

Spatio-temporal variation in macroinvertebrate assemblages of glacial streams in the Swiss Alps

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SUMMARY

1. Changes in water chemistry, benthic organic matter (BOM), and macroinvertebrates were examined in four different glacial streams over an annual cycle. The streams experienced strong seasonal changes in water chemistry that reflected temporal changes in the influence from the source glacier, especially in water turbidity, particulate phosphorus and conductivity.
2. Nitrogen concentrations were high (nitrate-N values were 130–274 $\mu\text{g L}^{-1}$), especially during spring snowmelt runoff. Benthic organic matter attained $>600 \text{ g m}^{-2}$ dry mass at certain times, peaks being associated with seasonal blooms of the alga *Hydrurus foetidus*.
3. Macroinvertebrate taxon richness was two to three times higher (also numbers and biomass) in winter than summer suggesting winter may be a more favourable period for these animals. Benthic densities averaged 1140–3820 ind. m^{-2} , although peaking as high as 9000 ind. m^{-2} . Average annual biomass ranged from 102 to 721 mg m^{-2} , and reached $>2000 \text{ mg m}^{-2}$ at one site in autumn.
4. Taxa common to all sites included the dipterans *Diamesa* spp. and *Rhypholophus* sp., the plecopterans *Leuctra* spp. and *Rhabdiopteryx alpina*, and the ephemeropterans *Baetis alpinus* and *Rhithrogena* spp. Principal components analysis clearly separated winter assemblages from those found in summer.

Keywords: alpine, Chironomidae, Ephemeroptera, insect, kryal, Plecoptera, seasonality, stream

Introduction

Glacier-fed streams and rivers are ubiquitous features of arctic and alpine environments at high altitudes and latitudes, and are coined kryal systems (Steffan, 1971). Kryal streams are distinctive, being characterized by low temperatures, high seasonal and diel discharge fluctuations, high loads of suspended solids from glacial flour, and low channel stability (Milner & Petts, 1994; Ward, 1994; Füreder, 1999). These habitat features of glacial streams are important 'filters' (*sensu* Tonn, 1990) that constrain the kinds and abundances of aquatic insects able to persist in them (Milner & Petts, 1994; Ward, 1994). Indeed, it is generally believed that the low temperature ($<2^\circ\text{C}$) and channel

instability of kryal streams limit most assemblages to species of *Diamesa* (Chironomidae) (Steffan, 1971; Milner & Petts, 1994).

The biota of kryal streams has been little studied; the first report of the macroinvertebrate fauna being that of Steinböck (1934). Other early authors, including Thienemann (1941), Illies (1961), Saether (1968), Bretschko (1969), and Steffan (1971), found that glacier-fed streams were dominated by chironomids of the genus *Diamesa*. Later researchers also documented the predominance of *Diamesa* in kryal systems (e.g. Kawecka, Kownacka & Kownacki, 1971; Kownacka & Kownacki, 1972) and provided the rationale for the conceptual model proposed by Milner & Petts (1994) for the longitudinal zonation of glacial stream benthos. The latter proposed that changes in the longitudinal distribution of benthic invertebrate communities were a function of increasing temperature and channel stability, with Orthocladinae, Baetidae,

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Simuliidae, Nemouridae and Chloroperlidae successively becoming more common further downstream. Milner & Petts (1994) suggested that deviations from this qualitative model may be caused by time since glaciation (e.g. Milner, 1987, 1994) or by resets caused by the presence of tributaries and lakes, or changes in catchment morphology. In line with this idea, Burgherr & Ward (2000) found distinct differences in zoobenthic assemblage structure in a kryal and an adjacent proglacial lake (i.e. a lake at the glacier terminus) outlet.

Other than the studies cited above, there is a general paucity of information on the zoobenthos of glacier-fed streams (but see Flory & Milner, 2000). Most of the earlier studies also were limited in geographic breadth, many being completed, for example, in the Tatra mountains of Poland (Kawecka *et al.*, 1971). We undertook the present study to examine spatial and temporal dynamics of macroinvertebrate communities in a number of different kryal streams in the Swiss Alps over an annual cycle. The results provide seasonal information on the biotic variation found among glacial streams in the Swiss Alps.

Methods

Study sites

The four glacial streams examined were in the Swiss Alps (Fig. 1). Site names refer to the glacier that provided the primary source of water to each stream. Sites ranged in altitude from 1320 (Oberer Grindelwald) to 2070 m a.s.l. (Lang) (Table 1). Catchment areas ranged from 6.2 km² at Steinlimi to 35.3 km² at

Morteratsch. All sites had sparse riparian vegetation except for Grindelwald where the glacier-snout terminus was below the treeline. The percentage of the catchment glaciated varied from 41% at Steinlimi to 62% at Grindelwald. Annual discharge exhibited typical maxima in summer during glacial ablation and minima in winter (Fig. 2). Water temperature rarely exceeded 2 °C in summer because of glacial ice melt; temperatures are typically near 0 °C in winter. Stream widths during summer ranged from about 5 m at Steinlimi to over 15 m at Morteratsch and Lang. Three of the glaciers lie on crystalline granite, while the Grindelwald glacier lies over dolomite bedrock, thus increasing the specific conductance of its stream.

Field and laboratory techniques

Study sites were visited monthly (when accessible) beginning in August or September 1998 and ending in September 1999. Lang and Steinlimi were inaccessible in late winter. On the initial visit to each stream, two sites were chosen for study: an upper site about 50–100 m from the glacial snout and a lower site 300–500 m downstream of the upper site. Only an upper site was established at Steinlimi. A water temperature logger (StowAway XTI, Onset Corp., Pocasset, MA, U.S.A., or Minilog, Vemco Ltd, Shad Boy, Nova Scotia, Canada) recording hourly was installed on the first sampling date at each site. Conductivity (WTW LF323 at 20 °C), turbidity (Cosmos, Fa. Zullig, Switzerland) as nephelometric turbidity units (NTU), and water temperature were determined in the field on each visit. In addition, a 1 L water sample was collected, placed on ice, returned to the laboratory, and filtered for analysis of nitrogen species (NH₄, NO₂, NO₂ + NO₃, dissolved-N, and particulate-N), phosphorus species (soluble reactive phosphorus, dissolved-P and particulate-P), dissolved organic carbon (DOC), particulate organic carbon (POC), total solids (TS), and ash-free dry mass (AFDM) following methods detailed in Tockner *et al.* (1997).

On each sampling date, five benthic samples were collected using a modified Hess sampler (0.042 m², 100 µm mesh). Sample locations at each site were selected haphazardly in riffle/run habitats. Samples were stored individually in labelled polyethylene bottles, and preserved with 4% formalin in the field. In the laboratory, macroinvertebrates were hand-picked from each sample using a dissecting microscope



Fig. 1 Map of Switzerland with locations of study streams. Dark lines delineate the major drainage basins within which each study glacier is situated.

Table 1 Location and general characteristics of the study systems. Elevation is at location of the glacial snout

Glacier	Drainage	Coordinates		Altitude (m a.s.l.)	Catchment area (km ²)	% Area glaciated
		Latitude	Longitude			
Morteratsch	Danube	46°26'	9°56'	2050	35.3	52
Steinlimi	Rhine	46°42'	8°24'	1920	6.2	41
Grindelwald	Rhine	46°39'	8°05'	1320	17.3	62
Lang	Rhone	46°26'	7°54'	2070	29.3	50

at 10× magnification. All invertebrates were identified to the lowest possible taxonomic unit (usually genus), counted, and dried at 60 °C for biomass determinations. The remaining benthic organic matter (BOM) was separated from the inorganic fraction of each sample by elutriation, dried at 60 °C until constant weight (c. 3–7 days), and weighed as dry mass.

Data analysis

The physical and chemical measures recorded for each site on different sampling dates, and macroinvertebrate taxon richness, density and biomass were

summarized as mean values, standard deviations (SD) and coefficients of variation (CV). Turbidity, specific conductance and particulate phosphorus were graphically presented to illustrate the seasonal changes in water quality. The most common groups of macroinvertebrates were described by their average densities and relative abundances (%). Benthic organic matter, and macroinvertebrate density and biomass also were plotted as monthly averages over the study period. Taxon richness was summarized for upper and lower sites for samples collected in summer and winter. Finally, principal components analysis was undertaken on $\log(x + 1)$ transformed density data (varimax rotated) of the most common macroinvertebrate taxa to further illustrate seasonal changes in assemblage structure among sites.

Results

Physical and chemical characteristics of the study streams

Average stream temperatures were <2.1 °C at all sites, being lowest at Morteratsch and highest at Steinlimi and lower Lang (Table 2). Conductivity was typically <50 $\mu\text{S cm}^{-1}$ except at Grindelwald where mean values reached >80 $\mu\text{S cm}^{-1}$ because of its dolomite dominated bedrock. Turbidity was high, reflecting the high loads of glacial flour during summer. Turbidity was much lower at Steinlimi (50 NTU) than in the other glacial streams. Concentrations of most nitrogen species, especially nitrate-N and dissolved-N, were high, likely, the result of the substantial atmospheric inputs of N in the study region (Malard, Tockner & Ward, 1999). Soluble reactive phosphorus levels were low, ranging from a mean of 0.8 $\mu\text{g L}^{-1}$ at Grindelwald to 2.6 $\mu\text{g L}^{-1}$ at Steinlimi. In contrast, particulate-P levels were much higher, being lowest at Steinlimi (31 $\mu\text{g L}^{-1}$) and highest at Lang (112 $\mu\text{g L}^{-1}$). Average DOC concentrations were always <0.5 $\mu\text{g L}^{-1}$. Average POC and AFDM values also were low,

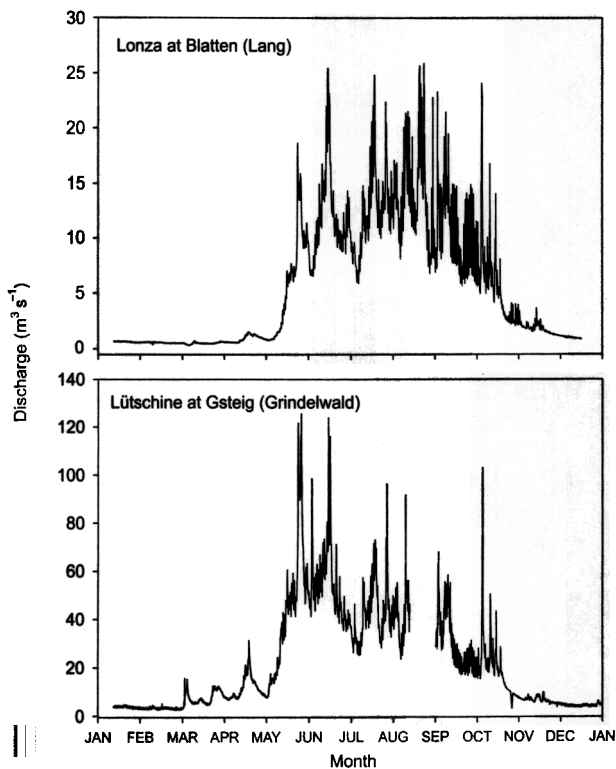


Fig. 2 Annual discharge patterns for two of the study streams (Lang and Grindelwald) during 1999. Although monitoring stations were located downstream of the study sites in each catchment, discharge patterns reflect the glacial influence on discharge in summer.

Table 2 Physical and chemical characteristics of the study sites as mean and coefficient of variation (CV). Sample size (*n*) represents the number of dates (i.e. different months) from which statistics were generated over the study period

Glacier (<i>n</i>)	Site	Parameter	Temperature* (°C)	Conductivity* (µS cm ⁻¹)	Turbidity* (NTU)	NH ₄ (µg L ⁻¹)	NO ₂ (µg L ⁻¹)	NO ₃ -N (µg L ⁻¹)	DN (µg L ⁻¹)	PN (µg L ⁻¹)	SRP (µg L ⁻¹)	DP (µg L ⁻¹)	PP (µg L ⁻¹)	DOC (µg L ⁻¹)	POC (µg L ⁻¹)	TS (mg L ⁻¹)	AFDM (mg L ⁻¹)
Mortersatsch <i>n</i> = 12	Upper	Mean	0.5	47	154	23	1.7	257	340	14	2.4	3.6	44	0.3	0.2	69	1.3
		CV	53	72	140	126	97	25	22	65	65	60	109	43	59	124	99
Mortersatsch <i>n</i> = 12	Lower	Mean	0.8	47	162	27	1.6	274	353	21	2.0	3.1	102	0.3	0.3	150	2.1
		CV	71	71	128	119	92	26	25	97	106	65	183	40	65	147	119
Steinlimi <i>n</i> = 10	Upper	Mean	1.9	22	50	19	0.9	130	217	12	2.6	5.6	31	0.5	0.2	31	0.8
		CV	60	66	60	162	63	40	57	62	95	137	81	105	40	74	73
Grindelwald <i>n</i> = 12	Upper	Mean	0.8	83	67	13	1.8	225	308	20	0.8	1.4	59	0.5	2.0	68	1.9
		CV	64	61	129	89	136	49	42	107	83	56	110	47	148	157	122
Grindelwald <i>n</i> = 12 (<i>n</i> = 8)	Lower	Mean	1.3	91	67	15	0.8	251	319	11	0.8	1.1	34	0.4	1.8	37	1.9
		CV	42	62	165	94	94	43	35	94	118	74	137	44	223	151	118
Lang <i>n</i> = 9	Upper	Mean	1.3	53	121	20	1.0	139	191	14	1.1	1.9	112	0.4	0.5	128	2.2
		CV	60	54	40	60	50	44	30	35	70	62	61	69	53	38	68
Lang <i>n</i> = 9 (<i>n</i> = 4)	Lower	Mean	2.1	48	128	24	1.3	147	239	13	1.0	1.3	84	0.4	0.4	141	3.3
		CV	53	55	25	11	40	58	28	35	82	77	71	65	35	28	68

*Sample size for temperature, conductivity, and turbidity for noted sites.

typically <2.0 mg L⁻¹. Total solids ranged from 31 to 150 mg L⁻¹, being primarily derived from the glaciers (Table 2).

Most physical and chemical measures displayed high CVs (Table 2). These included turbidity, ammonia-N, particulate-P, total-solids and AFDM. These variables usually demonstrated high seasonal variability concomitant with changes in glacial flow characteristics. However, some variables showed relatively low CVs (values typically <60%), including temperature, specific conductance, nitrate-N, dissolved-N and DOC. Lang had lower CV values than the other sites because it could not be sampled during winter when parameters related to glacial melting, such as turbidity, are typically lower than in other seasons.

Seasonality in glacial influence was most evident for specific conductance, turbidity and particulate-P (Fig. 3). Specific conductance increased at all sites during winter when glacial melting was minimal and the streams were fed mostly by groundwater. In contrast, turbidity and particulate-P were much higher during summer when glacial melting peaked. The differences in response curves for these variables among glacial sites were related to catchment size and the percentage of each catchment that was glaciated. For example, Steinlimi showed the least variation among seasons for these constituents and it had the smallest catchment with the least amount of glaciation.

Biotic characteristics of study streams

Average BOM ranged from 40.9 g m⁻² at the lower Lang site to 178.4 g m⁻² at the lower Grindelwald site (Table 3). Coefficients of variation for BOM for each site were quite high, being lowest at Mortersatsch (CV = 84%) and highest at Lang (CV = 187%). The high CVs were indicative of strong seasonal changes in BOM (Fig. 4). Typically, BOM values were maximal in autumn (c. 600 g m⁻²) because of prolific growths of the alga *Hydrurus foetidus* (Villars) Trevisan, a chrysophyte commonly observed in these glacial streams. The BOM levels decreased in winter when channels were snow covered and algal biomass was low, and in summer when turbid waters reduced light penetration and potentially caused high scouring. Some sites, such as lower Grindelwald, also displayed peaks in BOM

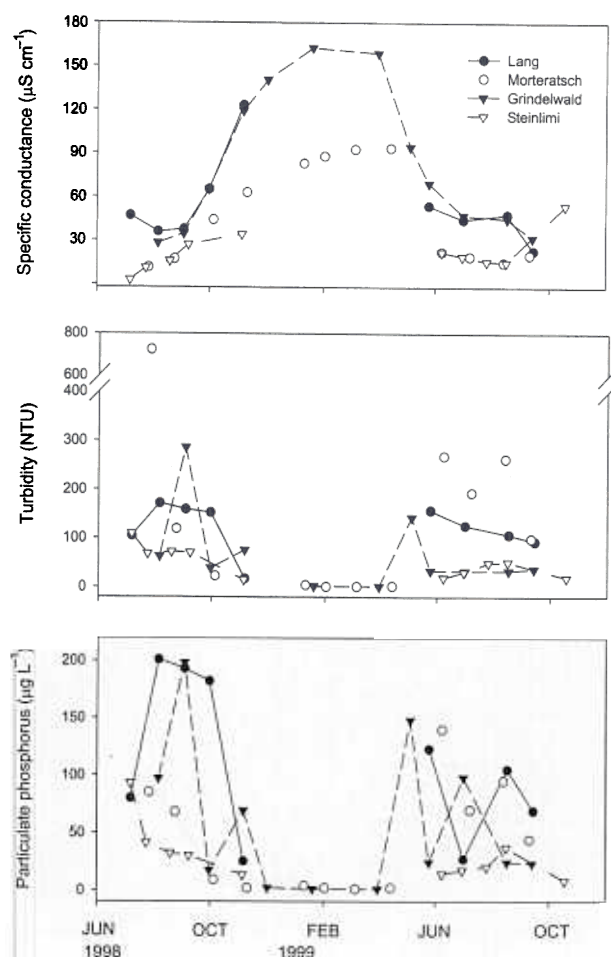


Fig. 3 Annual patterns of specific conductance, turbidity, and particulate phosphorus for the four glacial streams in the Swiss Alps. Note that Steinlimi and Lang were inaccessible during late winter. Symbols are specific collection dates.

biomass in spring prior to increases in glacial runoff (Fig. 4).

The average density of macroinvertebrates ranged from a low of 1139 ind. m⁻² at Lang to 3819 ind. m⁻² at Morteratsch (Table 3). The CVs varied widely, being lowest (<60%) at Morteratsch (both sites) and highest at upper Grindelwald (125%) and upper Lang (132%). Densities remained fairly constant at Morteratsch, the upper site in particular, but showed strong seasonal peaks at Steinlimi and Grindelwald (Fig. 5). Zoobenthic densities attained maxima between 6000 and 9000 ind. m⁻² at various times at most sites.

Mean biomass among sites showed similar patterns to density, being lowest at upper Lang (103 mg m⁻²) and highest at Morteratsch (721 mg m⁻²) (Table 3). The CVs also proved highly variable among sites, being lowest at upper Morteratsch (59%) and highest

at the upper Lang (144%) and Grindelwald (146%) sites. Biomass also showed strong seasonal peaks at all sites except Morteratsch upper, attaining maxima of over 1200 mg m⁻² at Grindelwald and even >1900 mg m⁻² at upper Morteratsch (Fig. 6). Peaks in biomass were observed most often in autumn and winter, whereas low values were found in late spring and summer.

Mean taxon richness was <5 taxa (in total) at all sites (Table 3), although 13 taxa in total were collected among sites. However, chironomids were identified only to family, although some larvae of *Diamesa* were later identified to species group. The CVs for taxon richness were relatively low (<60%), being <40% for five of the seven sites and <60% for the remaining two sites. However, mean taxon richness was much lower in summer than in winter when 3–4 additional taxa were recorded per site (Fig. 7).

Six taxa were predominant in these kryal streams: Chironomidae (Diamesinae), *Rhypholophus* sp., *Leuctra* spp., *Rhabdiopteryx alpina* Kührtreiber, *Baetis alpinus* Pictet, and *Rhithrogena* spp. (mostly *R. hybrida* Eaton and *R. loyolaea* Navas) (Table 4). The relative contributions made by these taxa varied widely among sites. For example, the Diamesinae comprised >80% of the macroinvertebrate numbers at Morteratsch and Steinlimi, but <50% at the other sites. *Rhypholophus* and *Leuctra* represented <5% of the assemblage at all sites, whereas *B. alpinus* typically constituted between 5 and 15% (<1% at Steinlimi). *Rhabdiopteryx alpina* was common at all sites with relative abundances ranging from 4% at Morteratsch to 49% at upper Grindelwald. *Rhithrogena* abundances ranged from 0.2% of the assemblage at Morteratsch to 13% at lower Lang. Other taxa frequently encountered but in low numbers included *Dicranota* sp., Empididae, *Perlodes intricata* Pictet, and other nemourid stoneflies (*Protonemura* in particular).

Principal components analysis based on the abundances of the six predominant taxa listed above separated sites into five groups (Fig. 8). The first axis was best explained (40%) by the abundances of *R. alpina*, *Rhithrogena*, and *B. alpinus*, whereas the second axis was associated with (24% of the variation) the abundances of chironomids (i.e. Diamesinae) and *Leuctra*. Lang and Grindelwald streams were grouped together, as were those at Morteratsch and Steinlimi. Within each of these groups the winter samples were grouped separately from the summer samples, except

Table 3 Amount of benthic organic matter, macroinvertebrate taxon richness, density and biomass averaged across dates for each site

Glacier	Site	Parameter	Benthic organic matter (g m^{-2})	Taxon richness (total)	Density (no. m^{-2})	Biomass (mg m^{-2})
Morteratsch $n = 12$	Upper	Mean	155.2	4.0	3819.7	721.0
		CV	84	35	53	59
Morteratsch $n = 12$	Lower	Mean	137.2	3.5	2845.5	599.8
		CV	95	37	57	93
Steinlimi $n = 8$	Upper	Mean	62.3	3.7	3261.5	288.5
		CV	114	33	80	76
Grindelwald $n = 10$	Upper	Mean	159.0	3.1	2692.4	372.0
		CV	111	46	125	146
Grindelwald $n = 10$	Lower	Mean	178.4	4.2	3054.4	529.8
		CV	103	37	85	93
Lang $n = 6$	Upper	Mean	126.3	2.6	1139.3	102.7
		CV	187	59	132	144
Lang $n = 6$	Lower	Mean	40.9	4.5	1213.3	180.6
		CV	171	34	113	98

CV = coefficient of variation.

that lower Lang was clearly distinguished from all other sites in summer.

Discussion

Results of the water analyses confirm that kryal streams have distinctive characteristics not shared by other stream types. All sites had low temperatures (annual mean $<2^{\circ}\text{C}$), high turbidity in summer from glacier flour (annual mean >50 NTU), and a distinct

flow regime (glacial source in summer, groundwater source in winter) as shown by Malard *et al.* (1999) for another glacial system in the Swiss Alps. However, the degree of glacial influence was closely associated with the kind and percentage of the catchment glaciated. Bedrock geology also played a strong role in the specific conductance of glacial stream water and explained the difference in ionic potential between Grindelwald and the other streams. Further, the small area of glaciated catchment at Steinlimi probably was

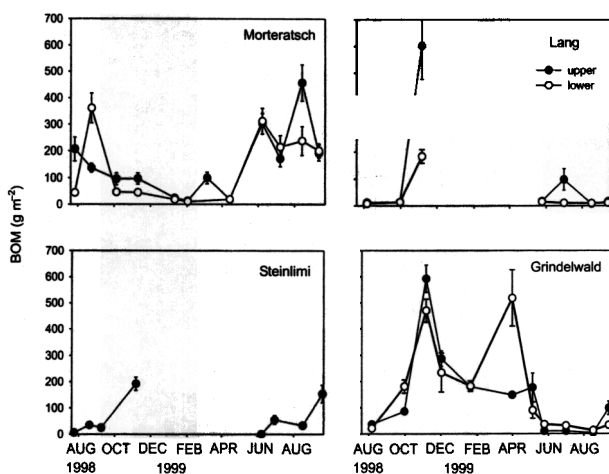


Fig. 4 Average quantity of benthic organic matter (BOM; dry mass) at each study site during the period of study. Bars represent ± 1 SD ($n = 5$ on each date). Note that Steinlimi and Lang were inaccessible during late winter.

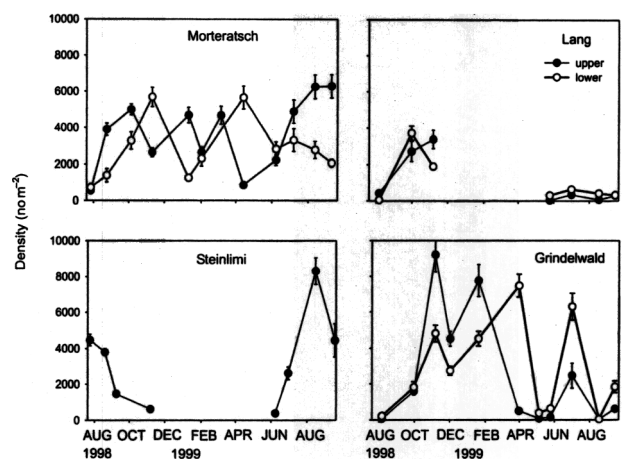


Fig. 5 Mean density of macroinvertebrates collected at the study sites during the period of study. Bars represent ± 1 SD ($n = 5$ on each date). Note that Steinlimi and Lang were inaccessible during late winter.

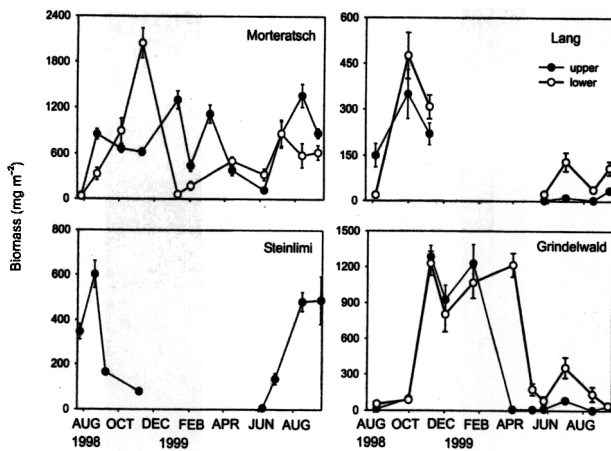


Fig. 6 Mean biomass (dry mass) of macroinvertebrates collected at the study sites during the period of study. Bars represent ± 1 SD ($n = 5$ on each date). Steinlimi and Lang were inaccessible during winter. Note scale differences among plots.

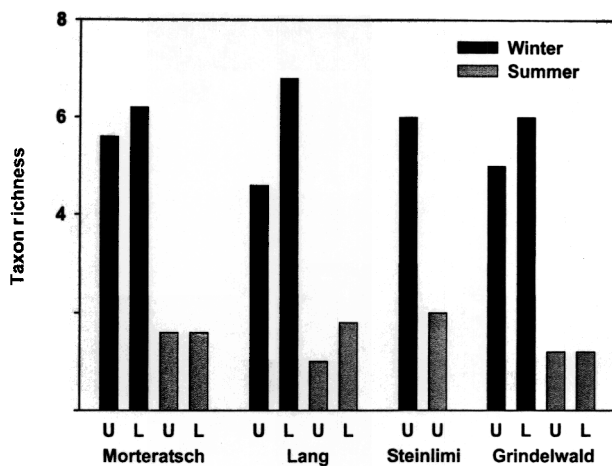


Fig. 7 Total taxon richness at each study site in winter and summer. U = upper site, L = lower site. Winter samples for Lang and Steinlimi are presented for late November, the last date these sites were accessible.

the reason for the lower turbidity values recorded in this stream. More research is needed to fully document the range of physical and chemical characteristics of glacial streams. For example, some kryal streams remain clear all year round with the reasons only partly understood (Ward, 1994) and geology differs considerably within and among geographic regions (e.g. Gíslason, Ólafsson & Adalsteinsson, 1998). These physico-chemical differences among glacial streams likely have a strong effect on zoobenthic distribution and abundance (*sensu* Southwood, 1977).

The amount (annual average) of BOM (dry mass) collected in the four glacial streams in this study fell within the range reported for open-canopied streams

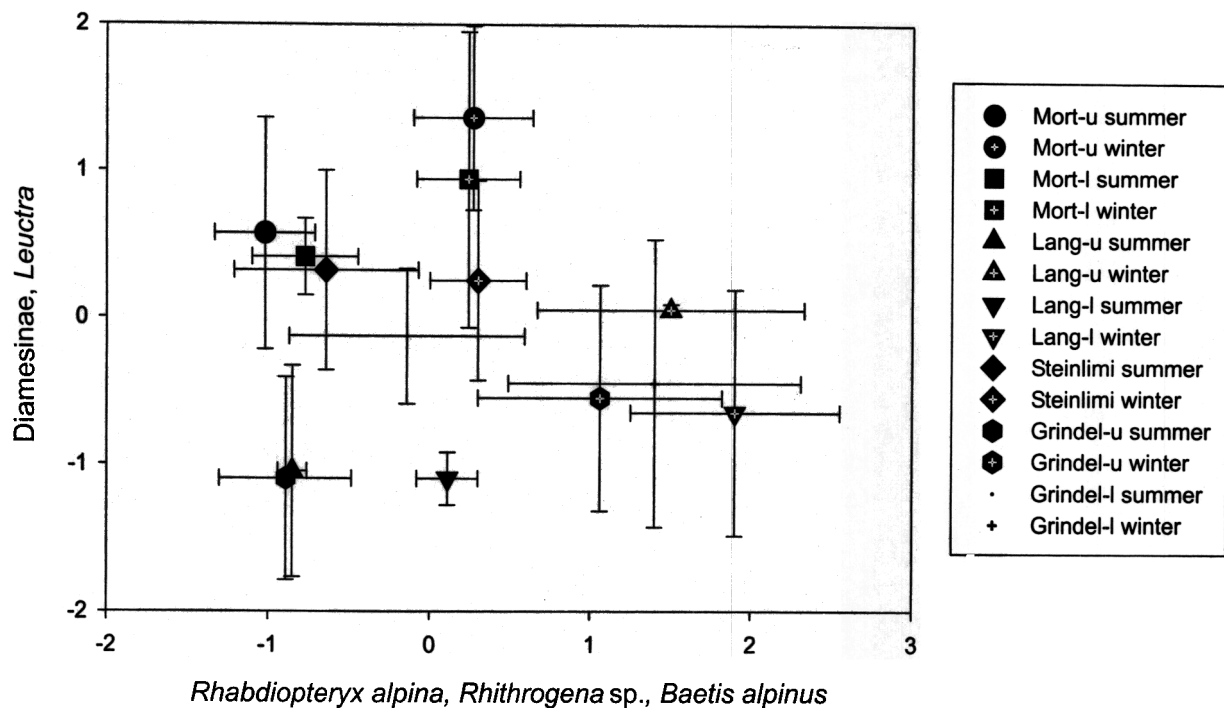
in other biomes (see Webster & Meyer, 1997). Average values in our study ranged from 41 to 180 g m⁻², comparable with typical values of <200 g m⁻² for arid and boreal streams. However, some streams in Alaska had average annual BOM values of only 20–56 g m⁻², and therefore were quite similar to the minimum observed in this study (41 g m⁻²). Maximum values for nonglacial streams that were forested ranged from about 1200 to over 6000 g m⁻² (Webster & Meyer, 1997). Our maximum BOM values (up to 600 g m⁻²) were associated with blooms of the chrysophyte *H. foetidus*, usually in autumn and, if channels were open, in winter. Clearly, primary production is an important avenue for organic matter generation and, potentially, a food resource for macroinvertebrates in alpine glacier-fed streams.

Our data suggest substantial variation in macroinvertebrate assemblages among kryal streams in the Swiss Alps. Thus, although the chironomids were a predominant component of the zoobenthos in all four glacial streams, especially during autumn and winter, other macroinvertebrate taxa commonly were found near the glacial snout as well. Indeed, Diamesanæ contributed <50% of assemblage abundances in two of the four glacial streams studied at both upstream and downstream locations. At these sites, *R. alpina*, *Rhithrogena*, and *B. alpinus* also were frequently collected. *Diamesa* groups (identified by B. Janecek, Universität für Bodenkultur, Vienna, Austria) common at the various sites included *D. latitarsis*-gr., *D. zernyi*-gr., *D. goetghebueri* and *D. bertrami* at Morteratsch; *D. zernyi*-gr., *D. bertrami* and *D. cinerella*-gr. at Grindelwald; and *D. cinerella*-gr. and *D. zernyi*-gr. at Lang.

Most studies of glacier-fed rivers have documented extremely low densities of macroinvertebrates (e.g. Kownacki, 1991; Gíslason *et al.*, 1998), and no studies have provided estimates of biomass (but see Milner, 1994; for biovolume measurements). Generally, our estimates of mean densities were similar to those found in temperate streams. For example, average densities in a number of streams sampled in central Idaho, U.S.A. over a 6-year period (Robinson, Minshall & Royer, 2000) ranged from 1700 to 9870 ind. m⁻², whereas average densities in our glacial streams ranged from 1140 to 3800 ind. m⁻². However, sampler mesh size was 250 µm in the Idaho study, compared with 100 µm in this study, suggesting that densities probably were higher in the Idaho study. Nevertheless, densities in our streams attained over 9000 ind. m⁻² at certain times

Table 4 Absolute and relative (%) average abundances (no. m⁻²) for the most common taxa collected at the study sites during the period of study. SD = Standard deviation, n = Number of collection dates

Glacier	Site	Parameter	Chironomidae	<i>Rhypholophus</i> sp.	<i>Leuctra</i> sp.	<i>Rhabdiopteryx</i> sp.	<i>Baetis alpina</i>	<i>Rhithrogena</i> sp.
Morteratsch n = 12	Upper	Mean	3196.3	55.3	179.5	189.5	221.8	8.3
		SD	2059.4	44.9	307.4	195.9	347.1	15.9
		%	83.0	1.4	4.7	4.9	5.8	0.2
Morteratsch n = 12	Lower	Mean	2408.1	67.7	53.9	120.8	294.8	12.7
		SD	1317.8	86.7	87.9	177.3	415.0	19.0
		%	81.4	2.3	1.8	4.1	10.0	0.4
Steinlimi n = 8	Upper	Mean	3109.9	52.7	12.5	228.0	27.7	22.5
		SD	2449.8	36.8	10.4	298.5	22.2	29.2
		%	90.1	1.5	0.4	6.6	0.8	0.7
Grindelwald n = 10	Upper	Mean	935.7	12.0	4.0	1355.8	423.9	21.6
		SD	1559.0	14.0	8.4	1905.7	751.8	24.1
		%	34.0	0.4	0.1	49.2	15.4	0.8
Grindelwald n = 10	Lower	Mean	1332.0	69.3	6.0	1435.2	149.7	102.0
		SD	1945.6	43.7	9.7	2021.1	197.6	165.9
		%	43.0	2.2	0.2	46.4	4.8	3.3
Lang n = 6	Upper	Mean	598.0	39.2	33.3	454.0	29.4	105.0
		SD	1086.7	37.2	64.1	888.7	49.3	155.4
		%	47.5	3.1	2.6	36.1	2.3	8.3
Lang n = 6	Lower	Mean	312.7	35.3	6.7	595.9	125.7	163.6
		SD	231.2	24.1	16.3	1068.2	159.2	137.2
		%	25.2	2.8	0.5	48.1	10.1	13.2

**Fig. 8** Principal components analysis ordination based on abundances of the six taxa common to all sites. Each symbol represents the mean factor score for that site from samples collected in winter or summer. Bars represent ± 1 SD. Mort = Morteratsch, Grindel = Grindelwald, u = upper site, l = lower site. Taxa noted on each axis had factor loadings greater than 0.70. Taxa associated with each axis showed positive relationships with that axis.

indicating the potential for extremely high densities in glacial streams (see Burgherr & Ward, 2000). Similarly, biomass values also fell within the range reported by Robinson *et al.* (2000), although tending to be in the lower quartile, and with substantial biomass peaks (e.g. $>1900 \text{ mg m}^{-2}$) at certain times of year.

The low densities cited by earlier authors may have been an artefact of restricting sampling to the summer, as access to many glacial stream systems is logistically constrained in winter. In the present study, however, high densities were found in the two glacial systems sampled throughout winter and taxon richness was considerably greater in winter than in summer (also see Schütz *et al.*, 2001). These results suggest that late autumn and winter may be favourable periods for macroinvertebrates in glacial streams, and is consistent with the findings of Burgherr & Ward (2000) who observed peaks of over $20\,000 \text{ ind. m}^{-2}$ in early winter and early spring in another glacial stream in the Swiss Alps. Glacial streams in Europe become much more benign from late autumn to early spring as glacial flow is minimal and water clarity high (Malard *et al.*, 1999), periphyton growth is dense (primarily because of *H. foetidus*; Ward, 1994; Uehlinger, Zah & Bürgi, 1998) and stream beds are highly stable (Füreder, 1999). Kownacka & Kownacki, (1972) found many kinds of chironomids inhabiting *H. foetidus* (an alga common in autumn/winter in our streams), the algal mats functioning both as habitat and food in streams of the Tatra Mountains. We also observed high numbers of chironomid adults under ice in a glacial stream (Val Roseg) during March prior to the opening of the channels in spring.

Principal components analysis clearly separated two groups of glacial streams; Grindelwald/Lang and Morteratsch/Steinlimi. The Grindelwald/Lang streams exhibited 1.5–2× greater monthly variation in macroinvertebrate densities and biomasses than the Morteratsch/Steinlimi streams suggesting other factors besides water chemistry or temperature were influencing assemblage dynamics. Milner & Petts (1994) suggested that channel stability was another critical factor limiting population persistence in glacial streams. Both Steinlimi (not sampled in late winter) and Morteratsch had relatively constant macroinvertebrate abundances throughout the year and both were dominated by *Diamesa* spp. The upper Morteratsch and Steinlimi both had stable channels with stream gradients $<2\%$ that may have allowed

Diamesa to maintain high densities even in summer. In contrast, channel stability in Grindelwald and Lang appeared to be much lower and stream gradients were substantially higher, thus potentially reducing population sizes in summer. Clearly, more research is needed to test the hypothesis that channel stability plays an important role in structuring macroinvertebrate assemblages in glacial streams.

We found little difference in assemblage structure between upstream and downstream locations within each stream despite distances between sites ranging from 300 to 500 m. Seasonal patterns in density, biomass and taxon richness also were quite similar between locations in a stream. Principal components analysis revealed a difference between upstream and downstream locations only at Lang, and then only in summer. Here, the lower site typically had higher average taxon richness, density and biomass than the upper site. Besides appearing less stable, the upper site also was more recent than the downstream one because of present trends in glacial recession. Consequently, stream reaches near the glacial snout may be in different stages of development than those further downstream as found in new streams in Glacier Bay, Alaska (Milner, 1987, 1994). Indeed, the longitudinal patterns observed in many glacier stream systems may simply be a function of stream age (Milner & Petts, 1994), although low temperature and habitat stability obviously play an important proximate role in structuring their zoobenthic assemblages along longitudinal gradients (Ward, 1994). Nevertheless, the similar or even higher densities of macroinvertebrates at the upper sites relative to the lower sites are certainly indicative of high colonization rates by some taxa, such as *Diamesa*.

In conclusion, our results indicate that considerable spatio-temporal variation exists in abiotic and biotic variables of glacier-fed streams in the Swiss Alps. Amounts of BOM were similar to those found in other open-canopied streams with minimal inputs of allochthonous litter; seasonal peaks were associated with blooms of the chrysophyte *H. foetidus*, a common alga in glacial streams. We found that although the chironomid *Diamesa* was a predominant component of the zoobenthos, other cold-adapted aquatic insects could be just as common in streams near the glacial snout. The differences in assemblage structure among the four kryal streams in this study appeared to be related more to channel stability than to low temperature. Although little studied, winter appears to be

an active and favourable period for aquatic insects, with more taxa and greater densities than in summer.

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