When the going gets tough, the tough get going: The enigma of survival strategies in harsh glacial stream environments

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Abstract

1. Glacier retreat is a key component of environmental change in alpine environments, leading to significant changes in physico-chemical characteristics and biological communities in glacier-fed rivers. While the overall effects of the environment on community structure of invertebrates are largely understood, its influence on functional strategies such as feeding habits of same species are not.

2. The aquatic larvae of the species-rich family Chironomidae, or nonbiting midges, are the first invertebrates colonising alpine headwaters, and the first macroinvertebrate consumers in these harsh environments. Species composition in the two subfamilies, Diamesinae and Orthocladiinae, is diverse and is strongly affected by the changing habitat conditions upon glacier retreat. Here, we show that Diamesinae have extremely flexible feeding strategies that explain their abundance, high body-mass and predominance in glacier-fed streams.

3. Along a multifactorial ecological gradient from benign to harsh, based on water temperature, sediment transport and degree of glacial influence, Diamesinae expanded their trophic niche area and covered more trophic levels when conditions harshened. In contrast, niche areas of Orthocladiinae remained small and were not related to this gradient. In Diamesinae, mean body-mass increased with harsher environmental conditions, but no such effects were found in Orthocladiinae.

4. As facultative predators and able to feed on diverse food sources, Diamesinae have evolved survival mechanisms that allow them to thrive and successfully reproduce in glacier-fed streams, which likely explains their predominance in these habitats.

5. Climate change-induced glacier retreat affects the global water balance, with many downstream effects, including on irrigation and domestic use, and our study deepens our understanding of its effects on animals that depend on glacier-melt.

KEYWORDS

glacial streams, niche breadth, omnivory, stable isotopes, trophic ecology
1 | INTRODUCTION

Alpine headwaters are of importance for downstream aquatic networks by providing multiple ecosystem services, including water, nutrients, organic matter or invertebrate prey for higher trophic levels (Milner et al., 2017). The heterogeneity of alpine streams is also vital for the biodiversity of invertebrates (Finn, Bonada, Murúa, & Hughes, 2011) and bacteria (Besemer et al., 2013). However, glaciers continue to retreat in alpine environments almost worldwide as a consequence of human-induced warming (IPCC, 2014), leading to alterations of the physical conditions in alpine glacier-fed stream ecosystems (e.g., altered water temperature, suspended sediment concentration and electrical conductivity) (Milner, Robinson, Rushforth, & Uehlinger, 2010). Consequently, in regimes (Biggs, 1996; Hieber, Robinson, Rushforth, & Uehlinger, 2001), the invertebrates seem to depend on in-stream primary consumers (scrapers, grazers, shredders, collector-filterers or predators) are mostly based on studies from lowland streams. Understandably, in harsh environments like alpine streams, the suitability and accuracy of this approach, as well as the degree of feeding on a restricted range of particle sizes among species are not known (Niedrist & Füreder, 2017). As input of terrestrial organic matter is generally low in glacial streams (Zah & Uehlinger, 2001), the invertebrates seem to depend on in-stream primary production. These basal food resources underlie considerable seasonal variations mediated by dynamics of disturbance and light regimes (Biggs, 1996; Hieber, Robinson, Rushforth, & Uehlinger, 2001; Uehlinger, Robinson, Hieber, & Zah, 2010). Consequently, in streams with glacial influence (the intensity depends on glacial extent and its melting activity), similar producer communities (dominance of filamentous chrysophyte Hydrurus foetidus, diatoms, epilithic bacteria and a lower abundance of cyanobacteria) represent the main food resources for grazing invertebrates (Cantonati, Corradini, Jütten, & Cox, 2001; Lods-Crozet et al., 2001; Rott, Cantonati, Füreder, & Pfister, 2006). Differences in abiotic conditions are thought to be of minor importance for the fatty acid composition within groups of benthic algae and cyanobacteria (Twining, Brenna, Hairston, & Flecker, 2016). Consequently, the uptake of ‘highly unsaturated fatty acids’, called HUFA’s, might mainly depend on how invertebrates can consume trophic resources in harsh environments (Füreder et al., 2003b; Milner, Brittain, Castella, & Petts, 2001; Zah & Uehlinger, 2001). As it is known for soil organisms (Gongalsky, Persson, & Pokarzhevskii, 2008), environmental stressors might affect invertebrates’ trophic niches, a specific aspect of an invertebrate’s fundamental niche (Hutchinson, 1957). Taxa living in streams with high glacial influence (high turbidity, low water temperature) might possess trophic strategies for coping with the environmental harshness such as omnivory (Füreder et al., 2003b), predatory or even cannibalistic activity (Clitherow et al., 2013). General characteristics of food webs in glacial streams have recently been illustrated (Clitherow et al., 2013; Füreder et al., 2003b). However, the role of key-environmental conditions in affecting the feeding strategies and trophic niche breadth of dominant invertebrate taxa remain unclear in alpine glacial streams.

Here, we present results from a study of six glacier-fed streams across a gradient of glacial influence in remote areas of the Austrian Alps. We studied the effects of in-stream habitat conditions on abundance and body mass of macroinvertebrates, and estimate food source preferences, and degree of feeding plasticity of dominant taxa. In particular, the objective of this study was to examine whether invertebrate feeding performance (in terms of preferred food sources) affects their trophic niche extension and their trophic height, over a gradient of glacial influence and associated living conditions (defined as environmental harshness and based on differences in water temperature, sediment load and degree of catchment glaciation) in alpine and subalpine glacial streams in the Hohe Tauern National Park. We analysed trophic properties of four taxa belonging to the dipteran family of nonbiting midges (Diptera: Chironomidae), which are known to be the first inhabitants (e.g., Lods-Crozet et al., 2001; Niedrist & Füreder, 2016), and thus the first connection between producers and consumers, in glacial headwater regions (Niedrist & Füreder, 2017). In particular, individuals of Diamesa steinboekci and Diamesa latitarsis-group I are among the first and dominant inhabitants of glacial headwater regions in the Alps (Lods-Crozet et al., 2001), but understanding of their survival strategies in these harsh environments is limited, but see Lencioni, Jousson, Guella, and Bernabb (2015) for potential molecular adaptations.

Resource use by species and populations in different environments can be quantified and compared using naturally occurring stable isotopes of carbon and nitrogen and trophic niche metrics (Layman, Arrington, Montaína, & Post, 2007). Exploring new statistical techniques (Bearhop, Adams, Waldron, Fuller, & MacLeod, 2004; Jackson, Inger, Parnell, & Bearhop, 2011), these metrics allow a clear refinement of feeding modes and niche extensions of consumers. We used novel Bayesian modelling to disentangle feeding preferences and to reliably quantify the trophic niche breadth (isotopic niche area) among four chironomid taxa. Based on earlier evidence from alpine stream studies (Füreder et al., 2003a,b), where
autochthonous food sources seemed to be a significant contributor in invertebrates’ diets, we employed the isotopic niche area to identify the diversity of resources assimilated by consumers. We hypothesised that i) independent from taxonomic identity, autochthonous food sources are more important than allochthonous material, and ii) to successfully sustain dominating populations in streams with harsh environmental conditions, taxa are forced to feed opportunistically. With this first application of trophic niche metrics combined with Bayesian modelling in alpine stream habitats, we provide insights into the enigma of survival strategies in harsh environments. This is ecologically significant as the ongoing retreat of glaciers causes important abiotic changes that can affect the stability and structure of invertebrate food webs in glacier-fed stream ecosystems (Niedrist & Füreder, 2017; Tunney, McCann, Lester, & Shuter, 2012).

2 | METHODS

2.1 | Sampling design

Samples were collected from six glacial streams in the Hohe Tauern National Park, Central Austrian Alps, in July and September 2015. All stream sites are part of a long-term river monitoring project, obtaining all necessary permits from the Hohe Tauern National Park council. The study design included alpine (above the treeline) glacial and subalpine (below the treeline) glacio-rhithral (mixture of glacial and nonglacial) stream reaches, located at elevations ranging from 1,354 to 2,216 m a.s.l. (Table 1).

All streams, being fed from glaciers with different extent within the catchment, are part of a space-for-time substitution, as they represent different stages of glacier retreat and its consequential environmental influence on the catchment and inhabitants (called environmental harshness). This broad ecological gradient was created by integrating crucial environmental factors shaping invertebrate communities in glacial streams (Niedrist & Füreder, 2016), namely mean water temperature, sediment load and degree of glaciation (% glacier cover in the catchment). These factors have been shown to mediate invertebrates distribution in glacial streams (e.g., Füreder, Schütz, Wallinger, & Burger, 2001; Khamis, Brown, Hannah, & Milner, 2016; Milner et al., 2001; Niedrist & Füreder, 2016). Such an approach decouples environmental conditions from spatial gradients and simulates multifactorial environmental change in glacial streams (Walker, Wardle, Bardgett, & Clarkson, 2010) and its effect on the functional performance of aquatic organisms.

2.2 | Characterisation of stream environments

All streams are continuously monitored in the long-term project monitoring Alpine rivers (Füreder & Schöner, 2013). For this study, we used data from July 2015 to characterise streams environmental conditions. At each site we continuously monitored stream water temperature with digital loggers (Onset Tidbit, MA, U.S.A.) throughout the year, filtered water (1 l) through pre-combusted Whatman GF/F filters (3× per site) and evaluated the discharge through depth/velocity transects using a vane wheel probe (Höntsch probe ZS25, Waiblingen, Germany). Mean sediment concentration (mg/l) was assessed by combusting filters at 450°C for 4 hr to calculate ash-free dry mass (AFDM) per liter. Consequently, we modelled the suspended load (particulate sediment carried in the body of the flow) in mg/s as the combination of discharge (l/s) and suspended solids (mg/l). The glacier cover in relation to the total catchment area (in %) was assessed using ArcVIEW 10.1 by digitising areal images.

2.3 | Sample collection

To characterise benthic chironomid communities, three multihabitat samples were taken at each site using a Surber sampler (mesh size 250 μm, area: 30 × 30 cm, 0.09 m²). We immediately preserved samples in 75% ethanol and stored them for further analyses in the laboratory. For stable isotope analysis, additional multihabitat samples were collected using a Surber sampler and spread on a white board. We manually removed Chironomid larvae, stored them separately in filtered stream water for 24 hr to allow evacuation of their digestive tracts, and rinsed them in distilled water before freezing (Füreder et al., 2003a,b). Additional chironomids were collected by hand searching. The rest of the multihabitat samples such as sand, algae, macrophytes, detritus and other allochthonous material (e.g., detritus and the gold alga Hydrurus foetidus) was frozen in the field and then separately sorted for every stream site in the laboratory.

| Site # | PC 1 scores | Elevation m a.s.l. | Coordinates WGS 1984 | Glaciated catchment % | meanT °C | Sediment load mg/s |
|--------|-------------|-------------------|-----------------------|------------------------|----------|-------------------|
| 1      | −1.48       | 1,433             | 47°01’06.1"N, 13°14’42.1"E | 5.51                  | 7.68     | 1.91              |
| 2      | −0.53       | 1,771             | 47°03’21.4"N, 13°12’25.5"E | 10.68                | 6.18     | 2.79              |
| 3      | −1.27       | 1,354             | 47°04’01.0"N, 13°09’53.7"E | 3.83                  | 7.71     | 17.87             |
| 4      | −0.57       | 1,828             | 47°00’38.5"N, 13°16’41.8"E | 14.5                  | 6.66     | 2.11              |
| 5      | 1.19        | 1,695             | 47°22’32.2"N, 12°26’37.3"E | 42.55                 | 6.21     | 515.21            |
| 6      | 2.66        | 2,216             | 47°59.72"N, 12°24’14.23"E | 48.36                 | 3.23     | 3,559.01          |
Epilithic biofilm was collected by scraping and washing the entire surface of submerged rocks \((n = 3)\) using a toothbrush and stream water. The material was concentrated onto pre-combusted Whatman GF/F filters and frozen in the field. We also collected additional benthic algae (esp. *Hydrurus foetidus*) by hand and froze them in the field.

### 2.4 | Sample processing

#### 2.4.1 | Chironomid community characterisation

We identified sampled chironomids to species or species-group level using published and unpublished keys (e.g., Ferrarese & Rossero, 1981; Rossero & Lencioni, 2015; Schmid, 1993) by mounting head capsules on slides using Euparal and examining them with 400× magnification. We measured the length of each individual from the antennal base to the procercus (a short structure where cerci originate) according to Nolte (1990) using an optical ocular ruler and calculated the body-mass of each taxon at each site using the available length-mass relationships (Benke, Huryn, Smock, & Wallace, 1999; Johnston & Cunjak, 1999; Nolte, 1990).

#### 2.4.2 | Analysis of stable carbon and nitrogen isotopes

All target consumers and potential food sources from each stream site were dried (48 hr, 55°C). Individuals of same Chironomid taxa (la) *D. steinboecki*, (b) *D. latitarsis-gr.I*, (c) *D. cinerella-gr.*, and (d) *Orthocladius luteipes* were dried before separately weighing individuals (0.2–1.2 mg) into tin capsules. The analysis of individual larvae enabled us to assess intraspecific variation and species’ isotopic niches. Potential food sources (mixed detritus including allochthonous sources, *Hydrurus foetidus* and epilithic biofilm on filters) were homogenised using a mortar and pestle before weighing them into tin capsules (2 mg for detritus and *Hydrurus*, >20 mg for biofilm onto filters) to ensure best representation of the sources. All samples were analysed for stable isotope ratio and percentage of carbon and nitrogen on a Delta V advantage (Thermo Scientific, Germany) continuous flow isotope ratio mass spectrometer (CF-IRMS) interfaced with an elemental analyser at the Stable Isotope Unit at the Free University of Bozen, Italy. Analytical standard deviation is ≤0.15% for both, \(\delta^{15}N\) and \(\delta^{13}C\), assessed using in-house standards (IAEA-600, IAEA-CH3, IAEA-NO3). Stable isotope values were calculated using the following equation:

\[
\delta X = \left[ \frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right] \times 1000
\]

where \(R\) is the ratio of heavy and light isotopes of the element \((X)\) in samples \(R_{\text{sample}}\) and standards \(R_{\text{standard}}\). Data were reported as \(\delta\) values, defined as the per mil (‰) deviation from the isotope standards (Pee-Dee Belemnite for carbon and atmospheric nitrogen for nitrogen).

### 2.5 | Data analysis

All statistical analyses and graphics were done in the open-source program R (v3.3.2) (R Core Team, 2015) using specific packages MixSIAR (v2.1.3) (Stock & Semmens, 2013) and SIBER (Jackson et al., 2011). Generally, statistical significance level was set to 0.05.

#### 2.5.1 | Gradient of environmental harshness and glacial influence

We combined the following environmental variables to order all sites gradually according to their abiotic conditions by performing a non-centred principal component analysis (PCA), similar to Ilg & Castella, (2006) and Niedrist, Cantonati, & Füreder (2018). In the analysis, we included monthly mean of the maximum daily water temperatures one month prior to sampling in July (mean water temperature), suspended load (sediment load) and relative glaciated area within the catchment (% glaciated catchment). The variable sediment load was log-transformed due to a skewed distribution. We used PC1 as the final multifactorial environmental harshness gradient, describing most of the environmental differences between the glacial stream sites (86.1%, Supporting Information Figure S1).

#### 2.5.2 | Abundance and mean body-mass of target species along gradient of environmental harshness

We calculated the relative abundance (% of all chironomids) and the mean body-mass (µg/individual) of chironomid taxa groups analysed for stable isotope ratios (A–D) and related them linearly to the degree of environmental harshness of the stream sites. We illustrated the degree of significant or nonsignificant changes of both, relative abundance and body mass, for all taxa groups along the whole gradient.

#### 2.5.3 | Estimating relative contributions of resources to the diet of Diamesa

To determine the most likely relative contributions of each food source to the diet of invertebrate groups, we used a Bayesian stable isotope mixing model, called MixSIAR (v2.1.3) (Stock & Semmens, 2013). Mean isotopic values of the sources were corrected for trophic fractionation prior to input in the model, applying family- and feeding guild-specific values from experimental studies (Bunn, Leigh, & Jardine, 2013; Jardine, Curry, Heard, & Cunjak, 2005). These were –0.32 ± 1.17‰ for \(^{13}\)C and 0.35 ± 0.82‰ for \(^{15}\)N (Jardine et al., 2005). Such family specific values deduced from feeding experiments reduce the reported uncertainty of stable isotope data using general fractionation factors (Alp, Peckarsky, Bernasconi, & Robinson, 2013). The food sources included in the MixSIAR model were (a) detritus, (b) epilithic bulk biofilm, and (c) the gold alga *Hydrurus foetidus*. Chironomids itself could not be included as food sources, as signatures of juvenile larvae was not available. We compared mean isotopic signatures of all sources between stream sites
(one-way ANOVA) and included them separately into the model, as isotopic signals slightly differed between stream sites. Consumers C: N ratios exceeded 3.5, ranging between 3.8 and 8.8. As high lipid contents (~5% for aquatic animals) are known to deplete isotopes δ13C signals, we made lipid normalisation of consumers’ δ13C signatures as suggested by (Post et al., 2007):

\[
\delta^{13}C_{\text{normalised}} = \delta^{13}C_{\text{untreated}} - 3.32 + 0.99 \times C:N
\]

We included 180 δ15N and δ13C signatures, 130 and 50 for consumers and sources, respectively. The MixSIAR model used Markov chain Monte Carlo simulation (MCMC) by running three replicate chains on the predefined chain Monte Carlo simulation (MCMC) by running three replicate

sumers and sources, respectively. The MixSIAR model used Markov
tures as suggested by (Post et al., 2007):

vironmental harshness with the analysis of Bayesian Standard Ellipses using SIBER. This is an innovative method to quantify the size (diversity) of the niche in terms of “trophic area” based on the variability of a population’s stable isotope (C and N) data. The ellipse corrected isotopic niche area is less influenced by extreme values or small samples and thus, represents more reliable estimates of niche extensions than the use of convex hulls, describing the smallest possible area in which all data points are enveloped (Jackson et al., 2011).

We included 130 consumer samples in this analysis. Posterior estimates (analogous to maximum likelihood in classical statistics) of isotopic niche areas for the four consumer groups at each site were modelled using Bayesian Standard Ellipses. The estimated areas (480,000 different simulations for each taxon in each glacial stream, a total of >10^7 simulated isotopic niche areas) were related to degree of environmental harshness using linear models, loess smoothing and by indicating confidence intervals.

2.5.4 Identifying taxon-specific niche breadth and variability between stream sites

The isotopic niche space size (\(\text{Area}_{\text{niche}}\)) and its variability of each consumer group were evaluated for each site along the gradient of environmental harshness with the analysis of Bayesian Standard Ellipses using SIBER. This is an innovative method to quantify the size (diversity) of the niche in terms of “trophic area” based on the variability of a population’s stable isotope (C and N) data. The ellipse corrected isotopic niche area is less influenced by extreme values or small samples and thus, represents more reliable estimates of niche extensions than the use of convex hulls, describing the smallest possible area in which all data points are enveloped (Jackson et al., 2011).

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3 RESULTS

The six glacial streams were separated mainly along the first component of the PCA, significantly explaining 86.1% of differences in water temperature, sediment load and degree of glaciation in the catchment between the sites, whereas the remaining two components described 8% and 5.95% (Supporting Information Figure S1). The gradient of environmental harshness (scores from the first component of the PCA) ranges from −1.48 (the less harsh site) to 2.66 (the most extreme site with cold water temperature, high sediment loads and high degree of glaciation within streams with higher relative abundances in harsher sites. The taxa-specific dominance, however, changed along the gradient of environmental harshness. While group C (D. cinerella–gr.) and D (O. luteipes) were a constant fraction of the chironomid community in all glacial stream sites with 10.4 ± 1.2% and 4.9 ± 1.1%, respectively, the abundance of D. steinboecki and D. latitarsis-gr. I significantly increased with increasing harshness. On the right end of the gradient, chironomid populations were dominated by D. steinboecki (49.2 ± 5.9% of all chironomids) (Figure 2a), their mean relative abundance increased significantly by 33.8% (Figure 2b, simple linear model, \(p < 0.001\)). The abundance of D. latitarsis-gr. I increased for 15.4% along the harshness gradient (Figure 2b), but this relationship was not significantly different from zero (\(p > 0.05\)).

The mean individual body-mass of Diamesa taxa increased along the gradient of environmental harshness (simple linear models, \(p < 0.05\)), whereas no significant change was observed for O. luteipes (\(p > 0.05\)). The averaged body-mass of D. steinboecki was highest in harsh glacial stream sites with 184.18 ± 31.63 μg/individual. Along the entire investigated gradient of environmental conditions, the average body-mass increased significantly for D. steinboecki (127.76 μg/individual; 100, 156, 50% credible intervals

![FIGURE 1] Gradient of environmental harshness. Noncentred analysis of principal components (nPCA) of stream sites and associated environmental habitat conditions: mean daily maximum water temperature in July (mean water temperature), transported amount of sediment per second (sediment load), and percentage of glaciation within streams catchment (% glaciated catchment). For explanatory power of residual components, see Supporting Information Figure S1.
D. latitarsis-gr. I (89.7 µg/individual; 67, 112, CI), and D. cinerella-gr. (58.12 µg/individual, 43, 73, CI). In contrast, the body-mass of O. luteipes did not change (Figure 3).

The potential food sources for grazing invertebrates in the glacial streams had uncorrected signatures that generally ranged from /C0 2.09 to /C0 0.49 for d15N and /C0 29.53 to /C0 23.74 for d13C for epilithic biofilm, from /C0 6.69 to /C0 4.21 for d15N and /C0 36.96 to /C0 26.22 for d13C for Hydrurus foetidus and –4.80 to –2.76 for d13C and –30.01 to –22.82 for d15C for detritus (Figure 4a). Nitrogen and carbon stable isotope signatures of analysed potential food sources were significantly different between streams for epilithon and Hydrurus foetidus (MANOVA, F10,24 = 5.5 and 8.6, p < 0.01, Pillay = 1.40 and 1.56, partial r² = 0.70 and 0.78, respectively), but not for detritus (p = 0.07). Hence, classical baseline correction for d13C and d15N was needed. Generally, the isotope values from Hydrurus foetidus, epilithic biofilm and detritus were consistent with those analysed in other regions in the Alps (Fürer et al., 2003b; Zah, Burgherr, Bernasconi, & Uehlinger, 2001) with –26.79 ± 1.74 (d13C) and –1.25 ± 0.41 (d15N) for epilithic biofilm, –32.63 ± 2.60 (d13C) and –5.59 ± 0.67 (d15N) for Hydrurus foetidus and –26.66 ± 1.69 (d13C) and –3.65 ± 0.60 (d15N) for detritus. This suggests a homogeneous signature of the dominant primary producers and food sources in glacial streams fed by depleted glacial organic carbon (Fellman et al., 2015). However, only epilithic biofilm was enriched in 13C in harsher environments as d13C was significantly related to degree of environmental harshness (F1,16 = 23.1, p < 0.001).

Isotopic signatures of chironomids ranged between –29.69 and –14.56 for d13C and –6.43 and –0.8 for d15N (Figure 4b). While signatures of D. steinboecki and D. latitarsis-gr. I varied with a standard deviation of 2.12 and 3.09 for d13C and 1.34 and 1.44 for d15N, less variation was found for D. cinerella-gr. and sampled Orthocladiinae (O. luteipes) with standard deviations of 1.56 and 1.49 for d13C and 1.08 and 0.55 for d15N. Consumer d13C values were significantly different between groups across glacial streams along the environmental harshness gradient. Carbon signals were significantly

**FIGURE 2** Relative abundance of dominant chironomid taxa groups (a) Diamesa steinboecki, (b) D. latitarsis-gr. I, (c) D. cinerella-gr., and (d) Orthocladius luteipes across glacial streams with differing degree of environmental harshness. Significant and nonsignificant linear relationships are indicated with solid and dashed lines, respectively (left). The barplot (right) illustrates the significant (dark grey) and non-significant (light grey) mean increase or decrease (slope*length of gradient) of taxa-specific (a–d) abundance relative to all chironomid individuals.

**FIGURE 3** Mean body-mass of dominant chironomid taxa groups (a) Diamesa steinboecki, (b) D. latitarsis-gr. I, (c) D. cinerella-gr., and (d) Orthocladius luteipes across glacial streams with differing degree of environmental harshness. Significant and nonsignificant relationships are indicated with solid and dashed lines, respectively (left). The barplot (right) illustrates the significant (dark grey) and nonsignificant (light grey) mean increase or decrease (slope*length of gradient) of taxa-specific (a–d) mean individual body-mass in µg per individual.
more $^{13}$C-depleted at sites with higher environmental harshness ($F_{1,21} = 20, p < 0.001$). Similarly, $\delta^{15}$N signatures increased significantly with increasing degree of environmental harshness for taxa *D. steinboecki* and *D. latitarsis*-gr. I for around 2–3‰ (simple linear models, $p < 0.05$ and $p < 0.001$), suggesting an increase of their trophic level (Figure 5a,b). Together with rising mean $\delta^{15}$N values, the variation of $\delta^{15}$N signatures (standard deviation) between individuals at each site increased for the groups *D. steinboecki* ($R^2 = 0.81, p < 0.05$) and *D. latitarsis*-gr. I, but not for the other groups (Figure 5).

### 3.1 Proportional contribution of potential food sources to chironomid diets

The posterior distribution of estimates from MixSIAR suggests that the relative contribution of investigated potential food sources for chironomids differed substantially between different streams (Figure 6). Mixing modelling revealed a similar pattern of food preference of all *Diamesa* taxa along changes of environmental harshness. While detritus contributed on average $>50\%$ to the diet of *Diamesa* in less harsh glacial streams, the same taxa fed predominantly on...
epilithic biofilm and less on detritus in harsh environments (Figure 6a–c). In contrast, detritus was the dominant food source (>60%) for *O. luteipes* in all streams. The mean contribution of epilithic biofilm was highest for *D. steinboecki* in the harshest stream environment (80%; 73, 87, CI) and lowest for *O. luteipes* (4%; 2, 9, CI) at intermediate harsh conditions (Figure 6a,d). The modelled mean contribution of *Hydrurus foetidus* ranged between 3.6 and 14.2% for *D. steinboecki*, between 3.6 and 14.2% for *D. latitarsis*-gr. I, between 7.6 and 31% for the other *Diamesa* taxa, and from 6.5% and 28.2% for *O. luteipes* (Figure 6a–d).

### 3.2 Individual isotopic niche breadth along environmental harshness

Individual variation in the diet of *D. steinboecki* and *D. latitarsis*-gr. I was significantly related to investigated environmental conditions in streams (*p* < 0.05, Figure 5). For both taxa, these relationships are likely driven by larger deviations in δ¹⁵N instead of δ¹³C. Based on SIBER’s standardised ellipses, the modelled isotopic niche area (standard ellipse area) of *D. steinboecki* and *D. latitarsis*-gr. I increased with increasing environmental harshness (Figure 7a,b). Both groups had the maximum extent of their isotopic niche area in site 5 (area of 7.9 and 9.9 cm² for *D. steinboecki* and *D. latitarsis*-gr. I, respectively). Standard deviations of all simulated estimations for isotopic areas of *D. steinboecki* and *D. latitarsis*-gr. I were also highest for site 5 (4.52 and 5.67, respectively; Table 2). In contrast, the niche area of *D. cinerella*-gr. and *O. luteipes* did not vary across investigated stream sites (Figure 7c,d). Their niche area remained small (area < 1.91 ± 1.09 cm² and < 0.58 ± 0.26 cm², respectively) and standard deviations were low for all habitats along the gradient (0.47 and 0.2 for *D. cinerella*-gr. and *O. luteipes*, respectively; Table 2).

### 4 DISCUSSION

We applied stable isotope analysis coupled with novel Bayesian mixing modelling to disentangle differing resource use and trophic niche variability of the dominant chironomid taxa in glacial streams with differing environmental conditions. Taxa already known to dominate the harshest glacial stream habitats in the Alps (e.g., Fürered et al., 2001; Lods-Crozet et al., 2001; Niedrist & Fürered, 2016) were found to depend on epilithic biofilm as a food source but also on plastic feeding behaviour as strategies to survive cold, dynamic and resource poor living conditions (=harsh conditions). In streams with less harsh conditions, the same taxa showed reduced feeding plasticity, a potential consequence of higher competition and resource partitioning (Castella et al., 2001).

#### 4.1 Body-mass of dominant chironomids in alpine and sub-alpine glacier-fed streams

The observed high densities of *D. steinboecki* and *D. latitarsis*-gr. I, dominating the invertebrate fauna in the investigated harsh glacial streams, support the general longitudinal patterns of invertebrate taxa according to the general model for glacier-fed streams (Milner et al., 2001) and previous studies in the European Alps (Fürered et al., 2001; Lods-Crozet et al., 2001). In addition to their dominance in terms of abundance, our results show that populations of the
genus *Diamesa* found in harsh environments have a mean body-mass, multiple times higher than the body-mass of the same taxa in more moderate glacial streams. Most pronounced was the mean difference in body-mass of *D. steinboecki*, the species known to dominate glacier-fed headwaters in the European Alps (Lods-Crozet et al., 2001), which was more than 125 g between larvae in the most benign and the harshest glacial streams (equals a mean increase of 226%). In contrast, no increase in relative abundance and mean body-mass was found for *Orthocladius luteipes*, a generalist species.

The implication of this is that withstanding harsh conditions in dynamic glacial stream habitats is likely allowing the pioneer invertebrate species to benefit from low competition in that they can acquire the available food sources in these environments. In less harsh environments with higher diversity (Milner et al., 2001) and higher densities of other invertebrates, higher competition leads to enhanced resource partitioning within the invertebrate community (Chase & Leibold, 2003; Tilman et al., 1997), but also results in a more balanced body mass of present taxa.

### 4.2 Primary producers in glacier-fed streams

The isotopic composition of benthic food resources for stream invertebrates are reported to be highly variable between sites (Zah & Uehlinger, 2001), potentially depending on current velocity and water temperature, which are important factors for the physiological discrimination of carbon isotopes by plants (MacLeod & Barton, 1998). However, our analysis of different primary consumers from several catchments in the Central Alps at the same time identified considerable isotopic differences between *H. foetidus* and epilithic biofilm in all glacial streams, but less variance when comparing the

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**TABLE 2** Summary of bayesian estimates for isotopic niches of chironomid taxa in glacier-fed streams based on the analysis of naturally occurring bulk stable isotopes ($\delta^{13}C$ and $\delta^{15}N$) of their tissue. Values are given as median ± standard deviation (SD) of 480,000 simulations (400,000 for *Orthocladius luteipes*)

| Stream site # | 1 - *Diamesa steinboecki* | 2 - *Diamesa latitarsis-gr. I* | 3 - *Diamesa cinerella-gr.* | 4 - *Orthocladius luteipes* | 5 | 6 |
|---------------|----------------------------|-------------------------------|-----------------------------|-----------------------------|-----------------------------|-----------------------------|
| Median        | 0.44                       | 0.88                          | 0.36                        | 0.20                        | 0.27                       | 0.20                       |
| SD            | 0.24                       | 0.59                          | 0.20                        | 0.11                        | 0.18                       | 0.11                       |
| Median        | 0.29                       | 0.74                          | 0.50                        | 0.27                        | 0.30                       | 0.27                       |
| SD            | 0.20                       | 0.50                          | 0.34                        | 0.18                        | 0.34                       | 0.18                       |
| Median        | 0.26                       | 3.12                          | 1.02                        | 0.58                        | 0.54                       | 0.58                       |
| SD            | 0.18                       | 2.09                          | 0.42                        | 0.58                        | 0.30                       | 0.58                       |
| Median        | 1.90                       | 1.54                          | 1.91                        | 0.54                        | 0.14                       | 0.12                       |
| SD            | 1.27                       | 1.04                          | 1.08                        | 0.30                        | NA                         | 0.12                       |
| Median        | 7.93                       | 9.99                          | 1.91                        | 0.14                        | NA                         | NA                         |
| SD            | 4.52                       | 5.67                          | 1.08                        | 0.12                        | NA                         | NA                         |
| Median        | 5.57                       | 6.32                          | 1.91                        | NA                          | NA                         | NA                         |
| SD            | 3.14                       | 3.54                          | 1.91                        | NA                          | NA                         | NA                         |
same resources from different sites. Thus, stable isotope signals from H. foetidus and epilithic biofilm (without thalli of H. foetidus) were also highly variable in our sites, but differentiable thanks to the analysis of samples from several catchments and the same stream type.

The δ13C signatures of epilithic biofilm, which usually is a consortium of autotrophic and heterotrophic bacterial cells and algal assemblages (Gesierich & Rott, 2012; Robinson & Kawecka, 2005; Wilhelm, Singer, Fasching, Battin, & Besemer, 2013), were significantly related with the gradient of environmental harshness between our sites. We observed a depletion of δ13C in harsher environments (streams experiencing higher glacial influence). This potentially indicates the incorporation of glacial carbon, enriched in 13C through (streams experiencing higher glacial influence). This potentially indicates the incorporation of glacial carbon, enriched in 13C through microbial fractionation (Anesio, Hodson, Fritz, Psenner, & Sattler, 2009; Anesio & Laybourn-Parry, 2012), into heterotrophic bacterial cells within the epilithic biofilm, as reported by several authors (Bardgett et al., 2007; Fellman et al., 2015; Singer et al., 2012). Glacially derived organic carbon is highly bioavailable (Singer et al., 2012) and thus stimulates and sustains food webs in glacier-fed streams.

4.3 Consumers in glacier-fed streams

Generally, there is little connection between riparian vegetation and the water of glacier-fed streams, which mainly depend on the interplay between sediment loads and conditions related to glacial melting dynamics (Milner et al., 2009; Smith, Hannah, Gurnell, & Petts, 2001; Zah & Uehlinger, 2001). Besides the direct effect of flow pulses and glacial runoff variability on benthic communities (Brown, Dickson, Carrivick, & Füreder, 2015; Cauvy-Fraunié et al., 2016), our results demonstrate a reduced availability and thus a reduced consumption of allochthonous material by invertebrates in harsh glacier-fed streams. In such stream habitats with little input and low retention of allochthonous plant material, chironomids predominantly feed on epilithic biofilm (including early stages of Hydrurus foetidus). In less harsh environments with more benign habitat conditions, detritus becomes the dominant food source for invertebrates. We clarify the statement by Zah & Uehlinger (2001) that allochthonous material would be important only in groundwater fed channels and conclude that, depending on glacial activity and the interplay of discharge, sediment load and water temperature, allochthonous material is used by invertebrates as food sources in calm glacier-fed streams, when available. Overall, our results indicate a shift within the diet of Diamesa taxa from autochthonous food sources in harsh glacier-fed streams to a more mixed and allochthonous-based food (detritus) in more benign glacial stream ecosystems.

Generally, the relative food source contribution was different for all invertebrate groups between glacial streams with distinct habitat templates. However, all Diamesa taxa exhibited similar food source contributions along the gradient of environmental harshness with higher inputs from epilithic biofilm in harsh environments, likely reflecting the adaptations to dominate alpine headwater regions (Füreder, 2007; Füreder et al., 2001; Lencioni et al., 2015; Lods-Crozat et al., 2001). In contrast, the non-Diamesa taxa Orthocladius luteipes, a common species in alpine streams (Niedrist & Füreder, 2016), fed quite differently (mostly autochthonous and allochthonous detritus in all stream habitats, less on H. foetidus with only little contribution of epilithic biofilm). The different use of resources by both groups (Diamesa and Orthocladius) points to the ecological differences between distinct genera and species within invertebrate families (e.g., chironomids) that may appear uniform. This might motivate ecologists to avoid coarse taxonomic grouping in future studies.

Our finding that selected invertebrate species (D. steinboecki and D. latitarsis –gr.) are able to inhabit considerably different extensions of isotopic niche areas supports our initial hypothesis that alpine stream invertebrates are forced to plastic feeding habits when conditions are harsh. Previous studies suggested a less specialised feeding, a higher degree of omnivory and lower connectivity of invertebrates living in dynamic stream systems (Clitherow et al., 2013; Füreder et al., 2003b). However, conclusions of these pioneer works were geographically or methodically limited. Recent progress in the development of applicable Bayesian mixing models allows the consideration of diet variability, statistically robust mixing models (Bearhop et al., 2004; Jackson et al., 2011; Semmens, Ward, Moore, & Darimont, 2009), and thus imply reliable conclusions derived from stable isotope data. Our work expands the initial findings on the trophic plasticity of invertebrates in harsh environments (Füreder et al., 2003b) by statistically disentangling niche variability of same invertebrate taxa along a gradient of environmental conditions related to glacier retreat. Furthermore, after analysing chironomid populations from several catchments, together with suggestions from previous work (Clitherow et al., 2013; Füreder et al., 2003b), we assume that omnivorous feeding is a widespread survival strategy for pioneer invertebrates in harsh glacier-fed streams. Such behaviour leads to body-masses of individual larvae exceeding the estimations from larvae living in benign streams. In benign glacial riverine ecosystems, together with a higher diversity of benthic communities (Brown et al., 2007), isotopic niche areas are small, indicating a specialisation/restriction of invertebrate species to certain food particles. Thus, our results suggest that in less harsh glacial streams diversity and isotopic niche area are associated with increasing trophic niche differentiation (Tilman et al., 1997) triggered by the availability and the higher input of allochthonous food sources to the stream ecosystem. Consequently, higher competition for the available resources limits the body-mass of larvae.

4.4 Perspectives for invertebrates in glacial streams

Considering recent climate predictions and simulations (IPCC, 2014) the wastage of glaciers, a prominent signal of anthropogenic climate change (Vaughan et al., 2013), may accelerate (Radic & Hock, 2011) and even lead to disappearing glaciers within short times (Zemp et al., 2009). As a consequence, in-stream habitat conditions in glacier-fed streams will ameliorate, generally supporting the diversity of invertebrate communities (Milner et al., 2009) and the biomass of autochthonous primary producers in alpine streams (Rott et al.,
2006; Uehlinger et al., 2010). However, little was known regarding the trophic roles of invertebrates inhabiting glacier-fed streams (Niedrist & Füreder, 2017), but see Füreder et al. (2003a) and Clitherow et al. (2013).

Here, we show that feeding plasticity is a strategy to acquire enough of the biomass of patchily distributed producers in dynamic glacier-fed streams. In analysing the isotopic niche breadth (food source diversity) along streams with differing environmental conditions, our work demonstrates that considerable flexibility in invertebrate feeding activities (this includes predatory activity) is required to dominate harsh glacier-fed streams. In less harsh sites, our results indicate that the same species are restricted to specific food sources. However, how invertebrate predation and cannibalism (Clitherow et al., 2013) contribute to the diet of Diamesa taxa in harsh glacial streams was not quantifiable using stable isotope modelling due to technical limitations and remains to be studied. We suppose that predation or cannibalism could have contributed to the increased niche area and the higher mean trophic level of species in harsh sites. However, Clitherow et al. (2013) detected such feeding links directly at a glacier snout but they were rarely observed in sites further downstream (Niedrist & Füreder, 2017).

We hypothesise that as glaciers recede in mountainous regions (Zemp et al., 2009) and do not further contribute to stream flow, the food web of more diverse invertebrate assemblages will be mainly sustained by seasonal primary production and less by bacteria within the epilithic biofilm fed by glaciers organic carbon (Fellman et al., 2015). Additionally, we suppose that the expected decrease of nutritional quality due to shrinking glacial activity (Niedrist, Cantonati & Füreder, 2018) will further affect the overall production of invertebrate grazers in alpine streams.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

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