

Using Fossil Midges from Saltspring Island, British Columbia to Infer Changes
in Temperature Over the Last 14,000 Years

by

Jillian Lemmen
B.Sc.(H), Queen's University, 2013
B.Ed., Queen's University, 2014

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of the Requirements for the Degree of

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Supervisory Committee

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Abstract

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Fossil midge remains from a sediment core from Lake Stowell, Saltspring Island (48°46'54"N, 123°26'38"W) were used to produce quantitative estimates of mean July air temperature over the last 14,000 years. Chironomid and *Chaoborus* remains were identified, and multiple models of past temperatures based on transfer functions of northern North American calibration datasets were evaluated. The selected model was used to create the first quantitative paleotemperature estimates for the Gulf Islands region.

Inferred paleotemperatures at Lake Stowell varied between 12.1 °C and 18.6 °C over the last 14,000 calendar years. Several major climate phases were identified based on changes in paleotemperature. The base of the record is characterised by a cool late-glacial interval with a minimum inferred July temperature of 12.1 °C. Inferred temperatures generally increased by ~4 °C between ~14,200 and 10,300 cal yr BP but this warming was interrupted by cooling, coincident with the Younger Dryas Chronozone, when inferred temperatures drop ~2 °C from the temperatures immediately preceding this interval. A warm early Holocene extends from ~10,300 to 8100 cal yr BP with temperatures regularly exceeding 16 °C. Following the early Holocene, inferred temperatures decreased to approximately 14.9 °C in the mid-Holocene. After a brief warm peak in the late Holocene, inferred temperatures cooled towards the present.

Inferred changes in paleotemperature from Lake Stowell are consistent with other paleoenvironmental studies conducted in southern British Columbia and throughout much of the Northern Hemisphere. Temperature changes at Lake Stowell are muted in comparison to continental sites, which may be due to the influence of marine conditions. This research provides context for other studies in the region, and contributes to our understanding of environmental change since the last glacial maximum.

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Introduction

Paleoenvironmental Studies and Environmental Proxies

Long-term environmental data are required to place recent ecosystem changes within the context of natural variability. There are limitations to the use of historical meteorological data, particularly on the timescale needed to capture natural variability before substantial anthropogenic influence and within long-term climate cycles. In order to understand long term changes in climate, climate needs to be inferred from natural archives, such as lake sediments (Smol et al. 2001a).

Lake sediments act as natural archives of environmental changes that occur through time within each lake and its catchment, as sediment is continually deposited in a sequential order on the lake bottom. As this sediment accumulates, environmental indicators, such as the remains of algae, plants, and insects, are incorporated into the sediment record. The biological remains and geochemical signals contained within the sediment record act as proxies for past changes in the environment, and, once a temporal chronology is determined for the record, can be used to infer changes in environmental conditions through time (Smol et al. 2001b).

Many different types of proxies can be analyzed in paleoenvironmental studies (Smol 2008). Pollen, diatoms (single-celled algae) and larval chironomids (non-biting midges) are the most commonly used biological proxies (e.g. Bennett et al. 2001; Larocque and Hall 2004; Stolze et al. 2007). Through identification and interpretation of these remains, it is possible to reconstruct past environmental conditions. Chironomid remains are particularly useful for quantitative reconstruction of past temperatures

because they are readily preserved and have well-defined quantitative relationships to environmental conditions.

Aquatic Midge Ecology

Chironomids (Chironomidae, order Diptera), or non-biting midges, are present on all continents and across a variety of aquatic and terrestrial habitats (Walker 2001). It has been estimated that there are greater than 4,000 species of chironomid that are completely aquatic in immature stages worldwide (Ferrington 2008). The chironomid life-cycle consists of four distinct stages; egg, larva, pupa and adult. Up to 90% of the life of a chironomid is spent in the first three stages, which are aquatic for the majority of chironomid species (Pinder 1995). Some genera of Orthocladiinae are considered terrestrial or semi-terrestrial, but these prefer moist soils for development (Pinder 1995). The final stage of the chironomid life cycle is a winged adult, capable of rapid dispersal (Williams 1996), although some dispersal may also occur due to drifting of egg masses in aquatic environments (Pinder 1995). The timing of this life cycle, and consequently the number of generations per year (voltinism) is highly variable across taxa and environmental gradients (Tokeshi 1995). Generally, warmer areas support higher voltinism, with temperate species having a univoltine or bivoltine life history, and tropical species exhibiting a multivoltine life history (Walker 2001).

Chaoborus, another member of order Diptera, is commonly included in chironomid-based paleoenvironmental studies. Also known as phantom midges, *Chaoborus* are predaceous feeding on zooplankton (Batt et al. 2015). *Chaoborus* species differ in size, colouration and migratory habit, which affects their susceptibility to

predation (Pope et al. 1973; Stenson 1978; Borkent 1981, Uutala 1990; Garcia and Mittelbach 2008). Most species of *Chaoborus* are capable of diurnal migration within the water column, generally only feeding in the upper waters at night, when visual hunting by fish is impaired (Garcia and Mittelbach 2008).

Chironomids in Paleoenvironmental Studies

Preservation Potential and Identification

During the larval stage of the chironomid life cycle, the chironomid develops a chitinous head capsule. As the larva grows, it passes through four instar stages. It is during the transition between these stages, as well as the final transition from larva to pupa, that the chitinous head capsule is shed. Head capsules are then incorporated into the sediment at the lake bottom, where they are preserved as a part of the natural record.

Variation in the morphological features of the head capsule allow for identification after the head capsule has been isolated from the sediment (Figure 1). The most prominent feature used for identification is the mentum, a toothed structure along the anterior ventral margin of the head capsule (Figure 2). The mentum itself is divided into median (Figure 2A) and lateral teeth (Figure 2B) and identifications can be made based on the number of teeth and their relative size, shape, and pigmentation patterns. In Tanypodinae, a fork-shaped structure called the ligula (Figure 2E) is used in identification in much the same way. The ventromental plates (Figure 2C) are also commonly used in identification based on their general shape and pattern of striations. Other features used in identification include mandibles, if present, the positioning of setae (Figure 2D), and general characteristics like overall size and pigmentation. *Chaoborus*

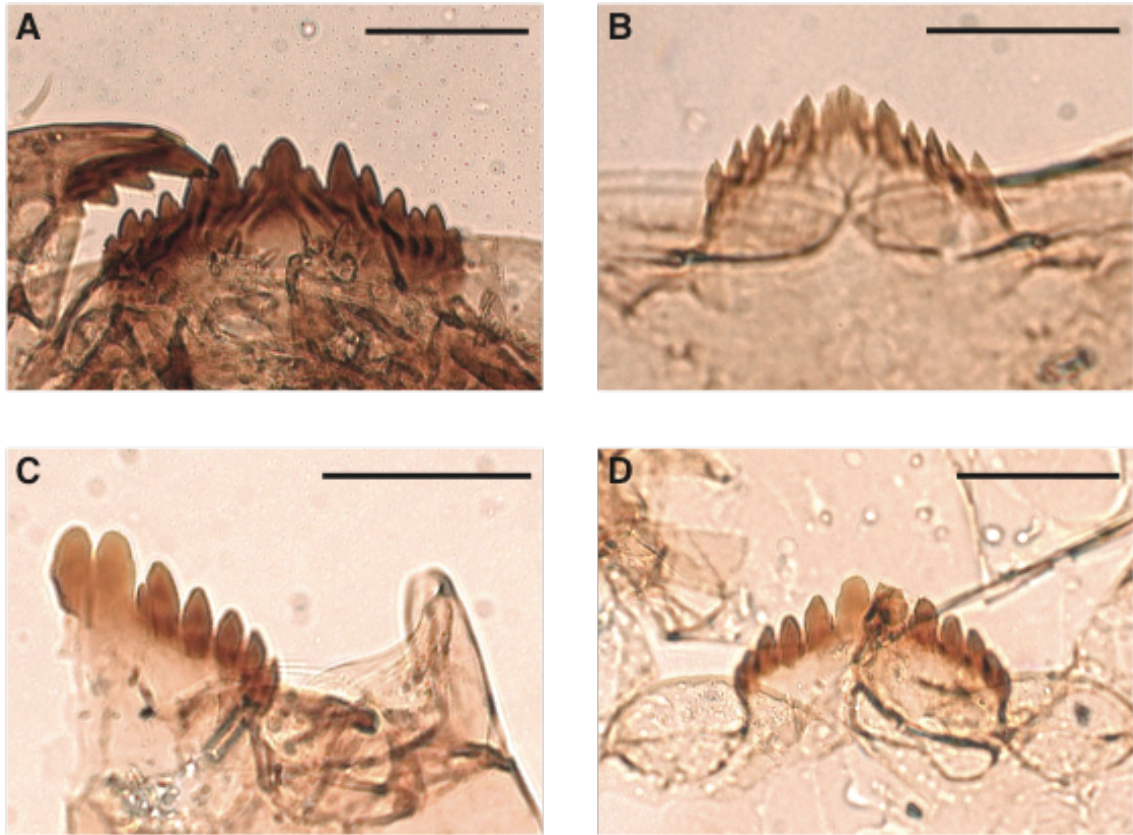


Figure 1. Select chironomid taxa from the Lake Stowell sediment record: A. *Chironomus*, B. Tribe Tanytarsini, C. and D. *Apedilum*, E. *Labrundinia*, F. *Polypedilum*, G. *Glyptotendipes*, H. *Dicrotendipes*. Black bar represents 50 μm .

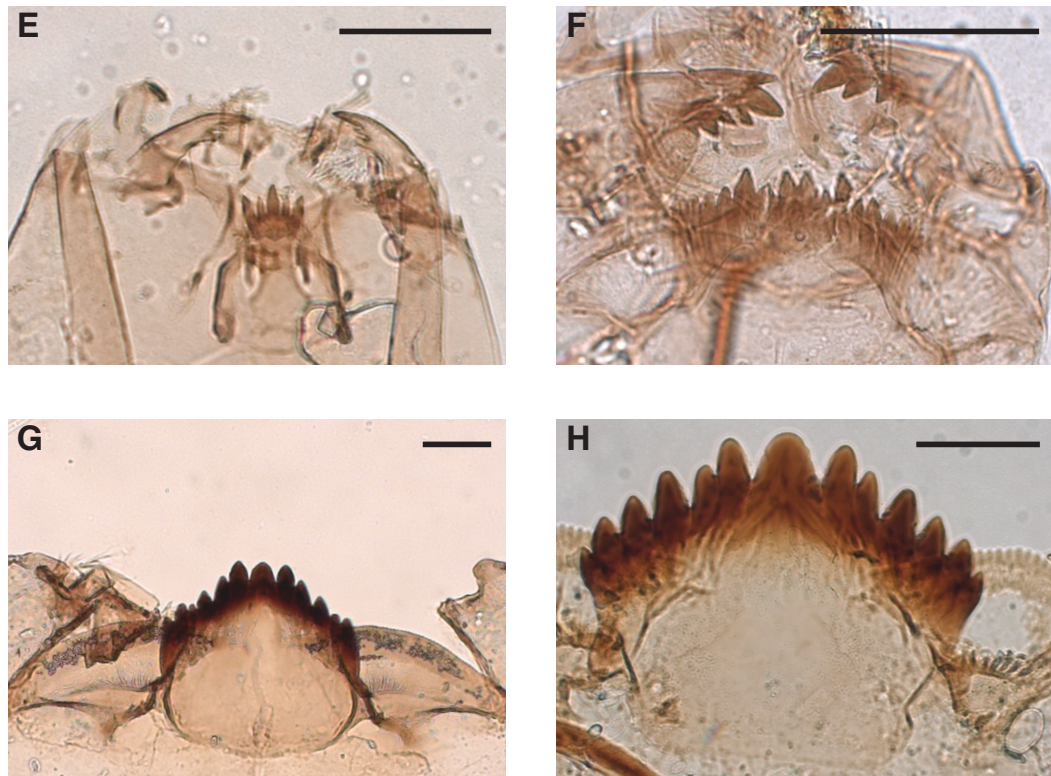


Figure 1 (continued). Select chironomid taxa from the Lake Stowell sediment record: A. *Chironomus*, B. Tribe Tanytarsini, C. and D. *Apedilum*, E. *Labrundinia*, F. *Polypedilum*, G. *Glyptotendipes*, H. *Dicrotendipes*. Black bar represents 50 µm.

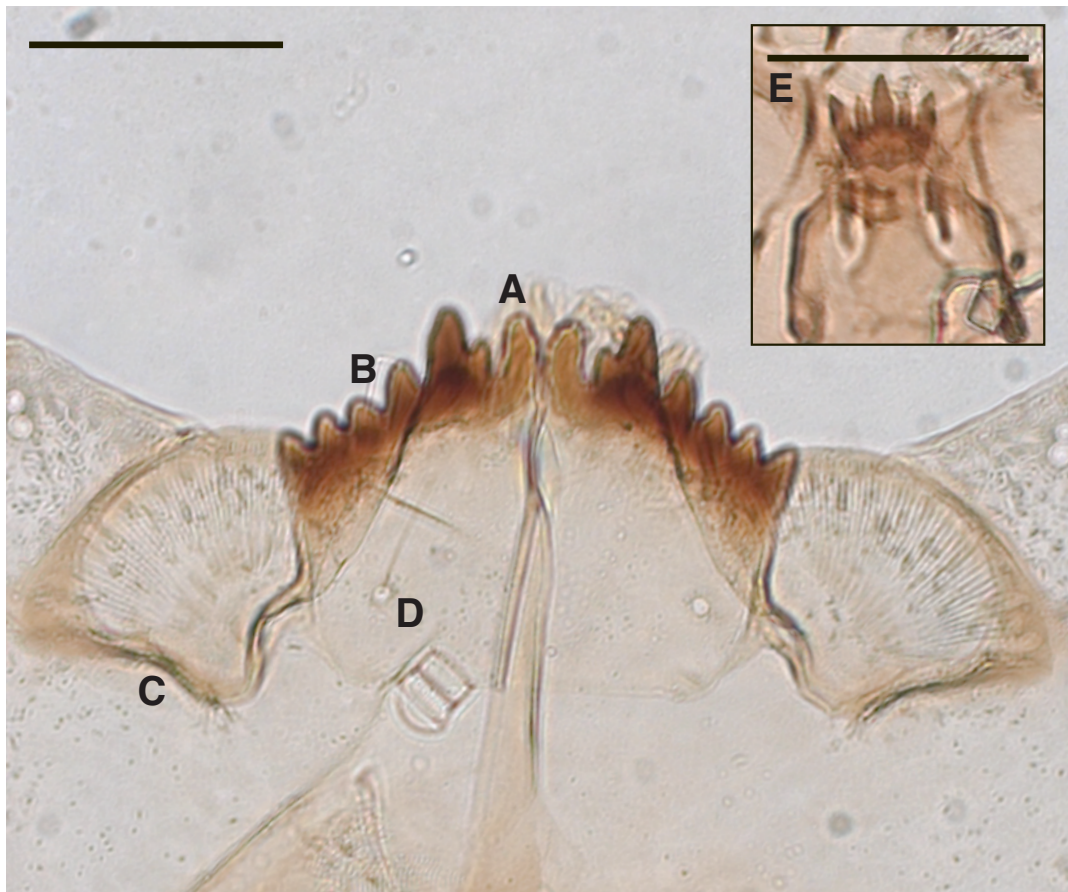


Figure 2. A *Microtendipes* head capsule showing the common features used in identification. A. median teeth of mentum, B. lateral teeth of mentum, C. striated ventromental plates, D. setae. Inset shows ligula (E) of Subfamily Tanypodinae. Additional identifying features not shown include the mandibles and antennal pedestals. Black bar represents 50 μm .

remains are identified by the shape, size and positioning of the subordinate tooth on the mandible (Uutala 1990).

Environmental Responses

Changes in chironomid assemblages have been linked to fluctuations in lake pH (e.g. Orendt 1999), lake depth (e.g. Kurek and Cwynar 2009), disturbance patterns (e.g. Tremblay et al. 2010) and trophic conditions (e.g. Brooks et al. 2001). Early studies using chironomids as environmental indicators investigated lake trophic status (Frey 1976; Sæther 1979). Through time, this initial focus on trophic status expanded to more specific conditions, such as oxygen availability and stratification. With the advent of more sophisticated statistical analyses and the development of large datasets of chironomid distributions, the relationship between chironomid assemblage composition and air temperature was recognized as a globally consistent explanatory variable for variation in chironomid assemblages (Eggermont and Heiri 2012). The mechanisms behind this relationship are complex and include both direct and indirect responses.

As ectotherms, chironomids exhibit direct physiological responses to changes in temperature that vary by taxa. Metabolic processes in chironomids respond directly to changes in temperature, with increased temperatures leading to increases in enzymatic and metabolic activities (e.g. Tatrai 1986) and respiration rates (e.g. Simčić 2005). Temperature also affects the growth and development rates of the larval and pupal stages in chironomids, with warmer than usual temperatures cueing emergence (Eggermont and Heiri 2012; Dickson and Walker 2015). Although increased temperature increases growth and development rates (Huryn and Wallace 1986), it does not do so without limit. Rather,

a threshold (optimum) value is reached where the increased energetic costs of metabolism begin to outweigh the benefits, which can result in stress and death (e.g. Gresens 2001; Reynolds and Benke 2005; Dickson and Walker 2015). The relationship between temperature, growth and development is also reflected in differences in voltinism among species, with observed values of 1/7 of a generation per year in arctic environments to upwards of five generations per year in tropical habitats (Tokeshi 1995). Voltinism can also vary within species, even within the same lake when microenvironmental conditions differ, with warmer environments leading to shorter generation times (Vannote and Sweeney 1980).

Temperature has also been found to affect the behaviour of both juvenile (Berg 1995) and adult chironomids (Armitage 1995). Many groups of chironomids are capable of feeding on multiple substrates such as detritus, algae, and animal matter (Berg 1995). While feeding strategy varies according to time of year or phase of life cycle, it can also vary due to the availability of a particular substrate, which may in turn be affected by temperature (Berg 1995). As well, many chironomids employ a variety of strategies to overwinter in lakes (Tokeshi 1995).

Chironomids respond faithfully to changes in air and water temperatures throughout the life cycle, and the winged adults are able to disperse rapidly to new environments when conditions are no longer suitable. On a practical level, modern air temperature data are easier to obtain at higher spatial and temporal resolutions than surface water temperature data, and where data are absent, it is easier to estimate (Eggermont and Heiri 2012). While there is debate on the mechanisms that explain the relationship between the distribution and abundance of chironomid taxa and temperature,

the link between chironomid assemblages and temperature is clear (Eggermont and Heiri 2012). The development of transfer functions (e.g. Walker et al. 1991) allows this relationship to be defined quantitatively, and has become the main focus of chironomid-based paleoenvironmental studies.

Chaoborus has also been included in studies that use aquatic midge remains to study paleotemperature (e.g. Barley et al. 2006). In addition to informing paleotemperature estimates, subfossil *Chaoborus* mandibles are used in paleolimnological studies to indicate past fish presence or absence. Fish commonly prey on *Chaoborus*, and high frequencies of *Chaoborus* remains are typically used to infer fishless conditions (Elser et al. 1987) with different species dominating depending on the abundance and diversity of fish species present (Uutala 1990).

Chironomids also respond to changes in salinity, with different taxa displaying different salinity optima and tolerances (Eggermont et al. 2006). This relationship is particularly clear and frequently used in studies of tropical lakes, where rainfall and evaporation have a strong effect on lake systems (Eggermont et al. 2006). Similar studies have also been conducted in lakes in semi-arid regions, where the combination of hydrology and geomorphology has resulted in fluctuations in salinity over the Holocene (e.g. Walker et al. 1995; Heinrichs et al. 1997).

Transfer Functions

Transfer functions are mathematical models that quantitatively define the relationship between abiotic and biotic components of a system (Birks et al. 2010). By understanding and quantifying the modern relationship between two variables of interest,

the resulting function can then be used to transform the biotic component, fossil assemblages, into quantitative estimates of abiotic variables such as temperature (Birks et al. 2010). These estimates are of particular value as they provide quantitative paleoenvironmental records that are independent of other paleoenvironmental proxy information.

To develop the mathematical model, calibration datasets are used to define the modern relationships between abiotic and biotic variables of interest. Calibration datasets are collections of ecologically important data from across environmental gradients, for example, the composition of chironomid communities in modern lakes along with environmental data (e.g., temperature, lake depth) from those same sites. These data are usually defined by multiple parameters relating to taxa such as minimum, maximum and optimal temperature values (e.g. Barley et al. 2006, Fortin et al. 2015), and in order to capture long gradients in temperature, calibration datasets often span substantial changes in latitude or elevation (e.g. Walker et al. 1997; Brooks and Birks 2001; Barley et al. 2006; Larocque et al. 2006). Multivariate statistical analyses allow for identification of the most important environmental variables that influence chironomid community composition within a certain dataset. In the case of chironomid communities, the primary explanatory variable is usually mean July temperature, though this can be manipulated depending on the environmental gradient being explored. For example, some studies have maximized changes in salinity, as opposed to changes in latitude or elevation, in order to understand the relationship between chironomid community composition and salinity (e.g. Walker et al. 1995; Eggermont et al. 2006). Once the explanatory variables are isolated, they can be used to develop mathematical models for predicting this variable

quantitatively from the assemblages. The resulting transfer function that explains the relationship between community composition and the environmental variable of interest (e.g. mean July air temperature) can then be applied to fossil assemblages to produce quantitative estimates of the variable of interest.

The first use of transfer functions in paleoenvironmental studies is attributed to Imbrie and Kipp (1971), who used fossil foraminiferal assemblages to infer sea surface temperatures and salinity in the Atlantic Ocean. Transfer functions for chironomids were first developed by Walker et al. (1991) using data from Atlantic Canada. Since then, transfer functions have been used to reconstruct paleotemperatures from chironomid remains in many regions of the world, with over 20 calibration datasets for air temperature currently published (Velle et al. 2010; Eggermont and Heiri 2012). In recent years, there has been much discussion as to the validity of transfer functions for use in paleoenvironmental studies (Velle et al. 2010; Brooks et al. 2012). Several assumptions need to be met in order for transfer functions to be considered valid (Juggins 2013) and much of the debate surrounding the use of transfer functions has focused on a perceived violation of these assumptions. The assumptions themselves can be divided into two main ideas: the biological component is related reliably to the abiotic component, and the transfer function itself is statistically valid. The relationship between chironomids and the environment has been well established (Velle et al. 2010; Eggermont and Heiri 2012), and through independent testing and refinement of transfer function development, the statistical validity of transfer functions has been strengthened. Telford and Birks (2011) developed the 'palaeoSig' test, which compares the proportion of variance within the fossil assemblage explained by the reconstruction to the proportion of variance explained

by reconstructions from transfer functions trained on random data. Reconstructions that explain more variability than 95% of the randomly constructed reconstructions are considered statistically significant (Telford 2015). With precautions in site and model selections, fossil chironomid assemblages have proven to be an ideal system for paleoenvironmental research because they can provide independent quantitative paleoclimate estimates and are particularly useful in multiproxy comparisons.

Modern Analogue Technique

The modern analogue technique compares modern assemblages within the training set to down-core fossil assemblages (Simpson 2007). The assumption, based in uniformitarianism, is that if modern and fossil assemblages are similar, so too are the environmental conditions in which they exist (Jackson and Williams 2004). Though contemporary midge-based paleotemperature reconstructions do not rely on modern analogues to provide quantitative estimates of temperature, testing for modern analogues within the training set allows for an evaluation of predictive power. That is, if good modern analogues exist within the training set, the paleotemperature estimate for that assemblage should be more reliable than one with poor modern analogues.

Most modern analogue testing uses squared chord distance as a measure of dissimilarity between modern and fossil assemblages. This technique allows for emphasis of the true climate signal in comparison to noise. Rare taxa are up-weighted slightly, so that they contribute to comparisons, but not so much that regional climate signals are disguised by local noise (Overpeck et al. 1985). Once the similarity between modern and fossil assemblages are quantified, a threshold value is imposed on the results to determine

good versus poor modern analogues (Jackson and Williams 2004). Poor modern analogues are associated with unique fossil assemblages. These are often indicative of some biological factor, such as migration, or environmental conditions not represented in the modern training set (Jackson and Williams 2004).

Paleoenvironmental Chironomid Studies in British Columbia

Some of the earliest research on chironomids as paleoenvironmental indicators in North America was done in British Columbia (Walker and Mathewes 1987, 1988, 1989a). Early descriptions of fossil chironomid assemblages (Walker and Mathewes 1987, 1988, 1989a) grouped species by thermal tolerance and provided insight into paleoclimate dynamics at a coarse taxonomic resolution. In one such study at Misty Lake on northern Vancouver Island, Walker and Mathewes (1989a) described a general three phase model, with cool temperatures during the late-glacial period, warming around ~10,000 ^{14}C yr BP to the Holocene thermal maximum, followed by gradual cooling to present day temperatures. A chironomid study at Hippa Lake on the west coast of Haida Gwaii did not detect any pattern of climatic change over the last 13,000 years (Walker and Mathewes 1988). These early studies relied heavily on the presence or absence of cold stenothermic taxa, particularly *Heterotrissocladius*, for inferring temperature change, and were done at relatively coarse temporal resolutions. While the Misty Lake study did indicate fluctuations in paleotemperature (Walker and Mathewes 1989a), the apparently stable conditions at Hippa Lake may be due to this coarse temporal resolution and/or the moderating effect of the ocean on a coastal lake.

With the advent of the use of transfer functions based on chironomid assemblages (Walker et al. 1991), midge-based paleoenvironmental studies in British Columbia shifted to quantitative analyses of July paleotemperature. Over a span of 10 years, paleotemperature reconstructions from multiple alpine sites in the Coast Mountain and Rocky Mountain ranges were produced (e.g. Pellatt et al. 2000; Palmer et al. 2002; Rosenberg et al. 2004; Chase et al. 2008). Supplemented by pollen and other paleoenvironmental proxies (e.g. Smith et al. 1998; Heinrichs et al. 2002; Stolze et al. 2007), these studies demonstrate a cohesive and stable pattern of Holocene temperatures in southern British Columbia. Most studies indicate rapid warming following deglaciation to a Holocene thermal maximum, followed by cooling to below-present temperatures in the late Holocene (e.g. Palmer et al. 2002; Heinrichs et al. 2002; Chase et al. 2008). Studies involving multiple sites note a temporal disconnect of these phases between sites (Chase et al. 2008), indicating that local microclimate may be an important influence. Transfer functions have also been used to investigate changes in salinity in several lakes in the interior of British Columbia (e.g. Walker et al. 1995; Heinrichs et al. 1997; Heinrichs and Walker 2006). These records suggest important variation in salinity at multiple sites in the region (Heinrichs et al. 2001).

Northern Hemisphere since the Last Glacial Maximum

A general pattern of paleoclimatic change in the Northern Hemisphere since the Last Glacial Maximum has been established. Much of these data come from the Northern Atlantic region (e.g. Alley et al. 1993; Bianchi and McCave 1999; NGRIP 2004), but the use of lake sediments has helped to produce a clearer picture of change over the

continental land masses, and given insight into regional variation and the influence of microclimate (e.g. Kaufman et al. 2004; Mayewski et al. 2004; Mann et al. 2009).

The period immediately following deglaciation was cool due to the influence that the remaining ice sheets still had on the surrounding regions. As the ice retreated, temperatures increased in a time-transgressive manner consistent with the position of remaining ice (Kaufman et al. 2004). Warming was interrupted, between ~13,000 and 11,500 cal yr BP, by abrupt cooling of 2-4 °C known as the Younger Dryas, which is recorded at sites across the Northern Hemisphere (e.g. Alley et al. 1993; Brooks and Birks 2000a; Kienast and McKay 2001). The Younger Dryas is a more or less synchronous event in the Northern Hemisphere, observed in many environmental proxy records, from Greenland ice cores (Zielinski and Mershon 1997; Björck et al. 1998) to deep sea sediment cores off the coast of Japan (Ruan et al. 2015). Suspected to be caused by the collapse of the Laurentide Ice Sheet (Alley et al. 1993; Ruan et al. 2015), the extent of the Younger Dryas appears to be far reaching.

Following the cool temperatures of the late-glacial and Younger Dryas, temperatures increased to a Holocene thermal maximum (HTM). This has been attributed to an increase in summer thermal insolation (Berger and Loutre 1991). Walker et al. (2008) refer to this transition as “the clearest signal of climatic warming” available in many climatic records. Across the Arctic, the initiation of the HTM varies from more than 12,000 cal yr BP to 5000 cal yr BP, with areas most distal to major ice sheets experiencing warming first (Kaufman et al. 2004). Variation occurs not only in timing, but in magnitude of change in temperature. Cuffey et al. (1995) suggested that early Holocene warming is exaggerated in the Arctic and more constrained in low mid-latitude

areas. The identification of the timing and amplitude of the HTM based on inferences from biological proxies is particularly variable, as biological responses to climate forcings are time transgressive by nature (Björck et al. 1998).

Following the HTM, changes in temperature became increasingly dominated by regional influences, leading to a complex pattern of smaller amplitude warming and cooling events (O'Brien et al. 1995). In general, temperatures following the HTM gradually cooled to modern conditions, but a number of widely recognized events punctuate this slow decrease, such as the 8.2 ka cooling, Medieval Climate Anomaly, and Little Ice Age (e.g. Bianchi and McCave 1999; Mann et al. 2009; Ruan et al. 2015). As with many small amplitude changes, the influence of local environmental conditions (e.g. topography, elevation) become increasingly important. In some regions, the influence of indigenous populations on environmental conditions is overlaid on potential climate signals (Sugimura et al. 2008; Wang et al. 2012; Hallmann et al. 2013).

Research Objectives

The overarching goal of my research is to produce quantitative estimates of mean July air temperature for the last 14,000 years in the Gulf Islands region. In order to accomplish this, a lake sediment core was collected from Lake Stowell on Saltspring Island, and chironomid head capsules and *Chaoborus* mandibles were isolated and identified to the highest taxonomic resolution possible to produce a biostratigraphy of these subfossil remains. Through the use of published modern calibration datasets and transfer functions, mean July air temperatures spanning the last 14,000 years were inferred. This research demonstrates the value of using subfossil chironomid remains as

an independent and quantitative proxy for past temperature, and, in turn, furthers our understanding of paleoenvironmental changes on the south coast of British Columbia.

Study Site and Regional Paleoenvironmental History

The Gulf Islands and Saltspring Island

The Gulf Islands are part of an archipelago of hundreds of islands, including the San Juan Islands, that is located along the inner coasts of southern British Columbia and northwest Washington. Saltspring Island (Figure 3), located immediately east of Vancouver Island, is the largest and one of the more southern Gulf Islands. The Gulf Islands are underlain by sedimentary rocks of the Late Cretaceous Nanaimo Group, and metasedimentary and igneous rocks of the Late Devonian Sicker Group, with granitic rocks on the south end of Saltspring Island (England and Calon, 1991; Greenwood and Mihalyuk 2009). The bedrock is overlain by the brunsolic soils that dominate the region (Meidinger and Pojar 1991).

The region has warm, dry summers and mild, wet winters. As the Gulf Islands sit in the rainshadow of the Vancouver Island Ranges and Olympic Peninsula, these islands receive much less precipitation than other portions of the coast (Demarchi 2011). Mean annual precipitation on Saltspring Island is 1070 mm/yr, with most precipitation falling between October and April and a very small portion falling as snow (Cusheon Lake station; Environment Canada 2015a). Saltspring Island has reduced seasonality of temperature, with mean daily temperatures ranging from 2.4 °C in December to 16.2 °C in August (Cusheon Lake station; Environment Canada 2015a).

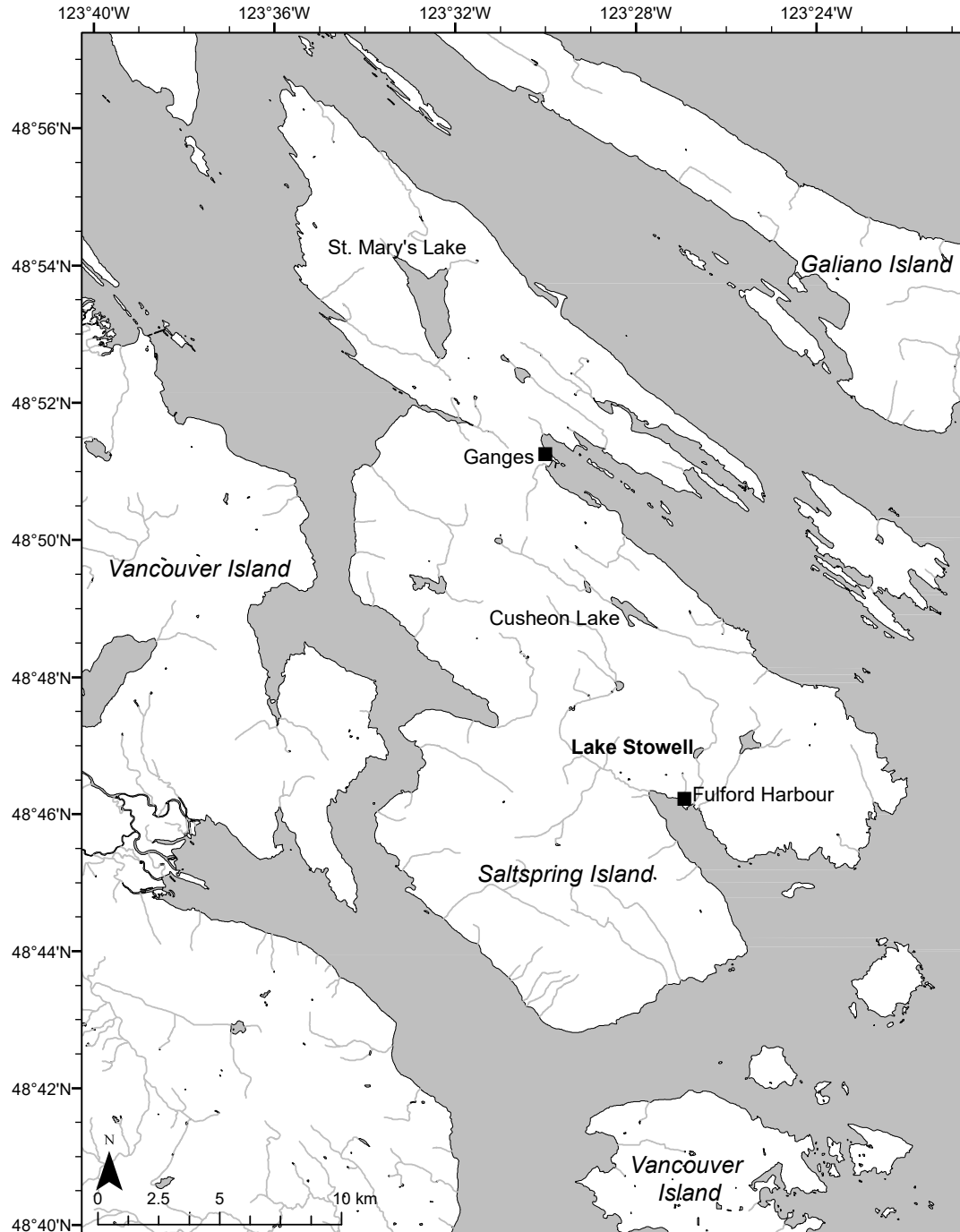


Figure 3. Site map of Lake Stowell on Saltspring Island, British Columbia. Additional sites indicated are the location of weather stations at Cusheon Lake and St. Mary's Lake, as well as centres of population at Fulford Harbour and Ganges.

These mild temperatures support a long growing season. The region is dominated mostly by Douglas-fir forests and many plant species found in the area are at the northernmost end of their range (Meidinger and Pojar 1991). Other common tree species include western redcedar, grand fir and red alder. The region is also known for Garry oak ecosystems, characterized by Garry oak and arbutus trees, and an understory dominated by grasses and wild flowers (Meidinger and Pojar 1991).

Lake Stowell

Lake Stowell (48°46'54"N, 123°26'38"W) is a small, oligo-mesotrophic lake, located on the southern end of Saltspring Island (Figure 3) at 70 m above sea level (asl) (Bednarski and Rogers 2012). There is a small, poorly-defined inflowing stream at the north end of the lake. The lake is surrounded by a riparian fringe with a small wetland and outlet at the south end of the lake. Lake Stowell has a surface area of 4.6 ha, a maximum depth of 7.5 m (Sprague 2009), and is thermally stratified from mid-April to late September (McKean 1981). In July 2015, water temperature was 24.6 °C at the surface and remained stable to a depth of 2.5 m, and then decreased, reaching 7.4 °C at 6.5 m (Appendix A; Figure A1). The summer of 2015 was particularly warm with drought conditions extending along much of the south coast of British Columbia. Mean July air temperature was almost 3 °C warmer at Saltspring Island in 2015, compared to 1981-2010 climate normals (Environment Canada 2015a; 2015b). In July 2008, Ormond et al. (2011) measured epilimnion temperature to be 22.7 °C with a similar temperature profile to that measured in 2015. Chlorophyll *a* (1.6 µg/L) and phosphorus levels (7 µg/L) are low and typical of oligotrophic to mesotrophic lakes in the region with high

dissolved oxygen (90.8%) and moderate dissolved organic carbon (5.1 mg/L) (Ormond et al. 2011; Table A1). Limnological variables measured in July 2015 can be found in Appendix A (Table A1).

Lake Stowell is easily accessed along Beaver Point Road on Saltspring Island and is used for recreational swimming and fishing, with a dock along the shore and a floating raft near its center. The lake is surrounded by private property consisting of forested and cleared land, and there are several small commercial farms in the vicinity of the lake. Rainbow trout, cutthroat trout and threespine stickleback are found in the lake at present (Ministry of Environment 2015). Lake Stowell has been stocked with cutthroat trout since 1927 and rainbow trout since 1974 (Ministry of Environment 2015).

Paleoenvironmental History of the Gulf Islands

Glacial History

During the Last Glacial Maximum, known regionally as the Fraser Glaciation, the Gulf Islands were covered by the Juan de Fuca Lobe of the Cordilleran Ice Sheet. The Cordilleran Ice Sheet covered most of British Columbia as well as southern Yukon and Alaska, mostly bounded by the Canadian Cordillera, but occasionally extending beyond the Rocky Mountains and Coast Mountains (Clague and Ward 2011). Ice extended onto the continental shelf, reaching the shelf edge in some regions (Clague and James 2002). As deglaciation began, the continental shelf and marine areas were the first to become ice free (Clague and James 2002). The southwest edge of the ice sheet thinned and retreated, leading to rapid deglaciation of the Juan de Fuca Strait region, starting around 17,000 calendar years before present (cal yr BP) and lasting only a few hundred years (Mosher

and Hewitt 2004). The Strait of Georgia was deglaciated shortly afterwards and was mostly ice-free by ~13,200 cal yr BP (11,300 ^{14}C yr BP; Barrie and Conway 2002). These ice free channels allowed for the establishment of modern ocean dynamics around Vancouver Island by 11,500 cal yr BP (Dallimore et al. 2008). The modern extent of ice cover in alpine regions was established approximately 10,000 cal yr BP (Clague et al. 1982).

Sea-level Change

The coast of British Columbia has seen dynamic changes in sea level due to glacio-isostatic crustal rebound as well as the release of water contained within ice sheets across the Northern Hemisphere. Sea-level changes differ by region and are affected by many factors including mantle viscosity, thickness and duration of ice cover, and tectonics (Hetherington and Barrie 2004).

In the Gulf Islands and southern Vancouver Island region, relative sea level immediately following deglaciation (~14,000 cal yr BP) was +70-100 m above modern sea level (Fedje et al. 2009; James et al. 2009). Relative sea level then dropped rapidly reaching levels comparable to modern approximately 13,200 cal yr BP (James et al. 2009), and continued to drop to a lowstand of 10-40 m below modern at approximately 11,200 cal yr BP (Fedje et al. 2009; Barrie and Conway 2002). Sea-level has since slowly risen, reaching modern levels around 4000 cal yr BP (James et al. 2009).

Climate History

The post-glacial climate history of coastal British Columbia has been inferred from studies using many different paleoenvironmental indicators (Figure 4). Changes in temperature following the last glaciation and through the Younger Dryas chronozone were relatively rapid, lending to the need for high resolution quantitative analyses for this period. However, environmental changes immediately following deglaciation and the associated changes in sea level are not recorded in a number of studies from the Gulf Islands region (e.g. McCoy 2006; Sugimura et al. 2008; Lucas and Lacourse 2013) because their paleoenvironmental records are limited to the Holocene epoch. Increasing temperatures following the last glacial maximum and Younger Dryas cooling of $\sim 3^{\circ}\text{C}$ between $\sim 12,900$ - $11,600$ cal yr BP have been identified in marine and lake sediment records from the wider region (e.g. Mathewes 1993; Mathewes et al. 1993; Kienast and McKay 2001; Brown and Hebda 2002, 2003; Lacourse 2005; Lacourse et al. 2012; Gavin et al. 2013).

Paleoenvironmental studies have provided some insight into the climate and vegetation history of southern Vancouver Island and the Gulf Islands during the Holocene. Pellatt et al. (2001) describe relatively mild temperatures with an open landscape from $11,450 - 10,350$ cal yr BP based on a high resolution study of a marine sediment core from Saanich Inlet. Warm early Holocene conditions have been inferred from fossil pollen analyses of lake sediments from nearby Pender Island (Lucas and Lacourse 2013) and Orcas Island (Leopold et al. 2016). This warm early Holocene is seen in paleoenvironmental records throughout the Pacific Northwest region, where it is

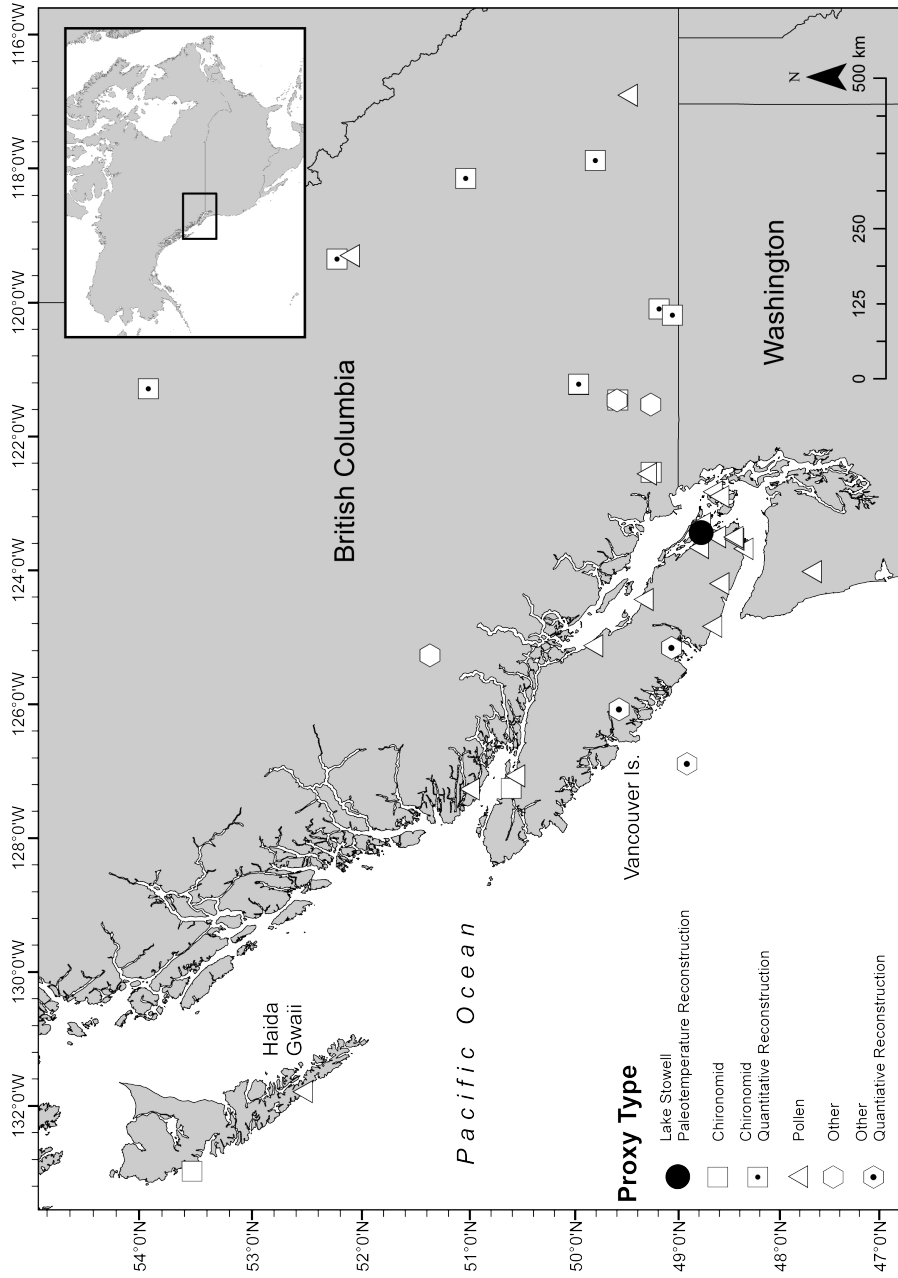


Figure 4. Regional map showing other paleoenvironmental studies cited in the text. Lake Stowell is symbolized by a round marker. Studies are identified by the type of proxy that was analyzed: chironomid (square), pollen (triangle) and other (hexagon). Quantitative paleotemperature reconstructions are indicated by a black dot. Studies include: Mathewes and Heusser (1981); Walker and Mathewes (1987); Walker and Mathewes (1988); Walker and Mathewes (1989b); Smith et al. (1998); Pellatt et al. (2000); Kienast and McKay (2001); Pellatt et al. (2001); Brown and Hebda (2002); Palmer et al. (2002); Hallett et al. (2003); Rosenberg et al. (2004); Lacourse et al. (2005); Brown et al. (2006); Hay et al. (2006); McCoy (2006); Stolze et al. (2007); Chase et al. (2008); Sugimara et al. (2008); Zhang et al. (2008); Gavin et al. (2011); Lacourse et al. (2012); Coulthard et al. (2013); Gavin et al. (2013); Lucas and Lacourse (2013); Courtney Mustaphi and Pisaric (2014); Lacourse and Davies (2015); and, Leopold et al. (2016).

usually the warmest interval of post-glacial paleoenvironmental records (e.g. Mathewes 1973; Mathewes and Heusser 1981; Palmer et al. 2002; Zhang et al. 2008; Walsh et al. 2010). Paleotemperature reconstructions support this inferred warm period, showing increases of up to 4 °C from cooler late-glacial conditions (e.g. Palmer et al. 2002; Walker and Pellatt 2003; Chase et al. 2008). An abundance of macroscopic charcoal in early Holocene lake sediments suggest that forest fires played an important role in local forest dynamics (e.g. Brown and Hebda 2002; Hallett et al. 2003; Courtney Mustaphi and Pisaric 2014).

The early Holocene was followed by cooler temperatures and increased precipitation after ca. 8000 cal yr BP, and a gradual transition to the mild and moist climate that is characteristic of the region today (Pellatt et al. 2001; Palmer et al. 2002; Rosenberg et al. 2004; Lacourse 2005; Brown et al. 2006; Stolze et al. 2007; Chase et al. 2008; Gavin et al. 2011; Leopold et al. 2016). Modern conditions were established within the past 3500 cal yr (Walker and Pellatt 2003; Briles et al. 2005), although fluctuations in temperature, precipitation and fire frequency still occurred (e.g. Heusser et al. 1985; Lepofsky et al. 2005; Chase et al. 2008; Lucas and Lacourse 2013; Bringué et al. 2016). Studies involving multiple sites (e.g. Chase et al. 2008) note a temporal disconnect in phases of temperature change, indicating small-scale differences in climate and highlighting the time-transgressive nature of paleoenvironmental change. This general pattern of temperature change (i.e. a cool late-glacial, followed by a warm early Holocene with cooling to modern temperatures) extends throughout the Pacific Northwest and much of the Northern Hemisphere (e.g. Brooks and Birks 2000b; Kaufman et al. 2004;

Velle et al. 2005a; Luoto et al. 2014), with variation in the timing and magnitude of change.

Anthropogenic Influences

Archaeological evidence from Orcas Island and San Juan Island indicate human occupation in the early Holocene (Fedje et al. 2009). Throughout the Gulf Islands, many shell middens and other cultural deposits have been dated to approximately 4000 cal yr BP (Fedje et al. 2009). Oral histories concerning the construction and use of clam gardens date back approximately 2000 years (Deur et al. 2015), and one such site is located along the west shore of Fulford Harbour on Saltspring Island (Wyatt 2015). The presence of this site as well as the recognized practice of prescribed burns before European settlement make it likely that indigenous peoples were inhabiting this area as well as influencing natural ecological processes throughout the neoglacial period if not earlier (Pellatt et al. 2001; Wyatt 2015).

Materials and Methods

Lake Sediment Core Collection

A 768.5 cm sediment core was collected from Lake Stowell, Saltspring Island at a water depth of 7.24 m. The core was collected in 1 m segments using a 5 cm-diameter Livingstone piston corer (Wright et al. 1984). Core segments were halved along their long axis and both halves were wrapped in waterproof plastic and aluminum foil, and stored at 4 °C. One half was left undisturbed for archive purposes. The uppermost 70 cm of sediment was sampled using a modified clear tube piston corer and extruded in the lab at 1 cm intervals.

Radiocarbon Dating and Age-Depth Model

In order to develop a chronology for the sediment core, six plant macrofossils were submitted to Beta Analytic in Miami, Florida, for radiocarbon dating through accelerator mass spectrometry. Radiocarbon ages were calibrated to calendar years using the IntCal13 calibration dataset (Reimer et al. 2013). These ages, along with ages for the Mazama tephra (Egan et al. 2015) and surface sediments (–63 cal yr BP), were used to build an age-depth model. The model was fit using Stineman interpolation (Stineman 1980) with the ‘stinepack’ (Johannesson et al. 2012) and ‘clam’ (Blaauw 2010) packages in the R statistical environment (R Core Team 2016).

Chironomid Analysis

Sediment subsamples were taken at 5-6 cm intervals along the length of the core to a depth of 604 cm, coinciding with sample depths used for pollen analysis in another study. An additional three samples were taken below this depth in the marine clay, only one of which (at 610 cm) contained a sufficient concentration of head capsules to be included in the fossil aquatic midge stratigraphy. A minimum of 50 head capsules is required from each subsample in order to obtain a representative sample (Quinlan and Smol 2001). To achieve this minimum, subsample volume in this study varied between 2 and 8.5 cm³. The majority of samples had a volume of 2 to 2.5 cm³, with the much larger samples being taken at the uppermost (0 and 6 cm) and lowermost (603 and 610 cm) sample depths. Preparation of these sediment samples for chironomid analysis was based on methods outlined in Walker (2001). Sediment subsamples were treated with warm 5% KOH for 5 min and then gently washed through 90 µm mesh using distilled water. The larger fraction (>90 µm) was visually examined in a Bogorov counting tray at 20-40× magnification under a stereomicroscope. Chironomid head capsules, both halved and whole, and *Chaoborus* mandibles were hand-picked using forceps and transferred to cover slips for mounting on slides with Entellan (Walker 2001).

For each subsample, a minimum of 50 complete head capsules were identified per subsample as recommended by Quinlan and Smol (2001), except those at 0 cm and 610 cm where this was not possible due to extremely low head capsule concentrations. Identification was done using a Zeiss A2 light microscope at 200-630× magnification and selected head capsules were photographed at 200-400× magnification with a Zeiss M1 AxioImager system (Figures 1 and 2). Identification was done to the highest possible

taxonomic resolution, usually to genus, and was aided primarily by Holarctic taxonomic guides (Brooks et al. 2007; Andersen et al. 2013). Online identification guides (Walker 2007; Cranston 2010) were also consulted for regional specificity and additional photographic aids. Oliver and Roussel (1983), Barley (2004) and Larocque-Tolber (2014) were also used in identification of select specimens. Identification of chironomid head capsules was based primarily on the mentum or ligula, ventromental plates, and, if present, antennal pedestals and mandibles (Figure 2). *Chaoborus* mandibles were identified based on the dichotomous key developed by Uutala (1990) focusing primarily on the morphology and position of the subordinate tooth.

Complete head capsules and head capsules with more than half of the mentum or ligula were counted as whole individuals, and head capsules broken along the midline of the median tooth were counted as half individuals. Fragments with less than half of the median tooth or missing the median tooth altogether were considered unidentifiable. Taxa counts of identified and unknown head capsules were summed and are presented as percent composition. Unidentifiable head capsules and those from early instars were excluded from the sum. This head capsule sum was divided by sample sediment volume to calculate head capsule concentrations (head capsules/cm³). Influx of head capsules (head capsules/cm²/cal yr) was calculated by dividing head capsule concentration for each sample by the corresponding sediment accumulation rate in the age-depth model.

Numerical Analyses

Zones with significant differences in chironomid assemblage composition were identified using 'psimpoll' software (Bennett 2007), which uses a broken-stick model to

test for statistical significance (Bennett 1996). Numerical zonation was done using six different divisive and agglomerative clustering techniques, after square-root transformation of the percentage data. Only taxa that accounted for greater than 5% of the sample sum were included in the cluster analyses. A threshold of 2% yielded similar results.

Taxonomic richness was estimated using rarefaction analysis in ‘psimpoll’ software (Bennett 2007), based on the number of taxa present in each sample with a set count of 50 head capsules. The uppermost and bottommost samples were excluded from rarefaction due to low head capsule counts. Diversity was evaluated using Hill’s N2 measure of diversity (Hill 1973). Referred to as measures of true diversity (Jost 2006), Hill’s numbers are a suite of diversity measures that calculate the effective number of taxa within a sample (Birks et al. 2016). This number depends upon the distribution of the proportional abundances of the taxa. For example, a sample with an effective taxa of y , regardless of how many taxa are actually present and in what proportions, is considered as diverse as a sample with exactly y evenly distributed taxa (Birks et al. 2016). Hill’s N2 reflects the number of abundant taxa within a sample, and as such, is related to Simpson’s diversity measure (Birks et al. 2016). Evenness was calculated using $E_{1/D}$,

$$E_{1/D} = \frac{1/D}{S}$$

where D is Simpson’s Index, the sum of the squared proportions of taxa in an assemblage, and S is the total number of taxa present in a sample (Smith and Wilson 1996). All richness and evenness calculations were performed at a common taxonomic resolution i.e., genus or morphotype.

Estimation of Paleotemperature

Several models for estimating July paleotemperatures from the fossil chironomid assemblages at Lake Stowell were evaluated. Paleotemperatures at Lake Stowell were estimated using the calibration datasets and transfer functions of Barley et al. (2006) and Fortin et al. (2015) in C2 software version 1.7.6 (Juggins 2014), following the approaches outlined in those studies. All species composition data were square-root transformed percentage data, and taxa that were rare or absent in the original models were not included in the reconstructions, with the exception of *Apedilum*, due to its importance in the Lake Stowell record. July temperature data for the calibration datasets were obtained from New et al. (2002). All reconstructions are based on 2 component bootstrapped weighted average partial least squares (WA-PLS) with 9999 bootstraps for cross validation, and use root mean square error of prediction (bootstrapped) and bootstrapped r^2 for model evaluation.

Model A is based on the original transfer function of Fortin et al. (2015). The calibration dataset included 435 lakes from across Canada and Alaska, with most sites located north of 55° latitude. These sites are from a variety of environments, including high elevation lakes in the Canadian Cordillera and Alaska, low elevation lakes in the Northwest Territories, Nunavut and Quebec, and lakes throughout the Canadian Arctic Archipelago. Fortin et al. (2015) removed one of these sites, a particularly deep lake in the high Arctic, from their model after identifying it as an outlier, and as such, the final model was run using 434 sites. This model included all identified chironomid head capsules from 70 taxa as well as unknown head capsules in the calculation of percent composition.

Model B used the calibration dataset and transfer function developed by Fortin et al. (2015) but was built on a subset of the original data that consisted of the 145 sites that make up the Barley et al. (2006) calibration dataset. These sites are located along a north-south transect from southern British Columbia, through the Yukon and into Alaska, with additional sites in the Arctic Archipelago. In essence, Model B applies Fortin et al.'s (2015) transfer function to the sites in Barley et al. (2006). Like Model A, Model B included all identified chironomid head capsules from 70 taxa as well as unknown head capsules in the calculation of percent composition.

Models A and B were run both with and without early instar head capsules included in the unknown category. As this did not significantly change model output, early instars were excluded from the final model runs because not all sites in Fortin et al.'s (2015) calibration dataset included counts of early instars in the percentage calculations.

Model C is based on the calibration dataset and transfer function in Barley et al. (2006). A total of 145 sites were included in the original dataset as described in Model B. Barley et al. (2006) excluded nine sites that were identified as outliers; however, Fortin et al. (2015) showed that these sites were not outliers, and as such all 145 sites were included in this model. This model is based on all identified chironomid head capsules from 63 taxa including *Chaoborus* mandibles, but unlike Fortin et al. (2015), unknown head capsules were excluded from the sum in percent calculations.

These three models were then tested for statistical significance as well as modern analogue conditions. Statistical significance of the temperature reconstructions was tested using the 'palaeoSig' package (Telford 2015). The proportion of variance within the

fossil assemblages explained by the reconstructions was compared to reconstructions from transfer functions trained on random data (Telford 2015). Model-based reconstructed temperatures that explain more variability than 95% of the randomly generated reconstructions are considered significant (Telford 2015). Using the ‘analogue’ package (Simpson and Oksanen 2016) in R, fossil assemblages from the Lake Stowell sediment core were compared to modern assemblages from the sites in the training sets. Squared chord distance (SCD) between the fossil and modern assemblages were compared to the distribution of values among the training sets. SCDs greater than the 5th percentile of this distribution were identified as having no modern analogues (Simpson 2007).

Results

Sediment Stratigraphy and Chronology

The sediment core retrieved from Lake Stowell was 768.5 cm in length. From 0-579 cm, the sediment is dark brown gyttja. A 2-cm layer of tephra at 330.5-332.5 cm is likely derived from the Mt. Mazama eruption. From 579-604 cm, inorganic content increases, resulting in a light brown gyttja. The remainder of the core (604-768.5 cm) consists of light grey clay that, based on an abundance of marine diatoms (T. Lacourse, unpublished data), was deposited in a brackish to marine environment.

An age-depth model (Figure 5) was developed using the calendar age equivalents of the six AMS radiocarbon ages on plant macrofossils (Table 1), the established age of the Mt. Mazama tephra (7584 – 7682 cal yr BP; Egan et al. 2015), and an age of –63 cal yr BP for the top of the sediment core. This model estimates the age of the basal organic sediments at 604 cm to be 14,011 cal yr BP (13,835-14,195 cal yr BP 95% confidence interval), which is consistent with models of sea-level change for the Gulf Islands region (James et al. 2009).

Sediment accumulation rates estimated from the age-depth model are generally low and never exceed 0.08 cm/cal yr (Figure 5). Sediment accumulation rates are about 0.04 cm/cal yr throughout most of the record, but there is an interval of markedly lower rates (~0.02 cm/cal yr) between about 5300 and 3000 cal yr BP. Maximum rates of 0.08 cm/cal yr occur in the uppermost sediments.

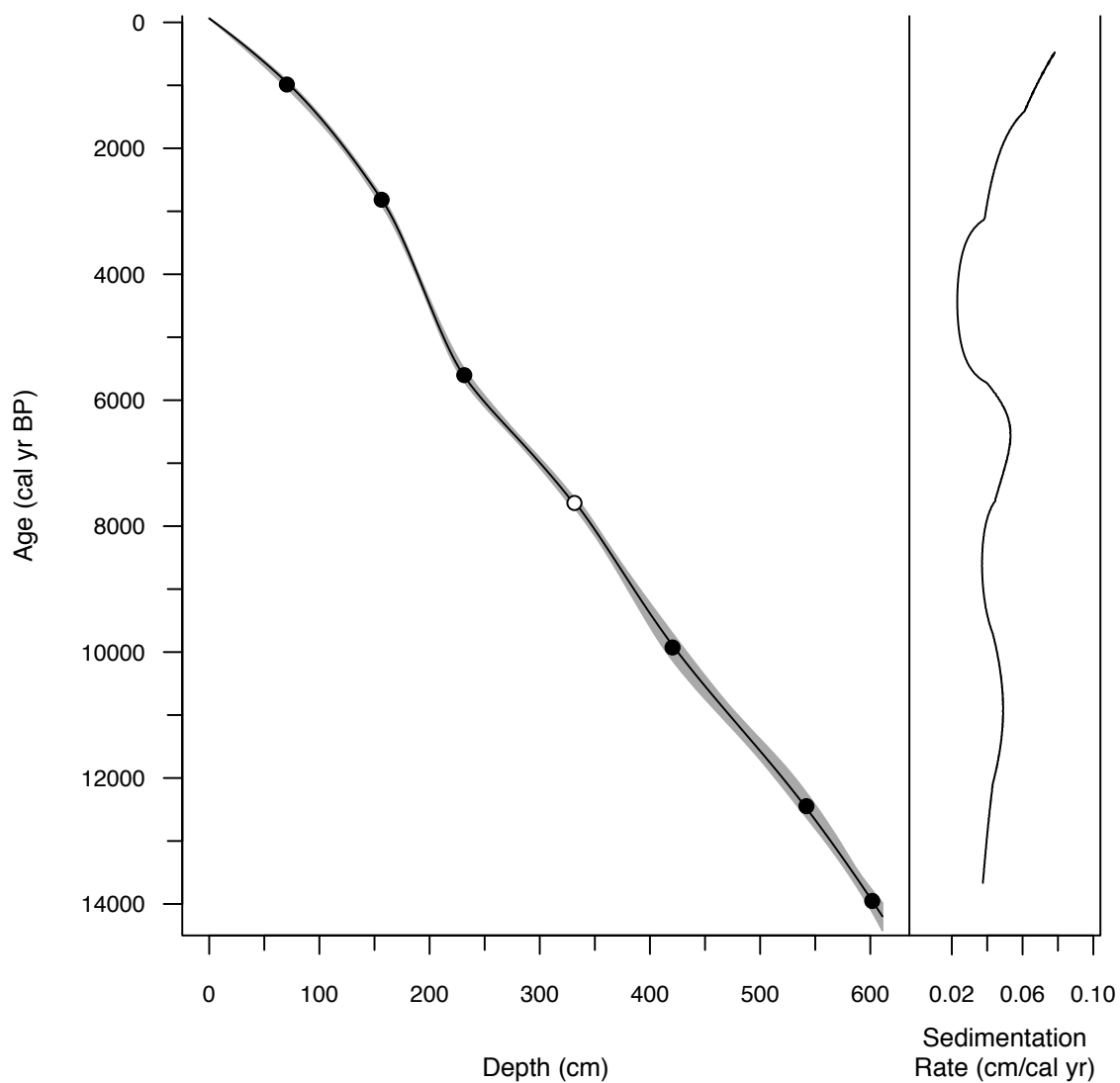


Figure 5. Age-depth model and associated sediment accumulation rates for the Lake Stowell sediment core. Grey bands show the 95% confidence intervals for the model. Solid black circles represent the calendar age equivalents of AMS radiocarbon ages on plant macrofossils (Table 1). The solid white circle represents the estimated age of Mt. Mazama tephra from Egan et al. (2015).

Table 1. AMS radiocarbon ages and calibrated calendar ages of six plant macrofossils recovered from the Lake Stowell sediment core as well as the estimated age of the Mt. Mazama tephra from Egan et al. (2015).

Depth (cm)	Material	Lab Code	AMS Radiocarbon Age (¹⁴ C yr BP ± 1σ)	Calendar Age Range ^a (cal yr BP)
70–71	<i>Pseudotsuga menziesii</i> needle and unidentified plant debris	Beta-365557	1040 ± 30	920 – 1050
156–157	<i>Pseudotsuga menziesii</i> seed	Beta-353388	2710 ± 40	2750 – 2880
231–232	Unidentified seed	Beta-283076	4880 ± 40	5490 – 5710
330.5–332.5	Mazama tephra	–	–	7580 – 7680 ^b
420–421	Poaceae stem	Beta-353390	8820 ± 40	9700 – 10,150
542	<i>Nuphar</i> seed	Beta-353392	10,520 ± 50	12,240 – 12,650
601.5–602	Woody twig	Beta-283077	12,100 ± 60	13,780 – 14,120

^a 2σ age range rounded to the nearest 10 yr

^b Egan et al. (2015)

Chironomid Assemblages

Chironomid head capsules were identified in a total of 121 samples spanning the last 14,200 cal yr. The mean time span between samples is 120 cal yr and individual samples represent 10 to 45 cal yr. A minimum of 50 head capsules were identified in all samples except the uppermost (0 cm) and bottommost (610 cm) samples because concentrations were too low to obtain this sample size. All head capsules present in each sample were examined. In most samples, greater than 60 head capsules were identified, with the largest sample size in an individual sample of 177 head capsules. Over the course of the record, 100 different taxa were identified in these samples. Taxa in the Tanytarsini group (Tanytarsina undifferentiated, *Tanytarsus*) and *Chironomus anthracinus*-type dominate much of the record (Figure 6). Several taxa including *Cricotopus/Orthocladius*, *Phaenopsectra flavipes*-type and *Einfeldia* are consistently present at low abundance. Many of the taxa present in the fossil assemblage prefer littoral habitat. Rheophilic taxa are rare. Assemblage diagrams of uncommon and rare taxa are included in the Appendix (Figures A2 and A3).

Numerical zonation of the chironomid assemblage data yielded similar results across the six techniques (Figure 7). Zonation based on optimal splitting by sum-of-squares was selected as best describing changes in chironomid assemblages within the sediment core. This technique identified six statistically significant zones that were consistent with multiple zonation techniques and highlighted important changes in the chironomid assemblages. The uppermost zone was deemed a subzone of the larger zone beneath it, based on similarity in composition and because it contains only two samples.

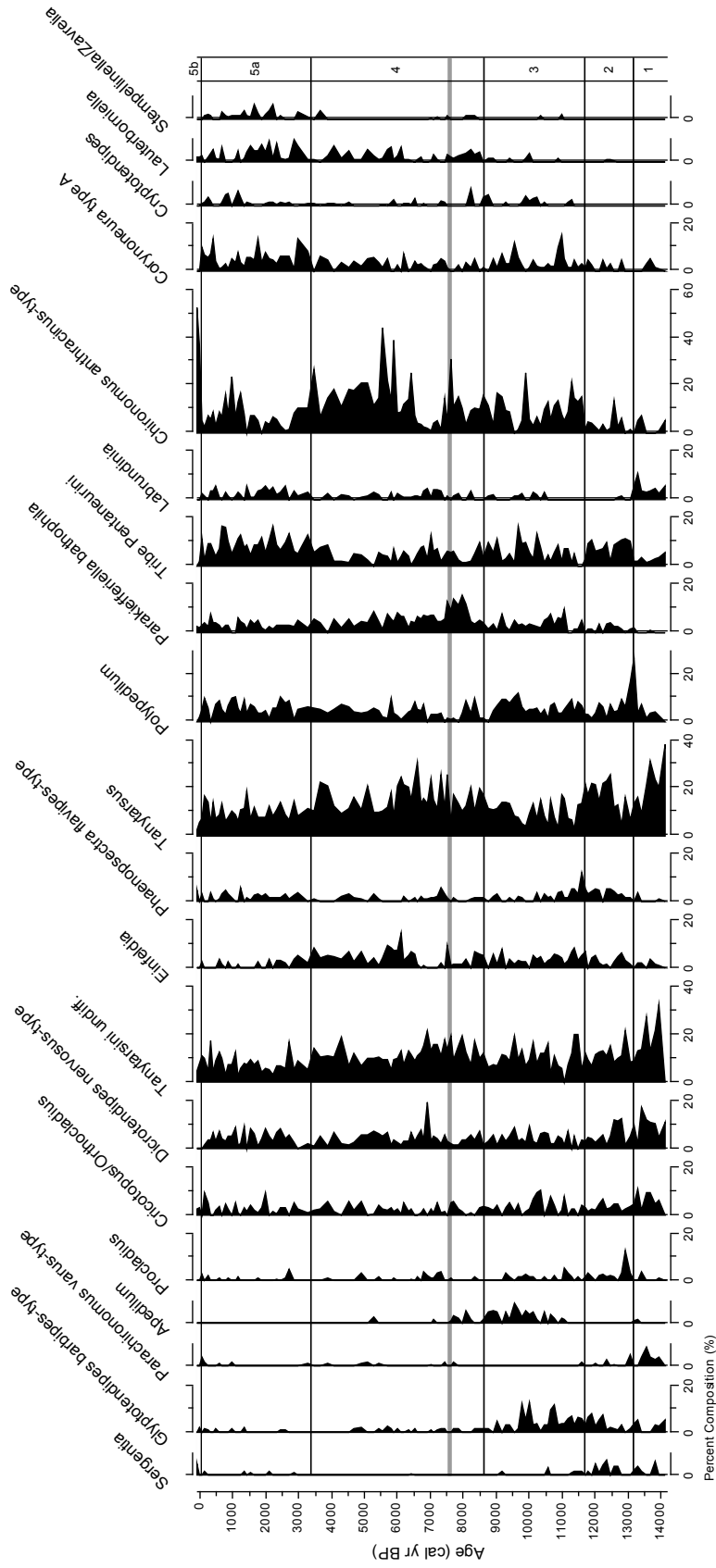


Figure 6. Percent composition of select chironomid taxa in the Lake Stowell sediment core, with zonation based on optimal splitting by sum-of-squares. Taxa are arranged left to right based on abundance through time (cal yr BP). The grey line across the diagram shows the stratigraphic position of the Mt. Mazama tephra.

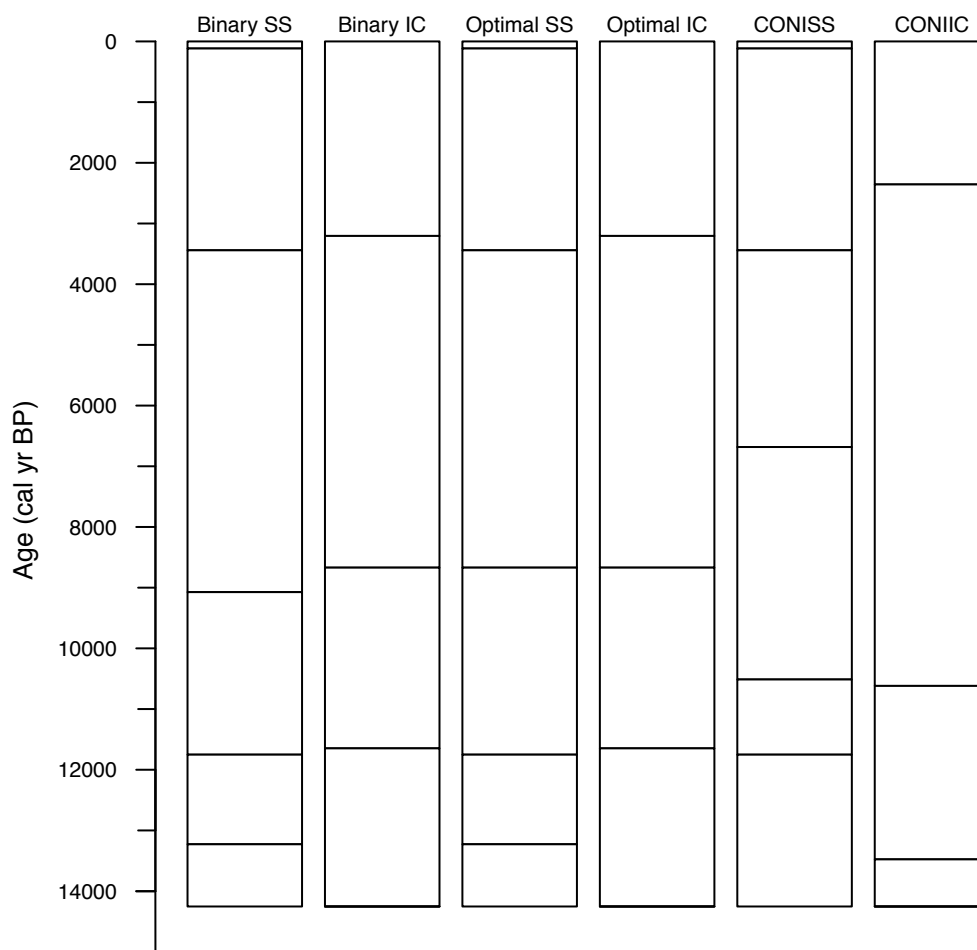


Figure 7. Results of six different zonation techniques applied to the chironomid assemblages from the Lake Stowell sediment core: binary splitting by sum-of-squares (Binary SS), binary splitting by information content (Binary IC), optimal splitting by sum-of-squares (Optimal SS), optimal splitting by information content (Optimal IC), constrained cluster analysis by sum-of-squares (CONISS), and constrained cluster analysis by information content (CONIIC). Only taxa that accounted for greater than 5% of sample sums were included in the cluster analyses. Horizontal lines indicate statistically significant zone boundaries. Optimal SS was selected as the model for best describing changes in chironomid assemblages within the sediment core.

Zone 1: 611 – 571 cm (~14,200 – 13,170 cal yr BP)

Zone 1 is comprised of eight samples from the late-glacial period. Head capsule concentrations and accumulation rates in this zone are relatively low compared to the rest of the sediment core, but increase through the zone (Figure 8). This zone is dominated by Tanytarsini and *Tanytarsus* spp. (Figure 6). Altogether, this group accounts for ~40% of the total chironomid assemblage in this zone with higher percent composition in the more basal samples. Zone 1 includes taxa at lower abundances that are found at both warm and cool sites within the calibration datasets. *Dicrotendipes nervosus*-type, a type adapted to warm July air temperatures, is consistently present, accounting for ~10-20% of the chironomid assemblages in this zone. *Sergentia* and *Cricotopus/Orthocladius*, found at cool sites, and *Labrundinia* and *Parachironomus varus*-type, found at warm sites, are present at 5-10% relative abundance. There is a peak in warm-adapted *Polypedilum* of 27% at the transition into Zone 2.

Zone 2: 571 – 506 cm (~13,170 – 11,690 cal yr BP)

Zone 2 consists of 13 samples that span the late-glacial to early Holocene transition. Head capsule concentration and accumulation rates increase to almost double that in the previous zone, with mean values of 38 HC/cm³ and 840 HC/cm²/cal yr, respectively (Figure 8). This zone is characterized by a continued dominance of Tanytarsini, constituting ~30% of the chironomid assemblage, and a continued low-level presence of *Sergentia* and *Cricotopus/Orthocladius* (Figure 6). Taxa associated with warm air temperature decrease in this zone, with *D. nervosus*-type declining to below

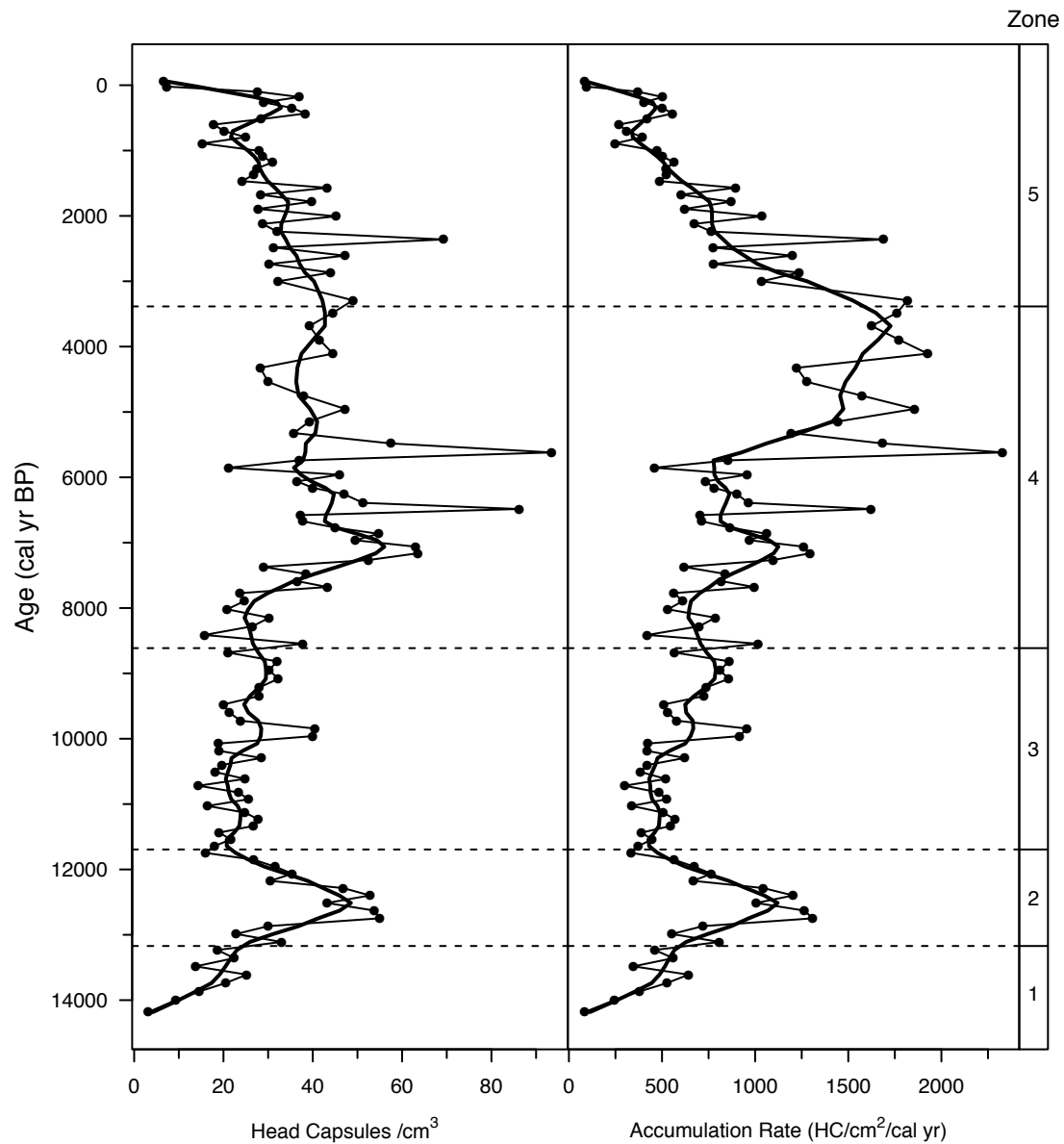


Figure 8. Chironomid head capsule concentrations and accumulation rates for the Lake Stowell sediment core. Thick black lines are locally weighted (LOWESS) regression lines with a span of 0.07 at 10 iterations.

5%, and *Labrundinia* and *P. varus*-type nearly absent. Pentaneurini increases in abundance to almost three times the levels observed in Zone 1. *Procladius* reach a peak abundance of 13% at the beginning of this zone, and decline throughout, becoming increasingly rare throughout the record. *Phaenopsectra flavipes* begins to appear consistently in this zone, reaching 5.5% at 12,400 cal yr BP. There are fewer taxa associated with submerged macrophytes compared to surrounding zones. Zone 2 marks the end of the continued substantial presence of *Sergentia*.

Zone 3: 506 – 371 cm (~11,690 – 8610 cal yr BP)

Zone 3 contains 27 samples and coincides with the early Holocene. Head capsule concentrations and accumulation rates decrease from the previous zone to mean values of 25 HC/cm³ and 565 HC/cm²/cal yr, respectively (Figure 8). Zone 3 is characterized by the presence of warm-adapted *Apedilum*, which appears almost exclusively in this zone (Figure 6), as well as an increase in *Chironomus anthracinus*-type. *Chironomus anthracinus*-type comprises ~10% of the chironomid assemblage in this zone, exceeding 20% in some samples, which is more than three times the percent abundance of previous zones. Taxa associated with cool sites in the calibration dataset such as *Sergentia* become increasingly rare, occurring only sporadically in Zone 3. Tanytarsini also decreases in relative abundance to ~20% of the total assemblage. In addition to the presence of *Apedilum*, other warm-adapted taxa increase in abundance in Zone 3. *Glyptotendipes barbipes*-type, present in older samples, increases in percent composition within this zone, while *Cryptotendipes* appears for the first time in the record. *Labrundinia* reappears

at 10,500 cal yr BP and establishes a consistent, low level presence of 1-5% for the remainder of the record.

Zone 4: 371 – 174 cm (8610 – 3390 cal yr BP)

Zone 4 is the largest zone with 39 samples extending through the middle Holocene. The highest levels of head capsule concentrations and accumulation rates occur in this zone, roughly double that observed in Zone 3 with mean values of 42 HC/cm³ and 1100 HC/cm²/cal yr, respectively (Figure 8). Both head capsule concentrations and influx values reach their maxima at approximately 5600 cal yr BP. As a result of relatively low sediment accumulation rates between ~5000 and 3000 cal yr BP, the trends between head capsule concentrations and accumulation rates diverge towards the end of Zone 4, with concentrations decreasing and accumulation rates remaining fairly high with values regularly exceeding 1500 HC/cm²/cal yr.

The Tanytarsini group is the dominant taxon in Zone 4, with similar percent composition to Zone 2 (Figure 6). *Chironomus anthracinus*-type is slightly more abundant in this zone than in the previous zone, and reaches a peak of ~45% at approximately 5600 cal yr BP, coincident with a peak in head capsule concentrations and accumulation rates. Taxa adapted to warm water decline through this mid-Holocene zone. For example, *Apedilum* is present before the Mazama tephra, and then nearly disappears. *Glyptotendipes barbipes*-type decreases to rare, sporadic appearances until approximately 4500 cal yr BP, where it disappears from the record until late in Zone 5. The decrease in *G. barbipes*-type is accompanied by decreases in other taxa (e.g., *Corynoneura* type A, *Apedilum*) that are also typically associated with submerged vegetation.

A mixture of cool- and warm-adapted taxa are present in this zone. Cool-adapted *Parakiefferiella bathophila*-type reaches peak abundance of ~7% immediately before the Mazama tephra, and then persists at low levels for the remainder of the record. Warm-adapted taxa such as *Labrundinia* and *Lauterborniella* also persist at relatively low percentages. Pentaneurini is also present at levels around 5%. Although there is a short absence following the Mazama tephra layer, *Einfeldia*, another warm-adapted taxon, is at its most abundant in this zone, increasing in abundance to a maximum of 14% at ~6200 cal yr BP.

Zone 5: 174 – 0 cm (~3390 cal yr BP to the present)

Zone 5 consists of two statistically significant subzones coinciding with the late Holocene. Head capsule concentrations and accumulation rates decrease consistently in this zone, with a sharp decrease to the lowest observed levels of 7 HC/cm³ and 84 HC/cm²/cal yr, respectively in the uppermost sample (Figure 8).

Zone 5a contains 30 samples and is characterized by an increased number of taxa present in comparison to Zone 4. There is a decrease in the proportions of the previously dominant Tanytarsini as well as *Chironomus anthracinus*-type with mean percentages of 20% and 8%, respectively (Figure 6). Pentaneurini and *Corynoneura* type A sustain frequencies of 10 to 20% for much of this zone. Several previously rare taxa that are present at warm sites in the calibration dataset reach peak relative abundances in this zone. This includes *Lauterborniella*, which has the second highest temperature optimum of all taxa identified in the record and reaches its peak abundance of 9% at ~2100 cal yr BP. Other warm-adapted taxa (e.g., *Stempellinella/Zavrelia*, *Labrundinia*,

Cryptotendipes) sustain populations at <5% of the total throughout this zone. Zone 5b consists of only the two uppermost samples, which are characterized by a dramatic increase in *Chironomus anthracinus*-type to ~50% of the total chironomid assemblage.

Taxonomic Richness, Diversity and Evenness

Richness varies between 13.2 and 25.0 taxa, averaging 19.0 taxa/sample over the course of the entire record (Figure 9). Richness is initially low, at 13.2 taxa/sample, in the late-glacial interval, gradually increasing through to ~12,900 cal yr BP, when it stabilizes at ~19 taxa/sample. The early Holocene, approximately 11,500 to 8200 cal yr BP, is characterized by high richness. These high levels begin to decrease during the latter part of the early Holocene. After ~9000 cal yr BP, richness decreases through the middle Holocene to levels similar to those in the late-glacial. Richness generally increases after 6000 cal yr BP, reaching a maximum of 25.0 taxa/sample at approximately 2100 cal yr BP. This period of increased richness is not as stable or as extended as in the early Holocene, and richness decreases from this point to the present.

Diversity ranges from 8.6 to 27.2 effective taxa throughout the core (Figure 9). Diversity is low in the late glacial with the lowest measure of effective taxa in the bottommost sample at 14,200 cal yr BP. Diversity increases from this low point to 18.1 effective taxa at ~13,000 cal yr BP, and fluctuates around this value for the majority of the record. There are a few anomalously low values in the early and middle Holocene where diversity is similar to that observed before 13,500 cal yr BP. There is a minor increase in diversity in the late Holocene, where the maximum Hill's N2 of 27.2 effective

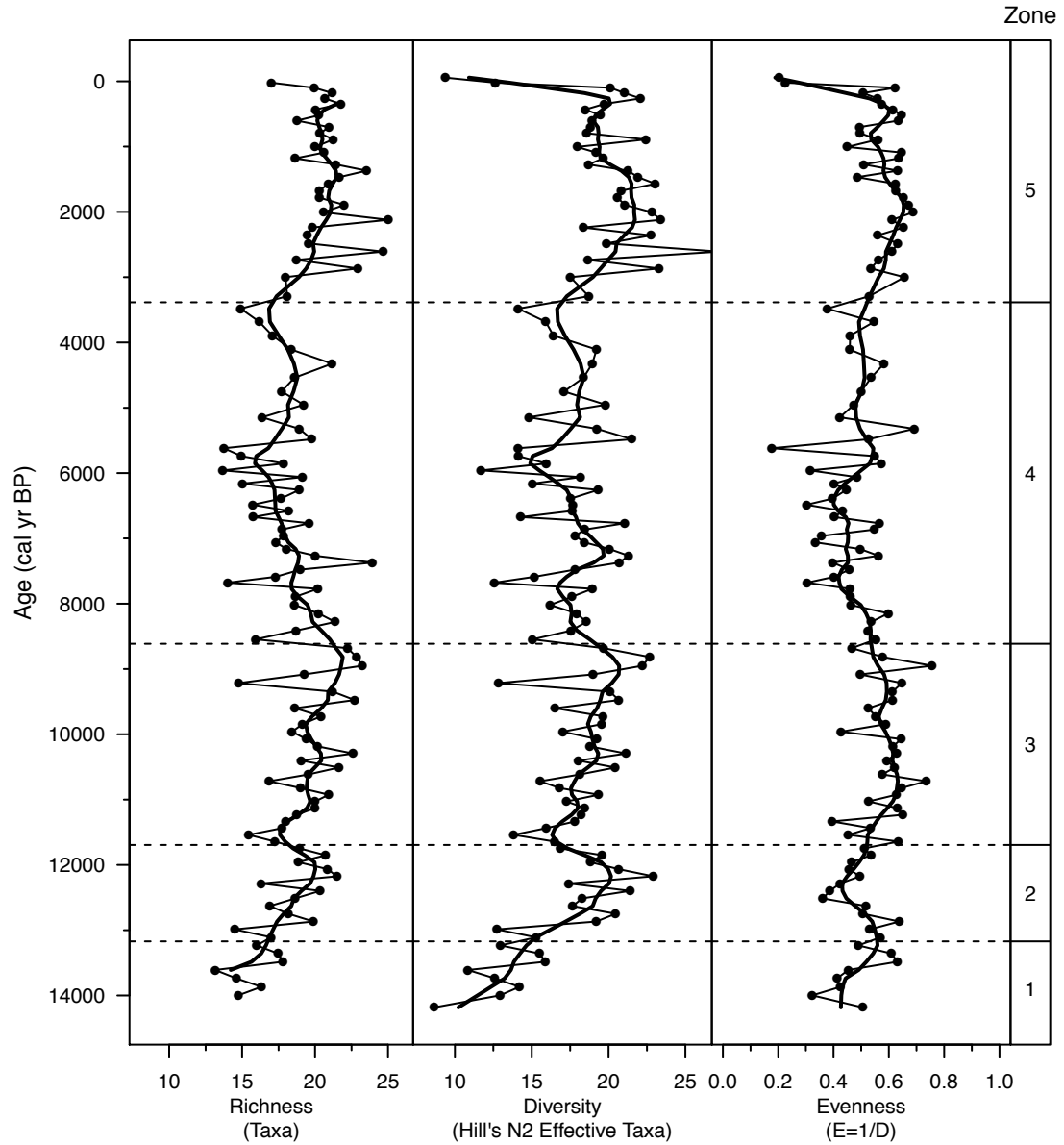


Figure 9. Richness, diversity and evenness of the Lake Stowell chironomid assemblages. The uppermost and bottommost samples were excluded from richness calculations due to low sample sizes. Thick black lines are locally weighted (LOWESS) regression lines with a span of 0.07 at 10 iterations.

taxa is observed at ~2600 cal yr BP. Diversity remains high before decreasing dramatically in the two uppermost samples to 12.6 and 9.4 effective taxa, respectively.

Evenness is fairly consistent throughout the chironomid record, fluctuating around 0.5 for the majority of the record (Figure 9); however, evenness is generally higher in the early and late Holocene than in the mid-Holocene. Evenness drops to its lowest value of 0.18 at ~5600 cal yr BP and is similarly low in the two uppermost samples. These isolated minima are associated with dramatic increases in the abundance of *Chironomus anthracinus*-type.

Chaoborus

Chaoborus mandibles were found up to a depth of 474 cm (~11,000 cal yr BP), but only occur consistently at numbers greater than two individuals in the top 100 cm (~1500 cal yr BP) (Figure 10). *Chaoborus* mandibles in most samples are either *C. flavicans* or *C. trivittatus*. *Chaoborus* (*Sayomyia*) occurs sporadically and *C. americanus* is limited to surface sediments. In the uppermost sediment sample (0-1 cm), *Chaoborus* mandibles account for 48% of all identified aquatic midge remains, with 27% identified as *C. flavicans* and 11% as *C. trivittatus*. At 6-7 cm, *Chaoborus* account for 20% of all identified aquatic midge remains, with the two dominant taxa occurring in equal abundance. Below this level, *Chaoborus* never comprise >5% of the total subfossil assemblage, and only occur above 3% once.

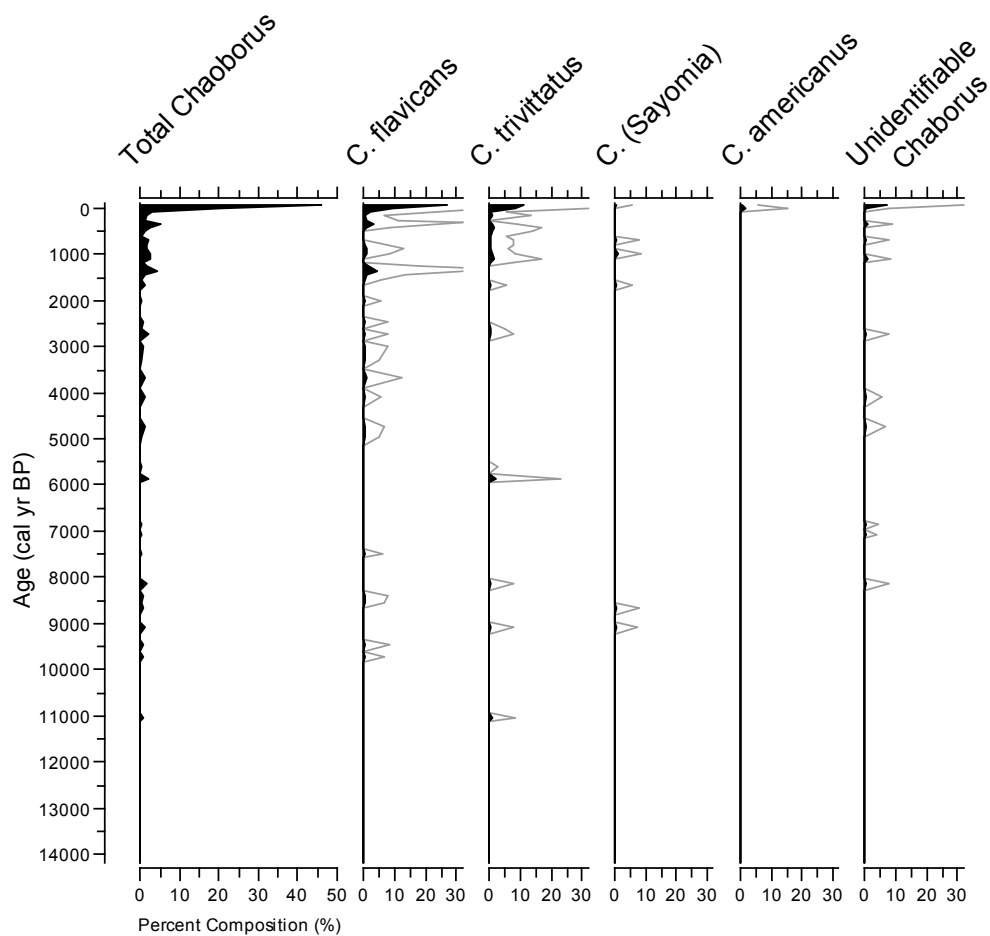


Figure 10. Percent composition of *Chaoborus* taxa in the Lake Stowell sediment core. Grey lines represent a 10× exaggeration of relative abundance. Percentages are based on all identified aquatic midge remains.

Inferred July Paleotemperature

Summary of Model Results

All three models exhibit broadly similar changes in July paleotemperature, differing primarily in the magnitude of temperature change. Inferred temperatures are lowest in the most basal samples, and then warm from this late-glacial minimum until a brief cooling between ~13,000 and 11,700 cal yr BP that coincides with the Younger Dryas chronozone. Temperatures then rapidly increase to an extended plateau of higher temperatures from 10,500 to 8000 cal yr BP. This early Holocene warm period is followed by generally cooler inferred temperatures in the mid-Holocene until about 3000 cal yr BP. Inferred temperatures reach a local peak around 2000 cal yr BP before cooling to present.

Model A estimates the largest range of temperatures followed by Model B and Model C. Although none of the models are statistically significant, Model A performs well in the modern analogue technique with 85% of fossil samples having good analogues in the full Fortin et al. (2015) calibration dataset, compared to only 51% and 47% in Models B and C, respectively. Model A also has a substantially lower maximum bias than Models B and C (Table 2). What follows is a breakdown of each model focusing on the paleotemperature estimates produced by each model and their associated performance. As none of the models were found to be statistically significant, it is important to apply them with caution.

Model A

Paleotemperature estimates based on the full calibration dataset published by Fortin et al. (2015) range between 12.1 °C and 18.6 °C (Figure 11A). Significance testing indicates that this model does not explain a significant amount of variation within the fossil assemblages ($p = 0.45$) (Figure 12A). However, only 18 fossil samples (i.e., 15% of all Lake Stowell samples) were identified as having poor analogues in the modern calibration dataset (Figure 12B). This model has a root mean square error of prediction (RMSEP) of 1.87 °C and a bootstrapped r^2 of 0.725 (Table 2).

The coolest reconstructed temperatures in the record are found in the most basal samples. Although the lowermost samples (13.6 – 13.8 °C) are warmer than those immediately following, inferred temperatures reach a local minimum of 12.5 °C around 13,700 cal yr BP before increasing. This increase in temperature is relatively rapid, reaching values around 15 °C within 500 cal yr. This rapid warming is interrupted by a cooler period from approximately 13,000 – 11,900 cal yr BP with a minimum of 12.1 °C at ~12,300 cal yr BP. Inferred temperatures rise after this cool period, with estimated July temperatures generally greater than 14.5 °C. This warming is increasingly rapid, particularly between 11,000 and 10,500 cal yr BP when temperatures increase approximately 3 °C in 500 years.

An extended period of stable, warm temperatures is present from 10,300 to 8100 cal yr BP. During this period, estimated temperatures regularly exceed 16 °C, with a maximum temperature of 18.3 °C around 9800 cal yr BP. Slightly cooler temperatures are inferred between 9500 and 9200 cal yr BP, coincident with a single *Sergentia* head capsule and a slight decrease in *Labrundinia*.

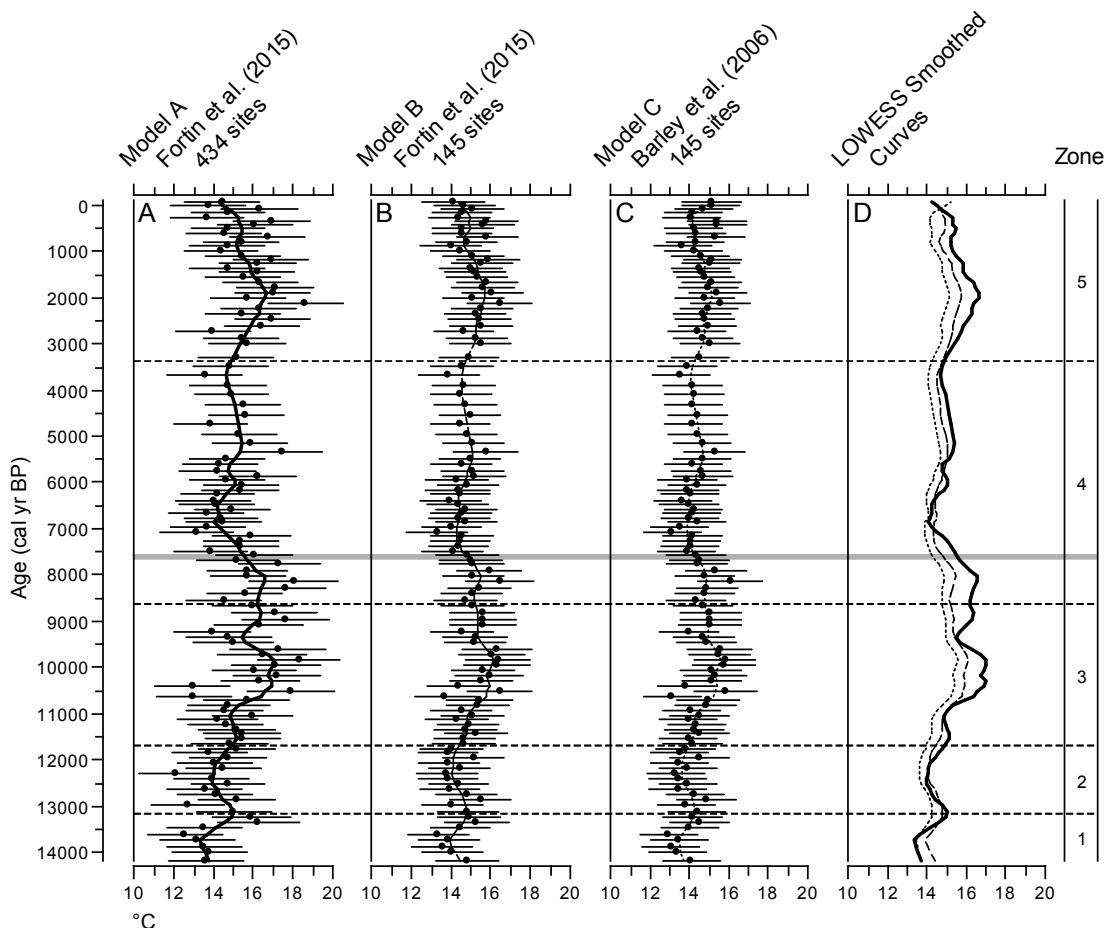


Figure 11. Mean July temperature reconstructions for the Lake Stowell sediment core. A. Model A based on the full Fortin et al. (2015) dataset and transfer function, B. Model B based on a subset of the Fortin et al. (2015) dataset and transfer function, and C. Model C based on the Barley et al. (2006) calibration dataset and transfer function. Black circles represent temperature estimates and horizontal lines represent root mean square error of prediction (A - 1.87 °C; B - 1.56 °C; C - 1.48 °C). The smoothed lines on all figures are locally weighted (LOWESS) regression lines with a span of 0.07 at 10 iterations. All three smoothed curves are presented together in (D) to allow for direct comparison. The solid black line represents Model A, the dashed line represents Model B, and dotted line represents Model C. The grey band across the diagram shows the stratigraphic position of the Mt. Mazama tephra.

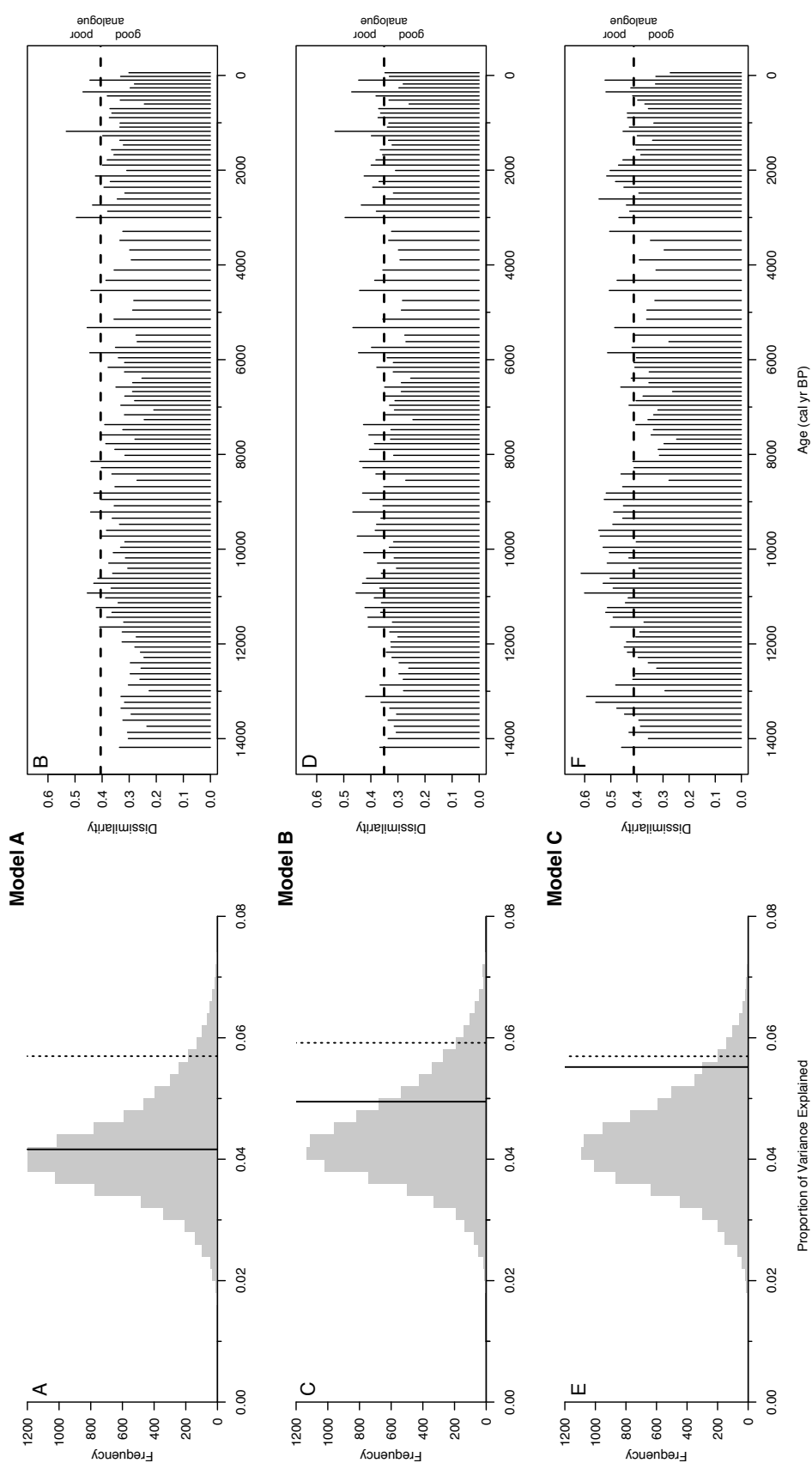


Figure 12. Model evaluation for the three models shown in Figure 11. Histograms in panels A, C and E show the distribution of variance within the fossil assemblages explained by transfer functions trained on random data: the thin dotted line represents the 95% quantile of this distribution, and the solid vertical line represents the proportion of variance explained by the paleotemperature reconstruction. Modern analogue conditions are shown in panels B, D and F: vertical lines represent the dissimilarity between individual samples and modern sites, and the dashed horizontal line represents the 5th percentile of dissimilarities, separating good and poor modern analogue conditions.

Table 2. Performance statistics of the three July temperature transfer functions applied to the Lake Stowell chironomid stratigraphy.

Performance Indicator	Model A	Model B	Model C
Bootstrapped r^2	0.725	0.826	0.838
RMSEP ^c (°C)	1.87	1.56	1.48
Maximum Bias	2.13	3.55	3.48
Proportion Variance Explained	0.04	0.05	0.05
palaeoSig test (p -value)	0.45	0.24	0.07
PCA Axis 1	0.11	0.12	0.11
Min. July Temperature (°C)	12.14	13.30	12.93
Max. July Temperature (°C)	18.63	16.49	16.08
Temperature Range (°C)	6.49	3.19	3.15
Good Modern Analogues (%)	85	51	47

^c Root Mean Square Error of Prediction

Following this warm period, inferred temperatures decrease reaching a local minimum around 7000 cal yr BP. Temperatures then increase slightly, stabilizing about 5500 cal yr BP at approximately 14.9 °C and corresponding generally with Zone 4 of the chironomid assemblage. Inferred temperatures increase at the beginning of Zone 5, gradually reaching ~17 °C around 2000 cal yr BP before decreasing towards the present.

Model B

Model B is based on a subset of Fortin et al. (2015) dataset with the same parameters as the original model. Temperature estimates range between 13.3 °C and 16.5 °C (Figure 11B), with a RMSEP of 1.56 °C and bootstrapped r^2 of 0.826 (Table 2). Significance testing indicates that this model does not explain a significant amount of variation within the fossil assemblages ($p = 0.24$) (Figure 12C). The modern analogue technique identified 59 samples (i.e., 50% of all Lake Stowell samples) as having poor modern analogues in this subset of the Fortin et al. (2015) calibration dataset (Figure 12D).

Temperature estimates in the most basal part of the core are consistently cool, with a local minimum of 13.4 °C occurring at ~13,600 cal yr BP. After this late-glacial minimum, inferred temperatures begin to increase, reaching upwards of 15 °C. A cooler period from 12,700 – 12,000 cal yr BP interrupts this warming, and temperatures decrease to a local minimum of 13.8 °C at 12,300 cal yr BP. Inferred temperatures gradually increase from this point to a sustained warm period between 10,300 and 7800 cal yr BP, when temperatures regularly exceed 15 °C. Inferred temperature estimates then drop by about 1°C and fluctuate around 14.6 °C through the middle Holocene. After 2700 cal yr BP, temperatures increase with a brief period of inferred temperatures comparable to those in the early Holocene, peaking at 2100 cal yr BP. Following this peak, inferred temperatures decrease to present, with increased variation between samples.

Model C

Temperature estimates based on the Barley et al. (2006) calibration dataset and transfer function range between 12.9 °C and 16.1 °C (Figure 11C) with a RMSEP of 1.48 °C and a bootstrapped r^2 of 0.879 (Table 2). As with Models A and B, significance testing indicates that Model C does not explain a significant amount of variation within the fossil assemblages ($p = 0.07$), although this model is the closest to achieving statistical significance (Figure 12E). The modern analogue technique identified 64 samples (i.e., more than half of all Lake Stowell samples) as having poor modern analogues in the Barley et al. (2006) calibration dataset (Figure 12F).

The most basal temperature estimates are the coolest part of the record with inferred temperatures at a minimum of 12.9 °C around 13,600 cal yr BP. Inferred

temperatures then increase slightly, reaching upwards of 14.5 °C before cooling by 0.5 °C between 12,700 and 11,700 cal yr BP. Inferred temperatures increase from this point, and a sustained period of warm temperatures extends from 10,500 to 7900 cal yr BP, when mean inferred temperature is ~15.2 °C. Temperatures at the beginning of this period are warmer (15.8 °C) than those estimated at the end (14.9 °C). Beginning around 7800 cal yr BP, inferred temperatures decrease and stabilize around 14.2 °C. Around 3000 cal yr BP, temperatures increase by about 1.5 °C to a local maximum at 2000 cal yr BP followed by a return to inferred temperatures of ~15 °C. In the uppermost samples, temperatures increase rapidly by about 1 °C.

Discussion

Chironomid Assemblages at Lake Stowell

Lake Stowell has a rich and diverse assemblage of chironomids throughout its entire record, with rarefaction estimates regularly exceeding 18 taxa/sample. In other paleoenvironmental studies, this level of richness is typically only observed in the warm early Holocene (e.g., Palmer et al. 2002; Porinchu et al. 2003). In a study of modern lake sediments across British Columbia, Walker and Mathewes (1989b) found elevated diversity at low elevation sites, such as coastal lakes. These low-elevation sites contain more species of the tribe Chironomini, compared to Orthoclaadiinae, than high elevation sites (Walker and Mathewes 1989b). While Lake Stowell has approximately the same number of Chironomini and Orthoclaadiinae taxa, Chironomini are much more abundant. However, most taxa are present at low relative abundances, a pattern that is typical of other coastal lakes in British Columbia (e.g. Walker and Mathewes 1989a). Relatively subtle changes in chironomid community composition over time are in contrast to higher elevation, continental lakes, where more dramatic changes in taxa are observed at times of environmental change (e.g. Smith et al. 1998; Pellatt et al. 2000; Palmer et al. 2002; Rosenberg et al. 2004).

As with many chironomid-based studies across British Columbia (e.g. Palmer et al. 2002; Rosenberg et al. 2004; Chase et al. 2008), much of the Lake Stowell chironomid record is dominated by Tanytarsini. This group is ubiquitous throughout the region (Walker and Mathewes 1989b) but tends to be most abundant in cool late-glacial and mid- to late Holocene assemblages (Walker and Mathewes 1988; Smith et al. 1998). The

other dominant taxon of the Lake Stowell record, *Chironomus*, is also common in the region, and generally occurs most commonly in early Holocene assemblages (e.g. Walker and Mathewes 1989a; Smith et al. 1998; Rosenberg et al. 2004).

Cold-stenotherms are often restricted to late-glacial assemblages (Walker and Mathewes 1988; Kaufman et al. 2012). Taxa indicative of cold-water conditions include *Heterotrissocladius*, *Stictochironomus* and *Sergentia*. These taxa are uncommon in the Lake Stowell sediment core; only *Sergentia* occurs consistently throughout the late-glacial at levels greater than 5%. *Sergentia* is also one of the few oligotrophic-mesotrophic taxa identified in the Lake Stowell record. As most other chironomid studies in British Columbia were conducted at high elevation or continental sites, late-glacial conditions presumably were cooler than in the Gulf Islands, leading to higher abundances of cold-adapted taxa than at Lake Stowell. In addition, some of these sites are fed by glacial meltwater (e.g. Palmer et al. 2002), further depressing temperature and creating more favourable conditions for taxa such as *Sergentia*. At lower elevation sites such as Lake Stowell, cold-stenotherms are usually restricted to the earliest sediments following deglaciation (e.g. Walker and Mathewes 1988, 1989a).

At Lake Stowell, several warm-water taxa (e.g., *Parachironomus varus*-type, *Dicrotendipes* and *Labrundinia*) account for a substantial portion of the late-glacial chironomid assemblages. Walker and Mathewes (1988, 1989a) noted the presence of *Dicrotendipes* during the late-glacial at other low-elevation coastal lakes in British Columbia at similar abundances to those observed in the Lake Stowell record. A comparatively diverse late-glacial assemblage is common to these coastal lakes (Walker and Mathewes 1988, 1989a). The Lake Stowell assemblages contain additional warm-

adapted taxa not observed in the records of more northern sites, and this, along with the absence of oligotrophic cold-stenotherms other than *Sergentia* make the late-glacial assemblage of Lake Stowell distinctive within the published literature for the region.

The bottom-most assemblages at Lake Stowell may be influenced by environmental conditions other than temperature. Chironomid assemblages are known to respond to changes in salinity (e.g. Walker and Heinrichs 1995; Heinrichs et al. 2001). Since Lake Stowell is an emergent coastal lake, the transition from a marine/brackish environment to a freshwater lake in the early development of the lake likely had an effect on the earliest chironomid assemblages. This transition is clearly demarcated in the sediment record through a change from marine clay to organic lake sediments and since approximately 14,000 cal yr BP, a freshwater environment has been constant within the lake.

Another distinguishing feature of the Lake Stowell sediment core is the presence of *Apedilum* in early Holocene sediments. *Apedilum* appears to be uncommon in British Columbia, and is not included in the published data from a survey of modern lake sediments conducted by Walker and Mathewes (1989b). It has been identified in both the Cariboo-Chilotin and Okanagan regions of British Columbia, and has been present in the Okanagan region since the early Holocene (Rück et al. 1998). Although *Apedilum* is present in the calibration datasets used in this study (Barley et al. 2006; Fortin et al. 2015), it is rare throughout the Holarctic region and it was excluded from the original transfer functions of Barley et al. (2006) and Fortin et al. (2015) for this reason. *Apedilum* has been identified in modern invertebrate communities in the southeastern US (Jacobsen

and Perry 2007; Tronstad et al. 2007) and Argentina (Donato et al. 2008; Epele et al. 2012) where summer temperatures are much higher.

The early Holocene at Lake Stowell is characterized by minor increases in the abundance of warm-adapted taxa and decreases in taxa associated with cool temperatures in the calibration datasets, such as *Tanytarsus*. At other sites in British Columbia, multiple warm-adapted taxa such as *Stempellina/Zavrelia* and *Dicrotendipes* markedly increase in abundance during the early Holocene (Smith et al. 1998; Pellatt et al. 2000; Palmer et al. 2002; Chase et al. 2008). At Lake Stowell, *Stempellina/Zavrelia* is nearly absent from the early Holocene and *Dicrotendipes* does not dramatically change in abundance relative to older assemblages. Only *Chironomus anthracinus*-type, a warm-adapted taxon in British Columbia that is common during the early Holocene (e.g. Smith et al. 1998; Chase et al. 2008), increases markedly in abundance at the beginning of the early Holocene in the Lake Stowell record.

The middle Holocene assemblages at Lake Stowell are characterized primarily by decreases in taxa that are associated with warm summer air temperature sites and submerged macrophytes, with corresponding increases in the Tanytarsini group. These assemblages are similar to assemblages from across the province (e.g. Palmer et al. 2002; Rosenberg et al. 2004). The late Holocene is characterized by the increased relative abundance of many previously infrequent taxa, such as *Lauterborniella*, *Stempellinella/Zavrelia*, and *Labrundinia*, which are adapted to warm conditions. This overall increase in warm-adapted taxa during the late Holocene is in contrast to the majority of chironomid studies across southern British Columbia, where the late Holocene is differentiated by a decrease in the presence of warm-adapted taxa (e.g. Smith

et al. 1998; Chase et al. 2008) and in some cases, the return of cold stenotherms (Walker and Mathewes 1989a; Pellatt et al. 2000).

The two uppermost samples are dominated by *Chironomus*, which prefers eutrophic habitats and is often one of the first taxa to dominate after rapid environmental change (Brooks et al. 2007). Although its dominance in the uppermost sediments may be in part an artefact of smaller sample sizes, the dramatic increase in *Chironomus* coincides with increased anthropogenic influence on the lake and surrounding watershed in the form of large scale settlement of Saltspring Island and the establishment of farms over the last 100 years (Hamilton 1969).

***Chaoborus* and Fish at Lake Stowell**

The analysis of *Chaoborus* mandibles in the Lake Stowell sediment core is limited due to the low concentrations of preserved remains. In recent sediments, four species of *Chaoborus* were distinguished, although most were identified as either *C. flavicans* or *C. trivittatus*. Both of these species are capable of diurnal migration within the water column, and therefore avoiding predation (Uutala 1990). *Chaoborus flavicans* is a particularly common species in low-elevation lakes throughout Canada (Lamontagne et al. 1994; Wissel et al. 2003). The dominance of *Chaoborus* species that can avoid predation is expected at Lake Stowell, given that there are established populations of threespine stickleback, rainbow trout and cutthroat trout that occur both naturally and due to recent stocking. However, *C. americanus* mandibles occur sporadically in the uppermost sediments, which is surprising as this species is reported in the literature as being restricted to fishless lakes (Uutala 1990; Walker 2001; Quinlan and Smol 2010).

In recent years, there has been a move towards identification of *Chaoborus* mandibles to species to better understand the conditions that influence their presence and abundance (e.g. Wissel et al. 2003; Quinlan and Smol 2010). While both *C. flavicans* and *C. trivittatus* are found in lakes with fish, they have also been found in fishless lakes (Garcia and Mittelbach 2008), and therefore they are not definitive indicators of past fish presence. Similarly, *C. americanus* is not restricted to fishless lakes since mandibles of this species occur in the surface sediments at Lake Stowell, though they are rare. Wissel et al. (2003) found *Chaoborus (Sayomyia)* populations are controlled more by their response to other *Chaoborus* than by the presence of fish.

The results at Lake Stowell, in combination with studies on the modern ecology of *Chaoborus*, do not support the use of fossil *Chaoborus* mandibles as simple indicators of past fish presence or absence in paleolimnological studies. The characterization of lakes into broad categories of fish and fishless using *Chaoborus* mandibles is too general to capture the details of limnological properties influencing *Chaoborus* populations. Quinlan and Smol (2010) proposed a more nuanced, hierarchical response categorization of lakes based on oxygen availability and dissolved organic carbon (DOC) as well as the presence and abundance of fish within thermally stratified lakes. A model such as this may identify factors aside from fish presence that affect *Chaoborus* populations and allow for a better understanding of paleolimnological conditions. According to Quinlan and Smol (2010), *Chaoborus* are abundant when hypolimnetic oxygen levels are low, which is consistent with modern conditions at Lake Stowell (Ormond et al. 2011). In addition, *C. trivittatus* dominates when there are ‘few’ species of fish, while *C. flavicans* dominates when there are ‘abundant’ fish species and high DOC, which is also more or

less consistent with modern conditions at Lake Stowell. However, past oxygen availability and DOC levels at Lake Stowell cannot be reliably inferred from *Chaoborus* mandibles due to small sample sizes (Quinlan and Smol 2010).

Evaluation of Inferred Paleotemperatures

Paleotemperature reconstructions were developed from the Lake Stowell chironomid record using three different combinations of calibration sets and transfer functions (Figure 11) to determine the best model for this site. The performance statistics of all three models were similar: bootstrapped r^2 for all models exceed 0.72, and root mean square error of prediction (RMSEP) ranged between 1.48 and 1.87 °C (Table 2). In each case, RMSEP was substantially lower than the range of paleotemperatures inferred by the models. Maximum bias was lowest in Model A (Table 2). The most pronounced difference among the models was the amplitude of inferred temperature changes. Model performance in this study is comparable to other studies including, for example, that of Upiter et al. (2014), where two transfer functions based on separate calibration datasets were applied to one paleoenvironmental record. Barley et al. (2006) was one of the datasets investigated by Upiter et al. (2014), and returned the smallest range of temperatures, as was the case in this study at Lake Stowell.

Significance Testing

Significance testing of the three paleotemperature models, using the ‘palaeoSig’ test developed by Telford and Birks (2011), indicated that no model was statistically

significant (Table 2). Accordingly, the paleotemperature reconstructions should be treated cautiously.

Telford and Birks (2011) highlight the limitations and complexities associated with this particular significance test. The ‘palaeoSig’ test may produce false positives when data are spatially autocorrelated and there are a number of possible reasons for Type II errors (Telford and Birks 2011). These include a low number of effective species, a small number of fossil samples used in the reconstruction, and poorly performing transfer functions (Telford and Birks 2011; Salonen et al. 2013), none of which appear to be an issue in the present study. Telford and Birks (2011) also indicate that limited variability in the quantitative reconstruction may cause failure of the ‘palaeoSig’ test, which likely plays a part in explaining the results at Lake Stowell, where the maximum range of temperatures within the models is 6.5 °C. Four chironomid-based paleotemperature reconstructions were tested by Telford and Birks (2011). The two that produced significant results ($p < 0.05$; Brooks and Birks 2000a, 2000b) had much larger ranges in their reconstructed temperatures than those that did not (Velle et al. 2005b; Brooks 2006). Relatively low variability in the Lake Stowell reconstructions likely explains why all three models were not deemed statistically significant by the ‘palaeoSig’ test.

Additional testing of the performance of the ‘palaeoSig’ test has raised other potential problems with interpretation of the test results. Payne et al. (2016) tested the significance of 30 testate amoeba-based water table reconstructions using the ‘palaeoSig’ test and found that only five were statistically significant ($p < 0.05$), with 17 of the remaining reconstructions having p -values that exceeded 0.40. In examining both the

reconstructions that passed and failed the significance testing, Payne et al. (2016) were unable to identify a common reason for either based on the weaknesses identified by Telford and Birks (2011). Luoto et al. (2014) showed that the size of the training set alone can have a dramatic effect on whether a reconstruction reaches statistical significance. Larger training sets, even those containing smaller training sets that test as significant, tend to return higher p -values (Luoto et al. 2014). This is demonstrated with the models applied to the Lake Stowell record: Model A, which consists of 434 sites, has a higher p -value ($p=0.45$) than Model B ($p=0.24$), which is built using the same model conditions but on a subset ($n=145$) of the same sites. Although it has been suggested that this test ‘may be overly pessimistic’ (Payne et al. 2016), the results of the test have been qualified by the developers as a tool for interpretation of results (Telford and Birks 2011). A quantitative significance test is an excellent step to standardizing a field where subjective judgements are common; however, a holistic understanding of transfer functions and ecological factors are necessary to evaluate the results.

Modern Analogue Technique

To identify modern analogues, fossil assemblages were compared to the modern assemblages in each of the models. Model A, based on the full Fortin et al. (2015) calibration dataset, provided the greatest number of good modern analogues (85%). The number of poor analogues was much higher in the other two models, both of which had ~50% poor modern analogues throughout the Lake Stowell record. In Models B and C, the majority of the Lake Stowell samples without good analogues in the modern calibration datasets occur during warm intervals, primarily the early and late Holocene

(Figure 12). As all three models are based on datasets dominated by ‘cold’ sites located mostly at northern latitudes or high elevations, this pattern is not unexpected. Training sets aim to establish a gradient along a single environmental variable. In this case, the training sets used latitude as a way to expand the temperature gradient, with cooler conditions in the north and warmer conditions in the south. Lake Stowell is at the extreme southern end of this temperature gradient. As a result, chironomid assemblages at Lake Stowell from cool intervals are similar to modern assemblages in more northern lakes and chironomid assemblages from warmer intervals have fewer modern analogues. Poor analogues conditions in Model A are infrequent and occur sporadically throughout the core. Due to this high proportion of good modern analogues as well as strong performance statistics, Model A, based on the full Fortin et al. (2015) calibration dataset, was selected as the best paleotemperature reconstruction for the Lake Stowell record.

Changes in Temperature over the Last 14,000 years

Changes in inferred summer temperature at Lake Stowell over the last 14,000 years are generally consistent with regional (e.g. Palmer et al. 2002; Rosenberg et al. 2004; Chase et al. 2008) and Northern Hemisphere (e.g. Bartlein et al. 1998; Barron et al. 2003; NGRIP 2004; Marcott et al. 2013) paleoclimate reconstructions (Figure 13). The climate history of British Columbia has been divided into several major phases (Mathewes 1973; Heusser et al. 1985; Hebda 1995; Palmer et al. 2002) that are reflected in the Lake Stowell record. In comparison to continental sites, changes in temperature are slightly muted, possibly reflecting the proximity to coastal waters, which has a moderating effect on temperature. Inferred temperatures are coolest in the late glacial

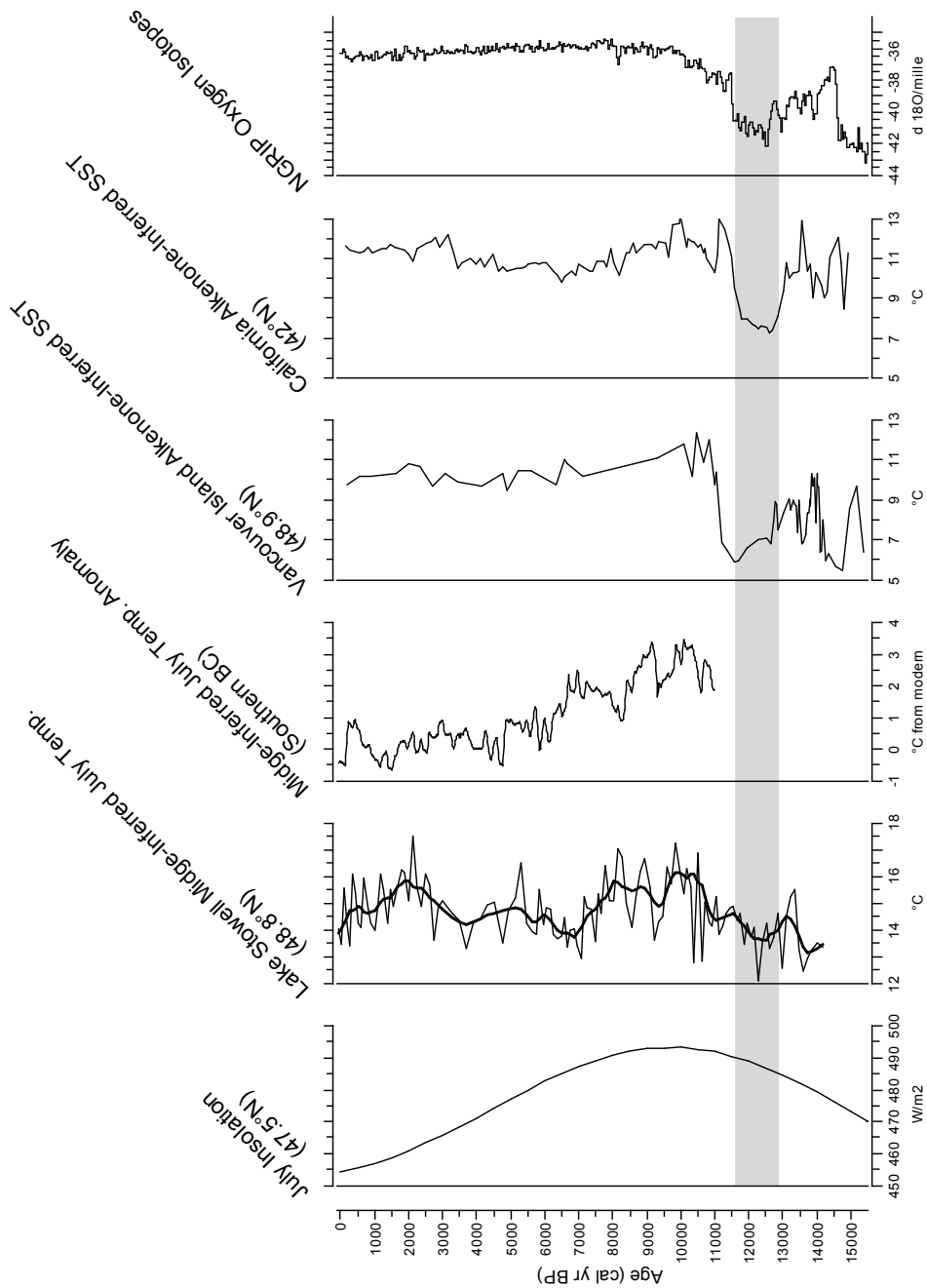


Figure 13. Selected paleoenvironmental reconstructions from the Northern Hemisphere: July insolation at 47.5°N from Berger and Loutre (1991), midge-inferred July temperatures from Lake Stowell with LOWESS smooth, midge-inferred July temperature anomaly for southern BC from Gavin et al. (2011), alkenone-inferred sea surface temperatures from Kienast and McKay (2001) and Barron et al. (2003), and the $\delta^{18}\text{O}$ record from NGRIP (2004). Grey band marks the Younger Dryas chronozone.

period with rapid warming to an early Holocene thermal maximum. After a period of stable, warm climate, inferred temperatures decrease through the middle Holocene, followed by a period of subtle warming in the late Holocene and decreasing inferred temperatures towards to the present. As the Lake Stowell sediment core dates back further than many other studies in the region and represents the most detailed quantitative paleotemperature reconstruction in the immediate area, new insight is gained into changes in temperature during the late-glacial and Younger Dryas time periods, as well as the details of Holocene temperature dynamics in the Gulf Islands.

Deglaciation and the Late-Glacial

During the late-glacial period, ice retreated from glacial maxima, with the Strait of Georgia being mostly ice-free by 13,200 cal yr BP (11,300 ^{14}C yr BP; Barrie and Conway 2002), though ice was still present in the region at high elevations until $\sim 10,000$ cal yr BP. The cooling influence of Northern Hemisphere ice sheets and abundant glacial meltwater is evident in the late-glacial portion of the Lake Stowell record. The paleotemperature reconstruction indicates a cool late-glacial period, with a minimum temperature of $12.5\text{ }^{\circ}\text{C}$, $\sim 2\text{ }^{\circ}\text{C}$ cooler than inferred modern temperature. Globally during this time period, there was cyclical warming and cooling, with identified climate events such as the Bølling, Older Dryas and Allerød periods (e.g. Björck et al. 1998; Ruan et al. 2015); however these fluctuations in temperature would not be apparent in the Lake Stowell record because of the temporal resolution of the record. It is also possible that these cyclical signals are not reflected in the record due to an insensitivity to change at Lake Stowell. The few lake sediment cores from western Canada that extend into this early late-glacial period indicate the establishment of forest communities during this time

frame (e.g., Mathewes 1993; Lacourse et al. 2005), which indicates some amount of warming coming out of the last glaciation.

Quantitative estimates of late-glacial temperatures have also been produced at sites in the interior of British Columbia (e.g. Palmer et al. 2002; Rosenberg et al. 2004; Chase et al. 2008), capturing the transition from a freshly deglaciated landscape into the Holocene. Palmer et al. (2002) report late-glacial mean July air temperatures of 8-10 °C at sites in southern British Columbia, which is 2-3 °C lower than their uppermost samples and similar to late-glacial temperature estimates reported by Chase et al. (2008) for southeastern British Columbia. In a regional synthesis, Walker and Pellatt (2003) describe the period between deglaciation and 11,500 cal yr BP as up to 4 °C cooler than present. Similarly, to the south in the Siskiyou Mountains of Oregon, mean annual temperatures during the late-glacial were at least ~3 °C cooler than present (Briles et al. 2005). Although reconstructed paleotemperatures from Lake Stowell are higher than those from continental sites, the difference relative to modern temperature is similar.

Climatic inferences from other paleoenvironmental studies along the south coast of British Columbia suggest similar patterns to the quantitative reconstructions in the region. Many regional paleoenvironmental studies based on pollen and charcoal (e.g. Mathewes 1973; Brown and Hebda 2002; Lacourse 2005; Gavin et al. 2013) describe the late-glacial period as cool or cold, with infrequent fires. Walker and Mathewes (1987, 1988) indicate cool, oligotrophic conditions in the late-glacial portion of chironomid records from coastal lakes in Haida Gwaii, Vancouver Island and the southern mainland coast of British Columbia; however, paleotemperatures were not inferred from these assemblages, so a direct comparison is not currently possible. Consistent with both

paleoenvironmental indicator studies and paleotemperature reconstructions, paleotemperatures at Lake Stowell increase through this period towards the Holocene.

Younger Dryas Chronozone

Throughout much of the Northern Hemisphere, the Younger Dryas chronozone marks a brief period of cooler conditions between ~12,900 and 11,700 cal yr BP (Björck et al. 1998; Steffensen et al. 2008), likely caused by an influx of freshwater into the North Atlantic Ocean from the melting Laurentide Ice Sheet that initiated rapid cooling (Alley et al. 1993; Mix et al. 1999; Steffensen et al. 2008; Ruan et al. 2015). As such, sites around the North Atlantic express the clearest signals of this event (e.g. Levesque et al 1996; Brooks and Birks 2000a; Martrat et al. 2014; Pawlowski et al. 2015). At Lake Stowell, a cooling signal of ~2-3 °C is visible between ~13,000 and 11,700 cal yr BP, the timing of which is similar to cooling recognized at other sites in the region (e.g. Mathewes 1993; Lacourse 2005; Kienast and McKay 2001). Some sites in British Columbia do not show evidence of a Younger Dryas cooling event during this time (e.g. Lacourse et al. 2005, 2012), but in a recent synthesis of midge-inferred paleotemperature estimates for southern British Columbia, Gavin et al. (2013) suggested that temperatures were 2.5 °C cooler than present during the Younger Dryas chronozone. Kienast and McKay (2001) inferred a similar decrease of ~3 °C in sea surface temperatures using alkenone records from a sediment core collected from the western Canadian continental slope, approximately 250 km west of Lake Stowell (Figure 4). This cooling is recorded elsewhere along the Pacific coast of North America, including a >3 °C cooling further south off the coast of California (Barron et al. 2003).

Early Holocene

Across the Northern Hemisphere, the transition into the Holocene was characterized by rapid warming in association with a contraction of the northern polar vortex (O'Brien et al. 1995) and increased summer insolation (Figure 13; Berger and Loutre 1991; Clegg et al. 2011). Major climatic changes are observed globally (NGRIP 2004; Mayewski et al. 2004, Marcott et al. 2013); however, the Holocene thermal maximum is time transgressive, with regional differences due, at least in part, to differences in the timing of deglaciation and proximity to ice sheets (e.g. Kaufman et al. 2004; Andersen et al. 2004). The warm period associated with the Holocene thermal maximum at Lake Stowell fits well within the local timing and amplitude documented by other studies in the region (e.g. Pellatt et al. 2001; Palmer et al. 2002; Chase et al. 2008; Gavin et al. 2013).

The early Holocene is the warmest portion of the Lake Stowell record, with inferred temperatures regularly exceeding 16 °C. This period extends from 10,300 to 8000 cal yr BP, coincident with warm and dry conditions inferred from nearby Saanich Inlet (Pellatt et al. 2001) and across the Pacific Northwest (e.g. Heusser et al. 1985; Walsh et al. 2010; Courtney Mustaphi and Pisaric 2014). Absolute temperatures at Lake Stowell during this time are higher than midge-inferred temperatures at high elevation and/or continental sites in British Columbia (e.g. Palmer et al. 2002; Chase et al. 2008); however, temperatures compare favourably to estimates based on fossil pollen assemblages closer to Lake Stowell. Mathewes and Heusser (1981) predicted early Holocene temperatures greater than 16 °C at Marion Lake located 310 m asl in Golden Ears Provincial Park, approximately 85 km northeast of Saltspring Island. There is also

agreement in the relative amount of change in the temperature estimates for the early Holocene. At Lake Stowell, early Holocene estimates exceed the late-glacial by 4-5 °C, and modern temperatures by 2-3 °C. A similar difference is observed in chironomid-based temperature reconstructions from the southern interior of British Columbia, where early Holocene temperatures exceed modern by 3-4 °C (Palmer et al. 2002; Chase et al. 2008).

Middle Holocene

As the Holocene progressed, temperatures began to gradually cool in western North America and across the Northern Hemisphere (e.g. Kienast and McKay 2001; Barron et al. 2003; Gavin et al. 2013; Marcott et al. 2013). At Lake Stowell, there is no evidence of the '8.2 ka event', a widely recognised cooling event (Alley et al. 1997; Morrill and Jacobsen 2005); however, the temporal resolution of the record is too coarse to assess this. Temperature estimates at Lake Stowell decrease after ~8000 cal yr BP with temperatures fluctuating around ~14.9 °C for much of the mid-Holocene. This moderate decrease in temperature is consistent with regional paleoenvironmental records and similar in timing to cooling observed in other paleoenvironmental studies in the region (e.g. Smith et al. 1998; Pellatt et al. 2001; Palmer et al. 2002; Stolze et al. 2007; Leopold et al. 2016).

Late Holocene

Globally, environmental changes became increasingly regional in scope in the late Holocene (O'Brien et al. 1995). Many paleotemperature reconstructions from southern

British Columbia suggest continuous cooling from the mid-Holocene to the present (e.g. Palmer et al. 2002; Chase et al. 2008). Other paleoenvironmental proxies also indicate a cool, moist climate in the region with increasing anthropogenic influence (e.g. Brown and Hebda 2002; Hay et al. 2006; Gavin et al. 2011).

The Lake Stowell paleotemperature reconstruction differs from this general pattern in that it shows a short-lived warming after 3500 cal year BP, peaking around 2000 cal yr BP, before cooling to modern temperatures. The warming recorded at Lake Stowell is not unprecedented in the regional paleoclimatic literature. Rosenberg et al. (2004) identified a warming signal in the late Holocene from a chironomid-based paleotemperature reconstruction at a high elevation lake in southern British Columbia. Mathewes and Heusser (1981) and Heusser et al. (1985) identified slight warming trends in the late Holocene based on pollen records from southern British Columbia and Alaska. Late Holocene warming is also evident in some marine cores from the northeastern Pacific Ocean. Barron et al. (2003) observed an increase in winter sea surface temperature off the coast of California ~3200 cal yr BP, based on alkenone records. This warming, which contrasts with the cooling suggested by many pollen records from the region, may reflect in part an intensification of ENSO cycles (Barron et al. 2003). Nearer to Lake Stowell, estimates of sea surface temperature suggest a slight warming at ~2300 cal yr BP, which has been interpreted to reflect an intensification of the Aleutian Low that brings warm southern currents up the coast of British Columbia (Patterson et al. 2011; Hallmann et al. 2013). The dominating effect of marine circulation patterns on sea surface temperatures would likely influence near-shore climates such as at Lake Stowell,

potentially explaining differences in temperature dynamics between coastal and more continental sites in the southern interior of British Columbia.

Charcoal records from across the Pacific Northwest show a late Holocene increase in charcoal around 2000 cal yr BP (e.g. Brown and Hebda 2002; Hallett et al. 2003; Gavin et al. 2013; Courtney Mustaphi and Pisaric 2014; Lacourse and Davies 2015). Most studies attribute this increase to expanding indigenous populations throughout the Pacific Northwest, and not an increase in temperatures. However, other factors that may have contributed to the increase in charcoal abundance include increased biomass, increased lightning frequency, or other climate factors (e.g. Hallett et al. 2003; Sugimura et al. 2008; Lucas and Lacourse 2013).

The late Holocene record from Lake Stowell also differs from many other paleoclimatic records in the region in that it does not show clear evidence of the Medieval Climate Anomaly (MCA; 1000 – 700 cal yr BP) or the Little Ice Age (LIA; 550 – 250 cal yr BP). As these were relatively short-lived events, it is likely that the limited temporal resolution of the Lake Stowell record prevents definitive identification of these events, despite the presence of high frequency changes in temperature during the late Holocene. Other paleoenvironmental studies in the Vancouver Island region that had a higher temporal resolution than was achieved in the Lake Stowell record found evidence for changes in fire frequency (Lucas and Lacourse 2013), the extent of glaciers (e.g. Coulthard et al. 2013; Mood and Smith 2015), and climate and marine productivity (Bringué et al. 2016) that coincide with the MCA and LIA.

Sensitivity to climatic change, or a lack thereof, may be a complicating factor in the interpretation of inferred paleotemperatures from Lake Stowell. Traditionally, in

British Columbia, sites selected for paleotemperature reconstructions based on reconstruction of paleotemperatures based on fossil chironomid assemblages have been located at or near elevational treeline. Ecotones such as those that exist at treeline are particularly sensitive to environmental changes, and thus, these changes are more readily reflected in the fossil record. Lake Stowell is well below treeline and changes in climate are moderated by proximal ocean waters. Accordingly, the lake and its faunal community are likely buffered from environmental changes. At Hippa Lake on the north coast of British Columbia, Walker and Mathewes (1988) observed a fairly stable chironomid assemblage over the last 11,000 years. This stability was attributed to an insensitivity to changes in climate due to hydrological factors as well as low elevation (Walker and Mathewes 1988). While changes in inferred paleotemperature are seen in the model selected here, the apparent muting of amplitude of change and the amount of error associated with the model may be indicative of this insensitivity.

Conclusion

Summary

A quantitative paleotemperature reconstruction for the past 14,000 cal yr was constructed from subfossil chironomid assemblages at Lake Stowell using a large calibration dataset and transfer function from northern North America. The resulting mean July air temperature profile is consistent with major changes in climate on both regional and hemispheric scales. The temperature changes in the Lake Stowell record are muted in comparison to continental sites, likely due to the influence of ocean waters. The record from Lake Stowell extends further into the late-glacial than many other paleotemperature reconstructions in the region, providing evidence of a cooling event on the Pacific coast of North America that is coincident with the Younger Dryas chronozone. During much of the postglacial interval, temperature dynamics were similar in many regions of the Northern Hemisphere, and this is seen in the similarities between the Lake Stowell record and continental reconstructions in the southern interior of British Columbia (e.g. Palmer et al. 2002, Chase et al. 2008). Overall, this reconstruction supports the use of chironomid-based quantitative reconstructions in paleoenvironmental studies and contributes to regional knowledge of changes in paleoclimate.

Study Limitations and Future Research

The lack of good modern analogues for 15% of the Lake Stowell chironomid samples is a complicating factor in this paleotemperature reconstruction. A good transfer function should have modern sites with similar zoographic and environmental

characteristics as the potential downcore assemblages. The modern calibration dataset used for the Lake Stowell paleotemperature reconstruction covered large latitudinal and elevational gradients providing good modern analogues for much of the Lake Stowell chironomid record, particularly in the cooler portions of the record. However, as Lake Stowell is at the southern extreme of the calibration set, some samples during periods of elevated temperature lacked good modern analogues. Warm-adapted *Apedilum* is common in early Holocene samples at Lake Stowell but uncommon in the modern calibration dataset, and as such, inferred paleotemperatures during the early Holocene may be underestimated. This highlights the need for extension of calibration datasets into southern continental Canada and the northern United States. A small calibration dataset consisting of high-elevation sites in California exists (Porinchu et al. 2002), but there is a large gap in North American gradients that needs to be filled in order to include the best possible modern analogues for low elevation, mid-latitude sites such as Lake Stowell.

In the creation and application of transfer functions, a consistent problem is taxonomic resolution and harmonization (e.g. Brooks et al. 2012; Jiang et al. 2013; Milošević et al. 2014). Chironomids have been intensively studied in many areas of the world and have well defined ecological optima and tolerances. These have been widely used in the analysis of chironomid fossil assemblages and several comprehensive taxonomic guides exist (e.g. Brooks et al. 2007; Andersen et al. 2013). While taxonomic resolution has improved considerably with the advent of calibration datasets and the sharing of taxonomic knowledge, there is still a lack of clarity in the identification of some taxa (e.g. *Parakiefferiella* sp B type in Barley 2004; Walker 2007). Some of this confusion is due to the minor morphological differences that are used for identification,

and how these features translate from written description to the variation of real world observation. For example, the differentiating feature between several species of *Cricotopus/Orthocladius* is the angle of the first lateral tooth, which with wear, distortion or inherent variation among individuals, can be difficult to assess definitively. Issues also arise in the identification of individuals when key features, such as the mandibles or antennal pedestals, are missing. As a result, the identification of chironomid head capsules is driven to a coarser taxonomic resolution than some would desire.

While high taxonomic resolution would seem beneficial for paleoenvironmental studies, as this allows ecological optima to be more clearly defined, increased resolution may also contribute to misidentification of specimens (Type I error) (Velle et al. 2010). Therefore an optimal taxonomic resolution is one where differences in taxa are recognized and appreciated, but not so precise that misidentification is common. Several researchers (e.g. Velle et al. 2010; Milosevic et al. 2014) have argued that the current level of taxonomic resolution in North America and Europe is at this so-called optimum, while improvements are needed in other regions (e.g. Africa, South America). Velle et al. (2010) have suggested that future research should focus on improving our understanding of how chironomid taxa respond to environmental variables, rather than on differentiating between species to the point where identification becomes muddled and negatively affects quantitative paleoenvironmental reconstructions.

The Lake Stowell chironomid record fills a gap in our understanding of paleoenvironmental changes following the last glacial maximum on the south coast of British Columbia. As the first quantitative paleotemperature record from the Gulf Islands, this research provides context for other paleoenvironmental studies and contributes to our

understanding of regional environmental changes. Pollen and charcoal analyses are currently being conducted on the same sediment core from Lake Stowell. Combining all of these paleoenvironmental proxies will help form a more holistic understanding of postglacial environmental change on the south coast of British Columbia.

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Appendix: Supplemental Tables and Figures

Table A 1. Limnological measurements at Lake Stowell, Saltspring Island taken on 6 July 2015.

Limnological Properties	Lake Stowell	
Secchi depth (m)	2.28	
Dissolved organic carbon (mg/L)	5.6	
Total organic carbon (mg/L)	5.8	
	<u>0.1 m</u>	<u>0.5 m</u>
pH	7.77	7.77
Conductivity ($\mu\text{S}/\text{cm}$)	102.8	103.4
Temperature ($^{\circ}\text{C}$)	24.6	24.6

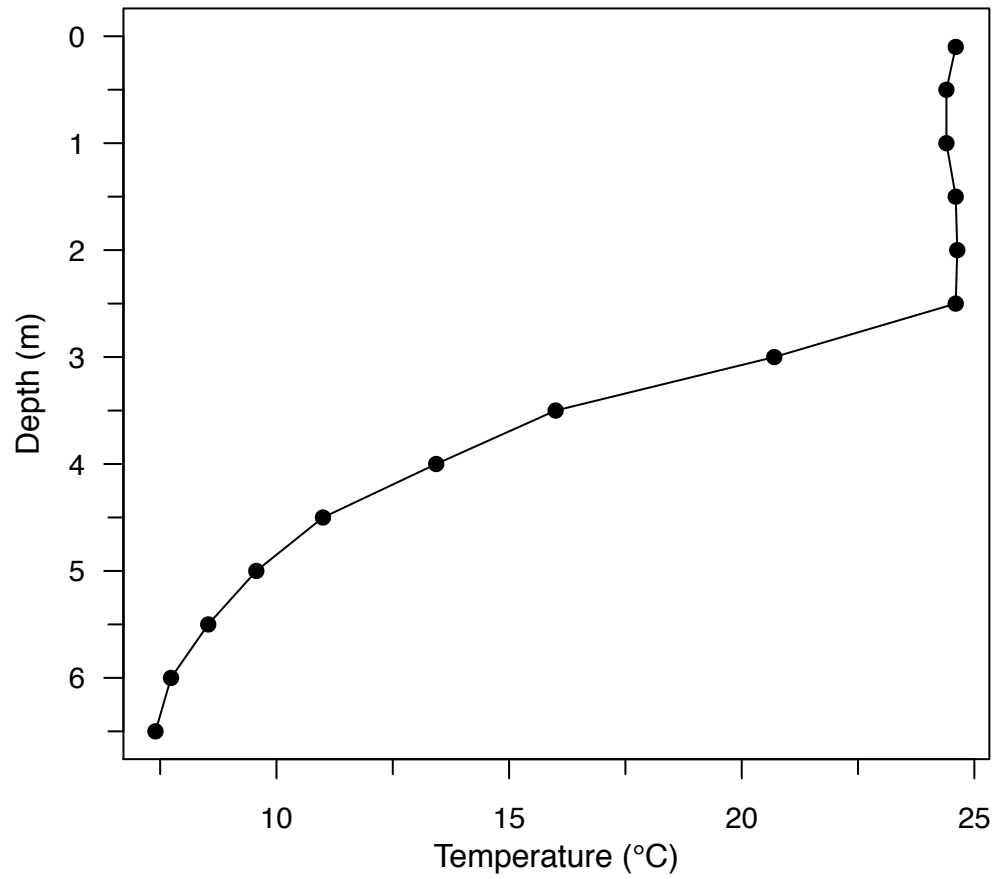


Figure A 1. Water temperature profile for Lake Stowell based on measurements taken on 6 July 2015.

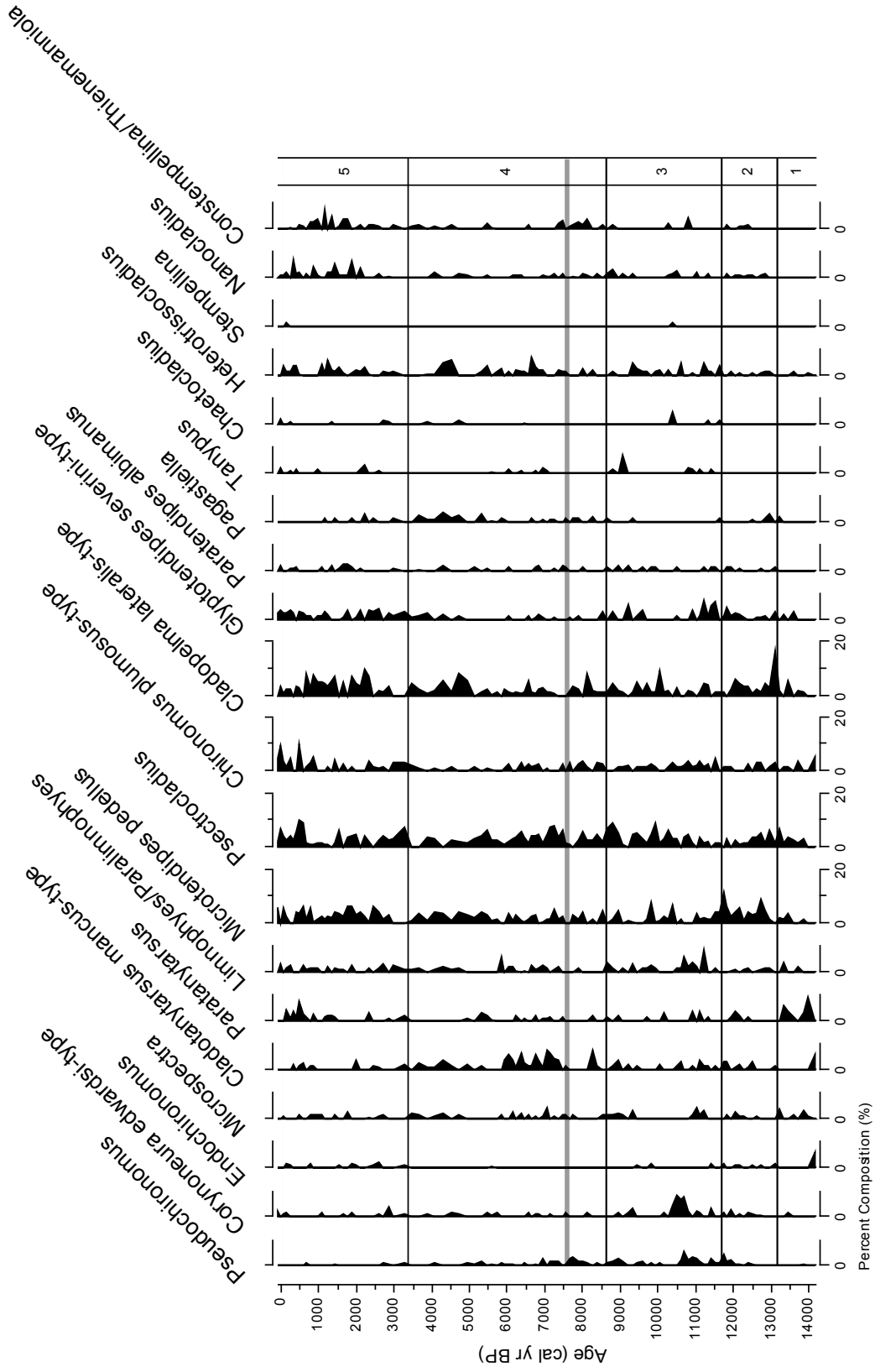


Figure A 2. Percent composition of uncommon chironomid taxa in the Lake Stowell sediment core, with zonation based on optimal splitting by sum-of-squares. Taxa are arranged left to right based on abundance through time (cal yr BP). Unknown head capsules are also included. The grey line across the diagram shows the stratigraphic position of the Mt. Mazama tephra.

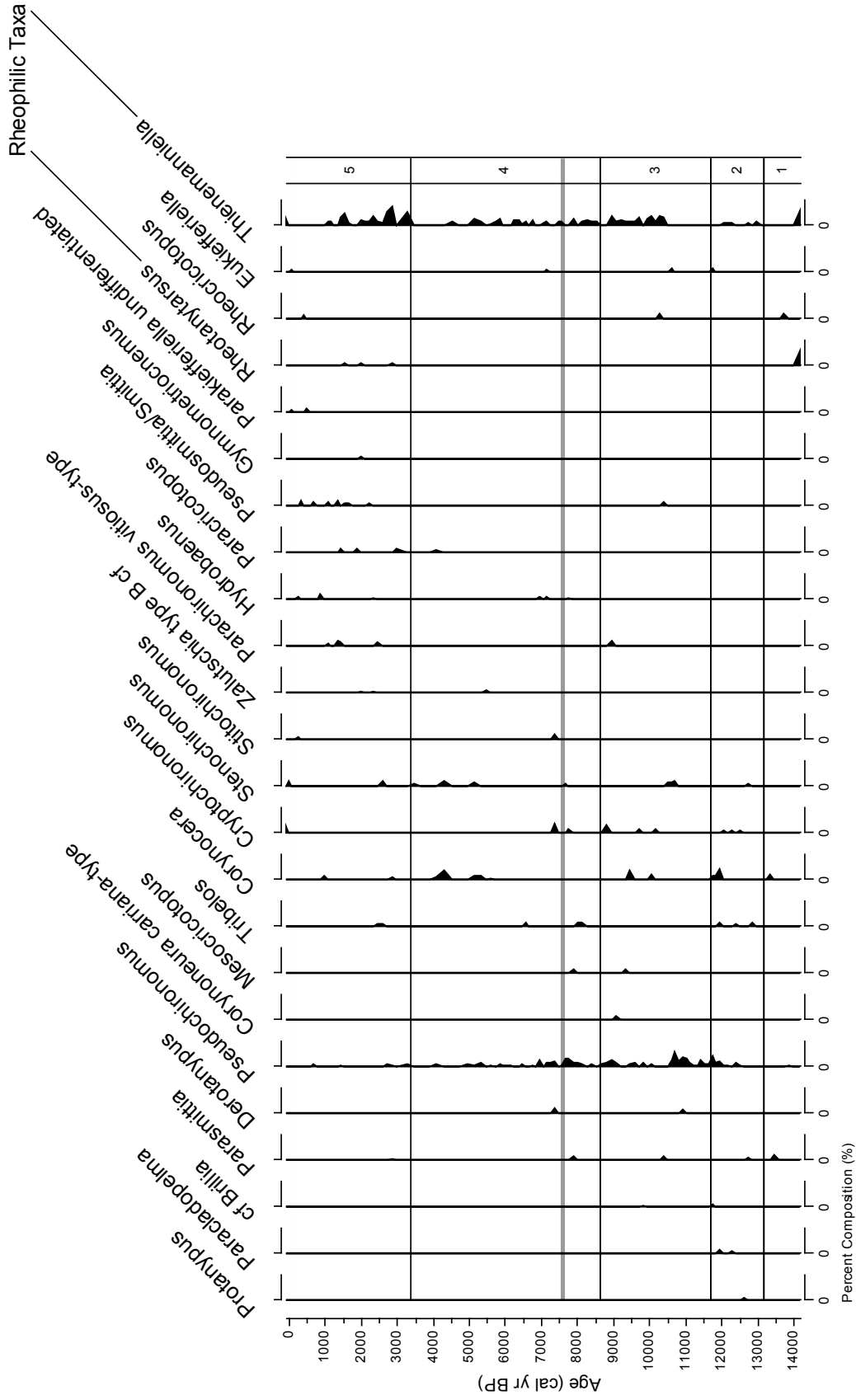


Figure A 3. Percent composition of rare (<5%) chironomid taxa in the Lake Stowell sediment core, with zonation based on optimal splitting by sum-of-squares. Taxa are arranged left to right based on abundance through time (cal yr BP) with a separate grouping of rheophilic taxa. The grey line across the diagram shows the stratigraphic position of the Mt. Mazama tephra.