Macrobenthic invertebrate richness and composition along a latitudinal gradient of European glacier-fed streams

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SUMMARY

1. The influence of 11 environmental variables on benthic macroinvertebrate communities was examined in seven glacier-fed European streams ranging from Svalbard in the north to the Pyrenees in the south. Between 4 and 11 near-pristine reaches were studied on each stream in 1996–97.

2. Taxonomic richness, measured at the family or subfamily (for Chironomidae) levels for insects and higher levels for non-insects, increased with latitude from Svalbard (3 taxa) to the Pyrenees (29 taxa).

3. A Generalized Additive Model (GAM) incorporating channel stability [Pfankuch Index (PFAN)], tractive force, Froude number (FROU), water conductivity (COND), suspended solids (SUSP) concentration, and maximum temperature explained 79% of the total deviance of the taxonomic richness per reach. Water temperature and the PFAN of stability made the highest contribution to this deviance. In the model, richness response to temperature was positive linear, whereas the response to the PFAN was bell-shaped with an optimum at an intermediate level of stability.

4. Generalized Additive Models calculated for the 16 most frequent taxa explained between 25 (Tipulidae) and 79% (Heptageniidae) of the deviance. In 10 models, more than 50% of the deviance was explained and 11 models had cross-validation correlation ratios above 0.5. Maximum temperature, the PFAN, SUSP and tractive force (TRAC) were the most frequently incorporated explanatory variables. Season and substrate characteristics were very rarely incorporated.

5. Our results highlight the strong deterministic nature of zoobenthic communities in glacier-fed streams and the prominent role of water temperature and substrate stability in determining longitudinal patterns of macroinvertebrate community structure. The GAMs are proposed as a tool for predicting changes of zoobenthic communities in glacier-fed streams under climate or hydrological change scenarios.
Introduction

Current climate change scenarios indicate proportionally more detectable impacts at both high altitude and latitudes (Roots, 1989; Beniston, Diaz & Bradley, 1997; Beniston, 2000). The precise distribution of climate change cannot be established, especially for complex mountain regions, but in areas where ‘coupled transitions in vegetation and precipitation patterns occur, geomorphological systems may be near thresholds of change and ecological systems may be more vulnerable’ (Poff, 1992). Among the potentially sensitive ecological systems, Grimm (1993) proposed streams as models to examine the consequences of climate changes. Indeed, running water systems and their biota can be regarded as catchment-scale integrative monitors for a set of hydrological, thermal and biotic variables that might be modified by climate change. It follows that arctic and alpine running waters can be regarded as research foci in such a context, and their communities considered to be as much under threat as terrestrial alpine communities (New, 1995).

Kryal streams and rivers dominated by glacial flow provide comparatively the highest amount of published information compared with other types of alpine and arctic running waters (Ward, 1994). Kryal zoobenthic communities appear to be largely controlled by thermal and substrate stability variables. Following the conceptual model by Milner & Petts (1994), it seemed possible to model the longitudinal distribution of macrofauna in glacial streams on the basis of environmental variables. However, unlike lowland streams in which climate change is thought to lead to an increase in water temperature (Stefan & Sinokrot, 1993; Hogg et al., 1995; Sinokrot et al., 1995), the anticipated glacier ablation would result in a decrease in stream water temperature and therefore a downstream expansion of the kryal influence and associated fauna (McGregor et al., 1995). There might be considerable variation however, depending on glacier size and geographical location, and kryal streams fed by small glacial areas might even undergo a reduction in their kryal fauna.

The recent availability of powerful statistical techniques has led to the current expansion of predictive habitat distribution models (Guisan & Zimmermann, 2000). Generalized Additive Models (GAMs) are a non-parametric extension of multiple regressions and Generalized Linear Models (GLM) (Hastie & Tibshirani, 1990). Generalized Additive Models are flexible exploratory and modelling tools as they allow for linear and non-linear response shapes, for both continuous and factor variables, and for a combination of those within a single model. They are less restrictive than classical linear regressions or GLMs because they are more data than model driven. Yee & Mitchell (1991) provided a comprehensive introduction to GAM modelling in ecology. Since then, GAMs became more frequently used to model species response to environmental variables, especially in vegetation sciences (e.g. Leathwick, 1995; Heegard, 1997; Bio, Alkemade & Barendregt, 1998; Lehmann, 1998; Austin, 1999; but see Brosse & Lek, 2000 for fish microhabitat modelling or Fewster et al., 2000 for birds). Yee & Mitchell (1991) concluded that GAMs are appropriate for modelling potential changes in species distributions resulting from global warming.

The goal of this study was to develop predictive models for macroinvertebrate taxonomic richness, and the abundance of major macroinvertebrate taxa along longitudinal/altitudinal gradients in glacial rivers. Development of these models also represents an attempt to test the validity of and add a quantitative component to the conceptual model proposed by Milner & Petts (1994). Generalized Additive Models were applied in this study because their data-driven smoothing regression technique has been shown to provide improvements over classical regression models, especially because of the avoidance of the a priori assumption of fixed response shapes (Bio et al., 1998). The data used for model development originated from seven glacial streams covering a wide European latitudinal gradient from Svalbard to the Pyrenees (Brittain & Milner, 2001). They were studied under a common protocol within the ‘Arctic and Alpine Stream Ecosystem Research’ project (AASER) (Brittain et al., 2000; Brittain & Milner, 2001).

Methods

The individual studies carried out under the AASER project are detailed in Brittain et al. (2001), Gislason et al. (2001), Lods-Crozet et al. (2001), Maiolini & Lencioni (2001), and Snook & Milner (2001).
Reaches and sampling regime

The reaches were located in seven glacier-melt dominated streams (Brittain & Milner, 2001). The glacial streams formed a latitudinal and altitudinal gradient across Europe from the Pyrenees in the south to Svalbard in the north (Table 1). A common protocol was used for determining the major geomorphological, physical, chemical and biological components of these streams.

Four to eight 15 m long reaches were defined in each stream to represent the different sectors identified on the basis of valley and channel geomorphology. In each stream, the first reach was as close to the glacial snout as possible. The second reach was typically within 1000 m of the glacier snout and upstream of any major tributary input. The downstream limit of the study sector was where a fully developed invertebrate community occurred, i.e. where Chironomidae were at least associated with Ephemeroptera (Baetidae and other families), Plecoptera (Nemouridae, Chloroperlidae and other families), and Trichoptera. This downstream limit was derived from preliminary surveys of the streams. It was applied within zoogeographical constraints to account for the fact that certain taxa are absent from northern and arctic catchments.

At each reach, except Bayelva on Svalbard, field surveys were carried out at three time periods during both 1996 and 1997: immediately post spring snowmelt (June), in mid-summer during the ice melt (August) and at low water level (September). These time periods will be referred to as ‘seasons’. The results obtained at a given reach and a given sampling season served as units in the analyses. These units will be referred to as ‘reach-date’. The snowpack precluded some samplings in upstream reaches in June. As the ice free season on Svalbard is short and because of logistic constraints, Bayelva was sampled only during early July and late August 1997.

Geomorphological and environmental variables

Geomorphological description (width of valley floor, of all active channels, slope) was carried out at the onset of the project. The stream bottom component of the Pfankuch’s index (PFAN) (Pfankuch, 1975) was used to assess channel stability by scoring five variables (rock angularity, bed-surface brightness,
particle packing, percentage stable materials, scouring, presence and type of aquatic vegetation). Scores were summed to provide an overall index of channel stability with a potential range of 15–70 (high scores representing unstable channels at the reach scale).

During a 5-day sampling period at each field survey, water temperature, level, discharge, conductivity and suspended solids (SUSP) were monitored at minimum and maximum flows on the upstream and downstream reach. At each of four transects installed at all reaches, the wetted channel width to a maximum depth of 0.5 m and depth/velocity profiles were determined. At the reach scale, average current velocity and average depth were combined to calculate an average Froude number (FROU, dimensionless), according to Statzner et al. (1988):

$$FROU = \frac{U}{(g \cdot D)^{0.5}}$$

with $U$: mean current velocity, $g$: gravity acceleration, $D$: mean water depth (from the depth profiles).

The reach slope and water depth were combined to calculate tractive force (TRAC, dyn cm$^{-1}$) (shear stress) according to Statzner et al. (1988):

$$TRAC = g \cdot S \cdot D \cdot \rho$$

with $g$: gravity acceleration, $S$: reach slope, $D$: mean water depth, $\rho$: water density.

Digital temperature loggers placed in streams throughout the study period monitored water temperature continuously at most reaches. Visual or manual assessments at each point of the depth/velocity profiles were used to record the bed-sediment composition, which was expressed for the reach as the percentage cover of four categories (boulders >20 cm, coarse gravel 5–20 cm, fine gravels 0.2–5 cm, and fine particles <0.2 cm). An index of substrate diversity (SUDI) was calculated at the reach scale as Simpson’s diversity index:

$$SUDI = \frac{1}{\sum p_i^2}$$

with $p_i$: proportion of the $i$th substrate category.

Three stones were collected at random in each reach at each sampling date, and benthic algae were scraped off the upper surface (area $3 \times 3$ cm) and washed onto a GF/C filter. Chlorophyll a (CHLO) was then determined in the laboratory according to standard methods (APHA, 1992).

Eleven environmental variables were selected among the available field measurements for use in the analyses. This selection was primarily based on the necessity to reduce redundancy among the set of explanatory variables within the regression procedures. The correlation coefficients for the 10 continuous variables selected are provided in Table 2. Three variables were associated to hydraulic energy and channel stability (PFAN, TRAC, FROU), three to substrate description [percentage cover by boulders (BOUL), percentage cover by fine sediment (FINE), and SUDII]. Conductivity (COND) served as an integrated description of the longitudinal gradient in each stream. The temperature variable retained (TEMP) was the maximum temperature recorded for one given reach over the entire study period. Benthic CHLO was used as an indicator of available food source for primary consumers. Suspended solids

<table>
<thead>
<tr>
<th>Variable</th>
<th>Code</th>
<th>PFAN</th>
<th>TRAC</th>
<th>FROU</th>
<th>BOUL</th>
<th>FINE</th>
<th>COND</th>
<th>CHLO</th>
<th>SUSP</th>
<th>SUDI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pfankuch index</td>
<td>PFAN</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Tractive force</td>
<td>TRAC</td>
<td>-0.41**</td>
<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
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<td></td>
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<tr>
<td>Froude number</td>
<td>FROU</td>
<td>-0.01</td>
<td>0.26**</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>% Boulders</td>
<td>BOUL</td>
<td>-0.58**</td>
<td>0.50**</td>
<td>0.12</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>% Fine sediment</td>
<td>FINE</td>
<td>0.15*</td>
<td>-0.32**</td>
<td>-0.15</td>
<td>-0.32**</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Conductivity</td>
<td>COND</td>
<td>-0.06</td>
<td>0.01</td>
<td>-0.17*</td>
<td>0.02</td>
<td>-0.12</td>
<td></td>
<td></td>
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<td></td>
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<tr>
<td>Chlorophyll a</td>
<td>CHLO</td>
<td>0.17*</td>
<td>0.17*</td>
<td>0.10</td>
<td>-0.10</td>
<td>-0.23**</td>
<td>-0.33**</td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Suspended solids</td>
<td>SUSP</td>
<td>0.14</td>
<td>-0.13</td>
<td>&lt;0.01</td>
<td>-0.07</td>
<td>0.16*</td>
<td>0.17*</td>
<td>-0.36**</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Substrate diversity</td>
<td>SUDI</td>
<td>0.14</td>
<td>0.02</td>
<td>-0.03</td>
<td>-0.31**</td>
<td>0.28**</td>
<td>0.01</td>
<td>0.02</td>
<td>-0.02</td>
<td></td>
</tr>
<tr>
<td>Temperature</td>
<td>TEMP</td>
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<td>0.10</td>
<td>-0.08</td>
<td>0.26**</td>
<td>-0.03</td>
<td>0.08</td>
<td>-0.17*</td>
<td>-0.16*</td>
<td>0.12</td>
</tr>
</tbody>
</table>

**$r$ significantly different from 0 at $P < 0.01$.  
* $r$ significantly different from 0 at $P < 0.05$.  
No asterisk: $r$ not significantly different from 0 ($P > 0.05$).
(SUSP) was the average concentration measured for each reach-date. Season (SEAS) was also included as a discrete explanatory variable. After examination of the distribution of the continuous variables, TRAC, COND, CHLO and SUSP were log-transformed to provide a more homogeneous spread for the calculation of the response curves in the regression models.

**Invertebrate sampling**

Within each sampling reach, 5–10 replicate kick samples were collected for invertebrates using a standard pond net (30 × 30 cm) with a mesh size of 250 μm, disturbing the substrate for a period of 30 s, within an area of 30 × 30 cm. Densities in number of individuals per m² were averaged among the samples. In the case of Western Jökulsá (WJO), 10 stones were collected at each reach and macroinvertebrates removed. The surface area of each stone was then traced on a paper and used to calculate invertebrate densities (Gislason, Ólafsson & Adalsteinsson, 1998). All invertebrate densities were $\log_{10}(x + 1)$ transformed prior to statistical analyses.

Invertebrate identification was to the lowest level possible. However, numerous young instars and taxa difficult to identify (e.g. Chironomidae, Limnephilidae) made it difficult to carry out homogeneous analyses at species or even genus level across all reaches and dates. Hence, the subfamily or family level for insects, and higher levels for non-insects, were used throughout for constructing models.

**Statistical analyses**

Regressions of reach taxonomic richness and of individual taxa density against environmental variables were carried out using GAMs (Hastie & Tibshirani, 1990). Generalized Additive Models express the relationship between a response variable ($Y$) and dependent variables (or predictors) ($X_i$) by:

$$ Y = \text{link linear predictor (LP)} $$

and:

$$ LP = \alpha + \Sigma f_i(X_i) + \varepsilon $$

Therefore, LP is the linear predictor. The ‘link’ function is a transformation used to accommodate different response distributions (e.g. log for a Poisson distribution, logit for a binomial one). $\alpha$ is a constant, and $\varepsilon$ the error term. The $f_i$s are smooth functions, estimated individually for each predictor by a scatterplot smoother. The models are additive in the predictors effects (Hastie & Tibshirani, 1990).

Generalized Additive Model calculations were carried out in the S-PLUS software (Anonymous, 1998), using a set of functions developed to perform generalized regression analyses and spatial prediction (GRASP; Lehmann, Leathwick & Overton, 1999). A quasi-Poisson family was used for the response variables (taxonomic richness or individual taxa density) to accommodate under- or over-dispersed Poisson data by estimating their dispersion parameter instead of using the default value of 1 (Leathwick & Austin, 2001). A cubic smoothing spline method was chosen to smooth the continuous environmental variables, using either one or three degrees of freedom (d.f.). Stepwise model selection was used to select variables to be retained in the final model. Starting from a model incorporating the more detailed smoothing (d.f. = 3) for all the dependent variables given as input, a stepwise selection procedure drops variables or modifies smoothing parameters for all variables successively, dropping at each loop the variable responsible for the lowest deviance reduction. The procedure stops when no further change can be found that provides a significant deviance reduction (Hastie & Tibshirani, 1990; Chambers & Hastie, 1993).

Diagnostic procedures for the GAMs included: (1) $F$-test for non-parametric effects to test the significance of each selected variable (Hastie & Tibshirani, 1990), (2) calculation of the percentage of deviance explained by the models (an equivalent of the coefficient of determination in classical regression models), (3) contributions of each explanatory variable expressed as a deviance reduction associated to dropping the variable from the model, (4) correlation ratio ($r_1$) between observed and predictive values, (5) correlation ratio ($r_2$) between observed and predictive values derived from cross-validation. In this last procedure, nine of ten of the data were used to recalculate a selected model, which was then used to predict the response on the remaining one of ten of the data. The procedure was repeated 10 times, and cross-predicted responses were compared with observed data to check the stability of the model.
Results

Taxonomic richness

A set of 169 reach-dates (reaches sampled on different dates) was obtained from the seven streams, providing a total of 40 macroinvertebrate taxa collected from 1049 individual kick or stone samples. Average densities for each taxon are given in Appendices 1 and 2. Altitudinal and latitudinal gradients of taxonomic richness are summarized in Fig. 1. At only three reach-dates were no organisms found (Svalbard and Iceland, at the uppermost reaches WJO01 and BAY01). The taxonomically richest reach was TAI35, the downstream reach in the Pyrenees, with 28 taxa. Three distinct ‘regions’ can be distinguished according to the number of taxa recorded per site: the Alps and the Pyrenees (TAI – 29 taxa, CON – 28 taxa, MUT – 23 taxa), Scandinavia (BRI, LEI and WJO, each with 17 taxa), and Svalbard (BAY – 3 taxa).

Two outlying Icelandic reaches influenced by geothermal activity (WJO02 and WJO03) were omitted from subsequent richness models because of the highest temperature maxima recorded in the entire data set (14 and 18 °C, respectively) were associated with a very low taxonomic richness (5 taxa).

Plots of taxonomic richness against the two major variables incorporated in the Milner & Petts (1994) model, maximum temperature and PFAN of channel stability, revealed a clear trend of increasing richness with increasing temperature, and a more complex response to channel stability (Fig. 2). Richness peaked between 30 and 35 PFAN units. Above 35 (i.e. in the more unstable reaches examined in the present study) a marked reduction in taxonomic richness was observed with no values above 15 taxa. The variability of the taxonomic richness per reach was also higher below 35 PFAN units.

GAMs for taxonomic richness

Generalized Additive Model for taxonomic richness started with 11 variables, including season as categorical variable (Table 3). Six variables (PFAN, TRAC, FROU number, COND, suspended sediment and maximum temperature) were retained in the analysis.
regression model ($F$-test, $P \leq 0.01$), explaining 79% of the total deviance of taxonomic richness. The validation diagnostics were high: $r_1 = 0.90$ for simple validation and $r_2 = 0.87$ for cross-validation. Maximum water temperature was the most important variable explaining variations in taxonomic richness (five times higher than the PFAN). SUSP, COND, FROU and TRAC were comparable but made low contributions. The shape of the response curves varied for the variables retained in the model (Fig. 3). Tractive force, COND and temperature were incorporated as linear functions (d.f. = 1 for the spline smoother), while the PFAN, FROU and SUSP etc. were more complex (d.f. = 3 for the spline smoother). Tractive force, temperature and COND had a general positive influence on taxonomic richness, suspended solids a negative one. Pfankuch index was incorporated with a sigmoid response and an optimum between 30 and 40 units. For PFAN, FROU and SUSP, the confidence bands (Fig. 3) evidenced a lack of accuracy in some parts of the gradients, because of a lower number of data.

GAMs for individual taxa

Generalised Additive Model regressions were only calculated for the 16 most frequent taxa. These were the 16 taxa occurring in more than 24% of the 169 reach-dates (four plecopteran, two ephemeropteran, two trichopteran, seven dipteran families and subfamilies, and oligochaetes).

Table 4 summarizes the environmental variables kept in the final regression models and their relative contributions. These variables were selected for incorporation in the models at the $P = 0.01$ level. Ten models explained more than half of the total deviance of their respective taxon density, six of them explained more than 60% deviance. Cross-validation and simple validation correlation ratios were on average high, with five models above $r_2 = 0.7$ for cross-validation. Models for the families of Plecoptera, Ephemeroptera and Trichoptera gave on average a higher explained deviance and stability than those for the families of Diptera and for the oligochaetes. The model that explained the highest deviance (79.1%)}
and had the highest cross-validation ($r^2 = 0.85$) was obtained for Heptageniidae. Models explaining a deviance <30% and with cross-validation $r^2 < 0.5$ were obtained for Diptera (Diamesiinae, Simuliidae and Tipulidae), and oligochaetes.

Maximum temperature and concentrations of suspended solids were incorporated in 14 and 15 models, respectively, of a total of 16. Temperature made the greatest contribution to the model in 11 cases, whereas suspended solids was the most important variable only once. Other frequently incorporated variables were PFAN and TRAC, both contributing significantly to 10 models. Variables related to substrate characteristics (BOUL, FINE, and SUDI) and SEAS, were very rarely retained. The response curves for the variables retained in the 16 models and their confidence bands (twice the standard error) are presented in Fig. 4. Confidence bands were usually wider at both ends of all gradients where the density of observations was lower. Regression models for the non-Diptera insects all showed similar trends, all incorporating a linear, or quasi-linear positive influence of TRAC (or FROU, for the Limnephilidae) and more complex responses for PFAN of stability. The contribution of temperature for the same groups was also positively linear or quasi-linear (Leuctridae, Baetidae, Heptageniidae), or showed an inflexion around 10 °C (Taeniopterygidae, Limnephilidae), or between 10 and 15 °C (Nemouridae, Perlodidae, Rhyacophilidae). Models for Chironomidae proved very distinct from the non-Diptera insects. The model for Orthocladiinae incorporated a negative linear contribution of TRAC and FROU. The model for Chironominae incorporated a negative linear response to PFAN and a V-shaped response to FROU. The regression model for Diamesiinae was the most distinct; it did not incorporate TRAC, FROU or PFAN, but variables associated to substrate characteristics (BOUL and SUDI) and with an optimum temperature response between 6 and 7 °C.

Relationships between the actual abundance of individual taxa and the environmental variables were back-calculated using the GAM general equation presented in the statistical analyses section above. These calculations were carried out for the four most commonly selected variables in the GAM regressions (maximum temperature, suspended sediments, TRAC and PFAN) (Figs 5–8). Taxa were represented only when the considered variable had been selected in the GAM model. Each curve expresses the taxon’s predicted response to a given environmental variable, in the absence of influence of the other variables selected in the model. Examination of the curves allows a comparison of the modelled sensitivity of the taxa to the range of environmental change.

Response curves for temperature (Fig. 5) varied from positively increasing (e.g. Heptageniidae, Baetidae, Taeniopterygidae) to bell-shaped (e.g. Diamesiinae, Chironominae, Simuliidae). Rapid increases in invertebrate densities were noticeable in the low

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**Fig. 3** Response functions for the reach taxonomic richness on the six environmental variables incorporated in the GAM. The dashed lines are approximate 95% confidence intervals around the smooth function. PFAN: Pfankuch Index of channel stability (dimensionless), TRAC: tractive force (log transformed dyn cm$^{-1}$), FROU: Froude number (dimensionless), COND: water electrical conductivity (log transformed $\mu$S cm$^{-1}$), SUSP: suspended solids (log$_e(x+1)$ transformed mg L$^{-1}$), TEMP: maximum reach temperature (°C). Vertical axes are scaled according to the dimensionless linear predictor.
temperature range in Diamesinae and Orthocladiinae, as was a clear shift in temperature preference among the three chironomid subfamilies. Responses for TRAC (Fig. 6) tended to have a similar positive trend, except for Orthocladiinae, the abundance of which decreased with TRAC. Responses for PFAN (Fig. 7) proved more varied, from increasing (e.g. Taeniopterygidae, Baetidae) to decreasing (Oligochaeta, Chironominae), and bell-shaped curves with an optima at 30–40 index units (Leuctridae, Heptageniidae, Rhyacophilidae, Empididae). Increasing concentrations of suspended solids (Fig. 8) had generally strong negative effects on abundance (Tipulidae, Heptageniidae, Rhyacophilidae, Leuctridae, and Nemouridae). However, some taxa maintained occurrences over the whole range of suspended solids concentrations (Perlodidae, Baetidae, Orthocladiinae, Simuliidae, Empididae), even when the abundance was high relative to the taxon’s average abundance (Diamesiinae, Limnephilidae). The only positive trend was obtained for Limoniidae.

Discussion

The data presented here represent the first published attempt to compare and model taxonomic richness among a set of glacier-fed streams distributed across a wide latitudinal gradient. Comparative studies of faunal assemblages and richness in similar streams located at different latitudes are rare (Jacobsen, Schultz & Encalada, 1997). Although described at a relatively high taxonomic level and based upon a limited set of streams, the observed latitudinal pattern allowed the distinction of geographical regions with taxon richness increasing at lower latitudes. Less than seven taxa were observed in the upstream reaches near the glacial source in all seven streams. Divergence between regions is manifest in the downstream gradient of taxonomic enrichment. There were more than 15 taxa in the Pyrenean and Alpine streams, whereas 10–15 taxa were recorded in the Scandinavian streams and less than five on Svalbard. The relative importance of factors responsible for the increasing taxon richness towards lower latitudes is still a matter of debate (Chown & Gaston, 2000), although biogeographical factors such as isolation and glacialiation certainly play a role (Milner et al., 2001). Our findings are consistent with this general latitudinal trend, and call for a further regionalization of
Fig. 4 Response functions for the log-transformed density of the 16 most frequent taxa on the environmental variables incorporated in their respective GAMs. The dashed lines are approximate 95% confidence intervals around the smooth function. PFAN: Pfankuch Index of channel stability (dimensionless), TRAC: tractive force (log, transformed dyn cm⁻¹), FROU: Froude number (dimensionless), COND: water electrical conductivity (log, transformed μS cm⁻¹), SUSP: suspended solids (log, (x + 1) transformed mg L⁻¹), TEMP: maximum reach temperature (°C), SEAS: ‘season’, BOUL: percentage cover by boulders, FINE: percentage cover by fine sediment (<0.2 cm), CHLO: chlorophyll a concentration (log, (x + 1) transformed mg m⁻²), SUDI: dimensionless index of substrate diversity. Vertical axes are scaled according to the dimensionless linear predictor.
Fig. 4 (Continued).
Fig. 4 (Continued).
models for kryal river communities. Such models should be developed within the context of more refined arctic and alpine ecoregions and their associated taxonomic pools. Lindegaard & Brodersen (1995) described such a regionalization of taxonomic pools in alpine and subalpine streams at the species level for Chironomidae.

Unlike Brosse & Lek (2000) who found limitations and shortcomings in the use of GAMs for modelling roach (Rutilus rutilus L.) microhabitats in lakes, the models produced here, both for total taxonomic richness, and for individual taxa, displayed on average high levels of explanation and stability. Among the 16 GAMs for individual taxa, the average percentage of explained deviance was 53% (range: 25–79%). This compares favourably with the values of 15% (range: 3–72%) and 13% (range: 1–66%) obtained by Bio et al. (1998) for two series of GAMs of the occurrence of 120 wetland plants. Correlation ratios over 0.7 obtained here in the cross-validation procedures confirmed the stability that can be reached for some of the models. As underlined by Peeters & Gardeniers (1998) in the case of logistic regression models, ‘weak models’ (i.e. models accounting for a small proportion of explained deviance) can result either from the model being inadequate (i.e. selected explanatory variables are irrelevant for the given taxon), or from the taxa having a wide ecological tolerance for the environmental factor considered. In the present study, the four weakest models for individual taxa explained between 25 and 30% of the total deviance. These four taxa (Diamesinae, Simuliidae, Tipulidae and Oligochaeta) had the highest level of ubiquity among the taxa sampled, at least over the temperature and PFAN gradients (Milner et al., 2001). For example, Diamesinae (occurring in 95% of the reach-dates) maintained

Fig. 5 Response functions on the maximum reach temperature for the abundance of the 14 taxa for which temperature was incorporated in the GAM. Abundance is expressed as the density of individuals per m² on a log₁₀ scale. Responses are smoothed with loess functions.
densities between 100 and 10 000 individuals m\(^{-2}\) across these two gradients. However, the model for Orthocladiinae (occurring in 86\% of the reach-dates, and also covering almost the complete range of temperature and PFAN) reached more than 50\% of explained deviance, with good validation criteria, notably on account of a strong relative contribution of temperature to their GAM. Indeed, the case of the four ‘weaker’ models may indicate that the taxonomic level considered here is too imprecise to allow accurate

\[ \text{Fig. 6 Response functions on tractive force (log}_e\text{ scale) for the abundance of the 10 taxa for which tractive force was incorporated in the GAM. Abundance is expressed as the density of individuals per m}^2\text{ on a log}_{10}\text{ scale. Responses are smoothed with loess functions.} \]

\[ \text{Fig. 7 Response functions on Pfankuch’s channel stability index (dimensionless) for the abundance of the 10 taxa for which the index was incorporated in the GAM. Abundance is expressed as the density of individuals per m}^2\text{ on a log}_{10}\text{ scale. Responses are smoothed with loess functions.} \]
modelling. For example, Diamesinae as a subfamily may not respond to the temperature or longitudinal gradient, although individual species do (Kownacka & Kownacki, 1975; Rossaro, 1991). This is certainly also the case for oligochaetes, although less documented at high altitudes (Ward, 1994).

Examination of the response curves for taxonomic richness and individual taxa conform with existing knowledge about the ecology of these organisms. A clear case is the shift of the optimum towards higher temperature in the Chironomidae, where the sequence Diamesinae/Orthocladiinae/Chironominae is consistent with results obtained by Rossaro (1991) or Lindegaard & Brodersen (1995) and others. Channel stability (as measured by the PFAN) led to the most diversified response shapes in the present study, illustrating the advantage of smoothed curves over traditional linear models in their capability to account for varied responses (e.g. the plateau-shaped responses of Perlodidae). Bell-shaped responses to channel stability of Leuctridae, Rhyacophilidae, Heptageniidae, and total taxonomic richness, appear to support the intermediate disturbance hypothesis (Ward & Stanford, 1983). In these cases, highest densities or richness were observed around the middle of the potential range of the stability index. However, data about detailed relationships between environmental variables and the density of taxa are mostly not available for glacier-fed streams. For example, suspended sediment was incorporated in the taxonomic richness GAM and in all taxa GAMs but one. The response curves for this variable were strongly negative in 11 taxa, confirming the detrimental effects of high levels of suspended solids on large parts of the aquatic fauna, although empirical data documenting the effects are still limited (Ward, 1992).

Fig. 8 Response functions on suspended solid concentration (log e scale) for the abundance of the 15 taxa for which suspended solid concentration was incorporated in the GAM. Abundance is expressed as the density of individuals per m² on a log₁₀ scale. Responses are smoothed with loess functions.
In general, the models obtained here support the idea that the fauna of glacial streams is strongly controlled by physical constraints (Milner & Petts, 1994; Milner et al., 2001). This strong physical control probably helps to explain the less successful modelling attempts with GAMs where habitat complexity and biotic interactions play more prominent roles (Brosse & Lek, 2000). However, Saether (1968) and Flory & Milner (1999, 2000) suggested that under certain conditions interspecific competition may influence Chironomidae succession and community structure even in glacial streams.

Season was very rarely incorporated in the models as an explanatory variable. However, although year-round faunal monitoring of alpine streams are seldom (Lavandier, 1979; Lavandier & Décamps, 1984), evidence suggests that sampling outside the late spring – late summer period brings a different picture of glacial stream biota (Füreder et al., 2001; Schütz et al., 2001).

Results of the modelling approach provide a means for evaluating the conceptual framework proposed by the Milner & Petts (1994). First, the significance of the predictive models implemented here confirms the existence of significant longitudinal trends in macroinvertebrate community structure at the family/subfamily level. Secondly, the high frequency of incorporation in the GAMs, and high contribution to deviance reduction, of maximum temperature, PFAN and TRAC, strongly confirm the primary importance of temperature and channel stability in shaping richness and composition of macrobenthic assemblages in glacier-fed streams. Suspended sediments were not initially considered as an important determinant in Milner & Petts (1994) framework. Incorporation of this factor in all but one of the models generated here and the differences in sensitivity exhibited by different taxa point to its value as a predictive variable. One other notable departure from Milner & Petts’s (1994) model in terms of longitudinal distribution is the observation of taxa, such as Oligochaetae, Orthocladiinae, Tipulidae, Simuliidae, and Taeniopterygidae, at lower temperatures than predicted, that is in reaches where the maximum temperature recorded did not exceed 2 °C.

In the early 1990s, it was recognized that predictions of the effects of climate change on the ecology of running waters were highly speculative (Oswood, Milner & Irons III, 1992; Poff, 1992; Ward et al., 1992). However, if the downscaling improvement of climatic scenarios advocated by Beniston, Diaz & Bradley (1997) actually leads to more accurate regional anticipations of climatic and glacier trends, then the predictive models elaborated here could serve as a basis for the forecast of changes in the associated glacial stream communities. In turn, these models could be used to forecast and map potential changes in suitable habitats for a given type of kryal community under different scenarios of environmental changes (as addressed by Sinokrot et al. (1995) for fish habitats). Furthermore, the models could serve to define reference conditions for glacial streams affected by other types of impacts (e.g. water abstraction) (Petts & Bickerton, 1994; McGregor et al., 1995). Such developments require the development of local relationships between projected trends in glacier dynamics and the concomitant variations in the variables retained in the models, such as suspended sediment concentrations and water temperature.

To further the development and validation of predictive models for glacial river macroinvertebrate communities, there would be a need to incorporate hydrological variables describing exchanges or relations between surface- and groundwater. Such variables have been shown to influence the stream conditions and temperature (Malard, Tockner & Ward, 1999; Ward et al., 1999). As suggested by Death (1995), it would also be necessary to test the invertebrate response to stability over a narrow range of the other variables, and especially temperature.

Regarding the biotic variables considered for prediction, the species-level models mentioned earlier are currently under elaboration, but the implementation of trait- or attribute-based models, an approach pioneered by Snook & Milner (in press) for glacial streams, might be a way to circumvent limitations associated with the biogeography of species, and to provide more general models for the sensitivity of functional groups of taxa.

The models developed here, concern only kryal rivers. However, groundwater or snow-fed tributaries can contribute greatly to the overall biodiversity of glacial catchments (Ilg et al., 2001; Zah & Uehlinger, 2001), but are predicted to react differently to climate change than kryal streams (McGregor et al., 1995). It is therefore a need to encompass all types of water supply and their associated fauna in predictive models if predictive scenarios are to be developed at the catchment scale.
Acknowledgments
The project, Arctic and Alpine Stream Ecosystem Research (AASER), was financed by the European Commission (project ENV-CT95-0164) and the Swiss Federal Office for Education and Science (project BBW 95.0430). We thank M. Gessner for valuable comments that improved the clarity of the text. Jessica Müller-Castella kindly edited some of the graphics.

References


Kownacka M. & Kownacki A. (1975) Gletscherbach-Zuckmücken der Ötztaler Alpen in Tirol (Diptera:


(Manuscript accepted 5 September 2001)
Appendix 1  Average densities (individuals.m$^{-2}$) for the taxonomic groups in the Pyrenean (TAI) and Alpine (CON, MUT) study reaches. Averages are calculated over all kick samples (5–10) and six sampling dates

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## Appendix 2

Average densities (individuals m\(^{-2}\)) for the taxonomic groups in the Scandinavian study reaches (including Svalbard – BAY). Averages are calculated over all kick or stone samples (5-10) and six sampling dates (except Svalbard with only two dates).

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