SUBFOSSIL CHIRONOMIDS (INSECTA: DIPTERA) AND CLIMATIC CHANGE AT HIGH ELEVATION LAKES IN THE ENGELMANN SPRUCE-SUBALPINE FIR ZONE IN SOUTHWESTERN BRITISH COLUMBIA

by

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B. Sc., The University of British Columbia, 1995

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE

in

THE FACULTY OF GRADUATE STUDIES

(Department of Zoology)

We accept this thesis as conforming to the required standard

THE UNIVERSITY OF BRITISH COLUMBIA

October 1998

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Abstract

Because very little is known about past climate change in the Ashnola region of southwestern British Columbia, a stratigraphic analysis of fossil head capsules of chironomids (Diptera: Chironomidae) was performed for two lakes located at treeline (approx. 2250m) in southernmost B. C.: North Crater Lake and Lake-of-the-Woods. Distinct changes in the chironomid (non-biting midge) communities implied changes in climate throughout the Holocene (10 000 yr. B. P. to present). Prior to 10 000 yr. B. P., cold conditions are indicated by the lack of temperate taxa and the presence of coldstenotherms such as Sergentia and Heterotrissocladius. The early Holocene (after 9500 yr. B. P.) in both lakes shows rapid increases in the abundance and diversity of warm-adapted taxa (e.g., Dicrotendipes, Microtendipes, Polypedilum and Cladopelma), while coldindicators disappear. This is indicative of warm, dry (i.e., xerothermic) conditions. Just prior to Mazama ash deposition, and later in the mid-Holocene, several warm-adapted taxa decrease in both lakes. This coincides with the warm, yet moist conditions of the mesothermic. The late-Holocene assemblages (~ 4500 yr. B. P. to present) indicate continued cooling with a continued reduction in diversity and abundance of warm-adapted taxa. Furthermore, cold-stenothermsreappear in Lake-of-the-Woods.

To quantitatively assess these inferred climate changes, temperature reconstructions were performed using a newly-developed chironomid-paleotemperature inference model. Reconstructed temperatures are generally in agreement with those changes inferred qualitatively from the stratigraphic diagrams. For both lakes, mean summer temperatures were cold in the late-glacial (8-10 °C). Inferred temperatures increase rapidly in the early-Holocene, with the highest inferred temperatures (12-16 °C) occurring during the xerothermic interval (9500 to 7000 yr. B. P.). Both lakes show a slight drop in temperature just prior to the Mazama eruption. This cooling trend continues thereafter at North Crater Lake, to present day. The cooling trend begins slightly later at Lake-of-the-Woods, after 5400 yr. B. P. For both lakes, this inferred cooling trend is consistent with

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the time of neoglaciation in B. C., as inferred from glacial and paleobotanical evidence. For comparison, paleotemperature reconstructions were done for Cabin Lake and 3M Pond, located slightly northwest of my sites. The reconstructed temperatures for these lakes show similar trends as those inferred for North Crater Lake and Lake-of-the-Woods.

As diversity often changes with changing community assemblages, diversity was also assessed quantitatively using the Shannon-Wiener Diversity Index. The inferred diversity changes within cores, parallel the inferred climate and temperature changes. Diversity is low during cold intervals, such as in the late-glacial. Diversity increases in the early-Holocene, corresponding with the warm reconstructed temperatures. Diversity drops in the late-Holocene (after 5400 yr. B. P.), and this is consistent with the cooler conditions of the neoglacial.

Community trajectory analysis for both lakes showed that while species assemblages of the late-glacial did not reassemble in the neoglacial, distinct late-glacial, early Holocene and late-Holocene stages of development were indicated throughout the history of each lake.

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Acknowledgments

I would like to thank my co-supervisors, Drs. Ian Walker and Geoff Scudder for their guidance, advice and support throughout this study. Special thanks to Dr. Ian Walker for starting me on this path many years ago as a summer research assistant, and for guiding me with patience and kindness ever since. I also thank the other members of my committee, Drs. Bill Neill and Gary Bradfield for their helpful comments. A multitude of thanks to Sandra Rosenberg for chironomid head capsule processing, picking and her friendship. I also wish to thank Markus Heinrichs for his much appreciated support, advice and shared laughs over the years. Thank you to the gang in the Project Lab at O. U. C. for the laughter and the friendships. Thanks are extended to Dr. Martin Evans, for providing the core from Lake-of-the-Woods, and to Dr. Martin Adamson for the generous use of microscopes.

A special thank you to Kevin Brulotte for his never-ending patience, support and computer expertise. To Adriana Lauran, a big thank you to a wonderful friend who was there through it all.

This thesis was funded by Forest Renewal British Columbia grant HQ96037-RE to Drs. Richard Hebda and Ian Walker.

Dedication

This thesis is dedicated to those people who have made me the person I am today. Especially my parents, Barry and Linda, who always made me believe I could do anything I set my mind to - and who are always there when I do. To my partner Kevin Brulotte for all the encouragement and help - but most of all for just

being there.

Chapter I

Introduction

1.1 Global Warming and Paleoclimate

Proof of a general rise in mean global temperature has been observed by researchers examining long-term (decades to millenia) temperature records and tree-rings (Strahler and Strahler 1992). Furthermore, scientists examining Antarctic ice cores have noted a strong correlation over the past 160, 000 years between temperatures as determined from oxygen isotopes in the ice and the concentration of CO_2 (measured via air bubbles also trapped in glacier ice) in the atmosphere (Raynaud *et al.* 1993). Increased concentrations of atmospheric CO_2 are associated with higher temperatures. At the present time, levels of CO_2 are higher than ever before, and researchers predict that a warmer climate will ensue, as concentrations of greenhouse gases increase (Harrington 1987, Houghton and Woodwell 1989).

Current climate models have determined that mean global surface temperatures with a doubling of CO_2 are expected to increase between 3.5 and 5.2 °C (Wetherald 1991). These temperatures and predictions as to the magnitude, geographic extent and timing of global warming and future climatic behavior are based on complex General Circulation Models (GCM's), different versions of which vary somewhat in their predictions (Bunce 1994). These models have been developed using present day climatic data, but are commonly tested with reference to paleoclimate data (Walker 1995). The latter is important as changes in temperature predicted for the future are similar in magnitude, to the difference between present day global temperatures and temperatures of the last ice age (Bunce 1994). Hence, studies examining climatic changes that occurred with the last deglaciation (~ 10 000 yr. B.P.) are potentially good analogues for what changes may be seen during global warming, occurring now, and projected to occur in the future (Smol *et al.* 1991, Walker 1993). In other words, in order to be able to understand present day climate and the causes and implications of future climate change, a detailed understanding of past climate change is

essential (Smol 1988, 1990). Furthermore, paleoclimate records from around the world are required in order to have a detailed profile of past changes in climate (Smol 1988). In terms of resolution, obviously the higher the resolution the better, and the more data the better. Thus data on sites 10km apart would offer a higher resolution than those hundreds of kilometres apart.

Lake sediments record changes that occur in the environment, including the direct and indirect effects brought about by climatic change (Smol *et al.* 1991). Also, many physical and biological, as well as chemical indicators, are found within lacustrine sediments (Smol 1990). Almost all fossils of past biota can be used to infer past climate and, in fact, many of these fossil indicators may be more sensitive indicators of climatic change than other physical and chemical proxy data (Smol 1990, Hengeveld 1998). This statement reflects recent work conducted on the ecological characterization of indicator organisms (thermal optima, etc.) via surface sediment studies (see Walker *et al.* 1997). Furthermore, Smol (1992) argues that because paleolimnologists can obtain very high resolution in lake sediments, this means that the impact of climate change on an area and its inhabitants can be deciphered better than by examining the output of any general circulation model.

How extensive global climate warming will be, and who and what will be affected, is controversial. Models provide basic, broad-scale predictions for events such as melting of ice-caps, changes in agriculture, expansion of deserts in temperate areas, decline in rainfall in temperate areas such as the Canadian Prairies, and increased rainfall in areas of India and Africa (Francis and Hengeveld 1998). Such predictions are, however, very general, and an entire area will not be affected uniformly, owing to differences in topography, elevation, etc.

British Columbia is ecologically diverse because of the latitudinal and elevational ranges, and diverse landforms. This province extends from 48 °12' to 60 ° 00' north in latitude. Elevation within the province ranges from 0 m at sea level to 4680 m at the top of

the highest mountain. Add to this Pacific humid air masses from the west coast, and mountain ranges that extend from northwest to southeast, and the result is very different climates all over the province (Farley 1979). This has led researchers to conclude that for British Columbia itself, it is not possible to predict and put forth one overall present day and future climatic picture (Kimmins and Lavender 1992). Therefore, because of the uncertainties regarding climate change and its impact throughout B. C., it only seems logical that data for regional and local ecosystem-level responses to climatic change be obtained.

In British Columbia, forestry is one of, if not the most important component of the economy. It accounts for not only ~ 50% of all export activity, but also for ~ 50% of manufacturing jobs, and over a quarter of total provincial economic activity (Kimmins and Lavender 1992). Climatic change will impact forests directly by affecting the growth and reproduction of tree species, and indirectly by altering the frequency of major disturbances (e.g., fire and insect outbreaks). It is therefore imperative that we develop a better understanding of climate processes, both past and present so that we can better prepare for possible future climate states.

Late-glacial and Holocene climate change has been examined in British Columbia, with the evidence coming mainly from studies on paleobotanical indicators, namely pollen and plant macrofossils (e.g., Alley 1976, Clague *et al.* 1992, Hebda 1995, Mathewes and Heusser 1981, Mathewes and King 1989, Pellatt and Mathewes 1997). Paleoclimate studies using midge remains (chironomids), as in this research, are of recent origin.

From these various proxy indicators, paleoclimate reconstructions have revealed distinct fluctuations in British Columbia's climate over the Holocene. Overall, Hebda (1995) concludes that three major Holocene climatic intervals are evident in B. C. The first of these was a warm, dry interval (aptly named the "xerothermic") that existed after deglaciation, from ca. 9500 - 7000 yr. B. P. Following this, from ca. 7000 - 4500 yr. B.P. there existed an interval where climate was warmer than present, but wetter than

during the xerothermic. This is referred to as the "mesothermic". The third interval, which showed a change to more modern conditions, extends from ca. 4500 yr. B. P. to present. During this interval, Hebda (1995) believes that cooler temperatures and increased precipitation prevailed. Evidence for neoglaciation, the readvance of mountain glaciers, has been observed in many areas during this time (e.g., Clague and Mathewes 1996, Ryder 1989).

Over the entire province, however, these events seem not to have been entirely synchronous, and the magnitude of the changes also varies among regions. For instance, the warm, dry xerothermic interval on the coast may have begun sooner and ended earlier than in the interior (Hebda 1995). Also, climatic changes in northern British Columbia appear to have occurred later than similar shifts in southern British Columbia. Furthermore, evidence of some climatic events found on the coast is entirely lacking farther inland. An example of this is recent evidence showing a cooling event on the coast similar to the Younger Dryas oscillation of Atlantic Canada (Mathewes 1993, Mathewes et al. 1993). Detailed reviews of what is known to date concerning climatic changes in B. C. based on pollen studies (published and unpublished) can be found in Hebda (1995) and Mathewes (1985). However, the province is very complex and what paleoecological data exists is limited and widely spaced across the province and its regions. To complete the record of paleoclimatic/paleoenvironmental changes that have occurred throughout the regions of B. C., more data need to be amassed. Relatively little paleoclimatic/paleoenvironmental information is available for the southwestern interior of British Columbia (Hebda 1995). It is advantageous to perform more paleoclimatic analyses in British Columbia, because although paleoclimate data exists, there is not very much of it. Furthermore, using chironomids is also advantageous, because lags in temperature reconstructions can occur with pollen, while the same does not occur with chironomids (Wilson et al. 1993). Furthermore, the more independant data that is amassed the better.

This will only make the inferences concerning climate change stronger, but also act as a cross-check against what pollen studies reveal.

1.2 Climatic Change and Disturbance

My research focuses especially on climatic change and disturbance in the Engelmann Spruce-Subalpine Fir (ESSF) biogeoclimatic zone, the highest forested zone in British Columbia's southern interior region (Meidinger and Pojar 1991). Begon *et al.* (1990) define disturbance as ". . . an event that removes organisms and opens up space which can be colonized by individuals of the same or different species." There are several notable disturbance agents that exist in the ESSF. The principal disturbance agents are probably climate, fire and volcanic tephra deposition. Wind, landslides/avalanches, and insects also contribute to disturbance within the forest.

The impact that climate change can have on ecosystems results in it being considered a major long-term natural disturbance factor. For instance, climate change plays a critical role in altering vegetation patterns (Hebda 1995) and is known to influence other short-term disturbance factors. Paleoecological studies have shown that disturbance regimes, such as fire, are not constant from century to century, but seem to have changed as climate changed (Davis 1994).

Climate change can impact on vegetation in the ESSF by causing shifts in location of vegetation communities. Many of the biogeoclimatic zones in the province of B.C. would change their location geographically by moving further north or higher in elevation, if temperatures were to increase anywhere from 1-6 C. For instance, the range of a forest community could move north 300-600 km or have an upwards increase in elevation of 300-600 m (Kimmins and Lavender 1992). Vegetation shifts have occurred before, for example, during the warm, dry xerothermic interval (9000 to 7000 yr. B.P.). Research has shown that treeline was higher than present in the xerothermic based on the evidence of fossil wood and macrofossils found above present treeline in many places in southern and coastal B. C. and Alberta (e.g., Clague *et al.* 1992, Luckman and Kearney 1986, Pellatt

and Mathewes 1994). Just how forest communities will respond to potential climate change however is unknown, again, owing to the complexity of climate change itself and the unreliability of predictions (Kimmins and Lavender 1992).

Wind, landslides/avalanches, plant pathogens and insect pests can also act upon forest ecosystems, but the extent of their impact may not be so significant. Wind as a disturbance agent can cause tree fall. Large amounts of tree fall could increase erosion. Landslides and avalanches can denude areas of vegetation. These areas then may be prone to further erosion. A final disturbance agent could be biological, namely insects and plant pathogens. When forests are stressed, due to climatic changes such as hotter, drier climes they become more susceptible to attacks by pathogens such as fungi, as well as insect outbreaks (Kimmins and Lavender 1992). For example, the insect that inflicts the most damage on trees in the subalpine zone of the southern Rockies is the spruce beetle (Dendroctonus rufipennis Kirby). These outbreaks are believed to be caused by a combination of mild winter conditions as well as blow-downs and logging, as the insects infect fallen trees first (Veblen et al. 1994). Similarly in eastern Canada, outbreaks of spruce budworm occur when there have been summer droughts. During summers of drought in B. C., there are outbreaks of bark beetle (Kimmins and Lavender 1992). Trees can be killed by outbreaks and infestations of certain insect pests and pathogens. Therefore, as insects, like plants, are adapted to certain climatic conditions, climate could have a secondary effect on insect outbreaks. Cooler climatic conditions may impede outbreaks.

An understanding of climatic change and disturbance may come through paleoecological analyses of indicator organisms such as chironomids. The study of fossil organisms and their environment is the essence of paleoecology, and as a science it focuses not only on the past, but also on recent environmental processes (Walker 1995).

There are advantages to such a paleoecological approach to study disturbance. First, records of disturbance regimes, such as climate change, dating back thousands of

years are not available. Thus, information about long-term disturbance has to be obtained from proxy data. These proxy data may come from a variety of indicators. A continuous record can often be found in lake sediments (Smol 1988). Secondly, conventional studies (i.e., non-paleoecological studies) that last 5-20 years do not allow for a full understanding of environmental variability. Thirdly, direct manipulation of an area is extremely expensive and, depending on spatial and temporal scale, may be impossible. Since disturbance intervals in forests can range in duration from decades to centuries, conventional studies are slow to provide relevant information (Smol *et al.* 1991). Given these difficulties, paleoecological data are valuable for understanding forest and lake processes, and, particularly in this study, how they respond to climatic disturbance.

The objectives of this research are to first assess the timing and magnitude of climatic changes in this area. These changes were inferred first based on inspection of the data in the chironomid stratigraphic diagrams. I have subsequently inferred temperatures quantitatively using a newly-developed paleotemperature inference model for British Columbia. Finally, I have used the chironomid data to explore patterns in ecosystem development as revealed by community trajectories, and changes in both richness and diversity.

Chapter II

The Chironomidae

Chironomidae are members of the true flies (Diptera). Adults resemble mosquitoes, although they do not bite. Most do not have a proboscis (Walker 1987). Adults are winged, although some taxa have underdeveloped wings and are unable to fly (e.g., *Corynocera*). Chironomids are found in most aquatic ecosystems as well as moist soils, holes in trees, peat and animal dung (Coffman and Ferrington 1984, Walker 1987). In freshwater ecosystems the larvae of these flies are among the most abundant benthic macroorganisms, along with oligochaetes (Hofmann 1988, Walker 1987, 1993). Unlike oligochaetes however, chironomid larvae leave behind an abundance of fossil evidence.

Chironomids have four life stages: egg, larva, pupa and adult (Coffman and Ferrington 1984, Walker 1987). The life cycle is depicted in Figure 1. The larvae shed their exoskeleton four times, each time shedding a sclerotized head capsule which becomes incorporated into sediments. As head capsules are composed of chitin, they preserve well and result in an abundant fossil record (Hofmann 1988, Walker 1987). Furthermore, as rates of sedimentation are quite high in lacustrine systems, high temporal resolution analyses of chironomids are possible. The life span of a chironomid varies depending on both species and habitat. The larval stage can last anywhere from two weeks to a few years. Species from arctic regions have the longest life cycles. Chironomid adults usually only live a few days, with some species surviving for a few weeks (Coffman and Ferrington 1984, Walker 1987).

Chironomids are known to respond to a variety of environmental influences making them ideal indicators of disturbance. Each species is adapted to specific ecological conditions and habitat, thus, their fossil assemblages indicate environmental conditions that existed during sedimentation (Hofmann 1988). This is why ecological characterization





of taxa is so important. Knowing accurately ecological requirements (or autecology) of taxa allows researchers to reconstruct and interpret past environments from the fossil assemblages (Smol 1990). Determination of the environmental requirements of each species has come a long way, considering that less than ten years ago there was a dearth of ecological information (Walker 1987). The ecological optima and tolerances of chironomid species can be efficiently determined using subfossil chironomid remains derived from surface sediment samples (Walker 1987, 1995, Walker *et al.* 1991a). These modern samples and the derived ecological information are then compared with fossil data, allowing for quantitative paleoenvironmental reconstructions (Walker 1995).

Chironomid communities are affected by the oxygen content of water (Hofmann 1988). If oxygen concentrations are high, certain species are present. If oxygen concentrations are depleted one species may disappear and be replaced by another species which can survive in low oxygen environments (Hofmann 1988, Walker 1987, 1993, 1995). One such species that can survive at low O_2 is *Chironomus anthracinus* Zett., as the larvae contain hemoglobin.

The availability of oxygen is correlated with lake trophic status and productivity (Hofmann 1988, Walker 1987). When trophic changes occur, such as an increase in nutrients and hence an increase in lake productivity, a dramatic response in chironomid communities is seen (Walker 1987). This is because different chironomid taxa are found in the profundal zone of oligotrophic, mesotrophic and eutrophic lakes, depending upon their oxygen and food requirements (Walker 1993). With high nutrient loads coming in from the surrounding catchment, a lake can become highly productive and hence eutrophic. This lowers the oxygen concentration in the hypolimnion. Consequently, chironomid fossil assemblages have been used to assess eutrophication due to human settlement and other environmental changes brought about by humans (Walker 1987, 1993). The use of chironomids as paleoecological tools to assess eutrophication can be seen in studies by Walker *et al.* (1993) and Warwick (1980).

Chironomids are sensitive to changes in acidity as well as salinity of water (Hofmann 1988, Walker 1987, 1993, 1995). Chironomids have been found in very acidic waters, and faunal changes do occur with increased acidification. For instance, several species increase in abundance (e.g., *Chironomus, Sergentia, Psectrocladius* and *Zalutschia*) when water pH decreases (Hofmann 1988, Walker 1987, 1993).

The use of chironomids as paleosalinity indicators is very recent. Even though early studies showed that chironomid fauna changed with respect to changing salinities in B. C. saline lakes (e.g., Cannings and Scudder 1978), very few paleosalinity studies have been done. This is because, like pH, salinity optima of species were unknown (Walker *et al.* 1995). However, a very recent study by Walker *et al.* (1995) of chironomid remains from a suite of B. C. saline lakes determined that summer salinity levels affected their distribution. This further led to the development of a chironomid-salinity inference model for use with chironomid paleoecological data (See Walker *et al.* 1995). This model is important for detecting shifts between fresh and saline water conditions and can also help in paleoclimate reconstructions. Although salinity is affected by nutrient and mineral influx into a lake, it is also affected by changes in climate. Temperature changes affect evaporation and precipitation in an area. Increased temperature results in increased evaporation, and this can lead to higher salinities (Hofmann 1988, Walker 1993, Walker *et al.* 1995).

Chironomid distributions are highly correlated with summer temperatures and this suggests that climate, directly or indirectly, has an effect on their distributions (Hofmann 1988, Walker 1987, 1995, Walker *et al.* 1991a). Indirectly, climate change affects composition by acting on lake ecosystems. For instance, increased nutrient levels may result owing to increased weathering at higher temperatures. This can result in changes to lake trophic status, as mentioned earlier. These nutrients, can affect chironomid faunal composition. However, it might also be argued that productivity would decrease with warming since nutrients might be trapped beneath a more stable thermocline. Climate can

also impact indirectly by changing water levels, and higher temperatures may also result in increased biological activity and lake productivity. Furthermore, nutrient inputs to a lake are affected by vegetation around the lake, itself dependent on climate (Walker 1987). Directly, a change in climate increases or decreases water temperature (Hofmann 1988, Walker 1987, Walker and Mathewes 1987). At colder water temperatures, those species adapted to warmer environs may not be able to complete their life cycles (Smol 1990).

Before 1987, how chironomids were related to climate was essentially unexamined. The first study to actively explore the potential of using chironomids as indicators of paleoclimate was performed by Walker and Mathewes (1987). After examining fossil remains from a coastal lake core, they then compared the inferred climate changes, determined from the chironomid stratigraphy, with the climatic history inferred from an earlier palynological study of the lake. Overall, when compared to the existing pollen data, Walker and Mathewes (1987) found that the chironomid-inferred climate changes corroborated the independent inferences determined by pollen. From this evidence, chironomids became credible paleoclimatological indicators. Furthermore, studies at that time showed that modern-day fauna are strongly correlated with climate. Members of the subfamilies Chironominae and Tanypodinae are mostly warm-adapted species. Found at lower elevations, these taxa undergo rapid growth during the summer. Cold-adapted taxa are members of the subfamilies Orthocladiinae and Diamesinae which are found in cold climate arctic/alpine areas. These species grow in the winter months (Walker 1987, Walker and Mathewes 1987).

The use of chironomids as paleoclimate indicators has not been universally accepted, and some controversy has existed as to their use. The debate persisted from 1987 through to 1992 and many papers have been written. Interested readers are referred to Walker (1995) for a list of these publications.

However, a solid understanding of just how chironomids relate to climate was lacking. In order to determine just how chironomid composition is influenced by climate,

Walker and Mathewes (1989a) undertook a gradient analysis. This involved examining surficial sediments in 30 lakes across an altitudinal gradient. This analysis improved on the general classification of subfamilies with regards to their ecological requirements by providing information about actual genera and species groups, and their distribution according to altitude. The research showed that lower elevation species were not found in the subalpine/alpine zones at higher elevations (Walker and Mathewes 1989a). Walker and Mathewes (1989a) were further able to place chironomid fauna into three different groups depending on where each individual taxon occurred: low to mid-elevation taxa, high elevation taxa (containing the cold-stenotherms) and widely distributed taxa. This study allowed the researchers to conclude that climate was having an impact (directly or indirectly) on species composition - that in fact the range of many taxa may be temperature limited (Walker and Mathewes 1989a). This research further substantiated the idea that chironomids were potentially good proxy indicators of climate. However, information on actual temperature optima and habitat preferences for each species were still lacking.

Multivariate analyses on surficial lake sediment samples allowed researchers to determine which environmental factors influence the composition of the fauna (Walker *et al.* 1991a, Wilson *et al.* 1993). Research by Walker *et al.* (1991a) used canonical correspondence analysis (CCA), a multivariate analytical technique. Through the analysis of fossil chironomid surface sample data from 26 lakes in Labrador and Quebec, and measured environmental variables, Walker *et al.* (1991a) determined that summer surface-water temperatures as well as lake depth were the factors that were most strongly correlated with the distribution and abundance of chironomids (Walker *et al.* 1991a). Their study indicated that Axis 1 in a CCA was most strongly correlated with temperature (r=-0.70).

Using these data, a weighted-averaging model of the chironomid-temperature relationship was developed. This chironomid-temperature transfer function allowed reconstruction of past climates from fossil chironomid assemblage data (Walker *et al.* 1991a). However, while this model permitted quantitative reconstructions of past climate

regimes, it had limitations in that it could only be used for chironomid data in eastern Canada and its accuracy was limited. More surface sample data from other lakes in the area was required to improve the accuracy of the inferred temperatures (Walker *et al.* 1991a).

The aforementioned model was expanded by Wilson *et al.* (1993). Ecological data encompassing lakes from Devon Island, N. W. T. south to Nova Scotia and New Brunswick were added. Due to this increase in data, more accurate paleotemperature reconstructions could be obtained (Wilson *et al.* 1993). This chironomid-temperature inference model has since been used in other paleoclimate studies. This model has only recently been improved yet again, with more surface sample data from eastern Canada, and including sites from Maine (see Walker *et al.* 1997).

This model provides good temperature inferences with a jack-knifed root-meansquare-error of prediction (RMSEP_{*jack*}) of 2.26 C but is only applicable for Atlantic Canada (Walker *et al.* 1997). In order for accurate paleotemperature reconstructions to be performed elsewhere, transfer functions need to be developed for each region. This is occurring. For instance, in parts of Europe, the power of quantitative paleoclimate reconstructions has led to the development of transfer functions in Norway, Finland and Switzerland (Lotter *et al.* 1997, Olander *et al.* 1997). Until now however, no paleotemperature inference model existed for western Canada. My study marks the development of the first chironomid-temperature inference model for use in British Columbia. This model was developed using elevation data, and temperature lapse rates (the rate that temperature decreases with increases in elevation), as well as chironomid fossil data. Its development and use in this research will be detailed in another section.

Lastly, chironomids can be affected by predator-prey relationships. Chironomids constitute a major component of the diet of many freshwater animals, both invertebrate and vertebrate. In addition many chironomids prey on other chironomid species (Tokeshi 1995). However, little is known in regards to predator-prey relations between chironomids and their predators, except for the influence of fish (Tokeshi 1995). Studies show that

densities of chironomids decrease with increased predation, yet as seen below, this in itself is inconclusive overall.

It is known that various chironomid larvae are preyed upon differently depending upon their foraging behavior. Those that are free-living (e.g., *Procladius*, *Thienemanniella*), and those tube-dwellers that leave their tubes frequently to feed, are preyed upon more than other larvae (Goyke and Hershey 1992, Hershey 1987, Tokeshi 1995). Overall though, smaller chironomids are preyed upon more than larger larvae, beçause larger larvae are able to construct more secure tubes and are also able to burrow deeper into sediment (Tokeshi 1995). Experimental research has verified this (Hershey 1987). The tubes serve as an anti-predator device.

As mentioned, they have many possible predators. First, they can prey on one another, with several species being considered predatory. However, the effect of chironomid predators on each other (in terms of community impact) has hardly been studied (Tokeshi 1995). Fish are important predators of chironomids. Fish are believed to be selective chironomid consumers, with some feeding on larvae while others feed on pupae and adults (Pinder 1986). Fish are also believed to be size-selective, with smaller chironomids being the preferred prey. This selectivity is likely due to chironomid habitat and refuge use, etc. (Tokeshi 1995). Fish can then impact on all stages of the chironomid life-cycle. However, just how and if fish predation does influence chironomid population size is still inconclusive. Some studies have shown that densities of chironomids do not change when fish numbers decrease, or when fish are completely excluded from an area. Conversely, some studies have shown density changes in chironomids when predators were or were not there (Tokeshi 1995). Salamanders and other amphibians are known predators of chironomids as well. They have been seen to reduce species richness of certain invertebrates by 53%. They are also shown to be size-selective like fish (See Blaustein et al. 1996). Turtles are another possible predator in aquatic ecosystems.

Finally, waterfowl feed on various macroinvertebrates including the Chironomidae (Tokeshi 1995). Chironomids make up portions of the diet of young diving ducks as well as some dabbling ducks. It is further believed that the distribution of population size in some birds is influenced by whether chironomids are available as a food source at certain times of the year (Pinder 1986).

Predators can have both direct and indirect effects on prey. Indirectly, they can impact on other predators of chironomids in the same food web (Tokeshi 1995). That is, trophic cascades can occur when top predators (be it salamanders, fish, birds, etc.) impact on their prey populations and this trickles down to affect the trophic levels below. This was seen in the salamander study of Blaustein *et al.* (1996). The patterns then seen are a result of chironomid communities reacting to various types of predation pressures and are highly variable. On top of this there is the effect of habitat. This can affect not only what chironomid taxa are found in a certain area, but it also impacts on the efficiency with which predators are able to forage for their food (Tokeshi 1995). All these possible interactions then make predation impacts on community composition and abundance hard to determine and interpret.

Predation is a disturbance factor and could possibly account for changes seen in chironomid communities. However, in terms of paleoecological studies such as this, it would be very difficult to ascertain, for several reasons. One is that records of gut contents, of fish for example, do not extend back 10 000 years. Records of ingestion by birds (such as the waterfowl mentioned) also do not exist. Furthermore, birds are migratory. Records also do not exist for other possible predators.

Predator-prey interactions also depend on what predators are actually in an area. There are no complete faunal records for either of my study lakes, nor the surroundings. Those records that exist are scant in information and are entirely based on casual observations (Steve Matthews, *pers. commun.*). Even if complete faunal records were available, they would only account for a few decades. Even then, the interactions and

associations between members of trophic chains would be virtually impossible to interpret. Thus, while predation could be a potential disturbance factor, I was not able to examine its role in my study.

The power of chironomids as tools for paleoecological/paleolimnological research is undeniable. In terms of climate change, they may in fact be more sensitive than other proxy data (i.e., pollen). This is due to the fact that chironomids are able to respond faster to changes in climate due to their short life spans. Furthermore, they are able to disperse quickly and efficiently because of their wings (Walker *et al.* 1991a, Walker *et al.* 1991b, Walker 1993). A time lag may exist between when climate change occurs and when vegetation responds, because many plants require suitable soils and many species (such as trees), unlike chironomids, have extremely long life spans and inefficient dispersal mechanisms(Wilson *et al.* 1993).

Chapter III

Methods

3.1 Study Sites

The study lakes, North Crater Lake and Lake-of-the-Woods, are located within the Kamloops Forest Region of the southwestern interior of British Columbia, Canada (Fig. 2). Both lakes are located in the Okanagan Range of the North Cascade Mountains, and fall within the ESSF (Engelmann Spruce - Subalpine Fir) biogeoclimatic zone. This is the highest forested zone in the southern two thirds of the British Columbia interior (Meidinger and Pojar 1991). Forests in this zone are continuous at lower and mid elevations, with subalpine parkland found at higher elevations (Lloyd *et al.* 1990).

My study lakes fall more specifically within the very dry, cold subzone of the ESSF (ESSFxc) (Lloyd *et al.* 1990). In the Kamloops Forest Region, this subzone encompasses both the highest forested elevations as well as the driest. Vegetation of this subzone is characterized by the climax tree species, Engelmann Spruce (*Picea engelmannii* Parry) and subalpine fir (*Abies lasiocarpa* (Hook) Nutt.). Lodgepole pine (*Pinus contorta* Dougl.) is also present in stands due to fire, as well as white bark pine (*Pinus albicaulis* Engelm.). A poorly developed shrub layer consisting of black huckleberry (*Vaccinium membranaceum* Dougl.) and white-flowered rhododendron (*Rhododendron albiflorum* Hook) is often found on steep, north-facing slopes and in depressions. Furthermore, presence of the herb Sitka valerian (*Valeriana sitchensis* Bong.) distinguishes the ESSF from all other zones (Lloyd *et al.* 1990). Both lakes are found at the upper reaches of this zone, at or just below treeline (Fig. 3 and 4).

The ESSF zone has a continental climate. This consists of long, cold winters with a high snow cover (remaining until late May) and cool, short summers (Lloyd *et al.* 1990). As climate plays an important part in the classification of B. C.'s biogeoclimatic zones (Pojar *et al.* 1987), some important ESSFxc environmental variables are presented in Table 1. Both Rice (1947) and Melcon (1975) have produced detailed accounts of the geology in



Figure 2: Location of study sites within British Columbia.

| Mean annual temperature | 1.7 ° C |
|----------------------------------|----------|
| Mean annual precipitation | 565 mm |
| Mean annual snowfall | 321 cm |
| Mean frost-free period | 45 days |
| Mean growing season temperature | 9.3 ° C |
| Mean growing season | 233 mm |
| precipitation | |
| Mean growing degree days (> 5 C) | 764 days |

Table 1: Selected environmental variables for the ESSFxc subzone (Lloyd et al. 1990).











Figure 4: Aerial photograph of Lake-of-the-Woods and the four other lakes making up the core area of Cathedral Provincial Park (1:25 000).

this area.

North Crater Lake (120 ° 1' W, 49 ° 4' N) is located on the north shoulder of Crater Mountain. Sitting at 2120 m asl (above sea level), it is at the uppermost reaches of treeline (Fig. 3). This lake has an area of approximately 1.5 ha, with no inlet or outlet present. Maximum water depth is approximately 1.7m (I. R. Walker, *pers. commun.*). The name "North Crater Lake" is commonly used by local residents, but has not been formally designated at this time. Thus, it may eventually be formally adopted, unless a traditional First Nations name is available.

Lake-of-the-Woods (120 ° 11' W, 49 ° 3' 45'' N) is one of five lakes located within the core area of Cathedral Provincial Park (Fig. 4). Situated at 2050 m asl, this cirque basin lies about 240 m below treeline (Evans 1997). The lake has an area of approximately 3.06 ha, and a maximum depth of 3.6 m (Evans 1997). An inlet stream, which is fed by Pyramid Lake, flows into this lake, at the south end. An outlet stream is very close to the inlet stream (Fig. 5). Water from these lakes drains into the Ashnola River, which is a tributary of the Similkameen River.

North Crater Lake and Lake-of-the-Woods were chosen as study sites for their size as well as their location. Paleoecologists/ paleolimnologists prefer small lakes with well protected basins and moderate depth. This is because larger lakes with long water retention times are less likely to show a response to short term trends such as nutrient loading, increase in temperature, etc. These larger lakes dampen fluctuations recorded in sediments particularly as sediment deposition may be irregular (Smol *et al.* 1991).

Although much research has already been conducted within my study area, particularly in Cathedral Provincial Park (e.g., Evans 1997, Melcon 1975, Ratcliffe and Turkington 1987, Ratcliffe and Turkington 1989, Saunders and Bailey 1996), my research constitutes the first paleoenvironmental/paleoecological investigation for the Cathedral Lakes and surrounding area, including Crater Mountain.



N

Depth Metres



Figure 5: Bathymetry of Lake-of-the-Woods, Cathedral Provincial Park, British Columbia (Courtesy of Evans 1997).

Both study lakes are small and surrounded by protective basins. They are sufficiently deep to ensure that the sediments have been little disturbed, yet sufficiently shallow that the records will be dominated by temperature sensitive littoral species. Furthermore both lakes are located very near alpine treeline. Treeline is an ecotone boundary whereby the distribution of plants is determined by growing season temperature as well as precipitation and snowpack. Hence treeline is very sensitive to climatic changes (Luckman and Kearney 1986, Pellatt and Mathewes 1997). As climate exerts a strong control on this area, lakes located at treeline are likely to be sensitive to even the smallest climatic changes. As chironomids are directly affected by temperature changes the chironomid stratigraphies obtained from these lakes are likely to reveal any past climatic fluctuations.

3.2 Coring procedures

Several cores from North Crater Lake were obtained in the summer of 1995 in ~ 1.7 m of water with a Livingstone piston corer with a core tube diameter of 5 cm. One 3m sediment core was obtained and extruded on site. Stratigraphy of the core was documented and the core was then sectioned, usually in 5 cm increments, and the sections stored in sealable, plastic sampling bags. One centimetre sections were taken around major disturbance events as indicated by volcanic ash and around regions of expected faunal changes (i.e., clay/gyttja interfaces). This material was transported to Okanagan University College (O.U.C.) in Kelowna, and stored at ~ 4 °C for further analysis.

Core A9 from Lake-of-the-Woods was obtained from Dr. Martin Evans, from the Geography Department at the University of British Columbia. This 4m core was also obtained with a Livingstone corer in 1 - 2m of water, in the summer of 1995. Location of the coring site can be seen in Figure 5. The core was extruded in the field and 1m sections were wrapped in cling film. After being placed in plastic sheaths and then in plastic tubes, these sections were transported in core boxes and stored at room temperature at U.B.C. for

later use (M. Evans, *pers. commun.*). On being made available to this study, the core was sectioned in a manner similar to the North Crater Lake core, with stratigraphy documented.

3.3 Chronology

In order to establish chronological time sequences, samples for bulk radiocarbon dating were removed from both cores. From the North Crater Lake core, five increments were removed for dating, while three increments were removed from the Lake-of-the-Woods core. AMS radiocarbon dating was performed on a sixth sample from North Crater Lake. All radiocarbon dating was performed by Beta Analytic Inc. using methods as outlined by Beta Analytic Inc. at their website (www.radiocarbon.com). These methods conform closely to standard radiocarbon protocols as described for example by Olsson (1986). Table 2 shows the sample depths and conventional 14 C dates obtained for both lakes. It should be noted that errors provided with radiocarbon dates reflect errors with precision of measurements and not accuracy of measurements. Despite high precision measurements, inaccurate dates can be obtained from hardwater lakes. Often called the hardwater effect, it results when carbon is released from carbonate rocks (e.g., limestone) as they dissolve, and then becomes incorporated into the tissues of aquatic organisms. Hence, these tissues give older ¹⁴C dates than normal, due to this ancient C derived from the carbonate rock (Walker 1993). This isn't expected to be a problem in this case, because hardwater lakes are rare at higher elevations, and both catchments in this study are underlined by metamorphic as well as sedimentary rocks. For instance, Lake-of-the-Woods is underlain by granodiorite (Evans 1997). Secondly, two volcanic tephras were found in the sediment cores. The two tephra layers are from Mount Mazama (6730 B.P.) (Hallett et al. 1997) and a prehistoric eruption of Mt. St. Helens called St. Helens Y (3390 ± 130 B.P.) (Fulton 1971). The tephra layers were found in both the core from North Crater Lake, as well as the Lake-of-the-Woods core. Identification was based primarily on stratigraphic position within the cores. However, Evans (1997) identified these two
| Core/Depth | Lab #: | ¹⁴ C yr. B. P. |
|---------------------|--------------|---------------------------|
| CL 85 - 95 cm | Beta - 91829 | 1890 ± 90 B.P. |
| CL 135 - 140 cm | Beta - 90297 | 3080 ± 90 B.P. |
| CL 190 - 195 cm | Beta - 90298 | 5470 ± 90 B.P. |
| CL 240 - 245 cm | Beta - 90299 | 8150 ± 100 B.P. |
| CL 267.5 - 275.5 cm | Beta - 90300 | 9540 ± 100 B.P. |
| CL 280 - 284 cm | Beta - 90289 | 10290 ± 80 B.P. |
| A9 140 - 150 cm | Beta - 94805 | 5450 ± 90 B.P. |
| A9 241 - 250 cm | Beta - 94806 | 8580 ± 80 B.P. |
| A9 341 - 350 cm | Beta - 94807 | 10200 ± 70 B.P. |

Table 2: Radiocarbon dates for North Crater Lake (CL series) and Lake-of-the-Woods (A9 series) sediments. (Error statisitics indicate ±1 s.d. based on decay count errors only (www.radiocarbon.com)).

tephras in almost all of his Cathedral Lake cores (which included 12 - 15 cores from each lake) and based his identifications on chemical analysis. These tephras then act as separate chronostratigraphic markers, independent of radiocarbon analysis.

3.4 Chironomid Analysis

For both lakes, subsamples of sediment were removed at various intervals for chironomid analysis. In both cores, these subsamples spanned the interval from Late-glacial time (>10 000 yr B. P.) to the present. In North Crater Lake one subsample was taken every 10 cm to the 100 cm level. After that subsampling occurred every 5 cm to the base of the core. Subsampling was at higher resolution around major disturbance events, as were evident from volcanic tephras, and charcoal layers. Each subsample consisted of 0.3 ml to 1 ml of sediment. The volume examined was varied in order to obtain at least fifty identifiable head capsules per increment, while trying to retain as much sediment as possible for complementary analyses by other scientists.

The Lake-of-the-Woods core was subsampled in a similar manner. In total, 63 subsamples of at least 1 ml each were obtained from the Lake-of-the-Woods core for chironomid analysis. For North Crater Lake 47 subsamples were examined. In both lakes, most subsamples provided more than one hundred head capsules. North Crater Lake subsamples had an average of 422 head capsules. The minimum number identified was 65 head capsules while the maximum number of head capsules per subsample was 901.5. The standard deviation was 202.6. For Lake-of-the-Woods, each subsample on average had 184 head capsules. The minimum number was 54 while the largest number per subsample was 564.5. The standard deviation was 103.1.

Once the samples were extracted from the sediment core, they were first treated with 10% HCl to remove calcium carbonate. Subsequent procedures for processing the sediment, to concentrate the head capsules, for sorting the head capsules, and for identifying and counting, follow procedures outlined by Walker *et al.* (1991a). These include deflocculating each sample in warm 5% KOH and sieving on a 95 µm Nitex[®]

mesh. The sediment retained on the mesh was then washed into a beaker using distilled water. Hand - sorting of chironomid head capsules, along with other fossils from the sample was done in a Bogorov counting tray at 50× magnification. Isolated head capsules of Chironomidae, Ceratopogonidae and *Chaoborus* mandibles were mounted on glass slides using Entellan [®] mounting medium.

Using various compound microscopes, chironomid identifications were completed at $100 \times$ to $400 \times$ magnification. The chironomid remains were identified mainly to the generic level with reference to keys by Walker (1988), Oliver and Roussel (1983), Wiederholm (1983), and an extensive photo reference collection. The system of nomenclature adopted follows Walker (1988), such that when two genera cannot be separated from head capsule remains, both names separated by a slash are given (e.g., *Brillia/Euryhapsis* = *Brillia* and *Euryhapsis*). Whole head capsules, or broken ones with more than half of the mentum, were counted as one head capsule. Those with precisely half the mentum were counted as half, while fragments that consisted of less than half were not counted. At least 50 identifiable chironomid head capsules were required from each level in order to perform detailed analyses of the data.

Raw data obtained from chironomid identifications and counts were then used to produce chironomid stratigraphic diagrams for both lakes. This was done using the programs TILIA version 2.0 b.4 (Grimm 1993) and TILIA-GRAPH version 2.0 b.5 (Grimm 1991, unreleased) developed by Eric Grimm (Illinois State Museum, Research and Collections Centre, 1920 South 10 1/2 Street, Springfield, IL 62703).

The data were converted to proportions and then square-root transformed prior to doing a stratigraphically constrained incremental sum-of-squares cluster analysis (using the computer program CONISS). The cluster analysis was done in order to determine where major changes in chironomid composition occurred throughout the core. The incremental sum-of-squares method is first of all a hierarchical agglomerative form of cluster analysis with the idea of minimizing the total dispersion within each cluster. It is sometimes

referred to as Ward's method, minimum variance, sum of squares, error sum of squares and optimal agglomeration (Grimm 1987). Stratigraphically constrained sum-of-squares cluster analysis is a variation on this where only stratigraphically adjacent clusters are merged (Grimm 1987). Ultimately the number of zones that I recognized was based on inspection of the CONISS output, not by any *a priori* criteria. For further details concerning the method of stratigraphically constrained incremental sum-of-squares cluster analysis as performed by CONISS, see Grimm (1987).

3.5 Climatic Inferences

In order to examine relationships between the chironomid data and past climates, further statistical analysis was performed.

The first of these was the construction of a temperature inference model for use in southern British Columbia. Surface sample data from across southern B. C. and adjacent Alberta were used in the modeling program CALIBRATE version 0.82 (Juggins and ter Braak 1997) to develop and apply a temperature inference model. Another program, WAPLS version 1.1 (Juggins and ter Braak 1996) was ultimately used to determine sample specific errors for the best model (see ter Braak and Juggins 1993).

The surface sample data set consisted of 51 lakes ranging from the Rockies to the Queen Charlotte Islands. The surface sample data comprised those sites assessed by Walker and Mathewes (1989a), as well as additional surface sample data more recently analyzed (Smith and Walker, unpublished). The lakes and their locations, elevations and mean July air temperatures are listed in Table 3. Since few of the lakes are situated near climate stations, I have estimated the mean July temperature (Temp. (°C) in Table 3) at each lake based on mean July air temperatures recorded at nearby climate stations (Source: Canadian Climate Normals, 1951-1980), and assuming a temperature lapse rate of 6.5 °C/1000m (Barry and Chorley 1987, Strahler and Strahler 1992).

| | 1 | | | | | |
|--------------|-------------------|---------------|---------------|--------------|------------|--------------------|
| | LAKE NAME | ELEVATION (m) | LONGITUDE (W) | LATITUDE (N) | TEMP. (°C) | CLIMATE STN. |
| Rockies | Ptarmigan Lk. | 2330 | 116°4.5' | 51°29' | 8.1 | Yoho Boulder Creek |
| | Hidden Lk. | 2270 | 116°6.5' | 51°29.1' | 8.4 | Yoho Boulder Creek |
| | Opabin Lk. | 2270 | 116°18.7' | 51°20.4' | 8.4 | Yoho Boulder Creek |
| | Hungabee Lk. | 2240 | 116°19.1' | 51°20.5' | 8.6 | Yoho Boulder Creek |
| | Lk. Annette | 1970 | 116°12.5' | 51°19.3' | 10.4 | Yoho Boulder Creek |
| | Mud Lk. | 1600 | 116°10.5' | 51°26.3' | 12.8 | Yoho Boulder Creek |
| QCI | Hermit Thrush Pd. | 550 | 131°54.4' | 52°41.3' | 10 | Tasu Sound |
| | Hippa Lk. | 230 | 132°58.4' | 53°31.9 | 12.1 | Tasu Sound |
| Southwestern | Chlorine Lk. | 2090 | 122°9.2' | 50°20.5' | 6.6 | Pemberton B. C.FS |
| B. C west of | Aqua incognito | 1970 | 122°10.2' | 50°20.4' | 7.4 | Pemberton B. C.FS |
| Cascades | Blowdown Lk. | 2030 | 122°9'6" | 50°21'7" | 7.0 | Pemberton B. C.FS |
| | Upper Kidney Lk. | 2090 | 122°8.75' | 50°21.25' | 6.6 | Pemberton B. C.FS |
| | Lower Kidney Lk. | 2060 | 122°10.0' | 50°21'3" | 6.8 | Pemberton B. C.FS |
| | Russet Lk. | 1870 | 122°51.9' | 50°1.4' | 4.4 | Squamish |
| | Black Tusk Lk. | 1750 | 123°1.6' | 49°57.6' | 5.2 | Squamish |
| | Helm Lk. | 1720 | 123°1.4' | 49°58.0' | 5.4 | Squamish |
| | Mimulus Lk. | 1720 | 123°1.8' | 49°57.5' | 5.4 | Squamish |
| | N. Elfin Lk. | 1480 | 122°59.2' | 49°47.2' | 7.0 | Squamish |
| | S. Elfin Lk. | 1480 | 122°59.2' | 49°47.1' | 7.0 | Squamish |
| | Lost Lk. | 069 | 122°56.1' | 50°7.7' | 12.1 | Squamish |
| | Stump Lk. | 200 | 123°7.3' | 49°47.3' | 15.3 | Squamish |
| | Alice Lk. | 180 | 123°7.3' | 49°46.7' | 15.4 | Squamish |
| | Nita Lk. | 625 | 122°59.6' | 50°6.0' | 12.5 | Squamish |
| | Upper Adit | 1875 | 122°51.8' | 50°02' | 4.4 | Squamish |
| | Lower Adit | 1845 | 122°51.8' | 50°02' | 4.6 | Squamish |
| | Mystery Lk. | 1140 | 122°56.0' | 49°22.5' | 12.6 | Grouse Mtn. |
| | Goldie Lk. | 066 | 122°65.1' | 49°22.3' | 13.6 | Grouse Mtn. |
| | Yew Lk. | . 945 | 123°12.7' | 49°24' | 13.9 | Grouse Mtn. |
| | Marion Lk. | 300 | 122°33.0' | 49°19.0' | 15.8 | U.B.C. RF Admin. |
| | Mike Lk. | 220 | 122°32.3' | 49°16.5' | 16.3 | U.B.C. RF Admin. |
| | Coleman Pond | 1680 | 121°44.0' | 48°48.6' | 6.9 | Cultus Lake |

Table 3: Names, elevations and mean July air temperatures for the 51 lakes from which surface sample data were used to construct the chironomid-paleotemperature inference model.

| | LAKE NAME | ELEVATION (m) | LONGITUDE (W) | LATITUDE (N) | TEMP. (°C) | CLIMATE STN. |
|------------------|-------------------|---------------|---------------|--------------|------------|--------------|
| | Hayes Lk. | 1460 | 121°43.3' | 48°51.5' | 8.3 | Cultus Lake |
| - | Highwood Lk. | 1250 | 121°40.5' | 48°51.9' | 9.7 | Cultus Lake |
| | Upper Twin Lk. | 1570 | 121°41'8" | 49°45' | 7.6 | Cultus Lake |
| | Picture Lk. | 1250 | 121°40.6' | 48°51.9' | 9.7 | Cultus Lake |
| | Hicks Lk. | 60 | 121°42.0' | 49°20.5' | 17.6 | Agassiz CDA |
| | Deer Lk. | , 60 | 121°40.5' | 49°22.0' | 17.6 | Agassiz CDA |
| | Trout Lk. | 90 | 121°44' | 49°21' | 17.4 | Agassiz CDA |
| | Misty Lk. | 70 | 127°15.7' | 50°36.3' | 13.2 | Port Hardy |
| | Frozen Lk. | 1180 | 121°27'40" | 49°35'25" | 11.4 | Hope A. |
| Southern | Lightning Lk. | 1225 | 120°50'05" | 49°03'30" | 14.5 | Manning Park |
| interior-east of | Shavawn Pond | 2000 | 121°13.8' | 49°58.3' | 8.8 | Merritt STP |
| or in Cascades | Kelly Pond | 1980 | 121°13.0' | 49°59.3' | 8.9 | Merritt STP |
| | Cabin Lk. | 1830 | 121°13.2' | 49°58.4' | . 9.9 | Merritt STP |
| | 3M Pond | 1950 | 121°13' | 49°59' | 9.1 | Merritt STP |
| | Stoyama Tarn | 2030 | 121°12.8' | 49°58.9' | 8.6 | Merritt STP |
| - | Natashia Pond | 2005 | 121°13.8' | 49°58.3' | 8.8 | Merritt STP |
| | Pellat Pond | 2060 | 121°13.85' | 49°58.4' | 8.4 | Merritt STP |
| | Roundabout Pond | 1905 | 121°12.42' | 49°58.7' | 9.4 | Merritt STP |
| | North Crater Lk. | 2120 | 120°1' | 49°4' | 10.6 | Mt. Kobau |
| | Lake-of-the-Woods | 2050 | 120°11' | 49°3'45" | 11.1 | Mt. Kobau |

The best technique for developing a chironomid-temperature inference model was determined from a series of modeling trials using different regression techniques. These regression methods included weighted averaging (with inverse and classical deshrinking, also with and without tolerance down-weighting), weighted- averaging partial least squares regression, and partial least squares regression. All trials were run first using untransformed percent species data and later with square-root transformed percent species data helps to reduce the influence of the most abundant species. The model chosen was the one which had the lowest jack-knifed root-mean-square-error of prediction (RMSEP) and the highest jack-knifed r².

In order to illustrate what impact a minimum sample size of fifty head capsules might have on inferred temperatures, or if sample size affects the temperature reconstructions, a simple test was performed based on a sample of one hundred head capsules from the 92.5 cm depth in the Lake-of-the-Woods core. This depth was chosen because there was a large number of head capsules. Temperature inferences were repeatedly calculated for this sample, in the first instance based on a single head capsule, then based on two head capsules, and repeatedly to one hundred head capsules. Each head capsule was added to the calculations in the same order as it had been identified from the original subsample. This illustrates the rate at which the temperature inferences will converge towards a stable value. The results of this analysis are presented in Figure 6. One can see that as the number of head capsules increases the temperature inferences become increasingly stable. Little change in the temperatures is evident where the number of head capsules exceeds 45. Since my samples contained at minimum 50 head capsules, and generally more than 100 head capsules, variations in subsample size probably had little impact on the inferred temperatures.

Figure 6: Increasing sample size and its impact on inferred temperature for depth 92.5 cm in the Lake-of-the-Woods core.



3.6 Diversity, Richness and Community Trajectories

Diversity changes within the cores were determined using the Shannon-Wiener Diversity Index calculated using the natural log (ln) H'=- Σ (p_i)(ln p_i). This was done in order to obtain a more quantitative interpretation of the diversity changes as depicted in the stratigraphic diagrams. To reduce the effect of sample size on richness, the species richness for each sample was based on the first fifty head capsules listed and identified from each sample. To address concerns that variations in the number of head capsules identified from subsamples might adversely influence the diversity and richness estimates, both diversity and richness estimates for the 92.5 cm Lake-of-the-Woods subsample were repeatedly calculated in the same manner as described in section 3.5 (i.e., based on 1, 2,100 head capsules). The estimated diversity value increased as the number of head capsules included in the calculation increased. However, for subsample sizes greater than 45 head capsules little effect was evident. This can be seen in Figure 7a). Richness increased continuously until a sample size of 65-70 head capsules. This can be seen in Figure 7b). A comparison of this result to one using all head capsules reveals the same trends.

Finally, in order to objectively address the question of whether species assemblages have recurred over time, as climate warmed and subsequently cooled, ordination analyses were performed. Selection of the most appropriate indirect ordination technique (Correspondence Analysis (CA), Principal Components Analysis (PCA), or Detrended Correspondence Analysis (DCA)) depends on the length of the first ordination axis as assessed from species scores. If the length of the first ordination axis is less than 1.5 standard deviation units (s. d.), PCA is appropriate. CA is recommended for first axes between 1.5 and 3.0 s.d. units, whereas DCA is better when axes are greater than 3.0 s.d. units in length (I. R. Walker, *pers. commun.*). As the first axis length for both lakes was greater than 3.0 s.d., DCA was appropriate.

Figure 7: Increasing sample size and its impact on both diversity and species richness for depth 92.5 cm in the Lake-of-the-Woods core.



a)



b)

According to Jongman et al. (1987), Hill (1973) introduced CA into ecology by the algorithm of reciprocal averaging and this is an extension of weighted averaging. The first axis in CA can be calculated by 1) assigning initial arbitrary scores to each site; 2) calculating initial species scores as weighted averages of the site scores; 3) calculating a new set of site scores as weighted averages of the species scores; 4) rescaling (deshrinking) the site scores to prevent the range of scores from getting smaller and smaller with successive iterations. Steps 2 through 4 are then iterated until little change in the site scores occurs from one iteration to the next. The second and subsequent axes are calculated in a similar manner but with the added constraint that they must be orthogonal to (uncorrelated with) earlier axes. DCA is a modification of CA that is intended to remove the arch effect, or horseshoe effect, that is evident in many ordination methods. In my DCA ordinations, detrending was acheived by means of a third order polynomial. This statistical analysis was performed using the program CANOCO version 3.12 developed by ter Braak (1991). DCA is an indirect gradient analysis or ordination technique. The purpose of ordination is to arrange species or samples along axes that represent different unknown environmental variables (Jongman et al. 1987). In this arrangement, species that are close together have similar ecology, and similarly, samples that are close together have similar species composition; those that are far apart have dissimilar composition (Jongman et al. 1987). Based on known species characteristics, these axes may then be recognized as distinct, but abstract environmental variables.

CHAPTER IV

Qualitative Interpretation of Results and Discussion

4.1 Radiocarbon Chronology

Radiocarbon dates from basal lake sediments (Table 2)provide a good indication of when deglaciation occurred, such that plants and other biota could begin to colonize. ¹⁴C dates from organic gyttja just above the clay at both study lakes indicate that deglaciation of the southwestern interior highlands occurred approximately 10 300 B.P. North Crater Lake has a basal radiocarbon date of 10 290 ± 80 B.P., whereas a basal date of 10 200 ± 70 B.P. exists for Lake-of-the-Woods.

These dates are consistent with ¹⁴C dates obtained in a recent paleoecological study of two lakes to the northwest of mine at Stoyoma Mountain, in the Cascade Mountains (Smith 1997). As the location, as well as the basis for that study, parallel my research, Smith's (1997) research will form the basis of comparisons with my results. Smith (1997) has Accelerator Mass Spectrometry (AMS) dates of 10 090 \pm 70 B.P. and 10 000 \pm 320 B.P. in Cabin Lake and 3M Pond, respectively. One study in the interior has shown that deglaciation may have begun earlier, perhaps by 13 000 B.P. (Hebda 1995). However, researchers question this date, suggesting that it may have been contaminated via coal or carbonates, yielding an anomalously old date (I. R. Walker, *pers. commun.*). Otherwise, the oldest date for the interior is 11 000 \pm 180 B.P. (Mathewes 1985).

4.2 Head Capsule Concentrations

Chironomid head capsule concentrations for both lakes are presented in Figures 8 and 9. As is evident, concentration of head capsules at each sampling interval varied within the sediment of both lakes. In North Crater Lake concentration varied from 1796 ml^{-1} at 197.5 cm to 29 ml^{-1} at 292.5 cm. Head capsule concentrations were highest in the middle of the core from 172.5 to 197.5 cm. The lowest concentrations appeared at the base of the core from 270.5 to 292.5 cm.





In Lake-of-the-Woods the chironomid head capsule concentrations varied from 564.5 ml⁻¹ at 375.5 cm to 54 ml⁻¹ at 72.5 cm. As with the North Crater Lake core, there was no definite pattern in chironomid increase or decline within this core. Unlike North Crater Lake though, the highest concentrations of head capsules appeared at the base of the core. There was, however, a noticeable difference in head capsule concentrations between the cores. North Crater Lake had an extraordinarily high concentration in each interval sampled compared to Lake-of-the-Woods. The presence of such high numbers was quite remarkable considering that highly organic sediment from small lakes produces on average between 50 to 100 head capsules ml⁻¹ (Walker 1987). However, much higher concentrations, almost 8000 ml⁻¹, were found in a lake in Alaska (Livingstone *et al.* 1958). Thus concentrations can and do vary greatly among lakes.

Chironomid stratigraphic diagrams, based on the percent of total identifiable chironomid head capsules at each depth are presented in Figures 10 and 11. Chironomid taxa as well as *Chaoborus* and identified Ceratopogonidae are listed along the top of each diagram. Taxa are separated into cold and warm water groupings using current information regarding their temperature preferences as determined by Walker *et al.* (1997). Taxa placed in these two groups are known to have narrow thermal tolerances. As a result of these well-defined, narrow ranges, these taxa are the best for delineating paleotemperature changes (Walker *et al.* 1997). Figure 12 shows head capsules of some cold-indicative chironomids, while Figure 13 shows representative genera indicative of warm environments. The remaining taxa are those that are least valuable in inferring changes in paleoclimate. These include the stream - inhabiting or "rheophilous" taxa (i.e., *Eukiefferiella/Tvetenia, Brillia/Euryhapsis, Doithrix/Pseudorthocladius, Corynoneura/Thienemanniella, Parametriocnemus, Rheocricotopus*), broad taxonomic groups like subtribe Tanytarsina, and eurythermic groups like *Procladius* and *Psectrocladius*,







abundances are expressed as percentages (region in black); expanded stippled region illustrates 10× Figure 10: Percentage chironomid stratigraphy for North Crater Lake, Crater Mtn., B. C. Species exaggeration.

Figure 11: Percentage chironomid stratigraphy for Lake-of-the-Woods, Cathedral Lakes, B. C. Species abundances are expressed as percentages (region in black); expanded stippled region illustrates 10× exaggeration.

Figure 12: Head capsules characteristic of some cold-indicative genera : a)*Heterotrissocladius*(400×), b) *Sergentia*(200×)

For both lakes there are four distinct chironomid assemblages (as determined by CONISS), representing inferred climatic changes over the course of the past 10 000 years.

4.3 North Crater Lake Stratigraphy

The 28 chironomid taxa identified in the core from North Crater Lake show distinct fluctuations in their abundances. The chironomid diagram is divided into four zones, based on stratigraphically -constrained incremental-sum-of-squares cluster analysis (Fig. 10). This analysis determines where major changes in chironomid composition occur. The lithology of the core can be seen on the left side of the diagram. Zone NCC-1 falls from 295-268 cm and encompasses the late-glacial period. Zone NCC-2 encompasses the early Holocene and is found from 268-232.5 cm. The mid-Holocene is encompassed by Zone NCC-3 from 232.5-168 cm. The most recent sediments, from ~ 3700 yr. B.P. to present, are found in Zone NCC-4 (168-0 cm).

Zone NCC-1 (295-268 cm):

The chironomid assemblage in this zone represents a late-glacial, coldstenothermous community, including two cold-stenotherms, *Heterotrissocladius* (<5% of fauna) and *Sergentia*. Cold-stenotherms such as these are most common in arctic/alpine lakes where waters are cold and O_2 saturated, but also occur in the profundal zone of deep temperate, oligotrophic lakes that seasonally stratify (Sæther 1979, Walker and MacDonald 1995). *Heterotrissocladius* occurs in more highly oxygenated waters than *Sergentia* (Walker *et al.* 1993). *Sergentia* is more common in mesotrophic lakes or lakes with moderate O_2 depletion (Walker 1990, Walker *et al.* 1993). *Heterotrissocladius* is a very common taxon in late-glacial sediments and has been seen in many studies of late-glacial sediments on both the western and eastern coasts of Canada (Walker *et al.* 1991b).

Low head capsule concentrations also characterize this part of the core (See Fig. 8). Smith (1997), saw a similar cold-stenothermous, late-glacial community in Cabin Lake, indicating similar cold climatic conditions.

Near the top of this zone the appearance of warm-water taxa, particularly Chironomus and Dicrotendipes, is very obvious, while an abrupt decline is seen in the relative abundances of cold-stenotherms. These changes suggest a shift in temperature from cold to warmer conditions. Taxa such as Chironomus and Dicrotendipes are most commonly littoral inhabitants of warm, low-elevation forested lakes (Walker et al. 1991a). However, Chironomus as well as other taxa, such as Psectrocladius and Procladius, are quite common in shallow arctic (or high elevation) ponds where temperatures are relatively warm (Walker 1990). As seen, Procladius is common in this late-glacial zone and throughout the Holocene, but never encompassing >26% of the fauna. Heterotrissocladius does not occur in shallow ponds or lakes because temperatures are too warm in summer and the ponds are possibly too O₂ deficient in the winter (Walker and MacDonald 1995). Furthermore, as shallow lakes do not stratify, cold-stenotherms are not able to migrate to a cool, protected profundal zone. As is evident, *Heterotrissocladius* peaks in this zone and then is absent throughout the rest of this core, suggesting shallow and warm conditions throughout the Holocene. This change in chironomid composition, where Heterotrissocladius and associated taxa decrease in abundance just after deglaciation, is seen in most chironomid studies of north temperate lakes (Walker 1995).

Subtribe Tanytarsina and *Psectrocladius* constitute the majority of the fauna in this zone. Tanytarsina comprise up to 47%, and *Psectrocladius* up to 48% of the fauna respectively. The huge peaks of *Psectrocladius* in this zone are intriguing. *Psectrocladius* is eurythermic. However, it is also found in acidic waters (Walker 1987, Walker and Mathewes 1989b). These sudden peaks in relative abundance may indicate weakly acidic conditions. The possibility of acidic conditions at this time may be corroborated by the appearance of *Zalutschia*, which is seen here and no where else in the core. *Zalutschia* is an indicator of water rich in humic matter and Fe (Sæther 1979, Walker *et al.* 1991a). Fe is usually bound to the humic matter in such situations (I. Walker, *pers. commun.*). *Zalutschia* lakes are also commonly somewhat acidic (Walker 1987). A study by Walker

and Paterson (1983) shows peaks in *Zalutschia* as acidity increased at Wood's Pond in New Brunswick. A similar peak in *Psectrocladius* was not seen in the late-glacial assemblage of Cabin Lake (Smith 1997).

Diatom species composition is strongly influenced by water pH. Thus, in the future, diatom analyses could be used to test my deduction. Furthermore certain chrysophytes are also very sensitive to pH, and leave identifiable remains in lake sediments.

Zone NCC-2 (268-232.5 cm):

This early Holocene assemblage shows a dramatic increase in the abundance and diversification of warm water taxa while cold-stenotherms disappear. Particularly abundant are members of the tribe Chironomini, such as *Chironomus, Dicrotendipes, Cladopelma, Microtendipes* and *Polypedilum*. Several of these chironomids have their highest abundances in this zone, such as *Dicrotendipes*, where it comprises up to 22% of the fauna. Similarly, *Cladopelma* and *Microtendipes* peak here, constituting 8% and 14% of the total chironomid fauna respectively. *Chaoborus* is a good indicator of warm temperatures (Walker *et al.* 1997), and is prominent in this zone.

The appearance and dominance of these warm-adapted taxa suggests a shift to much warmer climatic conditions. Temperate taxa are able to complete their life-cycles as environmental temperatures increase, and they are able to do this fast. These chironomids undergo rapid development in summer and are known to have ≥ 1 generation per season, (Walker 1987). They are therefore capable of producing a greater number of head capsule remains per season. This could at least partially explain why the density of head capsules in this zone, is high. The number of macroinvertebrate taxa in lakes is positively correlated with maximum summer temperature (Hoffman *et al.* 1996).

A significant change is observed in many of these taxa prior to deposition of the Mazama ash. Here, many taxa decline in abundance. There may be several possible reasons for this decline. The most plausible would appear to be a period of cooling

beginning prior to the eruption of Mt. Mazama. A pollen-climate transfer function has suggested that a period of cooler temperatures and increased precipitation began just before this eruption (Mathewes and Heusser 1981).

Pollen analysis being conducted in parallel with my study will provide an independent test for the existence of the inferred cooling. The inferred temperatures based on chironomid composition are consistent with the early Holocene xerothermic interval proposed by Mathewes (1985) as lasting from approximately 9500 to 7000 B.P. Smith (1997) also reports comparable changes in chironomids, including a decline in coldstenotherms and an increase in both diversity and abundance of temperate taxa. It would thus appear that this area of B. C. was, at that time, under the strong influence of increasing temperatures.

Tanytarsina, which are mostly littoral species of temperate lakes, but which are often found in cold, profundal high oxygen environments, continue to be prevalent in this zone as does *Procladius*. The sharp decline in *Psectrocladius* in this zone is obvious. Here it constitutes only about 19% of fauna at its peak, possibly owing to changes in alkalinity. This could be tested through diatom or chrysophyte analyses. The appearance and subsequent decline of *Monopsectrocladius* may also be related to such a change in water alkalinity. *Monopsectrocladius* was found by Walker *et al.* (1985) to be a common taxon in highly-acidic bog pools. The fact that it decreases in abundance close to the top of this zone suggests a possible return to more neutral conditions.

Zone NCC-3 (232.5-168 cm):

A continued decline in warm-water taxa, including *Chironomus, Dicrotendipes, Cladopelma* and Pentaneurini characterises this mid-Holocene assemblage. Several become rare to extinct in the upper parts of this zone. However, the continued presence of littoral warm-water taxa, particularly *Polypedilum* (constituting up to 19% of the community) and *Pagastiella*, both increasing in local abundance, would indicate that although temperatures may have dropped somewhat, they remain fairly warm. This is

corroborated by *Chaoborus* which remains very abundant. Tanytarsina (82%) and *Procladius* (25%) attain some of their highest abundances. *Procladius* is found in lakes at all elevations as well as in both littoral and profundal zones of lakes (Walker and Mathewes 1989a).

The time interval encompassed by this zone falls in the mesothermic period, previously defined on the basis of pollen analysis (Hebda 1982, 1995). This period represents a decrease in temperature as well as a gradual shift to increased moisture (Hebda 1982). The time of the mesothermic interval is from 7000-4500 B.P. in the interior of B.C. (Hebda 1982, 1995). Grasslands in the interior had their minimum range from 4500-3000 B.P. meaning that climate was both cool and moist (Hebda 1982).

The highest head capsule concentrations are found in both this zone and the latter (NCC-2)(Fig. 6). These concentrations support the thesis that climatic conditions were fairly warm, as greater abundances and diversity usually occur in low elevation lakes where maximum summer temperatures are the highest (Hoffman *et al.* 1996, Walker and Mathewes 1989a).

A similar inferred climate was seen at this time in Cabin Lake (Smith 1997). The zone for Cabin Lake encompasses roughly the same time period as in this study, with similar declines in local abundance of several warm-adapted taxa. Unlike North Crater Lake however, the mid-Holocene period for Cabin Lake encompasses a reappearance of cold-stenothermous taxa. The more northerly geographic location of Cabin Lake may have resulted in a stronger cooling signal.

Zone NCC-4 (168-0 cm):

The chironomid community in this late-Holocene zone shows further changes in composition. The relative abundances of many warm-water or temperate taxa continue to decrease. Several taxa such as *Cladopelma* and *Microtendipes* disappear altogether. Most noticeable is the dramatic decline in *Chaoborus*. *Chaoborus* is considered a low to midelevation taxon. It is extremely rare in the arctic, and is characteristic of warm, shallow

lakes south of treeline (Walker 1987, Walker and MacDonald 1995). These continued reductions in abundances suggest continued cooling in the late-Holocene up to the present-day.

The chironomid assemblage in the late-Holocene zone of Cabin Lake follows similar changes in composition. This reaffirms the suggested late-Holocene cooling throughout the region.

4.4 Lake-of-the-Woods Stratigraphy

The chironomid diagram for Lake-of-the-Woods is also arranged into four distinct chironomid assemblage zones, based upon the results of stratigraphically constrained incremental sum-of-squares cluster analysis (Fig. 11). As in North Crater Lake, there are distinct fluctuations in the abundances of the over 40 chironomid taxa identified. The fact that there are many more distinct taxa in this core could prove significant. Zone LWC-1 appears to encompass the late-glacial period, and is found from 381-357.5 cm. The early Holocene is encompassed by Zone LWC-2, from 357.5-298 cm. Zone LWC-3 is a large zone, 298-117.5 cm, and represents the mid-Holocene. Zone LWC-4, from 117.5-0 cm, encompasses the late-Holocene to present-day sediments.

Zone LWC-1 (381-357.5 cm):

The radiocarbon date for the base of this core, indicates that it penetrates into lateglacial sediments. However, the chironomid fauna is not a typical late-glacial assemblage, since it lacks a distinct cold-stenothermous community. A brief, but strong, peak in *Sergentia* occurs near the top of this zone. Two other cold-stenotherms are briefly present (*Heterotrissocladius, Stictochironomus*), but only at minimal levels. The highest head capsule counts were also recorded for this basal zone (See Fig. 9). Usually low head capsule concentrations are found in late-glacial sediments, and these are considered a reflection of the cold, unproductive, late-glacial conditions.

Several warm-water taxa, particularly *Dicrotendipes, Chironomus*, tribe Pentaneurini, and *Pseudochironomus* are already common. *Dicrotendipes*, is a littoral

inhabitant of warm, low-latitude temperate lakes (Walker *et al.* 1991a, Wiederholm 1983). *Pseudochironomus*, making up >10% of fauna, is found in areas south of treeline (Walker 1990, Walker and MacDonald 1995). A good indicator of warm water conditions, this chironomid is usually found in sandy or gravelly substrata in the littoral zone of mesotrophic to oligotrophic lakes (Walker *et al.* 1997, Wiederholm 1983). The presence of these taxa suggests warm conditions already at this time. As with North Crater Lake, this lake is relatively shallow (3.6 m deep). Its waters would warm quickly following the shift to warmer temperatures. North Crater Lake however, may possibly have had local ice persisting longer around it than Lake-of-the-Woods at this time. Cold meltwater may thus have influenced North Crater Lake, unlike Lake-of-the-Woods.

A brief decline in warm-water taxa and increase in *Sergentia* was noted at the top of this zone. *Sergentia*, a cold-stenotherm, is indicative of cold environmental conditions (Walker *et al.* 1997). This taxon contains hemoglobin, and as such is characteristically found in lakes with moderate oxygen depletion (Levesque *et al.* 1996, Walker 1990). It is therefore found not only in arctic or high elevation lakes, but also in the profundal zone of mesotrophic lakes (Walker *et al.* 1993). The disappearance of *Sergentia* and ultimate reappearance in small numbers of warm-adapted taxa, at the top of this zone, suggests a shift in temperatures in LWC-1 from warm to cold and quickly back to warm conditions.

Smith (1997) appears to have picked up a similar signal in his core from Cabin Lake. Close-interval chironomid sampling around these changes is needed to better resolve this event. As well, additional dates from this interval would better establish the time period, and whether it might possibly correlate with the event recorded by Smith (1997).

As in North Crater Lake, there is a huge *Psectrocladius* peak (52%) in this zone. It and the eurythermic *Procladius* (27%) are the most abundant taxa. The presence of *Psectrocladius* could possibly indicate weakly-acidic conditions. The succession and maturation of vegetation to a forest-like state can cause a slight increased acidity. For example, Rhodes and Davis (1995) have determined three means by which a lake can

become naturally acidified. First, soils become acidified owing to the build-up of forest litter and degradation of humus. Secondly, vegetation biomass retains base cations; thus, these ions cannot easily move to the lake. Thirdly, as forest vegetation succeeds from hardwood to conifers, soils become acidified.

This site (Fig. 4), lies in forest just below treeline. Ministry of Environment reports show that all of the Cathedral Lakes, including Lake-of-the-Woods, are weakly acidic, but are not sufficiently acidic to endanger the fish populations. Lake-of-the-Woods has viable populations of cutthroat trout (Matthews 1986). Changes of pH between 6.5 and 7.5 occur in many lakes and streams. These changes usually do not impact on plants or animals (Horne and Goldman 1994).

Conversely, any disturbance (e.g., fire, avalanche) of the forest vegetation could result in a rapid pH increase. Vegetation plays an important role in reducing erosion due to stabilization of soils and uptake of nutrients from the surrounding soils (Horne and Goldman 1994). Disturbance of forest allows base cations to be released via ash and eroded soil. Also, pH increases due to the destruction of forest litter following disturbance (Rhodes and Davis 1995). Such disturbances may have occurred around the observed decline of *Psectrocladius* in LWC-1. Forthcoming pollen analyses and charcoal analyses may allow us to discern an increase in early successional pollen types, and charcoal. A peak in charcoal would indicate fire.

Zone LWC-2 (357.5-298 cm):

The chironomid community present in this second zone is typical of the early-Holocene situation in B. C. treeline lakes (see for example Smith 1997). There is a prominent increase in the diversity of warm-water taxa, with increases particularly in *Cladopelma, Microtendipes, Pagastiella* and *Polypedilum*. Several, such as *Pagastiella* (19%) and *Polypedilum* (25%) attain there greatest abundances within this zone. *Chaoborus,* another warm water indicator, abruptly appears and maintains a constant presence until the most recent part of the core. Few cold-stenothermous taxa are present;

thus, warm conditions are indicated. As with North Crater Lake, this lake is shallow and located near treeline. It is therefore sensitive and responsive to climatic changes. Many chironomids reach their upper elevational limits near treeline (Walker and Mathewes 1989b). The beginning of this zone falls at the very beginning of the xerothermic interval as defined by Hebda (1995), Mathewes (1985), and Mathewes and King (1989).

Within this zone there is also an increase in rheophilous taxa and others closely associated with stream environments, particularly *Eukiefferiella/Tvetenia* and *Diamesa*. *Diamesa* occurs in mountain streams which are fed by melting ice, thus having very low temperatures (Pinder 1995). The latter are joined further downstream by *Eukiefferiella/Tvetenia* species which are eurythermic and inhabit all types of moving water (Wiederholm 1983). *Psectrocladius* decreases dramatically in abundance in this zone, never constituting >20% of the fauna throughout the rest of the core.

Of special interest is the appearance of *Orthocladius (Symposiocladius) lignicola* Kieffer. This orthoclad mines in submerged hardwood, actually ingesting wood fibers. It is widely distributed in lakes south of treeline, both in North America and Europe (Pinder 1986, Walker 1988, Wiederholm 1983). Its presence provides further evidence for the presence of trees in the vicinity of Lake-of-the-Woods by this time. Climatic conditions were clearly warm enough, and growing seasons long enough, to support trees. This corroborates the warmer temperatures inferred from other constituents of the chironomid community.

Because of oxygen depletion, *Orthocladius (Symposiocladius) lignicola* does not mine deep into wood. It is found just slightly below the wood surface (Berg 1995). O. (*Symposiocladius) lignicola* is more common on alder than conifer wood (Berg 1995). Pollen and macrofossil analyses will allow us to detect alder presence around this time. Alder is common in early successional vegetation and as a component of subalpine riparian vegetation. The appearance of this wood-mining species indicates the presence of fallen logs, and is thus an indication of some type of disturbance, possibly owing to an insect

infestation, pathogen, or fire. Without further evidence we can only speculate as to the nature of this disturbance.

Zone LWC-3 (298-117.5 cm):

This zone encompasses a portion of the xerothermic, as well as the mesothermic period as defined by Hebda (1995) and Mathewes (1985).

Early in this zone warm-water taxa increase. Several reach their greatest abundances in this zone, particularly *Stempellinella/Zavrelia*, *Glyptotendipes* and *Microtendipes*, which constitute much of the fauna (21%). *Stempellinella* is a warm-water taxon commonly occurring on sandy substrates in clear water lakes (Walker 1987). *Glyptotendipes* is common in shallow lakes, with high substrate heterogeneity, or high macrophyte presence (Gilinsky 1984, Walker and MacDonald 1995). From the great abundance and high diversity of Chironomidae, it would appear that warm conditions prevailed early in this zone.

As in North Crater Lake and at Cabin Lake many of these warm-water taxa decrease in abundance prior to deposition of the Mazama tephra. A sharp decline is observed in *Microtendipes*, *Cladopelma* and *Glyptotendipes*. *Microtendipes* later reappears in great numbers, unlike other taxa (e.g., *Glyptotendipes*) which disappear at the top of the zone or which show minimal abundances (e.g., *Cladopelma*) throughout the rest of the core.

This decrease in diversity and abundance is suggestive of cool conditions beginning prior to the eruption, as also inferred from North Crater Lake and other studies (Mathewes and Heusser 1981, Smith 1997). A relatively great abundance and diversity of rheophilous taxa remain, and may indicate higher precipitation.

Lake-of-the-Woods is fed by a stream. An increase in stream volume could ultimately lead to an increase in the rheophilous (stream inhabiting) taxa being brought into Lake-of-the-Woods. Increased run off, via both overland and groundwater flow, would enhance the erosional process, carrying mineral sediments into the lake. This would result in periodic episodes of increased sediment deposition. The presence of *Stempellinella* in

such high abundance throughout this zone suggests this. *Stempellinella*, occurs commonly in more minerogenic sediments, constructing sand cases in which to reside (Walker 1987).

The dramatic and abrupt appearance within this zone of two *Corynocera* species (*Corynocera* A and B) in large numbers is quite intriguing. Although there were brief peaks of both in LWC-2, their presence is dramatic in LWC-3. The specific identity of these *Corynocera* is uncertain. They are intermediate in appearance between the two *Corynocera* taxa (*Corynocera* nr. *ambigua* Zett. and *Corynocera* oliveri Lind.) found in coastal B. C. Pictures of *Corynocera* A and B can be seen in Figure 14.

Corynocera ambigua is a species that has never been recorded in British Columbia, although it has a Holarctic distribution. A similar species having a darker and more variable mentum was noted by Walker (1988) in B. C. Thus it has been referred to as *C*. nr. *ambigua*. *Corynocera* nr. *ambigua* is known to be typical of cold, oligotrophic lakes and ponds on the coast (Walker and Mathewes 1988). The second *Corynocera* to be found in B. C. is *Corynocera oliveri*. It appears to be the dominant chironomid in most coastal subalpine lakes (Walker 1988). Recent analysis of B. C. surface samples shows that other species may also be present (I. R. Walker, *pers. commun.*).

Interestingly, abundance of *Corynocera* increased during the mesothermic, perhaps responding to cooler temperatures. However, although *Corynocera* seem more common at high elevations and latitudes, they are sometimes abundant in temperate lakes (Brodersen 1998) in Denmark. Although *Corynocera* are often abundant is association with Characeae algae, there seems to be no obligate relationship. Thus, more studies of this enigmatic genus are needed (Brodersen, *pers. commun.*). The fact that two new, as yet unclassified, types of *Corynocera* may exist in British Columbia, and the fact that this marks the first time that a distinction has been made between *Corynocera* inland (previously only done on coastal studies), could prove very significant.

Figure 14: Pictures of subfossil remains of unidentified *Corynocera* species from Lake-of-the-Woods, B. C.: a) *Corynocera* A (400×), b) *Corynocera* B (400×).

Zone LWC-4 (117.5-0 cm):

As in North Crater Lake a dramatic decline in warm-water midges is evident in this late-Holocene assemblage. Many disappear completely (i.e., *Cladopelma, Microtendipes, Pseudochironomus, Stempellinella/Zavrelia* and *Chaoborus*) indicating continued cooling in the late Holocene. These cooler conditions are substantiated by the concurrent appearance of the cold-stenotherms *Sergentia* and *Heterotrissocladius*, in greater numbers than during the late-glacial. As in North Crater Lake, the climatic cooling would have resulted in both extended ice cover over the lake as well as colder summer water temperatures.

The timing of the shift to cold-stenothermous taxa coincides with neoglaciation and glacial readvances observed in the northern Coast Mountains, Canadian Rockies and throughout other areas of the Canadian Cordillera (Clague and Mathewes 1996, Luckman 1993, Ryder 1989). It would appear that the coldest part of this cooling regime occurred in the middle of this zone, as indicated by peaks in both *Heterotrissocladius* and *Sergentia*. Further radiocarbon dating around these peaks would better define the timing of these events, perhaps allowing correlations with specific glacial advances or maxima during the neoglacial. Similar reappearances of cold stenotherms and subsequent decreases in warmadapted chironomids occur in Cabin Lake (Smith 1997). Thus, this cooling is not a localized event.

Corynocera (type A 38% and type B 30%) remain abundant in this zone to the surface. Stream taxa continue to be locally abundant.

4.5 Possible significance of predator-prey interactions

The impact of predator-prey interactions on the chironomid communities in both lakes, is very hard to determine. Not only do scant records exist as to possible predators, but there are also so many other variables that can act upon and mask interactions among predators and prey, such as their ecosystem, habitat, etc. Climate change, as seen, is one of them, itself having secondary effects throughout aquatic ecosystems.

There are apparently no fish present at North Crater Lake (I. R. Walker. *pers. commun.*). This is related to the location of this lake and the fact that it has no inlet, or outlet and consequently no spawning area. Sherk and Rau (1996) noted that the chironomid *Procladius* tends to dominate in lakes where no fish are present. This could explain why this taxon is somewhat more abundant in North Crater Lake than in Lake-of-the-Woods. However, their study has been contradicted by others showing that *Procladius* spp. and other predatory chironomids are most abundant when fish are present (Gilinsky 1984). Clearly, other factors such as other predators, habitat, etc. have to be taken into consideration. Other types of vertebrate predators, for example salamanders or frogs, could be present. Salamanders are sometimes the main predators in lakes with no fish, as noted by Hoffman *et al.* (1996) in lakes of the Cascade Mountains in Washington and Oregon. However, no vertebrate records exist for North Crater Lake.

Water from the immediate area of both lakes drains into the Ashnola River which is a tributary of the Similkameen River. The Similkameen itself is a small river tributary of the Okanagan River and ultimately the Columbia River system (McPhail and Carveth 1992). These rivers are quite warm during summer months and are clearer and less turbulent than the larger Columbia, but have similar fish present as in the lower Columbia and its tributaries. For instance, the Columbia has 43 species of fish present, 27 of which are native and believed to be survivors of the last glaciation (McPhail and Carveth 1992). However, unlike the Columbia, the smaller rivers draining the interior plateau have several barriers (i.e., falls and rapids) that impede fish movement. The Similkameen has a barrier at Similkameen Falls, above which only rainbow trout and longnose dace occur (McPhail and Carveth 1992). Such physical barriers and the very high gradient of the headwater streams have prevented fish populations from naturally reaching the alpine/subalpine lakes. The Cathedral Lakes were initially stocked in the 1930's with cutthroat trout (Bull 1979). Four of the lakes in Cathedral Provincial Park, including Lake-of-the-Woods, now support

healthy fisheries with natural fish reproduction. Restocking of the lakes is not required (Bull 1979, Matthews 1986).

Lake-of-the-Woods is considered to have the best spawning habitat of all the lakes in the park because it has an outlet (Matthews 1986). It is believed that trout from Lake-ofthe-Woods may move to Pyramid Lake via the stream connecting the two lakes. Thus, the lake acts as a feeder to Pyramid Lake (Matthews 1986). Fish growth in such alpine lakes is known to be limited because of low mineral content in the water, low yearly heat budget and low food supplies, owing to a shorter growing season at these elevations (Matthews 1986).

Fish presence has been known to affect both species abundance and composition of benthic macroinvertebrates (Gilinsky 1984, Hoffman et al. 1996). Hoffman et al. (1996) assessed the impact of vertebrate predators, including fish, on nearshore macroinvertebrates. Their study had four different predation categories from lakes with vertebrate predators to lakes with none. Those lakes with fish, had either cutthroat trout (as in Lake-of-the-Woods) or rainbow trout. Even though chironomids were not examined, the study showed conclusively that vertebrate predators had an impact on the distributions of macroinvertebrate taxa (Hoffman et al. 1996). Furthermore, cutthroat trout introduced into a lake in Washington state, drastically reduced macroinvertebrate densities in both profundal and pelagic zones (Hoffman et al. 1996). Extrapolating these findings to Lakeof-the-Woods, we can assume that fish could probably have an impact on chironomid communities in terms of predator-prey relationships. The fish may be having an impact as seen by chi-square analysis performed on chironomid composition between surficial samples (post-stocking) and those samples prior to stocking. This can be seen in Table 4 showing the percent abundance of fauna in the first three samples from this lake (pre- and post-stocking). The chi-square test on the raw count data (i.e., before being transformed to percentages) between the 2.5 and 12.5 cm intervals indicates a significant difference

| Taxa: | 2.5 cm | 12.5 cm | $\frac{22.5 \text{ cm}}{22.5 \text{ cm}}$ |
|---------------------------------|--------|---------|---|
| Corynoneura/Thienemanniella | 3.3 | 4.0 | 6.8 |
| Heterotrissocladius | 6.6 | 1.0 | 3.8 |
| Tanytarsina | 35.0 | 24.7 | 27.5 |
| Nanocladius cf. distinctus | 0.4 | 1.6 | 0.8 |
| Corynocera type A | 7.4 | 21.7 | 10.6 |
| Corynocera type B | 15.6 | 9.9 | 22.6 |
| Dicrotendipes | 3.7 | 3.0 | 3.0 |
| Zalutschia | 0.8 | 1.3 | |
| Sergentia | 3.3 | 2.0 | 6.0 |
| Procladius | 3.3 | 5.9 | 0.8 |
| Cricotopus/Orthocladius | 2.1 | 2.3 | 2.3 |
| Psectrocladius | 2.1 | 4.3 | 1.5 |
| Rheocricotopus | 2.1 | 1.0 | 3.0 |
| Pagastiella cf. ostansa | 0.8 | 2.0 | 0.8 |
| Chironomus | 2.9 | | 1.5 |
| Parakiefferiella cf. bathophila | 0.8 | | 0.4 |
| Psectrocladius (Allo or Meso) | 1.6 | | 0.8 |
| Doithrix/Pseudorthocladius | 0.8 | | |
| Polypedilum, | 1.6 | | |
| Stempellinella | | 1.0 | 0.8 |
| Eukiefferiella/Tvetenia | | 3.0 | 1.1 |
| Monopsectrocladius | | 0.7 | 0.8 |
| Cladopelma | | 0.7 | |
| Brillia/Euryhapsis | | 0.7 | |
| Pentaneurini | | 0.7 | 0.8 |
| Glyptotendipes | | | 0.4 |
| Microtendipes | | | 0.4 |
| Protanypus | ` | | 0.4 |

Table 4: Percent abundance of each taxon present in the top three samples of Lake-of-the-Woods: 2.5 cm (post-stocking), 12.5 cm (pre-stocking) and 22.5 cm (pre-stocking).
between these two levels (p<0.025), whereas the probability is p<0.10 but > 0.05 between the 12.5 and 22.5 cm intervals. Thus, there doesn't appear to be a large difference between pre- and post-stocking, but it is significant, whereas the difference between the lower two samples is not significant. In an analysis of gut contents from forty-six cutthroat trout from Quiniscoe Lake, another of the Cathedral Lakes, Matthews (1986) found that 40% of stomach contents were chironomids; however, no studies have been conducted to determine what chironomid taxa were eaten.

An initial inventory of birds, mammals and amphibians began in Cathedral Provincial Park in 1979, based on casual observations, but is surely incomplete (S. Matthews, pers. commun.). Amphibians were observed (Bufo boreas Baird and Girard or Western Toad) near the outlet of Lake-of-the-Woods, or heard (Rana pretiosa Baird and Girard or Spotted Frog) in reeds bordering the lake. No salamander records are available, however, some bird sightings were recorded (Bull 1979). Thus, other vertebrate predators do occur. These could possibly impact on chironomid communities, but to determine this would involve a completely new study, including a comprehensive inventory of every possible predator (invertebrate and vertebrate) and every possible interaction. Overall however, predator-prey relationships and the impact on prey communities may be difficult to elucidate. Some studies have shown species diversity to increase when predation occurs, as competitive relationships between prey species are suppressed (Gilinsky 1984). Conversely, in other studies species richness and density increase when predators are absent (Gilinsky 1984). In addition, records of types of predators present, do not go back 10 000 years, or even 100 years. Predators will have changed through time. Moreover, while predation may structure benthic communities, the impact depends not only on the species involved, but also on other factors that could interact or have secondary effects such as: the season, the complexity of habitat, and environmental disturbances to name a ¢ few.

Chapter V

Quantitative Paleotemperature Reconstructions

Chironomids are good indicators for paleoclimatological reconstructions, with changes in their faunal composition allowing inferences to be made concerning post-glacial temperature and climatic changes.

With advances in statistical methods, much research has recently been devoted to quantitatively inferring paleotemperatures from fossil midge assemblages. For instance, an improved chironomid-paleotemperature inference model has recently been developed for Eastern Canada (Walker *et al.* 1997). Furthermore, similar models have been constructed for use in various parts of Europe (Lotter *et al.* 1997, Lotter *et al.* in press). In conjunction with my research, I have developed a similar inference model for southern British Columbia, the results of which are presented below.

5.1 Results

As indicated in the methods section, a series of trials was used to find the best model for inferring temperatures from chironomid larval remains. The methods used encompassed Weighted Averaging (with and without tolerance downweighting; with classical vs. inverse deshrinking), Weighted Averaging Partial Least Squares, and Partial Least Squares Regression. These various regression methods were applied to square-root transformed as well as untransformed species data. r_{jack}^2 and RMSEP_{jack} (jack-knifed rootmean-squared-error of prediction) were obtained via the resampling technique (leave-oneout jack-knifing) employed in the computer program CALIBRATE (Juggins and ter Braak 1997). The jack-knifed error statistics (r_{jack}^2 and RMSEP_{jack}) obtained for the various model trials are shown in Tables 5 and 6.

I have presented only the jack-knifed error statistics in Tables 5 and 6 because these provide a more accurate and realistic assessment of the errors associated with each model (Lotter *et al.* 1997, Walker *et al.* 1997). The r_{jack}^2 varied from 0.17 to 0.70, whereas the

RMSEP_{*jack*} varied from 5.20 to 1.98, among these trials. From the two tables, it is evident, on the basis of the highest r^2_{jack} and the lowest RMSEP_{*jack*}, that the best model is the 2 component WA-PLS model for square-root transformed percentage species data. Walker *et al.* (1997) report that this method out-performed the others in eastern Canada as well. Figure 15 illustrates the relationship between the WA-PLS predicted temperatures and the observed temperatures. The modeled, or predicted temperatures fit the observed data well with the model explaining 70% of the variance in the observed temperatures, with no obvious outliers. Thus, I have used this model to reconstruct past temperatures for my sites (Fig. 16 a, b). The error bars in the graphs represent sample-specific errors as obtained by WA-PLS. These errors are obtained in two steps: 1) jack-knifing is used to obtain standard errors of the WA-PLS species coefficients and 2) these standard errors are then used to estimate sample specific standard errors of prediction. Also to permit a comparison with other lakes in the area, this new temperature inference model has been applied to Smith's (1997) square-root transformed percentage species data from Cabin Lake and 3M Pond (Fig. 16 c, d) (Smith *et al.*, unpublished).

The chironomid-inferred paleotemperature reconstruction for North Crater Lake (Fig. 16a) indicates distinct fluctuations in temperature. Mean July temperatures are inferred to have been cold in the late-glacial. The lowest temperature inferred for this period is 8.4 °C. Temperatures are inferred to have increased after this, over the 270.5 to 259.5 cm interval, after about 9500 yr. B.P. The highest inferred temperature of 14.4 °C is predicted for the 261.5 and 259.5 cm levels. Temperatures are then inferred to have dropped slightly just below the Mazama ash. The highest inferred temperatures are inferred for the xerothermic interval as defined by Mathewes and Heusser (1981). The inferred temperatures suggest a cooling trend after the Mazama eruption. This is most obvious, over the 220.5 to 202.5 cm interval, prior to 5400 yr. B. P., where temperatures

| | r^2_{jack} | RMSEP _{iack} |
|--------------------------|--------------|-----------------------|
| Weighted averaging: | | |
| Inverse deshrinking WA | 0.5788 | 2.3304 |
| WA _{tol} | 0.6457 | 2.1692 |
| Classical deshrinking WA | 0.5896 | 2.5202 |
| WA _{tol} | 0.6558 | 2.2055 |
| WA-PLS: | | |
| 1 Component | 0.5788 | 2.3304 |
| 2 Components | 0.6076 | 2.2578 |
| 3 Components | 0.5618 | 2.4472 |
| 4 Components | 0.4895 | 2.8149 |
| 5 Components | 0.4069 | 3.2794 |
| 6 Components | 0.3646 | 3.5957 |
| PLS: | | |
| 1 Component | 0.5071 | 2.7923 |
| 2 Components | 0.4571 | 3.2046 |
| 3 Components | 0.3334 | 3.8452 |
| 4 Components | 0.2541 | 4.3790 |
| 5 Components | 0.1877 | 4.9255 |
| 6 Components | 0.1704 | 5.2035 |

Table 5: Comparison of output from modelling trials with untransformed species data: using weighted averaging (WA) (with inverse and classical deshrinking, and with and without tolerance down-weighting), weighted averaging partial least squares (WA-PLS), and partial least squares (PLS) techniques.

| | r^2_{jack} | RMSEP _{iack} |
|--------------------------|--------------|-----------------------|
| Weighted averaging: | | |
| Inverse deshrinking WA | 0.6853 | 2.0133 |
| WA _{tol} | 0.6774 | 2.0957 |
| Classical deshrinking WA | 0.6952 | 2.0935 |
| WA _{tol} | 0.6916 | 2.0693 |
| WA-PLS: | | |
| 1 Component | 0.6848 | 2.0207 |
| 2 Components | 0.6959 | 1.9779 |
| 3 Components | 0.6415 | 2.1648 |
| 4 Components | 0.6217 | 2.2380 |
| 5 Components | 0.6157 | 2.2711 |
| 6 Components | 0.6151 | 2.2899 |
| PLS: | | |
| 1 Component | 0.6430 | 2.1450 |
| 2 Components | 0.6033 | 2.3046 |
| 3 Components | 0.5528 | 2.4976 |
| 4 Components | 0.5338 | 2.5786 |
| 5 Components | 0.5429 | 2.5406 |
| 6 Components | 0.5500 | 2.5471 |

Table 6: Comparison of output from modelling trials: same as Table 5 but using squareroot transformed species data.



Predicted vs Observed Mean July B.C. Temperatures



cool to 10.1 °C. A brief warming is inferred around 186 cm, after which temperatures cooled substantially, to a low of 9.6 °C at 82.5 cm, after about 1900 yr. B. P. The inferences suggest that temperatures remained cool up until the present-day, where the inferred temperature is 10.7 °C.

The inferred temperatures for Lake-of-the-Woods (Fig. 16b) are higher overall, but follow a similar pattern to the changes seen in North Crater Lake. Cool temperatures occur prior to 10 000 yr. B.P., from approximately 380.5 to 365.5 cm, at the base of the core. The coldest inferred temperature of 8.7 °C occurs at 370.5 cm. Temperatures rose gradually after this, reaching a maximum inferred temperature of 16.4 °C at 275.5 cm, before the 8580 yr. B.P. radiocarbon date. The inferred temperatures for the entire 350.5 to 220.5 cm interval suggest stable and warm conditions. These warm inferred temperatures occur during the xerothermic. A dramatic temperature drop is inferred between 220.5 and 210.5 cm, slightly below the Mazama ash. Temperatures increased following this interval, returning to temperatures almost as warm as those before Mazama. However, after 5400 B. P. the inferred temperatures reveal a cooling trend to the present day. The lowest inferred temperature (10.9 °C) occurred at the 81 cm level. This inferred cooling trend is consistent with the time of neoglaciation in B. C.

Interestingly, the paleotemperature reconstructions for Cabin Lake and 3M Pond (Smith *et al.*, unpublished), using the same WA-PLS temperature inference model show similar temperature trends to those obtained for North Crater Lake and Lake-of-the-Woods. Cabin Lake (Fig. 16c) in particular shows a parallel profile. Mean July inferred temperatures were particularly cold in the basal part of the Cabin Lake core. A minimum late-glacial temperature of 5.4 °C was inferred. Between 333.5 and 323.5 cm the inferred temperatures rose from 6.4 to 14.3 °C, before about 8900 yr. B.P. Temperatures remained warm for a period, but then cooled slightly prior to deposition of the Mazama



Figure 16: Comparison of chironomid-inferred paleotemperatures for a) North Crater Lake, and b) Lake-of-the-Woods calculated using the new WA-PLS model, along with the paleotemperature inferences for c) Cabin Lake and d) 3M Pond (Walker, Smith and Palmer, unpublished). The error bars represent estimated standard errors of prediction.



b) Inferred paleotemperatures for Lake-of-the-Woods, B. C.



c) Inferred paleotemperatures for Cabin Lake, B. C.



d) Inferred paleotemperatures for 3M Pond, B. C.

ash. The warm inferred temperatures for this zone provide additional evidence for an early Holocene xerothermic. Temperatures are cooler than the xerothermic, but relatively stable until around 120.5 cm, before about 2400 yr. B. P. Thereafter, a cooling trend occurs, extending to the present-day. The inferred temperature at the top of this core is 9.3 °C.

For 3M Pond (Fig. 16d), the reconstruction shows temperatures rising from the base of the core to 13.9 °C at 44.5 cm. As the base of the core dates to 10 000 years B.P., the warming seen pertains to the onset of the warm, dry xerothermic interval. Except for a maximum inferred mean July temperature of 14.1 °C at the 36.5 cm interval, temperatures show a cooling trend after this. A dramatic drop in temperatures is inferred between 28.5 and 26.5 cm, prior to about 3500 yr. B. P. From 3500 years B. P. to present, temperatures remain cool. A minimum inferred temperature of 6.0 °C occurs at the 12.5 cm level. As in North Crater Lake and Lake-of-the-Woods, the late-Holocene cooling trend inferred for both Cabin Lake and 3M Pond is consistent with the concept of neoglaciation (See Clague and Mathewes 1996, Luckman 1993, Ryder 1989). With the error bars taken into account, each pair of individual points (reconstructed temperatures) on any of the four graphs presented are not significantly different. However, the overall trend in the four lakes is very similar. The trends suggest rather strongly that a regional pattern in temperature change occurred, with rapid warming around 10 000 years ago and then cooling in the mid- to late-Holocene.

5.2 Discussion

Comparison of temperatures quantitatively reconstructed from the new paleotemperature inference model to those changes inferred qualitatively by mere inspection of chironomid presence or absence in the stratigraphic diagrams (Chapter V, and Smith 1997), shows that these inferences are generally in agreement.

What is interesting in both temperature inference diagrams (Fig. 16 a,b) is how the high resolution sampling that was conducted immediately above and below Mazama ash

determined virtually nothing in terms of a cooling effect based on temperatures inferred from the chironomid assemblages. The idea existed that after the eruption, cooler climatic conditions may have resulted almost immediately owing to the supposed ash cloud. There is no definite indication of this resulting from the chironomid assemblage. While many species continue to decrease after Mazama (as seen in the stratigraphic diagrams, Fig. 10 and 11), this is probably because of other environmental disturbance factors such as the long-term cooling effect of the mesothermic as well as increased precipitation. The usefulness of this new inference model is also clearly evident when compared with the only other quantitative paleotemperature reconstruction available for B. C. Mathewes and Heusser (1981) applied their transfer function to stratigraphic pollen data obtained from Marion Lake, in the U. B. C. Research Forest near Maple Ridge, B. C. Their transfer function converted stratigraphic pollen counts to estimates of mean July temperature and mean annual precipitation (Mathewes and Heusser 1981). Figure 17 shows the results of their reconstructed temperatures.

From Mathewes and Heusser's (1981) reconstruction, it is apparent that deglaciation in the area of Marion Lake was complete prior to 12 000 years ago. Minimum temperatures occurred at the base of the core and rose by about 2 °C to maximum values near 10 000 years B.P. Temperature was observed to increase fastest between 10 500 and 10 000 years B.P. (Mathewes and Heusser 1981). The graph shows that the warmest inferred temperatures occurred from 10 000 to about 7500 years B.P. Mathewes and Heusser (1981) refer to this time period as the early Holocene xerothermic. A drop in temperature begins around 7500 B. P. and lasts until 6000 years B.P. Temperatures show little change between 6000 and 4000 years ago. Thereafter, temperatures appear to gradually increase, ever so slightly, to the present-day (Mathewes and Heusser 1981).

The inferred temperature reconstructions based on chironomid assemblages for North Crater Lake and Lake-of-the-Woods (Fig. 16 a,b) follow trends similar to those seen



Figure 17: Diagram of mean July temperatures (°C) reconstructed using pollen data derived from a sediment core from Marion Lake, B. C. (Adapted from Mathewes and Heusser 1981).

in Marion Lake, although there are also some differences. In all three lakes, minimum temperatures occur in the late-glacial period, at the base of all cores. However, basal dates in North Crater Lake and Lake-of-the-Woods are younger than the basal date obtained at Marion Lake. Radiocarbon dates from the southwest coast of B. C., indicate that deglaciation had begun there by about 13 000 years B.P. Deglaciation inland, such as in the southern interior occurred later (Hebda 1995, Mathewes 1985).

It would be expected then, that as deglaciation occurred later in the interior, that the maximum temperatures seen in both North Crater Lake and Lake-of-the-Woods would occur later than those seen for sites on the coast. This is indeed the case. Maximum temperatures are not seen until after about 9500 B.P. in both North Crater Lake and Lake-of-the-Woods (see Fig. 16 a, b). In my reconstructions and Mathewes and Heusser's (1981) reconstruction, this rapid warming is succeeded by a prolonged warm period, the "xerothermic", when temperatures remained high, and relatively stable. Unlike Marion Lake however, this xerothermic period persists after 7500 years B.P. in my reconstructions. In both North Crater Lake and Lake-of-the-Woods these high temperatures actually persist after the Mazama eruption (6730 B.P.). Mathewes (1985) suggested that the xerothermic may have lasted longer inland, and thus, this interval of warm, dry conditions may be time transgressive (did not occur simultaneously in all regions) in nature, even within British Columbia.

This is not to say, however, that the cooling observed before and after the Mazama eruption at Marion Lake was not detected in North Crater Lake or Lake-of-the-Woods. A cooling trend is observed, but it is not so strong as that seen in Marion Lake. Temperatures cool slightly in North Crater Lake, but only after about 6000 B.P. At Lake-of-the-Woods inferred temperatures increase slightly, at this time.

After 4000 years B.P. temperatures increase slightly in the Marion Lake reconstruction. A temperature shift also occurs in both North Crater Lake and Lake-of-the-Woods, however, this shift is opposite to that of Marion Lake. My reconstructions indicate

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that a cooling trend occurs beginning around 5000 years B.P. in both lakes. This signal is stronger at Lake-of-the-Woods, with the cooling becoming more pronounced around 3000 B.P. These cooler climatic conditions are consistent with the concept of a late Holocene neoglacial period (Clague and Mathewes 1996, Ryder 1989).

Readvances of glaciers were readily apparent beginning about 5000 years ago (Mathewes 1985). Major glacier advancement and expansion in many parts of the Cordillera of B. C. occurred between about 3300 and 1900 years ago. For instance, Bugaboo Glacier in the Columbia Mountains began to readvance prior to 2400 B. P. In south-central B. C., on the Shuswap Highlands, a major glacial advance occurred between 3400 and 2400 B. P. (Ryder 1989). Similarly, in the north Coast Mountains, several glacial advances occurred about 2800 years ago (Clague and Mathewes 1996).

However, it is only in the past several centuries that glaciers have reached their maximum extent, a time period referred to as the "Little Ice Age". The Little Ice Age transpired throughout the world (Clague and Mathewes 1996, Luckman 1993, Ryder 1989). The timing of it however, may be slightly different even within B. C. and Alberta. In the Coastal Mountains of southern B. C., the Little Ice Age is believed to have begun about 900 years ago and continued for about 700 years (Ryder 1989). Further north in the Coast Mountains, glaciers readvanced prior to 500 years ago, perhaps beginning almost 1000 years ago (Clague and Mathewes 1996, Ryder 1989). In the Canadian Rockies, glacier readvances began more than 600 years ago (Ryder 1989). In fact in the Canadian Rockies the Little Ice Age may have begun about 900 years ago (Clague and Mathewes 1996, Luckman 1993).

Tree-ring chronologies in the Rocky Mountains have shown that periods of cooler temperatures preceded moraine development (or glacier readvances). These periods are reviewed by Luckman (1993), and show that major glacial advances continued to occur well into the late 19th century. Glaciers throughout B. C., have receded from their maximum Little Ice Age extents, and this recession is ongoing (Luckman 1993, Ryder

1989). Standstills and readvances have interrupted this recession, for example, from 1960
- 1970. Some glaciers even readvanced slightly in the 1970's and early 1980's (Luckman 1993).

Overall, the trends and patterns seen in my temperature reconstructions are consistent with one another, and with Mathewes and Heusser's (1981) reconstruction. However, when compared with the province-wide synthesis of climate history compiled and prepared by Hebda (1995) there are discrepancies in the timing and extent of each interval. Hebda (1995) based his reconstruction on a multitude of palynological studies, and does indicate that the duration of intervals varied among regions. But, the timing of events and climatic trends proposed by Hebda (1995) for the southern interior are sometimes at odds with findings from my research. This suggests that the climatic history of the southern interior requires further study.

The time of deglaciation fits well with Hebda's (1995) summary for high elevation sites. Also, the appearance of *Orthocladius (Symposiocladius) lignicola* is consistent with the presence of trees, or forest vegetation at Lake-of-the-Woods by 10 000 yr. B. P. Hebda (1995) from the study of a lake located in the Interior Douglas Fir biogeoclimatic zone near Kamloops, B. C., determined that immediately after deglaciation *Pinus contorta* (or lodgepole pine) forest was present, possibly as a component of the pioneering vegetation. Hebda (1995) suggests that there was a warm interval in the Holocene, and he split it into two parts.

The first, from 9500-7000 B.P. he refers to as the early Holocene warm, dry "xerothermic interval". This name was proposed earlier by Mathewes and Heusser (1981). Hebda (1995) suggested that a warm but wet "mesothermic interval" occurred from 7000-4500 B.P. In this interval, temperatures are warmer than present, but not so warm as during the xerothermic interval. Precipitation was at levels comparable to those of the present day. Temperatures in the early Holocene xerothermic were postulated to be anywhere from 2 - 4 °C warmer than late-glacial/deglaciation temperatures and modern day

temperatures (Hebda 1995). The temperature reconstructions for North Crater Lake and Lake-of-the-Woods (Fig. 16 a,b) also show a 2 - 4 °C increase. However, these temperatures remained higher for longer than Hebda (1995) suggests.

In the southern interior, temperatures were believed to be at their maximum between 9500 - 7000 years B.P. (Hebda 1995). It is during this time that the grass and sagelands of the interior were at their maximum range, up to 1300 m asl. In both lakes, but particularly evident in Lake-of-the-Woods (See Fig. 16 b), these maximum temperatures began around 9500 years B.P., but remained high long after Mazama ash deposition (at 6730 B.P.) to about 6000 years B.P. Research performed by Kearney and Luckman (1983) also shows in the Rocky Mountains, that temperatures remained high until about 6000 B.P. According to Hebda (1995), this should not be the case for the southern interior. By 7000 years B.P. Hebda (1995) indicates that temperatures in the southern interior, although warmer than present, were cooler than during the xerothermic. Precipitation had increased and this lasted to about 4500 B.P. In fact, in southern B. C., this precipitation increase is believed to have begun close to 8000 years ago (Hebda 1995) at which time the range of grassland began to shrink. Since the xerothermic interval persists longer at my sites, it is to be expected that the so called "mesothermic" period would occur later also.

Unfortunately, the moist environmental conditions inferred through pollen analysis cannot be tested via chironomid analysis, except possibly through an increase in rheophilous taxa. Chironomids are known to be sensitive temperature indicators; thus, one would expect them to easily pick up the cooler conditions of the mesothermic. However, their assemblages suggest that the mesothermic may not have been as cool as suggested. From the paleotemperature reconstructions it is somewhat difficult to ascertain both the beginning and end of this mesothermic interval although cooler temperatures begin to show around 5400 years ago (Fig. 16 a,b). Interestingly, treeline evidence from Clague and Mathewes' (1989) analysis, showed high, warm temperatures between 9100 and 7600

yr. B. P. Following this, a gap occurred in which no logs were found above treeline at their sites. Then, from 6000 to 5100 yr. B. P., records of logs are once again found above present treeline. This is indicative of a return to warmer conditions (Clague and Mathewes 1989). Thus, the increase in temperatures inferred as occurring after Mazama deposition in Lake-of-the-Woods is possible.

Hebda (1995) suggests that the transition from the "mesothermic" climate to the cooler, moister modern climate occurred 5000 - 4000 years B.P. and is most apparent around 4000 B.P. for the southern interior. Palynological evidence suggests a possible further cooling between 4500 - 3000 years ago (Hebda 1995). My research suggests a continuous cooling from 5400 yr. B.P. to the present day. Neoglacial ice advances and cooler conditions are indicated by diverse climate proxy records at this time.

It is possible that the timing and extent of climatic changes may have varied even within the southernmost interior. For instance, Alley (1976) determined that climate was cool and moist, and trees were abundant in the Okanagan Valley at Kelowna by 6800 B.P. This is very different from my conclusion. However, Alley's (1976) "bog" site was likely very sensitive to local "edaphic" conditions, and may not provide a good climate proxy record.

Chapter VI

Diversity, Richness and Community Trajectories

Paleoecological data are potentially valuable, not only in reconstructing past environments, but also as a means to address some purely theoretical issues in ecology. Deevey recognized this potential in his early research, as succinctly expressed in the title of his paper, "Coaxing history to conduct experiments" (Deevey 1969). For example, we may seek answers to questions such as the following. As biotic communities gradually become established, is there a distinct successional pattern of species richness and diversity that has repeatedly occurred in lakes? If a lake is temporarily perturbed by a climatic change, or other disturbance, will a community with the same biotic composition reestablish itself if and when environmental conditions return to the original state? I have attempted to address these questions by examining stratigraphic patterns in both diversity and richness and also by examining community trajectories, as portrayed in ordinations for my study sites.

6.1 Community Trajectories: Do original cool assemblages reassemble when cooling returns?

The results of the trajectory analysis based on Detrended Correspondence Analysis (DCA) are presented in Figures18 and 19. In Figure 18, the first axis accounts for 35.6% of the variance in species data. Axis 2 accounts for an additional 11.7% of the variance in species data. Similarly for Figure 19, axis 1 accounts for 21% of variation in the species data, while axis 2 accounts for an additional 13.6% of variance in the species data. As indicated on page 38, the axes represent hypothetical environmental gradients as determined by the method of DCA. It is evident from the trajectories that original species assemblages are not recurring over time. For example, in the trajectory for North Crater Lake, three somewhat distinct assemblages are suggested. The two lowermost samples dating prior to 10 000 yr. B. P., have high scores on axis 2. Those samples, ranging from 270.5 to 233.75 cm and dating from around 9500 to 6800 yr. B. P. are scattered to the right of the









origin (i.e., high on axis 1). The remaining samples, dating from just prior to Mazama, to the present day, are located to the left of the origin. These samples are low on both axis 1 and axis 2. Similarly, for Lake-of-the-Woods, there are also three distinct groupings. The five lowermost samples have fairly high scores on axis 1 and like North Crater Lake, date prior to 10 000 yr. B. P. Those samples ranging from 355.5 to 112.5 cm, and dating from around 10 000 to 4800 yr. B. P. are clustered around the origin and most are low on both axis 1 and 2. A final group of eleven samples from the 102.5 cm level to present day have high scores on axis 2. The trajectory for both lakes starts and ends in completely different locations. Thus, in answer to the question: original assemblages did not recur as cool conditions returned in the late Holocene.

Other trajectory analyses have been performed on data from chironomid assemblages. For instance, a trajectory analysis was obtained from chironomid samples that encompassed late-glacial time in Atlantic Canada. The analysis focused on how chironomid assemblages responded to the "brief" (approximately 1000 yr.) cooling episode that is referred to as the Younger Dryas (Wilson *et al.* 1993). There, as in my trajectory analysis, the trajectory for the two lakes end up in different locations, although they do fluctuate.

Regardless of the fact that the chironomid communities did not re-establish in either of the lakes in my study, the possibility of this recurrence of species in space and time has generated much debate. This is because in the past there have been differences in the major concepts of what defines a community, or community structure. According to Krebs (1994) certain people believe that communities tend to move toward dynamic stability. That is, that exact repetition of the same associations (or species assemblages) never recurs spatially or temporally. On the other side, people believe that species are organized into integrated communities and that these groups of species recur consistently in both space and time (Krebs 1994, Wilson *et al.* 1996).

Much of the work on recurrence of species assemblages has been performed on plants and plant communities. For example, Wilson *et al.* (1996) examined roadside vegetation to see if species assemblages recurred at different sites. They sampled roadside vegetation sites at nearby locations in both southern New Zealand and eastern Spain. Each site had subsites (50m apart in New Zealand and on opposite sides of the road in Spain). Each site was composed of two adjacent quadrats. They found that associations (or assemblages of species) almost always recur. While their analysis shows species recurring spatially, it does not demonstrate a recurrence temporally within the same site or stand, and, thus is not directly comparable to mine.

Perhaps, the results from a study by Levesque *et al.* (1996) are more pertinent. They made comparisons of late-glacial chironomid communities among four New Brunswick lakes. At all sites the chironomid assemblages changed in response to cold climatic conditions during the Killarney Oscillation (a cooling event prior to the Younger Dryas that interrupted climatic warming following deglaciation). However, the precise nature of the changes differed for each site (See Levesque *et al.* 1996). Interestingly, within lakes, the researchers found that those assemblages that occurred during the Younger Dryas cooling in all four lakes were nearly identical to assemblages found in the bottom sediments of the same cores (immediately following deglaciation). Did original species assemblages recur? Most of the taxa were present during both time periods, but nevertheless several slight differences were readily apparent. A few taxa that were present during the Younger Dryas interval were not found in the basal sediments (Levesque *et al.* 1996).

It is difficult to accurately assess why species assemblages do, or do not, recur from paleoecological data. At my sites, cooler conditions returned in the late-Holocene, but conditions may not have returned to precisely their original state. Other factors relevant to the lake and its environment may have changed. For example, while cold conditions returned, the water chemistry could have differed significantly between the late-glacial and

the late-Holocene. This could perturb chironomid communities enough to account for differences in the assemblages.

What is apparent though, particularly in Lake-of-the-Woods, are three different groupings of samples. These groupings might represent three distinct climatic or environmental states in the lake's history.

6.2 Diversity and Richness

Associated with changing faunal assemblages are often changes in diversity. Thus the changes apparent in my stratigraphic diagrams were assessed quantitatively using a diversity index. The adequacy of the sample size was first assessed by plotting diversity versus actual numbers of head capsules in each sample. A regression analysis was performed on these data for each lake. The regression analysis showed that there was no positive correlation between diversity and sample size. For instance, the regression analysis for North Crater Lake produced an adjusted $r^2 = -0.0018$ with a significance (prob.) of 0.344. Regression analysis of actual numbers versus diversity for Lake-of-the-Woods produced an adjusted $r^2 = 0.0684$ with a significance (prob.) of 0.0217. For Lakeof-the-Woods this plot had a significant negative decreasing slope. If sample size was having an effect, the slope would however be expected to be positive. Thus, sample size is apparently not having a significant effect. Similarly, actual numbers in each sample were plotted versus richness, and a regression analysis performed. Regression showed a significant correlation between sample size and richness for North Crater Lake, with an adjusted $r^2 = 0.0262$ with a significance (prob.) of 0.0001. There was no significant correlation between richness and sample size in Lake-of-the-Woods. Here adjusted $r^2 = -$ 0.0140 with a significance (prob.) of 0.7071. As there was a significant correlation in North Crater Lake, richness was determined from the first fifty head capsules identified in each sample so as to eliminate the effect of sample size.



a) Diversity changes within the North Crater Lake core.

Figure 20: Diversity and richness of the chironomid assemblages from North Crater Lake and Lake-of-the-Woods.



North Crater Lake Species Richness

b) Richness of the assemblages within the North Crater Lake core.





d) Richness of the assemblages within the Lake-of-the-Woods core.

For North Crater Lake (Fig.20 a, b) few taxa were recorded in the late-glacial assemblage (i. e., prior to 10 000 years B. P.), the fewest recovered being six. This is reflected in the diversity values which are also low for the late-glacial. Diversity and species richness increased from 10 000 years B. P. onward to 236 cm (about 8000 B.P.). Diversity started to decline just prior to the Mazama eruption, and continued to slowly drop until about 5500 years B. P. Richness of the assemblages followed a parallel trend, except for a brief peak and maximum number of thirteen taxa at the 217.5 cm interval. From 5500 years B. P. to 3000 years B. P. diversity increased gradually, as the number of taxa remained steady. After 3000 years B. P., diversity dropped and has remained low to the present. Richness has oscillated between 5-8 species for the past 5500 years. Some of these top-most samples had the lowest number of taxa since the late-glacial.

At Lake-of-the-Woods diversity was very low in the three samples at the base of the core (Fig. 20 c,d). As few as six taxa were recovered during this time. The number of taxa identified rose gradually, together with diversity, attaining a maximum value around 295 cm. A maximum of nineteen different taxa was found in these samples. From 290 to 230 cm (approximately 8 000 B. P.) diversity remained high and relatively constant. Taxonomic richness during this interval was somewhat lower on average, but fluctuated. Diversity declined quite rapidly prior to the Mazama eruption. Thereafter it gradually increased until about 5500 years B. P. Richness was lower, but the number of taxa tended to increase by 5450 years B.P. Diversity tended to decline thereafter with species richness ranging between eleven and eighteen.

Overall the richness, and particularly the inferred diversity changes (Fig. 20), appear to parallel the changes in temperature inferred for my sites. In Zone 1, the cold, late-glacial interval, diversity and richness are low. The brief drop in diversity at 370.5 cm for Lake-of-the-Woods, corresponds to the inferred reversion to cooler temperatures. For both lakes, assemblages are both richer and more diverse in Zone 2. This corresponds with very warm reconstructed mean July temperatures. In Zone 3 species richness and

diversity dropped prior to the Mazama eruption, paralleling a drop in inferred temperatures. Richness and diversity trends remained high after Mazama, in Zone 3, but at North Crater Lake, diversity and species richness both dropped in Zone 4, remaining low to the present day. This is consistent with the cooler inferred temperatures of the neoglacial period. For Lake-of-the-Woods, diversity declined slightly after 5400 years B. P. Diversity dropped more dramatically from 65 cm to the present day, paralleling the trend to cooler temperatures during the neoglacial.

Studies by Walker and Mathewes (1989a) and Levesque *et al.* (1996), have documented similar diversity changes. Walker and Mathewes' (1989a) research showed that the coldest lakes (those at high elevations) had much lower diversity than warm low elevation lakes. Similarly, Levesque *et al.* (1996) examined richness and diversity changes in late-glacial chironomid assemblages in New Brunswick lakes. Richness and diversity were lowest immediately following deglaciation and during the Younger Dryas at all sites. This corresponds to times of the coldest inferred temperatures. Richness and diversity increased during warm intervals. In each case, the evidence suggests that climatic conditions strongly influenced the diversity changes.

It is also obvious that both diversity and richness are higher overall in Lake-of-the-Woods than North Crater Lake. There are several plausible reasons for this. For example, Walker and Mathewes (1989a) showed that diversity and richness of faunal assemblages were reduced at cold high elevation lakes compared to low elevation lake sites. North Crater Lake is situated 70 m higher in elevation than Lake-of-the-Woods. Slightly lower temperatures at North Crater Lake are perhaps enough to impact on the life-cycles of warmadapted taxa, and their ability to reproduce, develop, and disperse.

Other factors that can affect the distribution and diversity of fauna include chemistry of water, diversity and types of benthic substrates present, predators, and ability to disperse (Hoffman *et al.* 1996). For instance, Hoffman *et al.* (1996) examined forty-one oligotrophic lakes in the Northern Cascade Mountains of Washington, over a range of

altitudes, in an effort to determine what factors affected the distribution of macroinvertebrates such as chironomids. They found that as one moved from forest to alpine lakes, the number of taxa decreased: 86% of all taxa were collected from forest lakes; 61% of all taxa were collected from subalpine lakes; 16% of all taxa were collected from alpine lakes. These findings mirror those of Walker and Mathewes (1989a). Hoffman *et al's*. (1996) study determined that the number of taxa was positively correlated to maximum lake temperature and negatively correlated to elevation. Elevation then, and associated factors (e.g., ice presence, duration of ice and snow cover, temperature, etc.) seem to affect macroinvertebrate distribution.

Similarly, moving from forested lakes to alpine lakes, substrates in microhabitats change. Inorganic substrates (silt, sand, etc.) prevail in subalpine and alpine zone lakes. Organic substrates (emergent/submergent vegetation, lake grasses, sedges, coarse wood, organic detritus, etc.) are more prevalent in forest lakes (Hoffman *et al.* 1996). The diversity of organic substrates (submerged vegetation) will ultimately increase the number of microhabitats available for organisms. In fact, the study determined that there were three aspects of habitat that impacted on the distributions of macroinvertebrates: maximum water temperature, water chemistry and the substrates present in the shoreline zone (Hoffman *et al.* 1996).

Submerged vegetation is able to increase richness and diversity in several ways. It adds stability to littoral areas, it acts as a food source for various macroinvertebrates, and more importantly, it acts as a refuge for prey from predators (Gilinsky 1984, Hoffman *et al.* 1996). Gilinsky (1984), like Hoffman *et al.* (1996), showed that increased macrophyte presence, hence increased heterogeneity, resulted in increased species richness and density. She also determined that increased heterogeneity increased the stability of predator-prey relationships by keeping certain populations safe from predation. Overall, macrophytes formed a refuge from predators and increased the complexity of the surroundings so that predation efficiency decreased (Gilinsky 1984). Hence, increased areas of refuge,

decreased predation and increased heterogeneity ultimately relate to increased species richness and diversity.

Extrapolating these findings to the geographic location of my study lakes may help to explain the lower diversity and richness in North Crater Lake versus Lake-of-the-Woods. Compared to the latter, North Crater Lake lies in a very exposed basin near the top of Crater Mountain, and would not be as protected from the elements as Lake-of-the-Woods, which sits in a cirque basin. Furthermore, aerial photographs (Fig. 4) reveal that Lake-of-the-Woods, is also completely surrounded by dense forest. Lake-of-the-Woods is deeper and has an inlet through which organic matter (fallen logs, debris, etc.) may enter the lake. Lake-of-the-Woods, therefore, will not only have warmer temperatures, but also a greater array of organic substrates in the nearshore zone. All of these factors, are likely contributing to the differences in diversity between my sites. It is not difficult to imagine that changes in these variables temporally may also account for post-glacial diversity changes evident within my cores.

Chapter VII

Conclusions

The chironomids have revealed climatic changes that occurred throughout the Holocene in southwestern B. C., based on changes in their community assemblages.

Stratigraphic analysis of these non-biting midges from North Crater Lake and Lakeof-the-Woods showed that cold climatic conditions existed in the late-glacial (prior to 10 000 yr. B. P.). Cold-stenothermous chironomids such as *Heterotrissocladius* and *Sergentia* formed the major part of the chironomid assemblages at this time. Soon after 10 000 yr. B. P., there was a prolific increase in abundance and diversity of warm-adapted taxa. While genera such as *Microtendipes, Dicrotendipes, Pagastiella* and *Polypedilum* flourished after 10 000 yr. B. P. cold-stenotherms disappeared. The presence of these warm-adapted taxa portray rapid warming and high temperatures associated with the xerothermic period. While several taxa declined in abundance prior to the eruption of Mt. Mazama (6730 yr. B. P.), others remained fairly abundant, indicating that conditions remained warm until about 5000 yr. B. P. A significant drop in many of these taxa occurred thereafter in both lakes. This change and return of cold-stenotherms in Lake-ofthe-Woods, signifies a shift to cooler climatic conditions. This shift is consistent with the concept of neoglaciation in B. C. My research also led to the discovery of two, as yet unidentified *Corynocera* taxa.

My research indicated some discrepancies between the climate history as based on numerous palynological studies and chironomid paleotemperature inferences. My research indicates the xerothermic period lasted well beyond 7000 yr. B. P. Similarly, the cooler climatic conditions of the mesothermic (7000 to 5400 yr. B. P.) are not particularly evident in my paleotemperature reconstructions. As chironomids are thought to be more sensitive and able to respond faster to climatic shifts, those changes elucidated from the chironomid research may prove more reliable as a record of climate change.

Diversity and richness changes within the cores of both lakes, parallelled the reconstructed climatic changes. Diversity was low during the cold late-glacial. Conversely, both diversity and richness increased during times of increased warmth. Several distinct stages of development of the lake faunas were revealed by ecosystem trajectories, but there was no evidence that species assemblages comparable to those of the late-glacial, reassembled with late-Holocene neoglacial cooling.

In the future, B. C., including the southern interior, will be subject to further climatic changes. As can be seen in historical records of temperature and CO₂ concentrations, among other things, temperatures are warming and will likely get warmer. Climate models indicate that temperature may increase by 2-6 °C, yielding temperatures similar to those seen during the xerothermic. What does this mean? Ecosystem-level changes will conceivably occur that will impact all levels of biological life: water systems and availability, plant communities, animal populations, etc. Vegetation (e.g., trees) will migrate towards higher latitudes and elevations. Plant species unable to deal with such warm temperatures will be extirpated, perhaps replaced by others. The state of B. C. forests and the forest industry will likely change dramatically. We, as scientists, researchers, economists, laborers, need to understand and appreciate the significance of this possible change and plan for the future. This may mean changes in forest management including especially silviculture practices. Furthermore, as B. C. is so topographically and geographically diverse, further detailed paleoclimate studies need to be undertaken in order to understand the possible extent and impact of future climate change in this province.

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