

Ephemeropteran and Plecopteran communities in glacial rivers

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Abstract

From a study of glacier-fed catchments along a European latitudinal and climatic gradient, the relationships between the distribution of mayfly (Ephemeroptera) and stonefly (Plecoptera) nymphs and environmental variables were explored. Canonical Correspondence Analysis (CCA) and Generalised Additive Models (GAMs) demonstrated clear responses of mayfly and stonefly generic composition and taxa richness to environmental gradients, notably maximum water temperature and channel stability as these change downstream of glacial sources. GAMs developed for aquatic insects are well suited to detect environmental impacts, including climate change.

Keywords: macroinvertebrates, generalised additive models, canonical correspondence analysis, temperature, channel stability.

Introduction

Milner and Petts (1994) characterised glacier-fed rivers as having maximum water temperatures below 10°C, the peak of the annual hydrograph in summer with marked diurnal fluctuations and turbidity levels exceeding 30 NTU. They proposed that benthic macroinvertebrate communities in glacier-fed rivers displayed longitudinal trends driven by two principal variables, maximum water temperature and channel stability. Near the glacial source where water temperatures are <4°C and channel stability low, chironomids, especially the genus *Diamesa*, were suggested to dominate the community. However, at higher channel stabilities and where maximum water temperatures exceed 4°C, the mayfly family, Baetidae, and the stonefly families, Nemouridae and Chloroperlidae, would be among the taxa added to the community.

In the future, climatic changes will influence the hydrological regime of arctic and alpine rivers in a variety of ways, but the influence on glacier meltwater may be particularly significant (McGregor *et al.*, 1995). Increased glacial runoff may have a significant effect on flow, temperature and sediment transport regimes. Reduced stream temperatures from increased contributions of glacial meltwater and decreased channel stability from changed runoff patterns and altered sediment loads will potentially reduce the diversity of zoobenthic communities in glacier-melt dominated rivers (McGregor *et al.*, 1995). This may cause an increase in the relative abundance of a number of key taxa, which may thus act as a potential key indicator taxa for climate change effects in glacier-fed rivers (Melack *et al.*, 1997).

Until the recent AASER project (Arctic and Alpine Stream Ecosystem Research) (Brittain and Milner, 2001) no comparative studies had been made on glacier-fed catchments on a broader geographical scale using the same approach and methods. This paper analyses data from this project, together with another glacier-fed system, to develop predictive models for ephemeropteran and plecopteran taxonomic richness and composition in glacial rivers.

Material and Methods

The data used for model development originated from glacial catchments covering a wide European latitudinal gradient from Norway via the Alps to the Pyrenees (Brittain and Milner, 2001, Table 1). They were studied under a common protocol within the "Arctic and Alpine

Stream Ecosystem Research” project (AASER) (Brittain *et al.*, 2000; Brittain and Milner, 2001). Additional data were also included from an ongoing investigation of the macroinvertebrate fauna of the River Rhône in the Swiss Valais, upstream of its confluence with the Mutt, one of the glacier-fed rivers in the AASER project (Table 1).

Four to eight 15 m long reaches were defined in each river to represent the different sectors

identified on the basis of valley and channel morphology (Castella *et al.*, 2001). At each reach in the six glacier-melt dominated streams, field surveys were carried out during three time periods: 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.

Table 1 – Location and characteristics of the glacier-fed rivers used in the present analyses (partly after Brittain and Milner, 2001).

River	Taillon	Conca	Mutt	Rhône	Dalelva	Leirungsåi
Code	TAI	CON	MUT	RHO	BRI	LEI
Region	Pyrenees	S. Alps	NW. Alps	NW. Alps	W. Norway	E. Norway
Latitude, Longitude	43°06'N 0°01'W	46°06'N 10°36'E	46°33'N 8°24'E	46°33'N 8°24'E	61°40'N 6°50'E	61°24'N 8°41'E
Altitudinal range of study reaches (m a.s.l.)	1870-2500	1300-2830	1800-2600	1800-1850	10-340	970-1550
Distance of study reaches from glacier (m)	50-1500	350-4600	5-3600	700-800	199-7100	200-24600
Maximum altitude of catchment (m a.s.l.)	2975	3463	3099	3630	1915	2159
Catchment area (km ²)	6.4	4.15	7	30	25.6	401
Glacier area (km ²)	0.224	0.185	0.6	17.4	22	1.24
Glacier status	retreating	retreating	retreating	retreating	advancing	retreating
Precipitation (mm), mean 1996/97	3022	1497	1595	1595	1270	800
Discharge range (m ³ s ⁻¹)	0.29-0.36	0.29-2.05	0.56-1.48	0.8-12.7	0.5-35.2	0.38-6.23
No. of study reaches	4	7	5	3	5	7
Treeline altitude (m a.s.l.)	1600	2000	2000	2000	600	1050

Environmental variables

The stream bottom component of the Pfankuch index (PFAN) (Pfankuch, 1975) was used to assess channel stability (high scores representing unstable channels). During a five-day sampling period at each field survey, water temperature, water level, discharge, conductivity and suspended solids were generally monitored at minimum and maximum flows on the upstream and downstream reach. At each reach, average current velocity and average water depth were combined to calculate an average Froude number (FROU, dimensionless), according to Statzner *et al.* (1988). The reach slope and water depth were combined to calculate tractive force (TRAC, dyn cm⁻¹) (shear stress) according to Statzner *et al.* (1988). 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 boulders (>20cm), coarse gravel (5-20 cm), fine gravels (0.2-5cm), and fine particles (<0.2cm). An index of substrate diversity (SUDI) was calculated at the reach scale (Castella *et al.*, 2001). Benthic primary biomass was estimated in each reach on each sampling date, using Chlorophyll *a* determination (APHA, 1992).

Eleven environmental variables were selected among the available field measurements for use in the analyses, basically to reduce redundancy among the set of explanatory variables by including those least correlated (Castella *et al.*, 2001). Three variables were associated with hydraulic energy and channel stability (TRAC, FROU, PFAN), three to substrate description (percentage cover by boulders – BOUL, percentage cover by fine sediment – FINE, and SUDI). 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 chlorophyll *a* (CHLO) was used as an indicator of available food source for primary consumers. Suspended solids (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 and CHLO were log-transformed and SUSP transformed into a categorical variable to provide a more homogeneous spread for the calculation of the response curves in the regression models.

Invertebrate sampling and taxa included in the analysis

Within each sampling reach, 5 to 10 replicate kick samples were collected for invertebrates using a standard pond net (30 cm x 30 cm) with a mesh size of 250 µm. The substrate was disturbed for a period of 30 seconds, within an area of 30 x 30 cm. Identification of Plecoptera and Ephemeroptera was made at least to genus, apart from the Taeniopterygidae.

Statistical analyses

Three techniques were used to analyse the mayfly/stonefly data and the accompanying environmental variables. Firstly, the faunal data, expressed as presence/absence of the genera (plus Taeniopterygidae) per reach-date were processed by a between-reach Correspondence Analysis to ordinate the 92 non-empty reaches-dates on the basis of their faunal composition. This analysis maximises the differences between reaches (Dolédéc and Chessel, 1987, 1989)

Canonical Correspondence Analysis (CCA) (Ter Braak, 1986) was used to determine relationships between the environmental variables recorded at each reach and their respective mayfly/stonefly community (presence/absence data). In the CCA biplots, axes represent the most important environmental gradients along which

the fauna was distributed. The significance of the CCA axes was determined by Monte-Carlo permutation testing (10 000 permutations).

Regressions of reach taxonomic richness against the 11 environmental variables (including season) were carried out using Generalised Additive Models (GAMs) (Hastie and Tibshirani, 1990). Generalised Additive Models (GAMs) were applied 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). GAMs are a non-parametric extension of multiple regressions and Generalised Linear Models (Hastie and Tibshirani, 1990). Details concerning GAMs and the techniques used in the present study are given in Castella *et al.* (2001).

Taxa occurring in less than 5% of the reaches-dates were omitted from the Correspondence Analysis and CCA, but included in the GAM for taxonomic richness. The Correspondence Analyses were carried out using the ADE-4 software (Thioulouse *et al.*, 1997). GAM calculations were carried out using the GRASP set of functions (Lehmann *et al.*, 2003) implemented in the S-PLUS software (Anonymous, 1998).

Table 2 - Frequency of taxa in a given reach of the glacial rivers studied (no. of dates on which the taxa occurred / no. of dates samples). Taxa and reaches are presented according to their position in the between-reach correspondence analysis. Distance from glacial source and total number of taxa are also given.

	LEI03	LEI06	LEI05	BRI05	BRI03	BRI04	BRI02	BRI01	MUT02	MUT03	RHO2	MUT04	CON02	MUT05	CON03	RHO1	CON04	CON08	RHO3	TAI35	TAI03	
Distance from glacier (k)	3.9	15	11	5.0	1.9	2.6	1.0	0.12	0.20	0.35	0.75	1.7	1.1	3.6	1.5	0.70	2.6	4.6	0.80	1.5	1.4	
<i>Capnia</i>	0.75	0.40	0.50	0.60	0.50	0.75	0.67															
<i>Amphinemura</i>	0.25	0.80	0.50	0.60		0.25															0.33	
Taeniopterygidae			0.25	0.60	0.75	0.75	0.33	1.00	0.60	0.83	0.33	1.00	1.00	0.67	1.00		0.83	0.67				
<i>Nemoura</i>	0.5			0.40			0.33					1.00		1.00			1.00	1.00				
<i>Baetis</i>		0.60	0.75	0.20		0.75	0.67		0.60	1.00	1.00	1.00	0.60	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.80
<i>Leuctra</i>			0.25				0.33		0.20	0.33	0.33	1.00	0.80	0.67	0.67	0.33	1.00	0.83	0.67	1.00	0.60	0.60
<i>Protonemura</i>						0.25	0.33			0.17	0.67	1.00	1.00	0.67	1.00	0.67	1.00	1.00	1.00	0.67	0.40	
<i>Dictyogenus</i>									0.20	0.83		1.00	0.40	0.33	0.17	0.33	0.83	0.67	0.67			
<i>Rhithrogena</i>										0.50	0.33	1.00	0.80	1.00	1.00	0.67	0.83	1.00	1.00	1.00	0.80	
<i>Siphonoperla</i>												0.50		1.00	0.33		1.00	1.00		1.00	0.50	
<i>Isoperla</i>													0.20		0.50		0.67	0.83				
<i>Ecdyonurus</i>														0.67			0.33	0.83			1.00	
<i>Epeorus</i>																		1.00	0.33		0.17	
<i>Perlodes</i>															0.17		0.67	0.33			0.50	0.80
<i>Capnioneura</i>																				0.67	1.00	
No. of taxa	3	3	5	5	2	5	6	1	4	6	5	8	7	9	9	5	11	12	6	10	6	

Results

The between-reach Correspondence Analysis of the taxa x reach matrix showed three distinct groups : the two Norwegian sites (BRI, LEI), the sites from the Alps (RHO, CON, MUT) and the site in the Pyrenees (TAI) (Fig. 1, Table 2). The F1 axis explained 38% of the variation, while the F2 axis explained 20%. Plecopteran and ephemeropteran taxonomic richness varied across the European gradient, being highest in the Taillon

in the French Pyrenees and lowest in Leirungsåi, in Norway. In the ordination there was a strong heterogeneity within the Norwegian reaches in comparison with other sites, especially the catchments in the Alps.

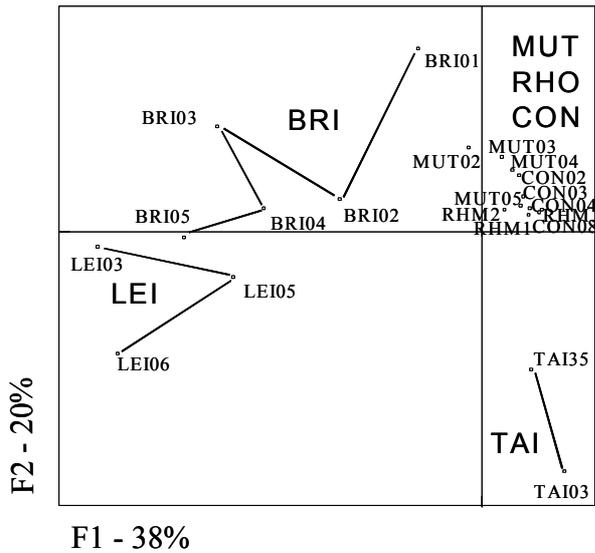


Fig. 1 – Between-reaches Correspondence Analysis of data from six glacier-fed rivers, based on 15 Ephemeroptera/Plecoptera taxa.

The Canonical Correspondence Analysis of taxa x reach x 10 environmental variables (season excluded) was highly significant (Monte Carlo permutation test $p < 0.0001$), although only 24% of taxonomic variation was explained (Fig. 2). The following taxa were best explained: *Isoperla* (53%), *Siphonoperla* (43%), *Epeorus* (43%). Taxa with the lowest level of explanation were *Nemoura* (9%), *Amphinemura* (13%), *Leuctra* (14%). The major contributory environmental variables were maximum water temperature (TEMP), the Pfanckuch index of channel stability (PFAN), chlorophyll *a* (CHLO) (along axis F1); tractive force (TRAC), percentage cover of boulders (BOUL), suspended solids (SUSP) and Froude number (FROU) (along axis F2).

The GAMs for taxonomic richness started with 11 variables, including season as categorical variable. Using a significance level of 0.01, three variables were retained in each of the regression models for ephemeropteran and plecopteran richness.

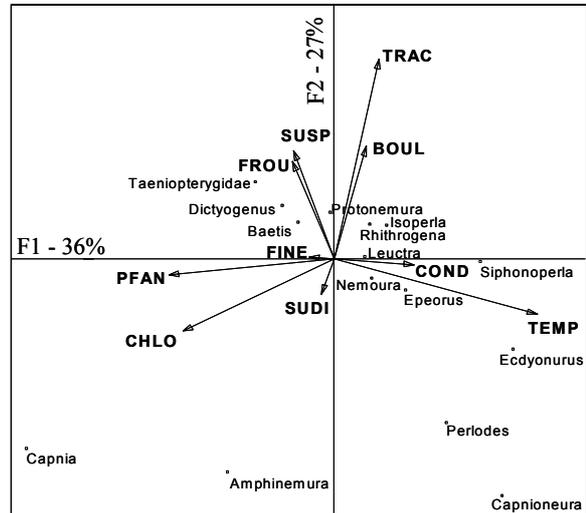


Fig. 2 – Canonical Correspondence Analysis of 15 Ephemeroptera/Plecoptera taxa, 92 reaches and 10 environmental variables (season excluded).

The results from the GAMs are presented as response curves (Figs. 3, 4). Response curves are the additive terms building up the model. All curves should be read with the environmental variable on the X axis and the dimensionless linear predictor as Y axis. Variations along this Y axis indicate the response of taxonomic richness to the given environmental variable.

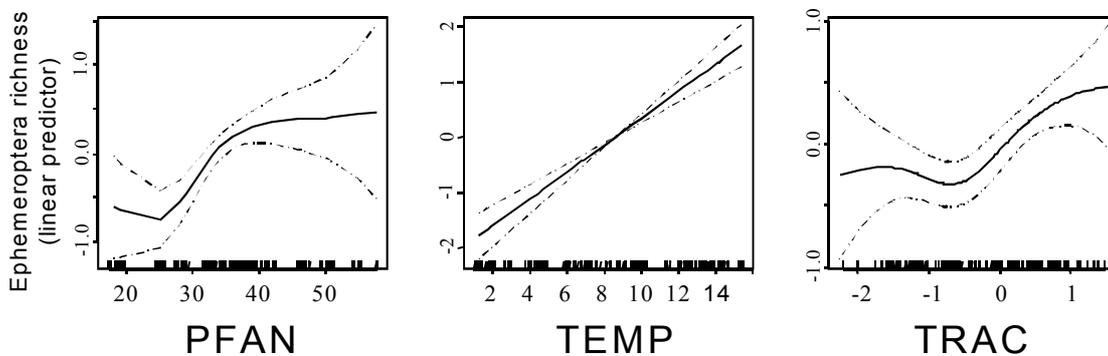


Fig. 3 - Response functions for Ephemeroptera taxonomic richness in relation to the three environmental variables incorporated in the GAM. The dashed lines are approximate 95% confidence intervals around the smooth function. PFAN: Pfanckuch index of channel stability (dimensionless), TEMP: maximum reach temperature ($^{\circ}\text{C}$), TRAC: tractive force (\log_e transformed dyn cm^{-1}). Vertical axes (taxonomic richness) are scaled according to the dimensionless linear predictor.

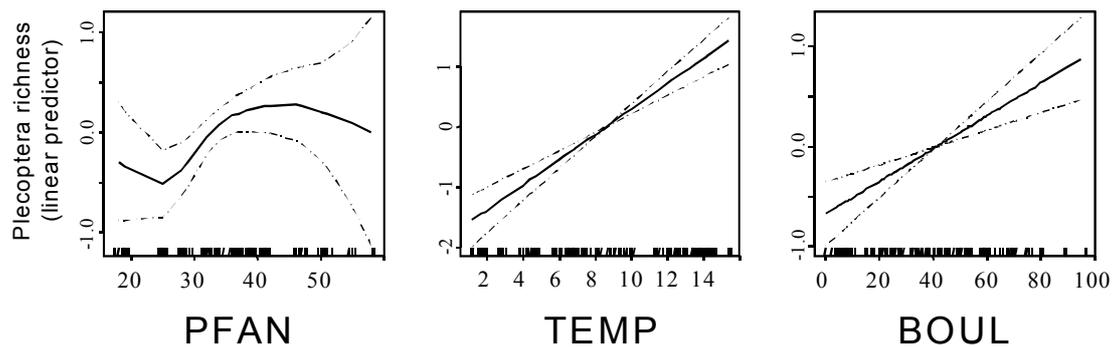


Fig. 4 - Response functions for Plecoptera taxonomic richness in relation to the three environmental variables incorporated in the GAM. The dashed lines are approximate 95% confidence intervals around the smooth function. PFAN: Pfankuch index of channel stability (dimensionless), TEMP: maximum reach temperature ($^{\circ}\text{C}$), BOUL: percentage cover by boulders. Vertical axes (taxonomic richness) are scaled according to the dimensionless linear predictor.

The GAMs for taxonomic richness had cross-validation correlation ratios between prediction and observation of 0.65 (Plecoptera) and 0.70 (Ephemeroptera), thus indicating stable models (Figs. 3, 4). The percentage of deviance explained was also reasonably high, 49% for Ephemeroptera and 43% for Plecoptera. Maximum water temperature (TEMP) and the Pfankuch index of channel stability (PFAN) were included in both models, while percentage boulders (BOUL) was included in the Plecoptera model and tractive force (TRAC) in the Ephemeroptera model. The shape of the response curves varied for the variables retained in the model (Figs. 3, 4). Temperature and percentage boulders were incorporated as positive linear functions, while the Pfankuch index and tractive force were more complex sigmoid functions.

Discussion

The mayfly and stonefly assemblages, as with most taxa of aquatic insects (Illies, 1965, 1978) are quite different in the Pyrenees, the Alps and in the Norwegian mountains, even at the generic level. This is clearly illustrated in the Correspondence Analysis in which the three regions are quite distinct. However, there is considerable overlap between the three regions, several genera, such as *Baetis*, *Leuctra* and *Nemoura*, occurring throughout Europe (Illies, 1965, 1978). Nevertheless, a number of genera, such as *Dictyogenus* and *Epeorus*, are absent from northern Europe. Ephemeroptera and Plecoptera are weak fliers (Brittain, 1982; Petersen *et al.*, 1999), which limits their dispersal. The absence of the stonefly genus *Capnia* in samples taken in the Alps is unexpected as it has been recorded from the Rhône and other sites in the Alps during

winter and early spring. However, the adults emerge in the spring, only appearing again as small nymphs late in the autumn. Since spring comes earlier in the Alps compared to the mountains of northern Europe, *Capnia* had already emerged by June in the Alps, but was still emerging further north.

Within Europe there is a general decrease in species richness with increasing latitude, partly a consequence of geographic isolation and colonisation and extinction processes associated with the last major Ice Age (Illies, 1965, 1978; Brittain 1990; Brittain and Milner, 2001). This also applies to taxonomic richness in glacial rivers, both generally and for Ephemeroptera and Plecoptera, increasing along a gradient from Scandinavia via the Alps to the Pyrenees (Castella *et al.*, 2001). The Norwegian reaches show considerable heterogeneity. This is related to the substantial environmental gradients represented in these systems and the influence of tributaries and lakes along the river systems (Brittain *et al.*, 2001). For example the river flows from the Briksdal glacier at an altitude of only 340 m a.s.l., well below the tree-line. There is therefore a much more rapid transition to the lowland environment in many of the environmental factors, although the influence of glacial meltwater is retained throughout most of its course due to a succession of glacial tributaries (Brittain *et al.*, 2001).

In the Canonical Correspondence Analysis, the genera *Nemoura*, *Amphinemura* and *Leuctra* had the lowest level of explanation. This is perhaps not surprising as these are large genera containing many species, many of which are widespread throughout Europe and occur in a wide variety of habitats (Illies, 1978). An analysis at the species level would probably provide better discrimination.

The importance of water temperature as a major environmental variable in determining the distribution of aquatic insects including mayflies and stoneflies is well documented (Ward and Stanford, 1982; Brittain, 1990). The present analysis of communities in glacier-fed rivers, whereby maximum water temperature is a major explanatory variable both in the Canonical Correspondence Analysis and the GAMs, confirms this. With the exception of Southern Hemisphere glacial systems, where Leptophlebiidae (Ephemeroptera) occur close to the glacier (Milner *et al.*, 2001a), mayflies and stoneflies are generally absent at upstream reaches close to glacial sources where maximum water temperatures rarely if ever rise above 2°C. However, as water temperatures increase downstream, a number of mayfly and stonefly genera are able to successfully colonise, particularly when T_{\max} rises above 4°C.

Channel stability is also an important variable in both GAM models for taxonomic richness, although the relationship is non-linear, there being a tendency for higher richness at intermediate stabilities, in accordance with the intermediate disturbance hypothesis (Connell, 1978; Ward and Stanford, 1983). Lake (2000) suggested that invertebrate diversity was more strongly regulated by intermediate-level disturbances at the regional scale across streams than at the reach scale within streams and our GAM analyses would appear to support this conclusion.

The other two major variables in addition to maximum temperature and channel stability which contributed significantly to the GAM models were tractive force (shear stress) for Ephemeroptera and percentage cover by boulders for Plecoptera. The relationship for tractive force showed a positive sigmoid relationship with highest richness at high levels of tractive force. There was a linear relationship between percentage boulders and plecopteran richness. A high percentage cover by boulders provides microhabitats that may be utilised by a number of stonefly species, as well as providing a degree of stability in an otherwise unstable environment.

GAMs are a powerful tool that have recently been applied to invertebrate taxonomic richness in glacier-fed rivers (Castella *et al.*, 2001; Milner *et al.*, 2001b). In the present study the use of GAMs has confirmed the importance of water temperature and channel stability in determining mayfly and stonefly richness. Using the same approach it is possible to develop predictive models for individual genera. Preliminary

analyses indicate that this is certainly feasible for many mayfly and stonefly genera in glacial rivers and that many of the models have high predictive power. The deterministic nature of mayfly and stonefly communities in glacial rivers makes them suitable objects for monitoring environmental impacts, especially related to climate change (McGregor *et al.*, 1995) and GAMs are an appropriate modelling tool to monitor and predict potential changes in species distributions resulting from global warming.

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