

Article

Glacial Stream Ecology: Structural and Functional Assets

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Abstract: High altitude glacier-fed streams are harsh environments inhabiting specialized invertebrate communities. Most research on biotic aspects in glacier-fed streams have focused on the simple relationship between presence/absence of species and prevailing environmental conditions, whereas functional strategies and potentials of glacial stream specialists have been hardly investigated so far. Using new and recent datasets from our investigations in the European Alps, we now demonstrate distinct functional properties of invertebrates that typically dominate glacier-fed streams and show significant relationships with declining glacier cover in alpine stream catchments. In particular, we present and argue about cause-effect relationships between glacier cover in the catchment and temperature, community structure, diversity, feeding strategies, early life development, body mass, and growth of invertebrates. By concentrating on key taxa in glacial and non-glacial alpine streams, the relevance of distinct adaptations in these functional components becomes evident. This clearly demonstrates that further studies of functional characteristics are essential for the understanding of peculiar diversity patterns, successful traits and their plasticity, evolutionary triggered species adaptations, and flexibilities.

Keywords: invertebrates; glacier retreat; Chironomidae; Diamesinae; adaptation; harshness

1. Introduction

Freshwaters at high altitude and latitude are often strongly influenced by snow and ice cover of the catchment, resulting in temporal (seasonal) and spatial (longitudinal) variabilities in environmental conditions (e.g., [1–4]). Glacial streams and rivers are for this reason considered as harsh ecosystems, because melting glacial ice in summer contributes significantly to the rough environmental key conditions (low water temperature, increased discharge dynamics, instable substrate and riverbed, increased turbidity and sediment load). Dependent on the size, volume, and mass of the glacier in proportion to the catchment area, a specific degree of harshness shaping and affecting of distinct biological characteristics has typically been observed (e.g., [5,6]). Such harsh environmental conditions in glacier-fed streams and rivers have caused specific adaptations in the biological communities over evolutionary timescales. Today's result is a diverse flora and fauna in these ecosystems, consisting of key taxa of benthic algae and periphyton [7,8] and invertebrates, such as the insect family Chironomidae, the chironomid subfamily Diamesinae, and species within the chironomid genera *Diamesa* and *Prodiamesa* [6]. Besides the typical structural components of biodiversity, functional characteristics and patterns in glacial streams and rivers have rarely been studied (but see [9–13]).

Glacial streams are not only special ecosystems with certain environmental harsh conditions and typical biological characteristics, with their location at higher altitude and latitude, they are facing considerable effects from climate change. Retreating glaciers as a conspicuous result of climate

warming will alter environmental conditions, as glacial share in runoff and coherent degrees of harshness typically depend on catchment glaciation.

Differing habitat conditions between streams, and also changing conditions within same waters, produce a mosaic of distinct habitat templates in alpine streams and consequently shape benthic invertebrate communities. In theory, individual traits and the phenotypic plasticity of distinct species limit their range of suitable habitat conditions for their occurrence [13–15], which in summary mediate the composition of occurring invertebrate communities.

While research upon impacts of glacier retreat has focused mostly on the effects for the biodiversity of invertebrates (as reviewed in [16]) and the composition of their communities, far less attention has been given to functional aspects of biota, such as potential consequences for their egg development, their trophic performance, and the acquisition of body-mass. As such functional characteristics might affect population fitness, or also ecosystem functions of alpine streams, such as secondary production, functional aspects of invertebrates—apart from mediating the occurrence of species—seem to be of high importance for the ecological integrity of alpine stream networks.

Here, we present results from an ongoing long-term monitoring of alpine rivers and reanalyzed data from recent studies in order to highlight the relationship between structural and functional properties of glacial stream ecology and the diverse environmental conditions and changes. In remote streams with glacial and non-glacial influence, we assessed invertebrate community metrics, as well as functional aspects such as egg development, body mass formation, trophic preferences, and strategies, and related these with the extend of glacial cover in the respective hydrological catchments. The objective of this study was thus to examine structural and functional assets of biota in glacier-fed streams, and how these might be affected by glacier retreat.

It was the specific aim, by considering multiple structural and functional aspects of alpine stream ecology in regard of glacier retreat, (i) to provide new insights into the limits for most invertebrates and the strategies of glacial stream specialists to survive and successfully reproduce in these harsh environments, and (ii) to come up with a more holistic approximation of consequences due to glacier retreat in alpine stream ecosystems.

2. Materials and Methods

2.1. Study Design

This study was built upon recent field surveys carried out on alpine streams and rivers within our long-term monitoring program. Besides presenting data on environmental conditions, as well as structural and functional characteristics (assessments in 2014), we re-analyzed some experimental raw data from already published sources (physiological data [17], isotope data [18], and experimental data [19], assessments in 2014, 2015, and 2017, respectively), where we think these new results specifically mirror functional assets in harsh environments, such as glacial rivers. We specifically aimed at defining cause-effect relationships (glacier cover vs. functions) by overlaying the invertebrate community data and environmental settings with the functional characteristics. These results are analyzed along a gradient of glacier-cover in the catchments.

2.2. Study Area

Glacial and non-glacial streams were studied in six catchments in the Hohe Tauern National Park in the Central Austrian Alps (Figure 1), where pristine catchments with limited direct anthropogenic influences (such as pollution or hydromorphological alterations) allow conclusions about environmental situations and changes. All selected stream sections are part of a long-term river monitoring project and are located at elevations ranging from 1354 to 2216 m a.s.l. (above sea level).

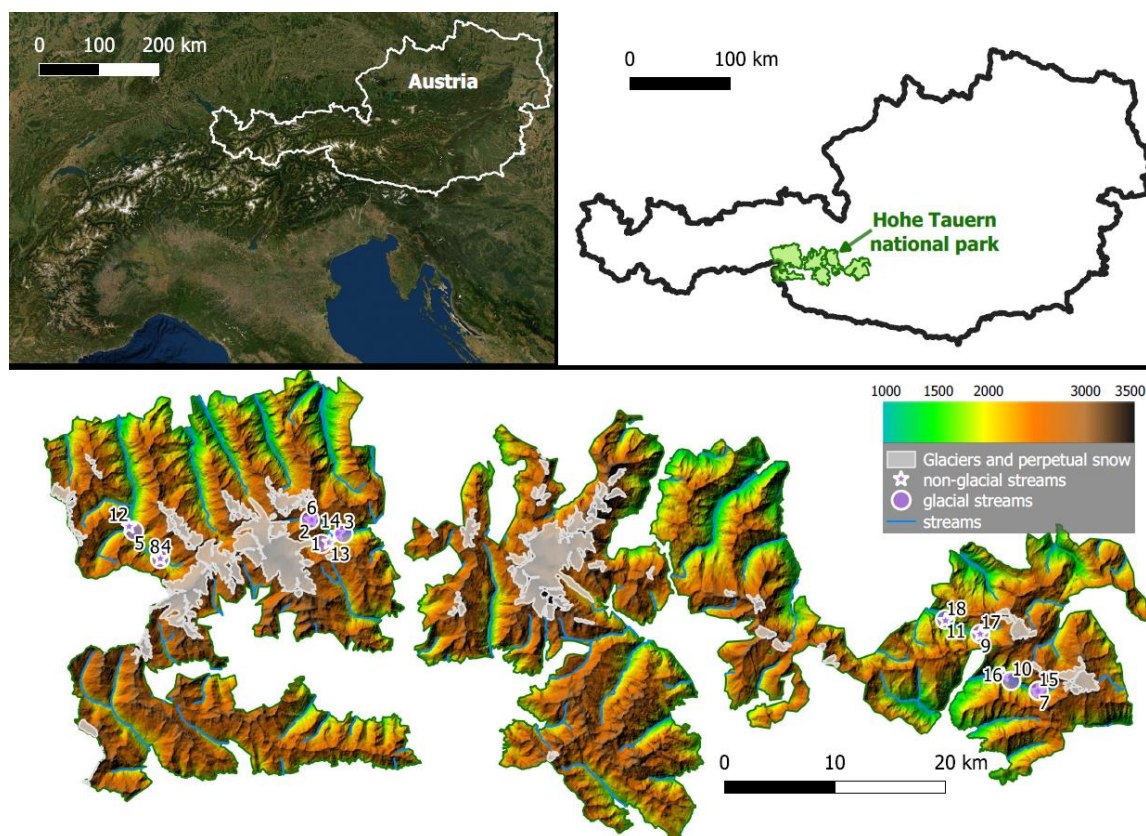


Figure 1. Map of the European Alps, Austria with the Hohe Tauern National Park, Austria, and the sampled stream sections in glaciated and non-glaciated catchments. Colored gradient indicates the distinct elevations within valleys of this mountain range, and circles (glacial streams) and stars (non-glacial streams) locate the sampled reaches. Additional information on study site features are presented in Table 1.

2.3. Physical and Chemical Habitat Variables

The degree of glaciation of each catchment was measured using QGIS [20] and CORINE land-cover data, and was expressed as the ratio of glaciated to total catchment area (%). Stream water temperature was monitored continuously (every 30 min) using digital data loggers (Tidbit; Onset, Bourne, Massachusetts) and averaged for a 1 month period before the sampling dates. Suspended solids were quantified via filtering 1–2 L water through pre-combusted Whatman GF/C filters on site and followed by a loss-on-ignition estimation (combustion at 450 °C for 4 h) in the laboratory. Together with the estimated discharge via depth/velocity-transect measurements using a vane wheel probe (ZS25; Höntzsch, Waiblingen, Germany), we modeled the inorganic sediment load (sediment load in mg/s) as the combination of suspended sediment concentration (mg/L) and discharge (L/s).

2.4. Invertebrate Community Structures

At each site, in July, we took six samples of aquatic invertebrates with a Surber sampler (0.09 m², 100 µm mesh size) by sampling mesolithal (cobble), macrolithal (coarse cobble), and megalithal (boulders) substrates, which represent the main microhabitats in these streams, leading to a total of 108 samples of invertebrate communities. We preserved all samples immediately in 75% ethanol, identified all groups to the resolution possible, and expressed the community composition using conventional summary metrics for glacier-fed streams, such as invertebrate abundance, taxa richness, or the relative abundance of the dipteran family Chironomidae or its subfamily Diamesinae.

2.5. Egg Development in Glacial Streams

To assess the potential influence of degree glacier cover in the catchment on the egg development of alpine stream invertebrate species, we used experimental data from Schütz and Füreder [19] and compared the identified day-degree demands at distinct breeding temperatures between typical glacial specialists (Diamesinae) and other chironomid species. We then used this published data set (day-degree demand per breeding temperature level, Schütz and Füreder [15]) and combined it with the environmental characters (water temperature and catchment glacier cover) and invertebrate communities of sampled glacial and non-glacial streams in the Hohe Tauern national park. This allowed us to (a) verify the validity of the experimental breeding experiments for alpine streams, and (b) to transfer experimental relationships between water temperature and breeding success to the temperature conditions in the here sampled streams.

2.6. Bulk Stable Isotopes and Individual Body Mass of Chironomid Populations

To quantify the potential relationship between glacier influence and trophic performance, as well as the body size of the invertebrates, we used available isotopic niche data of chironomids from Niedrist et al. [18], calculated the isotopic space of each population per stream, and related that to degree of glaciation in the respective catchments. The original data are stable isotope ratios of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) of individual chironomid larvae belonging to the taxa (A) *Diamesa steinboeckii*, (B) *Diamesa latitarsis*-gr.I, (C) *Diamesa cinerella*-gr., and (D) *Orthocladius luteipes*, which were sampled in July 2015 using a Surber sampler (mesh size 250 μm). These samples were taken from six different streams with differing catchment glacier cover. In this new analysis of that dataset, we quantified the relationship between each populations' isotopic niche between classes of catchments with differing glacier cover (0%, <15%, 15%–39%, 40%–80%).

To assess the relationship between body mass and glaciation in the catchment, original body mass data of all chironomid taxa belonging to the subfamilies Diamesinae and Orthoclaadiinae (obtained by Niedrist et al. [17] in the same 18 stream reaches in July 2014) was related with the relative glacier-cover in the respective catchments.

2.7. Data Analysis

Relationships between structural community measures (abundance, taxa number, relative abundance of Diamesinae) and glacier cover were tested using simple linear models, considering model diagnosis.

Taxon-specific isotopic niche breadth (isotopic area in ‰^2 , quantified via Bayesian Standard Ellipses using SIBER [21]) and its variability of each consumer group per study stream were related with glacial contribution to the glacial stream. For this, the estimated areas per population and sites (in total $>10^7$ simulated isotopic niche areas) were related to degree of glacial cover in the respective catchments, indicating median and quantile distribution.

We grouped the individual body mass of each chironomid larvae ($\mu\text{g individual}^{-1}$) per group of sites (catchments grouped by ratio of glaciated area: 0%, <15%, 15%–39%, 40%–80%) and compared the mean body mass of the two subfamilies Orthoclaadiinae and Diamesinae.

3. Results

3.1. Invertebrate Taxa Number and Dominance of Diamesinae

In total we identified 204 different taxa in the 18 study streams with their distinct environmental characteristics (Table 1), with most taxa colonizing streams with intermediate and no glacial influence (Table S1). Invertebrate taxa richness increased significantly as catchment glacier cover decreased, with on average +1.5 taxa every 10% decrease ($p < 0.05$, Figure 2A). In streams with high glacial contribution, invertebrate communities were dominated by Chironomidae, for which relative abundance ranged between 71% and 98% (interquartile range). Within the Chironomidae, the relative abundance of larvae

belonging to the subfamily Diamesinae decreased considerably and significantly with decreasing glacier cover in the streams' catchments ($p < 0.05$, Figure 2B). This relationship indicated a reduction of their relative abundance by 8% when glacier cover in the catchment decreased by 10%. While the glacial stream specialists Diamesinae dominated the invertebrate community in glacial streams, the relative abundance of the other chironomid subfamily Orthocladiinae gained with decreasing glacier cover in the catchment ($p < 0.05$).

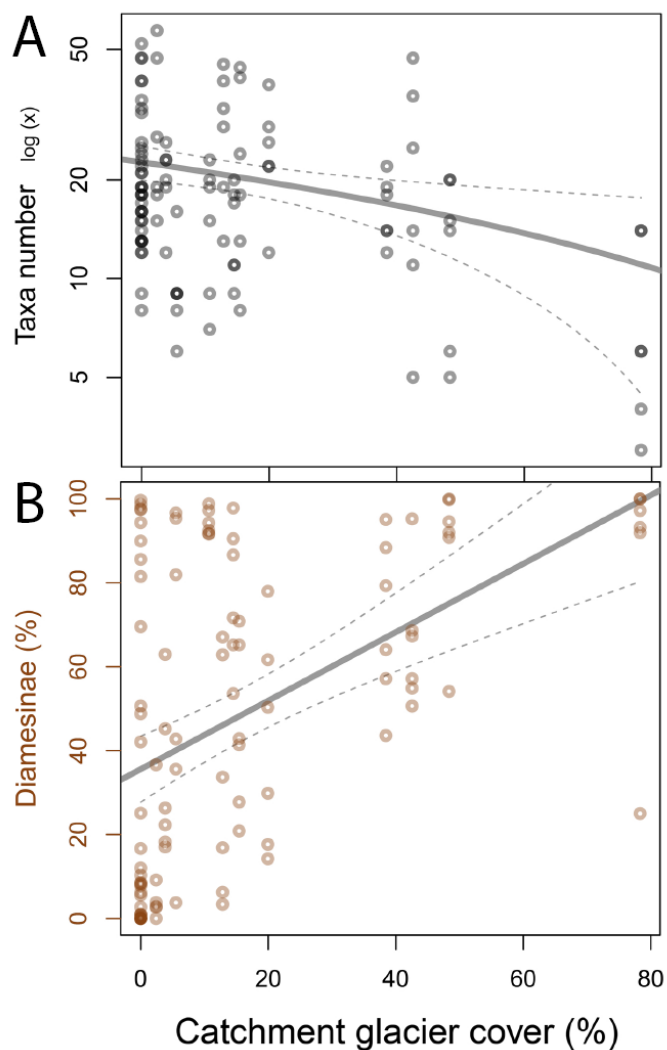


Figure 2. Relationship between catchment glacier cover and the invertebrate community measures (A) taxa number and (B) relative abundance of Diamesinae. Bold lines indicate the linear model fit, dashed lines represent statistical 95% confidence intervals.

3.2. Development of Eggs and Larvae in Relation to Catchment Glacier Cover

In development experiments with chironomid eggs, the degree-day demand until successful hatching was lowest in coldest treatments (2 °C) for all species, but was not related to the habitat conditions (no significant difference between eggs from glacial or non-glacial streams). The averaged original dataset revealed that at the coldest treatment, Diamesinae had a lower day-degree demand (36.2 ± 7.2) than Orthocladiinae with 52.8 ± 11.8 (Figure 3A,B). As highlighted in the original study [19], the averaged degree-day demand across chironomid species was also significantly higher with a higher breeding temperature. The lowest demand was found for Diamesinae in the coldest breeding temperature (2 °C) with on average 36.2 ± 7 degree-days, whereas the highest demand of the same subfamily was at 12 °C with 95.7 ± 18.8 degrees-day (Figure 3B). Linking the experimental dataset

and the invertebrate community data in sampled reaches, we found that the taxa selected for the experiments in [19] were dominant, especially in streams with high glacier cover in the catchment (Figure 3D). While the selected *Diamesa* taxa contributed considerably to the occurring invertebrate communities in cold and highly glaciated streams (Figure 3D), the contribution of Orthocladiinae taxa selected for the experiment was only marginal in natural non-glacial study streams (Figure 3C). The temperatures selected for breeding experiments in [19] represent significantly ($p < 0.001$) a negative relationship between catchment glacier cover (in %) and water temperature of the study streams and reflect the natural gradient of summer water temperatures in the same reaches (compare experimental and natural water temperature range, e.g., Figure 3B vs. Figure 3D).

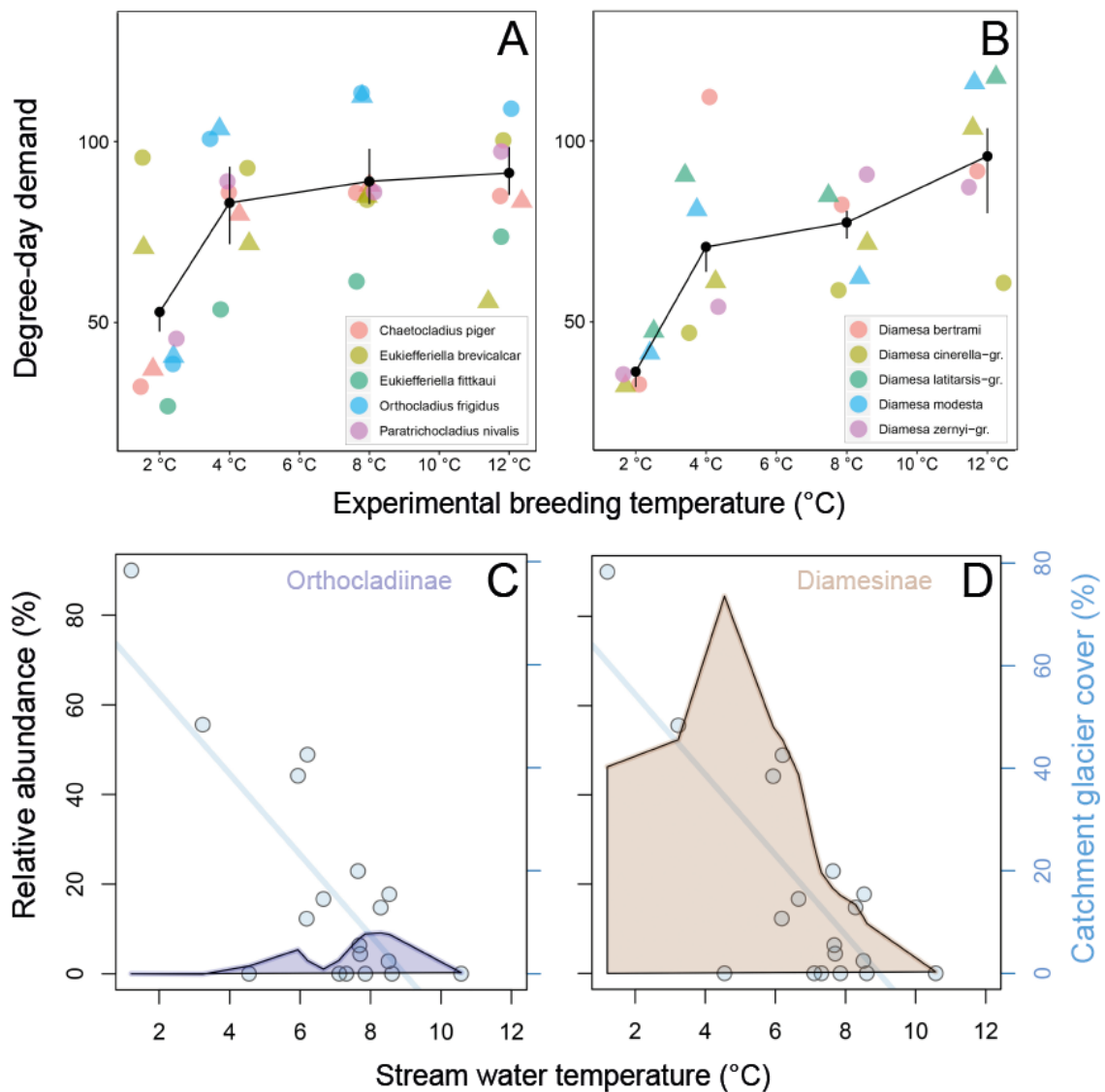


Figure 3. Experimentally derived degree-day demand for successful egg development of Orthocladiinae (A) and Diamesinae (B) species (summarized data (means) from [19]) and their relative contribution to invertebrate communities in studied streams in the present study with Orthocladiinae (C) and Diamesinae (D). The significant relationship ($p < 0.001$) between catchment glacier cover and water temperature is presented in (C) and (D). Dots represents the studied stream sites, representing the catchment glacier cover (y-axis) and the mean temperature one month prior sampling (x-axis). The solid line delineates the modelled linear relationship. Color areas (in (C) and (D)) indicate relative abundances in study streams of the same taxa selected for experiments (those listed in (A) and (B)).

Body mass of Diamesinae were significantly higher in stream habitats where glaciers covered more than 15% of the catchment areas, whereas this was not observed for Orthocladiinae (Figure 4). In total, 18,167 individuals were measured, most of which had a body mass between 14.4 and 29.8 μg (Orthocladiinae) and 42.9 and 77.5 μg (Diamesinae) in catchments with <15% glacier cover. While for Orthocladiinae we observed no difference in streams with differing glaciation in the catchment, we found that most Diamesinae had a higher body mass in streams draining highly glaciated catchments (15%–39%, Figure 4B) ranging between 75.8 and 128 μg . The larvae with the highest individual weight of 270 μg was a Diamesinae from streams with high glacial input (15%–39% glaciation).

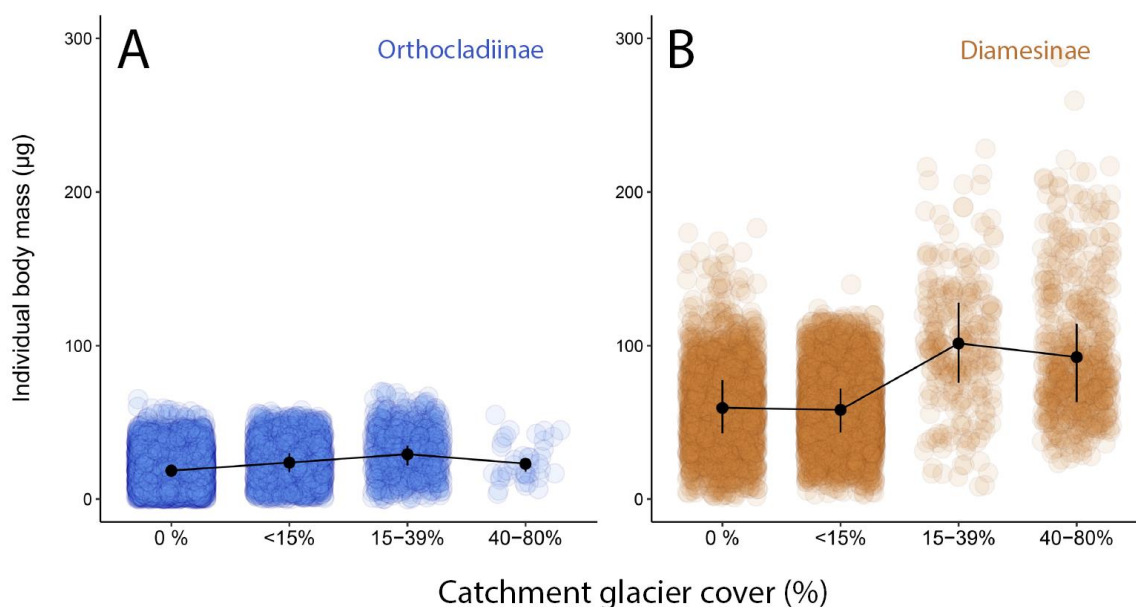


Figure 4. Individual body mass of chironomid subfamilies Orthocladiinae (A) and Diamesinae (B) from groups of streams draining catchments with varying degree of glacier-covered catchment areas (0%–80%). Single points represent weights of individual chironomid larvae whose weights were determined via length measurements and using available length-mass relationships [22,23]. Black dots represent the mean of each group, vertical lines limit the 25% and 75% quartiles of the respective data points.

3.3. Trophic Strategies in Glacier-Fed Streams Related to Catchment Glacier Cover

When relating the trophic niche dataset to the glacier cover in the respective catchment (%), we found that, among the investigated glacial stream specialist taxa, especially *Diamesa steinboeckii* and *D. latitarsis*-gr.I had significantly larger isotopic niche areas (>10 times higher, Figure 5A) in glacial streams with higher glacier cover, whereas the niche of other taxa (also *Diamesa* taxa) remained constant, regardless of the distinct ratio of glaciated catchment area. Streams with high glacial cover in the catchment also had lower water temperatures and higher sediment transport, but these relationships were not linear and not the same (Figure 5B).

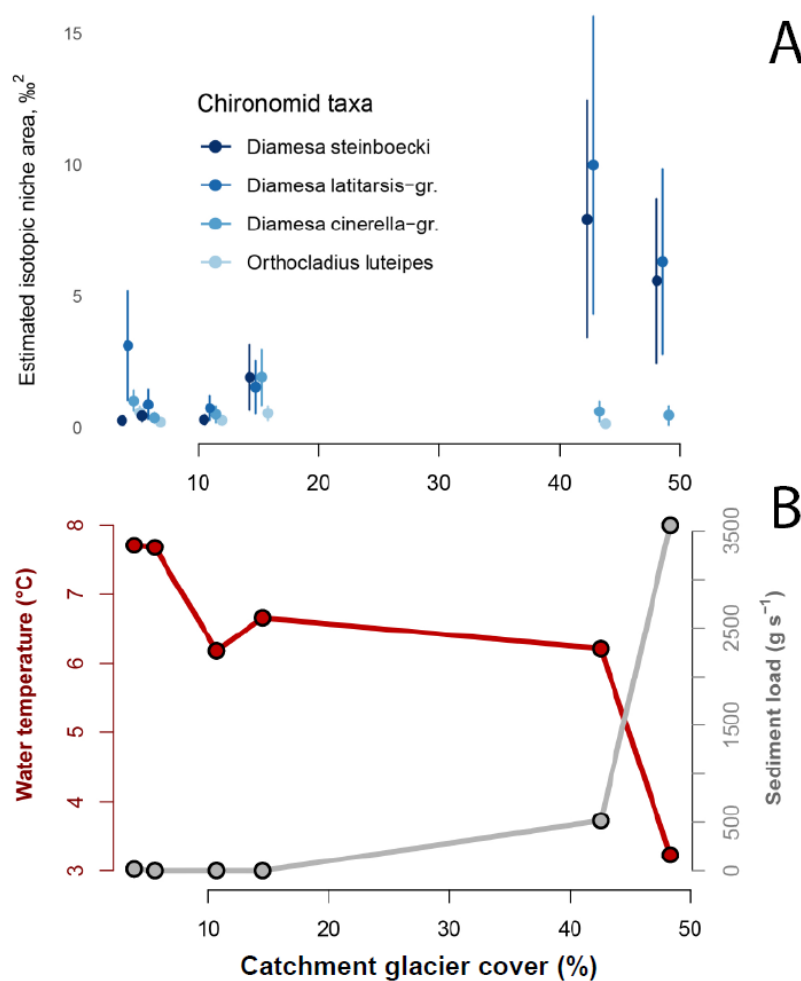


Figure 5. Estimated isotopic niche area (standard ellipse area) of chironomid populations of four chironomid taxa (see legend) from six glacial streams (from [18]) re-analyzed and related with the extend of glacier cover in the respective catchment (%) (A), which habitats differ in water temperature (°C, in red) and sediment load (g s^{-1} , in grey, B). Here, presented mean and most probable isotopic niche areas (in the $\delta^{15}\text{N} \times \delta^{13}\text{C}$ isotopic space) were limited using Stable Isotope Bayesian Ellipses in R (SIBER, Jackson et al. 2011) and examined using estimation statistics (using 480,000 (400,000 for *O. luteipes*) bootstrapped samples).

4. Discussion

4.1. Invertebrate Communities in Glacier-Fed Streams Were Dominated by Diamesinae

The dominance of species of the chironomid subfamily Diamesinae in glacier-fed streams is a well-known phenomenon (e.g., [5,24]), which is also confirmed by our results. With decreasing glaciation in the catchment, their absolute abundance remains constant, but their relative contribution to the total invertebrate community decreases sharply. In the most glaciated stream sections only a few *Diamesa* species (*D. steinboeckii*, *D. latitarsis-gr.I*, *D. cinerella*, and *D. zernyi*) occur regularly. A second subfamily, the Orthocladiinae, which also dominates in cold streams, shows generally a reverse pattern [25]. With decreasing degree of glaciated catchment area their relative abundance is increasing [26]. Despite the fact that this regular and obvious correlation can serve as an excellent indicator for defining significant effects on the community structure and diversity caused by declining glaciers, we can have a closer look if there are specific functional traits present in these taxa which, in the case of the Diamesinae, enables them to overcome and live in harsh environmental conditions, whereas others (Orthocladiinae) lack these traits.

4.2. Functional Assets in Glacial Streams

The harshness of glacial streams (cold water temperatures, short snow-free periods, or dynamic physical habitat conditions [27]) was long assumed to limit the growth of the invertebrate species that survive there [28,29]. In contrast to such assumptions, however, it has been shown that glacial stream specialists typically grow faster in harsh glacial streams or reach higher body mass than the same species in non-glacial streams [17,30]. The driving circumstances behind this certainly include the low level of competition in glacial streams [5,18], the sufficient availability of autochthonous and nutritious food resources [17], but also the combination of functional plasticity and special strategies, which are presented and reviewed as follows (and is summarized in Table 2). Although previous studies have highlighted individual functional aspects of glacial stream specialists, this work combined several adaptations and strategies of these taxa and illustrated dependencies on degree of catchment glaciation.

4.2.1. Fast Development of Eggs and Larvae

The larval community of glacial streams, dominated by chironomids [24], faces cold and dynamic living conditions not only during their larval stage, but also during their egg development [31], which is the first critical step for the emergence and occurrence of invertebrate species and key for population replenishment. Particularly in glacial streams, in addition to avoiding and tolerating freezing temperatures [32], the successful and timely completion of this stage is necessary for the species to find suitable living conditions as larvae. As for all ectotherms, this first life stage of glacial stream invertebrates is generally temperature-dependent [31,33,34]. Although so far cold-stenothermal species have been assumed to develop most efficiently at low temperatures [35,36], recent laboratory experiments on glacial stream specialist species has revealed their high plasticity against a wide range of temperatures [19], which is not restricted to cold-stenotherm taxa, as confirmed by our results. Thus, species classified as cold-stenotherm in cold waters can comply with a lower number of degree-days until hatching of the larvae, when compared to warmer situations. Conversely, this may mean that glacial stream invertebrates possess a certain plasticity of key fitness-associated traits, such as their reproductive performance, and, in times of warming alpine streams (Niedrist and Füreder, in prep.), that the egg development of specialists itself does not appear to be sensitive to climate change.

Apart from the egg development, it has recently been shown that glacial stream specialist species, in contrast to alpine stream generalists, grow faster in harsh environments (as evidenced by [30]) or produce more biomass than the same taxa in temperate streams [17]. Above a certain threshold of glacial influence, the dominant Diamesinae species are able to enlarge their body mass above the known level, which might be beneficial for their reproductive success.

4.2.2. Special Trophic Strategies

The harshness-dependency variability of body mass of glacial stream specialists can partly be explained by their plastic feeding strategy, which has previously been observed in the variability of isotopic C signatures [10–12]. In dynamic environments such as glacier-fed streams, where food sources might be patchily distributed due to dynamic riverbeds, glacial river specialists seem to be forced into opportunistic omnivorous or even cannibalistic [37] feeding behavior.

Indeed, an assessment based on stable isotope analysis of chironomid populations in different glacier-fed stream habitats revealed that selected chironomid taxa (*Diamesa steinboecki* and *D. latitarsis*-gr.A) exhibit considerably different isotopic niche areas (Figure 5A), indicating a variable diet of the populations when conditions are most dynamic and harsh [18]. While the trophic performance of other taxa (*Diamesa cinerella*-gr. and *Orthocladius luteipes*) was not related to environmental conditions in the streams, the isotopic niches of these two typical first colonizers in high glacial streams were many times higher in sites with harsh living conditions compared with that of populations of same species living in more benign habitats (Figure 5A). From these results, we can conclude that the possibility of

such a plastic feeding behavior within populations is an additional adaptation of these taxa for the survival and dominance in glacier-fed stream.

The harsh conditions in some of the observed glacier-fed streams are based not only on single environmental conditions, but also on the combination of low mean water temperatures, high sediment loads, and generally high levels of glaciation in the catchment (Figure 5B). During climate change and glacier retreat, same habitat properties are expected to change in combination [4,38,39], which in turn means that the trophic and the consequential ecological niche of glacial stream specialists will change. Catchment glacier cover, however, is generally indicating the various gradients of single environmental factors.

In alpine glacier-fed streams, where the short snow-free period is dominated by dynamic river runoff and unstable riverbeds, and where allochthonous organic inputs are typically low, the uptake of enough nutritious food is essential to successfully colonize and reproduce in these environments. Despite the importance of this component, it has long been unclear whether invertebrates in harsh glacial streams can choose between all food sources, or if they have to feed on anything they can find [10,11]. In performing gut content analyses of *D. steinboeckii* and *D. latitarsis* in an Austrian glacier-fed stream and in comparing the relative content of particles with its availability in the habitats of the larvae, these larvae were found to actively select high-quality food sources, namely, benthic diatoms and chrysophytes, but to avoid the low-quality food sources such as cyanobacteria [40]. Thus, such selective feeding can additionally contribute to the success of the glacial stream specialists in harsh glacial streams, as the primary producers diatoms and chrysophytes (e.g., the brown algae *Hydrurus foetidus* [41,42]) are known to possess distinct physiological properties (different nutritional quality according to fatty acid content and composition [43]). Knowing that such a high nutritional diet can enhance the reproductive success for animals ranging from invertebrates to humans [44], this selective feeding traits of few glacial stream chironomids can be seen as advantageous over other invertebrates in glacial streams.

4.3. Synthesis and Perspectives

Overall, this study revealed that invertebrate communities in glacier-fed streams possess distinct structural and functional properties, in contrast to other alpine stream types. The demonstrated functional plasticity of glacial stream specialists emphasizes a strong adaptation of key taxa to successfully live and survive in these cold and dynamic habitats and it significantly adds to the understanding why only specific taxa can survive and form stable populations in these harsh environments and others cannot.

Glacial streams and rivers play a crucial role in feeding lowland running waters in and around mountain areas, such as the European Alps. About 10% of the earth's land surface is covered by glaciers, which contribute significantly to freshwater availability and distribution. Over the last 170 years, these glaciers have been shrinking steadily, but in recent decades rapidly [45]. This glacier loss has already led to changes in the hydro-morphology and the ecology of river networks, and these are assumed to intensify in the future [46]. Major changes are to be expected not only in run-off and bed-load dynamics, but also in riverine biodiversity and biological community patterns, before we sufficiently understand evolved abilities and adaptations of plant and animal species.

In this respect, studies and experiments for elucidating life-cycle strategies and larval development in the highly adapted invertebrate species are needed. Schütz and Füreder [30] showed that with regular sampling efforts, they were able to conclude on a remarkable larval growth and development in chironomid larvae in the upper-most sections of a glacial river. The here documented similar trend of higher body-mass of chironomid larvae in highly glaciated catchments is another example that extreme environmental conditions may exclude several alpine stream taxa but favor the occurrence of glacial stream key taxa. With these studies [17,18,30] (and results presented here) we may conclude that when the essential needs, i.e., nutrient availability and quality, of robust species are guaranteed, they are able

to successfully live, grow, and reproduce even at harshest conditions. In amplifying storage of mainly autochthonous organic matter in the ecosystem they enrich the stream food chain at the initial links.

Little is known on the early development of alpine and arctic stream invertebrates. Schütz and Füreder [19] investigated for the first time the potential effect of water temperature on the egg development of 10 cold-adapted chironomid species from glacier- and spring-fed alpine and sub-alpine streams, employing rearing experiments at four different temperature levels. In their comparisons, they found that fast egg development contributed to the success of alpine chironomid species in harsh environments. Our application of functional characteristics again indicates that a fast egg development, together with a fast larval growth, seems to successfully contribute towards the evolutionary fitness of harshness-adapted chironomid species under extreme living conditions that exclude many other benthic species.

These aspects clearly demonstrate that further studies of functional characteristics are essential for the understanding of peculiar diversity patterns, successful traits and their plasticity, evolutionary triggered species adaptations, and flexibilities. Besides distinct structural characteristics and community patterns, knowledge about functional abilities and performance of glacial stream taxa under harsh environmental conditions is needed, especially when recent estimations and reports forecast their rapid changes by the effects of climate and environmental change.

Table 1. Site numbering, location, and environmental character of study sites with average invertebrate taxa number across six surber samples per stream (July 2014): WGS 84 = World Geodetic System 1984, maxT = maximum daily mean water temperature (during one month prior to sampling).

| # Site | Coordinates WGS 84 | Catchment Glacier Cover (%) | maxT | Transported Solids (mg/s) | Taxa Richness |
|--------|---------------------------|-----------------------------------|--------------|------------------------------|------------------|
| 1 | 47°6′50.7″N, 12°25′5.8″E | 78.3 | 1.42 ± 0.1 | 215.2 ± 17.4 | 8 ± 5 |
| 2 | 47°8′0.2″N, 12°24′11.8″E | 48.4 | 4.97 ± 1.11 | 3559.0 ± 142.6 | 13 ± 7 |
| 3 | 47°7′22.4″N, 12°26′37.7″E | 42.6 | 7.75 ± 0.84 | 515.2 ± 46.6 | 23 ± 16 |
| 4 | 47°5′50.8″N, 12°13′34.2″E | 38.4 | 7.68 ± 1.62 | 11.9 ± 0.9 | 17 ± 4 |
| 5 | 47°7′9.4″N, 12°11′37.2″E | 19.9 | 9.68 ± 1.62 | 16.8 ± 0.9 | 25 ± 9 |
| 6 | 47°7′59.8″N, 12°24′19.2″E | 15.4 | 12.99 ± 3.23 | 0.1 ± 0.2 | 25 ± 15 |
| 7 | 47°0′38.7″N, 13°16′40.8″E | 14.5 | 9.17 ± 1.89 | 2.1 ± 0.3 | 14 ± 5 |
| 8 | 47°5′51.3″N, 12°13′35.2″E | 12.8 | 11.24 ± 2.30 | 1.2 ± 0.3 | 30 ± 12 |
| 9 | 47°3′21.4″N, 13°12′25.7″E | 10.7 | 7.54 ± 1.46 | 2.8 ± 0.3 | 16 ± 6 |
| 10 | 47°1′5.9″N, 13°14′43.2″E | 5.5 | 9.23 ± 1.20 | 1.9 ± 0.3 | 10 ± 3 |
| 11 | 47°4′0.9″N, 13°9′53.6″E | 3.8 | 8.66 ± 0.92 | 16.8 ± 1.4 | 21 ± 5 |
| 12 | 47°7′22.1″N, 12°11′15.0″E | 2.4 | 10.58 ± 1.48 | 1.9 ± 0.3 | 31 ± 17 |
| 13 | 47°6′56.1″N, 12°25′38.4″E | 0.0 | 9.59 ± 1.16 | 0.0 ± 0.2 | 35 ± 14 |
| 14 | 47°7′23.1″N, 12°26′12.6″E | 0.0 | 9.38 ± 1.50 | 1.1 ± 0.3 | 32 ± 10 |
| 15 | 47°0′36.8″N, 13°16′38.4″E | 0.0 | 9.07 ± 1.09 | 0.1 ± 0.2 | 15 ± 4 |
| 16 | 47°1′22.5″N, 13°14′9.3″E | 0.0 | 13.08 ± 1.66 | 1.2 ± 0.3 | 15 ± 5 |
| 17 | 47°3′20.7″N, 13°12′25.1″E | 0.0 | 4.80 ± 0.52 | 0.2 ± 0.2 | 16 ± 2 |
| 18 | 47°3′57.7″N, 13°9′55.7″E | 0.0 | 10.25 ± 1.20 | 1.6 ± 0.3 | 22 ± 7 |

Table 2. Structural and functional assets in glacial stream community and key invertebrate taxa.

| Asset | Evidence | References |
|--|---|---------------|
| Structure | | |
| Dominance of chironomidae | Chironomidae usually represent most of the benthic invertebrate community | [5,6,25] |
| Ratio Diamesinae/Orthoclaadiinae | The proportion of Diamesinae in benthic habitats is high and positively related to glacier cover/glacial influence | e.g., [14,26] |
| Distinct succession of invertebrate families | Depending on the habitat template, invertebrate families successively colonize glacier-fed streams along their longitudinal dimension | e.g., [5] |
| Diversity and abundance | Diversity rises and falls along a hump shape harsh-benign gradient, whereas abundance increases with decreasing harshness. | [1,47] |
| Seasonal patterns | Significant difference in community structure in winter samples | [48,49] |
| Spatial and temporal heterogeneity | Dominance of certain taxonomic groups in the invertebrate community varies considerably between habitat types, along the longitudinal succession of streams, and between different seasons. | [6,14,50–52] |
| Function | | |
| Cold-hardiness | Cold river specialists (Diamesinae) possess cold hardiness mechanisms that allows winter-activity and survival at sub-zero temperatures | [32] |
| Feeding plasticity | Populations of same glacial river specialist species have variable feeding niches, depending on the harshness of the habitat | [11,18] |
| Food exploitation | Specificity in food items | [40] |
| Body mass variability | The body mass of same glacial river specialist species is positively related with habitat harshness, whereas other species have consistent body-mass | [17,30] |
| Trait variability | Relative abundance and variability of species traits are related to degree of glacial influence on particular stream habitats | [9,13] |
| Life-cycle adaptation | Alpine stream chironomid species (and especially for glacial river specialists) have lower degree-day demand and faster development as larvae at colder water temperatures | [17,19,30] |

Supplementary Materials: The following are available online at <http://www.mdpi.com/2073-4441/12/2/376/s1>, Video S1: Most taxa colonizing streams with intermediate and no glacial influence.

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