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Water Flow Dynamics of Groundwater-Fed Streams and Their Ecological Significance in a Glacierized Catchment

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Abstract

Subsurface flow pathways of groundwater-fed streams were characterized on a floodplain terrace of the Toklat River, Alaska, in summer 2008, to establish the influence of local physicochemical variability upon macroinvertebrate communities. Streams proximal to the valley side (A sites) and to the main meltwater channel (B sites) were studied. Chloride and natural isotopic tracers ($\delta^{18}O$ and $\delta^{2}H$) were used to identify water sources and flow pathways. Results indicated that flow in B sites was dominated by seepage of glacial meltwater through the alluvial aquifer. Streamflow at sites situated at higher elevations was ephemeral, and commenced with the seasonal rise in the groundwater table. In contrast, the physicochemistry of A sites was characteristic of seepage from valley-side debris fans, which maintained perennial flow to streams at lower elevations. Macroinvertebrate diversity was lower in ephemeral streams, likely due to colonization constraints. In June macroinvertebrate abundance was significantly positively correlated with the percentage contribution to streamflow from debris-fan seepage ($p < 0.05$) and with fine particulate organic matter concentration (FPOM) ($p < 0.05$); FPOM was correlated with debris fan seepage ($p < 0.05$). These relationships were not evident in July and August, when organic matter availability increased. Our study demonstrates that flow pathways and organic matter availability significantly influence macroinvertebrate communities in these groundwater-fed streams.

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Introduction

Interactions between groundwater and surface water (GW-SW) influence catchment hydrology, solute fluxes, and ecological diversity, and are potentially vulnerable to climate change (Ward et al., 1999; Brown et al., 2007; Robinson et al., 2009). Despite a growing recognition of the importance of GW-SW interactions, there remains a "relative paucity of [hydrological] studies investigating groundwater systems in present-day glacierized environments" (Robinson et al., 2009). Groundwater-fed streams are an important habitat for macroinvertebrate communities within glacierized catchments (Ward et al., 1999; Brown et al., 2003), as studies within alpine areas have suggested that streams fed by groundwater may support higher taxa abundance than those fed largely by surface snow and ice-melt (Brown et al., 2003). The difference in taxa abundance is attributed to characteristically higher water clarity, and reduced variability in stream temperature and discharge of groundwater-fed streams (Brown et al., 2003). Climate change may have significant implications for the macroinvertebrate communities of groundwater-fed streams (Brown et al., 2007), as glacial recession is predicted, in the long term, to increase groundwater contributions relative to surface water (Milner et al., 2009). However, the association between groundwater flow and macroinvertebrates may be more dynamic than has yet been established, as differences in water sources and groundwater flow pathways create local variations in stream physicochemistry (i.e. in both the physical and chemical characteristics of streams) (Brunke and Gonser, 1997; Malard et al., 1999; Ward et al., 1999), which may influence macroinvertebrate communities. A significant research gap remains in quantifying the influence of variability in groundwater hydrology on macroinvertebrate communities in glacierized catchments.

Several aspects of groundwater-fed stream physicochemical variability have been attributed to the length of individual groundwater flow pathways; the length reflects the distribution and connectivity of permeable deposits, through which water flow pathways develop (Ward et al., 2002; Robinson et al., 2008). Flowpath length may regulate the degree of attenuation of groundwater temperature and flow (Brunke and Gonser, 1997) whereby with increasing pathway length the amplitude of daily stage and temperature variations becomes increasingly reduced and out of phase with that of the waters at their original source. Locally variable heterogeneous landscape structure may therefore result in marked physicochemical variability within individual groundwater flow pathways. For example, the series of locally variable hydrological facies units, characteristic of valley-bottom fluvio-glacial deposits (Anderson, 1989; Robinson et al., 2008) may create local differences in subsurface water residence times, and associated variations in the degree of flow and temperature attenuation between individual streams sourced from alluvial aquifers.

Individual facies units can vary considerably in size from the laterally extensive valley train, or sandur, in Iceland (Robinson et al., 2008, 2009) to small, discrete fluvial-glacial deposits in alpine areas (e.g. Val Roseg, Swiss Alps; Malard et al., 1999). In some cases, rates of subsurface flow through these valley-bottom deposits may be substantial: Poole et al. (2002) found high rates of seepage of waters from the main river channel into the

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underlying alluvial aquifer on the Nyack floodplain of the Middle Fork Flathead River, Montana, with ‘springbrooks’ downstream that were sustained by groundwater flow through the upper alluvial aquifer. Malard et al. (1999) also distinguished a variety of channel types along a 2.6 km floodplain reach in Val Roseg, including the main channel, ‘groundwater channels’ fed by the alluvial aquifer, and ‘springs’ sustained by groundwater discharge at the valley side.

The facies units of valley-side colluvial deposits (e.g. debris fans and talus cones) may also be locally variable and discontinuous. These deposits have a higher permeability close to the surface enabling preferential subsurface flow along lateral pathways perpendicular to the valley axis (Clow et al., 2003). In addition, seepage into a dense matrix towards the base of the colluvium may result in flow with a longer residence time (Roy and Hayashi, 2009). During precipitation or snow- and ice-melt, as levels of saturation increase, additional preferential flowpaths may develop, as connectivity between individual permeable facies units increases (Sidle et al., 2000; Anderson et al., 2009).

Physicochemical characteristics of groundwater-fed streams are also influenced by seasonal and spatial variations in the contributions of source waters and flow pathways. Through the summer, rainfall becomes dominant over snowmelt (Sueker et al., 2000), increasing the relative contribution of precipitation to groundwater recharge. Ice-melt contributions to streamflow also increase during this period (Collins et al., 2002). Spatial variations in flow pathway contributions include the reduction in relative importance of debris-fan seepage with increasing distance from the valley side (Hjulstrom, 1955). Furthermore, streamflow permanence may vary with local topography; due to the marked seasonal fluctuation of water tables within glacierized catchments, reflecting glacial ablation (Robinson et al., 2008), only sites situated sufficiently close to the water table may demonstrate perennial flow. Together with the potential for variability in degree of flow and temperature attenuation (i.e. the reduction in amplitude of daily variability compared with that of the source), these factors may result in considerable local temporal and spatial variations in physicochemistry of groundwater-fed streams within glacierized catchments (Sueker et al., 2000; Robinson et al., 2008).

Groundwater displays marked temporal and spatial trends in isotopic and chemical signatures (Robinson et al., 2009). Sources and flow pathways of groundwater-fed streams thus can be identified by comparing variations in the isotopic composition of source waters, with variability in groundwater-fed streams. The δ^{18}O values of snow are lighter than rain, due to low temperatures during snow formation reducing evaporation (Theakstone, 2003). Through fractionation, the δ^{18}O values of some sources may alter throughout the season; the δ^{18}O value of snowmelt increases during the melt period, as isotopically heavier meltwater is generated at the snowpack surface, and infiltrates, via diffusion, through airspaces (Moser and Stichler, 1974). Seasonal variation in δ^{18}O values of glacial meltwater is reduced, as ice rarely undergoes fractionation, due to limited interstitial air space restricting diffusion (Moser and Stichler, 1974). Seasonal variability in δ^{18}O of glacial meltwater reflects a combination of isotopic fractionation of snowmelt from the glacier surface, buffered by contributions from several non-fractionating ice-melt sources (supra-glacial, englacial and subglacial). Where several water sources are present, additional hydrochemical tracers, such as Chloride (Cl^-) may be used to aid differentiation. Chloride is introduced to the catchment by rainfall, and concentrations are subsequently increased by evaporation (Hayashi et al., 1998), mineral dissolution (Anderson et al., 2003), or saltwater intrusion.

The ecological significance of groundwater flow heterogeneity is associated with its influence on the variability of stream temperature and discharge, organic matter concentrations, and degree of flow permanence. Higher streamflow and temperature variability results in reduced macroinvertebrate community persistence (Townsend et al., 1987) and macroinvertebrate diversity (Death and Winterbourn, 1995); the degree of flow regime attenuation might therefore influence macroinvertebrate community composition. Furthermore, groundwater may be influential through the distribution of organic matter, which can be entrained by through-flow and discharged into surface waters (Boissier and Fontvieille, 1995). Organic matter is an important energy source for macroinvertebrates, which may aggregate upon patches of the resource in otherwise resource-depleted environments (Tiegs et al., 2008). Flow permanence, determined by local topography, groundwater source, and flow pathways, has also been established as a key driving factor in macroinvertebrate community composition (McCabe, 1998) with intermittent and ephemeral streams typically supporting lower species diversity (Wood et al., 2005).

In general, past ecological research has largely compared macroinvertebrate communities between groundwater-fed streams and surface water sources (Friberg et al., 2001; Brown et al., 2006). However, local variability in the physicochemistry of groundwater-fed streams may influence their capacity to support high macroinvertebrate abundance and diversity (Turnbull et al., 1995; Soulsby et al., 1997). Accordingly, implications of climate change may be more site specific than previously considered. A quantitative association between physicochemical variability in groundwater-fed streams and macroinvertebrates has yet to be established. Consequently, this study aimed to establish local heterogeneity in the physicochemistry of streams fed entirely by groundwater, in the floodplain of the Middle Fork of the Toklat River, Denali National Park, Alaska, and to investigate the influence of this variability upon macroinvertebrate communities. The specific objectives were:

1. to establish the sources and flow pathways of water contributing to groundwater-fed streamflow;
2. to characterize and determine key driving processes of local spatial and temporal variability in groundwater physicochemistry; and
3. to assess the influence of physicochemical variability of groundwater-fed streams upon the macroinvertebrate community.

Methodology

FIELD SITE

A floodplain terrace in the middle fork of the Toklat River, in Denali National Park (63°29′19.54″N, 149°57′54.05″W), Alaska, was selected for study in summer 2008 (Fig. 1, A). Given an extensive network of streams fed entirely by groundwater, the likelihood of differences in subsurface water routing to streams across the terrace, and the proximity to the Park Access Road (2 km), the site was considered ideal for studying local spatial and temporal variability in groundwater-fed stream physicochemistry. These groundwater-fed systems on terraces are relatively widespread throughout Alaska, but have yet to be studied in detail. The terrace investigated here is situated on an eastern section of the glacial floodplain, ~12 km from the glacial margin, at a point where the floodplain is ~1300m wide (Fig. 1, B). The terrace is

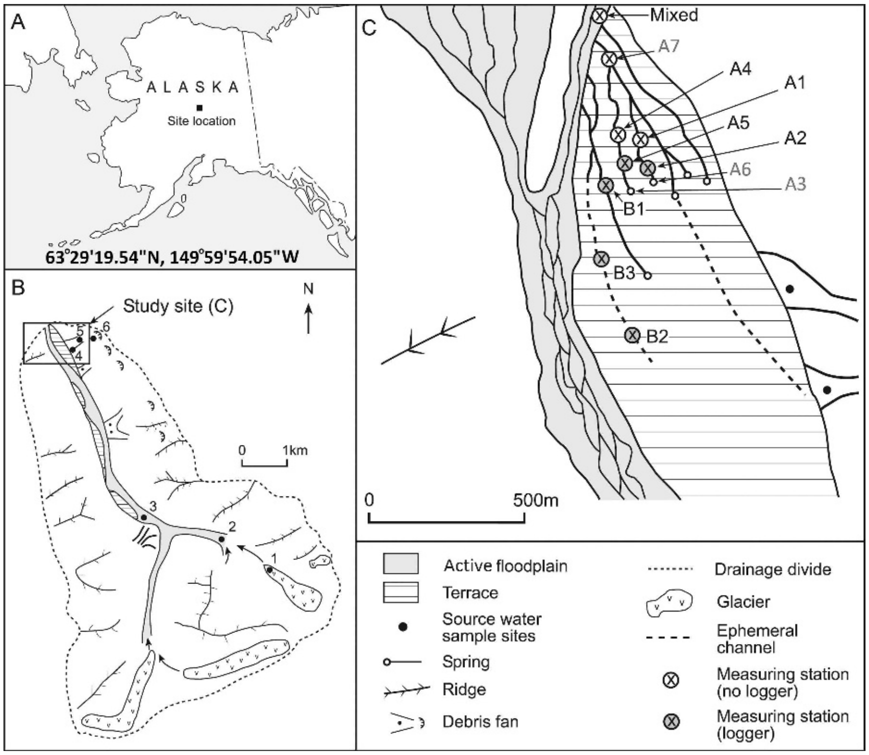


FIGURE 1. Study site schematic. (A) site location within state of Alaska. (B) Catchment overview including source water sampling sites 1 = Ice, 2 = GMW_{term}, 3 = GMW_{riv}, 4 = DFS_{deep}, 5 = $\text{DFS}_{\text{shallow}}$, 6 = snow. (C) Groundwater-fed stream sampling site schematic; sites where water chemistry and hydrology were monitored are labeled in black text, sites where only piezometer nests were inserted are labeled in gray text.

adjacent to the current active outwash plain (Fig. 2, A and B) and is approximately 600 m wide at its largest extent, extending for 2200 m along the valley bottom with a down-valley gradient of 2%. Several debris fans and talus cones are situated proximal to the terrace. These colluvial deposits extend across what are otherwise vegetated valley sides, and isolated perched wetlands occur along both margins of the floodplain.

The main Toklat River is a braided, north-flowing tributary of the Yukon River. Flow is predominantly derived from ice-melt and snowmelt from three small valley glaciers upstream. The upstream catchment is ~115 km^2 with elevations ranging from 1835 m to the south, to 1197 m in the valley bottom. The underlying geology comprises calcareous and siliceous strata, and along the valley sides are Triassic calcareous sedimentary and submarine basalt, and Paleocene volcanic units (Wilson et al., 1998). The sedimentary units in the valley bottom are inferred to comprise basal glacial till, overlain by fluvial-glacial outwash deposits, and colluvium along the valley side (products of extensive paraglacial weathering; Ballantyne and Benn, 1994).

The down-valley margins of the terrace are elevated marginally (~1 m) above the active floodplain, while at the head of the terrace, the surfaces are at approximately the same elevation. The groundwater-fed streams flow from a series of springs, which cross the down-valley (northern) margin of the terrace, before discharging into the main Toklat River (Fig. 1, C). Stream reaches (20 m) selected for study demonstrated similar stream morphology (an absence of bars, or riffle and pool sequences), and stream beds of small to medium cobbles overlying coarse gravel. Stream channel widths ranged between study sites from 0.23 to 5.3 m, and mean discharge (calculated throughout the study period) from 0.01 to 0.1 m^3 s^{-1} (Table 1). Mean monthly precipitation in summer 2008 was ~162 mm, and in winter was ~116 mm, while mean daily temperatures for the 2008 study period (recorded 5 km to the north at the Toklat Road Camp) were 11.8 °C (day) and 4.7 °C (night) (WRCC, 2008).

DATA COLLECTION AND ANALYSIS

Eleven sites were selected for study; 10 were groundwater-fed streams, situated upon the terrace (Fig. 1, C). Sites situated proximal to the valley sides were termed A sites (A1, A2, A3, A4, A5, A6, and A7), and those close to the glacial meltwater channel, were termed B sites (B1, B2, and B3). Sites B2 and B3 were ephemeral. The 11th site, the 'mixed channel,' was situated at the foot of the terrace and received flow from all groundwater-fed streams, and, intermittently, from the main Toklat channel.

Hydrology

Piezometer nests were installed at each groundwater-fed site (Fig. 1, C; sites A1, A2, A3, A4, A5, A6, A7, B1, B2, and B3). Each nest comprised two piezometers (5 cm outer diameter with 0.4 cm diameter holes drilled over basal 6 cm) installed to depths of 0.5 and 1 m below the surface using a piezometer installation system similar to that described by Baxter et al. (2003). The elevations of individual piezometers were determined by Electronic Distance Measurer (EDM) survey, with heights expressed relative to an arbitrary value of 0 cm at the lowest site on the terrace (A7). Piezometer water levels were monitored twice daily from 17 June to 9 September 2008. Spatial variations in water table elevations across the field site were interpolated, by Kriging, using a 90 m × 260 m grid from individual hydraulic head measurements at a depth of 50 cm.

In-stream water temperatures and levels were logged at five of the sites using *in situ* thermistors and pressure transducers (Fig. 1, C). Stream-bed water temperatures were also monitored at 20 cm depth at A2 and B1, and at 50 cm depth at A5 and B3. Measurements were taken continuously throughout the study period, with sensors scanned at 10-s intervals, from which 15-min mean values were derived. Water levels were also monitored within the main braided glacial meltwater channel; however, due to flooding, bank collapse, and sediment deposition, results were

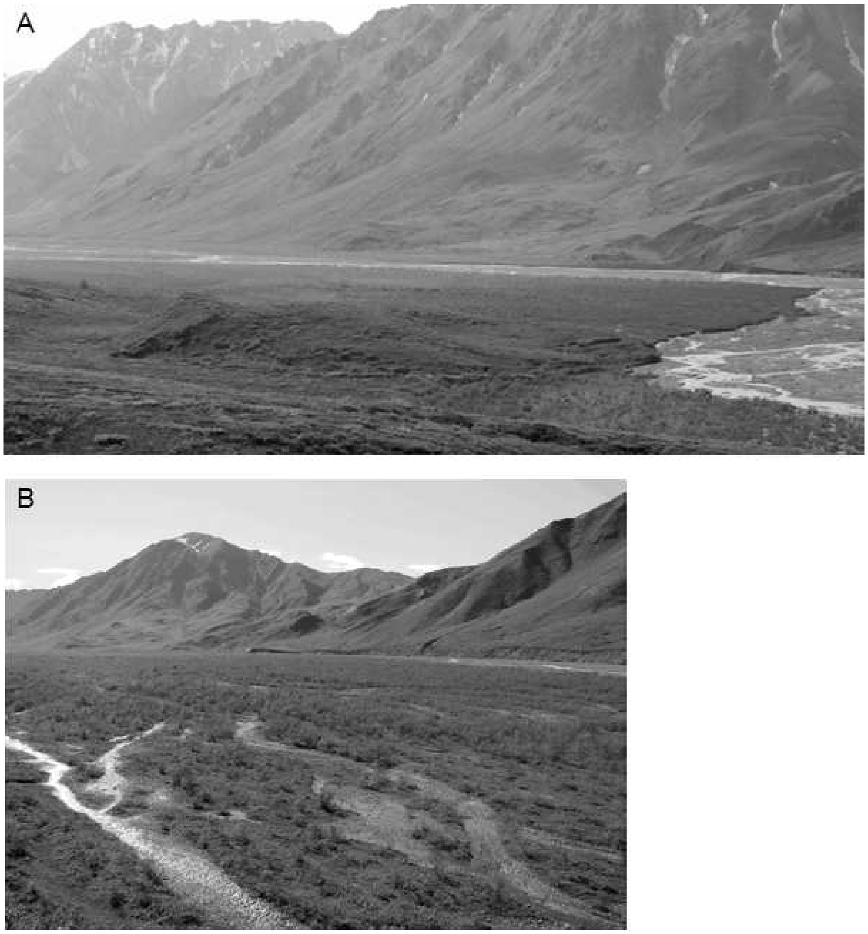


FIGURE 2. (A) View southwest across the valley showing terrace and active floodplain (the terrace is behind the bluff and extends up-valley for 2200 m) (8 June 2007). (B) View of terrace looking upstream (south), depicting network of groundwater-fed streams, with active floodplain observed on right (22 August 2008).

only obtainable from a single braid, from 22 August to 1 September.

Water Isotopes and Chemistry

From 30 May to 8 September 2008, water was sampled at 14-day intervals from groundwater-fed streams of sufficient depth to enable collection (A1, A2, A4, A5, B1, B2, and B3), and from the mixed channel site. Sampling of all water sources and potential flow pathways contributing to groundwater-fed streamflow was also undertaken. Sources sampled included precipitation, glacier ice-melt, glacial meltwater collected immediately below the terminus of the principal glacier (GMW_{term}), and snow meltwater (Fig. 1, B). Snow meltwater was sampled from the terminus of the snowpack, at the summit of the debris fan located adjacent to the terrace. Potential contributory flow pathways, flowing proximal to the terrace, were identified as glacial meltwater, sampled a short distance upstream of the terrace (GMW_{riv}); water flowing down the surface of the debris fan ($DFS_{surface}$); and debris fan seepage flow (DFS_{deep}) (Fig. 1, B). Water samples collected for isotopic analysis were taken using 2 mL vials, which were filled and tightly sealed to avoid evaporation during storage. Samples were also taken in 30 mL Nalgene polyethylene bottles for subsequent analysis of Chloride (Cl^-) concentration; these samples were filtered through 0.45 μL nylon membrane filters and refrigerated prior to analysis using an Anion Dionex ICS 2000 (instrumental precision <0.25 ppm).

Analysis of δ^2H and $\delta^{18}O$ was carried out using an Isoprime continuous-flow mass-spectrometer at the University of Birmingham, U.K. δ^2H analyses were undertaken using a chrome

TABLE 1

Comparative channel dimensions and seasonal mean discharge of groundwater-fed streams and main Toklat River channel: channel width gives distance between tops of adjacent stream banks; channel depth gives mean distance between stream bank top and stream bed at several intervals across the stream.

Site	Channel Width (cm)	Channel Depth (cm)	Mean stream discharge (m^3/s)	Stream discharge standard deviation
A1	230.0	18.04	0.01	0.005
A2	240.0	21.97	0.01	0.003
A4	280.0	24.10	0.02	0.005
A5	270.0	19.64	0.01	0.003
B1	530.0	54.04	0.06	0.016
B2	300.0	16.63	0.04	0.007
B3	440.0	18.32	0.10	0.084
Main Toklat River	500.0	23.90	0.55	0.048

reduction method on a Eurovector Elemental Analyzer preparation line. Internal precision for δ^2H is usually better than 1‰. $\delta^{18}O$ analyses were undertaken using an equilibration technique. Internal precision for $\delta^{18}O$ is typically 0.08‰, external precision is better than 0.12‰.

Ecology

Using a Surber Sampler (330 μm mesh), five replicate benthic macroinvertebrate samples were collected from each site at monthly intervals and preserved in 90% ethanol. Macroinvertebrates were identified to species wherever practical, and Simuliidae and Chironomidae were identified to family. This level has no significant effect upon determination of spatial distributions of invertebrate communities (Morris and Brooker, 1980). Mean abundance was calculated for the five replicates of each site, and expressed per m^2. Shannon's Index of macroinvertebrate diversity was calculated, and a Mann-Whitney U test used to determine the difference in diversity between streams fed by debris fan seepage waters (DFS) and those fed predominantly by GMW_{riv}.

Substrate collected in the Surber samples was dried at 65 °C, and sieved into coarse (>1 mm) and fine (<1 mm) fractions, prior to ashing at 540 °C for 2 hours, to determine ash-free dry mass. Organic matter content of both fractions was calculated, and expressed in mg/m^2. Algal matter was also collected at each site, at monthly intervals, from the upper surfaces of four randomly selected stones. The surface of each stone was scrubbed with a toothbrush, and materials washed into a 24 mL polypropylene container. Stone surface area was recorded. Samples were frozen, and stored in the dark to limit light degradation. After freeze drying, chlorophyll pigments were extracted in 90% acetone for 24 hours. Absorbance was determined at 750, 664, 647, and 630 nm wavelengths using a spectrophotometer. Concentrations of chlorophyll *a*, *b*, *c* and total chlorophyll were calculated using the equations of Sterman (1988), outlined in Ledger et al (2006).

Results

ISOTOPIC SIGNATURES

The isotopic composition of the Toklat water samples collected in 2008 are presented with a local meteoric water line (LMWL; Fig. 3, A). LMWLs are derived from the isotopic analyses of rainfall samples within a catchment. It was not possible, however, to fully characterize the annual isotopic variability within the Toklat catchment, due to the strong seasonality of precipitation in Alaska (snowfall predominance in winter, and rainfall in summer), and sampling only being possible during a summer field season. Therefore, the next nearest available LMWL based on the GNIP database is also provided, from Barrow, some 917 km to the north, for reference (IAEA/WMO, 2006). All Toklat samples lay close to the Barrow LMWL.

Water sources and water flow pathways sampled demonstrated distinct $\delta^{18}O$ signatures (Fig. 3, A; Table 2) including precipitation, snowmelt, glacial ice, surface flow from the debris fan ($DFS_{surface}$), debris fan subsurface flow (DFS_{deep}), and glacial meltwater from both the terminus (GMW_{term}) and the main meltwater channel (GMW_{riv}). The isotopic composition of debris fan and rainfall sources varied considerably throughout the season (Table 2), whilst that of groundwater-fed streams remained the most consistent.

The seasonal average $\delta^{18}O$ of precipitation (Table 2) was similar to both DFS_{deep} and $DFS_{surface}$. The average $\delta^{18}O$ values of snowmelt, GMW_{riv}, and GMW_{term} were considerably lower. Precipitation demonstrated the highest range in isotopic composition (Fig. 3, A) across all sources throughout the study period (20.26‰). The range of $DFS_{surface}$ $\delta^{18}O$ was lower than that of precipitation (8.90‰), but still relatively high compared with GMW_{term} (2.26‰) and GMW_{riv} (3.04‰). Unlike precipitation, however, $\delta^{18}O$ of $DFS_{surface}$ progressively increased throughout the season, irrespective of rainfall composition (Fig. 3, B). The average $\delta^{18}O$ of groundwater-fed streams was greater than that of GMW and snowmelt, but lower than DFS and rainfall; seasonal variation at 1.5‰ was lower than all source waters. The mixed channel at the base of the terrace had a low average $\delta^{18}O$ signature, more comparable to that of the GMW.

Marked isotopic variability was observed between perennial A sites, which were situated closer to the valley side, and B sites, of which most were ephemeral, which were situated closer to the GMW channel. Generally A sites had higher $\delta^{18}O$ values (Fig. 4, A), similar to DFS sources (Fig. 3, A; Table 2), and streamflow of A sites responded rapidly to precipitation (Fig. 4, B and C). However, hydrological and isotopic characteristics of A sites altered over the season; stream stage was initially relatively constant, but pronounced diurnal flow maxima were observed from 16 July (A2) and 16 August (A5). At A2, where these variations were most pronounced, the response of stream stage to precipitation also increased. Variations in the isotopic composition of groundwater-fed streams were directly connected to their respective hydrological regimes, with the $\delta^{18}O$ values responding to changes in stream depths. Accordingly, during the more hydrologically variable period at A2 and A5, and during periods of heavy or extensive rainfall (>4 days), the greatest $\delta^{18}O$ values were observed.

Sites B1, B2, and B3 generally had lower $\delta^{18}O$ values (Fig. 4, A), which were more similar to the low $\delta^{18}O$ values of GMW_{riv} (Fig. 3, A; Table 2). Stream stage within these sites was less responsive to precipitation; streamflow increased only following heavy or extended periods of continual rainfall (>4 days). At these sites the greatest $\delta^{18}O$ values were also associated with rainfall events of this duration; on 26 June, 25 July, and 11 August the $\delta^{18}O$ of B1 and B3 was higher than at all other sites (Fig. 4, A). During these extensive rainfall events the $\delta^{18}O$ of groundwater streamflow of all sites was greater, to some degree, irrespective of the isotopic composition of rainfall. B sites exhibited gradual increases in flow throughout the season (Fig. 4, D–F). B3 demonstrated two seasonal peak stage maxima, first in mid-June and second in early July (Fig. 4, F). The more attenuated flow regimes of B1 and B2, indicated by lower amplitudes of daily streamflow variations, demonstrated a similar flow peak in early August.

Seasonal differences in $\delta^{18}O$ values were observed between ephemeral and perennial streams (Fig. 5). Early in the season, during baseflow conditions, $\delta^{18}O$ was lower at all sites and closer to $\delta^{18}O$ values of 'meltwater' (snow or glacial). Subsequently, progressive seasonal increases in $\delta^{18}O$ values occurred within almost all perennial streams: A1–A3, A5, and B1. Following the initial increase from lower to higher $\delta^{18}O$ values within the first month of study, B2 and B3 (ephemeral streams) did not demonstrate further progressive increases in $\delta^{18}O$ values.

HYDROLOGICAL VARIABILITY

Throughout the season, increases in water table elevation were observed at all sites, although the magnitude of the water table increase was significantly greater at sites at higher elevations (Fig. 6, A) ($p < 0.01$). This reflects the significant down-valley surface

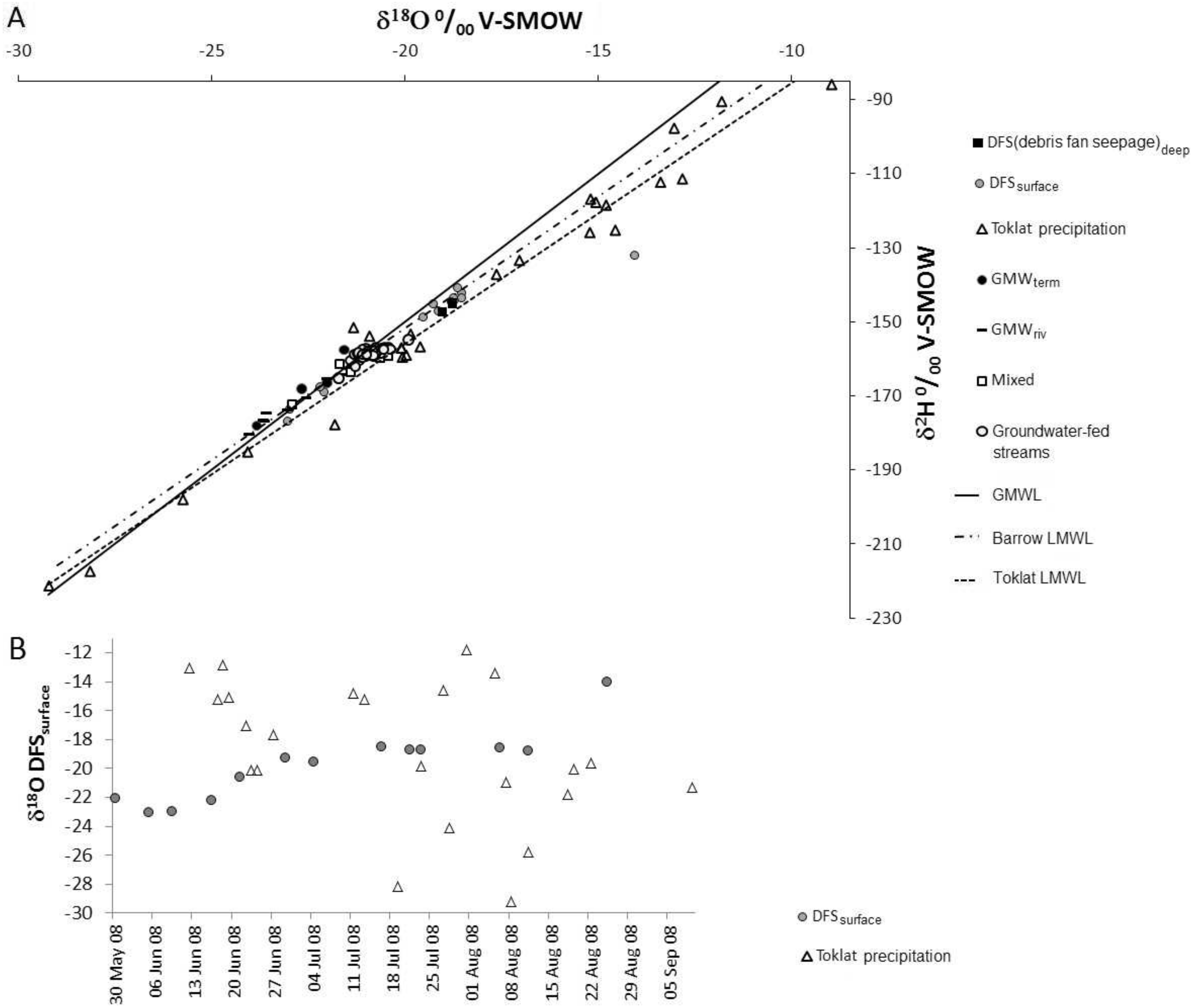


FIGURE 3. (A) Isotopic composition of source waters and groundwater-fed streams; Toklat local meteoric water line (LMWL): $\delta^2H = 7.05\ \delta^{18}O - 14.9$ (local rainfall data collected over 2008 study season); Barrow LMWL: $\delta^2H = 7.12\ \delta^{18}O - 9.13$ (7 year GNIP data set); global meteoric water line (GMWL): $\delta^2H = 8\ \delta^{18}O + 10$ (Craig et al., 1961). (B) Comparison between seasonal rise in $\delta^{18}O$ values of $DFS_{surface}$, and variable $\delta^{18}O$ values of precipitation.

gradient (2%) of the terrace (Fig. 6, B); the upstream sites at highest elevations (B2 and B3) experienced ephemeral flow. Streamflow commenced here later in the season as the water table rose to the surface. Greatest increases in water levels were observed in the initial months of study, stabilizing by early August.

Marked differences in degrees of flow attenuation were determined between sites (Fig. 7, A). Despite similarities in isotopic characteristics between GMW_{riv} and B sites, only B3 demonstrated distinct diurnal flow variability, corresponding with that of GMW_{riv} (Fig. 7, B). All A sites demonstrated low diurnal flow variability.

CL⁻ CONTENT

The average Cl^- concentration of DFS_{deep} was 15 times greater than that of any other source (Table 2). Although the standard deviation of Cl^- within DFS_{deep} was high, individual values were all markedly higher (at least 8 times) than, and therefore distinct from, all other sources and pathways. Average chloride concentrations of groundwater-fed streams were relatively high, compared to GMW, $DFS_{surface}$, and snow meltwater. The high Cl^- concentrations of DFS_{deep} are the most likely source of Cl^- to the groundwater streams. Given the distinct Cl^- signature, the proportional contribution of DFS_{deep} to each stream can be estimated using a simple mixing model:

$$DFS_{deep}\% = \left(\frac{S_u}{S_D}\right) \times 100 \qquad (1)$$

where $DFS_{deep}\%$ is percentage contribution of water to the site from DFS_{deep} waters, S_u is the concentration of Cl^- in the groundwater-fed stream, and S_D the average Cl^- concentration of DFS_{deep}.

By comparing $\delta^{18}O$ values with Cl^- concentrations within sites, two groups of streams were distinguished (Fig. 8, A). Group 1 streams encompassed all A sites. These had high, seasonally increasing Cl^- concentrations (Fig. 8, B), which corresponded at most sites with seasonal increases in $\delta^{18}O$ values. Significant

TABLE 2

Seasonal average $\delta^{18}O$ and Cl^- signatures of source waters, flow pathways, and groundwater-fed streams.

Source	$\delta^{18}O$ (‰)	SD	No. samples	Cl^-(mg L^{-1})	SD	No. samples
Rainfall	−18.22	5.08	25	1.76	—	1
DFS_{surf}	−19.45	2.30	11	0.56	0.18	11
DFS headwaters	−18.64	—	1	0.08	—	1
DFS snowmelt	−22.54	0.64	2	0.20	0.07	2
DFS_{deep}	−18.91	0.18	2	25.8	14.5	2
Snowmelt proximal to glacier	−22.99	—	1	0.14	—	1
Glacial melt (GMW_{term})	−22.53	0.98	4	0.34	0.2	4
Toklat main river(GMW_{riv})	−22.86	0.95	9	0.24	0.25	9
Groundwater streams	−20.93	0.302	45	2.67	1.13	45
Mixed	−21.29	0.772	8	1.97	1.14	8

correlations were identified between $\delta^{18}O$ values and Cl^- concentrations at A2 and A5. A4 did not demonstrate seasonal increases in $\delta^{18}O$ values, however Cl^- concentrations at this site were characteristically high, and increased throughout the season in a similar manner to comparable A streams (Fig. 8, B). At all A sites the relationship between $\delta^{18}O$ and Cl^- weakened following heavy or extended rainfall events; $\delta^{18}O$ increased disproportionately to Cl^-.

Group 2 incorporated streams B2 and B3; Cl^- concentrations were low at both sites, and not significantly correlated with $\delta^{18}O$ (Fig. 8, A). B1 and the mixed channel alternated between Groups 1 and 2 during the study season. In early summer, low Cl^- concentrations were observed at B1, with no correlation to $\delta^{18}O$ values (Group 2); thereafter a seasonal increase in Cl^- concentration was recorded (Fig. 8, B), associated with increases in $\delta^{18}O$ (Group 1) (Fig. 8, A), although this correlation varied with precipitation. Finally, during periods of peak glacial melt (as indicated by seasonal stage maxima in B3 [Fig. 7, A]), low Cl^- concentrations and $\delta^{18}O$ values were observed in the mixed channel (Group 2) (Fig. 8, C), which demonstrated marked increases in stream turbidity at this time. At all other times, higher Cl^- and $\delta^{18}O$ values were observed (Group 1).

MACROINVERTEBRATE DIVERSITY

Macroinvertebrate diversity in streams fed by DFS_{deep} was significantly higher throughout the study period, increasing from June to August (Fig. 9, A), than in streams with a higher GMW_{riv}

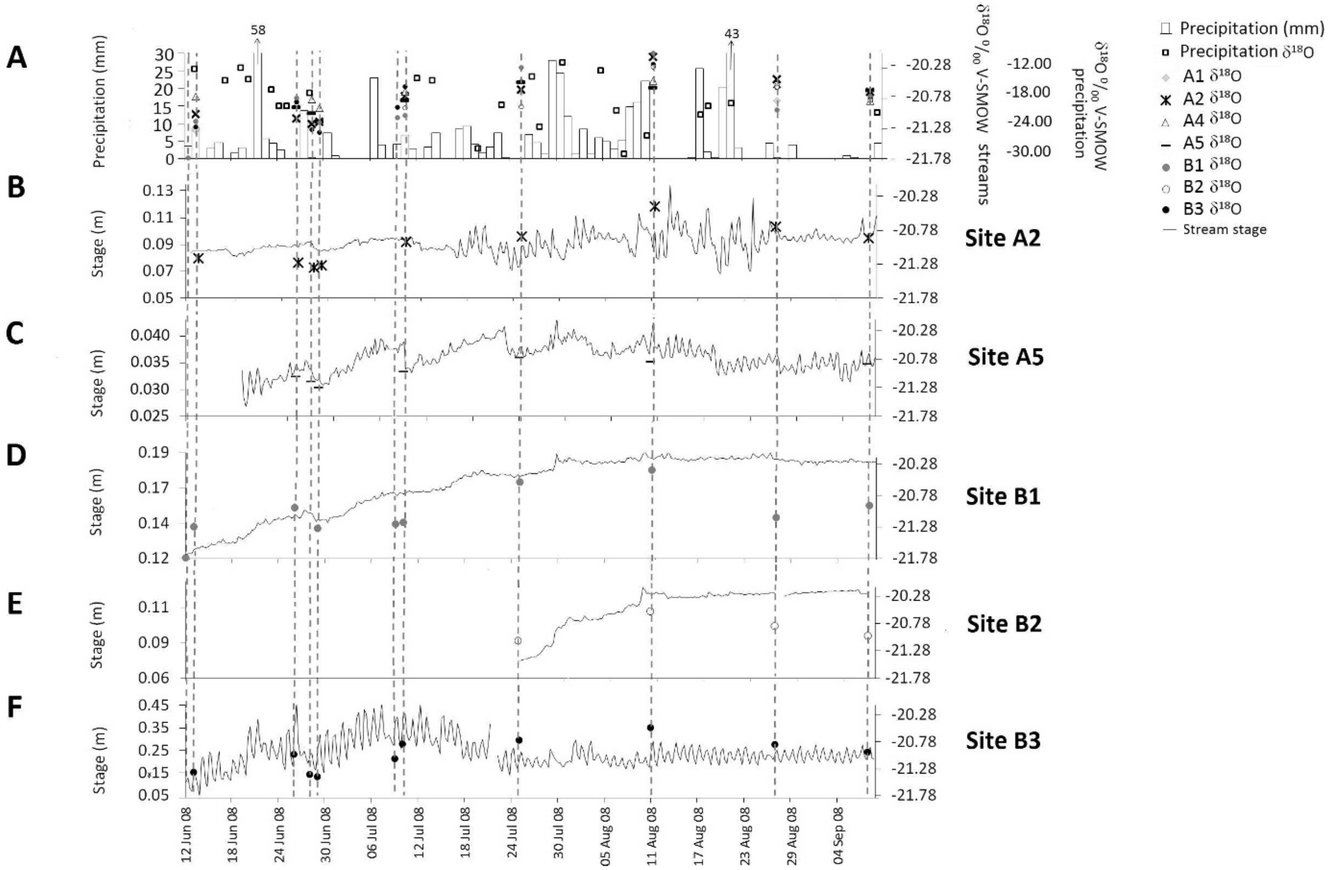


FIGURE 4. Comparisons of (A) variations in daily rainfall totals and the $\delta^{18}O$ values of all groundwater-fed streams; with variability in stream stage and $\delta^{18}O$ values of sites (B) A2, (C) A5, (D) B1, (E) B2, and (F) B3. Vertical lines highlight comparative sampling dates between streams.

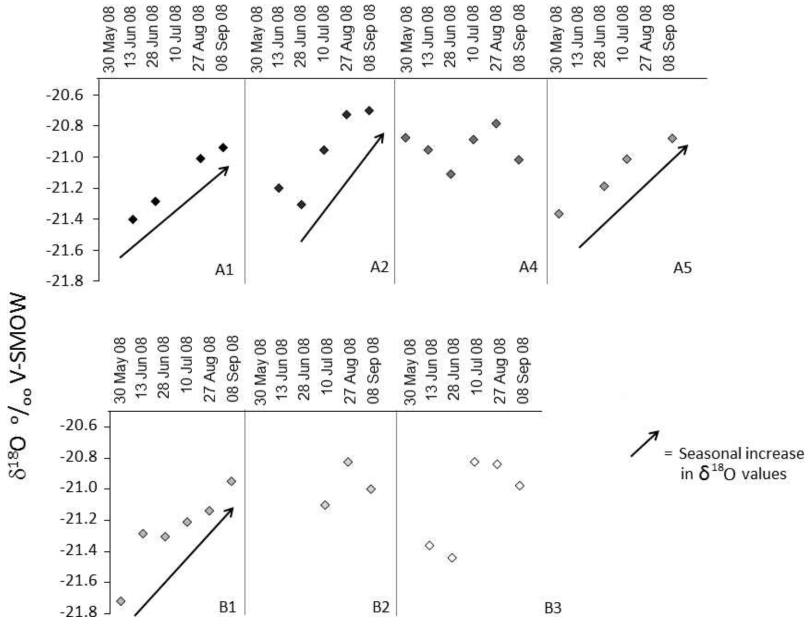


FIGURE 5. Differing degrees of seasonal increase in $\delta^{18}O$ values within perennial (A streams and B1) and ephemeral (B2 and B3) groundwater-fed streams.

contribution ($p < 0.001$; Table 3) where diversity remained limited (sites B2 and B3). Macroinvertebrate abundance of the mixed channel varied; in June, when GMW_{riv} had not yet inundated the mixed channel, due to low glacial ice-melt, macroinvertebrate abundance was comparable to that of the groundwater-fed streams (Fig. 9, B). Following peak glacial ice-melt, macroinvertebrate abundance of the mixed channel declined by 93% and did not significantly recover upon subsequent disconnection from GMW_{riv} in late July. The diversity of the mixed channel remained analogous to that of the groundwater-fed streams despite GMW_{riv} additions to the channel, until August, when diversity decreased (Fig. 9, A) in association with a higher relative dominance of Chironomidae, which increased from 43% in July to 93% in August.

In June the proportional contribution of DFS_{deep} to groundwater-fed streams was significantly correlated with fine particulate organic matter concentration (FPOM) (Fig. 10, A). At this time these two variables were also significantly correlated with macroinvertebrate abundance (Fig. 10, B and C). These associations were not observed in subsequent months. Increases in all organic matter fractions (fine and coarse) were observed at almost all sites from June to July (Fig. 10, D and E), with further increases observed in August. Chlorophyll increased at all sites in August (Fig. 10, F). The dissociation of relationships between DFS_{deep}, macroinvertebrate abundance, and FPOM in July and August corresponded with increases in availability of organic resources.

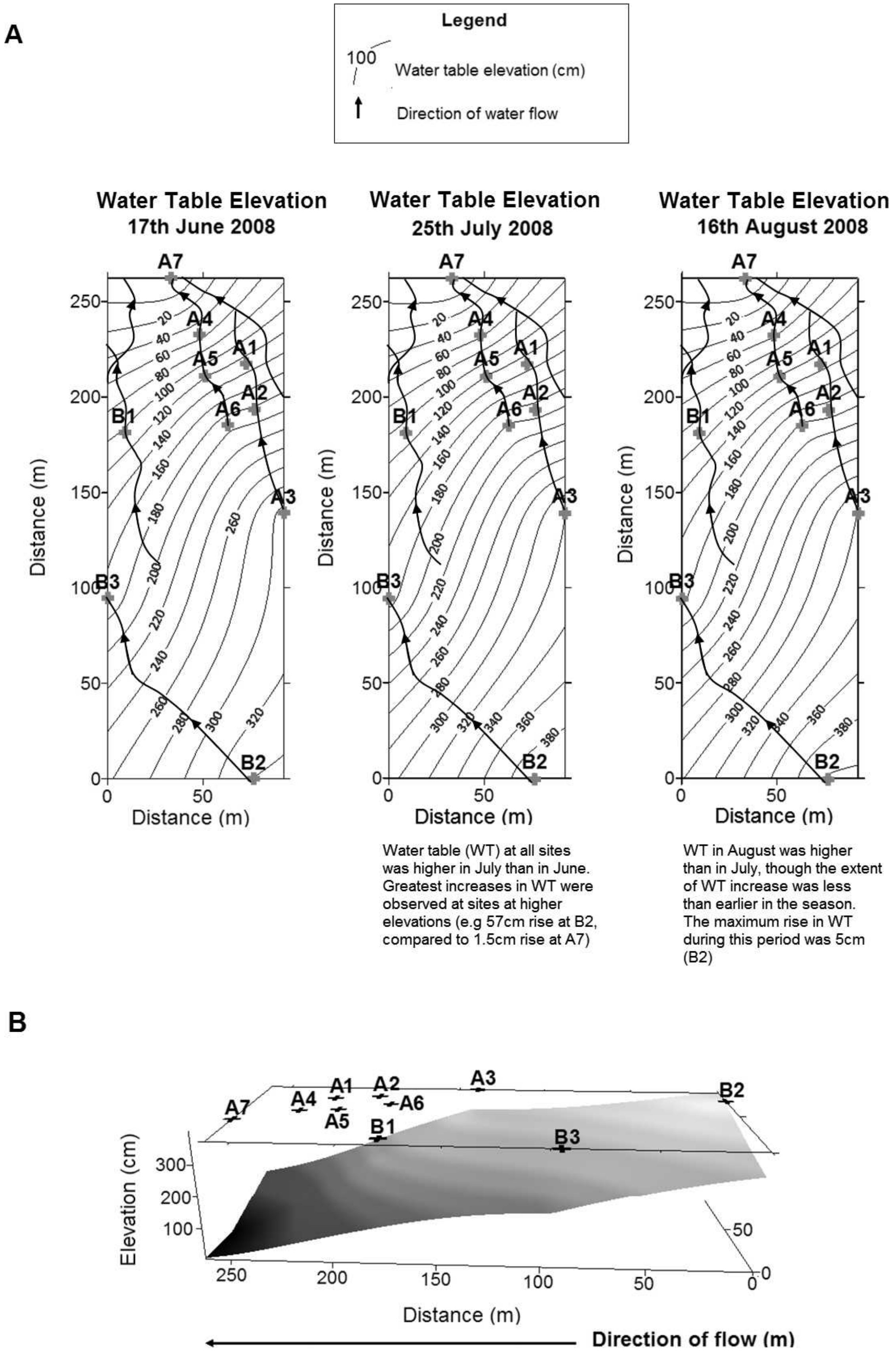
Discussion

WATER SOURCES AND FLOW PATHWAYS OF GROUNDWATER-FED STREAMS

The Barrow LMWL provides a more complete representation of the annual meteoric water input than the summer data collected from the study site. Although situated some distance from Denali National Park, the similarity in gradient between the Barrow LMWL and general trend in water samples derived from the Toklat catchment suggests that the systems were influenced by precipitation of similar isotopic signatures, supporting the use of this LMWL as a comparison in the study. Additionally, the proximity of Toklat surface and groundwater samples to the Barrow LMWL indicates that little evaporation has occurred and is therefore an unlikely cause of $\delta^{18}O$ differences between sources and groundwater-fed streams (Fairchild et al., 1999). Distinct isotopic signatures enabled identification of water sources and flow pathways contributing to groundwater-fed streamflow (Gibson et al., 2005); as the mean $\delta^{18}O$ value of groundwater-fed streams was intermediate between those of GMW_{riv} (lower $\delta^{18}O$ values) and the DFS flow pathways (higher $\delta^{18}O$ values), it was concluded that both were present within stream flow. Moreover, results indicated that streams may receive variable contributions to flow from these pathways, as the $\delta^{18}O$ of groundwater-fed streams differed between sites and over time.

Three flow pathways were associated with the valley side; a surface pathway ($DFS_{surface}$) and two subsurface pathways. Of the subsurface pathways, the first was situated at depth within the valley-side profile where waters likely had a long residence time (DFS_{deep}) (Fig. 11). This pathway acted as a perennial baseflow and principal source of Cl^- to the groundwater-fed streams. Evaporation can cause elevated Cl^- concentrations (Hayashi et al., 1998), however the isotopic compositions do not support this; localized mineral dissolution is therefore more likely. Flow through the less permeable, fine matrix of lower debris fan layers (Clow et al., 2003) may extend water contact time with rock facies, and enable mineral dissolution of evaporites. The Cl^- concentration of this 'older' DFS_{deep} groundwater would be increased to levels much greater than in initial atmospheric inputs (Anderson et al., 2003), explaining the higher Cl^- concentrations observed in DFS_{deep}, with minimal alteration in $\delta^{18}O$ values. Halites and anhydrites, although not specified in a general geological description of the national park (Wilson et al., 1998), could be found within the late Triassic calcareous sedimentary rocks of the valley sides.

The presence of a second subsurface flow pathway within the valley side is suggested by streamflow response to precipitation events, with increases in stage and $\delta^{18}O$ values, and no increase in Cl^- concentrations. This demonstrates contribution to streamflow from a rapid response pathway, potentially through the highly permeable near-surface sediments of the debris fan (Roy and Hayashi, 2009) ($DFS_{shallow}$) (Fig. 11). The $\delta^{18}O$ values of precipitation were buffered prior to reaching the groundwater-fed



Water table (WT) at all sites was higher in July than in June. Greatest increases in WT were observed at sites at higher elevations (e.g 57cm rise at B2, compared to 1.5cm rise at A7)

WT in August was higher than in July, though the extent of WT increase was less than earlier in the season. The maximum rise in WT during this period was 5cm (B2)

FIGURE 6. (A) Seasonal variations in water table elevation across floodplain terrace (cm). (B) Digital elevation model of groundwater-fed streams (cm), depicting surface topography.

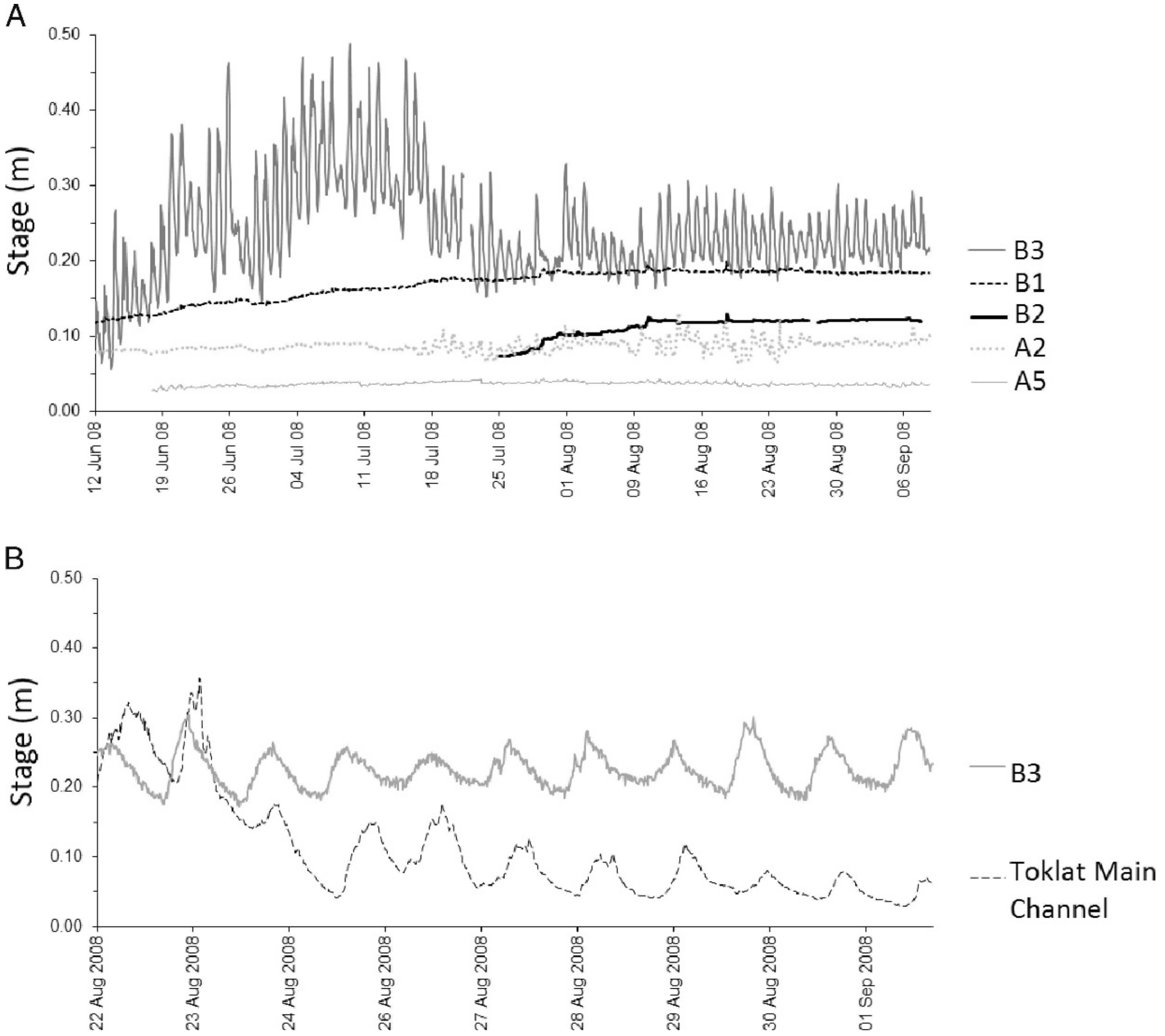


FIGURE 7. (A) Stream stage of groundwater-fed streams, illustrating flow attenuation. (B) Correspondence in flow regimes of less-attenuated B3 and GMW_{riv}.

streams; irrespective of the characteristically variable $\delta^{18}O$ values of rainfall, in-stream $\delta^{18}O$ values were persistently greater following precipitation. This may result from mixing of rainwater with antecedent soil moisture upon valley sides, which increases $\delta^{18}O$ and reduces variation (Rogers et al., 2005). In conjunction with the similarity between mean precipitation $\delta^{18}O$ values and DFS pathways, this buffering mechanism indicates that the most likely pathway of the heavier in-stream $\delta^{18}O$ values, following rainfall, is through the valley side. Reduced in-stream Cl^- concentrations relative to $\delta^{18}O$ values, also observed following rainfall, likely reflect the increased relative contribution of $DFS_{shallow}$ in groundwater-fed streams, with the rate of water flow through this pathway sufficient to minimize mineral dissolution (Swoboda-Colberg and Drever, 1993). Alternatively, evaporite deposits may be highly localized, and the $DFS_{shallow}$ flow pathway may bypass the minerals. The relative reduction in Cl^- concentration following rainfall suggests a time lag in the contributions of the two subsurface DFS pathways, and hence a difference in residence times.

The seasonal increases in $\delta^{18}O$ values observed within all DFS waters may be attributed to isotopic fractionation of snow meltwater. However, enrichment of $\delta^{18}O$ within $DFS_{surface}$ was 9‰, greater than expected for fractionation (Taylor et al., 2002). As average rainfall $\delta^{18}O$ values were higher than those of snowmelt, isotopic enrichment may additionally reflect the increasing dominance of rainfall, with seasonal snowmelt reductions (Sueker et al., 2000).

The final flow pathway comprises subsurface seepage from GMW_{riv} (Fig. 11), characterized by lower $\delta^{18}O$ values and low Cl^- concentrations. These waters are envisaged to derive from meltwater seepage through the river bed of the main Toklat River upstream, into the alluvial deposits of the floodplain terrace (e.g. Malard et al., 2002). GMW_{riv} seepage emerges onto the terrace as groundwater-fed streams at points where the terrace surface slopes down-valley to intersect the local water table. Mixing of the three subsurface pathways results in the intermediate $\delta^{18}O$ values and Cl^- concentrations observed in the groundwater-fed streams.

VARIABILITY IN PHYSICOCHEMICAL COMPOSITION OF GROUNDWATER-FED STREAMS

As Malard et al (1999) found in the Val Roseg in the Swiss Alps, results indicated that the three primary sources (snow, glacial ice, and rainfall) contributing to groundwater flow varied in both their relative contribution and flow pathway over space

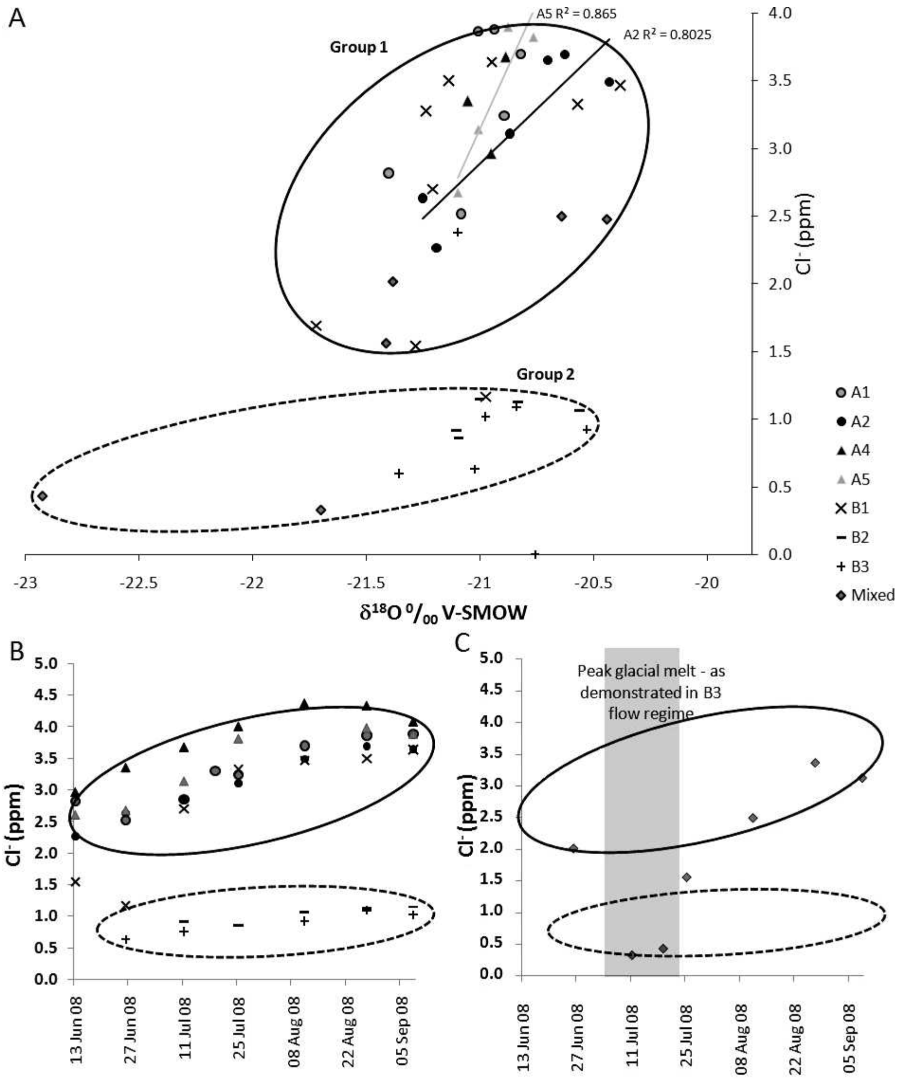


FIGURE 8. (A) Temporal co-variation of Cl$^-$ concentrations and δ^{18}O values within study sites. (B) Difference in Cl$^-$ concentrations between groups 1 and 2; seasonal increase in concentration depicted in group 1. (C) Seasonal variability in Cl$^-$ concentrations in mixed site.

and time. This contributes to marked local spatial and temporal variability in the physicochemistry of groundwater-fed streams.

Spatial Variability

Seasonal and spatial trends in the physicochemistry of the groundwater-fed streams can be attributed to differences in the proportional contributions from DFS flow pathways and GMW$_{riv}$ seepage. The proximity of the A streams to the valley side, lack of mid-summer flow maxima, and the perennial flow indicates that these streams received a significant flow contribution via seepage from the DFS pathways. The relatively high δ^{18}O values and seasonal increase in δ^{18}O values observed within A streams are also characteristic of DFS waters. This conclusion is further supported by high Cl$^-$ concentrations, indicative of DFS$_{deep}$ contributions, in addition to seasonal enrichment of both Cl$^-$ and δ^{18}O.

Cl$^-$ enrichment reflects several interacting processes. Cl$^-$ concentrations within valley-side flow pathways, and hence within A streams, were low at the start of the study season. During high discharge events solute concentrations from mineral dissolution are reduced (Frumkin, 1994); therefore, when large volumes of snow meltwater with low Cl$^-$ concentration values passed through DFS$_{deep}$ at the start of the study season (Sueker et al., 2000), lower Cl$^-$ concentrations were conveyed to the A streams. Following peak snowmelt, reduced snow meltwater contributions resulted in an increased dominance of rainfall (with higher Cl$^-$ concentrations) to groundwater recharge (Sueker et al., 2000). Percolating in smaller volumes through the valley side, rain water, further enriched in Cl$^-$ through mineral dissolution, was released from DFS$_{deep}$ into the groundwater-fed streams. The seasonal increase in Cl$^-$ concentrations of A streams therefore likely resulted from gradual increases in percentage contributions of rainfall (Sueker et al., 2000). The large range in Cl$^-$ concentration of DFS$_{deep}$ can thus be explained by variation in discharge and associated solute concentration and mineral dissolution (Frumkin, 1994). As rainfall dominance produced characteristic enrichment in δ^{18}O and Cl$^-$ within DFS flow pathways, the positive associations observed in A streams between δ^{18}O and Cl$^-$ further support the presence of this flow pathway.

The closer proximity of B streams to GMW$_{riv}$, seasonal-maxima, and generally lower δ^{18}O values, suggest a higher contribution from GMW$_{riv}$ seepage. At B2 and B3 ephemeral flow and lack of seasonal δ^{18}O enrichment further support this. The lack of seasonal increase in δ^{18}O might be attributed to the lower degree of fractionation typical of glacial ice-melt (Souchez and Lorrain, 1991; Moser and Stichler, 1974). Initial low δ^{18}O values likely reflect a high snowmelt contribution to glacial meltwater flow, from the glacier surface, early in the season (Collins, 1979). Through the summer, relative contributions of

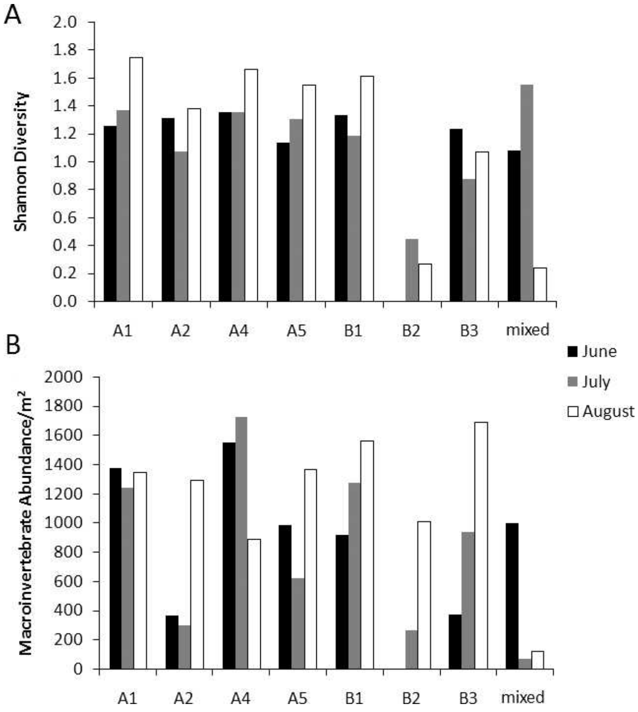


FIGURE 9. Macroinvertebrate (A) species diversity and (B) abundance of all study sites by month, demonstrating variability throughout the study season.

TABLE 3

Summary of average taxa abundance (throughout study period), indicating differences between stream types. Stream location of maximum taxa abundance is highlighted.

Taxa	Perennial	Ephemeral
Chironomidae	416.06	670.23
Zapada haysi	339.251	38.95
Oreogeton spp.	131.59	68.62
Baetis bicaudatus	88.37	5.11
Simuliidae	85.33	19.78
Ecclisomyia spp.	27.76	25.81
Chelifera spp.	6.97	—
Baetis tricaudatus	4.62	2.12
Oligochaetae	3.79	0.86
Alaskaperla ovibovis	3.15	1.29
Plumiperla diversa	3	0.86
Tipula spp.	2.86	11.18
Clinocera spp.	2.28	0.86
Isoperla petersoni	1.57	0.43
Ephydra spp.	1.13	0.43
Isotomidae	0.71	2.99
Limniphora spp.	0.71	0.43
Pericoma spp.	0.43	—
Hexatoma spp.	0.14	2.98
Megaleuctra spp.	0.14	0.43
Serromyia spp	—	1.72

glacial ice meltwater are increased as the transient snowline rises (Collins et al., 2002). This ice-melt contribution may buffer the fractionation effect of snowmelt; therefore, seasonal δ^{18}O enrichment does not occur. Moreover, following peak snowmelt there was little increase in the low Cl^- concentrations at these sites, suggesting limited or no connection with DFS_{deep}. Accordingly there was no association between δ^{18}O values and Cl^- concentrations, indicating limited contributions from sources experiencing differences in snowmelt and rain-fall dominance (DFS sources). Finally, the close correspondence between the flow regimes of B3 and GMW_{riv} demonstrates that the marked daily variations observed at B3 are likely as a result of a close, less attenuated, connection with GMW_{riv}.

Although B1 was characteristic of B streams in its presence of mid-summer flow maxima and proximity to GMW_{riv}, it also demonstrated seasonal increases in δ^{18}O values and perennial flow, similar to that of A streams. This might indicate a mixed contribution of groundwater flow pathways at B1, with a DFS_{deep} baseflow component and additional input from GMW_{riv} seepage. This mixture of flow pathways is further substantiated by Cl^- analysis. The high Cl^- concentrations and seasonal enrichment observed are indicative of DFS_{deep} baseflow. Differences observed between B1 and other B sites, despite a similar proximity to GMW_{riv}, are likely due to the lower elevation of B1, which is sufficiently close to the water table to maintain a perennial DFS_{deep} seepage baseflow component.

In the mixed channel, reductions in δ^{18}O values during periods of connectivity to GMW_{riv} (observed initially by marked increases in stream turbidity) can be attributed to the addition of glacial meltwater (low δ^{18}O values) to the previously predominantly groundwater-fed stream. Reductions in δ^{18}O values in the mixed channel, indicative of connectivity to GMW_{riv}, coincided with peak glacial melt from mid-June to late July (observed in B3), suggesting that connectivity to the main Toklat channel occurred during times of peak meltwater flow. The mixed channel becomes inundated with GMW_{riv} flow as discharge, and therefore number of active channels, of the main glacial meltwater channel increases (Warburton, 1994). Reductions in Cl^- observed during peak melt were therefore likely due to the low Cl^- content of GMW_{riv}. Associations between δ^{18}O and Cl^- observed during groundwater dominance of mixed channel flow is likely attributed to contributions from DFS_{deep}.

Temporal Variability

Short-term and seasonal variability in the physicochemistry of A and B streams was observed, in addition to that reflecting snowmelt reduction. Short-term variability may result from a rising water table following prolonged precipitation, enhancing connectivity between previously isolated preferential flow pathways (Anderson et al., 2009; Sidle et al., 2000). This process appeared to create pathways between B sites and the isotopically enriched and rapidly responsive $DFS_{shallow}$, indicated by step increases in stage and concurrent uncharacteristically high δ^{18}O values. A streams, situated closer to the valley sides, demonstrated increases in stage and δ^{18}O values following less extensive precipitation events, although the degree of this response was enhanced following periods of extended rainfall. The weakening of the positive association between δ^{18}O and Cl^- might be attributed to temporary increases in $DFS_{shallow}$ contribution, with high δ^{18}O values and low Cl^- concentrations.

The seasonal increase in water table reflects progression of the melt season, with increased GMW_{riv} flow resulting in greater subsurface infiltration of water. As water levels continued to rise until intersecting the surface, water table increases were particularly marked at higher elevations. Accordingly, streams began to flow at successively higher points as the summer progressed. Seasonal increases in streamflow observed at B sites might therefore be attributed to water table rises, of up to 60 cm, produced by peak mid-summer meltwater flows. Sites at the lowest

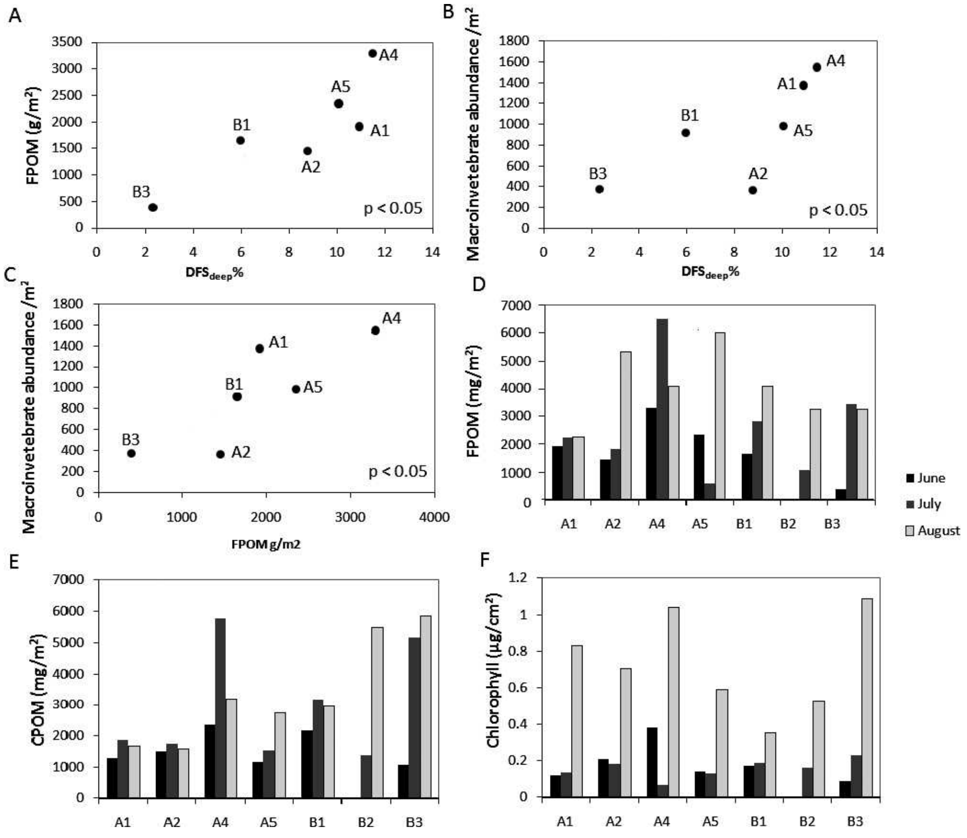


FIGURE 10. Interrelationships between (A) fine particulate organic matter (FPOM) and relative contributions from the debris fan deep pathway (DFS$_{deep}$%) in June; (B) macroinvertebrate abundance and DFS$_{deep}$% in June; (C) macroinvertebrate abundance and FPOM in June; (D) seasonal variability in FPOM; (E) seasonal variability in coarse particulate organic matter (CPOM); and (F) seasonal variability in chlorophyll concentration.

points of the terrace sustained perennial flow as they lay at a sufficiently low elevation to maintain surface flow supplied by DFS$_{deep}$, despite winter reductions in water table height. Seasonal increases in the diurnal variability of streamflow observed at A sites, concurrent with increases in streamflow at B sites, may indicate an influx of GMW$_{riv}$ seepage following the rise in the water table. Differences in emergence times of GMW$_{riv}$ seepage at A sites might reflect variations in flow attenuation and sediment permeability (Ward et al., 2002).

The results suggest that each groundwater-fed stream is characterized by a balance of inflows derived from three subsurface flow pathways: (1) ephemeral subsurface seepage from the main glacial meltwater channel (GMW$_{riv}$ seepage); (2) perennial flow through the base of an adjacent debris fan on the

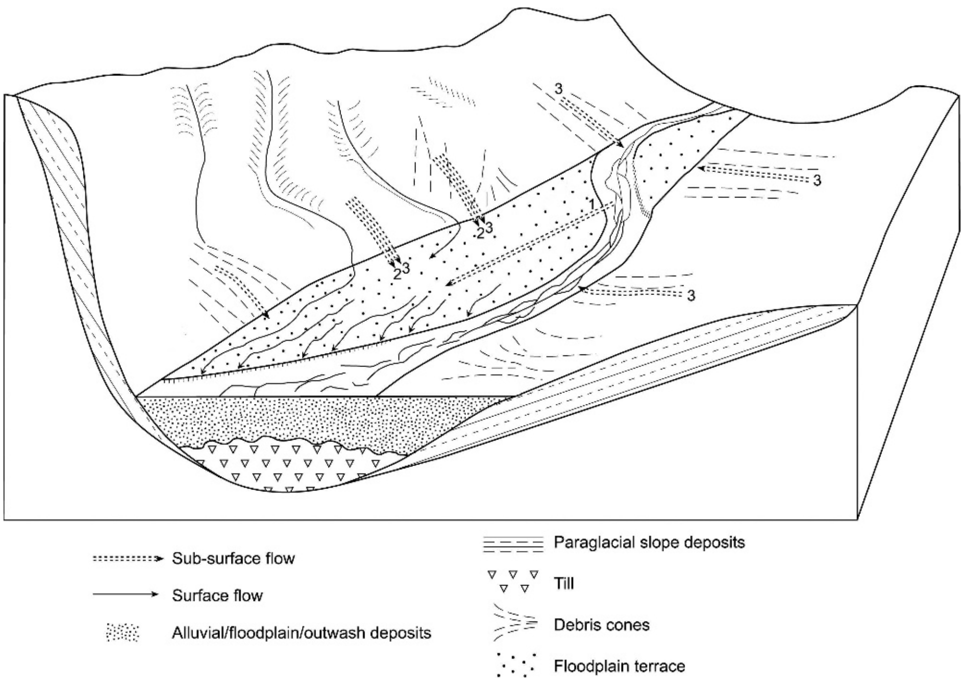


FIGURE 11. Schematic of groundwater flow pathways contributing to stream flow on a floodplain terrace of the Toklat River catchment (after Ballantyne, 2002; Fig. 30). (1) GMW$_{riv}$: subsurface flow of glacial-fed river through alluvial aquifer, along the valley axis; (2) DFS$_{deep}$: subsurface flow near debris fan base, within a dense matrix; and (3) DFS$_{shallow}$: subsurface flow near the debris fan surface, within a permeable matrix.

valley side (DFS_{deep}); and (3) rapid-response near-surface flow through the debris fan ($DFS_{shallow}$). The relative contribution of each pathway to individual groundwater-fed streams varies and may be significant given predicted long-term reductions in meltwater supplies resulting from climate change-associated glacial recession (Milner et al., 2009). Results indicate glacial recession may influence each groundwater-fed stream individually: B2 and B3, fed almost solely by glacial meltwater, may cease to flow, whereas streams derived from DFS_{deep} could maintain active stream flow with greater relative rainfall recharge contributions. Given the local variations in physicochemistry and climate change implications between each groundwater-fed stream, 'groundwater' in this catchment cannot be regarded as homogeneous.

INFLUENCE OF GROUNDWATER PHYSICOCHEMICAL VARIABILITY ON MACROINVERTEBRATE COMMUNITIES

The higher macroinvertebrate abundance and, later in the study season, macroinvertebrate diversity found within groundwater-fed streams relative to the mixed channel indicate that these systems are hotspots of diversity (as found by Brown et al., 2003, 2007) supported by high water clarity and stability of temperature and discharge (Brown et al., 2003). Within the mixed channel the high macroinvertebrate abundance and diversity observed during June might be attributed to an absence of glacial influence and dominance of groundwater as greater water clarity and Cl^- concentrations were observed at this time. Following the influx of glacial meltwater, the reduction in macroinvertebrate abundance but continued high diversity might be attributed to high meltwater discharge reducing all taxa (Resh et al., 1988). Macroinvertebrate abundance did not increase significantly once glacial waters receded, potentially due to longer term reduction of habitat suitability, e.g. deposition of glacial fines (Angradi, 1999) and removal of refugia. Alternatively, recolonization of the mixed channel may require a more significant time period (Scrimgeour et al., 1988).

The significant positive relationships observed in June between macroinvertebrate abundance, $DFS_{deep}\%$, and FPOM suggest that during this month DFS_{deep} was a principal source of FPOM, and macroinvertebrate community distribution reflected the availability of this resource. The relationship between $DFS_{deep}\%$ (sourced from valley-side through-flow) and FPOM might be explained by transport of particulate matter within subsurface environments (McDowell-Boyer et al., 1986). Through-flow may entrain organic matter from perched wetlands and deeper soils of the valley sides, which is discharged at points of upwelling groundwater (Boissier and Fontvieille, 1995). Organic matter is an important energy source (Buffam et al., 2001), and during periods of low resource availability macroinvertebrates may aggregate upon isolated patches of high organic matter concentration (Tiegs et al., 2008) such as those provided by DFS_{deep}.

The absence of a significant relationship between $DFS_{deep}\%$ with FPOM and macroinvertebrate abundance in July and August could reflect increased availability of alternative organic matter resources, with regrowth of streamside foliage in summer and subsequent fall of leaf litter (increasing FPOM and CPOM). Leaf abscission is also associated with enhanced periphyton production (resulting in greater chlorophyll concentrations) (Rosemond et al., 2000) as it reduces streambed shading. The relationship between macroinvertebrate distribution and groundwater flow became weaker when food resources were no longer constrained to isolated patches at points of DFS_{deep} discharge.

Despite seasonal variability in relationships between macroinvertebrate abundance and groundwater flow pathways, macroinvertebrate diversity within DFS_{deep}-fed streams was, overall, significantly higher than within streams supplied by higher proportions of GMW_{riv}. Lower macroinvertebrate diversity observed in all streams during June is attributed to lower organic matter availability; many taxa are phenologically adapted to hatch in months when resource availability is greatest (Cummins et al., 1989), therefore in perennial streams diversity seasonally increases with increasing organic matter resources. However, in ephemeral streams fed by GMW_{riv} seepage, despite seasonally increasing organic matter availability, diversity remained limited. This is likely due to low flow permanence (Fonseca and Hart, 2001); taxa were limited to those with specialist traits, e.g. drought resistant eggs, and multivoltinism, such as Chironomidae (Williams, 1996).

Although the strength of the association between macroinvertebrate abundance and characteristics of groundwater-fed streams varied seasonally in association with availability of alternative organic matter resources, the significant difference in diversity between perennial streams (derived from DFS_{deep} seepage) and ephemeral streams (derived from GMW_{riv} seepage) demonstrates a more sustained influence of groundwater flow pathways upon the macroinvertebrate community. Results also indicate climate change implications upon macroinvertebrate communities within groundwater-fed streams may be highly localized due to the dynamic stream physicochemistry. Given the potential for future reduction of GMW supplies (Milner et al., 2009), macroinvertebrate communities within streams fed solely by GMW_{riv} seepage demonstrate a high potential vulnerability to glacial recession. Perennial streams fed by groundwaters from DFS_{deep} could be more resilient to climate change; the diversity of macroinvertebrates within these streams could increase as perennial groundwater contributions increase relative to glacial meltwater (Brown et al., 2007). However, as additional stream properties (e.g. organic matter content) can vary markedly over a relatively small scale, the effect of glacial recession will be complex. Groundwater should therefore be regarded as having a dynamic influence upon macroinvertebrate communities.

Conclusion

There are marked local spatial and temporal variations in the physicochemistry of groundwater-fed streams in glacierized catchments, reflecting variability in the proportional contribution of waters derived from distinct flow pathways. On a floodplain terrace of the Toklat River, spatial variations in flow pathway contributions were determined to be primarily a function of topography. Proportional flowpath contributions also varied on a seasonal and rainfall-event scale. Resultant physicochemical differences between streams significantly influenced macroinvertebrate communities, but seasonal increases in organic matter availability weakened the association between these variables and macroinvertebrate abundance. In resource depleted environments, flow pathways determining organic matter entrainment may therefore have a significant influence upon the maximum macroinvertebrate abundance which can be supported.

A degree of vulnerability to climate change-induced glacial recession of groundwater-fed streams and macroinvertebrate communities was established, dependent upon groundwater source. Streams fed solely by glacial meltwater seepage were considered more vulnerable, given low macroinvertebrate diversities supported and potential for cessation of flow with long-term reductions in meltwater supplies. Perennial streams sustained by valley-side baseflow, supporting higher macroinvertebrate diversities, were placed at a lower risk. Understanding of groundwater flow in glacierized systems is therefore essential in establishing the influence of groundwater upon macroinvertebrate communities, and the future implications of climate change.

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