THE HYDROECOLOGY OF GROUNDWATER-FED STREAMS IN A GLACIERISED CATCHMENT

by

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Abstract

Groundwater flow typically provides stable stream habitat within glacierised floodplains. However, spatio-temporal differences within and between groundwater flow pathways can create marked variability in the physicochemical characteristics of groundwater-fed streams. Research conducted on a floodplain terrace of the Toklat River, Denali National Park, Alaska, predominantly from May to September 2008, determined the influence of groundwater flow dynamics upon benthic and hyporheic macroinvertebrate assemblages.

During periods of resource depletion benthic macroinvertebrate abundance was dependent upon contributions from specific flow pathways (DFS_{deep}), which supplied fine particulate organic matter. Dynamics of groundwater flow pathways influenced macroinvertebrates throughout the summer, however, with higher diversity observed in perennial streams which received groundwater flow from DFS_{deep}. Ephemeral flow pathways of glacial seepage supported lower diversity.

Within the hyporheic zone, environmental stability of surface waters was influential, as this reflected the sub-surface residence time of percolating waters; nested routes of flow within each flow pathway, of varying length or permeability, created differences in the environmental stability of each stream. Macroinvertebrate diversity in the hyporheic zone was higher at sites of lower surface environmental stability, suggesting possible migration into the hyporheic zone. Digital remote sensing used to estimate the spatial extent of groundwater upwellings within two national parks in Alaska indicated that these groundwater-fed habitats are widespread.

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Glossary of frequently used abbreviations

CPOM	Coarse particulate organic matter
DFS	Debris fan seepage
DFS_{deep}	Debris fan seepage (deep subsurface flow pathway)
$DFS_{shallow}$	Debris fan seepage (shallow subsurface flow pathway)
$DFS_{surface}$	Debris fan seepage (surface flow)
FPOM	Fine particulate organic matter
GMW	Glacial meltwater
GMW_{riv}	Glacial meltwater (of the main Toklat river channel)
GMW_{riv} seepage	Subsurface seepage of glacial meltwater originating from the main Toklat river channel
GMW_{term}	Glacial meltwater (of the glacial terminus)
HZ	Hyporheic zone
LMWL	Local meteoric water line
GMWL	Global meteoric water line
NDVI	Normalised Vegetation Index
TOM	Total organic matter

1.Introduction

It has been established that within glacierised catchments, streams deriving flow from groundwater may support higher ecological diversity (Brown et al., 2007), due to associated increased habitat stability. However when groundwater is considered as a stable feature, the established physicochemical dynamics of groundwater systems, reflecting variability within and between groundwater flow pathways, are overlooked. Such variability could influence macroinvertebrate communities. A better understanding of the complex hydro-ecological interactions occurring within glacierised catchments is required, to establish groundwater as a dynamic influence upon freshwater ecosystems. By studying the macroinvertebrate communities of seven streams fed solely by upwelling groundwater, within a glacierised catchment, this study addresses research gaps with respect to groundwater as a dynamic influence upon freshwater ecosystems.

1.1 Introduction

There is a relative paucity of research considering shallow groundwater hydrology within glacierised catchments (Robinson et al., 2009), likely due to the relative inaccessibility of study areas (Tockner et al., 2002). However knowledge of groundwater:surface water interactions in these environments is essential in understanding the influence of groundwater-fed streams upon freshwater ecosystems, and the potential implications of climate change-associated glacial recession (Brown et al., 2007a; Robinson et al., 2009). Glacial recession is predicted, in the long term, to result in an increase in the percentage of groundwater contribution to glacierised catchments (Brown et al., 2007_a; Milner et al., 2009), following the eventual depletion of frozen water stores and reduction in meltwater supply (Clow *et al.,* 2003). Furthermore, ecological research in these environments has focused largely upon glacial meltwater (Brown et al., 2007), and patterns of macroinvertebrate communities with distance from the glacial terminus (e.g. Milner et al., 2001; Ilg and Castella, 2006; *inter alia*). Few studies within glacierised catchments have considered the ecological significance of groundwater contributions; Brown *et al* (2007) therefore suggest the need for an integrated study between a) contributions from different water sources, b) physicochemical habitat and c) stream biota.

The composition and function of many freshwater ecosystems is dependent upon groundwater (Hattan and Evans, 1998; Murray *et al*., 2004; Boulton and Hancock, 2006; Murray *et al*., 2006), which is typically characterised by low variability in flow and temperature (Brunke and Gonser, 1997), and high water clarity. Where shallow groundwater supplies stream flow, hotspots of high nutrient concentrations may result (Coleman and Dahm, 1990). The difference between surface and groundwater-fed streams is particularly marked within glacierised catchments, as streams fed by glacial meltwater and snow-melt demonstrate extreme daily flow and temperature amplitudes, and high turbidity (Fureder *et al.,* 1998*;* Malard *et al*., 2001). Groundwater-fed streams therefore generally support higher ecological diversity, providing habitats for macroinvertebrate communities (Stanford and Ward, 1993; Boulton *et al*., 1998; Barquin and Death, 2006). These communities have key roles in nutrient cycling (Merritt *et al*., 1984) and are influential in the functioning of riverine ecosystems (Cummins, 1974; Cummins and Klug, 1979).

However a number of significant research gaps remain; groundwater is typically considered to be relatively homogenous (Poole *et al.,* 2006), and established physicochemical variability within groundwater systems (Malard *et al*., 1999; Ward *et al*., 1999) and its influence upon macroinvertebrates has been overlooked. Groundwater may originate from several different sources (glacial, snow-melt and rainfall) (Brown et al., 2007), and follow a variety of individual flow pathways (Robinson et al., 2009). The residence time of groundwater may vary within and between these flow pathways, influencing the degree to which water clarity, and stability of flow and temperature regimes are increased (Brunke and Gonser, 1997). In addition, flow permanence of groundwater streams may be determined not only by characteristics of water sources and flow pathways, but also by the local topography (Sophocleous, 2002), for example the position of a stream relative to fluctuating water table elevations. Organic matter concentrations of each flow pathway may also vary, depending on the proximity to vegetation, and the residence time and velocity of groundwater flow (Boissier and Fontvieille, 1995; Brown et al., 1999). Each of these factors may affect macroinvertebrate abundance and diversity.

A better understanding of the complex hydro-ecological interactions occurring within glacierised catchments is required, to establish groundwater as a dynamic influence upon freshwater ecosystems. This research therefore focuses upon the effects of local spatial and temporal variability in groundwater flow dynamics upon benthic and hyporheic macroinvertebrate communities. Research was undertaken in the Toklat River Basin, Denali National Park, Alaska, on several streams situated upon a fluvial terrace, fed solely by upwelling groundwater (Fig. 1).

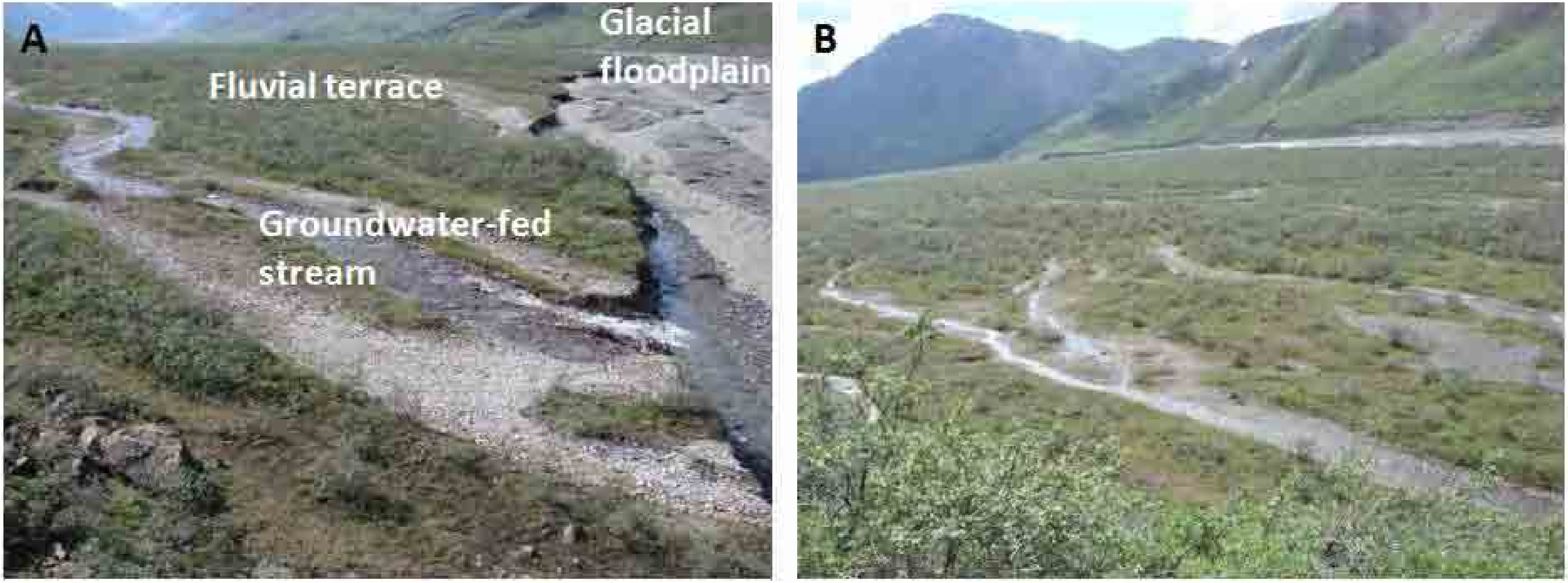

Fig. 1: Site photographs depicting A) the fluvial terrace, elevated above the current active glacial floodplain, and the contrast in water clarity between groundwater-fed streams and the main glacial channel; B) the geographical extent of the groundwater-fed streams

1.2 Groundwater flow pathways

Current research has highlighted marked local physicochemical differences between groundwater-fed streams (Ward *et al.*, 1999), reflecting, in part, differences within and between subsurface flow pathways of glacierised catchments. Flow pathways form between permeable facies units, which are typically found within valley bottom fluvio-glacial deposits, valley-side colluvial deposits, and bedrock aquifers (Robinson *et al*., 2008; Clow *et al.,* 2003). Within an individual flow pathway, flow regimes and residences times may vary, reflecting several nested routes of flow created by the locally variable, discontinuous subterranean structure of the hydrogeologic facies (Anderson, 1989). These routes of groundwater flow, nested within a single flow pathway, are subsequently referred to as a flow route (Fig. 2).

Flow route length has been linked to variability in temperature and flow attenuation (Brunke and Gonser, 1997), whereby diurnal variations of groundwater-fed streams fed by rhithral (snow-melt) or kryal (ice-melt) sources become increasingly reduced and out of phase with those of the source waters. Where there are significant differences in flow routes between individual groundwater-fed streams, corresponding variations in flow attenuation may be determined (e.g Hoehn and Cirpka, 2006). Additionally, flow attenuation may be temporarily reduced where preferential flow pathways develop between highly permeable hydrogeological facies units, predominantly during saturation (Sidle *et al.,* 2000).

Differences between streams in attenuation of stream flow can result in marked differences in stream bed porosity; for example greater variability in stream flow may result in reduced sediment compaction (Brunke and Gonser, 1997) and increased local permeability (Fowler and Death, 2001). Flow regimes may also influence scouring and deposition of rocks, in addition to their angularity and brightness. Here the bottom component of the index of

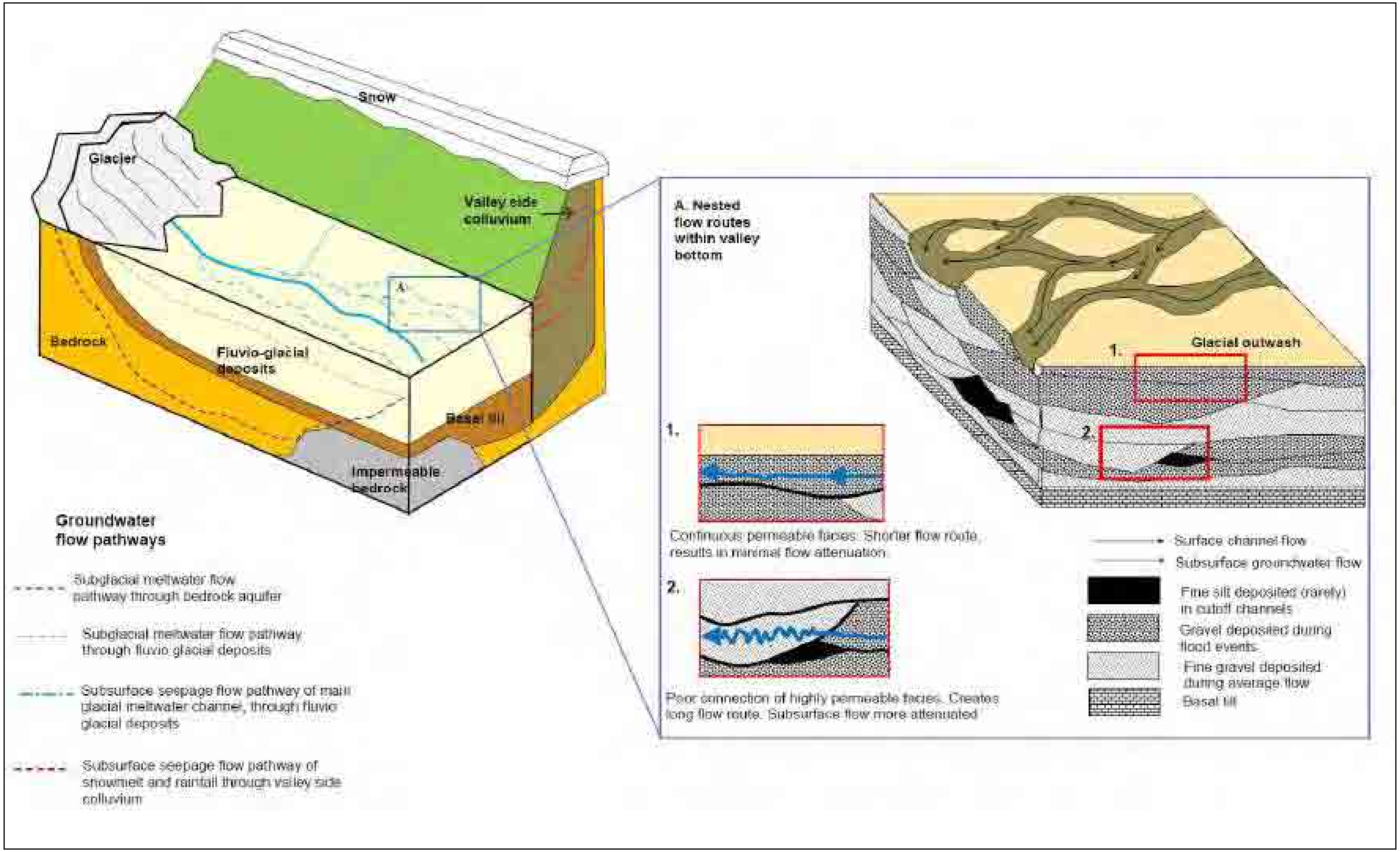

Fig.2: Flow pathways and nested flow routes within a glacierised catchment (adapted from Anderson, 1989)

Pfankuch stability can be used as an indicator of differences in channel stability between areas (Pfankuch, 1975; Death and Winterbourn, 1994; Brittain *et al*., 2001).

Local variability between groundwater-fed streams may also reflect differences *between* flow pathways. Groundwater flow pathways and topographical location can influence stream flow permanence (Ward *et al*., 1999). Ephemeral subsurface seepage is typically associated with the main glacial river channel (Parriaux and Nicoud, 1990; Ward *et al*., 1999), whereas perennial baseflow might be derived from flow pathways with a longer residence time, such as deep within the valley side (Clow *et al*., 2003). However, water tables within glacierised catchments fluctuate markedly with seasonal glacial ablation (Robinson *et al*., 2008), and only channels sufficiently close to the water table at its minimum level in winter will demonstrate perennial flow.

Water flow pathways may also influence the amount of organic matter contained within the groundwater-fed stream. Groundwater may entrain organic matter by throughflow (Boissier and Fontvielle, 1995); accordingly if the pathway directs flow through areas with more dense vegetation, or flow rate is rapid, organic matter entrainment will be higher. Flow pathways within valley-sides might therefore be expected to contain higher organic matter concentrations than those passing through glacial floodplains, which have very little vegetation (Richmond, 1960).

1.3 Ecological influence

Benthic macroinvertebrates are sensitive to environmental conditions, including water temperature (Hynes, 1970; Milner and Petts, 1994), flow velocity (Edington, 1968; James *et al*., 2008), stream bed porosity (Olsen and Townsend, 2003), organic matter abundance

(Anderson and Sedell, 1979; Lepori and Malmqvist, 2007), flow permanence (McCabe, 1998) and the variability of these factors over time (Hax and Golladay, 1998). Macroinvertebrate distributions might therefore be expected to be influenced by marked heterogeneity in these variables between streams, reflecting differences in groundwater flow pathways.

The relationships between environmental variables of streams and macroinvertebrates are not limited to surface waters, but extend downwards into the hyporheic zone (Boulton *et al.*, 1998), as macroinvertebrates seek refuge from the relative instability of surface conditions. The hyporheic zone is an area of transition situated beneath streams, composed of saturated sediments where mixing of groundwater and surface-water occurs (Schwoerbel, 1961). The use of the hyporheic zone as a refuge has been predominantly investigated in relation to a response to discrete disturbance events within surface streams (Fowler and Death, 2001). However, macroinvertebrates are also influenced by environmental variability (Death and Winterbourn, 1995). The influence upon hyporheic macroinvertebrate communities of groundwater flow dynamics, creating marked local differences in stream stability, hydrological regime, and water chemistry, has not yet been determined. It is unclear, for example, whether the degree of environmental variability caused by differences in flow pathways and lengths of flow routes might be sufficient to give rise to specific differences in groundwater fauna between groundwater-fed streams.

By investigating the influence of groundwater flow dynamics upon macroinvertebrate communities, this study will address research gaps on the wider effects of groundwater streams on macroinvertebrate communities within glacierised catchments. By conducting research within a subarctic catchment on several groundwater-fed streams, this project aims to gain a better understanding of the intrinsic eco-hydrological interactions operating within glacierised catchments. Research of this nature will enhance our understanding of glacierised catchments as early warning systems for climate change.

1.4 Aims and objectives

The overall aim of the research was to determine how **groundwater flow dynamics influence macroinvertebrate communities within a glacierised catchment**. In order to address this, the specific objectives of the research were to:

- characterise the physicochemical characteristics of groundwater flow pathways within a fluvial terrace, and determine the degree of local variability in environmental stability;
    - establish the water sources and flow pathways associated with areas of groundwater-fed streams; and
    - determine local physicochemical variability in groundwater, and identifying key driving processes;
    - create an index of environmental stability, using key physicochemical variables.
- determine the influence of variability in groundwater flow dynamics upon the benthic and hyporheic macroinvertebrate community;
    - determine associations between benthic macroinvertebrate community distribution and local physicochemical variables;
    - establish the relationships between individual benthic taxa and spatial and temporal groundwater dynamics;

    - establish the extent to which environmental stability (or additional physicochemical variables) of groundwater-fed streams influences macroinvertebrate distribution within the hyporheic zone
    - ascertain how ecological traits of individual taxa might determine different uses of the hyporheic zone
- develop a methodology of groundwater upwelling site identification through remote sensing, in order to put the results of the study into context, and to facilitate future research within glacierised catchments;
    - use digital remote sensing to identify areas of groundwater upwellings within glacierised catchments;
    - assess the accuracy of the methodology; and
    - determine the extent of groundwater upwellings within Denali National Park, and compare the results with those of the adjacent National Park, Wrangell St Elias.

Preliminary research was undertaken over a six week period during the summer of 2007 (Appendix A), with the main study carried out from May to September, 2008.

1.5 Methodology

1.5.1 Field site

To minimise the likelihood of encountering complicating anthropogenic influences when studying the physicochemistry of catchment hydrology, a study site within Alaska was selected for this research, as the environments of the National Parks are relatively pristine (Milner *et al.*, 2006). The Toklat River catchment within Denali National Park was chosen due to ease of access. Although there are several extensively glacierised areas within Alaska, offering potential study sites for this research, many are in extremely isolated areas (Robinson et al., 2009). A 148km mile road, stretching though the centre of Denali National Park, provided access to a fluvial terrace which supports an extensive network of groundwater-fed streams (Fig. 3), located only 3km from the road.

The terrace, which is situated upon an active glacial floodplain, with multiple streams fed solely by groundwater, therefore offered an opportunity to study physicochemistry and macroinvertebrate communities at multiple sites.

Figure 3: Network of groundwater fed streams on fluvial terrace, Toklat River catchment, Denali National Park

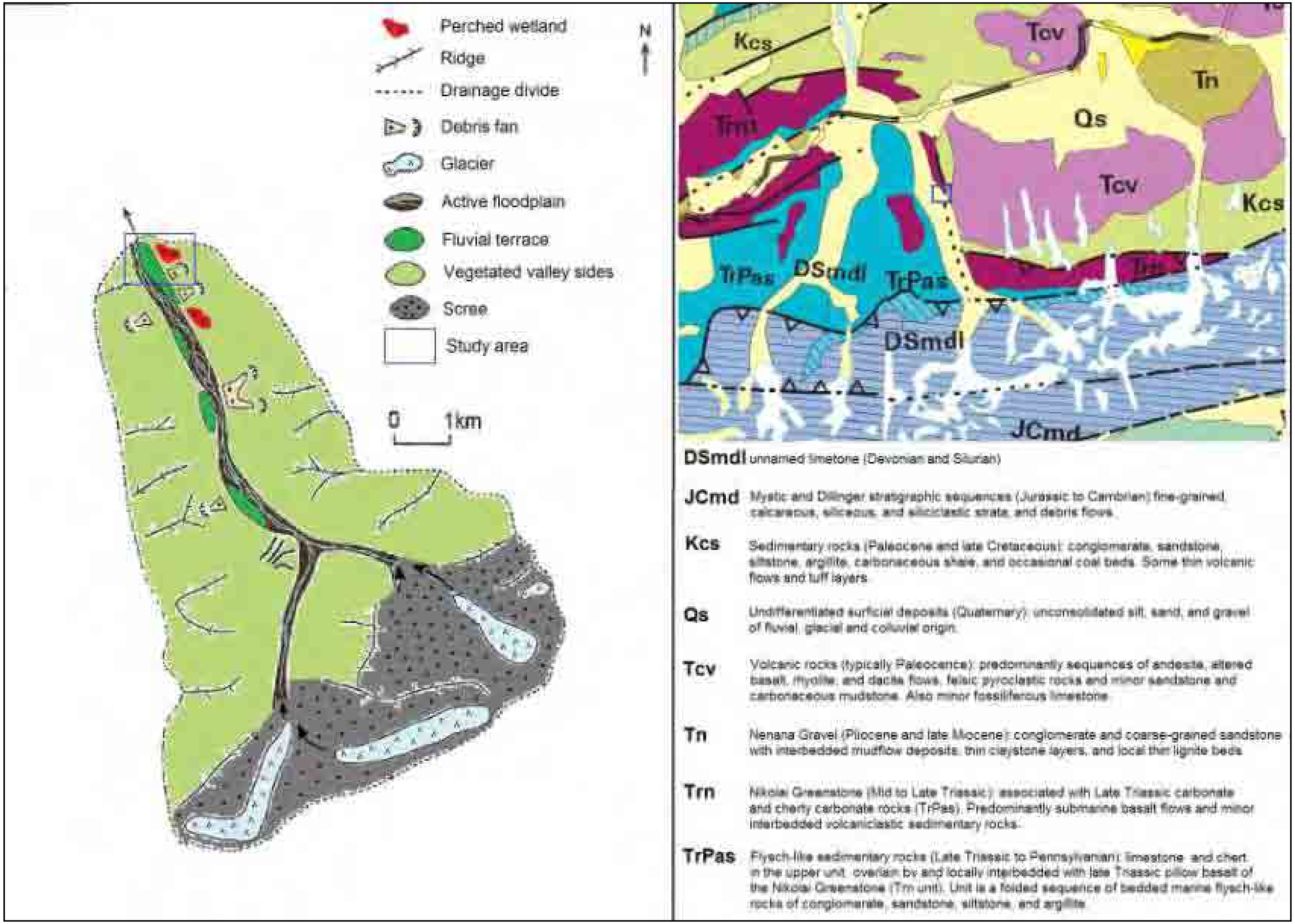

Figure 4: A) Key geomorphological features of the Toklat catchment B) Geology of the Toklat catchment and surrounding area (Wilson et al., 1998)

The geology and geomorphology of the Toklat catchment are locally highly variable. At the head of the catchment are several glaciers (Fig. 4A) underlain by calcareous and siliceous strata (Fig. 4B). Valley sides to the East and West, are predominantly extensively vegetated, and support isolated perched wetlands, which extend to within close proximity of the fluvial terrace. The geology of the valley sides is highly variable; to the East are several geological units (Fig. 4B), including Triassic calcareous sedimentary, Triassic submarine basalt, and Paleocene volcanic and sedimentary rocks. To the West the geology is primarily Triassic calcareous sedimentary. Due to the steep incline of the valley slopes, gravitational reworking of rockfall debris has formed debris fans and talus cones (Fig. 4A); only here was vegetation absent (Fig. 5). Snow packs were present at the summit of these valleys in May, though rapidly dispersed as the study season progressed.

Figure 5: Debris fan proximal to fluvial terrace, prior to completion of snowmelt

A braided glacial channel, the Toklat River, flows Northwards, across the valley bottom (Fig. 6). The river flows around the Western and Northern banks of the terrace, forming an active floodplain, which is around 1,300m wide at the study site location. The unconsolidated silts, sands and gravel of the active floodplain are glacial, fluvial and colluvial in origin.

Figure 6: Active floodplain of the Toklat River, (upstream orientation)

Approximately 12km from the terminus of the glaciers lies a fluvial terrace, across which flow a network of groundwater-fed streams (Fig.7). The topography of the terrace is locally variable, and individual streams appear to emerge at points where the water table intersects the terrace surface. Ten groundwater-fed streams were studied, each with individual reaches of ~20m. Sites were chosen for their comparability; the channel bottom substrate within each study reach was similar, consisting of small to medium cobbles overlying coarse gravel. Bed morphology was also relatively homogenous, with no large riffle and pool sequences. The locations of the groundwater-fed streams varied from those proximal to the valley sides, termed A streams (Fig 8A-C and Fig. 9 A-D), to those closer to the main glacial meltwater channel, termed B streams (Fig 10 A-C), of which sites B2 and B3 were ephemeral (Fig. 7).

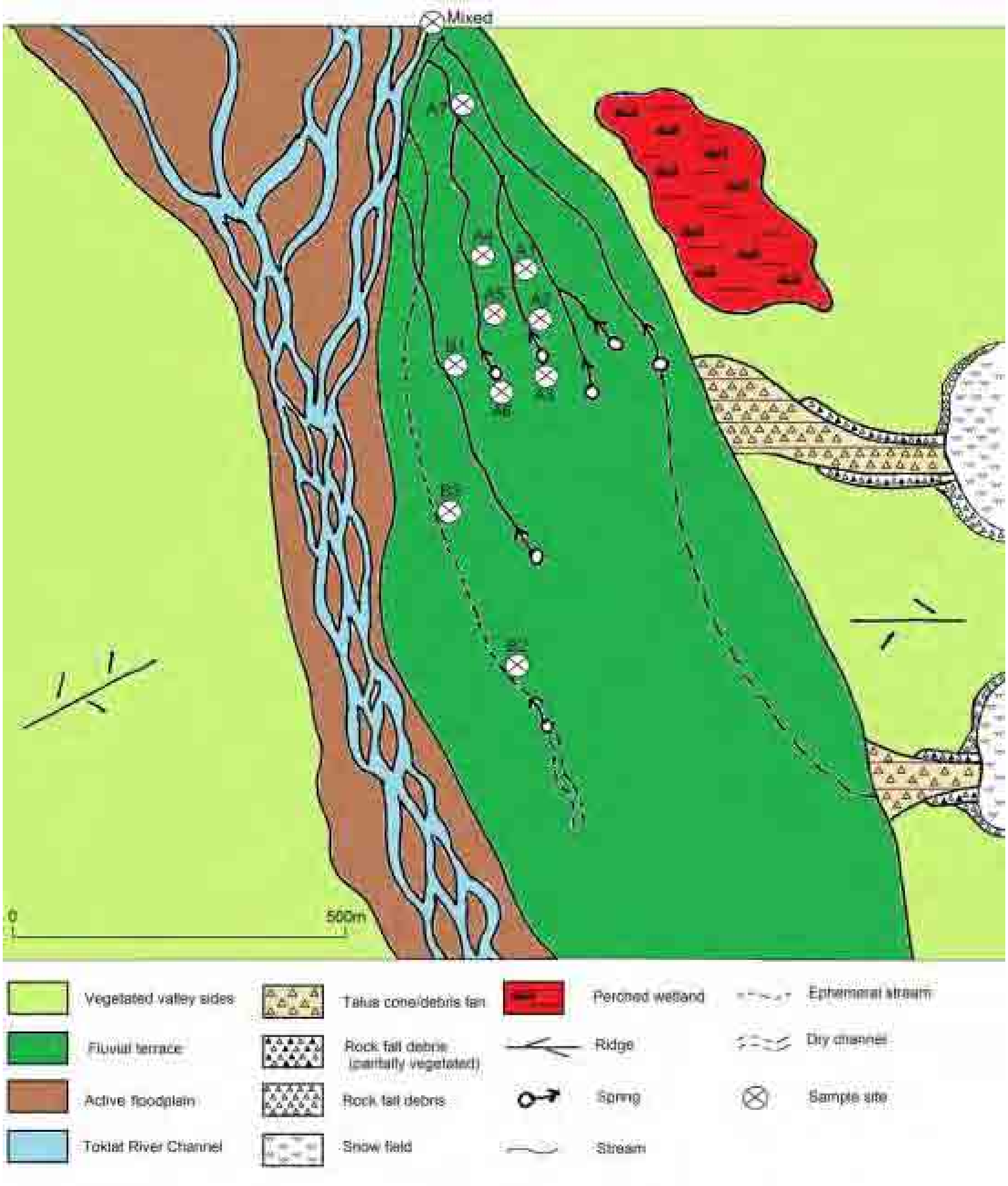

Figure 7: Field site schematic

The variety of potential water sources (snowmelt, rainfall and glacial meltwater) in close proximity to these sites made the terrace an ideal choice for research into variability in physicochemistry and macroinvertebrate communities between streams.

Figure 8: Site photographs of sites A) A1 B) A2 C) A3

Figure 9: Site photographs of sites A) A4 B) A5 C) A6 D) A7

Figure 10: Site photographs of sites A) B1 B) B2 C) B3

1.5.2 Data collection and analysis

Due to the multidisciplinary nature of this study a combination of methods were implemented, including ecological, hydrological, chemical and digital remote sensing. During a six week preliminary field investigation in 2007 many of these methods were tested, and adapted, prior to their application in the main 16 week study season of 2008.

1.5.2.1 Hydrology

To establish the flow and temperature regimes of the groundwater-fed streams, in-stream water temperature and water pressure was recorded automatically at five of the sites (Fig. 7; A2, A4, B1, B2 and B3), using data loggers with pressure transducers and temperature loggers. Hyporheic temperatures were also monitored continuously at a depth of 20cm (A2 and B1) and 50cm (B3). In 2008 sites B2 and B3 were determined to be ephemeral. Following this discovery, temperature loggers were left in-situ at multiple sites throughout June 2008 to June 2009 to determine stream flow permanence.

In 2007 several data loggers were lost throughout the study period due to animal attack, human interference and flooding. Data from this season was therefore sporadic, and a comparison of hydrological data between multiple sites was possible for only a very short period of time (Appendix Ai). In 2008 several steps were taken to mitigate these issues: all *in-situ* equipment was concealed with vegetation, covered in non-reflective grey plastic, and labelled as research property. In addition, multiple dataloggers were placed in glacial streams, to minimise data loss following bank collapse and flood damage.

The hydraulic gradient at each site was established through measurements of hyporheic water levels in nested piezometers during 2008. Given the potential for large diurnal variations in water levels within glacierised catchments, hyporheic water levels were monitored twice daily, at piezometer nests installed at all ten groundwater-fed sites (Fig. 7; A1, A2, A3, A4, A5, A6, A7, B1, B2 and B3). Each nest comprised two piezometers (5cm outer diameter, 0.4cm holes drilled over basal 6cm) installed to depths of 0.5 and 1m below the surface using an installation system described by Baxter *et al.,* (2003).

Also in 2008, on five occasions, surface water velocities and channel cross sections were determined at 10cm intervals across each groundwater-fed stream, at points adjacent to each piezometer nest. To determine individual channel cross sections, measurements of stream channel dimensions, river depth and flow velocity were taken (at 1/6 depth). The cross sections were used in conjunction with the water velocity measurements to create stream rating equations for each site. This enabled site discharge to be estimated continuously during the study period.

At each site, substrate size was determined by measuring the *b* axis of 100 randomly selected stones (Burgherr *et al*., 2002) and D_{50} calculated. The bottom component of the Pfankuch Stability Index (PSI) was determined, incorporating scores for rock angularity, brightness, particle consolidation and size distribution, scouring and deposition, and abundance of aquatic vegetation (Pfankuch, 1975).

1.5.2.2 Ecology

Benthic macroinvertebrate samples were collected using a Surber sampler (mesh 330 µm), and preserved in 90% ethanol. During sampling in 2007 only five sites were sampled (A1, A5, B1, B2 and B3). Differences in abundance and diversity both between sites and between the two dates (July and August) were established (Appendix Aii). To further investigate spatial and seasonal variability in macroinvertebrate distribution in 2008, it was decided to extend both the range of sites (to include A2 and A4), and the study period (macroinvertebrates were sampled every 4 weeks for 3 months). Sampling began at the downstream extent of the study reach, and progressed upstream; five replicate samples were taken at each site. Macroinvertebrates were identified to species wherever possible.

Organic material, collected in the Surber sampler, was separated from the macroinvertebrates, and dried at 65°C. This was then sieved into coarse (>1mm) and fine (<1mm) fractions, prior to ashing in a furnace at 540°C for 2 hours. Fine particulate organic matter (FPOM) and coarse particulate organic matter (CPOM) concentrations were calculated (mg/ m^2) by determining the ash free dry mass. This is a method commonly used in ecological research (Scrimgeour and Winterbourn, 1989; Lancaster and Hildrew, 1993; Scarsbrook and Townsend, 1993) as organic matter concentrations associated with each replicate macroinvertebrate sample are determined. The five macroinvertebrate and organic matter replicates (FPOM and CPOM) at each site are expressed as average abundance (or concentration) per m^2.

Algal matter was also collected at these four week intervals from each site, from the upper surfaces of four randomly selected stones, in accordance with the method outlined by Ledger and Hildrew (1998). The surface was scrubbed with a toothbrush, and materials washed into a 24 ml polypropylene container. Stone surface area was recorded. Samples were stored in black bin liners to limit light interactions, and frozen. Upon analysis, samples were freeze dried, and chlorophyll pigments extracted in 90% acetone for 24 hours. Absorbance was determined at 750, 664, 647 and 630nm wavelengths using a spectrophotometer. Concentrations of chlorophyll *a*, *b*, *c* and total chlorophyll were calculated using the Sterman (1988) equations, as outlined in Ledger *et al* (2006).

Macroinvertebrates were sampled from the hyporheic zone, in both 2007 and 2008, from 15cm and 30cm. In 2007 two alternative methods were trialled; colonisation pots, and pump sampling. Pump sampling was carried out through the installation of white PVC tubes (5cm in diameter, with a series of 0.4cm perforations drilled along the basal 6cm) to 15cm and 30cm depths within the stream bed. After six weeks a hand-pump was used to extract 0.5 litres of water from the tubes; Hunt and Stanley (2000) identified 0.5 litres as containing the best quantitatively representative sample of macroinvertebrates. However, several uncertainties were identified in pump sampling during 2007, which led to the favouring of the colonisation pot method in 2008. These issues included a difficulty in establishing the precise depth from which water was being sampled (Pusch *et al.*, 1998), which would likely depend on suction velocity and pressure; these variables are difficult to control with a hand-pump. In addition there was the potential for macroinvertebrates to cling to substrates, and thus for preferential sampling of particular taxa (Fraser and Williams, 1997). As a result of this, or perhaps due to siltation of the piezometer perforations, no macroinvertebrates were recovered through the piezometer suction method.

In 2007 colonisation pots consisting of pairs of cylindrical steel cages (15cm in height, 8cm diameter, mesh size 1cm^2), were inserted into the river bed, at adjacent points, to depths of 15 & 30cm. Individual pots were used to prevent macroinvertebrate movement between depths during extraction. Holes were excavated by hand to the appropriate depth, and each colonisation pot was packed with sediment in stratigraphic order. Due to the coarse substrate (small to medium cobbles overlying coarse gravel), coring methods could not be used to insert the pots. Pots were inserted in the holes, and the remaining substrate was placed around pot margins and over the top, whilst ensuring that the cable extended to the surface. Colonisation pots were then left *in-situ* for six weeks, as at least four weeks is required to enable macroinvertebrate colonisation (Coleman and Hynes, 1970). However upon extraction, significant water loss from the pots led to concerns of sampling bias towards macroinvertebrate capable of clinging to substrate within the pots (Scarsbrook and Halliday, 2002) (Appendix iii).

In 2008 the pots were re-designed; a tarpaulin bag with reinforced top and cable was placed around the base of each pot before inserting the pot in the excavated hole (Fig. 11). During extraction the cable was pulled vertically, driving the wire-reinforced tops to the surface and extending the tarpaulin bags. The water-proof bags minimised water loss, therefore reducing macroinvertebrate sampling bias. Sediment was placed in bags with 90% ethanol and subsequently rinsed and filtered through 0.63 µm mesh (Scarsbrook and Halliday, 2002). Due to the quantity of fine sediment, some macroinvertebrates were poorly preserved and thus only identified to family level.

Figure 11: colonisation pot design of 2008, including folded tarpaulin bag with wire-reinforced rim

1.5.2.3 Water Chemistry

To distinguish between water sources and flow pathways, natural isotopic tracers were used (δ^{18}O and δ^{2}H) (Robinson *et al*., 2009). Although both δ^{18}O and δ^{2}H were analysed, δ^{18}O is predominantly presented in the thesis, as this enabled a comparison with several similar studies which had used this isotope in their research (Bottomley *et al.,* 1986; Taylor *et al.,* 2002; Theakstone, 2003). During 2007, from mid-June to August, water samples were collected at 14-day intervals at all groundwater-fed streams. These were taken using 2ml vials, and retained for isotope analysis. To avoid evaporation during storage the vials were completely filled and tightly sealed. In addition a single sample was taken from the glacial terminus (12km upstream), and a stream flowing down the alluvial fan, which was proximal to the fluvial terrace. δ^{18}O and δ^{2}H data of 2007 (Appendix Aiv and Av) demonstrated that the groundwater-fed streams were likely fed by a combination of at least two isotopically distinct water sources. However to determine the relative contributions of each source to the streams, with a higher degree of confidence, a more intense study regime was required, including additional water sources, and a longer study season to incorporate seasonal variation.

In 2008 the study was repeated, from 30th May to 8th September. During this period every rainfall event was sampled. In addition four expeditions were made to sample the glacial terminus, during which water from all streams between the terrace and the glacier was also collected. Surface runoff from the debris fan/talus cone was sampled every two weeks, due to the presence of a large snowpack at the summit. Samples of this snowmelt, directly from the terminus of the snowpack, were also collected. Additionally the groundwater-fed streams and glacial meltwater of the main Toklat River channel, upstream of the terrace, were also sampled, every two weeks. The two week sampling regimes coincided with the four week intervals of the ecological sampling regimes, to enable correlations between variables.

During the 2008 study season, water samples were simultaneously taken in 30ml Nalgene polyethene bottles, for analysis of additional natural tracers, such as Chloride (Cl^-), to aid differentiation between water sources and flow pathways. These samples were filtered through 0.45 µl nylon membrane filters and refrigerated prior to analysis using an Anion Dionex ICS 2000 (instrumental precision <0.25ppm). In-stream pH was also monitored monthly.

1.5.2.4 Digital Remote Sensing

In 2007 several Landsat satellite images of Denali National Park and of Wrangel St Elias National Park were used to determine the extent of the groundwater-fed stream habitat. Due to the low resolution of the data set (30m) groundwater-fed streams could not be directly identified. As a result a vegetation proxy was used; the more stable banks and nutrient rich flows of streams fed by shallow groundwater (Valett *et al*., 1994; Dent *et al.,* 2000) have been observed to contain more dense vegetation (Hayashi and Rosenberry, 2001). A normalised vegetation indices (NDVI) was therefore applied to the dataset. However lakes and rivers derived from non-glacierised catchments were also included in the dataset, and as a result of images being taken on different dates, data between images was not directly comparable.

In 2009 reforms were made to the methodology. Datasets were first corrected for between-image variance, making images directly comparable (Chander *et al*., 2009). Glacierised catchments were then isolated through the application of a normalised turbidity index, as only these areas were relevant to the study. These areas of high turbidity were subsequently created as a separate dataset, and the vegetation proxy (NDVI) applied. The location of groundwater upwellings within glacierised catchments could then be accurately identified.

1.6 Outline of thesis

The thesis consists of four manuscripts, all of which have been, or will be, submitted for publication. The format of the chapters has been written accordingly:

Chapter two, entitled “Water flow dynamics of groundwater-fed streams and their ecological significance within a glacierised catchment”, aims to characterise the groundwater flow pathways and their physicochemical heterogeneity within the Toklat catchment. The primary associations between groundwater flow dynamics and macroinvertebrate communities are also explored.

Chapter three, entitled “Influences of the flow dynamics of groundwater-fed streams upon benthic macroinvertebrates, in a glacierised catchment” more fully explores the associations between the heterogeneous nature of groundwater flow and macroinvertebrate communities. Here the responses of individual taxa to physicochemical variables are assessed, and spatial and temporal variability in macroinvertebrate distribution determined.

Chapter four, “Comparisons of environmental stability between groundwater upwellings on a glacial floodplain; influences on hyporheic fauna”, investigates the vertical extent of the influence of groundwater flow dynamics. Several variables are combined into a multivariate index of environmental stability, which is then used in analysing the potential of the hyporheic zone of groundwater-fed streams as a refugia.

Chapter five, “Determination of groundwater upwelling sites using remote sensing of Landsat data”, scales up the research, to ascertain the spatial extent of groundwater upwellings within Alaska. Through digital remote sensing, a GIS-based model is developed, isolating areas of groundwater upwelling within glacierised catchments. The model seeks to optimise resource use in study site identification, a primary issue behind limited research within these areas.

The final chapter draws together the conclusions from the four manuscripts.

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2. WATER FLOW DYNAMICS OF GROUNDWATER-FED STREAMS AND THEIR ECOLOGICAL SIGNIFICANCE IN A GLACIERISED CATCHMENT

Subsurface flow pathways of groundwater-fed streams were characterized on a fluvial 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 glacial meltwater seepage. Streamflow at sites situated at higher elevations was ephemeral, and commenced with a seasonal rise in groundwater-table. In contrast, A sites comprised physicochemistry 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) (*$p<0.05$*); and FPOM was correlated with debris fan seepage (*$p < 0.05$*). These relationships were not evident in July and August, when organic matter availability increased. Results demonstrate that flow pathways and organic matter availability significantly influence macroinvertebrate communities in these groundwater-fed streams.*

2.1 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 these 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 streams fed by groundwater may support higher taxa abundance than those fed largely by surface snow and ice-melt (Brown et al., 2007). The difference in taxa abundance is attributed to characteristically higher water clarity, and reduced variability in stream temperature and discharge (Brown et al., 2003) of groundwater-fed streams. Climate change may have significant implications for the macroinvertebrate communities of groundwater-fed streams (Brown et al., 2007_a), 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 (Brunke and Gonser, 1997; Malard et al., 1999; Ward et al., 1999), which may influence macroinvertebrate communities.

Several aspects of groundwater-fed stream physicochemical variability have been attributed to variability in the length of flow route within and between groundwater flow pathways. Within flow pathways there may be several nested routes of flow, of variable length and thus residence time, which influence the hydrological variability of groundwater (Fig. 2); the length reflects the distribution and connectivity of permeable deposits (Ward et al., 2002; Robinson et al., 2008). Early work on Icelandic sandurs (Hjulstrom, 1955) revealed how the length of flow route regulated the turbidity of groundwater-fed streams. More recently, flow route length has also been linked to the degree of groundwater temperature and flow attenuation (Brunke and Gonser, 1997), whereby in glacial or snow-melt catchments, as the length of flow route increases, the amplitude of daily variations within subsurface waters become increasingly reduced and out of phase with that of the source.

Locally heterogeneous landscape structure may therefore result in marked physicochemical variability within individual 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 degrees of flow and temperature attenuation between individual streams sourced from alluvial aquifers. Similarly, the hydrogeologic facies of sedimentary units along valley-sides are variable and discontinuous (Anderson *et al*., 2008), and seepage through valley-side colluvial deposits (talus cones and debris fans) may follow one of two distinct pathways (Clow *et al*., 2003). First, preferential flow within highly permeable layers close to the surface results in rapid, ephemeral, near-surface water flow. This is a rapid response pathway, supplied by snow-melt and summer precipitation (Roy and Hayashi, 2009). Second, vertical seepage of water into the dense matrix towards the base of the colluvial structure results in longer residence times, and perennial groundwater baseflow. Preferential flow routes may however develop during saturation where disconnected, highly permeable facies become linked (Sidle, 2000). The distribution of flow routes may therefore vary spatially and temporally as precipitation, or snow- and ice-melt alter the vertical distribution of water within the flow route network, and potentially increase the number of active flow routes within a flow pathway (Sidle, 2000; Anderson *et al*., 2008).

Seasonal variations in contributions from individual sources and flow pathway may be observed. For example, seasonal discharge maxima from upper valley slopes are associated with spring peaks in snow-melt. The system then alters from being snow-melt to rainfall dominated (Sueker *et al*., 2000), and the percentage contribution of precipitation to groundwater recharge increases. Summer peaks in glacial meltwater discharge reflect the timing of ice-melt as the transient snow line rises during the summer (Smith *et al*., 2001; Collins *et al.,* 2002). Flow pathway contributions may also vary spatially; percentage contributions to groundwater-fed streams from debris-fan seepage may reduce with distance from the valley side (Hjulstrom, 1955). Together with the potentially large local scale variations in degree of attenuation of stream flow and temperature regimes, these factors result in considerable local spatial and temporal variations in the physicochemistry of groundwater-fed streams in glacierised catchments (Sueker *et al*., 2000; Robinson *et al*., 2008).

The dynamics of groundwater flow display marked trends in isotopic and chemical composition over time. Nonreactive tracers such as δ^{18}O may therefore be used to discriminate between water sources of a glacierised catchment (rainfall, snow-melt and ice-melt). The δ^{18}O values of waters derived directly from rainfall may vary considerably, as the isotopic composition of precipitation varies both within and between events (Ladouche *et al*., 2001), depending on the origin of the rainfall water. The δ^{18}O values of water comprised predominantly from snow-melt are initially much lighter than those of rainfall-fed systems. This is due to the lower temperatures during which snow is formed, resulting in less evaporation and therefore lower $\delta^{18}O$ values (Theakstone, 2003). However, the overall $\delta^{18}O$ composition of snow-melt increases throughout the melt period due to fractionation. Isotopically heavier meltwater is generated at the surface of the snowpack, exposed to evaporation, and subsequently infiltrates through air spaces within the snowpack via diffusion (Moser and Stichler, 1974). Glacier ice-melt does not normally demonstrate fractionation (Souchez and Lorrain, 1991), as limited interstitial air space restricts diffusion (Moser and Stichler, 1974). However the isotopic composition of glacial meltwaters (GMW) reflects several water sources, including seasonal snow-melt from the surface of the glacier, glacier ice, melting firn, superimposed ice, regelation ice and subglacial water (Theakstone, 2003). Seasonal variations in the $\delta^{18}O$ of GMW therefore typically reflect a combination of isotopic fractionation of the snow-melt from the glacier surface, buffered by contributions from glacial ice-melt.

Sources and flow pathways of groundwater-fed streamflow may be identified by comparing seasonal variations in isotopic composition of all potential contributory sources, with variability in the groundwater-fed streams. Additional unreactive hydrochemical tracers, such as chloride (Cl^-), may also aid differentiation between mixed water sources. 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 dynamics is related to its influence upon in-stream variability of temperature and discharge, organic matter and nutrient concentrations, and degree of flow permanence. Higher variability of stream flow and temperature result in reduced macroinvertebrate community persistence (Townsend *et al*., 1987) and macroinvertebrate diversity (Death and Winterbourn, 1995). Furthermore, organic matter, which may be entrained by throughflow and discharged at points of upwelling groundwater (Boisser and Fontvielle, 1995), is an important energy source for macroinvertebrates. Taxa may aggregate upon patches of organic matter in otherwise resource depleted environments (Tiegs *et al.,* 2008). In addition, water sources, groundwater flow pathways and local topography will determine the duration of active channel flow (Poff *et al*., 1997); flow permanence has been established as a key driving factor in macroinvertebrate community composition (McCabe, 1998). Intermittent and ephemeral streams typically support lower diversities, requiring either seasonal re-colonisation, or specialist adaptation by macroinvertebrates to facilitate survival during dry periods (Wood *et al.,* 2005).

In general, 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 not, however, yet been established. Consequently this study aimed to establish local heterogeneity in the physicochemistry of streams fed entirely by groundwater, in the floodplain 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 water sources and flow pathways associated with areas of groundwater-fed streams;
2. to determine local physicochemical variability in groundwater, and identifying key driving processes; and
3. to assess the influence of physicochemical variability of groundwater-fed streams upon the macroinvertebrate community.

2.2 Methodology

2.2.1 Field site

A fluvial terrace, elevated ~1m above the active glacial floodplain of the middle fork of the Toklat River, in Denali National Park (63°29'19.54"N, 149°57'54.05"W), Alaska (Fig. 12 A) was selected for study in summer 2008. The site, located within two miles of an access road, was ideal for studying local spatial and temporal variability in groundwater-fed stream physicochemistry, given the extensive network of streams fed entirely by groundwater, proximity to several water sources (i.e snow-melt, glacial meltwater and rainfall), and locally varying topography (ranging over 2.5m in elevation). These groundwater-fed systems on terraces are relatively widespread throughout Alaska, but have never before been studied in detail.

The terrace is situated on an eastern section of the glacial floodplain, ~12 km from the glacial margin, where the floodplain is ~1300m wide (Fig. 12B). Several debris fans and talus cones, with snow-capped summits early in the season, are situated proximal to the terrace. These colluvial deposits lie on otherwise vegetation-covered valley sides, with isolated perched wetlands, extending along the East and West floodplain margins. The main Toklat River is a braided, north flowing tributary of the Yukon River; flow is predominantly derived from ice-melt and snow-melt 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. Beneath the glaciers are debris flows, underlain by 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 valley-bottom consists of glacial, fluvial and colluvial deposits.

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. 12C). Stream reaches (20m) 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. Mean monthly precipitation in summer 2008 was ~ 162mm, and in winter was ~ 116mm, 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^{o}C (night) (WRCC, 2008).

2.2.2 Data collection and analysis

2.2.2.1 Water isotopes and chemistry

Eight streams were selected for study; 7 streams were situated upon the terrace and fed solely by upwelling groundwater (A1, A2, A4, A5, B1, B2 and B3) (Fig.12 C). One stream, situated at the foot of the terrace, received combined flow from all groundwater-fed streams, and also intermittently from the main Toklat channel ('mixed' channel). From 30th May to 8th September 2008, water samples were collected at 14-day intervals at all sites and from the main glacial Toklat River (GMW_{riv}). Additional sampling of individual water sources was undertaken, including ice-melt, snow-melt, debris fan seepage flow, rainfall and GMW (sampled from immediately below the terminus of the principal glacier, GMW_{term}) (Fig. 12B).

Water samples were taken using 2ml vials, and retained for isotope analysis. The vials were completely filled to ensure minimal headspace and tightly sealed to avoid evaporation during storage. Samples were also taken in 30ml Nalgene polyethene 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 <0.25ppm).

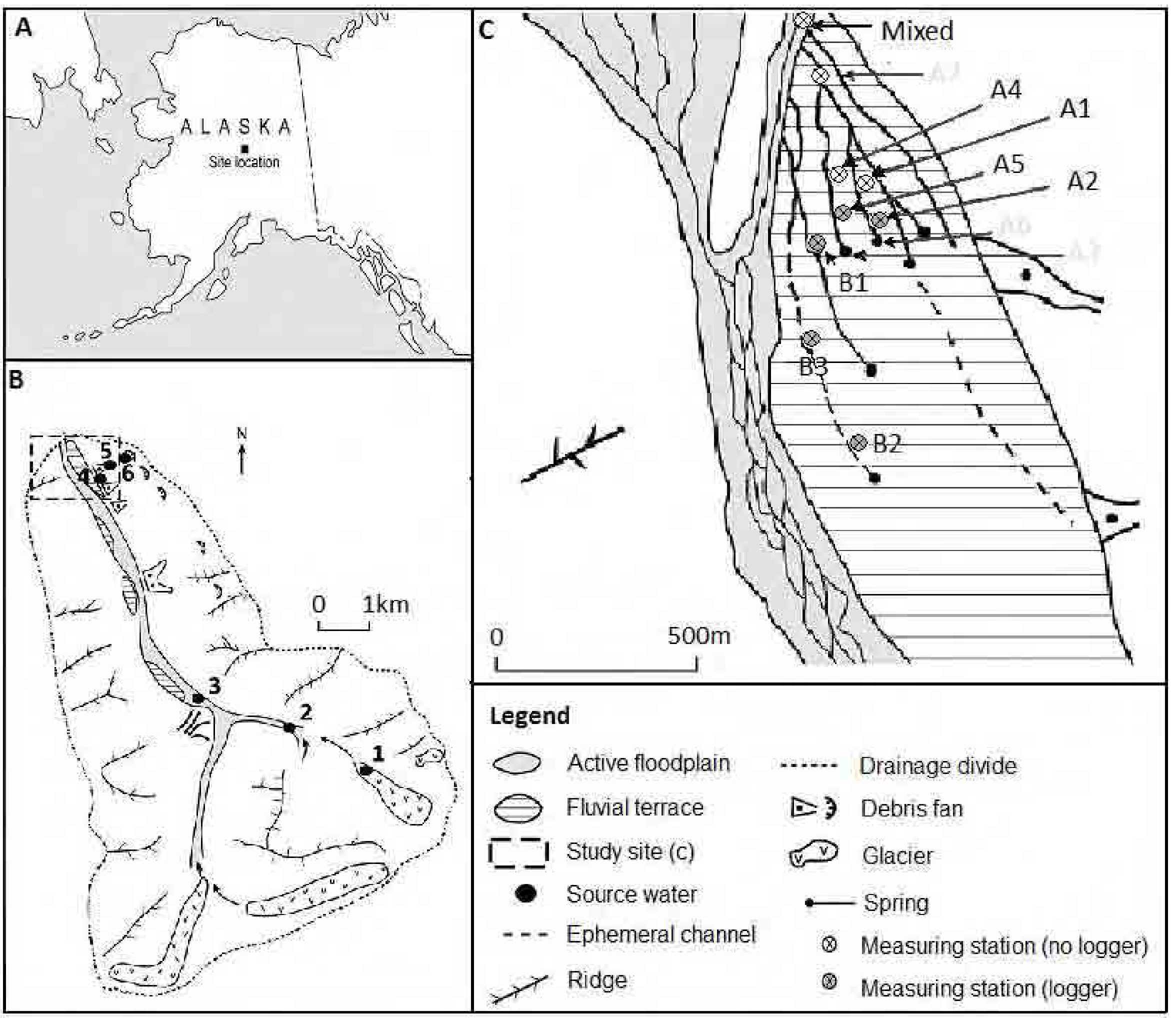


Fig. 12: Study site schematic. A) site location within state of Alaska B) catchment overview including source water sampling sites 1 = Ice, 2 = GMW_{term} 3 = GMW_{riv} 4 = DFS_{deep} 5 = $DFS_{shallow}$ 6 = snow C) sampling sites in groundwater-fed streams; chemistry and ecological sampling locations (black), additional piezometer nests (grey)

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

Eurovector Elemental Analyzer preparation line. Prior to analysis, two pulses of reference H_2 were injected to carry out a correction for H_3^+. Next, approximately 0.3 µl of sample was injected and reduced to hydrogen, at 1050°C over a chromium metal catalyst (Morrison *et al.*, 2001). Internal precision for δD was usually within 1 per mil. $\delta^{18}O$ analyses were undertaken using an equilibration technique. 200 µl samples were pipetted into glass exetainers and sealed with a piercable lid and rubber septum. Samples were left for 7 hours to equilibrate with a mixed gas (95% He, 5% CO_2), allowing the headspace CO_2 to assume the $\delta^{18}O$ composition of the water. The headspace gas was then analysed on the Isoprime mass-spectrometer. The internal precision for $\delta^{18}O$ is typically 0.08 per mil, external precision is within 0.12 per mil.

2.2.2.2 Hydrology

Piezometer nests were installed at 10 locations as indicated in Fig. 12C (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 relative elevations of individual piezometers was determined by surveying with a LEICA Geo electronic distance measurer, and piezometer water levels were monitored twice daily from June 17th to Sept. 9th 2008. Spatial variations in water table elevations across the field site were interpolated using a 90 m x 260 m grid from individual hydraulic head measurements at a depth of 50 cm, by Kriging.

In-stream water temperatures and levels were logged at 5 of the groundwater-fed sites, and in the main glacial meltwater river channel, using in-situ thermistors and pressure transducers (Fig. 12C and Appendix B). Stream bed water temperatures were also measured at 20cm depth, at A2 and B1, and at 50cm depth at A5 and B3. Measurements were taken continuously, with sensors scanned at 10-s intervals, from which 15-min mean values were derived. Gemini TinyTag thermistors were placed at selected sites and left *in situ* from June 2008 to June 2009, to determine flow permanence of streams. Perennial channels were identified where in-stream temperature, or that of a location directly upstream, constantly exceeded O°C throughout the year (Appendix C). Ephemeral streams were characterised either by in-stream temperatures falling significantly below 0°C (during winter), or at several sites, by the observed absence of flow.

2.2.2.3 Ecology

Benthic macroinvertebrates were sampled, using a Surber Sampler (330µm mesh), and preserved in 90% ethanol. Five replicates were taken at all nine sites, at four week intervals. Macroinvertebrates were identified to species wherever practical; Simuliidae, Chironomidae and Isotomidae were identified only to family. This level has not been reported to have a significant effect upon determination of spatial distributions of invertebrate communities (Morris and Brooker, 1980). Mean abundance was calculated at each site, on each sampling occasion (expressed as abundance per m^2). Substrate collected in the Surber sampler was dried at 65^{o}C, and sieved into coarse (>1mm) and fine (<1mm) fractions. This was weighed prior to ashing at 540^{o}C for 2 hours, to determine ash free dry mass. Organic matter content of both coarse and fine fractions were then calculated, and expressed in milligrams/m^2. Shannon's index of macroinvertebrate diversity was calculated (Shannon, 1949).

$$H = -\sum P_i \ln(P_i) \qquad 1.$$

A Mann-Whitney U test used to determine the difference in diversity between channels fed by debris fan flow pathways (DFS) and those fed predominantly by GMW_{riv} seepage.

Algal matter was also collected at four week intervals from each site, from the upper surfaces of four randomly selected stones. The surface was scrubbed with a toothbrush, and materials washed into a 24 ml polypropylene container. Stone surface area was recorded. Samples were stored in black bin liners and frozen to limit light interactions. Upon analysis, samples were freeze dried, and chlorophyll pigments extracted in 90% acetone for 24hours. Absorbance was determined at 750, 664, 647 and 630nm wavelengths using a spectrophotometer. *Concentrations* of chlorophyll *a*, *b*, *c* and total chlorophyll were calculated using the Sterman (1988) equations, as outlined in Ledger *et al* (2006).

2.3 Results

2.3.1 *Isotopic signatures*

The isotopic composition of water samples collected in 2008 are compared with the Toklat local meteoric water line (LMWL) and Barrow LMWL (917km North) (IAEA/WMO, 2006) in Fig. 13A; LMWLs were derived from rainfall samples of the respective catchments. All samples lay close to the Barrow LMWL. Water sources of groundwater-fed streams demonstrated distinct $\delta^{18}O$ signatures (Fig. 13A, Table 1), including precipitation, snow-melt, glacial ice, surface flow from the debris fan ($DFS_{surface}$), sub-surface flow from the debris fan ($DFS_{subsurface}$) and GMW from both the terminus of the glacier and the main meltwater channel (GMW_{term} and GMW_{riv}). Samples differed markedly in their range along the Barrow LMWL, with isotopic composition of groundwater-fed streams remaining the most consistent, and that of debris fan pathways and rainfall altering considerably throughout the season.

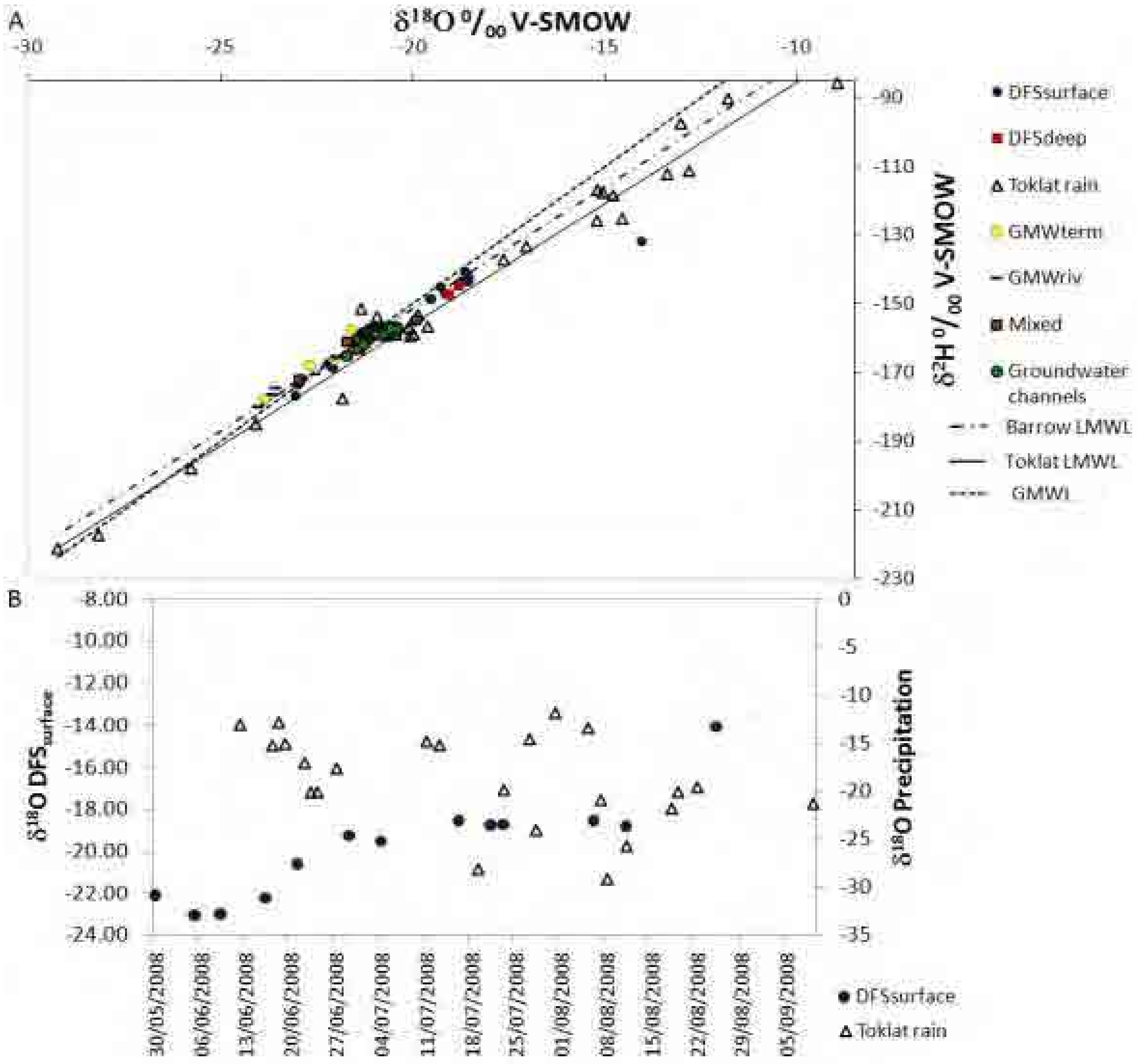


Fig. 13: A) Isotopic composition of source waters and groundwater-fed streams. Toklat local meteoric water line (y = 7.05x – 14.9) calculated using rainfall data collected over study season of 2008. Barrow meteoric water line (y = 7.12x – 9.13) calculated from GNIP dataset spanning 7 years. Global meteoric water line = 8x + 10 B) The marked seasonal rise in δ^{18}O values of DFS$_{surface}$ observed, irrespective of precipitation δ^{18}O values.

The seasonal average δ^{18}O of precipitation (Table 1) was similar to both DFS$_{deep}$ and DFS$_{surface}$; the average δ^{18}O value of snow-melt, GMW$_{riv}$ and GMW$_{term}$ were considerably lower. Precipitation demonstrated the highest range in isotopic composition across all sources throughout the study period (20.26 ‰), with δ^{18}O reflecting storm moisture origin. The range of DFS$_{surface}$ δ^{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 the δ^{18}O value of DFS$_{surface}$ progressively increased throughout the season, irrespective of rainfall origin (Fig. 13B). The average δ^{18}O of groundwater-fed streams was greater than that of GMW$_{riv}$, GMW$_{term}$ and snow-melt, but lower than DFS$_{surf}$, DFS$_{deep}$ and rainfall. Seasonal variation of groundwater-fed streams, at 1.5 ‰, was lower than that of all source waters. The mixed channel at the base of the terrace had a low average δ^{18}O signature, more comparable to δ^{18}O values of the GMW rivers.

Source	**δ^{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 below snowpack	-22.44	0.64	2	0.20	0.07	2
DFS$_{deep}$	-18.91	0.18	2	25.8	14.5	2
Snow-melt	-22.99	-	1	0.14	-	1
Glacial melt (GMW$_{term}$)	-22.53	0.98	4	0.34	0.2	4
Toklat main stream(GMW$_{riv}$)	-22.86	0.95	9	0.04	0.25	9
Groundwater streams	-20.97	0.302	45	2.87	1.13	45
Mixed	-21.38	0.722	8	1.73	1.14	8

Table 1: Seasonal average δ^{18}O and Cl^- signatures of source waters and upwelling sites

Marked variability was observed between A-sites, situated closer to the valley-side, and B-sites situated further towards GMW$_{riv}$. Generally A-sites had higher δ^{18}O signatures (Fig. 14C), similar to DFS flow pathways, and streamflow of A-sites responded rapidly to precipitation (Fig. 14 A,B), however this response altered over the season. Although stage was initially relatively constant, pronounced diurnal flow maxima were observed from July 16th (A2), and August 16th (A5). At A2 where these variations were most pronounced, the response of stage to precipitation became more marked. Variations in isotopic composition of the groundwater streams were directly connected to their respective hydrological regimes, with the δ^{18}O values responding to changes in stream depths. Accordingly, during the more hydrologically variable period at A2 and A5, increases in $\delta^{18}O$ values were greatest at A2.

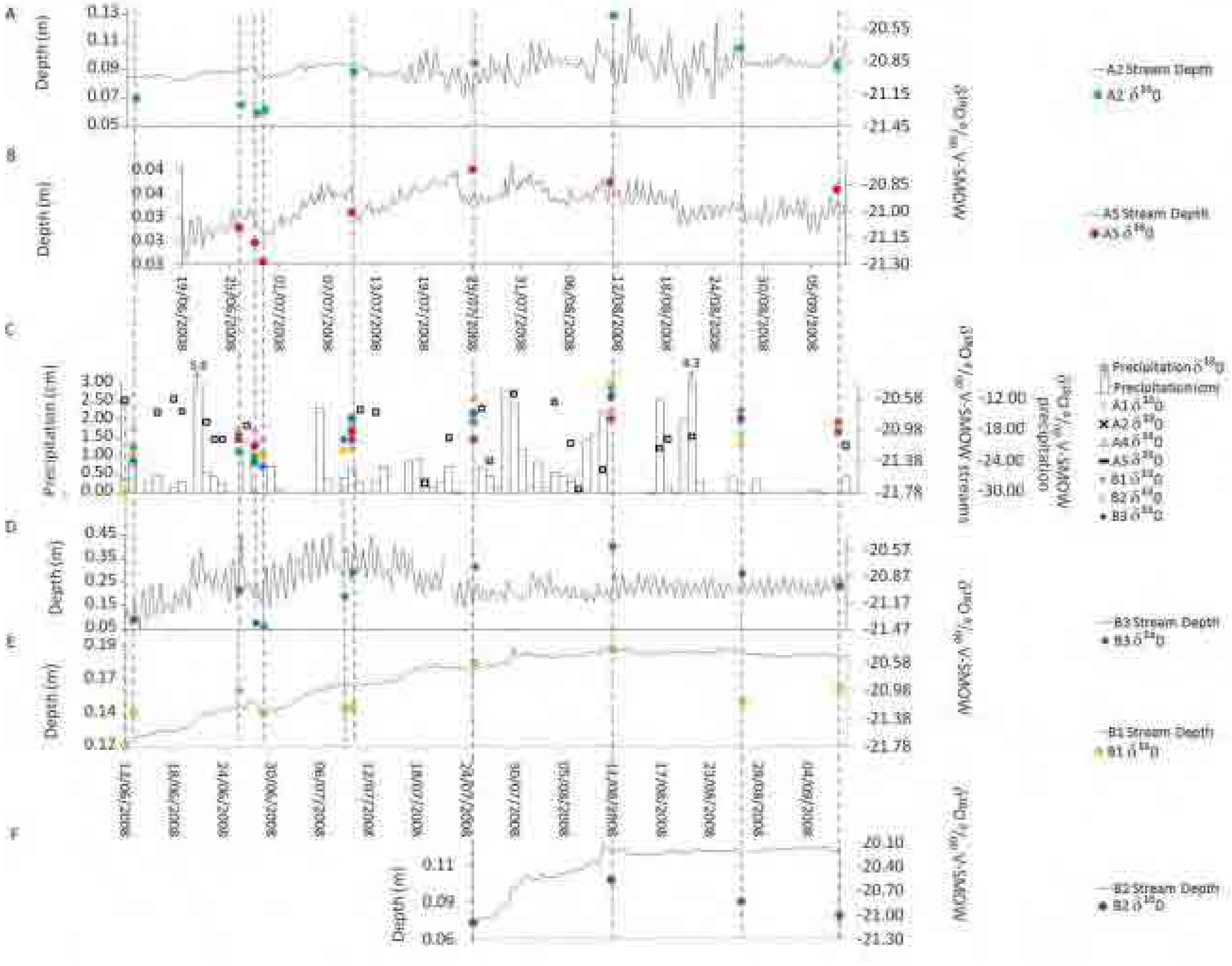


Fig. 14: Variations in flow regime (stream depth) and $\delta^{18}O$ values of groundwater-fed streams with rainfall

Sites B1, B2, and B3 generally had the lowest $\delta^{18}O$ signatures, more similar to GMW_{riv} (Fig. 14C). River stage within these sites was generally less responsive to precipitation; streamflow increased only following heavy or extended periods of continual rainfall (>4 days). Notable increases in $\delta^{18}O$ were observed only during these events; on June 26th, July 25th and August 11th the $\delta^{18}O$ of B1 and B3 was higher than at all other sites (Fig. 14C). During these events the $\delta^{18}O$ of groundwater streamflow of all sites increased to some degree, irrespective of the isotopic composition of rainfall. B-sites exhibited clear seasonal changes in flow regime, with gradual increases in flow throughout the season (Fig. 14D, E, F). B3 demonstrated two seasonal peak stage maxima, firstly in mid-June and secondly in early July (Fig. 14D). A similar flow peak was observed at B1 and B2, in early August, under more attenuated flow regimes, demonstrated by reduced amplitude of daily stage maxima.

Seasonal differences in δ^{18}O values were observed between ephemeral (B2 and B3) and perennial streams (A1-A5 and B1) (Fig. 15). During baseflow conditions early in the season, δ^{18}O was lower at all sites and closer to δ^{18}O values of meltwater (snow and glacial). Subsequently, progressive seasonal enrichment of isotopic composition occurred within almost all perennial channels; A1-A3, A5 and B1. Following the initial increase in δ^{18}O values within the first month of study, B2 and B3 (ephemeral streams) did not demonstrate further progressive isotopic enrichment.

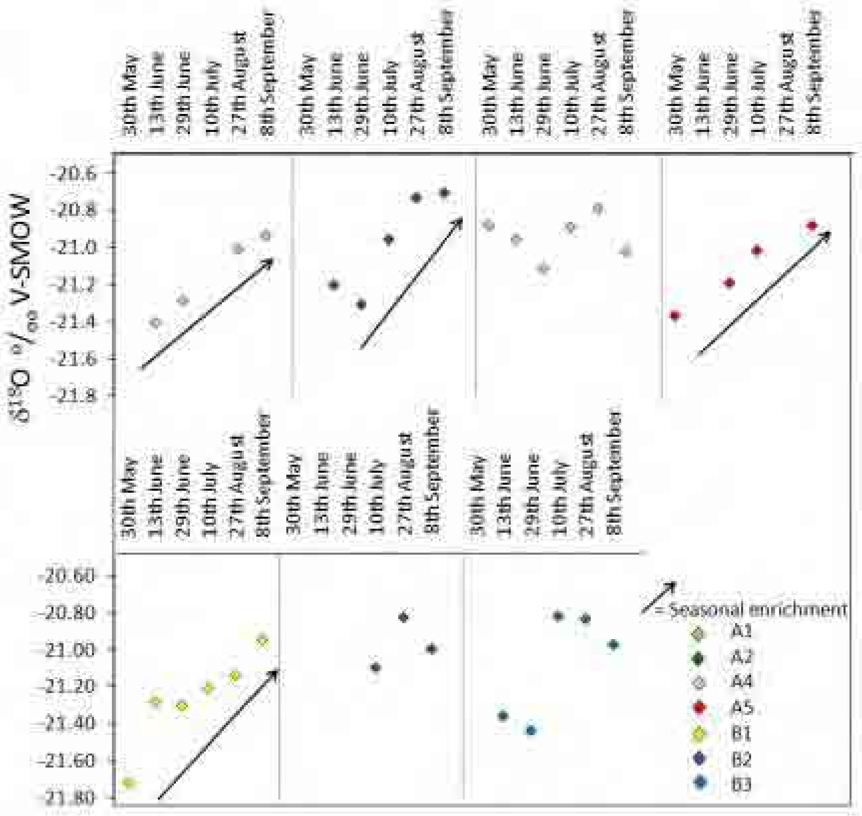
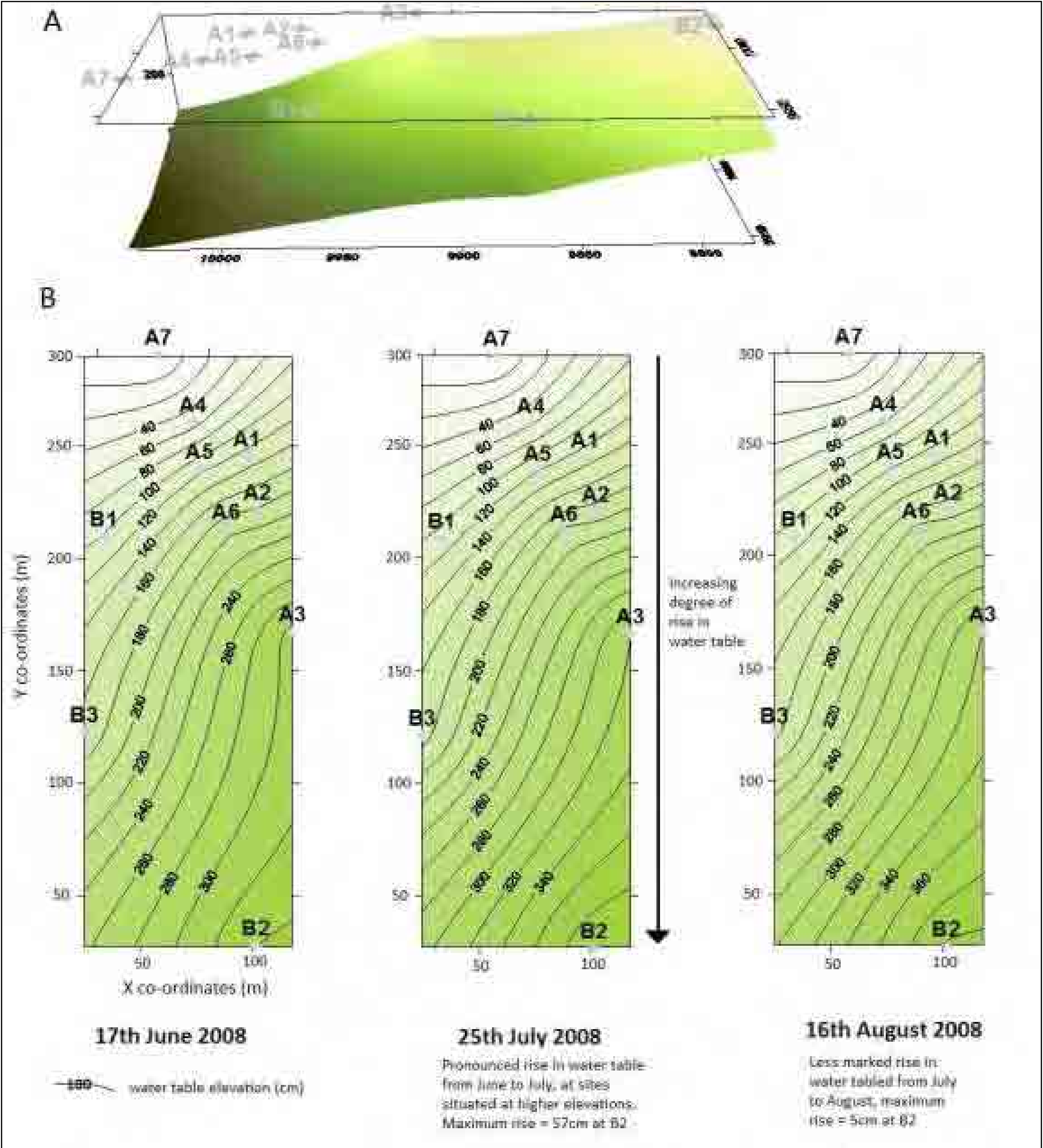


Fig. 15: Differing degrees of seasonal enrichment in δ^{18}O within perennial and ephemeral groundwater-fed streams

2.3.2 *Hydrological variability*

The flow regimes of the groundwater-fed streams varied throughout the season, and increases in interpolated water table elevation were observed across all sites. The greatest increases in piezometer water levels were observed during the initial months of study, stabilising by early August (Fig. 16B). The extent of the water-table increase was significantly positively correlated with site elevation ($p < 0.01$), reflecting the significant surface gradient across the terrace (Fig. 16A), with upstream sites generally situated at higher elevations.



17th June 2008

25th July 2008

Pronounced rise in water table from June to July, at sites situated at higher elevations. Maximum rise = 57cm at B2

16th August 2008

Less marked rise in water tabled from July to August, maximum rise = 5cm at B2

Fig. 16 A) Elevation of groundwater fed streams; B) seasonal variations in interpolated water table elevation across fluvial terrace

These streams were ephemeral, with flows commencing later in the season as the water-table rose to intersect the surface.

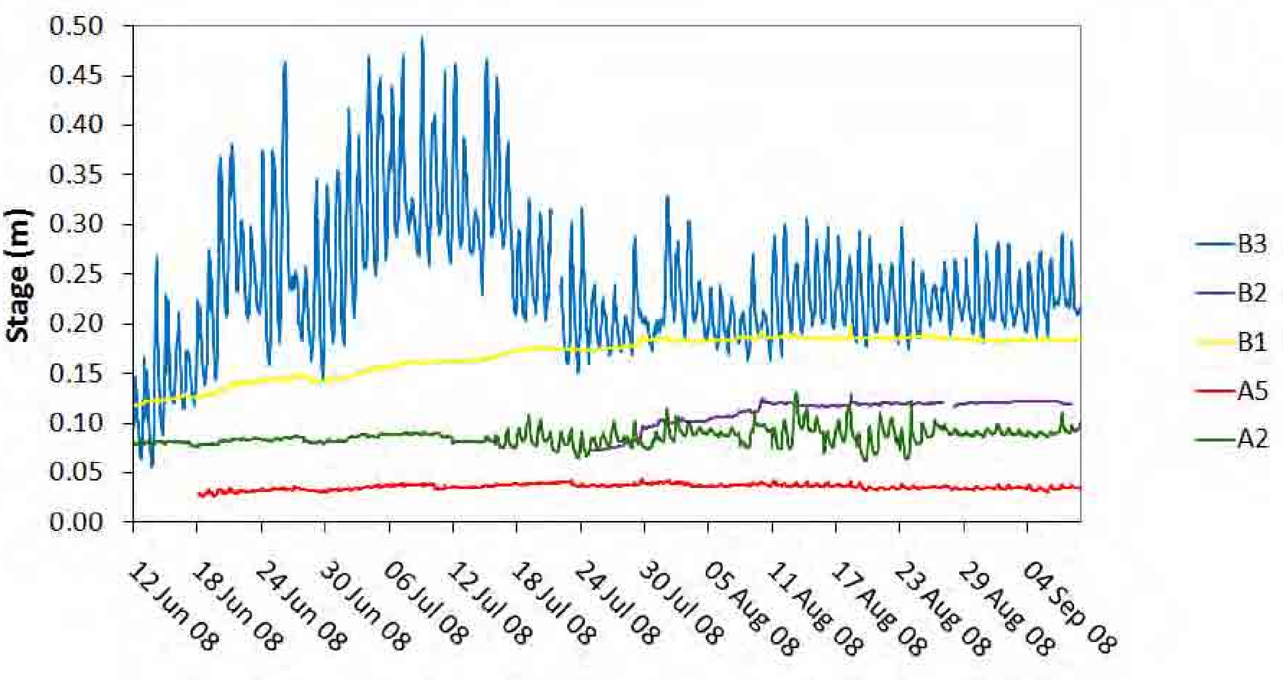


Fig. 17: Stream stage of all groundwater-fed streams, illustrating different degrees of flow attenuation

Marked differences in degrees of flow attenuation were determined between sites (Fig. 17). Despite similarities in isotopic characteristics between GMW_{riv} and B-sites, only B3 demonstrated distinct diurnal flow variability. All A-sites demonstrated reduced flow variability.

2.3.3 *Cl^- content*

The Cl^- concentration of DFS_{deep} was 15 times greater than that of any other water source or flow pathway (Table 1). GMW_{riv}, GMW_{term}, snow meltwater and $DFS_{surface}$ had the lowest Cl^- concentrations, whilst the average chloride concentrations of groundwater channels were relatively high. The high Cl^- concentration of DFS_{deep} is the most likely source of Cl^- to the groundwater-fed streams. With a distinct Cl^- signature, the proportional contribution of DFS_{deep} to each stream can be estimated using a simple mixing model:

$$DFS_{deep}\% = \left(\frac{S_u}{S_D}\right) \times 100 \tag{2.}$$

Where $DFS_{deep}\%$ is the percentage contribution of water to the site from DFS_{deep} waters, S_u is the concentration of Cl^- at the upwelling site, and S_D the average Cl^- concentration of DFS_{deep}.

By comparing $\delta^{18}O$ values and Cl^- concentrations within individual groundwater-fed streams (Fig. 18), two groups of streams were distinguished. Group 1 streams encompassed all A-sites. These had relatively high Cl^- concentrations, which increased throughout the season, and corresponded at most sites with seasonal isotopic enrichment; significant correlations were identified between $\delta^{18}O$ values and Cl^- concentrations at A2 and A5. Although A4 did not demonstrate seasonal isotopic enrichment, this site had similarly high Cl^- concentrations to other A streams, with comparable temporal variability. Following extended rainfall events $\delta^{18}O$ dissociated from Cl^-.

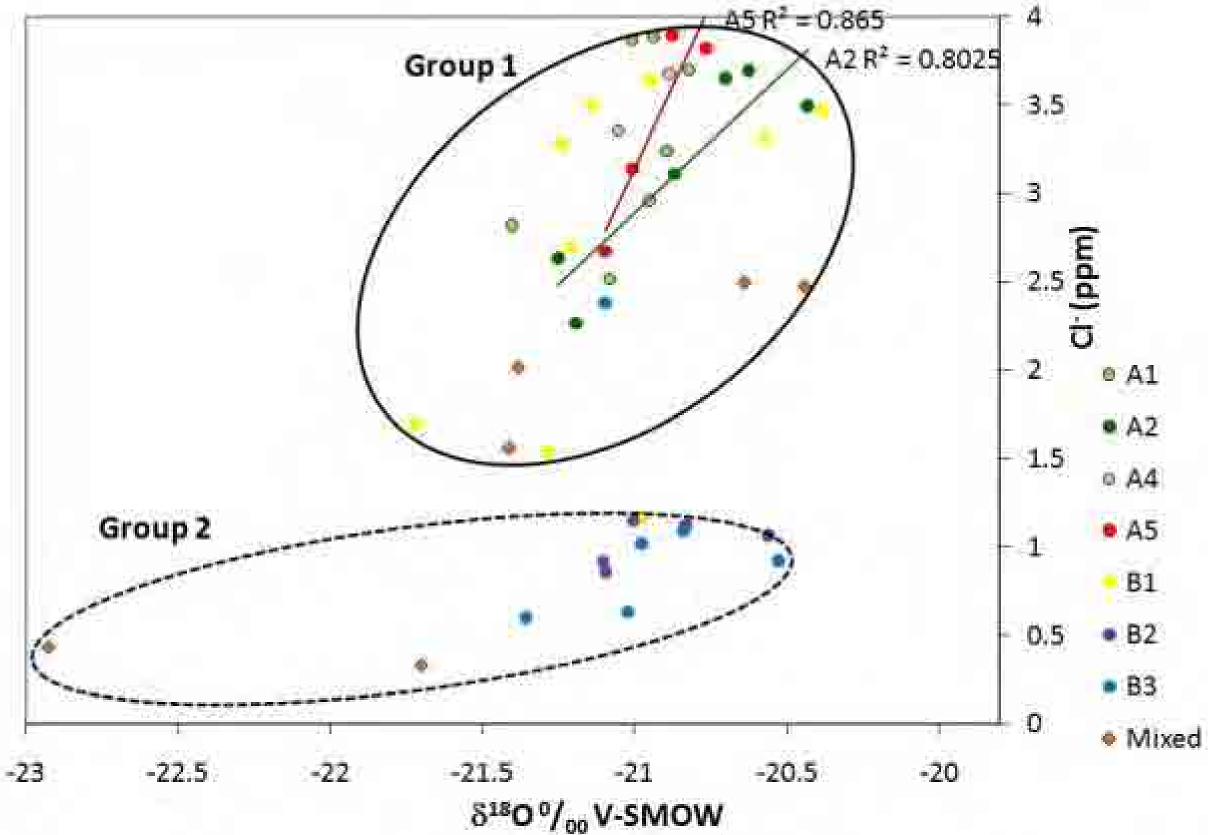


Fig. 18 Temporal co-variation of Cl^- concentrations and $\delta^{18}O$ values within streams

Group 2 consisted of sites B2 and B3. Both sites had low Cl^- concentrations and no significant correlation with $\delta^{18}O$ (Fig. 18). 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. 19i), associated with increases in $\delta^{18}O$ (group 1). The relationship between $\delta^{18}O$ and Cl^- also varied with precipitation. Finally, during periods of peak glacial melt (as indicated by seasonal stage maxima in B3; Fig. 17), low Cl^- concentrations (Fig. 19ii) and $\delta^{18}O$ values were observed in the mixed channel (Group 2). At all other times, higher Cl^- and $\delta^{18}O$ values were observed (Group 1) (Fig 18).

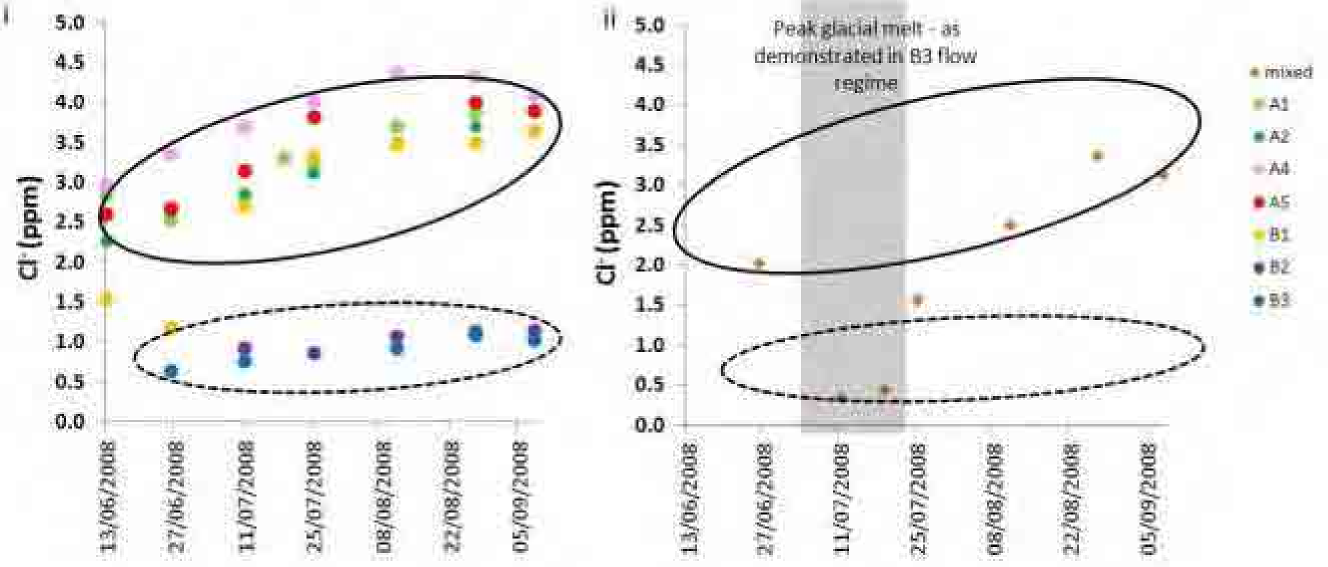


Figure 19 i. Seasonal differences in chloride concentrations between perennial streams (A streams and B1) and B streams, and ephemeral streams (B2 and B3); ii. seasonal varability in chloride concentration of mixed channel

2.3.4 *Macroinvertebrate communities*

Macroinvertebrate diversity was significantly higher within groundwater-fed streams fed by DFS water flow pathways, than in channels fed predominantly by seepage from GMW_{riv} ($p<0.01$). Macroinvertebrate abundance of the mixed channel was markedly lower than that of groundwater-fed streams, except in June when glacial melt was low, and hence connection to GMW_{riv} had not been initiated. During this month abundance was relatively high and comparable to that of the groundwater-fed streams (Fig. 20A). Following peak glacial melt macroinvertebrate abundance declined by 93% and did not significantly recover upon subsequent disconnection from GMW_{riv}. Macroinvertebrate diversity of the mixed channel however remained analogous to that of groundwater-fed streams until later in the season (Fig. 20B), when a reduction in diversity was associated with a higher relative dominance of Chironomidae, increasing from 43% in July to 93% in August.

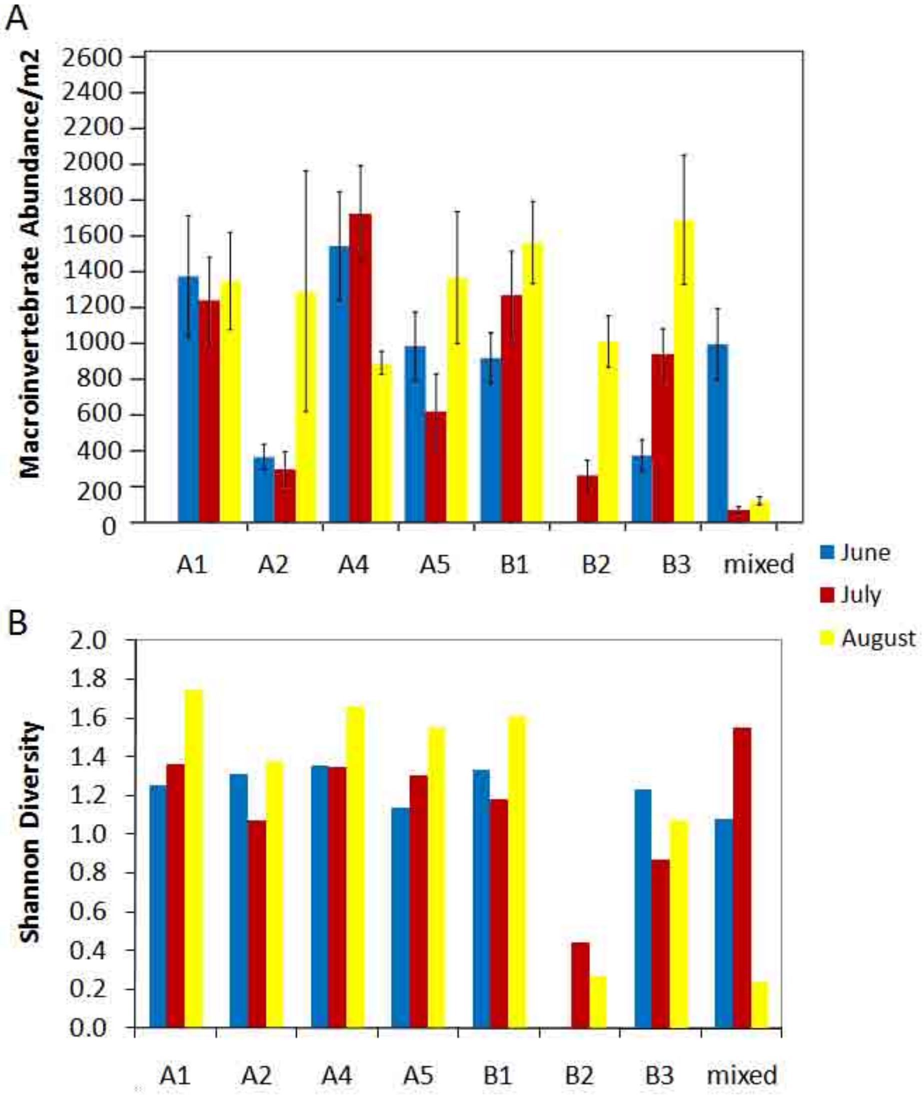


Fig. 20: Monthly variability in macroinvertebrate A) abundance and B) diversity of all study sites, demonstrating seasonal trends in macroinvertebrate distributions

A significant correlation was determined in June between proportional contribution of DFS$_{deep}$ to groundwater-fed streams and concentration of fine particulate organic matter (FPOM) (Fig. 21A). At this time a significant correlation was also determined between macroinvertebrate abundance and both DFS$_{deep}$% and FPOM (Fig. 21B and 21C). Subsequent dissociation of these relationships corresponded with increases in organic matter and chlorophyll concentration (Fig. 21D, E, F) observed in July and August.

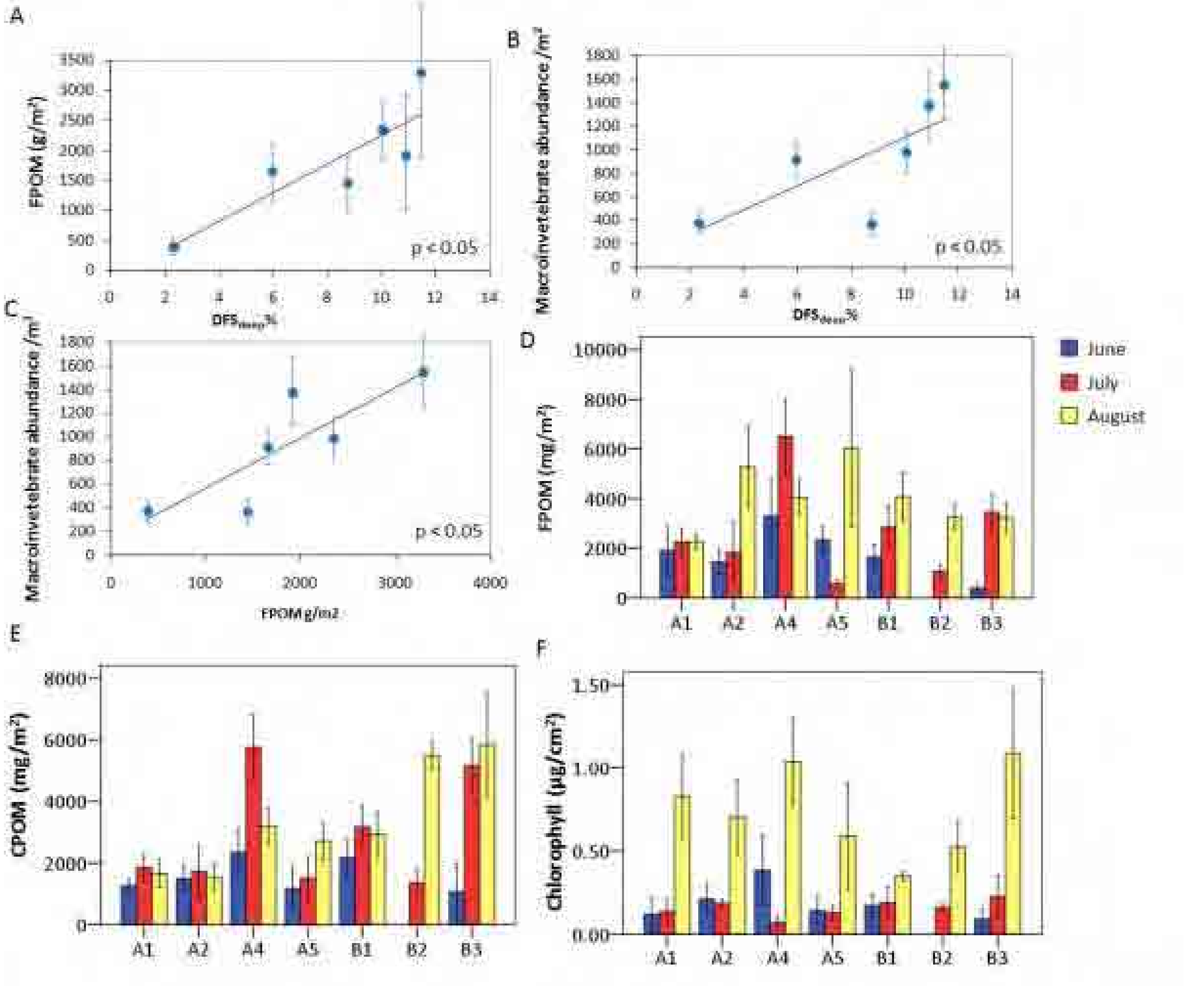


Fig. 21: Demonstration of interrelationships between A) relative contributions from DFS$_{deep}$ and FPOM in June, B) relative DFS$_{deep}$ contributions and macroinvertebrate abundance in June C) association between macroinvertebrate abundance and FPOM D-F) seasonal variability in organic resources

2.4 Discussion

2.4.1 *Water sources and flow pathways*

As the Barrow LMWL, created from the Global Networks of Isotopes in Precipitation (GNIP) dataset, included winter precipitation, it provided a more complete representation of the annual meteoric water input than rainfall data collected from the study site in summer. The proximity of samples to the LMWL indicates evaporation to be an unlikely cause of δ^{18}O differences between sources and groundwater-fed streams (Fairchild et al., 1999). Results suggest that the groundwater-fed streams were fed both by seepage from the valley-side debris fans (higher δ^{18}O values), and from GMW_{riv} (lower δ^{18}O values). Distinct isotopic signatures enabled identification of water sources and flow pathways contributing to groundwater-fed stream flow (Gibson *et al.,* 2005); as the mean δ^{18}O value of groundwater-fed streams was intermediate between those of GMW_{riv} and the DFS flow pathways, 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 δ^{18}O of upwelling channels 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 (Fig. 22), where waters likely had a long residence time (DFS_{deep}) due to the less permeable, fine matrix of the lower layers of the debris fan (Clow et al., 2003). This pathway acted as a perennial baseflow and principal source of Cl^- to the groundwater-fed streams. A possible explanation for the higher Cl^- concentrations is evaporation of water in the active root zone, during infiltration into the subsurface (Peters and Ratcliffe, 1998). However as samples did not deviate from the LMWL, evaporation is unlikely (Anderson et al., 2008$_a$). A more likely explanation is localised mineral dissolution; increased contact time with rock facies in this flow pathway may enhance mineral dissolution of evaporites, and the Cl$^-$ concentration of this groundwater may be increased to levels much greater than in initial atmospheric inputs (Anderson et al., 2003). Halites and anhydrites are specified within the site description (Wilson et al., 1998), but could be found within the late Triassic calcareous sedimentary geological facies units of the valley-sides. This would explain the higher Cl$^-$ concentrations observed in DFS$_{deep}$, with minimal alteration in δ^{18}O values.

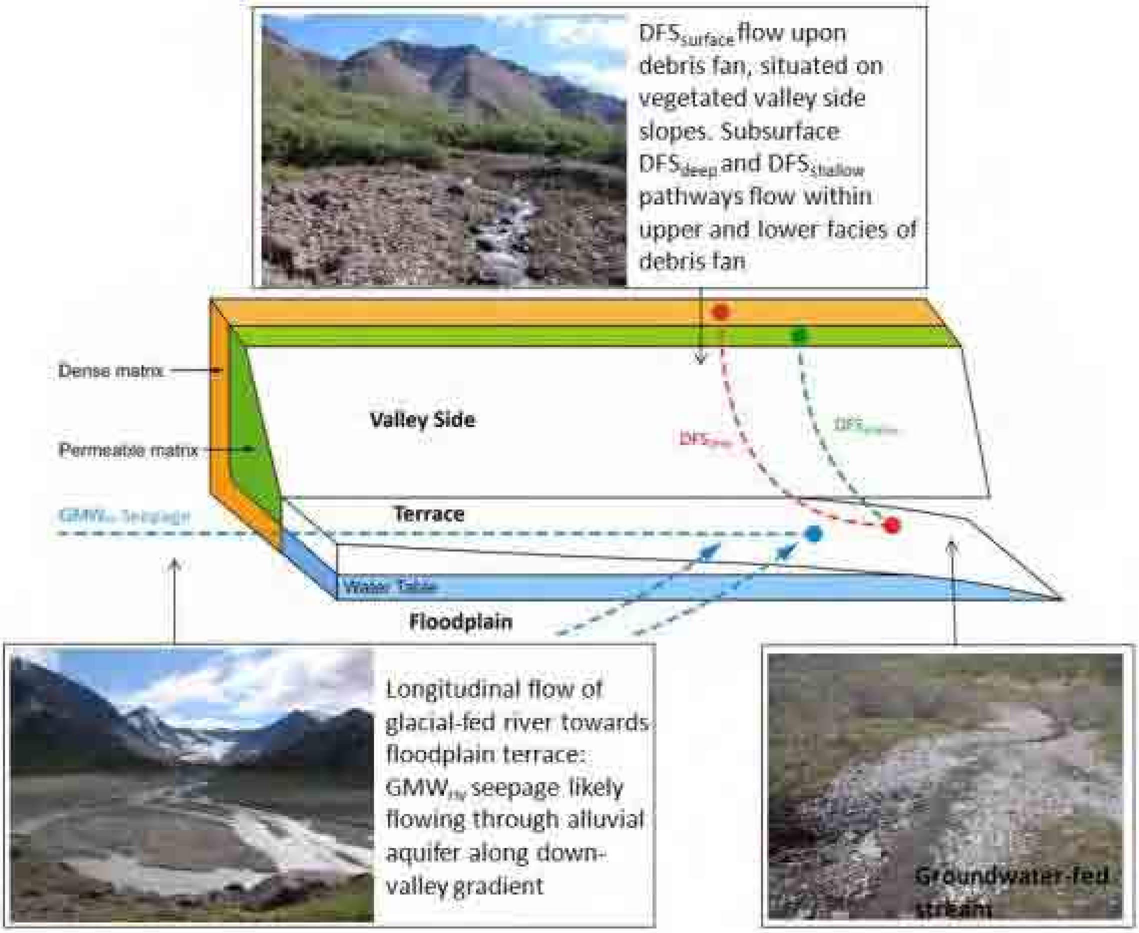


Fig. 22: Schematic of groundwater flow pathways contributing to stream flow on a fluvial terrace of the Toklat River catchment

The presence of a second subsurface flow pathway within the valley side was indicated by simultaneous increases in stage and δ^{18}O values, and reductions in Cl$^-$ concentrations detected within groundwater-fed streams, in response to precipitation events. This demonstrates contributions from a rapid response pathway, potentially through the highly permeable near-surface sediments of the debris fan (de Jong *et al.,* 2004; Roy and Hayashi, 2009) (Fig. 22). The δ^{18}O values of precipitation were however buffered prior to reaching sites of groundwater upwelling; irrespective of the characteristically variable δ^{18}O values of rainfall, in-stream δ^{18}O values persistently increased following precipitation. This may occur via the mixing of rainwater with antecedent soil moisture upon valley sides, which increases δ^{18}O and reduces variation (Rodgers, 2005). In conjunction with the similarity between mean precipitation δ^{18}O values and DFS pathways, this buffering mechanism indicates the most likely pathway of the heavier in-stream δ^{18}O values, following rainfall, to be through the valley side. Reduced in-stream Cl$^-$ concentrations relative to δ^{18}O values, also observed following rainfall, may reflect the increased relative contribution of DFS$_{\text{shallow}}$ in groundwater-fed streams, with the rate of water flow through this pathway sufficient to minimise mineral dissolution (Swoboda-Colberg and Drever, 1993). Alternatively halite deposits may be highly localised, and flow through DFSshallow may bypass the mineral completely. The reduction in Cl$^-$ concentration suggests a time lag in the relative contributions, and hence in residence times, of the two subsurface DFS pathways.

The seasonal enrichment of δ^{18}O observed within all DFS waters may be attributed to isotopic fractionation of snow-melt water (Moser and Stichler, 1974), whereby water released from snowpacks is progressively enriched by between 3-5 ‰, until all meltwater is utilised (Taylor *et al.,* 2002). Seasonal isotopic enrichment of DFS$_{\text{surface}}$ is, however, 9 ‰, suggesting additional processes may be responsible. As the average $\delta^{18}O$ value of rainfall was much higher than that of snow-melt, the isotopic enrichment may additionally reflect seasonal reductions in snow-melt supply, and the subsequent transition from a snow-melt to a rainfall dominated catchment (Sueker *et al*., 2000).

The final flow pathway comprises subsurface connections between GMW_{riv} and groundwater-fed streams (Fig. 22); these waters have a lower $\delta^{18}O$ value and a low Cl^- concentration. This pathway is analogous to lateral subsurface seepage described in the literature (Ward *et al.,* 2001); however due to the strong topographic gradient in this catchment, the predominant glacial subsurface flow pathway is likely to be through seepage along the valley axis, creating an alluvial aquifer (e.g. Malard et al., 2002). Mixing of the three subsurface pathways results in the intermediate $\delta^{18}O$ values and Cl^- concentrations observed in the groundwater-fed streams.

2.4.2 ***Local scale variability in physicochemical composition of groundwater-fed streams***

Our results indicated that, as Malard *et al* (1999) found of the Val Roseg in the Swiss Alps, the three primary sources (snow, ice and rainfall) contributing to groundwater flow varied in both their relative contribution and flow pathway over space and time. This contributes to marked local spatial and temporal variability in the physicochemistry of groundwater-fed streams.

2.4.2.1 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, the lack of mid-summer flow maxima, and the perennial nature of flow indicates that these streams received a significant contribution to flow via seepage from the DFS pathways. The relatively high δ^{18}O values and seasonal isotopic enrichment 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 increases in Cl^- concentration, which were positively associated with the seasonal enrichment of 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, following preferential leaching of Cl^- from snowpacks during peak snow-melt (Helliwell *et al.*, 1998). Small groundwater reservoirs cannot buffer against high volumes of water (Bottomley *et al.*, 1986), therefore low Cl^- concentrations were released from DFS_{deep} into streams during snowmelt, as large quantities of meltwater, low in Cl^- concentration, were rapidly flushed through this pathway. Following peak snow-melt, progressively reduced snow meltwater contributions result in an increased dominance of rainfall (Sueker *et al.*, 2000), which had a higher Cl^- concentration. Permeating in smaller quantities through the valley-side, rainfall water, further enriched in Cl^- through mineral dissolution, was released from DFS_{deep} into the groundwater-fed streams. In summary, the seasonal increase in Cl^- concentrations of A streams therefore likely resulted from gradual increases in percentage contributions of rainfall (Sueker *et al.*, 2000). As rainfall dominance produced characteristic seasonal variations in δ^{18}O and in Cl^- within DFS flow pathways, the positive associations observed in A streams between δ^{18}O and Cl^- further indicated the dominance of this flow pathway. Dissociation of the relationship following rainfall reflects inputs from the $DFS_{shallow}$ temporary flow pathway.

The closer proximity of B streams to GMW_{riv}, seasonal-maxima, and generally lower $\delta^{18}O$ values are suggestive of a higher contribution from GMW_{riv} seepage. Ephemeral flow and lack of seasonal $\delta^{18}O$ enrichment at B2 and B3 further supports this. Initial low $\delta^{18}O$ signatures likely reflect high volumes of snow-melt released into the glacial meltwater channel from the glacier surface early in the season (Collins, 1979). The ensuing lack of $\delta^{18}O$ enrichment potentially reflects increases in relative contributions of ice meltwater to flow which undergoes significantly less fractionation than snow (Souchez and Lorrain, 1991; Moser and Stichler, 1974). The progressive rise in transient snowline throughout the summer and resultant increase in ice-melt (Collins, 1989) would greatly buffer fractionation effects of the snow-melt contributions from the glacier surface. At these sites, following peak snow-melt, there was no increase in Cl^- concentrations which remained low throughout the study period, suggesting limited or no connection with DFS_{deep}. As a result there was no association between $\delta^{18}O$ values and Cl^- concentrations, indicating limited contributions from sources transforming between snow-melt and rain-fed dominated systems (DFS sources).

Site B1, although demonstrating perennial flow and seasonal isotopic enrichment, similar to A streams, was more similar to other B sites in its proximity to GMW_{riv}, and presence of mid-summer flow maxima. This indicates a more mixed inflow of groundwater flow pathways to this site, with a strong input from GMW_{riv} seepage, and a DFS_{deep} baseflow component. 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. In addition dilution of Cl^- following precipitation events of greater than four days suggests temporary connections were formed between $DFS_{shallow}$ and B1 during high rainfall events. Temporal initiation of preferential flow pathways during high discharge events has been observed in several studies (Tsuboyama et al., 1994; Uchida et al., 2005). Differences observed between B1 and other B sites, despite similar proximity to GMW_{riv}, and thus a significant flow contribution from GMW_{riv} seepage, are due to the lower elevation of B1, being sufficiently close to the water table to maintain a perennial valley-side seepage baseflow component.

In the mixed channel, reductions in $\delta^{18}O$ 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 $\delta^{18}O$ values) to the previously predominantly groundwater-fed stream. As reductions in $\delta^{18}O$ of the mixed channel, and hence periods of connectivity to GMW_{riv}, coincided with peak glacial melt throughout mid June to late July (determined from the B3 flow regime), this suggests that connectivity to the main Toklat channel occurred during times of peak meltwater flow. Increased meltwater discharge results in significant alterations to the surface channels of the main glacial river (Warburton, 1994); glacial meltwater may overtop the channel sides, and flow into the mixed channel, which is situated upon a slightly elevated section of the floodplain immediately below the terrace. The reductions in Cl^- also observed during this time were likely due to the low Cl^- content of GMW_{riv}. Associations between $\delta^{18}O$ and Cl^- observed during groundwater dominance of mixed channel flow, is likely attributed to contributions from DFS_{deep}.

2.4.2.2 Temporal variability

In addition to seasonal variations in Cl^- and $\delta^{18}O$ observed in A streams, reflecting reductions in snow-melt from the valley-side, short-term and seasonal variations in subsurface flow pathways were observed in both A and B streams, resulting from water table increases, enhancing connectivity between previously isolated preferential flow pathways (Anderson, 2008; Sidle *et al.*, 2000). Although B sites were predominantly fed by GMW_{riv} seepage, temporary rises in water table following prolonged precipitation events created pathways between the B sites and isotopically enriched and rapidly responsive $DFS_{shallow}$. This was observed by step increases in stage, and concurrent uncharacteristically high $\delta^{18}O$ values. A sites situated closer to the valley sides, demonstrated enhanced connectivity following less extensive precipitation events.

The observed seasonal increase in water table reflects progression of the melt season (Robinson et al., 2008), with increased GMW_{riv} flow resulting in greater subsurface infiltration of water. As the water table continued to rise until it intersected the surface, water table increases were particularly marked at higher elevations. Accordingly streams began to flow at progressively higher points throughout the summer. Seasonal increases in streamflow observed at B sites might therefore be attributed to water table rises produced by peak mid-summer meltwater flows. Sites at the lowest 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. A similar process occurred at A4 and A5; with differences in emergence times of GMW_{riv} seepage reflecting variations in flow attenuation and sediment permeability (Ward *et al.,* 2002) i.e. water followed different routes of flow, with different residence times, within the flow pathway.

The results suggest that each groundwater-fed stream is characterised 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 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 spatially and temporally, 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 recession may differentially influence each groundwater-fed stream. B2 and B3, fed almost solely by glacial meltwater, may cease to flow, whereas streams derived from DFS_{deep} may maintain active channel flow, increasing their percentage content of rainfall recharge. Given the local variations in physicochemistry and climate change implications between each groundwater-fed stream, 'groundwater' in this catchment cannot be regarded as homogeneous.

2.4.3 *Influence of spatial variations in groundwater hydrology on macroinvertebrate communities*

Groundwater upwellings are recognised as hotspots of macroinvertebrate biodiversity (Brown *et al.*, 2007), due to increased thermal and discharge stability, and water clarity (Brown *et al.*, 2003). The markedly higher macroinvertebrate abundance and, later in the study season, macroinvertebrate diversity, found within groundwater-fed streams relative to the mixed channel supports this widely held observation. The uncharacteristically high macroinvertebrate abundance and diversity found within the mixed channel during June might be attributed to the absence of glacial influence and dominance of groundwaters prior to and during this period, with associated greater channel stability and water clarity observed at this time. Following the influx of glacial waters (initially observed by a reduction in water clarity), the reduction in abundance, with maintenance of relatively high diversity, might be associated with the sampling of macroinvertebrates so shortly after meltwater inundation; general reduction of all taxa by high discharge may have occurred (Resh *et al.*, 1988; Cardinale et al., 2006). Subsequent reductions in biodiversity may be attributed to ensuing recolonisation and dominance by specially adapted multivoltine Chironomidae (Williams, 1996). Macroinvertebrate abundance did not recover once glacial waters receded, potentially due to longer term reduction of habitat suitability, e.g. deposition of glacial fines and reduction in pore space (Angradi, 1999) or removal of refugia. Alternatively recolonisation of the mixed channel following restoration of groundwater-flow dominance may require a longer period of time (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. Transport of particulate matter within subsurface environments is widely recognised (McDowell-Boyer et al., 1986) and valley-side through-flow (the source of DFS flow) may therefore entrain organic matter, which is discharged at points of groundwater upwelling (Boisser and Fontvielle, 1995), and thus the A sites and B1, which received greater relative contributions from DFS_{deep}, had higher organic matter concentrations. Organic matter is an important energy source (Polis *et al.*, 1997; Buffam *et al.*, 2001), and during periods of low resource availability, macroinvertebrates are therefore likely to aggregate upon ‘resource islands’ (Webster and Waide, 1982) of patches of high organic matter concentration (Tiegs *et al.*, 2008), such as those provided by upwelling DFS_{deep}.

The absence of a significant relationship between DFS_{deep}% with organic matter and macroinvertebrate abundance in July and August could reflect increased availability of alternative organic matter resources, resulting from establishment of streamside vegetation, leaf litter fall, and reductions in streambed shading and associated enhanced periphyton production (Rosemond *et al.*, 2000). As food resources were no longer constrained to isolated patches at points of DFS_{deep} discharge, the relationship between macroinvertebrate distribution and groundwater flow pathway weakened.

Despite seasonal variability in relationships between macroinvertebrate abundance and groundwater flow pathways, macroinvertebrate diversity within DFS_{deep} -fed streams was still overall significantly higher than within streams supplied by higher proportions of GMW_{riv} throughout the study period. Lower macroinvertebrate diversity observed in all streams during June is attributed to lower organic matter availability; diversity seasonally increases in perennial streams with organic matter resources, as many taxa are phenologically adapted to hatch in months when resource availability is greatest (Cummins *et al.*, 1989). Flow permanence (Smith *et al.*, 2003) and associated re-colonisation requirements of the glacially-fed ephemeral streams restrict increases in diversity, despite observed increases in organic matter availability. Here, as colonisation is limited to specialists adapted to the habitat, e.g. Chironomidae, spatial distribution of many taxa cannot reflect habitat preferences (Fonseca and Hart, 2001). Thus although resources increase within ephemeral streams throughout the season, aggregation of macroinvertebrates at sites of greater resources results predominantly in higher numbers of only a few specially adapted macroinvertebrates, potentially through the process of active drift (Oliver *et al.*, 1971). For example, at site B3 the relative abundance of Chironomidae rose from 83 to 94% between July and August; accordingly macroinvertebrate diversity decreased.

During periods of low organic matter availability, the ecological capacity of the groundwater-fed streams is governed by water sources and pathways. Although relationships between macroinvertebrate abundance and flow pathways are weakened following the increase in alternative sources of organic matter, significant differences in diversity subsequently observed between perennial streams (derived from DFS_{deep} seepage) and ephemeral streams (derived from GMW_{riv} seepage) demonstrates the sustained influence of groundwater flow pathways upon the macroinvertebrate community.

The implications of climate change upon macroinvertebrate communities within groundwater-fed streams are highly localised. Given the potential for future cessation of GMW supplies (Milner et al., 2009) macroinvertebrate communities within streams fed solely by glacial meltwater seepage demonstrate a high potential vulnerability to glacial recession, especially when considering their relatively low macroinvertebrate diversity. Perennial streams fed by groundwaters from snowmelt and rainfall could be more resilient to climate change; the diversity of macroinvertebrates within these streams may infact increase, as the reductions in glacial meltwater results in a relative increase in contributions from perennial sources (Brown et al., 2007_a). However as additional characteristics of groundwater (e.g. organic matter content) vary to such a marked extent over a relatively small scale, influences of glacial recession will be complex. Groundwater should therefore be regarded as having a dynamic influence upon macroinvertebrate communities.

2.5 Conclusion

Marked local spatial and temporal heterogeneity may occur in the physicochemical characteristics of groundwater-fed streams in glacierised catchments, reflecting variability in the proportional contribution of waters derived from distinct sources and flow pathways. On a fluvial terrace of the Toklat River, spatial variations in flow pathway contributions reflected both proximity to respective flow pathways and local topography. Contributions from flow pathways to stream flow varied both on a seasonal and rainfall-event scale. Resultant physicochemical differences between streams significantly influenced macroinvertebrate communities, but seasonal increases in organic matter availability reduced the influence of these variables upon macroinvertebrate abundance. In resource depleted environments, groundwater flow, entraining organic matter, may have a significant influence upon the maximum macroinvertebrate abundance which can be supported.

Seasonally reduced macroinvertebrate diversity was observed in groundwater-fed streams sourced from glacial meltwater of the main Toklat River (GMW_{riv}) compared with those sustained by valley-side baseflow. This demonstrated a potential differential vulnerability of macroinvertebrates to climate change between groundwater-fed streams. Understanding of groundwater flow in glacierized systems is essential in establishing the influence of groundwater upon macroinvertebrate communities, and the future implications of climate change.

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3. THE INFLUENCE OF GROUNDWATER FLOW DYNAMICS UPON BENTHIC MACROINVERTEBRATES, IN A GLACIERISED CATCHMENT

The influence of variability in flow pathways upon macroinvertebrates was studied in 7 groundwater-fed streams from May to September, 2008, within the Toklat River floodplain, Alaska. Higher macroinvertebrate diversity was supported by streams which derived a greater proportion of groundwater flow from perennial seepage, through a dense matrix, deep within a debris fan (DFS_{deep}). Streams fed almost solely by glacial meltwater seepage (GMW_{riv} seepage) supported lower macroinvertebrate diversity. Seasonal trends in macroinvertebrate distribution were determined within both ephemeral and perennial streams, through the use of a detrended correspondence analysis. Significant relationships were found in June between source water composition (DFS_{deep}%), fine particulate organic matter (FPOM) and macroinvertebrate abundance, indicating that during this month macroinvertebrates aggregated upon FPOM, which was predominantly supplied by DFS_{deep}. Subsequently, increases in alternative sources of organic matter reduced the influence of DFS_{deep}-derived FPOM upon benthic macroinvertebrates, and weakened the relationship between macroinvertebrate abundance and DFS_{deep}%. Resource tracking was indicated by the continued association of macroinvertebrate abundance with organic matter throughout the study period, although this varied between taxa, depending upon specific traits. The results indicate that the spatially and temporally dynamic groundwater flow pathways had an equally dynamic influence upon macroinvertebrate communities.

3.1 Introduction

Groundwater inflow may strongly influence the macroinvertebrate community structure of surface streams, (Brown *et al*., 2003), by increasing stream temperature, flow stability and water clarity. Groundwater flow is, however, highly dynamic, and the interaction of various groundwater sources and flow pathways can create marked local variations in physicochemical characteristics of streams (Ward *et al*., 1999; Füreder *et al*., 2001). This local variability in physical habitat (flow permanence and attenuation) and in resource availability (nutrient and organic matter concentrations) may influence macroinvertebrate communities (Turnbull *et al*., 1995; Soulsby *et al*., 1997). Groundwater flow may therefore be a more complex ecological driver of macroinvertebrate communities than previously established.

Variability in groundwater flow pathways is linked to the discontinuous, heterogeneous nature of the local subterranean structure (Anderson, 1989). As groundwater flow pathways in arctic and alpine streams are formed between permeable deposits within the valley bottom, valley side and bedrock aquifers (Robinson, 2008), local discontinuity in the structure of these deposits may create local variations in the routes of groundwater flow (Anderson, 1989). These various flow routes, nested within a single flow pathway, are characterised by different degrees of diurnal variability in flow and temperature regimes (Robinson *et al*., 2008), reflecting local differences in groundwater residence time (Fig. 2). Reduced variability in water temperature and flow typically result in greater macroinvertebrate abundance (Brown *et al*., 2007). Additionally, groundwater source, flow pathways and local topography influence the length of active channel flow (flow permanence), which is a key variable in macroinvertebrate community composition

(McCabe, 1998). Streams with low flow permanence (ephemeral streams) typically support lower diversity than streams sustaining active flow throughout the year (perennial streams) (Wood *et al.,* 2005), reflecting the need for seasonal re-colonisation, or specialist adaptation within ephemeral streams.

Groundwater flow pathways may also influence the availability of food resources, such as dissolved and particulate organic matter (DOM and POM), and nutrient concentrations of streams. Groundwater can potentially entrain organic matter by throughflow (Boissier and Fontvieille, 1995); flow pathways through deeper soils may therefore discharge greater concentrations of DOM and POM to river channels (Polis *et al*., 1997; Buffam *et al*., 2001). This influence may vary seasonally, as groundwater-derived organic matter is potentially ecologically significant only during periods of low alternative resource availability. In temperate streams autumnal leaf fall is an alternative source of allochthonous matter (Hill *et al.*, 2001), and increases light penetration to the stream bed, enhancing periphyton growth (autochthonous materials) (Rosemond *et al.*, 2000).

Organic matter is an important energy source for benthic communities of arctic and alpine streams where resources are sparse (Cowan and Oswood, 1984; Ward, 1994; McKnight and Tate, 1997; Tiegs *et al*., 2008). Positive associations between macroinvertebrates and organic matter have been established (Grimm, 1994 *in* Rowe and Richardson, 2001), and attributed to aggregation of macroinvertebrates upon resources (Tiegs *et al.,* 2008; Dobson and Hildrew, 1992; Richardson, 1991). Aggregation is most marked in resource depleted environments (Tiegs *et al*., 2008) where accumulations of resources serve as habitat patches (Palmer, 2000; Eggert and Wallace, 2003) or 'resource islands' (Webster and Waide, 1982; Benfield *et al*., 2001). The ability of taxa to locate resource patches, and to redistribute in accordance with temporal variations in resource availability, is termed ‘resource tracking’ (Rowe and Richardson, 2001; Hart and Robinson, 1990). Although several mechanisms of resource tracking have been identified, active and passive drift are widely accepted as the dominant processes (Rowe and Richardson 2001; Richardson, 1991; Kohler, 1985).

Active drift occurs as macroinvertebrates emigrate from sites of low resource availability, by entering the water column (Hansen and Cross, 2007), moving upstream along the stream bed (Townsend and Hildrew, 1976; Williams and Williams, 1993; Fengolio *et al*., 2002) or entering the benthic zone from the hyporheic zone (Williams, 1977). Conversely, passive drift occurs as large numbers of macroinvertebrates are ‘accidentally’ dislodged into the water column, predominantly during spates (Hart and Fineli, 1999). Associations between macroinvertebrates and organic matter may also be non-linear, due to the simultaneous influences of multiple variables upon communities. The facultative feeding nature of many macroinvertebrates may complicate the resource tracking relationship as some taxa can alter their diet according to resource availability or developmental stage (Mihuc and Minshall, 1995; Moore, 1977).

The influence of local scale variations in groundwater dynamics may vary depending upon temporal shifts in physicochemical variables, and taxa-specific traits. Therefore this study aims to assess not only the relationship between groundwater flow pathways and macroinvertebrate distribution, but also to incorporate additional physicochemical variables in examining the temporal and spatial dynamics between the physical environment and macroinvertebrate communities, in streams fed solely by upwelling groundwater in the floodplain of the Toklat River, Denali National Park, Alaska with the objectives of:

1) exploring the local spatial and temporal variability in physicochemical variables within groundwater-fed streams;
2) determining associations between benthic macroinvertebrate community distribution and local physicochemical variables; and
3) establishing the relationships between individual taxa and spatial and temporal groundwater dynamics.

3.2 Methodology

3.2.1 Field site

In summer, 2008, a fluvial terrace was selected for study; it is elevated ~1m above the current active glacial floodplain of the Toklat River, Denali National Park, Alaska ($63^{o}29'19.54''$N, $149^{o}57'54.05''$W; Fig. 23A). Mean monthly precipitation in summer 2008 was ~ 162mm, and in winter was ~ 116mm, 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^{o}C (night) (WRCC, 2008). The site was ideal for studying the macroinvertebrate communities of groundwater-fed streams, due to the extensive network of streams, fed entirely by groundwater, flowing across the terrace, and the proximity of the site to an access road (<2 miles).

The Toklat River is a braided, north flowing tributary of the Yukon River, and flow is predominantly derived from ice-melt and snow-melt of three small valley glaciers upstream. The terrace is ~12km from the glacial margin, where the floodplain is ~1300m wide (Fig. 23B). Vegetation-covered valley sides, supporting isolated perched wetlands, extend along the east and west margins of the floodplain, along which additionally lie several debris fans and talus cones. The catchment upstream is ~115km^2. Beneath the glaciers lie debris flows of Silurian and Devonian calcareous strata, whilst along the valley sides are Triassic calcareous sedimentary and submarine basalt, and Paleocene volcanic geologic units (Wilson et al. 1998). The valley bottom consists of unconsolidated clasts of glacial, fluvial and colluvial origin.

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. 12C). Stream reaches (20m) 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. These streams demonstrate variable hydrological characteristics (Table 2).

Site	**Flow pathway**	**Flow Permanence**	**Average Discharge (cumecs)**	**Average Temperature (°C)**
A4	Debris fan seepage	Perennial	0.016	---
A5	Debris fan seepage	Perennial	0.004	4.03
A2	Debris fan seepage	Perennial	0.006	4.45
A1	Debris fan seepage	Perennial	0.012	---
B3	Glacial seepage	Ephemeral	0.093	5.34
B1	Glacial and debris fan	Perennial	0.051	3.50
B2	Glacial seepage	Ephemeral	0.041	3.69

Table 2: Site characteristics (determined in Chapter 2)

3.2.2 Data collection

Seven groundwater-fed streams were studied from May 30th to September 9th 2008. Nested piezometers were inserted to depths of 50cm and 100cm at each site (Fig.23C); stream depth and hydraulic head in each tube was monitored twice daily, and pH and electrical conductivity (EC) were monitored monthly. Thermistors and pressure transducers were inserted at five of the upwelling points (A2, A5, B1, B2 and B3), at the surface, and at depths of 20cm (A2 and B1) and 50cm (B3), recording average readings of stream stage and temperature at 15 minute intervals (Appendix B). Gemini Tinytag Plus thermistors were placed at selected sites and left *in situ* from June 2008 to June 2009, to determine the length of active channel flow. Perennial streams were identified where in-stream temperature, or that of a location directly upstream, constantly exceeded 0°C throughout the year (Appendix C). Ephemeral streams were characterised either by in-stream temperatures falling significantly below 0°C (during winter), or at several sites, by the observed absence of flow.

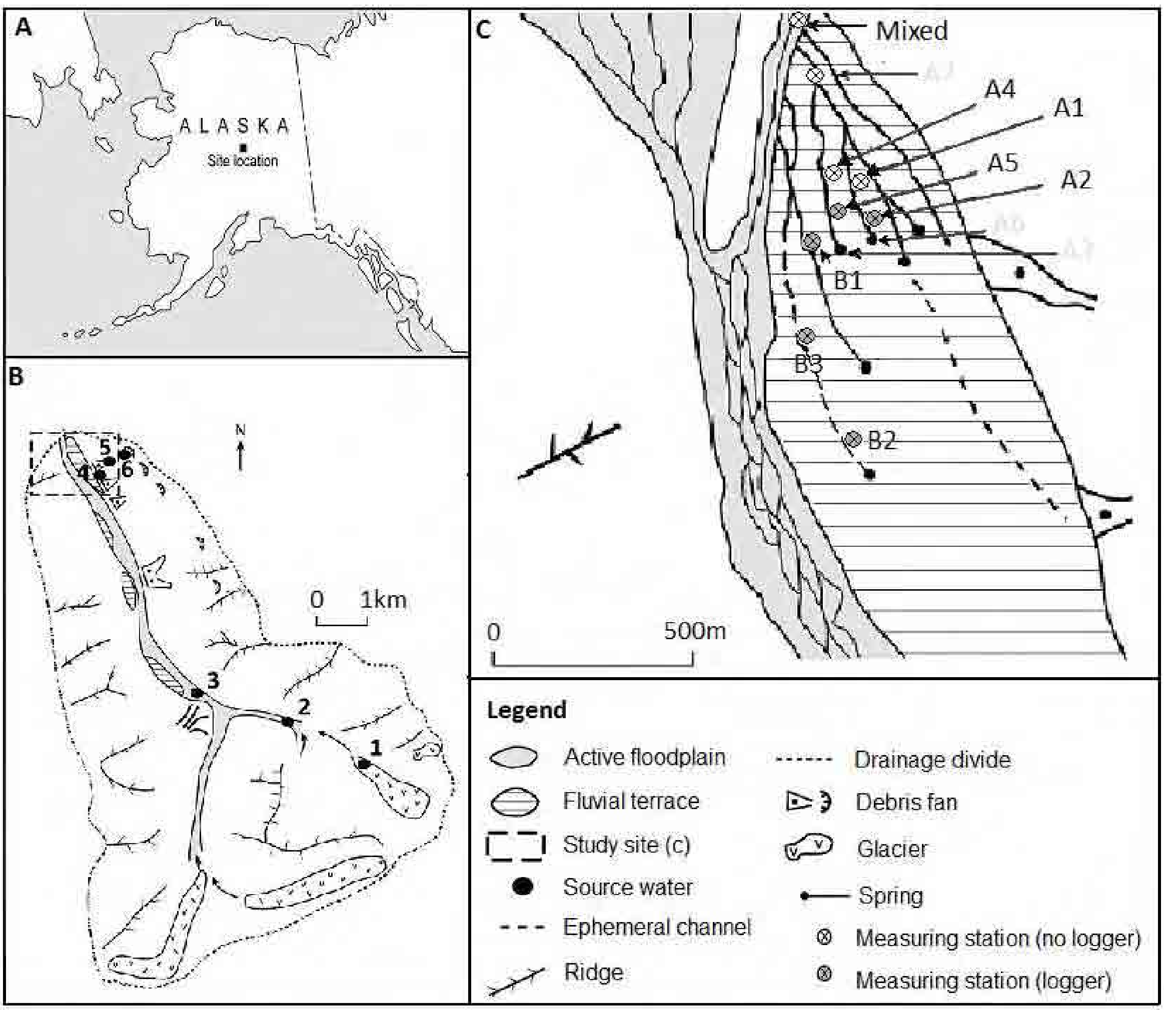

Fig. 23: Study site schematic. A) catchment overview B) sampling sites on groundwater-fed streams C) site location within state of Alaska

Channel cross sections were measured at three week intervals, whereby stream channel dimensions, river depth and flow velocity were measured (at 1/6 depth). Flow duration curves, and hence stream discharge data, were calculated. At each site, substrate size was determined by measuring the b axis of 100 randomly selected stones (Burgherr *et al*., 2002) and D_{50} calculated. The bottom component of the Pfankuch Stability Index (PSI) was determined, incorporating scores for rock angularity, brightness, particle consolidation and size distribution, scouring and deposition, and abundance of aquatic vegetation (Pfankuch, 1975).

Periphyton was collected monthly at each site, from the upper surfaces of four randomly selected stones. The surface was scrubbed with a toothbrush, and biofilm washed into a 24ml polypropylene container. Stone surface area (cm^2) was calculated by tracing the outline of the rock onto an acetate sheet, and weighing from the mass (g) of the tracing (Ledger and Hildrew, 1998). Samples were stored in the dark, and frozen. During analysis 10ml of each sample was freeze dried, and Chlorophyll pigments extracted in 90% acetone for 24 hours. Absorbance was determined using a spectrophotometer, at 750, 664, 647 and 630nm. Concentrations of chlorophyll *a*, *b*, *c* and total chlorophyll were calculated using the Sterman equations (1988), outlined in Ledger *et al* (2006).

Five replicate benthic macroinvertebrate samples were collected monthly at each site, using a Surber sampler (mesh 330µm), and preserved in 90% ethanol. Macroinvertebrates were identified to species wherever practical; Simuliidae, Chironomidae and Isotomidae were identified only to family. Abundance was expressed per m^2. Gut analysis of a predator *Oreogeton* spp (family: Empididae) was carried out, to determine its dominant prey. Organic material collected in the Surber sampler, having been separated from the macroinvertebrates, was dried at 65°C, and sieved into coarse (>1mm) and fine (<1mm) fractions, prior to ashing in a furnace at 540°C for 2 hours. Ash free dry mass was determined by re-weighing, and both fine particulate organic matter (FPOM) and coarse particulate organic matter (CPOM) were calculated (mg/m^2).

Water samples were collected at 14-day intervals at all sites. Additional water sampling was undertaken at higher points in the catchment (Fig. 23B) to investigate specific water sources (e.g. ice-melt, snow-melt, debris fan seepage flow and rainfall). Samples were collected from the centre of the streams, using pre-rinsed Nalgene poly-ethene bottles, filtered through 0.45 µm nylon membrane filters to remove organic matter and suspended sediment, and refrigerated. Samples were then analysed for Cl^- using an Anion Dionex ICS 2000; instrumental precision was 0.25 ppm.

Precise topographical measurements of the study area, including individual sites and river courses, were taken using a LEICA Geo electronic distance measurer (EDM). Relative site elevations were then calculated and interpolated on a 90m x 260m grid, using the Kriging method.

3.2.3 Data analysis

Direction of subsurface water movement was determined by calculating the hydraulic gradient (HG) of each piezometer nest. HG was calculated as the difference between the stream water level and the water level in the 50cm piezometers divided by the vertical distance. A positive gradient indicated that the direction of water movement was vertically upward. Stream rating equations were also derived for each cross section, enabling stream discharge to be estimated (continuously) for each site, for the entire study period.

Diurnal variations in temperature, river stage and river discharge were assessed using an index of variation, similar to that employed by Fowler and Death (2001). The diurnal stage variation index (DSVI) is a measure of the average difference between minimum (S_{min}) and maximum stage values (S_{max}) for every 24 hour period during the study (24 hours was chosen given the strong diurnal variation in flow):

$$DSVI = \sum \left(\frac{S_{\max} - S_{\min}}{n} \right) \qquad 3$$

The same calculation was used to produce a Diurnal Temperature Variation Index (DTVI) and a Diurnal Discharge Variation Index (DDVI).

High concentrations of Cl^- were measured within seepage from a dense matrix, deep within a debris fan (DFS_{deep}). Concentrations within DFS_{deep} were approximately 85 times greater than in samples of snow and glacial meltwater, and therefore Cl^- concentrations were used in a simple groundwater mixing model to determine the proportional contribution of DFS_{deep} seepage from the debris fan, to total flow at each upwelling site.

$$DFS_{deep}\% = \left(\frac{S_u}{S_D} \right) \times 100 \qquad 4$$

Where $DFS_{deep}\%$ is the percentage contribution of water at each site derived from DFS_{deep}, S_u is the concentration of Cl^- at upwelling sites, and S_D the average Cl^- concentration of debris fan seepage.

An integrated hydrological approach was used to investigate interactions between groundwater contributions from specific flow pathways and ecological processes. Accordingly, to determine whether there was a significant relationship between macroinvertebrate community diversity and groundwater flow pathways, the study related flow pathway contributions, determined from the groundwater mixing model, to a measure of macroinvertebrate diversity using Spearman's Rank Correlation. Macroinvertebrate diversity (H) was calculated using Shannon's index of diversity (Shannon, 1949):

$$H = -\sum P_i \ln(P_i) \qquad 5$$

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

To assess the influence of physicochemical variables upon individual taxa, variations in macroinvertebrate data were summarised using detrended correspondence analysis (DCA), and an ordination biplot created by independent correlations of axis 1 and axis 2 sample scores with physicochemical variables. The DCA with independent non-parametric analysis of additional variables was chosen in preference to a detrended canonical correspondence analysis (DCCA), which uses multiple linear regression to directly constrain relationships between sites and samples to the measured variables (Ter Braak, 1986; McCune, 1997), and is suitable for larger datasets. Variables used in the ordination were discharge, DDVI, DSVI, pH, Cl^- concentration, chlorophyll, FPOM, CPOM, HG, sediment particle size, site elevation and PSI. Temperature data (DTVI) were not included in the DCA as this was measured at only five of the seven sites, and was therefore correlated separately with corresponding species data, using Spearman's Rank Correlation.

A Mann-Whitney U test was carried out between macroinvertebrate diversity of ephemeral and perennial streams, and between the diversity of streams in each month. To determine the significance of environmental variables upon individual taxa, the six most dominant taxa (accounting for 96% of the total community abundance) were correlated individually with each variable, using Spearman's Rank correlations. Due to the strong seasonal gradient of macroinvertebrate distribution, determined by the DCA, correlations were calculated separately for each month.

3.3 Results

A significant difference was determined between macroinvertebrate diversity of perennial streams, fed by higher percentage contributions from $DFS_{deep,}$ and ephemeral channels, fed by higher contribution of glacial meltwater seepage ($p<0.01$); this difference was most marked during July and August (Fig.24A). Additionally within perennial streams there was a significant increase in macroinvertebrate diversity in August ($p<0.01$); this was not observed within ephemeral streams, although macroinvertebrate abundance increased (Fig. 24B).

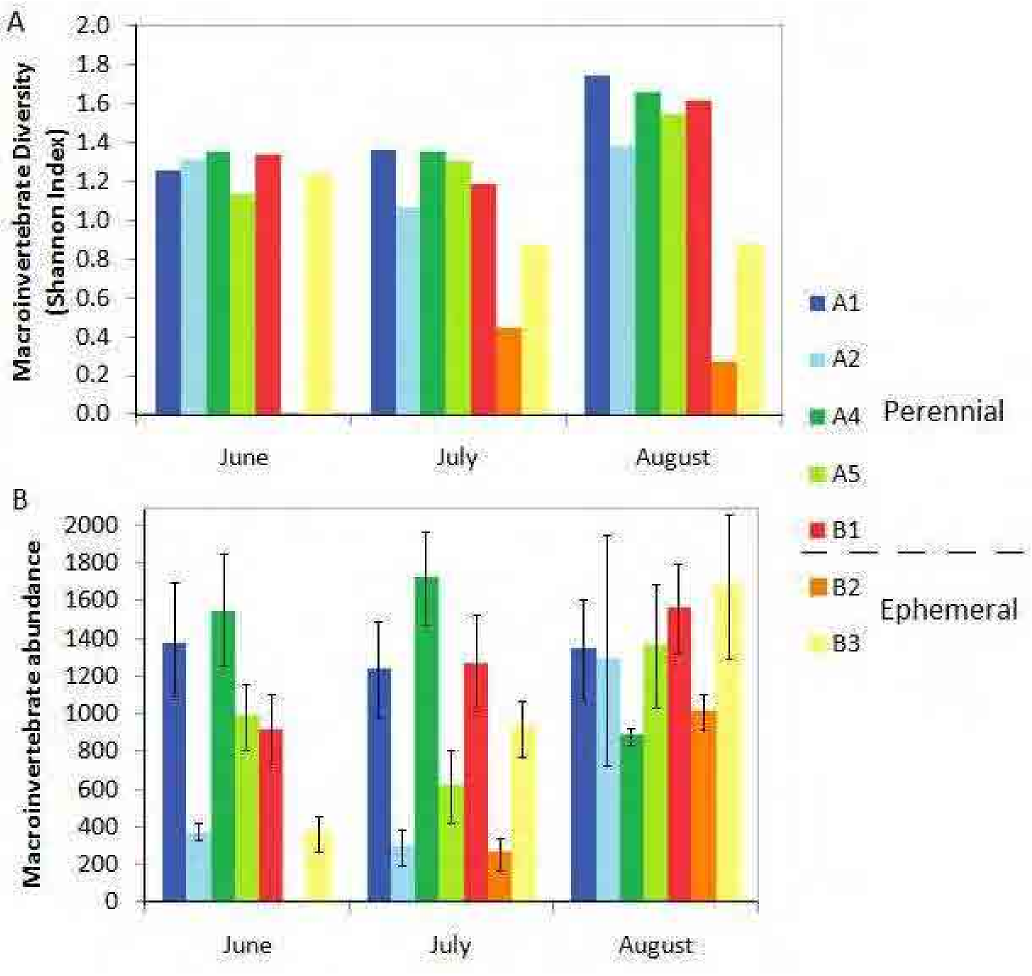

Fig. 24: Seasonal variability in A) the macroinvertebrate diversity within ephemeral and perennial streams B) macroinvertebrate abundance.

During June there was a significant positive correlation between macroinvertebrate abundance and $DFS_{deep}\%$ ($p < 0.05$) (Fig. 25A), between FPOM and $DFS_{deep}\%$ ($p<0.05$) (Fig. 25B), and between macroinvertebrate abundance and FPOM ($p<0.05$) (Fig. 25C). Following increases in organic matter concentrations during July and August across the study site, macroinvertebrate abundance and FPOM were no longer correlated to $DFS_{deep}\%$. However macroinvertebrate abundance continued to be associated with organic matter (FPOM, CPOM and total organic matter, $p<0.05$, Fig. 25 D,E,F).

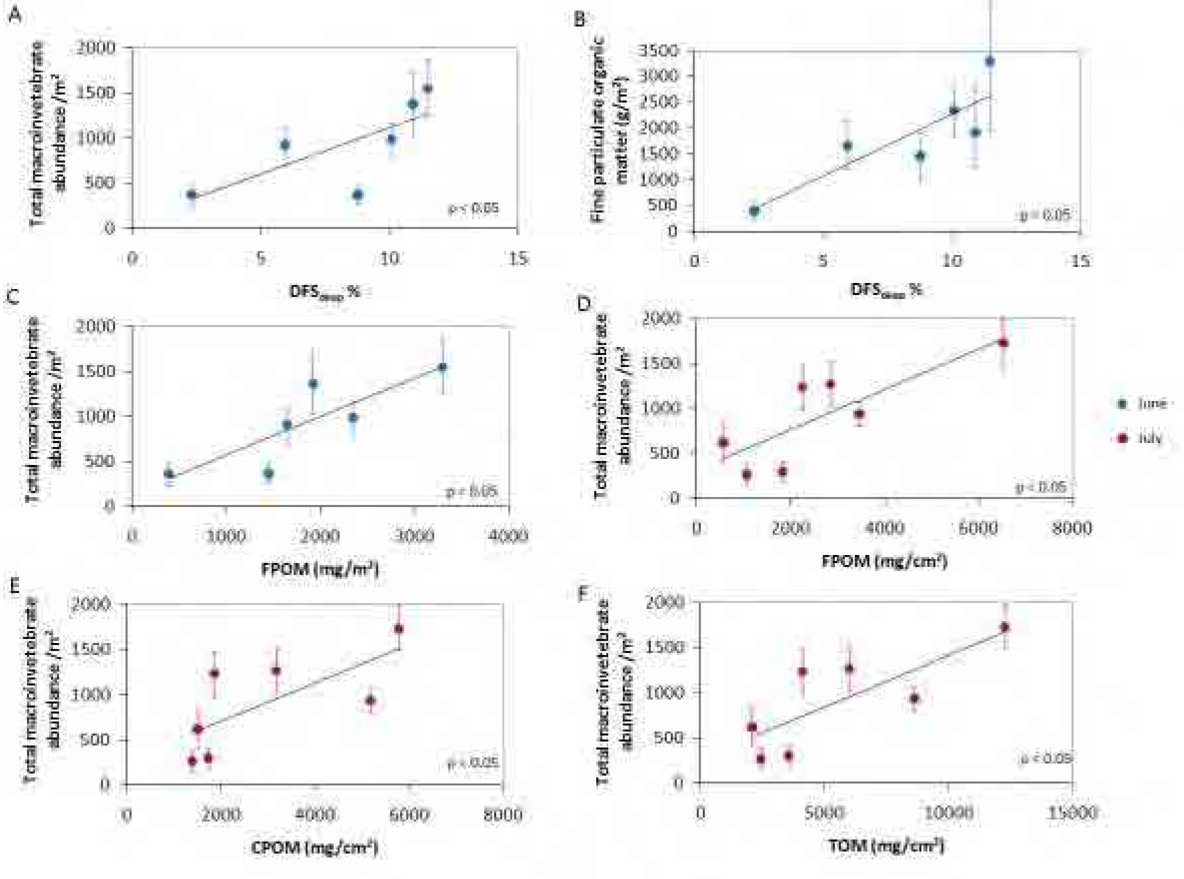

Fig. 25: Spearman's Rank correlation between A) macroinvertebrate abundance and $DFS_{deep}\%$ in June B) FPOM and $DFS_{deep}\%$ in June C) abundance and FPOM in June D) abundance and FPOM in July E) abundance and CPOM in July and F) abundance and total organic matter (TOM) in July

Results demonstrated seasonal variation within each of the seven sites (Fig. 26); sites on axis 1 were positioned primarily according to sample date, and on axis 2 according to site location, with a cumulative percentage variance of 90%. Perennial streams were grouped into 3 monthly clusters from left to right; June and July (similar in macroinvertebrate distribution), and August. Ephemeral streams were grouped into only two clusters; June, and July/August. In both ephemeral and perennial streams a gradient of June through to August was determined, with the high (axis 1) eigenvalue of 0.316 suggesting that this seasonal gradient was particularly strong, accounting for 58% of the variance in taxa distribution.

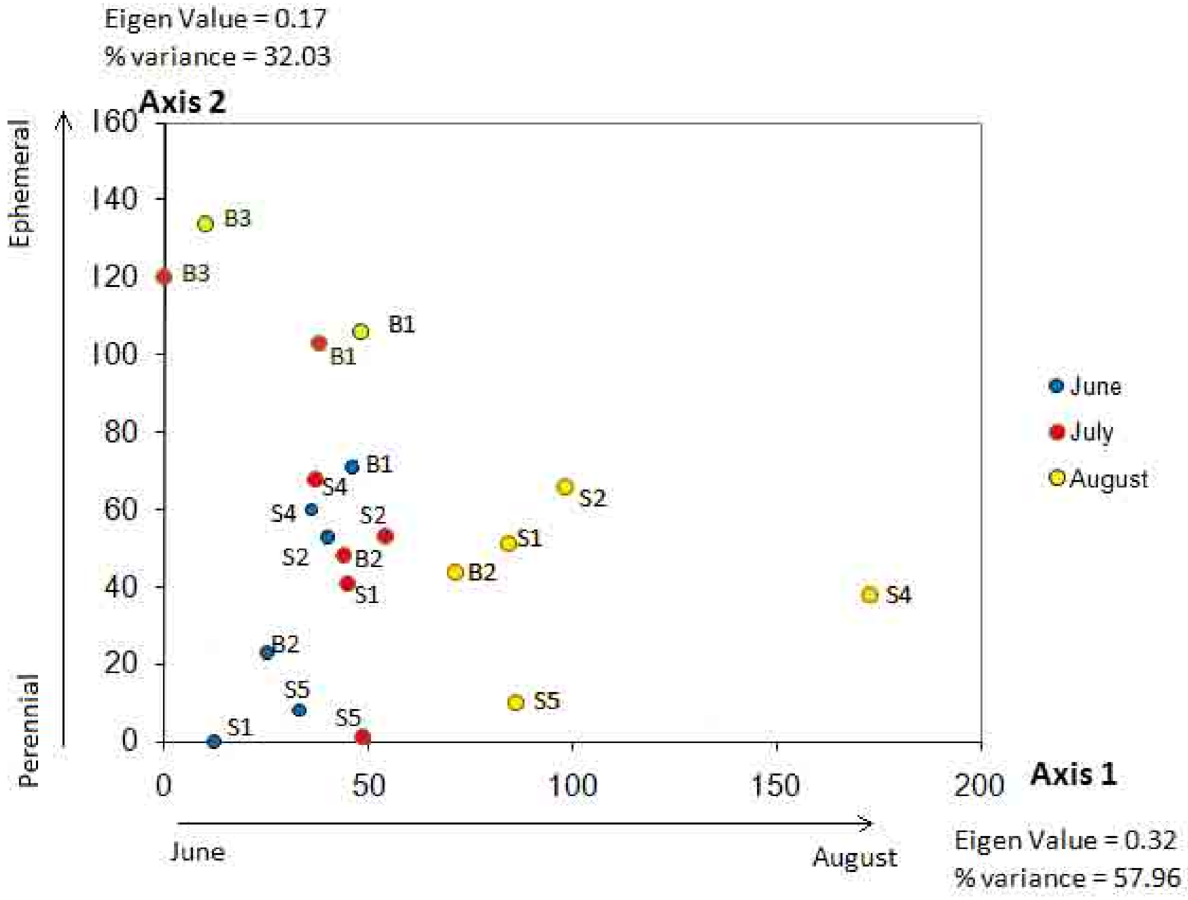

Fig. 26: Detrended correspondence analysis of macroinvertebrate taxa and sample sites, demonstrating strong seasonal gradient om axis 1

The ordination biplot (Fig. 27) indicated that ephemeral streams in June, and perennial streams in June and July were similar in macroinvertebrate composition, supporting a higher abundance of *Baetis tricaudatus, Baetis bicaudatus, Clinocera* spp., *Zapada haysi* and *Alaskaperla ovibovis.* The macroinvertebrate composition of streams differed in subsequent months; ephemeral streams supported a higher abundance of Chironomidae and Isotomidae in the July/August period, whereas perennial streams supported a higher abundance of *Ecclisomyia* spp, *Isoperla petersoni, Plumiperla diversa,* and *Oreogeton* spp. The strong seasonal gradient of axis 1 indicated that variables significantly correlated with this axis influenced taxa on a seasonal basis, while variables correlated more strongly with axis 2 created differences in macroinvertebrate communities between sites (Table 3).

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

Table 3: DCA independent Spearman's Rank correlations of physicochemical variables (** $p < 0.01$; * $p < 0.05$; $^@$ $p < 0.1$)

DFS_{deep}% (positively correlated on axis 1 and negatively on axis 2) therefore varied with the macroinvertebrate community both temporally (increasing in concentration from June to August), and spatially (with greater DFS_{deep}% in perennial than in ephemeral streams). FPOM was correlated in a similar manner, indicating a seasonal increase in concentrations, and a gradient of FPOM concentration between sites which was similar to that of DFS_{deep}%. D_{50} and site elevation (positively correlated on axis 2) varied predominantly between sites; ephemeral streams were situated at higher elevations and were characterised by greater sediment sizes.

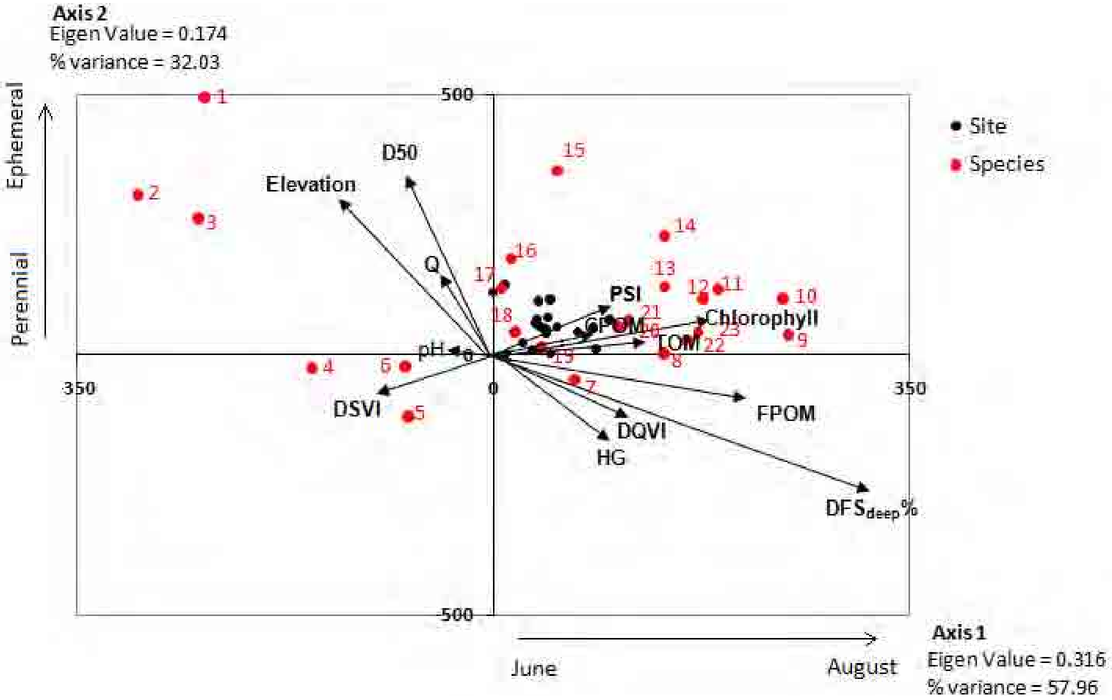

Fig. 27: Ordination biplot of detrended correspondence analysis, with independently correlated physicochemical parameters. Taxa: 1) *Serromyia* spp. 2) *Hexatoma* spp. 3) *Megaleuctra* spp. 4) Oligochaetae spp. a 5) *Baetis bicaudatus* 6) *Chelifera* spp. 7) *Zapada haysi* 8) *Plumiperla diversa* 9) Simuliidae 10) *Ephydra* spp. 11) *Limniphora* spp. 12) *Ecclisomyia* spp. 13) *Pericoma* spp. 14) *Tipula)* 15) Hydrocarnia 16) Isotomidae 17) Chironomidae 18) Oligochaeta spp.b 19) *Alaskaperla ovibovis* 20) *Baetis tricaudatus* 21) *Clinocera* spp. 22) *Oreogeton* spp. 23) *Isoperla petersoni*

Several of the variables demonstrated a degree of autocorrelation which differed between months. In June elevation was significantly negatively correlated with FPOM ($p<0.09$), and with total organic matter (TOM) ($p<0.05$) (Fig. 28A, 28B); and in July was strongly negatively correlated with CPOM ($p<0.09$) (Fig. 28C). Concentrations of autochthonous and allochthonous matter varied throughout the study period. FPOM generally increased in all streams from June to August (Fig. 28D) and chlorophyll increased in August by a magnitude of ~4.5 times (Fig. 28E). CPOM increased by varying degrees from June to August (Fig. 28F), increasing at all sites in July, but only increasing further at sites A5, B2 and B3 in August.

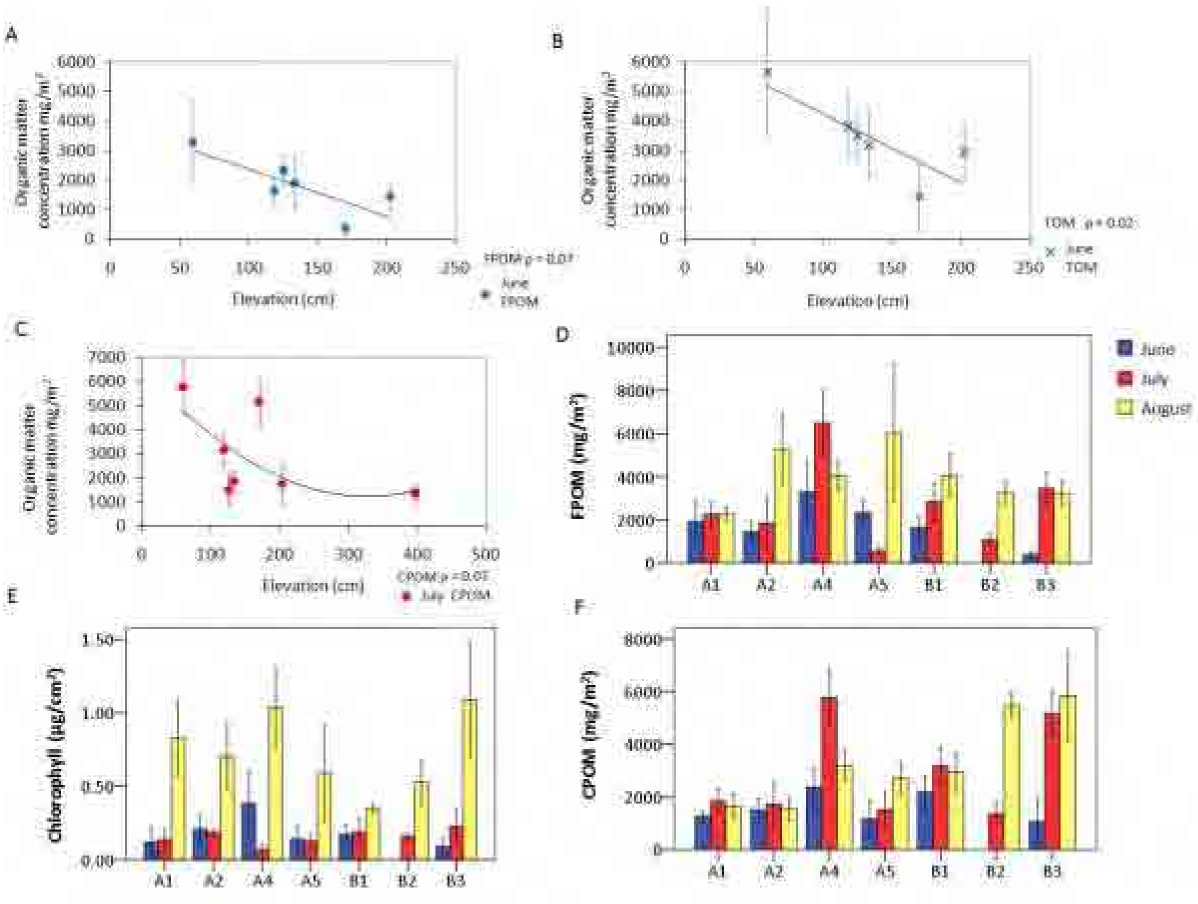

Fig. 28: Seasonal heterogeneity in organic matter distribution in groundwater-fed streams A) correlation between elevation and FPOM in June B) correlation between elevation and TOM in June C) correlation between elevation and CPOM in July D) seasonal increase in FPOM throughout study period E) increase in chlorophyll concentrations in August F) site-specific increases in CPOM

Associations between the six most dominant taxa and physical variables differed throughout the study period and between taxa (Table 4).In June several taxa were directly correlated to groundwater flow pathway (DFS_{deep}%), FPOM and site elevation (*Z. haysi*, Chironomidae, *B. bicaudatus*) (Fig. 29 A, B, C). Simuliidae, found only at site A4 during June, also demonstrated positive correlations with these variables. *Ecclisomyia* spp. however demonstrated a significant correlation with an alternative organic resource (CPOM). Abundance of

Ecclisomyia spp. during June was low (total abundance = 4.8) with taxon collected only at sites A4 and B1 (sites of highest CPOM). The predator *Oreogeton* spp. maintained a significant positive relationship with Chironomidae throughout June and July (≤0.05) (Fig. 29 D, E), and thus was indirectly associated with the food resource of Chironomidae (organic matter). Gut analysis of *Oreogeton* spp. confirmed the presence of Chironomidae.

Taxa	**June**		**July**		**August**	
	Positive	**Negative**	**Positive**	**Negative**	**Positive**	**Negative**
Zapada haysi	DFS_{deep}%*** FPOM***	Pfankuch*** D50***	CPOM$^{\$}$	site elevation ** D50***	pH***	site elevation *** TOM**
Chironomidae	DFS_{deep}%*** FPOM* TPOM***	site elevation**	TOM** CPOM** FPOM**	site elevation**	D50** CPOM** TOM**	DFS_{deep}%$^{\$}$
Ecclisomyia	CPOM** TOM**	site elevation**	CPOM** FPOM** TOM**	site elevation**	Bottom Pfankuch*	-
Oreogeton	Chironomidae ** FPOM***	site elevation$^{\$}$	Chironomidae ** CPOM** FPOM** TOM**	site elevation**		site elevation**
Baetis bicaudatus	DFS_{deep}%*** FPOM*** TOM***	site elevation**	CPOM$^{\$}$	site elevation**	DFS_{deep}%** TOM*** CPOM*** Chlorophyll$^{\$}$	Pfankuch$^{\$}$ D50** Chironomidae **
Simuliidae	DFS_{deep}%$^{\$}$ FPOM$^{\$}$ CPOM**	site elevation$^{\$}$	Site elevation**	-	Site elevation$^{\$}$	Discharge*** CPOM**

Table 4: Spearman's Rank correlations between taxa and physicochemical variables (* p < 0.01; ** p <0.05; *** p ≤0.1; $^{\$}$non linear relationship)

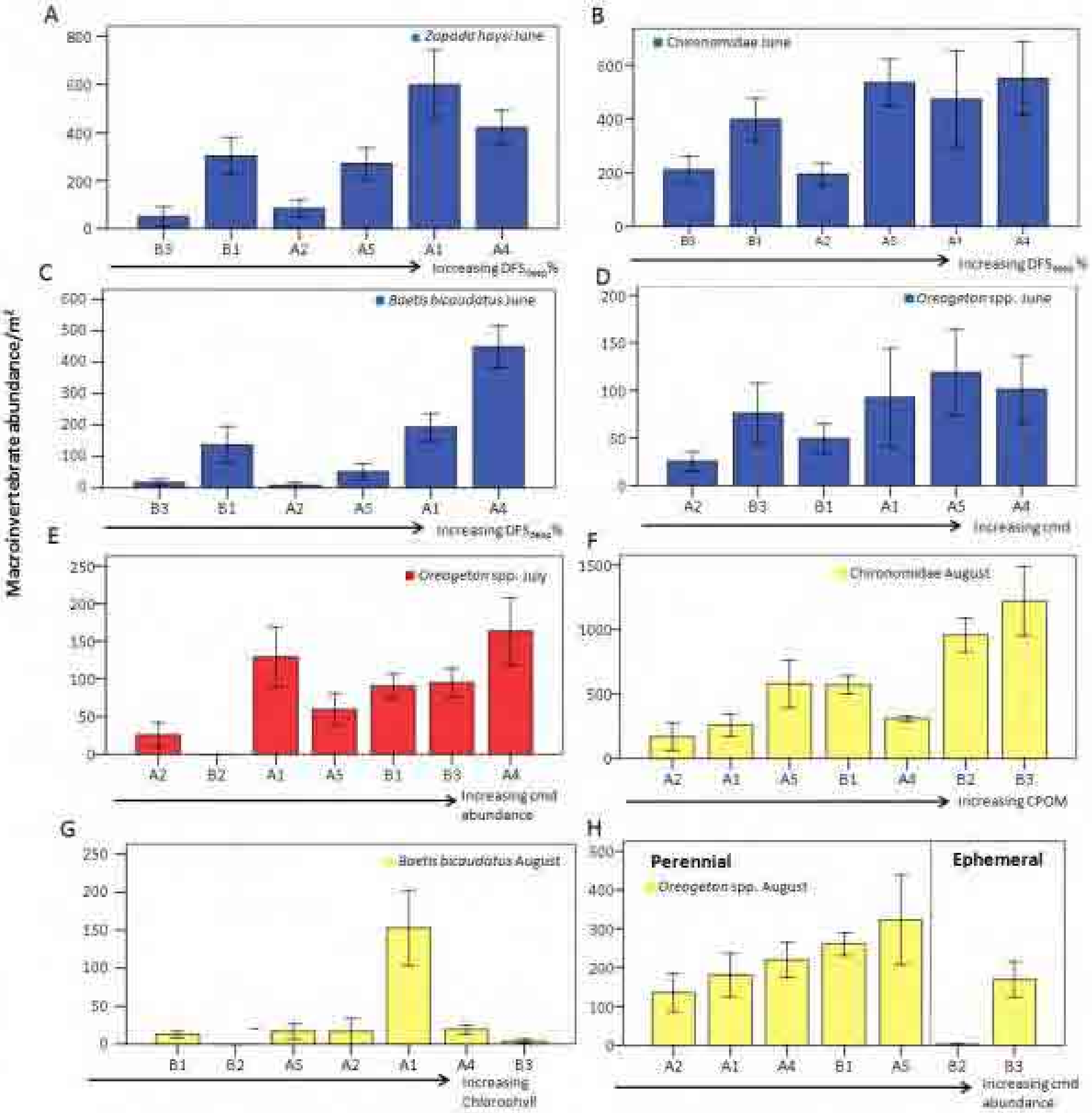

Fig. 29: Seasonal variability in taxa distributions: A, B, C, association in June between Z.*haysi*, Chironomidae and *B. b*ichaudatus with DFS$_{deep}$%; D, E, relationship between *Oreogeton* spp. and Chironomidae in June and July; F, association in August between Chironomidae and CPOM, found in high numbers in ephemeral streams; G, relationships between *B. bicaudatus* and chlorophyll in August; H, association in August between *Oreogeton* with Chironomidae, displaying low distribution in ephemeral streams

In July, despite altered distribution of organic matter concentrations, several taxa continued to demonstrate positive associations with resources (*Z. haysi*, Chironomidae, *B. bicaudatus*, *Ecclisomyia* spp. and *Oreogeton* spp.), predominantly associated with CPOM. Abundance of *Ecclisomyia* had risen markedly throughout July (total abundance = 122) and was now established in four of the seven streams. Despite initially establishing in the site furthest downstream in June, Simuliidae was increasingly found at upstream sites, demonstrating a positive correlation with stream elevation throughout July and August.

Associations between taxa abundance and resources were limited in August, with only Chironomidae and *Baetis bicaudatus* (Fig. 29 F, G) continuing to demonstrate positive correlations The latter also demonstrated strong associations with TOM, chlorophyll, sediment grain size and PSI during this month. However although *Oreogeton* spp. did not maintain significant associations with Chironomidae during this month, strong associations were observed within perennial streams (Fig. 29H). Abundance of *Ecclisomyia* spp., having increased since July, was significantly positively associated with PSI during August, and was now established in all seven streams. No significant relationship was found between macroinvertebrates and stream temperature variability.

3.4 Discussion

This study established the association of local variations in sources and flow pathways of groundwater-fed streams upon macroinvertebrate distributions. Macroinvertebrate diversity and abundance were primarily associated with availability of organic matter, and with water flow pathways (contributions to surface flow from DFS_{deep}). Diversity was associated with duration of active channel flow, reflecting site proximity to the water table, and thus the relative contribution of the perennial DFS_{deep} groundwater seepage. DFS_{deep} seepage was also found to support higher macroinvertebrate abundance during periods of limited resource availability, as this flow pathway likely supplied FPOM to the surface streams. Stability of flow, temperature and also of the stream channel, reflecting local variability in nested routes of groundwater flow (residence time), were less influential. Whilst we recognise that such an observational study demonstrates correlation, and not causation, we to draw upon existing literature to provide plausible explanations for the associations determined.

Significant differences between macroinvertebrate diversity and channel type (ephemeral channels fed almost solely by GMW_{riv} seepage, and perennial streams receiving a greater contribution from DFS_{deep}) may reflect an influence of groundwater flow dynamics upon macroinvertebrate community distribution. Low diversity in ephemeral channels might be attributed to recolonisation constraints; for example the predominant recolonisation mechanism of ephemeral streams available to the univoltine taxa was upstream migration, involving low numbers of individuals (William and Hynes, 1976; Fengolio *et al*., 2002). As a result, high relative abundance of the multivoltine Chironomidae was observed within ephemeral streams, an effective coloniser with drought resistant eggs (Gray, 1981; Williams, 1996).

Diversity in perennial channels increased throughout the season, which can perhaps be attributed to increases in organic matter availability in July and August. Many taxa (e.g. shredders) have phenological adaptations, responding to temporal variations in resource availability (Cummins *et al*., 1989). The absence of *Ecclisomyia* spp. in most streams until this time might therefore reflect the synchronised timing of hatching with leaf litter fall (Cummins *et al*., 1989; Bjelke *et al*., 2005). Diversity in ephemeral streams did not increase, likely reflecting constraints on mid-season colonisation due to the univoltine nature of taxa (Robinson *et al.,* 1992), and distance from the colonising pool of macroinvertebrates within the perennial streams (McCarthur and Barnes, 1985; Fritz and Dodds, 2005). Moreover, increased relative abundance of Chironomidae within ephemeral sites during these months may reflect aggregation of the taxon upon resources, coupled with limited competition.

The strong positive relationship between DFS_{deep}% and FPOM in June potentially indicates that organic matter is supplied to the streams by groundwater seepage through the debris fan, situated upon the valley-sides. The transport of particulate matter within subsurface environments, in addition to that of dissolved matter, has been widely recognised (McDowell-Bower et al., 1986). Entrainment of organic matter by throughflow, within the heavily vegetated, deeper soils of the valley-sides (Boisser and Fontvielle, 1995), may increase the organic matter content of DFS_{deep} waters. This flow pathway may therefore provide a valuable resource of FPOM during periods of low alternative organic matter availability. As positive associations between organic matter and macroinvertebrate communities typically indicate community aggregation upon resources (Richardson, 1991; Dobson and Hildrew, 1992), the results suggest that in June macroinvertebrates aggregated upon sites of greater DFS_{deep} discharge, which supplied FPOM resources to stream flow.

Groundwater is potentially an important resource for benthic systems otherwise deprived of allochthonous and autochthonous vegetation for much of the year (Zah *et al*., 2001). The alteration in macroinvertebrate association from flow pathways and associated FPOM in June, to CPOM in July, might be explained by increases in organic matter concentrations from alternative sources in later months. Allochthonous and autochthonous inputs increase as streamside vegetation becomes established, leaf litter falls (Cowan and Oswood, 1984), and subsequently streamside shading is reduced (Rosemond *et al*., 2000; Hill *et al*., 2001). DFS_{deep} ceased to be the predominant supplier of FPOM, following the increased availability of organic matter resources in later months. Dependence upon the flow pathway for organic matter supplies was reduced and accordingly the relationship between macroinvertebrate abundance and DFS_{deep} weakened. The continual association between macroinvertebrates and organic matter (FPOM, CPOM and total organic matter) throughout July, despite lack of correlation with DFS_{deep}%, might indicate that macroinvertebrates demonstrated resource tracking – the temporal covariance in redistribution of organic matter and macroinvertebrates (Rowe and Richardson, 2001; Melody and Richardson, 2004; Tiegs *et al.*, 2008).

3.4.1 Variables influencing the macroinvertebrate community

In addition to temporal and spatial variability in organic resources, several variables influenced macroinvertebrate community distribution. The positive relationship between sediment size (D_{50}) and macroinvertebrate abundance might be attributed to refugia provided by larger substrates (Hart and Finelli, 1999) both in the hydrodynamic dead zone (Reynolds *et al.*, 1991) and in the larger interstitial pore spaces (Davy-Bowker *et al.*, 2006). These pore spaces entrain greater quantities of organic matter (Downes *et al.*, 2000), and are likely to facilitate macroinvertebrate movement between the surface and the hyporheic zone in search of food or refugia. Larger substrates also increase surface area for colonisation and foraging (Ellner *et al.*, 2001).

The significant relationship between macroinvertebrate abundance and site elevation, a proxy for distance downstream, was attributed to the accumulation of organic matter within stream channel systems; sites situated at lower elevations were located in down-valley areas of the terrace, and received FPOM not only directly from upwelling groundwater, but also from dead or decaying macroinvertebrates, leaf litter reworked into FPOM, and streamflow transportation from upstream sites of groundwater upwellings. In addition to direct inputs of CPOM from adjacent streamside vegetation, these sites may also receive portions of that CPOM from upstream which decomposes at a slower rate (Cushing *et al.,* 1993) as shredders demonstrate a selective preference for highly microbially colonised leaf matter (Cummins and Klug, 1979). The strong relationships observed between CPOM, site elevation and macroinvertebrate abundance during July may therefore reflect increased CPOM quantities with establishment of streamside vegetation. This association further demonstrated the influence of resource distribution upon the macroinvertebrate community.

Active drift was likely the dominant mechanism of resource tracking by which macroinvertebrates within the groundwater-fed streams were associated with organic matter, as observed by Richardson (1991) and Rowe and Richardson (2001). However, this is a taxa-specific process, being dependent upon taxa mobility, diet and instar stage (e.g. nutritional requirements), therefore monthly inter-specific interactions should be considered.

3.4.2 Variables influencing individual taxa

Relationships observed between abundance of individual taxa and resource availability throughout June and July support the suggestion that taxa within this stream network aggregate upon resource patches (Dobson and Hildrew, 1992; Richardson, 1991). The maintenance of associations between individual taxa and resources (FPOM in June, and CPOM in July and August) despite alterations in resource distribution over time, is again suggestive of resource tracking (Rowe and Richardson, 2001). Weaker correlations between some taxa and organic matter in August might be indicative of reduced resource limitations following leaf fall.

Positive correlations between the abundance of *Z. haysi,* Chironomidae, *B. bicaudatus* and Simuliidae and organic resources ($DFS_{deep}\%$, FPOM and site elevation) during June might indicate resource aggregation, highlighting relationships between flow pathway contributions, FPOM, and downstream concentration processes. The significant correlation of *Ecclisomyia* spp. with CPOM also demonstrates aggregation at resources; as a facultative grazer, *Ecclisomyia* spp. may consume CPOM during resource scarcity (Zhang *et al*., 2003). In addition, the low abundance of this taxon may indicate a phenological adaptation; hatching is delayed until later months, when resource availability is greater (Cummins *et al*., 1989). Finally, the positive association of *Oreogeton* spp. with Chironomidae indicates possible predation by *Oreogeton* spp., supported by gut analysis. Similar findings were recorded by Parker and Huryn (2006) in an arctic mountain stream.

Throughout July the continuation of associations with resources (CPOM) of *Z. haysi*, *B. bicaudatus*, Chironomidae, *Ecclisomyia* spp. and *Oreogeton* spp., at downstream sites, might suggest further resource aggregation, and hence resource tracking. Changes from associations of several taxa from FPOM in June to CPOM in July may be related to dependence of earlier instars upon finer materials (Oliver, 1971; Richardson, 1992), or upon increased availability of CPOM during this month. Simuliidae however did not aggregate at sites of higher resources in July; abundances during this month were greater at upstream sites, irrespective of resource availability. Lower abundance downstream could be related to competition with *Z. haysi*. Alternatively *Oreogeton* spp., known predators of Simuliidae (Bay, 1974; Werner and Pont, 2003) were predominantly located downstream, and may control population numbers (Sommerman, 1962). Simuliidae remained at upstream sites in August, supporting indications that they developed favourably upstream where competition and predation stressors were potentially lower.

In August, following further increases in CPOM at some sites, and availability of additional food types, associations with resources were increasingly taxa-specific, likely reflecting individual traits. The lack of association between *Z. haysi* and CPOM may indicate that resource supplies for this taxon were greater than population densities at several sites. As taxa aggregation occurs predominantly in resource depleted environments (Tiegs *et al.,* 2008), increased availability of CPOM at some sites may reduce associations between taxa and resources, as resource 'islands' (Webster and Waide, 1982; Benfield *et al.,* 2001) become less isolated. Alternatively, alterations in associations could reflect resource quality, as this may also influence macroinvertebrate distribution (Eggert and Wallace, 2003). Shredders in particular preferentially consume detritus highly colonised with microbial matter (Anderson and Sedell, 1979). Less limited by resource availability in August, *Z. haysi* may have aggregated in areas of higher resource quality. Associations have been made between stream acidity and reduced shredder abundance, reflecting limited microbial activity at lower pH, which reduces detritus quality (Mulholland *et al*., 1992). The positive associations observed between *Z. haysi* abundance and pH during August might therefore indicate more selective resource tracking of higher quality organic matter.

Unlike *Z. haysi,* Chironomidae maintained a positive association within CPOM in August, indicative of continual resource tracking throughout the study period. As active drift is a recognised behavioural trait of this family (Oliver, 1971), it is likely that this is the dominant mechanism involved. The degree to which macroinvertebrates use emigration to avoid food limitation, and to compete for access to resources is taxa-specific (Rowe and Richardson, 2001); this may explain the persistence of *Z. haysi* at downstream sites despite relocation of Chironomidae. It is possible that due to higher population densities, Chironomidae remained closer to a resource/density threshold, and therefore continued to demonstrate active drift. Higher abundance at ephemeral sites reflect enhanced colonisation capabilities, attributed to physiological and behavioural traits. These include drought resistant eggs (Gray, 1981; Williams, 1996) which enable Chironomidae to rapidly colonise channels following flow initiation. Activation of eggs by progressive initiation of stream-flow upstream of sites (Williams and Hynes, 1976$_a$) may enable a continual downstream influx of Chironomidae, sustaining active drift in ephemeral streams.

Oreogeton spp. maintained associations with Chironomidae in all perennial streams; however colonisation of ephemeral streams was limited, despite significant increases in prey at these sites. This is likely due to the need for long distance upstream migration; colonisation of ephemeral streams is predominantly dependent upon upstream migration from perennial sites, and numbers involved are low (William and Hynes, 1976; Fengolio *et al.*, 2002). Although sites B2 and B3 offered optimum habitat conditions, colonisation limitations may have restricted macroinvertebrate distribution (Fonseca and Hart, 2001).

In addition to maintaining associations with CPOM in August, *B. bicaudatus* were associated with periphyton. This taxon may adapt its diet to suit resource availability (Brown, 1961; Mihuc and Minshall, 1995). Weaker associations between taxa distribution and resources in August may be due to the availability of multiple food sources. Alternatively as *B. bicaudatus* cease food consumption immediately prior to emergence (Moore, 1977), alterations in distributions and weak relationships might be partially explained by differences in larval stages and associated nutritional requirements.

The correlation of *Ecclisomyia* spp. with Pfankuch stability in August may reflect instar stage. Several species of later instars of cased caddis, including *Ecclisomyia* spp., have demonstrated a propensity to move between the benthic and hyporheic zone (Wright-Stow *et al.,* 2006) to collect well conditioned CPOM, which more mature larvae are better able to consume (Winterbourn and Wright-Stow, 2003). Later instar *Ecclisomyia* spp. may therefore assemble in sites of higher disturbance, where increased sediment porosity facilitates movement between zones (Brunke and Gonser, 1997). As *Ecclisomyia* spp. typically hatch in late summer, populations during June and July were likely to have been predominantly early instars, remaining at the surface, utilising benthic resources. In August however, a more mature population of *Ecclisomyia* spp. potentially relocated to areas of greater porosity, optimising resource availability.

Associations between flow pathway variability and both macroinvertebrate abundance and diversity might suggest that groundwater flows influence macroinvertebrate communities, Distinct temporally and spatially dynamic variability of groundwater flow pathways were associated with the physicochemical variables of recipient streams and with macroinvertebrate communities in a more complex manner than previously established. Variability in temperature and flow, and channel stability, reflecting local routes of groundwater flow, were less significantly associated with the benthic community.

3.5.Conclusion

These results suggest that the availability of organic matter appears to be the varaiable most strongly associated with benthic macroinvertebrate distribution in groundwater-fed streams in the Toklat catchment. Given the strong dependence of macroinvertebrates upon organic matter established in the literature, the results might indicate that organic matter distribution influenced macroinvertebrate communities. The degree to which groundwater flow pathways were associated with the macroinvertebrate community varied spatially, temporally and between taxa. Results indicate that during June, FPOM was predominantly supplied by the DFS_{deep} flow pathway, a resource upon which several taxa aggregated. However, as alternative supplies of organic matter became available, in greater concentrations, correlations were observed between these same taxa, CPOM and distance downstream, likely demonstrating the use of resource tracking to associate with sites of higher resource concentration downstream. Distribution was no longer related to DFS_{deep}%, likely as this flow pathway ceased to be the predominant source of organic matter to the groundwater-fed streams. A delicate seasonal balance in subarctic systems between resource depletion and surplus was observed. Due to the barriers to many taxa in colonising ephemeral streams in large numbers, differences in diversity between ephemeral and perennial groundwater-fed streams were observed, and many taxa could not track resources within ephemeral sites.

In conclusion positive correlations between both macroinvertebrate abundance and individual taxa with contributions from DFS_{deep} seepage indicated that groundwater flow pathways may be a key driving factor of macroinvertebrate communities in groundwater-fed streams. The strength of this relationship was dependent upon taxa-specific traits, and occurred primarily in locations or during seasons where alternative allochthonous resources were scarce. However, following increases in organic matter availability only perennial streams, fed by higher DFS_{deep} contributions, could support associated increases in macroinvertebrate diversity. Studies into macroinvertebrate ecology in streams receiving flow from groundwater within arctic and alpine environments, should therefore consider groundwater as a spatially and temporally dynamic influential factor.

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4. INFLUENCE OF ENVIRONMENTAL STABILITY OF GROUNDWATER-FED STREAMS ON HYPORHEIC FAUNA, ON A GLACIAL FLOODPLAIN, DENALI NATIONAL PARK, ALASKA

The influence upon hyporheic macroinvertebrates of differences in environmental stability, reflecting local variability in groundwater residence time, was investigated at depths of 15cm and 30cm, within groundwater-fed streams in an Alaskan glacierised floodplain. Surface-water temperature, streamflow, stream bed stability and sediment size were measured in summer 2008, and combined into a multivariate index of environmental stability. The hydraulic gradient, pH, organic matter availability and water chemistry were also measured to characterise local variability between groundwater-fed streams. Hyporheic macroinvertebrate diversity was significantly positively correlated to the multivariate index of environmental stability, with reductions in diversity at the surface; this is potentially indicative of greater macroinvertebrate use of the hyporheic zone at less stable sites. Two uses of the hyporheic zone were identified. Firstly, a refugia response was indicated by contrasting surface and hyporheic distribution patterns of several taxa, correlated with several environmental variables. These included variability in water temperature and channel stage, stream bed stability and availability of organic matter. Secondly, covariance in surface and hyporheic distribution of some taxa dependent upon stream bed stability and resource availability suggested the use of the hyporheic zone as an extension of the benthic habitat. Local differences in groundwater residence time between groundwater-fed streams created sufficient environmental instability in some streams to elicit a macroinvertebrate response.

4.1 Introduction

The use of the hyporheic zone as a refuge by macroinvertebrates has been predominantly investigated in relation to discrete disturbance events, such as floods, spates and droughts (Palmer et al. 1992; Cooling and Boulton, 1993; Dole-Oliver et al. 1997; Matthaei et al. 1999). However there is a paucity of information regarding the association between macroinvertebrates and the frequency of disturbance events, or ‘environmental stability’ (Dole-Olivier, 1997), which is characterised by flow and temperature regimes and measures of river channel stability (Fowler and Death, 2001; Death and Winterbourn, 1994). Limited research in this area has established that macroinvertebrates may demonstrate a refugia response to variability in environmental stability (Death and Winterbourn, 1995; Fowler and Death, 2001). Local differences in environmental stability might be found between groundwater-fed streams, reflecting differences in water sources, flow pathways, and groundwater residence time (Ward et al. 1999). However it has not been established whether the degree of local variability in environmental conditions observed between groundwater-fed streams is of sufficient magnitude or frequency to constitute a disturbance, and therefore to influence distribution within the hyporheic zone.

Spatial and temporal variations in the physicochemistry of groundwater-fed streams may arise both from differences within and between flow pathways. First, streams may receive groundwater flow from different sources which have followed distinct flow pathways. In glacierised catchments, the characteristics of groundwater-fed stream flow may be influenced by subsurface seepage from the main glacial channel (Malard et al. 2000), with contributions increasing seasonally with glacial ablation (Collins, 2002), or from valley side seepage. Temporal variability in physicochemical characteristics may result from seasonal transitions from snow-melt to rain-fed catchments (Theakstone, 2003). Second, physicochemistry might also be influenced by conditions that vary within a single flow pathway, such as groundwater residence time (Brunke and Gonser, 1997). Both valley-bottom and valley-side deposits are typically heterogeneous, characterised by a series of locally variable hydrogeologic facies (Robinson et al. 2008). Water within these facies may therefore follow several alternative routes of flow (Fig. 2), which differ in groundwater residence time, reflecting the permeability and connectivity of the sedimentary facies (Robinson et al. 2008; Ward et al. 2002). Attenuation of daily flow and temperature maxima may occur, whereby in areas of lower sediment porosity the amplitude of diurnal temperature and discharge variability becomes progressively reduced and out of phase with that demonstrated by the source (e.g. Hoehn and Cirpka, 2006). This attenuation might occur to different degrees within different routes of flow, reflecting the variability in groundwater residence time, and length of flow pathway (Brunke and Gonser, 1997). Flow attenuation may affect not only temperature and stage variability (Brunke and Gonser, 1997), but also substrate stability, bed load transport, bed sediments and associated benthic communities (Milner et al. 2001).

Macroinvertebrates are particularly sensitive to environmental variables including water temperature (Hynes, 1970; Milner and Petts, 1994), flow velocity (Edington, 1968; James et al. 2008), dissolved oxygen (Nebeker, 1972; Connolly et al. 2004), stream bed porosity (Olsen and Townsend, 2003), organic matter abundance (Anderson and Sedell, 1979; Lepori and Malmqvist, 2007) and the variability of these factors over time (Hax and Golladay, 1998). As the hyporheic zone, an extensive transition zone situated between the groundwater and surface water habitat, is a stable area typically only affected by high discharge events

(Matthaei et al. 1999) and generally well developed in permeable glacierised floodplains (Battin et al. 2003), it may provide refuge for macroinvertebrates from in-stream disturbance. To seek refuge however several conditions must be fulfilled; macroinvertebrates must be sufficiently stressed (James et al. 2008), i.e the disturbance must be of sufficient magnitude to alter surface conditions to a degree requiring macroinvertebrate relocation (James et al. 2008; Olsen and Townsend, 2005; Del Rosario and Resh, 2000). Additionally relocation will only occur where interstitial space, food availability and several other physicochemical variables permit (Williams. 1984). Thus macroinvertebrate responses to instability may be specific to individual taxa (Palmer et al. 1995), and be dependent upon their individual traits e.g. temperature tolerance, feeding habits and mode of movement (Usseglio-Polatera *et al*., 2000).

The influence of variability in environmental conditions of groundwater-fed streams on macroinvertebrate communities has yet to be considered in detail. In particular, it is unclear whether local variability in flow dynamics can create disturbance of sufficient frequency and magnitude to elicit macroinvertebrate relocation, and thus whether groundwater-fed streams, subject to different degrees of environmental variability, will display marked differences in hyporheic fauna. Accordingly, in this paper we use a multivariate index of environmental stability (a combination of several surface environmental variables) in addition to a range of physicochemical variables, to determine the influence of local differences in environmental stability between groundwater-fed streams on hyporheic macroinvertebrate diversity and distribution, in a glacierised catchment in Denali National Park, Alaska. The objectives of the study were:

1. to determine the local variability in environmental stability, and in additional physicochemical variables between groundwater-fed streams;
2. to establish the extent to which environmental stability (or additional physicochemical variables) of groundwater-fed streams influences macroinvertebrate distribution within the hyporheic zone; and
3. to ascertain how ecological traits of individual taxa might determine different uses of the hyporheic zone.

4.2 Methodology

4.2.1 Field site

Areas of groundwater upwelling were studied across the floodplain of a section of the middle fork of the Toklat River in Denali National Park, Alaska (63°29’19.54”N, 149°57’54.05”W) (Fig. 30A), at a point ~12km from its source, where the valley bottom is 1300 m wide (Fig. 30B). The site was selected for the study of the influence of varying environmental stability upon macroinvertebrates within the hyporheic zone, due to the extensive network of groundwater-fed streams (Fig. 30C), and the proximity of the terrace to several water sources (snow-melt, glacial ice-melt and rainfall), likely to influence stream hydrology and physicochemistry.

The Toklat is an extensively braided north flowing tributary of the Yukon River.Total monthly precipitation was 162mm, and in winter was 116mm, while mean daily temperatures recorded throughout the study period at the Toklat Road Camp (5 km to the north) were 11.8°C (day) and 4.7°C (night) (WRCC, 2008). A significant proportion of river flow was derived from ice- and snow-melt from a number of small valley glaciers upstream. The area of the upstream catchment is ~115km^2 with elevations ranging from 1835m to the south, to 1197m in the valley-bottom, with the interfluves ranging in height from 1350m to 1319m to the east and west respectively. The study site comprised a fluvial terrace, 0.9km^2 in area, on the eastern side of the valley. The surface of the terrace, at its downstream extent, lies approximately 1m above the current floodplain. A series of 10 - 15 groundwater springs emerge, in most cases from clearly defined springheads, and flow across the down-valley (northern) margin of the terrace, before joining the Toklat River downstream.

The underlying geology comprises Devonian and Silurian clastic and carbonate rocks in the north of the catchment, with Triassic calcareous sedimentary and submarine basalt, and Paleocene volcanic units (Wilson et al., 1998) along vegetation-covered valley sides, upon which are situated several debris fans and talus cones. The valley-bottom consists of glacial, fluvial and colluvial deposits.

4.2.2 Data collection

The main study period extended from July 24thth to September 4th 2008, during which time seven streams, fed solely by groundwater discharge, were studied across the fluvial terrace. Surface and hyporheic measurements of physicochemical variables were taken. Hyporheic water levels were monitored twice daily, at piezometer nests installed at the locations indicated in Fig. 30C (sites A1, A2, A4, A5, B1, B2 and B3). Each nest comprised two piezometers (5cm outer diameter, 0.4cm holes drilled over basal 6cm) installed to depths of 0.5 and 1m below the surface using an installation system described by Baxter *et al.,* (2003).

On five occasions surface water velocities were determined at 10cm intervals across each groundwater-fed stream at points adjacent to each piezometer nest. In-stream water temperature and water pressure was recorded automatically at the 7 sites using data loggers with pressure transducers and temperature loggers (Appendix B). Temperatures were also monitored continuously at a depth of 20cm (A2 and B1) and 50cm (B3). Throughout June 2008 to June 2009, Gemini Tinytag Plus recorders monitored in-stream temperatures at selected sites. These data were used to determine stream flow permanence.

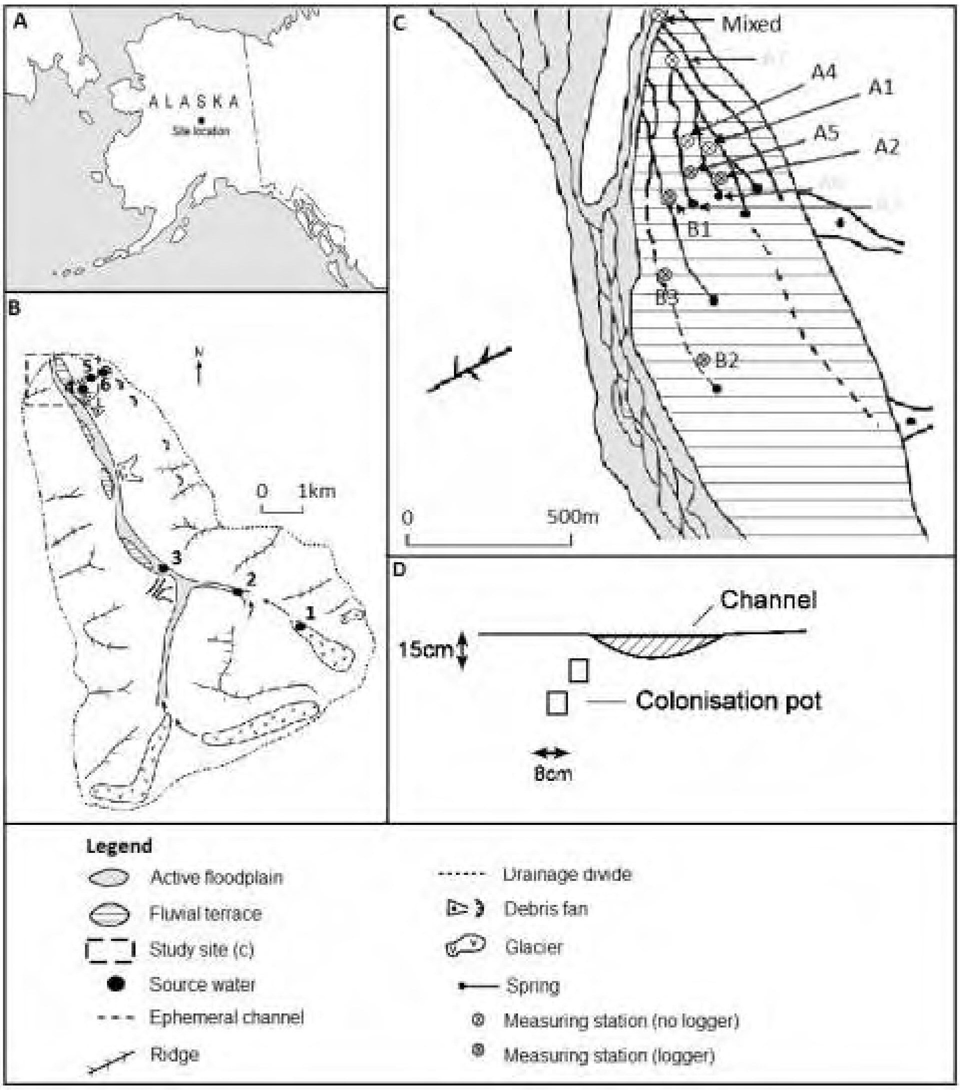


Fig. 30: Schematic of field site location and sampling sites A. Toklat catchment B. Sampling sites C. Colonisation pot distribution within hyporheic zone D. Site location within State of Alaska

Colonisation pots, comprising cylindrical steel cages (15cm in height, 8cm diameter, mesh size 1cm^2), were inserted into the river bed at adjacent points to depths of 15 & 30cm below the surface at five sites, A1, A4, B1, B2 and B3 (Fig. 30D). Individual pots were used to prevent macroinvertebrate movement between depths during extraction. Holes were excavated by hand to the appropriate depth, and each colonisation pot was packed with sediment in stratigraphic order. The process of inserting the colonisation pots was problematic due to the coarse substrate (small to medium cobbles overlying coarse gravel). Given the installation time, and the narrow channel width, only one pair of pots could be installed per site. In our study, a tarpaulin bag with reinforced top and cable was placed around the base of each pot (to facilitate subsequent removal) before inserting the pot in the excavated hole. Remaining substrate was placed around pot margins and over the top, whilst ensuring that the cable extended to the surface. Colonisation pots were then left *in-situ* for six weeks to enable macroinvertebrate colonisation.

During extraction the cable was pulled vertically, driving the wire-reinforced tops to the surface and extending the tarpaulin bags. This minimised macroinvertebrate loss. Sediment was placed in bags with 90% ethanol and subsequently rinsed and filtered through 0.65 µm mesh. Due to the quantity of fine sediment, some macroinvertebrates were poorly preserved and thus only identified to family level. Hence all macroinvertebrates were grouped to family level to determine diversity.

At the end of the study period, five replicate benthic macroinvertebrates samples were collected at all sites using a Surber sampler (350 µm mesh), and preserved in 90% ethanol. These provided reference samples of the surface benthos (Fowler, 2002). Surface abundances were calculated as a mean of the 5 replicates. Although the mesh of the Surber samples, compared with the waterproof tarpaulin used in the colonisation pots, may lead to underestimation of smaller taxa within surface samples, this study compared macroinvertebrate distribution between sites at the surface to distribution between sites within the hyporheic zone; direct comparisons of abundance between surface and hyporheic sites are not made. The difference in sampling methodology did not therefore influence the conclusions. Organic material collected in the Surber sampler, having been separated from the macroinvertebrates, was dried at 65°C, and sieved into coarse (>1mm) and fine (<1mm) fractions, prior to ashing in a furnace at 540°C for 2 hours. Ash free dry mass was determined by re-weighing, and both fine particulate organic matter (FPOM) and coarse particulate organic matter (CPOM) were calculated (mg/m^2).

Colonisation pots and Surber sampling sites were located within 2m of temperature and pressure sensors, except at A1 and A4, where representative water pressure and temperature data were taken from measurements at A2 and A5 respectively. These sites were within ~ 4m of each pot (Fig.30C). Temperature and river stage data from these loggers are referred to as sites A1 and A4, to correspond with colonisation pot samples. Surface pH was measured twice using a Myron meter during the six week period. The bottom component of the Pfankuch Stability Index (PSI) (Pfankuch, 1975) was also evaluated at the conclusion of macroinvertebrate data collection. This involved summing scores assigned to rock angularity and brightness, particle consolidation and size distribution, scouring and deposition, and abundance of aquatic vegetation. It was thought that the bottom component of the index would have the greatest relevance to the benthic community (Death and Winterbourn, 1994). Substrate size was determined at each site at this time, by measuring the b axis of 100 randomly selected stones (Burgherr *et al.,* 2002), and the D_{50} was subsequently calculated. Macroscale Channel Stability (MSS) was also measured and calculated at each site. MSS is a dimensionless measure of the total width of wetted channel, measured at three points over a 15m reach (W1, W2 and W3) divided by the total active channel width, taken at the same three locations (V1, V2 and V3) (Snook and Milner, 2001):

$$\mathrm{MSS} = \frac{(W1/V1)\ (W2/V2)\ (W3/V3)}{3} \tag{6}$$

Surface-water samples were collected at 14-day intervals at all upwelling sites, supplemented by extensive water sampling throughout the catchment, to characterise sources of subsurface flow (including samples of glacial meltwater, snow-melt, debris fan seepage flow and rainfall), using the natural tracer Chloride (Cl^-). Water samples were collected from mid-channel flow, in Nalgene poly-ethene bottles, pre-rinsed with de-ionised water. Samples were filtered through 0.45µm nylon membrane filters, and refrigerated. Using an Anion Dionex ICS 2000 samples were then analysed for Cl^- concentration (instrumental precision for the analysis was 0.25ppm).

4.2.3 Data analysis and Stability Index calculations

Flow permanence of individual groundwater-fed streams was assessed using 2008 over-winter data of streamflow temperature. Perennial streams were identified where site water temperature, or that of a location directly upstream, exceeded 0^{o}C throughout the year (Appendix C). Ephemeral streams were characterised either by in-stream temperatures falling significantly below 0°C (during winter), or at several sites, by the observed absence of flow.

The hydraulic gradient (HG) for each piezometer nest was calculated as the difference between the stream water level and the water level in the 50cm piezometers, divided by the vertical distance. Also, Stream Rating equations derived for each cross section, enabled stream discharge to be estimated continuously for each site, during the study period. Mean discharges over the summer were calculated for each site and used in the subsequent analysis.

The thermistor at B2 malfunctioned; regression analysis was run between the known water temperature of this site over a one-week period prior to data logger malfunctioning, and all other streams during the same time period (15th July 2008 to 22nd July 2008). A strong relationship was observed between water temperature at B2 and B3 (p = 0.01) enabling calculation of water temperature at site B2 for the 6 week period.

Variability in stream stage and temperature were assessed using an index similar to that employed by Fowler and Death (2001). Measures of variability were used due to the inadequacies identified in previous studies when using a mean to make comparisons between channel types (Burgherr *et al.*, 2002; Tockner *et al.*, 1997). The Diurnal Stage Variation Index (DSVI) is calculated by determining the difference between the minimum (S_{min}) and maximum stage values (S_{max}) for every 24 hour period over the 6 week study season (the time period of 24 hours was chosen due to the strong diurnal variation in flow):

$$\mathrm{DSVI} = \sum \frac{(S_{max} - S_{min})}{n} \qquad 7$$

Where n = number of values

The same technique was followed to determine a Diurnal Temperature Variation Index (DTVI) for each site using proximal surface stream water temperatures

A multivariate index of environmental stability was calculated, based upon the technique described by Death and Winterbourn (1994), which incorporates five surface environmental variables: variability in stream stage (DSVI) and stream temperature (DTVI), the bottom component of PSI, MSS, and sediment size (D_{50}). A principal components analysis (PCA) was performed to reduce these five variables to one multivariate indicator of stability (Death and Winterbourn, 1994; Townsend *et al.*, 1997; Burgherr *et al.,* 2002). The PCA correlation method was chosen, as this method standardises the numerically heterogeneous variables, prior to analysis. As in Death and Winterbourn (1994), axis 1 scores from the PCA were then rescaled (lower values indicate greater stability), and applied as the stability index. The environmental stability index was correlated with Shannon's Diversity Index (representing macroinvertebrate diversity at family level) using Spearman's Rank Correlation. A Kruskal-Wallis test was used to investigate whether differences in diversity between depths were significant.

Cross correlations between taxa and physicochemical variables were performed using Spearman's Rank Correlation to identify interspecific interactions. The variables used in the analysis included mean discharge (over the study period), mean hydraulic gradient, pH, Pfankuch Stability Index, MSS, DSVI, DTVI, FPOM, CPOM, Cl^- and the multivariate index of environmental stability. Although, within a site, depth is generally considered the primary determinant of interstitial biota distribution (Dole, 1985 *in* Dole-Olivier *et al.,* 1997), when determining variation between sites, within-depth analysis is required, as in Dole-Olivier *et al.*, (1997). Accordingly, as the primary focus in this study was between site variation, 15cm and 30cm datasets were analysed separately. Finally, comparisons were made between the surface and hyporheic distributions of taxa between sites.

4.3 Results

4.3.1 Physicochemical processes

In-stream temperature at B1, and upstream of A1 and A4, constantly exceeded $0^{o}C$ throughout the year (Appendix C), indicating perennial flow at these sites. The stream beds were dry at B2 and B3 at the start of the field campaign in May 2008. Water table elevations increased throughout the study period, which led to the initiation of streamflow as the rising water-table intersected the stream bed (first at B3, followed by B2). Additionally, analysis of water samples revealed high concentrations of Cl^- at a stream fed by seepage through colluvial deposits upon the valley side (15ppm) (DFS_{deep}), and lower concentrations in the main glacial channel (0.3ppm) (GMW_{riv}). Cl^- concentrations within groundwater-fed streams were highest at A1, A4 and B1 (3.35ppm, 4ppm, and 3.1ppm respectively), but comparatively low at B2 and B3 (1.02 and 0.9ppm respectively).

Mean diurnal stage variations (DSVI) differed markedly between sites (Fig. 31A). DSVI at A4, B1 and B2 was relatively low (mean DSVI at stream B2 was 0.003), and constant over time. At A1 and B3 the DSVI was more variable and, on average, much greater (mean DSVI at site B3 was 0.05). Similarly in-stream DTVI exhibited low variability at B2 and A4 (0.5 and 0.6 respectively; Fig. 31B). Much larger daily variations in temperature were observed at B1, A1, and B3 (DTVI of 1.42, 2.05, and 2.34 respectively). Subsurface temperatures, monitored at A1, B1 and B3 to characterise the hyporheic zone, revealed significant differences in temperature stability between the surface and hyporheic zone at all dual-monitored sites

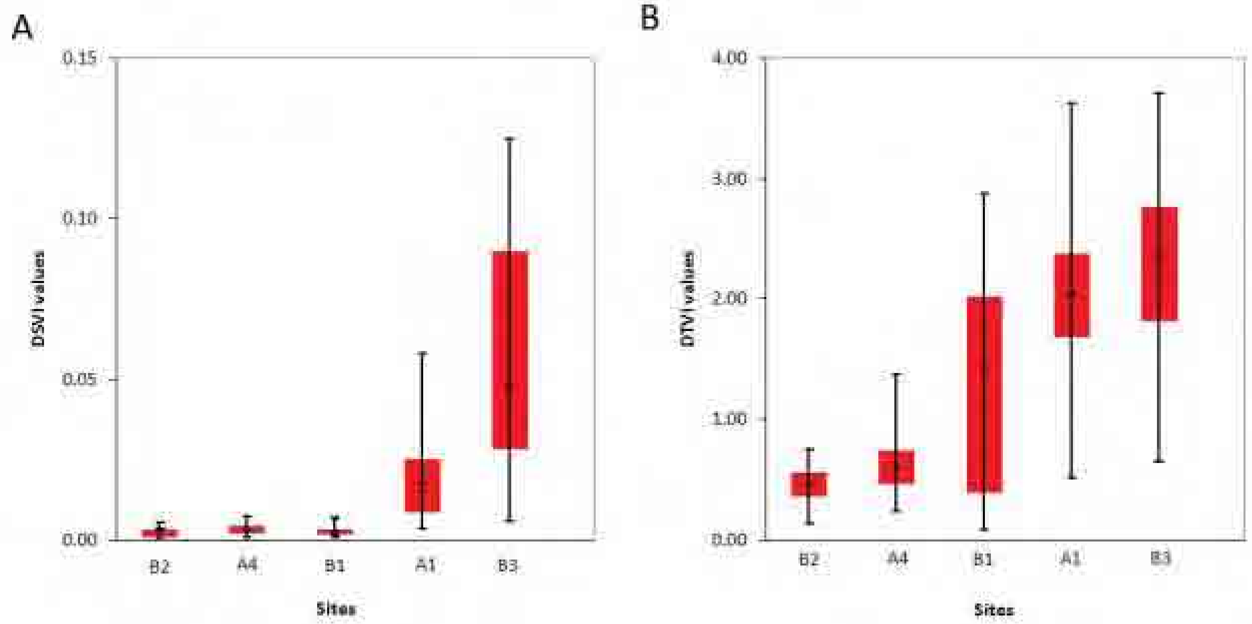
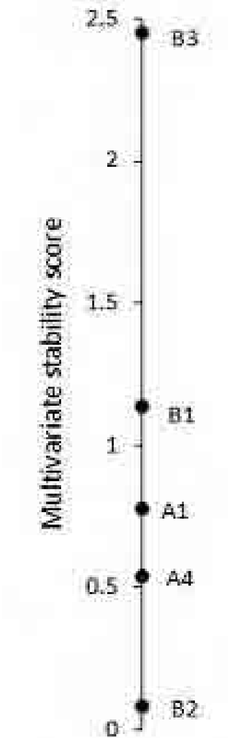


Fig. 31 Heterogeneity in A) DSVI and B) DTVI between groundwater-fed streams; box plots indicate mean value, and upper and lower quartiles

(p<0.01); the hyporheic zone demonstrated lower temperature variability than surface flow throughout the study.

The PCA of the multivariate environmental stability score determined that 65% of axis 1 variability was accounted for by DSVI, DTVI, PSI, MSS and sediment size; all individual variables contributed to this relatively equally. Axis 2 accounted for an additional 16%. Death and Winterbourn (1994) demonstrated how the PCA ordination technique effectively integrates multiple individual measures of instability into a single index. Here the rescaled scores indicate that B3 is the most stable, and B2 the least stable site (Fig. 32, Table 5).



Site	Axis 1	Axis 2	Stability index
B2	-0.9150	-0.5515	0.085
A4	-0.4564	0.6988	0.5436
A1	-0.2184	-0.0260	0.7816
B1	0.1374	0.115	1.1374
B3	1.4524	-0.1328	2.4524

Table 5: PCA axis 1 and 2 scores, and re-scaled stability index

Fig. 32: Multivariate environmental stability scores created from re-scaled axis 1 scores of PCA. The five variables used as indicators of stability in the PCA represent mean values

4.3.2 Macroinvertebrate community dynamics

Mean taxa richness within benthic sites was 12.6, and mean total abundance 99.85. Mean taxa richness and abundance within the hyporheic zone were considerably lower; at 15 and 30cm richness was 5.4 and 4.2, and abundance 39.2 and 22.2 respectively.

Macroinvertebrate diversity and abundance at 15cm was predominantly greater than at 30cm (Fig. 33A and 33B). However, a Kruskal-Wallis test indicated no significant difference between the two hyporheic depths.

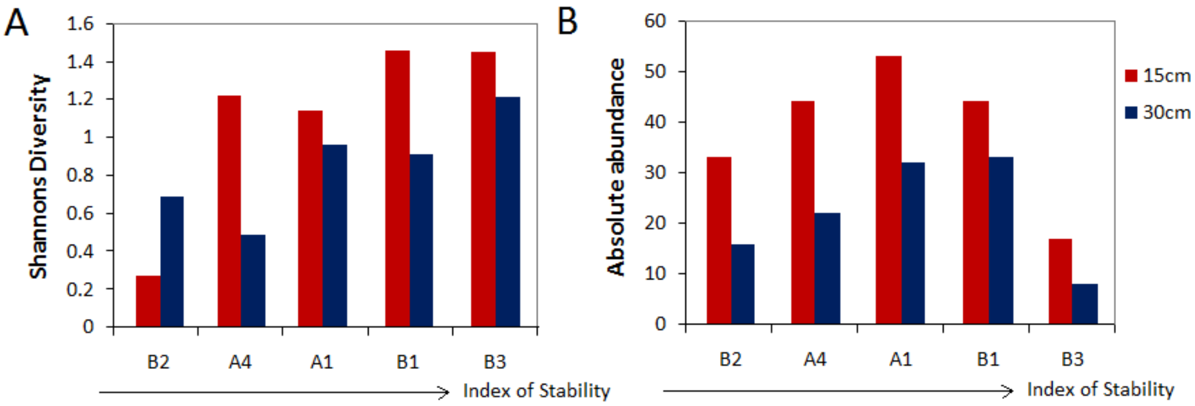


Fig. 33: Between-site and depth distribution of hyporheic macroinvertebrate A) diversity and B) abundance

A significant positive relationship was determined between macroinvertebrate diversity within the hyporheic zone and sites of lower surface environmental stability ($p < 0.01$; Fig. 34A). The correlation between benthic macroinvertebrate diversity and environmental stability was not significant. A significant quadratic association ($p <0.05$) between hyporheic abundance and index of environmental stability was determined (Fig. 34B), which diverged from the significant positive association between benthic macroinvertebrate abundance and environmental stability ($p<0.05$).

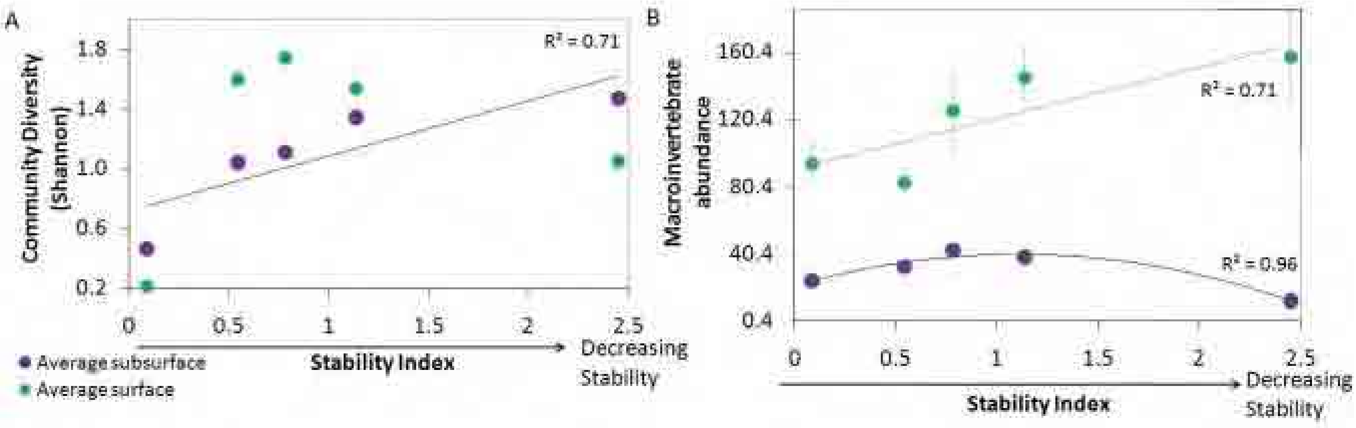


Fig. 34: Index of stability with average surface and hyporheic macroinvertebrate A) Shannon's diversity and B) abundance

Several significant correlations were determined between individual taxa and environmental variables (Table 6) which were compared to surface macroinvertebrate distributions (Fig. 35).

Taxa	**15cm**		**30cm**	
	Positive	Negative	Positive	Negative
Chironomidae		PSI*	Cl^-*	FPOM*, TOM*
Empididae	Stability index**			
Nemouridae	PSI$^@$ Cl^{-*}		PSI*, D50*, Stability index*	
Tipulidae		DTVI*, stability index*		
Chloroperlidae			DSVI*, pH**,	FPOM**
Baetidae	DSVI*, DTVI*, pH*	FPOM*		
Limnephilidae	PSI$^@$	CPOM$^@$	PSI$^@$	CPOM$^@$

Table 6: Spearman's correlation between taxa abundance and physicochemical variables (*= sig at 0.05 level,** = sig at 0.01 level, @ = non-linear relationship) DSVI diurnal stage variation index; DTVI diurnal temperature variation index; PSI Pfankuch stability index; D50 sediment size; MSS macro scale stability; FPOM fine particulate organic matter, CPOM coarse particulate organic matter, TOM total organic matter, Cl^- Chloride

At 15cm depth a significant positive relationship between Empididae and the multivariate index of environmental stability contrasted with a negative, though not significant surface distribution (Fig. 35A). Nemouridae demonstrated a significant positive relationship with Cl^- concentration, and a non-linear relationship with PSI, and Chironomidae a significant negative relationship with PSI. Both demonstrated higher hyporheic abundance at sites where surface abundance was low (Fig. 35B and 35C). Similarly Baetidae, positively correlated with both DTVI and DSVI, and negatively with FPOM, demonstrated contrasting surface and hyporheic distributions (Fig. 35D and 35E). Surface abundance of Limnephilidae demonstrated a positive association with PSI, and hyporheic abundance at 15cm demonstrated a non-linear relationship with both PSI (Fig. 35F) and CPOM (Fig. 35G).

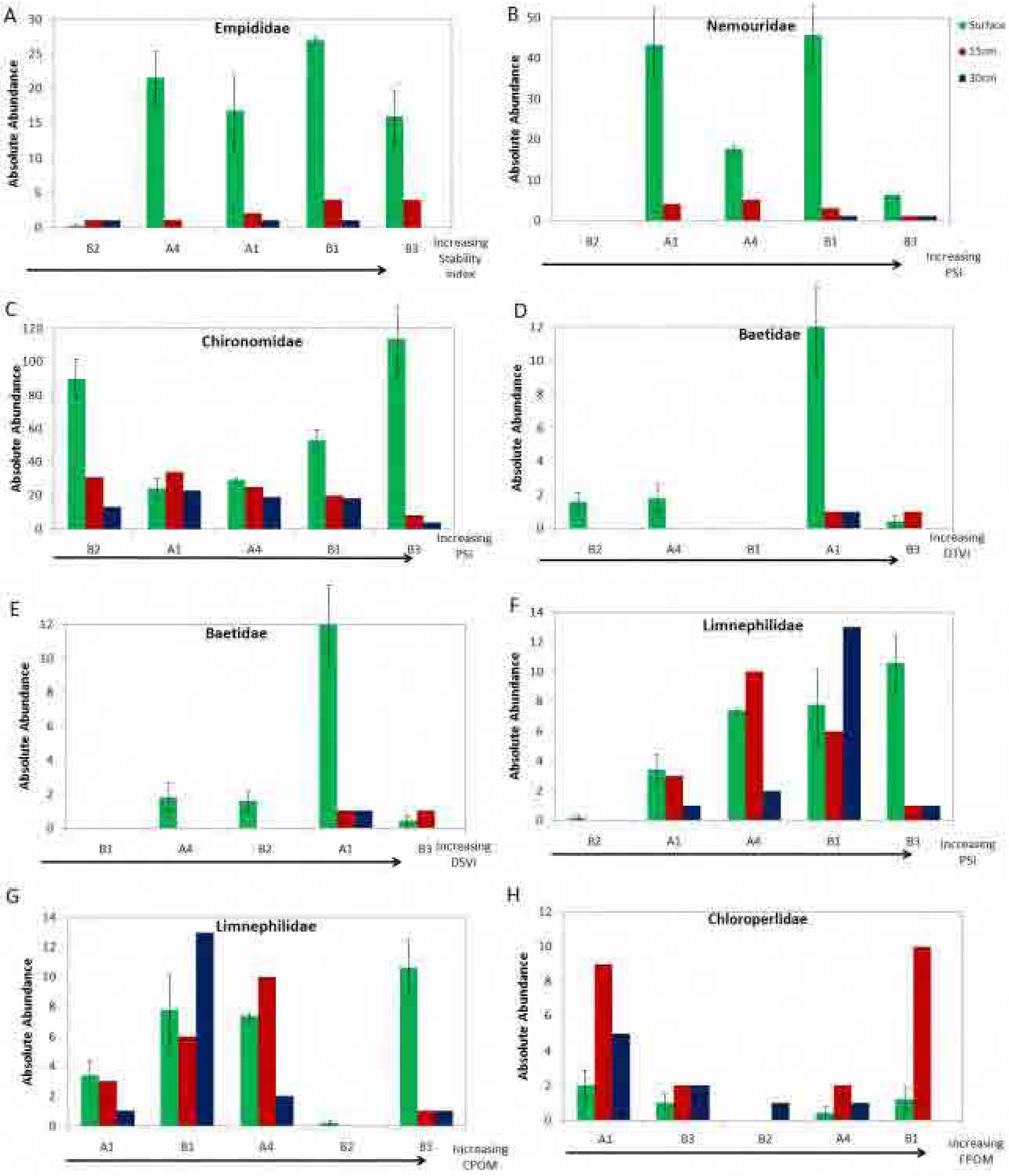


Fig. 35: Comparisons between the distribution of surface and hyporheic macroinvertebrates. A) Empididae, B) Nemouridae, C) Chironomidae, D) and E) Baetidae, F) and G) Limnephilidae, H) Chloroperlidae

At 30cm Chironomidae and Nemouridae continued to demonstrate contrasting surface and subsurface abundances. At this depth Nemouridae was significantly positively correlated to PSI and the multivariate index of environmental stability. Chironomidae was significantly positively correlated to Cl^- and negatively to CPOM. Hyporheic and surface distributions of Limnephilidae corresponded at 30cm, as did those of Chloroperlidae (Fig. 35H). Limnephilidae maintained the non-linear correlations with CPOM and PSI, and Chloroperlidae was significantly positively correlated to DSVI and negatively to FPOM.

4.4 Discussion

Prior to this research, the hyporheic zone had been identified as a refugia for macroinvertebrate taxa, predominantly with regard to discrete disturbance events within surface streams (Matthaei *et al.*, 1999; Palmer *et al.,* 1992). However findings from this study might indicate that macroinvertebrates also use the hyporheic zone in response to local variability in environmental stability. This variability was created by differences between sites in the attenuation of groundwater which contributed to streamflow, reflecting local differences in groundwater residence time. The research therefore indicates that groundwater flow dynamics may create sufficient levels of variability to elicit macroinvertebrate relocation.

4.4.1 Physicochemical heterogeneity of groundwater-fed streams

Cl^- may be used as an indicator of proportional contribution of valley side seepage flow, due to the markedly higher concentrations within the DFS_{deep} flow pathway, situated within the valley side. The ephemeral regimes of B2 and B3, combined with their lower Cl^- concentrations, suggests these streams receive less flow from the DFS_{deep} pathway, but a high contribution from GMW_{riv} seepage. The opposite extremes of DSVI and DTVI observed between the two streams demonstrate different degrees of flow and temperature regime attenuation, reflecting variations in the residence time of the glacial meltwater (Hoehn and Cirpka, 2006). This suggests there is a difference in the length of the flow routes within the GMW_{riv} pathway to B2 and B3, with B3 potentially linked to the glacial meltwater channel by a shorter flow route. Similarly within the perennial streams of higher Cl^- concentrations, the low DTVI of A4 suggests that this stream is connected to the perennial DFS_{deep} flow pathway via a longer flow route than A1.

Reduced flow attenuation in a glacial environment affects substrate stability, increases bed load transport and disrupts bed sediments and associated benthic communities (Milner *et al.,* 2001). This would account for the greater PSI, MSS and sediment size found at A1 and B3. Although all environmental variables ranked A1 and B3 as the least stable sites, no two sets of variables scaled the sites in the exact same order. A degree of variability existed between individual stability indicators (Death and Winterbourn, 1994) illustrating the need for a multivariate index of stability in characterising streams. The PCA multivariate analysis indicated that A1, B1 and B3 were the least stable streams. The hyporheic zone of these less stable sites might therefore be expected to support a greater diversity of macroinvertebrates than A4 and B2.

4.4.2 Influence of surface environmental stability upon macroinvertebrate distribution

The significant positive relationship between the multivariate index of environmental stability and the hyporheic macroinvertebrate diversity suggests small variations in surface environmental stability (reflecting variations in length of flow routes), may influence the distributions of hyporheic taxa. The absence of a correlation between surface benthos diversity and the stability index suggests environmental stability does not influence distribution of benthic macroinvertebrate diversity within the groundwater-fed streams of the fluvial terrace; the relationship between hyporheic macroinvertebrates and environmental stability is independent of surface macroinvertebrate diversity. At relatively less stable sites, the observed increase in diversity at hyporheic zones compared to the reduction in surface diversity might indicate a wider diversity of macroinvertebrates moving from the surface into the hyporheic zone; macroinvertebrates may use the hyporheic zone as a refuge from “substrate movement and flow variance” (Fowler and Death, 2001). The significantly more stable environment which was observed within the hyporheic zone demonstrates its potential to act as an effective refugia. The distribution of macroinvertebrates below the surface might therefore be attributed to a refugia response. However, the hyporheic zone may also be occupied more permanently, effectively being used as an extension of the surface habitat (Winterbourn and Wright-Stow, 2002). Here a reduction in stream stability may be associated with an increase in streambed porosity (Brunke and Gonser, 1997), thus facilitating macroinvertebrate migration between habitats.

The relationships between absolute abundance and index of stability within benthic and hyporheic zones differed from those of diversity, indicating greater abundance at less stable sites at the surface, and a quadratic relationship within the hyporheic zone. Together with the macroinvertebrate diversity associations, this might indicate reduced numbers of a dominant species at sites of lower stability within the hyporheic zone (e.g Chironomidae). The use of grouped communities in the analysis of relationships can mask the movements of individual taxa; consequently the relationships between individual families and stream stability should also be examined (Palmer *et al*., 1995).

4.4.3 Effects of ecological traits upon uses of the hyporheic zone

Contrasting distributions of taxa abundances between surface and hyporheic habitats, and differences between taxa in responses to environmental variables, indicate the potential for different uses of the hyporheic zone depending upon site characteristics, and the tolerance of the taxa. The divergent hyporheic and benthic macroinvertebrate distributions suggest that taxa within the hyporheic community may be more strongly affected by variations in environmental variables than by the factors determining surface macroinvertebrate abundance. This is potentially indicative of a refugia response (Dole-Olivier *et al.*, 1997).

4.4.3.1 Refugia

The relationships between Nemouridae and channel bottom stability (as indicated by PSI) at both 15 and 30cm, and of the multivariate environmental stability index at 30cm, may indicate a refugia response to reduced stream bed stability. At sites of least stability (as indicated by PSI and the multivariate index of environmental stability), reductions in abundance observed at 15cm correspond with the establishment of Nemouridae at 30cm, indicative of deeper migration at sites of higher relative instability. The contrasting negative relationship at the surface, although not significant, might indicate movement from the surface to the hyporheic zone at sites of reduced environmental stability. Such responses to in-stream instability were observed by Fowler and Death (2001). The relationships observed between Empididae and multivariate environmental stability at 15cm might be attributed to similar processes.

The significant positive correlations of Baetidae with DSVI and DTVI at 15cm may additionally indicate sensitivity to variability in temperature and stream stage. Relocation of Baetidae from the surface in areas of higher temperature variability is suggested by the contrast between higher hyporheic abundances and lower surface abundances. The more stable water temperatures within the hyporheic zone would provide a more suitable habitat for Baetidae in relatively unstable streams, given their preference for more stable temperature regimes (Hose *et al.*, 2005). The similar relationship observed between Baetidae and DSVI may result from higher stage variability, causing increased porosity, and facilitating macroinvertebrate entry into the hyporheic zone. However, the significant negative relationship with FPOM observed at this depth may also indicate that this taxon enter the hyporheic zone at sites of low food availability. When food availability is low, Baetidae perform more extensive searches of the surrounding habitat (Kohler, 1984), therefore higher abundances within the hyporheic zone may reflect increased foraging.

The significant negative relationship between Chironomidae abundance and channel stability (PSI) within 15cm of the hyporheic zone, with contrasting surface and hyporheic abundances, might again indicate a refugia response. Uniquely, highest hyporheic Chironomidae abundance was observed at sites of greater surface stability. Chironomidae have a high tolerance for instability, but are typically poor competitors, and thus abundance is reduced where conditions are less extreme (Milner and Petts, 1994). Where the competitive ability of taxa is weak, refuge will be sought in order to facilitate its co-existence (aggregation theory; Ward *et al.,* 1998), which in the case of Chironomidae may be the hyporheic zone at more stable sites. Owing to several behavioural and physiological traits, low stream permanence may strengthen the competitive ability of the Chironomidae (Williams and Hynes, 1976; Gray, 1981), reducing the need for the taxa to seek refuge, and potentially explaining the low hyporheic abundance at B2. Again the significant negative relationship between FPOM and Chironomidae at 30cm might also indicate a degree of food searching behaviour in the taxa. At sites of lower organic availability taxa may use the hyporheic zone as a food resource, searching for patches of settled organic matter, deep within the substrate (Winterbourn and Wright-Stow, 2002). This is supported by the significant positive relationship with Cl^- at this depth; greater FPOM concentrations may be entrained within the hyporheic zones of these sites, supplied by DFS_{deep} flow pathways (Boissier and Fontvieille, 1995). Hyporheic zones with greater Cl^- concentrations may therefore be capable of sustaining greater numbers of Chironomidae.

4.4.3.2 Surface habitat extension

Unlike macroinvertebrates demonstrating refugia responses, distributions of Limnephilidae (at 30cm) and Chloroperlidae closely reflected those at the surface, which may indicate continual movement of taxa between the surface and the hyporheic zone. The even distribution between zones suggests the hyporheic zone may be used as a permanent extension of the surface habitat, as opposed to a temporary refuge.

Uniquely, surface abundance of Limnephilidae was positively correlated to PSI; hyporheic abundance also appears to be influenced by both PSI and organic matter, indicated by the quadratic relationships at 15cm and 30cm. Limnephilidae move preferentially to greater depths, driven by increased likelihood of encountering food resources (Winterbourn and Wright-Stow, 2002; Wright-Stow *et al.*, 2006; Godbout and Hynes, 1982). Taxa typically display preferences for different degrees of sediment porosity (Wood and Armitage, 1997), and available physical space is a primary limiting variable determining hyporheic distribution (Maridet *et al.*, 1992). Limnephilidae (a cased caddis) therefore requires a minimum pore space to move deep into the hyporheic zone. In less stable sites this space will be made more readily available, as alterations in sediment porosity enable easier access (Brunke and Gonser, 1997). As a result greater abundances of Limnephilidae might be expected at less stable sites. However, equally, at sites of higher organic matter availability there is a reduced need for the taxa to migrate into the hyporheic zone in search of food. The optimum abundance of Limnephilidae are therefore found at sites of low organic matter and high PSI (B1). This may explain the quadratic nature of the relationships.

The significant positive association between the abundance of hyporheic (15 and 30cm) and benthic Chloroperlidae again suggests use of the hyporheic zone as a more permanent habitat. Nymphs of most genera of this family remain predominantly hyporheic, rising to the surface as late instars, just prior to emergence (Surdick, 1985). This would explain the low abundances observed at the surface, and correlation between habitats, as greater larvae abundances within the hyporheic zone support greater abundances for emergence at the surface. Positive relations between Chloroperlidae and DSVI at 30cm might be explained by greater stage variance driving early instar Chloroperlidae to greater depths to reach suitable habitat stability. Alternatively, the negative association with FPOM might suggest that Chloroperlidae move deeper into the hyporheic zone in search of food, at sites of low resource availability.

This study suggests, therefore, that in the case of several taxa examined, differences between groundwater-fed streams in degree of variability in environmental stability, and in additional physicochemical variables, were sufficient to result in significant differences in their abundance within the hyporheic zone.

4.5 Conclusion

The results demonstrate that within a relatively small fluvial terrace, the environmental stability of groundwater-fed streams may vary sufficiently to produce clear differences in macroinvertebrate communities and in the response of individual taxa. Differences between streams in environmental stability, created predominantly by local variability in groundwater residence times within subsurface flow routes, were demonstrated as a significant driver of macroinvertebrate distribution at a community scale. However on a taxa-specific level several additional physicochemical variables proved influential.

The results highlighted two potential uses of the hyporheic zone. Firstly it was used as a refuge from relatively small variations in the surface stream environment (environmental stability), and a suite of physicochemical variables, at ranges found less favourable by specific taxa – Chironomidae, Nemouridae, Empididae and Baetidae. Chironomidae, Nemouridae and Baetidae may have additionally used the hyporheic zone as a food resource at sites of reduced surface organic matter availability, or in areas where subsurface organic matter content was higher. Secondly, the hyporheic zone may be used as a more permanent extension of the surface habitat – by Limnephilidae and Chloroperlidae.

The study demonstrates that local scale variability can be of sufficient magnitude to elicit responses in taxa in subarctic environments, perhaps because here taxa may live close to their tolerance levels, or due to a scarcity of resources.

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5. DETERMINATION OF GROUNDWATER UPWELLING SITES USING REMOTE SENSING OF LANDSAT DATA

A method for identifying sites of upwelling groundwater, using digital remote sensing, was developed, in order to quantify the spatial extent of groundwater-fed streams within two National Parks, in Alaska. This larger spatial scale provides a better depiction of the overall distribution of points of groundwater upwelling, both within and between glacial floodplains. Chromaticity valuations were used to create a relative normalised index of turbidity, to isolate the glacial floodplains of both Denali and Wrangell St Elias National Park. Subsequently a normalised vegetation index is calculated, highlighting areas of high chlorophyll concentration within the floodplains. The 'hotspots' of chlorophyll were compared with higher resolution imagery, to determine the accuracy of site classifications.

It was determined that 30m resolution Landsat TM and ETM data can be used to accurately determine areas of groundwater upwelling within glacierised floodplains. This methodology will enable detailed comparative studies to take place between sites of groundwater upwelling, which might otherwise have been prevented due to the difficulties experienced in identifying suitable study sites.

5.1 Introduction

Areas of upwelling groundwater have been identified as key macroinvertebrate community drivers within glacierised systems (Brown *et al*., 2003). Groundwater-fed streams typically demonstrate higher taxa abundance and diversity compared to glacial rivers, due to the greater water clarity and physical channel stability of the upwellings (Ward *et al*., 1999). Additionally, greater nutrient concentrations may be supplied to macroinvertebrate communities where upwellings are fed by shallow groundwater flow (Coleman and Dahm, 1990). Macroinvertebrate diversity may, however, be significantly influenced by climate change, and associated glacial recession, as relative contributions of groundwater are eventually increased (Milner *et al*., 2009). Knowledge of the key habitats of macroinvertebrates is therefore crucial to the understanding and monitoring of glacierised riverine ecosystems, not only because given their sensitivity to change macroinvertebrates may be used as an indicator of climate change (Brown et al., 2007), but also as they play key roles in ecosystem functioning (Cummins and Klug, 1979; Lessard and Hayes, 2003) and nutrient cycling (Merrit et al., 1984).

Arctic and alpine catchments are relatively little studied, reflecting their remote locations and relative inaccessibility (Tockner *et al*., 2002). Therefore, despite the importance of groundwater upwellings, these freshwater ecosystems have not been extensively researched in subarctic environments. Large scale studies, comparing sites between several glacierised catchments are rare; one limitation has been the difficulty in locating suitable study sites. If limited to ground reconnaissance, identification of upwelling sites is laborious and costly due to the size of glacierised catchments, which are typically located in remote areas. A site identification method is therefore required which will optimise resource use and establish a broader understanding of groundwater upwelling dynamics.

Areas characterised by upwelling groundwater are typically associated with isolated sites of dense vegetation (Hayashi and Rosenberry, 2001) which contrast markedly with the non-vegetated active glacial floodplain (Zah and Uehlinger, 2001; Uehlinger *et al.,* 2003). This occurs whereby metabolism by nitrifying bacteria within groundwater flow pathways (Jones *et al*., 1995; Dahm *et al.,* 1998) results in elevated nitrate and phosphate concentrations at sites of groundwater discharge (Valett et al, 1994; Dent *et al.,* 2000). The nutrients are conveyed to both the stream and riparian zone through subsurface flow pathways extending from the active channel (Harner and Stanford, 2003), and in combination with reduced flow variability (resulting in greater bank stability) both algal and riparian vegetation growth are increased. Although the 30m resolution of the Landsat remote sensing images preclude the identification of individual groundwater channels within the floodplains, extensive vegetated areas growing within and between groundwater upwelling channels may be depicted on a larger scale.

Through the use of freely available satellite imagery therefore, sites of groundwater upwelling may be identified remotely; this would significantly reduce resource expenditure, enable larger scale comparative studies between upwellings sites, and establish the full extent and significance of these habitats.

This study therefore aims to

1. develop a methodology of identifying groundwater upwellings, using digital remote sensing;

2. assess the accuracy of the methodology; and

3. determine the extent of groundwater upwellings within Denali National Park, and compare the results with those of the adjacent National Park, Wrangell St Elias.

5.2 Methodology

5.2.1 Study sites

Two areas within interior Alaska were identified for study, each was ~ 200,000km^2. The first comprised a region in and around Denali National Park and Preserve (Fig. 36), and the second, Wrangell St Elias National Park and Preserve.

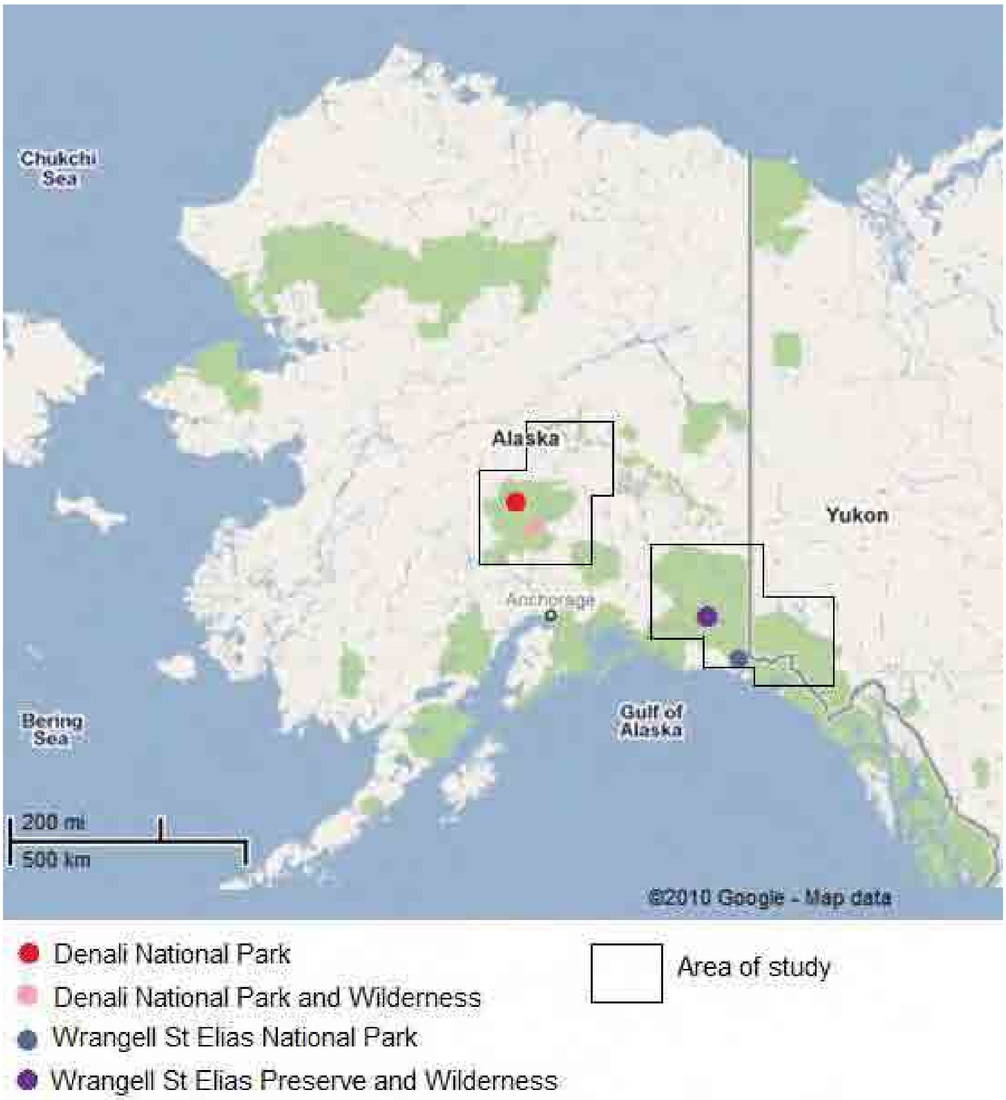

Figure 36: Locations of study sites for digital remote sensing data acquisition

Both areas are characterised by extensive glacierised floodplains, with additional snow-melt, rainfall and groundwater stream sources (Thorson and Bender, 1985; Anderson *et al*., 2003). Denali was selected as a control site, which could be used to determine model accuracy, based upon existing knowledge of groundwater upwelling locations. The replicative potential of remote sensing techniques was assessed by applying the method to the Wrangell St Elias dataset.

5.2.2 Data collection

Landsat images (30m resolution) were selected from the NASA Landsat orthorectified database, and each band downloaded as a separate image (.tif file); only the first five bands of the spectrum (blue, green, red, near infra red and far infrared) were required for the study. As each Landsat image measures ~34,000km^2, and images overlap by ~ 60%, six images were required to create each National Park scene. The majority of the image data was acquired from Landsat 5 TM and Landsat 7 ETM satellites covering the period 2000 to 2002. Although images within these scenes span a wide range of dates and satellite models, they represent the most recent Landsat images of highest quality (lowest cloud cover, with least pixel damage, taken during the growing season), as outlined in the orthorectification procedure used by NASA (Tucker *et al*., 2004). The high quality of this data reduces the need for atmospheric adjustments. Although more recent images are available, high cloud cover, data errors or data acquisition outside of the growing season (May-September) precluded them from study.

5.2.3 Data analysis - digital image processing

Although orthorectification of data provided by NASA resulted in similar atmospheric quality of images, several factors may create differences between images, and thus some degree of image processing is required. Remotely sensed data within each image band is provided as a series of rescaled radiance values (1-255); dissimilarities between images in sun angle and intensity, satellite angle, and satellite model may significantly alter these values. These differences were removed via a series of image corrections applied to each image band. Image processing was conducted using raster calculator in ArcMap 9.3. First, image data values were converted from model-specific radiance values (Q_{cal}) taken by either Landsat 5 TM or Landsat 7 ETM, into at-sensor spectral radiance (L_λ), a common radiometric scale (Chander *et al.*, 2009). The following conversion was performed, as outlined by the Landsat Project Science Office (2002), using constants provided in Chander *et al.*, (2009).

$$L_\lambda = \frac{LMIN_\lambda - LMAX_\lambda}{Q_{cal\max} - Q_{cal\min}}\left(Q_{cal} - Q_{cal\min}\right) + LMIN_\lambda \qquad 8$$

Where

L_λ = common radiometric scale
$LMAX_\lambda$ = maximum rescaled at sensor radiance value
$LMIN_\lambda$ = minimum rescaled at sensor radiance value
Q_{cal} = original model-specific radiance value
Q_{calmin} = minimum calibrated pixel value of satellite (= 1 for Landsat 5 and 7)
Q_{calmax} = maximum calibrated pixel value of satellite (= 255 for Landsat 5 and 7)

Next, to reduce variability resulting from differences in the date of Landsat image acquisition, at-sensor spectral radiance was converted to in-planetary albedo (TOA reflectance) using the equation given by Markam and Barker (1986) (below). This accounts for differences in sun angle, variation in distance between the sun and the earth, and in exoatmospheric solar irradiance arising from different spectral bands in relatively clear images (Chander *et al.*, 2009; Landsat Project Science Office, 2002).

$$TOA_{reflectance} = \frac{\prod . L_{\lambda}.d^{2}}{ESUN_{\lambda} . \cos\varnothing_{S}} \qquad 9$$

Where

$\prod$ = 3.142
L_{λ} = at-sensor spectral radiance
d = distance from the earth to the sun
$ESUN_{\lambda}$ = mean solar exoatmospheric irradiance
$\varnothing_{S}$ = Solar zenith angle (degrees)
All values (except $\prod$ and L_{λ}) are sensor, band or date specific, and again are summarised in Chander *et al*., (2009).

To identify groundwater-fed streams in glacierised floodplains, a measure of chromaticity was used, which identifies differences in water clarity (Bukata *et al*., 2001). However the narrow channel width of many groundwater-fed streams, and coarse resolution of the Landsat dataset (30m) prevented direct identification of the upwellings within glacial floodplains. Therefore a two-step process was used, first a conversion from $TOA_{reflectance}$ to the chromaticity measure was undertaken, to identify and remove larger non-glacial rivers and lakes from the Landsat scenes. Second, an NDVI was created to identify characteristic areas of high chlorophyll concentration within the remaining glacial floodplains, maintained by the high nutrient contents and stability of groundwater upwellings.

5.2.3.1 Relative normalised turbidity index

The colour of a water body is a result of interactions between downwelling solar irradiance and upwelling light reflectance of organic and inorganic compounds within that water (Jerome *et al*., 1994). Chromaticity measurements, adapted by Alföldi and Munday (1978) from the CIE 1931 measurements, may therefore be used as remote sensing indicators of water clarity. This transformation involves a brightness normalisation (Mouchot *et al*., 1991) of corrected $TOA_{reflectance}$ bands 2, 3 and 4 (green, red and near infra red):

Chromaticity X = band2/(band2+band3+band4) 10
Chromaticity Y = band3/(band2+band3+band4) 11
Chromaticity Z = band4/(band2+band3+band4) 12

These values may be plotted as coordinates in a 'chromaticity triangle' (Lindell *et al.*, 1986). However as strong positive correlations have been established between the Chromaticity X value and degrees of water clarity (Mouchot *et al*., 1991), Chromaticity X may be used as an indicator of turbidity (lower values indicate higher turbidity). Given that the aim of the method is to establish potential field sites with minimal resource expenditure, ground-truthing of turbidity data was not undertaken. As a result, the chromaticity values were not calibrated indicators of turbidity, but represent a relative normalised turbidity index.

Following the determination of turbidity (or chromaticity), further corrections for atmospheric haze are often undertaken (Lindell *et al.,* 1986). An assessment of between-image variance in chromaticity determined the level of accuracy to be within 2%. Correction for atmospheric haze is a time consuming process, and given the existing high accuracy level (low between-image variance), and the low resolution required to separate between the extremes of turbid and clear streams, this step was not considered necessary.

Two separate scenes were subsequently created, consisting of a mosaic of all turbidity images within each park. Snow and glacial ice were removed from each scene using the methods described by Dozier (1989). A snow mask was created, consisting of three layers; the first depicted bright snow, the second separated shaded snow from bright soil and rocks, and the third separated snow from cloud. TM band 1 saturates over bright snow and ice, thus displaying very low $TOA_{reflectance}$ values (Rosenthal and Dozier, 1996); at a threshold value (≤0.2) this is considered snow (Dozier, 1989). Shaded snow was distinguished from bright soil and rocks using the algorithm:

$$(Band2 - Band5) / (Band2 + Band5) \qquad 13$$

again using a threshold value (≤0.4) to create a second binary snow mask. Finally band 5 was used to separate snow from cloud with the threshold value of ≥0.25. A composite mask of all three criteria was created for each image, and a mosaic of the mask created for each park scene. Once applied as a ‘snow mask’ onto existing park turbidity scenes this successfully removed the majority of snow and ice from the datasets.

To identify and extract rivers from the dataset for further analysis, the use of bands 5 and 7 was considered, but due to the high $TOA_{reflectance}$ of the turbid glacial streams, this method was not appropriate. Density slicing of band 5 was also considered. However $TOA_{reflectance}$ values of glacial streams in the higher turbidity range, and some land classifications significantly overlapped. As a result several steps were taken. First the turbidity index was used to separate the majority of rivers from streams; the lower 10th percentile of values were removed, this was successful in removing terrestrial components of both scenes, and general background ‘noise’. Secondly, to remove large groundwater streams and lakes, the upper 90th percentile of turbidity values were identified and removed. Some rhithral streams remained; such streams could not easily be removed due to their high turbidity.

The removal of terrestrial components of the scenes also removed all mid-channel bars, and significant central portions of glacial floodplains. Such areas may contain upwelling hotspots, and were therefore required in the analysis. To re-introduce missing floodplain sections, with minimal time expenditure, a terrestrial vector mask was created. Using the glacial stream file as a mask, raster calculator was used to identify all non-glacial scene components. The resultant raster image was converted into a vector. All 'missing' areas of glacial floodplains and mid-channel bars had been surrounded by the extracted glacial rivers, and were therefore isolated vector shapes. As a result, by deleting the largest vectors within the two scenes (five or six shapes in each case) only the isolated vectors of interest remained. This vector file was then converted back to a raster, and used as a mask on the original (snow-free) turbidity index scene. This created, for both study areas, a scene consisting of sections of floodplains and mid-channel bars. These scenes were then mosaiced with the relevant glacial river scenes, creating park scenes of complete glacierised floodplains.

Finally partial density slicing of band 5 $TOA_{reflectance}$ values was undertaken. Using histograms within ERDAS imagine, the $TOA_{reflectance}$ value in band 5 which represented land values significantly different to those of rivers could be determined. All values above this point were removed. This was then applied to the park scenes of complete glacierised floodplains as a 'cleanup' operation. In isolation this method left significant portions of land. However in combination with river extraction through turbidity values, and snow and ice removal, it isolated additional land pixels, which could be subsequently removed, thus reducing model error.

The accuracy of the model in determining glacial floodplains was then assessed, using a percentage accuracy of pixel classification method, adapted from Ward *et al.,* (2000). Assessment sites were chosen using a random number generator to depict coordinates within the park scenes, which were then used as centroids for 800 square pixel areas. An RGB colour composite image, or where available, a digital satellite photograph were superimposed upon the model, and the accuracy of classification of each pixel value within the assessment grid square (glacial or non-glacial) determined.

5.2.3.2 Normalised vegetation index

Using $TOA_{reflectance}$ corrected bands 3 and 4, a mosaic of normalised vegetation indices was created for each park scene. NDVIs were calculated for each individual image within the scene using the formula

$$\mathrm{NDVI} = \frac{\mathrm{band3} - \mathrm{band4}}{\mathrm{band3} + \mathrm{band4}} \qquad 14$$

An NDVI representative of only areas within glacierised floodplains was created by masking the mosaic NDVI of each park scene with the glacierised floodplain scene, using the floating point operation in raster calculator. NDVI returns a value of between 1 and -1, with positive values indicating the presence of vegetation (Zhou *et al.*, 2001; Weiss *et al.*, 2004). Upwelling areas were therefore identified as isolated areas of positive NDVI values. NDVI values at hotspot locations previously identified in ground reconnaissance surveys within Denali National Park were recorded. Additionally, the overall accuracy of hotspot identification by the model was assessed using high resolution aerial photography of the sites; coordinates of each upwelling were obtained from the model and entered into Google Earth (25cm resolution) whereby the presence or absence of upwelling channels was confirmed.

5.3 Results and discussion

Model classification accuracy distinguishing between glacial floodplain and non-glacial floodplain pixels (Table 7) was determined at 94.3% for Denali National Park, and 87.8% for Wrangell St Elias National Park, using a methodology adapted from Ward *et al* (2000). The majority of misclassification in both datasets arose from misclassification of snow or ice as glacial floodplains; percentage accuracy of Wrangell St Elias was reduced by the higher percentage coverage of glaciers within the study area.

Scene	**Number of test sites**	**Pixels in test site images**	**Misclassified**	**% accuracy**	**% Land cover class of misclassification**		
					Snow/ice	Land	Snow-melt stream
Denali	13	10400	594	**94.3**	68	23	9
Wrangell St Elias	13	10400	1270	**87.8**	94	4	2

Table 7: Assessment of land cover accuracy with respect to glacial stream data extraction using relative normalised turbidity index

Within the National Park and Preserve of both Denali and Wrangell St Elias, 12 and 15 areas of upwelling groundwater were identified respectively, consisting of uncharacteristically high chlorophyll concentrations within otherwise barren glacierised floodplains. The most notable upwelling hotspots were on the East Fork of the Toklat River (Fig. 37) and the main Toklat River (Fig. 38) in the Denali National Park dataset, and on the Gakona River (Fig. 39) and the White River (Fig. 40) in the Wrangell St Elias dataset, all of which had NDVI scores greater than 0.4.

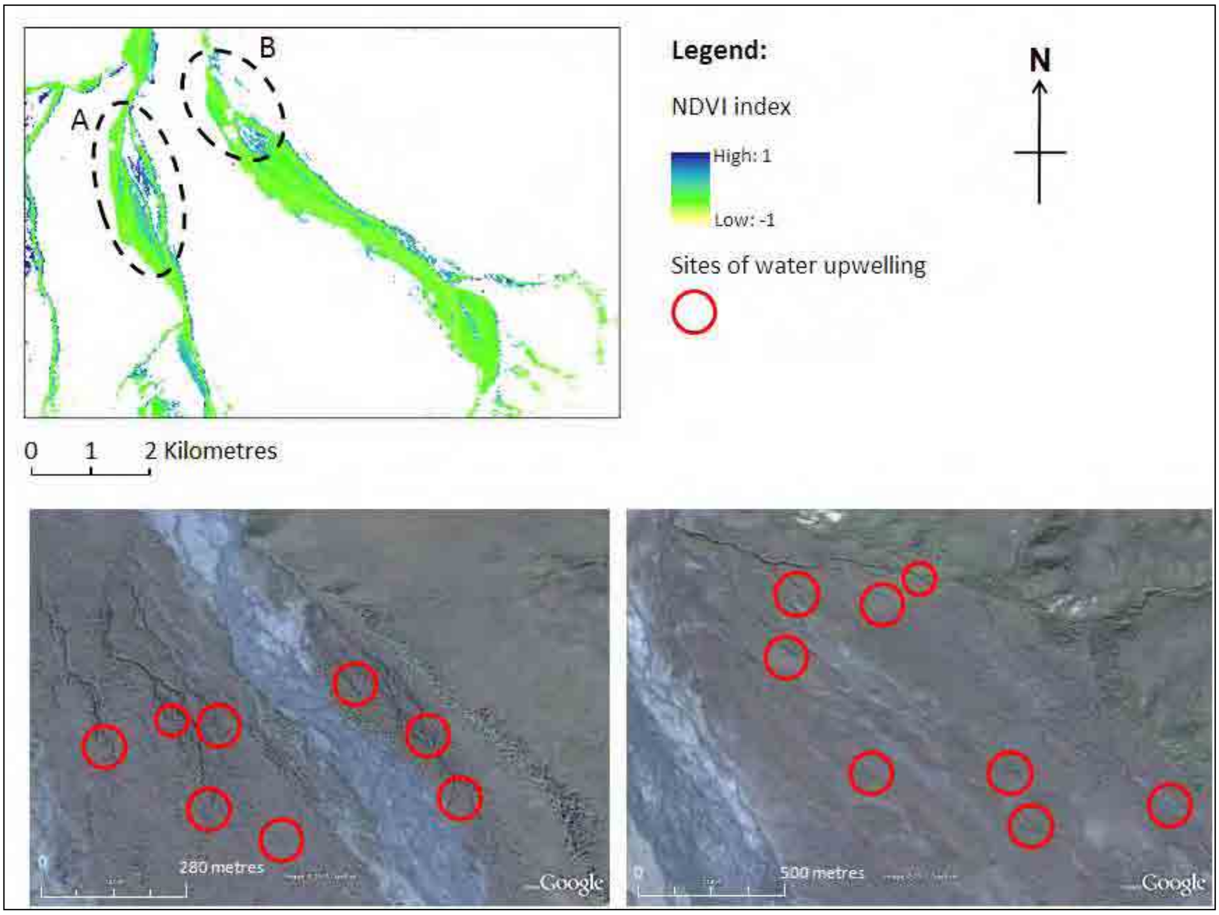

Fig. 37: Sites of groundwater upwelling on the East Fork of the Toklat River; assessment of model accuracy using GeoEye satellite imagery from Google Earth (25cm resolution)

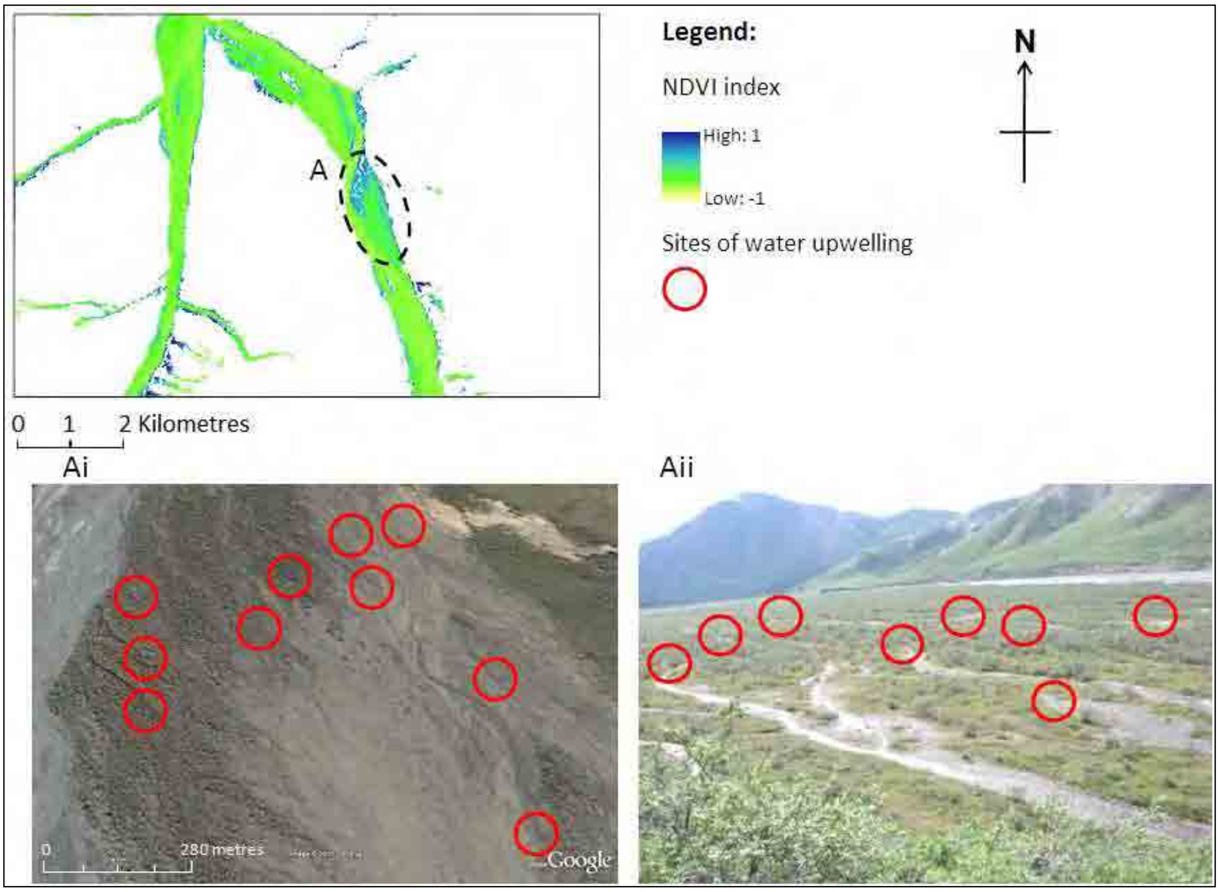

Fig. 38: Groundwater upwelling on the main Toklat River; assessment of model accuracy using (Ai) GeoEye satellite imagery from Google Earth (25cm resolution) and (Aii) ground truthing from site visitation

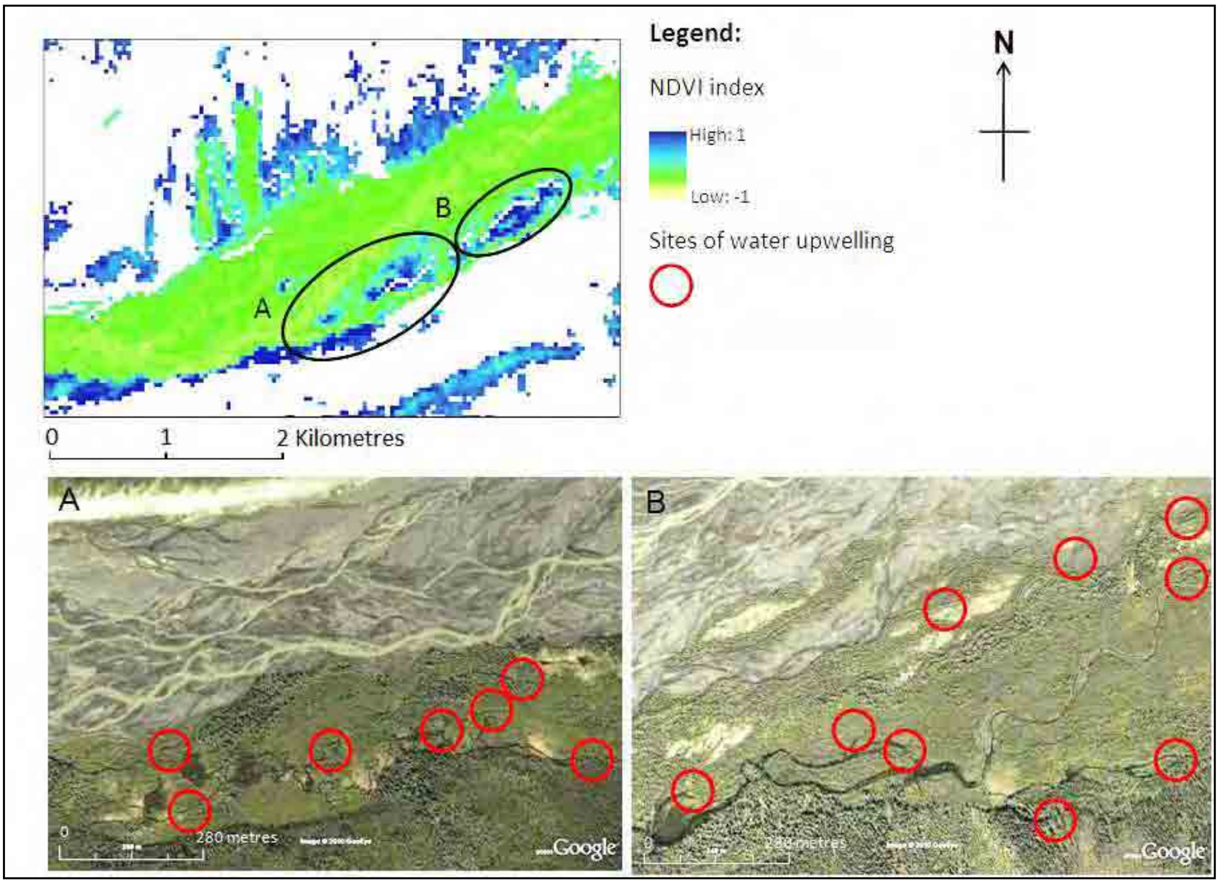

Fig. 39: Groundwater upwelling on the Gakona River; assessment of model accuracy using GeoEye satellite imagery from Google earth (25cm resolution)

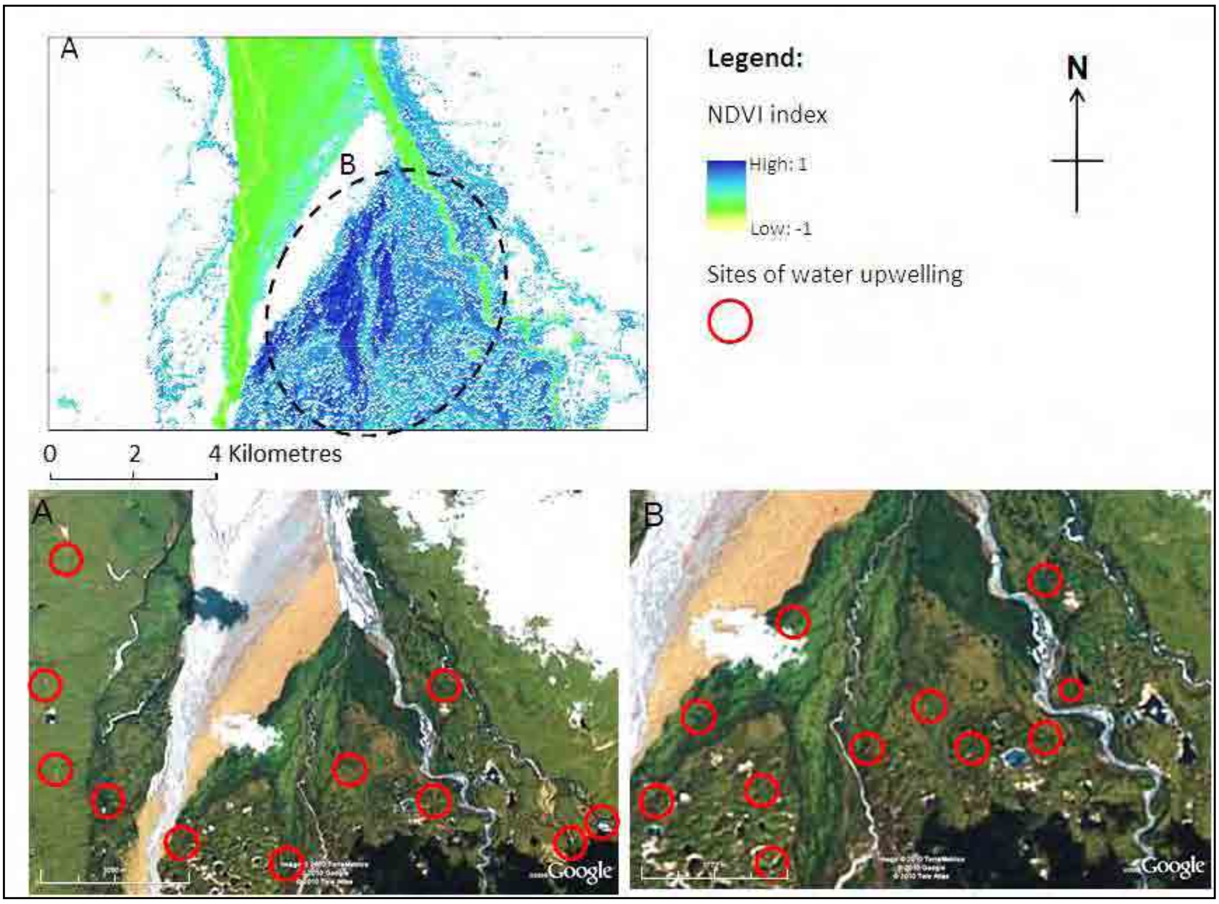

Fig. 40: Upwelling hotspots proximal to glacial headwaters of the White River, upstream of Canyon Mill; tributary to the Yukon. Assessment of model accuracy using Terrametrics satellite imagery (Google Earth) (15m resolution)

Total potential study areas for Denali and Wrangell St Elias were calculated at ~13,044m^2 and ~15,176m^2 respectively. The presence of all upwellings at identified hotspots was confirmed through the use of Google Earth imagery, which depicted the emergence of small clear water channels within or in close proximity to the glacial floodplains (Fig. 37A-40B). Furthermore upwelling areas previously identified by ground surveying studies within Denali National park were successfully identified by the remote sensing methodology; these include the East Fork of the Toklat River, the fluvial terrace of the main Toklat river (Fig. 38 Aii), and McKinley Bar.

This study demonstrates that remote sensing can be used to identify areas of groundwater upwelling on glacierised floodplains. The confirmation of the existence of several of the upwelling sites by ground reconnaissance and photographic images supports its use as a precursor to ground surveys, focusing resources in a more economical manner. The high percentage accuracy of the model in both scenes indicates that the risk of overestimating glacierised habitat, predominantly to include snow and ice accumulations, is acceptable. The characteristics of glaciers or snow topped mountains differ significantly to those of glacial streams and may easily be identified within the Landsat images and ignored. Additionally, the areas of snow and ice have no vegetation, and are therefore not subsequently identified within the model as upwelling hotspots. The potential to mistake an area covered by perennial ice as an area of upwelling groundwater is therefore minimal.

Further ground truthing of the methodology would confirm the predictive ability of the model. The knowledge of existing hotspots proved the predictive power of the NDVI in determining upwellings within glacial floodplains, and comparisons with higher resolution imagery suggests additional areas of high NDVI scores were accurately identified as upwelling areas. However site visitation would eliminate the possibility of overestimation of groundwater upwellings. Regardless of possible overpredictive characteristics of the model, this method successfully focuses resources upon a reduced number of study areas, by the isolation of 12 and 15 potential hotspots within two 200,000km^2 areas.

Although upwellings smaller than 30m^2 may be overlooked due to the 30m resolution of Landsat TM and ETM data, the technique identifies the largest and potentially therefore the most ecologically significant upwelling hotspots in glacierised catchments in both study areas. Additionally, the modelling technique could prove invaluable as finer resolution images, obtained through private satellite imaging companies, become more widely available.

The repeatability of the methodology, demonstrated by the high accuracy upon application of identical methods upon both Denali National Park and Wrangell St Elias datasets, suggests that remote sensing methods may be used successfully in many glacierised catchments. Othorectified Landsat images are now freely available for all areas (excluding Antarctica), and thus the potential for use of this methodology throughout arctic and subarctic catchments is economically less restrictive than costly and time consuming ground surveying techniques.

The large numbers of upwellings, covering a total of 28,221m^2, identified in Denali and Wrangell St Elias National Parks illustrates the frequency with which these habitats occur within subarctic catchments, and highlights the need for further study into these unique environments. Comparisons of upwelling systems within and between catchments could prove valuable to the understanding of habitat systems. With the use of remote sensing techniques, identification of suitable study sites will become more economically viable.

5.4 Conclusion

The use of remote sensing to identify sites of groundwater upwelling within glacierised catchments proved highly successful. This method presents a viable alternative to extensive field reconnaissance, demonstrating 94% accuracy in identifying glacierisied catchments, and 100% accuracy in determining upwelling areas, within Denali National Park. The repetition of the methodology, although marginally less accurate, at 83%, remained highly effective. Areas predominantly misclassified as glacial floodplains (snow and ice) were not subsequently misclassified as upwelling hotspots, and as a result the variation in model accuracy is not a cause for concern; in both instances all upwelling hotspots identified by the model were subsequently confirmed as sites of groundwater upwelling. This method substantially reduces problems in site identification of remote areas, and provides a step forward for studies of groundwater upwellings in glacierised catchments.

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CONCLUSION

A synopsis of the research findings are presented and wider implications discussed. Finally possibilities for further research are suggested.

6.1 Introduction

The aim of the research was to determine how physicochemical dynamics of groundwater flow influence macroinvertebrate communities within a glacierised catchment. Specific objectives were to:

1) characterise the physicochemical characteristics of groundwater flow pathways within the fluvial terrace, and determine the degree of local variability in environmental stability;
2) determine the influence of variability in groundwater flow dynamics upon the benthic and hyporheic macroinvertebrate community; and
3) develop a methodology of groundwater upwelling site identification through remote sensing, in order to put the results of the study into context, and to facilitate future research within glacierised catchments.

This study addressed research gaps in the effects of groundwater channels on macroinvertebrate communities within glacierised catchments, by investigating the influence of local physicochemical variability in groundwater-fed streams, reflecting dynamics of groundwater flow. Research was conducted upon several streams, fed solely by groundwater, situated upon a fluvial terrace, within the Toklat River floodplain; a subarctic glacierised catchment within interior Alaska. The research established a better understanding of ecohydrological interactions within glacierised catchments, in benthic and hyporheic zones, and analysed the geographical extent of these habitats, addressing wider issues of site location within remote areas.

6.2 Local groundwater flow dynamics: physicochemistry and environmental stability

The natural tracers $\delta^{18}O$ and Cl^- indicated that water followed three distinct subsurface flow pathways to supply the groundwater-fed streams; deep and shallow flow through a debris fan (DFS_{deep} and $DFS_{shallow}$,) and glacial meltwater seepage (GMW_{riv} seepage). Marked local spatial and temporal variations were determined in the physicochemistry of the groundwater-fed streams, reflecting variability in the proportional contribution of waters derived from these distinct pathways. During June, the concentration of fine particulate organic matter (FPOM) was significantly higher at sites receiving greater contributions from DFS_{deep}. However, this relationship was not found in subsequent months following establishment of streamside vegetation (July) and leaf litter fall (August). Spatial variations in contributions from individual flow pathways to groundwater-fed streams were attributed both to local topography (vertical distance from the water table) and proximity to the flow pathway. Perennial streams, situated proximal to the valley-sides and at lower elevations received baseflow from $DFS_{deep;}$ ephemeral streams derived a greater proportion of flow from GMWriv seepage. Proportional contributions between flow pathways also varied temporally, both as a result of rainfall and seasonal variability in snow and ice-melt.

Nested flow routes, of varying length and residence time were determined within each individual flow pathway. Marked differences were observed between sites in diurnal stage and temperature variation indices (DSVI and DTVI), independent of the dominant flow pathway (e.g Hoehn and Cirpka, 2006). Differences in DSVI and DTVI likely reflect local variations in attenuation of flow and temperature regimes, suggesting the length of flow route within a single pathway is highly variable. Hydrogeologic facies are locally variable (Robinson *et al.,* 2008), reflecting fluctuating sediment supplies and flow regimes during unit formation (Smith, 1985). As flow route length and hence residence time reflects the distribution and connectivity of permeable deposits (Ward *et al.,* 2002) (as illustrated in Fig. 2) this would explain the local variability in regime attenuation. Reduced attenuation of flow may affect substrate stability, increase bedload transport and disrupt bed sediment (Milner *et al.*, 2001), which would account for the higher Pfankuch Index of stability (PSI), Macroscale channel stability (MSS) and sediment size (D_{50}) observed within channels of less attenuated flow regimes. Accordingly, the multivariate index of environmental stability, combining individual measures of local variability (DSVI and DTVI, PSI, MSS and D_{50}), demonstrated higher variability in channels with reduced regime attenuation.

Seasonal flow maxima, physicochemistry and organic matter concentrations were closely related to relative contributions from water sources and flow pathways from the valley sides and the main glacial meltwater channel of the Toklat River. However, variability in channel stability between sites was primarily determined by flow regime attenuation, reflecting flow route lengths and groundwater residence time, which was dependent upon local substrate permeability and connectivity. This varied independently of relative contributions from the major flow pathways.

6.3 Influence of local flow pathway variability upon benthic and hyporheic macroinvertebrates

Over the summer of 2008, the influence of local variability both between groundwater flow pathways and in environmental stability upon macroinvertebrate communities was determined, through correlating abundance and diversity of macroinvertebrates, sampled simultaneously with physical variables throughout the study period.

6.3.1 Benthic macroinvertebrate communities

Macroinvertebrate abundance and diversity within groundwater upwellings has been recognised as being significantly higher than those within alternative water sources (Friberg *et al.*, 2001; Brown *et al.*, 2006). However, previous research has not fully explored the ecological significance of the heterogeneous nature of groundwater-fed systems. Links between marked local variability in the physicochemical composition of groundwater streams (Malard *et al.*, 1999; Ward *et al.*, 1999) and macroinvertebrate community distributions, although acknowledged (Turnbull *et al.*, 1995; Soulsby *et al.*, 1997), had not previously been established. Results presented in Chapters 2 and 3 provide significant correlations between variability in physicochemical composition of groundwater-fed streams, and macroinvertebrate community composition, establishing that groundwater-fed streams vary in their capacity to sustain higher macroinvertebrate abundance and diversity.

The results suggested that water flow pathways are a key driving factor in benthic macroinvertebrate community structure on this fluvial terrace. The influence of flow pathways upon macroinvertebrate abundance varied depending upon traits and tolerance of taxa, and occurred primarily during periods of low resource availability. During June FPOM was predominantly supplied by the DFS_{deep} flow pathway, and correlations were observed between taxa, FPOM and flow pathway relative contribution (DFS_{deep}%). However when alternative sources of organic matter became available in subsequent months, correlations were no longer observed between taxa and flow pathways, as DFS_{deep} seepage ceased to be the predominant source of organic matter to the groundwater-fed streams. Correlations observed between taxa, CPOM and distance downstream likely demonstrate resource tracking. However following the increases in organic matter availability, only perennial streams, deriving a greater proportion of streamflow from DFS_{deep}, supported associated increases in macroinvertebrate diversity. Ephemeral streams, fed by GMW_{riv} seepage, had significantly lower macroinvertebrate diversity throughout this period. This was potentially due to colonisation and resource tracking constraints faced by univoltine taxa in ephemeral streams.

Glacial recession will likely lead to an elevated contribution of groundwater to streamflow in many glacierised catchments, and have significant implications for macroinvertebrate abundance and diversity (Ward *et al.*, 1999; Brown *et al.*, 2007). However, these results indicate that the influence of groundwater, and thus of climate change, upon macroinvertebrate communities, may be more dynamic than previously envisaged. The significance of an increase in the relative contribution of groundwater to glacierised catchments resulting from glacial recession may vary depending upon water sources and flow pathways.

6.3.2 Hyporheic macroinvertebrate communities

Variability in environmental conditions has been identified as a driver of macroinvertebrate movement into the hyporheic zone (Death and Winterbourn, 1995; Boulton *et al.,* 1998; Fowler and Death, 2001). However, the potential influence of differences in flow pathways and local variations in flow route residence time, inducing local variability in physicochemical variables between groundwater-fed streams, has not previously been determined. In this context, the results presented in this thesis demonstrated that surface environments of groundwater-fed streams varied sufficiently to produce clear differences in hyporheic macroinvertebrate communities. Unlike the distribution of surface macroinvertebrate diversity however, the predominant driver of hyporheic macroinvertebrate distribution on a community level was not organic matter, and hence the relative contribution to flow of the three flow pathways (DFS_{deep}, $DFS_{shallow}$ and GWM_{riv} seepage) was not a significant influence. Macroinvertebrate diversity within the hyporheic zone was predominantly related to environmental stability, increasing in diversity with reductions in stability (as indicated by the multivariate index of environmental stability). Local differences in stability between streams likely reflect variability in flow route residence time. Individual taxa demonstrated relationships with several additional physicochemical variables.

Two potential uses of the hyporheic zone were highlighted in Chapter 4. Firstly, it was used as a refuge (Palmer et al. 1992; Cooling and Boulton, 1993; Dole-Oliver et al. 1997), where the hyporheic abundance of specific taxa demonstrated contrasting distribution to that of surface macroinvertebrate abundance. This may suggest macroinvertebrates relocated from the surface at sites of unfavourable conditions, such as high daily variability of temperature and flow, lower channel stability or low availability of food. Secondly, the hyporheic zone may have been used as a more permanent extension of the surface habitat (Surdick, 1985; Winterbourn and Wright-Stow, 2002) where distributions of macroinvertebrate abundance were similar both within the hyporheic zone and at the surface. Some taxa were identified as utilising sites of greater pore space (created through reduced stream bottom stability) as access to food resources within the hyporheic zone. Other taxa were phenologically adapted to spend the majority of their nymphal stage within the hyporheic zone.

Thus, the results indicate that local differences in environmental stability and additional physicochemical variables between groundwater-fed streams were sufficient to induce differences in macroinvertebrate distribution throughout the hyporheic zone.

6.3.3 Summary

Benthic and hyporheic macroinvertebrate community structure was influenced by different aspects of in-stream physicochemical heterogeneity created by groundwater flow dynamics (Fig. 41). Distribution of abundance of benthic macroinvertebrates (Fig. 41A) was primarily associated with organic matter availability, and diversity with length of active channel flow; both factors were influenced by local variability between flow pathways supplying groundwater to the surface streams.

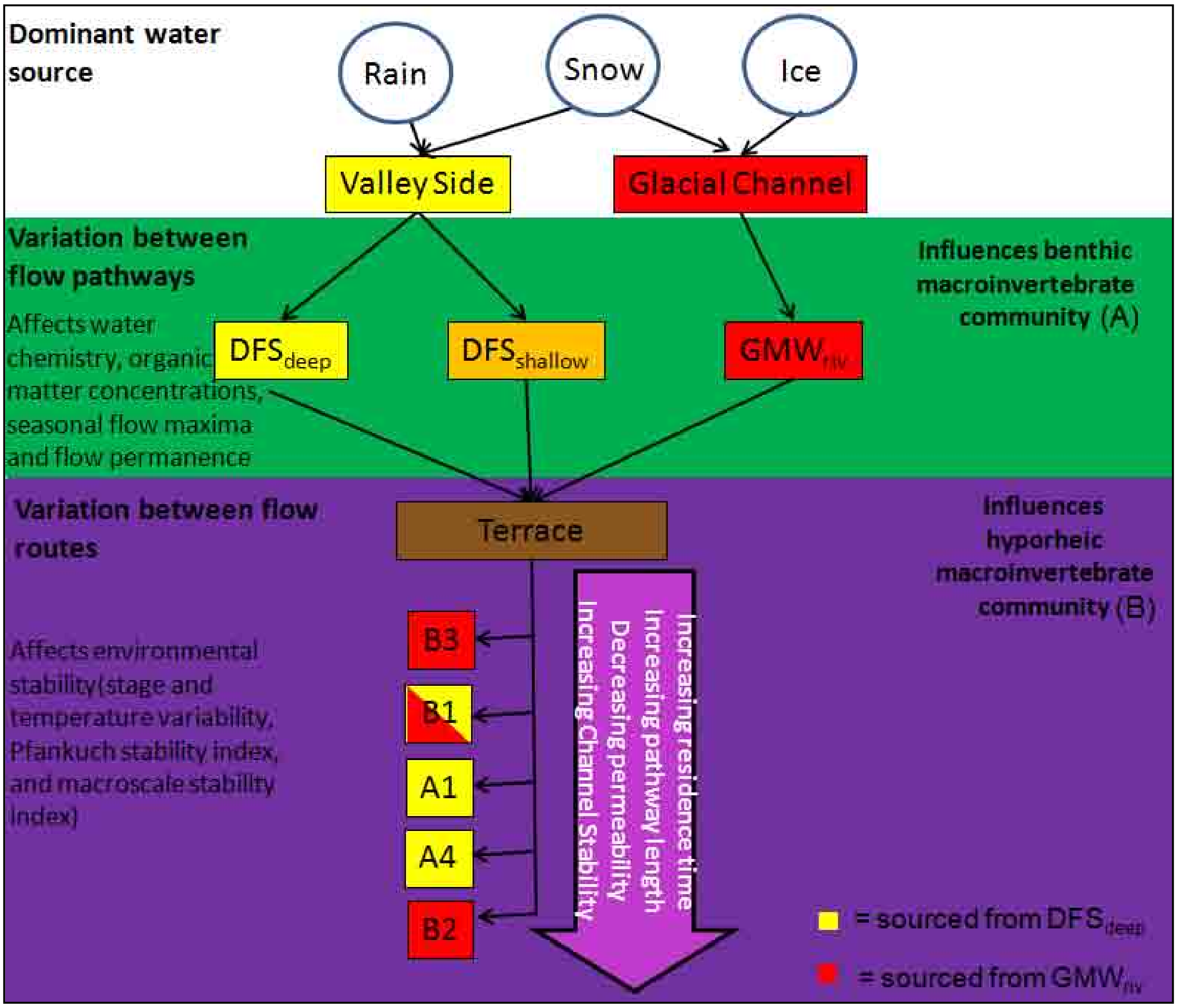

Fig. 41: Conceptual summary of the influence of groundwater flow dynamics upon benthic and hyporheic macroinvertebrate communities

Conversely, within the hyporheic zone (Fig. 41B), macroinvertebrates were influenced not by variation between flow pathways, but by nested routes of flow. Diversity was greatest at sites of lower environmental stability, likely resulting from differences between streams in residence time of flow routes. Most taxa within the hyporheic zone responded to surface variability in stream stage, temperature or PSI.

As groundwater characteristics vary to such an extent over a relatively small scale, groundwater should not be treated as a generic influence upon macroinvertebrate communities. Effects upon benthic and hyporheic macroinvertebrate communities should be considered as spatially and temporally dynamic, reflecting variability in water sources and flow pathways, and associated physicochemical attributes.

6.4 Methodology for remote identification of upwelling groundwater

To determine the extent of groundwater-fed streams within Denali National Park, and the potential for further research, a method of site identification using digital remote sensing was developed in Chapter 5, using LANDSAT images. Within glacierised catchments in Denali National Park, an area of ~13,044m^2 was found to contain upwelling groundwater, at 12 individual sites. The existence of upwellings at identified hotspots was confirmed through subsequent use of high resolution (0.5m) Google Earth imagery, which depicted the emergence of small clear water channels within the glacial floodplains. The model was highly successful, with a 94.3% accuracy of glacierised catchment detection, and a subsequent 100% accuracy of identification of upwelling areas. This method substantially reduces problems of *in-situ* identification of remote areas, and provides a step forward for studies of groundwater upwellings in glacierised catchments.

The model was also applied using images from Wrangel St Elias National Park, to demonstrate the repeatability of the method. Here accuracy was slightly lower, at 87.8% for catchment identification, likely due to the higher percentage ice cover of the area. However, again subsequent accuracy of hotspot identification was 100%. Fifteen sites of upwelling were identified within this park, with a total area of ~ 15,176m^2. This large number of upwellings, covering such a large spatial extent, illustrates the frequency of occurrence of these habitats within subarctic catchments, highlighting the need for further study. With the use of remote sensing techniques, identification of potential study sites will become economically viable, and comparisons of upwelling systems within and between catchments may be undertaken. This is essential to the understanding of these habitat systems.

6.5 Wider implications and future research

The results of this research have implications for climate change impact studies. Previous predictions (Brown et al., 2007; Milner et al., 2009) suggested reductions in glacial meltwater supplies, resulting from climate change-induced glacial recession, would increase macroinvertebrate diversity of streams receiving groundwater flow. However we suggest that the impacts upon macroinvertebrate communities of groundwater-fed streams will be highly localised; communities within streams fed solely by glacial meltwater seepage demonstrate a high potential vulnerability to glacial recession, especially when considering their relatively low macroinvertebrate diversity. Perennial streams fed by groundwaters from snowmelt and rainfall could be more resilient to climate change; here macroinvertebrate diversity may increase, as the reductions in glacial meltwater results in a relative increase in contributions from perennial sources (Brown et al., 2007). However as additional characteristics of groundwater (e.g. organic matter content) vary to such a marked extent over a relatively small scale, influences of glacial recession will be complex. Groundwater should therefore be regarded as having a dynamic influence upon macroinvertebrate communities. These habitats are clearly important in Alaska, when considering their geographical extent, as indicated by remote sensing.

Future research should include the incorporation of additional sites of upwelling groundwater, as identified by digital remote sensing, to scale up the investigation and provide further replications. Comparisons of hydroecological relationships occurring at other, similar study sites, would substantiate that the trends observed in data collected from the Toklat River catchment could be more widely applied to additional systems. This research should be applied to regions outside of Alaska, and of North America, to assess possible wider reaching and long term implications resulting from climate change.

In addition, as the relationships between abundance of benthic macroinvertebrates and flow pathways occurred predominantly during periods of resource depletion, sampling of all physicochemical variables during winter should be carried out. Through inter-annual studies, the temporal extent of this depletion and thus of the dependence of taxa upon resources supplied by flow pathways might be established. Currently, due to the difficult environmental conditions, inter-annual variability of subarctic taxa (e.g. Cowan and Oswood, 1984) is not well known. Here digital remote sensing might be used to identify suitable study sites which can be accessed throughout the year.

Further research might look to incorporate organic matter tracing through the use of fluorescence or absorbance spectroscopy. Although the major source of organic matter to the catchment in June 2008 was determined to be the DFS_{deep} pathway, the sources of these organic contributions were not directly traced. Fluorescence and absorbance spectroscopy might be used to optically determine the various sources of dissolved organic matter (DOM) (McKnight *et al.,* 2001; Baker and Spencer, 2004). This would provide greater insights into the spatial and temporal availability (sources and sinks) of organic resources available to macroinvertebrate communities.

The source of seasonal increases in in-stream organic matter might be determined through the use of isotopic tracers, such as $\delta^{13}C$ and $\delta^{15}N$ (McKnight *et al*., 2003). Dissolved organic carbon (DOC) fractions within DOM may demonstrate distinct $\delta^{13}C$ values, particular to the source (Schiff *et al*., 1990). Similarly characteristic $\delta^{15}N$ values of dissolved organic nitrogen (DON) may be determined (Gebauer and Schulze, 1991; Sebestyen *et al*., 2008), although microbial processes may influence these values (McKnight *et al*., 2003) and must also be considered.

Finally, more extensive hydrological models might be created through the daily sampling of isotopic and chemical groundwater-fed streams and predominant flow pathways (DFS_{deep} and GMW_{riv}), in addition to all rainfall events. Spatial and temporal variability in relative percentage contribution of every flow pathway to the groundwater-fed streams might be calculated if hourly sampling of groundwater-fed streams during and following rainfall events were undertaken, as this would provide additional information on the rate of flow transmission through the temporary pathways ($DFS_{shallow}$) (Ladouche *et al.*, 2001).

6.6 References

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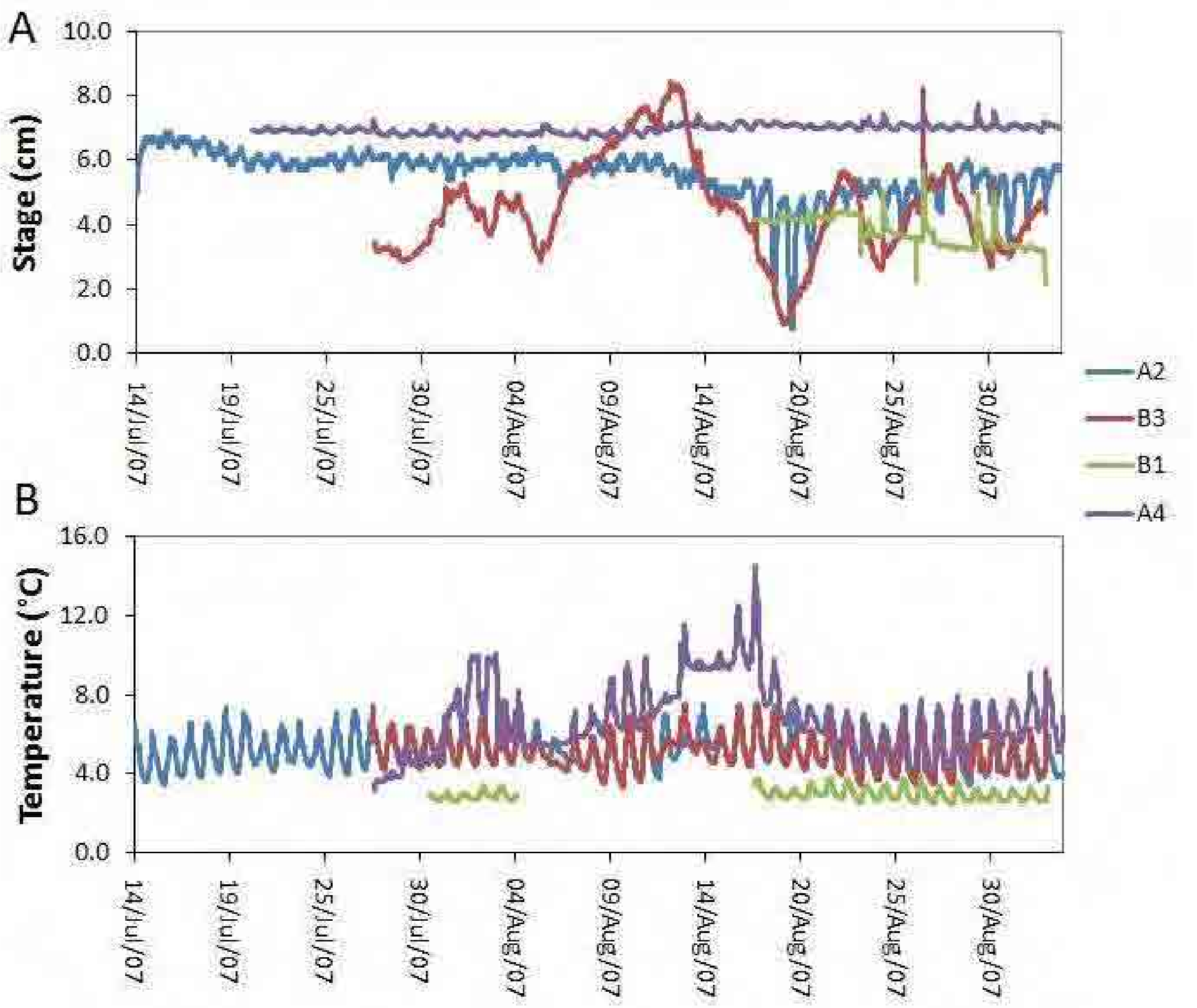
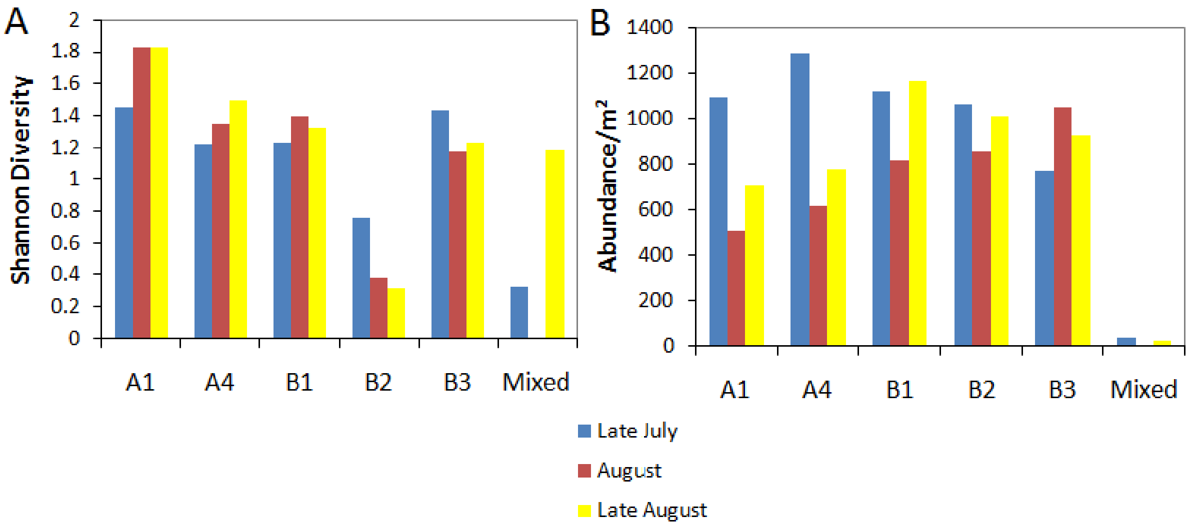
APPENDICES

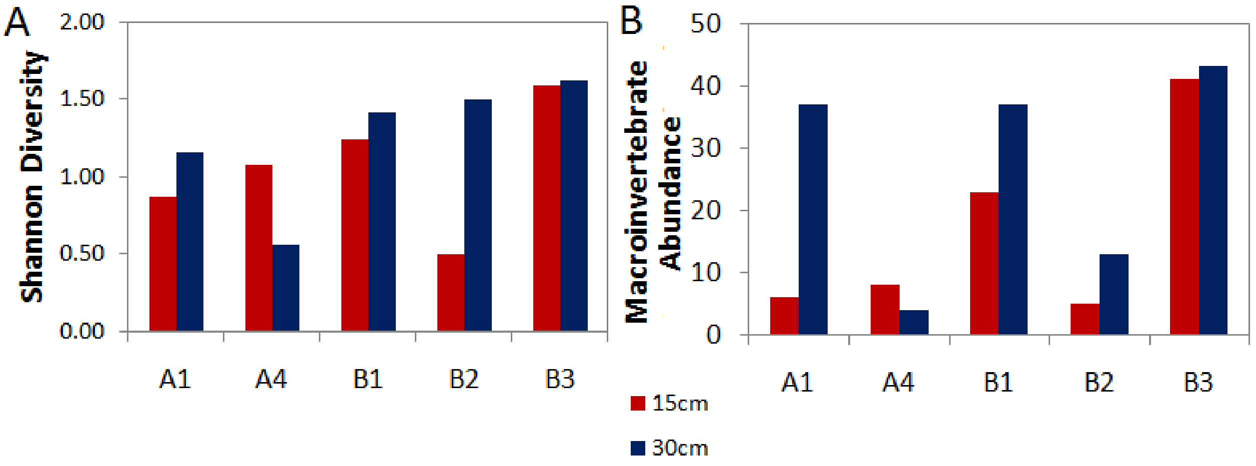
APPENDIX A: Presentation of data from initial six week study season in 2007



APPENDIX Ai: A) Stream temperature and B) flow regimes of groundwater-fed stream in summer 2007



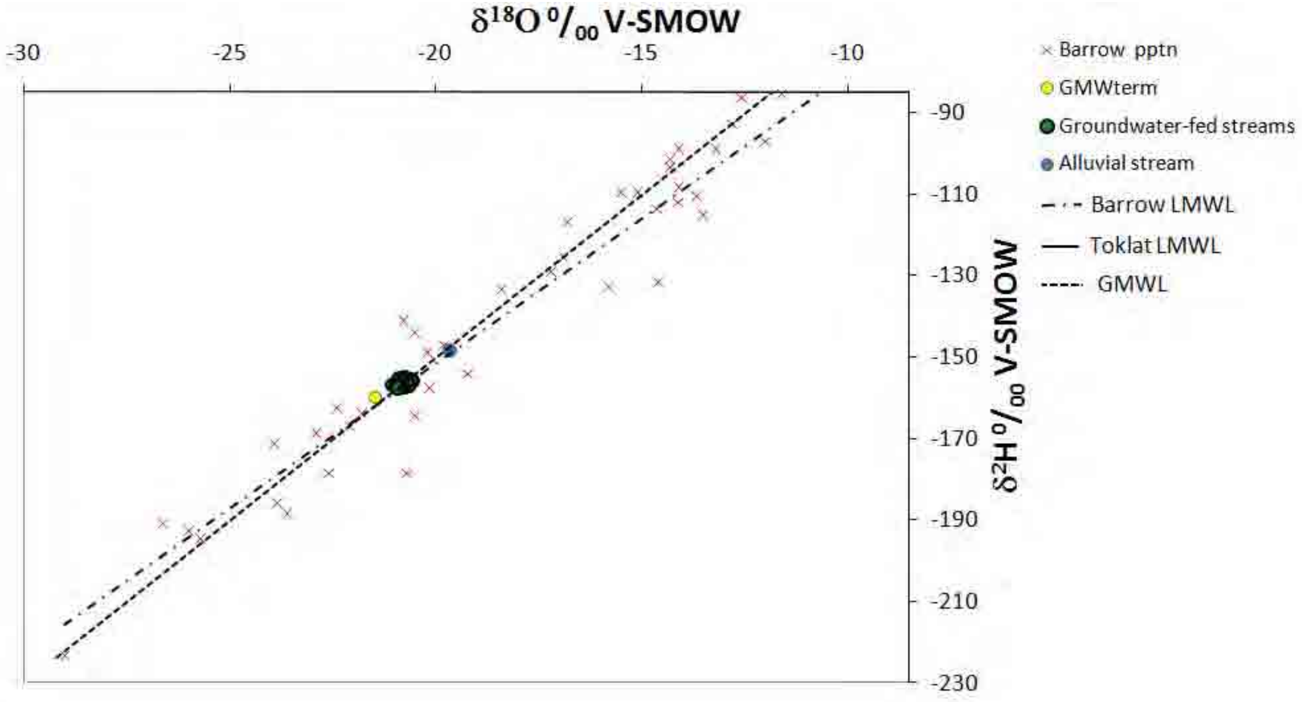
APPENDIX Aii: A) Macroinvertebrate diversity and B) abundance within groundwater-fed streams in 2007



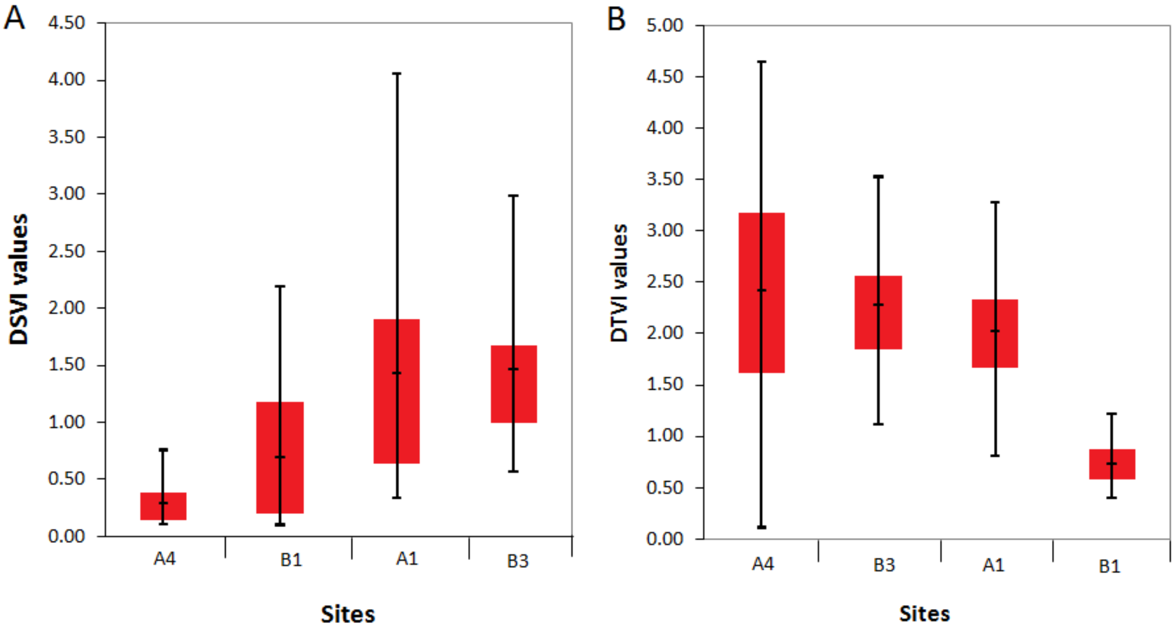
APPENDIX Aiii: A)Hyporheic macroinvertebrate diversity and B) abundance in groundwater-fed streams of 2007

Site	Cl^-	δ^2H	$\delta^{18}O$	pH
A1	3.39	-156.08	-20.81	7.8
A4	4.75	-155.59	-20.86	8.1
B1	3.14	-156.94	-20.73	8.2
B2	0.01	-157.07	-20.83	8.0
B3	0.01	-156.68	-20.82	8.3
Glacial meltwater	0.016	-159.92	-21.48	-

APPENDIX Aiv: Mean water chemistry values of groundwater-fed streams, in summer 2007



APPENDIX Av: Isotopic composition of source waters and groundwater-fed streams in 2007. Barrow local meteoric water line (y = 7.12x – 9.13) calculated from GNIP dataset spanning 7 years. GMWL = 8x + 10

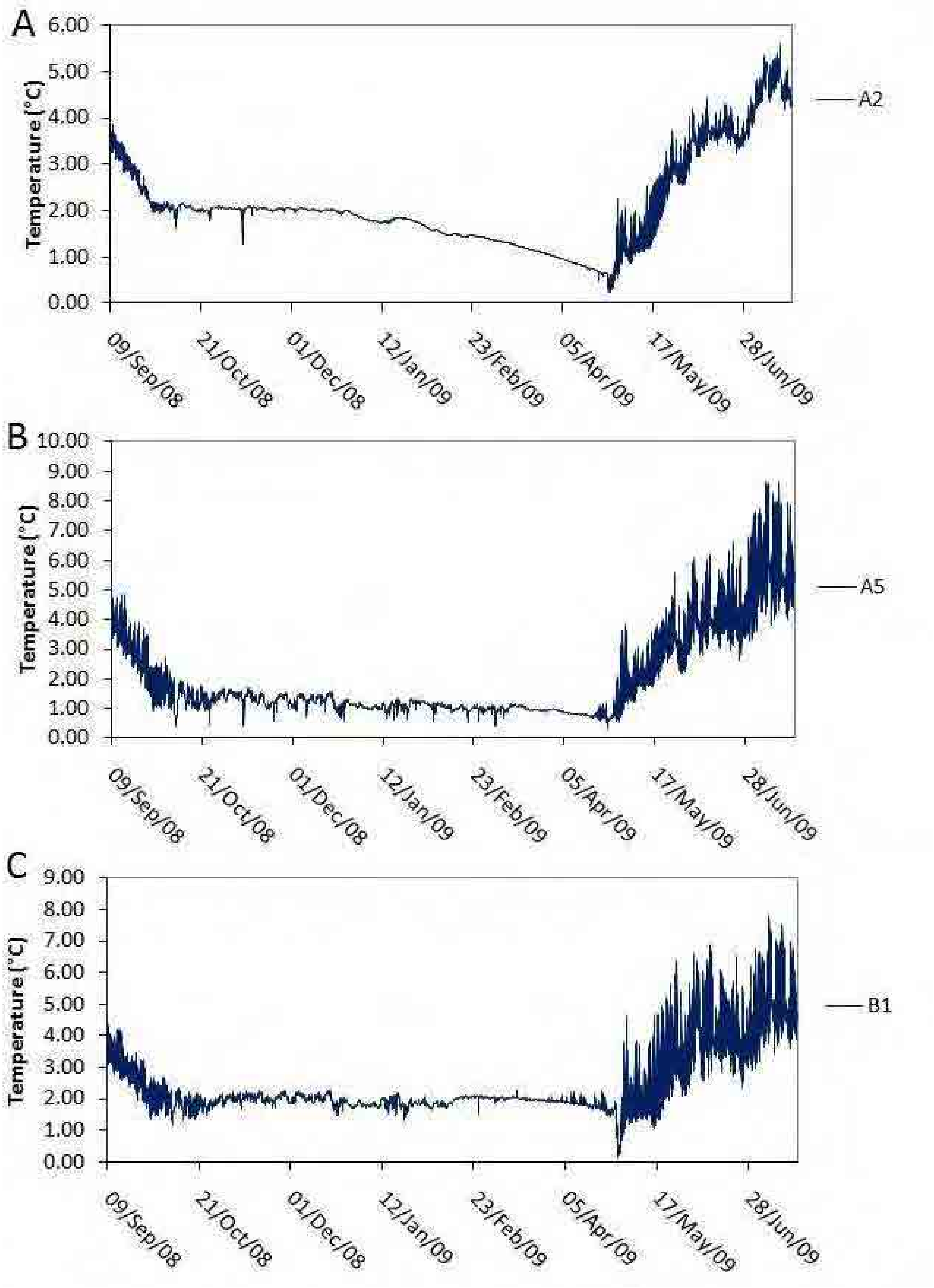


APPENDIX Avi: A) Diurnal stage and B) temperature variability of groundwater-fed streams in summer 2007

APPENDIX B: Equipment used in hydrological measurements of groundwater-fed streams

Site	Measurement	Depth	Equipment
A2	Stream temperature and depth	Surface	Gemini TinyTag Plus and Druck Pressure Transducer
	Hyporheic temperature	20cm	Temperature Probe and CR10X datalogger
A5	Stream temperature and depth	Surface	In-Situ Minitroll
	Hyporheic temperature	50cm	In-Situ Minitroll
B1	Stream temperature and depth	Surface	Gemini TinyTag Plus and Druck Pressure Transducer
	Hyporheic temperature	20cm	Temperature Probe and CR10X datalogger
B2	Stream temperature and depth	Surface	Trutrak Pressure Transducer
B3	Stream temperature and depth	Surface	In-Situ Minitroll
	Hyporheic temperature	50cm	In-Situ Minitroll

APPENDIX C: Annual temperature regimes of perennial streams A)A2, B)A5, C) B1. This demonstrates baseflow seepage from DFS_{deep}



APPENDIX D: List of taxa found in groundwater-fed streams in Denali National Park, Alaska.

Order	**Family**	**Genus**	**Species**
Plecoptera	Nemouridae	*Nemoura*	**arctica**
		Zapada	**haysi**
	Perlodidae	*Isoperla*	**pertersoni**
	Chloroperlidae	*Alaskaperla*	***ovibovis***
		Plumiperla	***diversa***
	Leuctra	*Megaleuctra*	**spp.**
Ephemeroptera	Baetidae	*Baetis*	**bicaudatus**
		Baetis	**tricaudatus**
Tricoptera	Limnephilidae	***Ecclisomyia***	**spp.**
Diptera	**Chironomidae**		
	Psychodidae	*Pericoma*	spp.
	Ceratopogonidae	*Serromyia*	spp.
	Simuliidae		
	Tipulidae	***Tipula***	**spp.**
		Hexatoma	**spp.**
	Empididae	***Chelifera***	**spp.**
		Clinocera	**spp.**
		Oreogeton	**spp.**
	Muscidae	***Limniphora***	**spp.**
	Ephydridae	***Ephydra***	**spp.**
Arachnida	**Hydracarina**		
Collembola	*Isotomidae*		