A comparison of benthic macroinvertebrate assemblages among different types of alpine streams

MÄGGI HIEBER,* CHRISTOPHER T. ROBINSON,[†] URS UEHLINGER[†] AND J. V. WARD[†]

ECOVIA, Hackenrüti, Wolhusen, Switzerland
[†]*Department of Limnology, EAWAG/ETH, Überlandstrasse, Dübendorf, Switzerland*

SUMMARY

1. Benthic macroinvertebrate assemblages were compared among a diverse array of first-order alpine tundra streams of the Swiss Alps.

2. A principal components analysis separated sites into three main groups: rhithral streams, rhithral lake outlets, and kryal sites including outlets and streams. Rhithral streams contained the most diverse and taxon rich assemblages, being colonised by both non-insect taxa and Ephemeroptera, Plecoptera, Trichoptera and Diptera.

3. Rhithral lake outlets supported high densities of non-insect taxa such as Oligochaeta, Nemathelminthes and crustaceans. Despite low taxon richness, kryal sites had high Ephemeroptera and Plecoptera abundances. Chironomidae were most common at all sites.

4. Collector-gatherers were dominant at all sites, whereas filter-feeders were rare. Scrapers and shredders were more common in streams than lake outlets.

5. Water temperature and algal standing crops were higher at rhithral lake outlets than rhithral streams, perhaps providing more favourable habitat for non-insect taxa. Glacial runoff was the dominant factor influencing macroinvertebrate assemblages of kryal streams and kryal lake outlets. Alpine lakes influenced the environmental conditions of their outlets and, consequently, their macroinvertebrate assemblages unless being constrained by a glacial influence.

Keywords: glacial, habitat filters, kryal, lake outlet, rhithral, Swiss Alps

Introduction

Steinmann (1907) noted that the stream habitat influences biotic assemblage composition and taxon specific traits. Later, Southwood (1977, 1988) suggested that the habitat provides the templet on which characteristic life-history strategies are evolved. Because of the hierarchical nature of stream networks (Minshall, 1988), habitat characteristics of streams act at different scales. For instance, geological, lithological and hydrological settings are primary determinants of stream environments at large scales such as regions, whereas substrate, water depth and velocity, and input of organic matter play key roles in organism distribution at smaller scales such as between riffles and pools (Frissell *et al.*, 1986). These scaled habitat features can be viewed as nested filters through which species in the regional pool must 'pass' to be present at a given site, consequently dictating the local distributions of organisms and ultimately assemblage composition (Tonn, 1990; Poff, 1997).

The insularity and distinctiveness of alpine streams, defined as mountain headwaters situated above tree-line (Ward, 1994), act as major, coarse-level constraints on stream organisms (Mani, 1990). Common habitat features of alpine streams are low temperature, short growing seasons, an often highly fluctuating discharge regime, turbulent well-oxygenated

Correspondence: Christopher T. Robinson, Department of Limnology, EAWAG/ETH, Überlandstrasse 133, CH-8600 Dübendorf, Switzerland. E-mail: robinson@eawag.ch
Present address: J. V. Ward, 2298 Todd Street, Eugene, Oregon, 97405, U.S.A.

water, and a low input of organic matter (Mani, 1990; Ward, 1994; Zah & Uehlinger, 2001). At a lower hierarchical level, alpine streams can be differentiated into kryal streams dominated by glacier-melt, rhithral streams being snow-fed, and krenal or groundwater-fed streams, each having distinctive habitat conditions (Steffan, 1971; Ward, 1994). In this sense, a dominant feature defining environmental conditions among alpine streams is the origin of water and associated differences in flow and temperature regime.

Lake outlets, an ecotone forming the longitudinal transition zone between lentic and lotic habitats, represent another distinct stream type (Naiman *et al.*, 1988; Samways & Stewart, 1997). Alpine lake outlets can be viewed as subtypes of either rhithral or kryal streams. Depending on lake size, outlets typically have attenuated variation in flow and temperature and a moderated seasonality in other physical-chemical characteristics (kryal lake outlets, in particular), leading to a relatively stable stream habitat (Milner & Petts, 1994; Burgherr & Ward, 2000; Hieber *et al.*, 2002). Consequently, alpine lake outlets presumably provide more benign habitats for benthic organisms than those found in other alpine streams, and potentially harbour a distinct assemblage of macroinvertebrates. However, the magnitude of influence by an upstream lake differs depending on season and can be controlled and offset by glacial discharge (Burgherr & Ward, 2000; Hieber *et al.*, 2002). The few studies on alpine lake outlets reported invertebrate assemblages to be similar to those of other alpine streams (Kownacki *et al.*, 1997; Burgherr & Ward, 2000; Donath & Robinson, 2001). In contrast, lake outlets below treeline typically have a distinct macroinvertebrate community dominated by filter-feeding invertebrates, presumably resulting from high concentrations of transported organic material and more stable flow and temperature regimes (Illies, 1956; Carlsson *et al.*, 1977; Brönmark & Malmqvist, 1984; Harding, 1994).

The goal of this study was to compare benthic macroinvertebrate assemblages of different alpine stream types in relation to their respective habitat conditions. Zoobenthic assemblages of four different stream types were examined: rhithral and kryal streams and rhithral and kryal lake outlets. It was expected that macroinvertebrate assemblage structure would differ between rhithral and kryal streams, and especially between lake outlets and streams. An earlier paper documented habitat conditions in the different stream types (Hieber *et al.*, 2002). A secondary objective was to compare assemblage characteristics between alpine lake outlets with those of low elevation lake outlets.

Methods

Study sites

Detailed site descriptions, locations and habitat characteristics are given in Hieber *et al.* (2002), with a short summary presented here. All study sites were first-order headwater streams above treeline at elevations between 1930 and 2500 m a.s.l. in the Swiss Alps (Table 1). Sites consisted of alpine lake outlets and non-outlet streams of rhithral and kryal origin in three

Table 1 Location and general characteristics of the study sites. Notations of the study sites as used in the text.

Site	Notation	Origin	Stream type	Drainage	Elevation (m a.s.l.)	Slope (%)	Pfankuch index
Lago Nero	LN	r	L	Po	2387	5	25
Puoz Minor	PM	r	L	Danube	2336	9	29
Lago Bianco	LB	r	L	Po	2076	4	29
Jörisee	JS	r(k)	L	Rhine	2489	5	24
Moesa	M	r	S	Po	2300	16	19
Güglia	G	r	S	Danube	2310	10	37
Lej Roseg	LR	k	L	Danube	2159	2	49
Steinsee	SS	k	L	Rhine	1934	4	50
Tschierva	TG	k	S	Danube	2100	4	58
Steinlimi	SG	k	S	Rhine	2090	2	37

Origin of the water: k, kryal; r, rhithral; r(k), rhithral with a partial glacial influence.
Stream type: L, lake outlet; S, (non-lake outlet) stream.
Pfankuch's index of channel bed stability: ≤15, 'excellent'; 16–30, 'good'; 31–45, 'fair'; and 46–60, 'poor'.

of the four major drainages in Switzerland (Rhine, Danube and Po). The Jörisee outlet is rhithral in origin but partially influenced by glacial discharge from a small higher order proglacial lake. Lake outlets were sampled at a distance of 10–30 m below each lake. Study sites had slopes ranging from 2% to 16%, median depths of 11–28 cm, average baseflow widths of 3–12 m, and substrate of a pebble/cobble matrix. Channel stability, determined using the stream bottom component of the Pfankuch's index (Pfankuch, 1975), was 'good' ($\leq$30) at rhithral lake outlets and rhithral stream Moesa (M); 'fair' (31–45) at rhithral stream Güglia (G) and kryal stream Steinlimi (SG); and 'poor' (46–60) at kryal lake outlets and kryal stream Tschierva (TG) (see Table 1 for site notations). Catchments were typically characterised by bare rock, with sparse vegetation of grass and low shrubs of alder (*Alnus* sp.) and willow (*Salix* sp.). All sites were in the crystalline area of the Swiss Alps, where bedrock mainly consists of granite and gneiss (Spicher, 1980).

Field collections

Where accessible, 10 sites were sampled monthly to bimonthly between June 1998 and September 2000, comprising on average two annual cycles. On each date, we collected benthic macroinvertebrates, benthic organic matter (BOM), periphyton and seston, and recorded physical and chemical water characteristics (also see Hieber *et al.*, 2002). Three quantitative samples (Hess-sampler, 0.04 m^2, 100-µm mesh) of benthic invertebrates and organic matter were collected randomly from each site. Benthic invertebrates were collected qualitatively with a kick-net at sites where heavy snow cover precluded the use of a Hesssampler. In addition, a composite 5-min qualitative kick-sample (100-µm mesh) was collected seasonally from the most common habitat types at each site. This latter sample provided a semi-quantitative assessment of the benthic assemblage to compare both invertebrate richness and density. All benthic samples were preserved with formalin for later analysis.

Water depth and velocity (MiniAir 2, Schiltknecht AG, Gossau, Switzerland) at $0.6 \times$ depth were measured to characterise the habitat conditions for each benthic sample. Periphyton was sampled by collecting 10 stones (*b*-axis = 2.8–14.0 cm, median = 7.0 cm) from predominant instream habitats at each site. The stones were stored at −25 °C until processed in the

laboratory. Four samples of transported particulate organic (POM) and inorganic matter (PIM) (seston) were collected using a nylon drift net (100-µm mesh) for 60–180 s at approximately $0.6 \times$ depth. The sampling period depended on the extent of clogging of the net by transported sediments, particularly in kryal sites, or organic particles. Velocity was recorded at the net aperture to express seston per unit volume of water (m^3), and the contents of each sample were stored at −25 °C until processed in the laboratory.

Organic matter

Benthic organic matter was estimated from each Hess sample standardised to unit area (m^2). After removing macroinvertebrates, the remaining benthic material from each sample was dried at 60 °C, weighed to the nearest 0.1 mg, ashed for 3 h at 500 °C, and then reweighed to calculate BOM as ash-free dry mass (AFDM).

Periphyton was removed from each stone by scrubbing with a metal bristle brush. Two aliquots of 3–5 mL of the algal suspension from each stone were filtered through pre-ashed glass fibre filters (Whatman GF/F), dried at 60 °C, weighed to the nearest 0.1 mg, and reweighed after ashing for 3 h at 500 °C. We calculated the surface area of each stone as the area of an ellipsoid based on measurements of the *a*- and *b*-axis following Uehlinger (1991) to standardise AFDM concentrations to unit area (m^2).

Each seston sample was filtered through a weighed pre-ashed glass fibre filter (Whatman GF/F), dried at 60 °C and weighed to the nearest 0.1 mg to determine total transported particulate matter (PM). Each filter was then ashed for 3 h at 500 °C and reweighed to calculate POM as AFDM. PIM was estimated as the difference between PM and POM.

Macroinvertebrates

In the laboratory, all macroinvertebrates were handpicked from each sample, identified to the lowest possible taxonomic level and counted using a dissecting microscope. Although many groups were identified to species, further analyses were based on genus or (sub-) family level to include early instar larvae that that could not be identified to species. Regardless, most genera were present as only one species, resulting in similar structure in composition.

Hydrozoa, Nemathelminthes, Oligochaeta, Hydracarina, Cladocera, Copepoda, Ostracoda and Collembola were not identified further. Functional feeding guilds were assigned according to Moog (1995). Invertebrates such as Nemathelminthes and Crustacea that were not identified enough to classify into functional feeding guilds were combined as an 'undefined group'.

Density, richness and Simpson's index of diversity (*D*) were calculated for each benthic sample. Densities are given as individuals per square metre for Hess-samples and as individuals per 5-min sample for kick-net samples. Simpson's index of diversity (*D*) was calculated using the formula

$$D = \sum \frac{n_i(n_i - 1)}{N(N - 1)},$$

where n_i is the number of individuals in the *i*th species and *N* the total number of individuals. High *D*-values indicate a more equal distribution of taxa, although the total number of taxa present may be low. In contrast, high taxon richness associated with low *D*-values indicates a strong dominance by one or a few taxa and the presence of many rare taxa. Simpson's index is weighted towards the most abundant species and is less sensitive to species richness than the Shannon–Wiener index (Magurran, 1991). Diversity analyses were performed using Pisces 2.3 (Pisces Conservation Ltd, Lymington, U.K.).

Statistical analyses

Habitat characteristics. Because the sampling design was unbalanced between the different sites, we used analysis of covariance (ANCOVA) to test for differences in habitat characteristics among sites with date as the covariate, and ANOVA to test for differences among dates within each site (Sokal & Rohlf, 1995). If differences were detected (significance level of *P* = 0.05), Tukeys HSD test was used to determine which values actually differed. All data were $\ln(x + 1)$ transformed to meet the assumptions of a normal distribution (Sokal & Rohlf, 1995).

Macroinvertebrates. Differences in assemblage composition among sites were analysed using principal components analysis (PCA). The applicability of PCA to determine general spatial and temporal patterns among study sites was tested by checking the raw

data and calculating the length of gradient using a detrended component analysis (DCA). A gradient length ≥4 SD indicates an unimodal response of the data, requiring correspondence analysis (ter Braak & Verdonschot, 1995). However, the data clearly showed linear responses (length of gradient ≤2.6 SD), thereby allowing the PCA. We analysed invertebrate data by means of a covariance matrix PCA after $\ln(x + 1)$ transformation and centering to reduce strong inter-taxonomic differences in densities. Because of the two different sets of invertebrate data (i.e. qualitative kick-net and quantitative Hess samples), two separate analyses were performed. Invertebrate densities (number per square metre) of the replicate Hess samples for each sampling date and site were averaged per taxon, whereas invertebrate assemblages of the kick-nets were kept as density/sample. Principal component analyses were computed using the ADE-4 software (Thioulouse *et al.*, 1997).

Invertebrate–habitat relationship. Density, taxon richness, Ephemeroptera, Plecoptera and Trichoptera (EPT) taxa, non-insect taxa, and Simpson's index of diversity were analysed using regression against different environmental variables. To assess for general environmental variables that explained differences among macroinvertebrate assemblages, we included the various invertebrate indices per sampling date and site in a stepwise multiple regression. Environmental variables were omitted if correlated ($r > 0.8$). Regression was calculated with two sets of variables: (i) variables at the reach scale within each stream at different dates (i.e. water chemistry, mean daily temperature, turbidity, velocity, water depth, POM, PIM, BOM and periphyton AFDM) were compared to test for seasonal changes; and (ii) a further set of variables (mean of the above tested variables) was compared between streams including general stream characteristics that were the same at all sampling occasions (i.e. slope, annual degree days (DD_a), and Pfankuch stability index). In the regression models, the limit for regression was set for an adjusted $r^2 = 0.3$ and the significance level at $P = 0.05$. In multiple regression analyses, the adjusted r^2-value allows one to compare among regressions with different numbers of variables. The magnitude of the standardised regression coefficient *Beta* indicates the relative contribution of each independent variable.

Unless otherwise stated all statistical analyses were performed using Statistica 5.1 (Statsoft, 1995).

Results

Habitat characteristics

Detailed analyses regarding physical, chemical, morphological, and stability measures characterising the study streams have previously been reported in Hieber *et al.* (2002). Briefly, average velocity, measured above each Hess sample, ranged from 0.23 to 0.56 m s^{-1} and was highest at kryal sites ($\geq$0.48 m s^{-1}). Average water depth ranged from 0.11 to 0.29 m and was highest at the lake outlets LB, LR and SS (>0.25 m) and lowest at rhithral sites ($\leq$0.2 m, except the rhithral lake outlet LB). BOM ranged on average from <2 g m^{-2} at kryal sites to 14 g m^{-2} at the rhithral L. Bianco outlet (Fig. 1). Concentrations of BOM were higher at rhithral sites (average 3–14 g m^{-2}) compared with kryal sites, and reached peak concentrations >30 g m^{-2} at the rhithral L. Bianco outlet. Periphyton organic matter (AFDM) was lowest at kryal sites (on average $\leq$10 g AFDM m^{-2}) and highest at rhithral lake outlets LB, PM and JS (on average >20 g AFDM m^{-2}). Periphyton AFDM was as low at rhithral streams as at kryal sites, whereas BOM concentrations were more similar to rhithral lake outlets. Transported POM ranged on average from 0.01 to 0.1 g m^{-3}. Concentrations of POM were highest at rhithral streams and the kryal stream TG but showed no distinct differences between kryal and rhithral sites (Fig. 1).

Macroinvertebrates

Sixty-seven taxa were collected during the study of which 33 were EPT taxa, 21 were Diptera, and 13 were Collembola, Coleoptera and non-insects (Appendix 1). The most common taxa were the turbellarian *Crenobia alpina* Dana, Nemathelminthes, Oligochaeta, ephemeropterans *Baetis alpinus* Pictet and *Rhithrogena* spp., plecopteran *Leuctra* spp., and chironomid subfamilies Diamesinae and Orthocladiinae.

Assemblage composition. Rhithral streams supported the highest number of taxa (35 taxa from a total of 50 taxa based on genus level) with between 20 and 25 taxa at rhithral lake outlets and kryal Roseg outlet and
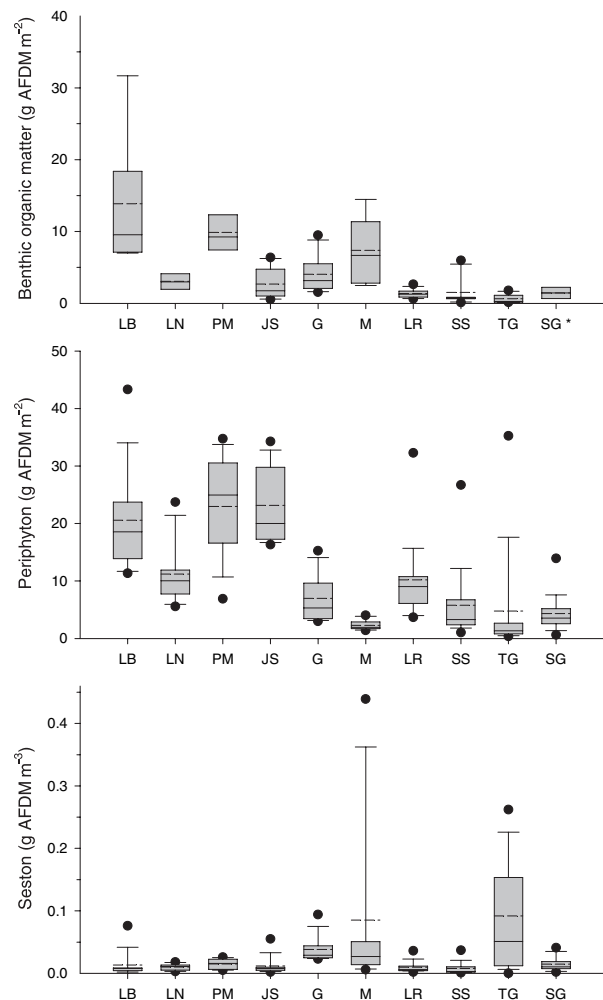

Fig. 1 Concentrations of benthic (from Hess samples), periphytic and sestonic (as AFDM) organic matter at 10 different sites (notations defined in Table 1). Box plots show the median (solid line), mean (dotted line), 25th and 75th percentile (▨), 10th and 90th percentile (low and high whiskers), and 5th and 95th percentile (●) for all measurements during the study period. *Concentrations available only for two sampling dates.

<18 taxa at other kryal sites (Table 2). About one-third of the taxa present at each site were EPT taxa with the greatest taxon richness at rhithral streams (13 EPT taxa = 38%) and the lowest richness at kryal Steinsee outlet (three EPT taxa = 25%). Simpson's index of diversity (*D*) was highest at rhithral streams (*D* = 3.9) and lowest at kryal sites (D $\leq$ 1.3; Table 2). Simpson's *D* was also high at the two lake outlets LN and JS (D $\geq$ 3.7) although taxon richness was $\leq$23, but was low at rhithral L. Bianco outlet (*D* = 1.8).

The PCA using macroinvertebrate abundance collected by both qualitative kick-net and quantitative

Table 2 Total and EPT taxon richness and Simpson's index of diversity (*D*) for each study site (notations and types defined in Table 1). Indices are calculated at the genus/family level.

| Site | Type | Taxon richness | | Simpson's diversity *D* |
		Total	EPT	
LN	rL	20	6	3.7
PM	rL	24	7	2.8
LB	rL	25	8	1.8
JS	rL	23	9	3.9
M	rS	34	13	3.9
G	rS	35	13	3.9
LR	kL	22	11	3.5
SS	kL	12	3	1.1
TG	kS	17	6	1.3
SG	kS	12	6	1.2

Hess samples grouped the 10 study sites into three main groups: (i) rhithral streams, (ii) rhithral lake outlets, and (iii) kryal sites with lake outlet sites and stream sites not being separated into distinct groups (Fig. 2). Non-insect taxa such as Oligochaeta, Nemathelminthes and the crustaceans Copepoda, Ostracoda and Cladocera defined axis-1 of the PCA, whereas Ephemeroptera-Plecoptera-Diptera (EPD) taxa such as *B. alpinus*, *Rhithrogena* spp., small unidentifiable heptageniids, *Leuctra* spp., Limoniidae and Psychodidae defined axis-2 (Fig. 2). Rhithral lake outlets were separated from other sites primarily by the non-insect taxa on axis-1. Kryal sites were situated along axis-2 following a gradient from Steinsee outlet and Tschierva stream being characterised by the absence of most taxa, to Steinlimi stream and Roseg outlet being characterised by the presence of EPD taxa. Jörisee outlet site was situated closer to the kryal sites reflecting its glacial influence, but was the most distinct site from the others (Fig. 2). Samples of each site and date varied in their position in the PCA ordination and no clear temporal patterns were obvious.

Functional feeding guilds. Collector-gatherers were dominant at all sites (on average 40–98%), reflecting high densities of Chironomidae (except for Tanypodinae being predators) and Oligochaeta (Fig. 3). Scrapers, mainly represented by ephemeropteran larvae, and shredders, comprising plecopteran and trichopteran larvae, reached highest relative abundances (up to 20%) at rhithral and kryal streams and kryal Roseg outlet. In rhithral lake outlets, the second dominant 'undefined' group (up to 40%) included primarily

Nemathelminthes and Crustacea. Filter feeders were least abundant and reached highest values (5%) only at rhithral P. Minor outlet.

Macroinvertebrate–habitat relationships.

Multiple linear regressions of the various invertebrate indices gave different results depending on the scale of the independent (physical-chemical) variables (Table 3). In general, the inclusion of between stream characteristics resulted in better regressions (higher adjusted r^2), although not necessarily in an increase in statistical significance (*P*). Density and number of non-insect taxa were best explained by instream reach scale variables, whereas total and EPT taxon richness and Simpson's *D* were best explained by including general stream variables that varied little among seasons. Density and richness of non-insect taxa were both positively related to mean daily temperature (*beta* ≥ 0.4) and negatively, but less strongly, to turbidity (*beta* ≤ −0.2). Additionally, periphyton organic matter (*beta* = 0.27) and velocity (*beta* = −0.19) were included in the regression model towards explaining non-insect density. Total density also was best explained by mean daily temperature (*beta* = 0.38); however, the adjusted r^2 of 0.22 indicates a low explanatory value (Table 3).

The most significant variables in the regression model for total and EPT taxon richness and Simpson's *D* were slope and the bottom component of the Pfankuch index, indicating the stronger influence of general stream characteristics compared with the seasonally changing within stream variables. Slope was positively related (*beta* ≥ 0.43) to the different indices, reflecting the high taxon richness and diversity in rhithral streams. However, Pfankuch index was negatively related (*beta* ≤ −0.26) to these indices, reflecting the low taxon richness and diversity of kryal sites. In addition, water depth was positively related to EPT taxon richness (*beta* = 0.30), indicating the influence of temporal changes in instream characteristics.

Discussion

Macroinvertebrate assemblages of alpine streams

Although macroinvertebrates showed distinct differences in assemblage structure between rhithral

(a) Qualitative kick-net samples:
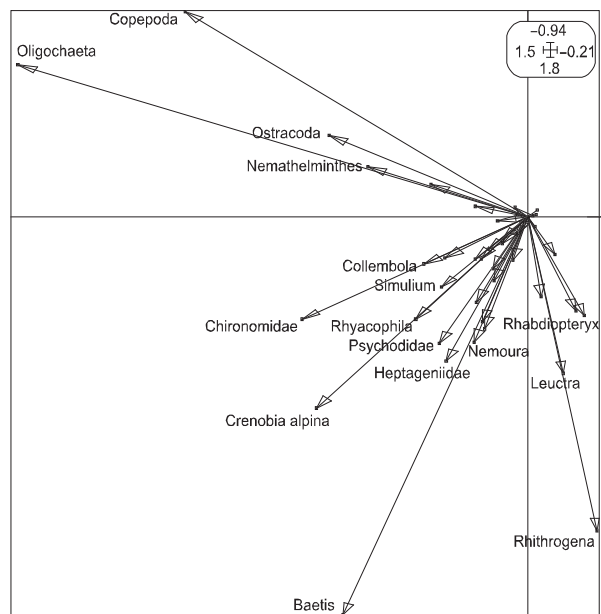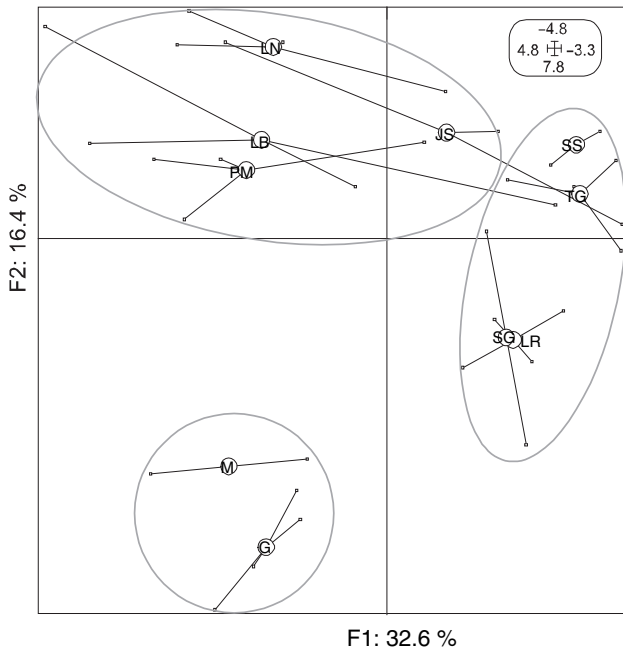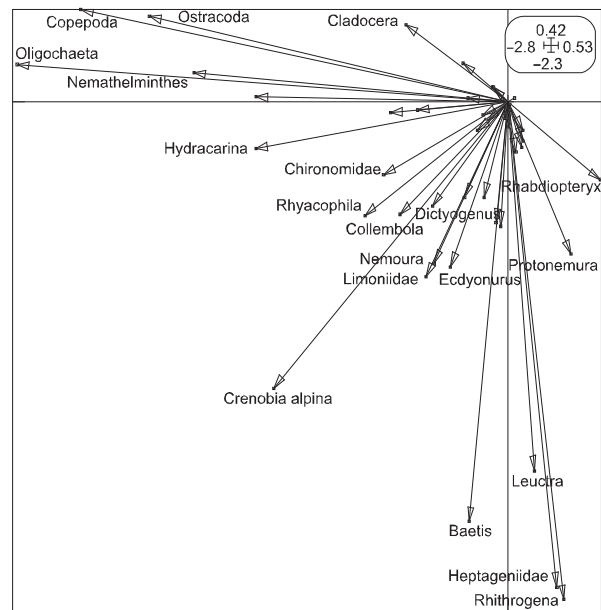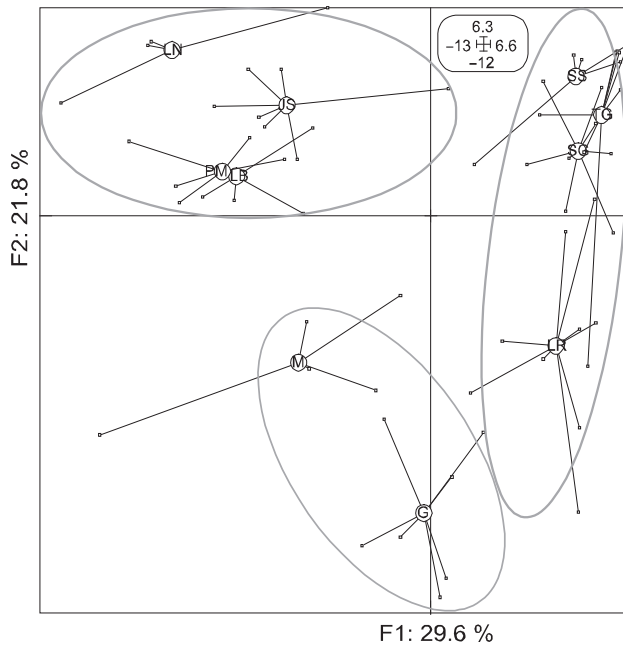

(b) Quantitative Hess samples:

Fig. 2 Ordination from a principal component analysis of invertebrate abundances at 10 alpine study sites based on (a) qualitative kick-net samples, and (b) quantitative Hess samples. In the factor map, small circles represent the average score for each study site and are connected by lines to actual scores for each sampling date (dates are not labelled as a matter of clearness). Grouping of sites is highlighted with large circles. In the taxa ordination, length and direction of each arrow indicates the contribution of each respective taxon to axes F1 and F2. The F1 axis explained 32.6% and the F2 axis 16.4% of the variation for the qualitative samples, and 29.6% and 21.8% for the Hess samples.
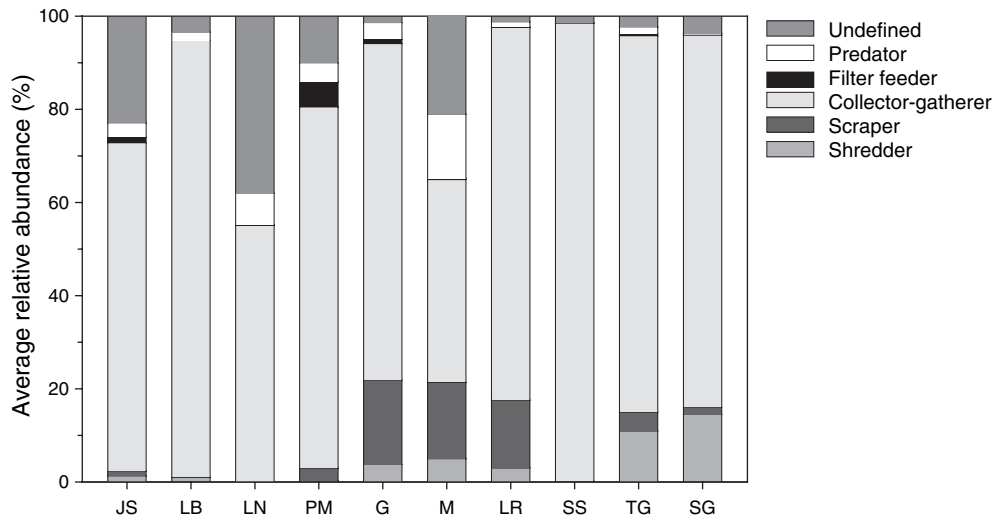
Fig. 3 Average % abundance of the main functional feeding guilds at each study site (notations defined in Table 1).

Table 3 Results of stepwise multiple regression analyses between macroinvertebrate density and diversity indices and (1) instream environmental variables at reach scale and (2) mean instream variables combined with general stream variables by sampling date (1) and site

Dependent variable	(1) Instream			(2) Mean instream + general stream		
	Independent variable	Adjusted r^2	*P*	Independent variable	Adjusted r^2	*P*
Total density	+mean temp., −POC	0.22	<0.001	+mean temp., −POC	0.23	<0.001
EPT density	+BOM, −PIM	0.12	<0.001	−Pfankuch, +slope, +BOM	0.21	0.01
Non-insect density	+mean temp., +Per.OM, −velocity, −turbidity	**0.58**	**0.001**	+DD$_a$, +mean temp.	0.70	0.37
Total taxon richness	−turbidity, +mean temp.	0.25	<0.001	+slope, −Pfankuch	**0.61**	**0.03**
EPT taxon richness		0.08	0.001	+slope, −Pfankuch, +depth	**0.36**	**0.04**
Non-insect taxon richness	+mean temp., −turbidity	**0.45**	**<0.001**	+DD$_a$, +slope, +mean temp., −NO$_2$-N+NO$_3$-N	0.65	0.55
Simpson's *D*		0.10	0.001	+slope, −Pfankuch	**0.39**	**<0.001**

Only variables with *P* < 0.05 are listed following decreasing beta-values with relationship indicated with '+' and '−'.
P-value denotes significance level of the regression model. Numbers given in boldface are regression models with adjusted $r^2 \geq 0.4$ and *P* < 0.05.
POC, particulate organic carbon; EPT, Ephemeroptera, Plecoptera and Trichoptera; BOM, benthic organic matter; PIM, particulate inorganic matter; OM, organic matter; DDa, annual degree days.

streams, rhithral lake outlets and kryal sites, many taxa were common to most study sites, as shown in other studies of alpine stream invertebrates (e.g. Kawecka, Kownacka & Kownacki, 1971; Snook & Milner, 2001; Burgherr, Ward & Robinson, 2002). Differences among assemblages were based more on the relative abundances of taxa than on taxon presence or absence. The similarity of invertebrate assemblages from the three different drainages suggests colonisation of these alpine regions originated from a similar species pool.

Chironomidae dominated all sites, reaching up to 100% at some kryal sites. Rhithral streams represented a combination of assemblages of both rhithral lake outlets and kryal sites, and were the most diverse streams that included high densities of non-insect taxa such as Oligochaeta, Nemathelminthes and crustaceans. Most of the common and abundant taxa found in the present study, especially in rhithral streams, are frequently found in other alpine streams throughout central Europe, and include the mayflies *B. alpinus* and *Rhithrogena loyolaea* Navas, stoneflies *Nemoura*

mortoni Ris, *Leuctra* spp. and *Protonemura* spp., caddisflies *Rhyacophila* spp. and various limnephilid species, dipterans such as Diamesinae, Simuliidae, and Limoniidae, and the turbellarian *C. alpina* (Steinmann, 1907; Kawecka *et al.*, 1971; Lavandier & Décamps, 1984; Burgherr *et al.*, 2002). Others, however, occurred only locally, being recorded in only a few studies (e.g. the stonefly *Rhabdiopteryx alpina* Kühtreiber).

Kryal sites generally were characterised by low taxon richness and dominance by the chironomid subfamily Diamesinae. Other taxa occasionally occurring in these sites included the ephemeropteran families Baetidae and Heptageniidae, plecopteran families Nemouridae, Leuctridae and Taeniopterygidae, and other dipterans such as Orthocladiinae and Limoniidae. Taxon richness varied among kryal sites, and other taxa commonly found in kryal streams (see Milner *et al.*, 2001) occurred only in low abundances at some of our kryal sites (e.g. Perlodidae, Simuliidae) or were absent (e.g. Rhyacophilidae, Chironominae, Empididae, Tipulidae). The invertebrate assemblages of kryal sites also showed no general differences between lake outlets and streams. A higher taxon richness and more diverse assemblage was found at the kryal Lej Roseg outlet compared with its respective kryal stream, supporting patterns found by Burgherr & Ward (2000). In contrast, the same number of taxa occurred at the Steinsee outlet and its respective stream. This particular outlet, however, appeared to be frequently disturbed by bank landslip and erosion (M. Hieber, personal observation).

Invertebrate assemblages of rhithral lake outlets differed substantially in their relative abundances from rhithral streams as well as from kryal sites. Rhithral lake outlet assemblages were strongly dominated by non-insect taxa such as Oligochaeta, Nemathelminthes, and the crustaceans Copepoda and Ostracoda. Crustaceans are common in lake outlets of all altitudes and can be of both benthic and planktonic origin (Kreis, 1921; Richardson & Mackay, 1991; Kownacki *et al.*, 1997; Donath & Robinson, 2001). Oligochaeta occurred in streams and lake outlets, similar to the patterns found by Illies (1956) in Lapland lake outlets and streams.

Filter-feeding taxa typically dominate lake outlet assemblages (Richardson & Mackay, 1991). However, most studies have been conducted on low- and mid-altitude lake outlets below treeline. In the present study, collector-gatherers significantly dominated all sites and filter-feeding taxa (here mainly Simuliidae) generally were rare, being abundant at only one rhithral outlet (average relative abundance of 5%). It appears that the distribution patterns of filter-feeding insects in alpine environments are rather inconsistent. Filter feeders are abundant in some alpine lake outlets (Bushnell, Foster & Wahle, 1987; Harding, 1994; Kownacki *et al.*, 1997; Donath & Robinson, 2001), but low in abundance or absent in others (Kownacka & Kownacki, 1972; Harding, 1994; Burgherr & Ward, 2000). Clearly, the macroinvertebrate assemblages of alpine lake outlets, being dominated by collector-gatherers, differ substantially from those of low- and midland lake outlets.

Invertebrate assemblages and habitat characteristics

Assemblage patterns among streams were influenced by different habitat characteristics of the individual stream types. Dominant habitat variables controlling taxon richness and diversity were slope, Pfankuch bottom index of channel stability and mean daily water temperature. Temperature is a key factor controlling differences in assemblage composition as well as individual life history traits (Steinmann, 1907; Dodds & Hisaw, 1925; Steffan, 1971; Ward & Stanford, 1982; Rossaro, 1991). It also is one of the most apparent abiotic variables related to changes along altitudinal gradients (Ward, 1985; Jacobson, Schultz & Encalada, 1997). Our study sites differed significantly in their temperature characteristics and mean daily temperature was a main determinant of temporal differences in invertebrate densities, particularly for non-insect taxa.

The period of snow and ice cover (Dodds & Hisaw, 1925; Kownacka & Kownacki, 1968) and flow interruption by freezing or drying (Dodds & Hisaw, 1925; Kawecka *et al.*, 1971; Donath & Robinson, 2001) further influence invertebrate assemblages in alpine streams. For example, temporary alpine lake outlets have invertebrate assemblages dominated by taxa able to complete development within a few months such as Simuliidae and Chironomidae, thereby persisting during unfavourable periods as terrestrial adults (Kownacka & Kownacki, 1972; Kownacki *et al.*, 1997; Donath & Robinson, 2001). We only have observational information on the length of ice and snow cover or possible freezing of our study streams.

Lago Nero and its outlet with the longest coverage of ice and snow and the lowest number of degree days supported a lower taxon richness compared with the other rhithral lake outlets. No sites were dry during the study, but freezing may have been possible at the outlet of P. Minor, based on the low average depth (11 cm) and small lake area (0.7 ha), perhaps favouring taxa with short life cycles (e.g. Simuliidae).

Lake outlets have been shown to have higher concentrations of seston that are expected to support filter-feeding taxa such as Simuliidae (Richardson & Mackay, 1991). In the present study, seston concentrations were rather low at all sites, whereas the inorganic fraction was as high or up to 10 times higher than the organic fraction (Hieber, Robinson & Uehlinger, 2003), and was probably the main reason for the low densities of Simuliidae.

Another important structuring force in alpine streams, glacial streams in particular, is channel stability and hydraulic stress resulting from strong seasonal and diel discharge fluctuations (Ward, 1994; Friberg *et al.*, 2001; Milner *et al.*, 2001), and many models have included channel stability in explaining invertebrate distribution patterns (Townsend & Hildrew, 1994; Death, 1995; Milner *et al.*, 2001). In our study, multiple linear regression showed a negative relation between channel stability and macroinvertebrate richness and Simpson's diversity. In addition, within our kryal sites, taxon richness was highest in the kryal Lej Roseg outlet which had the highest maximum water temperature and the highest channel stability. This result concurs with Milner *et al.* (2001) who suggested that macroinvertebrate occurrence in glacial streams is controlled by maximum water temperature and channel stability.

Relative abundances were best explained by in-stream differences in mean daily water temperature, similar to streams and lake outlets in Greenland (Friberg *et al.*, 2001). In the present study, however, regression with total density was of low explanatory value (adjusted $r^2 = 0.22$), whereas density of non-insect taxa was positively correlated with mean daily temperature and periphyton biomass and negatively with velocity and turbidity. Copepoda and Ostracoda were mainly derived from upstream rhithral lakes, and occurred primarily in low flowing clear habitats. In the present study, high Oligochaeta densities were found attached to moss and during periods of high periphytic biomass that corresponded to times of high mean daily water temperatures. Organic matter not only serves as a food source but also acts as substratum on which to live (Minshall, 1984). In alpine streams, benthic algae, and moss and macrophytes in particular, may have provided a distinct habitat for non-insect taxa such as Oligochatea.

Lake outlets as 'hot spots' in alpine environments?

We initially expected alpine lake outlets to provide more benign lotic habitats in an otherwise harsh alpine environment, and thus be inhabited by a temporally more constant and diverse macroinvertebrate assemblage. However, we found that the invertebrate assemblages in alpine rhithral lake outlets only differed from respective streams in the relative contribution of individual taxa, and not in their overall composition. The glacial influence on channel stability seemed to be the dominant factor affecting invertebrate assemblages of kryal lake outlets, overriding any ameliorating effect of the lake. Rhithral lake outlets were characterised primarily by a higher water temperature and algal biomass than rhithral streams, thus providing a more favourable habitat for non-insect taxa. Our results indicate that the distinctiveness of lake-outlet assemblages declines with increasing elevation and glacial influence.

In summary, we conceptualise the different environmental features that distinguish the habitats of our alpine stream systems as nested 'filters' that 'screen' the species in the regional species pool by their functional attributes, thus dictating the proximate structure of the invertebrate assemblage within a stream (Fig. 4; after Poff, 1997). At the largest scale, climate determines the inter- and intra-annual hydrologic and thermal regime that influences intermittency and permanence of flow and thus, 'filters' the alpine assemblage from the regional species pool. At the next level, the primary water source, i.e. the presence of a glacier, influences channel stability and seasonality, leading to a further constraint on population distribution. Channel type represents another 'filter'. Here, depending on its size, the presence of an upstream lake affects environmental conditions in the outlet, such as water temperature and seasonality, although still being strongly influenced by the presence of glaciers. By acting more as sinks than as sources, alpine lake outlets have lower concentrations of transported organic matter than other lakes, so that
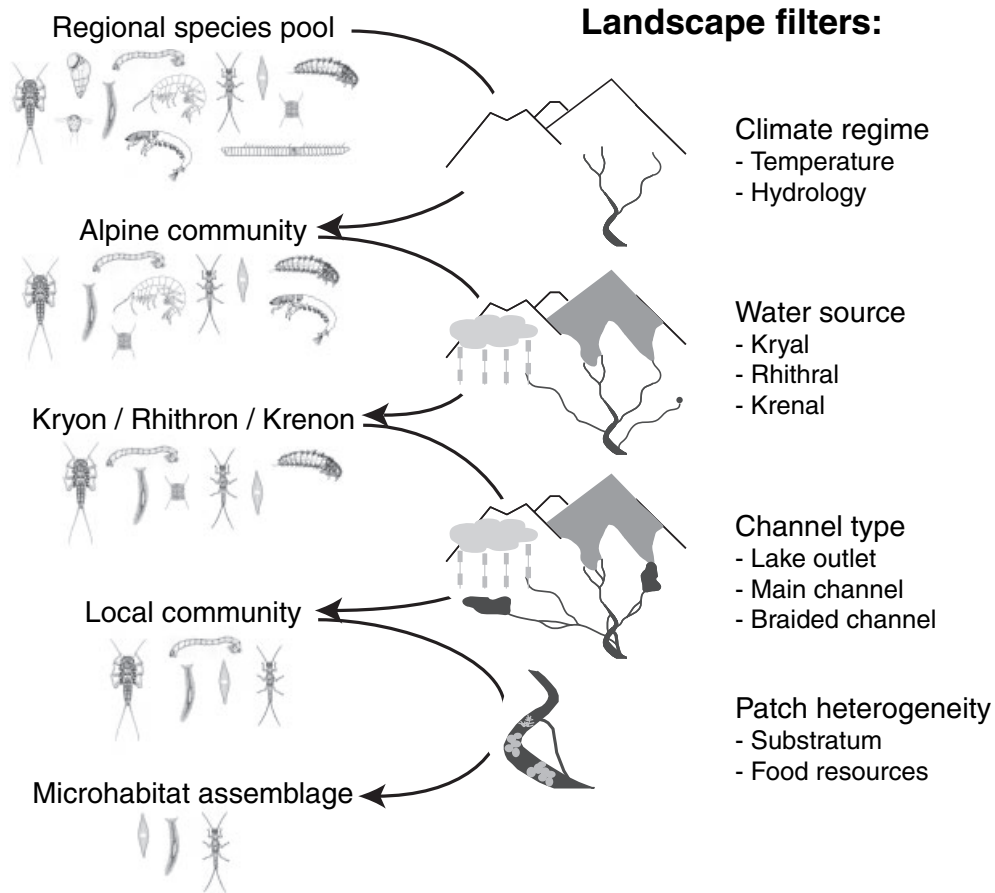
Landscape filters:

Regional species pool

Alpine community

Kryon / Rhithron / Krenon

Local community

Microhabitat assemblage

Climate regime
- Temperature
- Hydrology

Water source
- Kryal
- Rhithral
- Krenal

Channel type
- Lake outlet
- Main channel
- Braided channel

Patch heterogeneity
- Substratum
- Food resources

Fig. 4 Conceptual model of landscape filters (sensu Poff, 1997) determining the assemblage composition in different alpine stream types. Each hierarchical level represents an environmental feature and the dominant habitat characteristics that further 'filter' the invertebrate species.

assemblages shift from an expected filter feeder dominated to a collector-gatherer dominated assemblage. Lastly, within a stream reach, differences in substratum or food resources can favour certain species such as the Oligochaeta in the present study. Although not addressed in this study, biotic interactions may further constrain some species distributions.

References

ter Braak C.J.F. & Verdonschot P.M.F. (1995) Canonical correspondence analysis and related mutlivariate methods in aquatic ecology. *Aquatic Sciences*, **57**, 255–289.

Brönmark C. & Malmqvist B. (1984) Spatial and temporal patterns of lake outlet benthos. *Verhandlungen der Internationalen Vereinigung der Limnologie*, **22**, 1986–1991.

Burgherr P. & Ward J.V. (2000) Zoobenthos of kryal and lake outlet biotopes in a glacial flood plain. *Verhandlungen der Internationalen Vereinigung der Limnologie*, **27**, 1587–1590.

Burgherr P., Ward J.V. & Robinson C.T. (2002) Seasonal variation in zoobenthos across habitat gradients in an alpine glacial floodplain (Val Roseg, Swiss Alps). *Journal of the North American Benthological Society*, **21**, 561–575.

Bushnell J.H., Foster S.Q. & Wahle B.M. (1987) Annotated inventory of invertebrate populations of an alpine lake and stream chain in Colorado. *Great Basin Naturalist*, **47**, 501–511.

Carlsson M., Nilsson L.M., Svensson B. & Ulfstrand S. (1977) Lacustrine seston and other factors influencing the blackflies (Diptera: Simuliidae) inhabiting lake outlets in Swedish Lapland. *Oikos*, **29**, 229–238.

Death R.G. (1995) Spatial patterns in benthic invertebrate community structure: products of habitat stability or are they habitat specific? *Freshwater Biology*, **33**, 455–467.

Dodds G.S. & Hisaw F.L. (1925) Ecological studies on aquatic insects. IV. Altitudinal range and zonation of mayflies, stoneflies, and caddisflies. *Ecology*, **6**, 380–390.

Donath U. & Robinson C.T. (2001) Ecological characteristics of lake outlets in Alpine environments of the Swiss Alps. *Archiv für Hydrobiologie*, **150**, 207–225.

Friberg N., Milner A.M., Svendsen L.M., Lindegaard C. & Larsen S.E. (2001) Macroinvertebrate stream communities along regional and physico-chemical gradients in Western Greenland. *Freshwater Biology*, **46**, 1753–1764.

Frissell C.A., Liss W.J., Warren C.E. & Hurley M.D. (1986) A hierarchical framework for stream habitat classification: viewing streams in a watershed context. *Environmental Management*, **10**, 199–214.

Harding J.S. (1994) Variations in benthic fauna between differing lake outlet types in New Zealand. *New Zealand Journal of Marine and Freshwater Research*, **28**, 417–427.

Hieber M., Robinson C.T. & Uehlinger U. (2003) Seasonal and diel patterns of invertebrate drift in different alpine stream types. *Freshwater Biology*, **48**, 1078–1092.

Hieber M., Robinson C.T., Uehlinger U. & Ward J.V. (2002) Are alpine lake outlets less harsh than other alpine streams? *Archiv für Hydrobiologie*, **154**, 199–223.

Illies J. (1956) Seeausfluß-Biozönosen lappländischer Waldbäche. *Entomologisk Tidskrift*, **77**, 138–513.

Jacobson D., Schultz R. & Encalada A. (1997) Structure and diversity of stream invertebrate assemblages: the influence of temperature with altitude and latitude. *Freshwater Biology*, **38**, 247–261.

Kawecka B., Kownacka M. & Kownacki A. (1971) General characteristics of the biocoenosis in the streams of the Polish High Tatras. *Acta Hydrobiologica*, **13**, 465–476.

Kownacka M. & Kownacki A. (1968) The influence of ice cover on bottom fauna in the Tatra streams. *Acta Hydrobiologica*, **10**, 95–102.

Kownacka M. & Kownacki A. (1972) Vertical distribution of zoocenoses in the streams of the Tatra, Caucasus and Balkan Mts. *Verhandlungen der Internationalen Vereinigung der Limnologie*, **18**, 742–750.

Kownacki A., Dumnicka E., Galas J., Kawecka B. & Wojtan K. (1997) Ecological characteristics of a high mountain lake-outlet stream (Tatra Mts, Poland). *Archiv für Hydrobiologie*, **139**, 113–128.

Kreis A. (1921) Die Jöriseen und ihre postglaziale Besiedlungsgeschichte. *Internationale Revue der gesamten Hydrobiologie und Hydrographie*, **IX**, 189–212, 241–288, 451–490.

Lavandier P. & Décamps H. (1984) Estaragne. In: *Ecology of European Rivers* (Ed. B.A. Whitton), pp. 237–264. Blackwell Scientific Publications, Oxford.

Magurran A.E. (1991) *Ecological Diversity and Its Measurements*. Chapman & Hall, London.

Mani M.S. (1990) *Fundamentals of High Altitude Biology*. Aspect Publications Ltd., London.

Milner A.M. & Petts G.E. (1994) Glacial rivers: physical habitat and ecology. *Freshwater Biology*, **32**, 295–307.

Milner A.M., Brittain J.E., Castella E. & Petts G.E. (2001) Trends of macroinvertebrate community structure in glacier-fed rivers in relation to environmental conditions: a synthesis. *Freshwater Biology*, **46**, 1833–1847.

Minshall G.W. (1984) Aquatic insect-substratum relationships. In: *The Ecology of Aquatic Insects* (Eds V.H. Resh & D.M. Rosenberg), pp. 358–400. Praeger Publishers, New York.

Minshall G.W. (1988) Stream ecosystem theory: a global perspective. *Journal of the North American Benthological Society*, **7**, 263–288.

Moog O. (1995) *Fauna Aquatica Austriaca*. Wasserwirtschaftskataster, Bundesministerium für Land- und Forstwirtschaft, Wien.

Naiman R.J., Décamps H., Pastor J. & Johnston C.A. (1988) The potential importance of boundaries to fluvial ecosystems. *Journal of the North American Benthological Society*, **7**, 289–306.

Pfankuch D.J. (1975) *Stream Reach Inventory and Channel Stability Evaluation*. U.S.D.A. Forest Service, Missoula, Montana.

Poff N.L. (1997) Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. *Journal of the North American Benthological Society*, **16**, 391–409.

Richardson J.S. & Mackay R.J. (1991) Lake outlets and the distribution of filter feeders: an assessment of hypotheses. *Oikos*, **62**, 370–380.

Rossaro B. (1991) Chironomids and water temperature. *Aquatic Insects*, **13**, 87–98.

Samways M.J. & Stewart D.A.B. (1997) An aquatic ecotone and its significance in conservation. *Biodiversity and Conservation*, **6**, 1429–1444.

Snook D.L. & Milner A.M. (2001) The influence of glacial runoff on stream macroinvertebrate communities in the Taillon catchment, French Pyrenees. *Freshwater Biology*, **46**, 1609–1623.

Sokal R.R. & Rohlf F.J. (Eds) (1995) *Biometry: the Principles and Practice of Statistics in Biological Research*. W. H. Freeman and Company, New York.

Southwood T.R.E. (1977) Habitat, the templet for ecological strategies? *Journal of Animal Ecology*, **46**, 337–365.

Southwood T.R.E. (1988) Tactics, strategies and templets. *Oikos*, **52**, 3–18.

Spicher A. (1980) *Geologische Karte der Schweiz., Schweizerische Geologische Kommission*. Bundesamt für Landestopographie, Wabern.

Statsoft I. (1995) *STATISTICA for Windows (Computer Program Manual)*. Tulsa, OK.

Steffan A.W. (1971) Chironomid (Diptera) biocoenoeses in Scandinavian glacier brooks. *Canadian Entomologist*, **103**, 477–486.

Steinmann P. (1907) Die Tierwelt der Gebirgsbäche – eine faunistisch-biologische Studie. *Annales de Biologie Lacustre*, **2**, 30–162.

Thioulouse J., Chessel D., Dolédec S. & Olivier J.-M. (1997) ADE-4: a multivariate analysis and graphical display software. *Statistics and Computing*, **7**, 75–83.

Tonn W.M. (1990) Climate change and fish communities: a conceptual approach. *Transactions of the American Fisheries Society*, **119**, 337–352.

Townsend C.R. & Hildrew A.G. (1994) Species traits in relation to a habitat template for river systems. *Freshwater Biology*, **31**, 265–275.

Uehlinger U. (1991) Spatial and temporal variability of the periphyton biomass in a prealpine river (Necker, Switzerland). *Archiv für Hydrobiologie*, **123**, 219–237.

Ward J.V. (1985) Thermal characteristics of running waters. *Hydrobiologia*, **125**, 31–46.

Ward J.V. (1994) Ecology of alpine streams. *Freshwater Biology*, **32**, 277–294.

Ward J.V. & Stanford J.A. (1982) Thermal responses in the evolutionary ecology of aquatic insects. *Annual Review of Entomology*, **27**, 97–117.

Zah R. & Uehlinger U. (2001) Particulate organic matter inputs to a glacial stream ecosystem in the Swiss Alps. *Freshwater Biology*, **46**, 1597–1608.

(Manuscript accepted 24 August 2005)

Appendix 1 List of all taxa found at any site

Taxa		FFG	JS	LB	LN	PM	G	M	LR	SS	TG	SG
Cnidaria	Hydrozoa	P		++								
Plathelminthes	*Crenobia alpina* Dana	P	+	++	0	++	++	++	+	+	0	
Nemathelminthes			+	++	++	++	+	+	+	0	+	+
Oligochaeta		C	++	+++	+++	++	+	++	0	+	+	+
Arachnida		P	+	+	++	+	+	+		0	+	
Bivalvia	*Sphaerium corneum* Linnaeus	F	+									
Crustacea	Cladocera			++	++							
	Copepoda		++	++	+++	++	+	++	0			
	Ostracoda		++	++	++	++	+	++				
Collembola			0	+	+	++	++	+	+	+	+	
Coleoptera	Coleoptera sp.1									0		
	Ochthebius sp. (adult)	A	+			0						
	Helophorus sp. (larvae)	A						0				
Ephemeroptera	*Baetis alpinus* Pictet	AC	+	+		++	+++	++	++		+	++
	Ecdyonurus spp.	A	0			0	+	++	+			
	Rhithrogena spp.	A	+				++	++	++	+	++	++
Plecoptera	*Nemoura mortoni* Ris	S		++			++	+				
	Nemurella pictetii Klapalek	AC							+		0	
	Protonemura spp.	S		+		+	++	+	+	+	++	+
	Capnia vidua Klapalek	S							+			
	Leuctra spp.	S	+	0	+	+	++	++	+		++	++
	Rhabdiopteryx alpina Kühtreiber	S		+			+	+	+			+++
	Dictyogenus alpinum Pictet	P	+		+		++	+	0			
	Isoperla spp.	P				0		++	+			
	Perlodes intricatus Pictet	P	0	+	0	+	+					
	Siphonoperla montana Pictet	P					0					

Appendix 1 (*Continued*)

Taxa		FFG	JS	LB	LN	PM	G	M	LR	SS	TG	SG
Trichoptera	*Hydropsyche* spp.	F		0	+							
	Rhyacophila spp.	P		+	+		+	++				
	Acrophylax zerberus Brauer	S	+		+		+	0	+	0	0	+
	Annitella obscurata/Melampophylax melampus	S				+						
	Chaetopteryx villosa/fusca	S	+									
	Drusus spp.	A(PF)	+				+	+				
	Plectrocnemia conspersa Curtis	P						0				
Diptera	Ceratopogonidae	P					+					
	Chironomidae		++	+++	+++	+++	+++	++	++	++	++	++
	Diamesinae	C	++	++		+	++	+	+++	+++	++	+++
	Orthocladiinae	C	++	+++	++	++	+++	++	++			+
	Tanypodinae	P		+	+			+				
	Chironominae	C	++	+++	+	+	+	+	0			
	Dixidae	F					+					
	Dolichopodidae	P		0			+	+				
	Empididae	P				+	+	+				
	Limoniidae		+	+	+	+	+	+	+	+	+	+
	Dicranota spp.	P				0	+					
	Rhypholophus spp.	C								+		+
	Psychodidae	C		+			++	0				
	Simuliidae	F	0			++	++	+	+		+	
	Prosimulium spp.	F			0	++	+	+	+		+	
	Simulium spp.	F		0	0	+	+	0				
	Stratiomyidae	SA									0	
	Thaumaleidae	AC					0	+				
	Tipuliidae	S					+	0				
	Diptera sp.1										0	

Empty cell: taxon not found; 0: taxon found only once at the respective site; +: <4; ++: 4–64; +++: >64 individuals per average sample. JS, Jörisee; LB, Lago Bianco; PM, Puoz Minor; G, Güglia; M, Moesa; LR, Lej Roseg; SS, Steinsee; TG, Tschierva; SG, Steinlimi. FFG, functional feeding guild; A, scraper; C, collector; F, filter feeder; P, predator; S, shredder (after Moog, 1995).