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# Disruption of a longitudinal pattern in environmental factors and benthic fauna by a glacial tributary

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## SUMMARY

1. In the upper Rhône catchment (Swiss Alps), modifications in the longitudinal pattern of environmental conditions and the benthic macroinvertebrate fauna were investigated in a glacier-fed stream (Rhône) at its confluence with a smaller glacier-fed tributary (Mutt) in June, August and September 1998. The distance to the source glacier was greater for the Mutt than for the Rhône.
2. Environmental conditions were harsher for the biota in the main stream upstream of the confluence than in the tributary. The tributary upstream of the confluence was characterised by higher taxonomic richness and abundance of the zoobenthos than the Rhône upstream.
3. Although environmental conditions in the main stream were little modified by the tributary, the fauna was richer and more diverse below the confluence. During the period of ice melt, colonisation from the Mutt led to the occurrence of faunal elements atypical of glacial streams in the main glacial stream upstream of the confluence, where water temperature remains below 4 °C.
4. Although contributing an average of only 10% to the Rhône discharge, the Mutt tributary is suggested to be the faunal driver of the system.

*Keywords*: benthic communities, confluence, environmental conditions, heterogeneity, kryal stream, Swiss Alps

## Introduction

Interest in the ecology of glacial streams, especially in Europe, has been growing during the last decade. The environmental conditions determining faunal patterns in kryal streams were reviewed by Milner & Petts (1994) and Ward (1994). Milner & Petts (1994) proposed a conceptual model for the longitudinal pattern in invertebrate assemblages downstream of glaciers. In this model, downstream faunal changes (i.e. increasing taxonomic diversity and zoobenthic biomass) are related to two major driving variables: water temperature, which increases with distance downstream of the glacier margin, and channel stability. Zoobenthic communities are hypothesised to become more complex when environmental conditions are less harsh. Harshness is considered here as a gradient of combined environmental conditions. It decreases with increasing water temperature, conductivity and channel stability, and with decreasing discharge and daily flow fluctuations. In this sense, summer conditions are usually harsher than those of spring in northern-hemisphere glacial streams.

These patterns were subsequently studied *in situ* across a latitudinal gradient of European glacial systems (Brittain & Milner, 2001). The response of benthic invertebrate taxonomic richness and density to the environmental parameters was described and a modelling approach based upon environmental

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variables proposed by Castella *et al.* (2001), Milner *et al.* (2001) and Brittain *et al.* (in press).

Possible modifications of the model of faunal succession by natural disrupting factors such as tributaries, lakes and valley confinement were pointed out by Milner & Petts (1994) and Milner *et al.* (2001). Whereas valley confinement may only have an impact on channel stability, the presence of a tributary or lake in a glacial system is expected to modify the stability of the system as well as the water temperature, the latter depending on the nature of the disruptor (water origin, size, flow characteristics). In the present study, the impact of a tributary is considered in a field situation where two glacier-fed streams of different size (the main Rhône and the tributary Mutt) join at a point where their benthic communities are expected to be different, given the relative distance to the glacial front (Milner & Petts, 1994). We hypothesised that the Rhône, 1 km downstream from its glacier snout, could not offer suitable conditions for development of the more diverse fauna of its tributary, the Mutt (3.6 km downstream from its glacier).

The objective of this paper is to document possible differences in environmental conditions and benthic communities in the Rhône upstream and downstream of the Mutt confluence, in relation to those occurring in the Mutt itself. This comparison includes (i) average values of faunal and environmental conditions at the sites, (ii) seasonal changes and (iii) spatial variability, which may differ as a consequence of tributary influence. The effects of the tributary on the system and inputs to the Milner & Petts' conceptual model (1994) are discussed.

## Study area

### General description

The Rhône alluvial plain, or 'Gletschbode', is located in the upper catchment of the Rhône river at the upper end of the Goms Valley (Canton of Valais) in the central Swiss Alps (Fig. 1). The major water source of the Rhône river is the Rhône glacier (area 10.2 km$^2$). Below the glacier snout, situated at an altitude of 2210 m a.s.l., the Rhône river flows down a 400-m-high granite cliff (slope 63%) and enters an alluvial plain (mean elevation: 1790 m a.s.l.; length: 2000 m; slope: 2.6%; width of the main channel: 10–15 m; width of the plain: 20–100 m). During the last century, the retreat of the Rhône glacier has left valley moraine deposits (Fenn & Gurnell, 1987) and a braided channel pattern. A few hundred metres downstream of the upper limit of the 'Gletschbode', the Mutt, the major tributary of the Rhône in this upper catchment, joins the Rhône. The Mutt river (length: 3600 m) originates from the Mutt glacier (area 0.6 km$^2$). The upper part of the Rhône is a kryal segment (Ward, 1994), where water temperature rarely exceeds 4 °C. Mean annual discharge of the Rhône in 1998 was 2.88 m$^3$ s$^{-1}$ and its hydrograph reveals a discharge peak in summer with large daily flow fluctuations (data from the Swiss National Hydrological and Geological Survey). Water turbidity during summer is high because of glacial flour. The Mutt basin is characterised by a different geology, including a carbonate outcrop. In its lower course, the Mutt still has a glacial signature (Milner & Petts, 1994; Ward, 1994) including summer peaks in discharge and suspended sediments, but with an

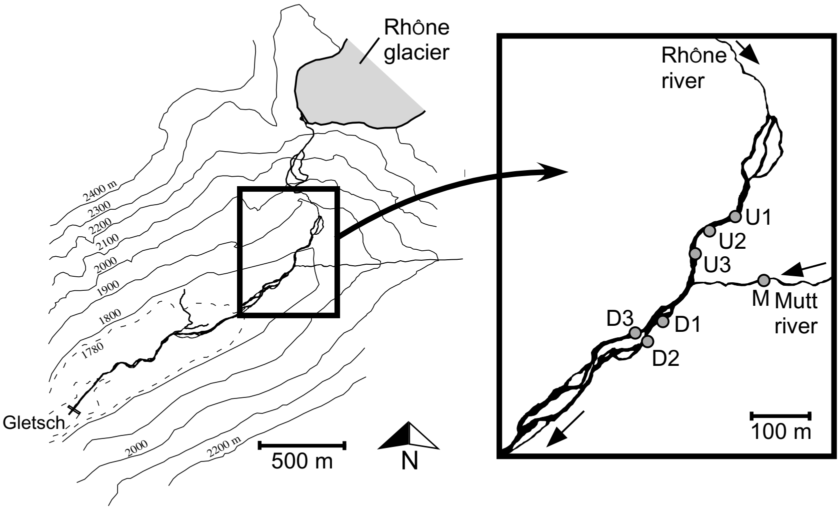

**Fig. 1** Location of sampling sites on the main glacial stream (Rhône River) and its glacial tributary (Mutt River), in the central Swiss Alps.

extended snow-melt period and a significant groundwater contribution (Ilg *et al*., 2001; Lods-Crozet *et al*., 2001). Daily flow fluctuations occur in summer, when there is an increase in sediment transport and turbidity. Water temperature in summer can exceed 13 °C near the confluence with the Rhône.

Highly diverse thickets of *Salix* spp. and *Alnus viridis* (Chaix) DC and herbaceous alpine vegetation are predominant in the alluvial plain, with some *Larix decidua* Miller. Some islands formed in the Rhône are colonised by vegetation typical of glacial stream alluvium (Cariocion bicoloris-atrofuscae) (Gallandat, Gobat & Roulier, 1993; Schubiger-Bossard, 1988).

### *Study sites*

The study sites were close to the confluence of the two glacial streams (Fig. 1). Three 'upstream' sites (U1, U2, U3) were along the left bank of the Rhône, upstream of the confluence. Here, the Rhône consisted of a single 15-m-wide channel, whereas downstream of the confluence, the Rhône had a braided pattern. The three 'downstream' sites were: D1 along the main channel, D2 on the left bank of the left channel and D3 on the right bank of the right channel. One site (M) was located on the Mutt 100 m upstream of the confluence. The Rhône upstream and downstream of the confluence will be referred to as 'sectors'.

The sites were assigned as 15-m-long reaches of the river. When water depth exceeded 0.6 m, the site was restricted to the area between the bank and 0.6 m depth.

## Materials and methods

The sites were investigated three times in 1998 during the three major annual hydrological phases: in June (10–17.6) during snow melt (J), in August (17–25.8) during ice melt (A) and in September (24.9–1.10) at low water level (S). These sampling periods will be referred to as 'seasons'. The field protocols followed closely those established for similar purposes in the EU-project 'AASER' (Brittain *et al*., 2000; Brittain & Milner, 2001; Castella *et al*., 2001).

### *Site level data*

During a 3-day period in each season, electrical conductivity and suspended solids were monitored at minimum (morning) and maximum (evening) flows. Electrical conductivity was measured in the field with a portable conductivity meter at a reference temperature of 25 °C (WTW Cond 330I; WTW GmbH, Weilheim, Germany). Water samples (250 mL) were taken in the water column and filtered through a weighed filter (RC55, 0.45 μm pore size, Schleicher & Schuell, Dassel, Germany) to measure suspended sediment concentration. The filter was dried at 105 °C for 30 min and cooled in a dessicator before re-weighing. Four cross-sectional profiles per site were used to assess depth, current velocity and bed sediment composition. The latter was evaluated by visual or tactile assessment of the occurrence of one of four substrate categories (<0.2 cm; 0.2–5 cm; 5–20 cm; >20 cm) at each of a minimum of 10 points along every cross-profile. Grain size distribution of the stream bed sediment was also assessed using Wolman's method by measurement of the width of 100 randomly selected stones (Leopold, Wolman & Miller, 1964). An index of substrate diversity was calculated from all grain size data at the site level as Simpson's diversity index (Castella *et al*., 2001):

$$\text{Simpson index} = 1/(\Sigma p_i^2)$$

where $p_i$ is the proportion of the $i$th substrate category. Water temperature was recorded continuously during the study year at most of the sites with digital temperature loggers (Orion tinytalk, Chichester, U.K. and Elpro-Buchs, Buchs, Switzerland). Daily mean and maximum water temperatures were calculated for a 70–98-day period (depending on logger functioning) between the beginning of July and mid-October for all sites except U3 and D1. At the site level, average current velocity ($U$) and average water depth ($D$) were combined to calculate an average Froude number (dimensionless) according to Statzner, Gore & Resh (1988):

$$\text{Froude number} = U/(g \cdot D)^{0.5}$$

where $g$ is the gravity acceleration. The site slope ($S$) and average water depth ($D$) were combined to calculate tractive force (shear stress) according to Statzner *et al*. (1988):

$$\text{Tractive force} = g \cdot S \cdot D \cdot \rho$$

where $g$ is the gravity acceleration and ρ is the water density, dyn cm$^{-1}$. Once during the study the stream bottom component of the Pfankuch index (Pfankuch,

1975) was used to assess channel stability (range of 15–70, high scores representing unstable channels). Benthic algal biomass was estimated for each site in each season by scraping a 3 × 3-cm patch of periphyton from the upper surface of five randomly selected stones. The scraped samples were filtered onto GF/C filter (Whatman, Maidstone, UK) and the pigments were extracted with 90% aqueous acetone for 2 h at 4 °C in the dark and exposed to ultrasonic waves. Chlorophyll *a* was determined by spectrophotometry (Perkin-Elmer uv/vis Lambda 2) (modified from APHA, 1992). The 1998 discharge records for the gauging station at Gletsch, 1.5 km downstream of the confluence, were supplied by the Swiss National Hydrological and Geological Survey. The relative contributions of the upper Rhône and the Mutt were calculated for each month using the data given by Bernath (1991). The Rhône and Mutt discharges were then estimated from the daily averages recorded at the Gletsch gauging station.

### *Kick sampling*

Ten sampling points were chosen randomly within each site. Depth, flow velocity and bed sediment composition were recorded at each of the 10 points before benthic sampling. The fauna was then collected into a 250-μm-mesh pond net at these points by kick-sampling within a 30 × 30-cm area for 30 s. The fauna was sorted, counted and identified under a dissecting microscope (Leica MZ12, Heerbrugg, Switzerland). The coarse benthic organic matter (>1 mm) contained in the kick samples was sorted, dried and weighed.

## Statistical analyses

To obtain the same level of identification for all seasons, taxa were grouped consistently at different taxonomic levels for multivariate analysis (family level for Diptera except for chironomids; species, genus or family for stoneflies, mayflies and caddisflies). Taxa represented by fewer than six individuals were not included in multivariate analyses, but were used to calculate species richness and total abundance. Data provided at the site level were used to compare the mean characteristics of the sites, whereas data collected at the individual kick sample level were used for comparisons of faunal and environmental heterogeneity within sites. Multivariate analyses were carried out with the ADE-4 software (Thioulouse *et al.*, 1997); correlations coefficents and univariate statistics were obtained using S-PLUS 2000 (MathSoft, Seattle, WA, U.S.A.).

### *Site level analyses*

Exploration of the total environmental data set allowed selection of 13 weakly correlated site variables for 21 sites-seasons (sites sampled at different seasons): Froude number, chlorophyll *a*, conductivity, maximum water temperature, tractive force, median of the substrate size, mean of water depth, variance of water depth, Pfankuch index, suspended sediments, % cover by fine sediment, substrate diversity index, coarse benthic organic matter. This data set was processed by principal component analysis (PCA). Coarse benthic organic matter, conductivity and chlorophyll *a* were log transformed prior to analysis.

The data set comprising the mean number of individuals per kick sample for each of the 25 taxa in the 21 sites-seasons was $\log_{10}(x + 1)$-transformed before undertaking correspondence analysis (CA) or PCA. Non-parametric tests (Mann–Withney) were used to compare the abundance of taxa as well as total taxonomic richness, between groups of sites and between seasons.

Between-group PCA and CA, and associated Monte–Carlo permutation tests (Dolédec & Chessel, 1987, 1989) were used to determine the significance of spatial (i.e. between sectors) and temporal (i.e. between seasons) differences in the multivariate ordinations.

### *Kick level analyses*

The total faunal data (209 kicks; one kick sample was lost) and environmental data (depth, substrate grain size, coarse benthic organic matter (log-transformed) and mean flow velocity (log-transformed) were used to assess heterogeneity of the environment and faunal composition. Three approaches were used to assess and compare within-site heterogeneity.

Within-group CA and PCA were carried out in order to measure within-‘site-season’ (i.e. a site in a given season) faunal and environmental heterogeneity. Within-group ordinations were carried out according to Dolédec & Chessel (1987, 1989, 1991) and allowed description and measurement of inertia within groups of rows after an initial ordination. The groups considered here were the sets of 30 kick-level faunal or environmental data per 'site-season'. The output of these within-group ordinations was one within-group inertia value per 'site-season'. Differences in within-'site-season' inertia between upstream and downstream sites were tested with Wilcoxon tests.

Mood tests [non-parametric dispersion comparison test, Rossini (1997)] were used on each continuous environmental variable (depth, coarse benthic organic matter and mean flow) to supplement the above-mentioned multivariate within-group inertia. These test for differences in variability between the upstream and downstream sites with all seasons grouped. They were processed after transformation of the values in order to obtain the same median in the groups compared.

Heterogeneity in substrate grain size was summarised by calculating Simpson's diversity index for each site-season. Differences in upstream and downstream values were tested by a Wilcoxon test.

## Results

### General environmental conditions at the sites

Water temperature was lowest at the U sites (2.3 ± 0.3 °C) (Table 1) and was not significantly different at U1 and U2 (Mann–Withney for paired data, $P = 0.7$). Water temperature did not exceed 4 °C at the U sites. Difference were significant for all other pairs of sites ($P < 0.001$). The Mutt was warmer than all other sites and the water temperature in D2, just downstream, was a little higher than at D3. Although significantly warmer, the water temperature at D3 was very similar to that of the U sites (Fig. 2a).

Daily mean discharge of the Rhône at Gletsch fluctuated between 1.1 and 16.2 $m^3 s^{-1}$, with a mean of 7.3 ± 3.5 $m^3 s^{-1}$ over the study period (Fig. 3a). During that period, the Mutt contributed an average of 10.9% to the Rhône discharge measured at Gletsch.

At the U sites, conductivity was very low and very stable (10 ± 5 $\mu S\ cm^{-1}$) (Table 1). The Mutt had a much higher conductivity with a mean value of 155 ± 45 $\mu S\ cm^{-1}$. The D sites exhibited intermediate conductivity values, with quite high conductivity at D1 and D2, although falling again at D3.

**Table 1** General characteristics of the sampling sites in the Rhône–Mutt area

| | U1 | U2 | U3 | D1 | D2 | D3 | M |
|---|---|---|---|---|---|---|---|
| Distance from glacier (m) | 1000 | 1050 | 1100 | 1300 | 1350 | 1350 | 3500 |
| Daily mean water temperature ± SD (°C) | 2.3 ± 0.3 | 2.3 ± 0.4 | Logger lost | Logger lost | 3.1 ± 0.5 | 2.4 ± 0.4 | 6.7 ± 2.0 |
| $T_{max}$ (°C) | 3.8 | 3.9 | – | – | 5.9 | 5 | 14.1 |
| Conductivity mean ± SD ($\mu S\ cm^{-1}$) | 10.7 ± 5.1 | 10.5 ± 5.1 | 10.3 ± 5.2 | 74.5 ± 35.1 | 58.5 ± 29.9 | 18.3 ± 12.1 | 154.5 ± 44.7 |
| Conductivity range ($\mu S\ cm^{-1}$) | 3.4–18.1 | 3.3–17.8 | 2.9–17.8 | 21.1–113.2 | 14.5–92.5 | 3.1–39.3 | 75.7–210 |
| Suspended sediments mean ± SD ($mg\ L^{-1}$) | 205 ± 197 | 187 ± 186 | 215 ± 236 | 151 ± 162 | 144 ± 133 | 175 ± 141 | 252 ± 469 |
| Suspended sediments range ($mg\ L^{-1}$) | 15–797 | 13–824 | 12–913 | 6–628 | 7–488 | 14–553 | 0.5–1480 |
| Average zoobenthos abundance (ind. $m^{-2}$) | 188–794 | 237–1403 | 237–1476 | 85–1263 | 638–3189 | 37–1971 | 233–2746 |

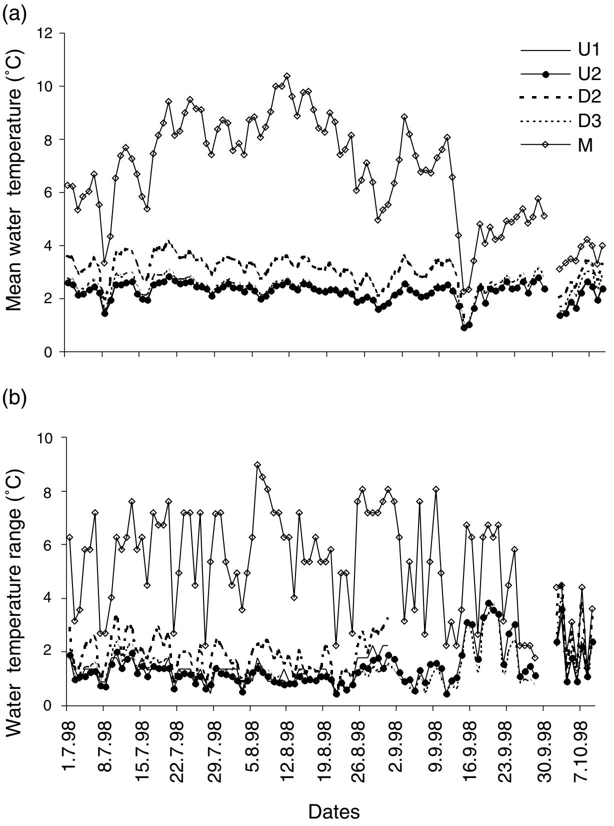

**Fig. 2** (a) Daily average water temperature at five sites on the upper Rhône and Mutt rivers over the study period; (b) daily ranges of water temperature ($T°_{\max}$–$T°_{\min}$) at the five sites over the study period.

Mean suspended sediment values ranged from 144 to 252 mg L$^{-1}$ (Table 1). Maximum values were 40–100 times higher than the minimum for the Rhône sites and up to 3000 times higher than the minimum for the Mutt.

Ordination of the site parameters (13 variables × 21 sites-seasons) by PCA separated the upstream sites (U) from the others along the F1 axis (Fig. 4a). The F2 axis separated the Mutt (M) from the others. D1 and D2 tended to be more similar to the Mutt and D3 to the U sites along F2. The difference between the U, D and M sectors was highly significant (37% of the total variability associated with between-sector differences; Monte–Carlo permutation test: $P < 0.001$). The U sites were characterised by substrate instability (high Pfankuch scores), large substrate grain size and high and variable water depth. The Mutt contrasted with the U and D sites (particularly D3), in having higher maximum water temperature, conductivity and tractive force.

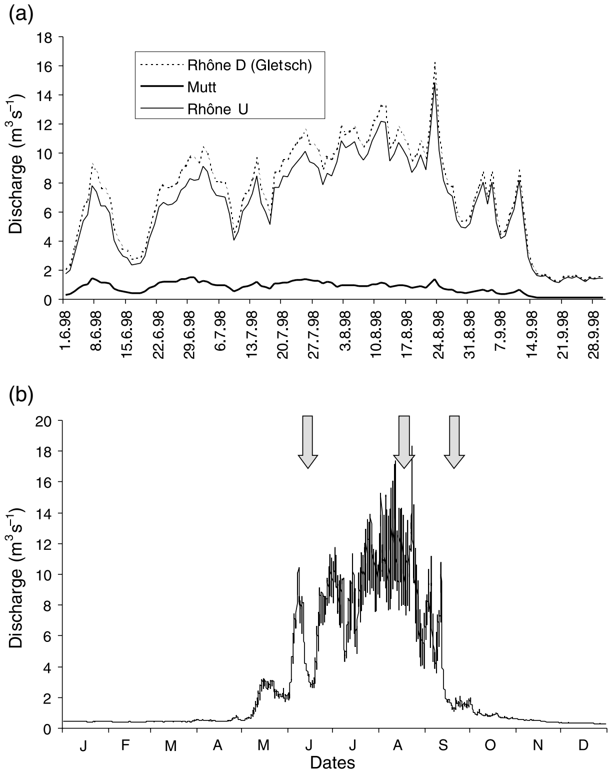

**Fig. 3** (a) Daily average discharge over the study period. Rhône D (Gletsch): Gletsch gauging station (see Fig. 1); Rhône U and Mutt: estimates based upon the relative contributions calculated from Bernath (1991); (b) hourly average discharge of the Rhône at the Gletsch gauging station during 1998. Arrows indicate the sampling periods.

### *Seasonal changes in environmental conditions*

Water temperature exhibited major daily fluctuations from spring to autumn (June to end of September 1998) (Fig. 2b). During this snow- and glacier-melt season, daily variations were about 3 °C for U and D sites and about 4–6 °C for the Mutt. During winter (November 1998–May 1999), variations in temperature were less, and for at least 5 months, water temperature remained below 1 °C at the U sites, below 2 °C in the Mutt and below 1.5 °C at D3. This period of low temperature variation began when discharge dropped below 0.6 m$^3$ s$^{-1}$ and ceased when discharge exceeded this value in May 1999.

The June samples were taken after a 7-day period with high flow during which discharge increased from 2 to 10 m$^3$ s$^{-1}$ before falling rapidly again (Fig. 3b). During the June sampling period, mean discharge was 4.5 ± 2.2 m$^3$ s$^{-1}$. Daily mean discharge exceeded 8 m$^3$ s$^{-1}$, continuously, from 19 July to 25

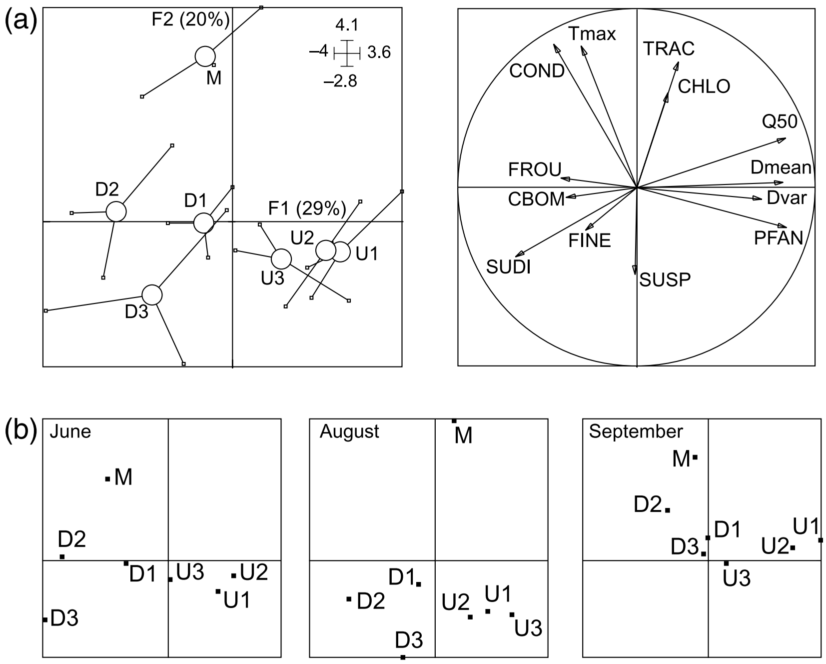

**Fig. 4** Ordination by principal component analysis (PCA) of the 21 sites-seasons (sites sampled in different seasons) according to 13 environmental variables. (a) Left plot, ordination of sites-seasons along the first two ordination axes (F1 and F2) (samples grouped by sites). Right plot, correlation between environmental variables and the same axes. FROU: Froude number; CHLO: chlorophyll *a* (log); COND: conductivity (log); Tmax: maximum water temperature; TRAC: tractive force; Q50: median of the substrate grain size; Dmean: mean of the water depth; Dvar: variance of the water depth; PFAN: Pfankuch index; SUSP: suspended sediments (log); FINE:% cover by fine sediment; SUDI: substrate diversity index; CBOM: coarse benthic organic matter (log); (b) ordination of sites-seasons along the first two ordination axes (F1 and F2). Each plot represents the samples for one season.

August. During 1998, daily fluctuations exceeded 3 $m^3 s^{-1}$ for 51 days, >4 $m^3 s^{-1}$ for 30 days and >5 $m^3 s^{-1}$ for 19 days. The September samples were taken during a low flow period when daily discharge mean remained below 2 $m^3 s^{-1}$ for 2 weeks, and daily fluctuations were <1 $m^3 s^{-1}$.

At the upstream sites, conductivity was very constant throughout the study period and stayed under 5 $\mu S\ cm^{-1}$ during ice melt (August) (Fig. 5a). During that period mean conductivity in the Mutt decreased and high daily conductivity fluctuations occurred, with lower values at the end of the afternoon when ice melt contributed most to the discharge. Conductivity at D1 and D2 during June and September was intermediate between values for the Mutt and for the U sites, with higher values for D1. In August, D1 and D2 exhibited low conductivity, but values were still higher than for the U and D3 sites. The annual pattern of conductivity at D3 was very similar to that at the U sites, with some higher variability in June and September.

Suspended sediments (Fig. 5b) did not vary significantly between sites, either in June, or in September (Kruskall–Wallis, $P < 0.005$), although differences were significant in August. The mean for June was 152 ± 73 mg $L^{-1}$, with lower values in the Mutt (17.7 ± 7.4 mg $L^{-1}$). In September the water was clear, and the suspended sediment level was very low (18.2 ± 8.8 mg $L^{-1}$). In August, suspended sediment loads were very high and variable (394 ± 317 mg $L^{-1}$), especially in the Mutt. This variability was associated with high daily discharge fluctuations. Water was clearer in the morning (216 ± 108 mg $L^{-1}$) and more turbid in the afternoon (571 ± 358 mg $L^{-1}$) when the ice-melt contribution was greatest.

The higher dispersion of D sites on the factorial map of the PCA (Fig. 4a) indicated an increase in variability of conditions downstream of the confluence. In August, during the high-discharge period, conditions at all the D sites were mostly differentiated from the Mutt (Fig. 4b). In September, conditions at the D sites were more similar and 'closer' to those in the Mutt. The situation in June was intermediate.

Between-season differences were also significant in the PCA ordination (21.3% of the variability associated with between-season difference; Monte–Carlo permutation test: $P = 0.003$). The seasonal effect was mainly because of very high chlorophyll *a* concentrations and almost no suspended sediments in September.

### *Environmental heterogeneity at the microhabitat level*

Most environmental parameters measured did not differ significantly in their variability within the upstream and downstream sectors in all three seasons, except for coarse benthic organic matter,

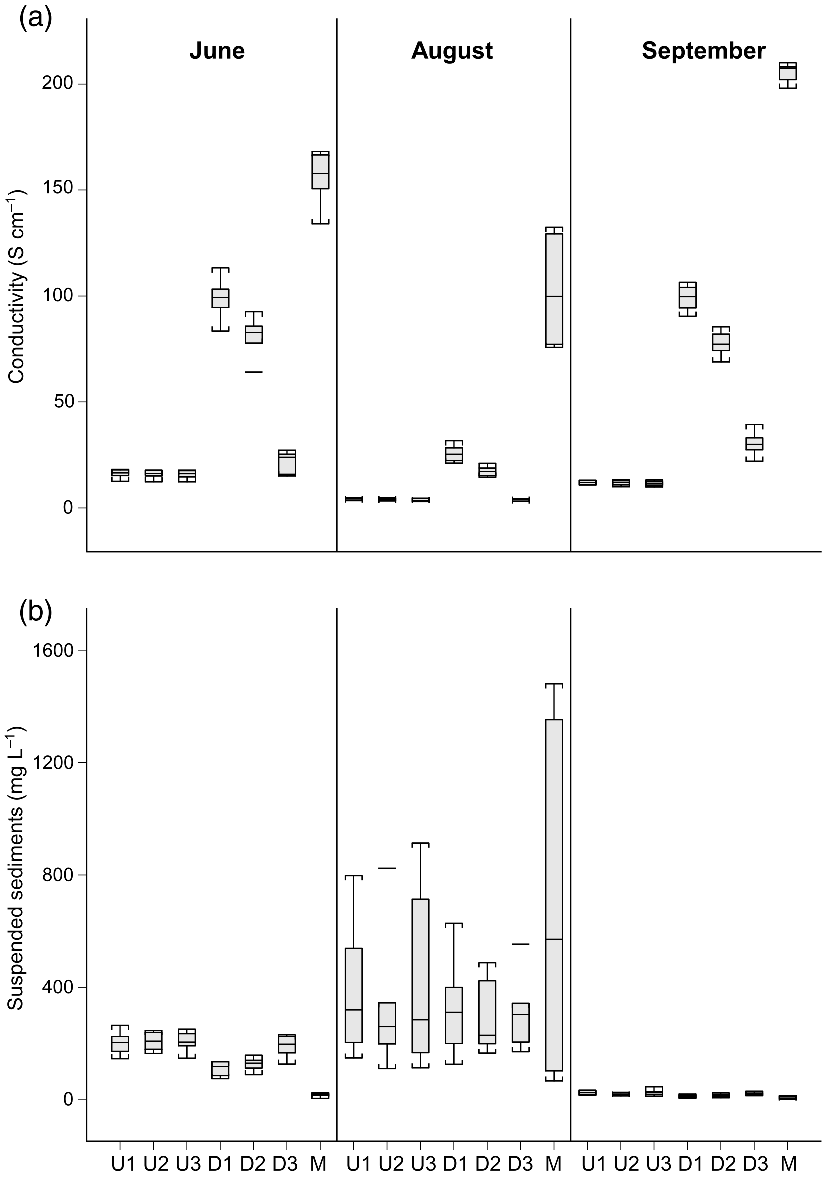

**Fig. 5** Box-plots of two environmental parameters measured during the monitoring periods. (a) Conductivity; (b) suspended sediment concentrations. The vertical boxes represent the interquartile range (Q25–Q75) around the site median (horizontal thick line). Upper and lower whiskers are drawn to the nearest value not beyond Q75 + 1.5 (Q75 − Q25) and Q25 − 1.5 (Q75 − Q25), respectively.

which was significantly more variable downstream from the confluence in June and August (Mood test: $P < 0.001$), and mean flow and depth which were more variable upstream than downstream from the confluence in June (Mood test, respectively, $P < 0.05$ and $P < 0.01$). With all seasons grouped, the result remained significant for organic matter (Mood test: $P < 0.001$) and for depth (Mood test: $P < 0.05$). The within-'site-season' inertia measured from a PCA (210 kicks × three variables) (Fig. 6a) and taken as an overall index of environmental heterogeneity, also did not differ significantly between upstream and downstream sectors (one-sided Wilcoxon test: $P = 0.07$). Heterogeneity of substrate grain size (Fig. 6b) was significantly higher downstream from the confluence than upstream (one-sided Wilcoxon test: $P < 0.05$).

### *Faunal composition*

A complete list of fauna is given in Table 2, including taxa that were not considered in the 25 taxa × 21 sites-seasons data set used for multivariate analyses.

The fauna was dominated by chironomids, that contributed more than 65% of total abundance (*Diamesa*: 57%; Orthocladiinae: 7%; Chironominae: <1%), followed by *Baetis alpinus* (Pictet) 17.7% (Table 2). Nemouridae represented almost 5% and

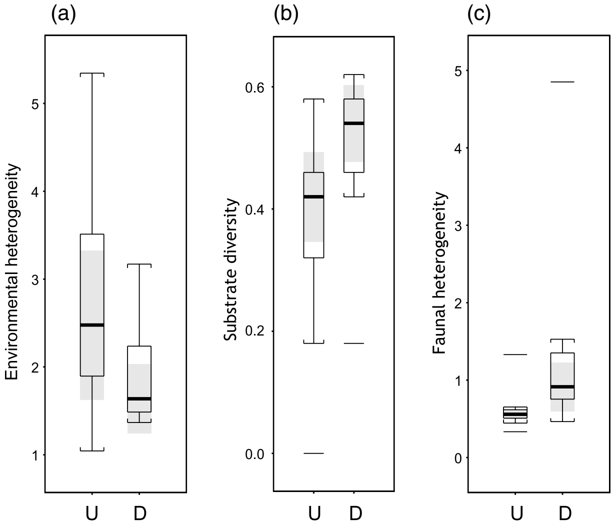

**Fig. 6** Box-plots of environmental heterogeneity (a), substrate diversity (b) and faunal heterogeneity (c). Environmental and faunal heterogeneities are measured from the within-'site-season' PCA and CA, respectively. The substrate diversity index is the Simpson diversity index applied to the site substrate-category composition. The vertical boxes represent the interquartile range (Q25–Q75) around the site median (horizontal thick line). Upper and lower whiskers are drawn to the nearest value not beyond Q75 + 1.5 (Q75 − Q25) and Q25 - 1.5 (Q75 − Q25), respectively. Grey areas are 95% confidence intervals around the median. $n = 9$ for the upstream and downstream sites.

Empididae, Blephariceridae (*Liponeura cinerascens minor* Bischoff) and Heptageniidae 1–5%. The remaining taxa were even scarcer.

The fauna was also dominated by chironomids at the sector level (U, D, and M), but the proportions of chironomid taxa varied. The U sites were dominated by *Diamesa* gr. *A* (>50% of total abundance) and *Diamesa* gr. *B* (17.8%). Orthocladiinae represented only 4% of total abundance. At the D sites the contributions of *Diamesa* gr. *A* (24.5%) and *Diamesa* gr. *B* (29.5%) were similar, whereas Orthocladiinae represented about 8% of total abundance. In the Mutt *Diamesa* gr. *A* (33%) and Orthocladiinae (13%) dominated and *Diamesa* gr. *B* represented only 5.5% of total abundance. *Baetis alpinus* was the second or third most abundant taxon in all sectors, with a contribution of 17.4–18.9%.

### Faunal differences between sites

Ordination of the 25 taxa × 21 sites-seasons data set by CA separated the sites into two groups (Fig. 7a): the first group including the upstream sites (U) and the downstream site D3, the second one including the Mutt, D1 and D2. Between-group differences were not significant (23% of the variability, but $P = 0.35$). Ordination of the same data set by PCA produced quantitative but not qualitative differences between the same two groups of sites (U+D3/D1+D2+M) (Fig. 7c,d) with a significant between-group difference (19.2% of variability; $P = 0.001$).

Mean overall abundance was not significantly different between the two groups of sites identified in the ordinations (Mann–Whitney test; $P = 0.64$) and ranged from 37 to 3189 ind. $m^{-2}$. Taxonomic richness (Table 2) was significantly higher in the second group of sites (D1 + D2 + M) than in the first one (U + D3) (Mann–Whitney unilateral test; $P < 0.001$). *Ecdyonurus, Capnia*, Dixidae and Thaumaleidae were absent from the first group of sites. Comparisons between the two groups at the taxa level gave significant differences (Mann–Withney unilateral test; $P < 0.025$) for 12 more taxa, which were less abundant in the first group of sites: *Rhithrogena nivata* (Eaton), *Rhithrogena degrangei* Sowa, Heptageniidae (other than *Ecdyonurus* and *Rhithrogena*), Orthocladiinae, Limoniidae, Blephariceridae, Perlodidae, *Rhabdiopteryx alpina* Kühtreiber, *Siphonoperla* sp., Nemouridae, Limnephilidae and *Rhyacophila* sp.

### Seasonal faunal changes

Ordination of the fauna by CA emphasised a seasonal shift in the composition of the fauna (Fig. 7b). The faunal contrast between the groups of sites (U+D3/D1+D2+M) was greatest in August, whereas in September, site D3 had a fauna more similar to that of the second group of sites.

On the factorial plot of the PCA for the same data set, the seasonal variability of the second group of sites was higher than that of the first group (Fig. 7c,d). Between-season differences were significant (33% of the variability; $P < 0.001$).

Overall mean abundance was lower in August (37–638 ind. $m^{-2}$) than June (653–1476 ind. $m^{-2}$) and September (794–3189 ind. $m^{-2}$) (Mann–Whitney for paired data; $P < 0.002$), but there was no significant difference between the latter seasons. Taxonomic richness (Fig. 8) was higher in the second group of sites (D1 + D2 + M) in August and September (Mann–Whitney unilateral test; $P < 0.025$). In September, taxonomic richness at D3 tended to be more

**Table 2** Taxonomic composition and abundance (ind. m$^{-2}$) per site. Each column is calculated from 10 individual kick samples

| | June | | | | | | | August | | | | | | | September | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | U1 | U2 | U3 | D1 | D2 | D3 | M | U1 | U2 | U3 | D1 | D2 | D3 | M | U1 | U2 | U3 | D1 | D2 | D3 | M |
| *Diamesa* gr. A[*] | 340 | 671 | 372 | 510 | 84 | 135 | 380 | 159 | 213 | 198 | 9 | 295 | 32 | 145 | 378 | 669 | 736 | 255 | 58 | 976 | 782 |
| *Diamesa* gr. B[†] | 139 | 359 | 201 | 99 | 84 | 99 | 38 | 23 | 19 | 24 | 19 | 50 | 4 | 7 | 153 | 132 | 277 | 417 | 1667 | 400 | 175 |
| Other Diamesinae[‡] | | | 1 | | | | | | | | 1 | | | 2 | | | | | | | 3 |
| Orthocladiinae | 35 | 73 | 138 | 48 | 66 | 57 | 82 | 4 | 3 | 4 | 14 | 82 | | 33 | 13 | 12 | 15 | 104 | 308 | 97 | 388 |
| Chironominae | | 3 | 93 | 3 | 4 | 12 | 1 | | | | | | | | | | | | | | |
| Simuliidae | 12 | 38 | 55 | 11 | 41 | 11 | 3 | | | | | 1 | | | | | | 2 | | | 1 |
| Limoniidae | | | 2 | 4 | 12 | 3 | 2 | | | | 4 | 2 | | 3 | 4 | 7 | 12 | 30 | 33 | 10 | 34 |
| Blephariceridae | 1 | 4 | 2 | 47 | 36 | | 260 | | | 1 | | 5 | | 4 | | | | | | | 10 |
| Psychodidae | | | 1 | | | 1 | | | | | | | | | | 1 | 5 | 6 | 1 | 3 | |
| Empididae | 1 | 2 | 3 | 1 | 14 | 2 | 1 | | | 1 | | 11 | | 2 | 20 | 18 | 65 | 110 | 192 | 98 | 66 |
| Thaumaleidae[§§] | | | | | | | 1 | | | | 1 | | | 1 | | | | | | | |
| Dixidae[§§] | | | | | | | | | | | | | | | | | | | 1 | | 1 |
| *Baetis alpinus* (Pictet) | 109 | 230 | 301 | 223 | 318 | 159 | 147 | 1 | 2 | 5 | 9 | 48 | | 10 | 215 | 269 | 215 | 163 | 476 | 272 | 592 |
| *Ecdyonurus picteti* Meyer-Dür | | | | | | | 1 | | | | | 1 | | | | | | 3 | 2 | | 2 |
| *Rhithrogena loyolaea* Navàs | 2 | | 4 | 3 | 25 | | 1 | 1 | | 1 | | 4 | | 1 | | 2 | 2 | 2 | 6 | 4 | 1 |
| *Rhithrogena endenensis* Metzler *et al*. | | | | | 12 | | | | | | 3 | | | | | | 1 | | 6 | 1 | |
| *Rhithrogena nivata* (Eaton) | | | 1 | 2 | 1 | | 7 | | | | 3 | 3 | 1 | | | 1 | | 2 | 26 | 3 | 47 |
| *Rhithrogena degrangei* Sowa | | | | | 2 | | | | | | | | | 2 | | | | 1 | 16 | 1 | 1 |
| Other Heptageniidae[§] | | | 1 | 6 | 14 | | 6 | | | | 2 | 8 | | 3 | | 2 | 2 | 8 | 12 | 10 | 12 |
| *Siphonoperla* spp. | | | | 1 | 2 | | | | | | | 2 | | 3 | | | | 14 | 7 | 3 | 9 |
| Perlodidae[¶] | | | 1 | 4 | 15 | | 15 | | | | 9 | 13 | | 4 | 1 | | 1 | 27 | 86 | 8 | 119 |
| *Rhabdiopteryx alpina* Kühtreiber | | | | 1 | 13 | | 1 | | | | | 3 | | 3 | | 1 | | 44 | 86 | 42 | 226 |
| Nemouridae[**] | 9 | 14 | 278 | 24 | 186 | 15 | 18 | | | 3 | 7 | 99 | | 3 | 4 | 4 | 2 | 32 | 121 | 29 | 188 |
| *Leuctra* spp. | | 1 | 7 | 2 | 2 | | 1 | | | | | | | | 6 | | 4 | 9 | 4 | 8 | 14 |
| *Capnia* spp. | | | | | | | | | | | | | | | | | | | 2 | | 4 |
| Limnephilidae[††] | 4 | 6 | 14 | 2 | 10 | | 1 | | | | 1 | 10 | | 4 | | | | 20 | 31 | 1 | 17 |
| *Rhyacophila* spp.[‡‡] | 1 | | 1 | | 4 | | 12 | | | | 3 | 1 | 1 | 3 | | 1 | | 14 | 48 | 5 | 54 |
| *Lithax niger* (Hagen)[§§] | | 1 | | | | | | | | | | | | | | | | | | | |
| Total abundance (ind. m$^{-2}$) | 653 | 1403 | 1476 | 991 | 945 | 494 | 978 | 188 | 237 | 237 | 85 | 638 | 37 | 233 | 794 | 1119 | 1337 | 1263 | 3189 | 1971 | 2746 |
| Number of taxa | 11 | 12 | 19 | 18 | 21 | 10 | 20 | 5 | 4 | 8 | 14 | 18 | 3 | 18 | 9 | 13 | 14[¶¶] | 20 | 23[¶¶] | 19 | 23 |

[*] *Diamesa bertrami*, D. gr. *steinboecki*, D. gr. *latitarsis* and D. gr. *aberrata*.

[†] *Diamesa insignipes, D.* gr. *cinerella* and *D.* gr. *zernyi.*

[‡] Incl. *Boreoheptagyia* and *Pseudokiefferiella*.

[§] Incl. *Epeorus alpicola, Rhithrogena alpestris, Rh.* cf. *gratianopolitana*.

[¶] Incl. *Perlodes intricatus, Dictyogenus* sp.

[**] Incl. *Nemoura mortoni, Protonemura* sp.

[††] Incl. *Allogamus uncatus, Drusus discolor, Acrophylax zerberus, Cryptothrix nebulicola, Pseudopsilopteryx zimmeri.*

[‡‡] Incl. *Rhyacophila intermedia, Rh. torrentium*.

[§§] Taxa represented by fewer than six individuals and not included in the multivariate analyses.

[¶¶] The number of taxa has been increased by one because of the presence of *Epeorus alpicola*.

similar to that of the second group of sites. There was no significant difference in June, either between the two groups, or between the upstream and downstream sectors. In August, 15 taxa were not found in the first group of sites and taxonomic richness was very different between the two groups, ranging from 3 to 8 in the first and 14 to 18 in the second. In September, richness ranged from 9 to 14 taxa at the U sites and 19–23 at the D and M sites.

### Faunal heterogeneity at the microhabitat level

The within-'site-season' inertia measured from CA (209 kick × 25 taxa) and taken as an overall index of

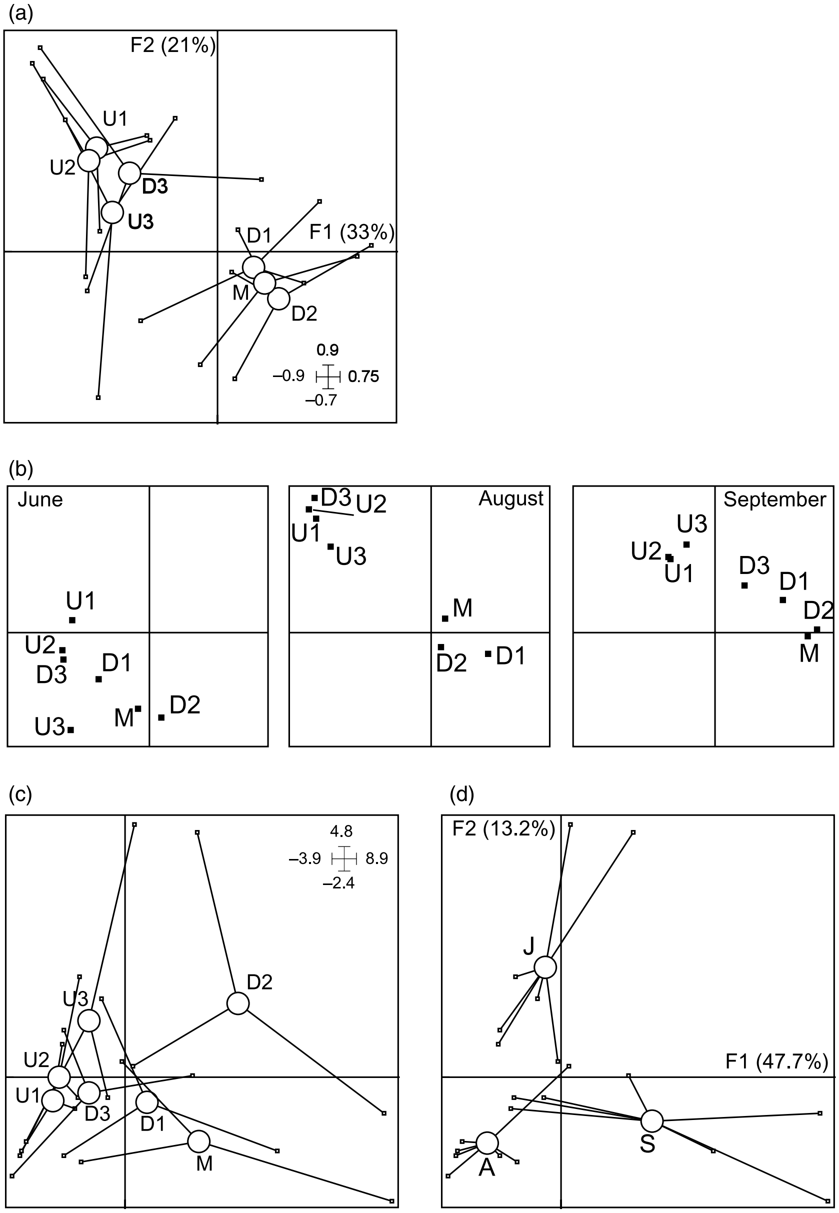

**Fig. 7** Multivariate ordination of the 21 sites – seasons according to their faunal composition (25 taxa). (a) and (b) ordination by correspondence analysis (CA)–(a) samples are grouped by sites; (b) each plot represents the samples for one season. (c) and (d) ordination by principal component analysis (PCA) – (c) samples are grouped by sites; (d) samples are grouped by seasons.

faunal heterogeneity was significantly lower at the upstream sites (one-sided Wilcoxon test: $P = 0.005$) (Fig. 6c).

## Discussion

### *Environmental and faunal influence of the tributary*

The Rhône sites upstream of the confluence were characterised by well-defined environmental conditions. The kryal signature of the upper sector of the Rhône was seen in water temperatures below 4 °C, conductivity around 10 $\mu$S cm$^{-1}$ and a discharge peak during summer. The fauna, characterised by low taxonomic richness, also exhibited seasonal changes. The taxonomic composition of the three upstream sites was homogeneous. The downstream sites differed from the upstream ones both in their environmental conditions and faunal composition. However, according to the multivariate ordinations, the macrobenthic fauna and the environmental conditions did not describe differences between the sites in the same way. In the environmental data set, the sites were grouped according to their location (U/D/M), whereas

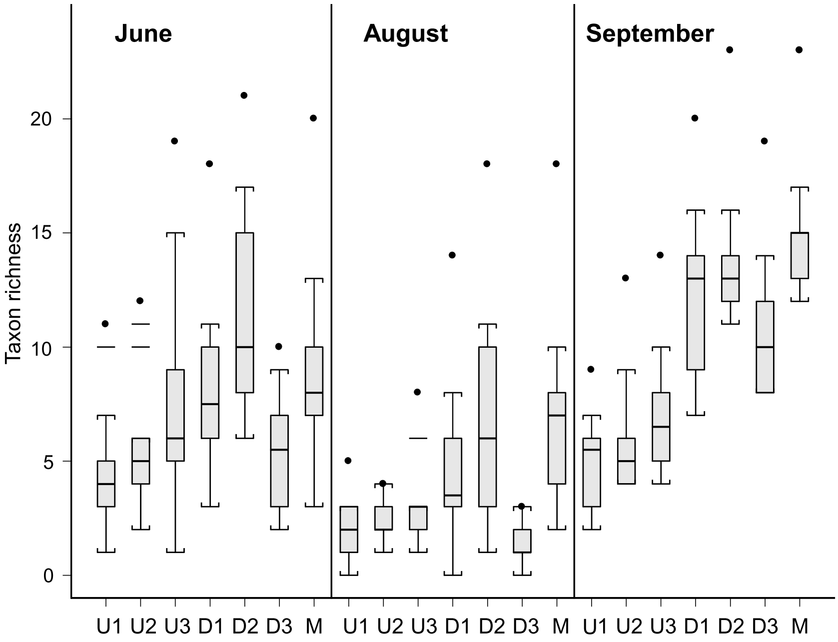

**Fig. 8** Box-plots of the number of taxa per kick sample and total number of taxa (black dots) at each site. The vertical boxes represent the interquartile range (Q25–Q75) around the site median (horizontal thick line). Upper and lower whiskers are drawn to the nearest value not beyond Q75 + 1.5 (Q75 − Q25) and Q25 − 1.5 (Q75 − Q25), respectively.

the fauna provided a different grouping of the sites (M + D1 + D2 and U + D3). It is clear that entry of the Mutt led to a richer and more diverse fauna (similar to that of the Mutt) at the Rhône left bank downstream sites. This occurred despite the fact that the environmental conditions were presumed to be harsher for the biota in the Rhône than in the Mutt itself. This indicates that the tributary fauna was not as sensitive as expected, to the environmental conditions.

Examination of the seasonal patterns identified further discrepancies between fauna and environmental conditions. During August, there was a clear difference between environmental and faunal patterns. The similarity of the fauna in the Mutt and the two left bank downstream sites contrasted with the differing environmental conditions predominating at all downstream sites compared with those in the Mutt. The very high discharge of the Rhône compared with the Mutt during August, and its much lower and stable water temperature (low daily range), may prevent Mutt taxa colonising the right side channel (D3), on the far side of the Rhône River. During August, the Mutt had much higher daily mean of water temperature and a daily temperature range about four to six times greater than the upstream Rhône sites. Water temperature and discharge could thus play a major role in determining the spatial distribution of some invertebrate taxa during August. In September, at low discharge and lower and more homogeneous water temperatures, the presence of a homogeneous (in terms of composition) richer and more abundant fauna in the Mutt and at all downstream sites coincided with more homogeneous environmental conditions. Low discharge in the Mutt as well as the Rhône, and smaller differences in daily ranges of water temperature, could then enable nearly all Mutt taxa to colonise downstream channels of the Rhône.

Comparison of the upstream–downstream variability of environmental conditions demonstrated a downstream diversification of substrate and amounts of organic matter, together with a reduction in downstream variability of water depth, which may be related to a decrease in mean slope below the confluence and an ensuing increase in channel stability. Faunal heterogeneity increased downstream of the confluence with the Mutt. One reason could be that the tributary introduced greater habitat heterogeneity through increased organic matter inputs and sediment supply, possibly key parameters for faunal diversification. Input of sediments from the Mutt was seen in the nature and composition of the sediment in the braided Rhône floodplain delta. Important modifications to the Rhône–Mutt confluence morphology have been observed after major Mutt floods (C.M. Schubiger-Bossard, personal communication). Confluence of the two glacier-fed streams induces geomorphological processes, which produce modifications to the channel pattern and transform the single-thread upper Rhône into a network of channels that contribute to downstream habitat diversification.

### *Inputs to the conceptual model of benthic community succession in glacier-fed rivers*

The importance of tributaries as potential modifiers of the longitudinal continuum of both environmental conditions and benthic communities in glacial streams has been emphasised by Milner & Petts (1994) and Milner *et al.* (2001), but studies focusing on such disrupting factors remain rare. Published studies on the modifications induced by a tributary on a glacial stream provide some information concerning the response of the fauna downstream of a confluence, but information on the environmental modifications at the confluence is scarce. In the few studies considering a glacial or colder tributary flowing into a larger glacial stream, there was a simplification of the fauna, or a delay in the establishment of the downstream sequence of the fauna in the main stream (Kawecka, Kownacki & Kownacka, 1978; Petts & Bickerton, 1994; Brittain *et al.*, 2001). In other studies, tributaries have been described as enhancing downstream development of the fauna in the glacial stream, according to Milner & Petts (1994), when the tributary was spring-fed (Kownacki, 1991), had mixed water source containing a high groundwater contribution (Snook & Milner, 2001), or was non-glacial (Brittain *et al.*, 2001). The opposite results, indicating a weak influence on glacial streams from non-glacial tributaries with a diversified fauna, have been reported from a study in the Swiss Mutt basin (Ilg *et al.*, 2001) and in a drift study in Norway (Saltveit, Haug & Brittain, 2001). In the latter case, it was suggested that most benthic taxa of the non-glacial tributary were unable to establish viable populations in the main glacial channel. In fact, in that study, no fauna was recorded in main-channel benthic samples in July, when conditions were harshest, but a few taxa drifted from the tributary into the main channel. Although Saltveit *et al.* (2001) considered the non-glacial tributary of little importance for colonisation of the glacial stream, it could be seen as a potential source of colonists through drift or oviposition if environmental conditions ameliorate (increase in channel stability and temperature) in the main channel (Milner *et al.*, 2001).

Another way in which a tributary can modify the conceptual model for glacier-fed rivers (Milner & Petts, 1994; Milner *et al.*, 2001) was revealed by the present study of the Rhône–Mutt confluence. Thus, the glacier-fed tributary, because of its greater distance from its source, was warmer, more stable and had fewer glacial characteristics than the main glacial river. The tributary did not modify environmental conditions substantially in the Rhône, but enabled a large range of benthic invertebrate taxa to colonise the main glacial stream. A rich benthic fauna was found at the downstream sites during all sampling seasons, particularly at the two left bank sites, even during high flow conditions in August. In fact, taxa that were not expected below 8 °C, or only in small numbers (Milner *et al.*, 2001), were present at the downstream sites although maximum water temperature did not exceed 6 °C. These were *Rhithrogena* spp., *Ecdyonurus picteti* Meyer-Dür and *Epeorus alpicola* Eaton (Heptageniidae), Nemouridae, *Leuctra* spp., *Rhyacophila* spp. and Chironominae. The stonefly *Perlodes intricatus* (Pictet) was found at the left bank downstream sites in all sampling seasons, but was absent from the Mutt (this study; Ilg *et al.*, 2001; Lods-Crozet *et al.*, 2001). This demonstrates that a richer and more diverse benthic fauna is able to establish itself downstream of the confluence, and that individual species can complete their life cycles in the Rhône. At the upstream sites of the Rhône some faunal elements atypical of glacial rivers may develop at least during low flow periods when the environmental conditions are less harsh. In June and September, taxonomic groups that occur strictly above 4 °C during the period of ice melt in European glacier-fed rivers (Milner *et al.*, 2001) were present in the upper part of the Rhône [*Dictyogenus* spp. (Perlodidae), Limoniidae, Limnephilidae, Chironominae, *Rhithrogena* spp. and *Epeorus alpicola* (Heptageniidae), Rhyacophilidae]. Other groups like Simuliidae, Nemouridae and Leuctridae were also observed at the upstream sites, although they are rarely reported to be present below 4 °C (Milner *et al.*, 2001). The presence of these taxa at the upstream sites during one part of the year argues for the ability of these organisms to colonise the upper part of the Rhône when conditions ameliorate, although they are not able to accomplish the whole of their life cycles there. Two taxa atypical of glacial rivers, *Rhithrogena loyolaea* Navàs (Heptageniidae) and *Protonemura* sp. (Nemouridae), were even found upstream of the

Rhône–Mutt confluence in August during the ice-melt period. The presence of these taxa at the upstream sites in August indicates that certain cold adapted organisms with good dispersal ability are able to colonise the kryal upstream reach of the Rhône. However, they may not successfully complete their life cycles there. In fact, the enrichment and diversification of the fauna at the Rhône sites downstream of the confluence clearly has a positive effect on the fauna of the upstream Rhône sites by enabling colonisation by certain taxa, for example by female upstream flight (Thomas, 1975; Müller, 1982; Winterbourn & Crowe, 2001).

The overall characteristics of the confluence system studied, are synthesised in Fig. 9. Although the main glacial Rhône River dominates the hydrology and certain environmental conditions (discharge, temperature, conductivity), the Mutt tributary is the structuring element of the system with regard to the fauna. In this sense, the Mutt may be considered to be the 'main channel' and the Rhône a 'disruptor' having a slightly disruptive effect on the fauna at the confluence, mainly by modifying downstream habitats both spatially and temporally. It should also be emphasised that the Mutt tributary is important as a biodiversity pool for colonisation of the upper Rhône and for the diversification of populations and their life cycle strategies.

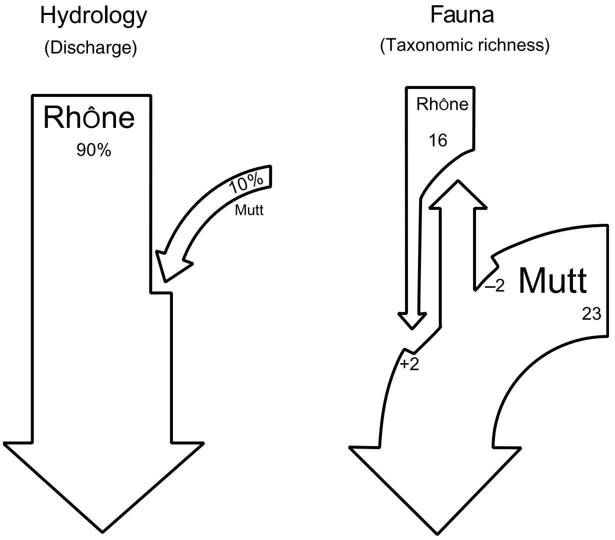

**Fig. 9** Schematic comparison of the relative importance of the Rhône and the Mutt rivers at the confluence with regard to hydrology and taxonomic richness. The width of the arrows is proportional to the discharge in percentage and the number of species, respectively.

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