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Vulnerability of alpine stream biodiversity to shrinking glaciers and snowpacks

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Abstract

Climate change poses a considerable threat to the biodiversity of high latitude and altitude ecosystems, with alpine regions across the world already showing responses to warming. However, despite probable hydrological change as alpine glaciers and snowpacks shrink, links between alpine stream biota and reduced meltwater input are virtually unknown. Using data from the French Pyrénées, we demonstrate that taxonomic richness and total abundance of stream macroinvertebrates increase significantly as meltwater (snow melt and glacier melt) contributions to river flow decrease. Macroinvertebrate species showed a gradation of optimum meltwater conditions at which they persist. For example: *Habroleptoides berthelemyi* (Ephemeroptera), *Perla grandis* (Plecoptera) and *Rhithrogena* spp. (Ephemeroptera) increased in abundance when meltwater contributions to streamflow decrease, whereas in contrast, *Rhyacophila angelieri* (Trichoptera) and *Diamesa latitarsis* spp. (Diptera) decreased in abundance. Changes in alpine stream macroinvertebrate community composition as meltwater contributions decline were associated with lower suspended sediment concentration, and higher water temperature, electrical conductivity and pH. Our results suggest α diversity (at a site) of streams presently fed by meltwaters will increase with future meltwater reductions. However, β diversity (between-sites) will be reduced as snow melt and glacier melt decrease because the habitat heterogeneity associated with spatiotemporal variability of water source contributions will become lower as meltwater contributions decline. Extinction of some endemic alpine aquatic species (such as the Pyrenean caddis fly *R. angelieri*) is predicted with reduced meltwater inputs, leading to decreases in γ diversity (region). Our identification of significant links between meltwater production and stream macroinvertebrate biodiversity has wider implications for the conservation of alpine river ecosystems under scenarios of climate change induced glacier and snowpack loss.

Keywords: biodiversity, climate change, endemic, French Pyrénées, river

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Introduction

Climate change poses a considerable threat to global biodiversity because of its potential for species extinction (Harte *et al*., 2004; Thomas *et al*., 2004). Alpine ecosystems, widely distributed throughout both hemispheres in mountainous regions above the permanent treeline, will respond rapidly to anticipated global temperature rise (Beniston, 2000). Species loss could be considerable because the range of micro-climates leads to extensive small-scale habitat diversity and thus high biodiversity (Körner *et al*., 2005). Several studies have already documented the vulnerability of alpine terrestrial plant and animal species to recent warming (e.g. Nagy *et al*., 2003; Körner *et al*., 2005). However, our knowledge of how alpine aquatic ecosystems will respond to climate change is limited, despite the likelihood of marked hydrological change as snowpacks and glaciers shrink (Barnett *et al*., 2005).

Glacier mass-balances show consistent decreases over the last century in most regions of the world and retreat may be accelerating in many locations (Dyurgerov & Meier, 2000; IAHS (ICSI) – UNEP – UNESCO, 2005).

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Negative glacier mass-balance is frequently attributed to a warmer climate, leading to major shifts in water sourcing of alpine streams with glacier- and snow-melt reductions (Barnett *et al*., 2005), proportionally greater groundwater contributions (Brown *et al*., 2006b) and changes in proglacial riverscape dynamics (Malard *et al*., 2006). These changes are likely to have significant, widespread consequences for the fauna of alpine stream ecosystems that are strongly influenced by river channel stability, water temperature and suspended sediment concentration, properties determined by relative meltwater contributions and valley geomorphology (e.g. Milner *et al*., 2001a). The chironomid *Diamesa* typically dominates European glacier-fed rivers where maximum water temperature is $<2\,^{\circ}$C and river channel stability is low. Further downstream from the glacier margin (as channels become more stable and water temperature increases), Ephemeroptera, Plecoptera and Trichoptera (EPT) genera become more dominant along with Simuliidae and other chironomids (e.g. Chironominae; Castella *et al*., 2001; Milner *et al*., 2001a).

Despite the influence of meltwater on alpine stream ecosystems, no studies have quantified links between water source (i.e. snow, glaciers and groundwater) contributions and macroinvertebrate community structure (Brown *et al*., 2003). If we are to accurately predict the response of alpine stream biota to reduced meltwater production under global climate change scenarios, it is critical that this relationship is defined across a continuum of meltwater to groundwater contributions to streams, and the underlying causal mechanisms identified. Understanding these fundamental hydroecological relationships is essential for devising effective conservation strategies for alpine rivers (Hannah *et al*., in press), particularly because the biogeographical isolation of many mountain ranges, and increasing habitat loss and fragmentation (Monaghan *et al*., 2005), severely restrict migration opportunities for species at risk of extinction due to ensuing meltwater reductions.

This study examines benthic macroinvertebrate community structure (total abundance and diversity) and the abundance of individual macroinvertebrate species in relation to water source contributions in the Taillon-Gabiétous basin, French Pyrénées, where glaciers exhibit high climatic sensitivity and have been in long-term retreat (Hannah *et al*., in press). Benthic macroinvertebrates were collected from, and water source contributions estimated for, three streams draining nested sub-basins with glacierized areas between 2% and 6%. The study aims were: (1) to provide an insight into the vulnerability of alpine river system α, β and γ diversity to meltwater reductions; (2) to determine the response of individual species to reduced meltwater contributions, and; (3) to examine the implications of meltwater reduction for alpine stream conservation strategies. The research design allowed the adoption of an analogue approach to predict stream macroinvertebrate community changes with shifts in meltwater contribution to alpine stream flow.

Methods

Study area

Field observations were made in the Taillon-Gabiétous basin, Cirque de Gavarnie, French Pyrénées (43°6′N, 0°10′W; Fig. 1) between 26 June and 3 September 2002 and 2003. Briefly, the basin covers 6.4 km^2 and ranges from 3144 to 1880 m at the most downstream site. The basin is characterized by steep slopes (30–70°) and glacially overdeepened sub-basins containing the Taillon (0.17 km^2) and Gabiétous (0.09 km^2) Glaciers. The upper basin (Pic du Taillon/Pic des Gabiétous) drains Marboré sandstone interspersed with Cenomanian/Turonian limestone outcrops, and sandy limestone of the Santonien and Conacien series. The lower basin (Vallée des Pouey Aspé) is a wide, gentle gradient valley composed mainly of carboniferous shale and Cenomanian/Turonian limestone. The study area is described in more detail by Hannah *et al*. (in press).

Water source contributions and physicochemical habitat variables

Water source contributions were estimated for three sites using hydrochemical data to inform end member mixing analyses (see Brown *et al*., 2006b for full details). Sites A and C were on the Taillon Glacier stream, up- and down-stream, respectively, of the confluence with the groundwater-dominated Tourettes stream (Site B; Fig. 1). Glacierized area for Site A, B and C was 6%, 2% and 4%, respectively. Dilute snow melt and ice melt, and slower routed subglacial waters (Brown *et al*., 2006b) were combined to provide an indication of the relative contribution of meltwater (snow melt and glacier ice melt) vs. groundwater to streamflow. Stream pH was measured twice weekly at each site using a Jenway 3150 portable meter (Barloworld Scientific Ltd, Dunmow, UK). Stream discharge, suspended sediment concentration, water temperature and electrical conductivity were measured every 10 s and averaged over 15 min using Campbell Scientific CR10/21X and Gemini TinyTag dataloggers (see Brown *et al*., 2006a, b for full details). Channel stability was estimated by calculating the bottom component of the Pfankuch Index, which incorporates measurements of rock angularity/embedding/colour and aquatic vegetation cover (Pfankuch, 1975). Habitat measurements were repeated for each macroinvertebrate sampling occasion.

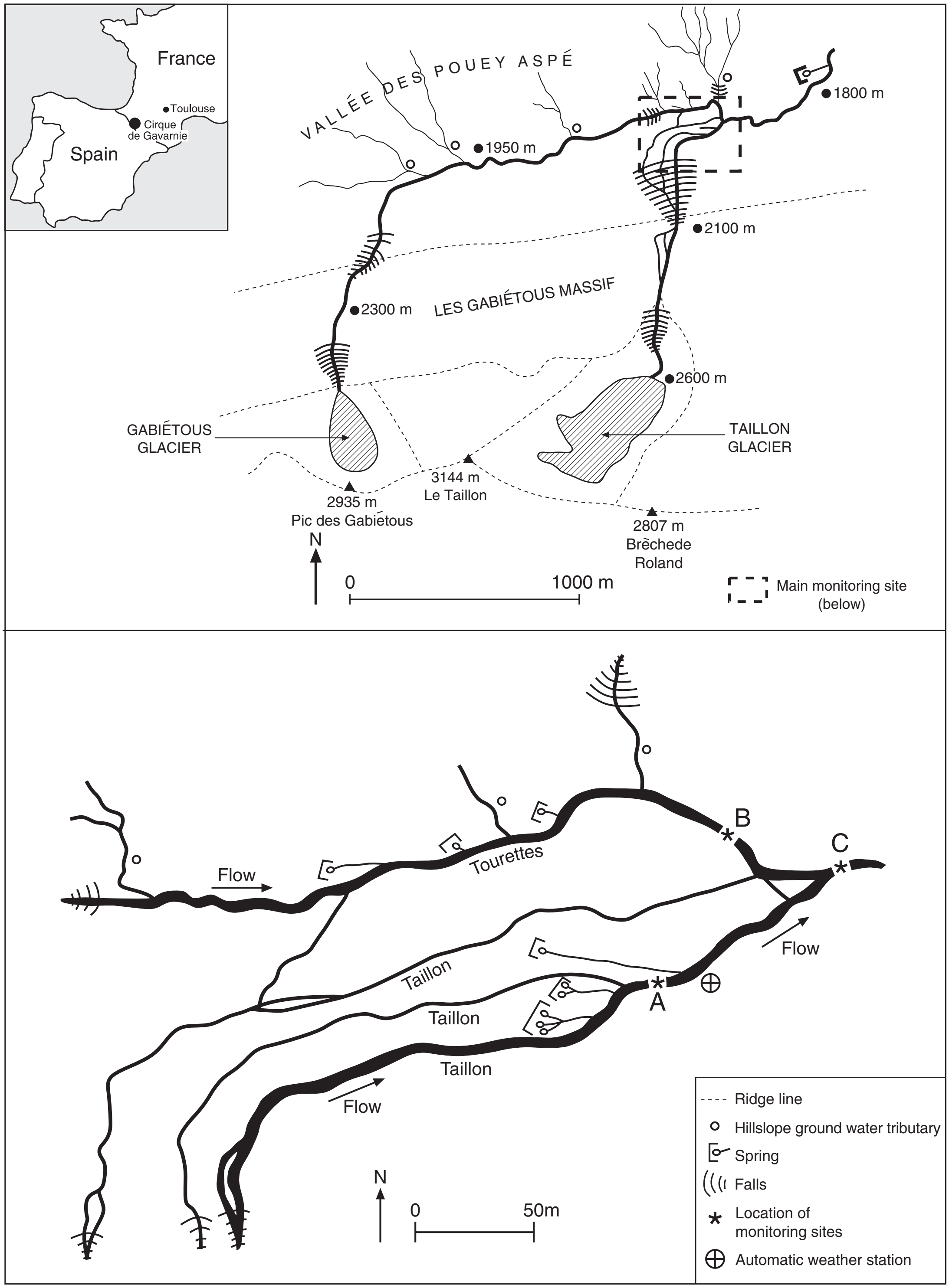

Fig. 1 Map of the Taillon-Gabiétous basin showing location of monitoring sites.

Stream macro invertebrates

Five 0.1 m^2 Surber samples (250 μm mesh net) were collected six times at each of the three sites throughout both melt seasons (biweekly, late June–early September; $n = 36$) following methods detailed by Brown *et al*. (2006c). Organisms were preserved in 4% formaldehyde in the field, then sorted under a light microscope (×10 magnification) and stored in 70% ethanol. Where possible, EPT and Chironomidae were identified to species but other taxa could only be identified confidently to genus/family. Chironomidae were identified following methods detailed by Snook & Milner (2001). Taxonomic publications used for identification were detailed by Snook & Milner (2002). Replicate sample data for each site/sampling occasion were pooled (Woodward *et al.*, 2002) to prevent patch-scale spatial variability affecting reach-scale comparisons of water source contributions and stream macroinvertebrate communities.

Data analysis

Environmental variables (meltwater contributions and physicochemical habitat variables) were tested for normality using the Kolmogorov–Smirnov test, and relationships between meltwater and macroinvertebrate communities examined using linear regression (Zar, 1999) in SPSS version 14.0. An initial detrended correspondence analysis (DCA) in CANOCO version 4.5 showed low species turnover along Axis 1 (Lepš & Šmilauer, 2003). Therefore, redundancy analysis (RDA) was used to test the influence of environmental variables (meltwater contributions and habitat) on stream macroinvertebrate communities. Number of days from start of study was included as an additional explanatory 'habitat' variable to test for seasonal/interannual effects. Macroinvertebrate data were $\log_{10}(x+1)$ transformed and centred by species before analysis. Forward selection was used to test if meltwater and habitat variables explained a significant ($P<0.05$) proportion of the species variance. The significance of the environmental variables was tested against 5000 Monte-Carlo permutations. To separate the variance attributed to the water source contributions and stream habitat variables, variance partitioning (partial RDA) was used following the method of Borcard *et al.* (1992).

To determine the optimum and tolerance of meltwater contributions for individual taxa, a weighted average transfer function with inverse deshrinking was calculated using C^2 version 1.4.3 (Juggins, 2003). β diversity (variation in community composition between each pair of the 36 samples) was calculated using Bray–Curtis dissimilarity coefficients (Bray & Curtis, 1957). Bray–Curtis coefficients of 0 indicate identical samples (i.e. low β diversity) and values of 1 indicate complete dissimilarity between samples (i.e. high β diversity). All statistical tests were considered significant where $P<0.05$.

Results

Taxonomic richness, total macroinvertebrate abundance and number of EPT genera all increased significantly ($P<0.05$) as meltwater contribution decreased (Fig. 2).

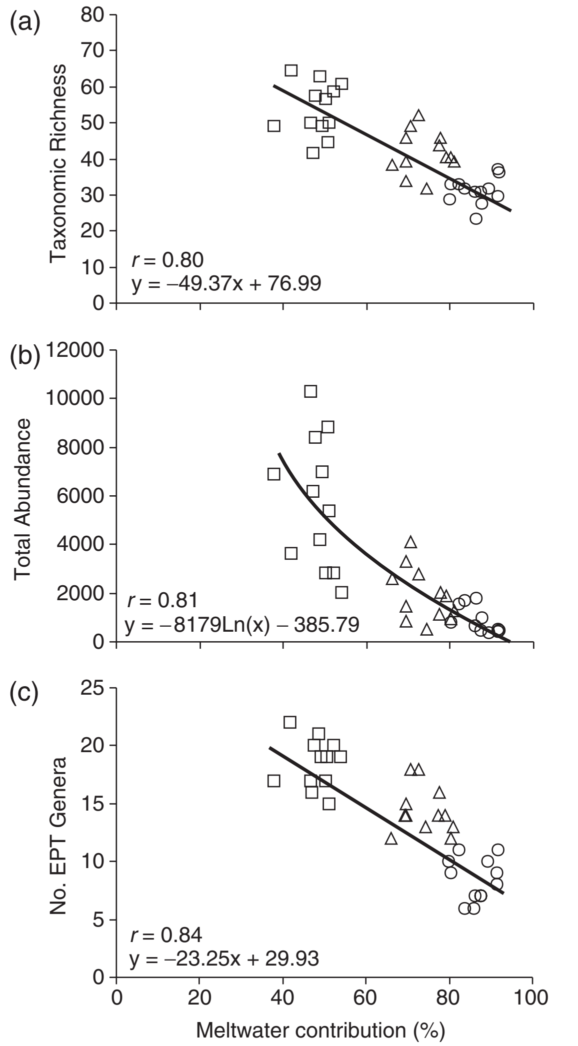

Fig. 2 Relationships between meltwater contribution to total streamflow and: (a) invertebrate taxonomic richness, (b) total invertebrate abundance (# m^{-2}), and (c) number of Ephemeroptera, Plecoptera and Trichoptera genera. All correlations significant at $P<0.01$. (Site A = ○; Site B = □; Site C = △).

Of the 102 macroinvertebrate taxa identified across the three streams, the lowest taxonomic richness (25) corresponded with 86% meltwater contribution and the highest taxonomic richness (63) streams with 42% meltwater contribution. Total macroinvertebrate abundance and the number of EPT taxa increased significantly with meltwater reduction (Fig. 2b and c). β diversity ranged from 0.24 to 0.99 but decreased significantly as meltwater contribution was reduced (Fig. 3).

Axes 1 and 2 of the RDA accounted for 45.7% of the total species variance and 73.8% of the species–environment relation. Species–environment correlations were 0.95 for both axes 1 and 2. Forward selection identified that all the environmental variables, except the Pfan-

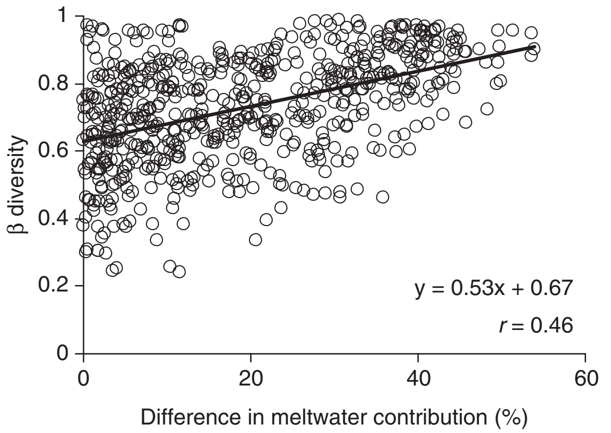

Fig. 3 Relationship between beta diversity (measured by calculating the Bray–Curtis dissimilarity index between samples) and difference in meltwater contribution between samples ($n = 630$). Correlation is significant at $P < 0.0001$.

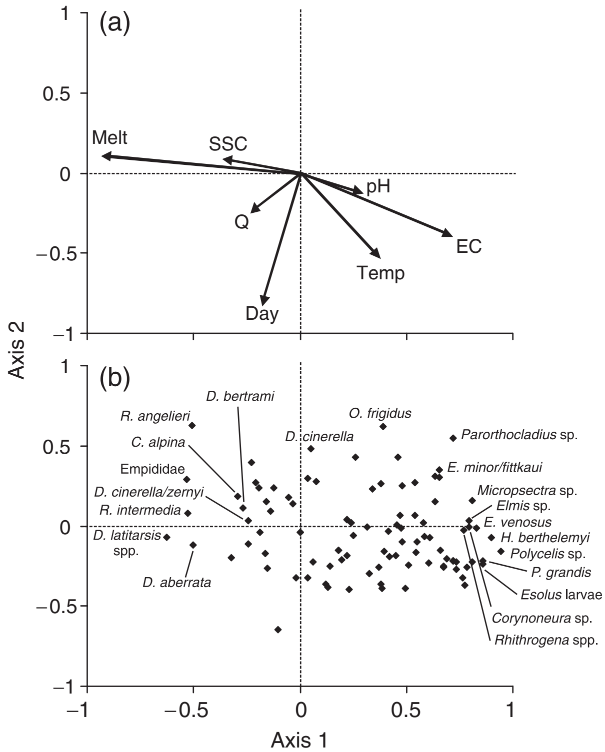

Fig. 4 Redundancy Analysis (RDA) ordination diagrams of (a) environmental variables, and; (b) macroinvertebrate taxa (with selected species highlighted). Melt, meltwater contribution; day, days since start of study; SSC, suspended sediment concentration; Q, stream discharge; Temp, water temperature; and EC, electrical conductivity. Species abbreviations follow Table 1 except *Crenobia alpina*, *Diamesa aberrata*, *Diamesa bertrami*, *Ecdyonurus venosus* and *Rhyacophila intermedia*.

kuch stability score, explained significant amounts of the species variance. Overall, meltwater contribution accounted for the greatest proportion of the total canonical eigenvalues (54%; $F = 18.093$; $P < 0.001$). However, meltwater contribution was correlated with suspended sediment concentration, water temperature, pH and electrical conductivity (Fig. 4). Number of days since beginning of study accounted for 13% of the total canonical eigenvalues. Variance partitioning indicated that meltwater contribution alone accounted for 27.8% of the species variance along axes 1 and 2. Most macroinvertebrate species showed a clear preference for low meltwater conditions (high axis 1 scores) with higher water temperature, pH and electrical conductivity and lower suspended sediment concentration (Fig. 4).

The weighted averaging model gave a root mean square error of prediction of 7%, jack-knifed R^2 of 0.78 and maximum bias of 13%. At the species level, macroinvertebrates clearly showed different responses to meltwater contribution to streamflow. *Pseudokiefferiella parva* had the highest meltwater contribution optimum of all taxa collected (89%; tolerance = 3%) and Ancylidae had the lowest (46%; tolerance 6%). The 20 most abundant taxa (averaged across the 36 samples), were dominated by Chironomidae, and all had optimum meltwater contribution levels of 50% or greater (Table 1). Of these 20 taxa, *R. angelieri* and *Diamesa latitarsis* spp. both had the highest optimum meltwater contributions (77%) and displayed similar tolerance levels. Nevertheless, a gradation of meltwater contribution optima was evident among the most abundant taxa. A more detailed comparison of *Habroleptoides berthelemyi*, *Perla grandis* and *Rhithrogena* spp. abundance in relation to meltwater contributions showed that species also displayed a range of meltwater contribution thresholds below which they were observed in streams (i.e. *H. berthelemyi* <60%, *P. grandis* <80%, *Rhithrogena* spp. <90%; Fig. 5).

Discussion and conclusions

This study yields new insights into alpine stream macroinvertebrate community response to glacier and snowpack reductions. Firstly, alpine stream benthic macroinvertebrate communities and individual species were strongly influenced by reduced meltwater contributions to streamflow. Therefore, these ecosystems are clearly at risk of alteration under scenarios of future climate and hydrological change (cf. Walther *et al.*, 2002). Secondly, although stream macroinvertebrates taxonomic richness and abundance increased significantly with decreased meltwater contribution to streamflow, the vulnerability of individual species adapted to meltwater stream habitats is overlooked by research at

Table 1 Meltwater contribution optimum and tolerance values for the 20 most abundant taxa (in order of decreasing optimum)

Taxa	Optimum (%)	Tolerance (%)
Rhyacophila angelieri	77	12
Diamesa latitarsis spp.	77	11
Diamesa cinerella/zernyi	71	16
Diamesa cinerella	69	17
Orthocladius frigidus	68	17
Simuliidae	67	16
Rhithrogena spp.	66	17
Diamesa zernyi	66	18
Parametricnemus stylatus	65	17
Baetis alpinus	65	17
Eukiefferiella minor/fittkaui	64	18
Esolus angustatus	62	15
Parorthocladius sp.	61	16
Esolus larvae	60	15
Perla grandis	58	14
Rheotanytarsus sp.	57	16
Polycelis sp.	57	14
Micropsectra sp.	55	13
Corynoneura sp.	52	13
Habroleptoides berthelemyi	50	9

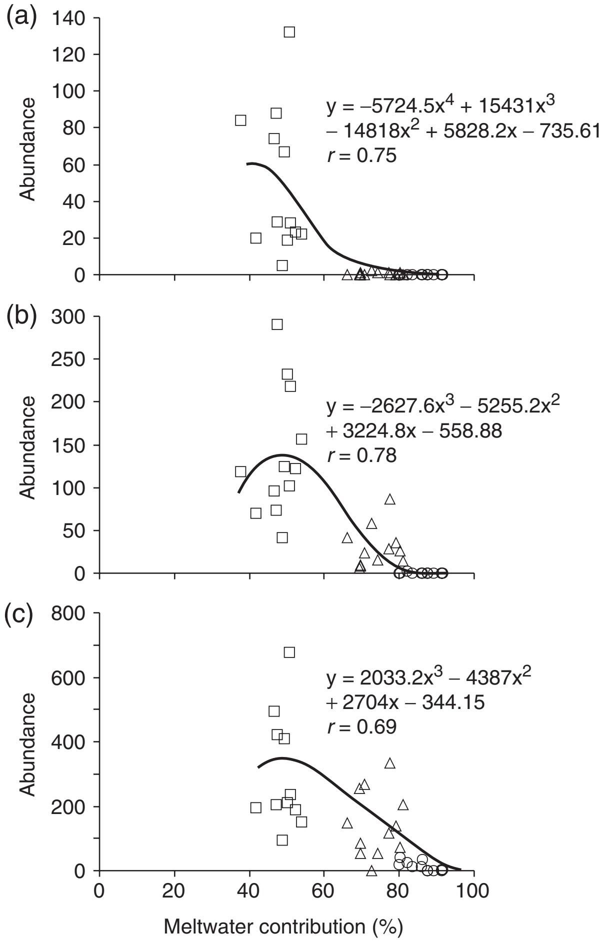

Fig. 5 Relationships between meltwater contribution to total streamflow and abundance (# m^{-2}) of selected taxa: (a) *Habroleptoides berthelemyi*, (b) *Perla grandis*, and (c) *Rhithrogena* spp. (symbols as per Fig. 2).

the community level. This finding demonstrates a need for highly resolved taxonomy in future alpine stream studies to accurately assess ecosystem response to changes in meltwater contribution to stream flow.

Our results suggest that α diversity (at a site) and total abundance of macroinvertebrates of alpine streams currently fed by meltwater will increase as snow melt and glacier melt decrease. Owing to concurrent increases in species richness with total macroinvertebrate abundance, one interpretation could be that α diversity simply increased due to meltwater reductions because more individuals were collected. However, the same operator collected all samples using the same method; therefore, abundance and richness were higher where meltwater contribution was lowest, similar to findings from comparable studies of meltwater and groundwater streams (e.g. Füreder *et al*., 2001). Higher macroinvertebrate abundance with meltwater reductions could subsequently benefit populations of fish and other freshwater insectivores by providing greater food resources, although a lack of detailed food webs for alpine streams precludes more detailed predictions. Conversely, reductions in meltwater production will lead to lower β diversity (between streams) in alpine basins. This reduction is likely because the current spatiotemporal variability of water source contributions (i.e. the mosaic of meltwater, groundwater and mixed streams; Brown *et al*., 2003) is responsible for high habitat heterogeneity (Malard *et al*., 2006) in alpine river systems. If meltwater contributions decline, the physicochemical habitat (e.g. water temperature, chemistry and suspended sediment concentration) across alpine streams that are currently either predominantly groundwater or meltwater fed will become more homogenous. In more extreme cases, some alpine meltwater streams could cease to flow (Uehlinger *et al*., 2006) once meltwater sources become depleted. An increase in the number of ephemeral streams and period of dewatering has potential for marked impacts on alpine macroinvertebrate biodiversity. However, further study is needed to determine the effects of dewatering in addition to the scenario of meltwater reductions examined herein.

Although meltwater contribution plays a key role influencing alpine stream macroinvertebrates, it is important to identify the mechanisms linking cause (meltwater contribution) and effect (macroinvertebrate community response). The results of this study demonstrate that reduced meltwater contributions were associated with lower suspended sediment concentration, and higher water temperature, pH and electrical conductivity. Lower suspended sediment concentration is typically favourable for stream invertebrates because abrasion is lower and primary producer food resources become more available due to increased light penetration (Milner *et al*., 2001a). Because few macroinvertebrate taxa are adapted to cold habitats, increasing water temperature plays a key role allowing macroinvertebrates to colonize as meltwater contributions decrease. Increasing water temperature has also been suggested as a key driver of changes in biological communities of Arctic and alpine lakes (e.g. Sorvari *et al*., 2002; Smol *et al*., 2005; Thompson *et al*., 2005). Therefore, similar causal mechanisms may drive biological community change in both high-altitude and high-latitude rivers and lakes, although further work is clearly required to test this hypothesis.

Although stream macroinvertebrate community metrics (e.g. species richness, abundance) have been offered as potential early indicators of hydrological change in alpine river systems (Milner *et al*., 2001a; Körner *et al*., 2005), they have not previously been quantitatively linked with meltwater contributions to streamflow. The approach detailed herein is a first indication of how macroinvertebrate taxa within these stream communities could be used as indicators of alpine hydrological change. The clear gradation of meltwater contribution optima for macroinvertebrate taxa is a significant finding because it could potentially be developed further to underpin a novel biomonitoring approach for assessing the extent of meltwater contributions to other alpine rivers (where such hydrological insight is lacking). However, data are also required for extremes of meltwater contribution (cf. this study with data only for meltwater contributions between 38% and 92%) to understand species' optima and tolerances more accurately. Although meltwater thresholds for individual species have not previously been demonstrated, they must be related to glacier retreat in similar ways to which successional sequences occur in aquatic and terrestrial systems following deglaciation (e.g. Milner *et al*., 2000; Hodkinson *et al*., 2004).

At present, it is not possible to firmly predict wider alpine stream biodiversity vulnerability to glacier and snowpack loss but this study represents a very important step to advancing our understanding, as it is the first to demonstrate quantitative relationships between macroinvertebrate communities and meltwater contributions. Some endemic species such as *H. berthelemyi* will increase in abundance as meltwater contributions decrease. However, lower abundance of *R. angelieri* and *D. latitarsis* spp. as meltwater contributions to streamflow decrease indicate these species are adapted to habitat conditions in predominantly meltwater-fed streams (e.g. low water temperature, high suspended sediment). *R. angelieri* is endemic to the Pyrénées where widespread glacial retreat is currently occurring (Hannah *et al*., in press), so it is probable that this caddis fly will become extinct with a decrease in meltwater contributions to stream flow as snowpacks and glaciers continue to retreat. For endemic macroinvertebrates adapted to alpine meltwater stream habitats (e.g. *R. angelieri*), migration to other alpine areas is unlikely because of the low biogeographical connectivity of many mountain ranges (minimizing the potential for aquatic invertebrate dispersion via larval drift or adult flight), and increasing habitat loss and fragmentation (Monaghan *et al*., 2005). Thus, although changing habitat conditions in alpine streams may allow species from lower altitudes to colonize, extinctions driven by reduced meltwater contributions will lead to an overall reduction of regional-scale (γ) diversity.

Although our results are based on one French Pyrenean river basin, the loss of aquatic species with meltwater reductions is likely to affect endemic species in other alpine basins. Milner *et al*. (2001b) highlighted how some species of mayfly are unique to New Zealand glacial or alpine streams, and Rossaro *et al*. (2006) discussed several species of chironomid found only in glacier-fed rivers of the European Alps. Our hypothesis that strict cold-stenothermal species, such as those belonging to the *Diamesa latitarsis* group, could be particularly at risk of extinction from glacial retreat and reduced meltwater contributions is supported by Rossaro *et al*. (2006), who observed that these chironomids are no longer found in the Apennine region where glaciers have vanished.

We recognize that this 2-year study in the French Pyrénées only provides an initial evaluation into the vulnerability of alpine stream biodiversity to shrinking glaciers and snowpacks. Further detailed assessments of alpine stream macroinvertebrate populations and their relationships with meltwater contributions are required in other mountain river basins to identify at risk species, and to inform global alpine conservation strategies. In addition to broadening the spatial dimension, studies are required over longer time-scales to assess the effects of changes in peak meltwater production timing, as well as meltwater contribution magnitude discussed herein. Such studies are required immediately to enable a more accurate assessment of extinction risk from climate change than current estimates, which are based only upon terrestrial species (Pounds & Puschendorf, 2004). Where any stream invertebrate populations were found to potentially have long-term futures (i.e. in areas where vestigial glaciers may persist into future), these sites need to be granted special conservation status to prevent additional human pressures (e.g. Schiermeier, 2004). However, in regions such as the Pyrénées, at the southern margin of contemporary European glaciation, rapid warming may lead to the complete loss of glaciers and reductions in seasonal snowpack cover. Therefore, it may be impossible to prevent the loss of species adapted to meltwater stream conditions as climate warms and snowpacks and glaciers shrink. Clearly, this extinction scenario for alpine stream macroinvertebrates is undesirable in terms of biodiversity conservation. Hence, our observations and hypotheses lend further weight to calls for minimizing greenhouse gas emissions to reduce climate change driven glacier and snowpack loss.

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