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The macroinvertebrate communities of two contrasting Norwegian glacial rivers in relation to environmental variables

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SUMMARY

1. Macroinvertebrate communities in two Norwegian glacial rivers, one in the western fjords (Dalelva) and one in the eastern mountains (Leirungsåi), were investigated during three time periods in 1996 and 1997.
2. Channel stability variables (substratum heterogeneity/Pfankuch index/hydraulic stress) and water temperature accounted for 54% of the total inertia in the principal components analysis (PCA) ordination of environmental variables. The importance of these variables was confirmed by cluster analysis.
3. The two rivers were well separated in the ordinations, with Leirungsåi showing much greater heterogeneity. This is explained by differences in altitudinal range, terrestrial vegetation and the importance and nature of tributary inputs.
4. Channel stability and temperature were also important in determining faunal communities in the two glacial rivers, supporting the main determining variables in the conceptual model of glacial streams (Milner & Petts, 1994). However, clear temporal differences were apparent in the data, the two rivers being more similar during the summer period of high discharge dominated by glacial meltwater. During spring and especially during autumn environmental conditions and the macroinvertebrate fauna differed both within and between rivers.
5. Diamesinae dominated in the upper reaches of both rivers, with Orthocladiinae becoming more common downstream. The dominance of Diamesinae persisted further down Dalelva because of the continued influence of glacial tributaries, whereas in Leirungsåi the influence of non-glacial tributaries led to a change towards a greater proportion of Orthocladiinae. Lakes modified macroinvertebrate communities in both river systems.

Keywords: glacial rivers, macroinvertebrates, environmental variables, ordination

Introduction

Within the alpine zone three stream ecosystem types have been identified: kryal streams which are glacial meltwater fed, rhithral streams which are snowmelt dominated, and krenal streams which are groundwater

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Table 1 General characteristics of the two Norwegian glacial river catchments studied

Catchment	Dalelva	Leirungsåi
Altitudinal range of study reaches (m a.s.l.)	10–340	970–1550
Tree-line (m a.s.l.)	600	1050
Catchment area at downstream limit (km^2)	25.6	400.9
Maximum altitude in catchment (m a.s.l.)	1960	2159
Glacier area (km^2)	22*	1.24
Precipitation (mm year^{-1})	*c.* 1270	*c.* 800
Discharge range (m s^{-1})	0.5–35.2	0.4–6.2
Distance of study reaches from snout (m)	100–7100	200–24 600

*The glacier, Briksdalsbreen, is an arm of a large plateau glacier, with an area of 487 km^2.

fed (Ward, 1994). Distinct longitudinal zonations in zoobenthic fauna have frequently been identified in alpine streams (e.g. Elgmork & Sæther, 1970; Kownacka & Kownacki, 1972; Ward, 1986, 1994; Kownacki, 1991; Rundle, Jenkins & Ormerod, 1994).

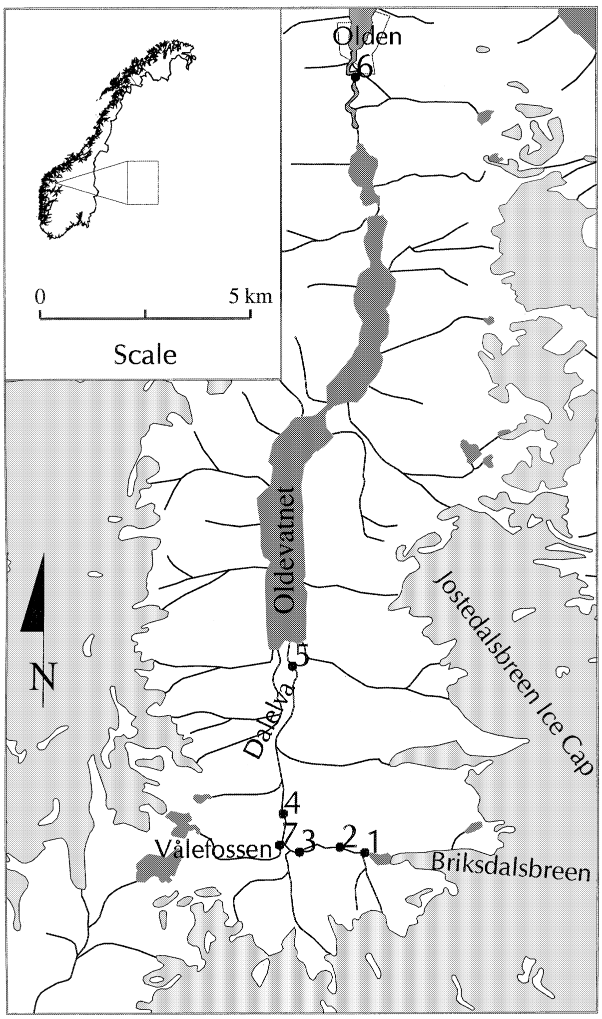

Fig. 1 Location of the study reaches in the glacial river, Dalelva in Briksdal, western Norway. Glacial area is shaded light grey.

Hynes (1970) noted that chironomids, especially *Diamesa*, dominated in glacial streams, although taxa such as mayflies and stoneflies colonized lower reaches. Immediately below glacial snouts even chironomids may be absent (Petts & Bickerton, 1994). On the basis of the European and North American literature, Milner & Petts (1994) proposed a conceptual model describing a conceptual zonation of zoobenthos with increasing distance from a glacier margin with respect to two principal environmental variables, water temperature and channel stability. A community dominated solely by *Diamesa* species was predicted at water temperatures less than 2 °C, while between 2 and 4 °C other Diamesinae, Orthocladiinae and Simuliidae would be added to the community. Further downstream when temperatures were >4 °C, Baetidae, Nemouridae and Chloroperlidae would

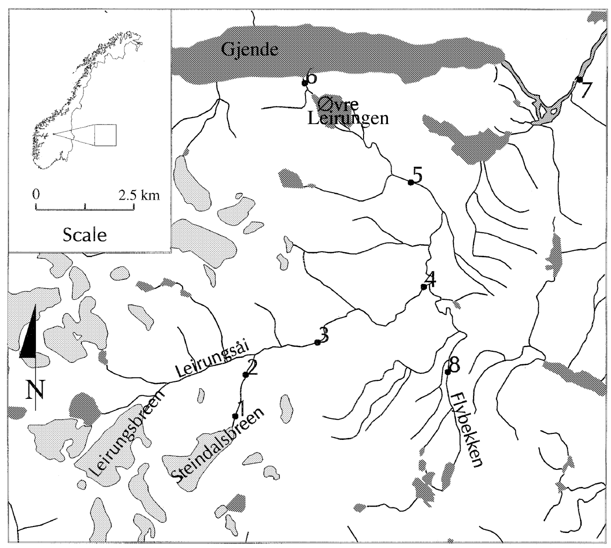

Fig. 2 Location of the study reaches in the glacial river, Leirungsåi in the Jotunheimen Mountains, central southern Norway. Glacial area is shaded light grey.

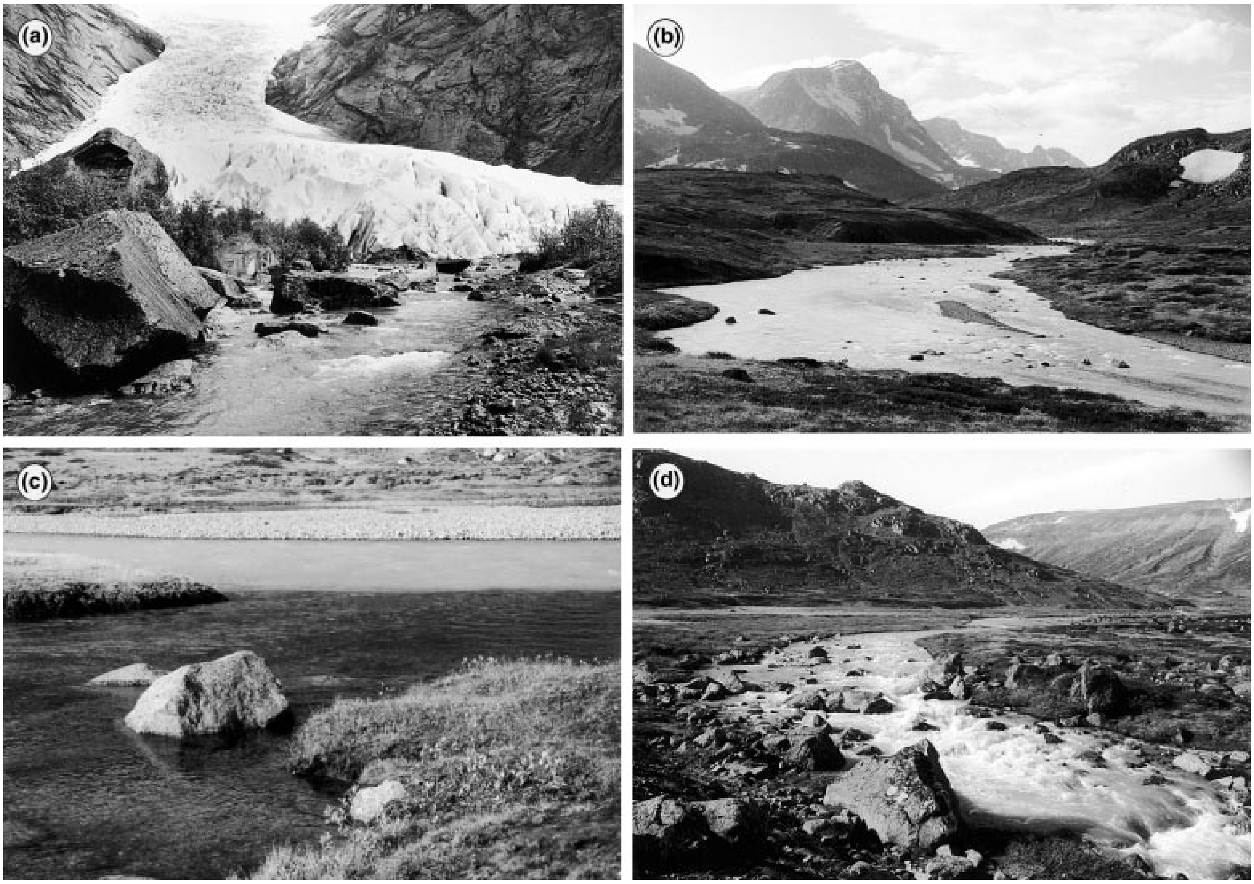

Fig. 3 Study rivers in Norway: (a) the advancing glacier, Briksdalsbreen, and the reach BRI01; (b) Leirungsåi 200 m downstream of reach LEI03; (c) inflow of non-glacial tributary between reaches LEI03 and LEI04; (d) Leirungsåi 800 m above LEI04.

likely be found. With the development of a more stable substratum, representatives of the Trichoptera as well as other Ephemeroptera, Plecoptera and Diptera may colonize.

Apart from a detailed study of chironomids in a glacial river at Finse in central southern Norway (Sæther, 1968) and studies related to the potential impact of hydropower development in Jostedalen (Fjellheim, Raddum & Schnell, 1988), there have been no studies of the fauna of Norwegian glacial rivers and streams. In the study at Finse (Sæther, 1968), the glacial stream was relatively recent because of the retreat of the glacier, and the fauna was dominated by two *Diamesa* species. In Jostedal, Chironomidae, notably Diamesinae, also dominated in the upper reaches near the glaciers, although clear gradients within the Fåbergstøl sandur towards a more diverse fauna with several mayfly and stonefly taxa were evident (Fjellheim & Raddum, 1982). Steffan (1971) investigated the chironomid fauna of glacial brooks in northern Sweden. The fauna resembled the Finse stream in the upper reaches, but lower down Simuliidae were also abundant together with *Diamesa*. There have been several investigations of the zonation of the zoobenthos in non-glacial mountain streams in Norway (e.g. Lillehammer & Brittain 1978; Solem, Steinkjer & Bretten, 1987) and faunal assemblages have been shown to be clearly related to the zonation of terrestrial vegetation and to the extent of allochthonous organic matter inputs.

This study had three main objectives: (1) to describe longitudinal distribution patterns in stream zoobenthic communities below two Norwegian glaciers, one downstream of an advancing glacier in an oceanic climate, and one below a retreating glacier with a continental climate; (2) to determine the principal environmental variables influencing benthic distributions in such systems; and (3) to assess the validity of the conceptual model of Milner & Petts (1994) for Norwegian glacial rivers.

Methods

Study areas

Two contrasting glacial river systems were studied, Dalelva and Leirungsåi (Table 1, Figs 1–3). Dalelva is situated in the western fjords (61°40′N, 6°50′E), with a moderately oceanic climate, giving high precipitation and relatively mild winters. The source glacier, Brikdalsbreen, is an arm of the Jostedalsbreen Icecap, the largest glacier on mainland Europe (487 km^2). Increased winter precipitation over the last decade resulted in an unprecedented glacial advance, and Briksdalsbreen advanced 390 m between 1988 and 1996, almost covering a proglacial lake and destroying established birch forest (Winkler *et al.*, 1997). The geology of the area is dominated by gneiss bedrock covered by moraine material of varying thickness. The tree-line is at about 600 m a.s.l. Six reaches were studied in the main stem of Dalelva, from BRI01 100 m from the glacial snout at 340 m a.s.l. to BRI06 19 km from the snout at 10 m a.s.l. (Fig. 1, Table 2). The river is bordered by riparian birch and alder forest for most of its length, although its width is reduced to a few metres in the pasture areas downstream of BRI04. Channel width varies from *c.* 10 m at BRI01 below the glacier to *c.* 20 m at BRI06. The river flows through two lakes, Oldevannet and Floen, between reaches BRI05 and BRI06. A non-glacial tributary, Vålefossen (BRI07), flowing into the main river at 150 m a.s.l. between reaches BRI03 and BRI04, was also investigated. Discharge data for BRI05 during 1996 and 1997 are given in Fig. 4.

Leirungsåi is located in the eastern part of the Jotunheimen Mountains of central southern Norway (62°40′N, 6°50′E), with a continental climate characterized by moderate precipitation coupled with low winter temperatures and relatively high summer temperatures. Glaciers in this region have retreated considerably during the last 100 years and are still slowly retreating. The cirque glacier, Steindalsbreen, the source of the study river, has retreated steadily at a rate of *c.* 9 m per year since a glacial maximum

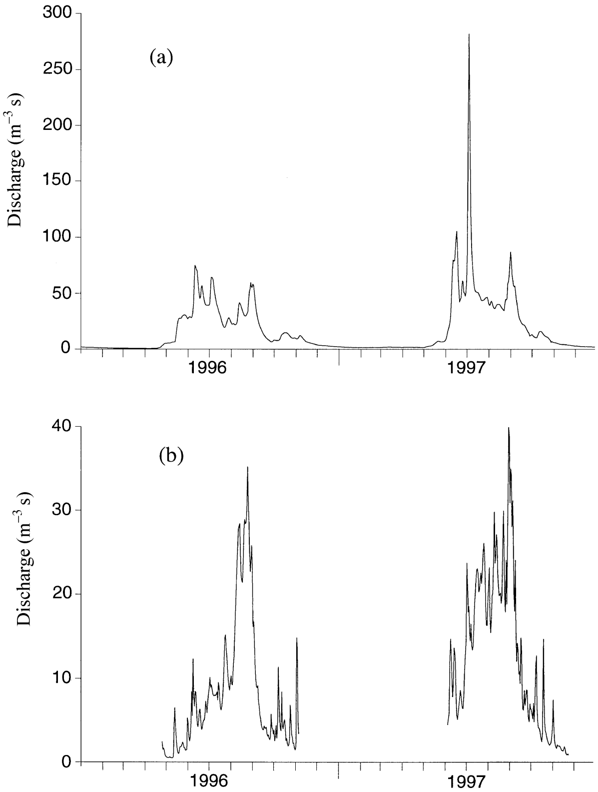

Fig. 4 Discharge data for (a) the river Sjoa (8 km below LEI07) and (b) reach BRI05 (Kvamme Bru) during 1996 and 1997. Data supplied by the Norwegian Water Resources and Energy Directorate.

Table 2 Study reaches in Dalelva (BRI) and Leirungsåi (LEI) analysed in this study

Reach	Distance from glacier (km)	Altitude (m a.s.l.)	Slope (m m^{-1})
BRI01	0.12	340	0.034
BRI02	1.0	300	0.018
BRI03	1.9	180	0.067
BRI04	2.6	70	0.021
BRI05	5.0	40	0.007
LEI01	0.2	1550	0.080
LEI02	1.6	1380	0.034
LEI03	3.9	1270	0.008
LEI04	7.6	1150	0.106
LEI05	11.0	1100	0.007
LEI06	15.0	986	0.051

around 1800 (S. Winkler, personal communication). The area is part of the Caledonian thrust complex, the Jotundekkene, dominated by gabbros and gneiss. There are also extensive areas of quaternary deposits of moraine material from the Ice Age. The glacial stream flows out of Steindalsbreen at *c*. 1550 m a.s.l., joining a larger glacial stream at 1330 m a.s.l. to form the river, Leirungsåi (Fig. 2). Seven reaches were studied in the main stem of Leirungsåi, from LEI01 200 m from the glacial snout at 1550 m a.s.l. to LEI07 23 km from the snout at 970 m a.s.l. (Fig. 2, Table 2). A major non-glacial tributary, Flybekken (LEI08) flows into Leirungsåi at 1150 m a.s.l., just downstream of LEI04. The river passes through a shallow lake, Øvre Leirungen, before flowing into the large glacial lake, Gjende (984 m a.s.l.). Most of the catchment (400 km^2) is above the tree-line (*c*. 1050 m a.s.l.), encompassing several other glaciers and peaks over 2000 m. There is no riparian vegetation at LEI01, lichens and grass occur at LEI02, scattered willow bushes at LEI03 and more dense willow at LEI04 and LEI05. LEI06 and LEI07 are below the tree-line and bordered by birch forest. Channel width varies from *c*. 1 m at LEI01 to about 10 m at LEI07. There was no gauging station in Leirungsåi, but survey data from Leirungsåi and continuous discharge data from a gauging station 8 km downstream of LEI07 (River Sjoa) (Fig. 4) indicated a more pronounced spring snowmelt peak compared with Dalelva and a slightly later peak in glacial melt. The discharge data from the River Sjoa also show less short-term variation, the effect of several above-lying lakes.

Physico-chemical variables

The protocols developed during the collaborative project 'Arctic and Alpine Stream Ecosystem Research' (AASER) for geomorphological, physical, chemical and biological components formed the basis of the sampling programme in both catchments (Brittain, Lencioni & Maiolini, 1998; Brittain *et al*., 2000; Brittain & Milner, 2001). Reaches, 15 m long, were identified, with the first reach as near the glacier as possible, and subsequent reaches accounting for major shifts in stream and channel morphology and tributary inputs. Field surveys were carried out in 1996 and 1997 during three periods: preglacial ice melt (late spring), mid-summer peak ice melt and the autumnal period of low discharge.

The reaches in Dalelva were sampled during the following periods in 1996: 10–14 June, 12–15 August/ 2–13 September and 14–18 October. As discharge was extremely high during August 1996 it was not possible to collect biological samples until early September. In 1997 the reaches were sampled during the following periods: 26–30 May, 27–30 July and 13–17 October. The reaches in Leirungsåi were sampled during the following periods in 1996: 10–14 June, 12–15 August/12–13 September and 14–18 October. Here again discharge was too high during August 1996 to take biological samples so they were taken in early September. In 1997 samples were taken in Leirungsåi during the following periods: 26–30 May, 27–30 July and 13–17 October.

Discharge and samples for analysis of sediment transport were taken at all reaches during the field survey periods. A permanent discharge and suspended solids gauging station was in operation at BRI05. At most other stations the salt dilution method (Hongve, 1987) was used to measure discharge during the field periods and create a relationship between discharge and water level when discharge could not be directly measured. Samples of suspended solids were taken in midstream whenever possible in 1 or 5-L bottles, depending on concentrations, and subsequently analysed by the Department of Hydrology, Norwegian Water Resources and Energy Directorate.

Digital temperature loggers were installed at BRI01, 03, 05, 06 and 07. In Leirungsåi, temperature loggers were located at LEI01, 03, 04, 05, 06, 07 and 08. The loggers at BRI07 and LEI04 were lost during floods. The loggers at BRI01, 03, 07 and LEI01, 04, 06, 07, 08 were of the Tinytag® type (Gemini Data Loggers (UK) Ltd., Chichester, UK) and recorded during the survey season, while the loggers at the others reaches were manufactured by Aanderaa A/S (Bergen, Norway), and recorded throughout the year.

The stream bottom component of the Pfankuch index of stream stability (Pfankuch, 1975) was used to assess the channel stability of each reach. Five variables (rock angularity, bed-surface brightness, particle packing, per cent stable materials, scouring and aquatic vegetation) were summed to provide an overall index of channel stability with high scores representing unstable channels at the reach scale.

In addition to the Pfankuch index of bed stability, two further stability parameters, shear stress and Reynolds number were calculated (Statzner, Gore &

Resh, 1988; Gordon, McMahon & Finlayson, 1992). Painted tracer stones of different size classes were also used to assess disturbance as suggested by Townsend, Scarsbrook & Dolédec (1997), but the high turbidity of the glacial waters hindered recovery. Substratum size was determined by visual assessment at each reach or contact at each point on the velocity/depth transects. The following categories were used: boulders (>20 cm), coarse gravels (5–20 cm), fine gravels (0.2–5 cm), inorganic sand (0.01–0.2 cm), inorganic silt (<0.01 cm) and mud (organic silt and clay) (<0.01).

Biological communities

Biological communities were sampled during the same periods as the physico-chemical variables with the exception of August 1996 in both rivers. Discharge was too high to allow benthic sampling so the biological sampling was undertaken 2 weeks later. To assess the biomass of epilithic algae, three stones were collected at random in each reach during each survey period. The benthic algae were scraped off the upper surface (area 3×3 cm) and washed onto GF/C filters. Chlorophyll *a* was subsequently extracted in the laboratory and quantified spectrophotometrically [American Public Health Association (APHA), 1992].

Five, 30-s replicate kick samples for benthic macroinvertebrates were taken at all reaches during all sampling periods. A standard net, with an opening of 30×30 cm and a mesh size of 250 μm was used. At the same position as the kick samples, water velocity, water depth and size distribution of sediment particles were estimated during the 1997 fieldwork. The invertebrate kick samples were preserved in 70% ethanol in the field and subsequently sorted and identified in the laboratory. The percentage organic matter in each kick samples was estimated by loss on ignition (Dean, 1974).

Data analyses

An initial correspondence analysis (CA) clearly indicated that there were major differences between the glacial rivers and their non-glacial tributaries, BRI07 and LEI08 were excluded from the subsequent analyses of the two glacial systems. The study reaches below large lakes (BRI06, LEI07) were also excluded from the present analysis for the same reason.

Examination of correlations between the six sediment size classes (boulders, coarse gravels, fine gravels, sand, silt and mud) revealed that boulders and coarse gravels were correlated and that mud and silt categories were only rarely recorded. For these reasons only boulders, fine gravels and sand were retained for subsequent ordinations. However, a Simpson diversity index (Cellot *et al.*, 1994) was applied to the full grain size data to provide an assessment of substratum heterogeneity.

As there were significant correlations between mean temperature and temperature range ($r = 0.76$) and between minimum and maximum temperatures ($r = 0.80$), only minimum temperature and temperature range were retained in the subsequent analysis. These were poorly correlated ($r = 0.23$).

These selections resulted in a set of 11 poorly correlated variables belonging to different parameter sets, six of which were log-transformed. These variables were: reach slope, depth at time of survey (log), average water velocity, per cent boulders, Simpson index of substratum diversity, Pfankuch index of bed stability, minimum temperature (log), temperature range (log), suspended solids (log), per cent organic material in kick samples (log) and chlorophyll *a* concentration (log). Thus, variables within the parameter sets hydraulic energy, substratum heterogeneity, substratum stability, temperature, suspended solids and macroinvertebrate food availability, were represented.

The environmental data matrix of these 11 variables was analysed by principal components analysis (PCA) (Hotelling, 1933; Legendre & Legendre, 1998). The sites and dates in Dalelva (BRI) and Leirungsåi (LEI) were subsequently clustered using the first three axes of the PCA ordination and Ward's (1963) second order moment clustering algorithm. For each of the 11 variables, a one-way ANOVA was used to test for differences between the two rivers, the 11 reaches, the six sampling dates and the 12 river × data sets, respectively.

The environmental data was then jointly analysed with the faunal data using co-inertia analysis (COIA) (Dolédec & Chessel, 1994). This allows the simultaneous ordination of two data matrices sharing the same set of rows. It calculates co-inertia axes maximizing the covariance of the factorial scores generated in the separate ordinations of the two input files (in this study a PCA of the environmental variables and a CA of the faunal data). COIA provides therefore an ordination of the common structure of the two data sets that maximizes simultaneously (i) the variance of the factorial scores from the separate tables, and (ii) their correlation. COIA generates factorial scores which can be used for graphical displays as in standard ordination methods. Although invertebrates were typically identified to species, most taxa were grouped into families to provide a more uniform data set. The faunal data are average values, $\log(x + 1)$ transformed, for the kick samples analysed at each reach (usually five) on each of the six dates. Multivariate data analyses and associated graphs were produced with the ADE-4 programme library (Thioulouse *et al.*, 1997).

Results

In the PCA of the environmental data, three factorial axes were retained on the basis of the shape of the decrease in the eigenvalues according to the criteria advocated by Diday *et al*. (1982), Saporta (1990) and others. These three axes accounted for 54% of the total inertia (Fig. 5). The main explanatory variables generally belonged to two principal groups: variables associated with channel stability (e.g. substratum heterogeneity, Pfankuch index) and water temperature. Slope, per cent organic material and chlorophyll *a* played minor roles in this data ordination. There was a higher heterogeneity between the six reaches in Leirungsåi than between the five reaches in Dalelva (Fig. 5), as substantiated in the box plots of selected environmental variables (Fig. 6). A minor temporal effect was also obvious. These differences were also tested by ANOVA. All variables apart from average water velocity, minimum temperature and per cent organic material, showed significant differences between the two glacial rivers (Table 3). The higher heterogeneity between the reaches in Leirungsåi was mostly related to a very conspicuous upstream–downstream gradient from LEI01 to LEI06. Such a gradient was not so obvious within Dalelva (see F1 × F2 factorial plot of the reaches in Fig. 5c). The temporal effects were mainly related to seasonal variations in depth and velocity, being high in Dalelva during summer and low during autumn in Leirungsåi. The importance of stability, substratum and temperature variables and the clear separation of the two rivers was substantiated by the cluster analysis.

Chironomidae dominated at all sites throughout the six sampling periods (Fig. 7), with Diamesinae and Orthocladiinae being almost the only families represented. There was a shift from Diamesinae in the upper reaches to Orthocladiinae in the low reaches in both rivers. However, although a few Orthocladiinae were recorded right up to the glacier in Dalelva, Diamesinae retained their dominance further downstream than in Leirungsåi. Many species of Diamesinae (e.g. *Diamesa bertrami* Edwards, *D. davisi* gr., *D. latitarsus* gr., *D. zemyi/cinerella* gp.) and Orthocladiinae (e.g. *Eukiefferiella claripennis* gr.), were recorded in both these Norwegian rivers (see also Lods-Crozet *et al*., 2001), although chironomid species richness was higher in Dalelva.

Simuliidae were the second most abundant taxa. Oligochaeta were well represented at all reaches in Dalelva, but only found at the lowermost reaches in Leirungsåi (Fig. 7). Tipulidae were recorded in most reaches in both streams, although absent close to the glacier. Capniidae, Taeniopterygidae and Nemouridae, were also recorded in most middle and lower reaches, especially during spring and autumn. These three families were also recorded frequently at the second reach below the glacier (BRI02), located 1 km below the glacial snout. Ephemeroptera and Trichoptera were uncommon in both glacial streams: Baetidae were recorded in reach two in Dalelva and Limnephildae in reach three in Leirungsåi, otherwise these two orders were largely restricted to the lower reaches of both rivers.

The joint analysis of the environmental and faunal data by COIA proved highly significant (permutation test, $P = 0$). The taxa were mostly ordinated along a diagonal across the F1 × F2 factorial plane (Fig. 8). This gradient was principally associated (from top right to bottom left) with increasing stability (decreasing Pfankuch index and suspended solids, increasing per cent boulders) and temperature (increasing minimum temperature). The COIA also confirmed the contrast between the two glacial streams seen in the environmental data. The environmental and faunal data were both more homogeneous during the summer high discharge periods, than during spring or autumn. In July, both in 1996 and 1997, the differentiation between the two streams tended to disappear at high discharges.

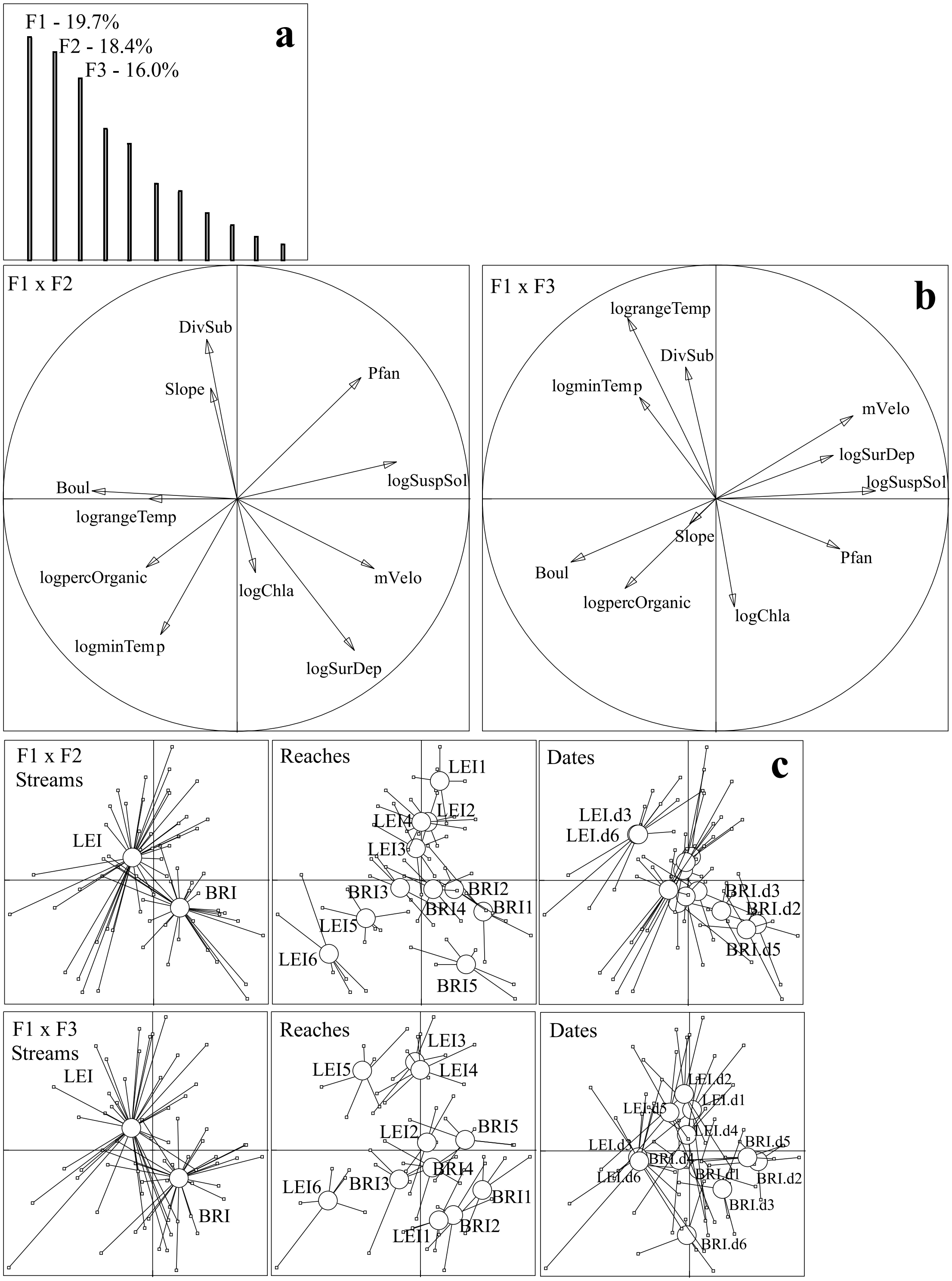

Fig. 5 Principal components analysis (PCA) ordination of the 11 reaches (on six sampling dates) by 11 environmental variables for two Norwegian glacial rivers. (a) Percentage of variance explained by each factorial axis; (b) F1 × F2 and F1 × F3 correlation circles of the 11 environmental variables; (c) F1 × F2 and F1 × F3 factorial plots of the reaches grouped according to river, reach and date.

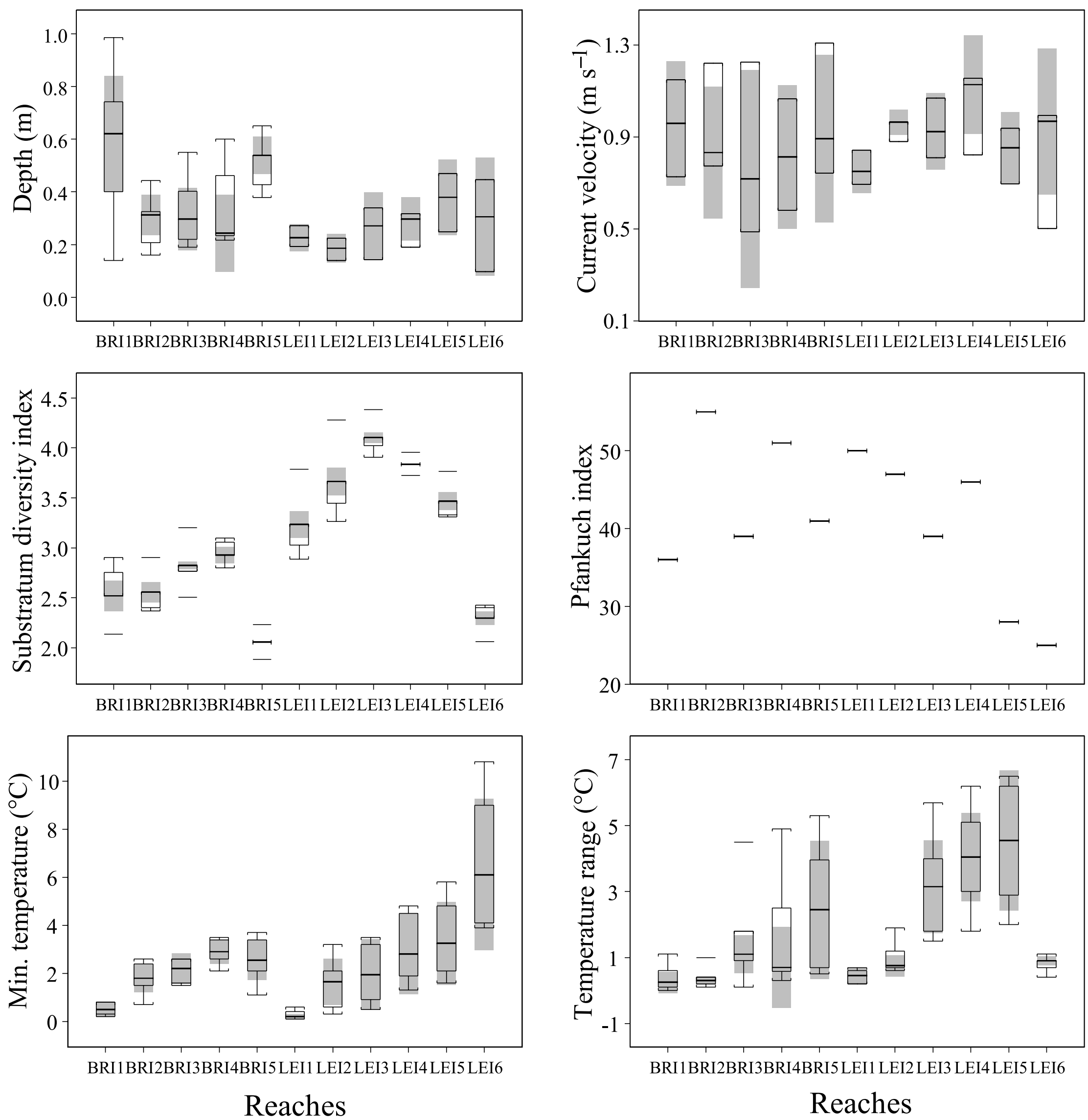

Fig. 6 Box-plots for six environmental variables in a total of 11 reaches in Dalelva and Leirungsåi. The vertical boxes depict the interquartile range (Q25–Q75) around the median (horizontal thick line). The grey areas are 95% confidence intervals around the median. Upper and lower whiskers are located at Q25 − 1.5(Q75 − Q25), and Q75 + 1.5(Q75 − Q25), respectively. Outliers, falling outside this interval, are represented by single lines. Only single values are plotted for the Pfankuch stability index because its value was constant for a given reach across all sampling dates.

Discussion

The upper reaches of both glacial rivers were dominated by Diamesinae, in particular the genus *Diamesa*. This genus is generally considered to be cold-adapted (Oliver, 1983), although recent studies (Rossaro, 1991; Flory & Milner, 1999; Lods-Crozet *et al*., 2001) have recorded *Diamesa* at water temperatures up to 15 °C. Other factors, including substratum stability and lack of other potential taxa in the vicinity may at least in part explain the lack of colonization by other taxa despite favourable water temperatures (Milner & Petts, 1994). Nevertheless, water temperature is in many cases a major variable influencing the life cycles, species diversity and distribution of aquatic insects (e.g. Ward, 1992; Williams & Feltmate, 1992; Jacobsen, Schultz & Encalada, 1997; Füreder, 1999). It is also one of the major deterministic variables in the conceptual model for glacial streams proposed by Milner & Petts (1994).

Table 3 Results of one-way ANOVA of selected environmental variables. Probability levels are given for all significant differences (see also box plots in Fig. 4)

Environmental variable	Between rivers	Between reaches	Between dates	Between rivers × dates
Reach slope	*	NS	NS	NS
Depth at survey (log)	***	**	*	***
Average water velocity	NS	NS	***	***
Per cent boulders	***	***	NS	NS
Substratum diversity	***	***	NS	***
Pfankuch index	*	NS	NS	NS
Minimum temperature (log)	NS	***	NS	NS
Temperature range (log)	*	***	NS	NS
Suspended solids (log)	*	*	***	***
Per cent organic material (log)	NS	*	*	**
Chlorophyll *a* (log)	**	NS	***	***

*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$, NS: non-significant.

The crucial role of temperature was confirmed in the present study of two Norwegian glacial rivers. Water temperature separated sites in the analysis of environmental variables and was also a major variable in explaining the gradient in benthic communities in both rivers.

In addition to temperature, the most active variables in analyses of the environmental data from the

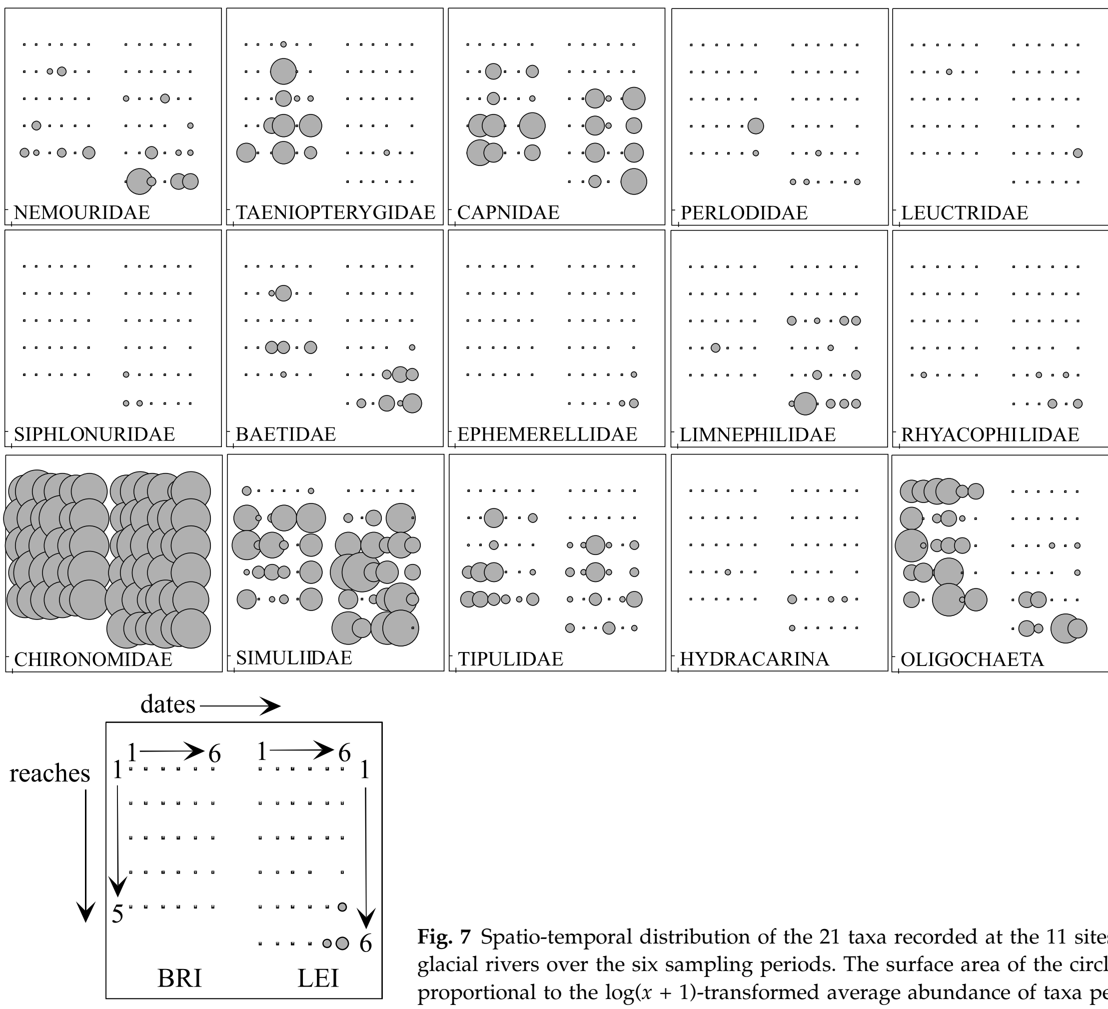

Fig. 7 Spatio-temporal distribution of the 21 taxa recorded at the 11 sites in the two glacial rivers over the six sampling periods. The surface area of the circles is proportional to the log(x + 1)-transformed average abundance of taxa per kick sample.

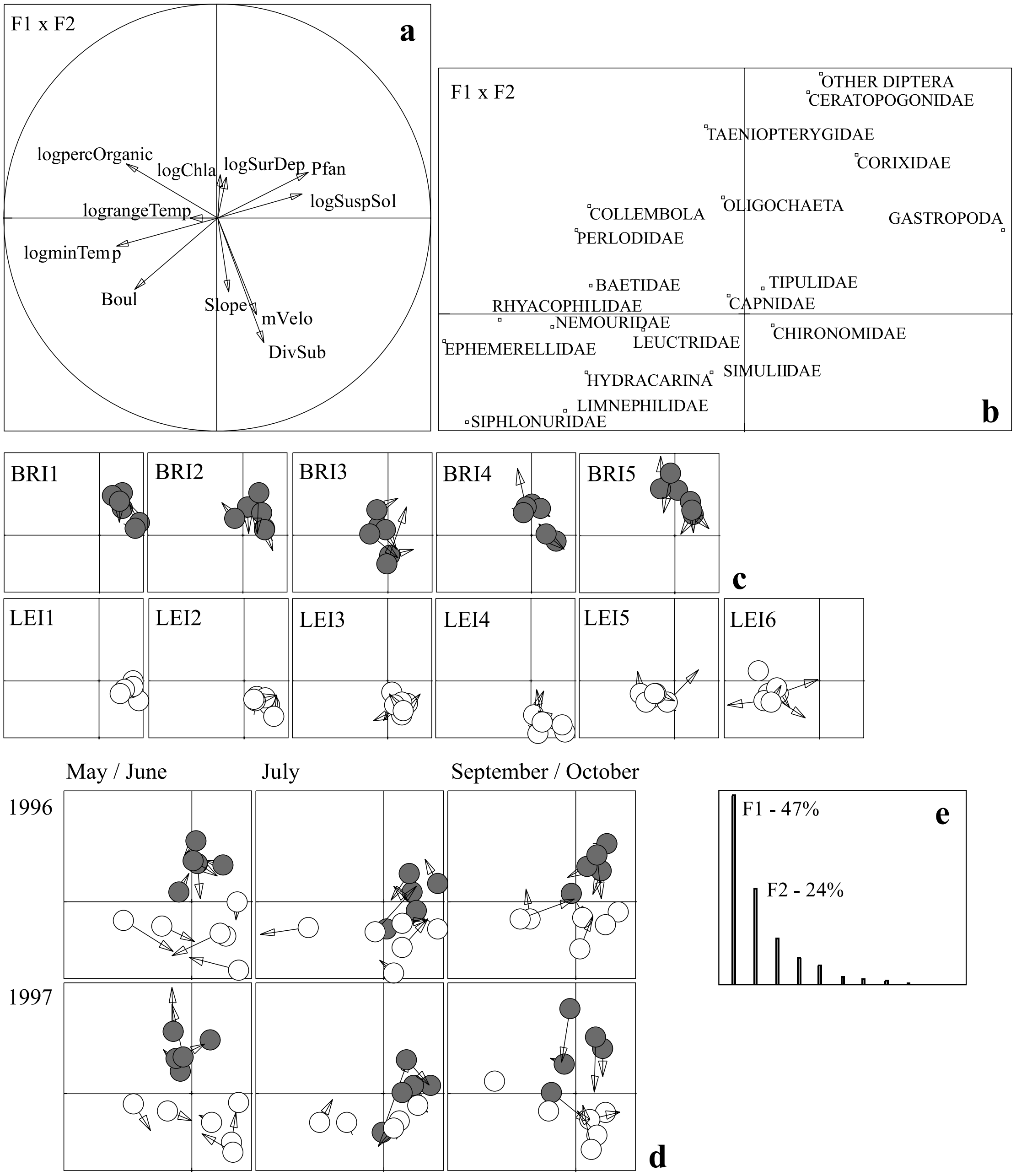

Fig. 8 First factorial plane (F1 × F2) of the co-inertia analysis (COIA) between 11 environmental variables and 21 taxa recorded in 11 reaches/dates in Dalelva and Leirungsåi. (a) Correlation circle of the 11 variables; (b) factorial plot of the 21 taxa; (c) ordination of the reaches/dates split up according to reaches; (d) ordination of the reaches/dates split up according to sampling dates; (e) percentage of inertia explained by the co-inertia axes. In (c) and (d) the circles are the reaches/dates as ordinated by the environmental variables, the tips of the arrows are the reaches/dates as ordinated by the taxa.

two glacial rivers, Dalelva and Leirungsåi, were associated with substratum stability (substratum heterogeneity, Pfankuch index of channel stability and hydraulic stress). This provides support for the role of substratum stability as a main explanatory variable in Milner & Petts's (1994) conceptual model.

Within river differences between the reaches in Leirungsåi indicated by the PCA, CA and COIA, were a function of the downstream gradient. This can be explained by a number of factors. There was a much greater altitudinal gradient in Leirungsåi compared with Daleelva, thereby creating greater heterogeneity between reaches. In addition, the Dalelva reaches analysed were completely within birch forest along a 5-km gradient, while Leirungsåi spanned a gradient from high alpine tundra to subalpine birch forest over a distance of 15 km. Although Dalelva received many tributaries, most were glacial and relatively large in comparison with the main stem. This tended to arrest community development and retain the characteristics of the reaches near the glacier and delaying the change towards a downstream situation with higher water temperatures and increased substratum stability. This was also reflected in the continued dominance of Diamesinae over Orthocladiinae in Dalelva far from the glacial source. It was only after the river passed through two large lakes that orthoclads became more abundant. Non-glacial tributaries were more common in Leirungsåi leading to a more rapid change in the chironomid community from one dominated to by Diamesinae to one in which Orthocladiinae were well represented or even dominant. The shift towards a more diverse benthic community in Leirungsåi was also advanced by the river's passage through two major lakes in the lower reaches. The data from Dalelva and Leirungsåi thus confirm the contention of Milner & Petts (1994) that tributary inputs and lakes would modify downstream patterns of macroinvertebrate community development.

Seasonal changes in glacial rivers can be marked (Uehlinger, Zah & Buergi, 1998; Brittain *et al*., 2000; Robinson, Uehlinger & Hieber, 2001). In this study such effects were principally related to high discharge and water velocity in Dalelva during the summer period of glacial melt and contrasting low values of the same variables in Leirungsåi during the autumn. The environment and the fauna of these two glacial rivers were both much more homogeneous during the summer period of high discharge. Milner & Petts's (1994) conceptual model was shown to be an accurate predictor of faunal change in glacial systems during the summer period. However, it did not account for seasonality reflected in the faunal composition of the two Norwegian glacial rivers, although sampling was restricted to the snow-free period. Although Chironomidae, notably *Diamesa*, clearly dominated in the upper reaches, other taxa were present, especially during spring and autumn as stability increased. This was particularly apparent in the upper reaches of Dalelva, where Oligochaeta, Taeniopterygidae, Capniidae, Simuliidae, Tipulidae and even Baetidae were recorded. The potential for colonization, both from drift from non-glacial tributaries (Saltveit, Haug & Brittain, 2001) and from ovipositing adults is greater in this river, which runs through low altitude birch forest, compared with Leirungsåi which is located above the tree-line in its upper and middle reaches.

Despite the high resilience of lotic communities (Ward *et al*., 1998), physical disturbance and the degree of habitat stability are also clearly important and play a major role in structuring benthic macroinvertebrate communities (Sidle & Milner, 1989; Death, 1995; Death & Winterbourn, 1995; Matthaei, Uehlinger & Frutiger, 1997; Townsend *et al*., 1997). Minshall & Petersen (1985) suggested that stream communities should be viewed as an interplay between stochastic and deterministic forces. Although stochastic processes, including the chance occurrence of immigrants from non-glacial tributaries certainly occur, deterministic forces appear to govern the macroinvertebrate communities of glacial rivers. The communities of the two Norwegian glacial rivers were clearly predictable both spatially and temporally. Severe summer spates will reduce benthic densities, and drift, both within the main river and from tributaries, is probably the main route for recolonization in the middle and lower reaches (Matthaei *et al*., 1997). However, nearer the glacier the continued presence of *Diamesa* and similar taxa is ensured by a combination of larval and pupal morphological adaptation to extreme disturbance (Steffan, 1971), colonization by ovipositing adults (Milner, 1994) and possibly upward movement from hyporheic and backwater refugia. Small-scale movements to refuge microhabitats (Lancaster, 1999) with less severe flow and disturbance may also occur during summer spates.

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References

APHA (1992) *Standard Methods for the Examination of Water and Wastewater*, 18th edn. The American Public Health Association 1015, Washington, DC, 1422 pp.

Brittain J.E. & Milner A.M. (2001) Ecology of glacier-fed rivers: current status and concepts. *Freshwater Biology*, **46**, 1571–1578.

Brittain J.E., Lencioni V. & Maiolini B. (1998) Arctic and Alpine Stream Ecosystem Research (AASER). *Proceedings of the Fourth Ny-Ålesund Seminar, the Arctic and Global Change*, Ravello, Italy, pp. 123–126. Italian National Research Council, Italy.

Brittain J.E., Adalsteinsson H., Castella E., Gislason G.M., Lencioni V., Lods-Crozet B., Maiolini B., Milner A.M., Petts G.E. & Saltveit S.J. (2000) Towards a conceptual understanding of arctic and alpine streams. *Verhandlugen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie*, **27**, 740–743.

Cellot B., Dole-Olivier M.J., Bornette G. & Pautou G. (1994) Temporal and spatial environmental variability in the Upper Rhne River and its floodplain. *Freshwater Biology*, **31**, 311–325.

Dean W.E. (1974) Determination of carbonate and organic matter in calcareous sediments and sedimentary rocks by loss on ignition: comparison with other methods. *Journal of Sediment Petrology*, **44**, 242–248.

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.

Death R.G. & Winterbourn M.J. (1995) Diversity patterns in stream benthic communities: the influence of habitat stability. *Ecology*, **76**, 1446–1460.

Diday E., Lemaire J., Pouget J. & Testu F. (1982) *Elements D'analyse de Données*. Dunod, Paris, 462 pp.

Dolédec S. & Chessel D. (1994) Co-inertia analysis: an alternative method for studying species–environment relationships. *Freshwater Biology*, **31**, 277–294.

Elgmork K. & Sæther O.R. (1970) Distribution of invertebrates in a high mountain brook in the Colorado Rocky Mountains. *University of Colorado Studies, Series in Biology*, **31**, 114 pp.

Fjellheim A. & Raddum G.G. (1982) Ferskvannsbiologiske undersøkelser i åbergstølsdeltaet, Jostedal i Sogn og Fjordane, i forbindelse med planlagt utbygging av Breheimen. *Rapport Laboratorium for Ferskvannsøkologi og Innlandsfiske, Universitetet i Bergen*, **49**, 57.

Fjellheim A., Raddum G.G. & Schnell Ø.A. (1988) Konsesjonsbetingete ferskvanns-biologiske undersøkelser i Jostedalsvassdraget, Sogn og Fjordane. *Rapport Laboratorium for Ferskvannsøkologi og Innlandsfiske, Universitetet i Bergen*, **64**, 157.

Flory E.A. & Milner A.M. (1999) The role of competition in invertebrate community development in a new stream in Glacier Bay National Park, Alaska. *Aquatic Ecology*, **33**, 175–184.

Füreder L. (1999) High alpine streams: cold habitats for insect larvae. In: *Cold-Adapted Organisms – Ecophysiology, Enzymology, Molecular Biology* (Eds R. Margesin & F. Schinner), pp. 181–196. Springer-Verlag, Heidelberg.

Gordon N.D., McMahon T.A. & Finlayson B.L. (1992) *Stream Hydrology. An Introduction for Ecologists*. John Wiley & Sons, Chichester, 526 pp.

Hongve D. (1987) A revised procedure for discharge measurement by means of salt dilution method. *Hydrological Processes*, **1**, 267–270.

Hotelling H. (1933) Analysis of a complex of statistical variables into principal components. *Journal of Educational Psychology*, **24**, 417–441, 498–520.

Hynes H.B.N. (1970) *The Ecology of Running Waters*. Liverpool University Press, Liverpool, UK, 555 pp.

Jacobsen 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.

Kownacka M. & Kownacki A. (1972) Vertical distribution of zoocenoses in the streams of the Tatra, Caucasus and Balkans Mts. *Verhandlugen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie*, **18**, 742–750.

Kownacki A. (1991) Zonal distribution and classification of the invertebrate communities in high mountain streams in South Tirol (Italy). *Verhandlugen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie*, **24**, 2010–2014.

Lancaster J. (1999) Small-scale movements of lotic macroinvertebrates with variations in flow. *Freshwater Biology*, **41**, 605–619.

Legendre P. & Legendre L. (1998) *Numerical Ecology*. Second English Edition. *Developments in Environmental Modelling*, Vol. 20. Elsevier, Amsterdam, 853 pp.

Lillehammer A. & Brittain J.E. (1978) The invertebrate fauna of streams in Øvre Heimdalen. *Holarctic Ecology*, **1**, 271–276.

Lods-Crozet B., Lencioni V., Ólafsson J.O., Snook D.L., Velle G., Brittain J.E., Castella E. & Rossaro B. (2001) Chironomid (Diptera: Chironomidae) communities in six European glacier-fed streams. *Freshwater Biology*, **46**, 1791–1809.

Matthaei C.D., Uehlinger U. & Frutiger A. (1997) Response of benthic invertebrates to natural versus experimental disturbance in a Swiss prealpine river. *Freshwater Biology*, **37**, 61–77.

Milner A.M. (1994) Colonization and succession of invertebrate communities in a new stream in Glacier Bay National Park, Alaska. *Freshwater Biology*, **32**, 53–70.

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

Minshall G.W. & Petersen R.C. (1985) Towards a theory of macroinvertbrate community structure in stream ecosystems. *Archiv für Hydrobiologie*, **104**, 49–76.

Oliver D.R. (1983) The larvae of Diamesinae (Diptera: Chironoimidae) of the Holarctic region – keys and diagnoses. *Entomologica Scandinavia Supplement*, **19**, 115–131.

Petts G.E. & Bickerton M.A. (1994) Influence of water abstraction on the macroinvertebrate community gradient within a glacial system: La Borgne d'Arolla, Valais, Switzerland. *Freshwater Biology*, **32**, 375–386.

Pfankuch D.J. (1975) *Stream Reach Inventory and Channel Stability Evaluation*. US Department of Agriculture Forest Service, Region 1, Missoula, MT, 26 pp.

Robinson C.T., Uehlinger U. & Hieber M. (2001) Spatiotemporal variation in macroinvertebrate assemblages of glacial streams in the Swiss Alps. *Freshwater Biology*, **46**, 1663–1672.

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

Rundle S.D., Jenkins A. & Omerod S.J. (1993) Macroinvertebrate communities in streams in the Himalaya, Nepal. *Freshwater Biology*, **30**, 169–180.

Sæther O.A. (1968) Chironomids of the Finse Area, Norway, with special reference to their distribution in a glacier brook. *Archiv für Hydrobiologie*, **64**, 426–453.

Saltveit S.J., Haug I. & Brittain J.E. (2001) Invertebrate drift in a glacial river and its non-glacial tributary. *Freshwater Biology*, **46**, 1777–1789.

Saporta G. (1990) *Probabilités, Analyse Des Données et Statistique*. Editions Technip, Paris, 493 pp.

Sidle R.C. & Milner A.M. (1989) Stream development in Glacier Bay National Park, Alaska, USA. *Arctic and Alpine Research*, **21**, 350–363.

Solem J.O., Steinkjer J. & Bretten S. (1987) Distribution and seasonal abundance of adult stoneflies (Plecoptera) in the Dovrefjell National Park, South Norway. *Fauna Norvegica Serie B*, **34**, 45–50.

Statzner B., Gore J.A. & Resh V.H. (1988) Hydraulic stream ecology: observed patterns and potential applications. *Journal of the North American Benthological Society*, **7**, 307–360.

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

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.

Townsend C.R., Scarsbrook M.R. & Dolédec S. (1997) Quantifying disturbance in streams: alternative measures of disturbance in relation to macroinvertebrate species traits and species richness. *Journal of the North American Benthological Society*, **16**, 531–544.

Uehlinger U., Zah R. & Buergi H. (1998) The Val Roseg project: temporal and spatial patterns of benthic algae in an Alpine stream ecosystem influenced by glacier runoff. In: *Hydrology, Water Resources and Ecology in Headwaters* (Eds K. Kovar, N.E. Tappeiner, N.E. Petters & R.G. Craig), pp. 419–424. IAHS Press, Wallingford, UK.

Ward J.H. (1963) Hierarchical grouping to optimize an objective function. *Journal of the American Statistical Association*, **58**, 236–244.

Ward J.V. (1986) Altitudinal zonation in a Rocky Mountain stream. *Archiv für Hydrobiologie Supplement*, **74**, 133–199.

Ward J.V. (1992) *Aquatic Insect Ecology: 1. Biology and Habitat*. Wiley, Chichester, UK, 438 pp.

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

Ward J.V., Bretschko G., Brunke M., Danielopol D., Gibert J., Gonser T. & Hildrew A. (1998) The boundaries of river systems: the metazoen perspective. *Freshwater Biology*, **40**, 531–569.

Williams D.D. & Feltmate B.W. (1992) *Aquatic Insects*. CAB International, Wallingford, UK, 358 pp.

Winkler S., Haakensen N., Nesje A. & Rye N. (1997) Glaziale Dynamik in Westnorwegen – Ablauf und Ursachen des aktuellen Gletschervorstoßes am Jostedalsbreen. *Petermanns Geographische Mitteilungen*, **141**, 43–63.

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