Ecosystem responses to Holocene climate variability through the analysis of high-resolution lake sediment cores from Southwestern Québec, Canada

Thesis submitted in partial fulfillment of the requirements for the degree of Doctorate in Philosophy in Geography

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Abstract

Lake biotic responses to natural climate variability, fire disturbances, and human impacts over the Holocene were studied at two proximate sites in southwestern Québec. Sediments from Lac Noir and Lac Brûlé had annually deposited laminations (varves), enabling for the precise dating of continuous time-series and high-resolution analysis of subfossil diatom assemblages.

The Lac Noir (45°46'31"N, 75°8'23"W, 176 m a.s.l.) record spanned ~11000 years of the Holocene. Stratigraphic changes in diatom assemblages of the lake could be divided into early, mid-, and late periods, broadly paralleling Milankovitch-scale climate intervals and vegetation changes inferred from regional palynological records. The early Holocene (11.1-8.0 ka) climate was cooler and dry, vegetation in the region was comprised of *Picea*-dominated woodlands, and the lake diatom flora included primarily benthic taxa. Warming in the mid-Holocene (8.0-3.6 ka) allowed for stabilization of soils and forests in the catchment, stronger thermal stratification in the lake, and resultant increases in oligo-mesotrophic diatom taxa such as *Discostella stelligera*. During the late Holocene (3.6 ka to present), an increase in the abundance of deciduous trees (e.g. *Betula* and *Alnus*) in response to cooling led to nutrient-enrichment and higher overall lake productivity.

The record from Lac Brûlé (45°43'09"N, 75°26'32"W, 270 m a.s.l.) encompassed the last ~1200 years of the late Holocene. Generalized additive models (GAM) revealed a tight coupling between diatoms and catchment-mediated processes (e.g. vegetation and disturbances), which were closely aligned with climate variations. During the Medieval Warm Period (800-1300 CE), pollen-based inferences of warmer summer temperatures were associated with high abundances of *Cyclotella bodanica* var. *intermedia* and *Cyclotella rossii*; this signalled oligotrophic lake conditions and prolonged thermal stratification. The onset of the Little Ice Age (1450-1850 CE)

marked a cooling in the region, and a decline in *Tabellaria flocculosa* str. IIIp indicated increased nutrient loading from the catchment area. Situated less than 300m from Lac Brûlé are remnants of the Wallingford-Back Mine, which ran from 1924-1972 CE; activities at the mine resulted in local changes to nutrient availability and primary productivity at this site.

In previous studies of both Lac Noir and Lac Brûlé, pollen records had indicated overall similarities in the vegetation histories in response to climate variability during the late Holocene. Diatom assemblages were influenced by individual lake conditions and were thus unique to each site; nevertheless, they were closely linked with local and regional patterns of vegetation composition. A main point of difference in the paleo-records from both lakes was attributed to a local fire in the Lac Brûlé catchment at 1345 CE, which caused an early decline in hemlock (*Tsuga*). The decrease in hemlock was seen at Lac Noir only centuries later, and diatoms in each lake responded according to vegetation changes within their own respective catchments.

This research shows that high-resolution sampling of lake sediments is able to detect diatom responses to both long-term and abrupt changes in the environment. Individual sites show similarly timed responses of other proxy-indicators, such as pollen and cladocera, to climate and land-use changes. However, distinct differences in the aquatic biota of well-dated proximate sites can be used to identify influences of regional climate variations, which are sometimes masked by localized, non-climatic processes.

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CHAPTER ONE

Introduction and Literature Review

1.1 Context and research objectives

Climate and land-use changes have impacts on the health of lake aquatic communities, which are mostly sensitive to changes in their surrounding environment (Johnstone et al. 2016). This thesis investigates the influences of natural climate variability, catchment-related processes such as fire and human disturbances, and internal lake dynamics on aquatic biota in southwestern Québec. Sampling sediment cores at high-resolution for analyses allows for better understanding of the nature of both abrupt and long-term changes in aquatic communities, which can help to inform future lake management strategies. Each main chapter (2, 3, and 4) builds upon this by addressing the following specific research objectives:

Objective 1: Reconstruct a high-temporal resolution history of diatom responses to climate variability and catchment- related processes

Previous high-resolution paleoecological studies from southwestern Québec show abrupt vegetation (pollen) and zooplankton (cladocera) community responses to climatic variations and human disturbances in the late Holocene (Cooper et al. 2016; Lafontaine-Boyer and Gajewski 2014; Paquette and Gajewski 2013; Williams et al. 2002). Key periods of interest in these studies were the Medieval Warm Period (~800-1300 CE), the Little Ice Age (~1450-1850 CE), and post- Euro-Canadian settlement (~1850-present). In Chapter 2 of this thesis, the main objective was to determine if diatom communities showed similarly timed responses to these periods during the last ~1200 years. Annually laminated (varved) sediments from Lac Brûlé were

analyzed for diatoms at high-temporal resolution, and comparisons to existing pollen (Lafontaine-Boyer and Gajewski 2014) and cladocera (Cooper et al. 2016) records from the same lake were used to identify and explain complex interactions between aquatic biota and the surrounding catchment area, as well as between different lake trophic levels.

Objective 2: Compare paleo-records of two proximate lakes in southwestern Québec to identify differences between regional- and local-scale responses in diatom communities

High-frequency climatic events (e.g. droughts) and/or catchment-related processes have localized effects which alter the rate and timing of ecological change amongst individual sites (Williams et al. 2011; Paine et al. 1998). This disrupts regional synchronicity in paleo-records as major climate events, such as the Medieval Warm Period and Little Ice Age, should theoretically trigger near- to simultaneous responses in terrestrial and aquatic biota (Williams et al. 2011). The replication of paleolimnological studies at regional-scales is therefore helpful in distinguishing between the effects of natural climate variability and non-climatic processes (Battarbee 2000). The main objective of Chapter 3 was to replicate the diatom analysis from Chapter 2 at a second nearby lake, and to compare the two high-resolution diatom records. Varved sediments from Lac Noir, southwestern Québec, were thus analyzed at high-resolution for diatoms. Comparisons of the paleo-records from Lac Brûlé and Lac Noir (diatoms and pollen) showed distinct points of difference within the past 1200 years, attributed to a local fire at Lac Brûlé in 1345 CE and anthropogenic disturbances in the more recent histories of the lakes. The results of this chapter strengthen our understanding of the influences of localized processes on aquatic biota, and their potential to cause significant and long-lasting effects within these communities.

Objective 3: Extend a high-resolution fossil record to the early Holocene to better understand the role of climate in structuring the long-term ecology of the lakes in southwestern Québec

Climate variability is comprised of diverse modes which oscillated at various time-scales (Viau et al. 2002, 2012; COHMAP Members 1988); this causes uncertainty in quantifying the frequency, magnitude, spatial extent and scale interactions of Holocene climate variations (Viau et al. 2006). Studies have shown that orbital- to decadal-scale changes in climate were significant in driving vegetation dynamics across North America (Viau et al. 2006; Shuman et al. 2005; Grimm and Jacobson 1992), which in turn affected aquatic ecosystems in southern Québec and Ontario throughout the Holocene (Beck et al. 2016; Moos et al. 2009; Huvane and Whitehead 1996; Sreenivasa and Duthie 1973). The main objective of Chapter 3 was to better understand the role of climate and vegetation succession in structuring the long-term ecology of lakes in southwestern Québec. To study these effects, a varve chronology was developed spanning the past ~11000 years at Lac Noir, and the previous high-resolution diatom record from the lake (Chapter 3) was extended to encompass the entire Holocene (Chapter 4). Results were compared to regional palynological records from nearby sites, providing a long-term perspective of lake ontogeny, as well as links between aquatic and terrestrial ecosystems. Lakes with varved sediments spanning the Holocene are rare; Lac Noir was thus an ideal site for paleolimnological research, and this study filled a gap in knowledge in terms of providing a long-term, high-resolution diatom record for the region.

1.2 Literature Review

1.2.1 Consequences of climate change and human impacts on lake ecosystems

In recent decades, lake ecosystems in eastern North America have been subjected to a number of negative consequences associated with climate change and increases in anthropogenic activities (IPCC 2007). By the end of the 21st century, global climate models (GCMs) project an increase in mean annual temperature of 1 to 5°C (Boulanger et al. 2017; IPCC 2007), which is likely to have continued impacts on lake ecosystem health (Johnstone et al. 2016) and resilience (Schindler 2001). Lakes may become more vulnerable in the future to acidification (Schindler et al. 1996), accelerated eutrophication (Tremblay et al. 2014; Reavie and Smol 2001), declines in species richness (Velghe et al. 2012), and oxygen depletion (IPCC 2001), amongst others. Predictive modelling of future conditions can help to inform lake conservation and management efforts, although such methods must take into account the inherently dynamic nature of biotic communities in response to rapid changes in the environment (Paus 2013; Keith et al. 2009; Williams et al. 2002).

1.2.2 Paleolimnological approaches and fossil assemblages

Predicting what happened in the past, or "hind-casting", can be useful in anticipating how ecosystems may react to future environmental conditions (Smol 1992). However, increasingly complex and novel patterns of change have the potential to alter modern biotic assemblages such that they will become non-analogous with fossil records (Keith et al. 2009; Jackson and Williams 2004). It is thus important to have a comprehensive understanding of the mechanisms or external forcings driving community-level responses in aquatic and terrestrial ecosystems; to accomplish this, paleolimnological studies should use multi-site, multi-proxy approaches when possible

(Adrian 2009). Replication of lake paloenvironmental studies at regional-scales, for instance, can help to differentiate between responses driven by general climate forcing and those triggered by local climate events or stochastic processes (Battarbee 2000). In addition, multi-proxy studies can identify potential links between aquatic biota at different trophic levels and catchment-related processes (Battarbee 2000), which may otherwise go unnoticed. Ecosystem reactions to direct and indirect external forcings are often documented as shifts in subfossil assemblages, such as diatoms (phytoplankton), chrysophytes (phytoplankton), cladocera (zooplankton), and pollen (vegetation) (Battarbee et al. 2001).

Diatoms are unicellular organisms capable of photosynthesis, and typically account for more than half of the primary production in freshwater systems (Smol 2008). They are a type of algae from the class Bacillariophyceae, and use silica to form intricate cell walls (or frustules). Each individual frustule is microscopic in size (2-200 μm), and is comprised of two valves connected by girdle bands. The size, shape and sculpturing of the valves is important for distinguishing between diatom species in fossil remains (Appendix A), and each species has specific habitat preferences or ecological tolerances, such as affinities for open water versus substrates, or high/low nutrient and pH levels (Cohen 2003). The good preservation and diversity of diatoms in lake sediments make them an ideal proxy indicator of past lake conditions, such as total phosphorous (TP) content, pH, primary productivity, and specific conductivity (Tremblay et al. 2014; Smol 2008, Birks 2001). Diatom analysis is thus widely used to address questions related to the physical, chemical and biological reactions of lakes to climate and environmental changes (Battarbee et al. 2001; Cohen 2003; Dixit et al. 1988).

Chrysophytes are algae from the class Chrysophyceae or Synurophyceae, and similarly to diatoms they are used as environmental indicators due to their high abundance in lake

sediments and wide ecological diversity. Each chrysophyte cell in the class Synurophyceae is covered in 30 to >200 siliceous scales; these microscopic scales are distinguishable and can be linked to different chrysophyte species based their external morphology, thus making them useful for paleoenvironmental reconstructions (Zeeb 2002). Each cell also produces siliceous resting cysts (or statospores), however relatively few morphotypes are linked to the species that produce them (Smol 1985; Kristiansen 1986; Duff et al. 1997). Munch (1980) suggests that chrysophyte scales are more easily identifiable than cysts, and are perhaps more useful in paleolimnological studies given that they are produced by cells with more consistency than are cysts. As a whole, the ratio of chrysophytes relative to diatoms is often used as an indicator of lake nutrient status (Smol 1985; Kristiansen 1986); chrysophytes tend to be favored in acidic and/or nutrient-poor lakes, whereas diatoms are generally more prevalent in alkaline and eutrophic waters (Kristiansen 1986; Zeeb 2002).

Cladocera are aquatic arthropods from the class Branchiopoda, and are found in most freshwater systems worldwide (Korhola et al. 2001). They respond quickly to changes in climate, water chemistry, lake depth, and aquatic vegetation (Cooper et al. 2016), but also have an important role in the aquatic food web as both a producer and consumer (Korhola et al. 2001). Diatoms are an important component in the dietary needs of cladocera, as they provide energy for growth and reproductive processes; single-celled diatoms (e.g. *Stephanodiscus* and *Cyclotella*) are a typical source of food in the spring, and larger colonial diatoms (e.g. *Asterionella formosa* and *Fragilaria*) are primarily consumed in the summer months (Carotenuto and Lampert 2004). Long-term changes in cladoceran communities may therefore exert various degrees of predation pressure on diatoms within the trophic structure of lakes.

Fossil pollen assemblages in lake sediments reflect past terrestrial vegetation dynamics

in response to climate fluctuations, anthropogenic impacts, and/or other biotic (e.g. grazing) and abiotic (e.g. fire) influences. For example, an increase in *Ambrosia* (ragweed) pollen is often used as an indicator of Euro-Canadian settlement and subsequent land clearance. Pollen from an individual site typically represents a regional record of vegetation history, as it is produced by plants within an area of 10-100 km in diameter around the lake (Traverse 2005); however, micro-scale changes in the immediate catchment area of lakes can often lead to dissimilarities among even the closest sites. There are a number of different pathways or means by which vegetation or soils can impact aquatic communities. Forests in general play a significant role in terms of cycling nutrients such as nitrogen, phosphorus and sulfur to lakes (Foster and Bhatti 2006), which are limiting resources for diatoms; sources of these nutrients are atmospheric, geologic, and/or anthropogenic. Changes in terrestrially derived dissolved organic carbon (DOC) inputs to lakes often act to influence diatoms by attenuating light, or by potentially releasing bound nutrients into the water column through photolysis (Seekell et al. 2015). Lastly, but not exclusively, soil acidity is controlled in part by the composition of forest stands in the surrounding area (Rawlence 1992); runoff through leaf litter and soils can cause changes in the pH of nearby lakes, which will ultimately influence the structure of aquatic communities.

1.3 Study Region

This study focuses on two lakes with varved sediments in southwestern Québec, located approximately 60 km north-east of Ottawa and within 25 km of each other (Fig. 1.1; Panels B-D). Lac Brûlé and Lac Noir are both situated on the Grenville Province, consisting mainly of metamorphic and igneous bedrock (Baer et al. 1977); specifically, Lac Brûlé is underlain by quartzite, paragneiss, pegmatite and granite (Lafontaine-Boyer and Gajewski 2014), while Lac Noir is underlain by granite, sillimanite, garnet, biotite and gneiss (Paquette and Gajewski 2013).

Resistance of hard granitic or gneiss bedrock to weathering could fail to replenish base cations in lake catchments following high- precipitation events (Smol 2008; Houle et al. 2006; Beck 2013), which are expected to increase in frequency and magnitude as a result of climate change within the region (Mailhot et al. 2009). This has implications for lake acidity and subsequently for aquatic biota, which are heavily influenced by the bedrock geology. Furthermore, lakes in southwestern Québec generally have a lower acid neutralizing capacity than those in the rest of the province (ANC < 100/μeq L^{-1}), indicating that the study region could potentially be more vulnerable to acidification processes (Dupont 1990).

In recent decades, increased observations of eutrophication and cyanobacterial blooms have also been noted in several lakes within southwestern Québec (Varin 2016), which could reflect a higher risk of decline in lake ecosystem health (Tremblay et al. 2014; Reavie and Smol 2001). Overall lake productivity is significantly influenced by total phosphorus, which is a key limiting nutrient for algal growth and often increases as a result of human-induced disturbances in the landscape (Hall et al. 1999; Schindler 1974). In southern Québec and Ontario, modern diatom-based inference models have been created to reconstruct pH, and nutrients such as total phosphorus and dissolved iron (Varin 2016; Tremblay et al. 2014; Velghe et al. 2012; Enache and Prairie 2002; Philibert et al. 2003; Reavie and Smol 2001; Dixit et al. 1988). In the Outaouais region near Lac Brûlé and Lac Noir (Fig 1.1; Panel B), Varin (2016) created a training-set consisting of 31 lakes, partially overlapping with a cladocera training-set by Cooper et al. (2016); these studies showed that the lakes had a very narrow range in TP, preventing paleolimnological reconstructions of this nutrient in down-core sediments. Additional lakes could help to construct a more robust transfer function with better performance, however differences between studies in regards to lake characteristics and taxonomic identifications often make it difficult to integrate multiple training-

sets (Juggins 2013; Telford and Birks 2009), as was shown in Cooper (2015).

Diatom records that characterize long-term trends of environmental changes (beyond the past few hundred years) are typically found outside of the study region, and are located (i) to the west near the Winnipeg River Drainage Basin (Karmakar et al. 2015; 2014; Haig et al. 2013; Philibert et al. 2003), (ii) eastward towards Montreal (Hausmann et al. 2011), or (iii) southward in the northeastern United States (Köster et al. 2005; Bradbury et al. 2002; Huvane and Whitehead 1996). Some exceptions exist, including a 1000-year record from Heney Lake (Varin 2016), and a longer 11000-year record from Pink Lake (Jones et al. 1984), both of which are situated within 100 km of Lac Brûlé and Lac Noir (Figure 1.1; Panel B). This thesis will aim to improve the long-term paleo-environmental history of an under-studied region.

1.4 General paleo-environmental history in southwestern Québec

During the transition from the last glacial period to the early Holocene, environmental changes in eastern North America were largely controlled by impacts of the Laurentide Ice Sheet on global atmospheric circulation patterns (Booth et al. 2005). The eventual retreat of the ice sheet triggered gradual changes in these circulation patterns (Webb et al. 2003), as reflected by alterations to the structure and distribution of vegetation and aquatic biota over time. Influences of lake catchment processes, such as vegetation succession and soil development, have been shown to be relevant in governing aquatic communities throughout the Holocene; interpretations of diatom assemblages are therefore stronger when accompanied by pollen records (Fritz and Anderson 2013; Puusepp and Kangur 2010; Moos et al. 2009; Jones et al. 1984).

1.4.1 Deglaciation and the early Holocene

Deglaciation began near the Great Lakes region and St. Lawrence Lowlands between 13-12 ka (Richard 1994), after which organic sediments accumulated in developing lake basins (Anderson 1987). High levels of solar radiation in the early Holocene led to a warming of 3-4°C by 10.0 ka (Viau et al. 2006; Fuller 1997), and ice had retreated from all of southeastern Canada and northeastern United States by 12-10 ka (Jacobson et al. 1987). Sudden collapses in ice domes over present-day Hudson Bay triggered brief periods of climate reversal, such as the 9.2 and 8.2 ka events which were cool and dry (Gregoire et al. 2012; Alley and Agustsdottir 2005). In the absence of large-scale continental ice, mechanisms such as non-linear responses to orbital forcing, solar variation, and volcanic events had strong influences on climate change during the Holocene (Booth et al. 2005; Mayewski et al. 2004).

Following deglaciation in southern Québec and Ontario, the landscape was sparsely covered by herbaceous and shrub tundra, and total pollen accumulation rates were low (Richard 1994). The subsequent succession to a boreal-type forest led to increased relative abundances of *Populus* and *Picea* (Fuller 1997; Mott and Farley-Gill 1981). An abrupt increase in *Pinus banksiana* and *P. resinosa* at ~10.0 ka initiated a transition towards a mixed-forest (Fuller 1997), and Overpeck et al. (1992) suggest that modern-day vegetation assemblages of eastern North America were established by 9.0 ka. During the 8.2 ka cooling event, vegetation shifted across many eastern North American sites (Alley and Agustsdottir 2005); records indicate increases in cold-tolerant species, such as *Picea* and *Abies* in Québec (Lavoie and Filion 2001), *P. banksiana* and *P. resinosa* in southern Ontario (Fuller 1997), and *Betula* in Maine (Shuman et al. 2002).

The dominance of small benthic diatoms (e.g. *Staurosirella pinnata*) in assemblages of

the early Holocene indicated low productivity associated with the initial stages of lake ontogeny (Moos et al. 2009). The expansion of boreal forests and development of soils in lake catchments correlates with increases in planktonic taxa (e.g. *Cyclotella* species), reflecting increased nutrient inputs and/or decreased lake turbidity (Moos et al. 2009; Huvane and Whitehead 1996). Low diatom concentrations in the early-Holocene also suggest this period was relatively unproductive in relation to the rest of the Holocene record (Moos et al. 2009).

1.4.2 The mid-Holocene and onset of Neoglaciation

Maximum warm temperatures were reached between 6.0-3.0 ka, followed by a period of gradual cooling termed "Neoglaciation" (Viau et al. 2006). Within this period, an abrupt drought at 4.2 ka affected many regions in central and eastern North America, and has been linked with changes in sea surface temperature patterns (Wanner et al. 2008).

Vegetation changed rapidly in the late-glacial and early Holocene periods, but reached a period of relative stability in the mid-Holocene after 7.0 ka (Williams et al. 2004). *Pinus* spp. eventually became the dominant taxa, but gradually decreased as shade-tolerant species (e.g. *Tsuga, Fagus,* and *Betula*) became more abundant (Keizer 2015; Fuller 1997). An abrupt decline in eastern hemlock (*Tsuga canadensis*) occurred at ~5.5 ka, and was thought to be the result of a widespread pathogen outbreak (Davis 1981). Alternatively, Foster et al. (2006) suggest that low moisture availability in the mid-Holocene was a potential cause for the decline, which recovered by ~3.0 ka (Fuller 1997) and marked the onset of Neoglacial cooling (Viau et al. 2006).

Fragilaria crotonensis and *Aulacoseira* species increased in the mid-Holocene, indicative of warming, low lake-levels, and/or more turbulent conditions (Karmakar et al. 2015;

Moos et al. 2009). The mid-Holocene was also characterized as a period of transition in species composition, culminating in increased relative abundances of planktonic taxa (e.g. *Discostella stelligera*) by at least 4.0 ka (Karmakar et al. 2015). Studies recorded increased percentages of *D. stelligera* and *Tabelleria flocculosa* following the widespread decline in *Tsuga*, which signalled nutrient enrichment from the catchment (Beck 2013; Huvane and Whitehead 1996). Another abrupt change occurred at 4.2 ka in response to a well-known drought period in the mid-west; records from Elk Lake, Minnesota showed a peak in diatom influx signalling high lake productivity (Booth et al. 2005). Varve thickness at Elk Lake increased due to greater moisture availability immediately prior to and following the drought, suggesting that it was a discrete drought event rather than a long-term change in climate (Booth et al. 2005).

1.4.3 The late Holocene and Euro-Canadian settlement

In the past ~2.0 ka, two distinct millennial-scale climate variations have been identified; the Medieval Warm Period (MWP; ~800-1300 CE) and the Little Ice Age (LIA; ~1450-1850 CE) (Viau et al. 2012). In southern Québec and Ontario, the MWP was 0-1.5°C warmer than the LIA, although both periods were cooler than present conditions (Lafontaine-Boyer and Gajewski 2014; Paquette and Gajewski 2013; Gajewski 1988). Among the proposed factors influencing the climate of the MWP is a synchronization of the La Niña and a warm phase Atlantic Multidecadal Oscillation (AMO) (Haig et al. 2013; Trouet et al. 2009). Low summer insolation, strong tropical volcanic activity, and glacial advances are associated with the LIA (Keizer 2015; Wanner et al. 2008). Initial settlement and expansion of Euro-Canadian activities in southwestern Québec (~1820-1875 CE; Smith 1967) corresponded broadly with the end of the LIA in the region (Gajewski 1988).

Pollen records show that there were higher percentages of *Tsuga*, *Betula* and *Fagus* during the MWP, while *Pinus strobus* and *Alnus* had low relative abundances (Paquette and Gajewski 2013; Gajewski 1988). During the LIA, coniferous species such as *Pinus*, *Picea* and *Abies* became more abundant as hardwood taxa declined (Paquette and Gajewski 2013). The influence of European settlement on the region was marked by an increase in herbaceous pollen, most notably *Ambrosia* (Lafontaine-Boyer and Gajewski 2014; Paquette and Gajewski 2013).

In northwestern Ontario, diatom-based inferences of lake level changes show evidence of regional aridity associated with the MWP (Karmakar et al. 2014), such as a lower ratio of planktonic taxa to mid-depth or benthic diatom species indicating decreased effective moisture (Haig et al. 2013). Following the MWP, lake levels increased at ~1400 CE signalling a transition towards a wetter environment, consistent with the onset of the Little Ice Age (Haig et al. 2013). In more recent sediments of the past ~150 years, sharp increases in *D. stelligera* are consistent with the *Ambrosia* rise (Beck et al. 2016), indicating environmental changes driven by human colonization and land disturbance (Friel et al. 2014). Lake eutrophication following the expansion of human populations has also been inferred by increases in *Stephanodiscus minulutus* and *F. crotonensis* (Varin 2016).

To summarize, diatom records spanning the past 11.0 ka show an overall association with a three- part division of the Holocene into early, mid- and late periods, beginning at ~11.0 ka, 8.2 ka, and 3.0 ka, respectively (Karmakar et al. 2015; Moos et al. 2009). These responses track orbital-scale variations in climate, as well as abrupt millennial- to decadal-scale periods of change. Shifts in diatom assemblages are closely aligned with regional records of vegetation succession, which suggests that aquatic and terrestrial ecosystems are tightly inter-linked and responded together to climate forcing and large-scale disturbances (e.g. colonization by Euro-

Canadians). Such connections are the basis of this thesis, and are discussed in detail in the following chapters.

1.5 High-resolution analysis in varved lake sediments

To enable comparisons of aquatic and terrestrial ecosystem changes at local- to regional-scales, paleolimnological studies require fossil data from multiple individual sites with accurate chronologies (Björk and Wohlfarth 2001). Age-control methods often include AMS-radiocarbon dating (^{14}C) for sediments less than ~40000 years old, and ^{210}Pb dating for the uppermost 150 years. In areas such as eastern North America, biostratigraphic methods could also be used to date lake sediments; for example, by comparing the *Ambrosia* pollen rise to historical records. However, the development of age-depth models and subsequent high-resolution sampling is more precisely achieved in varved sediment sequences, which record changes on continuous time-scales and at very short intervals (e.g. seasonal, yearly, decadal, etc.) (Ojala et al. 2012; Lotter and Strum 1994).

Specific environmental and morphometric conditions are required for the formation of annually varved sediments; lakes should be deep enough to prevent circulation to the base of the water column, flat-bottomed, and permanently or periodically hypoxic to inhibit the presence of organisms that may cause bioturbation of the sediments (O'Sullivan 1983). Lakes fitting some or all of these requisites are uncommon, and it is difficult to identify whether or not varves will be present prior to retrieving sediment cores. Thus, paleolimnological studies often rely on other (potentially less reliable) dating methods in the absence of sediments with varved sequences.

Simultaneous varve- counts on replicate cores (cross-dating), as well as independent age-depth models (e.g. using ^{14}C dates), are used to validate the accuracy of varve chronologies. A normal margin of error for varve counts is ± 1-4%; however, cores spanning several millennia

are more likely to have higher chronological errors (Ojala et al. 2012; Renberg 1983). To reduce potential errors, cores are divided into sections delineated by distinctive marker layers (Fig. 1.2; Panel B, C) or marker bands (Fig. 1.2; Panel D), whereby counts are resolved in these sections. Varve counts can also be performed by two (or more) researchers to resolve differences between their results and to further estimate errors. Dependent on the sampling resolution required, cores with varved sediments are typically subsampled at 5-year or 10-year intervals. Varve thickness measurements for each interval allow for precise estimates of concentrations and accumulation rates of the subfossil assemblages (Fig. 1.2; Panel E).

1.5.1 Varve composition at Lac Brûlé and Lac Noir

In their paper, Ojala et al. (2012) emphasize that knowledge of varve formation processes in addition to estimations of dating error-range are essential to the development of varve-based chronologies. Several different methods were used in a previous study of Lac Brûlé to analyze the composition of varves in the lake sediments from this site, including adhesive tape preparations, polyethylene glycol, thin sections, and smear slides; results of the analyses suggest that Lac Brûlé sediments should be characterized as having carbonaceous organic varves (Lafontaine-Boyer and Gajewski 2014). These type of varves form when calcite is precipitated into the water column and settles to the bottom of the lake, leaving behind a whitish layer in the sediments (Zolitschka et al. 2015). This typically occurs during late spring and early summer when increased temperatures and photosynthetic activity affect the solubility of calcium carbonate ($CaCO_3$) in the water (Zolitschka et al. 2015). In the fall and winter, plant detritus and minerogenic components are deposited as dark, fine grained layers in the sediments (Dickman 1979). At Lac Brûlé, annual laminations (or varves) alternate between these seasonally deposited layers, with each couplet representing one year of deposition (Fig. 1.2; Panel A). At Lac Brûlé, this seasonality was confirmed by the smear

slides; the light layers had increased percentages of calcite, silt and plant material, as well as a high ratio of centric to pennate diatoms indicative of spring and summer algal blooms (Lafontaine-Boyer and Gajewski 2014); the dark layers had a higher concentration of pennate diatoms in comparison to the light layers, which would be expected later in the year during the fall months (Zolitschka et al. 2015). Individual varves were not studied in great detail at Lac Noir, but strongly resembled those from Lac Brûlé in terms of overall appearance and thickness; this suggests that the processes involved in the genesis of the varves at both lakes were similar. For each site, the annual nature of varves was tested independently with ^{14}C and ^{210}Pb dating (discussed separately in each of the following chapters).

1.6 Thesis organization

This thesis is presented in article format, and each of the three main chapters represents a manuscript written for a peer-reviewed journal. The chapters are presented in order of which they were completed. Laboratory work, diatom analysis, statistical analyses, creation of the figures/tables, and manuscript preparations were completed by the author of the thesis. The work was guided by the thesis supervisor, Konrad Gajewski, who co-authored each of the manuscripts.

Chapter 2: **Neil, K.,** Gajewksi, K. 2017. The impacts of late-Holocene climate variability and watershed-lake interactions on diatom community structure in Lac Brûlé, southern Québec. *Ecosphere, 8, Issue e01886,* 1-17.

Chapter 3: **Neil, K.,** Gajewski, K. 2017. A high-resolution paleolimnological study of climate and human impacts on Lac Noir, Québec over the past 1000 years [*Accepted in Quaternary Research*].

Chapter 4: **Neil, K.,** Gajewski, K. 2018. An 11,000-year record of diatom community responses to climate and terrestrial vegetation changes, southwestern Québec [*Submitted to Ecosphere*].

Within these chapters are extensive references to three previously published studies of Lac Brûlé and Lac Noir. I co-authored one of these papers (Cooper et al. 2016), however the manuscript was based on a Master's thesis by Cooper (2015) and is therefore not included as part of this thesis. Below are brief descriptions of how the studies relate specifically to this research;

(i) Paquette, N., Gajewski, K. 2013. Climatic change causes abrupt changes in forest composition, inferred from a high resolution pollen record, southwestern Québec, Canada. *Quaternary Science Reviews, 75*: 169–180.

In their paper, the authors developed a 1000-year, varve-based chronology for Lac Noir, as well as a high-resolution pollen record (10-year intervals) using the lake sediments. They found that vegetation closely tracked millennial- to decadal-scale climate changes, and forests were also largely impacted by the arrival of Europeans to the region. The authors estimated European colonization of the region slightly early at ~1810 CE, although their chronology was later adjusted by Lafontaine-Boyer and Gajewski (2014) to better compare with the nearby Lac Brûlé paleo- record and to fit more reasonably with historical records (Smith 1967). For my thesis, I used remaining sediments from the Lac Noir core to analyze diatoms (Chapter 4), which were directly comparable to the pollen record. Following Lafontaine-Boyer and Gajewski (2014), I used the adjusted Lac Noir chronology.

(ii) Lafontaine-Boyer, K., Gajewski, K. 2014. Vegetation Dynamics in relation to late Holocene climate variability and disturbance, Outaouais, Québec, Canada. *The Holocene, 24*: 1515-1526.

The authors of this paper created a 1200-year varve based chronology for Lac Brûlé, and compared the pollen record from the lake to that of nearby Lac Noir (Paquette and Gajewski 2013). Most notably, they found a difference in the timing of a *Tsuga* decline between the two lakes that was attributed to a local fire in the Lac Brûlé catchment and which ultimately masked the regional climate signal. For my thesis, I retrieved another core with varved sediments from Lac Brûlé, and used the chronology from Lafontaine-Boyer and Gajewski (2014) to resolve the varve counts. I used shorter time-intervals (5-years) to obtain better resolution in certain key periods of interest, and used sediments from the core to analyze diatoms for the site (Chapter 3).

(iii) Cooper, E., **Neil, K**., Gajewski, K. 2016. Spatial and temporal cladoceran community responses to environmental change and anthropogenic impacts in southwestern Québec. *Écoscience, 23(3-4)*: 97-112. DOI: 10.1080/11956860.2017.1286895

This paper was based on a Master's thesis by Cooper (2015), however I worked on the core chronology, reanalyzed the data, re-created the figures, and prepared the manuscript for publication in the journal *Écoscience*. The paper summarizes changes in cladoceran assemblages at Lac Brûlé for the past 1200 years as they relate to pollen-based paleoclimate reconstructions from Lafontaine-Boyer and Gajewski (2014). In my thesis, I refer to these cladoceran communities in my interpretations of the Lac Brûlé diatom record (Chapter 3).

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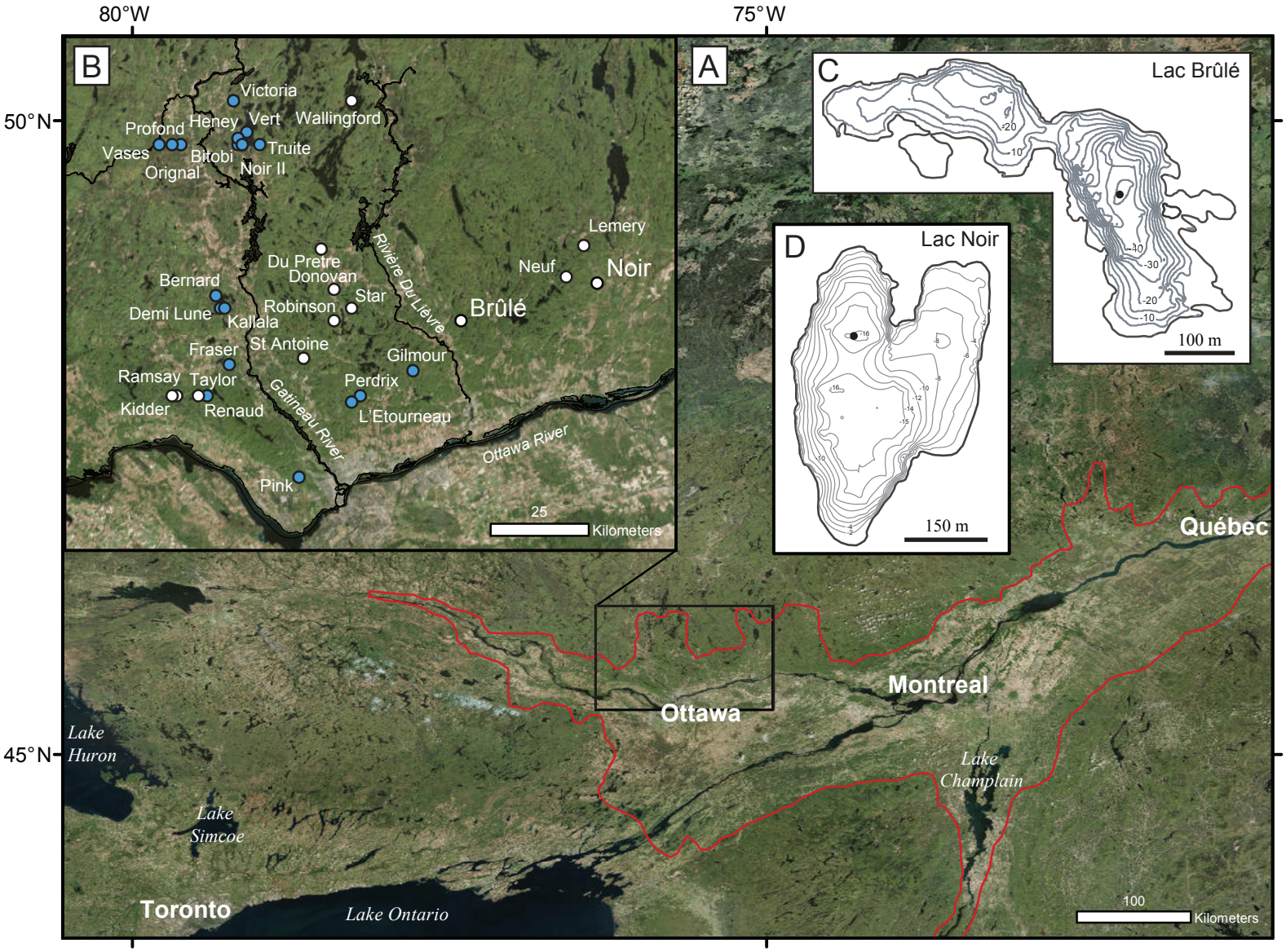
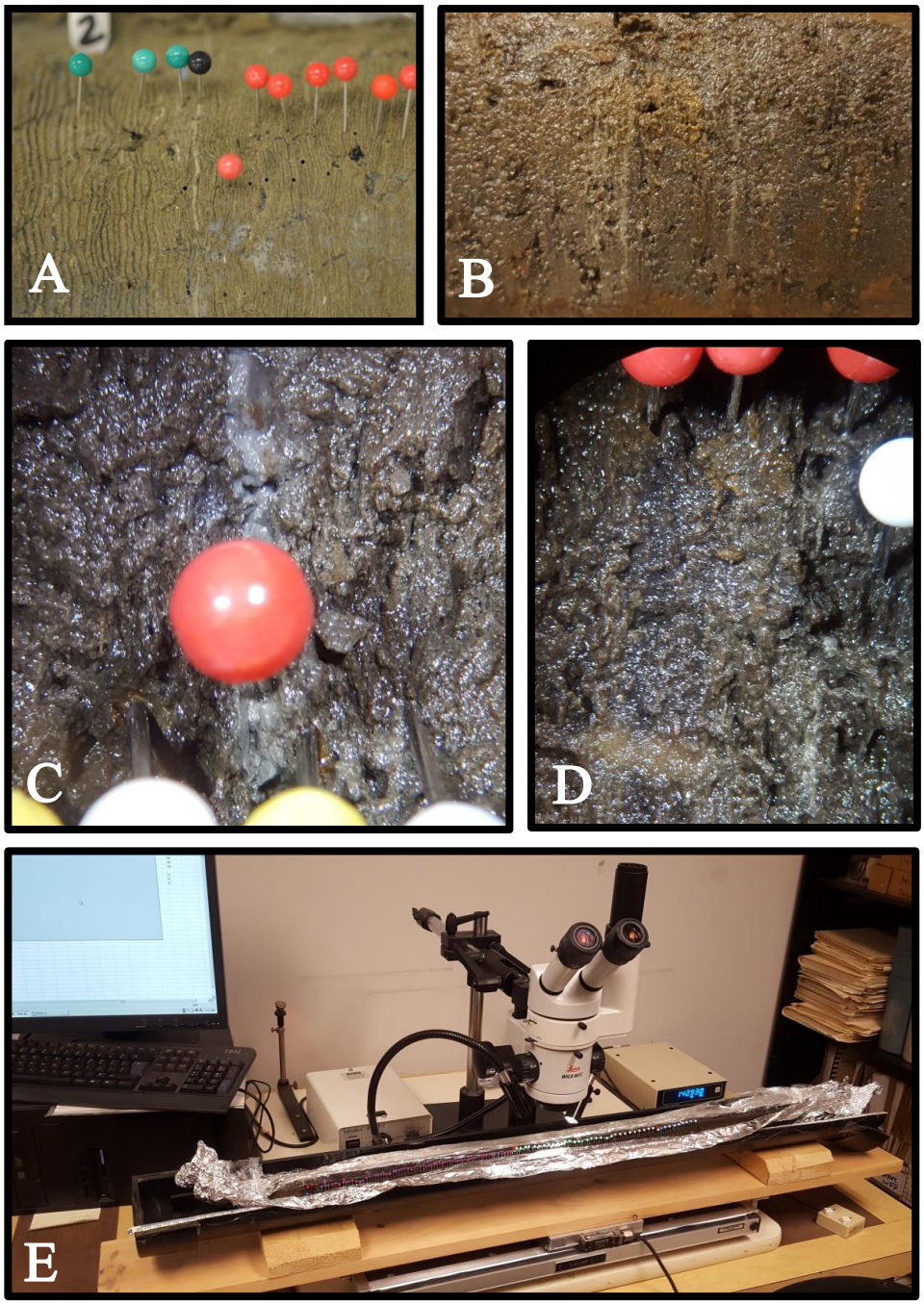


Figure 1.1: A) Location of the study area in southwestern Québec, Canada, where two varved lake sediment cores were analyzed for diatoms. The red line represents an estimate of the previous extent of the Champlain Sea following deglaciation (after ~13,000 cal. yr. BP; Rodrigues 1992). B) Lakes from which modern surface samples were analyzed for cladocera (all lakes marked by circles; Cooper et al. 2016), and diatoms (blue circles; Varin 2016). Varved lake sediment cores were retrieved from Lac Brûlé and Lac Noir (bold) for down-core analyses. C) and D) Bathymetry of Lac Brûlé and Lac Noir; the black dot in each lake represents the location from which the sediment cores were retrieved.



Panel A: Photo by Karelle Lafontaine-Boyer 2013; Panel B-E: Photos by Karen Neil 2018

Figure 1.2: Varved lake sediments from Lac Brûlé and Lac Noir; A) A couplet of one light and one dark layer represent a single year of deposition. Ten-year intervals at Lac Brûlé are marked by the red and green pins. The black pin shows a grey marker layer used to cross-correlate multiple cores (Photo credit: Karelle Lafontaine-Boyer); B) Varves in the Lac Noir sediment core, which also have distinct grey marker layers; C) Sediments at the base of the Lac Noir core. The red pin marks a distinct grey marker layer at ~11000 years before 2010. To the right of the pin, the lighter sediments indicate higher minerogenic content; D) A marker band is indicated between the first two red pins, distinguishable from marker layers by its darker color and wider length (sometimes spanning 10-20 varve couplets); E) Acu-Rite linear encoder and Quick-Check readout with Measure J2X software, used to measure varve thicknesses

CHAPTER TWO

Impacts of late-Holocene climate variability and watershed-lake interactions on diatom communities in Lac Brûlé, Québec

Abstract

A high-resolution diatom analysis of a varved sediment sequence from Lac Brûlé, southwestern Québec, was used to study temporal patterns of environmental change in the late Holocene. Key periods of interest in the record included the Medieval Warm Period (~800-1300 CE), the Little Ice Age (~1450-1850 CE), and post- Euro-Canadian settlement (~1850-present). Subfossil diatom assemblages were compared to previously-published pollen, cladocera, and sediment records from Lac Brûlé, revealing complex dynamics between terrestrial vegetation succession, nutrient fluxes, and trophic interactions. Generalized additive models (GAM) showed a response to long-term climate variability in the diatom record, although it was not the most influential driver of community changes at Lac Brûlé. Catchment-mediated processes instead played the largest role in governing the structure of diatom assemblages in the lake. For example, nutrient loading following a local fire in the watershed at 1345 CE led to an abrupt and significant increase in *Fragilaria* spp. Human activity associated with deforestation and the Wallingford-Back Mine (1924-1972 CE) also had strong impacts on the landscape, which triggered further responses in the aquatic communities of Lac Brûlé.

Keywords: Bottom-up / top-down; cladocera; diatom; European settlement; generalized additive models (GAMs); 'Little Ice Age'; 'Medieval Warm Period'; mine impact; paleolimnology; pollen; varve.

2.1 Introduction

There are many complex pathways through which terrestrial and aquatic ecosystems respond to external forcings and their interactions (Winder and Schindler 2004). It is thus challenging to anticipate when and how ecological communities will react to present and future changes in the environment (Johnstone et al. 2016), and to address potential issues regarding ecosystem management. Developing strategies to deal with environmental change requires not only an understanding of the direct and indirect mechanisms influencing current ecosystem responses (Alric et al. 2013), but also an expanded temporal perspective of these changes (Foster et al. 1990). Numerous paleolimnological studies, for example, demonstrate the ability of lake sediment analysis to accurately reconstruct ecosystem responses to external stresses (Smol et al. 2001), especially when sampled at high temporal resolution.

In southwestern Québec and southeastern Ontario, paleo-studies have shown that climate variability in the late Holocene had a significant influence on temperate forests and aquatic communities. Pollen-based inferences indicate that temperature and precipitation were important drivers of vegetation dynamics during well-established climate regimes, namely the Medieval Warm Period (800-1300 CE) and the Little Ice Age (1450-1850 CE) (Lafontaine-Boyer and Gajewski 2014; Paquette and Gajewski 2013). During these periods, phytoplankton and zooplankton assemblages were responsive to direct climate impacts on lake hydrologic and thermal budgets (Haig et al. 2013; Cooper et al. 2016). However, indirect catchment-mediated processes (e.g. vegetation composition and productivity, fire, soil development) also play an integral role in governing the structure and function of lacustrine ecosystems (Fritz and Anderson 2013; Anderson 2000). Since the settlement of Euro-Canadians in the region (1820s–present), interactions between ongoing climate change and anthropogenic activities have also triggered abrupt shifts in biotic communities (Lafontaine-Boyer and Gajewski 2014; Paquette and Gajewski

2013; Cooper et al. 2016).

The aim of the present study was to use a paleolimnological approach to hierarchize the impacts of climate variability and local landscape pressures on diatom assemblages over the past 1200 years at Lac Brûlé, southwestern Québec. Focus was placed on diatoms as they are well preserved in lake sediments (Smol and Stoermer 2001), they are sensitive to different types of external forcings (e.g. climate, nutrient inputs, and herbivory), and as primary producers they form the base of the aquatic food web. High-resolution data from previous studies, including paleo-records of sediment composition, pollen (Lafontaine-Boyer and Gajewski 2014), and cladocera (Cooper et al. 2016) were integrated into analyses of the diatoms; this permitted an understanding of the effects of lake catchment and trophic interactions (Puusepp and Kangur 2010) on the diatom communities.

2.2 Methods

2.2.1 Study Site

Lac Brûlé (45°43'09''N, 75°26'32''W, 270 m) is a small meromictic lake located in the Gatineau Hills of southern Québec, approximately 40 km northeast of Ottawa, Ontario. The lake is approximately 25 ha, is well encased by steep hills, and has a maximum depth of 43 m, thus ideal conditions for the formation of lake sediments with varves. In autumn of 2013, the lake was characterized as ultra-oligotrophic; total phosphorous was 4 μgL^{-1}, total nitrogen was 170 μgL^{-1}, and chlorophyll-α was 0.5 μgL^{-1} (Cooper et al. 2016). At the surface of the lake the pH was 8.35 and specific conductance (SC) was 119 μmgL^{-1}, and at approximately 30 m depth there was a strong chemocline (Cooper et al. 2016).

The lake catchment area is mostly forested, and characterized as mixed conifer-hardwood comprised of red and white pine (*Pinus haploxylon and diploxylon.*), spruce (*Picea*), eastern

hemlock (*Tsuga canadensis*), maple (*Acer spp.*), red oak (*Quercus rubra*), yellow birch (*Betula alleghaniensis*), and American beech (*Fagus grandifolia*) (Lafontaine-Boyer and Gajewski 2014). Deforestation and agriculture following Euro-Canadian settlement (after the 1820s) in the region was likely limited to the river valleys (Smith 1967), the closest of which (*Rivière du Lièvre*; Figure 1.1, Panel B) is 6 km from Lac Brûlé. The total catchment area to lake area ratio is relatively low (~ 6:1).

The only historical evidence of human impacts in the immediate watershed of the lake is from operations at the Wallingford-Back Mine, which was open from 1924-1972 CE (Leroux 2012). The mine is located 300 m north of Lac Brûlé, with a private access road running directly alongside the northern shore. A small stream connecting a pond at the mine to Lac Brûlé may intermittently drain into the lake, though there was no indication of water flow in June of 2016. There are other small inflow channels to the lake, and one output stream on the eastern side of the lake. Currently, several cottages and permanent houses are located around small lakes in the region, but only one cabin exists on Lac Brûlé and it was constructed after the 1980s.

2.2.2 Coring and Chronology

Sediment cores were retrieved from the deepest basin of Lac Brûlé (43 m depth) in two separate field seasons using freeze-corers. For a previous study (Lafontaine-Boyer and Gajewski 2014), a set of four continuously laminated (varved) cores was retrieved in 2012, one of which was sampled for pollen analysis. Lafontaine-Boyer and Gajewski (2014) established a varve-based chronology for the lake sediments by cross-dating these four cores, using distinct marker layers as tie points between the cores. The annual nature of varves was verified with smear slides, and the chronology of the core chosen for pollen analysis (BV13) was independently validated using ^{14}C dating (Fig. 2.1). In 2013, an additional core (BV14) was retrieved from the same lake

basin, and analyzed for both cladoceran remains (Cooper et al. 2016) and diatoms (this study). Varve counts from the BV14 core were resolved with those of the four 2012 cores (Fig. S2.1), with an estimated error of <1% in the resulting chronology.

2.2.3 Laboratory analysis

Varve thickness of the BV14 core was measured at five-year intervals, using an Acu-Rite linear encoder and Quick-Check readout with Measure J2X software. The core was then sectioned at five- or ten-year intervals, with higher sampling resolution taken during significant time periods. Determination of these periods (e.g. the Medieval Warm Period and Little Ice Age) was guided in part by the pollen record from the 2012 core. Sediment subsamples of 0.25 cm^3 were extracted from each section of the core, and processed for diatoms following standard protocols (Battarbee et al. 2001). A microsphere suspension of $5x10^6$ spheres mL^{-1} was prepared from a stock solution, and a pre-determined amount was added to each subsample after cleaning to enable the calculation of fossil diatom concentration and accumulation rates.

2.2.4 Microscope slide preparation and counting

A small amount of diatom suspension, diluted with distilled water, was pipetted onto a clean coverslip and left to evaporate at room temperature to attain an even spread of dried diatoms over the coverslip. A drop of Naphrax was then used to mount the coverslips onto permanent slides. A minimum of 500 individual diatom valves per slide were counted and identified under oil emersion at 1000x magnification, using a Nikon 90i microscope. Identifications were based on Antoniades et al. (2008), Siver et al. (2005) and Patrick and Reimer (1975; 1966). Chrysophyte scales were counted concurrently for each microscope slide to estimate the relative proportions of scales to diatom valves.

2.2.5 Statistical Analyses

A total of 21 diatom taxa were selected for statistical analysis, based on the criterion that each individual taxon had greater than 3% relative abundance in at least one of the 194 samples counted. Rare species were grouped into categories of 'other benthics' and 'other planktonics', and all relative abundance data was Hellinger transformed prior to data analysis (Legendre and Gallagher 2001). Principal components analysis (PCA) was chosen to summarize patterns of diatom community changes through time (Legendre and Birks 2012). To compare the fossil diatom communities with existing pollen, cladocera and sediment records from Lac Brûlé, samples were aggregated into 10-year time intervals. This returned 123 continuous samples between 785-2005 CE for which all taxonomic and sediment data were available. Changes in the diatom, pollen and cladocera assemblages at this 10-year sampling resolution were each quantified with PCAs using the package 'vegan' (Oksanen et al. 2008) in R3.2.5 statistical software (R Core Team 2013). Significant principal components (PCs) in each ordination were selected using scree plots of the axis eigenvalues, and represented the main taxonomic trends in subsequent analysis.

Using the 'mgcv' package (Wood 2008; 2011) in R, generalized additive models (GAMs) were used to separate and quantify the influences of several individual forcing variables (e.g. climate derived from local pollen records) on diatom community structure in Lac Brûlé. This type of modelling uses a sum of smooth functions to reveal local patterns in the relationships between predictor and response variables (Simpson and Anderson 2009). As such, GAMs are applicable in multi-proxy paleolimnological studies where the effects of variables can often change through time, and are potentially amplified or dampened during significant periods (e.g. the MWP, the LIA, and Euro-Canadian settlement).

In this study, changes in the scores of each significant diatom PC axis were considered as the response variable in the GAMs (four individual models). The following predictor variables

were introduced in each model; pollen PC axes 1-3 (representing vegetation responses to climate and disturbances), the ratio of chrysophyte scales to diatom valves (CS/DV; representing lake trophic status), and cladocera PC axes 1-3 (representing predation pressures). The GAMs were fit using restricted maximum likelihood (REML) smoothness selection, and thinplate splines with a value of k=9 for each basis dimension. A shrinkage method approach was also used to place a second penalty on each smooth term (Marra and Wood 2011). Evidence of autocorrelation was seen in the models explaining diatom PC axis 1 and 4; however, fitting generalized additive mixed models (GAMMs) with various autoregressive processes failed to resolve the correlation structure in the residuals. Thus, we used the models without correcting for autocorrelation, but recognize that this potentially led to poorer function estimates (Kohn, Schimek, and Smith 2000).

2.3 Results

2.3.1 Diatom assemblage zones

The diatom record from Lac Brûlé was dominated by planktonic species (~40-80%), including *Discostella stelligera* (Cleve & Grunow) Houk & Klee 2004, and other *Cyclotella* species, *Asterionella formosa* Hassal 1850, and *Aulacoseira* spp. Fragilarioids and benthic diatoms were less abundant throughout most of the record (15-60%), and were mainly represented by *Fragilaria* spp., *Achnanthidium minutissimum* (Kützing) Czarnecki 1994, and *Tabellaria flocculosa* str. IIIp (Roth) Kützing 1844 (Fig. 2.2). The fossil diatom percentage diagram was divided into three major zones (and four subzones) based on a principal components analysis of the main taxa (Fig. 2.3).

D. stelligera was relatively abundant at the beginning of zone A (715-1350 CE), but declined rapidly from ~55% to 25% of the total diatom sum around 850 CE (Fig. 2.2). This marked

the transition between zones A1 and A2, and was associated with an increase in *Cyclotella bodanica var. intermedia* Manguin ex Kociolek & Reviers 1996 and *A. formosa*, as well as the near disappearance of *Aulacoseira* spp. Species such as *Cyclotella rossii* Håkansson 1990 and *T. flocculosa* str. IIIp maintained relatively consistent abundances throughout zone A (~10% and 5% respectively). In zone A1, the summed abundance of all planktonic species was greater than the average for the whole record. Planktonic species percentages fell below average from 850 CE to 1100 CE, and remained close to average for the remainder of zone A2.

Zone B (1350 CE-1875 CE) was divided into two subzones, based on several transitions in the diatom assemblages. In zone B1, *D. stelligera* increased slightly, while *C. bodanica var. intermedia* and *C. rossii* declined rapidly from 20% to under 5% of the total diatom sum. *Fragilaria crotonensis* Kitton 1869 had a prominent peak (~13.5%) in 1375 CE, but returned to lower abundances of <5% for the remainder of zone B. At the end of zone B1, *T. flocculosa* str. IIIp decreased to <1% relative abundance. In zone B1, benthic and fragilarioid species were still outnumbered by planktonic species, though they did increase to above average values in comparison to the rest of the record. *D. stelligera* abruptly increased at the beginning of zone B2, reaching a maximum abundance of ~75% of the total diatom sum in 1460 CE. Following this peak, *D. stelligera* decreased again to ~50%. An increase in *Aulacoseira* spp. was also seen at around 1650 CE. Throughout the zone, both *C. bodanica var. intermedia* and *C. rossii* gradually increased in abundance towards percentages seen earlier in the record. Abundances of planktonic species were consistently above average in Zone B2.

Zone C (1875 CE-2010 CE) was characterized by high abundances of *Cyclotella michiganiana* Skvortzov [Skvortzov] 1937, *F. crotonensis*, and *A. minutissimum* in comparison with the earlier record. The relative abundances of these three species peaked at ~ 15%, 40%, and 8.5% of the total diatom sum, respectively. At the beginning of the zone, *D. stelligera* represented

roughly 20-45% of the diatom assemblage. At 1970 CE, *D. stelligera* increased abruptly to ~65%, and reached a peak in 2010 CE. When *F. crotonensis* peaked in 1935 CE, benthic and fragilarioid species outnumbered planktonic species in the diatom record by a ratio of 3:2. Following this, planktonic species began to increase in abundance, reaching around 80% of the total diatom sum at the top of the record.

Total diatom accumulation rates (DAR; also known as influx) for Lac Brûlé were relatively low until 1700 CE when they increased slightly, and reached maximum values in 2005 CE (Fig. 2.3). High frequency oscillations of DAR in zone B2 were interpreted as a function of batch number during processing, possibly resulting from slight differences in concentrations of microspheres added to sample vials on different dates. Long-term trends spanning the entire record, however, did not appear to be affected by this variance. The CS/DV in Lac Brûlé was highest near the beginning of zone A2, with a long-term trend of decreasing values from 925 CE to present date (Fig. 2.3).

2.3.2 Principal Components Analysis

Approximately 52% of the total variance in diatom assemblages was explained on the first four axes of a principal components analysis (Fig. 2.3, Fig. S2.3; component 1: 19.4%; component 2: 13.2%; component 3: 11.4%; component 4: 8.0%). The first component represented changes in the composition of *D. stelligera*, *F. crotonensis*, and *Staurosirella pinnata* (Ehrenberg) D.M. Williams & Round 1988, with negative scores in zones A1 and A2, positive scores in zone B2, and large positive scores in zone C after 1950 CE. The second component was positively loaded on *C. rossii* and negatively loaded on *C. michiganiana* and *A. minutissimum*. This component had high positive scores in zone A1 and negative scores in zones B1 and C. The third component was correlated with rarer taxa, including positive contributions of *Cymbopleura* spp. and *A.*

minutissimum versus those of *Aulacoseira* spp. and *Achnanthidium gracillimum* (F. Meister) Lange-Bertalot 2004. This component showed a trend of positive scores in zone A2, and highly variable (though mostly negative) scores from 1430 CE to present. The fourth component was correlated with *F. crotonensis*, having positive scores in zones B1 and C.

2.3.3 Generalized additive models (GAMs)

GAMs were used to show the contributions of seven forcing variables on fitted diatom PC axis scores at Lac Brûlé; pollen PC axis 1 and 3 (interpreted as watershed disturbances), pollen PC axis 2 (climate), chrysophyte scale/diatom valve ratio (CS/DV; lake trophic status) and cladocera PC axis 1, 2 and 3 (predation pressure). In each of the four GAMs (Fig. 2.4-2.7), cladocera PC axis 3 had zero contribution to the fitted scores and was therefore not shown in the figures. Together, the seven variables explained 63.0%, 60.7%, 49.2% and 57.6% of the variance in the fitted diatom PC axis 1-4 scores, respectively (Fig. 2.8).

In the first GAM explaining the fitted diatom PC axis 1 scores, watershed disturbances (pollen PC axis 1) contributed the most to the fitted values (p-value < 0.001). At ~1345 CE, there was an abrupt shift from positive to negative values in the time series representing the effects of watershed disturbance on diatom PC axis 1 scores (Fig. 2.9A), signalling an important disturbance event in the record. Another shift towards greater negative values at around 1900 CE indicated a second disturbance event with similar consequences for the diatom community. Climate (pollen PC axis 2) also had significant influences on the fitted diatom PC axis 1 scores, though not as consistently throughout the record. Figure 2.9B, however, shows changes from positive to negative y-axis values (and vice-versa) that marked three important climatic periods in the mid to late Holocene; 800-1450 CE, 1450-1900 CE, and 1900-2010 CE. Finally, lake trophic status (CS/DV)

was only significant after 1675 CE.

In the second GAM explaining the fitted diatom PC axis 2 scores, trends were influenced by several covariates. Pollen PC axis 1 again showed a sudden shift at ~1345 CE, interpreted as a response to disturbance in the watershed (Fig. 2.10A). However, unlike in the first model, pollen PC axis 3 showed a significant change to positive y-axis values at ~1860 CE, again indicating an abrupt disturbance event (Fig. 2.10C). Climate (pollen PC axis 2) was the most influential contributor to the fitted diatom PC axis 2 scores, and showed the same climatic periods identified in the first GAM (Fig. 2.10B). Predation pressure was mostly significant for brief periods in the oldest and most recent sediments of the record (cladocera PC axis 1; Fig. 2.10E), but also showed similarities to the pollen PC axis 2 time series (cladocera PC axis 2; Fig. 2.10F).

Only lake trophic status (CS/DV) was significant in contributing to the fitted diatom PC axis 3 scores, where y-axis values became more positive at ~1345 CE, and again at ~1700 CE (Fig. 2.11D). In the fourth GAM, climate (pollen PC axis 2) and predation pressure (cladocera PC axis 1) were the only significant contributors to fitted diatom PC axis 4 scores (Fig. 2.12B and 2.12E).

2.4 Discussion

2.4.1 The Medieval Warm Period (MWP; ~800-1450 CE)

In this study, very few samples from the earliest section of the core (subzone A1) were available for input in the GAMs; this restricted interpretations of terrestrial and aquatic assemblages to the past 1200 years of the late Holocene, beginning with the onset of the Medieval Warm Period at ~800 CE in southwestern Québec. In the MWP, terrestrial vegetation in southwestern Québec was characterized as temperate conifer-hardwood forest dominated by hemlock, white pine, maple, beech, and birch (Lafontaine-Boyer and Gajewski 2014; Paquette and

Gajewski 2013). At Lac Brûlé, this led to a pollen-based reconstruction of generally warmer climatic conditions (Lafontaine-Boyer and Gajewski 2014) consistent with sites across eastern North America (Gajewski 1988; Viau et al. 2012), and formed the basis of the interpretation of the PC axes (above). Regional aridity and droughts associated with the MWP were recorded by multiple lake-level studies west of Lac Brûlé (Haig et al. 2013; Booth et al. 2006; 2012). In contrast, the Lac Brûlé pollen record indicated variability in reconstructed precipitation values throughout the MWP; conditions were relatively dry until ~1000 CE, after which they became predominantly wetter (Lafontaine-Boyer and Gajewski 2014). There is therefore little evidence to suggest that droughts were occurring in the MWP further east in southwestern Québec or in southeastern Ontario (Keizer et al., 2015).

The GAMs showed a defined period from ~800-1450 CE where climate (PC axis 2) in the MWP was a significant contributor to fitted diatom trends (Fig. 2.9; panel B). At the onset of the MWP, increased abundances of *C. bodanica* var. *intermedia* and *C. rossii* in Lac Brûlé (Fig. 2.2) signalled lower available nutrient concentrations associated with the warming summer temperatures (Bracht et al. 2008; Findlay et al. 1998). During this period the high ratio of chrysophytes to diatoms (Fig. 2.3; Smol 1985), as well as the relatively high percentages of *T. flocculosa* str. IIIp (Fig. 2.2; Puusepp and Kangur 2010), indicated oligotrophic conditions in the lake. As temperatures rose above average for the late Holocene, increased thermal stability may have favoured lighter planktonic diatoms (e.g. *Cyclotella*) over more heavily silicified *Aulacoseira* spp. (Harris, Cumming, and Smol 2006). As conditions became wetter towards the end of the MWP, erosion of the soils in the Lac Brûlé catchment area and subsequent nutrient loading would have been more prominent. This is evidenced by a gradual decline of chrysophytes in relation to diatoms after 1000 CE (Fig. 2.3).

The cladoceran assemblages of Lac Brûlé during the MWP also revealed relatively high

abundances of *Bosmina longirostris*, a species commonly correlated with warmer temperatures (Fig. S2.2; Cooper et al. 2016). However, the presence of *B. longirostris* would typically indicate lake eutrophication (Luoto et al. 2008), contradicting the diatom- and chrysophyte-based inferences of nutrient poor conditions in the MWP. If cladoceran assemblages were responding to changes in lake trophic status (through bottom-up controls), we would have expected to see a positive correlation between *B. longirostris* and CS/DV values. The lack of such a relationship suggests that top-down influences on cladoceran assemblages (e.g. changes in temperature affecting cladocera metabolism and/or fish predation pressures) may have been more relevant in governing community structure during this period.

2.4.2 The Little Ice Age (LIA; ~1450-1850 CE)

At approximately 1450 CE, the expansion of white pine, spruce, and alder (*Alnus*), as well as a decline in beech, marked the onset of regional cooling associated with the Little Ice Age in southwestern Québec (Lafontaine-Boyer and Gajewski 2014) and southeastern Ontario (Keizer et al., 2015). Deteriorating climatic conditions during this period favoured coniferous species adapted to colder and moister conditions, while hindering the regeneration of hemlock after a major fire in the lake catchment area (discussed below). After 1600 CE, there was an abrupt decline in the accumulation of beech and maple pollen at Lac Brûlé (Lafontaine-Boyer and Gajewski 2014) and also around a second lake within 25 km of the study site (Paquette and Gajewski 2013). This event was interpreted as a rapid cooling in the region that persisted for approximately 100 years.

The timing of the LIA (~1450-1850 CE) as well as a considerable influence of climate on fitted diatom trends was demonstrated by the GAMs. The diatom record of Lac Brûlé showed an increase in the abundance of *D. stelligera* at the onset of the LIA cooling (Fig. 2.2), though this species would typically be linked with warmer climates (Perren et al. 2009). Fritz and Anderson

(2013) proposed that an expansion of *D. stelligera* prior to 20th century warming may have resulted from climate-induced mixing of the water column, or nutrient loading from catchment-driven processes. As Lac Brûlé is surrounded by steep and high hills, it is unclear if changes in wind regimes would have had significant influences on diatom assemblages in the lake. However, nutrient enrichment in the LIA was evidenced by relatively low abundances of *C. bodanica* var. *intermedia* and *T. flocculosa* str. IIIp (Wolin and Stoermer 2005), as well as the continued decline of chrysophytes relative to diatoms (Smol 1985). Given the uncertainty associated with interpretations of *Cyclotella* (or *Discostella*) patterns in paleolimnological studies, future work would benefit from improved knowledge of the ecological preferences of individual species within this genus (Saros and Anderson 2015). During the coldest and driest period reconstructed from the Lac Brûlé pollen record (1600-1700 CE; Lafontaine-Boyer and Gajewski 2014), the only significant change in the diatom assemblages was a brief peak in *A. formosa* (Fig. 2.2). This suggests that worsening conditions in the LIA did not have strong adverse effects on aquatic assemblages; instead, climate during this cold period may have been a hindrance primarily to terrestrial plant production (Lafontaine-Boyer and Gajewski 2014).

The cooler temperatures associated with the LIA favoured the presence of cold-tolerant cladocera species, as evidenced by an increase in the representation of *Daphnia longispina* (Cooper et al. 2016). Furthermore, percentage abundances of the smaller-sized *B. longirostris* decreased in relation to larger-sized species (*Eubosmina longispina* and *D. longispina*). Lower temperatures in the LIA may have caused a top-down cascading effect in the ecosystem; extended ice-cover could have caused oxygen depletion in the lake, leading to higher fish kills and reduced predation pressures on larger cladocera species, which would have been more easily detected by predators (Luoto et al. 2008, Cooper et al. 2016).

2.4.3 Impacts of fire disturbance in the Lac Brûlé watershed

As interpreted in Lafontaine-Boyer and Gajewski (2014), a large influx of charcoal in the Lac Brûlé sediment record at around 1345 CE signalled a local fire in the watershed. Several changes were seen in the pollen record at this time, most notably a rapid decline in hemlock percentages which subsequently failed to recover to levels found prior to the fire.

In the GAMs, there was an abrupt shift in the contribution of watershed disturbances (pollen PCA axis 1) to fitted diatom scores at 1345 CE (Fig. 2.9, 2.10; panel A); this confirmed that external forcing in the catchment area (a fire) played a significant role in governing diatom community structure in Lac Brûlé. An abrupt increase in varve thickness immediately following the fire indicated heavier accumulation of allocthonous materials in the lake basin as a result of increased erosion in the watershed (Lafontaine-Boyer and Gajewski 2014). Additionally, high charcoal and dissolved organic carbon (DOC) inputs into the lake caused more shading and lower light penetration through the water column (Philibert et al. 2003). These poor light conditions favoured the more tolerant *Fragilaria* species (Anderson et al. 2008), which showed a peak in relative abundance at this time. Reduced light availability was also marked by a decline in planktonic diatom abundance, particularly for species with more heavily silicified valves (e.g. *C. bodanica* var. *intermedia*) (Gall 2015).

Cladoceran assemblages showed subtler changes associated with the fire at 1345 CE; the GAMs also indicated that trophic interactions (cladocera PC axis 1 and 2) did not contribute significantly to fitted diatom scores at this time (Fig. 2.9-2.11). However, small increases in the accumulation rates of littoral cladoceran species (*Alonella excisa*, *Chydorus brevilabris*, and *Sida* undiff.) after the fire signalled greater nutrient inputs and DOC in the lake (Cooper et al. 2016), consistent with the inferences made from both the pollen and diatom records.

2.4.4 Regional and local anthropogenic influences in the 19th-21st century

The first European settlement along the Ottawa River and its tributary valleys occurred in the early 1820s, increasing towards the middle of the century as the lumber trade expanded (Smith 1967). The impacts of anthropogenic land-use changes on regional forest ecosystems was reflected as a rise in *Ambrosia* pollen in Lac Brûlé sediments at 1860 CE (Lafontaine-Boyer and Gajewski 2014), slightly after initial colonization of the region. Historical records describe logging activities along the *Rivière du Lièvre* (approximately 6km from the study site) and in the surrounding *Lièvre* valley (Smith 1967), although the extent and proximity of these activities to Lac Brûlé remains unclear. Regardless, the pollen record showed decreased pollen accumulation rates of white pine, beech, and hemlock after 1860 CE, reflecting selective logging of these species within the region. In the mid to late 19th century, fire associated with logging and the practice of burning forests for agriculture (Johnstone et al. 2016) was evidenced by increased charcoal accumulation rates in the sediment record, as well as an increase in the relative abundance of shrub and herbaceous pollen as the forest canopy opened (Lafontaine-Boyer and Gajewski 2014). Human-induced fire activity in the immediate watershed of Lac Brûlé, however, was unlikely due to the steep sloping topography surrounding the lake, making it unsuitable for extensive use.

Regional-scale anthropogenic activities thus led to significant impacts on vegetation composition, which ultimately exerted bottom-up controls on diatom communities of Lac Brûlé. For example, land clearance and conversion could have led to the mobilization of previously fixed nitrogen compounds (Vitousek et al. 1997), effectively altering the water chemistry of nearby lake ecosystems. The Lac Brûlé diatom record showed an increase in the abundance of *A. minutissimum* after 1860 CE (Fig. 2.2), indicating a response to an influx of nitrogen and DOC associated with Euro-Canadian settlement in the general area (Pappas 2010). Diatom assemblages also showed a post-settlement pattern of succession from *C. bodanica var. intermedia* to *C. michiganiana*, similar

to several other diatom records from the upper Great Lakes (Wolin and Stoermer 2005; Garrison and Wakeman 2000). Increased nutrient loading as a result of regional deforestation activities in the late 19th century likely drove this shift in diatom species, as higher total nitrogen favoured *C. michiganiana* over *C. bodanica var. intermedia* (Wolin and Stoermer 2005).

In contrast to the rather distinct shifts seen in both the pollen and diatom assemblages during the 19th century, the cladoceran communities of Lac Brûlé showed minimal responses to these anthropogenic impacts. This could be explained by weaker bottom-up controls on the lake ecosystem towards the top of the food web (McQueen et al. 1989). Given the wide range of ecological tolerance of the two dominant cladocera species in the record (*B. longirostris* and *E. longispina*), they also would have been more resilient against environmental changes associated with early human settlement.

Anthropogenic impacts in the immediate watershed of Lac Brûlé also affected the aquatic communities of the lake, most notably during the operation of the Wallingford-Back Mine from 1924-1972 CE (Leroux 2012). Immediately following the opening of the mine, the diatom record showed an abrupt increase in benthic *Fragilaria* species (Fig. 2.2), which were able to out-compete the previously dominant *D. stelligera* for resources (Köster et al. 2005). Small peaks in *A. formosa* and *Aulacoseira* spp. at this time indicated nutrient enrichment (Wolin and Stoermer 2005), potentially through a connection between the tailing pond of the mine and Lac Brûlé, and/or incoming dust from the nearby access road. Furthermore, the relative abundance of cladocera species *B. longirostris* in the 20th century showed an almost identical profile to that of *Fragilaria crotonensis.* This substantiated the inference of increased nutrients and inputs of DOC associated with exploitation of the Wallingford-Back Mine (Cooper et al. 2016). After the closure of the mine in 1972 CE, the relative abundance of *Fragilaria crotonensis* and *B. longirostris* decreased, again very abruptly. The GAMs also showed a change in the contribution of watershed disturbances

(pollen PC axis 1) to diatoms trends at this time (Fig. 2.9; panel A), further indicating that the mine was a significant factor influencing lake community structure.

The abrupt responses of diatom assemblages to late Holocene climate variability, natural watershed disturbances (e.g. fire), and anthropogenic stressors demonstrates the importance of paleolimnological studies with high-resolution sampling. More generally, the ecosystems of southwestern Québec have shown significant responses to past climatic changes and local forcings on a timescale similar to that of the current global warming. The coherent, immediate and coupled responses of watershed dynamics and lake communities to the fire in 1345 CE coincidentally occurred as the climate was deteriorating in the Little Ice Age. The impacts of the fire on both terrestrial and aquatic systems lasted longer than would otherwise be predicted given the nature of this disturbance. The rapid response and subsequent recovery of the lake to impacts from the Wallingford-Back Mine would also have been difficult to predict without the long-term perspective offered by this paleolimnological study. Finally, the methodology we have applied here permitted the identification of the different and interacting forcings on Lac Brûlé and its surroundings, on a timescale particularly relevant to the understanding of current climate change and land-use impacts.

2.5 Conclusions

(1) Integrating paleo-records of terrestrial (pollen) and aquatic (diatoms, cladocera) biota in paleolimnological studies provides insight into the complexities of watershed-lake interactions, as well as the functioning of aquatic ecosystems at different trophic levels.

(2) At Lac Brûlé, the diatom record showed trends associated with two distinct millennial-scale climate variations in the late Holocene. In the Medieval Warm Period (MWP), oligotrophic

conditions and thermal stratification in the lake were associated with pollen-based inferences of warmer summer temperatures. The expansion of *D. stelligera* at the onset of regional cooling in the Little Ice Age (LIA) was thought to be primarily driven by catchment-mediated processes (nutrient loading), rather than direct climatic influences.

(3) Watershed-lake interactions were thus important drivers of change for aquatic communities; in this study, GAMs revealed that diatoms responded most strongly to disturbances in the Lac Brûlé catchment area. For example, at around 1345 CE a local fire triggered an abrupt response in the vegetation of the surrounding watershed (a rapid decline in hemlock), which consequently impacted the diatom community of the lake. The fire occurred concurrently with the transition from the MWP to the LIA; replication of paleolimnological studies in the region is thus needed to identify the response of diatoms (and other proxies) to this change in climate regimes in the absence of major disturbances in the watershed.

(4) Regional deforestation as a result of Euro-Canadian settlement in the region in the early to mid-1800s had a strong influence on the water chemistry of Lac Brûlé, which in turn affected the diatom assemblages. This is further evidence to support the conclusion that terrestrial vegetation dynamics are strongly correlated with aquatic community structure.

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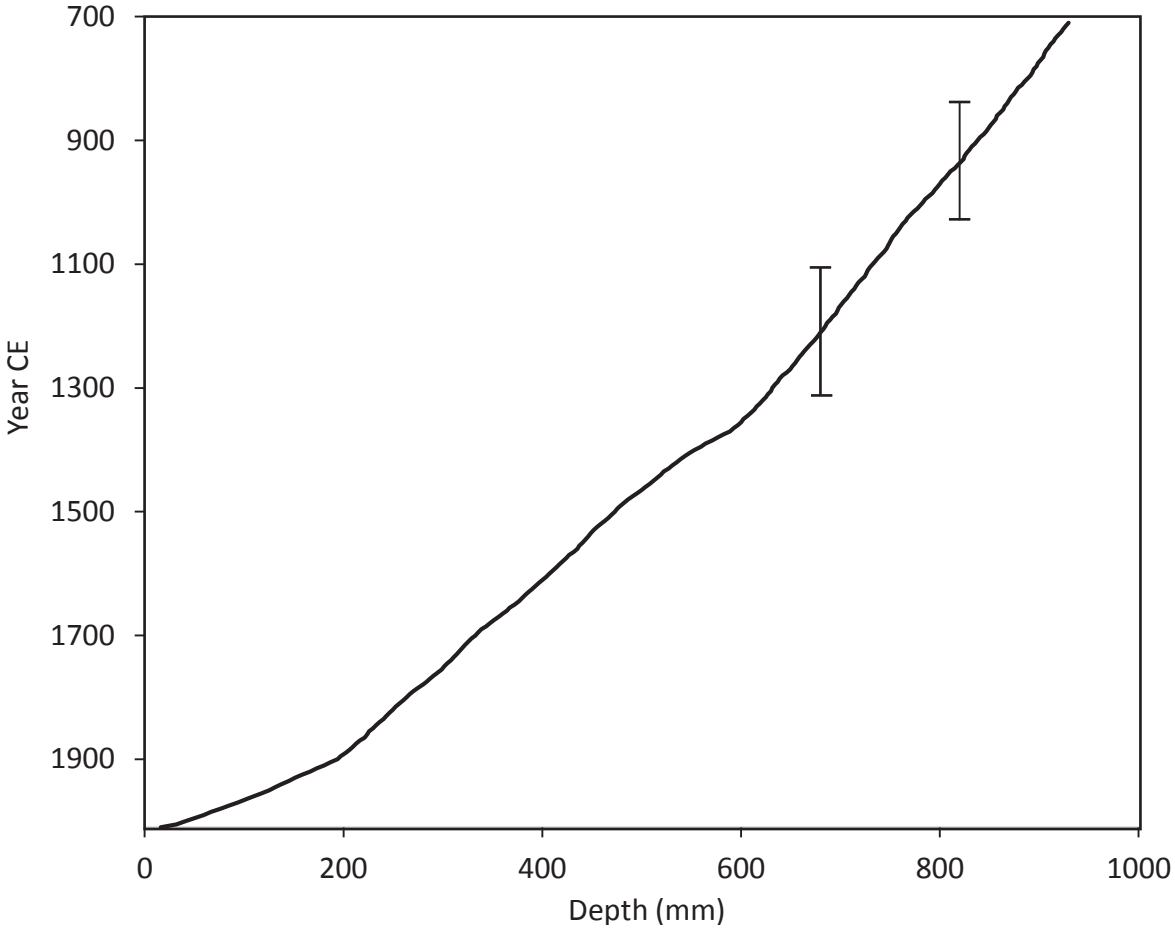


Figure 2.1: Varve-based chronology (age-depth curve) for the Lac Brûlé sediment core. The solid curve is the cumulative varve thickness for each depth interval, plotted against age. The chronology used in this study was resolved with that of sediment core collected from Lac Brûlé in 2012 (BV13; Lafontaine-Boyer and Gajewski 2014; see text for details). The two vertical lines show calibrated radiocarbon determinations with an error range of two standard deviations for the BV13 core from Lafontaine-Boyer and Gajewski (2014)

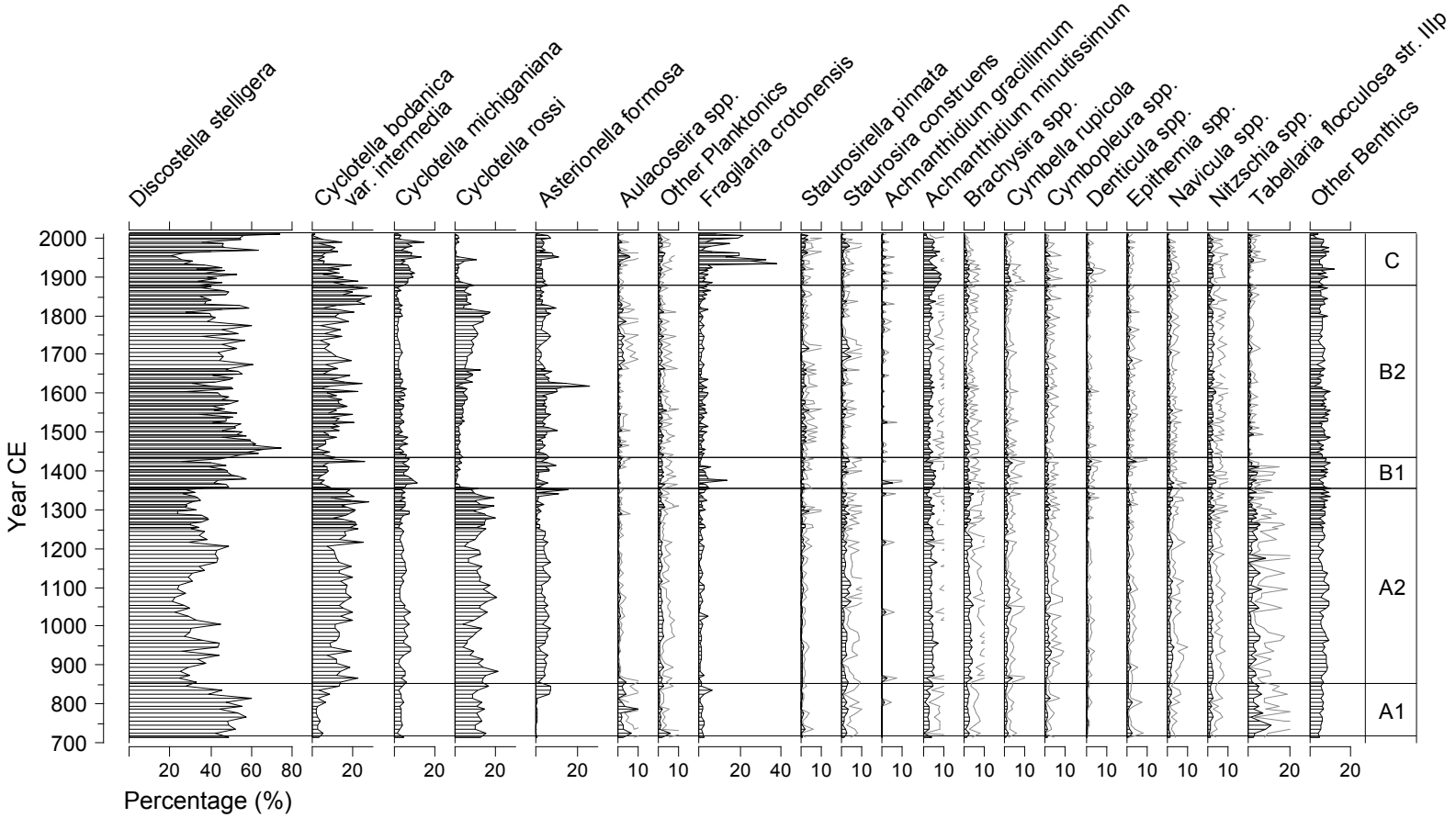


Figure 2.2: Diatom taxa representing >3% relative abundance in at least one sample, identified in the sediment core from Lac Brûlé, southwestern Québec. Sampling intervals are shown by the horizontal black lines in each profile. A 3x exaggeration (grey line) is applied to taxa representing a smaller portion of the total diatom sum

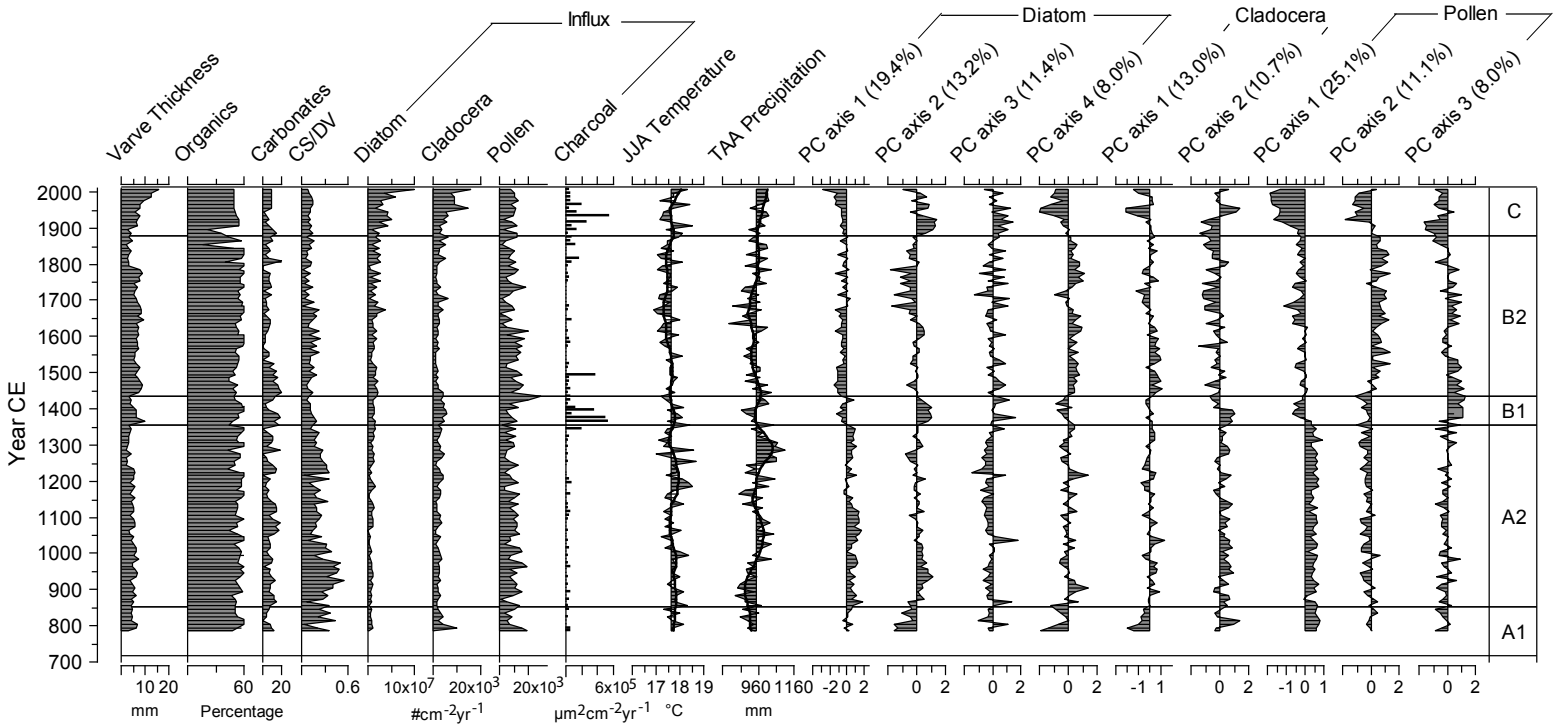


Figure 2.3: Paleo-environmental summary for Lac Brûlé, southwestern Québec, including sediment characteristics, total influx (accumulation rates) of aquatic/terrestrial biota and charcoal, paleo-climate reconstructions (derived from local pollen; Lafontaine-Boyer and Gajewski 2014) and primary ecological trends in aquatic (diatom, cladocera) and terrestrial (pollen) taxa. The CS/DV represents a ratio of scaled chrysophytes relative to diatom valves calculated for each sample. Ecological trends are summarized with a principal components analysis (PCA), and significant axes are shown for each taxonomic group; percentage variance explained by each axis is indicated in brackets. Data for the organic/carbonate content, pollen and charcoal influx, and paleo-climate reconstructions are from Lafontaine-Boyer and Gajewski (2014), and cladocera influx data are from Cooper et al. (2016)

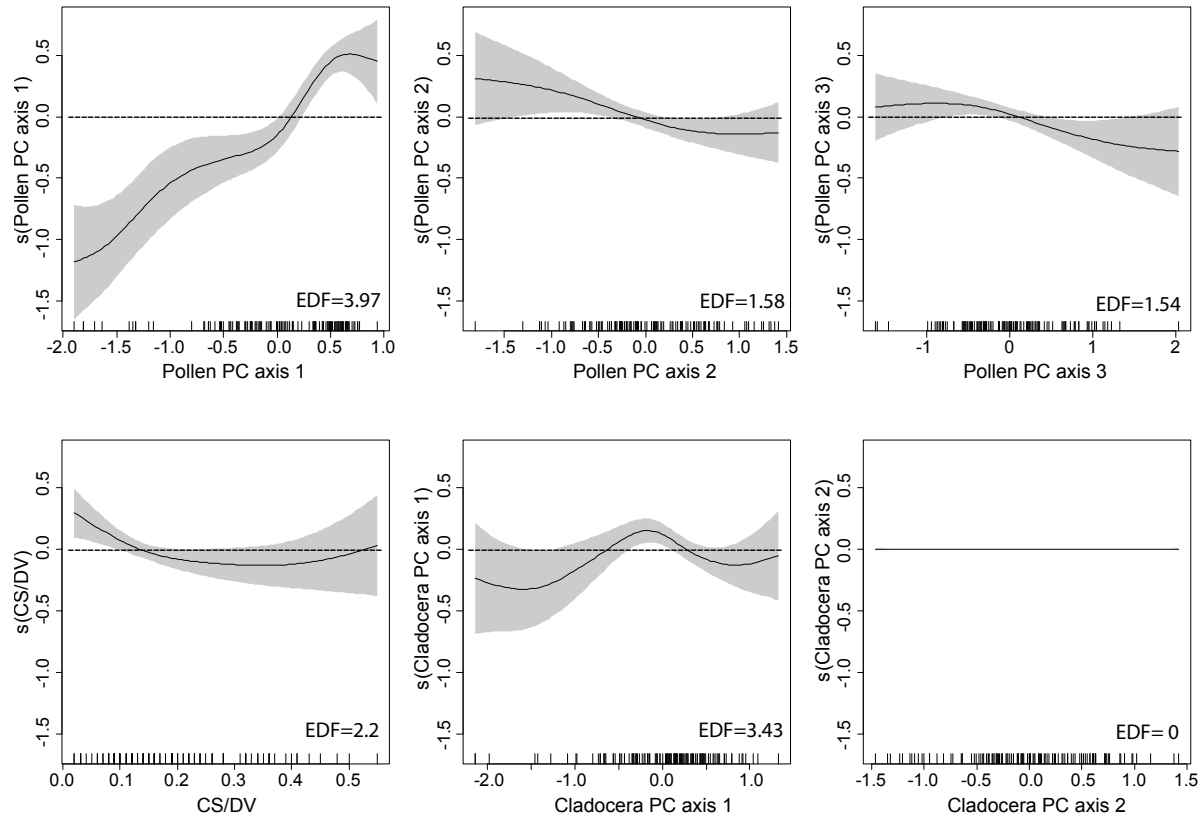


Figure 2.4: Fitted smooth functions of variables in the final GAMs for the Lac Brûlé diatom PC axis 1 scores. The distribution of observed values for each variable is indicated by tick marks on the x-axis (inside each panel). Pointwise confidence intervals (95%) are indicated by grey bands; where they touch the dashed zero line, the contribution of the variable is not statistically significantly different from the intercept. Effective degrees of freedom (EDF) are shown for each variable, where a value of 1.0 indicates a linear relationship

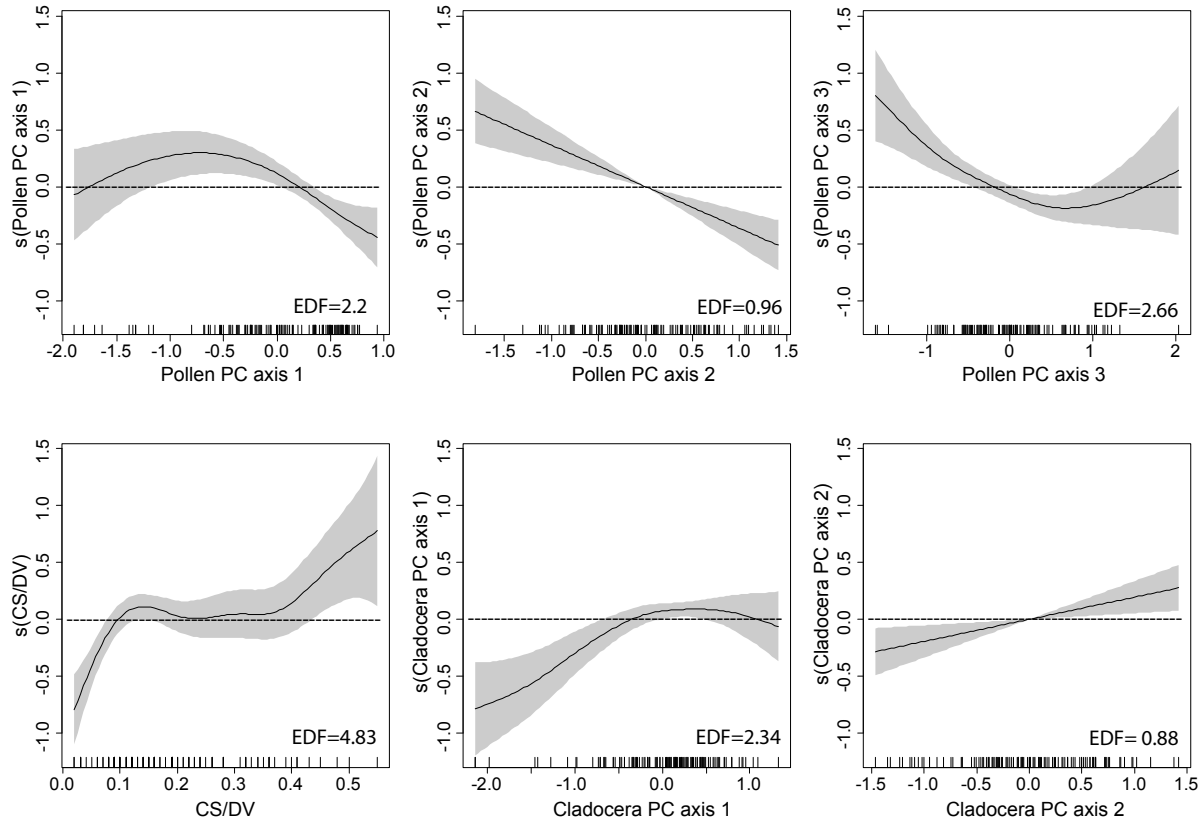


Figure 2.5: Fitted smooth functions of variables in the final GAMs for the Lac Brûlé diatom PC axis 2 scores. The distribution of observed values for each variable is indicated by tick marks on the x-axis (inside each panel). Pointwise confidence intervals (95%) are indicated by grey bands; where they touch the dashed zero line, the contribution of the variable is not statistically significantly different from the intercept. Effective degrees of freedom (EDF) are shown for each variable, where a value of 1.0 indicates a linear relationship

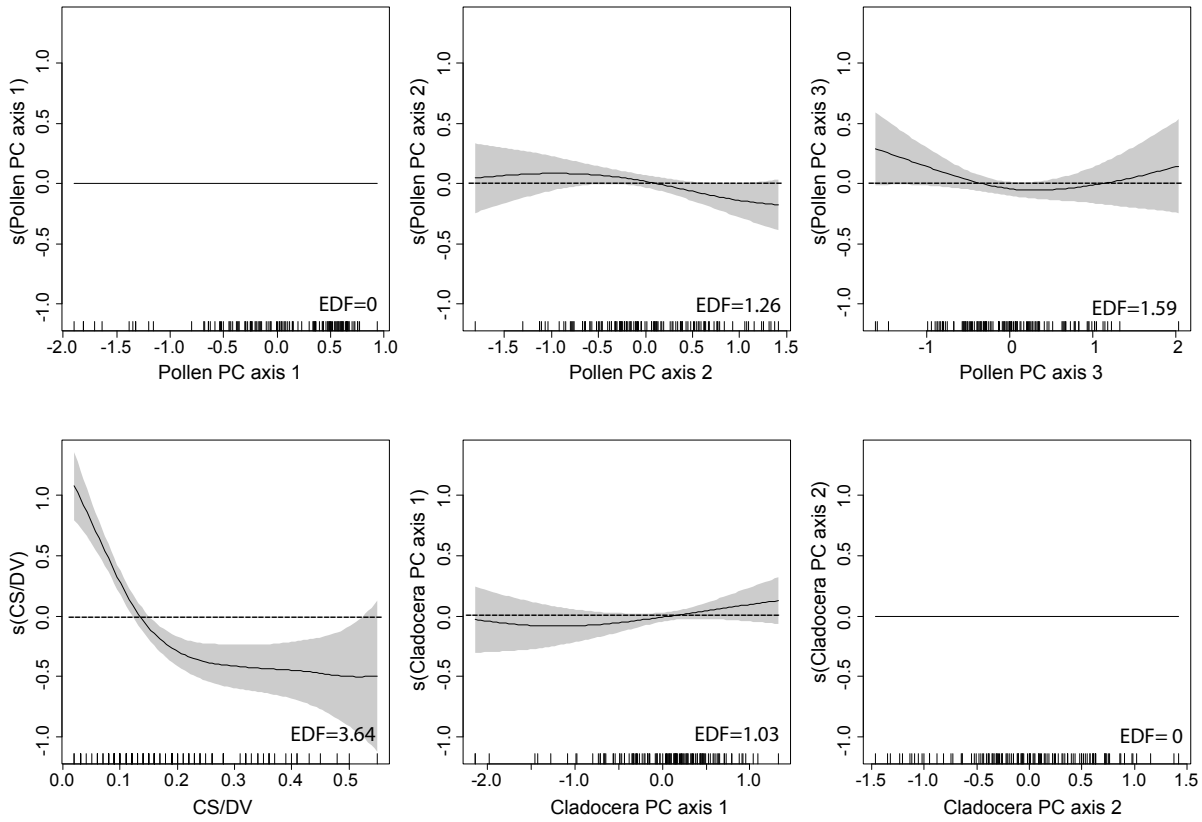


Figure 2.6: Fitted smooth functions of variables in the final GAMs for the Lac Brûlé diatom PC axis 3 scores. The distribution of observed values for each variable is indicated by tick marks on the x-axis (inside each panel). Pointwise confidence intervals (95%) are indicated by grey bands; where they touch the dashed zero line, the contribution of the variable is not statistically significantly different from the intercept. Effective degrees of freedom (EDF) are shown for each variable, where a value of 1.0 indicates a linear relationship

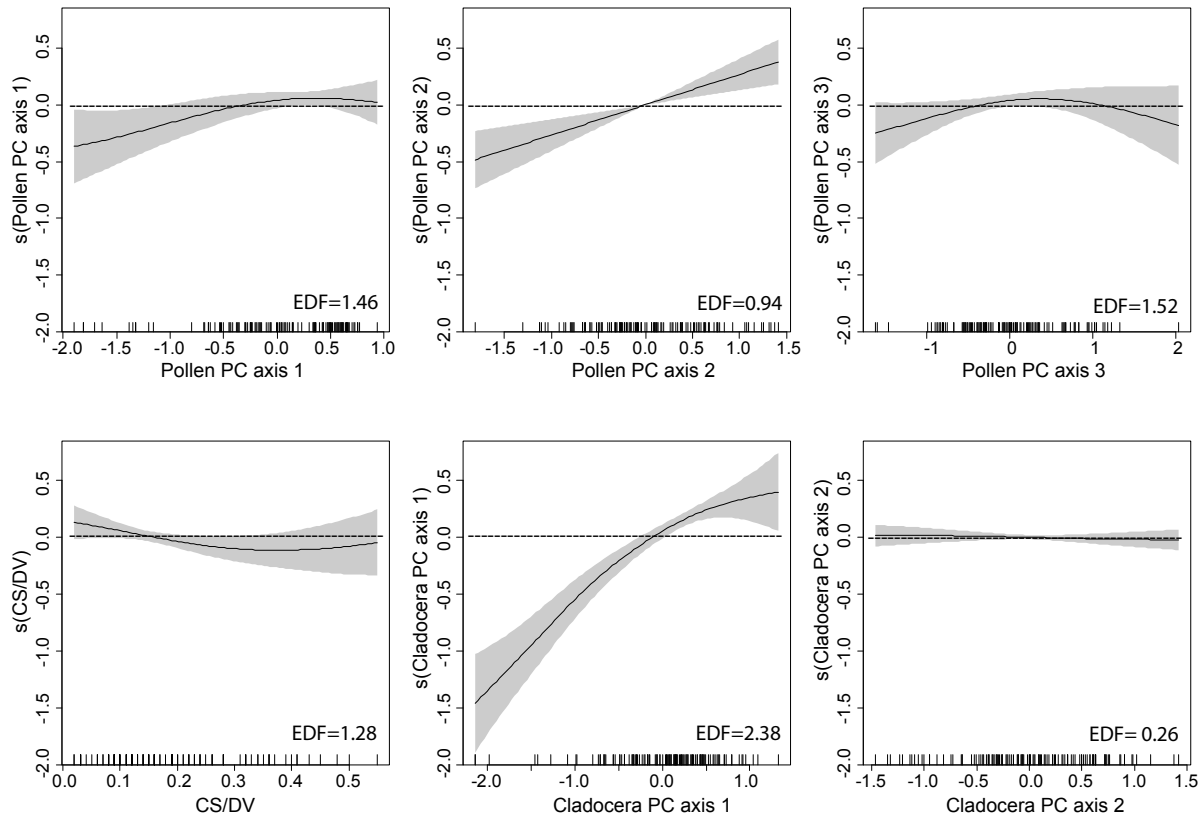


Figure 2.7: Fitted smooth functions of variables in the final GAMs for the Lac Brûlé diatom PC axis 4 scores. The distribution of observed values for each variable is indicated by tick marks on the x-axis (inside each panel). Pointwise confidence intervals (95%) are indicated by grey bands; where they touch the dashed zero line, the contribution of the variable is not statistically significantly different from the intercept. Effective degrees of freedom (EDF) are shown for each variable, where a value of 1.0 indicates a linear relationship

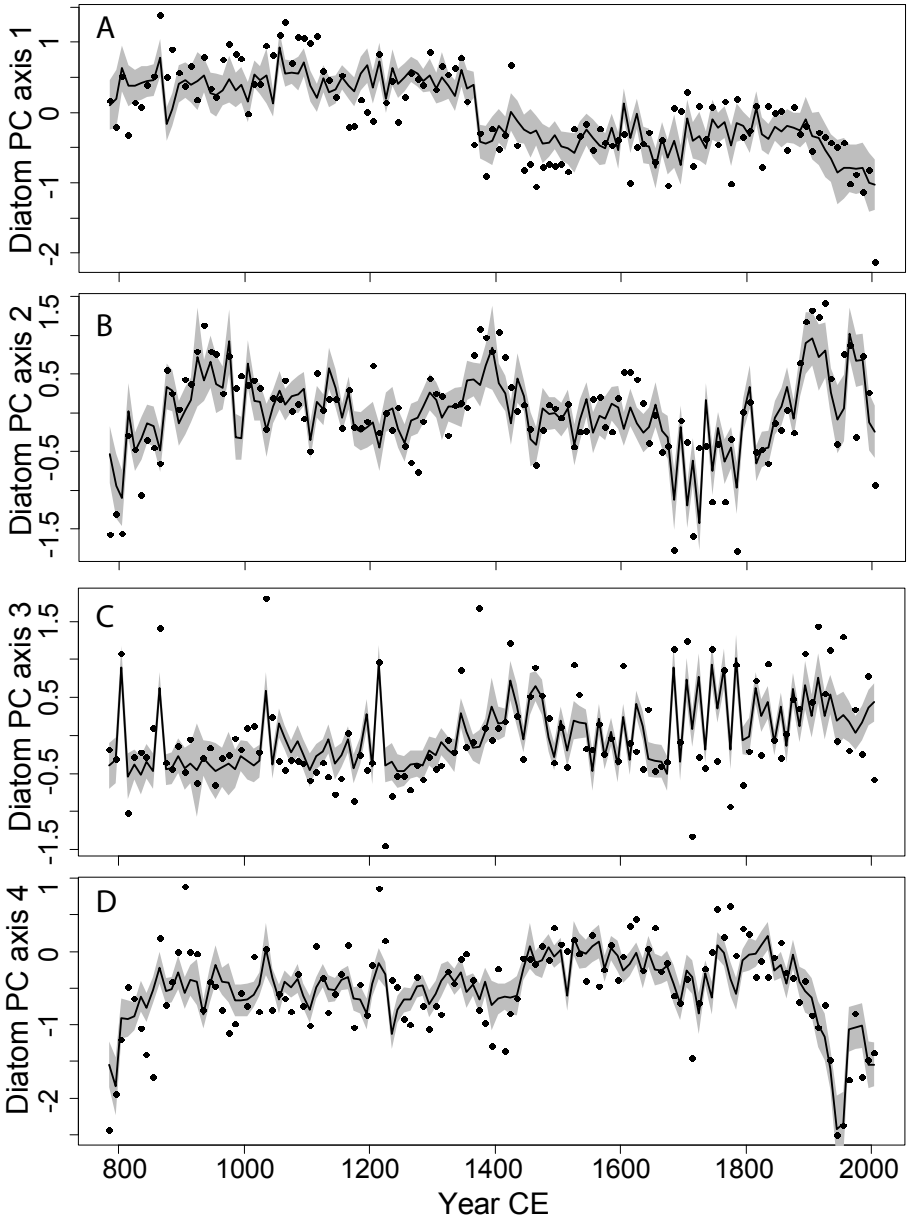


Figure 2.8: Observed (dots) and GAM fitted values (line) for diatom PC axis 1, 2, 3, and 4 scores (A-D) for the Lac Brûlé core. A 95% pointwise confidence interval on the fitted values is shown by the gray band.

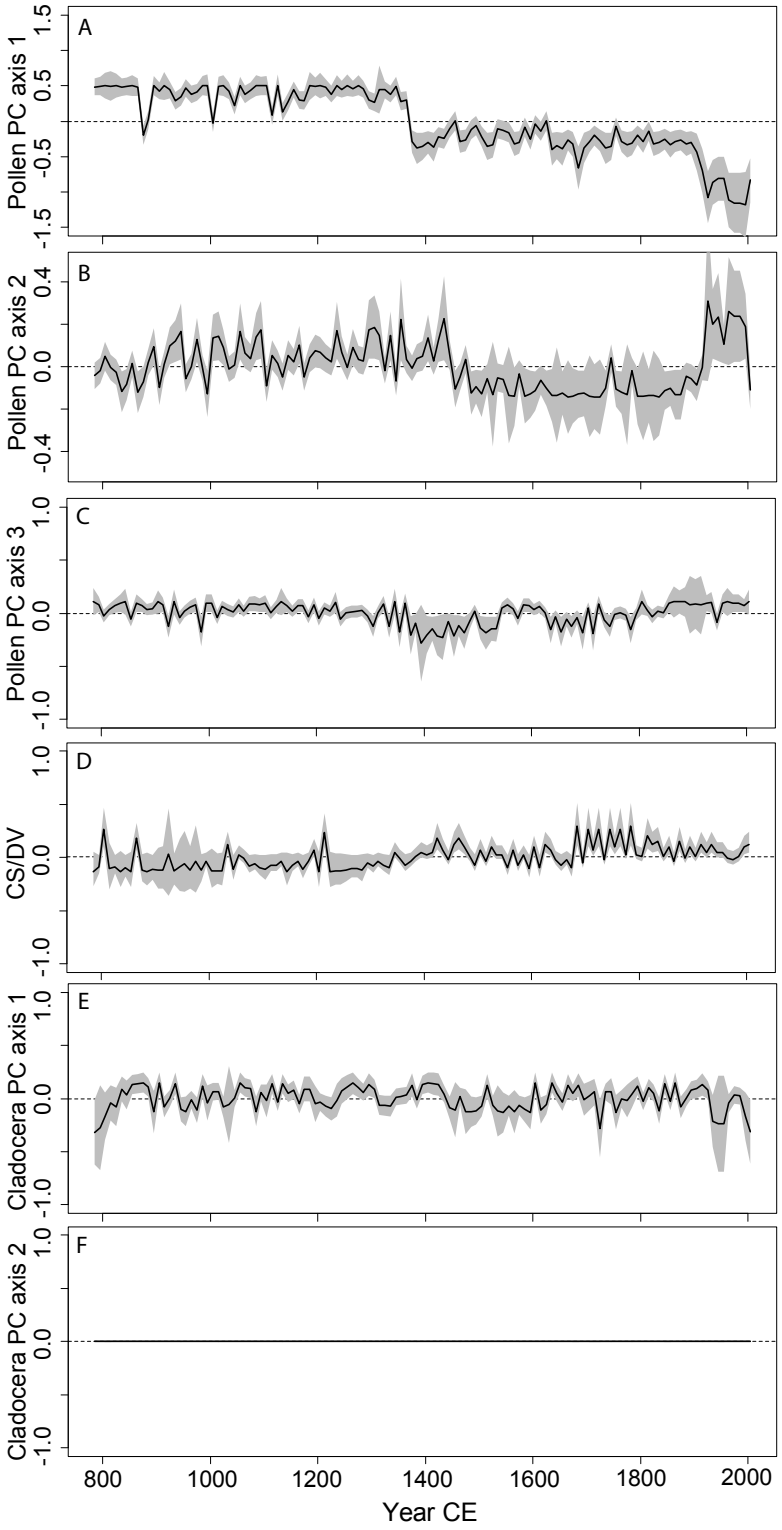


Figure 2.9: Contributions of environmental indicators to the fitted diatom PC axis 1 scores in the final GAM model for Lac Brûlé. The grey band is an approximate 95% pointwise confidence interval on the contribution. Where the band encompasses the dashed zero line, the contribution of the variable is not statistically significantly different from the intercept

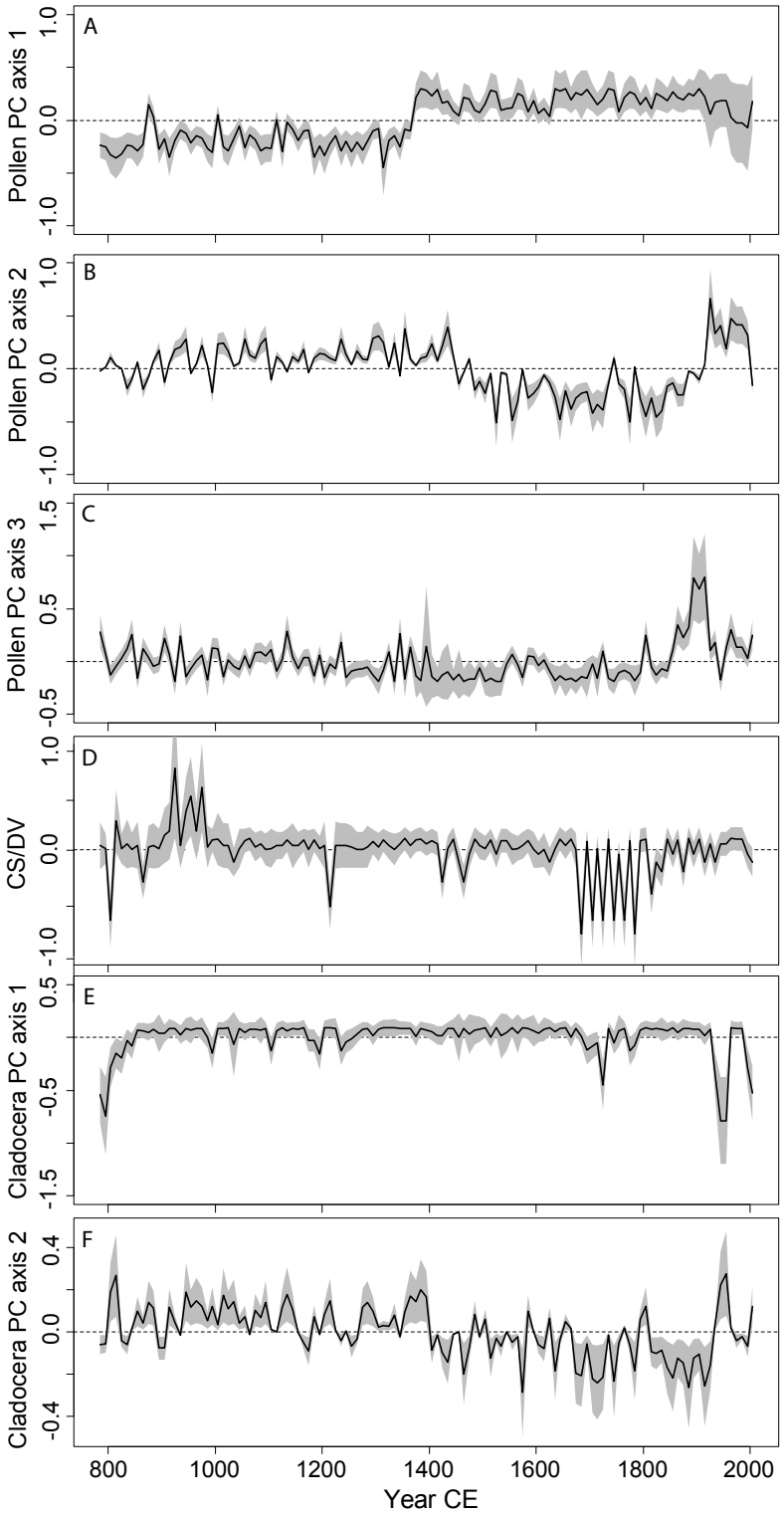


Figure 2.10: Contributions of environmental indicators to the fitted diatom PC axis 2 scores in the final GAM model for Lac Brûlé. The grey band is an approximate 95% pointwise confidence interval on the contribution. Where the band encompasses the dashed zero line, the contribution of the variable is not statistically significantly different from the intercept

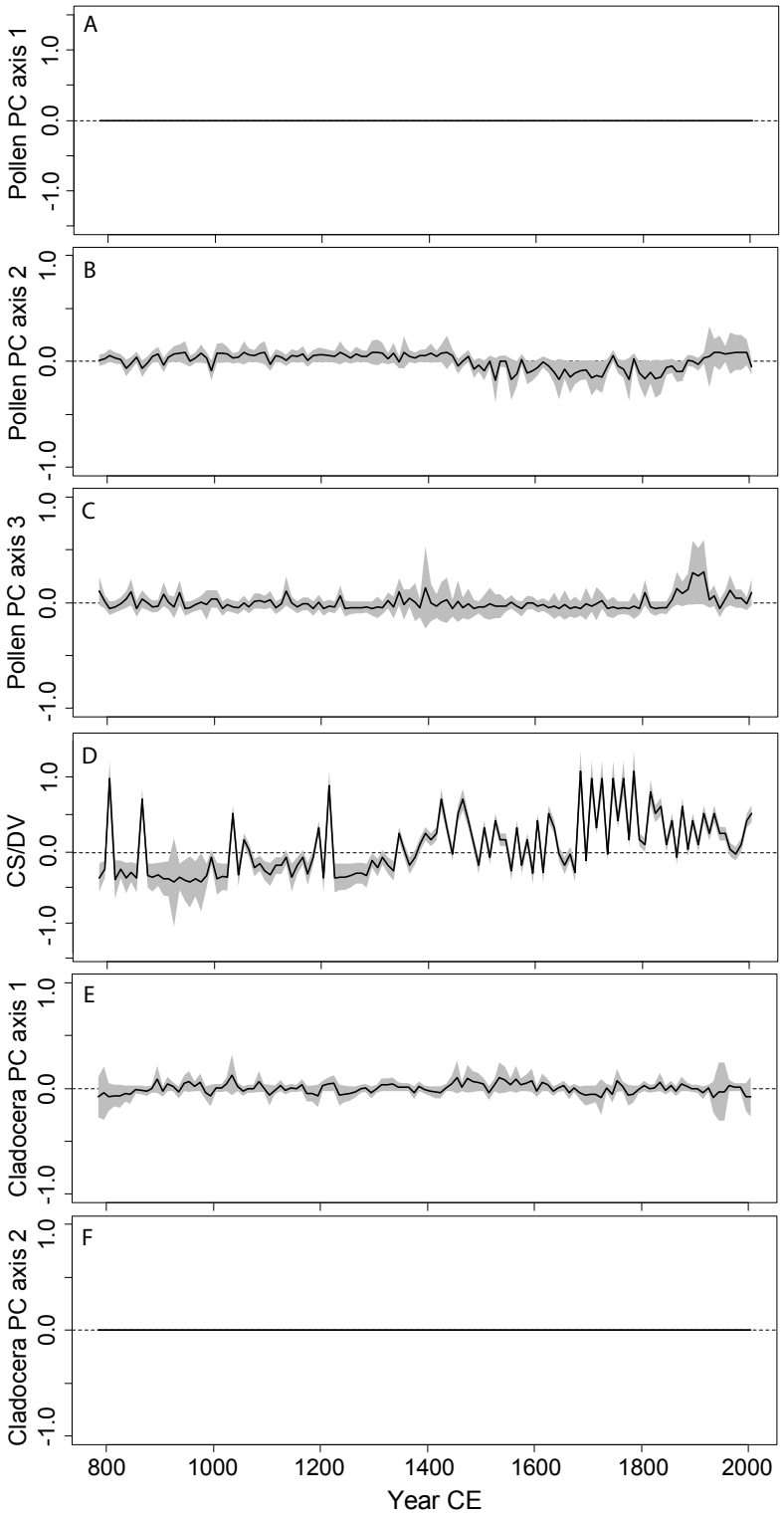


Figure 2.11: Contributions of environmental indicators to the fitted diatom PC axis 3 scores in the final GAM model for Lac Brûlé. The grey band is an approximate 95% pointwise confidence interval on the contribution. Where the band encompasses the dashed zero line, the contribution of the variable is not statistically significantly different from the intercept

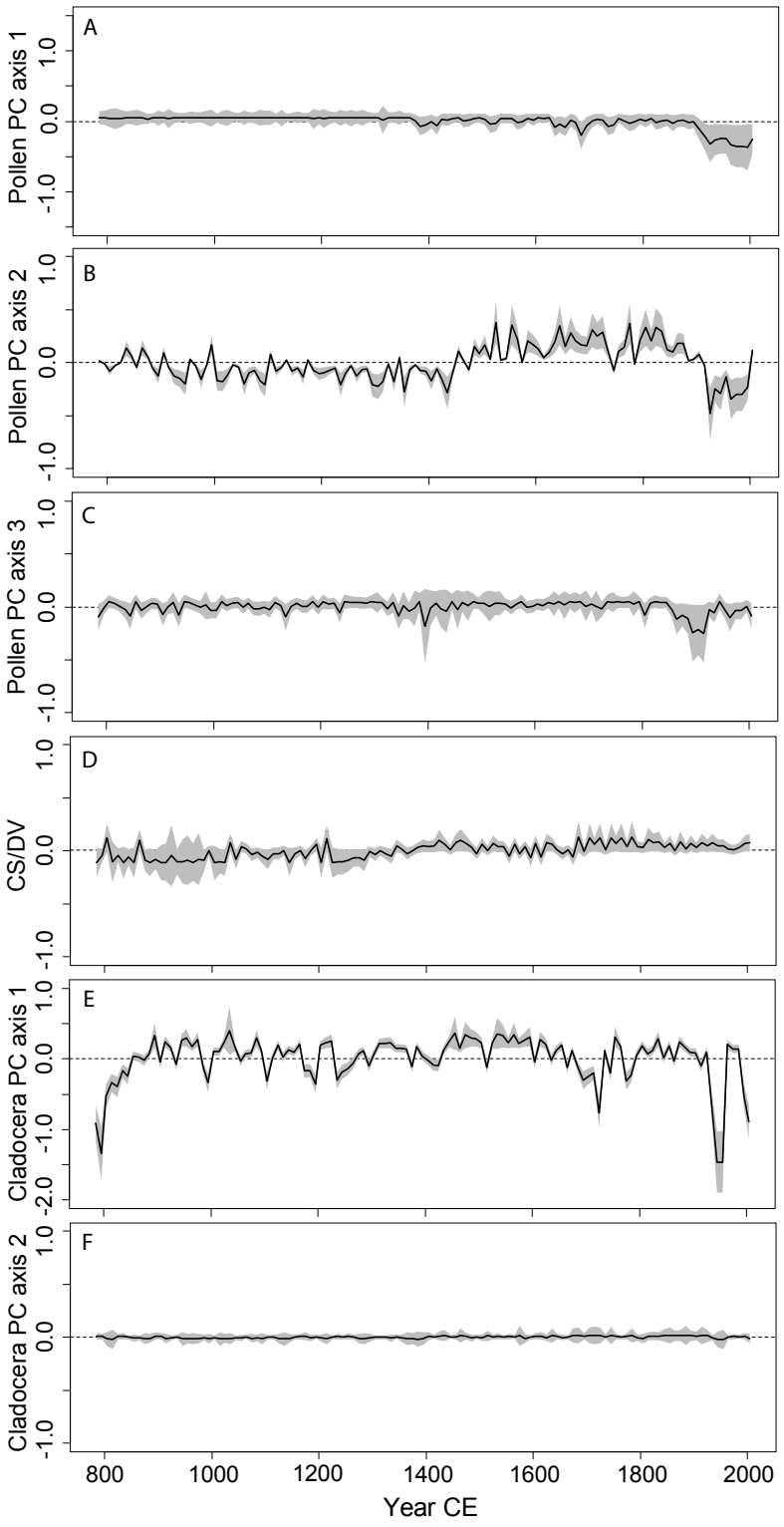


Figure 2.12: Contributions of environmental indicators to the fitted diatom PC axis 4 scores in the final GAM model for Lac Brûlé. The grey band is an approximate 95% pointwise confidence interval on the contribution. Where the band encompasses the dashed zero line, the contribution of the variable is not statistically significantly different from the intercept

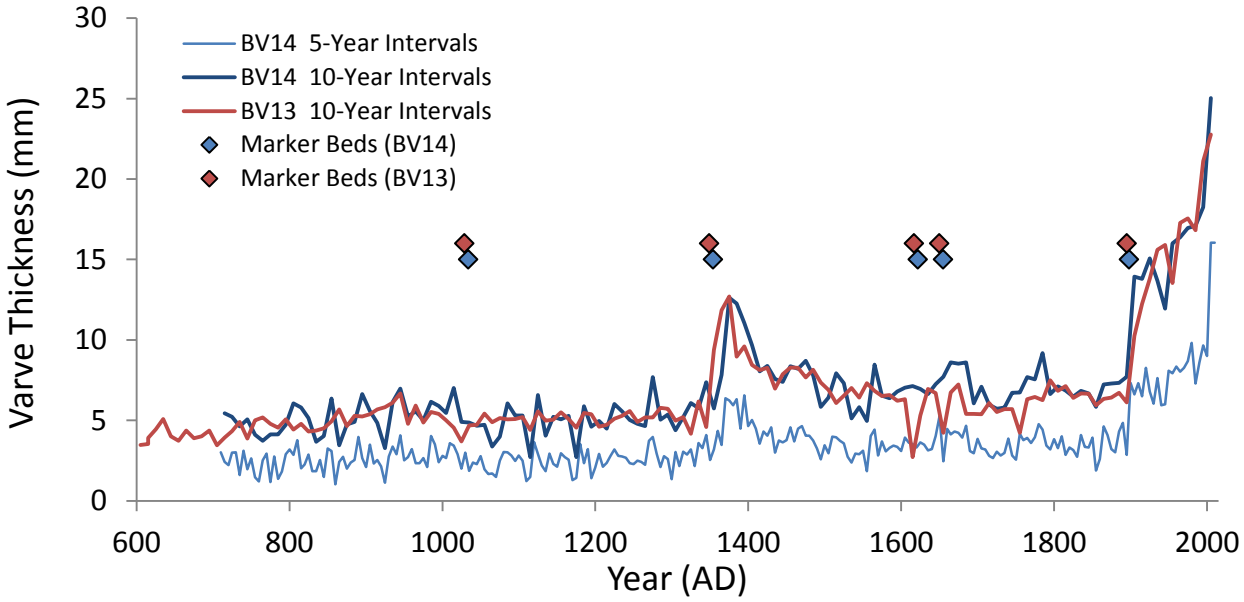


Figure S2.1: Varve thickness comparison between lake sediment cores from Lac Brûlé; BV13 (Lafontaine and Gajewski 2014) and BV14 (Neil and Gajewski 2017). The varve thickness for core BV14 at 10-year intervals was calculated by summing 5-year interval pairs down the length of the core

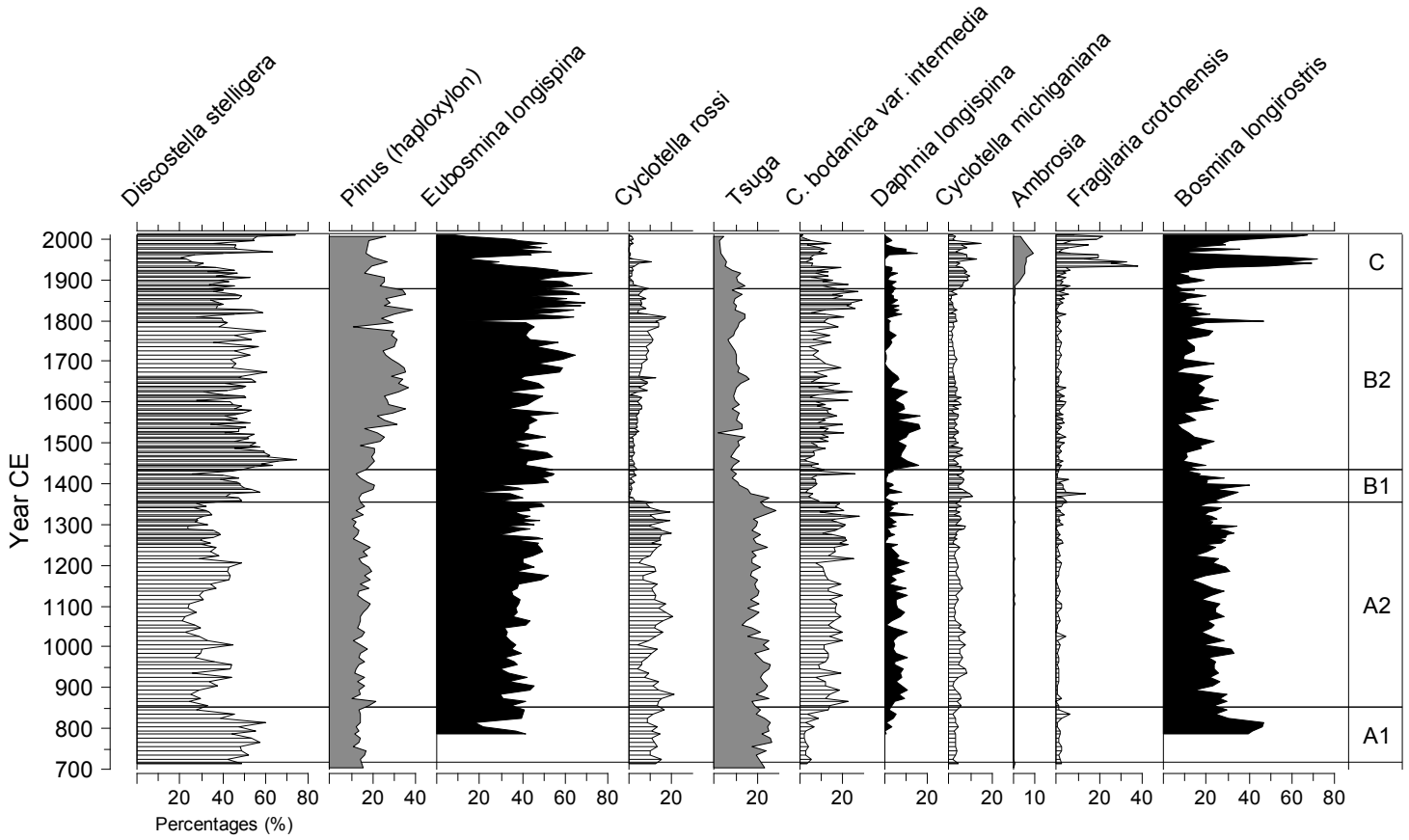


Figure S2.2: Direct comparisons of the relative abundance profiles for select taxa from Lac Brûlé; diatom data comes from Neil and Gajewski (2017) (white/hatched profiles), pollen data comes from Lafontaine-Boyer and Gajewski (2014) (solid grey profiles), and cladocera data comes from Cooper et al. (2016) (solid black profiles)

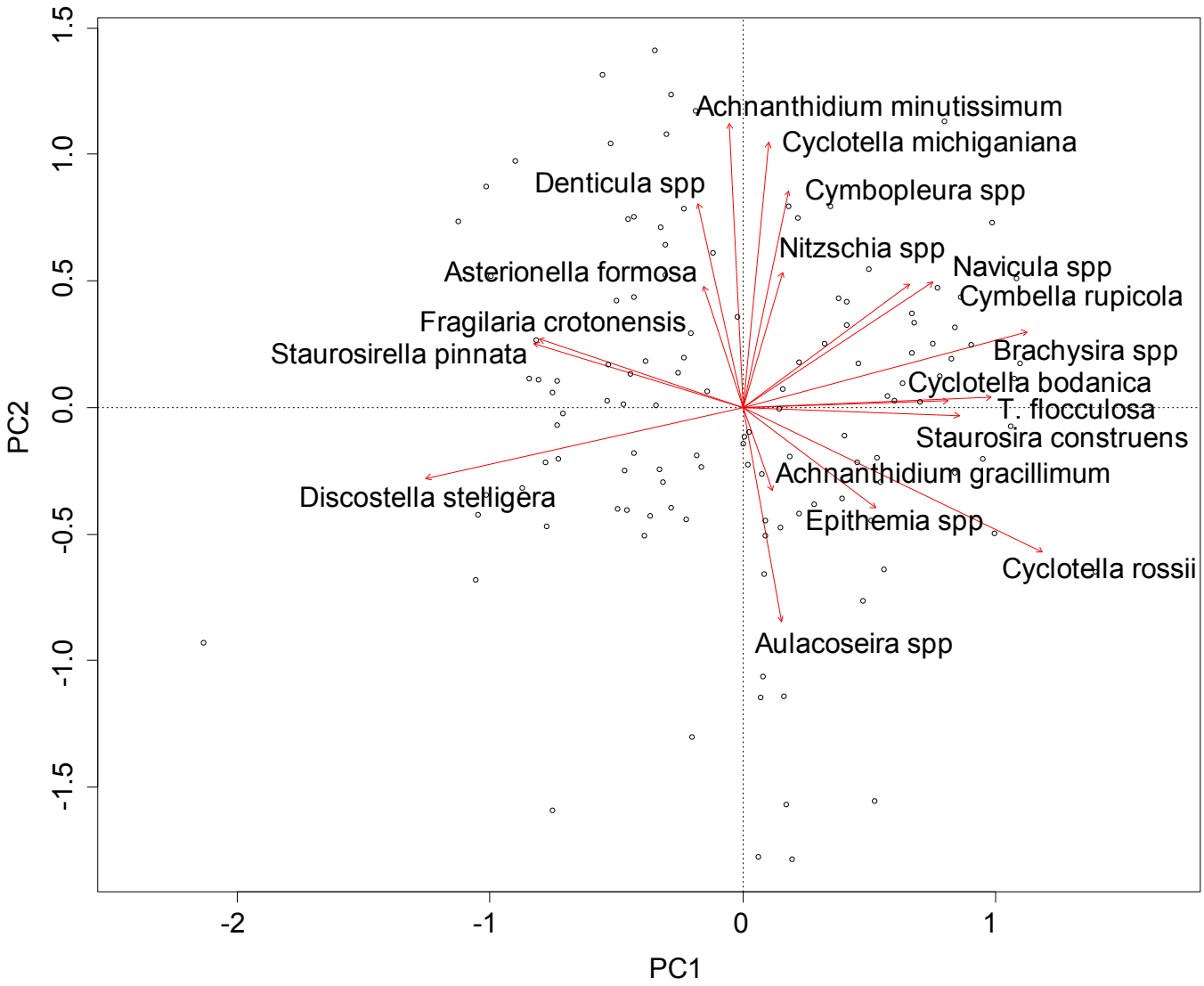


Figure S2.3: Biplot of a principal components analysis, performed on Hellinger transformed diatom percentages from Lac Brûlé, southwestern Québec, Canada. Taxa chosen for this analysis represent >3% relative abundance in at least one sample. Dots indicate sample scores, and red arrows show loadings of the diatom taxa

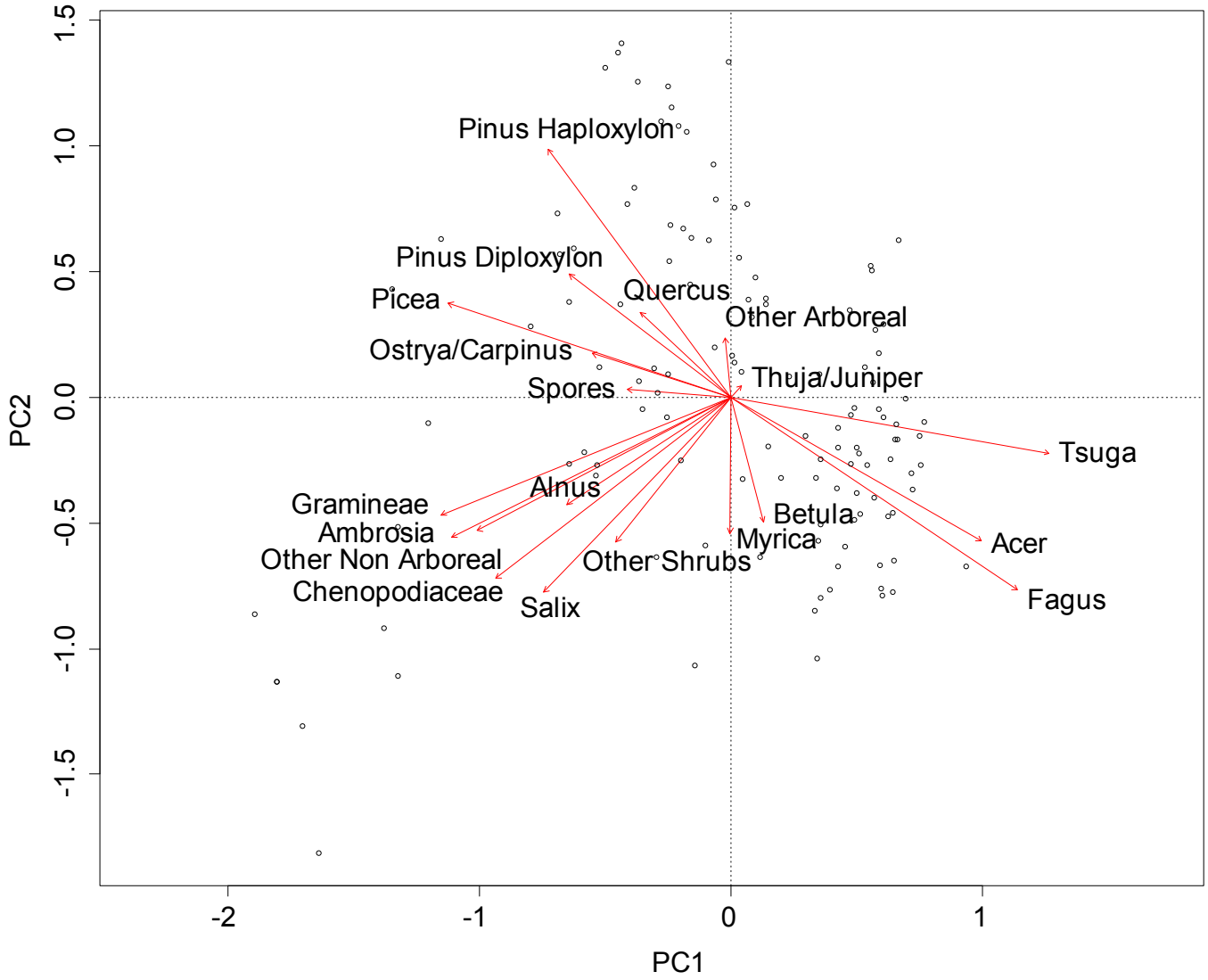


Figure S2.4: Biplot of a principal components analysis, performed on Hellinger transformed pollen percentages from Lac Brûlé, southwestern Québec, Canada (data from Lafontaine-Boyer and Gajewski 2014). Dots indicate sample scores, and red arrows show loadings of the pollen taxa

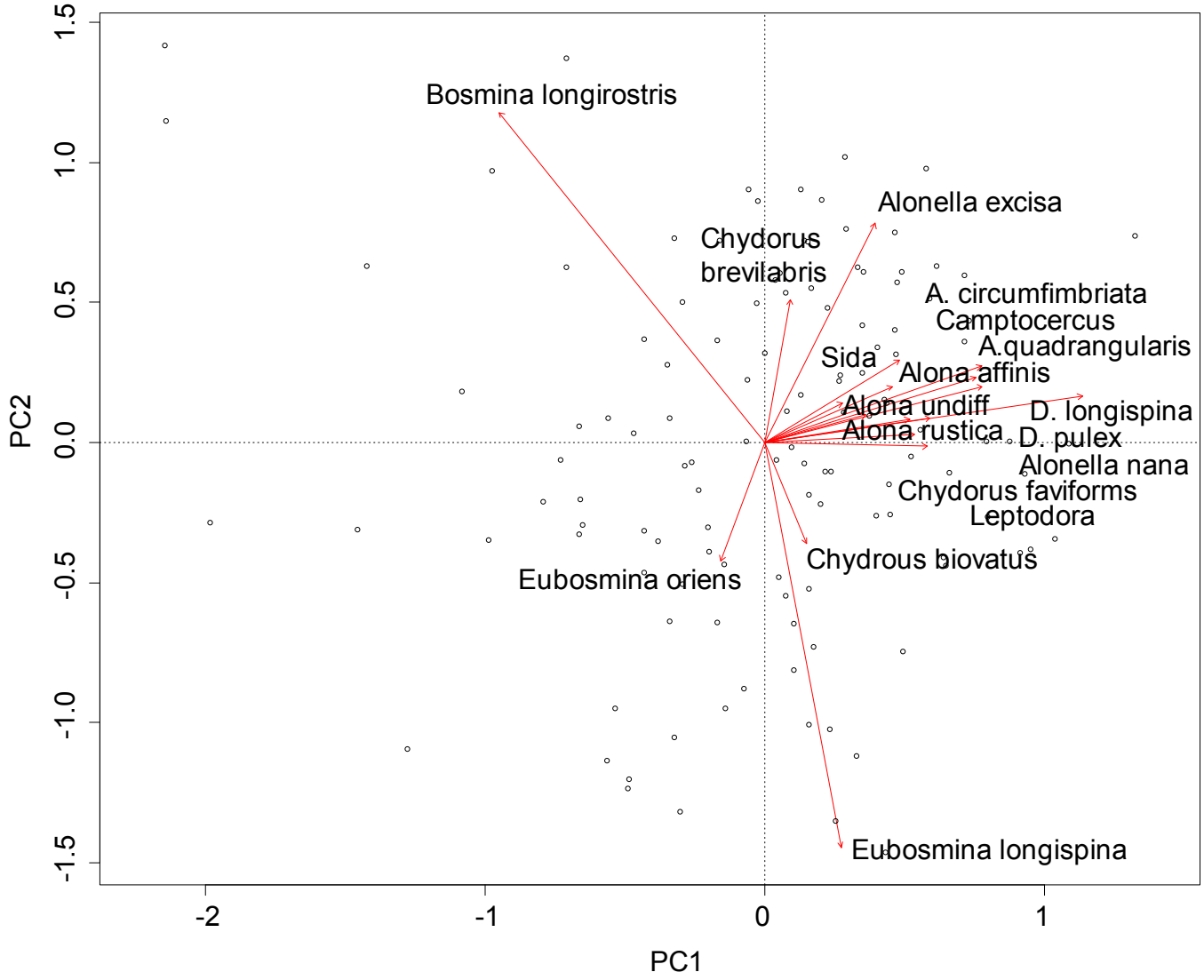


Figure S2.5: Biplot of a principal components analysis, performed on Hellinger transformed cladocera percentages from Lac Brûlé, southwestern Québec, Canada (data from Cooper et al. 2016). Dots indicate sample scores, and red arrows show loadings of the cladocera taxa

CHAPTER THREE

A high-resolution paleolimnological study of climate and human impacts on Lac Noir, Québec over the past 1000 years

Abstract

Diatom assemblages in lake sediments of Lac Noir, southwestern Québec, were studied at a resolution of ten years to determine principal drivers of primary producers for the past ~1000 years. Generalized additive modelling (GAM) revealed strong links between broad-scale climate intervals of the Late Holocene, forest composition and succession, and diatom flora. During the Medieval Warm Period (MWP; ~1200 CE) and onset of cooler temperatures in the Little Ice Age (LIA; ~1450-1850 CE), increases in *Tabellaria flocculosa* str. IIIp at the expense of *Discostella stelligera* reflected low lake productivity. At 1630 CE, an abrupt shift to cooler-than-average temperatures and dry conditions at the peak of the LIA triggered a decline in hemlock (*Tsuga*), replaced by disturbance and cool-adapted pollen. Greater nutrient availability and soil erosion in the catchment led to a corresponding and rapid increase in diatoms with higher optima for nitrogen, such as *Asterionella formosa* and *Fragilaria crotonensis.* After 1860 CE, an increase in pollen of taxa associated with disturbances signalled the arrival of Euro-Canadians, and associated nutrient inputs to the lake triggered increases in S*tephanodiscus minutulus* and *Achnanthidium minutissimum*. Overall results of the study indicate that climate played an important underlying role in lake-ecosystem dynamics, however disturbances affecting forest composition in the watershed had more direct influences on the diatoms of Lac Noir.

Keywords: Diatom, Varve, Holocene, paleolimnology, 'Medieval Warm Period', 'Little Ice Age', generalized additive models (GAMs), European settlement

3.1 Introduction

In southern Québec and Ontario, global climate models (GCMs) project a rise in annual mean temperature of 1-5°C by the end of the 21st century (Boulanger et al. 2017). This will undoubtedly trigger significant changes in lake health and productivity in the region (Barker et al. 2005), as climate plays a major role in freshwater ecosystem dynamics (Bradshaw et al. 2005). In small, temperate lakes, for example, greater primary production in response to warmer temperatures could ultimately lead to lake anoxia, with indirect impacts on higher trophic levels (Dove-Thompson et al. 2011). Variations in precipitation, including periods of sustained droughts, could also alter lake hydrological cycles, increasing their vulnerability to deteriorating water quality and eutrophication (Barker et al. 2005).

Changes in forest vegetation and catchment soils associated with climatic variability and human disturbances also exhibit strong influences on lake water chemistry and aquatic biota (Carignan and Steedman 2000). The close coupling of watershed processes and lake ecosystems is documented in paleolimnological studies; for example, Beck et al. (2016) noted a shift to a more nutrient-rich catchment surrounding Wishart Lake, southern Ontario, following the mid-Holocene decline of hemlock (*Tsuga canadensis*), which ultimately led to the eutrophication of the lake. Studies from southern Ontario and Québec describe significant responses of aquatic communities to human-induced disturbances following Euro-Canadian settlement (Neil and Gajewski 2017; Ekdahl et al. 2007). Climate change, as well as sustained and potentially increased impacts of anthropogenic activities in the future, will likely present challenges for predicting how lake ecosystems will respond and recover to environmental changes (Johnstone et al. 2016).

Paleo-records and historical data document responses of vegetation and aquatic taxa to major climatic variations of the late Holocene (Williams et al. 2002), such as the Medieval Warm Period (MWP; ~800-1200 CE) and the Little Ice Age (LIA; ~1450-1850 CE). However, local

forcings or disturbances (e.g. fire, anthropogenic activity) often mask these broad climatic signals in the data as they alter the rate and timing of ecological change among sites (Williams et al. 2011; Paine et al. 1998). This was demonstrated in a study which compared the vegetation histories from two proximate lakes, Lac Noir and Lac Brûlé, in southern Québec (Lafontaine-Boyer and Gajewski 2014). A decline in hemlock pollen at Lac Noir was attributed to cooling temperatures during the LIA, but a similar decrease occurred centuries earlier at Lac Brûlé in response to a local fire in the watershed (Lafontaine-Boyer and Gajewski 2014). To distinguish the effects of climate and non-climatic processes on watershed-lake interactions, replication of multi-proxy studies within a limited spatial area is thus necessary.

The purpose of this study is (1) to analyze aquatic primary producers (diatoms) in Lac Noir in relation to environmental changes and nutrient fluxes, and (2) to understand their responses within the context of regional paleo-records of the late Holocene in southern Ontario and Québec. Diatoms are good indicators of lake response to external forcings, as they are abundant, respond rapidly to physical/chemical changes in the water column, and are typically preserved in lake sediments (Stoermer and Smol 2001). Generalized additive models (GAMs) are used to hierarchize the influences of external forcings on diatom assemblages, and to identify ecological responses linked to regional climate variability and/or site-specific factors. Results of the diatom analysis are compared with a previous study of Lac Noir, in which climate and vegetation changes of the past 1000 years were identified through a high-resolution pollen analysis of the lake sediments (Paquette and Gajewski 2013). The overall results are compared to those from the nearby Lac Brûlé (Neil and Gajewski 2017).

3.2 Methods

3.2.1 Study site

The study area is located in southwestern Québec, 60 km north-east of Ottawa (Fig. 3.1). Lac Noir (45°46'32.89"N, 75°08'05.65"W, 176m) is the main site for which data is presented here; it is a small lake (25 ha), has continuously laminated sediments, with a maximum depth of ~16 m (Paquette and Gajewski, 2013). In 2013, the pH of the lake was 7.7 near the surface, and the conductivity was 20.0 μScm^{-1}. Based on low concentrations of total phosphorous (9 μgL^{-1}), total nitrogen (260 μgL^{-1}), and chlorophyll-α (0.59 μgL^{-1}) at this time, the lake was characterized as ultra-oligotrophic (Cooper et al. 2016).

Lac Noir is underlain by Pre-Cambrian Shield (mainly granite bedrock), and is situated within a transition zone between the boreal (to the north) and deciduous forest (to the south). The mixed forest surrounding the lake is dominated by red and white pine (*Pinus resinosa, Pinus strobus*), white and black spruce (*Picea glauca, Picea mariana*), eastern hemlock (*Tsuga canadensis*), yellow birch (*Betula alleghaniensis*), American beech (*Fagus grandifolia*), various species of maple (*Acer saccharum, Acer pensylvanicum, Acer rubrum, Acer negundo*), and green and speckled alder (*Alnus crispa, Alnus rugosa*). The closest long-term weather station to Lac Noir (Notre-Dame de la Paix) records mean daily temperatures ranging from -11.9°C in January to 19.1°C in July (Environment Canada 2017). Total annual precipitation in the region is 985 mm, approximately 30% of which falls as rain in the summer months (June, July, August) (Environment Canada 2017).

There are a few small inflow streams at the northern shoreline of Lac Noir, and one main outflow stream to the south. The catchment area to lake area ratio is approximately 10:1, and human activity in the watershed is restricted; there are currently two small summer cabins on the shore. A

few small towns and agricultural fields are located ~1 to 2 km east of the lake, but immediately to the west the landscape is relatively steep and appears undisturbed.

3.2.2 Sampling and chronology

In 2010, three continuously-laminated sediment cores were collected from Lac Noir. Paquette and Gajewski (2013) identified the laminations as annual varves (confirmed by ^{210}Pb and ^{14}C dating), and cross-correlated the varved sequences from each of these cores to establish a chronology for the site. The majority of the core (6.6-91 cm) was sectioned into 10-year intervals based on the varve chronology; however disturbances in the uppermost 6.5 cm prevented varves from being counted. Instead, results from ^{210}Pb dating were used to assign ages to samples corresponding with this upper section of the core (see Paquette and Gajewski 2013 for details). To enable direct comparisons of diatoms with the previously published, high-resolution pollen record from Lac Noir, subsamples in this study were taken from the same 10-year intervals of the core used by Paquette and Gajewski (2013) in their analyses.

In their study, Paquette and Gajewski (2013) estimated Euro-Canadian settlement at ~1810 CE based on a rise in *Ambrosia* pollen at Lac Noir. Historical records indicate that European colonization of the region began in the early 19th century, but human activities impacting the environment (e.g. logging, agriculture) only increased in the second half of the century (Smith 1967). In 2014, a palynological study of a nearby lake with varved sediments, Lac Brûlé, recorded an increase in *Ambrosia* pollen at 1860 CE (Lafontaine-Boyer and Gajewski 2014). Following Lafontaine-Boyer and Gajewski (2014), we revised the Lac Noir chronology in this study to place the *Ambrosia* rise at 1860 CE. The varves from the Lac Brûlé core were undisturbed in the upper section and thus likely more accurate, and an increase in *Ambrosia* at 1860 CE seems to fit more reasonably with the historical record of the region.

3.2.3 Laboratory analysis

From the same sections of the Lac Noir sediment core used for the palynological study, subsamples averaging ~0.02g of dry sediment were extracted into 20-mL glass vials in 2017 for diatom analysis. Hydrogen peroxide (30%) was added to each vial and left to digest in a water bath at 80°C for 3-4 hours (Battarbee et al. 2001). To enable estimations of diatom influx rates, a known volume of microsphere solution (concentration of $5.0x10^6$ spheres/mL) was added to each subsample. A small amount of diatom slurry was diluted with deionized water before being pipetted onto a cleaned coverslip. The coverslips were left to air dry in a dry hood, after which they were permanently mounted onto microscope slides with Naphrax. Diatoms were identified with a Nikon 90i microscope at 1000x magnification under oil emersion, using Antoniades et al. (2008), Siver et al. (2005) and Patrick and Reimer (1975; 1966) as taxonomic references. For each sample, a minimum of 500 diatom valves were counted; these counts were translated into both relative abundance data, and influx rates for each diatom species. Chrysophyte scales were enumerated on each slide, and a chrysophyte scale-to-diatom valve index (CS/DV) was calculated following Karmakar et al. (2015).

3.2.4 Numerical analysis

Using the "vegan" package in the statistical program R3.2.5 (R Core Team 2013), diatom assemblages consisting of the most abundant taxa (>3% relative abundance in at least one sample) were summarized with principal components analysis (PCA). Prior to the PCA, species relative abundance data were Hellinger transformed (Legendre and Gallagher 2001). Significant PCA axes were identified using a scree plot of the axis eigenvalues, and the diatom percentage diagram was divided into biostratigraphic zones based solely on changes in the scores of the PCA. For each of the 110 samples from Lac Noir, additional data from Paquette and Gajewski (2013) were available

for analysis, including pollen percentages (summarized with a separate PCA), pollen influx, loss-on-ignition, charcoal influx, and reconstructed June-July-August (JJA) temperature and precipitation, derived from the pollen data using the Modern Analogue Technique.

Generalized additive models (GAMs) were generated using the "mcgv" package in R (Wood 2008; 2011) to assess the degree to which individual external forcings influenced the Lac Noir diatom community. The response variable in each GAM was one of three significant diatom principal components (PC) axes. The predictor variables included pollen PC axes (representing vegetation responses to both climate and watershed disturbances), pollen influx (representing productivity of terrestrial vegetation), percent organics and carbonates (representing erosional processes and allochtonous inputs), CS/DV (representing lake trophic status), and micro-charcoal influx (representing fire disturbances). Parameterization of the GAMs included an REML smoothness selection, a shrinkage method by double penalty approach on each of the smoothing terms (Marra and Wood 2011), and thin plate splines as the type of basis dimension.

3.3 Results

3.3.1 Diatom biostratigraphy and environmental data

A total of 130 diatom species were identified from the sediment samples, fifteen of which occurred with >3% relative abundance in at least one sample (Fig. 3.2); only these more abundant species are shown. Three of the taxa dominated the fossil assemblages, and when combined accounted for 45% to 80% of the total diatom sum: *Discostella stelligera* (Cleve & Grunow) Houk & Klee 2004, *Tabellaria flocculosa* str. IIIp (Roth) Kützing 1844, and *Fragilaria crotonensis* Kitton 1869 (Fig. 3.2). More detailed changes in the Lac Noir diatom record (Fig. 3.2) and environmental variables (Fig. 3.3) throughout the late Holocene are described in this following

section in relation to four major biostratigraphic zones. Note that these zones were defined based solely on changes in the diatom assemblages, as summarized by a PCA (Fig. 3.4; discussed below). *Zone A (1050-1430 CE):* In zone A, the relative abundance of *D. stelligera* declined steadily. *T. flocculosa* str. IIIp represented on average 30% of the total diatom sum, and *F. crotonensis* percentages fluctuated gradually, reaching a minimum for the record at the boundary between zones A and B (<5%). In 1150 CE, *Aulacoseira tenella* (Nygaard) Simonsen 1979 first appeared in the record, increasing at 1300 CE (Fig. 3.2). Diatom influx was relatively low and did not significantly change in zone A (Fig. 3.3). There was a slight decrease in CS/DV just before 1200 CE, which coincided with a brief peak in charcoal influx (2 consecutive samples), and a small decline in pollen influx occurred at ~1250 CE (Fig. 3.3).

Zone B (1440-1630 CE): At the beginning of zone B, *A. tenella* abruptly disappeared and remained absent from the rest of the record. The relative abundance of *T. flocculosa* str. IIIp increased up to a maximum of 52% in 1570 CE, before declining rather abruptly (Fig. 3.2). Total diatom, pollen, and charcoal influx rates and CS/DV were stable throughout zone B (Fig. 3.3).

Zone C (1640-1860 CE): In zone C, *D. stelligera* began to increase, reached a peak in relative abundance at ~1700 CE, and then declined to ~20% of the total diatom sum at the end of the zone. The percentage of *T. flocculosa* str. IIIp was initially low (<5%), when *Asterionella formosa* Hassal 1850, *F. crotonensis*, and *Staurosira pinnata* (Ehrenberg) D.M. Williams & Round 1988 were more abundant. Despite this initially low relative abundance, *T. flocculosa* str. IIIp quickly stabilized at ~25% of the total diatom sum in the rest of the zone. *S. pinnata* grew in abundance more gradually, reaching a peak of 25% only at the end of zone C (Fig. 3.2). At the beginning of the zone, CS/DV and pollen influx declined abruptly and remained relatively low, while aquatic pollen rapidly increased (Fig. 3.3). Total diatom influx showed a single peak at 1690 CE, most likely caused by a low microsphere count for that sample which created a false signal in

the data. At the beginning of the zone, there was also an abrupt decrease in JJA precipitation to values below the long-term average for the record which persisted throughout the zone.

Zone D (1870-2010 CE): The relative abundance of *F. crotonensis* began to increase in zone D, at the same time that *T. flocculosa* str. IIIp and *A. formosa* declined. At 1900 CE, *Stephanodiscus minutulus* (Kützing) Cleve & Möller 1882 appeared abruptly in the record, reaching a brief peak at 1920 CE before declining. At the same time, *Achnanthidium minutissimum* (Kützing) Czarnecki 1994 showed a small increase in relative abundance. After 1940 CE, *D. stelligera* declined by 20%, while some of the rarer taxa increased slightly (*Cyclotella distinguenda* Hustedt in Gams 1928, *Staurosira construens* Ehrenberg 1843, *Planothidium* spp. and *Psammothidium* spp.) (Fig. 3.2). Total diatom, pollen, and charcoal influx increased at the beginning of zone D, and subsequently decreased at the end of the zone. Aquatic pollen and CS/DV only increased after 1930 CE, but kept rising throughout the zone.

3.3.2 Principal Components Analysis

The principal components analysis (PCA) explained 41% of the variance in the diatom assemblages on the first three axes (Fig. 3.4; component 1: 17%; component 2: 14%; component 3: 10%). The first diatom PC axis represented changes in the composition of *T. flocculosa* str. IIIp, *F. crotonensis*, and *S. minulutus* (Table 1). It had positive values in zones A and B (1050-1630 CE), negative values in zone C (1640-1860 CE), and larger negative values in zone D (1870-2010 CE) (Fig. 3.4). The second diatom PC axis had more high frequency variability, but with two rather distinct shifts from negative to positive values; the first is the transition between zones B and C, and the second occurred in zone D at 1900 CE. The second component was positively loaded on *D. stelligera*, and negatively loaded on *S. pinnata* and *Psammothidium* spp. Finally, the third diatom PC axis had decreasing values at the transition between zones A and B, mostly negative

values throughout zone C, and an abrupt increase to positive values in zone D at 1900 CE. This axis was positively correlated with *A. tenella*, *A. minutissimum*, and *Nitzschia* spp.

As mentioned previously, the biostratigraphic zones were defined strictly by changes in the diatom PC axes. However, major changes in the Lac Noir pollen record, summarized in a separate PCA (Fig. 3.4; Table 3.2), occurred at the same key points in time. Likewise, a PCA including both species data (diatom and pollen principal components) and environmental variables from Lac Noir showed clear groupings of samples associated with each of the major biostratigraphic zones (Fig. 3.5).

3.3.3 Generalized additive models

In the first GAM, predictor variables explained 71% of the variance in the fitted diatom PC axis 1 scores. The largest contributor to the fitted values was pollen PC axis 1 (p-value <0.001), which was interpreted as an indicator of both climate and watershed disturbances. In the time series representing the effects of this variable on the fitted diatom PC axis 1 scores (Fig. 3.6), two abrupt shifts towards negative values at ~1630 CE and ~1870 CE indicate rapid and synchronous changes in pollen and diatom assemblages. There were also shifts in the percent organics time series (towards positive values this time), though they lagged the dates above by ~40-60 years. Only one other variable, percent carbonates, was significant in this GAM, for a brief period between 1720-1870 CE.

Approximately 51% of the variance in the fitted diatom PC axis 2 scores was explained in the second GAM. The scores were most strongly influenced by percent organics in this model, with significant contributions occurring after 1920 CE (Fig. 3.7). The time series representing the contributions of charcoal and pollen influx were rather similar (e.g. a simultaneous peak at 1890 CE). Changes in the time series representing the effects of pollen PC axis 2 were more

gradual, and closely resembled the biostratigraphic zones (defined by the diatom PCA). This predictor variable was interpreted as an indicator of climate.

Finally, 43% of the variance in the fitted diatom PC axis 3 scores was explained in the third GAM. Several predictor variables contributed significantly to the fitted values, with the most influential being percent organics and pollen PC axis 1 (Fig. 3.8). Temporal trends in the contribution time series showed results similar to those from the GAMs described above.

3.4 Discussion

3.4.1. Zone A: Culmination of the Medieval Warm Period (1050-1430 CE)

The varve-based chronology from Lac Noir indicated an age of 1050 CE for the bottom of the core, which in southern Québec corresponded to the latter part of the Medieval Warm Period (MWP; ~800-1200 CE; Viau et al. 2006; 2012). A local pollen record from the lake showed higher abundances of deciduous taxa and *Tsuga* during this period, as well as relatively low abundances of northern taxa (e.g. *Picea*) or taxa indicative of disturbance (e.g. shrubs, herbs, *Pinus strobus*). This led to a pollen-based summer (JJA) temperature reconstruction that was 0.5-1.0°C warmer than the long-term average for the late Holocene, with relatively high JJA precipitation (Paquette and Gajewski 2013). During the MWP, diatom assemblages in Lac Noir were dominated overall by *T. flocculosa* str. IIIp and *D. stelligera*. In addition to a greater proportion of chrysophytes relative to diatoms (CS/DV), this signalled an oligotrophic, circumneutral to slightly acidic lake, with limited primary productivity (Smol 1985; Köster et al. 2005; Puusepp and Kangur 2010; Karmakar et al. 2015).

The generalized additive models (GAMs) showed that during the MWP, the Lac Noir diatom communities were influenced by the composition of the surrounding forest (pollen PC axis 1), likely

through changes in lake chemistry associated with the leaf litter quality. This also suggests that there was an overall association of the diatom flora with relatively warm and stable climatic conditions.

Broad-scale climate forcing (e.g. temperature, precipitation) could be interpreted as key drivers of aquatic responses (Williams et al. 2011), though this is not necessarily reflective of a direct relationship. Instead, shifts in diatom communities are often associated with secondary factors and catchment-mediated processes controlled by climate, such as DOC inputs, water turbidity, pH, nutrient concentrations, and light availability, amongst others (Morabito et al. 2012; Fritz and Anderson 2013; Rühland et al. 2015; Neil and Gajewski 2017). *Tsuga*-dominated forests, for example, are associated with humic-rich soils and greater inputs of dissolved organic carbon (DOC) to nearby lakes (Engstrom and Wright 1984). These types of environments would favor diatom taxa more tolerant of high DOC such as *T. flocculosa* str. IIIp (Camburn and Charles 2000; Faulkenham et al. 2003) and *A. tenella* (Haig et al. 2003), both of which were abundant in Lac Noir when *Tsuga* percentages were at their maximum for the late Holocene.

Towards the end of the MWP several records from southern Ontario and Québec (including Lac Noir), as well as the New England states (U.S.), showed a relatively synchronous response of diatom communities to gradual climate cooling (Philibert et al. 2003; Köster and Pienitz 2006; Neil and Gajewski 2017). In Connecticut, U.S., the rise of *A. tenella* in Bates Pond at ~1150 CE was interpreted as a response to cooling temperatures and reduced thermal stratification (Köster and Pienitz 2006). This taxon also appeared in Lac Noir at ~1150 CE and increased after 1300 CE, coinciding with cooling and greater seasonal rainfall reconstructed from the local pollen data (Paquette and Gajewski 2013). *A. tenella* is a heavily silicified diatom more commonly found in lakes with turbulent waters and high DOC (Harris et al. 2006; Haig et al. 2013; Rühland et al. 2015). In the MWP, high-frequency variations in precipitation may have led to seasonal mixing of Lac Noir

as well as greater inputs of humic-rich allogenic sediments and DOC from the catchment (Köster and Pienitz 2006; Stager et al. 2017), thus creating optimal conditions for *A. tenella*.

3.4.2. Zone B: Onset of the Little Ice Age (1430-1630 CE)

Subtle changes in the pollen record (e.g. an increase in *Pinus* and *Picea*, decline in *Tsuga* and *Fagus*) at 1430 CE were accompanied by an increase in *T. flocculosa* str. IIIp at the expense of *D. stelligera*, suggesting that this marked the initial onset of Little Ice Age (LIA) cooling in the region. An overall increase in the abundance of boreal taxa would result in greater soil acidity and inputs of DOC from the catchment (Fritz and Anderson 2013), and could explain the slight shift towards more acid-tolerant taxa such as *T. flocculosa* str. IIIp (Faulkenham et al. 2003) at Lac Noir. Lake pH could be impacted by weathering processes as well; for instance, an extended period of higher than average JJA precipitation inferred from the Lac Noir pollen record (Paquette and Gajewski 2013) may have resulted in heavier losses of base cations from the surrounding soils, leading to a slightly more acidic lake environment (Boyle 2007; Fritz and Anderson 2013).

While the timing of the LIA at Lac Noir is in phase with intervals commonly used to define the period in eastern North America (Mann et al. 2008; Gajewski 1988; Viau et al. 2006; 2012), the PCA of combined environmental variables (Fig 5) showed that diatom assemblages from Zone A (the MWP) and Zone B (the onset of the LIA) overlapped. This indicates that there was a smooth transition from one period to the next, and changes within the lake and in its surrounding catchment were not pronounced. The GAMs (Fig 6, 7, 8) confirmed that this transition was indistinct, and revealed only slight responses in diatom communities to vegetation changes and/or disturbances (pollen PC axis 1 and 2), which was expected given minimal changes in local pollen assemblages at this time (Fig S1).

3.4.2 Zone C: Peak of the Little Ice Age (1630-1860 CE)

At 1630 CE, the Lac Noir pollen record showed a decline in pollen influx (Fig 3), as well as the replacement of *Tsuga* and *Fagus* by *Betula*, *Pinus strobus*, and *Alnus* in the catchment (Fig S1), which was interpreted as a rapid shift to a cool climate and dry conditions associated with the peak of the LIA (Paquette and Gajewski 2013). Within the lake, there was a decline in *T. flocculosa* str. IIIp percentages and CS/DV values, and increases in *A. formosa*, *F. crotonensis*, *D. stelligera*, *S. pinnata*, as well as total diatom influx; overall this indicated a shift to a slightly more nutrient-rich lake with relatively higher productivity (Smol 1985; Wolin and Stoermer 2005; Köster et al. 2005; Pappas 2009; Puusepp and Kangur 2010) in comparison to that of the earlier record.

The GAMs showed sharp breaks in the time series representing the influences of vegetation and disturbances on diatom communities in Lac Noir (pollen PC axis 1 and 2; Fig 6-8), signalling that changes in the surrounding forest were abrupt and had significant impacts on the diatom flora of the lake. For instance, deteriorating climatic conditions triggered disturbances and openings in the forest canopy, as evidenced by increasing abundances of *Alnus*, *Pinus strobus*, and other shrubs in local and regional pollen records (Paquette and Gajewski 2013; Lafontaine-Boyer and Gajewski 2014). The initial opening of the forest in addition to enhanced soil erosion in the LIA (Stevenson et al. 1990) likely facilitated transport of nutrients to nearby lakes (Hall and Smol 1993), promoting primary productivity. Changes in terrestrial vegetation composition have been shown to affect leaf litter quality and nutrient availability within lakes (Rawlence 1992). Forests comprised of broad-leaved taxa (e.g. *Betula* and *Alnus*) contribute more nitrates (NO_3-) and phosphorus (P) to lakes through erosion and runoff than those dominated by conifers (e.g. *Tsuga*), favoring diatoms indicative of meso-eutrophic lake conditions (Hall and Smol 1993; Beck et al. 2016). Diatoms such as *A. formosa* and *F. crotonensis* are more competitive than *Tabellaria* sp. in lakes with moderate-

to-high levels of N and silica (Saros et al. 2005; Arnett et al. 2012), and are indicators of eutrophication in temperate lakes (Lotter 1998). Increases in these taxa at Lac Noir thus support an inference of higher nitrogen concentrations (likely the primary limiting nutrient) and overall lake productivity during the peak of the LIA.

In contrast to the MWP, declining percentages of *Tsuga* as well as cooler and dry climatic conditions at the peak of the LIA (Paquette and Gajewski 2013) may have led to less acidic waters and low DOC inputs, evidenced by an increase in *D. stelligera* and benthic alkaphilous taxa (e.g. *S. pinnata*) at the expense of *T. flocculosa* str. IIIp (Faulkenham et al. 2003; Lavery et al. 2014). Studies of Arctic and temperate lakes report conflicting findings in regards to optimal lake and/or climatic conditions for *D. stelligera*, even in sites within close proximity to one another (Saros et al. 2015). Some studies suggest that *D. stelligera* is more abundant in warm conditions with greater thermal stratification (Rühland et al. 2015; Perren et al. 2009); however, at Lac Noir, as well as at other sites, there seams to be a definitive association of this small centric taxon to N-concentrations (Neil and Gajewski 2017; Fritz and Anderson 2013), or even climate cooling as was described by Saros et al. (2015) in relation to Neoglaciation.

During the peak of the LIA, the Lac Noir diatom record again closely resembled that of Bates Pond in Connecticut (Köster and Pienitz 2006). At Bates Pond, increased abundances of benthic *Fragilaria* spp. (*S. pinnata* included) at 1640 CE were interpreted as a response to cooling climate conditions and prolonged seasonal ice cover. At other sites, extended ice cover has been shown to trigger internal releases and mobilization of P from lake sediments (Kirilova et al. 2009). *S. pinnata* has a slightly higher weighted-average for total phosphorus (TP) and total nitrogen (TN) than other diatom taxa such as *Tabellaria flocculosa* str. IIIp (Christie et al. 2003; Hall and Smol 1996), and thus increases in this taxon at Lac Noir may have signalled either internal or external nutrient loading during the cool, dry phase of the LIA. Increased abundances of small benthic *Fragilaria* spp. could

indicate an expansion of the littoral zone as well (Karst and Smol 2000); at Lac Noir, low inferred JJA precipitation and greater abundances of aquatic macrophytes during the peak of the LIA (Fig 3; Paquette and Gajewski 2013) may have therefore led to optimal conditions for *S. pinnata*.

3.4.3 Zone D: Post-settlement (1870 CE to present)

The initial settlement and subsequent expansion of Euro-Canadian activities in southern Québec (~1820-1875 CE; Smith 1967; Neil and Gajewski 2017) corresponded broadly with the end of the LIA in the region (Gajewski 1988). The impacts of human-induced land clearance and burning of forests for agriculture in the region were prominent in the Lac Noir record after 1870 CE; there was an abrupt increase in herbaceous pollen (*Ambrosia*, Poaceae, Plantaginaceae, *Rumex*) coinciding with an influx of micro-charcoal in the lake sediments (Paquette and Gajewski 2013). Disturbance associated with the colonization, such as logging or burning, may have increased the inputs of minerogenic materials to the lake (Rosén and Hammarlund 2007), possibly evidenced by a decline in organic matter content (Fig. 3).

Abrupt changes in the GAMs at 1870 CE confirm significant responses of the diatom flora to direct and indirect impacts of catchment disturbances (pollen PC axis 1 and percent organics; Fig 6-8). Both climate (pollen PC axis 2) and terrestrial productivity (pollen influx) were also influencing factors on the lake ecosystem, although their contributions to diatom trends were gradual and subtler. Peaks in *A. minutissimum* and *S. minutulus* were recorded at Lac Noir from 1870-1930 CE, slightly after initial settlement when anthropogenic activities and associated impacts on the landscape were high (Smith 1967). Regional deforestation as a result of land clearance and logging likely triggered the release of nutrients, particularly N, within the catchment (Vitousek et al. 1997; Neil and Gajewski 2017), which ultimately caused the changes seen in the diatom flora at Lac Noir during this period; for instance, *A. minutissimum* is known to be responsive to nitrogenous influxes and pollution

(Pappas 2009). Multiple mechanisms related to human activities further contribute to the loading of P in lake ecosystems, including the use of fertilizers and manure in agricultural fields (presently located as close as 1 to 2 km east of Lac Noir), septic leaching into local groundwater and surface water, or atmospheric deposition of dust particles (Riemersma et al. 2006). Diatom calibration sets of lakes in southern Ontario and Québec suggest that *S. minutulus* has a weighted-average (optima) of 549.5 μgL^{-1} for TN (Christie et al. 1993) and 17.0 μgL^{-1} for TP (Tremblay and Pienitz 2014). The peak in *S. minutulus* between 1870-1930 CE at Lac Noir was therefore reflective of meso-eutrophic conditions associated with anthropogenic activities, and indicated TN and TP values that were roughly double those observed in the modern surface sample collected from Lac Noir soon after the core was retrieved (Cooper et al. 2016).

Greater atmospheric N deposition caused by fossil fuel combustion, agricultural practices and other anthropogenic activities have been noted in recent decades, as evidenced by a rise in *A. formosa* and *F. crotonensis* in North American lakes (Hall and Smol 1996; Saros et al. 2005; Arnett et al. 2012; Sheibley et al. 2014). Similar increases in these taxa were seen at Lac Noir after Euro-Canadian settlement, suggesting that this activity has had substantial influences on lakes in southern Québec. After 1930 CE, the Lac Noir diatom record showed signs of progression towards a less productive ecosystem (e.g. disappearance of *S. minutulus,* higher CS/DV values, an increase in *T. flocculosa* str. IIIp), similar to that observed during the MWP. Human impacts on vegetation were less pronounced, and regional temperatures were once again warmer than the long-term average for the Late Holocene (Paquette and Gajewski 2013; Lafontaine-Boyer and Gajewski 2014). The more recent change in lake trophic state could be explained by a reduction in phosphorus concentrations resulting from better management practices (Riemersma et al. 2006), or perhaps the ability of early successional forests to better retain nutrients (Hall and Smol 1996).

3.4.4 Lac Noir and Lac Brûlé: a regional comparison of diatom/pollen records

A comparison of the paleo-records from Lac Brûlé and Lac Noir (25km apart) showed that vegetation surrounding each of the two sites responded to environmental changes similarly in timing and direction of change, with some exceptions (Lafontaine-Boyer and Gajewski 2014). Diatom community composition was more unique to each lake as a result of local catchment-scale characteristics, including basin morphometry, habitat availability, water chemistry, and disturbances (Blanco 2014). Regardless, most of the pollen taxa and several of the abundant diatom species were common to both sites and were directly comparable (Fig. 3.9).

Inconsistency in the pollen records of the two lakes was mainly attributed to a decline in *Tsuga* that occurred earlier in Lac Brûlé at 1345 CE, in response to a fire in the watershed (Fig. 3.9; indicated by a peak in charcoal influx). This disturbance was considered to be local, as there was no equivalent response in the Lac Noir record, despite the relatively close proximity of the two lakes (Lafontaine-Boyer and Gajewski 2014). At Lac Brûlé, the *Tsuga* decline triggered an influx of nutrients and dissolved organic carbon (DOC) into the lake, also resulting in poorer light penetration through the water column (Neil and Gajewski 2017; Cooper et al. 2016). This was reflected in the diatom assemblages as a decrease in the relative abundance of *T. flocculosa* str. IIIp. However, the overall nutrient status of Lac Brûlé did not appear to be greatly affected by the fire in the watershed, as CS/DV values did not show any major changes at this time (Neil and Gajewski 2017).

At Lac Noir, a similar decrease in *Tsuga* occurred later in the record at 1630 CE, and coincided with the deteriorating conditions at the peak of the LIA. At this time, most of the plant taxa represented in both lakes (e.g. *Pinus strobus*, *Fagus*) declined in abundance after exceeding a threshold that reduced growth and reproductive success. The Lac Noir record also revealed a tight coupling between diatom assemblages and abrupt, climate-driven vegetation responses in the

catchment area. Greater nutrient availability associated with the shift in forest composition may have resulted in a more productive lake ecosystem, again evidenced by a decline in *T. flocculosa* str. IIIp and a peak in the percentages of *F. crotonensis* and *A. formosa*. As the decline in *Tsuga* was accompanied by additional changes in terrestrial vegetation at Lac Noir, such as a decline in *Fagus*, there were greater consequences for the nutrient status of the lake (e.g. a rapid decline in CS/DV values that was absent from the Lac Brûlé record).

Local forcings were responsible for triggering site-specific changes in the diatom records of Lac Brûlé and Lac Noir. For example, in both lakes, diatom assemblages in the uppermost samples representing the last 100 years were dissimilar as they responded individually to changes in their respective catchments. At Lac Brûlé, diatoms responded abruptly to impacts associated with the opening and closing of the Wallingford-Back Mine (1924-1972 CE), located approximately 300m north of the lake (Neil and Gajewski 2017). Mining operations did not significantly affect the surrounding vegetation, though increases in the percentages of *F. crotonensis* to well above previous values indicated nutrient enrichment of the lake associated with human activity. Diatom assemblages from Lac Noir were relatively undisturbed in comparison, with major changes only occurring concurrently with vegetation shifts in the catchment after 1860 CE.

3.5 Conclusions

The timing of zone boundaries delineated by the diatom assemblages match major shifts in pollen relative abundance and influx, as well as peaks in charcoal input to the sediment and, to a certain extent, transitions in sediment organic matter and carbonates. This indicates a close coupling of the lake ecosystem to terrestrial vegetation dynamics in the watershed and surrounding region. Multi-proxy paleolimnological studies with sampling at high-resolution are thus necessary

to unraveling the intricate dynamics of climatic and terrestrial influences on aquatic communities. These types of studies not only provide necessary details regarding the succession of past communities, but also represent a key component in forecasting future responses to climate variability and human-induced disturbances.

3.6 References

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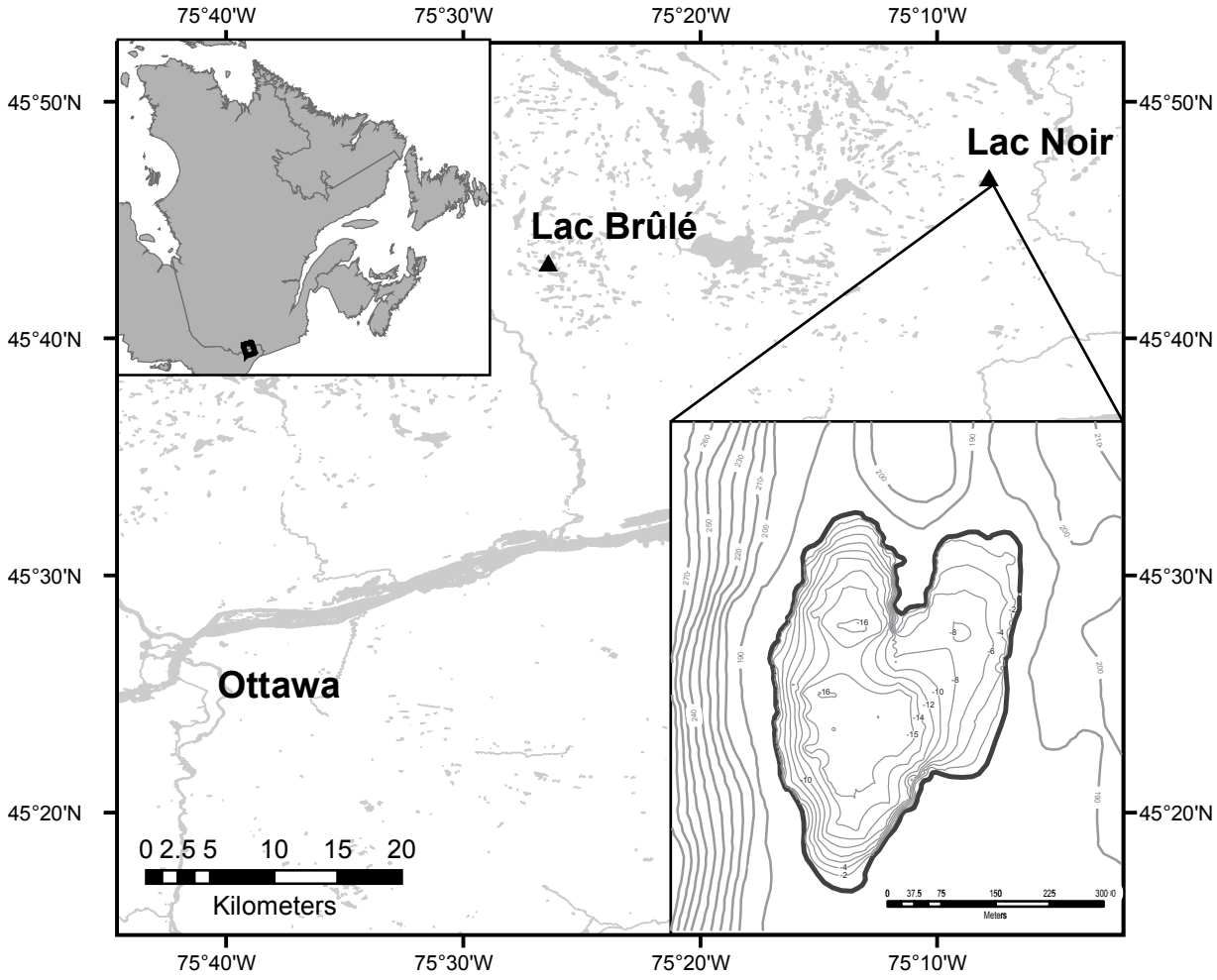


Figure 3.1: Map of the location, surrounding topography and bathymetry of Lac Noir, southwestern Québec

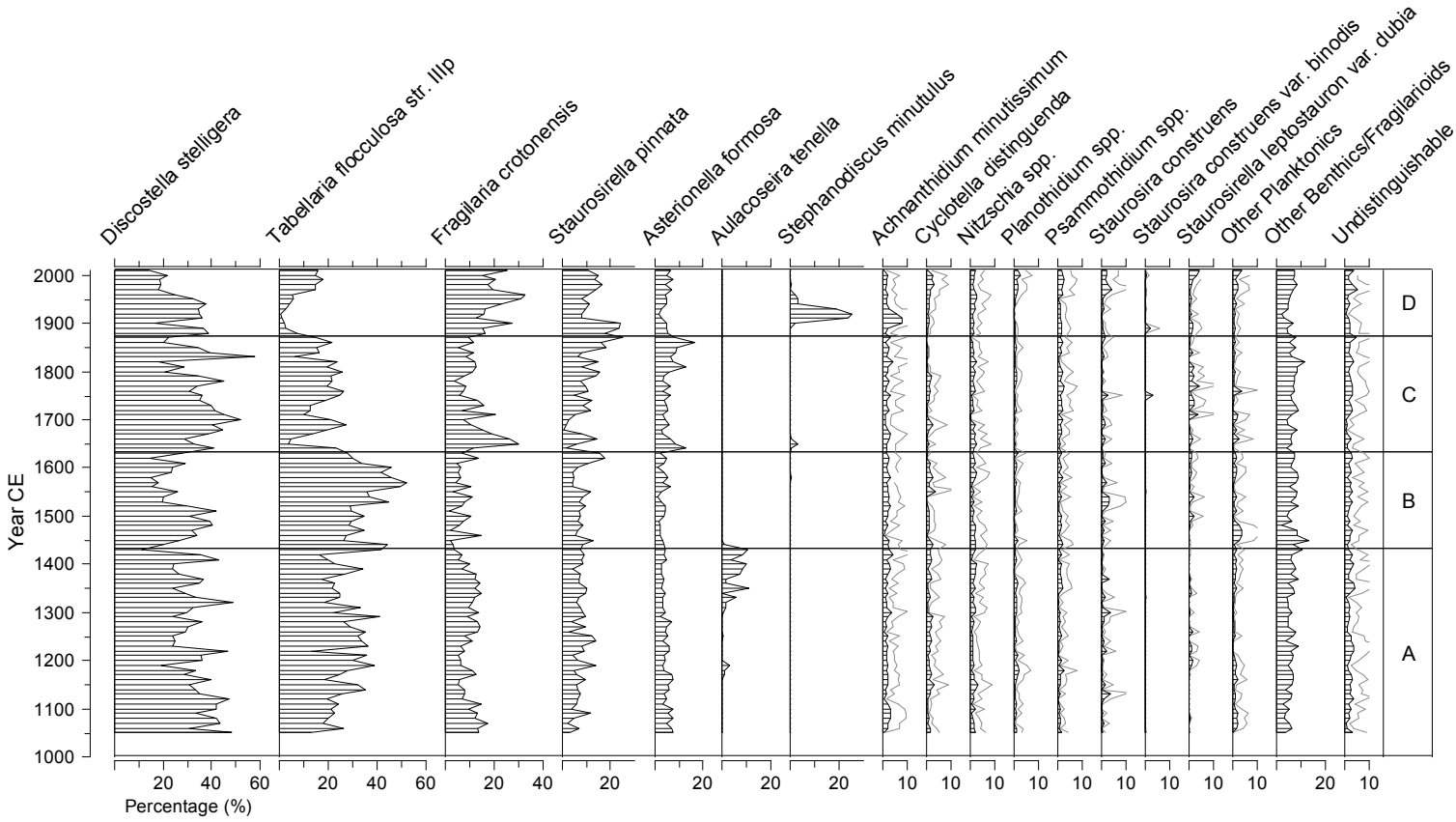


Figure 3.2: Lac Noir diatom stratigraphy, expressed as percentages of total diatom abundance. Taxa with ≥ 3% relative abundance in at least one sample are shown. Sampling intervals are shown by the horizontal black lines in each profile. A 3x exaggeration (grey line) is applied to taxa representing a smaller portion of the total diatom sum

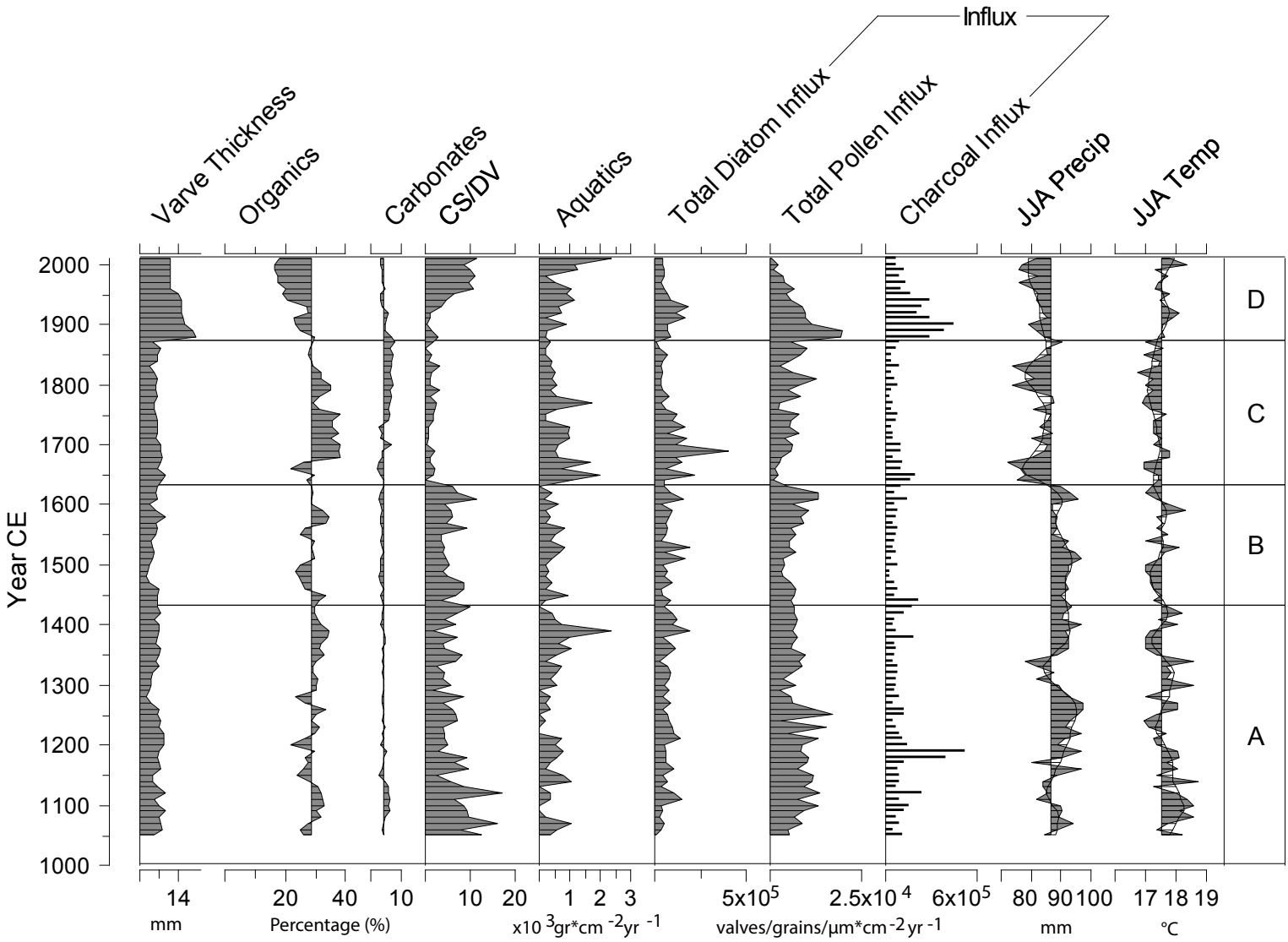


Figure 3.3: Paleo-environmental summary for Lac Noir, southwestern Québec, including sediment characteristics, the ratio of scaled chrysophytes relative to diatom valves (CS/DV), total influx (accumulation rates) of aquatic macrophytes, diatoms, pollen and charcoal, and paleo-climate reconstructions (derived from local pollen using the modern analogue technique). All data (with the exception of CS/DV and diatom influx) was obtained from Paquette and Gajewski (2013)

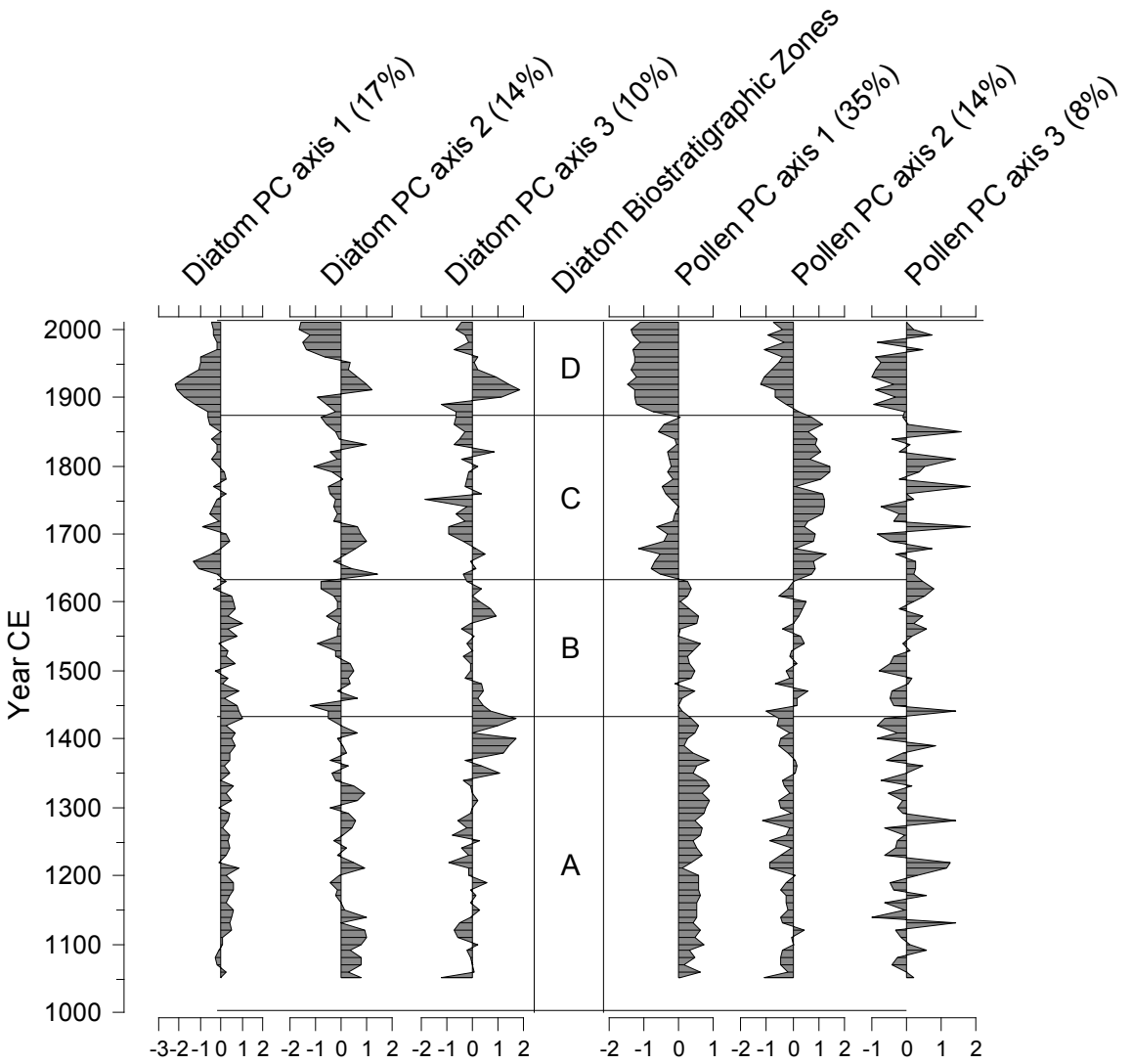


Figure 3.4: Diatom and pollen principal components sample scores for Lac Noir (see tables 1-2 for loadings). Only significant PCA axes are shown. Explained variance of each axis is indicated as a percentage. The division of the diagram is based solely on changes in the diatom PCA. The pollen PCA axes were derived from the pollen record of Paquette and Gajewski (2013)

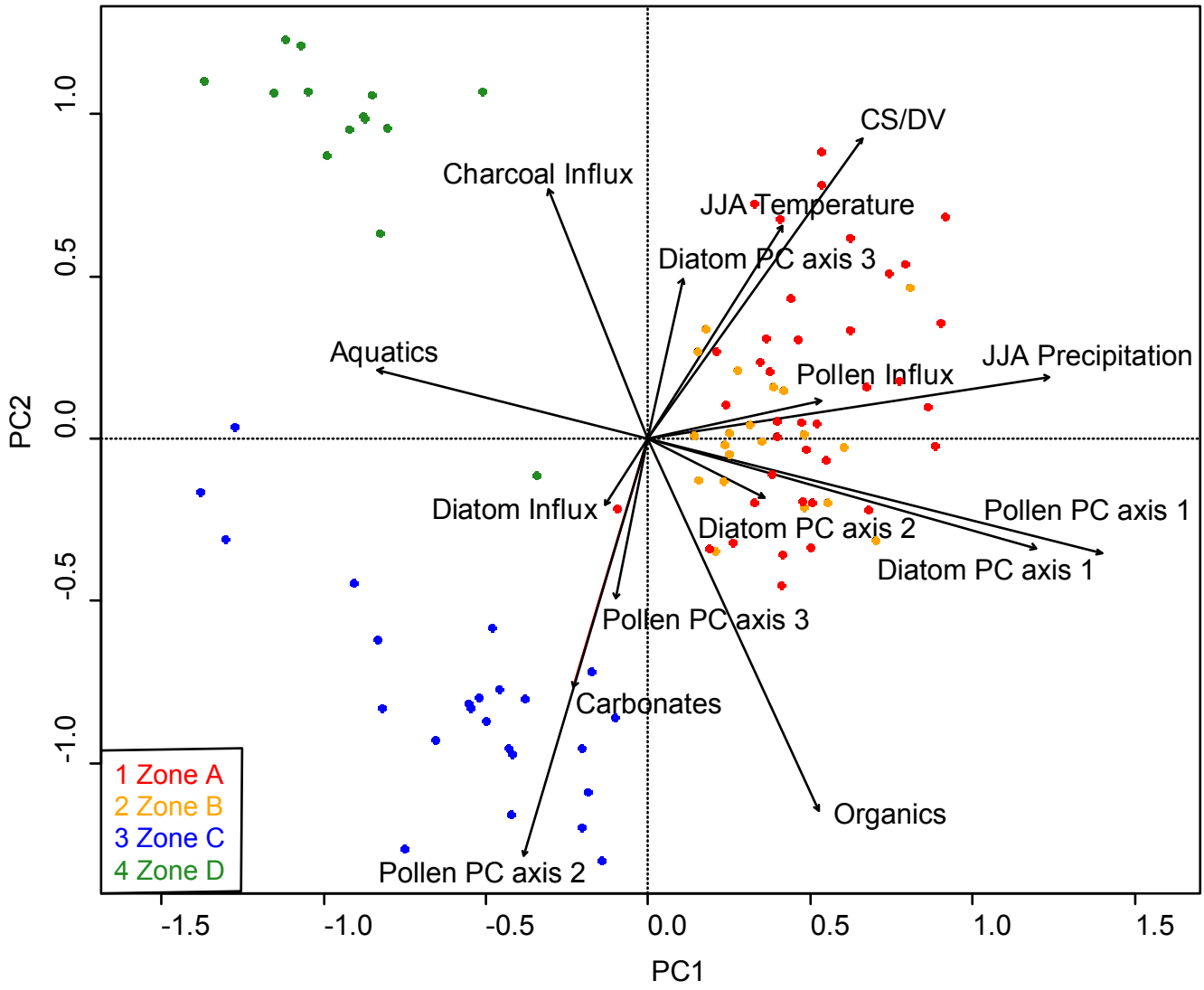


Figure 3.5: Biplot of a principal components analysis (PCA) incorporating fossil diatom and pollen assemblages (summarized with separate PCAs) and environmental variables from samples in Lac Noir, southwestern Québec. Dots represent the sample scores and are colored based on the biostratigraphic zones defined by the diatom PCA (see Fig 3.4)

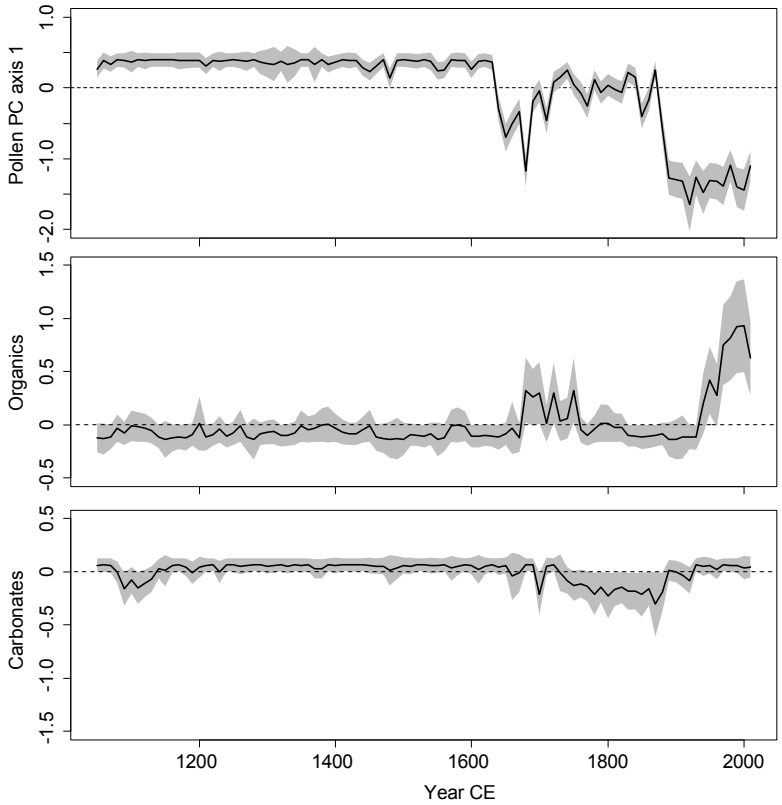


Figure 3.6: The contributions of environmental variables to the fitted diatom PC axis 1 scores in the final GAM model for Lac Noir. A 95% pointwise confidence band is shown by the grey band. In the time series, the contribution of the variable is considered significantly different from the intercept when the grey band does not intersect the dashed zero line

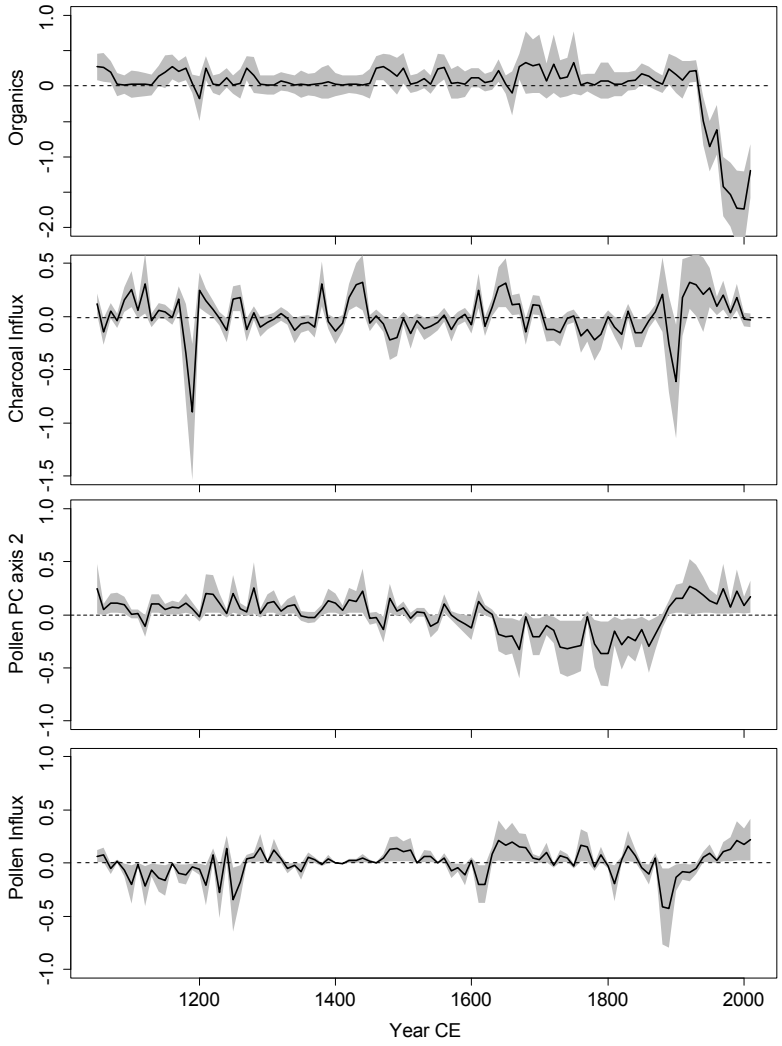


Figure 3.7: The contributions of environmental variables to the fitted diatom PC axis 2 scores in the final GAM model for Lac Noir. A 95% pointwise confidence band is shown by the grey band. In the time series, the contribution of the variable is considered significantly different from the intercept when the grey band does not intersect the dashed zero line

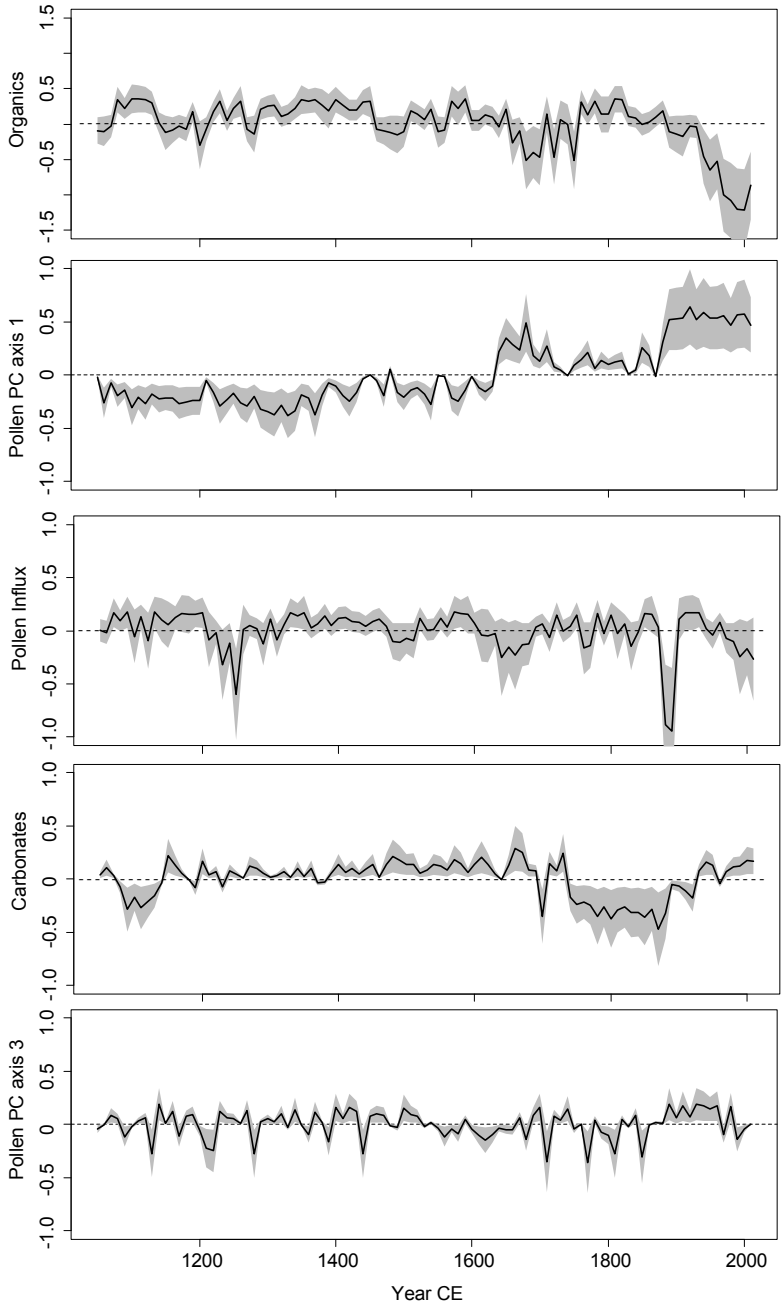


Figure 3.8: The contributions of environmental variables to the fitted diatom PC axis 3 scores in the final GAM model for Lac Noir. A 95% pointwise confidence band is shown by the grey band. In the time series, the contribution of the variable is considered significantly different from the intercept when the grey band does not intersect the dashed zero line

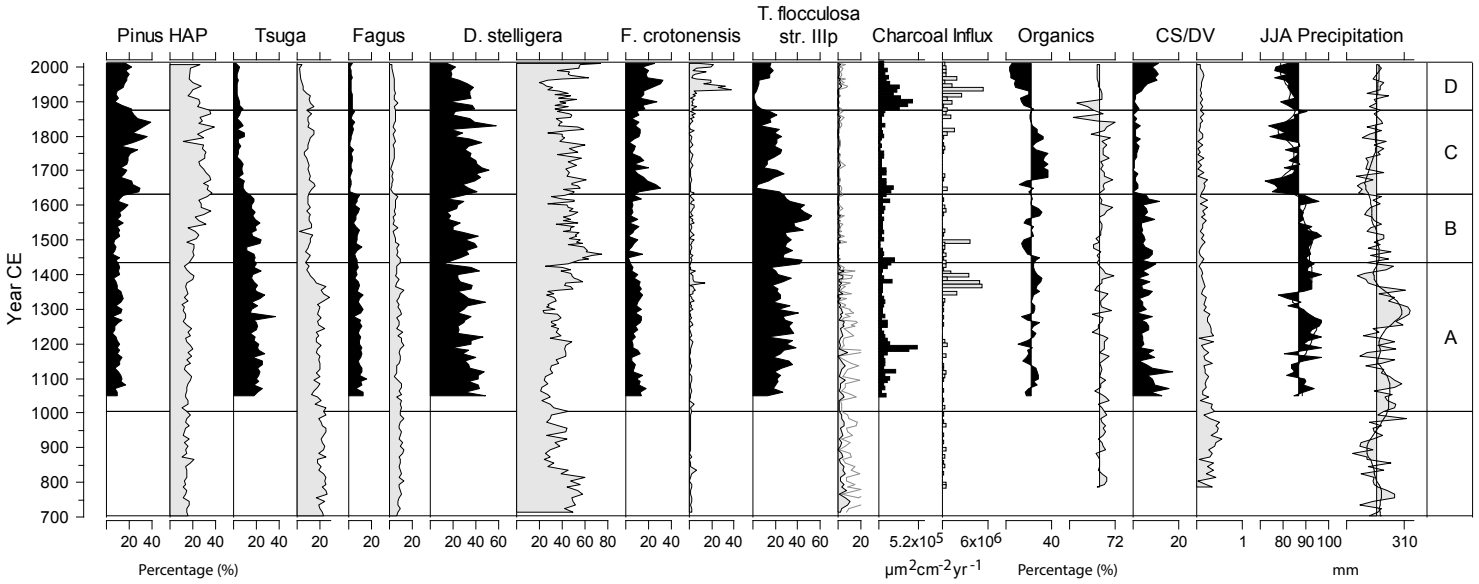


Figure 3.9: Comparison of selected pollen and diatom percentages and environmental variables from Lac Noir (Black; this study; Paquette and Gajewski 2013) and Lac Brûlé (Grey; Neil and Gajewski 2017; Lafontaine-Boyer and Gajewski 2014)

Table 3.1: Loadings and explained variance (eigenvalues) of a principal components analysis on diatom percentages from Lac Noir, southwestern Québec

	Component		
Taxon	1	2	3
Discostella stelligera	-0.145	1.084	-0.545
Tabellaria flocculosa	1.330	-0.130	0.020
Fragilaria crotonensis	-1.082	-0.102	-0.109
Staurosirella pinnata	-0.524	-0.993	0.047
Asterionella formosa	-0.267	-0.093	-0.568
Aulacoseira tenella	0.549	-0.013	0.799
Stephanodiscus minutulus	-1.110	0.287	0.610
Achnanthidium minutissimum	-0.632	-0.123	0.797
Cyclotella distinguenda	0.567	-0.096	0.167
Nitzschia spp.	0.121	-0.161	0.754
Planothidium spp.	0.636	-0.652	-0.355
Psammothidium spp.	-0.315	-0.873	0.092
Staurosira construens	0.023	-0.606	-0.591
Staurosira construens var. binodis	-0.259	-0.219	-0.582
Staurosirella leptostauron var.dubia	-0.672	-0.823	-0.343
Other Planktonics	0.066	-0.451	0.293
Other Benthics/Fragilarioids	0.465	-0.919	0.152
Eigenvalues	0.17	0.14	0.10

Table 3.2: Loadings and explained variance (eigenvalues) of a principal components analysis on pollen percentages from Lac Noir, southwestern Québec (Paquette and Gajewski 2013)

	Component		
Taxon	1	2	3
Pinus diploxylon	-0.956	-0.097	0.836
Pinus haploxylon	-0.615	1.019	0.040
Picea	-0.689	0.521	0.425
Abies	-0.364	0.898	-0.211
Tsuga	1.283	-0.456	0.115
Acer	0.866	-0.783	-0.202
Betula	0.378	0.171	-0.370
Fagus	1.248	-0.580	-0.116
Other arboreal spp.	-0.276	0.202	-0.173
Alnus	-1.285	0.188	-0.250
Salix	-0.842	0.097	-0.270
Other shrub spp.	-0.612	-0.465	0.966
Asteraceae	-0.842	-0.317	-0.653
Ambrosia	-1.153	-0.489	-0.479
Poaceae	-1.214	-0.576	-0.348
Plantaginaceae	-0.796	-0.613	-0.412
Rumex Type	-0.929	-0.733	0.177
Other non-arboreal spp.	-0.748	-0.699	0.452
Eigenvalues	0.35	0.14	0.08

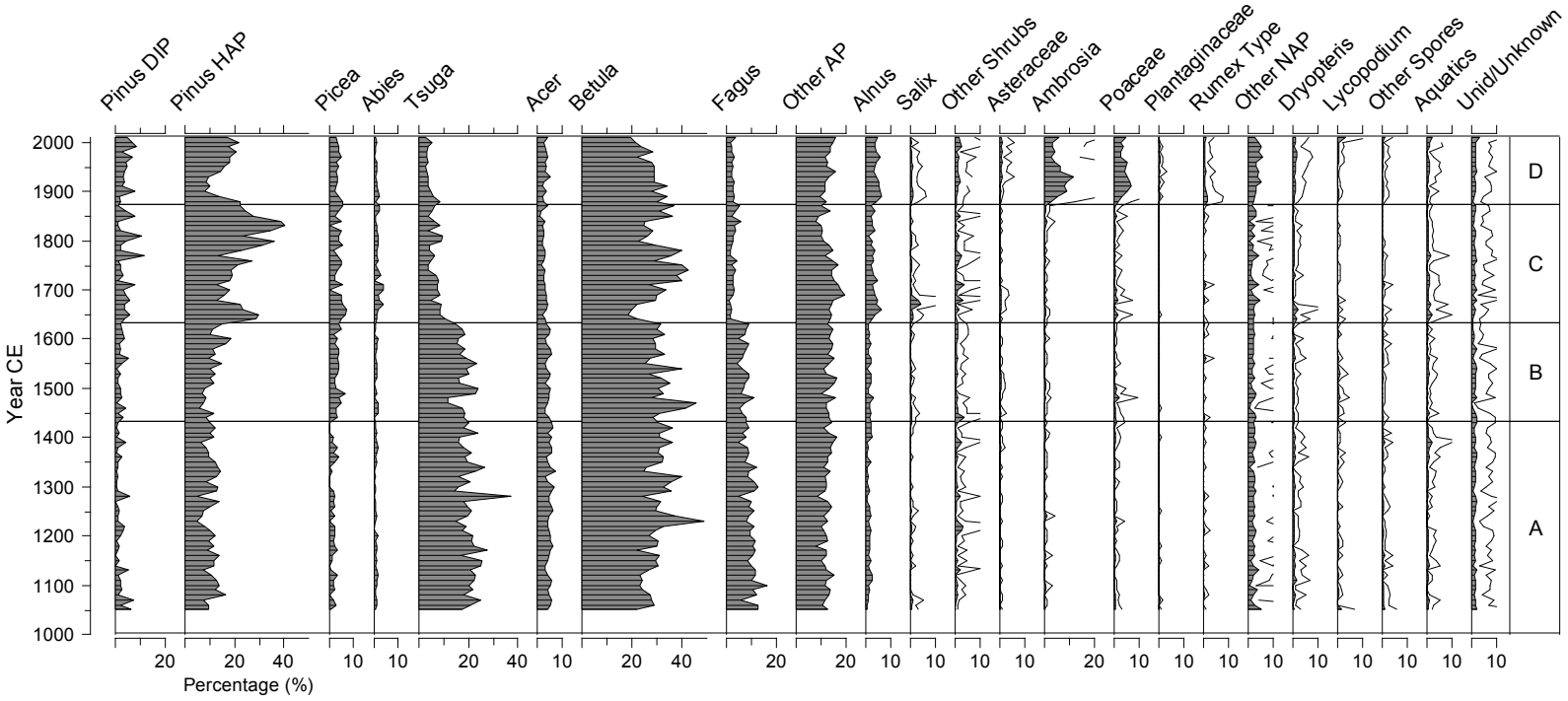


Figure S3.1: Pollen percentage diagram for Lac Noir, southwestern Québec. Data was obtained from Paquette and Gajewski (2013), but their chronology was corrected in this study (see text for details). Unfilled grey lines represent a 5x exaggeration

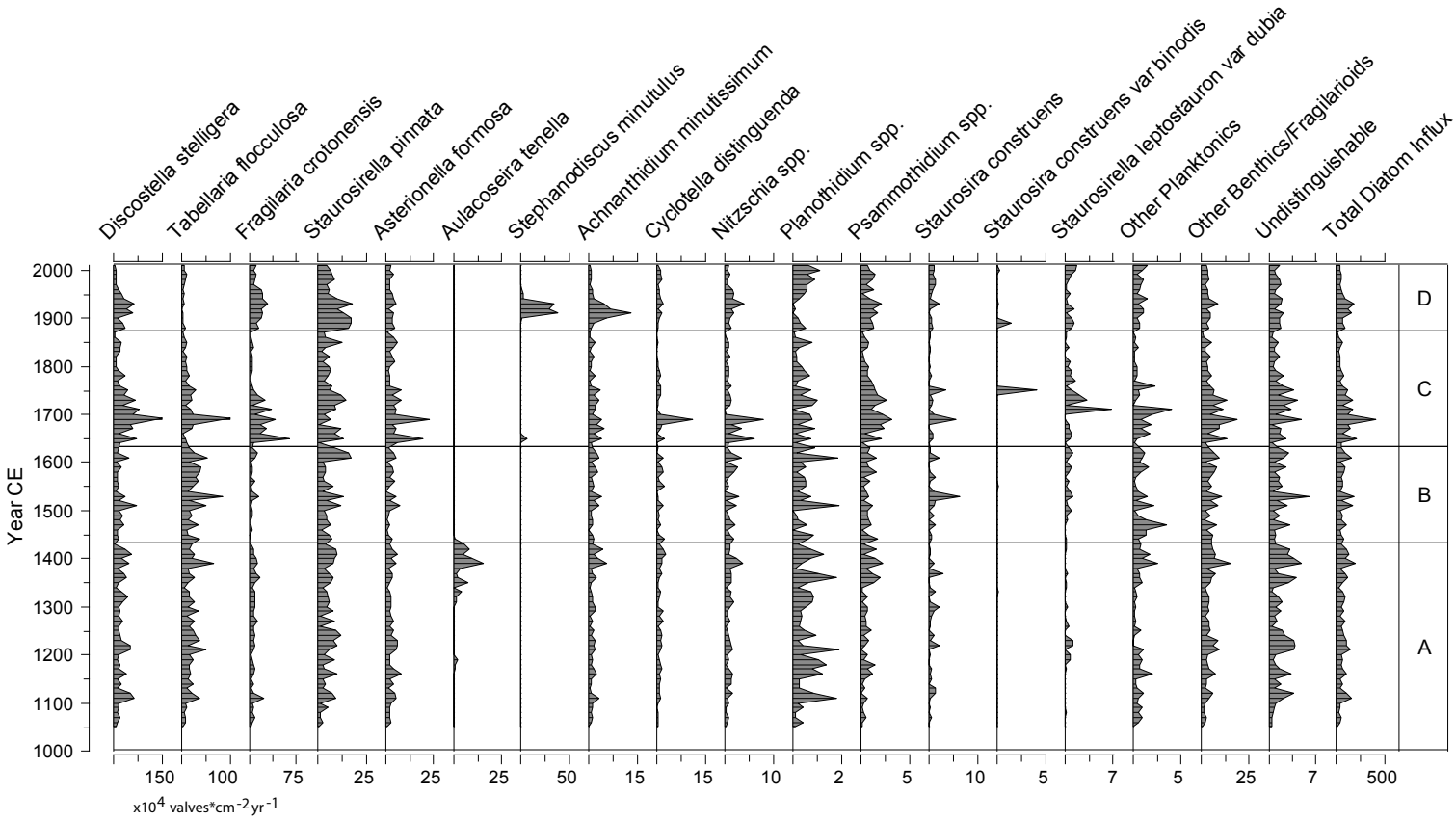


Figure S3.2: Diatom accumulation rates from Lac Noir, southwestern Québec, for the past 1000 years

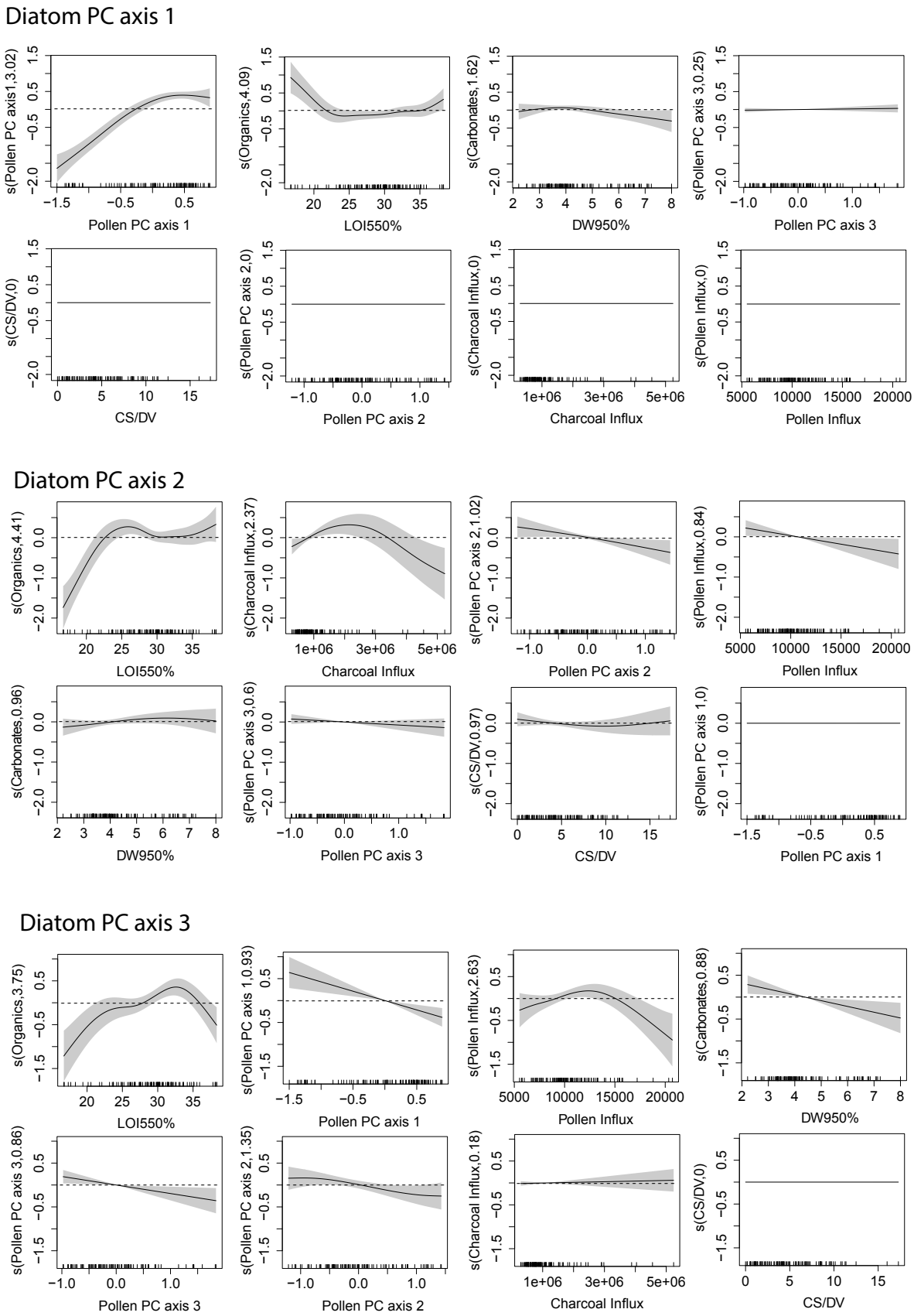


Figure S3.3: Generalized additive model (GAMs) fitted smooth functions of variables from Lac Noir for each of the significant diatom principal components axes. Observed values for each variable are indicated by tick marks on the x-axis (inside each panel). Pointwise confidence intervals (95%) are indicated by the grey bands; where they touch the dashed zero line, the contribution of the variable is not statistically significantly different from the intercept

CHAPTER FOUR

An 11,000-year record of diatom community responses to climate and terrestrial vegetation changes, southwestern Québec

Abstract

A high-resolution diatom sequence was developed from a continuously-laminated lake sediment core in southwestern Québec, which spanned the Holocene (~11000 years). Changes in the diatom record were synchronous with patterns of vegetation succession inferred from regional palynological studies, demonstrating significant influences of terrestrial ecosystems on lake water chemistry and aquatic communities. Principal components analysis delineated three major diatom biostratigraphic zones corresponding broadly to Milankovitch-scale climate intervals. Benthic alkaphilous diatoms were abundant when the landscape was sparsely vegetated by *Picea*-dominated woodland in the early Holocene (11.1-8.0 ka), when post-glacial climate conditions were inferred as relatively cool and dry. Warming in the mid-Holocene (8.0-3.6 ka), resulted in a stabilization of forests and soils in the catchment. The percentages of shade-tolerant tree species (*Tsuga, Fagus,* and *Betula*) increased during this time, and planktonic diatom taxa (*Discostella stelligera* and *Fragilaria tenera*) were abundant in the lake. The well-known decline in *Tsuga* across eastern North America at ~5.5 ka corresponded to a shift towards eutrophic lake conditions for several centuries, indicated by an increase in benthic diatom taxa and a higher ratio of chrysophytes relative to diatoms. Neoglacial cooling in the late Holocene (3.6 ka to present) triggered an initial decline in *D. stelligera*, which later recovered as a result of nutrient inputs associated with increased abundances of hardwood, deciduous species (*Betula* and *Alnus*) in the catchment. In addition to providing a high-resolution record of lake ontogeny for the region, the full Holocene record from this lake adds a new perspective on the spatial extent of regional aridity

during the Medieval Warm Period (1.2-0.8 ka).

Key Words: diatom, Holocene, lake ontogeny, paleoclimate, pollen, *Tsuga*-decline, varve

4.1 Introduction

Climate variations operated at various spatial and temporal-scales during the Holocene (Viau et al. 2002; COHMAP Members 1988), resulting in complex patterns of ecological change (Soranno et al. 2014). Responses of aquatic and terrestrial biota to these climate variations are documented by multi-proxy and regional paleolimnological studies, which have identified multi-scale interactions in the past (Birks et al. 2012), and can lead to improved predictive modelling of future changes (Paus 2013). Annually-laminated (varved) lake sediments, in particular, offer added opportunities to study ecosystem changes, as they can be used to generate precisely-dated, high-resolution chronologies to illustrate gradual and/or abrupt changes in subfossil assemblages (Ojala et al. 2012; Zolitschka et al. 2005; O'Sullivan 1983). Among paleolimnological fossils, diatoms are considered ideal indicators of past environments given their ecological diversity and sensitivity to changes in lake water chemistry and nutrient availability (Stoermer and Smol 2001; Battarbee 2000), while pollen is typically used to reconstruct vegetation dynamics and overall climate conditions (Smol et al. 2001).

Sediment records dating to early stages of lake formation ~11000 years ago in Québec and Ontario show that diatom communities responded to orbital-scale climate variations during the Holocene (Karmakar et al. 2015; Haussmann 2011; Moos et al. 2009). High-resolution studies spanning the last ~1200 years show synchronous responses in biota (e.g. pollen, diatoms, and cladocera) to millennial- to decadal-scale climate intervals in southern Québec (Cooper et al. 2016; Neil and Gajewski 2017) as well. Studies of lake ontogeny, the natural aging process of a lake

(Whiteside 1983), suggest that aquatic communities are also highly responsive to vegetation succession and soil development in their respective lake catchments (Fritz and Anderson 2013; Puusepp and Kangur 2010; Boyle 2007; Engstrom et al. 2000), perhaps more so than to direct climate impacts.

The aim of this paper was to analyze diatom assemblages in a continuously-varved lake sediment core in order to provide a long-term perspective of aquatic changes spanning the entire Holocene. The diatom record is interpreted in the context of palynological records from nearby sites (Lafontaine-Boyer and Gajewski 2014; Paquette and Gajewski 2013; Fuller 1997; Mott and Farley-Gill 1981) to develop a more comprehensive environmental history for the region, which will improve our understanding of lake responses to both natural climate variability and non-climatic processes.

4.2 Methods

4.2.1 Study Site

The study area is located towards the northern edge of the Ottawa-St. Lawrence Lowland, which was deglaciated ~13000 cal. yr. BP (Parent and Occhietti 1988). Marine transgression of the Champlain Sea following ice retreat is evidenced at several sites by marine clay deposits and fossils found in lake sediments (Rodrigues 1992). The Champlain Sea receded by ~11600 cal. yr. BP due to isostatic rebound, and organic sediment began to accumulate in lake basins across southwestern Québec and Ontario (Anderson 1987). The site chosen for this study, Lac Noir (Fig. 4.1; 45°46’31.9’’N, 75°8’6.23’’W, 176 m a.s.l.), is situated within the mapped boundary of the Champlain Sea in southwestern Québec (Rodrigues 1992). A core retrieved from the lake in 2012 had 5.24 m of continuously varved sediments, with an additional 30 cm of clay material at its base.

Lac Noir is relatively small (surface area = 25 ha), oligotrophic (total phosphorus (T =

0.009 mgL^{-1}) and circumneutral (pH = 7.7). The water is hypoxic (dissolved oxygen = 3%) at the maximum lake depth (~16 m). The predominant vegetation around the lake is red and white pine (*Pinus* spp.), yellow birch (*Betula alleghaniensis*), with some eastern hemlock (*Tsuga canadensis*), American beech (*Fagus grandifolia*), maple (*Acer* spp.) and alder (*Alnus* spp.). The watershed surrounding the lake is relatively undisturbed by human activities, though there were some changes to the landscape associated with Euro-Canadian settlement in the region beginning at ~1860 CE (Neil and Gajewski, subm; Paquette and Gajewski 2013); the region was logged and settlements and farmland extended up the river valleys from the Ottawa River. Mean annual, summer and winter temperatures at the closest weather station are 4.8°C, 17.9°C and -9.9°C respectively, and total annual precipitation is 985 mm (Environment Canada 2017).

4.2.2 Sediment collection and cross-correlation

At Lac Noir, previous studies analyzed the uppermost 0.9 m of a frozen sediment core. The core had annually deposited layers determined to be varves, enabling for precise dating of the sediment which was used to prepare a continual series of diatoms (Neil and Gajewski, subm.) and pollen (Paquette and Gajewski 2013) at high temporal resolution (every 10-years). In 2012, a modified Livingstone piston corer was used to retrieve a longer, complete core from the deepest part of the lake in 1-m sections (drives). The uppermost drive included the water/sediment interface while the bottom of the lowermost drive was comprised of dense clay; this suggests that the full sediment profile, also varved, was recovered. A second complete core was retrieved to fill potential gaps between 1-m sections of the first core sequence, and more importantly to estimate chronological errors in varve counts (below). The magnetic susceptibility of both cores was measured with a Bartington™ MS2C meter and loop sensor, with the exception of the uppermost drives comprised of unconsolidated sediments. The cores were cross-correlated by matching peaks

in magnetic susceptibility, as well as distinctive marker beds (consisting of single layers or thicker bands) present in both cores. A composite magnetic susceptibility curve was then calculated by averaging values from both cores at 1-cm resolution.

4.2.3 Chronology and varve thickness

Varve couplets consisting of one dark and one light layer of deposition were counted in each core, with pins placed at 10-year intervals (ten couplets) to develop the varve chronology. Varve counts were completed independently by two researchers and on each core sequence, and were resolved in sections delineated by distinctive marker beds. Percentage errors of the varve counts were calculated for individual drives, and in sections between marker beds (Table 4.1). AMS ^{14}C dates of 22 samples from the cores (Table 4.2) were used in the package "BACON" (Blaauw and Christen 2011) in version 3.4.0 of the software R (R Core Team 2013) to create an age-depth model (Fig. 4.2); this model was derived independently from the varve counts, and was strictly used for the purposes of verifying the varve chronology. A 2nd order polynomial regression fit through the ^{14}C-dates was also shown for comparison. In the following sections, references to ^{14}C-calibrated dates are written as 'cal. yr. BP'. Varve-ages used to describe stratigraphic changes in the Lac Noir core are written as 'ka' (thousands of years before 2010).

Following validation of the varve chronology, the thickness of each 10-year interval was measured using an Acu-Rite linear encoder and Quick-Check readout with Measure J2X software at a precision of 0.0001 mm (VoorTech Consulting, Holderness, New Hampshire, USA). Where varve thickness measurements overlapped between the two core sequences, an average varve thickness measurement was calculated to create a composite curve.

4.2.4 Diatom processing and identification

Sediment subsamples of ~0.25 cm^3 were extracted from the 10-year intervals of the cores at a resolution of 100 years between 0.9-5.24 m, and at every 20 years between 2.47-2.79 m and 4.33-4.53 m. The subsamples were processed for diatoms following standard protocols (Battarbee et al. 2001), and 1.0 mL of a microsphere suspension ($5x10^6$ spheres mL^{-1}) was added to each subsample after digestion and cleaning to estimate diatom accumulation rates. Slides were prepared by allowing small amounts of diatom suspension (diluted with deionized water) to evaporate on clean coverslips, after which they were mounted onto permanent microscope slides with Naphrax. A minimum of 500 individual diatom frustules was enumerated for each slide using a Nikon 90i microscope at 1000x magnification under oil emersion. Identifications were made using Antoniades et al. (2008), Siver et al. (2005), and Patrick and Reimer (1966, 1975) as references. Chrysophyte scales were also enumerated on each slide to estimate their proportions relative to diatom valves, but were not further identified.

4.2.5 Statistical analysis

In a previous study of Lac Noir, diatom assemblages were analyzed in 97 samples from the uppermost 0.9 m of a frozen core (Neil and Gajewski, subm.). In this study, an additional 169 samples were counted for diatoms between 0.9-5.24 m, and statistical analyses were run on the combined 266 samples spanning the entire length of the core. Diatom relative abundance data was graphed using the program C2 (version 1.7.6; Juggins, 2014); only the more prominent taxa representing >4% of the total diatom sum in at least one sample were shown (Fig. 4.3) and used in subsequent analyses. Using the "vegan" package in the program R (R Core Team 2013), a detrended correspondence analysis (DCA) of the diatom assemblages produced a gradient length of <2.5 standard deviation units. A principal components analysis (PCA; Fig. 4.4) was therefore

chosen to summarize variations in species relative abundance data (Legendre and Birks 2012), which were Hellinger transformed prior to analysis (Legendre and Gallagher 2001). Significant changes in the first three components of the PCA (Table 4.3; Fig. 4.5) were used to delineate diatom assemblage zones and subzones in the stratigraphic diagrams.

4.3 Results

4.3.1. Development and verification of chronology

A total of 11160 individual varves (years) were counted between 0-5.24 m. Distinctive marker beds were identified which allowed for the cross-correlation of 10-year intervals between the two cores. Marker layers were pale-grey to white and were thin, approximately the width of an individual varve. Marker bands differed, as they were comprised of visibly darker sediments (black or grey) and sometimes spanned the width of up to 20-30 varves.

Independent, resolved varve counts by two researchers were completed on individual drives from both cores (~1 m long), and for smaller sections between marker beds (~5 cm long). If sections delineated by marker beds were present where both core sequences overlapped, error estimates were calculated using four varve counts (by each researcher and per core; Table 4.1). Based on the differences in varve counts, the estimated chronological error for individual drives ranged from 1.5-6.7%. When varve counts were replicated between distinct marker beds, the estimated error was 1.4-4.1%. Counts were therefore within a normal margin of error for a varve chronology (Ojala et al. 2012; Renberg 1983). Differences in the varve counts were also random rather than systematic; for example, one researcher did not consistently count more varves than the other.

An independent Bayesian age-depth model (Fig. 4.2; grey shaded area) was generated using AMS ^{14}C dating of 22 evenly distributed samples throughout the cores in order to validate

the varve chronology (Fig. 4.2; solid black line). The two chronologies were very similar, only deviating from each other slightly between 1.0-2.3 m, and again from 3.5-4.5 m. The maximum difference between the mean age of the ^{14}C-based chronology and varve-age at any given depth was less than 500 years. A 2nd order polynomial regression fit through the ^{14}C-calibrated dates (Fig. 4.2; solid red line) seemed to be a better overall fit in comparison to the varve chronology, with a maximum of 450 years separating the two at any given depth. The differences between these three age-depth models were determined to be reasonable, with each one likely to produce comparable results in regards to the interpretation of the Lac Noir paleo-record. Thus, varve-ages were chosen to describe temporal changes in the sedimentary and biostratigraphic data.

One small section (4 cm) in the lowermost drive (5.12-5.16 m) of the core had varves that were disturbed and undistinguishable. The number of years in this section was interpolated using average accumulation rates of adjacent, undisturbed sediments. Finally, below the oldest varve counted (11160 years) there was ~30 cm of clay material which comprised the base of the core. A single ^{14}C date taken in this clay at 5.40 m was dated at ~11650 ± 347 cal. yr. BP, but no samples were analyzed for diatoms from this depth.

4.3.2 Sedimentological data

Magnetic susceptibility was highest in the clay sediments at the base of the Lac Noir core (43.5 CGS units), and decreased rapidly (Fig. 4.5). A small peak was dated between 8.9-8.4 ka, where values increased to 4.95 CGS units before decreasing again. At ~7.5 ka there was another small and broad increase, after which magnetic susceptibility was low for an extended period (<1.0 CGS units). Values increased briefly between 2.5-1.7 ka, and there was a final abrupt peak at 0.92 ka (5.8 CGS units).

Varve thickness did not vary greatly between 11.1-5.5 ka, averaging ~35 mm for the 10-year intervals in this period (Fig. 4.5). Values were slightly higher between 5.0-4.1 ka (~50 mm), decreased until 3.0 ka, after which they gradually increased again with greater variability for ~2.0 ka years. Varve thicknesses reached a peak at ~2.1 ka (87 mm), followed by a plateau and a second peak at ~1.1 ka (130 mm). Varve thickness once again declined until ~0.5 ka, before rising again until the present. There were 54 marker layers and 14 marker bands identified in the core; marker layers were spaced fairly regularly throughout the core, whereas the marker bands were only present between 11.0-9.0 ka and 2.5-0.8 ka (Fig. 4.5).

4.3.3 Diatom biostratigraphy

The majority of diatom taxa identified in the Lac Noir sediments were rare, with only 23 of the 160 taxa having relative abundances greater than 4% in at least one sample (Fig. 4.3). Three major biostratigraphic zones and six subzones were distinguished based on changes in the assemblages of these more abundant diatom taxa, as summarized by a PCA (Fig. 4.4).

At the beginning of Zone A (11.1-8.0 ka), up to 35% of the diatom assemblages was comprised of *Aulacoseira ambigua* (Grunow) Simonsen 1979, however this taxon declined abruptly by 10.9 ka. Subzone A1 was mainly dominated by benthic fragilarioid taxa such as *Staurosirella pinnata* (Ehrenberg) Williams & Round 1988, *Staurosira construens* Ehrenberg 1843, and *Staurosirella leptostauron* var. *dubia* (Grunow) M.B.Edlund 1994, together accounting for ~50% of the assemblages. Other notable benthic taxa with relatively higher percentages in subzone A1 were *Navicula* spp., *Nitzschia* spp., and *Amphora pediculus* (Kützing) Grunow 1875.

At 10.7 ka, *Stephanodiscus minutulus* (Kützing) Cleve & Möller 1882 increased and remained relatively abundant throughout the rest of Zone A. At the boundary between subzones A1 and A2 (9.5 ka), *Aulacoseira pusilla* (F.Meister) A.Tuji & A.Houk 2004 and other

undifferentiated *Aulacoseira* species increased abruptly to 25% and 20%, respectively. Towards the end of subzone A2, benthic/fragilarioid diatoms were gradually replaced by planktonic taxa, including *Tabellaria flocculosa* str. IIIp (Roth) Kützing 1844, *Discostella stelligera* (Cleve & Grunow) Houk & Klee 2004, and *Fragilaria crotonensis* Kitton 1869. High-resolution sampling in subzone A2 between 9.0-8.3 ka showed high variability in *Aulacoseira* species, where in several instances they quickly shifted from being present at relatively high abundances to being absent from the record (and vice-versa).

Diatom assemblages in Zone B (8.0-3.6 ka) were dominated by planktonic taxa. The relative abundances of *S. minutulus* and *F. crotonensis* decreased in subzone B1, while *T. flocculosa* str. IIIp and *Aulacoseira tenella* (Nygaard) Simonsen 1979 increased. Subzone B2 (6.9 ka) was marked by an increase in *Asterionella formosa* Hassal 1850, *D. stelligera*, and *Fragilaria tenera* (W.Smith) Lange-Bertalot 1980, as well as a rapid decline in *A. pusilla*. By the end of subzone B2 (3.6 ka), *D. stelligera* had gradually increased to a peak of ~55% of the diatom assemblage.

Zone C (3.6 ka – present) began with an initial decline in *A. formosa, D. stelligera*, and *F. tenera*. *D. stelligera* recovered, and quickly rose to about 60% by 2.8 ka. *A. tenella* and other undifferentiated *Aulacoseira* species increased in subzone C1, and declined again at ~1.7 ka. In subzone C2 (1.0 ka - present), the relative abundance of *A. formosa* was low, and *D. stelligera* decreased slightly. Both *T. flocculosa* str. IIIp and *F. crotonensis* showed small increases, as well as the small benthic species *S. pinnata*. In the uppermost sediments, there was an abrupt peak in *S. minutulus* at 0.1 ka, reaching up to 25%. In Chapter 3 of this thesis, detailed changes in the diatom assemblages of subzone C2 are described at decadal resolution for the past ~1.0 ka years.

Total diatom concentration (DC) and accumulation rates (DAR) shared similar profiles in the Lac Noir record; they both had a series of dips and peaks, each lasting for several millennia (Fig. 4.5). Periods of high DC and DAR were reached at ~8.7, 4.5 and 2.3 ka, with low points at 7.0 and 3.2 ka. Several individual peaks in DC and DAR were also seen in the record, many of which corresponded to the 10-year intervals that included a marker layer or band. A sudden decline in DC and DAR after 1.0 ka (subzone C2) could be explained by different batches of microsphere solution used in Neil and Gajewski (subm.) and this study; however, the timing also corresponds to changes in diatom relative abundances (independent of DC and DAR), as well as high varve thicknesses.

The ratio of chrysophyte scales to diatom valves (CS/DV) was below the long-term average in Zone A and gradually increased until 6.0 ka (Fig. 4.5). Values decreased to below average in subzone B2 between 6.0-4.7 ka, and increased very abruptly at the start of Zone C (3.6 ka). Following a slow decline, CS/DV values ultimately fell below the long-term average in subzone C2 between 0.86-0.50 ka.

The first three axes of a principal components analysis (PCA; Table 4.3) explained 30%, 10% and 8% of the variance in the diatom assemblages of Lac Noir (Fig. 4.5), respectively. The first axis had positive values in Zone A (11.1-8.0 ka), neutral to slightly decreasing values in Zone B (8.0-3.6 ka), and negative values in Zone C (3.6 ka – present). This axis was positively loaded on *Stephanodiscus hantzschii* Grunow 1880 and *S. minutulus*, as well as small fragilarioid and benthic taxa such as *S. construens*, *S. pinnata*, *Amphora pediculus* (Kützing) Grunow 1875, *Achnanthes* spp., *Navicula* spp., and *Nitzschia* spp. It was negatively loaded on *D. stelligera* and *T. flocculosa* str. IIIp. The second axis had negative values only in the lowermost (A1) and uppermost subzones (C2), and positive values in all other subzones. This axis was positively loaded on fragilarioid and benthic taxa, and negatively loaded on *Aulacoseira* species (*A. pusilla*,

tenella) and *F. tenera*. The third axis had positive values in subzone A1 (11.1-9.5 ka), negative values in subzones A2 and B1 (9.5-6.9 ka), and zero to slightly positive values throughout the rest of the record (6.9 ka-present). This axis was positively loaded on *S. minulutus* and *F. crotonensis*, and negatively loaded on *F. tenera*. The PCA scores (Fig. 4.4) show that the diatom assemblages varied more in the older sediments (subzones A1, A2, and B1), and were more closely related in the younger, recently deposited sediments (subzones B2, C1, and C2), as shown by the distribution of samples in ordination space.

4.4 Discussion

4.4.1 Deglaciation in southern Québec and Ontario

At Lac Noir, the oldest ^{14}C date was estimated to be 11600 cal. yr. BP, and sediments corresponding to this date were retrieved from clay material below the oldest varve (11.160 ka). In southern Québec and Ontario, deglaciation occurred at ~13000 cal. yr. BP (Richard 1994), followed closely by transgression of the Champlain Sea. Many lake basins in the region have evidence of organic sediments overlaying marine clay deposits, indicating a date of ~11600 cal. yr. BP to mark the recession of the Champlain Sea from the region (Rodrigues 1992). The varve chronology for Lac Noir, coupled with the lack of marine diatom species in the record, suggests that basal sediments from the core accumulated in freshwater conditions at the onset of the early Holocene, after complete evacuation of the Champlain Sea from the study area.

4.4.2 Diatom responses to Holocene climate variability

The Lac Noir diatom assemblages were divided into three major biostratigraphic zones (A-C; Fig. 4.5), which correspond broadly to Milankovitch-scale climate intervals (COHMAP Members 1988) and are closely aligned with the three-part division of the Holocene proposed by

Walker et al. (2012). Zone A (11.1-8.0 ka) is associated with cool and dry conditions inferred in the early Holocene, followed by rapid warming until 8200 cal. yr. BP (Walker et al. 2012). Zone B (8.0-3.6 ka) is considered as the mid-Holocene, which included several climate regimes such as a cool period from 8200-6000 cal. yr. BP, rapid warming at 6000 cal. yr. BP, and gradually increasing temperatures until 3000 cal. yr. BP (Walker et al. 2012; Viau et al. 2006). Finally, Zone C (3.6 ka to present) is associated with late-Holocene or "Neoglacial" cooling (Viau et al. 2006). Superimposed on long-term trends were abrupt, millennial-scale changes in the diatom record that again paralleled climate oscillations, including (i) a warming between 1200-800 cal. yr. BP termed the Medieval Warm Period, and (ii) a cool period from 360-160 cal. yr. BP known as the Little Ice Age (Viau et al. 2012; 2002).

Recent studies of long-term lake development report strong links between climate-driven vegetation dynamics, soil development and the succession of aquatic biota (Fritz and Anderson 2013; Fritz and Engstrom 1995). The early Holocene, for example, was relatively cool and dry in eastern North America (Walker et al. 2012; Viau et al. 2006), which resulted in lakes surrounded by sparse vegetation, soil instability, and high rates of erosion (Fuller 1997; Mott and Farley-Gill 1981). Inputs of mineral-rich sediments to lakes were greater in newly deglaciated regions, as indicated by elevated magnetic susceptibility recorded in Québec and Ontarian lake sediments (Friel et al. 2014; Fuller 1997) and at the base of the Lac Noir core (Fig. 4.5). Benthic diatom taxa, such as *S. pinnata*, *S. construens* and *S. leptostauron* var. *dubia*, are regarded as early colonizers (Bradshaw et al. 2000); they typically represent the initial ontogenetic phases of lakes (Lu 2014), and are common in low light environments with prolonged ice cover and shallow depths (Lavery et al. 2014; Puusepp and Kangur 2010). These benthic fragilarioid taxa dominated the early Holocene assemblages at Lac Noir (Fig. 4.3), reflecting the overall severe conditions inferred from pollen and climate reconstructions at this time (Viau et al. 2006; Fuller 1997; Mott and Farley-Gill

1981).

At Lac Noir, high nutrient availability resulting from enhanced erosion and run-off in the early Holocene (Fuller 1997) could be inferred from corresponding increases in taxa with high optima for total phosphorus, such as *A. ambigua, S. hantzschii,* and *S. minutulus* (Enache and Prairie 2002). Relative abundances of meso-eutrophic *F. crotonensis* and *A. formosa* (Pappas 2010) were high, and those of oligo-mesotrophic *D. stelligera* and *T. flocculosa* str. IIIp (Puusepp and Kangur 2010) were low. The proportion of chrysophytes relative to diatoms (CS/DV) is another indicator of lake trophic status (Smol 1985); low CS/DV in the early record (Fig. 4.5) supported an inference of high overall nutrient availability and primary productivity.

Temperatures increased during the early Holocene in eastern North America until ~8,200 cal. yr. BP (Viau et al. 2006). Diatom studies have shown positive correlations between rising temperatures, extended ice-free growing seasons, and shifts towards planktonic-dominated taxa (Rühland et al. 2015; Podritske and Gajewski 2007). At Lac Noir, a rapid decline in benthic taxa from 10.5-9.5 ka (Fig. 4.5) may be attributed to climate-driven changes in ice cover dynamics, but could also be related to increasing water levels as the lake moved out of the initial stages of development (Haig et al. 2013; Moos et al. 2009).

Between 8.9-8.4 ka there was a peak in magnetic susceptibility at Lac Noir (Fig. 4.5) that coincided with a period of melt water pulses and discharge events triggered by sudden collapses in ice domes over present-day Hudson Bay (Gregoire et al. 2012). These collapses caused rapid, century-scale periods of climate cooling at ~9.2 ka and ~8.2 ka, which affected many regions in the Northern Hemisphere (Walker et al. 2012; Flietmann et al. 2008; Alley and Agustsdottir 2005; Webb et al. 2003). At Lac Noir, the peak in magnetic susceptibility aligns with the earlier 9.2 ka event described by Fleitmann et al. (2008), and the mean July temperature curve (Viau et al. 2006; Fig. 4.5) showed a notable decline of ~0.2°C around this time. A slight offset in timing between

sedimentary changes in the core and this cooling could be attributed to a number of reasons; for example (i) an error in the varve chronology could account for a small time gap (several hundred years), and/or (ii) the loop sensor measuring magnetic susceptibility may have caused a displacement of the peak, as it takes an average across several centimeters. Nevertheless, climate cooling at around 9.2 ka appeared to have little to no effect on the overall aquatic ecosystem at Lac Noir. Only brief disappearances in *A. pusilla* at this time, and again at ~8.2 ka, indicate a potential link to vegetation changes in the catchment; for example, an increase in cold-tolerant species could have led to higher soil acidity, which is not optimal for *A. pusilla* (Denys et al. 2003). However, a local vegetation history may be needed to support this interpretation.

Transitioning to the mid-Holocene, climate conditions reached a point of relative stability in comparison to the early Holocene (Viau et al. 2006), promoting the growth of forests more resistant to large-scale fire disturbances in the region (Fuller 1997; Clark et al. 1996). Developed soils under a more closed forest canopy would have been more effective in binding phosphorous (Fritz and Anderson 2013), thereby limiting nutrient supplies to lakes as they were instead stored in the biomass and soils within catchment areas. In Québec and Ontarian lake studies, the mid-Holocene was characterized by gradual shifts in overall diatom flora, culminating in peak abundances of planktonic taxa (namely *D. stelligera*) by at least 4000 cal. yr. BP (Karmakar et al. 2015). A slow progression towards oligotrophic conditions signalled by increased planktonic taxa could be explained by less nutrients inputs from the more stable lake catchments. At Lac Noir, there were indications that the site followed a similar pattern of natural oligotrophication; CS/DV was slowly increasing, oligo-mesotrophic *T. flocculosa* str. IIIp was more abundant than in previous zones, and meso-eutrophic taxa (e.g. *S. minutulus, A. formosa,* and *F. crotonensis*) declined. An abrupt increase in *D. stelligera* occurred at 7.0 ka and was followed by a more gradual rise until ~4.0 ka, also consistent with other diatom records from Québec and Ontario.

At ~3200 cal. yr. BP, reduced summer insolation associated with the rapid onset of Neoglacial cooling (Viau et al. 2006) was linked to subtle changes in pollen and diatom records across eastern North America (Beck et al. 2016; Friel et al. 2014; Fuller 1997; Gajewski, 1988, 1987). Millennial-scale oscillations in temperature during Neoglaciation reflected a "saw-tooth structure", where rapid warming was followed by steadily cooling periods (Viau et al. 2006). At Lac Noir, the sudden declines in taxa typically associated with warmer temperatures (e.g. *D. stelligera* and *F. tenera*; Rühland et al. 2003) may have indicated a pronounced response to cooling beginning at ~3.6 ka. Fluctuations in *D. stelligera* seem to correlate with millennial-scale changes in temperature, possibly indicating a more direct relationship to climate; however, the ecological preferences of this species are still not well understood (Saros and Anderson 2015).

Paleo-records and associated climate reconstructions often infer increased moisture during Neoglaciation (Beck et al. 2016; Viau and Gajewski 2008). This could have effects on the sediment accumulation rates (SAR) of lakes; for example, some studies suggest that lower SAR accompanied periods of cooling and/or drought (Adams and Finkelstein 2010; Booth et al. 2005), and increases in SAR were recorded during periods of higher precipitation, erosion and lake productivity (Blair et al. 2015; O'Sullivan 1983). At Lac Noir, varve thicknesses (or SAR; Fig. 4.5) were low in the early and mid-Holocene, but increased after 3.0 ka when temperatures were cooling. This, coupled with gradual decreases in CS/DV, could indicate enhanced erosion in the catchment, which may have led to nutrient-enrichment and a resultant shift towards more eutrophic lake conditions (Blair et al. 2015).

During the past ~2.0 ka, millennial-scale climate variations had significant impacts on aquatic ecosystems in the study area (Cooper et al. 2016; Neil and Gajewski 2017). Pollen-based climate reconstructions showed that the Medieval Warm Period (MWP; 1.2-0.8 ka) was 0-1.5°C warmer than the Little Ice Age (LIA; 0.36-0.16 ka), although both periods were cooler than present

(Lafontaine-Boyer and Gajewski 2014; Paquette and Gajewski 2013; Viau et al., 2012; Gajewski 1988). In relation to the full Holocene record, there were subtle indications at Lac Noir that regional aridity during the MWP extended east towards the southern Québec/Ontario border. Benthic taxa (e.g. *S. pinnata*) increased at 1.0 ka while more prominent planktonic taxa (e.g. *D. stelligera*) decreased, possibly in response to reduced effective moisture and/or lower lake-levels (Haig et al. 2003). Varve thicknesses (or SAR) declined immediately prior to 1.0 ka, concurrent with the onset of the MWP and also potentially indicative of drier conditions (Booth et al. 2005). Previous studies of the lake and surrounding region on a shorter time-scale (the last 1,200 years) found little evidence of regional aridity in the MWP (Neil and Gajewski 2017; Lafontaine-Boyer and Gajewski 2014; Paquette and Gajewski 2013). This suggests that a long-term perspective may perhaps be needed to detect more subtle responses of pollen and diatoms to climate.

During a peak of cooler temperatures in the LIA, the Lac Noir record showed a decrease in *T. flocculosa* str. IIIp and CS/DV, and increases in *F. crotonensis* and *A. formosa*. This may have signalled nutrient-enrichment resulting from enhanced erosion in the catchment during this period (Neil and Gajewski, subm.; Puusepp and Kangur 2010; Pappas 2010; Köster et al. 2005; Wolin and Stoermer 2005; Smol 1985). Towards the end of the LIA, diatom responses to climate were slightly obscured by Euro-Canadian settlement and subsequent impacts of land clearance in southern Québec (Smith 1967). Nevertheless, a brief peak in *S. minutulus* to percentages only seen during the early Holocene was attributed to increased human activity in the catchment (Neil and Gajewski, subm.; Finney et al. 2002).

4.2.3 Influences of vegetation on watershed-lake interactions

Terrestrial ecosystems and associated run-off from soils not only influence the type and amount of materials transferred to lakes, but effectively alter lake water chemistry and ultimately

aquatic organisms (Fritz and Anderson 2013). Changes to forests in lake catchments typically represent a more direct influence on lake ecosystems rather than does the reconstructed climate, and a history of these changes is thus essential for more detailed interpretations of fossil diatom assemblages in paleolimnological studies. Pollen records from some sites in southern Québec and Ontario, including Lac Brûlé, Lac Noir, High Lake, Graham Lake, Ramsay Lake, and Pink Lake (Lafontaine-Boyer and Gajewski 2014; Paquette and Gajewski 2013; Fuller 1997; Mott and Farley-Gill 1981), provide a general context of regional-scale vegetation change for the study area, and are discussed below as they relate to the Lac Noir diatom record for the Holocene.

Vegetation at the beginning of the early Holocene was mainly comprised of herbaceous or shrub tundra along with trees such as *Picea glauca* and *Thuja-Juniperus* (Fuller 1997), as they were able to establish in minerogenic sediments following ice retreat (Perren et al. 2012). Acidic soils in this coniferous woodland may have resulted in a lower pH of lakes within the region (Puusepp and Kangur 2010; Huvane and Whitehead 1996), which would have affected aquatic community structure. Taylor et al. (1987) suggest that there is a near total absence of *Cyclotella* (including *D. stelligera*) in lake waters below pH 5.5; the low relative abundances of this genus in the early Lac Noir record could therefore imply a response to higher lake acidity during this time. At 9.5 ka, a rapid increase in *A. pusilla* signalled a shift to a more alkaline environment with greater turbidity (Karmakar et al. 2015; Denys et al. 2003), synchronous with a regional decline in *P. glauca* and associated with a warming of 3-4°C (Viau et al. 2006; Fuller 1997; Mott and Farley-Gill 1981).

Fuller (1997) suggests that greater fire frequency and/or intensity in the early Holocene may have stimulated the initial establishment of a continuous forest cover after 9500 cal. yr. BP, comprised of early successional taxa such as *Pinus banksiana, P. resinosa*, *Betula* and *Pinus strobus*. The presence of several darker bands of sediment between 11.1-9.0 ka followed by an

extended period during which they were absent (~6500 years), as well as rapidly decreasing magnetic susceptibility, could indicate more organic-rich inputs to the lake as vegetation and soils developed and stabilized in the catchment.

Widespread climate cooling at 9200 and 8200 cal. yr. BP (Flietmann et al. 2008; Alley and Agustsdottir 2005) affected forests across multiple sites in eastern North America (Shuman et al. 2002). For example, brief expansions of more cold-tolerant species, such as *P. banksiana or P. resinosa* in southern Ontario (Fuller 1997) and *Picea* and *Abies* in Québec (Lavoie and Filion 2001), were indicative of cooler climate conditions. Disappearances of *A. pusilla* at Lac Noir coinciding roughly with the 9.2 and 8.2 ka events signalled a brief lowering of lake pH (Denys et al. 2003), potentially linked to an influx of coniferous trees in the catchment and subsequent acidic run-off (Huvane and Whitehead 1996).

Although the composition of the forests changed rapidly throughout the late-glacial and early Holocene, they reached a point of relative stability by ~7000 cal. yr. BP (Williams et al. 2004). At this time, *Pinus* was being gradually replaced by shade tolerant taxa such as *Tsuga, Fagus,* and *Betula* (Webb III et al. 1993; Fuller 1997), affecting soil composition in the region. Forests comprised of *Tsuga* were rich in humic acids (Engstrom and Wright 1984), potentially leading to increased acidity in proximate lakes. A slight increase in dystrophic *A. tenella* signaled inputs of dissolved organic carbon (DOC) and/or a change in the water color at Lac Noir, potentially from leaching of humic-rich soils (Huvane and Whitehead 1996). Decreased pH was also reflected by a decline in *A. pusilla* (Denys et al. 2003), consistent with expansion of *Tsuga* populations in the region (Fuller 1997).

At ~5500 cal. yr. BP an abrupt and widespread decline in *Tsuga* occurred across many sites in eastern North America; hypotheses as to the cause of such an event include a widespread pathogen outbreak or reduced moisture availability (Davis 1981; Foster et al. 2006; Webb et al.

2003; Fuller 1997). At Wishart Lake (East of Lake Superior), increased abundances of *D. stelligera* and *T. flocculosa* str. IIIp at ~5000 cal. yr. BP were associated with nutrient enrichment following the decline of *Tsuga*-dominated forests, which were replaced with more broad-leaved species (Beck et al. 2016). Similarly at Lac Noir, a shift towards eutrophic conditions is inferred between 6.0-5.0 ka (i.e. low CS/DV values), and minor increases in benthic taxa from ~5.5 to 5.0 ka may indicate a brief dry period (Haig et al. 2013).

Tsuga percentages began to recover between 3200-3700 cal. yr. BP along with increases in *Alnus* and *Fagus* (Fuller 1997; Mott and Farley-Gill 1981), marking the onset of Neoglacial cooling (Viau et al. 2006) in southern Québec and Ontario. Changes in *Tsuga* were once again linked to an increase in *A. tenella* at Lac Noir, suggesting that this species may have been fairly responsive to inputs of humic-rich soils from the catchment. Studies generally reveal subtle, less-pronounced responses of terrestrial and aquatic biota to cooler and wetter conditions inferred during Neoglaciation (Friel et al. 2014; Fuller 1997; Magnuson et al. 1997). However, the abrupt centennial-scale changes recorded in the Lac Noir diatom assemblages starting at 3.6 ka suggest that the lake responded quickly at first to deteriorating climate conditions. A local history of vegetation may be needed to ascertain if changes in the catchment affected the diatoms in the lake directly, or if they were instead responding to a regional signal in climate.

During the MWP, *Tsuga* and *Fagus* percentages decreased while deciduous hardwood taxa increased (e.g. *Betula, P. strobus* and *Alnus*). Deterioration of the climate at the peak of the LIA led to cooler conditions, which were associated with increases in certain deciduous species characteristic of disturbance (*Betula* and *Alnus*; Paquette and Gajewski 2013). The change in leaf-litter quality associated with these changes in the catchment likely resulted in more nutrient-rich soils (Beck et al. 2016; St. Jacques et al. 2000); at Lac Noir, increased abundances of *S. pinnata* and *F. crotonensis*, as well as a decline in CS/DV occurred between ~1.0 ka to present, supporting

an inference of increased nutrient inputs to the lake.

The influence of Euro-Canadian settlement and human-induced impacts on the region at ~0.15 ka was marked by an increase in herbaceous pollen, most notably *Ambrosia* (Lafontaine-Boyer and Gajewski 2014; Paquette and Gajewski 2013). Diatoms responded to human activity in the region as well; for example, a brief and significant increase in *S. minutulus* and *A. minutissimum* was likely due to an influx of nitrogen and DOC following land clearance and logging (Neil and Gajewski 2017; Pappas 2010; Vitousek et al. 1997). Overall, the Lac Noir record shows a well-established and continuous connection between vegetation dynamics and diatom responses for the entire Holocene, suggesting that these proxies should be observed together when possible in future paleolimnological studies (Puusepp and Kangur 2010).

4.4.4 Thermal stratification and/or mixing in varved lakes

In addition to climate and vegetation influences, other factors such as wind activity have been shown to cause changes to lake circulation and stratification, which consequently affect water chemistry and diatom flora (Haussmann 2011). While the preservation of varves in a lake typically signifies an absence of wind-driven turbulence within the water column, studies have shown that stratification and/or mixing can be inferred in lakes with continuous, undisturbed varved sediments (Ekdahl et al. 2007; Bradbury et al. 2002; Dean 2002; O'Sullivan 1983). For example, Baier et al. (2004) used the diatom record from a varved sediment core to infer dynamic lake mixing in the early- to mid-Holocene between 9000-6000 cal. yr. BP, which they attributed to abrupt seasonal temperatures differences (e.g. cold winters, stormy springs, warm summers). Similarly at Lac Noir, increased abundances of *A. pusilla* and other *Aulacoseira* species between ~9.5-6.0 ka (Fig. 4.3; subzone A2-B1) indicated enhanced mixing, as these diatoms are heavily silicified valves and require relatively turbulent conditions to transport them to the photic zone (Karmakar et al. 2015;

Harris et al. 2006). In contrast, a rapid decline in *A. pusilla* beginning at ~7.0 ka (subzone B2), as well as increases in *D. stelligera* and *F. tenera*, signalled extended thermal stratification of the lake (Michelutti et al. 2015; Lavery et al. 2014). Stratification is typically associated with warmer and more stable climatic conditions (Rühland et al. 2003) which characterized the mid-Holocene (Viau et al. 2006). Also seen in the mid-Holocene was an increase in CS/DV to values above the long-term average, possibly attributed to the more competitive nature of chrysophytes in thermally stratified waters (Sandgen 1988).

4.5 Conclusions

This study demonstrates that a long-term perspective of ecosystem change throughout the Holocene is particularly valuable, and provides added data to inform previous work in the region focusing on shorter temporal scales (e.g. the past 2.0 ka). Sparse vegetation inferred in the early Holocene (Fuller 1997) was associated with early ontogenetic phases at Lac Noir, fostering soil instability and enhanced erosion; benthic alkaphilous diatoms with high tolerances for poor conditions (Puusepp and Kangur 2010) thrived in this post-glacial environment. Temperature increases during the mid-Holocene (Viau et al. 2006) allowed for the stabilization of forests and soils in the region (Mott and Farley-Gill 1981), which led to increased stratification and gradual oligotrophication of Lac Noir. The abrupt onset of Neoglacial cooling then triggered changes in diatom assemblages, such as a rapid and brief decline in *D. stelligera* more typically associated with warming (Rühland et al. 2008). Wet conditions during Neoglaciation (Beck et al. 2016) also led to increased varve thicknesses and higher inferred nutrient inputs to the lake. Millennial-scale changes in temperature associated with the Medieval Warm Period and the Little Ice Age favoured deciduous, broad-leaved taxa in the catchment, resulting in a shift towards eutrophic lake conditions. Finally, increases in human activities within the catchment associated with European

settlement showed distinct influences on diatom communities at Lac Noir.

Climate variations during the Holocene were largely driven by orbital-scale solar forcings (COHMAP Members 1988) and these affected the broad-scale evolution of the vegetation in the region. This in turn had a significant influence on the chemistry and aquatic biota at Lac Noir. Analysis of vegetation in lake catchments and at regional-scales should therefore be considered as essential for interpretations of subfossil diatom assemblages, and overall watershed dynamics should be taken into account for future planning and management of lakes within the region.

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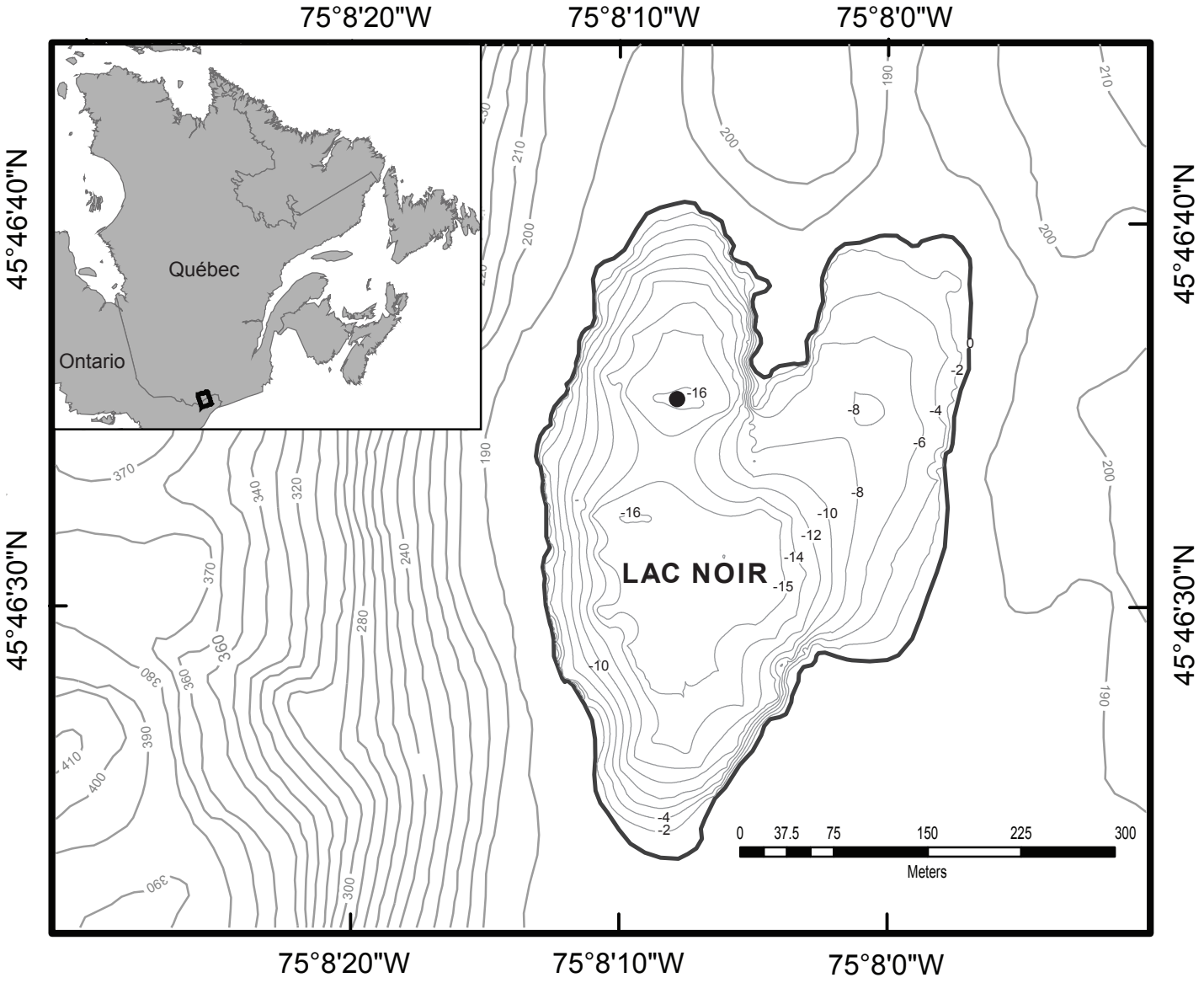


Figure 4.1: Map showing the location, local topography, and bathymetry of Lac Noir, southwestern Québec. Cores were collected from the deepest part of the lake (~16 m; marked by circle) in 2012 CE

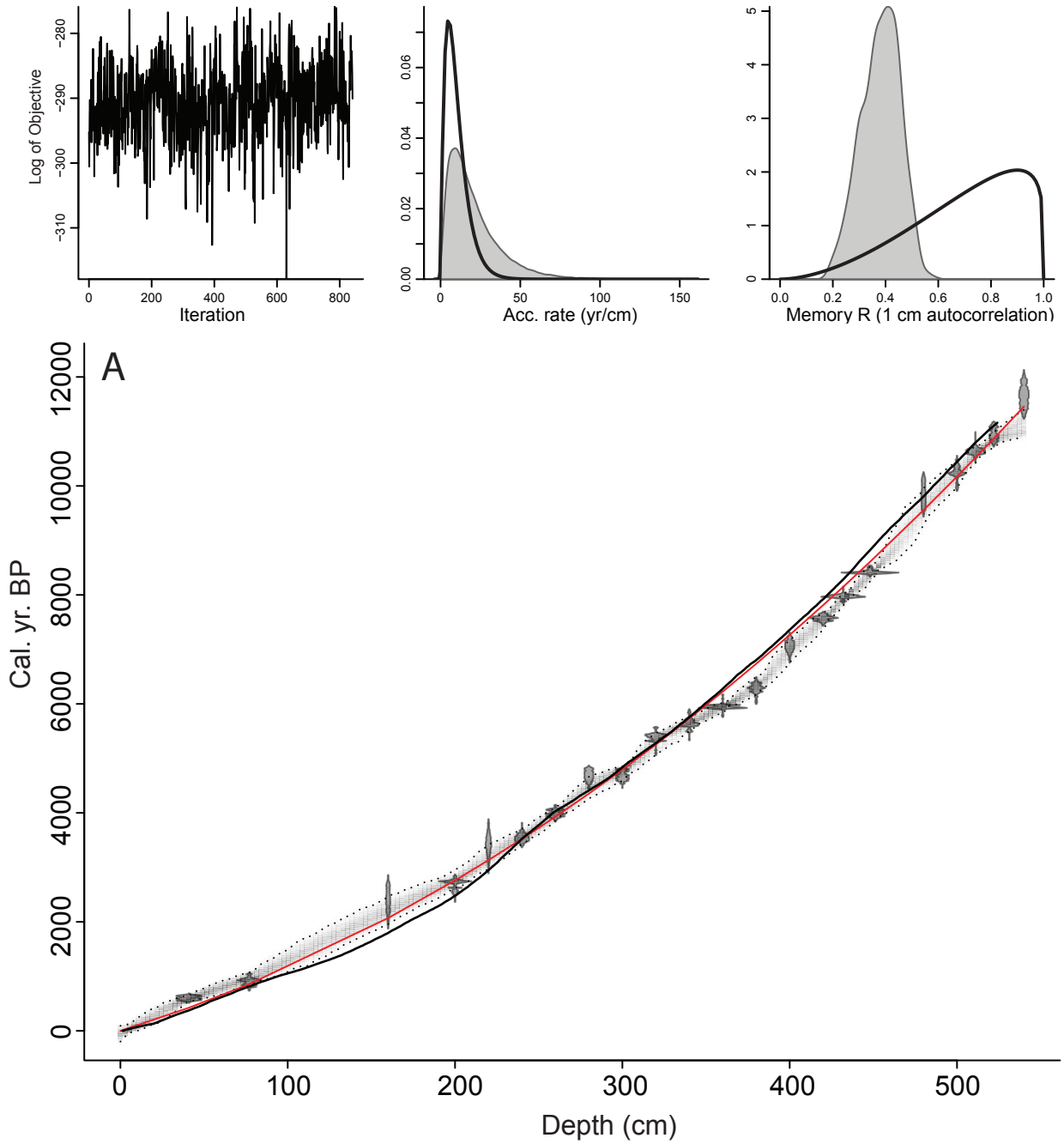


Figure 4.2: A) Varve-based age-depth model for the Lac Noir core (solid black line). An independent age-depth model generated using R software package "BACON" is shown; grey symbols represent the twenty-two AMS 14C dates and their probability distributions, the grey shaded area indicates iterations of the model outlined by a 95% confidence interval (dotted grey lines). The solid red line shows a 2nd order polynomial regression fit through the calibrated 14C dates. The inset graphs at the top show; (left) the number of MCMC iterations used to generate the grey shaded area of the BACON model; (centre) The prior and posterior distributions of accumulation rates for the BACON model; (right) The prior and posterior distributions of the autocorrelation in accumulation rates (memory) for the BACON model.

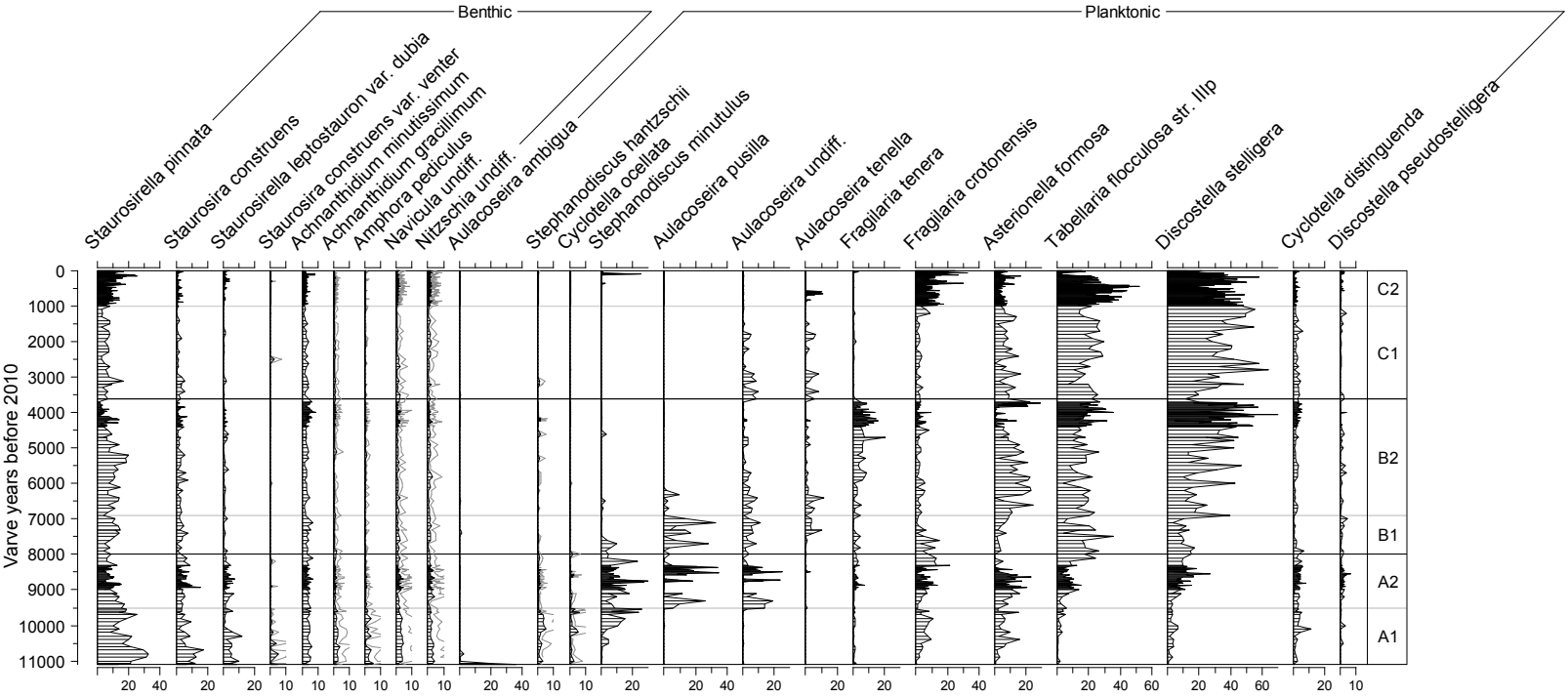


Figure 4.3: Diatom relative abundances of major taxa (>4% relative abundance in at least one sample) from Lac Noir, southwestern Québec. Sampling intervals are shown by horizontal black lines in each profile. A 3x exaggeration (grey line) is applied to less abundant taxa

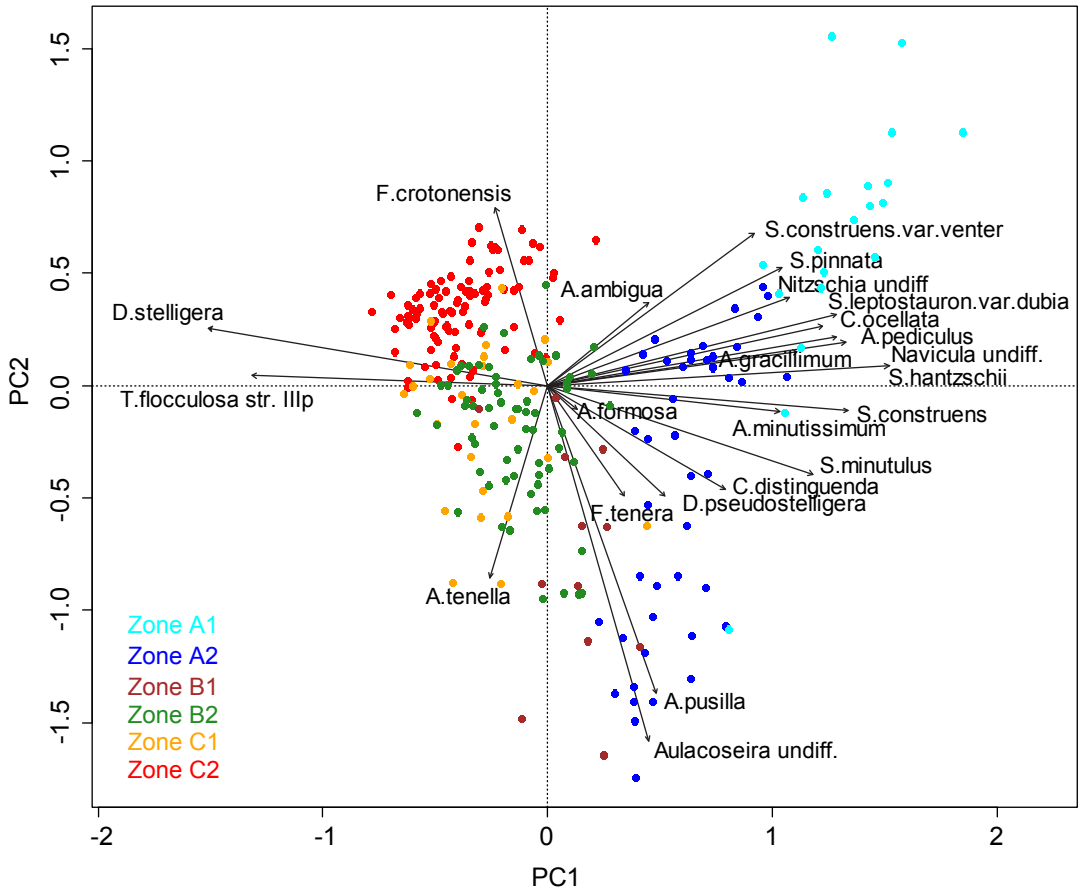


Figure 4.4: Biplot of the first two axes of a principal components analysis (PCA) on fossil diatom assemblages from Lac Noir. Dots represent the sample scores, and are colored based on the biostratigraphic zones defined by the PCA

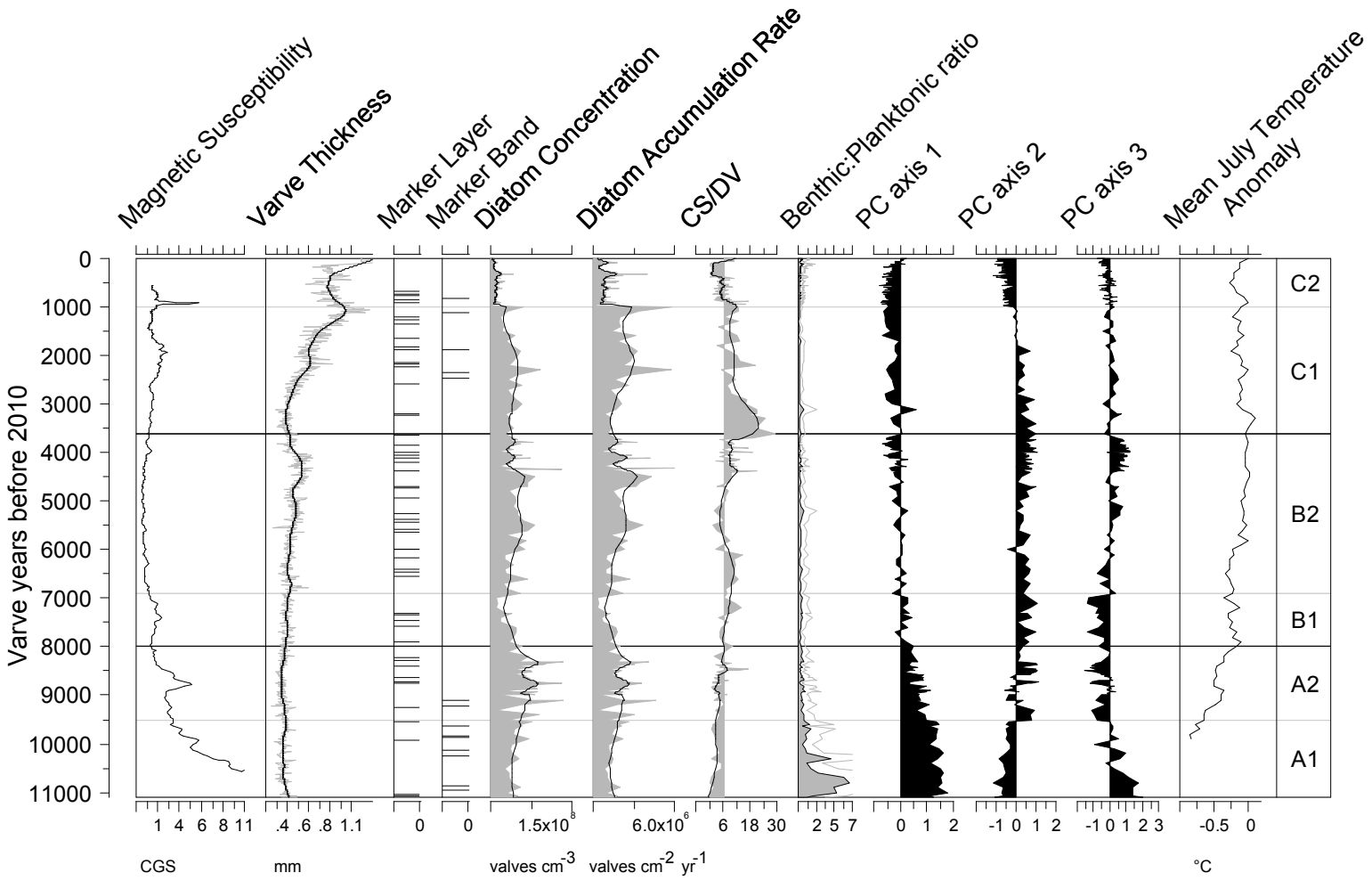


Figure 4.5: Sedimentary and diatom data, and PCA scores from the Lac Noir core. Data from the most recent sediments (subzone C2) was obtained from previous studies (Neil and Gajewski [*in press*]; Paquette and Gajewski 2013). Magnetic susceptibility (truncated at the bottom) and varve thickness curves are composites based on average values from two overlapping core sequences. CS/DV is the ratio of scaled chrysophytes relative to diatom valves. Mean July temperature data was obtained from Viau et al. (2006), and truncated at 10.0 ka to better illustrate variability in the mid- to late Holocene

Table 4.1: Number of varve couplets counted on two different core sequences from Lac Noir. Replicated counts (by two researchers) and percentage errors are provided for individual drives, and between distinct marker beds. The chronology of drive 0 (0-0.91 m) was developed by Paquette and Gajewski (2013). Where sections delineated by marker beds overlapped in the two core sequences, four counts were completed (one per researcher and one per core)

Drive #	Varve Count #1	Varve Count #2	Interval	% Error
*0	-	-	-	2.3
6	710	761	-51	6.7
1	898	880	18	2.0
7	812	800	12	1.5
2	1469	1540	-71	4.6
10	1835	1760	75	4.3
Drive - Marker Bed ID				
8-A to 8-B	159	163	-4	2.5
8-H to 8-I	189	194	-7	3.6
3-A to 3-B	192	196		
3-I to 3-J	173	174	-6	3.4
9-A to 9-B	179	175		
9-G to 9-H	121	121	-5	4.1
4-A to 4-B	124	126		
4-G to 4-H	219	222	-3	1.4
5-BB to 5-DD	318	312	6	1.9

Table 4.2: Radiocarbon dates and calibrated ages BP (before 1950 CE) from Lac Noir, southwestern Québec. The two youngest dates (LN-41 and LN-77) were obtained from Paquette and Gajewski (2013). Samples are based on plant material.

Sample ID	Laboratory no.	Depth (cm)	Conventional radiocarbon age (BP)	Calibrated 14C age ranges (1σ probability distribution)
LN-41	Beta - 276987	41-42	580 ± 40	540-562 (33.0%) 593-637 (67.0%)
LN-77	Beta - 276988	77-78	980 ± 40	799-813 (13.0%) 826-866 (43.0%) 1901-924 (43.0%)
KLN DR7 160-163	UOC-5286	160-163	2346 ± 168	2770-1989 (95.4%)
KLN DR2 200-203	UOC-5287	200-203	2599 ± 43	2790-2692 (78.6%) 2636-2614 (4.2%) 2594-2466 (12.7%)
KLN DR2 220-223	UOC-5288	220-223	3201 ± 141	3731-3063 (93.3%)
KLN DR2 240-242	UOC-5289	240-242	3310 ± 51	3644-3445 (91.4%)
KLN DR2 260-261	UOC-5290	260-261	3660 ± 30	4085-3899 (95.4%)
KLN DR2 280-283	UOC-5291	280-283	4159 ± 64	4844-4524 (95.4%)
KLN DR2 300-302	UOC-5292	300-302	4134 ± 26	4821-4568 (95.0%)
KLN DR2 320-322	UOC-5293	320-322	4639 ± 38	5469-5302 (95.4%)
KLN DR2 340-341	UOC-5294	340-341	4894 ± 58	5748-5577 (87.9%) 5534-5480 (6.9%)
KLN DR2 360-361	UOC-5295	360-361	5183 ± 25	5990-5907 (95.4%)
KLN DR2 380-382	UOC-5296	380-382	5492 ± 63	6414-6180 (94.2%)
KLN DR2 400-403	UOC-5297	400-403	6170 ± 71	7251-6896 (95.4%)
KLN DR2 420-421	UOC-5298	420-421	6708 ± 43	7660-7500 (95.4%)
KLN DR2 432-433	UOC-5299	432-433	7149 ± 27	8014-7936 (95.4%)
KLN DR2 448-449	UOC-5300	448-449	7621 ± 27	8450-8379 (95.4%)
KLN DR2 480-482	UOC-5301	480-482	8769 ± 155	10214-9526 (95.4%)
KLN DR2 500-502	UOC-5302	500-502	9078 ± 65	10434-10152 (93.2%)
KLN DR2 511-512	UOC-5303	511-512	9404 ± 33	10728-10555 (95.4%)
KLN DR2 522-524	UOC-5304	522-524	9610 ± 35	11159-11050 (24.5%) 11039-10775 (70.9%)
KLN DR2 540-543	UOC-5305	540-543	10080 ± 82	11997-11315 (95.4%)

Table 4.3: Taxon loadings and explained variance (eigenvalues) of a principal components analysis performed on the diatom assemblages of the Lac Noir core (Fig 4.4)

	Component		
Taxon	1	2	3
Aulacoseira ambigua	0.45	0.37	-0.27
Aulacoseira pusilla	0.48	-1.37	0.58
Aulacoseira tenella	-0.26	-0.85	0.01
Aulacoseira undifferentiated	0.45	-1.58	0.24
Cyclotella distinguenda	0.79	-0.46	-0.73
Cyclotella ocellata	1.22	0.26	0.14
Discostella pseudostelligera	0.52	-0.49	0.74
Discostella stelligera	-1.51	0.26	-0.37
Stephanodiscus hantzschii	1.52	0.09	0.04
Stephanodiscus minutulus	1.18	-0.39	0.66
Achnanthidium gracillimum	1.11	0.15	-0.47
Achnanthidium minutissimum	1.03	-0.12	-0.44
Amphora pediculus	1.29	0.22	-0.48
Asterionella formosa	0.13	-0.11	0.33
Fragilaria crotonensis	-0.23	0.79	1.25
Fragilaria tenera	0.34	-0.49	-1.21
Navicula undifferentiated	1.33	0.19	-0.10
Nitzschia undifferentiated	1.08	0.39	0.07
Staurosira construens	1.34	-0.11	-0.23
Staurosira construens var. venter	0.92	0.68	-0.13
Staurosirella leptostauron var. dubia	1.29	0.32	0.11
Staurosirella pinnata	1.04	0.52	0.45
Tabellaria flocculosa str. IIIp	-1.32	0.04	-0.37
Eigenvalues	0.30	0.10	0.08

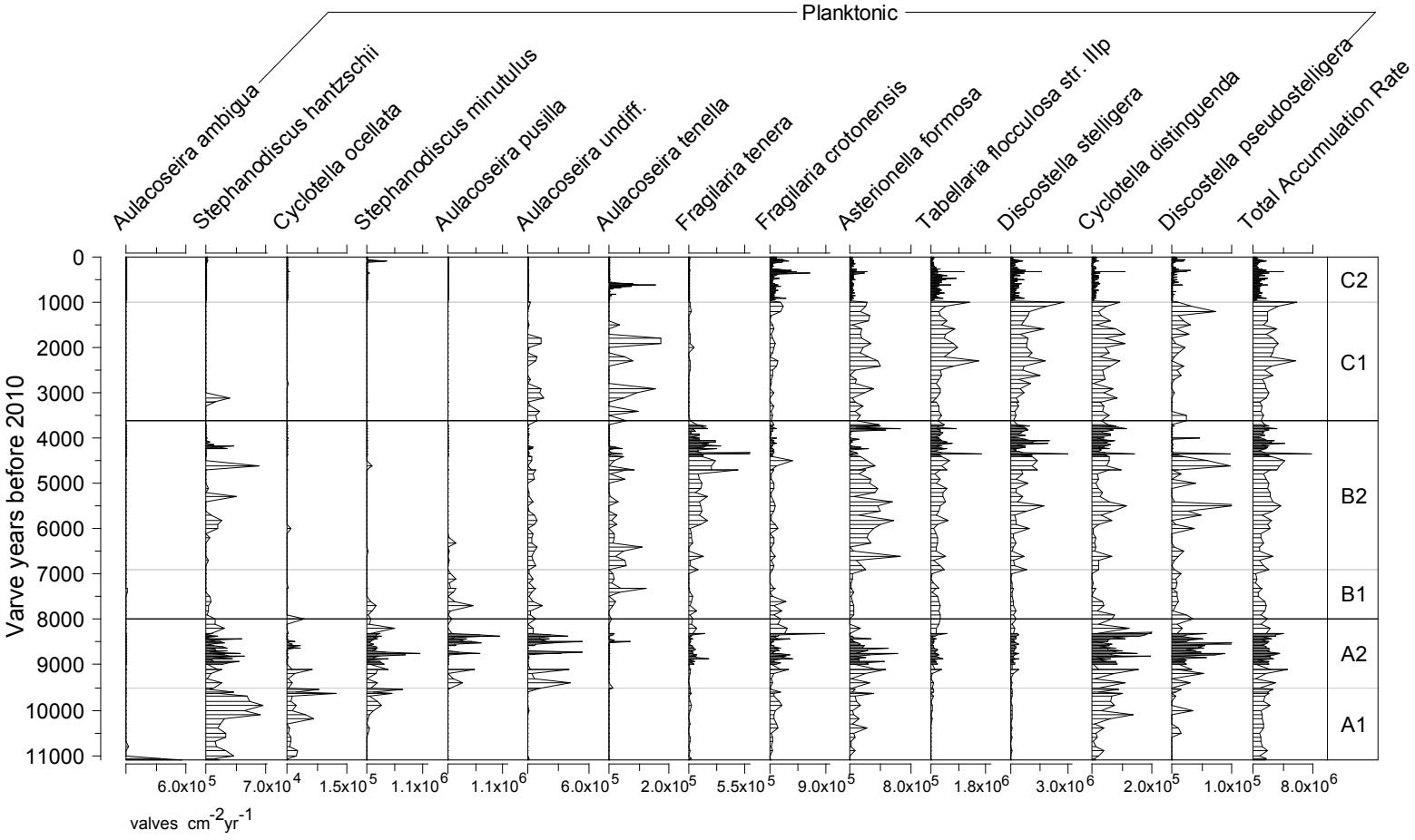


Figure S4.1: Diatom accumulation rates of major planktonic diatom taxa (>4% relative abundance in at least one sample) from Lac Noir

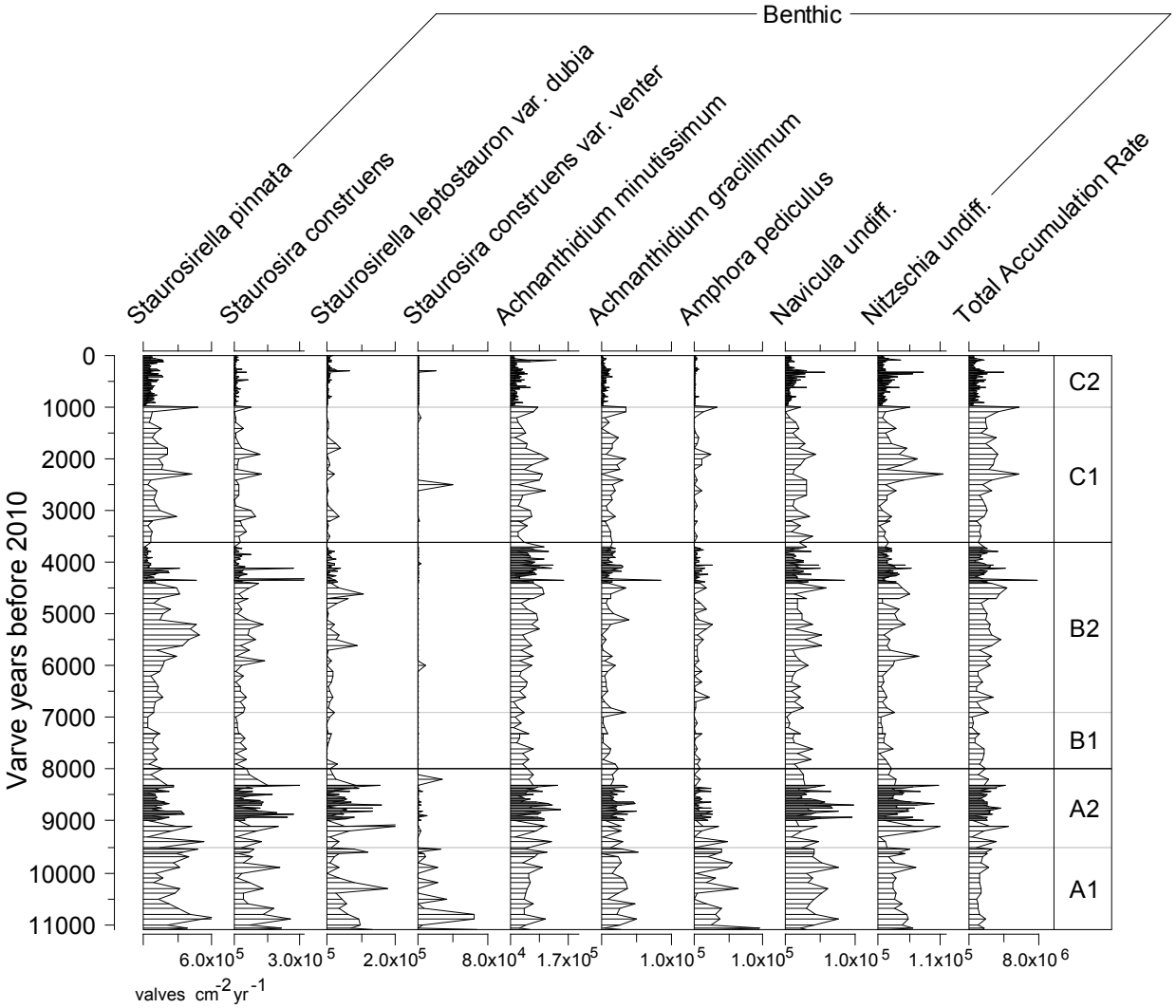


Figure S4.1: Diatom accumulation rates of major planktonic diatom taxa (>4% relative abundance in at least one sample) from Lac Noir

CHAPTER FIVE

Summary, research limitations, and future directions

5.1 Summary

The high-resolution paleo-records spanning ~1200 years at Lac Brûlé and ~11000 years at Lac Noir, southwestern Québec, revealed marked shifts in diatom community composition that were largely attributed to catchment-related processes rather than direct consequences of climate variability. Terrestrial ecosystems track both short- and long-term variations in temperature and precipitation (Lafontaine-Boyer and Gajewski 2014; Paquette and Gajewski 2013; Shuman et al. 2005; Williams et al. 2002; Fuller 1997; Gajewski 1988), however aquatic biota seem to respond more readily to hydrochemistry changes in lake catchments (Fritz and Anderson 2013; Anderson 2000; Engstrom and Hansen 1985). The general findings of this study are consistent with several multi-proxy records in eastern North America that show strong associations between climate, vegetation succession and composition, soil characteristics and aquatic biota over the Holocene (Puusepp and Kangur 2010; Moos et al. 2009; Huvane and Whitehead 1996; Jones et al. 1984).

Objective 1: Reconstruct a high-temporal resolution history of diatom responses to climate variability and catchment- related processes

At Lac Brûlé, pollen (terrestrial) and cladocera (zooplankton) records were integrated along with analyses of fossil diatom assemblages by using generalized additive models (GAMs), which hierarchize the contributions through time of forcing variables (such as climate interpreted from pollen assemblages) on a specific predictor variable (Alric et al. 2013; Simpson and Anderson 2009), e.g. diatoms trends in this study. Lac Brûlé diatom communities were significantly influenced by watershed disturbances, most notably as a result of (i) a local fire at 1345 CE, (ii)

the regional impacts of Euro-Canadians during the 19th century, and (iii) operations at the Wallingford-Back Mine from 1924-1972 CE. Each of these events influenced the surrounding forest (Lafontaine-Boyer and Gajewski 2014), which in turn altered the lake chemistry. These disturbances were further associated with inferred nutrient increases (e.g. from charcoal, dissolved organic carbon inputs, and nitrogen mobilization), reflected in changes to the overall composition of diatom flora within the lake.

Immediately following a fire at 1345 CE, for example, there was an abrupt decline of hemlock (*Tsuga*) in the catchment, and large influxes of charcoal were recorded in the Lac Brûlé sediments (Lafontaine-Boyer and Gajewski 2014). This led to higher nutrient inputs and reduced light availability (Philibert et al. 2003), which favoured diatom taxa with tolerances for a wider range of conditions (e.g. *Fragilaria crotonensis*) (Anderson et al. 2008). Littoral cladoceran taxa also increased as a result of high nutrient concentrations following the fire (Cooper et al. 2016); however, cladoceran communities generally showed less distinct shifts in response to disturbance events, unlike those seen in the pollen and diatom records.

Human-induced disturbances were also a large contributing factor to diatom trends. Land clearance and the burning of forests following Euro-Canadian settlement (Jonhstone et al. 2016) may have triggered mobilization of nitrogen compounds within lake catchment areas (Vitousek et al. 1997), which resulted in higher abundances of diatom taxa with high optima for nitrogen (e.g. *Cyclotella michiganiana* and *Achnanthidium minutissimum* at Lac Brûlé) (Neil and Gajewski 2017; Wolin and Stoermer 2005). As well, a nearby mine was responsible for a brief period of increased nutrients between 1924-1972 CE at Lac Brûlé, indicated by a rise in *Fragilaria crotonensis* and *Asterionella formosa* (Neil and Gajewski 2017; Köster et al. 2005; Wolin and Stoermer 2005), as well as the cladoceran species *Bosmina longirostris* (Cooper et al. 2016).

The record of biotic responses at Lac Brûlé is particularly relevant to our understanding of

the risks associated with potentially increased and long-lasting impacts of disturbances on lake ecosystem health in the future. For example, terrestrial and aquatic biota responded abruptly and significantly to the local fire at 1345 CE, and studies indicate that a return to pre-disturbance conditions following such an event is typically on the order of less than ten years (Paterson et al. 2002). However, Lafontaine-Boyer and Gajewski (2014) suggest that the inability of hemlock to regenerate following the fire was perhaps due to worsening conditions as the climate transitioned into the Little Ice Age. The combined interactions of disturbances and rapid changes in climate can thus lead to significant and persistent effects (Johnstone et al. 2016) in terrestrial ecosystems, but also by extension to aquatic biota within surrounding lakes.

While disturbances in the catchment were perhaps the dominant forcing responsible for governing diatom communities at Lac Brûlé, there was a strong climate signal recorded in the responses of several paleo-indicators at this site, and reflected again in the GAMs. Pollen-based climate reconstructions indicated a period of higher temperatures from ~800-1300 CE associated with the Medieval Warm Period (MWP), during which time forests were dominated by hemlock, white pine, maple, beech, and birch (Lafontaine-Boyer and Gajewski 2014; Gajewski 1988). The Lac Brûlé record showed high relative abundances of *Tabellaria flocculosa* str. IIIp and *Bosmina longirostris,* and a larger ratio of chrysophytes to diatoms during this period; this was indicative of relatively stable and oligotrophic lake conditions (Cooper et al. 2016; Puusepp and Kangur 2010; Smol 1985).

The onset of the Little Ice Age (LIA) at ~1450 CE is well documented in studies across eastern North America (Viau et al. 2012, 2006; Mann et al. 2008; Gajewski 1988). At Lac Brûlé, a shift to regionally cool temperatures was indicated by declines in beech and other hardwoods, as well as increases in white pine, spruce, and alder; this also occurred during a time when the forest may have still been recovering from the preceding fire event at 1345 CE (Lafontaine-Boyer and

Gajewski 2014). During the LIA, Lac Brûlé diatom assemblages showed an increase in *Discostella stelligera*, and a decrease in *Tabellaria flocculosa* str. IIIp, which was interpreted as a response to nutrient enrichment originating from the lake catchment area (Neil and Gajewski 2017; Saros et al. 2015; Fritz and Anderson 2013). Studies of Arctic and temperate lakes have reported increases in *Cyclotella* species (including *Discostella stelligera*) in response to recent global warming and thermal stratification Rühland et al. 2015; Perren et al. 2009); however, results of this study suggest other mechanisms may be influencing species within this genus. This has implications regarding the use of *Cyclotella* as indicators of warming trends, as our study shows an equally significant rise in *Discostella stelligera* during a well-established period of cooling climatic conditions.

Objective 2: Compare paleo-records of two proximate lakes in southwestern Québec to identify differences between regional- and local-scale responses in diatom communities

Diatom assemblages at Lac Noir were compared not only to other proxy-indicators from the lake, but also to paleo-records from the nearby Lac Brûlé. As previously discussed, aquatic biota from Lac Brûlé were significantly influenced by local disturbances in the lake's catchment area; this chapter was therefore relevant to understanding how diatoms from Lac Noir reacted to late Holocene climate changes in the absence of major disturbance events. Principal components analysis and GAMs revealed that Lac Noir diatom assemblages were again closely aligned with the vegetation composition of the surrounding catchment, primarily driven by Holocene climate variability.

Much like those from Lac Brûlé, the diatom assemblages of Lac Noir indicated relatively stable and oligotrophic lake conditions throughout the Medieval Warm Period (MWP); however, responses to the onset of the Little Ice Age (LIA) seemed to occur much less abruptly at the latter

site. The Lac Noir pollen record showed slight increases in cool-adapted taxa (e.g. white pine and spruce) at ~1450 CE, however pronounced cooling at the peak of the LIA (~1630 CE) was associated with abrupt increases in white pine and alder, as well as corresponding declines in both hemlock and beech (Paquette and Gajewski 2013). In the absence of a local fire at Lac Noir, the greatest changes in forest composition therefore occurred at the peak of the LIA, when temperatures had reached their lowest point in the last 1000-years (Paquette and Gajewski 2013).

Changes in the Lac Noir catchment during the peak of the LIA had significant influences on diatom assemblages within the lake; for example, *Asterionella formosa, Staurosirella pinnata* and *Fragilaria crotonensis* increased abruptly, while *Tabellaria flocculosa* str. IIIp percentages, as well as the ratio of chrysophytes to diatoms, declined. These changes signalled an overall shift towards a more productive lake ecosystem with higher nutrient availability (Puusepp and Kangur 2010; Pappas 2010; Köster et al. 2005; Wolin and Stoermer 2005; Smol 1985), perhaps resulting from increased soil erosion and/or changes in leaf litter quality within the catchment (Beck et al. 2016; Rawlence 1992; Stevenson et al. 1990).

European colonization and subsequent land-use changes in southern Québec and Ontario, signalled by increases in herbaceous pollen and micro-charcoal influxes (Paquette and Gajewski 2013), triggered substantial responses in Lac Noir diatom assemblages. Peaks in *Stephanodiscus minutulus* and *Achnanthidium minutissimum* indicated a brief period during which nutrients increased (Finney et al. 2002) between 1870-1930 CE, after which the lake seemed to have been less disturbed and returned to conditions similar to those of the early record during the MWP. In comparison, the Lac Brûlé diatom record continued to show signs of eutrophic conditions associated first with the Wallingford-Back Mine (1924-1972 CE), but also in the modern assemblages (e.g. high relative abundances of *Discostella stelligera* and *Fragilaria crotonensis*). Lac Noir is fairly isolated with little human activity in the immediate catchment, whereas Lac

Brûlé is publicly accessible and, despite the closure of the nearby Wallingford-Back mine, is a site still frequented by local residents and tourists. Changes on the order of decades were therefore captured due to the high-temporal resolution used in this study, which revealed very distinctive local histories for each lake.

Within a regional context, this study shows that some lakes may need to be prioritized in terms of management of forests and human activities in their respective catchment areas. For example, proposals have been put forward to transform the remnants of the Wallingford-Back Mine into an official tourist attraction, which would lead to a significant increase in traffic and impacts. There could be significant and lasting impacts on the nearby Lac Brûlé, which should therefore be taken into consideration for future planning.

Objective 3: Extend a high-resolution fossil record to the early Holocene to better understand the role of climate in structuring the long-term ecology of the lakes in southwestern Québec

Lac Noir is one amongst few lake sediment records that are continuously laminated (varved) and span the entire Holocene period (~11000 years). In the absence of a local pollen record for the site dating beyond the last 1000 years (Paquette and Gajewski 2013), changes in the Lac Noir diatom assemblages were discussed within the context of regional palynological studies, including those by Mott and Farley-Gill (1981; Ramsay Lake, Pink Lake) and Fuller (1997; High Lake, Graham Lake). Long-term changes in Lac Noir diatom communities showed a close association with climate (Viau et al. 2006), early lake ontogeny (Moos et al. 2009), and the development of forests and soils (Fuller 1997; Huvane and Whitehead 1996) following retreat of the Laurentide ice sheet from southwestern Québec.

Biostratigraphic changes in the Lac Noir diatom assemblages indicate three major zones corresponding to overall climate changes in the early, mid-, and late Holocene (Viau et al. 2006;

Walker et al. 2012), and were consistent with other long-term diatom records from southern Québec and Ontario (e.g. Karmakar et al. 2015; Haussmann 2011). Climate conditions at the start of the Holocene were cool and dry, and the diatom assemblages at Lac Noir were comprised primarily of benthic taxa (e.g. *Staurosirella pinnata* and *Staurosira construens*) typical of the early phases of lake ontogeny (Bradshaw et al. 2000; Lu 2014; Lavery et al. 2014; Puusepp and Kangur 2010). Warming in the mid-Holocene was associated with enhanced thermal stratification and a gradual shift to oligotrophic conditions (Karmakar et al. 2015); this was evidenced at Lac Noir by increases in *Tabellaria flocculosa* str. IIIp, *Discostella stelligera*, and in the ratio of chrysophytes relative to diatoms, as well as decreases in meso-eutrophic taxa, such as *Stephanodiscus minutulus* and *Fragilaria crotonensis*. Diatom taxa with tolerances for warmer conditions (e.g. *Fragilaria tenera* and *Discostella stelligera;* Rühland et al. 2003) declined at the onset of Neoglacial cooling, although the latter species recovered gradually despite the persistent cooler temperatures. The diatom record therefore reflects a general link to orbital-scale climate (COHMAP Members 1988), although when studied alongside local and regional pollen records can provide a much more detailed and comprehensive understanding of the mechanisms driving changes in the diatom flora.

Forest composition had major influences on physical, chemical and biological properties of soils (stability, pH) and lakes (stratification, pH, nutrient concentration, aquatic biota) within the region. For example, *Picea*-dominated woodlands in the early Holocene (Fuller 1997) were associated with higher acidity at Lac Noir, interpreted based on low relative abundances of *Discostella stelligera* and *Aulacoseira pusilla* at this time (Denys et al. 2003; Taylor et al. 1987). As well, expansion of *Tsuga* in the mid-Holocene (Fuller 1997; Mott and Farley-Gill 1981) was correlated with higher percentages of *Aulacoseira tenella*, reflecting leaching of humic-rich soils into the lake via the catchment (Huvane and Whitehead 1996). This study thus confirms a well-

established and continuous influence of vegetation composition on diatom flora throughout the Holocene, and shows that there is a distinct advantage in comparing multiple proxy-records when possible at any given site.

The previous chapters of this thesis discussed centennial- to decadal-scale diatom responses to climate intervals, including the Medieval Warm Period and Little Ice Age, as well as natural and human-induced disturbances. The extended Lac Noir record was sampled at a slightly lower temporal resolution (every 100-years, and in some sections at every 20-years), however abrupt changes were still noted in both the sediments and the diatom assemblages. A peak in magnetic susceptibility, for example, was attributed to climate cooling at 9.2 ka and 8.2 ka, resulting from sudden ice dome collapses over the present-day Hudson Bay area (Flietmann et al. 2008; Alley and Agustsdottir 2005). However, these events seemed to have had little impact on overall diatom communities of the lake. Additionally, a widespread decline in hemlock (*Tsuga*) at ~5500 cal. yr. BP lasted for several centuries; this event triggered nutrient increases in the lake as inferred from increased relative abundances of *Discostella stelligera* (Beck et al. 2016), and a decline in the ratio of chrysophytes relative to diatoms (Smol 1985). These results show that well-dated, high-resolution records are necessary in assessing the timing and magnitude of major environmental changes, and analyses of varved lake sediments are perhaps the best way to accomplish this.

5.2 Future directions

Using paleolimnological approaches as a means of understanding the mechanisms driving ecosystem change are only one component of a research effort needed for better lake management practices. Long-term changes on the order of centuries and/or millennia are informative in terms of studying natural variability in aquatic communities through time, as well as their linkages with climate and catchment-related processes. However, connecting this to the scale of anthropogenic

impacts now and in the future can be challenging given the complexity with which humans interact with the environment. Questions arise regarding ecosystem thresholds or "tipping points" (Maslin 2004), the ability of organisms to adapt or recover following major disturbances (Johnstone et al. 2016), and dissimilarity or high-frequency variability between local-scale responses (e.g. diatom assemblage changes) and regional-scale driving forces (e.g. climate). As the demand increases for lake ecosystems services, such as safe drinking water and/or recreational activities, it is critical to consider the vulnerability of lakes, especially as they relate to continued anthropogenic activities.

Quantitative reconstructions are useful tools in paleolimnological research (Birks 2001) as a means of determining lake ecosystem health. Modern diatom calibration- or training-sets are often used to infer past nutrient levels and/or lake pH (Varin 2016; Tremblay et al. 2014; Velghe et al. 2012; Enache and Prairie 2002; Philibert et al. 2003; Reavie and Smol 2001; Dixit et al. 1988). This could then be applied to answer questions about pre- or post- industrial conditions, for example, as a measure of anthropogenic impact on lake ecosystems. Moreover, quantitative reconstructions can provide insights into optimal conditions for individual diatom species in relation to a range of physical (water depth, bedrock geology) and chemical (pH, nutrient concentrations) parameters. Down-core analyses of variables, such as total phosphorous (TP), could improve the quality of interpretation in terms of diatom responses to natural climate variability, disturbances, and other proxy-indicators (pollen and cladocera). Within the study region, attempts to reconstruct TP in down- core sediments using modern diatom and cladocera training-sets were unsuccessful (Varin 2016; Cooper et al. 2016). This was due to a narrow range in TP across the sampled lakes; however, expanding the dataset could help to create a more robust and better performing transfer function, which could then be applied to the Lac Brûlé and Lac Noir sediment cores.

Another avenue for future research in the region could be to evaluate the potential risk of droughts on ecological succession within the context of future warming trends for the region

(Cook et al. 2004). Paleoclimate records from mid-continental U.S. have indicated occurrences of mega-droughts in the mid- to late Holocene, ranging temporally from multi-year to multi-decadal events (Williams et al. 2011; Booth et al. 2005). Several particularly dry periods that affected the Central Plains to the Great Lakes region are associated with (i) the 4.2 ka drought, (ii) late 16th century droughts, and (iii) droughts of the 1930s (Booth et al. 2005). However, the eastward extent of these events and accompanying environmental impacts are not well defined, as there is a lack of high resolution drought-sensitive records towards the southern Québec/Ontario border (Lafontaine and Gajewski 2014; Booth et al. 2006). Lake-level studies within eastern study sites could therefore help to address these questions, which were not fully resolved in this thesis. Cores from Lac Brûlé and Lac Noir were retrieved from the deepest parts of the lake basins where the varves were preserved; however, deep cores do not always reflect variations in lake levels of the past (Haig et al. 2013). Cores taken at a depth near the modern benthic-to-planktonic diatom boundary are more likely to capture climate-driven changes in water level (Karmakar et al. 2015), although they are also likely to have disturbed sediments. Research using this B:P diatom boundary technique on well-dated sediment cores could perhaps confirm whether or not severe droughts occurred in southern Québec and Ontario in the past.

This thesis has provided evidence to show that critical information can be gained from replicating multi-proxy studies within a relatively small spatial scale. Diatom assemblages, in particular, appear to be especially sensitive to disturbances within their respective catchments; however, studies such as those mentioned above have also shown that there can be a large degree of variability in fossil assemblages within sediment cores from different areas of the lake basin (e.g. shallow, deep). Without multiple replicate cores from the same lake, it is perhaps more difficult to separate the random ‘noise’ in paleo-records generated at one site from the broader signal in the data. More studies of this nature are therefore needed.

Finally, this study has shown numerous benefits in regards to the uses of annually-laminated lake sediments for high-resolution paleolimnological studies. However, Lac Brûlé and Lac Noir only represent two of potentially many sites in southwestern Québec, or other regions in eastern North America, that have sediments with varves. Given that it is a challenge to find lakes with varves (especially in such close proximity), it could be unrealistic to assume that this type of study could be easily replicated in the future or in other regions. It may therefore be beneficial to compare sampling strategies in lake sediments with and without varves to assess whether similar results could be achieved between the two.

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APPENDIX A
Diatom list and photomicrographs

Table A1: Diatoms occuring in Lac Brûlé and Lac Noir sediments. Diatoms listed in bold occur in higher relative abundances (>3 or 4% of the total diatom sum in each lake), and are shown in stratigraphic diagrams in Chapters 2-4. Photomicrographs of select species are shown in plates 1-9. Numbers after the species names correspond to the numbers used in the figures.

Genus species (Fig. number)	**Authority**
Achnanthes undulorostrata	R.L.Lowe & A.R.Sherwood 2009
Achnanthidium deflexum	(C.W.Reimer) J.C.Kingston 2000
Achnanthidium minutissimum (3)	**(Kützing) Czarnecki 1994**
Achnanthidium gracillimum	**(F.Meister) Lange-Bertalot 2004**
Achnanthidium reimeri (4)	(Camburn) Ponader & Potapova 2007
Achnantidium exiguum (1, 2)	(Grunow) Czarnecki 1994
Amphora minutissima (5)	W.Smith 1853
Amphora ovalis var. pediculus (6, 7)	**(Kützing) Grunow 1875**
Aneumastus rostratus (8)	(Hustedt) Lange-Bertalot 2001
Asterionella formosa (9)	**Hassal 1850**
Aulacoseira alpigena	(Grunow) Krammer 1991
Aulacoseira ambigua (10)	**(Grunow) Simonsen 1979**
Aulacoseira canadensis	(Hustedt) Simonsen 1979
Aulacoseira italica (11)	(Ehrenberg) Simonsen 1979
Aulacoseira lirata (12)	(Ehrenberg) R.Ross 1986
Aulacoseira nivalis	(W.Smith) J.English & Potapova 2009
Aulacoseira pusilla (13, 14)	**(F.Meister) A.Tuji & A.Houk 2004**
Aulacoseira subarctica	(Otto Müller) E.Y.Haworth 1990
Aulacoseira tenella (15, 16)	**(Nygaard) Simonsen 1979**
Brachysira brebissoni (17)	R.Ross 1986
Brachysira microcephala (18)	(Grunow) Compère 1986
Brachysira ocalanensis	H.A.Shayler & P.A.Siver 2004
Brachysira styriaca (19)	(Grunow) R.Ross 1986
Brachysira zellensis (20)	(Grunow) Round & D.G.Mann 1981
Caloneis bacillum (21)	(Grunow) Cleve 1894
Caloneis silicula (22)	(Ehrenberg) Cleve 1894
Cavinula cocconeiformis	(W.Gregory ex Greville) D.G.Mann & A.J.Stickle 1990
Cavinula pseudoscutiformis	(Hustedt) D.G.Mann & A.J.Stickle 1990
Cavinula pusio	(Cleve) Lange-Bertalot 2004
Cavinula scutelloides	(W.Smith) Lange-Bertalot 1996
Cavinula vincentii (23)	Antoniades & P.B.Hamilton , nom. inval. 2008
Chamaepinnularia mediocris	(Krasske) Lange-Bertalot & Krammer 1996
Chamaepinnularia soehrensis	(Krasske) Lange-Bertalot & Krammer 1996
Cocconeis lineata (24)	Ehrenberg 1849
Cocconeis placentula	Ehrenberg 1838
Craticula ambigua (25)	(Ehrenberg) D.G.Mann 1990
Lindavia intermedia (27)	**(Manguin ex Kociolek & Reviers) Nakov, Guillory, Julius,**
Synonym: *Cyclotella bodanica var. intermedia*	**Theriot & Alverson ex W.C.Daniels, Novis & Edlund**
Cyclotella distinguenda (28)	**Hustedt in Gams 1928**
Cyclotella meneghiniana (29)	Kützing 1844
Cyclotella michiganiana (30)	**Skvortzov [Skvortzov] 1937**
Pantocsekiella ocellata (31)	**(Pantocsek) K.T.Kiss & E.Ács 2016**
Synonym: *Cyclotella ocellata*	
Discostella pseudostelligera (32)	**(Hustedt) Houk & Klee 2004**
Synonym: *Cyclotella pseudostelligera*	
Cyclotella radiosa	(Grunow) Lemmermann 1900
Pantocsekiella rossii (33)	**(H.Håkansson) K.T.Kiss & E.Ács 2016**
Synonym: *Cyclotella rossii*	
Cymbella cistula	(Ehrenberg) O.Kirchner 1878
Cymbella cymbiformis	C.Agardh 1830

Genus species (Fig. number)	**Authority**
Cymbella hustedtii	Krasske 1923
Cymbella rupicola (35)	**Grunow in A.W.F.Schmidt 1881**
Cymbella sinuata var. antiqua (36)	(Grunow) Cleve 1894
Cymbopleura inaequalis	(Ehrenberg) Krammer 2003
Cymbopleura metzeltinii	Krammer 2003
Cymbopleura naviculiformis	(Auerswald ex Heiberg) Krammer 2003
Denticula tenuis (37)	Kützing 1844
Diatoma moniliformis	(Kützing) D.M.Williams 2012
Discostella stelligera (34)	**(Cleve & Grunow) Houk & Klee 2004**
Homotypic synonym: ***Cyclotella stelligera***	
Encyonema silesiacum	(Bleisch) D.G.Mann 1990
Entomoneis ornata	(Bailey) Reimer 1975
Epithemia adnata (38)	(Kützing) Brébisson 1838
Epithemia gibba	(Ehrenberg) Kützing 1844
Epithemia reichelti (39)	Fricke 1904
Epithemia smithii (40)	Carruthers 1864
Epithemia sorex (41)	Kützing 1844
Eucocconeis alpestris (42)	(Brun) Lange-Bertalot 1999
Eucocconeis flexella (43)	(Kützing) Meister 1912
Eucocconeis laevis	(Østrup) Lange-Bertalot 1999
Eunotia diodon	Ehrenberg 1837
Eunotia elegans (46)	Østrup 1910
Eunotia formica	Ehrenberg 1843
Eunotia incisa	W.Smith ex W.Gregory 1854
Eunotia naegelii	Migula 1905
Eunotia pectinalis (44)	(Kützing) Rabenhorst 1864
Eunotia praerupta	Ehrenberg 1843
Eunotia tetraodon (45)	Ehrenberg 1838
Fragilaria crotonensis (47)	**Kitton 1869**
Fragilaria mesolepta	Rabenhorst 1861
Fragilaria mesolepta	Rabenhorst 1861
Fragilaria tenera (48)	**(W.Smith) Lange-Bertalot 1980**
Fragilariforma bicapitata	(A.Mayer) D.M.Williams & Round 1988
Frustulia crassinervia	(Brébisson ex W.Smith) Lange-Bertalot & Krammer 1996
Geissleria acceptata	(Hustedt) Lange-Bertalot & Metzeltin 1996
Gliwiczia calcar	(Cleve) M.Kulikovskiy, Lange-Bertalot & A.Witkowski 2013
Gomphonema acuminatum (59)	Ehrenberg 1832
Gomphonema apicatum (60)	Ehrenberg 1854
Gomphonema brebissonii	Kützing 1849
Gomphonema gibba	J.H.Wallace 1960
Gomphonema intricatum (61)	Kützing 1844
Gomphonema pseudosphaerophorum	H.Kobayasi 1988
Gomphonema subtile (62)	Ehrenberg 1843
Gomphonema truncatum (63)	Ehrenberg 1832
Gomphonema truncatum var. turgidum (64)	(Ehrenberg) R.M.Patrick 1975
Grunowia tabellaria (51)	(Grunow) Rabenhorst 1864
Gyrosigma acuminatum	(Kützing) Rabenhorst 1853
Halamphora thumensis (58)	(A.Mayer) Levkov 2009
Hippodonta capitata	(Ehrenberg) Lange-Bertalot, Metzeltin & Witkowski 1996
Hippodonta capitata subsp. Iberoamericana	Metzeltin, Lange-Bertalot & García-Rodríguez 2005
Iconella tenera	(W.Gregory) Ruck & Nakov 2016
Karayevia clevei (56)	(Grunow) Bukhtiyarova 1999
Karayevia laterostrata	(Hustedt) Bukhtiyarova 1999
Karayevia suchlandtii	(Hustedt) Buktiyarova 1999
Lemnicola rostellata	(Cleve-Euler) Chudaev 2015
Lindavia affinis	(Grunow) Nakov, Guillory, Julius, Theriot & Alverson 2015

Genus species (Fig. number)	**Authority**
Lindavia antiqua (26)	(W.Smith) Nakov, Guillory, Julius, Theriot & Alverson 2015
Lindavia delicatula	(Hustedt) T.Nakov et al. 2015
Luticola nivalis	(Ehrenberg) D.G.Mann 1990
Luticola ventricosa	(Kützing) D.G.Mann 1990
Mastogloia grevillei (49, 50)	W.Smith 1856
Meridion anceps	(Ehrenberg) D.M.Williams 1985
Meridion circulare (65)	(Greville) C.Agardh 1831
Meridion circulare var. constrictum	(Ralfs) Van Heurck 1880
Navicula aurora	Sovereign 1958
Navicula cryptonella	Lange-Bertalot 1985
Navicula flatheadensis	Bahls 2011
Navicula minnewaukonensis	Elmore 1921
Navicula sabiniana	R.M.Patrick 1959
Neidium affine (66)	(Ehrenberg) Pfitzer 1871
Neidium hitchcockii (67)	(Ehrenberg) Cleve 1894
Neidium iridis	(Ehrenberg) Cleve 1894
Nitzschia fonticola (53)	(Grunow) Grunow 1881
Nitzschia semirobusta (52)	Lange-Bertalot 1993
Pinnularia borealis (69)	Ehrenberg 1843
Pinnularia divergens var. sublinearis	Cleve 1895
Pinnularia metzeltinii	Krammer 2000
Pinnularia nodosa (70)	(Ehrenberg) W.Smith 1856
Pinnularia septentrionalis	Krammer 2000
Placoneis abiskoensis (71)	(Hustedt) Lange-Bertalot & Metzeltin 1996
Placoneis anglophila	(Lange-Bertalot) Lange-Bertalot 2005
Planothidium abbreviatum	(Reimer) Potapova 2012
Planothidium apiculatum	(R.M.Patrick) Lange-Bertalot 1999
Planothidium calcar (54)	(Cleve) M.B.Edlund 2001
Planothidium dubium	(Grunow) Round & Bukhtiyarova 1996
Planothidium frequentissimum	(Lange-Bertalot) Lange-Bertalot 1999
Planothidium haynaldii	(Schaarschmidt) Lange-Bertalot 1999
Planothidium lanceolatum (55)	(Brébisson ex Kützing) Lange-Bertalot 1999
Planothidium rostratum	(Østrup) Lange-Bertalot 1999
Platessa hustedtii	(Krasske) Lange-Bertalot 2004
Psammothidium didymum	(Hustedt) L.Bukhtiyarova & Round 1996
Rhopalodia musculus	(Kützing) Otto Müller 1900
Rossithidium pusillum (83)	(Grunow) Round & Bukhtiyarova 1996
Sellaphora alastos	(M.H.Hohn & Hellerman) Lange-Bertalot & Metzeltin 1996
Sellaphora bacillum	(Ehrenberg) D.G.Mann 1989
Sellaphora pulchra	Enache & Potapova 2009
Sellaphora rectangularis (68)	(W.Gregory) Lange-Bertalot & Metzeltin 1996
Stauroneis gracilis	Ehrenberg 1843
Stauroneis smithii (72)	Grunow 1860
Staurosira construens (74, 75)	**Ehrenberg 1843**
Staurosira binodis (77)	**(Ehrenberg) Lange-Bertalot 2011**
Synonym: *Staurosira construens var. binodis*	
Staurosira venter (73)	**(Ehrenberg) Cleve & J.D.Möller 1879**
Synonym: *Staurosira construens var. venter*	
Staurosira leptostauron (57)	(Ehrenberg) Kulikovskiy & Genkal 2011
Staurosirella leptostauron var. dubia (76)	**(Grunow) M.B.Edlund 1994**
Staurosirella pinnata (79)	**(Ehrenberg) Williams & Round 1988**
Stephanodiscus hantzschii (81)	**Grunow 1880**
Stephanodiscus minutulus (82)	**(Kützing) Cleve & Möller 1882**
Surirella amphioxys	W.Smith 1856
Synedra cyclopum	Brutschy 1922
Tabellaria flocculosa str. IIIp (78, 80)	**(Roth) Kützing 1844**
Ulnaria contracta	(Østrup) E.A.Morales & M.L.Vis 2007

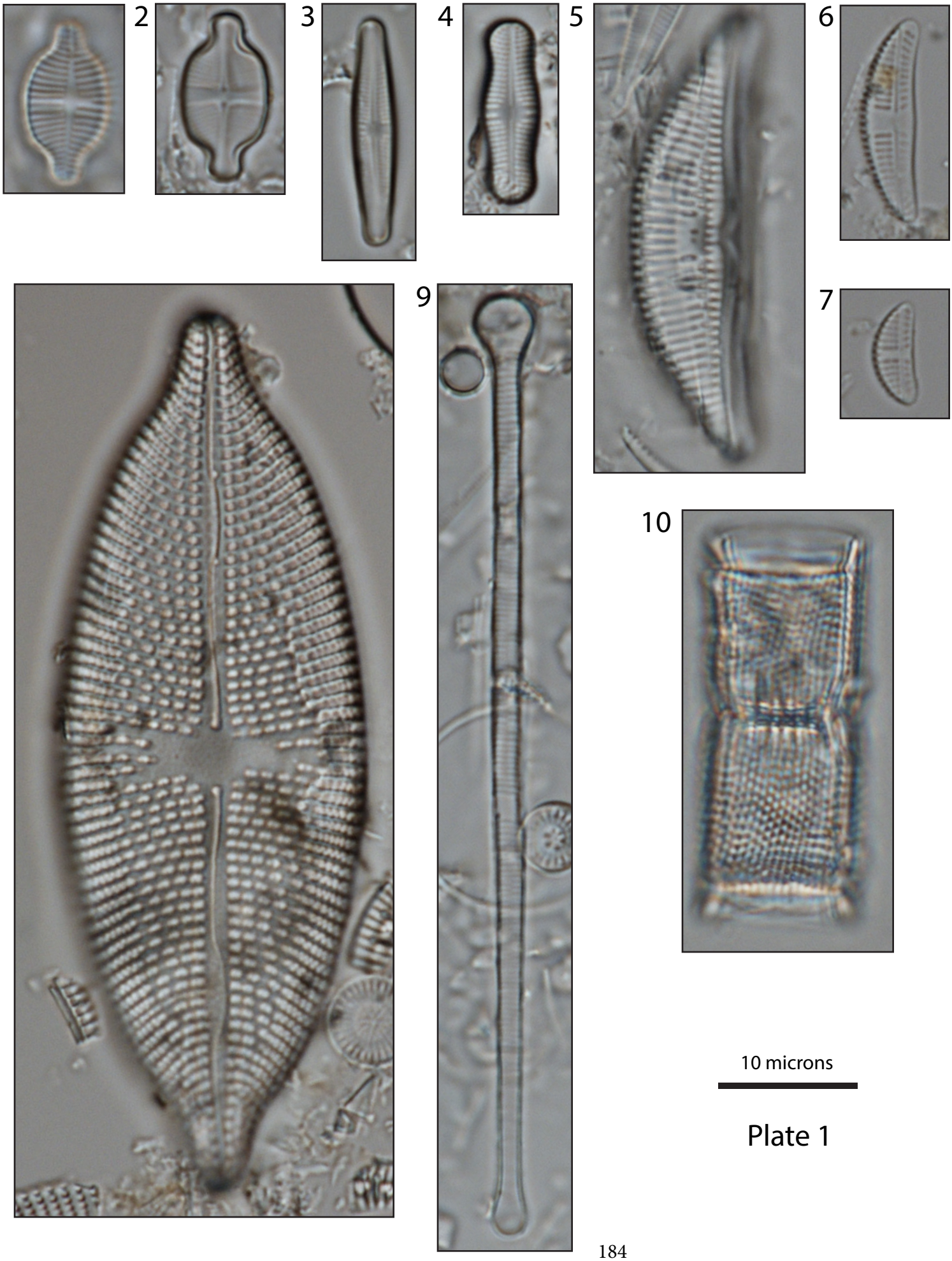
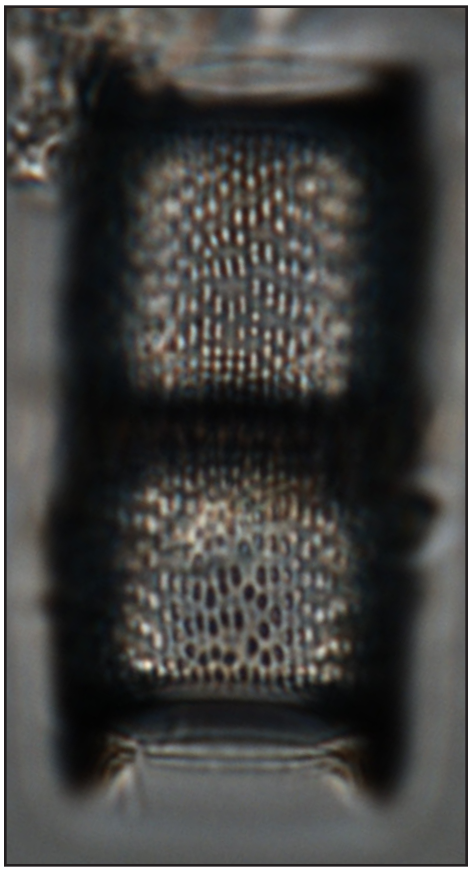
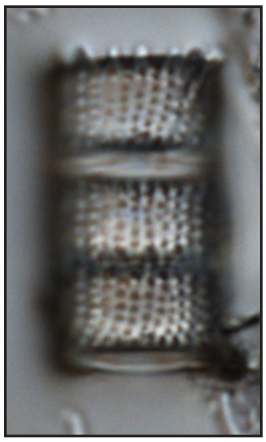
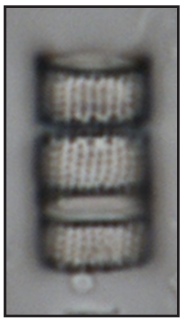
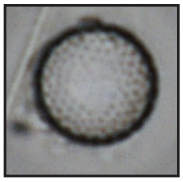


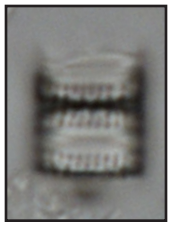
Plate 1

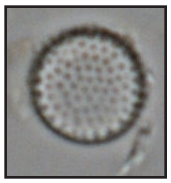












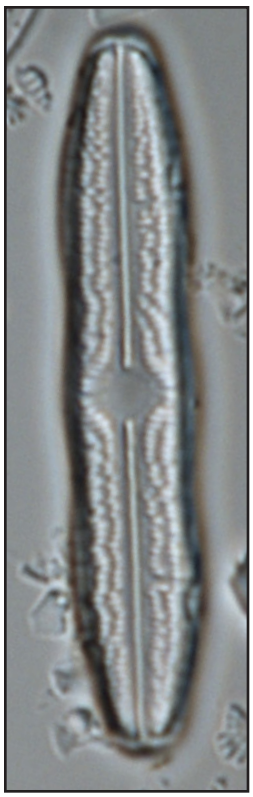


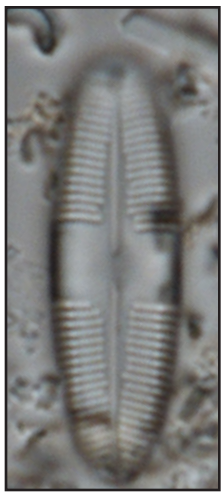


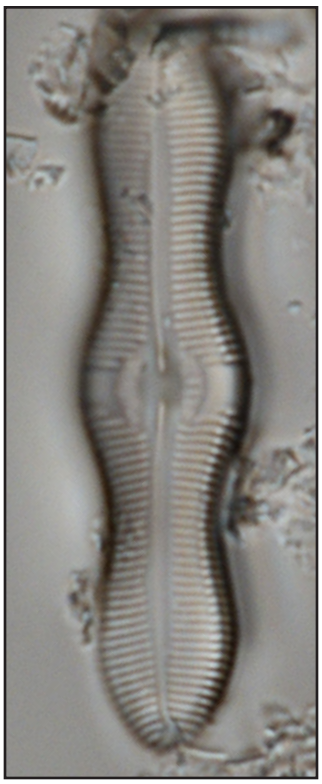


10 microns

Plate 2





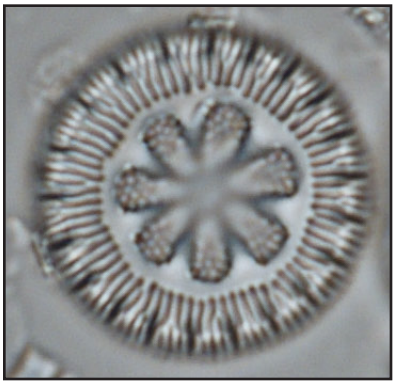


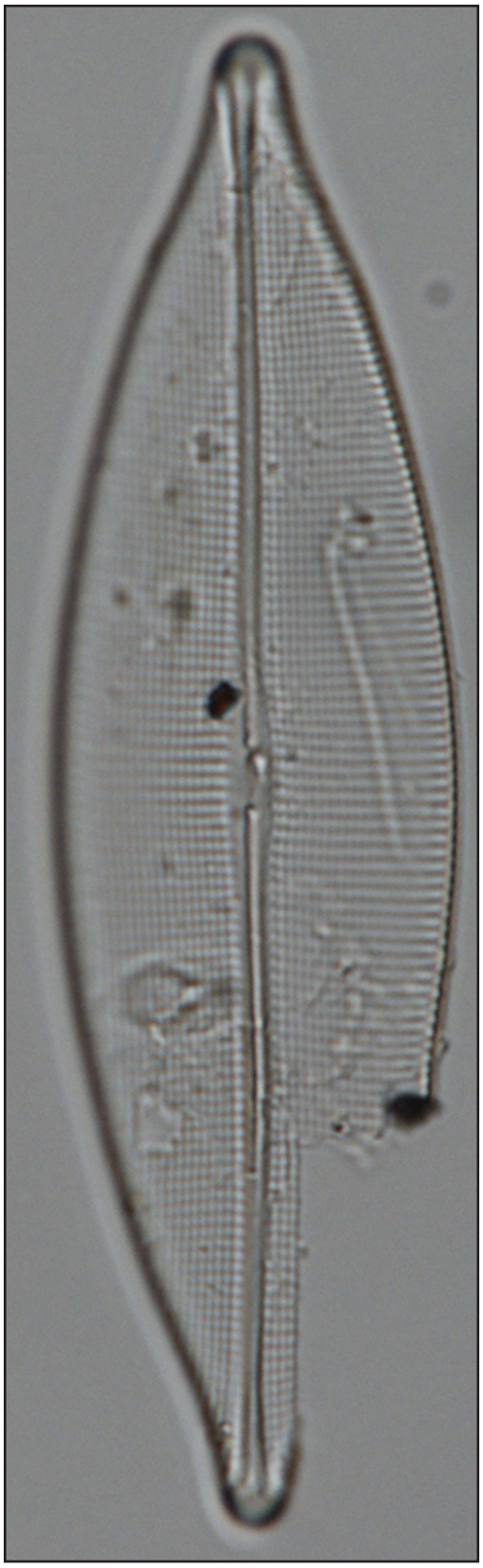


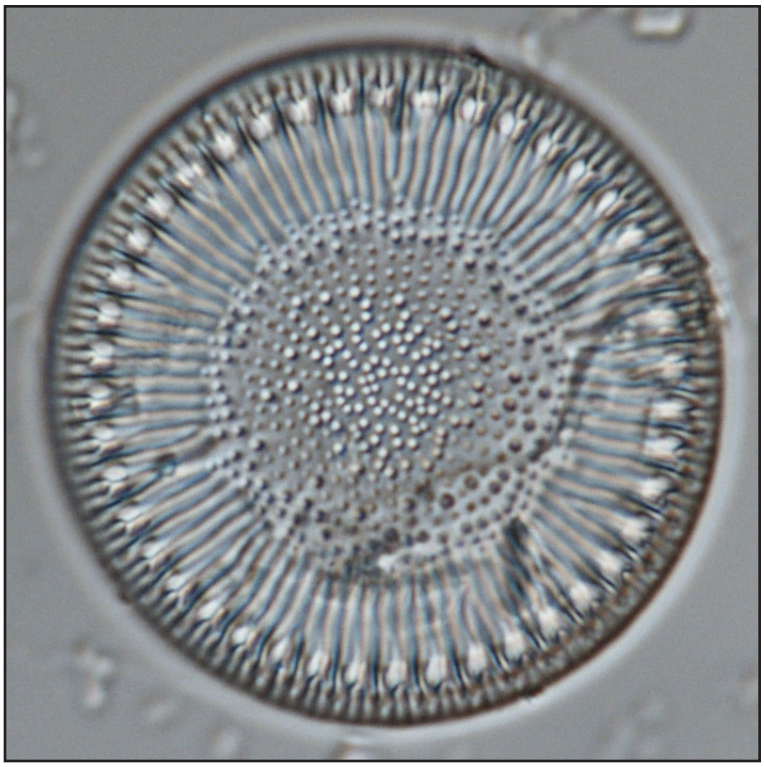
10 microns

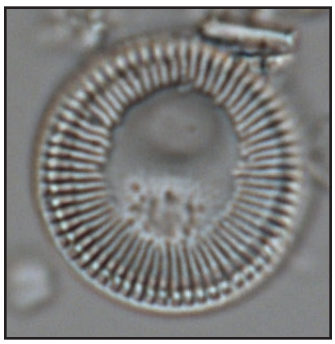
Plate 3

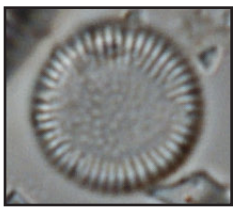


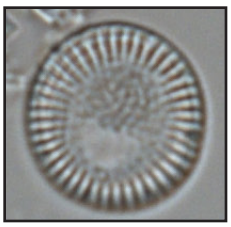


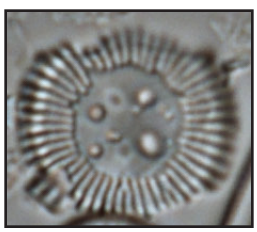




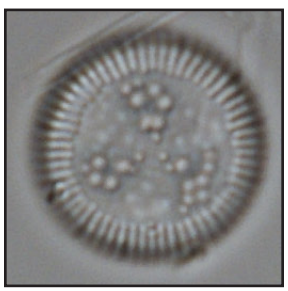














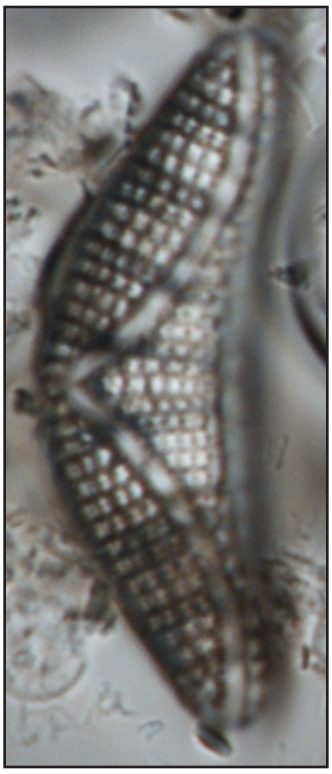














10 microns

Plate 4

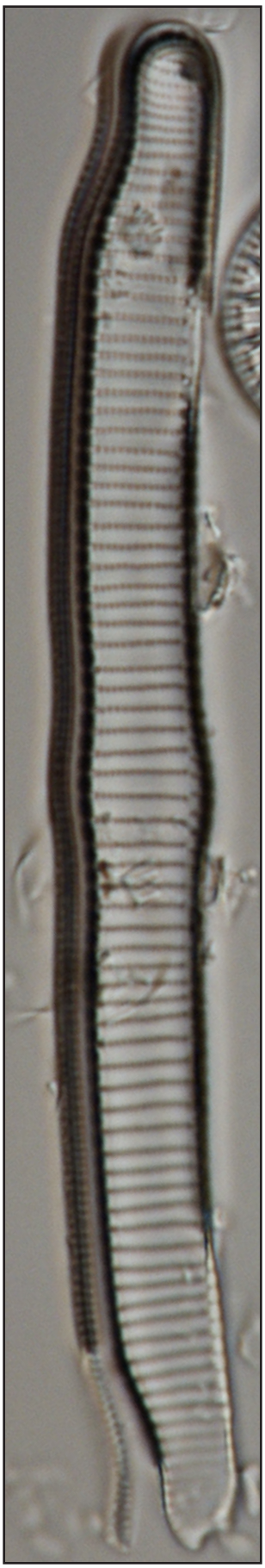
42



43



44



45

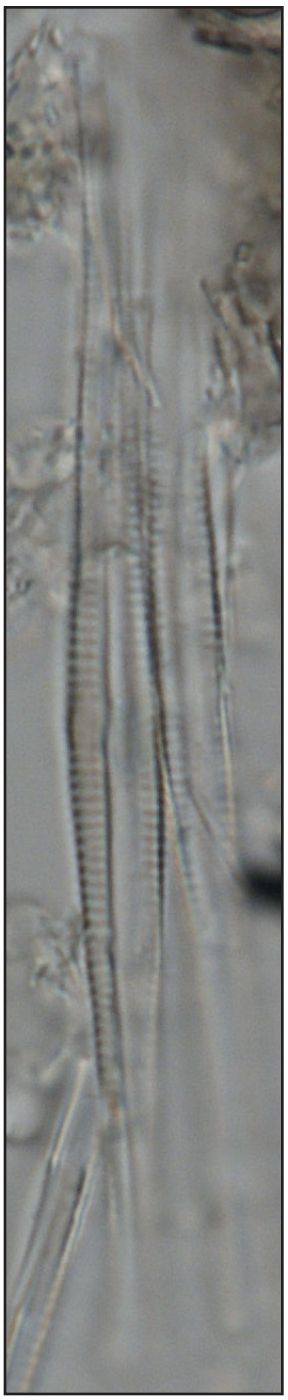


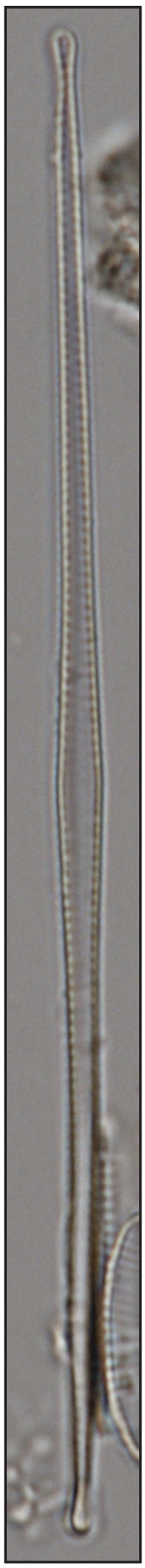
46



10 microns

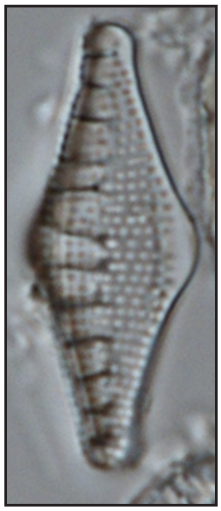
Plate 5









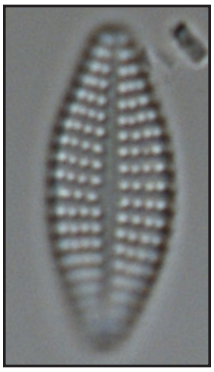












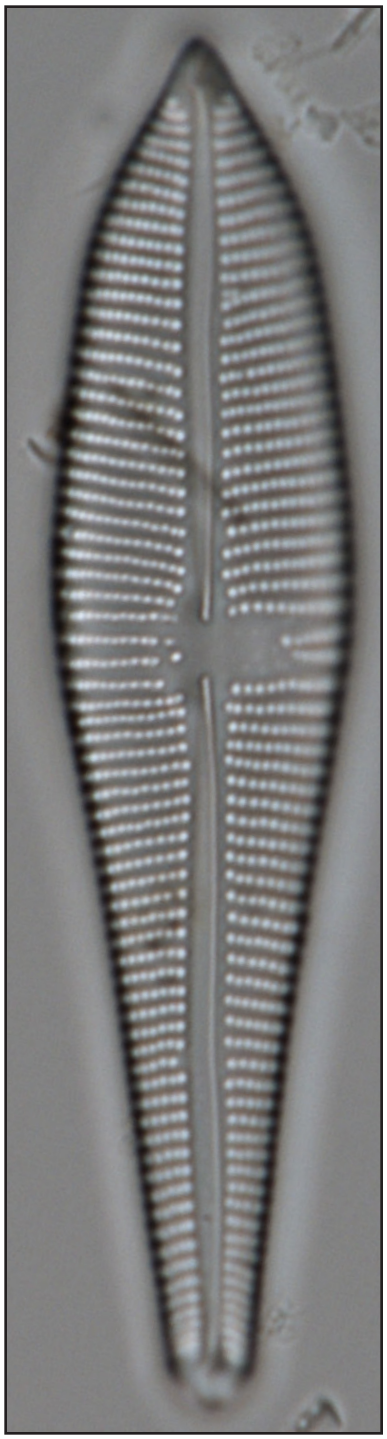




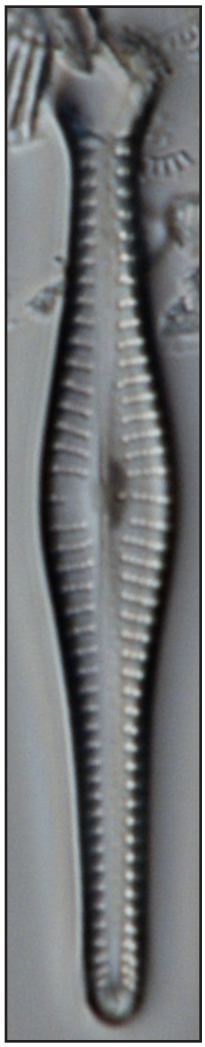
10 microns

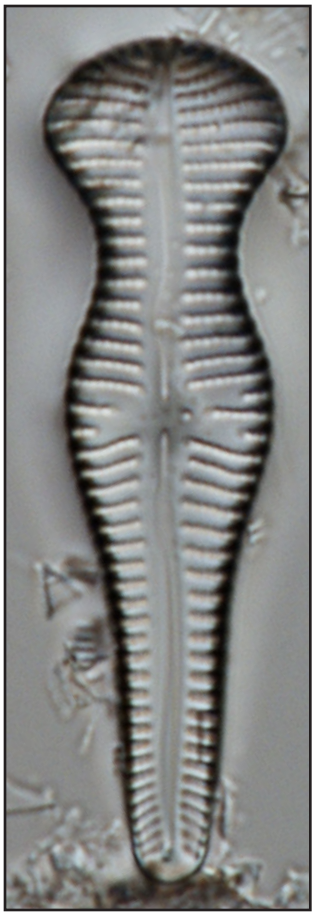
Plate 6





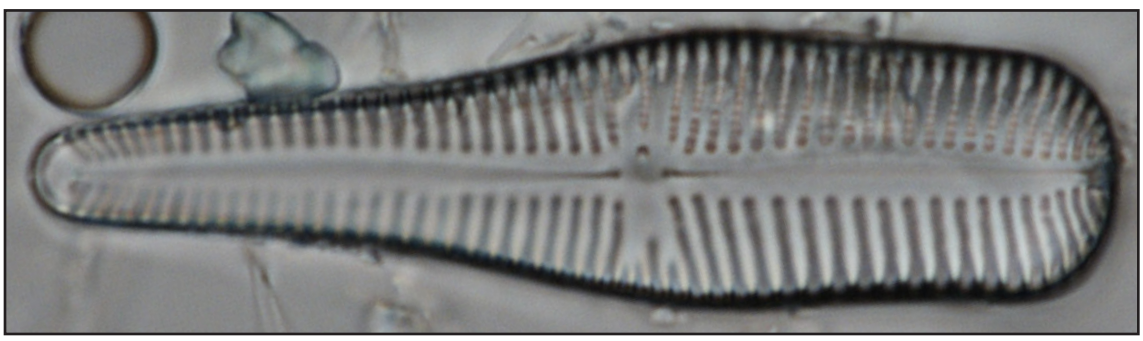




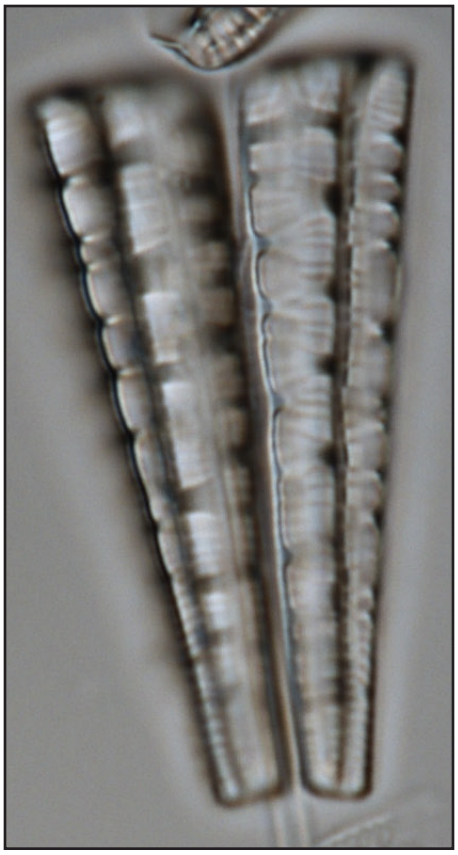


10 microns

Plate 7

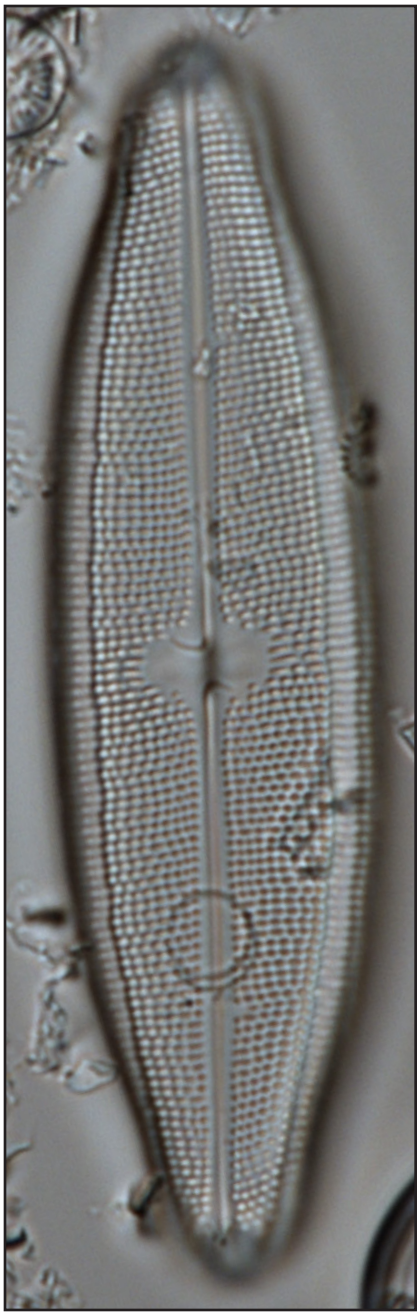


65



10 microns

66



67

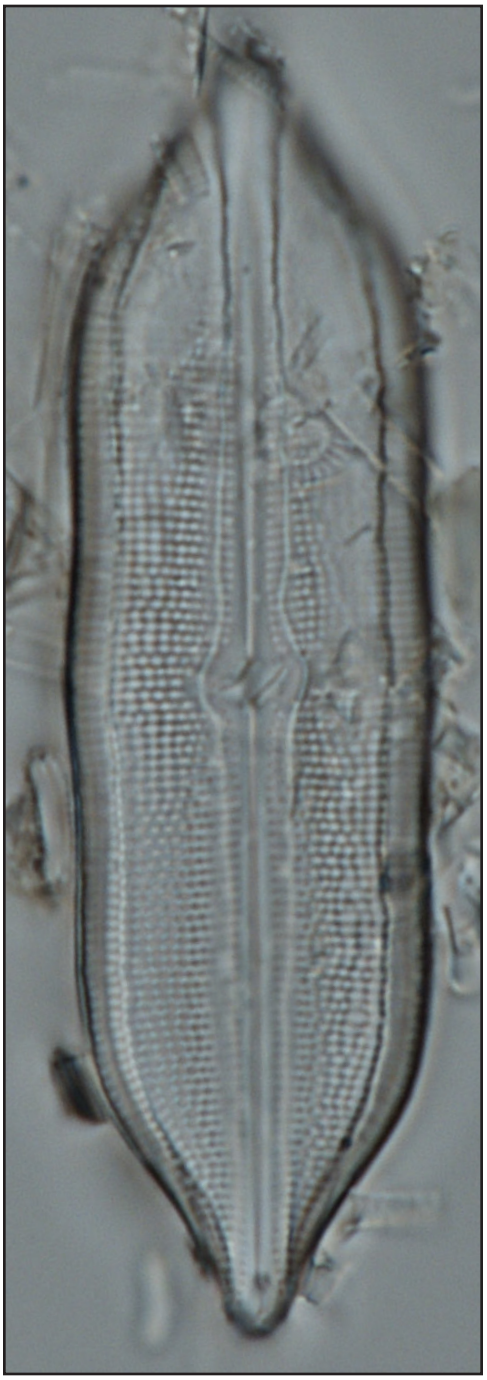


Plate 8

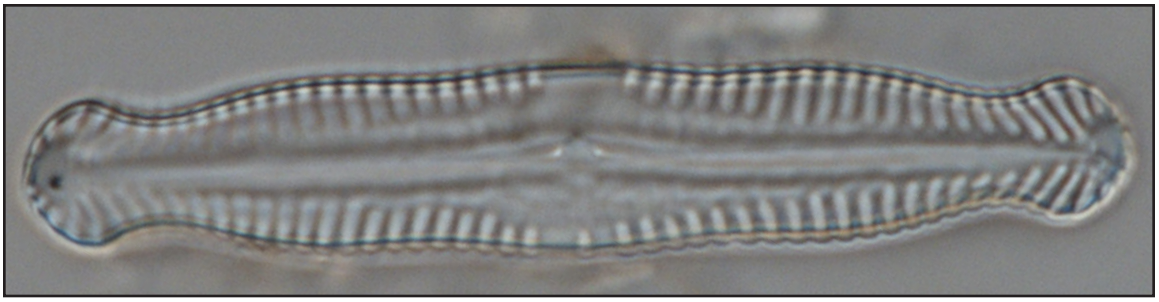
68

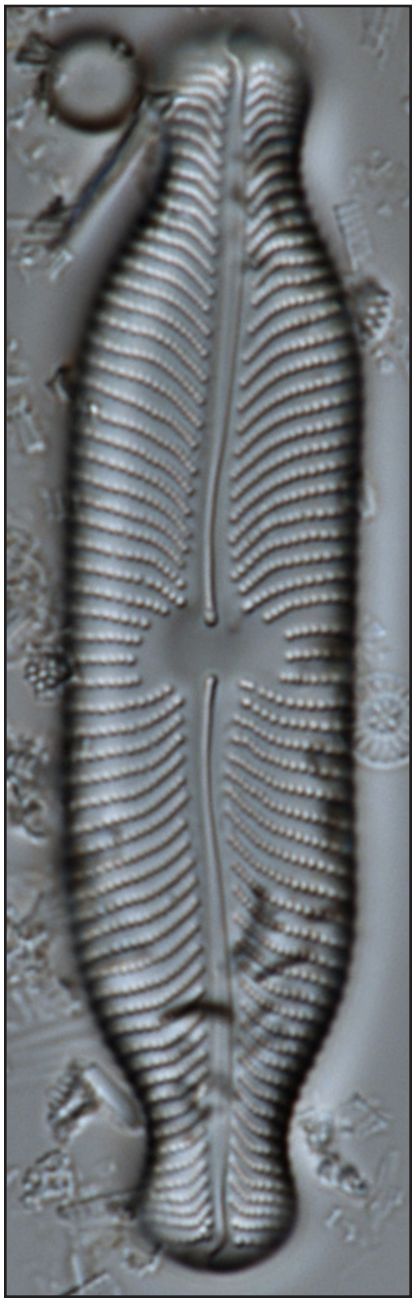


69



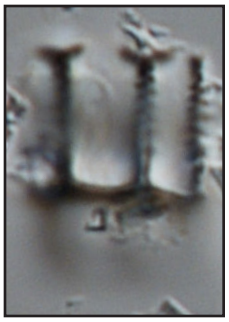
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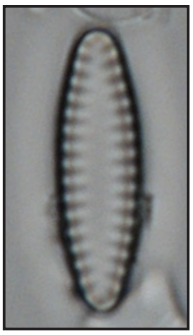


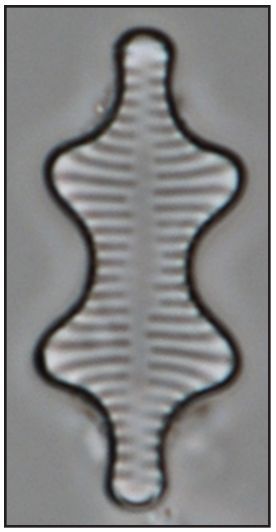






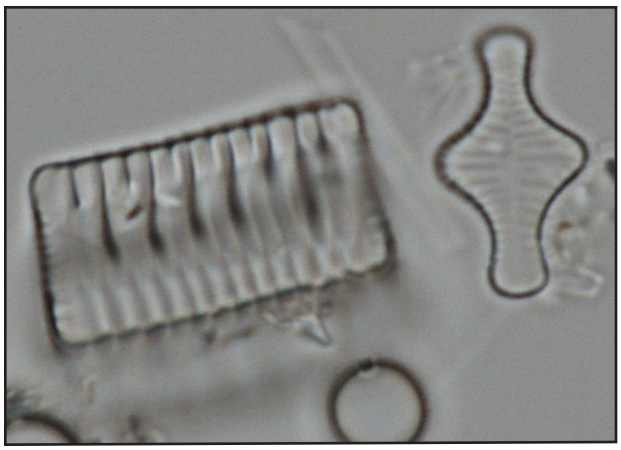


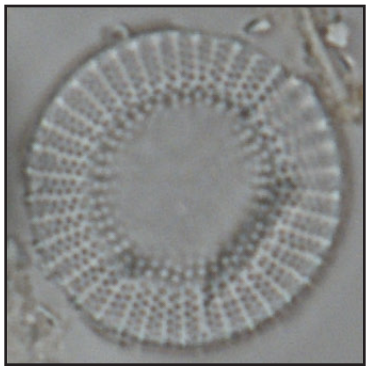


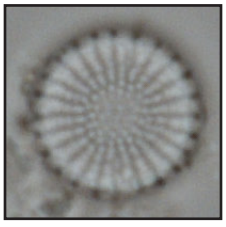


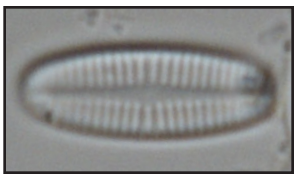












10 microns

Plate 9