Dietary and stable isotope ($\delta^{13}C$, $\delta^{15}N$) analyses in alpine Ephemeroptera and Plecoptera

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Abstract

Headwater streams are intimately tied to their water sources, regional climate, and stream-side and upland vegetation as they define abiotic and biotic conditions. In the case of alpine headwater streams, altitude is also a factor as it directly affects water sources, climate, and vegetation. While previous studies have elucidated longitudinal and seasonal patterns of community structure associated with changes in local environmental conditions in alpine streams, little is known about nutrients, and food availability and utilization. In the Austrian Central Alps, we studied physicochemical conditions, food resources (i.e., benthic CPOM and FPOM, DOM, seston, Aufwuchs) and bottom faunas in nine reaches that contrasted in stream type (glacial versus non-glacial systems), riparian vegetation (above and below the treeline), and season (autumn versus spring). Gut content and stable isotope ($\delta\ ^{13}C$, $\delta\ ^{15}N$) analyses were used to estimate the utilization of food in nine dominant species (Ephemeroptera – *Baetis alpinus*, *Rhithrogena loyolaea*, *Rhithrogena nivata*; Plecoptera – *Dictyogenus fontium*, *Leuctra* sp., *Nemoura* sp., *Protonemura* sp., *Rhabdiopteryx alpina*, *Siphonoperla* sp.). Gut content indicated detritus was the dominant food consumed in all streams. Stable isotope analysis suggests several species feed opportunistically on algae, especially in glacial streams. Thus, it appears that autochthonous production can be important in glacial streams, in spite of long snow cover, frequent flooding, and high turbidity.

Keywords: glacier-fed, spring-fed, streams, organic matter, food availability.

Introduction

Physico-chemical and biological conditions within a stream reflect a wide variety of factors, including local and regional climate, chemical characteristics of watershed geology and water sources, landscape and channel geomorphology, riparian and upland vegetation, and the species that inhabit that stream. These factors directly or indirectly influence water temperature, solar radiation, substrate composition and distribution, temporal and spatial variation in flow, nutrient concentration and availability, input and fate of organic matter (coarse, fine, and dissolved material) from terrestrial sources, and the survival and growth of microbes, algae, macrophytes, invertebrates and vertebrates within the stream.

The harsh climate in alpine landscapes causes specific conditions and may affect alpine streams directly (e.g., through low water temperature, presence of ice and snow) or indirectly (e.g., by inhibiting growth of riparian vegetation), causing alpine streams to differ from headwater streams at lower elevations. Harsh environmental conditions can cause alpine streams to differ both in structure (e.g., fewer species, lower densities) and function (e.g., lower growth and production rates, food webs skewed towards different food sources) relative to headwater streams that are commonly studied.

For example, low temperature can significantly decrease growth rates and increase development times (e.g., from ≤ 1 yr to 2-4 yrs) for some aquatic insects (Humpesch, 1979; Brittain, 1990). Similarly, low temperature, extended periods of snow cover, turbidity, and low nutrient concentrations can severely limit algal and macrophyte (i.e., autochthonous) production in glacier-fed streams (Steffan, 1971, 1972, 1974; Milner and Petts, 1994; Ward, 1994). The absence of riparian and upland trees (and often shrubs and bushes) in alpine meadows results in more direct solar radiation and less allochthonous organic matter (e.g., leaves and wood) reaching alpine streams.

In alpine and arctic regions, running water ecosystems are particularly affected by their discharge patterns, which depend greatly on their prevailing water sources (glacier, groundwater) and regional climate conditions (snowmelt, rain). Based on prevailing physico-chemical conditions and biological assemblages, these stream reaches have been assigned to specific stream types: kryal, rhithral and glacio-rhithral streams or rivers (Steffan, 1974; Braukmann, 1987; Milner and

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Petts, 1994; Ward, 1994; Füreder, 1999). In several investigations (for relevant publications see reviews by Milner and Petts, 1994; Ward, 1994; Füreder, 1999), faunistic patterns and possible adaptations of the fauna to alpine conditions have been discussed, characterizing the glacial stream fauna as a very specific assemblage.

While increasing scientific interest in glacial streams elucidated longitudinal and seasonal patterns of community structure (Brittain *et al.*, 2000; Füreder *et al,*. 2000; Schütz *et al.*, 2000; Füreder *et al.*, 2001; Gislason *et al.*, 2000; Tockner *et al.*, 1997), various aspects in alpine streams and especially in glacial streams still remain unclear, like the availability of food resources, food web structure, strategies of aquatic invertebrates (adaptations and life cycles) and the taxonomy of sometimes dominant invertebrate groups.

In this paper we focus on food availability and food consumption and utilisation by species of Ephemeroptera and Plecoptera typical for alpine stream reaches. In particular, the main objectives treated here were to 1) evaluate differences in the abundance in Ephemeroptera and Plecoptera, when stream types (glacial *vs*. spring-fed) and stream segments (above *vs*. below the tree line) are compared, 2) estimate the role of food availability by means of organic matter concentration, gut content and stable isotope analysis in Ephemeroptera and Plecoptera taxa, 3) complement the gut content approach by stable isotope analysis, and 3) draw some conclusions in order to explain ecosystem function of alpine streams.

Material and Methods

We examined these questions in six alpine streams: four glacier-fed and two spring-fed streams near Obergurgl, Ötztal, Tyrol, Austria (Fig. 1; Table 1). Sampling was conducted in 5 sites above treeline and 4 sites below treeline in late winter (at the end of snow cover – winter aspect) and autumn (summer aspect) in order to assess spatial and seasonal heterogeneity.

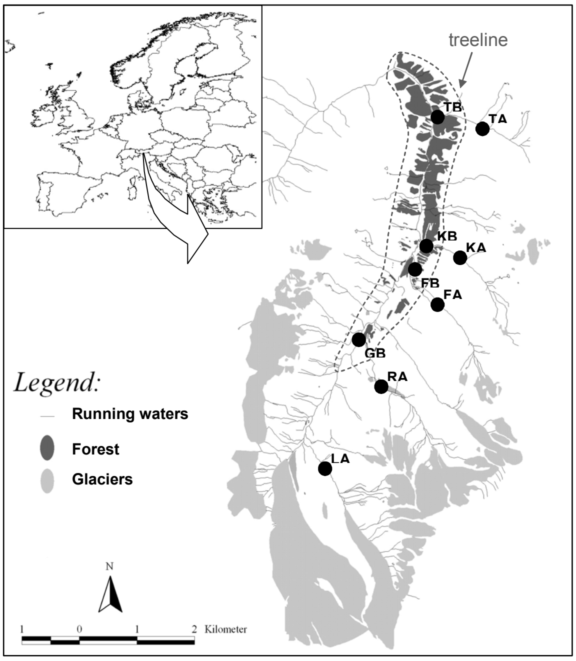

Fig. 1 - Map of the investigation area around Obergurgl, Ötztal, Tirol, Austria (Map produced by C.M.E. Hansen)

Food resources were described from estimates of benthic particulate organic matter (FPOM, CPOM), seston transport, and periphyton (Chl a concentration). Particulate organic matter was sorted from 5 invertebrate benthic samples collected at each site. Particulate matter was separated into different fractions, i.e. material greater than 640 µm and finer material (< 100 µm, > 100µm) with standard sieves. Seston (organic particles suspended in the water column) was collected by filtering a minimum of 1 L stream water (2 replicates) through a pre-weighed filter (GF/C, pore size <0.5 µm). All of these organic matter samples were dried at 60°C for 24 h, and then ashed in a muffle furnace at 450°C for 1 h (Wallace and Grubaugh, 1996). Measures of organic matter were reported as dry mass and/or ash free dry mass. DOM was measured as DOC.

Table 1 - General characteristics of streams and sampling sites

Strema	Origin	Site	Altitude (m a.s.l.)	Site *vs.* treeline	Catchment area (Km^2)
Königsbach	non-glacial	KA	2240	above	4.4
		KB	1850	below	5.8
Timmelsbach	non-glacial	TA	2100	above	3.6
		TB	1600	below	6.3
Ferwallbach	glacial (60 %)	FA	2380	above	4.1
		FB	1960	below	7.9
Rotmoosache	glacial	RA	2280	above	10.4
Langtaler Bach	glacial	LA	2440	above	10.7
Gurgler Ache	glacial	GB	2030	below	39.1

Table 2 - Ephemeroptera and Plecoptera taxa used for gut content and stable isotope ($\delta\ ^{13}C$, $\delta\ ^{15}N$) analysis. Feeding type categories follow Merritt and Cummins (1996) and Moog (1995), bold letters indicate dominant feeding role; number of "+" indicate different abundance classes from low (+), frequent (++) to high (+++)

	Feeding type Merritt & Cummins 1996	Feeding type Moog 1995	Benthos	Gut content	$\delta^{13}C$ $\delta^{15}N$
Ephemeroptera					
Baetis alpinus PICTET, 1843-1845	coll gath	graz/detr	+++	x	x
Rhithrogena loyolaea NAVAS, 1922	coll gath	graz/detr	++	x	x
Rhithrogena nivata (EATON, 1871)	coll gath	graz/detr	+	x	x
Plecoptera					
Dictyogenus fontium (PICTET, 1841)	pred	**Pred**	+	x	x
Leuctra sp.	shred/detr	shred/graz/**detr**	++	x	x
Nemoura sp.	shred/detr	shred/**detr**	+	x	x
Protonemura sp.	shred/detr	**shred**/graz/detr	+	x	x
Rhabdiopteryx alpina KÜHTREIBER, 1934	shred/detr	**shred**/graz/detr	+	x	x
Siphonoperla sp.	coll gath/pred	shred/graz/detr/**pred**	+	x	x

Table 3 - Summary of organic matter fractions (FPOM, CPOM), organic seston and organic Aufwuchs (numbers are means, BPOM benthic organic matter). Details can be found in Füreder *et al.* (2003).

	Season		**Stream Type**			Above	Below	
	Autumn	Spring	Glacial	Glacial (-FB)	Spring-fed	**Treeline**		Average
Seston ($\mu g\ L^{-1}$)	627	1578	1678	1939	383	1030	1194	1102
Biofilm ($mg\ m^{-2}$)	722	596	751	522	550	610	721	659
BPOM ($g\ m^{-2}$)	864	3940	1473	867	3342	1794	3079	2402

Algae biomass was estimated as chlorophyll a content of algae attached to rocks. Three stones were collected at random at all sites, and periphyton from the surface of each stone was scraped off using a toothbrush. The scrapings were washed with distilled water onto a 4.7 cm GF/C filter. The filter was then wrapped with aluminum foil and placed in a thermos. In the laboratory (within 1 month of collection in cool and dark storage), filter papers were processed by grinding each filter separately in a tissue grinder at 500 rpm for 1 minute in 2 ml 90% acetone solution. After grinding the sample was flushed into a screw-cap centrifuge tube with an additional 10 ml 90% acetone solution and allowed to extract for a period of 2 hours at 4 °C in dark conditions. The sample was then centrifuged for 20 minutes at 500 rpm before analysis by a spectrophotometer.

Stable isotope signatures were obtained for leaves and wood from riparian vegetation, wind-borne detritus embedded in snow pack, and submerged detritus (seston, DOM, FPOM, CPOM), macroalgae, and periphyton from the streams. The structure and function of the benthic invertebrate assemblages were described concurrently with estimates of density and functional feeding group composition and with estimates of density, dietary composition, and energy utilization (stable isotope analysis) for selected Ephemeroptera and Plecoptera species (Table 2).

For stomach content and stable isotope analyses, representative individuals from each reach were collected with tweezers and placed in separate sample bottles. Some specimens were frozen for stomach content analysis while others were kept alive in water for 24 h to allow food material to be excreted before stable isotope analysis. To describe stomach contents, the mid- and foreguts were removed from about 10 preserved larvae of each species, stomach contents were transferred to separate slides, and percent compositions by volume of the major food items were estimated for each individual. Specimens selected for stable isotope analysis (ten to twenty individuals per taxon and site) were washed with distilled water and dried at 60°C for 24 h. At least 100 µg of tissue was used for dual isotope analysis of δ13C and δ15N, respectively. Three or more replicates per species, site, and season were taken. Dual isotope was also performed from the major food resources for comparison with primary and secondary consumers (Hershey and Peterson, 1996).

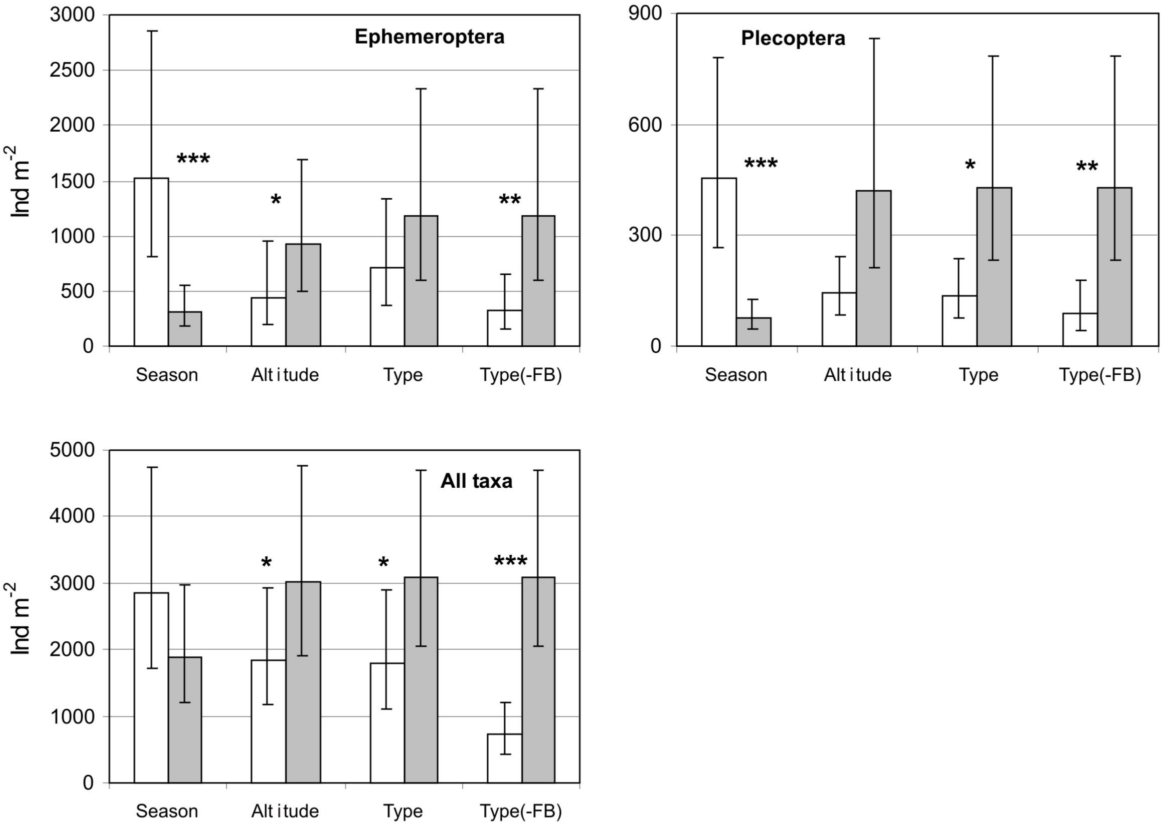

Fig. 2 - Seasonal (white: autumn, grey: spring), altitudinal (white: above, grey: below treeline) and stream-type (white: glacial, grey: spring-fed) comparisons of abundances in the studied streams (columns are means; bars indicate upper and lower confidence limits; asterix show significance levels, where * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$)

Results

Organic matter content of suspended material (Table 3) averaged from 383 $\mu g\ L^{-1}$ in the spring-fed streams to 1678 µg L in the glacier-fed streams. When the mixed-origin stream Ferwallbach was not considered, suspended organic matter increased to a mean of 1939 $\mu g\ L^{-1}$. Suspended organic matter concentration was higher in spring (1578 $\mu g\ L^{-1}$) compared to autumn (627 $\mu g\ L^{-1}$) as well as below the treeline (1194 $\mu g\ L^{-1}$) compared to alpine meadows (1030 $\mu g\ L^{-1}$). The average concentration of suspended organic matter when all stream types and both seasons were considered was 1102 $\mu g\ L^{-1}$.

The organic portion of the biofilm on rocks was on average higher in the glacial streams (751 $mg\ m^{-2}$) but reached almost the same mean, when the glacial streams (excluded Ferwallbach) were compared to the spring-fed streams (522 *vs*. 550 $mg\ m^{-2}$). Biofilm development was higher in autumn (722 $mg\ m^{-2}$) compared to spring (596 $mg\ m^{-2}$). The average content of organic matter in the biofilm was 659 $mg\ m^{-2}$ with a higher value below the treeline (721 $mg\ m^{-2}$) compared to reaches above (610 $mg\ m^{-2}$).

Benthic organic matter concentration (mean 2402 $g\ m^{-2}$) was higher in spring (3940 $g\ m^{-2}$) and below the treeline (3079 $g\ m^{-2}$) compared to autumn (864 $g\ m^{-2}$) and reaches above (1794 $g\ m^{-2}$). When both seasons were considered, glacial streams had lower BPOM concentration than spring-fed streams, 867 $g\ m^{-2}$ and 1473 $g\ m^{-2}$ (when including Ferwallbach) compared to 3342 $g\ m^{-2}$.

The comparison of abundances of all taxa but especially Ephemeroptera and Plecoptera resulted in significant differences by season and also by stream type (Fig. 2). When Ferwallbach was not included in the comparison, the abundances in the glacial streams were significantly different when compared to the spring-fed streams (Ephemeroptera and Plecoptera $P < 0.01$; all taxa $P < 0.001$). Differences between altitudes were significant for Ephemeroptera ($P < 0.05$) and all taxa ($P < 0.05$). Autumn abundances of both Ephemeroptera and Plecoptera were all significantly higher than those in spring ($P < 0.001$).

Gut content analysis of selected Ephemeroptera and Plecoptera taxa (see Table 2 for taxa list) showed a dominance of detritus, both in glacial streams as well as in spring-fed streams (Fig. 3). In the analysed taxa, algae and diatoms were detectable to a minor portion. In glacial streams the relative amount of algae and diatoms in gut contents was higher below the treeline compared to areas above; in the spring-fed streams it was equally distributed. Plant fragments reached a higher portion in the spring-fed streams than in the glacial streams, where they were evident only below the treeline. Inorganic matter of gut content was somewhat higher in Ephemeroptera and Plecoptera taxa from the glacial streams.

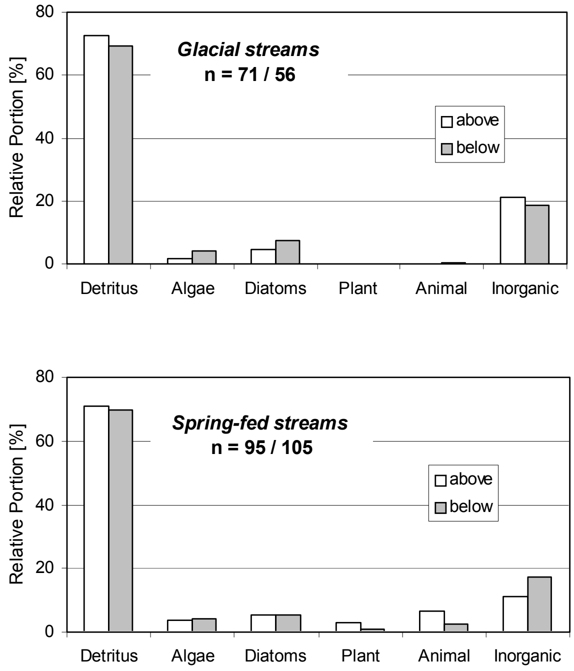

Fig. 3 - Relative portion of gut content in Ephemeroptera and Plecoptera (considered together) sampled above (white columns) and below (grey columns) the treeline; n is the number of examined animals.

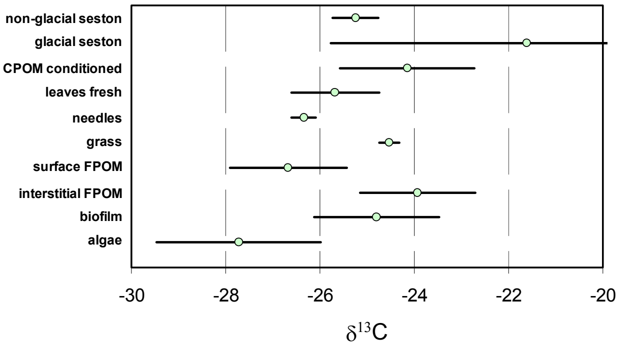

Fig. 4 - Carbon isotopic signals of potential food items. Details can be found in Füreder *et al.* (2003).

As described in detail in Füreder *et al.* (2003), stable isotope signatures differed greatly among samples and available food types. Relatively fresh or unconditioned coarse particulate organic matter (CPOM) collected as needles (–26.3), leaves (–25.7), and grass (–24.5) from along the stream had distinct stable isotope signatures relative to filamentous algae (*Hydrurus*) (–27.7) (Fig. 4). Conditioned CPOM (–24.2) collected in the stream had a variable signature, presumably because of the mixture of different sources and degree of conditioning, but appeared more similar to grass than needles or leaves. Biofilm (–24.8) was high compared with filamentous algae. Fine particulate organic matter (FPOM) from the streambed surface (–26.7) appeared more similar to algae than to terrestrial sources. Interstitial FPOM (–23.9) was more similar to conditioned terrestrial sources. Seston in glacier-fed streams was highly variable (mean = –21.6 ± 4.2) compared with seston from non-glacial streams (mean –25.2 ± 0.5).

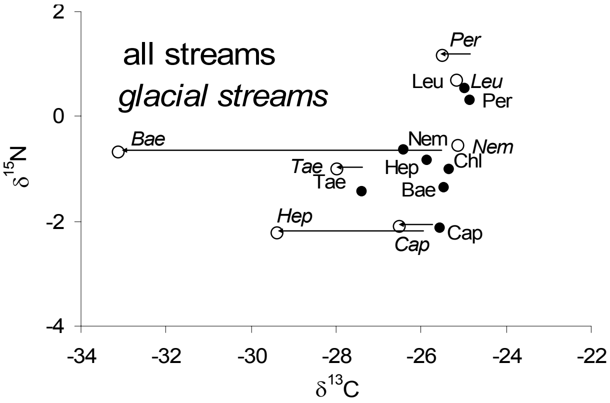

Fig. 5 - Carbon and nitrogen isotopic ratios for Ephemeroptera and Plecoptera families. Black letters indicate mean isotopic ratios from all streams and sites; grey shows results from glacial streams.

Carbon and nitrogen signals in the Ephemeroptera and Plecoptera families overlapped, however distinct patterns were evident when both isotopes were considered together (Fig. 5). When all streams were considered, Capniidae, Baetidae, Taeniopterygidae, Heptageniidae, Chloroperlidae and Nemouridae had lower N signals, while Leuctridae and Perlodidae had higher ones. Their carbon signals ranged between –24 and –28. Taeniopterygidae showed the lowest $\delta^{13}C$ and Capniidae the lowest $\delta^{15}N$.

In glacial streams the carbon signals were much lower than the average from all streams, this was most evident in Baetidae (from –25.5 to –

30.1), Capniidae (from –25.6 to –26.5), Heptageniidae (from –25.8 to –29.4), Perlodidae (from –24.9 to –25.5) and Taeniopterygidae (from –27.4 to –28.0).

Discussion

The differences among invertebrate assemblages in alpine streams reflect the different environmental conditions that are characteristic of the individual stream types such as degree of glacial influence (e.g., glacier-dominated versus spring-fed streams; Schütz, 1999; Füreder *et al.*, 2000; Schütz *et al.*, 2000; Füreder *et al.*, 2001; Schütz *et al.*, 2001), geology of the watershed (e.g., calcareous versus siliceous rocks), and disturbance timing and intensity (e.g., seasonal floods from snow-melt versus more stable flow from groundwater inputs; Milner and Petts, 1994; Ward, 1994; Tockner *et al.*, 1997).

Our comparison of the relative availability of autochthonous and allochthonous food resources in high elevation streams that flow through alpine meadows and through downstream forests delivered interesting results. Especially, when the individual stream types were considered, most differences were significant. Glacial streams were found to be different from non-glacial systems, having less aquatic invertebrate species and lower abundances, influenced by the harsh environmental conditions in these systems (Ward, 1994; Milner and Petts, 1994; Füreder, 1999). Previous investigations from 1996 through 1998 in a glacier-fed and a spring-fed stream of the Obergurgl area, helped to understand seasonal and longitudinal patterns of hydrological and physico-chemical conditions and their effect on the stream fauna (Schütz, 1999; Füreder *et al.*, 2001; Schütz *et al.*, 2001) and to explain the significance of differences between the two stream types. In our study, the significant difference of Ephemeroptera and Plecoptera abundance between glacial and non-glacial streams is another example of the importance of water origin for the structure and function of alpine stream ecosystems.

Organic matter availability also differed between the stream types. Average benthic POM in spring-fed streams was four times higher than in glacial streams, however biofilm reached equal mean values in both stream types. Although low temperature, extended periods of snow cover, turbidity, and low nutrient concentrations were made responsible for limited algal growth in glacier-fed streams (Steffan, 1971; 1972; 1974; Milner and Petts, 1994; Ward, 1994), specific seasonal conditions may favour biofilm development. Then, more direct solar radiation and the release of limiting nutrients from glacial sediments (phosphorus) and snow melt (nitrate) may enhance algal growth. Seasonal analysis of invertebrate taxa number and abundance provided further evidence of periods with favourable conditions in glacier-fed systems (Füreder *et al.*, 2001; Schütz *et al.*, 2001).

With increasing distance from the source, seasonal and diurnal dynamics may change; due to incoming tributaries these dynamics either increase (glacier-fed tributaries) or decrease (with incoming groundwater). In addition, the tree line is supposed to provide additional changes in environmental conditions, supporting the system with higher levels of allochthonous organic matter reaching alpine streams.

Our results on ingested food by Ephemeroptera and Plecoptera demonstrated the limited information obtained from principal dietary component analysis in alpine streams because detritus was the dominant item, which was impossible to assign to a food source. Under- or overestimation of filamentous algae and diatoms as clearly identifiable autochthonous primary producers, depending on differing digestions and/or remaining fragments was possible. But also in taking the whole gut for analysis, we might have counted digested food and therefore overestimated the food item "detritus". Finally, the results might just be a reflection of previously consumed matter and correspond little with assimilation and growth.

In contrast, recent stable isotope analysis were shown to provide important information on the relative importance of autochthonous and allochthonous organic matter for invertebrates (Zah *et al.*, 2000, 2001; Füreder *et al.*, *in press*). Zah *et al.* (2000) found shifts in the diet when they compared sites close to the glacier to sites close to the valley edge and further downstream. Correspondingly, the lower signals in glacial-stream mayflies and stoneflies compared to spring-fed stream species in our study provided equal information, autochthonous algae being an important food in glacial streams. Indirect evidence is supplied by relatively high biofilm standing crops in the glacial streams, which reached the same level as in the spring-fed streams.

The relative role of autochthonous and allochthonous processes in driving animal communities has been extensively debated, especially for glacial headwater streams. In-stream primary production in glacial headwater streams has been considered to be low due to a high disturbance frequency and high turbidity (Steffan, 1971, 1972, 1974). However, some authors reported also relatively high algal biomass at certain periods of time (Uehlinger *et al.*, 1998). Our results of low C signals in aquatic insects of glacial streams are evidence that primary production is more important in glacial stream than previously assumed. Ephemeroptera and some Plecoptera species were more closely tied to algal carbon in glacial streams than in spring-fed streams. Also, Diptera and Ephemeroptera above the tree line showed lower C signals than their downstream relatives (Füreder *et al. in press*), reflecting the importance of in-stream carbon in streams with limited potential for terrestrial inputs.

Our study also demonstrates the importance of using simultaneously Carbon and Nitrogen stable isotopes to increase the resolution of results. The food resource biofilm, that could be related with the amorphous detritus found in gut content of larvae inspected in the present study, presented C signatures in the range of different allochthonous organic matter (grass, fresh and conditioned leaves and FPOM). Therefore primary consumers (both ephemeropterans and plecopterans), which similarly ranged between –28 and –26 $\delta^{13}C$ values, could not be definitely related to any specific food item. Additional information is provided by the N signatures, when considering an increase about 3 units between trophic levels (Peterson and Fry, 1987). While most ephemeropterans and plecopterans had N signals between –1 and –2, Leuctridae and Perlodidae were placed around +1, leading to the assumption that they may occupy predatory feeding habits. Interesting in the case of Leuctridae, assigned by Moog (1995) and, Merrit and Cummins (1996) to shredders, grazers and detritivores, is, that a considerable part of their food consists of animal tissue.

This shift of diets in taxa of Ephemeroptera and Plecoptera demonstrates the flexibility of feeding modes in glacial stream species, which is important to overcome periods of low food quality and quantity. When the whole fauna was considered (Füreder *et al.*, *in press*), smaller differences between trophic levels (based on N) combined with the high degree of overlap in food consumption (based on C) suggested that the opportunistic and omnivorous nature of stream insect feeding is intensified in alpine streams, especially above the tree line where primary production is important but restricted to a short period by long winter cover. In glacier-fed streams, primary production is restricted to an even shorter period by increased flow, substrate movement, and turbidity (Ward, 1994; Milner and Petts, 1994). Thus, aquatic consumers in alpine streams have no choice but to feed on a variety of food types, depending on what is available at a specific time or place. Apart from predators and filter feeders, which exhibited relatively limited variation, alpine stream insects are very opportunistic feeders, which may be an important strategy in the harsh abiotic conditions of alpine streams.

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