The Response of Cladoceran Communities to the Climatic Changes of the Late Holocene Southwestern Québec

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Abstract

This thesis focuses on a chronological analysis of the cladoceran communities from a sediment core of a small oligotrophic lake in southwestern Québec, Canada over the past 1250 years. The sediments of the lake were varved, which allowed for accurate dating. A previously-published pollen study of the lake provided a record of the paleoclimatic and landscape changes in the region. The core was then used to infer how changes in temperature and landscape changes impacted the taxonomic composition of the cladoceran community through time. Cladoceran diversity was high throughout most of the Medieval Warm Period and into the Little Ice Age and decreased during the modern period in response to increased temperatures and anthropogenic impacts. *Daphnia* and plant-associated species greatly decreased in the past 100 years. This shift, combined with increased temperatures and changes in the landscape opened up a niche for the colonization by the smaller *Bosmina longirostris*. The modern communities are unlike most of what was observed throughout the past millennium.

Résumé

Cette thèse se concentre d'un analyse chronologique des communautés cladoceran, d'une carotte du sedimentaire qui vien par un petit lac oligotrophique dans la sud-ouest de Québec, Canada, 1250 années passé. Dans le lac, les sedimentaire sois varvée, à cause de ça on peut avoir la datation précise. Une étude pollen qui était publié pour le lac, fournir les changes paléoclimatique et demanagement du paysage dans la region. On y utilisé la carotte pour identifier comment le température et les déménagements du paysage, avait affecté la composition taxonomique de la communauté cladorceran quand le temps traverses. La diversité du cladoceran est pleine pendent la période Petit Optimum Médiévale à la petit peu dans le Petit Age Glaciaire, et diminué dans la époque moderne au cause d'augmenté température chaud, et l'affect anthropologique. Des associés espèces de plante, *Daphina* était diminué pendant les 100 années passées. Cette décalage plus la température augmenté, et les changes du paysages sont découvre une niche pour la colonisation de la plus petit *Bosmina longirostris*. Les communautés modern était au contraire qui été observée dans tout le dernier millénaire

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List of Abbreviations

AMO: Atlantic Multidecadal Oscillation
CA: Correspondence Analysis
CAR: Cladoceran accumulation rate
CCA: Canonical Correspondence Analysis
DCA: Detrended Correspondence Analysis
DI: Deionized water
LIA: Little Ice Age
MWP: Medieval Warm Period
PCA: Principal Components Analysis
PDO: Pacific Decadal Oscillation
NO_x: Nitrogen oxides
RDA: Redundancy Analysis
SO_x: Sulphur oxides

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1. Introduction

Climatic and Environmental Background

In aquatic environments, the increased temperatures resulting from anthropogenic warming have led to extended growing seasons, increased production, increased algal blooms and increased stratification in temperate and northern regions (Schindler, 2001). Concern over the potential impacts of current climatic change has sparked interest in the climates of the past, in the search of analogues to the current warming and to better understand the natural variation of biological communities in response to environmental changes. This is often done using information obtained from climatological proxies such as ice-cores or pollen to reconstruct past temperatures and using the remains of fauna in sediments to determine the ecosystem response to these changes. Using these records we are able, for example, to divide up the past into periods of relatively warmer and cooler climates compared to modern standards (Gajewski, 1988).

Pollen records document the changing vegetation of the past. Plant species live under specific environmental conditions and thus their allow us to infer temperature, moisture and soil characteristics of the particular region. Climatic reconstructions indicate that over the past 1500 years, North America has experienced two major climatic regimes, which are called the Medieval Warm Period (MWP) and the Little Ice Age (LIA) (Gajewski, 1988).

Ostracod-inferred temperatures from the Chesapeake Bay region indicate increased oceanic temperatures from 600-1400 CE (Cronin et al., 2010). Similarly, a temperature increase is observed from approximately 675-1375 CE in the region of eastern Canada (Lafontaine-Boyer, 2013), and from 800-1300 CE in the western Great Lakes (Booth et al., 2006). This period is referred to as the Medieval Warm Period (MWP). The MWP is

characterised by La Niña-like conditions (Pederson et al., 2005; Wahl et al., 2012) with increasing temperatures and drier climates throughout much of North America, particularly in the central-western regions of the United States and Canada (Booth et al., 2006). These changes may be associated with a cool phase in the Pacific Decadal Oscillation (PDO) and a warm phase in the Atlantic Multi-decadal Oscillation (AMO) (Pederson et al., 2005; Booth et al., 2006). Warmer temperatures are indicated by decreases in coniferous taxa *Pinus* and *Picea* and increases in deciduous taxa such as *Acer* and *Fagus* in eastern North America (Laird et al., 2003; Paquetteand Gajewski, 2013; Lafontaine-Boyer, 2013). Parts of central North America were much drier than periods since and after this, and experienced mega-droughts (Booth et al., 2006; Laird et al., 2012), while regions to the east tended to be less affected in terms of changes in precipitation (Lafontaine-Boyer, 2013). Diatom records from northwestern United States and northwestern Ontario indicate decreased lake levels due to increased drought frequency (Schmeider et al., 2011).

The Little Ice Age (LIA) followed the MWP and lasted approximately four centuries into the mid-19th century (Pederson et al., 2005; Mann et al., 2009). In mountainous regions of North America, the LIA began around the 13th to the 14th century with the onset of glacial advances brought about by decreased temperatures and/or increased moisture supplies (Fagan, 2000; Matthews & Briffa, 2005). This period was generally cooler and wetter than the present day and the MWP (Cronin et al., 2003). The LIA was associated with El Niño-like conditions in the north Pacific and a positive PDO phase (Pederson et al., 2005; Cronin et al., 2010). Pollen records from across North America indicate a decrease of 1-3°C during this time period (Viau et al., 2006; 2012; Viauand Gajewski 2009). A rapid transition from the MWP to the LIA was indicated in eastern Canada with a sharp increase in *Pinus* and *Picea* and a decrease in *Acer* and *Tsuga* from pollen records in laminated sediments

(Paquette and Gajewski, 2013; Lafontaine-Boyer, 2013). In eastern Canada, the LIA can be divided into sub-phases that are characterised by an increase or decrease of specific taxa in the pollen record (Lafontaine-Boyer, 2013).

In southeastern Canada, the first subdivision of the LIA (1375-1410 CE) was characterised by a decrease in *Tsuga* and *Acer*. *Acer* and *Tsuga* continued to decrease into the 17th century and *Salix* and *Betula* decreased from 1450-1700 CE. Abundances of *Pinus* and *Picea* pollen began to increase rapidly (Lafontaine-Boyer, 2013) during this time period with a brief increase in *Quercus* and *Alnus* towards the end of this period. *Betula* and *Fagus* began to increase in abundance towards the end of the LIA (1700-1860 CE) (Paquetteand Gajewski, 2013; Lafontaine-Boyer, 2013). The end of the LIA is indicated by a decrease in *Pinus* abundance and by an increase in *Acer*, *Fagus*, *Betula* and herbaceous plants (Lafontaine-Boyer, 2013); it coincided with the settlement of the area by Europeans. Temperatures began to increase towards the end of the LIA, indicated by a return of temperate taxa. Towards the end of the period there are indications of increased anthropogenic disturbance from European settlement in eastern North America.

The current warming trend that has been observerved as a result of anthropogenic activities has resulted in increased evapotranspiration, which has led to decreased water levels and ground water reserves (Schindler2001). Increased frequencies of toxic algal blooms threaten wildlife and drinking water supplies (Woodward et al., 2010; Taranu et al., 2015). Recent warming led to longer ice-off periods and decreased levels of dissolved oxygen in aquatic ecosystems; this resulted in shifts in the invertebrate populations and fish kills (Schindler et al., 2001; Jeppesen et al., 2001a). The increase in planktivorous fish populations reduced the populations of zooplankton; this combined with increased populations of phytoplankton uncoupled trophic interactions in food webs in many areas

(Winderand Schindler, 2004). Global climatic changes also exacerbate the impact of eutrophication on the aquatic ecosystems (Winderand Schindler, 2004).

Historically, anthropogenically-sourced acidification has been one of the foremost problems facing freshwater ecosystems in northeastern North America, Europe and other regions worldwide. Primary sources of acidification in northeastern North America consist of atmospheric sulphur and nitrogen oxide (SO_x and NO_x) emissions from metal smelting plants and other industrial sources, which precipitate into lakes (Jefferies et al., 2000; Jeziorski et al., 2008; Smol 2008). These activities have led to increased deposition of sulphurous and nitrogenous oxides and subsequently increased dissolved H^+ ions in nearby and regional water systems. As a result of their location on granitic rock watersheds and nutrient-poor soils, the lakes of the Canadian Shield are particularly vulnerable to additions of ions (Watmoughand Arhene, 2008; Walseng et al., 2003). This consequently lowers the pH and alters ecological communities. As a result of decreased grazing pressures brought about by decreased populations of Daphniids (Jeziorski & Yan, 2006; Jeziorski et al., 2008), acidification also leads to increased algal blooms (Walseng et al., 2003). In addition to acidification, lakes have also suffered from eutrophication (Schindler et al, 2001).

Lakes and rivers typically receive nutrient inputs from their catchments, therefore, septic-water runoff, increased agriculture, the use of detergents and fertilizers, and similar factors add nutrients to lakes. At a local scale, the eutrophication of lakes has led to increased macrophyte growth (Schindler et al., 1971), reduced transparency, shifts in fish populations towards smaller planktivorous fish (Jeppesen et al., 2001a), and increased blooms of cyanobacteria (Schindler, 2001; Taranu et al., 2015). The decrease in large piscovorous fish leads to decreased grazing pressures from zooplankton and increased algal growth (Jeppesen et al., 2001a). Increased biological production as a result of increased

phosphorus (Brooks et al., 2001) results in increased decomposition rates and oxygen depletion in the hypolimnion (Schindler, 1971; 1974). As the amount of phosphorus in the water column increases, floating algae begin to outcompete rooted plants for sunlight (Carpenter, 2005). Without rooted plants, sediment phosphorus becomes resuspended more easily, creating a positive feedback loop (Carpenter, 2005; Carpenter et al., 2001). Ultimately, the increased influx of nutrients may lead to increased ecosystem variability and decreased predictability (Cottingham et al., 2000). Human-induced eutrophication of freshwater inland lakes has become a major stressor impacting the diversity and composition of freshwater ecological communities in modern times (Brodersen et al., 1998; Dodson et al., 2000).

To track how ecosystems respond to environmental change, the remains of organisms extracted from lake sediments are used to infer the changes in ecological communities over time in response to environmental variability of the past. In addition, by understanding the niches of these organisms and their responses to environmental stimuli, we are able to infer changes in the environment over time where records are scarce.

Cladocera as Paleoecological Indicators

Paleoecology is the study of past environments and past interactions of organisms. A "paleoenvironmental proxy" is an organism that preserves well in strata over time, is relatively easy to identify, is niche-specific and responds in a known-way to changes in the environment. By recovering the remains of these organisms, we are able to infer aspects about the environment that they lived in and how it changed through time with changing species representations and community relations.

Cladocera are microscopic aquatic arthropods belonging to the class Branchiopoda. There are approximately 400 species in 80 genera that can be found in almost any freshwater body in the world, with the greatest diversity in the temperate regions (Korhola & Rautio, 2001). Their short generation time enables these organisms to quickly respond to stresses in an aquatic environment (Frey, 1986); the species diversity and richness of Cladocera changes more rapidly in response to environmental stress in comparison to longer-lived organisms (Frey, 1960; Korhola & Rautio, 2001). Upon death and moulting, their exoskeletons break up into constituent parts which are identifiable to the genus and even species levels (Frey, 1960; Korhola & Rautio, 2001). The exoskeletons of Cladocera are composed of chitin, which preserves well in lake sediments (Korhola & Rautio, 2001), making them useful as palaeoceological indicators (Frey, 1960).

Cladocera can be divided into to two groups; pelagic and littoral. Pelagic species are mostly open-water swimmers and inhabit the upper part of the water column while littoral species inhabit the vegetated areas associated with the sediment-water interface near the shoreline (Korhola & Rautio, 2001). Pelagic Cladocera tend to be generalists whereas littoral species are more habitat specific (Whiteside et al., 1978; Whitesideand Swindol, 1988). Pelagic species tend to comprise 80% or more of the subfossil assemblages recovered from the sediments, particularly in deep lakes (Kattel et al., 2007). Sediment cores are typically taken from the central deepest part of the lake and therefore most of the aquatic habitat above is pelagic while littoral organisms would need to be carried from the margins of the lake to the centre on water currents (Katel et al., 2007). Since littoral organisms are rarer in sediments, their remains account for a greater proportion of the living assemblage than what has been preserved from a central core. Therefore, changes in the species composition of littoral organisms generally account for greater change in ecology than do changes in percent

abundance of pelagic species (Whitesideand Swindol, 1988). This relationship is not as clear in shallow lakes with depths less than 5 m (Katel et al., 2007; Nevalainen et al., 2011), where littoral taxa dominate the communities.

Cladocera incorporate calcium (Ca) directly from the water as a component in their shells; some taxa have higher Ca demands than others (Jeziorski & Yan, 2006). The differences in calcium content make certain species good indicators of changes in acidity and calcium depletion in lakes. In addition to their sensitivity to calcium, many species are habitat specific, responding to changes in vegetation abundances as well as to changes in trophic interactions. As a result of properties such as these, the remains of Cladocera in lake sediments have been used as palaeoecological proxies to reconstruct past aquatic vegetation structure (Frey, 1968; Whiteside, 1978; Whitesideand Swindol, 1988), to infer eutrophication (Krause-Dellinand Steinberg, 1986; Broderson et al., 1998; Jeppesen, 2001b) and acidification processes (Jeziorski et al., 2012; Walseng et al., 2003), in the reconstruction of predator-prey dynamics (Kerfoot et al., 1975; 1977; Korosi et al., 2013) and in the tracking of changes in temperatures (Nevalenin et al., 2010).

Species within the family Chydoridae are indicators of the type of littoral vegetation, which are often governed by nutrient composition. Species typically found in sand and muddy sediments with little to no vegetation are primarily from the genus *Alona—Alona circumfimbriata, A. rustica* and *A. intermedia* (Whiteside et al., 1978), as well as other less common species *Monospilus dispar, Acroperus harpae* and *Chydorus piger* (Whiteside et al., 1978; Whitesideand Swindol, 1988). These species tend to be poor swimmers and detritivores (Frey, 1968; Korhola & Rautio, 2001). *A. quadrangularis, A. affinis* and *Chydorus brevilabris* are typically present among littoral vegetation. *C. brevilabris* (referred to as *C. sphaericus* in Europe) is a generalist plant-dwelling organism that prefers dense

vegetation and is also tolerant of high phosphorus levels (Broderson et al., 1998); however, this species is highly adaptive and is able to live in a wide variety of habitats. It is able to vertically migrate and live among the floating beds of algae and cyanobacteria in highly eutrophic waters (Jeppessen et al., 2001b; Albert et al., 2010). *Alonella* species are exclusively plant dwellers (Whiteside & Swindol, 1988; Tremel et al., 2000). They tend to inhabit near-shore floating leafed vegetation and dense macrophytes of shallow lakes. They graze on epiphytic algal particles and on floating decaying organic matter (Frey, 1968; Whiteside et al., 1978; Tremel et al., 2000). These species are also oligotrophic clear water indicators (Albert et al., 2010). Other macrophytic taxa include *Eurycercus, Camptocercus, Graptoleberis* and *Pleuroxus* (Whiteside et al., 1978; Whiteside & Swindol, 1988).

Changes in aquatic vegetation are in turn related to changes in the nutrient concentrations (Broderson et al., 1998), specifically phosphorus, which is often the limiting nutrient in an aquatic ecosystem and the primary determinant of primary production and algal growth (Schindler, 1974; Brooks et al., 2001). As eutrophication progresses in the water column, shifts in aquatic vegetation structure occur, particularly in shallow lakes (Schefferand Egbert, 2007). As long as rooted macrophytes are present in the water column, the environment will tend to remain in a clear water state (Schefferand Egbert, 2007). This leads to an increase in littoral species, particularly *A. affinis* and *C. brevilabris* (Albert et al., 2010). However, as phosphorus increases in the water column, planktonic algae become more abundant and begin to shade and out-compete rooted macrophytes (Schindler, 1974; Schefferand Egbert 2007). Decaying macrophytes release more phosphorus into the water column and may create an anoxic hypolimnetic environment (Smol, 2008). The anoxic environment causes the phosphorus in the sediment to be released from iron, which creates a positive feedback loop (Smol, 2008). Hypereutrophic environments dominated by algae tend

to have a decreased diversity of Cladocera (Broderson et al., 1998). The increase in pelagic resources tends to cause a shift towards the dominance of pelagic Bosminids and *C. brevilabris* over other species (Jeppessen et al., 2001b; Davidson et al., 2011). Using these relations, Broderson et al (1998); Jeppeson et al., (2001b) constructed a transfer function of Chydoridae phosphorus tolerances using the species assemblages and phosphorus levels in Danish lakes.

Cladocera are often used as indicators of acidification. The high Ca content in the shells of Daphniidae makes them particularly vulnerable to changes in acidity (Jeziorski & Yan, 2006), and *Daphnia* populations tend to decrease significantly once the pH drops below 6.5 (Jeziorski & Yan, 2006; Jeziorski et al., 2008). Individuals of *Daphnia pulex* complex, as a result of their smaller size, have lower Ca requirements and are slightly more tolerant of acidic conditions when compared to the larger *D. longispina* (Walseng et al., 2003; Jeziorski et al., 2006). Shifts from *D. longispina* to *D. pulex* may be interpreted as the beginnings of acidification stress in lakes. Further increases in acidity lead to the increased dominance of Bosminidae at the expense of Daphniidae species in the pelagic zone as well as the increased overall abundance of littoral organisms (Walseng et al., 2003; Korosi & Smol, 2012c). Littoral organisms, particularly chydorids, are—compared to daphniids— calcium-poor species that tend to be more acid tolerant. The species *A. rustica, A. intermedia*, and *Alonella excisa* are acidophilous and exhibit maximum abundances when pH is less than 7 (Krause-Dellinand Steinberg, 1986; Walseng et al., 2003). *Alona affinis, Chydorus faviforms, Eurycercus* and *Graptoleberis testudinaria* tend to prefer circumneutral waters (Krause-Dellinand Steinberg, 1986; Walseng et al., 2003). *A. quadrangularis, Camptocercus* spp. and *Pleuroxus* spp are alkophilous species and tend to be most abundant in waters above pH 7 (Krause-Dellinand Steinberg, 1986). Finally, some species are indifferent or tolerant to

changes in acidity, such as *C. brevilabris*, *Alonella nana* and *Acroperus harpae* (Dellinand Steinberg, 1986). The presence/absence of one particular species of Cladocera cannot tell us the pH of a lake at a given time; however, by looking at the entire assemblage and the species proportions at a specific time, we may be able to determine the acidity of the ecosystem. Cladocera are also often used in conjunction with other paleoecological proxies such as diatoms and Chrysophytes to interpret changes in acidity; many diatom and chrysophyte acidification transfer functions have been developed to determine pH from taxonomic assemblages using lakes of a known pH as calibration (Batterbee et al., 1999; Batterbee et al., 1990).

Cladocera occupy an intermediate position in the food web, being impacted by both producers and consumers (Korhola et al., 2001). Cladocera are typically preyed upon by small planktivorous fish as well as other larger arthropods. The different pressures that these two groups of predators exert on the cladoceran community leave a mark on their morphology and on their size distributions (Kerfoot, 1975; 1977; Dodson, 1974; Korosi, 2013). Predators will often have a preference for prey with particular traits and hence prey with traits that predators find undesirable will survive preferentially over individuals with more desirable traits (Dodson, 1974; Boersma et al., 1998). Hence prey will continue to evolve anti-predator mechanisms. In order to keep up, predators evolve better abilities to capture prey in an evolutionary "arms race", which is called the "red-queen hypothesis" (Van Valen, 1979). In the case of Cladocera, individuals develop morphological features that deter predators, they may adapt behaviourally or evolve life history strategies adapted towards predator evasions (Tollrian, 1995). Morphological defenses are the most widely studied and are readily identifiable in lake sediments. The development and maintenance of these traits often incurs an energetic cost; thus, in the absence of threats, individuals without

these features will often have a competitive advantage over individuals possessing defensive traits (Kerfoot, 1977). This creates a negative feedback loop that allows for rapid replacement of individuals and the tracking of responses to changes in trophic interactions.

Different species of *Daphnia* often develop horns and neck spines in response to different kairomones produced by predators in the water column (Dodson et al., 1984; Tollrian 1995; Boersma et al., 1998).The ratio of *Daphnia* to the sum of *Daphnia* and *Bosmina* extracted from lake sediments can give a good indication of the prevalence of planktivorous fish in the aquatic ecosystem (Kerfoot, 1975). This is because *Daphnia* are much larger than *Bosmina* and are therefore more likely to be observed and eaten by small fish species (Jeppesen et al., 1996; Kerfoot, 1975). The spines and horns of *Daphnia* spp. do not preserve well in lake sediments, however.

In recent years, the study of cyclomorphsis in response to predation pressures in Bosminidae species has grown as a result of easily identifiable traits and their high fidelity in the lake sediments (Korosi et al., 2013). Small planktivorous fish are visual predators and therefore tend to select larger individuals over smaller ones (Twiningand Post, 2013; Korosi et al., 2013), whereas most invertebrate predators are gape dependent and select small individuals that require less handling time compared to larger ones (Zaret and Kerfoot, 1975; Kerfoot, 1977; Labaj et al., 2013). The difference in selectivity results in differential survival of individuals within the community. Many studies have been able to refine this technique showing that small body size and curved antennules are specifically indicative of fish predation (Sanford, 1993) and that *Bosmina* populations that are heavily predated upon by *Chaoborus americanus* larvae have larger mucros (Labaj et al., 2014). Therefore, higher representations of large-bodied individuals with elongated antennules and tail structures (mucros) indicate greater predation pressures by invertebrates over fish; while, higher

representations of smaller individuals in Bosminidae would be indicative of increased predation pressures from planktivorous fish over invertebrates. This differential survival is preserved in the sediments and thus we are able to track changes in predation regimes over time using these measurements.

Cladocera tend to have broad temperature tolerances, and therefore species assemblages are not often used as paleoclimate indicators, as is done with pollen (Korhola & Rautio, 2001). In order to interpret past climates from Cladocera, more indirect inferences must be used (Smol, 2008; Nevalainen et al., 2010). For example, Cladocera reproduce parthenogenically throughout most of the year and reproduce sexually during times of stress (Korhola & Rautio, 2001). During times of stress resulting from decreased temperatures or increased ice cover, the proportion of asexually-produced males in communities increases and the Cladocera begin to reproduce sexually as a means of survival (Kultti et al., 2011; Dodsonand Frey, 1991). When Cladocera reproduce sexually, they produce eggs that are encased in the carapace (called an ephippium) that sinks to the bottom after moulting (Kulti et al., 2011). The eggs enter diapause until favourable conditions arise (Dodsonand Frey, 1991: 731). These cases are resistant to freezing, desiccation and even digestion (Jeppsen et al., 2003). They have been known to remain viable for at least 150 years (Kultti et al., 2011). Observing the changes in the proportion of ephippia preserved in the sediment over time allows for the inference of increases and decreases in the length of the ice over period in the past (Kultti et al., 2011). Jeppsen and colleagues (2003) developed a model to track temperature changes over time using *Bosmina.* They determined that temperature is proportional to the sum of the number of carapaces and the number of ephippia divided by number of ephippia in the sediment for a given time interval. In addition to ephippia, the percentage of males compared to females of some species can infer colder climates

(Nevalainen et al., 2012). For example, an increased proportion of Chydoridae ephippia around 13.2-11.0 ka represented a cold period during the Pleistocene/Holocene transition in Finland (Nevalainen et al, 2012; Kultti et al., 2011). Ephippia have also been used in resurrection ecology (Kerfootand Weider, 2004; Kultti et al., 2011) in which we have been able to hatch eggs found in sediments to determine taxonomic composition of the past community and infer ecology by means of genetic analysis. The genome of the individuals that were resurrected in adapted to the past environment we are thus able to infer environmental properties using this technique (references).

In addition to predicting the relative length of ice-on time, Nevalelainen and colleagues (2011) determined that the ratio of pelagic organisms to littoral organisms in the community is related to depth of the lake, provided that surface area and other properties remain somewhat constant. As depth increases, the proportion of water that is in contact with the sediment decreases and therefore the proportion of pelagic habitat to littoral habitat increases (Nevalainen et al., 2011). Tracking changes in water depth of closed basin lakes over time can allow the inference of changes in precipitation and thus the aridity of the climate (Nevalainen et al., 2011); however, the morphology of the lakes needs to be considered.

Using Cladocera, we are able to track community and ecological changes in response to changes in habitat, nutrient content, acidity, predator-prey relationships and climate in order to better understand how ecosystems change over time. These phenomena do not exist in a vacuum; the cladoceran community is the product of the response to a variety of different stressors acting upon it at any given time. Eutrophication can lead to excessive macrophyte growth (Schindler et al., 1971; Roelofs, 1983), with a total loss of macrophytes in later stages (Brothers et al., 2013). Therefore in the earlier stages of eutrophication we

would expect to see an increase in littoral species, while in later stages we would expect a shift back towards pelagic species (Brothers et al., 2013; Vermaire et al., 2012; 2013). Acidification often leads to decreased populations of small planktovorous fish and a dominance of invertebrate predators (Walseng et al., 2003). Ecological phenomena interact to create a dynamic ecosystem. These interactions can often make it harder to determine specific stressors that organisms are responding to. Cladocera respond to a variety of conditions and by understanding how they respond we are able to better understand how aquatic ecosystems change over time in response to different types of stressors.

In this thesis, I will reconstruct past community interactions and infer changes in habitat structure through time using Cladocera as a paleoecological proxy. These interactions will be interpreted in the context of environmental change in a lake ecosystem. A detailed chronology of the lake sediments will be provided using annually-laminated lake sediments (Lafontaine-Boyer & Gajewski). The climatic record will also allow us to determine the impact of changing temperatures and regional vegetation on the taxonomic composition.

Formation of Laminated Sediments in Lakes

Varves are a specific type of annual lamination formed in lake sediments that consist of at least two layers of different composition (Ojala et al., 2000). The use of annually laminated sediments from these lakes allow for accurate dating. By "cross-dating" the individual layers, an accurate chronology may be developed (Stokesand Smiley, 1996).

The most common type of varve in temperate regions is biogenic/clastic (O'Sullivan, 1983; Zillen et al., 2002). These layers typically form in environments with a strong seasonal climate, characterized by winter ice-cover, spring floods, summer stratification, seasonal

algal blooms and autumn storms (Ojala et al., 2002). This change in conditions creates seasonal differences in accumulation of materials within the sediments. Darker, fine grained bands are formed during the winter while lighter-coloured material is deposited in during the summer months (O'Sullivan, 1983; Larsen et al., 1998). Dickman (1979) determined that the lighter bands are usually the result of excess CO_2 combining with calcium to form calcium carbonate which precipitates to the bottom to form calcite deposits while the darker bands are from decaying organic matter that falls to the bottom at the end of each growing season. As a result, this seasonality allows for the identification of years and even individual seasons (O'Sullivan, 1983).

The formation of varves often occurs in relatively deep lakes with steep sloped edges, a flat bottom (which prevents the slumping of the sediments) and at least seasonal anoxia below the hypolimnion (Dickman, 1979; Zillen et al., 2002; O'Sullivan, 1983). The anoxicia prevents bioturbation and slows down the rate of decay, allowing layers of organic material to subsequently build up year after year. In addition to being relatively deep, many of these lakes are meromictic, possessing a chemocline (Dickman, 1979; O'Sullivan, 1983). This chemocline creates a difference in density which further prevents the mixing of the bottom layer with the oxygenated part of the water column, preventing disturbance (Dickman, 1979). The formation of varves allows for accurate dating and the excellent preservation of biological remains in lake sediments. Using these high-resolution records, we are able to identify key events in the history of ecosystems and connect changes in community structure to known disturbances that occurred throughout history.

Lac Brûlé

Lac Brûlé (45.72° N, 75.43° W 270 m; Figure 3.1) is a small deep lake (10 hectares by 43 metres deep) located in the Municipality of Mulgrave-et-Derry in the western part of the Regional County Municipality of Papineau (Lafontaine-Boyer, 2013). It is located in the mixed deciduous-coniferous forests characteristic of the Canadian Shield (Braun et al., 1950). The lake is relatively well sheltered by large hills. There is minimal development in the area with only one cottage on the lake. The local geology of the area consists of quartzite, paragneiss, pegmatite and granite (Ministere du resources naturelles, 2013). The average annual temperature of the area is 5°C and it has an average monthly total precipitation of 1054 mm (Lafontaine-Boyer, 2013). The lake is oligotrophic (TP = 4 μgL^{-1}, TKN = 170 μgL^{-1}) with a conductivity of 120 μScm^{-1}, a pH of 8.35 and a calcium concentration of 22.8 mgL^{-1} at the surface; measurements were taken from the surface of the lake October 5th 2013 prior to autumn overturn.

Lac Brûlé is a meromictic lake with a chemocline that occurs around 30 m (Figure 1.1). Below the chemocline, the phosphorus increases to 7.6 mgL^{-1}, nitrogen to 153 mgL^{-1}, the conductivity to 1234 μScm^{-1}, and the pH decreases to 6.2. There is also a sharp increase in calcium and other metals at the monolimnion.

When the results of a lake profile collected in this study are compared those published in Lafontaine-Boyerand Gajewski (2014), the curves of temperature, pH, and specific conductance are relatively similar, however, dissolved oxygen content decreased to very low levels in 2012, whereas the oxygen content increased below the chemocline in our study. This is likely a measuring error; in 2013 we used a Van Dorn bottle to collect a water sample and bring it to the surface for oxygen measurements, as our hydro-lab was only able

to reach 25 m depth (Figure 1.1). However, measurments taken by Lafontaine-Boyer in 2012 were taken from the deepest part using a dissolved oxygen probe with a cable in excess of 50 m (Lafontaine-Boyer & Gajewski, 2014). Opening the bottle and inserting the probe the may have oxygenated the water.

A pollen analysis of Lac Brûlé was conducted using a core to reconstruct trends in the regional vegetation over time and infer past climates (Lafontaine-Boyer & Gajewski, 2014). Lafontaine-Boyer & Gajewski (2014) determined that a large forest fire occurred around 1375 CE, and that this affected the sedimentation in the lake.

Cladoceran fossils were extracted from a second core collected from Lac Brûlé and were analysed to reconstruct community composition in relation to changes in vegetation composition and climatic variation that were inferred from the pollen record. Using the changes in community composition we were also able to infer changes in habitat structure and species interactions in response to climatic changes and other regional environmental stimuli.

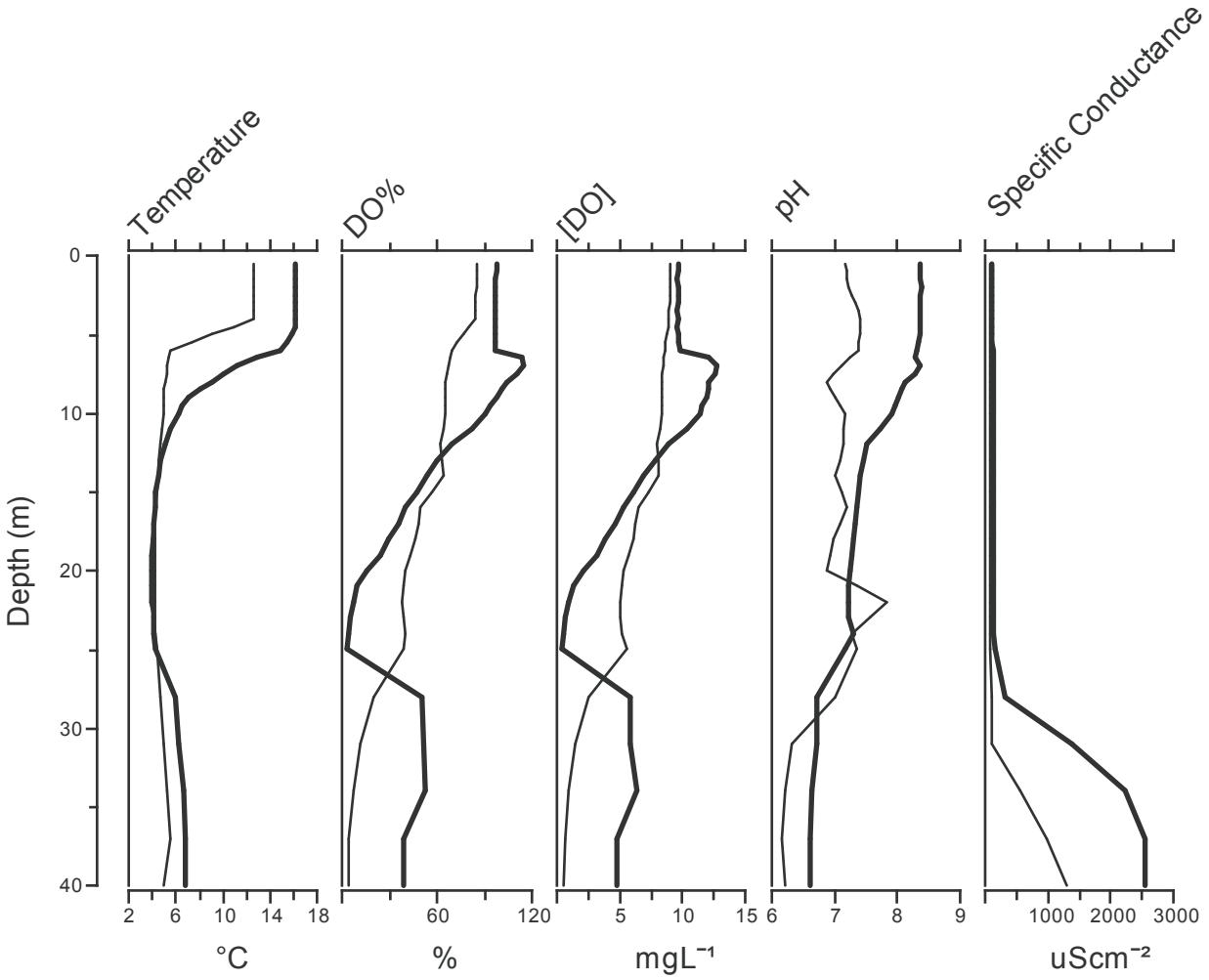

Figure 1.1: A comparison of Lac Brûlé depth profiles taken October 6th 2013 (bold) and June 2012 (Lafontaine-Boyer & Gajewski, 2014). The diagram shows temperature (°C), percent oxygen saturation, dissolved oxygen concentration (mgL^{-1}), pH and specific conductance (μScm^{-1}) as a function of depth.

Objectives

The objectives of this thesis were to track the ecological changes in the Lac Brûlé ecosystem in response to climatic changes, changes in catchment vegetation and anthropogenic impacts through time using Cladocera as a paleoecological proxy. This is done through the analysis of the cladoceran remains from a sediment core on a high-resolution time scale.

The thesis is written in article format, consisting of an introduction, two main articles (Chapters 2 and 3), followed by an overall conclusion to the thesis (Chapter 4). The first part (Chapter 2) is the study of the recently-deposited Cladocera from a series of lakes from the Gatineau Hills area of SW Québec. These data were combined with similar surface sediment analysis done in the area of Eastern Canada (Desellas et al., 2008). The purpose of this first part was to aid in the interpretation of the sediment core. The cladoceran assemblages were compared to the chemical composition and other abiotic factors of the lakes. Multivariate analyses were used to characterize the relation between the community and the abiotic environment. First, a Principal Components Analysis (PCA) of the different measured variables within the lakes was used to determine which environmental variables accounted for the most variation in the lakes and how these variables are related to one another. A Correspondence Analysis (CA) was then used to determine relationships between the taxa extracted from the surface sediments, as well as how similar the lakes are to one another in terms of species compositions. A final step was a Redundancy Analysis (RDA) (or a Canonical Correspondence Analysis (CCA)) that indicates the influence of the environmental variables on the cladoceran species as well as the interspecies relationships.

This allows us to infer the environmental preferences of the various taxa in the cladoceran community (Borcard et al., 2011; Crawley, 2013).

In the second part of this thesis (Chapter 3), the changes in the community composition of cladoceran species through time in a sediment core from lac Brûlé will be used to reconstruct changes in aquatic environment over the past 1200 years. This information will be combined with records of vegetation and reconstructed temperature and precipitation over the last 1200 years derived from the pollen record (Lafontaine-Boyer & Gajewski) to infer the impact of the changing climate on cladoceran community composition.

Unfortunately, the environmental gradient in the modern sample set was found to be too small, thus it was not possible to develop a useful model that could be used for a quantitative reconstruction downcore. Furthermore, analogues for the subfossil assemblages could not be found in the modern samples (Appendix 1). Thus, the two chapters of the thesis could not be analysed together numerically. These results of Chapter 2 will be instead be used in a qualitative way to aid in the interpretation of the core (Chapter 3). In the future, these results from Chapter 2 can be combined with other studies to produce such a transfer function for a wider area.

Predictions

For this thesis, a series of predictions were made with reference to how the community will respond to past environmental conditions. Using remains of these organisms in the lake sediments, we will be able to track changes through time, and link these changes in community composition with key climatic events and other environmental conditions, determined from the independent climatic record through time.

1. There will be a greater abundance of Daphnia species during preindustrial times compared recent times. This is because Daphnia tend to prefer cooler waters (Whiteside et al., 1978). The decrease in *Daphnia* should most pronounced in warmer periods such as the 1940s, 1990s and into the new millennium. In addition to the warming climate and increased nutrients, the abundances of Daphniids will also likely be decreasing as a result of less Ca in the water (if a decrease in Ca concentrations can be implied) (Halland Smol, 1996; Jeziorski & Yan, 2006). The decrease in *Daphnia* will also likely be coupled with an increase in the representation of Bosminidae and in acidophilic species, particularly *Alona rustica, Alonella excisa* and *Chydorus brevilabris* with acidification (if shown to occur).

2. *Daphnia* will increase in abundance during the LIA as a result on cooler waters and decreased stratification. *Daphnia* are more efficient grazers and should thus out-compete Bosminidae during times of low primary productivity (DeMot and Kerfoot, 1982).

3. *Chydorus brevilabris* and other plant-associated species will increase in abundance during periods of increased temperatures, due to increased macrophyte growth and primary production, which would have increased the availability of their habitat. Conversely, there should be an increase in the representation of *Alona*, *Leydigia*, *Acroperus* and other mud and sediment dwelling taxa (particularly *A. rustica* and *A. circumfimbriata*) during cooler periods.

4. Lafontaine-Boyer and Gajewski (2014) described the occurrence of a large forest fire around 1375 CE in the vicinity of Lac Brûlé. With the fire will come shifts in cladoceran community composition consistent with increased nutrient and cation influx, and decreased sunlight penetration into the water. Changes in community composition will include increased representation of pelagic species and an increase in the representation of *Alona* and other sediment-dwelling taxa. The changes in the community after theimpact of the fire dissipates from the record should allow for the tracking of the recovery of community post change. The post fire ecology of the lake should revert to a similar state that is consistent with the climatic regime of the time.

2. Cladoceran Communities of Southwestern Québec Lakes

Abstract

Cladoceran remains were counted and identified from surface sediments collected from thirty-one lakes in the Gatineau Hills region of Québec, Canada. A Redundancy Analysis was used to determine the influence of the chemical concentrations and morphological features of the lakes on the taxonomic composition of the organisms. The lakes were circumneutral to alkaline with moderate to high concentrations of calcium and other ions. The nutrient content of the lakes ranged from oligotrophic to meso-eutrophic. Principal Components Analysis showed that the concentration of calcium, magnesium and sulfate, the pH and the specific conductance of the lakes was influenced by the composition of the watershed bedrock. The communities of the lakes were primarily dominated by pelagic species; *Bosima longirostris* was the most commonly found species. *Chydorus brevilabris/biovatus* was the most commonly found littoral organism. The pelagic species were primarily influenced by the concentrations of metals and lake depth, while the littoral species were mostly influenced by the nutrient concentrations and area.

Introduction

Eutrophication, acidification and calcium loss are major stressors on the biological communities of Canadian Shield lakes in northeastern North America. With increasing human impacts on aquatic ecosystems it is necessary to better understand the role that water chemistry plays in influencing the biodiversity and the distribution of organisms within them; allowing for a stronger comprehension of how changing environmental conditions impact the abundances and composition of species within ecosystems through time and space.

Sediments that collect at the bottom of lakes contain the remains of organisms that once lived within the ecosystems, from algae and other plants to fish and larger animals (Smol, 2008). Studies of lake sediments show that cores taken from the central, deepest part of the lake integrate organismal remains from the entire aquatic community (e.g., Frey, 1960; Smol, 2008; Korhola & Rautio, 2001). As a result, the surface sediments taken from this location provide a snapshot of the distribution of the biota within the ecosystem at the time of deposition. Combining this information with chemical concentrations and other environmental variables of the lakes allows us to infer the relationships between the distribution of organisms and the environments they live in. The results can be used to interpret fossil assemblages of the past, where environmental records are scarce, and to predict how organisms will respond to changing environments.

Cladocera are crustacean arthropods that inhabit most freshwater lakes and ponds worldwide. They graze on algae and decaying plant matter (Korhola & Rautio, 2001). Their exoskeletons are composed of chitin, which preserves well in lake sediments (Korhola & Rautio, 2001), making them useful as palaeoceological indicators (Frey, 1960). Cladocera incorporate calcium (Ca) directly from the water as a component in their shells and some

taxa have higher Ca demands than others (Jeziorski & Yan, 2006). The shells of *Daphnia* spp., for example, are composed of twenty times as much Ca as other cladoceran taxa (Walseng et al., 2003). It is this high calcium requirement that makes them sensitive to changes in Ca concentrations and pH (Jeziorski & Yan, 2006) in lakes, and good indicators of lake acidity. Hard-shelled taxa that do not incorporate as much Ca into their exoskeletons are better able to survive acidic conditions; this group consists of the families Bosminidae, Chydoridae, and Holopeididae.

Bosminidae and Holopeidiae are generalist pelagic taxa that live in the upper part of the water column (Korhola & Rautio, 2001), while Chydoridae species live among the sediments and aquatic vegetation of the shallow littoral and benthic zones (Whiteside & Swindol, 1988); this group of species is habitat specific. *Chydorus, Pleuroxus, Eurycercus and Camptocercus* species are macrophytic and live among submerged vegetation. *Alonella* spp. are epiphytic and live on or amongst emergent floating leafed plants, while most *Alona* spp. are mud and rock dwelling organisms that inhabit sediments, and rock surfaces (Whiteside & Swindol, 1988). Thus, the fluctuations in the relative abundances of these taxa in sediment cores may be interpreted as changes in lake water chemistry, macrophyte cover and vegetation composition (Davidson et al., 2010).

Changes in aquatic vegetation are in turn related to changes in the nutrient concentrations (Broderson et al., 1998; Bos and Cummings, 2003), specifically phosphorus, which is often the limiting nutrient in an aquatic ecosystem and the primary determinant of primary production and algal growth (Broderson et al., 1998; Brooks et al., 2001). As a result of ecological relationships such as these, the remains of Cladocera in lake sediment cores have been used as palaeoecological proxies to determine the responses of aquatic ecosystems to changes in chemical composition from stressors such as eutrophication

(Broderson et al., 1998; Albert et al., 2010) and acidification (Jeziorski et al., 2012; Walseng et al., 2003), or in the reconstruction of past aquatic vegetation structure and predator-prey dynamics (Davidson et al., 2011; Korosi et al., 2013).

The cladoceran communities of southwestern Québec have been relatively understudied compared to other Canadian Shield areas in eastern Canada, including lakes in south-central and northern Ontario (Desellas et al., 2008; Kurek et al., 2011; Walseng et al., 2003, Pinel-Alloul et al., 1990). As a result of the surrounding landscapes and granitic watersheds (Watmough and Ahrene, 2008), lakes on the Canadian Shield are typically characterised as nutrient poor (Kurek et al., 2011) and low in dissolved ions (Walseng et al., 2003; Jeziorski et al., 2008). Recent lake acidification in the Canadian Shield is a direct result of increased atmospheric sulfur dioxide (SO_x) inputs from coal-burning power plants and other activities such as metal smelting in the Greater Sudbury region (Jefferies et al., 2000) and logging (Hall & Smol, 1996). These activities have led to increased deposition of dissolved ions in soft water, nutrient poor lakes (Walseng et al., 2003), lowering the pH and altering the ecological communities.

This study examines the influence of the water chemistry and lake morphology on the cladoceran community abundances in circumneutral lakes with moderate to high Ca levels in southwestern Québec. Lakes in southwestern Québec are of interest because, compared to lakes just to the north in the Abitibi region of the province (Auclair et al., 1993) and in adjacent areas of southern and northeastern Ontario (Walseng et al., 2003; Jeziorski et al., 2008; 2013; 2014), they have not acidified greatly in the last one hundred years (Dupont, 1992; Jefferies et al., 2000). As a result, the lakes in this region contain, on average, higher Ca concentrations and higher pH compared to lakes in adjacent regions on the Canadian

Shield (Dupont, 1992) that have been impacted by acidification. These conditions should influence the cladoceran communities of these lakes.

The lakes are located in southwestern Québec, on the Canadian Shield between 45.4 and 46.2^{o}N and between 75.0 and 76.2^{o}W (Figure 2.1). Many of these lakes are situated on marble bedrock with others on paragneiss, granite, sable, syenite and gabbro (Wilson, 1964). The lakes are primarily surrounded by mixed deciduous-coniferous forests that are dominated by maple (*Acer),* birch (*Betula),* cedar (*Thuja),* and pine (*Pinus*) (Braun, 1950).

Materials and Methods

Field Methods

Surface sediment samples were collected during the summer to early autumn months of 2013. The depth of the lakes was assessed using a depth sounder and a Glew-gravity corer was used to collect sediments from the deepest part of each of the lakes. Cores were extruded using a core-extruder into one centimetre subsections. The sediment was placed in plastic bags and stored in a refrigerator at 4°C. Later, the first centimetre of sediment was used as a surface sample for the preparation, identification and analysis of organismal remains.

Surface pH and specific conductance of the lakes was measured on site using a pH/conductivity probe. The chemistry and the chlorophyll concentrations of the surface water were measured by sampling three litres of water from the surface using acid-washed Nalgene bottles. Two litres were used to measure the concentration of Chlorophyll-α in the water while the remainder was analysed for total phosphorous and total nitrogen (filtered and unfiltered), metal and ion concentrations by the City of Ottawa Water Treatment Centre. The

extraction of chlorophyll-α was carried out following the protocol from Burnison (1980) and concentrations were calculated following Jeffrey and Humphrey (1975).

Cladocera Sample Preparation

Extraction of the cladoceran remains from the sediment followed the protocol of Korhola & Rautio (2001). One to three millilitres of sediment were sampled from the uppermost centimetre from each of the lakes. The samples were deflocculated in 150 mL of 10% potassium hydroxide (KOH) solution at 70-80^{o}C for 30 minutes with continuous stirring. This was done to break up any larger particles and separate the organisms from the sediment. After 30 minutes, the solution was left to cool to 40^{o}C before being strained through a 30 µm filter and washed with deionized (DI) water until the water ran clear. The remaining material on the filter was poured into a 5 mL vial with DI water. Five drops of 95% ethanol were added to preserve the samples and one drop of safrarin-red was used to stain the organisms for identification.

Slides were prepared by first placing one drop of glycerine onto a microscope slide. Using an aliquot pipette, with the opening of the tube cut to one millimetre in diameter, 100 µL of sample was pipetted onto each slide and excess water was allowed to evaporate on a warming plate at 70°C. Once the water evaporated sufficiently, one to two 22 X 22 mm cover slips were placed over the samples and sealed using nail polish.

Identification

Slides were viewed under a Nikon Eclipse 90i light microscope at 200X magnification, increased to 400X when required. Individual skeletal components were identified to genus

and species where possible. The fossilized components (e.g., carapace, headshield) were noted and the length was measured to the nearest 50 µm using NIS Elements Br 3.0 Software. Between 125 and 150 specimens or a maximum of 10 slides per site were counted to obtain an appropriate estimate of species composition (Kurek et al., 2010) within each of the lakes.

Since there is no single guide to the identification of cladoceran subfossils in lake sediments for North America, an assortment of sources were used for the identification, including Bos (2001), Sweetman (2006), Korosi & Smol (2012a and b), De Melo & Hebert (1994), Brandelova et al (1972), and Szerocynska & Sarmaja-Korjonen (2007). To distinguish between genera within the family Bosminidae the curvature of the antennules, the length and roundness of the rostrum, the shape of the carapace, the presence/absence of pectin on the mucrones (De Melo and Hebert, 1994), position of head pores and the overall size of the individuals were used (Korosi & Smol, 2012a). The carapace and head strucutres of Daphniidae are rarely found in sediments as these components are rich in Ca compared to that of other claodceran taxa and thus do not preserve well over time (Frey, 1986; Korhola & Rautio, 2001; Korosi & Smol, 2012a); typically, only the postabdominal-claws and occasional ephippia are recovered (Korhola & Rautio, 2001; Korosi & Smol, 2012a). The presence/absence of larger teeth at the base of the postabdominal claw was used to distinguish between *Daphnia pulex* and *D. longispina* species complexes (Korosi & Smol, 2012a). The identification of remains in the family Chydoridae was carried out using Sweetman (2006), Bos (2001) and Korosi & Smol (2012b). Other, less common, groups were identified using Korosi & Smol (2012a).

Data Analysis

Using the statistical programme R (R Foundation, 2013), a Principal Components Analysis (PCA) of the chemistry and the physical features of the lakes was performed to summarize the variability and relationships between these variables. Chemicals that were present above the detection limit in at least 50% of the lakes were retained for the analysis. Environmental variables were transformed to approximate normal distributions (Table 2.2). Those that could not be so transformed (this typically occurred as a result of containing two or more values that were more than two standard deviations from the mean in one direction) were removed from the analyses.

A detrended Correspondence Analysis (DCA) was performed on the species abundances from the lakes to determine the gradient in standard deviation units of the community composition. This gradient determined whether linear (PCA) or nonlinear methods (Correspondence Analysis; CA) should be used to summarize the distribution of the species within the group of lakes (Borcard et al., 2011). Only species or taxonomic groups that represented at least 1% of the assemblages in at least five of the lakes were retained for numerical analyses, leaving 15 taxonomic groups. Taxa that did not meet this criterion were lumped into either of the "Other Pelagic" or "Other Littoral" categories. *Chydorus brevilabris* and *C. biovatus* were grouped together as *C. brevilabirs/biovatus* due to their morphological similarities. Species abundances were transformed using the Hellinger transformation (Legendre & Gallagher, 2001; Legendre & Legendre, 2012), which down-weighs the importance of the most abundant species. The gradient of the DCA was found to be less than 2.5 standard deviation units; therefore, a PCA of the species abundances was used to summarize the taxonomic relationships among species in the communities and between lakes, and a Redundancy Analysis (RDA) was used to determine the influence of

the environmental variables on the distribution and abundances of the taxa in the lakes (Borcard et al., 2011; Legendre & Birks, 2012). The Variance Inflation Factor (VIF) of each variable was calculated to determine the colinearity of the variables to one another in space; variables with a VIF greater than 7 were removed from the RDA one at a time. Forward selection was used to determine the variable that had the greatest influence on the abundance of the organisms within the lakes (Borcard et al., 2011).

Results

Lake Environments

Most of the lakes were relatively small, with approximately two-thirds less than 20 ha in area, and relatively shallow, with two-thirds less than 20 m deep. The median area of the lakes was 11.5 ha and the median depth was 17.2 m. The remainder of the lakes were mostly larger in area and relatively deep, with a few small and deep lakes. Most of the lakes in the series stratified to some degree (the most notable acception being Lac Des Vases). The nutrient content of lakes ranged from oligotrophic to meso-eutrophic with phosphorus concentrations between 3 and 43 μgL^{-1}, with an average of 8 μgL^{-1}, and nitrogen concentrations from 160 to 630 μgL^{-1} with an average of 310 μgL^{-1} (Table 2.2). The pH ranged from 7.2 to 8.7, with an average of 8.1, and specific conductance ranged from 20 to 245 μScm^{-1}, with an average of 125.3 μScm^{-1}. Ca concentration ranged from 6.4 to 42.9 mgL^{-1} with an average concentration of 19.2 mgL^{-1}; all lakes in the series contained calcium levels above the threshold required for the survival of *Daphnia* spp. (Table 2.1) (Jeziorski & Yan, 2006). The sodium (Na) concentration of the lakes ranged from 0.4 to 15.3 mgL^{-1} with an average concentration of 2.3 mgL^{-1}.

Cladoceran Communities

Cladoceran remains were abundant in the lake sediments, with a total of 30 taxa identified. Taxonomic richness ranged from 6 in Lac Profond to 22 in Lac Gilmour, with an average of 13 ±1 (95% confidence interval) species per lake. Shannon's diversity index ranged from 0.8 in Lac Bitobi to 2.0 in Lac à Perdrix of with an average of 1.34. Neither of these indices were strongly correlated with any of the environmental variables measured.

The dominant taxa in the lakes were *Bosmina longirostris* and *Eubosmina longispina* with average percent abundances of 54.2 and 11.5% respectively (Figure 2.2). *Daphnia* abundance ranged from 0 to 38% with an average of 5.2%, making up more than 25% of the species assemblages only in Lac à Perdrix (Figure 2.2). The lakes were primarily dominated by pelagic species, which accounted for at least 75% of the biota in 75% of the lakes. The two lakes that were not dominated by pelagic organisms were Lac Donovan and Lac Fraser. Littoral species made up over 90% of the community in Lac Donovan (Figure 2.2); this lake had an unusually high Na concentration which likely resulted in the anomalous community and the scarcity of organisms found within its sediments. Littoral organisms made up 62% of the community composition in Lac Fraser (Figure 2.2).

The dominant littoral taxon was the *Chydorus brevilabris/biovatus* complex with an average percent abundance of 9.8% (Figure 2.2). *Alona* species represented between 0 and 24% of the species assemblages with an average abundance of 5.5%. The remaining littoral cladoceran taxa cumulatively accounted for between 0 and 37% of total species abundance with an average of 1.2% (Figure 2.2).

Data Analysis

Prior to conducting statistical analyses, three lakes that were determined to fall outside of the population of oligotrophic environments, were removed from analysis. The lakes removed from subsequent data analyses were the meso-to-eutrophic lakes Lac Noir and Lac Renaud (Table 2.1), and Lac Donovan, which had an unusually high Na concentration (15.3 mgL^{-1}) that likely resulted in the scarcity of organisms and the anomalous community found within the sediments. This left 28 lakes in the data set. Environmental variables Barium and Boron could not be transformed to a normal distribution and were removed from the analysis. It would not be possible to produce useful ordinations, had these sites and variables been retained.

The first component of the PCA of the environmental variables from the 28 lakes accounted for 35.8% and the variation and the second for 20.3%. The first axis was negatively correlated with most of the ions, the specific conductance, and the pH; while the second axis was positively correlated with the depth along with with sodium (Na) and chlorine (Cl) concentrations and, to a lesser extent and negatively correlated with the nutrient concentrations of the lakes (Figure 2.3). The transitional metals loaded positively on the first axis and were negatively correlated with the pH (Figure 2.3).The lakes had a tendency to cluster by the type of rock that they were located on. Lakes that received negative scores on the first axis had a tendency to be on marble rock. These lakes had higher Ca, Mg, and sulfate (SO_4) concentrations, higher specific conductances, and pH. Lakes that received positive scores on the second axis were lower in nutrients and were deeper compared to lakes that received positive scores on this axis. Lakes that contained higher concentrations of transitional metals tended to be more acidic; while lakes that had higher specific conductance had higher concentrations of metal and non-metal ions, and a higher pH (Figure

2.3). Lakes that were at higher elevation tended to be deeper, lower in nutrients, and had a lower pH.

The first component of the PCA on the cladoceran communities accounted for 19.8% and second accounted for 13.7% of the variation. Species within the same genus tended to be highly correlated with one another (Figure 2.4). Lakes that received negative scores on the first axis tended to have high proportions of Bosminidae species and contained lower abundances of Chydoridae species. *Alonella* species loaded positively on the second axis; while *Alona* species loaded negatively on this axis. *Eurycercus* and *Camptocercus* were correlated with the *Alona* species, while *Pleuroxus* was highly correlated with *Chydorus brevilabris/biovatus* and with the *Daphnia* species.

An RDA was used to illustrate the influence of the environmental variables on the relative organismal abundances. Na, Cl, Al, Sr and Mn were highly collinear to one another and to other variables in the ordination (VIF > 7) and were thus removed from the RDA. The first two components of the Redundancy Analysis accounted for a total of 55.1% of the total constrained variation (30.6% and 24.5% respectively; Figure 2.5). *Alonella excisa, Alona quadrangularis* and *Chydorus brevilabris*/*biovatus* were correlated with the nutrient concentrations, with pH and area of the lakes. Taxa *Pleuroxus, Eurycercus, A. rustica* and *A. nana* loaded negatively on the first component and negatively on the second; these species tended to be found in lakes together. The abundances of *Daphnia* species was influenced by the Ca, Mg, K and SO_4 concentrations. *Bosmina longirostris* was influenced by the silicon (Si) concentrations of the lakes. Deeper lakes tended to contain higher abundances of Bosminidae species than shallower lakes; *Eubosmina oriens* was most prominent in the deepest lakes (Figure 2.5). Forward selection determined total phosphorous to be the most significant variable in determining the distribution of organisms within the lakes.

Discussion

The Principal Components Analysis of environmental variables showed, as expected, that lakes on marble had higher Mg and Ca concentrations as well as higher a specific conductance and pH than those situated on other types of bedrock (Table 2.1; Figure 2.3). Marble rock is composed of calcium carbonate (Watmough and Ahrene, 2008); while other bedrock types are have higher percentages of silicates. This high calcium content gives the marble lakes a higher buffering capacity against acidification compared to lakes that are not on marble (Watmough & Ahrene, 2008; Jeziorski et al., 2008). The watershed composition of the lakes influences their chemical compositions, which subsequently influences the composition of the cladoceran communities and hence the ecology of the lakes.

The cladoceran communities were dominated by pelagic species with a high representation of Bosminidae. The prevalence of pelagic organisms was related to the maximum depth of the lakes, as has been demonstrated in other studies (e.g. Jeppesen et al., 2003; Nevalainen et al., 2010). As depth increases, the proportion of water that is in contact with the sediment decreases and therefore the proportion of pelagic habitat to littoral habitat increases (Nevalainen et al., 2011). The representation of *Daphnia* species was associated with the concentration of Ca and the pH of the lakes, consistent with the conclusions of Jeziorski and Yan (2006). As a result of their high Ca requirements, *Daphnia* become disadvantaged in Ca poor lakes (Jeziorski et al., 2014) and Bosminidae species tend to out-compete them to become the dominant taxon. On the other hand, as Ca concentrations increase, representations of Daphniidae also increase (Jeziorski et al., 2008) because they are better able to maintain their shells (Jeziorski et al., 2012), and are more efficient grazers than other pelagic taxa (Demot & Kerfoot, 1982). The results from the RDA however, indicate

that Ca and pH are not the only factors determining the abundance of *Daphnia* (Figure 2.5). As Ca is not a limiting resource in these lakes, other factors that were not measured in this study, such as competition and predation, may play a stronger role in influencing the relationships between Bosminidae, Daphniidae and calcium in these lakes. The pelagic species were influenced by the lake depth and the concentration of ions in the lakes, whereas littoral taxa were strongly influenced by the nutrient content and the area of the lakes.

Littoral cladocerans consisted primarily of epiphytic and macrophytic species *Chydorus brevliabris/biovatus, Alona quadrangularis*, *Camptocercus* spp., *Pleuroxus* spp., *Alonella excisa* and *A. nana* (Whiteside & Swindol, 1988; Hann and Karrow, 1984; Whiteside et al., 1978). Lakes with higher phosphorus and nitrogen concentrations tended to have higher proportions of *C. brevilabris/biovatus* complex, *A. quadrangularis* and other taxa that inhabit macrophytic communities than the more oligotrophic lakes (Whiteside et al., 1988). More oligotrophic lakes on the other hand, had higher representations of species that live on bare sediment, such as *A. circumfimbriata*, *A. rustica* and pelagic taxa. *C. brevilabris* (*C. sphaericus*) are inefficient grazers and tend to thrive in more eutrophic waters (Broderson et al., 1998; Plath & Boersma, 2001); they also have the ability to inhabit surface blooms of algae and cyanobacteria which are common in eutrophic ecosystems (Plath & Boersma, 2001). The relationship observed between littoral organisms and nutrient concentrations found in this study is expected; increased nutrient concentrations in oligotrophic systems lead to increased primary production and abundance of littoral vegetation (Vermaire et al., 2008; 2012), whereas with much higer nutrient concentrations, from mesotropic to eutrophic conditions, algae begin to outcompete macrophytes for nutrients and sunlight. The shift towards algal production in eutrophic environments leads to decreased habitat for littoral Cladocera and increased prominence of pelagic species

(Vermaire et al., 2008; 2012). The RDA showed that the epiphytic species *A. excisa* was more abundant in larger, shallow lakes. Larger and shallower lakes have greater littoral zones relative to the entire ecosystem compared to smaller, deeper lakes and therefore have increased habitat for emergent plants and epiphytic species. The influence of nutrients and area on the communities was more prominent in shallower lakes than in deeper lakes, where the littoral zones contributed a much larger portion of the aquatic ecosystem.

C. brevilabris/biovatus was the most abundant taxon in Lac Donovan. Very few organisms were collected from the surface sediment of this lake; therefore the high percentage of *C. brevilabris/biovatus* may be a result of its tolerance to high sodium conditions of the lake (Bos and Cummings, 2003). Bosminidae and other pelagic Cladocera have poor osmotic regulation abilities (Korhola & Rautio, 2001) and were likely unable to survive the high sodium conditions of the lake. Alternatively, *C. brevilabris* is also able to vertically migrate and to act as a pelagic species (Plath & Beorsma, 2001). The near absence of Bosminidae and Daphniidae in Lac Donovan likely opened up a niche that was able to be filled by *C. brevilabris/biovatus* in the absence of competition.

The results of this study show that environmental variables influence the structure and the composition of the cladoceran communities in these lakes. The communities of these lakes are more strongly influenced by the changes in the nutrient composition and morphological characteristics than they are by the pH and related concentrations of ions, compared to other lakes on the Precambrian Shield, where acidification has had a larger impact on lake chemistry and on aquatic ecology. Further studies on species diversity and environmental variability would be required to determine whether these moderate to high-calcium, and high pH lakes have undergone Ca loss and changes in acidity in the past, which

would have led to changes in community composition in the last century in response to anthropogenic disturbances and to climatic changes.

Table 2.1: Location, morphometry, watershed geology, and principal chemical characteristics of study lakes in southwest Québec, Canada.

#	Lakes	Lat. (°)	Long. (°)	Geology	Elev. (m)	Area (ha)	Depth (-m)	Specific Cond. (μScm^{-1})	pH	TP (mgL^{-1})	TKN (mgL^{1})	Ca (mgL^{-1})
1	Bernard	45.76	-76.00	Marble	166	450	24.0	148	8.39	0.007	0.30	23.5
2	Bitobi	46.00	-75.95	Marble	150	38	19.4	96	8.30	0.004	0.33	13.6
3	Brûlé	45.72	-75.44	Granite	252	12	42.0	119	8.35	0.003	0.17	22.8
4	Demi-	45.74	-75.99	Marble	192	9.6	15.0	205	8.22	0.004	0.29	37.5
5	Donovan	45.77	-75.73	Marble	192	8	5.0	245	7.75	0.013	0.37	29.6
6	Du Pretre	45.84	-75.76	Sable	180	11	32.0	80	8.11	0.008	0.16	11.9
7	Fraser	45.65	-75.97	Sable	153	7.5	4.0	225	8.30	0.005	0.34	33.4
8	Gilmour	45.64	-75.55	Marble	136	11	42.0	132	8.70	0.005	0.29	11.6
9	Heney	46.02	-75.93	Marble	150	1590	32.0	234	8.70	0.012	0.28	19.4
10	Kallala	45.74	-75.98	Marble	199	8	9.0	113	8.16	0.007	0.40	38.1
11	Kidder	45.60	-76.09	Syenite	212	12	17.0	55	7.36	0.003	0.17	7.8
12	Lemery	45.84	-75.16	Granite	236	7	14.5	104	7.20	0.005	0.23	7.8
13	Létournea	45.60	-75.67	Marble	128	28	4.0	160	8.30	0.010	0.34	16.2
14	Neuf	45.79	-75.20	Paragneiss	238	7.4	30.0	21	7.20	0.006	0.25	6.4
15	Noir	45.78	-75.13	Gabbro	177	10	30.0	20	7.70	0.009	0.26	10.6
16	Noir II	46.01	-75.95	Marble	150	11	7.2	120	8.32	0.023	0.59	25.7
17	Orignal	46.00	-76.08	Marble	181	74	27.2	158	8.60	0.008	0.42	19.3
18	Perdrix	45.59	-75.69	Marble	156	40	27.1	82	8.00	0.007	0.27	24.9
19	Pink	45.47	-75.81	Paragneiss	164	10	20.0	239	8.25	0.005	0.19	42.9
20	Profond	46.00	-76.10	Marble	180	148	35.3	227	8.00	0.004	0.19	11.6
21	Ramsay	45.60	-76.10	Syenite	204	8.2	8.7	60	7.31	0.007	0.34	7.8
22	Renaud	45.60	-76.02	Syenite	203	11.5	8.0	70	7.21	0.043	0.63	8.7
23	Robinson	45.72	-75.73	Paragneiss	227	16	8.0	61	7.65	0.005	0.24	7.4
24	St. Antoine	45.66	-75.80	Sable	230	40	9.0	65	7.65	0.006	0.24	8.2
25	Star	45.74	-75.69	Paragneiss	311	7	50.0	39	7.96	0.003	0.21	6.6
26	Taylor	45.60	-76.04	Syenite	210	48	20.0	75	7.72	0.005	0.25	9.6
27	Truite	46.00	-75.90	Marble	181	9.6	17.5	129	8.60	0.006	0.23	33.2
28	Vases	46.00	-76.13	Paragneiss	179	45	0.8	103	8.51	0.009	0.47	19.0
29	Vert	46.00	-75.94	Marble	156	19	13.4	159	8.63	0.007	0.4	26.1
30	Victoria	46.07	-75.96	Marble	151	52	7.2	132	8.12	0.007	0.34	19.8
31	Wallingfor	45.58	-75.69	Paragneiss	168	6.8	13.5	210	8.44	0.004	0.31	34.1

Table 2.2: Summary statistics of the water chemistry of study lakes in southwestern Québec and the transformation used to approximate a normal distribution prior to statistical analyses.

Variables	Units	Minimum	Maximum	Mean	Standard Deviation	Transformation
Elevation	Metres above sea-level	128	311	187.5	39.2	untransformed
Area	Hectares	6.8	1590	89	290.0	Sqrt ($\log_{10}(x)$)
Depth	Metres	1	50	19	13.0	untransformed
pH	pH	7.20	8.70	8.06	0.46	untransformed
Specific Conductance	μScm^{-1}	20	245	125	67	untransformed
TP (Total Phosphorus)	mgL^{-1}	0.003	0.043	0.008	0.007	$Log_{10}(x)$
TKN (Total Kjehldahl Nitrogen)	mgL^{-1}	0.16	0.63	0.31	0.11	$Log_{10}(x)$
(Chlα) Chlorophyll-α	μgL^{-1}	0.15	1.93	0.58	0.35	$Log_{10}(x)$
Ca (Calcium)	mgL^{-1}	6.4	42.9	19.2	10.9	$Log_{10}(x)$
SO_4 (Sulfate)	mgL^{-1}	2.8	12.9	6.3	2.70	$Log_{10}(x)$
Cl (Chlorine)	mgL^{-1}	0.2	27.8	2.9	5.30	$Log_{10}(x)$
Mg (Magnesium)	mgL^{-1}	0.6	9.0	2.7	2.0	$Log_{10}(x)$
Na (Sodium)	mgL^{-1}	0.4	15.3	2.3	2.90	$Log_{10}(x)$
Si (Silicon)	mgL^{-1}	0.24	2.98	1.35	0.75	$Log_{10}(x)$
K (Potassium)	mgL^{-1}	0.2	1.4	0.7	0.30	$Log_{10}(x)$
Sr (Strontium)	mgL^{-1}	0.027	0.400	0.110	0.095	$Log_{10}(x)$
Fe (Iron)	mgL^{-1}	0.0007	0.299	0.043	0.070	$Log_{10}(x)$
Al (Aluminum)	mgL^{-1}	0.0009	0.080	0.014	0.016	$Log_{10}(x)$
Mn (Manganese)	mgL^{-1}	0.001	0.037	0.010	0.009	$Log_{10}(x)$

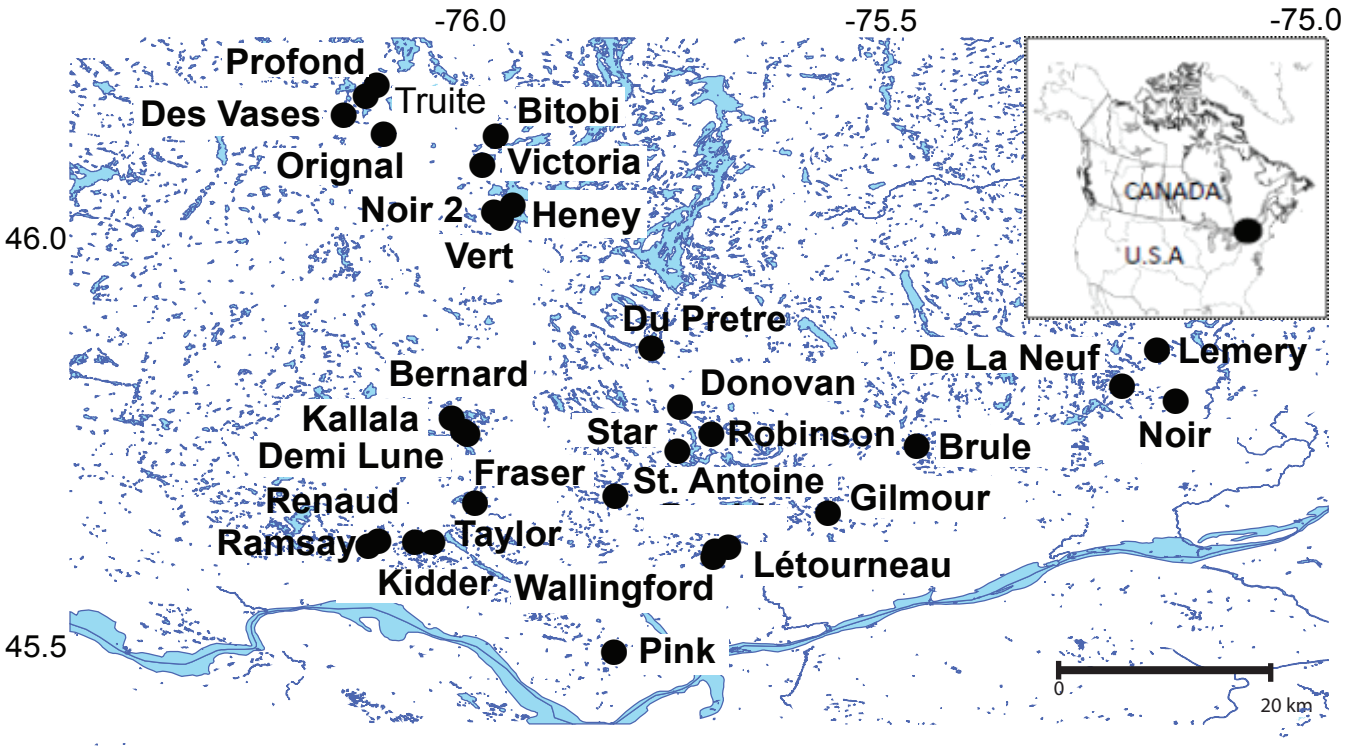

Figure 2.1: Map the Outaouais region of Québec showing locations of lakes sampled in this study.

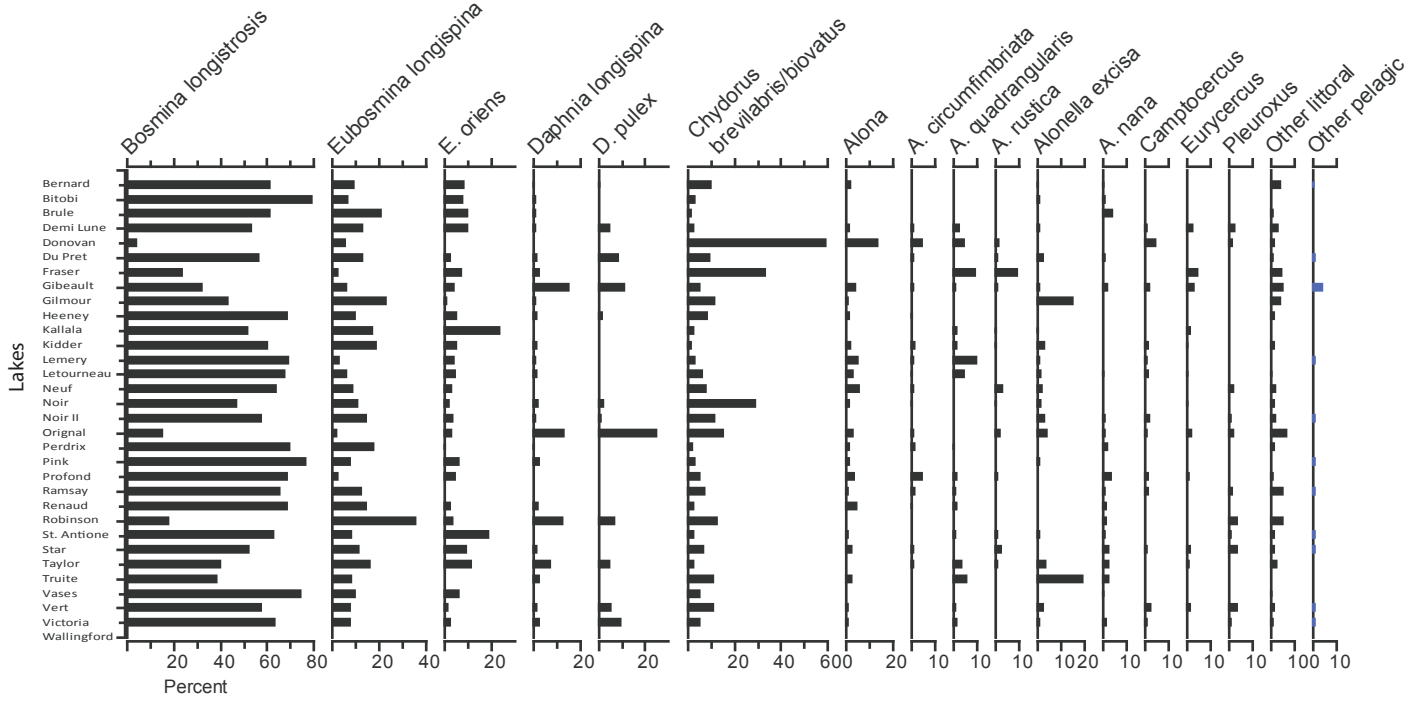

Figure 2.2: Percent abundances of cladoceran taxa in lakes from southwestern Québec. Only taxa with at least 1% abundance in at least 5 lakes are shown; rare taxa are summarized into "Littoral other" and "Pelagic Other".

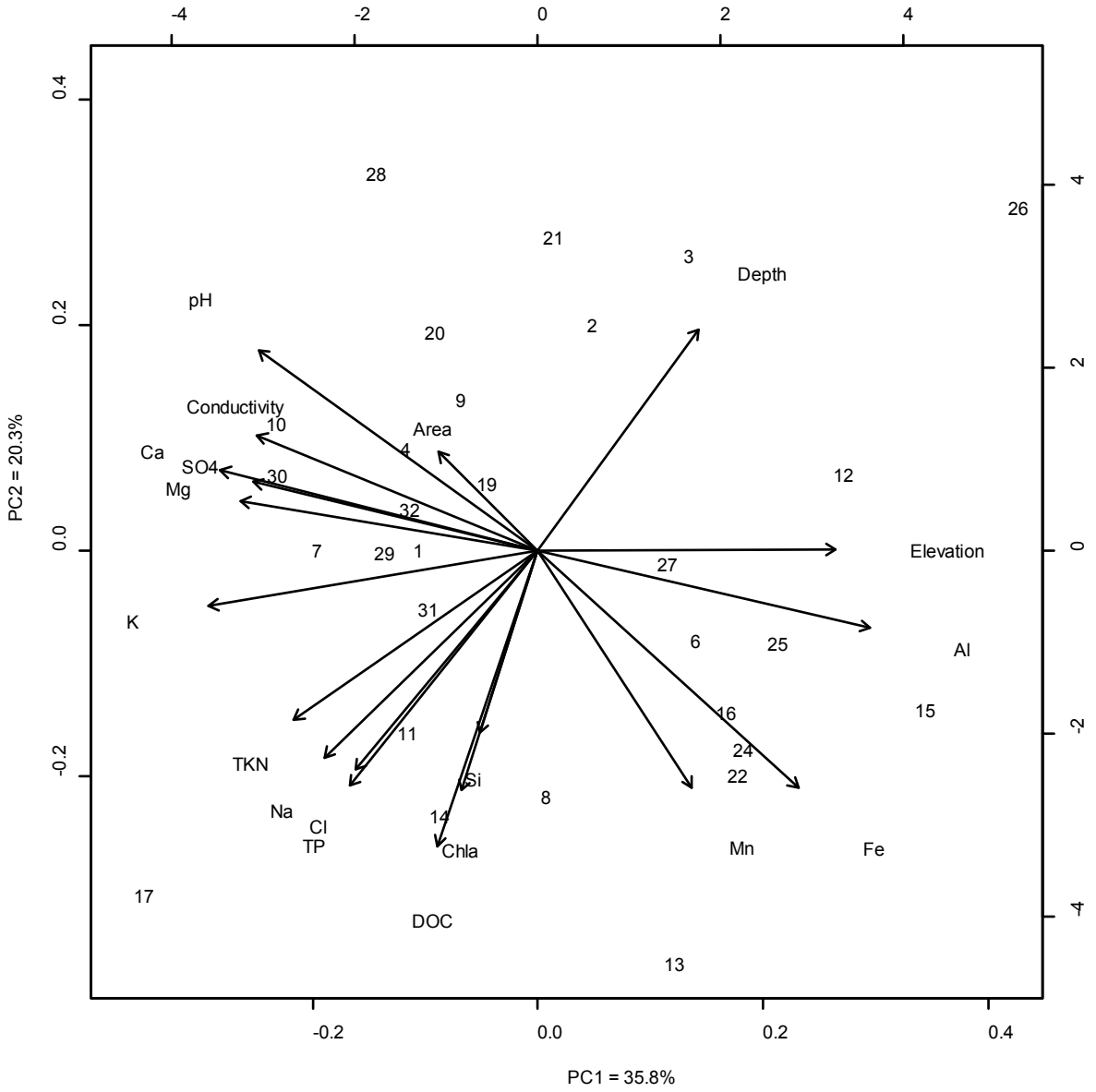

Figure 2.3: Principal Component Analysis biplot of environmental variables in 28 study lakes from southwest Québec. See Table 1 for site names.

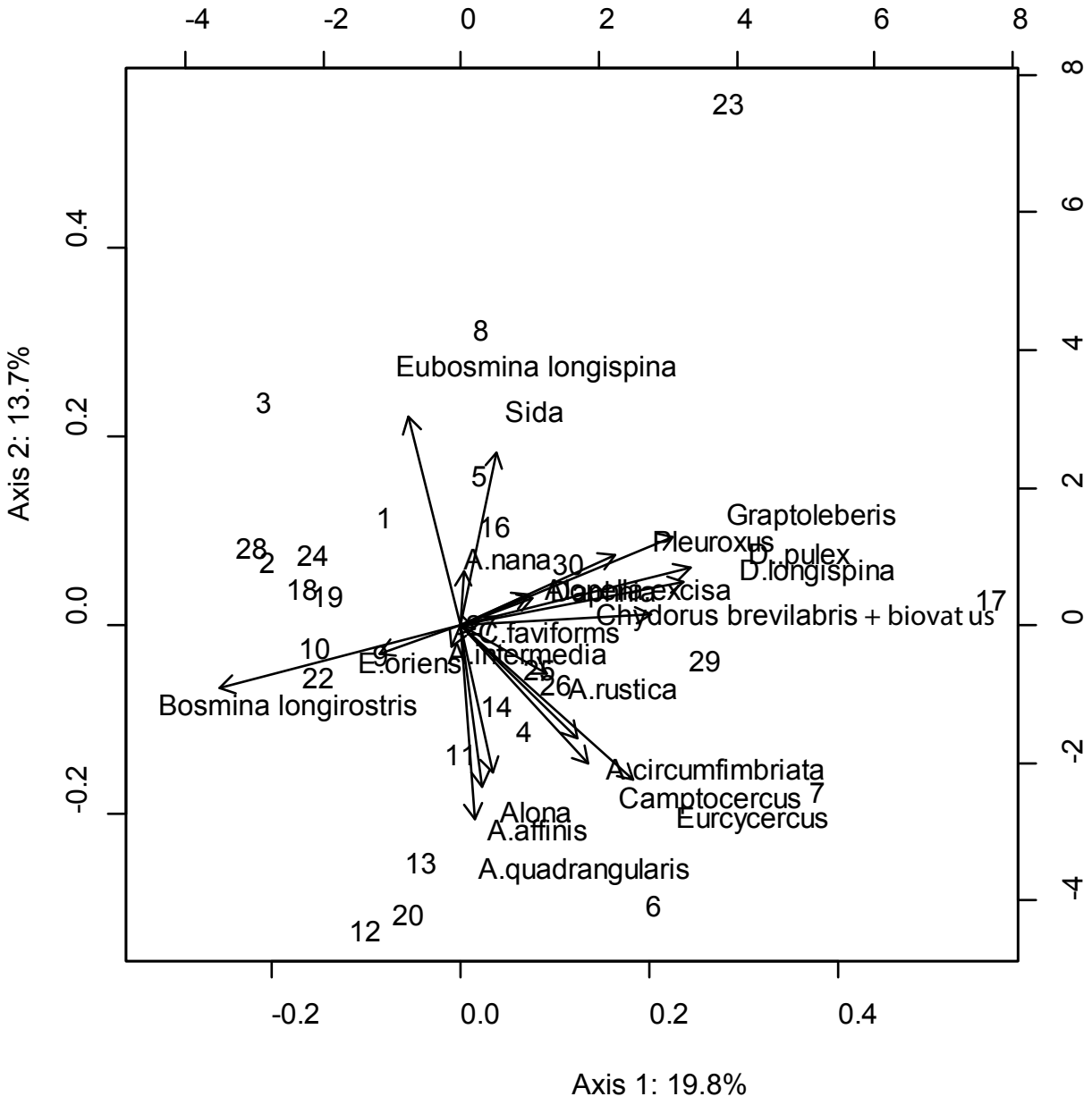

Figure 2.4: Principal components analysis of the species abundances within the 28 lakes. Species percent abundances are transformed using the Hellinger transformation. See Table 2.1 for site names.

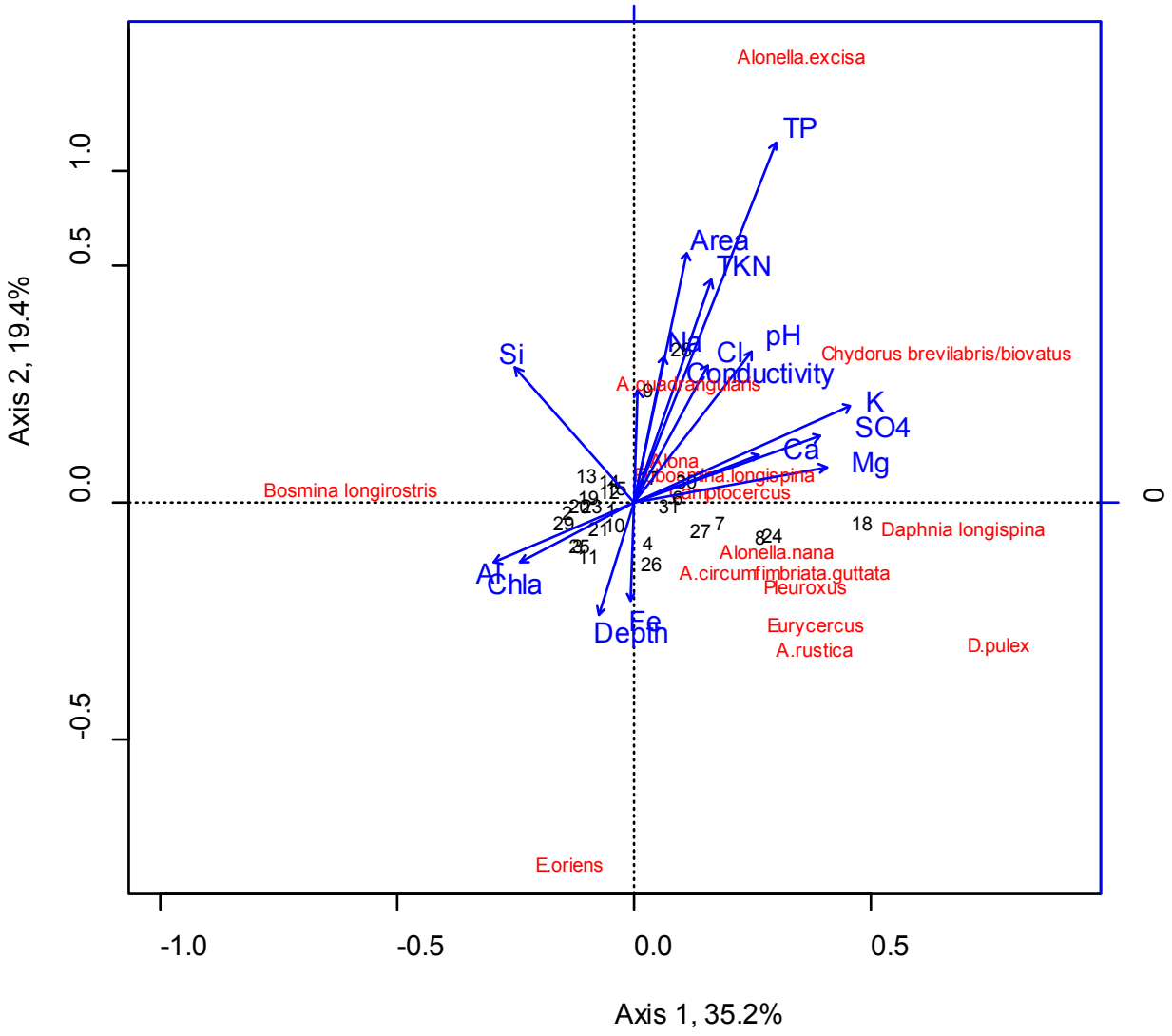

Figure 2.5: Redundancy Analysis comparing the relative abundance of the Cladocera within the lakes to the environmental variables. See Table 1 for site names and Table 3 for species codes.

3. Response of Cladoceran Communities to Climatic Events of the Late Holocene in Lac Brûlé, Southwestern Québec

Abstract

The long-term changes of the cladoceran communities of a small oligotrophic lake in south-western Québec, Canada were investigated. The sediments of the lake were varved, which allowed for accurate dating. A pollen record of the lake provided a paleoclimate reconstruction and information regarding landscape changes in the region (Lafontaine-Boyer & Gajewski). This record was used to infer how the cladoceran community responded to climatic events and to changes in the landscape. The changes in species composition were subsequently used to infer habitat structure, and nutrient conditions of the lake in response to the climatic events of the past.

Cladoceran diversity was high throughout most of the Medieval Warm Period and into the Little Ice Age and decreased during the modern period due to increased temperatures and anthropogenic activities in the region. *Daphnia* and plant associated species greatly decreased in the past 100 years, implying a decrease in aquatic vegetation. The lower *Daphnia* populations combined with increased temperatures left the pelagic zone open for colonization by the smaller *Bosmina longirostris*. This study shows that the modern communities of the lake are unlike most of what was observed throughout the past millennium.

Introduction

In aquatic environments, current increasing temperatures from anthropogenic climate change have resulted in many changes, including increased nutrient inputs, increased stratification, increased productivity from longer growing seasons, increased hypolimnetic anoxia, increased frequency of algal blooms, and shifts in trophic interactions (Schindler, 2001; Woodward et al., 2010).

In the past millennium, prior to the current anthropogenic warming, North America experienced two major climatic periods characterized by long-term warmer and colder than average temperatures, known as the Medieval Warm Period (MWP) and the Little Ice Age (LIA) (Mann et al., 2009; Ahmed et al., 2013). In eastern North America, the MWP persisted from approximately 750 CE to 1250 CE, although dates vary depending on region (Gajewski, 1988; Pederson et al., 2005; Cronin et al., 2010; Paquette & Gajewski, 2013; Lafontaine-Boyer & Gajewski). This period was characterized by warmer than average temperatures and dry conditions throughout much of North America, particularly in the midwestern United States. The MWP transitioned into the Little Ice Age (LIA) sometime during the 14th century CE, and persisted into the early 19th century (Ahmed et al., 2013; Gajewski, 1988). The LIA was characterized by cooler than average temperatures and by glacial expansions in the north and in alpine regions. Temperatures increased towards the end of the LIA leading into current conditions.

Paleoenvironmental studies from lake sediments utilize the remains of biological material to reconstruct past communities and to understand how they have changed through time in response to regional changes in the environment, such as climatic variability and changes in water chemistry. When the lake sediments are annually-laminated (varved) an

accurate chronology can be developed, which allows for tracking of species abundances and the computation of accumulation rates on a high-resolution time scale.

Cladocera are widely used as paleoenvironmental indicators due to their responses to changes in water chemistry, lake depth, aquatic vegetation, and trophic interactions (Kurek et al., 2010; Desellas et al., 2008; 2011; Nevalainen et al., 2011; Davidson et al., 2010b; Brodersen et al., 1998; Walseng et al., 2003). The communities of Cladocera usually do not respond directly to past temperature variations but indirectly to changes in their environment that are often associated with climate. The ratio of ephippia to carapaces of chydorids in the sediments has also in the past been used to track and reconstruct changes in temperature as this is an indication of sexual reproduction and environmental stress (Nevalainen et al., 2012).

This study investigates the dynamics of the cladoceran communities in a lake in the Outaouais region of eastern Canada in response to the climatic variability of the MWP, the LIA and current anthropogenic warming. We use the varved sediments of an oligotrophic lake, Lac Brûlé, that has received little direct human impact from settlement and recreation, to observe the impact of past climate variability on the aquatic community. This study will help us to better understand how aquatic communities respond to climate change on longer time scales than possible using lake monitoring. Using a previously-published pollen record from the lake (Lafontaine-Boyer & Gajewski), we will be able to connect the cladoceran communities to changes in regional vegetation and to temperature changes reconstructed using this record. This study will allow us to connect changes in the community structure to climatic transitions in the landscape and disturbances in the landscape through time to better infer community drivers.

Study Site

Lac Brûlé is a small, deep lake situated in the Mulgrave-Derry region of the Gatineau Hills in southern Québec (45.72°N, 75.43°W, 270m) (Figure 1). The watershed of the lake is also very small, only 3-4 times the size of the lake. The lake is situated on granitic-parangneise rock (Ministere du resources naturelles, 2013) and is surrounded by temperate mixed hardwood forests characteristic of the Canadian Shield (Burns & Honkala, 1990; Richard, 1993). The lake is nestled among hills, sheltering it from the wind, with one cabin located on the shore of the lake (Lafontaine-Boyer & Gajewski). It is approximately 10 hectares in area with a maximum depth of 42 m.

Methods

Field Methods

Lac Brûlé was sampled by Lafontaine and Gajewski (2014) for pollen analysis (2012 core), and a new core was collected for this study in 2013 (BV14). A 90-cm core was taken from the deepest part of lac Brûlé (42 metres depth) using a freeze corer packed with dry ice. The corer was sent to the bottom of the lake where the sediment adhered to the outer surface. Once the sediment was retrieved, it was carefully removed from the corer, packed in aluminum foil and placed in dry ice to be transported to the University of Ottawa where it was kept cold storage at -25°C. Two 2 L water samples were taken using acid-washed bottles from the surface and from 31 m depth. One litre was used to measure surface chlorophyll α concentrations while remainder was analyzed for total phosphorous and total nitrogen (filtered and unfiltered), metal and ion concentrations by the City of Ottawa Water Treatment Centre.

Varve Counting and Sediment Sample Preparation

The BV14 core was continuously laminated, and each varve was defined as a couplet comprised of one dark and one light layer (Ojala et al., 2012). The varved chronology of a core previously taken in 2012 was validated using Carbon-14 dating and was used as a standard against which the other cores were compared to (Lafontaine-Boyer & Gajewski, 2014). The BV14 core was cross-dated using distinct marker layers (a standard dendrochronological technique; Lamoureux, 2001; Stokes & Smiley, 1996) that were defined from the 2012 core and lined up with BV14 and from four separate previously collected sediment cores (Lafontaine-Boyer & Gajewski; Karen Neil unpublished data). Once the marker-layers were lined up, the cross-dated varves were counted in annual couplets and marked at 5-year intervals. An Acu-Rite linear encoder and Quick-Check readout with Measure J2X software was used to measure the BV14 varve thickness at the 5-year intervals (five couplets). The core was subsequently sectioned using an exacto-knife and samples were placed into 20 mL scintillation vials.

Samples were analyzed at five-year intervals for the periods from 1795-2010 CE and from 1245-1420 CE, and at ten year intervals from 1415-1795 CE and 785-1235 CE. This was done to allow for the analysis of more rapid changes occurring during the European period (the past 200 years) as well as during the transition between the Medieval Warm Period and the Little Ice Age (1245-1420 CE). This totaled to 164 sampling levels for the core.

Cladocera Sample Preparation

Extraction of the cladoceran remains from the sediment followed the protocol of Korhola & Rautio (2001). Half a milliliter of sediment from each designated layer was used as a sample; the samples were deflocculated in 100 mL of 10% Potassium Hydroxide (KOH) solution at 70-80°C for 30 minutes with continuous stirring. This was done to break up any larger particles and separate the organisms from the sediment. After 30 minutes, the solution was left to cool to 40°C before being strained through a 30 µm filter and washed with deionized (DI) water until the water ran clear. The remaining material on the filter was poured into a 5 mL vial with DI water and left to settle.

Once the sediment had settled to the bottom of the bottle, the remaining water was removed using an aloquott pipette, and one tablet of Lycopodium spores (batch #938934) containing a known number of spores (10679 ± 426) was added to each sample along with three drops of 10% hydrochloric acid to dissolve the tablet. This was used to estimate the concentration of cladoceran remains in each sample and by multiplying by the sedimentation rate, the cladoceran accumulation rates could be estimated (Kerfoot, 1974; Szerocynska, 2007). Three mL of DI water were added along with five drops of 95% ethanol to preserve the samples and one drop of safrarin-red to stain the organisms for identification.

Slides were prepared by first placing one drop of glycerine onto a microscope slide. Using an aliquot pipette, with the opening of the tube cut to one millimetre in diameter, 50 µL of sample was pipetted onto each slide and excess water was allowed to evaporate on a warming plate at 70°C. Once the water evaporated sufficiently, one to two 22 X 22 mm cover slips were placed over the samples and sealed using nail polish.

Identification

Slides were viewed under a Nikon Eclipse 90i light microscope at 200X magnification, increased to 400X when required. Individual skeletal components were identified to genus and species where possible. The fossilized component (e.g., carapace, headshield) was noted and the length was measured to the nearest 50 μm using NIS Elements Br 3.0 Software. Between 100 and 150 specimens per level were counted to obtain an estimate of species composition and abundances (Kurek et al., 2010). Total counts of individual components were used to determine relative abundances of taxa within the study. In cases where it was clear that two or more components were derived from the same individual, due to proximity and articulation, only one component was counted.

Since there is no single guide to the identification of cladoceran subfossils in lake sediments for North America, an assortment of sources were used for the identification, including Bos (2001), Sweetman & Smol (2006), Korosi & Smol (2012a and b), De Melo & Hebert (1994), Brandelova et al (1972); Szerocynska & Sarmaja-Korjonen (2007). To distinguish between genera within the family Bosminidae the curvature of the antennules, the length and roundness of the rostrum, the shape of the carapace, the presence/absence of pectin on the tail structures (mucros) (De Melo & Hebert, 1994), position of head pores, and the overall size of the individuals were used (Korosi & Smol, 2012a). The carapaces and head structures of Daphniidae species are rarely found in sediments as their soft, Ca-rich shells do not preserve well over time (Frey, 1986; Korhola & Rautio, 2001; Korosi & Smol, 2012a); typically, only the chitinized postabdominal-claws and occasional ephippia are recovered (Korhola & Rautio, 2001; Korosi & Smol, 2012a). The presence/absence of larger teeth at the base of the postabdominal claw was used to distinguish between *Daphnia pulex* and *D. longispina* species complexes (referred to from this point forward as

D. pulex and *D. longispina respectively*) (Korosi & Smol, 2012a). The identification of remains in the family Chydoridae was based on Sweetman & Smol (2006), Bos (2001) and Korosi & Smol (2012b). Less common groups were identified following Korosi & Smol (2012a).

Data Analysis

Cladoceran abundances were compared to reconstructions of temperature and precipitation, charcoal influx and the abundances of pollen taxa from Lafontaine-Boyer and Gajewski (2014) to achieve an understanding of the impact of environmental changes on the Cladoceran communities. Using the changes in the Cladoceran species abundances, we are also able to infer changes in macrophyte composition and aspects of water chemistry.

Cladoceran concentrations were calculated by multiplying the number of individuals counted by total number of *Lycopodium* spores per tablet over the number counted in the corresponding sample divided by the volume of sample used per level (Kerfoot, 1974). Cladoceran accumulation rates (in the sediments) (CARs) were subsequently calculated by multiplying the concentration by the varve thickness in centimentres per year for that interval. These two measurements were used as proxies for biological production of the Cladoceran populations.

Statistical Analyses were done using the statistical programme R (R Core Team, 2013). A Principal Components Analysis (PCA) of the cladoceran taxa was performed to summarize changes in community structure through time. Relative cladoceran abundances were transformed using the Hellinger transformation (Legendre & Gallagher, 2001; Borcard et al., 2011; Legendre & Legendre, 2012), which using the squared-cord distance to down-weigh the importance of the most abundant taxa in the sample emphasizes

abundances of rare taxa. To eliminate rare species and chance occurrences, only species that were present at greater than one percent in at least 2 samples were used in this analysis, all other taxa were grouped, leaving 21 taxonomic groups. The rarefied species diversity was calculated using the "rarefy" function in the Vegan package to obtain diversity measurements by year, controlling for sample size (Oksanen, 2014).

A constrained cluster analysis was performed using the "coniss" option under the "chclust" function in the Rioja R package (Juggins, 2014), and the resemblance between samples was calculated using Euclidean distance. This created a number of biostratigraphic zones based on the similarity of species abundances and community composition through time. However, comparisons are local; once there is a zone transition, you cannot return to the previous group, even if the subsequent sample further up in the stratigraphic column resembles a sample further below. Therefore an unconstrained cluster analysis was also performed using Euclidean distance and Ward's method (Crawley, 2013). This standard cluster analysis created groups based on the similarity of the taxonomic assemblages, irrespective of their stratigraphic position in the core. The first analysis creates groups (zones) based on time and shows changes over timescales of centuries to millennia, whereas the second analysis compares assemblages throughout the core and shows decadal changes in the community.

Results

Lake Chemistry

Chemistry measurements were collected in the autumn of 2013, prior to turnover. Lac Brûlé is ultra-oligotrophic with a total phosphorus content of 4 μgL^{-1}, a total nitrogen

content of 170 μgL^{-1} and chlorophyll-α content of 0.5 μgL^{-1}. The pH of the lake is 8.35 and specific conductance at the surface of 119 μScm^{-1}. The calcium and sodium content of the surface water is 22.8 and 0.8 mgL^{-1} respectively. The lake was determined to be meromictic by Lafontaine-Boyer and Gajewski (2014), and contains a strong chemocline at about 30 m depth, leading to sediments that are laminated (varved), allowing for accurate dating (Lafontaine-Boyer & Gajewski). There is a sharp increase in the concentration of phosphorus to 7.6 mgL^{-1} and nitrogen to 163 mgL^{-1} in the hypolimnion. The concentration of calcium also rises significantly, reaching 117.7 mgL^{-1}.

Cladoceran Communities

The dominant taxon in the sediments was *Eubosmina longispina* which gradually increased in abundance between 785 and 1915 CE (Figure 2). In the 20th century, *Bosmina longirostris* increased rapidly to maximum values between 1940 and 1950 CE; it subsequently decreased and has been increasing since 1990 CE. Other taxa highly represented throughout the sequence were *Eubosmina oriens* and *D. longispina*.

The first two Principal Components of the cladoceran assemblages accounted for 11.0% and 8.4% of the variance respectively (Table 1; Figure 3). The scores on the first component were correlated with the abundances of *Daphnia* spp. and of the littoral taxa and closely aligned with the Rarefied Shannon's Diversity Index. The second component was positively correlated with the variation in *B. longirostris* and negatively with *Eubosmina longispina* (Figure 2; Table 1). The assemblages from the present period (zone 5) and from the deepest part of the core (zone 1) received similar scores compared to other sections throughout the core. Most of the scores on the first component shifted from

negative in zone 2 to positive in zone 3, and those of the second component were negative in zone 4.

The first zone (785-815 CE) was characterized by a high percent abundance of *B. longirostris* and lower representations of *Daphnia* spp. and of most littoral species, specifically *Chydorus* spp. and *Alona* spp.; however, there were some *Alonella* spp. individuals present (Figure 2). This zone was also characterized by low overall diversity. The second zone (825-1410 CE) was characterized by a decrease in abundance of *B. longirostris*, which continued to decrease throughout the period. The abundance of *Daphnia* spp. was higher than in the previous zone and remained relatively constant at about 8% during the Zone 2. There was a relatively high abundance of littoral species compared to the previous zone, particularly of *Alona* spp. during this period, which contributed to the high overall diversity (Figure 2). *Eubosmina longispina* steadily increased during this zone. Zone 3 (1415-1665 CE) was marked by increased representation of *Daphnia* species, higher than any other time the core, which was sustained throughout this period (Figure 2). The percent abundance of *E. longispina* continued to increase throughout this zone. The diversity in this zone was slightly higher than previous zones. The PCA scores for this zone were positive on the first component and generally negative on the second (Figure 3). Zone 4 (1675-1930 CE) was marked by high abundances of *E. longispina* and low representations of *Daphnia* (Figure 2). Abundances of *Alona* spp. and *Chydorus* spp. remained relatively constant throughout this period; however, there was a decrease in the abundance of most other littoral species (Figure 2). Species diversity was low throughout this period as a result. The last zone (1935-2010 CE) was marked by a sharp increase in the representation of *B. longirostris* and a decrease in *E. longispina*. Community diversity during this period was relatively low.

Varve thickness was averaged for each biostratigraphic zone to observe changes in sedimentation rates associated with cladoceran community changes. Varve thickness was 0.67 ± 0.1 mm year^{-1} in zone 1, decreased to 0.55 ± 0.04 mm year^{-1} in zone 2 and increased in zone 3 to 0.78 ± 0.04 mm year^{-1} (Figure 4). Thickness remained similar (0.80 ± 0.08 mm year^{-1}) in zone 4 and increased in the uppermost, more unconsolidated sediments to 1.84 ± 0.32 mm year^{-1} (Figure 4). Cladocera Accumulation Rates (CARs; also called influx) is a measures of secondary production (Figure 4), taking into account sedimentation rates. Accumulation rates were high the first zone and decreased into the second zone with an even greater decrease moving into zone 3 (even with increased varve thickness). This pattern was observed in all taxa except for *Daphnia* species during zone 2 and 3. While the accumulation rates for most of the species decreased from zone 2 into zone 3, *Daphnia* accumulation rates remained relatively constant (Figure 4). Accumulation rates increased in zone 4 and accelerated in the uppermost zone 5. This acceleration is seen in most taxonomic groups, particularly in *B. longirostris, D. longispina*, *Alona* spp. and *C. brevilabris* (Figure 4).

An unconstrained cluster analysis was also performed on the cladoceran assemblages to infer community changes at the decadal level and to observe similarity between communities throughout the core; note that the group numbers do not imply any ordering and they are not associated with the zone numbers (Figure 3). The first group contained moderate to high representations of E. longispina with high representations of littoral species compared to other groups; diversity was high throughout this group. This group mostly contained assemblages from zones 2 and 3 in the constrained analysis. The second group contained relatively high representations of *Alona* spp., *Alonella* spp. and *Daphnia* species along with low representations of *B. longirostris* and high representations

E. longispina. Overall diversity was high in this group. This group was mostly found in samples from zone 3 and some from zone 4. The third group contained the second highest representatiosn of *B. longirostris* in the core. This group also contained overall high representations of *Daphnia* and of littoral species and hence high overall species diversity compared to other groups. The fourth group contained the lowest representations of *B. longirostris* and the highest of *E. longispina* and of *E. oriens* in the core. These samples were marked by low representations of *Daphnia* with increased representations of littoral species but continued low diversity. This group was found mostly in zone 3 and 4. The fifth group contained the highest representations of *B. longirostris* for the core and low representations of most other species in the communities. Consequently, there was low species diversity in this group.. This group was found only in the lowermost and uppermost sediments, in zones 1 and 5.

Discussion

The reconstructed temperatures of the first two zones defined by the constrained cluster analysis were warmer than average (Figure 3; Lafontaine-Boyer & Gajewski); these two zones (785-1410 CE) likely represent the Medieval Warm Period (MWP) and the transition into the Little Ice Age (LIA) for this region (Paquette & Gajewski, 2013; Lafontaine-Boyer & Gajewski). The cladoceran community during the MWP was characterized by relatively high representations of *B. longirostris* and lower abundances of *E. longispina* and of *Daphnia* species compared to other parts of the core. As predicted, littoral species were relatively abundant, particularly macrophyte-associated taxa such as *Alonella* spp. and *Chydorus brevilabris* (Frey, 1960; Whiteside et al., 1978; Whiteside & Swindol, 1988). Secondary production was high during this interval, as indicated by high cladoceran

accumulation rates (290 individuals cm^{-2} $year^{-1}$) (CAR) in the sediment (Figure 4), corresponding to high population numbers. Charcoal influx increased around the year 1375 CE, towards the end of zone 2 (Figure 3); this increase in charcoal was also accompanied by an increase in values of the second Principal Component of the cladoceran assemblages and a slight increase in relative abunandces of *B. longirostris* (Figure 2). The fire coincided with the climate transition into the LIA, and induced a permanent change in the regional vegetation, as seen in the decrease in *Tsuga* pollen and the increase in *Pinus* and *Picea* pollen abundances. Temperatures decreased from the end of zone 2 and continued through zone 3 (1415-1665 CE), (LIA; Figure 3; Lafontaine-Boyer & Gajewski). The abundance of *E. longispina* and *Daphnia* spp. increased during this time, and diversity was high in the early part of the LIA. There was a slight decrease in the abundance of *Alonella* spp. and an increase in *Alona* species in zone 3, suggesting an overall decrease in the abundance of aquatic vegetation in the littoral zone and an increase in bare littoral sediments (Whitesideand Swindol, 1988). The increase in the representation of *Daphnia* spp. in the lake between 1380 CE and 1675 CE (Figure 3) is likely a response to reduced temperatures as *Daphnia* spp. tend to be more abundant in cold lakes with decreased stratification (Gillooly & Dodson, 2000; Plath & Boersma, 2001; Boersma et al., 2001). The other significant response to the lower temperatures was a decrease in cladoceran production as evidenced by a decrease in CARs from an average of 282 ± 34 individuals cm^{-2} $year^{-1}$ to 825 CE to 1410 to 223 ± 47 individuals cm^{-2} $year^{-1}$ between 1415 and 1665 CE (Figure 4). This decrease is seen in all species except for *Daphnia* spp. The sustained accumulation rates of *Daphnia* species during zone 3 in conjunction with the decreased accumulation rates of most other species, Bosmindae species in particular, is why there was an increase in the relative abundances of

Daphnia species in the beginning of the LIA. Although other species were affected, the *Daphnia* were comparatively not.

Temperatures remained low during the transition from zone 3 to zone 4 and increased towards the end of zone 4 (Figure 3; Lafontaine-Boyer & Gajewski). *Daphnia* spp. abundances decreased from zone 3 into zone 4; this zone is also marked by a decrease in overall diversity, primarily due to a decrease in the abundances and diversity of littoral species and *Daphnia* spp. (Figure 3.2). This likely indicates a decrease in littoral vegetation abundances (Tremel et al., 2000). The cold temperatures and the reduced growing season of the LIA favoured *Eubosmina* spp. and *Daphnia* spp. over warm-temperature preferring *B. longirostris* (Figure 2; Gillooly & Dodson, 2000; Nevalainen et al., 2014). Species diversity began to decrease in the middle of zone 4 (around 1800 CE) with a small increase in *Daphnia* spp. likely in response to the colder temperatures of this time.

Temperatures began to increase around 1860 CE and increased to today beyond what was observed in the reconstruction of the MWP (Figure 3). Charcoal influx and the percent abundance of *Ambrosia* in the pollen record also increased at this time, indicating increased disturbance in the landscape from the arrival of Europeans (Lafontaine-Boyer & Gajewski). The final zone (1935 CE to present) is marked by a shift in the cladoceran community from one dominated by *E. longispina* throughout much of the MWP and the LIA to a community dominated by *B. longirostris* and the near absence of *Daphnia* and littoral species. This shift also coincided with an increase in the abundance of shrubs in the region and the continued increase in charcoal influx suggesting increased frequency of fires and landscape modifications linked to anthropogenic activities (Lafontaine-Boyer & Gajewski). It also approximately coincides with the time the Black Mine was being exploited (Leroux, 2012); the road to the mine passes along the north shore of the lake. These disturbances likely led to

an increase in allochotonous materials into the lake, particularly nutrients and organic carbon (Watmough et al., 2003), which would have led to increased nutrient availability for algal production, decreased transparency and decreased macrophyte growth. The increased algal production would have subsequently supported the shift towards *B. longirostris* over *Eubosmina* spp. The brief decrease in the abundance of *B. longirostris* in zone 5 coincided with a decrease in charcoal influx and a brief increase in the representation of littoral organisms and *Daphnia* species around 1950 CE (Figure 3). This is likely due to decreased disturbance, which may have resulted in less erosion and subsequently decreased nutrient inputs. Charcoal influx rates increased again around 1965 CE and were once again accompanied by an increase in the representation of *B. longirostris,* a decrease in *E. longispina,* and a decrease in diversity again. The strong association between *B. longirostris* abundances and the charcoal influx from the region into the lake suggests that the effects from fires and other changes in the region did have a local impact on the cladoceran communities of the lake throughout the core. The increased temperatures along with the changes in the aquatic environment from anthropogenic activities during the European period led to an increase in planktonic productivity and food availability which opened up a niche for the smaller pioneer species *B. longirostris,* in the absence of competition from other pelagic species (Plath & Boersma, 2001; Gillooly & Dodson, 2001) as a result of increased temperatures and anthropogenic activities. This indicates that rather than responding directly to temperature, the Cladocera are instead responding to the secondary impacts of temperature on the landscape and in the aquatic environment. CARs begin to accelerate towards the end of zone 4 (1900 CE) and into zone 5, indicating continued increased production in response to the increased temperatures and disturbances in the ecosystem.

The unconstrained cluster analysis illustrates community variability within each

zone, compared to the stratigraphically-constrained analysis which indicates long-term gradual changes in the community. The unconstrained analysis more clearly shows that increased *B. longirostris* abundances coincide with increased charcoal deposition in the watershed. Communities from the very bottom of the core are similar to those from the very top; unfortunately, there are too few levels in the first zone to understand the reasons for this resemblance. Groups 1 and 4 in the unconstrained analysis roughly correspond to zones 2 and 4 respectively, indicating less variation in the communities through time during these periods and more during zones 1, 3 and 5, where more rapid changes in temperature, pollen composition, and charcoal influx rates were found to occur.

The impact of post-Little Ice Age warming on the landscape was magnified by the arrival of Europeans and forestry practices in the greater region that disturbed the forests leading to more abundant shrubs and early successional trees such as white pine (Braun, 1950; Lafontaine-Boyer & Gajewski). The response of the cladoceran community to this shift was a decrease in the abundance of *Daphnia* spp. and littoral species. Although *B. longirostris* abundances were relatively high during the MWP, they were not as high as they have been over the past 100 years. In addition, the community of the MWP was more diverse than it is today. Current temperatures have surpassed those of the MWP; anthropogenic changes shifted the community and parts of the ecosystem beyond what was seen during the MWP with comparable temperatures. However, due to the lack of independent records of fish populations within the lake, the role of fish populations in shifting community composition cannot be ruled out (Jeppesen et al., 1996; Davidson et, 2010a and b).

Even in a lake that has experienced little direct impact from eutrophication, recreation or settlement or anthropogenic activities from the greater region and potentially

from the mine, the regional anthropogenic effects on the landscape combined with a warmer climate have had a noticeable impact on the aquatic communities. This change was greater than what was experienced during the MWP and the transition into the LIA and likely would likely not have been caused by an increase in temperature alone, as seen by the comparison with the MWP. It also shows that hat there was more variability in the community during periods of where there was more variability in the temperatures of the region and changes in the landscape. Using the deep, ultra-oligotrophic Lac Brûlé, we were able to track the impact of climate changes and changes in the landscape on the cladoceran communities (Schindler, 2009). This allows for a better understanding of how disturbances in the region, combined with climatic changes, impact aquatic ecosystems.

These results indicate distinct communities develop in relation to temperature and changes in the landscape. The oligotrophic character allows us to better connect the changes in the community to changes in the landscape and to climatic change than in more productive lakes, where changes in nutrient concentrations can mask these effects (Schindler, 2001; Woodward et al., 2010). This study shows that the current community of the lake is not comparable to any other time in the past 1200 years as a result of climatic events and disturbances in the landscape from human impact. It also shows clear examples of the relationship between three competing species under different temperature regimes and disturbances in the aquatic ecosystem.

Table 3.1: Loadings of the Principal Components on the cladoceran taxa in the core from Lac Brûlé

Species	PC1	PC2
Bosmina.longirostris	-0.30	0.54
Eubosmina.longispina	0.05	-0.62
E.oriens	-0.05	-0.04
Daphnia	0.10	0.21
D. longispina	0.40	-0.08
D. pulex	0.19	0.03
Alona	0.18	-0.03
A. affinis	0.23	0.03
A. quadrangularis	0.25	0.05
A. circumfimbriata	0.29	0.05
A.rustica	0.21	0.08
A. intermedia	-0.02	-0.17
A. costata	0.11	-0.08
C. brevilabris	0.14	0.18
C. faviforms	0.13	0.05
Alonella.excisa	0.21	0.31
A. nana	0.24	-0.01
Camptocercus	0.27	0.01
Graptoleberis	0.02	0.09
Pleuroxus	0.15	0.21
Eurcycercus	0.11	-0.06
Acroperus	0.19	0.03
Sida	0.25	0.14
Leptodora	0.20	0.03
Other	0.13	-0.07

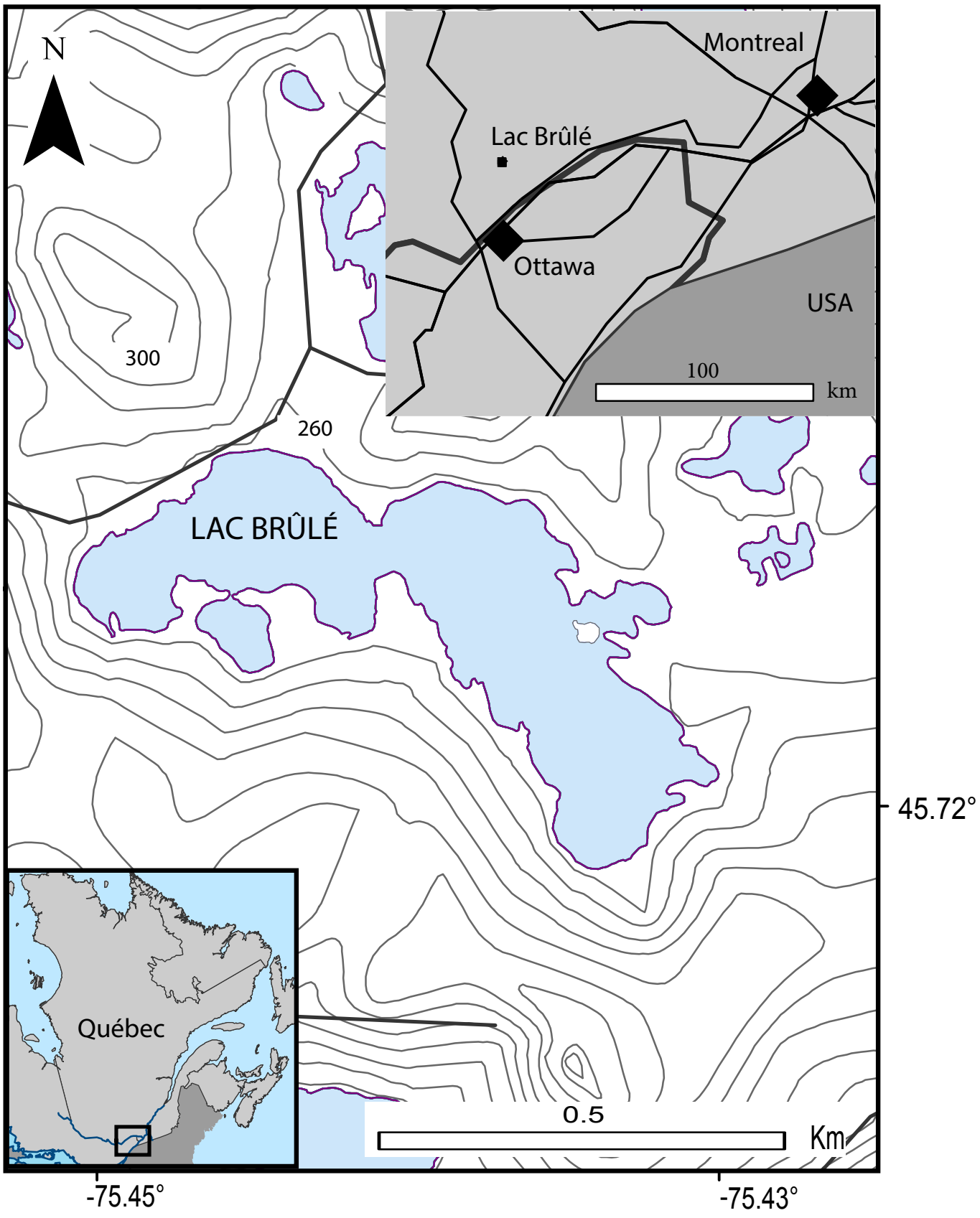

Figure 3.1: Topographic map of the area surrounding Lac Brûlé (45.72°, -75.44°), Southwestern Québec; the core was collected from the deepest part of the lake at 42 m.

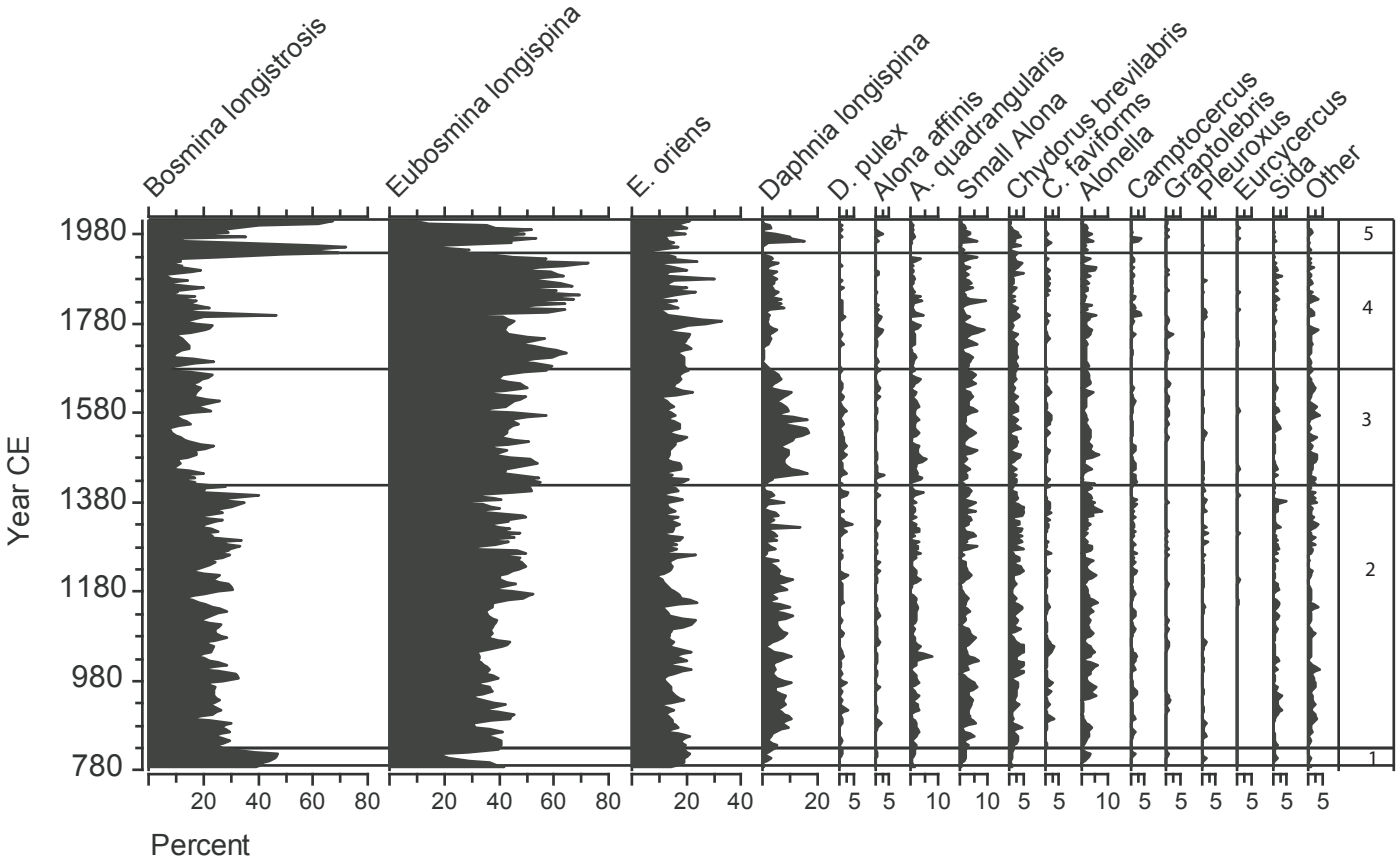

Figure 3.2: Stratigraphic diagram of the percent abundances of cladoceran taxa in Lac Brûlé. *Alona circumfimbriata, A. rustica, A. costata, A. intermedia* and other small unidentified *Alona* subfossils have been lumped into the category "Small Alona". Zones are determined using the constrained cluster analysis shown in Figure 3. Only taxa which make up at least one percent of the assemblage in at least two samples are listed, all others are combined into the column title "Other".

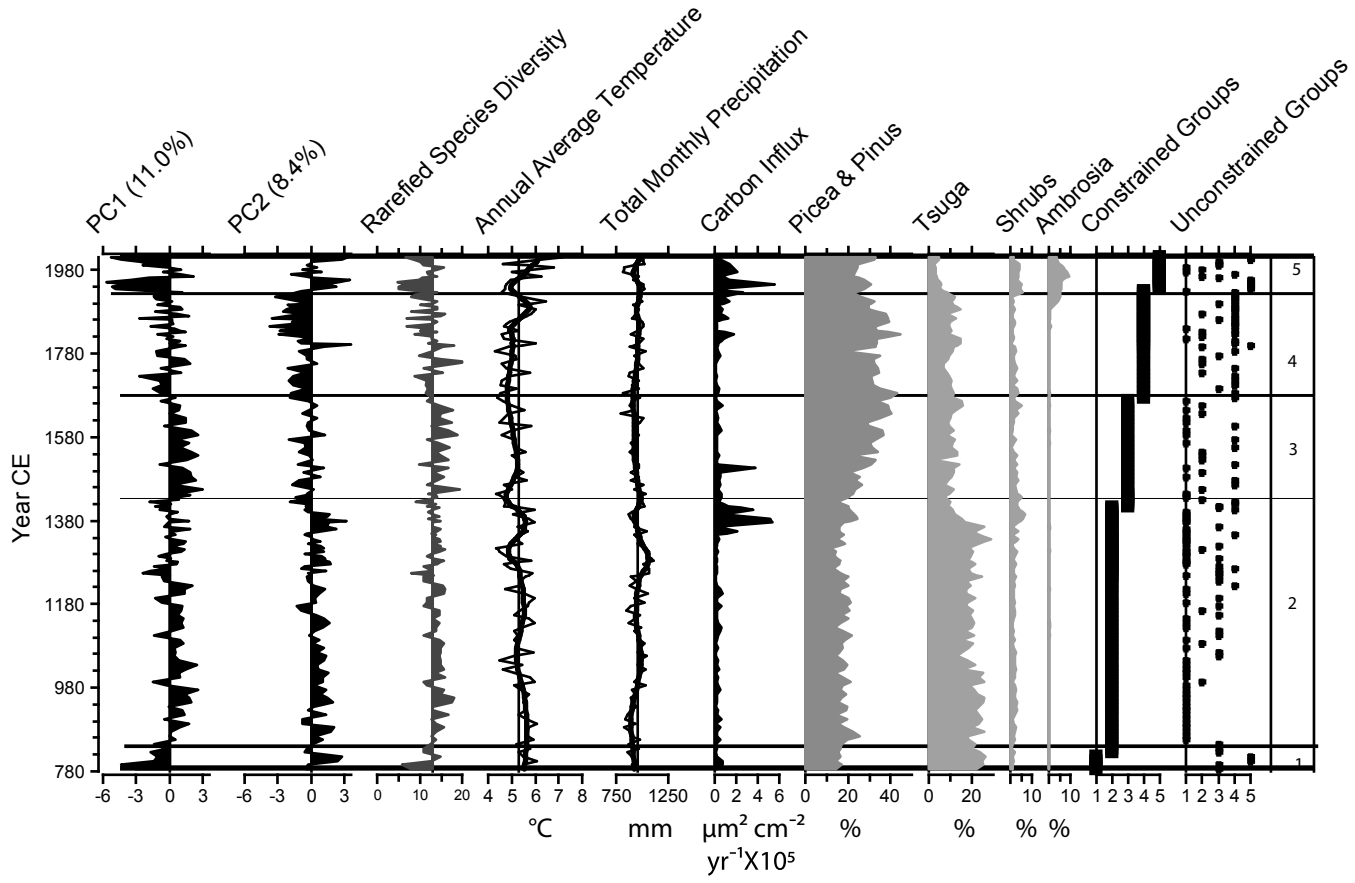

Figure 3.3: Principal Components Analysis (PCA) scores (species percentages transformed using the Hellinger transformation (Borcard et al., 2011)) of the Cladocera species, community diversity, Rarefied Diveristy Index, temperature and precipitation reconstructed using the pollen record, charcoal influx rates, abundances of key tree species summarized from Lafontaine-Boyer and Gajewski (2014), and group membership of sites using constrained and an unconstrained cluster analyses of the species abundances transformed by the Hellinger transformation.

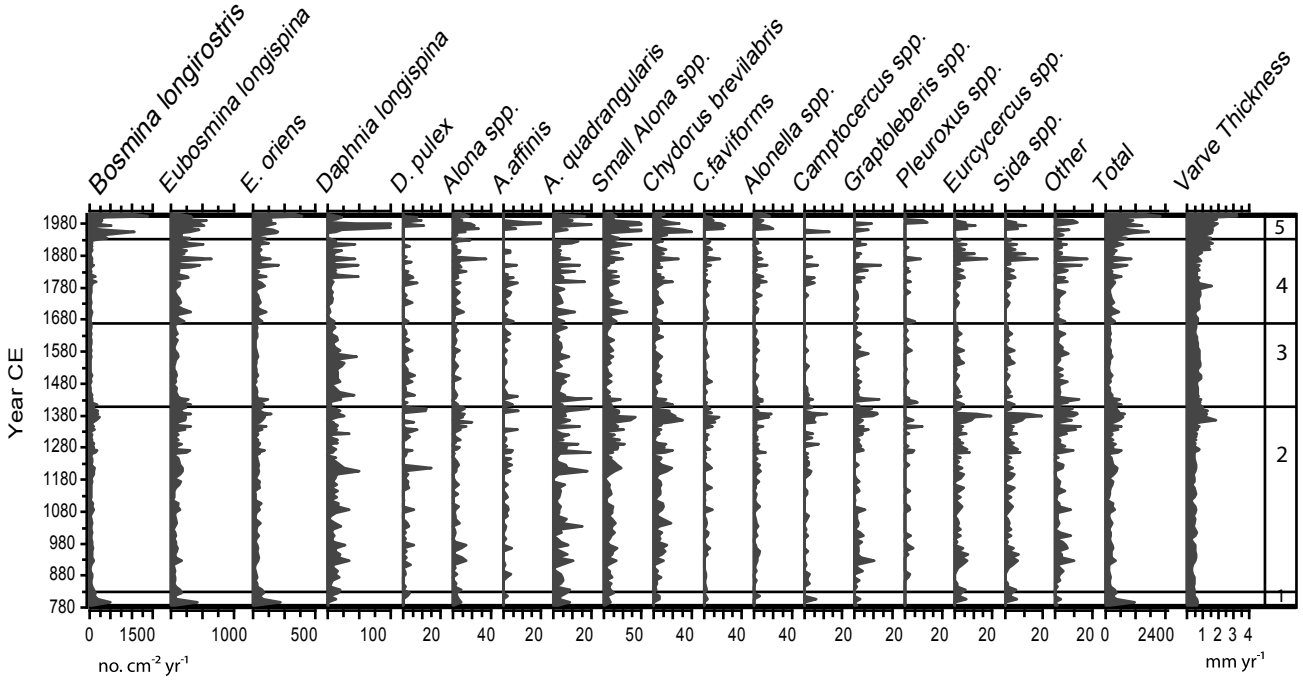

Figure 3.4: Accumulation rates in individuals cm^{-2} yr^{-1} by species, total cladoceran accumulation rates and varve thickness in millimetres. Zonations were determined using the biostratigraphic cluster analysis from Figure 3.

4. Conclusions

Cladocera are widely used as paleoecological indicators due to their diversity, their fidelity of preservation in lake sediments, their identifiability, and for their responses to changes in habitat structure and to nutrient/mineral concentrations in the aquatic ecosystem. This study began with an analysis of cladoceran communities across a series of lakes in the region of southwestern Québec. Most of the lakes in the region had a pH above 7 and were situated on marble-calcium carbonate rock. A Principal Components Analysis (PCA) on the environmental variables was used to determine the relationships among the lakes. The PCA of the environmental variables was subsequently combined with a PCA of the cladoceran communities of the corresponding lakes in a redundancy Analysis (RDA). The RDA was used to determine the influence of environmental factors on the species composition and relations within the region.

The results were consistent with most other studies concerning the response of cladoceran communities to variation in environmental variables (eg: Broderson et al, 1998; Desellas et al, 2008; 2011; Kurek et al, 2011). The pelagic species were more responsive to depth and to mineral concentrations while littoral organisms responded to nutrient and chlorophyll concentrations and to lake surface area. Oligotrophic lakes contained higher relative abundances of *Alona* species and pelagic taxa while lakes with higher phosphorus concentrations tended to have higher representations of plant dwelling taxa such as *C. brevilabris*, *Eurycercus*, and *Pleuroxus*. The cladoceran communities of these lakes were more heavily influenced by the nutrient concentrations and morphological characeristics than by pH and related ion concentrations compared to other studies.

Cladoceran communities were extracted from the varved sediments of Lac Brûlé in the Mulgrave-Derry region of southwestern Québec to reconstruct community changes and to infer changes in habitat structures and nutrient concentrations in response to climatic changes inferred from the pollen record. A Canonical Correspondence Analysis (CCA) of the time series data was plotted passively on a CCA of the surface samples of the Québec study combined with surface samples from a study conducted in central Ontario (Desellas et al., 2008. Unfortunately, few analogues of the down-core assemblages were found in the modern samples and hence these samples could not be used to quantitatively interpret the fossil data. Prior to the study, we had predicted that *Daphnia* abundances would decrease into the present day as a result of warmer temperatures and decreasing Ca trends. We predicted that this would likely be most noticeable in the warmest periods: the 1940s and the 1990s into the new millennium. *Daphnia* populations would likely be replaced by low calcium counterparts including *Bosmina* and *Eubosmina.* Secondly, we predicted that diversity would be highest during preindustrial times and would decrease into modern day. Thirdly, we expected an increase in plant associated organisms with warmer temperatures and lastly, that the fire that had occurred in the area of Lac Brûlé around 1375 CE would have resulted in an increase in the abundance of *Alona* species and in the abundance of pelagic species as a result of decreased macrophyte growth and increased nutrient input.

The relative abundances of *Daphnia* spp. did indeed increase into the present day with the increasing temperatures; however, Ca did not appear to be a factor in this decrease. As well, *Daphnia* abundances were not shown to have decreased particularly during the 1940s or 1950s. With decreases in the abundances of Daphnia came increased in the relative abundances of *Bosmina* and *Eubosmina* spp.

The community was more diverse from the middle of the Medieval Warm Period to the middle of the Little Ice Age (865-1660 CE) after which diversity decreased rapidly (1665-1860 CE) with the colder temperatures. In spite of the temperature increase in the modern period, charcoal influx into the lake and landscape changes impacted the aquatic environment negatively. This is documented by continued low abundances of littoral organisms and of *Daphnia* along with the shift to *B. longirostris* during the past 100 years and overall low diversity. The loss in forest cover would have led to an increased influx of materials from the surrounding area into the lake which would have altered the ecological conditions. The increased nutrient influx led to increased primary production, leading to shifts towards Bosminidae over Daphniidae. The diversity was relatively high throughout the preindustrial periods but there was a shift towards higher abundances of *Alona* and *Daphnia* during colder periods as a response to decreased primary productivity. Therefore, rather than responding directly to temperature, the organisms appear more to be responding to secondary impacts of temperature and anthropogenic activities in the surrounding landscape on the aquatic environment.

The study showed that *B. longirostris* abundances were indeed higher during warmer periods, particularly during the new millennium and from 785-825 CE, but while *E. longispina* was more associated with colder temperatures. Disturbances in the region, such as charcoal influx and changes in vegetation composition however, appeared to have a larger influence on abundances of *B. longirostris* than any direct temperature effects. The shifts in species composition around the times of the increase in charcoal influx from the watershed indicate that the impact of the fire was likely local on the lake. Figure 3.4 indicated an increase in the accumulation rates of *Alona* species during this time; however, the relative abundances did not change with the charcoal influx. *Bosmina* abundances increased in each

case of an increase in the accumulation rates of Charcoal on the landscape, thus showing a tendency for the taxon to respond to fire on the landscape and the subsequent changes in the aquatic environment.

Using the deep, oligotrophic Lac Brûlé, we were able to track the impact of climate changes in the landscape on the cladoceran communities on a high-resolution timescale to better understand how disturbances and climatic changes impact aquatic ecosystems. More studies of a comparable resolution are needed in order to further understand the impact of recent climatic events on freshwater ecosystems. In addition, information on fish abundances should also be incorporated to assess the impact of changing climate and anthropogenic activities on species abundances and trophic interactions.

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Appendix 1: Surface Sediment Calibration

Surface sediment samples were collected from 31 lakes in the region of southwestern Québec and analysed for their cladoceran communities. These data were combined with those from a study by Desellas et al (2008) on cladoceran-environmental relations in the region of central Ontario. Using a CCA, the communities were related to environmental variables from the spatial series of lakes to determine organismal preferences. A CCA of the species variation in Lac Brûlé through time was passively plotted onto the surface-sample CCA using the timetrack program in the analogue R package (Simpson, 2007). This was done to track the changes in community composition through time relative to the communities of the surface sediments and the environmental calibration. Unfortunately, few analogues were found from the modern samples for down core assemblages and thus the calibration set was inadequate for this study (Figure A1.1). However, this suggests that either Lac Brûlé is different from most lakes in the vicinity, or that recent changes have greatly altered the cladoceran communities of the region beyond what was seen in Lac Brule throughout the late Holocene.

Table A1.1: Numbers used to designate lakes in Figure A1.1. See Figure 2.1 and Desellas et al (2008) for locations

#	Lake				
1	Bernard	30	Vert	59	McKay
2	Bitobi	31	Victoria	60	Moot
3	Brûlé	32	Wallingford	61	Nunikani
4	Demi-Lune	33	Axe	62	Pearceley
5	Donovan	34	Basshaunt	63	Pincher
6	Du Pret	35	Bigwind	64	Plastic
7	Fraser	36	Blue Chalk	65	Red Pine
8	Gibeault	37	Bonnechere	66	RedChalkE
9	Gilmour	38	Brandy	67	RedChalkM
10	Heeney	39	Buck	68	Saw
11	Kallala	40	Chub	69	Sherborne
12	Kidder	41	CinderEast	70	Smoke
13	Lemery	42	CinderWest	71	Solitaire
14	Letourneau	43	Cradle	72	Timberwolf
15	Neuf	44	Crosson	73	Walker
16	Noir	45	Crown	74	Young
17	Noir II	46	Delano		
18	Orignal	47	Devine		
19	Perdrix	48	Dickie		
20	Pink	49	Glen		
21	Profond	50	Hamer		
22	Ramsay	51	Harp		
23	Renaud	52	Healey		
24	Robinson	53	Heney		
25	St. Antione	54	Kimball		
26	Star	55	Leech		
27	Taylor	56	Leonard		
28	Truite	57	Little Clear		
29	Vases	58	Maggie		

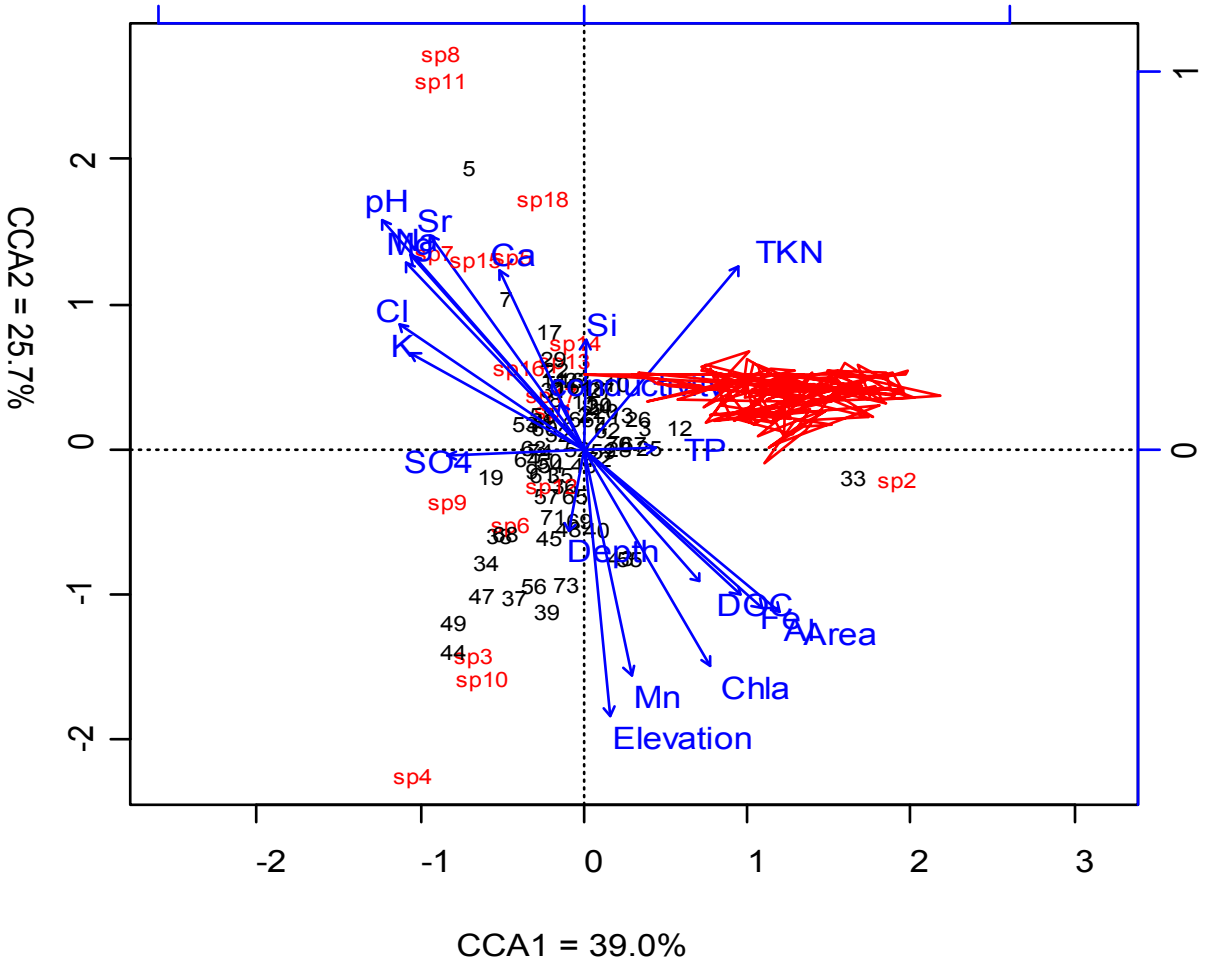

Figure A1.1: Canonical Correspondence Analysis (CCA) of the Lac Brûlé cladoceran community time series (Chapter 3) plotted passively over the CCA of the present-day cladoceran communities from the Québec lakes (Chapter 2) combined with cladoceran communities from central Ontario (Desellas et al., 2008) calibrated to the environmental variables. See Table A.1 for corresponding lakes names.

Appendix 2: Data Tables

Table A2.1: Location, geology, area, depth, acidity and specific conductances of lakes collected for the surface analysis from southwestern Québec.

Lake	Latitude	Longitude	Elevation (metres above sea level)	Geology	Area (hectares)	Depth (metres)	pH	Specific Conductance (μScm^{-1})
Bernard	45.76	-76	166	Marble	450	24	8.39	147.9
Bitobi	46	-75.95	150	Marble	38	19.4	8.30	96
Brûlé	45.72	-75.44	252	Granite	12	42	8.35	118.9
Demi-Lune	45.74	-75.99	192	Marble	9.6	15	8.22	205.1
Donovan	45.77	-75.73	192	Marble	8	5	7.75	245
Du Pretre	45.84	-75.76	180	Sable	11	32	8.11	80
Fraser	45.65	-75.97	153	Sable	7.5	4	8.30	225.03
Gilmour	45.64	-75.55	136	Marble	11	42	8.70	131.5
Heney	46.02	-75.93	150	Marble	1590	32	8.70	234.5
Kallala	45.74	-75.98	199	Marble	8	9	8.16	112.9
Kidder	45.6	-76.09	212	Syenite	12	17	7.36	55
Lemery	45.84	-75.16	236	Granite	7	14.5	7.20	104
L'etourneau	45.6	-75.67	128	Marble	28	4	8.30	159.8
Neuf	45.79	-75.2	238	Paragneiss	7.4	30	7.20	20.5
Noir	45.78	-75.13	177	Gabbro	10	30	7.70	20
Noir II	46.01	-75.95	150	Marble	11	7.2	8.32	120
Orignal	46	-76.08	181	Marble	74	27.2	8.60	157.5
Perdrix	45.59	-75.69	156	Marble	40	27.1	8.00	82.4
Pink	45.47	-75.81	164	Paragneiss	10	20	8.25	239
Profond	46	-76.1	180	Marble	148	35.3	8.00	226.9
Ramsay	45.6	-76.1	204	Syenite	8.2	8.7	7.31	60
Renaud	45.6	-76.02	203	Syenite	11.5	8	7.21	69.8
Robinson	45.72	-75.73	227	Paragneiss	16	8	7.65	61.3
St. Antoine	45.66	-75.8	230	Sable	40	9	7.65	65.5
Star	45.74	-75.69	311	Paragneiss	7	50	7.96	39
Taylor	45.6	-76.04	210	Syenite	48	20	7.72	75
Truite	46	-75.9	181	Marble	9.6	17.5	8.60	129.1
Vases	46	-76.13	179	Paragneiss	45	0.8	8.51	102.8
Vert	46	-75.94	156	Marble	19	13.4	8.63	158.8
Victoria	46.07	-75.96	151	Marble	52	7.2	8.12	131.7
Wallingford	45.58	-75.69	168	Paragneiss	6.8	13.5	8.44	210

Table A2.2: Chemistry measurements in mgL-1 of the lakes collected for the surface sample analysis

Lake	TP	TKN	Chla	SO4	Na	Ba	Mn	Ca	Mg	K	Cl	Al
Bernard	0.007	0.30	0.006	9.20	1.60	0.01	0.01	23.55	3.90	0.69	1.60	0.007
Bitobi	0.004	0.33	0.002	3.40	1.80	0.01	0.01	13.60	1.90	0.71	0.90	0.007
Brûlé	0.004	0.17	0.005	6.60	0.80	0.01	0.00	22.80	1.00	0.40	0.60	0.010
Demi-Lune	0.004	0.29	0.004	7.70	2.30	0.02	0.00	37.50	6.80	0.82	4.30	0.015
Donovan	0.013	0.37	0.006	4.20	15.30	0.01	0.02	29.60	1.80	0.69	27.80	0.018
Du Pretre	0.008	0.16	0.01	4.70	1.00	0.01	0.01	11.90	1.30	0.40	0.80	0.020
Fraser	0.005	0.34	0.003	8.40	4.80	0.02	0.01	33.40	4.80	1.09	5.10	0.005
Gilmour	0.005	0.29	0.005	4.70	2.00	0.03	0.00	11.60	3.60	0.82	2.20	0.005
Heney	0.011	0.28	0.005	7.60	2.50	0.01	0.00	19.40	2.60	0.94	3.10	0.003
Kallala	0.007	0.40	0.010	4.60	2.00	0.02	0.02	38.05	7.60	0.92	0.90	0.004
Kidder	0.003	0.17	0.005	6.40	0.70	0.01	0.01	7.80	1.00	0.21	0.20	0.011
Lemery	0.005	0.23	0.007	6.00	8.60	0.01	0.04	7.80	1.20	0.83	13.50	0.034
L'etourneau	0.010	0.34	0.010	3.70	2.40	0.06	0.04	16.20	2.20	0.78	2.60	0.009
Neuf	0.006	0.25	0.004	2.80	1.40	0.01	0.01	6.40	0.60	0.26	1.30	0.080
Noir	0.009	0.26	0.006	3.90	2.00	0.01	0.01	10.60	0.90	0.48	2.80	0.047
Noir II	0.023	0.59	0.02	10.00	3.60	0.01	0.00	25.65	3.00	1.40	5.00	0.001
Orignal	0.008	0.42	0.002	7.60	0.80	0.01	0.00	19.30	2.60	0.55	0.20	0.012
Perdrix	0.007	0.27	0.004	9.70	1.60	0.09	0.01	24.85	1.90	0.86	1.60	0.005
Pink	0.005	0.19	0.005	9.00	1.60	0.02	0.00	42.90	2.40	0.60	0.90	0.006
Profond	0.004	0.19	0.007	4.70	0.90	0.01	0.00	11.65	2.20	0.60	0.30	0.004
Ramsay	0.007	0.34	0.007	4.90	1.70	0.02	0.01	7.80	1.30	0.29	1.30	0.016
Renaud	0.043	0.63	0.006	2.90	0.70	0.02	0.02	8.70	2.30	0.24	0.30	0.013
Robinson	0.005	0.24	0.008	3.10	1.60	0.01	0.02	7.40	1.30	0.60	1.30	0.016
St. Antoine	0.006	0.24	0.004	3.60	0.90	0.01	0.01	8.20	1.40	0.43	0.80	0.019
Star	0.003	0.21	0.002	3.30	0.40	0.00	0.00	6.60	0.80	0.20	0.20	0.035
Taylor	0.005	0.25	0.006	4.10	0.70	0.01	0.01	9.60	2.90	1.21	0.40	0.015
Truite	0.006	0.23	0.003	12.90	0.80	0.02	0.00	33.20	9.00	0.97	0.20	0.003
Vases	0.009	0.47	0.003	7.50	1.40	0.02	0.00	18.95	4.00	0.72	1.20	0.008
Vert	0.007	0.40	0.006	10.20	3.00	0.01	0.00	26.10	2.20	0.88	4.00	0.003
Victoria	0.007	0.34	0.004	8.20	1.90	0.01	0.02	19.80	2.40	0.80	1.00	0.003
Wallingford	0.004	0.31	0.005	9.70	2.00	0.08	0.01	34.10	1.90	0.69	2.80	0.005

Lake	Si	Fe	B	Sr	Zn	Ni	Cu	Pb	Ag	Ti
Bernard	2.3	0.0134	0.008	0.06	0.0006	0.0003	0.0006	0.0001	0.0001	0.0003
Bitobi	1.2	0.0125	0.004	0.0913	0.001	0.0004	0.0008	0.0001	0.0001	0.0006
Brûlé	0.91	0.0048	0.0058	0.1348	0.0028	0.0008	0.0006	0.0001	0.0001	0.0002
Demi-Lune	1.06	0.0056	0.0083	0.0867	0.001	0.0004	0.0006	0.0001	0.0001	0.0004
Donovan	0.95	0.0448	0.0124	0.1406	0.0021	0.0002	0.0024	0.0003	0.0001	0.0007
Du Pretre	1.72	0.046	0.0058	0.0599	0.0018	0.0003	0.0006	0.0001	0.0001	0.0003
Fraser	0.66	0.0142	0.0208	0.1001	0.0012	0.0006	0.0006	0.0001	0.0001	0.0003
Gilmour	0.96	0.00755	0.0187	0.0763	0.0006	0.0006	0.0009	0.0001	0.0001	0.0002
Heney	1.38	0.00205	0.007	0.1117	0.0006	0.0004	0.0006	0.0001	0.0001	0.0002
Kallala	2.5	0.01515	0.0134	0.0858	0.0012	0.0006	0.0006	0.0001	0.0001	0.0002
Kidder	1.86	0.0306	0.0057	0.0312	0.0016	0.0002	0.0006	0.0001	0.0001	0.0002
Lemery	2.94	0.1917	0.0042	0.0648	0.0023	0.0033	0.0008	0.0002	0.0001	0.0007
L'etourneau	1.47	0.0125	0.0113	0.208	0.0011	0.0004	0.0006	0.0001	0.0001	0.0006
Neuf	1.77	0.046	0.0059	0.0271	0.0038	0.0003	0.0006	0.0001	0.0001	0.0011
Noir	0.56	0.0602	0.0049	0.0643	0.0013	0.0003	0.0012	0.0001	0.0001	0.0038
Noir II	2.98	0.0021	0.0087	0.2049	0.0006	0.0004	0.0006	0.0001	0.0001	0.0002
Orignal	0.24	0.00425	0.0054	0.0288	0.0006	0.0003	0.0008	0.0001	0.0001	0.0002
Perdrix	0.54	0.00685	0.0178	0.3173	0.0006	0.0003	0.0007	0.0001	0.0001	0.0002
Pink	0.77	0.0048	0.0131	0.2889	0.0017	0.0004	0.0006	0.0004	0.0001	0.0003
Profond	1.01	0.0014	0.003	0.0277	0.0006	0.0002	0.0006	0.0001	0.0001	0.0002
Ramsay	0.6	0.1834	0.0084	0.0352	0.0024	0.0002	0.0043	0.0001	0.0001	0.0004
Renaud	0.88	0.2993	0.0128	0.0421	0.0018	0.0002	0.0006	0.0003	0.0001	0.0006
Robinson	1.74	0.0733	0.0047	0.0407	0.0016	0.0002	0.0006	0.0002	0.0001	0.0003
St. Antoine	0.9	0.163	0.0088	0.0478	0.0014	0.0003	0.0013	0.0001	0.0001	0.0006
Star	0.75	0.024	0.0106	0.06	0.0014	0.0003	0.0006	0.0001	0.0001	0.0003
Taylor	1.21	0.0378	0.0136	0.0411	0.0014	0.0002	0.0006	0.0001	0.0001	0.0008
Truite	0.87	0.0007	0.0043	0.0428	0.0006	0.0006	0.0006	0.0001	0.0001	0.0002
Vases	2.44	0.00575	0.0051	0.0624	0.0006	0.0003	0.0007	0.0001	0.0001	0.0002
Vert	0.68	0.0007	0.0069	0.2481	0.0006	0.0003	0.0006	0.0001	0.0001	0.0002
Victoria	1.39	0.0148	0.0049	0.1377	0.0013	0.0003	0.0006	0.0001	0.0001	0.0002
Wallingford	2.58	0.0119	0.0258	0.4006	0.0013	0.0007	0.0008	0.0002	0.0001	0.0003

Lake	Co	Cr	U	As	Bi	Be	Cd	Se	NO_3
Bernard	0.0001	0.0001	0.0001	0.0002	0.0001	0.0001	0.0001	0.0002	0.02
Bitobi	0.0006	0.0001	0.0001	0.0002	0.0002	0.0001	0.0001	0.0002	0.02
Brûlé	0.0024	0.0001	0.001	0.0002	0.0001	0.0001	0.0001	0.0003	0.02
Demi-Lune	0.0018	0.0001	0.0003	0.0002	0.0001	0.0001	0.0001	0.0002	0.02
Donovan	0.0006	0.0001	0.0001	0.0002	0.0001	0.0001	0.0001	0.0002	0.02
Du Pretre	0.0006	0.0001	0.0001	0.0002	0.0001	0.0001	0.0001	0.0002	0.7
Fraser	0.0008	0.0001	0.0003	0.0003	0.0001	0.0001	0.0001	0.0002	0.02
Gilmour	0.0001	0.0002	0.0001	0.0003	0.0001	0.0001	0.0001	0.0002	0.02
Heney	0.0001	0.0001	0.0001	0.0002	0.0001	0.0001	0.0001	0.0002	0.02
Kallala	0.0006	0.0001	0.0003	0.0002	0.0001	0.0001	0.0001	0.0002	0.02
Kidder	0.0008	0.0001	0.0001	0.0002	0.0001	0.0001	0.0001	0.0002	0.02
Lemery	0.0006	0.0002	0.0001	0.0002	0.0001	0.0001	0.0001	0.0002	0.14
L'etourneau	0.0009	0.0001	0.0001	0.0003	0.0001	0.0001	0.0001	0.0002	0.02
Neuf	0.0006	0.0001	0.0001	0.0002	0.0001	0.0001	0.0001	0.0002	0.02
Noir	0.0017	0.0001	0.0001	0.0002	0.0001	0.0001	0.0001	0.0002	0.02
Noir II	0.0006	0.0002	0.0001	0.0002	0.0001	0.0001	0.0001	0.0002	0.02
Orignal	0.0001	0.0001	0.0001	0.0002	0.0001	0.0001	0.0001	0.0002	0.05
Perdrix	0.0001	0.0002	0.0001	0.0003	0.0001	0.0001	0.0001	0.0002	0.02
Pink	0.0006	0.0003	0.0002	0.0004	0.0001	0.0001	0.0001	0.0002	0.02
Profond	0.0001	0.0001	0.0001	0.0002	0.0001	0.0001	0.0001	0.0002	0.1
Ramsay	0.0006	0.0001	0.0001	0.0002	0.0001	0.0001	0.0001	0.0002	0.02
Renaud	0.0017	0.0001	0.0001	0.0003	0.0001	0.0001	0.0001	0.0002	0.02
Robinson	0.0006	0.0002	0.0001	0.0002	0.0001	0.0001	0.0001	0.0002	0.02
St. Antoine	0.0006	0.0001	0.0001	0.0002	0.0001	0.0001	0.0001	0.0002	0.08
Star	0.0006	0.0001	0.0001	0.0002	0.0001	0.0001	0.0001	0.0002	0.02
Taylor	0.0006	0.0022	0.0001	0.0002	0.0001	0.0001	0.0001	0.0002	0.02
Truite	0.0001	0.0002	0.0001	0.0002	0.0001	0.0001	0.0001	0.0002	0.02
Vases	0.0001	0.0001	0.0001	0.0002	0.0001	0.0001	0.0001	0.0002	0.02
Vert	0.0001	0.0001	0.0001	0.0002	0.0001	0.0001	0.0001	0.0002	0.02
Victoria	0.0006	0.0001	0.0001	0.0002	0.0001	0.0001	0.0001	0.0002	0.02
Wallingford	0.0006	0.0004	0.0002	0.0002	0.0001	0.0001	0.0001	0.0002	0.02

Table A2.3 cladoceran surface sediment counts from lakes in southwestern Québec

Lake	*Bosmina longirostris*	*Eubosmina longispina*	*E.oriens*	*Sida*	*Daphnia (unidentified)*	*D.longispina*	*D.pulex*	*Chydorus brevilabris*	*C.biovatus*
Bernard	86	13	12	1	1	1	1	8	6
Bitobi	92	8	9	0	0	1	0	4	0
Brûlé	74	25	12	1	0	1	0	2	0
Demi-Lune	64	16	12	1	0	1	6	1	2
Donovan	3	4	0	0	0	0	0	34	6
Du Pret	74	17	3	1	1	2	11	12	0
Fraser	10	1	3	0	0	1	0	6	8
Gibeault	98	0	8	0	0	0	0	6	0
Gilmour	41	8	5	0	1	19	14	4	2
Heeney	52	28	1	3	0	1	0	13	1
Kallala	89	13	7	0	0	2	2	6	5
Kidder	73	24	33	0	0	0	0	1	3
Lemery	83	26	7	0	0	2	0	1	1
Letourneau	64	3	4	0	0	1	0	3	0
Neuf	88	8	6	0	0	2	0	5	3
Noir	80	11	4	0	0	0	0	10	0
NoirII	69	16	3	1	0	3	3	36	7
Orignal	73	19	5	0	1	1	1	15	0
Perdrix	21	3	4	1	0	18	34	21	7
Pink	89	23	1	1	0	1	0	1	2
Profond	97	10	8	0	1	3	0	4	0
Ramsay	83	3	5	1	0	0	0	5	2
Renaud	80	15	0	1	0	0	0	5	4
Robinson	98	21	4	0	0	3	0	2	2
St. Antione	20	40	4	4	0	14	8	6	8
Star	73	10	22	2	0	0	0	2	1
Taylor	67	15	12	1	1	2	0	6	5
Truite	40	16	11	0	0	7	5	3	0
Vases	28	6	0	0	0	2	0	8	0
Vert	97	13	8	0	0	0	0	7	0
Victoria	67	9	2	0	1	2	6	11	2
Wallingford	74	9	3	0	1	3	11	4	2

Lake	*C.piger*	*C. faviforms*	*Alona (unidentified)*	*A.circumfimbriata*	*A.quadrangularis*	*A.rustica*	*A.affinis*	*A.intermedia*
Bernard	0	4	3	0	0	0	0	0
Bitobi	0	0	0	0	0	0	0	0
Brûlé	0	0	0	0	0	0	0	0
Demi-Lune	0	1	2	1	3	0	1	1
Donovan	0	0	9	3	3	1	0	0
Du Pret	0	0	0	1	0	1	0	0
Fraser	1	0	0	0	4	4	0	0
Gibeault	0	1	0	0	1	1	0	0
Gilmour	1	1	5	1	1	1	1	0
Heeney	0	1	1	0	0	0	0	0
Kallala	0	1	2	1	0	0	1	0
Kidder	0	0	0	0	2	1	0	0
Lemery	0	1	3	2	2	1	0	0
Letourneau	0	0	5	1	9	0	0	0
Neuf	0	1	4	1	6	0	0	0
Noir	0	0	8	1	0	4	1	0
Noir II	1	0	2	1	0	1	0	0
Orignal	0	1	0	0	0	0	1	0
Perdrix	14	0	4	1	0	3	0	0
Pink	0	0	2	2	1	0	0	1
Profond	0	0	2	0	0	0	0	0
Ramsay	0	0	4	5	2	1	0	0
Renaud	1	0	1	2	1	0	0	0
Robinson	0	0	7	1	2	0	0	0
St. Antione	0	0	0	0	0	0	0	0
Star	0	0	1	0	1	1	0	0
Taylor	0	0	3	1	0	3	0	1
Truite	0	0	0	1	4	1	3	0
Vases	0	0	2	0	4	0	0	0
Vert	0	0	0	0	0	0	0	0
Victoria	0	0	1	0	1	0	1	0
Wallingford	0	0	1	0	2	0	0	0

Lake	*Alonella excisa*	*A. nana*	*A. puchella*	*Camptocercus*	*Eurycercus*	*Graptoleberis*	*Pleuroxus*	*Leptodora*
Bernard	1	1	0	0	0	0	0	0
Bitobi	1	1	0	0	0	0	0	0
Brûlé	0	5	0	0	0	0	0	0
Demi-Lune	1	0	0	1	3	0	3	0
Donovan	0	0	0	3	0	0	1	0
Du Pret	3	1	1	0	0	0	0	0
Fraser	0	0	1	0	2	0	0	0
Gibeault	2	0	0	0	0	1	0	0
Gilmour	1	3	1	3	4	1	0	4
Heeney	18	0	0	0	0	1	0	0
Kallala	0	0	0	0	0	0	0	0
Kidder	1	0	0	0	2	0	0	0
Lemery	4	0	0	2	1	1	0	0
Letourneau	1	0	0	1	0	0	0	0
Neuf	2	1	0	2	1	0	0	0
Noir	3	0	0	0	0	1	3	0
Noir II	2	0	0	0	1	0	0	0
Orignal	4	1	0	2	0	0	1	0
Perdrix	6	1	0	1	3	3	3	0
Pink	0	3	0	0	0	0	0	0
Profond	1	0	0	0	0	0	0	0
Ramsay	0	4	0	2	1	0	0	0
Renaud	0	1	0	2	0	3	2	1
Robinson	0	2	0	0	0	0	0	0
St. Antione	0	2	0	0	0	2	4	0
Star	1	1	0	0	0	0	1	0
Taylor	0	3	0	1	2	0	4	0
Truite	4	3	0	0	1	0	0	0
Vases	14	2	0	0	0	0	0	0
Vert	0	1	0	0	0	0	0	0
Victoria	3	0	0	3	2	1	4	0
Wallingford	1	2	0	1	0	1	1	0

Lake	*Leydigia*	*Holopedium*	*Acroperus*	total
Bernard	0	0	1	139
Bitobi	0	0	0	116
Brûlé	0	0	0	120
Demi-Lune	0	0	0	120
Donovan	0	0	1	68
Du Pret	0	0	0	130
Fraser	1	0	0	42
Gibeault	0	0	0	118
Gilmour	0	0	1	126
Heeney	0	0	0	120
Kallala	0	0	0	129
Kidder	0	0	0	140
Lemery	0	0	0	137
Letourneau	0	1	0	93
Neuf	0	0	0	130
Noir	0	0	0	125
Noir II	0	0	0	146
Orignal	0	0	0	126
Perdrix	0	0	3	133
Pink	0	0	0	127
Profond	0	0	0	126
Ramsay	0	0	0	120
Renaud	0	0	0	120
Robinson	0	0	0	142
St. Antione	0	0	0	112
Star	0	1	0	117
Taylor	0	0	0	130
Truite	0	0	0	99
Vases	0	0	0	66
Vert	0	0	1	127
Victoria	0	0	0	116
Wallingford	0	0	0	116

Table A2.3: cladoceran Lac Brûlé time series counts from varved core. All individuals observed were recorded, and up to approximately 125 individuals counted per site

Year CE	*Bosmina longirostris*	*Eubosmina longispina*	*E. oriens*	*Daphnia (unidentified)*	*D. longispina*	*D. pulex*	*Alona (unidentified)*	*A.affinis*	*A. quadrangularis*	*A. circumfimbriata*
2010	91	12	29				1			
2005	84	19	24	1	1	0	1	0	1	0
2000	49	43	21		3	1	1		1	1
1995	41	51	27		4				1	
1990	30	57	15			1	1		1	
1985	42	59	22		1		1	2	1	2
1980	11	50	20		5		2	3	1	
1975	46	47	10		13	1	2	0	2	
1970	12	58	14		11		1		1	1
1965	14	46	15		17		4	1		1
1960	41	60	21	2	3		1		1	
1955	80	23	15	1	1		1			
1950	94	19	22							
1945	74	38	12				1			
1940	91	30	5							
1935	61	45	15							
1930	32	56	20		4		6			2
1925	13	65	15		4		2		4	
1920	13	62	27		2				2	1
1915	8	84	9		7					
1910	14	74	15	0	3	1	1	0	1	0
1905	12	56	16		2		2			2
1900	24	58	25		2		1		1	
1895	18	67	16		6	0	2	1	1	
1890	5	54	11		3		2	1		1
1885	6	61	13		3		1		1	
1880	5	29	18		3		1		1	
1875	18	67	19		5	1	1		1	1
1870	6	75	16		5		4		1	
1865	16	75	15		3					1
1860	26	55	26		5	2	3	0	1	
1855	13	76	17		5		1		1	1
1850	13	65	29		7		1	1	2	
1845	7	70	16		4		2			
1840	19	62	15		2				4	1
1835	8	58	6		6		3		1	
1830	17	42	16		3	1	5		4	2
1825	19	84	12		9	1	2		1	1
1820	17	54	14		4	1	2	1	1	
1815	28	55	22	1	10	1	1		1	
1810	9	53	8		2	1	1	1	1	
1805	21	65	13		1	1	1		2	
1800	50	13	14		3	1		1	5	1
1795	28	58	25		3	3	3	3		1
1785	14	53	39		2			1		
1775	30	56	27		3		2		5	
1765	23	46	13		6		5	3	1	3
1755	13	55	27		3	1	2	2	2	1
1745	15	70	25		4		1		2	

Year CE	*Bosmina longirostris*	*Eubosmina longispina*	*E. oriens*	*Daphnia (unidentified)*	*D. longispina*	*D. pulex*	*Alona (unidentified)*	*A.affinis*	*A. quadrangularis*	*A. circumfimbriata*
1735	20	64	26		3	2	3	1	2	4
1725	19	73	28							
1715	13	85	21		1		2		1	
1705	13									
1695	26	51	21				1	1	1	2
1685	14	81	26		2		1		1	2
1675	8	74	27		4	1		2	2	2
1665	32	57	24		8		3			3
1655	26	51	24	1	9		2		5	2
1645	20	60	20		5	1	4	1	2	1
1635	21	56	17	1	3	1	1	2		
1625	23	43	29		14		2		3	2
1615	21	65	14		10	2	2	2	1	1
1605	33	58	16		6		2		3	1
1595	21	55	20		11	1			4	2
1585	29	42	16		12	3	4	1	2	2
1575	12	76	21		7	1	1		2	2
1565	16	58	18		22	1	1		4	1
1555	19	59	22		7	2		1	2	1
1545	9	57	23		21		2	1	2	2
1535	11	54	17	2	21	1	5		4	1
1525	15	52	26		15	2	3		1	1
1515	19	66	21		13	2	1			
1505	31	46	20	1	8	3			4	1
1495	21	53	17		12	1	6		3	
1485	23	48	18		12	3		1	4	1
1475	27	133	32	0	21	1	3	1	15	2
1465	15	71	23		10	1			3	
1455	12	56	24	1	14	1	2	1	2	1
1445	25	52	14		20	3	2	1	3	
1440	15	58	19	2	14	1	2	4	2	
1435	21	68	15		4		1	1	5	
1430	14	64	27		5				5	
1425	22	71	24		2				1	
1420	20	68	19		2	1	1	1		
1415	37	64	18		1		1	1	1	
1410	27	67	21		1		1	1	1	1
1405	24	62	20		1	1	3		2	
1400	25	58	18		4	4	4		6	
1395	49	34	13		5	3	2	2	2	2
1390	39	51	22	1	2		1		1	1
1385	31	52	24		3		2		1	
1380	36	18	14		8		3		2	2
1375	44	45	17		3		2			
1365	34	50	17		0				2	1
1360	28	35	19		3	2	7		2	
1355	34	46	17		6		2		1	
1350	27	65	14		8		1		1	2
1345	22	67	23	1	3		3		3	2
1340	34	54	17		5	2	3			
1335	33	59	20		4	2	2	2		1
1330	19	33	16		1	4	3	1	2	
1325	23	47	18		16				2	1
1320	29	56	20	1	2	1	1		4	
1315	32	50	19		4	3	2		4	
1310	25	58	13		5	2	3	1		2

Year CE	*Bosmina longirostris*	*Eubosmina longispina*	*E. oriens*	*Daphnia (unidentified)*	*D. longispina*	*D. pulex*	*Alona (unidentified)*	*A.affinis*	*A. quadrangularis*	*A. circumfimbriata*
1305	53	90	32	3	12	1	6	1	4	1
1300	28	58	24		3		3	1		
1295	44	41	23		7		1		1	
1290	39	39	67	20		1				5
1285	38	38	51	22	2	3			1	1
1280	42	42	42	15	1	3		3		3
1275	36	36	34	20		6		2		3
1270	37	37	60	19		2	1		1	1
1265	33	33	64	12		2			1	5
1260	35	35	44	28	1	1	1	1		2
1255	25	25	44	15			1			2
1250	28	28	65	20		8				1
1245	31	31	62	18		3		1	2	1
1235	26	26	63	19		6		2	0	1
1225	21	21	64	20		9		3	2	3
1215	32	32	50	11	1	7	4	1		2
1205	29	29	51	14	1	14		1	1	5
1195	39	39	61	16		6	1			1
1185	41	41	49	19	1	12	1	1		
1175	25	25	65	21		3	1	1		
1165	17	17	64	24		7	1	3	1	3
1155	25	25	51	32		3	2	1		2
1145	27	27	44	12		12				3
1135	38	38	47	17		5		4	1	3
1125	29	29	46	18	3	14			2	3
1115	23	23	50	30		7	1	2		3
1105	34	34	49	28		7				1
1095	32	32	49	20		8		3	1	2
1085	32	32	49	18		12	2	1	1	1
1075	36	36	45	17	2	9		1	1	2
1065	24	24	51	18		4		2	2	2
1055	31	31	54	17		1		2		5
1045	28	28	39	27		5	1	3		2
1035	23	23	43	20		14	2		1	10
1025	29	29	42	26		8		2	1	3
1015	39	39	47	17		5	1	2		3
1005	24	24	47	28	1	6		1		
995	41	41	45	20		5	1		1	2
985	46	46	55	16		7		2		3
975	28	28	42	17	1	14	3	7		4
965	32	32	48	19		6		4	2	
955	29	29	46	18	1	6	1	1		2
945	31	31	39	21	1	11	0	1		4
935	32	32	42	24		9	1	5		1
925	27	27	52	12		10		4		3
915	34	34	43	20		7	4	1	1	4
905	30	30	58	16	2	10		3		
895	19	19	57	19	0	14	1			1
885	40	40	40	20	2	9	1	3	3	3
875	34	34	40	22	1	12			1	3
865	38	38	53	16		6		1		4
855	31	31	46	28		4		3		3
845	39	39	54	24		3	1	1		1
835	31	31	52	25		7		3		3
825	39	39	51	25		5	1	1		2
815	60	60	23	27	0	1	1	2	1	2

Year CE	*Bosmina longirostris*	*Eubosmina longispina*	*E. oriens*	*Daphnia (unidentified)*	*D. longispina*	*D. pulex*	*Alona (unidentified)*	*A.affinis*	*A. quadrangularis*	*A. circumfimbriata*
805	61	61	29	25		4		2		1
795	57	57	50	26				1		1
785	50	50	53	18		1		1		2

Year CE	*A.rustica*	*A.intermedia*	*A. costata*	*Chydorus brevilabris*	*C.biovatus*	*C.faviforms*	*C.piger*	*Alonella excisa*	*A.nana*	*A.pulchella*
2010				1				1		
2005	0	0	0	1	0	0	0	0	0	0
2000								1	1	
1995	2	1		1				1	2	
1990				1				1	1	
1985	2			3	1	1		2	1	
1980	1	1		3		1		2	2	
1975				4	1	0			2	
1970	1			2					2	
1965	2			2		1		2	3	
1960				1		3		1		
1955				5		1		2		
1950				1				1		
1945	1							3		
1940				4				1		
1935				3				1		
1930				2					1	
1925	1		1	2		1		2	2	
1920				3					1	
1915	1			5						
1910	0	1	0	3	1	0	0	1		
1905				1	2			3	3	
1900	1			2		2		3	3	
1895				1		1		1		
1890				5				1	1	
1885	1			1		1		2	1	
1880					1	1				
1875	2			2				1	1	
1870	1			2		2		1	2	
1865		1				1				
1860	3			3	0	0		2	1	
1855				1	1	2		3		
1850					1				1	
1845						1		1		
1840	1			2				2		
1835									1	
1830	2			2				1		
1825	2									
1820				1				3	1	
1815				3	1			1		
1810				2				2		
1805	1			2						
1800	1			3	1	2		4	2	
1795	1			5				4	1	
1785	1			1		1		1	1	
1775	3			2				1	1	
1765	1	1						3	1	
1755	1	1		4		1		1	3	
1745		1		1		2		1		
1735	2			4				3		1
1725	1			3				1	1	
1715				3				1	1	
1705	3	1		4				1	1	
1695	1			2				1	1	
1685		1		4				1	3	
1675	1			3		1		2		

Year CE	*A.rustica*	*A.intermedia*	*A. costata*	*Chydorus brevilabris*	*C.biovatus*	*C.faviforms*	*C.piger*	*Alonella excisa*	*A.nana*	*A.pulchella*
1665	2			3				2	2	
1655	1			3		1		3	1	
1645	1	1		1				3	1	1
1635				1	1	1				
1625	1			1		3		6		
1615	3			2	2			1	1	
1605	1			1					2	
1595	1	1		4		1		1	1	
1585	1		1	4					1	
1575						3			2	
1565	1			4		3		1	2	
1555	1			1		2	1	2		
1545				5				3	1	
1535	1					2		3	1	
1525				3				3	1	
1515	1			4				1	2	
1505		1		2	1			4	1	
1495	2					2		2	2	
1485			1	5		1		4	5	
1475	2	0	0	7	0	2	0	2	1	0
1465	1							1		
1455	2			3				3	2	
1445				1		0		1		
1440	1			3				1		
1435			2	1		1				
1430	2			3		2		1		
1425				3		1				
1420	1			2				5	1	
1415				2		2		2		
1410	2			1				4	1	
1405	1	1		1				1	1	
1400		1		3					2	
1395				3				4		
1390				4		1		3	2	
1385				3				3		
1380	1			1		2		5		
1375	4			4		2		2	3	
1365				7		2		5	2	
1360				5		1		5	4	
1355	1			7		3		2	3	
1350				6				4	2	
1345				2					2	
1340	2			2		2		2	1	
1335	1			4			1	2		
1330				3		1		2	1	
1325						1		2		
1320	1			6		1		1	2	
1315	1			5		1			1	
1310	1			2				1	2	
1305	6	0	0	10	0	0	0	1	2	0
1300	2			3				1		
1295	1	1		5				2		
1290	3			7		2		3		
1285	1			2				1	1	
1280	1			3		1		4	1	

Year CE	*A.rustica*	*A.intermedia*	*A. costata*	*Chydorus brevilabris*	*C.biovatus*	*C.faviforms*	*C.piger*	*Alonella excisa*	*A.nana*	*A.pulchella*
1275				6				2	3	
1270								4		
1265				2		3				
1260	1			2					1	
1255				3					1	
1250		1		2	3			5	1	
1245	2			2				4		
1235	1			5				2		
1225	1			7		2		2	2	
1215	3			2				5	2	
1205	1			2		1		3		
1195				3		1		1		
1185				1				3		
1175				1				3		
1165				3		1		3	1	
1155	2			2		1		3	5	
1145	2			5		2		3		
1135	1			7		1		5	1	
1125	1			2				3		
1115	1			4				3	1	
1105				2		1		3		
1095				5		1		4		
1085	1							3	3	
1075	5			2		1		2		
1065	1			3		2		1		
1055	1			7		4		3	1	
1045				4	3	3		5	1	
1035				3		1		3	1	
1025	1	1		3		1		1		
1015	1			9		1		5	3	
1005	2			3				3	2	
995				7		1		4		1
985	2			1		1		2		
975				4		4		3	1	
965	1			4				4	3	
955	1			3		3		3	1	
945	1	1		3				5	2	
935	1			2		1				
925		1		4		2		1		
915	2			2				1		
905				1		1				
895	3			2		4			1	
885	3			1				1	1	
875				6		1		4	1	
865				1				2	1	
855	1			4				3	1	
845				4				1	1	
835	1			2		1			1	
825		1		2						
815	1			1				3	1	
805	1			1				2	1	
795				1						
785				1						

Year CE	*Camptocercus*	*Graptoleberis*	*Pleuroxus*	*Eurcycercus*	*Acroperus*	*Sida*	*Leptodora*	*Latona*	*Leydegia*	*Holopedium*
2010		1								
2005	0	1								
2000										
1995				1						
1990		1			1					
1985	1				2	1				
1980							1			
1975		1		0		1				
1970	4			1						
1965	3					1				
1960							1			
1955			1							
1950										
1945										1
1940										
1935										
1930	1					1				
1925	1						1			
1920	1									
1915						1	1			
1910										
1905	1				1	1				1
1900		1				2				
1895				0						
1890	1	1				1				
1885	1					3	1			
1880										
1875	1		2			1	1			
1870	1				1	2				
1865										
1860	1	0		0		1				
1855	1	1				2				
1850	1		1	1			2			
1845										
1840	2				2	1				
1835	1					2	3			
1830					1	1	1			
1825										
1820	1					1				
1815	2					1				
1810			1	1		1	1			
1805	4		2	0				2		
1800	4		1		1		1			
1795	1	1	2			1				
1785	1	1				1				
1775										
1765					2		1	1		
1755	2	3	1			1	1			
1745							1			
1735				1		1				
1725						1				
1715	1	1					1			
1705		1								
1695							1			
1685							1			

Year CE	*Camptocercus*	*Graptoleberis*	*Pleuroxus*	*Eurycercus*	*Acroperus*	*Sida*	*Leptodora*	*Latona*	*Leydegia*	*Holopedium*
1665						1				
1655						1	1			
1645		2			1	1				
1635	1					2	2			
1625			1			1	1			
1615	1	1			1	1				
1605	2	1								
1595	1				1	1	3			
1585	1	1	1	1	2	3				
1575		1					5			
1565						1	1			
1555	1	1				2				
1545	1					4				
1535	1		2							
1525		1	1		1	1	2			
1515										
1505	2					1	1	1		
1495	2					1				
1485					1		2			
1475	2				2		5			
1465	2		1			1	2			
1455	2		1	1		2	1		1	
1445			1				1			
1440	2					2				
1435	2		1		1		2			
1430	2		1				3			
1425	3				2					
1420			1		3	1				
1415	1					1				
1410			1			1	1			
1405			1							
1400						1	3			
1395				1			1			
1390	1		1				3			
1385	3		2			2	2			
1380		1	1			6	3			
1375	3		1			2				
1365			1		1	2	1			
1360	1		2			2	1			
1355	1					1	1			
1350	1					1				1
1345	2				2	1	1			
1340						1	1			
1335	1					1	2			
1330	1					1	3			
1325	1		2		1	3	2			
1320						1	2			
1315	2	1	1			1				
1310	1		3	1			1			
1305	2	1	0	0	0	2	2	0	0	0
1300	1					1	2	1		
1295						2	1			
1290	1	1	3				1			
1285	2		1		1	2	2			
1280	1					2				
1275	1	1				3	2			

Year CE	*Camptocercus*	*Graptoleberis*	*Pleuroxus*	*Eurcycercus*	*Acroperus*	*Sida*	*Leptodora*	*Latona*	*Leydegia*	*Holopedium*
1265	3				1	2				
1260		1	1							
1255	1									
1250	1		1			2				1
1245	2									
1235	0		1			1				
1225	3		1		1		1			
1215	1					1		1		
1205	1		1	1						
1195		1	1			2				
1185	1					3	1			
1175	2						1			
1165	1							1		
1155				1		3	1			
1145			1		2	2	2			
1135	2		1					1		
1125	2					3				
1115		1				1	1			
1105	1					1				
1095	2	1			1	2				
1085	1				1	1	2			
1075						1	1			
1065		1	2				1			
1055		1	1			1	1			
1045	1					1	1			
1035	3					1	1			
1025	2		1			3				
1015	1						2			
1005	2		1		2	2	3			
995										
985						1	3			
975	1				1		1		1	
965	1				2	2	1			
955	3		1			1	1			
945	2	1			1	4	1			
935		2				2	2			
925	1					2	3			
915	1	1	1			4	1			
905	1					2	2			
895	2					1	4			
885			2		2					
875			1		1					
865	2		1				2			
855	1		2			1				
845						1	1			
835						2				
825						1				
815	2	1				1				
805			2			2	1			
795										
785							1			

Year CE	*Polyphemus*	*Kurzia*	*Cerodaphnia*	*Ophoryxus gracilis*	*Diaphansoma*	*Anchistropus*	total
2010							135
2005							135
2000							122
1995							132
1990							110
1985							144
1980							102
1975							130
1970							108
1965							112
1960							135
1955							130
1950							130
1945							130
1940							131
1935							125
1930							125
1925							114
1920							112
1915							116
1910							116
1905							103
1900							125
1895							114
1890		1					88
1885							96
1880							59
1875							124
1870		1					120
1865							112
1860							129
1855							125
1850							123
1845							101
1840							113
1835							86
1830							97
1825							131
1820							101
1815							127
1810							83
1805							113
1800							107
1795							140
1785							117
1775							130
1765							110
1755						1	126
1745							123
1735			1				138
1725		1					128
1715							131
1705							142

Year CE	*Polyphemus*	*Kurzia*	*Cerodaphnia*	*Ophoryxus gracilis*	*Diaphansoma*	*Anchistropus*	total
1695							109
1685							137
1675							129
1665						1	138
1655							131
1645							126
1635			1				111
1625		1					131
1615							131
1605						1	127
1595							129
1585							127
1575							133
1565							134
1555					1		125
1545		1					132
1535							126
1525			1				129
1515							130
1505						1	129
1495							124
1485			1				130
1475			1				259
1465							131
1455							132
1445							124
1440							126
1435							125
1430							129
1425							129
1420							126
1415							131
1410							131
1405							119
1400							129
1395							121
1390							133
1385							128
1380							103
1375							132
1365							125
1360							117
1355							125
1350							133
1345							134
1340							126
1335							135
1330							91
1325							119
1320							128
1315							127
1310							121
1305							229

Year CE	*Polyphemus*	*Kurzia*	*Cerodaphnia*	*Ophoryxus gracilis*	*Diaphansoma*	*Anchistropus*	total
1300							128
1295							129
1290							154
1285							131
1280							126
1275							121
1265							128
1260							129
1255							119
1250							92
1245							139
1235							128
1225							127
1215							142
1205							124
1195							127
1185							133
1175							133
1165							124
1155							131
1145							134
1135							117
1125							134
1115		1					128
1105							128
1095						1	128
1085							132
1075							131
1065							126
1055							116
1045							130
1035							124
1025							130
1015							129
1005							136
995							128
985							128
975							139
965							132
955							132
945							123
935							130
925							124
915							122
905							128
895	1						128
885							130
875							133
865							128
855							128
845							131
835							132
825							128

Year CE	*Polyphemus*	*Kurzia*	*Cerodaphnia*	*Ophoryxus gracilis*	*Diaphansoma*	*Anchistropus*	total
815							129
805							127
795							132
785							136
							127

Table A2.4: Number of *Lycopodium* spores counted, volume of sediment used for sample, concentration in individuals mL^{-1}, the varve thickness in millimetres and cladoceran influx in individuals cm^{-2} yr^{-1}.

Year CE	*Lycopodium* count	volume (mL)	Concentration	Varve Thickness	Influx
2010	400	0.75	4796.55	16.036	299.1114
2005	418	0.50	6885	16.034	429.4
2000	500	0.50	5201.592	9	577.9547
1995	1270	0.50	2215.729	9.67	229.1343
1990	740	0.25	6337.784	8.58	738.6694
1985	260	1.00	5903.446	7.286	810.2451
1980	469	0.50	4636.324	9.814	472.4194
1975	660	0.25	8398	8.694	965.9535
1970	1141	0.50	2017.83	8.262	244.2302
1965	508	0.50	4700.031	8.028	585.4548
1960	475	0.50	6058.8	8.358	724.9103
1955	510	0.25	10868	7.926	1371.183
1950	400	0.50	6928.35	8.084	857.0448
1945	1119	0.25	4953.244	6.01	824.167
1940	700	0.50	3989.511	5.934	672.314
1935	969	0.25	5500	7.642	719.7069
1930	836	0.50	3187.5	6.034	528.2565
1925	902	0.50	2694.293	6.796	396.4527
1920	750	0.50	3183.488	8.274	384.758
1915	450	0.50	5495.307	6.492	846.4736
1910	872	0.50	2835.881	7.312	387.8393
1905	1625	0.50	1351.233	6.61	204.4226
1900	1171	0.50	2275.619	7.334	310.2835
1895	662	0.25	7342.151	2.87	2558.241
1890	1215	0.25	3088.04	4.844	637.4978
1885	1045	0.25	3916.8	4.318	907.0866
1880	910	0.25	2764.312	3.018	915.9417
1875	1384	0.25	3819.988	3.21	1190.028
1870	403	0.25	12695.58	4.092	3102.537
1865	1700	0.25	2808.96	4.624	607.474
1860	508	0.50	5413.429	2.608	2075.701
1855	1260	0.25	4229.762	1.892	2235.604
1850	478	0.25	10971.19	3.942	2783.153
1845	630	0.25	6835.295	3.31	2065.044
1840	1575	0.50	1529.482	3.362	454.9322
1835	775	0.50	2365.61	4.09	578.3888
1830	836	0.25	4947	2.746	1801.529
1825	958	0.50	2915.092	3.164	921.3312
1820	1268	0.25	3396.085	3.312	1025.388
1815	250	0.50	10829.54	2.852	3797.175
1810	662	0.25	5345.601	4.006	1334.399
1805	1200	0.50	2007.445	3.27	613.8976
1800	500	0.50	4562.052	3.838	1188.653
1795	1052	0.25	5673.992	3.19	1778.681
1785	1400	0.50	1781.576	7.874	226.2606
1775	1434	0.50	1932.594	8.718	221.6786
1765	1350	0.50	1737.022	8.718	199.2455
1755	1184	0.50	2268.639	7.524	301.5203
1745	843	0.50	3110.456	7.524	413.4045
1735	677	0.50	4345.471	7.94	547.2886

Year CE	*Lycopodium* count	volume (mL)	Concentration	Thickness	Influx
1725	1402	0.50	1946.294	7.94	245.1252
1715	765	0.50	3650.533	5.396	676.5258
1705	600	0.25	10090.52	5.396	1870
1695	712	0.50	3263.57	6.864	475.4619
1675	530	0.50	5188.721	5.896	880.0408
1665	1202	0.50	2447.491	5.896	415.1104
1655	916	0.50	3048.753	5.456	558.7891
1645	960	0.50	2797.988	5.456	512.8276
1635	633	0.50	3738.227	6.442	580.2899
1625	1308	0.50	2135.06	6.442	331.4281
1615	842	0.50	3316.696	6.812	486.8902
1605	1080	0.50	2506.839	6.812	368.0034
1595	1388	0.50	1981.284	7.762	255.2543
1585	990	0.50	2734.733	7.762	352.3233
1575	1138	0.50	2491.471	8.164	305.1777
1565	832	0.50	3433.428	8.164	420.5571
1555	1300	0.50	2049.808	8.438	242.9258
1545	1458	0.50	1930.025	8.438	228.7301
1535	1660	0.50	1618.113	6.934	233.3593
1525	1472	0.50	1868.221	6.934	269.4291
1515	1252	0.50	2213.53	9.296	238.1164
1505	984	0.50	2794.738	9.296	300.6387
1495	1540	0.50	1716.514	6.35	270.3172
1485	830	0.50	3338.964	6.35	525.8211
1475	2511	1.00	1099.435	7.122	154.3716
1465	1250	0.50	2234.126	7.122	313.6937
1455	1166	0.50	2413.358	6.858	351.9041
1445	702	0.50	3765.573	4.142	909.1194
1440	841	0.50	3193.898	3.712	860.425
1435	542	0.50	4916.513	3.008	1634.479
1430	450	0.50	6111.16	4.574	1336.065
1425	585	0.50	4700.892	4.064	1156.716
1420	816	0.50	3291.75	4.322	761.6266
1415	310	0.50	9008.574	3.558	2531.921
1410	771	0.50	3622.125	4.5	804.9166
1405	568	0.5	4466.271	5.036	886.8688
1400	642	0.50	4283.523	4.642	922.7754
1395	687	0.5	3754.699	6.562	572.1882
1390	490	0.5	5786.314	4.492	1288.138
1385	443	0.5	6159.603	6.32	974.6207
1380	786	0.5	2793.58	5.952	469.3515
1375	501	0.5	5616.719	6.244	899.5385
1365	896	0.5	2974.051	9.2	323.2664
1360	640	0.5	3897.197	4.356	894.6733
1355	884	0.5	3014.423	3.202	941.4188
1350	535	0.5	5299.615	2.546	2081.546
1345	375	0.5	7617.632	4.094	1860.682
1340	1600	0.5	1678.793	3.272	513.0784
1335	407	0.5	7071.081	3.59	1969.66
1330	833	0.5	2328.857	2.166	1075.188
1325	645	0.5	3933.088	3.194	1231.399
1320	604	0.5	4517.722	2.882	1567.565
1315	1106	0.5	2447.908	3.052	802.0668
1310	677	0.5	3810.16	2.156	1767.235
1305	1023	0.5	4772.065	3.032	1573.9
1300	687	0.5	3971.913	1.36	2920.524

Year CE	*Lycopodium* count	volume (mL)	Concentration	Thickness	Influx
1295	508	0.5	5413.429	2.598	2083.691
1290	460	0.5	7136.896	2.772	2574.638
1285	500	0.5	5585.316	2.108	2649.581
1280	544	0.5	4937.625	2.94	1679.464
1270	320	0.5	8527.2	3.728	2287.339
1265	242	0.5	11363.73	2.238	5077.626
1260	568	0.5	4466.271	2.418	1847.093
1255	842	0.5	2329.283	2.498	932.459
1250	597	0.5	4963.487	2.294	2163.682
1245	525	0.5	5197.531	2.338	2223.067
1235	546	0.5	4958.582	5.57	890.2302
1225	592	0.5	5113.439	6.018	849.6908
1215	675	0.25	7832.391	6.014	1302.36
1205	312	0.5	8677.519	5.174	1677.139
1195	391	0.5	7251.391	4.488	1615.729
1185	1104	0.5	2568.201	5.034	510.1711
1175	433	0.5	6104.924	4.976	1226.874
1165	360	0.5	7757.383	3.464	2239.429
1155	628	0.5	4548.745	4.618	985.0033
1145	900	0.5	2771.34	5.562	498.2632
1135	1037	0.5	2754.689	5.89	467.6891
1125	995	0.5	2742.416	4.97	551.794
1115	992	0.5	2750.71	2.724	1009.805
1105	346	0.5	7886.428	3.87	2037.837
1095	560	0.5	5024.957	5.296	948.8212
1085	421	0.5	6633.392	5.68	1167.851
1075	750	0.5	3581.424	5.076	705.5603
1065	805	0.5	3071.911	4.416	695.6319
1055	812	0.5	3412.98	5.228	652.8271
1045	451	0.5	5861.268	4.786	1224.67
1035	564	0.5	4913.723	4.05	1213.265
1025	1054	0.5	2609.129	5.12	509.5955
1015	992	0.5	2922.629	6.582	444.0336
1005	663	0.5	4115.692	5.15	799.1636
995	488	0.5	5591.607	2.72	2055.738
985	584	0.5	5073.976	3.724	1362.507
975	580	0.5	4851.683	5.314	913.0001
965	510	0.5	5517.6	5.31	1039.096
955	575	0.5	4560.198	5.306	859.4418
945	682	0.5	4063.548	5.832	696.7676
935	703	0.5	3760.216	6.062	620.293
925	346	0.5	7516.751	5.542	1356.325
915	814	0.5	3352.216	3.99	840.1544
905	719	0.5	3795.138	3.196	1187.465
895	650	0.5	4263.6	3.374	1263.663
885	571	0.5	4965.489	3.634	1366.398
875	642	0.5	4250.318	4.74	896.6915
865	845	0.5	3229.236	5.062	637.9367
855	777	0.5	3594.154	4.664	770.6163
845	642	0.5	4383.14	4.24	1033.759
835	360	0.5	7579.733	4.872	1555.774
825	310	0.5	8871.039	5.02	1767.139
815	512	0.5	5287.863	4.912	1076.519
805	420	0.5	6699.943	6.338	1057.107
795	175	0.5	16567.13	7.014	2362.009
785	1109	0.5	2441.286	6.24	391.2317