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Water source dynamics influence macroinvertebrate communities across groundwaterfed streams in a glacierized catchment

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Water source dynamics influence macroinvertebrate communities across groundwater-fed streams in a glacierized catchment

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Abstract Groundwater contributions to streamflow significantly influence the structure and function of riverine ecosystems, particularly in glacierized catchments where there are marked differences in water sources and subsurface flow paths. Here, we investigated spatial and temporal variation in relationships between water sources, flow paths, physical and chemical processes, organic matter, microbial biofilms, and macroinvertebrates across groundwater-fed streams in the glacierized Toklat River catchment of Denali National Park, Alaska. Streams fed predominantly by seepage from the valley sides were perennial, whereas streams sustained by glacial meltwater seepage were ephemeral. Differences in environmental conditions between flow regimes appeared to influence spatial and temporal patterns of organic matter, linking to macroinvertebrate community dynamics. Macroinvertebrates in perennial streams were supported by fine particulate organic matter from subsurface flow paths during summer, transitioning to a combination of fine particulate matter and leaf litter in autumn. In comparison, macroinvertebrates inhabiting ephemeral streams, which only flowed during autumn, were supported by leaf litter. Some macroinvertebrate taxa were unaffected by turnover in organic matter, indicating potential plasticity in organic matter resource use. Findings highlight the importance of considering spatial and temporal variation in groundwater-fed streams, considering that projected hydrological changes under a changing climate may have significant implications for these systems.

This paper is dedicated to the memory of Jill Crossman and was revised and published after her untimely passing.

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Introduction

Groundwater contributions to streamflow in glacierized catchments are vitally important and typically

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create biodiversity hotspots (Murray et al., 2004; Boulton & Hancock, 2006; Murray et al., 2006) by sustaining low variability in flow and water temperature regimes, and high water clarity, when compared to other water sources (Füreder et al., 2001; Malard et al., 2001; Barquin & Death, 2006). Nevertheless, groundwater-fed streams vary in their degree of flow permanence ranging from ephemeral to perennial (Wood et al., 2005; Brown et al., 2007a). In glacierized catchments, this variability in groundwater contributions is a significant driver of macroinvertebrate community composition, yet this topic has generally been overlooked.

Groundwater flow pathways in glacierized catchments typically lie within the most permeable deposits of the valley bottom, valley side, and in bedrock aquifers (Robinson et al., 2008). As a result, features such as river terraces, which are often composed of coarse fluvial deposits, may support groundwater upwellings in glacierized river catchments (Malard, 2003). Groundwater permeating these deposits can be derived from multiple sources, for example, glacial meltwater can infiltrate the underlying alluvial aquifer and then discharge to the surface further down the valley (Malard et al., 1999; Crossman et al., 2011). Alternatively, precipitation can percolate through colluvial and alluvial deposits and remerge at lower elevations when the water table intersects the surface (Crossman et al., 2011). Furthermore, groundwaters can be routed through deposits via different flow pathways (Anderson, 1989), resulting in multiple different types of streams originating on river terraces. The combined effects of water sources and flow paths lead to marked heterogeneity in instream conditions within river terrace streams (e.g., hydrology and physical and chemical processes), as well as influencing the riparian ecotones surrounding the stream channels (Stromberg & Merritt, 2016). This variation in streams and riparian habitats across river terraces is responsible for their role as hotspots of terrestrial and aquatic biodiversity in an otherwise fluvial landscape (Crossman et al., 2012).

Across streams, there may be physical and environmental differences resulting from variation in the relative contributions of groundwater to total stream flow (Kath et al., 2016), the interactive effects of distinct groundwater sources (e.g., snowmelt, surface seepage, and glacial melt), and associated water flow pathways (e.g., deep or shallow subsurface flows) (Khamis et al., 2016). Although physical and chemical variables are generally more stable in groundwater-fed streams than in other stream types, there can still be considerable variability in these variables in groundwater-fed streams in glacierized catchments (Robinson et al., 2008; Windsor et al., 2017; Durkota et al., 2019). Notably, habitat patches within streams can differ in their environmental conditions in response to their proximity to groundwater discharges (Mathers et al., 2017; Crespo-Pereez et al., 2020). Patches close to areas of groundwater exhibit different organic matter and macroinvertebrate community dynamics depending upon the source of groundwater. These characteristics generate variability across spatial and temporal scales in both physical and chemical habitat (flow permanence and environmental stability) and resource availability (nutrient and organic matter concentrations) within and across stream systems (Boulton & Hancock, 2006; Sertić Perić et al., 2021). In turn, this variation influences the biotic communities inhabiting these systems, including microbial biofilms (Colls et al., 2019) and macroinvertebrates (Windsor et al., 2017).

Climatic and associated hydrological change threatens the ecological integrity of groundwater-fed streams in glacierized catchments. For example, estimates in the Toklat catchment in Denali National Park (Alaska, USA) suggest that snow- and glacial meltwater may contribute to an increase in groundwater flow by 2070 (Crossman et al., 2013a). As such, changes in the contributions of groundwater from different water sources are likely to influence the environmental and biological conditions present. Here, we investigate the complex spatial and temporal dynamics of the relationship between macroinvertebrate communities and their physiochemical environment. In doing so, we highlight the role of potential climate change-induced stresses on freshwater communities within glacierized catchments. The specific objectives of the study were to assess:

(i) The spatial and temporal variability in environmental and physical variables (e.g., water source contributions, flow regime, water temperature) in different groundwater-fed streams across the Toklat Catchment in Denali National Park, and;

(ii) The relationships between environmental, physical, and chemical variables and benthic macroinvertebrate communities (overall structure and individual taxa)

Our hypothesis was that we would be able to distinguish between the physical and chemical variables and macroinvertebrate communities associated with different groundwater types. We accomplished these objectives during an intensive summer field campaign sampling perennial and ephemeral streams in a glacierized valley of the Toklat River in Alaska.

Methods

Site description

The Toklat River is a braided north-flowing, glacier-fed tributary of the Yukon River which derives a substantial percentage of its total flow from valley glaciers in its headwaters. The upstream catchment is ~115 km^2 in area, ranging in elevation from 1,835 to 1,197 m. Mean annual precipitation is ~2,400 mm of which ~2,000 mm falls as snow, while mean annual June to September daily air temperature in 2008 (recorded 5 km to the North at the Toklat Road Camp) was 11.8 °C (day) and 4.7 °C (night) (WRCC, 2008). The underlying geology is dominated by Devonian and Silurian clastic and carbonate rocks, with Quaternary and Neogene sediments along the valley sides (Gilbert et al., 1984). Extensive debris fans and talus cones have formed along the valley margins with glacial and fluvial-glacial deposits in the valley bottom.

From May 30th to September 8th, 2008, we studied seven sites across four groundwater-fed streams arising across a fluvial terrace (0.9 km^2 area) on the floodplain of the middle fork of the Toklat River in Denali National Park, Alaska (63°29′19.54″ N, 149°57′54.05″ W). These streams, in comparison to a barren active floodplain, support a dense marginal vegetative community including soapberry [*Shepherdia canadensis* (L.) Nutt.] and dwarf birch (*Betula nana* L.), alongside other riparian specialist plants. Sites were selected to represent different groundwater and riparian conditions (see Table 1). Upstream (A2, A5, B2) and downstream (A1, A4, B3) sites within the same streams were used to compare local variations in the levels of groundwater influence as determined by local flow paths, which were in turn related to the position of the site on the alluvial terrace (Fig. 1). The riparian vegetation associated with individual streams varied, depending on proximity to the active channel, and also the hydrological conditions in the surrounding terrace sediments.

To contextualize the following analyses, precise topographical measurements of the study area, including the position of the channels on the terrace and the elevation of individual sites, were mapped using a Geo electronic distance measurer (LEICA, Wetzlar, Germany).

Water source contributions

A total of 70 water samples were collected at 14-day intervals across all sites and additional samples were collected higher up the catchment to represent specific water sources (e.g., ice-melt, snowmelt, debris fan seepage flow and rainfall). Stream water samples were collected from the center of the stream using

Table 1 Site characteristics of the seven groundwater-fed study streams on the mid-Tolkat floodplain (DFS$_{deep}$ = debris fan side [deep]; GMW$_{riv}$ = glacial meltwater [river])

Site	Flow pathways and sources	Flow permanence	Mean discharge (cumecs)	Mean water temperature (°C)
A1	DFS$_{deep}$	Perennial	0.012	–
A2	DFS$_{deep}$	Perennial	0.006	4.45
A4	DFS$_{deep}$	Perennial	0.016	–
A5	DFS$_{deep}$	Perennial	0.004	4.03
B1	GMW$_{riv}$ and DFS$_{deep}$	Perennial	0.051	3.50
B2	GMW$_{riv}$	Ephemeral	0.041	3.69
B3	GMW$_{riv}$	Ephemeral	0.093	5.34
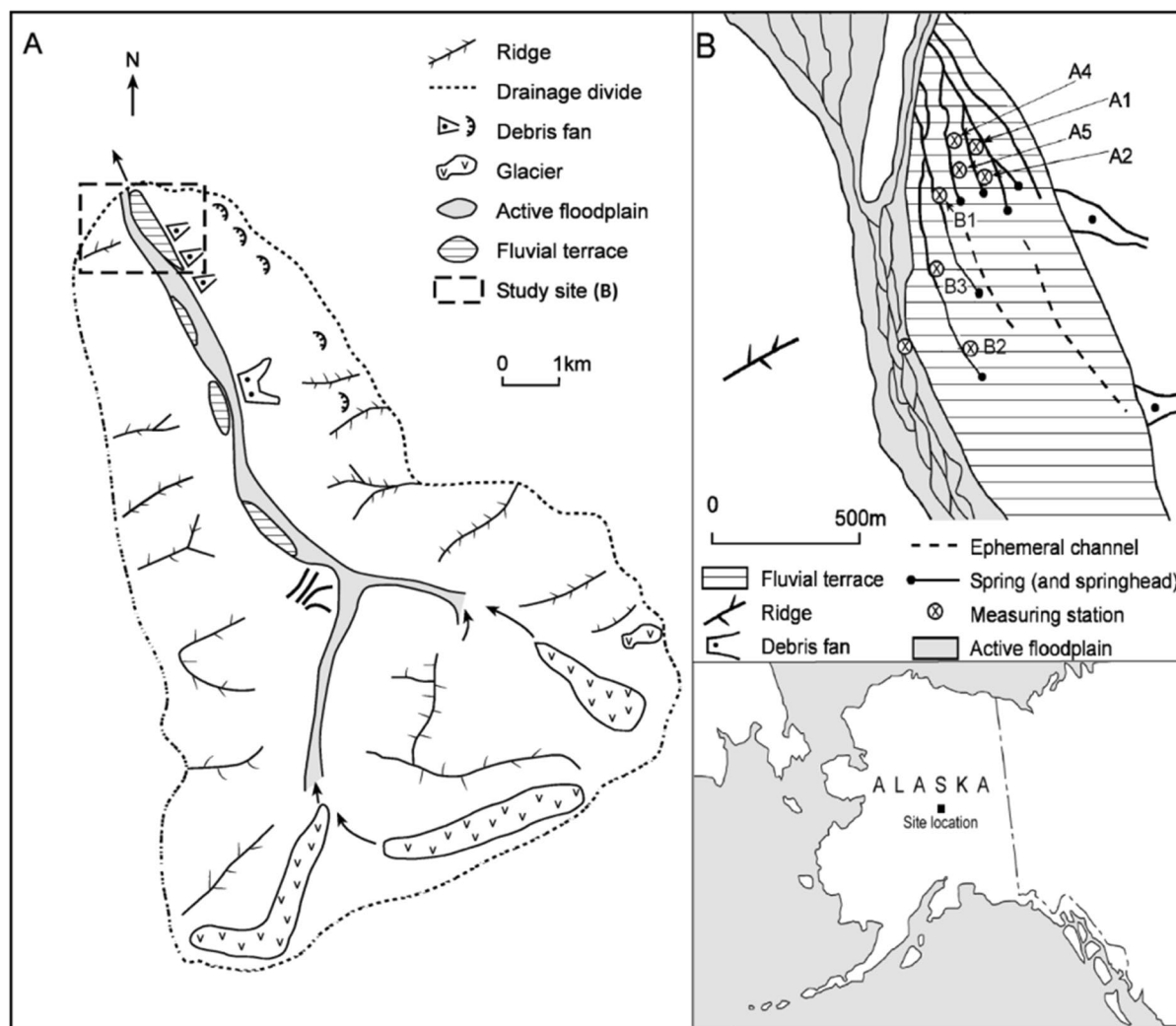
Fig. 1 Study site schematic. **A** is a catchment overview. **B** is the groundwater channel sampling site schematic. Site location within state of Alaska (bottom right)

acid-rinsed Nalgene polyethylene bottles. Samples were filtered through 0.45 μm nylon membrane filters and refrigerated prior to analysis. In the laboratory, chloride (Cl⁻) concentrations (ppm) were measured using an ICS 2000 (Dionex, Sunnyvale, USA). Instrumental precision for the analysis of Cl⁻ was 0.25 ppm.

Concentrations of Cl⁻ in deep groundwater from the debris fan site (DFS_{deep}) were approximately 85 times greater than in samples of snow and glacial meltwater; therefore, we used Cl⁻ measurements across stream samples and water sources to

estimate the proportional contribution of DFS_{deep} from the debris fan to the total flow for each groundwater stream. Estimates were made using a groundwater mixing model, with the groundwater end-member estimated from high Cl⁻ concentrations observed in waters from DFS_{deep}:

$$DFS_{deep}^{\%} = \left(\frac{S_u}{S_D} \right) \times 100$$

where $DFS_{deep}^{\%}$ was the percentage contribution of water at each site that was derived from DFS_{deep}, S_u was the concentration of Cl⁻ at upwelling sites, and

S_D was the mean Cl^- concentration of debris fan seepage (Crossman et al., 2011).

Flow pathways

Stream depth and hydraulic head were measured twice daily from June 17th to September 2nd, 2008, using nested piezometers inserted to depths of 50 cm and 100 cm at each sample site (Fig. 1). Within the piezometers, Level TROLL 500 pressure transducers (In-Situ Inc., Fort Collins, USA) were used to log water level and the direction of subsurface water movement was determined by calculating the hydraulic gradient at each piezometer nest (dividing the difference between stream water level and the water level in the piezometers at 50 cm depth by the vertical distance). A positive gradient indicated groundwater discharge. To provide additional context and confirm the contributions of different flow paths, pH and electrical conductivity (EC) were monitored monthly using a HI 98,127 multimeter (Hanna Instruments, Woonsocket, USA).

Fig. 2 Seasonal variability in the association of macroinvertebrate taxon diversity with flow pathway contributions from DFS_{deep} to groundwater-fed streams
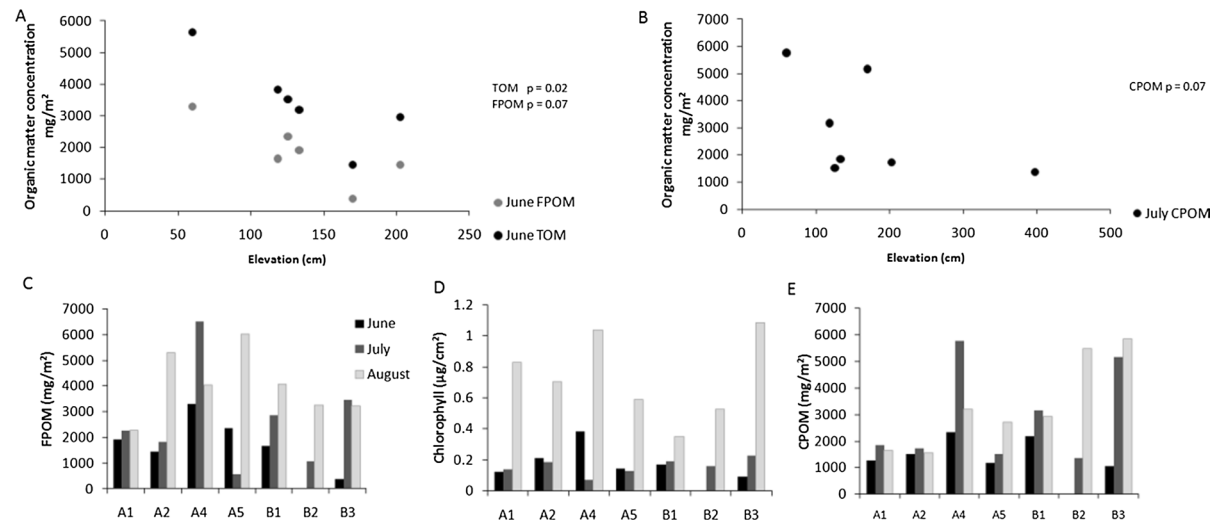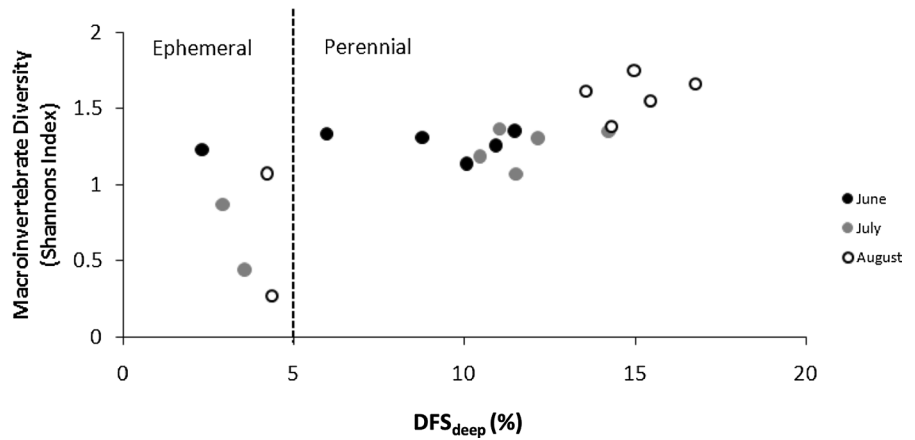
Fig. 3 Seasonal heterogeneity in physical and chemical characteristics of groundwater-fed streams. **A** Correlation between elevation (cm relative to lowest point on terrace) and mean TOM and mean FPOM in June. **B** Correlation between elevation and mean CPOM in July. **C** Seasonal changes in FPOM throughout study period. **D** Temporal variation in chlorophyll concentrations in August. **E** Site-specific increases in CPOM

Physical and chemical variables

Stream morphology

Stream channel dimensions, water depth, and flow velocity were measured at 1/6 depth every 3 weeks over the study period, and stream discharge and flow duration curves were subsequently estimated. At each site, predominant substrate size was determined by measuring the *b*-axis of 100 randomly selected stones

(Burgher et al., 2002) and D_{50} was calculated. The bottom component of the Pfankuch Stability Index was also determined, incorporating scores for rock angularity, brightness, particle consolidation and size distribution, scouring and deposition, and aquatic vegetation (Pfankuch, 1975). The bottom component of this index describes the stability of the material in the streams that is almost always underwater with higher scores being more unstable.
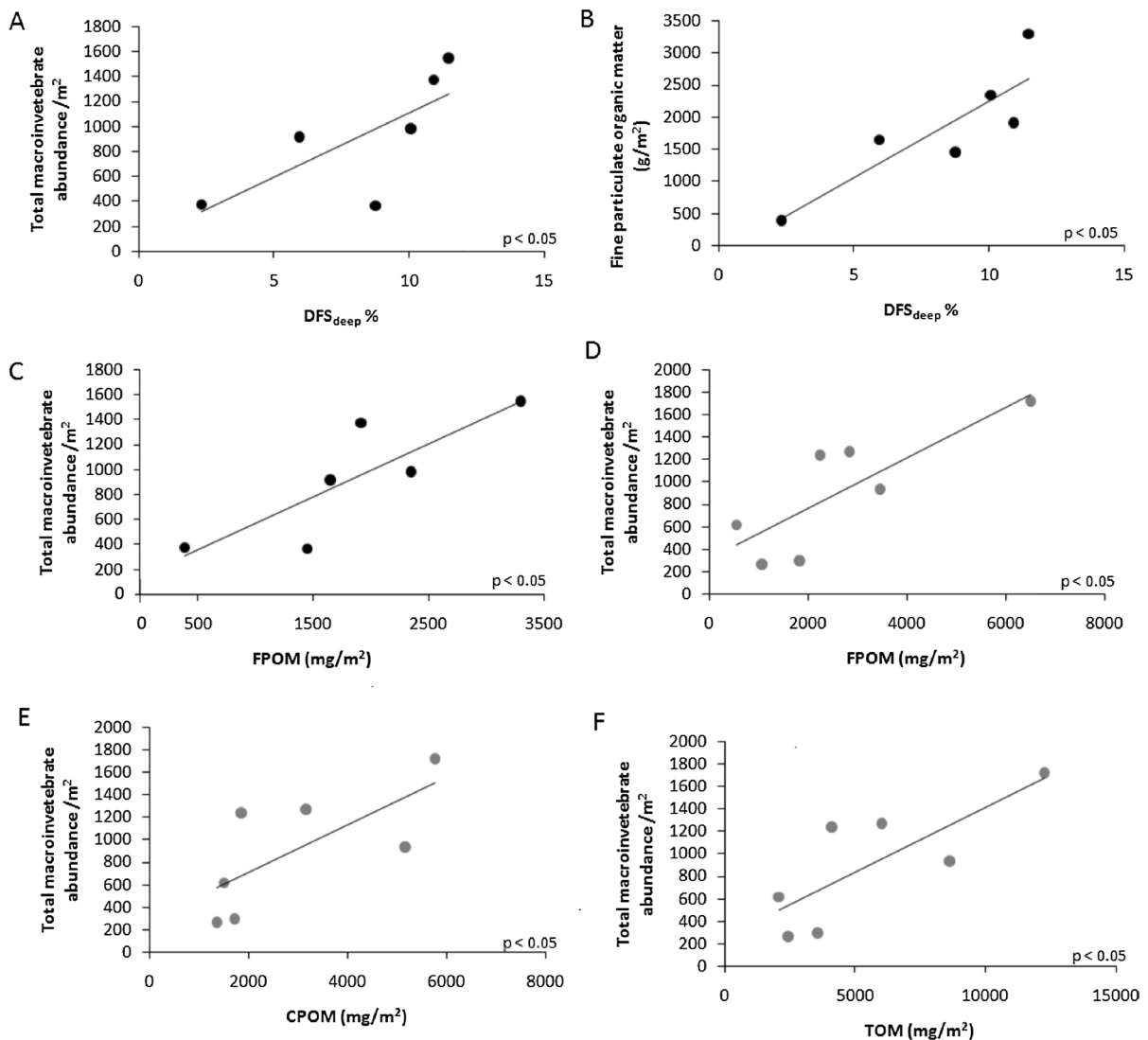
Fig. 4 Relationships between flow pathways, organic matter concentrations, and macroinvertebrate abundances. **A** Macroinvertebrate abundance and %DFS_{deep} in June. **B** FPOM and %DFS_{deep} in June. **C** Abundance and FPOM in June. **D** Abundance and FPOM in July. **E** Abundance and CPOM in July. **F** Abundance and TOM in July. Lines represent relationships and are not statistically derived from Spearman's rank correlations

Stream discharge

Stream stage (m) was measured across streams using Level TROLL 500 pressure transducers (In-Situ Inc., Fort Collins, USA). These transducers were placed at the surface of the stream bed, and at a depth of 50 cm, across five of the sample sites (A2, A5, B1, B2, and B3), and mean stream stage was logged at 15-min intervals. Stream stage data were combined with stream rating equations derived for each cross section, enabling stream discharge to be estimated for each site, over the entire study period.

Water temperature

Stream water temperature (°C) was measured using Tinytag Plus thermistors (Gemini, Chichester, UK), inserted at the surface across five of the sample sites (A2, A5, B1, B2, and B3) at 15-min intervals. Perennial streams were identified as those where in-stream temperatures exceeded 0 °C throughout the year (Brown et al., 2006a).

Diurnal variations in water temperature, stream stage, and discharge were assessed using an index of variation (Fowler & Death, 2001). The diurnal stage variation index (DSVI) was derived using the following equation:

$$DSVI = \frac{1}{n} \sum_{i=1}^{n} \left(S_{max} - S_{min} \right)$$

where S_{min} and S_{max} were the minimum and maximum stage values for every 24-h period throughout the study season (24 h was chosen because of the strong diurnal variation in flow) (Crossman et al., 2013b). Similarly, indices for Diurnal Temperature Variation (DTVI) and Diurnal Discharge Variation (DDVI) were determined.

Microbial biofilms

Samples of microbial biofilms were collected monthly at each site following the protocol described in Ledger and Hildrew (1998). For each sample, the surface area (cm^2) of four randomly selected stones was calculated by tracing the stone outline onto an acetate sheet. Surfaces were then scraped into a 50 ml tube frozen and stored in the dark until analysis. The sample mass was measured using a microbalance (Ohaus, Parsippany, USA) to estimate the biofilm mass per unit area (g cm^{-2}). A 10 ml subsample was freeze dried and chlorophyll pigments were extracted in 90% acetone for 24 h. Absorbance at 750, 664, 647, and 630 nm was determined using a spectrophotometer (Hanna Instruments, Woonsocket, USA), and total chlorophyll was calculated (Sterman 1988).

Benthic macroinvertebrates

Five replicate benthic invertebrate samples were collected monthly at each site using a Surber sampler (0.093 m^2, mesh 330 μm) and preserved in 90% ethanol. Flotation was subsequently used to separate macroinvertebrates from gravel and heavier organic materials, by the addition of a saturated solution of MgSO$_4$. The remaining mineral portion of the sample was examined for cased-caddisfly larvae and other macroinvertebrates that were not extracted via flotation.

Macroinvertebrate taxa were identified using Thorp and Covich (2001). Individuals were identified to species, wherever possible, but Simuliidae and Chironomidae were only identified to family. The abundance of different taxa was enumerated, and macroinvertebrate diversity (H) was calculated using Shannon's Index of Diversity (Shannon & Weaver, 1949)

$$H = - \sum P_i \ln(P_i)$$

where P_i is the relative abundance of each taxon, calculated as the proportion of individuals of a given taxon to the total abundance within the sample.

Organic matter

Organic material collected in the Surber samples was first dried at 65 °C and then sieved into coarse (> 1 mm) and fine (< 1 mm) fractions. The weight of each fraction was measured using a microbalance (Ohaus, Parsippany, USA) prior to ashing in a furnace at 540 °C for 2 h. Ash-free dry mass was then determined by re-weighing the different organic matter

fractions. From these data, the ash-free dry mass of FPOM and CPOM, as well as total organic matter (TOM), was calculated per unit area (mg m^{-2}).

Data analysis

Objective 1: Spatial patterns in environmental and physical variables

Patterns of environmental and physical variables across sites were evaluated in relation to their elevation by correlating different variables (e.g., TOM, FPOM, CPOM, site elevation, and flow permeance) using a series of Spearman's rank-order correlations.

Objective 2: Relationships between environmental variables and macroinvertebrate communities

Metrics for macroinvertebrate communities (total abundance and Shannon–Weaver index) were related to water source contributions, TOM, CPOM, FPOM, and site elevation using Spearman's rank-order correlations. A Mann–Whitney U test was carried out between the macroinvertebrate diversity of ephemeral and perennial streams as diversity data were not normally distributed. Comparisons of variance in macroinvertebrate abundance between sites within and between months were completed using ANOVA, with P-values generated using F-tests.

Variation in macroinvertebrate community structure and relationships with physical and chemical variables were analyzed using detrended correspondence analysis (DCA; Hill & Gauch, 1980). DCA is an ordination technique that detrends (divides the axes into segments and centers the second axis on zero) and equalizes the weighted variance of taxon scores along the axis segments. Similar communities occur closer together on both axes. Axis 1 and Axis 2 sample scores from these analyses were correlated against physical and chemical variables (discharge, DDVI, DSVI, pH, EC, Cl$^-$ concentration, chlorophyll, FPOM, CPOM, HG, sediment particle size, site elevation, and the Pfankuch Stability Index). A DCA with independent non-parametric analysis of additional variables was selected, rather than a detrended canonical correspondence analysis which uses

multiple linear regression to directly constrain relationships between sites and samples to the measured variables (Ter Braak, 1986), as it is more appropriate for smaller datasets. Water temperature data (DTVI) were not included in the DCA as this was only measured at five sites, and thus, temperature was correlated separately using Spearman's rank-order correlation.

To determine the significance of environmental variables for individual taxa abundance, the six most dominant taxa (96% of total abundance) were correlated individually with each variable for each month (due to the strong seasonal gradient of macroinvertebrate distribution correlations) using Spearman's rank-order correlation.

Results

Water source contributions and flow paths

Characteristics of the seven sample sites were spatially and temporally variable at a range of scales (Table 1). Sites at the low elevation end of the terrace (A1–A5 and B1) were perennial, with high percent DFS$_{deep}$. In contrast, sites further up the terrace (B2 and B3) were ephemeral, reflecting their higher elevation, with markedly lower DFS$_{deep}$ contributions (Fig. 2). As glacial seepage (GMW$_{riv}$) contributed more flow to the ephemeral streams, flow was only initiated after the infiltration of seasonal meltwater and precipitation raised the water table to intersect the surface.

Organic matter was similarly variable: TOM and FPOM were negatively correlated with elevation in June ($P < 0.01$; Fig. 3a). FPOM generally increased in all streams from June to August (Fig. 3c) and total chlorophyll in microbial biofilms increased in August by a factor of ~4.5 (Fig. 3d). Notably, FPOM, total chlorophyll, and CPOM were lowest in almost all sites in June (Fig. 3e).

Variation in macroinvertebrate communitie*s*

Macroinvertebrate diversity was significantly correlated with percent DFS$_{deep}$ ($P < 0.01$; Fig. 2) and was higher in perennial channels than ephemeral channels ($P < 0.01$). The relationship between

macroinvertebrate diversity and site elevation (a proxy for flow permanence; see *Water source contributions and flow paths*) was also significant ($P < 0.05$), with the highest diversity at lower elevation sites (perennial streams).

At all sites except A4, macroinvertebrate abundance was highest during August and significantly higher at B2 and B3 ($P < 0.01$). During June, macroinvertebrate abundance (Fig. 4a, b) was significantly correlated with percent DFS_{deep} and FPOM ($P < 0.05$; Fig. 4c). FPOM and percent DFS_{deep} were themselves significantly correlated ($P < 0.05$). During July and August, macroinvertebrate abundance was not significantly associated with DFS_{deep}. However, macroinvertebrate abundance was still significantly

correlated with FPOM and also CPOM ($P < 0.05$, Fig. 4d, e).

Seasonal variation at each of the seven sites was evident in the DCA (Fig. 5a). Sites on Axis 1 were plotted primarily according to the time of sampling, and on Axis 2 to site location (cumulative variance 90%). Perennial streams were grouped into clearly defined monthly clusters (June, July, and August). Ephemeral streams were grouped into two clusters, June and July/August. This seasonal gradient for both stream types along Axis 1 accounted for 58% of the variance in taxa distribution.

Ephemeral streams in June and perennial streams in June and July supported similar macroinvertebrate community structure (Fig. 5b), characterized by a higher abundance of *Baetis tricaudatus* Dodds, 1923, *Baetis bicaudatus* Dodds, 1923, *Clinocera* spp., *Zapada haysi* (Ricker, 1952), and *Alaskaperla ovibovis* (Ricker, 1965). In late July/August, ephemeral channels supported a higher abundance of Chironomidae and Collembola whereas perennial channels supported a higher abundance of *Oreogeton* spp., *Ecclisomyia* spp., *Isoperla petersoni* Needham & Christenson, 1927, and *Plumiperla diversa* (Frison, 1935). The strong seasonal gradient of DCA Axis 1 indicated that significantly correlated variables

Table 2 Significant Spearman rank correlations of environmental variables on the first two axes of an independent DCA of sites using macroinvertebrate abundance (**$P < 0.01$; *$P < 0.05$)

Axis 1 (seasonal)	Axis 2 (site)
DFS_{deep}%** (+ve)	DFS_{deep}%* (−ve)
Fine particulate organic matter* (+ve)	D50** (+ve)
	Elevation** (+ve)

Table 3 Significant Spearman's Rank Correlations between the six most abundant taxa and physical and chemical variables (***$P < 0.01$; ** $P < 0.05$; * $P \leq 0.1$; [a]qualitative non-linear relationship observed in the data)

Taxa	June		July		August	
	Positive	Negative	Positive	Negative	Positive	Negative
Zapada haysi	DFS_{deep}%* FPOM*	Pfankuch* D50*	CPOM[a]	Elevation** D50*	pH*	Elevation* TOM**
Chironomidae	DFS_{deep}%* FPOM*** TPOM*	Elevation**	TOM** CPOM** FPOM**	Elevation**	D50** CPOM** TOM**	DFS_{deep}%[a]
Ecclisomyia	CPOM** TOM**	Elevation**	CPOM** FPOM** TOM**	Elevation**	Pfankuch***	-
Oreogeton	Chironomidae** FPOM*	Elevation[a]	Chironomidae** CPOM** FPOM** TOM**	Elevation**		Elevation**
Baetis bicaudatus	DFS_{deep}%* FPOM* TOM*	Elevation**	CPOM$	Elevation**	DFS_{deep}%** TOM* CPOM* Chlorophyll[a]	Pfankuch[a] D50** Chironomidae**
Simuliidae	DFS_{deep}%[a] FPOM[a] CPOM**	Elevation[a]	Elevation**	–	Elevation$	Discharge* CPOM**

A

Eigen Value = 0.174
% variance = 32.03

B
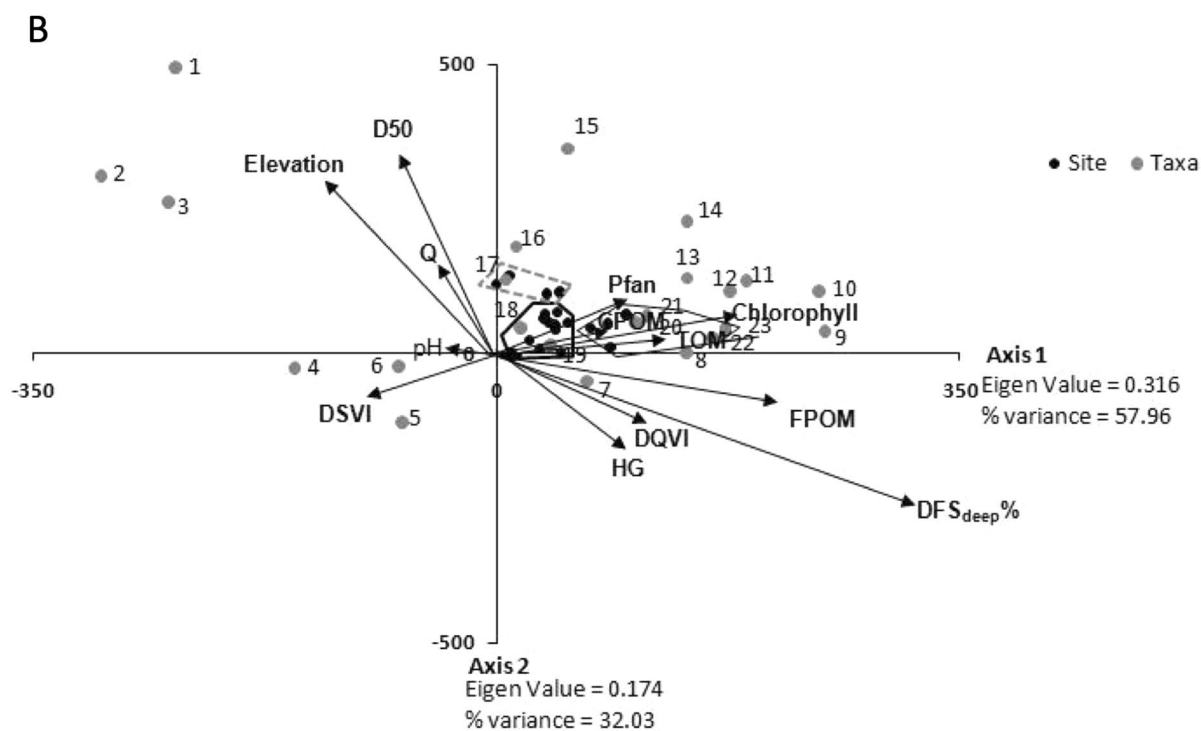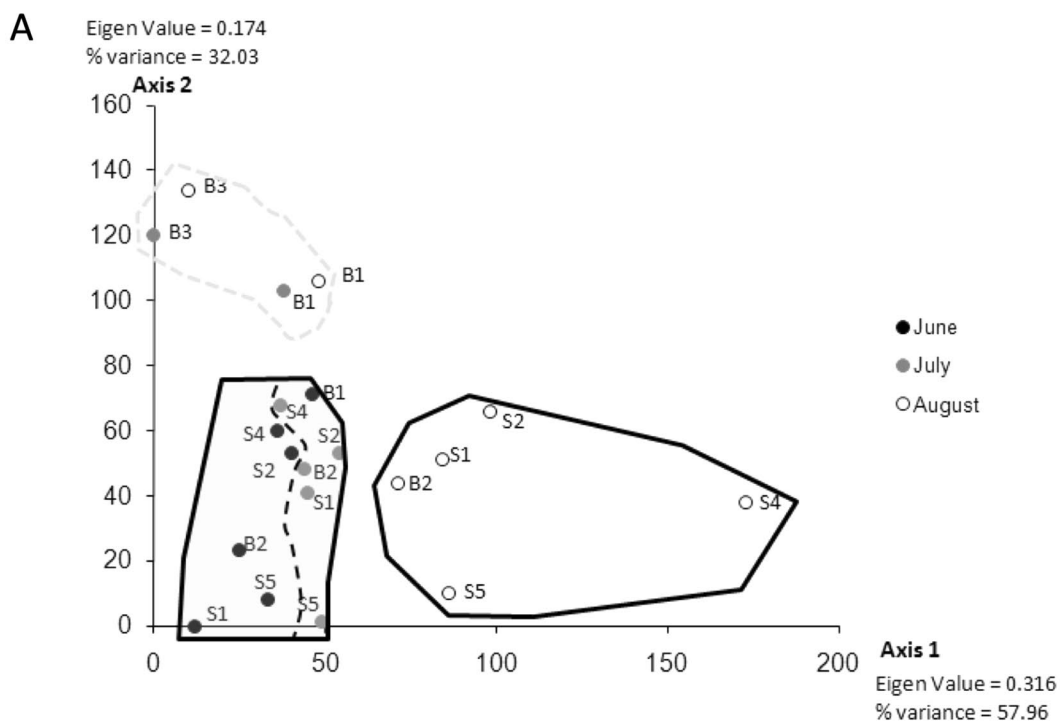
◄**Fig. 5** Community variation in macroinvertebrates. **A** Detrended correspondence analysis of macroinvertebrate taxa and sample sites. **B** Ordination biplot of detrended correspondence analysis, with independently correlated physical and chemical variables. Taxa: **1** Ceratopogonidae, **2** *Hexatoma* spp., **3** *Megaleuctra* spp., **4** Oligochaetae spp. A, **5** *Baetis bicaudatus,* **6** *Chelifera* spp., **7** *Zapada haysi,* **8** *Plumiperla diversa,* **9** Simuliidae, **10** *Ephydra* spp., **11** *Limniphora* spp., **12** *Ecclisomyia* spp., **13** Physchodidae, **14** *Tipula* spp., **15** Hydracarina, **16** Collembola, **17** Chironomidae, **18** Oligochaetae spp. B, **19** *Alaskaperla ovibovis,* **20** *Baetis tricaudatus,* **21** *Clinocera* spp., **22** *Oreogeton* spp., **23** *Isoperla petersoni*

influenced taxa on a seasonal basis, while variables that correlated more strongly with DCA Axis 2 were accounted for by between site differences (Table 2). $DFS_{deep}\%$ (positively correlated on DCA Axis 1 and negatively on DCA Axis 2) therefore influenced macroinvertebrate communities, both seasonally (increasing in concentration from June to August) and between sites (with greater DFS_{deep} seepage concentrations in perennial streams).

Patterns of dominant macroinvertebrate taxa

The relationship of the six most dominant taxa with physical and chemical variables varied seasonally (Table 3). In June, several taxa (*Z. haysi*, *B. bicaudatus,* Chironomidae, and Simuliidae [the latter found only at site A4 during June]) were correlated to water flow pathway ($DFS_{deep}\%$), FPOM, and site elevation (Fig. 6a–c). *Ecclisomyia* spp., although low in abundance in June and only collected at sites A4 and B1, had a significant correlation with CPOM. The abundance of the predator *Oreogeton* spp. was significantly associated with abundance of their prey Chironomidae throughout June and July ($P \leq 0.05$) (Fig. 6d, e).

In July, despite the change in FPOM availability, several taxa continued to demonstrate positive associations with TOM (*Z. haysi*, Chironomidae, *B. bicaudatus*, *Ecclisomyia* spp., and *Oreogeton* spp.), predominantly related to CPOM availability. *Ecclisomyia* spp. abundance increased markedly to become established in four of the seven stream sites. Despite initially establishing in the site furthest downstream in June (A4), Simuliidae were increasingly found at upstream sites, demonstrating a positive correlation with stream elevation throughout July and August.

Fewer taxa were associated with organic matter in August, with only Chironomidae and *Baetis*

bicaudatus continuing to demonstrate a positive correlation (Fig. 6f, g). *B. bicaudatus* also demonstrated a strong association with chlorophyll, sediment grain size, and the Pfankuch Stability Index during this month. *Oreogeton* spp. maintained significant associations with Chironomidae in perennial streams during August but not in ephemeral streams (Fig. 6h). *Ecclisomyia* spp., found at all seven stream sites, was significantly associated with the Pfankuch Stability Index.

Discussion

Groundwater-fed streams were strongly influenced by local variation in water source and flow path dynamics. Here, we found that in a glacierized catchment spatial and temporal variation in these variables influenced physical and chemical conditions and as a result the macroinvertebrate communities. Across the stream sites studied, macroinvertebrate communities were related to the duration of active flow in the channels, and its subsequent influence on physical and chemical processes and organic matter dynamics. Overall, these findings highlight the combined influence of flow regime stability and organic matter content as drivers of macroinvertebrate community structure and abundance across groundwater-fed streams in glacierized catchments.

Spatial and temporal variation in environmental conditions

Spatial variation in the physical and environmental conditions present across groundwater steams on the river terrace was high, with the largest differences occurring between perennial and ephemeral streams. Perennial streams were at lower elevations on the river terrace in comparison with ephemeral streams, and there were differences in water source contributions with perennial streams supported by groundwater from DFS_{deep} (seepage from the valley sides), whereas ephemeral channels water source was predominantly GW_{river} (DFS_{deep}, snow and glacial meltwater) groundwater associated with the alluvial aquifer. These patterns align well with findings from previous studies which have also found spatial variation in water sources contributions at local scales in
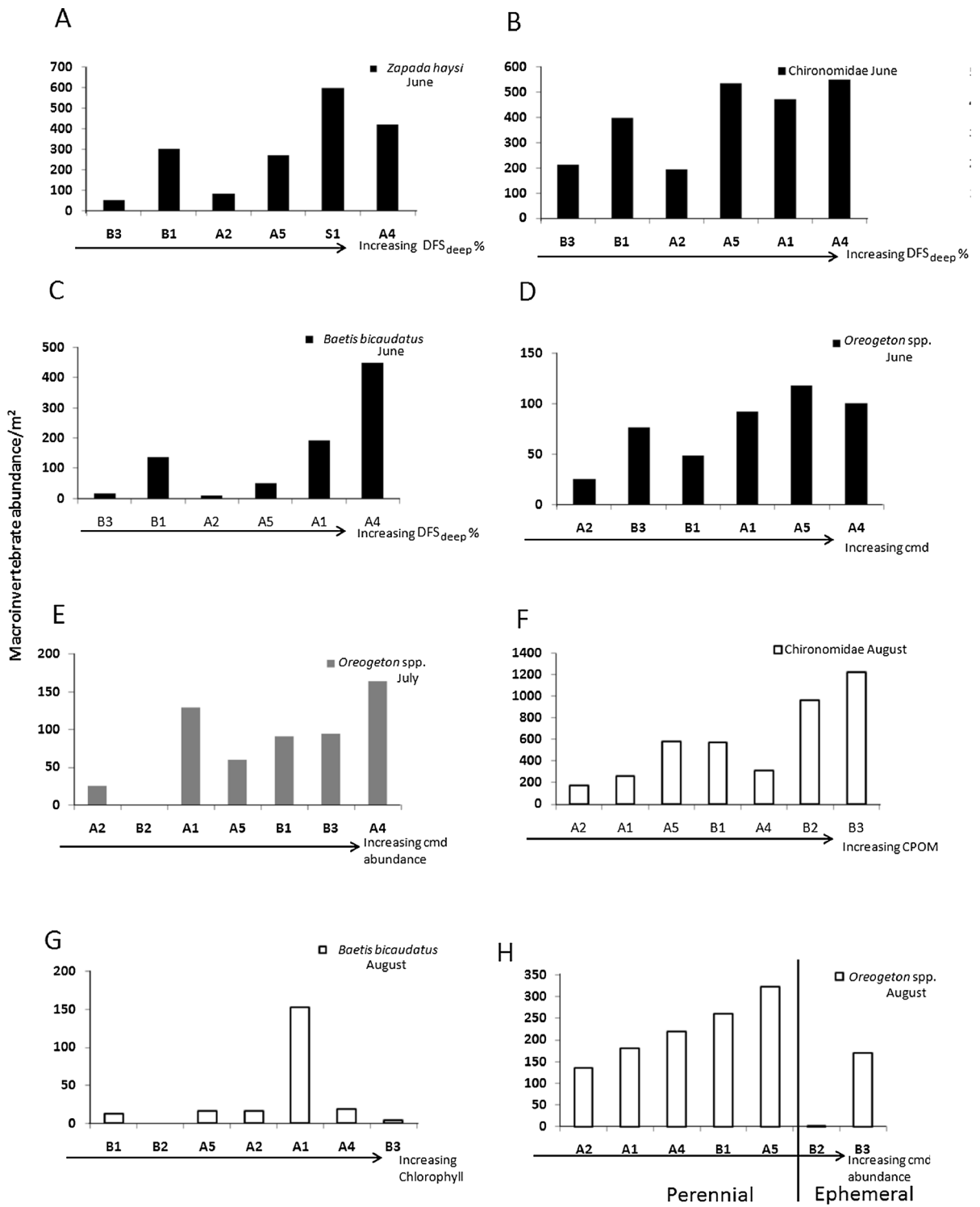
◄**Fig. 6** Seasonal variability in distribution of individual taxa with relation to physiochemical variables. **A** *Zapada haysi*, **B** Chironomidae, and **C** *Baetis Bicaudatus* to DFS$_{deep}$%. **D** and **E** The distribution of *Oreogeton* spp. associated with that of Chironomidae throughout June and July, respectively. **F** and **G** Association of Chironomidae and *Baetis bicaudatus* with resource availability throughout August. **H** Difference between association of *Oreogeton* spp. with Chironomidae within perennial and ephemeral streams during August

glacierized catchments (Alther et al., 2019; Zuecco et al., 2019), which concluded that flow permanence strongly influenced environmental conditions within streams (Brown et al., 2006a).

Temporal variation in environmental conditions within streams was also high. Ephemeral streams only started flowing in late summer with increases in glacial meltwater contributions to groundwater. More specifically, changes in water sources and flow paths influenced organic matter dynamics, with increases in TOM and total chlorophyll (from microbial biofilms) with highest levels observed in August. This pattern coincides with leaf fall and in-stream degradation, as well as peak primary productivity. Patterns such as this were expected in this study, but yet are uncommon for streams in glacierized catchments, which are typically supported by low levels of allochthonous organic matter due to poorly developed riparian ecotones on highly disturbed glacial floodplains (Zah & Uehlinger, 2001).

Factors influencing variation in macroinvertebrate communities

Macroinvertebrate abundance, diversity, and community composition varied spatially, across streams with different degrees of flow permanence, demonstrating the important influence of groundwater dynamics. Overall, perennial streams maintained a higher macroinvertebrate abundance and diversity in comparison with ephemeral groundwater-fed streams. Higher macroinvertebrate diversity in perennial streams can be attributed to the greater channel stability and the permanence of flow (Wood et al., 2005; Brown et al., 2006b, 2007b; Milner et al., 2020). Conversely, the low macroinvertebrate diversity observed in ephemeral channels is likely a result of flow intermittency.

There were, however, temporal variations in macroinvertebrate communities across the stream sites. For example, diversity in perennial channels increased throughout the summer (June to August) likely due to the response of macroinvertebrate taxa to increasing OM availability, particularly CPOM, in July and August. In contrast, diversity in ephemeral streams was invariant, likely reflecting limitations on colonization due to distance from the macroinvertebrate colonizing pool in the perennial streams (McArthur and Barnes 1985; Fritz and Dodds 2005) as well as the influence of short summer seasons and thus opportunities for dispersal. Colonization of ephemeral stream reaches predominantly depends upon seasonal upstream migration from perennial reaches (William & Hynes, 1976; Fengolio et al., 2002) and aerial dispersal, which across the streams studied here already had low macroinvertebrate abundance. Although flow stability is likely to be the main determinant of spatial and temporal variations in macroinvertebrate community composition (see Milner et al., 2020), a series of co-varying physical and chemical variables may be responsible for the patterns observed across these groundwater-fed streams.

Organic matter dynamics was particularly variable across and within streams. The strong positive relationship between FPOM and DFS$_{deep}$%, and subsequently macroinvertebrate abundance across flowing streams in June, indicates the potential for FPOM transport to streams by groundwater flowing through colluvial deposits on the floodplain margins (Boissier & Fontvielle, 1995). Certainly, FPOM entrainment by waters percolating through the more densely vegetated and deeper soils on the valley sides would increase the FPOM content of DFS$_{deep}$ waters providing a valuable carbon resource to macroinvertebrates during periods when CPOM was limited (Richardson, 1991; Dobson & Hildrew, 1992). Furthermore, increases in CPOM due to leaf litter inputs in late July and August would explain the shift in the association of macroinvertebrates from FPOM in June to CPOM in late July and August across stream sites.

Irrespective of the organic matter source (FPOM or CPOM), there was a continued correlation between macroinvertebrate taxa and organic matter, indicative of resource tracking (Hart & Robinson, 1990; Rowe & Richardson, 2001). Two dominant mechanisms of tracking have been identified: (1) active (a deliberate emigration from sites of low to high resource availability) and (2) passive (accidental dislodgement) (Richardson, 1991; Kohler, 1985; Rowe & Richardson, 2001). However, the facultative feeding

nature of some macroinvertebrates may complicate the resource tracking relationship where taxa alter their diet according to resource availability or developmental stage (Mihuc & Minshall, 1995; Moore, 1977). Here, this may be the case as the relationships between TOM and macroinvertebrates are most marked in resource-depleted environments, such as arctic and alpine streams (Tiegs et al., 2008).

Conclusions

Our findings presented here demonstrate that groundwater sources and flow paths are key variables influencing macroinvertebrate community structure in groundwater-fed streams. Our results also highlight the importance of changes in the source and timing of groundwater flow, in the context of wider uncertainties of the extent (and reliability) of the contribution to flow from snow- and ice-melt and summer rainfall. Climate change is likely to affect these streams by altering the proportional contribution of individual water sources to streamflow. This may be highly complex (e.g., Liu et al., 2020) and at present is poorly known (Jyvasjarvi et al., 2015). Given projections that maximum glacier water yield in Alaska will occur in 2060 under a RCP of 2.6 and 2090 under a RCP of 8.5 (Huss & Hock, 2018), glacier meltwater is likely to increase throughout the second part of this century in Alaska. Consequently, ephemeral streams, fed through the snow and glacial melt water, are likely to run longer over the summer and with potentially greater flow.

To determine the full extent of climatic influences on these terraces, further research is needed into the relative importance of winter macroinvertebrate diversity and abundance on summer community composition and into seasonal changes in groundwater sources associated with receding glaciers and snowpacks feeding deep aquifers.

Data availability The data behind the paper are available on application to the corresponding author.

Declarations

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