

Ecology of glacier-fed rivers: current status and concepts

JOHN E. BRITTAIN* and ALEXANDER M. MILNER†‡

*Freshwater Ecology and Inland Fisheries Laboratory (LFI), Natural History Museums and Botanical Garden, University of Oslo, Norway

†School of Geography and Environmental Sciences, University of Birmingham, Edgbaston, Birmingham, U.K.

‡Institute of Arctic Biology, University of Alaska, Fairbanks, Alaska, U.S.A.

SUMMARY

1. This paper is an introduction to a special issue of *Freshwater Biology* containing papers dealing with various aspects of the ecology of glacier-fed rivers.
2. Using similar field protocols, a wide range of glacier-fed systems were studied across Europe from the French Pyrenees to Svalbard within the framework of the European Commission project, Arctic and Alpine Stream Ecosystem Research (AASER). Recent investigations from other parts of Europe together with New Zealand and Greenland are also reported. This work has advanced our knowledge of the functioning of these types of rivers and has led to the modification and quantification of the conceptual model of Milner & Petts (1994).
3. Glacier-fed rivers, by virtue of the dominance of physical variables in shaping macroinvertebrate communities, are not only good indicators of climate change, but also may be suitable testing grounds for examining ecological concepts.

Keywords: alpine, arctic, glacier-fed rivers, hydrological change, macroinvertebrates, model

Introduction

Ecological zonation within cold regions may be defined on the basis of general climatic criteria. The treeline in undisturbed environments approximates the position of the mean 10 °C July isotherm and forms the dividing line between subalpine/subarctic woodlands and the treeless alpine/tundra areas (Remmert, 1980). Above the treeline, the environment is generally characterized by snow beds, bare rock surfaces, skeletal soils and prostrate vegetation except close to river margins, where riparian growth can be extensive especially in the low alpine. Permanent snowfields and glaciers dominate at higher altitudes.

Between the permanent snowline and the treeline, three general types of stream ecosystem have been identified (Steffan, 1971; Ward, 1994): the kryal, or glacier-melt dominated system; the rhithral, or seasonal snowmelt-dominated system; and the krenal, or spring-fed system. However, valley glaciers can extend through the treeline and glacier-melt dominated streams can persist for considerable distances downstream reaching sea-level at higher latitudes (Brittain *et al.*, 2001; Lods-Crozet *et al.*, 2001a). Furthermore, snow and ice cover may vary significantly over small spatial scales, and different stream segments will display characteristics that reflect the relative proportions of the different runoff sources: glacier melt, snowmelt and spring-flow. Each source generates a characteristic seasonal hydrological signature and runoff of different physical (temperature and suspended sediment load) and chemical quality (Sharp *et al.*, 1998; Brittain *et al.*, 2000).

Correspondence: John E. Brittain, Freshwater Ecology & Inland Fisheries Laboratory (LFI), Natural History Museums and Botanical Garden, University of Oslo, P.O. Box 1172 Blindern, N-0318 Oslo, Norway. E-mail: j.e.brittain@nhm.uio.no

Concepts

From a synthesis of European and Alaskan literature, Milner & Petts (1994) proposed a conceptual model (Fig. 1) to predict the gradient of zoobenthic communities in rivers downstream of glacial margins as determined by two principle variables, water temperature and channel stability. Water temperature conveys broadly predictable trends to the longitudinal pattern of invertebrate community structure in glacial rivers and determines the point downstream at which certain taxa may colonize within a stable channel (Milner, 1994). However, even if water temperature is suitable, channel instability may delay colonization and allow some cold tolerant taxa to remain dominant in the community. Chironomid larvae of the genus *Diamesa* were suggested as the typical sole inhabitants when $T_{\max} < 2\text{ }^{\circ}\text{C}$, but are joined by other Diamesinae, Orthoclaadiinae and Simuliidae when $T_{\max} > 2\text{ }^{\circ}\text{C} < 4\text{ }^{\circ}\text{C}$ (Milner & Petts, 1994; Ward, 1994).

This conceptual model also recognizes that, discontinuities in the downstream gradient of zoobenthic communities may be caused by lakes. These act as thermal and hydrological regulators, and by changing stream valley morphology. Lakes embedded in the river course also influence solute loadings, turbidity patterns, and geomorphological dynamics of down-

stream river sections (see also Ward & Stanford, 1983). Tributaries may act in a similar way. For example, glacial tributaries may retard zoobenthic community development, while non-glacial tributaries may enhance it (Brittain *et al.*, 2001). The general theme outlined by Milner & Petts (1994) is further superimposed by variations in the structure and functioning of stream ecosystems both between and within catchments.

Differences in stream types within arctic and alpine areas typically relate to varying hydrological regimes during the summer, which affect in particular suspended sediment load, turbidity, hydraulic stress and bedload transport. During the winter fewer differences exist as many streams and rivers are dominated by groundwater inputs (Tockner *et al.*, 1997; Malard *et al.*, 1999). Other factors, such as the extent of snow and ice cover, may nevertheless give rise to differences in incident radiation, water temperature and primary production (Schütz *et al.*, 2001). These points highlight the range of stream types found in high latitude and altitude environments, although they fail to link the fundamental hydrological effects of runoff on stream biota.

Many alpine areas are typified by sharp gradients in environmental conditions, giving rise to ecosystem patchiness and thereby isolation (Jeník, 1997). As a result of differences in altitude and thereby climate

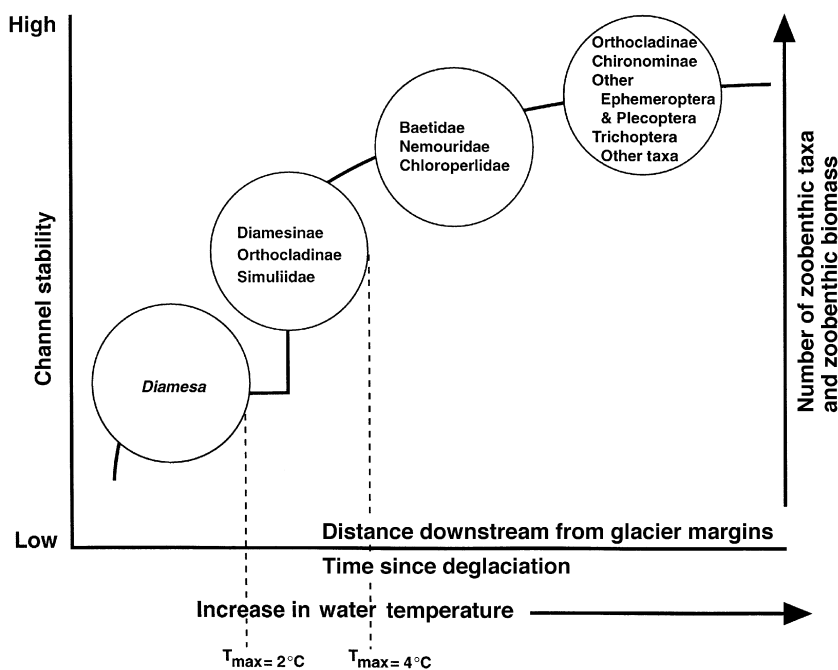


Fig. 1 Conceptual model proposed by Milner & Petts (1994) for the distribution of benthic macroinvertebrates downstream of glacial sources.

there are major changes along alpine rivers both in riparian vegetation (Lillehammer & Brittain, 1978; Petersen *et al.*, 1995; Jeník, 1997; Zah & Uehlinger, 2001) and in instream conditions such as temperature (Burgherr & Ward, 2001; Malard *et al.*, in press). Different water sources, for example snowmelt and glacier melt as well as the extent and nature of groundwater inputs, can also give rise to major environmental gradients over short distances which are reflected in faunal composition (Malard *et al.*, 1999; Füreder *et al.*, 2001). The winter period of ice and snow cover also significantly reduces the potential window for dispersal (Schütz *et al.*, 2001). The problem of isolation also applies to several arctic and subarctic areas, both island archipelagos and non-glaciated areas between glaciers. Nevertheless, the heterogeneous nature of stream types in such catchments, particularly in floodplain areas (Gurnell *et al.*, 1999; Smith *et al.*, 2001), provides potential sources of colonizers to the zoobenthos. Dispersal can take place via drift of immature stages and adult flight so that the response of zoobenthic communities within the main glacial river to hydrological change can be rapid. Recent research on invertebrate colonization following glacial retreat (Milner, 1994) support this contention, although more information is required on the dispersal ability and degree of population interaction within and between catchments of this nature.

Historical changes

The stream ecosystems of cold regions are 'young' in geological terms; they are also relatively rare today.

During the Pleistocene, continental glaciers covered about 32% of the earth's land surface and glacial rivers would have been widespread (Embleton & King, 1975; Goudie, 1992). Today, only some 10% of the land surface remains covered by glaciers. Glacier-fed rivers have been replaced by snowmelt and rainfall dominated rivers; a change reflected by adjustments of channel morphology and one that has been well-documented by palaeoenvironmental studies of river valleys throughout the temperate zone (e.g. Starkel *et al.*, 1991).

Glacial area has also varied over historic time scales. The 'Little Ice Age' between about 1550 and 1850, was the latest and most dramatic episode of Neoglaciation. The twentieth century was characterized by a general retreat of glaciers in the European Alps and in northern Europe (Fig. 2). However, the widespread retreat of glaciers in the European Alps seems to have been arrested in the 1960s and subsequently the termini of many glaciers have slowly re-advanced, although overall increases in area have been small (Kasser, 1983). In northern Europe a similar retreat has been documented throughout much of the last century. However, many of the western glaciers in Norway have also begun to advance, some of them dramatically, over the past few years because of increased winter precipitation (Fig. 3, Winkler *et al.*, 1997). In North America, there has been a general pattern of glacial retreat over the past 50 years, although in Alaska there was an increase in glacial mass in the 1970s (Mayo & March, 1990). However, this increase was not sustained (Melack *et al.*, 1997).



Fig. 2 The Rhone Glacier in 1825 (a) and in 1998 (b), illustrating the dramatic changes during the last two centuries. The glacier has retreated almost to the top of the steep rock face, thereby creating a glacial floodplain with another glacier-fed river, the Mutt, leading to a substantial increase in spatial and temporal habitat diversity.

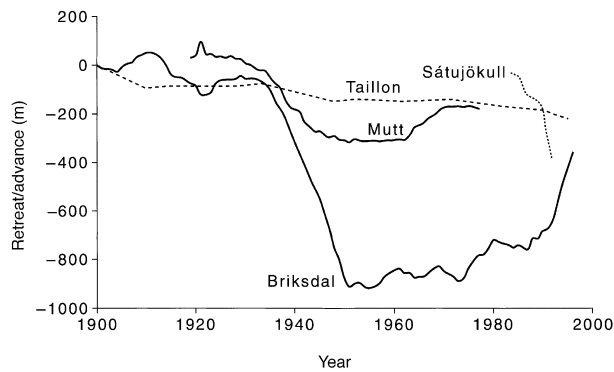


Fig. 3 Patterns of glacial retreat and advance shown by selected European glaciers (Data supplied by the Norwegian Water Resources and Energy Directorate (Briksdal); National Energy Authority, Iceland (Sátujökull); Versuchsanstalt für Wasserbau Hydrologie und Glaziologie of the Swiss Federal Institute of Technology (ETH), Zurich (Mutt)).

Anthropogenic impacts

In the future, climatic changes will influence the hydrological regime of arctic, alpine and mountain streams in a variety of ways, but the influence on glacier meltwater may be particularly significant (McGregor *et al.*, 1995). Changes in the magnitude and variability of a range of climate determinants of glacier behaviour, as a result of an enhanced Greenhouse effect, will have important implications for the future hydrogeomorphological and thermal dynamics of glacial streams. Water resources developments, such as water diversions for hydro-electric power developments, water abstraction and land-use changes, can also have marked impacts upon these stream ecosystems, particularly on benthic communities (e.g. Boon, 1988; Brittain & Saltveit, 1989; Petts & Bickerton, 1994). Stream macroinvertebrate communities are widely used to monitor changes in water quality as a result of human impact, notably with regard to organic pollution and acidification (Rosenberg & Resh, 1993). However, knowledge of environmental variables determining macroinvertebrate distribution is a necessary prerequisite for using zoobenthos as bioindicators of environmental change in arctic and alpine running waters (Fig. 2).

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, most notably *Diamesa* spp., which may thus act as a potential key indicator taxa for climate change effects in glacier-fed rivers (Melack *et al.*, 1997).

Ecological processes

The functioning of glacier-fed stream and river ecosystems in arctic and alpine regions is less well known than that of forest and lowland systems for a number of reasons. Studies have historically been largely restricted to the window of the ice-free season, because of the logistical problems of sampling in the winter. However, significant progress over the last decade has helped to redress this balance. Although these systems initially appear unstable, characterized by lower biodiversity than lowland clearwater streams, glacier-fed stream ecosystems may be unique among lotic systems in supporting predictable macroinvertebrate communities because of the overriding dominance of physical variables in determining community structure. Certain taxa groups, such as Chironomidae, may display considerable species richness and notably glacial floodplains can represent hot-spots of environmental and species diversity in view of their considerable temporal and spatial heterogeneity (Tockner *et al.*, 1997; Ward *et al.*, 1998). The generally low complexity and high degree of predictability of glacially influenced systems may also be an advantage, not only making them better indicators of environmental change, but also as a suitable testing ground for examining ecological concepts. The ability of the macroinvertebrates of glacier-fed streams and river ecosystems to cope with such environmental heterogeneity, through a range of life cycle and colonization strategies, indicates that their distribution patterns, in a similar manner to their lowland counterparts, are a sensitive indicator of both natural and anthropogenic changes.

An overview of recent research summarized in this special issue

One of the recent main research thrusts has been the international co-operative project entitled, 'Arctic and Alpine Stream Ecosystem Research (AASER)' (Brittain

et al., 1998) which was the first attempt to undertake a co-ordinated study of a wide variety of glacier-fed stream ecosystems in Europe. The study was a co-operative effort between several institutions: the University of Oslo, Norway (Freshwater Ecology and Inland Fisheries Laboratory), the University of Birmingham, U.K. (School of Geography and Environmental Sciences), the University of Geneva, Switzerland (Laboratory of Ecology and Aquatic Biology), the University of Iceland, Reykjavik (Institute of Biology), the Trento Museum of Natural Sciences in Italy and the National Energy Authority of Iceland. The primary aim of AASER was to identify the primary physical and chemical variables determining the distribution of macroinvertebrates in glacially influenced catchments along a latitudinal and climatic gradient across Europe with which to test the validity of the Milner & Petts (1994) conceptual model outlined earlier in this paper. The AASER project, financed by the European Union and the Swiss Federal Office for Education and Science, covered 3 years of study from 1996 to 1999.

The AASER study sites were selected to represent a latitudinal gradient from 43°N in the French Pyrenees to 79°N on the arctic archipelago of Svalbard, and in degree of continentality from the oceanic climates of Iceland and Western Norway to the more continental climates of the Alps and Eastern Norway (Table 1, Brittain *et al.*, 2001; Castella *et al.*, 2001; Gislason *et al.*, 2001; Lods-Crozet *et al.*, 2001b; Maiolini & Lencioni, 2001; Saltveit *et al.*, 2001; Smith *et al.*, 2001; Snook & Milner, 2001). The study areas also represented the types of glacial situation present in Europe at present: retreating, advancing and 'stable'. Faunal diversity was also very different across sites being highest in the Alps and the Pyrenees, decreasing northwards. On Svalbard, isolated from mainland Europe, many taxa were not found, and Chironomidae dominated the freshwater fauna, both in glacial and non-glacial systems (Lods-Crozet *et al.*, 2001a). Some systems contained lakes as well as substantial tributary influence (Brittain *et al.*, 2001; Saltveit *et al.*, 2001), enabling evaluation of their effect on the pattern of macroinvertebrate distribution.

Fieldwork and subsequent analyses were carried out according to a standard protocol (Brittain & Saltveit, 1997) to ensure uniformity in data collection. Within each catchment, climatic and hydrological data were collected (including temperature, solutes

and suspended sediments); physical habitat characteristics were assessed (geomorphological assessment); and epilithic algae and zoobenthos were sampled. All data were entered into a single database to facilitate inter-site comparisons.

In addition to the AASER project, recent research on the zoobenthos of glacial rivers has been undertaken in the Bernia Massif of Switzerland and in the Tyrolean Alps, Austria. The Swiss site was the Val Roseg catchment, which contains a complex floodplain, providing an extensive interplay between glacial, groundwater and snowmelt channels (Malard *et al.*, 1999). Wide-ranging studies have made a significant contribution to our understanding of both abiotic and biotic processes in glacial floodplains (e.g. Burgherr & Ward, 2001; Zah & Uehlinger, 2001). In the Tyrol, studies have been undertaken in two parallel catchments, one spring-fed (Königsbach) and one glacier-fed (Rotmoosache) (Füreder *et al.*, 2001; Schütz *et al.*, 2001). Both these studies and a more general study encompassing several sites throughout the Swiss Alps (Robinson *et al.*, 2001) have included sampling during winter. Much of our knowledge of glacial rivers is based on data collected during the spring, summer and autumn. However, despite logistical problems, only year-round studies can give us the correct understanding of overall ecosystem structure and functioning and the life history patterns of the aquatic fauna.

Although recent research on glacier-fed rivers has been concentrated on European systems, studies have recently been undertaken in other areas of the world including New Zealand (Milner *et al.*, 2001) and Greenland (Friberg *et al.*, 2001). These studies widen the geographical scope of the European studies above and also provide insight into how deterministic patterns are in the downstream distribution of benthic macroinvertebrates across regions with substantially different faunas. The studies documented in this issue culminate in a synthesis paper that incorporates the development of a modified conceptual model, supported by quantitative data, that is applicable to a wide range of glacier-fed systems (Milner *et al.*, 2001).

Acknowledgments

This special issue of *Freshwater Biology* has its origins in the project, 'Arctic and Alpine Stream

Table 1 Location and characteristics of the glacier-fed rivers investigated in the AASER project

| River system | Code | Region | Co-ordinates | Max. altitude of catchment (m a.s.l.) | Catchment | | Precipitation (mm), 1996/97 | Number of study reaches | Distance of reaches from glacier (m) | Alitudinal range of river studied (m a.s.l.) | Discharge range (m ³ s ⁻¹) | Treeline altitude (m a.s.l.) |
|--------------|------|-----------------------|---------------------|---------------------------------------|---|---------------------------------|-----------------------------|-------------------------|--------------------------------------|--|---|------------------------------|
| | | | | | area at downstream reach (km ²) | Glacier area (km ²) | | | | | | |
| Taillon | TAI | Pyrenees | 43°06'N, 0°01'W | 2975 | 6.4 | 0.2 | † | 4 | 50–1500 | 1870–2500 | 0.3–0.4 | 1600 |
| Conca | CON | S.E. Alps | 46°06'N, 10°36'E | 3463 | 4.2 | 0.2 | 1497 | 7 | 350–4600 | 1300–2830 | 0.3–2.1 | 2000 |
| Mutt | MUT | N. Alps | 46°33'N, 8°24'E | 3099 | 7 | 0.6 | 1595 | 5 | 5–3600 | 1800–2600 | 0.6–1.5 | 2000 |
| Dalelva | BRI | W. Norway | 61°40'N, 6°50'E | 1915 | 25.6 | 22* | 1270 | 5 | 100–7100 | 10–340 | 0.5–35 | 600 |
| Leirungsåi | LEI | Central Norway | 61°24'N, 8°41'E | 2159 | 400 | 1.2 | c. 800 | 7 | 200–24600 | 970–1550 | 0.4–6.2 | 1050 |
| W-Jökulsá | WJO | Central Iceland | 64°50'N, 18°45'W | 1800 | 840 | 68 | 662 | 11 | 5–45000 | 160–860 | 25–31 | No trees† |
| Bayelva | BAY | Spitsbergen, Svalbard | 78°55'N, 11°50'E | 742 | 30.9 | 12 | 483 | 4 | 300–2900 | 5–50 | 0.01–15.6 | No trees |

*Part of a large plateau glacier with an area of 487 km².

†c. 300 mm recorded during July and August.

‡The natural treeline, without anthropogenic impacts, would be 300–400 m a.s.l.

Ecosystem Research (AASER)', which was supported by the European Commission (contract ENV-CT95-0164) and the Swiss Federal Office for Education and Science (project BBW 95.4390). We are extremely grateful for their financial support and also for the encouragement of the Scientific Officer in the European Commission, Dr Hartmut Barth. Our colleagues in AASER and in the other projects reported in this issue are thanked for their contributions and for valuable discussions on the theme of glacier-fed rivers. The data concerning glacial retreat and advance was kindly supplied from a number of sources. We wish to thank the following referees who have kindly reviewed papers in this issue: Emmanuel Castella, Lynda Corkum, Mike Dobson, Nikolai Friberg, Leo Füreder, Paul Giller, Angela Gurnell, Jill Lancaster, Jean-Luc Peiry, Mark Oswood, Chris Robinson, Jon Sadler, Klement Tockner, Urs Uehlinger, James Ward and Mike Winterbourn. We are especially grateful to Mark Gessner, whose meticulous editing improved the final versions of a number of papers. Finally, we wish to thank all the authors for their patience and understanding in the face of comments, criticisms and ultimatums from the reviewers and editors.

References

- Boon P.J. (1988) The impact of river regulation on invertebrate communities in the U.K. *Regulated Rivers*, **2**, 389–409.
- 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., Lencioni V. & Maiolini B. (1998) Arctic and Alpine Stream Ecosystem Research (AASER). In: Proceedings of the fourth Ny Ålesund Seminar, the Arctic and Global Change, Ravello, Italy, pp. 123–126. Italian National Research Council, Italy.
- Brittain J.E. & Saltveit S.J. (1989) A review of the effect of river regulation on mayflies (Ephemeroptera). *Regulated Rivers*, **3**, 191–204.
- Brittain J.E. & Saltveit S.J. (Eds) (1997) Arctic and Alpine Stream Ecosystem Research (AASER). Unpublished Scientific Report to the EU Commission. *Freshwater Ecology and Inland Fisheries Laboratory*. University of Oslo, Norway.
- 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 glacial rivers in relation to environmental variables. *Freshwater Biology*, **46**, 1723–1736.
- 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.
- Castella E., Adalsteinsson H., Brittain J.E. *et al.* (2001) Macroinvertebrate richness and composition along a latitudinal gradient of European glacier-fed streams. *Freshwater Biology*, **46**, 1811–1831.
- Embleton C. & King C.A.M. (1975) *Glacial and Periglacial Geomorphology*, 2nd edn. Wiley, New York.
- 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.
- Füreder 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.
- Goudie A. (1992) *Environmental Change*. Clarendon Press, Oxford.
- Gurnell A.M., Edwards P.J., Petts G.E. & Ward J.V. (1999) A conceptual model for alpine proglacial river channel evolution under changing climatic conditions. *Catena*, **38**, 223–242.
- Jeník J. (1997) The diversity of mountain life. In: *Mountains of the World* (Eds B. Messerli & J.D. Ives), pp. 199–231. Parthenon Publishing Group, New York.
- Kasser P. (1983) Influences of changes in the glacierised area on summer runoff in the Porte Du Scex drainage basin of the Rhone. *Proceedings of a Symposium on the Hydrology of Glaciers*, International Association de Science Hydrologique, Publication No. **95**, Pp. 221–225.
- Lillehammer, A. & Brittain, J.E. (1978) The invertebrate fauna of streams in Øvre Heimdalen. *Holarctic Ecology*, **1**, 271–276.
- 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., Tockner K. & Ward J.V. (1999) Shifting dominance of subcatchment water sources and flow paths in a glacial floodplain, Val Roseg, Switzerland. *Arctic, Antarctic and Alpine Research*, **31**, 135–150.
- Mayo L.R. & March R.S. (1990) Air temperature and precipitation at Wolverine Glacier, Alaska; Glacier growth in a warmer wetter climate. *Annals of Glaciology*, **14**, 191–194.
- McGregor G., Petts G.E., Gurnell A.M. & Milner A.M. (1995) Sensitivity of alpine stream ecosystems to climatic change and human impacts. *Aquatic Conservation*, **5**, 233–247.
- Melack J.M., Dozier J., Goldman C.R., Greenland D., Milner A.M. & Naiman R.J. (1997) Effects of climate change on inland waters of the Pacific Central Mountains and Western Great Basin of North America. *Hydrological Processes*, **11**, 971–992.
- Milner A.M. (1994) Colonization and succession of invertebrate communities in a new stream in Glacier Bay National Park, Alaska. *Freshwater Biology*, **32**, 53–70.
- Milner A.M., Brittain J.E., Castella E. & Petts G.E. (2001) Trends of macroinvertebrate community structure in glacier-fed rivers in relation to environmental conditions: a synthesis. *Freshwater Biology*, **46**, 1833–1846.
- 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.
- Petersen R.C., Gislason G.M. & Vought L.B.M. (1995) Rivers of the Nordic countries. In: *River and Stream Ecosystems* (Eds C.E. Cushing, K.W. Cummins & G.W. Minshall), pp. 295–341. Elsevier, Amsterdam.
- Petts G.E. & Bickerton M.A. (1994) Influence of water abstraction on the macroinvertebrate community gradient within a glacial system: La Borgne d'Arolla, Valais, Switzerland. *Freshwater Biology*, **32**, 375–386.
- Remmert H. (1980) *Arctic Animal Ecology*. Springer-Verlag, Berlin.
- 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.
- Rosenberg D.M. & Resh V.H. (Eds) (1993) *Freshwater Biomonitoring and Benthic Macro-Invertebrates*. Chapman & Hall, New York.
- 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.
- Sharp M., Richards K.S. & Tranter M. (1998) *Glacier Hydrology and Hydrochemistry*. John Wiley and Sons, Chichester.
- 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.
- Starkel L., Gregory K.J. & Thornes J.B. (1991) *Temperate Palaeohydrology*. Wiley, Chichester, UK.
- Steffan A.W. (1971) Chironomid (Diptera) biocoenoses in Scandinavian glacier brooks. *The Canadian Entomologist*, **103**, 477–486.
- 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 ecosystem (Val Roseg, Switzerland). *Archiv für Hydrobiologie*, **140**, 433–463.
- Ward J.V. (1994) Ecology of alpine streams. *Freshwater Biology*, **32**, 277–294.
- Ward J.V., Bretschko G., Brunke M., Danielopol D., Gibert J., Gonser T. & Hildrew A. (1998) The boundaries of river systems: the metazoan perspective. *Freshwater Biology*, **40**, 531–569.
- Ward J.V. & Stanford J.A. (1983) The serial discontinuity concept of lotic systems. In: *Dynamics of Lotic Ecosystems* (Eds T.D. Fontaine & S.M. Bartell), pp. 29–42. Ann Arbor Science, Ann Arbor, MI.
- Winkler S., Haakensen N., Nesje A. & Rye N. (1997) Glaziale Dynamik in Westnorwegen – Ablauf und Ursachen des aktuellen Gletschervorstoßes am Jostedalbreen. *Petermanns Geographische Mitteilungen*, **141**, 43–63.
- Zah R. & Uehlinger U. (2001) Particulate organic matter inputs to a glacial stream eco-system in the Swiss Alps. *Freshwater Biology*, **46**, 1597–1608.

(Manuscript accepted 5 September 2001)