribute only marginally (0.13%) to total runoff in the north Italian province of South Tyrol.

To assess hydrological shifts related to climate change in alpine environments, Milner et al. (2009) stress the importance of taking into account the dynamic interactions between snowmelt, ice melt, and groundwater contribution to the stream flow. In the early stages of glacier retreat, water discharge is increasing due to higher energy inputs from the atmosphere, earlier melting of reflective snow cover, and the consequent lower ice albedo

(Milner et al., 2009). For instance, Finn et al. (2010) detected hydrological changes in the Roseg Valley (Switzerland) as consequence of 52 years of glacial retreat (i.e. from 1955 to 2007). Such changes include a significant increase in short-term flow variability, higher flow maxima during summer and lower minima during winter, and an earlier onset of spring runoff. In the advanced stages of glacier retreat, glacial runoff exceeds a hydrological tipping point referred to as "peak water" (Huss et al., 2017; Huss and Hock, 2018), and decreases due to prolonged glacier shrinkage and fragmentation (Stahl et al., 2008). As glaciers retreat, split, and disappear, the importance of air warming (energy fuelling the melting process) gradually drops, whilst the progressively rising snowline and the earlier onset of the seasonal snowmelt also reduces the role of the snowpack as a natural water reservoir (Stewart, 2009; Zierl and Bugmann, 2005; Huss et al., 2017). As a result, many Alpine streams may run dry in summer in the near future, especially in warm and dry years (Zierl and Bugmann, 2005). Moreover, the marked diel and seasonal discharge fluctuations are substituted by an increased dependency on stochastic precipitation events and on groundwater sources (Milner et al., 2009), with an increased flashiness of water regime due to the decreased buffering capacity exerted by the cryosphere (Huss et al., 2017).

The contribution of rock glaciers to Alpine water flow is anticipated to increase substantially in the future. In fact, the ice loss in rock glaciers, although slower than for typical mountain glaciers, will likely increase throughout warmer and prolonged summers. In addition, new rock glaciers may form in areas left uncovered by glaciers, through different and complex mechanisms that involve e.g. the evolution of debris-covered glaciers or the accumulation of ice and detritus under favourable slope settings (Whalley and Martin, 1992; Clark et al., 1998; Zasadni, 2007; Schoeneich et al., 2011; Anderson et al., 2018). In addition, Wagner et al. (2016) stress the potential hydrological contribution from fossil rock glaciers (i.e. with no more creeping activity and no residual ice) due to their water storage capacity during dry periods and buffering potential during flood events, and suggest that in the long-term, the catchments rich in rock glaciers may be influenced by these landforms even when deglaciation has finished. Research on the contribution of permafrost to mountain hydrology has been mainly conducted on streams fed by rock glaciers. However, Rogger et al. (2017) considered also talus fans and Little Ice Age tills of a 5 km^2 catchment in the Ötztal Alps (Austria), and modelled that the complete disappearance of permafrost would reduce flood peaks by up to 19 % and increase runoff by up to 17 % during recession periods. This suggests that the water buffering capacity of Alpine slopes will likely change in the future not only due to snow cover and glacier loss but also due to permafrost thaw.

1.3.2. Geomorphology

Glacier-fed streams represent an important source of sediments for the river basin level, with a significant proportion transported as bedload (Gurnell et al., 2000; Mao et al., 2019). The formation and reworking of glacial deposits left uncovered after glacier retreat promotes the formation of actively braiding proglacial reaches (Church and Ryder, 1972) with high width-depth ratios (Milner and Petts, 1994). Meltwater outburst events can be a key geomorphic driver for fluvio-glacial deposits (Gurnell et al., 2000). In addition, new lakes can form in the glacial forelands, with an increased likelihood of glacier outburst floods (GLOFs) and related hazards (e.g. Emmer et al., 2015; Haeberli et al., 2016; Carrivick and Tweed, 2016; Otto, 2019). Though rare in high mountain environments, thermokarst (i.e. ice-thaw formed) lakes can occur in permafrost conditions, as reported by Kääb and Haeberli (2001) on a rock glacier in the Swiss Alps. As deglaciation proceeds and glaciers shrink, fragment, and ultimately disappear, sediment transport gradually decreases, giving way to a period of incision of previously accumulated sediments (Church and Ryder, 1972; Fleming and Clarke, 2005) and a shift to more stable forms such as single-thread channels with higher sinuosity (Milner and Petts, 1994; McGregor et al., 1995, Gurnell et al., 2000). As the rapid uplift of the vegetational belts occurring in the Alps (Rogora et al., 2018) suggests, riparian vegetation may exert an increasing hydromorphological role in stabilizing the channels in the late phases of glacier retreat. However, in glacier forelands, the succession rate from pioneer and herbaceous stages to shrubs is very slow, as it usually spans over more than a century (Gurnell et al., 2000; Eichel, 2018). Furthermore, preliminary findings from the Rocky Mountains (USA) suggest that the homogenisation of alpine vegetation will favour riparian herbaceous species at high elevations (McKernan et al., 2018), where shrubs may not act as hydromorphological drivers as they do in lower reaches.

1.3.3. Alpine stream habitat types

Water origin is considered the main driver of the habitat conditions in alpine streams, so that three major stream types were originally identified and described (see Ward, 1994): kryal (glacier-fed), krenal (groundwater-fed) and rhithral (snowmelt/precipitation-fed), each type characterized by different water temperature, channel form and stability, discharge patterns, turbidity, electrical conductivity and hydrochemistry (for a detailed description see Brown et al., 2003; Milner et al., 2010). Since the contribution of the different water sources to stream discharge shows high spatial heterogeneity and pronounced seasonality, a classification of stream types based on a longitudinal sub-division has been proposed (see summary by Füreder, 1999), and a more complex habitat classification based on the relative proportion of each source (snow, ice, precipitation, groundwater) to water flow has been developed by Brown et al. (2003) and Brown et al. (2009). However, a substantial gap in all these classifications is represented by the lacking inclusion of alpine permafrost as a water source. This omission needs to be addressed as active rock glacier outflows exhibit a particular set of habitat conditions, typically being clear waters (<5 NTU) at low and stable temperatures (0.5-1.5°C). High electrical conductivities (up to 1000 µS cm^{-1}), due to high concentrations of selected cations (Ca^{2+}, Mg^{2+}) and anions (SO_4^{2-}, NO_3^-) are also commonly observed, especially during base-flow conditions in the late summer/autumn (Williams et al., 2006; Baron et al., 2009; Thies, et al., 2013; Krainer, 2015: Carturan et al., 2016; Rotta et al., 2018). Because deglaciation causes changes in the contribution of different water sources, an increased abundance of krenal and rock glacial habitats can be anticipated, along with the uplift of kryal habitats following retreating glacier margins. However, it is very likely that the habitat framework under glacier loss will be catchment specific and dependent on local geological and geomorphological conditions interacting with the new climatic setting.

1.3.4. Water and sediment quality

Water temperature

In deglaciating alpine areas, water temperature of glacier-fed streams increases due to air warming, reduced discharge and decreased ice-melt (Milner et al., 2009). For the Alps, this was observed in nine Swiss catchments, showing a rise of 2-7°C in summer temperatures for upper stream reaches since the late 90's (Robinson and Oertli, 2009; Finn et al., 2010; Robinson et al., 2014). As rock glacier outflows (Carturan et al., 2016) and high-elevation springbrooks (von Fumetti et al., 2017) are characterized by low and constant water temperatures, they may become cold refuge areas after the glacier loss (Hotaling et al., 2017). However, deglaciation may also narrow longitudinal temperature gradients, as detected by Finn et al. (2010) in the Roseg valley (autumn period, 1997-2007), and therefore reduce the extent of cold habitat conditions downstream.

Availability of carbon, nitrogen and phosphorus

Melting of the cryosphere releases carbon, nitrogen, and phosphorus to freshwaters. Glaciers accumulate and store organic carbon (OC), which derives from in-situ microbial production and atmospheric deposition of vascular plants, soil, and aerosol combustion products, as detected by Singer et al. (2012) in a study of 26 Austrian glaciers. The authors found that this ice-locked organic matter was highly labile, and demonstrated a positive correlation between DOC bioavailability and age, which ranged between 600-8,500 years BP. Glacial carbon is conveyed by glaciers and eventually released to freshwaters through the melting process (Singer et al., 2012; Hood et al., 2015), and supports kryal food webs (Fellman et al., 2015). Based on the limited research to date, rock glacier streams typically show DOC concentrations similar to those found in glacial streams, but this carbon seems to be less labile, as it was found studying three mountain areas in the USA (Fegel et al., 2016). Hence, in the initial phases of deglaciation, glacier retreat is accompanied with a boosted delivery of ancient and particularly labile carbon to freshwaters. This may have ecological consequences, since OC enhances stream metabolism via microbial uptake (Singer et al., 2012), with potential bottom-up trophic effects. However, after the "peak water" has occurred and the load of labile carbon from glaciers fades, shifts in allochthonous inputs to streams are anticipated, with enhanced loads of more recalcitrant organic carbon provided by rock glaciers (Fegel et al., 2016) and increased organic matter from vegetation colonizing upstream areas (Zah and Uehlinger, 2001).

Nitrogen pulses arising from spring snowmelt are commonly observed in Alpine catchments and are associated with dry and wet deposition and with biological processes occurring in winter (Kuhn, 2001). Deposition of nitrogen from the air in Alpine valleys is linked with intense urbanization, and agricultural and industrial activities in the surrounding areas

(Rogora et al., 2006). A reduced deposition of nitrogen compounds in the Alps has been observed starting from the end of the 20th Century (Rogora et al., 2016) as a consequence of the reduction of atmospheric emissions agreed by international protocols (EEA, 2016). Nevertheless, nitrate concentrations in water >100 µg L^{-1} are commonly found in streams originating from ablating glaciers (Uehlinger et al., 2010) and active rock glaciers in the Alps (Thies et al., 2013; Krainer, 2015; Lösch et al., 2015a) as in other mountain ranges (e.g. Barnes et al., 2013; Fegel et al., 2016). However, the causes of these high concentrations (e.g. microbial production, release from the ice melt and permafrost thaw) are still debated, and no major ecological effects have been observed worldwide (Slemmons et al., 2013). Artificially increased concentrations of nitrates and phosphates in five Swiss glacier-fed streams did not trigger any periphyton accrual (Rinke et al., 2001), suggesting that other environmental factors, such as turbidity and scouring, inhibit nutrient-driven algal growth. Since these limiting factors are commonly absent in rock glacier outflows, primary producers may be more sensitive to nitrogen inputs there, even if other features may still limit algal growth, such as low temperatures or high UV radiation. This topic, however, remains unstudied for this stream type worldwide.

Phosphorus is also supplied to alpine streams by glacier ablation, mainly through the physical erosion and weathering of rocks (Hodson, 2006). However, most of the phosphorus released by glaciers in Alpine and Arctic areas was found to be associated with clay particles, and only a minor fraction consisted of soluble reactive phosphorus (SRP) loosely aggregated with the sediment (Hodson et al., 2004). Thus, higher rates of glacier ablation likely increase the export of phosphorus to downstream environments, as detected by Robinson et al. (2014) in eight Swiss glacier-fed streams from 1998 to 2011. Even if particulate phosphorus is not bioavailable, the minerals may become dissolved under favourable conditions after the deposition of suspended sediments (Hodson et al., 2004), suggesting potential long-term effects once deposited sediments are remobilized. Notably, high loads of bioavailable SRP have been demonstrated in ice fields in Alaska (Hood and Berner, 2009) and Greenland (Hawkings et al., 2016). SRP contribution by mountain glaciers still remains understudied, although very low concentrations (<3 µg L^{-1}), consistent with those of krenal streams, have been found in kryal (e.g. Rott et al., 2006; Uehlinger et al., 2010) and rock glacial waters (Rotta et al., 2018) in the Alps.

Legacy contaminants

Alpine glaciers store air-borne anthropogenic contaminants and convey them to freshwaters via ice melting. These include persistent organic pollutants (POPs, i.e. industrial chemicals, pesticides, and by-products of combustion processes and chemical reactions), black carbon, i.e. dark aerosol produced from the combustion of fuels (Daly and Wania, 2005; Hodson, 2014), and trace elements (Gabrielli et al., 2008; Carling et al., 2017). The proximity of the Alps to several highly industrialized regions makes this mountain range particularly sensitive to input and accumulation of POPs, but their release from glaciers has also been observed in Himalaya and the Rocky Mountains (Miner et al., 2017). As POPs are mostly delivered through wet deposition, especially with snow, the seasonal snowmelt is an important source of these contaminants for freshwaters (Bizzotto et al., 2009). Moreover, as the accumulation zone of glaciers represents a temporary storage for snow, toxic and even banned substances can be released decades after their production. This intensifies with progressive deglaciation, with potential effects to surface water quality (Bogdal et al., 2009). Accordingly, concentrations of organochlorine chemicals and pesticides were found to be much higher in glacial compared to non-glacial streams in several Italian catchments, and concentrations increased 10-fold from snowmelt to ablation periods where seasonality was assessed (Villa et al., 2006; Bizzotto et al., 2009). Since the content of organic matter in glacier-fed streams is low and the organic pollutants can be mainly found in the dissolved phase, with a low potential for suspended sediment absorption, these compounds can be potentially bioavailable to organisms (Slemmons et al., 2013). Bizzotto et al. (2009) studied the variability in the concentrations of POPs in different macroinvertebrate feeding groups over summer, finding higher concentrations in the kryal than in krenal streams. However, bioaccumulation could not be confirmed, as the higher concentration in predators was attributed to their high lipid content, and a direct uptake from water was suggested for all organisms. The highest release of POPs from glaciers to freshwaters may be expected to coincide with “peak water”, after which a gradual decrease is not necessarily accompanied by a reduced ecological effect, due to the persistence of these substances in the environment (Jones and Voogt, 1999).

Trace elements

Permafrost thaw is known to influence the inorganic chemistry of waters worldwide (Colombo et al., 2018a), and insights into the potential consequences of thawing rock glaciers on water quality have come from several case studies in the Alps. Acidic waters (pH=5-5.5) has been found in lakes (Ilyashuk et al., 2014) and streams (Thies et al., 2013) fed by thawing rock glaciers. Further, high concentrations of trace elements (e.g. Al, Ba, Ni, Zn, Mn, Co, Sr), often exceeding the EU limits for drinking waters, have been reported in Austrian (Thies et al., 2007; 2013) and Italian (Krainer, 2015; Nickus and Thies, 2015; Colombo et al., 2018b; Rotta et al., 2018) rock glacial freshwaters. Even if the debate on the causes of the particular water chemistry in active rock glacier outflows is still ongoing, internal ice thaw is considered as a key driver for the enrichment of solutes and trace elements, and for the acidification of waters in catchments with sulphide-bearing lithology (see Colombo et al., 2018a).

High concentrations of trace elements (Al, Ti, Fe, Co, U, Mn, Fe) have been reported even for glacier-fed streams, in the Swiss (Brown and Fuge, 1998) and Italian Alps (Rotta et al., 2018), especially during baseflow conditions, and attributed to the rock weathering associated with the glacial/subglacial flow. However, the bulk downstream export is considered to be greater during the ablation period, when the highest discharge offsets lower concentrations (Mitchell et al., 2001). Thus, it may be expected that the highest concentrations of trace elements in Alpine streams, and the greatest associated biotic effects, will be reached during the last phases of glacier shrinkage, under decreased average discharge and ice/rock ratio from glaciers in parallel with an increased hydrological significance of thawing rock glaciers. In addition, climatic changes (e.g. more frequent dry periods, reduced snow cover) are capable of enhancing the mobilization of naturally-occurring trace metals through enhanced weathering processes in glacier-free areas, as detected in the Pyrenees (Zaharescu et al., 2016). This may cause high loads of trace elements to freshwaters, even when deglaciation has finished.

1.4. EFFECTS OF DEGLACIATION ON STREAM COMMUNITIES

Among the large body of literature covering different aspects of Alpine streams, we found only twenty-four published papers (hereafter identified with * at first citation) that specifically address the impact of deglaciation on stream biota (Figure 1.3). Among them, three papers investigate waters affected by permafrost thaw. Eighteen studies are based on a synchronic approach that substitutes space for time in order to predict future developments and trends linked to glacier retreat. Diachronic studies based on long-term surveys are still a minority (three), but they will likely increase in the future driven by the growing interest in Alpine deglaciation, both within and outside the scientific community. Here, we briefly summarize the available knowledge on the biotic communities and the food webs of Alpine streams, identify the observed or predicted ecological effects of deglaciation, and draw comparisons - where possible - with other alpine areas.

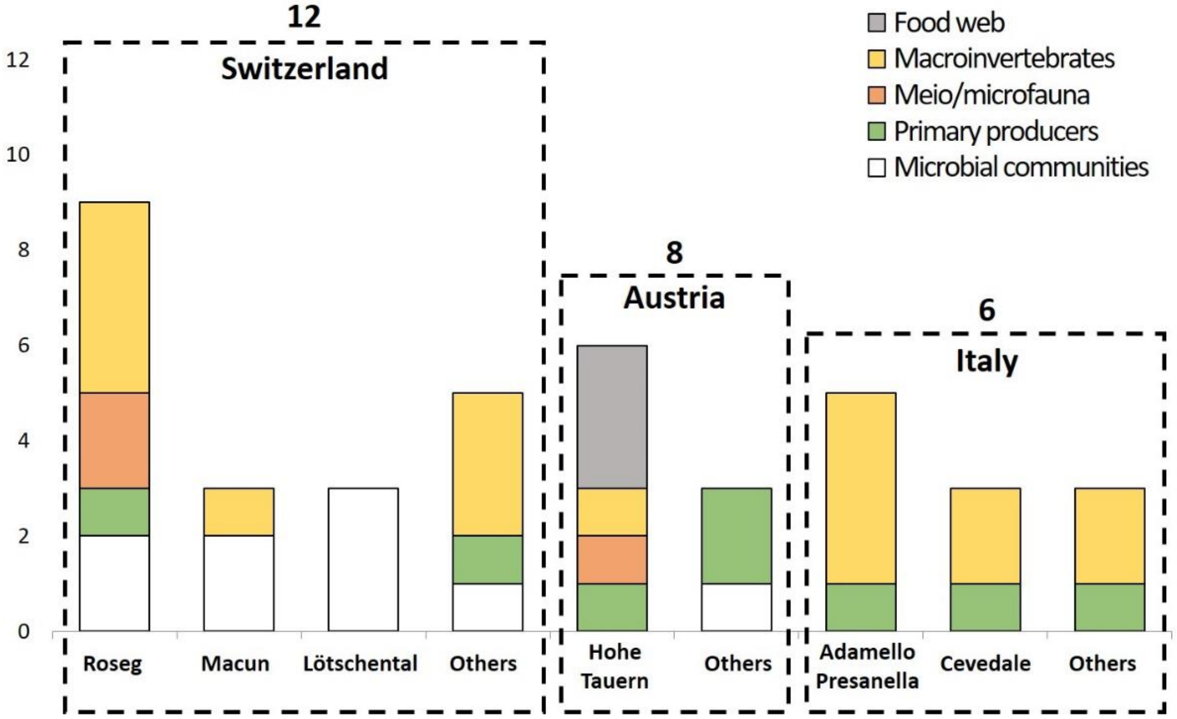


***Figure 1.3**. Distribution of 24 research papers specifically focusing on the effects of deglaciation on alpine stream biota in the European Alps, ordered by study area/country and the investigated biotic component. Articles covering more than one catchment/country have been split into different counts. The papers have been chosen as they specifically address the topic at least in the scope of the research or treat it extensively in the discussion or conclusions. Considered papers are marked in the main text with * the first time of citation.*

1.4.1. Microbial communities

Stream microbial communities represent the trophic connection between nutrients, producers, and consumers (Battin et al., 2016). Microbes drive several biogeochemical and metabolic processes, including nitrogen uptake and transformation, methanogenesis, iron cycling, photosynthesis, and respiration (Freimann et al., 2013[*]), which also occur in glaciers (Anesio and Laybourn-Parry, 2012). In fact, despite their extreme habitat conditions, glaciers and ice sheets are considered as a proper biome (Anesio and Laybourn-Parry, 2012). As such, they are autotrophic systems hosting viruses, prokaryotes and algae (Anesio et al., 2017), and exporting organisms and nutrients to the heterotrophic glacier-fed streams (Anesio et al., 2009).

In Alpine streams, the strong seasonality shapes the traits of stream microbial communities, as investigated by Battin et al. (2004) in the Rotmoos (Austria) and by Freimann et al. (2013; 2014) in three Swiss catchments. During the spring snowmelt, the pulsed release of airborne organic material accumulated and processed over winter, triggers a stage of active metabolism and bacterial growth. In this phase, the enhanced hydrological linkage within the river network and between streams and groundwater, soil and vegetation results in high uptake and transport of DOC, nutrients, and microbes in freshwaters. In summer, the harsh physical conditions (e.g. high turbidity and scouring) during glacial ablation hinder microbial production in kryal habitats, which are dominated by small-sized, specialist microorganisms during this period (Freimann et al., 2013). Because of the reduced disturbance and the persistent release of labile DOC and nutrients from the melting ice, autumn represents a favourable ecological window in kryal, promoting shifts in the community composition and a dominance of larger-sized bacteria (Battin et al., 2004). Because of a less pronounced seasonality in habitat conditions, krenal and rhithral assemblages are dominated in all seasons by large and generalist bacteria that can cope with smaller changes by solely adapting cell metabolism (Freimann et al., 2013).

Research on Alpine stream sediments has shown that glacier-fed streams have lower bacterial diversity, abundance and community biomass, and bacterial carbon production compared to non-glacial streams, and these different stream types host distinct communities (Battin et al., 2001; Battin et al., 2004; Logue et al., 2004; Freimann et al., 2014[*]). A relatively higher abundance of α-Proteobacteria and a lower abundance of Eubacteria was found in the Rotmoos glacier-fed stream compared with rhithral and krenal habitats (Battin et al., 2004). This difference coincides with findings from US mountains (Fegel et al., 2016), Himalaya (Liu et al., 2011), the Arctic and the Antarctic (Marghesin and Miteva, 2011; Van Horn et al., 2016). A high diversity found close to the glacier snout in the Rotmoos was attributed to bacterial inputs from the glacial environment (*Archaea*, *Proteobacteria*, *Bacteroidetes*, *Actinobacteria* and *Cyanobacteria* are typical dwellers of glaciers; Anesio et al., 2017), whereas bacterial carbon production and specific growth rates increased when proceeding downstream from the glacier snout, along with the reduction of *Archaea* abundance and in concomitance to increasing algal biomass in the biofilm (Battin et al., 2001). The progressive increase in bacterial α-diversity in water and biofilm downstream from the glacier seems to reflect the increased contribution from different sources (Wilhelm et al., 2013*), again witnessing the importance of hydrological connectivity in the catchment.

While most research on microbial communities has focused on glacial environments and streams, only few studies have been conducted to date on permafrost-fed waters in the Alps. Preliminary studies on bacterial diversity in rock glacier ponds (Mania et al., 2018) and running waters (Tolotti et al., 2018) agree with the outcomes of studies conducted in North America (Fegel et al., 2016), which show that rock glacier outflows host more abundant and diverse bacterial communities than kryal streams, with a high proportion of typical soil taxa in streambed sediments.

In addition to the loss of microbial glacier specialists (e.g. *Archea*), climate change and deglaciation may generate consequences for microbial communities by means of altered hydrological pathways. For instance, it is possible that the loss of cryosphere will also influence krenal microbial communities, due to the hydrological connection between glacial and groundwater flow in Alpine catchments (little studied, but see Ward et al., 1999; Cuffey and Paterson, 2010). After the “peak water” (i.e. maximum water flow associated with glacier loss, see 3.1), the reduced loads of organic carbon, phosphorus and nitrogen from glaciers may be paralleled by increased organic matter inputs from terrestrial vegetation and enhanced primary production in streams. Such a shift may trigger changes in the bacterial community composition and the associated functional activity, with consequent large-scale changes in the nutrient cycling and the overall ecosystem functioning. Freimann et al. (2013) claim that future stream networks in groundwater-dominated catchments will be more suitable for generalist bacterial taxa typical of krenal habitats, with a consequent loss of kryal specialists. Bacterial α-diversity is predicted to increase upstream due to the habitat amelioration (e.g. reduced scouring and turbidity), while differences between stream types and seasons will decrease, resulting in a general reduction of β-diversity (Wilhelm et al., 2013, Freimann et al., 2013). Responses to the changing physical and chemical conditions are expected to be more pronounced and complex for sediment bacteria, since microbial heterotrophs in epilithic biofilms benefit from algal exudates, while the epipsammic biofilms rely much more on external sources for DOC (Wilhelm et al., 2014).

Freshwater fungi, or “aquatic hyphomycetes” (see Bärlocher, 2016), which play a key role in the decomposition of organic matter (Gessner and Robinson, 2003), are affected differently by deglaciation when compared to other microbes. In fact, previous findings from studies in Swiss (Gessner et al., 1998; Gessner and Robinson, 2003) and Austrian Alps (Eisendler-Flöckner et al., 2013*) outlined that low allochthonous inputs rather than harsh habitat conditions (e.g. low water temperature, scouring) inhibit fungal diversity and abundance. Leaf bag experiments in the Swiss Alps, showed lower biomass (represented by concentrations of ergosterol in leaves) in kryal reaches than in the other stream types (Gessner et al., 1998; Gessner and Robinson, 2003), while a studied rock glacial stream showed similar concentrations than springbrooks (Robinson and Jolidon, 2005*). Because of the uplift of vegetational belts, fungal biomass and the associated breakdown of organic matter is expected to rise due to increased input of allochthonous material (Robinson and Jolidon, 2005). Shifts in riparian species composition may involve changes in the quality of organic matter being processed by fungi, with consequences on fungal biomass, and rates of colonization and sporulation (Gessner and Robinson, 2003). Changes in fungal communities may also trigger bottom-up effects along the food web. In fact, aquatic hyphomycetes have an important role in the nutrition of invertebrates (Bärlocher, 1985), especially in glacier-fed streams where they represent a high-quality food for meiofauna (Eisendle-Flöckner et al., 2013).

1.4.2. Primary producers

Alpine streams are harsh habitats for primary producers, because of intense UV radiation, low concentrations of nutrients, low temperatures and a long-lasting snow-cover. The harshest habitat conditions in kryal habitats (high turbidity and scouring) support lower periphytic biomass compared to more benign krenal habitats throughout the year, as demonstrated by Uehlinger et al. (2010)* in the Swiss Alps. A conceptual model of periphyton accrual in alpine streams based on these results points to the importance of different catchment features (e.g. climate, patterns of snow cover, and stream flow) and stream habitat conditions (light and UV, bedload, turbidity, temperature, and phosphorus availability) on a seasonal basis, and defines favourable periods (i.e. spring and autumn) as "windows of opportunity" (WO) enhancing algal productivity (Uehlinger et al., 2010). Seasonality also drives the composition of algal communities in different alpine stream types (Hieber et al., 2001). Kryal habitats are typically dominated by diatoms, whereas cyanobacteria (*Chamaesiphon sp.*, *Lyngbya sp.*) and the cosmopolitan golden algae *Hydrurus foetidus* exhibit temporary blooms during low-flow periods (Ward, 1994; Uehlinger et al., 1999; Hieber et al., 2001). During summer, pioneer and stress-tolerant species with cosmopolitan distribution (e.g. *Achnantidium minutissimum*, *Hannea arcus*), characterized by reduced motility and strong adhesion to substrate, dominate the diatom community of glacier-fed streams worldwide (Cantonati et al., 2001; Hieber et al., 2001; Gesierich and Rott, 2012), while others rest in reduced form (e.g. *H. foetidus* in their basal stage, Niedrist, Cantonati and Füreder, 2018).

Compared to kryal streams, communities from lake outlets, krenal, and rhithral streams, exhibit a higher algal diversity and a less pronounced seasonality, as found in the Swiss Alps, where diatoms exhibited a high diversity, and Cyanobacteria and *H. foetidus* have been found increasingly dominant over summer (Uehlinger et al., 1998; Hieber et al., 2001).

Deglaciation is anticipated to have several consequences for primary production and algal diversity. Uehlinger et al. (2010) proposed that an earlier snowmelt may open or reinforce the spring WO, since UV radiation is a limiting factor for alpine freshwater organisms (e.g. Sommaruga, 2014) and UV levels are less intense in spring. Likewise, the autumn WO could expand because of a later snowfall. Biotic interactions may represent other possible triggers for WO shifts. For instance, in glacier-fed streams the macroinvertebrate community may become increasingly abundant and diverse in an ameliorated environment, and grazers may limit periphyton growth (Milner et al., 2009; Uehlinger et al., 2010). On the other hand, changes in the stream biofilm involving primary producers may propagate to the heterotrophic component, which might benefit from algal exudates, as hypothesized by Battin et al. (2016). Glacier retreat enhances algal species richness due to the decreased environmental harshness induced by ablation (Milner et al., 2009). Fell et al. (2018)* recently studied the diversity patterns of diatoms in three Austrian valleys, where a gradient in glacier cover in the catchment was used as a proxy for glacier retreat. These authors identified several diatom taxa peculiar to high glacier cover and predict a β-diversity decline associated with glacier loss. This confirms previous research in the Hohe Tauern (Austria), where Rott et al. (2006) detected a pattern of decreasing richness as a function of increased percent glaciation in the catchment. Glacier retreat may also lead to shifts in community structure, as the increased habitat stability and temperature, and reduced scouring, potentially enhance taxa abundances of specific groups and the overall persistence of algal communities. This may favour typical rhithral cyanobacteria (e.g. *Phormidium, Oscillatoria)* and loosely attached (e.g. *Navicula*) or aggregated (e.g. *Cymbella*, *Gomphonema*) diatom taxa in previously hostile reaches. *H. foetidus*, the main kryal macroalgae, may take advantage of the improved habitat conditions and potentially anticipate its blooms because of nutrient pulses induced by earlier snowmelt (Milner et al., 2009). Due to the hydrological connectivity between glacial flow and groundwater, cascading effects of deglaciation may cause shifts in krenal communities with high conservation value. In fact, Alpine springbrooks are recognized as rich and diversified habitats hosting a significant number of peculiar, rare, and Red List diatom species (Cantonati et al., 2012). Although glacier loss will cause local extinctions of rare and stenoecious diatoms, other threatened or rare species may benefit from the pristine conditions of high mountains (Fell et al., 2018), thus posing a challenge for conservation policies aimed at preserving alpine sites from local pressures.

Algal communities are still poorly investigated in streams influenced by permafrost thaw worldwide. A preliminary study on two rock glacial streams (Ötztal Alps, Austria) during autumn baseflow conditions (Thies et al., 2013*), outlined higher proportions of acidophilous and acidobiontic taxa in association with lower pH values and higher concentrations of trace metals. Species richness was lower in the reference streams (rhithral) and in the rock glacial stream not affected by acidification and high metal concentrations, which were mainly inhabited by circumneutral taxa. It was found, however, that habitat diversity is the main driver for taxa richness in a community otherwise dominated by the stress tolerant *Achnantidium minutissimum.* A recent study on headwaters fed by glaciers and permafrost (rock glaciers and talus) in the Italian Central Alps confirmed pH and trace metals as key drivers for diatom diversity in streams influenced by permafrost, and discovered higher richness in glacio-rhithral than in rock glacial habitats (Rotta et al., 2018*). These studies suggest that the effects of thawing permafrost on the diatomic community can be mediated by acid-rock drainage. Furthermore, catchments with low buffering capacity and streams with reduced habitat diversity may be more sensitive to chemical changes induced by rock glacier thaw, especially after the "peak water" when the decreasing glacial influence is paralleled by increased permafrost influence.

In contrast to the more widely studied diatoms and algae, relatively little is known about bryophytes in Alpine streams, despite their abundance and the presence of rare or endangered species (Gesierich and Rott, 2004). Given that mosses establish on stable substrates (e.g. Stream Bryophyte Group, 1999), they can be used as an indicator of reduced glacial influence. We propose that bryophyte colonization may trigger positive feedbacks capable of increasing channel stability in glacio-rhithral sections with ongoing glacier retreat, and thereby enhancing algal and invertebrate diversity and biomass (e.g. Lencioni and Rossaro, 2005; Rotta et al., 2018).

1.4.3. Macroinvertebrates

Macroinvertebrates represent the most studied biotic component of alpine streams worldwide (Fell et al., 2017). Originally, this research field developed following the review papers by Ward (1994) on alpine stream habitat classification, and by Milner and Petts (1994) on the characterisation of glacial rivers. These papers triggered an outburst of studies worldwide and especially in Europe, starting from AASER project (Castella et al., 2001; Brittain and Milner, 2001) and continuing to the present (see Milner, 2016). Despite the abundant literature on alpine stream communities, especially those of kryal and krenal habitats, to our knowledge very little is known about the macroinvertebrates dwelling in rock glacier-fed streams, and the environmental determinants of community characteristics. The project PERMAQUA (www.permaqua.eu) represents a first preliminary attempt to study the diversity and distribution of macroinvertebrates in Alpine streams (Lösch et al., 2015a) and lakes (Thaler and Tait, 2015) affected directly or indirectly by rock glacier thaw.

Community composition and diversity

Alpine streams host different zoobenthic communities depending on the habitat type (e.g. Ward, 1994) and season (e.g. Milner and Petts, 1994; Brittain and Milner, 2001; Milner et al., 2001). In summer, when the differences between habitats are greatest, insect larvae of the orders Ephemeroptera, Plecoptera, Trichoptera (EPT) and Diptera are usually found with different abundances and diversity in krenal, rhithral, and lake outlets, and in the mid and lower sections of glacier-fed streams (Maiolini and Lencioni, 2001; Füreder et al., 2001; Hieber et al., 2005). Chironomidae represent the most abundant and widely distributed taxon of alpine streams (Milner and Petts, 1994; Castella et al., 2001; Lods-Crozet et al., 2001a; Milner et al., 2001) and are the exclusive group dwelling in proglacial reaches in the Alps (e.g. Füreder, 1999; Lencioni and Rossaro, 2005; Niedrist et al., 2016; Lencioni, 2018[*]).

The chironomids of genus *Diamesa* are the most adapted to glacial conditions, especially low temperatures and low channel stability, and dwell at low abundances in harsh kryal habitats (e.g. Milner and Petts, 1994; Niedrist et al., 2016; Rossaro et al., 2016[*]; Lencioni, 2018). Downstream, temperature and channel stability increase so that other chironomid subfamilies (Orthocladiinae, Chironominae) gradually enter the community. These groups share their habitat with Oligochaeta, other Diptera (Empididae, Limoniidae, Simuliidae), Plecoptera and Ephemeroptera, which gradually enter the community with different patterns according to the mountain sector (e.g. for Austria see Füreder et al., 2001; for Italy see Maiolini and Lencioni, 2001; for the Switzerland see Lods-Crozet et al., 2001b).

The decrease of glacial influence when proceeding downstream from the glacier snout, leads to the amelioration of habitat conditions (Füreder, 2012), which in turn favours high abundance and diversity of benthic communities (Milner et al., 2001). However, taxa diversity commonly shows a unimodal pattern as a function of glacial influence (Füreder, 2012). For instance, in an extensive study located in the central Alps, Füreder et al. (2002) detected a peak of EPT and total number of taxa at 1-10% GCC (glacier cover in the catchment, i.e. the percentage of the catchment covered by glaciers), and Füreder (2007) recorded this diversity peak at 1-15% GCC in the Hohe Tauern Austrian Alps. Thus, the observed patterns of taxa distribution in glacier-fed streams (Brittain and Milner, 2001) provide the potential to predict shifts in zoobenthos as consequence of glacier retreat. Jacobsen et al. (2012)* conducted a meta-analysis of taxa distribution in glacier-fed streams in three world mountain regions (Alps, Alaska, Ecuadorian Andes), modelling α, β and γ diversity as a function of GCC. For the Alps, a loss of regional (γ) diversity starting from 30-50% GCC, together with a predicted loss of up to 16% species with total glacier disappearance. The authors also forecast a decrease in taxa turnover (β diversity), as the decreasing glacial influence induces a loss of habitat and biological heterogeneity between catchments (see also Lencioni et al., 2007a; Lencioni, 2018). In contrast, local taxa richness (α diversity) is predicted to increase in kryal sites, whereas diversity hotspots (i.e. maximum richness sites in the catchment), located at 5-30% GCC, move upstream following glacier retreat. Thus, maximum taxa richness in the catchment is expected to decrease along with glacier disappearance.

During the initial phases of increased runoff related to negative glacier mass-balance, Milner et al. (2009) predict a decrease in abundance and diversity with a concomitant shift towards communities dominated by Diamesinae and Orthocladiinae chironomids. After the "peak water", the decreased glacier contribution to stream discharge may cause an increase of taxa diversity and abundance. A loss of cold-stenothermal species and the colonisation by other taxa was detected by Rossaro et al. (2016) and Lencioni (2018), as typical kryal species have been found at increasingly higher altitudes in the Alps over the last decades, in parallel to the colonisation of upstream reaches by Orthocladiinae and Nemouridae (Lencioni, 2018). In general, although results from diachronic research are still scarce, they are confirming what has been predicted by models and studies that substitute space for time. In particular, shifts in biodiversity, abundance, and drift patterns have been observed in a wide range of Alpine catchments (Table 1.1), together with upstream migration of communities associated with different glacial influence. However, the ecological shifts associated with deglaciation may not be as deterministic as models predict. For instance, glacier retreat is accompanied by changes in the steepness of longitudinal gradients for community' diversity. For example, invertebrate diversity (expressed with the Shannon index) increased more steeply downstream of the Swiss Tschierva glacier during summer, following ten years of glacier retreat (Finn et al., 2010*). These steeper environmental gradients may act as ecological barriers, hindering the upstream colonisation of organisms. Under scenarios of rapid environmental change associated with fast glacier retreat, taxa with limited ability for dispersal may not be able to keep pace with the changing conditions (Brown et al., 2018*). Within this context, new insights come from the biogeographical role of rock glacial communities. Lösch et al. (2015b)* investigated five streams fed by rock glaciers in South Tyrol (Italy) and found a dominance of Diamesinae and Orthocladiinae chironomids, and the presence of Plecoptera, Ephemeroptera and Trichoptera. The authors report the presence of cold-stenothermal species (*Diamesa spp*), which suggests that rock glacial streams can act as refuge areas after the glacier loss. However, preliminary findings from the Solda Valley (Italy) showed that rock glacial communities have similar composition to those of krenal and glacio-rhithral habitats, suggesting the potential for these streams to act as stepping-stones for the colonisation of upstream reaches during the last phases of glacier retreat (Brighenti et. al., 2018).

Ecological traits and functional diversity

As each organism exhibits a specific set of traits (e.g. maximal size, voltinism, resistance forms, attachment to substrate, feeding habits) that allow facing the habitat and community interactions, ecological communities can be analysed in terms of their functional diversity, which is strictly bound to the ecosystem functions (see Laureto et al., 2015). In this context, habitat acts as a filter for the ecological traits expressed by organisms (Poff, 1997). In Alpine settings, Ilg and Castella (2006) found an increasing functional diversity with increasing distance from the glacier and the consequential reduction of glacial influence in two Swiss (Rhone and Mutt) and one French (Romanche) glacier-fed streams. Glacial influence (GI, synthesized by combining water temperature, conductivity, suspended solids and channel stability) correlated negatively with body size, and positively with univoltinism/semivoltinism, absence of resistance forms, and abundance of crawling and deposit feeding organisms. Similarly, Füreder (2007) found that GCC correlates positively with the abundance of habitat specialists, rheobionts clingers with streamlined/flattened body, univoltinism/semivoltinism, cold adaptations, omnivory, and mobility of the adults in the Hohe Tauern (Austria).

Milner et al. (2009) predicted that a decreased glacial influence in alpine catchments will lead to stream communities dominated by generalists, with fewer taxa characterized by omnivory, flattened body shape and adaptation to low temperatures, and more taxa with low mobility. Increased nutrient availability and a more benign habitat will favour larger body size and the overall traits diversity. In an extensive study on the deterministic patterns structuring the functional responses of macroinvertebrate communities to glacier regression covering different biogeographic regions worldwide, Brown et al. (2018)* found a general pattern of increasing functional diversity with decreasing glacier cover, and selected traits exhibiting the same pattern across different regions. In contrast to the outcomes outlined for the Alps (Ilg and castella, 2006; Füreder, 2007), Brown et al. (2018) found fewer generations per year and a longer generation time associated with a lower glacial influence. These outcomes suggest that life history traits must be considered to better assess macroinvertebrates responses to changing seasonal time constraints. Studying *Allogamus uncatus* (Trichoptera) in the Roseg catchment (Switzerland), Shama and Robinson (2009) found a longer time to reach pupation, higher growth rates and a bigger adult mass along a gradient of distance from glaciers for permanent streams. Likewise, a later onset of snow accumulation, and the longer duration of favourable autumn conditions, may enhance oviposition and egg hatching, as observed by Schütz et al. (2001) in the Rotmoosache for *Baetis alpinus* in two contrasting years. Thus, deglaciation during summer and snowpack shifts during winter may interact, causing synergic effects on Alpine stream biota, with shifts in the life cycles and life histories of taxa, that are known to be influenced by the seasonality of snow cover and temperature patterns (Füreder, 1999; Lencioni, 2004). We also suggest that shifts in life cycles might be reflected in the seasonality of the community composition, which was found to be pronounced in Alpine streams (Robinson et al., 2001; Schütz et al. 2001; Brown et al., 2015; Lencioni and Spitale, 2015).

1.4.4. Meiofauna

An important and to date poorly-investigated aspect of alpine stream ecology is the use of the hyporheic habitat by benthic taxa, which are small enough to dwell in the interstices. In fact, most of them are categorized as “meiofauna” (from Mare, 1942). The hyporheic habitat is more stable than the benthic one, and hosts more stable communities, especially in glacier-fed streams where the low substrate stability and the high streambed porosity facilitate the vertical migration of invertebrates (Malard et al., 2001[*]; Crossman et al., 2012; Lencioni and Spitale, 2015). Fauna exclusive to the hyporheic habitat are dominated by crustaceans, and harpacticoid copepods are typical dwellers of Alpine stream hyporheos. In addition, larval stages of insects use the hyporheic zone as a nursery, temporary refuge, and biological corridor (Malard et al., 2001; Malard, 2003; Malard et al., 2003[*]; Lencioni et al., 2007b), and even micro/meiofaunal invertebrates (e.g. nematodes, rotifers) dwell in kryal habitats (Eisendle, 2008; Eisendle-Flöckner et al., 2013).

Despite the paucity of published research on meiofauna in Alpine streams, there is evidence that kryal hyporheic communities change along the altitudinal gradient and depend on both glacial influence (water temperature and abundance of organic matter) and groundwater contribution/upwelling (Malard et al., 2003; Maiolini et al., 2006; Lencioni et al., 2007b; Raschioni et al., 2007; Lencioni and Spitale, 2015). In the Alps, meiofaunal cold-stenothermals were found to be strictly bound to glacier-fed streams (Husmann, 1975; Cottarelli et al., 2001; 2005; Malard, 2003; Maiolini et al., 2006; Raschioni et al., 2006; Eisendle, 2008), and one species of Alpine copepod, so far endemic, has been described (Cottarelli et al., 2005). Thus, changes in the community structure of these smaller invertebrates can be predicted as a consequence of glacier retreat. In the benthos, Eisendle-Flöckner et al. (2013) found a decreasing taxonomic richness of Nematoda and Rotifera and a decreasing abundance and maturity of Nematoda, as a function of GI (water temperature, channel stability and conductivity as proxy). In the hyporheos, during the initial stages of increased glacial influence, meiofaunal diversity may drop in glacial floodplains, since it was found to be strictly related to groundwater upwelling contribution and habitat diversity (Malard et al., 2001; Malard, 2003). On the long-term, the decline of glacial influence may be paralleled by the loss of cold-stenothermals, and the upstream colonization by other taxa (Malard et al., 2003). Such upstream migration might be possible in the hyporheic zone, which can act as an ecological corridor. This was demonstrated by evidence of invertebrate taxa in the hyporheos far above their benthic altitudinal limit (Malard et al., 2001; Malard et al., 2003). However, the sensitivity and response of meiofauna to deglaciation, and its contribution to the biodiversity and complexity of food webs in alpine streams is still understudied and further research still needed.

1.4.5. Food webs

In alpine streams, autochthonous production is low because of the overall environmental harshness, which limit primary producers (Uehlinger et al., 2010). Further, allochthonous inputs are scarce because of a sparse and simplified vegetation (Zah and Uehlinger, 2001). Both limitations are highest in kryal habitats, where inputs of organic matter are mainly provided by the aeolian transport (Zah and Uehlinger, 2001; Füreder et al., 2003a) and by glacier ablation (Singer et al., 2012). In particular, the ablation process was found to be important in fuelling the food webs of streams in Alaska, where Fellman et al. (2015) demonstrated via stable isotope and radiocarbon analysis of different trophic levels that up to 36% of the carbon assimilated by consumers had a glacial origin. Although this topic remains to be investigated in the Alps, Niedrist and Füreder (2018)* speculate that glacial carbon is incorporated in the epilithic biofilm of kryal streams in the Hohe Tauern, as witnessed by $\delta^{13}C$ depletion in this matrix, which depends on glacial influence. Generally, the strong limitations in both autochthonous and allochthonous production, and the natural absence of fish in high mountains (Adams et al., 2001), result in simple alpine stream food webs, especially in proglacial reaches (Clitherow et al., 2013*). Gut content and stable isotope analyses undertaken in several streams in the Austrian (Füreder et al. 2003a; 2003b; Clitherow et al., 2013) and Swiss (Zah et al., 2001; di Cugno and Robinson, 2017) Alps revealed a widespread omnivore behaviour of invertebrates. Opportunistic feeding strategies, such as predation in the shredder *Leuctra sp.* and the filter-feeder *Prosimulium sp.*, and cannibalism in the collector *Diamesa latitarsis/steinboecki* were also detected. In addition, Niedrist and Füreder (2017) found that selective feeding may be more important in *Diamesa* than previously assumed. In fact, stable isotope and gut content analyses on this taxon in the Hohe Tauern revealed the selective preference for *H. foetidus* and diatoms and the avoidance of cyanobacteria. Niedrist and Füreder (2018) further demonstrated along a gradient of glacial influence that, unlike Orthocladiinae, the detritivore Diamesinae are capable of shifting their diet and feeding on the available epilithic biofilm in kryal reaches, which is demonstrated to have a higher nutritional quality in harsh than in benign streams (Niedrist et al., 2018*).

The demonstrated opportunistic feeding behaviour may represent an ecological buffer for organisms facing climate change and deglaciation in alpine streams (di Cugno and Robinson, 2017). With the progression of glacier retreat and the rise of the treeline and vegetational belts, allochthonous inputs will increase in the upper stream reaches and vegetation will gain importance for the stream metabolism. Further, even if these advantages may be initially counterbalanced by the increased environmental harshness caused by boosted glacial influence, the transiently augmented contribution of ancient and labile organic carbon from thawing glaciers may enhance stream food webs across microbial uptake in biofilms (Singer et al., 2012; Fellman et al., 2015, Niedrist and Füreder, 2018). After the "peak water" period, the habitat amelioration may support periphyton and *H. foetidus* accrual, resulting in increased autochthonous production. However, more external and internal inputs fuelling the system will not necessarily determine more complex food webs. In fact, Niedrist and Füreder (2017) suggest that the dietary quality of periphyton may change due to shifts in the taxa composition in the biofilm assemblage, resulting in non-predictable shifts in higher trophic levels. Niedrist et al. (2018) demonstrated a higher nutritional quality of periphyton in harsher kryal sites, pinpointed as an explanation for higher *Diamesa* body mass in reaches with high glacial influence, where competition with other taxa is absent. This is in line with the opinion of Fell et al. (2017), who suggested that biotic interactions rather than habitat conditions will determine the ecosystem shifts in ameliorated environments. Very simple food webs such as those of kryal habitats may be sensitive to changes affecting single nodes, and radical shifts may be determined by local extinctions and by the entry of larger-sized taxa (Clitherow et al., 2013). The upstream colonization by predators, such as the observed colonisation of new habitats by *Siphonoperla sp.* in Roseg Valley (Finn et al 2010), may exert important top-down effects on such simple food webs and may thus affect the ecosystem functioning. This was demonstrated by the experimental introduction of a predatory stonefly (*Perla grandis*) in mesocosms set up in the French Pyrenees, where Khamis et al. (2015) found that the introduced predator caused an abundance depression of *Baetis alpinus*, together with changes in the feeding guild structure and body size spectrum.

Since no food web studies have been conducted in rock-glacier fed streams so far, it is difficult to fully appreciate how permafrost thaw influences stream food webs, with the exception of a potential uptake and bioaccumulation of heavy metals in affected headwaters. In fact, Ilyashuk et al. (2014) analysed various trace elements (Cu, Zn, Pb, Ni, Cr, Al, Fe, Ti, Mn, V) in tissues of key taxa from different trophic levels (selected from mosses, worms, chironomids and aquatic beetles) in the rock glacier influenced lake Rasass (South Tyrol, Italy) and in the adjacent non-affected pond. This assessment proved that trace element concentrations in body tissues were higher in the lake than in the pond, where concentrations in water and sediment were significantly lower.

Table 1.1. *Observed changes in zoobenthos diversity specified by cited references on studies in Italian and Swiss catchments*

Area	Period / reaches	Shifts in the community	References
Carè Alto (Adamello Massif)	1996, 1997, 2005 and 2013	No observed changes in α-diversity for Chironomidae community. Observed reduction of β and γ diversity. Newly-formed reaches rapidly colonized by *Diamesa sp.*	Rossaro et al. 2016
Conca, Niscli, Cornisello, Amola, Careser, Noce Bianco, Trobio catchments	1997-2013 summer campaigns covering different glacial influence reaches	Upstream migration of cold stenothermal (*Diamesa sp*) and eurieucious (*Baetis alpinus*, Orthocladiinae, Nemouridae, Limoniidae, Empididae, Oligochaeta) taxa. Concomitant increase of functional diversity and redundancy.	Lencioni, 2018
Morteratsch, Steinlimi, Tschierva, Roseg, Lang, Stein, Oberaletsch, Fiesch catchments	1998 - 2009 – 2011 (mid-summer) upstream reaches on glacier-free forelands	Newly-formed reaches rapidly colonized by *Diamesa sp.* β-diversity increase associated with reduction of Chironomidae and expansion of Ephemeroptera and Plecoptera taxa in the communities. Increase of γ-diversity with the entry of Diptera Blephariceridae and Trichoptera in the community	Robinson et al., 2014
Roseg Valley	1997 - 2007/08 (spring to autumn)	Newly-formed reaches rapidly colonized by *Diamesa sp* and other Diamesinae (increased α-diversity). Increase of γ-diversity with the entry of *Syphonoperla sp* (Plecoptera), *Ecdyonurus sp* (Ephemeroptera Heptageniidae) *Liponeura sp.* (Diptera Blephariceridae) and *Ryacophila torrentium* (Trichoptera)	Finn et al., 2010
Swiss National Park (Macun catchment)	2001/2008 mid-summer series in ponds and streams	Decrease of zoobenthos densities and taxa richness (α-diversity) in rock glacier influenced streams between 2001-2004 and 2005-2008, with similar trend for lake outlets and krenal	Robinson and Oertli 2009*
Swiss National Park	1999/2013 monthly samplings from spring to late autumn. Downstream reaches at 1707-1750 mt, low glacial contribution	No observed changes in α-diversity but shifts in the community composition and abundance. Observed increase in abundance of Simuliidae and *Leuctra sp.* and decrease of Heptageniidae for the glacier fed river (Fuorn) and of *Protonemoura sp* for the rock glacier fed (Aqua) stream	Sertić-Perić et al., 2015*
Roseg Valley	1997/98 – 2008/09 (monthly year-round campaigns)	In the downstream sections (glacio-rhithral) of the retreating glacier stream, drift densities of Chironomidae (and overall community) decreased (especially in spring and autumn) and Ephemeroptera/Plecoptera drift density increased (especially in spring and winter)	Sertić Perić and Robinson, 2015*

1.5. ECOSYSTEM TRAJECTORIES FOR ALPINE STREAMS

Space for time studies and long-term monitoring are contributing to the understanding of shifts in Alpine stream ecosystems triggered by deglaciation, but much more specific research is needed. Our conceptual model (Figure 1.2) is an attempt to illustrate the complex interactions between drivers of habitat change under scenarios of deglaciation and the predicted outcomes for Alpine stream ecosystems. In our model, glacier retreat and permafrost thaw interact with other climate-driven processes (vegetational shifts, snow cover changes) and with specific topographic, geomorphic, and geologic features at the catchment level. At this scale, interactions between global and local drivers determine changes in the hydrology and habitat conditions of streams. Progressive deglaciation gradually decreases the glacier contribution to streamflow, which in turn is partially offset by permafrost thaw and contributions from rock glacier outflows, resulting in a longer-term flow originating from degrading cryosphere. Increasingly unpredictable atmospheric precipitation may also become a significant hydrological driver after glacier loss (Milner et al., 2009).

The intermediate disturbance hypothesis (Connel, 1978) predicts that the performance of biological communities peaks under conditions of intermediate environmental stress. Accordingly, Füreder (2012) proposes that functional diversity, taxa abundance and diversity, as well as habitat diversity and food availability in alpine streams, are lowest when glacial influence is highest, reach a peak under the moderate harshness of intermediate glacier cover in the catchment, and decline again with decreasing glacial influence as habitat amelioration occurs. All changes in habitat conditions at various time scales affect the stream biota and food webs. A decrease in β and γ diversity and an increase in α-diversity have been anticipated in many studies regarding bacteria, algae, and invertebrates, and have already been observed in benthic invertebrates in long term studies (see Table 1.1). Reduction and loss of cold-stenothermal populations and the spread of krenal and rhithral species provide early warning signals of warming-triggered ecological shifts. Ecosystem responses occur at different levels of organization and thus shape the overall system functioning (Woodward et al., 2010).

The potential pathways for the colonization of glacier-fed streams by invertebrates depend on the ecological traits of each taxon and are different depending on season and hydrological connectivity in the catchment. Active migration across the terrestrial and aerial environments is essentially undertaken by the adults of insects (Bilton et al., 2001). Additional dispersal pathways by resistant forms (diapausing eggs for crustaceans) and parasite stages attached to insect adults and birds (e.g. water mite juveniles) have been proposed as potential pathways for meiofaunal colonisation in Alaskan streams (Robertson and Milner, 1999). In kryal habitats, active migration occurs upstream along the hyporheic corridor, and during winter within the benthic habitat of those reaches that do not freeze or run dry. The alpine hyporheic corridor also allows lateral migration between streams, as well as vertical shifts between the hyporheic and benthic zones (Bruno et al., 2012; Lencioni and Spitale, 2015). Within this context, the role of the catchment-specific hydrological connectivity is crucial for benthic life in alpine streams, as locations characterized by high hydrological connectivity (e.g. debris along steep slopes, abundance of alluvial plains) are potentially subject to faster colonization rates. It is, however, especially important to find out whether rock glacial streams can provide a long-lasting refuge for cold-stenothermals and/or sources of species for colonisation of surrounding streams after glacier loss.

1.6. CONCLUDING REMARKS AND FUTURE RESEARCH PERSPECTIVES

We provided a first extensive summary of the shifts in alpine stream ecosystems arising from both glacier retreat and rock glacier thaw with a focus on the European Alps. These insights inform about changes that occur across alpine systems worldwide (e.g. Himalaya, Rocky Mountains, Andes, New Zealand Alps), whilst recognising their differences in terms of climate and hydrology, glacier and permafrost cover, and local and regional human pressures.

Despite that the Alps are relatively well studied in comparison to other mountain ranges, considerable knowledge gaps still exist. To date, most studies on alpine stream biota have been concentrated in a few hotspots, e.g. the Val Roseg in Switzerland or the Hohe Tauern in Austria, but further research is needed across a wider range of catchments, especially in the Western Alps.

Very little is known on the hydrological significance of permafrost (including pervasive permafrost, talus fans, Little Ice Age till) for high mountain catchments. Despite the forecasted hydrological importance of rock glaciers for mountain hydrology, their increasing role in shaping stream ecology is still severely understudied. Research on streams fed by rock-glaciers under degrading permafrost conditions is therefore urgently needed for several key reasons. First, these freshwater habitats may serve as ecological refugia for cold-stenothermals biota and gain increasing conservation value. Secondly, permafrost thaw alters the physical and chemical properties of streams, causing water contamination and related problems for drinking waters (Sapelza, 2015). Thirdly, the so far limited studies in the Alps, supported by a few findings from outside Europe, show that streams fed by active rock glaciers are characterized by peculiar habitat conditions, which differ from those of other alpine stream types recognised so far. As a consequence, the role of rock glaciers in driving and modulating Alpine stream ecology is likely to become even more important in the near future.

Based on the review of existing knowledge on ecosystem shifts in alpine streams under glacier retreat and rock glacier thaw, we identify several key research priorities, and provide suggestions on how knowledge gaps may be addressed:

1. We advocate the need for an understanding of the interactions between the autotrophic and the heterotrophic components of biofilms, and on their relative importance and role in nutrient cycling. This will provide important insights into the food quality for primary consumers and allow predictions of future situations. In particular, there is the need for a deeper understanding of the ecological role of fungi and bacteria in alpine stream food webs.
2. Further investigations on community composition of primary producers in different stream types, and an understanding of the drivers and limiting factors for algal accrual during windows of opportunity, will lead to better predictions of future shifts in abundance and

biomass increase and timing. Little is known about aquatic mosses diversity in alpine streams, and about their importance as hydromorphological drivers and detritus traps.

3. Invertebrate meio/microfauna, such as Copepoda, Ostracoda, Nematoda, Rotifera and Tardigrada, remain understudied in Alpine streams. Further work is particularly needed on species distribution, their autoecology, and their sensitivity to deglaciation, which helps in recognizing their functional and ecological role in Alpine stream ecosystems.
4. For macroinvertebrates, interest in the intraspecific diversity loss linked to climate change has been increasing in recent years (e.g. Finn et al., 2013; 2014). Despite a recent study on *Baetis alpinus* diversity (Leys et al., 2016), no specific research has been published so far on the loss of cryptic species related to deglaciation in the Alps. In addition, the phenotypic plasticity of organisms, and their physiological responses to environmental changes deserve further investigation (e.g. Lencioni et al., 2013).
5. For future food web studies, we call for better knowledge about the trophic and functional role of species in Alpine contexts, also based on molecular fingerprinting combined with stable isotope analysis and Bayesian mixing modelling (Niedrist and Füreder, 2018). Considering smaller invertebrates in food web studies, when possible, will also give a more comprehensive picture on the ecological role of hyporheos. Studies of the effects of POPs pollution and nutrient (P, N, OC) loads from glaciers into the food web are also limited. To the best of our knowledge, the ecological effects (e.g. uptake, biomagnification) of metals in both rock glacier- and glacier-fed streams have not been investigated so far.

In conclusion, our current understanding of the impacts of deglaciation on alpine stream ecology is largely based on fragmented data. A combination of high frequency logging and remote sensing would provide datasets with increased spatial and temporal resolution and the potential to derive valuable insights into the processes underpinning habitat and stream ecosystem changes in response to deglaciation. Advances in the analysis of such large datasets are currently creating collaborative opportunities for interdisciplinary and international research groups working on permafrost (International Permafrost Association, https://ipa.arcticportal.org). Such innovative scientific networks and novel approaches are needed to advance knowledge on the significance of mountain permafrost loss for freshwater ecosystems and place the resulting ecological impacts in the global context. International scientific networks can also provide a vital role in guiding management and policy making at the local, regional, and global scales.

CHAPTER 2

After the peak water: the increasing influence of rock glaciers on Alpine river systems

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2.1. INTRODUCTION

Current human-accelerated climate change is leading to a rapid loss of cryosphere globally (IPCC, 2013; Huss et al., 2017). In the European Alps, 76-97% of the present glacier volume is predicted to vanish within this century (Beniston et al., 2018), and the majority of glaciers to disappear within a few decades, as most of them are very small (<0.5 km^2; Huss and Fischer, 2016). Several Alpine catchments have already surpassed the hydrological tipping point of maximum average discharge associated with glacier wastage, in relation to summer and total annual flows (Huss and Hock, 2018). After this "peak water", on the long-term discharge declines and seasonal maxima shift to the snowmelt peak of early summer (Beniston et al., 2018). The rapid glacier recession in alpine catchments is paralleled by an increased hydrological role of stochastic precipitation (Milner, Brown and Hannah, 2009; Milner et al., 2017), and by an increased prevalence of paraglacial features (i.e. adjustments in the landscape following glacier loss) and periglacial (i.e. conditioned by frost) processes driven by a slower and prolonged permafrost ice thaw (Haeberli, Schaub and Huggel, 2016). Rock glaciers are common and evident forms of mountain permafrost (Jones, Harrison, Anderson and Whalley, 2019), and their internal ice represents an important water reservoir globally (Jones, Harrison, Anderson and Betts, 2018).

Water origin is a key control of alpine stream ecosystems since it influences the habitat template (i.e. the combination of different physical and chemical conditions) in which biotic communities reside and interact along the river continuum (Hannah et al., 2007; Milner et al., 2009). Accordingly, different alpine stream types have been originally described (Ward, 1994): kryal (glacier-fed), krenal (groundwater-fed), and rhithral (snowmelt/rainwater fed). In the lower part of the catchments, the term "glacio-rhithral" is commonly used to reflect the contribution from different water sources (Füreder, 1999). Outflows from rock glaciers are commonly observed in the Alps as in other mountain ranges (Jones et al., 2019). However, to date no research has focused on characterizing the distinctive habitat template of such running waters (Brighenti et al., 2019a). Rock glacier-fed (hereafter referred to as "rock glacial") streams exhibit particular hydrological and chemical conditions, comprising cold (<1.5°C) and clear waters with high electrical conductivity associated with high concentrations of major ions and, often, trace elements (Thies, Nickus, Tolotti, Tessadri and Krainer, 2013; Colombo et al., 2018a; Rotta et al., 2018a). Solute concentrations typically increase from spring to autumn, when the baseflow can be sustained by thawing internal ice (see Colombo et al., 2018a). Due to their cold waters, rock glacial streams were found to decrease summer water temperature in tributaries along the river continuum, thus extending refuge areas for cold-adapted species (Harrington, Hayashi and Kurylyk, 2017). In general, rock glaciers (including fossil forms, i.e. those without ice) and other landscape features including talus bodies, moraines, and tills represent important groundwater sources (Clow et al., 2003; Wagner, Pauritsch and Winkler, 2016; Winkler et al., 2016; Rogger et al., 2017; Harrington, Mozil, Hayashi and Bentley, 2018) that are able to influence the quantity and quality of running waters in alpine catchments (Liu, Williams and Caine, 2004; Weekes, Torgersen, Montgomery, Woodward and Bolton, 2015; Engel et al., 2019). However, most research to date has focused on the hydrology of single landforms (e.g. for talus bodies see Muir, Hayashi and McClymont, 2011; for moraines Winkler et al., 2016; for rock glaciers Harrington et al., 2018; Winkler et al., 2016), and we are not aware of any study attempting a longitudinal characterisation of stream conditions under their combined influence at the catchment scale. In fact, glaciers are generally considered as the major hydroecological driver during the snow-free season in glacierized catchments (e.g. Ilg and Castella, 2006; Brown, Milner and Hannah, 2010).

Our research therefore aimed to characterize the habitat features of rock glacial streams and appraise the seasonal and diurnal patterns of glacial, periglacial, and paraglacial influence along glacier-fed streams. We tested two hypotheses: H1) Rock glacier outflows represent a distinct alpine stream type, with different physical and chemical conditions when compared to kryal, krenal and glacio-rhithral habitats; H2) Rock glaciers influence stream conditions along the river continuum, in catchments with small glacier cover and fading glacial influence. We investigated the physical and chemical characteristics of different stream types within a glacierized catchment, and characterized the influence of glaciers, permafrost, mountain landforms, and groundwater on the stream habitat conditions moving downstream from the glacier snout.

2.2. STUDY AREA

The Solda Valley (Figure 2.1A) is located in the Central Italian Alps, in the Ortles/Cevedale massif. The climate is typically alpine, with average temperatures ranging from 10.6 °C in July to -5.3 °C in January and an average annual precipitation of 860 mm (Autonomous Province of Bolzano/Bozen – APB, 2018a) at Solda village (1900 m a.s.l., 1982/2012 period). The research was conducted in the upper Solda and Zay subcatchments, which both have their closing section in Solda village. The area hosts several glaciers (World Glacier Monitoring Service - WGMS, 2018) and active rock glaciers occurring above ~2700 m a.s.l. (APB, 2018b). Three tectonic units of the Austroalpine domaine (Ortles, Zebrù and Peio) merge in the valley resulting in a complex geology (Montrasio et al., 2015). To reduce this bedrock variability, we selected the study sites (Table 2.1, Figure 2.1B) within the crystalline basement (Campo Nappe), mainly composed of gneisses and quartzphyllytes.

The upper Solda subcatchment (area 20 km^2, maximum elevation 3902 m a.s.l.) hosts several glaciers covering 32% of the total area (APB, 2018b). Among these, the North-oriented Suldenferner (1.05 km^2, mean elevation 2986 m a.s.l.) is a debris-free glacier that has experienced considerable retreat during the last decades (320 m during 1920-2016 period; WGMS, 2018). Sampling sites (Figure 2.1B) included the stream originating from this glacier (S1, S2), the permanent outflow (SRG) of an active rock glacier (area 0.072 km^2) located in the alpine belt, and one of the several springs originating from the slopes in the subalpine belt (i.e. SKN, Table 2.1).

The smaller Zay subcatchment (11 km^2, 3546 m a.s.l., Figure 2.1C) is geologically more homogeneous (gneisses, with some intrusions of amphibolites in the lower section). Three small glaciers (area <0.5 km^2) cover 8 % of the subcatchment area. Among them, the North-oriented Ausserer Zay (0.3 km^2) is a debris-covered glacier that retreated 260 m from 1897 to 2007 (WGMS, 2018), and additional 90 m from 2008 to present (comparison between the present front and the 2008 orthophoto of the APB, 2018). The main stream of the subcatchment (Zay Stream) originates from this glacier (station Z1), whereas no other major surface runoff originates from the other glaciers (Figure 2.1C). The Zay Stream has a complex flow path (Figure 2.1C, Table 2.1): 400 m below the glacier snout (Z3), the stream feeds a small lake (0.044 km^2, 2772 m a.s.l.) whose outflow immediately sinks into moraine debris. The moraine outflow (Z4), located 200 m downstream, runs beside the body of an active rock glacier (0.09 km^2, 2719 m a.s.l. front), and joins with its outflow (ZRG, Table 2.1) in a small glacial floodplain (Z5, Table 2.1). Downstream, the closing section (Z6) of the glacial cirque (5.2 km^2) also drains a series of three proglacial lakes without any evident outlet, and a huge rock glacier (0.42 km^2) that feeds a very small spring not directly connected with the Zay Stream. Beyond the glacial cirque, the stream seeps into the debris of a talus slope, from which it re-emerges after a distance of 600 m and an elevation 290 m lower (Z7, Figure 2.1C). The slopes of this lower part of the subcatchment are occupied by some intact and several relict rock glaciers without any evident superficial outflow. In the sub-alpine belt, groundwater-fed tributaries, including the one where the ZKN station is located, join the Zay Stream before station Z12. In the lower part, the stream flows through a coniferous forest (Z13) before reaching the Solda village (Figure 2.1).

Figure 2.1 A) Location of the study area and of the two subcatchments; B) Upper Solda; and C) Zay with location of the sampling stations and main geomorphic drivers. Station codes as in Table 2.1. D) Hypsographic curve of Zay stream, with indication of the monitoring stations.

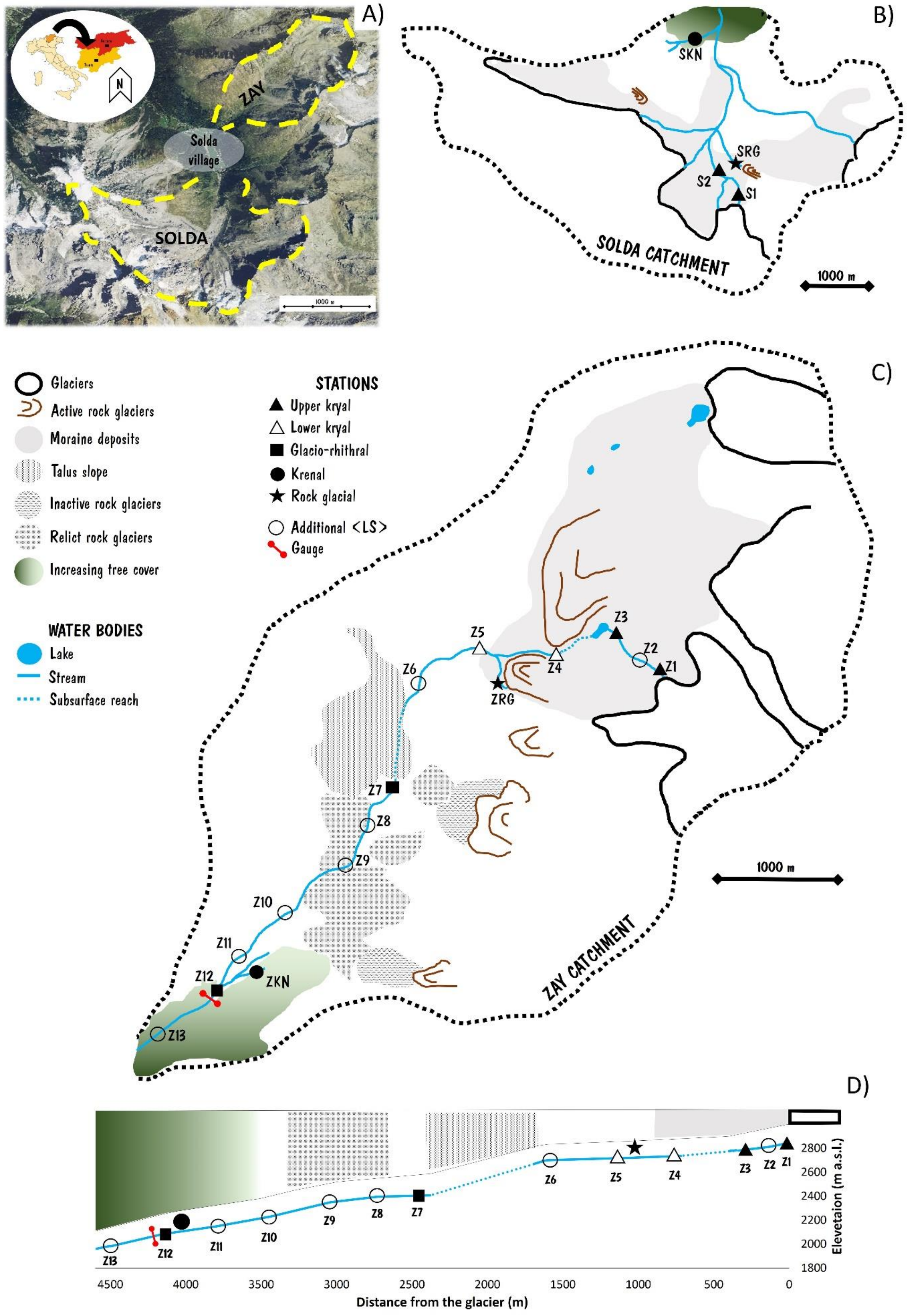

Table 2.1. Main features of sampling stations. Code^{LS}= only longitudinal survey undertaken. Lat/Lon= coordinates referring to WGS84, UTM32N. Alt= elevation (m a.s.l.). Dist = distance from the spring (km). Slope = % average slope, obtained with clivometry maps (Autonomous Province of Bolzano/Bozen, 2018). Channel type derived from Rinaldi et al. (2016). Veg= Riparian vegetation, classes: 0=sparse/absent, 1=discontinuous alpine heat, 2= continuous alpine heat, 3= alpine heat with sparse trees and shrubs 4= canopy from trees and shrubs. Moss= abundance of mosses in the channel, classes: 0=0-5%, 1=5-10%, 2=10-30%, 3=30-50%. Different kryal habitats (i.e. upper and lower stations) are classified in this work according to the distance from the glacier snout.

Catchment	Code	Lat/Lon	Alt	Dist	Slope	Habitat type	Channel type	Veg	Moss	Bedrock[c]
Zay	Z1	625.249/ 5.156.172	2845	0	55	Upper kryal	Single-thread, straight	0	0	Orthogneiss (Quartzphyllyte)
Zay	Z2^{LS}	624.690/ 5.156.263	2811	0.13	10	Upper kryal	Double-thread	0	0	Orthogneiss
Zay	Z3	625.039/ 5.156.377	2780	0.34	18	Upper kryal	Single-thread, straight	1	0	Orthogneiss
Zay	Z4[a]	624.691/ 5.156.262	2736	0.72	10	Lower kryal	Single-thread, straight	1	3	Orthogneiss
Zay	Z5	624.278/ 5.156.281	2717	1.13	2	Lower kryal	Glacial floodplain Multi-thread	1	1	Orthogneiss
Zay	Z6^{LS}	623.870/ 5.156.156	2699	1.61	1	Lower kryal	Single-thread, sinuous	1	1	Orthogneiss
Zay	Z7	623.744/ 5.155.463	2407	2.38	4	Glacio-rhithral	Single-thread, sinuous	2	3	Orthogneiss, Flaser paragneiss
Zay	Z8^{LS}	623.696/ 5.155.423	2395	2.73	5	Glacio-rhithral	Single-thread, sinuous	2	3	Orthogneiss, Flaser paragneiss
Zay	Z9^{LS}	623.574/ 5.155.234	2350	3.04	35	Glacio-rhithral	Single-thread, sinuous	3	2	Orthogneiss, Flaser paragneiss
Zay	Z10^{LS}	623.446/ 5.155.015	2228	3.44	17	Glacio-rhithral	Single-thread, straight	3	3	Orthogneiss, Flaser paragneiss
Zay	Z11^{LS}	623.131/ 5.154.761	2148	3.8	20	Glacio-rhithral	Multi-thread	3	3	Orthogneiss, Flaser paragneiss
Zay	Z12[b]	622.893/ 5.154.517	2084	4.15	25	Glacio-rhithral	Multi-thread: anabranching	4	2	Orthogneiss, Flaser paragneiss
Zay	Z13^{LS}	622.681/ 5.154.270	1982	4.5	40	Glacio-rhithral	Single-thread, straight	4	2	Flaser paragneiss, Orthogneiss (Amphibolites)
Zay	ZRG	624.401/ 5.156.088	2718	0	2	Rock glacial	Single-thread, sinuous	2	1	Orthogneiss
Zay	ZKN	622.936/ 5.154.442	2160	0	22	Krenal	Single-thread, straight	4	3	Flaser paragneiss
Solda	S1	622.586/ 5.148.841	2710	0	15%	Upper Kryal	Single-thread, straight	0	0	Orthogneiss, Phyllades, Amphibolites, (Prasinites and Serpentinites)
Solda	S2	622.250/ 5.149.314	2560	0.7	10%	Upper Kryal	Multi-thread: braided	0	0	Phyllades, Amphibolites, Quartzites (Prasinites, Serpentinites)
Solda	SRG	622.737/ 5.149.517	2586	0.05	25%	Rock glacial	Single-thread, straight	2	3	Orthogneiss, Quartzphyllytes, Micaschists (Andesites)
Solda	SKN	622.298/ 5.151.224	2105	0.1	65%	Krenal	Single-thread, straight	3	2	Orthogneiss, Quartzphyllytes, Amphibolites (Dolomite)

2.3. METHODS

Streams were investigated during two consecutive years (2017, 2018). Sites (Figure 2.1, Table 2.1) were sampled during five-day campaigns conducted in three main periods of the alpine summer: snowmelt (3rd week of June), glacier ablation (end July/beginning of August), and flow recession (1st week of September). Several additional field-trips were undertaken during summer 2018 for discharge measurements and supplementary surveys. We designed two types of survey, differing in aims and monitored parameters: extensive surveys and longitudinal surveys.

2.3.1 Extensive surveys

These surveys (N=6) characterized the physical and chemical conditions of streams as a function of water origin. At each subcatchment, we selected one groundwater-, one rock glacier-, and one glacier-fed stream. Additionally, four stream sections of mixed origin were selected along the Zay Stream (Figure 2.1C). A total of twelve stations (reaches) of ~50 m length each were investigated.

Water temperature, electrical conductivity (EC), and turbidity were recorded with portable probes (WTW-Cond-3310 and WTW-Turb-430IR, Germany). Water level was recorded (in 2018) by measuring the water surface elevation at fixed iron rods. Discharge (not assessed at ZRG and Z5 because the very wide and shallow channels prevented complete transversal mixing) was measured with the salt-dilution method (Gordon, MacMahon and Finlayson, 1992) during periods of maximum and minimum flow, and was used to build flow-rating curves associated with water level. A gauging station equipped with a level-meter pressure transducer (Keller AG Messtechnik, Switzerland) was deployed near the Zay closing section (Z13, 2081 m a.s.l.) for continuous recording at 10 min intervals. All extensive survey stations were instrumented with temperature data-loggers (HOBO© WaterTempProv2, Onset, Germany), with 30 min interval records. Temperature datasets were used to calculate the maximum (T_{max}), minimum (T_{min}), average water temperature (T_{avg}) and temperature range ($dT= T_{max}-T_{min}$) for each survey week.

Water samples for chemical analyses were collected in 500 mL polyethylene bottles and preserved at 4°C until analysis at the Hydrochemistry laboratory of the Edmund Mach Foundation. Alkalinity, pH, EC, CO_3^-, Ca^{2+}, Mg^{2+}, Cl^-, Na^+, K^+, total nitrogen (TN), NH_4^+-N, NO_3^--N, total phosphorus (TP), PO_4^--P, SO_4^{2-} and SiO_2, were determined according to standard methods (APHA-AWWA-WPCF, 2017). Stream water for the determination of trace elements was filtered with cellulose acetate membranes (0.45 µm) into acid washed 100 mL polyethylene bottles and acidified at 1-1.5% with >65% HNO_3 until delivered to Ecoresearch S.r.l. laboratory (Bolzano), where concentrations of Be, B, Na, Mg, Al, K, Ca, Ti, V, Cr, Mn, Fe, Co, Ni, Cu, Zn, As, Se, Rb, Sr, Mo, Ag, Cd, Sn, Sb, Ba, Tl, Pb, U, Bi, P were measured using a ICP-MS ICAP-Q, Thermo Fischer analyser. Water samples for the determination of Dissolved Organic Carbon (DOC) were collected in clean, pre-acidified (65% HNO_3), 100 mL polyethylene bottles and preserved at 4°C until delivered to Dolomiti Energia S.p.a. laboratory (Trento).

To identify the major runoff components for each station and sampling time, precipitation, snowmelt, ice-melt and stream water samples were collected in 50 mL polyethylene bottles. A time-integrated precipitation sample was collected each month (from May to October) in rainwater containers built by following the IAEA (2014) standards, and placed nearby SRG and ZRG stations. Snowmelt and ice melt samples were taken from dripping snow patches and glacier surface rivulets at each sampling occasion. Isotopic analysis of δ^2H and δ^{18}O was conducted with a laser spectroscope (Picarro L2130i, precision: 0.1‰ for δ^2H, 0.25‰ for δ^{18}O) at the laboratory of the Free University of Bozen/Bolzano.

Channel stability was assessed with the Pfankuch index (Pfankuch, 1975), obtained by recording metrics describing: upper banks (landform slope, mass-wasting, debris jam potential, vegetation, channel capacity); lower banks (rock content, obstructions, undercutting, deposition); and the streambed (rock angularity, brightness, particle packing, clasts size, scouring and deposition, aquatic vegetation). Scores assigned to each variable are summed in order to achieve the index, with low and high scores associated with stable and unstable channels, respectively. An aliquot of water (250-3000 mL) was collected and filtered in the field through GF/C Whatman glass microfiber filters, that were stored frozen (<-20°C) until the determination of suspended solids concentration, which was calculated as ash-free dry mass (AFDM, g L^{-1}) following Hauer and Lamberti (1996). The organic detritus was sampled with a Surber net (100 µm mesh, 506 cm^2 frame) by disturbing different substrates (i.e. mosses, boulders, cobbles and gravel) according to their relative abundance in the channel (five total replicates). Samples were preserved in 90% ethanol and devoid of invertebrates and fragments of living mosses under a dissecting microscope. Organic detritus was calculated as ADFM (g m^{-2}). The coarse (≥ 1 mm) and fine (< 1 mm) fractions were separated with a sieve to calculate the detritus ratio (coarse/fine).

2.3.2. Longitudinal surveys

These surveys (N=3) estimated the diel and seasonal variability of glacier influence on habitat conditions along the river continuum. Longitudinal surveys were conducted at the Zay subcatchment, where we selected 13 monitoring points (Figure 2.1D), that included all extensive survey stations and additional sites that were added to obtain a more regular spacing. Monitoring was undertaken on days without precipitation during the extensive survey campaigns of 2018. Two teams assigned respectively to the upper (Z1-Z6) and lower (Z7-Z13) stations of the subcatchment measured water temperature, EC, turbidity and water level every three hours starting from 7 AM (five runs of approximately 60 min each), proceeding downstream (ZKN and ZRG were included). Portable conductivity (WTW-Cond-3310, WTW-Cond-3210) and turbidity (WTW-Turb-430IR) meters were previously cross-calibrated in the laboratory to ensure comparable recording between the two teams. Station Z1 was not sampled in June as it was covered with snow. Due to safety reasons (dry thunderstorm), 4 PM and 7 PM runs in lower Zay (Z7-Z13) were not undertaken in September. Six additional surveys with morning, mid-day and afternoon runs were conducted in different weeks respect to longitudinal surveys, and were included in the calculation of the glacial indices (see below). The data recorded by the gauging station at Z13 and the data-loggers were used to provide information about the discharge and temperature patterns of the period and guarantee that the longitudinal survey data were representative of each hydrological period. The Pfankuch index was assessed for all the longitudinal survey stations. Discharge measurements were conducted using the salt dilution method at Z2, Z3, Z4, Z6, Z8, Z11 during seasonal discharge minima and maxima, to evaluate the discharge range, and flow rating curves were developed.

2.3.3. Data analysis

To detect the different components of the water flow, mixing diagrams for each subcatchment were produced by plotting δ^2H against SiO_2 values, where silica was assumed as a proxy for groundwater contribution (Ward, Malard, Tockner and Uehlinger, 1999; Brown, Hannah and Milner, 2003; Liu et al., 2004; Brown et al., 2006). In addition, we used a tracer-based runoff separation and produced two-member mixing models. Accordingly, mass balance equations 1 and 2 were applied to separate discharge into two flow components (Blaen, Hannah, Brown and Milner, 2014):

$$Qgw / Qi = (Cm - Ci) / (Cm - Cgw) \qquad \text{(Equation 1)}$$

$$Qi = Qm + Qgw \qquad \text{(Equation 2)}$$

where Q denotes discharge and C the solute (Silica) concentrations. Subscripts gw, m and i refer to groundwater, melt water, and sampling site water, respectively.

We assumed that meltwater was driven by the snowmelt or the ice melt (for both found below the detection limits, i.e. 0.05 mg L^{-1}). The groundwater component was defined as the highest value at krenal sites (for both SiO_2 = 4.3 mg L^{-1}). The uncertainty was calculated following Genereux (1998) and accounting for the error propagation where data were pooled together.

The extensive survey dataset was analysed by Principal Component Analyses (PCA), with Kaiser normalization and Varimax rotation, to visualize the environmental variables associated with different stations and sampling date. Trace elements were analysed in a separate PCA from the other environmental variables, in order to account for bedrock composition variability. Stepwise forward selection, discarding the variables not strongly correlated (correlation coefficient <0.5) to any other in the correlation matrix, was used to choose the variables. Water isotopes (analysed separately), detritus ratio (redundant with organic detritus), suspended solids (redundant with turbidity), and trace elements above the detection limits for less than 6 samples were excluded from the multivariate analyses.

The longitudinal survey dataset was analysed to compute the glacier influence and its spatial and temporal trends. The Glaciality Index proposed by Ilg and Castella (2006) uses the normalized values of water temperature, EC, 1/suspended solids, and 1/Pfankuch (only bottom component) to produce a non-centred PCA, where the PC1 scores are taken as values of the index. We used a similar approach and built our Index of Glacial Influence (IGI) by using

1/water temperature, 1/EC, turbidity, and Pfankuch (upper banks, lower banks and bottom components) in order to obtain increasing IGI values associated with increasing glacial influence. The IGI values were eventually obtained by adding to PC1 scores the minimum value of them, to achieve all positive numbers. Given the large seasonality of the glacier influence in alpine catchments (e.g. Milner and Petts, 1994; Brown et al., 2003), we designed a specific index of Seasonal Glacier Influence (SGI), reflecting the large seasonal variability of habitat conditions driven by the presence of glaciers. This index was obtained using the same method employed for the calculation of the IGI by using the following variables in the PCA: Pfankuch index; total averages of turbidity; 1/water temperature; 1/EC; and the standard deviation values of turbidity and EC. We cross-compared (non-parametric Spearman correlation, ρ) our calculated indices with the total area occupied by glaciers in the underlain catchment area (Glacier cover in the catchment) and the Glacial Influence index of Jacobsen and Dangles (2012), calculated as a function of distance from the glacier and its area.

Ggplot2 package in R version 3.6.0 (R Development Core Team, 2017) was used to produce biplots of mean and standard deviation of the variables across the gradients over the season. Pairwise comparisons (Table 2.2) were made to analyse differences in all the analysed variables between sample groups (i.e. months, stream types). Due to non-normal distribution (Shapiro-Wilk, $P<0.5$), even after data transformation, and/or inhomogeneous variances (Levene, $P>0.5$), we used the non-parametric Wilcoxon rank-sum and the Kruskal-Wallis tests, with post-hoc Mann-Whitney test and Bonferroni corrections. The softwares SPSS (v.25, IBM, 2018) and R were used to analyse the data.

Table 2.2. *Results from the pairwise comparisons analyses. The values of the post-hoc test (Mann-Whitney test adjusted by the Bonferroni correction for multiple tests) are reported where differences are significant, according to the corresponding α-value and df. Stream type codes: UK= Upper Kryal, LK= Lower Kryal, GR= Glacio-rhithral, KN= Krenal, RG= Rock glacial, all= all other stream types. Month codes: JUN= June, AUG= August, SEP= September, all= all other periods. Proglacial= Z1-Z3, Others= Z4-Z13. See text for further details on measured variables.*

Variable	Groups	N	p-value	Test statistic	df	Post-hoc <0.001	Post-hoc <0.01	Post-hoc <0.05
EXTENSIVE SURVEYS								
Pfankuch index	Stream type	68	<0.001	H=52.4	4	UK>GR,KN, RG		UK>LK
Turbidity	Stream type	68	<0.001	H=42.5	4	UK>KN,RG		UK>GR
Suspended Solids	Stream type	63	<0.001	H=43.6	4	UK>KN,RG	UK>GR, LK	
SiO_2	Stream type	63	<0.001	H=51.6	4	UK<RG,KN	UK<GR, LK	
Organic detritus	Stream type	67	<0.001	H=54.4	4	UK<GR,RG, KN	LK<KN	
Detritus ratio	Stream type	67	<0.001	H=43.4	4	UK<GR,KN	RG<KN	
Total P	Stream type	68	<0.001	H=25.3	4	UK>GR,KN	LK<KN	UK>RG
T_{max}	Stream type	65	<0.001	H= 32.7	4	RG<KN,GR	RG<LK	RG<UK
T_{avg}	Stream type	65	<0.001	H= 44.7	4	RG<KN,GR UK<KN,GR		
dT	Stream type	65	<0.001	H=20.4	4	RG<UK	RG<LK	RG<GR
$\delta^{18}O$	Month	67	<0.001	H=19.5	2	JUN<SEP		
$\delta^{2}H$	Month	67	<0.001	H= 20.2	2	JUN<SEP		AUG<SEP
Turbidity	Month at UK	24	0.006	H= 11.3	2		SEP<AUG	SEP<JUN
Electrical conductivity	Month at UK	24	0.003	H= 10.1	2			SEP>all
NO_3^-	Month at UK	24	<0.001	H=16.8	2	SEP<AUG		SEP>JUN
Ca^{2+}	Month at UK	24	0.005	H= 10.5	2			SEP>all
Mg^{2+}	Month at UK	24	0.031	H= 6.9	2			
SO_4^{2-}	Month at UK	24	0.011	H= 9.0	2			SEP>all
Turbidity, Pfankuch index	ZRG>SRG	12	0.002	U=36.0				
Electrical conductivity, Ca^{2+}, Mg^{2+}, SO_4^{2}, HCO_3^-, pH	SRG>ZRG	12	0.002	U=21.0				
K^+	SRG>ZRG	12	0.041	U=5.0				
Total N	SRG>ZRG	12	0.026	U=32.0				
Rb	Solda<Zay	70	<0.001	U=863.5				
Sr	Solda>Zay	70	0.001	U=304.0				
Ba	Solda>Zay	70	0.037	U=415.0				
U	Solda<Zay	70	0.003	U=816.0				

Mn	Stream type	70	<0.001	H=48.9	4	UK>all		
As	Stream type	70	<0.001	H=41.0	4	KN<GR,RG UK>RG		KN<LK UK<LK
U	Stream type	70	<0.001	H=29.71	4	KN<RG	KN<LK,GR UK<RG	
Sr	Stream type	70	0.013	H=12.71	4			UK<RG
LONGITUDINAL SURVEYS								
Water temperature	Proglacial < others	173	<0.001	U=4893				
Electrical conductivity	Proglacial < others	173	<0.001	U=3938				
Turbidity	Proglacial > others	173	<0.001	U=6				
IGI	Proglacial > others	173	<0.001	U=91.6				
SGI	Proglacial > others	13	0.007	U=0				
Discharge	Month at proglacial	40	<0.001	H=27.5	2			JUN>SEP
Electrical conductivity	Month at proglacial	40	0.017	H=8.1	2	SEP>all		
IGI	Month	173	<0.001	H=30.8	2	SEP<all		
Water temperature	Month	173	0.004	H=10.9	2			SEP<AUG
Turbidity	Month	173	<0.001	H=41.6	2	AUG>all		
Electrical conductivity	Month	173	<0.001	H=106.9	2	SEP>all		
Discharge	Month	173	<0.001	H=29.4	2	SEP<JUN	AUG<JUN	SEP<AUG

2.4. RESULTS

2.4.1 Discharge patterns, water origin and temperature profiles

The hydrograph at Zay gauging station (Figure 2.2) revealed major peaks during the snowmelt period (first week of June in 2017, last week of May in 2018). In both years, discharge decreased during summer, especially after early September, with superimposed secondary peaks associated with rainfall events in July and August (Figure 2.2).

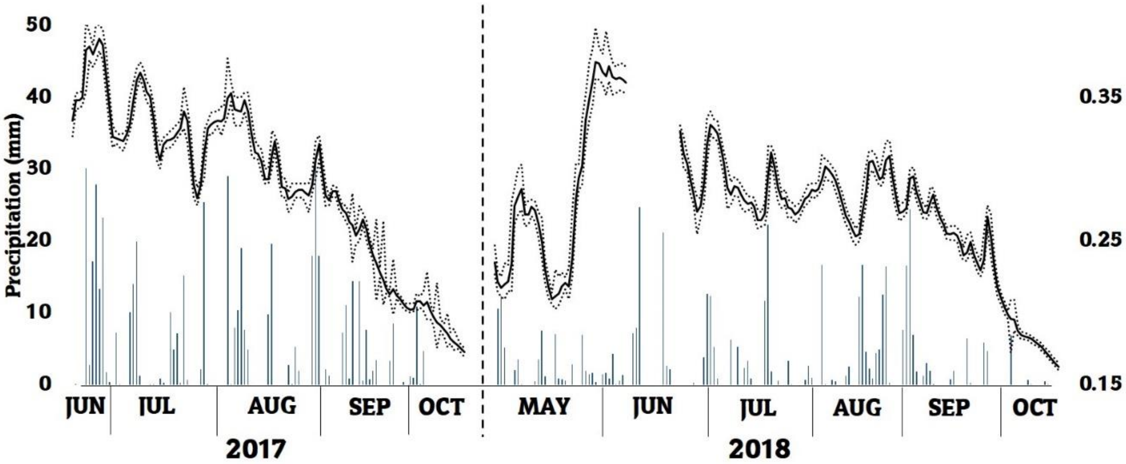

Figure 2.2. *Comparison of daily average water level (continuous line) and maximum and minimum values (dashed lines) at Z13 (2084 m a.s.l., 4.2 km far from the glacier snout) and total rainfall (columns) for both summers (until the 15th October). Gauging stations deployed on 23th June 2017. Precipitation measured at the closest meteorological station, in Solda (Autonomous Province of Bolzano/Bozen, 2018). The water stage gap in 2018 is due to a defect logging period on 9-23 June.*

Discharge decreased consistently from the snowmelt to recession period along the whole Zay stream (Figure 2.3), including the proglacial sites (Z2-Z3), where it was 55 ± 10 L s^{-1} in June, 35 ± 17 L s^{-1} in August, and 13 ± 10 L s^{-1} in September (longitudinal surveys means and standard deviations). Discharge at the Suldenferner snout (all extensive survey measurements always at 10-11 AM), exhibited a different trend, with the highest values recorded in August (136 L s^{-1}), intermediate values in June (113 L s^{-1}), and much lower values in September (12 L s^{-1}) surveys.

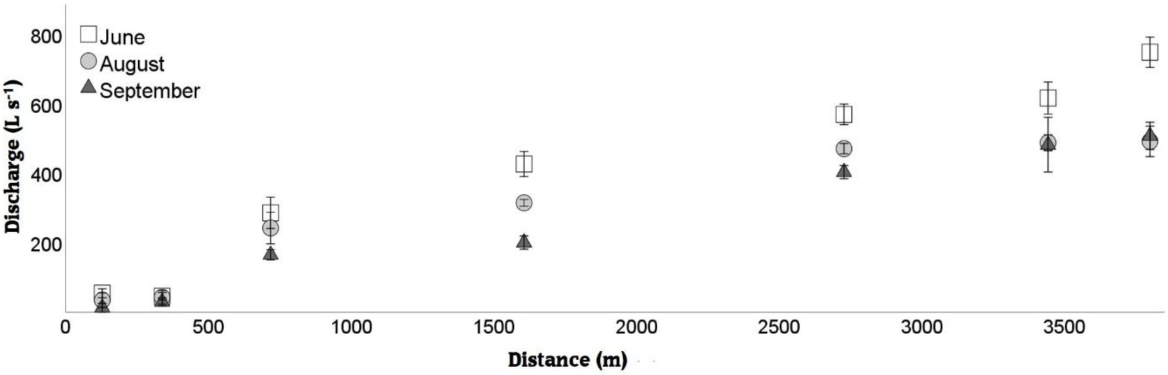

Figure 2.3. *Discharge diel variability along the Zay Stream during the three longitudinal survey campaigns at different stations. Error bars indicate 95% confidence interval.*

Seasonal variations of both $\delta^{18}O$ and δ^2H revealed a significant isotopic enrichment from June to September (Table 2.2), in line with a decreased influence from the melting snow. This seasonality is shown in the mixing space of δ^2H and SiO_2 (Figure 2.4), where all stream samples are included in the range of the potential water sources for both subcatchments. With very low silica concentrations (<0.3 mg L^{-1}), snowmelt (-140.3 to -89.7 ‰) and ice melt (-105.5 to -89.5 ‰) delineate an end-member of isotopic depleted waters, and precipitation a second end-member of isotopically enriched (-91.2 to -38.8 ‰) waters. Sampling station waters were in the isotopic range of snowmelt and ice melt, and differed in terms of silica concentrations, with lowest values for the upper kryal (0.6 ± 0.4 mg L^{-1}) and highest for krenal sites (3.7 ± 0.8 mg L^{-1}) at each extensive survey. Rock glacial, lower kryal, and glacio-rhithral sites exhibited similar silica concentrations at each extensive survey, intermediate between kryal and krenal. Accordingly, the mixing models (Table 2.3) revealed for all periods an increased groundwater contribution from the upper kryal sites (14.1 ± 9.9 % overall mean and SD), to the lower kryal (44.4 ± 10.8 %) and glacio-rhithral (48.3 ± 13.0 %) stations, and to the krenal sites (84.9 ± 19.6 %). Rock glacial streams revealed a high proportion of groundwater contribution (49.2 ± 12.7 %), without any significant difference between ZRG and SRG (Table 2.3).

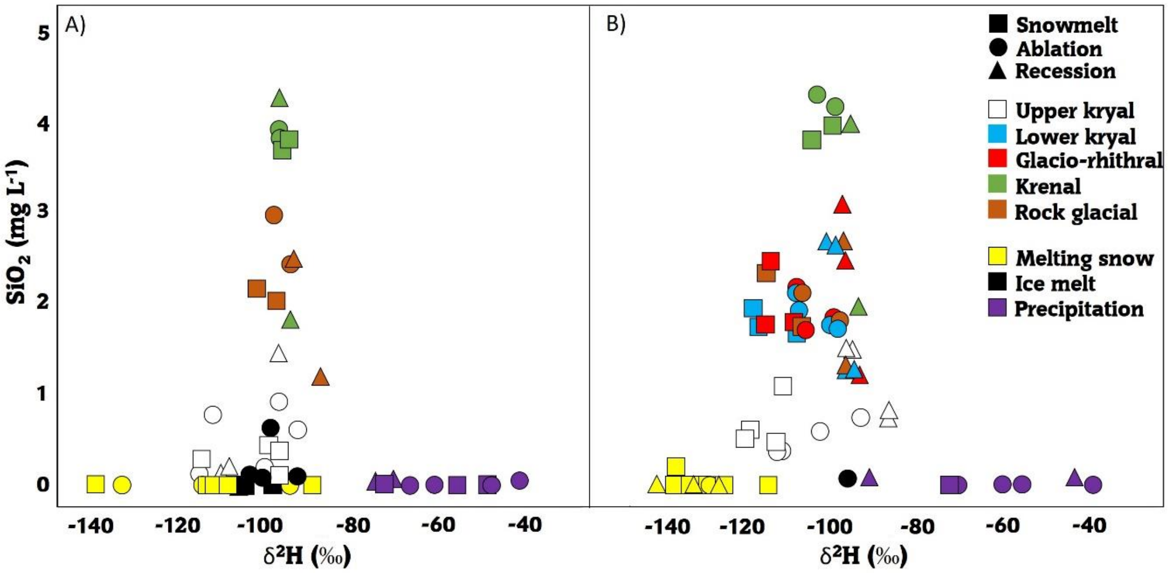

Figure 2.4. Mixing space of δ^2H and Silica (SiO_2) for a) Solda and b) Zay stations, including samples from potential runoff components, i.e. melting snow, supraglacial ice melt and precipitation. Different shapes indicate distinct hydrological periods: "Snowmelt", glacier ablation ("Ablation"), flow recession ("Recession"), pooling together several sampling dates.

Table 2.3. Groundwater contribution (%) resulting from the two end-member mixing analysis (groundwater versus snowmelt/ice melt, Silica concentrations as proxy). For each of the summer periods we provide the groundwater % range across the survey stations, and the mean and standard deviation values for each stream type. With the exceptions of Z1 snowmelt and Z12 (one sample), single numbers indicate the same value in both years. The relatively small values of groundwater contribution during recession are due to snow melting in the days prior to the September 2017 field campaign.

Station	Snowmelt	Ablation	Recession
Upper kryal	**10.0 ± 6.0**	**12.0 ± 6.1**	**20.1 ± 13.4**
S1	2.3	4.7-7.0	2.3-4.7
S2	9.3-18.6	9.3-20.9	14.0-34.9
Z1	14.0	9.3-18.6	18.6-34.9
Z3	11.6	9.3-14.0	16.3-34.9
Lower kryal	**42.6 ± 3.6**	**43.6 ± 4.0**	**46.5 ± 18.8**
Z4	46.5	41.9-48.8	30.2-62.8
Z5	39.5-41.9	39.5-44.2	30.2-62.8
Glacio-rhithral	**47.3 ± 9.4**	**45.0 ± 5.9**	**52.7 ± 22.6**
Z7	41.9	39.5-44.2	27.9-58.1
Z12	58.1	51.2	72.1
Krenal	**89.0 ± 2.9**	**97.1 ± 4.4**	**68.6 ± 28.3**
SKN	86.0-88.4	90.7-100.0	41.9-93.0
ZKN	88.4-93.0	97.7-100.0	46.5-93.0
Rock glacial	**48.3 ± 6.9**	**54.7 ± 12.1**	**44.8 ± 18.3**
SRG	46.5-51.2	58.1-69.8	27.9-58.1
ZRG	39.5-55.8	41.9-48.8	30.2-62.8

Temperature data-loggers showed different patterns according to stream type (Figure 2.5). Low water temperature with reduced diel fluctuations characterized the Zay glacier outlet (Z1, T= 0.7 ± 0.5°C), where diel fluctuations increased in mid-summer, but remained limited when compared to downstream stations. Marked diel fluctuations characterized Z3, where water temperature (T= 2.1 ± 1.2°C) even exceeded 8°C during warm days after the snowmelt (with up to 8°C fluctuations). Moving downstream, the outlets from the moraine (Z3, T= 2.5 ± 0.5°C) and the talus body (Z7, T= 4.7 ± 0.8°C) exhibited increasingly high average temperatures but less pronounced diel fluctuations, compared to Z3. The krenal station ZKN showed constant and relatively low water temperature in summer (T= 3.1 ± 0.3°C), with slight diel fluctuations of maximum 1°C. Rock glacial streams exhibited unique patterns (Figure 2.5), with low water temperatures slightly increasing over the season, and almost absent diel fluctuations (1.2 ± 0.1°C for both ZRG and SRG). The temperature profile of SRG exhibited more pronounced daily fluctuations than ZRG, and showed transient (0.5-1.5 hrs) peaks (up to 2.6°C) associated with rainfall events. Also the upper kryal station showed transient temperature peaks, apparently associated with rainfall events, although these fluctuations were less frequent and minor (not shown).

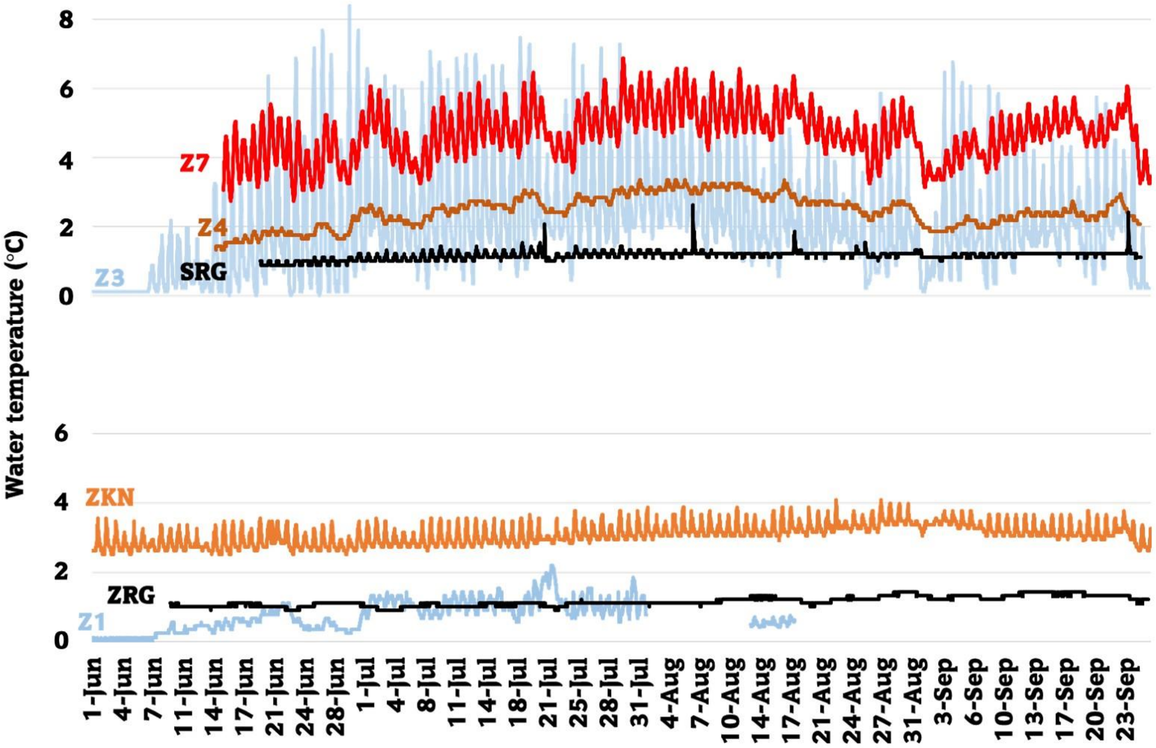

Figure 2.5. *Temperature profiles for key stations in summer 2018, from the 1st of June to the 27th of September. Interruptions for the Z1 profile are caused by sensor emergence from water.*

2.4.2 Extensive surveys

The first two components of the PCA with the retained environmental variables (Figure 2.6) explained 72.6% of the total variance, and the variable loadings are summarized in Table 2.4.

Table 2.4. *Variable loadings of the environmental and trace element principal component analyses (after VariMax rotation). Bold numbers indicate strong correlation (<-0.6 or > 0.6). Var. exp.= variance explained*

Environmental features			Trace elements		
	PC1	**PC2**		**PC1**	**PC2**
Var. exp.	44.8%	27.9%	Var.exp.	41.4%	33.2%
EC	**0.98**	0.15	Sr	**0.98**	0.04
SO_4^{2-}	**0.98**	0.07	Ba	**0.95**	0.05
Ca^{2+}	**0.98**	0.13	As	**0.78**	-0.21
Mg^{2+}	**0.97**	0.08	Rb	0.03	**0.89**
K^+	0.35	**0.67**	Al	-0.03	**0.85**
Turbidity	-0.27	**-0.72**	U	0.06	**0.71**
SiO_2	0.11	**0.91**			
Pfankuch	-0.11	**-0.81**			
NO_3^-	0.23	0.55			
T_{avg}	-0.29	**0.65**			
Organic detritus	-0.08	**0.76**			

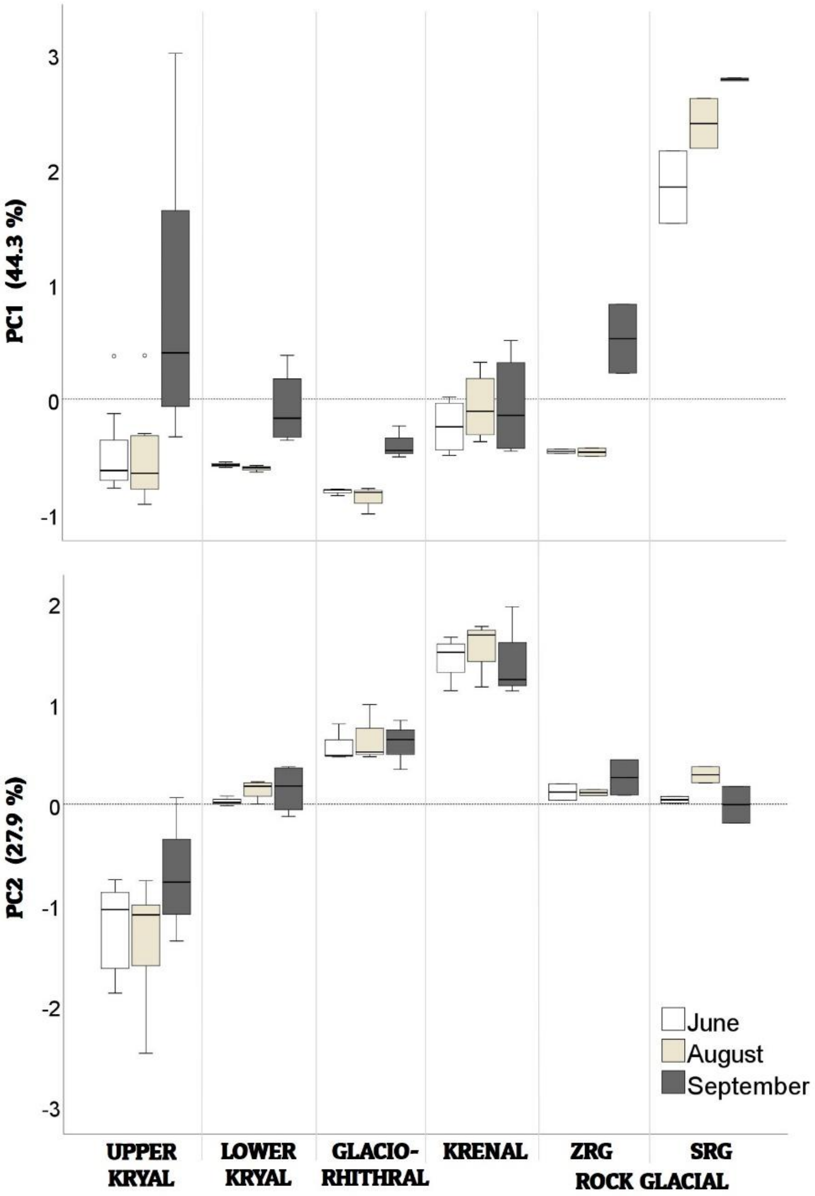

Figure 2.6. *Boxplots of the two principal components resulting from the retained environmental variables. Boxes are clustered in terms of sampling timing, and grouped in terms of stream type except for rock glacial streams for which boxes of single stations are provided.*

Samples were clearly separated according to stream type and seasonality. Upper kryal stations could be distinguished in terms of their low PC1 and PC2 values. Accordingly, pairwise comparisons (Table 2.2) showed that upper kryal stations had significantly higher Pfankuch index (i.e. channel instability), suspended solids, turbidity, and total P, and lower SiO_2, organic detritus, and detritus ratio compared to the other stream types. However, in September, the upper kryal stations exhibited significantly lower turbidity values and higher EC, NO_3^-, SO_4^{2-}, Ca^{2+}, than in June and August (Table 2.2), and the strong seasonal variability of the habitat conditions was also identified in the PCA by a progressive shift towards positive values of PC1 and PC2 (Figure 2.6). Samples from upper kryal to lower kryal, glacio-rhithral, and krenal stations were distributed along a gradient of decreasing water turbidity and increasing channel stability, water temperature and abundance of organic detritus (Figure 2.6). In fact, a strong negative correlation (ρ=-0.84, P<0.001) was identified between PC1 values and the Jacobsen Index of glaciality in the catchment. Within each stream type, the PC values shifted from June to September along a gradient of increasing solute concentrations (Figure 2.6). Nevertheless, this variability was minimal for krenal stations (confirmed by non-significant differences among the three periods in the variables). At each sampling occasion krenal stations exhibited the highest values of SiO_2, organic detritus, and detritus ratio among stations, although differences in mean values were significant only when compared to upper kryal stations (Table 2.2). Rock glacial streams exhibited significantly lower T_{max} and dT compared to all other stream types, and the lowest T_{avg} except for those of kryal stations. However, only SRG can be clearly distinguished in Figure 2.6, due to the particularly high values of PC1, while ZRG scores are placed in the same range of lower kryal stations except for September values, that are associated with increased PC1 scores. In fact, the two rock glacial streams exhibited clear differences in water chemistry, with SRG showed significantly higher pH, EC, Ca^{2+}, Mg^{2+}, SO_4^{2-}, HCO_3^-, K^+, Pfankuch index values, and lower turbidity and total nitrogen than ZRG (Table 2.2). In both rock glacial streams, NO_3^- levels (108-272 µg L^{-1}) were comparable to those of glacio-rhithral and lower kryal in all samples, and showed highest values in September, while PO_4^- concentrations (1-5 µg L^{-1}) were among the highest of all stream types in all periods.

In the PCA undertaken with the retained trace elements (As, Sr, Ba, Al, Rb and U), 74.7 % of the variance was explained by the first two components (Figure 2.7, Table 2.5). One outlier (Z3, September 2017) was removed before running the analysis because of extremely high concentrations of Al and Fe (see Discussion). All June samples except SRG plot close to the PCA axes origin, due to low concentrations of trace elements. At the krenal sites, trace element concentrations remained for the whole season close or below the detection limits. For the other stream types, August and September samples are spread along the two PC axes in Figure 2.7, and clearly differ in the two subcatchments, with upper kryal and rock glacial samples from Solda grouped along PC1 (increasing As, Sr, Ba) and Zay samples grouped along PC2 (increasing Al, Rb, U). The pairwise comparisons (Table 2.2) confirmed this pattern (higher values of Rb and U and lower values of Ba and Sr at Zay), and provided further detail on the distinction between habitats based on the trace elements discarded in the PCA. In fact, upper kryal exibited significantly higher values of Mn (up to 22.3 µg L^{-1}) compared to all other stream types. The highest trace elements concentrations were detected in September at both Zay (U, Mn and in 2017 Fe, Al, Rb) and Solda (As, Sr, U, and Ba, Ni, Cu, Rb only in this month) upper kryal. U exhibited high concentrations along the entire Zay stream over this period, with higher values in the proglacial sections (68.1-88.3 µg L^{-1}) than downstream (6.6-35.7 µg L^{-1}). High concentrations of trace elements were also detected in rock glacial waters, in particular SRG that showed the highest concentrations of As (22-36 µg L^{-1}), Sr (29.5-614 µg L^{-1}) and Ba (11.8-24 µg L^{-1}) among stations in all periods (Figure 2.7). In September, concentrations of U at ZRG (53.2-81.9 µg L^{-1}) were comparable to those of Zay upper kryal, and higher than those of the nearby lower kryal sites (6.6-35.7 µg L^{-1}).

Table 2.5. *Variable loadings for the Principal Component Analysis used to build the indices of Glacial Influence. Bold numbers indicate correlation > 0.6 or <-0.6.* [a]*based on single datapoints.* [b]*based on the whole dataset mean and SD.*

Index of Glacial Influence (IGI)[a]			**Stationary Glacier Influence (SGI)**[b]	
	PC1	PC2		PC1
1/EC	**0.91**	0.16	Turbidity SD	**1.00**
Turbidity	**0.85**	-0.20	Turbidity average	**0.99**
Pfankuch index	**0.72**	-0.55	Pfankuch index	**0.98**
1/water temperature	0.52	**0.81**	Conductivity SD	**0.86**
			1/average water temperature	**0.78**
			1/average EC	**0.70**

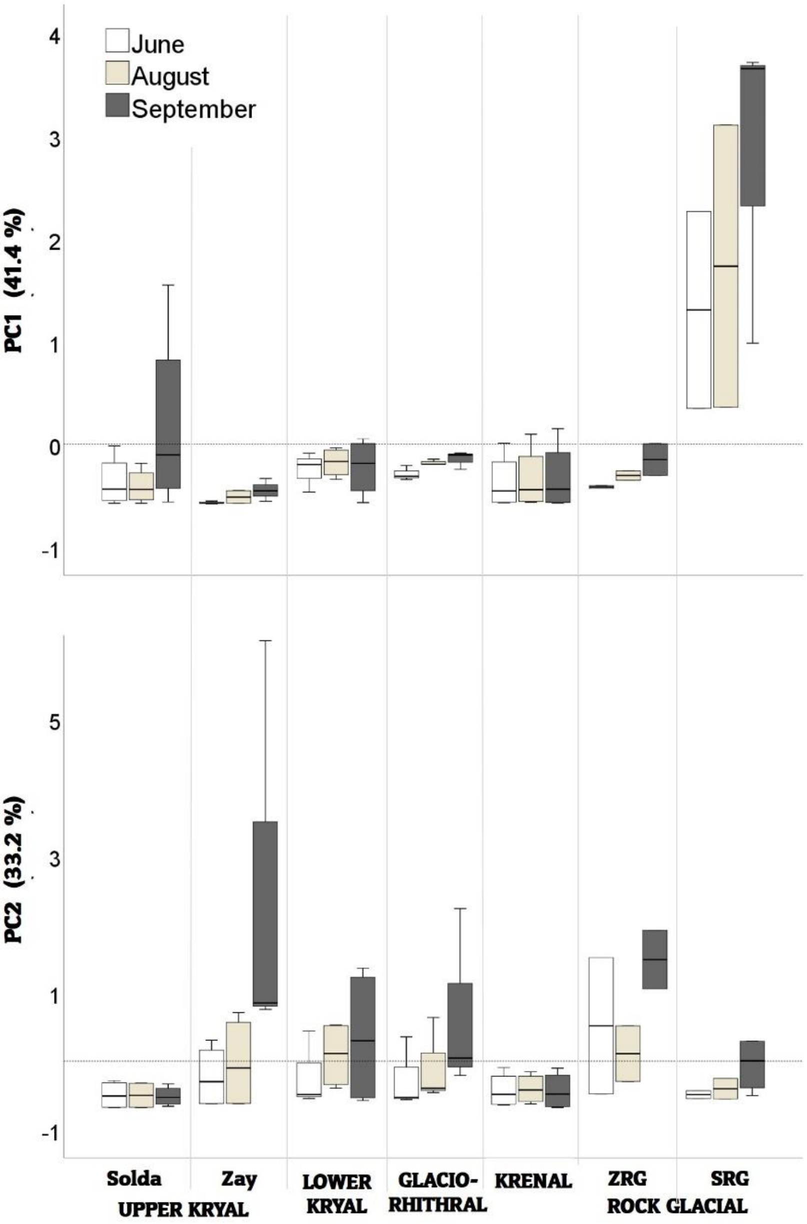

Figure 2.7*. Boxplots of the two principal components resulting from the retained trace elements. Boxes are clustered in terms of sampling timing, and grouped in terms of stream type except for upper kryal and rock glacial streams, for which boxes of different catchments and single stations are provided respectively.*

2.4.3. Longitudinal surveys

The first component of the PCA used to build the Index of Glacial Influence explained 59.1% of the total variance (see Table 2.5 for the loadings). In the PCA run to build the Seasonal Glacier Influence (SGI), the first component alone accounted for 79.4% of the variance and was strongly driven by all the parameters included in the analysis (Table 2.5). Both IGI and SGI were significantly correlated ($P<0.001$) with distance from the glacier and elevation (correlation coefficient $\rho=-0.80$ for IGI, $\rho=-0.98$ for SGI), Jacobsen Index ($\rho=0.8$; $\rho= 0.98$), and the glacier cover in the catchment ($\rho=0.66$; $\rho=0.85$). Longitudinal patterns were similar for both IGI and SGI (Figure 2.8) exhibiting significantly higher values (Table 2.2) in the proglacial reaches (Z1-Z3) compared to further downstream (Z4-Z13), with a sharp reduction from station Z4, i.e. downstream of the lake and the moraine. Longitudinal variations of both indices were stronger in the proglacial reaches than below the lake, reflecting a rapid reduction of the glacial influence moving downstream from the glacier snout on a daily (IGI) and seasonal (SGI) basis. IGI exhibited a clear seasonality, with lowest values during the flow recession compared to both snowmelt and glacier ablation periods. These longitudinal and temporal patterns of the indices corresponded closely to those of channel stability, water temperature, EC, turbidity, and discharge recorded along the stream.

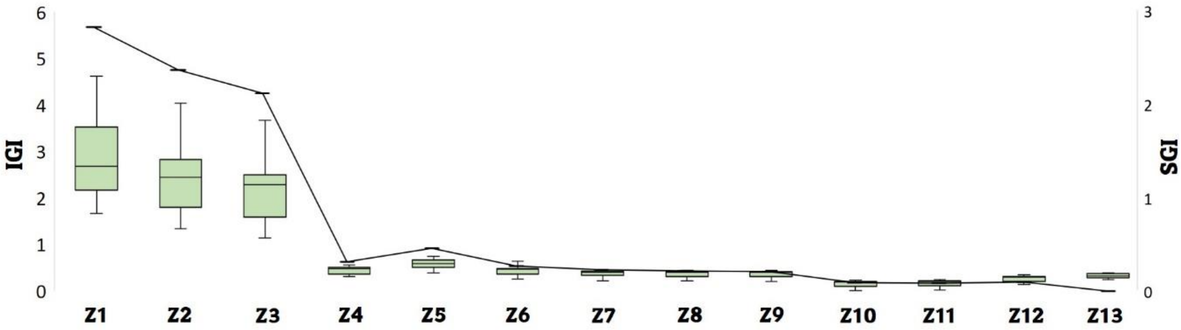

Figure 2.8. *Indices of glacial influence. Seasonal Glacier Influence (SGI, black line), and the Index of Glacial Influence (IGI) boxplot for all stations and seasons. The supplementary LS campaigns were included for the calculation of the indices.*

The Pfankuch index had the same longitudinal trend as the IGI, with relatively high values recorded at the floodplain station (Z5), driven by high values of the bottom component, and below station Z10, driven by high values of the upper and lower bank components (Figure 2.9). The index showed a strong negative correlation with distance from the glacier ($P<0.001$, $\rho= -0.80$).

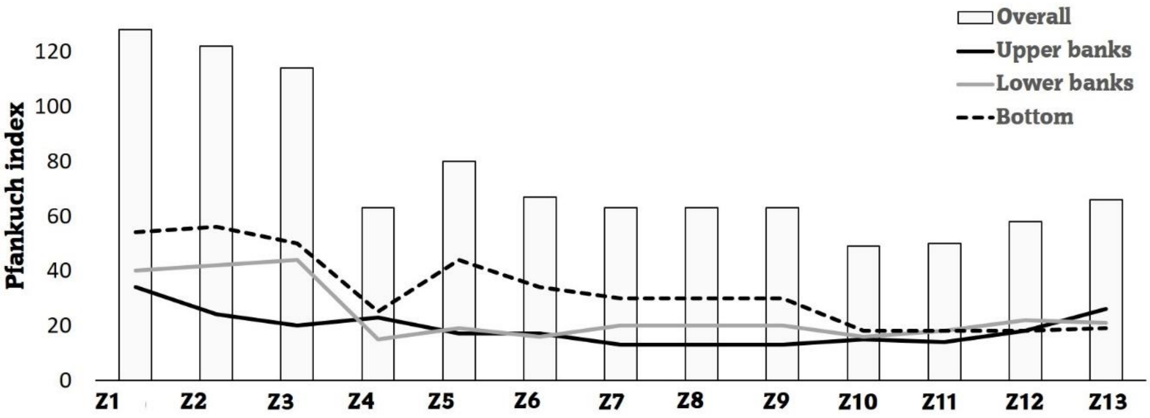

Figure 2.9. *Longitudinal variations of the Pfankuch index (columns) and its components (lines).*

All stations above the proglacial lake (Z1-Z3) showed significantly higher turbidity and lower water temperature and EC compared to the stations downstream (Z4 to Z13) in all periods (Figure 2.10). These proglacial reaches showed a clear seasonality, with the recession period characterized by significantly lower discharge, and higher EC compared to the periods of snowmelt and glacier ablation (which did not differ significantly from each other in relation to these parameters). Below the lake (Z4 to Z13), the Zay stream showed sudden shifts in terms of decreased turbidity (up to 6-fold) and increased EC (3-fold) during snowmelt and glacier ablation, compared to proglacial stations, and decreased water temperature compared to Z3. Moving downstream from the moraine outlet, EC increased slightly during snowmelt and glacier ablation, especially in the lower part of the subcatchment (below Z10), and showed a positive peak below the junction with the rock glacial stream (Z5). This peak was particularly pronounced (228.8 ± 8.0 µS cm^{-1}) and sharp during the recession period, with a rapid decrease in EC just below this station. The seasonal increase of EC was also found at ZRG (Figure 2.10), with highest values during recession (295.9 ± 7.6 µS cm^{-1}, 4-fold increase with respect to the previous periods), corresponding to the highest levels recorded at Zay. At ZRG, the longitudinal surveys confirmed seasonally low and constant water temperature (1.2 ± 0.1°C), while turbidity (8.3 ± 5.2 NTU) values were always comparable to those recorded below the talus body. ZKN was characterized by consistently clear (1.2 ± 1.1 NTU) and cold (3.2 ± 0.3°C) waters in all longitudinal surveys, and EC showed a small seasonality (130.0 ± 7.1 µS cm^{-1}) as well, with higher values compared to all other stations (including ZRG) during snowmelt and glacier ablation but not during recession, when EC was higher (not significantly) than at stations Z10-Z13 and Z1-Z4.

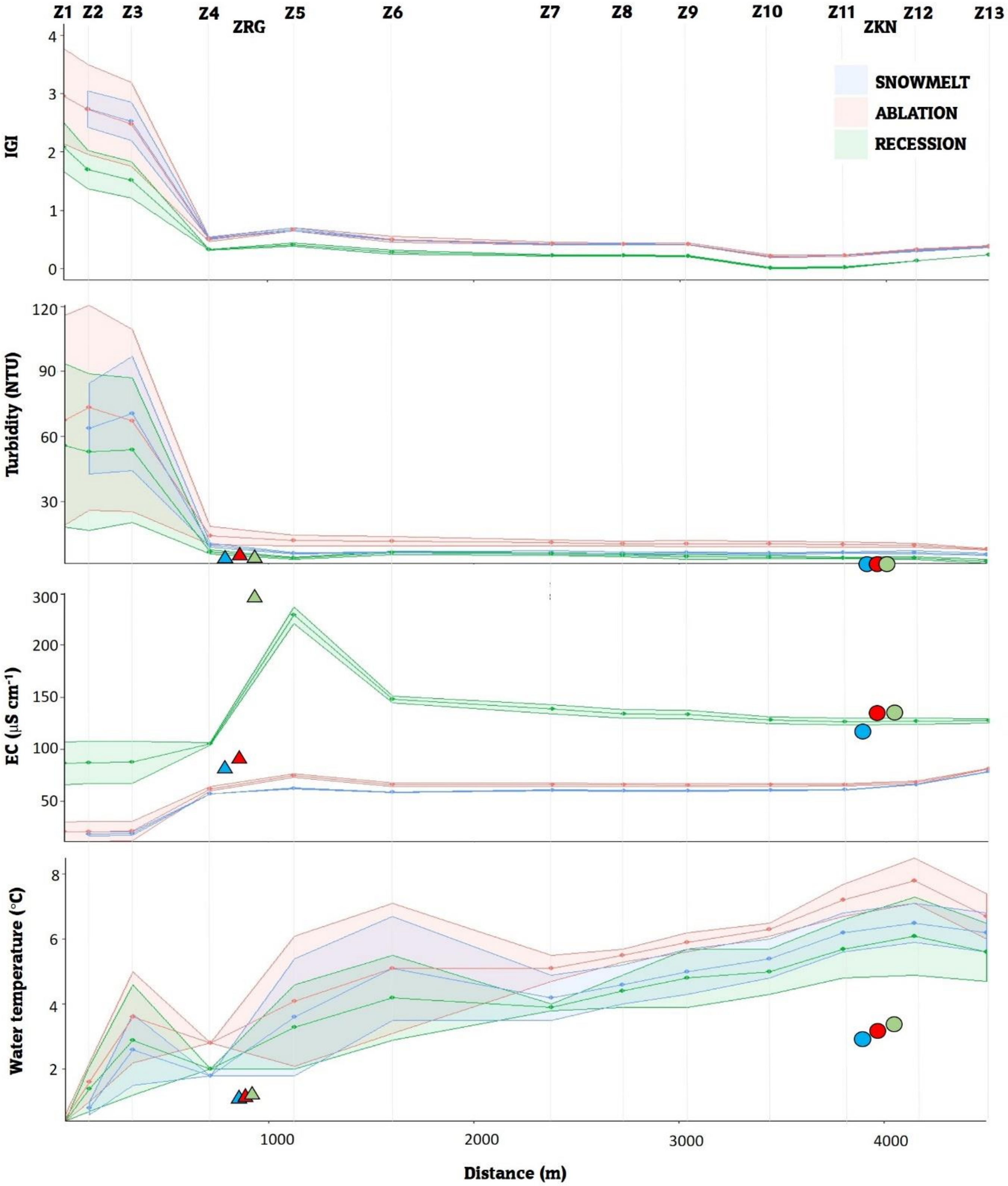

Figure 2.10. *Longitudinal patterns of the IGI, turbidity, electrical conductivity and water temperature for the three hydrological periods (snowmelt, "ablation" i.e. glacier ablation, "recession" i.e. flow recession), each calculated over all daily samplings. Mean (point) and standard deviation (area) of each sampling station and period (colours). Values for ZRG (triangles) and ZKN (circles) stations are inserted in each plot according to their position along the longitudinal gradient.*

Different patterns of diel fluctuations appeared to be associated with different seasonal phases (Figure 2.11), although it was not always possible to disentangle the timing of minima and maxima in the parameters, and the values recorded from stations downstream of the moraine (especially Z4 and Z7-Z13) showed very little diel variability (Figure 2.10). Water temperature generally showed morning minima (in all periods) and mid-day (in the recession period) to afternoon (in the snowmelt and glacier ablation periods) maxima. These timings were confirmed by the analysis of the temperature data-loggers (which recorded, for the proglacial stations as well, the actual minima during the night, when in-situ field measurements could not be undertaken). Turbidity showed a comparable diel pattern across all periods in the proglacial reaches (Z1-Z3), with afternoon maxima and morning minima. A clear opposite trend was observed in the lower part of the subcatchment (Z7-Z13) during glacier ablation, where maxima were recorded in the early morning and minima in the late afternoon. A spatial pattern in EC values was observed during glacier ablation, when all the upper stations showed morning maxima (except Z4) and afternoon minima (except Z4 and Z6), while the lower stations (Z7/Z13) had morning minima and afternoon maxima. Discharge values showed similar patterns for all stations and across all periods, with morning minima and afternoon maxima where variations could be detected. Finally, IGI diel cycles appeared to be most strongly related to the trends recorded for turbidity, with a weaker contribution from the other parameters structuring the index (Figure 2.11).

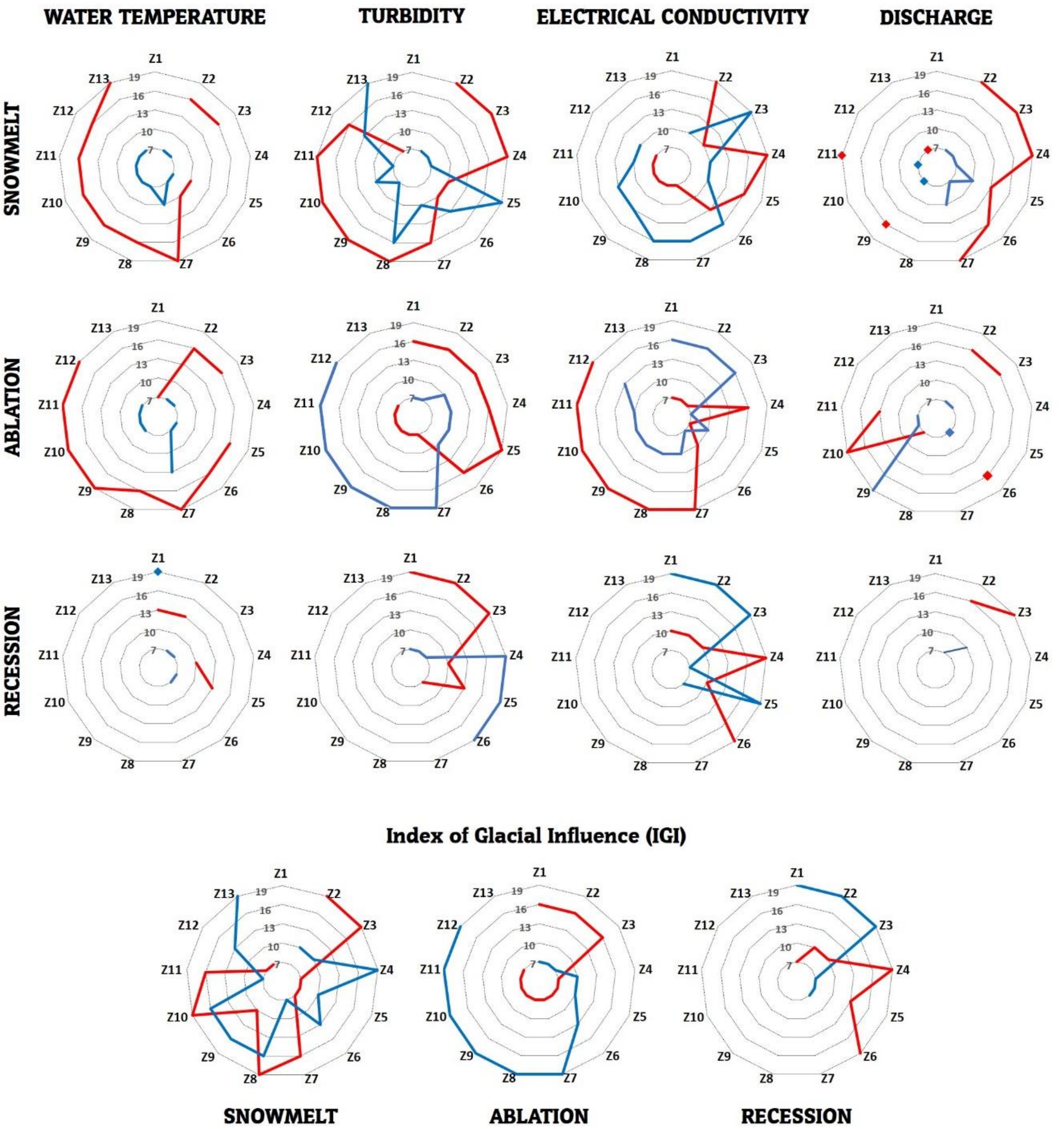

Figure 2.11. *Timing of the minima (blue) and maxima (red) values of each variables for each hydrological period (snowmelt, "ablation" i.e. glacier ablation, "recession" i.e. flow recession), measured at 3 hours interval over 12 h. Stations and timings with constant values not represented in figures. The incomplete dataset for stations Z7/Z13 for the flow recession phase does not allow to provide results for this part of the subcatchment.*

2.5. DISCUSSION

This study combined field sampling, to characterize the physical and chemical water quality and habitat parameters of alpine streams, with high-frequency monitoring to investigate the longitudinal gradients of glacial influence in different periods of the Alpine summer. Using this combined survey design we addressed both research hypotheses: i) we identified key habitat features that distinguish rock glacial streams from other stream types (H1) and ii) we demonstrated the role of an active rock glacier in shaping the stream habitat conditions along the river continuum, in a catchment where the hydrological imprint of glaciers is fading because of the prolonged retreat and the influence from the paraglacial landscape is increasing (H2).

2.5.1. Discharge and water sources

Discharge patterns suggest a greater hydrological role of the glacier in Solda than in Zay. In fact, the discharge at the Suldenferner outflow was an order of magnitude higher than at the Ausserer Zay glacier, with major peaks during the period of glacier ablation. In contrast, discharge maxima at the upper kryal stations (and along the entire stream) at Zay occurred in the early summer, i.e. during the snowmelt period. This seasonal dynamic, combined with the extreme reduction of the glacier during the last few years (WGMS, 2018), provides evidence that the Zay subcatchment was well over the peak water. In fact, a similar condition was observed for small glaciers in Switzerland (Huss and Fischer, 2016), where anticipation of the seasonal peak discharge and decreased average discharge were observed in 1961-1990 following glacier retreat, and were associated with the exceedance of peak water. At the catchment scale, the reduced hydrological contribution from predictable glacier cycles is paralleled by an increased relative importance of melting snow and a larger dependency on stochastic precipitation patterns, as reported for several catchments in the Alps and the Pyrenees (Milner et al., 2017).

At Zay, the progressive groundwater contribution in the lower sections suggested by mixing models is in line with previous studies in alpine settings, where silica was found to be a good indicator of groundwater (Ward, Malard, Tockner and Uehlinger, 1999; Brown et al., 2003; Liu et al., 2004; Brown et al., 2006). However, the isotopic composition of water (assessed during baseflow conditions) indicates that at least part of the groundwater flow in Zay was associated with the routing of glacial- and snow melt waters. This meltwater contribution to groundwater recharge was also demonstrated by Ward et al. (1999) in a highly glacierized catchment, and our results suggest that glaciers are still able to provide a notable contribution to water fluxes even in catchments with a small glacier cover.

2.5.2. Stream types

Despite the differences in the hydrochemistry of the two studied subcatchments reflecting the prevalence of different bedrock, our study has provided further evidence that water origin is a key driver in structuring habitat conditions in alpine streams (e.g. see Ward, 1994; Brown et al., 2003). The upper kryal stations were characterised by the harshest and most variable habitat conditions among all surveyed stations. In fact, highly unstable channels with very turbid and cold waters, enriched in total phosphorus (product of the glacial physical erosion; see Hodson, 2007) and depleted in other solutes, were typical of the snowmelt and glacier ablation periods. Shifts to clear waters with a steady flow occurred in September, when a 10-fold increase in EC was detected compared to August. Multiple energy fluxes (e.g. net radiation and sensible heat) influence the ablation process on glaciers (Hannah, Gurnell and McGregor, 2000), and ice ablation is reduced or absent during autumn and winter (Cuffey and Paterson, 2010). Accordingly, autumn discharge from glaciers is typically dominated by the baseflow (see Table 2.3), which is mostly driven by the subglacial/englacial contribution associated with waters enriched in solutes (Sharp, 2006) and metals/metalloids (Mitchell, Brown and Fuge, 2001). Accordingly, highest concentrations of major ions (Ca^{2+}, Mg^{2+}, SO_4^{2-}, NO_3^-) and trace elements were recorded in this period in both glacier-fed streams. Interestingly, As (S2), U (the entire Zay Stream), Fe and Al (Z3, 2017) were found above the EU/EPA limits for drinking water in September, likely as a result of the local lithology and the presence of metal ores in the upper Zay (siderite at manganese; Baumgarten, Folie and Stedingk, 1998).

As previously reported for highly (e.g. Milner and Petts, 1994; Füreder, 2012; Finn, Räsänen and Robinson, 2010) and poorly (e.g. Smith, Hannah, Gurnell and Petts, 2001; Khamis, Brown, Hannah and Milner, 2016) glacierized basins, a gradient of habitat amelioration was detected along the glacier-fed stream. This steep gradient we observed was associated with decreasing turbidity and trace element concentrations, and increasing channel stability, average water temperature, nitrate concentrations, and abundance of organic detritus, the latter due to higher inputs from the surrounding vegetation and increased retention from bryophyte mats.

Water temperature represents the main environmental variable that discriminates rock glacial streams from the other habitats, as very low (<1.2°C) and constant values were recorded at both rock glacial streams. Carturan et al. (2016) suggested a low and constant temperature during summer as the only reliable water proxy allowing identification of the permafrost presence in rock glaciers. However, the studied rock glacial streams were also characterized by clear waters, with an abundance of organic detritus that was comparable to glacio-rhithral stations. Despite the scarce loads from the surrounding vegetation (patchy alpine grassland), this indicates a higher retention capacity of rock glacial compared to kryal habitats, which is also due to the higher coverage of mosses and higher channel stability. Nutrient levels, i.e. nitrates and phosphates, were also high and comparable to those of glacio-rhithral sections, and potentially support primary production (Uehlinger, Robinson, Hieber and Zah, 2010). High nitrate levels are commonly found in rock glacier outflows and have been attributed to microbial production into the rock glacier bodies, where the ice thaw may promote the nitrogen flushing from microbially active sediments (Williams, Knauf, Cory, Caine and Liu, 2007; Baron, Schmidt and Hartman, 2009; Barnes, Williams, Parman, Hill and Caine, 2014).

Although it was not possible to clearly discriminate rock glacial streams according to water isotopes, these streams exhibited concentrations of silica comparable to those of lower kryal and glacio-rhithral stations in all periods, suggesting a considerable part of the baseflow associated with the groundwater component. This is in line with the literature on rock glacier hydrology stating that these landforms act as unconfined aquifers in mountain slopes (e.g. Krainer and Mostler, 2002; Jones et al., 2019). The enrichment of solutes and trace elements in rock glacier outflows is commonly attributed to the thaw of internal ice and to the associated weathering of freshly exposed rock particles (Williams, Knauf, Caine, Liu and Verplanck et al., 2006; Ilyashuk, Ilyashuk, Psenner, Tessadri and Koinig, 2018; Colombo et al., 2018b; Munroe, 2018). Accordingly, the high values of EC, major ions, and trace elements, we observed increasing over the season, are consistent with data reported in the literature on rock glacier hydrology (e.g. Millar, Westfall and Delany 2013; Williams et al., 2006; Mair et al., 2015; Colombo et al., 2018a) and suggest that part of the rock glacial baseflow in late-summer came from permafrost thaw, in addition to the groundwater fraction, and this increased as summer progressed. As observed in other case studies (e.g. Colombo et al., 2018a; Rotta, 2018), trace elements were found at high concentrations in rock glacial waters at Solda (As, Sr and Ba) and Zay (U, Rb), with concentrations of As (all Solda samples, up to 3-fold in September) and U (Zay, up to 3-fold in September) exceeding the EU/EPA limits for drinking water.

In stark contrast to all the patterns described above, we observed some striking differences between the two rock glacier outflows. While the Solda rock glacial stream exhibited high EC, Ca^{2+}, Mg^{2+}, SO_4^{2-} that made this stream unique among all stations, the Zay rock glacial stream showed intermediate conditions between the Solda rock glacial and the lower kryal/glacio-rhithral stations, especially during the snowmelt period. The differences could be related in part to local topographic (channel stability) and geological features (pH and trace elements). However, we suggest that the seepage of kryal waters across the rock glacier debris, observed in the field, might play a crucial role in structuring the chemistry of rock glacial waters at Zay. In fact, turbidity and δ^2H values were consistently similar to those found in the adjacent lower kryal stations. The decreasing glacial influence from June to September was balanced by an increasing role exerted by the groundwater component and the thawing permafrost, as shown by a 3- to 4-fold increase of EC, ions and trace element concentrations. In addition, as summer progressed and the influence of glacier ablation dropped, the distinction between the two rock glacial streams became less pronounced. This provides insights on the mutual interactions between glacial and periglacial processes in deglaciating environments (see also Jones et al., 2019). In fact, rock glaciers can originate from the progressive evolution of a debris-covered glacier, under a continuum process along which the decreasing glacial influence is paralleled by increasing periglacial/permafrost conditions as deglaciation progresses (Anderson, Anderson, Armstrong, Rossi and Crump, 2018). Accordingly, the Zay rock glacial stream may represent a hydrological evidence of this glacial to periglacial transition, as the Zay rock glacier shows evidences of glacial origin from the same debris-covered glacier that feeds the Zay stream. Whatever its origin, the Solda rock glacier appears to be completely isolated from any glacial influence. Accordingly, its outflow may represent an ideal “hydrological end-member” of periglacial influence that the Zay rock glacial stream may reach in the late stages of deglaciation, when this stream becomes completely detached from the glacier imprint.

2.5.3. Glacial influence along the river continuum

The longitudinal surveys at Zay suggest that in the late stages of glacier retreat, under a declining and low discharge from glaciers, the paraglacial landscape exerts a strong influence on stream habitat conditions. Within this context, our new index (SGI) seems to capture the average influence of the glacier at the reach level, reflecting harsh summer conditions and a large seasonal variability of stream parameters. In turn, the IGI best reflected the diel cycles associated with the glacial influence in different periods and was a good indicator of the glacial imprint in proglacial sections. However, the collected data suggest that atmospheric conditions (e.g. solar radiation, air temperature) exerted a greater influence than the glacier over the water temperature, as values of 5-6°C were reached just 300 m below the glacier in all longitudinal survey periods. This is in line with the findings from another poorly glacierized basin in the French Pyrenees, where Khamis, Brown, Milner and Hannah (2015) found atmospheric conditions as the primary driver of the energy budgets in a glacier-fed stream during the snow-free period, under low discharges from the small glacier.

In our study, local conditions such as slope gradients seemed to override the glacier influence on channel stability in all stations below the lake, and this was reflected in the non-linear behaviour of the IGI proceeding downstream. In fact, a high glacial influence was restricted to the proglacial sections, where pronounced diel and seasonal variations of discharge, turbidity, EC, were those typical of highly glacierized areas (e.g. Milner and Petts, 1994; Milner, Brittain, Castella and Petts, 2001, Castella et al., 2001). Proglacial lakes are known to have a great buffering capacity for alpine river networks, as they can smooth water temperature variability, trap sediments, and stabilize downstream discharge (Milner and Petts, 1994, Finn et al., 2010). Also in our study, the turbid proglacial lake acted as an efficient environmental buffer and trap for suspended solids along the river continuum, as confirmed by significant reductions in IGI and SGI values below the lake compared to the inlet, in combination with decreased average values of turbidity (up to an order of magnitude) and Pfankuch index. Nevertheless, some environmental features showed unexpected patterns that cannot be explained by the presence of the lake alone. In fact, water temperature at the moraine outlet, extremely constant on a diel and daily basis, was always lower than in the lake inlet, whereas EC was higher downstream the moraine compared to upstream sites for all periods and timings. Furthermore, three surveys of the lake waters (downstream shore) at different timings during the glacier ablation survey revealed warm conditions (6.4-8.9°C) with turbidity and EC values lower but the same order of magnitude as the inflowing stream. Lower water temperatures and higher EC values at the moraine outlet during snowmelt and glacier ablation are probably the result of processes occurring in the hypogeal flow across the moraine debris. In fact, coarse blocky deposits in alpine settings are able to buffer atmospheric temperatures in summer and to cool infiltrating warmer waters (Jones et al., 2019). In addition, proglacial moraines are generally considered as potential groundwater storage systems (Langston, Bentley, Hayashi, McClymont and Pidlisecky, 2011). Accordingly, the moraine outlet may combine the seepage of stream/lake waters with the groundwater flow, and this is corroborated by a larger groundwater component revealed by mixing models in that station compared to the upstream ones. Thus, while the turbidity drop was caused by both the lake and the moraine, the increased EC and the decreased water temperature was likely driven by the moraine baseflow.

Although not capable of cooling waters in the tributary, as found by Harrington et al. (2017) in a glacier-free catchment, the rock glacial stream does represent an important driver within the river continuum at Zay. This is demonstrated by the rise of EC below the confluence during the recession phase compared to previous periods which can be explained by the increased contribution of permafrost-influenced waters from the rock glacier. However, the decreased values of EC from the first to the second station downstream from the junction indicate an incomplete mixing of lower kryal and rock glacial waters at the upper site, which was located ca. 60 m below the confluence where the channel was very wide (20 - 30 m) and shallow (< 1 m).

The decreasing trends of turbidity below the glacial cirque reflect the linearly decreasing influence of the glacier, whereas the downstream increase of discharge and EC may reflect the increasing contribution from groundwater sources. Although some storage capacity has been reported in talus slopes (e.g. Sueker, Ryan, Kendall and Jarrett, 2000), water flow across these bodies is often rapid as these landforms typically consist of coarse blocky materials (Muir et al., 2011). In our study, similar water characteristics above and below the talus body suggest the stream water probably had a short residence time. However, minor diel fluctuations recorded for all parameters at the talus outlet compared to the upstream station are probably due to some buffering effect exerted by the talus debris, leading to relatively stable habitat conditions.

In the lower section of Zay, the observed longitudinal increase in EC values during snowmelt and glacier ablation can be explained by the contribution of krenal streams enriched in solutes, which also accounted for the lowering of turbidity and water temperature observed along the Zay stream. However, during the flow recession the EC continued to decline proceeding downstream from the glacial cirque, most likely due to the contribution from krenal tributaries being unable to increasing EC as during the previous periods. This explanation is supported by the observed inactivity and reduced flow from several springs in this period.

The longitudinal gradients of EC recorded during the recession period, with a dominant influence from the rock glacier and negligible effect from groundwater tributaries, were also confirmed by additional longitudinal surveys (16-24/9, 4/10), and were driven by concentrations of Ca^{2+}, Mg^{2+}, SO_4^{2-} and HCO_3^-. Thus, despite the seepage of kryal waters into the debris of the active rock glacier, its outflow was capable of driving an inversion of the EC gradients along the entire Zay stream in late summer, exerting a significant influence on the stream hydrochemistry for more than 3 km downstream, until the Zay closing section. Furthermore, a previous study conducted along the main river of the Solda catchment revealed, in September, an increase of EC below the junction with the Zay Stream (Engel et al., 2019), and this suggests an even wider hydrological influence exerted by the Zay rock glacier requiring further investigation. Despite the water contribution from rock glaciers currently being considered as negligible from a catchment-scale perspective in the Alps (Krainer, Mostler and Spötl, 2007; Krainer, Chinellato, Tonidandel and Lang, 2011; Geiger, Daniels, Miller and Nicholas, 2014), our results demonstrate that these landforms can have a significant role in shaping the stream habitat conditions along the Alpine river networks.

Our results provide new insights into how we sample the physical, chemical, and biological characteristics of alpine streams in the late phases of glacier retreat. In fact, the typically large diel fluctuations commonly attributed to glacier-fed systems, and driven by the cycles of glacier ablation, were only restricted to the proglacial sections. All stations below the lake showed a negligible diel variability in EC, turbidity, and discharge, and water temperature cycles were associated with the atmospheric conditions rather than the glacier ablation patterns. In contrast, rock glacial streams showed consistent physico-chemical variables, although we identified large and transient variations in water temperature and EC (increasing at ZRG, decreasing at SRG) associated with rainfall events (not shown). Thus, on the basis of the habitat parameters analysed, only krenal sites seem to be decoupled from both diel and daily patterns and from weather conditions, and a sampling strategy accounting for seasonality is important for all stream types.

2.6. CONCLUSIONS

Recent research on alpine stream ecosystems is beginning to show that the hydrological role of mountain permafrost is expected to increase as glaciers recede due to climate change (Jones et al., 2019). Our results provide evidence to support previous findings on the hydrology and hydrochemistry of outflows from thawing rock glaciers, and clearly highlight the distinctive nature of these habitats. In fact, rock glacial streams exhibit constantly cold and clear waters, stable channels favouring the retention of organic detritus, and high concentrations of solutes and trace elements that increase over the season under the influence of thawing permafrost.

In alpine catchments with a small glacier cover, in which peak water has been surpassed, the low discharge from glaciers allows other driving forces, such as weather conditions and the contribution from non-glacial tributaries, to exert an increased hydrological influence. Within this context, the paraglacial landscape (i.e. proglacial lakes, moraines, talus bodies) and permafrost increasingly shape the habitat conditions of streams. Our research points to the importance of rock glacial streams in driving the hydrochemistry of alpine river networks, namely under permafrost thaw conditions, and for a long distance downstream.

Under continued climate change in the Alps (Gobiet et al., 2014), a sustained glacier recession in combination with a prolonged snow-free period may further boost the hydrological importance of active rock glaciers. Late summer/autumn can be considered as a “hot period” in deglaciating catchments because the combination of low discharges, a higher proportion of subglacial contribution, and the prolonged permafrost thaw cause an intense release of solutes and trace elements, with potentially significant effects on stream ecology and for drinking water quality. Given the scarce consideration dedicated so far to mountain permafrost, and its increasing hydroecological importance, we call for more research on the role of rock glaciers and the paraglacial landscape on the river continuum. As rock glacial streams have distinct habitat characteristics, increased research will provide valuable insights on their future ecological role in glacier-free alpine catchments.

CHAPTER 3

Thawing rock glaciers and paraglacial features drive stream invertebrate patterns in a deglaciating Alpine area

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3.1 INTRODUCTION

The present climate change and the consequent deglaciation (IPCC, 2013) are leading to rapid shifts in mountain ecosystems such as alpine streams (Huss et al., 2017). The anticipation of the snowmelt period and the declining hydrological contribution from glaciers are increasing the capacity of other water sources to shape the hydrology and ecology of alpine river networks (Milner et al., 2009). These water sources include summer precipitation, whose future trends are still uncertain, and groundwater provided by talus slopes, moraines and rock glaciers (Brighenti et al., 2019b). In particular, the role of permafrost ice as a long-term water source is increasing, given its lower rate of shrinkage compared to that of glacier ice (Jones, Harrison, Anderson & Whalley, 2019). Recently, Brighenti et al. (2019b) suggested that the outflow from thawing rock glaciers (i.e. ice-containing and creeping debris mantles, that are typical expressions of mountain permafrost; see Jones et al., 2019) should be considered a particular habitat, given the unique environmental conditions that include constantly clear (< 5 NTU) and cold (< 1.5°C) waters and stable channels. Rock glacial waters in catchments with volcanic/metamorphic bedrocks commonly present high electrical conductivities (EC = 300-1000 µS cm^{-1}) associated with high concentrations of solutes (including nutrients such as NO_3^- and PO_4^-) and trace metals that increase over summer under the influence of thawing permafrost (Colombo et al., 2018). Despite their recognized importance in contributing to the hydrological diversity of alpine river networks, little research has focused so far on the biota of such streams (Brighenti et al., 2019a). In fact, glacier retreat is regarded as the main ecological driver for alpine river networks, because it induces a rapid loss of β-diversity, modifications in the functional traits and ecosystem processes, and promotes upstream dispersal of downstream communities (e.g. Hotaling, Finn, Giersch, Weisrock & Jacobsen, 2017; Milner et al., 2017). Stream invertebrates are the most investigated biotic component in alpine stream studies (Fell, Carrivick & Brown, 2017): streams fed by glaciers (i.e. kryal) host specialist taxa that are able to face the harsh conditions brought by the glacial influence (high turbidity, low water temperature, unstable channels) and benefit from the absence of competitors (Lencioni, 2018). As the glacial influence decreases (in space and/or time), the habitat amelioration, provided also by groundwater contribution (Khamis, Brown & Hannah, 2016) or by the presence of lakes (Hieber, Robinson, Uehlinger & Ward, 2005), allows other taxa to enter the community, thus enhancing the complexity of stream food webs (Niedrist & Füreder, 2017) and the communities' functional performance and diversity (Brown et al., 2017). Accordingly, the ecosystem progressively shifts from environmental filtering towards an increasing biotic control, as the assemblage complexity boosts the relative importance of community interactions in driving the ecosystem functioning (Fell et al., 2017). Within this context, little attention has been paid so far to the role of aquatic bryophytes in alpine streams (Suren, 1999; Gesierich & Rott, 2004; Rotta et al., 2018). Stream bryophytes are efficient microhabitats and traps for organic detritus (Stream Bryophyte Group [SBG], 1999), which is a limited resource in alpine streams due to the low allochthonous inputs, especially in the highly unstable glacier-fed streams (Niedrist & Füreder, 2017). This role is particularly relevant in deglaciating alpine catchments, as aquatic mosses are generally absent in the upper kryal but can colonise new reaches as soon as the ameliorated conditions allow for it (Milner et al., 2017; Brighenti et al., 2019b). As rock glacial streams, originating at the same elevation as kryal systems, typically host extensive mosses mats (authors' personal observation), they may provide additional sources for bryophyte colonisation (via propagules, see SBG, 1999) of glacier-fed streams during deglaciation. This is particularly relevant in alpine settings, where the upstream dispersal from aquatic bryophytes (SBG, 1999) and the terrestrial vegetation (Gurnell, Edwards, Petts & Ward, 2000) are very low (i.e. involve decades).

Different community metrics have been used to assess the effects of deglaciation on alpine stream invertebrates. Amongst them, diversity indices (e.g. Shannon, species richness) and invertebrate density (i.e. abundance) are the most used. Recently, body size and biomass have shown to be promising indicators of the ecological performance of alpine stream invertebrates and a tool complementing the information on their response to climate change (Niedrist, Cantonati & Füreder, 2018). Since the biomass of a population is mediated by the body size of the individuals (e.g. Brown, Gillooly, Allen, Savage & West, 2004; Hauer & Lamberti, 2007), this metric can provide additional information on the energy use (Pagel, Harvey & Godfray, 1991), ecological performance (Brown, Allen & Gillooly, 2007) and nutrient cycling (Hall et al., 2007) by organisms, and on the interactions within the food web (Cohen, 2007). In general, abundance, body size and biomass can be used as complementary proxies to describe the quantitative relationships between the organisms and their environment, and between organisms in their ecological communities (e.g. Hoste-Danilow et al., 2013; Pakulnicka & Zawal, 2018).

Aim of the present study was to assess the ecological shifts in stream invertebrate communities associated with late stages of glacier retreat. We selected a high mountain catchment of the European Alps, where we studied the communities of different stream types (i.e. fed by permafrost, glaciers, groundwater, and of mixed origin). In addition, we assessed the ecological influence of a proglacial lake, a moraine body and rock glaciers, that have been already found to strongly shape the physical and chemical conditions along the glacier-fed river continuum (Brighenti et al., 2019b). In particular, we tested four main hypotheses: H1) Where present, bryophyte mats enhance the invertebrate production; H2) Different stream types are characterized by distinct benthic invertebrates abundance, biomass and body size patterns; H3) The paraglacial landscape enhance invertebrate production and diversity along the glacier-fed streams; H4) Given their unique habitat settings, rock glacial streams host a different invertebrate community compared with the other stream types.

3.2 STUDY AREA

The Solda Valley (South Tyrol, Italy) is located in the European Alps and hosts several glaciers undergoing rapid recession (World Glacier Monitoring Service [WGMS], 2018), rock glaciers and paraglacial features such as moraine deposits, talus bodies and tills (Montrasio et al., 2015; Autonomous Province of Bolzano/Bozen [APB], 2018). A set of sampling stations (Figure 3.1, Table 3.1) underlain by metamorphic bedrock (primarily ortogneisses and quartzphyllites) was selected in the nival, alpine and subalpine belts of the Zay and Solda subcatchments, in order to represent distinct stream types according to their origin and distance from the glacier. The two upper kryal stations along the Zay stream (Z1, Z3) are separated from the lower kryal ones by a proglacial lake and a subterranean reach across a moraine deposit. Below the moraine (Z4), the Zay stream flows parallel to a rock glacier mantle, whose outflow (ZRG) converge with the Zay stream in a glacial floodplain (Z5). From there, the stream seeps into a talus slope that separate lower kryal with glacio-rhithral sections. These include the reach below the talus body (Z7) in the alpine belt, and the reach in the subalpine belt (Z12) close to the subcatchment closing section (Figure 3.1; Figure 3.1). The remaining stations include the two Solda (SKN) and Zay (ZKN) krenal streams (subalpine belt), and two upper kryal (S1, S2) and one rock glacial (SRG) streams in the Solda subcatchment (nival belt). Brighenti et al. (2019b) found that the hydrology, hydrochemistry and physical habitat of Zay stream was strongly influenced by the presence of the lake and the moraine; as a result, the lower kryal sections exhibited much clearer waters, higher channel stability and EC values compared with upper kryal sites (Figure 3.1). The same study showed that ZRG habitat was influenced by the interactions between groundwater, permafrost and glacier contribution, because the rock glacier and the glacier were still hydrologically-connected; that ZRG waters in turn exerted a clear influence on the hydrochemistry of the Zay stream below the confluence, especially during autumn, when glacial influence was low and permafrost influence high; that SRG showed distinct habitat conditions that were strongly influenced by permafrost dynamics, and allowed to distinguish this stream from krenal, glacio-rhithral and kryal habitats in the study area (Brighenti et al., 2019b).

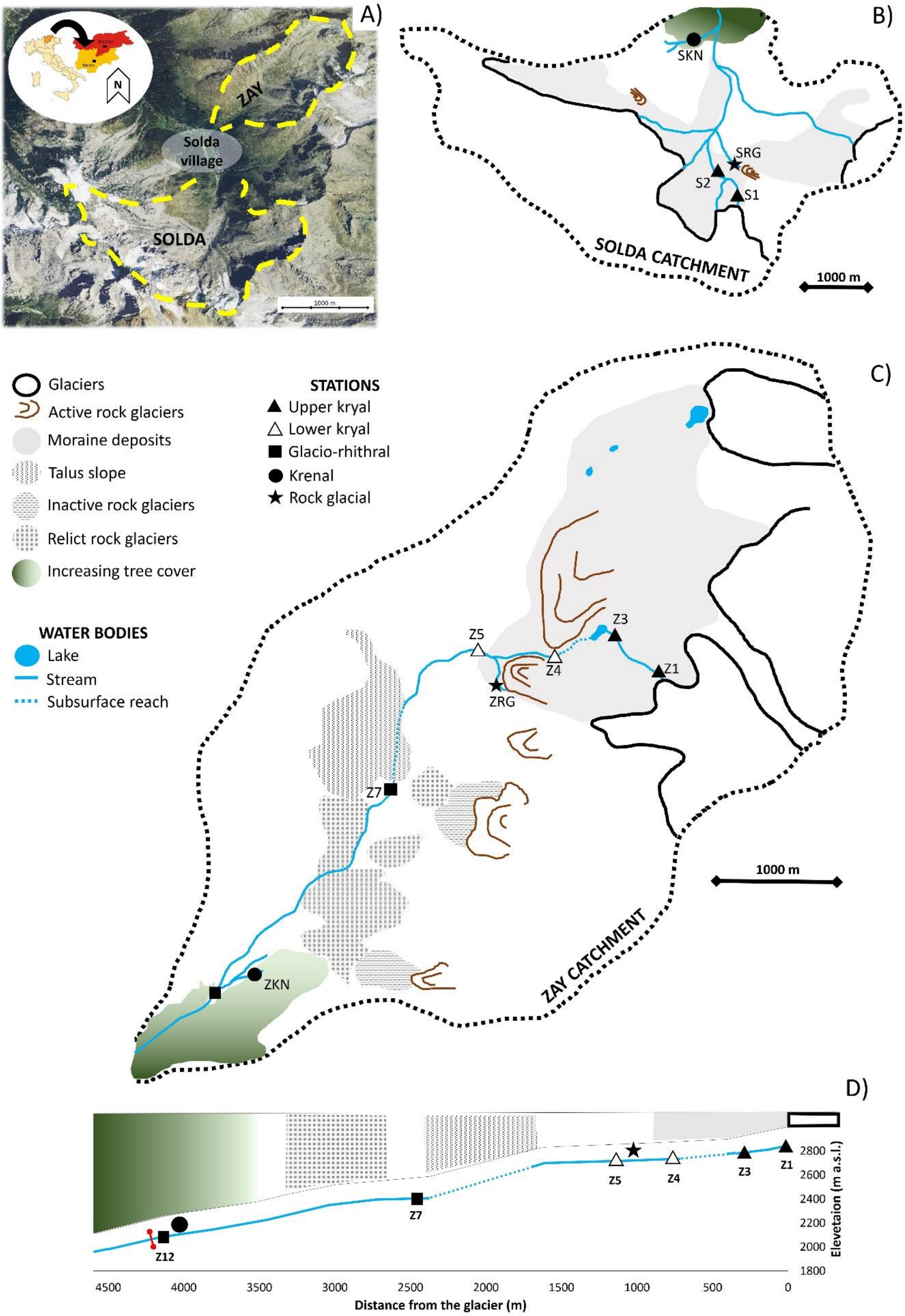

Figure 3.1. A) Geographic location of the study area; Schematic hydromorphological setting and locations of the sampling stations for: B) Upper Solda subcatchment; C) Zay subcatchment; D) Hypsographic curve of Zay stream, with the position of the sampling stations along the distance from the glacier gradient.

Table 3.1. *Main features of sampling stations. Alt= elevation (m a.s.l.). Dist = distance from the spring (km). Slope = % average slope, calculated from maps (Autonomous Province of Bolzano/Bozen, 2018). Channel type attributed following Rinaldi et al. (2016). Veg= Riparian vegetation, classes: 0=sparse/absent, 1=discontinuous alpine heat, 2= continuous alpine heat, 3= alpine heat with sparse trees and shrubs 4= canopy from trees and shrubs. Moss= abundance of mosses in the channel, classes: 0=0-5%, 1=5-10%, 2=10-30%, 3=30-50%. Pfan= bottom component of the Pkankuch index, proxy for the instability of the substrate. T= average water temperature, from 15 June to 25 September 2017 and 2018. Turbidity measured in NTU. EC measured in µS cm^{-1}. See Brighenti et al. (2019b) for more details on the sampling stations. [a]station added in August 2017. [b] station added in June 2018.*

Catchment	Code	Alt	Dist	Slope	Habitat type	Channel type	Veg	Moss	Pfan	T	Turbidity	EC	pH
Zay	Z1	2845	0	55	Upper kryal	Single-thread, straight	0	0	54	0.93 ± 0.75	40.6 ± 28.1	92.1 ± 99.3	6.3 ± 0.6
Zay	Z3	2780	0.34	18	Upper kryal	Single-thread, straight	1	0	50	2.04 ± 1.71	51.1 ± 26.5	86.3 ± 90.0	6.2 ± 0.6
Solda	S1	2710	0	15%	Upper Kryal	Single-thread, straight	0	0	58	1.04 ± 0.66	123.9 ± 99.7	35.3 ± 37.2	8.0 ± 0.8
Solda	S2	2560	0.7	10%	Upper Kryal	Multi-thread: braided	0	0	59	2.83 ± 1.65	60.8 ± 51.0	288.5 ± 192.5	7.5 ± 0.4
Zay	Z4[a]	2736	0.72	10	Lower kryal	Single-thread, straight	1	3	25	2.48 ± 0.79	11.4 ± 3.3	81.2 ± 22.0	6.6 ± 0.2
Zay	Z5	2717	1.13	2	Lower kryal	Glacial floodplain Multi-thread	1	1	44	3.01 ± 1.62	11.2 ± 5.3	103.7 ± 53.7	6.8 ± 0.3
Zay	Z7	2407	2.38	4	Glacio-rhithral	Single-thread, sinuous	2	3	30	4.66 ± 0.88	11.9 ± 5.7	80.4 ± 27.2	6.7 ± 0.2
Zay	Z12 [b]	2084	4.15	25	Glacio-rhithral	Multi-thread: anabranching	4	2	30	7.05 ± 3.58	8.2 ± 3.4	93.5 ± 26.3	6.8 ± 0.3
Zay	ZKN	2160	0	22	Krenal	Single-thread, straight	4	3	18	3.10 ± 0.29	1.0 ± 0.3	133.8 ± 7.7	6.8 ± 0.3
Solda	SKN	2105	0.1	65%	Krenal	Single-thread, straight	3	2	37	4.52 ± 1.22	7.3 ± 0.2	213.4 ± 21.2	7.5 ± 0.2
Zay	ZRG	2718	0	2	Rock glacial	Single-thread, sinuous	2	1	30	1.16 ± 0.14	10.5 ± 6.7	121.2 ± 75.4	6.7 ± 0.3
Solda	SRG	2586	0.05	25%	Rock glacial	Single-thread, straight	2	3	18	1.17 ± 0.14	2.2 ± 0.6	506.5 ± 81.8	7.5 ± 0.1

3.3 METHODS

3.3.1 Field activities

The selected stations were investigated over two consecutive years (2017, 2018) in the same periods of the alpine summer (June, August and September). The complete physico-chemical characterization of each sampling site (Table 3.1) is available in Brighenti et al. (2019b). In order to estimate the biomass of the epilithic biofilm, two filter sets, for the determination of organic biomass and Chl-*a* concentration, respectively, were prepared for each sampling site. Accordingly, three-five cobbles were randomly chosen in the permanently wet streambed, and a known area was delimited by a plastic frame and brushed with a toothbrush. This was then washed in a falcon vial filled with deionized water, which was in turn filtered in the field through GF/C Whatman pre-cleaned glass filters with a portable vacuum pump (Mityvac MV8030, USA). Filters were frozen (-20°C) within 4 hours from collection and transported in thermal bags to the laboratory. In order to compare the capacity of organic matter decomposition of different stream types, the “poplar sticks” method was used by following Arroita et al. (2012). Accordingly, common tongue depressors made of *Betula* sp. wood were numbered and hole drilled. Then, they were oven dried (60°C) for four days and weighted. Each stick was labelled, positioned and fixed in the streambed. Five sticks were deployed randomly in each sampling station (i.e. SRG, ZRG, Z2, Z4, Z5, ZKN and SKN) in early summer 2018 (end of June/beginning of July depending on the accessibility of sites) and were collected in autumn after 86-91 days. They were carefully packaged so to avoid any damage and material loss during transport, and carried to the laboratory within 24 hours. Before sampling the zoobenthic community, each station was examined for the assessment of the relative abundance of organic (bryophyte mats, *Hydrurus foetidus*) and inorganic (sand, gravel, cobbles, boulders) microhabitats. A Surber sampler (mesh size 100 µm, 506 cm^2 area) was then used to collect zoobenthos from each microhabitat, with a number of replicates proportional to the relative abundance in the stream reach, for a total of 5 replicates (0.25 m^2). To collect invertebrates, inorganic substrates were manually disturbed following Merritt, Resh & Cummins (2016), whereas *Hydrurus foetidus* and bryophytes were repeatedly shaken and rubbed underwater, bryophyte fragments were repeatedly rinsed in water in a tray, whose content was filtered with the remaining sample, and discarded, in order to collect only the associated detritus and invertebrates. Samples from mineral substrates (pooled together), bryophyte mats and *Hydrurus foetidus* were kept in separated bottles, filtered with a 100 µm mesh size filter and preserved in 95% ethanol in the field.

3.3.2 Laboratory activities

For the assessment of epilithic Chl-*a* concentrations, the first set of filters were first shredded in 20 mL acetone 90% with an Ultraturrax ®T25 (Thermofisher, Italy) and extracted overnight at 4°C in the dark in a 50 ml vials. After the extraction, the content of each vial was filtered through GF/F Whatman glass filters into glass vials. Spectrophotometer was used to estimate, before and after acidification, the Chl-*a* and Pheophytine-*a* concentrations (µg cm^{-1}), following Steinmann, Lamberti & Leavitt (1996). The second set of filters was oven dried (1 hr, 110°C) and ashed (1 hr, 550°C) for the assessment of the epilithic biomass, expressed in AFDM (g m^{-2}) and calculated following Steinmann et al. (1996). The collected wooden sticks (Arroita et al., 2012) were tap-water washed, brushed and dried in aluminium containers in the oven at 60°C for 4 days. After weighting, they were ashed in the furnace (550°C, 4 hours) and reweighted for the assessment of AFDM.

Invertebrates and bryophytes fragments were removed from each Surber samples under a dissecting stereomicroscope (Motic SMZ-168, Leika MZ-12-5), and the remaining fraction was processed to assess the abundance of organic detritus. Accordingly, invertebrate- and bryophyte-free detritus was filtered with a 1 mm mesh sieve to separate coarse and fine fractions. The resulting aliquots were placed in separated aluminium vials and oven dried (60°C) 48-72 h. After weighting, detritus was ashed in a furnace (550°C) for 4 hours and reweighted. The benthic organic matter (BOM) content in each specific microhabitat (i.e. mineral, bryophyte mats, *Hydrurus foetidus*) was then calculated as ash free dry mass (ADFM, g m^{-2}), resulting in the combination of coarse (CPOM ≥ 1 mm) and fine (FPOM < 1 mm) fractions. Invertebrate-devoided *Hydrurus foetidus* was processed without any further treatment, given the practical limitations in separating detritus from algal filaments. Benthic invertebrates were determined at the species (Plecoptera, Ephemeroptera, Trichoptera), genus (Mollusca, Chironomidae Diamesinae), subfamily (other Chironomidae), family (other Diptera, Oligochaeta) or order (Copepoda, Hydrachnidia, Ostracoda, Tardigrada, Nematoda) level by using a stereomicroscope (Leika MZ-12-5) and a light microscope (Leica DC-300F) and following the available manuals (Consiglio, 1980; Belfiore, 1983; Campaioli, Ghetti, Minelli & Ruffo, 1994; Lencioni, Marziali & Rossaro, 2007; Waringer & Graf, 2011). The body length of each specimen was measured following Méthot et al. (2012) using a graph paper (0.5 mm precision) placed under the Petri dish (see Supplementary S1).

The invertebrate community metrics were characterised in all three summer periods for each station (see Supplementary S2), resulting in the whole 2017 set of collected samples, and 22 additional 2018 samples examined to assess the possible interannual variability, achieve all periods for Z1 (not accessible in June 2017) and Z4 (added in August 2017) and ensure comparisons with the sampling station added in 2018 (i.e., Z12).

3.3.3 Data analysis

The Autothrophy Index – AI (Apha, 1985), which is the ratio AFDM/Chl-*a* (same scale) in biofilm, was used to assess the trophic status of epilithic communities. The breakdown rate of organic matter was calculated for each station as the average value between the wooden sticks of each station, using the negative exponential model proposed by Peters & Cummins (1974), and was estimated both over days (k-day^{-1}) and over degree days (k-°day^{-1}). For the analyses of BOM, conversions were applied when different microhabitats were compared. In fact, living bryophytes and their propagules represented a considerable fraction of what found among cobbles and boulders, and were sampled as part of the "mineral" microhabitat.

Therefore, adjustments were applied to the BOM from the mineral microhabitat, by applying the following equation:

$$BOM_{adj} = BOM_{min} * \%_{min}$$

Where BOM_{adj} is the storage capacity of the mineral substrate alone, BOM_{min} the raw outcome from the laboratory analysis, $\%_{min}$ the percentage of detritus stored in the mineral fraction of the sample. The latter parameter, estimated for each station in a subset (about 50%) of samples, could only be calculated for the CPOM, given the practical limitations brought by the leaching of the fine fraction from bryophytes in the sample. The $\%_{min}$ was calculated as (CPOM in the mineral fraction)/(CPOM in the mineral fraction + CPOM collected in moss fragments associated with the mineral fraction).

To calculate the biomass of invertebrates, size-mass exponential equations ($DM = a\ L^b$, were a and b are taxon-specific constants) were applied to estimate the dry mass (mg m^{-2}) of each genus (Ephemeroptera, Plecoptera, Trichoptera: EPT) or family (Diptera, Oligochaeta) in each sample, following the most accurate estimates found in literature for each taxon (Nolte, 1990; Breitenmoser-Würsten & Sartori, 1995; Benke et al., 1999; Johnston & Cunjack, 1999; Giustini et al., 2008; Zwick & Zwick, 2010; Méthot et al., 2012; see Supplementary S1). Pupae and meiofaunal taxa (i.e. Hydrachnidia, Copepoda, Nematoda, Tardigrada, Ostracoda) were excluded. The total biomass was estimated for each taxon, sampling site, date and microhabitat by adding together the body mass of its individuals in the community. Average “taxon body mass” was estimated by applying size-mass equations to the mean size of each taxon. The average “individual body mass” in the sample was calculated as the weighted mean of the average individual biomasses of each taxon.

Invertebrates diversity was assessed by calculating richness (i.e. total number of taxa) and the Shannon index, using the package *vegan* (R core team, 2012). Stream communities were analysed with a non-metric multidimensional scaling (NMDS) in *vegan*, based on a Bray-Curtis distance matrix calculated from log(x+1) transformed taxa abundances. We ensured the convergence of solutions at a reasonable stress value (<0.2), and the Shepard plot was examined to ensure strong correlation between the interpoint distances in the original versus the final configuration of dissimilarities in a two-dimensional space. Spearman correlation between log(x+1) transformed taxa abundances and the NMDS axes scores was estimated, to identify the most important taxa driving the NMDS configuration. To test significant differences in community composition between stations and stream types, we performed an analysis of similarity (ANOSIM; Clarke, 1993) using the function *adonis* from package *vegan*.

Pairwise comparisons were run to analyse differences in environmental and community variables among groups for the factors: sampling month (three levels: June, August, September), stream type (five levels: upper kryal, lower kryal, glacio-rhithral, krenal, rock glacial), and habitat type three levels: mineral substrates, bryophyte mats, *Hydrurus foetidus*), using the software SPSS (v.25, IBM, 2018). Samples with only one microhabitat were discarded from the analysis when pairwise comparisons were undertaken according to microhabitat. Due to non-normal data distribution (t-test, $P<0.5$) and/or inhomogeneous variances (Levene test, $P>0.5$) among groups, persisting even after transformation, we used non-parametric Mann-Whitney (two groups) or Kruskal-Wallis (> two groups) tests, with post-hoc Bonferroni correction applied to control Type-I error.

Linear Mixed Effect Models (LME) were run using the *lme4* R package (Bates, Maechler & Bolker, 2012) to analyse the importance of different fixed (stream type, microhabitat, month, turbidity, BOM) and random (station, taxon) effects in driving the abundance of detritus and the community metrics (see Figure 3.3). Plots of residuals were inspected to ensure their homoscedasticity and normality, and p-values were obtained by likelihood ratio tests of the "full model" with the effect in question against the model without the effect in question or "null model" (Figure 3.3). Patterns of community metrics as a function of environmental gradients were investigated with regression models, choosing the best fit (R^2) between linear and logistic regression. Where the distribution was wiggly, we only performed correlation analyses (Spearman or Pearson, depending on the distribution) instead of generalized additive models, because of the low number of points along the environmental gradients (i.e. distance from the glacier; $N=7$).

3.4 RESULTS

3.4.1 Epilithic biofilm

Epilithic biomass did not differ significantly among stream types. We recorded significantly lower Chl-*a* values ($H\geq20.5$, $p\leq0.023$) and significantly higher Autotrophic Index – AI scores ($H\geq22.9$, $p\leq0.008$) in the upper kryal compared to the other stream types, which in turn did not significantly differ from each other in both indices (Figure 3.2). AI was significantly higher in the upper kryal of Solda than Zay ($U=14$, $p=0.001$), driven by very low Chl-*a* concentrations (Figure 3.2). Month was an important driver of AI, given significant differences between the full and the null (only stream type considered) mixed models (Figure 3.3). Chl-a and epilithic biomass values were higher in the lower kryal stations than in the other stream types (Figure 3.2).

***Table 3.2**. Biological proxies for the sampling stations. Values indicate minimum and maximum for each station, mean and standard deviation (95% confidence) for each habitat. Chl-a is expressed in μg cm^{-2}, epilithic biofilms in g m^{-2}, AI = Autotrophic Index is dimensionless. K is expressed in positive numbers and thousands. Abundance values are expressed in thousand ind m^{-2}, total biomass in g m^{-2}, average body mass in μg ind^{-1} (dry mass).*

Stations	Chl-a	Epilithic	AI/1000	10^{3} k (day^{-1} - °day^{-1})	Abundance (thousands)	Biomass	Body mass	Richness	Shannon
Upper kryal	**0.14 ± 0.18**	**16.5 ± 9.3**	**90.3 ± 165.6**		**1.5 ± 2.1**	**0.1 ± 0.2**	**37 ± 37**	**6 ± 3**	**0.6 ± 0.4**
SI	0.00 - 0.02	8.9 - 35.3	48.8 - 752.1		0.1 - 0.3	0 - 0.02	7 - 22	5 -7	0.8-1.3
S2	0.01 - 0.17	14.7 - 30.0	8.9 - 207.6		0.5 - 1.7	0.02 - 0.06	6 - 32	6 - 8	0.4-0.9
Z1	0.03 - 0.59	2.7 - 37.6	1.41 - 26.5	0.37 - 0.23	0.2 - 2.7	0 - 0.6	10 - 129	2 - 3	0.1-0.6
Z3	0.02 - 0.61	5.3 - 18.1	73.5 - 92.8		1.0 - 8.1	0.02 - 0.4	27 - 92	2 - 8	0.5-1.0
Lower kryal	**3.9 ± 4.3**	**46.7 ± 92.5**	**0.9 ± 1.1**		**18.2 ± 30.5**	**1.3 ± 0.5**	**256 ± 251**	**12 ± 2**	**1.2 ± 0.4**
Z4	1.6 - 14.3	6.5 - 92.5	0.2 - 0.6		3.0 - 93.0	1.3 - 1.8	6 - 308	10-11	0.8-1.2
Z5	0.8 - 7.8	5.1 – 299.0	0.4 - 3.8	0.65 – 0.15	1.9 - 11.7	0.5 - 2.1	37 - 779	11-15	1.0-1.7
Glacio-rhithral	**1.4 ± 1.1**	**24.8 ± 23.0**	**1.7 ± 1.0**		**63.5 ± 42.3**	**3.7 ± 1.7**	**56 ± 25**	**26 ± 4**	**1.5 ± 0.3**
Z7	0.5 - 2.2	14.0 - 57.7	0.9 - 3.3	0.88 – 0.20	60.1 - 133.4	3.4 - 6.1	29 - 87	20-28	1.0-1.5
Z12	0.7 - 3.6	4.3 - 63.4	0.5 - 1.8		21.2 - 28.9	1.6 - 2.6	53 - 85	25-31	1.5-2.1
Krenal	**0.7 ± 0.6**	**10.8 ± 5.3**	**3.1 ± 3.1**		**50.6 ± 40.6**	**1.3 ± 0.8**	**63 ± 101**	**27 ± 4**	**1.4 ± 0.4**
ZKN	0.3 - 2.1	3.6 - 20.5	0.3 - 1.2	0.95 – 0.25	38.1 - 130.2	1.0 - 2.5	7 - 45	27-30	1.1-1.6
SKN	0.1 - 0.7	8.9 - 17.0	1.6 - 9.5	0.60 – 0.09	14.4 - 47.9	3.2 - 1.8	16 - 270	19-31	1.1-2.0
Rock glacial	**1.2 ± 0.7**	**19.6 ± 15.4**	**1.9 ± 1.8**		**30.0 ± 22.3**	**1.3 ± 1.2**	**139 ± 174**	**15 ± 6**	**1.3 ± 0.4**
SRG	0.5 - 2.3	1.3 - 22.1	0.2 - 3.1	0.52 - 0.44	25.1-45.8	1.0 - 1.5	7 - 460	19-22	1.1-1.8
ZRG	0.8 - 2.6	8.4 - 53.0	0.9 - 6.8	0.28 – 0.26	1.2-73.1	0.1 - 4.0	15 - 43	7-13	0.9-1.6

Table 3.3 (NEXT PAGE). *Linear mixed effect models performed and associated results. For each of the models, we list: the "full" against the "null" model (response variable ~ fixed effects), and the df, χ^2 and p-value resulting from their comparison (ANOVA), the intercept and estimate values of the fixed effects and the standard deviation explained by the random effects and residual. Where two random effects were present, they were crossed. Cross-comparisons between the effects are not displayed. Estimate values of months (Jun=June, Sep=September) are listed in the comparison with August, stream types in the comparison with glacio-rhithral, and the microhabitat "moss" (i.e. bryophyte mats) is compared with mineral substrate.*

[1] we summarize for all taxa only the estimates that underline differences of body mass associated with bryophytes; note that only taxa with a sufficient number of samples (>10) and density (>20 ind m^{-2}) were used for the analyses, and only those with an estimate value > |0.3| are displayed. Hydrurus foetidus was excluded from the analyses due to the low number of cases (N=3).

Model	**Full model**	**Null model**	**(df) χ^2, p-value**	**Int.**	**Fixed effects estimate**	**Random effect(s) SD**
Chl-*a*	Chl-*a*^{log} ~ Stream type * month	Chl-*a*^{log}= Stream type	(10)16.18,0.09	-0.24	Jun= 0.59; Sep=0.59 Upper kryal= -2.28; Lower kryal= 0.91; Krenal= -1.38; Rock glacial= -0.06	Station=0.72 Residual=0.73
Epilithic	AFDM^{log} ~ Stream type * month	AFDM^{log}~ Stream type	(10)28.0,0.002	2.09	Jun= 0.33; Sep=1.30 Upper kryal= -0.15; Lower kryal= 0.13; Krenal= 0.19; Rock glacial= -0.15	Station=0 Residual=0.78
Autotrophy index	AI^{log}= Stream type * month	AI^{log}= Stream type	(10)20.1, 0.03	0.04	Jun=-0.27; Sep=0.71 Upper kryal= 2.18; Lower kryal= -0.74; Krenal= 1.55; Rock glacial= -0.85	Station=0.89 Residual=0.90
Benthic organic matter	BOM^{log} ~ Microhabitat * stream type	BOM^{log} ~ Microhabitat	(8)48.3, <0.001	0.59	Moss = 0.62 Upper kryal= -0.25; Lower kryal= 0; Krenal= 0.23; Rock glacial= 0.24	Station=0.09 Residual=0.21
Biomass	Biomass^{log} ~ Microhabitat * stream type	Biomasss^{log} ~ Microhabitat	(8)20.4, 0.009	3.41	Moss= 0.24 Upper kryal= -1.23; Lower kryal= -0.46; Krenal= -0.48; Rock glacial= -0.59	Station=0 Residual=0.37
Abundance	Abundance^{log} ~ Microhabitat * stream type	Abundance^{log} ~ Microhabitat	(8)15.7, 0.046	4.33	Moss= 0.65 Upper kryal= -1.19; Lower kryal= -0.39; Krenal= 0.08; Rock glacial= -0.61	Station=0.15 Residual=0.34
Biomass	Biomass^{log} ~ BOM^{log} + Turbidity^{log}	Biomass^{log} ~ BOM ^{log}	(1)4.7, 0.03	2.59	Turbidity= -0.29 BOM= 0.14	Station=0.60 Residual=0.54
Body mass	Body mass^{log} ~ Microhabitat + stream type	Body mass^{log} ~ Microhabitat	(8)10.4, 0.24	4.9	Moss= -0.14 Upper kryal= 0.78; Lower kryal= 0.30; Krenal= -1.04; Rock glacial= -0.21	Station= 0.72 Taxon= 1.55 Residual= 1.30
Body mass	Body mass^{log} ~ Taxon * microhabitat	Body mass^{log} ~ Taxon	(27)30.4, 0.30	5.87	Moss= -0.22 [1]In bryophytes: *Baetis*= -0.34; *Dictyogenus*= -0.48; Plecoptera juveniles= -0.82; Goeridae= -0.52; *Protonemura*= 0.61; *Rhithrogena*= -1.90; *Rhabdiopteryx*=0.48; Enchytraeidae= 0.44	Station=0.62 Residual= 1.17

3.4.2 Availability and degradation of organic detritus

Benthic organic matter (BOM) was lower in the upper kryal sites, with an increasing trend moving from lower kryal, glacio-rhithral and krenal habitats, and intermediate values for rock glacial sites (Figure 3.2, Figure 3.1). Along the Zay stream, distance from the glacier was a good predictor of the BOM in the channel (Figure 3.4). There was a strong positive correlation between BOM and CPOM/FPOM (Spearman ρ= 0.73, p<0.001). CPOM/FPOM significantly decreased with elevation (Figure 3.4). Where present in the channel, bryophyte mats stored significantly higher BOM than the mineral substrates (U=329, p<0.001; Figure 3.2). Models showed that the habitat type was an important mediator of this difference (Figure 3.3); in fact, krenal and glacio-rhithral sites showed the highest difference between the amounts of BOM stored in the two substrates (Figure 3.2). Despite the low number of sampling stations (N=7) hindered any statistical significance, breakdown rates of organic matter (k-day^{-1}) was positively correlated with the availability of CPOM in the channel (Pearson r=0.54, p=0.11). In turn, k-day^{-1} was correlated with the total biomass of invertebrates in the channel (r=0.652, p=0.07). In fact, the lowest value for k-day^{-1} (Figure 3.2) occurred in the upper kryal; the value increased moving downstream along the glacier-fed stream and reached the highest numbers at ZKN (krenal), with intermediate values for SRG (rock glacial stream). ZRG and SKN showed lower k-day^{-1} compared to their stream type counterparts, with the former showing values comparable with Z1 (Figure 3.2). Breakdown rate in k-°day^{-1} was much more homogeneous among stations, although SKN still showed low values despite relatively warm waters (500 days). K-°day^{-1} was much higher at SRG than at all other stations (Figure 3.2).

Table 3.4. *Regression analyses. The best response variable among environmental drivers was chosen according to the highest R^2 value, between BOM, CPOM, FPOM and CPOM/FPOM. To ensure homoscedasticity: [1]one outlier was removed (Z4 June 2018); ^{log} log(x+1) transformation was applied to the dataset.*

Response	Predictor	Model	R^2	F-statistic	p-value	b
CPOM/FPOM ^{log}	Elevation	Logaritmic	0.55	79.0	<0.001	-0.83
BOM ^{log}	Distance from the glacier	Linear	0.74	80.3	<0.001	0.20
Richness	Distance from the glacier	Linear	0.86	147.5	<0.001	5.08
Shannon	Distance from the glacier	Logaritmic	0.66	34.2	<0.001	0.21
Abundance ^{log}	Distance from the glacier	Logaritmic	0.51	20.9	<0.001	0.30
Biomass ^{log}	Distance from the glacier	Logaritmic	0.64	35.8	<0.001	0.36
Total biomass ^{log}	Total abundance ^{log}	Linear	0.76	128.1	<0.001	1.00
Taxon biomass ^{log}	Taxon abundance ^{log}	Linear	0.44	272.6	<0.001	0.64
[1]Abundance ^{log}	BOM ^{log}	Linear	0.73	105.9	<0.001	1.88
Biomass ^{log}	BOM ^{log}	Logaritmic	0.48	37.7	<0.001	1.09
Richness	BOM ^{log}	Linear	0.74	118.4	<0.001	20.13
Shannon	BOM ^{log}	Linear	0.35	22.0	<0.001	0.74
Abundance ^{log}	Turbidity ^{log}	Linear	0.53	45.4	<0.001	-1.26
Biomass ^{log}	Turbidity ^{log}	Linear	0.49	35.8	<0.001	-1.40
Richness	Turbidity ^{log}	Linear	0.46	34.6	<0.001	-12.50
Shannon	Turbidity ^{log}	Linear	0.29	16.3	<0.001	-0.53

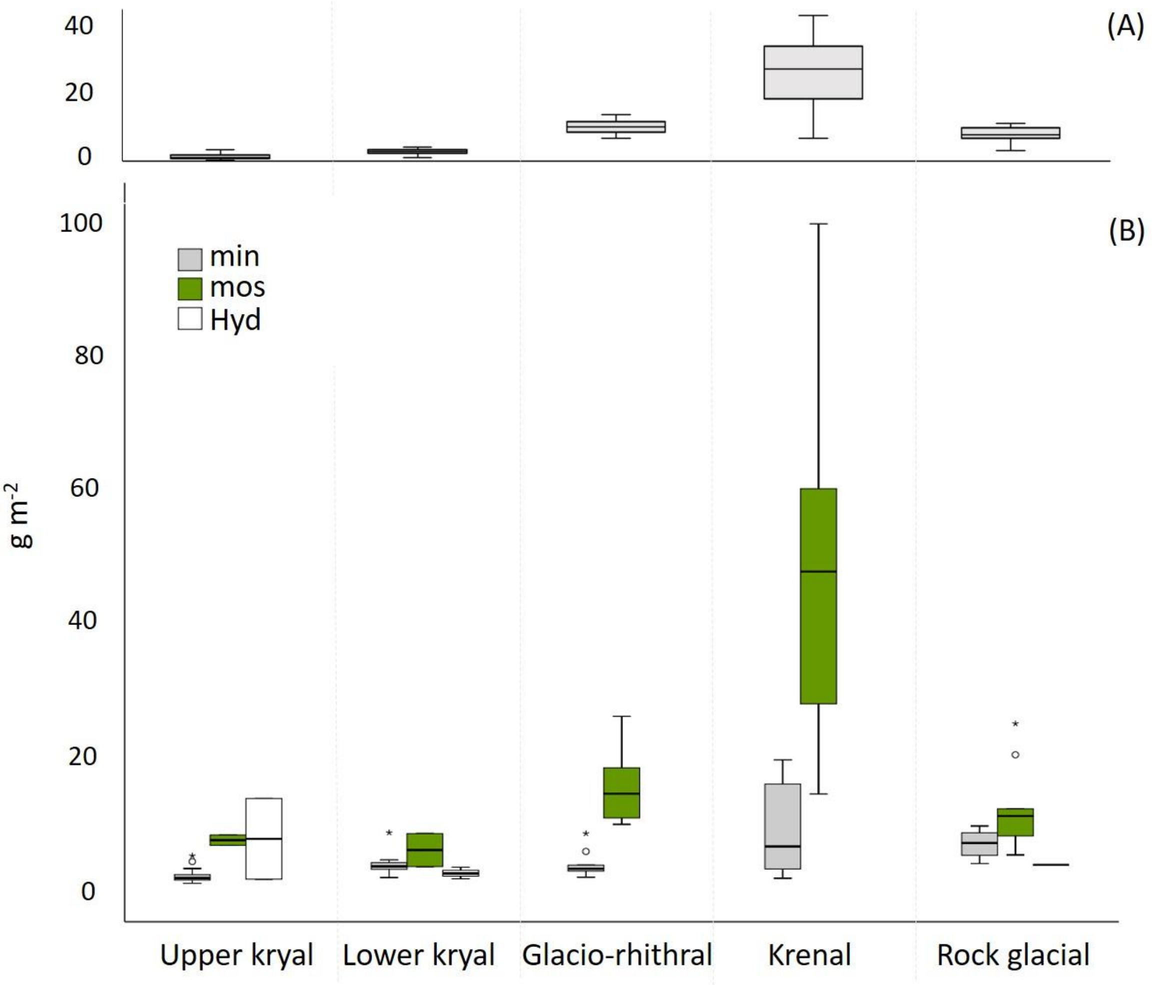

Figure 3.2. *Boxplot of total benthic organic matter (BOM) in the channel, expressed as ash free dry mass (g m^{-2}), for each stream type over all sampling dates; A) BOM in the channel for different stream types, accounting for the relative proportion of different microhabitats; B) BOM in different microhabitats (min= mineral substrate, mos= bryophyte mats and Hyd= Hydrurus foetidus patches) for each stream type. Values associated with mineral substrate corrected accounting for the abundance of bryophytes in the sample (i.e. BOM$_{adj}$, see text).*

3.4.3 Diversity and composition of stream communities

Taxa richness (H=35.7, p<0.001) and Shannon index (H=21.2, p<0.001) differed significantly among stream types. Both diversity metrics were lowest in the upper kryal sites and increased moving downstream to lower kryal and glacio-rhithral habitats (Figure 3.2, Figure 3.3). The highest values for both indices were recorded in the krenal sites, without any significant difference between ZKN and SKN. Diversity (U=11.3, p=0.001) and richness (U=10.7, p=0.001) were significantly higher in rock glacial habitat compared to the upper kryal one. However, SRG had significantly higher richness than ZRG (U=5.4, p=0.02), and the Shannon index among the highest in the catchment (Figure 3.3, Figure 3.2). The distance from the glacier was a good predictor of taxa richness and Shannon diversity along the Zay stream (Figure 3.4). Taxa richness and diversity of bryophyte mats and mineral substrates did not significantly differ.

Despite the small number of samples (N=3), both diversity metrics were much lower in *Hydrurus foetidus* than in the bryophyte microhabitat (Figure 3.3, Figure 3.2).

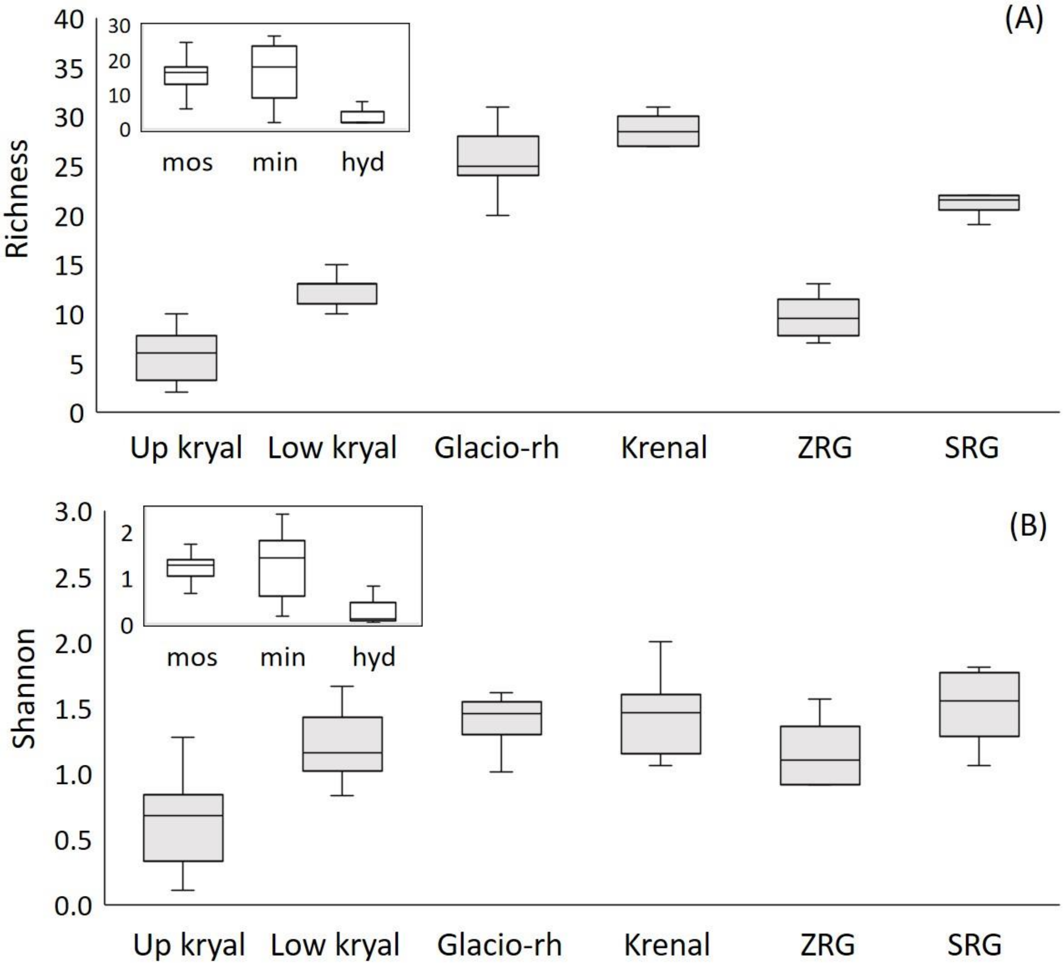

Figure 3.3. *Diversity metrics associated with different stream types (large boxplots) and microhabitats (small boxplots, legend as in Fig. 2) in each sampling date. A) Taxa richness (total number of taxa); B) Shannon index. NOTE: Rock glacial stations are kept separated.*

The NMDS plot (Figure 3.4), showed a separation of stations according to the habitat type (stress value= 0.12, R^2= 0.99 in the Shepard plot). The ANOSIM analysis confirmed significant differences among stations (R= 0.82, p= 0.001) and stream types (R= 0.59, p= 0.001). Those taxa that most contributed to the grouping of stations along the first two NMDS axes are summarized in Figure 3.5. We recognized three clusters of stations characterized by different community composition (see also supplementary S2) in the NMDS space. A first group comprised the upper kryal communities, dominated by the Chironomidae *Diamesa* sp. The sample scattering in the NMDS space associated with the upper kryal is likely due to the seasonal variability in abundances of Chironomidae, that included Orthocladiinae in the downstream stations Z2 and S2, and of accessory meiofaunal (Nematoda, Copepoda, Hydrachnidia, Tardigrada) and macroinvertebrate (Ceratopogonidae and Enchytraeidae, present in Z2) taxa. A second cluster included the lower kryal samples (where *Diamesa* outnumbered Orthocladiinae) and ZRG (where Orthocladiinae outnumbered *Diamesa*), and

Pseudodiamesa sp. was abundant along with Diptera (Empididae, Limoniidae, Pediciidae), Haplotaxidae and Trichoptera (*Acrophylax zerberus*). Other Diptera (Muscidae, Tipulidae, Simuliidae), *Drusus adustus*, Nemouridae, *Dictyogenus fontium*, *Baetis alpinus* were only found in the lower kryal in this cluster, whereas high numbers of Copepoda (mainly Cyclopoida) and Nematoda were found at ZRG and at Z5. The third cluster in the NMDS space included samples from SRG, krenal and glacio-rhithral stations, all characterised by a high number of EPT and Diptera taxa at high densities. In the glacio-rhithral stations, Orthocladiinae and Tanytarsini Chironomidae outnumbered the Diamesinae (the latter included *Pseudokiefferiella* sp. and a low number of *Diamesa* sp. and *Pseudodiamesa* sp.), Plecoptera (*D. fontium*, *Protonemura* spp., *Nemoura mortoni*, *Leuctra* spp., *Rhabdyopteryx alpina*) were collected at high densities, along with Ephemeroptera (*Baetis alpinus*, *Rhithrogena* spp.) and Trichoptera Limnephilidae (*Drusus adustus*, *D. discolor*). Both krenal stations showed the highest diversity of Trichoptera, the composition in these stations included *D. biguttatus* and *Micropterna lateralis* Limnephilidae, Rhyacophylidae spp. and the Goeridae *Lithax niger*; *Crenobia alpina*, Tanypodinae chironomids and the Gasteropoda *Gyraulus* sp. were collected only in these stations. At SRG, Orthocladiinae dominated the chironomid community as well, but Diamesinae (*Diamesa sp*, *Pseudokiefferiella sp*, *Pseudodiamesa sp*) showed a higher share compared to glacio-rhithral and krenal stations. On the contrary, the abundance and diversity of Plecoptera (*D. fontium*, *Isoperla rivulorum*, *Leuctra rosinae*, *Nemoura mortoni*, *Rhabdyopteryx alpina*), Ephemeroptera (*Baetis alpinus*, *Rhithrogena loyolaea*) and Trichoptera (*Drusus adustus*, *Drusus monticola*) was comparable with that of non-glacial sites.

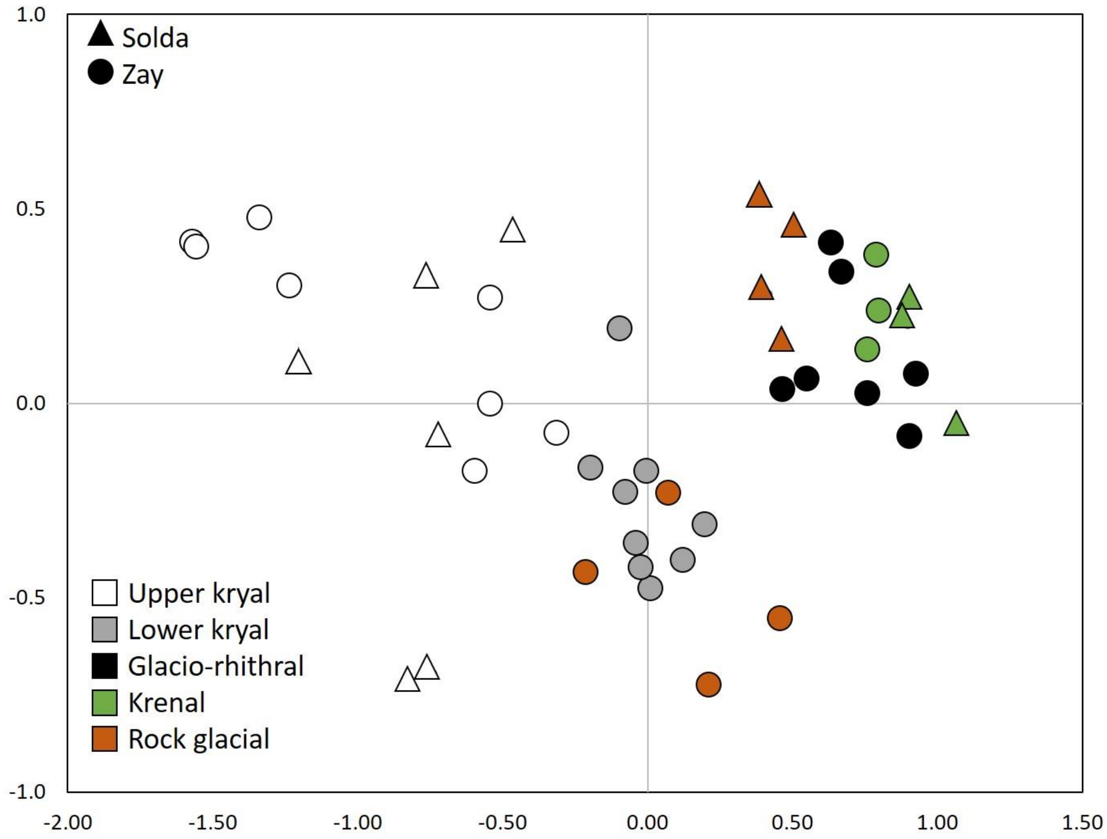

Figure 3.4. *Non-metric multidimensional scaling ordination biplot of sampling stations, according to catchment (geometric shapes) and stream type (colours), for the log(x+1) transformed dataset of taxa abundances.*

Table 3.5. *Correlation between NMDS axes scores and taxa (log(x+1)-transformed) abundances. Only taxa with |R|>0.5 are listed*

Taxon	NMDS1	NMDS2
Orthocladiinae	0.88	0.15
Enchytraeidae	0.82	-0.14
Baetis alpinus	0.78	0.40
Nemoura mortoni	0.73	0.53
Tanytarsini	0.72	0.30
Dictyogenus fontium	0.69	0.42
Protonemura nitida	0.69	0.28
Hydrachnidia	0.66	0.31
Leuctra rosinae	0.64	0.38
Simuliidae	0.60	0.23
Copepoda	0.60	-0.20
Protonemura brevistyla	0.57	0.33
Nematoda	0.57	-0.40
Limoniidae	0.56	0.38
Isoperla rivulorum	0.54	0.29
Rhithrogena loyolaea	0.54	0.12
Drusus adustus	0.53	0.41
Pediciidae	0.51	0.12
Pseudodiamesa sp	0.11	-0.54

3.4.4 Abundance, biomass and size of stream invertebrates

Abundance, total biomass and average body mass of invertebrates varied with different patterns among stream types and microhabitats (Figure 3.5). Overall, we found a positive linear relationship between the total abundance and the total biomass of invertebrates and, though weaker, between the total abundance and the total biomass for each taxon (Figure 3.4). The average body mass of each taxon was negatively correlated with their abundance in each sample ($\rho=-0.43$, $p<0.001$). The mean body size of invertebrates in each station was largest for ZRG and the lower kryal sites, and showed different patterns depending on the taxon, with generally increasing body mass moving downstream along the glacier-fed stream, highest values for Z12, and intermediate levels for krenal and rock glacial sites (Figure 3.5; Figure 3.6). We found significant differences in the average body mass of macroinvertebrates in different microhabitats, as bryophyte mats hosted significantly smaller individuals ($U= 146$, $p= 0.004$) on average. Mixed models that considered body mass as response variable revealed a primary importance of taxon as random effect, given its high standard deviation (Figure 3.3). When taxon was considered as fixed effect, most of the common taxa showed a negative response to bryophytes in terms of average body mass, and the stream type was not an important fixed effect (non-significant differences between the full and the null models, Figure 3.3). However, although for most of comparisons the low number of cases did not allow statistical comparisons, the microhabitat proved important for some taxa at some stations. For example, Chironomidae were (on average) four times smaller in the bryophytes of the upper kryal (Z3), where these mats were constantly emerged in autumn. On the contrary, at the Solda rock glacial stream (SRG) they were two times smaller in the mineral microhabitat. Bryophytes hosted smaller individuals compared to mineral substrates also for other stations and taxa: *Baetis alpinus* at krenal sites (on average ten times smaller in bryophytes compared to mineral substrates at ZKN) and at the SRG (1.8 times smaller), *Rhithrogena* sp in the krenal sites (where we only found first instars in bryophytes), Limnephilidae at Z12 and at both rock glacial sites, *D. fontium* at the glacio-rhithral stations.

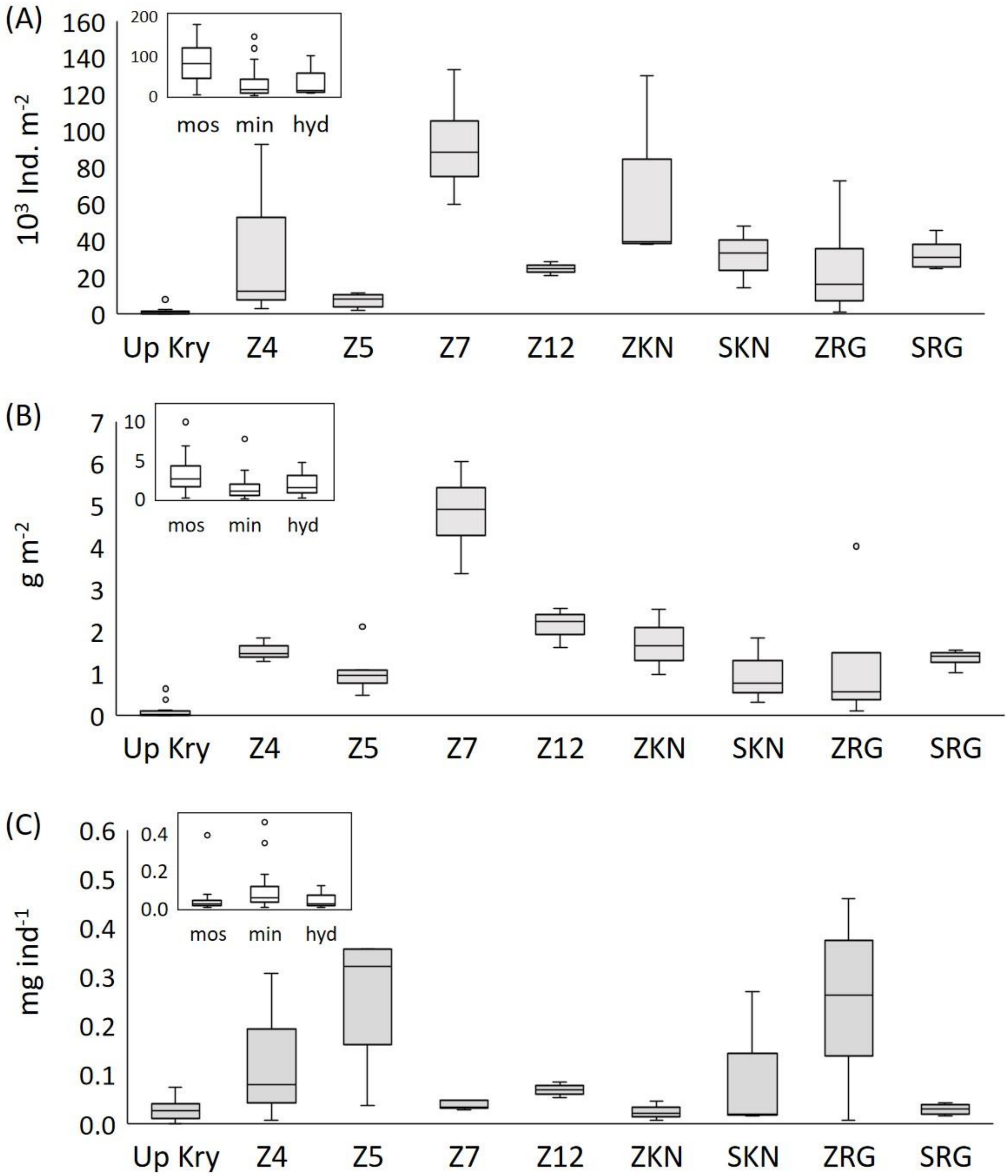

Figure 3.5. *Quantitative community metrics associated with the different sampling stations (large boxplots) and microhabitats (small boxplots, legend as in Fig. 2). A) Invertebrate abundance (i.e. density); B) Invertebrate biomass (meiofaunal taxa and pupae excluded); C) Average invertebrate body mass. Up Kry= Upper kryal stations, pooled together because of the little variability in the metrics.*

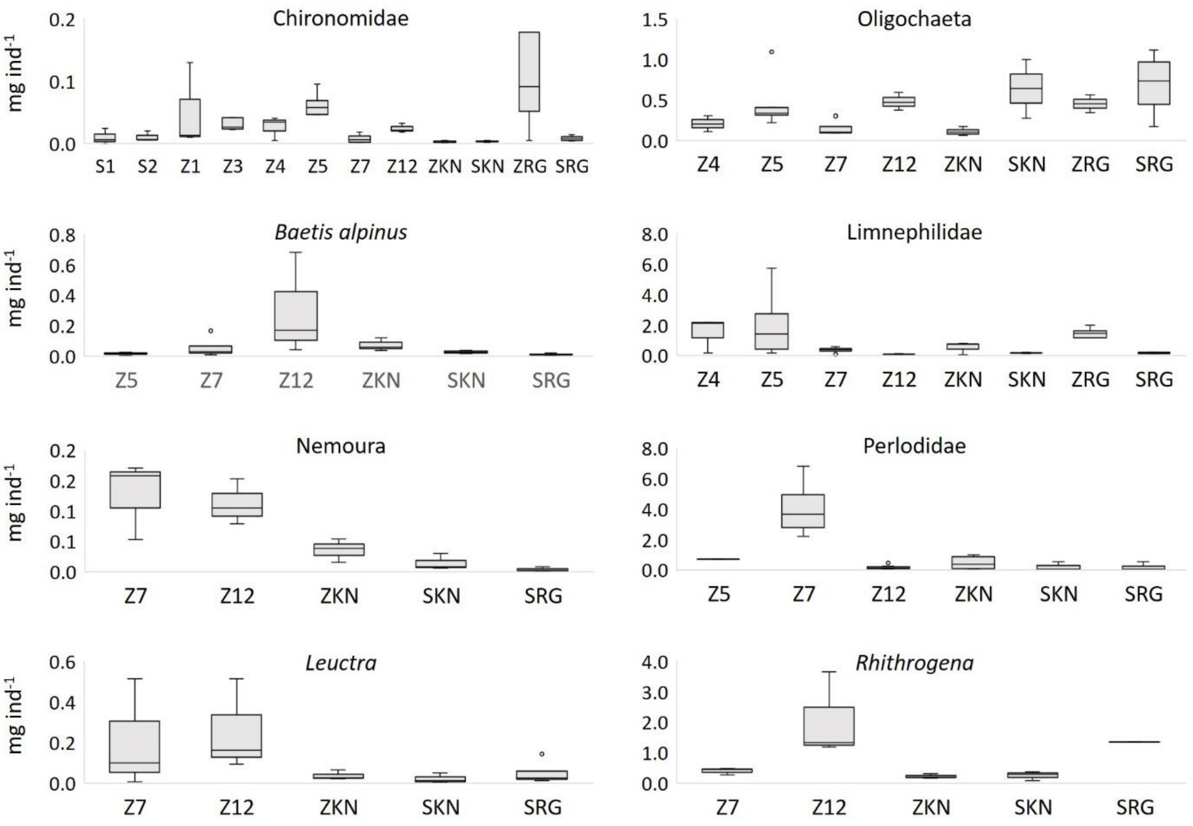

Figure 3.6. Boxplots of the average body mass (mg ind^{-1} of dry mass) of the most abundant taxa in each sampling station and date. For each sampling date, values of distinct microhabitats have been averaged according to the relative abundance of the habitat in the channel. Taxa belonging to the same order/family and/or with a similar size pattern are pooled together. Samples with a low number of specimens (<20 ind m^{-2}) have been discarded. One outlier is not indicated in the Chironomidae boxplot, corresponding to ZRG station (0.37 mg ind^{-1}). Oligochaeta only include Enchytraeidae and Naididae because of the low abundance of Haplotaxidae.

Biomass was significantly lower in the upper kryal compared to all other stream types ($H>16.2$, $p\leq0.036$ for all post-hoc pairwise comparisons), that did not show any significant difference between each other. Although regression models explained well the average biomass and abundance of communities as a function of the distance from the glacier, we observed evident peaks of both indices associated with station Z6 and a decline moving downstream to station Z12 (Figure 3.5). However, biomass did not show this pattern in the bryophyte mats, where it was similar between Z7 and Z12. In general, turbidity was negatively correlated with biomass and abundance of invertebrates whereas the BOM was positively correlated (Figure 3.4), and an asymptotic behaviour of abundance/biomass as a function of BOM and turbidity was detected (Figure 3.7). Regarding the comparisons between microhabitats, both abundance ($U=457$, $p<0.001$) and biomass ($U=415$, $p=0.002$) of invertebrates were significantly higher in the bryophyte mats than in the mineral substrate. Mixed models revealed the importance of the stream type in driving the invertebrate biomass and abundance in different microhabitats (Figure 3.3).

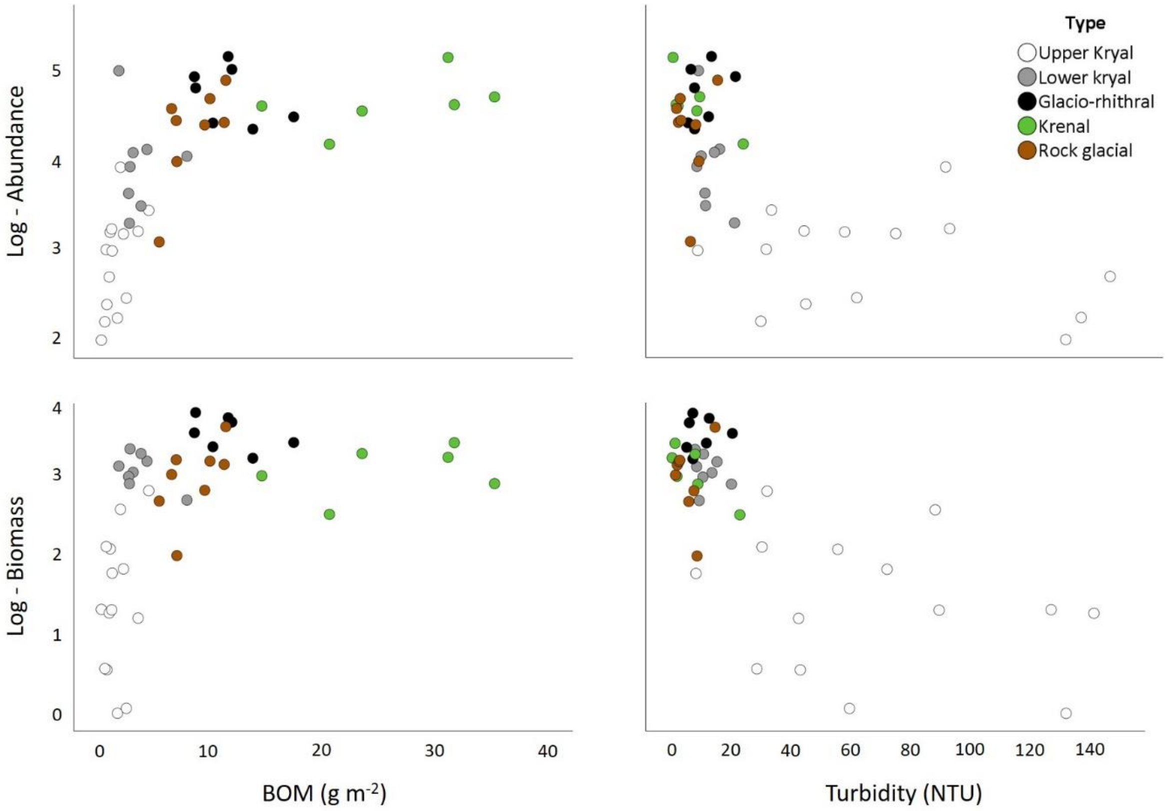

***Figure 3.7**. Scatterplots of abundance/biomass as a function of the availability of benthic organic matter BOM) and turbidity.*

3.5 DISCUSSION

Our work provides insights on the ecology of alpine river networks in the late stages of deglaciation, where the thawing permafrost and the geomorphic features of a landscape left uncovered by receding glaciers play an increasing role in driving habitat features and stream communities.

3.5.1 Biotic habitat settings in deglaciating catchments and their implications

Epilithic biofilm is an important driver of the biogeochemical cycles and influences the stream food webs, especially in alpine streams where allochthonous inputs of organic matter are low (Niedrist & Füreder, 2018). Epilithic production in our study was mostly dependent on the presence and abundance of *Hydrurus foetidus*, and this may have masked the potential existing differences among stream types in epilithic biomass and Chl-*a* concentration not due to this pervasive alga. However, the lower kryal stations always exhibited higher epilithic biomass and Chl-*a* concentrations compared to the other stream types, thus testifying the buffering effect exerted by the proglacial lake and the moraine body along the downstream gradient. The autotrophic index was particularly high in the upper kryal, likely due to the low biomass of the epilithic primary producers in the glacier-fed waters. In fact, although high concentrations of Cyanobacteria are known to boost the index (Biggs, 2000), *Hydrurus foetidus* and diatoms are considered as the major constituents of periphyton in proglacial sections (Hieber, Robinson, Rushforth & Uehlinger, 2001), where biofilms are dominated by heterotrophic bacteria (Battin et al., 2016; Tolotti, submitted), whose growth is boosted by the provisioning of a highly labile organic carbon from glaciers (Singer et al., 2012; Niedrist & Füreder, 2018). We suggest that the autotrophy index might be useful for assessing the influence of the glacier on the biofilm habitat template. In fact, in the proglacial sections of our study area, the glacial influence on the physico-chemical habitat was very high at Solda, and much lower at Zay (due to prolonged glacial wastage, see Brighenti et al., 2019b), with cascading effects on the aquatic communities. Therefore, the higher abundance and biomass of *Diamesa* sp. that we found at the Zay proglacial stations compared to Solda, may be attributable to a more benign habitat coupled with a higher trophic quality of the periphyton. In fact, *Diamesa* sp. exhibits a specialized grazing behaviour in sections with a high glacial influence (Niedrist & Füreder, 2017), and a high selectivity for diatoms and Crysophyceae has been demonstrated by Niedrist et al. (2018) in kryal sites of the Austrian Alps.

In our study, the availability of organic detritus increased moving downstream from the glacier snout under the enhanced retention capacity exerted by stable channels and by increased allochthonous inputs from vegetation, as also shown by Zah & Uehlinger (2001) in the Roseg Valley (Switzerland). The increased vegetation complexity (i.e. shrubs, trees) moving downslope in the Solda Valley was also responsible for the increased CPOM/FPOM in the channels.

We recorded a strong correlation between breakdown rates of organic matter (measured with the wooden sticks method) and the invertebrate biomass, which in turn changed according to the stream type. These results are partially in agreement with an extensive study conducted in the Swiss Alps, where Robinson & Jolidon (2005) estimated lower degradation rates in kryal streams, intermediate in rock glacial, and higher in krenal ones. These Authors estimated values of degradation an order of magnitude larger than in our study, but results are not comparable because they are based on leaf bag experiments, and leaves have a higher bioavailability compared to wooden sticks (Arroita et al., 2012). Interestingly, Robinson & Jolidon (2005) found that temperature had a primary role in driving degradation rates in all stream types. In contrast, although our temperature records refer to a data-logger placed close to the spring (20 meters upstream the sampling site), we found a two-fold faster breakdown rates (k-°day) for the Solda rock glacial stream compared to the other stations, likely attesting a high biological activity despite very cold conditions.

A key driver for the retention of organic detritus was represented by the bryophyte mats, which trapped on average four times the BOM than the mineral substrate. In our study, the role of bryophytes as detritus traps might have been underestimated, as: I) our sampling strategy involved the collection of a fraction of the total standing stock framed in the Surber-net, and II) the considerable amount of bryophytes found among the cobbles made it difficult to disentangle the role of the mineral substrate alone as detritus trap. Nonetheless, our results are in agreement with records in literature (see SBG, 1999). In the study most similar to ours, Suren (1991) found an average detritus storage three to six times higher in bryophytes compared to gravel substrates in alpine streams from New Zealand. The same author found that the total density of invertebrates was seven to ten times higher in the bryophyte mats, and our study is the first to demonstrate a similar condition in the European Alps. In fact, our results indicate the bryophytes as hosting 2.6-times the total number of invertebrates found in mineral substrates, and we demonstrated that the invertebrate biomass shows a similar behaviour (2.3-times on average), and an even more pronounced differences (3.5-fold) when only the total abundance and biomass of Chironomidae were considered. The invertebrate densities of 7 400-218 000 ind m^{-2} found by Suren (1991) were comparable to those of our study (5 260-177 440 ind m^{-2}) but Suren's BOM values were an order of magnitude higher, maybe because a different experimental design (i.e. the author completely removed mosses mats and only inspected gravel substrate as indicator of the mineral fraction) and study setting (i.e. different channel types and vegetation cover). We found that, on average, bryophytes hosted smaller macroinvertebrates compared with the mineral substrates. Despite the low number of cases, each single taxon showed strikingly evident smaller size in bryophytes, particularly at the krenal and rock glacial sites and even in the upper kryal if temporarily-submerged mosses where present. This confirms the role of bryophyte mats as a nursery refuge for alpine streams (SBG, 1999). For some taxa (e.g. *Rhithrogena* sp., *Baetis alpinus,* Limnephilidae), bryophytes may provide a thick canopy which helps hindering predation, and prevents food scarcity-driven competition. For other taxa (e.g. Chironomidae), mosses may represent a trophic and habitat refuge when the environmental harshness is high (upper kryal). Interestingly, Chironomidae average body mass was two times larger in bryophytes compared to mineral substrates in the Solda rock glacial stream, thus showing opposite trends compared to the other stations. We suggest that in this stream, the thick canopy represented by bryophyte mats might represent a thermal refuge against the very cold waters emerging from the rock glacier, and enhance the growth of individuals according to the metabolic theory of ecology (Brown et al., 2004). However, this also underscores the peculiarity of rock glacial streams, where the typical set of habitat and biotic conditions might trigger distinct ecological patterns.

3.5.2 Abundance, biomass, body size and diversity: different proxies for ecological shifts

The combined influence of glaciers, permafrost and the paraglacial landscape shaped the quantitative aspects of the invertebrate communities in the study area. Despite abundance and biomass showed consistent patterns, biomass estimates were much more homogeneous between and within stations than the abundance values. As expected, abundance tended to overrepresent the importance of small-sized and underrepresent that of the large-sized taxa, compared to biomass. For example, Chironomidae accounted for 74-96 % of the total abundance but only 13-62 % of the total biomass of macroinvertebrates at SRG, where Limnephilidae represented 2-11 % of the abundance and 21-77% of the biomass.

The abundance and biomass of invertebrates in the Solda Valley were related to the presence of organic detritus in the channel. Studies on alpine stream food webs (Zah, Burgherr, Bernasconi & Uehlinger, 2001; Füreder, Welter & Jackson, 2003a; 2003b; di Cugno & Robinson, 2017; Niedrist & Füreder, 2018) pinpoint that, while epilithic biofilm and *Hydrus* *foetidus* are the main basal resources in the autotrophic kryal systems, organic detritus is the primary food resource where the influence form the glacier is low (glacio-rhithral) or absent (krenal). As expected, we recorded lower invertebrate abundance and biomass in the upper kryal stations, with an increasing trend moving downstream to lower kryal, glacio-rhithral and krenal sites. Rock glacial streams exhibited intermediate levels between glacial and non-glacial streams. Nevertheless, we observed non-linear patterns of abundance and biomass along the Zay stream. The lower kryal station located below the lake/moraine outflow showed higher values compared with the downstream one, which was located below the confluence with the rock glacial stream. The ameliorated conditions of the physical habitat (higher channel stability, lower turbidity, increased detritus; see Brighenti et al., 2019b) well-explain the boosted values of abundance and biomass compared to the harsh kryal tributary of the lake. Furthermore, the solutes provided by the moraine baseflow improved the chemical conditions (increased electrical conductivity and major ions at Z4) and sustained both the primary (as shown by higher epilithic Chl-*a* concentration and bryophyte coverage) and secondary production (sharp increase of taxa richness and Shannon diversity compared to the lake inlet). The direct seepage of lake waters into the moraine debris prevented the possibility to discriminate the single effects of these two paraglacial features on the invertebrate production. However, the role of kryal lakes in increasing macroinvertebrate richness and density was negligible/low in studies conducted in the Swiss Alps (Burgherr & Ward, 2000; Sertić Perić & Robinson, 2015; Hieber et al., 2005) and Patagonia (Miserendino et al., 2018; Martyniuk, Modenutti & Balseiro, 2019). This suggests that the moraine exerted a stronger influence on the benthic invertebrate communities, compared to the Zay lake.

Studies conducted in the Austrian Alps (Füreder, 2007) and the Pyrenees (Khamis, Brown, Hannah & Milner, 2016), showed unimodal rather than linear responses of invertebrate community metrics as a function of the glacier influence. In our study, along the Zay glacier-fed stream, this occurred for abundance and biomass which showed evident peaks in the uppermost glacio-rhithral station (i.e. below the talus body, where the glacier cover in the catchment – GCC was 13.7 % and the groundwater contribution was estimated in the range of 57.8 ± 9.7 % by Brighenti et al., 2019b) but not at the catchment closing section, whereas the Shannon diversity and taxa richness showed a linear increasing trend rather than a unimodal response. For Khamis et al. (2016), the peaks of abundance and diversity corresponded to 40-60% meltwater contribution, whereas Füreder (2007) found the invertebrate abundance peaking at 15-30% glacier cover in the catchment (GCC, i.e. the area of the underlain catchment covered by glaciers), and taxa richness peaking at 0-15% GCC. This unimodal pattern may result from intermediate habitat harshness and reduced competition/predation in the community (Khamis et al., 2016). Within this context, the talus body might have had a role in improving the habitat conditions compared to the upstream stations (Brighenti et al., 2019b) shifting upstream the longitudinal gradients of the community metrics. For the same reason, the asymptotic behaviour of abundance and biomass of invertebrates that we observed in the bryophyte microhabitat when moving downstream along the Zay stream, might be due to a combination of: i) an overabundance of food resources in bryophytes as soon as the allochthonous input is sufficiently coupled with reduced physical disturbance, and/or i) reduced species interactions (i.e. low competition for food, effective predation avoidance).

Average macroinvertebrate body mass exhibited different patterns compared to abundance and biomass, with increasing trends along the glacier-fed streams and higher values at Zay in the rock glacial stream and at the glacial floodplain, located at the junction between lower kryal and rock glacial waters. These findings can be mostly related to the high average body mass of the caddisfly *Acrophylax zerberus* and of the chironomid *Pseudodiamesa sp*., and it is likely that the input of rock glacial tributary increased the average invertebrate body mass in the downstream glacier-fed reaches (for instance, by downstream dispersal) below the junction. The lentic character of rock glacial waters at Zay likely contributed to make the environment favourable for invertebrates, so that specimens could better allocate their energy to body growth and/or larger-sized taxa could survive. In fact, small size is a good adaptation to physical disturbance, as less energy the organism needs to survive, and more shelter areas are available (Füreder, 1999). However, exceptions to this assumption have been observed in glacier-fed streams. In the Austrian Alps, Schütz & Füreder (2018) found that *Diamesa* spp. specimens were larger close to the glacier than downstream, and Niedrist et al. (2018) demonstrated the same condition in a gradient of environmental harshness, with a positive correlation between harsh conditions (i. e., glacial influence) and the body mass of *Diamesa*. In line with these studies, we recorded the highest body mass in Chironomidae at the glacier margin (average DM= 141 µg/ind), where this taxon was mostly represented by *Diamesa*, compared to all other stations along the glacier-fed streams. However, this value was recorded in September, at the Zay glacier margin and not at Solda (where the average DM of Chironomidae scored 22 µg/ind), where the environmental harshness was much higher. Although our results are based on fewer observations and in different timings compared to Niedrist et al. (2018), they suggest a combined effect of habitat harshness and nutritional quality of biofilms. A boosted *Diamesa* body mass might be expected close to the glacier margins in the late stages of glacier retreat but not in the period of maximum glacial wastage, when the nutritional quality and biomass of epilithic biofilms are very low.

Taxa richness exhibited unimodal trends as a function of biomass, with highest richness values at the glacio-rhithral closing section and at the krenal sites, corresponding to intermediate biomass levels. Guo & Berry (1998) suggested that a hump-shaped relationship between biomass and taxa richness in environmental gradients results from a balance between decreasing environmental harshness (allowing biomass to increase) and increasing biomass which, beyond a certain peak, triggers mechanisms of competitive exclusion. Accordingly, the intermediate biomass values and high richness and Shannon diversity (among the highest in the catchment) of the Solda rock glacial stream might result from intermediate disturbance conditions (Connell, 1978): low competition coupled with intermediate habitat harshness, resulting from a combination between harsh (very low water temperature, high concentrations of trace elements) and benign (stable channels, clear waters, abundant organic detritus, favourable base chemistry) environmental conditions.

3.5.3 Paraglacial landscape and rock glaciers driving forces for invertebrate communities

Our study provides a first assessment of invertebrate community composition in streams fed by active rock glaciers, in comparison to communities influenced by different features of the paraglacial landscape, glaciers and groundwater.

Gradients in glacial influence primarily shape invertebrate communities. In agreement with other studies located in the European Alps (Brighenti et al., 2019a and references therein), we observed a dominance of *Diamesa* sp. in the proglacial sections, steep downstream gradients with the progressively increase of Orthocladiinae, other Diamesinae, Chironominae, Trichoptera, Plecoptera, Ephemeroptera and Diptera moving to lower kryal, glacio-rhithral and krenal stations. Overimposed to these gradients, the paraglacial complexity promotes high habitat variability: at Zay, where the presence of a diverse paragalacial landscape ameliorated the habitat conditions (Brighenti et al., 2019b), we observed a shift in the invertebrate abundance, biomass, and community composition below the lake/moraine, associated with the appearance of Trichoptera (*A. zerberus*) and *Pseudodiamesa* sp. The talus body had an influence as well, as it might have promoted the upstream dispersal and colonization by glacio-rhithral assemblages (*Diamesa* outnumbered by other Diamesinae, Orthocladiinae and Chironominae, high abundances of EPT taxa).

The results of our study provide the first evidence that rock glacial streams communities are clearly dissimilar from the upper kryal. However, in our study area, the two rock glacial streams strikingly differed from each other as a result of different local habitat setting and stable physical conditions (high channel stability, constant water level and water temperature). The Zay rock glacial stream has a distinctive highly lentic character (velocity <0.1 m s^{-1}), the stream bed is mainly composed of silt and flat boulders, and water is very cold and slightly turbid as it is influenced by glacial waters seepage. Solda rock glacial stream, on the other hand, has a clearly lotic character, streambed is almost devoid of fine sediment, and waters are very cold and clear. These habitat characteristics supported a more diverse and abundant community than at Zay; this community resembled those of krenal and glacio-rhithral sites yet with a higher share of *Diamesa* sp. and other Diamesinae. Krenal-like habitat conditions favoured the presence of a pool of taxa also detected in non-glacial stations, located 500 m elevation below and isolated by the highly turbid (up to 1200 NTU recorded) and unstable Solda glacier-fed stream (see Engel et al., 2019) along the only river pathway. In addition, the presence of permafrost provided very cold waters that favoured abundances of cold-adapted taxa (Diamesinae). Similar results were reported in a previous study from Lösch, Tolotti & Alber (2015) on five streams fed by active rock glaciers in South Tyrol (Eastern Alps), characterized by the presence of EPT taxa and Diptera, and by a high proportion of Diamesinae among all Chironomidae. These authors found, though at low densities, typical kryal specialist species that are commonly found in sections with very high glacial influence: *D. latitarsis*, *D. goetghebueri* and *D. steinboecki* (Rossaro, Montagna & Lencioni, 2016).

Unfortunately, we cannot draw any conclusion on the presence of such species in our study, given the low taxonomic precision of our identification.

Thawing rock glaciers often provide waters with high metal/metalloids concentrations (Colombo et al., 2018), with some ecological effect detected (see review in Brighenti et al., 2019a). For example, a strong control of pH and trace metal concentrations was found by Thies, Nickus, Tolotti, Tessadri & Krainer (2013) and, even in our study area, by Rotta et al. (2018), on the community composition of diatoms. The relatively high concentrations of trace elements (As, Sr, Ba) that we found in the Solda rock glacial waters did not seem to influence the invertebrate diversity, given the high abundance of Plecoptera and Ephemeroptera, which are considered as indicators of good water quality (Ghetti, 1995). The absence of these taxa in the Zay rock glacial stream might be due to the lotic conditions rather than the relatively high concentrations of U, that were high also downstream the confluence (lotic stream conditions), where the same taxa were present. We therefore suggest that, at these concentrations (e.g., As exceeding three times the EU standards for ecological quality), the effects of trace elements: i) might be absent/negligible for benthic invertebrates, ii) might be detectable at the level of organism (sub-lethal effect, see Ilyashuk, Ilyashuk, Psenner, Tessadri & Koinig, 2014) or iii) population (e.g. depressed abundance). According to Mayer-Pinto, Underwood, Tolhurst & Coleman (2010), it is difficult to estimate the effects of heavy metals on freshwater organisms, especially at relatively low concentrations in water and in natural settings. However, this topic should be further investigated, given the implications for metal bioaccumulation along the food web.

3.5.4 Biogeographical implications of rock glacial influence

Rock glacial streams not affected by glaciers represent benign habitats in a river network of harsh conditions. In fact, they share the same elevation with kryal streams but their physical conditions are strikingly milder and less variable (Brighenti et al., 2019b). For instance, the Solda "typical" rock glacial stream hosts a highly diverse invertebrate community that resemble those of non-glacial streams located in the lower part of the catchment. Due to their krenal-like character, rock glacial streams support extensive bryophyte mats that enhance the invertebrate biomass by trapping organic detritus and providing a refuge against predation/competition and a protection against the environmental harshness (e.g. UV penetration). All these factors seem to contribute to a very efficient ecosystem metabolism, as suggested by the fastest breakdown rates of organic matter estimated in our study. Rock glacial streams may therefore act as "stepping stones" under continued deglaciation, by speeding up the colonisation of the upper reaches of alpine river networks from non-glacial communities via drifting dispersal and oviposition from adult stages of insects. In our study area, an indicator of "drifting pressure" might be the unusual presence in the Solda glacial stream of *Rhabdyopterix alpina*, *Nemoura mortoni* and *Baetis alpinus* late instars in autumn (when ablation did not occur and habitat conditions were less harsh), just below the confluence with the rock glacial stream (data not shown). An indicator of "air dispersal pressure" might be the presence of a discrete number (52 ind. m^{-2}) of Plecoptera first instars in the upper kryal station located close (<500 m) to the rock glacier. Noteworthy, during summer ablation, Plecoptera were never recorded along the whole Solda stream.

Rock glacial streams may have a great conservation value, associated with another biogeographical implication in the latest deglaciation phases. In fact, If the presence of typically glacial *Diamesa* species will be confirmed by more accurate identification of our specimens and by other studies, these streams may be addressed as a long-lasting refuge for these cold-stenotherm species when glaciers will be disappeared, as permafrost ice thaw is much slower than that of the glacier ice (Haeberli, Schaub & Huggel, 2016) and may therefore maintain the exclusive habitat characteristics for longer. At the same time, even other taxa that are considered as "losers" according to their sensitivity to climate change (see e.g. Besacier-Montbertrand et al., 2019), that include rare, threatened and/or endemic species (e.g. *Drusus adustus*, endemic of the Eastern Alps, according to Waringer & Graf, 2011) may be favoured by the presence of rock glacial streams. In general, these habitats may therefore buffer the β-diversity loss predicted in deglaciating alpine areas in the long-term (e.g. Milner et al., 2017).

3.6 CONCLUSIONS

In glacierized alpine areas in the late stages of glacier retreat, the paraglacial features and the thawing permafrost increasingly shape the habitat conditions and biota of alpine streams by enhancing the landscape, geomorphological and riverscape diversity. We demonstrated, in the river system of our study area, the primary role exerted by bryophyte mats in boosting the organic detritus retention and the invertebrate production (H1), and provided insights on their role as multipliers of the habitat amelioration that alpine streams are experiencing because of glacier retreat. As such, bryophytes mediate the different patterns of abundance, biomass and mean body weight in different alpine stream types (H2). In the glacier forelands, the paraglacial landscape has a great influence on stream communities (H3): lake outlets and moraine baseflow enhance the invertebrate production and diversity across thorough habitat amelioration, and rock glacial streams that are still detaching from the glacial influence provide and additional source of biological diversity for tributaries, thanks to their different habitat and biological settings compared to glacier-fed streams. On the contrary, rock glacial habitats that are not influenced by glaciers host a distinct invertebrate community compared to the other stream types (H4), although partially comparable with non-glacial streams, and may represent biodiversity hotspots favouring the invertebrate diversity and productivity in deglaciating catchments. As such, they could represent stepping stones speeding-up the upstream colonisation of downstream communities following glacier retreat. At the same time, their conservation value as refuge areas for kryal specialists has still to be confirmed. As soon as the local human pressures are increasing in the European Alps, great efforts might be expected in the conservation and restoration of these habitats in the future glacier-free and stressors-rich landscapes, and we advocate for even greater efforts in preventing the spread of local but pervasive pressures that threaten alpine stream ecosystems.

CONCLUSIONS

This work contributes to the knowledge on the effects of deglaciation on alpine stream ecosystems. From the literature review and from the research undertaken in the study area, it emerges that the role of glaciers in shaping the habitat conditions and biotic communities is progressively fading in the Alps. In parallel, thawing rock glaciers and the other elements of the paraglacial landscape are increasingly emerging as drivers of the future trajectories of alpine river networks. A brief synthesis on the hydrological and ecological significance of rock glaciers, moraines, proglacial lakes and talus bodies in catchments experiencing glacier retreat is provided in Table I.

***Table I**. Influence of single glacial, paraglacial and periglacial features on the hydrology, habitat conditions and invertebrate communities along the river continuum of the study area. “x”= demonstrated effect, “P”= expected effect but not demonstrated in the present study, “?”= likely effect, but difficult to isolate it, “+”= positive influence,”-“= negative influence. NOTE: the biological effects of the proglacial lake and the seepage into the moraine debris could not be isolated and are therefore provided for both features.*

	Glaciers	Proglacial lake	Moraine	Talus body	Rock glaciers
Hydrology					
Meltwater contribution	x				P
Groundwater contribution			x	?	x
Habitat conditions					
Net sediment delivery	x				
Net sediment trapping		x	x		?
Water heating		x			
Water cooling	x		x		x
Physico-chemical buffering		x	x	x	
Solute export	x		x		x
Trace elements export	x				x
Invertebrate community					
Biomass	-	+	+	?	?
Abundance	-	+	+	?	?
Body mass	+	+	?		+
β-diversity	+				P
α-diversity	-	+	+	?	+

Thus, rock glaciers and the paraglacial landscape features enhance the riverscape diversity of alpine river networks and have a strong influence on their habitat conditions and benthic invertebrates. In the context of the general habitat amelioration caused by decreased glacier influence, major drivers of the invertebrate community patterns are represented by the interactions with the other communities in the channel (i.e. biofilm, aquatic bryophytes) and the linkages with the terrestrial system (i.e. allochthonous detritus). In particular, bryophyte mats enhance the storage of organic detritus in the channel, boost the invertebrate abundance and biomass and shape body size patterns in the channel. Given the increased contribution from the surrounding vegetation, and the increased storage capacity exerted by increasingly stable channels because of climate change and glacier retreat, organic detritus abundance is increasing in alpine river networks. Within this context, rock glacial streams may provide upstream sources for the spreading of aquatic bryophytes, speeding-up shifts in the communities and stream metabolism. This is a consequence of the "insularity" of rock glacial streams, at least for those non influenced by glacial waters, as demonstrated by benthic invertebrate communities that are similar to krenal and glacio-rhithral channels. Due to their biogeographical relevance as "stepping stones", streams fed by thawing rock glaciers might have a striking conservation value when glaciers vanish from the catchment. Thus, there is a pressing need of generalize knowledge and hypotheses through the investigation of other rock glacial streams from different areas in the Alps, in order to fully assess their ecological importance and inform nature conservation planning.

Rock glaciers are already considered as habitat of European concern and included as "*permanent glaciers"* in the Annex I of the Habitat Directive. Nevertheless, to comprise streams emerging from rock glaciers in the list of *priority habitats* (which according to the directive is the highest conservation status) would represent a courageous policy effort, that might protect them from the increasing local human pressures that alpine areas are experiencing, and enhance the protection of aquatic and terrestrial (Tampucci et al., 2017) organisms related to rock glaciers and glaciers, and therefore threated by alpine deglaciation.

Research perspectives

Several research perspectives arise from this work. In particular, the same research approaches applied to other high-mountain catchments might help to understand whether the relation patterns between habitat conditions and biota observed in Solda Valley could be extended to other mountain areas inside and outside the Alps, and to fully appreciate the magnitude and general validity of the outcomes. In particular, it would be very relevant to answer to these questions:

1. How widespread are rock glacial streams in the Alps? How many rock glaciers originate permanent outflows?
2. Do streams fed by thawing rock glaciers share common habitat conditions? If so, are there differences in habitat conditions and invertebrate communities between streams emerging from active, inactive and fossil rock glaciers?
3. How important are moraine debris and talus bodies in shaping habitat and biota of alpine river networks?
4. What is the contribution of solute export from thawing rock glaciers to the river networks downstream? How far this export can be distinguished downstream? In how many catchments can this phenomenon be detected? Is there any control exerted, besides by lithology, by other catchment-specific conditions?

Beyond these broad research perspectives, part of the large dataset collected was not included in the present dissertation because of the lack of time, and will be analysed in the next future. These forthcoming outcomes will be achievable thanks to the same multidisciplinary working group (involving experts in geology, hydrology and in the different aspects of freshwater ecology) that greatly improved the quality of the papers included in this dissertation. Tentative title and topic of the forthcoming outcomes are listed in the table below.

Table II. *Forthcoming research perspectives resulting from the additional data collected during the PhD 3-year field and laboratory activities.*

Authors	Topic	Title	Aims
Brighenti S., Tolotti M., Bruno M. C., Lencioni V., Bressan F., Vulcano C., Camin F.	Ecology	Characterisation of a rock glacial stream under a multitrophic approach	Analyse different communities (invertebrates, diatoms, bacteria) and the food webs of different alpine stream types (krenal, glacio-rhithral, kryal and rock glacial) to understand the emerging properties resulting from the community interactions and common/differing patterns in different communities and streams
Brighenti S., Engel M., Tolotti M., Bruno M. C., Bertoldi W., Comiti F.	Hydrology and hydrochemistry	Contrasting hydrochemical patterns of active rock glaciers	Understand the underlain reasons of the contrasting hydrochemistry in two active rock glaciers, and the differing responses of water temperature and electrical conductivity associated with precipitation events in the snow-free season
Tolotti M., Brighenti S., Bruno M. C., Camin F., Lami A., Mair W., Rose N., Giordani L.	Lake sediments, geochemistry, hydrochemistry, ecology	Lessons from the past: what future for alpine areas under deglaciation?	To reconstruct the influence of permafrost thaw and glacier retreat on the ecology of a high-mountain lake in the past millennia, in order to predict future ecosystem trajectories. Several chemical and biological proxies will be analysed to understand shifts in habitat and ecology of the lake associated with major climate changes occurred during the Holocene.
Tolotti M., Brighenti S., Bruno M. C., Cerasino L., Pindo M., Albanese D.	Microbial ecology	Microbiological communities of a deglaciating alpine area	Exploring seasonal evolution of bacterial communities in alpine river networks in relation with different water origin and environmental conditions, in order to understand possible future ecological implications within the context of alpine deglaciation
Tolotti M., Brighenti S., Bruno M. C., Cerasino L., Rotta F., Vulcano C.	Ecology	Diatom diversity in deglaciating alpine area	Investigating seasonal evolution of biodiversity, abundance and functionality of epilithic diatom communities of alpine river networks in relation with different water origin environmental conditions, in order to predict possible future ecological trajectories under progressive alpine deglaciation

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Supplementary material – S1

Supplementary S1, Chapter 3. Conversion factors for size-mass equations. Dry mass was obtained by applying the exponential equation DM= a Lb, where L is the body length (Méthot et al., 2012), a and b the conversion factors specific for each taxon.

Taxon	**a**	**b**	**reference**	**Taxon reference**	**notes**
Plecoptera juvenile	0.0049	2.562	Benke et al., 1999	Plecoptera	
Dictyogenus fontium	0.0067	2.695	Zwick & Zwick, 2010	*Dictyogenus fontium*	
Isoperla sp	0.0072	2.743	Giustini et al., 2008	*Isoperla grammatica*	
Protonemoura sp	0.0056	2.762	Benke et al., 1999	Nemouridae	
Nemoura sp	0.0019	3.588	Giustini et al., 2008	*Nemoura cinerea*	
Leuctra sp	0.0027	2.818	Giustini et al., 2008	*Leuctra* sp	
Rhabdiopteryx alpina	0.0072	2.655	Benke et al., 1999	Taeniopterigidae	
*Baetis alpinu*s	0.0100	2.550	Breitenmoser-Würsten & Sartori, 1995	*Baetis alpinus*	
Rhithrogena sp	0.0138	2.560	Breitenmoser-Würsten & Sartori, 1995	*Rhithrogena sp*	
Limnephilidae	0.0040	2.933	Benke et al., 1999	Limnephilidae	
Goeridae	0.0040	2.933	Benke et al., 1999	Goeridae	
Rhyacophilidae	0.0099	2.480	Benke et al., 1999	Rhyacophilidae	
Ceratopogonidae	0.0025	2.469	Benke et al., 1999	Ceratopogonidae	
Chironomidae	0.0018	2.617	Benke et al., 1999	Chironomidae	Other stations
Chironomidae	0.0021	2.803	Nolte, 1990	*Diamesa* sp	Only kryal
Chironomidae	0.0007	2.736	Nolte, 1990	*Micropsectra* sp	SRG: most specimens very slim
Blephariceridae	3.292	0.0067	Benke et al., 1999	Blephariceridae	
Dolichopodidae	0.0054	2.546	Benke et al., 1999	Empididae	Not found
Dixidae	0.0018	2.617	Benke et al., 1999	Chironomidae	Not found
Empididae	0.0054	2.546	Benke et al., 1999	Empididae	Not found
Limoniidae	0.0054	2.546	Benke et al., 1999	Empididae	Not found
Pediciidae	0.0054	2.546	Benke et al., 1999	Empididae	Not found
Muscidae	0.0054	2.546	Benke et al., 1999	Empididae	Not found
Psychodidae	0.0018	2.617	Benke et al., 1999	Chironomidae	Not found
Simuliidae	0.002	3.011	Benke et al., 1999	Simuliidae	
Thaumaleidae	0.0018	2.617	Benke et al., 1999	Chironomidae	Not found
Tipulidae	0.0054	2.546	Benke et al., 1999	Empidiidae	Not found
Elminthidae	0.0074	2.879	Benke et al., 1999	Elminthidae	
Gyraulus sp	0.9608	2.650	Mèthot et al., 2012	Planorbidae	
Lumbriculidae	0.1075	1.540	Mèthot et al., 2012	Oligochaeta	
Enchytraeidae	0.1075	1.540	Mèthot et al., 2012	Oligochaeta	
Haplotaxidae	0.1075	1.540	Mèthot et al., 2012	Oligochaeta	
Naididae	0.1075	1.540	Mèthot et al., 2012	Oligochaeta	
Crenobia	0.0082	2.168	Benke et al., 1999	Turbellaria	

Supplementary material – S2

Supplementary S2, Chapter 3. List of taxa abundances. For each station and taxon, abundances (ind. m-2) for each microhabitat (min=inorganic substrate, mos= bryophyte mats, mix= microhabitat replicates (min, mos) pooled in the same sample, san= sand/silt, bou= boulders, Hyd= Hydrurus foetidus) are provided. The number of Surber replicates is provided for each microhabitat in the sampling (five total replicates).

June 2017 station	**S1**	**S2**	**Z3**	**Z5**	**Z7**	**Z7**	**ZKN**	**ZKN**	**SKN**	**ZRG**	**ZRG**	**ZRG**	**SRG**	**SRG**
microhabitat	min	min	mix	min	min	mos	min	mos	mix	san	bou	mos	min	mos
n° replicates	5	5	5	5	4	1	3	2	5	2	2	1	3	2
TURBELLARIA														
Crenobia alpina (Dana, 1766)	0	0	0	0	0	0	0	0	32	0	0	0	0	0
NEMATODA	4	0	68	1056	0	0	0	0	1328	240	0	120	0	0
OLIGOCHAETA														
Lumbriculidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Haplotaxidae	0	0	0	16	0	0	0	80	0	0	20	0	0	10
Enchytraeidae	0	0	12	112	40	160	107	320	48	20	230	480	67	250
Naididae	0	0	0	0	10020	3040	0	0	0	0	0	0	0	0
TARDIGRADA	0	0	0	96	0	160	0	0	0	0	10	0	0	160
HYDRACHNIDIA	8	4	1424	48	240	480	1653	4320	432	0	0	20	7	100
CRUSTACEA														
Ostracoda	0	0	0	0	0	0	293	240	0	0	10	0	0	0
Copepoda	0	0	0	96	140	800	4000	5680	0	0	180	0	0	0
COLLEMBOLA	16	20	0	96	0	0	0	0	48	0	0	0	27	240
EPHEMEROPTERA														
Heptagenidae														
Rhithrogena juv	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhithrogena sp.	0	0	0	0	380	0	80	320	32	0	0	0	13	0
Rhitrogena loyolaea Navàs, 1922	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhitrogena semicolorata - Gr.	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Baetidae														
Baetis alpinus(Pictet, 1834)	0	0	0	0	2500	6080	5520	12560	240	0	0	0	33	60
PLECOPTERA														
Plecoptera juv	0	0	0	0	0	160	453	0	0	0	0	0	107	0
Perlodidae														
Dictyogenus fontium(Ris, 1896)	0	4	0	0	240	0	53	480	0	0	0	0	53	80
Isoperla cf. *rivulorum (Pictet, 1841)*	0	0	0	0	0	0	267	480	0	0	0	0	7	80
Chloroperlidae														
Chloroperla susemicheli Zwick, 1967	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Taeniopterygidae														
Rhabdiopteryx alpina Kühtreiber, 1934	0	0	0	0	40	0	0	0	0	0	0	0	47	0
Nemouridae														
Protonemoura sp	0	0	0	0	20	0	35	40	24	0	0	0	0	0

June 2017 station	**S1**	**S2**	**Z3**	**Z5**	**Z7**	**Z7**	**ZKN**	**ZKN**	**SKN**	**ZRG**	**ZRG**	**ZRG**	**SRG**	**SRG**
microhabitat	min	min	mix	min	min	mos	min	mos	mix	san	bou	mos	min	mos
n° replicates	5	5	5	5	4	1	3	2	5	2	2	1	3	2
Protonemoura brevistyla (Ris, 1902)	0	0	0	0	60	0	267	880	0	0	0	0	0	0
Protonemoura nitida (Pictet, 1835)	0	0	0	0	120	0	3013	7680	48	0	0	0	0	0
Protonemoura cf. *lateralis* (Pictet, 1835)	0	0	0	0	40	160	0	0	0	0	0	0	0	0
Protonemura nimborum (Ris, 1902)	0	0	0	0	0	0	320	1040	304	0	0	0	0	0
Proronemura cf. *caprai* (Aubert, 1954)	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nemoura mortoni (Ris, 1902)	0	0	0	0	1660	160	240	480	224	0	0	0	240	750
Leuctridae	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Leuctridae/capnidae sp	0	0	0	0	40	0	4	40	0	0	0	0	47	13
Leuctra major Brink, 1949	0	0	0	0	240	0	80	0	0	0	0	0	0	0
Leuctra rosinae Kempny, 1900	0	0	0	0	0	0	27	160	320	0	0	0	260	770
Leuctra cf. *teriolensis* Kempny, 1900	0	0	0	0	60	0	0	0	0	0	0	0	0	0
Leuctra braueri Kempny, 1898	0	0	0	0	0	0	0	0	0	0	0	0	0	0
THYSANOPTERA	0	0	0	0	0	0	0	0	0	0	0	0	0	0
TRICHOPTERA														
Rhyacophilidae														
Rhyacophila intermedia McLachlan, 1868	0	0	0	0	0	0	0	0	16	0	0	0	0	0
Rhyacophila pubescens Pictet, 1834	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Limpnephilidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Drusus monticola (McLachlan, 1867)	0	0	0	0	0	0	27	0	0	0	0	0	33	430
Drusus cf. *adustus* (McLachlan, 1867)	0	0	0	0	600	160	0	80	0	0	0	0	1333	2800
Acrophylax zerberus Brauer, 1867	0	0	0	80	20	0	27	80	0	100	30	220	0	0
Micropterna lateralis (Stephens, 1837)	0	0	0	0	0	0	27	240	0	0	0	0	0	0
Drusus discolor (Rambur, 1842)	0	0	0	0	0	0	0	0	64	0	0	0	0	0
Goeridae														
Lithax niger (Hagen, 1859)	0	0	0	0	0	0	27	160	0	0	0	0	0	0
COLEOPTERA														
Coleoptera sp	0	0	0	0	0	0	0	0	0	0	0	60	0	0
Elminthidae	0	0	0	0	0	0	0	0	0	0	0	0	7	0
DIPTERA	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tipulidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Limoniidae	0	12	0	16	100	0	107	240	32	0	0	0	13	0
Pediciidae	0	0	0	0	20	0	0	0	16	0	0	0	0	0
Simuliidae	0	0	4	0	40	0	373	1440	48	0	0	0	0	0
Ceratopogonidae	0	0	4	0	0	0	0	0	0	0	0	0	0	0

June 2017	station	**S1**	**S2**	**Z3**	**Z5**	**Z7**	**Z7**	**ZKN**	**ZKN**	**SKN**	**ZRG**	**ZRG**	**ZRG**	**SRG**	**SRG**
	microhabitat	min	min	mix	min	min	mos	min	mos	mix	san	bou	mos	min	mos
	n° replicates	5	5	5	5	4	1	3	2	5	2	2	1	3	2
Chironomidae															
Diamesinae															
Diamesa sp		64	360	68	7952	629	707	2518	2080	0	100	7950	0	533	18400
Pseudodiamesa sp		0	0	0	544	0	0	0	0	0	10	0	20	0	0
Pseudokiefferiella sp		0	0	0	0	2507	4952	0	0	0	0	0	0	13	13590
Boreoheptagyia sp		0	0	0	0	0	0	0	0	0	0	0	0	0	0
Orthocladiinae		0	100	8	544	30529	106113	88982	135200	10928	2000	3790	16380	4747	39960
Chironominae		0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tanytarsini		0	0	0	0	975	707	10073	3120	213	0	0	0	0	0
Chironomini		0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tanypodinae		0	0	0	0	0	0	0	0	107	0	0	0	0	0
Psychodidae		0	0	0	0	0	0	27	0	0	0	0	0	0	0
Blephariceridae		0	0	0	0	0	0	0	0	0	0	0	0	0	0
Empididae		8	0	4	16	60	0	0	80	0	0	0	0	20	20
Dolichopodidae		0	0	0	0	20	0	0	0	0	0	0	0	0	0
Muscidae (*Lispe* sp)		0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dixidae		0	0	0	0	0	0	0	0	16	0	0	0	0	0
Thaumaleidae		0	0	0	0	0	0	0	80	0	0	0	0	0	0
MOLLUSCA - Planorbidae															
Gyraulus sp		0	0	0	0	0	0	0	0	0	0	0	0	0	0

August 2017	station	**S1**	**S2**	**Z1**	**Z3**	**Z4**	**Z4**	**Z5**	**Z7**	**Z7**	**ZKN**	**ZKN**	**SKN**	**SKN**	**ZRG**	**ZRG**	**ZRG**	**SRG**	**SRG**
	microhabitat	min	min	min	min	min	moss	min	min	mos	min	mos	min	mos	san	mos	min	min	mos
	n° replicates	5	5	5	5	4	1	5	3	2	4	1	4	1	2	1	2	3	2
TURBELLARIA																			
Crenobia alpina (Dana, 1766)		0	0	0	0	0	0	0	0	0	0	0	0	480	0	0	0	0	0
NEMATODA		8	0	0	60	300	1280	5600	8213	11800	5080	2800	400	3840	81840	30720	8080	1067	800
OLIGOCHAETA																			
Lumbriculidae		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Haplotaxidae		0	0	0	0	40	0	32	160	0	0	0	0	160	0	0	0	27	0
Enchytraeidae		0	0	0	0	20	320	80	533	400	2080	240	0	480	160	5760	5120	800	160
Naididae		0	0	0	0	0	0	0	4747	4360	0	0	0	0	0	0	0	0	80
TARDIGRADA		56	16	0	0	0	320	0	107	960	0	0	0	0	1840	19360	8320	133	320
HYDRACHNIDIA		8	0	0	4	0	0	0	533	600	400	720	360	4640	0	1120	400	53	0
CRUSTACEA																			
Ostracoda		0	0	0	4	0	0	0	53	0	200	160	40	0	0	0	0	0	0
Copepoda		88	48	0	20	0	0	576	587	1040	2520	5760	1160	320	0	68160	2800	107	0
COLLEMBOLA		0	0	48	92	20	1760	512	107	0	0	0	200	0	0	320	0	53	80
EPHEMEROPTERA																			
Heptagenidae																			
Rhithrogena juv		0	0	0	0	0	0	0	693	0	0	0	368	0	0	0	0	0	0
Rhithrogena sp.		0	0	0	0	0	0	0	213	0	0	0	240	160	0	0	0	0	0
Rhitrogena loyolaea Navàs, 1922		0	0	0	0	0	0	0	0	0	600	0	480	0	0	0	0	0	0
Rhitrogena semicolorata - Gr.		0	0	0	0	0	0	0	0	0	80	0	120	0	0	0	0	0	0
Baetidae																			
Baetis alpinus(Pictet, 1834)		0	0	0	0	0	0	176	15147	6240	760	1040	520	4960	0	0	0	293	320
PLECOPTERA																			
Plecoptera juv		0	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Perlodidae																			
Dictyogenus fontium(Ris, 1896)		0	0	0	0	0	0	16	640	0	160	0	40	0	0	0	0	53	240
Isoperla cf. *rivulorum (Pictet, 1841)*		0	0	0	0	0	0	0	0	0	200	160	0	0	0	0	0	0	0
Chloroperlidae																			
Chloroperla susemicheli Zwick, 1967		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Taeniopterygidae																			
Rhabdiopteryx alpina Kühtreiber, 1934		0	8	0	0	0	0	0	160	0	0	0	0	0	0	0	0	2107	0
Nemouridae																			
Protonemoura sp		0	0	0	0	0	0	0	25	0	40	80	20	40	0	0	0	0	0
Protonemoura brevistyla (Ris, 1902)		0	0	0	0	0	0	0	107	40	80	160	0	480	0	0	0	0	0

August 2017	station	**S1**	**S2**	**Z1**	**Z3**	**Z4**	**Z4**	**Z5**	**Z7**	**Z7**	**ZKN**	**ZKN**	**SKN**	**SKN**	**ZRG**	**ZRG**	**ZRG**	**SRG**	**SRG**
	microhabitat	min	min	min	min	min	moss	min	min	mos	min	mos	min	mos	san	mos	min	min	mos
	n° replicates	5	5	5	5	4	1	5	3	2	4	1	4	1	2	1	2	3	2
Protonemoura nitida (Pictet, 1835)		0	0	0	0	0	0	16	267	0	1000	1680	160	800	0	0	0	0	0
Protonemoura cf. *lateralis* (Pictet, 1835)		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Protonemura nimborum (Ris, 1902)		0	0	0	0	0	0	0	0	0	0	160	0	160	0	0	0	0	0
Proronemura cf. *caprai* (Aubert, 1954)		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nemoura mortoni (Ris, 1902)		0	0	0	0	0	0	0	693	40	200	800	240	1760	0	0	0	0	80
Leuctridae		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Leuctridae/capnidae sp		0	0	0	0	0	0	0	25	0	40	40	40	0	0	0	0	53	27
Leuctra major Brink, 1949		0	0	0	0	0	0	0	53	0	80	0	0	0	0	0	0	0	0
Leuctra rosinae Kempny, 1900		0	0	0	0	0	0	0	0	0	40	160	1120	0	0	0	0	1013	240
Leuctra cf. *teriolensis* Kempny, 1900		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Leuctra braueri Kempny, 1898		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
THYSANOPTERA		8	0	4	0	0	0	16	0	80	40	80	0	0	0	160	0	0	0
TRICHOPTERA																			
Rhyacophilidae																			
Rhyacophila intermedia McLachlan, 1868		0	0	0	0	0	0	0	0	0	0	0	0	160	0	0	0	0	0
Rhyacophila pubescens Pictet, 1834		0	0	0	0	0	0	0	0	0	0	0	0	320	0	0	0	0	0
Limpnephilidae		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Drusus monticola (McLachlan, 1867)		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	53	400
Drusus cf. *adustus* (McLachlan, 1867)		0	0	0	0	0	0	16	747	40	40	0	40	0	0	0	0	1680	3600
Acrophylax zerberus Brauer, 1867		0	0	0	0	220	0	80	0	0	0	0	0	0	320	480	80	0	0
Micropterna lateralis (Stephens, 1837)		0	0	0	0	0	0	0	0	0	80	0	40	0	0	0	0	0	0
Drusus discolor (Rambur, 1842)		0	0	0	0	0	0	0	0	0	0	0	0	320	0	0	0	0	0
Goeridae																			
Lithax niger (Hagen, 1859)		0	0	0	0	0	0	0	0	0	160	80	0	0	0	0	0	0	0
COLEOPTERA																			
Coleoptera sp		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Elminthidae		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
DIPTERA		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tipulidae		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Limoniidae		0	0	0	20	0	0	0	0	40	120	80	40	0	0	160	0	53	80
Pediciidae		0	0	0	0	0	0	0	107	0	40	0	0	0	0	0	80	107	80
Simuliidae		0	0	0	0	0	0	16	0	40	40	0	40	0	0	0	0	0	0
Ceratopogonidae		0	0	0	0	0	0	0	0	0	80	0	240	0	0	0	0	27	80
Chironomidae																			

August 2017	station	**S1**	**S2**	**Z1**	**Z3**	**Z4**	**Z4**	**Z5**	**Z7**	**Z7**	**ZKN**	**ZKN**	**SKN**	**SKN**	**ZRG**	**ZRG**	**ZRG**	**SRG**	**SRG**
	microhabitat	min	min	min	min	min	moss	min	min	mos	min	mos	min	mos	san	mos	min	min	mos
	n° replicates	5	5	5	5	4	1	5	3	2	4	1	4	1	2	1	2	3	2
Diamesinae																			
Diamesa sp		8	1568	188	1260	7800	19840	3664	14313	563	403	936	186	0	0	0	0	2453	8480
Pseudodiamesa sp		0	0	0	0	0	1920	704	0	0	0	0	0	0	3120	2880	3280	0	0
Pseudokiefferiella sp		0	0	0	0	0	0	0	3340	11258	0	0	0	0	0	0	0	160	3360
Boreoheptagyia sp		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Orthocladiinae		0	40	0	92	280	3200	192	95420	73175	20129	35083	5092	98560	640	3360	0	4427	22160
Chironominae		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tanytarsini		0	0	0	0	0	0	0	954	844	268	702	1118	2880	0	640	0	0	0
Chironomini		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tanypodinae		0	0	0	0	0	0	0	0	0	0	0	124	0	0	0	0	0	0
Psychodidae		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Blephariceridae		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Empididae		0	8	0	0	0	0	0	160	80	0	0	0	0	0	0	0	80	80
Dolichopodidae		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Muscidae *(Lispe* sp)		0	0	0	0	20	0	0	53	0	0	0	0	0	0	0	0	0	0
Dixidae		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thaumaleidae		0	0	0	0	0	0	0	0	0	0	0	120	0	0	0	0	0	0
MOLLUSCA - Planorbidae																			
Gyraulus sp		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

September 2017 station	**S1**	**S2**	**Z1**	**Z1**	**Z3**	**Z4**	**Z5**	**Z7**	**Z7**	**ZKN**	**ZKN**	**SKN**	**SKN**	**ZRG**	**ZRG**	**SRG**	**SRG**
microhabitat	min	min	min	Hyd	min	min	min	min	mos	min	mos	min	mos	bou	san	min	mos
n° replicates	5	5	4	1	5	5	5	3	2	4	1	4	1	1	4	3	2
TURBELLARIA																	
Crenobia alpina (Dana, 1766)	0	0	0	0	0	0	0	0	0	0	80	940	160	0	0	0	0
NEMATODA	20	4	0	0	0	0	5616	53	0	360	160	80	3360	1100	7300	0	0
OLIGOCHAETA																	
Lumbriculidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Haplotaxidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	27	0
Enchytraeidae	4	0	0	0	0	32	928	373	4640	680	320	0	480	80	40	80	240
Naididae	0	0	0	0	0	0	0	4480	13600	0	0	0	0	0	0	0	0
TARDIGRADA	4	0	0	0	0	0	16	0	80	0	80	0	480	80	300	0	400
HYDRACHNIDIA	4	4	0	40	0	0	16	160	480	720	3840	340	12480	0	0	27	80
CRUSTACEA																	
Ostracoda	0	0	0	0	0	0	0	0	0	360	160	0	0	0	0	0	0
Copepoda	232	4	0	0	0	0	256	53	320	3120	7920	6860	40000	67900	2620	53	480
COLLEMBOLA	4	0	60	0	80	0	16	107	0	0	80	60	640	60	0	0	160
EPHEMEROPTERA																	
Heptagenidae																	
Rhithrogena juv	0	0	0	0	0	0	0	0	0	36	0	0	0	0	0	0	0
Rhithrogena sp.	0	0	0	0	0	16	0	0	0	0	0	60	0	0	0	27	0
Rhitrogena loyolaea Navàs, 1922	0	0	0	0	0	0	0	0	0	280	0	140	0	0	0	0	0
Rhitrogena semicolorata - Gr.	0	0	0	0	0	0	0	0	0	80	0	60	0	0	0	0	0
Baetidae																	
Baetis alpinus(Pictet, 1834)	0	0	0	0	0	16	224	15787	47040	800	4000	800	3520	0	0	187	880
PLECOPTERA																	
Plecoptera juv	4	0	0	0	0	0	0	160	0	0	240	7080	2560	0	0	0	0
Perlodidae																	
Dictyogenus fontium(Ris, 1896)	0	0	0	0	0	16	0	320	80	160	480	20	160	0	0	107	640
Isoperla cf. *rivulorum (Pictet, 1841)*	0	0	0	0	0	0	0	0	0	120	480	0	480	0	0	27	240
Chloroperlidae																	
Chloroperla susemicheli Zwick, 1967	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Taeniopterygidae																	
Rhabdiopteryx alpina Kühtreiber, 1934	0	0	0	0	0	0	0	0	0	0	0	60	160	0	0	2027	0
Nemouridae																	
Protonemoura sp	0	0	0	0	0	0	0	27	80	40	80	80	160	0	0	0	0
Protonemoura brevistyla (Ris, 1902)	0	0	0	0	0	0	0	0	160	80	160	160	480	0	0	0	0

September 2017 station	**S1**	**S2**	**Z1**	**Z1**	**Z3**	**Z4**	**Z5**	**Z7**	**Z7**	**ZKN**	**ZKN**	**SKN**	**SKN**	**ZRG**	**ZRG**	**SRG**	**SRG**
microhabitat	min	min	min	Hyd	min	min	min	min	mos	min	mos	min	mos	bou	san	min	mos
n° replicates	5	5	4	1	5	5	5	3	2	4	1	4	1	1	4	3	2
Protonemoura nitida (Pictet, 1835)	0	0	0	0	0	0	0	107	80	1480	5440	160	1120	0	0	0	0
Protonemoura cf. *lateralis* (Pictet, 1835)	0	0	0	0	0	0	0	0	160	0	0	0	0	0	0	0	0
Protonemura nimborum (Ris, 1902)	0	0	0	0	0	0	0	0	0	0	0	340	2720	0	0	0	0
Proronemura cf. *caprai* (Aubert, 1954)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nemoura mortoni (Ris, 1902)	0	52	0	0	0	16	0	1600	1440	320	480	400	4160	0	0	3573	1680
Leuctridae	0	0	0	0	0	0	0	53	80	0	0	3080	0	0	0	0	0
Leuctridae/capnidae sp	0	0	0	0	0	0	0	53	80	0	0	3080	0	0	0	0	0
Leuctra major Brink, 1949	0	0	0	0	0	0	0	53	0	320	160	0	0	0	0	0	0
Leuctra rosinae Kempny, 1900	0	0	0	0	0	0	0	0	0	400	640	1060	6880	0	0	1787	1360
Leuctra cf. *teriolensis* Kempny, 1900	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Leuctra braueri Kempny, 1898	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
THYSANOPTERA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
TRICHOPTERA																	
Rhyacophilidae																	
Rhyacophila intermedia McLachlan, 1868	0	0	0	0	0	0	0	0	0	0	80	0	0	0	0	0	0
Rhyacophila pubescens Pictet, 1834	0	0	0	0	0	0	0	0	0	0	0	40	0	0	0	0	0
Limpnephilidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Drusus monticola (McLachlan, 1867)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	240	0
Drusus cf. *adustus* (McLachlan, 1867)	0	0	0	0	0	0	16	800	1040	120	0	100	320	0	0	1093	240
Acrophylax zerberus Brauer, 1867	0	0	0	0	0	256	240	107	0	200	1440	0	0	60	80	0	0
Micropterna lateralis (Stephens, 1837)	0	0	0	0	0	0	0	0	0	200	0	0	320	0	0	0	0
Drusus discolor (Rambur, 1842)	0	0	0	0	0	0	0	0	0	0	0	120	160	0	0	0	0
Goeridae																	
Lithax niger (Hagen, 1859)	0	0	0	0	0	0	0	0	0	760	80	0	0	0	0	0	0
COLEOPTERA																	
Coleoptera sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Elminthidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
DIPTERA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tipulidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Limoniidae	0	68	0	0	0	16	0	0	0	80	0	0	0	0	0	187	160
Pediciidae	0	0	0	0	0	0	32	0	0	0	160	60	0	0	0	0	0
Simuliidae	0	0	0	0	0	0	0	53	0	0	400	80	0	0	0	0	0
Ceratopogonidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chironomidae																	

September 2017	station	**S1**	**S2**	**Z1**	**Z1**	**Z3**	**Z4**	**Z5**	**Z7**	**Z7**	**ZKN**	**ZKN**	**SKN**	**SKN**	**ZRG**	**ZRG**	**SRG**	**SRG**
	microhabitat	min	min	min	Hyd	min	min	min	min	mos	min	mos	min	mos	bou	san	min	mos
	n° replicates	5	5	4	1	5	5	5	3	2	4	1	4	1	1	4	3	2
Diamesinae																		
Diamesa sp		20	784	1610	6800	920	1808	320	587	0	420	251	143	0	0	0	133	880
Pseudodiamesa sp		0	0	0	0	0	48	224	160	0	0	0	0	0	1000	440	0	0
Pseudokiefferiella sp		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3600
Boreoheptagyia sp		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Orthocladiinae		0	20	0	0	0	768	272	16533	108480	21019	38859	5041	54400	1500	740	5653	80080
Chironominae		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tanytarsini		0	0	0	0	0	0	0	267	0	561	251	761	0	0	0	0	240
Chironomini		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tanypodinae		0	0	0	0	0	0	0	0	0	0	0	95	0	0	0	0	0
Psychodidae		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Blephariceridae		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Empididae		0	32	0	0	0	48	0	0	80	0	0	0	0	0	0	27	320
Dolichopodidae		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Muscidae *(Lispe* sp)		0	0	0	0	0	0	0	107	400	0	0	0	480	0	0	53	0
Dixidae		0	0	0	0	0	0	0	0	0	0	0	40	160	0	0	0	0
Thaumaleidae		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MOLLUSCA - Planorbidae																		
Gyraulus sp		0	0	0	0	0	0	0	0	0	40	80	0	0	0	0	0	0

	June 2018										**August 2018**					
	Z1	**Z3**	**Z3**	**Z4**	**Z4**	**Z5**	**Z7**	**Z7**	**Z12**	**Z12**	**Z3**	**Z3**	**Z4**	**Z5**	**Z12**	**Z12**
microhabitat	min	min	mos	min	Hyd	min	min	mos	min	mos	min	mos	min	min	min	mos
n° replicates	5	4	1	4	1	5	3	2	3	2	4	1	5	5	4	1
TURBELLARIA																
Crenobia alpina (Dana, 1766)	0	0	0	0	0	0	0	0	20	0	0	0	0	0	0	0
NEMATODA	0	0	800	200	0	1120	427	2400	2400	3200	50	0	0	160	2000	1040
OLIGOCHAETA																
Lumbriculidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Haplotaxidae	0	0	0	0	0	16	0	320	0	0	0	0	0	0	0	0
Enchytraeidae	0	0	0	20	0	176	533	1360	360	1920	20	0	0	32	180	320
Naididae	0	0	0	0	0	0	7200	16000	0	0	0	0	0	0	0	0
TARDIGRADA	0	0	160	0	0	0	0	240	20	720	0	0	0	0	0	0
HYDRACHNIDIA	0	0	0	60	0	0	0	400	20	160	20	0	0	0	80	0
CRUSTACEA																
Ostracoda	0	0	0	0	0	496	0	0	180	160	0	0	0	32	660	80
Copepoda	0	0	0	20	0	256	80	160	60	0	60	0	0	32	0	80
COLLEMBOLA	8	0	0	40	0	16	0	0	0	0	20	0	0	32	60	320
EPHEMEROPTERA																
Heptagenidae																
Rhithrogena juv	0	0	0	0	0	0	0	0	40	0	0	0	0	0	0	0
Rhithrogena sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhitrogena loyolaea Navàs, 1922	0	0	0	0	0	0	80	0	60	0	0	0	20	16	60	0
Rhitrogena semicolorata - Gr.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Baetidae																
Baetis alpinus(Pictet, 1834)	0	0	0	0	0	0	987	2000	1100	1120	0	0	0	16	920	720
PLECOPTERA																
Plecoptera juv	0	0	0	0	0	0	0	0	580	720	0	0	0	0	60	2000
Perlodidae																
Dictyogenus fontium(Ris, 1896)	0	0	0	0	0	0	27	0	100	0	0	0	0	64	1140	3680
Isoperla cf. *rivulorum (Pictet, 1841)*	0	0	0	0	0	0	0	0	580	720	0	0	0	0	100	640
Chloroperlidae																
Chloroperla susemicheli Zwick, 1967	0	0	0	0	0	0	0	0	0	0	0	0	0	0	20	0
Taeniopterygidae																
Rhabdiopteryx alpina Kühtreiber, 1934	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nemouridae																
Protonemoura sp	0	0	0	20	0	0	0	0	40	80	0	0	0	0	100	80

	June 2018										August 2018					
	Z1	**Z3**	**Z3**	**Z4**	**Z4**	**Z5**	**Z7**	**Z7**	**Z12**	**Z12**	**Z3**	**Z3**	**Z4**	**Z5**	**Z12**	**Z12**
microhabitat	min	min	mos	min	Hyd	min	min	mos	min	mos	min	mos	min	min	min	mos
n° replicates	5	4	1	4	1	5	3	2	3	2	4	1	5	5	4	1
Protonemoura brevistyla (Ris, 1902)	0	0	0	0	0	0	0	0	80	0	0	0	0	0	20	240
Protonemoura nitida (Pictet, 1835)	0	0	0	0	0	0	53	0	100	800	0	0	0	0	40	0
Protonemoura cf. *lateralis* (Pictet, 1835)	0	0	0	0	0	16	80	640	0	1280	0	0	0	16	20	240
Protonemura nimborum (Ris, 1902)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Proronemura cf. *caprai* (Aubert, 1954)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	20	0
Nemoura mortoni (Ris, 1902)	0	0	0	0	0	0	27	0	220	240	0	0	0	0	300	0
Leuctridae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	80	0
Leuctridae/capnidae sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	80	0
Leuctra major Brink, 1949	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Leuctra rosinae Kempny, 1900	0	0	0	0	0	0	0	0	100	80	0	0	0	0	40	0
Leuctra cf. *teriolensis* Kempny, 1900	0	0	0	0	0	0	0	0	0	80	0	0	0	0	0	0
Leuctra braueri Kempny, 1898	0	0	0	0	0	0	0	0	40	0	0	0	0	0	40	0
THYSANOPTERA	0	0	0	400	0	0	0	0	0	0	20	0	0	0	20	0
TRICHOPTERA																
Rhyacophilidae																
Rhyacophila intermedia McLachlan, 1868	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhyacophila pubescens Pictet, 1834	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Limpnephilidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Drusus monticola (McLachlan, 1867)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Drusus cf. *adustus* (McLachlan, 1867)	0	0	0	0	0	0	53	0	0	0	0	0	40	0	0	0
Acrophylax zerberus Brauer, 1867	0	0	0	120	2080	336	80	560	60	0	0	0	240	208	20	80
Micropterna lateralis (Stephens, 1837)	0	0	0	0	0	0	0	0	40	400	0	0	0	0	0	0
Drusus discolor (Rambur, 1842)	0	0	0	0	0	0	0	0	0	9600	0	0	0	0	1140	4400
Goeridae																
Lithax niger (Hagen, 1859)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
COLEOPTERA																
Coleoptera sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Elminthidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
DIPTERA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tipulidae	0	0	0	20	0	0	0	0	0	0	0	0	0	0	0	0
Limoniidae	0	0	0	0	0	0	0	0	0	0	10	0	0	0	80	0
Pediciidae	0	0	0	0	0	0	0	0	20	0	0	0	0	0	0	0
Simuliidae	0	0	0	0	0	16	0	0	720	6080	0	0	0	0	100	640

	June 2018										August 2018					
	Z1	**Z3**	**Z3**	**Z4**	**Z4**	**Z5**	**Z7**	**Z7**	**Z12**	**Z12**	**Z3**	**Z3**	**Z4**	**Z5**	**Z12**	**Z12**
microhabitat	min	min	mos	min	Hyd	min	min	mos	min	mos	min	mos	min	min	min	mos
n° replicates	5	4	1	4	1	5	3	2	3	2	4	1	5	5	4	1
Ceratopogonidae	0	0	0	0	0	0	0	0	0	0	10	0	0	0	0	0
Chironomidae																
Diamesinae																
Diamesa sp	152	280	1920	80360	97600	1600	3793	0	462	0	4490	19680	2240	96	0	0
Pseudodiamesa sp	0	0	0	0	0	0	0	0	0	0	0	0	0	128	0	0
Pseudokiefferiella sp	0	0	0	0	0	0	1517	21718	346	17488	0	0	0	0	99	6240
Boreoheptagyia sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Orthocladiinae	0	20	3360	10040	0	112	9861	65154	1269	41972	470	0	60	1120	8903	57600
Chironominae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tanytarsini	0	0	0	0	0	0	455	1448	20	720	0	0	0	0	198	0
Chironomini	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tanypodinae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Psychodidae	0	0	0	0	0	0	0	0	0	160	0	0	0	0	0	0
Blephariceridae	0	0	0	0	0	0	0	0	20	0	0	0	0	0	0	0
Empididae	0	0	0	0	0	0	0	80	0	0	0	0	0	0	60	0
Dolichopodidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Muscidae *(Lispe* sp)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dixidae	0	0	0	0	0	0	0	0	20	0	0	0	0	0	0	0
Thaumaleidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MOLLUSCA - Planorbidae																
Gyraulus sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

September 2018 station	**Z12**	**Z12**	**ZRG**	**ZRG**	**SRG**	**SRG**
microhabitat	min	mos	min	san	min	mos
n° replicates	4	1	3	2	3	2
TURBELLARIA						
Crenobia alpina (Dana, 1766)	0	0	0	0	0	0
NEMATODA	80	1600	0	0	480	480
OLIGOCHAETA						
Lumbriculidae	0	0	0	0	0	0
Haplotaxidae	0	0	0	0	0	80
Enchytraeidae	240	160	0	160	160	320
Naididae	0	0	0	0	0	0
TARDIGRADA	0	80	0	0	0	240
HYDRACHNIDIA	60	240	0	240	53	400
CRUSTACEA						
Ostracoda	180	240	0	0	0	0
Copepoda	0	400	480	0	0	80
COLLEMBOLA	0	0	0	0	0	160
EPHEMEROPTERA						
Heptagenidae						
Rhithrogena juv	0	0	0	0	0	0
Rhithrogena sp.	0	0	0	0	0	0
Rhitrogena loyolaea Navàs, 1922	180	0	0	0	53	0
Rhitrogena semicolorata - Gr.	0	0	0	0	0	0
Baetidae						
Baetis alpinus(Pictet, 1834)	80	2400	0	0	160	720
PLECOPTERA						
Plecoptera juv	80	400	0	0	0	0
Perlodidae						
Dictyogenus fontium(Ris, 1896)	1420	160	0	0	1760	80
Isoperla cf. *rivulorum (Pictet, 1841)*	60	1600	0	0	107	0
Chloroperlidae						
Chloroperla susemicheli Zwick, 1967	0	80	0	0	0	0
Taeniopterygidae						
Rhabdiopteryx alpina Kühtreiber, 1934	0	0	0	0	2027	80
Nemouridae						
Protonemoura sp	0	160	0	0	0	0
Protonemoura brevistyla (Ris, 1902)	0	0	0	0	0	0

September 2018 station	**Z12**	**Z12**	**ZRG**	**ZRG**	**SRG**	**SRG**
microhabitat	min	mos	min	san	min	mos
n° replicates	4	1	3	2	3	2
Protonemoura nitida (Pictet, 1835)	0	2560	0	0	0	0
Protonemoura cf. *lateralis* (Pictet, 1835)	20	160	0	0	0	0
Protonemura nimborum (Ris, 1902)	0	0	0	0	0	0
Protonemura cf. *caprai* (Aubert, 1954)	0	0	0	0	0	0
Nemoura mortoni (Ris, 1902)	60	1440	0	0	53	0
Leuctridae	0	0	0	0	0	0
Leuctridae/capnidae sp	0	0	0	0	0	0
Leuctra major Brink, 1949	0	0	0	0	0	0
Leuctra rosinae Kempny, 1900	80	160	0	0	1227	640
Leuctra cf. *teriolensis* Kempny, 1900	0	0	0	0	0	0
Leuctra braueri Kempny, 1898	40	0	0	0	0	0
THYSANOPTERA	20	0	0	0	0	0
TRICHOPTERA						
Rhyacophilidae						
Rhyacophila intermedia McLachlan, 1868	0	0	0	0	0	0
Rhyacophila pubescens Pictet, 1834	0	0	0	0	0	0
Limpnephilidae	0	0	0	0	0	0
Drusus monticola (McLachlan, 1867)	0	0	0	0	0	0
Drusus cf. *adustus* (McLachlan, 1867)	0	0	0	0	1813	3360
Acrophylax zerberus Brauer, 1867	500	9760	107	0	0	0
Micropterna lateralis (Stephens, 1837)	0	0	0	0	0	0
Drusus discolor (Rambur, 1842)	100	3600	0	0	0	0
Goeridae						
Lithax niger (Hagen, 1859)	0	0	0	0	0	0
COLEOPTERA						
Coleoptera sp	0	0	0	0	0	0
Elminthidae	0	0	0	0	0	0
DIPTERA	0	0	0	0	0	0
Tipulidae	0	0	0	0	0	0
Limoniidae	100	0	0	0	53	160
Pediciidae	0	80	0	0	53	0
Simuliidae	0	0	0	0	0	0
Ceratopogonidae	0	0	0	0	0	0
Chironomidae						

September 2018	station	**Z12**	**Z12**	**ZRG**	**ZRG**	**SRG**	**SRG**
	microhabitat	min	mos	min	san	min	mos
	n° replicates	4	1	3	2	3	2
Diamesinae							
Diamesa sp		0	0	80	80	373	5680
Pseudodiamesa sp		0	0	107	1200	0	560
Pseudokiefferiella sp		0	0	0	0	0	5680
Boreoheptagyia sp		0	0	0	0	0	0
Orthocladiinae		1720	57600	80	80	2187	31360
Chironominae		0	0	0	0	0	0
Tanytarsini		340	880	0	0	0	0
Chironomini		0	0	0	0	0	0
Tanypodinae		0	0	0	0	0	0
Psychodidae		60	240	0	0	0	0
Blephariceridae		0	0	0	0	0	0
Empididae		0	0	0	0	0	0
Dolichopodidae		0	0	0	0	0	0
Muscidae *(Lispe* sp)		100	80	0	0	0	0
Dixidae		0	0	0	0	0	0
Thaumaleidae		0	0	0	0	0	0
MOLLUSCA - Planorbidae							
Gyraulus sp		0	0	0	0	0	0

Supplementary material – S3

Supplementary S3, Conclusions. Dissemination of results. Participation to congresses and meetings, and additional published papers.

Meeting/conference	Place	Date	Authors	Title
XXXIII congress of the International Society of Limnology – SIL	Torino, Italy	July 2016	Brighenti, S., Iacobuzio, R, Rolla., M., von Hardenberg, A., Bassano, B. & Tiberti, R.	Poster: Resilience of alpine lakes invertebrates after the eradication of introduced brook trout *Salvelinus fontinalis*
International meeting on the conservation of high mountain lakes	Ceresole Reale (TO), Italy	July 2017	Brighenti, S., Bruno, M. C., Tolotti, M., Wharton, G., Pusch, M. & Bertoldi, W.	Poster: Ecological shifts of stream ecosystems in deglaciating Alpine areas
			Brighenti, S., Iacobuzio, R., Rolla, M. & Tiberti, R.	Oral presentation: Resistant streams and resilient lakes: recovery of high mountain macroinvertebrates along with a fish eradication campaign
XXVII congress of the Italian Society of Ecology - S.It.E. (2017)	Napoli, Italy	September 2017	Brighenti, S., Bruno, M. C., Tolotti, M., Wharton, G., Pusch, M., & Bertoldi, W.	Oral presentation: Effects of deglaciation on Alpine stream ecosystems: preliminary results Co-chair in the session “Extreme environments)
			Brighenti, S., Iacobuzio, R., Rolla, M. & Tiberti, R.	Poster: Macroinvertebrate community recovery along with alien fish eradication in high mountain lakes
LimnoAlp – SIL Austria meeting (2017)	Innsbruck, Austria	October 2017	Brighenti, S., Bruno, M. C., Tolotti, M., Wharton, G., Pusch, M., Holtz, T. & Bertoldi, W.	Oral presentation: Habitat characterization of Alpine streams in a deglaciating catchment
EUCOP 18 – European Conference on Permafrost (2018)	Chamonix, France	June 2018	Brighenti, S., Engel, M., Bruno, M. C., Tolotti, Comiti, F. & Bertoldi, W.	Poster: Rock glacier outflows: a distinct a alpine stream type?
			Engel, Brighenti, S., M., Bruno, M. C., Tolotti & Comiti, F.	Poster: Multi-tracer approach for characterizing rock glacier outflow
XXVII congress of the Italian Society of Ecology - S.It.E. (2018)	Cagliari, Italy	September 2018	Brighenti, S., Engel, M., Bruno, M. C., Tolotti & Bertoldi, W.	Poster: Stepping stones or shelter areas? The role of rock glaciers in the context of Alpine deglaciation
XV Italian meeting of young researchers in stream ecology (2019)	Ostana (TO), Italy	May 2019	Brighenti, S., Bruno, M. C., Tolotti, M., Wharton, G., Camin, F., Holtz, T. & Bertoldi, W	Oral presentation: Alpine stream ecosystems under increased influence of rock glaciers (Awarded as third best presentation)

Symposium of European Freshwater Science – SEFS11 (2019).	Zagreb, Croatia	July 2019	Brighenti, S., Bruno, M. C., Tolotti, M., Engel, M., Wharton, G., & Bertoldi, W. Brighenti, S., Tolotti, M., Bruno, M. C., Bressan, F., Camin, F., & Bertoldi, W.	Oral presentation: Influence of the paraglacial landscape along the river continuum in a deglaciating Alpine catchment Oral presentation: Characterisation of a rock glacial stream under a multitrophic approach. (Awarded as third best student presentation)
International Symposium of the International Society of River Science – ISRS6 (2019)	Wien, Austria	September 2019	Brighenti, S., Bruno, M. C., Tolotti, M., Wharton, G., Pusch, & Bertoldi, W.	Oral presentation: Streams fed by active rock glaciers: habitat, biota and conservation value
Meeting on the research in the Stelvio National Park	Bormio, Italy	October 2019	Tolotti, M., Brighenti, S., & Bruno, M. C.	Oral presentation: Investigating the influence of permafrost on the ecology of Alpine freshwaters

Papers published during the PhD period, not related to the programme:

- Tiberti, R., Nelli, L., Brighenti, S., Iacobuzio, R., Rolla, M. (2017). Spatial distribution of introduced brook trout *Salvelinus fontinalis* (Salmonidae) within alpine lakes: evidences from a fish eradication campaign. *The European Zoological Journal*, *84*, 73-88.
- Tiberti, R., Bogliani, G., Brighenti, S., Iacobuzio, R., Liautaud, K., Rolla, M., von Hardenberg, H. & Bassano, B. (2018). Recovery of high mountain Alpine lakes after the eradication of introduced brook trout Salvelinus fontinalis using non-chemical methods. *Biological Invasions, 21(3), 875–894.*
- Tiberti, R., & Brighenti, S. (2019). Do alpine macroinvertebrates recover differently in lakes and rivers after alien fish eradication? *Knowledge and Management of Aquatic Ecosystems*, *420*(37), 1-11.