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Effects of snow cover on the benthic fauna in a glacier-fed stream

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SUMMARY

1. Alpine streams above the tree line are covered by snow for 6–9 months a year. However, winter dynamics in these streams are poorly known. The annual patterns of macroinvertebrate assemblages were studied in a glacial stream in the Austrian Alps, providing information on conditions under the snow.
2. Snow cover influenced water temperature, the content of benthic organic matter and insect development. Taxa richness and abundance of macroinvertebrates did not show a pronounced seasonal pattern. The duration of the autumn period with stable stream beds was important in determining the abundance and composition of the winter fauna.
3. There were significant differences in species composition between summer and winter. Two potential strategies in larval survival were evident: adaptation to the extreme abiotic conditions in summer (e.g. *Diamesa* spp.) or avoidance of these conditions and development during winter (e.g. Ephemeroptera and Plecoptera).
4. A comparison of a stream reach with continuous snow cover and a stream reach that remained open throughout winter showed that conditions under snow are suboptimal. At the open stream site, with higher water temperatures and greater food supply (benthic organic matter content), abundance and taxa richness was higher and larval growth was faster. Several taxa were found exclusively at this site.
5. Winter conditions did not provide an entirely homogeneous environment, abiotic conditions changed rapidly, especially at the onset of snowfall and at snowmelt. Continuous monitoring is necessary to recognize spatial and temporal heterogeneity in winter environments and the fauna of alpine streams.

Keywords: benthic fauna, glacial stream, snow cover, winter sampling

Introduction

Milner & Petts (1994) and Ward (1994) presented an overview and synthesis of studies conducted in glacial streams and described typical features, such as low water temperatures, large diel flow fluctuations, unstable stream beds, turbid waters, dominance of *Diamesa* species (in the uppermost reaches), paucity of organic resources and sparse growth of microphytes. Milner & Petts (1994) proposed a conceptual model predicting the longitudinal distribution of the fauna along environmental downstream gradients, mainly water temperature and stream bed stability. More recently, studies within the EU-project Arctic and Alpine Stream Ecosystem Research (AASER) (Brittain *et al*., 2000) have been conducted in several European ecoregions to evaluate the validity of this conceptual model for a wide range of arctic and alpine glacier-fed streams. As it was not the objective of this project to evaluate the applicability of the model for the winter months, sampling was restricted to the snow-free season.

Abiotic conditions during winter, including the physico-chemical nature of stream waters and the

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influence of snow and ice, have been investigated more intensively than the biota. Water chemistry of glacial streams changes between summer and winter from glacial meltwater-dominated to groundwater-dominated conditions (Tockner *et al*., 1997). During snowmelt, preferential elution of ions from the snow can cause peaks of solutes in the stream water (Johannessen & Henriksen, 1978; Tranter *et al*., 1987; Helliwell *et al*., 1998) and also ice break-up can have a major influence on current velocity, water temperature, concentrations of suspended solids and substrate scouring (Prowse, 1994; Scrimgeour *et al*., 1994).

Alpine regions above the tree line are covered by snow for 6–9 months a year. However, due to problems of sampling under the snow, few investigations on stream invertebrates have been performed during winter. As a result, only a few recent studies of the biota of glacial streams in Switzerland and Austria have included winter sampling (Füreder *et al*., 1998; Burgherr & Ward, 2000; Robinson, Uehlinger & Hieber, 2001), although Bretschko (1969) had described macroinvertebrate assemblages in glacial streams during winter, that differed markedly from summer assemblages, thus being more similar to the fauna of spring-fed streams. The results of the more recent studies have shown that invertebrates respond to the seasonal changes of their environment, which confirmed the findings of Bretschko (1969) that the assemblages in glacial streams show particular winter aspects in terms of taxa richness, composition and abundance. In the present paper we report data on macroinvertebrate assemblages in streams in the Ötztal Alps over a complete 2 year period including winter, in order to provide continuous year-round information. The main objective was to investigate how the fauna of glacier-fed streams is influenced by the changing environmental conditions from summer to winter and to determine how macroinvertebrates survive the conditions of low water temperatures and lack of light.

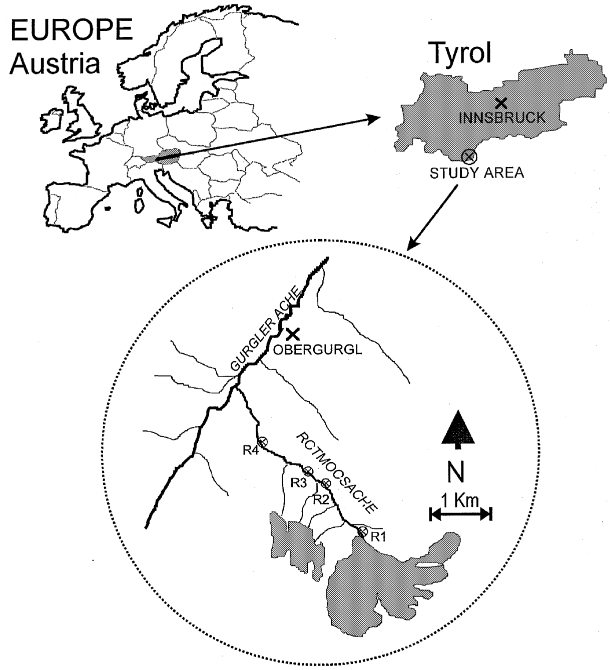

Fig. 1 Study area in the upper Ötztal with glacial stream Rotmoosache and sampling sites R1, R2, R3, R4, glacier areas grey shaded.

Methods

Study area

The study sites were located along a glacial stream, Rotmoosache, in the Ötztal Alps near Obergurgl (Tyrol, Austria) close to the Italian border (46°50′ N/ 11°03′ E) (Fig. 1). The valley has a north-west exposure. The catchment geology is characterized by crystalline gneiss, with dominant rocks consisting of easily weatherable gneiss and micaschists, and of marble and hornblende in the southern part of the catchment (Frank *et al*., 1987). We investigated four sites above the tree line at altitudes between 2250 and 2450 m a.s.l. (Table 1). The sites were selected to take account of the morphology of the valley, altitude and different periods of glacial retreat.

Macroinvertebrates

Sampling was carried out monthly from July 1996 to June 1998. Benthic samples were taken with a Surber sampler (0.09 m^2, 100 μm mesh, 3–5 replicates per site). Water temperature was recorded permanently by dataloggers (Onset Stow Away®Temp, Onset Stowaway, MA, USA). It was not possible to take some of the winter samples, either because of dry and frozen sites or because of avalanche danger, especially at R1 and R3.

Benthos samples were preserved in the field with ethanol (80%) and subsequently separated into three size fractions: > 670 μm, 250–670 μm and 100–250 μm. The invertebrates were sorted and counted under a dissecting microscope and determined to species

Table 1 Characterization of the Rotmoosache and sampling sites R1–R4. All values are mean ± SD

Steam characteristics	Summer		Winter	
Discharge (Ls^{-1})	1515 ± 736		289 ± 196	
Suspended solids (mg L^{-1})	208 ± 239		1.5 ± 3.0	
Conductivity (μS cm^{-1})	89 ± 47		208 ± 44	
pH	8.1 ± 0.4		7.95 ± 0.1	
Sampling sites	R1	R2	R3	R4
Altitude (m a.s.l.)	2450	2300	2270	2250
Distance to source (m)	0	1200	2050	3350
Sub-catchment size (km^2)	3.7	7.1	8.4	10.3
Glaciated area (%)	84	52	48	40
Ice free	Recently	1920	1850	Before 1850

where possible, using current keys. The remaining taxa were determined to genus, subfamily, class or subclass.

Fine benthic organic matter (FBOM) was expressed as percent ash-free dry matter (loss on ignition) of the pooled material remaining from the benthic samples after the invertebrates had been removed. This substrate material had a grain size <1 mm and >100 μm.

Data treatment

Between-sample comparisons of abundance and taxa richness were performed using the Kruskal–Wallis test (Statistix, 2000). The program CANOCO (ter Braak, 1988; ter Braak & Smilaur, 1998) was used to perform an indirect gradient analysis on the data of the benthic samples from R2 and R4. According to the gradient length, a linear model [Principal Components Analysis (PCA)] was chosen and individual numbers were log(x + 1) transformed.

Results

Discharge

Stream discharge declined strongly as air temperatures declined in September and at the onset of snowfall (Fig. 2). The final peak in autumn was caused by heavy rainfall in October 1996, but then air temperatures fell rapidly and discharge stabilized at baseflow values with little fluctuation during winter. The first and second snowmelt peaks corresponded to increases in air temperature. After the second peak in June 1997, snow had no further detectable influence on discharge, whereas rainstorms and glacial melt affected discharge during the summer months.

Water temperature

Although snow cover formed in October/November, some reaches of the stream remained open longer than others. This heterogeneous pattern was reflected in the water temperature (Fig. 3), with daily variations until the snow cover was completely closed and water temperatures stabilized between 0 and 1 °C. At R2, diel temperature fluctuations started again in May under the snow cover, about 1 month before the stream was again free of snow.

Site R4, however, behaved very differently (Fig. 3). Snow did not cover the stream during winter, most probably as a result of groundwater upwelling. This open stream reach varied between 10 and 30 m in length. During the coldest months of winter, solar radiation did not cause an increase in stream water temperature, but later, in March, April and May, marked diel fluctuations of water temperature were observed.

Benthic organic matter

The FBOM content did not follow a seasonal pattern. Mean values did not differ significantly between summer and the snow-covered sites in winter (Fig. 4). However, the differences in FBOM between the snow-covered site R2 and the snow-free site R4 were significant ($P < 0.01$, Mann–Whitney *U*-test) during winter (Fig. 4). At R4, the increase in water temperature from February to May was followed by a strong increase in FBOM (1.02 ± 0.77%), because of a

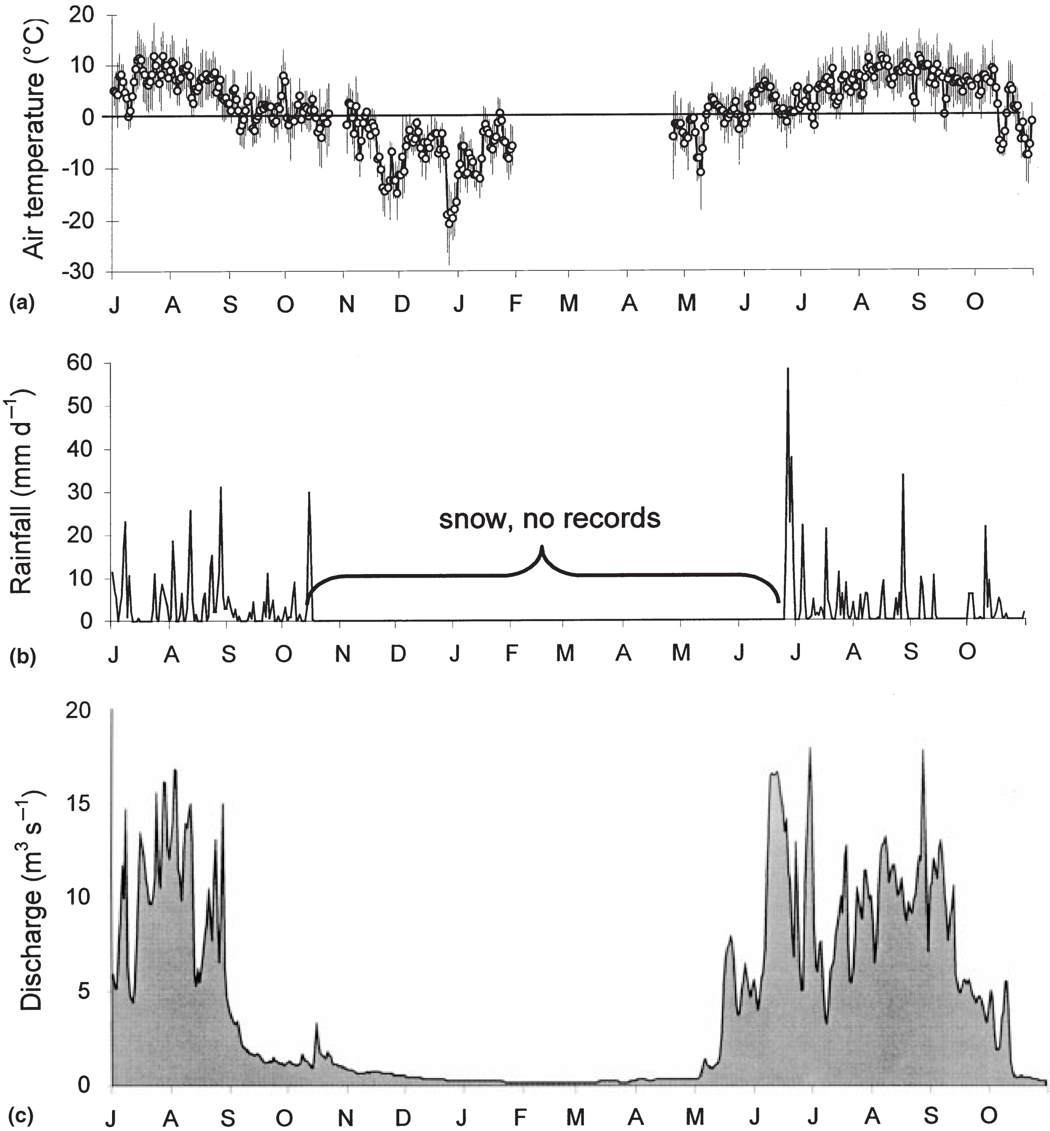

Fig. 2 (a) Air temperature, (b) rainfall from July 1996 to October 1997 in the Rotmoos valley (data from the climate station of R. Kaufmann, unpublished data) and (c) average daily discharge of the gauging station in Obergurgl, Gurgler Ache from June 1996 to October 1997 (Tyrolean hydropower company, data provided by the Tyrol government, Hydrographical service).

dense growth of the alga *Hydrurus foetidus*. At R2, the values remained low (0.23 ± 0.09%), and no growth of *Hydrurus* was observed.

Macroinvertebrates

Taxa richness and abundance varied between sites and seasons but there was no distinct annual pattern (Fig. 5). Abundance was generally higher during the first year of sampling (July 1996–June 1997) compared with the second. Significantly lower abundances were found at times of maximal discharge in summer (August 1996, September 1997), at R2 in the second winter (January 1998) and at R4 during snowmelt (June 1998). The abundance peaks were caused by numerous small larvae of a single taxon, *Baetis* in March 1997 and *Diamesa* in July 1996 and 1997 at R2 and in April 1998 at R4. The difference between abundance in the first and the second winter was also mainly caused by the different densities of *Baetis* larvae. They constituted about 87% to the total macroinvertebrate density at the two

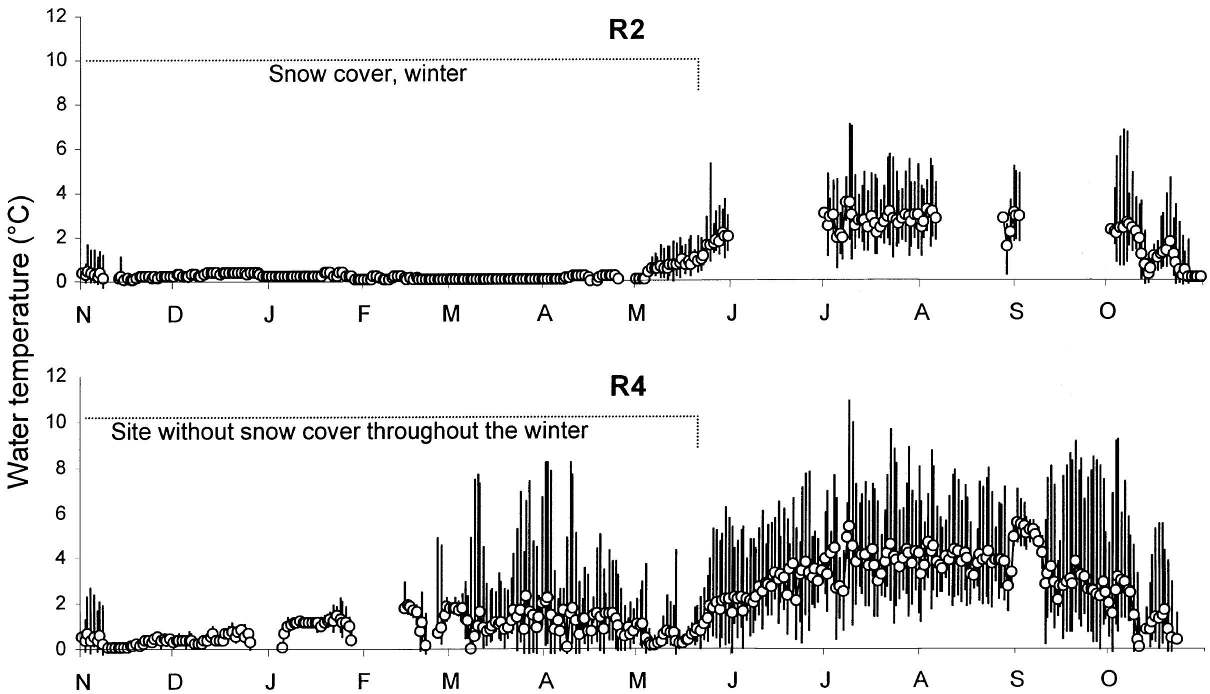

Fig. 3 Daily means, minima and maxima of water temperature in the Rotmoosache at the sites R2 and R4, November 1996 to October 1997.

sites during the 1996–97 winter, but only 1.5% during the 1997–98 winter.

During the first winter, taxa richness at R2 was not different from summer, but in the second winter it decreased significantly in January. At R4, the number of taxa was low during the summer months, increased in autumn and generally remained high throughout the winter months, declining significantly with snowmelt.

A total of 74 different taxa were identified in this study (see Appendix). Most taxa were found in early and late winter, fewer taxa in autumn and during snowmelt and the lowest taxa numbers during early and late summer. Several taxa were restricted to particular periods: 38 taxa were mostly collected during early and late winter, some mainly during snowmelt (eight taxa) and early summer (eight taxa), five in autumn, and one (*Smittia* sp.) only during the period of maximal discharge in mid-summer. Sixteen taxa occured at similar densities throughout the year.

In late winter, it is necessary to distinguish again between the snow-covered site R2 and the open site R4 (Appendix). When only winter samples of snow covered sites are taken into account, 4% of the taxa were found predominantly in late winter. Including samples of the open site R4, this percentage increases to 34. Five taxa were exclusively found in samples from R4 in winter [*Eukiefferiella minor* (Edwards), *Protonemoura* sp., *Pseudosmittia* sp., *Tvetenia bavarica* (Goethgebuer) Syrphidae].

Baetis alpinus Pictet, the dominant mayfly, showed a different size distribution at the snow-covered and the snow-free sites (Fig. 6). In July/August 1996 mature larvae ready to emerge were recorded, while from August to October mainly small larvae with a high percentage in the 250–670 μm size fraction occurred. At R4, the larvae grew continuously during winter and were most abundant in March. At site R2, under the snow, development was slower and the situation in June was similar to February/March at the open site. A similar pattern of development was observed for larvae of *Rhabdiopteryx alpina* Kühtreiber.

Indirect gradient analysis

The site scores and species scores (separate plots for different faunal groups) of the PCA for the first two axes are shown in Fig. 7. The first axis explained about 40% of the faunistic variance. The samples were

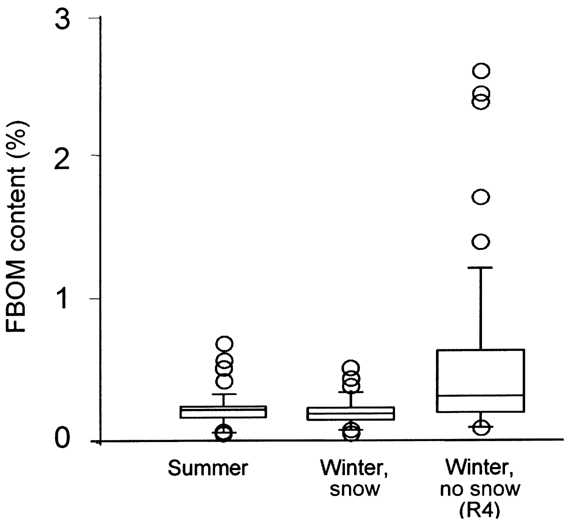

Fig. 4 Box-and-whisker plots (median, 75th, 90th percentile) of fine benthic organic matter (FBOM), content between September 1996 and June 1998.

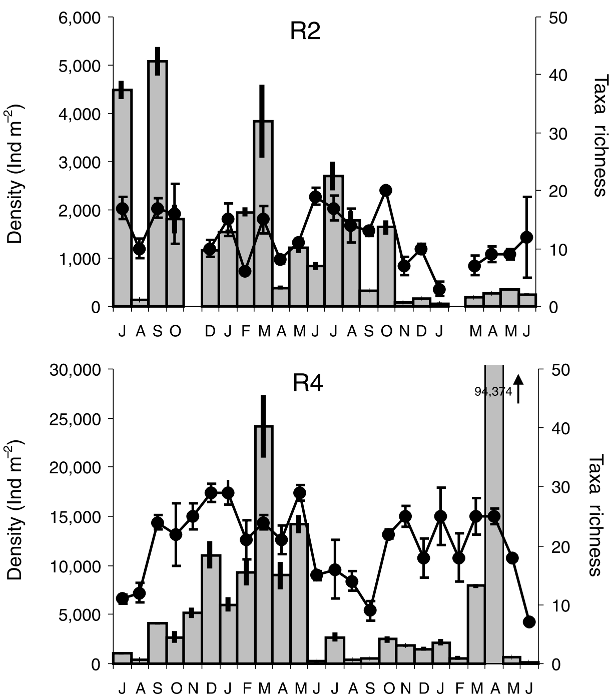

Fig. 5 Macroinvertebrate density (Individuals m^{-2} ± SD), represented by columns, and number of taxa (±SD), represented by dots, at the sites R2, snow covered in winter, and R4, snow-free in winter, from July 1996 to June 1998.

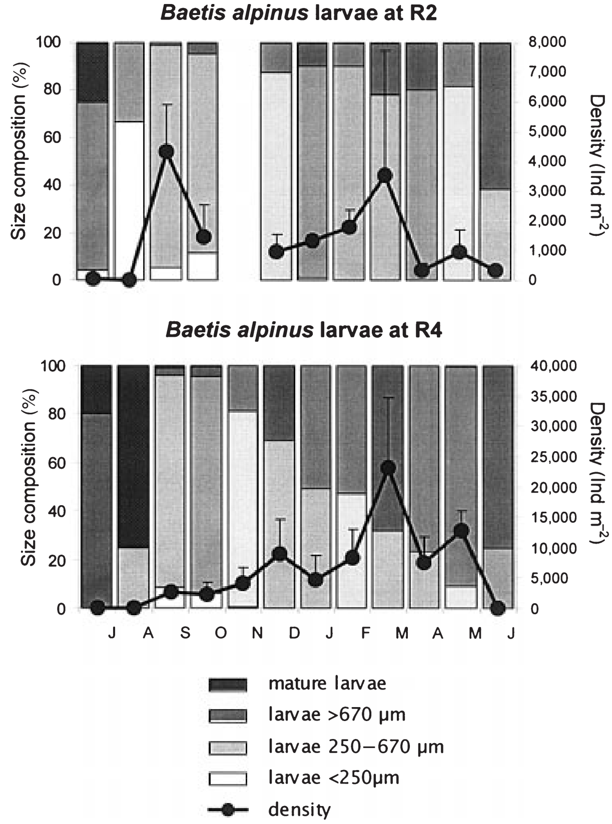

Fig. 6 Size composition of *Baetis alpinus* larvae and *Baetis* density (±SD) at the sites R2, snow-covered in winter, and R4, snow-free in winter, from July 1996 to June 1997.

distributed along this axis according to the season (Fig. 7a). Snowmelt samples overlapped to some degree with summer samples. The winter samples were divided. Those adjacent to the snowmelt samples (i.e. the winter samples of the snow covered site R2) were distributed along axis 1. The winter samples from the open site R4 formed a distinct cluster together with the autumn samples.

Individual taxa showed different vector directions (Fig. 7b–g; species not represented in the diagrams lay close to the origin). Diamesinae were correlated with the summer samples, Ephemeroptera and Plecoptera pointed towards autumn samples and winter samples from R4. The arrangement of the other groups was less distinct, most taxa being distributed within the autumn and R4 winter area. Only few species were correlated with snowmelt or with the snow covered site, R2.

The abundance displayed for several key taxa in the PCA (i.e. taxa with long vectors) along the first two axes may be arranged as an annual chronosequence (Fig. 8) following the seasonal pattern of the site scores (Fig. 7a). *Diamesa latitarsis*-gr. represents the *Diamesa* species found mostly during summer, although a few individuals were also recorded throughout the year. Thaumaleidae were found in snowmelt samples and also under the snow. Nematoda appeared mostly

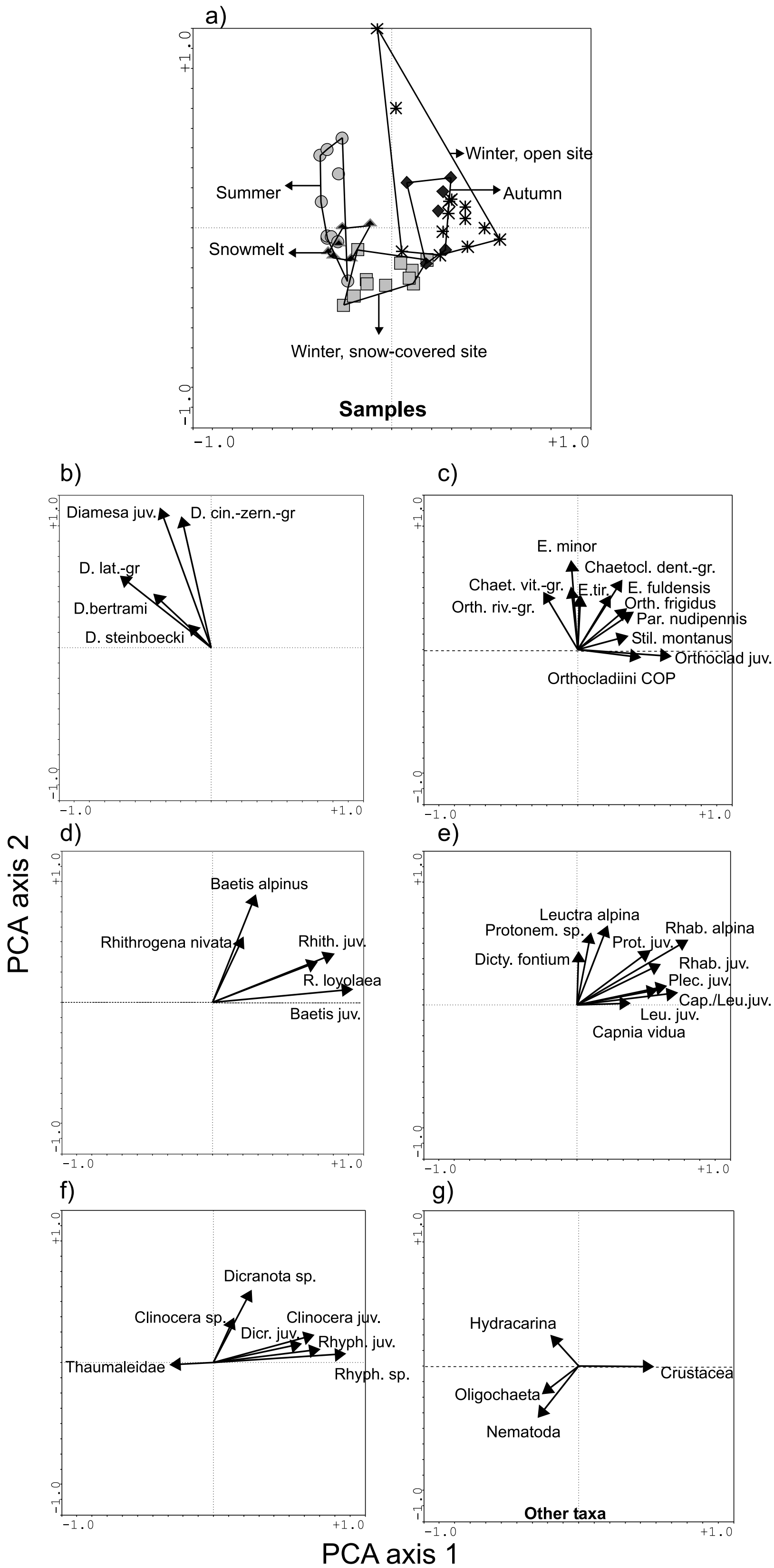

Fig. 7 First two axes of the principal components analysis of macroinvertebrate data from R2 and R4, July 1996 to June 1998 (axis 1: 40.2% of total variance, axis 2: 22% of total variance); site scores (a) with different symbols for the samples of different periods: summer (◍), snowmelt (▲), winter – snow covered site R2 (▨), autumn (◆), winter – snow-free site R4 (✱), and species scores separately for the different groups: Diamesinae (b), other Chironomidae (c), Ephemeroptera (d), Plecoptera (e), other Diptera (f), other taxa (g); for full species names see Appendix.

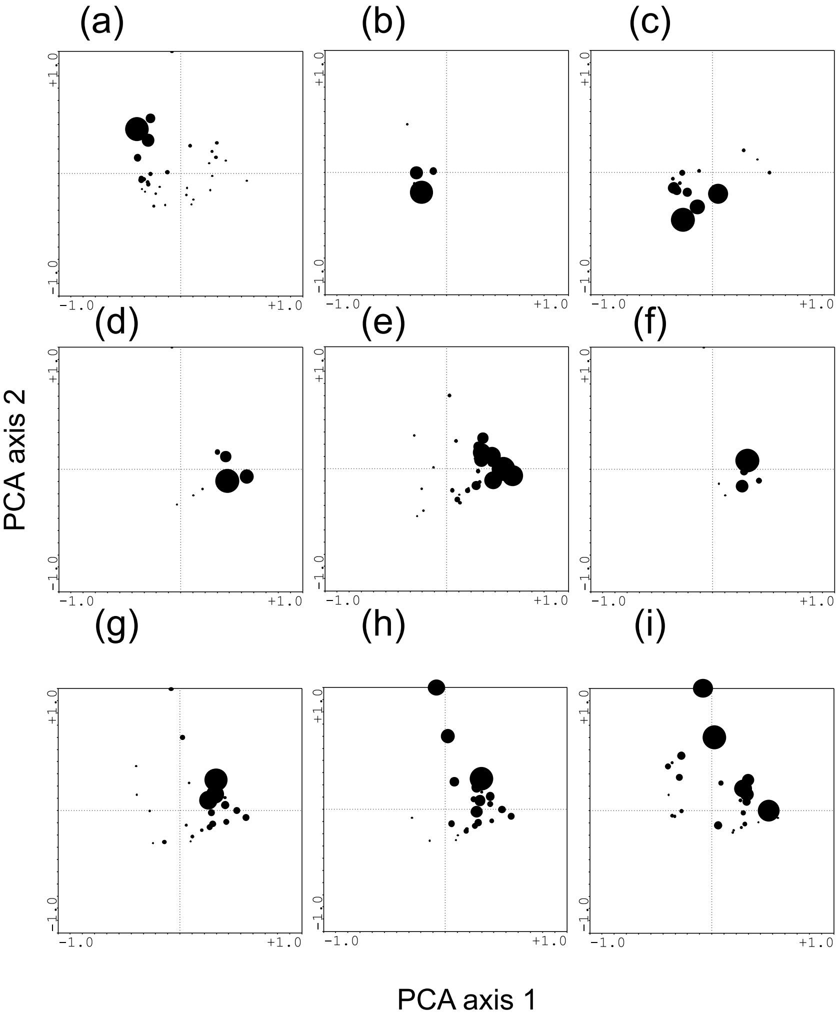

Fig. 8 Arrangement of nine key taxa along the first two axes of the PCA (see Fig. 7a); dot size represents relative abundance in the sample; *Diamesa* lat.-gr. (a), Thaumaleidae (b), Nematoda (c), Crustacea (d), *Rhypholophus* sp. (e), *Capnia vidua* (f), *Rhithrogena loyolaea* (g), *Rhabdiopteryx alpina* (h), *Baetis alpinus* (i).

at R2 in winter. Six different taxa represented the species that were mainly found in autumn and winter. Crustacea were found in low densities in autumn and at the snow covered site and most of them appeared in winter at R4. *Rhypholophus* sp. was more widely distributed among the autumn and winter samples, although single individuals were also found during the other seasons. *Capnia vidua* Klapalek was exclusively found during winter, whereas *Rhithrogena loyolaea* Navas and *Rhabdiopteryx alpina* had highest densities in autumn and winter at R4. *Baetis alpinus* were found throughout the year but the highest densities were recorded at the open site in winter.

Discussion

Abiotic conditions during winter in the Rotmoosache were very different from summer. Water temperature and discharge were low but stable and mainly groundwater-influenced, channel stability was high and snow cover prevented light penetration. These conditions were similar to those found in other winter investigations of alpine streams (Tockner *et al.*, 1997).

In this and other year-round studies, changes in the species assemblages reflected observed environmental changes, with additional taxa appearing in winter and some typical summer taxa disappearing (Bretschko, 1969; Schütz, 1999; Füreder *et al.*, 2000; Robinson *et al.*, 2001). Increases in biomass and taxa richness of macroinvertebrates in winter have also been observed (Burgherr & Ward, 2000; Robinson *et al.*, 2001). The benthic fauna of the Rotmoosache changed in composition between summer and winter and significant differences in Chironomidae abundance and taxa richness have been detected (Füreder *et al.*, 2001).

The results regarding the complete invertebrate assemblage were not so clear. At times we observed high taxa richness and high densities under the snow, but in other months these values were not different from those in summer.

Abundance and taxa richness

In our samples, the total abundance of macroinvertebrates was mainly influenced by single species, like *B. alpinus* or *Diamesa* sp., that are able to produce extremely high numbers of larvae if conditions are favourable. Results from R2 show that abundance can be either high or low under the snow, with variations between months and different years. There were no significant differences in the abiotic stream conditions between the two studied winter seasons, despite major differences in *B. alpinus* densities. An explanation for the varying contribution of *Baetis* larvae in the two winters can be found in the autumn situations. The favoured emergence period of *B. alpinus* in North Tyrol is from mid-July to beginning of October (Ritter, 1985). In 1996, the autumn, typified by low discharge and a stable stream bed, lasted from the end of August to the end of October, providing good conditions for oviposition and egg hatching. In 1997, in contrast, high discharge lasted until mid of September, so the benign period was much shorter. Eggs and newly hatched *Baetis* larvae may have been killed by meltwater floods or carried downstream. As a result, the total density of *Baetis* remaining in the stream for winter was much lower than the year before. The duration of the stable autumn conditions may have also been an important factor for other species and hence for taxa richness, composition and density of the winter fauna.

Species composition

Robinson *et al*. (2001) found different seasonal macroinvertebrate assemblages in several glacial streams in the Swiss Alps. They only used six common taxa for a PCA, but this was sufficient to separate summer from winter samples. In our analysis, samples were also clearly separated according to their composition, which varied seasonally. Winter, autumn and summer samples formed distinct groups along the first two axes, and within the winter samples the open site R4 and the snow-covered site R2 were also separated.

Diamesa spp. are characteristic and abundant in glacial streams during summer (Steffan, 1971; Kownacka & Kownacki, 1975; Milner & Petts, 1994; Ward, 1994). In the Rotmoosache, we found high Diamesinae densities in summer, but under the snow only a few individuals were collected. R. Burger (personal communication) found highest emergence rates for the *Diamesa* species in the Rotmoosache in August 1997, which corresponds to the date when the abundance of *Diamesa* spp. in the benthic samples decreased. As we did not find high numbers of small *Diamesa* larvae under the snow, they do not seem to overwinter in the uppermost layer of the substratum. Possibly they overwinter as eggs or as larvae in the hyporheic zone.

Baetis and *Rhithrogena* are common genera of the fauna in glacial streams at some distance from the glacier snout (Ward, 1994; Weichselbaumer, 1997). In the Rotmoosache, numbers in the summer samples did not give a realistic impression of the densities these species can reach. For *B. alpinus* nearly 70% of all sampled individuals were found in winter, for *R. loyolaea* about 66% and for *R. nivata* Eaton, a mayfly very typical of glacial streams, 85%. Thus, the contribution of these taxa to the total biomass production of glacial streams is underestimated when extrapolated solely from summer sampling.

Capnia vidua is typical of alpine streams and emerges very early (Kühtreiber, 1934). Previously this species has not been described for glacial streams at an altitude above 2000 m, possibly because only their early, unidentifiable larval instars are found in summer. W. Wallinger (personal communication) collected 29 adult individuals of *C. vidua* from April to May 1997 in emergence traps in the Rotmoosache, which corresponded to the collection of the benthic larvae of the same cohort from November to May. Most of the other Plecoptera [*Rhabdiopteryx alpina, Protonemoura* sp., *Leuctra alpina* Kühtreiber] also typically emerge in spring (Kühtreiber, 1934) and so must develop during winter under the snow cover. Many Plecoptera have the ability to grow at low temperatures under snow cover (Brittain, 1983). As shown in the PCA, all Plecoptera species in the Rotmoosache are associated with winter conditions, but only *Rhabdiopteryx alpina* was abundant enough in our samples to demonstrate larval growth during winter.

The absence of predators as a typical attribute of glacial streams (Ward, 1994) is not totally true for the Rotmoosache. Several predators were collected, mainly during autumn and winter (*Clinocera* sp., *Dicranota* sp., *Dictyogenus fontium* (Ris), *Perlodes* sp., Hydracarina). Such predators may affect the community structure during this part of the year.

Crustacea and Nematoda prefer the hyporheic zone; with groundwater dominance in autumn and winter, the contribution of these groups to the benthic fauna increases. Malard *et al*. (2001) found for Oligochaeta that their distribution in a glacial stream was closely related to interactions between surface water and groundwater. They concluded that the hyporheic zone can be a source for colonization of benthic habitats in periods of suitable environmental conditions. Crustacea and Nematoda can be indicators of the active seasonal migration of species between hyporheic and benthic habitats.

Life-cycle strategies

The survival of populations in the extreme environment of glacial streams obviously requires special strategies. Organisms living in high alpine streams have developed physiological and behavioural adaptations to cope with low water temperature and freezing in winter (for a review see Füreder, 1999). Two evolutionary successful strategies in glacial streams are adaption to the unstable stream conditions during summer (summer species) or avoidance of these conditions (winter species). These strategies were both found in the Rotmoosache: *Diamesa* spp. as the summer species and most Plecoptera and Ephemeroptera as the winter species.

The periods of relatively stable stream conditions are early summer (between snowmelt and icemelt), autumn and winter. The early summer window is very short (Schütz, 1999), while autumn and winter provide a longer period of stable conditions. However, the winter months also have disadvantages: water temperature is always low, close to 0 °C, the stream is snow-covered and autotrophic production impeded. A snow pack of 0.5 m attenuates 99.5% of the photosynthetically active radiation (Uehlinger, Zah & Bürgi, 1998). Summer species can overwinter in a more or less inactive state, often involving long egg development or diapause (Oliver, 1971). The winter species have to develop in complete darkness and at very low temperatures, which slows growth and prolongs development time (Oliver, 1971; Brittain, 1983; Nolte & Hoffmann, 1992) as shown by the differences between R2 and R4 in the development of *B. alpinus* larvae. However, improved food quality or, in the Rotmoosache, stable stream beds, can outweigh the disadvantage of low temperature (Anderson & Cummins, 1974).

The type of nutrient source available for the macroinvertebrates under the snow is unknown as we cannot distinguish if the source of FBOM in the Rotmoosache was allochthonous or autochthonous. Zah & Uehlinger (2001) suggested that terrestrial organic matter that reaches the stream from the catchment during low flow in autumn might be stored and serve as food source for overwintering species. Biofilms are a potential source for energy and nutrient for the benthic fauna in winter, but have been little investigated in glacial streams. Recent studies in the Rotmoosache have shown that the structure of the biofilm (matrix and bacterial composition) shows high spatial and temporal dynamics depending on glacial influence, presence of chlorophyll *a* and flood events (Battin *et al*., 2001) but we do not know how the biofilm changes during winter. In terrestrial ecosystems, investigations concerning the role of microorganisms during snow cover have shown that the microbial activity supports nival food webs and serves as a base for energy transfer to larger invertebrates (Jones, 1999).

Another disadvantage for species developing in winter is the snow layer and its influence on successful emergence. We frequently found adult specimens in winter, mostly chironomids, in the small cavities above the stream surface. Similarly, Robinson *et al*. (2001) observed chironomid adults under the ice, perhaps waiting for the stream opening. However, if these specimens find a mating partner, they can theoretically complete their life cycle under the snow cover.

A prerequisite for the two life-cycle strategies to be successful is the active or passive movement between different reaches of the stream or even between different water bodies, stream channels, the hyporheic zone and groundwater (Ward *et al*., 1998). Species found exclusively in one habitat during one period are expected to spend the rest of the year in a different habitat. Drift behaviour, especially at the onset of snowfall or during snowmelt, may also be a component of the seasonal avoidance strategy (Brittain & Eikeland, 1988).

Snow-free winter conditions

The situation at R4 in winter with no snow cover and open water was very favourable for the macroinvertebrates. It entailed many advantages like stable stream bed, clear water, algal growth, high values of FBOM and in late winter diurnal increases of water temperature. Environmental conditions resembled more the autumn conditions than the winter conditions under the snow. This was also reflected by the macroinvertebrate assemblages of these winter samples, which were more similar to autumn samples than to winter samples of the snow-covered site R2.

From the specific but not uncommon situation at R4 one may conclude that conditions under snow cover are only suboptimal for many species. They are able to survive and reproduce, but their production and growth rates are relatively low. When the stream remains open, abiotic and biotic conditions are much more benign, abundance and taxa richness increase and larval development is faster. Winter situations such as at R4 may be considered as 'hot spots' of species diversity and abundance in glacial streams.

Although our results are far from drawing a complete picture of the winter dynamics in glacial streams, they give some insight into 'what goes on under the snow'. The period of snow cover does not provide a completely homogeneous, static environment, and the faunistic compostion also changes from the beginning of snowfall to early winter, late winter and snowmelt. To recognize and understand the dynamics and processes during the winter months, continuous monitoring is necessary. Special focus should be given to the timing of changes: snowfall and snowmelt. Discharge, water temperature and light conditions change rapidly during these short periods. Field work in winter entails substantial methodological and practical difficulties, but for a comprehensive understanding of the ecology of alpine streams, knowledge of the winter conditions and their effects on the stream fauna is clearly a prerequisite.

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Appendix Taxa list of the Rotmoosache (all sites) from June 1996 to July 1998; taxa arranged after their season of highest relative density; values display percent of all sampled individuals of this taxon that were collected in this season. Values >50% are shaded

	SM	ES	MS	A	EW	LW	LW, R2	LW, R4
Prosimulium sp.	100.0							
Thaumaleidae juv.	100.0							
Boreoheptagyia sp.	100.0							
Brillia modesta (Meigen)	100.0							
Cricotopus sp.	100.0							
Thaumalea sp.	85.7	14.3						
Oligochaeta	50.1	7.5	17.4	6.6	10.5	8.0		8.0
Coleoptera	50.0	50.0						
Nematoda	46.3		2.6	2.3	8.7	40.1	37.1	3.1
Limnephilidae juv.		100.0						
Eukiefferiella devonica/ilkyensis		100.0						
Pseudokiefferiella parva (Edwards)		68.0			32.0			
Heleniella sp.		68.0			32.0			
Orthocladius rivicola-gr.	5.8	60.1	4.9			29.2		29.2
Turbellaria		53.4		8.9	37.7			
Diamesa latitarsis-gr.	11.0	51.3	28.5	4.0	0.7	4.5	1.0	3.5
Diamesa steinboecki (Goetghebuer)	0.4	50.5	6.2	41.2		1.6	1.6	
Diamesa bertrami (Edwards)		41.4	20.5	37.2	0.9			
Smittia sp.			100.0					
Diamesa insignipes (Kieffer)				100.0				
Eukiefferiella fittkaui (Lehmann)				100.0				
Tanytarsini juv.				100.0				
Plecoptera juv.		0.5	0.6	74.8	18.0	6.1	3.4	2.7
Rhypholophus juv.	5.1	1.3	3.1	56.0	15.6	19.0		19.0
Clinocera sp.		20.3	7.7	44.2	4.6	23.2	11.6	11.6
Prodiamesa sp.					100.0			
Eukiefferiella brevicalcar/tirolensis					100.0			
Heterotrissocladius scutelatus (Goetghebuer)					100.0			
Capnia vidua (Klapalek)					91.7	8.3		8.3
Stilocladius montanus (Rossaro)					81.5	18.5		18.5
Orthocladiini 'COP'	4.2				79.0	16.8		16.8
Crustacea					73.8	26.2	6.3	19.9
Pseudodiamesa branickii (Nowicki)	11.4		19.0	9.5	60.2			
Capnia/Leuctra juv.		0.8		38.7	51.6	8.8		8.8
Dicranota juv.	1.4			22.3	48.2	28.2		28.2
Orthocladiinae juv.	11.9	4.9	3.7	7.8	46.3	25.4	1.9	23.5
Drusinae juv.	12.7	15.8		27.5	44.0			
Rhabdiopteryx juv.		15.1	4.6	34.7	42.2	3.4		3.4
Clinocera juv.	4.2		1.2	30.3	39.6	24.7	4.9	19.8
Eukiefferiella minor (Edwards)						100.0		100.0
Protonemura sp.						100.0		100.0
Pseudosmittia sp.						100.0		100.0
Tvetenia bavarica (Goetghebuer)						100.0		100.0
Syrphidae						100.0		100.0
Chaetocladius vitellinus-gr.	2.7					97.3	10.8	86.5
Leuctra alpina (Kühtreiber)				1.6	1.3	97.1	2.8	94.4
Diamesa juv.	0.4	5.0	0.6	1.2	0.1	92.7	0.1	92.6
Rhithrogena nivata (Eaton)		1.9	2.5	1.2	4.8	89.6	23.9	65.7
Eukiefferiella fuldensis (Lehmann)	1.5	7.6			5.4	85.5	3.1	82.4
Protonemura juv.				0.4	15.8	83.8	2.8	81.0
Chaetocladius dentiforceps-gr.					18.7	81.3		81.3
Baetis juv.	0.6	0.4	0.1	8.3	16.5	74.2	7.5	66.6
Diamesa cinerella-zernyi-gr.	0.5	21.6	3.2	1.6	0.6	72.5	0.1	72.4

Appendix (Continued)

	SM	ES	MS	A	EW	LW	LW, R2	LW, R4
Diamesa sp.			14.7	14.7		70.6		70.6
Dictyogenus fontium (Ris)					30.6	69.4		69.4
Limnophyes sp.	17.1		14.3			68.6		68.6
Tvetenia calvescens (Edwards)		21.4			10.1	68.5		68.5
Parorthocladius nudipennis (Kieffer)				2.7	30.1	67.2		67.2
Leuctra juv.			0.5	0.9	31.6	67.0	2.1	64.9
Hydracarina	33.3					66.7	44.4	22.2
Dicranota sp.	6.3	6.8		7.6	13.5	65.8	7.3	58.5
Rhithrogena juv.	2.0	1.7	0.7	10.6	19.4	65.6	9.8	55.7
Baetis alpinus (Pictet)	1.7	8.7	3.5	17.4	5.4	63.4	0.9	62.5
Leuctra rosinae (Kempny)	10.1			28.6	5.9	55.4	35.3	20.2
Perlodes intricatus (Pictet)					44.7	55.3		55.3
Thienemanniella sp.	5.3	33.0	8.8			52.9		52.9
Rhypholophus sp.	1.5		0.4	18.1	27.4	52.5	3.8	48.7
Corynoneura lobata (Edwards)	22.6	10.6	9.4	4.7	1.7	50.9		50.9
Perlodidae juv.			19.8	11.9	20.7	47.6	23.8	23.8
Rhabdiopteryx alpina (Kühtreiber)			0.1	29.9	23.0	47.0	1.9	45.0
Rhithrogena loyolaea (Navas)	1.0	1.5	3.2	27.8	21.2	45.2	2.2	43.0
Orthocladius frigidus (Zetterstedt)	10.0		2.1		42.8	45.1	5.0	40.1
Eukiefferiella brevicalcar (Kieffer)	5.2	28.2	14.4		7.1	45.1		45.1
Eukiefferiella tirolensis (Goetghebuer)	10.1	29.5	7.0	11.2	5.0	37.1	6.7	30.4
Number of taxa found in this season	37	33	32	38	49	52		

SM = snowmelt, ES = early summer, MS = mid-summer, A = autumn, EW = early winter, LW = late winter.