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Longitudinal and seasonal distribution patterns of the benthic fauna of an alpine glacial stream (Val Roseg, Swiss Alps)

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SUMMARY

1. Seasonal changes in longitudinal patterns of environmental conditions and macroinvertebrate community distributions were examined in an alpine glacial stream (Roseg River, Switzerland).
2. Physico-chemical parameters reflected seasonal changes in glacial influence via shifts in water sources and flowpaths (glacial meltwater versus ground water), and were best described by turbidity, particulate phosphorus and specific conductance. High nitrogen concentrations indicated snowmelt was the main water source in June.
3. Macroinvertebrate densities and taxon richness were highest during spring (4526 m^{-2} and 16 taxa, all sites combined) and late autumn/early winter (8676–13 398 m^{-2} with 16–18 taxa), indicating these periods may be more favourable for these animals than summer when glacial melting is maximal. *Diamesa* spp. (Chironomidae) dominated the fauna at the upper three sites (>95% of zoobenthos) and were abundant at all locations. Other common taxa at lower sites (1.2–10.6 km downstream of the glacier terminus) included other chironomids (Orthocladiinae, Tanytarsini), the mayflies *Baetis alpinus* and *Rhithrogena* spp., the stoneflies *Leuctra* spp. and *Protonemura* spp., blackflies (*Simulium* spp., *Prosimulium* spp.), and Oligochaeta.
4. Co-inertia analysis revealed a strong relationship between environmental conditions and benthic macroinvertebrate assemblages. Furthermore, it elucidated temporal variability in longitudinal response patterns, as well as a similarity in temporal patterns among individual sites.
5. Our results suggest that zoobenthic gradients are not solely related to temperature and channel stability. Seasonal shifts in sources and pathways of water (i.e. extent of glacial influence), and periods of favourable environmental conditions (in spring and late autumn/early winter) also strongly influenced zoobenthic distributions.

Keywords: glacial, kryal, macroinvertebrates, Chironomidae, Ephemeroptera, Plecoptera

Introduction

Treeline and the permanent snowline comprise two important boundaries for life in alpine environments. Above treeline the alpine zone is characterized by sedge-mat vegetation that gradually fades into grass hummocks and cushion plants in the subnival zone (Landolt, 1992). Three principal types of stream ecosystems can be distinguished in areas of high altitude (Ward, 1994): kryal (glacier-melt dominated), krenal (groundwater-fed) and rhithral (seasonal snowmelt dominated). Environmental harshness (low temperatures and scarce food resources) is a general feature of these alpine streams. Because of heterogeneity in the climate, geomorphology and hydrology of

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alpine environments, alpine stream networks often form a complex mosaic of kryal, krenal and rhithral segments (Ward, 1994; McGregor *et al.*, 1995).

Kryal stream segments are characterized by (1) year-round low temperatures ($T_{\max} = 4$ °C), (2) large diel flow fluctuations in summer with peaks in late afternoon from glacial melting, (3) highly turbid water from suspended rock flour through glacial scouring and (4) usually low channel stability close to the glacier, but with increasing stability downstream (Milner & Petts, 1994; Ward, 1994). Furthermore, instream environmental conditions depend on distance from the glacier terminus, season, and the contribution of non-glacial water sources. Downstream of the kryal segment, a glacio-rhithral zone, fed by a mixture of water sources, can extend for a considerable distance, with temporal changes in discharge and temperature reflecting the relative proportion of glacial influence (Füreder, 1999).

Alpine streams play an important role in river systems throughout the world (Füreder, 1999), and may be more affected by global climate change and anthropogenic impacts than mountain streams at lower altitude (Chapin & Körner, 1994; McGregor *et al.*, 1995). Despite a well-documented interest in high mountain streams and their fauna at the beginning of the 20th century (Steinmann, 1907; Thienemann, 1912; Steinböck, 1934; Dorier, 1937), most later studies have dealt principally with hydrology, glaciology, geomorphology and physico-chemical attributes (e.g. Gurnell & Fenn, 1985; Röthlisberger & Lang, 1987; Prowse, 1994; Gurnell *et al.*, 1999). In contrast, comprehensive studies examining longitudinal distribution patterns of alpine benthic communities are few (e.g. Saether, 1968; Steffan, 1971; Kownacka & Kownacki, 1972; Kownacki, 1991), and typically of limited duration or intensity. Year-round studies, such as conducted by Lavandier & Décamps (1984) in the Estaragne, an alpine headwater stream in the French Pyrenees, are scarce although of major importance to understand temporal dynamics.

Synthesizing the available literature on the ecology of glacial-fed streams, Milner & Petts (1994) proposed a qualitative model that relates longitudinal gradients of zoobenthic communities to temperature and channel stability; both being a function of distance from the glacier terminus and time since deglaciation. Close to the glacier, where summer temperatures typically do not exceed 2 °C, chironomids of the genus *Diamesa* generally dominate, or are the sole animals found. Where maximum temperatures are between 2 and 4 °C, other Diamesinae, Orthocladiinae and Simuliidae are typically present. When water temperatures exceed 4 °C, Baetidae, Nemouridae and Chloroperlidae typically colonize glacial streams. Further downstream, other Ephemeroptera, Plecoptera and Diptera, as well as Trichoptera, are predicted to appear. Milner & Petts (1994) also suggested that modifications of downstream patterns may result from tributaries, changes in valley confinement and lakes. For example, Burgherr & Ward (2000) reported distinct differences in the zoobenthic communities of a kryal channel and an adjacent proglacial lake outlet stream.

The study of relationships between faunal assemblages and their environment is a central theme of community ecology. Whenever possible, the inherent spatial and temporal variation of both the environment and the faunal assemblage should be considered (e.g. Borcard, Legendre & Drapeau, 1992; Franquet, Dolédec & Chessel, 1995) to gain a better understanding of the ecological phenomenon under study (Resh & Rosenberg, 1989). Ordination techniques, designed to summarize and simplify complex data sets, provide a powerful tool for analysing patterns of biotic assemblages, and relating them to measured environmental variables (ter Braak & Verdonschot, 1995). Recently, co-inertia analysis has been proposed as an alternative to canonical correspondence analysis for the study of relationships between faunistic data and environmental measurements (Dolédec & Chessel, 1994). This technique is particularly suitable for the simultaneous detection of faunistic and environmental features in studies of ecosystem structure.

The principal objective of this study was to relate longitudinal patterns in macroinvertebrate assemblages to environmental conditions in the glacial-fed Roseg River, Switzerland. Specifically, the following questions were addressed: (1) Do environmental conditions exhibit distinct patterns with increasing distance from the glacier terminus and across seasons? (2) Are there predictable spatio-temporal patterns reflected in zoobenthic assemblages? (3) Is there concordance among environmental and biotic gradients? Because the relationship between fauna and environment may vary in space and time, we use an approach to separate the spatial variability among sampling dates and the temporal variability among sampling sites.

Methods

General description of the study area

The study was conducted in the Val Roseg located in the Bernina Massif of the Swiss Alps (9°53′57″ E, 46°29′28″ N). The 11.3 km long Roseg River (Ova da Roseg) drained a catchment area of 66.5 km^2, of which 30% was covered by glaciers, 40% was bare rock or glacial till without vegetative cover, and 9% was used for pasture. Bedrock consists of granite and diorite of the Bernina-, Corvatsch- and Sella-Nappes, which all belong to the austroalpine nappes. Altitude ranged from 1760 m a.s.l. (confluence with Bernina River) to 4049 m a.s.l. (Piz Bernina). Precipitation averaged 1600 mm year^{-1}, of which 50% is snow (1951–80; Spreafico, Leibundgut & Weingartner, 1992). Glacial meltwater from the Tschierva and Roseg glaciers was the primary water source of the Roseg River. Mean annual discharge of the Roseg River was 2.76 m^3 s^{-1} (1955–97; Swiss Hydrological and Geological Society). Discharge peaked in late summer when diel flow fluctuations also were highest. In winter, the system was fed largely by groundwater.

Treeline was about 2300 m a.s.l. in the Val Roseg, with subalpine coniferous forests restricted to the lower parts of the valley slopes, whereas no trees occurred on the fluvio-glacial gravel of the valley floor. Dominant tree species were larch (*Larix decidua* Mill.), stone pine (*Pinus cembra* L.) and mugo pine (*P. mugo* Turra). Shrubs consisted mainly of green alder [*Alnus viridis* (Chaix) DC] and willow (*Salix* spp.). In the lower alpine zone, mat-grass (*Nardus stricta* L.) vegetation was dominant. Curved sedge (*Carex curvula* All.) characterized the middle and upper alpine zone. In the subnival zone, sparse hummocks of curved sedge tussocks occurred, otherwise only lichens and mosses developed.

Study sites

Five distinct reaches characterize the Roseg River: an unstable braided proglacial reach (length 900 m) below Tschierva glacier (Fig. 1), a lake outlet stream below proglacial Lake Roseg (length 950 m), a single thread channel incised in glacial till (length 600 m), the main glacial flood plain (length 2750 m), and a canyon-constrained reach that extends downstream to the river mouth at Pontresina (length 7050 m) (Figs 2 and 3a). In the main flood plain, six distinct channel types can be distinguished (Tockner *et al.*, 1997).

Ten sampling sites (Fig. 3a) were located along the main channel (thalweg) of the Roseg River from just below terminus of the Tschierva glacier (site M1) down to the river mouth (site M10), covering an altitudinal gradient from 2150 to 1760 m a.s.l. For comparison with previous work on the hydrology and ecology of this glacial river system, sites numbered M1–M10 in this paper corresponded to codes M-20, M-15, M-10, M-1, M10, M12, M20, M30, M32 and M40 used in previous papers (Tockner *et al.*, 1997; Malard, Tockner & Ward, 1999; Ward *et al.*, 1999). Some general site characteristics are summarized in Table 1.

Fig. 1 Pro-glacial area below Tschierva Glacier.

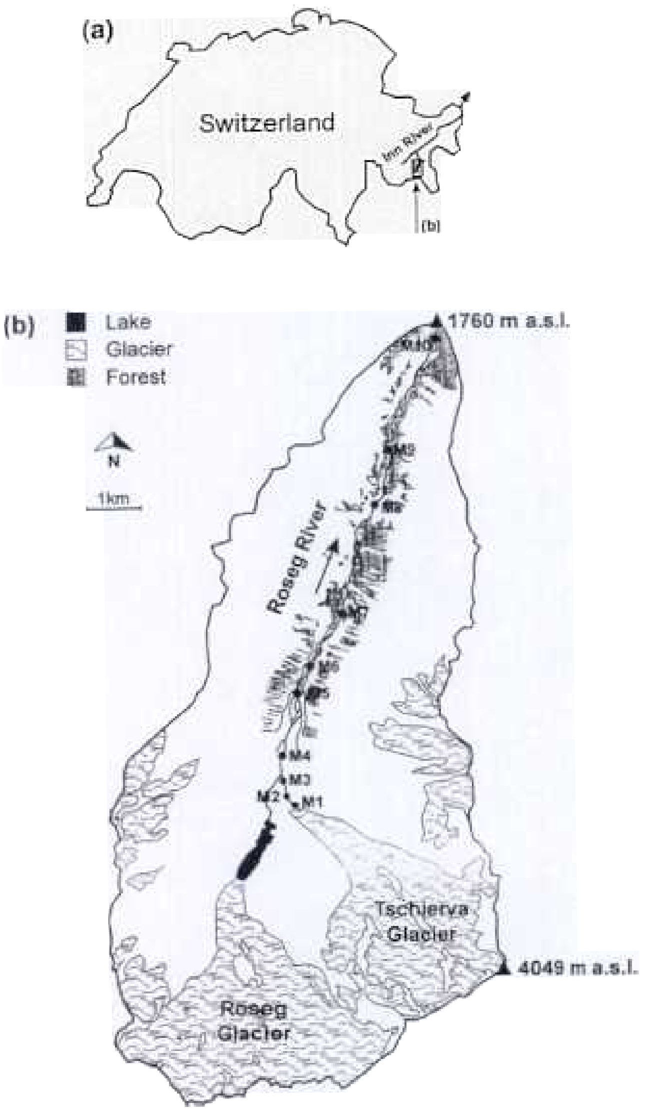


Fig. 2 (a) Geographical location of the Val Roseg study site in the Bernina Massif of the Swiss Alps. (b) Catchment area of the Val Roseg and indication of glaciers, lakes and forests. Black circles indicate locations of sampling sites.

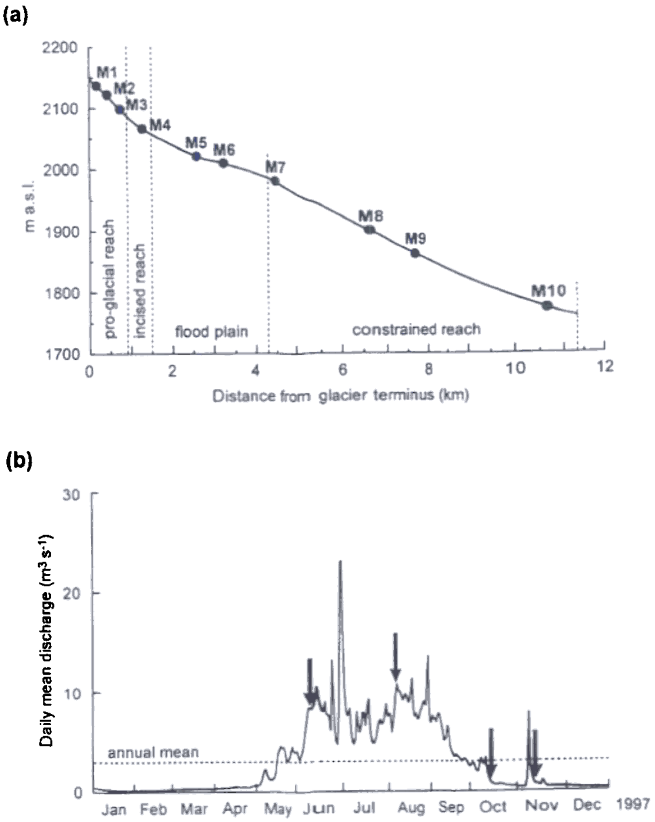


Fig. 3 (a) Longitudinal and altitudinal location of sampling sites along the Roseg River. Dashed lines indicate reach borders. (b) Annual discharge of the Roseg River in 1997. Arrows indicate sampling dates for environmental variables and macroinvertebrates.

Samples were collected in June (increasing discharge), August (high discharge), October (decreasing discharge) and November 1997 (low and constant discharge) (Fig. 3b). For sites M1 and M2, samples were collected only in August and October.

Data collection and analysis

Physico-chemical parameters were collected in the morning at each site and sampling date to minimize the influence of daily discharge fluctuations and ensure data comparability. Turbidity was determined with a portable turbidity meter (Cosmos; Züllig, Switzerland). Specific conductance and temperature were measured in the field using a pocket conductivity meter (WTW LF323-B; Wissenschaftliche-Technische Werkstätten, Germany). Suspended solids (SS) were estimated according to American Public Health Association (APHA) (1989). Nitrate (NO_3–N) was determined according to Downes (1978) and modifications by Stöckli (1985). Soluble reactive phosphorus (SRP) was analysed according to the molybdenum blue method (Vogler, 1965). Particulate nitrogen (PN) and particulate phosphorus (PP) were quantified as NO_3–N and SRP after digestion with $K_2S_2O_8$ at 121 °C (Ebina, Tsutsui & Shirai, 1983). Dissolved organic carbon (DOC) was measured by wet oxidation with subsequent acidification and IR-detection of CO_2, whereas total inorganic carbon (TIC) was measured as CO_2 with a Horiba IR-detector after samples had been acidified and heated to 860 °C. For further details see Tockner *et al.* (1 997). Continuous temperature records (1 h intervals; StowAway XTI tempera-

Table 1 General characteristics of the sampling sites. Means and ranges in parentheses are given for near-bed velocity and annual mean temperature. Annual degree days are expressed as centigrade temperature units (CTU)

Site	Reach type	Altitude (m a.s.l.)	Distance from glacier terminus (m)	Near-bed velocity (m s^{-1})	Annual mean temperature (°C)	Annual degree days (CTU)
M1	Proglacial	2137	147	0.45 (0.22–0.74)	–	–
M2	Proglacial	2122	414	0.67 (0.39–0.96)	0.42 (0.00–0.92)	154
M3	Proglacial	2096	769	0.46 (0.19–0.69)	0.68 (0.00–1.86)	248
M4	Incised	2064	1324	0.48 (0.05–0.76)	1.00 (0.00–3.54)	365
M5*	Flood plain	2021	2579	0.40 (0.13–0.64)	1.82 (0.00–4.83)	666
M6	Flood plain	2009	3218	0.45 (0.29–0.62)	–	–
M7	Constrained	1981	4389	0.39 (0.24–0.59)	2.59 (0.00–6.11)	945
M8	Constrained	1901	6612	0.42 (0.15–0.68)	–	–
M9	Constrained	1862	7659	0.50 (0.13–0.80)	–	–
M10	Constrained	1773	10642	0.49 (0.10–0.73)	2.64 (0.00–6.73)	964

*In contrast to all other sites, site M5 was not permanently flowing. Surface water was not present from mid December 1996 to the first half of April 1997, and mid-December 1997 to the second half of April 1998.

ture loggers, Onset Corporation, U.S.A.) were available for six of the 10 sites (U. Uehlinger, personal communication). Near-bed current velocities were measured at the same positions where benthic samples were taken using a flow meter (Mini Air 2; Schiltknecht Messtechnik AG, Switzerland). Substrate size was assessed in the field by measuring 100 randomly selected stones (b-axis, width). Initiation of sediment transport was used as a measure of channel stability because it was also considered as a useful disturbance threshold for benthic macroinvertebrates. Estimates of dimensionless critical shear stress (based on channel geometry and grain size distributions; Gessler, 1965) were used to determine the critical discharge at which bed sediments start to move, using the software FLUSSBAU (Laboratory of Hydraulics, Hydrology and Glaciology, Swiss Federal Institute of Technology, Zurich, Switzerland).

Three Hess samples (area 0.043 m^2, 100 μm mesh size) from randomly selected locations in riffle/run habitats were collected at each site and date, and preserved in 4% formalin. In the laboratory, macroinvertebrates were sorted, counted and identified to the lowest practical taxonomic level for most groups using a dissecting microscope. However, all Chironomidae were identified to subfamilies and tribes, and species groups were qualified for some *Diamesa* spp. Limnephilid caddiesflies also were pooled, as identification to the species level is only possible using fifth instar larvae (Waringer & Graf, 1997). Nematoda, Hydrachnellae, Crustacea and Oligochaeta were not identified further. After removal of invertebrates, the remaining material from each sample was split into two fractions (>1 and <1 mm), dried at 60 °C, weighed, ashed at 550 °C and reweighed for determination of coarse and fine benthic organic matter (BOM) as ash-free dry mass (AFDM).

Macroinvertebrate community analyses included estimates of mean densities, taxon richness and Simpson's index of concentration (SI) as a measure of diversity.

$$SI = \Sigma[(n^2 - n)/(N^2 - N)]$$

where n is the number of individuals in a species, and $N = \sum n$. As recommended by Rosenzweig (1995), SI values were converted to –ln SI such that values increase as the number of species does, independently of sample size.

Co-inertia analysis (CIA) was used to simultaneously examine the structure in the environmental and faunistic data, and to identify the corresponding variations (i.e. co-structure) of these two structures (Dolédec & Chessel, 1994). Co-inertia analysis is a two-table ordination method, as is canonical correspondence analysis (CCA). However, CIA enables the joint analysis of tables having similar (even low) as well as different numbers of environmental variables, species, and/or samples (Dolédec & Chessel, 1994). In contrast, in CCA a small number of environmental variables is required to predict the faunistic structure, otherwise it would be reduced to a simple correspondence analysis of the faunistic table. Environmental data were normalized to ensure equal weights for all variables, whereas the faunistic data were $\log_{10}(x + 1)$ transformed and centred to reduce strong intertaxonomic differences in densities. A Monte-Carlo permutation test was used to check the significance of the co-structure between the two data sets as revealed by CIA. The temporal and spatial components of variation in the two data sets were examined using within-class CIA (Franquet & Chessel, 1994; Franquet *et al.*, 1995). All multivariate analyses were computed using the ADE-4 software (Chessel & Dolédec, 1996; Thioulouse *et al.*, 1997).

Results

Environmental conditions

A detailed description of the physico-chemical templet of the Val Roseg was previously summarized (Tockner *et al.*, 1997; Malard *et al.*, 1999); therefore, only a selection of parameters distinctive for kryal streams will be presented here. Substrata at all sites consisted mainly of cobbles and boulders. Average particle size (*b*-axis, width) ranged between 9 and 12 cm. Estimates of critical shear stress indicated that bed sediments in the main channel of the Roseg River start to move if discharge exceeds 8 m^3 s^{-1}. This threshold was exceeded on 41 days in 1997; 15x in June, 6x in July, and 20x in August. Daily mean water temperature in the main channel ranged from 0.00 to 0.92 °C at site M2, 0.00 to 4.83 °C at M5, and 0.00 to 6.73 °C at M10. Annual degree days increased from 154 centigrade temperature units (CTU) at site M2, to 666 CTU at M5, and 964 CTU at M10 (Table 1). Nitrate (NO_3–N) was the dominant nitrogen species (87%) in the surface water of the Roseg River (Malard *et al.*, 1999). The average nitrate concentration was highest in June at 421 ± 17 µg L^{-1} (mean ± SD), and between 180 and 266 µg L^{-1} on the other sampling dates (Fig. 4a). Specific conductance (Fig. 4b) was lower during the peak of glacier melting (36 ± 5 µS cm^{-1} in August, 38 ± 5 µS cm^{-1} in October) and highest in November (69 ± 7 µS cm^{-1}) when glacial melting was minimal. Intermediate levels were found in June (55 ± 9 µS cm^{-1}) when snowmelt was still the main source of water, but glacier melting already started.

Turbidity and particulate phosphorus (PP) (Fig. 4c,d) peaked in August because of glacier melting and associated high loads of glacial flour, with an average of 84 ± 11 nephelometric turbidity units (NTU) for turbidity and 49 ± 16 µg L^{-1} for PP. In June and October (when discharge was increasing and decreasing, respectively) intermediate levels were observed (turbidity: 51 ± 13 and 58 ± 18 NTU; PP: 29 ± 7 and 29 ± 6 µg L^{-1}), whereas during low flow in November minimum values were recorded (13 ± 12 NTU for turbidity, 11 ± 5 µg L^{-1} for PP). Turbidity and to a lesser extent PP reached substantially higher values in the incised reach compared with the

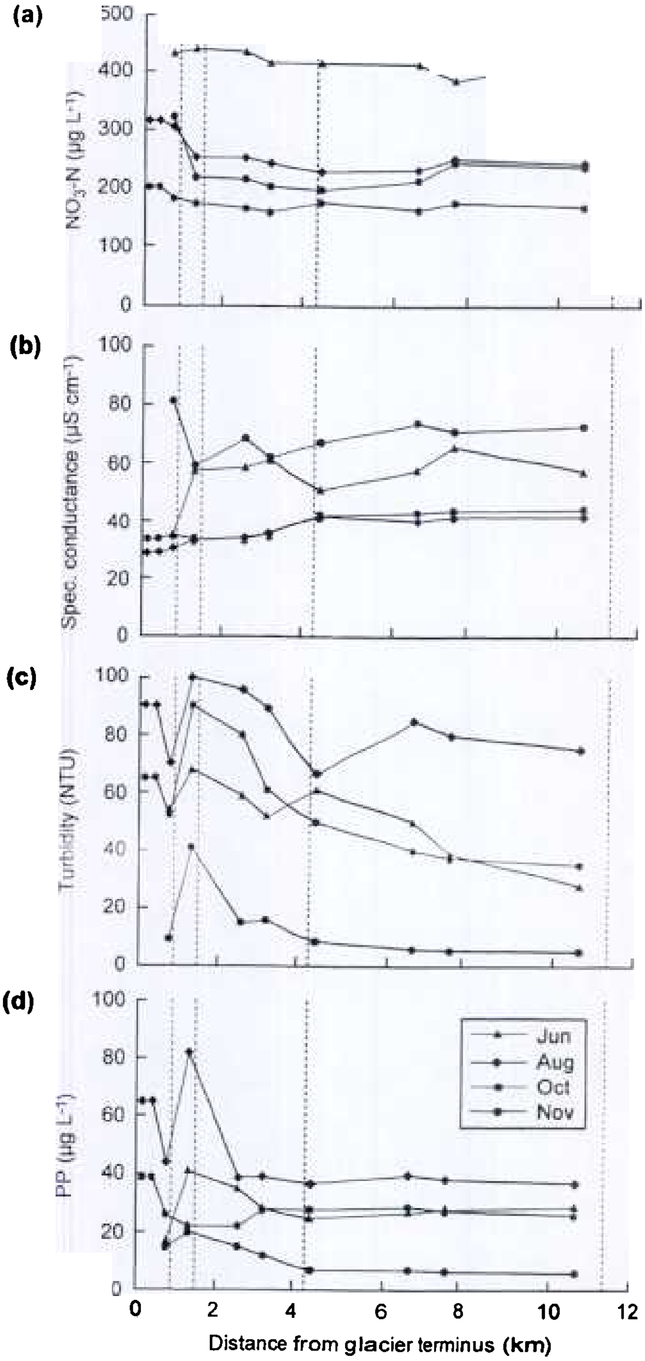


Fig. 4 Longitudinal patterns of (a) NO_3–N, (b) specific conductance, (c) turbidity and (d) particulate phosphorus (PP) on each sampling date. Dashed lines indicate reach borders. Order of sampling sites and names shown in Fig. 2a.

proglacial area, whereas further downstream values were attenuated again. Overall, longitudinal patterns in physico-chemical parameters exhibited pronounced seasonal changes.

Macroinvertebrates

Total densities of macroinvertebrates ranged from 116 m^{-2} (M2 in August) to 24 380 m^{-2} (M10 in October), varying along both temporal and spatial dimensions. Lowest densities, all sites combined, were found in August (1472 ± 1355 m^{-2}), intermediate in June (4526 ± 2723 m^{-2}) and November (8676 ± 4434 m^{-2}), and highest in October (13 398 ± 6113 m^{-2}). Generally, average densities per site increased with increasing distance from the glacier terminus (Table 2). Coefficients of variations were highest in the proglacial reach (M1–M3), decreased to a minimum at M6, and then increased again downstream to M10.

The number of taxa recorded at a site ranged from 1 to 26. Lowest taxon richness was found within the proglacial reach (M1–M3), followed by a progressive increase to M6 at the lower end of the flood plain, then similar richness at the four lowermost sites (Table 2). Overall, Chironomidae, *Baetis alpinus* Pictet, *Rhithrogena* spp., *Leuctra* spp., *Protonemura* spp., Simuliidae, and Oligochaeta were the predominant taxa (Table 3). Other taxa generally made up <1% of the total community, although some exceptions on certain dates and sites occurred (e.g. *Rhypholophus* sp. comprised 6–13% in the proglacial area in August, *Crenobia alpina* c. 3% at M3 and M4 in August, and Limnephilidae 7% at M10 in October). The few large individuals of limnephilid Trichoptera were identified as *Acrophylax zerberus* Brauer and *Drusus biguttatus* Pictet. Taxa not used in multivariate analyses (<0.05% of the assemblage or semiaquatic) were not included in Table 3. These were *Ecdyonurus picteti* Meyer-Dür, *Dictyogenus* spp., *Siphonoperla* spp., *Rhyacophila intermedia* McLachlan, Ceratopogonidae, and Collembola.

Diamesa spp. was the only genus of Chironomidae found close to the glacier terminus. Orthocladiinae first appeared at M3, but in low abundance. At M4, relative densities of *Diamesa* spp. declined by c. 30%, whereas the share of Orthocladiinae further increased. Further downstream, the ratio of *Diamesa* spp. to Orthocladiinae varied between 1 and 4. Tanytarsini always constituted a minor part of total Chironomidae present. Common *Diamesa*-groups found, were *D. steinboecki*-gr., *D. latitarsis*-gr., *D. bertrami*-gr., *D. cinerella-zernyi*-gr., and *D.* cf. *incallida*. *Baetis alpinus* was c. 2.5x more abundant than *Rhithrogena* species. *Rhithrogena loyolaea* Navàs and *R. nivata* Eaton were the two predominant *Rhithrogena*-species at all sites, while *R. alpestris* Eaton and *R. degrangei* Sowa were most abundant in the constrained reach. Simpson's Index was low in the proglacial reach, but increased in the incised reach and the flood plain, and reached a maximum at sites in the constrained reach (Table 2).

Relationships between fauna and environment

The co-structure between the environmental and faunistic data sets revealed by CIA was highly significant, as confirmed by a Monte-Carlo permutation test ($P = 0$). The first two CIA axes explained 81.1 and 14.5% of the total inertia. Turbidity, PP and SS were negatively related to Factor 1 of CIA, while TIC and specific conductance showed a positive relationship (Fig. 5a). Factor 2 was related to temperature, NO_3–N, PN and BOM in the positive region. Axis F1 of the corresponding faunistic structure (Fig. 5b) was best explained by Orthocladiinae, *Proto-*

Table 2 Mean ± 1 SD, and in parentheses coefficients of variation (CV in percentage) for densities, taxon richness, and Simpson's index (–ln SI) of the macroinvertebrate communities at the 10 sampling sites

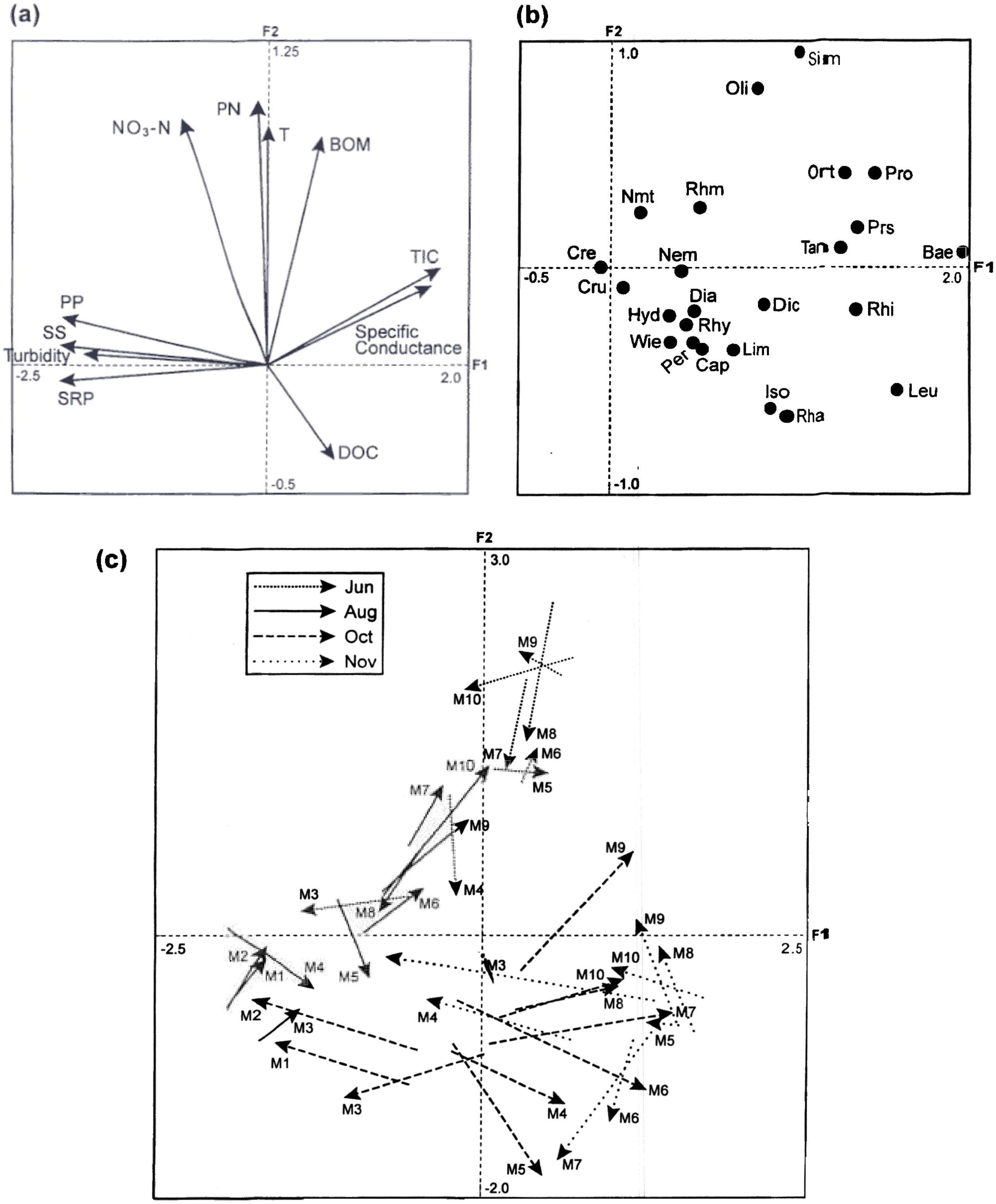
Site	Density (m^{-2})	Taxon richness	Simpson's Index (–ln SI)
M1	2632 ± 3536 (134)	5 ± 1 (16)	0.27 ± 0.37 (134)
M2	2469 ± 3327 (135)	2 ± 1 (71)	0.21 ± 0.29 (141)
M3	5417 ± 8020 (148)	8 ± 1 (6)	0.38 ± 0.39 (104)
M4	5048 ± 4562 (90)	11 ± 4 (36)	0.71 ± 0.39 (54)
M5	8438 ± 5237 (62)	16 ± 4 (26)	1.11 ± 0.41 (37)
M6	7936 ± 4504 (57)	20 ± 5 (25)	1.21 ± 0.35 (29)
M7	8136 ± 5991 (74)	20 ± 4 (20)	1.42 ± 0.10 (7)
M8	9138 ± 7074 (76)	19 ± 3 (16)	1.43 ± 0.27 (19)
M9	8504 ± 7074 (83)	19 ± 2 (12)	1.46 ± 0.44 (30)
M10	8415 ± 10753 (128)	18 ± 5 (30)	1.34 ± 0.50 (37)

Table 3 Absolute mean abundances (m^{-2}) for the predominant taxa collected at the sampling sites during the study period. For the other taxa only presence (x) or absence (–) at a site are reported because on average they contributed <1% to the total numbers. SD = standard deviation. Abbreviations for each taxon used in Figs 4–6 are shown in parentheses

	Sampling sites									
	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10
Predominant taxa										
Diamesa spp. (Dia)										
Mean	2593	2457	5194	3217	2287	1795	1928	2281	3490	4560
SD	3536	3344	7935	2980	1510	864	1779	2721	5474	7987
Orthocladiinae (Ort)										
Mean	0	0	29	153	833	985	1963	1868	1087	1091
SD	0	0	19	123	954	408	1242	1286	468	996
Tanytarsini (Tan)										
Mean	0	0	0	6	58	74	142	83	78	45
SD	0	0	0	12	91	64	175	95	51	66
Baetis alpinus Pictet (Bae)										
Mean	0	0	2	963	1392	2023	2279	1868	1128	366
SD	0	0	4	1348	1523	2194	2168	2456	1267	540
Rhithrogena spp. (Rhi)										
Mean	4	0	25	289	2236	527	291	248	256	169
SD	6	0	41	377	3039	574	226	207	221	150
Leuctra spp. (Leu)										
Mean	0	0	37	105	748	1688	552	250	122	118
SD	0	0	50	169	806	1979	633	299	140	129
Protonemura spp. (Pro)										
Mean	0	0	45	83	593	285	159	99	78	21
SD	0	0	84	78	903	236	170	43	44	15
Simulium spp. (Sim)										
Mean	0	0	0	21	37	74	107	83	810	205
SD	0	0	0	43	64	101	54	141	813	235
Prosimulium spp. (Prs)										
Mean	0	0	0	6	19	16	165	333	421	229
SD	0	0	0	7	34	22	216	551	711	231
Oligochaeta (Oli)										
Mean	8	4	5	2	6	109	85	1576	640	775
SD	11	6	7	4	7	82	73	1798	468	635
Other taxa										
Crenobia alpina Dana (Cre)	–	–	x	x	x	x	x	x	x	x
Nematoda (Nmt)	–	–	x	x	x	x	x	x	x	x
Hydrachnellae (Hyd)	–	–	–	–	–	x	x	x	x	x
Crustacea (Cru)	x	–	x	–	x	x	–	x	x	x
Rhaphdiopterix alpina Kühtreiber (Rha)	–	–	–	x	x	x	x	x	x	x
Nemoura spp. (Nem)	–	–	–	–	–	x	x	x	x	x
Capnia sp. (Cap)	–	–	–	–	x	x	x	–	x	x
Isoperla spp. (Iso)	–	–	–	x	x	x	x	x	x	x
Perlodes intricata Pictet (Per)	–	–	–	–	x	x	x	x	x	–
Limnephilidae (Lim)	–	–	–	–	x	x	x	x	x	x
Rhabdomastix sp. (Rhm)	–	–	–	–	x	x	x	x	x	x
Wiedemannia sp. (Wie)	x	–	–	x	x	x	x	x	x	x
Dicranota sp. (Dic)	–	–	x	x	x	x	x	x	x	x
Rhypholophus sp. (Rhy)	x	x	x	x	x	x	x	x	x	x

nemura spp., *Prosimulium* spp., Tanytarsini, *B. alpinus*, *Rhithrogena* spp., and *Leuctra* spp., whereas axis F2 was described by Oligochaeta, *Simulium* spp., *Rhabdiopteryx alpina*, and *Isoperla* spp.

The co-structure between the fauna and the environment is best illustrated by plotting standardized environmental and associated faunistic scores together on the F1 × F2 factorial plane and to link



ig. 5 Results of the co-inertia analysis (CIA) of 11 environmental variables and 24 taxa from 10 sampling sites and four dates. a) Ordination diagram of the 11 normalized environmental variables in the CIA. Codes are given in material and methods. (b) Position of axa on the CIA F1 × F2 plane. Codes are given in Table 3. (c) Standardized co-inertia scores of the environmental and faunistic data ets projected onto the F1 × F2 factorial map. Arrows link environmental scores (beginning of an arrow) to faunistic ones (arrowhead). n (a) the longer an arrow and the closer to an axis the stronger the relationship to this factor; in (c), in contrast, arrows measure the trength of the co-structure between the fauna and the environment, so the shorter the arrow the better the agreement between the two structures.

the two positions by an arrow (Fig. 5c). The length of the arrow is then a measure of the strength of the co-structure; the shorter this distance the better the agreement between the two structures. In general, all arrows indicated good agreement between the two structures. On the F1 × F2 factorial map, four overlapping groups could be distinguished that corresponded to the four sampling dates. However, the dispersion of sampling sites varied from one date to another. The environmental separation of the June samples on axis F2 was caused by high concentrations of NO_3-N, whereas the other three dates were separated by a gradient of glacial influence along axis F1. High discharge from glacial melting resulted in high values of particle variables in August, whereas glacial melting no longer occurred in November and ground water contributed a large proportion to stream water, as reflected by marked increases in specific conductance and TIC.

The ordination separated samples from June/August and October/November along the positive diagonal (lower left to upper right) (Fig. 5c). This is attributable to the lower density and taxon richness of samples from June and August compared with those from October and November. Additionally, there existed a downstream increase in densities and taxon richness within each sampling date. These results demonstrate an important overlap between a temporal effect, mainly caused by a changing glacial influence, and a different spatial (i.e. longitudinal) response pattern.

A spatial typology was investigated by means of a within-date CIA. The existence of a significant co-structure was confirmed (permutation test, $P = 0$), with Factor 1 (90.6%) explaining most of the observed co-structure, and Factor 2 contributing only marginally (4.8%). Within-date environmental gradients were related to downstream changes in glacial influence (Fig. 6a). Although longitudinal patterns differed among dates, three groups of sites were observed (Fig. 6c). Sites M1–M3 in the proglacial reach, and M6 in the lower flood plain together with sites M7–M10 in the constrained reach formed two distinct groups, and the group formed by sites M4 and M5 reflected the transition between them. This pattern was clearest in August and October, but less distinct in June, and even weaker in November, indicating conditions were most homogenous on this last date. Sites in the constrained reach (M7–M10), which were fringed by forest, exhibited higher BOM concentrations than sites located further upstream (Fig. 6a,b). By comparing Fig. 6b,c, seasonal shifts in taxonomic composition can be observed; they are most evident at sites in the flood plain and in the constrained reach.

Last, the temporal stability of macroinvertebrate assemblages at each site assessed using a within-site CIA had a significant co-structure ($P = 0$). The first two axes explained 97.3% of the total inertia (F1 = 80.1%, F2 = 17.2%). The F1xF2 factorial plane showed a distinctive seasonal shift for all sampling sites (counter-clockwise from June to November) that became even more distinct with increasing distance from the glacier terminus (Fig. 7c). Positions of June samples on the F1xF2 factorial map (Fig. 7c) were related to high concentrations of NO_3–N (Fig. 7a), while sample positions in August could be attributed to high levels of turbidity, SS and PP. November samples reflected the substantial contribution of ground water (specific conductance, TIC, and to a lesser extent DOC), whereas October samples showed a transitional shift between the declining glacial influence and the increasing proportion of ground water to stream water. Faunistically, Simuliidae and Oligochaeta contributed highly to the total community at downstream sites in June (Fig. 7b,c). In October and November, several taxa of Ephmeroptera, Plecoptera and limoniid Diptera were responsible for site separation (Fig. 7b,c).

Discussion

Environmental conditions

Stability was closely related to the hydrograph of the Roseg River. Moving bed sediments reduced channel stability from June to August. During the remaining time of the year, discharge did not exceed the threshold of 8 $m^3\ s^{-1}$, indicating channel stability was higher than during the summer snow and ice melting period. Maximum annual temperatures in the proglacial reach (M1–M3) were below 2 °C, and thus are considered metakryal (Ward, 1994). The strong increase in maximum annual temperature at M4 can be attributed to an attenuation of environmental conditions resulting from the influence of the proglacial lake outlet stream. The hypokryal starts

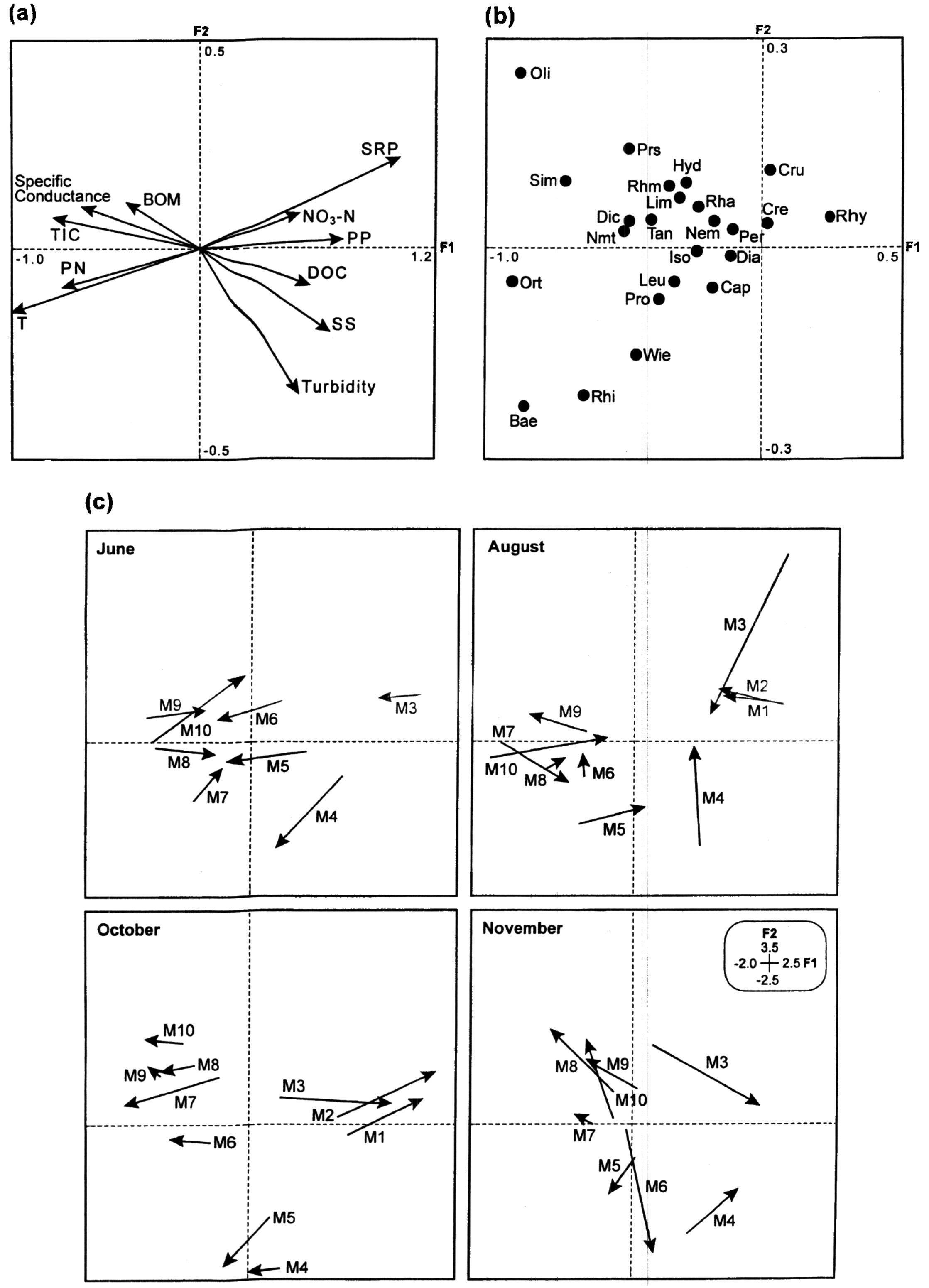


Fig. 6 Within-date co-inertia analysis (CIA) (spatial typology). (a) Co-inertia scores of the environmental parameters, and (b) of the taxa on the F1 × F2 factorial plane. (c) Standardized co-inertia scores of sampling sites of the environmental and faunistic data sets onto the F1 × F2 factorial maps for each sampling date. In (a) the longer an arrow and the closer to an axis the stronger the relationship to this factor; in (c), in contrast, arrows measure the strength of the co-structure between the fauna and the environment, so the shorter the arrow the better the agreement between the two structures.

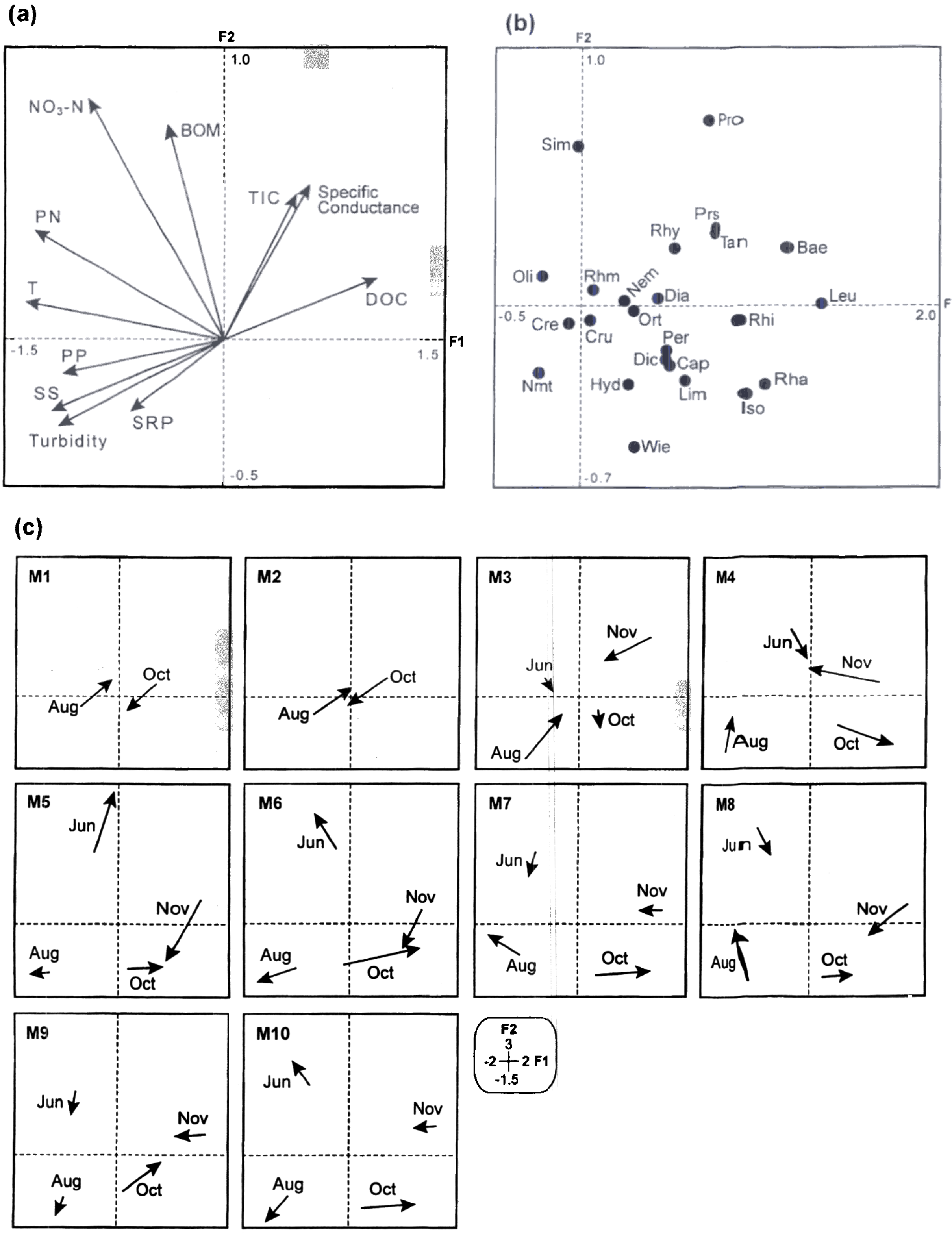


Fig. 7 Within-site co-inertia analysis (CIA) (temporal typology). (a) Co-inertia scores of the environmental parameters, and (b) of the taxa on the F1 × F2 factorial plane. (c) Standardized co-inertia scores of sampling dates of the environmental and faunistic data sets onto the F1 × F2 factorial maps for each sampling site. In (a) the longer an arrow and the closer to an axis the stronger the relationship to this factor; in (c), in contrast, arrows measure the strength of the co-structure between the fauna and the environment, so the shorter the arrow the better the agreement between the two structures.

downstream of the confluence and extends to the head of the flood plain. Sites M5–M10 all have maximum temperatures >4 °C, being characteristic of a glacio-rhithral zone (Füreder, 1999). Annual degree days never exceeded 1000 CTU even at the lowermost site. Our data are partially comparable with those of Lavandier (1974) in the River Estaragne (France). He reported 500 CTU at the uppermost site at 2350 m a.s.l. and 1000 CTU at the lowermost site at 1850 m a.s.l. compared with only 154 and 964 CTU, respectively, in this study.

As in many other mountain areas (Charles, 1991), NO_3–N concentrations in surface water of the Val Roseg were highest in spring meltwaters. High elevation catchments are sensitive to atmospheric deposition of pollutants such as inorganic nitrogen because they are released from the snowpack in the form of a pulse during snowmelt, magnifying the concentration of pollutants stored in the seasonal snowpack (Williams & Tonnessen, 2000). The discharge peak in August, because of glacial melting of the Tschierva and Roseg glaciers, was associated with high turbidity and PP values. High concentrations of PP associated with glacial flour have been reported elsewhere (Bretschko, 1966). The peak in turbidity at site M4 is most likely attributable to the proglacial Lake Roseg, because larger sediment particles settle in the lake. Therefore, SS in the lake outlet stream comprise of a much higher fraction of smaller particles compared with the kryal stream originating from the Tschierva Glacier, which led to the increase in turbidity below the confluence of the two streams. With decreasing discharge in October, specific conductance was still low, indicating that the contribution of englacial water had not significantly changed. At low and constant discharge in November, the contribution of ground water had increased markedly, as shown by high values of specific conductance. Seasonal shifts in sources and flow paths of water in the Val Roseg catchment determine the degree of glacial influence (Malard *et al.*, 1999), and have important implications for the biota.

Benthic macroinvertebrate assemblages

In general, Chironomidae, especially the genus *Diamesa*, were a predominant constituent of the zoobenthos in the glacial stream of Val Roseg. Larvae of the genus *Diamesa* were the sole inhabitants close to the glacier snout, as reported for many glacier-fed streams in the European Alps (Bretschko, 1969), Tatra Mountains (Kownacka & Kownacki, 1972), Scandinavia (Steffan, 1971), and the Rocky Mountains (Elgmork & Saether, 1970). In contrast, glacial streams influenced by water abstraction (e.g. Petts & Bickerton, 1994), were devoid of fauna for 200–500 m below the glacier snouts. Although, *Diamesa* chironomids are generally considered cold-stenotherms (Oliver, 1983), some species (e.g. *Diamesa steinböcki*) may occur at warmer temperatures (Rossaro, 1991; Milner, 1997).

Ephemeroptera, Plecoptera and other taxa, however, also made substantial contributions to benthic assemblages. Within the genus *Baetis* only *B. alpinus* was found. The absence of *B. melanonyx* Pictet, another common species of this region, is attributed to the high altitude of the Val Roseg and the crystalline substratum (Sartori & Landolt, 1999). These authors report a univoltine life cycle for *B. alpinus* >1500 m a.s.l. with animals overwintering as larvae, which is consistent with our findings. Within the genus *Rhithrogena*, *R. loyolaea* and *R. nivata* were the two most abundant species at most sites, corresponding to their expected altitudinal optima between 1700 and 2200 m a.s.l. (Sartori & Landolt, 1999). In contrast, *R. alpestris* and *R. degrangei* were only abundant at the more downstream sites because they have their altitudinal optima in the lower alpine zone and in the upper subalpine zone (Sartori & Landolt, 1999). *R. loyolaea* usually has a univoltine life cycle in the Swiss Alps (Sartori & Landolt, 1999), but Lavandier (1981) showed that larval development requires 3 years above 2100 m in the French Pyrenees. Unfortunately, life cycles of many alpine stream insects are poorly known, although there is a general agreement that the number of generations per year decreases with increasing altitude, and that low temperature at high elevation is likely responsible for later emergence (Ward, 1992). Furthermore, seasonal changes in quantity and quality of food sources are expected to influence population dynamics of macroinvertebrates (Ward, 1992; Füreder, 1999). For example, high turbidity, abrasion by SS and bed-load transport during summer high flow effectively limit benthic primary production (Milner & Petts, 1994; Ward, 1994; Uehlinger, Zah & Bürgi, 1998).

Total zoobenthic density ranged over two orders of magnitude, being lowest in August (116 m^{-2}) and highest in October (24 380 m^{-2}). Similar values were found by Lavandier & Décamps (1984) in the French Pyrenees although other studies of glacial streams report much lower densities (e.g. Kownacki & Kownacka, 1973; Gislason, Olafsson & Adalsteinsson, 1998). Several factors may be responsible for these differences. Sampling in other studies was typically restricted to the summer period, when sites are easily accessible. Different sampling techniques, as well as differences in mesh size used, additionally confound comparability of results.

Total densities, taxon richness and SI of diversity showed similar trends, suggesting that changes in density and diversity of benthic communities are most likely attributable to (1) spatial phenomena (reduced harshness with increasing distance from the glacier), and (2) temporal phenomena (more favourable periods in spring and late autumn/early winter than in summer).

Relationships between fauna and environment

Co-inertia analysis clearly demonstrated the relationship between environmental conditions and benthic community structure. Furthermore, it revealed the existence of a strong overlapping spatio-temporal pattern. Within-class analyses eliminate such spatial or temporal effects and enable the examination of changes in the spatial co-structure among sampling dates, and the temporal stability in observed longitudinal patterns. The results of these analyses can be interpreted as follows: (1) Seasonal changes in glacial influence (i.e. shifts in sources and flow paths of water) comprised of a key factor structuring benthic macroinvertebrate assemblages. (2) Although longitudinal response patterns of zoobenthos varied across seasons, individual sites exhibited similar temporal patterns.

In general, our results conform quite well to the model of Milner & Petts (1994); however, some substantial deviations were found. For example, Orthocladiinae were collected at M3, although maximum annual temperatures ($T_{\max}$) were still <2 °C. Ephemeroptera and Plecoptera were found below a $T_{\max}$ of 4 °C at sites M3 and M4, especially in October and November, but to a lesser extent also at other times. In accordance to our findings, Thomas (1975) reported that *B. alpinus* can complete its whole life cycle even if water temperature is always between 0 and 3 °C. Burgherr & Ward (2000) reported similar findings in another study comparing a kryal stream with a lake outlet channel. Overall, Milner & Petts's (1994) conceptual model predicted macroinvertebrate distribution patterns accurately during glacial melt in summer, but did not account for seasonal changes in assemblage patterns. However, temporal patterns play an important role in the understanding of ecological dynamics within and between glacial streams, as our results and those from other studies (Brittain *et al.*, 2001; Robinson *et al.*, 2001) imply. Consequently, we postulate that, besides temperature and channel stability, a complex interplay of factors determines the distributions of populations in glacial streams. In particular, important environmental characteristics involved in the habitat templet and thus related to macroinvertebrate life histories in glacial streams include sources and flowpaths of water, which in combination with discharge reflect changes in glacial influence.

Longitudinal distribution patterns of macroinvertebrates also could be a result of stream age because a stream near the glacier terminus may be in a different stage of development than the same stream further downstream (Milner, 1987, 1994). However, such a site-specific temporal succession can be constrained by alternating cycles of glacial recession and advance. For example, M3 in the Roseg River has been ice-free since 1955, and M2 since 1971, whereas M1 was again covered by the glacier between 1979 and 1991.

Conclusions

In summary, our results show that zoobenthic communities in the Roseg River exhibit a high spatio-temporal variation because of seasonal shifts in glacial influence. During periods of favourable environmental conditions (spring and late autumn/early winter) invertebrate density and taxon richness peak, and cold-adapted taxa other than just *Diamesa* spp. can occur rather close to the glacier terminus. Such periods are characterized by (1) highly stable stream beds as shown in this study and reported elsewhere (Füreder, 1999), (2) minimal sediment transport, shear stress and turbidity are minimal (Uehlinger *et al.*, 1998), and (3) accompanied accrual of benthic algae, especially the chrysophyte *Hydrurus foetidus* Kirch, enhancing food availability for zoobenthic organisms.

Future modifications and refinements of the conceptual model of Milner & Petts (1994) should account for temporal patterns reported in this study and other investigations (Robinson *et al.*, 2001). Other factors to consider include biogeographical patterns [e.g. *Diamesa* is absent in some regions (Willassen & Cranston, 1986)], endemic species that may co-occur with *Diamesa* in metakryal stream segments (Brodsky, 1980), glacial streams that remain clear all year (e.g. in the Colorado Cordillera; Ward, 1994), and differences in geology, topography and riparian vegetation among river basins within and among geographical regions (e.g. Gislason *et al.*, 1998).

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