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## An Investigation of Epiphytic Diatom Substrate Specificity and Its Use in Paleolimnology

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A thesis submitted in partial fulfillment of the requirements for the Master of Science degree in Geography

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## **ABSTRACT**

Submerged macrophyte communities are an important component of lake ecosystems that can be altered by anthropogenic disturbances. In the absence of direct monitoring, it is difficult to know how these communities respond to such disturbance. This thesis investigated the potential of epiphytic diatoms preserved in lake sediments to record submerged macrophyte community composition. Epiphytic diatoms from *Chara* sp., *Myriophyllum spicatum* and *Potamogeton robbinsii* were sampled from Gilmour Bay, Ontario, Canada to assess whether submerged macrophyte species were characterized by distinct diatom communities. Principal components analysis indicated overlap, but analysis of similarity suggested there were differences in diatom community composition. A tool was developed and applied to Gilmour Bay nearshore sediment samples to reconstruct past submerged macrophyte community composition, but reconstruction was hindered by abundant *in situ* epipelagic and epipsammic diatoms. This research shows that differences in epiphytic diatom communities offer new opportunities for paleolimnological reconstructions.

**Keywords:** Paleolimnology, Epiphytes, Diatoms, Submerged Macrophytes, *Chara*, *Myriophyllum spicatum*, *Potamogeton robbinsii*

## **SUMMARY FOR LAY AUDIENCE**

Aquatic plants are important in lakes, helping to maintain clear water and reduce algal abundance by uptake of nutrients. Invasive aquatic plants (i.e., those that do not naturally occur in the lake) can be introduced from boat traffic or household aquariums and potentially replace native plants causing a shift in the aquatic plant community. Changes in the aquatic plant community can affect nutrient availability (i.e., nitrogen and phosphorus) in the lake since not all plants use nutrients the same way. Knowing how the aquatic plant community has changed over time can therefore help to understand changes in nutrient availability and consequential changes that occur in lake ecosystems.

Unfortunately, direct long-term monitoring of aquatic plants is rare. One way to solve this problem is to study sediment (i.e., mud) records collected from the bottom of lakes. New sediment is deposited on top of older sediment, creating an archive that can span thousands of years. Preserved in sediment are fossils of organisms that inhabited the lake when the sediment was deposited, acting as a snapshot of environmental conditions from that time. Some of these fossils are potential indicators of aquatic plant communities.

This research explored how diatoms (a type of microscopic algae found in almost all lakes and well preserved in lake sediments) that live on aquatic plants could be used to track changes in aquatic plants over time. Samples from three aquatic plants, including one invasive species, were collected from Gilmour Bay, Ontario, Canada, and their diatom communities studied. The results identified that the diatom community living on different aquatic plants can be differentiated, although there is overlap among plants. Using this knowledge, an attempt was made to identify the historic aquatic plant community from diatoms preserved in sediment using key diatoms associated with specific aquatic plants. Unfortunately, in the sediment samples collected, diatoms living directly on the sediment overwhelmed the diatoms from aquatic plants, making it difficult to assess the historic aquatic plant community. However, the technique showed promise, and this research provides the foundation for future research aimed at using fossil diatoms to track changes in aquatic plant communities.

## **CO-AUTHORSHIP STATEMENT**

Although this thesis is presented as a monograph, I plan to submit parts of my thesis for publication, and therefore have included a co-authorship statement. I collected all the field samples, with field assistance from Soomin Lee, Jacob Walker, and Dr. Katrina A. Moser. Water samples were analyzed by the Ontario Ministry of Environment, Conservation, and Parks at the Dorset Environmental Science Centre. I prepared all samples for diatom analyses. I performed all diatom analyses (i.e., identification and enumeration), as well as all statistical analyses presented here. Dr. Katrina A. Moser provided guidance on the research design and data analysis and interpretation. I prepared the original draft of the thesis and worked with Dr. Katrina A. Moser to edit and improve that draft, and she will be listed as a co-author on any and all subsequent publications of this work.

*This thesis is dedicated to my mother, who instilled in me at a young age a fiery passion for learning and discovery that burns brightly to this day. All my love.*

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## **LIST OF ABBREVIATIONS**

ANOSIM	Analysis of Similarities
cal yr BP	calendar years before present
ECCC	Environment and Climate Change Canada
EPS	Extracellular Polymeric Substances
MOE	Ontario Ministry of the Environment
MOECP	Ontario Ministry of the Environment, Conservation and Parks
PCA	Principal Components Analysis
PC1	Principal Components Analysis axis 1
PC2	Principal Components Analysis axis 2

## 1 INTRODUCTION

Lakes are an important storage compartment for global freshwater and a key part of the global hydrologic cycle. Freshwater accounts for 2.59% of the total water supply, and of that only 0.014% is easily accessible surface water (la Rivière, 1989). Lakes comprise half of this accessible water, but more importantly are key in hydrologic and biogeochemical processes such as carbon sequestration (Cole et al., 2007), local heat flux and associated weather and climate effects (Balsamo et al., 2012), and trophic interactions with terrestrial food webs (Polis et al., 1997).

Humans have historically benefitted from the abundant food and freshwater that lakes provide, as well as recreation and enjoyment for those who visit or live near them. In the past, a lake used for these purposes has generally low nutrients (i.e., nitrogen and phosphorus), and clear water, which has historically been described as a “high ecological status lake”, meaning little to no anthropogenic alteration (Moss, 2015). Generally, such lakes, at least in temperate regions, support a diverse submerged aquatic plant community (hereafter referred to as submerged macrophytes) (Moss, 2015). However, stressors, including the introduction of nutrients due to anthropogenic activities (i.e., agriculture, leaky septic tanks, stormwater runoff, etc.) or warming temperatures caused by global climate change, have the capacity to impact these ecosystems and catalyse a shift from submerged macrophyte- to algae-dominated waters (Kosten et al., 2009). Even systems with little to no direct anthropogenic alteration may be affected, likely due to nutrient mobilization from more frequent extreme precipitation events or atmospheric deposition of nutrients through dust, as evidenced by the continent-wide reduction in low nutrient systems observed in recent years (Stoddard et al., 2016). These transitions and their ecological consequences can be difficult to reverse, including algal blooms, anoxic conditions, and fish kills (Carpenter, 2005).

To understand better how lakes are responding to anthropogenic stressors and predict future responses, it is necessary to have knowledge about the natural variability of the lake and trajectories of ongoing change. Unfortunately, long-term records of environmental conditions are often lacking in detail or absent entirely (Smol, 2008;

2010). To circumvent this issue, paleolimnologists have developed numerous methods using proxies preserved in sediment cores to infer past environmental conditions. One such method, developed by Reavie & Smol (1997) and expanded by Vermaire et al. (2011), focused on reconstructing submerged macrophyte biomass, a reduction of which is a hallmark of a lake's transition to an algal dominated system. The proxy used in these reconstructions were diatoms, a type of protist that live in many different lake environments. The diatoms found living on submerged macrophytes were distinct from the diatoms on other substrates (i.e., rocks, filamentous algae, and wood) allowing for the inference of temporal changes in submerged macrophyte abundance from diatoms preserved in sediment cores. In these previous studies, multiple submerged macrophyte species were grouped together and treated as one macrophyte unit. However, not all submerged macrophytes species are ecologically equivalent. Different macrophyte species utilize nutrients differently (Carpenter & Lodge, 1986), therefore a change in macrophyte community composition can affect overall nutrient availability in lake ecosystems. It is therefore critical to know how macrophyte communities have changed throughout time to understand changes in nutrient availability better; however, methods are presently not available to do this. Although other studies have identified subtle differences in the diatom community composition among species of macrophytes (Comte & Cazaubon, 2002; Messyasz et al., 2009; Rojas & Hassan, 2017), the paleolimnological application of these differences remains relatively unexplored (Rojas and Hassan, 2017). The overall goal of my research is to investigate the diatom community composition of different submerged macrophyte species to determine whether fossil diatoms can be used to track changes in submerged macrophyte community composition. This goal is broken into two key research questions:

- 1) **How does the epiphytic diatom community differ among species of submerged macrophytes?**
- 2) **How can these differences be used in paleolimnological research to reconstruct submerged macrophyte community composition?**

Submerged macrophytes create differences in available diatom habitats by differences in their physical structure and chemical interactions with the surrounding environment



(Blindow, 1987). Thus, because diatoms exhibit habitat specificity among the unique microhabitats of different substrates (i.e., rocks, wood, macrophytes), diatoms are also anticipated to exhibit microhabitat specificity among species of submerged macrophytes (Douglas & Smol, 1995). If differences in diatom community composition living on distinct macrophyte species can be identified, then it may be possible to track changes in submerged macrophyte communities through time. This will help to understand better how submerged macrophyte communities have responded to changing limnological conditions and predict how they may change in the future. My research will additionally develop preliminary protocols for reconstructing changes in submerged macrophyte community composition using fossil diatoms preserved in lake sediment cores with attention to coring location and analytical techniques. The development of such protocols is an important first step in expanding the tools available to lake managers in their efforts to predict, track, prevent, and repair harmful environmental changes in lake ecosystems.

## **2 BACKGROUND INFORMATION**

### **2.1 Overview**

The overall goal of this section is to provide an overview of the literature pertinent to the research presented in this thesis and provide the reader with an understanding of important concepts that support it.

This review provides an overview of: 1) the role of submerged macrophytes in lake ecosystems, 2) the ecology of native and invasive submerged macrophyte species common to temperate lakes in southern Ontario, 3) diatom ecology and substrate specificity, and 4) paleolimnological methods to reconstruct submerged macrophyte abundance and composition.

### **2.2 The Role of Submerged Macrophytes in Lake Ecosystems in Relation to Anthropogenic Disturbance**

The nearshore zone (Figure 2.1) of many lake ecosystems is abundant with aquatic macrophytes, which refers to a diverse group of aquatic photosynthetic organisms including macroalgae of the divisions Chlorophyta, Xanthophyta, and Rhodophyta, Bryophyta (mosses and liverworts), Pteridophyta (ferns), and Spermatophyta (seed-bearing plants) (Chambers et al., 2008). Submerged macrophytes both influence and respond to the lake ecosystem in a variety of physical and biogeochemical ways. For example, submerged macrophytes help to sequester nutrients that may otherwise increase nutrient delivery to the offshore zone of the lake (Kufel & Kufel, 2002; van Donk et al., 1993). Submerged macrophytes also create habitat for zooplankton, which are crucial to controlling phytoplankton biomass (Celewicz-Goldyn & Kuczynska-Kippen, 2017; Timms & Moss, 1984; van Donk & van de Bund, 2002). Furthermore, physical properties of the nearshore environment such as light availability, temperature, and water flow are affected by macrophyte type and abundance (Carpenter & Lodge, 1986). For

example, submerged macrophytes reduce mixing in the littoral zone and create areas of thermal stratification in shallow waters (Andersen et al., 2017b). Therefore, a change in submerged macrophyte abundance can have a substantial impact on the overall lake ecosystem (Irvine et al., 1990; Jeppesen et al., 1997; Nakamura et al., 2008). Such effects can be potentially confounded by eutrophication and climate change.

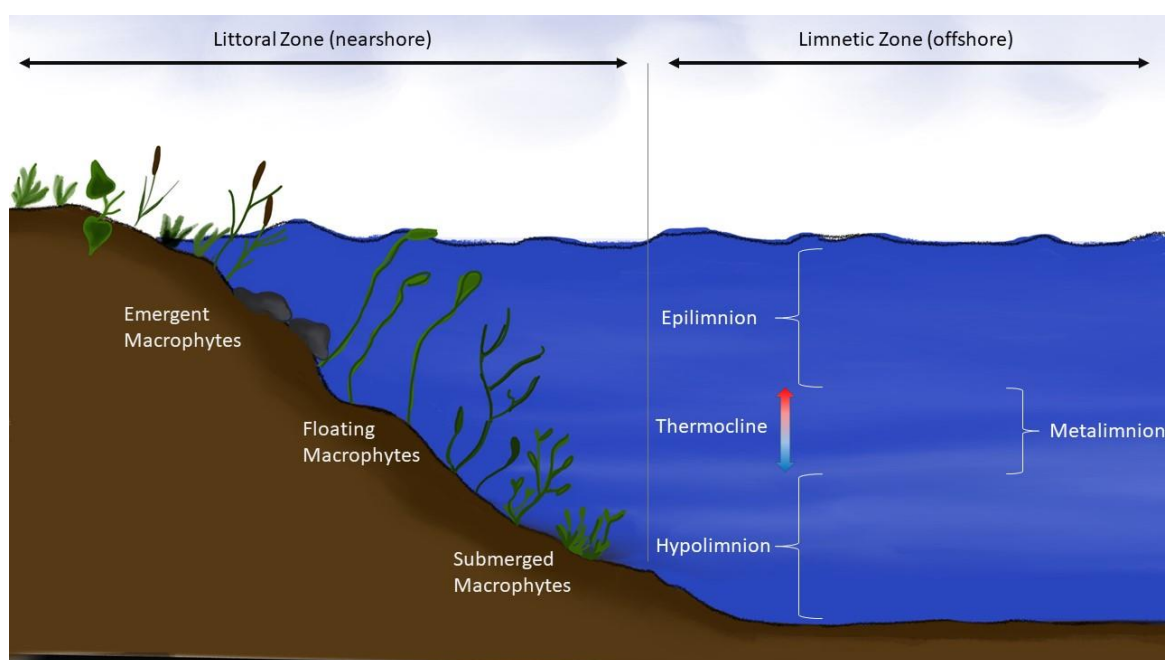


Figure 2.1 A thermally stratified, dimictic lake ecosystem during summer stratification.

Aquatic macrophytes grow in the photic zone (i.e., where light penetrates through the water column) of the nearshore environment. Macrophytes can be grouped broadly into three groups: 1) emergent, where part of the macrophyte extends above the surface of the water; 2) floating, where most of the macrophyte lives underwater but part of it floats on the surface, and 3) submerged, where the macrophyte exists entirely beneath the surface of the water. Figure drawn by Kestrel McNeill, adapted from Lake Access (2005).

Anthropogenic eutrophication, or the enrichment of a waterbody with nutrients due to human activity, has impacted lakes around the world (Stoddard et al., 2016). Eutrophication can lead to several effects including increased algal production, anoxic bottom water, and biodiversity losses (Schindler et al., 1971; Smith, 2003). These changes, in turn, affect submerged macrophytes and nearshore communities. For example, eutrophication can lead to increased algal production, which reduces overall light availability (Middelboe & Markager, 1997). Because different species of submerged macrophytes have different light requirements for growth, increased algal blooms can trigger changes in macrophyte community composition (Middelboe & Markager, 1997; Sand-Jensen & Madsen, 1991). Studies of the nutrient/primary producer relationship characterize it as a continuum, where the alternative dominance of charophytes (Chlorophyta macroalgae), submerged angiosperms (Spermatophyta seed-bearing plants) and phytoplankton represent alternative stable states of lake trophic status (Scheffer & van Nes, 2007). A change in submerged macrophyte community composition (e.g., charophyte to angiosperm) may therefore be an indicator of environmental change driven by eutrophication.

The effects of eutrophication are further complicated by climate change. Research of temperate lakes has indicated a reduction of macrophytes with warmer temperatures (Hargeby et al., 2004; Kosten et al., 2009). For example, milder winter temperatures lead to earlier ice-break up, which allows for earlier wind-induced resuspension of sediment particles and a reduction in light availability for submerged macrophytes at a critical period for their growth (Hargeby et al., 2004). It has also been reported that lakes in these regions have been able to sustain macrophyte abundance even in the presence of high nutrients. Although the exact reason for this phenomenon is unclear, it may be due to strong macroinvertebrate periphyton grazing triggered by reduced predation as a result of partial fish kills occurring during ice-covered winters (Kosten et al., 2009). Warming temperatures, therefore, may decrease the resiliency of the submerged macrophyte community to increased nutrients.

Although submerged macrophytes may be common in many lakes, it is worth noting that their absence does not necessarily indicate a disturbance. For example, otherwise clear,

low nutrient arctic lakes may have limited macrophyte growth because of the year-round cold temperatures (Lauridsen et al., 2020). Similarly, high nutrients and algal production may occur naturally in lakes underlain by phosphate-rich volcanic rock even in the absence of anthropogenic activity (Murphy et al., 1983); the high algal production causes low water transparency and results in a complete decline of submerged macrophytes (Dondajewska et al., 2020). This highlights the need to consider geographic context when conducting lake research, especially as it pertains to the unaltered, reference state of the lake. In southern Ontario, where temperatures are warm in the summer and the reference state of most lakes is generally low in nutrients (Hall & Smol, 1996), a diverse community of submerged macrophytes is expected.

### **2.3 Native Submerged Macrophytes in Southern Ontario Lakes**

Southern Ontario lakes have a diverse community of native submerged aquatic vegetation. Some examples include Canadian waterweed (*Elodea canadensis*), muskgrass (*Chara* spp.), pondweeds (e.g., *Potamogeton amplifolus*, *P. richardsonii*, *P. robbinsii*), watermilfoils (e.g., *Myriophyllum sibiricum*, *M. verticillatum*), wild celery (*Vallisneria americana*), and many others (Ginn, 2011; Grabas et al., 2012; Hogsden et al., 2007). This review is focused on the general ecology of *Chara* spp. and *Potamogeton* spp. as studies have identified that *Chara* spp. tend to decline during a shift from macrophyte-dominated to phytoplankton-dominated systems and are often replaced with *Potamogeton* spp. (Ozimek & Kowalczewski, 1984). This shift is thought to occur due to reduced light availability, which may be caused by eutrophication (Blindow, 1992) or warming temperatures (Favot et al., 2019), both of which affect southern Ontario lakes.

*Chara* is a type of macroalgae commonly mistaken for higher order plants due to their erect central stalks with whorled branchlets (Chambers et al., 2008). *Chara* was first described in the 1700s and is present globally, with over 400 species identified worldwide (Linnaeus, 1753; Moore, 1986); at least 84 species of *Chara* have been identified in North America (Scribailo & Alix, 2010). *Chara* spp. prefer alkaline lakes as they can utilize bicarbonate as a source of carbon during photosynthesis (Kufel et al., 2016; Van den Berg

et al., 2002). *Chara* spp. have a complex morphology and high phenotypic plasticity, meaning one genotype can produce different observable morphological traits (Schneider et al., 2016). Unlike other submerged macrophytes that may be identified by gross morphological features, to identify *Chara* to species level requires significant knowledge of their structural complexities (Scribailo & Alix, 2010). This is at least partly why *Chara* species are not differentiated in research and represented as “*Chara* spp.” (e.g., Ginn, 2011; Madsen et al., 2015; Ozimek & Kowalczewski, 1984). Some species of *Chara* are unique from other macrophytes in their ability to overwinter, storing nutrients in plant biomass beyond the growing season and acting as an effective nutrient sink (Kufel & Kufel, 2002). Therefore, a replacement of *Chara* with other macrophyte species may amplify the effect of increased nutrients (e.g., increased algal production) in previously *Chara* dominated systems.

*Potamogeton* spp. are native and widespread in North America and are adapted for a wide range of aquatic environments with varying physical and biogeochemical characteristics (Pip, 1987). The growth form of *Potamogeton* is variable in terms of shoot length or leaf size and species can exhibit phenotypic plasticity; *Potamogeton richardsonii* exemplifies this, with multiple growth forms that differ widely in leaf dimension and internode length depending on environmental conditions (Spence & Dale, 1978). Additionally, some *Potamogeton* spp. have floating leaves at some point in their seasonal life cycle (Chambers et al., 2008; Chambers & Kalff, 1987). Although all submerged macrophytes rely on light availability for their survival, some *Potamogeton* spp. are bottom dwellers, meaning they produce shorter shoots than other macrophytes and can be especially limited by light availability (Chambers & Kalff, 1987), a reduction in which is a common consequence of eutrophication.

Although a decline of submerged macrophytes may affect lake ecosystems, so too may the overabundance of submerged macrophytes. Dense submerged macrophyte cover can reduce mixing in the littoral zone and create areas of thermal stratification in shallow waters (Andersen et al., 2017b). Prolonged thermal stratification and the decay of organic matter in the shallow, nearshore environment may lead to localized hypoxic or anoxic conditions and trigger the release of nutrients from sediment (Andersen et al., 2017a;

Boros et al., 2011). Such conditions may be caused by the introduction of a non-native submerged macrophyte species, which can rapidly take over and upset the natural abundance of native vegetation. Therefore, the introduction of non-native submerged macrophytes may create a mechanism for macrophyte loss and a shift to a turbid, phytoplankton-dominated system (Vilas et al., 2017).

#### **2.4 *Myriophyllum spicatum* Invasion and its Effect on the Nearshore Environment**

In Ontario lakes, *Myriophyllum spicatum* (Eurasian watermilfoil) is a non-native submerged macrophyte. A perennial, vascular macrophyte, *M. spicatum* is characterized by its branched and leafy shoot, finely dissected and feather-like leaves, and differentiated from native species of *Myriophyllum* by a pink terminal spike (Aiken et al., 1979). *M. spicatum* has a high photosynthetic rate and high light requirement that is reflected by its growth pattern of creating a dense overhead canopy near the water surface (Madsen et al., 1991). Although *M. spicatum* grows in water down to 10 m deep, it is most abundant between 1 to 4 m of water (Aiken et al., 1979; Nichols & Shaw, 1986).

*M. spicatum* is ubiquitous in Eurasia and was first observed in North America in the 1800s, likely initially introduced to the Chesapeake Bay area from shipping ballast (Aiken et al., 1979; Reed, 1977). The establishment of *M. spicatum* as a dominant species is reported in Ontario lakes as far back as the 1960s, but it was not widely recognized as a nuisance until the 1970s (Aiken et al., 1979; Crowder & Painter, 1991). Its early proliferation in North America is attributed to its widespread use in aquariums (Reed, 1977), but continued proliferation is attributed to its notable ability to colonise through fragments (Vári, 2013). Fragments can be formed by external forces such as wave action, animal feeding, or human activities, but *M. spicatum* also exhibits the ability to autofragment as a means of rapid propagation (Vári, 2013; Xie & Yu, 2011). Populations of *M. spicatum* typically grow rapidly, persisting for 5 to 10 years, and then rapidly decline (Carpenter, 1980).

The rapid proliferation of *M. spicatum* can lead to lowered light availability for other submerged macrophytes, and consequently, a loss of native submerged macrophyte abundance and species richness (Boylen et al., 1999). The effects of *M. spicatum* on overall primary production in nearshore environments, however, is minimal, although previous studies have identified a preference of higher level organisms to derive energy from native macrophytes rather than non-native species (Kovalenko & Dibble, 2014; Van Goethem et al., 2020). In addition, dense mats of *M. spicatum* can harbour harmful *Escherichia coli* bacteria (Mathai et al., 2019). This has the potential to influence water quality negatively in the littoral zone and has important public health implications for recreational water use (Mathai et al., 2019).

## **2.5 Diatom Ecology and Substrate Specificity**

Diatoms (class: *Bacillariophyta*) are unicellular protists that are characterized by a cell wall composed of opaline silica (Barron, 1993). Diatoms are responsible for about 45% of global primary production, despite representing only 1% of the Earth's photosynthetic biomass (Field et al., 1998). Diatoms have existed for approximately 100-200 million years and their role in primary production has continued to be important to the oxygenation of our atmosphere (Benoiston et al., 2017). There are many diatom species, with one estimate suggesting over 30,000 diatom species exist globally (Mann & Vanormelingen, 2013). The diversity in species is important, since different diatom species occupy different ecological niches that vary with environmental variables such as temperature, nutrients, and pH (Cumming et al., 1995). By gaining knowledge of the ecological conditions associated with different diatom species, they can be used as a proxy indicative of those environmental conditions. Because of this, and because the opaline silica cell walls of diatoms make them resistant to degradation and are well preserved in sediment (Smol, 1997), paleolimnologists utilize fossil diatoms to study environmental change in lake ecosystems (e.g., Clerk et al., 2000; Hadley et al., 2013; Reavie & Smol, 2001).



Some diatoms attach directly to the surface of macrophytes; such diatoms are known as epiphytes. However, diatoms do not attach to macrophytes only; they may also be found living on rocks (epilithic), sediment (epipelic), sand (epipsammic), wood (epidendric) or free-floating in the water column (planktonic) (Douglas & Smol, 1995). Attaching to a substrate offers diatoms improved stability and resistance to currents (Stevenson, 1996), which is important for less buoyant diatoms to remain in the photic zone rather than being swept offshore and sinking (Acuña et al., 2016). However, each substrate is a unique environment. For example, sand and rocks are hydrodynamically energetic environments and more susceptible to the effects of surface and internal wave action (Cantonati & Lowe, 2014; Pla-Rabés & Catalan, 2018). Some substrates may offer nutrient enrichment, such as silica in the case of rocks and sediment (Douglas & Smol, 1995) or phosphorus in the case of macrophytes (Burkholder & Wetzel, 1990). Macrophytes also provide diatoms with better access to light due to their elevated position in the water column (Cattaneo & Kalff, 1979). These examples are not meant to be an exhaustive list, but they illustrate how substrates have different physical, biological, and chemical environments which diatoms may exploit depending on their habitat requirements.

Early studies of epiphytic diatom ecology showed similar diatom communities between macrophytes and morphologically similar artificial macrophyte substrates (Cattaneo & Kalff, 1979), leading to the “neutral substrate hypothesis”, which states that there is no significant effect of macrophyte substrate on the epiphytic diatom community. However, this hypothesis has been challenged in other studies that identified subtle differences in diatom community composition among different substrates and different species of macrophytes (e.g., Comte & Cazaubon, 2002; Messyasz et al., 2009; Rojas & Hassan, 2017). The differences in diatom community composition may be explained by comparing key physical, biological, and chemical differences among macrophytes.

Arguably the clearest distinction (at least upon preliminary inspection) among submerged macrophytes are the morphologies of different species. For example, *Myriophyllum spicatum* (and other *Myriophyllum* spp.) has finely dissected leaves, whereas macrophytes from the genera *Vallisneria* and *Potamogeton* have more simple and broad leaf architectures. Epiphyte density is reported to be lower on broad leafed macrophytes

compared to finely dissected leaves (Celewicz-Gołdyn & Kuczyńska-Kippen, 2017; Laugaste & Reunanen, 2005). The reason for this could be a reduction in the movement speed of water through finely dissected leaves. Studies on bryophytes determined finely dissected bryophytes slow the movement of water (Knapp & Lowe, 2009; Suren et al., 2000), thereby protecting epiphytes from being swept away. The effects of different plant morphologies on water movements may also influence epiphytic diatom community composition.

Diatom species attach to substrates in different ways, utilizing extracellular polymeric substances (EPS) in the forms of mucilaginous stalks, pads, adhering films, fibrils and cell coatings, which differ in adherence strength (Hoagland et al., 1993; Woods & Fletcher, 1991). Therefore, the ability of individual diatom species to remain attached to surfaces is variable, and it follows that epiphytic diatoms with weaker attachments would benefit from a reduction in the movement speed of water associated with a finely dissected leaf architecture. Not only can the physical structure of submerged macrophytes affect epiphytic diatom community composition, but so can the chemistry of macrophyte microhabitats.

Some macrophytes have a protective adaptation where they produce compounds known as allelochemicals, which inhibit the growth of diatoms and other epiphytes. This is because epiphyte growth can reduce submerged macrophyte access to light (Sand-Jensen & Søndergaard, 1981). The degree to which macrophytes produce allelochemicals vary among macrophyte species (Hilt & Gross, 2008), with species such as *M. spicatum* having a higher allelopathic potential than *Chara* spp. and some species of *Potamogeton* not exhibiting any allelopathic tendencies. While some epiphytic diatoms are sensitive to these compounds (Wium-Anderson et al., 1982), others appear unaffected by them (Berger & Schagerl, 2004; Hilt, 2006).

In addition to allelochemicals, submerged macrophytes of the genus *Chara* are commonly encrusted with calcium carbonate owing to its greater ability to utilize bicarbonate as a source of carbon during photosynthesis (Kufel et al., 2016; Van den Berg et al., 2002). Carbonate ions produced as a by-product of this reaction readily bind with dissolved calcium ions, leading to calcium carbonate encrustations (Kufel et al., 2016). These

calcium carbonate encrustations create alkaline zones on the surface of the macrophyte (Pukacz et al., 2014); for every bicarbonate ion taken up by the macrophyte, one hydroxide ion is excreted to maintain electron neutrality (Lucas & Smith, 1973; Van den Berg et al., 2002). Diatom species that prefer more alkaline environments may, therefore, prefer *Chara* as a substrate. The result of the physical, chemical, and biological differences among substrates is a distinct diatom assemblage associated with different substrates.

In order to apply observed differences in modern epiphytic diatom assemblages to investigate past submerged macrophyte communities, fossil diatoms found in lake sediments must be utilized. However, studies of epiphytic diatoms are lacking compared to their planktonic counterparts. A recent search of the Web of Science database (Thomson Reuters, New York) (search based on topic: planktonic/planktic diatoms and epiphytic/periphytic diatoms; all journals; all years; accessed January 11, 2021) yielded almost 4000 results, of which the ratio of papers on planktonic diatoms outnumbers epiphytic diatoms approximately 5:2). These results are similar to a 2013 search (Pouličková et al., 2014) based on similar search terms, indicating a continuation of the trend to focus on planktonic diatoms. Furthermore, the use of epiphytic diatoms in paleolimnology to determine past submerged macrophyte community composition is limited, even though epiphytic diatoms can potentially provide valuable information on nearshore zone changes (Kelly et al., 2016; Letáková et al., 2018).

## **2.6 Tracking Changes in Submerged Macrophyte Community Composition using Paleolimnology**

The relationships between submerged macrophytes and limnological conditions are complex, with shifts in both submerged macrophyte community composition and abundance being affected by and influencing lake properties. It is therefore helpful to know how submerged macrophyte community composition has changed over time and its relationship to changing limnological conditions. Unfortunately, long-term data sets of actual water quality measurements, such as pH, nutrient concentrations, temperature, and

salinity, are scarce. Globally, there are fewer than 50 limnological data sets longer than 35 years (Rosenzweig et al., 2008), and analysis of one international journal dedicated to environmental monitoring and assessment revealed that approximately 90% of the research articles had monitoring windows less than 3 years in duration (Smol, 2008; 2010).

In the absence of direct, long-term (decades to centuries) monitoring of environmental variables, paleolimnology can provide these records using proxies preserved in lake sediments as substitutes for measured environmental conditions (Smol, 2008). To track changes in macrophyte communities, proxies from macrophytes, including pollen, plant macrofossils, and *n*-alkanes have been used, although each of these has its limitations.

Pollen has been used effectively to reconstruct invasive emergent macrophytes, cattails (*Typha latifolia*, *Typha angustifolia* L. and *Typha x glauca* Godr.), at the regional and local scale (Rippke et al., 2010; Shih & Finkelstein, 2008). However, pollen generally is not ideal for investigating aquatic macrophytes as aquatic plant pollen is typically less than 5% of the total pollen preserved in lake sediments, even in lakes with abundant aquatic vegetation (Boxem et al., 2018; Edwards et al., 2000).

Plant macrofossils, which generally are preserved in close proximity to the plant that they originated from, could be more useful than pollen for tracking changes in macrophyte communities because they effectively identify the dominant plants in the littoral zone (Zhao et al., 2006). However, the reproductive ecology of the plant (i.e., number of seeds produced and the dispersal mechanisms) can significantly affect the abundance of macrofossils preserved in sediment (Bishop et al., 2018). This can lead to an over- or underrepresentation of specific macrofossils in sediment.

The chain length of *n*-alkanes, a lipid produced by aquatic and terrestrial vegetation, preserved in lake sediments have been used to differentiate among submerged, emerged, and terrestrial vegetation (Ficken et al., 2000). Although the average *n*-alkane chain length is different between submerged macrophytes and algae, the average chain length among species of submerged macrophytes is too similar to allow for the differentiation of submerged macrophyte taxa (Liu & Liu, 2016).

Fossil remains of diatoms that live on aquatic macrophytes may offer the best opportunity to track changes in the aquatic plant community; however, such studies are limited, especially in southern Ontario. To infer past littoral habitats of the St. Lawrence River, Reavie & Smol (1997) used the microhabitat specificity of diatoms on filamentous algae, rocks, and submerged macrophytes to develop an inference model which was applied to fossil diatoms in sediment cores to identify shifts in nearshore habitat, such as a relative increase in total macrophyte populations. Models like this have been improved to include semi-quantitative reconstructions of submerged macrophyte biomass (Vermaire et al., 2011) and have been successfully employed in paleolimnological investigations of Québec lakes (Vermaire et al., 2012; 2013). These investigations did not differentiate among submerged macrophytes species using diatoms because preliminary findings indicated no significant differences in epiphytic diatom community composition (Reavie & Smol, 1997; Vermaire et al., 2011). An attempt to decouple submerged macrophyte species in these reconstructive models was not made but is warranted based on emerging research which indicates that diatom communities vary among species of submerged macrophytes (e.g., Comte & Cazaubon, 2002; Messyasz et al., 2009; Rojas & Hassan, 2017). If diatom community composition is distinct on different submerged macrophytes, then it may be possible to use changes in diatom assemblages preserved in lake sediments to track changes in submerged macrophytes over time.

### 3 STUDY AREA

#### 3.1 The General Geology and Geography of Chandos Lake and Gilmour Bay

Chandos Lake (44°49'30" N, 77°58'30" W) is located in Peterborough County near the Township of Apsley in North Kawartha, Ontario, Canada (Figure 3.1). Chandos Lake is situated within the Grenville Province of the Canadian Shield and is situated in metamorphosed rocks (Heaman et al., 1982). Most of Chandos Lake is situated in monzonites, quartz monzonites and marble (Heaman et al., 1982). Between 13,000 to 15,000 calendar years before present (cal yr BP), Pleistocene glaciers retreated across what is now southern Ontario (Gao, 2011). Glaciers scoured the land, carving out thousands of lakes, including Chandos Lake (Shaw & Hewitt, 1962). Poor drainage and swampy areas in the surrounding terrain also contributed to the creation of the lake. Glaciofluvial deposits in the area surrounding Chandos Lake are rare (Shaw & Hewitt, 1962).

Chandos Lake resides in the Dfb climate zone according to the Köppen-Geiger climate classification model (Kottek et al., 2006), meaning it has a humid, snowy climate with warm summers. Canadian climate normal data for 1981-2010 from the nearby Peterborough monitoring station indicate an average daily temperature of -8.4 °C in January and 20.7 °C in July, annual rainfall of 144.5 mm and annual snowfall of 182.1 cm (Environment and Climate Change Canada [ECCC], 1981-2010).

The forest surrounding Chandos Lake is Great Lakes – St. Lawrence Forest (Rowe, 1972). The forests in this area contain a diverse mix of tree species including both coniferous and deciduous trees. Common species include sugar maple (*Acer saccharum*), yellow birch (*Betula lutea*), beech (*Fagus grandifolia*), white pine (*Pinus strobus*), balsam fir (*Abies balsamea*), and red oak (*Quercus rubra*) (Cambon, 1994; Thompson, 2000). European colonisation and logging activities began in the Chandos Lake area in the early 1860s with a report from 1913 indicating that 68% of the area had been logged (Cole, 1989; Howe & White, 1913). Modest forest recovery occurred from 1910 to 1950

before cottage development began following the Second World War (Brunger, 2009; Cole, 1989).



Figure 3.1 Map illustrating the location and shape of Chandos Lake in Ontario, Canada.

Figure drawn by Karen VanKerkoerle, © 2021 Department of Geography and Environment, Western University, K. VanKerkoerle. Base map source: DMTI Spatial Inc. This figure is reproduced with the express permission of the copyright holder (Appendix A).

### 3.2 Lake and Watershed Properties

Chandos Lake is large relative to many other small lakes in the area with a surface area of 16.68 km<sup>2</sup>, a max depth of 45.7 m and a mean depth of 12.85 m (Ontario Ministry of the Environment [MOE], 1986). The shoreline is well developed with over 1200 cottages populating Chandos Lake (Moser, 2019). There are several small creeks originating from Lakes Tallan, Clydesdale, and Lasswade, as well as underground springs, that flow into Chandos Lake (MOE, 1972). Chandos Lake discharges into the Crowe River, part of the Trent River System. During periods of elevated water level following spring melt, the Crowe River may reverse flow into Chandos Lake, but the effect is thought to be minimal (MOE, 1986). There are three large bays on Chandos Lake – West Bay, South Bay, and Gilmour Bay. This study is focused on Gilmour Bay (44°47'4" N, 77°57'8" W), attached by a narrow inlet to the southeast end of Chandos Lake.

Gilmour Bay is itself a complex ecosystem, but it is much smaller than Chandos Lake. Small lakes may be more sensitive to anthropogenic and climatic disturbances and respond more quickly to their effects (Gerten & Adrian, 2001; Adrian et al., 2009; Yang et al., 2016; Mrdjen et al., 2018). Preliminary research supports this hypothesis, indicating Gilmour Bay appears more impacted than Chandos Lake (Hollingshead, 2017). Considering their similar geographic and climatic conditions, this presents the opportunity to study Gilmour Bay as an analogue for the main lake, where impacts in Gilmour Bay might reflect future changes to Chandos Lake.

Gilmour Bay has a surface area of 0.65 km<sup>2</sup>, a max depth of 27.4 m, and a mean depth of 8.51 m (MOE, 1986). Both Chandos Lake and Gilmour Bay appear to be dimictic since they are well stratified in both summer and winter. Previous measurements by the MOE (1972; 1986) showed that the concentration of nutrients in the main part of Chandos Lake is low, classifying it as oligotrophic; whereas hypolimnetic anoxia and epilimnetic total phosphorus between 10-20 µg/L in Gilmour Bay classify it as oligo-mesotrophic (classifications based on Wetzel, 2001; Table 13.18). More recent water chemistry measurements from epilimnetic waters in the center of Gilmour Bay also indicate oligotrophic status, but hypolimnetic measurements show elevated phosphorus (Table 3.1,



3.2) and anoxia (Figure 3.2). Notably, these measurements did not capture lake turnover when hypolimnetic phosphorus can be introduced into the epilimnion during mixing, which could lead to a different classification. A peak in oxygen at ~7 m (Figure 3.2), likely indicates a chlorophyll-*a* maximum, which is suggestive of nutrient limitation in the surface waters in August (Fee, 1976). Monthly Secchi measurements from Gilmour Bay during summer 2019 indicate an increase in light penetration over the summer season, ranging from 2.5 m in May to 4.8 m in August (Table 3.1).

Relative to other lakes on the Canadian Shield (Ontario Ministry of Environment, Conservation and Parks [MOECP], 2020), Gilmour Bay has high alkalinity and calcium values (Spring surface water alkalinity = 47.6 mg/L, calcium = 21.4 mg/L; Table 3.1) compared to what is commonly reported for Canadian Shield lakes (alkalinity  $\leq$  60 mg/L and calcium  $\leq$  5 mg/L; Bodo, 1992; Jeziorski et al., 2008) and lower values than what is commonly reported for lakes in Paleozoic bedrock to the south (alkalinity  $\geq$  120 mg/L and calcium  $\geq$  30 mg/L values; Barbiero et al., 2006; Bodo, 1992). This is probably due to the erosion of marbles and monzonites, both metamorphic rocks containing calcite, from the catchment of Chandos Lake. As a result, Gilmour Bay and Chandos Lake represent a transition in limnological conditions between two distinct ecozones (Precambrian Canadian Shield and Paleozoic southern Ontario), and may therefore support a more diverse community of submerged macrophytes.

Table 3.1 Monthly limnological measurements from Gilmour Bay during the 2019 summer season.

Samples were collected by David Zilkey and analysis was completed by the Dorset Environmental Science Centre. “E” represents epilimnion measurements, “H” represents hypolimnion measurements. Additional measurements are provided in Appendix B.

Limnological Variable	May 30, 2019		June 23, 2019		July 29, 2019		August 31, 2019	
	E	H	E	H	E	H	E	H
pH	7.76	7.18	7.91	7.26	7.86	7.06	7.77	7.00
Alkalinity (mg/L CaCO <sub>3</sub> )	47.6	49	52.4	50.2	51.8	51.7	52.7	55.7
Calcium (mg/L)	21.4	21.3	22.3	21.6	20.5	19.9	19.7	18.6
Total Phosphorus (µg/L)	9.5	15.9	8.6	15.5	5.8	50.7	6.1	157.5
Total Nitrogen (µg/L)	273	266	308	290	288	375	293	805
Secchi depth (m)	2.5		2.5		4.5		4.75	

Table 3.2 August, 2014 water chemistry from Gilmour Bay (Hollingshead, 2017).

Epilimnetic samples were taken approximately 0.5 m below the water surface with a Nalgene ® bottle lowered by hand and hypolimnetic samples were taken at approximately 18 m depth using a Van Dorn sampler. “E” represents epilimnion; “H” represents hypolimnion; < LOD represents less than limit of detection. Nitrate and Nitrite LOD = 2 µg/L; Nitrite Nitrogen LOD = 1 µg/L; Soluble Reactive Phosphate-Phosphorus LOD = 0.9 µg/L. Table obtained from Hollingshead (Table 4, 2017), © Kelly Hollingshead. This table is reproduced with the express permission of the copyright holder (Appendix A).

Chemical Symbol	Name	Gilmour Bay	
		E	H
TN (N µg/L)	Total Nitrogen	277	1,150
TP (P µg/L)	Total Phosphorus	7	140
NH <sub>3</sub> (N µg/L)	Ammonia Nitrogen	3	543
NO <sub>2</sub> +NO <sub>3</sub> (N µg/L)	Nitrate and Nitrite	<LOD	<LOD
NO <sub>2</sub> (N µg/L)	Nitrite Nitrogen	<LOD	<LOD
SRP (P µg/L)	Soluble Reactive Phosphate-Phosphorus	<LOD	41
DOC(C mg/L)	Dissolved Organic Carbon	5.0	5.0
DIC(C mg/L)	Dissolved Inorganic Carbon	10.9	12.1
Cl (mg/L)	Chloride	10.77	14.78
SO <sub>4</sub> (mg/L)	Sulphate	4.21	3.03
Na (mg/L)	Sodium	6.26	9.03
K (mg/L)	Potassium	0.81	1.03
Ca (mg/L)	Calcium	20.37	21.25
Mg (mg/L)	Magnesium	1.41	1.59
SiO <sub>2</sub> (Si mg/L)	Dissolved Silica	0.70	2.77
Chl-a (µg/L)	Chlorophyll-a	2.37	3.13

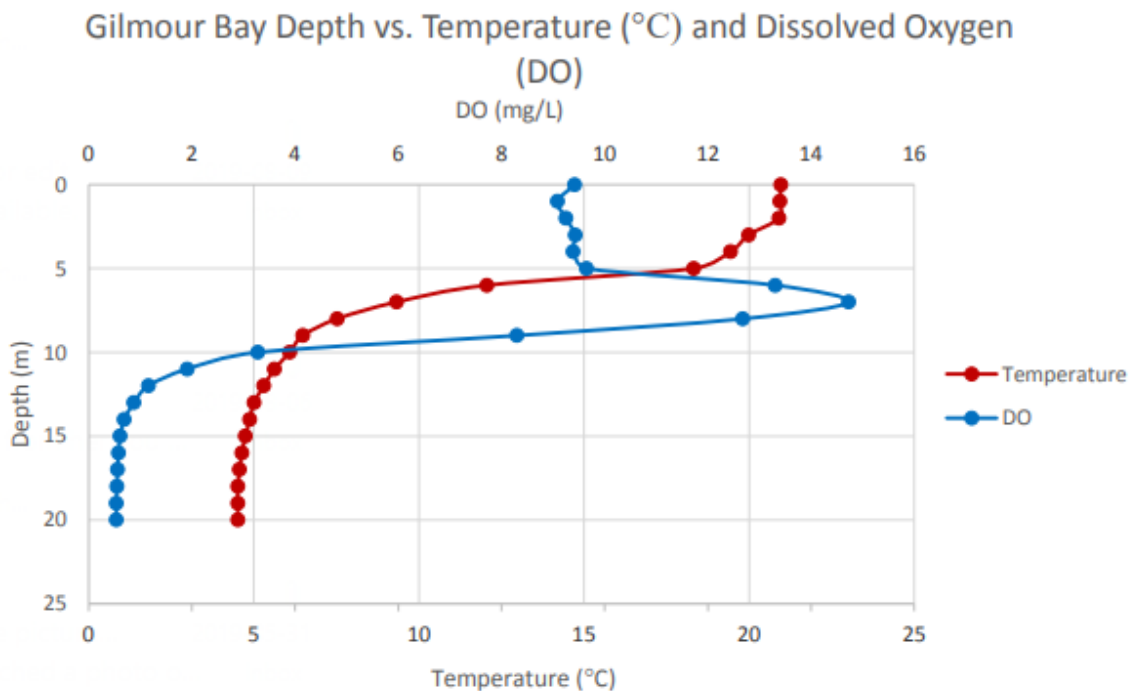


Figure 3.2 August 2014 dissolved oxygen and temperature profiles from Gilmour Bay.

Gilmour Bay is anoxic below ~11 m depth. Figure obtained from Hollingshead (Figure 7C, 2017), © Kelly Hollingshead. This figure is reproduced with the express permission of the copyright holder (Appendix A).

Extensive aquatic plant growth is limited to a few areas of shoreline around the lake, including sites in Gilmour Bay (Appendix C) (MOE, 1972). A mix of aquatic vegetation is found at Chandos Lake including both submergent and emergent plant species.

Common plants reported in the 1970s included pondweeds (*Potamogeton robbinsii*, *P. pectinatus*, *P. zosteriformis*), bur reed (*Sparganium* sp.), and bulrush (*Scripus* sp.) (MOE, 1972; 1986). In the Kawartha Lakes region where Chandos Lake is located, a rapid disappearance of *M. spicatum* from Lakes Chemong, Buckhorn, and Scugog were noted in the late 1970s, with circumstantial evidence suggesting that insect grazing by *Acentria nivea* was responsible for the shift back to native vegetation (Painter & McCabe, 1988). *M. spicatum* was present in Chandos Lake as noted by the 1972 report but was not identified in the 1986 report (MOE, 1972; 1986). Present day observations by Chandos Lake residents indicate widespread presence of *M. spicatum*, suggesting its abundance increased following the 1986 report (K. Baker, personal communication, May 27, 2019). *Chara* is not identified in either report, but it is unclear whether that is due to its absence from the nearshore environment or a conscious decision to exclude *Chara* since it is a macroalgae. Regardless, present day observations indicate its presence in the nearshore environment.

## 4 METHODS

### 4.1 Field Methods

#### 4.1.1 Submerged Macrophyte Collection

To determine the epiphytic diatom community composition of submerged macrophytes, I collected macrophyte samples from Gilmour Bay in late August 2019. Late summer sample collection ensured ample epiphytic diatom growth and was prior to fall/winter macrophyte dieback (Vermaire et al., 2011). Samples were collected from a macrophyte-rich area of the bay (Figure 4.1) that was identified from previous research by the MOE (Appendix C) to ensure enough samples were available from one site for analysis. Boat traffic and recreation in the collection area was minimal and unlikely to disturb the study site. The submerged macrophyte community at this location was primarily *Potamogeton robbinsii*, *Myriophyllum spicatum*, and *Chara* sp. (hereafter referred to as *Chara*) based on visual inspection (for photos of submerged macrophytes, see Appendix D). A total of 30 macrophyte samples were collected with ten complete individuals (i.e., roots, leaves, stems, etc.) of each species. This sample size was similar to previous studies (Reavie & Smol, 1997; Rojas and Hassan, 2017; Vermaire et al., 2011). *P. zosteriformis* and *P. pectinatus* were also observed but were much less abundant at the time of sampling and were not collected. Sampling was conducted from a boat using an extended grabber tool (Figure 4.2). The grabber tool was attached to the base of the macrophyte and a gentle pulling force was applied to collect the macrophyte while minimizing disturbance to both the surrounding sediment and the epiphytic diatom community. Samples were removed from the water and placed into a clean, dry, re-sealable plastic bag, rather than bagging underwater (Vermaire et al., 2011). This was done to reduce the likelihood of epiphytic diatom detachment during transport from the field to the laboratory and the potential for contamination from diatoms in the water. Samples were kept in a cool, dark environment until returned to the laboratory where they were stored at 4 °C while awaiting processing.

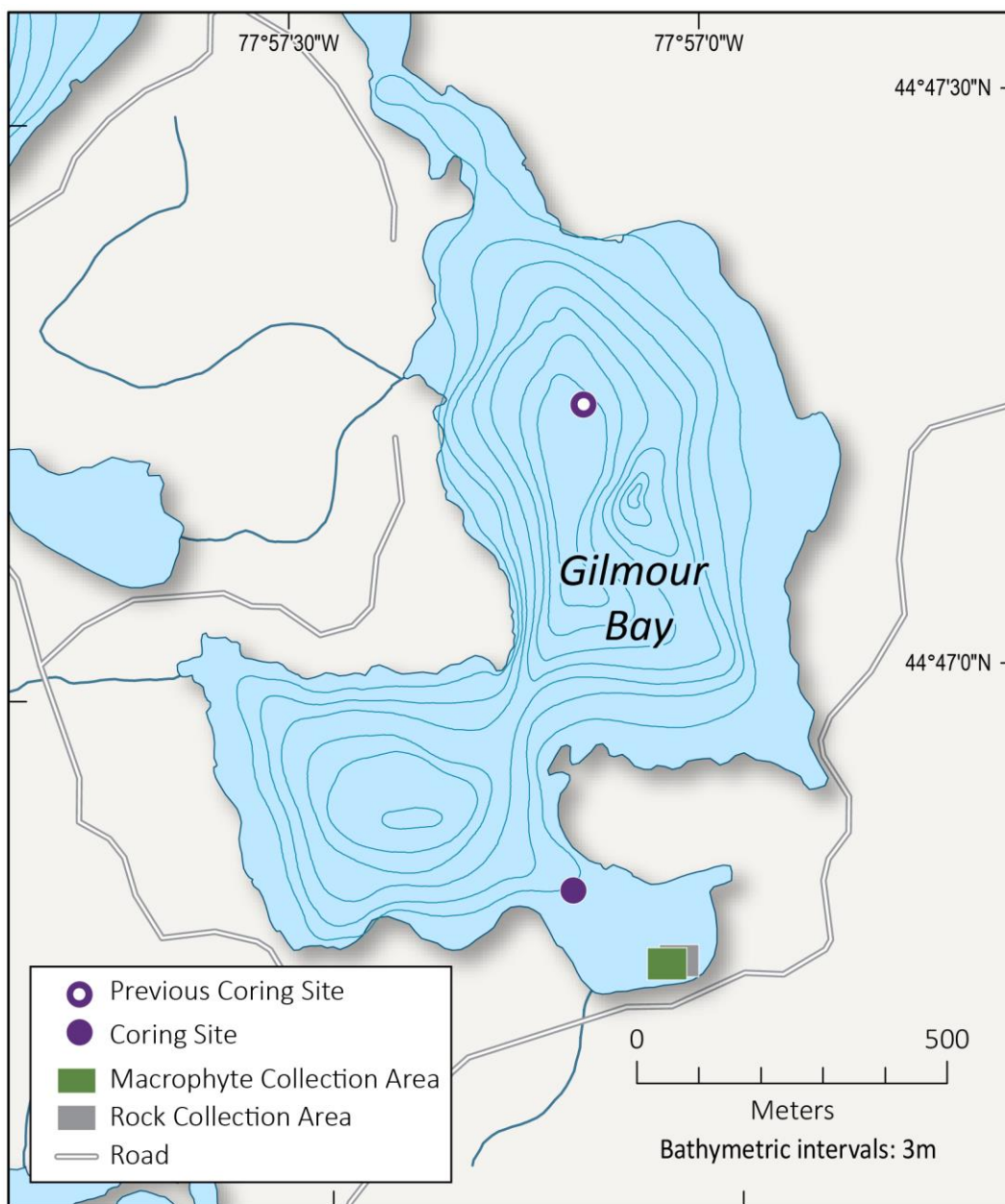


Figure 4.1 Bathymetric map indicating Gilmour Bay sampling locations.

Figure drawn by Karen VanKerkoerle, © 2021 Department of Geography and Environment, Western University, K. VanKerkoerle. Base map source: DMTI Spatial Inc. This figure is reproduced with the express permission of the copyright holder (Appendix A).

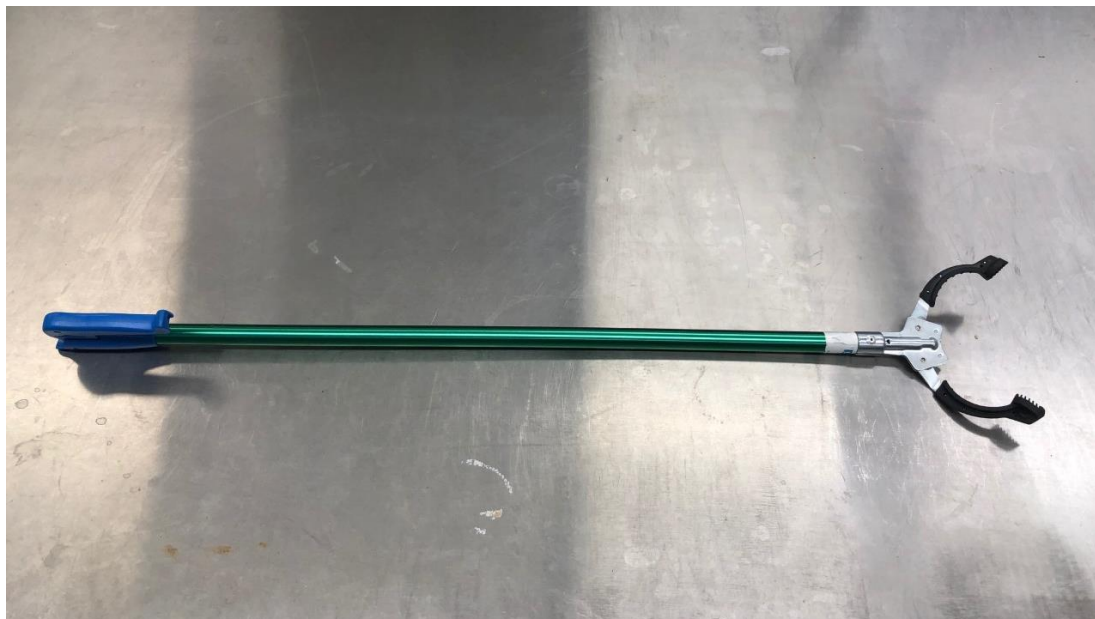


Figure 4.2 Image of extended grabber tool used for submerged macrophyte collection.

The tool was rinsed between each sample collected to reduce the likelihood of contamination between samples. Photo taken by David Zilkey.

#### 4.1.2 Rock Sample Collection

Reavie & Smol (1997) and Vermaire et al. (2011) indicated epiphytic diatoms were distinct from epilithic diatoms. To confirm this was also true in Gilmour Bay, three rock samples were collected for analysis of epilithic diatoms. Samples were collected away from direct macrophyte contact along the shoreline of the macrophyte-rich area to avoid contamination of epiphytic diatoms. Samples were kept in a cool, dark environment until returned to the laboratory where they were stored at 4 °C while awaiting processing.

#### 4.1.3 Nearshore Sediment Core Collection and Extrusion

Two nearshore sediment cores (Figure 4.3) were obtained from the littoral zone of Gilmour Bay near the macrophyte-rich area of the bay (Figure 4.1). The purpose for obtaining nearshore sediment cores was to apply the results of the epiphytic diatom



survey to fossil diatoms preserved in sediment to reconstruct changes in submerged macrophyte community composition. The cores were obtained at a water depth of 3 m. A shallower location was avoided to ensure no sediment mixing due to wave action and avoid *in situ* epipelagic and epipsammic diatom growth. The proximity of the coring location to the shore was expected to represent changes in the nearshore environment rather than a spatially integrated sample of the entire lake as is expected when cores are collected from the centre of the lake (Charles et al., 1991). The surface sediment was assumed to represent modern littoral habitat conditions, while the bottom sediment was assumed to represent historical littoral habitat conditions. The cores were taken 1 m apart from each other using a messenger triggered gravity core (Glew, 1989; 1991) (6.5 cm internal tube diameter). Using a specialized vertical extruder (Glew, 1988), sediment cores were sectioned at continuous 0.5 cm intervals to minimize stratigraphic disturbance, however, only three of these sediment samples are presented here. Sub-sampling was completed in the field immediately after sediment core collection. Sub-samples were placed into Whirl-Pak® bags and kept in a cool, dark environment until returned to the laboratory where they were stored at 4 °C while awaiting processing.

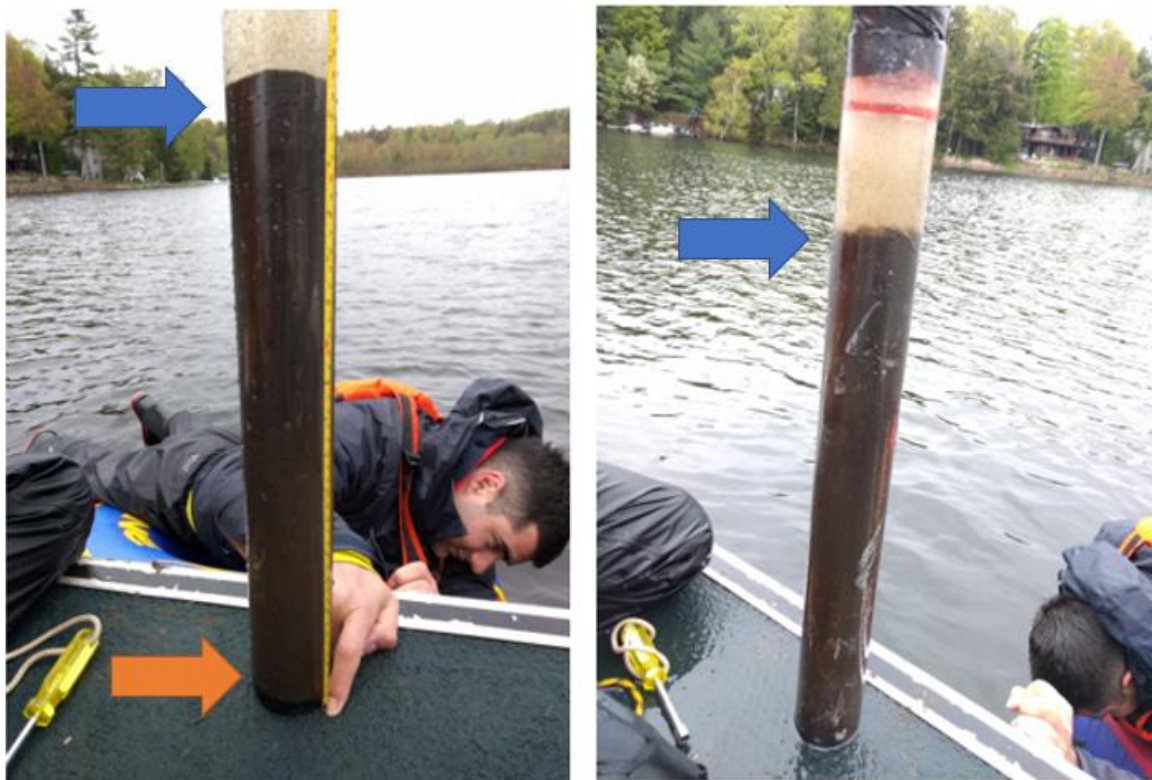


Figure 4.3 Photograph of nearshore sediment cores obtained from Gilmour Bay.

Nearshore cores were obtained from the nearshore coring location in Gilmour Bay (Figure 4.1). 19-GB-03-C1 (left) was 44 cm long and 19-GB-03-C2 (right) was 43 cm long. The blue arrows indicate surface sediment samples, representing modern conditions, obtained from each core. The orange arrow indicates the bottom sediment sample, representing pre-disturbance conditions, obtained from 19-GB-03-C1.

## 4.2 Laboratory Methods

### 4.2.1 Epiphytic Diatom Sample Preparation

Submerged macrophyte samples were prepared for diatom analysis in the Lake and Reservoir Systems (LARS) Research Facility at the University of Western Ontario. Approximately 3 cm of submerged macrophyte material including both stem and leaf were cut randomly from each sample and placed into a glass scintillation vial. Samples were treated with approximately 15 mL of 10% hydrochloric acid to remove any carbonates and aspirated after 24 hours at rest. Immediately following aspiration, samples were washed using approximately 15 mL of Type 1 (18.2 M $\Omega$ -cm) deionized water. After an overnight settling period, samples were treated with approximately 15 mL of a 50:50 molar mixture of sulphuric and nitric acid to remove organic material. The samples were placed in a hot water bath for three hours to increase the rate of reaction before being left to settle for 24 hours. Because there was still considerable organic material remaining in the samples, samples were aspirated and a second application of the 50:50 molar mixture of sulphuric and nitric acid was applied. Following another three-hour hot water bath and 24-hour settling period, samples were aspirated and repetitively washed with 18.2 M $\Omega$ -cm deionized water until a neutral pH was reached (12-15 washes with 24 hours in between each wash to allow for settling). A vial containing only 18.2 M $\Omega$ -cm deionized water underwent the same procedures as a method to determine if contamination occurred during sample processing; if diatoms were found in this vial, then contamination among samples was likely. Approximately 1.5 mL of each slurry was added to a test tube and diluted with 18.2 M $\Omega$ -cm deionized water; four dilutions were made per slurry, each with approximately 2 mL more 18.2 M $\Omega$ -cm deionized water than the previous dilution, to ensure an appropriate amount of diatoms for enumeration. The diluted solutions were extracted and spread evenly onto a cover slip (cleaned with a 10% ethanol solution and Kimwipes®) using a Pasteur pipette. The cover slips were left to dry for a minimum of 24 hours until no water was visible. To ensure the cover slips were completely dry, each cover slip was briefly heated prior to mounting on glass slides (cleaned with a 10% ethanol solution and Kimwipes®) using ZRAX®, a mounting medium with a high refractive index (R.I. = 1.7).

#### 4.2.2 Rock and Sediment Diatom Sample Preparation

Rock and sediment samples were prepared for diatom analysis in the Lake and Reservoir Systems (LARS) Research Facility at the University of Western Ontario following standard procedures reported in Battarbee et al. (2001). For each rock sample, a toothbrush was used to remove epilithic diatoms and rinsed into a glass scintillation vial with 18.2 M $\Omega$ -cm deionized water. Samples were left to settle, and the 18.2 M $\Omega$ -cm deionized water was aspirated from the vial. For each sediment sub-sample, approximately 1 cm<sup>3</sup> of sediment was placed into a glass scintillation vial. Sample preparation procedures were identical to those outlined for epiphytic diatoms, except only one acid treatment was required to remove organic material.

#### 4.2.3 Diatom Analysis

Diatom identification followed taxonomic guidelines from *Diatoms of North America* (Spaulding et al., 2020) and Krammer & Lange-Bertalot (1986-1991). Each sample was enumerated using a Leica® E-600 light microscope equipped with Nomarski differential interference contrast (DIC) optics and 1000X magnification. A transect was counted beginning at the centre of a vertical edge and a minimum of 400 diatom valves were counted per slide to ensure a representative sample was collected. Digital photographs of common diatom taxa were taken using a Retiqua® digital camera (Appendix E).

### 4.3 **Statistical Methods**

#### 4.3.1 Modern Analysis

Diatom counts were converted into relative abundances prior to statistical analysis. As an assessment of heterogeneity, diatom species richness (i.e., the number of different diatom taxa present) was calculated for each sample and average species richness (i.e., the number of different species) was calculated for each substrate. For subsequent analysis, diatom taxa that were not present in at least four samples and in  $\geq 2\%$  abundance in at least one sample were excluded from statistical analysis. The remaining taxa are hereafter referred to as “common taxa”. To improve figure legibility, taxa were shortened to a six-character code (Table 4.1). Although excluding taxa based on low frequency can have an

impact on ordination results if many sites are sampled across a wide ecological gradient, generally excluding taxa with less than 2% abundance does not have marked effects on subsequent ordination and analyses (Lavoie et al., 2009). In this study, where only one site is considered, it is expected that removing infrequently present taxa will have little effect on the results.

Table 4.1 Common diatom taxa and their associated codename

<b>Taxon Code</b>	<b>Full Taxon Name</b>
AchExi	<i>Achnantheidium exiguum</i>
AchGra	<i>A. gracillum</i>
AchLat	<i>A. latecephalum</i>
AchMin	<i>A. minutissimum</i>
BraMic	<i>Brachysira microcephala</i>
CocPla	<i>Cocconeis placentula</i>
EnaLan	<i>Encyonema lange-bertalotii</i>
EncMic	<i>Encyonopsis microcephala</i>
EncSp	<i>E. sp.</i>
EpiRei	<i>Epithemia reichelti</i>
EpiTur	<i>E. turgida</i>
EunInc	<i>Eunotia incisa</i>
FraCap	<i>Fragilaria capucina</i>
FraCro	<i>F. crotonensis</i>
FraMes	<i>F. mesolepta</i>
FraTen	<i>F. tenera</i>
GomMin	<i>Gomphonema minutum</i>
GomPar	<i>G. parvulum</i> var. <i>parvulus</i>
LinInt	<i>Lindavia intermedia</i>
LinMic	<i>L. michigania</i>
NavCph	<i>Navicula cryptocephala</i>
NavCpt	<i>N. cryptotonella</i>
NavGer	<i>N. gerloffii</i>
NavRad	<i>N. radiosa</i>
NavSp1	<i>N. sp. 1</i>
NitDis	<i>Nitzschia dissipata</i> var. <i>media</i>
PlnFre	<i>Planothidium frequentissimum</i>
PltBah	<i>Platessa bahlsi</i>
PltCon	<i>P. conspicua</i>
PsaMic	<i>Psammothidium microscopium</i>
RhoGib	<i>Rhopalodia gibba</i>
RosAna	<i>Rossithidium anastasiae</i>
SelPup	<i>Sellaphora pupula</i>
StaCon	<i>Staurosira construens</i>
StePin	<i>Staurosirella pinnata</i>

A plot of relative abundances was created to visualize and compare the diatom community composition from each submerged macrophyte, rock, and sediment sample using the 'stratipLOT' function from the 'rioja' package (Juggins, 2020) in the R statistical program (R Core Team, 2020).

Cluster analysis was performed to assess whether samples could be grouped by substrate based solely on their diatom community composition, without prior input on the substrate from which each sample was obtained. A Bray-Curtis dissimilarity matrix was calculated using the 'vegdist' function from the 'vegan' package (Oksanen et al., 2019) and average hierarchical cluster analysis was applied using the 'hclust' function from the 'stats' package (R Core Team, 2020). A Bray-Curtis dissimilarity matrix, commonly used by ecologists in similar studies (e.g., Vermaire et al., 2011; Hao et al., 2017, Rojas & Hassan, 2017), was selected since it is sensitive to differences in abundance among species and weights abundant species more heavily than rare species (Ricotta & Podani, 2017).

Principal components analysis (PCA) was used to identify diatom taxa that differentiated the diatom community composition of submerged macrophytes, and therefore could be potentially used to track changes in submerged macrophytes over time using fossil diatoms. The PCA was performed to highlight which diatom taxa differentiate the diatom community composition among species of submerged macrophytes using the 'prcomp' function from the 'stats' package (R Core Team, 2020) and visualized using 'ggplot2' (Wickham, 2016). The PCA was standardized; variables were shifted to be zero centered and scaled to have unit variance to reduce the impact of outliers and extreme values.

To test whether there was a difference in the diatom community composition among species of submerged macrophytes, an analysis of similarity test (ANOSIM) based on a Bray-Curtis dissimilarity matrix was performed using the 'anosim' function from the 'vegan' package (Oksanen et al., 2019). The raw Bray-Curtis coefficients (previously calculated for cluster analysis) were converted to ranked values prior to the ANOSIM test. ANOSIM compares the mean of ranked dissimilarities between groups to the mean of ranked dissimilarities within groups. ANOSIM tests the null hypothesis that there is no difference between the means of two or more groups and returns an R statistic between -1

and 1 (Buttigieg & Ramette, 2014). The observed R statistic is compared to the null distribution of R, created with 999 permutations, to generate a measure of statistical significance (P). When  $R = 1$ , it suggests that samples within a group are more similar to each other than samples from another group, indicating dissimilarity between groups; when  $R = 0$ , it suggests there is no dissimilarity between groups; when  $R = -1$ , dissimilarity is greater within a group than between groups (Buttigieg & Ramette, 2014).

#### 4.3.2 Historical Analysis

As a preliminary test of whether fossil diatoms could be used to track changes in submerged macrophytes, I explored various diatom indices which were selected to highlight changes in the epiphytic diatom community. Indices were necessary since planktonic diatom species typically overwhelm the signal of benthic diatoms, particularly in higher production systems (Vermaire et al., 2011) and in deep lakewater cores (Moos et al., 2005). Diatom indices were determined to focus on the epiphytic diatom community. The numerator of each index was determined from the PCA, which identified indicator diatoms associated with specific submerged macrophytes. The denominator was a generalist epiphytic diatom taxon.



## 5 RESULTS

### 5.1 Diatom Community Composition of Submerged Macrophytes Compared to Other Substrates

To confirm that the diatom community compositions of the three submerged macrophyte species were distinct from rocks and surface sediment in Gilmour Bay, I compared the diatom community composition of these substrates. A total of 92 diatom taxa were identified in the 34 modern samples (30 macrophyte, two surface sediment, and two rock samples) and one historical sediment sample; the common taxa are shown in Figure 5.1 and are illustrated with photographic plates in Appendix E. The surface sediment samples presented in Figure 5.1 are the top interval (0-0.5 cm) of the nearshore sediment cores (Figure 4.3). Only one historical sediment sample retrieved from the bottom of one of the cores is included due to limitations in the paleolimnological investigation discussed in Chapter 6.2. Only two rock samples were included as the third sample did not have enough diatoms for enumeration.

The most common diatom, occurring in all samples, was *Achnantheidium minutissimum* (*Chara* mean =  $25 \pm 5.8\%$ ; *M. spicatum* mean =  $27 \pm 6.0\%$ ; *P. robbinsii* mean =  $29 \pm 5.3\%$ ; rock mean =  $21 \pm 4.5\%$ ; surface sediment, mean =  $15 \pm 2.3\%$ ) (Figure 5.1). Cluster analysis (Figure 5.2) showed that diatom communities on submerged macrophytes differed from rock scrapes and sediments. All species of submerged macrophytes contained a high relative abundance of *Cocconeis placentula* (*Chara* mean =  $16 \pm 5.2\%$ ; *M. spicatum* mean =  $28 \pm 16\%$ ; *P. robbinsii* mean =  $23 \pm 8.0\%$ ) compared to rock scrapes and surface sediment (rock mean =  $8.0 \pm 2.0\%$ ; surface sediment mean =  $3.6 \pm 0.23\%$ ). Rock samples were differentiated from all other samples by a higher relative abundance of *Epithemia reichelti* (mean =  $28 \pm 1.7\%$ ) and *Navicula* sp. 1 (mean =  $9.4 \pm 6.1\%$ ), neither of which were present on submerged macrophytes.

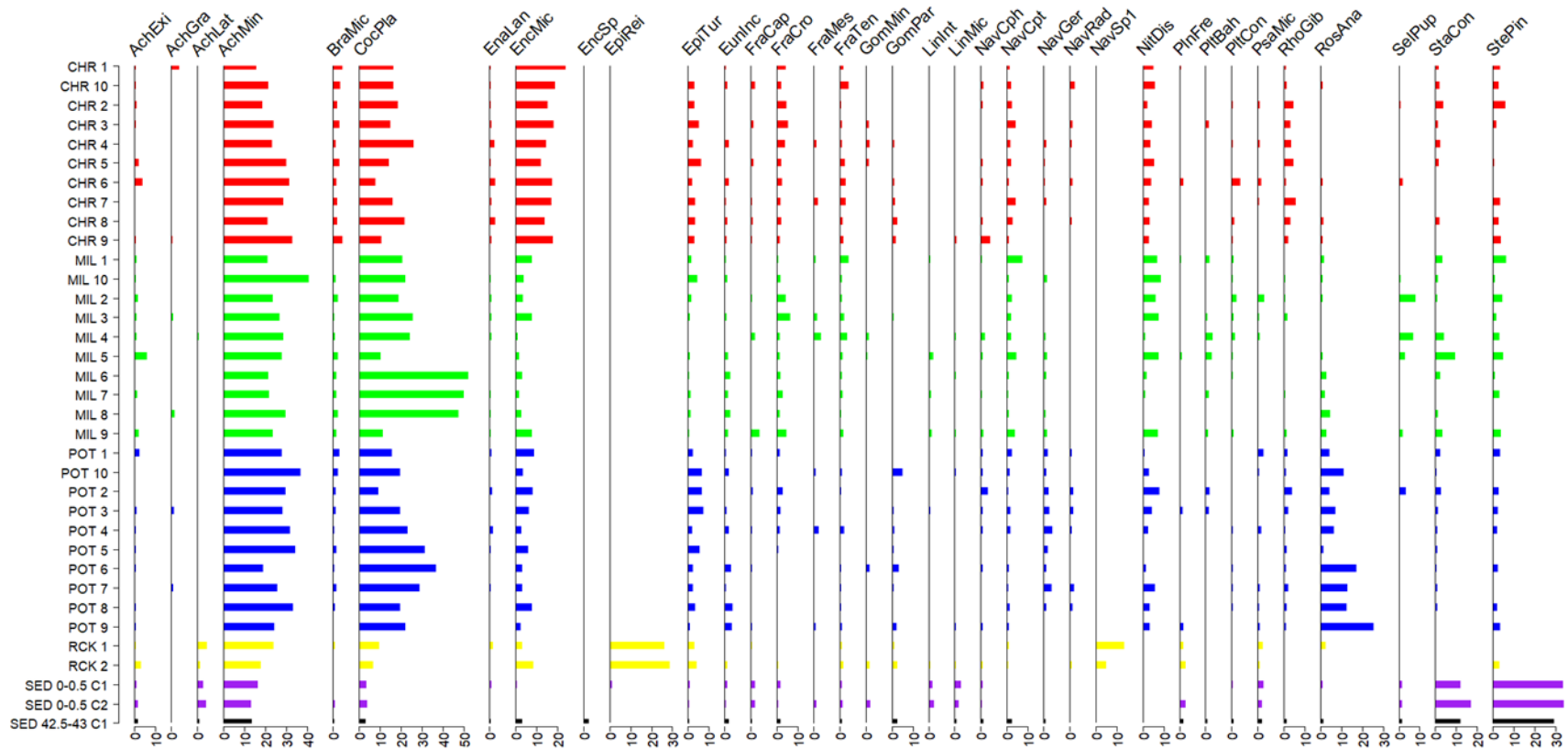


Figure 5.1 Relative abundances of common diatom taxa.

Diatom species are presented alphabetically; substrates are differentiated by colour (Red = *Chara*, Green = *M. spicatum*, Blue = *P. robbinsii*, Yellow = Rock, Purple = Surface Sediment, Black = Bottom Sediment). See Table 4.1 for full names of taxa.

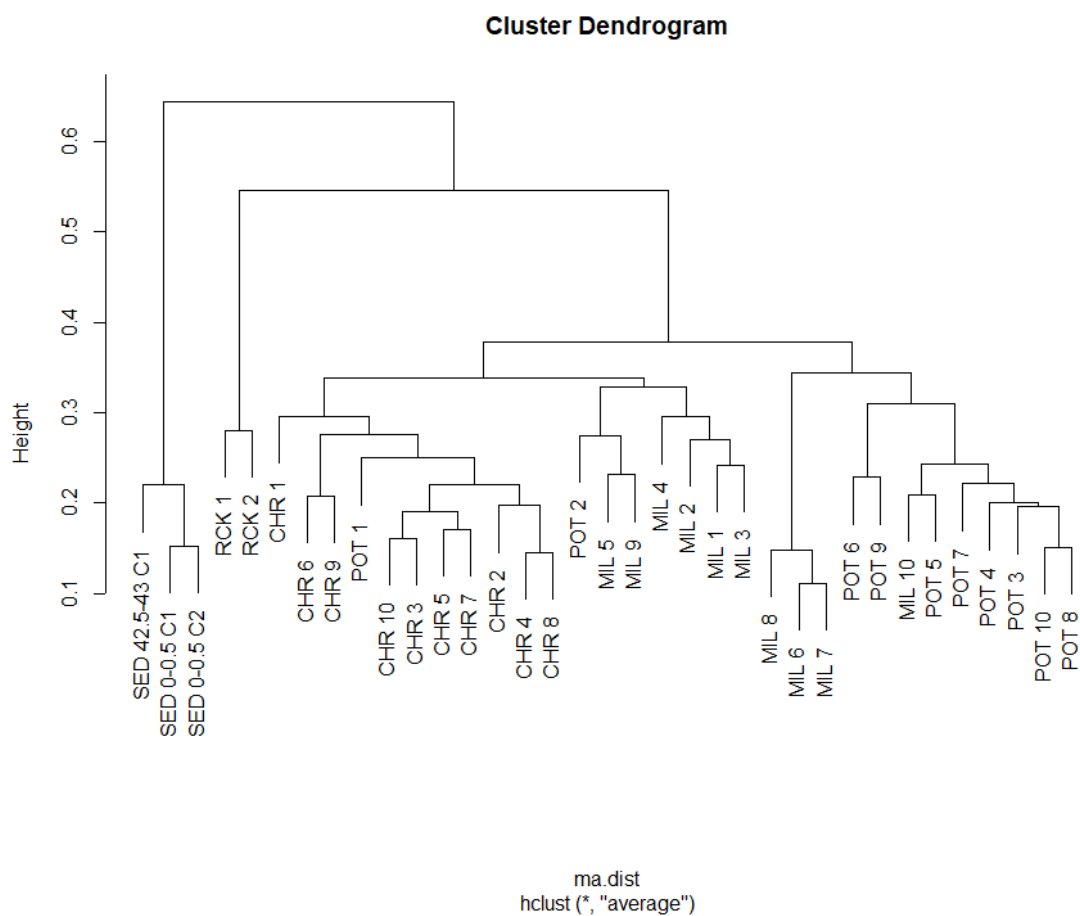


Figure 5.2 Dendrogram depicting the results of average-linking agglomerative hierarchical cluster analysis.

Samples are sequentially merged with their closest neighbouring cluster to form larger clusters. Closest neighbour is determined using the center of each cluster (average). CHR = *Chara*, MIL = *M. spicatum*, POT = *P. robbinsii*, RCK = rock, SED 0-0.5 C1/C2 = Surface Sediment, SED 42.5-43 C1 = Bottom Sediment.

Surface sediment samples were differentiated from all other samples by a much higher relative abundance of *Staurosirella pinnata* (*Chara* mean =  $2.6 \pm 1.8\%$ ; *M. spicatum* mean =  $3.0 \pm 2.1\%$ ; *P. robbinsii* mean =  $2.0 \pm 1.2\%$ ; rock mean =  $1.8 \pm 1.8\%$ ; surface sediment mean =  $34 \pm 0.038\%$ ) and *Staurosira construens* (*Chara* mean =  $1.4 \pm 1.2\%$ ; *M. spicatum* mean =  $2.7 \pm 2.8\%$ ; *P. robbinsii* mean =  $1.2 \pm 0.87\%$ ; surface sediment mean =  $15 \pm 3.4\%$ ). Although the nearshore sediment cores were expected to represent the littoral environment at the time of sampling, the high abundances of *Staurosirella pinnata* and *Staurosira construens*, both generalist epipelagic and epipsammic diatoms (Wilson et al., 1997), indicate these samples are more representative of the sediment environment.

The average diatom species richness differed slightly among modern samples with the greatest species richness observed on *Chara*, *M. spicatum* and in surface sediment (*Chara* mean = 29, *M. spicatum* mean = 29, *P. robbinsii* mean = 25, rock = 23, surface sediment = 29).

## 5.2 Diatom Community Composition of Different Species of Submerged Macrophytes

The ANOSIM that compared all three submerged macrophyte species returned an R statistic of 0.516 ( $P = 0.001$ ) (Figure 5.3). The ANOSIM would return an R statistic near 0 if the diatom communities of submerged macrophyte species were similar; conversely, if the diatom communities were distinct, it would return an R statistic of 1. The R value suggests that there were differences in the diatom community of each submerged macrophyte.

Cluster analysis showed that the diatom communities living on *Chara* were different from the other submerged macrophytes with the exception of one *P. robbinsii* sample (POT 1; Figure 5.2). The PCA results also indicated that the diatom community living on *Chara* was generally distinct from the other two submerged macrophyte species, with the exception of two *P. robbinsii* samples (POT 1 and POT 2, which are discussed further below; Figure 5.4; Figure 5.5). Furthermore, the results of the ANOSIM to assess the

dissimilarity between *Chara* and *M. spicatum* ( $R = 0.542$ ,  $P = 0.001$ ) and between *Chara* and *P. robbinsii* ( $R = 0.677$ ,  $P = 0.001$ ) showed that the diatom community of *Chara* is different from both *M. spicatum* and *P. robbinsii* (Figure 5.6).

Arrows on the PCA represent diatom taxa and the projection of the end of the arrow onto the principal components axis represents the amount that each taxon influences the position of the PCA axes (ter Braak, 1983). Arrows that plot in the same direction represent diatom species with similar distributions. Samples that plot close to the ends of an arrow have higher abundances of the taxa represented by that arrow. The PCA shows that diatom species associated with *Chara* included *Encyonopsis microcephala*, *Rhopalodia gibba*, *Brachysira microcephala*, *Fragilaria crotonesis* and *Encyonopsis lange-bertalotti*. Of those diatom taxa, Figure 5.1 shows that all but *Encyonopsis microcephala* appear infrequently or in low relative abundance; this makes them less suitable for paleolimnological reconstructions so they will not be discussed further. Therefore, the main difference in the diatom community composition of *Chara* is the high relative abundance of *Encyonopsis microcephala* (*Chara* mean =  $17 \pm 3.2\%$ ; *M. spicatum* mean =  $4.1 \pm 2.6\%$ ; *P. robbinsii* mean =  $5.2 \pm 2.5\%$ ) (Figure 5.1).

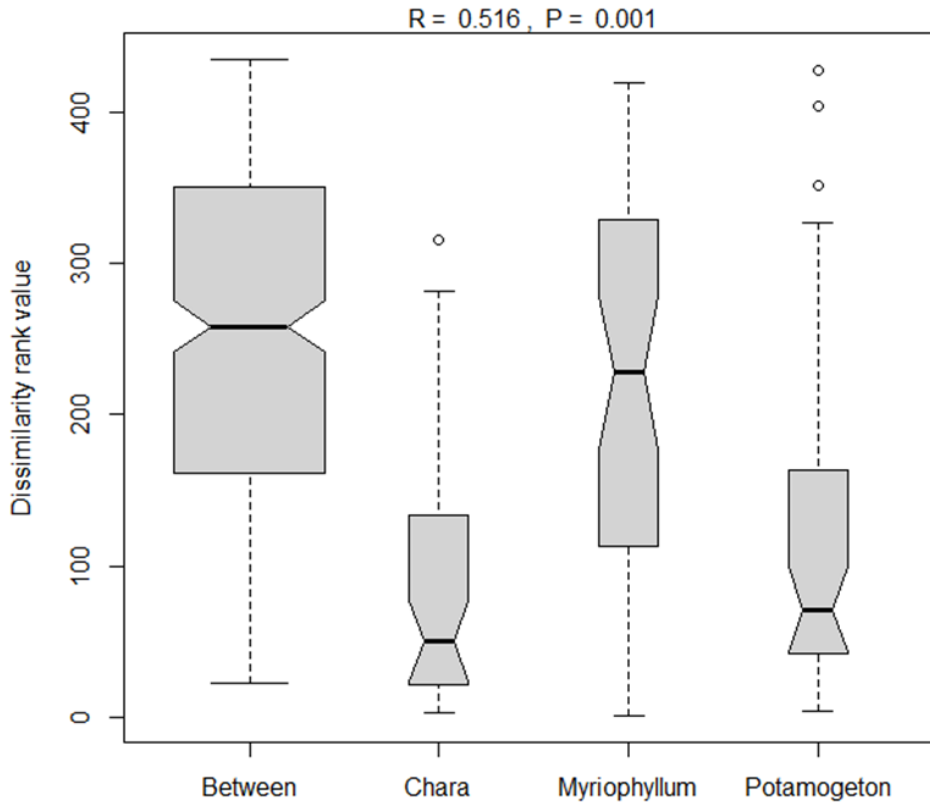


Figure 5.3 Analysis of Similarity (ANOSIM) comparing all submerged macrophytes.

R-value showing dissimilarity among macrophyte species. The bold horizontal bar indicates the median of dissimilarity values; boxes represent the interquartile range between the first and third quartiles (25<sup>th</sup> and 75<sup>th</sup> percentile, respectively); whiskers extend to the most extreme datapoint that is no more than 1.5 times the interquartile range (Q3-Q1); points outside of the whiskers are considered outliers. Chara = *Chara*, Myriophyllum = *M. spicatum*, Potamogeton = *P. robbinsii*.

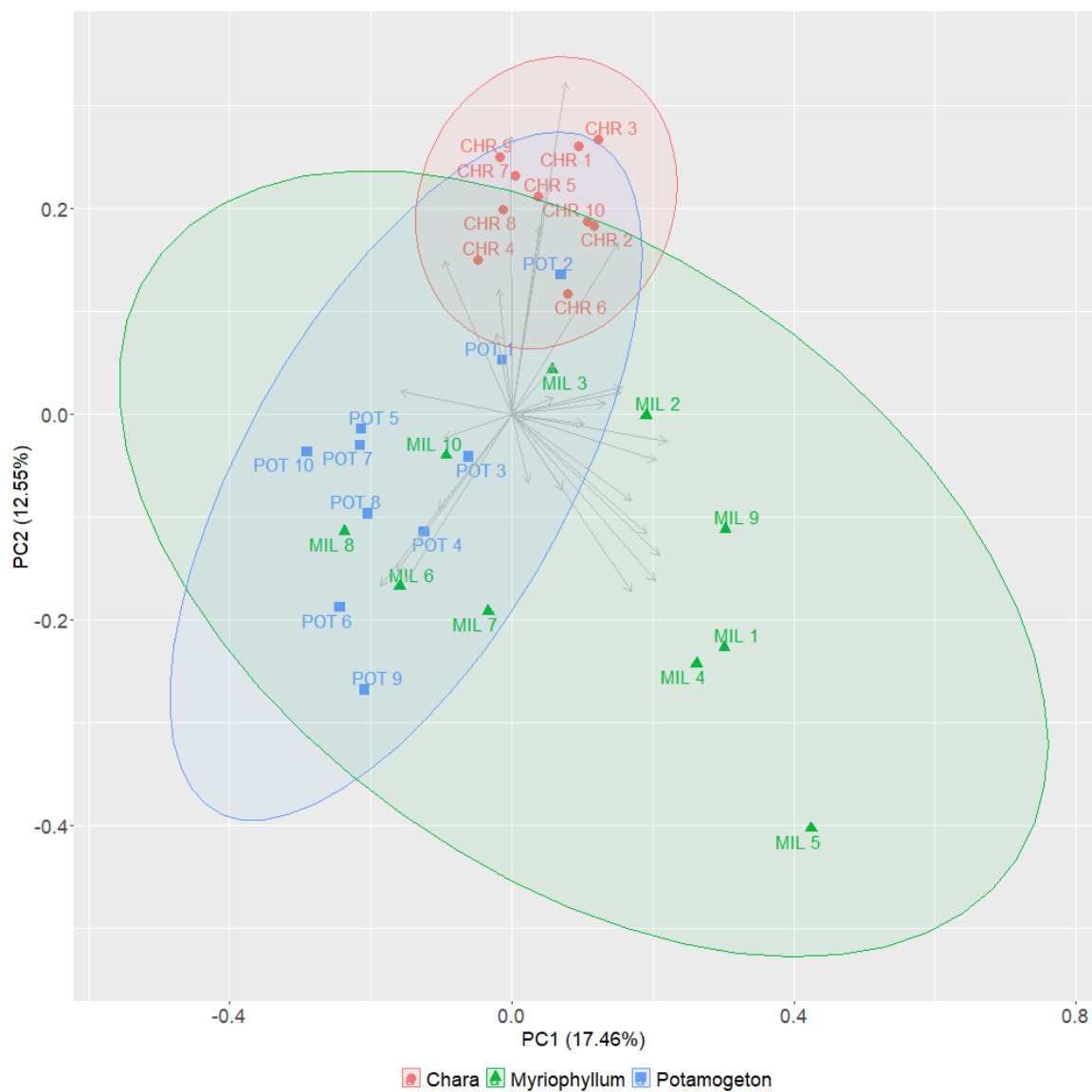


Figure 5.4 Principal components analysis (PCA) of epiphytic diatom assemblages with confidence ellipses.

Points represent diatom samples from different submerged macrophytes. Arrows represent diatom taxa shown in Figure 5.5. Ellipses indicate the 95% confidence ellipses. Chara = CHR = *Chara*, Myriophyllum = MIL = *M. spicatum*, Potamogeton = POT = *P. robbinsii*.

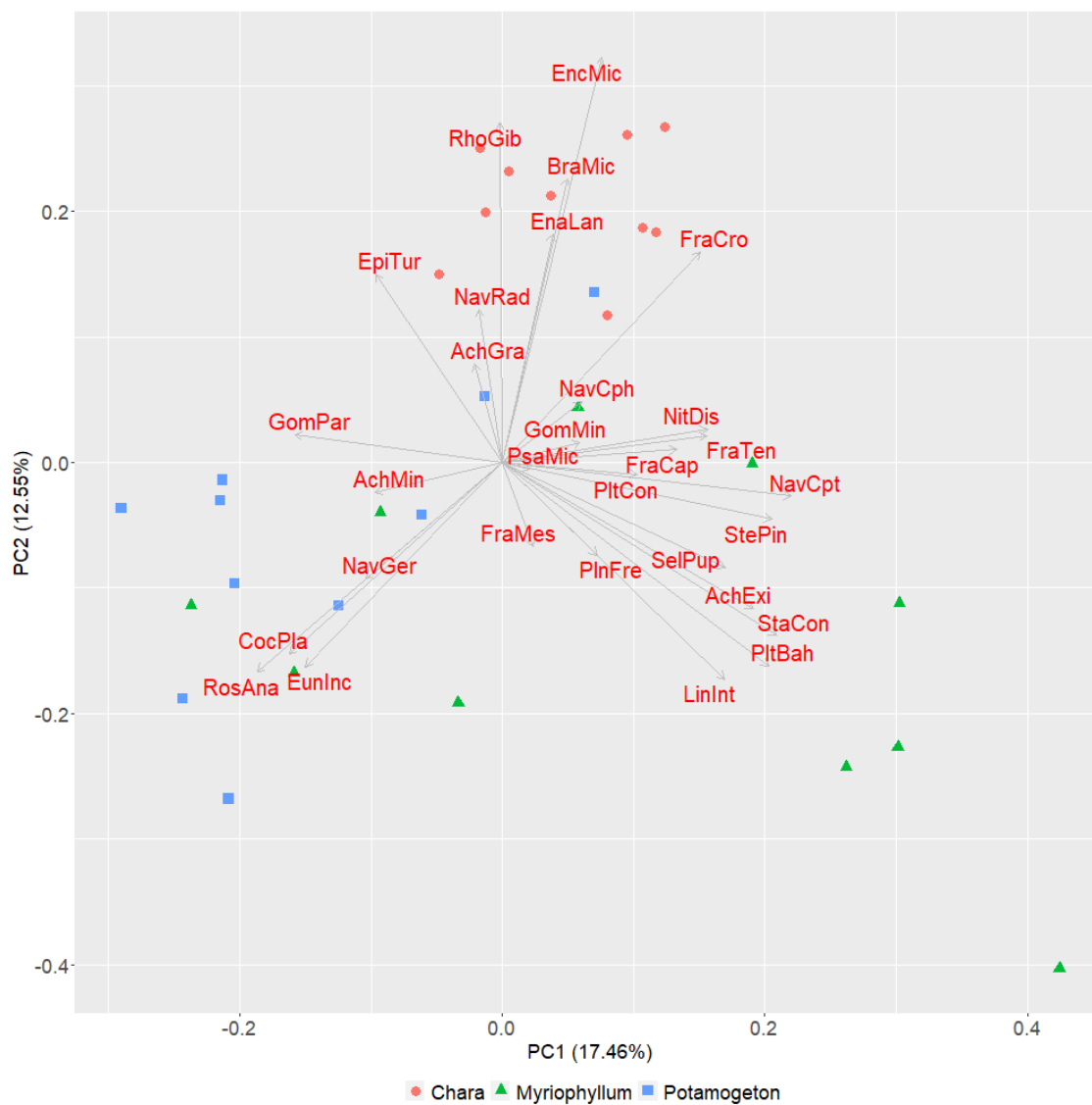


Figure 5.5 Principal components analysis (PCA) of epiphytic diatoms with arrows.

The length of each arrow corresponds to its magnitude of influence to determine the position of the principal components (PC1 and PC2) in multidimensional space. The total variance explained by the two principal components was low (Figure 5.4; PC1 = 17.46%, PC2 = 12.55%). See Table 4.1 for full names of taxa. Note: the scale is different from Figure 5.4 to accommodate the labels for each arrow.



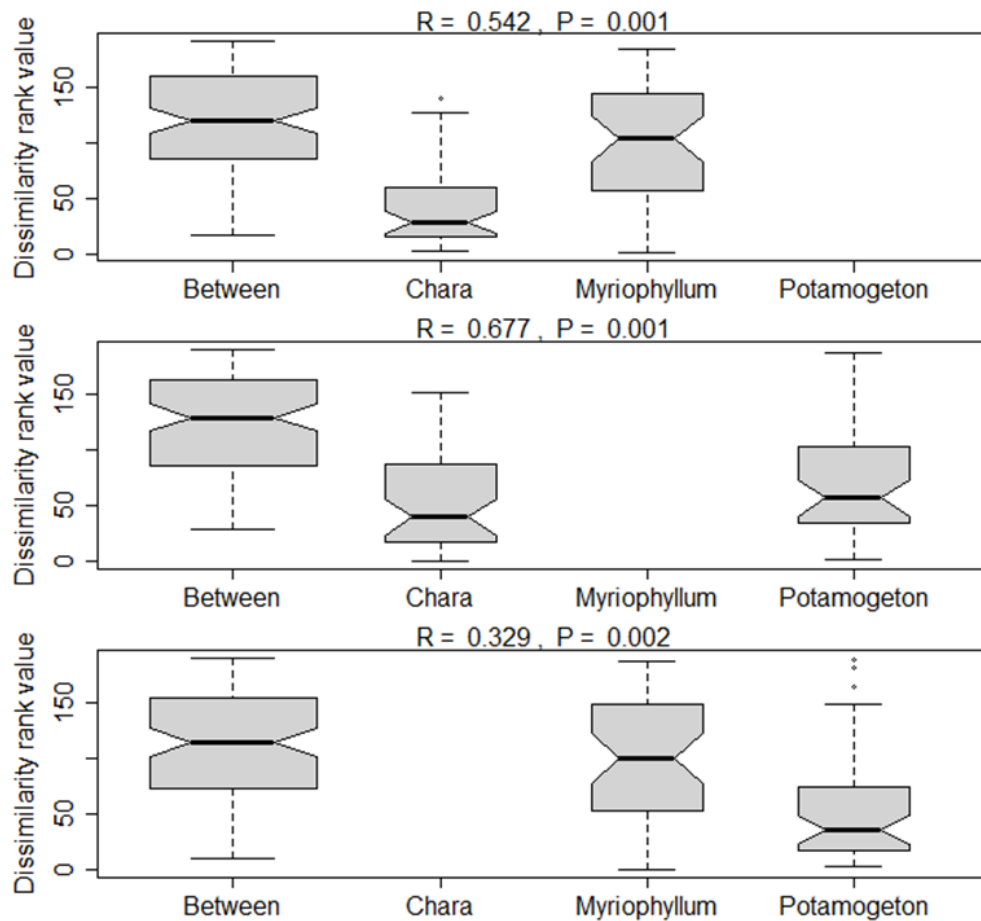


Figure 5.6 Analysis of Similarity (ANOSIM) comparing two macrophyte species per test.

R-value showing dissimilarity between submerged macrophyte species. The bold horizontal bar indicates the median of dissimilarity values; boxes represent the interquartile range between the first and third quartiles (25<sup>th</sup> and 75<sup>th</sup> percentile, respectively); whiskers extend to the most extreme datapoint that is no more than 1.5 times the interquartile range (Q3-Q1); points outside of the whiskers are considered outliers. Chara = *Chara*, Myriophyllum = *M. spicatum*, Potamogeton = *P. robbinsii*.

The PCA showed that *P. robbinsii* samples were less tightly grouped together than *Chara* samples, but still generally positioned together in the lower-left side of the PCA (Figure 5.4). The longest arrows pointing in the direction of the *P. robbinsii* group are *Rossithidium anastasiae*, *Cocconeis placentula*, *Gomphonema parvulum* var. *parvulus* and *Eunotia incisa* (Figure 5.5). However, Figure 5.1 showed that *Cocconeis placentula* was general to all submerged macrophyte species. Figure 5.1 also showed that *Gomphonema parvulum* var. *parvulus* and *Eunotia incisa* appeared infrequently or in low relative abundance, making them unsuitable for paleolimnological reconstruction, so they will not be discussed further. Therefore, *P. robbinsii* was mainly differentiated from the other two species by high abundances of *Rossithidium anastasiae* (*Chara* mean =  $0.44 \pm 0.55\%$ ; *M. spicatum* mean =  $1.8 \pm 1.3\%$ ; *P. robbinsii* mean =  $10 \pm 7.2\%$ ) (Figure 5.1). The two *P. robbinsii* samples that plotted within or close to the *Chara* group (POT 1 and POT 2) had relatively low abundances of *Rossithidium anastasiae* and *Cocconeis placentula* and higher abundances of *Encyonopsis microcephala* compared to the other *P. robbinsii* samples (Figure 5.1).

In terms of diatom community composition, *M. spicatum* samples showed much more variability as evidenced by the larger 95% confidence ellipses for *M. spicatum* (Figure 5.4) and the wide interquartile range of ranked dissimilarity values relative to *Chara* and *P. robbinsii* (Figure 5.6). *M. spicatum* samples lacked any indicator diatom taxa (i.e., a diatom taxon that appeared more frequently and in higher abundance on *M. spicatum* compared to other submerged macrophyte samples) (Figure 5.1). Four *M. spicatum* samples occurred within the *P. robbinsii* group (Figure 5.4). Three of these samples (MIL 6, 7, 8) had high relative abundances of *Cocconeis placentula* (Figure 5.1). Additionally, these three samples had slightly elevated abundances of *Rossithidium anastasiae* compared to other *M. spicatum* samples (Figure 5.1). The final *M. spicatum* sample in the *P. robbinsii* cluster (MIL 10) had a high relative abundance of *Achnanthydium minutissimum* (Figure 5.1); its position is therefore near the *Achnanthydium minutissimum* arrow (Figure 5.5). The remaining *M. spicatum* samples were dispersed, but generally plotted away from the *Chara* and *P. robbinsii* groups, close to the *Achnanthydium exiguum*, *Lindavia intermedia*, *Platessa bahlsi*, and *Staurosira construens* arrows (Figure 5.5). These species appeared infrequently or in low relative abundance in most *M.*

*spicatum* samples, so they will not be discussed further (Figure 5.1). The results of the ANOSIM to assess the dissimilarity between *M. spicatum* and *P. robbinsii* ( $R = 0.329$ ,  $P = 0.001$ ) indicated more overlap between the diatom communities on these macrophytes (Figure 5.6).

### 5.3 Potential Inferences of Past Submerged Macrophyte Habitat from Sediment Core Samples

There were many diatom taxa common to all three submerged macrophyte species. To infer past submerged macrophytes at Gilmour Bay, I made a preliminary attempt to develop a tool that reduces “noise” from the diatom taxa that are common to all submerged macrophytes and enhances the signal from indicator taxa. I focused on *Chara* and *P. robbinsii* because the ANOSIM identified the diatom communities of these macrophytes as the most dissimilar (Figure 5.6) and they each had high abundances of an indicator diatom (Figure 5.1). The indicator diatoms chosen were *Encyonopsis microcephala* for *Chara* and *Rossithidium anastasiae* for *P. robbinsii*. To emphasize the macrophyte diatom habitat rather than other littoral diatom habitats, key diatom taxa were divided by *Cocconeis placentula*, an abundant diatom common to all species of submerged macrophytes in this study (Figure 5.1) and plotted (Figure 5.7). *Chara* samples, which had high abundances of *Encyonopsis microcephala* and low abundances of *Rossithidium anastasiae*, plotted along the x-axis of the plot, whereas *P. robbinsii* samples, which had low abundances of *Encyonopsis microcephala* and high abundances of *Rossithidium anastasiae*, plotted along the y-axis of the plot. *M. spicatum*, which had low abundances of both key diatoms plotted near the origin of the plot.

The same ratios were plotted for surface and historical sediment. The position of the surface sediment samples relative to macrophyte samples indicates modern submerged macrophyte abundance and the position of the historical sediment sample indicates past macrophyte abundance. One modern surface sediment sample contained neither of the key diatoms and therefore plotted at the origin of both plots. The second modern surface sediment sample had a higher ratio for *Rossithidium anastasiae* and a lower ratio for

*Encyonopsis microcephala* and plotted near the *P. robbinsii* samples. This indicates that *P. robbinsii* is present in the modern submerged macrophyte habitat. The historical sample had high ratios of both key diatoms, indicating that both *Chara* and *P. robbinsii* were present.

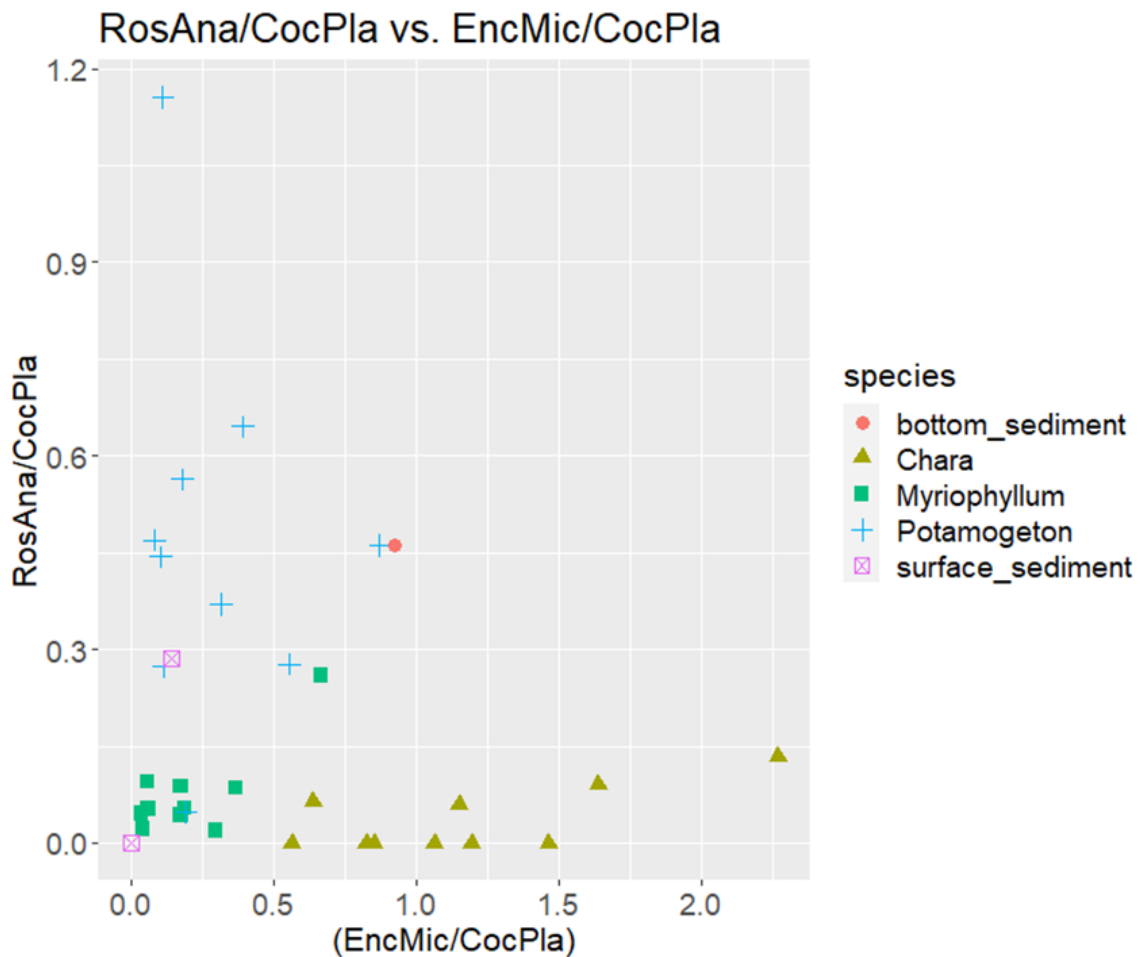


Figure 5.7 Ratio plot of key-to-generalist epiphytic diatoms.

The plot compares key epiphytic taxa (*Rossithidium anastasiae* and *Encyonopsis microcephala*) to the generalist epiphytic taxon *Cocconeis placentula*. The position of sediment samples indicates submerged macrophytes present at time of sediment deposition. If a sediment sample plots near the cluster of *Chara* or *P. robbinsii* samples, it indicates greater relative abundance of that macrophyte at the time of sediment deposition. This figure cannot inform on the presence of *M. spicatum* because it was not characterized by an indicator diatom taxon. See Table 4.1 for full names of taxa.

## 6 DISCUSSION

### 6.1 Is the Epiphytic Diatom Community Composition Distinct for Different Species of Submerged Macrophytes?

Although previous research has shown that it is possible to differentiate diatom community compositions among rocks, filamentous macroalgae, submerged macrophytes, and wood (Reavie & Smol 1997; Vermaire et al., 2011), it was unclear if diatom communities differed among submerged macrophyte species. My research indicates that there are differences in the epiphytic diatom community composition of different submerged macrophytes. Although there are several possibilities to explain these differences, including variations in microhabitat chemistry, allelopathy and leaf architecture, the observed differences are most likely related to alkaline microhabitats created by *Chara* and differences in leaf architectures between broad leaf (*P. robbinsii*) and dissected leaf (*M. spicatum* and *Chara*) macrophytes.

In accordance with the findings of previous research (Douglas & Smol, 1995; Reavie & Smol, 1997; Vermaire et al., 2011), my research indicated that diatom community compositions of submerged macrophytes differed from rocks and sediments. Rocks and sediments are predicted to have distinct diatom community compositions from macrophytes in part due to their increased exposure to wave action (Cantonati & Lowe, 2014; Pla-Rabés & Catalan, 2018) as well as their silica-rich environments (Douglas & Smol, 1995). In my study, diatom taxa such as *Epithemia reichelti* and *Navicula* sp. 1. were exclusively abundant on rock samples, while *Staurosira construens* and *Staurosirella pinnata* were abundant in surface sediment samples. *Staurosira construens* and *Staurosirella pinnata*, both characterized by a thick, highly silicified cell wall and a stout, flexible mucilaginous stalk, may be indicative of greater wind and wave action in areas with less macrophyte cover (Hoffman et al., 2020). The submerged macrophyte species were differentiated from rocks and sediments by a greater abundance of *Cocconeis placentula*, one of the most common generalist epiphytic diatoms in freshwater habitats (Jahn et al., 2009). *Cocconeis placentula* has an opportunistic growth strategy,

increasing in abundance despite high grazing pressure by invertebrates (Blindow, 1987; Underwood & Thomas, 1990). Grazing pressures are stronger on submerged macrophytes relative to floating macrophytes (Meerhoff et al., 2003) and the resistance of *Cocconeis placentula* to such pressures is likely due to its strong, adnate attachment mechanism (Rojas & Hassan, 2017; Underwood & Thomas, 1990).

More importantly, my research showed that the diatom community composition differed among submerged macrophyte species. The diatom community composition of *Chara* was generally distinct from the other submerged macrophyte species by higher abundance of *Encyonopsis microcephala*, which is commonly found in oligo-mesotrophic freshwater systems and is alkaliphilic (i.e., widely distributed in environments with  $\text{pH} > 7$ ) (Battarbee, 1984; Kennedy et al., 2019). The latter could explain its elevated presence on *Chara* samples. Compared to other submerged macrophytes, *Chara* has a superior ability to utilize bicarbonate as a source of carbon dioxide for photosynthesis, which leads to calcium carbonate encrustations on *Chara* when carbonate ions bind with calcium ions in solution (Kufel et al., 2016; Van den Berg et al., 2002). The process by which this occurs is complex and may be explained by either *cis* or *trans* models, as described by McConnaughey & Whelan (1997). In *cis* calcification, photosynthetic bicarbonate uptake releases hydroxide, which alkalizes the water surrounding *Chara* (McConnaughey & Whelan, 1997); in *trans* calcification, enzymes drive the exchange of calcium and hydrogen ions, creating alternating zones of acidic and alkaline conditions (McConnaughey & Whelan, 1997). A high degree of calcification is considered an indicator of the *trans* calcification model (Pukacz et al., 2014). *Chara* samples from Gilmour Bay were lacking extensive calcium carbonate encrustations upon inspection during field sampling and laboratory analysis. Therefore, the lack of a high degree of calcification on *Chara* samples suggests a “*cis*” physiology is more likely. In either case, the process creates an alkaline microhabitat on at least part of the macrophyte, which, in combination with the oligo-mesotrophic status of Gilmour Bay, explains the elevated presence of *Encyonopsis microcephala* on *Chara*. Depending on how far the alkaline zones created by *Chara* extend from the macrophyte, the zones could also alter the chemistry of nearby plants. Although I did not record the location of individual plant sample collection locations, an expanded alkaline zone around *Chara* individuals could

alter the water chemistry around other nearby submerged macrophytes and explain why two *P. robbinsii* samples (POT 1 and POT 2) had diatom community compositions similar to *Chara*. Another explanation for the similarity among POT 1 and POT 2 and *Chara* is that *Potamogeton* species are also calcareous aquatic plants (Prins et al., 1982). *Chara*'s superior ability to utilize bicarbonate for photosynthesis (Van den Berg et al., 2002) and *Potamogeton*'s tendency to shed calcium carbonate encrustations (McConnaughey & Whelan, 1997) would support the overlap only being present in some samples. Further research is necessary to determine the exact cause of the similarities between *Chara* and some of the *P. robbinsii* samples in this study.

Another possibility to explain differences in diatom communities of the different plant species is allelopathy. Allelochemicals from *Chara* have been shown to inhibit the growth of the diatom *Nitzschia palea* in laboratory settings (Wium-Andersen et al., 1982). However, whether these allelochemicals are produced in large enough quantities to inhibit diatom growth in natural systems is unclear. Studies have found abundant *Nitzschia palea* growth on *Chara* spp. in natural systems with no observed allelopathic effect on epiphytic diatom communities (Berger & Schagerl, 2004). Unfortunately, it cannot be evaluated whether the inhibition of *Nitzschia palea* was observed in *Chara* samples from Gilmour Bay since *Nitzschia palea* was not found in my samples from any substrate in Gilmour Bay. *Nitzschia palea* growth responds positively to nutrient enrichment (Marks & Power, 2001), and since Gilmour Bay is oligo-mesotrophic, it is likely the nutrient concentrations are not high enough to support *Nitzschia palea* growth.

Studies have also shown that *M. spicatum* produces allelopathic algicidal polyphenols that inhibit diatom microalgal enzymes (Gross & Sütfield, 1994; Leu et al., 2002).

Furthermore, in their review paper, Hilt & Gross (2008) ranked *M. spicatum* as a macrophyte with higher allelopathic potential than *Chara* spp. (medium allelopathic potential) and *Potamogeton* spp. (low, if any, allelopathic potential). Increased allelopathic activity would support the finding that key diatoms which differentiated *Chara* and *P. robbinsii* are not present on *M. spicatum*, while tolerant, generalist taxa (e.g., *Achnantheidium minutissimum* and *Cocconeis placentula*) are able to withstand these conditions, and therefore are present and abundant on all macrophytes in Gilmour Bay



(Jahn et al., 2009; Potapova & Hamilton, 2007). This could also explain why *M. spicatum* does not have an indicator diatom which differentiates its diatom community from that of the other submerged macrophytes. However, other research has indicated that epiphytic algae directly attached to *M. spicatum* have developed resistances to its allelopathic effects and are not as vulnerable as planktonic species (Hilt, 2006). Additionally, the average species richness of *M. spicatum* was the same as *Chara* (mean = 29) and both were greater than *P. robbinsii* (mean = 25) suggesting diatom species are not being reduced by the greater allelopathy of *M. spicatum*. It appears, therefore, unlikely that allelopathy is mainly responsible for the observed differences in the epiphytic diatom communities of different submerged macrophytes. Another possibility to explain the differences in epiphytic diatom community composition observed in my study are variations in leaf architecture.

Leaf architecture may affect diatom community composition by affecting the movement and speed of water around the submerged macrophyte (Laugaste & Reunanen, 2005; Suren et al., 2000). Finely dissected leaf architecture slows the movement of water around the leaves, thereby protecting epiphytes (Knapp & Lowe, 2009; Suren et al., 2000); conversely, a broad leaf architecture increases epiphyte exposure to wave action and currents. The leaf architecture of the macrophytes in this study were different. *M. spicatum* has finely dissected leaves while *P. robbinsii* has a more broad leaf architecture (Aiken et al., 1979; Chambers et al., 2008); as a macroalgae, *Chara* has branchlets of multinucleate cells that resemble dissected leaves, though not as fine as *M. spicatum* (Chambers et al., 2008).

The diatom community living on the broad leaf *P. robbinsii* was generally characterized by a higher abundance of *Rossithidium anastasiae*. Although it has been found primarily in oligo-mesotrophic, cold-water systems (e.g., Rocky Mountain lakes), *Rossithidium anastasiae* has been identified in fossil diatom records from a southern Ontario lake as *Rossithidium linearis*, a synonym for *Rossithidium anastasiae* (Potapova, 2012; Watchorn et al., 2008). One study (McGowan et al., 2018) identified *Rossithidium linearis* (i.e., *Rossithidium anastasiae*) as having prostrate attachment to rock samples, meaning one valve face of the diatom is attached to a surface by mucilage (Spaulding et al., 2020).

This attachment mechanism is relatively strong and would explain the presence of *Rossithidium anastasiae* on a broad leafed macrophyte with less shielding from currents and wave action than a finely dissected macrophyte. The broad leaves of *P. robbinsii* and lower average species richness of its diatom community supports this hypothesis and suggests that leaf architecture affects epiphytic diatom communities.

In addition to the protection from currents and wave-action offered by dissected leaves, leaf architectures may further impact epiphytic diatom community composition by some diatoms having microdistributional preferences for the edges of leaves (Cattaneo, 1978). The reason for this preference is not clear, but it was observed on both artificial and natural macrophytes, suggesting the advantage is physical, not biological, and may be linked to light availability or nutrient availability (Cattaneo, 1978). As a result of this preference, differences in the proportion of leaf edges to overall surface area among species of submerged macrophytes with different leaf architectures may contribute to differences in their diatom community compositions. One of the diatoms that had a preference for leaf edges was *Cocconeis placentula* (Cattaneo, 1978). *Cocconeis placentula* had a higher relative abundance on *M. spicatum*, which has a high proportion of its surface area as edges due to its finely dissected leaves, which may explain the higher relative abundances of this diatom on this macrophyte. Unfortunately, studies which consider the *in situ* spatial distribution of epiphytic diatoms are lacking and remains an area of future research that could improve our understanding of epiphytic diatom substrate specificity.

To separate the effects of leaf architecture from potential allelopathic effects, studies have used artificial macrophytes to simulate different growth forms of submerged macrophytes. One such study compared the epiphytes growing on three different artificial leaf growth forms; broad, dissected, and floating leaf architecture (Hinojosa-Garro et al., 2010). Although the findings from this research indicated that the diatom community of the floating macrophytes were most distinct, there were also differences between the broad and dissected leaf diatom community composition (Hinojosa-Garro et al., 2010). However, despite leaf architecture appearing to be an important factor in determining the epiphytic diatom community of submerged macrophytes, studies which utilize artificial

macrophytes to study the phenomenon may not be a complete substitute for natural macrophytes. Mesocosm experiments have indicated that diatom communities differ between artificial macrophytes and the natural macrophytes they are designed to simulate (Hao et al., 2017), so laboratory studies that isolate and observe the effects of morphology or allelopathy in shaping the epiphytic diatom community may not accurately represent natural systems. Decoupling the effects of leaf architecture and allelopathy in natural systems using natural macrophytes to confirm their relative importance in shaping epiphytic diatom communities remains an area of future research. Despite this gap in diatom ecology knowledge, the observed differences in epiphytic diatoms among species of submerged macrophytes may still be applied to fossil diatoms preserved in sediment cores to infer historical submerged macrophyte communities.

## **6.2 Is it Possible to Infer Submerged Macrophyte Community Composition using Fossil Diatoms?**

The results of the qualitative reconstruction of submerged macrophyte habitat availability indicated that the modern submerged macrophyte community was mainly comprised of *P. robbinsii*, while historical conditions were a mix of *P. robbinsii* and *Chara*. Considered alone, this might indicate that *Chara* was historically more abundant in Gilmour Bay. However, we know that the current submerged macrophyte community at Gilmour Bay includes *Chara*, so it is surprising that its key diatom, *Encyonopsis microcephala*, is not more abundant in the modern surface sediments. Furthermore, one of the modern sediment samples contained neither *Encyonopsis microcephala* or *Rossithidium anastasiae*, which would suggest that neither *P. robbinsii* nor *Chara* are present in the modern nearshore environment. However, direct observation indicates that both macrophytes are present. The reason that *Encyonopsis microcephala* and *Rossithidium anastasiae* are absent from the sediment samples could be the result of the sediment sampling location. If neither *P. robbinsii* nor *Chara* were located proximal to the sediment core sampling site, the diatoms associated with these submerged macrophytes may not be preserved in the sediments at the coring location. Variability in the epiphytic

diatom assemblages preserved in sediments collected from different locations should be examined by using an improved sampling design that includes a greater number of surface sediment samples to test how representative different coring locations are of the submerged macrophyte community.

The coring site location issue may be compounded by the nearshore coring location not capturing a strong epiphytic diatom signal. The epipelagic and epipsammic diatoms, *Staurosira construens* and *Staurosirella pinnata*, were highly abundant in both modern and historical sediment samples (Stoermer, 1981; Winter et al., 2000), and the relative abundance of *Encyonopsis microcephala* and *Rossithidium anastasiae* was therefore low, supporting the hypothesis that the coring location did not capture a strong epiphytic diatom signal. Coring location may be critical to tracking changes in submerged macrophyte communities and is discussed further in Chapter 6.3.

One of the challenges presented in past studies that sought to use epiphytic fossil diatom assemblages to track changes in the submerged macrophyte community is the lower abundances of littoral diatoms in deep water cores, especially in eutrophic systems (Vermaire et al., 2011). Planktonic diatom taxa are more abundant than littoral taxa in deeper, dimictic lakes, indicating that lake depth also impacts the relative abundance of littoral diatom taxa preserved in offshore sediment cores (Werner & Smol; 2005). In a lake in northwestern Ontario, Moos et al. (2005) collected a transect of surface sediment samples from depths ranging between 2 to 30 m; their findings indicated that diatom assemblages shifted to predominately planktonic taxa at depths greater than 8 m. I attempted to emphasize littoral diatom communities in the sediment record by obtaining a sediment core from ~3 m depth intending to capture a diatom signal of the submerged macrophyte community.

As expected, the sediment core taken from the nearshore environment did not have an abundance of planktonic diatom taxa. However, the introduction of signal dilution from epipelagic and epipsammic taxa was unexpected. A recent study has identified distinct diatom community zones: a shallow littoral zone hosting mainly epiphytic and epilithic species and a deeper littoral zone hosting mainly epipelagic and epipsammic taxa (Hofmann et al., 2020). Hofmann et al. (2020) indicated that sediment cores taken from light-

flooded depths are dominated by *in situ* epipellic and episammic species; if light was able to reach the sediment, the 3 m coring depth in Gilmour Bay was part of the deeper littoral zone which explains why the samples were dominated by epipellic and epipsammic diatom taxa. Although Secchi depth was 2.5 m when nearshore cores were collected in May 2019 (Table 3.1), future Secchi measurements were deeper and suggest light-flooded depths at the coring location were likely. Therefore, I expect a better coring location to capture changes in the submerged macrophyte community would be shallower than I cored for this research. However, regardless of the coring location, more surface sediment samples should be included to reduce the effect of sampling variability.

### **6.3 Proposed Improvements to This Study and Areas of Future Research**

Before taking further steps to improve our ability to track submerged macrophytes using epiphytic diatoms, determining the best coring location is critical. A sediment core that contains the best possible representation of epiphytic diatoms allows for the proper evaluation of whether the indices I have developed allow for the reconstruction of submerged macrophyte community composition. As identified by Hofmann et al. (2020), a coring location from the shallow littoral zone that is dominated by epiphytic and epilithic diatom taxa may alleviate the issue of epipellic and epipsammic diatoms dominating the samples. The core, therefore, should be taken from a shallower water depth where the epiphytic diatom signal is amplified, but not so shallow that wave action disturbs the sediment. It would be useful to follow Moos et al. (2005) and use a transect of sediment samples perpendicular to the shoreline to locate the best coring location to track changes in submerged macrophyte community composition. In this scenario, depth-constrained cluster analysis could be used, similarly to the methods employed by Hofmann et al. (2020), to separate nearshore diatom community-zones and identify the most appropriate location to take a core designed to reconstruct submerged macrophyte community composition. This step is crucial prior to seeking improvement of the indices themselves.

To improve the diatom indices and expand the applicability of this method to include more macrophyte species, it is important to gain a better understanding of what controls diatom distributions on submerged macrophytes. To do this, it would help to collect samples of all submerged macrophytes present, not just those which appear most abundant. This would ensure that the key diatom taxa identified in this study are truly representative of their associated submerged macrophyte. In Gilmour Bay, two additional *Potamogeton* species (*P. pectinatus* and *P. zosteriformis*) were identified at the time of sampling. Since *Potamogeton* species appear to have a lower allelopathic potential than other macrophytes (Hilt & Gross, 2008) and not all *Potamogeton* spp. have the same growth form, collecting all *Potamogeton* species will help clarify the role of leaf architecture in determining epiphytic diatom community composition relative to allelopathic activity.

Continued investigation of the differences in epiphytic diatoms associated with charophytes compared to higher order submerged macrophytes is warranted. Since *Chara* has a unique ability to overwinter and store nutrients in plant biomass (Kufel & Kufel, 2002), a change in its abundance may affect nutrient loads and is therefore of interest to lake managers. Furthermore, the loss of *Chara* populations and replacement with higher order macrophytes is a consequence of eutrophication (Ozimek & Kowalczewski, 1984), so studies of anthropogenic disturbances may benefit from further investigation of *Chara* epiphytes. An example of such a transition in macrophyte community between a higher order macrophyte and a charophyte where such a study could be useful is nearby Lake Scugog (Scugog Lake Stewards Inc., 2015; Harrow-Lyle & Kirkwood, 2020).

Seasonal sampling is thought to be less important in determining epiphytic diatom community composition than the nature of the host macrophyte (Majewska et al., 2013), but multiple sampling events might help emphasize the subtle differences in diatom communities among different submerged macrophytes. Seasonal variations in major environmental gradients (e.g., temperature, dissolved oxygen, water level) are thought to affect epiphytic diatom colonization (Öterler, 2018), so multiple sampling events may therefore highlight distinctions in diatom community composition among submerged macrophytes not captured by the single sampling event used for my research. Based on

other studies of epiphytic algae, monthly sampling would be appropriate (e.g., Öterler, 2017, Öterler, 2018; Tunca et al., 2014), but even capturing a spring, summer, and fall sample would improve the results and the potential applications for reconstructing submerged macrophyte community composition.

## 7 CONCLUSION

The research presented in this thesis agrees with the findings of previous studies that the diatom community composition of submerged macrophytes are distinct from those of rocks and sediments. Although past nearshore habitat studies grouped submerged macrophyte species together, citing no significant interspecies differences in epiphytic diatom community composition, the findings presented here suggest otherwise. The submerged macrophytes considered in this study had broad (*P. robbinsii*) or dissected (*M. spicatum*, *Chara*) leaf architectures, which appears important in determining differences among submerged macrophyte diatom communities. *P. robbinsii* was generally characterized by high abundances of *Rossithidium anastasiae*, a diatom with a relatively strong prostrate attachment mechanism that is well suited to the greater wave action associated with the broad leaf architecture of *P. robbinsii*. The lower average diatom species richness for *P. robbinsii* relative to *Chara* and *M. spicatum* further support the hypothesis that leaf architecture is important in determining the epiphytic diatom community.

A second important factor in determining the epiphytic diatom community is the water chemistry immediately surrounding the macrophyte. *Chara* was best distinguished from the other submerged macrophytes by consistently high abundances of *Encyonopsis microcephala*, an alkaliphilic diatom, attributed to the more alkaline microhabitat commonly found on *Chara* due to its calcium carbonate encrustations.

Although allelopathy was also considered as a factor affecting epiphytic diatom community of submerged macrophytes, evidence that evaluates this factor was not collected. Decoupling the effects of leaf architecture and allelopathy to confirm their relative importance in shaping epiphytic diatom communities remains an area of future research.

The differences in epiphytic diatom communities reported here may prove useful for reconstructions of the presence or absence of macrophyte species from nearshore sediment cores. Importantly, this would add to the available paleolimnological methods for lakes with similar limnological conditions to Gilmour Bay and create a basis for



developing one in those with different limnological conditions. A key next step to developing this method is to identify an appropriate nearshore coring location which avoids *in situ* epipelagic and epipsammic diatom growth by taking a transect of nearshore cores perpendicular to the shoreline. An improved understanding of how submerged macrophyte communities have changed in response to local and global stressors is crucial as we work collectively to manage the effects of such stressors on natural systems.

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## APPENDICES

### Appendix A. Copyright Permissions

Letter from Karen VanKerkoerle giving permission for Figures 3.1, 4.1.

#### David Rawn Zilkey

---

**From:** Karen Vankerkoerle  
**Sent:** January 11, 2021 11:04 AM  
**To:** David Rawn Zilkey  
**Subject:** Re: Permission to Use Copyright Material in a Master's Thesis

Dear Mr. Zilkey,

You have my permission to include "Map illustrating the location of Chandos Lake in Ontario, Canada" and "Bathymetric map indicating Gilmour Bay sampling locations" illustrations in the publication of your thesis entitled, "An Investigation of Epiphytic Diatoms for Reconstructing Historical Changes in Submerged Macrophyte Communities in Gilmour Bay, Chandos Lake, Ontario, Canada".

Karen VanKerkoerle  
 January 11, 2021



**Karen Van Kerkoerle**  
 Cartographic Specialist  
 Department of Geography and Environment  
 Western University



*Western University sits on the traditional territory of the Attawandaran, Anishinaabe, Haudenosaunee, and Leni-Lunaape Peoples.*

---

**From:** David Rawn Zilkey [REDACTED]  
**Sent:** January 11, 2021 10:56 AM [REDACTED]  
**To:** Karen Vankerkoerle [REDACTED]  
**Subject:** Permission to Use Copyright Material in a Master's Thesis

Date: January 11, 2021  
 Re: Permission to Use Copyright Material in a Master's Thesis

Dear Ms. VanKerkoerle,

I am a University of Western Ontario graduate student completing my Master's thesis entitled: "An Investigation of Epiphytic Diatoms for Reconstructing Historical Changes in Submerged Macrophyte Communities in Gilmour Bay, Chandos Lake, Ontario, Canada". My thesis will be available in full-text on the internet for reference, study, and/or copy. Except in situations where a thesis is under embargo or restriction, the electronic version will be accessible through the Western Libraries web pages, the Library's web catalogue, and also through web search engines. I will also be granting

Library and Archives Canada and ProQuest/UMI a non-exclusive license to reproduce, loan, distribute, or sell single copies of my thesis by any means and in any form or format. These rights will in no way restrict republication of the material in any other form by you or by others authorized by you.

I would like permission to allow inclusion of the following material in my thesis: "Map illustrating the location of Chandos Lake in Ontario, Canada" and "Bathymetric map indicating Gilmour Bay sampling locations", produced by yourself for the Department of Geography and Environment at Western University.

The material will be attributed through a citation.

Please confirm in writing or by email that these arrangements meet with your approval.

Sincerely,

David Zilkey

## Letter from Kelly Hollingshead giving permission for Table 3.2 and Figure 3.2

**RE: Permission to Use Copyrighted Material in a Master's Thesis**

Kelly Hollingshead [REDACTED]

Fri 2020-12-11 3:31 PM

**To:** David Rawn Zilkey [REDACTED]

Hi David,

Thanks for reaching out. You have my permission to use the table and figures identified in this email so long as they are referenced.

All the best,

Kelly

---

**From:** David Rawn Zilkey [REDACTED]**Sent:** December 11, 2020 12:14 PM**To:** Kelly Hollingshead [REDACTED]**Subject:** Permission to Use Copyrighted Material in a Master's Thesis

Date: December 11, 2020

Re: Permission to Use Copyright Material in a Master's Thesis

Dear Ms. Hollingshead,

I am a University of Western Ontario graduate student completing my Master's thesis entitled: "An Investigation of Epiphytic Diatoms for Reconstructing Historical Changes in Submerged Macrophyte Communities in Gilmour Bay, Chandos Lake, Ontario, Canada". My thesis will be available in full-text on the internet for reference, study, and/or copy. Except in situations where a thesis is under embargo or restriction, the electronic version will be accessible through the Western Libraries web pages, the Library's web catalogue, and also through web search engines. I will also be granting Library and Archives Canada and ProQuest/UMI a non-exclusive license to reproduce, loan, distribute, or sell single copies of my thesis by any means and in any form or format. These rights will in no way restrict republication of the material in any other form by you or by others authorized by you.

I would like permission to allow inclusion of the following material in my thesis: Table 4, Figure 6, and Figure 7 C from your report titled "Paleolimnological investigation of South Bay and Gilmour Bay, Chandos Lake, Ontario", published June, 2017 on [www.chandossier.com](http://www.chandossier.com), retrieved from <https://chandossier.files.wordpress.com/2016/12/kellys-final-report-june-23-2017.pdf>.

The material will be attributed through a citation.

Please confirm in writing or by email that these arrangements meet with your approval.

Sincerely,

David Zilkey

Excerpt from Report of Water Quality in Chandos Lake (1972) on use of material from the report presented in Appendix C

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## **Appendix B. Gilmour Bay Water Quality Measurements**

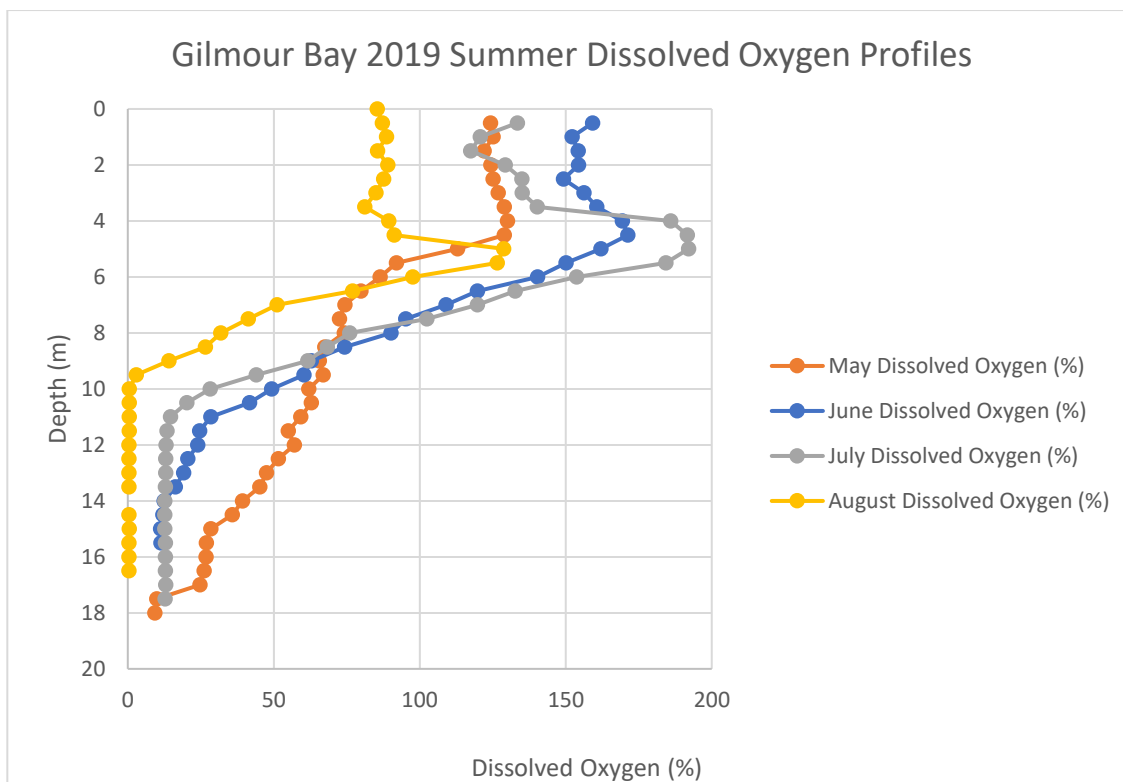
Limnological variables were measured and water samples collected four times between May and August 2019. The purpose of collecting these data was to confirm Gilmour Bay's current trophic status and water chemistry. Offshore limnological measurements (Figure 4.1) and water samples were obtained from the same location as the Lake Partner Program for easier comparison with past measurements (MOECP, 2020). Nearshore limnological measurements and water samples were collected from the nearshore sediment coring location (Figure 4.1). A YSI® ProPlus (YSI Incorporated, Yellow Springs, OH, USA) was used at the offshore site to collect a monthly water column profile of temperature, pH, specific conductance, and dissolved oxygen at 0.5 m increments from water surface to sediment. Samples were collected in pre-cleaned 1 L polyethylene bottles following three rinses with sample water. Samples were immediately filtered on-site and kept in a cool, dark environment until their analysis at the Dorset Environmental Science Centre (DESC) of the Ministry of Environment, Conservation and Parks (MOECP). Samples were refrigerated until analysis and arrived at DESC within 48 hours of collection.



Limnological characteristics of Gilmour Bay. “E” represents epilimnion measurements, “H” represents hypolimnion measurements. Samples collected by David Zilkey.

Laboratory analysis completed at Dorset Environmental Science Centre.

<b>Limnological Variable</b>	<b>May 30, 2019</b>		<b>June 23, 2019</b>		<b>July 29, 2019</b>		<b>August 31, 2019</b>	
	<b>E</b>	<b>H</b>	<b>E</b>	<b>H</b>	<b>E</b>	<b>H</b>	<b>E</b>	<b>H</b>
Dissolved Inorganic Carbon (DIC) (mg/L)	11.2	13.4	11.7	12.9	11.4	13.8	13.0	19.1
Dissolved Organic Carbon (DIC) (mg/L)	1.7	4.5	5.1	4.6	4.9	4.7	4.2	4.7
Sodium (mg/L)	9.11	11.7	7.92	9.51	6.95	9.41	7.33	9.74
Magnesium (mg/L)	1.49	1.59	1.51	1.57	1.36	1.46	1.42	1.54
Iron ( $\mu\text{g/L}$ )	30	40	30	70	30	310	20	1150
Manganese ( $\mu\text{g/L}$ )	9.6	102	12.4	126	7.7	553	9.6	893

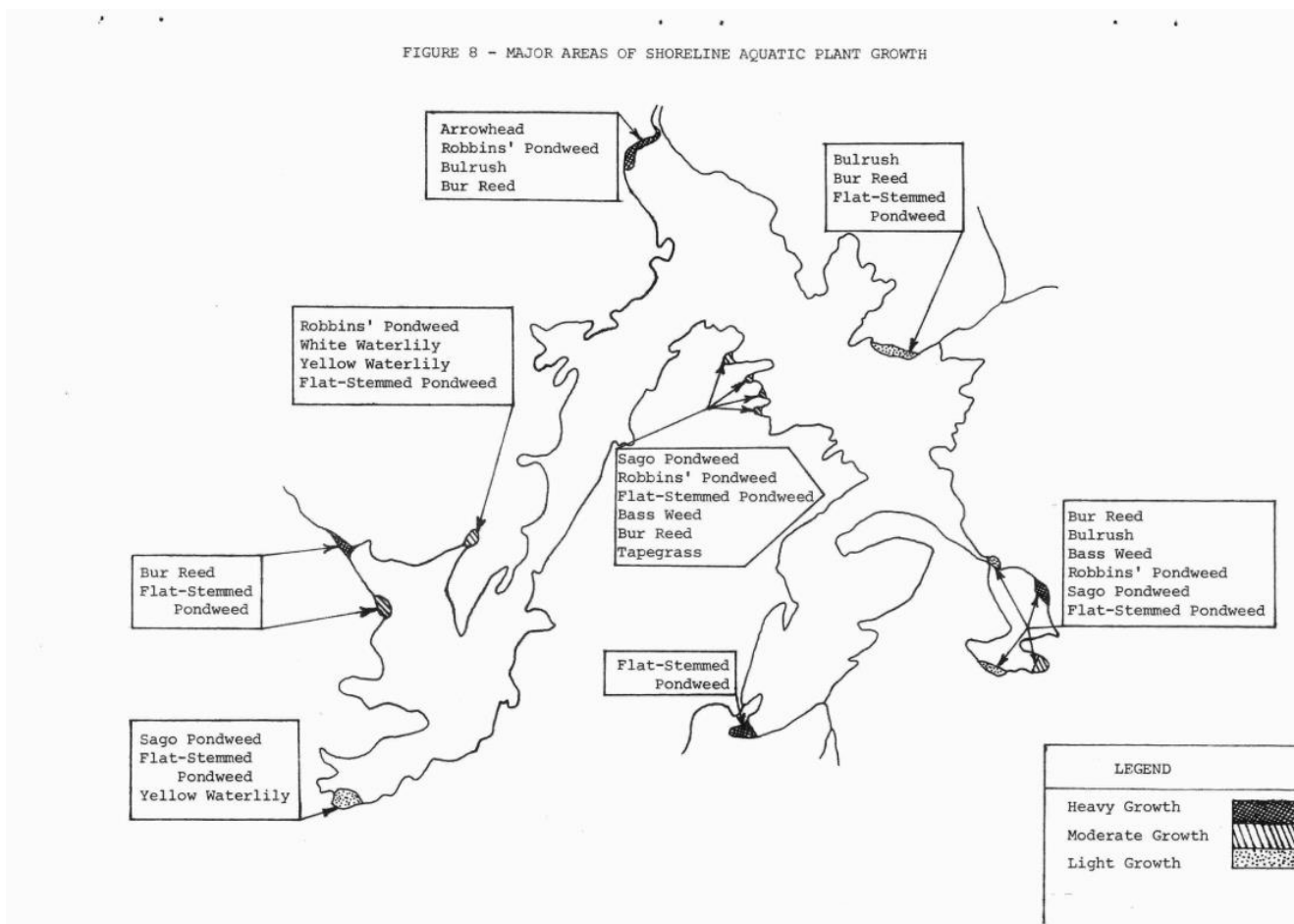


Gilmour Bay 2019 summer dissolved oxygen profiles (% air-saturated water). Profiles collected by David Zilkey. Note: In May 2019, the dissolved oxygen probe was submerged in sediment for the final two measurements (Depth = 17.5 m and Depth = 18.0 m)

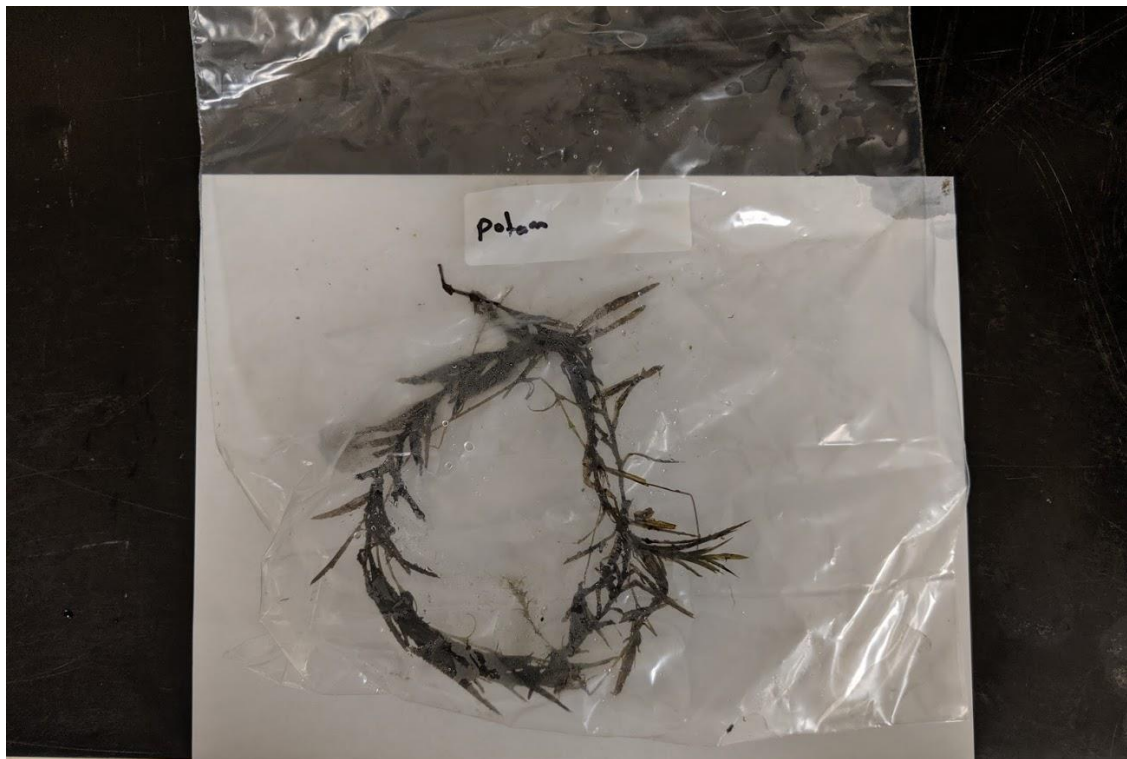
### **Appendix C. Ontario Ministry of Environment (1972) Aquatic Plant Survey of Chandos Lake**

The aquatic plant survey conducted by the Ministry of Environment (1972) is included as a reference for identifying macrophyte rich areas in Chandos Lake and Gilmour Bay. This map does not include every species identified, only those which appeared most abundant at the time of sampling. The biomass or relative abundance of macrophyte species were not included in the report.

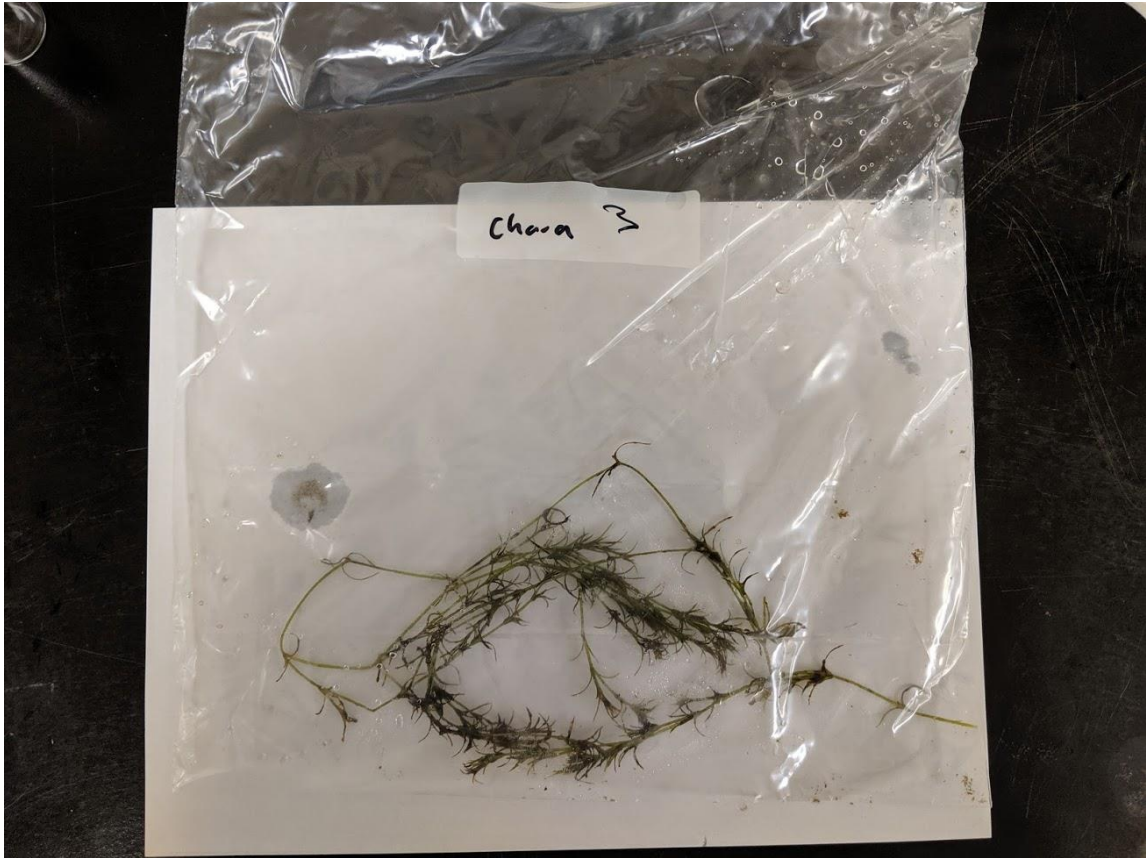
FIGURE 8 - MAJOR AREAS OF SHORELINE AQUATIC PLANT GROWTH



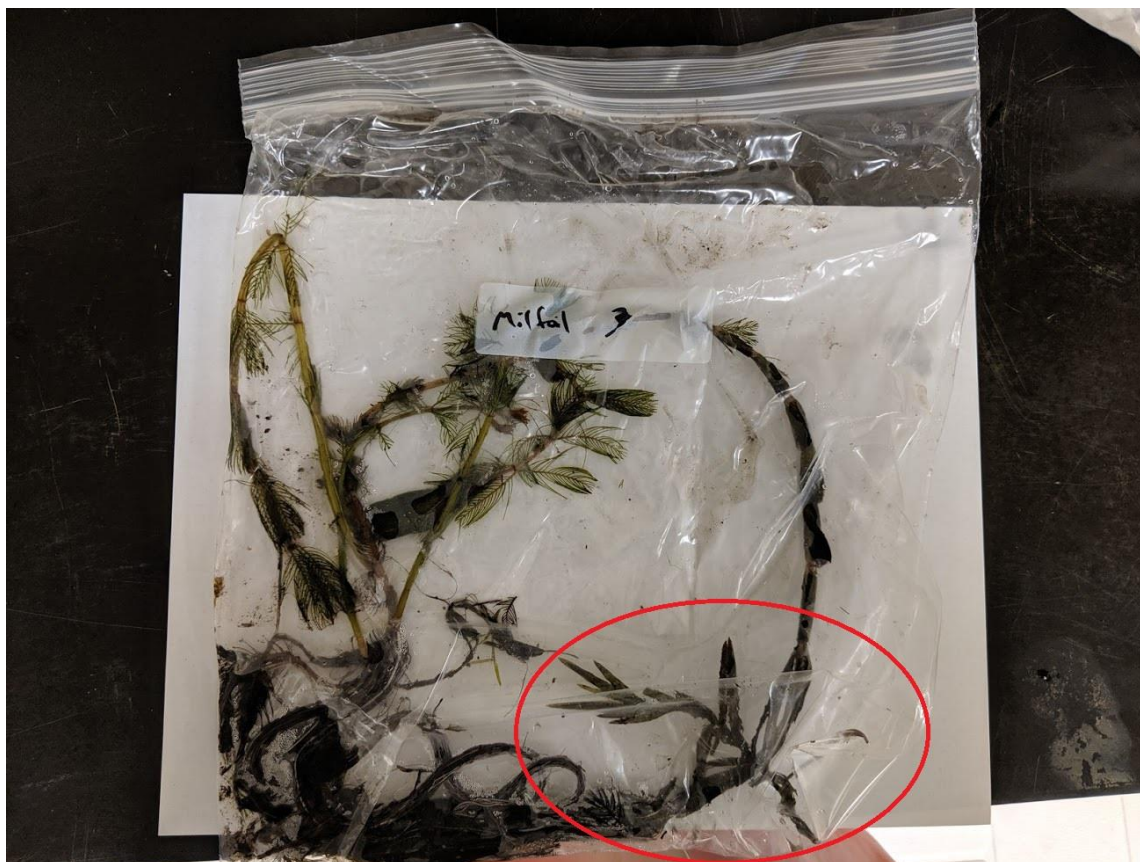
Map of aquatic plants observed in Chandos Lake and Gilmour Bay during the 1972 Ministry of Environment Aquatic Plant Survey (MOE, 1972), © Queen's Printer for Ontario. Reproduction of Crown Copyright material for non-commercial purposes, no permission required (Appendix A)

**Appendix D. Photos of Submerged Macrophytes from Gilmour Bay**

*Potamogeton robbinsii*.



*Chara* sp.



*Myriophyllum spicatum*. Note: A small piece of *Potamogeton robbinsii* was collected with this sample and is outlined in red but was not used for analysis.

## **Appendix E. Diatom Plates and Authorities**

Light micrographs of common diatom taxa recovered from Gilmour Bay and their respective authorities.

All micrographs are at 1000X magnification.



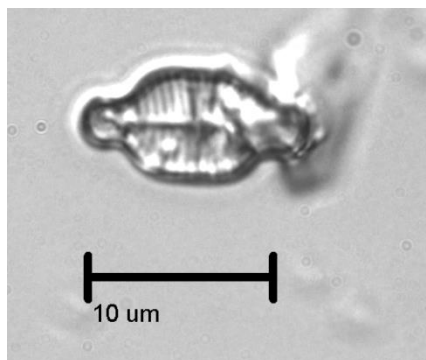
**PLATE 1**

**1-2:** *Achnanthydium exiguum* (Grunow) Czarn. 1994

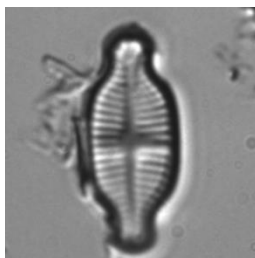
**3:** *Achnanthydium gracillimum* (Meister) Lange-Bertalot in Krammer and Lange-Bertalot  
2004

**4:** *Achnanthydium latecephalum* H. Kobayasi 1997

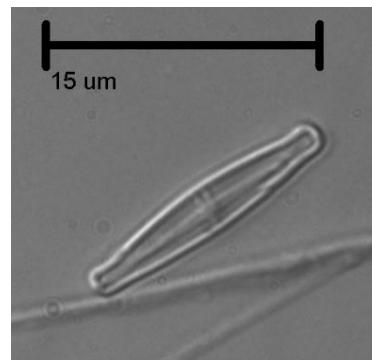
**5-6:** *Achnanthydium minutissimum* (Kütz) Czarn. 1994



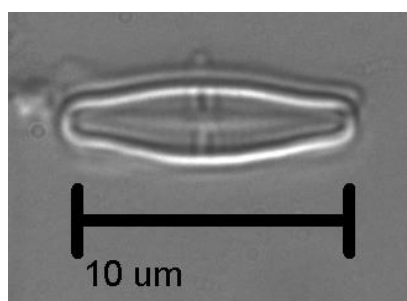
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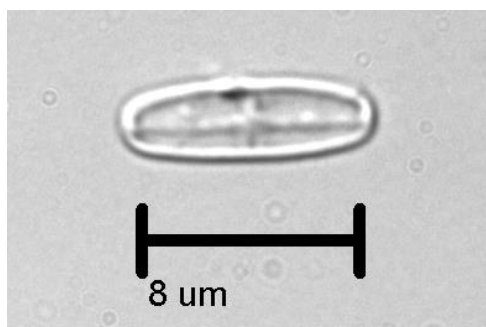
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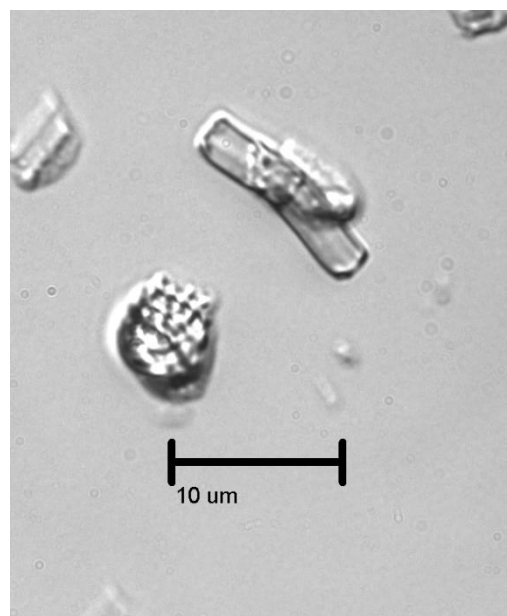
3



4



5



6

**PLATE 2**

**7:** *Brachysira microcephala* (Grunow) Compère 1986

**8:** *Cocconeis placentula* Ehrenb. 1838

**9:** *Encyonema lange-bertalotti* Krammer 1997

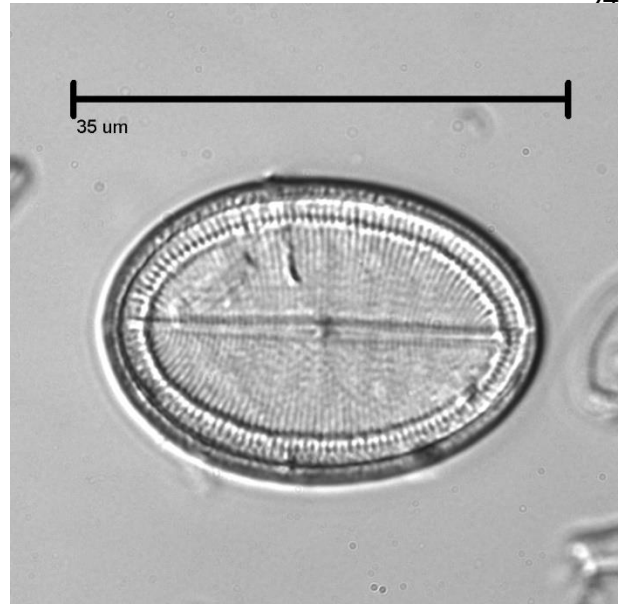
**10:** *Encyonopsis microcephala* (Grunow) Krammer 1997

**11:** *Encyonopsis* sp. 1

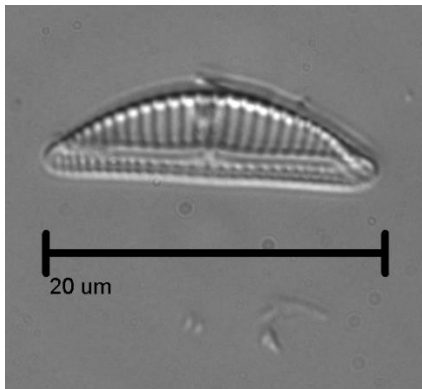
**12:** *Epithemia reichelti* Fricke in Schmidt et al. 1904



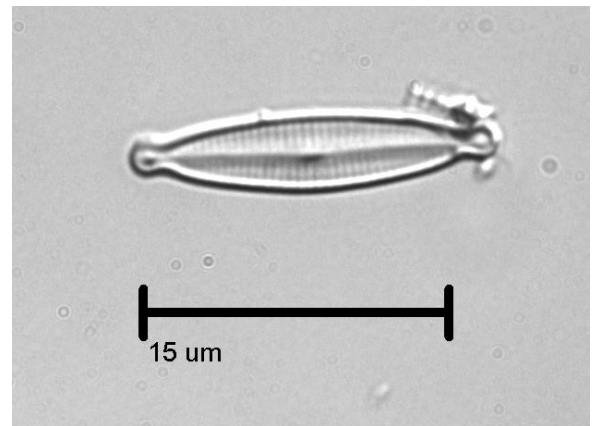
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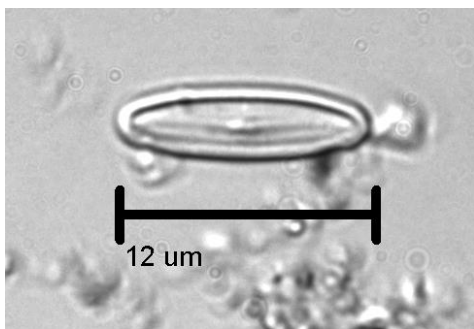
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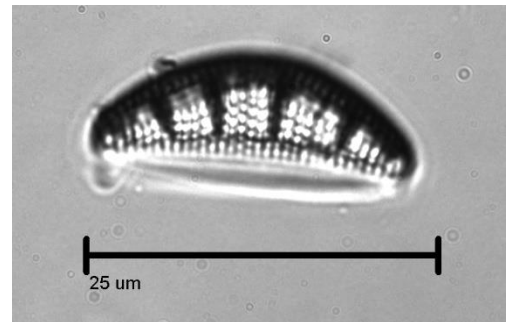
9



10



11



12

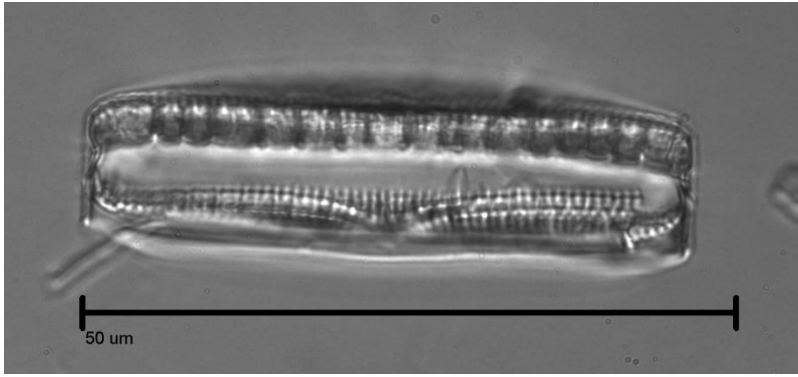
**PLATE 3**

**13:** *Epithemia turgida* (Ehrenb.) Kütz. 1844

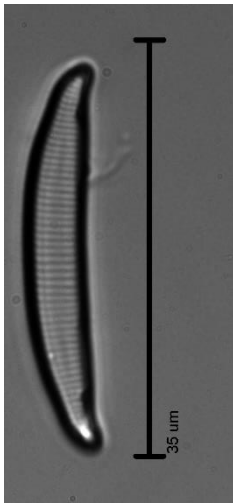
**14:** *Eunotia incisa* Gregory 1854

**15:** *Fragilaria capucina* Desmazières 1925

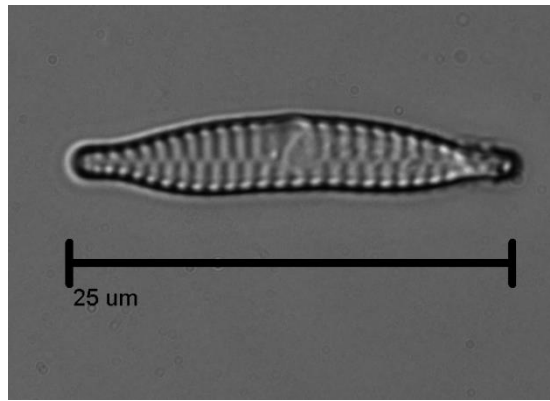
**16-17:** *Fragilaria crotonensis* Kitton 1869



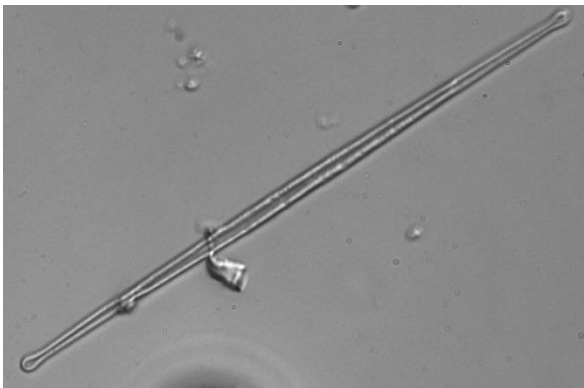
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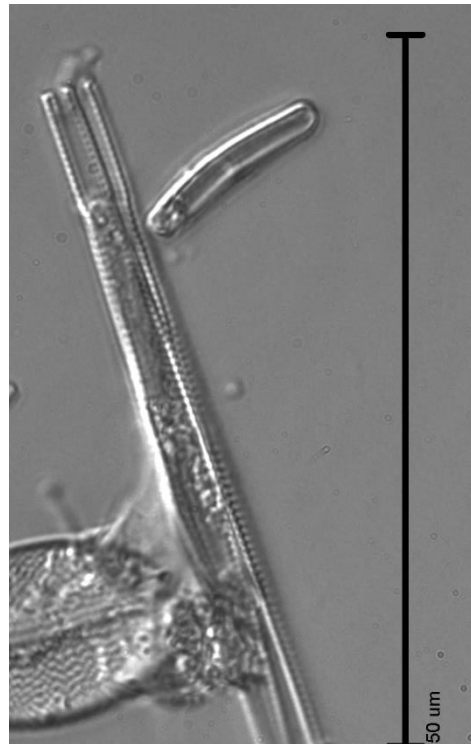
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**PLATE 4**

**18:** *Fragilaria mesolepta* Rabenh. 1861

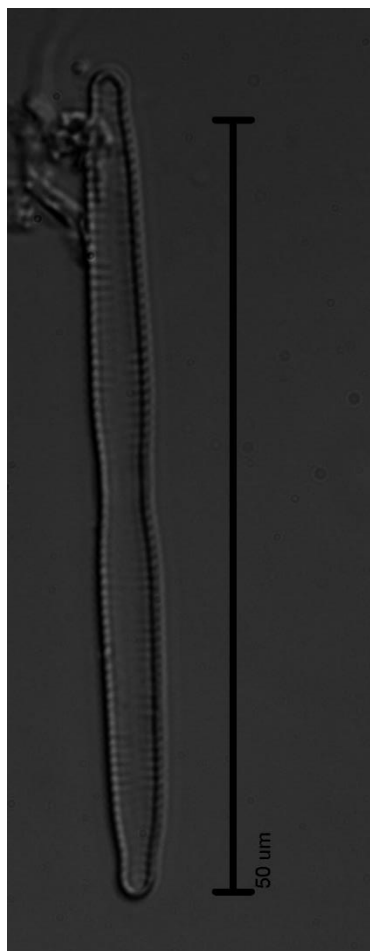
**19:** *Fragilaria tenera* (W. Sm.) Lange-Bertalot 1980

**20:** *Gomphonema minutum* Agardh 1831

**21:** *Gomphonema parvulum* var. *parvulus* Lange-Bertalot & Reinhardt in Lange-Bertalotti 1985

**22:** *Lindavia intermedia* (Manguin ex Kociolek and Reviers) Nakov et al. ex Daniels et al. 2016

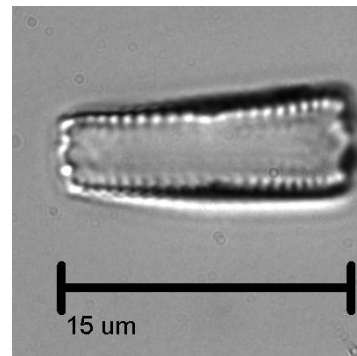
**23:** *Lindavia michigania* (Skvortzov) Nakov, Guillory, M. L. Julius, E. C. Ther. and A. J. Alverson 2015



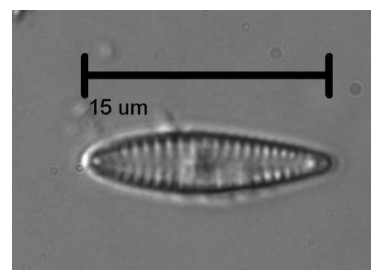
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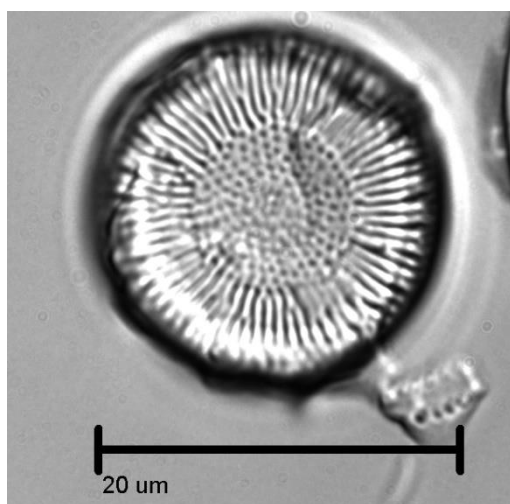
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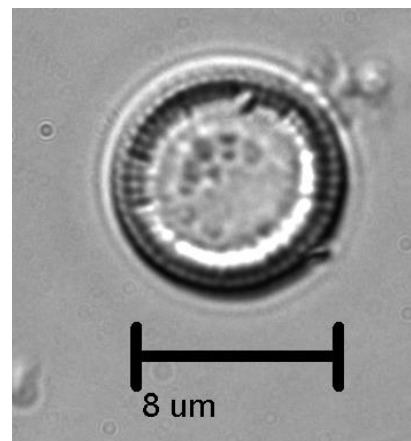
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**PLATE 5**

**24:** *Navicula cryptocephala* Kütz. 1844

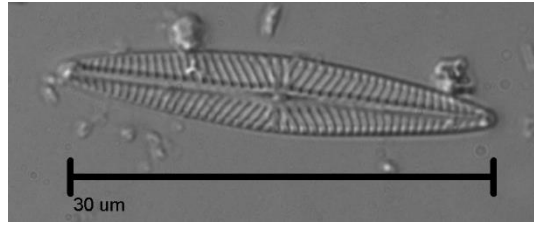
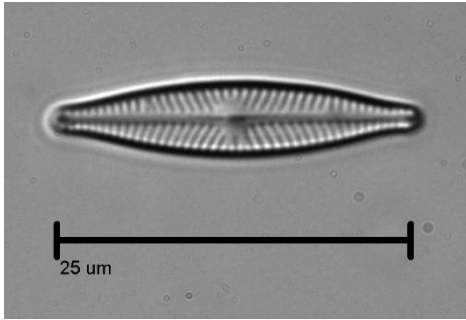
**25:** *Navicula cryptotonella* Lange-Bertalot in Krammer & Lange-Bertalot 1985

**26:** *Navicula gerloffii* Schimanski 1978

**27:** *Navicula radiosa* Kütz. 1844

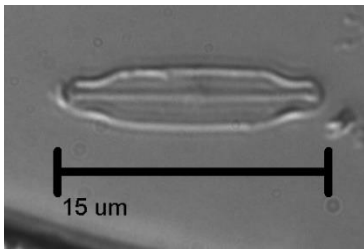
**28:** *Navicula* sp. 1

**29:** *Nitzschia dissipata* var. *media* (Hantzsch) Grunow 1881

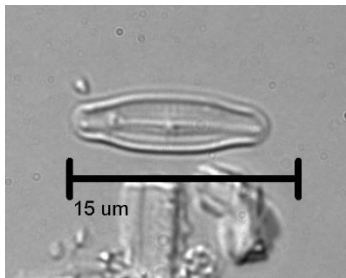


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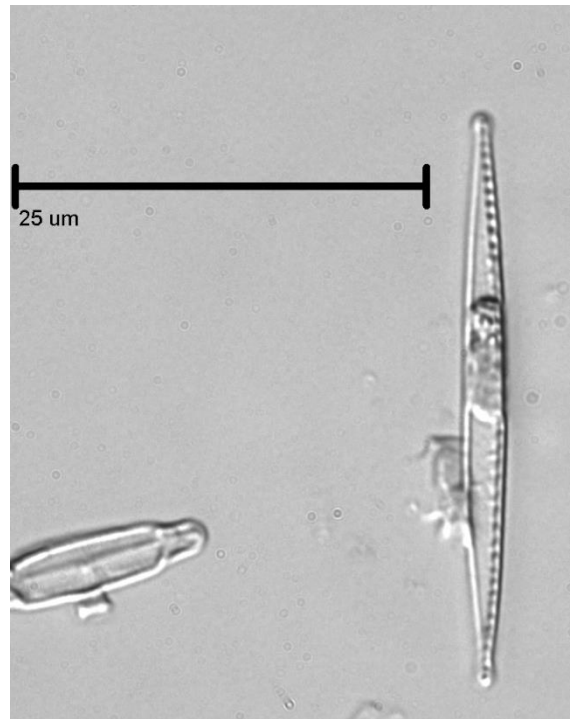
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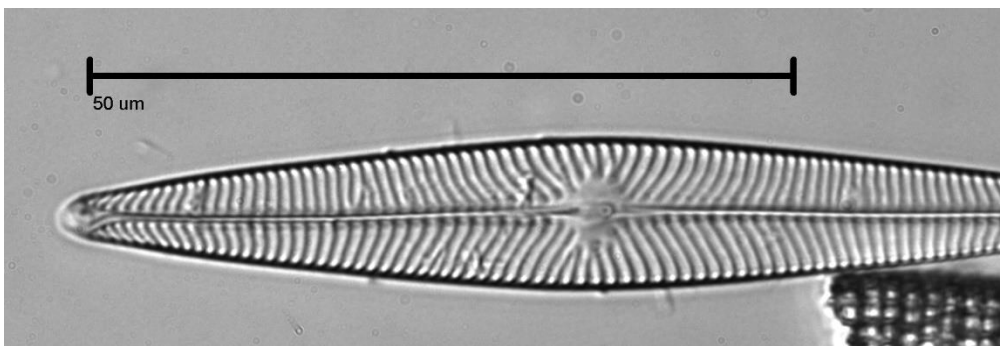
26



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**PLATE 6**

**30:** *Planothidium frequentissimum* Lange-Bertalot 1993

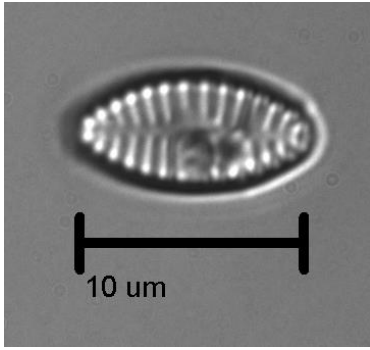
**31:** *Platessa bahlsi* Potapova 2012

**32:** *Platessa conspicua* (A. Mayer) Lange-Bertalot in Krammer & Lange-Bertalot 2004

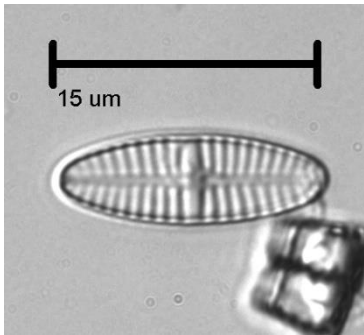
**33:** *Psammothidium microscopum* (Cholnoky) S. Blanco 2016

**34:** *Rhopalodia gibba* Ehrenb. (Kütz.) 1844

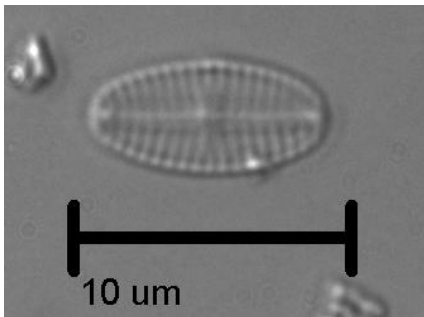
**35:** *Rossithidium anastasiae* (Kaczmarska) Potapova 2012



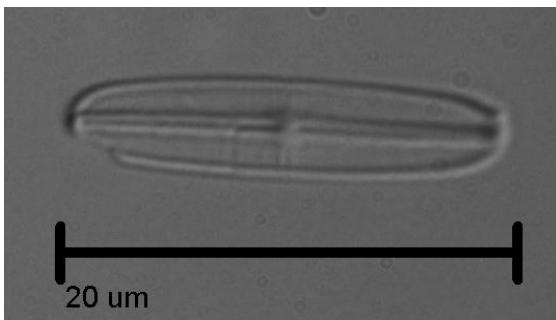
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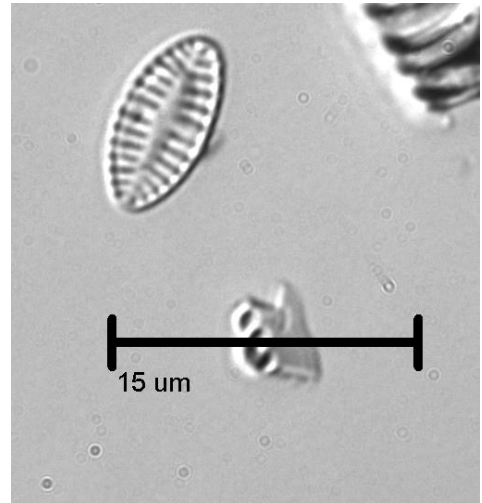
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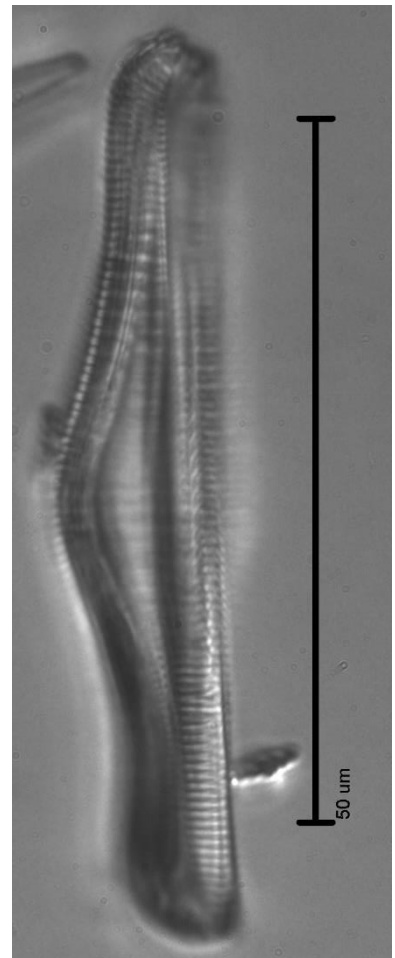
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31



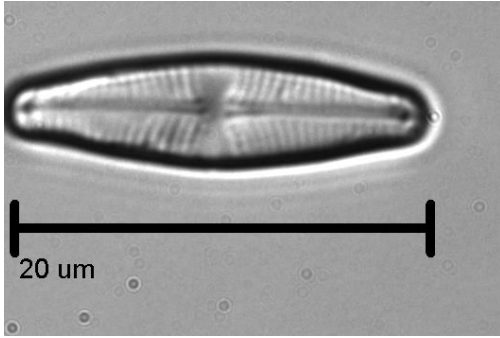
34

**PLATE 7**

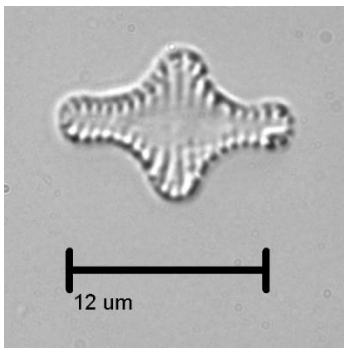
**36:** *Sellaphora pupula* (Kütz) Mereschkosky 1902

**37-38:** *Staurosira construens* Ehrenb. 1843

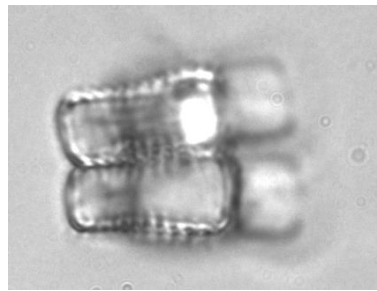
**39-40:** *Staurosirella pinnata* (Ehrenb.) D. M. Williams and Round 1987



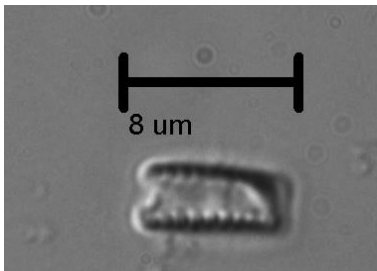
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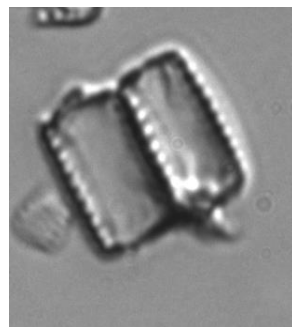
37



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## CURRICULUM VITAE

### Education

- 2018-2021    **MSc.**, Geography with Environment and Sustainability  
 University of Western Ontario, London, ON  
 Thesis title: An Investigation of Epiphytic Diatom Substrate Specificity  
 and Its Use in Paleolimnology
- 2013-2018    **BSc.**, Honours Earth and Environmental Sciences, Co-op  
 McMaster University, Hamilton, ON

### Conference Publications

- Armour, M-H., Boyce, J. I., & **Zilkey, D.** (2017). Geophysical signature of suspected and confirmed impact structures, Ontario, Canada. In *Geological Society of America Abstracts with Programs* (Vol. 49). Seattle, WA.  
<https://doi.org/10.1130/abs/2017AM-305212>

### Honours and Awards

- 2020-2021    **Mitacs**  
 Accelerate Internship Grant
- 2019-2020    **National Science and Engineering Research Council (NSERC)**  
 Canada Graduate Scholarship – Master’s Program

### Related Work Experience

- 2018-2020    Teaching Assistant, Department of Geography  
 Geography of Hazards, Climate Change, Weather and Climate  
 University of Western Ontario, London, ON
- 2017            Research Assistant, Algal Physiology and Nutrient Dynamics  
 Environment and Climate Change Canada, Burlington, ON
- 2016            Research Assistant, Great Lakes Issue Management and Reporting Section  
 Environment and Climate Change Canada, Burlington, ON