
Article:

Brown, LE, Dickson, N, Carrivick, J et al. (2015) Alpine river ecosystem response to glacial and anthropogenic flow pulses. Freshwater Science, 34 (4). 1201 - 1215. ISSN: 2161-9549

https://doi.org/10.1086/683062

FWS MS 14-043

Alpine river ecosystem response to glacial and anthropogenic flow pulses

Lee E. Brown[1,3], Neil E. Dickson[1,4], Jonathan L. Carrivick[1,5], Leopold Füreder[2,6]

[1]School of Geography and water@leeds, University of Leeds, Woodhouse Lane, Leeds, LS2 9JT UK

[2]Institute of Ecology, University of Innsbruck, Technikerstrasse 25, A-6020, Innsbruck, Austria

E-mail addresses: [3]l.brown@leeds.ac.uk; [4]neilsletterbox@gmail.com; [5]j.l.carrivick@leeds.ac.uk; [6]leopold.fuereder@uibk.ac.at

Received 3 April 2014; Accepted 16 January 2015; Published online XX Month 2015.

Abstract: Alpine glacier-fed river hydrology, chemistry, and biology can vary significantly in space and over diurnal to interannual time scales as a function of dynamic inputs of water from snow, ice, and ground water. The sensitivity of biota to these water-source dynamics potentially makes them susceptible to hydrological changes induced by anthropogenic activities, such as flow regulation, but most alpine studies have been focused on intact rivers during summer only. We examined the spatiotemporal dynamics of physicochemical habitat and macroinvertebrate assemblages in a high-altitude (>2000 m) floodplain in the European Alps over an 18-mo period. We present a novel insight into the river system and macroinvertebrate assemblage responses to natural glacier-melt-driven expansion–contraction of unregulated river sites and to intermittent flow pulses caused by hydropower regulation. Mainstem glacier-fed sites had cyclical seasonal dynamics in macroinvertebrate assemblage composition that shifted to be partly reminiscent of groundwater tributaries in winter then back to melt water in the following spring. Significant unimodal relationships were found between glacial influence and macroinvertebrate assemblage density, richness, Simpson's diversity, evenness, and β diversity. These relationships suggest that glacial influence can positively affect biodiversity where glacier melt water mixes with nonglacial water and habitat diversity is maximized. Regulation-induced flow pulses led to inconsistent responses among macroinvertebrates, with no significant effects in summer 2008 but increased density and decreased taxonomic richness in 2009. Assemblage composition was unaffected by reservoir releases despite significant increases in water temperature and discharge at these times. The effects of alpine river management for hydropower production on macroinvertebrate assemblages in this river system appear to be relatively minor, but further studies should be undertaken in other alpine locations to assess the generality of this finding.

Key words: flood-pulse, glacier, groundwater, hydropower, macroinvertebrate, reservoir

Alpine zones are found on all continents between the treeline and permanent snowline, and they host an array of glacier-melt, snowmelt, groundwater, and mixed-source rivers that provide considerable heterogeneity of habitat and biodiversity (Füreder 1999, Brown et al. 2003). Recent research has highlighted the potential loss of biodiversity from these systems with glacier retreat via alterations to river flow, water temperature, geomorphology, and water chemistry (Brown et al. 2007, Jacobsen et al. 2012, Cauvy-Fraunié et al. 2014). Alpine aquatic ecosystems appear to be particularly sensitive to environmental change because of strong system linkages between climate, water sources, physicochemical habitat conditions, and biodiversity (Hannah et al. 2007, Brown et al. 2009). Understanding of these linkages has developed mostly from space-for-time approaches, often used along gradients of meltwater contribution, catchment glacial cover, or multivariate glaciality indices (Milner et al. 2009). However, to date, detailed gradient studies on alpine rivers have focused on data collected during the summer melt season only. Thus, such approaches need to be evaluated more thoroughly over annual time scales.

Glacial river systems exhibit considerable seasonal physicochemical habitat change associated with the glacial flood pulse (Malard et al. 2006, Cauvy-Fraunié et al. 2014). Increased snow and ice melt during late spring/early summer leads to the lateral expansion of channel networks across floodplains, and melt water mixes with alluvial and hillslope ground water in varying proportions (Malard et al. 2006). Alpine braided flood plains are ideal for studying these hydrological gradients because rivers with different water sources are colocated within short distances and, thus, are not confounded by altitude, meteorological, or geological/pedological effects. For example, Burgherr et al. (2002) showed that high habitat heterogeneity across the Val Roseg, Swiss Alps, supported considerable macroinvertebrate biodiversity. Although a few investigators have examined stream temperature dynamics across floodplains above the treeline

(Carrivick et al. 2012, Dickson et al. 2012), the relationships among hydrology, physicochemical habitat, and macroinvertebrate assemblages have yet to be reported for these rivers. These alpine systems lack mature vegetation, so allochthonous detritus inputs to river food webs are relatively low. Groundwater stream dynamics in alpine regions also may differ from those below the treeline because lower vegetation biomass and lower temperatures should mean they are influenced less by evapotranspiration of soil/groundwater.

In addition to hydrological dynamics linked to meltwater inputs, many alpine river ecosystems, particularly in Europe, are compromised by anthropogenic regulation for hydropower generation (Füreder et al. 2002, Wehren et al. 2010). However, little is known about anthropogenic regulation effects on alpine rivers because most studies have focussed on sub-treeline rivers below the reflux point of hydroelectricity generating stations (e.g., Brunke 2002, Céréghino et al. 2002, Maiolini et al. 2003). An exception is the study by Petts and Bickerton (1994), which showed that abstraction close to the glacier margin in the Borgne d'Arolla, Switzerland, meant rivers were devoid of fauna because of intermittent flow and frequent turbid purging flows. In contrast, further downstream, the reduction of glacial melt as a proportion of flow (cf. ground water) ameliorated the harsh physicochemical habitat allowing a broader range of macroinvertebrates to colonize. High-altitude reservoir outflows can cause large changes in river discharge (Anselmetti et al. 2007, Wüest 2010) and water temperature (Dickson et al. 2012), but no investigators have yet examined the impacts of alpine reservoir releases on benthic macroinvertebrate assemblages. In Europe, such studies are vital to reconcile requirements of the Water Framework Directive (2000/60/EC) with those of the Renewable Energy Directive (2009/28/EC), particularly in alpine systems, which have unique biodiversity but significant potential for hydropower (Alpine Convention 2009).

We aimed to address the research gaps outlined above by undertaking a year-round study of macroinvertebrate assemblage distribution and diversity across the Eisboden floodplain, Hohe Tauern, Austria, which at certain times of the year is impacted partially by outflow from a hydropower reservoir. We tested the hypothesis that (H_1) the river physicochemical environment and macroinvertebrate assemblages would show a clear seasonal dynamic caused by natural hydrological changes linked to summer glacial meltwater pulses (Malard et al. 2006). We also expected that (H_2) benthic macroinvertebrate assemblages would show unimodal responses to physicochemical habitat dynamics linked to spatial dynamics (i.e., from predominantly ground water to glacial sites; Brown et al. 2007) and changes between time periods linked to the annual melt cycle. These responses should be a consequence of meltwater regimes restricting species to cold water/disturbances specialists, but mixing with warmer ground water, thereby maximizing diversity (Jacobsen et al. 2012). Last, we expected that (H_3) overspill from a storage reservoir in late summer would disturb the natural flow pulse and unimodal patterns of H_2, leading to significant changes in macroinvertebrate assemblages at impacted sites. We discuss our findings in the context of previous work on flood-pulse dynamics, alpine river ecosystems, and the effects of regulation flood flows.

METHODS

Study area and sampling design

The Ödenwinkelkees catchment (9.2 km^2, 19.5% glaciated) is partially within the Hohe Tauern National Park, central Austria (Carrivick et al. 2013). The catchment occasionally receives additional runoff from basins to the west via the Weiβsee hydropower storage lake (surface area = 0.5 km^2, maximum depth = 51 m, volume = 15.7 Mm^3, Dickson et al. 2012). The

Weißsee collects runoff directly from the Sonnblick Glacier river and water routed underground in culverts from Amartaler See (4.3 km west-southwest, 2276 m asl) and Salzplattensee (5.3 km west; 2294 m asl). The Weißsee is not used as a direct feed for hydropower generation. Instead, it serves as secondary storage with water routed to a larger downstream lake (Tauernmoossee) predominantly via the Eisboden and, occasionally, via a river and tunnels in an adjacent valley (Fig. 1).

We monitored 6 sites along part of the Eisboden River, which is sourced from the Ödenwinkelkees (terminus 2197 m asl). The 6 study sites were arrayed across a floodplain 1.5 km downstream from the glacier (2099 m asl; Fig. 2A–D). We selected sites on 3 river types: main glacial river (sites A, B), mixed channels (sites C, D), and groundwater tributaries (sites E, F), so that the contrasting hydrological dynamism would provide a gradient from harsh glacial systems to relatively benign groundwater streams. We selected the 2 main glacial river sites because they defined the main inputs (site A) and output (site B) of the Eisboden, and specifically because site B was known to be periodically affected by dam overspill and active water releases from the Weiβsee, whereas site A could serve as an unimpacted control. Overspill from the Weiβsee commenced on day 230 (19 August) in 2008 and 213 (1 August) in 2009, once the capacity of the reservoir was exceeded. Active water releases were more variable depending on when valves were opened in winter by the hydropower company (Fig. S1).

River environmental variables and benthic macroinvertebrate were sampled on 8 occasions: 3 times during the northern hemisphere summer of 2008, during December 2008 (winter) and March 2009 (spring), and then again 3 times in summer 2009. Summer sampling was undertaken at approximately monthly intervals (Table S1). Sites B and D, and to a lesser extent, site E were affected by overspill from the Weiβsee immediately before August 2008 and

2009 sampling. Overspill elevated water temperatures and discharge (Dickson et al. 2010).

A snowpack of up to 2.7 m depth covered the river system from December 2008 to March 2009 at sites unaffected by reservoir drawdown (sites A, C, and F). We used a dual-phase Leica GPS500 differential global positioning system (GPS; Leica Geosystems, Milton Keynes, UK) in real-time kinematic (RTK) mode, with a base receiver positioned at the Hinterer Schafbichl geodetic control point, with x,y accuracy of ± 0.05 m, to relocate snow-covered sampling sites and assess whether the channels had flowing water. At each site, we carefully excavated snow to locate and download data loggers (see below). Thus, we consistently found and sampled the same locations throughout the study. Site C was not flowing in December 2008, and no flow was observed at sites A, C, or F in March 2009. For channels that retained flow, we excavated a short length of channel (5–10 m) carefully to allow access to the river for macroinvertebrate sampling. To mitigate for any disturbance to benthic fauna during excavation, channel sections were covered with a tarpaulin and left undisturbed for 24 h prior to sampling (as per Schütz et al. 2001, personal communication).

River environmental variables

We measured water depth at each site for the duration of the study with either a Trafag DL/N 70 pressure transducer with integrated data logger (Trafag UK, Basildon, UK), or a Druck PDCR1830 pressure transducer (General Electric Company, Fairfield, Connecticut) connected to a Campbell Scientific CR1000 data logger (Campbell Scientific, Shepshed, UK). Instruments were deployed at river cross-sections where lateral migration was constrained by bedrock or vegetated banks. We used water depth to estimate discharge based on velocity-area or salt-dilution estimates (Dickson et al. 2012), with rating curves for all sites producing R^2 values

>0.90. We monitored water temperature continuously at each site with a Gemini Tinytag data logger (Gemini, Chichester, UK). All water pressure and water temperature data loggers recorded at 15-min intervals. Data were downloaded and internal clocks checked weekly during summer and every 3 mo during winter. A full description of the river thermal regimes was provided by Dickson et al. (2012). We measured electrical conductivity (EC) and pH at each site with a Hach HQ 40d meter (Hach Lange, Düsseldorf, Germany) immediately before every collection of macroinvertebrates. We collected river water samples (~500 mL) concurrently, and measured suspended sediment concentration (SSC) later in the laboratory by filtering samples through Whatman 0.45-µm cellulose nitrate filter papers, drying, and weighing. We assessed channel stability on each sampling visit using the bottom component of the Pfankuch index (Pfankuch 1975). We measured snow depth at each snow-covered site during winter sampling.

Macroinvertebrate sampling

We collected 5 replicate Surber samples (0.05 m^2, 250-µm-mesh net) randomly from different subhabitats (riffles, glides) at each site except A in December 2008 when the Surber net became clogged with ice because of extremely low water and air temperature and only 3 samples could be collected. We always collected samples in the morning to avoid patches of sediment wetted only during peak diurnal flow in late afternoon/evening. We preserved the samples in the field with 70% ethanol prior to subsequent sorting in the laboratory.

We sorted and stored macroinvertebrates in fresh 70% ethanol. We measured ash-free dry mass (AFDM) of benthic particulate organic matter (POM) in the remaining material, including algae, which were not separated from samples, by loss on ignition (Steinman et al. 2006). We initially sorted and counted macroinvertebrates under a light microscope (10× magnification).

We subsampled Chironomidae (*n* = 50/Surber sample), cleared them by soaking in 10% solution of KOH, mounted them ventral side up on slides using Euporal, and examined them at 200 to 1000× magnification (Epler 2001). We identified most individuals to species, except Plecoptera (genus), some Chironomidae (subgenus or genus), and most non-chironomid Diptera (family) (see Appendix S1 for keys). We separated taxa that could not be identified confidently to species level, but were clearly distinguishable based on gross morphological features, into morphogroups. We did not count Oligochaeta because of poor preservation.

Data analysis

We summarized spatial and temporal dynamics of the river system by using discharge and water temperature records to derive 3 indices based on continuous 15-min-resolution data over the 7 d prior to sampling dates: 1) Q = mean discharge, 2) T = mean water temperature, and 3) T_{max} = maximum water temperature. Continuous discharge and water temperature data were not available for site A for the week prior to sampling in June 2009 because a marmot severed the logger cables. We used a linear regression model constructed from 15-min data at sites A and B during the following week to approximate discharge ($r^2 = 0.94$, $p < 0.01$) and water temperature ($r^2 = 0.97$, $p < 0.01$) at site A to enable the calculation of indices (1, 2, and 3) for this sampling period. We used 1-way analysis of variance (ANOVA) to compare each of the physicochemical habitat variables between sites. We did not undertake temporal analyses because measurements of these variables were not replicated on each sampling occasion.

To illustrate the seasonal dynamics of river physicochemical habitat, we calculated a multivariate glaciality index using T, EC, SSC, and Pfankuch stability scores following methods by Ilg and Castella (2006) and Brown et al. (2010). The index provides a synthetic measure of physicochemical harshness in alpine rivers, based on 4 physicochemical variables that are considered to have strong influences on alpine river macroinvertebrate assemblages (Ilg and Castella 2006). We calculated reciprocals of the Pfankuch Index and SSC so that higher values of all constituent data sets equated to low glacial influence, then standardized all data from 0 to 1 prior to calculation of the index based on axis 1 scores from a non-centred principal components analysis (nPCA).

To quantify year-round macroinvertebrate assemblage dynamics at the 6 sites, we used replicate Surber sample data to calculate: 1) density (total number of macroinvertebrates/m^2), 2) taxonomic richness (number of taxa), 3) 1 – Simpson's index of diversity, 4) dominance, 5) mean and standard deviation of β-diversity (for each set of 5 replicates) calculated using Bray–Curtis dissimilarities (Whittaker 1972). Abundance data were $\log_{10}(x + 1)$-transformed prior to statistical analysis. We used analysis of variance (ANOVA) to test for differences in assemblage metrics among sites and sampling periods. Prior to statistical analyses, we tested individual data sets and model residuals for spatial (based on straight-line distance) and temporal (based on calendar day) autocorrelation using Mantel tests. This step was necessary because rivers were in close spatial proximity, some possessed direct up–downstream linkages, and some sets of samples (i.e., summer) were collected relatively closely in time. However, these Mantel tests did not reveal any need to correct for either spatial or temporal autocorrelation (Table S2).

We used nonmetric multidimensional scaling (NMDS) to visualize the extent to which macroinvertebrate composition across the floodplain followed clear seasonal cycles linked to the annual meltwater production cycle. The analysis was based on $\sqrt{(x)}$-transformed abundance data with Bray–Curtis dissimilarities in *vegan* in R (version 2.0-6; R Project for Statistical Computing, Vienna, Austria; Oksanen 2005) with 999 permutations. The replicate samples collected at each site/date were pooled prior to analysis to prevent patch-scale variability from impeding the site-scale comparison over time (Brown et al. 2006). The best 2-dimensional solution was retained following up to 200 restarts. The glaciality index was fitted to the solution post hoc using the *envfit* procedure with 999 permutations. This approach was preferred over direct ordination approaches such as RDA/CCA because NMDS makes no assumptions about the underlying data structure, and better represents the distances between samples in multivariate ordination space (Legendre and Legendre 1998). We undertook analysis of similarity (ANOSIM) on $\log_{10}(x + 1)$-transformed abundance data using Bray–Curtis dissimilarities to assess whether the taxonomic composition of macroinvertebrates differed between 1) all sites, 2) all sampling periods, and 3) sampling periods for individual sites.

We used generalized additive models (GAMs) to assess whether changes in macroinvertebrate assemblage metrics could be predicted from the physicochemical habitat gradient described by the glaciality index. Negative binomial, quasibinomial, or quasiPoisson distribution parameters were estimated following the recursive approach of Barry and Welsh (Barry and Welsh 2002), with Akaike's Information Criterion (AIC) values calculated to identify the best model fit (and for comparison with linear models). Optimum smoothing was selected using the cross-validation approach of Wood (2008).

Overspill flows from the Weißsee in both 2008 and 2009 provided an experimental framework to assess macroinvertebrate assemblage responses to high-altitude river regulation for comparison to the seasonal dynamics. We assessed the extent of any difference in macroinvertebrate assemblage metrics using general linear models (GLM) based on a before-after-control-impact (BACI) design between sites A and B. Results were Bonferroni corrected for multiple comparisons. ANOSIM was undertaken on $\log_{10}(x+1)$-transformed abundance data using Bray–Curtis dissimilarities to assess whether: 1) compositional differences between sampling periods were greater than those within periods, and 2) compositional differences between sites were greater than those within sites.

RESULTS

River environmental variables and glaciality gradients

Clear spatiotemporal differences in physicochemical habitat variables were evident between sites (Table 1). Most measured environmental variables showed variability across seasons and sites, with significant differences observed between sites for EC, channel stability, and Q (Table 1). In general, main-stem sites (A and B) had the harshest physicochemical habitat (i.e., lower maximum water temperature and channel stability, but high Q and SSC). Sites C and D (mixed channels) had intermediate habitat conditions, and sites E and F (ground water) had the least harsh conditions.

Temporal changes in surface hydrological connectivity affected the physicochemical variables and glaciality index scores at our study sites. During summer 2009, a greater proportion of flow from the main channel was routed across to the west side of the floodplain (Fig. 2C, D). This mainly affected sites C and D with higher mean discharges (i.e., in July 2009 vs 2008, site C up from 0.03 to 0.27 m^3/s, and Site D from 0.09 to 0.41 m^3/s) and lower mean river temperature (i.e., in July 2009 vs 2008, site C down from 4.6 to 3.4°C and site D from 5.3 to 3.3°C). The reach in which site E (ground water) was situated became connected with the mixed side channels feeding down the west side of the floodplain, which caused a doubling of mean discharge (0.01 to 0.02 m^3/s) and a slight decrease in temperature (5.4 to 5.1°C).

Axis 1 of the nPCA, which was used to derive the glaciality index, accounted for 60% of the cumulative variance and was negatively associated with all 4 habitat variables (SSC: –0.804, Pfankuch: –0.442, EC: –0.375, water temperature: –0.134; higher index values equal higher glaciality). A relatively wide gradient of glaciality index scores were generated from the physicochemical habitat data sets, and plots of the index per site over time showed only minimal differences between main-stem and mixed-channel sites A to D during the 2 summer monitoring periods (Fig. 3). Groundwater sites E and F had markedly lower glaciality index scores, but a clear pattern of increasing harshness emerged as both melt seasons progressed.

Continuous time-series of river temperature and discharge data sets (e.g., Fig. S1) showed that where rivers were flowing, diurnal variability in discharge and water temperature under snow packs was greatly suppressed during the winter months. Q, T, T_{max}, POM, and SSC were all markedly reduced at sites A and F during winter monitoring periods. Glaciality index scores showed consistently harsh habitats at sites A to D throughout the winter and spring seasons (Fig. 3). Site E had high glaciality scores during December 2008, but the site was much more benign in spring 2009. Site F differed from site E in having low glaciality scores during December 2008 before it ceased to flow.

Macroinvertebrate assemblage composition

More than 17,900 macroinvertebrates were identified, most of which (89% total abundance, 35 taxa) belonged to the Chironomidae. We also observed 11 non-Chironomidae Diptera taxa, 2 Ephemeroptera (*Baetis, Rhithrogena*), 7 Plecoptera (including *Leuctra*, *Nemurella*, *Protonemoura*, and *Perlodes*), and 9 Trichoptera (including *Acrophylax, Lithax*, and *Drusus*). Members of the Chironomidae subfamily Diamesinae were the most dominant taxa at sites A to D, except at site A in August 2008 when *Cheilotrichia* sp. (Limoniidae) dominated the relatively small assemblage (abundance = 40 individuals [ind]/m^2 vs total abundance = 56 ind/m^2). Sixty-six of the 71 taxa observed were found during the summer observation periods.

Macroinvertebrate assemblage density, taxonomic richness, dominance, and Simpson's diversity differed significantly among sites (Table 2), with a clear gradient from meltwater-dominated mainstem sites A and B to groundwater-dominated sites E and F. The composition of macroinvertebrates clearly differed across the river system (ANOSIM, $R = 0.27$, $p < 0.0001$; Fig. 4). These spatial differences were associated strongly with groundwater-fed sites E and F (Table S4). Glacier-dominated mainstem sites (A and B) generally had the most negative scores on NMDS axis 1, mixed sites (C and D) had slightly negative or neutral scores, whereas predominantly groundwater-fed sites (E and F) had positive scores on axis 1. The negative end of Axis 1 of the NMDS plot was associated strongly with Chironomidae taxa (particularly Diamesinae) and *Baetis alpinus*. At the positive end of axis 1, groundwater samples were associated with higher abundance of Trichoptera (particularly *Drusus monticola*) and the Orthocladiinae chironomids *Brillia modesta, Tvetenia*, and *Smittia*.

Forty-two of the 71 taxa observed were found during winter. Five of these were found only during winter (*Diamesa permacer/dampfyi* gr., *B. modesta*, *Smittia* sp., Nemouridae juv., and *Brachyptera* sp.), and *B. modesta* and *Smittia* sp. were observed only under snow cover. Assemblage composition for all samples differed over time (ANOSIM, $R = 0.25$, $p < 0.0001$). All sites differed from period to period, except site A and site E, for which periods 4 and 5 were similar (Table S3). A clear change in the macroinvertebrate assemblage occurred at sites A to D during winter, when assemblage composition became more closely associated with that at sites E and F along NMDS axis 1 (Fig. 4D). The total abundance of *Diamesa* fell drastically (>2600 ind/m^2 in August 2008 vs 660 ind/m^2 in December 2008). In contrast to summer sampling periods, *Acrophylax zebrus*, *Parapsectra* sp., *Heleniella serratosioi*, *Clinocera* sp., and *Dicranota* sp. were present in the winter assemblages. Overall, abundance and richness observed in the snow-covered groundwater river (Site F) were lower (632 ind/m^2, 20 taxa) during December 2008 than during all other sampling periods (abundance >1980 ind/m^2, 21–27 taxa).

Macroinvertebrate density, taxonomic richness, and Simpson's diversity had significant unimodal responses along the glaciality index gradient (Fig. 5A–C, Table 3), whereas dominance and the standard deviation of β diversity estimates were typically highest at the positive end of the glaciality spectrum and relatively similar across mid to low glaciality conditions (Fig. 5D).

River ecosystem response to reservoir overspill

Water temperature and discharge increased significantly at site B (Figs 6A, S1, Table S4) during periods of overspill, whereas physicochemical conditions at site A were relatively similar. Mean daily discharge increased from 1.93 to 2.66 m^3/s (38%) in 2008 and 2.55 to 4.04 m^3/s (58%) in 2009. No clear ecological effects of reservoir overspill were observed in 2008, but in 2009, abundance increased and taxonomic richness decreased at site B in comparison to site A (Fig. 6B, C, Table S4). β diversity also decreased at site B in 2009 (Fig. 6F), but the site × time interaction was not significant. Despite changes in some assemblage-level metrics (Fig. 6C–F), no significant difference was seen in overall assemblage composition (ANOSIM, Table 4).

DISCUSSION

This study has significantly enhanced our understanding of the spatiotemporal dynamics of physicochemical habitat and macroinvertebrate assemblages across a high alpine river–floodplain system throughout the year. It has provided novel insights into the year-round compositional dynamics of alpine river macroinvertebrate assemblages. First, the greatest distinctions among sites were observed in summer when glacial influence was high, whereas sites were more homogenous in winter when glacial influence diminished. These findings are comparable to those from lower altitude, sub-treeline floodplains (Burgherr et al. 2002, Malard et al. 2006). Second, macroinvertebrate assemblage descriptors displayed predominantly unimodal relationships with glaciality index scores and, thus, the gradient of meltwater-groundwater conditions. This finding, based on data collected year-round, adds weight to results of recent studies showing similar relationships from summer sampling campaigns (Jacobsen et al. 2012). Last, despite the widespread nature of regulation for hydropower across the European Alps (Bundi 2010), we found inconsistent or negligible effects of reservoir overspill/regulation on macroinvertebrate assemblages despite significant increases in river flow and water temperature. Each of these novel findings from the study is discussed in turn below.

Effects of meltwater pulses and glaciality gradients on alpine river ecosystems

Our results supported H_1 and the prevailing general consensus that during the summer melt season, different alpine floodplain river habitats are characterized by distinct physicochemical conditions and, thus, macroinvertebrate assemblages (Burgherr et al. 2002, Brown et al. 2003, Malard et al. 2006). Channel stability and water temperature are key physicochemical drivers influencing longitudinal trends in macroinvertebrate assemblages along proglacial rivers (Milner et al. 2001). In our study, these environmental variables varied relatively consistently in space and time in accordance with the glacial flow pulse. The effect of this spatial environmental heterogeneity in the Eisboden was that the lowest macroinvertebrate densities (maximum = 184 ind/m^2) and taxonomic richness (6) were observed at site A, which had harsh physicochemical conditions ($T_{max} < 2.8°C$, mean EC < 30 μS/cm, and low channel stability; Carrivick et al. 2013). The assemblage at site A during summer was typical of a European glacial river close to the glacial margin (Milner et al. 2001), and consisted predominantly of *Diamesa* with the occasional *Eukiefferiella claripennis* and *Cheilotrichia* sp. Macroinvertebrate density was significantly higher in the predominantly groundwater-fed sites (E and F) than in the main glacial river, and assemblages were more diverse, a finding supported by previous studies (e.g., Füreder 1999, Burgherr et al. 2002, Brown et al. 2007). Across the Eisboden, abundances of Trichoptera (with the exception of Psychomyiidae, the only caseless Trichoptera observed) were associated strongly with groundwater contributions. However, this higher abundance contrasted with a study in the French Pyrénées where Brown et al. (2007) found lower Trichoptera abundance in rivers with large groundwater components. A possible explanation is that, in the Eisboden, habitat conditions were too harsh at sites A to D during the summer melt season for Trichoptera taxa to establish in higher abundance than at sites in nearby groundwater rivers. This finding highlights the need for caution in assuming the generality of taxon–environment gradients across alpine habitats (see also Vaughan and Ormerod 2003).

Temperate and subarctic/arctic proglacial floodplains contract during winter as melt-driven inputs are drastically reduced or stop completely, and discharge becomes insufficient to maintain lateral surface connectivity or subsurface pathways feeding groundwater upwellings (Tockner et al. 2000, Malard et al. 2006). At sites on the Eisboden floodplain unaffected by the Weiβsee (sites A, C, and F), discharge declined drastically during autumn/winter to the extent that no surface water was observed during December at site C, and by March, no surface flow was seen at sites A or F. Sites B, D, and E were perennial and typically possessed low and diurnally stable discharge, river temperature, and SSC during winter when reservoir drawdown operations did not occur, as seen in previous studies (Füreder et al. 2001, Robinson et al. 2001, Schütz et al. 2001). These physicochemical habitat changes were reflected in the winter convergence of glaciality index scores.

A distinct shift in macroinvertebrate assemblage composition was observed in December in the main glacial channel at site A, and several taxa not found during summer were observed, including members of the Trichoptera, Plecoptera, Empididae, Pediciidae, and Chironomidae. For example, relatively high abundance of *Parapsectra* sp. was observed under snow at sites A, E, and F, and we found Chironomidae resembling *D. permacer* in winter. This species can tolerate extreme cold conditions and remains active when deep snow covers the ground (Hågvar 2010). We sampled site A only once during winter and collected only 3 subsamples, so the relatively modest increase in taxonomic richness from summer to winter may be a conservative representation of assemblage change. Nevertheless, these findings are supported by increases in diversity seen under winter snow cover elsewhere (see Burgherr and Ward 2001, Füreder et al. 2001, Robinson et al. 2001, Schütz et al. 2001) and are linked to the development of more diurnally benign conditions compared to summer. Thus, the main glacial river macroinvertebrate assemblage more closely resembled groundwater-fed stream assemblages in winter than at any other time of year, providing further support for H_1.

Relatively predictable expansion and contraction cycles of river ecosystems have been linked to flood and flow pulses (Junk et al. 1989, Malard et al. 2006). In the Eisboden, annual observations dating back to ~2001 suggest the main channel is almost always routed down the east side (S. Carver [University of Leeds, UK], personal communication). However, we observed a more stochastic event in August 2009 (see Fig. 1D and Carrivick et al. 2013) when a large volume of flow was routed down the west side. Site E was inundated with meltwater, especially during August, when previously it had no upstream connection to the main channel and was predominantly groundwater-fed. The macroinvertebrate assemblage responded rapidly to this hydrological shift, and composition became more similar to that in the glacial river than at any other time (NMDS). Concurrently, Heptageniidae and Limnephilidae juv. appeared in the main channel (site B) assemblage. These individuals were likely to have drifted downstream from inundated groundwater or mixed sites (Knispel and Castella 2003). However, the Limnephilidae observed at site B were juveniles, and their development probably would have been restricted in the harsh main-channel habitats (Lavandier and Décamps 1984).

Our study of 6 sites over 18 mo provided a broad spectrum of physicochemical conditions from relatively harsh (main channel glacier-fed) to relatively benign (groundwater channels). These harsh–benign (cf. Peckarsky 1983) differences were reflected in significant relationships between glaciality index scores and the responses of benthic macroinvertebrate assemblage density, richness, and Simpson's diversity, and supported H_2. We observed unimodal responses along the gradient, whereas previous investigators using the glaciality index have shown only linear responses (Ilg and Castella 2006, Brown et al. 2010). Similar unimodal findings were reported in a recent meta-analysis of macroinvertebrate assemblage responses to glacier loss. This meta-analysis suggested diversity peaks where glacial cover in catchments ranges from ~5 to 30% (Jacobsen et al. 2012). Our results, together with this previous analysis, further illustrate the potential for significant changes in aquatic biodiversity as glacial influence decreases beyond specific thresholds (Brown et al. 2007).

Effects of flow regulation on alpine river ecosystems

Few investigators have studied the effects of flow regulation on macroinvertebrate assemblages in high alpine rivers (but see Petts and Bickerton 1994). The Weiβsee affects the flow regime of the Eisboden in late summer/early autumn when overspill occurs once the reservoir reaches capacity, then during winter as a series of planned drawdown events to transfer water via the Eisboden to the Tauernmoossee. We did not study these planned events because the loss of surface flow at site A during winter and reduced sampling frequency meant a lack of suitable data for a before-after–control-impact (BACI) analysis. However, site B showed a major shift along NMDS Axis 1 in March 2009, whereas sites D and E did not. Therefore, these winter flow events warrant further detailed study. The only published study in which the authors investigated the effect of reservoir outflow on a high alpine river is one by Dickson et al. (2012), who showed significant increases in river temperature over the period detailed in our study. For mountain rivers, the effects of drawdown discharges on macroinvertebrate assemblages have been assessed in only subalpine systems (see Céréghino et al. 2002, Robinson et al. 2004, Dickson et al. 2012), and so the results of our represent a significant advance in understanding.

Overspill increased T by up to 3.2°C and T_{max} by up to 2.2°C at site B compared with the immediate pre-regulation period (see Dickson et al. 2012) and discharge by up to 58% of pre-overspill flows. Despite these habitat changes, and in contrast to H_3, we found inconsistent evidence for effects on the macroinvertebrate assemblage and changes to density and richness only in 2009. The macroinvertebrates *D. bertrami*, *D. cinerella/zernyi* gr., and *D. latitarsis* increased markedly at site B in August 2009, and overall density increased >10× from before overspill. This increase might have been related to a 58% increase in flow magnitude increase of 58%, on average, in 2009 (compared to 26% in 2008) with mean flows >4 m^3/s, which may have initiated bed movements. Macrroinvertebrates at site A responded similarly in both years before and after overspill, whereas those at site B lacked the late-summer increase in abundance in

2008. This result suggests that the increase in 2009 was not an annual phenomenon arising consistently as a result of overspill but was more likely to be associated with the stochastic rerouting of glacial river flow along the west side of the valley. The overspill did have a more apparent effect on taxonomic richness, which decreased relative to a marginal increase at site A. Some taxa that were unable to exist in the altered hydraulic conditions (Cauvy-Fraunié et al. 2014) may have emigrated at this time, thereby enabling the Chironomidae to become more abundant. The differences between years also may have been the result of a relatively large rainfall event that coincided with the commencement of overspill in 2009 such that site A was disturbed in parallel with the release of reservoir water into site B.

These findings contrast with decreases in the abundance and loss of some species altogether (e.g., *B. muticus*; see Céréghino and Lavandier 1998) following hydropeaking in the French Pyrenees. However, this difference might arise from the much higher altitude of our study sites (>2000 m vs 912 m) and its closer proximity to the glacial margin than the River Oriège sites. As such the macroinvertebrate assemblage of the Eisboden probably consisted of taxa better adapted to the extreme levels of disturbance and harsh physicochemical conditions associated with glacial rivers (Ilg and Castella 2006, Brown and Milner 2012). Common taxa included those with flattened (*Rhithrogena*, *Ecdyonurus*) or cylindrical bodies (*Esolus*, *Limnius*, *Limoniidae*, Empididae, Chironomidae), or crawlers and clingers (e.g., some Trichoptera), which are typically more tolerant of hydropeaking flows or are able to move to refugia (Maiolini et al. 2003). In addition, water temperature decreased as a consequence of water release into the River Oriège, which may have placed a greater physicochemical constraint on the survival and development of macroinvertebrates than the water temperature increases in the Eisboden. Year-round flow was sustained only at sites that were affected by drawdown from the Weiβsee reservoir. Whether Sites B, D, and E would have ceased to flow in winter without water contributions from the Weiβsee is impossible to say, but at the Val Roseg floodplain, Switzerland, Malard et al. (2006) found that although surface flow ceased at the upper part of the floodplain, upwelling sustained flow year-round in the lower half. The Weiβsee certainly did cause discharge to increase significantly at sites B and D and prevented formation of snow packs across the channels at some times. Only after drawdown stopped did snow packs start to accumulate over these river channels. Chironomidae abundance at sites inundated by drawdown waters (B and D) remained relatively high during winter, and this phenomenon has been observed elsewhere under natural flow regime conditions where rivers remain free of snow cover (see Robinson et al. 2001, Burgherr et al. 2002).

Conclusion

We have demonstrated considerable temporal variation in macroinvertebrate assemblages at sub-seasonal and interannual time scales. Quantifying these multiscale variations in alpine aquatic ecosystem dynamics, with a particular emphasis on what happens during winter and summer, is an essential step to understanding the consequences of climate change and anthropogenic modification (Milner et al. 2009). The macroinvertebrate assemblage in mainstem sites changed distinctly during winter. The shift showed that these habitats can support markedly different assemblages from those predicted at other times of the year (Milner et al. 2001). However, the re-imposition of harsh physicochemical conditions during the subsequent summer once again restricts the presence of some taxa from the macroinvertebrate assemblage in glacial rivers. The diversity of river habitats and ecosystems found across the relatively small Eisboden floodplain manifested as unimodal responses of biodiversity measures to glacial influence, a finding that further highlights the potential for significant changes in aquatic biodiversity as glacial influence decreases beyond specific thresholds (Brown et al. 2007, Füreder 2007, Jacobsen et al. 2012).

We have provided novel insights into the effects of reservoir overspill on river habitats and macroinvertebrate assemblages because previous studies in these environments were focused only on subalpine river reaches. Regulation has a relatively large effect on the physicochemical conditions in the Eisboden (Dickson et al. 2012), but in general, the macroinvertebrate assemblage seems surprisingly resilient to these disturbances in comparison with reports from subalpine rivers (e.g., Céréghino et al. 2002, Cortes et al. 2002). However, one cannot conclude in general that the effects of reservoir operation are limited because our study was restricted to a sampling program in a single basin, and we analyzed only summer overspill events. The hydropower station served by the Eisboden also has an expansive spatial footprint (see Fig. 1), and affects multiple rivers across several high alpine valleys. Therefore, it is essential that the effects of anthropogenic flow regulation for hydropower generation in alpine systems be assessed more widely to provide a fuller picture of any effects.

ACKNOWLEDGEMENTS

This research was supported primarily by a Natural Environment Research Council (NERC) studentship (NE/H527467/1) to NED. Additional support to LEB was provided by the Royal Society (International Outgoing Grant 2006/R4), and to LEB and JLC by the Royal Geographical Society–Institute of British Geographers with the Royal Institute of Chartered Surveyors (GFG 39/08) and University of Leeds Academic Fund for Learning and Teaching (2008). Steve Carver, Bob Dickson, Andy Evans, Will Hunt, James Farrell, Naomi van der Velden, and Jeff Warburton provided much appreciated field support. Two anonymous referees provided insights that improved significantly an earlier version of this paper.

LITERATURE CITED

Alpine Convention. 2009. Water and water management issues: report on the state of the Alps. Alpine signals. Special edition 2. Permanent Secretariat of the Alpine Convention, Innsbruck, Austria. (Available from: http://www.alpconv.org/en/alpineknowledge/rsa/water/default.html [last accessed 9 March 2015])

Anselmetti, F. S., R. Buhler, D. Finger, S. Girardclos, A. Lancini, C. Rellstab, and M. Sturm. 2007. Effects of alpine hydropower dams on particle transport and lacustrine sedimentation. Aquatic Sciences 69:179–198.

Barry, S., and A. H. Welsh. 2002. Generalized additive modelling and zero inflated count data. Ecological Modelling 157:179–188.

Brown, L. E., D. M. Hannah, and A. M. Milner. 2003. Alpine stream habitat classification: an alternative approach incorporating the role of dynamic water source contributions. Arctic Antarctic and Alpine Research 35:313–322.

Brown, L. E., D. M. Hannah, and A. M. Milner. 2007. Vulnerability of alpine stream biodiversity to shrinking glaciers and snowpacks. Global Change Biology 13:958–966.

Brown, L. E., D. M. Hannah, and A. M. Milner. 2009. ARISE: a classification tool for Alpine River and Stream Ecosystems. Freshwater Biology 54:1357–1369.

Brown, L. E., D. M. Hannah, and A. M. Milner. 2010. Predicting river ecosystem response to glacial meltwater dynamics: a case study of quantitative water sourcing and glaciality index approaches. Aquatic Sciences 72:325–334.

Brown, L. E., and A. M. Milner. 2012. Rapid loss of glacial ice reveals stream community assembly processes. Global Change Biology 18:2195–2204.

Brown, L. E., A. M. Milner, and D. M. Hannah. 2006. Stability and persistence of alpine stream macroinvertebrate communities and the role of physicochemical habitat variables. Hydrobiologia 560:159–173.

Brown, L. E., A. M. Milner, and D. M. Hannah. 2007. Groundwater influence on alpine stream ecosystems. Freshwater Biology 52:878–890.

Brunke, M. 2002. Floodplains of a regulated southern alpine river (Brenno, Switzerland): ecological assessment and conservation options. Aquatic Conservation: Marine and Freshwater Ecosystems 12:583–599.

Bundi, U. 2010. Alpine waters. Springer, Berlin, Germany.

Burgherr, P., and J. V. Ward. 2001. Longitudinal and seasonal distribution patterns of the benthic fauna of an alpine glacial stream (Val Roseg, Swiss Alps). Freshwater Biology 46:1705–1721.

Burgherr, P., J. V. Ward, and C. T. Robinson. 2002. Seasonal variation in zoobenthos across habitat gradients in an alpine glacial floodplain (Val Roseg, Swiss Alps). Journal of the North American Benthological Society 21:561–575.

Carrivick, J. L., L. E. Brown, D. M. Hannah, and A. G. D. Turner. 2012. Numerical modelling of spatio-temporal thermal heterogeneity in a complex river system. Journal of Hydrology 414/415:491–502.

Carrivick, J. L., M. Geilhausen, J. Warburton, N. E. Dickson, S. J. Carver, A. J. Evans, and L. E. Brown. 2013. Contemporary geomorphological activity throughout the proglacial area of an alpine catchment. Geomorphology 188:83–95.

Cauvy-Fraunié, S., P. Andino, R. Espinosa, R. Calvez, F. Anthelme, D. Jacobsen, and O. Dangles. 2014. Glacial flood pulse effects on benthic fauna in equatorial high-Andean streams. Hydrological Processes 28:3008–3017.

Céréghino, R., P. Cugny, and P. Lavandier. 2002. Influence of intermittent hydropeaking on the longitudinal zonation patterns of benthic invertebrates in a mountain stream. International Review of Hydrobiology 87:47–60.

Céréghino, R., and P. Lavandier. 1998. Influence of hypolimnetic hydropeaking on the distribution and population dynamics of Ephemeroptera in a mountain stream. Freshwater Biology 40:385–399.

Cortes, R. M. V., M. T. Ferreira, S. V. Oliveira, and D. Oliveira. 2002. Macroinvertebrate community structure in a regulated river segment with different flow conditions. River Research and Applications 18:367–382.

Dickson, N. E., L. E. Brown, and J. L. Carrivick. 2010. Hydroclimatological and anthropogenic influences on stream temperature dynamics of the Eisboden glacier-fed river, Austrian Alps. Pages 725–733 *in* Anon (editor). British Hydrological Society 3rd International Symposium. British Hydrological Society, London, UK.

Dickson, N. E., J. L. Carrivick, and L. E. Brown. 2012. Flow regulation alters alpine river thermal regimes. Journal of Hydrology 464/465:505–516.

Epler, J. H. 2001. Identification manual for the larval chironomidae (Diptera) of North and South Carolina. Division of Water Quality, North Carolina Department of Enviroment and Natural Resources, Raleigh, North Carolina.

Füreder, L. 1999. High alpine streams: cold habitats for insect larvae. Pages 181–196 *in* R. Margesin and F. Schinner (editors). Cold-adapted organisms: ecology, physiology, enzymology, and molecular Biology. Springer, Berlin, Germany.

Füreder, L. 2007. Life at the edge: habitat condition and bottom fauna of Alpine running waters.

International Review of Hydrobiology 92:492–513.

Füreder, L., C. Schütz, M. Wallinger, and R. Burger. 2001. Physico-chemistry and aquatic insects of a glacier-fed and a spring-fed alpine stream. Freshwater Biology 46:1673–1690.

Füreder, L., C. Vacha, K. Amprosi, S. Bühler, C. M. E. Hansen, and C. Moritz. 2002. Reference conditions of alpine streams: physical habitat and ecology. Water, Air, and Soil Pollution: Focus 2:275–294.

Hågvar, S. 2010. A review of Fennoscandian arthropods living on and in snow. European Journal of Entomology 107:281–298.

Hannah, D. M., L. E. Brown, A. M. Milner, A. M. Gurnell, G. R. McGregor, G. E. Petts, B. P. G. Smith, and D. L. Snook. 2007. Integrating climate–hydrology–ecology for alpine river systems. Aquatic Conservation: Marine and Freshwater Ecosystems 17:636–656.

Ilg, C., and E. Castella. 2006. Patterns of macroinvertebrate traits along three glacial stream continuums. Freshwater Biology 51:840–853.

Jacobsen, D., A. M. Milner, L. E. Brown, and O. Dangles. 2012. Biodiversity under threat in glacier-fed river systems. Nature Climate Change 2:361–364.

Junk, W. J., P. B. Bayley, and R. E. Sparks. 1989. The flood pulse concept in river-floodplain systems. Canadian Special Publication of Fisheries and Aquatic Sciences 106:110–127.

Knispel, S., and E. Castella. 2003. Disruption of a longitudinal pattern in environmental factors and benthic fauna by a glacial tributary. Freshwater Biology 48:604–618.

Lavandier, P., and H. Décamps. 1984. Estaragne. Pages 237–264 *in* B. A. Whitton (editor). Ecology of European rivers. Blackwell Scientific, Oxford, UK.

Legendre, P., and L. Legendre. 1998. Numerical ecology. Elsevier, Amsterdam, Netherlands.

Maiolini, B., L. Silveri, and V. Lencioni. 2003. Hydroelectric power generation and disruption of the natural stream flow: effects on the zoobenthic community. Studi Trentini di Scienze Naturali Acta Biologica 83:21–26.

Malard, F., U. Uehlinger, R. Zah, and K. Tockner. 2006. Flood-pulse and riverscape dynamics in a braided glacial river. Ecology 87:704–716.

Milner, A. M., J. E. Brittain, E. Castella, and G. E. Petts. 2001. Trends of macroinvertebrate community structure in glacier-fed rivers in relation to environmental conditions: a synthesis. Freshwater Biology 46:1833–1848.

Milner, A. M., L. E. Brown, and D. M. Hannah. 2009. Hydroecological response of river systems to shrinking glaciers. Hydrological Processes 23:62–77.

Oksanen, J. 2005. Vegan: R functions for vegetation ecologists. R Project for Statistical Computing, Vienna, Austria. (Available from: http://cc.oulu.fi/~jarioksa/softhelp/vegan.html)

Peckarsky, B. L. 1983. Biotic interactions or abiotic limitations? A model of lotic community structure. Pages 303–323 *in* T. D. Fontaine and S. M. Bartell (editors). Dynamics of lotic ecosystems. Ann Arbor Science, Ann Arbor, Michigan.

Petts, G. E., and M. A. Bickerton. 1994. Influence of water abstraction on the macroinvertebrate community gradient within a glacial stream system: La Borgne d'Arolla, Valais, Switzerland. Freshwater Biology 32:375–386.

Pfankuch, D. J. 1975. Stream reach inventory and channel stability evaluation. United States Department of Agriculture Forest Service, Region 1, Missoula, Montana, USA.

Robinson, C. T., S. Aebischer, and U. Uehlinger. 2004. Immediate and habitat-specific responses of macroinvertebrates to sequential, experimental floods. Journal of the North American

Benthological Society 23:853–867.

Robinson, C. T., U. Uehlinger, and M. Hieber. 2001. Spatio-temporal variation in macroinvertebrate assemblages of glacial streams in the Swiss Alps. Freshwater Biology 46:1663–1672.

Schütz, C., M. Wallinger, R. Burger, and L. Füreder. 2001. Effects of snow cover on the benthic fauna in a glacier-fed stream. Freshwater Biology 46:1691–1704.

Steinman, A. D., G. A. Lamberti, and P. R. Leavitt. 2006. Biomass and pigments of benthic algae. Pages 357–379 *in* F. R. Hauer and G. A. Lamberti (editors). Methods in stream ecology. Academic Press, New York, USA.

Tockner, K., F. Malard, and J. V. Ward. 2000. An extension of the flood pulse concept. Hydrological Processes 14:2861–2883.

Vaughan, I. P., and S. J. Ormerod. 2003. Improving the quality of distribution models for conservation by addressing shortcomings in the field collection of training data. Conservation Biology 17:1601–1611.

Wehren, B., B. Schädler, and R. Weingartner. 2010. Human interventions. Pages 71–92 *in* U. Bundi (editor). Alpine waters. Springer, Berlin, Germany

Whittaker, R. H. 1972. Evolution and measurement of species diversity. Taxon 21:213–251.

Wood, S. N. 2008. Fast stable direct fitting and smoothness selection for generalized additive models. Journal of the Royal Statistical Society Series B: Statistical Methodology 70:495–518.

Wüest, A. 2010. Downstream relevance of resevoir managment. Pages 235–246 *in* U. Bundi (editor). Alpine Waters. Springer, Berlin.

FIGURE CAPTIONS

Fig. 1. Map showing hydropower infrastructure associated with the Tauernmoossee dam, and consequent effects of regulation across numerous Alpine rivers. Boxed area shows location of the Eisboden river study site.

Fig. 2. Map (A), and photographs (B–D) of the study area with the locations of the 6 study sites and an overall view of the surface hydrological connectivity within the study area in June 2008 (B), and July (C) and August (D) 2009. Note the majority of flow from the Odenwinkelkees (top right) channelled along the east side of the floodplain in (B). The main Eisboden river flows from right to left (i.e., south–north).

Fig. 3. Temporal changes in the multivariate glaciality index over the duration of the study at mainstem (A and B), mixed (C and D), and groundwater (E and F) sites. High glaciality index values represent harsher conditions with more glacial influence. Missing data points correspond with the loss of surface flow at study sites during winter. Dates are formatted Mon-last 2 digits of the year.

Fig. 4. Nonmetric multidimensional scaling (NMDS) output for the main glacial river at sites A and B (A), mixed-source rivers (B), predominantly groundwater-fed channels (C), and the locations of selected taxa in the NMDS ordination space and the glaciality index vector ($R^2 = 0.45$, $p = 0.001$) (D). Arrows show the temporal progression of assemblage composition at each site. Broken arrows link successive samples where the river had an intermediate phase with no observed flow. Samples collected in December 2008 and March 2009 are labelled as Dec and Mar, respectively. *A.zebrus* = *Acrophylax zebrus*, *B.alpinus* = *Baetis alpinus*, *B.modesta* = *Brillia modesta*, *C.vitellinus* = *Chaetocladius vitellinus*, *D.dampfyi* = *Diamesa dampfyi*, *D.bertrami* = *Diamesa bertrami, Diamesa*

cinerella/zernyi gr., *D.latitarsus* = *Diamesa latitarsus*, *D.steinboecki* = *Diamesa steinboecki*, *D.monticola* = *Drusus monticola*, *E.claripennis* = *Eukiefferiella claripennis*.

Fig. 5. Relationships between the multivariate glaciality index (positive values = greater glacial influence) and $\log_{10}$(density) (A), taxonomic richness (B), 1 – Simpson's diversity index (C), dominance (D), mean of pairwise β diversity scores per site (E), and the standard deviation (SD) of pairwise β diversity scores per site (F). Filled circles are from December 2008 and March 2009, and lines denote generalized additive model (GAM) best fit (solid) and 95% confidence intervals (broken). Ind = individuals.

Fig. 6. Interaction plots showing changes in mean values (± 1 SD) of water temperature (A), $\log_{10}$(density) (B), taxonomic richness (C), 1 – Simpson's diversity (D), dominance (E), and β diversity (F) before and after the onset of Weißsee reservoir overspill which affected site B in 2008 and 2009. Asterisks denote significant differences between sites (see also Table S4). Connecting dashed lines denote a significant effect of time (before–after the release) on between-site differences.

Table 1. Mean (± 1 SD) values of environmental conditions for the 6 monitoring sites over the entire study and analysis of variance (ANOVA) results for differences in environmental conditions among sites. EC = electrical conductivity, POM = particulate organic matter, Q = mean discharge, T = mean temperature, T_{max} = maximum temperature.

Site	pH	EC (µS/cm)	Pfankuch Index	Suspended sediment (mg/L)	POM (g/m^2)	Q (m^3/s)	T (°C)	T_{max} (°C)
A ($n = 7$)	7.45 ± 0.28	30 ± 7	52 ± 0	0.14 ± 0.18	1.93 ± 2.04	1.22 ± 0.67	1.4 ± 0.7	2.8 ± 1.4
B ($n = 8$)	7.45 ± 0.39	32 ± 8	49 ± 0	0.14 ± 0.17	1.39 ± 0.83	1.67 ± 0.82	2.9 ± 2.1	4.7 ± 2.7
C ($n = 6$)	7.52 ± 0.30	30 ± 5	34 ± 0	0.11 ± 0.12	1.52 ± 0.66	0.20 ± 0.17	3.3 ± 1.4	8.4 ± 3.8
D ($n = 8$)	7.37 ± 0.41	32 ± 10	34 ± 0	0.07 ± 0.07	1.96 ± 1.31	0.32 ± 0.21	3.1 ± 2.5	5.9 ± 3.7
E ($n = 8$)	7.49 ± 0.40	46 ± 17	21 ± 4	0.002 ± 0.002	2.71 ± 1.90	0.02 ± 0.01	3.7 ± 2.5	7.2 ± 4.6
F ($n = 7$)	7.74 ± 0.41	64 ± 8	20 ± 0	0.002 ± 0.004	9.50 ± 15.37	0.01 ± 0.004	4.3 ± 2.1	6.3 ± 2.7
ANOVA (site)	$F = 0.818$ $p = 0.544$	$F = 12.2$, $p < 0.0001$	$F = 356.1$ $p < 0.0001$	$F = 2.196$ $p = 0.07$	$F = 1.769$ $p = 0.143$	$F = 17.82$ $p < 0.0001$	$F = 1.55$ $p = 0.197$	$F = 2.335$ $p = 0.06$

Table 2. Mean (±1 SD, $n = 5$) macroinvertebrate assemblage metrics for the 6 monitoring sites over the study period and factorial analysis of variance (ANOVA) results for differences in macroinvertebrate variables (replicated Surber sample data, $n = 209$) and β diversity ($n = 420$) among sites and sampling periods.

Site	Log_{10}(density)	Taxonomic richness	1 – Simpson's diversity	Dominance	β diversity
A	1.88 ± 0.29	5 ± 2	0.58 ± 0.15	0.55 ± 0.18	0.68 ± 0.20
B	2.74 ± 0.62	9 ± 3	0.55 ± 0.23	0.58 ± 0.20	0.58 ± 0.20
C	2.72 ± 0.43	10 ± 4	0.64 ± 0.13	0.50 ± 0.16	0.56 ± 0.21
D	2.91 ± 0.52	11 ± 4	0.65 ± 0.10	0.50 ± 0.12	0.52 ± 0.19
E	3.05 ± 0.68	21 ± 6	0.79 ± 0.09	0.35 ± 0.12	0.63 ± 0.20
F	3.37 ± 0.31	24 ± 3	0.78 ± 0.12	0.37 ± 0.14	0.56 ± 0.11
Site	$F = 78.0$	$F = 198.1$	$F = 77.7$	$F = 53.7$	$F = 2.19$
	$p < 0.0001$	$p < 0.0001$	$p < 0.0001$	$p < 0.0001$	$p = 0.14$
Period	$F = 1.13$	$F = 0.07$	$F = 0.65$	$F = 1.12$	$F = 1.27$
	$p = 0.29$	$p = 0.79$	$p = 0.42$	$p = 0.29$	$p = 0.26$
Site × period	$F = 1.65$	$F = 0.07$	$F = 0.85$	$F = 2.34$	$F = 0.20$
	$p = 0.20$	$p = 0.79$	$p = 0.36$	$p = 0.13$	$p = 0.66$

Table 3. Summary of general additive models (GAMs) of multivariate glaciality index vs macroinvertebrate assemblage metrics

Response variable	Summary statistics	% deviance explained
Log_{10}(density)	$F = 9.4$, $p < 0.001$	31.2
Taxonomic richness	$\chi^2 = 73.5$, $p < 0.001$	63.5
1 – Simpson's diversity	$F = 9.4$, $p < 0.001$	26.2
Dominance	$F = 9.4$, $p < 0.001$	33.7
Mean β diversity	Not significant	–
SD β diversity	$F = 9.4$, $p < 0.001$	24.9

Table 4. Analysis of similarity (ANOSIM) results with Bonferroni-corrected p-values for comparisons of sites A and B before–after reservoir overspill in 2008 and 2009.

	Site A - Before	Site B - Before	Site A - After
2008			
Site B - Before	$p = 1.0$, $R = –0.08$		
Site A - After	$p = 1.0$, $R = 0.13$	$p = 1.0$, $R = 0.32$	
Site B - After	$p = 1.0$, $R = -0.14$	$p = 1.0$, $R = –0.05$	$p = 1.0$, $R = 0.16$
2009			
Site B - Before	$p = 0.66$, $R = 0.38$		
Site A - After	$p = 1.0$, $R = –0.002$	$p = 0.56$, $R = 0.22$	
Site B - After	$p = 0.23$, $R = 0.38$	$p = 0.20$, $R = 0.59$	$p = 0.24$, $R = 0.34$

Figure1

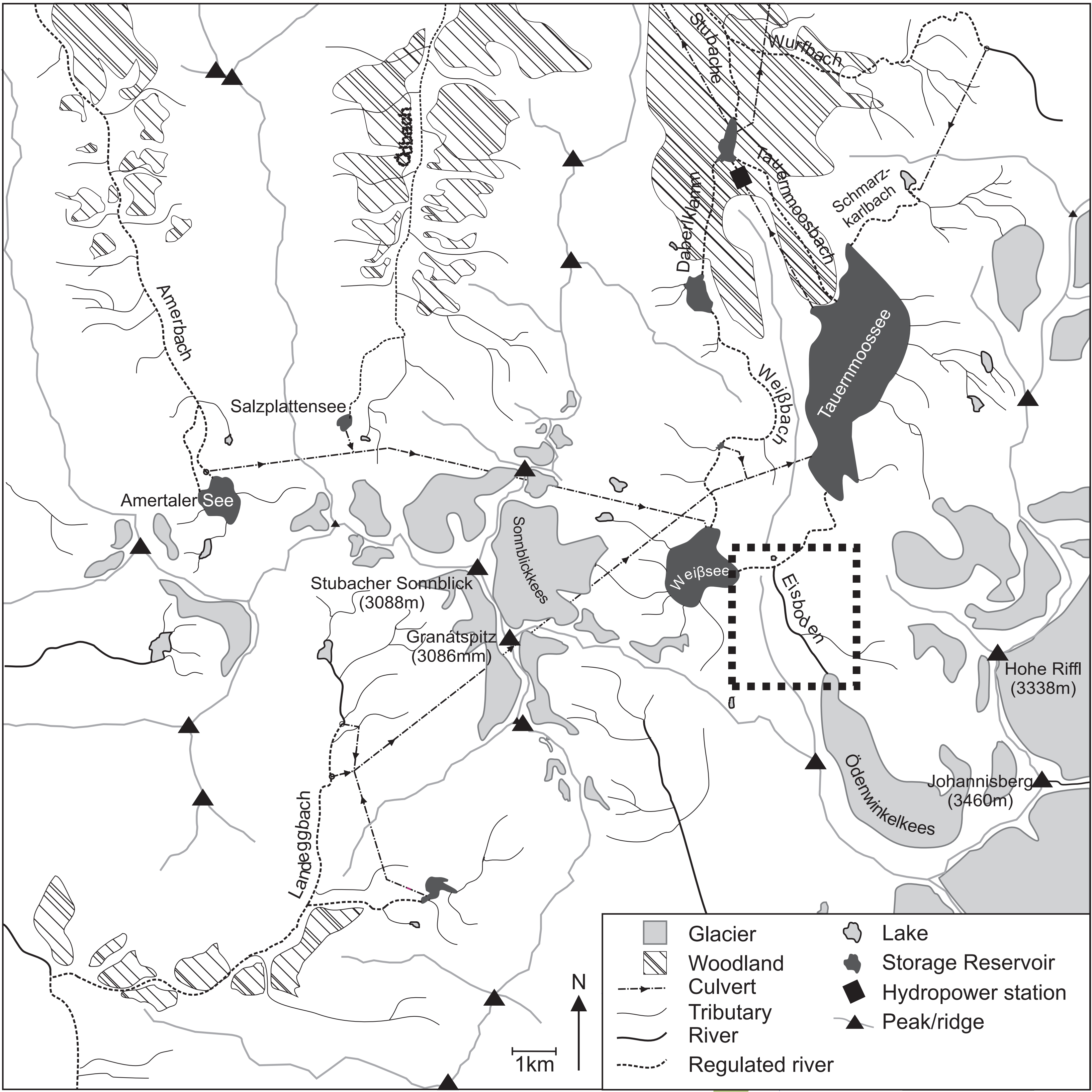

Stubache
Wurfbach
Ödbach
Tauernmoosbach
Schmarz-
karlbach
Daberklamm
Amerbach
Salzplattensee
Tauernmoossee
Weißbach
Amertaler See
Sonnblickkees
Weiβsee
Eisboden
Stubacher Sonnblick
(3088m)
Granatspitz
(3086mm)
Hohe Riffl
(3338m)
Ödenwinkelkees
Johannisberg
(3460m)
Landeggbach
N
1km
Glacier
Woodland
Culvert
Tributary
River
Regulated river
Lake
Storage Reservoir
Hydropower station
Peak/ridge

Figure2

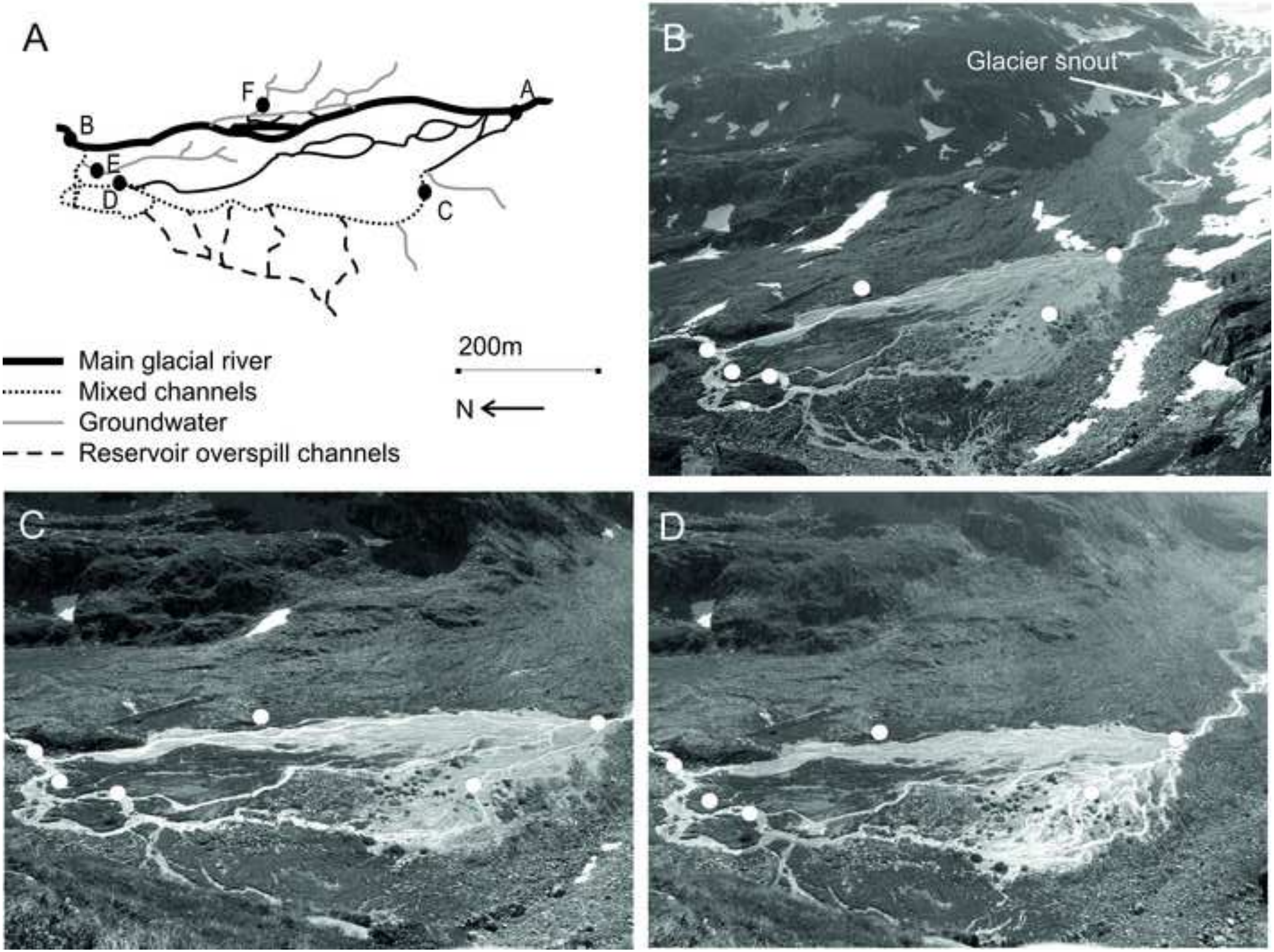

A
F
A
B
E
D
C
Main glacial river
Mixed channels
Groundwater
Reservoir overspill channels
200m
N
B
Glacier snout
C
D

Figure3

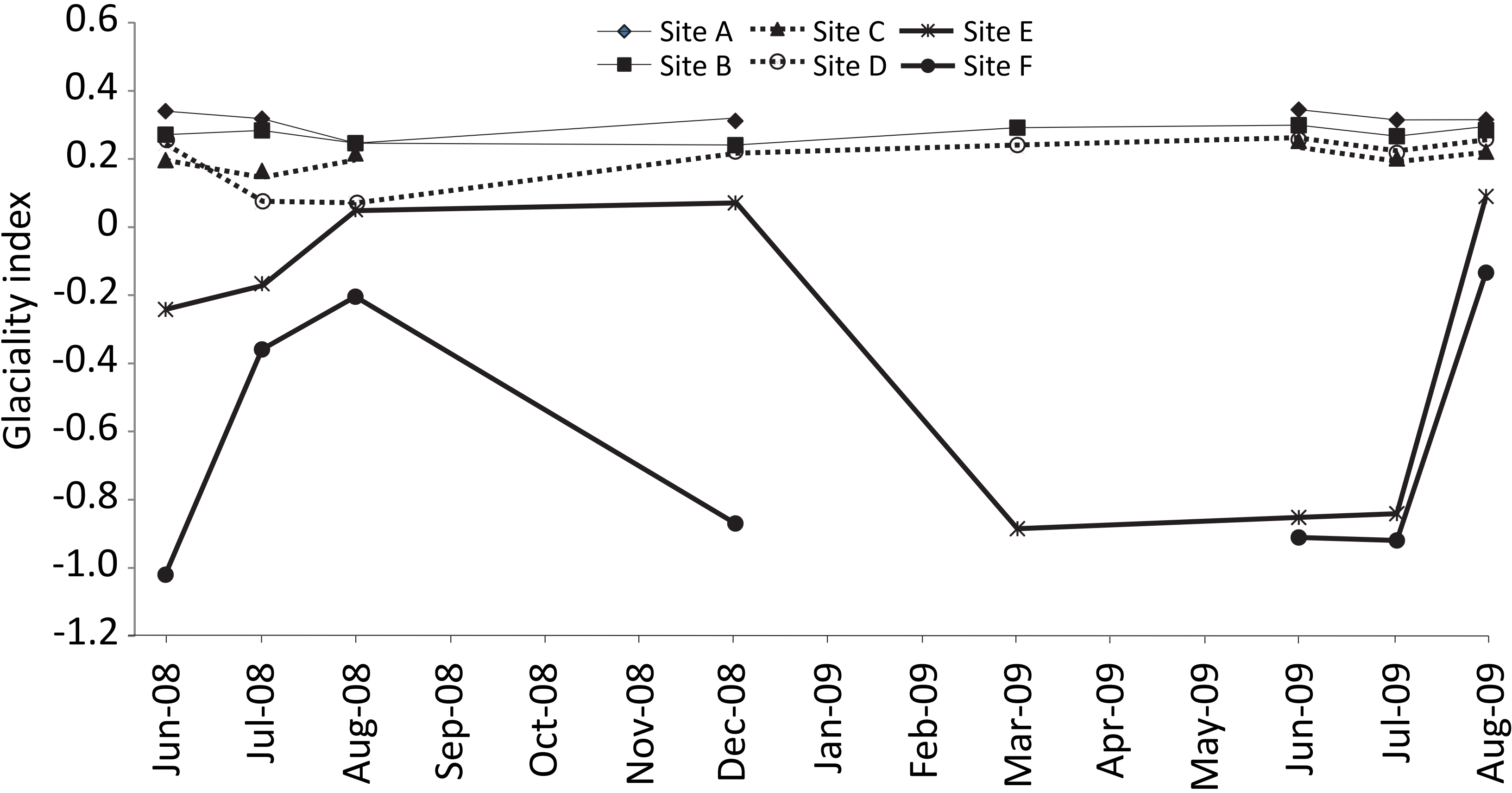

Site A
Site B
Site C
Site D
Site E
Site F
Glaciality index
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-1.0
-1.2
Jun-08
Jul-08
Aug-08
Sep-08
Oct-08
Nov-08
Dec-08
Jan-09
Feb-09
Mar-09
Apr-09
May-09
Jun-09
Jul-09
Aug-09

Figure4

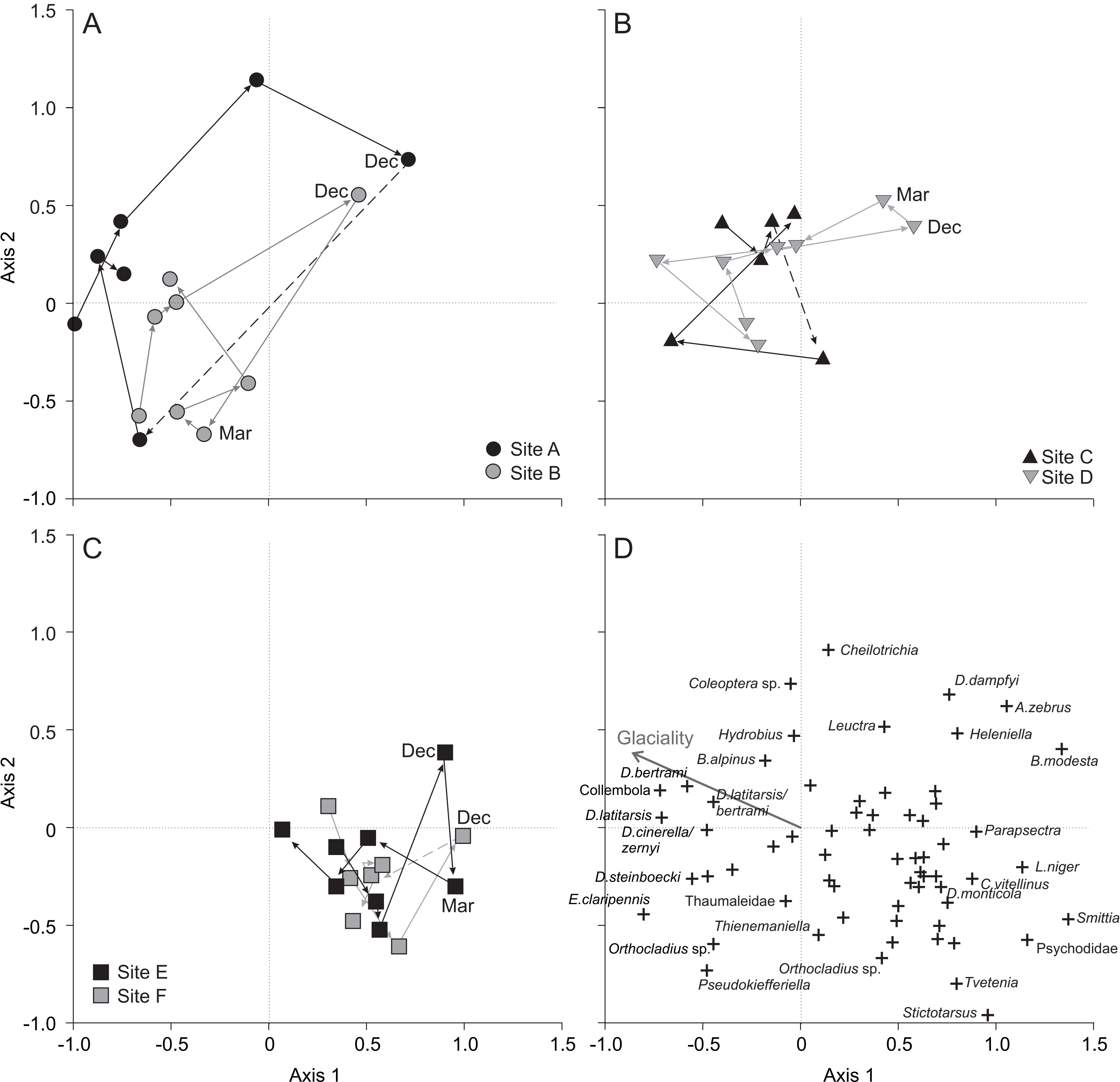

A
B
C
D
1.5
1.0
0.5
0
-0.5
-1.0
Axis 2
Axis 1
-1.0
-0.5
0
0.5
1.0
1.5
Dec
Dec
Mar
Site A
Site B
Mar
Dec
Site C
Site D
Dec
Dec
Mar
Site E
Site F
Cheilotrichia
Coleoptera sp.
D.dampfyi
A.zebrus
Hydrobius
Leuctra
Heleniella
Glaciality
B.alpinus
B.modesta
D.bertrami
Collembola
D.latitarsis/
bertrami
D.latitarsis
D.cinerella/
zernyi
Parapsectra
D.steinboecki
L.niger
C.vitellinus
D.monticola
E.claripennis
Thaumaleidae
Smittia
Thienemaniella
Orthocladius sp.
Psychodidae
Orthocladius sp.
Tvetenia
Pseudokiefferiella
Stictotarsus

Figure5

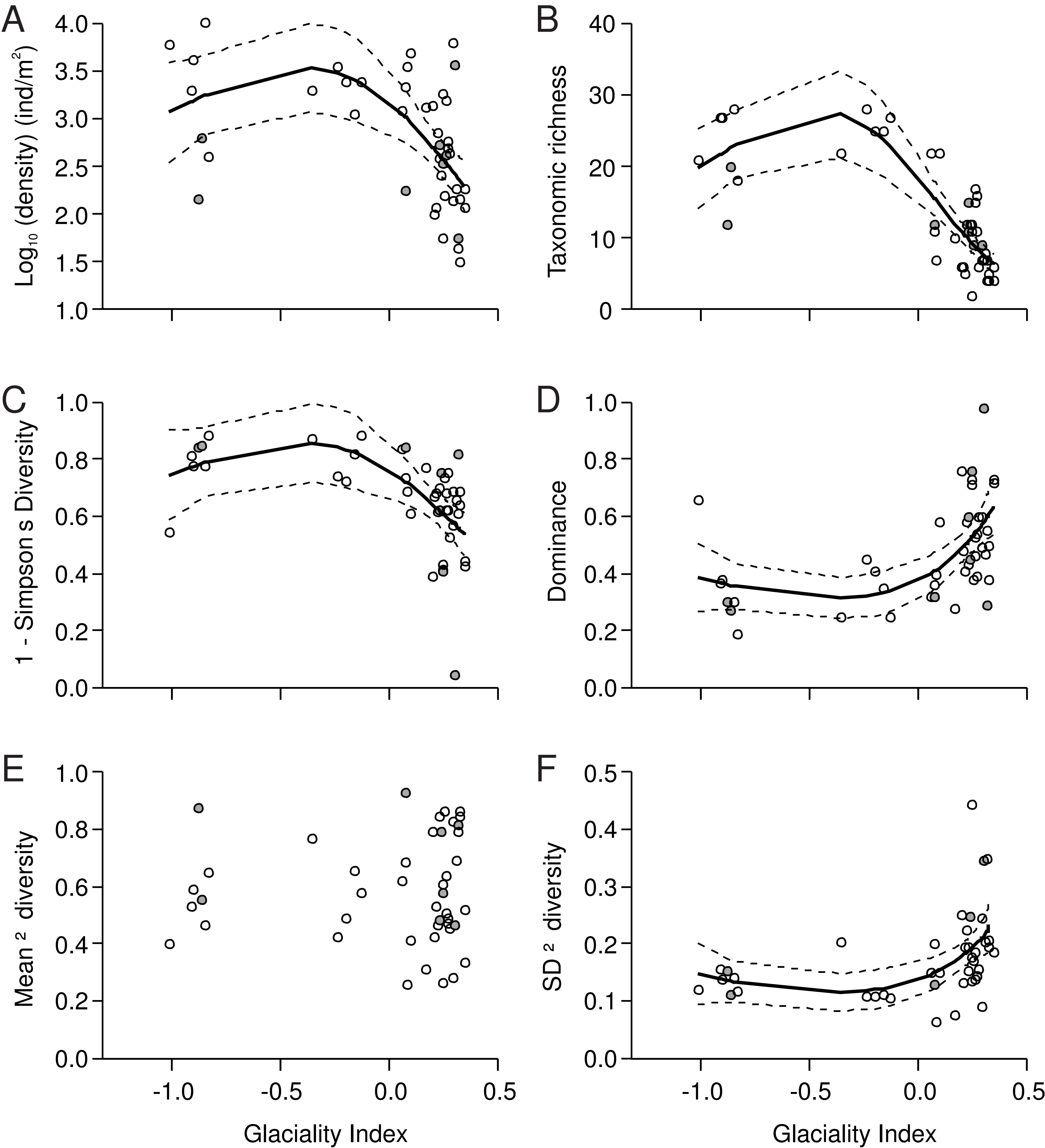
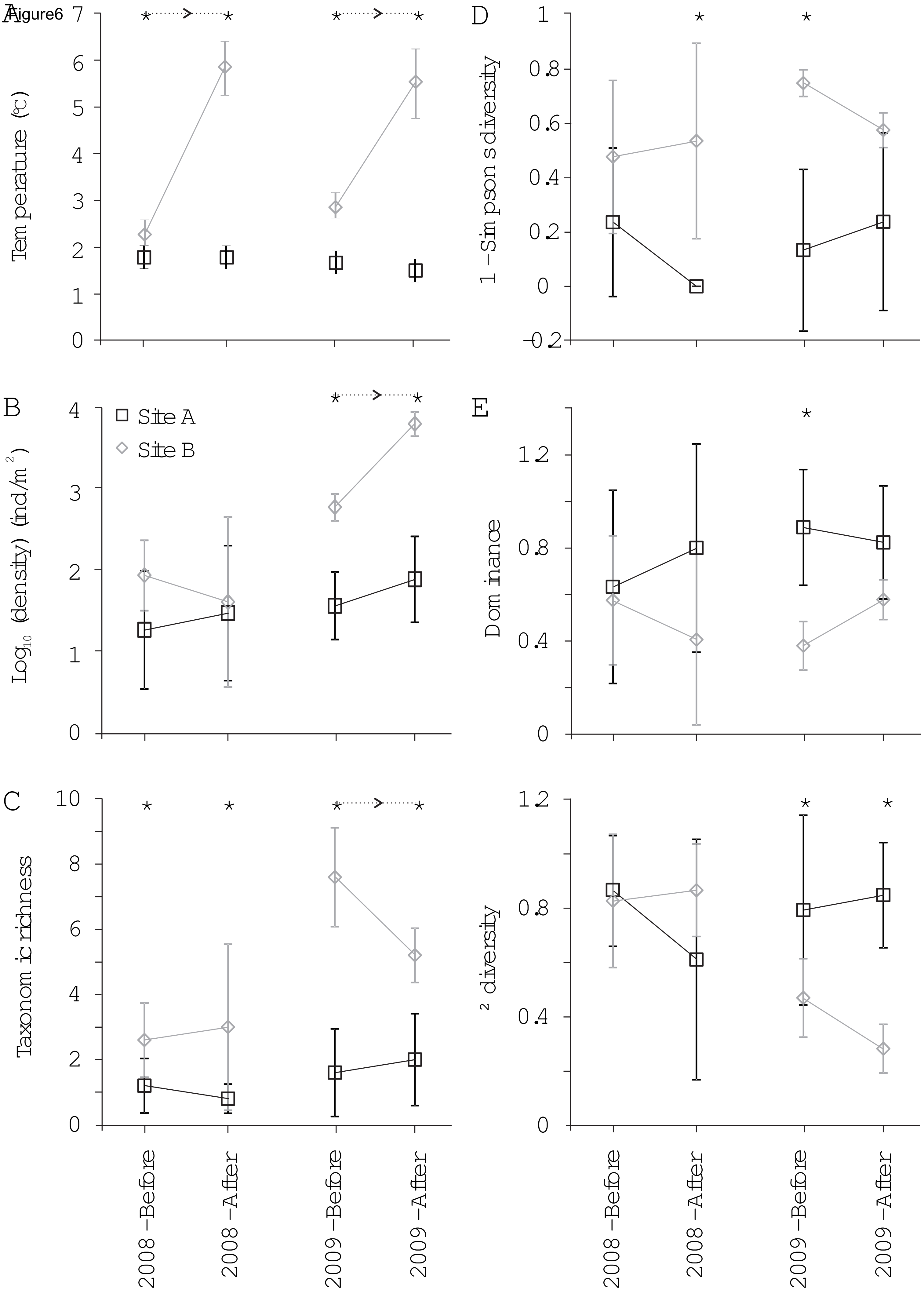

A
Log₁₀ (density) (ind/m²)
4.0
3.5
3.0
2.5
2.0
1.5
1.0
B
Taxonomic richness
40
30
20
10
0
C
1 - Simpson s Diversity
1.0
0.8
0.6
0.4
0.2
0.0
D
Dominance
1.0
0.8
0.6
0.4
0.2
0.0
E
Mean ² diversity
1.0
0.8
0.6
0.4
0.2
0.0
F
SD ² diversity
0.5
0.4
0.3
0.2
0.1
0.0
-1.0
-0.5
0.0
0.5
Glaciality Index
-1.0
-0.5
0.0
0.5
Glaciality Index

Figure6


A
Temperature (℃)
0
1
2
3
4
5
6
7
B
Log$_{10}$ (density) (ind/m^2)
0
1
2
3
4
Site A
Site B
C
Taxonomic richness
0
2
4
6
8
10
D
1 − Simpson s diversity
−0.2
0
0.2
0.4
0.6
0.8
1
E
Dominance
0
0.4
0.8
1.2
² diversity
0
0.4
0.8
1.2
*
2008 − Before
2008 − After
2009 − Before
2009 − After

FigureS1

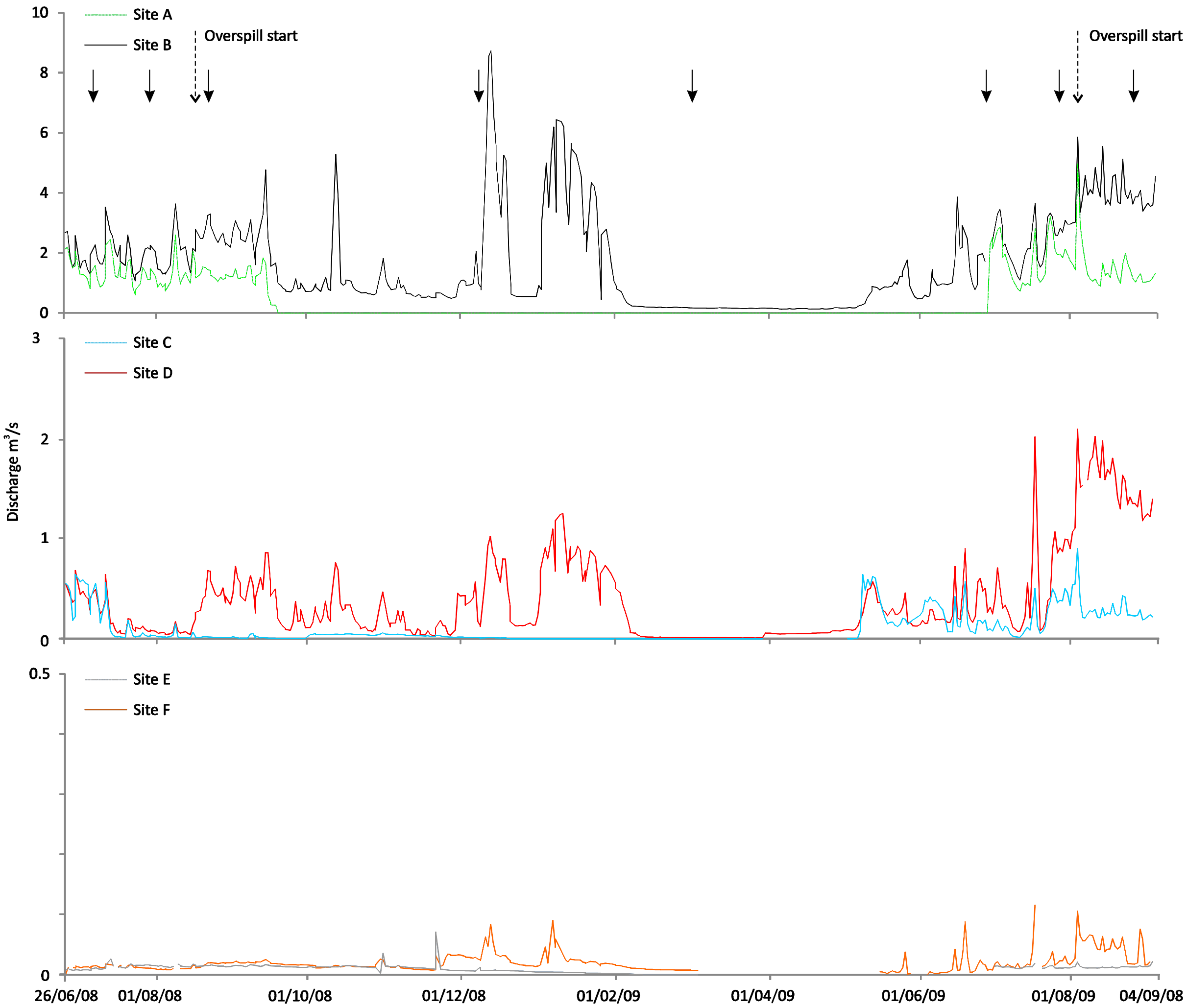


Fig. S1. Hydrographs from the 6 study sites. The distinct summer glacial flow pulse is evident at site A, whereas site B had regulated flows because of late summer overspill and reservoir drawdown in winter. Solid arrows show macroinvertebrate sampling times, and broken arrows show times when reservoir overspill commenced. Peaks at sites B and D between 1 January 2008 and 1 February 2009 coincide with reservoir drawdown releases.

Table S1. Sampling periods, with calendar days given in parentheses.

Sampling period	Year	Site A	Site B	Site C	Site D	Site E	Site F
June	2008	01/07 (183)	01/07 (183)	01/07 (183)	01/07 (183)	01/07 (183)	01/07 (183)
July	2008	31/07 (213)	31/07 (213)	31/07 (213)	31/07 (213)	01/08 (214)	01/08 (214)
August	2008	28/08 (241)	28/08 (241)	28/08 (241)	28/08 (241)	28/08 (241)	28/08 (241)
December	2008	09/12 (344)	09/12 (344)	No observed flow	09/12 (344)	09/12 (344)	09/12 (344)
March	2009	No observed flow	07/03 (66)	No observed flow	07/03 (66)	07/03 (66)	No observed flow
June	2009	30/06 (181)	30/06 (181)	30/06 (181)	30/06 (181)	30/06 (181)	30/06 (181)
July	2009	27/07 (208)	27/07 (208)	27/07 (208)	27/07 (208)	27/07 (208)	27/07 (208)
August	2009	27/08 (239)	27/08 (239)	27/08 (239)	27/08 (239)	27/08 (239)	27/08 (239)

TableS2

Table S2. *P*-values for Mantel tests testing for autocorrelation between sites for each time period, and periods at each site

Between sites for each period	Site A	Site B	Site C	Site D	Site E	Site F		
Richness	0.73	0.42	0.9	0.86	0.78	0.34		
Density	0.51	0.26	0.05	0.09	0.6	0.5		
Dominance	0.87	0.96	0.21	0.37	0.13	0.49		
1/S	0.89	0.99	0.13	0.42	0.17	0.49		
Beta mean	0.29	0.19	0.53	0.23	0.81	0.38		
Beta SD	0.97	0.74	0.31	0.64	0.36	0.78		
Between periods for each site	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**
Richness	0.69	0.55	0.26	0.33	0.34	0.45	0.35	0.41
Density	0.09	0.1	0.09	0.19	0.33	0.43	0.19	0.05
Dominance	0.89	0.69	0.05	0.49	0.34	0.17	0.31	0.44
1/S	0.87	0.92	0.06	0.65	0.33	0.17	0.33	0.46
Beta mean	0.45	0.41	0.65	0.62	0.34	0.08	0.15	0.1
Beta SD	0.39	0.46	0.05	0.33	0.49	0.5	0.16	0.2

Table S3. Analysis of similarity (ANOSIM) results between sites, period, and period for each individual site. Overall *R* and *p*-values are given next to each site name. Unshaded values denote pairwise *p*-values, and shaded values are pairwise *R* values.

Between sites

$R = 0.27$, $p < 0.0001$	A	B	C	D	E	F
A		0.447	1	0.063	0.0015	0.003
B	0.1317		1	1	0.009	0.0045
C	0.05804	0.02232		1	0.0075	0.0435
D	0.2455	0.03069	–0.03181		0.0405	0.003
E	0.5982	0.4983	0.303	0.3493		1
F	0.4754	0.5717	0.3044	0.4886	0.02734	

Between periods

$R = 0.25$, $p < 0.0001$	1	2	3	4	5	6	7	8
1		1	1	0.0616	0.2548	1	1	1
2	0.09259		1	0.042	0.0364	1	1	1
3	0.2315	0.0463		0.4984	0.4788	1	1	1
4	0.4324	0.4185	0.3213		1	0.0672	0.154	0.0672
5	0.3778	0.4389	0.3296	0.06944		0.4592	0.042	0.0532
6	–0.02963	0.1796	0.1704	0.4009	0.3278		1	1
7	0.2667	0.007407	0.08148	0.5343	0.437	0.2148		1
8	0.2352	–0.09259	0.04444	0.5176	0.487	0.2611	0.05	

Site A

$R = 0.22$, $p = 0.005$	1	2	3	4	5	6	7	8
1		0.1177	0.0152	0.0473	–	0.095	0.0319	0.4638
2	0.1563		0.1154	0.3333	–	0.464	0.6288	0.8604
3	0.7062	0.3125		0.3991	–	0.0667	0.0162	0.0597

4	0.8182	0.1429	0.03571			0.3297	0.1861	0.1855
5	–	–	–	–		–	–	–
6	0.7091	0.03571	0.4643	0.75	–		0.1914	0.4674
7	0.244	–0.09375	0.4094	0.1636	–	0.2		0.4406
8	0	–0.1281	0.35	0.2636	–	0.009091	–0.002	
Site B								
$R = 0.44$, $p < 0.0001$	1	2	3	4	5	6	7	8
1		0.0095	0.0104	0.008	0.01	0.308	0.0084	0.0081
2	0.328		0.554	0.0162	0.0228	0.3102	0.0367	0.0079
3	0.4281	–0.04062		0.0181	0.0072	0.2146	0.0162	0.0087
4	0.708	0.392	0.5531		0.0462	0.018	0.0078	0.0088
5	0.548	0.316	0.5688	0.348		0.0479	0.0081	0.0066
6	0.044	0.04	0.09687	0.46	0.24		0.0152	0.0076
7	0.832	0.28	0.3469	0.94	0.928	0.468		0.0087
8	1	0.392	0.5156	0.936	0.932	0.688	0.588	
Site C								
$R = 0.47$, $p < 0.0001$	1	2	3	4	5	6	7	8
1		0.0075	0.0081	–	–	0.2263	0.0096	0.3094
2	0.475		0.0065	–	–	0.0067	0.0078	0.0085
3	0.55	0.544		–	–	0.0083	0.0069	0.0077
4	–	–	–		–	–	–	–
5	–	–	–	–		–	–	–
6	0.08333	0.8125	0.8438	–	–		0.0404	0.0775
7	0.4125	0.912	0.94	–	–	0.3687		0.0165
8	0.05	0.314	0.44	–	–	0.1812	0.354	
Site D								
$R = 0.49$, $p < 0.0001$	1	2	3	4	5	6	7	8
1		0.0094	0.0092	0.0081	0.0074	0.2887	0.0082	0.0079

2	0.672		0.0079	0.0086	0.0089	0.0161	0.0078	0.007
3	0.496	0.432		0.0063	0.0097	0.0152	0.0449	0.1034
4	0.98	0.968	0.848		0.0844	0.007	0.0087	0.0074
5	0.466	0.528	0.396	0.198		0.0096	0.0083	0.0074
6	0.08	0.504	0.38	0.948	0.444		0.0066	0.1082
7	0.82	0.692	0.244	0.984	0.578	0.656		0.007
8	0.408	0.452	0.168	0.984	0.434	0.22	0.336	
Site E								
$R = 0.57$; $p < 0.0001$	1	2	3	4	5	6	7	8
1		0.0071	0.0073	0.0074	0.0074	0.0078	0.0083	0.0082
2	0.98		0.0074	0.0085	0.0067	0.0078	0.0079	0.0087
3	0.968	0.816		0.0081	0.0077	0.0088	0.0083	0.0081
4	0.42	0.384	0.484		0.1623	0.0137	0.024	0.008
5	0.444	0.484	0.632	0.142		0.0082	0.0075	0.0082
6	0.54	0.988	0.964	0.38	0.484		0.0097	0.0081
7	0.808	0.604	0.9	0.416	0.388	0.844		0.0089
8	0.756	0.836	0.896	0.486	0.536	0.876	0.448	
Site F								
$R = 0.70$, $p < 0.0001$	1	2	3	4	5	6	7	8
1		0.0163	0.0077	0.0085	–	0.0081	0.0148	0.0078
2	0.36		0.0086	0.0072	–	0.008	0.12	0.007
3	1	0.54		0.0081	–	0.0077	0.0083	0.0091
4	1	0.824	1		–	0.0076	0.0072	0.0081
5	–	–	–	–		–	–	–
6	0.548	0.556	1	0.948	–		0.0076	0.009
7	0.38	0.128	0.992	0.956	–	0.616		0.0071
8	0.92	0.396	0.588	1	–	0.86	0.724	

Table S4. Analysis of variance statistics for between-site and -period (before–after) comparisons of reservoir overspill releases.

	2008			2009		
Metric	Site	Period	Site × period	Site	Period	Site × period
Water temp.	$F = 503.4$	$F = 472.0$	$F = 470.8$	$F = 1134.5$	$F = 209.1$	$F = 291.2$
	$p < 0.0001$	$p < 0.0001$	$p < 0.0001$	$p < 0.0001$	$p < 0.0001$	$p < 0.0001$
Log$_{10}$ density	$F = 1.30$	$F = 0.029$	$F = 0.570$	$F = 97.15$	$F = 18.17$	$F = 4.879$
	$p = 0.27$	$p = 0.87$	$p = 0.46$	$p < 0.00001$	$p < 0.001$	$p = 0.042$
Richness	$F = 7.448$	$F = 0.0$	$F = 0.368$	$F = 62.235$	$F = 2.941$	$F = 5.765$
	$p = 0.015$	$p = 1.0$	$p = 0.55$	$p < 0.00001$	$p = 0.11$	$p = 0.029$
1-Simpsons	$F = 8.767$	$F = 0.389$	$F = 1.274$	$F = 22.431$	$F = 0.116$	$F = 1.911$
	$p = 0.011$	$p = 0.54$	$p = 0.28$	$p < 0.001$	$p = 0.74$	$p = 0.19$
Dominance	$F = 1.749$	$F = 0.01$	$F = 0.963$	$F = 20.535$	$F = 0.644$	$F = 2.501$
	$p = 0.21$	$p = 0.99$	$p = 0.34$	$p < 0.001$	$p = 0.43$	$p = 0.13$
β diversity	$F = 0.923$	$F = 0.724$	$F = 1.850$	$F = 41.962$	$F = 0.925$	$F = 3.106$
	$p = 0.35$	$p = 0.40$	$p = 0.19$	$p < 0.0001$	$p = 0.34$	$p = 0.09$

Appendix S1. Identification keys used in the study.

Elliott, J. M., U. H. Humpesch, and T. T. Macan (editors). 1988. Larvae of the British Ephemeroptera: a key with ecological notes. Freshwater Biological Association, Cumbria, UK.

Janecek, B. F. R. 1998. Diptera: Chironomidae (Zuckmücken). Bestimmung von 4. Larvenstadien mitteleuropäischer Gattungen und österreichischen Arten. Universität für Bodenkultur Wien (BOKU), Vienna, Austria. 117p

Klausnitzer, B. 1996. Käfer im und am Wasser. Die Neue Brehm-Bücherei, Bd. 567, Westarp Wissenschaften, Magdeburg.

Rivosecchi, L. 1984. Ditteri (Diptera). Guide per il riconoscimento delle species Animali delle acque interne Italiane. AQ/1/206. Consiglio Nazionale Delle Ricerche, Milan, Italy.

Schmid, P. E. (editor). 1993. A key to the larval Chironomidae and their instars from Austrian Danube Region streams and rivers: Part 1. Diamesinae, Prodiamesinae and Orthocladiinae. Wasser und Abwasser Supplementband 3/93: 513p.

Seitz, G. (editor). 1998 Bestimmungsschlüssel für die Präimaginalstadien der Kriebelmücken Deutschlands. Stand: 01.11.1998. Bayrisches Landesamt für Wasserwirtschaft (editor). Dienstbesprechung, Biologisch-ökologische Gewässeruntersuchung, München, Germany. Materialien 77:140–154.

Smith, K. G. V. 1989. An introduction to the immature stages of British flies: Diptera larvae, with notes on eggs, puparia and pupae. Royal Entomological Society, London, UK.

Waringer, J., and W. Graf. 1997. Atlas der österreichischen Köcherfliegenlarven; unter Einschluß der angrenzenden Gebiete. Facultas-Universitätsverlag, Vienna, Austria, 288p.

Wiederholm, T. 1983. Chironomidae of the Holarctic region. Keys and diagnoses. Part 1. Larvae.

Scandinavian Entomology 19:1–449.

Zwick, P. 2004. Key to the West Palaearctic Genera of Stoneflies (Plecoptera) in the Larval Stage. Limnologica 34:315–348.