PALAEOCLIMATE ANALYSIS OF SOUTHWESTERN YUKON TERRITORY USING SUBFOSSIL CHIRONOMID REMAINS FROM ANTIFREEZE POND

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ABSTRACT

Freshwater midges, consisting of Chironomidae, Chaoboridae and Ceratopogonidae, were assessed as a biological proxy for palaeoclimate in Beringia. The Beringia training set consists of midge assemblages and data for 25 environmental variables collected from 121 lakes in Alaska, British Columbia, Yukon and the Northwest Territories. Canonical correspondence analyses revealed that lake depth, mean July air temperature and seven other variables contributed significantly to explaining the midge distributions. Weighted averaging partial least squares (WA-PLS) was used to develop midge inference models for transformed depth (ln (x+1); r^2_{boot}=0.431, and RMSEP=0.574) and mean July air temperature (r^2_{boot}=0.507, RMSEP=1.345°C).

Antifreeze Pond in the southwest Yukon provides one of the oldest lacustrine records in eastern Beringia, though a precise chronology for the lower core remains elusive. Mean July air temperature and lake depth were inferred for the record using the WA-PLS models as well as the Modern Analogue Technique (MAT). Midge analysis revealed a sequence of five distinctive biostratigraphic zones that show general agreement with an existing pollen record (Rampton, 1971). Midge inferences point to a transition from cold and arid to warm and likely wetter conditions in the lower core. Midge remains were extremely rare through the organic poor middle zone; extrapolation from adjacent zones points to temperatures at least 2-3°C below modern. Temperature warmed to modern by 12,500 ^{14}C yr BP, then cooled again from 10,800 to 8,500 ^{14}C yr BP. By 8,000 ^{14}C yr BP, inferred temperatures recovered to modern, and varied little through the rest of the Holocene.

DEDICATION

To my grandfather Maurice V. Smith
whose constant engagement with the natural world
is truly infectious.

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1 Introduction

Climate has always impacted humans, influencing both where we live at regional and global scales, and how we feed and shelter ourselves. Cultures have thrived during periods of climatic stability only to weaken or disappear with changes in temperature, precipitation, or frequency of climate driven disasters (Brenner *et al.*, 2002; Núñez *et al.*, 2002). For all of human existence, climate has been a dynamic system. However, it is only in the past century that we have really begun to understand the components and processes which influence climate, and to recognize the roles they play in driving climate change (Bradley, 1999).

With a growing understanding of climate comes a new awareness of the potential effects of global climate change. Changes in precipitation and temperature threaten current agricultural regions, clean water sources, and communities dependent on a stable sea-level (Government of Canada, 2003). Our greatest asset in dealing with these threats is an ability to foresee what changes will occur, and how they will unfold. This requires sound knowledge of past climates, in order to understand the long term cycles and patterns of climate change. It is only by studying past changes, and the effects these had on past peoples and environments, that we begin to understand our current predicament, and to properly prepare for the future.

During the Last Glacial Maximum[1] (LGM, 26,000 - 14,000 ^{14}C yr BP), much of the Northern Hemisphere was covered by glaciers that scoured away sediments, erasing the palaeoecological records they contained (Bradley, 1999). Undisturbed by these glaciers was Beringia, a region extending from the Yukon, through Alaska, across the exposed Bering Land Bridge and into Siberia. With sediments extending back through the late Pleistocene, Beringia is an extensive repository for palaeoclimatic and palaeoecological data (Elias, 2001a). Beringia is located at sub-arctic and arctic latitudes, making it particularly sensitive to climate change. Extensive permafrost and short growing seasons

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[1] Terminology follows Elias (2001a).

characterize the modern landscape, and even small changes in climate can have pronounced effects on the environment and the life it contains.

To date, palaeoclimates in Beringia have been inferred primarily from pollen records. The full glacial was cold and dry, with increases in temperature and moisture through the late glacial before reaching near modern conditions at the start of the Holocene (Elias *et al.*, 1996; Lozhkin *et al.*, 1993). However, the broad picture of climate painted by pollen records contributes little to the quantitative data needed to answer questions such as: how cold and dry was the full glacial? How rapidly did climate ameliorate through the late glacial? Was the amelioration punctuated by any reversals? Beetle data obtained by Elias (2000, 2001b), provide the first quantitative estimates of temperatures during the full glacial, suggesting summer temperatures 2-4°C colder, and winter temperatures 8°C colder than at present.

Chironomids, as well as Ceratopogonidae and Chaoboridae, constitute the freshwater midges, another insect group whose usefulness as a palaeoclimatic indicator has been demonstrated (Porinchu and MacDonald, 2003; Walker *et al.*, 1997). Chironomid-temperature transfer functions have been developed, that allow for the reconstruction of mean July temperatures with errors of less than 2°C (Porinchu and MacDonald, 2003). When applied to lake sediment records with good chronology, these provide excellent high resolution temperature reconstructions. Similarly, where significant changes in lake depth have occurred, chironomid-depth transfer functions can illustrate these changes (Korhola *et al.*, 2000). As an independent indicator of palaeoclimates, chironomids have the potential to contribute new and much needed high resolution data, and to further our understanding of the nature of past climate changes.

The objectives of the research presented here are two-fold: 1) to create midge-temperature and midge-depth transfer functions for western Canada and Alaska, and 2) to reconstruct palaeoclimates of Eastern Beringia from midge analysis of Antifreeze Pond in southwest Yukon.

2 Literature Review

2.1 Palaeoecology of Eastern Beringia

2.1.1 Geography

In 1937 Hultén hypothesized a land bridge connecting Alaska to Siberia and called this land Beringia, after the Bering Strait (in Hopkins, 1996). Since then, the concept of Beringia has expanded to include contiguous regions to the east and west that remained unglaciated during the last glacial period. The western limit of Beringia is recognized as the Lena River in Siberia. This is a practical boundary and somewhat arbitrary as the ice-free landscape continued and expanded westward into Eurasia, with glaciers restricted to the Chukotka Mountains (Alfimov and Berman, 2001). Eastern Beringia is more clearly demarcated by glacial boundaries along the Alaska and Coastal Ranges in the south, and in the east by the Laurentide Ice Sheet reaching to the eastern foot of the Richardson Mountains (Hughes, 1972).

Eastern Beringia's mountains run east-west with the Brooks and Cordilleran Range located in the north and the Alaska and Coastal Range in the south. Most other features such as the major river systems and vegetation zones, run parallel to the mountains. To the far north is tundra; between the mountain ranges, uplands and lowlands alternate and boreal forest dominates with regions of muskeg. Coastal forest is found along the southern (formerly glaciated) foot of the mountains (Anderson and Lozhkin, 2001; Ritchie, 1984).

The modern vegetation of Eastern Beringia consists mainly of boreal forest and tundra (Anderson and Lozhkin, 2001; Muhs *et al.*, 2001; and Ritchie, 1984). The forests are dominated by *Picea glauca* (Moench) Voss and *Picea mariana* Mill., and filled out by other tree species including *Larix laricina* (Du Roi) K. Koch, *Betula papyrifera* Marsh., *Populus balsamifera* L., and *Populus tremuloides* Michx. Tundra is found in the north, and at higher elevations. Poaceae and Cyperaceae dominate with shrubs of *Salix* and *Betula*. Other vegetational types are scattered across the landscape including fell-field at high elevations and steppe slopes in areas too dry to support trees (Laxton *et al.*, 1996).

Climate in Alaska and the Yukon varies with distance from the oceans and local topography. In the north, air temperatures are influenced by the perennially frozen Arctic Ocean and are cold year round. In most of the Yukon and central Alaska, a continental climate creates warm summers and cold winters, with a temperature range of 40°C between the warmest and coldest months (Phillips, 1990). High air pressure and long days provide abundant clear sunny skies and an accumulation of summer heat. In winter, temperature inversions can lead to cold air in the valleys, with less extreme temperatures at higher elevations. Precipitation is moderate and peaks in late summer. Topography also has a strong influence on precipitation, with the wettest regions located on the south and west slopes of mountains. In the south, Alaska is under a maritime influence, and has a more moderate climate. Precipitation increases with proximity to the Pacific; inland, moderate levels of precipitation peak in late summer. Permafrost ranges from continuous through most of the north, to sporadic in southern Yukon (Natural Resources Canada, 2003).

2.1.2 The Palaeoenvironment from 26,000 to 10,000 ^{14}C yr BP

For over a century, miners and researchers in Beringia have been digging up fossils belonging to an interesting and now extinct assemblage of large mammals including mammoths, camels, bison, mastodons, horses, saber-toothed cats, giant beavers, and saiga antelope. In 1968, Guthrie, a mammalogist, published the first of a series of papers that sparked a vigorous debate over the character of the full glacial landscape in Beringia. From fossil records, including tooth morphology and stomach content of some frozen specimens, and observations of close relatives of the extinct species, he determined that the large fauna was predominantly composed of grazers, and secondarily browsers (republished in Guthrie, 1996). Guthrie reasoned that a more productive than present vegetation must have been necessary to support the diversity and dietary requirements of this megafauna. Guthrie put forth the hypothesis that the fauna was supported by a 'mammoth steppe', an extensive grassland contiguous with that of Eurasia. He proposed (Guthrie 1982, 1985) that it had the following properties:

- fertile and productive soils capable of providing sufficient quality and quantity of forage
- herbaceous vegetation with lots of grasses that were high in nutrients, and low in antiherbivory components
- a deeper thaw and longer growing season than at present
- shallow snow cover (from low snowfall and/or windy conditions) to permit winter grazing and browsing by fauna
- a firm dry substrate to support the foot morphology of the fauna
- a diversity of habitats to support varying dietary requirements

In a series of publications, Ritchie and Cwynar (Cwynar, 1982; Cwynar and Ritchie, 1980; Ritchie, 1984; Ritchie and Cwynar, 1982) challenged Guthrie's proposal of a mammoth steppe, based on pollen analyses of cores from two northern Yukon lakes. For the herb zone (33,000 to 14,000 ^{14}C yr BP), they note low pollen influx values suggesting sparse vegetation. They found pollen taxa of arctic and alpine vegetation, and interpreted the *Artemisia* and grass dominated assemblage to be analogous to the modern fell-field vegetation of the surrounding area. They concluded that there was no productive mammoth steppe; on the contrary, a sparse tundra or polar desert covered the landscape of eastern Beringia.

The strong evidence of both healthy and complex megafaunal communities, coeval with sparse vegetation, presented an apparent productivity paradox (Schweger *et al.*, 1982). This controversy was the fuel of much debate, and culminated in a heated exchange of articles between Guthrie and palynologist Colinvaux (Colinvaux, 1986; Colinvaux and West, 1984; Guthrie, 1985). The debate eventually deteriorated into a semantic argument over the definition of 'tundra', until a compromise of sorts was reached with the adoption of the term tundra-steppe, long used by the Russians (or the North Americanized 'steppe-tundra'). This term suggests ecotones of cohabiting steppe and tundra species, and supports a mosaic interpretation of a landscape that could have contained both tundra and steppe-like patches (developed by Schweger and Habgood, 1976; reiterated by many including Ager, 1982; Anderson and Brubaker 1996; Mathewes, 1991; Schweger *et al.*, 1982).

While use of the term tundra-steppe has been widely adopted by proponents of both sides, the debate as to what exactly this tundra-steppe was, is far from over. General vegetation trends were noted by Livingstone (in Colinvaux, 1967) and classified into three consecutive zones: herb, birch and alder. The herb zone is a prominent feature in cores spanning the LGM, although it varies in its dating, composition, and interpretation. A selection of studies is summarized in Table 2.1. The dominance of herbs is apparent, with frequent high percentages of grasses and *Artemisia*. This is the zone that is central to the productivity paradox. The range of results, conspicuous absence of *Artemisia* in some cores, and various interpretations of pollen influx levels are at the heart of this debate.

During the late glacial period and leading into the Holocene is an interval commonly referred to as the Birch Zone (studies summarized in Table 2.2). The birch zone is generally interpreted to indicate an amelioration of climate indicated by higher pollen accumulation rates, and an increase of shrubs, particularly of *Betula* (Colinvaux, 1967; Eisner and Colinvaux, 1992; Oswald *et al.*, 1999).

Palaeoecologists have used pollen stratigraphies to make generalized landscape reconstructions in Beringia. Some studies note, and it should be emphasized, that there are limitations to interpretations of high-latitude pollen data that must be recognized in order to maximize the quality of interpretations (see especially: Anderson and Brubaker, 1996; Cwynar, 1982). The common use of stratigraphies comparing taxa by percentage can mask important quantitative information about pollen estimates that change over time. However pollen influx levels, used to measure quantitative abundance and total productivity (Cwynar, 1982), are also problematic (Guthrie, 1985). Pollen accumulation rates can vary greatly from year to year in surficial samples (Ritchie, 1977), and inaccurate or insufficient dates in a core will invalidate influx estimates. Typically, tree and shrub taxa are over-represented and pollen can be blown in from distant vegetation

Table 2.1 A selection of Beringian pollen studies covering the herb zone (approx. 30,000 to 14,000 ^{14}C yr BP).

AUTHOR	LOCATION	DATES (^{14}C YR BP)	ZONE	TAXA[1]	INTERPRETATION[2]
Summary in Lozhkin *et al.*, 1993	western Beringia, (3 sites)	27,000 to 12,500	herb	Poaceae Cyperaceae *Artemisia* Caryophyllaceae	
Lozhkin *et al.*, 1993	Jack London and Sosednee Lakes, Upper Kolyma, Russia	22,000 to 12,500	herb	*Artemisia* 20-60% *Betula* to 30% *Alnus* to 30%	Artemisia- Poaceae tundra; (harsh herb tundra)
Elias *et al.*, 1996	Bering and Chukchi Sea floors (10 cores)	20,000 to 14,000		*Betula* 15-60% Poaceae 28-44% Cyperaceae 13-30% Sphagnum 26-58%	birch-graminoid tundra
Eisner and Colinvaux, 1992	Oil and Feniak Lakes, N Alaska	dating unreliable	herb	Cyperaceae 10-34% Poaceae 8-35% *Artemisia* to 25% other herbs	discontinuous xeric herb tundra; Oil Lake similar to modern high tundra of Banks Island
Oswald *et al.*, 1999	Tukuto Lake, NW Alaska	30,000 to 10,000	herb	herbs dominant Cyperaceae to 35% Poaceae 10-55% *Salix* 10-25%	sparse xeric tundra changing to mesic tundra
Anderson *et al.*, 1994a	Joe Lake, NW Alaska	26,000 to 14,000 (approx)	herb	Cyperaceae 30-40% Poaceae 20-30% *Salix* 5-15%	temporal mosaic of tundras; herb, mesic, and graminoid tundras

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[1] All references to the family Gramineae were replaced with the updated family name Poaceae

[2] Interpretations are those of respective author(s)

Table 2.1 continued

AUTHOR	LOCATION	DATES(^{14}C YR BP)	ZONE	TAXA	INTERPRETATION
Short *et al.*, 1992	Nushagak and Holitna Lowlands, SW Alaska	poor dating	transition zone	herbs dominant *Artemisia* Poaceae Cyperaceae moderate shrubs	transition from dry graminoid tundra to birch zone
Lea *et al.*, 1991	Nushagak Lowland, SW Alaska	Beyond radiocarbon dating limits	Flounder Flat complex	Cyperaeae 14-60% Poaceae 22-68% *Salix* 4-22% *Artemisia* 3-13%	
Cwynar, 1982	Hanging Lake, N Yukon	33,000 to 18,450	herb	total herb >60% Poaceae >30% *Artemisia* 10-40% *Betula* 10-40%	sparse vegetation; like local modern fell-field
Cwynar, 1982	Hanging Lake, N Yukon	18,450 to 14,600	Salix-Cyperaceae	total herb 25-65% Poaceae 15-27% *Salix* to 35% Cyperaceae to 53%	tundra mosaic
Cwynar and Ritchie, 1980	Lateral Pond, N Yukon	15,500 to 12,500	herb	Poaceae to 40% Cyperaceae to 25% *Artemisia* to 40% other herbs	sparse, discontinuous vegetation; herbaceous tundra (uplands), sedge-grass meadows (lowlands)

Table 2.2 A selection of Beringian pollen studies covering the birch zone (approx. 14,000 to 10,000 ^{14}C yr BP).

AUTHOR	LOCATION	DATES (^{14}C yr BP)	ZONE	TAXA[1]	INTERPRETATION[2]
Lozhkin *et al.*, 1993	Jack London and Sosednee Lakes, Upper Kolyma, Russia	12,500 to 9200		*Betula* to 60% *Alnus* to 60% *Larix* *Salix*	*Betula-Alnus* shrub tundra, then *Larix dahurica* woodlands
Elias *et al.*, 1996	Bering and Chukchi Sea floors (64 cores)	14,000 to 9000	Alaskan Birch	*Betula* 15-60% Poaceae 20-40% Cyperaceae 10-30% *Sphagnum* 5-50%	birch-heath-graminoid tundra with ponds
Eisner and Colinvaux, 1992	Oil and Feniak Lakes, N Alaska	dating unreliable	Birch	*Betula* to 70% Cyperaceae 15-50% *Alnus* to 30% *Salix* to 15%	
Eisner, 1991	Imnavait Creek, N Alaska	11,000 to 8000	Birch	*Betula* to 80% Cyperaeae 200%? Poaceae to 15% *Salix*	tundra mosaic of herb and shrub assemblages
Hu *et al.*, 1993	Wien Lake, central Alaska	12,500 to 10,500	Birch	*Betula* 65-75% Cyperaceae 10-20% *Salix* 10%	shrub *Betula* tundra; tussock tundra in mesic microsites

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[1] All references to the family Gramineae were replaced with the updated family name Poaceae

[2] Interpretations are those of respective author(s)

Table 2.2 continued

AUTHOR	LOCATION	DATES (^{14}C yr BP)	ZONE	TAXA	INTERPRETATION
Oswald *et al.*, 1999	Tukuto and Etivlik Lakes, NW Alaska	13,000 to 8000	Birch	*Betula* 20-50% Cyperaceae 20-45% *Salix* 15% *Populus*	mesic shrub tundra
Anderson *et al.*, 1994a	Joe Lake, NW Alaska	14,000 to 10,000	transitional	*Betula* 35-75% *Salix* 5-20% Cyperaceae 5-35% Poaceae 5-30%	*Betula* shrub tundra, and *Populus* woodland-*Betula* shrub tundra
Short *et al.*, 1992	Nushagak and Holitna Lowlands, SW Alaska	unreliable dating	Birch	*Betula* 30% Poaceae 25-40% Cyperaceae 7-25%	diverse, mesic, birch shrub tundra
Lacourse and Gajewski, 2000	Sulphur Lake, SW Yukon	11,250 to 10,250	Birch	*Betula* to 81% *Salix* 5-13% *Populus* *Alnus*	birch shrub tundra
Cwynar, 1982	Hanging Lake, NE Yukon	14,600 to 11,100	Birch	*Betula* to 80% herbs 20% *Salix* 10%	tundra with birch microhabitats
Cwynar, 1982	Lateral Pond, NE Yukon	12,500 to 7000	Birch	*Betula* to 70% *Salix* to 20% *Picea* to 20% herbs	shrub tundra; birch-heath shrub tundra on mesic sites, herb tundra on xeric sites

(Ritchie, 1977); insect pollinated taxa are rare. The minor presence of taxa with low pollen production rates can provide valuable information, and should be given consideration (as in Anderson *et al.*, 1994a; Cwynar, 1982; Cwynar and Ritchie, 1980). Taxonomic resolution has improved for some taxa (Brubaker *et al.*, 1987), while others remain undifferentiated and have broad ecological requirements that require careful consideration. Cwynar (1982) makes the point for *Artemisia*, commonly interpreted to represent steppe, whose different species are found on dry hills as well as riverbanks.

Integration of additional data sources into reconstructions is providing some excellent results. Elias *et al.* (1996) analysed pollen, macrofossils and insect assemblages from 20 cores retrieved from the Bering and Chukchi sea floors. Birch-graminoid tundra was interpreted from pollen, while macrofossils gave evidence of aquatic plant communities in small ponds. Insects indicated an arctic climate, and gave strength to his vegetation reconstructions. A mere 100 km away, a wealth of plant macrofossils has provided excellent local species specific data for vegetation reconstructions on the Seward Peninsula. Goetcheus and Birks (2001) recovered macrofossils from a preserved landscape buried at 18,000 ^{14}C yr BP by the Devil Mountain Lake tephra. *Kobresia* and *Draba* were dominant in the graminoid and forb rich vegetation. The soils were dry, alkaline, calcareous, and enriched with loess. This interpretation conjures up images of Guthrie's mammoth steppe. The sharp contrasts in these two sites with species specific data, and their strongly supported interpretations, add fuel to the fires of debate, and reinforce the dangers of making landscape level extrapolations from individual sites.

One of the few issues agreed upon by all parties in the tundra-steppe debate is that it has no exact modern analogue. Partial analogues, relics, and elements of tundra-steppe have been proposed in abundance. In the Kluane Lake region of the Yukon, Laxton *et al.* (1996) found increased grassland productivity (measured as biomass) at sites with active loess deposition. Walker *et al.* (2001) find analogous properties to Guthrie's steppe in what they term moist nonacidic tundra: vegetation with high vascular plant species richness, few antiherbivory chemicals and more nutrients, on calcium rich, moderately alkaline soils with sufficiently deep active layers. Inferred steppe relics have been noted in Siberia (Alfimov and Berman 2001; Yurtsev 2001), as well as on south facing bluffs of interior Alaska and Yukon (Edwards and Armbruster, 1989; Schwarz and Wein, 1997; Yurtsev, 2001).

2.1.3 The Palaeoclimate from 26,000 to 10,000 ^{14}C yr BP

The diversity of vegetation reconstructions leads to a fairly singular interpretation of the Beringian climate during the LGM: it was cooler and more arid than at present (Cwynar, 1982; Elias *et al.*, 1996; Lozhkin *et al.*, 1993; Oswald *et al.*, 1999). Windswept conditions were interpreted at some sites (Goetcheus and Birks, 2001; Oswald *et al.*, 1999). These could have lead to differential snow depths (Oswald *et al.*, 1999), and spring patches with varying moisture availability supporting the dry and mesic plant communities identified (Goetcheus and Birks, 2001). Winds are also believed to have carried loess that enriched soils (Goetcheus and Birks, 2001). In a review of 24 Alaskan sites, Anderson and Brubaker (1996) found east to west trends with colder and drier conditions in the east (also Lozhkin *et al.*, 1993). This is supported by data from Elias (1992) that indicates a maritime influence in southwestern Alaska, with more mesic conditions than the interior. Likewise, Alfimov and Berman (2001) summarize support for a cold maritime climate for the Land Bridge itself, characterized by cold wet summers, and catabatic winds in winter.

The palaeoclimate reconstruction of the palynologists agrees well with that of Guthrie (2001) and Vereshchagin and Baryshnikov (1982) based on interpretations of the megafauna's environmental requirements. LGM fauna such as horse, bison, musk ox and mammoth are well insulated with thick fur coats that enable them to withstand very cold temperatures. A difference in fur structures for the megafauna compared with those from modern arctic fauna suggests cooler temperatures than present. The greatest challenge to survival was likely access to winter food sources (Guthrie, 1985). The requirement for bare patches of ground or soft shallow snow cover implies dry windswept conditions (also Guthrie, 1985). In summer, firm dry ground was necessary to support the small hooves of the ungulates, most notably of horse and bison.

Through the late glacial and extending into the Holocene, climate change is noted. The birch zone indicates widespread warming and increased precipitation (Cwynar, 1982; Cwynar and Ritchie, 1980; Eisner and Colinvaux, 1992; Elias *et al.*, 1996; Oswald *et al.*, 1999; Short *et al.*, 1992). Some interpret warming to levels greater than present (Elias, 2000; Lozhkin *et al.*, 1993). Deeper thawing of permafrost likely resulted from the increased temperatures (Oswald *et al.*, 1999), and insulation from the increased snow cover (Short *et al.*, 1992).

Insect assemblages are being used to generate quantitative data on climate. Elias (2000, 2001b) found that summer temperatures for the LGM in Alaska were colder than modern by 2-2.5°C in Western Alaska, and 4°C in the interior. Winter temperatures were 8°C colder in both regions. Temperatures rose rapidly after 12,000 ^{14}C yr BP, peaked as much as 5-7°C above modern temperatures at 11,000 ^{14}C yr BP, and show a sharp cooling concurrent with the Younger Dryas event of 11,000 to 10,000 ^{14}C yr BP. Engstrom *et al.* (1990) also interpret a Younger Dryas record at 10,800 to 9,800 ^{14}C yr BP from a vegetation reversal in their south Alaskan core, although more evidence is needed before any conclusions can be drawn about such a signal in Beringia.

2.2 Chironomids as Indicators of Past Environments

2.2.1 Chironomids in Lake Sediments

The family Chironomidae, commonly referred to as non-biting midges, belongs to the order of true flies (Diptera). While the adult is airborne, the life cycle is dominated by an aquatic larval stage. The larvae have hard, chitinous head capsules, which are shed as the larvae literally outgrow their head capsules, and progress through four instar stages. The chitin in the head capsules is chemically inert, and the head capsules preserve well for tens of thousands of years (Frey, 1976).

These head capsules are ubiquitous in lake sediments, and typically dominate the invertebrate subfossil assemblages. With an estimated 15,000 plus species, chironomids can be found on all continents, and can tolerate environmental extremes such as those found in arctic ponds, saline lakes, at high altitudes, and at great depths (Cranston, 1995).

2.2.2 Sensitivity to Environmental Variables

Chironomid species are sensitive to environmental conditions, and the composition of taxa in a given sediment provides information about the environmental conditions in which the chironomids lived. Chironomid assemblages have been demonstrated to vary with temperature, oxygen level, salinity, acidity, and trophic status (Walker, 1995). Some environmental factors are represented by indicator taxa, as for example the halobiont *Cricotopus ornatus* Meigen, or members of the subfamily Diamesinae which are cold stenothermic. Where conditions allow for the deposition of undisturbed sediment over time, chironomid assemblages with radiocarbon dates can provide information about changing palaeoenvironmental conditions.

The abundance and wide distribution of chironomids combine with aspects of their life cycle to make them excellent proxy indicators. The mobility of the adult stage allows them to quickly disperse and re-colonize lakes as favourable conditions allow (Solem *et al.*, 1997). Generation times range from a few months to a few years (Tokeshi, 1995), and enable chironomids to respond rapidly to environmental changes.

For decades, literature accumulated documenting the relationships between chironomids and environmental factors such as oxygen availability (Carter, 1977), salinity (Cannings and Scudder, 1978; Heinrichs *et al.*, 1999), anthropogenic eutrophication (Dévai and Moldován, 1983; Wiederholm and Eriksson, 1979), acidification (Brodin and Gransberg, 1993; Henrikson *et al.*, 1982), lake siltation (Hofmann, 1983; Warwick, 1989), and climatic conditions (Hofmann, 1983; Walker and Mathewes, 1989a). With chironomids showing responses to so many related environmental variables, debate arose over which factors were most strongly influencing changes in chironomid distribution, especially through the late glacial.

2.2.3 Transfer Functions

This debate prompted Walker *et al.* (1991) to undertake the first study using multivariate statistics to explore the relationship between midge assemblages and various environmental variables. Walker *et al.* collected environmental data and sediment samples from 24 lakes along a north-south transect in Labrador. They found that midge assemblages correlated most strongly with lake surface-water temperature, and created the first midge transfer function from this data set.

The use of midge transfer functions for inferring past temperatures has endured controversy (Hann *et al.*, 1992; Korhola *et al.*, 2001; Seppälä, 2001; Walker and Mathewes, 1987, 1989b; Walker *et al.*, 1992; Warner and Hann, 1987; Warwick, 1989). The ecology of chironomids, including their relationship with temperature is poorly understood. However, despite these unknowns, transfer functions appear to 'work' for numerous biological proxies, and are now widely accepted by palaeoecologists (Ammann, 2000; Battarbee, 2000; Pienitz *et al.*, 1995). Several midge transfer functions have been published for parts of North America, and Europe. These have been used to reconstruct not only summer surface water temperature, but also mean July air temperatures and lake depth. The application of these midge transfer functions have provided high resolution quantitative estimates of past temperatures for numerous regions and have also been used to detect climatic events such as the Younger Dryas (Brooks and Birks, 2000; Cwynar and Levesque, 1995; Lotter *et al.*, 2000) and the Killarney Oscillation in North America (Levesque *et al.*, 1993).

3 Development of Midge Inference Models for Beringia

3.1 Introduction

Palaeoecologists seeking to quantify past environmental changes are relying increasingly on transfer functions that make use of biological proxies (Battarbee *et al.*, 2002; Lotter *et al.*, 1997). Midges have been shown to be an excellent proxy organism for climate, and have been used in transfer functions to reconstruct summer water and air temperatures (Brooks and Birks, 2001; Olander *et al.*, 1999; Walker *et al.*, 1997), and lake depth (Korhola *et al.*, 2000).

In addition to climate, the biogeographical distribution of chironomids can be affected by limits to the dispersal of certain species. For example, in Canada *Corynocera ambigua* is common and abundant in lakes of the northwest, but is absent east of Hudson Bay despite comparable temperatures and a range of lake depths. Regional limnological trends in variables such as extremes in chemistry or salinity also influence midge distribution, and can override the impacts of climate (Walker, 1995). To minimize the confounding influence of these factors, regional temperature models have been created for application in eastern Canada (Walker *et al.*, 1991, 1997), Switzerland (Lotter *et al.*, 1997), northern Fennoscandia (Olander *et al.*, 1999), and Norway (Brooks and Birks, 2001).

Alaska and Yukon form the eastern portion of Beringia, a region that remained unglaciated through the LGM. The sediments of this region are of great value for their potential to provide continuous palaeoclimatic records for the arctic extending back through the LGM. Few quantitative palaeoclimatic data exist for this region; no chironomid temperature or lake depth reconstructions have yet been published. The potential of midges as indicators in the Yukon and adjacent Northwest Territories (NWT) was explored by Walker *et al.* (2003). In this data set of 56 lakes from Whitehorse to Tuktoyaktuk, midge assemblages were statistically compared with 35 environmental variables.

The models presented here expand on the results of Walker *et al.* (2003). Lakes from Alaska and British Columbia (BC) are added to the data set, and temperature and depth transfer functions are created and tested. The inclusion of sites from a broader geographical area make these new models well suited for reconstructing temperature and lake depth throughout eastern Beringia.

3.2 Methods

3.2.1 Study Area

Data were collected from 147 lakes in northwest Canada and Alaska. The majority of these lakes fall along a roughly north-south transect, extending from Tuktoyaktuk, NWT to central BC 3000 km farther south (Fig. 3.1). The remainder of the sites form a parallel transect through the centre of Alaska. Collectively, these sites cover a range of latitude of 20°, longitude of over 30°, and are distributed through 6 ecozones in Canada alone (Natural Resources Canada, 2003).

At the north end of the range, sites are within the Arctic Circle, and lie within kilometers of the Beaufort Sea, frozen for over 8 months of the year (Natural Resources Canada, 2003). The landscape is treeless, and the tundra is underlain by permafrost. The arctic waters provide some moderating effect on climate, and temperatures at near-coastal sites are cold, though not extreme, year round. On the Tuktoyaktuk Peninsula, lakes are ice-free from late-June to early-October (Pienitz *et al.*, 1997). Farther inland, sites are subjected to some of the most extreme temperature ranges in Canada with a greater than 40°C difference between the mean temperatures of the warmest and coldest months (Phillips, 1990). Precipitation is low (about 300 mm per year) and falls mostly during late summer (Phillips, 1990). In contrast, the southern sites of central interior BC are located in evergreen needleleaf forest that is free of permafrost. Summer temperatures of 15°C are only ~4-5°C warmer than the northernmost sites, but with averages of about –8°C in the winter, are 20°C milder. Interior BC is also relatively dry with an annual precipitation of about 400 mm.

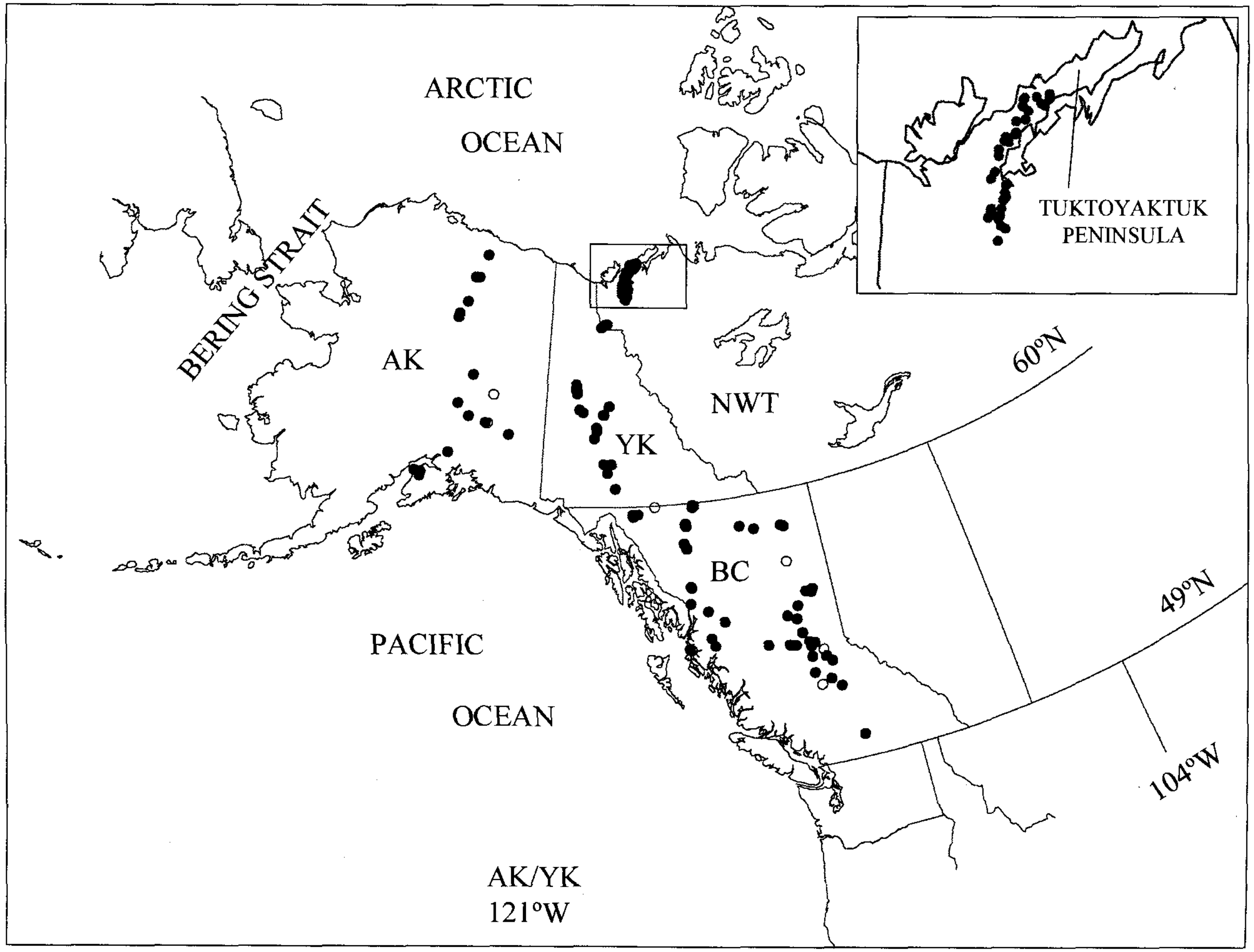

Figure 3.1 Location of the 121 lakes of the Beringia training set. Outliers are identified by open circles.

Between these north and south endpoints, climate and vegetation vary with latitude, elevation and topography. Elevation for all sites ranges from near sea-level to 1619 m asl. Alpine tundra is found at high elevation sites in the mountainous regions. Most sites are subject to a continental climate, with large daily and seasonal fluctuations. Winters are long and cold; summers are short and warm. Conditions are generally dry, with most of the precipitation falling during late summer.

Lakes selected for this study were ideally small, shallow and undisturbed. Lakes with little or no inflow were sought to ensure that all midge assemblages were influenced primarily by the local limnological and environmental data collected. Practical considerations dictated that most sites were also accessible by road.

The sites included in this model represent a compilation of 3 independent data sets. The 56 sites in the Yukon and adjacent NWT were collected in July 1990 by inflatable boat and on the Tuktoyaktuk Peninsula by helicopter. Chemical, diatom and midge data for these sites have previously been published (Pienitz *et al.*, 1995, 1997; Walker *et al.*, 2003). Samples and data from the Alaska sites were collected in summer of 1996. Midge analysis of 34 Alaskan lakes is presented here; chemical and diatom data for these and other lakes exist elsewhere (Gregory-Eaves *et al.*, 1999, 2000). These transects were extended south in August of 2001, with the addition of 57 BC lakes between Kelowna and Whitehorse. Data from the BC lakes are presented here for the first time. Most lakes are unnamed, and all are referred to by number (Alaska sites are prefaced by 'AK', BC by 'KW', and Yukon/NWT by 'U').

3.2.2 Midge Analysis

Sediment for midge analysis was obtained using a Kajak-Brinkhurst (Glew, 1989) or mini-Glew (Glew, 1991) gravity sediment corer. Samples were taken from approximately the deepest part of each lake, with the exception of lakes whose depths exceeded the 30 m limits of sampling equipment.

For each core, the top 1 cm of sediment was extruded on site, transferred to a Whirlpak® bag, and kept cool until analysis at a later date. The volume of sediment available for analysis varied among data sets depending on the type of corer and number of cores taken. For BC and Yukon/NWT, additional intervals of sediment were also extruded, and stored individually.

In the laboratory, midges were processed for picking following the protocol outlined by Walker *et al.* (1991). Samples were treated with warm 5% KOH to deflocculate sediment, and 10% HCl to dissolve carbonates. After each treatment, the samples were washed with de-ionized water on a 95-μm mesh sieve. The residue remaining on the sieve was transferred in small portions to a Bogorov tray for examination under a dissecting microscope. Head capsules of chironomids and ceratopogonids, as well as mandibles of chaoborids were picked, mounted on coverslips and preserved with Entellan® for identification at a later date.

Chironomids were identified primarily with reference to Oliver and Roussel (1983), Walker (1988, 2000) and Wiederholm (1983). Chironomid head capsules were only rarely identified to species, and more often to genus, or to groups of species or genera. A complete list of taxa and identification notes can be found in Appendix 1. Chironomid head capsules are often fragmented, especially those belonging to the subfamilies Tanypodinae and Orthocladiinae. Tanypodinae are often missing parts; provided there were sufficient parts for them to be identified, they were always counted as whole. For consistent and precise counting of all other subfamilies, fragments of head capsules without the median teeth were not counted (except *Cladopelma* and *Cryptochironomus* which are easily identified by the lateral teeth), those with exactly half the mentum were counted as a half, and those with all median teeth were counted as whole. Each ceratopogonid head capsule, and *Chaoborus* mandible was counted as an individual.

All samples from the Yukon/NWT data set were previously processed, mounted and identified. Detailed records of identifications and counts were compared with the taxonomy and counting procedures described above. Identifications were verified for several lakes to ensure consistent taxonomy, and specimens of less common taxa (for example *Apedilum*, *Derotanypus*, *Lasiodiamesa*, *Mesocricotopus*, *Metriocnemus*, *Pseudodiamesa*) were verified in all lakes. Taxonomy was harmonized, for example '*Dicrotendipes/Einfeldia/Glyptotendipes*' was lumped with *Glyptotendipes*, and the 3 different types of *Zalutschia* were matched up with those in the model. Tanytarsina were also lumped to match the groupings used in the model.

A minimum count of 75 identifiable chironomids per sample was used. This value was chosen as a conservative estimate of the number of head capsules required to be statistically representative of a given lake (Heiri and Lotter, 2001; Quinlan and Smol, 2001). The volume of sample required to meet this criterion ranged from 1 mL to over 30 mL, and depended on the characteristics of the lake as well as the water content of the sample. Samples were first processed from the 0-1 cm interval, and where needed, sediment from subsequent intervals was added to bring up the chironomid count. A number of lakes had low yields of chironomids and were excluded from further analysis. Reasons for low yields were apparent for some lakes (proglacial - KW18; man-made industrial lake - KW16; small sample volumes - AK17, AK21, AK23, AK28, AK32-34, AK36, AK37, AK40, AK42, AK44, AK45, AK48, KW17) but unknown for others (U08, AK27, AK41, AK51, KW09, KW22, KW36, KW37, KW47). One hundred and twenty one lakes met the 75 capsule criterion, and constitute the sites of the Beringia training set.

3.2.3 Environmental Variables

Physical, chemical and environmental data for the Alaska and the Yukon/NWT data sets were collected as part of independent studies, and are presented in greater detail elsewhere (Gregory-Eaves *et al.*, 2000; Pienitz *et al.*, 1997). For the purpose of simplification, only the 25 variables with data available for all 3 data sets (and values above the limits of detection in >50% of lakes) are described here (Table 3.1). Physical and environmental data were obtained from topographical maps (1:50 000) or collected in the field. Latitude (LAT) and longitude (LONG) were obtained at each site using a hand held geographical positioning system, and recorded in decimal format.

Table 3.1 The Beringia training set: environmental, limnological and chemical data for 121 lakes.

Lake	LAT	LONG	ELEV	SA	DEPTH	SECCHI	pH	COND	vegetation	JTEMP	Ca	Cl	Fe	K	Mn	Na	SO4	SiO2	TPU	TPF	DOC	DIC
	°N	°W	m	ha	m	m		uS/cm		°C	mg/L	mg/L	ug/L	mg/L	ug/L	mg/L	mg/L	mg/L	ug/L	ug/L	mg/L	mg/L
AK07*	64.12	145.50	290	29	4.0	2.6	8.3	132	FOREST	15.6	17.0	1.5	235	5.5	8	2.0	7.9	0.2	475.8	<0.2	257.0	16.0
AK13	64.52	147.52	160	9	4.0	0.7	9.3	75	FOREST	16.2	4.6	4.3	241	2.3	10	4.8	11.6	0.3	54.5	16.2	28.8	6.0
AK14	63.39	148.49	625	2	4.5	3.7	7.7	94	L-WOOD	13.2	13.2	1.1	98	0.9	6	2.2	7.4	0.3	11.3	6.0	19.0	12.0
AK19*	63.03	146.00	851	142	25.0	2.5	8.1	68	T-ALP	12.0	8.7	2.1	43	0.5	5	1.9	3.3	5.0	27.7	6.0	21.7	9.5
AK20	63.04	146.11	1029	17	3.0	3.0	7.5	6	T-ALP	11.6	0.3	0.2	22	0.2	1	<0.2	1.7	0.8	8.1	3.3	2.9	2.0
AK22	62.42	144.04	713	106	2.0	2.0	9.1	208	FOREST	13.5	30.3	0.6	25	1.3	13	3.9	36.8	2.1	19.3	7.5	20.0	19.5
AK24	66.58	150.23	395	40	1.2	1.2	7.5	21	L-WOOD	13.5	3.2	1.1	316	0.2	8	0.3	2.1	0.3	25.1	5.3	7.1	4.1
AK25	67.08	150.21	320	4	3.0	1.4	8.1	172	L-WOOD	14.8	29.0	0.4	208	0.4	20	0.7	7.7	0.8	21.1	9.8	192.0	23.9
AK26	67.39	149.44	431	17	0.8	0.8	8.4	324	L-WOOD	12.9	50.0	1.4	66	0.6	13	0.7	43.1	1.6	14.9	6.6	24.4	37.5
AK29	68.41	149.05	777	4	20.0	8.0	8.0	122	T-ARC	11.0	23.0	0.4	20	0.3	4	0.3	8.8	1.6	6.6	2.8	6.5	15.7
AK30	68.39	149.28	800	13	11.0	2.7	7.3	7	T-ARC	10.9	2.0	0.2	117	0.2	47	<0.2	<0.2	1.6	9.0	13.8	81.6	1.1
AK31	69.35	148.38	148	37	2.1	2.1	8.2	180	T-ARC	12.0	36.2	4.3	111	0.4	11	0.5	5.0	1.2	10.8	4.2	12.8	25.1
AK38	63.13	147.41	930	1	2.3	2.3	7.7	12	T-ALP	12.3	1.9	0.2	57	0.7	4	0.2	7.2	0.2	14.8	3.4	14.2	2.9
AK43	61.40	148.52	61	2	3.1	3.1	8.1	77	FOREST	11.6	16.6	0.7	22	0.3	1	0.6	5.8	2.9	1.3	1.2	9.2	10.2
AK46	60.32	150.50	71	35	6.0	3.9	7.8	28	FOREST	13.1	3.1	2.0	14	0.9	3	1.2	0.7	0.2	8.9	4.7	86.3	5.0
AK47	60.42	150.48	74	109	30.0	7.5	7.0	31	FOREST	14.8	4.1	1.3	10	0.6	3	1.0	1.7	0.2	3.3	2.1	105.0	5.1
AK50	60.42	151.19	35	3	2.6	2.3	7.1	12	FOREST	13.5	0.9	1.8	51	0.5	12	0.9	1.0	0.1	18.3	2.3	137.0	3.6
U03	60.44	135.02	625	21	17.5	5.0	8.5	490	FOREST	13.4	26.7	1.5	11	4.3	7	16.3	82.1	12.5	6.5	4.5	7.8	52.9
U05	61.42	135.17	1021	53	12.0	2.3	7.8	73	FOREST	11.8	16.6	0.6	76	0.6	4	2.0	3.9	7.9	8.7	4.9	8.6	12.4
U06	61.21	135.39	823	89	49.0	3.2	8.3	179	FOREST	12.4	44.2	0.9	16	1.2	12	4.6	24.5	9.3	5.1	4.3	10.1	33.1
U07	61.42	135.56	634	163	27.0	10.8	8.3	230	FOREST	13.6	50.3	0.9	6	1.9	7	7.6	29.0	9.2	4.9	3.5	8.4	40.8
U09	62.43	136.41	579	332	3.0	1.9	8.7	220	FOREST	14.8	37.6	1.3	17	2.8	21	4.3	23.8	7.3	15.4	0.2	26.9	30.8
U10	63.01	136.28	655	89	8.0	4.4	8.6	242	FOREST	14.3	37.7	1.5	6	2.9	17	4.4	28.9	6.5	12.0	8.1	14.2	35.1
U11	63.09	136.30	732	9	5.0	3.3	8.5	49	FOREST	14.2	7.8	4.2	50	1.6	adl	0.7	2.0	0.2	12.3	9.0	17.1	3.8
U12	63.39	135.54	579	23	9.2	6.0	8.4	149	FOREST	15.3	31.0	1.0	27	1.5	11	1.3	0.5	3.1	8.7	5.5	13.5	22.5
U13	63.59	135.24	701	10	10.1	3.6	7.8	45	FOREST	14.5	7.3	0.5	37	0.5	4	0.4	2.8	0.2	9.8	5.6	16.2	4.6
U14	63.59	135.22	701	23	16.5	11.5	8.3	260	FOREST	14.4	45.4	0.4	10	1.6	7	3.7	57.1	8.8	4.3	2.9	15.9	35.1
U15	63.39	135.51	594	24	3.0	1.5	7.5	46	FOREST	15.3	8.6	0.9	165	1.1	18	0.5	4.2	0.2	28.8	13.9	24.2	4.2
U16	63.45	137.43	610	80	5.0	2.8	7.6	42	FOREST	15.1	6.8	0.5	124	1.6	21	0.9	0.5	1.0	21.6	11.4	15.3	4.9
U17	63.51	138.02	610	19	7.0	1.7	8.2	24	FOREST	14.8	3.5	0.7	134	1.3	19	0.8	0.5	0.2	25.0	13.0	18.1	2.2
U18	64.35	138.18	1173	18	7.5	4.6	8.6	113	T-ALP	9.9	23.0	0.3	57	0.4	35	3.7	11.5	2.0	11.4	6.2	6.5	18.1
U19	64.39	138.23	1128	20	3.8	3.2	8.7	111	T-ALP	10.5	31.6	0.4	35	0.6	11	3.4	9.0	2.0	10.0	6.9	10.2	20.5

Table 3.1 continued

Lake	LAT °N	LONG °W	ELEV m	SA ha	DEPTH m	SECCHI m	pH	COND µS/cm	vegetation	JTEMP °C	Ca mg/L	Cl mg/L	Fe µg/L	K mg/L	Mn µg/L	Na mg/L	SO4 mg/L	SiO2 mg/L	TPU µg/L	TPF µg/L	DOC mg/L	DIC mg/L
U20	64.44	138.22	1097	14	1.9	1.9	9.3	39	T-ALP	11.3	9.7	0.4	664	0.1	22	0.3	1.9	0.4	23.1	14.1	12.3	5.7
U21	64.51	138.21	1006	144	3.8	3.7	7.5	32	T-ALP	11.3	5.8	0.6	127	0.4	17	0.3	4.1	0.3	7.8	4.9	11.4	3.8
U22	68.11	133.27	76	8	5.5	4.1	7.9	153	L-WOOD	13.4	39.2	6.1	53	1.0	11	2.3	38.9	3.2	10.3	7.9	17.8	14.4
U23	68.18	133.16	30	7	2.5	1.8	7.2	72	L-WOOD	13.4	13.9	3.7	287	0.7	11	1.6	13.2	0.9	17.5	11.3	10.6	4.6
U24	68.19	133.22	91	15	2.8	1.1	6.9	35	L-WOOD	12.9	6.5	2.0	1280	0.8	33	1.3	5.2	2.4	44.9	34.1	22.6	4.0
U25	68.24	133.42	122	1	3.0	3.0	7.8	140	L-WOOD	12.5	20.2	3.2	136	2.1	20	8.3	32.6	0.6	16.1	12.1	13.1	11.5
U26	69.28	132.49	18	85	2.0	2.0	8.1	100	T-ARC	9.6	9.1	15.4	170	1.1	14	8.2	1.9	0.1	15.3	7.1	6.6	6.3
U27	69.32	132.47	15	95	2.0	1.0	8.0	343	T-ARC	9.4	43.8	74.9	754	3.2	16	33.4	17.9	0.3	19.8	8.0	12.3	27.7
U28	69.33	132.45	15	170	2.0	1.2	7.8	145	T-ARC	9.3	19.3	18.9	376	1.8	13	9.4	6.0	0.3	16.7	8.1	6.7	12.9
U29	69.33	132.25	15	547	2.0	2.0	8.1	152	T-ARC	9.3	20.8	18.7	66	0.9	11	10.3	1.1	0.1	9.2	4.8	5.8	17.5
U30	69.35	132.04	21	196	4.0	3.2	8.0	179	T-ARC	9.2	26.9	21.4	81	1.2	11	10.4	24.7	0.1	12.6	6.0	18.2	19.6
U31	69.32	132.04	21	58	3.0	2.8	8.1	165	T-ARC	9.4	24.7	16.3	45	1.4	7	9.0	10.5	0.2	6.6	3.7	8.0	19.2
U32	69.28	132.12	21	74	9.0	6.0	8.0	198	T-ARC	9.6	36.2	13.2	16	1.4	6	7.6	9.2	1.5	3.0	2.9	4.8	27.4
U33	69.29	132.19	15	5	2.0	1.0	7.3	87	T-ARC	9.6	11.5	10.0	297	1.1	13	6.1	4.7	0.4	13.8	11.4	19.0	6.8
U34	69.25	132.40	24	116	2.5	2.5	7.9	159	T-ARC	9.8	24.0	17.4	153	1.4	46	9.7	3.0	0.6	13.7	6.3	10.7	17.9
U35	69.19	132.59	24	86	7.0	2.7	8.2	128	T-ARC	10.2	21.8	10.1	143	1.6	11	6.1	2.8	0.4	11.3	6.6	8.5	17.5
U36	69.10	133.16	21	103	4.0	3.2	8.4	105	T-ARC	10.7	18.3	7.2	93	1.2	18	4.7	1.4	0.4	20.8	6.2	9.6	14.1
U37	69.08	133.17	21	69	6.5	4.0	8.1	98	T-ARC	10.9	16.4	6.8	58	1.0	13	4.6	1.4	0.5	10.5	5.6	8.9	12.7
U38	69.07	133.11	21	50	3.0	3.0	8.2	139	T-ARC	10.9	24.2	8.9	39	1.3	16	7.3	2.1	0.6	13.3	5.3	9.6	20.8
U39	69.12	133.02	24	105	12.0	6.0	8.2	141	T-ARC	10.6	29.6	7.4	24	1.2	7	5.0	4.7	1.4	5.0	3.7	6.1	21.4
U40	69.13	133.00	24	82	3.0	2.5	8.2	104	T-ARC	10.5	18.9	8.2	165	1.2	18	4.9	0.8	0.6	13.1	10.3	10.1	13.3
U41	69.20	132.44	24	86	7.0	2.5	8.1	167	T-ARC	10.1	32.2	12.2	52	2.0	9	7.8	9.2	0.6	7.5	4.2	7.9	24.0
U42	69.03	133.27	46	85	15.0	7.0	7.8	150	T-ARC	11.0	20.8	5.2	21	0.9	adl	3.4	1.9	1.5	3.5	2.7	4.6	15.7
U43	68.59	133.28	30	36	14.0	7.0	7.5	105	T-ARC	11.3	14.0	5.6	19	1.0	14	3.1	1.6	0.8	5.0	3.2	5.7	10.3
U44	68.50	133.33	30	61	4.0	2.8	8.2	129	T-ARC	11.8	19.8	3.7	72	1.1	19	3.1	2.1	0.7	12.3	6.6	8.1	14.2
U45	68.46	133.39	76	65	2.0	1.5	6.9	65	T-ARC	11.7	7.8	1.9	348	0.9	23	2.2	12.9	1.9	17.8	12.6	11.8	3.4
U46	68.29	133.39	122	63	2.5	2.5	7.1	81	T-ARC	12.3	9.7	1.9	235	1.4	33	2.4	14.6	1.2	16.2	10.9	11.4	4.9
U47	68.28	133.38	122	21	1.5	1.5	8.3	220	L-WOOD	12.3	33.9	2.7	27	1.6	8	5.0	42.3	0.9	9.3	6.0	9.1	18.9
U48	68.25	133.35	114	96	1.5	1.0	8.6	71	L-WOOD	12.5	9.2	1.6	272	1.4	39	1.6	8.1	0.4	48.8	12.7	11.6	5.5
U49	68.23	133.25	84	5	3.5	0.7	6.6	41	L-WOOD	12.8	6.7	1.4	1660	0.5	61	1.4	9.1	3.3	43.9	21.2	21.5	2.0
U50	68.25	133.22	76	22	2.0	1.6	7.0	71	L-WOOD	12.8	9.2	5.2	774	1.1	50	4.9	9.3	0.8	28.6	24.3	29.9	3.9
U51	68.29	133.22	128	87	1.5	1.0	8.5	72	L-WOOD	12.3	10.2	2.0	771	1.2	43	4.2	3.8	1.7	55.1	13.6	17.2	7.4
U52	68.34	133.20	145	20	6.0	1.8	7.0	116	L-WOOD	11.9	12.6	1.7	348	1.1	72	7.2	49.4	1.5	9.7	6.6	11.3	1.8
U53	68.36	133.15	152	26	3.5	2.3	7.2	48	T-ARC	11.8	5.9	1.6	110	0.8	14	3.1	6.1	1.0	11.4	7.8	10.8	3.7

Table 3.1 continued

Lake	LAT °N	LONG °W	ELEV m	SA ha	DEPTH m	SECCHI m	pH	COND uS/cm	vegetation	JTEMP °C	Ca mg/L	Cl mg/L	Fe µg/L	K mg/L	Mn µg/L	Na mg/L	SO4 mg/L	SiO2 mg/L	TPU µg/L	TPF µg/L	DOC mg/L	DIC mg/L
U54	68.38	133.17	91	40	10.0	1.9	7.3	85	T-ARC	12.1	11.9	1.9	265	1.0	14	4.0	19.0	1.3	11.7	7.5	13.0	5.1
U55	68.42	133.15	30	88	18.5	3.5	7.7	70	T-ARC	12.2	10.4	2.5	160	1.0	20	2.1	3.2	0.6	9.0	7.2	8.5	7.4
U56	67.14	135.26	366	35	4.0	1.4	7.5	35	FOREST	13.5	5.5	0.7	612	0.8	23	0.8	7.6	1.0	35.4	14.5	12.3	2.4
U57	67.13	135.36	396	7	1.2	1.0	7.4	140	L-WOOD	13.4	9.5	0.5	607	1.1	44	0.9	31.9	0.5	40.5	16.8	9.8	2.1
U58	67.06	136.00	549	19	5.5	1.9	5.9	77	T-ALP	12.6	8.3	0.3	196	0.5	adl	0.7	39.0	1.9	9.8	4.5	3.9	0.3
U59	64.29	138.17	1387	4	15.5	9.5	7.9	65	T-ALP	10.2	12.8	0.2	37	0.1	11	0.2	15.2	1.7	4.0	2.8	3.1	5.5
KW02	49.54	120.10	1619	2	1.5	1.2	7.7	55	FOREST	12.5	10.0	1.7	119	0.9	11	2.3	4.7	3.7	n/a	11.0	16.0	5.9
KW03*	52.09	122.04	930	8	1.5	1.5	8.9	522	FOREST	15.6	23.5	12.4	32	24.4	6	27.3	<0.5	17.8	1550	1540	31.3	99.2
KW04	52.40	122.23	796	6	14.3	4.7	8.2	256	FOREST	15.0	43.6	0.7	<6	1.6	12	7.5	<0.5	20.4	13.0	6.0	8.8	48.6
KW05	53.19	122.21	908	14	12.5	2.6	8.0	19	FOREST	13.9	1.6	0.2	306	0.8	7	1.0	0.7	1.5	10.0	8.0	12.0	1.5
KW06	53.52	123.15	762	6	7.3	7.1	8.2	123	FOREST	13.8	18.8	3.6	12	1.4	1	3.2	1.0	15.0	4.0	<2	2.6	20.2
KW07	53.55	123.39	762	23	1.1	1.1	7.8	81	FOREST	12.0	3.0	15.8	127	0.8	15	10.0	<0.5	<0.1	18.0	14.0	8.5	4.8
KW08	54.03	125.03	939	31	8.5	2.9	8.4	77	FOREST	14.3	12.8	0.2	60	1.2	53	3.9	2.5	0.2	13.0	8.0	13.0	10.1
KW10	55.12	127.41	339	23	2.6	2.6	7.9	97	FOREST	14.7	16.0	2.9	73	0.6	15	3.4	9.0	5.8	8.0	7.0	3.8	10.1
KW11	54.19	128.33	183	6	8.7	6.7	8.1	38	FOREST	15.6	0.8	7.5	<6	<0.1	9	4.6	0.7	<0.1	4.0	2.0	1.7	0.8
KW12	55.42	128.46	251	8	7.25	5.7	8.1	121	FOREST	14.3	20.6	0.9	17	0.5	9	2.5	3.5	5.5	6.0	4.0	3.7	18.2
KW13	54.37	128.42	224	2	4.5	4.5	6.8	5	FOREST	15.0	<0.1	0.2	39	0.2	15	0.2	<0.5	<0.1	10.0	6.0	3.4	0.9
KW14*	54.14	130.07	73	2	8.5	0.8	5.4	17	FOREST	13.1	0.6	1.4	704	<0.1	10	1.5	0.8	3.9	17.0	12.0	13.6	1.3
KW15	54.17	130.16	60	2	0.75	0.6	6.6	43	FOREST	13.0	3.2	3.3	571	0.2	6	3.1	2.9	0.8	13.0	8.0	16.0	1.3
KW19	56.03	129.54	90	17	11	7.3	8.0	95	FOREST	12.1	17.6	0.3	64	0.3	10	0.7	10.6	3.8	2.0	<2	1.9	10.5
KW20	56.40	129.45	550	6	4	2.6	7.0	14	FOREST	12.7	1.4	<0.1	57	<0.1	6	0.9	0.6	3.3	8.0	5.0	9.6	1.4
KW21	56.43	129.47	599	42	12.8	4.4	7.8	32	FOREST	12.7	3.6	1.0	35	0.2	14	1.2	1.5	3.9	4.0	2.0	6.2	2.8
KW23	58.13	129.50	1205	42	11.8	4	8.0	45	T-ALP	10.6	7.7	0.8	31	0.9	8	1.0	1.9	5.8	6.0	2.0	3.0	5.8
KW24	58.15	129.51	1209	25	12.5	6.5	8.0	26	T-ALP	10.6	4.8	0.1	104	0.3	7	1.1	1.1	7.8	4.0	3.0	1.6	4.5
KW25	58.26	130.00	799	39	19.2	5.8	8.8	148	FOREST	11.8	23.5	0.6	12	1.1	11	4.8	5.3	6.3	7.0	4.0	4.7	23.0
KW26	59.06	129.44	785	9	1.2	1.2	7.5	53	FOREST	11.2	8.5	0.5	36	0.6	3	1.9	2.0	12.6	3.0	2.0	3.5	7.2
KW27	59.11	129.48	955	5	6	6	7.9	56	FOREST	10.1	8.7	0.7	15	0.8	1	1.5	5.2	8.9	<2	<2	0.9	6.0
KW28	59.13	129.44	957	11	20.3	8.3	8.0	65	T-ALP	10.5	12.0	0.4	77	0.5	13	1.3	7.2	6.8	<2	<2	1.1	7.8
KW29	59.50	129.08	802	6	12.5	8.4	8.4	215	FOREST	13.1	36.4	0.5	9	1.2	2	1.9	3.2	10.2	3.0	<2	3.6	41.6
KW30	59.52	129.09	842	16	2.5	2.5	8.3	170	FOREST	13.1	36.1	3.1	69	0.3	12	1.9	<0.5	7.5	7.0	5.0	17.8	30.8
KW31	59.55	129.06	835	6	5.1	4.2	8.4	192	FOREST	13.8	29.5	1.2	32	0.4	7	1.9	0.6	5.1	7.0	6.0	16.0	35.4
KW32*	59.57	132.00	790	6	2	2	7.7	75	FOREST	11.8	14.4	0.2	25	0.9	2	1.1	2.1	9.4	3.0	<2	4.2	13.1
KW33	59.41	133.43	713	25	5.3	3.6	9.0	287	FOREST	12.5	25.8	2.0	10	2.0	9	7.5	11.6	10.6	21.0	21.0	16.2	54.3
KW34	59.42	133.18	1268	9	4.6	3.1	7.9	31	FOREST	8.6	3.1	0.1	173	0.4	8	1.7	2.9	8.4	10.0	3.0	7.8	2.8

Table 3.1 continued

Lake	LAT °N	LONG °W	ELEV m	SA ha	DEPTH m	SECCHI m	pH	COND uS/cm	vegetation	JTEMP °C	Ca mg/L	Cl mg/L	Fe µg/L	K mg/L	Mn µg/L	Na mg/L	SO4 mg/L	SiO2 mg/L	TPU µg/L	TPF µg/L	DOC mg/L	DIC mg/L
KW35	59.36	133.41	758	41	13.8	8.32	8.8	448	FOREST	12.4	15.3	3.3	9	5.3	<1	7.2	37.3	9.1	5.0	3.0	19.7	86.0
KW38	58.51	125.44	1066	2	2.3	2.3	8.2	104	FOREST	10.7	26.3	0.3	6	<0.1	<1	<0.1	9.7	2.2	<2	<2	0.5	27.0
KW39	58.39	124.42	1289	2	2.2	2.2	9.0	125	FOREST	9.0	21.4	13.8	58	0.3	6	7.8	<0.5	0.1	5.0	4.0	5.5	19.3
KW40	58.37	122.42	482	19	1.6	1	7.1	50	FOREST	16.0	6.1	0.9	285	0.6	16	1.8	5.5	0.3	33.0	29.0	19.8	2.9
KW41	58.33	122.30	472	28	9.1	1.6	8.0	133	FOREST	16.6	27.5	0.2	225	0.3	49	1.9	7.6	3.9	19.0	9.0	21.6	19.3
KW42*	57.10	122.48	1205	8	3	0.8	6.6	13	FOREST	13.2	2.6	<0.1	855	0.4	12	0.3	<0.5	2.0	22.0	12.0	20.0	1.1
KW43	55.53	121.54	725	39	20	2.7	7.9	103	FOREST	14.5	14.7	6.2	235	1.1	29	6.3	7.3	1.4	11.0	7.0	12.1	10.6
KW44	55.48	121.31	706	38	5.5	2.6	7.9	189	FOREST	14.8	38.7	0.4	310	1.7	42	2.4	3.5	4.4	32.0	22.0	14.9	33.9
KW45	55.55	121.24	698	70	8.9	1.4	8.6	238	FOREST	15.0	49.1	1.0	47	5.4	47	3.4	9.3	4.5	36.0	12.0	17.2	39.8
KW46	55.23	122.37	868	95	30	8	8.5	109	FOREST	12.7	24.7	1.2	25	0.2	4	1.1	5.6	1.0	3.0	<2	1.7	18.1
KW48	55.03	123.26	1029	17	4.7	3.2	7.9	45	FOREST	12.3	8.6	<0.1	133	0.7	5	0.9	1.9	3.0	5.0	3.0	7.9	5.8
KW49	54.52	122.50	879	14	10.2	6.2	7.8	20	FOREST	13.7	2.7	<0.1	14	0.3	2	0.4	0.5	<0.1	4.0	3.0	5.0	2.6
KW50	54.18	122.39	709	8	6	1.7	7.6	141	FOREST	14.4	15.8	19.0	27	1.1	14	15.6	0.8	1.4	12.0	7.0	17.5	11.6
KW51	53.54	122.18	739	6	1.8	1.8	8.3	71	FOREST	14.7	11.4	1.5	382	0.6	33	2.2	0.8	2.8	10.0	8.0	14.5	9.7
KW52	53.44	122.17	823	6	13.2	7.7	7.7	67	FOREST	14.0	10.2	0.3	38	0.6	5	1.2	2.7	11.2	4.0	3.0	2.8	9.9
KW53	53.51	121.59	743	8	11.6	5.1	8.0	37	FOREST	13.9	6.7	<0.1	6	0.4	3	0.5	<0.5	0.4	7.0	4.0	7.0	5.8
KW54*	53.30	121.32	985	6	13	6.4	7.3	9	FOREST	13.0	0.6	<0.1	15	0.3	3	0.3	<0.5	<0.1	5.0	4.0	4.6	1.3
KW55	53.13	121.27	1053	6	10.4	3.7	7.9	24	FOREST	13.0	3.5	<0.1	56	0.2	20	0.5	0.6	1.4	5.0	4.0	7.6	3.1
KW56	52.59	121.08	992	6	11.1	5	8.0	154	FOREST	13.4	39.8	0.3	11	0.4	6	0.7	3.7	3.9	4.0	3.0	3.5	28.7
KW57	52.18	121.26	845	11	6.5	1.9	7.8	188	FOREST	14.4	37.0	0.8	10	0.9	28	6.5	1.3	13.6	21.0	12.0	15.2	36.2
KW58	51.57	120.53	1011	17	7.5	2.7	7.9	80	FOREST	14.0	14.0	0.2	110	0.8	12	1.2	0.6	8.1	10.0	7.0	11.8	13.2

* Outliers were not included in the models

Elevation asl (ELEV), and surface area (SA) for each lake were determined using topographical maps. Maximum depth (DEPTH) was assessed by use of a depth sounder where available, or by repeat sampling (except KW28 and KW46 where maximum depth exceeded equipment limits and sampling depth was substituted). From near the lake centre, secchi depth (SECCHI) was measured with a standard 22 cm secchi disk, and a pH reading was taken (BC: Beckman FΦ 255 pH/Temp/mV meter). Conductivity measurements (COND) were obtained using meters for the Alaska and Yukon/NWT data sets. Due to equipment failure during sampling, conductivity values for BC were estimated using a linear regression model developed from 300 paired salinity and conductivity measurements ($y = 0.8754x + 0.6446$, where $y = \log(\text{cond})$, $x = \log(\text{salin})$, $r^2=0.987$). The salinities used in this model were calculated as the sum of major cations and anions (Ca, Na, Mg, K, Cl, SO_4, and DIC). The vegetation was entered as binary variables after classification into one of the following 4 categories: arctic tundra (T-ALP), alpine tundra (T-ALP), lichen woodland (L-WOOD), or boreal forest (FOREST).

Mean July air temperatures (JTEMP) for all sites except those in the NWT were obtained from PRISM (Parameter-elevation Regressions on Independent Slopes Model) Climate Layers (Spatial Climate Analysis Service, 2001). These climatic data have a grid resolution of 2.5 min (~4 km), and are available in a Geographical Information System format. These climate maps were produced using a combination of data on elevation, climate normals (30 years), distance from oceans and topography. PRISM data is not yet available for NWT. Mean July air temperatures were estimated for NWT sites in the Mackenzie Delta using climate normals from 10 climate stations in proximity to the delta.

Water samples were obtained in the field for detailed chemical analysis in a laboratory. Samples were collected near the centre of the lake approximately 0.5 m below the lake's surface. Where necessary, samples were filtered and treated on site following the procedures outlined in the Analytical Methods Manual (Environment Canada, 1979, 1994a, b). Water samples were stored under cool and dark conditions. Those from Alaska and Yukon/NWT were submitted for analysis to the National Water Research Institute, Burlington, ON, while those from BC were analysed by Environment Canada's

Pacific Environmental Science Centre, Vancouver, BC. Values for the following variables were obtained for all 3 data sets: calcium (Ca), chloride (Cl), iron (Fe), potassium (K), manganese (Mn), sodium (Na), sulphate (SO_4), dissolved silica (SiO_2), total particulate and dissolved phosphorus (TPU), total dissolved phosphorus (TPF), dissolved organic carbon (DOC), and dissolved inorganic carbon (DIC).

3.3 Data Analysis

3.3.1 Data Screening

All taxon data are presented as percent abundances, and were square-root transformed prior to further analysis.

LAT, LONG and ELEV are fixed variables and so were entered as passive variables. Environmental variables with skewed distributions were transformed using $\ln(x + 1)$, where x was the given environmental variable. Collinearity of environmental variables was assessed using a series of detrended correspondence analyses (DCAs). Variables with an inflation factor ≥ 20 were eliminated one per DCA run until all remaining variables had values of <20. By this process, the variable FOREST was found to be redundant and was eliminated.

Sites with unusual midge assemblages or environmental characteristics were eliminated. A site was defined as an outlier if: (1) its sample score fell outside the 95% confidence interval of the sample score mean for both a DCA of the taxon data **and** a principal components analysis (PCA) of the environmental data; or (2) leverage diagnostics in canonical correspondence analysis (CCA) showed a sample to have an environmental variable with extreme influence (>8X). Following these criteria, AK07, KW03, KW14, KW32, KW42 and KW54 were eliminated. AK19 was also eliminated as it had significant abundances of rheophilous taxa (*Eukiefferiella/Tvetenia* and *Rheotanytarsus*).

Rare taxa, defined here as taxa that were present in fewer than 5% of the lakes (i.e., <6 lakes), were eliminated.

3.3.2 Ordinations

All ordinations were performed using the program CANOCO, version 3.12 (ter Braak, 1991). To take into consideration the potential effects of the 3 different data sets on ordination, AK, KW and U were entered as binary covariables.

A DCA was used to explore principal patterns of faunistic variation in the data set. The gradient length of species scores was relatively long (3.97 standard deviations), thus unimodal ordination techniques were used (ter Braak, 1995). The relationships between individual environmental variables and midge distributions were assessed using CCA. Statistically significant ($P \leq 0.05$) environmental variables were determined using forward selection in CCA. Variables were sequentially selected such that each selected variable accounted for the greatest proportion of the remaining variance. Forward selected variables and CCA axes were also tested for significance by running Monte Carlo permutation tests (with 999 unrestricted permutations, $P \leq 0.05$).

3.3.3 Model Development

The relationships between midges and both temperature (Brooks and Birks, 2000, 2001; Lotter *et al.*, 1997, 1999; Olander *et al.*, 1997, 1999; Walker *et al.*, 1991, 1997) and lake depth (Korhola *et al.*, 2000) have previously been demonstrated to be robust. To explore the relationships between midges and these two variables for this data set, CCAs constrained to temperature and depth respectively were run, and the first to second eigenvalues (λ_1 / λ_2) compared.

The program C2, version 1.4 Beta (Juggins, 2003) was used to develop and assess midge transfer functions for temperature and depth. Several unimodal regression-calibration techniques were used: simple weighted averaging (WA) and weighted averaging with tolerance downweighting (WA_{tol}) both with classical and inverse deshrinking, and weighted averaging partial least squares (WA-PLS). Each model was tested with 1000 bootstrap cycles, and evaluated by means of the bootstrapped co-efficient of determination (r^2_{boot}) and root mean squared error of prediction (RMSEP).

3.4 Results

3.4.1 Faunistic Description

Over 27,000 midge subfossils from 78 taxa were examined. Ranking of taxa by latitude, temperature and depth (Figs. 3.2-3.4) revealed patterns in the distribution of many taxa. For the temperature and depth graphs, only the taxa showing relationships with the variable were included. *Abiskomyia*, *Mesocricotopus*, *Zalutschia* type B, *Parakiefferiella nigra* type and *Eukiefferiella/Tvetenia* were restricted to deep lakes in the colder regions, the first two taxa being further restricted to only the northernmost lakes. *Zalutschia* type A, *Corynocera oliveri* type and *Derotanypus* (in low abundances, not graphed) showed a preference for cold and shallow lakes. *Sergentia*, commonly interpreted as a cold indicator (Palmer *et al.*, 2002; Walker, 1990), showed little relationship with temperature, but did show a clear pattern of higher abundances in the deeper lakes. The warm indicators (*Labrundinia*, *Chaoborus*, *Pseudochironomus* and *Glyptotendipes*) seemed to show little correlation with depth. A few of the most common taxa were truly eurytopic with uniform distributions across latitude, temperature, and depth. These included: other Tanytarsina, *Procladius* and other Pentaneurini. Both ceratopogonids and *Chaoborus* showed strong preferences for sites below treeline.

Corynocera ambigua and *Corynocera oliveri* type were mostly restricted to latitudes north of ~60° N. At these latitudes, they were common (found in 44% and 30% of lakes, respectively) especially in shallow lakes, and often attained high abundances within a lake (with maximums of 57% and 37% respectively). *C. oliveri* type was found in the colder regions, while *C. ambigua* showed no correlation with temperature.

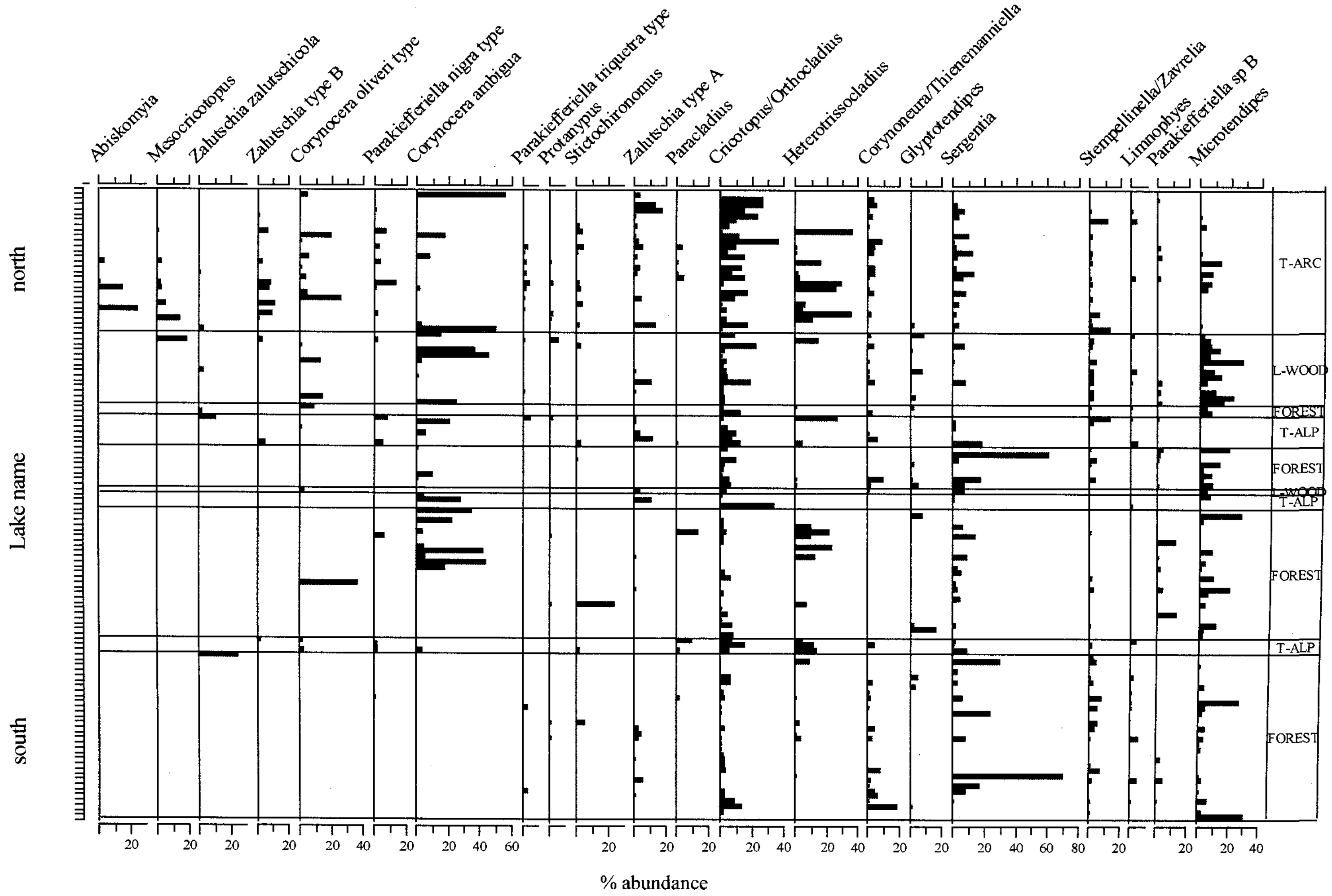

Figure 3.2 A chironomid diagram for the Beringia training set, with taxa ranked by latitude (N to S) as determined by a constrained CCA. All taxon abundances are presented as a % of the total identifiable chironomids. Taxa that were rare or never exceeded 5% have been omitted. Vegetation type is indicated at right with some abbreviations: T-ARC, arctic tundra; T-ALP, alpine tundra; L-WOOD, lichen woodland.

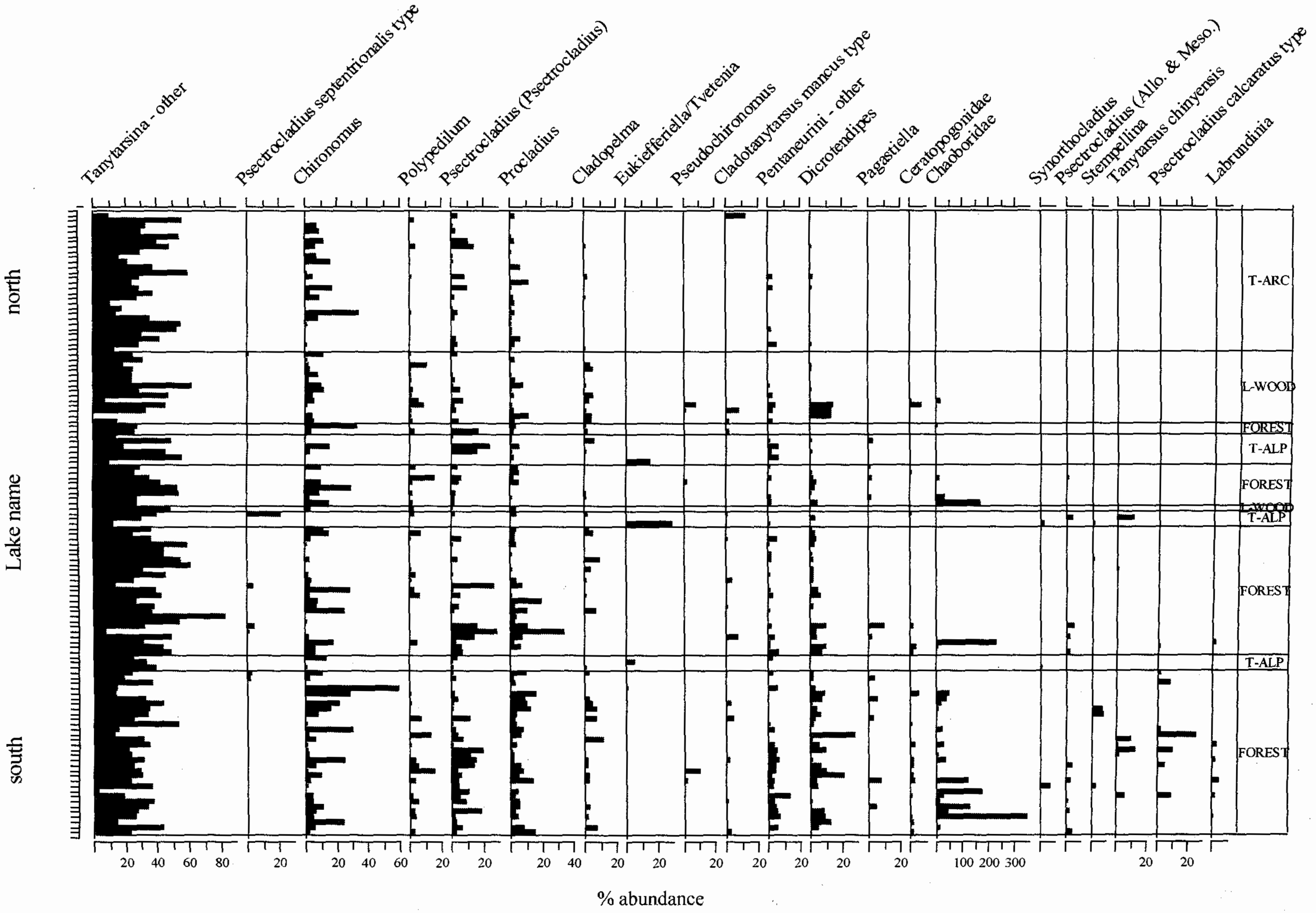

Figure 3.2 continued

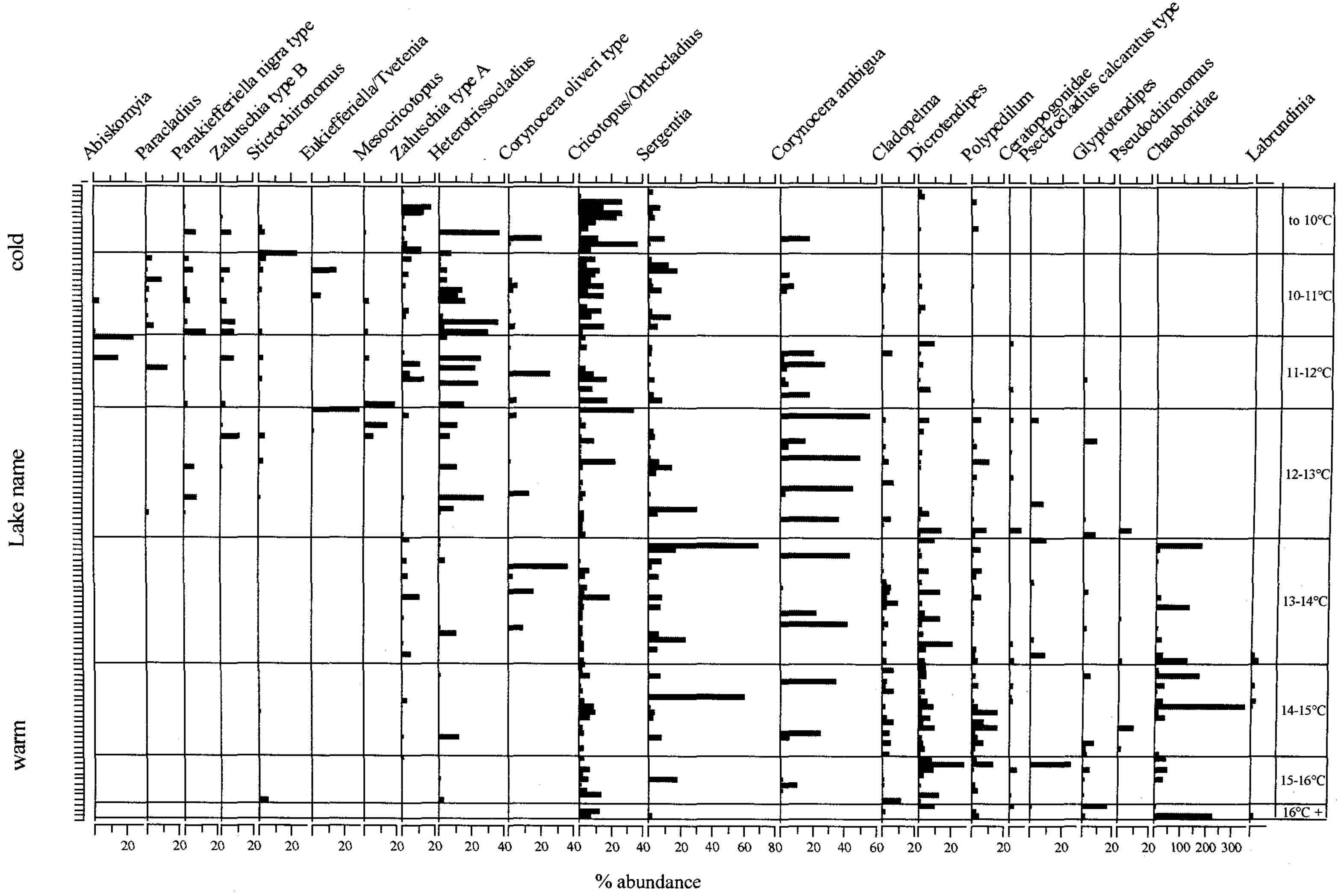

Figure 3.3 A chironomid diagram for the Beringia training set, with select taxa ranked by mean July air temperature (cold to warm) as determined by a constrained CCA. All taxon abundances are presented as a % of the total identifiable chironomids.

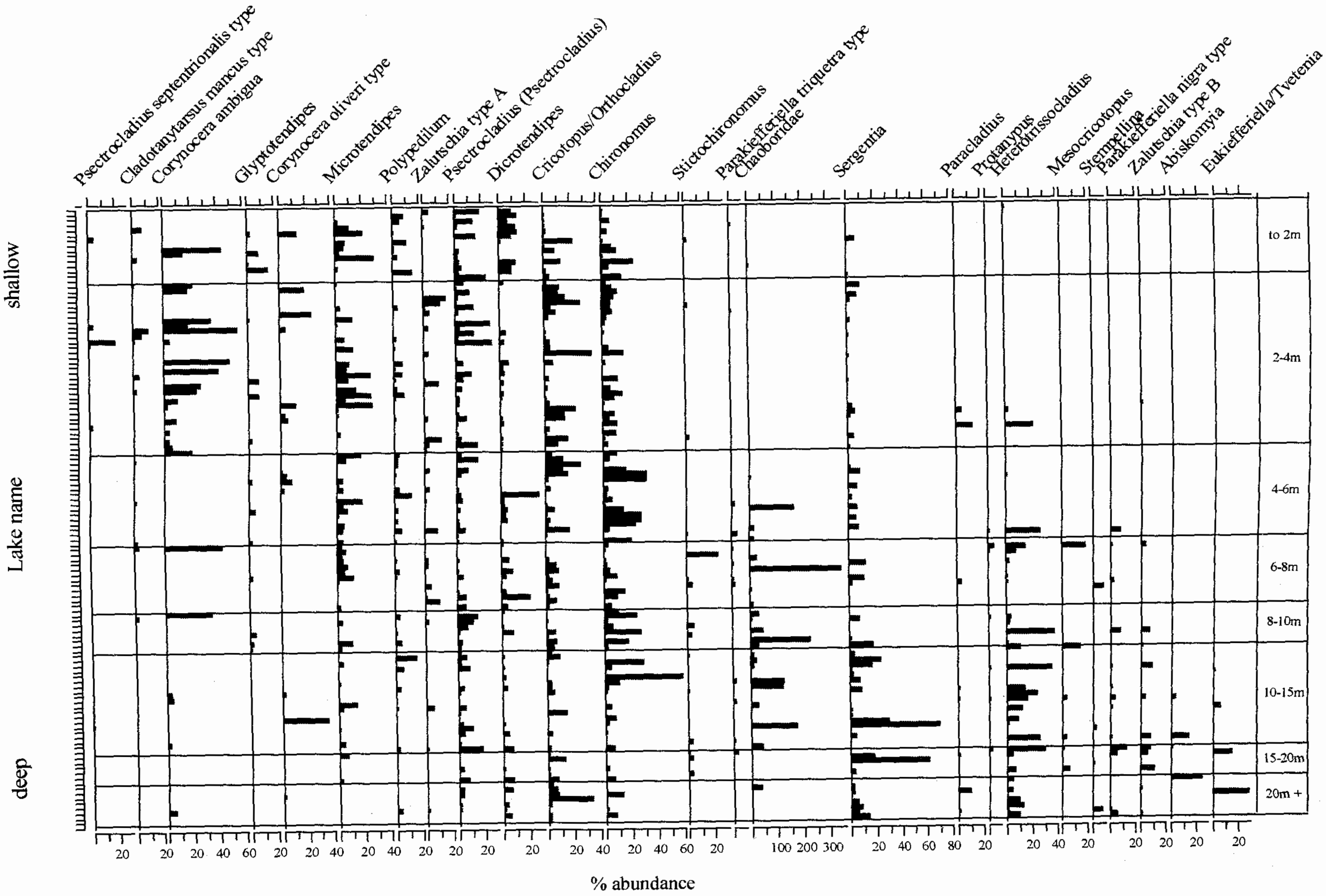

Figure 3.4 A chironomid diagram for the Beringia training set, with select taxa ranked by mean depth (shallow to deep) as determined by a constrained CCA. All taxon abundances are presented as a % of the total identifiable chironomids.

3.4.2 Ordinations

Ordination analyses included 60 taxa, 21 environmental variables and 114 sites. In order to determine the extent to which individual environmental variables contributed to variation, forward selection in CCA was performed. In the initial run (1), AK, KW and U were entered as covariables, and all variables were selected in the order dictated by forward selection. Ten environmental variables explained significant proportions ($P \leq 0.05$) of the explainable variance. In order, these were DEPTH, JTEMP, pH, DOC, T-ARC, Ca, DIC, TPU, SECCHI and SA (Table 3.2).

With the selection of each variable in forward selection, the relative importance of the remaining variables is re-evaluated. A variable will decrease in relative importance if it is correlated with (i.e., explains some of the same variation as) the variables already selected. Thus, a variable that initially appears important might escape selection, if it is correlated with variables already selected.

To test the robustness of the variables selected, a different order was forced by selecting TPU ahead of DEPTH, since both initially explained equal amounts of the variation (0.11/0.66). Run 2 produced similar results: TPU, DEPTH, JTEMP, DIC, Ca, T-ARC, SECCHI, Mn, DOC and SA. Run 3 was conducted without covariables, and again all variables were selected in the order dictated by the forward selection procedure. This produced ten significant variables: T-ARC, DEPTH, JTEMP, DIC, Ca, DOC, TPU, SECCHI, SO4 and SA. Again a different order was forced (run 4) by selecting the initially equal (0.12/0.78) JTEMP before T-ARC, with similar results: JTEMP, DEPTH, pH, T-ARC, SO4, DOC, TPU, Ca, DIC, SECCHI and SA. Nine variables were significant across all 4 runs, and were selected for a final CCA (without covariables). These were DEPTH, JTEMP, T-ARC, TPU, Ca, DIC, DOC, SECCHI and SA.

Patterns in data structure of the final CCA run were compared with those of correspondence analysis (CA) to explore the impact of the environmental data on species and site ordination. Similar patterns were observed as assessed both visually, and by

Table 3.2 Variance explained before and after forward selection in CCA. Results are presented for: run 1) CCA with covariables AK, KW and U, and all variables selected in the order presented; run 2) CCA with covariables AK, KW and U, TPU selected first, and all other variables selected in the order presented; run 3) CCA without covariables, and all variables selected in the order presented; and run 4) CCA without covariables, JTEMP selected first, and all other variables selected in the order presented.

Covariables AK, KW, U						No covariables					
Variable	Before forward selection	Added with selection run 1		run 2		Variable	Before forward selection	Added with selection run 3		run 4	
DEPTH	0.11	1	0.11	2	0.07	T-ARC	0.12	1	0.12	4	0.05
TPU	0.11	8	0.03	1	0.11	JTEMP	0.12	3	0.06	1	0.12
JTEMP	0.09	2	0.10	3	0.06	DEPTH	0.10	2	0.11	2	0.12
SECCHI	0.09	9	0.03	7	0.03	TPU	0.08	7	0.03	7	0.03
DOC	0.08	4	0.03	9	0.03	SECCHI	0.08	8	0.03	10	0.03
TPF	0.08					DOC	0.07	6	0.04	6	0.04
T-ARC	0.07	5	0.03	6	0.04	SA	0.06	10	0.03	11	0.03
Ca	0.05	6	0.03	5	0.04	Ca	0.06	5	0.06	8	0.04
DIC	0.05	7	0.03	4	0.05	TPF	0.05				
pH	0.04	3	0.05			COND	0.05				
Fe	0.04					pH	0.05			3	0.05
COND	0.04					DIC	0.05	4	0.05	9	0.04
T-ALP	0.04					Cl	0.04				
L-WOOD	0.03					Mn	0.04				
K	0.03					Fe	0.04				
Mn	0.03			8	0.03	SO4	0.04	9	0.03	5	0.04
SIO2	0.03					T-ALP	0.04				
SA	0.03	10	0.03	10	0.02	K	0.04				
Cl	0.03					L-WOOD	0.03				
Na	0.02					Na	0.03				
SO4	0.02					SIO2	0.03				
Sum of variance explained			0.47		0.48	Sum of variance explained			0.56		0.59
as a percent			71.21		72.73	as a percent			71.79		75.64
Total explainable variance	0.66					Total explainable variance	0.78				
Total variance	2.32					Total variance	2.32				

comparing CA and CCA values for the first 2 axes. Correlation between CA and CCA species scores of the first axis (r^2= 0.92) and second axis (r^2=0.47), and site scores for the first axis (r^2=0.96) and second axis (r^2=0.67) were good. This confirms that the environmental variables included in CCA capture the general patterns of species distribution observed in CA. As such, only CCA is further considered.

Eigenvalues for the first 4 axes of the final CCA account for 18.0% of the species variance (Table 3.3). Monte Carlo tests (999 unrestricted permutations) confirmed the significance of all four axes ($P=0.001$). Relationships between the significant environmental variables and the individual axes were examined through correlation coefficients, t-values and interset correlations (Table 3.4). All variables were significantly correlated with at least the first or second CCA axis ($P\leq0.05$). DEPTH showed a positive correlation with the first axis and negative correlation with the second axis. JTEMP showed negative correlations with both the first and second axes.

A biplot of the final CCA sample scores shows a good distribution of sites with respect to both axes (Fig. 3.5). Sites showed clustering by vegetation type with strong segregation of forest and arctic tundra sites along the temperature gradient. Arctic tundra sites clustered predominantly in the top right (coldest) quadrant. Forest sites clustered in the bottom left (warmest) quadrant, and also extended into adjacent quadrants. The majority of alpine tundra sites fell along the boundary between arctic tundra and forest sites. Sites with lichen woodland vegetation were interspersed with the forest sites in the top left (shallowest) quadrant.

The distribution of CCA species scores reflects the environmental preferences of individual taxa. Clustered near the right end of axis 1 were deep lakes of the colder regions, and the taxa associated with them (Fig. 3.6): *Abiskomyia*, *Mesocricotopus*, *Parakiefferiella nigra* and *Zalutschia* type B. Bordering the shallow northern lakes of the top quadrants were *Derotanypus*, *Corynocera* spp. and *Parachironomus*. Spanning the bottom quadrants *Einfeldia*, *Synorthocladius*, *Stempellina* and *Cyphomella/Harnischia/Paracladopelma* showed preference for deep lakes in the warmer regions. Taxa clustered

Table 3.3 Eigenvalues, taxon-environmental correlations, cumulative % variance and significance of the four axes for the final CCA.

	Axis 1	Axis 2	Axis 3	Axis 4	
Eigenvalue	0.227	0.090	0.060	0.041	
Taxon-environment correlations	0.850	0.794	0.711	0.728	
Cumulative % variance					
of taxon data	9.8	13.7	16.2	18.0	
of taxon-environment relation	42.2	58.9	70.0	77.5	
Significance (probability) of axis	0.001	0.001	0.001	0.001	
Sum of all unconstrained eigenvalues					2.325
Sum of canonical eigenvalues					0.539

Table 3.4 Canonical coefficients, their t-values and interset correlations for the final CCA.

	Canonical coefficients				t-values				Interset correlations			
	Axis 1	Axis 2	Axis 3	Axis 4	Axis 1	Axis 2	Axis 3	Axis 4	Axis 1	Axis 2	Axis 3	Axis 4
DEPTHt	0.54	-0.85	-0.33	0.04	5.35*	-6.80*	-2.06*	0.23	0.42	-0.50	-0.19	0.21
SAt	0.00	0.34	0.11	0.29	0.01	3.57*	0.93	2.50*	0.30	0.34	-0.13	0.17
JTEMP	-0.38	-0.45	-0.30	-0.24	-4.39*	-4.19*	-2.14*	-1.77	-0.53	-0.33	-0.28	-0.08
SECCHIt	0.09	0.69	-0.13	-0.10	0.81	4.74*	-0.72	-0.55	0.37	-0.32	-0.04	0.23
Cat	0.78	0.38	-1.12	-0.44	5.67*	2.26*	-5.09*	-2.13*	0.17	0.14	-0.50	0.36
TPUt	-0.06	0.43	-0.70	-0.69	-0.61	3.66*	-4.68*	-4.85*	-0.33	0.43	-0.26	-0.30
DOCt	0.00	0.41	0.22	0.65	0.03	4.23*	1.80	5.57*	-0.31	0.30	-0.06	0.19
DICt	-0.90	-0.31	0.41	0.98	-6.37*	-1.77	1.81	4.59*	0.01	0.06	-0.38	0.52
T-ARC	0.44	-0.06	0.04	-0.28	5.18*	-0.58	0.26	-2.18*	0.56	0.34	0.07	-0.01

*significant at $P \leq 0.05$

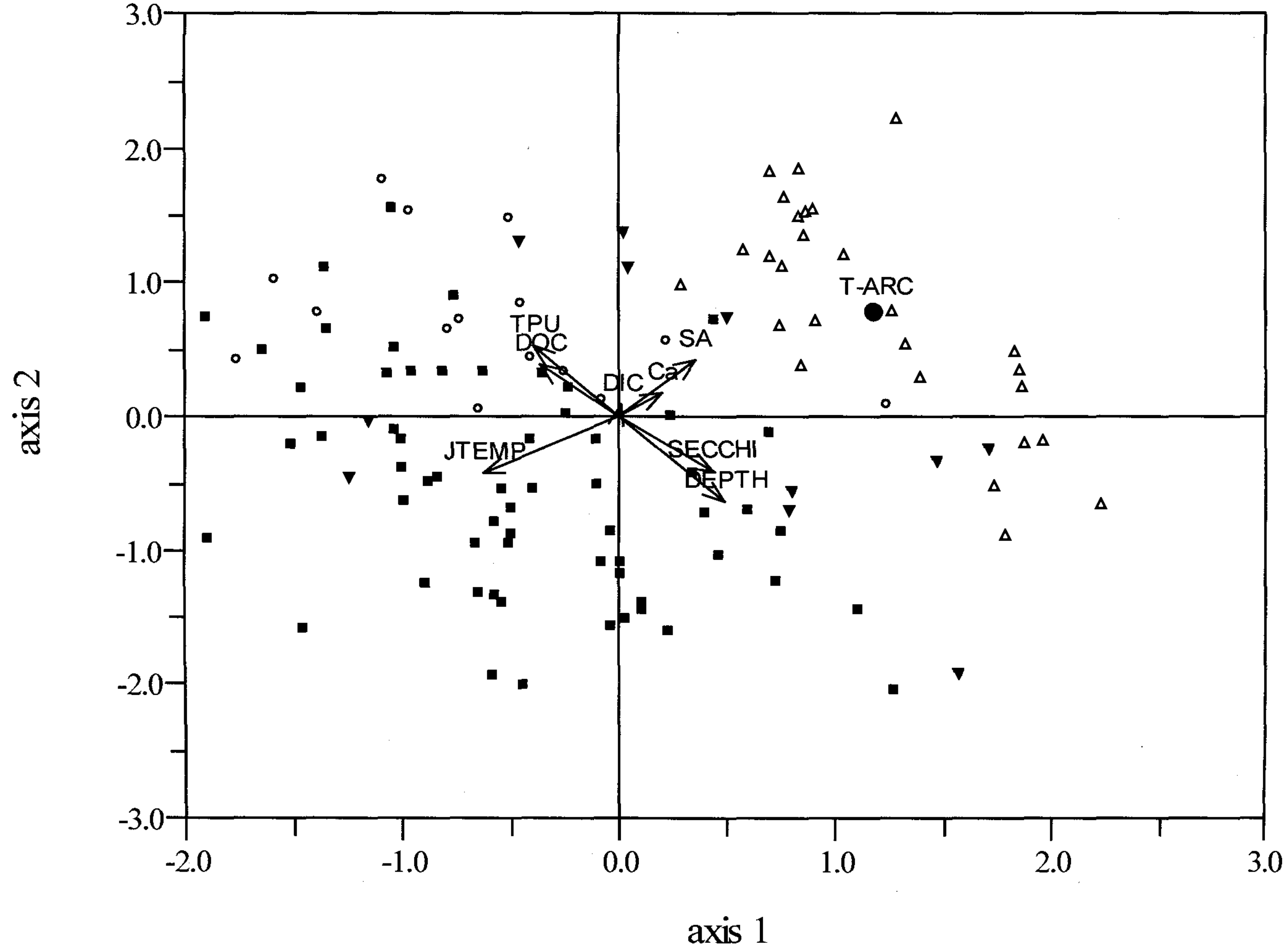

Figure 3.5 Canonical correspondence analysis ordination showing the dispersion of sites by vegetation type, relative to nine significant environmental variables. Symbols indicate: Δ arctic tundra, ▼ alpine tundra, ■ forest, o lichen woodland.

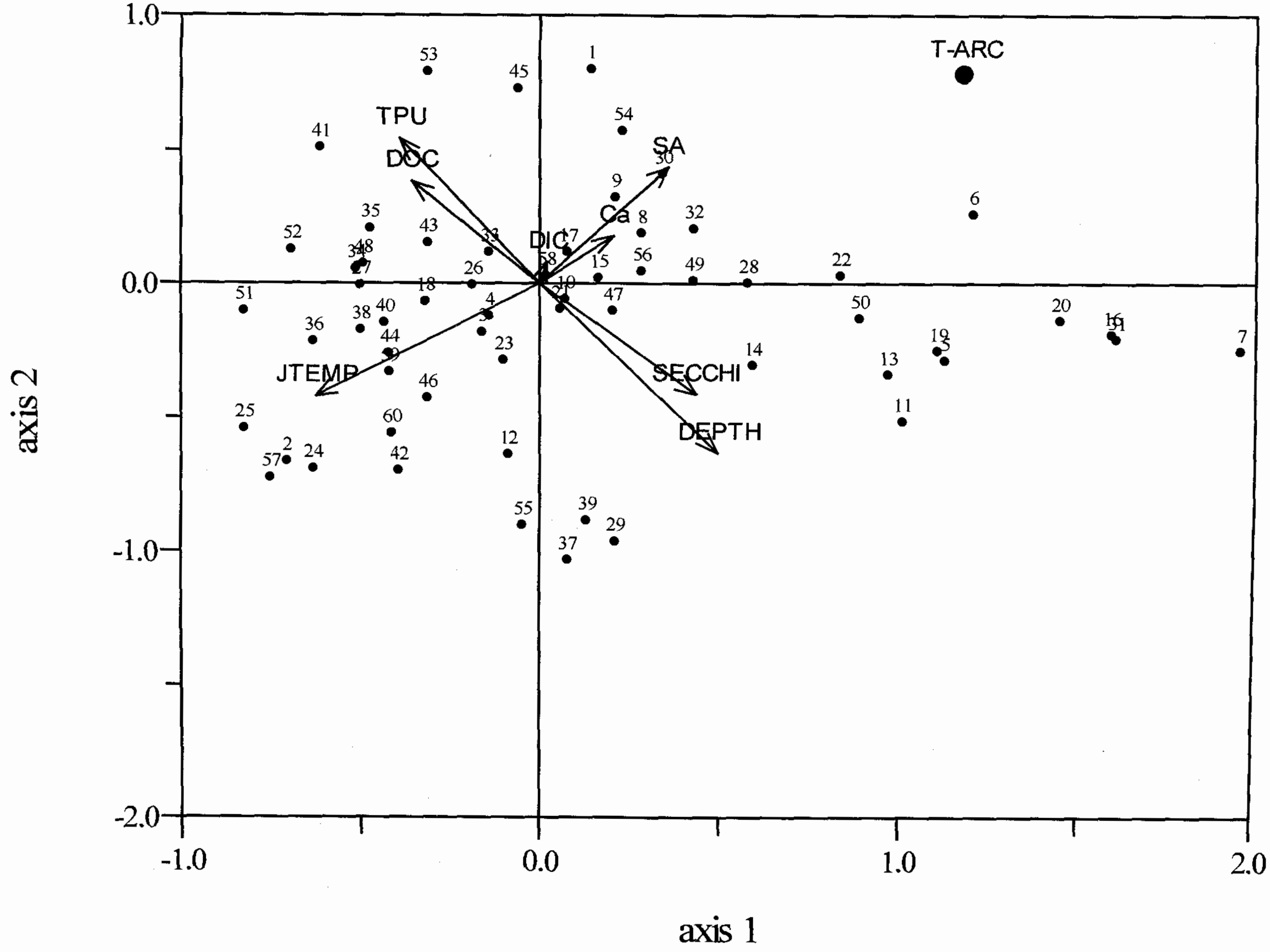

Figure 3.6 Canonical correspondence analysis ordination showing the dispersion of taxa relative to nine significant environmental variables. Taxon codes correspond with full taxon names listed in Table 3.6.

in the central part of the CCA show no distinctive environmental or vegetational preferences.

3.4.3 Model Development

Depth was the strongest variable overall, as it ranked first or second in all four runs of forward selection. Mean July air temperature was a close second, and ranked consistently in the top three variables. CCAs constrained first to depth, and then to temperature were run, and produced respective eigenvalue ratios of 0.354 (λ_1/λ_2=0.105/0.296), and 0.439 (λ_1/λ_2=0.122/0.278). WA and WA-PLS models were constructed using the screened training set (Table 3.5). For depth, WA-PLS with 2 and 3 components produced the strongest models as indicated by their coefficients of determination and RMSEP's. The 2 component model was selected as it was the simpler of the two models (r^2_{boot}=0.431, and RMSEP=0.574). For temperature, the WA-PLS model with 2 components (r^2_{boot}=0.507, RMSEP=1.345°C) was again selected over the WA-PLS model with 3 components.

Taxon specific optima and tolerances were generated using WA (Table 3.6). For depth, *Psectrocladius septentrionalis* type generated the shallowest optimum of 3.3 m, while the deepest was 14.4 m for *Abiskomyia*. For temperature, the range of optima was relatively narrow: the lowest optimum of 11.0°C was shared by *Paracladius* and *Abiskomyia,* and the highest was 14.4°C for *Labrundinia*. This narrow range results from a short gradient of mean July air temperatures for the sites (8.6°C to 16.6°C), as well as the tendency of WA to overestimate low values, and to underestimate high values. Beta values were generated by the WA-PLS models as coefficients to be used in calculating depth and temperature estimates.

Table 3.5 A comparison of WA and WA-PLS models for reconstructing a) depth, and b) mean July air temperature.

a) **depth**

		Apparent			Bootstrapped		
Model		r^2	RMSE	Max Bias	r^2	RMSEP	Max Bias
WA	inverse	0.454	0.530	1.327	0.346	0.594	1.424
	classical	0.454	0.787	0.593	0.354	0.784	0.894
WAtol	inverse	0.441	0.536	1.461	0.329	0.618	1.534
	classical	0.441	0.808	0.847	0.334	0.858	1.054
WA-PLS	1 component	0.454	0.530	1.313	0.346	0.596	1.419
	2 components	**0.634**	**0.434**	**1.110**	**0.431**	**0.574**	**1.385**
	3 components	0.722	0.379	0.911	0.434	0.601	1.315
	4 components	0.769	0.345	0.798	0.424	0.642	1.301
	5 components	0.788	0.330	0.745	0.404	0.688	1.293

b) **mean July air temperature**

		Apparent			Bootstrapped		
Model		r^2	RMSE	Max Bias	r^2	RMSEP	Max Bias
WA	inverse	0.490	1.300	2.686	0.403	1.433	2.893
	classical	0.490	1.857	1.952	0.412	1.862	2.413
WAtol	inverse	0.438	1.365	2.920	0.341	1.537	3.086
	classical	0.438	2.064	2.315	0.349	2.181	2.701
WA-PLS	1 component	0.490	1.300	2.719	0.403	1.432	2.921
	2 components	**0.676**	**1.036**	**1.862**	**0.507**	**1.345**	**2.435**
	3 components	0.744	0.921	1.597	0.504	1.406	2.474
	4 components	0.779	0.856	1.529	0.472	1.529	2.641
	5 components	0.794	0.827	1.491	0.449	1.641	2.758

Table 3.6 Values for all non-rare taxa for: taxon occurrence (i.e., percentage of 121 lakes in which taxon was present), and for each of depth and mean July air temperature: taxon range, WA optimum (bootstrapped), WA tolerance (bootstratpped) and WA-PLS Beta coefficient (bootstrapped).

			TEMPERATURE					DEPTH				
Taxon code	Taxon name	occurrence (%)	T-Min (°C)	T-Max (°C)	T-Opt (°C)	T-Tol (°C)	WAPLS Beta	D-Min (m)	D-Max (m)	D-Opt (m)	D-Tol (m)	WA-PLS Beta[1]
1	*Derotanypus*	12	8.6	15.3	11.6	1.8	2.8818	1.2	10.1	3.5	0.5	-0.9604
2	*Labrundinia*	9	12.0	16.6	14.4	1.0	23.6727	1.1	14.3	6.4	0.9	3.9806
3	Tr: Pentaneurini	72	9.0	16.6	12.8	1.6	13.4292	0.8	49.0	5.8	1.2	2.7880
4	*Procladius*	91	8.6	16.6	12.7	1.7	13.0641	0.8	49.0	5.2	1.0	1.7122
5	*Protanypus*	21	9.6	15.6	11.7	1.3	13.0012	1.2	49.0	9.5	1.0	3.2982
6	*Monodiamesa*	13	9.4	12.6	11.1	1.0	7.7458	1.5	15.5	7.1	0.7	0.0730
7	*Abiskomyia*	6	10.1	12.2	11.0	0.5	11.4044	7.0	20.0	14.4	0.3	5.3535
8	*Corynoneura/Thienemanniella*	56	9.2	16.2	12.1	2.0	9.0323	0.8	49.0	5.9	0.9	2.2680
9	*Cricotopus/Orthocladius*	87	8.6	16.6	12.0	1.9	7.3305	0.8	49.0	4.9	1.0	0.7112
10	*Doithrix/Pseudorthocladius*	14	10.1	16.2	12.6	1.7	15.8364	1.2	30.0	5.8	1.1	1.6604
11	*Eukiefferiella/Tvetenia*	6	9.3	15.0	11.3	1.6	3.8635	2.0	25.0	11.7	0.5	6.0073
12	*Heterotanytarsus*	6	12.3	14.2	13.3	0.7	15.0761	2.5	12.5	6.5	0.6	3.7825
13	*Heterotrissocladius*	46	9.4	16.2	11.8	1.5	13.2453	0.8	12.5	9.7	0.9	4.0634
14	*Hydrobaenus/Oliveridia*	9	9.3	14.8	12.0	1.3	13.2259	0.8	30.0	7.1	1.7	1.7842
15	*Limnophyes*	42	8.6	16.2	12.3	1.9	9.7472	1.1	49.0	5.2	1.0	1.0950
16	*Mesocricotopus*	9	9.6	12.6	11.5	0.8	15.4715	5.5	18.5	10.3	0.4	2.3794
17	*Nanocladius*	25	9.2	15.3	12.3	1.9	9.1530	1.1	25.0	5.1	0.9	1.2638
18	Orthocladiinae sp 2	10	8.6	16.2	12.6	2.1	10.2466	2.0	19.2	5.3	0.6	2.0736
19	*Paracladius*	18	9.6	12.3	11.0	0.9	6.0377	1.5	49.0	8.9	1.1	3.1928
20	*Parakiefferiella nigra* type	15	9.3	13.6	11.1	1.1	8.7054	2.0	49.0	11.1	0.9	4.1387
21	*Parakiefferiella* sp B	10	10.2	14.8	12.3	1.9	11.0725	2.0	30.0	5.9	1.1	2.6386
22	*Parakiefferiella triquetra* type	26	9.2	14.8	11.7	1.3	9.9799	1.2	49.0	6.9	1.0	1.5559
23	*Parametriocnemus/Paraphaeno.*	17	9.3	16.6	13.2	2.0	18.3451	2.0	49.0	7.2	0.9	4.0502
24	*Psectrocladius (Allo. & Meso.)*	18	9.0	16.6	12.8	1.8	8.3310	1.1	49.0	4.4	1.2	0.8703
25	*Psectrocladius calcaratus* type	15	11.3	16.0	13.4	1.3	10.6758	0.8	19.2	3.7	1.0	-0.2595
26	*Psectrocladius (Psectrocladius)*	88	8.6	16.6	12.6	1.9	15.9141	0.8	49.0	4.6	1.0	0.8969
27	*Psectrocladius septentrionalis* ty	18	10.7	15.3	12.4	1.2	8.6183	1.2	12.8	3.3	0.7	-1.6489
28	*Pseudosmittia /Smittia*	5	10.2	14.4	12.5	1.3	15.8874	1.5	15.5	6.7	0.7	1.2399
29	*Synorthocladius*	9	10.1	14.4	13.1	1.4	17.4376	6.0	49.0	11.5	0.6	7.8654
30	*Zalutschia* type A	51	8.6	15.0	11.6	1.7	3.9445	0.8	30.0	4.5	0.9	0.0814

Table 3.6 continued

Taxon code	Taxon name	occurrence (%)	TEMPERATURE T-Min (°C)	T-Max (°C)	T-Opt (°C)	T-Tol (°C)	WAPLS Beta	DEPTH D-Min (m)	D-Max (m)	D-Opt (m)	D-Tol (m)	WA-PLS Beta[1]
31	*Zalutschia* type B	14	9.4	14.8	11.2	1.1	10.7987	3.0	49.0	12.3	0.7	4.8788
32	*Zalutschia zalutschicola*	12	10.2	16.2	12.7	1.3	19.576	2.0	18.5	4.4	0.6	-1.28516
33	*Chironomus*	84	8.6	16.6	12.8	1.9	12.8042	0.8	49.0	5.2	0.9	1.94375
34	*Cladopelma*	59	9.0	16.2	13.2	1.5	16.6018	0.8	49.0	4.5	0.9	1.30735
35	*Cryptochironomus*	36	9.3	16.0	13.2	1.6	16.4181	0.8	30.0	3.7	0.9	-0.296425
36	*Cryptotendipes*	18	9.3	16.2	13.3	1.5	16.9933	1.1	49.0	4.1	1.3	0.359271
37	*Cyphomella/Harn./Paraclado.*	7	10.6	15.6	13.1	1.6	20.0024	3.1	30.0	8.6	0.8	4.52201
38	*Dicrotendipes*	74	8.6	16.6	13.2	1.6	16.0121	0.8	49.0	4.7	1.2	1.638
39	*Einfeldia*	8	10.6	16.2	13.3	1.7	20.0828	4.0	30.0	14.3	0.8	11.4998
40	*Endochironomus*	25	9.3	16.6	13.5	1.7	19.8728	1.5	20.0	5.1	0.8	2.41458
41	*Glyptotendipes*	31	9.3	16.2	13.5	1.7	19.0994	1.2	49.0	3.6	0.8	-0.48385
42	*Lauterborniella/Zavreliella*	5	12.3	14.8	13.9	1.0	22.3987	1.8	30.0	7.2	1.2	5.02421
43	*Microtendipes*	71	8.6	16.6	12.9	1.7	14.9005	1.1	49.0	4.3	0.9	0.265015
44	*Pagastiella*	33	9.0	15.3	13.0	1.5	14.1285	0.8	49.0	5.4	1.4	2.67344
45	*Parachironomus*	25	9.1	15.3	12.0	2.0	5.66057	1.2	20.0	3.9	0.7	-0.115844
46	*Paratendipes*	9	12.3	15.6	13.7	1.0	22.2211	1.5	49.0	7.8	1.2	5.48319
47	*Phaenopsectra flavipes* type	20	9.3	15.3	12.8	1.5	14.8707	1.5	49.0	6.9	1.3	4.11461
48	*Polypedilum*	64	9.2	16.6	13.3	1.6	17.077	0.8	49.0	4.4	1.0	0.857096
49	*Sergentia*	60	8.6	16.6	12.1	1.7	10.0495	1.2	49.0	7.6	1.2	4.35293
50	*Stictochironomus*	25	9.3	15.6	11.4	1.8	7.5431	1.5	49.0	6.8	0.9	1.20621
51	*Pseudochironomus*	19	10.9	15.3	13.8	1.1	21.1462	0.8	30.0	4.1	1.2	0.035675
52	*Cladotanytarsus mancus* type	20	8.6	16.2	12.8	1.9	11.0513	0.8	30.0	3.4	0.8	-0.355663
53	*Corynocera ambigua*	34	9.3	15.3	12.5	1.4	11.8048	1.5	30.0	3.5	0.7	-0.10634
54	*Corynocera oliveri* type	20	9.3	13.5	11.8	1.2	6.64839	0.8	20.3	3.5	0.9	-1.01217
55	*Stempellina*	13	10.6	16.0	13.2	1.2	17.244	1.6	30.0	10.0	1.0	7.21598
56	*Stempellinella/Zavrelia*	69	8.6	16.6	12.4	1.7	12.3629	1.2	49.0	5.7	1.0	1.70644
57	*Tanytarsus chinyensis*	9	8.6	15.6	13.3	1.6	16.8799	0.8	13.2	4.3	0.9	0.860915
58	Tanytarsina - other	100	8.6	16.6	12.4	1.8	11.3617	0.8	49.0	5.6	1.1	2.08447
59	Ceratopogonidae	35	10.6	16.0	13.5	1.2	17.9414	0.8	49.0	5.8	1.3	2.81537
60	Chaoborus	54	8.6	16.6	13.9	1.5	21.215	0.8	20.0	7.0	0.7	4.60289

[1] The beta coefficients will infer transformed depths, which must be converted to real depths by e^{beta} -1.

3.5 Discussion

3.5.1 Fauna

All taxa previously included in Canadian temperature models (Palmer *et al.*, 2002; Walker *et al.*, 1991, 1997) were also present in this training set. The higher number of taxonomic groupings here is attributed both to the increased taxonomic resolution of some groups (e.g., *Psectrocladius*, *Zalutschia*, other Tanytarsina; see Appendix 1), and to the presence of a greater number of taxa in this study's larger geographical area. The most significant additions were 3 species of *Corynocera*, which were common and often abundant in this training set, but were entirely absent in the eastern training sets. Among the taxa included in the other Canadian models, only *Pseudodiamesa* and *Tribelos* were rare in this training set, and excluded from the model.

Corynocera ambigua has generated discussion for its unusual morphology, and interesting temporal and spatial distributions (Brodersen and Lindegaard, 1999; Walker *et al.*, 2003). Distribution in the Beringia training set confirms *C. ambigua* as a primarily arctic/sub-arctic taxon, that is rare below ~60°N (i.e., only 7 head capsules were found in northern BC). The results of this study also support the conclusion by Brodersen and Lindegaard (1999) that temperature is not a limiting factor in the distribution of *C. ambigua*. Walker *et al.* (2003) suggest a Beringian refugium for this taxon during the last glacial interval, based on its present distribution and limited flight capabilities.

Some controversy surrounds the taxonomy and identification of *Corynocera oliveri* type. A well defined feature of this taxon is the presence of a large surface tooth on the mandible (Brooks, 2004; Walker, 2000). The median teeth are described as prominent or on a separate plane, and where the mandibles are absent, *C. oliveri* type is sometimes lumped with the similarly described *Tanytarsus lugens* type (e.g., Brooks and Birks, 2000; Rosén *et al.*, 2003). To further complicate matters, observations on subfossils from this training set and additional lakes from BC (lakes from Palmer *et al.*, 2002; Walker and Mathewes, 1988) revealed *C. oliveri* type mandibles on specimens with different mentum types (personal observation). For the Beringia training set, the identification of

C. oliveri type agrees with available descriptions, but is further restricted to a single mentum type by a dorso-lateral curvature of the mentum, and is confirmed by the appearance of a very subtle accessory tooth (or tooth-like shading) often visible between the median and first lateral teeth, as drawn in Wiederholm (1983; see Appendix 1 for further details). In the Beringia training set, *C. oliveri* type resembles *C. ambigua* in distribution: it is largely restricted to latitudes north of ~60°N, is moderately common, often abundant and is sometimes found in the same lakes as *C. ambigua*. Although it is absent from the warmest Yukon/NWT and Alaska regions, latitude appears to be the stronger determinant of distribution. Again, its distribution supports the hypothesis of a Beringia refugium for this taxon.

First reported by Walker and Mathewes (1988), *Corynocera* nr. *ambigua* was identified at 4 sites in this training set and shows no geographical overlap with the other two *Corynocera* spp. The composite records indicate a strongly western/coastal BC distribution for this taxon. This again supports the suggestion that *C.* nr *ambigua* survived the last glacial interval in a Queen Charlotte Island refugium (Walker and Mathewes, 1988). *Corynocera* nr. *ambigua* was rare in the training set, and excluded from the model.

3.5.2 Models and Training Set

As inference models get larger in terms of the number of sites, gradient lengths of the environmental variables typically increase too. The tradeoff in having a training set with more diverse sites can be larger errors, and weaker r^2 values. In a comparison of errors, this temperature model gives smaller error estimates ($RMSEP_{boot}$=1.35, $RMSEP_{jack}$ =1.28) than those for other Canadian models ($RMSEP_{jack}$= 1.98, Palmer *et al.*, 2002; $RMSEP_{jack}$= 1.87, Rosenberg *et al.*, 2004; $RMSEP_{jack}$ = 2.26, Walker *et al.*, 1997). This positive result can be partially attributed to a relatively narrow range of mean July air temperatures in the training set. However, the r^2 values (r^2_{boot}=0.51, r^2_{jack}=0.51) are weaker (r^2_{jack}=0.70, Palmer *et al.*, 2002; r^2_{jack}=0.73, Rosenberg *et al.*, 2004; r^2_{jack}=0.88, Walker *et al.*, 1997), as expected for this larger and more diverse training set. The weak

r^2_{boot} (0.43) for the depth model is again expected given the great diversity and range of depths in the training set. These results were also suggested by the ratios of the first to second eigenvalues (depth: λ_1/λ_2=0.35; temperature: λ_1/λ_2=0.44) in the constrained CCAs. These modest ratios (as compared with λ_1/λ_2=1.15 for Walker *et al.*, 1991) indicate the importance of multiple variables in explaining the distribution of taxa.

Forward selection in CCA indicates that at least nine environmental variables explained significant portions of the midge distribution. However, the gap between the variance explained by the significant environmental variables and the total variance (1.786; Table 3.3) indicates that the distribution of midge taxa is also affected by additional factors not included in the statistical analyses. For example water temperature (surface and profundal), lake substrate, sources of food (i.e., within lake flora and fauna) and predators (i.e., presence of fish) might also contribute significantly to the dispersion of midge taxa. Where practical, inclusion of additional variables could provide additional information on distribution of midge taxa.

For the environmental variables that were included, diverse sites that increase the gradient also increase the chance of capturing the conditions that correspond with past assemblages. This is especially important in Beringia, as it presents the potential to apply this model to some of the oldest midge assemblages in the country. To this end, at the cost of higher errors, future studies might benefit from an even longer gradient of temperatures. This could be achieved by (1) extending the transect farther north with sites from the Canadian high arctic, or (2) selecting a different measure of temperature that better captures the climatic gradient of the transect. The temperature gradient along the transect is greatest in the winter, suggesting an index that incorporates winter temperatures, as for example a simple mean annual temperature.

The paucity of quantitative climate data for Beringia makes these models important tools for data generation. However, some caution is suggested in the interpretation of the palaeotemperatures and palaeolake-levels derived from these models. Reconstructed mean July air temperature in particular is constrained by the short gradient (8.6°C to

16.6°C) captured in the training set. The depth gradient is large (<1m to 49 m), but so too is the error (for example, after correction to untransform the data, an inferred depth of 5 m would have error bars from 2-10 m). As Walker *et al.* (2003) point out, fluctuations in water-levels are often too small to be satisfactorily reconstructed. However, atypical fluctuations of as much as 18m have recently been identified in central Alaska (Abbott *et al.*, 2000; Barber and Finney, 2000; Bigelow and Edwards, 2001). In regions where large depth fluctuations have occurred, the midge depth model provides a means to detect and describe these changes. Of most importance is the usefulness of both models to illustrate past patterns (i.e., timing, magnitude and direction) of climatic change. Patterns generated by these models will contribute data that is independent of existing data, largely based on vegetation records.

In addition to providing data for the models, the training set provides an excellent database for climate reconstruction by the Modern Analogue Technique. Here again, the diversity of sites and assemblages captured by the long transect and environmental gradients is an asset. Where close analogues exist, temperature and depth can be reconstructed, and insights can be gained into additional elements of the palaeoenvironment such as vegetation type.

4 A Palaeoclimatic Reconstruction for Antifreeze Pond, Yukon Territory

4.1 Introduction

As scientists work to put current climate change in the context of long term patterns and cycles of change, an understanding of past climates is essential. Beringia is an excellent repository for such palaeoclimatic information. Composed of parts of Yukon, Alaska, the former Bering Land Bridge and adjacent Siberia, Beringia remained unglaciated throughout the Quaternary, and contains a wealth of climate sensitive proxies buried in its sediments.

Early palaeoclimatic studies in Beringia focused largely on pollen, and provide an understanding of the transition from a cold and dry full glacial to a warmer and wetter Holocene (Elias, 2001a). More recently, additional proxies have proven useful for addressing higher resolution questions in Beringia and elsewhere. Chironomids, diatoms, cladocera, loss-on-ignition and other indicators have all contributed to temperature reconstructions (Battarbee, 2000; Rosén *et al.*, 2003), lake-level reconstructions (Abbott *et al.*, 2000; Edwards *et al.*, 2000), and the detection of climate reversals (Levesque *et al.*, 1993). Chironomids (order Diptera) and other midges have been used repeatedly to produce high resolution temperature reconstructions with errors of less than 2°C. No midge temperature or depth reconstructions exist yet for Beringia.

Antifreeze Pond in southwest Yukon was first cored and the pollen analysed by Rampton (1969, 1971). Bulk sediment radiocarbon dates obtained by Rampton produced four near basal dates from 27,100 to 31,500 ^{14}C yr BP. These dates are older than most eastern Beringian cores, which often end with basal dates of late glacial age (for example Abbott *et al.*, 2000; Bigelow and Edwards, 2001; Hu *et al.*, 1993). While bulk sediment dates are less reliable than modern AMS dates, these old dates provided the impetus to revisit and reanalyse Antifreeze Pond.

The aim of this research is to produce a palaeoclimatic record of southwest Yukon by reconstructing mean July air temperature and depth from 1) recently developed Beringian midge models, and 2) Modern Analogue Technique used in conjunction with the Beringia training set.

4.2 Study Area

Antifreeze Pond (62°20.4′ N, 140°49.2′ W; 650 m asl), is situated about 5 km southeast of the community of Beaver Creek, Yukon, off the east side of the Alaska Highway (Fig. 4.1). This is located in the southeast corner of the Yukon, a mountainous region where the northwest-southeast trending St. Elias Mountains connect the Coastal Mountains of Alaska with those of BC.

Protected from the Pacific Ocean by the St. Elias Mountains, Antifreeze Pond is subjected to a pronounced continental climate (Wahl *et al.*, 1987). Summers are mild with a mean July air temperature of 13°C to 14°C (Spatial Climate Analysis Service, 2001; Wahl *et al.*, 1987), though daytime highs typically reach 18°C to 23°C and can hit extremes near 30°C (Wahl *et al.*, 1987). Winters are long and cold with four months below –20°C, and January the coldest of those at –28°C. The region receives approximately 400 mm of precipitation, most falling as rain during the summer months. The frost-free period extends from late June to mid August, and Antifreeze Pond falls on the transition between sporadic and extensive discontinuous permafrost. The climate is hard on vegetation, and Antifreeze Pond is surrounded by stunted black spruce forest and tussock muskeg, both typical for the region.

Antifreeze Pond is small, with a surface area of approximately 1 ha, and a diameter of 120 m. Late winter measurements gave a maximum lake depth of 119 cm, topped by 58 cm of ice. This is approximately equal to a summer depth of 1.7 m. There is no inflow to the pond; a small outlet exists to the west. Patches of peat are immediately adjacent to the pond, and the surrounding area is relatively flat. Rampton (1971) situates Antifreeze Pond on a moraine deposited by the Mirror Creek glaciation (tentatively equivalent to the Reid glaciation), and places the maximum extent of the McConnell glaciation (locally named the Macauley glaciation by Rampton) 6 km to the southeast.

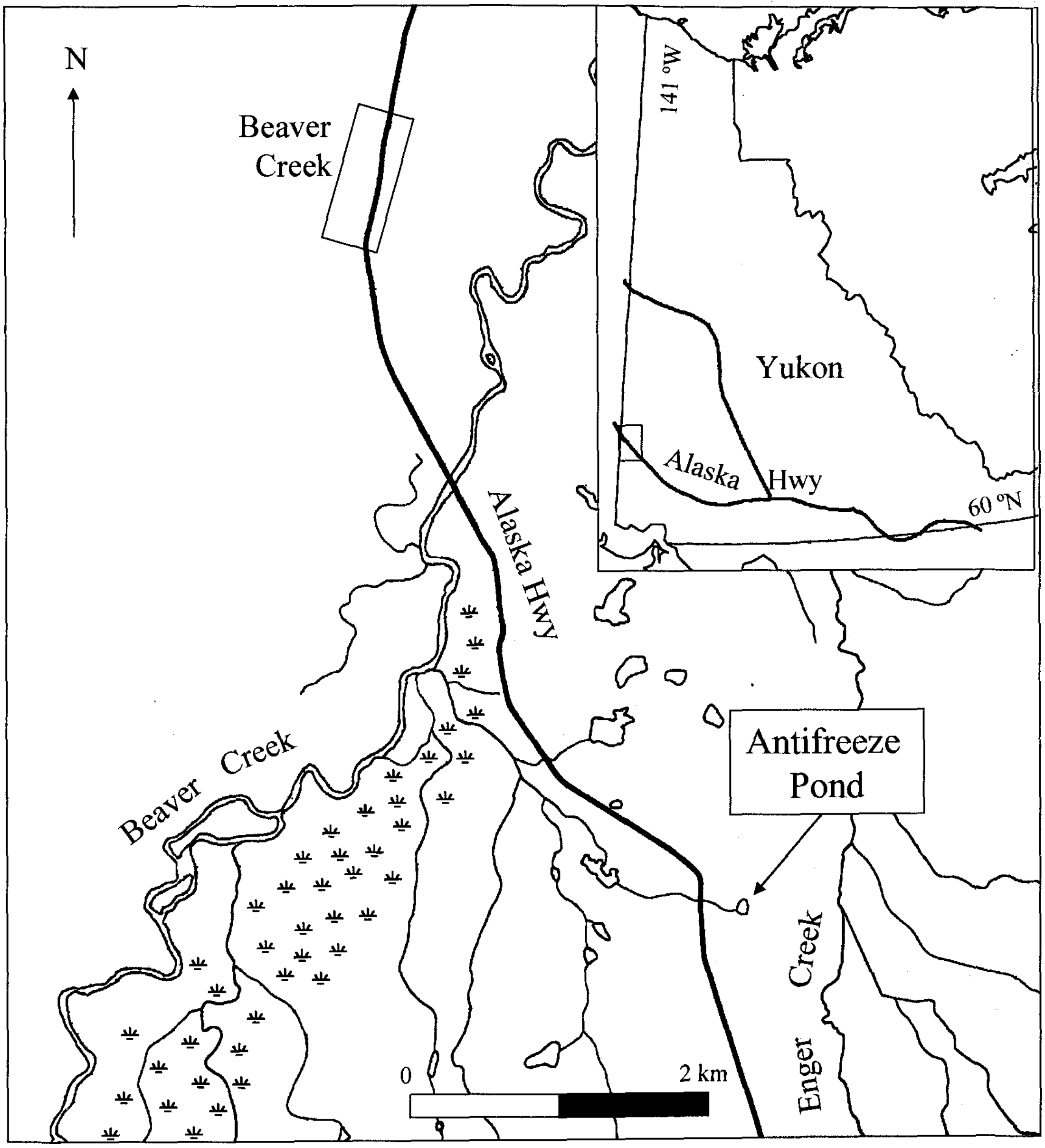

Figure 4.1 Map locating Antifreeze Pond in southwestern Yukon Territory.

4.3 Methods

4.3.1 Field and Laboratory Methods

Antifreeze Pond was cored through the ice in April of 2001. A modified Livingstone piston corer was used to retrieve two parallel cores near the deepest part of the pond. The first and second cores yielded 446 and 510 cm of sediment respectively. The cores were transported to the University of New Brunswick for storage until sampling.

The parallel cores were then carefully matched through comparison of their sediments, and the basal meter from the second core was patched to the first core to form a continuous 500 cm record. Samples from the patched record were obtained for loss-on-ignition (LOI), a measure of the organic content of a sample (Dean, 1974; Kurek *et al.*, 2004).

Up to 3 mL of sediment from each 0.5 cm interval were designated for analysis of midges. Midges were analyzed at 4 cm intervals, except between 368 and 256 cm where a preliminary analysis at 8 cm intervals showed chironomid remains to be rare. Midge processing and identification follows that outlined earlier in this thesis (3.2.2 Midge Analysis, paragraphs 3 & 4). For statistical significance, a target minimum of 50 identifiable chironomid head capsules per interval was used (Heiri and Lotter, 2001; Quinlan and Smol, 2001). However, concentration of chironomid head capsules varied greatly throughout the core, and several intervals yielded counts of less than 50 (488.5 cm, 368-256 cm, and 176-148 cm).

4.3.2 Chronology

Twenty six samples were obtained for AMS radiocarbon dating (Table 4.1). All samples were submitted to the Lawrence Livermore National Laboratory in Livermore, California for analysis. Dates of <20,000 ^{14}C yr BP were calibrated using CALIB 4.4 (Stuiver and Reimer, 1993).

Table 4.1 AMS radiocarbon dates for Antifreeze Pond.

Depth (cm)	Laboratory number	^{14}C age BP	Calibrated age* (cal. years BP)	Relative area under probability distribution	Material dated
40-40.5	CAMS-94344	2555 ± 30	2492 - 2596	0.347	unidentified wood fragments
			2608 - 2641	0.136	
			2706 - 2752	0.517	
50.5-51	CAMS-94354	2990 ± 35	3003 - 3006	0.002	unidentified wood fragments
			3038 - 3045	0.007	
			3062 - 3268	0.924	
			3286 - 3323	0.068	
58-58.5	CAMS-94345	2805 ± 35**	2787 - 2829	0.089	unidentified wood fragments
			2840 - 2990	0.911	
80.5-81	CAMS-94355	6100 ± 35	6803 - 6824	0.051	unidentified twig
			6857 - 7027	0.864	
			7076 - 7088	0.017	
			7126 - 7156	0.068	
104.5-105	CAMS-94346	6915 ± 45	7661 - 7838	1	unidentified wood fragments
114.5-115	CAMS-94356	2705 ±35**	2752 - 2862	1	unidentified wood fragments
120-120.5	CAMS-94347	8150 ± 60	9000 - 9290	0.992	spruce and unidentified wood fragments, 2 sedge achenes
			9360 - 9370	0.003	
			9390 - 9400	0.005	
142.5-143	CAMS-94357	8625 ± 35	9530 - 9633	0.812	unidentified twig
			9638 - 9695	0.188	
147-147.5	CAMS-94348	9630 ± 30	10759 - 10833	0.149	unidentified wood fragments
			10836 - 10958	0.427	
			10999 - 11018	0.021	
			11043 - 11047	0.003	
			11056 - 11165	0.399	
154.5-156	CAMS-94358	10110 ± 35	11343 - 11389	0.034	unidentified wood fragments
			11411 - 11507	0.105	
			11547 - 11773	0.581	
			11795 - 11986	0.234	
			12002 - 12107	0.047	

Table 4.1 continued

Depth (cm)	Laboratory number	^{14}C age BP	Calibrated age* (cal. years BP)	Relative area under probability distribution	Material dated
160-160.5	CAMS-94349	10805 ± 35	12634 - 12750	0.246	unidentified wood fragments
			12789 - 13007	0.724	
			13051 - 13098	0.031	
170-170.5	CAMS-94359	10780 ± 45	12628 - 12760	0.284	unidentified twig
			12776 - 13002	0.699	
			13056 - 13093	0.018	
179.5-181	CAMS-94350	12200 ± 30	13841 - 13929	0.054	22.5 *Hippuris vulgaris* seeds
			14069 - 14375	0.526	
			14613 - 15357	0.421	
189.5-191	CAMS-94360	12270 ± 60	13850 - 13910	0.021	18 *Eleocharis* seeds
			14080 - 14410	0.482	
			14570 - 15400	0.497	
189.5-191	CAMS-94351	12245 ± 45	13849 - 13917	0.029	40 *Hippuris vulgaris* seeds
			14079 - 14395	0.502	
			14590 - 15384	0.469	
199.5-201	CAMS-94361	12225 ± 35	13846 - 13922	0.038	22.5 *Hippuris vulgaris* seeds
			14076 - 14384	0.516	
			14602 - 15369	0.446	
219.5-221	CAMS-94352	12320 ± 60	14100 - 14450	0.449	11 *Eleocharis* seeds
			14530 - 15440	0.551	
229.5-231	CAMS-94362	12300 ± 35	13870 - 13889	0.005	11.5 *Hippuris vulgaris* seeds
			14097 - 14420	0.467	
			14560 - 15417	0.528	
229.5-231	CAMS-94353	12350 ± 50	14110 - 14460	0.426	17 *Eleocharis* seeds
			14530 - 15430	0.574	
230.5-231	CAMS-94363	12410 ± 110	14120 - 15440	1	unidentified twig
371.5-375.5	CAMS-107171	12900 ± 210	14350 - 16110	1	unidentified wood fragments
375.5-377	CAMS-95383	16480 ± 820	17690 - 21630	1	~2300 chironomid head capsules
449-450.5	CAMS-96823	15810 ± 150	18230 - 19570	1	~5000 chironomid head capsules
449-450.5	CAMS-94364	43830 ± 810	n/a	n/a	5 Potamogeton fruit stones
452-457.5	CAMS-107172	38010 ± 6640	n/a	n/a	unidentified wood fragments + 2 *Carex* seed coats
493-497	CAMS-107173	28170 ± 1110	n/a	n/a	unidentified wood fragments + 1 *Carex* seed

* CALIB 4.4, 2 sigma values (Stuiver and Reimer, 1993)

** Rejected AMS date

Twenty terrestrial and emergent macrofossil samples provided dates for the upper portion of the core. A date at 114.5 cm was rejected as it was out of line with both the underlying and older overlying dates. A second reversal occurred in the date at either 50.5 - 51 cm or 58 - 58.5 cm. The age at 58 cm was rejected as this allowed for a more constant rate of sedimentation. This interval also coincides with the appearance of semi-terrestrial chironomids suggestive of fluctuating water levels (see 4.4.1 Midge Stratigraphy) that could cause re-working of organic matter (Abbott *et al.*, 2000). A tephra layer at 30 cm, presumed to be the White River Ash, provides the youngest age at 1,250 ^{14}C yr BP (Clague *et al.*, 1995; Richter *et al.*, 1995). A depth-age model for the upper core is inferred by linear interpolation between the accepted AMS dates (Fig. 4.2).

In the lower core, terrestrial macrofossils were scarce and yielded only three samples (Table 4.1). A date was also obtained on an aquatic macrofossil. Chironomid head capsules were recently demonstrated to yield reliable radiocarbon ages (Fallu *et al.*, 2004), and two chironomid samples from the lower core were picked and dated. Unfortunately, the lower core ages are problematic and indicate either errors or reversals in dating (Fig. 4.2). Further, the sedimentation rate in the upper core is variable, and precludes extrapolation to a basal date.

A date of 43,830 ± 810 ^{14}C yr BP was obtained on five *Potamogeton* fruitstones (449 - 450.5 cm). Given the presence of underlying undisturbed laminae (at 490 - 500 cm), and given that *Potamogeton* is an aquatic, the fruitstones must have originated in the pond during the timespan represented by the core. Dates obtained on aquatic macrofossils are at risk of contamination with old carbon if a ^{14}C reservoir effect exists (Abbott and Stafford, 1996; Björck and Wohlfarth, 2001). At present, Antifreeze Pond is shallow with no evidence of carbonates or local limestone to suggest such an effect, though past sources of old carbon are hard to rule out (Hutchinson *et al.*, 2004).

Despite the reliable chironomid dates obtained by Fallu *et al.* (2004), two factors predispose the chironomid dates of this study to contamination errors. Firstly, these samples are older than the Holocene aged samples of Fallu *et al.* (2004), and thus any

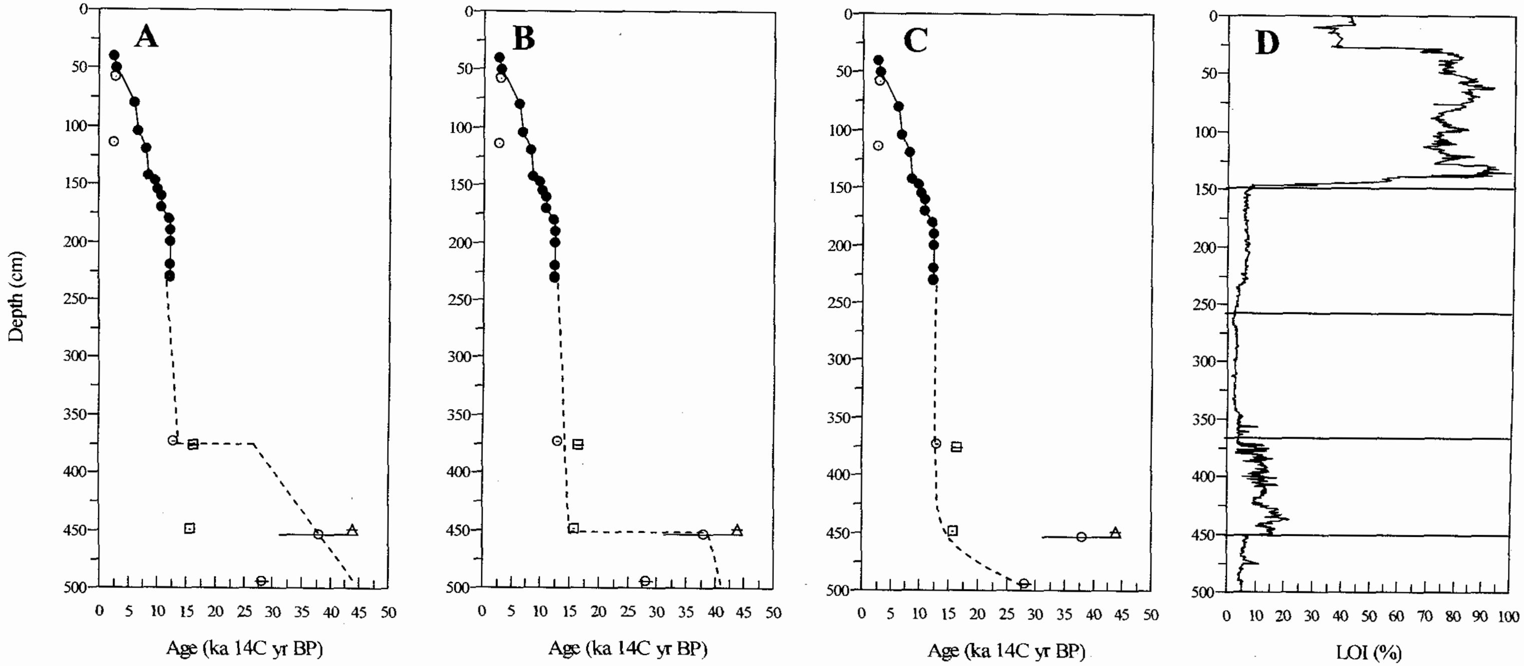

Figure 4.2 A-C) Depth-age profiles for Antifreeze Pond, showing all AMS radiocarbon dates with errors (small error bars not visible). In the upper core, linear interpolation (solid lines) between accepted dates was used to create a depth-age model. For the lower core, three possible chronologies (broken lines) are illustrated: A) chronology 1, B) chronology 2 and C) chronology 3. Source of dated material: ● terrestrial or emergent macrofossils (accepted), ○ terrestrial or emergent macrofossils (rejected in the upper core, status uncertain in the lower core), □ chironomid head capsules (status uncertain), Δ aquatic macrofossils (status uncertain). D) A loss on ignition (LOI) curve for Antifreeze Pond. The LOI curve is included for comparison, as the zonation reflects change in sediment and midge composition.

contamination with modern carbon would have a greater effect (i.e., produce a greater error) on the reported age of the sample. In addition, these chironomid samples have a greater probability of contamination from modern carbon, as they took longer to pick due to their larger sizes (~2300 and ~5000 chironomid headcapsules compared with an average of ~2000 for Fallu *et al.*). Despite efforts to maintain a clean work environment, foreign fibres had to be removed from both samples prior to submission.

Terrestrial macrofossils are the preferred material for radiocarbon dating, as they generally yield the most reliable dates (Björck and Wohlfarth, 2001). However, even the terrestrial macrofossil dates in the lower core are problematic. The two older dates are on macrofossils of mixed sources (unidentified wood fragments and *Carex* seed coats) and have very large errors (1110 and 6640 ^{14}C yr). In addition a reversal in these two older terrestrial dates exists. Reversals are often explained by a re-working of older material into younger sediments (Björck and Wohlfarth, 2001), though the older date is supported by the (admittedly also problematic) aquatic date.

Dates from all three source materials were obtained at ~450 cm, and gave a large age range of ~28,000 ^{14}C yr. There is the potential that some of this discrepancy can be attributed to contamination, as both the chironomid and aquatic samples are at risk of contamination. Important differences exist between the effects of contamination with younger and older carbon sources. To give some perspective on these effects, a comparison was done of the percentage of contamination that would be required to explain the different dates at 450 cm (Table 4.2). For simplification, all samples were assumed to be of the same real age, and only modern and dead (i.e., inactive) sources of carbon contamination were considered. Acceptance of the 15,810 ^{14}C yr BP chironomid date requires that a substantial >90% of the terrestrial and aquatic samples were contaminated with dead carbon. Acceptance of the 38,010 ^{14}C yr BP terrestrial macrofossil date requires significant contamination (51%) of the aquatic sample with dead carbon. This in turn requires a significant input of dead carbon into the watershed, as atmospheric exchange with this shallow lake would provide a modernizing influence on the carbon ratio. Acceptance of the 43,830 ^{14}C yr BP aquatic date, or even of a date

Table 4.2 A comparison of the theoretical contamination required to produce the three different radiocarbon dates at 450 cm.

Potential real age			Contamination[2]			Apparent age	
Age	% C	Fm[1]	Age	% C	Fm	Age	Fm
15,810	100.00	0.1397	n/a	0.00	n/a	15,810	0.1397
15,810	6.30	0.1397	dead	93.70	0	38,010	0.0088
15,810	3.08	0.1397	dead	96.92	0	43,830	0.0043
38,010	86.79	0.0088	modern	13.21	1	15,810	0.1397
38,010	100.00	0.0088	n/a	0.00	n/a	38,010	0.0088
38,010	48.86	0.0088	dead	51.14	0	43,830	0.0043
43,830	86.40	0.0043	modern	13.60	1	15,810	0.1397
43,830	99.55	0.0043	modern	0.45	1	38,010	0.0088
43,830	100.00	0.0043	n/a	0.00	n/a	43,830	0.0043
infinite	86.03	0	modern	13.97	1	15,810	0.1397
infinite	99.12	0	modern	0.88	1	38,010	0.0088
infinite	99.57	0	modern	0.43	1	43,830	0.0043

[1] Fm (Fraction modern) of carbon in a sample is calculated by $Fm=e^{-t/8033}$, where t is the age of the sample relative to a standard of 1950

[2] Two contamination sources are considered: dead (i.e., inactive), and modern carbon.

beyond the limits of radiocarbon dating, requires only 14% contamination with modern carbon in the chironomid sample, and less than 1% contamination of the terrestrial sample. If the samples are all of the same age, the discrepancy in dates is most easily attributed to contamination of the chironomid sample. This comparison supports an age of >38,000 ^{14}C yr BP for the lowest section of the core.

Rampton (1971) based his chronology on 10 bulk sediment radiocarbon dates (Table 4.3), and the correlation of his sediment profile with others in the region. Prominent in the sediment is a clayey silt layer that Rampton interpreted as loess deposited during the full glacial. Rampton's date of 13,500 ^{14}C yr BP for the upper boundary of the loess provides a defining date for the retreat of the McConnell glaciation (Fraser and Burn, 1997; Jackson *et al.*, 1991). At some localities in the region, a thin layer of tephra, presumed to be the Dawson tephra, is common near the base of the loess layer and provides a finite date of ~24,000 ^{14}C yr BP (Fraser and Burn, 1997; Froese *et al.*, 2002; Rampton, 1969). Bulk sediment samples in the lower core yielded four dates between ~27,000 and ~31,000 ^{14}C yr BP, but these were out of order and provide poor chronological control for the lower core.

Despite efforts to date the lower half of the core, a precise chronology remains elusive. The available dates are plagued by significant potential for error. Three possible chronologies are proposed here, though none satisfies all the evidence available, and other possibilities certainly exist.

Chronology 1. Chronology 1 agrees largely with Rampton, but with one modification. It infers a hiatus at ~375 cm such that the underlying two zones are of interstadial age, the overlying zone (~375 to ~250 cm) is sediment deposited near the end of the full glacial (i.e., early deglaciation), and the peak of the full glacial is absent from the record. This chronology attributes the two dates at ~375 cm to the overlying sediments, and rejects the chironomid date at ~450 cm (15,810 ^{14}C yr BP), and the terrestrial macrofossil date at ~495 cm (28,170 ^{14}C yr BP).

Table 4.3 Bulk sediment radiocarbon dates from Rampton (1971).

Depth (cm)*	Laboratory number	^{14}C age BP	Material dated
130-135	GSC-1040	5690 ± 140	detritus gyttja
173-178	GSC-1242	8710 ± 160	detritus gyttja
197-200	GSC-1042	9980 ± 150	gyttja
278-283	GSC-1110	13500 ± 300	clayey silt w organic detritus
392-412	GSC-1048	31500 ± 700	organic silt
395-404	GSC-1257	28500 ± 440	organic silt
417-432	GSC-1198	27100 ± 390	organic silt
502-520	GSC-1230	29700 ± 700	organic silt
base of adjacent bog	GSC-496	> 36000	organic silt

* In order to better correlate Rampton's published depths with those of this thesis, a correction of 110 cm has been subtracted based on the depth of the White River Ash.

Chronology 2: This chronology infers a hiatus at ~450 cm with the underlying sediments deposited during the interstadial, the overlying sediments deposited during the end of the full glacial (i.e., early deglaciation), and no sediments captured during the peak of the full glacial. This chronology accounts for the dating discrepancy at 450 cm, as the three dates could all be more or less accurate if the older two dates are associated with the lower zone, and the younger chironomid date with the overlying sediment. The terrestrial macrofossil date at ~495 cm (28,170 ^{14}C yr BP) is rejected.

Chronology 3: Chronology 3 infers a continuous record that extends back to the full glacial. Here, the lowermost three zones represent variation within the full glacial, with the basal zone (~500 to ~450 cm) deposited during the peak of glaciation, and the overlying two zones (~450 to ~250 cm) during deglaciation. The two older dates at ~450 cm (38,010 and 43,830 ^{14}C yr BP) are rejected.

4.3.3 Data Analysis

For statistical analyses, taxon abundances were calculated as a percent of total identifiable midges, while for graphing purposes taxon abundances were presented as a percent of total identifiable chironomids. Percent abundance data for midges were compiled and graphed using C2 v1.4 Beta (Juggins, 2003). Stratigraphically constrained zones were delimited with reference to CONISS (Grimm, 1987) in the program ZONE v1.2 (Juggins, 1991). Data were square root transformed for further analysis.

Intervals from Antifreeze Pond were compared with samples from a Beringia training set to assess the similarity between assemblages past and present. The Beringia training set consists of modern samples from 121 lakes from Alaska, Yukon, NWT and BC, and is described earlier in this thesis (3.2 Methods). Similarity was measured as the squared chord distance between closest analogues, using Modern Analogue Technique (MAT) in the program C2 v1.4 Beta (Juggins, 2003). First, the self-similarity of modern assemblages in the training set (excluding rare taxa and outliers, as defined in section 3.3.1 Data Screening) was assessed, and 75% and 95% confidence intervals for these values determined. Assemblages from Antifreeze Pond (excluding rare taxa, defined as above with intervals substituted for lakes) were then compared with those of the training set to determine the closest analogue for each interval. Squared chord distances greater than the 95% confidence interval were used to define intervals with no analogue, those less than the 75% confidence interval indicated good analogues, and those in between indicated weak analogues (Laing *et al.*, 1999).

Data were then entered into the models for inferring mean July air temperatures and depth that were developed from the Beringia training set earlier in this thesis (see 3.4.3 Model Development). Mean July air temperatures and depth were also inferred using MAT to compare intervals with lakes of the Beringia training set. Given the short gradient of temperatures in the Beringia training set, and the shallowness of Antifreeze Pond, the five best analogues (versus the standard 10) were used to calculate weighted averages of temperature and depth. This procedure was followed to ensure the sensitivity of reconstructions, although it came at the cost of higher sample specific errors.

4.4 Results

4.4.1 Midge Stratigraphy (Fig. 4.3)

Zone AF-1 (497.5-450.5 cm)

This basal zone consists of distinctive and unusual assemblages with a low taxon richness. *Cricotopus/Orthocladius* dominates, constituting ~30-70% of the assemblages; *Sergentia* is also prominent at ~10-30%. Low abundances of *Corynocera oliveri* type, *Chironomus*, *Zalutschia* sp A, *Procladius*, *Psectrocladius (Psectrocladius)*, Tanytarsina – other (not shown in fig. 4.3) and *Corynoneura/Thienemanniella* fill out the assemblages. The organic component in the basal sediments is low, with an average LOI of 5%. The assemblages and LOI throughout this zone are uniform until a sharp transition leads into zone 2.

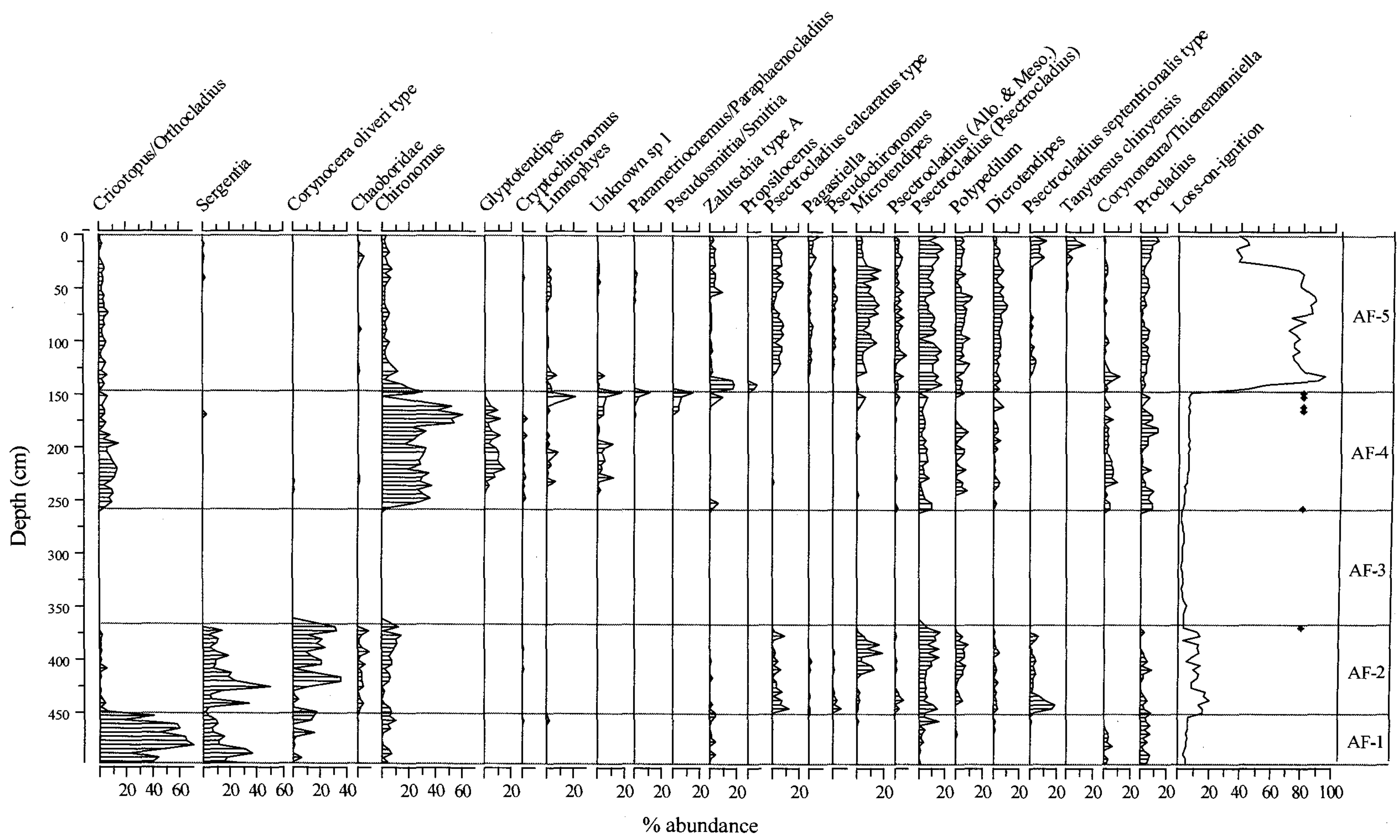

Figure 4.3 A chironomid stratigraphy for Antifreeze Pond. Select taxa are shown, and all taxon abundances are presented as a % of the total identifiable chironomids. Data is presented for intervals with greater than 15 chironomid head capsules; intervals with low counts (15-35 chironomid head capsules) are indicated by a ◆.

Zone AF-2 (450.5-366 cm)

The number of taxa present in zone AF-2 is twice that found in the previous zone. The formerly dominant *Cricotopus/Orthocladius* almost disappears (~1%), whereas *Sergentia* remains abundant (~10-50%). *Corynocera oliveri* type increases with peaks of up to 35%. The increased taxon richness is made up of *Psectrocladius calcaratus* type, *Psectrocladius septentrionalis* type and an increase in Chironomini taxa. LOI also increases to an average of 13%. Like AF-1, the assemblages within this zone are generally uniform.

Zone AF-3 (366-258 cm)

Chironomids were rare in this zone with samples averaging one chironomid/cm^3 (Table 4.4). These exceptionally low counts create unrepresentative percentage data, and so were omitted from the stratigraphy and reconstructions. LOI for this zone is the lowest in the core at about 3%.

Zone AF-4 (258-146 cm)

Cricotopus/Orthocladius increases from AF-2 levels to ~7%, while the formerly abundant *Sergentia* and *Corynocera oliveri* type are virtually absent. *Chironomus* (~32%) and *Cryptochironomus* (~1%) are at their maximum abundance in this zone, while *Glyptotendipes* (~5%) is entirely restricted to this zone. Some of the taxa found in zone AF-2 re-appear, for example *Psectrocladius* (*Psectrocladius*), *Polypedilum*, and *Dicrotendipes*, while others such as *Psectrocladius calcaratus* type, *Psectrocladius septentrionalis* type and *Microtendipes* do not. Four semi-terrestrial taxa appear in this zone: *Limnophyes*, *Parametriocnemus/Paraphaenocladius*, *Pseudosmittia/Smittia* and Unknown sp 1[2]. The top four intervals of this zone, with low counts (16-27 head

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[2] Unknown sp 1 is assumed to be semi-terrestrial based on its strong correlation with semi-terrestrial taxa here, and its co-occurrence with *Limnophyes* elsewhere (pers. obs.)

Table 4.4 Raw midge data (number of head capsules recovered) for intervals 260 to 360 cm of Antifreeze Pond.

depth (cm)	# of head capsules	taxa
260	5.0	Tanytarsina - other (3), *Chironomus* (1), *Cricotopus/Orthocladius* (1)
264	1.0	*Chironomus* (1)
272	0.0	
280	1.0	*Chironomus* (1)
288	0.0	
296	0.5	*Microtendipes* (0.5)
312	0.0	
320	3.5	Tanytarsina - other (2), *Chironomus* (0.5), *Polypedilum* (1)
328	0.0	
336	2.0	Tanytarsina -other (2)
344	0.0	
352	4.0	Tanytarsina - other (1), *Cryptochironomus* (1), chironomidae - unidentified (2)
360	1.0	*Procladius* (1)

capsules), require caution in their interpretation. The general uniformity of assemblages through the remainder of this zone shows that counts of ≥35 head capsules are sufficient to be statistically representative. LOI increases somewhat, but remains low at 6%.

Zone AF-5 (146-0 cm)

No taxa dominate this zone, rather the assemblages are composed of a diverse fauna. At the base of the zone, a peak in *Zalutschia* type A coincides with the appearance of *Propsilocerus*. Following this, there is a synchronous appearance (at 130 cm) of *Psectrocladius calcaratus* type, *Psectrocladius septentrionalis* type, *Pagastiella* and *Pseudochironomus*. Three semi-terrestrial taxa *Limnophyes*, *Parametriocnemus/ Paraphaenocladius* and Unknown sp 1 re-appear from 58-30 cm. At 30 cm, the deposition of the White River Ash further affects the assemblages: *Tanytarsus chinyensis* type appears, *Psectrocladius septentrionalis* type increases, and *Pseudochironomus* and *Microtendipes* decrease. LOI for the zone begins with a sharp increase to 94% (from 6% in the previous zone), then plateaus at 78% before dropping again to 42% following the White River Ash.

4.4.2 Temperature and Depth Reconstructions

The Beringia training set provided adequate analogues (squared chord distance ≤ 17.4) for the majority of intervals in Antifreeze Pond (Fig. 4.4). The oldest zone (AF-1) yielded good analogues (squared chord distance <14.1), for all but one interval. In zones AF-2 and AF-4, weak analogues (squared chord distance 14.1 to 17.3) dominated. The intervals with no analogues occurred primarily in AF-2, at the AF-4/AF-5 boundary (late glacial to Holocene transition), and following the deposition of the White River Ash at 30 cm. This method provides a conservative evaluation of analogues, and confirms that the Beringia training set (and models derived therefrom) provides a good fit for Antifreeze Pond.

The WA-PLS and MAT methods yielded very similar patterns in mean July air

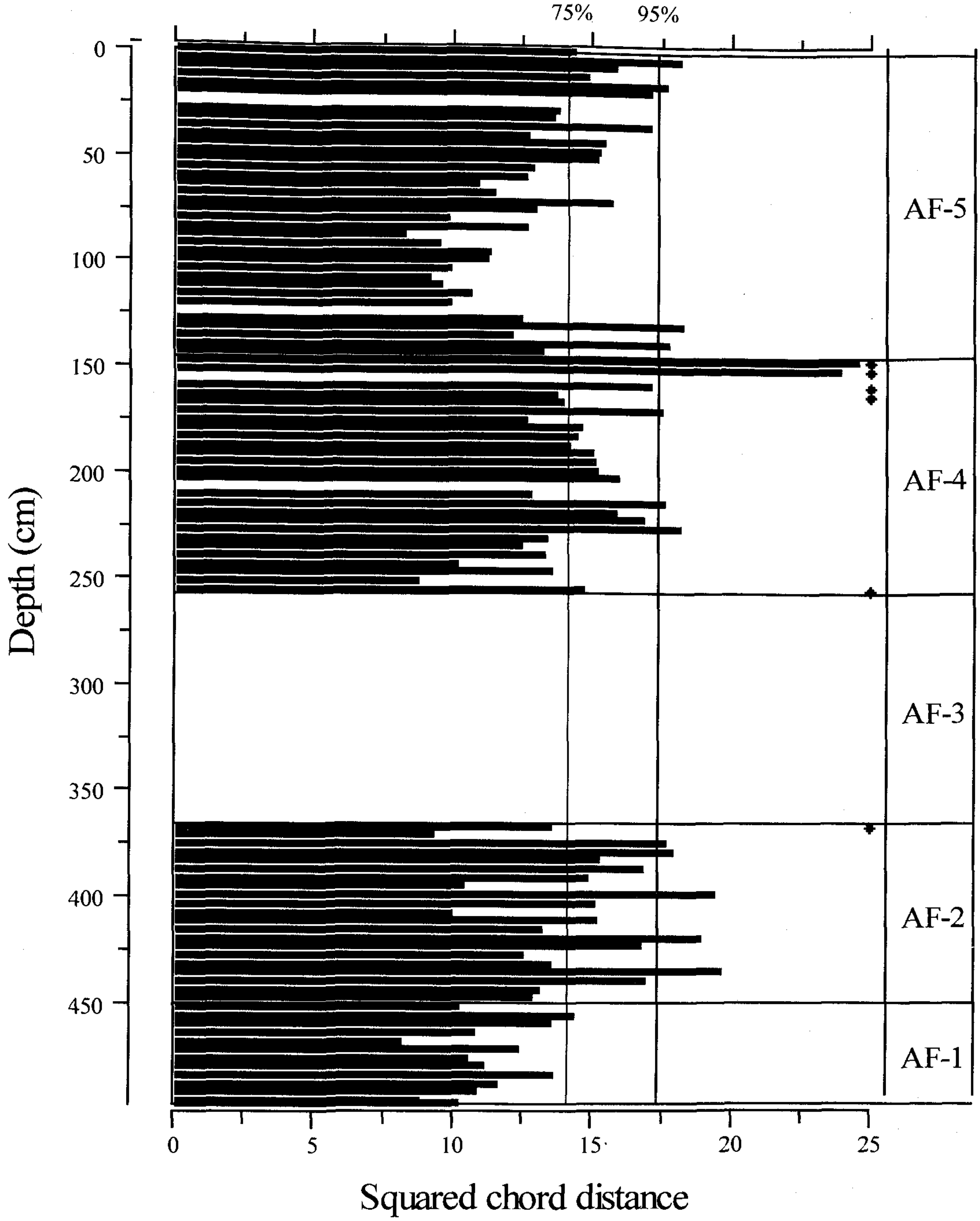


Figure 4.4 An analogue comparison of intervals from Antifreeze Pond with sites from the Beringia training set. Intervals with squared chord distances below the 75% confidence interval have good analogues, those between 75% and 95% have weak analogues, and those greater than 95% have no analogues. Intervals with low counts (15-35 chironomid head capsules) are indicated by a ◆.

temperature. Temperatures inferred by the WA-PLS model ranged from 8.9°C to 14.6°C (Fig. 4.5). The surface sample gave an inferred temperature of 13.0°C, well within the model error (1.3°C) of the modern temperature obtained from PRISM (13.2°C; Spatial Climate Analysis Service, 2001). For MAT, the temperature range was narrower at 9.7°C to 14.5°C, and the surface sample lower at 11.8°C. Lowess smooths were fitted to both reconstructions to highlight broad patterns of temperature change.

Changes in lake depth are complicated by the accumulation of sediment over time. With less accumulated sediment in the past, the overflow (i.e., maximum) depth of Antifreeze Pond would have been deeper than the present 1.7 m. Inferred depths are compared with inferred past overflow depths. These overflow depths are estimated by adding sediment depth to lake depth. For the upper two zones, WA-PLS and MAT inferred very similar patterns of lake level changes, however for the lower two zones, these patterns differed (Fig 4.6). For the basal zone (AF-1), the high quality of analogues supports the reconstruction inferred by MAT. For AF-2, the differences are significant, and it is unclear which is the more probable reconstruction. Again, lowess smooths were fitted to the data to highlight the patterns in the lake depth record.

For each zone, the climate as inferred by midges is compared with Rampton's (1971) climate inferences based on the pollen record. Correlation of the midge and pollen records was determined primarily by comparison of sediment descriptions for the two cores (Fig 4.7). Currently, the pollen record is being reanalysed (from the same cores as the midges) and will allow for better correlation between the midge and vegetation records.

Zone AF-1 (497.5-450.5 cm)

This basal zone represents the coldest and driest conditions captured by the midges. Temperatures for this zone inferred by WA-PLS and MAT respectively averaged 3.3°C and 2.3°C colder than modern. This is the only zone where the MAT inferred depth was

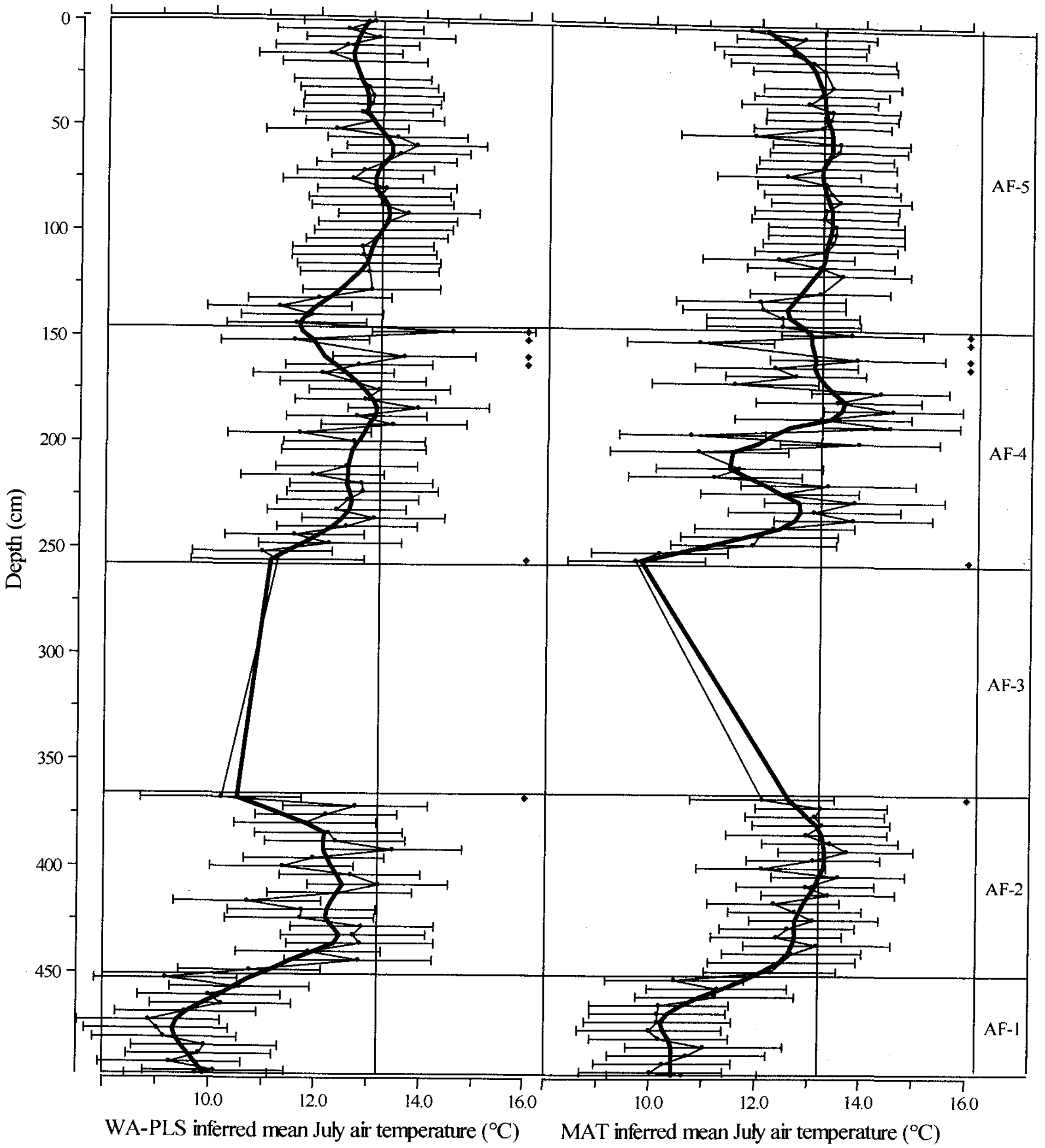


Figure 4.5 Mean July air temperatures as inferred by WA-PLS and MAT. Lowess smooths (thick lines) are superimposed on the temperature curves (thin lines). Error bars represent sample specific estimated standard errors of prediction. The modern mean July air temperature of 13.2°C is plotted for reference. Intervals with low counts (15-35 chironomid head capsules) are indicated by a ♦.

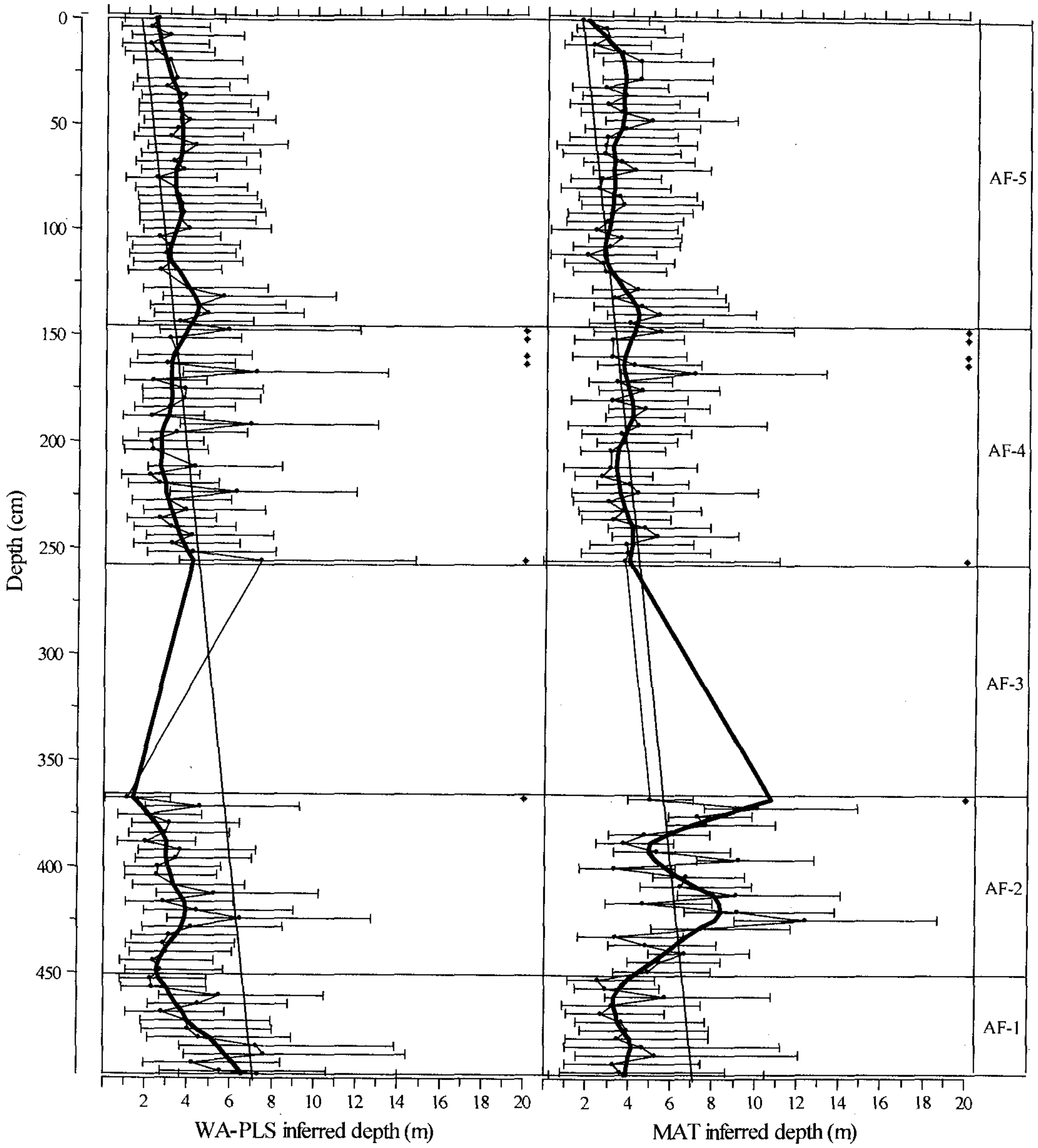
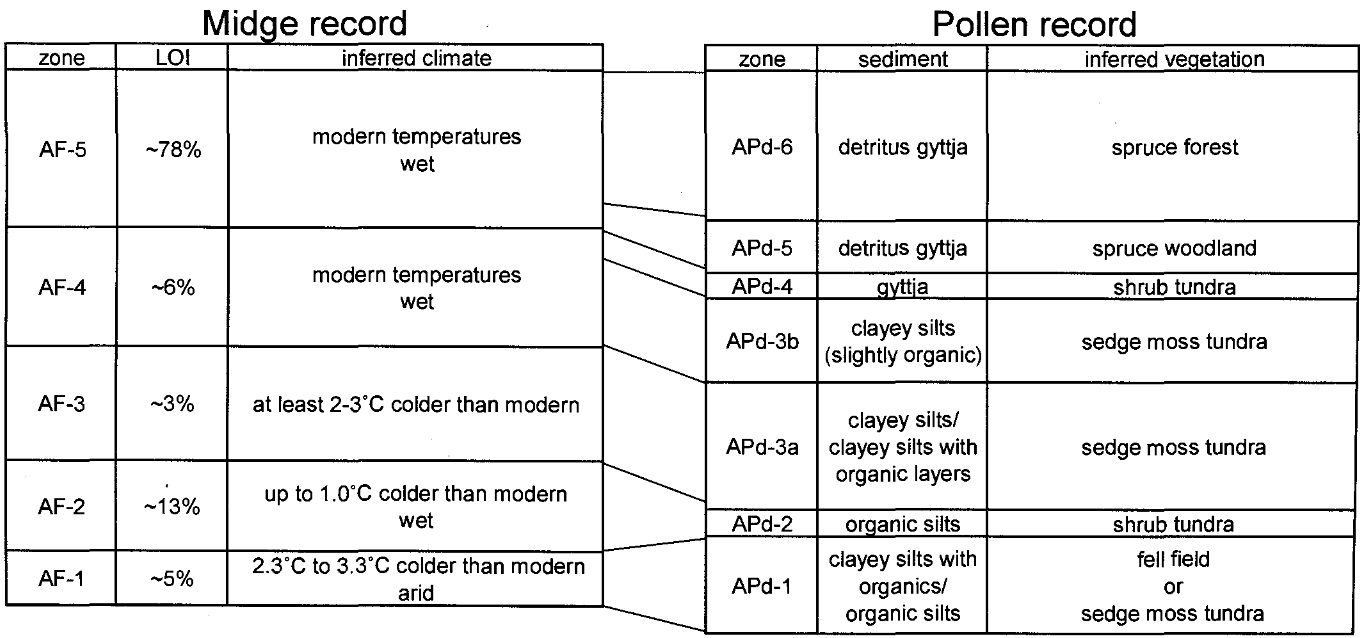


Figure 4.6 Depths as inferred by WA-PLS and MAT. The potential overflow level is plotted for reference. Lowess smooths (thick lines) are superimposed on the depth curves (thin lines). Error bars represent sample specific estimated standard errors of prediction. Intervals with low counts (15-35 chironomid head capsules) are indicated by a ♦.



Midge record

zone	LOI	inferred climate
AF-5	~78%	modern temperatures wet
AF-4	~6%	modern temperatures wet
AF-3	~3%	at least 2-3˚C colder than modern
AF-2	~13%	up to 1.0˚C colder than modern wet
AF-1	~5%	2.3˚C to 3.3˚C colder than modern arid

Pollen record

zone	sediment	inferred vegetation
APd-6	detritus gyttja	spruce forest
APd-5	detritus gyttja	spruce woodland
APd-4	gyttja	shrub tundra
APd-3b	clayey silts (slightly organic)	sedge moss tundra
APd-3a	clayey silts/ clayey silts with organic layers	sedge moss tundra
APd-2	organic silts	shrub tundra
APd-1	clayey silts with organics/ organic silts	fell field or sedge moss tundra

Fig. 4.7 A correlation of the midge record with Rampton's (1971) pollen record.

below the overflow level, at an average of about 4 m. At the base of the zone, the WA-PLS inferred depth was at overflow (~7 m), and then decreased rapidly to about 2 m. The good fit of modern analogues for these distinct assemblages prompts further examination. The group of closest analogues for this zone is dominated by the shallower tundra lakes (~2 - 4 m) of the Tuktoyaktuk Peninsula (north of treeline). Also, in a dataset collected by Walker and MacDonald (1995), four of the taxa from this zone (*Zalutschia*, *Corynoneura/Thienemanniella*, *Corynocera* and *Sergentia*) are found to be most common in shallow tundra lakes.

One of the distinctive features of this zone, is the high percentage of *Cricotopus/ Orthocladius* (~30-70%). In the Beringia training set, *Cricotopus/Orthocladius* never exceeds 37%, and the higher abundances are found most often at the northern end of the transect (Fig. 3.2). Even farther north, abundances of *Orthocladius* of up to 95% have been reported on Svalbard, in the high arctic north of Scandinavia (Brooks and Birks, 2004; Birks *et al.*, 2004). Again, these high percentages occur in the shallow lakes (less than ~3 m). This suggests that certain species within this taxon have characteristics which allow them to withstand the conditions imposed by extreme climates on shallow lakes. Given the ecology of *Cricotopus/Orthocladius*, *Sergentia*, *Zalutschia* sp A, *Corynoneura/Thienemanniella* and *Corynocera oliveri* type, the WA-PLS inferred depths are likely overestimates of the real depths. The location of good analogues at the northern limit of the transect and the similarity to assemblages of the high arctic, point to an environment even colder and more extreme than those captured in the Beringia training set.

Rampton's analysis of the pollen record leads to much the same interpretation. Pollen spectra indicate that sedge-moss tundra or fell-field covered the landscape, representing a much colder, and a drier climate than at present. Rampton interprets the low levels of tree pollen (*Picea* and *Alnus*) as indicating long distance transport.

Zone AF-2 (450.5 –366 cm)

The transition to AF-2 is marked by a sharp change in climate. Inferred mean July air temperatures warmed to modern (MAT) or nearly modern (1.0°C below modern; WA-PLS). This warming is reflected in the increased productivity, indicated by higher LOI and an increase in chironomid richness. Depth for this zone is problematic. WA-PLS infers a drop in lake level, to below overflow depths of about 2-4 m. In contrast, MAT infers a strong increase in lake level to depths of 5-8 m that fluctuate broadly at and above the overflow depth.

Rampton's pollen record reveals a very strong and sudden increase in *Betula* pollen for this zone. An increase in shrub birch is indicative of increasing moisture and temperature, and Rampton interprets a shrub tundra vegetation for this zone. This supports the MAT inferred increase in lake levels for this zone.

While inferred temperatures approach modern values, midge assemblages and LOI are different from modern. This points to environmental and climatic conditions different from those captured in the Beringia training set.

Zone AF-3 (366-258 cm)

Midges are too rare in this zone to provide temperature and depth reconstructions. The sediment in AF-3 consists of silt with very little organic matter (LOI ~3%). The near absence of midges in this zone is most likely caused by low levels of organic matter that reflect an unproductive environment with little available food. Temperatures at least 2-3°C below modern are inferred by extrapolation from the adjacent zones. Rampton interprets a cool and dry sedge moss tundra from the pollen record (pollen zone 3a).

Zone AF-4 (258-146 cm; 12,500+ to 9,400 ^{14}C BP)

With the re-appearance of midges, temperatures warmed to modern by 12,500 ^{14}C yr BP (Fig. 4.8). Following this, there was a rapid deposition of sediment between 230 and 180 cm (12,300 and 12,200 ^{14}C yr BP). MAT indicates the possibility that temperatures surpassed modern by 1°C at 11,500 ^{14}C BP. This possible warm peak was followed by a cold reversal at the transition to zone AF-5. Both reconstructions show a modest cooling (~1.0°C below modern) from 10,800 ^{14}C BP to 8,500 ^{14}C BP interrupted by a single warm interval at 9,700 ^{14}C BP. This warm interval (148 cm) is possibly an anomaly, as it is a low midge count interval with high semi-terrestrials that drive the inferred temperature up. Depth remained at the overflow level, though simultaneous peaks in four semi-terrestrial taxa are conspicuous, and suggest some fluctuation of water levels and/or peat development around the lake margin.

Coinciding with the re-appearance of midges, is the appearance of pollen from three aquatic taxa: *Potamogeton*, *Myriophyllum* and *Hippuris* (pollen zone 3b; Rampton, 1971). This indicates strong changes in the late glacial limnic environment. In the lower portion of zone AF-4, a sedge-moss tundra (pollen zone 3b) indicates a climate similar to that of the full glacial, with shrub tundra not far away. In the upper portion of zone AF-4 (pollen zone 4), *Betula* peaks again, indicating a change to shrub tundra. Peaks in *Sphagnum* and *Equisetum* spores, and Ericaceae pollen, suggest bog development around the lake. This shows excellent correlation with the peak in semi-terrestrial chironomids. The vegetation changes in the upper portion of the core indicate an increase in precipitation, likely to levels greater than during AF-2.

Zone AF-5 (146-0 cm; 9,400 ^{14}C BP to present)

The beginning of the top zone dates to ~9,400 ^{14}C BP, and marks the start of the Holocene record. A remarkable feature of this zone is the increase in organic matter from 6% LOI in the previous zone to 94% LOI at the beginning of this zone. Mean July air temperatures recover from the cold period by ~8,000 ^{14}C BP, and modern temperatures

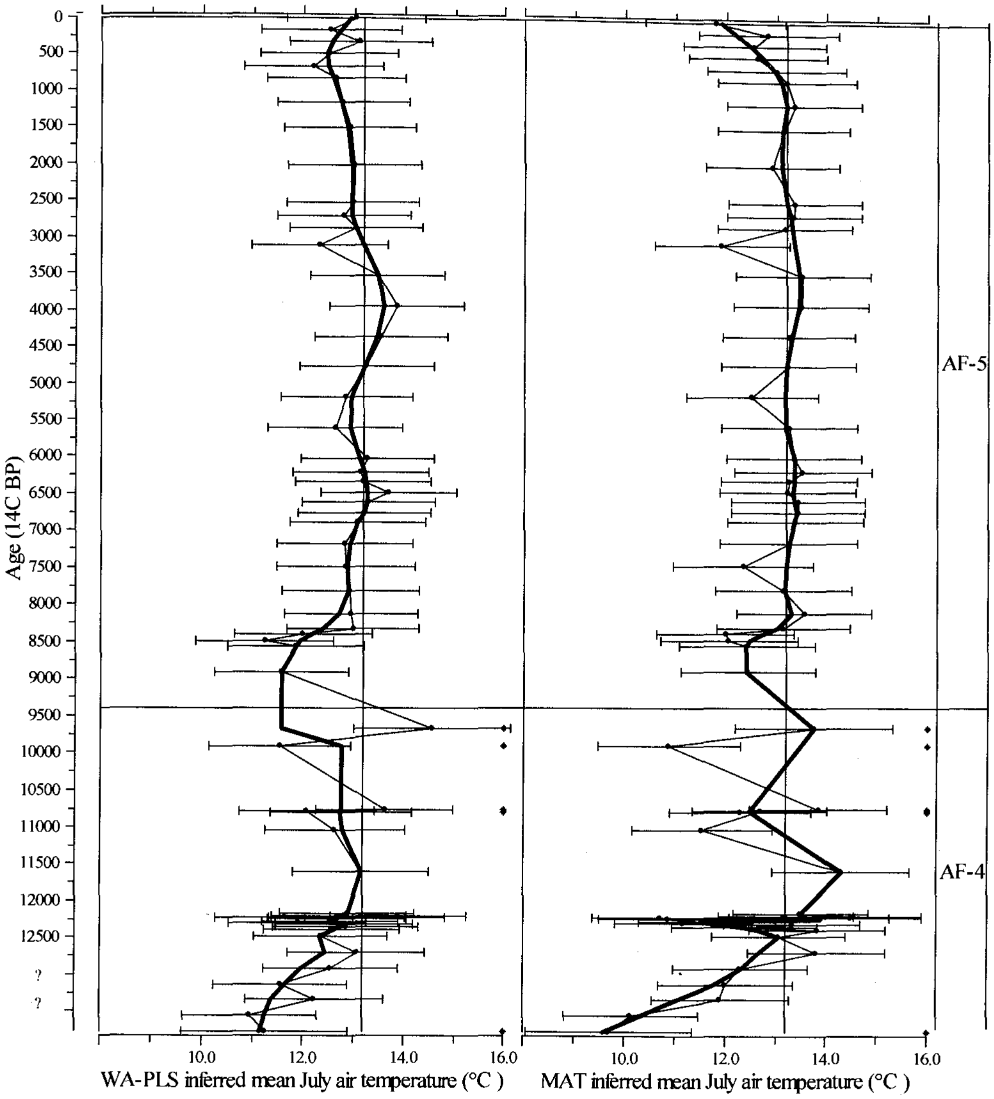


Figure 4.8 Mean July air temperatures for the late glacial and Holocene as inferred by WA-PLS and MAT, and plotted against age. Lowess smooths (thick lines) are superimposed on the temperature curves (thin lines). Error bars represent sample specific estimated standard errors of prediction. The modern mean July air temperature of 13.2°C is plotted for reference. Intervals with low counts (15-35 chironomid head capsules) are indicated by a ♦.

are sustained through the Holocene. Depth is at the overflow level (MAT and WA-PLS), and remains stable for most the Holocene. Following deposition of the White River Ash at 1,250 ^{14}C BP (Clague *et al.*, 1995; Richter, 1995), inferred temperatures decrease, especially those inferred by MAT. However, weak analogues for the uppermost intervals suggest some confounding influence from the tephra. The continued influence of the tephra in the top intervals is clear from the sustained drop in LOI.

4.5 Discussion and Regional Synthesis

The midge derived zones of Antifreeze Pond are based on robust changes in assemblages, and coincide with changes in LOI. These sharp transitions imply strong and rapid changes in the midge environment. The agreement between midge and pollen zones at several boundaries further demonstrates that many of these changes extended beyond the limnic environment, and were driven by climate. The vegetation record (pollen and macrofossils) is currently being re-analyzed, and should help to further resolve the relationships between the limnic and terrestrial environments, and climate.

A comparison of regional records is complicated by the poor chronological control for the lower portion of Antifreeze Pond. However, acceptance of any of the near basal dates makes Antifreeze Pond one of the older lacustrine records in eastern Beringia, as the majority of lakes yield basal dates of less than 14,000 ^{14}C yr BP (for example: Abbott *et al.*, 2000; Anderson *et al.*, 1994b; Bigelow and Edwards, 2001; Hu *et al.*, 1993; Oswald *et al.*, 1999). The problems at Antifreeze Pond are not unique: lacustrine and terrestrial sites that pre-date 14,000 ^{14}C yr BP are commonly plagued by poor chronology owing to gaps in the record, date reversals and/or a lack of finite dates (Anderson and Lozhkin, 2001).

There is good evidence to suggest at least a full glacial and possibly an interstadial age for some of the lower zones of Antifreeze Pond. A number of full glacial and interstadial records in east Beringia exist, though they are often plagued by dating problems

(Anderson and Lozhkin, 2001; Schweger and Matthews, 1991). A selection of some of the better dated of these records is discussed.

At the Fox permafrost tunnel, Hamilton *et al.* (1988) document a record extending from beyond the limits of radiocarbon dating through the Holocene. Lower and upper units of perennially frozen silts were deposited as loess during the interstadial and full glacial. Silt in the lower unit accumulated rapidly, and contains large ice wedges. The base of this lower silt unit is tentatively assigned a date of 43,000 ^{14}C yr BP, though several infinite dates at the boundary suggest this could be a minimum date. Assemblages above the base indicate a dry, open meadow with xeric conditions. Separating this lower unit from the upper silt unit is an unconformity characterized by little or no loess deposition, lenses of buried sod, thaw ponds, and the truncation of ice wedges. This unconformity formed during a period of deep thaw, and defines the Fox Thermal interval (Begét, 1990). Dates of 33,000 to 30,000 ^{14}C yr BP have been assigned to this interval, though large errors (>2000 yrs) on a number of the constraining dates, suggest that these ages are approximate. The development of ponds, and analyses of animal and plant remains, indicate not only warm, but also mesic conditions. This interval terminates with the onset of full glacial conditions, represented by the upper silt unit.

A similar climatic record is revealed by magnetic susceptibility analyses on loess sections in the Goldstream Valley near Fairbanks, Alaska. Begét (1990) and Begét and Hawkins (1989) used magnetic susceptibility to track changes in wind intensity, and thus infer changes in climate. The magnetic susceptibility records at four loess exposures are correlated with a magnetic susceptibility record from the well dated Fox permafrost tunnel (Hamilton *et al.*, 1988). The records show a warm (low wind intensity) Holocene, underlain by a cold (high wind intensity) full glacial, and below that a more variable interstadial. Within the interstadial, are two warm intervals, interrupted by a cold section. The chronology at the Fox permafrost tunnel correlates this cold section and the overlying warm interval with the lower silt unit and overlying Fox Thermal interval.

In the Isabella basin, also located near Fairbanks, Alaska, Matthews (1974) shows a vegetation response to the full glacial and two part interstadial. The inferred interstadial pollen record is comprised of two subzones. Matthews interprets the lower of these (zone Aa, including a bulk sediment date of >31,900 ^{14}C yr BP, I-4775) as indicating scattered spruce in an open sedge dominated vegetation. The late interstadial warming is captured by zone Ab (including a bulk sediment date of 34,900 ± 2950 ^{14}C yr BP, I-3083). Plant and animal macrofossils point to increases in moisture and temperature. Simultaneous increases in *Picea*, *Larix, Alnus* and *Betula* (shrub and arboreal macrofossils) indicate that a higher treeline accompanied the warming. Following this, steppe-like vegetation is inferred from high levels of *Artemisia* (to 30%) in the herb zone. From this, Matthews interprets a cold and arid full glacial climate.

In western Alaska, vegetation records reveal similarities at several sites that include and pre-date the herb zone: Imuruk Lake (Colinvaux, 1964), Joe Lake (Anderson *et al.*, 1994a), Kaiyak Lake (Anderson, 1985), Zagoskin Lake (Ager, 2003) and the Kvichak Peninsula exposure in Bristol Bay (Ager, 1982). Below the herb zone of the full glacial, the pollen record contains not only herb pollen, but also modest levels of *Betula* pollen. In a summary of western Alaskan sites, Ager (2003) characterizes this zone as herb tundra with birch, and assigns it to the interstadial.

Inferred temperatures for the full glacial are provided by the application of Mutual Climatic Range (MCR) analysis to beetle remains. Elias (2000, 2001b) inferred summer temperatures for the Last Glacial Maximum in Alaska of 4°C colder than modern in interior Alaska. MCR on beetle remains also estimates winter temperatures as 8°C colder than modern.

Lower Core - Chronology 1

Chronology 1 assumes a hiatus at ~375 cm that separates interstadial sediments (AF-1 & AF-2) from the overlying sediments deposited during the end of the full glacial (i.e., early deglaciation; AF-3). The peak of the full glacial occurred during the hiatus, and is not captured by the record. Here, the sequence of distinctive zones provides a basis for comparing Antifreeze Pond with a selection of regional records.

The sharp transition from a cold and arid zone (AF-1) to a warmer and possibly wetter zone (AF-2) is a prominent feature in the midge and pollen records at Antifreeze Pond. This pattern also turns up in the interstadial records from Fox permafrost tunnel, the Goldstream Valley loess and the Isabella basin pollen record (Begét, 1990; Begét and Hawkins, 1989; Hamilton *et al.*, 1988, Matthews, 1974). In addition, the peak in *Betula* pollen (45%) during AF-2, correlates with the interstadial herb with birch zone from several pollen records in western Alaska (Ager, 2003). For zone AF-3, a near absence of midges and very low levels of organic matter could be attributed to rapid sedimentation during deglaciation. The pollen record during AF-3 is dominated by herbaceous pollen and correlates well with the herb zone, widespread in eastern Beringia during the full glacial (Table 2.1).

If chronology 1 is accepted, Antifreeze Pond includes a two part interstadial with a cold and dry climate (temperatures ~2.5 to 3.5°C colder than modern) followed by an increase in moisture and a warming of mean July air temperatures to near modern. No midge inferred temperatures are available for the full glacial, however extrapolation from adjacent zones points to mean July air temperatures more than 2-3°C below modern for this period.

Lower Core – Chronology 2

Chronology 2 infers a hiatus in the sediment record at ~450 cm that separates interstadial sediments (AF-1) from the overlying sediments deposited during the end of the full glacial (AF-2 & AF-3).

According to chronology 2, AF-1 is near and possibly beyond the limits of radiocarbon dating with an upper boundary of 38,000 ^{14}C yr BP or older. The lack of finite dates for this zone, and for this time period at other sites, makes it very difficult to correlate this zone with other records. It is not clear whether AF-1 is coeval with the earlier cold phase of the interstadial as for chronology 1 (but why a hiatus during the late interstadial?), or with the warmer late interstadial (but suggests a very different vegetation and climate from the regional records). Following the hiatus (~450 cm), a productive environment (AF-2) is followed by rapid sedimentation (AF-3). This pattern does not appear within the full glacial in other vegetation records.

If chronology 2 is accepted, the poorly constrained interstadial is arid with mean July air temperatures 2-3°C below modern. Warm and wet conditions much like modern arise earlier than previously thought at ~16,000 ^{14}C yr BP. However, these near modern conditions are not continuous through the late glacial: they are punctuated by a zone of cold and dry conditions with high loess deposition. This would indicate that for the interstadial and full glacial record at Antifreeze Pond, local climatic conditions overrode any regional trends.

Lower Core – Chronology 3

Chronology 3 assumes a continuous record with the full glacial spanning zones AF-1 through AF-3. For AF-1 and AF-3, the evidence indicates a cold and arid climate, with a treeless landscape. This agrees with the full glacial climate and conditions inferred from the herb zone at other sites (Table 2.1). However, these zones are separated by a warm and wet zone (AF-2) beginning at ~16,000 ^{14}C yr BP. This fluctuation does not appear in other herb zone records. The warming inferred here differs from the late glacial warming at other sites in that it occurs much earlier, and is not sustained through the late glacial.

Acceptance of chronology 3 indicates a full glacial with a cold (mean July air temperatures 2-3°C below modern) and arid climate, punctuated by the appearance of conditions much like modern. While the cold and arid conditions are synchronous with regional patterns, the warm and wet interruption is not observed elsewhere and suggests a strong influence from local climate.

Upper Core

An increase in productivity at the start of AF-4 (shortly before ~12,500 ^{14}C yr BP), is shown by increases in LOI, midges and aquatic pollen. This boundary marks the start of the late glacial. Despite the increased productivity, the terrestrial pollen record shows little change at this transition. This suggests a higher sensitivity of the limnic environment to a change in climate. Towards the end of the late glacial, a sharp peak in *Betula* pollen indicates an increase in precipitation. In central Alaska, the increase in birch is dated to ~12,000 ^{14}C yr BP at two sites by AMS radiocarbon dating (Bigelow and Edwards, 2001). Bulk sediment dates at several sites give older dates of ~13,500 to ~12,500 ^{14}C yr BP (Anderson *et al.*, 1994b; Bigelow and Edwards, 2001; Hu *et al.*, 1993), and are likely influenced by a hard water effect. To the east, birch was established prior to 11,300 ^{14}C yr BP at Sulphur Lake, southwest Yukon (Lacourse and Gajewski, 2000). At Antifreeze Pond, Rampton's bulk date of ~10,000 ^{14}C yr BP for the birch peak is significantly younger than elsewhere, and lacks an explanation. The different timing in changes to the limnic and terrestrial environments points to a two-step climatic amelioration.

Midge inferred temperatures began rising before 12,500 ^{14}C yr BP, reached modern by ~12,000 ^{14}C yr BP, and possibly peaked about 1°C above modern (MAT) at 11,500 ^{14}C yr BP. Applying MCR to beetle remains, Elias (2000, 2001b) finds a similar pattern. The rapid temperature rise began 12,000 ^{14}C yr BP and peaked 11,000 ^{14}C yr BP at 5-7°C above modern.

Changing moisture regimes are also indicated by fluctuations in some or all of the four semi-terrestrial chironomid taxa through the late glacial and Holocene. Their greatest peak coincides with the rise of birch, and increases in spores of *Sphagnum* and *Equisetum* that point to bog development around the margins of the lake. This further supports an increase in available moisture, and places a date on the increase of ~10,700 to ~9,500 ^{14}C yr BP. Smaller peaks in some of the semi-terrestrial taxa occur at ~12,500 to ~12,000 ^{14}C yr BP and in the Holocene at ~3,500 to ~1,250 ^{14}C yr BP.

At Birch Lake in central Alaska, Abbott *et al.* (2000) have used seismic profiles and multiproxy sedimentary analyses to reconstruct changes in lake levels. From the late glacial to the Holocene, the dry basin was transformed into a full lake (a change of 18 m) through a series of fluctuations. The two largest increases in lake level occur from 12,700 to 12,200 ^{14}C yr BP and 10,600 to 10,000 ^{14}C yr BP. These dates show excellent correlation with moisture peaks inferred from the semi-terrestrial chironomids. A third rise is documented from 8,800 to 8,000 ^{14}C yr BP. Re-examination of the chironomid record shows a weak peak in two of the semi-terrestrial taxa that is tentatively interpreted as a moisture signal. Birch Lake attains overflow level by mid-Holocene, and so is unable to pick up any further moisture peaks (i.e., that suggested by the semi-terrestrial chironomids from ~3,500 to ~1,250 ^{14}C yr BP).

Using MCR on beetle remains, Elias (2000, 2001b) identifies a Younger Dryas cooling from 11,000 to 10,000 ^{14}C yr BP. Midge inferred temperatures also point to a cooling from 10,800 to 8,500 ^{14}C yr BP. While the onset of cooling coincides with the Younger Dryas, the sustained cooling beyond ~11,000 ^{14}C yr BP suggests that the Younger Dryas is not the driving force behind this cold period. In addition, this cooling is not reflected in the pollen record. Even in the chironomid record this cold period is curious, as it straddles two zones, and a very sharp increase in productivity (i.e., large increases in both LOI and chironomid concentration). Closer analysis of these intervals suggests that the inferred colder temperatures are driven in part by high percentages of *Zalutschia* type A (to 18%). In the Beringia training set, *Zalutschia* type A shows a preference for shallow lakes in cold regions. Though *Propsilocerus* has no influence on the inferred temperatures (it was absent in the Beringia training set), its appearance during this cold peak is noteworthy, as it has only been recorded at two other sites in North America (see Appendix 1). *Propsilocerus*' distribution at higher latitudes suggests it is a cold indicator (Sæther and Wang, 1996), and it is reported to prefer shallow, eutrophic lakes. This is consistent with temperature, depth and productivity inferences for Antifreeze Pond during its appearance in the record. The peaks of these two cold taxa also coincide with drops or delays in the appearance of several warm taxa (*Microtendipes*, *Pseudochironomus* and *Pagastiella*).

Temperatures attained modern values by 8,000 ^{14}C BP, and were relatively unchanged through the Holocene. Rampton's (1971) pollen record shows the staggered arrival of spruce (~8,700 ^{14}C BP) and alder (~6,000 ^{14}C BP) in the region. These dates agree generally with dates in central Alaska (Anderson *et al.*, 1994b; Bigelow and Edwards, 2001; Hu *et al.*, 1993).

5 Conclusion

Following the development of the first midge transfer function (Walker *et al.*, 1991), criticism arose regarding the role temperature plays in directly affecting the distribution of midge taxa (Hann *et al.*, 1992). Over a decade later, the ecological questions of how and why midges correlate with summer air temperature remain largely unanswered. Regardless, multivariate analyses conducted on the Beringia training set confirm that mean July air temperature is an important variable in determining midge distribution. In addition, these analyses show that mean July air temperature is strongly correlated with other variables (i.e., vegetation type, TPU) that also rank high in explaining midge distribution. This points to a complex, and likely indirect relationship between midges and mean July air temperature.

Whatever the specifics of the midge temperature relationship, it exists. This is demonstrated not only by multivariate analyses and model statistics, but also by the robust temperature reconstructions inferred using midge data. At Antifreeze Pond, both the WA-PLS model and MAT yielded very similar records of inferred temperature. These in turn showed excellent correlation with broad patterns in temperatures inferred locally from pollen, and regionally from vegetation and sediment analyses. Differences exist in temperatures inferred by midges and terrestrial pollen through the late glacial to Holocene transition. Reasons for this are not clear; possible explanations include a higher sensitivity to temperature change by the limnic environment, or a differential response in midges and terrestrial vegetation to strongly fluctuating temperatures.

The depth midge relationship was explored statistically and through application of a WA-PLS model and MAT to Antifreeze Pond. Multivariate analyses indicate that depth is the most important variable in explaining midge distribution in the Beringia training set. Despite this strong relationship, the WA-PLS model for depth is weaker than that for temperature as evaluated by the bootstrapped coefficient of determination (r^2_{boot}). The weaker correlation is attributed to the larger gradient of depths included in the model. Again, the relationship between midges and depth is complex. Though not available for the Beringia training set, temperature and O_2 levels at the water sediment interface are likely important variables that correlate with depth. In addition, depth varies within a lake depending on the shape of the basin, such that assemblages collected at maximum depth can be influenced by the lake's bathymetry.

Application of the WA-PLS model and MAT to reconstruct lake depth for Antifreeze Pond yields mixed results. Inferred WA-PLS and MAT depths for the late glacial and Holocene show excellent correlation. Further, both show a gradual shallowing consistent with the inferred accumulation of sediment in the basin during this period. This suggests a high sensitivity to subtle changes from both methods. Unfortunately, WA-PLS and MAT show contradictory trends for the lower portion of the core. The trend yielded by MAT is consistent with moisture changes inferred from the pollen at Antifreeze Pond, and from other regional records. However, it would be premature to generalize from this single site that it is the better approach. The discrepancy in results from both the WA-PLS model and MAT can best be resolved through the application of both approaches to lakes where the palaeo lake levels are known.

A very interesting correlation was observed here between semi-terrestrial chironomids and moisture at Antifreeze Pond. Although depth was at overflow through the late glacial and Holocene, peaks in four semi-terrestrial (i.e., depth or moisture sensitive) chironomids were conspicuous. Comparison of these peaks with the well documented palaeohydrology record of Birch Lake (Abbott *et al.*, 2000) in central Alaska showed remarkable correlation. Again, examination of other sites with well documented palaeohydrology records is necessary to determine whether this record is unique to Antifreeze Pond, or whether this approach can be applied elsewhere.

More than three decades after Antifreeze Pond was first cored (Rampton, 1969, 1971), a firm chronology is still lacking. New radiocarbon dates support a basal age in the full glacial or interstadial, and suggest several possible chronologies. Resolution of the chronology is important, as the acceptance of any of the options considered here has significant implications. If the climatic changes at Antifreeze Pond are synchronous with those in Alaska, this study provides some of the first quantitative climate data for eastern Beringia. If, on the other hand, the chronology supports climatic changes that are asynchronous with regional patterns, this could provide valuable information about the timing and nature of the McConnell glaciation's retreat.

Improvements to the Beringia training set suggest themselves already: additional lakes should be added, with particular emphases on expanding the temperature gradient, and filling out the depth gradient. The promising results yielded by midges at Antifreeze Pond re-affirm the value of midges as a proxy for climate. The continued application of, and improvement to, the Beringia training set and its models shows great promise for significant contributions to our understanding of climate change in eastern Beringia.

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APPENDIX

The following bolded taxa constitute a complete list of all taxonomic groups recognized and included in this training set. The primary references used for each taxon are provided. Where identifications emphasized features other than those described in the references, additional notes are provided. Ventromental plates are abbreviated as VP.

Order: Diptera
Family: Chironomidae
Subfamily: Podonominae
Lasiodiamesa (see Wiederholm, 1983)

Subfamily: Tanypodinae
Derotanypus (see Wiederholm, 1983)
Labrundinia (see Wiederholm, 1983)
other Pentaneurini (see Walker, 1988; Wiederholm, 1983)
Procladius (see Wiederholm, 1983)
Tanypus (see Wiederholm, 1983)

Subfamily: Diamesinae
Diamesa (see Wiederholm, 1983)
Potthastia (see Wiederholm, 1983)
Protanypus (see Wiederholm, 1983)
Pseudodiamesa (see Wiederholm, 1983)

Subfamily: Prodiamesinae
Monodiamesa (see Wiederholm, 1983)

Subfamily: Orthocladiinae
Abiskomyia (see Wiederholm, 1983)
Acamptocladius (see Wiederholm, 1983)
Brillia/Euryhapsis (see Walker, 2000; Wiederholm, 1983)
    Notes: median tooth often absent in half fragments, and mentum of very dark pigmentation.
Cardiocladius (see Wiederholm, 1983)
Corynoneura/Thienemanniella (see Wiederholm, 1983)
Cricotopus/Orthocladius (see Walker, 1988, 2000; Wiederholm, 1983)
    Notes: a highly variable group with more morphotypes than depicted in the references. Always 6 pairs of lateral teeth, 2nd lateral appressed to the 1st or independent, and VP very reduced and often ending in a dark 'knob'.
Doithrix/Pseudorthocladius (see Walker, 2000)
    Notes: identified primarily by the paired 4th & 5th pairs of lateral teeth and a slight indent in the edge of the mentum descending from the 5th lateral.
Eukiefferiella/Tvetenia (see Walker, 2000; Wiederholm, 1983)
Heterotanytarsus (see Walker, 1988; Wiederholm, 1983)
Heterotrissocladius (see Walker, 1988; Wiederholm, 1983)

Hydrobaenus/Oliveridia (see Walker, 1988, 2000; Wiederholm, 1983)

Limnophyes (see Walker, 2000; Wiederholm, 1983)

Notes: outer edges of mentum descending from the last laterals are straight and nearly parallel to each other.

Mesocricotopus (see Walker, 2000; Wiederholm, 1983)

Metriocnemus (see Wiederholm, 1983)

Nanocladius (see Walker, 1988, 2000; Wiederholm, 1983)

Orthocladiinae sp 2 (see Walker, 2000)

Notes: mentum similar to *Cricotopus/Orthocladius*, though taller and narrower with a slight concavity in each half, 6 pairs of lateral teeth though 1st pair separated from median tooth only by fine notches, and median tooth sometimes subdivided by additional notches, VP sometimes overlapping lateral teeth.

Paracladius (see Wiederholm, 1983)

Notes: whole mentum very pale and broad, single broad median tooth very pale at top edge with weak pigmentation partway down tooth, 6 small pigmented lateral teeth that can be hard to distinguish from each other, last lateral teeth often projecting out at a sharp angle relative to other laterals, VP sometimes overlapping lateral teeth.

***Parakiefferiella nigra* type** (see Walker, 1988; Wiederholm, 1983)

***Parakiefferiella* sp B type** (see Walker, 2000; *P.* cf *bathophila* in Walker, 1988)

Notes: this taxon is complex, with a gradient of intermediates between two distinctive morphotypes. While the morphotypes at the ends of the spectrum are easily separated, the continuum of intermediates makes it difficult to split this taxon into reliable groups. The co-occurrence in samples of the two morphotypes and intermediates suggests that no ecological information is gained by dividing this complex group, thus they have been lumped. At one end of the spectrum, specimens resemble *Parakiefferiella bathophila*, with the following features: a single median tooth broader than laterals and rounded or slightly pointed, 1st pair of lateral teeth appearing either as small accessory teeth attached to the median tooth or as independent teeth resembling the other lateral teeth, an additional 5 pairs of lateral teeth, individual lateral teeth are often hard to distinguish as they are somewhat squished together, and VP bulge out and overlap last lateral teeth. At the other end of the spectrum is the *Parakiefferiella* sp. B described in Walker (2000) with the following features: median tooth broader than laterals and slightly pointed, weak concavity in each half of the mentum, 1st pair of lateral teeth appearing either as accessory teeth cleaving off the median tooth or as independent teeth resembling the other lateral teeth, an additional 5 pairs of lateral teeth are easily distinguished, the shape of the last laterals is different from other laterals and creates a distinct angle with the other laterals, and VP rarely overlap last laterals.

***Parakiefferiella triquetra* type** (see Walker, 1988; Wiederholm, 1983)

Parametriocnemus/Paraphaenocladius (see Wiederholm, 1983)

Propsilocerus (see Wiederholm, 1983)

Note: the appearance of over a dozen subfossils of *Propsilocerus* in Antifreeze Pond is intriguing as this taxon is generally rare, and particularly so in North America. Additional specimens were also found at the same depths in nearby

Eikland Pond (pers. obs.), and subfossils have also been reported from a lake in Maine (Chase, 2004)

***Psectrocladius* (*Allopsectrocladius* & *Mesopsectrocladius*)** (see Wiederholm, 1983)

***Psectrocladius* (*Psectrocladius*)** (see Wiederholm, 1983)

***Psectrocladius calcaratus* type** (see Wiederholm, 1983)

***Psectrocladius septentrionalis* type** (see Wiederholm, 1983)

Pseudosmittia/Smittia (see Wiederholm, 1983)

Rheocricotopus (see Walker, 1988; Wiederholm, 1983)

Symposiocladius lignicola (see Wiederholm, 1983)

Notes: this taxon is synonymous with *Orthocladius (Symposiocladius) lignicola* in Walker (1988, 2000).

Synorthocladius (see Walker, 1988; Wiederholm, 1983)

Unknown sp. 1

Notes: this orthoclad is distinctive in its characteristics, and while it shares some similarities with other taxa, it has no exact match in Wiederholm (1983). The single median tooth is nipple shaped and broader than the laterals, it has 5 lateral teeth with teeth 4 & 5 somewhat paired, and an indentation in the edge of the mentum that descends from the 5th lateral. The VPs connect with and extend down from the median tooth; some specimens make it clear that these VPs are on a different plane than the lateral teeth. The edge of mentum continues down below the 5th lateral (and indentation) to give the appearance of a second set of VPs parallel to the first. Mandible with 4 inner teeth. The appearance of this taxon coincided with peaks in *Limnophyes*, *Parametriocnemus/ Paraphaenocladius* and *Pseudosmittia/Smittia*, and suggests that it is semi-terrestrial.

***Zalutschia* type A** (see Walker, 1988)

Notes: mental teeth medium to dark pigmentation, each median tooth with small accessory tooth unless worn, median teeth sometimes striated, 5 pairs of lateral teeth identical to each other, last laterals often lower and out of line with other laterals, and mandible with apical and 3 inner teeth all of same colour.

***Zalutschia* type B**

Notes: mental teeth medium to dark pigmentation, median teeth asymmetrical with peak on central side of each tooth, 1st lateral reduced and independent, 2nd to 6th laterals identical to each other, mandible with apical and 3 inner teeth all of same colour.

Zalutschia zalutschicola (see Wiederholm, 1983)

Notes: median teeth often paler than laterals, 1st pair of lateral teeth reduced and independent, 2nd to 5th pairs identical to each other, 6th pair reduced and sometimes hard to see, and mandible with pale apical tooth and 3 dark inner teeth.

Subfamily: Chironominae

Tribe: Chironomini

Apedilum (see Wiederholm, 1983)

Chironomus (see Walker, 1988; Wiederholm, 1983)

Cladopelma (see Walker, 1988; Wiederholm, 1983)

Cryptochironomus (see Walker, 1988; Wiederholm, 1983)

Cryptotendipes (see Walker, 1988; Wiederholm, 1983)

Cyphomella/Harnischia/Paracladopelma (see Walker, 1988; Wiederholm, 1983)

Dicrotendipes (see Walker, 1988; Wiederholm, 1983)

Einfeldia (see Wiederholm, 1983)

Endochironomus (see Walker, 1988; Wiederholm, 1983)

Notes: mentum is similar to that of *Phaenopsectra flavipes* type, *Sergentia, Stictochironomus* and *Tribelos*. Tops of teeth darker than the rest of the mentum and median teeth (or rarely, tooth) not much smaller than first laterals. VP differ from the usual 'fan' (or 'triangle') shaped Chironomini VP: the bottom portion of the 'fan' much reduced or absent giving the VP a somewhat 'bar' shaped appearance; the ends of the VP furthest from the mentum often appear rounded. On the VP, upper and lower bands of striations separated by a very small gap, with striations often curving away from mentum near upper margin of VP. Mandibles usually with 3 inner teeth.

Glyptotendipes (see Walker, 1988; Wiederholm, 1983)

Notes: a highly variable group, mentum broad or narrow, with single median tooth notched or simple, 6 pairs of lateral teeth, and VP with striations and ridges along top margin. This taxon also includes specimens originally identified as 'Dicrotendipes/Einfeldia/Glyptotendipes' in the Yukon/NWT dataset (Walker *et al.*, 2003).

Lauterborniella/Zavreliella (see Walker, 1988; Wiederholm, 1983)

Microtendipes (see Walker, 1988; Wiederholm, 1983)

Notes: a tiny median tooth occasionally visible between dominant pale median teeth.

Nilothauma (see Walker, 1988; Wiederholm, 1983)

Pagastiella (see Walker, 1988; Wiederholm, 1983)

Parachironomus (see Walker, 1988; Wiederholm, 1983)

Paralauterborniella (see Walker, 1988; Wiederholm, 1983)

Paratendipes (see Walker, 1988; Wiederholm, 1983)

***Phaenopsectra flavipes* type** (see Walker, 1988, 2000; Wiederholm, 1983)

Notes: Mentum narrower and usually darker than the similar taxa *Endochironomus, Sergentia, Stictochironomus* and *Tribelos*. VP with upper and lower bands of striations separated by a small gap, upper band of striations extends to upper margin of VP. A small indent appears in the VP where it is joined by the bottom edge of the mentum. Mandible with 3 inner teeth.

Polypedilum (see Walker, 1988; Wiederholm, 1983)

Sergentia (see Walker, 1988; Wiederholm, 1983)

Notes: VP with two bands of striations separated by a gap: striations near the upper margin appear as paired ticks while lower band of striation appears more 'normal' (i.e., evenly spaced striae). Median teeth shorter but not much narrower than 1st laterals. Mandible with 4 inner teeth. Compare this taxon with *Endochironomus, Phaenopsectra flavipes* type, *Stictochironomus* and *Tribelos*.

Stictochironomus (see Walker, 1988; Wiederholm, 1983)

Notes: similar to *Endochironomus, Phaenopsectra flavipes* type, *Sergentia* and *Tribelos*. Median teeth shorter and narrower than all other laterals. Median and 1st laterals of a squared shape (i.e., tops flat, not pointed). Upper part of VP with no striations; a lower band of striation may be present. Mandible with 3 inner teeth.

Tribelos (see Walker, 1988; Wiederholm, 1983)

notes: similar to *Endochironomus, Phaenopsectra flavipes* type, *Sergentia* and *Stictochironomus*. VP with upper and lower bands of striations; upper band does not extend to upper margin of VP (compare with *Phaenopsectra flavipes*). Mandible with 3 inner teeth.

Xenochironomus (see Wiederholm, 1983)

Tribe: Pseudochironomini

Pseudochironomus (see Walker, 1988; Wiederholm, 1983)

Tribe: Tanytarsini

***Cladotanytarsus mancus* type** (see Brooks, 2004; Walker, 2000)

Corynocera ambigua (see Walker, 2000; Wiederholm, 1983)

Notes: simple mentum with only 5 teeth, median and first pair of lateral teeth on separate plane from 2nd laterals, dorso-lateral curvature of mentum causes 2nd laterals to directly overlap 1st laterals, antennal pedestal elongate with no projection, and mandible with no visible teeth.

Corynocera* nr. *ambigua (see Walker, 1988, 2000)

Notes: mentum often very worn and with hard (or impossible) to distinguish teeth, mentum narrower than other Tanytarsini (resembling other *Corynocera* spp) and often dark, antennal pedestal elongate with small very blunt projection, and mandible with indistinct teeth.

***Corynocera oliveri* type** (see Brooks, 2004; Walker, 2000; Wiederholm, 1983)

Notes: an apparent dorso-lateral curvature to mentum (such that middle 3 teeth are never in focus at the same time as outer laterals), median tooth at least as wide as or often wider than first pair of laterals, first pair of lateral teeth taller and wider than other laterals and on the same plane as median tooth, a tiny and subtle accessory tooth (or tooth-like shading) between median and first laterals, 2nd to 5th pairs of laterals not on the same plane as the median trio and often squished together (i.e., overlapping), antennal pedestals elongate with no projection, and mandible with large surface tooth obscuring the inner teeth.

Identification keys for this taxon have relied heavily on the mandible (Brooks, 2004; Walker, 2000). This has created problems, as a survey of specimens from BC lakes (in addition to the Beringia training set) shows that more than one mentum type has a mandible matching the description for *C. oliveri* type. For this thesis, specimens were identified based on the above description of the mentum, and were confirmed (but not identified) by the mandible. The description of *C. oliveri* type given here is also consistent with specimens from Russia in the reference collection at University of New Brunswick, Canada (pers. obs).

Rheotanytarsus (see Wiederholm, 1983)

Stempellina (see Walker, 1988; Wiederholm, 1983)

Stempellinella/Zavrelia (see Walker, 1988; Wiederholm, 1983)

Tanytarsus chinyensis (see Brooks, 2004; Walker, 2000)

Tanytarsina other (see Brooks, 2004; Walker, 2000; Wiederholm, 1983)

Notes: undifferentiated Tanytarsina not belonging to any of the above listed groups.

Family: **Ceratopogonidae** (see Walker, 2000)

Family: **Chaoboridae** (see Uutala, 1990)