POSTGLACIAL CHANGES IN CHIRONOMID COMMUNITIES AND

INFERRED CLIMATE NEAR TREELINE AT MOUNT STOYOMA, CASCADE

MOUNTAINS, SOUTHWESTERN BRITISH COLUMBIA

by

Michael J. Smith
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Name: Michael Joseph Smith

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SOUTHWESTERN BRITISH COLUMBIA.

Examining Committee:

Chair: _____ Dr. L. Bendell-Young, Assistant Professor

_____
Dr. R. Mathewes, Professor, Senior Supervisor
Department of Biological Sciences, SFU

_____
Dr. I. Walker, Adjunct Professor
Department of Biological Sciences, SFU

_____
Dr. I. Hutchinson, Associate Professor
Department of Geography, SFU
Public Examiner

Date Approved:_____February 27, 1997_____

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ABSTRACT

Analysis of the distributions of chironomid (midge) and other dipteran subfossils from two high elevation lake sediment cores in the Cascade Mountains reveals changes in midge communities and inferred climate since the late-glacial. Cabin Lake and 3M Pond are located near treeline in the subalpine Engelmann Spruce/Subalpine Fir biogeoclimatic zone. Chironomid head capsule assemblages illustrate a characteristic late-glacial community (Cabin Lake only), and three distinct Holocene communities. In Cabin Lake, the late-glacial community is composed of cold-stenothermous taxa dominated by *Stictochironomus*, *Mesocricotopus*, *Heterotrissocladius*, *Parakiefferiella nigra*, *Sergentia*, *Protanypus*, and *Paracladius*, and warm water midges are absent or rare, indicating cold conditions. In both lakes the early Holocene is dominated by a diverse warm-adapted assemblage, corresponding to the warm climatic conditions of the xerothermic period. Cabin Lake's mid-Holocene zone records a decrease in relative abundance of the warm water community and is accompanied by an increase in cold-stenotherms. At 3M Pond this zone shows a dramatic loss in diversity of warm-adapted taxa, as the temperate genus *Dicrotendipes* dominates. This zone corresponds to the mesothermic period. Further cooling in the late Holocene (to modern conditions) is inferred from continued reduction of warm water midges and persistence (at Cabin Lake) or

appearance (at 3M Pond) of a cold-stenothermal community. This late Holocene cooling is similar in timing to Neoglacial advances in the Coast, Cascade, and Rocky Mountains of southern British Columbia.

Similarities in the timing of chironomid and vegetation community changes at these high elevation sites, along with the more rapid response time of the Chironomidae, support the sensitivity of midges to postglacial climatic change at high elevation sites.

Dedication

To all those who have contributed to molding my character
and making me the person I am today,

especially to my parents, Darrel and Bev
and to my wife, Christine

"Out of the strain of the doing

Into the peace of the done"

--- Julia Louise Woodruff

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INTRODUCTION

Climate plays a role in determining the abundance and distribution of many organisms as well as physical and chemical resources, upon which virtually all life depends. It largely determines the availability of water, which in turn affects health, and the abundance and distribution of crops and other plants which sustain all "higher" life forms (Watson et al., 1992). Thus, from a purely anthropocentric view, climate is a key to our food security and the availability of forest products. As a consequence, the potential ecological effects of today's human-induced global warming have become a leading area of research (Delcourt and Delcourt, 1991).

Over the past forty years, computer models have been developed which describe the physical processes that determine climate (Huggett, 1991). With these general circulation models (GCM's), predictions of future climatic directions become possible (COHMAP, 1988). Like any good scientific model, they must be tested to determine their level of reliability, and the best way to test them is through their predictive power in reconstructing past climates. Validation from independent lines of proxy climatic evidence is of great importance in determining the reliability of GCM's (Schweger and Hickman, 1989).

Instrumental records of climatic variation are relatively recent in human history and so provide inadequate perspectives on climatic variation over a long

time scale (Bradley, 1985). Paleoclimatology is the study of climate prior to the period of instrumental measurements, primarily using various proxy data, in the form of climate-dependent natural phenomena (Bradley, 1985). It is possible to synthesize different proxy data into a comprehensive picture of former climatic fluctuations, thus increasing the possibilities of identifying their causes and mechanisms.

The focus of this study concerns changes in climate since the last deglaciation in southern British Columbia. As will be illustrated in the following literature review, most studies in this region have involved the use of paleobotanical information to infer climate change, which show some discrepancies with respect to the timing of changes (Hebda, 1995).

This paleolimnological study utilizes fossil chironomid larval remains in the sediments of two high elevation lakes to infer changes in summer water temperatures since late-glacial time. In small lakes, water temperature in summer can be used to indirectly reconstruct air temperature, a key component of climate. Walker et al. (1991a) convincingly illustrate that summer surface water temperature is the key environmental variable in determining chironomid distributions. An important aspect of my study is the location of the two sites in the Engelmann Spruce-Subalpine Fir biogeoclimatic zone of British Columbia. Cabin Lake and 3M Pond lie very near alpine treeline, which is known to be very sensitive to the effects of climate on plant growth and distribution (Arno &

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Hammerly, 1984; Luckman & Kearney, 1986), and so it was anticipated that this ecotone boundary would also be sensitive in terms of chironomid distributions.

This work is being completed in conjunction with a study of pollen and plant macrofossils at the same sites by Pellatt (1996), thereby contributing independent proxy information for late-glacial and Holocene climatic change.

LITERATURE REVIEW

(1) Late-glacial and Holocene Climates in Southern British Columbia:

Climate is known to strongly influence broad-scale vegetation patterns and is often cited as a major cause of changes in species abundances and distributions (Mathewes, 1985). Thus, paleobotanical evidence using pollen and plant macrofossils is commonly used to determine past vegetation changes and to infer associated shifts in climate.

Reviews of the climate history of southern British Columbia (Mathewes, 1985; Hebda, 1995) have identified the timing of climatic events since the last deglaciation. All dates reported here are in uncalibrated radiocarbon years before present (^{14}C yr BP).

Mathewes (1985) reported that in the late-glacial, prior to 12,000 yr BP, the climate was cooler and drier than today. From *ca.* 12,000 yr BP until *ca.*

10,500 yr BP, cooler and wetter conditions have been inferred in both coastal (Mathewes, 1973) and interior (Hebda, 1995) regions. Transfer functions applied to the coastal Marion Lake pollen data (Mathewes & Heusser, 1981) gave a quantitative interpretation that supported the qualitative inferences given by Mathewes (1973). Recent evidence suggests that a cooling event around the time of the amphi-Atlantic Younger Dryas also occurred on the British Columbia coast (Mathewes et al, 1993; Mathewes, 1993). This evidence may prove very significant in terms of understanding the cause and geographic extent of this climatic event and its implications for global climate dynamics. Further evidence from various types of proxy indicators at more sites is needed to confirm this view of late-glacial deterioration to colder conditions.

A warm and dry early Holocene interval is evident from many studies in B.C., although the timing of the period of maximum warmth appears to be different at coastal and interior sites. Mathewes & Heusser (1981) quantitatively showed a rapid rise in temperature and decrease in precipitation around 10,000 yr BP, with a maximum July temperature and minimum annual precipitation between 10,000 yr BP to 7500 yr BP, aptly named the "early Holocene xerothermic interval". Hebda (1995) interprets a grassland maximum in the southern interior from 10,000 - 8000 yr BP to represent warmer and drier than present conditions, but correlates a "mesic grassland period" from 8000 - 4500 yr BP as being warmer than present but moister than the early Holocene.

Alley (1976) suggested a warm, dry interval between 8400 - 6600 yr BP from his study at Kelowna Bog, with a shift to moister and cooler conditions coinciding with Mazama Ash deposition (6800 yr BP). Cawker (1983) and Mathewes & King (1989) also inferred a warm, dry early Holocene that persisted until 6800 yr BP. Maximum warmth in the southern coast-interior transition was inferred to occur around 8000 - 9000 yr BP by Clague & Mathewes (1989) and Clague et al. (1992), based on growth of trees above present treeline at Castle Peak.

The mid-Holocene climate generally became cooler than the early Holocene xerothermic, but still remained warmer than present, and an increase in moisture is often noted (Hebda, 1995). The timing of this trend also does not appear to be synchronous over southern British Columbia. Hebda (1995) demonstrates an increase in moisture around 8000 yr BP in the southern interior grasslands, which remained warmer than today until *ca.* 4500 yr BP. Many studies identify a cooling and moistening trend beginning near the time of Mazama Ash deposition (Mathewes, 1973; Mathewes & Rouse, 1975; Heusser, 1983; Mathewes & King, 1989). This mid-Holocene stage was generally prevalent until *ca.* 4500 yr BP (Mathewes, 1985; Hebda, 1995).

The late Holocene climate change towards modern conditions is considered to begin at *ca.* 5000 yr BP, at which time signs of neoglacial readvances appear at high elevations (Clague, 1981; Ryder, 1989). Most paleobotanical studies show a cool and moist period beginning between 4500 -

4000 yr BP (Mathewes, 1985; Hebda, 1995) at both coastal and interior sites, which corresponds well with the proposed end of the eastern Hypsithermal as described by Ritchie (1987), and with significant shifts in climate in the U.S. interior northwest (Mehringer, 1985).

The timing of Holocene climatic changes appears to vary considerably between some sites in southern British Columbia. Mathewes (1985) views the Hypsithermal as a time-transgressive event here as in other parts of North America, and so these apparent discrepancies in fact may not be contradictory, especially in comparing sites in a region of extreme climatic and physiographic variability. Timing of changes may also reflect the proximity of each site to important ecotonal boundaries during gradual climatic changes.

(2) Chironomids as Indicators of Lake Typology:

A complete coverage of the historical development of this topic is beyond the scope of this review, and the reader is referred to comprehensive summaries by Brinkhurst (1974), Walker (1987,1993), and Hofmann (1988).

Early limnological studies involving chironomids were concerned with classifying lakes according to lake productivity. As outlined by Walker (1987), Einar Naumann introduced the lake types used today in trophic classification, describing very productive eutrophic lakes and unproductive oligotrophic lakes. August Thienemann used this same scheme, and matched specific chironomid

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genera with lake types, such as oligotrophic *Tanytarsus* lakes and eutrophic *Chironomus* lakes (Walker, 1987).

Later studies by Sæther (1975a, 1979) illustrated the continuous range of lake trophic states and representative chironomid communities. Sæther (1979) reviewed the various mathematical indices that summarized chironomid data in relation to eutrophication and proposed important refinements to increase the validity of this classification system.

It is important to note that this lake type classification scheme was originally intended to be based on benthic fauna of stratified lakes. The benthos are exposed to variations in nutrient and oxygen levels in their environment, which are reflected in the occurrence and distribution of these organisms (Sæther, 1979), and so it is suggested that changes in profundal chironomid taxa be examined separately from littoral taxa when considering trophic indicators (Kansanen et al., 1984; Hofmann, 1986; Walker, 1987). Hershey (1985) considered littoral taxa to be useful in lake typology in her study of an arctic lake, which appeared to illustrate a complex relationship between the effects of productivity and temperature. Sæther (1975a) discussed the occurrence of typical profundal chironomid species in the littoral zone of subarctic, arctic, and alpine lakes, and, along with Hofmann (1988), explained that in shallow lakes, climatic influences are likely to be more influential in determining chironomid distributions.

In addition to lake productivity, another factor that has been suggested to control chironomid community composition is the hypolimnetic oxygen regime. Using this system of classification, it was found that seasonal oxygen depletion in the profundal of stratified lakes gives rise to specific chironomid communities consisting primarily of *Chironomus* species (Oliver, 1971; Frey, 1976; Hofmann, 1988; Walker, 1993), which are used as indicators of eutrophic conditions. Another community (Brundin's *Tanytarsus lugens* community) is indicative of oligotrophic conditions in the profundal of stratified, temperate lakes in which there is a continually high oxygen content (Hofmann, 1988).

Once again, the complexities of the environmental factors influencing chironomid distributions can be noted. As Hofmann (1988) explains, the oxygen conditions in the profundal zone of lakes are closely related to productivity. Higher metabolic oxygen demands in productive, eutrophic lakes leads to oxygen depletion in the hypolimnion of stratified lakes, and so chironomids such as the hemoglobin-bearing *Chironomus* dominate (Walker, 1987). Conversely, unproductive, oligotrophic lakes may benefit profundal chironomids that require high oxygen levels, such as the genus *Heterotrissocladius* (Sæther, 1975b).

Many recent paleolimnological studies of fossil chironomids have employed the notion of chironomid communities as indicators of lake types (Wiederholm & Eriksson, 1979; Devai & Moldovan, 1983; Kansanen, 1985; Merilainen & Hamina, 1993; Walker et al., 1993). Clearly, conclusions made

from studies such as these should take into account the close interrelationships between trophic state, oxygen conditions, and climatic influences, and thus great caution must be applied to environmental reconstructions based on these changes in chironomid communities.

(3) Chironomidae in Paleoclimatic Investigations:

Larval chironomids have many attributes which make them applicable to paleolimnological studies and the reconstruction of paleoenvironments. These larvae inhabit the profundal and littoral regions of nearly all freshwater habitats (Walker, 1987). Among the freshwater invertebrates in the temperate zone, midges contribute the highest number of species, and their larvae generally are present in large numbers (Hofmann, 1988), along with the oligochaetes (Walker, 1993). Head capsules of moulted larval exoskeletons and dead larvae are well preserved in the sediments, allowing identification of these remains (Hofmann, 1986, 1988; Walker, 1987). Species are adapted to certain ecological conditions within a lake, so the chironomid fossil record is indicative of the ecological conditions at the time of sedimentation. Successional changes in chironomid fauna are documented vertically in the sediment, and these changes should reflect shifts in ecological conditions during lake development.

Using a single core to determine past whole-lake conditions raises the important question of how representative such a core can be, since the site of

sedimentation of chironomid remains is not necessarily the habitat of the living organisms (Hofmann, 1988). The deepest part of the lake appears to be the optimal site from which to obtain a complete and undisturbed sediment core (Hofmann, 1986, 1988). It has been determined that cores obtained from this region of a lake are highly reproducible, and so it can be assumed that a correct interpretation of lake conditions can be made from a single core (Schmah, 1993). Because deep basin cores contain a mixture of profundal, littoral, and pelagic remains, chironomid subfossils should be considered separately for analysis. The relative abundances of littoral vs. profundal species gives an indication of the influence of littoral species on the death assemblage (Hofmann, 1986).

Caution should also be exercised when equating chironomid life and death assemblages. Many studies on present chironomid ecology rely on samples taken at one time of year only, and taphonomic processes determine which taxa will be preserved, in what numbers, and where (Walker and Mathewes, 1989a). Comparisons of chironomid life and death assemblages have in fact shown relatively good correlation (Walker, 1987), and proper comparison of fossil and modern assemblages can minimize errors of interpretation. Studying recent fossil assemblages in surficial lake sediments is more cost efficient compared to conventional sampling, and, more importantly, the fauna is more comparable to the fossil assemblages retrieved from cores (Walker and Mathewes, 1989a).

(a) SALINITY

Ecological studies of chironomids in saline lakes have illustrated relationships between chironomid community composition and salinity levels (Cannings, 1975; Cannings & Scudder, 1978a,b; Hofmann, 1987; Williams et al., 1990).

The hydrologic budgets of lakes are related to climate, and significant fluctuations in lake levels are often correlated with periods of climatic change (Fritz, 1990). Therefore, the reconstruction of past changes in lake levels can provide a background for understanding modern hydrologic conditions and be a tool for predicting future hydrologic responses to changing climate. This information may also provide analogues of precipitation patterns during past warm periods, as well as a means of validating general circulation models used to simulate global climatic change (Fritz, 1990). Closed basin lakes in regions with a negative water balance are very good paleohydrologic and paleoclimatic recorders, as fluctuations in the balance of precipitation and evaporation result in lake level changes and concentration or dilution of dissolved salts. This information has been shown to be recorded in chironomid community composition, and so these organisms hold good potential in tracking changes in paleosalinities and associated climate.

Mees et al. (1991) reconstructed Holocene paleosalinities using chironomids in a study of Lake Melha, Africa, in which marked fluctuations in

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salinity were noted. Similarly, Verschuren (1994) inferred past salinities and lake level fluctuations from changes in chironomids archived in the sediments of Lake Oloidien, Kenya.

Chironomid remains in surficial sediments from 86 British Columbia lakes were used to assess the possibility of quantitatively reconstructing past salinities from fossil chironomid assemblages (Walker et al., 1995). Using canonical correspondence analysis (CCA), late summer salinity was found to be the environmental variable that explained most of the variance in the weighted averages of the taxa. The most appropriate weighted-averaging calibration function was used to produce a chironomid - salinity transfer function, which achieved close agreement at low to moderate salinities, but became poorer at salinities greater than 10 g/L. It was concluded that although chironomids appear to be very good indicators of transitions between freshwater and moderately saline waters, they cannot produce accurate estimates of salinity changes in highly saline waters (Walker et al., 1995).

The transfer function developed by Walker et al. (1995) was tested by Heinrichs (1995) in reconstructing paleosalinities of three lakes in the south-central interior of British Columbia, and comparing these inferred postglacial climate changes with accepted regional climatic trends. Salinity reconstructions at Mahoney and Kilpoola Lakes indicated a shift from freshwater to saline

conditions in the early Holocene, suggesting a temperature increase corresponding to the early Holocene xerothermic interval (Hebda, 1995).

(b) TEMPERATURE

Many studies involving chironomid physiology, behavior (Danks, 1971), and life cycles have shown that temperature is a very important limiting factor in the distribution of various chironomid taxa. Studies on emergence (Danks & Oliver, 1972a,b; Nordlie & Arthur, 1981), growth and development (Mackey, 1977), eclosion times (Kureck, 1979), and genetic diversity (Thorp & Chesser, 1983) have illustrated this temperature constraint. Pinder (1986) presents a good review of many related studies. Modern faunas do vary with climate, with the Orthocladiinae and Diamesinae occurring abundantly in cold arctic and alpine conditions, while the Chironominae and Tanypodinae are prominent at low altitudes and latitudes (Oliver, 1971; Walker & Mathewes, 1987a). Further evidence suggesting a chironomid-temperature relationship is shown by the fact that many temperate species that are absent from arctic and alpine habitats are also rare or absent from the cold profundal waters of temperate regions (Walker & Mathewes, 1989a). Conversely, most cold-stenothermous taxa common in arctic and alpine sites are predominantly limited to cold profundal regions of temperate lakes (Walker & Mathewes, 1987a, 1989b; Walker, 1990).

Work done by Walker & Mathewes (1987a), interpreting changing chironomid communities as a response to changing climate, was challenged by Warner and Hann (1987), who considered substrate characteristics and turbidity to be more important in regulating midge distributions. They proposed the wide geographical distribution of cold-stenothermous taxa as evidence against climate-related changes in chironomid faunas, and interpreted faunal changes as reflecting changes in allochthonous organic matter deposition and nutrients as a result of vegetation changes in the watershed that may have only been indirectly climatically controlled. Warner & Hann (1987) also assumed that freshwater invertebrate communities are not directly influenced by climate, since the aquatic environment acts as a strong buffer against climate change. Warwick (1989) also supported a role of sediment composition in determining the presence of chironomid taxa, referring primarily to his study in the Bay of Quinte (Warwick, 1980).

In response, Walker & Mathewes (1987b) argued that although many cold-stenotherms (such as *Heterotrissocladius*) are widely distributed, they are limited to cold northern or montane to alpine lakes, and are found only in the deep cold profundal regions of temperate lakes. Evidence against turbidity or substrate-controlled communities is given by the presence of *Heterotrissocladius* in both turbid waters of glacial lakes and very clear waters (Walker & Mathewes, 1989c). *H. marcidus* is the least cold-stenothermous species of the

genus, but is still restricted to relatively cold waters, although it is found on various types of substrates (Sæther, 1975b; Walker & Mathewes, 1987b). In addition, the very low sedimentation rates at approximately 10,000 years BP at Marion Lake, British Columbia (Walker & Mathewes, 1987a,b, 1989c), when the chironomid fauna changed, contradicts the suggested correlation with high sedimentation rates. In studying biotic and abiotic factors associated with diversity and density of larvae, Thorp and Chesser (1983) found that water temperature was the factor most strongly associated with chironomid assemblage changes, while particle size and organic content of the substratum were relatively unimportant.

Early studies (i.e., Thienemann, 1918; Brundin, 1949, 1956, 1958), as cited by Walker (1987), concerned with benthic lake classification in terms of trophic state also hinted at a relationship between chironomids, trophic state, and climate. Walker (1987) and Walker & Mathewes (1987a) explain this relationship, whereby higher temperatures and longer growing seasons lead to increased biological activity and productivity, and increased chemical weathering rates at higher temperatures contribute to higher nutrient levels. Thus, many taxa characteristic of oligotrophic conditions are cold-stenothermous, and taxa common in eutrophic waters are warm-adapted (Walker, 1987).

Walker (1987) reviewed some important preliminary studies of climate-related chironomid succession, illustrating good correspondence between climatic inferences based on chironomid data and trends shown by pollen-climate transfer functions. In the first study of postglacial chironomid succession in the Pacific Northwest, Walker & Mathewes (1987a) looked at changes in the fossil assemblages at Marion Lake, British Columbia. They discovered a prevalence of cold-stenotherms during late-glacial time, which they designated the "late-glacial *Heterotrissocladius* fauna", indicating cold conditions. At approximately 10,000 yr BP, reduction or complete loss of this fauna suggested rapid warming. The strong similarity between chironomid profiles in different geographic regions (British Columbia, New Brunswick, Germany) clearly reflects the fact that lake faunas independently respond to similar regional influences, most likely climate (Walker & Mathewes, 1987a). Further evidence of rapid climatic warming at Marion Lake at the Pleistocene/Holocene boundary was based on pollen-climate transfer functions (Mathewes & Heusser, 1981; Walker & Mathewes, 1987a). Similar changes in chironomid communities were observed at Mike and Misty Lakes (Walker & Mathewes, 1989a).

The next logical step in gaining confidence in chironomid-climate relationships came with a study of surficial lake sediments distributed across an altitudinal gradient (Walker & Mathewes, 1989b), which could be assumed to be

analogous to a latitudinal climatic gradient, since temperature decreases with increasing elevation (environmental lapse rate) (Oke, 1987). Here, it was again found that a typical *Heterotrissocladius* fauna was prevalent at higher, colder altitudes and in the bottom, oligotrophic waters of deep, temperate lakes, whereas many species common at lower elevations were absent at alpine and upper subalpine sites. Although horizontal and vertical climatic gradients are not linear functions of altitude or latitude, the parallel trends along altitudinal and horizontal climatic gradients strongly suggest that climate is either directly or indirectly influencing chironomid distribution.

A major advance in this research was attained with a statistical study of chironomid remains from surficial sediments of lakes in Labrador and Quebec, using canonical correspondence analysis (CCA) to quantitatively determine which environmental variables were most influential on chironomid distributions (Walker et al., 1991a). CCA (ter Braak, 1986) appears to provide the most appropriate means for analyzing the factors influencing biological distribution, where relationships between organisms and their environment can be used directly in reconstructing past environmental conditions, assessing several environmental variables independently using the same fossil data (Walker et al., 1991a). This study was initiated to test the importance of summer surface water temperature, maximum lake depth, and organic content of sediments in influencing relative abundances of fossil chironomid taxa.

Results showed that summer surface water temperature ($r = 0.79$, $p < 0.0001$) accounted for most of the explained variance (Walker et al., 1991a), and so a temperature-constrained CCA produced a weighted-averaging regression and calibration model of the chironomid-temperature relationship, which was used as a transfer function to predict summer surface water temperatures from fossil data.

Attempts to discredit climate as a factor in directing chironomid faunal changes were again attempted by Hann et al. (1992), but most of their comments were unsubstantiated or simply incorrect, and were dealt with adequately by Walker et al. (1992a).

From Walker et al.'s (1991a) work, chironomid-temperature relationships have been utilized to support the occurrence of an Allerød/Younger Dryas-age climatic oscillation in Atlantic Canada (Walker et al., 1991b; Wilson et al., 1993). The Allerød/Younger Dryas transition, which is well documented in Europe, marks a change from relatively warm conditions before 11,000 yr BP (Allerod) to a much cooler environment approximately 11,000 - 10,000 yr BP (Younger Dryas chronozone). Palynological and lithological evidence suggested late-glacial temperature fluctuations in Atlantic Canada that correlate well with this oscillation (Mott et al., 1986; Wright, 1989), but other independent evidence was needed to confirm this trend.

Continued expansion of the dataset and use of the chironomid-temperature transfer function were the result of studies of chironomids, pollen, and sediment organic content from sites in New Brunswick, Prince Edward Island, and Nova Scotia (Levesque et al., 1993a,b, 1994), and Maine (Cwynar & Levesque, 1995). In addition to support for Younger Dryas-age cooling, evidence of a short cold period in eastern North America just prior to the Younger Dryas, called the Killarney Oscillation (11,160 - 10,910 yrs BP), was discovered through very high resolution analyses. This period corresponds to the Gerzensee Oscillation in Switzerland and other events detected along the North Atlantic seaboard, suggesting a single event in the North Atlantic region, possibly causally related to the Younger Dryas.

Most recently, an improvement of this inference model was achieved by Walker et al. (in press). With further expansion of the surface sample dataset, more accurate temperature reconstructions and error estimates are expected.

STUDY SITES

Located in the Kamloops Forest Region of the southwestern interior of British Columbia, Mount Stoyoma (2283 m asl; 121°13' W; 49°59' N) is at the northern limit of the Cascade Mountains (Figure 1). The Cascades are primarily composed of strongly folded Paleozoic and Mesozoic sedimentary and volcanic rocks (Holland, 1976).
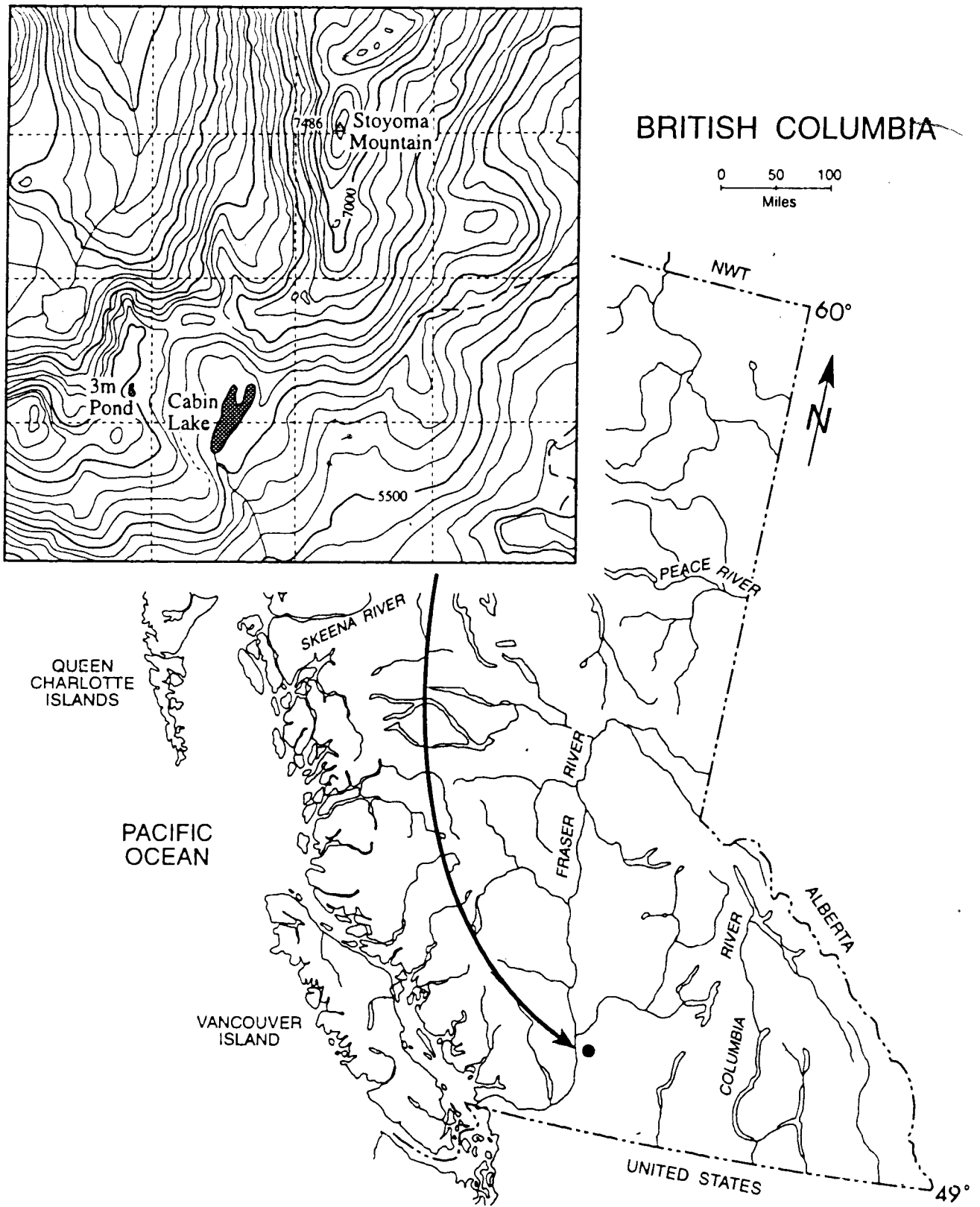
Figure 1: Map of British Columbia showing location of Mount Stoyoma in the Northern Cascade Mountains.
(Inset: topographic setting of study sites)

Vegetation reflects the environment and recent history of a given site, and thus is a key to ecosystem classification and identification (Lloyd et al., 1990; Pojar et al., 1991). In British Columbia, ecosystem classification is based on the relationship between ecosystems and climate, as climate has the greatest influence on the development of an ecosystem (Mitchell & Green, 1981). Utilizing this relationship, the ecosystems are divided into biogeoclimatic zones. The sites involved in this study lie in the Engelmann Spruce-Subalpine Fir biogeoclimatic zone (ESSF), which is the highest forested zone in the southern and central interior of British Columbia (Hebda, 1995). More specifically, the study sites are within the dry, cold Engelmann Spruce - Subalpine Fir subzone variant 2 (ESSFdc2) (Lloyd et al., 1990). Characteristic trees and shrubs include Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), whitebark pine (*Pinus albicaulis*), white-flowered rhododendron (*Rhododendron albiflorum*), and black mountain huckleberry (*Vaccinium membranaceum*) (Pellatt, 1996), producing continuous forest at lower and middle elevations in the zone, and subalpine parkland at higher elevations (Lloyd et al., 1990). The two sites involved here are at the upper regions near treeline, just below the alpine tundra biogeoclimatic zone.

Climate in the ESSF zone is continental, characterized by long, cold winters with high snow cover, and short, cool summers. Table 1 summarizes mean values for important environmental variables of the ESSFdc2 (Lloyd et al.,

Table 1: Mean values for selected ESSFdc2 climatic variables.
(Lloyd et al., 1990).

Annual precipitation	839 mm
Annual snowfall	635 cm
Annual temperature	- 0.2°C
Frost free period	45 days
Growing degree days (> 5°C)	579 days
Growing season precipitation	296 mm
Growing season temperature	8.0°C
Mean minimum January temperature	- 14.1°C

1990).

The two lake basins selected for paleoecological analysis were Cabin Lake (1850 m asl) and 3M Pond (1950 m asl). Both are located near present treeline, and are therefore expected to be sensitive to past climatic changes. Cabin Lake (Figure 2) lies within the dry southern Engelmann Spruce - Subalpine Fir Parkland (ESSFpe) and is surrounded by a well developed forest of Engelmann spruce and subalpine fir on the south, east, and west sides. The north slope forest was burned relatively recently, with abundant charred snags and open meadow vegetation. The lake has an area of approximately 4 ha, and a maximum water depth measured at 4.2 m. A small inlet stream is located at the north end which is active during the warmest months as snow melts at higher elevations, and an outlet stream is present at the south end, again probably only active when meltwater raises lake level.

Dominant trees and shrubs surrounding Cabin Lake include Engelmann spruce, subalpine fir, white-flowered rhododendron, partridgefoot (*Leutkea pectinata*), black mountain huckleberry, grouseberry (*Vaccinium scoparium*), pink mountain heather (*Phyllodoce empetriformis*), and mountain heather (*Cassiope mertensiana*) (Pellatt, 1996; Lyons, 1965).

3M Pond (Figure 3), within the transition between ESSFpe and the Dry Southern Alpine Tundra (ATd) (Mitchell & Green, 1981), is approximately 0.75 ha in area and has a maximum water depth of 1 m. Common trees and shrubs

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Figure 2: Photograph of Cabin Lake showing surrounding ESSF forest with Mount Stoyoma in the distance.

Figure 3: Photograph of 3M Pond with surrounding ESSF parkland.

surrounding the pond are subalpine fir, Engelmann spruce, whitebark pine, common juniper (*Juniperis communis*), white mountain heather, pink mountain heather, and partridgefoot, with a more prominent herb component than observed around Cabin Lake (Pellatt, 1996).

METHODS

Field and Laboratory:

Cabin Lake was sampled in July, 1993 using a modified Livingstone piston corer with a core tube diameter of 5 cm. A 399 cm sediment core was obtained from the deepest part of the lake. The five drives comprising the entire core length were extruded in the field and wrapped in cellophane and aluminium foil, and subsequently transported to Simon Fraser University (SFU) where they were stored at approximately 4°C for later analysis.

The Cabin Lake sediments were subsampled most commonly every 15 cm, with higher resolution sampling in regions of expected faunal change (i.e., late-glacial basal clay and basal clay/gyttja interface). Subsamples consisted of 0.5 ml or 1 ml of sediment, but up to 10 ml of sediment were necessary in some intervals to obtain sufficient numbers of chironomid head capsules for analysis (at least 30). All subsamples were stored in glass vials in 2 ml of distilled water and kept refrigerated at 4°C until analyzed.

Coring of 3M Pond was done using the methods outlined above in August, 1993. A 74 cm sediment core was removed from the deepest region of the pond and transported to SFU.

Subsampling of 3M Pond was usually done at 2 cm or 4 cm intervals in the top half of the core (0 - 35 cm), and every 8 cm in the bottom half (35 - 67 cm). Again, 0.5 ml or 1 ml (but up to 2 ml) subsamples were placed in 2 ml of distilled water in glass vials and stored at approximately 4°C for future analysis.

Isolation of chironomid head capsules, *Chaoborus* mandibles, and ceratopogonid head capsules generally followed the procedures outlined by Walker (1987). Sediment samples were deflocculated in 8% KOH at approximately 60°C for 60 minutes, followed by a thorough distilled water rinse on a 95 μm Nitex[r] mesh. Since carbonates were a very minor component of the sediments of both lakes, a treatment with HCl was not necessary. The residue retained on the sieve was back-washed into a beaker using distilled water, in which it was stored until sorted.

Sorting of the residue was done in a Bogorov counting tray under 25 - 50X magnification with a Wild M5 dissecting microscope. Remains were transferred to drops of water on a coverslip under 12X magnification using #4 or #5 forceps. Coverslips containing approximately 30 remains each were dried and mounted

onto glass slides using Permount[R] or Entellan[R] mounting medium for later identification.

Remains were identified under 100 - 400X magnification using various Zeiss compound microscopes. Identifications were based on descriptions given in keys by Walker (1988), Oliver & Roussel (1983) and Wiederholm (1983). Whole head capsules and fragments containing greater than half of the mentum were counted as one head capsule. Fragments that were exactly half of a head capsule were counted as one half, and fragments that consisted of less than half of the mentum were not counted. Most identifications were made at the generic level, although a few species identifications were possible. Broader taxonomic categories were necessary where the genus could not be determined (eg., subtribe Tanytarsina, *Cricotopus/Orthocladius, Corynoneura/Thienemanniella*).

Data Analysis:

Data were compiled on a spreadsheet using Tilia version 2.0 (Grimm, 1993), and chironomid percentage diagrams were produced using Tilia Graph version 1.17 (Grimm, 1991). A constrained sum-of-squares cluster analysis (CONISS) (Grimm, 1987) for percentage data was done to examine major changes in chironomid communities throughout the stratigraphy.

Chronology:

Ash Layers:

Tephra derived from Mount Mazama (6800 yr BP) (Hebda, 1995) is present in both Cabin Lake (246 - 253 cm) and 3M Pond (36 - 42 cm) sediment profiles. Cabin Lake also contains the Bridge River Tephra (ca. 2410 yr BP) (89.5-90.5 cm). Identifications of tephra using microprobe analysis were made by Dr. Jerry Osborne and Glen DePaoli (University of Calgary).

Radiometric Dating:

AMS radiocarbon dating (by IsoTrace Radiocarbon Laboratory, Toronto, and Center for Accelerator Mass Spectrometry, Lawrence-Livermore National Laboratory) was used to determine the ages of organics at two points in 3M Pond's sediment profile, and three points for Cabin Lake, and all dates given in this study are in uncalibrated radiocarbon years before present (^{14}C yr BP), datum 1950. Table 2 shows sediment depths, types, and ages of samples from Cabin Lake and 3M Pond. Regression analysis (Grimm, 1993) was utilized to interpolate radiocarbon ages at key intervals of chironomid community change.

Table 2: AMS radiocarbon dates for 3M Pond and Cabin Lake

Sample Identification	Sample Description	Lab #	Age (^{14}C yr BP)
3M Pond (65-67 cm) 3M94-B-21	conifer needles	TO-5329 (Isotrace)	10,000 ± 320
3M Pond (24-26 cm) 3M94-A-25	conifer needles	TO-5330 (Isotrace)	3530 ± 60
Cabin Lake (306 cm) CLJL94-5-12	carbonized wood	TO-5205 (Isotrace)	8910 ± 120
Cabin Lake CL-324 cm	pollen	29826 (CAMS)	10,090 ± 70
Cabin Lake CL-368-370 cm	leaf fragments	29829 (CAMS)	9860 ± 60

(Errors presented as ± 1s)

RESULTS

Figures 4 & 5 illustrate head capsule counts for each taxon, as a percentage of the total number of identifiable chironomid head capsules in each sampling interval. The chironomid taxa, along with *Chaoborus* and Ceratopogonidae, are separated into typical warm and cold water assemblages according to current information regarding their thermal optima and tolerances (Walker et al., in press). Figure 6 shows examples of head capsules from common cold and warm-adapted taxa. The remaining uncategorized taxa consist of "rheophilous" (flowing water) groups (i.e., *Brillia/Euryhapsis, Doithrix/Pseudorthocladius, Corynoneura/Thienemanniella, Rheocricotopus, 'Eukiefferiella & Tvetenia, Parametriocnemus, Smittia/Pseudosmittia, Synorthocladius*), eurythermic groups (i.e., *Psectrocladius, Procladius*), and broad taxonomic categories (i.e., subtribe Tanytarsina, *Cricotopus/Orthocladius*), all of which are of relatively little value in assessing paleotemperature regimes.

Cabin Lake

The basal sediments (399 - 324 cm) of Cabin Lake consist of a dark grey clay with two distinct bands (369 - 364 cm, 357 - 355 cm) of very dark grey mixed organic/inorganic material which are graded coarse to fine. A relatively uniform dark brown to black gyttja was deposited above 324 cm. The remainder

Figure 4: Chironomid percentage diagram for Cabin Lake stratigraphy.

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3M Pond, Mount Stoyoma
Chironomid % Diagram

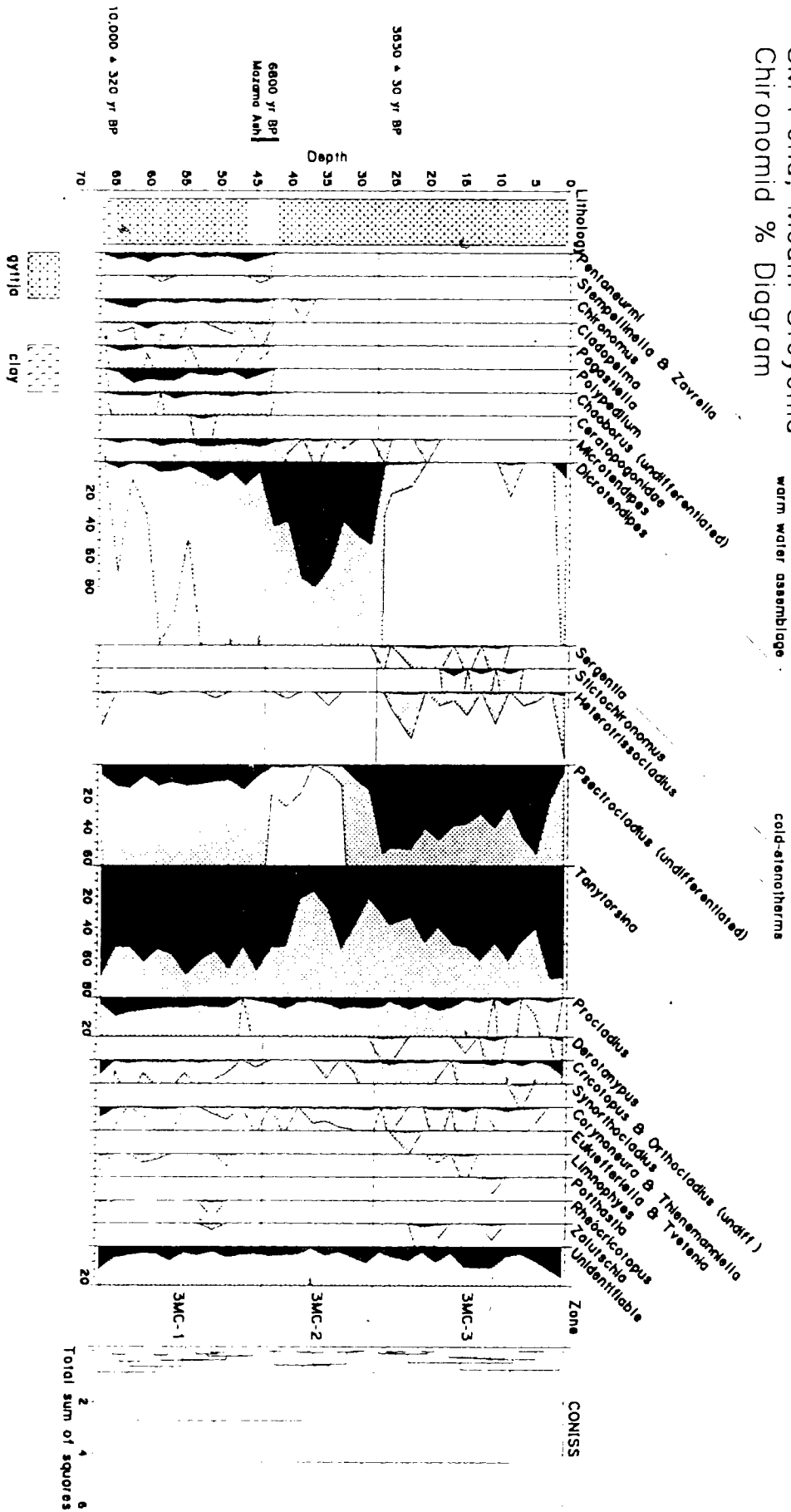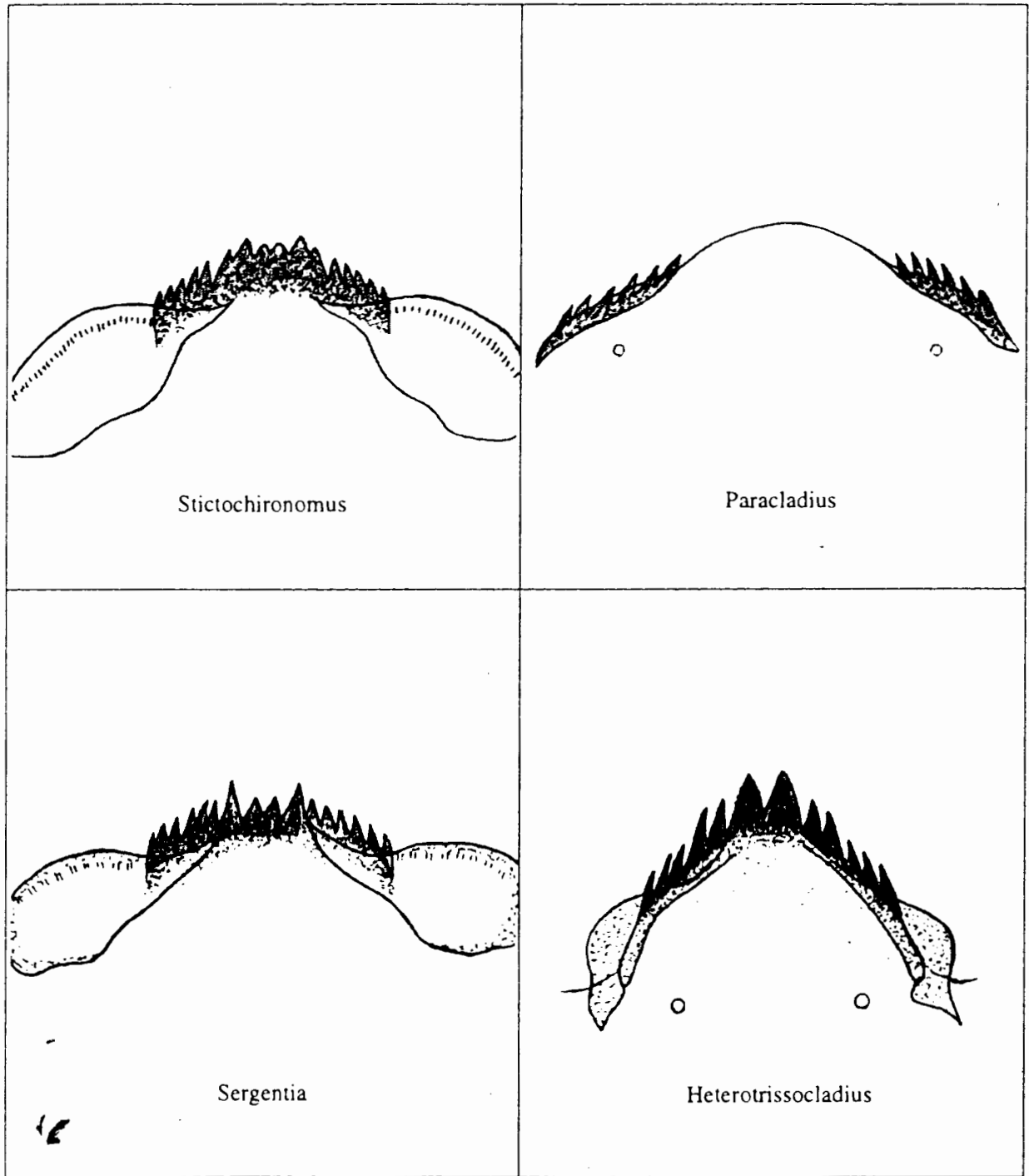Figure 5: Chironomid percentage diagram for 3M Pond stratigraphy.

Figure 6a: Mentum and ventromental plate characteristics of typical cold-stenothermic chironomid taxa found at Cabin Lake and /or 3M Pond (drawings adapted from Walker (1988)).
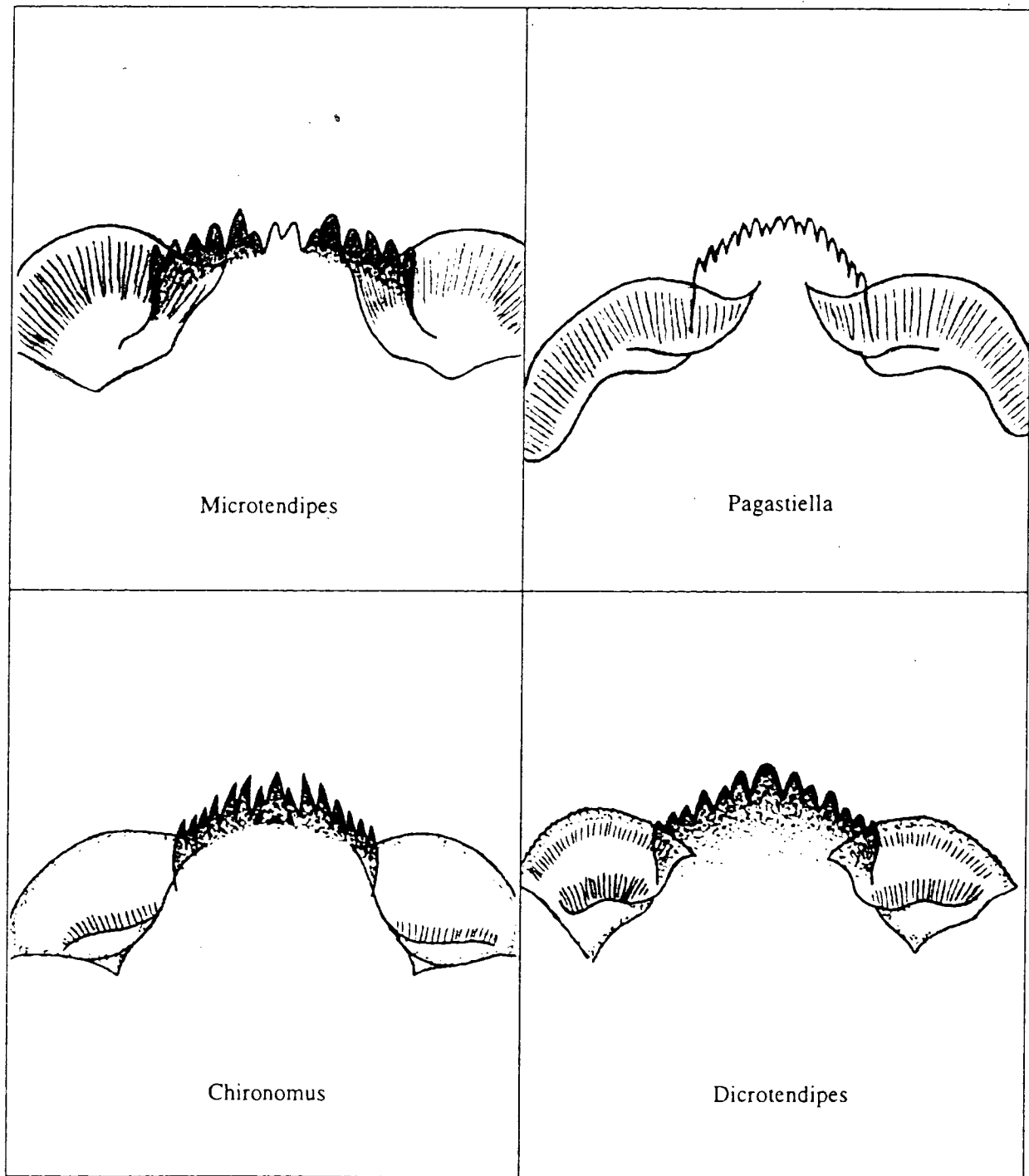
Figure 6b: Mentum and ventromental plate characteristics of typical warm water chironomid taxa found at Cabin Lake and 3M Pond (drawings adapted from Walker (1988)).

of the sediment profile consists of dark gyttja, with the exception of two tephras at 252.5 - 247 cm (identified as Mazama ash) and 90.5 - 89.5 cm (identified as Bridge River tephra).

A sample of carbonized wood at 306 cm was dated at 8910 ± 120 yr BP (Table 2). It should be noted that a previous core of the lake also provided a date of 9319 ± 120 yr BP a few centimetres above the clay/gyttja interface. Dates of pollen at 324 cm and leaf fragments at 368 - 370 cm (both within the clay) were 10,090 ± 70 and 9860 ± 60 yr BP, respectively. Therefore, it was assumed that the clay was deposited rapidly at the late-Pleistocene/Holocene boundary at ca. 10,000 yr BP. Mazama ash deposition has a widely accepted age of 6800 yr BP (Hebda, 1995), and the Bridge River tephra has been dated to 2410 yr BP (Clague et al., 1995).

The chironomid fossil record of Cabin Lake has been divided into four zones, determined by a constrained sum-of-squares cluster analysis (Grimm, 1987), which places boundaries where the greatest changes in chironomid community composition occur (Figure 4). Zone CC-1 (399 - 330 cm) represents late-Pleistocene sediments before ca. 10,000 yr BP near the clay/gyttja transition. Zone CC-2 (330 - 265 cm) encompasses the early Holocene, between ca. 10,000 yr BP and ca. 7220 yr BP. Zone CC-3 (265 - 112 cm) spans the mid-Holocene between ca. 7220 yr BP and ca. 3210 yr BP. The most recent

sediments make up zone CC-4 (112 - 0 cm), representing ca. 3210 yr BP to present.

Zone CC-1:

The late-glacial assemblage primarily consists of the widespread Tanytarsina group (up to 54%) and typical oligotrophic, cold-stenotherms (*Paracladius*, *Parakiefferiella nigra*, *Mesocricotopus*, *Stictochironomus*, *Protanypus*, and *Heterotrissocladius*), along with *Sergentia*, which characterizes cold, mesotrophic waters (Walker, 1990). An interesting feature of this zone is the brief peaks in the relative abundances of some typical warm-adapted chironomids (*Chironomus*, *Stempellinella* & *Zavrelia*, *Parakiefferiella* cf. *bathophila*, *Dicrotendipes*) and the *Dasyhela* type of ceratopogonid, which occur at the time of increased deposition of organic sediment prior to the Holocene.

The predatory *Procladius* also makes up a significant proportion of the late-glacial assemblage (up to 33%), and remains relatively abundant throughout the Holocene.

Zone CC-2:

The beginning of the Holocene is characterized by a sudden disappearance of most of the cold-stenotherms, with only *Heterotrissocladius* and *Sergentia* persisting as very small proportions of the faunal assemblage. In

conjunction with this trend, significant increases in the warm-adapted chironomids occur. Most notably, *Chironomus, Stempellinella & Zavrelia, Pagastiella, Microtendipes,* along with various *Chaoborus* species rapidly become major faunal elements in the early Holocene. The eurythermic Tanytarsina and *Procladius* approach their lowest levels in this zone, which may be a result of less production in these groups or simply because of a greater prevalence of other taxa. Unfortunately, sedimentation rates are not available and so influx rates could not be determined.

This zone also shows an increase in proportions of the rheophilous *Corynoneura/Thienemanniella* group, and the eurythermic *Psectrocladius* and *Corynocera*.

Zone CC-3:

Just prior to Mazama ash deposition, a major shift in fauna occurs. Although this mid-Holocene zone still supports a large warm-adapted group of chironomids, a notable reduction in *Stempellinella & Zavrelia* and *Pagastiella* is seen, and *Sergentia*, a cold-water genus, reaches significant proportions (up to 27%) of the community composition. *Heterotrissocladius* also reaches levels comparable to its late-glacial contribution.

Chironomus remains a dominant genus through this zone (up to 27%), with *Microtendipes* consistently making up approximately 5% of the community.

Other important warm-water taxa comprising this zone are *Dicrotendipes* and *Parakiefferiella* cf. *bathophila*, with *Chaoborus* mandibles reaching their greatest proportion.

Tanytarsina (37%) and *Procladius* (34%) again attain significant relative abundances in the mid-Holocene, and various rheophilous taxa continue to be consistently represented in small proportions.

Zone CC-4:

The most recent late Holocene sediments reveal a dramatic decrease in the relative contribution of warm water taxa as a group, with many genera becoming locally extinct and others reaching their minimum Holocene values. *Sergentia* remains relatively abundant, with *Heterotrissocladius* retaining its typical late-glacial abundance at the beginning and end of this interval. Possibly significant is the reappearance of *Paracladius*, a strongly cold-stenothermous taxon (Walker et al., in press), in the late Holocene fossil assemblage.

Procladius remains a dominant faunal element, whereas Tanytarsina reaches its maximum extent (61%), surpassing its late-glacial assemblage contribution. Rheophilous taxa continue to be deposited into the lake, although a slightly less diverse group is evident in the late Holocene.

3M Pond

The core taken from 3M Pond contains a uniformly grey basal clay from 65.5 - 73 cm. Above 65.5 cm, various shades of gyttja, ranging from black to olive grey to the green surface sediments, make up the remainder of the core. Mazama ash (6800 yr BP) was also present in the stratigraphy between 46 - 42 cm.

In addition to the dated tephra, two AMS radiocarbon dates were obtained for core chronology. Conifer needles found at the clay/gyttja interface (66 cm) produced a date of 10,000 ± 320 yr BP, corresponding with the late-Pleistocene/Holocene boundary, as expected. Similar needles were isolated from 24 - 26 cm (near major chironomid zone boundary), giving a date of 3530 ± 60 yr BP (Table 2).

Changes in chironomid communities in 3M Pond can also be divided into three Holocene zones (Figure 5), as in Cabin Lake. Rarity of head capsules in the clay prevented the extraction of information regarding the late-glacial at 3M Pond. Thus, zone 3MC-1 (66 - 44 cm) represents the early Holocene, from 10,000 yr BP to the time of Mazama ash deposition at 6800 yr BP. Zone 3MC-2 encompasses the mid-Holocene from 6800 yr BP to ca. 3950 yr BP at 27.5 cm. Zone 3MC-3 represents the late Holocene, spanning ca. 3950 yr BP to present.

Zone 3MC-1:

The early Holocene was dominated by Tanytarsina, making up approximately 60% of the faunal assemblage. The eurythermic *Psectrocladius* (7 - 16%) and *Procladius* (up to 12%) also significantly contribute to this assemblage. A distinct and diverse warm water assemblage is clearly evident, composed primarily of the tribe Pentaneurini, *Chironomus*, *Cladopelma*, *Polypedilum*, *Microtendipes*, *Dicrotendipes*, *Chaoborus*, and other minor components. Not surprisingly, a lack of cold-stenothermic chironomids is apparent, with only three *Heterotrissocladius* head capsules being found. A very minor allochthonous contribution is possible due to the presence of *Cricotopus/Orthocladius*, *Corynoneura/Thienemanniella*, *Limnophyes*, *Rheocricotopus*, and *Zalutschia*.

Zone 3MC-2:

Following Mazama ash deposition, a major shift in the faunal assemblage occured, with most of the warm-adapted taxa becoming locally extinct or reduced to a very minor component of the community. An exception to this trend is the rapid increase in the relative abundance of *Dicrotendipes* (up to 80%), also a typical temperate genus. A significant reduction in the relative abundances of Tanytarsina and *Psectrocladius* may be the result of decreased production or an artefact of the dominance of *Dicrotendipes*. Again, influx data are lacking, and

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so the cause of this change remains uncertain. The contributions of *Procladius*, *Cricotopus/Orthocladius*, and *Corynoneura/Thienemanniella* show little change from the early Holocene.

Zone 3MC-3:

Another major zone boundary is evident at 27.5 cm, when *Dicrotendipes* rapidly declines in relative abundance to near extinction. All other warm-adapted chironomids disappear, with the exception of *Microtendipes*, which persists for a short time as a very minor faunal element. Offsetting the disappearance of *Dicrotendipes* is the now abundant littoral *Psectrocladius* (up to 57%), which dominates the late Holocene along with Tanytarsina (32 - 72%).

The emergence of cold-stenotherms (*Heterotrissocladius*, *Stictochironomus*, *Sergentia*) in this zone is significant, as it represents their first appearance as a distinct community in the Holocene sediments.

Procladius, *Cricotopus/Orthocladius*, and *Corynoneura/Thienemanniella* remain relatively unchanged until the most recent sediments, and there again exists a minor rheophilous contribution, as in the early Holocene. The appearance of *Derotanypus* in the late Holocene freshwater assemblage is surprising, as this genus is common in saline waters.

DISCUSSION

Changes in chironomid assemblages through postglacial time could be the result of many different environmental influences, but at Cabin Lake and 3M Pond on Mount Stoyoma, these community shifts can be explained by direct or indirect climatic effects, which closely correspond to other Holocene paleoclimate reconstructions in southwestern British Columbia.

Cabin Lake

Zone CC-1:

The late-glacial midge assemblage clearly contains a significant cold-stenothermous community, including *Paracladius*, *Parakiefferiella nigra*, *Mesocricotopus*, *Stictochironomus*, *Protanypus*, *Heterotrissocladius*, and *Sergentia* (Figures 4 & 6a).

Paracladius is a characteristic genus in high arctic and alpine lakes (Walker, 1990; Walker et al., in press), and often is found in the cold profundal zone of large, deep, oligotrophic temperate lakes. This cold-stenotherm is largely absent from shallow ponds of arctic and alpine sites, where summer temperatures can be much higher than those of larger, deeper lakes nearby, and where winter anoxia can result from long winters and freezing of bottom waters (Walker & Mathewes, 1989b).

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Parakiefferiella nigra occurs widely in subarctic and arctic areas, as well as alpine and subalpine lakes (Walker, 1990; Walker & Mathewes, 1989b; Walker et al., 1992b), and in temperate latitudes is restricted to cold profundal zones of large, deep oligotrophic lakes (Walker et al., 1991a; Walker & MacDonald, 1995).

Mesocricotopus is typical of high arctic lakes and the larvae are normally found in oligotrophic to mesotrophic waters (Levesque et al., 1996; Walker et al., in press). Levesque et al. (1996) present the first positive identification of this genus in Canadian fossil assemblages.

Stictochironomus also has a low optimal temperature (Walker et al., in press) and is most commonly associated with arctic and alpine sites, as well as the deep, cold profundal waters of temperate lakes (Walker, 1990; Walker & Mathewes, 1989b; Walker & MacDonald, 1995), but may occur (different species?) in warmer mesotrophic waters (Sæther, 1979; Walker & Mathewes, 1989a).

Protanypus is similarly widely distributed in arctic and alpine lakes (Walker, 1990; Walker & Mathewes, 1989b), as well as in many deep, cold waters of temperate lakes (Walker & MacDonald, 1995).

The genus *Heterotrissocladius* has been identified as a common element of cold water assemblages (Walker & Mathewes, 1987a,b; Walker & Mathewes, 1989a,b,c). These midges are typical of arctic to subarctic and alpine to

subalpine waters (Walker & Mathewes, 1989b), and are common in the deep profundal regions of temperate lakes. In addition, *Heterotrissocladius* has been shown to be well represented in late-glacial chironomid assemblages from British Columbia, New Brunswick, Michigan and Germany (Walker & Mathewes, 1987a).

Sergentia is also a cold-stenotherm (Walker et al., in press), and is often found under the same temperature regimes as the above taxa. An important difference with respect to most other cold-stenothermic taxa is the occurrence of *Sergentia* in mesotrophic waters (Walker, 1990; Levesque et al., 1996). This genus contains hemoglobin and can thus tolerate moderate oxygen depletion due to the increased biological oxygen demand in moderately productive waters, or from winter anoxia in bottom-freezing shallow waters (Walker & Mathewes, 1989b; Walker et al., 1991a; Levesque et al., 1996).

This diverse cold-adapted assemblage, along with the rarity of typical temperate, warm water chironomids, provides evidence of a cold, late-glacial climate at this high elevation site. Alpine tundra conditions during late-glacial time are also indicated by the presence of subalpine/alpine herb pollen in these sediments (Pellatt, 1996).

Initially, the appearance of an interesting peak of warm-adapted midges between 340 cm and 370 cm, within the late-glacial cold community of Cabin Lake, suggested the possibility of a shift in temperature from cold to warm and

back to cold, possibly similar to the proposed Older Dryas-Allerød-Younger Dryas shifts which occurred in Europe (Wright, 1989), Atlantic Canada (Walker et al., 1991b; Wilson et al., 1993), and the Pacific Northwest of North America (Mathewes, 1993; Mathewes et al., 1993). Although this interval contains two distinct bands of very dark grey mixed organic/inorganic material within the basal clay, radiocarbon dating revealed little difference in ages between this interval and the clay/gyttja boundary at 330 cm (Table 2). Thus, at this time, a Younger Dryas-age event cannot be verified at this site. Higher resolution chironomid sampling and more dates at this radiocarbon plateau may shed more light on the nature of this apparent temperature shift.

Zone CC-2:

The beginning of the Holocene is accompanied a dramatic reduction of cold-stenotherms, as *Sergentia* and *Heterotrissocladius* become very rare, and other typical late-glacial taxa become locally extinct. The rapid diversification and dominance of warm water taxa in the early Holocene suggests a shift from late-glacial cold conditions to a warm climate, which persisted to ca. 7220 yr BP (Figure 4). Warmer water temperatures would inhibit cold-stenothermous taxa from completing their life cycles (Oliver, 1968, 1971; Danks & Oliver, 1972a,b), whereas the warm water taxa would utilize sufficiently high temperatures necessary for completion of their life cycles.

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Although it may appear that the decline of oligotrophic taxa and dominance of the eutrophic indicator *Chironomus* suggests a eutrophication process in the early Holocene, it should be recalled that Cabin Lake was shallow, probably with less than 7.5 m maximum depth at that time, and no indication of thermal stratification is evident in the sediment. Cabin Lake was likely very well mixed in the summer. Thus, it would be unwise to apply the lake typology system as discussed earlier to explain the chironomid community shift at the beginning of the Holocene. Kansanen and Aho (1981) and Hofmann (1978) explain that in unstratified lakes bottom temperatures can be high, and so the cold-stenothermal deep-water species, which are usually important components of the oligotrophic fauna, may be absent in shallow, oligotrophic lakes, not because of eutrophy and its associated summer bottom oxygen depletion (Hofmann, 1986, 1988; Walker, 1987), but simply due to high temperatures.

Hofmann (1983, 1986) notes that during late-glacial cold conditions, the cold-stenothermic community common in oligotrophic waters may have occurred in the littoral zone, as is observed in arctic and subarctic lakes, and so would not reflect trophic state or oxygen conditions in deeper waters.

A community dominated by *Chironomus* usually suggests eutrophic conditions, but a study of chironomids in Lake Mallasvesi, Finland, challenges this generalization (Kansanen et al., 1984). Lake Mallasvesi is oligotrophic to

mesotrophic and irregularly stratified, with high hypolimnetic temperatures in both summer and winter. Thus, rather than indicating trophic state, the *Chironomus* community reflects climatic conditions, either directly through temperature effects on the larvae, or indirectly as high temperatures would cause increased oxygen consumption and lead to decreased oxygen concentration in deep waters (Kansanen et al., 1984).

Pellatt's (1996) vegetation analysis of Cabin Lake postglacial sediments reveals total pollen concentrations at their highest in the early Holocene. High extra-local or regional transport of diploxylon pine and *Alnus viridis* pollen suggest that open/dry conditions existed around Cabin Lake in the early Holocene. Relatively high values of *Picea*, haploxylon pine, *Artemisia*, and Poaceae pollen support this hypothesis (Pellatt, 1996). Thus, agreement of the paleoclimate reconstruction (with respect to temperature) using fossil vegetation and chironomid community composition is consistent with coastal British Columbia's early Holocene xerothermic period (Mathewes, 1973, 1985; Mathewes & Heusser, 1981; Hebda, 1995).

Zone CC-3:

The chironomid zone encompassing the mid-Holocene (ca. 7220 yr BP to ca. 3210 yr BP) supports a well defined warm water chironomid community, although there is a significant decrease in the relative abundances of

Stempellinella/Zavrelia and *Pagastiella* (Figure 4). The contemporaneous presence of the cold-stenotherm *Sergentia* appears to be contradictory to the diverse warm-adapted community in the shallow, unstratified lake.

In considering temperature requirements alone, it appears that the reduction in some warm water taxa and prominence of *Sergentia* (and to a small extent *Heterotrissocladius*) suggests cooling following the early Holocene (Zone CC-2), but warmer than present. The most probable explanation for the apparently discrepant coexistence of cold and warm water taxa centers on the fact that Cabin Lake is shallow and situated at a high elevation. Walker and Mathewes (1989b) compare taxa common in lakes versus shallow ponds of the arctic and high elevations. Cold-stenotherms such as those prevalent in Cabin Lake's late-glacial sediments are typical of the deeper basins, whereas a completely different community is found in shallow ponds, including *Chironomus, Cricotopus/Orthocladius, Procladius, Psectrocladius*, Tanytarsini, and *Sergentia* (note these taxa throughout zone CC-3). In these shallow waters, bottom freezing in the winter often leads to anoxia (Walker, 1987; Walker & Mathewes, 1989b; Walker et al., 1991a), which would exclude cold-stenotherms that require the high oxygen concentrations found in oligotrophic waters. *Sergentia*, in contrast, thrives in cold waters with moderate oxygen depletion (Walker, 1990). Timing of development also is important in explaining the coexistence of both cold and warm water taxa, as cold-adapted taxa grow most

predominantly and quickly in winter, whereas warm-adapted chironomids grow more rapidly through the summer (Oliver, 1971; Walker, 1987). Therefore, the different developmental timing patterns can allow *Sergentia* and the various warm water taxa to inhabit Cabin Lake in any given year.

Another climatic factor which could contribute to winter anoxia in Cabin Lake during the mid-Holocene is increased precipitation. Although not discernible from the chironomid assemblage directly, more precipitation would produce greater snow pack on the lake and lead to longer winter conditions, as the time required for the snow to melt would be extended and anoxic conditions would persist for a longer period. A small but more diverse assemblage of rheophilous taxa in this zone may suggest increased precipitation, as a greater volume of melting snow from higher elevations could carry more stream taxa into Cabin Lake.

The presence of pollen types indicative of relatively wet conditions (i.e., *Abies*, Cyperaceae, Ericales) reveal that conditions were wetter during the mid-Holocene than in the late-glacial or early Holocene at Cabin Lake (Pellatt, 1996). In addition, high pollen concentrations and low spruce/pine ratios indicate a climate warmer than present, while an increase in some subalpine taxa suggests a decrease in temperature with respect to the early Holocene (Pellatt, 1996). Therefore, the chironomids and vegetation at Cabin Lake both

indicate a climate that corresponds with the mesothermic period noted in southwestern British Columbia (Hebda, 1995).

Pellatt (1996) distinguishes a second pollen zone in the more recent sediments of chironomid zone CC-3, as typical subalpine vegetation becomes established and further decrease in temperature is inferred. This continued cooling of the latter part of the mid-Holocene is not as obvious in the chironomid stratigraphy, although the cold-stenotherm *Heterotrissocladius* becomes more abundant and the relative contribution of *Chironomus* declines. As Pellatt (1996) suggests, the mid-Holocene may have been a time of continued gradual cooling rather than a stable temperature state, and this is evident from the chironomid profile although further zones are not as distinct. Higher resolution chironomid sampling may have better illustrated this subtle trend.

Zone CC-4:

The late Holocene (ca. 3210 yr BP to present) brought a further reduction in the relative abundances of the warm water taxa, as many genera become locally extinct and others reach their lowest Holocene values (Figure 4). Conversely, the cold-stenothermous *Sergentia* and *Heterotrissocladius* essentially retain their mid-Holocene community contributions, and *Paracladius*, although rare, appears again for the first time since the late glacial.

This significant change in the chironomid assemblage suggests further cooling in the late Holocene, and is consistent in timing to glacial advances in the Canadian Rocky Mountains, Coast Mountains, and northern Cascade Mountains (Porter & Denton, 1967; Ryder & Thomson, 1986; Luckman et al., 1993).

Although the late Holocene appears to represent a discrete climate state based on chironomid temperature inferences, Pellatt (1996) further subdivides this period based on vegetation changes.

3M Pond

Zone 3MC-1:

The first chironomid assemblage zone in 3M Pond sediments corresponds to the early Holocene (ca. 10,000 to 6800 yr BP), since a late-glacial community was not found (Figure 5). The most prominent feature of the early Holocene with respect to paleoclimatic reconstruction is the diverse warm water midge community and absence of cold-stenotherms. Clearly, the water of 3M Pond was quite warm to support this assemblage. With a maximum depth of less than 1.7 m during this time, the shallow waters would warm very quickly after the snow and ice melt, and likely attain sufficiently high temperatures to exclude cold water taxa (Hofmann, 1983; Kansanen & Aho, 1981; Kansanen, 1985; Walker & Paterson, 1983).

Pollen and plant macrofossil analyses of early Holocene sediments indicate relatively dry conditions, but indicators of warm temperatures, other than high pollen concentrations, are lacking (Pellatt, 1996). Taken together, palynological and chironomid evidence suggest that the early Holocene was warm and dry from 10,000 yr BP until the the time of Mazama ash deposition, coinciding with the observed xerothermic in coastal British Columbia (Mathewes, 1985; Hebda, 1995) and the southern interior of British Columbia (Mathewes & King, 1989; Hebda, 1995).

Zone 3MC-2:

The dramatic shift in chironomid community composition following Mazama ash deposition involves the local extinction of most warm water taxa, with the exception of the rapid and substantial increase in relative abundance of the warm-adapted *Dicrotendipes* (Figure 5). This major change does not include the appearance of cold-stenothermous taxa, but the decreased diversity, especially involving warm water chironomids, may indicate cooling.

Hoffman et al. (1996) have shown that the number of nearshore macroinvertebrate taxa is positively correlated to water temperature and inversely related to elevation in lakes of Washington's North Cascades National Park Service Complex. Low elevation forest lakes were found to have the

highest number of taxa and highest maximum lake temperatures, whereas alpine sites had lowest number of taxa and lowest maximum temperatures.

Walker and Mathewes (1989b) indicate that a decrease in chironomid diversity with increasing elevation in coastal British Columbia may reflect a relationship between diversity and temperature, although they warn against uncautious interpretations based on assemblage diversity alone. Smol (1981) suggests great care in making paleoecological interpretations of diversity measures, preferring that interpretations be based on the ecology of specific taxa. Recall that in the case of 3M Pond, the loss of diversity involves warm water taxa specifically.

Thorp and Chesser (1983), in their study of larval midges in a cooling reservoir in South Carolina, show that water temperature was the environmental factor most strongly associated with changes in chironomid assemblage diversity, with a significant relationship between diversity and average and maximum water temperatures. More recently, Levesque et al. (1996) found that both chironomid species richness and diversity were lowest during the coldest parts of the late-glacial (following deglaciation and during the Younger Dryas) in four New Brunswick lakes, whereas during the warmer periods richness and diversity were higher.

Consistent with this interpretation, Pellatt (1996) infers mid-Holocene temperatures as warmer than present from plant macrofossils and high levels of

local conifer pollen, but cooler than in the early Holocene. Thus, the chironomid and vegetation compositions within this zone correspond well with Hebda's (1995) mesothermic period.

The reason for the dominance of *Dicrotendipes* over the other warm water taxa is not clear. The majority of this genus' larvae are found on the surface of aquatic vegetation, and among vegetation on rocks, logs, or similar substrata (Epler, 1988). The larvae also feed on a great variety of organic substrates, from coarse to fine detrital particles, to algae and vascular plants (Coffman, 1984). A possible explanation for the success of *Dicrotendipes* after the deposition of Mazama ash may concern habitat and food choices. The accumulation of volcanic ash in the shallow basin of 3M Pond could have greatly disturbed most habitats in which chironomid larvae were living, but *Dicrotendipes* was relatively less affected than the other taxa at this time. This may have been due to the flexibility of food types and the ability of the larvae to live on the large surface area of vegetation rather than directly on the sediment surface.

Tokeshi (1995) reports that for epiphytic species in one study, the time to reach 95% of the mean natural density after complete denudation of a macrophyte habitat was less than two weeks, and Davies (1976) reviews that in Volta Lake, the Chironomidae, and specifically *Dicrotendipes*, dominated the colonization of new substrates within 25 days.

Although 3M Pond did not support a large macrophyte community throughout the Holocene, Pellatt (1996) found that the number of *Carex* seeds increased at approximately 6800 yr BP, with a complimentary increase in Cyperaceae (sedge) pollen percentages at this time. Sedges would have been growing on the margins of 3M Pond, and it is likely that many plants were partly submerged. If this was the case, the larvae of *Dicrotendipes* would have had the habitat availability necessary to be relatively less affected by disruption as a result of Mazama ash deposition. An expanded knowledge of the ecology of each chironomid species is necessary to support this type of interpretation of community changes.

Zone 3MC-3:

The main shift in chironomid assemblages between the middle and late Holocene occurred at 28 cm in the core (ca. 3950 yr BP) (Figure 5). This change involved the dramatic reduction in *Dicrotendipes* relative abundance, which was replaced primarily by the eurythermic *Psectrocladius*. Thus, the late Holocene assemblage contained few warm water taxa, with *Dicrotendipes* and *Microtendipes* persisting very rarely and sporadically. Accompanying this trend is the appearance of a cold-stenothermic community which includes *Sergentia*, *Stictochironomus*, and *Heterotrissocladius*. Although the cold-stenotherms are not a dominant group in terms of the community as a whole, their presence,

55

along with the disappearance of warm-adapted taxa, indicates cooling in the late Holocene.

The timing of this shift in the community coincides, as at Cabin Lake, with the timing of glacial advances in northwestern North America (Porter & Denton, 1967; Ryder & Thomson, 1986). As the climate cooled at 3M Pond, water temperatures would have decreased, causing the exclusion of chironomid larvae with high temperature optima and tolerances, attaining cool enough summer temperatures to support cold-stenothermal taxa. This correlates well with the cool, modern subalpine conditions indicated by decreased needle abundance and diversity, and decreased local pollen productivity at the site after ca. 3530 yr BP (Pellatt, 1996).

CONCLUSIONS

In viewing the changes in chironomid assemblages and vegetation at both Cabin Lake and 3M Pond since the late-glacial, a clear correlation in the timing of these shifts becomes apparent (Figure 7).

The late-glacial cold-stenothermal chironomid community found in the Cabin Lake basal sediments, along with the rarity of temperate taxa, indicates cold conditions before ca. 10,000 yr BP. After this time, diverse warm water chironomid assemblages comprise a significant proportion of the communities at Cabin Lake and 3M Pond, corresponding to the warm early Holocene

Cabin Lake

3M Pond

| midges | pollen | | midges | pollen | macros |

¹⁴C
yr BP

0
1000
2000
3000
4000
5000
6000
7000
8000
9000
10,000

Cabin Lake:
midges column: CC-4, — 3210 —, CC-3, — 7220 —, CC-2, ~10.000, CC-1
pollen column: CP-5, CP-4b, — 2410 —, CP-4a, — 4800 —, CP-3, — 7000 —, CP-2, — 9320 —, CP-1

3M Pond:
midges column: 3MC-3, — 3950 —, 3MC-2, — 6800 —, 3MC-1, ~10.000, no data
pollen column: 3MP-4, — 2870 —, 3MP-3, — 6800 —, 3MP-2, ~10.000, 3MP-1
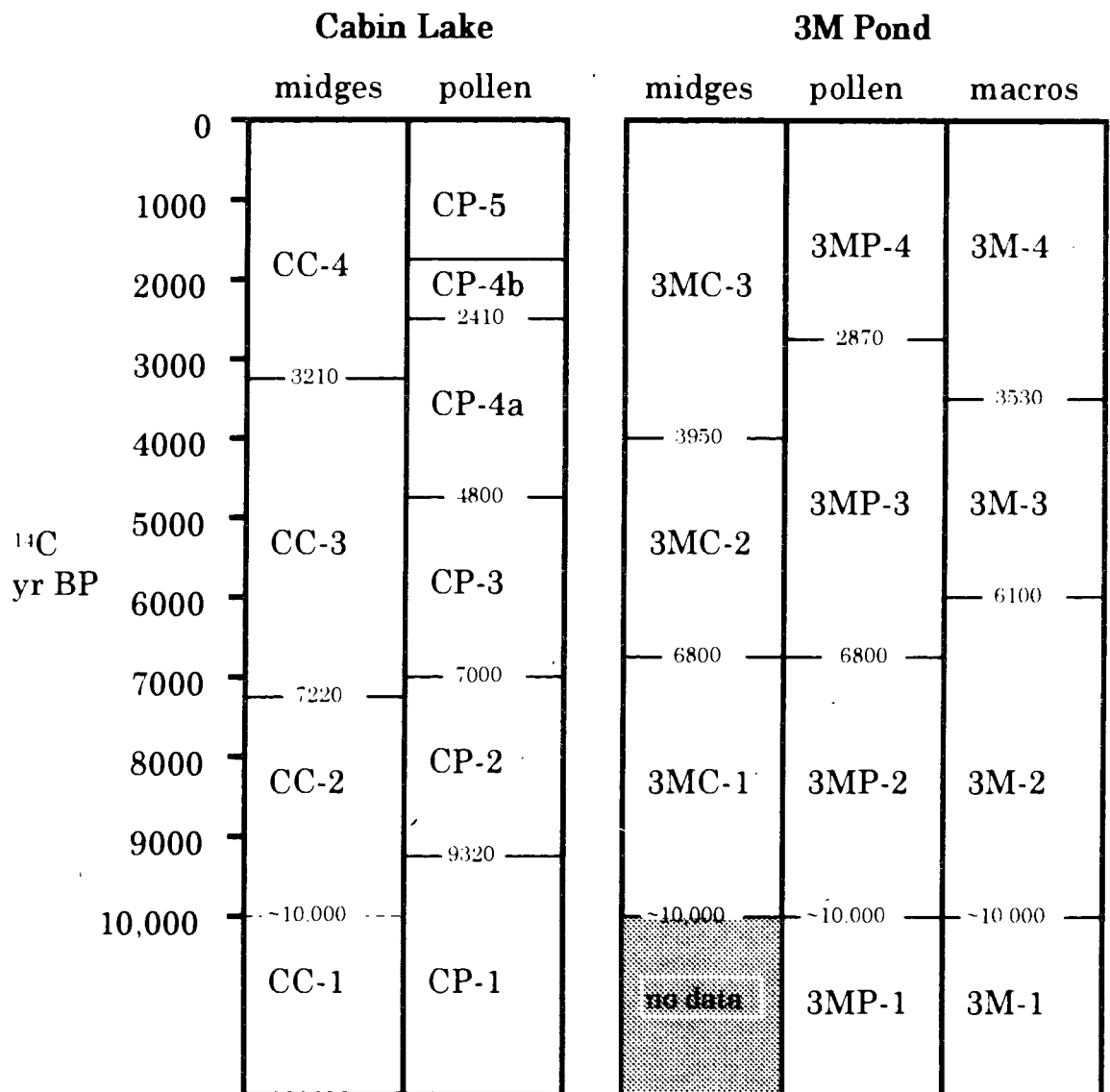macros column: 3M-4, — 3530 —, 3M-3, — 6100 —, 3M-2, ~10 000, 3M-1

Figure 7: Comparison in timing of zone changes for chironomids
and vegetation at Cabin Lake and 3M Pond.

Note: Approximate dates of zone boundaries were interpolated
through regression analysis (Grimm, 1993).

xerothermic period (Mathewes, 1985). Palynological evidence from Cabin Lake (Pellatt, 1996) suggests that this shift from late-glacial cold to early Holocene warm (and dry) conditions lagged behind the midge response by approximately 700 years (ca. 9320 yr BP). Pollen and macrofossil changes at 3M Pond occur at ca. 10,000 yr BP, suggesting a climate-related vegetation change at the more sensitive higher elevation site about 700 years prior to the lower elevation site.

The early Holocene xerothermic period persisted to ca. 7220 yr BP at Cabin Lake, at which time cooling is indicated by an increase in cold-stenotherms and a reduction in temperate midge taxa. At 3M Pond, the major decrease in relative abundance of warm-adapted chironomids occurred slightly later, at ca. 6800 yr BP. Evidence from pollen indicates local vegetation changes corresponding primarily to increasing moisture at ca. 6800 yr BP at 3M Pond and ca. 7000 yr BP at Cabin Lake (Pellatt, 1996). The midge-inferred cooling and vegetation changes indicative of increasing moisture closely correspond to the timing of the mesothermic period found in coastal and southwestern interior British Columbia sites (Hebda, 1995).

The termination of the mesothermic appears to be somewhat time-transgressive. Earliest indications of possible slight cooling are found in the Cabin Lake pollen assemblage at ca. 4800 yr BP, although a more dramatic drop in temperature is evident at ca. 2410 yr BP (Pellatt, 1996). Chironomid evidence suggests increasing cooling at ca. 3210 yr BP at Cabin Lake, and slightly earlier

at ca. 3950 yr BP at 3M Pond. Vegetation response lagged behind chironomid response at 3M Pond , where shifts in pollen at ca. 2870 yr BP and plant macrofossils at ca. 3530 yr BP indicate decreasing temperatures (Pellatt, 1996).

The timing of the mesothermic period's termination at Cabin Lake and 3M Pond coincides with Neoglacial advances. The Tiedemann advances on the Coast Mountains of British Columbia have been dated at approximately 3345 yr BP to 1300 yr BP (Ryder and Thomson, 1986), while the Burroughs Mountain Stade moraines of the Cascade Range were built ca. 3500 yr BP (Porter and Denton, 1967). In the Rocky Mountains, the Peyto, Robson, Yoho and Saskatchewan glaciers advanced between ca. 3300 yr BP and 2800 yr BP (Luckman et al., 1993). Earlier indications of cooling have been outlined for the Rockies at ca. 5000 yr BP (Luckman et al., 1993), the Coast Mountains at ca. 6000 yr BP (Garibaldi phase; Ryder and Thomson, 1986), and the Southern Cascade Glacier of the northern Cascade Mountains at ca. 4700 yr BP (Porter and Denton, 1967).

As Porter and Denton (1967) and Ryder and Thomson (1986) point out, the transition from relatively warm conditions of the early to mid Holocene to cooler and moister conditions was prolonged up to 2000 years, and the timing of the start of glacial advances varied regionally. Therefore, although the mesothermic period in southwestern British Columbia indicates wetter and slightly cooler conditions than the early Holocene xerothermic, its timing of

termination with Neoglaciation cannot be generalized throughout this entire region.

In summary, this study has shown that the Chironomidae are valuable in paleoclimatic reconstructions at sensitive high elevation sites, and that response times of midge communities to temperature changes are generally shorter than that of vegetation, as would be expected by the mobility and much shorter life cycles of chironomids. Similarities in the timing of vegetation and chironomid community changes on Mount Stoyoma, and their correlation with inferred climate shifts at other southwestern interior and coastal British Columbia sites clearly illustrate that shallow lakes at elevational treeline ecotone boundaries are very useful areas for future paleoclimatic studies involving chironomid-inferred temperature changes.

REFERENCES

Alley, N.F. 1976. The palynology and palaeoclimatic significance of a dated core of Holocene peat, Okanagan Valley, southern British Columbia. *Canadian Journal of Earth Sciences*, 13: 1131 - 1144.

Arno, S.F. and R.P. Hammerly. 1984. *Timberline - Mountain and Arctic Forest Frontiers.* The Mountaineers, Seattle.

Bradley, R.S. 1985. *Quaternary Paleoclimatology.* Allen and Unwin Inc., London.

Brinkhurst, R.D. 1974. The Benthos of Lakes. MacMillan Press, London.

Brundin, L. 1949. Chironomiden und andere Bodentiere der Südschweden Urgebirseen. *Report of the Institute of Freshwater Research, Drottningholm*, 30: 32 - 44.

Brundin, L. 1956. Die bodenfaunistischen Seetypen und ihre Andwendbarkheit auf die Südhalkugel. Zugleich ein Theorie der produktionbiologischen Bedeutung der glazialen Erosion. *Report of the Institute of Freshwater Research, Drottningholm*, 37: 186 - 235.

Brundin, L. 1958. The bottom faunistical lake type system and its application to the southern hemisphere. Moreover a theory of glacial erosion as a factor of productivity in lakes and oceans. *Verhandlungen der internationalen Vereingung theoretische und angewandte Limnologie*, 13: 288 - 297.

Cannings, R.A. 1975. A new species of *Chironomus* (Diptera: Chironomidae) from saline lakes in British Columbia. *Canadian Entomologist*, 107: 447 - 450.

Cannings, R.A. and G.G.E. Scudder. 1978a. Phenology of *Chironomus* spp. in saline lakes of central British Columbia. *Verhandlungen der Internationalen Vereinigung theoretische und angewandte Limnologie*, 20: 2641 - 2646.

Cannings, R.A. and G.G.E. Scudder. 1978b. The littoral Chironomidae (Diptera) of saline lakes in central British Columbia. *Canadian Journal of Zoology*, 56: 1144 - 1155.

Cawker, K.B. 1983. Fire history and grassland vegetation change: three pollen diagrams from southern British Columbia. *Canadian Journal of Botany,* 61: 1126 - 1139.

Clague, J.J. 1981. Late-Quaternary geology and geochronology of British Columbia: Part 2: Summary and discussion of radiocarbon-dated Quaternary history. *Geological Survey of Canada Paper,* 80-35: 1 - 41.

Clague, J.J., S.G. Evans, V.N. Rampton, and G.J. Woodsworth. 1995. Improved age estimates for the White River and Bridge River tephras, western Canada. *Canadian Journal of Earth Sciences,* 32: 1172 - 1179.

Clague, J.J. and R.W. Mathewes. 1989. Early Holocene thermal maximum in western North America: new evidence from Castle Peak, British Columbia. *Geology,* 17: 277-280.

Clague, J.J., R.W. Mathewes, W.M. Buhay, and T.W.D. Edwards. 1992. Early Holocene climate at Castle Peak, southern Coast Mountains, British Columbia, Canada. *Palaeogeography, Palaeoclimatology, Palaeoecology,* 95: 153 -167.

Coffman, W.P. 1984. Chironomidae, In: *An introduction to the Aquatic Insects of North America,* 2nd ed. (eds. R.W. Merritt & K.W. Cummins). Kendall/Hunt, Dubuque, pp. 551 - 652.

COHMAP members. 1988. Climatic changes of the last 18 000 years: observations and model simulations. *Science,* 241: 1043-1052.

Cwynar, L.C. and A.J. Levesque. 1995. Chironomid evidence for late-glacial climatic reversals in Maine. *Quaternary Research,* 43: 405 - 413.

Danks, H.V. 1971. Overwintering of some north temperate and arctic Chironomidae: II. Chironomid biology. *Canadian Entomologist,* 103: 1875 - 1910.

Danks, H.V. and D.R. Oliver. 1972a. Seasonal emergence of some high arctic Chironomidae (Diptera). *Canadian Entomologist,* 104: 661 - 686.

Danks, H.V. and D.R. Oliver. 1972b. Diel periodicities of emergence of some high arctic Chironomidae (Diptera). *Canadian Entomologist,* 104: 903 - 916.

Davies, B.R. 1976. The dispersal of Chironomidae larvae: A review. *Journal of the Entomological Society of South Africa*, 39: 39 - 62.

Delcourt, H.R. and P.A. Delcourt. 1991. *Quaternary Ecology - A Paleoecological Perspective*. Chapman and Hall, London. pp. 193-203.

Devai, G. and J. Moldovan. 1983. An attempt to trace eutrophication in a shallow lake (Balaton, Hungary) using chironomids. *Hydrobiologia*, 103: 169 - 175.

Epler, J.H. 1988. Biosystematics of the genus *Dicrotendipes* Kieffer, 1913 (Diptera: Chironomidae: Chironominae) of the world. *Memoirs of the American Entomological Society*, 36: 1 - 214.

Frey, D.G. 1976. Interpretation of Quaternary paleoecology of Cladocera and midges, and prognosis regarding usability of other organisms. *Canadian Journal of Zoology*, 54: 2208-2226.

Fritz, S.C. 1990. Twentieth-century salinity and water level fluctuations in Devils Lake, North Dakota: test of a diatom-based transfer function. *Limnology and Oceanography*, 35: 1771 - 1781.

Grimm, E.C. 1987. CONISS: a FORTRAN 77 program for stratigraphically constrained cluster analysis by the method of incremental sum of squares. *Computers and Geoscience*, 13: 13 - 35.

Grimm, E.C. 1991. *Tiliagraph 1.7* (computer software). Illinois State Museum, Research and Collections Center, Springfield, Il.

Grimm, E.C. 1993. *Tilia 2.0* (computer software). Illinois State Museum, Research and Collections Center, Springfield, Il.

Hann, B.J., B.G. Warner and W.F. Warwick. 1992. Aquatic invertebrates and climate change: a comment on Walker et al. (1991). *Canadian Journal of Fisheries and Aquatic Sciences*, 49: 1274 - 1276.

Hebda, R.J. 1995. British Columbia vegetation and climate history with focus on 6 ka BP. *Geographie physique et Quaternaire*, 49: 55 - 79.

Heinrichs, M.L. 1995. *Chironomid-based paleosalinity reconstruction of three lakes in the south-central interior of British Columbia, Canada.* Msc. Thesis, Simon Fraser University, Burnaby, British Columbia, Canada. 58p.

Hershey, A.E. 1985. Littoral chironomid communities in an arctic Alaskan lake. *Holarctic Ecology,* 8: 39 - 48.

Heusser, L.E. 1983. Palynology and paleoecology of postglacial sediments in an anoxic basin, Saanich Inlet British Columbia. *Canadian Journal of Earth Sciences,* 20: 873 - 885.

Hoffman, R.L., W.J. Liss, G.L. Larson, E.K. Deimling, and G.A. Lomnicky. 1996. Distribution of nearshore macroinvertebrates in lakes of the Northern Cascade Mountains, Washington, USA. *Archiv für Hydrobiologie,* 136: 363 - 389.

Hofmann, W. 1978. Analysis of animal microfossils from the Großer Segeberger See (F.R.G.). *Archiv für Hydrobiologie,* 82: 316 - 346.

Hofmann, W. 1983. Stratigraphy of Cladocera and Chironomidae in a core from a shallow North German lake. *Hydrobiologia,* 103: 235 - 239.

Hofmann, W. 1986. Chironomid analysis. In: Berglund, B.E. (Ed.), *Handbook of Holocene Palaeoecology and Palaeohydrology.* John Wiley & Sons Ltd., Chichester. pp. 715 - 727.

Hofmann, W. 1987. Stratigraphy of Cladocera (Crustacea) and Chironomidae (Insecta: Diptera) in three sediment cores from the central Baltic Sea as related to paleo-salinity. *Internationale Revue der gesamten Hydrobiologie,* 72: 97 - 106.

Hofmann, W. 1988. The significance of chironomid analysis (Insecta: Diptera) for paleolimnological research. *Palaeogeography, Palaeoclimatology, Palaeoecology,* 62: 501 - 509.

Holland, S.S. 1976. *Landforms of British Columbia: A Physiographic Outline.* Bulletin 48, British Columbia Department of Mines and Petroleum Resources, Victoria.

Huggett, R.J. 1991. *Climate, Earth Processes, and Earth History.* Springer-Verlag, Berlin. pp. 4-9.

Kansanen, P.H. 1985. Assessment of pollution history from recent sediments in Lake Vanajavesi, southern Finland. II. Changes in the Chironomidae, Chaoboridae and Ceratopogonidae (Diptera) fauna. *Annales Zoologici Fennici*, 22: 57 - 90.

Kanasnen, P.H. and J. Aho. 1981. Changes in the macrozoobenthos associations of polluted Lake Vanajavesi, Southern Finland, over a period of 50 years. *Annales Zoologici Fennici*, 18: 73 - 101.

Kansanen, P.H., J. Aho and L. Paasivirta. 1984. Testing the benthic lake type concept based on chironomid associations in some Finnish lakes using multivariate statistical methods. *Annales Zoologici Fennici*, 21: 55 - 76.

Kureck, A. 1979. Two circadian eclosion times in *Chironomus thummi* (Diptera), alternately selected with different temperatures. *Oecologia*. 40: 311 - 323.

Levesque, A.J., F.E. Mayle, I.R. Walker and L.C. Cwynar. 1993a. A previously unrecognized late-glacial cold event in eastern North America. *Nature*. 361: 623 - 626.

Levesque, A.J., F.E. Mayle, I.R. Walker and L.C. Cwynar. 1993b. The Amphi-Atlantic Oscillation: A proposed late-glacial climatic event. *Quaternary Science Reviews*, 12: 629 - 643.

Levesque, A.J., L.C. Cwynar and I.R. Walker. 1994. A multiproxy investigation of late-glacial climate and vegetation change at Pine Ridge Pond, southwest New Brunswick, Canada. *Quaternary Research*, 42: 316 - 327.

Levesque, A.J., L.C. Cwynar and I.R. Walker. 1996. Richness, diversity and succession of late-glacial chironomid assemblages in New Brunswick, Canada. *Journal of Paleolimnology*, 16: 257 - 274.

Lloyd, D., K. Angrove, G. Hope and C. Thompson. 1990. *A Guide to Site Identification for the Kamloops Forest Region*. British Columbia Ministry of Forests, Victoria.

Luckman, B.H., G. Holdsworth and G.D. Osborn. 1993. Neoglacial glacier fluctuations in the Canadian Rockies. *Quaternary Research*, 39: 144 - 153.

Luckman, B.H. and M.S. Kearney. 1986. Reconstruction of Holocene changes in alpine vegetation and climate in the Maligne Range, Jasper National Park, Alberta. *Quaternary Research*, 26: 244 - 261.

Lyons, C.P. 1965. *Trees, Shrubs and Flowers to Know in British Columbia*. J.M. Dent & Sons (Canada) Ltd, Vancouver.

Mackey, A.P. 1977. Growth and development of larval Chironomidae. *Oikos*, 28: 270 - 275.

Mathewes, R.W. 1973. A palynological study of postglacial vegetation change in the University Research Forest, southwestern British Columbia. *Canadian Journal of Botany*, 51: 2085 - 2103.

Mathewes, R.W. 1985. Paleobotanical evidence for climatic change in southern British Columbia during late-glacial and Holocene time, In: C.R. Harington, ed., *Climate Change in Canada 5: Critical Periods in the Quaternary Climatic History of Northwestern North America*. Syllogeus 55. pp.397 - 422.

Mathewes, R.W. 1993. Evidence for Younger Dryas-age cooling on the north Pacific coast of America. *Quaternary Science Reviews*, 12: 321-331.

Mathewes, R.W. and L.E. Heusser. 1981. A 12,000-year palynological record of temperature and precipitation trends in southwestern British Columbia. *Canadian Journal of Botany*, 59: 707 - 710.

Mathewes, R.W., L.E. Heusser, and R.T. Patterson. 1993. Evidence for a Younger Dryas-age cooling event on the British Columbia coast. *Geology*, 21: 101 - 104.

Mathewes, R.W. and M. King. 1989. Holocene vegetation, climate, and lake level changes in the Interior Douglas-Fir Zone, British Columbia. *Canadian Journal of Earth Sciences*, 26: 1811-1825.

Mathewes, R.W. and G.E. Rouse. 1975. Palynology and paleoecology of early postglacial sediments from the lower Fraser River Canyon of British Columbia. *Canadian Journal of Earth Sciences*, 12: 745 - 756.

Mees, F., D. Verschuren, R. Nijs and H. Dumont. 1991. Holocene evolution of the crater lake at Malha, Northwest Sudan. *Journal of Paleolimnology*, 5: 227 - 253.

Mehringer, P.J., Jr. 1985. Late-Quaternary pollen records from the interior Pacific Northwest and northern Great Basin of the United States, In: V.M. Bryant & R.G. Holloway, eds., *Pollen Records of Late-Quaternary North American Sediments*. American Association of Stratigraphic Palynologists Foundation, Dallas. pp. 167 - 189.

Merilainen, J.J. and V. Hamina. 1993. Recent environmental history of a large originally oligotrophic lake in Finland: a palaeolimnological study of chironomid remains. *Journal of Paleolimnology*, 9: 129 - 140.

Mitchell, W.R. and R.E. Green. 1981. *Identification and Interpretation of Ecosystems of the Western Kamloops Forest Region: Volume II: Dry and Subcontinental Climatic Regions*. British Columbia Ministry of Forests, Victoria.

Mott, R.J., D.R. Grant, R. Stea, and S. Occhietti. 1986. Late-glacial climatic oscillation in Atlantic Canada equivalent to the Allerod/Younger Dryas event. *Nature*, 323: 247-250.

Nordlie, K.J. and J.W. Arthur. 1981. Effect of elevated water temperature on insect emergence in outdoor experimental channels. *Environmental Pollution (Series A)*, 25: 53 - 65.

Oke, T.R. 1987. *Boundary Layer Climates*. Methuen & Co., New York. pp.51-54.

Oliver, D.R. 1968. Adaptations of arctic Chironomidae. *Annales Zoologici Fennici*, 5: 111 - 118.

Oliver, D.R. 1971. Life History of the Chironomidae. *Annual Review of Entomology*, 16: 211 - 230.

Oliver, D.R. and M.E. Roussel. 1983. *The Insects and Arachnids of Canada. Part 11: The Genera of Larval Midges of Canada, Diptera: Chironomidae*. Agriculture Canada Publication 1746. 263 p.

Pellatt, M.G. 1996. *Postglacial changes in vegetation and climate near treeline in British Columbia*. Ph.D. thesis, Simon Fraser University, Burnaby, British Columbia, pp. 177.

Pinder, L.C.V. 1986. Biology of freshwater Chironomidae. *Annual Review of Entomology*, 31: 1 - 23.

Pojar, J., D. Meidinger and K. Klinka. 1991. Concepts, In: D. Meidinger & J. Pojar, eds., *Ecosystems of British Columbia*. Research Branch, British Columbia Ministry of Forests, Victoria. pp. 9-37.

Porter, S.C. and G.H. Denton. 1967. Chronology of Neoglaciation in the North American Cordillera. *American Journal of Science*, 265: 177 - 210.

Ritchie, J.C. 1987. *Postglacial Vegetation of Canada*. Cambridge University Press. 178 p.

Ryder, J.M. 1989. Holocene glacier fluctuations (Canadian Cordillera), In: R.J. Fulton, ed., *Quaternary Geology of Canada and Greenland*. Geological Survey of Canada, Ottawa. Geology of Canada No. 1.

Ryder, J.M. and B. Thomson. 1986. Neoglaciation in the southern Coast Mountains of British Columbia: chronology prior to the late Neoglacial maximum. *Canadian Journal of Earth Sciences*, 23: 273 - 287.

Sæther, O.A. 1975a. Nearctic chironomids as indicators of lake typology. *Verhandlungen der Internationalen Vereinigung fur theoretische und angewandte Limnologie*, 19: 3127 - 3133.

Sæther, O.A. 1975b. Nearctic and Palaearctic *Heterotrissocladius* (Diptera: Chironomidae). *Bulletin of the Fisheries Research Board of Canada*, 193: 1 - 68.

Sæther, O.A. 1979. Chironomid communities as water quality indicators. *Holarctic Ecology*, 2: 65 - 74.

Schmah, A. 1993. Variation among fossil chironomid assemblages in surficial sediments of Bodensee-Untersee (SW-Germany): implications for paleolimnological interpretation. *Journal of Paleolimnology*, 9: 99-108.

Schweger, C.E. and M. Hickman. 1989. Holocene paleohydrology of central Alberta: testing the general-circulation-model climate simulations. *Canadian Journal of Earth Sciences*, 26: 1826-1833.

Smol, J.P. 1981. Problems associated with the use of 'species diversity' in paleolimnological studies. *Quaternary Research*, 15: 209 - 212.

ter Braak, C.J.F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology*, 67: 1167 - 1179.

Thienenann, A. 1918. Untersuchungen uber die Bezeihungen zwischen dem Sauerstoffgehalt des Wassers und der Zusammensetzung der fauna in Norddeutschen Seen. *Archiv für Hydrobiologie*, 82: 316 - 346.

Thorp, J.H. and R.K. Chesser. 1983. Seasonal responses of lentic midge assemblages to environmental gradients. *Holarctic Ecology*, 6: 123 - 132.

Tokeshi, M. 1995. Species interactions and community structure, In: *The Chironomidae: Biology and Ecology of Non-biting Midges*, eds. P.D. Armitage, P.S. Cranston, and L.C.V. Pinder. Chapman & Hall, London, pp. 297 - 335.

Verschuren, D. 1994. Sensitivity of tropical-African aquatic invertebrates to short term trends in lake level and salinity: a paleolimnological test at Lake Oloidien, Kenya. *Journal of Paleolimnology*, 10: 253 - 263.

Walker, I.R. 1987. Chironomidae (Diptera) in paleoecology. *Quaternary Science Reviews*, 6: 29 - 40.

Walker, I.R. 1988. *Late-Quaternary Palaeoecology of Chironomidae (Diptera: Insecta) From Lake Sediments in British Columbia*. Ph.D. Thesis, Simon Fraser University, Canada.

Walker, I.R. 1990. Modern assemblages of arctic and alpine Chironomidae as analogues for late-glacial communities. *Hydrobiologia*, 214: 223 - 227.

Walker, I.R. 1993. Paleolimnological biomonitoring using freshwater benthic macroinvertebrates. In: Rosenberg, D.M. & V.H. Resh, eds., *Freshwater Biomonitoring and Benthic Macroinvertebrates*. Chapman & Hall, New York. pp. 306 - 343.

Walker, I.R., A.J. Levesque, L.C. Cwynar and A.F. Lotter. In Press. An expanded surface-water palaeotemperature inference model for use with fossil midges from eastern Canada. *Journal of Paleolimnology*.

Walker, I.R. and G.M. MacDonald. 1995. Distributions of Chironomidae (Insecta: Diptera) and other freshwater midges with respect to treeline, Northwest Territories, Canada. *Arctic and Alpine Research*, 27:258 - 263.

Walker, I.R. and R.W. Mathewes. 1987a. Chironomidae (Diptera) and postglacial climate at Marion Lake, British Columbia, Canada. *Quaternary Research,* 27: 89 - 102.

Walker, I.R. and R.W. Mathewes. 1987b. Chironomids, lake trophic status, and climate. *Quaternary Research,* 28: 431 - 437.

Walker, I.R. and R.W. Mathewes. 1989a. Early postglacial chironomid succession in southwestern British Columbia, Canada, and its paleoenvironmental significance. *Journal of Paleolimnology,* 2: 1 - 14.

Walker, I.R. and R.W. Mathewes. 1989b. Chironomidae (Diptera) remains in surficial lake sediments from the Canadian Cordillera: analysis of the fauna across an altitudinal gradient. *Journal of Paleolimnology,* 2: 61 - 80.

Walker, I.R. and R.W. Mathewes. 1989c. Much ado about dead diptera. *Journal of Paleolimnology,* 2: 19 - 22.

Walker, I.R., J.P. Smol, D.R. Engstrom and H.J.B. Birks. 1991a. An assessment of Chironomidae as quantitative indicators of past climatic change. *Canadian Journal of Fisheries and Aquatic Sciences,* 48: 975 - 987.

Walker, I.R., R.J. Mott and J.P. Smol. 1991b. Allerod - Younger Dryas lake temperatures from midge fossils in Atlantic Canada. *Science,* 253: 1010 - 1012.

Walker, I.R., D.R. Oliver and M.E. Dillon. 1992b. The larva and habitat of *Parakiefferiella nigra* Brundin (Diptera: Chironomidae). *Netherlands Journal of Aquatic Ecology,* 26: 527 - 531.

Walker, I.R. and C.G. Paterson. 1983. Post-glacial chironomid succession in two small, humic lakes in the New Brunswick-Nova Scotia (Canada) border area. *Freshwater Invertebrate Biology,* 2: 61 - 73.

Walker, I.R., E. Reavie, S. Palmer, and R.N. Nordin. 1993. A palaeoenvironmental assessment of human impact on Wood Lake, Okanagan Valley, British Columbia. *Quaternary International,* 20: 51 - 70.

Walker, I.R., J.P. Smol, D.R. Engstrom and H.J.B. Birks. 1992a. Aquatic invertebrates, climate, scale, and statistical hypothesis testing: A response to Hann, Warner, and Warwick. *Canadian Journal of Fisheries and Aquatic Sciences,* 49: 1276 - 1280.

Walker, I.R., S.E. Wilson and J.P. Smol. 1995. Chironomidae (Diptera): quantitative palaeosalinity indicators for lakes of western Canada. *Canadian Journal of Fisheries and Aquatic Sciences,* 52: 950 - 960.

Warner, B.G. and B.J. Hann. 1987. Aquatic invertebrates as paleoclimatic indicators? *Quaternary Research,* 28: 427 - 430.

Warwick, W.F. 1980. Palaeolimnology of the Bay of Quinte, Lake Ontario: 2800 years of cultural influence. *Canadian Bulletin of Fisheries and Aquatic Sciences,* 206: 1 - 117.

Warwick, W.F. 1989. Chironomids, lake development and climate: a commentary. *Journal of Paleolimnology,* 2: 15 - 17.

Watson, H.L., M.C. Bach, and I.M. Goklany. 1992. Global vs. Climate Change, In: *Implications of Climate Change For Pacific Northwest Forest Management.* University of Waterloo, Waterloo. pp. 97-109.

Wiederholm, T. 1983. Chironomidae of the Holarctic Region, Keys and Diagnoses: Part 1 - Larvae. *Entomologica Scandinavica Supplement,* 19: 1 - 457.

Wiederholm, T. and L. Eriksson. 1979. Subfossil chironomids as evidence of eutrophication in Ekoln Bay, central Sweden. *Hydrobiologia,* 62: 195 - 208.

Williams, W.D., A.J. Boulton and R.G. Taaffe. 1990. Salinity as a determinant of salt lake fauna: a question of scale. *Hydrobiologia,* 197: 257 - 266.

Wilson, S.E., I.R. Walker, R.J. Mott and J.P. Smol. 1993. Climatic and limnological changes associated with the Younger Dryas in Atlantic Canada. *Climate Dynamics,* 8: 177 - 187.

Wright. H.E., Jr. 1989. The amphi-Atlantic distribution of the Younger Dryas paleoclimatic oscillation. *Quaternary Science Reviews,* 8: 295-306.