The diversity and composition of benthic macroinvertebrate assemblages in streams in the Mackenzie River System, Northwest Territories

by

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AUTHOR'S DECLARATION

I hereby declare that I am the sole author of this thesis. This is a true copy of the thesis, including any required final revisions, as accepted by my examiners.

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Abstract

Impending natural resources development and concern about the effects of climate change have spurred increased efforts to study and monitor aquatic habitats in the Mackenzie River system. As part of Environment Canada's attempt to survey the system in advance of the construction of the Mackenzie Gas Pipeline, benthic macroinvertebrates were sampled at 50 streams spanning the geographical range of the Mackenzie system in the Northwest Territories, Canada, to assess spatial patterns in diversity and assemblage structure and the environmental factors driving them. Replicated, quantitative D-net samples were collected during the late summer of 2005 through 2008, mostly at crossings of the proposed pipeline route.

373 macroinvertebrate taxa were recorded, mainly aquatic insects, which were identified to the genus or species levels; other groups were identified to higher taxonomic levels. Ephemeroptera and Plecoptera diversity declined along a latitudinal gradient, while Trichoptera diversity declined in the middle of the latitudinal range and rose towards the far north. Chironomidae (Diptera) increased in diversity and abundance towards the far north, becoming dominant in the northern sub-arctic forest and lowland tundra of the Mackenzie Delta. Diversity, measured as the average generic richness per stream, correlated with a composite environmental variable representing stream size, but not much else; spatial trends in local generic richness were only apparent in the far north of the study area. Regional diversity was assessed using rarefaction curves and showed a clear decrease from south to north across the study area for most taxa; the major exception was the chironomid subfamilies Orthocladiinae and Chironomini, the former being diverse throughout the study area and the latter increasing in diversity on the tundra. Odonata, Hemiptera and Coleoptera were well-represented in the south of the study area, but decreased sharply in diversity and abundance in the north; another common order, Megaloptera, was entirely absent from the study area, as were crayfish.

Community composition varied along a latitudinal gradient, with some species restricted to northern latitudes and many more species restricted to the southern areas. Composition varied by region, as did the environmental factors that control it. Streams in the north of the system are connected to hundreds of small lakes and tend to freeze in the winter, which increases habitat stability; assemblages in this region were characterized by relatively large chironomids that are usually associated with lentic habitats and by a lack of taxa that are intolerant to freezing. Substrate was the main factor explaining differences in assemblage composition in this region. Just to the south, alluvial streams are more common and permafrost is continuous with very shallow active layers, which likely results in intense discharge peaks and ice scour in the spring and flashy summer hydrographs. Invertebrates in this region were mainly short-lived, small sized orthoclads, baetids and chloroperlids; the annual disturbance regime seems likely to be an important factor shaping community composition in this region. Many streams in this region received input from saline springs, resulting in perennial flow, and these streams harboured several taxa that were absent or rare in other streams at similar latitudes, including several stoneflies (e.g. *Pteronarcys*, *Sweltsa*); the presence of flow during the winter was found to be a major factor affecting community composition in this region, which surrounded the town of Norman Wells, NT. Nutrient dynamics appeared to be important in structuring benthic assemblages in the southern portion of the study region, with high-nutrient streams supporting a diverse fauna which included many taxa that were absent in the north, while communities in low-nutrient streams were more similar to the northern alluvial stream fauna. There was no spatial distinction between low- and high-nutrient streams in the southern region, and the difference may be due to the local conditions of permafrost, which is patchy and discontinuous in the region.

Evidence that winter ice and permafrost conditions are important drivers of benthic invertebrate diversity and community composition in the Mackenzie system, along with the latitudinal gradients which are consistent with a temperature/climate gradient, raises the possibility that benthic assemblages may be useful as indicators of effects of global climate change on freshwater habitats in the Canadian north. More immediately, construction of the Mackenzie Gas Pipeline may affect stream habitat due to sedimentation, and plans for the operation of the pipeline have raised concerns about potential effects on permafrost conditions. Implications for development of a biomonitoring program utilizing benthic invertebrates and their potential as indicators of climate change are discussed.

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Chapter 1

Introduction: Physical and biotic characteristics of northern streams, with a focus on the Mackenzie River system

Few extensive surveys of lotic macroinvertebrates have been conducted in the Mackenzie River system, but, thanks to increasing natural resources development and the acute threat of climate change in the far north, increasing attention is being paid to aquatic ecosystems in the region. The Mackenzie River system spans the longitudinal and latitudinal ranges of the Northwest Territories and extends from boreal forest in the south, through subarctic forest to tundra in the north. The wide range of environmental conditions and climatic severity experienced by streams in the system leads to variable hydrological and disturbance regimes and availability of habitat and food resources over a latitudinal gradient. This range in conditions is likely to have a large effect on benthic invertebrate assemblages, as streams towards the north experience colder temperatures, shorter growing seasons, greater likelihood of freezing and ice scour, increasing dominance of the hydrological effects of permafrost, and limited allochthonous food inputs. Habitat stability may decrease towards the north due to spring ice scour and flashy summer flow patterns. In the far north of the Mackenzie system, the landscape and stream morphology of the Delta may ameliorate the seasonal disturbance regime (though freezing to the substrate during the winter is likely) and flooding in the spring facilitates nutrient exchange between the stream, surrounding water bodies and the landscape. These factors have the potential to pose constraints on benthic invertebrate life cycles, growth rates, environmental tolerances, behaviour, population dynamics, and most other aspects of their biology. While the response of any given species to arctic conditions is unique, the effects of a wide array of environmental conditions are integrated at the community or assemblage level. In this study, I use a spatial survey of benthic invertebrate assemblages in small streams across the Mackenzie River system in the Northwest Territories to examine latitudinal patterns in community composition and diversity.

This section provides an introduction to the study area and provides a brief overview of the environmental factors relevant to benthic invertebrates in high-latitude streams; where possible I have used studies specific to the Mackenzie River system, but the discussion should be applicable to small to mid-sized arctic and subarctic streams generally.

1.1 Physical and climate characteristics of the Mackenzie River System

Extending over 15° of latitude and portions of three provinces and two territories, the Mackenzie River drains an area of northern Canada (1.78 million km^2) larger than central Europe (Culp *et al.* 2005), delivering 333 km^3 of water and 118 million tonnes of suspended sediments to the Beaufort Sea each year (Brunskill 1986). The study area (Figure 1.1) is tributary streams north of the Peace-Athabasca delta, so encompasses a great diversity of climatic and geological conditions, spanning

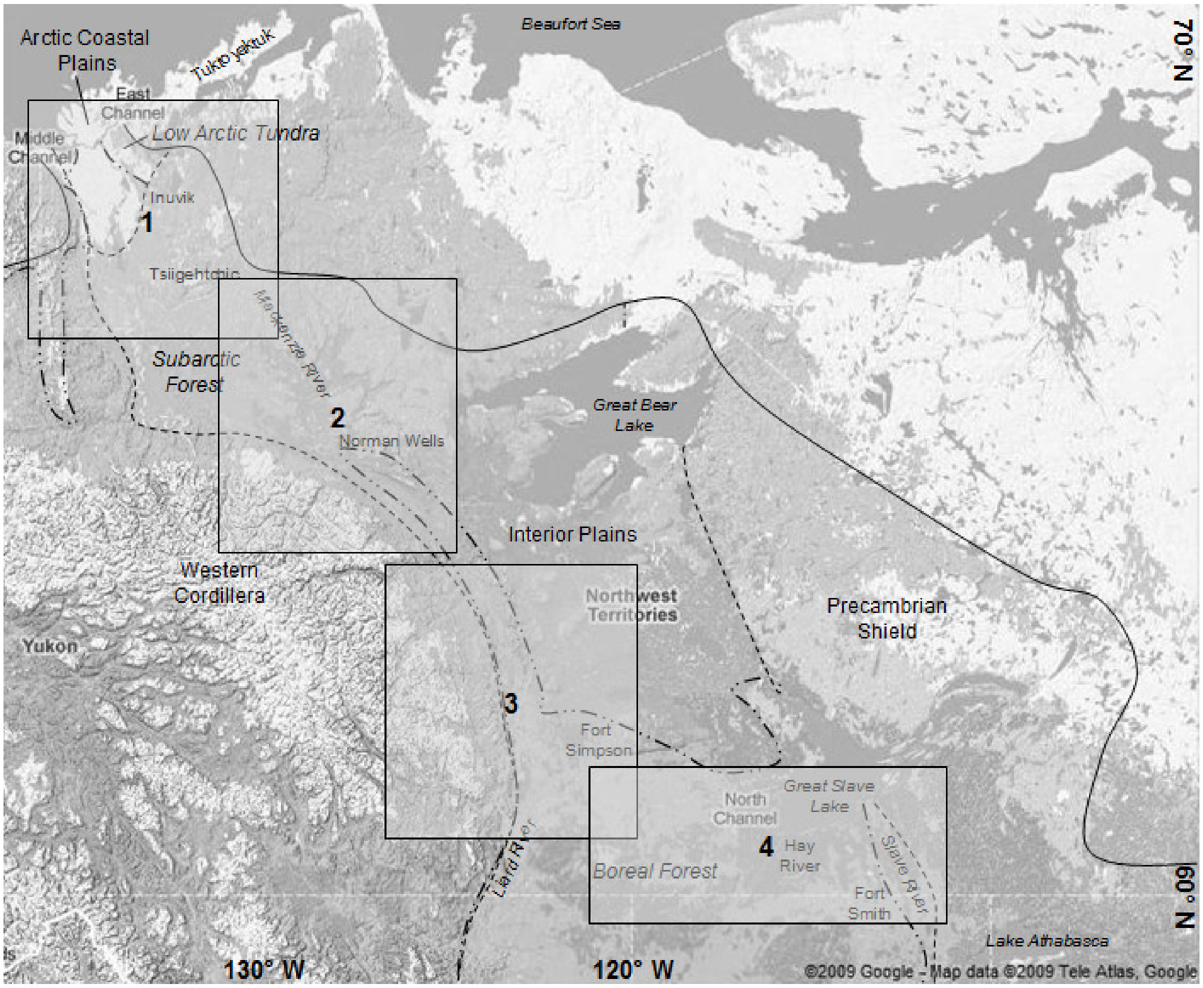

Figure 1.1 – Overview map of the Mackenzie River System in the Northwest Territories. Numbers and shaded areas indicate the areas covered by the regional maps on subsequent pages. Solid lines (—) indicate the boundaries of the Mackenzie basin, hatched lines (- - -) indicate boundaries of physiogeographic areas, and solid/hatched lines (— - - —) indicate boundaries of major vegetation zones. Regional Map 1 (Figure 2.1) shows sites in the far north and western cordillera; Regional Map 2 (Figure 2.2) shows sites surrounding Norman Wells; Regional Map 3 (Figure 2.3) shows sites in the Liard basin and surrounding areas; and Regional Map 4 (Figure 2.4) shows sites surrounding Great Slave Lake. Image obtained from Google Maps.

three biogeographic regions -the Interior Plains, Western Cordillera and Arctic Coastal Plains (Brunskill 1986) - and three major vegetation regions -boreal forest, subarctic forest and low arctic tundra (MRBC 1981). This range of environmental and geological conditions means that the hundreds of smaller tributary streams in the system experience diverse climatic, hydrologic and nutrient regimes. Unless otherwise noted, the sources for this section are the reviews by Brunskill (1986) and Culp *et al.* (2005).

Although the entire system can be considered northern, there is a distinct gradient of climatic severity, with lower temperatures, longer winters and decreasing solar radiation towards the north (Table 1.1). Permafrost is patchy and discontinuous in the south of the study area, but increases in thickness from 12 m on average near the confluence of the Mackenzie River main stem with the Liard River near Fort Simpson, to 60 m near Norman Wells, up to nearly 800 m on the arctic coastal plains, although in the Mackenzie Delta it may be as shallow as 10 to 50 m (Brunskill 1986). Precipitation on the west side of the river is up to four times higher annually than on the east side, which is why all of the major tributaries originate on the western edge of the basin (Culp *et al.* 2005). Differences in terrain and geology are interrelated with the relatively recent glacial history of the basin. Until about 12,000 to 14,000 years ago most of the system was covered by the Laurentide ice sheet, with scattered Cordilleran glaciers and refugia in the western mountains; as the ice receded the basin filled with glacial melt water and was covered by several very large lakes until about 9,000 to 10,000 years ago. The climate may have been warmer following the receding of the glaciers, since the Tuktoyaktuk peninsula, presently tundra, supported spruce forests until about 4,000 years ago (Brunskill 1986). Today the flat or rolling terrain of the interior plains, which comprises most of the study area, is overlying poorly drained sandstones, shales and limestones, usually with high soil organic contents. The western cordillera is mainly sedimentary rock, and the streams carry a high proportion of the summer precipitation (40 to 70%) as runoff and contribute most of the sediment load of the Mackenzie River main stem. Boreal forest predominates in the southern regions, and the range of mixed deciduous/coniferous forests extends northward in a narrow band on either side of the Mackenzie River. East and west of this band and north of Norman Wells is mainly subarctic forest, dominated by black spruce (*Picea mariana*), willow (*Salix* spp.) and alder (*Alnus viridis*). North of the treeline, sparse willows (*Salix herbacea*) grow along the edges of streams. Most streams in the subarctic plains and forest are shallow and probably freeze to their bottoms in the winter; some regions contain taliks which deliver perennial supplies of saline water.

Table 1.1 – Summer and winter climatic conditions in the Mackenzie River system. Source: Brunskill (1986).

	Summer			**Winter**			
	July mean temp. (°C)	June-July max photoperiod (hours per day)	Avg daily solar radiation (g cal cm^{-2})	Winter mean temp (°C)	December min photoperiod (hours per day)	Avg daily solar radiation (g cal cm^{-2})	Length of winter (days)
North of Great Slave Lake	10 to 16	24	450 to 550	(-23) to (-29)	0	10 to 25	200 to 250
South of Great Slave Lake	16 to 21	17	500 to 550	(-20) to (-26)	8	25 to 75	175 to 200

1.2 Physical & chemical characteristics of high-latitude streams

Arctic and sub-arctic lotic ecosystems are fundamentally defined by extremes of climate and seasonality. The flow regime is determined by complex interactions between stream morphology, permafrost conditions and ice formation, resulting in pronounced seasonal disturbance regimes in many streams. Ice formation during the long arctic winter can extend to the streambed, restricting habitat availability, reducing flow and limiting solar radiation and terrestrial inputs for much of the year, all of which limit the productivity of aquatic systems. However, the short growing season brings an influx of nutrients from snowmelt, extensive exchange of water and nutrients with the surrounding landscape and abundant sunlight that fuels high levels of primary production. These seasonal extremes pose considerable challenges to invertebrates attempting to inhabit the benthos of streams in the north.

McKnight *et al.* (2008) suggested a classification of arctic streams based on channel morphology and water source. The major types of channel are 1) “peat” channels, which are generally beaded series of deep pools and narrow runs over low gradients, with fine sediments and lots of organic matter (actual peat may or may not be present); and 2) alluvial channels, which usually have steeper gradients and coarser substrates. The major sources of water in the arctic are runoff from snow melt or precipitation (many streams are fed primarily by surface flow), springs (limited in areas of continuous permafrost to unfrozen areas called *taliks* (Woo *et al.* 2000)) and the melting of glaciers (which are limited in the Mackenzie system to high-latitude areas in the south, outside of the study area). Many streams alternate between the two morphologies or receive water from multiple sources, but broad differences between these stream types have important implications for flow conditions (Woo & Thorne 2003, Best *et al.* 2005, Huryn *et al.* 2005) and nutrient cycling (Brosten *et al.* 2006).

1.2.1 Seasonal variation in flow & the disturbance regime

The length of the winter season (air temperature under 0°C) varies in the Mackenzie system between approximately 6 months in the south and 8 months in the north; during this period average daily temperatures range from -20 to -29°C (mean daily January temperatures), but can be warmer during the short summer season, ranging from 10 to 21°C in July (Brunskill 1986). Although precipitation is usually highest in July or August, due to the long winter most of the annual precipitation arrives as snow and enters streams in a short but intense pulse in the spring (Culp *et al.* 2005). Most of the system, including the entire survey area of the present study, lies over continuous or discontinuous permafrost (MRBB 2009). The extent and seasonal dynamics of ice below and above ground largely determine inter-seasonal and, during the warmer seasons, intra-seasonal variation in flow and the severity of disturbance that accompanies peaks in discharge.

Annual peaks in discharge are driven by spring snowmelt, which contributes the majority of the annual discharge of most streams (Stewart *et al.* 1998), though groundwater may make a relatively large contribution in the southern Mackenzie system where permafrost is discontinuous (St Amour *et al.* 2005). When permafrost lies under a shallow active soil layer, water retention is low and there is usually a rapid increase in discharge in response to precipitation in the summer, resulting in the flashy hydrograph that is characteristic of a nival flow regime (Woo 2000). Although precipitation makes a relatively minor contribution to the water cycle, balanced by evaporation from thermokarst lakes or unfrozen soil (Rouse 2000), large, ephemeral increases in flow can occur in response to precipitation; these summer peaks can be mediated by the presence of lakes or wetlands along the stream course, or when inputs from glacial melt-water are substantial (Woo & Thorne 2003).

In stark contrast to the hydrologic variability of the growing season, flow during the winter is invariably reduced. Smaller streams usually freeze solid while larger streams may retain perennial flow (McKnight *et al.* 2008), but the propensity of a stream to freeze is determined by an array of factors. Shallow, narrow streams are less likely to freeze, though there is a question of cause and effect (Best *et al.* 2005); significant groundwater inputs can allow perennial flow (Huryn *et al.* 2005); and permafrost can cause unfrozen water to continue to cool after the ice cover has formed (Danks 2007). Outflows of large lakes are not likely to freeze, and larger rivers that receive relatively warm water from southern regions retain perennial flow (Prowse *et al.* 2006a). In frozen streams, aquatic habitat is effectively limited to small pockets of anoxic water that is usually high in solutes due to freezing out (Danks 2007), and flow is usually greatly reduced even in perennial streams (Power & Power 1995).

The onset of spring ice and snow melt varies according to air temperature (Prowse & Beltaos 2002) and its duration ranges from days to weeks, depending on the permeability of the active layer, water storage in lakes and ponds and re-freezing of melt water (Stewart *et al.* 1998). The stored precipitation from the previous 6 – 9 months is quickly released, and peak flow during this period can constitute over 50% the annual discharge, especially in channels mostly fed by runoff (Rouse 2000). Snowpack depth determines run-off levels in the spring, and can vary widely due to wind-driven drifts and sublimation (Rouse *et al*. 2003) and much of the total runoff ends up entrained by permafrost in lakes and wetlands (Prowse *et al*. 2006a). Ice melt accelerates as discharge accumulates downstream, resulting in large hydraulic forces and swift increases in temperature at the breakup front (Prowse & Culp 2003). In large, north-flowing rivers, ice break-up proceeds slower in the downstream regions than in the warmer headwaters, resulting in massive ice jams that can inundate floodplains for weeks at a time (Rouse *et al.* 1997); in the Mackenzie Delta, approximately 50,000 small floodplain lakes and ponds are connected each spring by ice-jam flooding (McKnight *et al.* 2008). Intense breakup events occur in the main channels throughout the Mackenzie system, particularly at major confluences (MRBC 1981).

Alongside the annual flow maxima induced by spring snowmelt, the breakup of ice can cause intense physical disturbance. Breakup can be characterized as 1) thermal, in which ice weakens gradually throughout the spring with little disturbance to the banks or sediments, or 2) dynamic, where attached ice is mechanically broken apart by the high spring discharge and significant scouring of the channel margins may occur (Scrimgeour *et al.* 1994). Peak annual suspended sediment loads usually occur during ice melt due to the scouring of margins and channel bottoms, and visible changes to the landscape (such as widened channels, slumping banks, and redirection of the stream course, sometimes forming oxbow lakes) are common (Prowse & Culp 2003). Ice with flowing water underneath it is more likely to undergo dynamic breakup while smaller streams with bedfast ice often remain frozen until later in the spring and break up thermally, avoiding both high spring flows and ice scouring (Best *et al*. 2005). The beaded morphology and low gradients characteristic of peat channels (e.g. in the Mackenzie Delta and lowland tundra) are not as conducive to transporting large amounts of sediment compared to alluvial channels (e.g. in the subarctic and boreal forest), and the former may experience relatively little mechanical disturbance in the spring (McKnight *et al.* 2008).

1.2.2 Seasonal variation in nutrient dynamics

Although spring ice melt causes a great deal of disturbance to stream habitats, it brings with it a pulse of nutrients that drives primary and secondary production through the summer. Runoff from snowmelt delivers large quantities of dissolved organic matter derived from terrestrial primary production into streams (McKnight *et al*. 2008) and ice scour liberates large amounts of dissolved and particulate carbon, nitrogen and phosphorus from the sediments and banks; peak concentrations of these nutrients usually coincide with spring ice breakup (Scrimgeour *et al.* 1994). Evidence from stable isotopes has shown that the food webs of small arctic streams are primarily fuelled by terrestrially derived carbon (Bunn *et al.* 1989), which, considering the limited vegetation of the arctic tundra could be mainly delivered in a pulse in the spring (Prowse & Culp 2003). Streams that flood in the spring may receive large additional inputs of nutrients from their floodplains (McKnight *et al.* 2008), often enhanced by biogeochemical and photochemical processing, particularly in the Mackenzie River delta (Lesack *et al.* 1998).

During the brief summer and autumn seasons, autochthonous primary production is severely limited by nutrient concentrations, specifically those of phosphorus (Peterson *et al.* 1993). Phosphorus is generally kept at low levels by a combination of factors, including adsorption or precipitation of inorganic phosphorus with iron hydroxides and calcium, respectively, as well as immediate utilization of available phosphorus by aquatic primary producers and microbes (Kling *et al.* 1992). Grazing by invertebrates is also likely to limit benthic primary production (Quesada *et al*. 2008), but phosphorus and (to a lesser extent) nitrogen limitation seem to be the key factors keeping epilithic algal production low, as indicated by unusually high abundances of benthic algae resulting from a long-term phosphorus enrichment experiment (Peterson *et al.* 1993; McKnight *et al.* 2008) and downstream of a sewage discharge in a stream near Resolute Bay, NT (Quesada *et al*. 2008). In drainages with continuous permafrost, precipitation flows quickly through the upper soil matrix, which is rich in organic matter (Rouse 2000), so such streams may receive periodic summer influxes of dissolved organic matter and other nutrients (McKnight *et al.* 2008). Hyporheic exchange is limited by active layer depth in streams running over continuous permafrost (Brosten *et al.* 2006); however, hyporheic biogeochemical processing in some arctic streams reaches rates similar to those found in temperate climates, and the hyporheos is an important source of dissolved nutrients to stream water (Edwardson *et al.* 2003). Alluvial stream types are generally more responsive to temperature changes than peat channels, which are insulated by organic material. Alluvial streams therefore tend to have deeper active layers underneath the stream during the summer; however, the insulating effect of peat channels permits the relatively shallow active layer to keep growing well into the fall, after alluvial channel active layers have begun to freeze (Brosten *et al.* 2006). Inputs of allochthonous coarse particulate organic matter (CPOM) are high in the autumn, but much lower than in temperate streams due to limited vegetation; however, the quality of the detritus may be higher since the proportion of woody debris is generally lower in arctic than in temperate streams (Cowan & Oswood 1983). A second pulse of CPOM usually occurs in the spring, as runoff from snow-melt flushes partially degraded organic matter into the streams (Cowan & Oswood 1983, Scrimgeour *et al*. 1994).

During the long winter, any water remaining in the channel is effectively cut off from terrestrial inputs by ice and snow cover and from groundwater inputs by permafrost, except in perennial streams fed by springs (Power & Power 1995, Danks 2007). The low angle of the sun limits the available light, and most of this is cut off by thick snow cover. Heterotrophic metabolism can quickly deplete the water of oxygen; however, if there is little snow cover (e.g. due to wind activity) and light can penetrate the ice, primary production can quickly saturate the water with oxygen (Prowse & Culp 2003). Winter in the arctic and sub-arctic is generally a long period in which water and nutrients are stored outside of the stream (in or under ice and snow), aquatic habitat is severely limited, and most hydrologic, biogeochemical and biological processes effectively come to a halt.

1.3 Benthic communities in high-latitude streams

The seasonal extremes of climate and disturbance in arctic and sub-arctic regions pose constraints on the growth rates, life cycles and habitat selection of stream invertebrates. Several orders of aquatic insects that are common in temperate streams (Odonata, Hemiptera, and Coleoptera) are rare at high-latitudes, and Megaloptera are entirely absent (Rautio *et al.* 2008). The Ephemeroptera, Plecoptera and Trichoptera are much less diverse than in temperate regions, and are represented by only a few families in the far north, although they are often abundant (Oswood 1989). Northern benthic communities are usually dominated by Diptera, especially Simuliidae and Chironomidae, the latter being the only common aquatic insect group in the high arctic (Hershey *et al.* 1995).

The ability to disperse among streams and watersheds is probably very important in the highly variable arctic environment (Miller & Stout 1989), and arctic lotic insect communities tend to reflect a mix of Nearctic and Palearctic influences (e.g. Irons 1988), with little evidence of biogeographic boundaries (Hershey *et al*. 1995). In the winter, the availability of unfrozen habitat is a major constraint on survival of many species (Power & Power 1995), while the scouring that accompanies dynamic ice break-up is a cause of significant mortality in the spring (Scrimgeour *et al.* 1994), although it also brings a pulse of nutrients and detritus, and may provide a level of disturbance that helps maintain biodiversity (Prowse 2001). The dominance of fine particulate organic matter as a food source in the summer may favour collector-gatherer and filter-feeding species over other functional feeding groups (Rautio *et al.* 2008). Stream type and source of water are important factors, as many taxa are limited to glacier- or spring-fed streams that retain perennial flow (Hoffsten & Malmqvist 2000, Huryn *et al.* 2005, Lencioni & Rossaro 2005).

This section provides a brief and general outline of the physiological, phenological and behavioural mechanisms used by lotic invertebrates to overcome seasonal constraints and take advantage of the short growing season. Although the seasonal cycles of physical disturbance, nutrient pulses and freezing/thawing are fairly predictable, it is important to note that variations in climate in one season can have large effects on the habitat and biota that often carry over into subsequent seasons (McKnight *et al*. 2008). Summer temperatures can determine rates of growth and emergence, thereby affecting the biomass of aquatic insects in subsequent summers (Hodkinson *et al.* 1996). The level of precipitation in the fall determines the amount of winter snowpack, which affects the freezing conditions of the stream and therefore habitat availability (Clifford 1969) and the duration of ice and snow cover, affecting adult emergence in the spring and summer (Finn & Poff 2008). Wind activity and snow capture by the surrounding terrain and vegetation during the winter determine the distribution of snow prior to melting, which partly determines the amount of runoff and the level of disturbance experienced in the spring (Rouse 2000). Because of the connection between seasonal climate and aquatic habitat characteristics, northern stream invertebrate communities may be strongly affected by climate change.

1.3.1 Adaptations to spring conditions

Streams that undergo dynamic ice breakup in the spring experience an annual period of intense disturbance when invertebrates may be mechanically damaged by ice scour or displaced by high flow (Scrimgeour *et al.* 1994). Since unfrozen habitat is often limited to a small portion of the channel (Power & Power 1995), ice scour can be very efficient in clearing large portions of the fauna from stream reaches, resulting in highly variable compositions of the summer communities (Miller & Stout 1989). Species with good dispersal capabilities (in the air or in the drift) can quickly re-colonize patches cleared by ice scour, so the effect of the intense disturbance is usually short-term (Young & Mackie 1991), and diversity in arctic streams is often stable (Prowse & Culp 2003), although patterns of abundance and dominance have been described as largely stochastic (Miller & Stout 1989, Milner *et al.* 2006). Streams that regularly experience extreme ice scour are probably not favourable to sessile macroinvertebrates (Sousa 1984).

The unpredictable nature of disturbance that accompanies dynamic ice breakup strongly favours insects with univoltine life cycles, since insects that spend more than one spring season in the same aquatic habitat have a higher chance of mortality. Emergence of adults of most univoltine species occurs in early spring (Clifford 1969), allowing dispersal to newly cleared habitats, e.g. *Ephemerella aurivillii* (Ephemerellidae); other species spend the winter as eggs or 1st instar larvae and grow rapidly in the spring (Ulfstrand 1968), possibly taking advantage of the seasonal nutrient pulse. Many species avoid the annual disturbance entirely by overwintering in habitats that are not exposed to ice scour. For example, *Leptophlebia cupida* (Leptophlebiidae) nymphs overwinter in deep pools and migrate along the banks in the spring to mature rapidly in small streams that had been frozen during the winter (Clifford 1969) or to warmer meltwater pools (DR Barton, pers. comm.). Some Plecoptera oviposit in lakes in the fall and then drift into streams after the snowmelt (Prowse 2001); others overwinter as eggs or dormant larvae or pupae in the hyporheic zone or in protected stream edges (Danks 2007).

Insects in streams that are frozen solid and undergo thermal break-up are usually protected from the worst of the spring disturbance, but they also face physiological and phenological constraints. Many insects can survive freezing (see below), but recrystallization of ice during thawing can cause internal mechanical damage (Danks 2007). Since the stream bed often does not thaw until late spring, the length of the growing season may be reduced by a month or more, and the spring pulse of nutrients and particulates may pass these habitats by, flowing overtop of the ice. Life cycles of two or more years are not uncommon (Ulfstrand 1968), and many species will delay emergence and enter diapause until the following year if they need to feed in the spring (Danks 1992b).

1.3.2 Effect of conditions during the growing season

The summer and autumn seasons are periods of intense activity and growth for most northern aquatic invertebrates. Many insects have adapted to the brief growing season by emerging as early as possible, as has been reported for many arctic mayflies, stoneflies and caddisflies (Ulfstrand 1968, Clifford 1969, Irons 1988, Stewart *et al* 1990, Giberson *et al*. 2007). Most of the early emerging species grow rapidly in the fall, coinciding with peak concentrations of CPOM, which is utilized rapidly (Cowan *et al.* 1983). Other univoltine species grow rapidly in early summer and emerge in time to oviposit and possibly hatch before the onset of freezing (Clifford 1969), while semivoltine species living in relatively stable habitats can grow slowly throughout the summer and emerge early in spring in the year that they complete development (Ulfstrand 1968, Danks 1992b). Multiple cohorts are commonly observed, and in arctic streams there is little synchronization of emergence;

this contrasts with the often tightly synchronized emergence of insects in northern lentic environments (Armitage 1995).

Streams with nival flow regimes experience unpredictable seasonal disturbance due to run-off related flow events, which may affect community composition by limiting the importance of biotic interactions (e.g. competition) (Poff & Ward 1989) and increasing temporal and spatial variability (Miller & Stout 1989). The dynamics of disturbance and resultant drift followed by recolonization of disturbed patches are thus likely to be important in northern streams in the summer (Townsend 1989), dependant on stream morphology, permafrost conditions and precipitation patterns; this topic is discussed further in the introductions to Chapters 3 and 4.

Limitations on adult dispersal are commonly overlooked, but likely are important in the far north (Danks 2007). The nature of the terrestrial vegetation covering the surrounding landscape affects the distance that aquatic insect adults migrate by offering shelter and opportunities for rest (Delettre & Morvan 2000), so the tundra landscape potentially limits the dispersal ability of many insects because of a lack of opportunities for shelter and rest. Many insects are limited by air temperatures that are lower than those required for flight. Loss or limitation of flight ability is common, and some insects mate on the ground or water surface rather than in the usual aerial swarms (Danks 2007). Reproduction via parthenogenesis is common in aquatic insects in the arctic, and allows perpetuation of the species without leaving the stream or finding a mate (Langton 1995, Giberson *et al.* 2007).

1.3.3 Adaptations to winter conditions

Arctic winters impose severe constraints on aquatic invertebrates in the form of sub-zero temperatures, limited food availability and frozen habitat, and most animals survive the season in a dormant state. Some invertebrates may be active under the ice in unfrozen habitat, but are susceptible to scouring by frazil or anchor ice (Martin *et al.* 2000). The propensity of a stream to freeze solid in the winter is major determinant of community composition (Huryn *et al.* 2005), and when a perennial stream anomalously freezes solid the effects can be long-lasting (Hoffsten 2003). Most species need to either cope with freezing or avoid it, and northern aquatic insects possess a variety of physiological and behavioural mechanisms to survive the winter. Excellent reviews of the current state of knowledge of the mechanisms involved are provided by Danks (2007) and Walters *et al.* (2009); the overview given here will necessarily be brief.

Although a few limnephilid caddisflies are capable of overwintering as adults in leaf litter under snow cover (Danks 2007), most arctic aquatic insects spend the winter as eggs or larvae. Eggs mostly avoid freezing by lowering their water content, but other mechanisms such as production of anti-freeze proteins are possible (Danks 2007). Larvae that cannot tolerate freezing must either select a habitat that is unlikely to freeze (e.g. Clifford 1969) or actively move away from the freezing front (Irons *et al.* 1993). However, these animals may still be susceptible to desiccation due to the high solute content of the unfrozen water or to anoxia due to limited photosynthesis and water flow in sealed off pockets of water, as well as to mechanical disturbance by frazil ice and slush.

Aquatic insects that survive encased in ice do so by two general mechanisms: 1) avoiding freezing by dehydration or by discouraging freezing (either by removing ice nucleators from the hemolymph or by producing antifreeze compounds or proteins) or 2) encouraging freezing of the extracellular matrix by producing ice nucleators while discouraging freezing or desiccation of cellular fluid using antifreeze compounds (Walters *et al.* 2009). Although the ability to survive freezing has been demonstrated in many chironomids and several limnephilids (Danks 2007), few physiological studies have been conducted on freeze-tolerance in aquatic insects. It is generally assumed that the mechanisms are similar to those found in terrestrial species, although aquatic insects face additional threats related to encasement in solid ice: inoculative freezing may induce ice crystal formation through the cuticle (Frisbie & Lee 1997) and mechanical damage may be incurred from high pressure since water expands as it freezes (Danks 2007). In most species that have been studied in detail, a period of acclimation is required for cold-tolerance to develop (Walters *et al.* 2009), and the ability to survive freezing is usually limited to only one life cycle stage (Bouchard *et al.* 2006). Most of the demonstrated freeze-tolerant species belong to the Diptera (especially Chironomidae and Empididae) (Irons *et al*. 1993), but they also include some limnephilids (Danks 2007) and a very common arctic stonefly, *Nemoura arctica* (Walters *et al.* 2009). Mechanical damage resulting from freezing and thawing is also a risk, and many chironomids construct special winter cocoons in response to low temperatures (Tokeshi 1995). Many northern caddisflies also construct special cocoons or simply modify their summer cases (Danks 2007). The case-building behaviours of these groups may represent a pre-adaptation to arctic conditions, and partly explain their relative diversity at northern latitudes.

1.4 Previous research on benthic invertebrates in the Mackenzie System

Lotic invertebrates in the sub-arctic regions of the Mackenzie River System have received very little attention compared to their Alaskan (Oswood 1989, Stewart *et al.* 1990, Huryn *et al.* 2005) and European (Malmqvist & Hoffsten 2000, Beketov 2008, Heino & Paasivirta 2008) counterparts, and even within Canada the aquatic insect fauna of the Yukon (e.g. several chapters in Danks & Downes

1997), Nunavut (Giberson *et al.* 2007) and the high arctic (Stocker 1972, Danks 1980, Andrews & Rigler 1985) have been studied more recently and extensively. Barton (1986) noted the lack of information on benthic invertebrates in the Mackenzie system, but remained the only published review of faunal surveys until Culp *et al*. (2005), who had very few updates to report. The watersheds of the upper Mackenzie System are subjected to greater anthropogenic influences (primarily flow regulation by the Bennett Dam on the Peace River and oils sands development along the Athabasca), and so have been studied more thoroughly (Barton & Wallace 1980, Shaw *et al.* 1990) and more closely monitored (e.g. the Regional Aquatic Monitoring Program in Alberta; RAMP 2008) than the regions north of Great Slave Lake. This study only concerns streams in the Northwest Territories, so the literature review given here is limited to studies from that region.

Most of the information on benthic invertebrates in the Mackenzie System, NT, has been gathered in response to interest in natural resources development, especially gas pipeline construction (Barton 1986), which was also the impetus for the current study. The hydrology and ecology of the main channels (the Liard, Slave and the Mackenzie River itself) are generally better studied than those of smaller tributary streams. Wiens *et al.* (1975) provided species lists from an extensive survey of streams, including a few Cordilleran streams that were sampled in this study, but provided only presence-absence data. Jessop *et al*. (1973) found that benthic invertebrates provided a major food resource for a diverse fish community in Rat River, a Cordilleran stream that flows into the Mackenzie Delta. McCarthy *et al*. (1997) conducted a baseline survey of the Slave River and reported a fauna dominated by Chironomidae and Oligochaeta. Tallman (1996) found a much more diverse aquatic insect fauna in the guts of fish (cited in Culp *et al*. 2005), but together these studies suggest that the benthic diversity of the mainstem is limited relative to the tributaries. MacDonald (1992) surveyed the length of the Liard River and reported a longitudinal transition between the high-elevation headwaters and the lowland confluence with the Mackenzie (cited in Culp *et al*. 2005). There have been a few studies on the potential effects of human activities on benthic communities, relating to sedimentation from construction of roads and pipeline crossings (Brunskill *et al.* 1973, Rosenberg & Snow 1975, Young & Mackie 1991) and accidental oil spills (Snow *et al.* 1975); these studies generally found the communities to recover rapidly from short-term anthropogenic disturbance.

Because the few studies listed above sampled different types of streams and identified the invertebrates to varying taxonomic levels, generalizations about the fauna are difficult. Most studies note the importance of Chironomidae and Simuliidae, which often compose over 50% of the fauna (Barton 1986), and several general are widespread across the system, including *Procladius,* *Chironomus, Dicrotendipes, Polypedilum, Cladotanytarsus, Micropsectra, Stempellina, Tanytarsus, Corynoneura, Cricotopus, Eukiefferiella, Orthocladius, Psectrocladius* and *Simulium* (Wiens *et al*. 1975). Other common insects include *Baetis*, *Ephemerella*, *Heptagenia* (Ephemeroptera), perlodid and nemourid Plecoptera, *Brachycentrus*, *Hydropsyche*, *Lepidostoma* and Limnephilidae (Trichoptera) (Wiens *et al.* 1975, Barton 1986, Culp *et al.* 2005). Barton (1986) observed that the representation of Plecoptera and Amphipoda increases towards the north while that of Ephemeroptera and Trichoptera increases towards the south, but also noted that differences in habitat types sampled among studies probably obscures important relationships. The fauna is believed to derive from Pleistocene refugia in both the east and the west, but dispersal has likely obscured historical biogeographic patterns, especially among some of the more widely distributed insect species, and seasonality and habitat characteristics (i.e. aspects of the landscape, hydrology and substrate) are likely more important determinants of the faunal composition (Barton 1986).

1.5 Ecological threats to the current state of the Mackenzie River System

1.5.1 Natural resources development

The vast majority of streams and rivers in the Mackenzie River System north of Lake Athabasca can be considered pristine, with undeveloped watersheds and few sources of anthropogenic pollution. Towns are small, with most limited to a few hundreds of people. Mines are few in number with active mines largely limited to diamond mines outside the Mackenzie River Basin. Oil has been extracted at Norman Wells since the late 1940s by drilling, with numerous drill pads located in the river. While there have been concerns over the years with these operations and their effects on fish health, there has been no evidence that these activities are contaminating the Mackenzie River.

The Mackenzie River Basin proper is rich in oil and gas reserves, with immense oil sands reserves in the Fort McMurray area in Alberta and gas and oil reserves in the Arctic Ocean, including the Beaufort Sea and Mackenzie River delta (Gautier *et al*. 2009). The immense gas and oil reserves in the Mackenzie River and Beaufort Sea area have been known for decades; in the early 1970s, environmental and social studies were conducted to investigate the feasibility of extracting these reserves and pumping oil and gas south in a pipeline. However, during this inquiry, which was headed by Justice Thomas R. Berger, issues related to Aboriginal land claims and creating conservation areas were not adequately addressed; Berger recommended a ten year moratorium on the development of the pipeline to deal with these issues (JRP-MGP 2010).

In recent years, the potential construction of the pipeline has been revisited. A new series of environmental impact assessments have been conducted with the findings presented by Imperial Oil Resource Ventures (2004). These findings and questions arising and addressed have been published in the recently released Joint Review Panel report (JRP-MGP 2010); unless otherwise noted, these are the sources of information in this section.

As currently planned, the gas fields would be developed by a consortium of oil companies, including Imperial Oil and Shell (which would operate one gas field each), ConocoPhillips and ExxonMobil (which would share the Parsons Lake operation), and a group representing aboriginal interests. There would be two drill pads in the outer Mackenzie River delta and one or two drill pads on Parsons Lake. Approximately 190 km of gathering pipeline (of varying diameter) would connect these gas fields to facilities in Norman Wells, and then a 1,220 km pipeline, about 30 cm in diameter, would carry the gas to existing pipeline systems in northern Alberta, where it will mostly be used to heat water from the Athabasca River to extract bitumen from the oil sands. With projected capital costs of over $16 billion (CDN), the extraction and transport systems will take approximately 4 years to complete, and operations could commence as early as 2014 (JRP-MGP 2010).

The buried pipeline system will run along the east side of the Mackenzie River as far as Jean-Marie River, where it will cross the Mackenzie and run into Alberta. The pipeline will cross approximately 700 waterways of varying sizes, and is therefore regulated under the *Fisheries Act*, which prohibits harmful alteration, disruption or destruction (HADD) of fish habitat, including food resources (e.g. benthic invertebrates). While physical conditions and fish populations at waterway crossings were surveyed for an initial environmental impact assessment (IORV, 2004), no benthic studies at stream crossings were conducted as part of this assessment, so this thesis addresses an important knowledge gap. The Department of Fisheries and Oceans (DFO), which enforces the *Fisheries Act*, has expressed the concern that knowledge of the physical and biological baseline conditions at many of the stream crossings is poorly developed (JRP-MGP 2010).

Most of the initial focus on the stream studies has been placed on the choice of construction method used at stream crossings. Four types of waterways were identified. Vegetated creeks are small, shallow, often ephemeral vegetated drainages or dispersed overland overflow. Active II streams freeze to the bottom or are dry in winter. Active 1 streams are perennial in flow or only freeze partially to the bottom while large rivers and streams have perennial flow and drainage areas generally >1000 km^2. Construction will take place during the winter, and vegetated and active II streams will be crossed using the open-cut method, in which a trench is dug straight across the stream. Other (more expensive and time-consuming) options are available for active I streams and large rivers with perennial flow including cutting under the creek/river bed. Isolated cut methods involve pumping water through pipes over or around the crossing site during construction, while the horizontal directionally drilled (HDD) method can place the pipeline under the stream without instream construction or trenching; this latter is more expensive and is currently planned for only 17 channel crossings, mainly large rivers. While current plans call for open cuts at all crossings other than the Active I and large river types, perennial streams that have not been shown to contain fish overwintering or spawning habitats may receive open cuts, as will crossings for which the more specialized isolation and HDD methods have been deemed unfeasible. Therefore, the effect of pipeline construction will theoretically be greatest on perennial (Active I) streams, particularly when the open cut construction method is used.

The Mackenzie Gas Pipeline would be the first North American below-ground, temperature-regulated pipeline constructed in continuous permafrost; changes in ground temperature around the pipeline as a consequence of this thermal regulation could impact permafrost and ultimately stream hydrology and morphology at the crossings. The pipeline running between Inuvik and northern Alberta facilities will operate with a seasonal temperature regime designed to minimize freezing-related physical stress, i.e. between 6°C in the summer and -8°C in the winter with an annual average of 1°C. Since ground temperatures are near the freezing point, the thermally-regulated pipeline could induce melting of the normally frozen ground and, during other times, freezing of ground that is normally seasonally thawed. The loss of permafrost around the pipeline crossings may lead to increased groundwater inputs and perennial flow and may also induce the formation of frost bulbs which can disrupt winter flow and scour the sediments in the spring. Pipeline damage may occur. These concerns may be accentuated by global warming. The potential for cumulative impacts are essentially unknown, as all other below-ground pipelines in arctic and sub-arctic North America either operate at ambient temperatures (e.g. near Norman Wells) or are located in areas with much colder permafrost, which can probably tolerate low levels of warming without reaching the melting point (e.g. in Alaska). Similar pipelines have been constructed in Siberia, where alterations of the landscape related to frost heave and thaw settlement have been observed, indicating the potential for impacts to permafrost dynamics.

1.5.2 Global climate change

Northern systems are highly susceptible to the effects of climate change; the Mackenzie River System is warming particularly rapidly. Annual average temperatures in the system have been rising by approximately 0.5 to 0.8 °C per decade, and winter temperatures have been rising by as much as 2 °C per decade (Stewart *et al.* 1998). General circulation models predict that a doubling of the concentration of atmospheric CO_2 could result in modest increases in summer temperature (2-4 °C) and large winter increases of 4 to 8 °C (Rouse *et al.* 1997). Rising sea levels, a result of melting sea ice, will strongly affect low-lying areas of the Mackenzie Delta (Lesack & Marsh 2007), and drill pad operations in the delta are expected to result in delta subsidence. Additionally, precipitation may increase by up to 10% annually as circulation patterns (currently mainly Arctic for most of the year) are altered, with increasing importance of Pacific air masses (Rouse *et al.* 1997). Changes in the timing and extent of river ice and intensity of spring flooding, lengthening of the growing season, and permafrost melting (with increases in active soil layer depth) have been predicted, and in many cases already observed (Prowse *et al.* 2006b). However, diverse physical and hydrological conditions, the complexity of potential feedback loops, and uncertainties about the effects of warming on atmospheric, hydrologic and biogeochemical cycles make even general predictions difficult.

The most substantial changes to northern streams are likely to result from increased temperatures particularly as they affect melting of the permafrost. Rising temperatures and increasing seasonal melting of surface permafrost have been observed in Alaska (Hinzman *et al.* 2005), and one model predicts that the Mackenzie basin will be free of surface permafrost (< 3 m deep) by the end of the 21st century (Lawrence & Slater 2005). While this will undoubtedly have large effects on the hydrology, nutrient supply and ecosystem structure of streams, the nature of these changes depend on a myriad of other factors, such as elevation and relief, watershed geology, changes in precipitation and concurrent effects on primary production and biogeochemical cycling (Prowse *et al.* 2006b). Permafrost prevents groundwater from reaching stream channels in the winter, and many streams that currently freeze to the substrate may become perennial as permafrost thawing increases (Huryn *et al.* 2005). Weathering of exposed rock will result in higher inputs of inorganic nutrients and solutes to streams (Prowse *et al.* 2006b), and increased rates of DOM production may increase inputs of organic nutrients from the watershed, although these latter may be offset by increased rates of mineralization (Lyons & Finlay 2008). Water storage in soils will increase, with important consequences for hydrology and nutrient cycling (Rouse 2000). Runoff flows through the organic soils of shallow active layers very quickly, resulting in flashy summer hydrographs in streams with continuous permafrost. Increased water retention will dampen the hydrograph (Rouse *et al.* 1997), increase the time available for microbial processing (Lyons & Finlay 2008), and, depending on changes in precipitation and terrestrial vegetation (Prowse *et al.* 2006b) decrease hydrologic inputs to streams as more water is lost to evaporation (Rouse 2000). While the magnitude and rate of hyporheic exchange may be increased by permafrost melting, they are limited by the morphology and flow rates of tundra streams (Zarnetske *et al.* 2008). Increasing water infiltration to the soils will probably result in the disappearance of many shallow thermokarst lakes in the north of the study area, and the landscape will likely become considerably drier as the permafrost melts (Hinzman *et al*. 2005).

In addition to permafrost melt, increasing air temperatures are likely to effect seasonal patterns and production levels. The ice-free growing season will increase in length as snowmelt begins earlier (Rouse *et al.* 1997); currently, onset of snowmelt is advancing by about three days per decade in many parts of the Mackenzie System (Woo & Thorne 2003). Since solar radiation at the onset of spring melt will be lower, melt will occur over a longer period of time, and the accompanying disturbance to stream channels may be less intense (Prowse *et al*. 2006b); however, thinner ice cover and perennial flow may increase the likelihood of dynamic breakup, so the implications for the seasonal disturbance regime are unclear (Scrimgeour *et al.* 1994). The combination of longer growing seasons, higher temperatures and increased phosphorus inputs from weathering is expected to dramatically increase aquatic primary productivity (Flanagan *et al.* 2003), although light limitation due to high DOC and turbidity, as well as grazing by consumers, may keep these increases in check (Wrona *et al.* 2006). Riparian CPOM inputs will probably increase substantially as vegetation zones shift north in response to warmer temperatures and permafrost melting (Hinzman *et al.* 2005). Major changes to aquatic habitat in the Mackenzie Delta will likely involve altered connectivity between the river, estuary and floodplain due to a combination of rising sea levels and decreased ice jamming in the main channels. Summer water levels in low elevation areas of the delta have been rising concurrently with sea levels (although the relationship is more complicated, since water level increases in the delta have exceeded sea level rises by approximately 3:1), while the connection times and extent of spring flooding of higher elevation streams further from the main channels has decreased (Lesack & Marsh 2007). Major changes to tundra streams in the system will therefore depend on their proximity to the river: low elevation streams will be flooded for longer periods of the growing season, while higher elevation streams could dry up in the summer unless precipitation increases substantially.

Predictions of future changes to the environment are made uncertain by the lack of understanding of the current and historical conditions of many of the processes involved and the feedback loops that connect them. Our ability to predict the effects on macroinvertebrates and other biological assemblages is limited even further by our general lack of knowledge of community organization (including competition and predation), population genetic structure, dispersal patterns and species-specific physiology, phenology and behaviour in the arctic. Many insects in northern regions are living near the limit of their environmental tolerances (Danks 1992a), so as temperature and nutrient availability increase and disturbances from freezing and discharge variation decrease, many species will see their ranges shift northwards as species adapted to warmer climates colonize new habitats and coldwater species are forced further north (Allan & Flecker 1993). Temperature alone can have substantial effects on the life histories and growth rates of aquatic insects, with faster growth, earlier emergence and smaller size at maturity associated with warmer temperatures (Hodkinson *et al.* 1996, Hogg & Williams 1996). Decreases in winter snowpack may have similar effects (Finn & Poff 2008), depending on changes in winter precipitation. Decreases in flow variability associated with permafrost melting will have consequences for community composition (Huryn *et al.* 2005), possibly reducing the high temporal and spatial variability of arctic macroinvertebrate communities (Miller & Stout 1989, Milner *et al.* 2006). The probability of substrate freezing during winter will decrease, which may allow successful colonization of species from perennial streams (Huryn *et al.* 2005), and it has been speculated that some freeze-tolerant populations may gradually lose this physiological ability (Danks 1992a).

If predictions of increased nutrient loading to streams are correct, the effect on stream macroinvertebrate communities could be profound (Huryn *et al.* 2005). The extent of these effects could depend on the level of nutrient enrichment (Hobbie *et al.* 1999). Due to the nutrient limitation of arctic streams, even small increases in phosphorus and nitrogen can increase primary production (primarily via increases in diatom abundance) and the abundance of benthic invertebrate grazers, as occurred in the first several years of a long term nutrient enrichment experiment in the Kuparuk River, Alaska (Peterson *et al*. 1993). At higher nutrient concentrations, there was a shift in primary producer dominance from diatoms to bryophytes (*Hygrohypnum* spp.), which increased habitat complexity and possibly sequestered nutrients (McKnight *et al.* 2008). This shift resulted in changes to the benthic macroinvertebrate assemblage, increasing the proportion of chironomids and *Ephemerella* while decreasing the proportion of *Baetis* and *Orthocladius*, the latter of which was the dominant chironomid prior to fertilization and in the control reach (Lee & Hershey 2000). Rising temperatures and longer periods of solar radiation are likely to magnify the increase in primary production rates (Flanagan *et al*. 2003), and, on a slightly longer timescale, increased CPOM from better developed riparian vegetation could further increase food resources available to benthic consumers. The heterotrophic microbial food web is a major component of total biomass in many aquatic arctic habitats (Wrona *et al.* 2006) and serves as an important link between primary production (allochthonous or autochthonous) and benthic consumers (McGoldrick *et al*. 2008). Understanding of the functioning of these heterotrophic communities in the arctic is poor, but given projected increases in temperature and inputs of nutrients, dissolved organic carbon (DOC), particulate organic carbon (POC) and dissolved inorganic carbon (DIC), rates of carbon processing by the microbial food web are likely to increase (Wrona *et al.* 2006). Overall, it seems that under many warming scenarios nutrient availability is unlikely to limit benthic invertebrate production to the degree it currently does, but the exact effects on assemblage composition cannot be predicted.

This M.Sc. thesis describes results and conclusions from a 2005 to 2008 survey of the benthic macroinvertebrate fauna in low to mid-order tributary streams along the entire length of the Mackenzie River in the Northwest Territories. Chapter 1 provides a general overview of the unique environmental conditions prevalent in northern streams and some of the common adaptations that allow stream macroinvertebrates to survive and thrive in the arctic and subarctic. The sites and measured environmental parameters are described in Chapter 2. Chapter 3 examines latitudinal trends in the number of species/genera and the differences in patterns of diversity among the major aquatic insect groups. Patterns of community assemblage are described in Chapter 4 and related to regional and local habitat characteristics. Chapter 5 summarizes the major findings of this thesis, discusses their relevance to biomonitoring and suggests potential implications of natural resources development and climate change to the benthic fauna of streams in the Mackenzie system.

Chapter 2

Habitat and water chemistry characteristics in the study area

2.1 Introduction

There is very little habitat information available about the majority of the sites used in this study; many had never been surveyed prior to an environmental impact assessment (IORV 2004) relating to the Mackenzie gas pipeline (JRP-MGP 2010). The purpose of this chapter is to analyze water chemistry and habitat variables measured as part of our survey, along with information from the 2004 EIS and mapping software, to provide a framework for analyzing the diversity and composition of benthic assemblages in later chapters.

2.2 Study sites and methods

2.2.1 Description and distribution of sites

Sites were selected in order to produce a latitudinal gradient of tributary streams covering the length of the Mackenzie System in the Northwest Territories. Many of the sites were located at proposed stream crossings of the Mackenzie Gas Pipeline; background information for these sites was provided by an environmental impact assessment relating to that project (IORV 2004). We generally limited sampling to streams that were comparable in size and flow conditions (i.e. large rivers and stagnant streams were excluded). Accessibility was also a factor limiting choice of sites; many of the streams were remote and in the summer could only be accessed by helicopter. Other streams were sampled at sites upstream of road crossings or near their confluence with navigable rivers.

Sampling locations are indicated on four regional maps (Figures 2.1, 2.2, 2.3 and 2.4; see Figure 1.1 for an overview). We sampled 56 sites over the four year (2005-2008) sampling period (Table 2.1), as well as some large river sites which were not included in this analysis (50 sites are indicated on figure one because some 2005 streams were sampled at 2-3 stations; see below). Due to the expense of travelling to isolated sites, we were able to sample each site only once, generally during the mid-to-late growing season (late July to early September). Sampling began by helicopter in 2005 working out of Norman Wells, NT (Figure 2.2). These streams generally had gravel-cobble substrate and flowed out of the foothills of the Norman Mountains directly into the Mackenzie River. Canyon Creek, Helava Creek, Oscar Creek and Vermillion Creek were sampled upstream and downstream of proposed crossing locations of the Mackenzie Gas Pipeline, and the latter two streams

Table 2.1 – Legend to numerical site labels on regional maps. Site numbers are ordered by latitude. Multiple stations at Oscar, Canyon, Helava and Vermillion Creeks have been condensed into one site due to the scale of the map.

Regional Map 1				Regional Map 2		Regional Map 3		Regional Map 4	
1	RPR-006.1	13	RPR-099	25	Tieda River	32	Dahadinni Creek	41	Red Knife tributary
2	Yaya River	14	Nello Creek	26	RPR-271	33	Hodgson Creek	42	Bouvier Creek
3	Zed Creek	15	Rengleng River	27	Chick Creek	34	Shale Creek	44	Little Buffalo River
4	RPR-032	16	Rat River	28	Oscar Creek	35	Stream 8	46	Sandy Creek
5	Hans Creek	17	Stream 3	29	Canyon Creek	36	Stream 7	47	Birch Creek
6	Stanley Creek	18	Thunder River	30	Helava Creek	37	Stream 6	48	Dettihih Dehe River
7	RPR-048	19	Stream 2	31	Vermillion Creek	38	Jean-Marie River	49	Salt River
8	RPR-058.6	20	Vittrekwa River			39	Birch River	50	Hornaday River
9	RPR-069	21	Stoney Creek			40	Poplar River		
10	RPR-070	22	Stream 1			43	Upper Blackstone River		
11	RPR-075	23	Treeline Creek			45	Trout River		
12	Travaillant Creek	24	Jackfish Creek						

were also sampled at their mouths, which were accessed by boat from the Mackenzie River. Tieda River was a relatively large river in the north of the Norman Mountains region. Chick Creek was located further from the Mackenzie River than the rest of the sites and flowed out of a small lake; nearby was RPR-271, a small vegetated creek.

In 2006 and 2007, we sampled streams in the far north of the Mackenzie System (Figure 2.1), working out of Inuvik, NT. All streams in the tundra and most in the taiga were accessible only by helicopter. RPR-006.1 and Yaya River were the northernmost sites, located between main channels in the Mackenzie Delta. Other tundra streams were RPR-032, Hans Creek and RPR-048, which flow west into the Mackenzie River, and RPL-001, which flows northeast through a network of lakes and pools into the Beaufort Sea. Taiga streams accessed by helicopter in 2006 were RPR-058.6 (just south of the treeline), RPR-069, RPR-070, RPR-075, Travaillant River, RPR-099, and, further to the south, Thunder River. The 2007 helicopter survey consisted of generally rocky, alluvial streams on the west side of the Mackenzie River which drain the Western Cordillera range. Rat River flows north to the Mackenzie Delta, while Vittrekwa River and Stoney Creek are tributaries of the Peel. These were

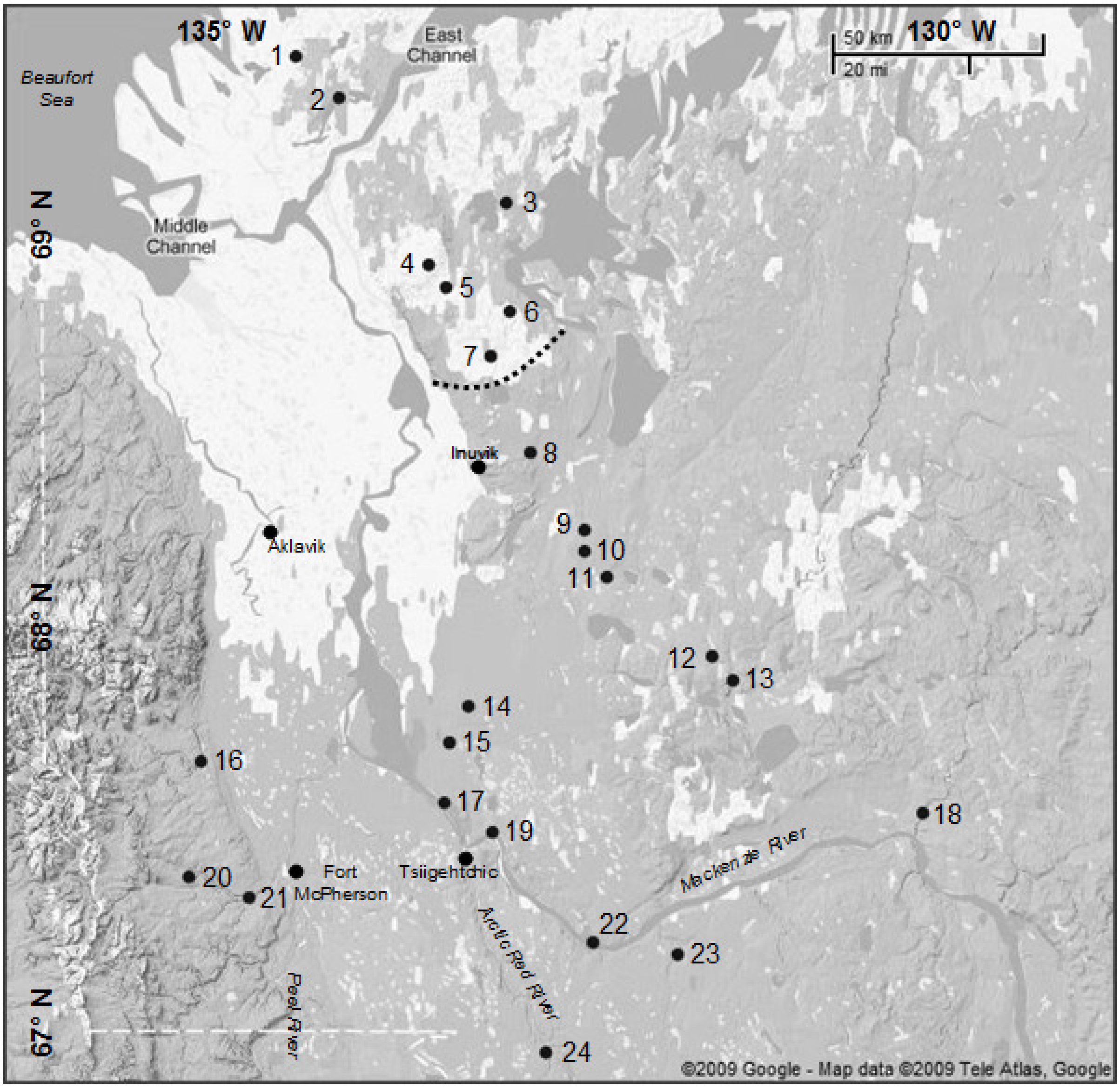

Figure 2.1 – Regional Map 1 (Northern sites). Numbers refer to sites as indicated in Table 2.1. Image obtained from Google Maps. The dotted line indicates the approximate location of the treeline.

sampled shortly following heavy rainfall, and were carrying considerably more than their base flows. Further to the south, Jackfish Creek is an Arctic Red River tributary and Treeline Creek (which is actually well south of the treeline) flows into the Mackenzie River. Two streams were sampled along the Dempster Highway in 2007: Nello Creek was a peat channel on flat terrain while Rengleng River was an alluvial stream in a steep valley, a sharp difference in landscape considering the streams were only about 12 km apart. Working out of Tsiigehtchic, we attempted to sample streams near the confluence of the Mackenzie and Arctic Red Rivers, but access was limited due to low water levels in

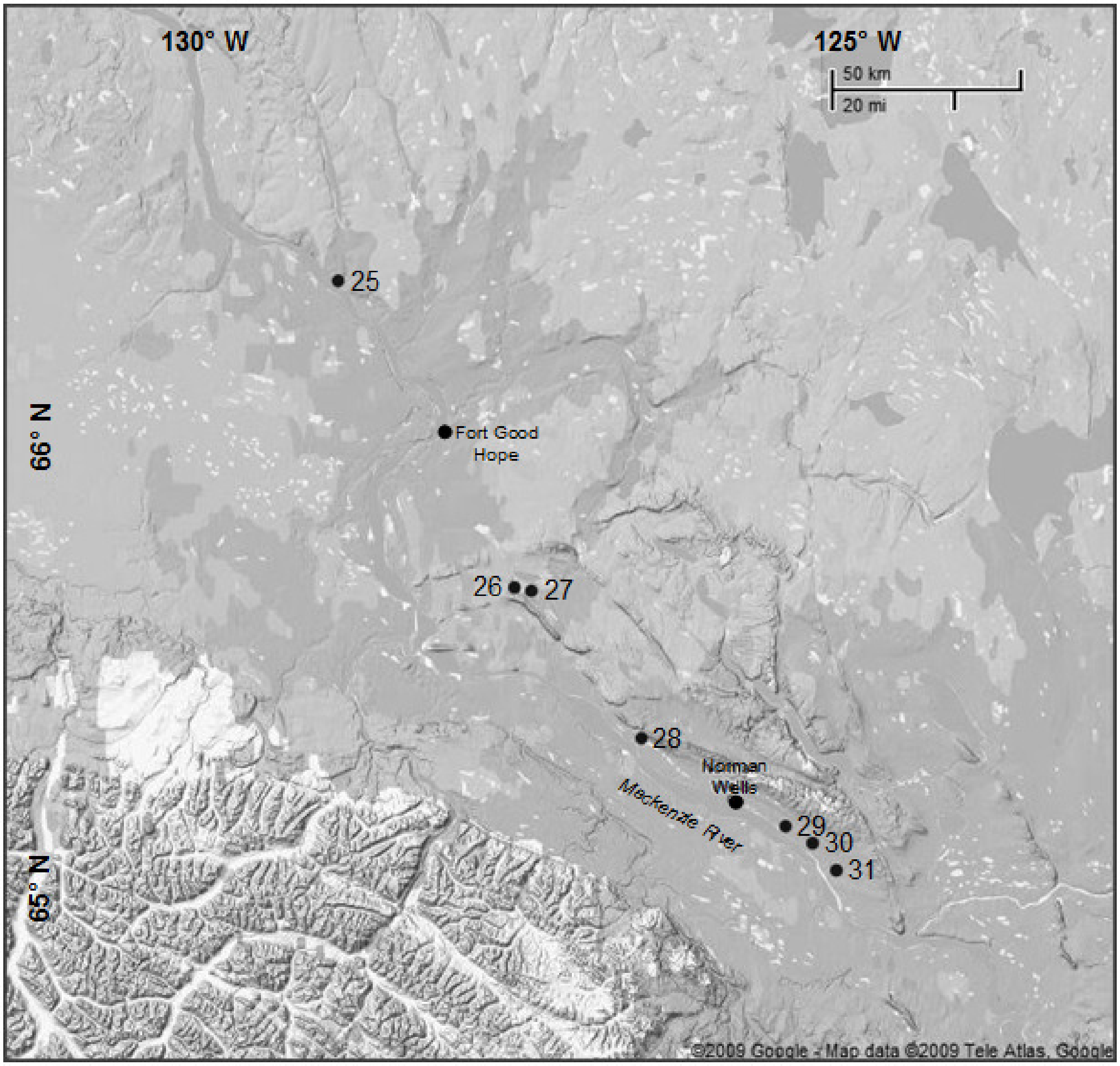

Figure 2.2 - Regional Map 2 (Norman Wells and surrounding area). Numbers refer to sites as indicated in Table 2.1. Image obtained from Google Maps.

the Arctic Red River and because the stream banks had often collapsed, covering the main channel with entangled shrubs and trees. The streams we sampled (Streams 1, 2 and 3) were generally small, possibly ephemeral streams which flowed directly into the Mackenzie River.

Samples from the Liard watershed (Figure 2.3) east to the start of the Mackenzie River at Great Slave Lake were collected by other workers from Environment Canada in 2006 and 2007. Laura Remple (DFO)'s collections in 2006 also included Stanley Creek in the tundra. Dahadinni River and Hodgson Creek were the only sites sampled along the long stretch between Norman Wells

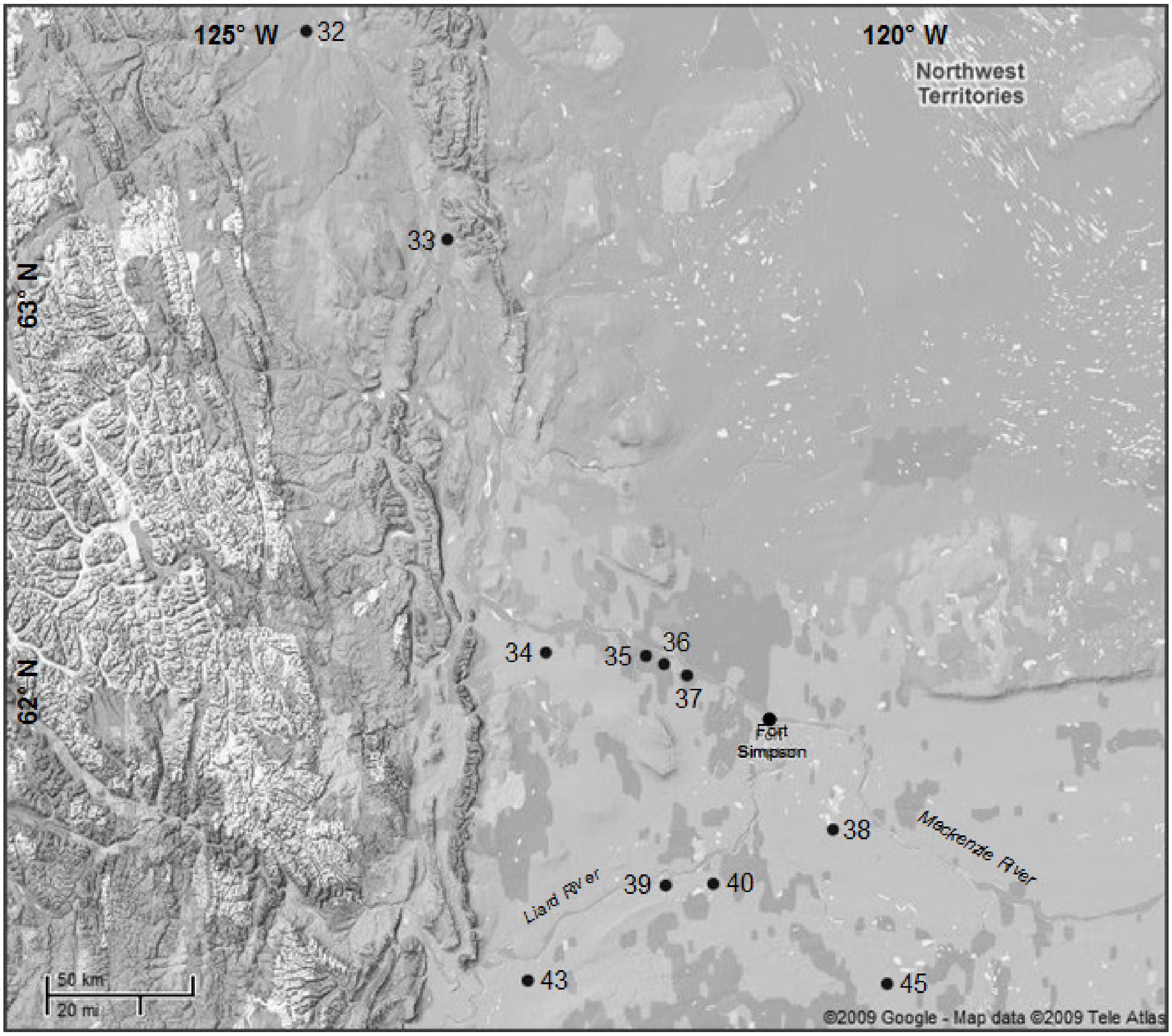

Figure 2.3 - Regional Map 3 (Liard basin and surrounding area). Numbers refer to sites as indicated in Table 2.1. Image obtained from Google Maps.

and the point where the Mackenzie River bends north; Shale Creek enters the Mackenzie just upstream of this bend. Streams 6, 7 and 8 are small streams flowing parallel to each other into the main stem. The Liard watershed is represented by Upper Blackstone River, Birch River and Poplar Creek. Jean-Marie River flows east from hills near the Liard River to the village of Jean-Marie, NT, where it enters the Mackenzie River. Further east, Bouvier Creek and an unnamed tributary of the Red Knife River flow directly into the Mackenzie. Trout River and Dehtihih Dehe River drain relatively high elevation areas well to the south of the Mackenzie main stem; the latter stream is by far the highest elevation sampled.

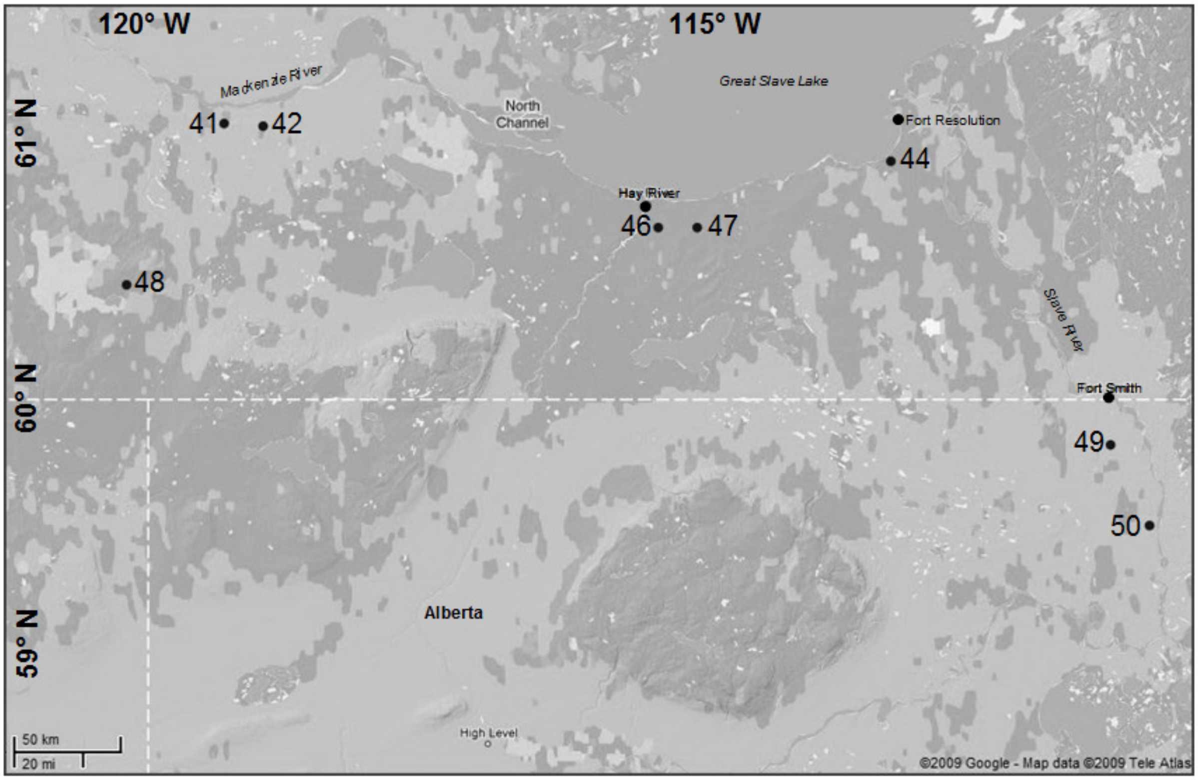

Figure 2.4 - Regional Map 4 (Great Slave Lake and surrounding area). Numbers refer to sites as indicated in Table 2.1. Image obtained from Google Maps.

In 2008, working out of Hay River and Fort Smith, NT, we sampled streams south of Great Slave Lake to just beyond the Alberta border (Figure 2.4) at highway crossings (upstream, where possible). Little Buffalo River (a large river), Sandy Creek (which was apparently blocked off downstream with very little flow) and Birch Creek flow north into Great Slave Lake a few kilometres beyond their sampling sites. Salt River and Hornaday River were tributaries of the Slave River in northern Alberta. Both of these streams contained large amounts of filamentous algae. Stream selection in the region south of Great Slave Lake was limited, as many of the potential sampling sites were either dry or blocked off (possibly by the highway); it was likely a very dry summer, with very little rainfall but with many forest fires occurring during the sampling period.

2.2.2 Collection of environmental variables

Slightly different suites of water chemistry and habitat variables were collected from year to year, so only those variables that were sampled consistently (i.e. those with values for all sites) have been used in this thesis. Composite water samples were collected from 2-3 sections of the reach for alkalinity, colour, specific conductivity, pH, total dissolved solids (TDS), total suspended solids

(TSS), turbidity, hardness, major ions, NH_3, NO_2/NO_3, total dissolved nitrogen (TDN), dissolved organic carbon (DOC), and total phosphorus (TP); treatment of the water samples and laboratory analysis were as described for a concurrent survey of lower Mackenzie lakes by Ogbebo *et al.* (2009a,b). Streamflow measurements were taken using a SonTek FlowTracker Handheld Acoustic Doppler Velocimeter with a 2D probe attached to a top setting wading rod set according to water depth. Flow measurements were taken for 40 seconds at multiple points along a stream transect. For streams less than 5 m wide, three flow measurements were taken at equidistant point; in wider rivers flow was measured at each 1 m interval from the bank; occasionally streams were not wadeable so measurements were only taken near the bank. Depth, surface temperature, specific conductivity, pH and DO were measured in the field using a YSI-Sonde. The latitude and longitude coordinates were recorded from GPS. We used qualitative assessments of macrophyte cover (0, 25, 50, 75 or 100%), substrate (from fine to coarse: Silt/Organic Material, Sand/Pebble, Gravel/Cobble, Cobble/Boulder) and habitat type (Run, Riffle or Pool; we did not sample any rapids). Winter conditions were inferred from observations in a preliminary environmental impact assessment produced by Imperial Oil (2004), and streams were classified as perennial, frozen or anoxic in the winter. Elevation, gradient, and the presence and position of upstream lakes were determined using Google Earth.

2.2.3 Data analysis

Each environmental variable was tested for normality prior to analysis (Shapiro-Wilk; $\alpha = 0.05$), and variables that deviated from normality were transformed until they achieved normality (square root, fourth root, or log transformations). The data were normalized prior to multivariate analysis. Plots of each variable against latitude were also examined visually to identify any broad spatial trends, which were evaluated using Pearson product-moment correlations. Variation in the environmental variables among the sites was examined with principal component analysis (PCA) using PRIMER v6.

We also split the local environmental variables into physical (elevation, gradient, width, depth, and velocity) and chemical (pH, specific conductivity, turbidity, TP, TDN, and NO_2/NO_3) components. This approach sometimes produces more ecologically interpretable principal components, which can be used as composite environmental variables in analyses of species richness (Heino & Paasivirta 2008). Latitude and longitude were not included so that the composite variables would be independent of spatial location. However, we also ran a multiple regression with the composite variables as the independent variables and latitude as the dependant variable to assess whether they were actually independent of latitude.

2.3 Results and discussion

The environmental variables we collected are presented in Appendices II-IV and are summarized in Table 2.2. The lack of prior information on many of the sites, combined with the fact that our site selection in the field was primarily based on accessibility and the presence of flowing water, justified the exclusion of sites with values far outside the usual range for any environmental variable even after transformation. Inclusion of these sites caused correlation and regression analyses to be dominated by one influential point, and prevented the PCA from producing ecologically explainable axes. These sites were: three Western Cordillera sites (Rat River, Stoney Creek and Vittrekwa River) which were sampled following heavy rain and had abnormally high turbidity (295, 1220, and 4520 NTU, respectively) and TP (0.421, 0.7235, and 1.52 mg/L); one tundra site (Stanley Creek) that had unusually high TP for the region (0.12 mg/L); one site (Dettihih Dehe River) that was far outside of the range of elevation of the rest of the sites (619 m); three sites (Trout, Dahadinni, and Little Buffalo Rivers) which were large rivers far above the range in wetted width (50, 46, and 45 m); and Salt River, which had abnormally high conductivity (19,399 µS/cm). An initial PCA also showed the tundra site RPR-006.1 (which could be accurately characterized as a trickle of water between two ponds) and the three remaining Great Slave region sites (which were physically distant from the rest of the sites and were sampled during an unusually dry summer) to have an inappropriately strong effect on the ordination of the environmental variables, and so were also excluded from the environmental data set. These exclusions left environmental data from 43 sites, consisting of variables that were normal after transformation and which produced two interpretable PC axes that accounted

Table 2.2 – Summary of environmental variables and the effect of the transformations applied (see text for details of transformations).

				Before transformation		After transformation	
Variable	Range	Min	Max	Mean	SD	Mean	SD
Latitude (°N)	9.876	59.437	69.313	65.369	2.909	65.369	2.909
Elevation (m)	237	6	243	109.957	75.849	109.957	75.849
Gradient (m/km)	45.9	0.1	46	9.081	9.87	1.54	0.491
Wetted width (m)	26.3	0.4	26.7	8.544	6.203	2.731	1.054
Depth (m)	0.89	0.11	1	0.382	0.204	0.767	0.0996
Velocity (m/s)	1.948	0.01	1.958	0.453	0.379	-1.283	1.273
pH	2.09	6.35	8.44	7.77	0.613	7.77	0.613
Spec Cond (µS/cm)	2151	40	2191	470.9	583.18	5.558	1.1
Turbidity (NTU)	19.5	0.4	19.9	4.901	4.759	1.359	0.36
TP (mg/mL)	0.0565	0.001	0.0575	0.0127	0.0121	-4.846	1.078
TDN (mg/mL)	1.175	0	1.175	0.429	0.327	0.597	0.272
NO_2/NO_3 (mg/mL)	0.112	0.005	0.117	0.0262	0.0272	-4.163	1.04

for 65.8% of the variation in the data. Any analysis that did not utilize the local physicochemical environmental variables included all sites, except as noted otherwise.

Four variables in particular had noticeable latitudinal gradients (Figure 2.5). Elevation decreased along the course of the Mackenzie River (Figure 2.5a; $r = -0.654$, $p < 0.001$), except for a few sites located in the mountain ranges just south of the sub-arctic lowlands. TDN (Figure 2.5b; $r = 0.355$, $p < 0.05$) was highly variable in the south but generally high in the north and low in the middle of the latitudinal range; TP showed a similar but less convincing gradient ($r = 0.251$, $p = 0.09$). Both pH (Figure 2.5c; $r = -0.688$, $p < 0.001$) and specific conductivity (Figure 2.5d; $r = -0.532$, $p < 0.001$) declined steeply beginning at about 66° of latitude, a condition likely related to the increasing contribution of runoff over the permafrost as a water source in the far north.

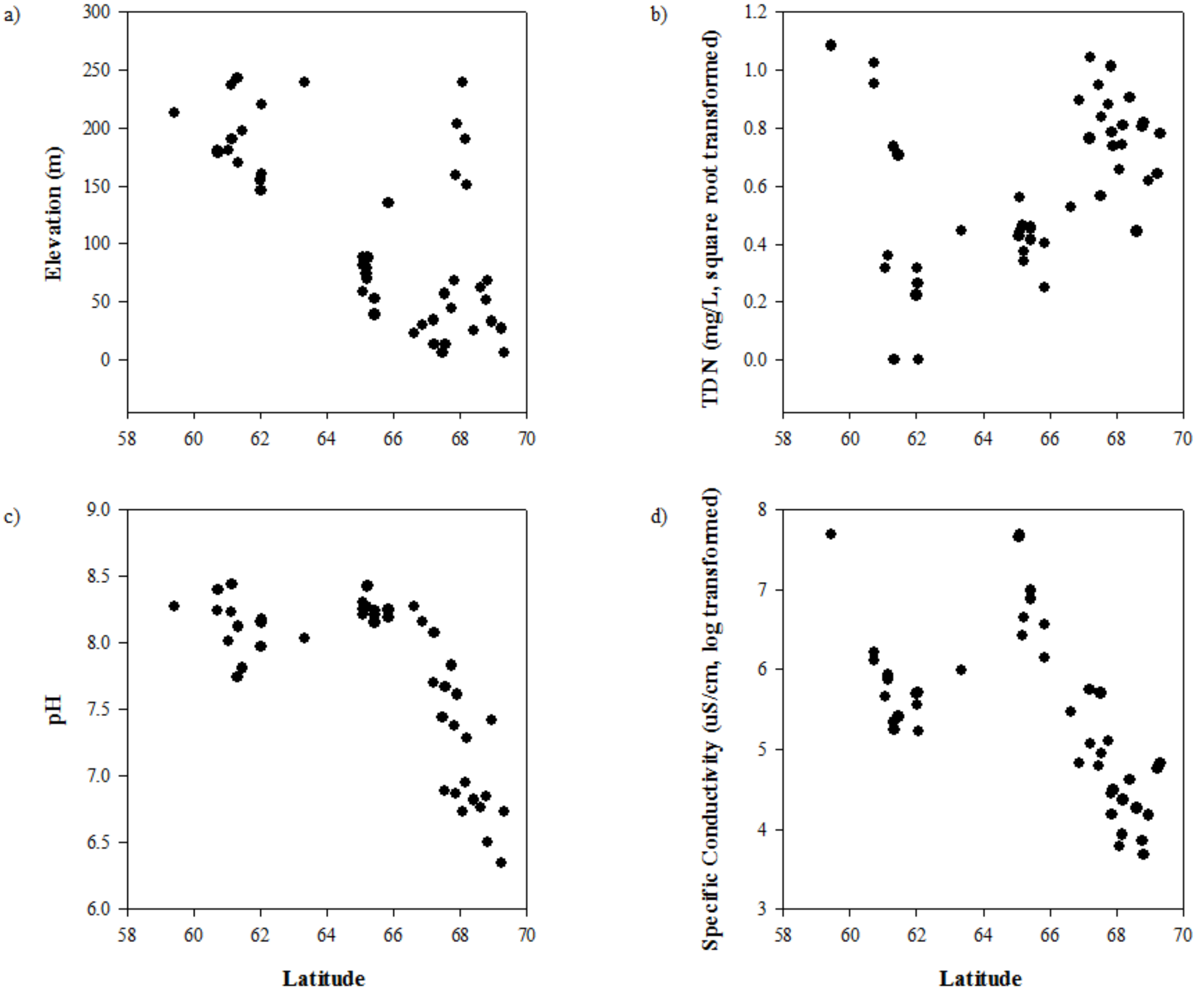

Figure 2.5 – Latitudinal gradients of selected environmental variables. Specific conductivity and TDN have been transformed (see Table 2.2).

The PCA of environmental variables at the 43 remaining sites (Figure 2.6) described 70.2% of the variation (39.4% on the 1st axis, 20.0% on the 2nd, and 10.7% on the 3rd). Due to the strong co-linearity between latitude and elevation, the latter variable was excluded from the PCA. PC1 and PC2 both had high loadings from latitude (Table 2.3). PC1 split the sites into two groups based on water chemistry and nutrients: sites in the arctic lowlands (both the tundra and the northern taiga) were of neutral pH and low conductivity, but had relatively high levels of dissolved phosphorus and nitrogen, while all sites south of approximately 67.5° N were slightly alkaline, had lower levels of dissolved nutrients, and variable but generally higher conductivity. PC2 arranged the sites along a gradient corresponding to stream size (with high loadings from wetted width and velocity). The ordination of

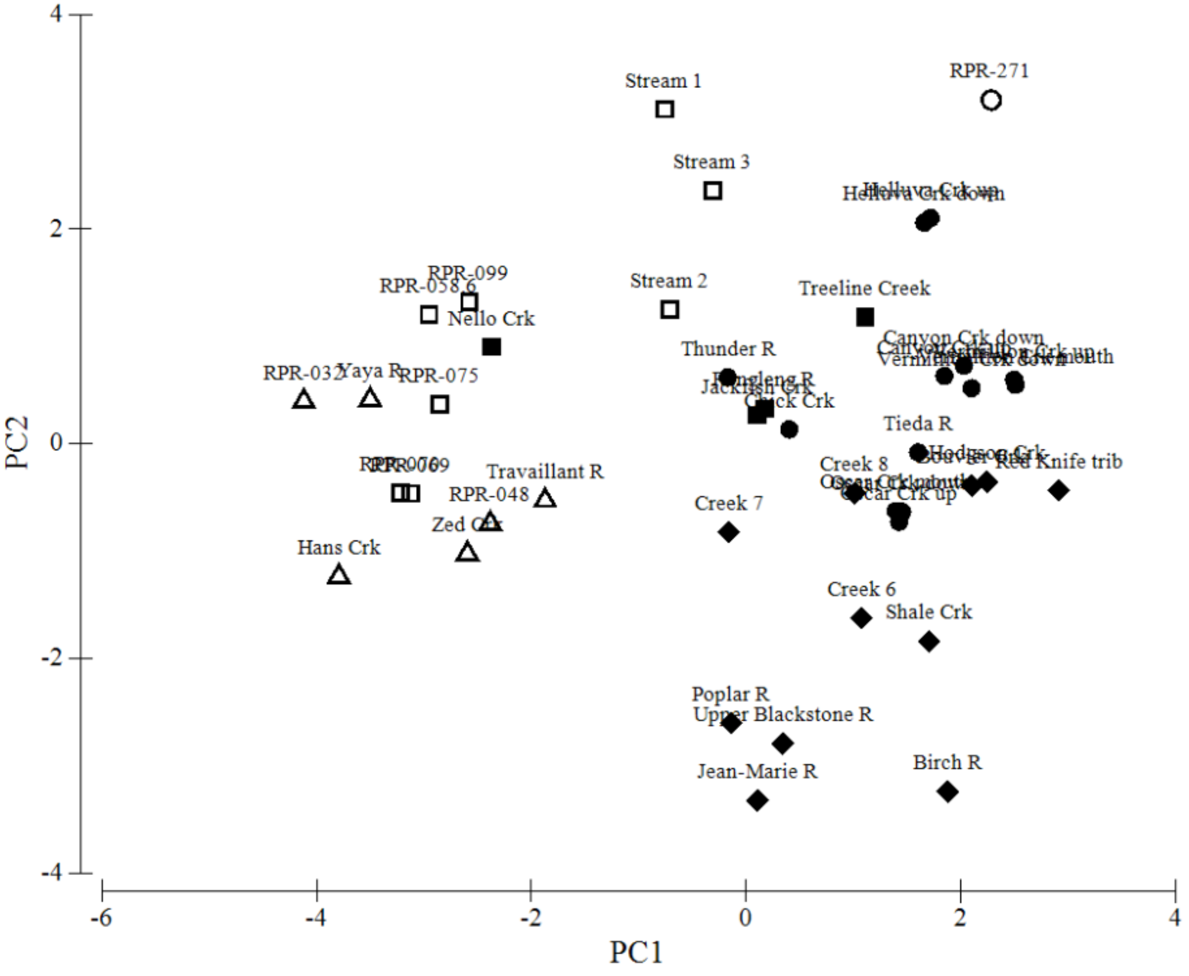

Figure 2.6 – PCA ordination of environmental variables. First two principal components are shown, and sites are labeled according to region; from north to south these are: tundra (triangles), taiga (squares), Norman mountains (circles) and Liard region (diamonds). Open shapes denote soft (sand or silt) substrate, while shaded shapes denote coarse (gravel, cobble or boulder) substrate.

the first two axes (Figure 2.6) suggested a latitudinal gradient in stream size among the second, larger group defined by PC1, with the largest streams in the south and the smallest in the north; the arctic lowlands group fell in the middle of the range of sites along PC2. PC3 primarily described a gradient from steep, highly turbid streams to low-gradient, low-turbidity streams, with little indication of a latitudinal trend. The PCA ordination also revealed a latitudinal trend in substrate type (Figure 2.6). Most far northern streams had soft, depositional-type substrate (silt or sand, with some small pebbles), while the majority of sites to the south of these regions had coarser substrates (gravel, cobble and/or boulders).

Table 2.3 – Loadings of the environmental variables on the first three principal component axes. Variables have been transformed to satisfy normality requirements as indicated in the text, and have been normalized. Loadings with absolute values higher than 0.3 are shown in bold.

Variable	PC1	PC2	PC3
Latitude	**-0.327**	**0.352**	0.278
Elevation	n/a	n/a	n/a
Gradient	0.162	**0.347**	**-0.615**
Wetted width	0.124	**-0.581**	0.157
Depth	-0.253	-0.299	0.263
Velocity	-0.036	**-0.456**	-0.23
pH	**0.434**	-0.023	-0.139
Specific Conductivity	**0.413**	0.075	0.107
Turbidity	-0.26	-0.221	**-0.469**
TP	**-0.339**	-0.033	-0.249
TDN	**-0.305**	0.247	0.172
NO_2/NO_3	**0.389**	0.062	0.235

Since the groupings indicated by the PCA were spatially distinct (on both the ordination and the map), we re-ran the analysis within both of these groups to obtain a finer picture of the distribution of environmental variables among the sites (Table 2.4). The first group, which consisted of the high-nutrient, low-pH and -conductivity sites in the tundra and northern taiga (Figure 2.7a), were ordinated along a slight latitudinal gradient of depth and TDN (PC1) and gradients of water chemistry (PC2) and stream size (PC3) that had little variation related to latitude (Table 2.4). The larger, southern group of sites (Figure 2.7b) fell into a distinct gradient of stream size, which increased from north to south (PC1). Along PC2, the northern-most group of sites (in the southern taiga region, east and west of the Mackenzie River) split from the rest on the basis of high TDN and low conductivity and pH. The 3rd principal component of this group of sites was primarily determined by gradient, pH and nutrients (TP and TDN), with no apparent latitudinal trend.

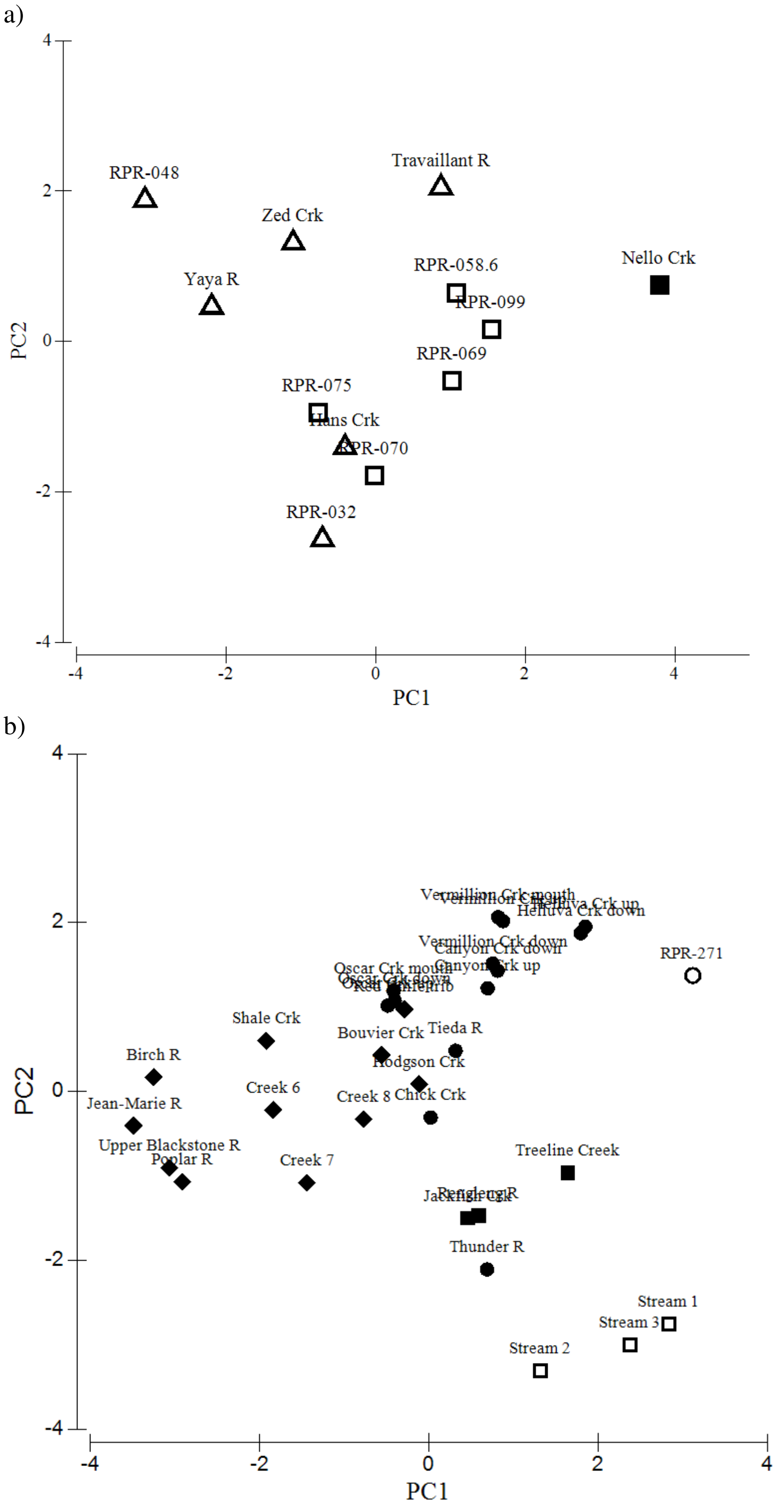

Figure 2.7 – Secondary PCA ordinations of environmental variables within groups defined by the initial PCA. a) Northern group, containing 12 tundra and northern taiga sites. b) Southern group, containing 31 southern taiga, mountains and plains sites. Symbols indicate region and substrate as described in Figure 2.6.

Table 2.4 – Principal component analysis of the environmental variables in the northern and southern groups of sites. Groups were defined by the initial PCA of all of the sites. Loadings with absolute values higher than 0.3 are shown in bold.

	Northern group			Southern group		
Variable	PC1	PC2	PC3	PC1	PC2	PC3
Latitude	**-0.404**	-0.074	0.279	**0.457**	-0.158	-0.249
Gradient	0.029	**-0.358**	-0.211	**0.327**	-0.062	**0.508**
Wetted width	0.039	0.048	**-0.566**	**-0.508**	0.015	-0.252
Depth	**-0.469**	-0.194	-0.129	**-0.337**	0.197	-0.17
Velocity	-0.211	0.007	**-0.398**	**-0.382**	-0.18	-0.003
pH	0.298	**0.318**	**-0.449**	0.004	**0.48**	**0.302**
Spec Cond	0.097	**0.489**	**0.34**	0.12	**0.533**	-0.02
Turbidity	0.285	**-0.354**	-0.104	-0.262	-0.298	0.282
TP	0.168	**-0.556**	0.142	-0.1	-0.031	**0.436**
TDN	**0.483**	-0.203	0.181	0.239	**-0.401**	**-0.31**
NO_2/NO_3	**0.359**	0.109	0.043	0.127	**0.366**	**-0.362**
Eigenvalue	3.33	2.17	1.75	3.01	2.32	1.73
% variation explained	30.2	19.7	15.9	27.4	21.1	15.7
Cum. % variation	30.2	50.0	65.8	27.4	48.5	64.2

The PCA analysis suggested grouping the sites into five regions: 1) tundra, located above the treeline; 2) northern taiga, located below the treeline but with water chemistry similar to the tundra streams; 3) southern taiga, in the arctic lowlands or the foothills of the Mackenzie Mountains, and with water chemistry similar to the southern sites; 4) Norman region, containing streams that drain the Mackenzie Mountains in the Norman Range and flow directly into the Mackenzie River, around Norman Wells; and 5) Liard region, south of the mountains, including some in the Liard watershed, roughly centered on Fort Simpson. The tundra and north taiga were grouped together in the initial PCA, and separated from each other on the basis of surrounding vegetation; the south taiga separated from the southern two groups on the basis of nutrients and pH/conductivity (although this group was still distinct from the north taiga in terms of water chemistry), and the mountains around Norman Wells and the plains in the Liard region were separated on the basis of their position along the gradient of stream size from the secondary PCA.

When the environmental variables were divided into physical variables and water chemistry variables, the resulting PCAs explained 64.9% of the variation in the former and 73.6% of the variation in the latter (Table 2.5). Each composite environmental variable was mostly determined by a combination of three of the original variables (those with loadings > 0.4), and were more ecologically interpretable than the overall PCAs that were used to classify the sites. The physical composite variables roughly described a gradient in stream size (PHYS1), from wide and fast to narrow and

Table 2.5 – Summary of principal component analyses of composite physical habitat and water chemistry variables. Loadings greater than 0.4 are in bold.

	Physical habitat variables			Water chemistry variables		
		PHYS1	PHYS2		WC1	WC2
Eigenvalues		2.06	1.19		3.56	0.851
% Variation explained		41.2	23.7		59.4	14.2
Loadings of environmental variables						
	Elevation (m)	-0.34	**0.589**	pH	**0.452**	0.282
	Gradient (m/km)	**0.444**	**0.592**	Spec Cond	**0.473**	0.136
	Wetted width	**-0.575**	0.171	Turbidity	-0.348	**0.501**
	Depth (m)	-0.394	**-0.43**	TP	-0.382	**0.449**
	Velocity (m/s)	**-0.449**	0.297	TDN	-0.325	**-0.657**
				NO_2/NO_3	**0.446**	-0.133

slow, and a gradient from high gradient, shallow streams to low-gradient, deeper streams, with a large input from elevation (PHYS2). The composite water chemistry variables described gradients in ionic composition (pH, spec. conductivity, and nitrates; WC1) and in turbidity and nutrients (WC2). The four composite variables (based on the site loadings on the first two axes of the physical and water chemistry PCAs) were predictive of latitude in a multiple regression analysis ($r^2 = 0.718$, $p < 0.001$), indicating they varied with latitude. As noted previously, several of these original variables were strongly correlated with latitude, and the composite variables reflected these latitudinal gradients to a large degree, especially with regards to elevation, stream size and ionic composition (the latitudinal gradient of WC1 was very similar to that of pH and specific conductivity, shown in Figure 2.5).

In this chapter, latitudinal gradients in habitat and water chemistry variables in the stream study sites were described. Variation in the environmental variables among the sites was characterized and composite physical and water chemistry variables were created to facilitate the analysis described in later chapters. Further, the sites were grouped into regions defined by the environmental variables. These results provide a framework for analyzing patterns of benthic invertebrate diversity (Chapter 3) and community composition (Chapter 4) across the Mackenzie River System.

Chapter 3

Species richness and abundance of aquatic insects in the Mackenzie River System

3.1 Introduction

Biodiversity, most simply expressed as species richness or species density (Gotelli & Colwell 2001), is among the most straightforward measures used to compare or describe communities (Pianka 1966). Diverse benthic invertebrate communities in streams have higher stability and resilience to disturbance or invasion (Vinson & Hawkins 1998), are associated with higher rates of nutrient processing (Jonsson *et al.* 2001, Jonsson & Malmqvist 2005) and may act as a source that permits the persistence of rare taxa (Allan & Flecker 1993), so diversity is a component of most biomonitoring programs, e.g. CABIN (Reynoldson *et al.* 2008), in one form or another. High levels of spatial and temporal variability have made discerning and explaining the patterns of benthic invertebrate biodiversity an ongoing concern of stream ecology (Vinson & Hawkins 1998, Clarke *et al.* 2008). The diversity of stream insects is affected by a hierarchy of environmental factors, from continent-scale variation in climate and geology to the microhabitat scales in which these generally tiny organisms live and grow. The number of taxa present in a stream or stream reach (*alpha* diversity) is a subset of the regional species pool or *gamma* diversity (Clarke *et al.* 2008) consisting of those species that have dispersed to the locality and can survive local environmental and biotic conditions (Minshall & Petersen 1985).

Recognition that the variation in local (*alpha*) diversity is greater than can be explained by local environmental conditions (e.g. Miller & Stout 1989, Milner *et al.* 2006) has led to an understanding of aquatic insect diversity that focuses on disturbance and dispersal as much as local habitat. Frequent disturbances such as freezing and flooding may clear patches of substrate, which can then be re-colonized, thereby keeping the patch “community” from reaching a stable equilibrium (Minshall & Petersen 1985). The constantly shifting assemblage of any particular patch of a frequently disturbed stream may not attain the maturity necessary for competition for space or food resources to lead to the exclusion of species (Townsend 1989, but see Miyake *et al.* 2003, Ledger *et al.* 2006) and disturbance may therefore act to increase or maintain diversity (Sousa 1984). In addition to in-stream dispersal, the diversity of aquatic insects is likely maintained by dispersal among streams in the adult stage (Palmer *et al.* 1996). The importance of aerial and aquatic dispersal in shaping the community and maintaining diversity has led to recent interest in the metacommunity concept (Leibold *et al.* 2004), which suggests that for aquatic insect communities, maintenance of species diversity at the regional (*gamma*) scale may be more important than at the scale of individual stream reaches (Clarke *et al.* 2008).

Broad scales of environmental gradients such as hydrology, climate and vegetation influence the diversity of the regional species pool (Schall & Pianka 1978, Vinson & Hawkins 1998, 2003). Drainage basin factors such as water chemistry and sediment and nutrient loadings have often been found to affect diversity (e.g. Malmqvist & Hoffsten 2000, Heino & Paasivirta 2008), although these are likely to be indirect effects (Vinson & Hawkins 1998). The temperature and hydraulic regime of the basin is thought to be an important factor determining diversity since variable conditions will provide optimal growth conditions for a greater number of species (Allan 2007), and the prediction that this variability will be greatest in mid-order streams (Vannote *et al.* 1980, Poff & Ward 1989) has been confirmed by several studies (e.g. Minshall *et al.* 1985, Malmqvist & Hoffsten 2000, Heino & Paasivirta 2008, Heino *et al.* 2008), although other studies are equivocal (Vinson & Hawkins 1998).

The latitudinal range of the Mackenzie River system spans an environmental gradient from temperate to arctic regions, providing an opportunity to examine large-scale latitudinal trends in diversity. Colder temperatures and shorter growing seasons in the north limit the number of species due to physiological and life cycle constraints (Rautio *et al.* 2008), and changes in vegetation related to light availability and permafrost depth may limit food quality and availability (Vinson & Hawkins 2003). The hemisphere scale latitudinal gradient in diversity is a fundamental finding of biogeography and is generally attributed to a combination of glacial and evolutionary history and increasing climatic severity towards the poles (Lomolino *et al.* 2006). Decreasing species or generic richness has been documented in many disparate groups of organisms (e.g. Schall & Pianka 1978, Roy *et al.* 2000). However, broad-scale studies of lotic invertebrate diversity are rare and often contradictory (Vinson & Hawkins 1998), have often focused on the diversity gradient between tropical and temperate latitudes to the exclusion of the north, and have led some to suggest that certain groups (e.g. Chironomidae) may be exceptions to the general pattern (Pianka 1966, McKie *et al.* 2005). Although many groups of aquatic insects (e.g. Coleoptera, Hemiptera, Odonata) are poorly represented in high-latitude streams (Oswood 1989), certain families of Diptera seem to be far more successful (Rautio *et al.* 2008) while other orders, such as the EPT orders (Ephemeroptera, Plecoptera, Trichoptera), often give conflicting results (Vincent & Hawkins 2003).

At local scales, greater habitat heterogeneity generally allows a greater number of species to co-exist (Allan 2007). Local substrate characteristics play an important role, and studies employing a variety of methods of substrate characterization have found a substantial effect on diversity (Barton 1980, others reviewed in Vinson & Hawkins 1998). The quantity, quality and diversity of food resources (e.g. algae and terrestrial detritus) likely play a similar role (Malmqvist & Hoffsten 2000), but are more difficult to describe or quantify. Gradients in the frequency and intensity of disturbance are likely to affect lotic insect diversity, e.g. frequent high flows driven by precipitation runoff over the permafrost in the summer (Power & Power 1995, Smidt & Oswood 2002), formation of frazil or anchor ice in perennial streams during the winter (Martin *et al.* 2000) and scour from ice break-up during spring melt (Scrimgeour *et al.* 1994, Prowse & Culp 2003). In streams that freeze solid during the winter, diversity may be limited because fewer species will be able to survive (Huryn *et al.* 2005), although a certain amount of recolonization by freeze-susceptible species probably occurs over the summer. Most likely, a combination of all of these factors serve to limit lotic insect biodiversity in the north, as every species present will need to possess physiological, behavioural or phenological adaptations that allow them to persist in these harsh environments (Hershey *et al.* 1995, Danks 2007).

As a first step toward describing the lotic insect fauna of the Mackenzie River system, this chapter will 1) describe the size and composition of the overall pool of aquatic insect diversity in streams of the Mackenzie River system; 2) examine the relationship between the physical and chemical attributes of stream habitat and the local generic richness of aquatic insect assemblages; but mostly 3) evaluate latitudinal trends in local and regional diversity across the basin.

3.2 Methods

3.2.1 Collection & identification of benthic invertebrates

Benthic samples were collected using a D-net with a 200 µm mesh and a mouth size of approximately 0.055 m^2. The substrate was disturbed by hand as far down as the sediments or rocks could be moved and organisms and debris were carried into the net by the flow. Four 0.055 m^2 patches of substrate were sampled for each replicate, so each replicate sampled 0.22 m^2. These quantitative samples were collected near the center of the stream (when accessible) and attempts were made to include as many different microhabitats as possible (e.g. if different vegetation, substrate or flow conditions were present); the method that was used prevented sampling in very deep water or areas with little or no flow. Sampling began at the downstream end of the sampling reach and proceeded upstream. The material collected was washed of fine silts through a 200 µm sieve using filtered stream water; large debris and clumps of algae were rinsed into the sieve and discarded. Three replicate samples were taken in most streams in 2006 - 2008; the number of replicates was occasionally limited by the supply of collecting jars due to limited storage space in the helicopter, and more replicates were taken at some sites in order to sample a greater number of habitats, usually when there were pools present in the stream reach. Damage during shipping resulted in the loss of a few samples from 2006 and 2007, and sites that were sampled by other researchers sometimes had fewer than three replicates. In 2005, many streams were sampled upstream and downstream of potential pipeline crossings and at the mouths of Mackenzie River tributaries, and these sites had up to six replicates taken at each reach; these reaches were considered as separate sites in the analyses. In 2006-2008, qualitative kick net samples using a CABIN-type approach (Reynoldson *et al.* 2008) were collected for comparison with the quantitative D-net samples; these are not used in any of the analyses in this thesis.

The samples were preserved in the field using buffered formalin; occasionally preservation was delayed several hours until they could be returned to the lab, with no observable effects on benthos quality. The samples were shipped to the University of Waterloo, where they were rinsed again through a 200 µm sieve and stored in 70% ethanol until they could be sorted. Sorting was performed under a dissecting microscope with the goal of extracting all macroinvertebrates; however, when total abundance ranged into the thousands the samples were subsampled ¼ to ½ of wet weight.

Animals were identified to the lowest practicable taxonomic level. I attempted to identify aquatic insects to species where possible, but the frequent occurrence of immature nymphs and larvae often made even genus-level identification difficult. Chironomids were generally identified to genus, to species if possible. Simuliidae were generally identified only to the family level. Amphipoda were usually identified to genus; most other Crustacea were identified to Order. Gastropods were identified to family. Other non-arthropods were identified to Class or, in the case of nematodes, Phylum. Since the focus of this chapter is trends in number of genera, groups that were identified only to higher levels cannot be included; the following analysis is therefore limited to aquatic insects.

3.2.2 Data analysis

To determine whether a latitudinal gradient in diversity was present, generic richness in all D-net samples were compared across the study area. The relationship between latitude and local overall generic richness, as well as the local generic richness of each major group of insect (Orders and chironomid subfamilies and tribes), were analyzed using regression analysis and Pearson product moment correlation analysis. Both linear and polynomial regressions were used to assess latitude as a predictor of local diversity, under the assumption that any relationships present may not be entirely linear, and the regression model that best fit the data was used. Pearson correlation coefficients were calculated to provide a simple measure of the direction and magnitude of the correlation. A similar analysis was used to assess latitudinal gradients in abundance; these data were log-transformed due to the high variability in abundance among genera and samples.

To assess the effect of local conditions on the diversity and abundance of the major groups of aquatic insects, the residuals from the latitude regressions were used, since the purpose was to examine the variation in local diversity and abundance that could not be explained by latitude alone. The relationship between the composite environmental variables and the residual variation in local generic richness and abundance were examined using Pearson product moment correlation coefficients; since the principal components, although theoretically orthogonal to each other, were found to be highly correlated with each other as well as latitude, multiple regression was deemed to be inappropriate. An analysis of variance (ANOVA) was used to assess the effect of substrate on local diversity and abundance; this analysis was repeated using two-factor fixed effect ANOVAs, with region (defined in Chapter 2) as the second factor to assess the effect of substrate while taking latitudinal variation into account. Because of the uneven sampling of substrates among the regions, the interaction factor for the 2-way ANOVA could not be calculated.

Finally, latitudinal gradients in regional diversity were examined by comparing the size of the regional species pools among the five regions (defined in Chapter 2) using rarefaction curves. These were constructed by pooling all of the samples within each region and then calculating the expected number of genera per individual (ES_n, Sanders-Hurlbert method; n is the number of individuals) for each number of individuals up to the lowest total abundance of the five regions (in the case of the rarefaction curves for all insects, this was 4000 individuals). This was repeated for each common insect order and chironomid subfamily, with the range of rarefaction determined for each by the minimum regional abundance.

3.3 Results

3.3.1 Abundance & generic richness of aquatic insects

The overall generic richness and abundance of the benthic assemblages observed in the 149 samples from 43 sites used in this analysis are summarized in Table 3.1. Out of the more than 86,000 individual invertebrates counted, there were 57,478 immature aquatic insects belonging to 233 genera from 58 families. Abundance generally tracked generic richness (Figure 3.1), as groups that were more diverse tended to also be more abundant.

A majority of genera were classified as rare or very rare, occurring in fewer than 5% of all samples, while very common species that were found in more than 25% of all samples only

Table 3.1 – Diversity, generic richness, and abundance of major groups of aquatic insects. Averages and ranges represent values observed for each 0.22 m^2 sample; raw abundances for each sample were multiplied by 4.54 to obtain abundance/m^2. Average generic richness and abundance were determined from non-zero values (i.e. average richness and abundance of each group where it occurred).

Taxonomic group	# of families observed	# of genera observed	Generic richness per sample - average (SD)	Range in generic richness per sample	% of total generic richness	Total # of individuals collected	% of total abundance	Abundance per m^2 - average (SD)	Range in abundance per m^2
Ephemeroptera	9	26	3.1 (1.8)	0 - 8	11.2	8,274	14.4	242.2 (475.8)	0 – 3,772.7
Odonata	4	5	1.1 (0.3)	0 - 2	2.1	13	0.02	7.3 (5.4)	0 – 18.2
Plecoptera	8	21	2.2 (1.1)	0 - 6	9.0	2,282	4.0	73.1 (138.0)	0 – 594.7
Hemiptera	2	4	1 (0)	0 - 1	1.7	13	0.02	7.3 (4.1)	0 – 13.6
Trichoptera	14	30	2.4 (1.3)	0 - 7	12.9	2,047	3.6	82.6 (116.2)	0 – 531.2
Coleoptera	6	15	1.2 (0.5)	0 - 3	6.4	393	0.7	63.1 (190.7)	0 – 871.7
Diptera	15	132	13.1 (6.1)	1 - 29	56.7	44,456	77.3	975.2 (2,081.6)	4.5 – 20,993.0
non-Chironomid Diptera[a]		36	2.9 (1.3)	0 - 6	15.5	4,704	8.2	133.5 (319.2)	0 – 2220.1
Ceratopogonidae		5	1.1 (0.3)	0 - 2	2.1	427	0.7	28.1 (46.8)	0 – 290.6
Empididae		7	1.2 (0.4)	0 - 2	3.0	714	1.2	30.4 (39.0)	0 – 263.3
Tipulidae		11	1.2 (0.5)	0 - 3	4.7	537	0.9	35.0 (100.3)	0 – 780.9
Chironomidae		96	10.5 (5.3)	1 - 24	41.2	39,752	69.2	898.5 (2,177.4)	4.5 – 20,806.8
Tanypodinae		14	2.1 (1.2)	0 - 7	6.0	3,798	6.6	132.1 (189.8)	0 – 780.9
Diamesinae		3	1.1 (0.3)	0 -2	1.3	65	0.1	12.7 (9.1)	0 – 31.8
Podonominae		1	1 (0)	0 - 1	0.4	37	0.06	84.0 (112.1)	0 – 163.4
Orthocladiinae		43	5.2 (2.5)	0 - 12	18.5	12,505	21.8	321.4 (508.5)	0 – 3,069.0
Chironominae		35	4.2 (2.5)	0 - 11	15.0	23,350	40.6	706.4 (2,204.6)	0 – 19,417.6
Tanytarsini		11	2.6 (1.5)	0 - 7	4.7	21,283	37.0	655.1 (2,496.1)	0 – 19,267.8
Chironomini		23	2.7 (1.7)	0 - 7	9.9	2,063	3.6	114.4 (191.1)	0 – 1,203.1
Pseudochironomini[b]		1	1	0 - 1	0.4	4	0.007	18.2	0 – 18.2
Total	58	233	19.6 (8.9)	1 - 44	100.0	57,478	100.0	1,357.9 (2,803.4)	4.5 – 21,415.2

[a] Only ceratopogonids, empidids, and tipulids were identified to the generic level; all other families are counted as one "genus".

[b] Only one genus of Pseudochironomini was observed in only one sample, so standard deviations could not be calculated.

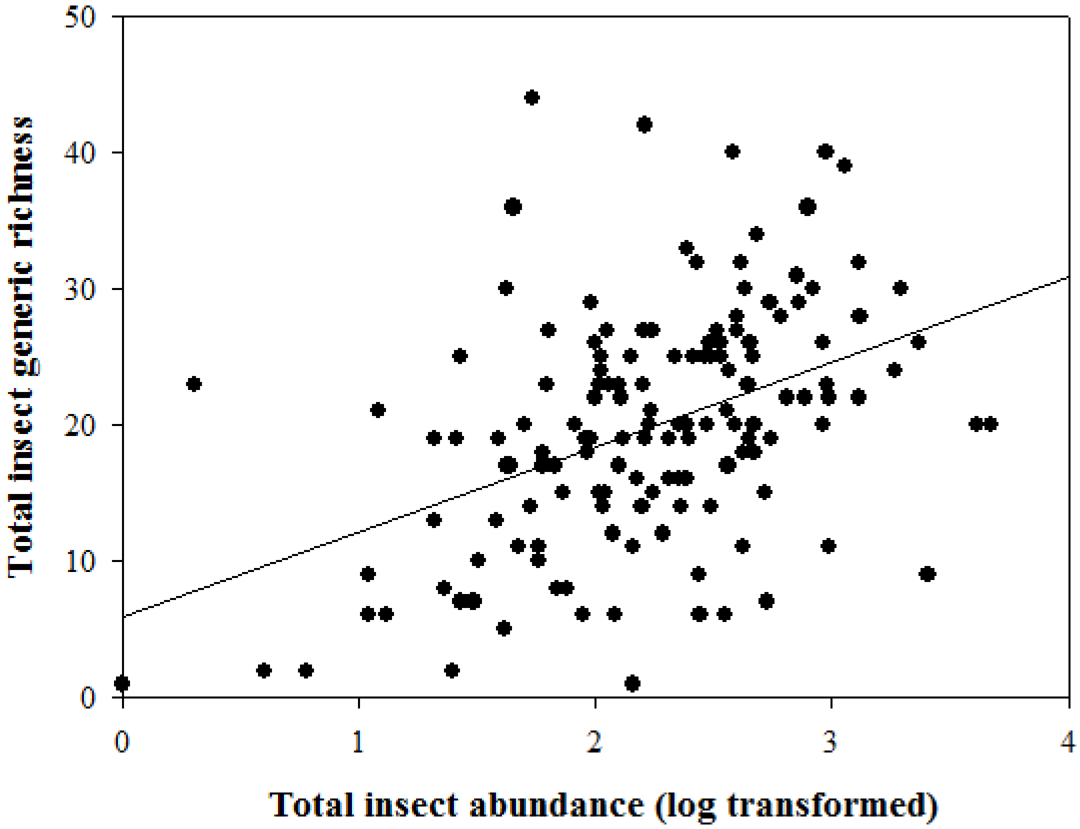

Figure 3.1 – Relationship between abundance and local generic richness. Abundance per sample is log-transformed and local number of genera is all insects per sample. Linear regression was significant with r^2=0.333, $p < 0.001$.

comprised approximately 10% of the total fauna. These trends held true for all major taxonomic groups except the Tanytarsini, which were mainly represented by a few common, abundant genera. Abundance values were log transformed for subsequent analyses due to the high variability and large standard deviations in the raw data (Table 3.1).

Odonata, Hemiptera, and Coleoptera were scarce throughout the study area, with the exception of the elmid *Optioservus*, which was abundant at a few sites, mainly in the south. Ephemeroptera, Plecoptera, and Trichoptera were similar in generic richness overall and on a per sample basis, but the Ephemeroptera were distinctly more abundant on average than the other two groups. Caddisflies were slightly more diverse than the mayflies and stoneflies, but had a higher proportion of rare genera. Only one caddisfly, *Brachycentrus americanus* (Brachycentridae), occurred in more than 25% of samples. Greater numbers of very common genera were found among the Ephemeroptera (the baetids *Baetis* and *Acentrella*, the heptageniid *Heptagenia*) and Plecoptera (the chloroperlid *Haploperla brevis*, the nemourid *Nemoura arctica* and the perlodid *Skwala americana*).

The order Diptera contributed most of the generic richness and abundance (Figure 3.2, Table 3.1), mostly from the Chironomidae. Most of the non-chironomid dipteran abundance came from the Simuliidae, which were highly abundant at some sites. The three families that were identified to genus level were mainly represented by a few common genera, notably *Probezzia* (Ceratopogonidae), *Chelifera* (Empididae), and *Leptotarsus* (Tipulidae). Chironomids, which represented approximately 40% of the overall generic diversity and 70% of overall abundance, were mainly represented by the subfamilies Tanypodinae, Orthocladiinae, and Chironominae, each of which had larger proportions of common genera than the other groups of insects. Although the Tanytarsini made a relatively small contribution to generic richness (only about a third the richness of the Chironominae), they represented a large proportion of the total and average abundance, which was in large part due to extremely high numbers of *Rheotanytarsus* at a few sites. Orthoclad abundance was also higher than most other groups, but this subfamily also made a large contribution to generic richness and had the largest number of common genera. Notably common chironomids were the *Thienemannimyia* group (Tanypodinae), *Corynoneura*, *Cricotopus*, *Eukiefferiella*, *Orthocladius*, and *Tvetenia* (Orthocladiinae), *Polypedilum* (Chironomini), and *Cladotanytarsus*, *Micropsectra*, *Rheotanytarsus*, and *Tanytarsus* (Tanytarsini). With the exception of the genus *Potthastia*, the Diamesinae were rare throughout the study area, and the Podonominae and Pseudochironomini were extremely rare, each represented by one genus at one site.

3.3.2 Latitudinal gradients in local generic richness and abundance

Overall local generic richness (Figure 3.3a) had no clear relationship with latitude. No significant correlation was found and a 2° polynomial regression was barely significant, but the low r^2 indicates that latitude is not a good predictor of total local generic richness. Ephemeroptera (Figure 3.3b) and Plecoptera (Figure 3.3c) tended to decrease in generic richness in the far north, but richness of both orders was highly variable throughout the rest of the latitudinal range. Trichoptera richness (Figure 3.3d) was best described by a 2^{nd} degree polynomial, lowest in the middle of the latitudinal range (mostly in streams draining hills in the Norman Range), and higher in the south and north, with no overall linear trend. The Diptera was the only group with a significant, linear, latitudinal trend in local richness, which was, notably, positive (Figure 3.3e). The three orders that were rare across the study area (Odonata, Hemiptera, and Coleoptera) decreased markedly in richness and abundance above approximately 62 °N; the low numbers and sparse distribution of these orders precluded statistical analysis.

The Chironomidae, as a whole, closely tracked the Dipteran latitudinal gradient in local

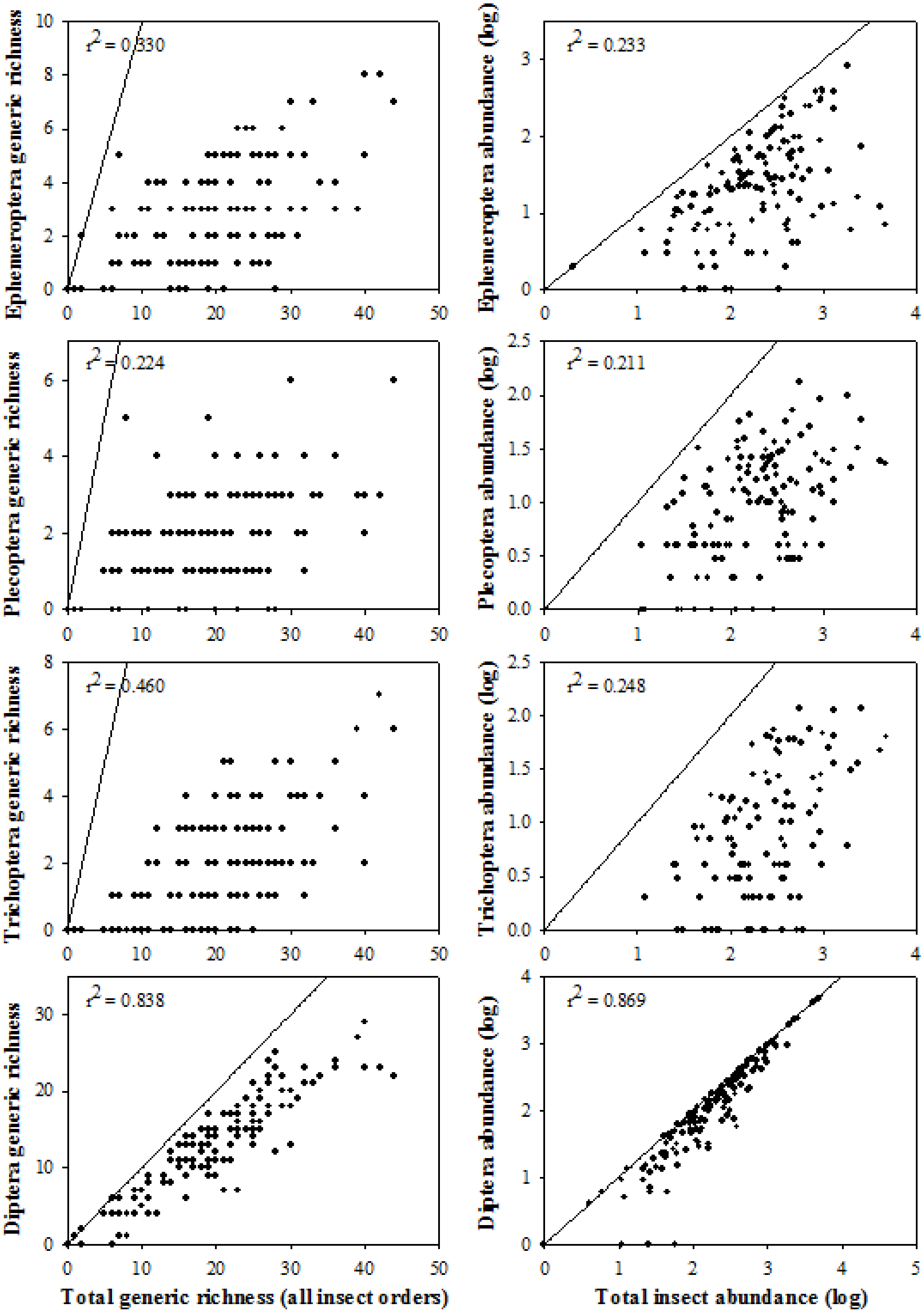

Figure 3.2 – Contribution of aquatic insect orders to overall generic richness and abundance. Only the most widespread, diverse and abundant orders are shown. Abundance values for individual samples are log transformed. r^2 values from linear regressions are indicated, and 1:1 lines are shown.

richness (Figure 3.4a), but significant positive latitudinal trends were found only in the subfamily Orthocladiinae (Figure 3.4c) and the tribe Chironomini (Chironominae) (Figure 3.4e). Pearson correlations between latitude and generic richness were positive for all groups, whether significant or not, although the maximum values of generic richness of the Tanytarsini (Chironominae) were recorded south of 66 °N. With the highest local richness, the Orthocladiinae most closely reflected the overall chironomid gradient. Chironomini generic richness had the strongest positive correlation with latitude, although the trend was best described by a 2° polynomial regression, reflecting the very low diversity of this tribe in some of the rocky streams in the Liard and Norman Wells regions.

3.3.3 Local environmental determinants of generic richness and abundance

Correlations among the composite environmental variables were low (Pearson $r < 0.4$) but consistently significant. Since there were significant correlations between latitude and several environmental variables and components of diversity, a conservative approach was used to evaluate relationships between the environmental variables and aquatic insect abundance and generic richness. Preliminary analyses showed that using raw generic richness and log-transformed abundance produced a much higher number of significant correlations than using the residuals from the latitudinal regressions shown in Figures 3.3 and 3.4. When both the biotic and environmental variables were represented by their residuals in the latitudinal regressions, there were significant correlations between most of the pairs of variables in Table 3.2. Therefore, correlating residual variation in generic richness and abundance against the composite variables (Table 3.2) appeared to minimize the chances of Type I errors.

Local generic richness was primarily correlated with stream size (PHYS1) for most groups of aquatic insects (Table 3.2), with higher richness in the larger streams (which in this set of sites corresponds to mid-order streams). The streams included in analysis are low- to mid-order (although we did not use stream order as an explicit variable); generic richness in the higher order rivers that were excluded from analysis was highly variable, from 11 in Dahadinni River and 21 in Little Buffalo River to 40 in Trout River and 37 in the Mackenzie River mainstem near Norman Wells. Exceptions to the stream size diversity gradient were found in the Orthocladiinae, whose generic richness did not correlate with any of the composite environmental variables, and the Plecoptera, which were slightly more diverse in streams with high altitude and gradient (PHYS2). PHYS 2 also correlated with the generic richness of the Tanypodinae and Tanytarsini, both of which were slightly more diverse in flat, lowland streams. The water chemistry variables showed little correlation with the generic richness of any group, with the exception of a very slight negative correlation between WC1 (which was a

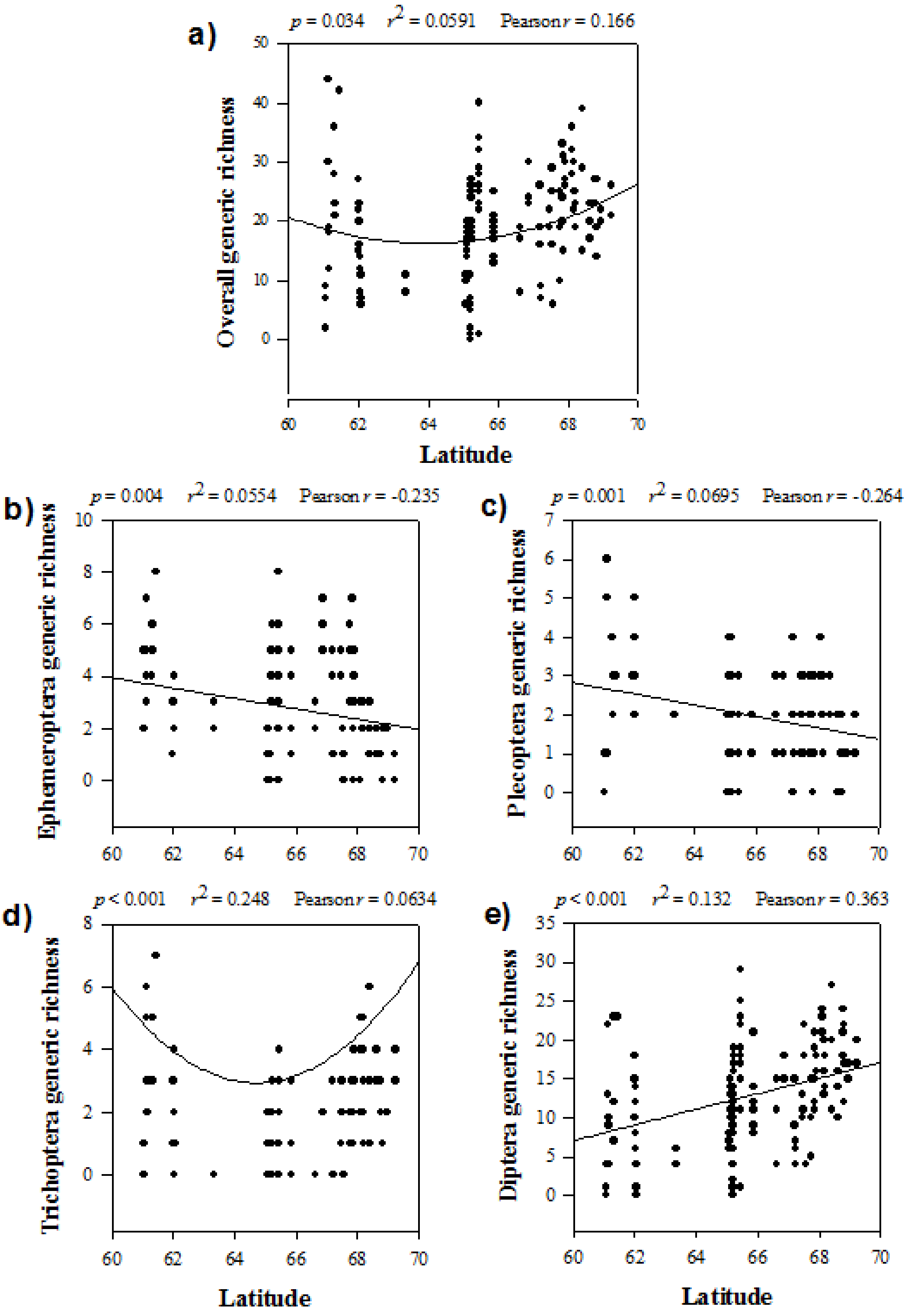

Figure 3.3 – Latitudinal gradients in local generic richness of aquatic insects, overall and among the major orders. Generic richness estimates are per sample. Pearson r values are given to indicate the direction of the correlation; *p* and r^2 values refer to linear regressions except for a) and d), which refer to 2° polynomial regressions. Only significant ($p < 0.005$) regression lines are shown.

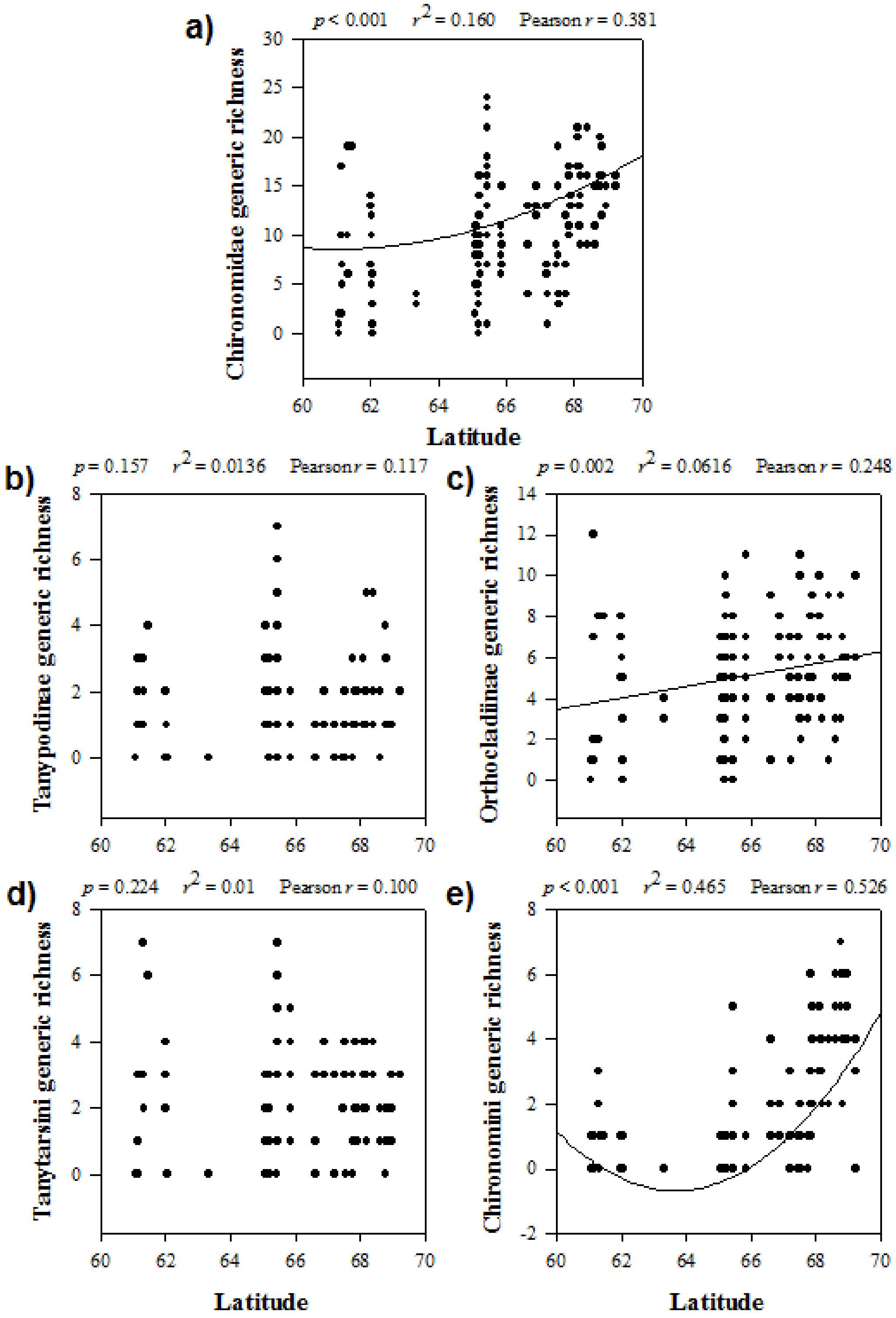

Figure 3.4 – Latitudinal gradients in local generic richness of the Chironomidae and its major subfamilies and tribes. Generic richness estimates are per sample. Pearson r values are given to indicate the direction of the correlation; *p* and r^2 values refer to linear regressions except for a) and e), which refer to 2° polynomial regressions. Only significant ($p < 0.005$) regression lines are shown.

Table 3.2 – Correlations between local generic richness & abundance and environmental variables. Values are Pearson correlation coefficients. Environmental variables are represented by site loadings on principal components of physical habitat variables (PHYS1 and PHYS2) and water chemistry variables (WC1 and WC2). Ecological interpretations of the principal components are indicated. Biological data (generic richness per sample and log abundance per sample) are represented by the residuals from the linear or polynomials regressions with latitude. Significant Pearson correlations ($p < 0.05$) are in bold.

	Local generic richness				Abundance per sample			
	PHYS1	PHYS2	WC1	WC2	PHYS1	PHYS2	WC1	WC2
	Stream size	Gradient	Chemistry	Nutrients	Stream size	Gradient	Chemistry	Nutrients
Overall	**-0.433**	-0.060	**-0.161**	0.020	**-0.216**	-0.080	-0.003	-0.028
Ephemeroptera	**-0.280**	0.025	-0.026	-0.028	**-0.203**	0.046	-0.076	0.037
Plecoptera	-0.0917	**0.244**	-0.147	-0.080	0.007	**0.236**	-0.027	-0.025
Trichoptera	**-0.283**	0.029	0.039	-0.040	**-0.286**	-0.113	-0.002	-0.034
Diptera	**-0.377**	-0.125	-0.087	0.066	**-0.176**	**-0.172**	0.055	-0.072
Chironomidae	**-0.430**	-0.154	-0.136	0.100	**-0.210**	**-0.200**	0.0503	-0.048
Tanypodinae	**-0.329**	**-0.210**	0.018	0.095	**-0.455**	-0.144	-0.045	0.087
Orthocladiinae	-0.074	0.055	0.036	-0.083	-0.014	-0.121	0.026	-0.139
Tanytarsini	**-0.327**	**-0.189**	-0.059	0.102	**-0.379**	-0.160	-0.179	0.106
Chironomini	**-0.430**	-0.154	-0.136	0.100	**-0.572**	**-0.227**	**-0.276**	**0.184**

gradient of pH and ionic composition) and overall diversity. Abundance was also mostly negatively correlated with PHYS1, again with the exception of the Plecoptera (correlated to PHYS2) and Orthocladiinae (correlated to none of the variables). Overall chironomid abundance was higher in flat, lowland streams, and the Chironomini, in addition to being more abundant in larger streams, were more abundant in flat, low-elevation, low-pH, low-conductivity, high-nutrient streams (i.e. they had significant correlations with all of the environmental variables), a result that was likely related to the consistently high abundance of this tribe in the northern regions of the study area.

Substrate, measured here as a categorical variable, by itself had little effect on the generic richness of most of the major groups (Figure 3.5). The Ephemeroptera and Plecoptera tended to be slightly more diverse and abundant on coarse substrates than on soft, but the clearest trends were seen in the Chironomini, which were much more diverse and consistently more abundant in streams with substrates composed primarily of silt, sand and organic matter. However, since substrate had a strong latitudinal component in this set of sites, with most of the soft substrates in the far north (Figure 2.6), the direct comparison of substrate types is probably misleading.

A 2-way ANOVA using latitudinal regions (defined in Chapter 2) and substrate type revealed much larger differences in generic richness and abundances due to region than to substrate (Table 3.3). The Ephemeroptera were still more diverse on coarse substrates than on soft, as were the Tanytarsini to a lesser extent (Table 3.4). Least square means for regions in the 2-way ANOVAs

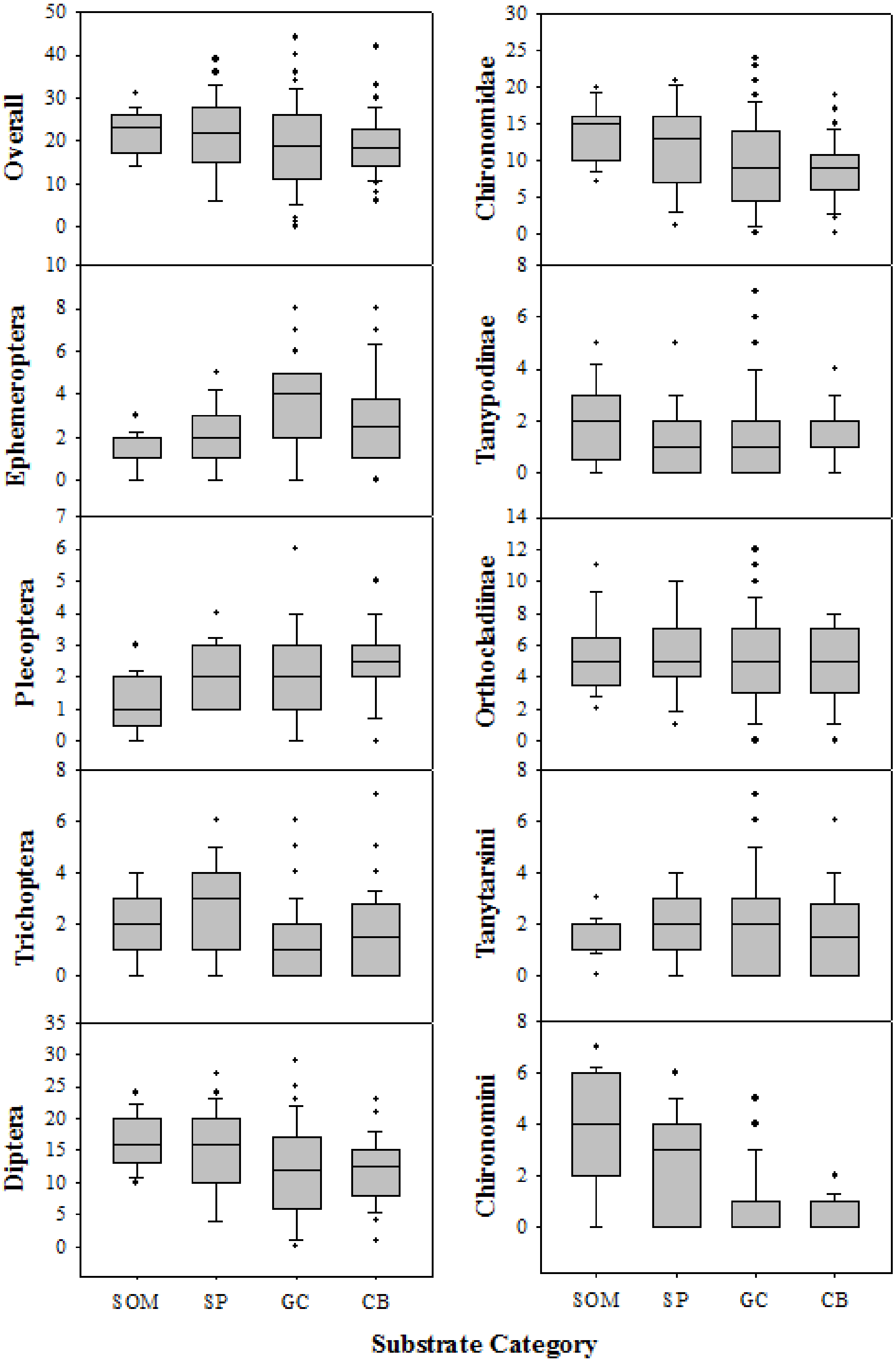

Figure 3.5 – Effect of substrate on local generic richness of the major aquatic insect groups. The upper and lower boundaries of the boxes represent 25th and 75th percentiles, respectively, and the line within the boxes represents median generic richness. Upper and lower whiskers indicate 90th and 10th percentiles, respectively, and the dots represent outlier values. SOM = Silt/Organic Material, SP = Sand/Pebbles, GC = Gravel/Cobble, CB = Cobble/Boulder (arranged in order of increasing coarseness).

Table 3.3 – 2-way fixed effect ANOVA table showing the effects of substrate type and location (region) on the local generic richness and abundance of aquatic insects. Significant differences ($p < 0.001$) are indicated in bold.

	DF	SS	MS	F	P		DF	SS	MS	F	P
Overall						Diptera					
Substrate type	3	293.8	97.9	1.3		Substrate type	3	38.1	12.7	0.4	0.761
Region	5	1718.8	343.7	4.6		Region	5	1480.7	296.1	9.1	**<0.001**
Residual	174	12917.2	74.2			Residual	174	5671.0	32.6		
Total	182	15003.6	82.4			Total	182	7533.3	41.4		
Ephemeroptera						Tanypodinae					
Substrate type	3	56.9	19.0	6.1	**<0.001**	Substrate type	3	4.5	1.5	0.9	0.428
Region	5	68.2	13.6	4.4	**<0.001**	Region	5	65.5	13.1	8.2	**<0.001**
Residual	174	537.5	3.1			Residual	174	279.2	1.6		
Total	182	679.3	3.7			Total	182	349.7	1.9		
Plecoptera						Orthocladiinae					
Substrate type	3	4.4	1.5	1.2	0.314	Substrate type	3	12.5	4.2	0.6	0.61
Region	5	59.0	11.8	9.5	**<0.001**	Region	5	105.0	21.0	3.1	**0.011**
Residual	174	216.1	1.2			Residual	174	1195.3	6.9		
Total	182	313.5	1.7			Total	182	1319.7	7.2		
Trichoptera						Tanytarsini					
Substrate type	3	10.9	3.6	1.5	0.209	Substrate type	3	29.0	9.7	3.9	**0.01**
Region	5	97.4	19.5	8.2	**<0.001**	Region	5	42.2	8.4	3.4	**0.006**
Residual	174	413.3	2.4			Residual	174	432.7	2.5		
Total	182	562.9	3.1			Total	182	497.4	2.7		
						Chironomini					
						Substrate type	3	9.7	3.2	1.9	0.126
						Region	5	134.4	26.9	16.0	**<0.001**
						Residual	174	292.3	1.7		
						Total	182	570.2	3.1		

Table 3.4 – Least square means of local generic richness for substrate groups and regions from 2-factor ANOVA. Values with the same letter are not significantly different (alpha = 0.05).

	Overall	Ephemeroptera	Plecoptera	Trichoptera	Diptera	Tanypodinae	Orthocladiinae	Tanytarsini	Chironomini
Substrate type									
Silt / Organic Matter	17.05	1.54 a	1.24	1.55	11.83	1.30	4.39	1.21 a	2.10
Sand / Pebbles	19.72	2.11 a	1.63	2.33	12.65	1.25	5.17	1.68 a,b	1.59
Gravel / Cobbles	22.50	4.01 b	1.84	2.47	13.43	1.79	4.90	2.7 b	1.82
Cobbles / Boulders	20.59	3.30 b	1.96	2.23	12.47	1.89	4.53	1.87 a,b	1.33
Region									
Tundra	24.08 a,b	1.97 a,c	1.19 a,c	3.04 a	17.69 a	2.25 a	5.87	2.73 a,c	3.67 a
Northern Taiga	27.23 a	3.34 a,b	2.58 b	3.17 a	17.83 a	2.40 a	5.87	2.82 a	3.28 a
Southern Taiga	14.12 c	2.66 a,b,c	1.66 a,b	0.89 b,c	8.71 b	0.35 b	4.33	0.99 b,d	0.84 b
Norman Mountains	16.68 b,c	1.75 c	1.56 a	0.73 c	12.33 b	1.66 a,d	5.10	1.61 a,c,d	0.60 b
Liard	16.95 b,c	2.51 a,b,c	2.55 b	2.05 a,b	9.08 b	0.75 b,c,d	3.95	1.20 b,c,d	0.96 b
Slave	20.71 a,b,c	4.19 b	0.46 c	2.99 a	9.94 b	1.95 a,c	3.36	1.84 a,c,d	0.91 b

generally matched the trends from the latitudinal regressions for the EPT orders, with declines in richness apparent in the mayflies (significantly) and stoneflies (not significantly) and low caddisfly richness in the middle regions. There was no clear relationship between dipteran richness and substrate, but a clear trend towards higher local least square means of richness in the tundra and northern taiga. This trend was apparent in each sub-group of the Chironomidae, and was highly significant for the Chironomini.

3.3.4 Gradients in regional diversity

Preliminary analyses showed that one tundra site (Zed Creek) contained huge numbers of *Rheotanytarsus* sp. (thousands per sample), which had an inordinate effect on the rarefaction curve for the tundra making regional diversity appear much lower than it actually was. We therefore excluded this site for the calculation of all rarefaction curves that included *Rheotanytarsus* (e.g. the overall, Chironomidae, and Tanytarsini curves); since there was nothing apparently unusual about the rest of the fauna, we included Zed Creek when we calculated the other curves. Rarefaction curves were not calculated for the Great Slave region because only five sites were sampled, and one of these (Salt River) yielded large numbers of a single species of aquatic insect – a member of the *Cricotopus (Isocladius) sylvestris* group, found at only one other nearby site).

Regional rarefaction curves of overall diversity, calculated for up to about 4000 individuals, showed a consistent trend of decreasing diversity with increasing latitude, with the exception of the tundra region, which had a curve similar to the Norman and Southern Taiga regions (Figure 3.6). This pattern contrasted with the lack of a clear latitudinal trend in local overall generic richness, although it is consistent with the 2° polynomial regression line (Figure 3.3a). The regional rarefaction curves of the major insect orders and major groups of chironomids, on the other hand, generally matched the trends in local richness.

The Ephemeroptera and Plecoptera were each most diverse in the Liard and Norman regions and least diverse in the northern taiga and tundra (Figures 3.7a, b). Mayfly diversity appeared to decline in steps, with sharp drops in ES_n between the Liard and Norman regions, and again between the southern and northern taiga regions. Low abundances of Ephemeroptera in the tundra (where only about 80 individuals were collected in total) meant that the rarefaction curve for that region had an early, and artificial, asymptote, but otherwise it closely matched the northern taiga curve. The stonefly curves declined from south to north in a more orderly manner; the difference between the curves was smallest in the south and greatest in the north, indicating an accelerating decline in diversity with increasing latitude. The Trichoptera regional diversity curves (Figure 3.7c) were

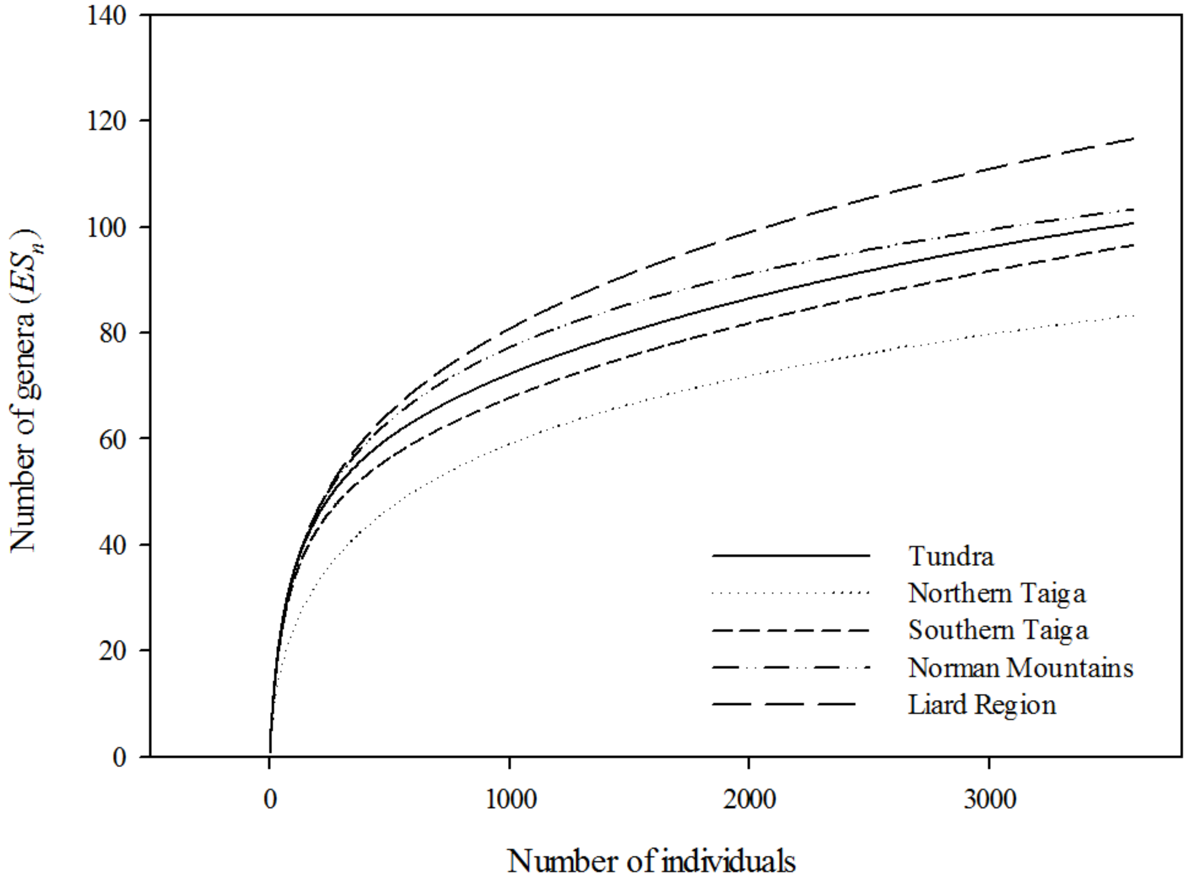

Figure 3.6 – Overall generic richness of latitudinal regions. Rarefaction curves are based on pooled abundance of genera across all samples within a region. Regions were defined in Chapter 2.

similar to the local diversity latitudinal gradient, with the lowest estimates in the Norman and southern taiga regions. However, the curve for the Liard region is well above the curves for the northern regions, and there is an indication of a dip in regional diversity between the northern taiga and the tundra, a pattern matched by comparison of the total number of genera collected in each region (Table 3.5), in which it should be noted that the Great Slave region had the 2nd-highest number of genera despite the low sampling effort. So, there is an indication of a negative latitudinal diversity gradient in the Trichoptera, although the pattern is more complex than in the other EPT orders. Regional diversity of the Diptera (Figure 3.7d) had little latitudinal trend, similar to the rarefaction curves for all aquatic insects except that the curves for the northernmost and southernmost regions were almost identical. This pattern differed from the latitudinal gradient in local dipteran richness, which had a positive linear regression. Among the major groups of chironomids, diversity of the Tanypodinae and Tanytarsini decreased with latitude, while the most diverse groups (Orthocladiinae and Chironomini) had patterns similar to the overall Diptera rarefaction curves. The Tanypodinae

(Figure 3.8a) had the most consistent decreasing latitudinal trend, with regional diversity clearly highest in the Liard region and lowest on the tundra, and the latter region's rarefaction curve reached a clear asymptote at approximately four genera. The exception was in the southern taiga, where low total abundance prevented calculation of a reasonable rarefaction curve (similar to the mayflies on the tundra). Asymptotes were also reached by several of the Tanytarsini regional rarefaction curves (Figure 3.8c), which decreased with latitude with the exception of the tundra, which appeared to approach and possibly exceed the diversity of the southern taiga. The crossing of the Liard and Norman region curves is indicative of a difference in the evenness of genera, with the Norman region quickly reaching a stable asymptote and the Liard curve rising more slowly due to the addition of rare species as more individuals were sampled.

The Orthocladiinae and Chironomini (Figures 3.8b, d) had similar trends in regional diversity, but the trend was much more apparent in the latter group. The Norman and taiga regions were approximately equivalent in diversity, and much lower than the tundra and Liard regions. In the case of the Orthocladiinae, these latter two regions had almost identical rarefaction curves, while Chironomini diversity was lower in the far northern region. The latter case reflects a greater proportion of genera that were either rare or occurred in low abundance on the tundra, since both the tundra and Liard curves eventually reach the same endpoint of 14 genera (Table 3.5).

3.3.5 Latitudinal trends in distributions of common genera

Among the EPT orders, the mayflies and stoneflies exhibited the clearest decline in diversity towards the north. In both orders, the regional rarefaction curves for the tundra and northern taiga lay well below the curves for the other regions, which is consistent with the sharp declines in local generic richness we observed above approximately 68 °N. Also, in both orders, the pool of genera on the tundra was about half the size of that of the northern taiga; this is not obvious in the Ephemeroptera rarefaction curves due to their very low abundance on the tundra. These primarily consisted of only the most widespread genera (*Acentrella* and *Baetis* for the mayflies; *Haploperla* and *Nemoura arctica* for the stoneflies). The regional rarefaction curves of the three southern regions consistently (but slightly) declined from south to north, due to the loss of burrowing mayflies, several baetid genera, and several plecopteran families (Capniidae, Perlidae, Pteronarcyidae, Taeniopterygidae). The taiga was basically limited to genera that were also common in the areas to the south, but the transition to the tundra saw the loss of almost all ephemerellids, heptageniids, leptophlebids, perlodids, and *Zapada* (Nemouridae), leaving a depauperate fauna consisting of the genera already mentioned. *Baetis* was an exception to the loss-of-genera trend, as the presence of this genus on the tundra was

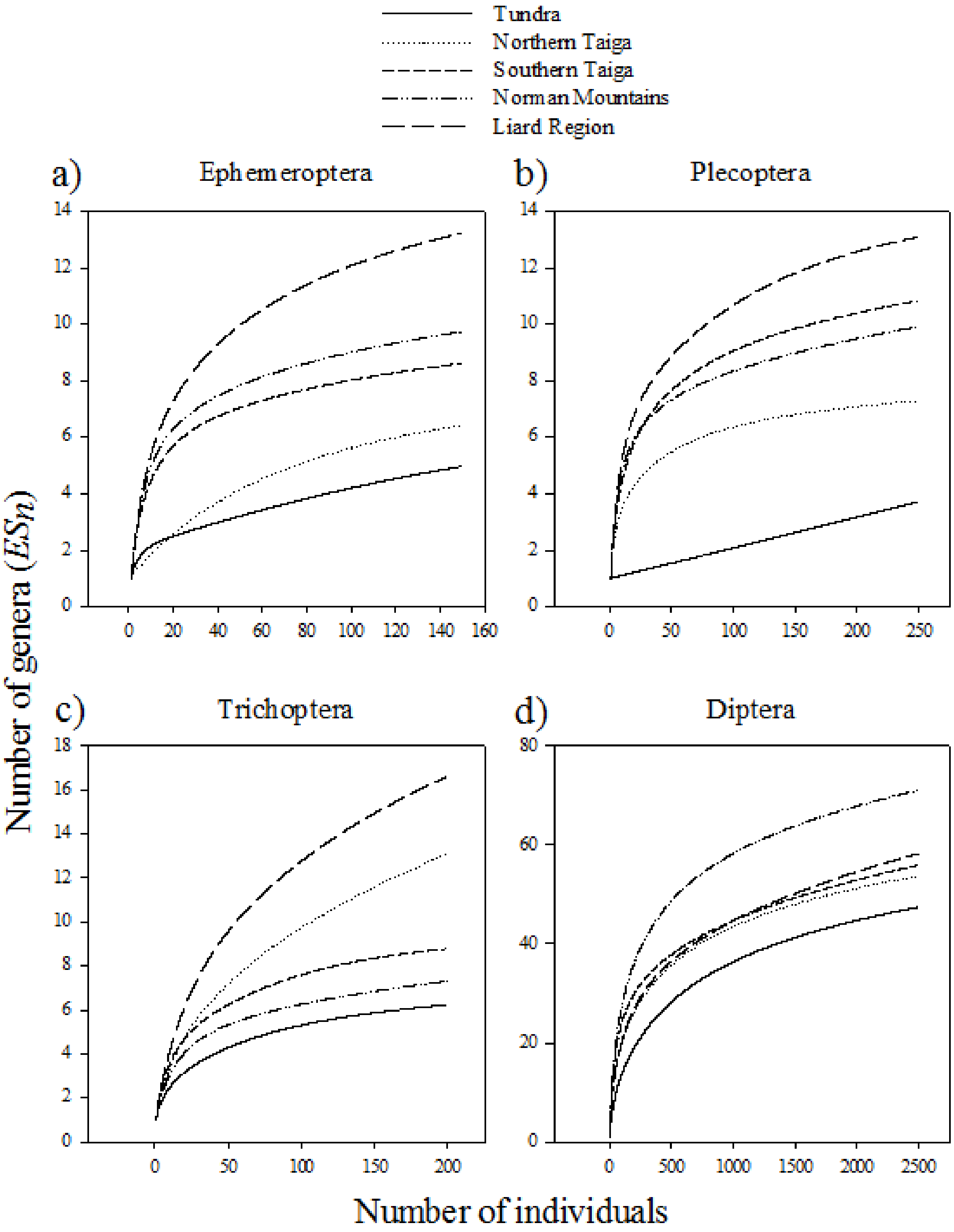

Figure 3.7 – Regional generic richness of major Orders of aquatic insects (Ephemeroptera, Plecoptera, Trichoptera, Diptera). Rarefaction curves are based on pooled abundance of genera across all samples within a region. Regions were defined in Chapter 2.

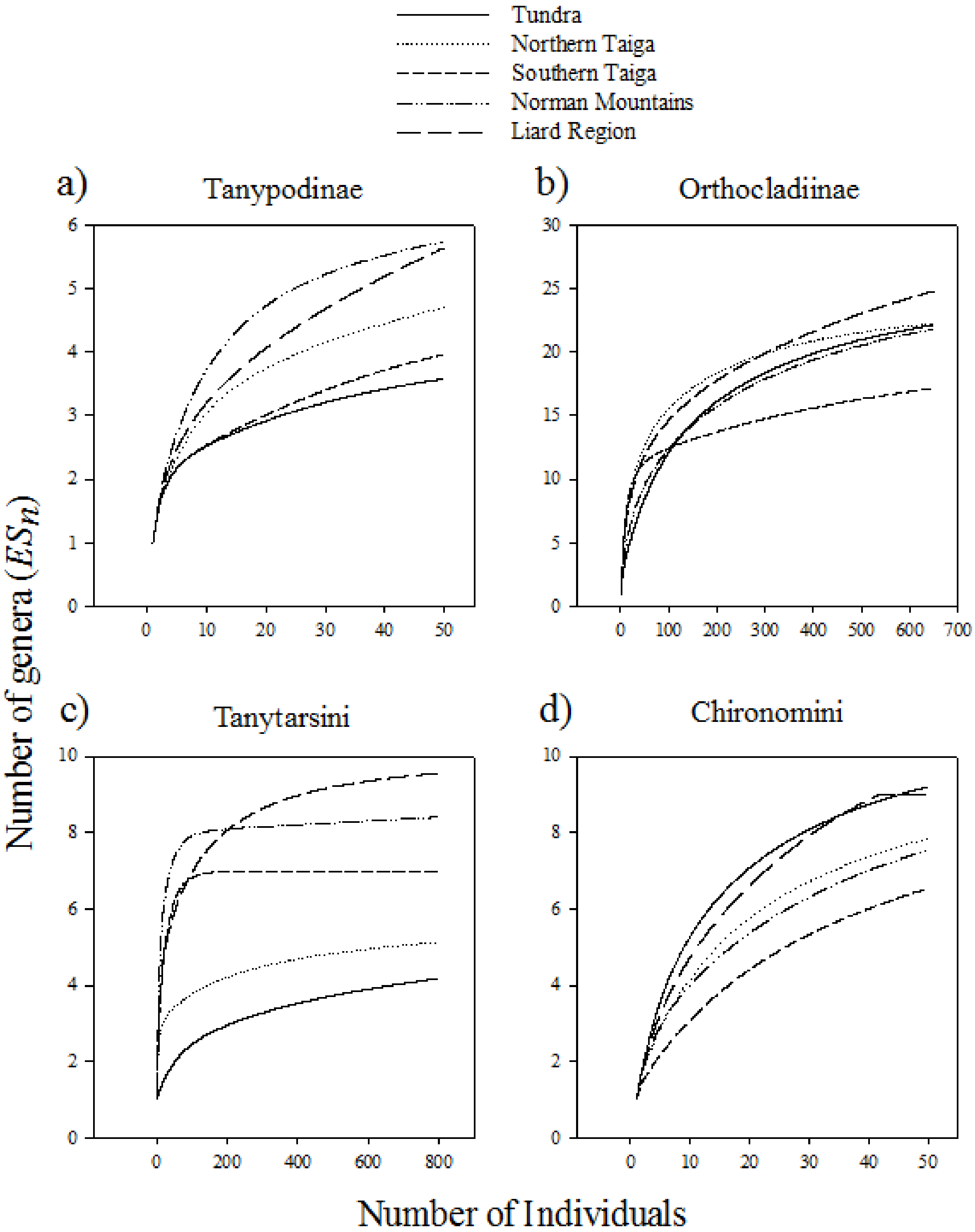

Figure 3.8 – Regional generic richness of subfamilies and tribes of Chironomidae (Tanypodinae, Orthocladiinae, Tanytarsini, Chironomini). Rarefaction curves are based on pooled abundance of genera across all samples within a region. Regions were defined in Chapter 2.

Table 3.5 – Total number of genera collected in latitudinal regions. Values are based on pooled counts across each region. Regions were defined in Chapter 2; the Great Slave region contains streams that drain into Great Slave Lake or Slave River.

	Great Slave	Liard	Norman Mountains	Southern Taiga	Northern Taiga	Tundra
Ephemeroptera	13	18	16	11	9	5
Odonata	5	1	2	0	2	0
Plecoptera	4	15	12	13	8	4
Hemiptera	5	2	0	0	2	0
Trichoptera	19	23	9	9	18	13
Coleoptera	10	6	6	3	3	5
Diptera	47	77	96	64	71	74
Chironomidae	35	62	67	47	54	54
Tanypodinae	6	10	11	4	8	5
Orthocladiinae	15	27	30	22	24	25
Tanytarsini	6	10	9	7	7	8
Chironomini	8	14	14	12	13	14
Other Diptera	12	15	29	17	17	20
Total	103	142	141	100	113	101

actually a replacement of widespread species (mainly *B. flavistraga* and *B. tricaudatis*) by the northern species *B. bundyae*. The other four tundra genera were apparently similar at the species level to the southern regions, but this could merely reflect a limitation in our taxonomic knowledge for these groups.

The pool of caddisfly genera was much smaller on the tundra than the southern-most region; the polynomial regression line was mainly determined by the loss of several families and genera in the Norman and southern taiga regions. The streams in the latter two regions were notable mainly for the dominance of hydropsychids (*Hydropsyche* in the Norman region and *Arctopsyche* in the southern taiga) and the absence (or very low abundance) of hydroptilids, philopotamids, phryganeids, and *Rhyacophila*, none of which were particularly common across the entire study area. The number of genera in the other regions declined from south to north, as shown by both the total number of genera collected (Table 3.5) and the rarefaction curves; the decline between the tundra and northern taiga may be even steeper than Figure 3.7c suggests, since the former curve appears to be approaching an asymptote while the latter does not. The trichopteran fauna of tundra around the Mackenzie Delta appears to be limited to the most widespread genera (*Brachycentrus americanus*, *Micrasema*, *Glossosoma*, but not *Hydropsyche* or *Rhyacophila*) and a few northern specialists, mostly limnephilids (e.g. *Grensia praeterita*, *Sphagnophylax meiops*) and phryganeids. The latitudinal gradient in local diversity is less clear (apart from the dip in the Norman mountains and southern taiga), but there is an indication that greater sampling effort at the southern end of the study area could have produced a clearer gradient: the 19 genera found in the Great Slave region came from only two streams, which were more diverse than all of the tundra sites put together.

Unlike the EPT orders, local generic richness of the Diptera increased with latitude, mainly due to the Chironomidae. Apart from that family, the Ceratopogonidae, Empididae, and Tipulidae were the major contributors to generic richness, since all other families were either monotypic in our collections, or were not identified past the family level (the Simuliidae were the major omission here, since they made up a large proportion of the fauna of some streams, and were most abundant in the taiga regions). The three families that were identified to genus showed no apparent latitudinal trends in diversity, and the other Diptera families (apart from the blackflies) were rare and generally low in abundance.

The Chironomidae were the most abundant and by far the most diverse group of insects across the study area, and were the major contributor to overall local generic richness and regional diversity. Only the Tanypodinae, however, had a clear latitudinal trend in regional diversity, and this was negative, with the tundra fauna basically limited to *Ablabesmyia*, *Procladius*, and genera in the *Thienemannimyia* group. The pattern seems to be one of species loss, similar to the Plecoptera (two common genera, *Labrundinia* and *Nilotanypus*, drop off north of the Liard region), but it is possible that taxonomic difficulties, especially with regard to the *Thienemannimyia* group, caused us to underestimate tanypode diversity in some regions.

Orthoclads, although highly variable in local generic richness, exhibited very little in the way of significant trends, in relation to either latitudinal or the environmental variables. This was the most diverse chironomid subfamily, and taxonomic difficulties make it difficult to draw clear conclusions as several genera (especially the widespread *Cricotopus*, *Eukiefferiella*, and *Orthocladius*) were diverse at the level of species or even species group, and the general biology of many orthoclads is not well described, let alone environmental tolerances and other relevant details. The Chironomini also displayed no evident loss of genera in the north, and in fact increased in local generic richness in the northern taiga and tundra. This tribe's latitudinal local richness gradient was similar to the Trichoptera, but with a greater and more consistent increase in the north. Neither the Orthocladiinae nor the Chironomini exhibited any clear trend with regard to species loss or gain over the latitudinal range; it is possible that a more detailed analysis of the assemblage composition will shed some light on these groups (Chapter 4).

The Tanytarsini were represented by relatively few genera, most of which were widespread and abundant in at least part of the study area. This was possibly the most thoroughly sampled group of insects, as indicated by the early asymptotes of the regional rarefaction curves (but again, generic-level identification likely obscures much greater levels of species diversity). Several closely related genera (*Constempellina*, *Stempellina*, *Stempellinella,* and *Neostempellina*) that were common in the southern regions were rare or absent in the taiga and tundra, likely due to the lack of coarse substrates in these northern regions. Others (*Cladotanytarsus*, *Rheotanytarsus*, and *Tanytarsus*) were present throughout the study area, and were generally more abundant in the far north, especially *Rheotanytarsus*, which was extremely abundant downstream of tundra lakes.

3.4 Discussion

We expected to find a latitudinal diversity gradient with decreasing numbers of genera towards the north, consistent with the classical diversity gradient found in most groups of animals, and suggested for some groups of stream invertebrates by the meta-analysis of Vinson & Hawkins (2003). In arctic and sub-arctic streams, this gradient is likely related to shorter growing seasons, higher probability of freezing of the substrate, and more frequent and less predictable disturbances (e.g. flooding) in the north. Frequent and unpredictable disturbance combined with short (approximately four month) ice-free seasons imposes severe life-cycle constraints on the benthos, selecting for species with fast life cycles and high dispersal ability (Danks 2007). Freezing of the substrate during the winter selects for freeze-tolerant species or those that are able to avoid freezing either by producing antifreeze compounds or by avoiding habitats that are likely to freeze (Frisbie & Lee 1997).

Direct comparisons with other studies of lotic invertebrate diversity are somewhat problematic because of differences in watershed size, number of streams sampled, sampling method and taxonomic resolution, all of which affect estimates of diversity (Vinson & Hawkins 1996, Gotelli & Colwell 2001). Our estimates of total genus richness were in line with those of the only previous survey the Mackenzie System (Wiens *et al.* 1975), which counted 274 non-simuliid insect genera (24 mayflies, 12 odonates, 17 stoneflies, 45 caddisflies, 19 beetles and 111 chironomids); our estimates were either very similar (26 mayflies, 21 stoneflies, 15 beetles) or slightly lower (233 total genera, 5 odonates, 30 caddisflies, 96 chironomids), possibly due to a lower sample size. Compared to large river systems in temperate North America the macroinvertebrate fauna of the Mackenzie River is somewhat depauperate; the Upper Mississippi basin contains almost twice the number of invertebrate taxa (over 430) than the Mackenzie, despite draining an area less than one third the size (589,500 km^2) (Delong 2005). Even some much smaller watersheds in temperate latitudes contain many more invertebrate taxa than were observed in the present study; for example, the St. John’s River in Florida (> 300 taxa; Smock *et al.* 2005) and the Flathead River (> 500 taxa; Stanford *et al.* 2005). Macroinvertebrate surveys in northern latitudes tend to reach estimates of overall diversity similar to what was found here for the Mackenzie system; in central Sweden, Malmqvist & Hoffsten (2000) found 247 non-chironomid species, while the Moose River system in northern Ontario contained 288 invertebrate taxa (Milner *et al.* 2005).

Evidence for the expected latitudinal diversity gradient was strongest for the rarest orders of aquatic insects. The Odonata, Hemiptera, and Coleoptera were virtually absent from the northern regions of the study area. None of these orders was particularly diverse overall, but a marked decrease in abundance was found for each. Multiple year life cycles are common in each of these groups, so it seems likely that the increasingly intense disturbance regime in the far north limits the success of these orders. Alternatively, no member of any of these groups has been demonstrated to survive or avoid freezing, so tolerance of winter conditions may play a role. Adult dragonflies were frequently observed, even at the far northern latitudes, but only near lakes and the Mackenzie River main channel (i.e. habitats that were unlikely to freeze). It is also possible that these had migrated from southern areas.

The Ephemeroptera, Plecoptera, and Trichoptera were present throughout the study area, and latitudinal gradients in diversity largely conform to those found by Vinson & Hawkins (2003). The present study has the benefit of a much larger sample size (they had six streams located above 60 °N, only one of which was located above the treeline), although our low sampling intensity likely underestimated diversity relative to the older study, which used data from surveys spanning multiple years and seasons. Even so, the range of local EPT generic richness and the latitudinal patterns in generic richness they found were similar to those present in the Mackenzie system. Overall, latitudinal trends in the Ephemeroptera and Plecoptera supported the predicted diversity gradient, and the general pattern of loss rather than replacement of genera is consistent with the hypothesis that increasingly unfavourable climatic factors limit the fauna to only the most widespread, ecologically tolerant species, such as the freeze-tolerant *N. arctica* (Walters *et al.*, 2009), or specialists, e.g. *B. bundyae* (Giberson *et al*. 2007). The Trichoptera, on the other hand, were without a clear north-to-south gradient in diversity, which could reflect the wide range of species-specific habitat requirements and feeding modes of this group (Wiggins, 1996). In comparison with other arctic watersheds, there is apparently a longitudinal gradient in the number of EPT taxa. Mayfly diversity in the eastern Canadian arctic is low, with 19 taxa recorded in the Moose River system (Milner *et al.* 2005) and only 16 species in Nunavut (Giberson *et al.* 2007), compared to the 26 genera recorded in this study; diversity increases further west, with over 30 species present in the Yukon River system (Bailey 2005) and 55 in an eastern Siberian system (Beketov 2008). A similar east-west gradient is apparent for the stoneflies, which decrease from 71 species in the Yukon River (Bailey 2005) to 21 genera in the Mackenzie (this study) to only 12 taxa in the Moose River (Milner *et al.* 2005). Caddisflies, while much more diverse in western North America with 145 species in the Yukon River (Bailey 2005) compared to 30 genera in this study and 45 in Wiens *et al*. (2005), do not decrease as much in the east, with a fairly diverse fauna of 34 taxa in the Moose River (Milner *et al*. 2005). Again, differences in the taxonomic level of identification and sampling effort among these studies limits the value of these comparisons.

The dominance of the Chironomidae in the far north can probably be attributed to adaptation to extreme cold conditions, although little is currently known about species-specific freeze-tolerance adaptations (Irons *et al.* 1993), and possibly to the fact that chironomids are mostly collector-gatherers, so the predominance of fine particulate food sources (as opposed to leaf litter) above the treeline may be more favourable to them than to other insect groups (Rautio *et al.* 2008). Substrate appeared to be a major determinant of chironomid richness and abundance, especially in the tribe Chironomini, which were much more diverse and abundant in the softer substrates that were predominant on the tundra. However, substrate does not account for the high diversity of this group in some rocky streams in the Liard region, so other factors such as food availability may be involved. Many Chironominae generally prefer soft substrates and lentic environments (McCafferty 1998) and the low gradient depositional streams and preponderance of lakes in the tundra is probably favourable to them; significant negative correlations with the composite physical environmental variables indicated that they were more abundant in large, low-gradient stream independent of latitude. Another possible factor driving chironomid diversity and abundance is the general lack of invertebrate predators in the far north. Since odonates, predatory stoneflies (e.g. Perlodidae) and caddisflies (e.g. *Rhyacophila* and *Hydropsyche*) and Megaloptera/Neuroptera are nearly absent in the northern extremes of the study area, as are many potential collector-gatherer competitors (e.g. most mayflies), many chironomids may be free of many potentially limiting biotic interactions on the tundra. Few large-scale surveys of arctic North American streams have attempted to include chironomids; Bailey (2005) estimated that over 100 chironomid taxa are present in the Yukon River basin, which is comparable to observations for the Mackenzie System of 96 genera (this study) and 111 genera (Wiens *et al.* 1975); diversity may be slightly lower in the east, as Milner *et al.* (2005) report 77 chironomid taxa in the Moose River system. Chironomid diversity in the Mackenzie Basin appears to be considerably higher than in northern Europe, as surveys of watersheds in Finland (Heino & Paasivirta 2008) and northern Italy (Lencioni & Rossaro 2005) recorded 49 and 53 chironomid genera, respectively.

The River Continuum Concept (Vannote *et al.* 1980) predicts that diversity should peak in mid-order streams, due to the higher habitat diversity present relative to very small or very large streams (Minshall *et al.* 1985), which can meet the habitat requirements of a greater variety of species. Apart from latitude, stream size (as expressed by the principal component corresponding to width, depth, and velocity) was the only environmental variable with a consistent correlation with local generic richness and abundance. Since our set of sites included mainly low- to mid-order streams, these results are consistent with the predictions of the RCC; other studies have also found diversity to be highest in mid-order streams (e.g. Minshall *et al.* 1985), including some in northern European systems (Malmqvist & Hoffsten 2000, Heino & Paasivirta 2008, Heino *et al*. 2008). Only two groups were not affected by stream size: Plecoptera were more diverse and abundant in smaller, high-gradient streams, consistent with their general preference for cool, well-oxygenated water, and the diversity and abundance of Orthocladiinae were not significantly correlated with any environmental variable. The Orthocladiinae were by far the most diverse group across the entire study area at the generic level; at the species level they were likely far more diverse, but consistent species identification in this group proved to be difficult. Assuming that taxonomic diversity corresponds to ecological diversity in this poorly understood subfamily, it seems reasonable that different kinds of streams could support similar numbers of orthoclad genera, and that the composition of the assemblages could be a better indicator of environmental conditions than the number of genera present at a given site (this will be examined in greater detail in Chapter 4).

Water chemistry variables had little correlation with local generic richness or abundance of any group of aquatic insect. Part of the reason for this is that the major gradients in water chemistry (pH, conductivity, and nutrients) were highly correlated with latitude, which made separation of these variables effectively impossible. Likewise, the effects of different kinds of substrate were difficult to separate from latitudinal gradients since the streams in the tundra and in the Mackenzie Delta were mainly soft-bottomed braided channels. However, other studies have also failed to find strong correlations between environmental and diversity variables (e.g. Heino *et al.* 2008), and some have suggested that patterns in stream macroinvertebrate diversity, especially of the chironomids, are essentially random as far as local environmental factors are concerned (Heino 2005).

Regional diversity and local generic richness of the EPT orders exhibited similar latitudinal patterns, but this was not so for the chironomids. Mean regional midge generic richness was consistently highest in the northernmost regions, but the southernmost region had the highest rarefaction curve for each chironomid subgroup, so the size of the regional genus pool would seem to underestimate local generic richness in the far north. In other words, northern taiga and tundra streams harboured a greater percentage of the regional species pool than streams in the southern regions. This may be related to the biotic interactions mentioned above, but could also have something to do with the disturbance regime (e.g. winter freezing and spring/summer flooding). Tundra streams are more likely to freeze solidly in the winter, limiting the number of potential predators and competitors; however, because the terrain is relatively flat and channel morphology is generally beaded, with many pools, they are less likely to experience catastrophic disturbance in the spring. So, if the majority of the fauna is able to withstand or otherwise cope with the winter conditions, the major source of disturbance is summer flooding driven by precipitation running off over the permafrost, which should, according to the intermediate disturbance hypothesis (Sousa 1984) increase the number of genera that occur on any given patch. This might lead to an essentially random assemblage of chironomids which is also subject to relatively low levels of predation and/or competition from other insect orders, and therefore not as susceptible to reduction by competitive exclusion. So, near the end of the growing season (e.g. at the time of sampling), most tundra streams contain a well-mixed chironomid fauna with a high proportion of the regional pool represented.

The extreme abundance of some Tanytarsini at a few tundra sites, most notably *Rheotanytarsus* in Zed Creek, just downstream of Parson Lake, had a strong effect on the rarefaction curves, which serves to highlight one of the important features of the rarefaction procedure. The curves represent diversity as well as dominance (or evenness), so if two regions (Region A and Region B) are equally diverse in total numbers of taxa, but Region A is dominated by one taxon while Region B has roughly equal numbers of all taxa, the curve of Region A will fall well below that of Region B. This is because the probability of picking an individual of the dominant taxon in Region A is so much higher than the probability of picking an individual belonging to any of the other taxa, especially in the lower parts of the curve.

The relationships between local taxonomic richness and regional diversity, between local richness and abundance, and between all three of these variables and small- and large-scale environmental factors are complex and exceedingly difficult to explain within a single study (Allan 2007). The attempt described in this chapter was limited in some ways because of the nature of the larger survey project: site selection was often based largely on accessibility, and the goal of sampling as many sites as possible within a brief time period limited the scope and detail in which local habitats could be assessed, and meant that each site could be sampled on only one occasion. On the other hand, all sites were sampled late in the growing season, which ensured that the communities were phenologically similar, and the sampling method was standardized, which facilitated direct comparison of local generic richness and abundance across streams. Information on the ecological conditions of the sites prior to sampling was extremely limited; some basic information was available for sites that fell along the proposed route of the Mackenzie Gas pipeline (IORV 2004), but the environmental status of many sites was completely unknown. For certain analyses, sites which had one or more environmental variable far outside the range of the rest of the sites were excluded to avoid spurious correlations with richness. Another potential limitation of our study is the fact that sites were sampled in different years, although there was considerable spatial overlap among years. Annual variation in both winter (Bradt & Wieland 1981) and summer (e.g. Hodkinson *et al.* 1996) conditions can have a large effect on abundance, but diversity, and to a lesser extent community composition, have been found to be less variable from year to year (Bradt & Wieland 1981), depending on the stability of the stream habitat (Milner *et al.* 2006). Lacking a rigorous, long-term sampling regime for each stream, the high variability in local richness and abundance could not be fully explained; broad spatial trends were apparent for some taxa, but a large stochastic element was unavoidable.

To summarize, there was little evidence of a latitudinal gradient in overall local generic richness, and weak evidence of a decrease in the regional pool of genera towards the north. However, latitude had a differential effect on the major groups of aquatic insects, as the diversity of the EPT orders decreased from south to north, while Diptera, and especially chironomid diversity, increased towards the north. Chapter 4 expands on this analysis by examining patterns of community composition across the Mackenzie River System.

Chapter 4

Patterns and drivers of benthic invertebrate assemblage composition in streams of the Mackenzie River System

4.1 Introduction

The composition of macroinvertebrate communities is influenced by the regional species pool, the ability of species to disperse to a site, the suitability of the habitat for growth and reproduction of the species that reach it, and the disturbance regime of the watershed or region (Allan 2007); in other words, a complex hierarchical filter of biotic and abiotic factors govern the species composition at a site and the way that composition varies over time. Species vary in their microhabitat requirements, environmental tolerances, life cycles and feeding methods, so the habitat template (Southwood 1988) is important in determining patterns of distribution and abundance. Low temperature and limited food availability in arctic and subarctic streams limit the growth of many species (Vinson & Hawkins 2003), and adaptations to avoid freezing during the winter and ice scour in the spring are necessary for survival in many northern streams (Prowse & Culp 2003, Huryn *et al.* 2005). Variability due to flow variation in the spring and summer may decrease the potential for competition and other biotic interactions between species (Townsend 1989), and possibly result in largely stochastic patterns of composition by periodically transporting organisms to different patches, reducing patterns attributable to local habitat variables (Miller & Stout 1989). Therefore, the macroinvertebrates present in a patch of stream benthos may be more properly referred to as an assemblage rather than a community, as the latter term implies predictable interactions and trophic connections between species; the two terms will be used interchangeably here, given the above caveats. The composition of communities or assemblages of aquatic macroinvertebrates can be altered as a result of environmental change, providing a useful basis for biomonitoring or assessment of impacts (e.g. Reynoldson *et al.* 1997), but it has also been suggested that the disturbance regime (in terms of spring ice scour and flashy summer flow) of many streams in the far north results in highly variable natural assemblages (Milner *et al.* 2006), which could lead to difficulties in defining a reference condition.

Studies of benthic assemblage composition of streams in the Canadian north have for the most part been limited to assessing the response to disturbances related to pipeline construction and operation (e.g. Rosenberg & Snow *et al.* 1975; Snow *et al.* 1975; Young & Mackie 1991) or to certain taxonomic groups (e.g. Cobb & Flanagan 1980), although there are a few more general studies from the Athabasca system (e.g. Clifford 1969, Barton 1980) as well as from the far north (Stocker 1972). There is a larger body of literature on streams in Alaska and northern Europe, especially Scandinavia and Finland. Several studies have found that, as in temperate streams, composition is related to the position along the river continuum (Oswood 1989, Smidt & Oswood 2002; Heino & Paasivirta 2008; Heino *et al.* 2009) and to characteristics of the substrate (Barton 1980, Lencioni & Rossaro 2005). A rare experimental study (Peterson *et al*. 1993) has shown fairly conclusively that nutrient limitation (especially phosphorus) has a strong effect on arctic stream communities, and low inputs of allochthonous CPOM likely limit the abundance of certain functional feeding groups (Cowan *et al.* 1983; Cowan & Oswood 1984). Strong spatial components to variation in assemblage composition have been found in Alaska (Oswood 1989; Smidt & Oswood 2002), Sweden (Malmqvist & Hoffsten 2000) and Siberia (Beketov 2008), with these patterns attributed to a variety of factors including latitude, altitude, longitudinal position (i.e. proximity to the outlet of the river system into the ocean), and permafrost conditions. Since these factors are often correlated with each other (and certainly are in the Mackenzie system; see Chapter 2), it is difficult to attribute changes in community composition to a single geographic variable. The availability of unfrozen habitat and the stability of flow and substrate during the growing season are important factors determining assemblage composition (Huryn *et al.* 2005), imposing physiological (Irons *et al.* 1993, Danks 2007) and phenological (Clifford 1969, Danks 1992b) constraints on growth and survival. However, the investigation of species-specific winter survival mechanisms of aquatic insects is still in the early stages (Ward & Stanford 1982; Danks 2007) and only a few species have been studied in any detail (Irons *et al.* 1993; Frisbie & Lee 1997; Bouchard *et al.* 2006; Walters *et al.* 2009).

In addition to factors that affect assemblage composition in all stream systems, such as substrate, water chemistry, stream size and others (Allen 2007), benthos in the study area is also likely to be affected by factors related to the arctic climate, which becomes more severe towards the north. The latitudinal gradient spanned by the Mackenzie River system comprises several factors which potentially affect composition, including altitude, temperature, permafrost conditions, longitudinal position, vegetation and major differences in terrain. Patterns of assemblage composition are expected to include an increase in the proportion of cold-hardy taxa towards the north, reflecting increasing climatic severity, and reflect the dramatic changes in terrain and hydrology in the far north where the rolling to mountainous terrain of the boreal forest gives way to the relatively flat and lake-dominated tundra and Mackenzie Delta. Winter ice conditions were expected to have a strong effect on composition by selecting for freeze-tolerant taxa. Low phosphorus and nitrogen levels likely lead to nutrient limitation in many of the streams, so small differences in nutrient availability seem likely to have relatively large effects on assemblage composition. Many arctic and sub-arctic species live near the limit of their environmental tolerance, and latitudinal patterns in the abundance of these species likely reflect the environmental latitude gradient, making them potentially useful indicators of climate change (Danks 1992a),

In this chapter, a multivariate analysis is used to investigate patterns of community composition of benthic macroinvertebrates in tributary streams of the Mackenzie River across a large-scale latitudinal gradient, and the relation of composition to local environmental variables such as substrate and water chemistry. Additionally, latitudinal trends in the abundance of common taxa are examined to identify potential indicators of climate change. Descriptions of the study sites and collection of environmental variables were given in Chapter 2 along with a summary of spatial patterns in those variables; benthos collection and sorting methods were given in Chapter 3.

4.2 Analytical Methods

The environmental variables were transformed to achieve normal distributions as described in Chapter 2, and the variables were then standardized across samples prior to multivariate analysis. The abundance data were log-transformed prior to analysis. This transformation was optimal for two reasons, the first being that it led to the lowest stress levels on the MDS ordination of sites. Second, the effect of transformations in non-parametric methods is to increase the relative influence of rare species. Since the level of identification used here varied among taxa, there were several widespread taxa that most likely represented multiple species (e.g. *Rheotanytarsus*, Pelycopoda, Oligochaeta, etc), so the transformation allowed the taxa that were identified to lower taxonomic levels to have more appropriate influence.

Multivariate analyses were carried out using the PRIMER v6 statistical package (Table 4.1). Initial tests were conducted using ANOSIM (analysis of similarity, a non- parametric, multivariate analog of ANOVA based on rank similarities) to check that the individual samples naturally grouped by stream or by site (at least three replicates were collected at each site, and some streams were sampled at more than one station) and to determine the resemblance coefficient (Jaccard or Bray-Curtis similarities based on logged or relative abundance) that maximized the differences between sites. From these tests, it appeared that Bray- Curtis similarity determined from log-transformed abundances averaged by site. Bray-Curtis similarities were also preferable because several routines in PRIMER are based on that coefficient, so all of our results were more directly comparable.

Next, non-metric multi-dimensional scaling (MDS) was used to ordinate the sites by community composition. In PRIMER, this is an iterative procedure in which the distance between

Table 4.1 – Description of multivariate analysis protocols in PRIMER v6.0 and their uses in the analysis of community composition in this chapter.

Method in PRIMER	Rationale	Use in this chapter
ANOSIM (Analysis of Similarities)	Comparison of similarities of multivariate patterns within and among groups of samples	1. Preliminary evaluation of grouping samples by site 2. Linking community composition to qualitative environmental variables 3. Used within the LinkTree protocol
Bio-Env	Identifies out of a set of variables the subset whose multivariate pattern best correlates with another fixed multivariate pattern corresponding to the same set of sites	Identification of the set of environmental variables that best correlates to the pattern of community composition
BV-Step	Similar to Bio-Env but uses a step-wise procedure allowing a greater number of variables to be analyzed	Identification of the subset of taxa that best correlates to the overall pattern of community composition
CLUSTER (Hierarchical Cluster Analysis)	Constructs a dendrogram using an agglomerative clustering protocol	Evaluation of the MDS ordination
LinkTree	Creates a linkage tree based on a resemblance matrix in which each split corresponds to a threshold value for one or more variables in another data matrix	Definition and characterization of site groups based on community composition and environmental variables
MDS (Non-metric Mulitdimensional Scaling Analysis)	Ordinates samples based on multivariate rank similarities	Ordination of sites by community composition
RELATE	Tests null hypothesis of no relationship between multivariate patterns in two sets of samples	1. Linking community composition to quantitative environmental variables 2. Linking community composition to spatial distribution of sites 3. Used within the Bio-Env and BV-Step protocols
SimPer (Similarity Percentages)	Evaluates the contribution of species to similarities within a group of samples and dissimilarities among groups of samples	Evaluation of the contribution of individual taxa to site groups and to significant differences in composition based on qualitative environmental variables

two sites represents the rank order of the relative dissimilarities of the sites. This method is sensitive to outliers, which can cause the majority of sites to be tightly clustered in a single group if a few of the sites are highly distinct. Five sites had to be removed on this basis, but each of these had an ecologically reasonable justification for removal, and these are described in the results section. The ordination was compared to an agglomerative, hierarchical clustering method (CLUSTER) to ensure that it adequately described the variation among sites.

Next, to link the invertebrate assemblages to spatial and environmental variables at the sites, the Bray-Curtis resemblances among assemblages were compared to the Euclidean distance matrix of the environmental variables at the sites as well as to a Euclidean distance matrix of the decimal coordinates of the sites, which represented the spatial distance among sites. These comparisons were made using RELATE, a non-parametric rank-based testing protocol. Differences in assemblages based on qualitative groupings of the sites (region, substrate, winter conditions, presence of an upstream lake, % macrophyte cover and habitat type).

The next step was to link individual environmental variables to the multivariate pattern across the sites. The Bio-Env procedure was used to exclude extraneous variables from the analysis by finding the subset of environmental variables whose Euclidean distance matrix best correlated to the Bray-Curtis resemblance matrix of the invertebrate assemblages. These variables were used as input into a binary, divisive linkage tree protocol called LinkTree, which uses a non-metric, non-linear and non-additive algorithm to divide the sites in such a way that maximizes the multivariate distance between groups of sites based on the assemblage data, but also so that each split in the tree corresponds to a threshold value for one or more of the environmental variables. The most interpretable results were obtained using a minimum group size of 3 sites, a minimum split size of 5 sites, and a minimum ANOSIM R value of 0.3 between groups. Based on these results, the sites were split into groups corresponding to both biotic and environmental variables.

The next step was to determine the species or higher taxa that were responsible for these groupings, and for the multivariate pattern of the sites. The BV-Step protocol was used to identify discriminating species (this is similar to Bio-Env, but uses a step-wise search for combinations of variables rather than analyzing every possible combination among the 370 species found). This procedure identified the set of species that best recreated the original Bray-Curtis resemblance matrix, as evaluated by the RELATE ρ statistic. BV-Step was run iteratively, removing the selected species after each analysis, until ρ was less than 0.7 (i.e. until the set of species returned by the procedure no longer produced an ordination similar to the original). This left a set of species that was almost entirely responsible for the multivariate pattern among sites.

SimPer (similarity percentages) was used to characterize the site groups; this is a method of pair-wise comparisons that gives percentage contributions from each species to the average Bray-Curtis similarities among all samples within a group and dissimilarities among all samples between groups. Species contributions to the average similarity/dissimilarity were compared to the contribution of the species to the standard deviation as a measure of the consistency of the presence in, or discrimination between, groups for each species. Correlations between environmental variables and assemblage composition on a more local scale were assessed within each group of sites with Bio-Env for continuous variables and ANOSIM for categorical variables. The set of discriminating species within each region was determined using BV-Step, as described above. Where significant differences were found among stream types (e.g. categorical variables), SimPer was used on the set of discriminating species to characterize differences in the fauna. The relationships between the continuous variables and the discriminating species were evaluated using Pearson correlation analysis.

Finally, I attempted to characterize large-scale patterns of community composition across the entire study area using Pearson correlations between latitude and the log-transformed abundance of each of the discriminating taxa as identified by BV-Step.

4.3 Results

4.3.1 Preliminary analysis & data handling

Preliminary analysis of the samples indicated that it was acceptable to pool samples based on the site or stream they came from (Table 4.2). The ANOSIM *R* statistic was slightly higher when samples were grouped by site rather than stream, indicating that there were significant differences between sites in the same stream for the few streams that were sampled at multiple stations (these were some of the 2005 Norman region streams, which were sampled upstream and downstream of proposed

Table 4.2 - Evaluation of sample groupings and resemblance coefficients. Values are the ANOSIM *R* statistics, which have a range of 0 to 1 and are highest when the differences among samples between groups are greater than the differences among samples within groups. All tests were significant with $p < 0.1$.

	Bray-Curtis resemblance		Jaccard similarity
	Log abundance	Relative abundance	
Sites	0.862	0.851	0.735
Streams	0.824	0.726	0.689

pipeline crossings), though these differences were usually smaller than the differences between streams. *R* was maximized when the resemblance matrix contained Bray-Curtis similarities determined from log abundance values, as opposed to Bray-Curtis similarities of relative (%) abundance or Jaccard coefficients, so these (Bray-Curtis similarities of log abundance) were used to construct resemblance matrices.

Initial MDS ordinations revealed five sites to be multivariate outliers that prevented interpretation of the ordination when included; these five sites were excluded from subsequent analyses. Three sites in the Slave region were excluded: Little Buffalo River was a large river sampled only along the banks; Sandy Creek had been blocked off upstream by a beaver dam and contained a fauna more characteristic of a pond (e.g. *Monoporeia*, several cladocerans, gyrinid beetles, coenagrionid damselflies and caenid mayflies); and Salt River was an apparently unusual stream with extremely high conductivity, abundant algae and a benthic assemblage dominated by a few taxa that were rare elsewhere (especially *Cricotopus* (*Isocladius*) *sylvestris*). Two streams in the Western Cordillera region were sampled a few hours after heavy rainfall, and had a limited assemblage consisting of a few species of clinging mayflies (e.g. *Serratella*, *Rithrogena*). It is likely that much of the fauna in these latter streams had either entered the drift, had burrowed deeper into the substrate or moved to the sides of the stream to avoid the drift and therefore was not sampled; since the sampling methods limited sampling to shallower areas, it is also possible that some of the areas sampled are dry under normal flow conditions.

4.3.2 Ordination of sites by community composition & relation to environmental variables

ANOSIM tests of differences among groups of sites defined by qualitative environmental variables were generally not significant (Table 4.3). The exceptions were region (as defined by PCA analysis of environmental variables in Chapter 2) and the presence/absence of a lake upstream, although there was a regional effect in the latter due to the preponderance of lakes in the tundra. No effect was found for substrate or % macrophyte cover (although the classification of these variables was rather coarse), habitat type (defined as riffles or runs), side (east or west) of the Mackenzie River, the presence of pooled areas at the site, or winter flow conditions (which were only known for a handful of the sites). On the other hand, RELATE tests determined that the variation in the quantitative habitat and water chemistry variables was significantly related to variation in assemblage composition ($\rho = 0.447$, $p < 0.1$), as was the spatial configuration of sites ($\rho = 0.32$, $p < 0.1$).

Table 4.3 - Differences among groups of sites based on qualitative variables among all sites (Global R) and within each site group. Values are ANOSIM R statistics for differences among the categories for each grouping. Winter conditions were unknown for the HNSS and LNSS site groups, and only one site in the FNS group had a lake upstream. FNS = Far Northern Streams, MNS = Mid-Northern Streams; HNSS = High-Nutrient Southern Streams, LNSS = Low-Nutrient Southern Streams and SNS = Small Northern Streams. Significant R statistics (*p* < 0.5) are in bold.

Grouping	Global R	FNS	MNS	HNSS	LNSS	SNS
Region	**0.261**	0.198	**0.449**	0.679	0.563	0.727
Substrate	0.098	**0.576**	-0.014	0.333	0.5	0.077
Winter Conditions	0.088	-0.084	**0.37**	n/a	n/a	0.778
Presence of lake upstream	**0.198**	n/a	**0.427**	-0.296	0.161	-0.32
% macrophyte cover	0.079	0.067	-0.068	0.679	0.563	0.179
Habitat type	0.156	0.153	0.004	-0.393	0	-0.045

MDS analysis produced an ordination with a stress level of 0.18 (Fig 4.1), which is within the acceptable range of stress levels that allows meaningful interpretation. Percent similarity among sites ranged from very low (< 20%), especially among the southern sites, to over 50% among many of the far northern sites. The wide range of similarities prevented simple classification of the sites using percent similarity values, as can be seen from the 20% and 30% similarity clusters indicated in Fig 4.1; at 20% most sites fall into one large group with several outlying clusters each of which contained

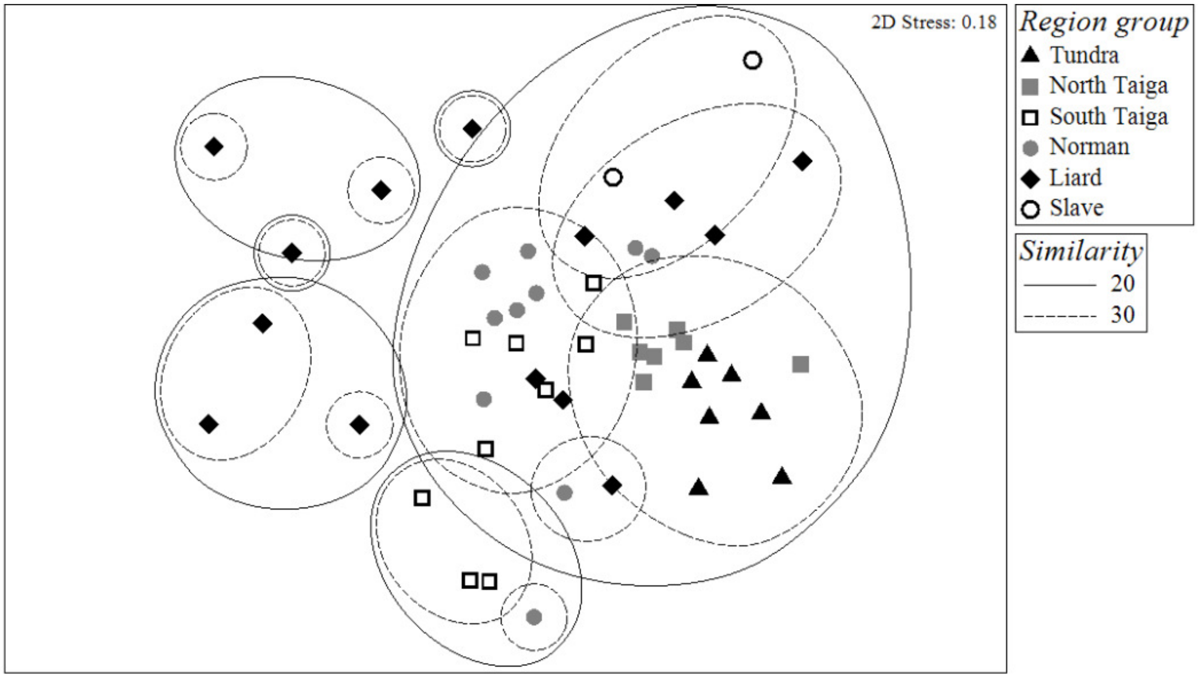

Figure 4.1 – MDS ordination of sites based on community composition. The stress level on the 2-dimensional ordination was 0.18. Sites are labeled by region (defined in Ch. 2). 20% and 30% similarity levels from CLUSTER analysis are shown.

only 1 to 4 sites, while at 30% there was more distinction between the northern groups of sites, but most southern sites split off into even smaller groups. Notably, however, the largest 30% similarity clusters were well defined geographically, with the northern taiga and tundra regions forming one group and most southern taiga and Norman Wells region sites forming another. The distribution of the regions across the ordination supports these observations, as the tundra and low-pH northern taiga streams formed a coherent group, most Norman and southern taiga streams were close together in the center of the ordination, and the Liard and Slave region sites were dispersed around the periphery.

The Bio-Env procedure returned a set of eight quantitative environmental variables that together correlated with the variation in assemblage composition ($\rho = 0.535$, $p < 0.01$). These were latitude, gradient, stream width, depth, turbidity, TP, TDN and NO_2/NO_3. Of these eight variables, only three had a consistent effect in the LinkTree analysis: latitude, stream width, and TP (Figure 4.2). Two groups of sites were consistently identified by the LinkTree analysis, regardless of the parameters used. Far Northern Streams (FNS) included all of the tundra and northern taiga region streams defined by latitude north of 67.8 °N, low pH and conductivity, and high TP and TDN (see Chapter 2). The second group (Mid-Northern Streams, MNS) consisted of most of the southern taiga and Norman regions, with exceptions discussed below. Splits among the Liard and Slave region sites were less consistent. This result is consistent with the MDS ordination, which showed the southern regions to be more variable than the northern ones. The reader should refer to Appendix I for a list of the abbreviations for site groups.

When forming the remaining groups we attempted to maximize the average similarity among sites within each group, taking into account consistent LinkTree groupings, the positions of the sites on the MDS ordination, and reasonable interpretations of the environmental variables. For the most part, these streams separated on the basis of wetted width (the widest streams were all in the south of the study area) and nutrients (TP is shown in Fig 4.2, but TDN and nitrates were identified as equivalently important factors when alternative parameter settings were used). However, comparison of the positions of these sites on the MDS ordination and the CLUSTER dendrogram suggests that nutrients, specifically TDN (which had greater variation than TP) was a better predictor of assemblage composition than width, and assigning the southern sites to high-TDN (High-Nutrient Southern Streams, HNSS) and low-TDN (Low-Nutrient Southern Stream, LNSS) groups led to higher average similarities within the groups than a classification based on wetted width. A fifth group (called Small Northern Streams (SNS), mostly for convenience) was defined as containing those sites which did not have a consistent position in the LinkTree analyses; however, these sites did form a relatively distinct group on the MDS ordination. These were generally small, northern streams, along

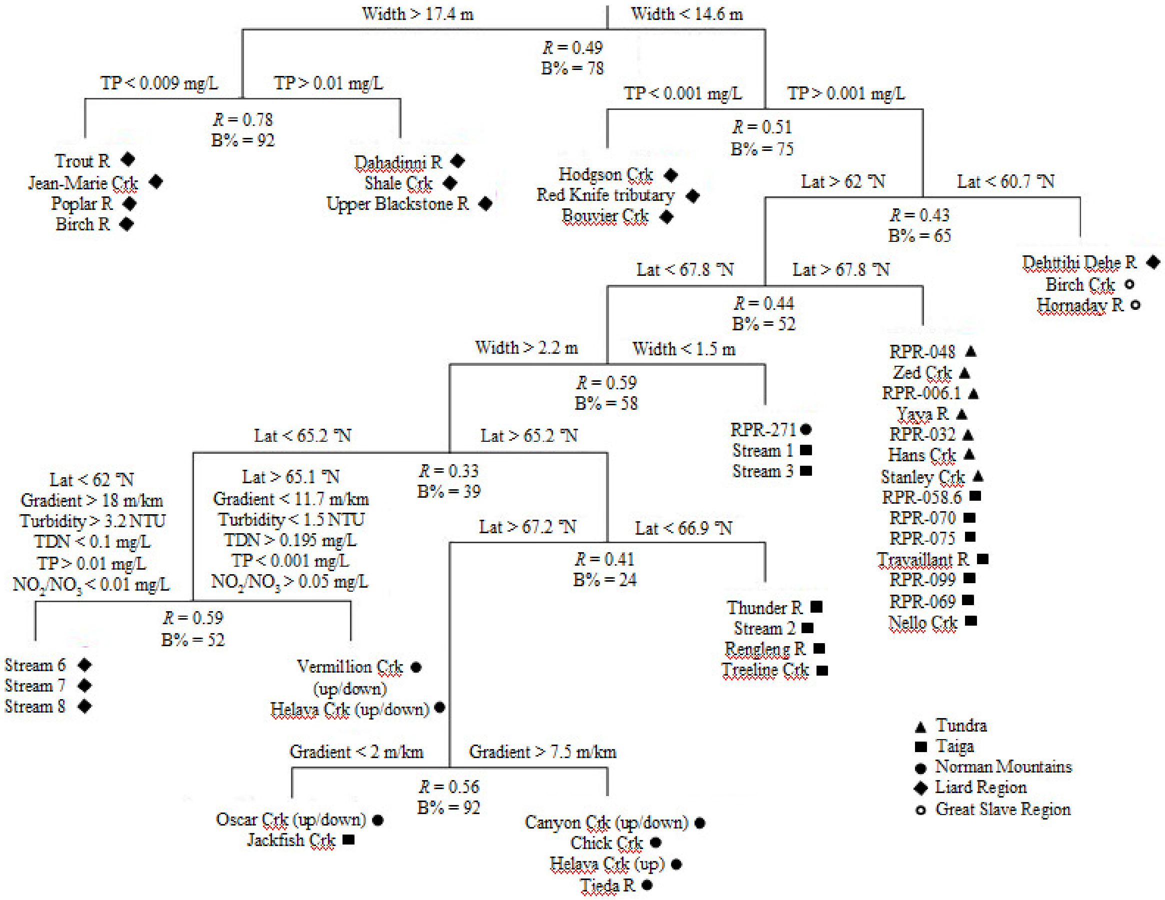

Figure 4.2 – Groupings of sites from LinkTree analysis. Symbols beside names indicate the region; a legend is included in the figure. *R* values refer to ANOSIM test statistics between the groups of sites at each split; B% is a rank-based measure of the difference between the groups. Minimum group size was set at 3, minimum split size at 5, and minimum *R* between groups at 0.3.

with Rat River (which was sampled during precipitation-related high flow), Helava Creek downstream of the pipeline crossing (which was physically and chemically similar to the upstream site, but with a much less diverse invertebrate fauna – there was also some indication that the dominant fish, slimy sculpin (*Cottus cognatus*) was less abundant than at the upstream site (MS Evans, *pers. comm.*) while no difference was observed upstream and downstream of other potential pipeline crossing sites in 2005) and Dehttihi Dehe River. Interestingly, the latter stream had a fauna similar to the small northern streams despite being in the Liard watershed, but was much higher in elevation than the rest of the Liard sites, suggesting a possible effect of climate along a gradient of elevation. This classification of sites into five groups left only three apparent outliers: Streams 6, 7 and 8 from the Liard region grouped with the MNS group in both the MDS and the LinkTree.

However, benthic assemblages in these sites contained distinct southern elements, such as *Capnia* and *Optioservus* spp., so they were placed in the LNSS group.

Average Bray-Curtis similarities within the groups ranged from 23.0 to 43.6 (Table 4.4). The highest within-group similarities occurred in the FNS and MNS groups, which were the most well-defined groups in the MDS (Figure 4.3), CLUSTER and LinkTree analyses. The HNSS group had the lowest similarity among its sites; this is not unexpected, since this group covers the largest geographical range (including the sites in the Slave region). With the exception of HNSS, within-group Bray-Curtis dissimilarities were lower than any among-group BC dissimilarities. The LNSS group was the least similar to the other groups; its relatively low dissimilarity with the MNS group was mainly due to Streams 6, 7 and 8; when these were excluded the dissimilarity between MNS and LNSS increased to 80.53 (but this caused the within-group similarity of LNSS to decrease to 19.71). The most similar groups were FNS and MNS, both of which were also relatively similar to the HNSS group. The highest dissimilarities were found between the two southern groups and the SNS group.

Table 4.4 - Average Bray-Curtis similarities/dissimilarities within & between the groups of sites. Site group abbreviations are as in the heading for Table 2 and in the text. Columns 1-4 contain the Bray-Curtis dissimilarity matrix for the site groups. Both average Bray-Curtis similarity and average Bray-Curtis dissimilarity are given for easier comparison; BC Diss = 100 – BC Sim.

Site Group	MNS	SNS	HNSS	LNSS	Average BC Similarity	Average BC Dissimilarity	# of sites
FNS	68.51	75.65	72.14	82.15	43.63	56.37	14
MNS		71.57	72.47	74.8	41.37	58.63	14
SNS			85.74	79.68	33.83	66.17	5
HNSS				84.11	23.02	76.98	6
LNSS					33.03	66.97	8

4.3.3 Community composition of site groups and correlations with local environmental variables

There was considerable variation in the average assemblage composition among site groups (Table 4.5). The FNS group was dominated by chironomids (especially Chironominae), blackflies and non-insects (particularly oligochaetes, mollusks and ostracods), with large contributions from only three EPT species, one from each order (*Baetis tricaudatis*, *Nemoura arctica* and *Brachycentrus americanus*). Total abundance was low in the SNS group and the assemblages consisted of a subset of the FNS fauna, with lower average abundance of all taxa except *N. arctica*. Virtually all taxa present in SNS were also present in the FNS group, but the former lacked several Ephemeroptera and Trichoptera genera, many Chironomini and Orthocladiinae, as well as most Mollusca and Crustacea.

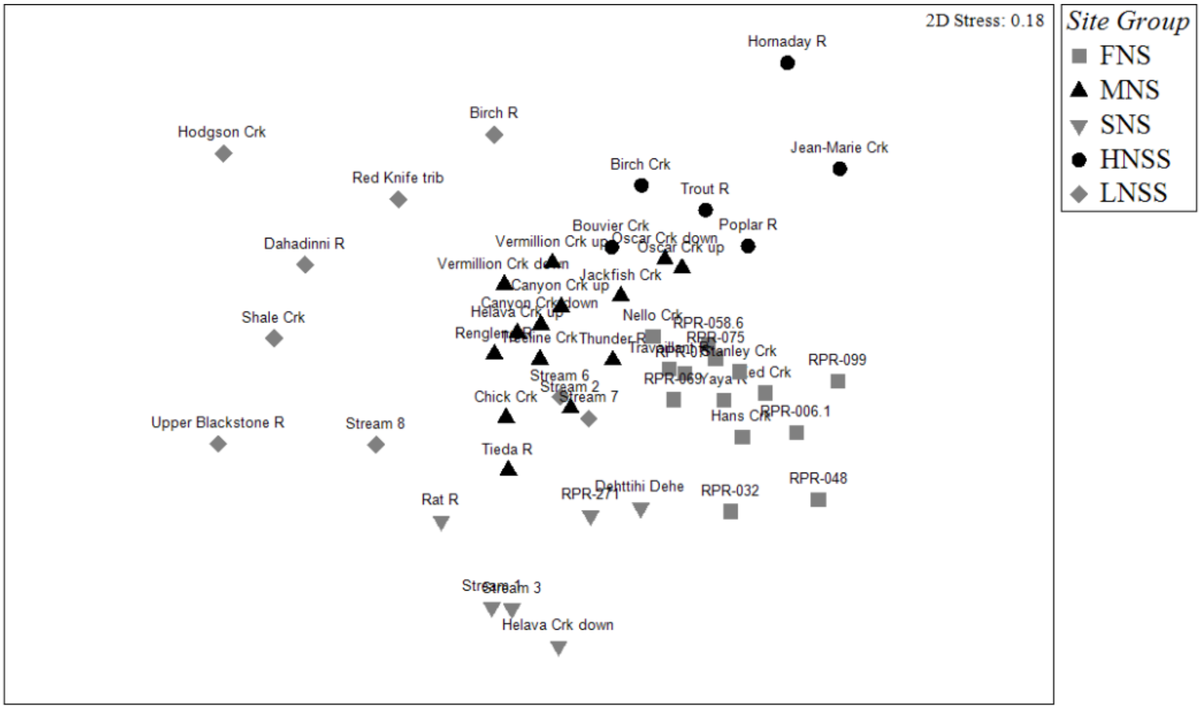

Figure 4.3 – **MDS ordination of sites indicating site groups**. Ordination is based on Bray-Curtis similarities of log-transformed abundance averaged by site. FNS = Far Northern Streams, MNS = Mid-Northern Streams, SNS = Small Northern Streams, HNSS = High-Nutrient Southern Streams, and LNSS = Low-Nutrient Southern Streams.

The assemblages in the MNS group were similar to those in the FNS in presence/absence terms, but patterns of average abundance were generally reversed; taxa that were abundant in the FNS tended to be less abundant in the MNS, and vice versa. Several taxa were present only in the two southern groups, including mayflies (*Acerpenna*, *Eurylophella*, *Tricorythodes*, *Ephemera*, *Parameletus*), the dragonfly *Ophiogomphus severus*, caddisflies (Hydropsychidae, several hydroptilid genera), the elmid *Optioservus*, and tanypode chironomids (*Labrundinia* and *Nilotanypus*). A few taxa were common in the north but rare or absent in the south, notably *Baetis bundyae*, *N. arctica*, *Micrasema*, *Procladius* and several genera in the tribe Chironomini. Among the southern groups of sites, the low-nutrient streams (LNSS) were lower in diversity and abundance than the high-nutrient (HNSS) group. The LNSS group contained both southern and northern species, generally with lower average abundance than in the HNSS group or the two northern groups. Although most taxa with southern distributions were present in the LNSS group, their average abundances were generally much lower than in the HNSS group, and the dominant taxa in the LNSS tended to be widespread across the entire study region (especially *Haploperla brevis* and oligochaetes).

Within the group of far northern streams, a large amount of variation in assemblage composition was due to differing substrates (Table 4.3, Figure 4.4). Most chironomids (especially Chironominae) and mollusks were more abundant on silt and organic matter (SOM), while sand and pebble (SP) substrates contained greater numbers of EPT, orthoclads and other Diptera (Table A5 in Appendix V). These two substrate types had an average dissimilarity of 64.26%; the two coarser substrate categories were represented by one site each within the FNS group, so comparisons with those groups were not possible. The abundance of most Ephemeroptera and Plecoptera mainly correlated with TDN concentrations, while velocity and % macrophyte cover were the primary determinants of the abundance of most Trichoptera (Table A9a in Appendix VI). Diptera abundance was generally correlated with depth, velocity and % macrophyte cover; most taxa were more abundant in shallow streams, but the direction of the correlation between the latter two factors varied among taxa. Turbidity had little effect on most taxa, with the exceptions of *Sergentia* (Chironomini) and water mites.

Within the MNS site group, assemblage composition varied significantly ($p < 0.5$) based on three categorical variables (Table 4.3). Latitude had an effect, with streams in the southern taiga differing from streams in the Norman region by 81.12% (average Bray-Curtis dissimilarity). The species that discriminate between the two regions in the MNS group displayed the following patterns (Table A6 in Appendix V): taxa that were widespread across the entire study area (e.g. *Acentrella insignificans*, *Orthocladius obumbratus*, *H. brevis*) were more abundant on average in the Norman (southern) region, while taxa that were common in the FNS group (e.g. *Baetis bundyae*, *Paramectriocnemus graminocola*, *Demicryptochironomus*) were more abundant in the southern taiga region. Most of the difference was due to increases in abundance of widespread taxa or to additional species in the Norman region; only two taxa were present in the southern taiga but not in the Norman region: *Lopescladius* and *Arctopsyche ladogensis*, which seemed to be replaced by *Hydropsyche* south of the taiga. Evidence indicating the winter conditions was available for approximately half of the sites, and perennial streams differed from streams that froze solidly by 75.17% on average (Figure 4.5, Table A7 in Appendix V). Many taxa were only present in perennial streams, including widespread genera such as *Baetis*, *Ephemerella* and *Cricotopus*; the few taxa that were only present in solidly frozen streams were rare throughout the study area. A third significant grouping was between sites with lakes upstream and those without (Figure 4.6, Table A8 in Appendix V). All filter-feeding taxa that contributed to the average dissimilarity between these stream types were more abundant (*Hydropsyche*, *B. americanus*) or exclusively present (*A. ladogensis*, *Dicrotendipes*) at sites with lakes upstream. Three of the continuous variables (gradient, width and conductivity) each

Table 4.5 – Average abundance of discriminating taxa in the site groups and their correlations between average site abundance and latitude. Site group abbreviations are as in Table 2 and the text. Average abundance values for each site are untransformed; when the average similarity for a taxa within a site group was > the SD of the similarity for that taxon within that group, it indicates that it is consistently present at a consistent level of abundance within the group; in this case the average abundance value is shown in bold. Significant Pearson r coefficients ($p < 0.05$) between abundance and latitude are in bold.

Table 4.5a – Major aquatic insect orders: Ephemeroptera (E), Odonata (O), Plecoptera (P), Trichoptera (T) & Coleoptera (C).

	FNS	MNS	SNS	HNSS	LNSS	R with latitude
Acentrella insignificans (E)	0.81	13.13	0.33	0	7.72	-0.039
Acentrella lapponicus (E)	0	1.08	0	88.78	3.04	**-0.44**
Acerpenna macdunnoughi (E)	0	0	0	3.06	0	-0.227
Acerpenna pygmaeus (E)	0	0	0	117.67	0	**-0.381**
Baetis spp. (E)	0.99	5.17	0.58	183.78	2.41	**-0.416**
Baetis bundyae (E)	0.69	0	4	0	0.33	**0.319**
Baetis flavistraga (E)	3.79	**13.37**	0.22	56.33	1.22	-0.207
Baetis tricaudatis (E)	31.39	2.39	0.28	52	0.7	0.00728
Eurylophella (E)	0	0	0	8.08	0	-0.268
Ephemera (E)	0	0	0	1.83	0.11	-0.238
Rithrogena (E)	0.48	6.8	0	16.25	0.59	-0.144
Tricorythodes (E)	0	0	0	22.72	0	**-0.344**
Paraleptophlebia (E)	0.39	12.69	0	21.139	0.04	-0.183
Parameletus (E)	0	0	0	0.33	0.61	-0.276
Ophiogomphus severus (O)	0	0	0	1.19	0.11	**-0.425**
Haploperla brevis (P)	4.38	**5.19**	2.58	9.75	**6.44**	-0.223
Plumiperla (P)	0.02	0.13	0	0.08	5.2	-0.129
Nemoura arctica (P)	**14.09**	1.82	**17.83**	0.08	0.18	**0.404**
Zapada (P)	1.65	2.33	0	1.86	1.63	-0.0915
Skwala americana (P)	0.4	1.4	0.67	6.25	0.5	-0.226
Beraea fontana (T)	0	0	0	0	0.07	-0.21
Brachycentrus americanus (T)	16.64	1.13	0.06	4.64	0.46	0.275
Micrasema (T)	4.58	0.59	0.42	0.08	0.63	**0.395**
Glossosoma (T)	1.74	0.68	0.58	0.25	1.04	0.06
Cheumatopsyche (T)	0	0	0	2.39	0	**-0.408**
Hydropsyche spp. (T)	0	3.68	0	**65.89**	0.76	**-0.505**
Hydropsyche bronta (T)	0	0	0	2.39	0.56	**-0.303**
Hydropsyche slossonae (T)	0	0	0	**11.03**	0.18	**-0.534**
Lepidostoma (T)	0.05	0	0	27.58	0.04	**-0.418**
Ithytrichia (T)	0	0	0	0.83	0	**-0.289**
Ochrotrichia (T)	0	0	0	4.33	0	**-0.324**
Oxyethira (T)	0.72	0.11	0	2.42	0.06	-0.01
Grensia praeterita (T)	1.01	0	0	0.75	0	0.111
Doliphilodes (T)	0	0.38	0	2.78	0	-0.203
Rhyacophila (T)	0.31	0.08	0.06	0.06	0.04	0.254
Optioservus (C)	0	0.36	0	38.61	0.15	**-0.466**

Table 4.5b – Chironomidae: Chironomini (C-CC), Tanytarsini (C-CT), Diamesinae (C-D), Orthocladiinae (C-O) and Tanypodinae (C-T). Maximum body size estimates from various chapters in Wiederholm (1983), as cited in text.

	FNS	MNS	SNS	HNSS	LNSS	R with lat	max length (cm)
Cryptochironomus (C-CC)	1.92	0.2	0	0.08	0.04	**0.287**	15
Demicryptochironomus (C-CC)	1.69	0.63	0	0.86	0	**0.347**	12
Dicrotendipes (C-CC)	2.88	4.02	0	0	0	**0.418**	11
Endochironomus (C-CC)	0.8	0.02	0	0	0	**0.357**	17
Phaenopsectra (C-CC)	0.41	0.01	0	0.33	0	0.192	8
Polypedilum scalaenum (C-CC)	**10.52**	0.7	0.58	0.67	0.13	**0.415**	14
Sergentia (C-CC)	2.73	0.07	0	0.33	0	**0.383**	18
Stictochironomus (C-CC)	1.15	0.76	0.36	0.22	0	0.164	14
Cladotanytarsus (C-CT)	65.6	18.57	1.33	12.67	0.7	0.247	5
Constempellina (C-CT)	0.38	4.34	0.94	2.08	0.07	0.08	5
Micropsectra (C-CT)	1.75	6.58	0.56	48.42	0.18	0.0406	8
Neostempellina (C-CT)	0	0.54	0	6.42	0	**-0.348**	
Rheotanytarsus (C-CT)	**294.7**	2.33	0	27.56	4.07	0.261	5
Stempellina (C-CT)	0.31	0.8	0.5	0.17	1.48	-0.0993	5
Stempellinella (C-CT)	0.02	3.71	0	133.86	0.11	**-0.302**	3
Tanytarsus (C-CT)	19.34	3.37	0.92	**79.58**	0.59	-0.13	9
Potthastia longimana (C-D)	**1.45**	0	0	0.08	0.04	**0.478**	10
Cardiocladius (C-O)	0	0.02	0.14	0	0.07	0.0046	11
Cricotopus trifascia (C-O)	5.46	0.24	0.33	2.83	0.24	-0.12	8
Cricotopus tristis (C-O)	3.64	3.84	0.06	2.33	0.33	0.145	8
Corynoneura (C-O)	5.03	**7.32**	2.75	69.11	1.13	-0.118	3
Eukiefferiella claripennis (C-O)	2.61	2.27	0	4.17	0	0.0735	7
Eukiefferiella gracei (C-O)	5.38	0.38	0	0	0.07	**0.304**	7
Euryhapsis (C-O)	8.44	0.17	0	1.33	0.74	0.149	8
Heleniella (C-O)	0.14	0.09	0.06	0	0.04	0.127	4.5
Krenosmittia (C-O)	0.19	**2.21**	1.33	0.42	0	0.052	3.5
Lopescladius (C-O)	0	1.07	0	26.56	0.11	**-0.328**	4
Nanocladius (C-O)	1.33	0.42	0	11.33	0	-0.141	5
Orthocladius spp. (C-O)	0.13	1.94	0.67	0	0.68	-0.0417	12
Orthocladius clarkei (C-O)	1.09	0.43	0	0	0.24	0.0484	12
Orthocladius lapponicus (C-O)	0.55	18.38	0.92	0	0.3	0.0246	12
Orthocladius obumbratus (C-O)	2.79	31.9	1	5.75	0.76	-0.0237	12
O. (Pogonocladius) (C-O)	0.21	0.07	0.06	0	0.04	0.169	12
Parakiefferiella (C-O)	0.94	0.33	0.39	0	0	0.264	4
Paramectriocnemus spp. (C-O)	1.05	6.09	1.06	**15.67**	0.15	-0.205	9
P. graminocola (C-O)	2.24	2.49	0.08	2.39	0	0.173	9
Paraphaenocladius (C-O)	0.96	0.56	1.78	0.25	0.04	**0.356**	6
Psectrocladius (C-O)	0.85	0.29	0.28	0.17	0	0.247	11
Symposiocladius (C-O)	1.44	0	0.56	0.28	0	**0.299**	6.5
Thienemanniella (C-O)	4.48	2.67	1	144.56	1.37	0.0143	3
Tvetenia bavarica (C-O)	15.57	**5.78**	**5.39**	1.33	1.43	**0.461**	7
Tvetenia discoloripes (C-O)	0.84	0.15	0	**45.36**	0	-0.235	7
Zalutschia (C-O)	0.6	0	0	0	0	0.266	7
Conchapelopia (C-T)	21.33	3.31	0.08	**7.72**	0.11	0.204	7
Hayesomyia (C-T)	0.09	1.73	0	3.67	0.04	-0.166	?
Labrundinia (C-T)	0	0.05	0	1.11	0.07	**-0.327**	5

Table 4.5b continued.

	FNS	MNS	SNS	HNSS	LNSS	R with lat	max length (cm)
Procladius (C-T)	6.84	0.17	0.08	0.11	0	**0.377**	11
Nilotanypus (C-T)	0	0.07	0	13.89	0.04	**-0.354**	3
Rheopelopia (C-T)	9.41	1.64	0	**4.33**	0	0.154	8
Thienemannimyia (C-T)	2.07	3.89	0	5.64	0.68	0.0117	10
Trissopelopia (C-T)	8.66	**3.67**	0.06	6.06	0.22	0.225	8

Table 4.5c – Other benthic invertebrates: non-Chironomid Diptera (Ceratopogonidae (D-C), Empididae (D-E), Simuliidae (D-S), Tipulidae (D-T)), Collembola (Co), Hydracarina (Ha), Annelids (A), Mollusca (M), Crustaceans (Cr) & Nematodes (N).

	FNS	MNS	SNS	HNSS	LNSS	R with lat
Probezzia (D-C)	0.59	0.62	0.06	1.83	0.04	-0.017
Chelifera (D-E)	2.18	**6.18**	1.5	1.75	0.61	0.147
Hemerodromia (D-E)	0.12	0.85	0	**8.42**	0.09	**-0.411**
Wiedemannia (D-E)	0	0.24	0	0	0.07	0.0815
Simuliidae (D-S)	**29.36**	**23.02**	5.44	249.11	4.56	0.0549
Dicranota (D-T)	0.48	0.4	0.72	0.39	0.11	-0.0821
Leptotarsus (D-T)	0.98	0.42	0.06	0	0.04	**0.295**
Rhabdomastix (D-T)	0	0	0	0	0.11	-0.0694
Collembola (Co)	0.71	0.15	0.56	3.33	0.04	-0.0242
Hydrodroma (Ha)	0	0	0	0.72	0	**-0.289**
Hygrobates (Ha)	3.98	0.83	0	1.78	0.56	0.216
Lebertia (Ha)	**8.96**	3.88	1.86	7.94	1.8	0.117
Sperchon (Ha)	3.64	4.11	2.28	**3**	0.54	**0.289**
Sperchonopsis (Ha)	0.09	0.45	0	0.69	0.07	-0.0751
Testudacaris/Torrenticola (Ha)	0.18	0.04	0	7.28	0.87	**-0.319**
Hydracarina (unID'd hard-bodied) (Ha)	0.45	0.27	1.06	0.42	0.04	0.0741
Hirudinea (A)	0.42	0.21	0	0.11	0	0.224
Oligochaeta (A)	**83.07**	**29.99**	**10.22**	**58.78**	**3.18**	**0.463**
Ancylidae (M)	0	0	0	0.58	0.5	**-0.309**
Lymnaeidae (M)	0.07	0.05	0.03	2.83	0.59	-0.232
Planorbidae (M)	**11**	0.77	0.28	**15**	0.43	0.144
Physa (M)	0.88	0	0	0.44	0	0.0793
Pelycopoda (M)	12.84	0.02	0	**5.83**	0	0.26
Gammarus lacustris (Cr)	0.01	0	0	7.83	0	**-0.361**
Hyallela (Cr)	0	0	0	1	0	**-0.289**
Cladocera (Cr)	18.64	1.51	0	2.47	0.33	**0.299**
Cyclopoida (Cr)	8.53	0.43	**1.44**	0.25	0.59	**0.327**
Ostracoda (Cr)	**32.56**	0.68	0.61	0.22	0.22	**0.544**
Nematoda (N)	**20.45**	0.52	0.42	**5.36**	1	0.252

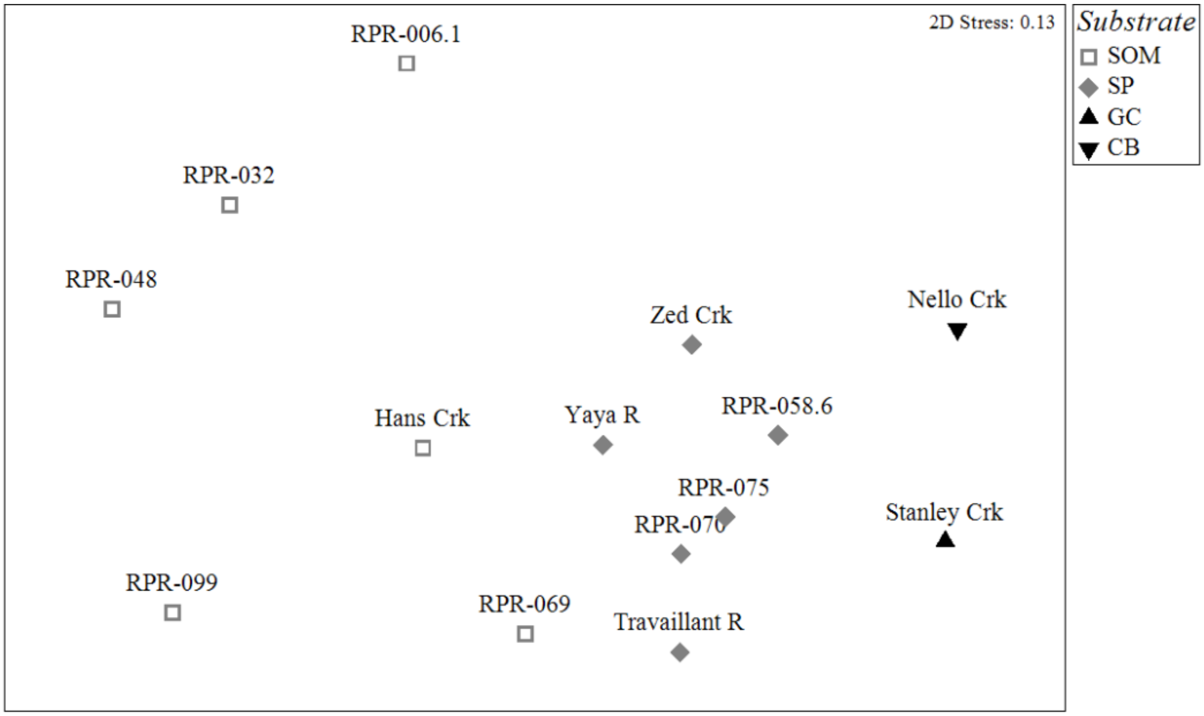

Figure 4.4 – MDS ordination of far northern streams (FNS group) showing the effect of substrate type. Ordination is based on Bray-Curtis similarities of log-transformed abundance data averaged by site. Sites are labeled by substrate type. SOM = Silt/Organic Matter, SP = Sand/Pebbles, GC = Gravel/Cobble, CB = Cobble/Boulder.

correlated with the abundances of several taxa (Appendix VI). Significant correlations between abundance and gradient or width were exclusively negative, and were positive for abundance and specific conductivity. The other two variables selected by Bio-Env, macrophyte cover and pH, were significantly correlated only with *B. americanus* and *Sperchon* (Hydracarina), which both apparently preferred slightly acidic streams.

Sites within the two southern site groups did not vary significantly with any categorical environmental variable (Table 4.3). Information on the winter conditions of these streams was not available. Within the HNSS group (which was more similar to the northern site groups than to the LNSS (Table 4.4)), elevation, gradient, velocity, conductivity and nitrates were identified by Bio-Env as correlating with variation in assemblage composition (Appendix VI). Taxa associated with the northern regions were positively correlated with latitude; this was significant only for *H. brevis*, but *Rithrogena*, *B. americanus*, *T. bavarica* and nematodes were also positively correlated. Abundances of some mayfly genera (*Ameletus*, *Serratella* and *Rithrogena*) were positively correlated with velocity and negatively with conductivity, while *Baetis* spp. had correlations in the opposite directions. *Optioservus* abundance was negatively correlated with velocity, and the abundance of *Hydropsyche*

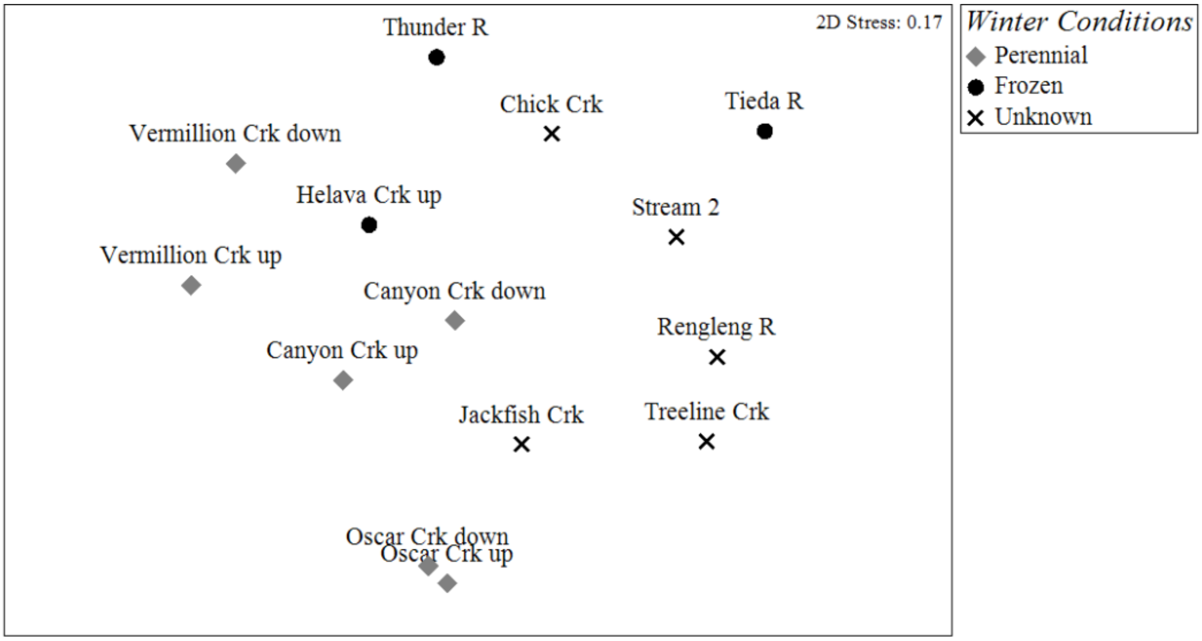

Figure 4.5 – MDS ordination of mid-northern streams (MNS site group) showing the effect of winter ice conditions. Ordination is based on Bray-Curtis similarities of log-transformed abundance data averaged by site. Sites are labeled by winter conditions as described in Imperial Oil (2004).

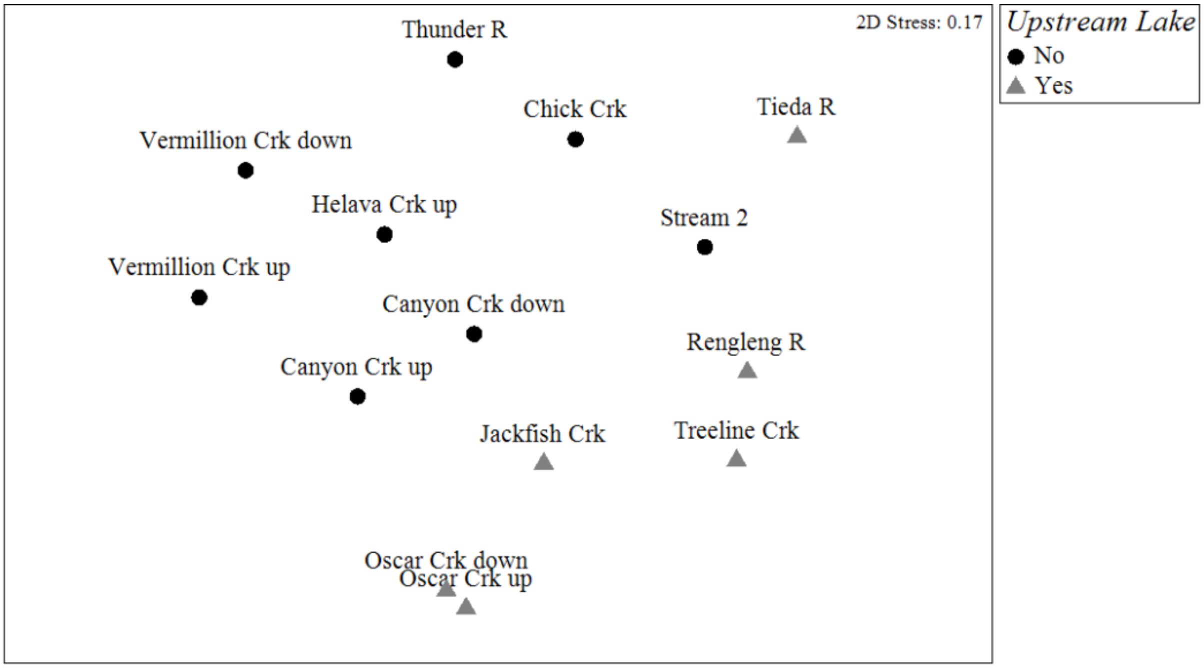

Figure 4.6 – MDS ordination of mid-northern streams (MNS group) showing the effect of having a lake upstream. Ordination is based on Bray-Curtis similarities of log-transformed abundance data, averaged by site. Sites are labeled according to whether or not a lake was present upstream.

morosa was strongly correlated with NO_2/NO_3 concentration. Few significant correlations between abundance and environmental variables were found in the LNSS group (Appendix VI). Most variation was apparently due to spatial (longitude) and physical (mainly depth) factors. The small number of sites in these two groups meant that these statistical tests had lower power than those for the northern regions, and no attempt was made to explain variation within the SNS group because it contained even fewer sites.

4.3.4 Latitudinal gradients in abundance of discriminating species

Among the taxa identified as important contributors to the multivariate ordination, approximately half had positive latitudinal gradients in abundance (Figure 4.7). With few exceptions, these were Diptera and non-insect invertebrates. Abundances of most EPT genera or species were negatively correlated with latitude, with the exceptions of *Baetis bundyae*, *Nemoura arctica* and *Micrasema* sp., which had significant positive correlations. A few other Trichoptera (*Brachycentrus americanus*, *Grensia praeterita* and *Rhyacophila* sp.) also increased in abundance towards the north, but the correlations were not significant. All other EPT taxa, as well as the sole representatives of the Odonata and Coleoptera, were negatively correlated with latitude, often significantly (Table 4.5). The

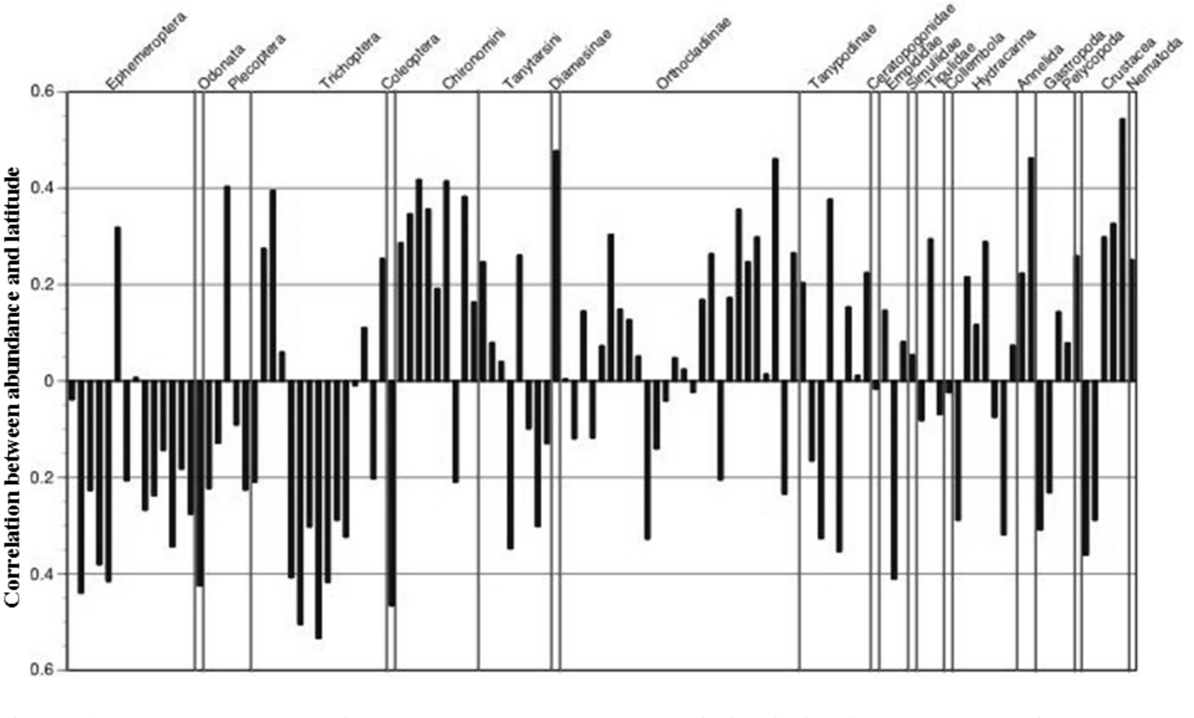

Figure 4.7 – Pearson correlations between log abundance of discriminating taxa and latitude. Major taxa groups are indicated above the figure; taxa are ordered as in Table 4.5, along with Pearson r values and significance ($p < 0.05$).

abundances of most genera of chironomids were positively and frequently significantly correlated with latitude. This trend was especially pronounced in the Chironomini and Diamesinae (represented here only by *Potthastia longimana*), while the other major chironomid groups varied in their latitudinal distributions. Latitudinal patterns of abundance varied widely among other families of Diptera and in the Hydracarina. Among the non-insect fauna, annelids, pelycopods, nematodes and micro-crustaceans (Copepoda, Cladocera and Ostracods) were positively correlated with latitude, while most gastropods and amphipods were negatively correlated.

4.4 Discussion

4.4.1 Relationships between local environmental factors and assemblage composition

Stream size is predicted to be an important determinant of benthic assemblage composition by the River Continuum Concept (Vannote *et al.* 1980), and variables relating to stream size have been found to correlate with changes in composition of various components of stream macroinvertebrate assemblages (e.g. Arscott *et al.* 2005; Lencioni & Rossaro 2005; Heino & Paasivirta 2008), including studies of high-latitude streams in Alaska (Oswood 1989; Smidt & Oswood 2002). While it would be ideal to compare streams of different orders, this information was not available for many of the streams. Of the four variables in this study that correlate with stream size (width, depth, velocity and gradient), no fewer than two were found to co-vary with community composition in each of the four site groups examined (Appendix VI). Since the study area only contained low- to mid-order streams, it is unlikely that predictable changes in habitat structure along a stream size gradient (e.g. substrate particle size, degree of riparian shading) were responsible, and the relationships of individual taxa with the stream size variables were often inconsistent. These results suggest a complex relationship between assemblage composition and stream size that possibly relates to the greater habitat diversity in mid-order streams relative to low-order streams (Minshall *et al.* 1985). If mid-order streams contain more different microhabitats than the smaller streams, then the observed assemblage would largely depend on which and how many microhabitats were actually sampled.

While there was little variation due to substrate type overall, within the far northern region there was a significant effect (Table 4.3); as noted, this was the only site group which contained a range of substrates, from coarse to soft. When it is properly measured, substrate is usually described as a dominating factor controlling benthic assemblages (Barton, 1980; Arscott *et al.* 2005). Many invertebrates require soft substrates to burrow into, while clinging or sedentary forms need hard and/or stable substrates. Arscott *et al.* (2005) found that sites located in a floodplain contained higher proportions of burrowing groups (Ephemeridae and Caenidae) and groups associated with pools (Corixidae and Gyrinidae) compared to streams with coarse substrate located nearer to the headwaters. While none of these families were present in the far north of the Mackenzie system, several chironomid genera were much more abundant in soft silt substrates than sandy, notably *Procladius*, *Corynoneura* and *Polypedilum* (Appendix V), the former two being primarily associated with lentic habitats and the latter two apparently tolerating a wide variety of aquatic habitats (compiled in Wiederholm 1983).

Water chemistry accounted for relatively little of the variation in assemblage composition. Gradients of pH and specific conductivity were notable only in the MNS site group, with streams decreasing in conductivity and pH towards the north of the region. The trend towards slightly acidic streams in the far north of the study area may be primarily due to the ubiquitous presence of continuous permafrost in these regions: runoff driven by precipitation and permafrost melt is a major source of water in the summer relative to groundwater inputs, and the humic material that builds up on top of the frozen layer on the tundra increases the acidity of runoff (McKnight *et al.* 2008). Aquatic macroinvertebrates vary widely in their tolerance to acidity (e.g. Malmqvist & Hoffsten 2000), but given the extreme changes in terrain, vegetation and substrate that occur over the same region as the pH gradient, it seems unlikely that the changes in the fauna seen between the MNS and FNS regions could be explained by the relatively small range of pH that was present among the study sites. Nitrate concentrations were identified as correlates of community composition, but apart from a significant positive correlation with *Hydropsyche morosa* in the HNSS group they did not seem to have much of an effect on the abundance of most taxa. Arscott *et al.* (2005) suggested that apparent effects of nitrate concentrations on macroinvertebrate assemblages are probably either due to their correlations with other variables along the longitudinal gradient of a river system or to anthropogenic influences, most likely the former in the sparsely populated Northwest Territories. High specific conductivity in streams in the Norman range likely indicates input from saline springs, which is consistent with earlier observations of perennial flow in these streams (IORV 2004).

The arctic temperature and light regimes limit nutrient delivery to streams from both terrestrial and autochthonous sources (Vincent *et al.* 2008). Soluble reactive phosphorus (SRP) concentrations are often near the limits of detection (Peterson *et al*. 1993), as was total phosphorus in this study, although TDN concentrations were often higher. A long-term experiment in a tundra stream in Alaska demonstrated that modest additions of phosphorus and nitrogen can increase growth of many benthic invertebrates (Peterson *et al.* 1993) and can lead to competitive interactions (e.g.

between *Prosimulium* and *Brachycentrus americanus*) that are not apparent otherwise (Hiltner & Hershey 1992); eventually, changes effected by the invasion of a bryophyte (*Hygrohypnum* spp.) restructured the benthic habitat and altered the community composition (McKnight *et al.* 2008). TP and TDN concentrations largely co-varied in streams in the study area, although TDN was more commonly the statistically significant variable, most likely because it had a much wider range of variation and occurred in higher concentrations. Nutrients appeared to be a limiting factor on the tundra and northern taiga, as the abundance of most mayflies as well as *Zapada* were positively correlated with TDN concentration (Appendix VI). Nutrient levels were also the basis for separating the Liard and Slave region sites into two groups. High-nutrient southern streams had a rich EPT fauna, while the low-nutrient southern streams had lower abundance of nearly all taxa (Table 4.5) and were more similar in composition to higher-latitude sites below the treeline (Table 4.4). This might indicate that northern assemblages may be limited by nutrient availability in addition to freezing. CPOM is certainly a limiting factor, especially to shredders north of the treeline, but was not measured in this study. Although there was little evidence of a significant shift in assemblage composition at the treeline in this study, extreme seasonality of nutrient inputs to northern streams leads to strong associations between the timing of growth and nutrient availability in other northern systems, with many shredders present at very low levels until hatching in late summer, leading to late autumn peaks in abundance (Cowan and Oswood 1984).

Among the other physical habitat variables, only the presence of an upstream lake had a significant effect on assemblage composition (Table 4.3). Downstream of lake outlets, the benthic fauna often consists of a mix of lentic and lotic elements (Malmqvist & Hoffsten 2000), and this was especially true on the tundra in the Mackenzie Delta. The presence of thousands of shallow lakes in the area meant that none of the northern sites were more than a few kilometers downstream of a lake and the generally soft substrate in these streams probably only heightened the lentic aspect of the assemblages. In the south, most streams drained steeper terrain, so upstream lakes occurred less frequently. Lencioni & Rossaro (2005) found that the presence of riffles and/or pools significantly affected chironomid assemblage composition, while Halwas *et al.* (2005) found little difference between habitat types for most other benthic invertebrates. The latter is more in line with the present results, and it may be that the way qualitative habitat types are defined in a given study largely determines whether significant effects are observed. Permafrost, which is present throughout the study area, is an important factor controlling hydrology and nutrient availability. Smidt & Oswood (2002) suggested that the presence of any permafrost in a watershed can have large effects on macroinvertebrate communities; unfortunately I do not have data at the scale required to assess this within the Mackenzie system, but it is undoubtedly a factor, especially in the southern regions where permafrost may be discontinuous.

4.4.2 Assemblage composition along the latitudinal gradient

The streams surveyed in this study spanned a latitudinal range that comprised a climatic gradient, from sub-arctic/near-temperate conditions in the south to arctic/sub-arctic conditions in the north. Towards the north, the growing season decreases in length while the duration of low temperature and snow cover increases and the probability of freezing increases in aquatic habitats. Disturbance due to spring melt becomes more severe and that due to periodic flooding in the summer more frequent in areas with continuous permafrost (e.g. Woo & Thorne 2003), although this may not be the case on the tundra due to lower precipitation and relatively flat terrain, and terrestrial vegetation becomes more limiting both as an allochthonous food source and as habitat for adult aquatic insects. Similar to other large surveys in Alaska (Oswood 1989) and Europe (summarized in Hoffsten & Malmqvist 2000), many families and even orders were extremely rare or absent at high latitudes in the Mackenzie system. Odonata, Hemiptera and Coleoptera were uncommon and, when present, represented by very few taxa (*Ophiogomphus severus*, Corixidae & Elmidae, respectively). The dominant Ephemeroptera were Baetidae, but the abundance of nearly all species decreased towards the north, and some families were absent from the far north, notably the burrowing mayflies (Ephemeridae), even though the soft substrate of the tundra would seem like an ideal habitat (at least in the summer). Similarly, plecopterans were limited to Nemouridae, Chloroperlidae and occasionally Perlodidae in the north; other families (Pteronarcyidae, Taeniopterygidae) were absent in the far north, and perlids were found only in the far south of the study area. Among the Trichoptera, brachycentrids and limnephilids were common at higher latitudes, if not very abundant, but case-less caddisflies were entirely absent from the far north.

On the other hand, Diptera, especially chironomids, were abundant and diverse in the far north of the study area. The generic-level identifications necessitated by current taxonomic information can obscure species-level patterns (especially in diverse, widespread genera, e.g. most Tanytarsini), but this limitation applied throughout the study area. The abundance of most genera of Orthocladiinae was positively correlated with latitude (Table 4.5b), but only a few genera or species (*Cricotopus trifascia*, *Eukiefferiella gracei*, *Euryhapsis* and *Tvetenia bavarica*) continued to increase into the northern taiga and tundra. The only common diamesid (*Potthastia longimana*) also increased in abundance towards the far north. Diamesinae and Orthocladiinae are often generalized as cold stenothermic groups (Lindegaard & Brodersen 1994), and many of the genera that increased towards the north in the forested part of the study area were of small size (Cranston *et al*., 1983) with fast multivoltine life cycles (Tokeshi 1995), e.g. *Cricotopus* (other than *C. trifascia*), *Corynoneura*, *Thienemanniella*, *Orthocladius* and *Eukiefferiella* (other than *E. gracei*). Chironomini are usually thought to prefer slightly warmer streams (Lindegaard & Brodersen 1994), yet along with certain Tanytarsini (*Cladotanytarsus*, *Rheotanytarsus* and *Tanytarsus*) and some tanypods (*Procladius*, members of the *Thienemannimyia* group), they were the dominant chironomids in the far northern site group. These far northern chironomids tended to be large, with maximum body length greater than 10 mm (Pinder & Reiss 1983), and members of several of these genera are known to have semivoltine life cycles (*Sergentia*, *Arctopelopia*, *Procladius*, *Cryptochironomus*; Tokeshi 1995) and/or reproduce parthenogenically (e.g. *Tanytarsus*, *Micropsectra*; Langton 1995). Genera that contain species that have been observed to overwinter as larvae within cocoons (*Cladopelma*, *Dicrotendipes*, *Endochironomus*, *Stictochironomus*, *Tanytarsus*; Tokeshi 1995) were, without exception, more abundant at higher latitudes.

The ability to survive in ice during winter is likely a major factor limiting the distributions of invertebrates in the Mackenzie system. Data pertaining to winter flow conditions (IORV 2004) were only available for sites in the FNS and MNS groups, and no stream in the FNS region maintained flow through the winter. Table A7 in Appendix V lists the species in the MNS group that appear to be most sensitive to freezing of the streambed (e.g. abundant in most streams of one type and absent or scarce in streams of the other type). It should be emphasized that many less common species, including most non-chironomid insects, were never found in streams that froze to the substrate (Appendix VII). In contrast to the suggestion by Huryn *et al*. (2005) that the presence of certain Plecoptera is indicative of perennial flow, both *Zapada* (Nemouridae) and *Skwala americana* (Perlodidae) were present in several streams that had been observed to freeze to the substrate. However, they were not very abundant, and since perennial streams were present in the region it is possible that the frozen streams were colonized in the spring by insects that were not necessary tolerant of freezing, or that there were unfrozen areas upstream which served as sources of colonization. Most other perlodids (*Diura bicaudata* being the most common) were absent from winter-frozen streams, as were the majority of mayflies (except *Acentrella insignificans*, *Baetis flavistraga* and *B. tricaudatus*) and all Odonata and aquatic Coleoptera. Non-insect taxa (e.g. bivalves, cladocerans) were more abundant in perennial streams than those that freeze solid, but sessile or non-emergent taxa were present in both types of streams.

Trends among the Chironomidae were less clear-cut; these insects can survive the winter using a variety of mechanisms including the construction of winter cocoons, migrating to small interstitial spaces in gravel substrate (where liquid water may be present throughout the winter) and physiological adaptations allowing survival encased in ice (Irons *et al.* 1993). Orthoclads were the dominant chironomids in the MNS region, and many genera (notably *Orthocladius*) were found in both types of streams, although a few (e.g. *Cricotopus mackenziensis*) were only found in perennial streams, and most Tanypodinae were absent or rare in frozen streams. The chironomid fauna of these frozen streams bore little resemblance to the frozen streams in the far north of the study area, which were dominated by Chironomini, Tanytarsini, *Procladius* and *Polypedilum scalaenum*.

There were positive correlations between abundance and latitude for several species that are known to survive freezing conditions as larvae. *Baetis bundyae* and many species of *Acentrella* (*A. insignificans* was dominant in the Mackenzie system) are often found in ephemeral ponds and streams in the north, overwintering in the frozen ground as eggs and hatching early in the spring (Giberson *et al*. 2007). The stonefly *Nemoura arctica* survives freezing by producing an array of ice-binding proteins and glycerols (Walters *et al*. 2009). *Diamesa mendotae* has been shown to tolerate temperatures well below zero (Bouchard *et al*. 2006); although this species was not observed in this survey, it is possible that *P. longimana* possesses a similar set of adaptations.

Equally important to winter conditions are the severe hydrological and physical disturbances that accompany ice break-up in the spring (Scrimgeour *et al.* 1994; Prowse & Culp 2003). In streams that experience regular ice scouring, the success of aquatic invertebrates is determined by their ability not only to avoid physical destruction during break-up but also to time their life cycles (i.e. diapause, hatching and emergence) to take immediate advantage of large quantities of nutrients available in the spring and to disperse to recently opened habitats (Miller & Stout 1989). Species that are able to survive the winter encased in ice are still susceptible to mechanical damage in the spring (Danks 2007), and abundance in perennial streams can be limited not only by scouring during break-up (Prowse & Culp 2003) but also by the formation of frazil or anchor ice during the winter (Martin *et al.* 2000). This extreme but predictable disturbance regime means that there is an annual cycle of re-colonization in northern streams, leading to high variability in assemblage composition among streams and among years (Miller & Stout 1989; Milner *et al.* 2006). Newly opened habitat is colonized in the spring by species that have survived the winter either in undisturbed habitat within the stream (e.g. deep pools or within the hyporheic zone, unless it freezes due to permafrost) or in nearby streams or lakes from which adult insects have dispersed, resulting in an essentially stochastic pattern of assemblage composition (Miller & Stout 1989) which may bear little relation to environmental factors that may be important in more stable habitats (Heino & Mykra 2008); it has even been suggested that community composition metrics commonly used for biomonitoring in temperate streams may be unsuitable in the far north due to high variability (Milner *et al.* 2006). Under this disturbance regime, fast-growing, highly motile taxa have an advantage (Miyake *et al.* 2003); in a boreal stream that experienced an anomalous, arctic-like winter, the insect fauna was found to recover much more quickly than populations of less vagile taxa (Hoffsten 2003), and the insect assemblage of Hodgson Creek in the Liard watershed (which was also sampled in this study) was observed to recover rapidly after a construction-related disturbance (Young & Mackie 1991).

The results were consistent with a latitudinal gradient of increasing disturbance towards the north, up until slightly below the treeline. Higher correlations between abundances of individual taxa and continuous environmental variables were found for the southern regions (Liard and Slave) than for the northern regions, and the grouping of southern sites into high- and low-nutrient streams was indicative of a strong effect of local environmental factors while the northern sites grouped mainly by region, indicating that dispersal may be a more important factor for that part of the study range. Streams in the mid-latitude group, especially those that completely froze in the winter, were dominated by small, fast-growing species that are likely univoltine, including Orthocladiinae, Tanytarsini (Tokeshi 1995), Baetidae (Clifford 1969) and Chloroperlidae (Stewart *et al.* 1990). Species that probably require up to two years for development, such as *N. arctica*, *Zapada* (Stewart *et al.* 1990) and *B. americanus* (Irons 1988), were also common regardless of the winter conditions, which indicates that they either tolerate/avoid freezing or overwinter in unfrozen habitats. Insects with longer life cycles, e.g. 2-4 years for *Pteronarcys* (Stewart & Stark 1988) were only present in perennial streams. It should be noted, however, that inferences from other studies should be made with caution, since life cycles can vary widely under different environmental conditions and tend to be longer in the north due to nutrient and temperature limitation (Stewart *et al.* 1990; Danks 1992b). Mollusca, Crustacea and other taxa of low vagility were not common in northern streams south of the treeline; on one hand, this may have been related to the coarse substrates in many of these streams, but the winter flow conditions also had a large effect on these taxa as indicated by their absence or very low abundances in streams in the MNS group that froze to the substrate.

The northernmost group of sites (FNS), which spanned the treeline near Inuvik, NT, contained a distinct fauna characterized by Chironominae, *Baetis* spp., *N. arctica*, Brachycentridae (*B. americanus* and *Micrasema*), Limnephilidae (especially *Grensia praeterita*, *Philarctus quaeris,* and *Sphagnophylax meiops*) and non-insects (oligochaetes, pelycopods, mites, cladocerans, ostracods and nematodes). The abrupt change in environmental conditions between the FNS and MNS sites seems likely to be attributable to a combination of permafrost depth and terrain, as the low-gradient streams in the FNS group are all connected to a network of thermokarst lakes, which become increasingly numerous towards the opening of the Mackenzie Delta into the Beaufort Sea. The streams connecting these lakes are physically characterized by low gradients, fine substrates with large amounts of organic material and relatively high summer temperatures due to the lack of shading. They are mainly peat streams according to the classification of McKnight *et al.* (2008), indicating that they experience relatively little scouring due to water retention and mediation of flow by thermokarst lakes and ponds, and the deeper pools may provide unfrozen habitat in the winter. There was some evidence that both of these factors had an effect on the benthic assemblages. Soft substrates (ranging from silt/organic matter to sand/pebbles) were common, and substrate type was the predominant factor explaining community composition within the region (Figure 4.4). Insects that are generally associated with coarse substrates (e.g. Heptageniidae, Hydropsychidae) were rare, but the abundance of Simuliidae indicated that the availability of surfaces for attachment was not a limiting factor; abundant macrophytes and embedded boulders may have provided sufficient solid surface area. All streams for which winter flow data were available either froze to the substrate or had small amounts of anoxic water below the ice, with the exception of Zed Creek, which was apparently perennial (IORV 2004). While not distinct in composition, Zed Creek had much higher abundance than any other northern stream (up to 4300 individuals/m^2), especially of *Rheotanytarsus* (up to 3700 ind/ m^2). Lentic influence on these streams was certainly an important factor: all FNS sites (except RPR-099) were within 10 km downstream (usually closer to 1 km) of a lake or large pond, and most of the invertebrates present are also associated with lentic habitats.

Habitat stability also seemed to play a major role in shaping community composition. The chironomid genera that were more abundant in the FNS than elsewhere tended to be those that can grow to relatively large sizes (Pinder & Reiss 1983; see maximum body length in Table 4.5b) and included several genera that have been observed to have semivoltine life cycles, e.g. *Sergentia, Cryptochironomus*, *Procladius* (Tokeshi 1995). Most invertebrates that do not have an aerial life stage were much more abundant in the FNS streams, with the exceptions of amphipods and gastropods. These trends, compared to those described above for the mid-latitude and southern site groups, suggest that streams habitats are more stable in the far north of the Mackenzie system, allowing prolonged life cycles in insects and the establishment of populations of sessile invertebrates. The disturbance regime is mostly related to climate, especially ice conditions during the winter, and not so much to the spring ice scouring and "flashy" summer flow patterns that are important factors in streams to the south. Freeze tolerance or avoidance has unfortunately not been studied at low taxonomic levels in the Chironomidae, but the freeze tolerant *N. arctica* (Walters *et al.* 2009) was consistently present at the FNS sites. The high average abundances of *B. americanus* and an unidentified species of *Micrasema* suggest that these too may be able to survive freezing. Several chironomid genera that were common to streams in the far north are known to contain species with adaptations to survive the arctic winter as larvae, including cessation of feeding (*Thienemanniella*), reduction of water content to avoid freezing (*Polypedilum*) or, in the case of several genera including *Dicrotendipes*, *Endochironomus*, *Stictochironomus*, and *Tanytarsus*, winter cocoon-building (Tokeshi 1995).

4.4.3 Rare species

Of the 377 species or higher taxa collected from the Mackenzie system, approximately 150 could be classified as rare (defined here as present at five or fewer sites). A disadvantage of the multivariate techniques used in the preceding analysis is that rare species are effectively eliminated from the data, since the sample size of their occurrence is too small to discriminate among groups of sites or to assess correlations with environmental variables. While eliminating or down-weighting rare taxa is desirable from a statistical and analytical point of view (not to mention the slight chance of occasional misidentifications), it also reduces the amount of information that can be gleaned from the data. Since the distributions of rare taxa may be of interest to naturalists and of potential significance to conservation efforts, I will end this chapter with notes on the distributions of distinctive rare species. There were five general patterns of occurrence (Appendix VII): 1) limited to the far north (from the taiga to the tundra); 2) limited to the far south (Liard and Slave regions); 3) limited to the middle latitudes (Norman region and southern taiga); 4) widespread (north and south) up to the treeline; and 5) widespread spanning the treeline.

With one exception (a damselfly found in a small, slow-flowing stream in the taiga) only Trichoptera and Chironomidae contained species or genera that were limited to the far north, reflecting the relatively high diversity of both of these groups on the tundra. The group of taxa with southern distributions included representatives of several families of Ephemeroptera and Trichoptera, most large Odonata, Hemiptera and Coleoptera, all perlid and taeniopterygid Plecoptera, and several sessile macroinvertebrates. Several genera were only found in perennial streams near Norman Wells, notably the mayflies *Epeorus* and *Metretopus* and the chloroperlid *Sweltsa*. A large number of taxa, although rarely collected, had widespread distributions. Many of these were identified to the genus level and may represent multiple species occurring in different regions. *Arctopsyche ladogensis* was occasionally found in rocky streams along the western edge of the study area, but was only abundant when other hydropsychids were absent. Lastly, the conchostracan *Lynceus brachyurus* was found in two sites, one a small shallow stream at its outlet to the Mackenzie main stem near Tsiigehtchic, NT (which also contained a rare corixid that keyed to *Oravelia pege*), the other also a shallow stream about 12 km from its outlet into Great Slave Lake.

There was an apparent pattern in the distributions of several rare disjunct and/or widespread insects involving a particular site. Oscar Creek is a mid-order, perennial stream in the Norman Region that drains into the Mackenzie River a few kilometers downstream of the sampling site. Fifteen of the rare disjunct/widespread insect taxa were found in Oscar Creek, 11 of which were found nowhere else in the northern half of the study region, not counting 4 insects (*E. canis*, *Endotribelos*, *Pagastiella* and *Parapsectra*) that were not collected elsewhere. *Diphetor hageni* (Baetidae), *Caenis*, *Aeshna* (Anisoptera) and *Labrundinia* (Tanypodinae) were found in the Slave region and Oscar Creek, while *Leptophlebia*, *Siphloplecton*, *Pteronarcys*, *Paratendipes* (Chironomini), *Neostempellina* (Tanytarsini), *Rheocricotopus* (Orthocladiinae) and *Natarsia* (Tanypodinae) were found in Oscar Creek and streams in the Liard region. The relatively large number of rare taxa (20 in total) in this stream, especially those that are more widely distributed in southern streams, seems to indicate that Oscar Creek may provide a habitat for relict southern species that cannot usually tolerate extreme northern conditions, and therefore provide a source of dispersal for these rare species, as well as for more common taxa.

4.4.4 Caveats regarding interpretation of the data

Although many of the study sites were selected on the basis of their proximity to the proposed route of the Mackenzie Gas Pipeline, the overriding factor that determined site selection, apart from the presence of flowing water (preferably with riffle habitat), was accessibility. Most streams in the far north of the study region are remote and only accessible during the summer by helicopter, so the availability of a safe, landing site often determined whether a stream was sampled (this was obviously more of an issue below the treeline than on the tundra). More southerly sites were selected mainly for their accessibility from roads and (in a few cases) navigable waterways. While it was possible to identify broad latitudinal features of the system and its fauna, ideally there would have been as many streams (and as many kinds of streams) sampled in the southern regions as the north. In consequence, the data do not conform to an ideal sampling design in terms of determining the relationships between local environmental variables and benthic assemblages, as opposed to climate-related regional variation. Substrate is a good example – while streams with soft substrate were common in the tundra and northern taiga, all of the streams to the south had primarily rock or gravel substrates, so differences in assemblage composition among different substrate types were only apparent in the far north. Other variables that could not be statistically separated from latitude included winter conditions (which obviously have some relationship with latitude), the presence/absence and distance to upstream lakes (this was confounded by the numerous lakes in the Mackenzie Delta), conductivity and pH (both exhibited a latitudinal gradient above approximately 67.8 °N). Therefore, local environmental variables explained little of the variation in assemblage composition across the entire study area in our analysis relative to the variation explained by latitude. These sampling design issues are hard to avoid in a system as physically heterogeneous as the Mackenzie, and it was possible to determine relationships between local conditions and assemblage composition within regions with greater validity. However, it should be recognized that differences in the variables that apparently determine composition within regions could be due to greater variation of those variables within some regions relative to others, rather than actual differences in the effect of the variables on the fauna of the different regions (Heino & Mykra 2008).

4.4.5 Summary: Large-scale spatial trends in assemblage composition

This chapter has documented a latitudinal gradient of community composition across the Mackenzie River system. The study area covered a wide range of physical, hydrological and climatic conditions, and the relationship of these factors with benthic assemblages is complex. The results suggest that a combination of nutrient availability, habitat stability, substrate characteristics, and winter ice conditions were largely responsible for the patterns that were found. However, since most environmental variables that were apparently related to assemblage composition were also correlated with latitude, it is difficult to isolate the effect of any one variable. For example, most far northern streams had soft substrates and were dominated by a soft-substrate fauna, but were completely lacking in burrowing Ephemeroptera and severely depleted of Odonata, Coleoptera and aquatic Hemiptera. This may be because they are unable to survive in frozen or anoxic sediments; other possible explanations for the absence of these taxa from the far north include lack of suitable adult habitat on the tundra and nutrient limitation.

In the southern portion of the study area, nutrient availability (exemplified by TDN) seems to be a major factor affecting benthic assemblages, as high-nutrient streams had many genera, families and even orders of insect that are characteristic of temperate streams but virtually absent in the northern regions, while assemblages in low-nutrient streams were similar to streams that were much higher in latitude. Further north, assemblages were dominated by small, short-lived insects as permafrost becomes more ubiquitous, summer flow becomes more variable and freezing during the winter becomes more likely. In the lowlands in the north of the study area, the landscape was dominated by thermokarst lakes and the assemblages contained a mixed lotic/lentic fauna, which was probably restricted to animals with long life cycles due to nutrient limitation and very short duration of the growing season, as well as adaptations to survive winter in frozen or anoxic sediments.

In summary, benthic community composition in the Mackenzie River System is structured along a latitudinal gradient related at least in part to temperature, permafrost and nutrient availability. Regional differences in assemblage composition reflect the latitudinal environmental gradient between the arctic and sub-arctic. The presence of flowing water during the winter, often from saline springs, is a determinant of community composition in northern regions, and continuous permafrost probably plays a role in controlling hydrology and nutrient dynamics during the growing season, with potential effects on benthic communities. Landscape characteristics are also important, as the relatively flat, lake-dominated northern landscape harboured a fauna dominated by chironomids, mollusks, crustaceans and oligochaetes, including a large proportion of lentic taxa, which was distinct from the more diverse fauna of the higher gradient alluvial streams that dominated to the south. The regional differences observed in the benthic fauna and the likelihood that they are driven by factors relating to climate and permafrost have implications for future biomonitoring efforts in the Mackenzie River System, which are discussed in Chapter 5.

Chapter 5

Applications & future directions

There has been renewed interest in aquatic habitats in the Mackenzie System in the past decade due to impending natural resources development and to recognition that the climate in the system (and in northern regions generally) is changing rapidly. The Mackenzie Gas Pipeline, if built, will cross hundreds of streams including many of the study sites; it will be the largest construction project ever undertaken in the Northwest Territories, and its ecological effects are uncertain because no analogous project has ever been attempted in arctic North America. Climate change is occurring more rapidly at high latitudes than elsewhere, and melting of the permafrost may cause large changes to stream hydrology and habitat. Before summarizing the findings of this project, this final chapter will review the potential effects of these two threats to the current state of streams and benthic macroinvertebrates in the Mackenzie River System, and discuss the feasibility of biomonitoring using benthic assemblages in light of the results of this study.

5.1 Potential impacts of pipeline construction on benthic communities

Impacts on benthic invertebrate communities during and after the construction of pipeline crossings are expected to mainly stem from increased sediment loads. These impacts include the physical effects of scouring and sediment deposition and limitation of food and oxygen availability due to increased turbidity and burial; additionally, the feeding mechanisms of filter feeders may become clogged by increased suspended sediment loads (Levesque & Dube 2007). In other environments, large increases in the density of macroinvertebrates in the drift in response to natural and construction-related increases in sediment loads have frequently been observed, accompanied by decreases in abundance in and downstream of the affected area (Rosenberg & Snow 1975, Young & Mackie 1991). The duration of these impacts is likely related to the physical characteristics of the stream in terms of the transport or retention of the sediment; if sufficient quantities of sediment are retained to permanently alter the benthic habitat, long-term alterations in community composition are possible. However, when the increased sediment inputs are short-term, macroinvertebrate assemblages can recover rapidly (Rosenberg & Snow 1975, Young & Mackie 1991, Levesque & Dube 2007). Organisms drifting from unaffected upstream areas and oviposition by aerial aquatic insects provide sources for colonization of the impacted stream length. Especially in northern streams, the large physical and hydrological disturbance that accompanies spring snow melt and ice breakup is often likely to swamp out the effects of increased sedimentation during construction by moving deposited sediment downstream and bringing in organisms from upstream; short-term reductions in abundance and diversity may not be observable after spring high flows have subsided (Rosenberg & Snow 1975, Young & Mackie 1991).

Once the pipeline is constructed, the major risk factor for aquatic habitats is the possibility of a pipeline rupture and a degraded stream bank; as the pipeline is carrying gas, impacts on benthos are likely to be short-lived and limited in distance. Other impacts may occur depending on how sewage is released from the various pumping stations located along the pipeline. Secondary impacts may also occur with snowmobile and all terrain vehicle traffic along the pipeline route and in the stream bed. While an oil spill is unlikely, studies of the impacts on lotic invertebrate assemblages from experimental oil spills indicate that these effects are also relatively short-lived, and recovery may be substantially complete following spring melt, despite catastrophic initial effects on abundance, diversity and drift rates (Snow *et al.* 1975, Miller *et al.* 1986). Invertebrates enter the drift to escape oil inputs (similar to the response to sedimentation), and potential toxic effects of the soluble fractions of oil may be mediated by decreased metabolism at low temperatures and the relatively low surface area to volume ratio of the mature overwintering larvae of many species (Miller *et al.*1986). Since natural seasonal variation in assemblages (e.g. Miller & Stout 1989) is often greater than changes due to short-term anthropogenic disturbances (Young & Mackie 1991), impacts on benthic invertebrate assemblages may not closely track impacts on other stream assemblages (e.g. fish, macrophytes) which do not have the high phenological variability/adaptability or dispersal ability of aquatic insects. However, where long-term impacts on stream habitat occur (e.g. substrate characteristics, bank slumping, chronic contamination), benthic assemblages may be more consistently affected and therefore serve as indicators of environmental impacts.

Many of the potential effects of pipeline-related alterations to permafrost dynamics may be similar to those expected to occur due to climate change, especially in areas that currently have continuous permafrost. These are discussed in the following section.

5.2 Potential impacts of climate change on benthic communities

The latitudinal survey described in this study is a substantial contribution toward establishing a baseline against which the effects of climate change on northern benthic macroinvertebrate assemblages can be monitored and assessed. Permafrost in the Liard and Slave basins is discontinuous and patchy, and if the contrast in macroinvertebrate assemblages between high-nutrient and low-nutrient streams in these regions is related to permafrost conditions, the conditions of these stream types may converge, resulting in greater macroinvertebrate species richness in the low-nutrient streams and less distinction between the macroinvertebrate assemblages of the stream types. Permafrost is continuous north of the Norman Wells area, and winter flow conditions were among the major determinants of assemblage composition in areas where perennial streams were present. These streams may become more stable in the spring and summer due to increased water retention in the active soil layer and less violent ice scour. This increased stability may affect benthic diversity because intermediate levels of disturbance (i.e. the flashy hydrograph of permafrost streams) are believed to maintain species richness and prevent dominance of a few species by continuously clearing new habitat (Townsend 1989, Huryn *et al.* 2005). However, as temperatures increase and nutrient levels rise, species currently limited to the south are likely to expand their distribution limits northwards. These invasions may act to stabilize or increase diversity, but the outcome may depend on the traits of the species that shift north and their interactions with the native species. One potential complicating factor is that the invading fauna could disproportionately consist of large predators, which are underrepresented in northern streams (e.g. Odonata, Hemiptera, many Plecoptera, Trichoptera, Megaloptera); the current fauna of northern streams, mainly collector-gatherers, might be ill-equipped to deal with large increases in predation. Shredders are also likely to increase in diversity and abundance, in tandem with the increasing abundance and diversity of leaf litter that will accompany northward shifts in terrestrial vegetation; it seems fairly safe to predict that autumn shredder abundances on the tundra will rise as the treeline moves north.

Ultimately, the conditions (i.e. the habitat template) of perennial and frozen streams may converge (Huryn *et al.* 2005), with an overall loss of species as those that specialize in frozen streams are pushed northwards. Although the diversity of any particular stream may increase as southern species invade and winter conditions become more tolerable, the overall diversity of the Mackenzie basin is more likely to decrease as the distributions of northern species are pushed towards the delta and the Arctic Ocean. This decline could be exacerbated by the potential drying up of stream channels due to permafrost melt, depending on precipitation trends. Streams in the far north of the study area, in and around the Mackenzie Delta, may be subject to very different effects from climate change. This region mostly contains peat channels connecting thermokarst lakes, has very shallow active soil layers, floods in the spring due to high discharge and ice jams, and was found to have a distinct stream invertebrate fauna dominated by chironomids, including many genera more often associated with lentic habitats; the dominant chironomid genera in the region tended to grow to a large maximum body length, which may be indicative of longer life cycles. The lentic aspect of the fauna may become more important in low-lying streams near the river, which are currently experiencing longer connection times to the river than in the past; streams further away and at higher elevations are being inundated for shorter periods of time, and are likely to dry out barring large increases in precipitation. However, even the lowland channels may be adversely affected by climate change, since melting of the permafrost has the potential to dramatically alter the landscape of the delta by draining thermokarst lakes, inducing sloughing of the banks, eventually remapping the channel network, probably with high inputs of sediment which may limit algal production (likely an important food source on tundra streams).

Climate-related changes to the hydrologic and nutrient cycles in the Mackenzie River system may have implications for areas far beyond the basin. The Mackenzie Delta floodplain is an important source of organic nutrients for to the Mackenzie estuary and the Beaufort Sea (Emmerton *et al.* 2008), and along with other major arctic river basins in the Palearctic is a major contributor of freshwater to the Arctic Ocean. If a combination of higher precipitation, permafrost melting and decreased retention of melt water in thermokarst pools (as examples of possible factors) lead to higher discharge, salinity in the Arctic Ocean may be affected, with potential consequences for global circulation patterns (Peterson *et al.* 2002, 2006). Since the processes that determine annual discharge occur throughout the river network, monitoring conditions of smaller streams may facilitate early detection of climate-related alterations of environmental processes. Given the uncertain predictions of the effects of warming in the arctic, benthic invertebrate assemblages of smaller streams may prove to be especially useful indicators as their composition integrates the effects of many environmental factors. If an annual sampling effort were maintained, differences in biomass, abundance and phenology due to climatic variation could become apparent within a few years (Hogg & Williams 1996). The short life spans and high dispersal capabilities of aquatic insects mean that their distributions may shift rapidly as environmental conditions change (Danks 1992a). This study provides regional and latitudinal baselines against which future climate-related change can be measured.

5.3 Implications for biomonitoring

Most monitoring programs have been developed for temperate systems, and the applicability of these designs to arctic and sub-arctic systems is limited by the variability of assemblage composition and the poor representation of many well-studied invertebrate groups characteristic of northern streams (Milner *et al.* 2006). The diversity and numerical dominance of chironomids in the Mackenzie River system means they will form an important component of any biomonitoring effort, requiring greater taxonomic expertise and, in many cases, species-level information. Conversely, the poor representation of non-Diptera orders means that many commonly used community metrics (e.g. %

EPT) may be of little use. Huryn *et al.* (2005) suggested that assemblage structure could be used as an indicator of perennial flow, and since the potential effects of both climate change and pipeline operation include changes to permafrost conditions, and therefore to the state of winter flow in streams, development of a community-level indicator of perennial flow specific to the Mackenzie System could be useful. This study demonstrated differences in assemblage composition of the late-summer fauna in streams that flow year-round versus those that freeze solidly in the Norman Wells region, suggesting that such an indicator can be developed; however, a larger sample size would be desirable, as would more detailed assessments of winter flow conditions than those supplied by Imperial Oil (2004).

Another challenge to biomonitoring in northern streams is the high inter-annual variability in assemblage composition caused by the seasonal climate and disturbance regimes. In Alaskan streams, Milner *et al.* (2006) found that species that were abundant in one year were often rare or absent in subsequent years under natural conditions, and this has serious implications for the definition of invertebrate communities to be expected in reference conditions. The resources available for this study did not allow estimation of variability among years. The inter-annual variability of macroinvertebrate assemblages in different regions of the Mackenzie System needs to be addressed to allow meaningful interpretation of monitoring results and to statistically demonstrate significant impacts. Additionally, if assemblage variability is related to the disturbance regime, then the rate of change from year to year could provide an indicator of permafrost conditions, as these are an important factor controlling the hydrological regime.

The strong regional component that we found in patterns of assemblage composition is a factor that should be taken into account in monitoring efforts using a reference condition approach, as has been recommended by DFO for the Mackenzie Gas Project (JRP-MGP 2010). Distinct assemblages were observed in the Mackenzie Delta/lowland tundra region and in the sub-arctic and boreal forest surrounding Norman Wells, representing different reference conditions in the two regions. Assemblage composition in the southern streams was more variable and had no evidence of a regional component; this may be because of lower sampling effort in these regions, or because conditions are more spatially variable in the southern end of the system (e.g. patchy discontinuous permafrost). In either case, further sampling in these regions is needed to establish reference conditions, especially in the areas of the Liard basin that the pipeline will pass through. The regional variability in assemblage composition means that a monitoring program for the MGP pipeline will need to take different regional reference conditions into account, and include a sufficient number of reference or control sites from each region. This is also applicable to local monitoring of pipeline crossings using a BACI design (also recommended by DFO); control sites from each region would need to be included.

There is currently no program in place to monitor environmental conditions in aquatic habitats in the Mackenzie River System. Although the Joint Review Panel for the Mackenzie Gas Project (JRP-MGP 2010) has recommended that a monitoring system be implemented to assess effects on fish and fish habitat, it remains unclear whether biomonitoring of benthic invertebrate assemblages will be included. Since the potential effects of climate change and industrial development are uncertain, benthic invertebrate assemblages may provide a useful indicator of altered stream habitat because they integrate many environmental factors. This study provides a baseline of the patterns of assemblage composition along environmental gradients in the Mackenzie System and of reference conditions in the different regions of the system, which can be used to plan monitoring efforts.

5.4 Conclusions and recommendations for future work

This study has shed light on the environmental factors that drive benthic invertebrate diversity and community composition in small streams in the Mackenzie River System. In addition to factors such as channel size and substrate, which affect benthic communities in river systems generally, elements of the arctic environment shape the fauna in the far north. Nutrient limitation, freezing of the substrate during the winter and ice scour in the spring limit the diversity and affect the composition of benthic invertebrates to varying degrees in different regions. Landscape characteristics seem to be important determinants of community composition through their effect on stream habitat, as the flat terrain of the tundra harbours limited, chironomid-dominated assemblages that contrast strongly with the relatively diverse assemblages in alluvial streams in the hills just to the south and the west. Diversity of Ephemeroptera and Plecoptera increase from north to south, with the northern fauna for the most part limited to the most widespread species; chironomids become more dominant towards the north and shift from assemblages dominated by orthoclads to those dominated by Chironominae, coinciding with a shift in landscape characteristics in the far north. Other common aquatic invertebrates (Odonata, Hemiptera, Coleoptera, Megaloptera) were rare across the system, but particularly in the far north. Future studies may want to examine whether the latitudinal gradients in diversity and composition described in this study are primarily due to the cold temperatures or the increased hydrologic effects of permafrost in the north; both of these factors likely have a role, as could other possibilities such as regional differences in precipitation, terrestrial vegetation and fish populations. The strong regional component to assemblage composition and the high diversity in landscape and climate may make the Mackenzie a good system to test hypotheses concerning the relative importance of dispersal versus selection by the habitat template, and diverse permafrost conditions, from patchy and discontinuous in the south to continuous in most areas of the far north, might provide a good system in which to study the effects on invertebrates of different hydrological regimes. A more complete picture of community dynamics probably necessitates sampling in multiple years to characterize interannual variability as well as sampling during multiple seasons, possibly even during the winter. Addressing these theoretical issues could also be helpful in the development of regional biomonitoring programs.

The conclusions of this study have implications for the development of programs utilizing benthic invertebrates to monitor the Mackenzie Gas Pipeline and the effects of global warming. Reference conditions need to be established on a regional basis, taking into account differences among the tundra, subarctic forest and boreal forest regions. Reference conditions also need to be established for different stream types among the regions. A number of perennial (Active I) and winter-frozen (Active II) streams should be included as these are likely to be affected by pipeline construction and climate change, and the reference streams should include sufficient variation in conditions of other factors that we found to affect benthic communities, including different types of substrate, lake outlets (especially in the north), sources of water (e.g. precipitation and permafrost melt versus springs) and permafrost conditions. A sufficient number and variety of reference sites (i.e. streams that will not cross the pipeline route) need to be included at a variety of latitudes in order to monitor impacts of pipeline construction and operation; establishing and monitoring reference conditions is especially important because impacts from the pipeline may be difficult to separate from changes due to warming. Additionally, sampling many sites could help identify diversity hotspots (such as Oscar Creek) and ecologically sensitive sites, which would be useful information for making conservation decisions. The interannual variability of benthic communities represents a major knowledge gap and should be addressed before construction of the pipeline begins; if surveys of the reference sites begin a few years before pipeline installation commences, then variability could be quantified, resulting in more robust interpretations of monitoring data.

Tributary streams and creeks in the Mackenzie River System have been relatively understudied given the importance of the system to the ecology of a vast swath of the Canadian north. The study described in this thesis builds on earlier surveys of benthic invertebrates in the system and provides ecological context to further our understanding of the factors governing their populations and communities and a baseline that can contribute to developing scientifically sound monitoring programs. The system is changing rapidly due to climate warming, and may be further altered by natural gas development and the construction of the pipeline system. Hopefully, this study will be useful in understanding and protecting stream habitats in the Mackenzie system heading into the future.

Appendix I

Abbreviations used in this thesis

Table A1 – Key to abbreviations used in this thesis.

Variable	Abbreviation	
Physiogeographic Region	ACP	Arctic Coastal Plain
	IP	Interior Plains
	WC	Western Cordillera
Vegetation Region	BF	Boreal Forest
	LAT	Low Arctic Tundra
	SAF	Sub-Arctic Forest
Watershed	AR	Arctic Red River
	GSL	Great Slave Lake
	KB	Kugmallit Bay (Beaufort Sea)
	L	Liard River
	MD	Mackenzie Delta
	MM	Mackenzie Main Stem
	P	Peel River
	S	Slave River
Dominant Substrate	SOM	Silt/Organic Material
	SP	Sand/Pebbles
	GC	Gravel/Cobble
	CB	Cobble/Boulder
Site group (Ch. 4)	FNS	Far Northern Streams
	MNS	Mid Northern Streams
	HNSS	High Nutrient Southern Streams
	LNSS	Low Nutrient Southern Streams
	SNS	Small Northern Streams
Winter conditions	P	Perennial
	F	Frozen
	A	Anoxic
	?	Unknown

Appendix II

Site location and sampling information

Table A2 - Location and sampling information for the study sites. See Appendix I for legends to abbreviations. Information on physiogeographic and vegetation regions is from Rosenberg & Barton (1986) and Brunskill (1986), respectively. Continued on next page.

Site	Sampling date	# of samples	Latitude	Longitude	Elevation (m)	PG Region	Veg. Region	Water shed	Up stream Lake (km)
Canyon Crk up	07/08/2005	6	65.2265	126.5224	88	IP	BF	MM	n/a
Canyon Crk down	07/08/2005	6	65.22256	126.5259	70	IP	BF	MM	n/a
Oscar Crk down	09/08/2005	6	65.43894	127.4314	53	IP	BF	MM	44
Oscar Crk up	09/08/2005	6	65.43961	127.4156	53	IP	BF	MM	44
Vermillion Crk down	10/08/2005	6	65.09178	126.1375	81	IP	BF	MM	n/a
Vermillion Crk up	10/08/2005	6	65.09753	126.1301	89	IP	BF	MM	n/a
Chick Crk	11/08/2005	6	65.85481	128.1342	135	IP	SAF	MM	n/a
RPR-271	11/08/2005	3	65.85547	128.1343	135	IP	SAF	MM	n/a
Helava Crk down	12/08/2005	6	65.18961	126.4207	74	IP	BF	MM	n/a
Helava Crk up	12/08/2005	6	65.19228	126.4199	79	IP	BF	MM	n/a
Tieda R	14/08/2005	3	66.62961	129.3371	23	IP	SAF	MM	18.23
Oscar Crk mouth	16/08/2005	3	65.43522	127.4598	39	IP	BF	MM	44
Vermillion Crk mouth	17/08/2005	3	65.07783	126.2069	59	IP	BF	MM	n/a
RPR-048	15/08/2006	3	68.61497	133.5691	62	ACP	LAT	MD	1.2
RPR-058.6	16/08/2006	3	68.40083	133.3091	25	ACP	SAF	MD	7.2
Yaya River	19/08/2006	3	69.23117	134.5803	27	ACP	LAT	KB	3.2
RPR-006.1	19/08/2006	5	69.313	134.7649	6	ACP	LAT	MD	0.9
Zed Creek	19/08/2006	3	68.95497	133.5401	33	ACP	LAT	MD	1.3
Thunder River	20/08/2006	3	67.53339	130.8519	57	IP	SAF	MM	n/a
RPR-099	20/08/2006	2	67.85961	132.0795	159	ACP	SAF	MD	0.4
Travaillant River	20/08/2006	3	67.90772	132.1931	203	ACP	SAF	MD	3.7
RPR-075	20/08/2006	3	68.09672	132.8259	239	ACP	SAF	MD	2.7
RPR-070	20/08/2006	3	68.16472	132.9815	190	ACP	SAF	MD	9.25
RPR-069	21/08/2006	3	68.19583	133.0525	151	ACP	SAF	MD	10.37
Hans Creek	21/08/2006	3	68.77322	133.7721	52	ACP	LAT	MD	0.7
RPR-032	21/08/2006	3	68.821	133.8568	68	ACP	LAT	MD	1.7
Stanley Crk	09/09/2006	1	68.70769	133.4478	56	ACP	LAT	MD	7
Hodgson Crk	16/09/2006	2	63.33771	123.4634	239	IP	BF	MM	n/a

Table A2, continued.

Site	Sampling date	# of samples	Latitude	Longitude	Elevation (m)	PG Region	Veg. Region	Water shed	Up stream Lake (km)
Dahadinni R	16/09/2006	1	63.94127	124.5333	116	IP	BF	MM	n/a
Dehtthih Dehe R	17/09/2006	2	60.45543	120.2034	619	IP	BF	MM	n/a
Trout R	17/09/2006	2	60.97816	120.572	331	IP	BF	MM	45
Jean-Marie R	18/09/2006	1	61.45286	121.0078	197	IP	BF	MM	33
Poplar R	18/09/2006	2	61.314	121.7293	243	IP	BF	L	n/a
Stream 1	29/07/2007	3	67.22972	133.0333	13	IP	SAF	MM	2
Stream 2	29/07/2007	3	67.47692	133.5753	6	IP	SAF	MM	n/a
Stream 3	30/07/2007	3	67.56192	133.7636	13	IP	SAF	MM	n/a
Rengleng R	31/07/2007	3	67.75564	133.8619	44	IP	SAF	MM	18.34
Nello Crk	31/07/2007	3	67.84269	133.6947	68	ACP	SAF	MM	1
Rat R	02/08/2007	3	67.65542	135.5348	99	WC	SAF	MD	n/a
Stoney Crk	02/08/2007	3	67.35189	135.012	28	WC	SAF	P	n/a
Vittrekwa R	02/08/2007	2	67.35189	135.3774	220	WC	SAF	P	1.7
Jackfish Crk	03/08/2007	3	66.88536	133.2627	30	IP	SAF	AR	13
Treeline Creek	03/08/2007	3	67.20178	132.396	34	IP	SAF	MM	22
Stream 6	15/08/2007	3	61.99256	121.928	155	IP	BF	MM	n/a
Stream 8	15/08/2007	3	62.03694	122.1374	160	IP	BF	MM	n/a
Shale Crk	15/08/2007	3	62.05608	122.8982	220	IP	BF	MM	n/a
Upper Blackstone R	16/08/2007	3	61.05608	122.8982	181	IP	BF	L	n/a
Birch R	16/08/2007	2	61.33211	122.0963	170	IP	BF	L	n/a
Stream 7	18/08/2007	3	62.025	122.0285	146	IP	BF	MM	n/a
Red Knife trib	18/08/2007	3	61.15175	119.3397	190	IP	BF	MM	27
Bouvier Crk	18/08/2007	2	61.13647	119.0143	237	IP	BF	MM	n/a
Little Buffalo R	22/07/2008	3	60.98489	113.7526	158	IP	BF	GSL	n/a
Birch Crk	23/07/2008	3	60.71818	115.3835	180	IP	BF	GSL	4
Sandy Crk	23/07/2008	3	60.73314	115.7115	179	IP	BF	GSL	n/a
Salt R	25/07/2008	3	59.81908	111.9671	190	IP	BF	S	7.31
Hornaday R	25/07/2008	3	59.43742	111.5004	213	IP	BF	S	n/a

Appendix III

Habitat measurements & observations

Table A3 - Habitat measurements & observations for the study sites. See Appendix I for legend to abbreviations. Winter flow information is from Imperial Oil (2004). Continued on next page.

Site	Wetted width (m)	Depth (m)	Vel. (m/s)	Grad. (m/km)	Surf. Temp (°C)	Habitat Type	Pools present	M-phyte Cover (%)	Dom. Subs.	Winter Flow
Canyon Crk up	6.7	0.3	0.3	13.9	15.28	Riffle	No	0	GC	P
Canyon Crk down	6.7	0.3	0.3	13.9	15.28	Riffle	No	0	GC	P
Oscar Crk down	12.2	0.3	0.31	1	12.74	Run	Yes	0	GC	P
Oscar Crk up	12.2	0.3	0.31	1	13.45	Riffle	Yes	0	GC	P
Vermillion Crk down	7.1	0.3	0.46	11.1	11.49	Riffle	Yes	0	CB	P
Vermillion Crk up	7.1	0.3	0.46	11.1	12.1	Riffle	Yes	0	CB	P
Chick Crk	4.3	0.3	0.7	16.9	9.13	Riffle	Yes	0	GC	?
RPR-271	0.4	0.2	0.07	42	9.45	Pool	Yes	75	SOM	?
Helava Crk down	2.2	0.5	0.04	11.7	10.44	Riffle	Yes	0	GC	F
Helava Crk up	2.2	0.5	0.04	11.7	11.7	Riffle	Yes	0	GC	F
Tieda R	14.6	0.27	0.53	7.5	11.82	Riffle	No	25	GC	F
Oscar Crk mouth	12.2	0.3	0.31	1	13.92	Run	Yes	25	GC	F
Vermillion Crk mouth	7.1	0.3	0.46	11.1	11.5	Run	Yes	0	CB	P
RPR-048	6.8	1	0.5882	3	14.81	Run	No	50	SOM	F
RPR-058.6	2	0.28	0.2057	1	12.8	Run	Yes	25	SP	F
Yaya River	1	0.84	0.4028	2	8.54	Run	No	25	SP	F
RPR-006.1	0.75	0.11	0.01	0.1	7.7	Run	Yes	25	SOM	?
Zed Creek	8.5	0.55333	0.6767	0.2	12.75	Run	No	25	SP	P
Thunder River	5.8	0.407	0.3388	4.2	10.95	Riffle	No	0	GC	F
RPR-099	8	0.29333	0.0312	2.2	13.86	Pool	Yes	75	SOM	A
Travaillant River	8.3	0.36667	0.7297	2.1	14.27	Riffle	Yes	25	SP	A
RPR-075	3.5	0.53	0.6954	13.4	13.93	Run	No	25	SP	F
RPR-070	6.2	0.66	1.0538	15.7	13.45	Run	Yes	50	SP	A
RPR-069	6.4	0.60667	0.4388	4	11.01	Run	Yes	50	SOM	F
Hans Creek	13.3	0.82	0.346	1.1	9.81	Run	No	25	SOM	?
RPR-032	3	0.7333	0.3154	5	9.42	Run	Yes	100	SOM	?
Stanley Crk	10.7	0.363	0.78	4	12.72	Run	Yes	0	GC	?
Hodgson Crk	10.3	0.223	0.57	18	8.23	Riffle	No	0	GC	A
Dahadinni R	46	0.654	0.51	4	3.94	Riffle	No	0	GC	?

Table A3, continued.

Site	Wetted width (m)	Depth (m)	Velocity (m/s)	Gradient (m/km)	Surface Temp (° C)	Habitat Type	Pools present	Macrophyte Cover (%)	Dom. Substrate	Winter Flow
Dehtthih Dehe R	4.5	0.547	0.14	7	5.13	Run	Yes	0	SP	P
Trout R	49.6	0.514	0.72	4	9.82	Run	No	0	GC	P
Jean-Marie R	24	0.74	1.35	0.1	10.5	Run	Yes	25	CB	P
Poplar R	23.3	0.577	0.44	1	7.35	Riffle	Yes	0	GC	?
Stream 1	1.3	0.13	0.11	46	9.96	Run	Yes	25	SP	?
Stream 2	5.5	0.19	0.68	24	14.68	Run	Yes	25	SP	?
Stream 3	1.5	0.12	0.36	17	12.18	Riffle	Yes	25	SP	?
Rengleng R	12	0.33	0.43	8	15.65	Riffle	Yes	25	GC	?
Nello Crk	4.2	0.25	0.31	4	14.17	Run	Yes	25	CB	?
Rat R	13.6	0.44	0.96	12	10.29	Riffle	No	0	CB	?
Stoney Crk	25	0.4	0.98	3	16.01	Riffle	No	0	CB	?
Vittrekwa R	20	0.46	0.82	86	15.4	Run	No	0	CB	?
Jackfish Crk	11	0.23	0.32	2	17.68	Riffle	No	0	CB	?
Treeline Creek	7	0.13	0.37	4	14.91	Riffle	No	0	GC	?
Stream 6	10.3	0.38	1.958	18	11.53	Riffle	No	0	CB	?
Stream 8	7.4	0.236	0.599	20	11.72	Riffle	No	0	CB	?
Shale Crk	17.4	0.308	0.511	6	14.57	Riffle	Yes	0	GC	?
Upper Blackstone R	22.3	0.3	0.69	3	12.45	Run	Yes	0	GC	?
Birch R	26.7	0.5	1.362	8	15.02	Run	Yes	0	CB	?
Stream 7	5.025	0.4	0.524	18	12.08	Run	Yes	25	CB	?
Red Knife trib	8.6	0.164	0.423	8	15.01	Riffle	Yes	0	CB	?
Bouvier Crk	13.2	0.268	0.1302	8	16.46	Run	Yes	75	GC	?
Little Buffalo R	45	0.55	0.01	1	21	Run	Yes	25	SOM	?
Birch Crk	7	0.29	0.01	4	16.01	Riffle	Yes	25	GC	?
Sandy Crk	9	0.4967	0.01	1	18.76	Pool	Yes	25	GC	?
Salt R	12	0.21	0.0608	3	17.9	Run	Yes	0	GC	?
Hornaday R	6	0.3167	0.0288	0.8	20.71	Run	Yes	25	CB	?

Appendix IV

Water chemistry measurements

Table A4 - Water chemistry and nutrient measurements for the study sites. Blank values were not recorded for that site. Continued on next page.

Site	pH	Spec Cond (µS/cm)	DO (mg/L)	Colour	Turbidity (NTU)	TP (mg/L)	TDN (mg/L)	NO_2/NO_3 (mg/L)
Canyon Crk up	8.43	771	10.15	5	1	0.005	0.141	0.02
Canyon Crk down	8.42	769	9.68	5	0.4	0.005	0.117	0.02
Oscar Crk down	8.24	976	9.7	20	3.6	0.005	0.204	0.04
Oscar Crk up	8.21	961	9.82	20	6.2	0.005	0.211	0.06
Vermillion Crk down	8.21	2160	10.69	5	1.5	0.005	0.313	0.05
Vermillion Crk up	8.25	2160	10.68	10	0.4	0.005	0.195	0.05
Chick Crk	8.245	463.5	11.49	15	8.995	0.0195	0.161	0.02
RPR-271	8.19	703	10.82	30	0.6	0.005	0.062	0.04
Helava Crk down	8.26	614	11.02	20	0.95	0.005	0.214	0.065
Helava Crk up	8.275	611	10.75	20	0.705	0.005	0.215	0.065
Tieda R	8.27	237	9.9	10	0.65	0.005	0.277	0.08
Oscar Crk mouth	8.15	1080	10.03	20	2.94	0.01	0.172	0.05
Vermillion Crk mouth	8.3	2110	10.89	5	0.5	0.005	0.182	0.05
RPR-048	6.76	71	9.68	11.05	1.85	0.0065	0.1965	0.005
RPR-058.6	6.82	102	8.69	114	5.75	0.0275	0.8195	0.005
Yaya River	6.35	117	10.52	33.15	6.2	0.017	0.4125	0.005
RPR-006.1	6.73	125	9.74	54.7	2.05	0.006	0.6115	0.005
Zed Creek	7.42	65	10.43	10.4	3.45	0.0255	0.383	0.005
Thunder River	6.89	299	9.84	18.8	1.05	0.001	0.319	0.0125
RPR-099	6.87	66	8.28	68.05	5.5	0.0285	0.616	0.005
Travaillant River	7.61	89	9.13	58.1	6.55	0.011	0.5425	0.005
RPR-075	6.73	44	9.07	15.75	4.05	0.0225	0.432	0.005
RPR-070	6.95	51	9.53	53.45	11.75	0.0325	0.554	0.005
RPR-069	7.28	79	10.4	127.5	19.9	0.0255	0.656	0.005
Hans Creek	6.85	47	10.31	95.4	11.3	0.039	0.6475	0.005
RPR-032	6.5	40	9.58	104	7.8	0.0575	0.669	0.005
Stanley Crk	7.52	72.6		40	10.03	0.12	0.38	0.015
Hodgson Crk	8.03	398.5		15	11	0	0.2	0.117
Dahadinni R	7.62	300.1		65	61.3	0.028	0.28	0.03
Dehtthih Dehe R	7.41	136.5		60	8.2	0.005	0.41	0.005

Table A4, continued.

Site	pH	Spec Cond (µS/cm)	DO (mg/L)	Colour	Turbidity (NTU)	TP (mg/L)	TDN (mg/L)	NO_2/NO_3 (mg/L)
Trout R	7.88	133.6		50	10.1	0.009	0.41	0
Jean-Marie R	7.81	222.8		65	1.76	0.008	0.5	0.026
Poplar R	7.74	208.5		55	10.1	0.009	0.54	0.027
Stream 1	8.07	159	11.63	147	10.085	0.015	1.09	0.01
Stream 2	7.44	120	10.38	123	4.785	0.00625	0.9	0.02
Stream 3	7.67	140	11.1	65.8	1.475	0.0025	0.7	0.005
Rengleng R	7.83	165	9.02	69.2	3.32	0.0025	0.775	0.05
Nello Crk	7.38	85	8.44	149	9.64	0.0225	1.025	0.0075
Rat R	8.2	343	11.67	21.65	295	0.421	0.415	0.21
Stoney Crk	8.21	212	10.16	53.75	1220	0.7235	0.38	0.085
Vittrekwa R	8.11	340	10.26	29.2	4520	1.52	0.38	0.13
Jackfish Crk	8.16	124	9.36	134	2.41	0.0025	0.8	0.019
Treeline Creek	7.7	311	7.38	30.9	1.45	0.0025	0.585	0.08
Stream 6	8.16	295	10.36		3.2	0.01	0.05	0.01
Stream 8	8.18	302	9.44		4	0.02	0.07	0.01
Shale Crk	8.15	187	9.82		2.7	0.01	0	0.03
Upper Blackstone R	8.01	287	9.91		16.2	0.02	0.1	0.01
Birch R	8.12	189	9.6		3.5	0	0	0.01
Stream 7	7.97	257	10.13		17.3	0.03	0.1	0.01
Red Knife trib	8.44	376	9.79		6.0	0	0.13	0.08
Bouvier Crk	8.23	356	9.38		2.5	0	0.13	0.01
Little Buffalo R	8.05	2411	8.21	52.95	2.465	0.0175	0.902	0.005
Birch Crk	8.24	499	8.24	36.3	0.415	0.0065	0.9085	0.0075
Sandy Crk	8.4	449	9.26	61.55	2.095	0.0175	1.05	0.005
Salt R	8.07	19399	9.1	48.1	0.665	0.0115	1.225	0.005
Hornaday R	8.27	2191	10.66	102.5	0.775	0.0255	1.175	0.005

Appendix V

Contrasts in community composition among stream types within regional site groups

Table A5 - Contrasts in average abundance of species between streams with SOM and SP substrates within the FNS site group. The ratio of average % dissimilarity to the standard deviation provides an absolute measure of the consistency of species abundance between the two site groups; ratios > 1 can be considered relatively consistent. SimPer analysis in PRIMER was used to obtain data for this and subsequent tables. Taxa are listed in order of their percent contribution to the dissimilarity between groups; the legend for the abbreviations can be found in the headings to Tables 4.5a-c. Continued on next page.

Species	Avg Abundance in Silt/Organic Matter	Avg Abundance in Sand/Pebbles	Avg % Dissimilarity	Avg % Diss / SD	% Contribution to Dissimilarity	Cumulative % Dissimilarity
Brachycentrus americanus (T)	0.667	29.056	4.41	3.63	6.85	6.85
Conchapelopia (C-T)	2.433	26.833	3.41	1.74	5.31	12.17
Trissopelopia (C-T)	1.822	18.389	3.28	1.92	5.11	17.27
Procladius (C-CC)	15.4	0.444	2.94	1.66	4.58	21.86
Nematoda (N)	2.933	34.556	2.72	1.56	4.23	26.08
Lebertia (Ha)	3.022	15.389	2.39	1.62	3.72	29.8
Nemoura arctica (P)	4.033	11.944	2.24	1.76	3.49	33.29
Haploperla brevis (P)	4.033	11.944	2.21	1.48	3.44	36.73
Oligochaeta (A)	26.544	44.278	2.01	1.73	3.13	39.86
Sergentia (C-CC)	5.822	0.556	1.92	1.5	3	42.85
Hygrobates (Ha)	1.556	6.278	1.86	1.35	2.9	45.75
Polypedilum scalaenum (C-CC)	12.778	11.778	1.7	1.66	2.65	48.4
Corynoneura (C-O)	9.74	1.944	1.7	1.01	2.65	51.05
Glossosoma (T)	0	3.111	1.58	1.31	2.46	53.5
Baetis tricaudatis (E)	2.344	7.056	1.52	1.08	2.36	55.87
Dicrotendipes (C-CC)	2.717	3.611	1.42	1.33	2.2	60.28
Cryptochironomus (C-CC)	2.917	1.556	1.36	0.98	2.12	62.4
Psectrocladius (C-O)	1.983	0	1.29	1.23	2.01	64.42
Tvetenia discoloripes (C-O)	0.189	1.778	1.23	1.31	1.92	66.34
Chelifera (D-E)	0.478	2.833	1.2	1.25	1.87	68.2
Ephemerella aurivillii (E)	1.333	1.778	1.14	0.92	1.77	69.98
Micropsectra (C-CT)	1.589	2.167	1.11	0.88	1.73	71.71
Endochironomus (C-CC)	1.367	0.5	1.03	1	1.6	73.31
Leptotarsus (D-T)	0.722	1.556	0.99	0.88	1.53	74.84
Physa (M)	1.989	0.056	0.96	0.75	1.49	76.33
Phaenopsectra (C-CC)	0.956	0	0.91	1.68	1.42	77.75
Limnophyes (C-O)	1.367	2.444	0.91	0.62	1.41	79.16
Paramectriocnemus (C-O)	0.111	0.5	0.88	0.64	1.37	80.53

Table A5, continued.

Species	Avg Abundance in Silt/Organic Matter	Avg Abundance in Sand/Pebbles	Avg % Dissimilarity	Avg % Diss / SD	% Contribution to Dissimilarity	Cumulative % Dissimilarity
Corynocera (C-O)	4.733	0	0.74	0.44	1.14	81.68
Cricotopus tristis (C-O)	0.056	0.944	0.73	1.08	1.14	82.81
Zalutschia (C-O)	1.356	0.056	0.69	0.69	1.07	83.88
Orthocladius lapponicus (C-O)	0	0.611	0.66	1.1	1.03	84.91
Dicranota (D-T)	0	1.11	0.64	0.49	1	85.91
Constempellina (C-CT)	0.111	0.667	0.57	1.03	0.89	86.79
Euorthocladius type III (C-O)	0	0.222	0.54	0.69	0.84	87.63
Skwala Americana (P)	0.222	0.556	0.53	1.07	0.83	88.46
Rhyacophila (T)	0.111	0.556	0.52	0.91	0.82	89.27
Eukiefferiella cyanea (C-O)	0	0.556	0.51	0.68	0.79	90.07

Table A6 – Contrasts of species abundance in streams in the MNS site group between those in the southern taiga region and those in the Norman mountains (regions defined in Chapter 2). Taxa are listed in order of their percent contribution to the dissimilarity between groups; the legend for the abbreviations can be found in the headings to Tables 4.5a-c. Continued on next page.

Species	Avg Abundance in Norman Region	Avg Abundance in South Taiga Region	Avg % Dissimilarity	Avg % Diss / SD	% Contribution to Dissimilarity	Cumulative % Dissimilarity
Orthocladius obumbratus (C-O)	53.83	2.667	5.97	1.19	7.36	7.36
Acentrella insignificans (E)	12.813	13.556	4.29	1.23	5.29	12.65
Orthocladius lapponicus (C-O)	32.125	0.056	4	0.81	4.93	17.58
Sperchon (Ha)	0.479	8.944	3.57	1.25	4.4	21.98
Haploperla brevis (P)	5.25	5.11	3.21	1.32	3.96	25.94
Paramectriocnemus (C-O)	9.1667	2	3.01	1.46	3.71	29.64
Paramectriocnemus graminocola (C-O)	0.687	4.889	2.98	1.24	3.68	33.32
Thienemannimyia (C-T)	6.437	0.5	2.92	1.31	3.6	36.92
Cricotopus mackenziensis (C-O)	5.104	0	2.85	0.98	3.51	40.43
Paraleptophlebia (E)	22.083	0.167	2.65	0.86	3.27	43.7
Hydropsyche (T)	6.437	0	2.64	1.18	3.25	46.95
Arctopsyche ladogensis (T)	0	8.44	2.47	0.69	3.04	49.99
Arctopelopia (C-T)	4.479	0	2.2	0.59	2.71	52.71
Hayesomyia (C-T)	2.896	0.167	2.02	1.36	2.49	55.2
Alluaudomyia (D-C)	1.75	0	1.98	0.94	2.44	57.64
Dicrotendipes (C-CC)	0.875	8.222	1.93	0.58	2.38	60.02
Ephemerella aurivillii (E)	2.146	0.056	1.76	0.95	2.17	62.19
Brachycentrus americanus (T)	0.437	2.056	1.68	0.97	2.07	64.26
Cladocera (Cr)	1.812	1.11	1.59	0.95	1.97	66.23
Baetis bundyae (E)	0.729	1.167	1.54	0.97	1.9	68.13

Table A6, continued.

Species	Avg Abundance in Norman Region	Avg Abundance in South Taiga Region	Avg % Dissimilarity	Avg % Diss / SD	% Contribution to Dissimilarity	Cumulative % Dissimilarity
Leucrocuta (E)	1.229	0.111	1.37	0.6	1.69	69.82
Planorbidae (M)	1.271	0.111	1.28	1.23	1.58	71.4
Demicryptochironomus (C-CC)	0.396	0.944	1.27	1.06	1.56	72.96
Paraphaenocladius (C-O)	0.354	0.833	1.15	1.09	1.42	74.38
Acentrella lapponicus (E)	1.812	0.111	1.13	0.86	1.39	75.77
Larsia canadensis (C-T)	2.417	0	1.09	0.68	1.35	77.12
Podmosta (P)	0.604	0.444	1.07	0.53	1.32	78.44
Lopescladius (C-O)	0	2.5	1.07	0.43	1.31	79.76
Psychoglypha (T)	0.646	0	1.06	1.13	1.31	81.07
Hexatoma (D-T)	6.396	0	1.04	0.5	1.28	82.35
Cyclopoida	0.708	0.056	1.02	0.73	1.25	83.6
Heterotrissocladius (C-O)	0.625	0	1.01	0.72	1.25	84.85
Diura bicaudata (P)	0.021	0.889	1.01	0.65	1.25	86.1
Ablabesmyia illinoensis (C-T)	3.667	0	0.98	0.54	1.21	87.31
Paramerina (C-T)	0.562	0	0.95	1.17	1.17	88.48
Synorthocladius (C-O)	1.646	0	0.86	0.62	1.06	89.54
Doliphilodes (T)	0	0.889	0.83	0.51	1.03	90.57

Table A7 - Contrast of species abundance between perennial and winter-frozen streams within the MNS site group. Refer to Tables 4.5a-c for abbreviations. Continued on next page.

Species	Avg Abundance in Perennial Streams	Avg Abundance in Streams that Freeze	Avg % Dissimilarity	Avg % Diss / SD	% Contribution to Dissimilarity	Cumulative % Dissimilarity
Orthocladius obumbratus (C-O)	24.167	100.06	5.55	1.32	7.38	7.38
Orthocladius lapponicus (C-O)	7.444	70.778	4.94	1.16	6.57	13.95
Cricotopus mackenziensis (C-O)	6.778	0	3.74	1.23	4.98	18.94
Thienemannimyia (C-T)	8.472	0.444	3.69	1.53	4.91	23.85
Acentrella insignificans (E)	8.667	2.889	3.3	1.2	4.39	28.23
Haploperla brevis (P)	4.583	12.833	3.18	1.34	4.23	32.46
Hydropsyche (T)	8.472	0.222	3.16	1.43	4.2	36.66
Arctopelopia (C-T)	5.972	0	2.97	0.7	3.95	40.61
Hayesomyia (C-T)	3.861	0	2.85	2.58	3.79	44.41
Paramectriocnemus (C-O)	11.583	1	2.75	1.31	3.66	48.06
Paraleptophlebia (E)	28.667	0	2.5	0.73	3.33	51.39
Ephemerella aurivillii (E)	2.861	0	2.34	1.16	3.11	54.5
Brachycentrus americanus (T)	0.306	3.333	2.13	1.01	2.84	57.34
Alluaudomyia (D-C)	1.583	1.5	2.07	1.02	2.75	60.09
Lopescladius (C-O)	0	5	2.03	0.66	2.7	62.79
Planorbidae (M)	1.667	0.111	1.6	1.46	2.12	64.92

Table A7, continued.

Species	Avg Abundance in Perennial Streams	Avg Abundance in Streams that Freeze	Avg % Dissimilarity	Avg % Diss / SD	% Contribution to Dissimilarity	Cumulative % Dissimilarity
Larsia canadensis (C-T)	3.22	0	1.46	0.84	1.94	66.86
Psychoglypha (T)	0.861	0	1.43	1.6	1.9	68.76
Acentrella lapponicus (E)	2.417	0	1.41	0.96	1.88	70.63
Hexatoma (D-T)	8.528	0	1.39	0.58	1.84	72.48
Ablabesmyia illinoensis (C-T)	4.889	0	1.3	0.64	1.74	74.21
Sperchon (Ha)	0.639	1.333	1.27	1.19	1.69	75.9
Leucrocuta (E)	0	0.889	1.25	1.24	1.66	77.56
Synorthocladius (C-O)	2.194	0	1.14	0.74	1.52	79.08
Cladocera (Cr)	2.389	0.222	1.12	0.78	1.49	80.58
Baetis bundyae (E)	0.972	0	1.04	0.7	1.38	81.96
Heterotrissocladius (C-O)	0.167	0.889	0.99	0.82	1.32	83.28
Paramectriocnemus graminocola (C-O)	0.806	0.444	0.99	1.63	1.32	84.6
Paramerina (C-T)	0.528	0.444	0.97	1.33	1.29	85.88
Podmosta (P)	0	0.889	0.95	0.66	1.27	87.15
Demicryptochironomus (C-CC)	0.528	0.333	0.78	0.9	1.03	88.18
Paraphaenocladius (C-O)	0.139	0.611	0.76	1.2	1.01	89.2
Plumiperla (P)	0.083	0.444	0.71	0.82	0.94	90.14

Table A8 - Contrast of species abundance between community composition in streams with & without lakes upstream within the MNS site group. Continued on next page.

Species	Avg Abundance in streams with no lake upstream	Avg Abundance in streams with lake upstream	Avg % Dissimilarity	Avg % Diss / SD	% Contribution to Dissimilarity	Cumulative % Dissimilarity
Orthocladius obumbratus (C-O)	55.625	0.278	6.24	1.39	7.78	7.78
Acentrella insignificans (E)	20.313	3.556	4.36	1.27	5.44	13.22
Haploperla brevis (P)	8.667	0.556	3.61	1.28	4.5	17.72
Orthocladius lapponicus (C-O)	32.125	0.056	3.47	0.76	4.33	22.04
Paramectriocnemus (C-O)	0.875	13.056	3.12	1.45	3.88	25.93
Sperchon (Ha)	1.521	7.556	3.08	0.99	3.84	29.76
Paraleptophlebia (E)	0.625	28.778	2.83	0.99	3.53	33.29
Arctopsyche ladogensis (T)	0	8.444	2.83	0.71	3.53	36.82
Paramectriocnemus graminocola (C-O)	1.104	4.333	2.82	1.14	3.51	40.33
Thienemannimyia (C-T)	3.167	4.861	2.44	1.16	3.05	43.38
Dicrotendipes (C-CC)	0	9.389	2.42	0.66	3.02	46.39

Table A8, continued.

Species	Avg Abundance in streams with no lake upstream	Avg Abundance in streams with lake upstream	Avg % Dissimilarity	Avg % Diss / SD	% Contribution to Dissimilarity	Cumulative % Dissimilarity
Hydropsyche (T)	1.208	6.972	2.23	1.05	2.78	49.17
Cricotopus mackenziensis (C-O)	4.729	0.5	2.16	0.78	2.7	51.87
Arctopelopia (C-T)	4.479	0	1.9	0.56	2.36	54.23
Hayesomyia (C-T)	0.708	3.083	1.77	1.27	2.21	56.44
Alluaudomyia (D-C)	1.75	0	1.71	0.87	2.13	58.57
Cladocera (Cr)	0.687	2.611	1.63	0.92	2.04	60.61
Brachycentrus americanus (T)	1.354	0.833	1.58	0.86	1.97	62.58
Baetis bundyae (E)	0.687	1.222	1.57	0.98	1.96	64.54
Ephemerella aurivillii (E)	0.937	1.667	1.48	0.87	1.85	66.38
Demicryptochironomus (C-CC)	0.167	1.25	1.37	1.1	1.71	68.09
Acentrella lapponicus (E)	0.104	2.389	1.3	1.01	1.63	69.72
Leucrocuta (E)	1.229	0.111	1.25	0.61	1.56	71.27
Paraphaenocladius (C-O)	0.542	0.583	1.25	1.08	1.55	72.83
Hexatoma (D-T)	0.021	8.5	1.24	0.58	1.55	74.38
Planorbidae (M)	0.479	1.167	1.24	1.31	1.54	75.92
Larsia canadensis (C-T)	0.083	3.111	1.23	0.78	1.53	77.45
Ablabesmyia illinoensis (C-T)	0	4.889	1.21	0.65	1.51	78.96
Diura bicaudata (P)	0	0.917	1.2	0.7	1.49	80.45
Podmosta (P)	0.937	0	1.05	0.51	1.31	81.76
Synorthocladius (C-O)	0.021	2.167	1.02	0.73	1.27	83.03
Doliphilodes (T)	0	0.889	0.96	0.52	1.19	84.23
Cyclopoida (M)	0.5	0.333	0.92	0.72	1.14	85.37
Lopescladius (C-O)	1.875	0	0.91	0.35	1.14	86.51
Heterotrissocladius (C-O)	0.625	0	0.87	0.68	1.09	87.6
Wiedemannia (D-E)	0.083	0.444	0.87	1.27	1.08	88.68
Psychoglypha (T)	0.458	0.25	0.79	0.86	0.98	89.66
Paramerina (C-T)	0.417	0.194	0.72	0.9	0.9	90.56

Appendix VI

Correlations between abundance of discriminating taxa and environmental variables

The following tables show correlations between abundance of discriminating taxa and environmental variables selected by Bio-Env. See Tables 4.5a-c for explanations of taxa abbreviations; taxa are in phylogenetic order.

Table A9a – Abundance/environment correlations in the Far Northern Streams (FNS). Continued on next page. Significant correlations ($p < 0.05$) are in bold.

	Depth	Velocity	% macrpht	Turbidity	TDN
Baetis flavistraga (E)	-0.289	-0.0642	-0.143	0.227	**0.563**
Baetis tricaudatis (E)	-0.285	-0.176	-0.188	0.388	**0.733**
Ephemerella aurivillii (E)	0.139	0.461	0.0828	0.482	0.0235
Serratella (E)	-0.285	0.0923	-0.145	0.299	**0.542**
Haploperla brevis (P)	-0.158	0.453	-0.216	0.279	0.147
Nemoura arctica (P)	-0.122	0.313	-0.357	0.408	0.217
Zapada (P)	-0.437	-0.325	-0.156	0.102	**0.689**
Skwala americana (P)	0.0572	0.617	-0.298	0.446	-0.124
Brachycentrus americanus (T)	0.00521	**0.587**	**-0.664**	0.0929	-0.0985
Glossosoma (T)	-0.00167	**0.533**	-0.514	0.0521	-0.285
Mystacides supulchralis (T)	-0.493	-0.419	0.214	-0.228	0.0994
Rhyacophila (T)	0.0805	0.415	-0.022	0.282	0.131
Bezzia/Palpomyia (D-C)	**-0.781**	**-0.601**	-0.243	-0.347	0.446
Cryptochironomus (C-CC)	0.0262	-0.15	0.425	0.313	0.245
Dicrotendipes (C-CC)	-0.248	-0.287	-0.0686	0.0433	0.391
Endochironomus (C-CC)	0.48	0.0413	0.452	-0.328	-0.335
Phaenopsectra (C-CC)	0.291	-0.412	0.431	-0.126	-0.0383
Polypedilum scalaenum (C-CC)	0.491	0.134	0.509	0.0361	-0.168
Sergentia (C-CC)	0.112	-0.374	0.294	**-0.547**	-0.241
Constempellina (C-CT)	-0.0894	0.0767	-0.214	0.15	0.435
Micropsectra (C-CT)	**-0.581**	**-0.606**	-0.00365	-0.243	**0.544**
Protanypus (C-D)	-0.138	-0.397	0.512	-0.28	0.166
Corynoneura (C-O)	**-0.558**	**-0.599**	0.262	-0.248	0.274
Cricotopus tristis (C-O)	-0.355	0.0453	-0.482	0.214	0.343
Eukiefferiella cyanea (C-O)	-0.0311	0.336	-0.489	0.129	-0.352
Orthocladius lapponicus (C-O)	-0.045	0.102	-0.27	0.0104	0.231
Orthocladius obumbratus (C-O)	-0.245	0.241	-0.471	0.244	-0.029
Paramectriocnemus (C-O)	0.0847	-0.292	**0.654**	0.0123	0.211
Paramectriocnemus graminocola (C-O)	-0.185	-0.153	-0.214	0.23	0.53
Psectrocladius (C-O)	-0.136	-0.405	0.173	-0.498	-0.277
Tvetenia discoloripes (C-O)	0.0892	0.194	-0.272	-0.389	-0.346
Zalutschia (C-O)	-0.491	-0.496	0.124	-0.429	0.109
Ablabesmyia illinoensis (C-T)	-0.124	-0.447	-0.16	-0.224	0.183

Table A9a, continued.

	Depth	Velocity	% macrpht	Turbidity	TDN
Procladius (Holotanypus) (C-T)	-0.183	**-0.687**	**0.592**	-0.328	0.0561
Conchapelopia (C-T)	-0.127	**0.605**	-0.475	0.103	-0.237
Trissopelopia (C-T)	0.14	0.452	-0.279	0.00476	-0.137
Chelifera (Ha)	-0.239	0.395	**-0.566**	0.176	0.118
Leptotarsus (Ha)	0.245	0.189	-0.239	0.0177	-0.112
Hygrobates (Ha)	0.0486	0.047	-0.385	0.4	0.443
Lebertia (Ha)	-0.0464	0.447	-0.388	0.434	0.331
Oxus (Ha)	0.195	-0.169	-0.0564	**0.557**	0.328
Sperchonopsis (Ha)	0.0668	0.113	0.119	**0.576**	0.282
Oligochaeta (A)	-0.096	0.407	**-0.74**	0.123	-0.0976
Physa (M)	-0.227	**-0.564**	0.401	-0.276	-0.0145
Harpacticoida (Cr)	-0.282	0.189	-0.424	0.123	-0.185
Nematoda (N)	-0.217	0.382	**-0.585**	0.101	0.0688

Table A9b – Abundance/environment correlations in the mid-northern streams (MNS). Significant correlations ($p < 0.05$) are in bold. Continued on next page.

	Gradient	Width	Macrophytes	pH	SpecCond
Acentrella insignificans (E)	0.409	-0.132	0.18	0.222	-0.195
Acentrella lapponicus (E)	**-0.672**	0.503	-0.153	0.21	0.303
Baetis bundyae (E)	-0.0616	0.101	0.182	-0.183	-0.196
Ephemerella aurivillii (E)	-0.398	0.311	-0.342	0.423	0.359
Leucrocuta (E)	0.345	-0.463	-0.086	0.23	-0.0273
Paraleptophlebia (E)	**-0.654**	0.402	-0.251	0.234	0.263
Haploperla brevis (P)	0.345	**-0.575**	-0.276	-0.247	0.335
Diura bicaudata (P)	-0.123	0.344	0.442	-0.18	-0.412
Brachycentrus americanus (T)	-0.394	-0.261	-0.329	**-0.724**	-0.213
Arctopsyche ladogensis (T)	-0.125	0.356	0.431	-0.155	-0.485
Hydropsyche (T)	-0.485	0.298	-0.343	0.398	0.441
Psychoglypha (T)	-0.0479	0.119	-0.395	0.519	**0.599**
Rhyacophila (T)	-0.307	0.0384	-0.242	-0.277	-0.445
Alluaudomyia (D-C)	0.345	-0.475	-0.32	0.34	**0.653**
Cryptochironomus (C-CC)	**-0.597**	0.397	-0.218	0.147	-0.267
Demicryptochironomus (C-CC)	**-0.775**	0.358	-0.273	-0.245	-0.297
Dicrotendipes (C-CC)	**-0.571**	0.359	-0.221	0.1	-0.293
Cricotopus mackenziensis (C-O)	0.081	0.0168	-0.352	0.374	**0.803**
Heleniella (C-O)	0.456	-0.194	0.0612	0.0817	0.132
Heterotrissocladius (C-O)	0.384	**-0.686**	-0.261	0.314	0.111
Orthocladius lapponicus (C-O)	0.29	**-0.559**	-0.288	0.309	0.45
Orthocladius obumbratus (C-O)	0.388	**-0.594**	-0.351	0.156	**0.539**
Paramectriocnemus (C-O)	**-0.706**	0.329	-0.4	0.37	0.172
Paramectriocnemus graminocola (C-O)	-0.138	0.113	0.36	-0.418	-0.53
Paraphaenocladius (C-O)	0.0765	-0.321	-0.0629	-0.0567	-0.471

Table A9b, continued.

	Gradient	Width	Macrophytes	pH	SpecCond
Synorthocladius (C-O)	**-0.705**	0.456	-0.222	0.196	0.317
Larsia canadensis (C-T)	**-0.692**	0.451	-0.237	0.204	0.381
Paramerina (C-T)	0.00754	-0.287	-0.387	0.47	0.507
Arctopelopia (C-T)	0.222	-0.0883	-0.225	0.205	**0.678**
Hayesomyia (C-T)	**-0.602**	0.438	-0.411	0.405	**0.568**
Thienemannimyia (C-T)	-0.424	0.291	-0.403	0.374	**0.587**
Wiedemannia (D-E)	-0.135	0.425	0.323	0.0015	-0.49
Hexatoma (D-T)	**-0.593**	0.383	-0.185	0.169	0.266
Sperchon (Ha)	-0.089	0.0908	0.356	**-0.643**	-0.437
soft mites (Ha)	0.449	-0.324	-0.262	0.375	0.143
Planorbidae (M)	-0.444	0.296	-0.299	0.251	0.372
Cladocera (Cr)	-0.372	0.185	0.0654	-0.28	-0.0655
Cyclopoida (Cr)	0.0568	-0.269	-0.191	0.187	0.156

Table A9c – Abundance/environment correlations in the high-nutrient southern streams (HNSS). Significant correlations ($p < 0.05$) are in bold.

	Elevation	Gradient	Velocity	SpecCond	Nitrates
Ameletus (E)	0.0566	-0.731	**0.956**	-0.591	0.701
Baetis flavistraga (E)	-0.46	0.125	-0.796	**0.968**	-0.497
Baetis tricaudatis (E)	-0.306	-0.0311	-0.646	**0.967**	-0.433
Serratella (E)	0.146	-0.374	**0.869**	-0.547	0.192
Rithrogena (E)	0.806	-0.113	0.712	-0.743	-0.031
Leptophlebia (E)	0.0997	0.0233	-0.0425	-0.287	0.588
Haploperla brevis (P)	**0.819**	0.369	0.179	-0.647	0.0192
Brachycentrus americanus (T)	0.496	0.283	-0.324	0.152	-0.142
Hydropsyche morose (T)	-0.145	-0.678	0.465	-0.281	**0.907**
Optioservus (C)	-0.374	0.626	**-0.876**	0.612	-0.429
Neostempellina (C-CT)	0.165	0.15	0.292	-0.501	0.506
Tvetenia bavarica (C-O)	0.606	0.706	-0.0646	-0.423	-0.202
Tvetenia discoloripes (C-O)	-0.187	-0.433	-0.208	0.796	0.147
Conchapelopia (C-T)	-0.462	-0.678	-0.0855	0.709	0.292
Rheopelopia (C-T)	0.0416	-0.6	0.738	-0.404	0.789
Nematoda (N)	0.678	0.407	0.0144	-0.594	-0.0133

Table A9d – Abundance/environment correlations in the low-nutrient southern streams (LNSS). Significant correlations ($p < 0.05$) are in bold.

	Longitude	Gradient	Depth	Nitrates
Acentrella insignificans (E)	-0.217	0.609	0.0208	-0.597
Baetis spp. (E)	0.406	-0.117	**0.854**	-0.48
Baetis flavistraga (E)	**-0.86**	0.0575	-0.529	-0.0599
Haploperla brevis (P)	0.439	-0.417	0.249	0.252
Isogenoides (P)	-0.653	0.437	-0.482	-0.0151
Skwala americana (P)	-0.0576	0.158	0.234	-0.496
Glossosoma (T)	-0.137	0.322	0.367	-0.37
Polypedilum scalaenum (C-CC)	-0.177	0.312	0.475	-0.459
Rheotanytarsus (C-CT)	-0.0524	0.302	0.537	-0.437
Corynoneura (C-O)	-0.156	0.578	0.16	-0.428
Euryhapsis (C-O)	0.0835	0.238	0.39	-0.293
Thienemannimyia (C-T)	-0.106	-0.00307	0.433	-0.312
Simuliidae (D-S)	-0.263	0.642	-0.0567	-0.399
Hygrobates (Ha)	**-0.872**	0.281	-0.552	0.187
Cyclopoida (Cr)	0.124	0.259	0.483	-0.318
Nematoda (N)	-0.143	0.613	0.0616	-0.39

Appendix VII

Occurrence of rare taxa in the site groups

Table A10 – Occurrence of rare taxa (present at fewer than five sites total). Site group abbreviations are explained in Appendix I. Continued on the next four pages.

Family/tribe	Genus/species	FNS	MNS	SNS	HNSS	LNSS
Baetidae	*Acerpenna macdunnoughi*				Birch Crk	
	Acerpenna pygmaeus				Hornaday Crk, Jean-Marie Crk, Poplar R	
	Callibaetis sp.				Little Buffalo R	
	Centroptilum sp.					Red Knife tributary
	Diphetor hageni		Oscar Crk		Birch Crk	
	Procloeon sp.				Sandy Crk, Poplar R	
	Pseudocloeon sp.		Oscar Crk, Treeline Crk			
Caenidae	*Caenis sp.*		Oscar Crk		Sandy Crk	
Ephemerellidae	*Attenella sp.*				Trout R	
	Ephemerella inermis		Rengleng R, Stoney Crk			
	Ephemerella infrequens					Shale Crk
	Eurylophella sp.				Jean-Marie Crk, Poplar R	
Ephemeridae	*Ephemera sp.*				Jean-Marie Crk	Birch R
	Hexagenia limbata				Little Buffalo R, Hornaday R	
Heptageniidae	*Epeorus (Iron) sp.*		Canyon Crk, Chick Crk			
	Stenacron sp.		Stoney Crk, Jackfish Crk, Treeline Crk			
	Stenonema sp.	RPR-032			Bouvier Crk	Stream 7, Birch R, Upper Blackstone R
Trichorythidae	*Tricorythodes sp.*				Birch Crk, Sandy Crk, Hornaday R	
Leptophlebiidae	*Leptophlebia sp.*		Oscar Crk		Bouvier Crk, Poplar R	
Metretopodidae	*Metretopus sp.*		Oscar Crk, Canyon Crk			

Table A10, continued.

Family/tribe	Genus/species	FNS	MNS	SNS	HNSS	LNSS
Siphlonuridae	*Siphloplecton sp.*		Oscar Crk		Jean-Marie Crk	
	Parameletus sp.				Bouvier Crk	Birch R
Aeshnidae	*Aeshna sp.*		Oscar Crk		Hornaday R, Sandy Crk	
	Somatochlora minor				Hornaday R, Birch Crk	
Libellulidae	*Epitheca canis*		Oscar Crk			
Coenagrionidae	*Amphiagrion sp.*	RPR-099				
	Coenagrion/Enallagma sp.	RPR-099			Sandy Crk	
Lestidae	*Lestes unguiculatus*				Sandy Crk	
Capniidae	*Capnia sp.*		Helava Crk			Red Knife tributary, Stream 7, Stream 8
Chloroperlidae	*Sweltsa sp.*		Oscar Crk, Canyon Crk			
Leuctridae	*Zealeuctra sp.*			RPR-271		
Nemouridae	*Amphinemura linda*		Nello Crk, Stream 2		Sandy Crk	
Perlidae	*Claasenia sabulosa*				Bouvier Crk, Poplar R	
	Phasganophora/Agnatina sp.				Trout R	
Pteronarcyidae	*Pteronarcys sp.*		Oscar Crk		Bouvier Crk, Trout R, Jean-Marie Crk	
Corixidae	*Hesperocorixa sp.*				Jean-Marie Crk	
	Sigarra alternata	RPR-099			Hornaday R, Birch Crk	
	Trichocorixa borealis				Salt R	
Gerridae	*Limnoporus sp.*				Hornaday R, Birch Crk	
	Trepobates sp.				Hornaday R	
Macroveliidae	*Macrovelia sp.*	Travaillant R		RPR-271		Upper Blackstone R
	Oravelia pege			Stream 1, Stream 2		
Apatanidae	*Apatania sp.*	Travaillant R	Jackfish Crk			Birch R
Beraeidae	*Beraea fontana*					Upper Blackstone R
Glossosomatidae	*Anagapetus sp.*	RPR-075	Treeline Crk, Stream 2			Stream 8
Hydropsychidae	*Arctopsyche ladogensis*		Treeline Crk, Jackfish Crk, Rengleng R		Trout R	Birch R

Table A10, continued.

Family/tribe	Genus/species	FNS	MNS	SNS	HNSS	LNSS
	Cheumatopsyche sp.				Hornaday R, Trout R, Poplar R	
Hydroptilidae	*Agraylea*	RPR-048, RPR-058.6				Red Knife tributary
	Ithytrichia sp.				Hornaday R	
	Ochrotrichia sp.				Hornaday R, Jean-Marie R	
	Stactobiella sp.		Canyon Crk		Hornaday R	Stream 7
Lepidostomatidae	*Theliopsyche sp.*			Detthihi Dehe R		
Leptoceridae	*Ceraclea sp.*	Travaillant R	Oscar Crk, Jackfish Crk			Red Knife tributary
	Mystacides supulchralis	Travaillant R, RPR-099, RPR-006.1				
	Oecetis sp.	RPR-058.6			Hornaday R, Bouvier Crk	Red Knife tributary
Limnephilidae	*Clostoeca disjuncta*				Jean-Marie Crk	Stream 8
	Dicosmoecus obscuripennis	Yaya R, RPR-058.6				
	Glyphopsyche irrorata				Sandy Crk	
	Limnephilus	RPR-006.1				
	Nemotaulius sp				Hornaday R, Little Buffalo R	
	Philarctus quaeris	RPR-099				
	Sphagnophylax meiops	RPR-006.1, Hans Crk, RPR-048	Canyon Crk			
Molannidae	*Molannodes tincta*	RPR-006.1, RPR-099				
Philopotamidae	*Chimarra sp.*				Hornaday R, Jean-Marie Crk	Stream 6
	Doliphilodes sp.		Rengleng R, Treeline Crk		Hornaday R, Sandy Crk, Birch Crk	
	Wormaldia sp.				Hornaday R, Bouvier Crk	
Phryganeidae	*Agrypnia sp.*	RPR-006.1, RPR-099				
	Fabria inornata	RPR-006.1			Hornaday R, Little Buffalo R	
Polycentropodidae	*Neureclipsis sp.*	RPR-058.6			Sandy Crk, Jean-Marie Crk	Stream 7
	Polycentropus sp.				Birch Crk.	

Table A10, continued.

Family/tribe	Genus/species	FNS	MNS	SNS	HNSS	LNSS
Dytiscidae		Hans Crk, RPR-099, RPR-006.1, RPR-058.6, RPR-048	Vitrekkwa R, Oscar Crk, Canyon Crk	Detthihi Dehe R	Hornaday R, Salt R, Sandy Crk, Birch Crk, Little Buffalo R	
Elmidae	not *Optioservus sp.*		Oscar Crk, Rat R	Stream 3	Birch Crk, Bouvier Crk,	Birch R
Gyrinidae					Hornaday R	
Haliplidae					Sandy Crk	
Chaoboridae	*Chaoborus sp.*				Sandy Crk	
Chironomini	*Chironomus sp.*	RPR-006.1	Oscar Crk	Detthihi Dehe R		
	Cladopelma lateralis	RPR-006.1				
	Cryptotendipes sp.	Travaillant R	Oscar Crk			Red Knife tributary
	Endotribelos sp.		Oscar Crk			
	Einfeldia sp.	RPR-006.1, Zed Crk, RPR-075				
	Glyptotendipes sp.	RPR-058.6	Thunder R			
	Harnischia sp.		Tieda R		Little Buffalo R	
	Pagastiella sp.		Oscar Crk			
	Parachironomus sp.	Hans Crk, Travaillant R	Oscar Crk		Trout R	
	Paratendipes sp.		Oscar Crk		Trout R	
	Saetheria tylus	Travaillant R	Treeline Crk			
	Stenochironomus sp.				Bouvier Crk	
	Tribelos sp.	Yaya R	Rat R			
Pseudochironomini	*Psuedochironomus sp.*	Yaya R				
Tanytarsini	*Corynoneura sp.*	RPR-006.1				
	Neostempellina sp.		Oscar Crk		Bouvier Crk, Poplar R, Jean-Marie Crk, Trout R	
	Parapsectra sp.		Oscar Crk			
	Paratanytarsus sp.	RPR-006.1, Zed Crk, RPR-075			Sandy Crk, Salt R	Stream 6
Diamesinae	*Diamesa sp.*		Treeline Crk			
	Protanypus sp.	RPR-006.1, RPR-032, RPR-048, Nello Crk				

Table A10, continued.

Family/tribe	Genus/species	FNS	MNS	SNS	HNSS	LNSS
Orthocladiinae	*Cardiocladius sp.*		Thunder R, Helava Crk	Stream 1, Stream 3		Stream 8
	Chaetocladius sp.	Yaya R, Travaillant R		RPR-271	Birch Crk	
	Cricotopus (Isocladius) aricomalis	RPR-058.6, Zed Crk				
	Cricotopus (Isocladius) sylvestris				Salt R, Hornaday R	
	Heterotanytarsus sp.	RPR-006.1, RPR-048, Nello Crk				
	Limnophyes sp.	RPR-006.1, RPR-058.6	Oscar Crk			
	Pseudorthocladius sp.		Canyon Crk, Vermillion Crk			
	Psilomectriocnemus sp.	RPR-006.1, Yaya R				
	Rheocricotopus sp.		Oscar Crk	Detthihi Dehe R	Bouvier Crk	
	Xylotopus sp.		Canyon Crk			
	Zalutschia sp.	RPR-006.1, RPR-032, Zed Crk				
Podonominae	*Trichotanypus posticalis*			RPR-0271		
Prodiamesinae	*Monodiamesa tuberculata*		Rat R			
Tanypodinae	*Coelotanypus sp.*		Vermillion Crk			
	Labrundinia sp.		Oscar Crk		Hornaday R, Sandy Crk	Red Knife tributary
	Natarsia sp.		Oscar Crk			Birch R
	Pentaneura sp.	Nello Crk				Stream 7
	Psectrotanypus sp.	RPR-032				
Oreoleptidae	*Oreoleptis sp.*		Vermillion Crk			
Ancylidae					Jean-Marie R, Poplar R	Birch R
Hydrobiidae				Stream 3		
Valvatidae					Bouvier Crk	Red Knife tributary
Amphipoda	*Hyallela azteca*				Hornaday R, Salt R, Little Buffalo R	
	Monoporeia sp.				Hornaday R, Sandy R	
Choncostraca	*Lynceus brachyurus*			Stream 2	Birch Crk	

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