

Trends of macroinvertebrate community structure in glacier-fed rivers in relation to environmental conditions: a synthesis

ALEXANDER M. MILNER,*† JOHN E. BRITTAIN,‡ EMMANUEL CASTELLAS and GEOFFREY E. PETTS*

*School of Geography and Environmental Science, University of Birmingham, Edgbaston, Birmingham, U.K.

†Institute of Arctic Biology, University of Alaska, Fairbanks, AK 99775, U.S.A.

‡Freshwater Ecology and Inland Fisheries Laboratory, Natural History Museums and Botanical Garden, University of Oslo, Oslo, Norway

§Laboratoire d'Ecologie et de Biologie Aquatique, University of Geneva, Geneva, Switzerland

SUMMARY

1. Generalized additive models (GAMs) were used to predict macroinvertebrate taxonomic richness and individual taxon diversity at the reach level across seven European glacier-fed river sites from a set of 11 environmental variables. Maximum water temperature and channel stability were found to explain the most deviance in these models.
2. Using this information, and data from other recent studies of glacier-fed rivers, a modified conceptual model based on Milner & Petts (1994) is presented which predicts the occurrence of macroinvertebrate families and subfamilies as determined by maximum water temperature ($T_{\max}$) and channel stability. This deterministic model only applies to the summer meltwater period when abiotic variables drive community structure.
3. Where maximum water temperature is below 2 °C, Diamesinae chironomids are typically the sole inhabitants, but where $T_{\max} > 2$ °C but < 4 °C Orthocladiinae are found and, where channels are more stable, Tipulidae and Oligochaeta also occur. Above 4 °C Perlodidae, Taeniopterygidae, Baetidae, Simuliidae and Empididae can be expected to be part of the glacier-fed river community, particularly in Europe.
4. At other times of the year when environmental conditions ameliorate, glacial rivers support higher macroinvertebrate abundance and diversity, with a number of taxa present that are not found during the summer melt period.
5. Dispersal constraints influence macroinvertebrate assemblages of many glacier-fed rivers located on islands and in some alpine areas.

Keywords: channel stability, Chironomidae, dispersal, glacier, rivers, temperature

Introduction

In high latitude and alpine regions, three main types of running waters have been described (Ward, 1994): kryal streams fed by glacial meltwater, rhithral

streams fed by snowmelt and rainfall, and spring-fed or krenal streams. Milner & Petts (1994) characterized glacier-fed rivers as having maximum water temperatures below 10 °C and the peak of the annual hydrograph in summer with marked diurnal fluctuations and turbidity levels exceeding 30 NTU. These characteristics are quite distinct from snowmelt/rainfall streams at this time of year.

Based on documented distributions, Milner & Petts (1994) suggested that benthic macroinvertebrate

Correspondence: Alexander M. Milner, School of Geography, University of Birmingham, Edgbaston, Birmingham B45 8LY, UK. E-mail: a.m.milner@bham.ac.uk

communities in glacier-fed rivers displayed longitudinal trends driven by two principal variables, maximum water temperature and channel stability (Fig. 1). Where maximum water temperatures are below 2 °C, *Diamesa* (Chironomidae) were suggested to dominate the community. If water temperatures increased, but channel stability remained low, it was predicted that *Diamesa* would remain dominant within the macroinvertebrate community. If channel stability increased then other Diamesinae, Orthocladiinae and Simuliidae would potentially colonize below a maximum water temperature of 4 °C. Above a maximum of 4 °C, additional taxa typically added to the community would be Baetidae, Nemouridae and Chloroperlidae. Identified modifiers of the situation depicted in the conceptual model are lakes (increased water temperature and channel stability downstream), tributaries (increased/decreased channel stability and increased water temperature) and valley confinement (usually increasing bed stability).

Milner & Petts (1994) suggested that their conceptual model provided a hypothetical framework for the investigation and comparison of glacier-fed rivers and their macroinvertebrates communities, but that field research was required for model validation. Since 1994 a significant amount of field research has been undertaken to further this aim, particularly by the Arctic and Alpine Stream Ecosystem Research

(AASER) programme (Brittain & Milner, 2001) and other relevant studies summarized within this special issue of *Freshwater Biology*. The principal aim of this paper is to synthesize these findings, and those of other studies undertaken since 1994, in a broader context and to evaluate to what extent they support the model of Milner & Petts (1994).

Methods

Study areas

Research within the AASER project was across a latitudinal gradient from Svalbard [79°N] to the French Pyrenees [43°N] (Brittain & Milner, 2001). Seven glacially influenced rivers were chosen for quantitative cross-site comparisons: the Taillon in the Pyrenees, France (Smith *et al.*, 2001; Snook & Milner, 2001), the Conca in the Alps, Italy (Maiolini & Lencioni, 2001), the Mutt in the Alps, Switzerland (Lods-Crozet *et al.*, 2001a), the Dalelewa and the Leirungssai in western and central Norway (Brittain *et al.*, 2001), the western branch of the Jokulsa in Iceland (Gislason *et al.*, 2001) and the Bayelva on Svalbard (Brittain & Milner, 2001; Lods-Crozet *et al.*, 2001b).

Other geographical areas included in this review are Greenland (Friberg *et al.*, 2001) and New Zealand (Milner *et al.*, 2001). Recent studies in two alpine

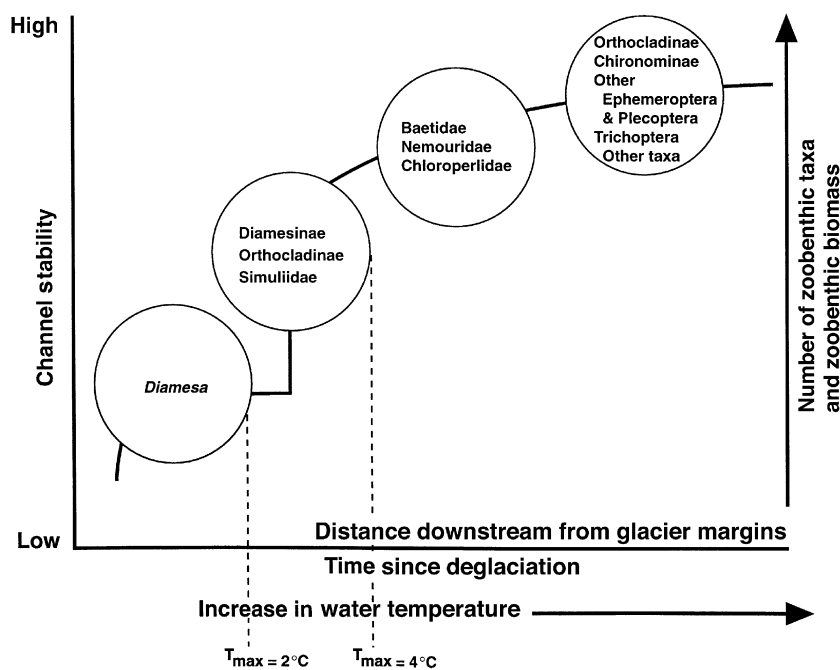


Fig. 1 Original conceptual model for the downstream distribution of macroinvertebrate taxa in glacier-fed stream (Milner & Petts, 1994).

glacial catchments, the Val Roseg in Switzerland (Burgherr & Ward, 2001; Robinson, Uehlinger & Hieber, 2001; Zah & Uehlinger, 2001) and the Rotmoosache in Austria (Füredér *et al.*, 2001; Schütz *et al.*, 2001) are also included.

Data collection

Macroinvertebrates and physicochemical data, including water temperature and channel stability [as described by the bottom component of the Pfankuch index [Pfankuch (1975)], were collected at the AASER sites over a 1 or 2-year period as outlined in Brittain & Milner (2001), Castella *et al.* (2001) and Snook & Milner (2001).

Statistical analyses

Based on the seven AASER sites, a generalized additive model (GAM) was determined, that predicts macroinvertebrate taxonomic richness (typically families, but subfamilies for Chironomidae and higher taxonomic units for noninsect taxa) at the reach level from a set of 11 environmental variables using the S-PLUS software (Anonymous, 1998). Overall taxonomic richness comprised 40 taxa. Maximum water temperature and the bottom component of the Pfankuch Index of channel stability (Pfankuch, 1975) were the variables that explained most of the deviance (measure of variance) in this GAM. These two variables also were consistently retained as contributive variables in the GAM models for explaining taxon density [i.e. water temperature in 14 of the 16 models and the Pfankuch Index in 10 of the 16 models]. Because of their importance, we used these two variables in the present analysis to compare the density response of the 16 taxa that occurred in more than 25% of the AASER sampling units (169 reach/dates corresponding to 39 sites in three different seasons over 2 years). A spline function was used to smooth the response of each taxon to the explanatory variable (Venables & Ripley, 1999) using the S-PLUS software (Anonymous, 1998).

Results

The data from the seven AASER sites clearly indicated that many taxa displayed a threshold temperature below which, they were not recorded (Fig. 2).

In addition to this threshold, the temperature range containing fewer than 10% of all occurrences was considered to be the 'low frequency' part of a taxon's range. For the Pfankuch Index, a value of about 40 (on a scale of 15–60 with high values indicating greater instability) was the upper threshold for the main occurrence of many taxa (Fig. 3). Diamesinae, Orthocladiinae, Simuliidae and Oligochaeta were the most abundant taxa on unstable substrates (Pfankuch Index >40), although only a single taxon (Heptageniidae) was absent in situations where the Index exceeded 40.

Relationships between the distributions of major invertebrate taxa and water temperature and channel stability at the seven AASER sites are summarized in Fig. 4. The lower temperature threshold for Orthocladiinae, Tipulidae and Oligochaeta was 2 °C. A threshold of 4 °C was apparent for Perlodidae, Taeniopterygidae, Baetidae, Simuliidae and Empididae, 6 °C for Limnephilidae and 8 °C for Nemouridae, Leuctridae, Heptageniidae, Rhyacophilidae and Chironominae. For six taxa (Leuctridae, Perlodidae, Rhyacophilidae, Chironominae, Empididae and Limoniidae) percent occurrence was less than 5% on unstable substrates (Pfankuch Index values >40).

Discussion

Ward (1997) emphasised the four dimensional nature of river systems incorporating longitudinal, lateral, and vertical components with a temporal scale superimposed on these spatial dimensions. The original conceptual model of Milner & Petts (1994) applies only to the longitudinal dimension of glacial river main channels, predicting downstream changes in macroinvertebrate community structure. However, there is considerable habitat heterogeneity in glacier-fed rivers flowing over alluvial floodplains that incorporate lateral components because of the occurrence of side channels, spring-fed groundwater channels and intermittently connected channels (Tockner *et al.*, 1997). Because, many glaciated valleys contain thick deposits of fluvio-glacial sediments, the vertical dimension introduced by subsurface (hyporheic) habitats also may be important (Malard *et al.*, 2001).

A modified conceptual model

On the basis of recent research summarized in this issue of *Freshwater Biology* and further synthesized

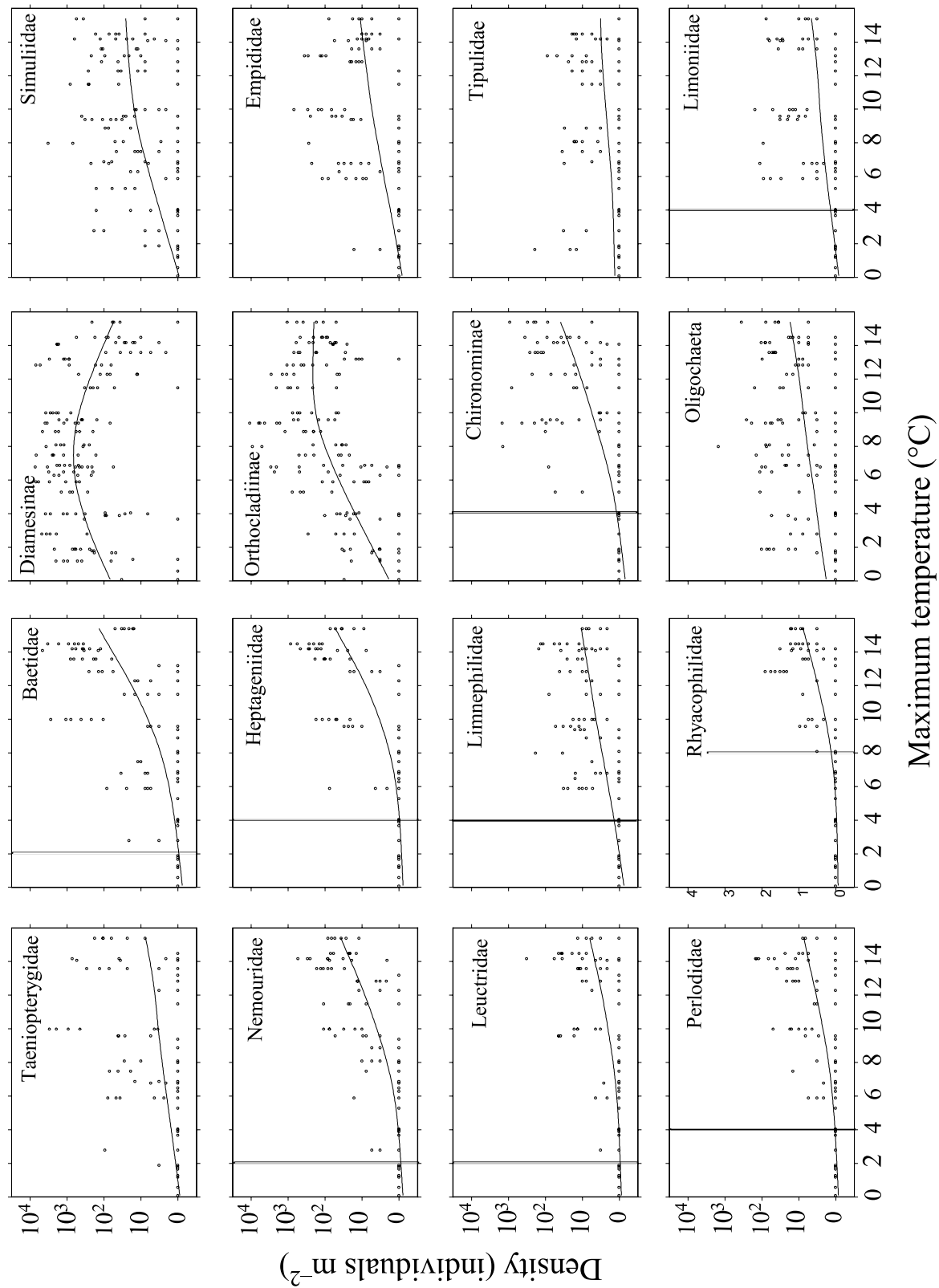


Fig. 2 Relationship between the density of 16 invertebrate taxa and the maximum water temperature recorded in seven glacier-fed streams. For each taxon, the density distribution in 169 reach dates was smoothed with a spline function. When represented, vertical bars indicate taxa for which no occurrences were recorded below 2, 4 or 8 °C.

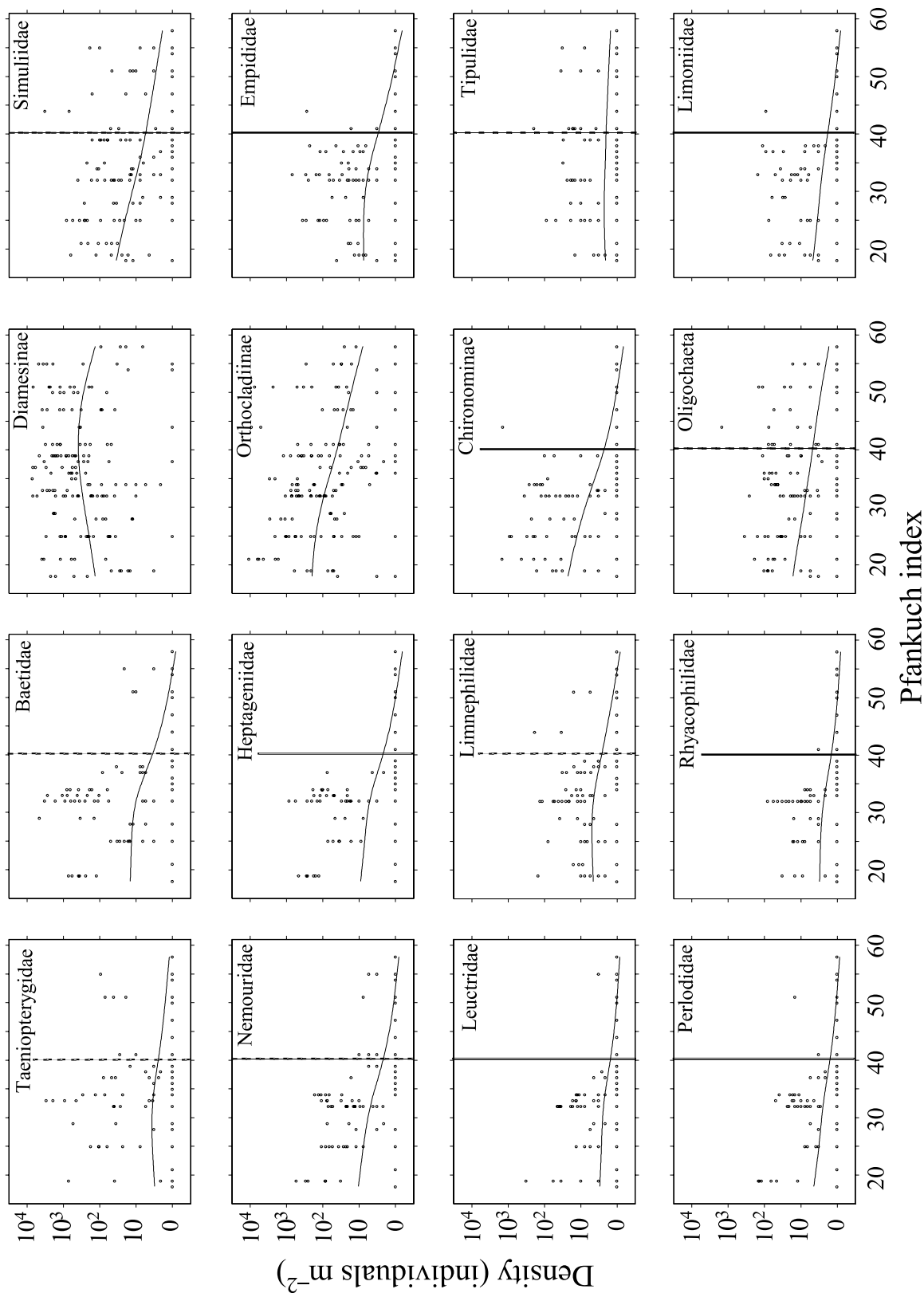


Fig. 3 Relationship between the density of 16 invertebrate taxa and the bottom component of the Pfanck Index of channel stability in seven glacier-fed streams. For each taxa, the density distribution in 169 reach dates was smoothed with a spline function. When presented, vertical bars indicate taxa for which <5% (solid bars), or <25% (dashed bars) of the occurrences were observed above a value of 40 for this index.

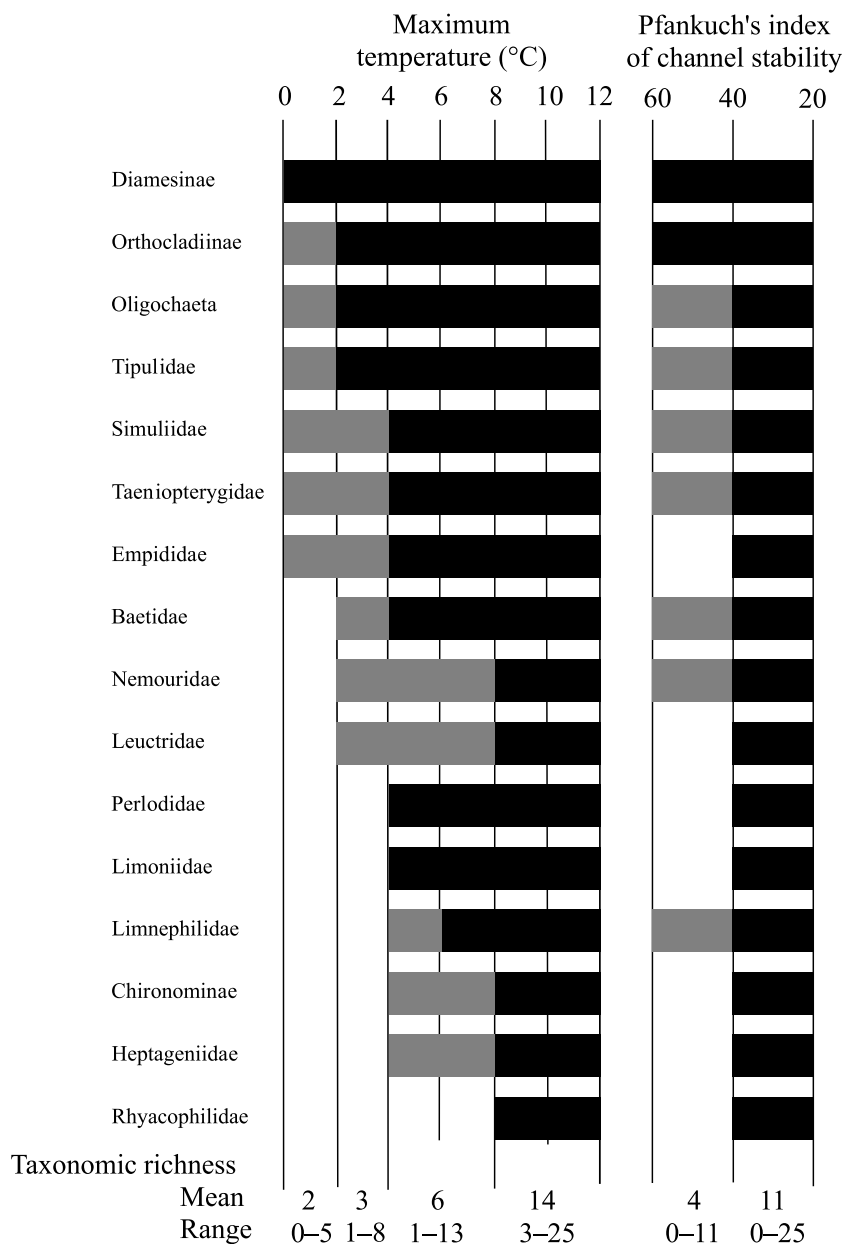


Fig. 4 Summary of relationships between the occurrence in seven glacier-fed rivers of 16 macroinvertebrate taxa and taxonomic richness at the reach scale with maximum water temperature and the bottom component of the Pfankuch Index of channel stability. For water temperature: white = no occurrence, grey = <10% of all occurrences, black = >10% of all occurrences. For the Pfankuch Index: white = <5% of all occurrences, grey = 5–25% of all occurrences, black = >25% of all occurrences.

here, the conceptual model for glacier-fed streams during the summer meltwater season (Milner & Petts, 1994) has been modified. However, it is still based on the expected common taxa at the family and sub-family (Chironomidae) levels (Fig. 5). Although *Diamesa* typically dominates glacier-fed rivers where maximum water temperature is <2 °C, other Diamesinae may also be present (e.g. *Pseudodiamesa* and *Pseudokiefferiella*), whereas in the original model Diamesinae other than *Diamesa* were predicted to colonize only when $T_{\max}$ was above 2 °C. Diamesinae are able to colonize habitats where the channel

stability is low (i.e. with a Pfankuch Index of 40–60). Similarly, some of the Orthocladiinae (Chironomidae) can typically colonize low stability habitats although where $T_{\max}$ is >2 °C but <4 °C. Oligochaeta and Tipulidae can also be present within this temperature range, although more typically where channel stability is greater (Pfankuch Index values <40). These last two taxa were not considered in the original model.

Above 4 °C, Perlodidae, Taeniopterygidae, Baetidae, Simuliidae and Empididae can be expected to colonize glacier-fed rivers, particularly in Europe.

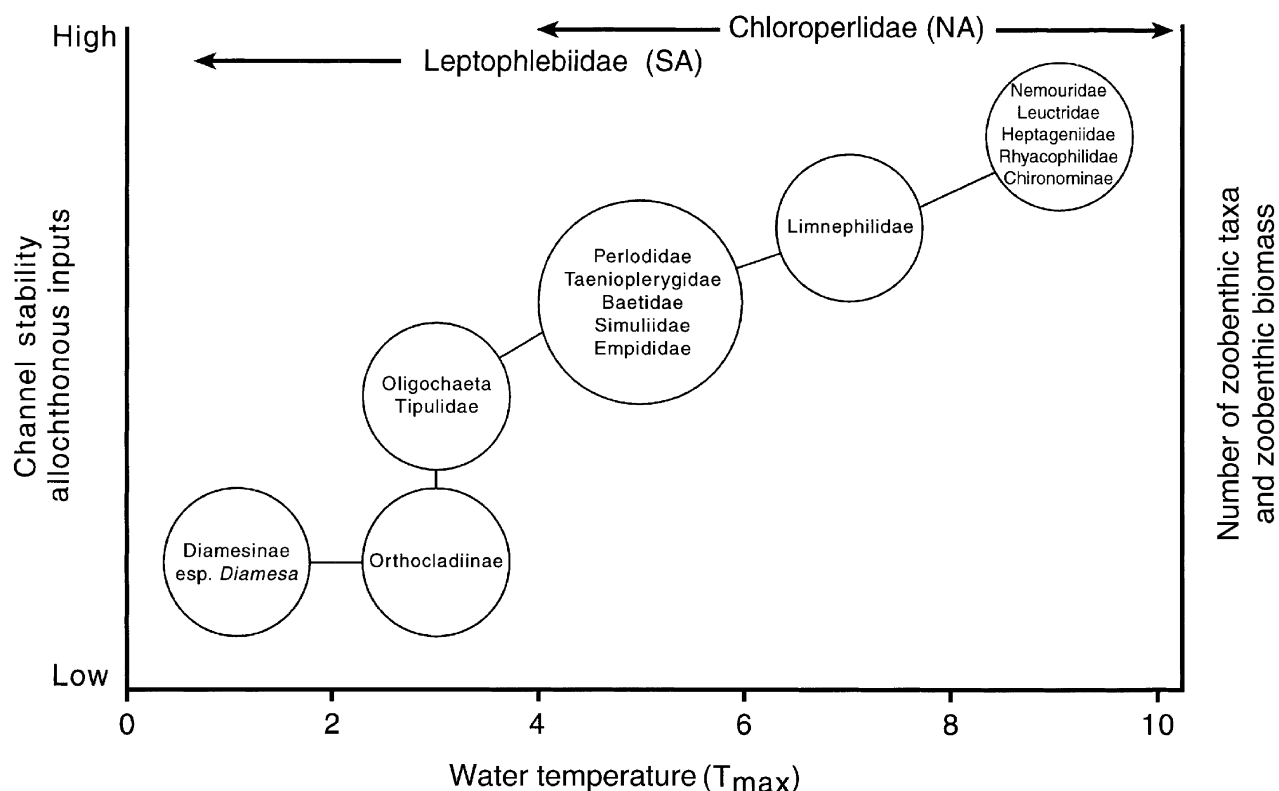


Fig. 5 Modified conceptual model describing the likely first appearance of macroinvertebrate taxa along an upstream-downstream continuum from the glacier margin with increasing water temperature and channel stability during the melt season for European glacier-fed rivers. Arrows indicate taxa that may be found across this temperature range in other geographical areas – SA = South America, NA = North America – see text for details).

In the earlier conceptual model, Simuliidae were considered to occur along with Orthocladiinae and other Diamesinae where maximum water temperature is 2–4 °C, however, although small numbers are found in this temperature range, the AASER intersite comparison indicate that Simuliidae are typically found above 4 °C. The two plecopteran families, Perlodidae and Taeniopterygidae, and the Empididae were not considered in the original model. The trichopteran family, Limnephilidae, can appear when T_{max} is between 6 and 8 °C, channel stability is enhanced (Pfankuch Index <40) and inputs of allochthonous material increase. Above 8 °C and below a T_{max} of 10 °C, Nemouridae, Leuctridae, Heptageniidae, Rhyacophilidae and Chironominae can be expected.

In the initial model it was proposed that Chloroperlidae and Nemouridae would colonize as T_{max} exceeds 4 °C, but this is not especially evident by the present GAM analysis. This finding may be related to

the overall scarcity of Chloroperlidae across the seven European AASER sites. Nevertheless chloroperlids were some of the first plecopterans to colonize glacially influenced streams in Alaska (Milner, 1994) and are therefore included in the updated model over the range of 4–10 °C. Nemouridae occurred between 2 and 8 °C at the European site in low densities but increased in abundance above 8 °C. In New Zealand, Milner *et al.* (2001) found the mayfly *Deleatidium* (Leptophlebiidae) close to the glacial margins below a T_{max} of 2 °C. In stream studies of the Patagonian Andes, Wais & Bonetto (1988) found that leptophlebiid mayflies (*Meridialaris*) and stoneflies mostly of the family Gryptopyterigidae dominated a glacier-fed catchment. In another South American study, Leptophlebiid mayflies were also dominant mayflies at temperatures of 3.8–4.8 °C (Misserendino & Pizzoton, 2000). Many of the northern hemisphere taxa, such as the mayfly family Heptageniidae and the stonefly families Nemouridae and Perlidae are either absent or

poorly represented in most parts of the southern hemisphere (Campbell, 1990; Zwick, 1990). This has led to considerable adaptive radiation among southern hemisphere taxa, especially among the Leptophlebiidae in which morphological convergence is widespread (e.g. Pescador & Peters, 1979; Campbell, 1990). As the occurrence of leptophlebiids is likely to be unique to the southern hemisphere generally, the family is not included in the main body of the present model. More information on southern hemisphere glacier-fed rivers and the characteristic taxa would be required to develop a generalized model for those regions.

The 'distance from glacier' legend included in the original conceptual model on the y axis with $T_{\max}$ has been removed in the revised model because diverse communities can be found close to glacier margins as long as water temperature and channel stability are relatively high. These conditions were observed at a number of AASER sites including the French Pyrenees (Snook & Milner, 2001), the Italian Alps (Maiolini & Lencioni, 2001) and the Swiss Alps (Lods-Crozet *et al.*, 2001a). Distance from glacier was originally used as a surrogate for 'time since deglaciation' but its predictive values is limited by such factors as rate of retreat or advancement of glaciers, altitudinal gradient, and the size of the river including the relative contributions of glacial meltwater and other sources of runoff. Channel development is a key process in invertebrate colonization but this is indexed by channel stability (Milner *et al.*, 2000).

Interestingly, with water temperature removed as a predictive variable in the GAM model, the relationship between overall taxa richness and the bottom component of the Pfanck Index of channel stability (Fig. 6) was found to be in accordance with the

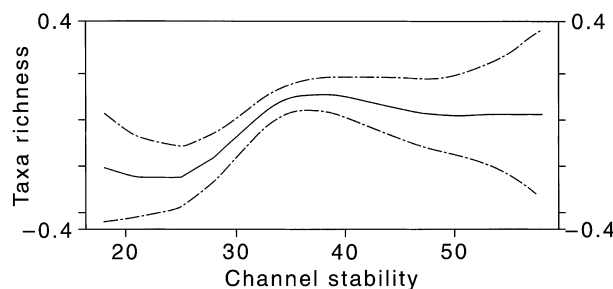


Fig. 6 General relationship of taxon richness with channel stability in glacier-fed rivers after removal of water temperature from the analysis. Dotted lines = ± 1 SD.

intermediate disturbance hypothesis (Connell, 1978), as richness was lower in both stable channels and the most unstable ones (Castella *et al.*, 2001). Both Ward & Stanford (1983) and Townsend, Scarsbrook & Doledec (1997) concluded that invertebrate diversity in running water was enhanced by increased spatial heterogeneity resulting from disturbances at intermediate frequencies, although a number of empirical studies have failed to provide support for this concept in streams (e.g. McCabe & Gotelli, 2000). However, 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 analysis would appear to support this conclusion.

Modifiers of the conceptual model

Milner & Petts (1994) suggested that the patterns identified in their conceptual model would be modified by lakes and tributaries. Studies in two Norwegian glacier-fed rivers, Dalelva and Leirungsåi, support this hypothesis, demonstrating that lakes affect downstream benthic communities (Brittain *et al.*, 2001). The interruption of the river course by lakes (Fig. 7) resulted in the amelioration of physical conditions further downstream allowing increased faunal diversity. Similarly, Burgherr & Ward (2000) found a more diverse community in a kryal lake outlet stream than a adjacent kryal stream without a lake, while Dorava & Milner (2000) showed that large lakes on glacier-fed rivers in southcentral Alaska enhanced salmon productivity 10 fold compared with systems without lakes. However, lakes close to or proximal to a glacier margin can eventually infill or become detached from the main channel, so that the enhancing influence on channel stability and water temperature is lost (Milner *et al.*, 2000). These changes 'reset' benthic communities downstream, which become less diverse and resemble earlier successional stages.

Tributaries can also be important modifiers of glacier-fed channels and their communities. In Dalelva, western Norway (Brittain *et al.*, 2001), downstream community development was affected by inputs from glacier-fed tributaries resulting in a continued dominance of Diamesinae. In contrast, in several nonglacial tributaries entering Leirungsåi, eastern Norway, a Diamesinae dominated commu-



Fig. 7 Glacier dammed lake Demmevatn in western Norway: increased faunal diversity and abundance downstream.

nity rapidly changed to one in which Orthocladinae were well represented or even dominant. Invertebrate drift from nonglacial tributaries can potentially lead to increased species diversity, but drift studies in Dalelva, western Norway (Saltveit *et al.*, 2001) suggest that most tributary species were unable to establish viable populations in the physically harsh main channel of the main glacier-fed river. However, should conditions ameliorate in the main channel, drift would undoubtedly be a main source of colonists. During spring and autumn a number of EPT species were in fact present in the upper reaches of the Daleva river. However, these species also occurred above non-glacial tributary inputs, indicating that colonization had taken place through routes other than drift from tributaries (e.g. as a result of ovipositing adults).

Vertical gradients in reach water temperature

Where glacially influenced streams flow across alluvial floodplains they may be influenced by upwelling

groundwater in the hyporheic mixing zone of stream and groundwater vertical gradients in temperature occur. Upwelling of groundwater to kyal reaches can produce higher annual thermal regimes in the hyporheic zone than in the overlying main channel. This situation has been documented in the Val Roseg floodplain, Switzerland where ephemeropteran and plecopteran taxa were found in some reaches below the upper substratum layer although the maximum temperature of surface water was only 2 °C (Malard *et al.*, in press). Surface samples of macroinvertebrates in these reaches indicated a community dominated by *Diamesa* with no other taxa present. Thus, in addition to longitudinal gradients in water temperature (Ward, 1994), there may be vertical thermal heterogeneity in some alluvial systems because of groundwater influence (Malard *et al.*, 2001a) and this can affect macroinvertebrate community structure.

Our modified conceptual model applies only to surface waters and does not incorporate diversity in macroinvertebrate community structure produced by vertical thermal heterogeneity. It must be borne in

mind, however, the more equable conditions in hyporheic zones may provide refugia during high summer flows of glacial runoff and so enable taxa to persist in channels where they would otherwise be eliminated.

Chironomid succession in glacier-fed rivers

The distribution of chironomid communities and changes in the distribution of Chironomidae taxa is of particular interest in glacier-fed rivers as the degree of glacial influence changes. Sixty-three taxa were found in six European glacial streams and reach scale comparisons between six European glacier-fed systems, based on these chironomid communities indicated water temperature and channel stability were the two most important variables separating Diamesinae from other chironomids at sites further from the glacier (Lods-Crozet *et al.*, 2001b). Some Diamesinae, including species of *Diamesa* and *Pseudodiamesa*, are able to complete their life cycle where water temperatures never exceed 2 °C. Burgherr & Ward (2001) even found a univoltine *Diamesa* species in a proglacial stream where only 154 degree days were accumulated per year, $T_{\max}$ was 0.96 °C and annual mean temperature 0.42 °C. While other taxa can withstand low water temperatures in this range, they require higher maximum temperatures to complete their life cycles and so maintain viable populations. Where channel stability is great enough, warmer temperatures permit other taxa to colonize reaches further downstream where glacial influence is reduced, or even reaches close to the glacier where glacial runoff is low (e.g. French Pyrenees – Snook & Milner, 2001). Even at times of the year when glacial inputs become low and the stream less turbid, notably in early spring and autumn, water temperature still remains low close to the glacier, potentially restricting the taxa present. The findings of Lods-Crozet *et al.* (2001b) for six European glacier-fed streams support the suggestion of Flory & Milner (1999) that populations of *Diamesa* can be maintained in warmer temperatures (>8 °C) in unstable channels where other chironomid taxa are not abundant. Indeed, the optimum temperature for *Diamesa* in Europe as indicated by the GAM models was 6–7 °C (Castella *et al.*, 2001).

The other chironomid subfamily strongly represented in glacier-fed streams are the Orthocladiinae. However, unlike the Diamesinae, most species

are confined to reaches where $T_{\max}$ exceeds 2 °C. Taxa typical of European glacier-fed streams were *Eukiefferiella claripennis* grp., *Orthocladius frigidus* (Zetterstedt), *Orthocladius rivicola* grp., and *Tvetenia*, while in streams of western Greenland, *Orthocladius thienemanni* Kieffer was the dominant member of this group (Friberg *et al.*, 2001). In two New Zealand glacier-fed rivers, *Eukiefferiella brundini* (Boothroyd & Cranston) was the dominant orthoclad (Milner *et al.*, 2001), and its distribution encompassing the entire length of these rivers from ice face to the sea (<1–10 °C). The Diamesini are absent from New Zealand but the endemic *Maoridiamesia* (Heptagyni) was present over a temperature range of 0.7–7.8 °C.

Food sources of macroinvertebrates in glacier-fed rivers

Steffan (1971) and Ward (1994) suggested that fine particulate organic matter transported by wind (e.g. pollen) is potentially an important food source for organisms in glacier-fed waters. However, retention is often low in turbulent fast flowing headwater streams and selective feeding on drifting organic particles is probably inefficient because of the large amount of suspended inorganic particles (Zah & Uehlinger, 2001). Where glacier-fed streams flow below the treeline, allochthonous particulate organic matter inputs can increase significantly (Brittain *et al.*, 2001; Zah & Uehlinger, 2001). However, where this organic input consists of conifer needles, the value to krynal systems may be limited because of low nutrient value (Robinson *et al.*, 2000). Using stable isotope analysis (Zah *et al.*, 2001) found that allochthonous inputs to an alpine glacier-fed system were important as a food source to macroinvertebrates only in groundwater fed channels close to the floodplain margin and their importance did not increase downstream as expected.

Instead, the dominant food sources in the main glacier-fed channels were epilithic diatoms and the filamentous chrysophyte, *Hydrurus foetidus* (Vill.) Kirchn. Zah *et al.* (2001) also showed that taxa, typically considered within one functional feeding group (e.g. shredders), were in fact highly omnivorous and that feeding plasticity was an important factor allowing benthic macroinvertebrates to persist under the physical extremes of temperature, turbidity and flow prevalent in glacial streams. *Hydrurus*

foetidus is common in glacier-fed streams throughout the European Alps and Northern Scandinavia (Ward, 1994; Lods-Crozet *et al.*, 2001a; Maiolini & Lencioni, 2001; Schütz *et al.*, 2001). These data correspond with a study in the Austrian Central Alps, where food availability in five glacial and spring-fed alpine streams was compared at sites above and below the tree line (Leo Füreder, unpublished data). Some taxa (e.g. *Baetis alpinus*) had a relatively ^{13}C depleted signal indicating periphyton as a predominant food source in the glacier-fed streams above the tree line.

Populations of epilithic diatoms and filamentous algae in lotic ecosystems display seasonal variations mediated by disturbance regimes and seasonality in light regimes (Biggs, 1996). Uehlinger *et al.* (1998) showed for example that algal biomass in a glacially influenced stream was low during summer, apparently because of high sediment transport, associated shear stress and turbidity but increased during autumn and late spring when physical conditions ameliorated. The increase was particularly evident in autumn when chlorophyll *a* levels exceeded 100 mg m^{-2} in reaches near the glacier margin. Groundwater influenced channels showed relatively high chlorophyll *a* levels throughout the winter months (Uehlinger *et al.*, 1998). This algal food source will be of importance to the taxa found in increasing numbers over the winter (Robinson *et al.*, 2001; Schütz *et al.*, 2001).

A recent study has shown that where basal glacial ice is temperate, water is present and, where organic carbon from glacially eroded soils is available, the subglacial environment beneath a high Arctic glacier can provide a viable habitat for microbes (Skidmore, Fight & Sharp, 2000). In the Rotmoosache stream, Austria, subglacial waters entrain these bacteria and wash them into the main channel where the bacteria adhere to sediment biofilms. The importance of these subglacial bacteria in sediment biofilms decreased downstream from the glacier snout (Battin *et al.*, 2001).

Gislason *et al.* (2001) found that bryophytes increased downstream of the glacial margin in an Icelandic stream and supported greater numbers of macroinvertebrates than upstream, particularly Orthocladiinae chironomids. Bryophytes accumulate fine particulate organic matter that constitute a food resource to detritivorous invertebrates (Suren, 1992; Suren & Duncan, 1999) and provide a colonization

surface for diatoms which in turn can serve as a food source (Suren & Winterbourn, 1992). During peak summer flows, when bed movements are greatest in glacial streams, larger substrata may also provide stable habitat for algal and invertebrate communities (Uehlinger, 1991; Biggs, 1996).

Temporal changes in glacier-fed rivers – elements of the harsh-benign concept

Peckarsky (1983) suggested that stream communities could be placed along a harsh-benign gradient of environmental conditions and, depending on this position, macroinvertebrate community structure could be regulated by different factors. Thus, under physically benign conditions communities would be influenced by biotic interactions, whereas in harsh environments biotic interactions would have a negligible influence on community structure. In glacier-fed rivers the relative harshness of the environment changes seasonally and macroinvertebrate community composition would be expected to reflect the changes in conditions. Burgherr & Ward (2001), Füreder *et al.* (2001), Robinson *et al.* (2001), and Schütz *et al.* (2001) showed that macroinvertebrate taxon richness and abundance were typically higher during periods (spring and autumn) when environmental conditions were more benign (lower flow and potentially more abundant and nutritious food resources, such as diatoms). Taxon richness and abundance can also be relatively high in winter (Robinson *et al.*, 2001; Schütz *et al.*, 2001). Thus, it appears that seasonal shifts in taxon richness and abundance in glacier-fed rivers are indeed driven by temporal changes in glacial discharge, which determines both T_{max} and channel stability regimes as summarized in Fig. 8. The variable level in richness and abundance during the winter is dependent on the degree of influence of groundwater on the main channel.

Some taxa in glacially influenced rivers are found only in surface waters during winter and spring, but not during summer when discharge is high (Füreder *et al.*, 2001; Robinson *et al.*, 2001; Schütz *et al.*, 2001). In nonglacially influenced rivers, summer is typically a period of insect emergence, egg laying and early instar development. However, the high flows in glacier-fed rivers make conditions less favourable for these activities and the life histories of many taxa are adapted to avoid these adverse conditions (Füreder

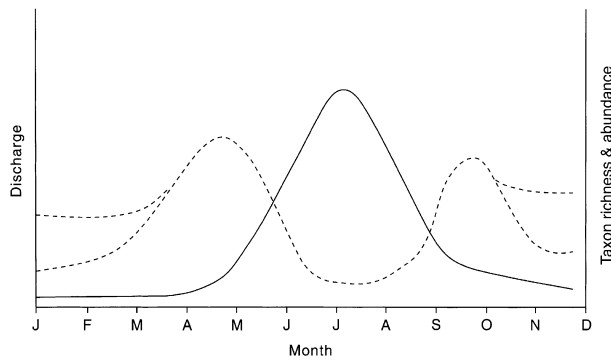


Fig. 8 Hypothetical relationship between taxon richness/macroinvertebrate abundance and discharge across the annual cycle (discharge is the driver for $T_{\max}$ and channel stability). In the winter, richness and abundance is variable depending upon degree of groundwater influence (see text).

et al., 2001; Saltveit, Haug & Brittain, 2001; Malard *et al.*, 2001b). Adaptations may include occupying the hyporheic zone as eggs or early instars to survive the high summer flows and the seeking of refugia in reaches dominated by snowmelt or groundwater inputs. Conversely some taxa such as *Diamesa*, dominate during the high flow conditions in summer, but are only found in low numbers at other times of the year. This life history pattern may have evolved to avoid greater potential competition under more benign conditions.

Biogeographical and dispersal influences on community structure

A final factor influencing macroinvertebrate community composition in glacier-fed rivers are dispersal constraints, which may limit faunal diversity. Many glacier-fed rivers are located on islands often at high latitudes, while some alpine areas are surrounded by extensive lowlands and thus also display an island character. Dispersal to these islands may involve crossing large tracts of unsuitable habitat thereby restricting the pool of potential colonizers (Fig. 9). Ephemeroptera and Plecoptera are weak fliers (Brittain, 1982; Petersen *et al.*, 1999), which limits their dispersal. Within Europe there is a general decrease in species richness with increasing latitude, a consequence of geographic isolation and colonization and extinction processes associated with the last major Ice Age (Illies, 1965; Brittain, 1990; Brittain & Milner, 2001). The occurrence of Oligochaeta in glacier-fed

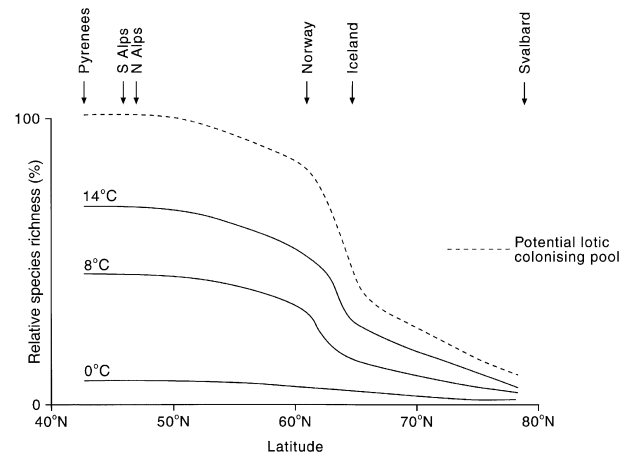


Fig. 9 Generalized relationship between latitude and species richness of benthic macroinvertebrates in glacier-fed rivers across Europe based on data from the AASER project, illustrating the lower numbers of potential colonizers of glacier-fed rivers at higher latitudes. Temperatures are maximum temperature for that stream reach.

rivers is noteworthy because it is dependent on dispersal mechanisms other than flight. (Malard *et al.*, 2001a) demonstrated the dispersal of oligochaetes via hyporheic pathways.

In glacier-fed streams on Greenland, no Plecoptera are found and Ephemeroptera are probably restricted to a single species of *Baetis* (Norrevang & Lundo, 1981; Friberg *et al.*, 2001). Only eight species of Trichoptera are known from Greenland across all river types (Norrevang & Lundø, 1981). On Svalbard, there are also no Plecoptera and only one species of Ephemeroptera with a very restricted distribution (O. A. Schnell, personal communication) and on Iceland aquatic insect species diversity is similarly low (Gislason, Olafsson & Adalsteinsson, 2000). Several taxa characteristic of Holarctic glacial rivers are absent in similar habitats on the southern hemisphere. For example, the plecopteran families Nemouridae and Chloroperlidae, the ephemeropteran family Baetidae and the chironomid tribe Diamesini, which includes *Diamesa*, do not occur in New Zealand (Milner *et al.*, 2001). However, representatives of the Southern Hemisphere families Gryopterygidae, Nesameletidae and the Diamesini tribe Heptagyini inhabit cold glacier-fed rivers along with 'cold-adapted' members of the cosmopolitan families Leptophlebiidae and Orthocladiinae. Similar assemblages probably occur in South America (M. J. Winterbourn, personal communication). Thus macroinvertebrate community

assemblages in glacier-fed streams in regions with markedly different species pools may make the application of conceptual models inappropriate or at least explain why a certain family is not found within the community assemblage.

In conclusion, the patterns described in the modified conceptual model are applicable only to the main channel during the glacier-melt season. At other times of the year, when glacial meltwater does not dominate stream flow, macroinvertebrate community structure may be markedly different (Brittain *et al.*, 2000; Füreder *et al.*, 2001; Robinson *et al.*, 2001; Schütz *et al.*, 2001). At these times the river will be more like a snowmelt or groundwater dominated system characterized by low sediment load and turbidity, and macroinvertebrate assemblages may be dominated by different taxa than during the high discharge period produced by peak ice melt in summer.

It is the spatio-temporal patterns of widely contrasting environmental conditions that make glacier-fed rivers unique. When glacial discharge is relatively low at periods other than summer, the river behaves predominantly as a groundwater or snowmelt fed system with lower discharge, turbidities and diurnal fluctuations, and higher conductivity (Burgherr & Ward, 2001). These conditions do not conform to the original definition of a glacier-fed river proposed by Milner & Petts (1994) and outlined in the introduction. Macroinvertebrate community structure shifts seasonally in response to these changes in environmental conditions. The same rationale applies to longitudinal changes downstream, which can alter habitat conditions within a short distance of the glacier, as has been observed in the French Pyrenees (Snook & Milner, 2001) and the Swiss Alps (Lods-Crozet *et al.*, 2001a). It is these temporal and longitudinal changes that ensure that the main channel of a glacier-fed system is not the unproductive habitat that is intuitively associated with these systems. This productivity is further enhanced by the variety of channel types across glacial alluvial floodplains and by the presence of vertical gradients between surface and ground water flowing in and beneath the main channel.

Acknowledgments

This paper arose out of the project, 'Arctic and Alpine Stream Ecosystem Research (AASER)', which

was supported by the European Commission (contract ENV-CT95-0164) and the Swiss Federal Office for Education and Science. We are extremely grateful for their financial support and encouragement. Our colleagues within the AASER project and in the other projects reported in this issue are thanked for their contributions and for valuable insights on the theme of glacier-fed rivers. We also wish to thank Mike Winterbourn and Mark Gessner for providing extensive comments on an earlier version that helped to substantially improve our manuscript and put us on the right track. Thanks also for review comments by Angela Gurnell, Chris Robinson, and James Ward.

References

- Anonymous (1998) *S-PLUS 4.5*. Data Analysis Products Division. MathSoft, Inc., Seattle, Washington.
- Battin T.J., Wille A., Sattler B. & Psenner R. (2001) Phylogenetic and functional heterogeneity of sediment biofilms along environmental gradients in a glacial stream. *Applied and Environmental Microbiology*, **67**, 799–807.
- Biggs B.J.F. (1996) Hydraulic habitat of plants in streams. *Regulated Rivers – Research and Management*, **12**, 131–144.
- Brittain J.E. (1982) The biology of mayflies. *Annual Review of Entomology*, **27**, 119–147.
- Brittain J.E. (1990) Life history strategies in Ephemeroptera and Plecoptera. In: *Mayflies and Stoneflies* (Ed. I.C. Campbell), pp. 1–12. Kluwer Academic Publishers, Dordrecht.
- Brittain J.E., Adalsteinsson H., Castella E., Gislason G.M., Lencioni V., Lods-Crozet B., Maiolini B., Milner A.M., Petts G.E. & Saltveit S.J. (2000) Towards a conceptual understanding of arctic and alpine streams. *Verhandlungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie*, **27**, 740–743.
- Brittain J.E. & Milner A.M. (2001) Ecology of glacier-fed rivers: current status and concepts. *Freshwater Biology*, **46**, 1571–1578.
- Brittain J.E., Saltveit S.J., Castella E., Bogen J., Bønsnes T.E., Blakar I., Bremnes T., Haug I. & Velle G. (2001) The macroinvertebrate communities of two contrasting Norwegian glacial rivers in relation to environmental variables. *Freshwater Biology*, **46**, 1723–1736.
- Burgherr P. & Ward J.V. (2000) Zoobenthos of Kryal lake outlet biotopes in a glacial flood plain. *Verhandlungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie*, **27**, 1587–1590.

- Burgherr P. & Ward J.V. (2001) Longitudinal and seasonal distribution patterns of the benthic fauna of an alpine glacial stream (Val Roseg, Swiss Alps). *Freshwater Biology*, **46**, 1705–1721.
- Campbell I.C. (1990) The Australian mayfly fauna: composition, distribution and convergence. In: *Mayflies and Stoneflies* (Ed. I.C. Campbell), pp. 149–153. Kluwer Academic Publishers, Dordrecht.
- Castella E., Adalsteinsson H., Brittain J.E. et al. (2001) Macrobenthic invertebrate richness and composition along a latitudinal gradient of European glacier-fed streams. *Freshwater Biology*, **46**, 1811–1831.
- Connell J.H. (1978) Diversity in tropical rain forests and coral reefs. *Science*, **199**, 1302–1310.
- Dorava J.M. & Milner A.M. (2000) Role of lake regulation on glacier-fed rivers in enhancing salmon productivity: the Cook Inlet watershed, southcentral Alaska, U.S.A. *Hydrological Processes*, **14**, 3149–3159.
- Flory E.A. & Milner A.M. (1999) Influence of riparian vegetation on invertebrate assemblages in a recently formed stream in Glacier Bay National Park. *Journal of the North American Benthological Society*, **18**, 261–273.
- Friberg N., Milner A.M., Svendsen L.M., Lindegaard C. & Larsen S.E. (2001) Macroinvertebrate stream communities along regional and physico-chemical gradients in Western Greenland. *Freshwater Biology*, **46**, 1753–1764.
- Füredér L., Schütz C., Wallinger M. & Burger R. (2001) Physico-chemistry and aquatic insects of a glacier-fed and a spring-fed alpine stream. *Freshwater Biology*, **46**, 1673–1690.
- Gislason G.M., Adalsteinsson H., Hansen I., Olafsson J.S. & Svavarsdottir K. (2001) Longitudinal changes in macroinvertebrate assemblages along a glacial river system in central Iceland. *Freshwater Biology*, **46**, 1737–1751.
- Gislason G.M., Olafsson J.S. & Adalsteinsson H. (2000) Life in glacial and alpine rivers in central Iceland in relation to physical and chemical parameters. *Nordic Hydrology. An International Journal*, **32**, 411–422.
- Illies J. (1965) Phylogeny and zoogeography of the Plecoptera. *Annual Review of Entomology*, **10**, 117–140.
- Lake P.S. (2000) Disturbance, patchiness, and diversity in streams. *Journal of the North American Benthological Society*, **19**, 573–592.
- Lods-Crozet B., Castella E., Cambin D., Ilg C., Knispel S. & Mayor-Simeant H. (2001b) Macroinvertebrate community structure in relation to environmental variables in a Swiss glacial stream. *Freshwater Biology*, **46**, 1641–1661.
- Lods-Crozet B., Lencioni V., Ólafsson J.O., Snook D.L., Velle G., Brittain J.E., Castella E. & Rossaro B. (2001a) Chironomid (Diptera: Chironomidae) communities in six European glacier-fed streams. *Freshwater Biology*, **46**, 1791–1809.
- Maiolini B. & Lencioni V. (2001) Longitudinal distribution of macroinvertebrate assemblages in a glacially influenced stream system in the Italian Alps. *Freshwater Biology*, **46**, 1625–1639.
- Malard F., Mangin A., Uehlinger U. & Ward J.V. (2001) Thermal heterogeneity in the hyporheic zone of a glacial floodplain. *Canadian Journal of Fisheries and Aquatic Sciences*, **58**, 1319–1335.
- Malard F., Lafont M., Burgherr P. & Ward J.V. Hyporheic versus benthic longitudinal patterns of Oligochaetes in a glacial river. *Arctic, Antarctic and Alpine Research* (in press).
- McCabe D.J. & Gotelli N.J. (2000) Effects of disturbance frequency, intensity, and area on assemblages of stream macroinvertebrates. *Oecologia*, **124**, 270–279.
- Milner A.M. (1994) Colonization and succession of invertebrate communities in a new stream in Glacier Bay National Park, Alaska. *Freshwater Biology*, **32**, 387–400.
- Milner A.M., Knudsen E.E., Soiseth C., Robertson A.L., Schell D., Phillips I.T. & Magnusson K. (2000) Colonization and development of stream communities across a 200-year gradient in Glacier Bay National Park, Alaska, U.S.A. *Canadian Journal of Fisheries and Aquatic Sciences*, **57**, 2319–2335.
- Milner A.M. & Petts G.E. (1994) Glacial rivers: physical habitat and ecology. *Freshwater Biology*, **32**, 295–307.
- Milner A.M., Taylor R.C. & Winterbourn M.J. (2001) Longitudinal distribution of macroinvertebrates in two glacier-fed New Zealand rivers. *Freshwater Biology*, **46**, 1765–1775.
- Misserendino M.L. & Pizzoton L.A. (2000) Macroinvertebrates of a fluvial system in Patagonia: altitudinal zonation and functional structure. *Archiv für Hydrobiologie*, **150**, 55–83.
- Nørrevang A. & Lundø J. (Eds) (1981) *Danmarks Natur – Grønland*. Politikens Forlag, Copenhagen, Denmark.
- Peckarsky B.L. (1983) Biotic interactions or abiotic limitations? A model of community structure. In: *Dynamics of Lotic Ecosystems* (Eds T.D. Fontaine & S.M. Bartell), pp. 303–324. Ann Arbor Science Publishers, Ann Arbor, MI, U.S.A.
- Pescador M.L. & Peters W.L. (1979) Phylogenetic relationships and zoogeography of cool-adapted Leptophlebiidae (Ephemeroptera) in southern South America. In: *Advances in Ephemeroptera Biology* (Eds J.F. Flannagan & K.E. Marshall), pp. 43–56. Plenum Press, New York.
- Petersen I., Winterbottom J.H., Orton S., Friberg N., Hildrew A.G., Spiers D.C. & Gurney W.S.C. (1999) Emergence and lateral dispersal of adult Plecoptera and Trichoptera from Broadstone Stream, U.K. *Freshwater Biology*, **42**, 401–416.

- Pfankuch (1975) *Stream Reach Inventory and Channel Stability Evaluation*. US Department of Agriculture Forest Service, Region 1, Missoula, MO, U.S.A.
- Robinson C.T., Gessner M.O., Callies K.A., Jolidon C. & Ward J.V. (2000) Larch needle breakdown in contrasting streams of an alpine glacial floodplain. *Journal of the North American Benthological Society*, **19**, 250–262.
- Robinson C.T., Uehlinger U. & Hieber M. (2001) Spatio-temporal variation in macroinvertebrate assemblages of glacial streams in the Swiss Alps. *Freshwater Biology*, **46**, 1663–1672.
- Saltveit S.J., Haug I. & Brittain J.E. (2001) Invertebrate drift in a glacial river and its non-glacial tributary. *Freshwater Biology*, **46**, 1777–1789.
- Schütz C., Wallinger M., Burger R. & Füreder L. (2001) Effects of snow cover on the benthic fauna in a glacier-fed stream. *Freshwater Biology*, **46**, 1691–1704.
- Skidmore M.L., Foght J.M. & Sharp M.J. (2000) Microbial life beneath a high Arctic glacier. *Applied and Environmental Microbiology*, **66**, 3214–3220.
- Smith B.P.G., Hannah D.M., Gurnell A.M. & Petts G.E. (2001) A hydrogeomorphological framework for ecological research on alpine glacial rivers. *Freshwater Biology*, **46**, 1579–1596.
- Snook D.L. & Milner A.M. (2001) The influence of glacial runoff on stream macroinvertebrates communities in the Taillon catchment, French Pyrénées. *Freshwater Biology*, **46**, 1609–1623.
- Steffan A.W. (1971) Chironomid (Diptera) biocoenoses in Scandinavian glacier brooks. *Canadian Entomologist*, **103**, 477–486.
- Suren A.M. (1992) Enhancement of invertebrate food resources by bryophytes in New Zealand alpine headwater streams. *New Zealand Journal of Marine and Freshwater Research*, **26**, 229–232.
- Suren A.M. & Duncan M.J. (1999) Rolling stones and mosses: effect of substrate stability on bryophyte communities in streams. *Journal of the North American Benthological Society*, **18**, 457–467.
- Suren A.M. & Winterbourn M.J. (1992) The influence of periphyton, detritus and shelter on invertebrate colonization of aquatic bryophytes. *Freshwater Biology*, **27**, 327–339.
- Tockner K., Malard F., Burgherr P., Robinson C.T., Uehlinger U., Zah R. & Ward J.V. (1997) Physico-chemical characterization of channel types in a glacial floodplain (Val Roseg, Switzerland). *Archiv für Hydrobiologie*, **140**, 433–463.
- Townsend C.R., Scarsbrook H.R. & Doledec S. (1997) Quantifying disturbance in streams: alternative measures of disturbance in relation to macroinvertebrate species traits and species richness. *Journal of the North American Benthological Society*, **16**, 551–544.
- Uehlinger U. (1991) Spatial and temporal variability of the periphyton in a pre-alpine river (Necker, Switzerland). *Archiv für Hydrobiologie*, **123**, 219–237.
- Uehlinger U., Zah R. & Burgi H.R. (1998) The Val Roseg project: temporal and spatial patterns of benthic algae in an alpine stream ecosystem influenced by glacier runoff. In: *Hydrology, Water Resources and Ecology in Headwaters* (Eds K.T.U. Tappeiner, N.E. Peters & R.G. Craig), pp. 419–425. IAHS Press, Wallingford, U.K.
- Venables W.N. & Ripley B.D. (1999) *Modern and Applied Statistics with S-PLUS*. Statistics and Computing. Springer, New York, 501 pp.
- Wais I.R. & Bonetto A.A. (1988) Analysis of allochthonous organic matter and associated macroinvertebrates in some streams of Patagonia (Argentina). *Verhandlungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie*, **23**, 1455–1459.
- Ward J.V. (1994) Ecology of alpine streams. *Freshwater Biology*, **32**, 277–294.
- Ward J.V. (1997) An expansive perspective of riverine landscapes: pattern and process across scales. *Gaia*, **6**, 52–60.
- Ward J.V. & Stanford J.A. (1983) The intermediate disturbance hypothesis: an explanation for biotic diversity patterns in streams. In: *Dynamics of Lotic Ecosystems* (Eds T.D. Fontaine & S.M. Bartell), pp. 347–356. Ann Arbor Science Publishers, Ann Arbor, MI, U.S.A.
- Zah R., Burgherr P., Bernasconi S.M. & Uehlinger U. (2001) Stable isotope analysis of macroinvertebrates and their food sources in a glacier stream. *Freshwater Biology*, **46**, 871–882.
- Zah R. & Uehlinger U. (2001) Particulate organic matter inputs to a glacial stream ecosystem in the Swiss Alps. *Freshwater Biology*, **46**, 1597–1608.
- Zwick P. (1990) Transantarctic relationships in the Plecoptera. In: *Mayflies and Stoneflies* (Ed. I.C. Campbell), pp. 141–148. Kluwer Academic Publishers, Dordrecht.

(Manuscript accepted 5 September 2001)