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Aquatic Macrophyte Communities in Five Sibley County (Minnesota) Lakes and the Factors that Affect their Distribution

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Aquatic macrophyte communities in five Sibley County (Minnesota) lakes and the factors

that affect their distribution

By

Samuel A Schmid

A thesis submitted in partial fulfillment of the requirements for the degree of

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ACKNOWLEDGEMENTS

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ABSTRACT

Aquatic macrophyte communities in five Sibley County (Minnesota) lakes and the factors that affect their distribution
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The purposes of this study are to 1) quantify the shifts in the macrophyte community structure of five lakes in Sibley County, and 2) to assess the relationships between the macrophyte communities and abiotic factors in these five lakes. In both the early and late growing season of 2019, point-intercept surveys were conducted on High Island Lake, Titlow Lake, Schilling Lake, Silver Lake, and Clear Lake. At each point, water depth was recorded, and all macrophytes sampled were identified and recorded as "present." There was not a late season survey conducted for High Island Lake in 2019 due to a dewatering event in the middle of the growing season. The macrophyte community shifts in individual lakes during the growing season were quantified by comparing the species presence/absence and mean species richness in the early season to the late season. Additionally, in the early season, a sediment core was retrieved at each point for analysis. All sediment cores were analyzed for particle size and sediment organic matter using the hydrometer method and loss on ignition respectively. In order to assess the relationships between the macrophyte community and abiotic factors at individual lakes, generalized linear regressions were ran with the mean species richness as the dependent variable and water depth, distance from shore, percent sand, percent silt, percent clay, and percent sediment organic matter as explanatory variables. In models where the residuals were spatially autocorrelated, a geographically weighted regression was ran using the variables of the highest performance model. The analyses of the macrophyte community shifts suggest that macrophyte phenology is a primary factor that affects the shifts in community structure over the growing season. The generalized linear regressions identify water depth, distance from shore, and percent silt as significant predictors of mean species richness in multiple models. Water depth and distance from shore are both negatively related to mean species richness in multiple models. Whether silt is positively or negatively related to mean species richness is dependent on the species composition of that lake.

CHAPTER 1 – LITERATURE REVIEW

In North America, surface freshwater systems are a highly important natural resource. The structure and function of these systems are affected by many factors (Wilson & Carpenter, 1999; Wetzel, 2001), including the aquatic macrophyte communities (Madsen et al., 1996, 2008; Wersal & Madsen, 2012). The term aquatic macrophyte refers to vegetation adapted to live in aquatic habitats, and includes angiosperms, ferns, mosses, and macroalgae (Wetzel, 2001). Macrophytes affect the structure and function of these systems by increasing biodiversity, contributing to primary productivity, improving water quality, providing food and habitat for animals, and mitigating flooding and erosion (Ozimek et al., 1990; Madsen et al., 1996, 2008; Scheffer, 2004; Wersal & Madsen, 2012). Additionally, aquatic macrophytes can improve the economic value (e.g., water storage, food, and recreation) of these systems (Wilson & Carpenter, 1999; Wetzel, 2001; Wersal & Madsen, 2012). The effects the aquatic macrophyte communities have on lake systems are influenced by the phenology and structure of the macrophyte community constituents.

Macrophytes and environmental factors

The majority of macrophytes in freshwater systems grow in the littoral zone, which is defined as the area between the pelagic zone (open water column) and the terrestrial landscape (Fig 1.1) (Wetzel, 2001; Madsen et al., 2008). In freshwater lake systems, the littoral zone has the greatest diversity and productivity, in part due to the prevalence of macrophytes (Ozimek et al., 1990; Wetzel, 2001; Madsen et al., 2008).

Macrophytes are usually organized into four categories: emergent macrophytes, rooted floating-leaved macrophytes, submersed macrophytes, and free-floating macrophytes (Wetzel, 2001; Scheffer, 2004). Light availability is the most limiting factor for macrophyte growth, especially rooted submersed macrophytes, and light availability in turn is influenced by water depth and turbidity (Barko & Smart, 1986; Strand & Weisner, 1996; Wetzel, 2001; Case & Madsen, 2004; Scheffer, 2004). Macrophyte abundance can also be affected by temperature, wave action, herbivory, and sediment properties (Case & Madsen, 2004; Wersal et al., 2006; Wersal & Madsen, 2011; Turnage et al., 2018). For example, plants will exhibit temperature preferences, and many plants have an optimal photosynthetic rate between 20-35°C (Santamaría et al., 2003; Bornette & Puijalon, 2011). Nutrients can also affect the structure of the macrophyte community. Both nitrogen and phosphorous are limiting factors for macrophyte growth, and an increase in either can result in a trophic cascade that alters the structure and function of the entire system (Lacoul & Freedman, 2006; Bornette & Puijalon, 2011). Specifically, phosphate loading often favors the phytoplankton community at the expense of the macrophyte community (Bornette & Puijalon, 2011).

Although these environmental factors may be limiting for aquatic plant growth, they may also receive feedback from the macrophyte community (Wetzel, 2001; Scheffer, 2004). Macrophytes have been shown to affect water quality by mitigating wave action that increases turbidity, reducing phytoplanktonic biomass via shading, and promoting water column clearing by supporting filter feeders (Scheffer, 1999; Madsen et al., 2001; Peterson & Heck, 2001; Zhu et al., 2006, 2015). Submersed aquatic vegetation

supports many freshwater fishes by providing habitat and food (Tate et al., 2003; Havens et al., 2005). The non-native macrophyte *Myriophyllum spicatum* L. (Eurasian watermilfoil) has also been shown to alter nutrient dynamics by lifting phosphorus out of the sediment and into the water column (Smith & Adams, 1986). In addition to these factors, macrophytes can have major effects in the structure of a lake by influencing its sediment properties.

Macrophytes and sediments

The sediment-plant interface is a site for many complex interactions that can affect the structure and function of lakes. Although macrophytes take up many nutrients from the water column, nitrogen, phosphorous, iron, and manganese are all primarily obtained from the sediment (Barko et al., 1991). Additionally, carbon is often bound to the sediment in the form of organic matter (Forsberg, 1989; Wetzel, 2001). In lake systems, two of the most well-studied nutrient cycles are the nitrogen and phosphorous cycles (Forsberg, 1989; Barko et al., 1991; Wetzel, 2001; Scheffer, 2004). These cycles are influenced by both biotic (e.g., metabolism, fixation, sequestration etc.) and abiotic (e.g., deposition, dissolution, diffusion etc.) processes (Barko et al., 1991; Wetzel, 2001; Scheffer, 2004). Even though both Nitrogen and Phosphorous are found in all constituents of the lake system, only N is readily present as a gas, whereas P is only rarely gaseous in the form of phosphine (Barko et al., 1991; Wetzel, 2001; Scheffer, 2004). Nitrogen is primarily found in the form of molecular N_2, ammonia (NH_4^+), nitrite (NO_2^-), and nitrate (NO_3^-); whereas P is predominately found in the form of phosphate

(PO_4^{3-}) (Wetzel, 2001). Nitrogen and phosphorus are often considered limiting in lake systems, however eutrophic systems are categorized as rich in nitrogen and phosphorus, which supports much higher productivity (Wetzel, 2001; Scheffer, 2004).

Lake sedimentation is further affected by many factors including: wind, land use, water depth, thermal stratification, and aquatic macrophytes (Wetzel, 2001; Scheffer, 2004). In Swan Lake, Blue Earth County, Minnesota, *Stuckenia pectinata* (L.) Böerner (sago pondweed) was found growing in sediments with greater clay contents (Madsen et al., 2006). Sago pondweed often grows in dense canopies that have the ability to reduce wave action and, consequently, mitigate sediment sorting, reduce resuspension, and promote sediment deposition in sites where it is prevalent (Kantrud, 1990; Madsen et al., 2001, 2006; Scheffer, 2004). In a laboratory experiment both *Acorus calamus* L. (sweet flag), an emergent plant, and *Vallisneria natas* L., a submersed plant, reduced sediment resuspension due to reduced water movement, though *A. calamus* reduced resuspension more than *V. natans* (Wu & Hua, 2014).

Aquatic vegetation affects the sedimentation of particles in lakes, and the texture of the sediment is related to the abundance and distribution of macrophytes. Various macrophyte species have expressed a preference for certain sediment textures (Koch, 2001). For instance, sago pondweed has been found growing more frequently in finer sediments in multiple studies (Koch, 2001; Case & Madsen, 2004; Madsen et al., 2006). Macrophyte sediment relationships are established because there is often an ecological tradeoff between coarser and finer sediments. Coarser sediments have a lower bulk density, which is more beneficial for root growth (Gerbersdorf et al., 2007). However,

coarser sediments have lower nutrient availability due to a lower cation exchange capacity (CEC) (Gerbersdorf et al., 2007). Conversely, finer sediments have a higher CEC at the expense of a greater bulk density (Gerbersdorf et al., 2007). The suspension and resuspension of sediment in lakes can be affected by wave action, lake depth, lake fetch, sediment loading, and benthic omnivorous fishes (Hamilton & Mitchell, 1996; Madsen et al., 2001; Rahman et al., 2008; Donohue & Molinos, 2009). The suspension and resuspension of benthic sediments is the principal contributor to turbidity: a light limiting factor (Madsen et al., 2001; James et al., 2004). Fine sediments can also limit submersed macrophyte growth by contributing to increased turbidity (James et al., 2004).

In addition to particle size, organic matter is another major constituent of sediment that is related to the abundance and distribution of aquatic macrophytes (Wetzel, 2001; Scheffer, 2004). Sedimentary organic matter (SOM) is a key factor that affects the movement of energy and carbon across trophic levels in lake systems (Carpenter et al., 2005; Xu et al., 2014). Organic carbon in a lake system can come from a source within the lake (autochthonous) or deposited into the system after it is produced from an outside source (allochthonous) (Wetzel, 2001). Macrophytes play an important role on the input and cycling of SOM into the sediment (Brenner et al., 2006). In Eastern Asia, a field study identified macrophyte communities as a primary, autochthonous source of SOM (Xu et al., 2014). However, some studies have found SOM to be an inhibitor to macrophyte growth (Barko et al., 1991). Macrophyte growth declined linearly as SOM concentration increased from 0% to 20%, but when SOM is in excess of 20% the inhibition on macrophyte growth plateaus (Barko et al., 1991). The

decomposition of SOM in hypoxic environments produces many compounds that may inhibit the growth of plants, which may be why macrophyte growth is negatively related to SOM (Barko et al., 1991; Koch, 2001).

The properties of lake sediments are major factors that affect the abundance and distribution of aquatic macrophytes, which fundamentally affects the structure and function of the aquatic plant community (Barko et al., 1991; Koch, 2001). Changes in these factors may alter the aquatic macrophyte community, which can initiate a trophic cascade that alters the structure and function of the entire lake system; and may facilitate invasion by non-native species.

Aquatic invasive species

Since the globalization of trade, many aquatic non-native plants have become invasive in North America. Non-native species are one of the greatest, modern, ecological threats, with over $120 billion in losses and damages caused in the United States every year (Pimentel et al., 2005). Aquatic weeds affect water quality and movement, animal food and habitat, recreation, transport, and land use (Rockwell, 2003; Pimentel et al., 2005). For example, economic costs from hydrilla (*Hydrilla verticillata* (L. f.) Royle) in Florida alone were estimated to reach $750 million by 2012 (Wersal & Madsen, 2012). Two of the most invasive aquatic macrophytes in Minnesota are *Myriophyllum spicatum* L. (Eurasian watermilfoil) and *Potamogeton crispus* L. (curlyleaf pondweed) (Woolf & Madsen, 2003; Roley & Newman, 2008).

Aquatic invasive species have multiple ecological mechanisms that aid in their invasion and proliferation. Eurasian watermilfoil is a submersed plant that can grow in very high densities (Nichols & Shaw, 1986; Smith & Barko, 1990). Eurasian watermilfoil has also been shown to alter the nutrient dynamics of lakes by "pumping" phosphorus that is bound to the sediment up into the water column, which can affect the trophic dynamics of the lake system (Smith & Adams, 1986). The rapid spread of Eurasian watermilfoil through the Midwest is driven by the plant's vegetative reproduction via fragmentation, which allows any shoot fragment to produce a new individual if it is secured to the substrate; in addition to its innate tolerance to a wide variety of environmental conditions (Nichols & Shaw, 1986; Smith & Barko, 1990; Fleming & Dibble, 2015). Eurasian watermilfoil is an herbaceous perennial that produces root crowns; these root propagules persist through the winter and initiate shoot growth the following growing season (Boylen et al., 1999).

Similarly, curlyleaf pondweed can form dense mats that not only out-compete natives, but also can alter the nutrient dynamics and hydrology of the invaded lakes and potentially change the trophic state of the lakes (Nichols & Shaw, 1986; Bolduan et al., 1994; Fleming et al., 2015). Growth of curlyleaf pondweed occurs rapidly in the early season, with the peak growth occurring in June and July in Minnesota (Nichols & Shaw, 1986; Bolduan et al., 1994; Woolf & Madsen, 2003). Asexual reproduction is the primary mode of reproduction for curlyleaf pondweed, which is driven by propagules called turions. These turions form on the axillary bud, accumulate in the sediment when the plant dies back in July, and will sprout during late fall. Sprouted turions will persist

during the winter, even under ice cover, and allow for growth in the early spring (Nichols & Shaw, 1986; Bolduan et al., 1994; Woolf & Madsen, 2003). This atypical phenology is often referred to as "winter annual". The explosive growth and subsequent dieback are often called a "Boom and Bust" life cycle and can displace native competitors, change hydrology, and alter nutrient cycling (Catling & Dobson, 1985; Bolduan et al., 1994; Turnage et al., 2018). In southern Minnesota, curlyleaf pondweed is one of the most prevalent aquatic invasive macrophytes, and these invasive mechanisms need to be considered when managing lakes in these areas (Woolf & Madsen, 2003).

Study location

Lakes are highly abundant in Minnesota, and this surface freshwater is a vital natural resource. State-wide, Minnesota has a higher abundance (~71%) of shallow lakes (<4.5m in depth) than deep lakes (>4.5m in depth) (Radomski & Perleberg, 2012). Deep lakes generally support a more diverse macrophyte community (Radomski & Perleberg, 2012). Conversely, the shallow lakes in Minnesota are more likely to be degraded, as their surrounding land use is most often agriculture (Radomski & Perleberg, 2012). Southern and western Minnesota have higher abundance of shallow lakes as this portion of the state is part of the Prairie Pothole Region (Guntenspergen et al., 2002). This vast region produces between 40% and 60% of North America's waterfowl population (Rosen et al., 1995; Guntenspergen et al., 2002). The Prairie Pothole Region is estimated at 700,000 km^2 and makes up a large portion of southwestern Minnesota (Guntenspergen et al., 2002) (Fig 1.2).

Sibley County, Minnesota is located in the southeastern tip of the Prairie Pothole Region (Fig 1.2). The most prominent land use in Sibley County is agriculture (Sibley County, 2018). The lakes in Sibley County are shallow and turbid, which is typical of eutrophic lakes (Wetzel, 2001) (Table 1.1). The high turbidity is generally a result of loose flocculent sediments that are high in organic matter (Wetzel, 2001; Scheffer, 2004). Even though the surface water resources of Sibley County are important, there has been no quantitative assessment of the aquatic vegetation communities in Sibley County for many decades. For this study, five high profile lakes in Sibley County (High Island Lake, Titlow Lake, Schilling Lake, Silver Lake, and Clear Lake) (Fig 1.2) were surveyed during the 2019 growing season to quantify macrophyte communities and sediment properties. The objectives of this study were to 1) quantify the seasonal shifts in macrophyte community structure within lakes, and 2) assess the relationships between the macrophyte community structure and abiotic factors, in the five Sibley County Lakes.

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TABLES

Table 1.1 Physical and geographic properties of the five study lakes in SibleyCounty, Minnesota, USA during the 2019 growing season.

	Latitude (°)	Longitude (°)	Total area (km^2)	Average depth (cm)	Secchi depth (cm)
High Island Lake	44.6678	-94.2103	6.99	167.6	149
Titlow Lake	44.5696	-94.2000	3.60	149.4	22
Schilling Lake	44.6959	-94.2103	3.55	167.6	86
Silver Lake	44.6185	-93.9710	2.92	164.6	10
Clear Lake	44.4566	-94.5147	2.04	228.6	29

FIGURES
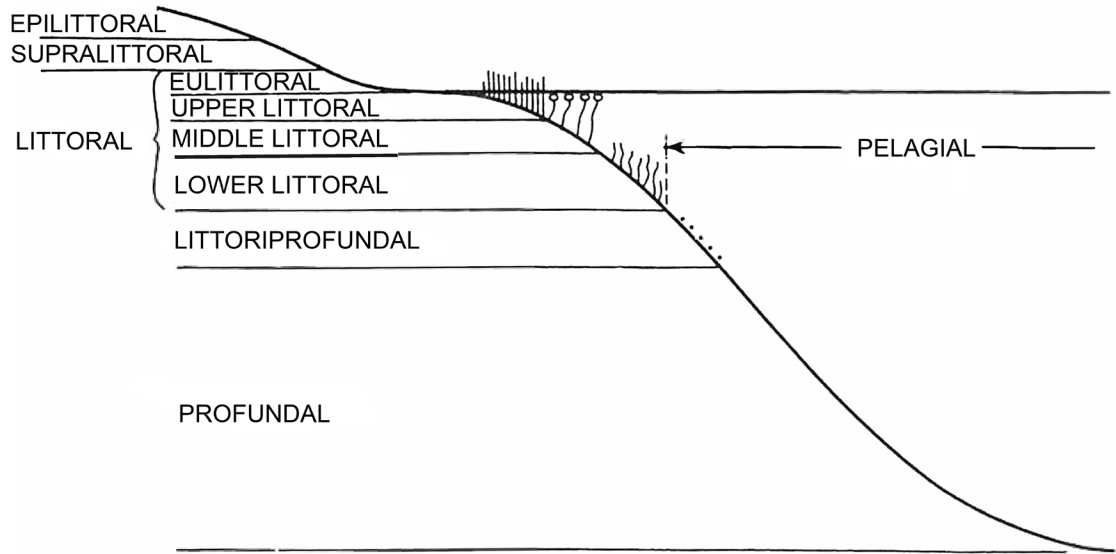
Fig 1.1 Typical lacustrine and macrophyte growth form zonation (Wetzel, 2001; p 131).
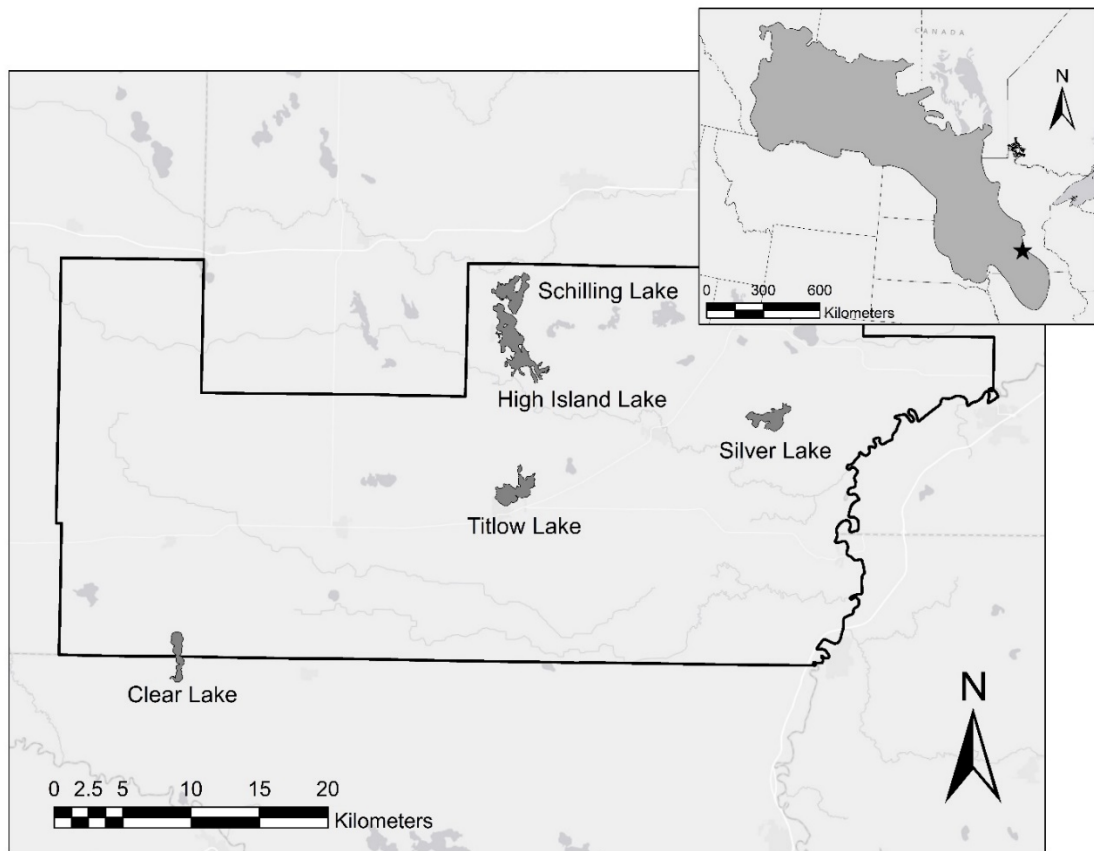
Fig 1.2 The five lakes in SibleyCounty, Minnesota that were surveyed during the 2019 growing season. The black line indicates the border of Sibley County. The inset shows the position of Sibley County (black star) in the Prairie Pothole Region located in Midwestern North America.

CHAPTER 2 - AQUATIC MACROPHYTE COMMUNITY SHIFTS IN FIVE
SHALLOW LAKES IN SIBLEY COUNTY, MINNESOTA

ABSTRACT

The aquatic macrophyte community is one of the driving factors that effects the structure and function of freshwater systems. The shallow lakes of Sibley County, Minnesota have been under studied, and the purpose of this study was to describe aquatic macrophyte communities in these lakes, as well as document seasonal changes in community structure in the presence of aquatic invasive plants. Entire lake surveys were conducted on five lakes using the point-intercept method in both the early growing season and late growing season in 2019. The dominant native macrophyte in Sibley Co. lakes was sago pondweed, with one lake (Schilling Lake) being dominated by curlyleaf pondweed, at least during the early season. Significant shifts in the macrophyte community were found in four lakes, and the shifts differed depending on the species composition and the presence/absence of aquatic invasive species. Schilling Lake had the greatest change in mean species richness, from 0.69 in the early season to 1.11 in the late season. The presence of curlyleaf pondweed in Schilling Lake was a primary driver for the community shift from early to late season. In Schilling Lake, curlyleaf pondweed had a frequency of 44.4% in the early season, which decreased to 13.9% in the late season. Conversely, sago pondweed had a frequency of 6.3% in the early season, which increased to 63.9% in the late season. Overall, all lakes in this study were relatively species poor compared to other large lakes in southern Minnesota.

INTRODUCTION

Aquatic macrophytes are one of the major factors that affect the structure and function of shallow lakes (Wetzel, 2001; Scheffer, 2004). Macrophytes increase biodiversity, contribute to primary productivity, mitigate flooding, improve water quality, and provide food and habitat for all other organisms (Ozimek et al., 1990; Madsen et al., 1996, 2008; Scheffer, 2004; Wersal & Madsen, 2012). In shallow, eutrophic systems, aquatic macrophytes are essential in moderating the intensity and frequency of algal blooms, a common disturbance in these systems (Takamura et al., 2003; Bakker et al., 2010). Aquatic macrophytes can reduce algal blooms by competing with algae for nutrients and light (Takamura et al., 2003; Bakker et al., 2010). Additionally, submersed aquatic vegetation can reduce the resuspension of lake sediment, which is a major source of autochthonous phosphorus that can promote algal blooms (Barko et al., 1991; Zhu et al., 2015). There is also evidence that suggests some aquatic macrophytes produce allelochemicals that inhibit the growth of phytoplankton (Körner & Nicklisch, 2002; Hu & Hong, 2008).

In southern Minnesota, one of the most dominant, native, aquatic macrophytes is *Stuckenia pectinata* (L.) Böerner (sago pondweed), a cosmopolitan, submersed species that is essential to the shallow lake ecosystem (Case & Madsen, 2004; Madsen et al., 2006; Wersal et al., 2006). It is an herbaceous perennial that produces tubers from which new shoots grow each season (Case & Madsen, 2004; Wersal et al., 2006). Sago pondweed is important for nutrient cycling, it provides habitat for fish and aquatic invertebrates, and its fruits and tubers are an important food source for waterfowl

(Kantrud, 1990; Wersal et al., 2005). The growth of sago pondweed is initiated with tuber germination in the spring, which typically reaches maximum growth in mid to late summer, and can form dense, monotypic canopies (Wersal et al., 2006). After it reaches its growth maximum, it will flower and then fruit. Shoot growth can persist into autumn at which point it will die back to its tubers and over-winter (Kantrud, 1990; Case & Madsen, 2004; Wersal et al., 2006). The phenology of sago pondweed is typical of submersed macrophytes in temperate North America.

Conversely, *Potamogeton crispus* L. (curlyleaf pondweed) is a widespread aquatic invasive macrophyte that is common in the upper Midwest (Woolf & Madsen, 2003). Like other aquatic invasive macrophytes, curlyleaf pondweed is harmful both economically and ecologically. It harms systems by changing habitat structure, altering nutrient cycling, and inhibiting recreation and navigation (Rockwell, 2003; Pimentel et al., 2005). Curlyleaf pondweed is a fast-growing perennial that can form thick, monospecific canopies that shade out native macrophytes, reduce biodiversity, and alter the structure and function of affected systems (Bolduan et al., 1994; Woolf & Madsen, 2003; Turnage et al., 2018). Compared to most other submersed macrophytes in temperate North America, curlyleaf pondweed has an atypical seasonal phenology. In the early spring, curlyleaf pondweed exhibits explosive shoot growth that forms dense canopies that can reach the surface in shallow lakes. Its maximum growth occurs in May and June at which point it flowers and forms turions, a rigid asexual propagule formed at the axillary buds (Bolduan et al., 1994; Turnage et al., 2018). In late June and into July, curlyleaf pondweed shoots senesce and the turions are deposited onto the sediment.

Turions then start to sprout in autumn, and its growth will persist through winter until spring when it initiates rapid growth (Woolf & Madsen, 2003; Turnage et al., 2018). This unconventional "boom-and-bust" phenology can drastically alter the community structure of lakes where it becomes established.

Macrophyte communities change over time, and the seasonal phenology of plants is a driving factor for shifts in lake community structure (Wersal et al., 2006; Sayer et al., 2010). In temperate North America, temperature and light availability are two of the most limiting factors on aquatic plant growth, especially sago pondweed and curlyleaf pondweed (Wersal et al., 2006; Turnage et al., 2018). Since the macrophyte community is so influential on the system as a whole, describing the macrophyte community is important for studying and managing lake systems. In Sibley County, Minnesota, to our knowledge, there have been no previous, quantitative assessments of the aquatic macrophyte communities. However, Schilling Lake in Sibley County, has a well-established population of curlyleaf pondweed that dominates the lake in the spring (Schmid & Wersal, 2020). The primary purpose of this study was to describe the macrophyte communities in five shallow lakes, as well as analyze seasonal shifts in macrophyte communities if they occur. Since seasonal phenology is a primary driver of aquatic plant community structure, the Sibley County aquatic macrophyte community will exhibit significant seasonal shifts depending upon the plant species present. Additionally, the infestation of curlyleaf pondweed in Schilling Lake will alter the macrophyte community dynamics over the growing season.

MATERIALS AND METHODS

Study site

The study took place in five natural, shallow lakes in Sibley County, Minnesota. Sibley County is situated in the Prairie Pothole Region of the Midwestern United States. The dominant land use in Sibley County, Minnesota is cultivated land which made up 79% of Sibley County's total land area in 2017 (Sibley County, 2018). The five lakes studied were High Island Lake, Titlow Lake, Schilling Lake, Silver Lake, and Clear Lake (Table 2.1; Fig 2.1). These systems are eutrophic to hypereutrophic lakes that are warm, productive, and turbid throughout the growing season. These lakes are primarily used for recreation including boating, fishing, and duck hunting. The dominant aquatic macrophytes in these lakes are *Ceratophyllum demersum* L. (coontail), curlyleaf pondweed, sago pondweed, and *Typha spp.* (cattails) (Schmid & Wersal, 2020).

Macrophyte surveys

The entirety of all five lakes (with the exception of High Island Lake) were surveyed during the early season (May-June) and late season (August-September) of 2019. High Island Lake was dewatered between the early season and late season surveys in order to repair a dam on High Island Creek. This drawdown prevented the execution of a late season survey on High Island Lake during 2019. Macrophyte surveys were conducted using the point-intercept method similar to other studies in southern Minnesota lakes (Woolf & Madsen, 2003; Case & Madsen, 2004; Madsen et al., 2006; Wersal et al., 2006). Survey points were arranged in a predetermined 150m grid for High Island Lake

(n=318), Titlow Lake (n=163), Schilling Lake (n=160), Silver Lake (n=129), and Clear

Lake (n=90); the same points were surveyed during both surveys. A ruggedized tablet

computer[1] with a spatial accuracy of 2 m, was used to navigate to each point. At each

point, a plant rake was deployed, and when it reached the benthos, it was retrieved, after

which plant species presence was recorded. Additionally, the depth at each point was

measured using a sounding rod. Spatial data were recorded electronically using software[2]

that also allowed for navigation to specific survey points as well as displaying and

collecting geographic and attribute data while in the field, thus reducing data entry errors

and post processing time (Wersal et al., 2010; Cox et al., 2014; Madsen et al., 2015).

Collected data were recorded in database templates using specific pick lists constructed

for this project (Appendix A). The survey grid is relatively large at 150m and the nature

of the point intercept method infrequently places sample points at or near the shore which

can cause an under-sampling of emergent and other shoreline vegetation. To address this

limitation, all observed species were qualitatively recorded (even if they were not present

at a sample point) and combined with the sampled species to produce a complete species

richness list. The species that were recorded qualitatively included both littoral and

shoreline plants that were observed, but missed by the survey. During each survey,

secchi depth was recorded in the center of the lake around noon on a clear day.

Statistical analyses

Plant species presence was averaged over all points sampled and multiplied by

100 to report the frequency of occurrence for each species. The shifts in the frequency of

individual species from early to late season were analyzed using a McNemar's test[3]. The

McNemar's test assesses the data's difference in correlated proportions for dichotomous

dependent variables that are not independent (Case & Madsen, 2004; Madsen et al., 2006,

2015; Wersal et al., 2006). In addition to percent occurrence, the mean species richness

was calculated as the average number of species per point from a specific survey. At

each lake (except High Island) the mean species richness values in the early season and

late season were compared using a Wilcoxon Signed Rank test[4] which compares the

changes in ranks of data from paired independent variables (Zar, 1999). Only

macrophytes that were recorded from the sample points in the surveys were used in the

McNemar's test and Wilcoxon Signed Rank test. All statistical analyses were conducted

at a $p \leq 0.05$ significance level.

RESULTS AND DISCUSSION

      Macrophyte data from the early and late season surveys showed a significant shift

in the macrophyte communities in every lake over the 2019 growing season (Table 2.2).

Schilling Lake had the greatest mean species richness in both the early (0.69) and late

season (1.11), and the shifts in the mean species richness from early to late season was

significant (p<0.001) (Table 2.2). Curlyleaf pondweed was the dominant macrophyte in

Schilling Lake during the early season survey with a sample frequency of 44.4% (Table

2.2). However, the presence of curlyleaf pondweed declined to 13.9% from early to late

season (p<0.001) (Table 2.2). Sago pondweed was found in only 6.3% of samples in the

early season, but it exhibited a significant increase in frequency to 63.9% in during the

late season survey (p<0.001) and became the dominant macrophyte in Schilling Lake (Table 2.2). High Island Lake had the second highest mean species richness (0.62) during the early season and had no data for a late season survey due to the draw-down in mid-summer, 2019 (Table 2.2). During the early season survey, sago pondweed was dominant in High Island Lake with a sample frequency of 49% (Table 2.2). Titlow Lake had a mean species richness of 0.16 in the early season and 0.28 in the late season (Table 2.2). Sago pondweed was the dominant macrophyte for the entire growing season with sample frequencies of 14.8% and 25.3% during the early season and late season surveys respectively. These data also showed that all five of these lakes were relatively species poor compared to other lakes in southern Minnesota (Madsen et al., 2006).

Schilling Lake exhibited the greatest shift in the macrophyte community from early to late season (Table 2.2). This shift is primarily driven by the infestation of curlyleaf pondweed in Schilling Lake. Curlyleaf pondweed is a canopy-forming, invasive macrophyte with an atypical seasonal phenology. The oppressive growth exhibited by curlyleaf pondweed in Schilling Lake during spring greatly outcompetes the native macrophytes for light, thereby suppressing their growth, and displacing them for much of the early season (Madsen et al., 1991; Bolduan et al., 1994; Fleming & Dibble, 2015) (Fig 2.2). Curlyleaf pondweed dominated most of the lake, and during the early growing season, sago pondweed only inhabited sections of the lake where curlyleaf pondweed was absent. The two species rarely co-existed at sample points surveyed (Fig 2.2). In the late season, after curlyleaf pondweed had senesced, the range of sago pondweed expanded significantly (Table 2.2; Fig 2.2). The seasonal senescence of

curlyleaf pondweed in the early summer likely resulted in a competitive release on the sago pondweed population that was then exploited by sago pondweed to become the dominant species in the lake. The mean species richness increased in the sample points largely due to increasing prevalence of sago pondweed, and coontail during the late season survey (Table 2.2). Additionally, Schilling Lake exhibited an increase in mean species richness as rare species that were not found during early season were sampled in the late season (e.i. slender naiad and muskgrass).

Similarly, Titlow Lake exhibited significant shifts in macrophyte population in 2019 (p=0.005) (Table 2.2). Sago pondweed was the dominant macrophyte in Titlow Lake. Change in sago pondweed was significant (P=0.013) (Table 2.2; Fig 2.3), and this magnitude of increase (44% increase between early and late season) may be more typical of a shallow lake in this region that is not infested with curlyleaf pondweed. Conversely, in Schilling Lake, the increase in sago pondweed was 89% between the early season and late season surveys. The large increase corresponds with the senescence of curlyleaf pondweed that infests Schilling Lake.

The increase in species richness in Schilling Lake over the growing season suggests that the dominance of invasive macrophytes can displace native species and decrease species richness (Boylen et al., 1999; Houlahan & Findlay, 2004; Fleming & Dibble, 2015). However, when the competitive pressure is released, native species are able to fill that niche, and species richness can increase. This is evident by the increase in sago pondweed frequency as well as the appearance of rare species in Schilling Lake. Invasive, canopy-forming plants are known to reduce the density and abundance of native

macrophytes (Madsen et al., 1991; Boylen et al., 1999; Santos et al., 2011). The phylogeny and life history of curlyleaf pondweed in northern North America is characterized by rapid, dense shoot growth that is high in intensity, but relatively short in duration (Woolf & Madsen, 2003; Turnage et al., 2018). The decline of curlyleaf pondweed in mid to late summer in tandem with the appearance of rare macrophytes in Schilling Lake during the late season suggests that curlyleaf pondweed infestation alone may not be enough to locally extirpate certain submersed macrophytes.

Since shallow, eutrophic lakes are characterized by high productivity, they often experience intense algal blooms that outcompete submersed aquatic vegetation for light and reduce habitat complexity (Phillips et al., 1978; Bakker et al., 2010). However, increases in the density and abundance of macrophytes is known to moderate the growth of algae in shallow lakes, thus improving their biodiversity (Takamura et al., 2003; Bakker et al., 2010). This suggests that a population of curlyleaf pondweed in a shallow, warm, hypereutrophic lake in North America may be more beneficial to the system if the alternative is a lake with prominent algal blooms, high turbidity, and low mean species richness like Silver Lake and Clear Lake. Further evidence is required to support these claims and future studies should involve long-term assessments of the effects of curlyleaf pondweed on native plant community structure in combination with environmental monitoring

Poor species richness in Silver Lake and Clear Lake is likely the result of algal blooms that raise the turbidity and shade out submersed aquatic vegetation (Table 2.1). Algal blooms are a primary driver in macrophyte decline in eutrophic and hypereutrophic

lakes, and occurrences of algal blooms can be reduced in waterbodies with higher macrophyte biomass (Phillips et al., 1978; Bakker et al., 2010). This would also be consistent with the long-term model that suggests that duration of plant dominance is reduced by prevalence of algal blooms in mid to late summer (Sayer et al., 2010). Lack of change in distribution of white waterlily in Silver Lake over the growing season is primarily driven by its life history (Fig 2.4). White waterlily is a floating-leaf macrophyte that allocates large portions of its biomass to thick, fleshy rhizomes. Compared to aquatic macrophytes that invest more biomass to shoot growth, the range and density of white waterlily tends to fluctuate less over the course of a growing season. Additionally, the floating leaves of white waterlily would render it largely unaffected by algal blooms and poor light transmittance later in the growing season, which are much more detrimental to submersed aquatic macrophytes. The algal bloom likely also explains why sago pondweed was found during the early season survey but was absent in the late season (Table 2.2). In Clear Lake, species richness was so poor that in both the early and late season, species were found in fewer than 10% of sample points (Table 2.2). Clear lake was the deepest lake surveyed and had poor water clarity. These factors combined to result in a very species poor plant community. Clear Lake is the most extreme example of the Sibley County lakes; that of a shallow, turbid lake that is nearly devoid of submersed aquatic vegetation.

In 2019, Sibley County lakes with relatively high species richness did experience significant shifts in the aquatic macrophyte community. Schilling Lake experienced the greatest shifts facilitated by infestation of curlyleaf pondweed. Surveys of these lakes

should be conducted annually to monitor the macrophyte communities and detect any new infestations of curlyleaf pondweed, or other non-native aquatic plant. The methodology should also be adopted and utilized in nearby counties to document macrophyte communities and the spread of aquatic invasive species in general. Overall, species richness in Sibley County lakes are consistent with similar Lakes in the region (Wersal et al., 2006; Radomski & Perleberg, 2012). Mean species richness of lakes in Sibley County ranged from 0.01 – 1.11 (Table 2.2). Sibley County lakes are species poor when compared to lakes outside of the region, where the mean species richness can range from 1-3 (Wersal et al., 2010; Cox et al., 2014; Madsen et al., 2015).

SOURCES OF MATERIALS

[1]Yuma 2, Trimble Navigation Limited, 935 Stewart Drive, Sunnyvale, CA 94085 USA

[2]Site Mate, Farm Works Information Management, P.O. Box 250, Hamilton, IN 46742 USA

[3]SAS software, SAS Institute, 100 SAS Campus Drive, Cary, NC 27513 USA

[4]SPSS Statistics, International Business Machines Corperation, 1 New Orchard Road, Armonk, NY 10504 USA

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TABLES

Table 2.1 Physical and geographical properties of all five study lakes in Sibley County, Minnesota 2019.

	Latitude (°)	Longitude (°)	Total area (km^2)	Average depth (cm)	Secchi depth (cm)	mean species richness
High Island Lake	44.6678	-94.2103	6.99	167.6	149	0.61(±0.05)
Titlow Lake	44.5696	-94.2000	3.60	149.4	22	0.16(±0.03)
Schilling Lake	44.6959	-94.2103	3.55	167.6	86	0.71(±0.07)
Silver Lake	44.6185	-93.9710	2.92	164.6	10	0.30(±0.08)
Clear Lake	44.4566	-94.5147	2.04	228.6	29	0.08(±0.03)

Table 2.2 Percent frequency values of individual macrophytes and mean species richness of sample points during early and late season surveys. Sample frequency values were compared using a McNemar's test and species richness values were compared using the Wilcoxon Signed Rank test.

	Species	Common name	Early season	Late season	p-value
			Sample frequency (%)		
High Island Lake	*Ceratophyllum demersum*	coontail	2.00		
	Lemna minor L.	lesser duckweed	2.80		
	Lemna trisulca L.	star duckweed	0.80		
	Schoenoplectus tabernaemontani (C.C.Gmel.) Palla	softstem bulrush	0.40		
	Stuckenia pectinata	sago pondweed	49.00		
	Typha spp.	cattail	4.80		
	Wolffia Columbiana H. Karst	Columbian watermeal	0.80		
	Mean species richness		0.62		
Titlow Lake	*Lemna minor*	lesser duckweed	0.62	3.09	0.103
	Phragmites australis (Cav.) Trin. ex Steud.	common reed	0.60		
	Stuckenia pectinata	sago pondweed	14.81	25.31	0.013
	Typha spp.	cattail	0.62	1.23	0.564
	Mean species richness		0.16	0.28	0.005
Schilling Lake	*Carex spp.*	true sedge	2.78	2.78	1.000
	Ceratophyllum demersum	coontail		0.04	
	Chara spp.	muskgrass		0.69	
	Lemna minor	lesser duckweed	2.08	9.72	0.005
	Lemna trisulca	star duckweed		0.69	
	Najas flexilis (Willd.) Rosk. & Schmidt	slender naiad		3.47	
	Phragmites australis	common reed	0.69		
	Potamogeton crispus	curlyleaf pondweed	44.44	13.89	<0.001
	Spirodela polyrhiza (L.) Schleid	greater duckweed		2.78	
	Stuckenia pectinata	sago pondweed	6.25	63.89	<0.001
	Typha spp.	cattail	15.28	5.56	0.006
	Wolffia columbiana	Columbian watermeal		1.39	
	Native mean species richness		0.24	0.97	<0.001
	Non-native mean species richness		0.45	0.14	<0.001
	Total mean species richness		0.69	1.11	<0.001
Silver Lake	*Carex spp.*	true sedge	1.68		
	Lemna minor	lesser duckweed	2.52	5.04	0.317
	Nympheae odorata Ait.	white waterlily	10.08	9.24	0.835
	Phragmites australis	common reed		0.84	
	Sagittaria latifolia Willd.	broadleaf arrowhead	0.84	0.84	1.000
	Stuckenia pectinata	sago pondweed	8.40		
	Typha spp.	cattail	6.72	4.20	0.405
	Mean species richness		0.30	0.20	0.050
Clear Lake	*Lemna minor*	lesser duckweed		1.11	
	Stuckenia pectinata	sago pondweed	7.78		
	Mean species richness		0.08	0.01	0.034

FIGURES
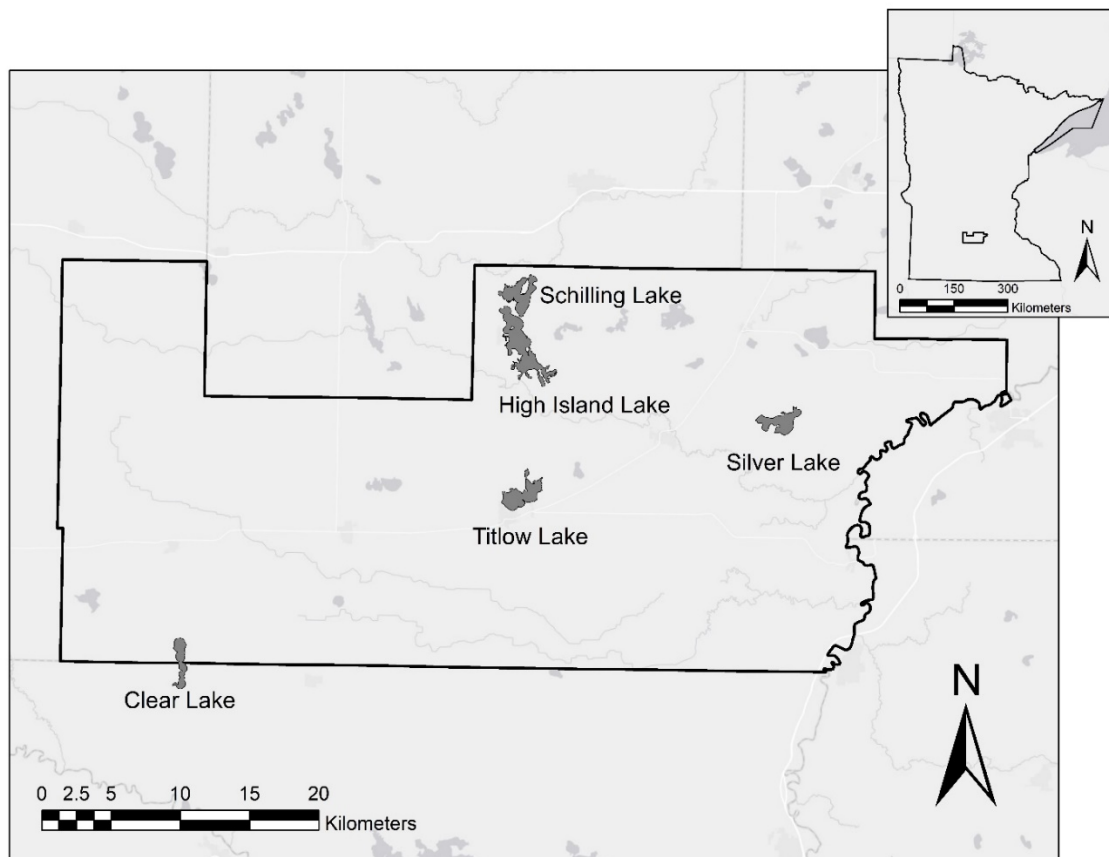
Fig 2.1 The five lakes that were surveyed in Sibley County, Minnesota. The black line indicates the extent of Sibley County. Surveys occurred during the early and late portions of the 2019 growing season.
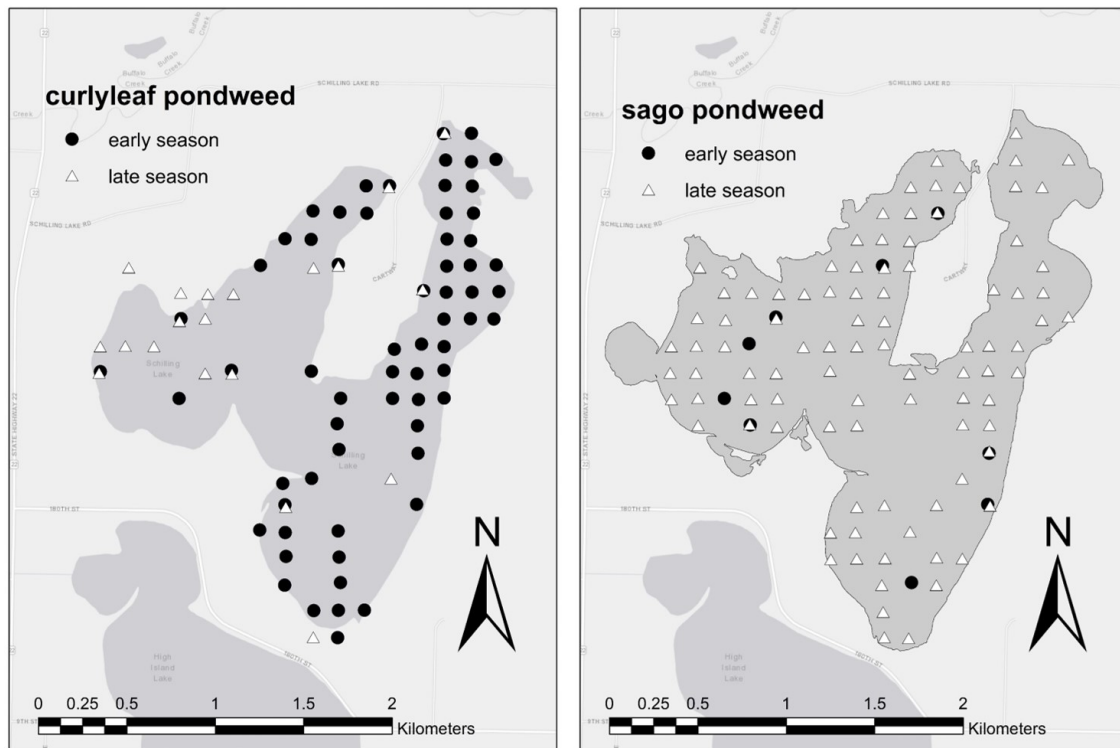
Fig 2.2 The distribution of curlyleaf pondweed (left) and sago pondweed (right) sampled in the early and late season surveys in Schilling Lake, Sibley County, Minnesota 2019.
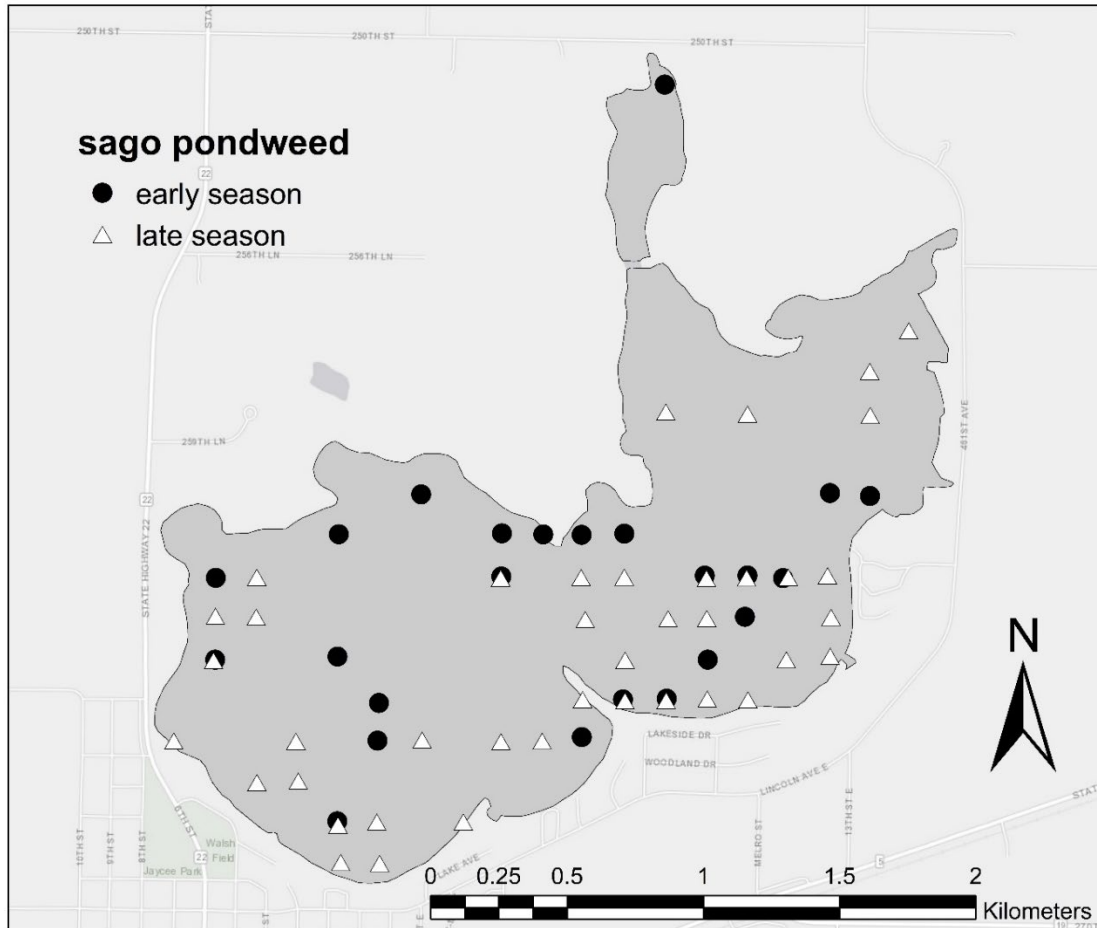
Fig 2.3 The distribution of sago pondweed sampled in the early and late season surveys in Titlow Lake, Sibley County, Minnesota 2019.
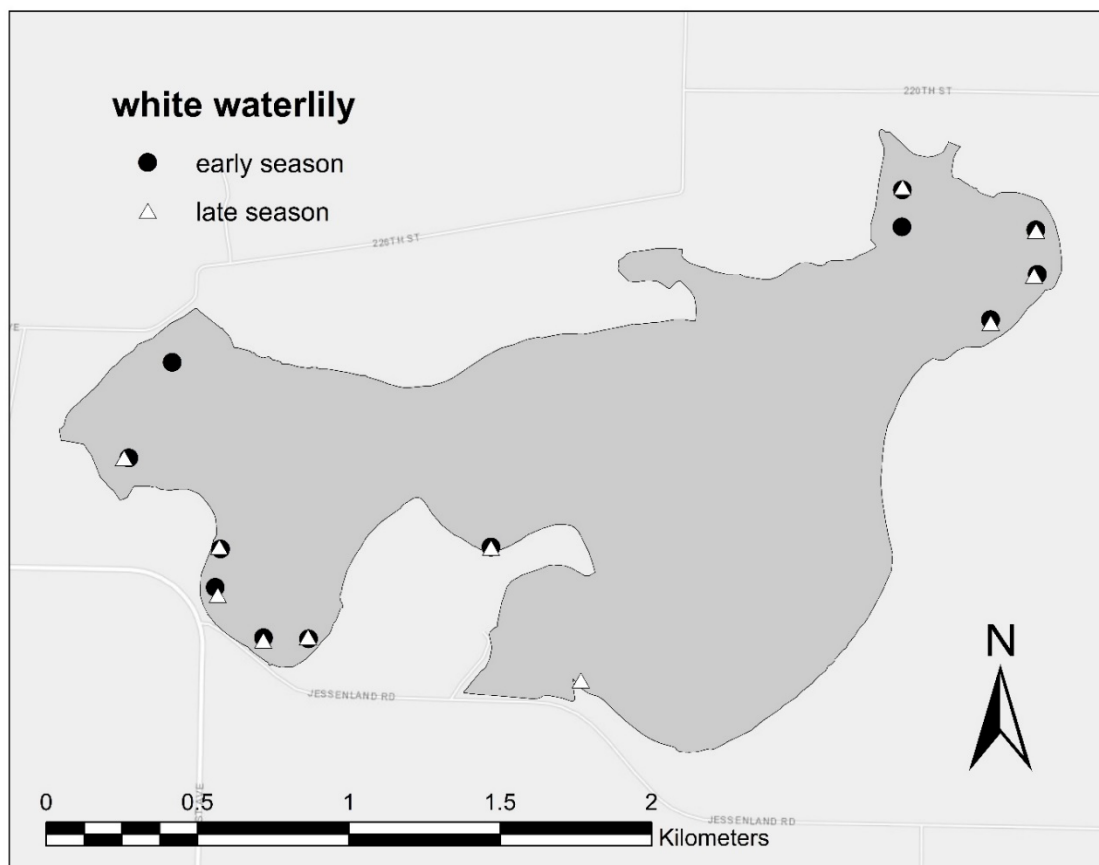
Fig 2.4 The distribution of white waterlily sampled in the early and late season surveys in Silver Lake, Sibley County, Minnesota 2019.

CHAPTER 3 - ABIOTIC FACTORS THAT AFFECT THE DISTRIBUTION OF
AQUATIC MACROPHYTES IN SHALLOW LAKES LOCATED IN SIBLEY
COUNTY, MINNESOTA, USA: A SPATIAL MODELING APPROACH

ABSTRACT

Aquatic macrophytes are an integral component of freshwater lake communities; therefore, understanding the factors that affect the aquatic macrophyte community structure is vital to the conservation and management of lakes. In Sibley County, Minnesota, USA, five lakes (High Island Lake, Titlow Lake, Schilling Lake, Silver Lake, and Clear Lake) were surveyed using the point-intercept method. At each point, the presence of macrophytes were recorded, water depth was measured, and a sediment sample was collected. Sediment samples were quantified by determining soil particle size and percent organic matter.  The richness of macrophytes in all five lakes was modeled with six explanatory variables: water depth, distance from shore, percent sand, percent silt, percent clay, and percent sediment organic matter. Mean species richness was negatively related to water depth and distance from shore, but silt was either negatively or positively related to mean species richness, depending on the macrophyte community structure. All mean species richness models had *pseudo*-R^2 values between 0.25 and 0.40. Individual species were also modeled for Schilling Lake using the same explanatory variables.

INTRODUCTION

Aquatic macrophytes are important primary producers and ecosystem engineers in freshwater systems (Koch, 2001). The majority of all aquatic vegetative growth occurs in the littoral zone, the transitional space between the profundal zone and the terrestrial

landscape (Fig. 1.1) (Madsen et al., 2008). Aquatic macrophyte communities influence

the structure and function of aquatic systems in many ways. Aquatic macrophytes

provide food and habitat for waterfowl, fish, and macroinvertebrates (Waters &

Giovanni, 2002; Wersal et al., 2005; Dibble & Pelicice, 2010). In addition to supporting

animal communities, aquatic macrophytes inhibit the growth of phytoplankton

allelopathically, and provide habitat for important filter feeders that graze on

phytoplankton. These interactions can mitigate the frequency and intensity of algal

blooms (Scheffer, 1999; Körner & Nicklisch, 2002; Takamura et al., 2003; Bakker et al.,

2010). Aquatic vegetation can also improve water quality by promoting the settling of

suspended sediment and inhibiting the resuspension of settled sediment by reducing wave

action in the water column (Barko & Smart, 1986; James et al., 2004). A diverse, aquatic

plant community can improve the ecological value of a lake system as a whole.

Understanding the factors that affect the composition of the aquatic macrophyte

community is important for managing aquatic systems and preserving their structure and

function. Light availability is considered the principal limiting factor for the growth of

aquatic macrophytes (Barko et al., 1985; Chambers & Kaiff, 1985; Lacoul & Freedman,

2006). Light is a rate limiting factor for the primary productivity of plants, and in aquatic

systems, light is often limited by the attenuation of light by the water column (Lacoul &

Freedman, 2006; Bornette & Puijalon, 2011). The light regime of a lake is the primary

driver for the niche partitioning of aquatic macrophytes throughout the littoral zones of

lakes (Barko et al., 1985). The typical structure of the littoral zone consists of

angiosperms at shallow depths and bryophytes and charophytes at deeper depths

(Chambers & Kaiff, 1985; Blindow, 1992). This zonation of the macrophyte community is primarily driven by the availability of light and the adaptations of plants to those light conditions. Light availability is also a strong determinant of macrophyte growth form. Lakes with very low light availability are often dominated by floating leaf and free-floating macrophytes that are adapted to grow leaves at the surface, where light is not limited (Lacoul & Freedman, 2006). Conversely, submersed macrophytes are generally more abundant in lakes where there is more light available in the water column (Lacoul & Freedman, 2006).

Water depth is also an important factor that affects the distribution of macrophytes in lakes. Many lakes have a maximum depth of macrophyte colonization that is shallower than the maximum depth of the lake (Chambers & Kaiff, 1985; Rooney & Kalff, 2000). When water depths in the middle of the lake exceed the maximum depth of colonization, a profundal zone is present with the littoral zone found around the margin. The profundal zone is typical in deep lakes; however, in shallow lakes it may be absent entirely. Water depth is often considered an inhibiter of macrophyte growth because the water column attenuates more light as depth increases. This also explains why macrophytes at lower depths are often better adapted to lower light conditions than macrophytes at shallower depths. These results show that density and abundance of macrophytes is negatively related to water depth (Barko et al., 1985; Cheruvelil & Soranno, 2008).

Another important factor that affects the abundance and distribution of aquatic macrophytes is the fetch of the lake system. In shallow lakes, one of the primary

determinants of wave action is fetch (Andersson, 2001; Lacoul & Freedman, 2006). Depending on the intensity of the wave energy, the effects of wave action may be positive or negative. In systems where wave action is very high, those forces may damage macrophytes and stimulate them to change their morphology; however, in systems where wave action is moderate, mixing of the water column by waves may benefit macrophytes by increasing nutrient availability (Madsen et al., 2001; Lacoul & Freedman, 2006; Bornette & Puijalon, 2011). Wave action may also contribute to suspension and resuspension of fine textured sediment that may affect community structure in various ways (Madsen et al., 2001; James et al., 2004).

One of the major factors that limits the growth of aquatic macrophytes is water turbidity, which is a major limiter of light availability (Barko et al., 1985; Lacoul & Freedman, 2006; Bornette & Puijalon, 2011). Turbidity in a lake system is mostly caused by suspension and resuspension of fine textured sediment (James et al., 2004). Suspended sediment can increase light attenuation and nutrients in the water column, which reduces light availability and can promote algal blooms, thus inhibiting the growth of submersed macrophytes (James et al., 2004; Zhu et al., 2015). However, aquatic macrophytes can affect the turbidity of lake systems. Many studies have found that the presence of aquatic macrophytes reduces wave action, and consequently reduces suspension and resuspension of fine sediments that contribute to turbidity (Barko et al., 1991; Madsen et al., 2001; Wu & Hua, 2014). The relationship between turbidity and aquatic macrophytes is complex, but abundant evidence implicates turbidity as a major

limiting factor for plant growth through limiting light availability (Barko et al., 1985;

Lacoul & Freedman, 2006; Bornette & Puijalon, 2011).

A lake's sediments are highly influential on the macrophyte community, and

interactions between sediment and macrophyte communities is highly complex (Barko &

Smart, 1986; Barko et al., 1991). While fine sediments can contribute to turbidity, but

sediment texture affects macrophytes in many other ways. For instance, *Stuckenia*

pectinata (L.) Böerner (sago pondweed) has shown a proclivity for growth in sediments

with abundant silt (Madsen et al., 1996; Koch, 2001; Case & Madsen, 2004). In Swan

Lake and Middle Lake, Nicollet County, Minnesota, USA, clayey sediment was

positively related the presence of sago pondweed, but negatively related to the presence

of *Vallisneria americana* Michx. (American eelgrass) (Madsen et al., 2006). Finer

sediment like silts and clays can be both beneficial and detrimental to macrophytes, and

effects are species specific. In finer sediments, macrophytes generally encounter a trade-

off between nutrients and bulk density (Gerbersdorf et al., 2007). Finer sediment

particles often have a higher affinity for cations, which improves cation exchange

capacity (CEC), elevating nutrient availability. However, reduced porosity of finer

sediments can inhibit root growth sediment density is greater and generally results in

more hypoxic sediments (Koch, 2001; Gerbersdorf et al., 2007).

Factors that affect the structure of the macrophyte community are highly

influential on the structure and function of lake systems. Lakes of Minnesota are very

diverse, and this is largely due to landscape diversity across the state. In Minnesota,

shallow lakes (maximum depth < 4.5 m) are more common than deep lakes (maximum

depth $\geq$ 4.5m) (Radomski & Perleberg, 2012). Regions with deeper and more

oligothrophic lakes have lakes with much greater mean species richness than regions with

shallow, eutrophic lakes (Radomski & Perleberg, 2012). Much of southern Minnesota is

situated in the Prairie Pothole Region, where lakes are much shallower and more species

poor than most other regions of Minnesota (Guntenspergen et al., 2002; Radomski &

Perleberg, 2012). The ecology and management of shallow lakes is fundamentally

different from deep lakes as they are generally warmer, more turbid, and more productive

than deep lakes (Scheffer, 2004). Managing lakes in southern Minnesota requires an

understanding of how certain physical and geographic factors affect the aquatic

macrophyte communities. The purpose of this study is to quantify the relationships

between mean species richness, lake sediment, and geographic factors in five major lakes

in Sibley County, Minnesota, USA.

MATERIALS AND METHODS

Study site

      This study took place in Sibley County, Minnesota, which is located in the Prairie

Pothole Region of North America (Guntenspergen et al., 2002) (Fig 3.1). Cultivated land

makes up ~79% of Sibley County's total land area (Sibley County, 2018). Dominant soil

series include Lester and Canisteo soil series, both of which are loams rich in silts and

clays that have a high CEC (National Resource Conservation Service, 1997). For this

study, five natural, shallow lakes were surveyed: High Island Lake, Titlow Lake,

Schilling Lake, Silver Lake, and Clear Lake (Table 3.1, Fig 3.1). These lakes are warm,

eutrophic to hypereutrophic systems, that are characterized by high productivity and turbidity throughout the growing season. Recreation is the primary use of these lakes, which primarily consists of boating, fishing, and duck hunting. Dominant submersed aquatic macrophytes in the study lakes were *Ceratophyllum demersum* L. (coontail), *Potamogeton crispus* L. (curlyleaf pondweed), and sago pondweed, with *Typha spp.* L. (cattails) being the dominant shoreline macrophytes in 2019 (Schmid & Wersal, 2021).

Lake surveys

Similar to other studies in southern Minnesota, all five lakes in Sibley County were surveyed using point-intercept surveys (Woolf & Madsen, 2003; Case & Madsen, 2004; Madsen et al., 2006; Wersal et al., 2006). For all five lakes, survey points were arranged in a 150m grid (Fig 3.2-3.6). These point grids were used to conduct macrophyte community and sediment surveys in May and June of 2019. During the surveys, these points were navigated to by watercraft under the direction of a GPS enabled ruggedized tablet which has a spatial accuracy of 2 m (Trimble Navigation Limited, Sunnyvale, California, USA). At each point, a plant rake was deployed and allowed to reach the benthos after which it was retrieved. All plants attached to the plant rake were identified and plant species presence was recorded. Sediment cores were also taken at each point by pushing a 5 cm diameter sediment corer into the benthos between 20 cm and 30 cm deep to collect an adequate sediment volume. Additionally, depth at each point was recorded using a sounding rod. All spatial data were recorded electronically using Site Mate software (Farm Works Information Management,

Hamilton, Indiana, USA) that records geospatial data and allows for the entry of geospatial attributes in the field, which reduces data entry errors and post-processing time (Wersal et al., 2010; Cox et al., 2014; Madsen et al., 2015). A pick list of aquatic macrophytes was constructed for these surveys that allowed for the recording of macrophyte species in a database template (Appendix A). Mean species richness was calculated for each lake by averaging the number of unique species at each point. Secchi depth was also recorded during surveys at each lake. Secchi depth was measured near the geographic center of the lake at mid-day during clear weather.

Sediment analyses

In order to estimate the sediment particle size and SOM, sediment cores were homogenized and dried in a forced-air drying oven for 48 hrs at 105°C. Composition of the fine-grained fraction (particle size) and percent organic matter were both calculated for all oven-dried using a minimum of 60 g of oven-dried sediment per sample.

Particle size of oven-dried sediment samples was estimated using the Bouyoucos hydrometer method (Bouyoucos, 1962). A 50 g portion of oven-dried sediment was weighed, and the exact weight was recorded (*m*). To disperse sediment aggregates, samples were pulverized using a combination of a mortar and pestle and a ceramic spur grinder. After pulverization, sediment samples were then combined with 100mL of a dispersal agent, which was a solution of 50g of sodium hexametaphosphate dissolved in 1L of distilled water. The mixture of sediment and dispersal agent was homogenized using a sediment mixer (SA-14, Gilson Company, Inc, Lewis Center, Ohio, USA). The

mixture sat for 24 hrs before it was mixed for another 2 min in the mixer. The mixture was then added to a 1,000 mL sedimentation cylinder and distilled water was added to bring the final volume to 1,000 mL. A blank cylinder was prepared by combining 100 mL of dispersal agent and 900 mL of distilled water. Samples in each cylinder were thoroughly mixed prior to the start of each test by capping the cylinder with a bung and inverting it multiple times. A hydrometer reading was taken at 40 s and 2 hrs after the start time. Hydrometer readings were taken from blank cylinders after each test reading and ambient air temperature was recorded. Test readings were then corrected by subtracting the blank reading from them and adding or subtracting by a factor of 0.1 for every degree below or above 20 °C, respectively. The corrected 40 s reading was represented as hydrometer 1 (H_1) and the corrected 2 hrs reading was represented as hydrometer 2 (H_2). Proportion of sand (P_{sand}), silt (P_{silt}), and clay (P_{clay}) in the sediment samples was estimated using the following formulae:

$$P_{sand} = 1 - \frac{H_1}{m}$$

$$P_{clay} = \frac{H_2}{m}$$

$$P_{silt} = 1 - (P_{sand} + P_{silt})$$

Proportions of sand, silt, and clay were multiplied by 100 to represent the percent of the sediment for which each constituent accounted.

The SOM of sediment samples was estimated using the loss on ignition (LOI) method (Dean, 1974; Heiri et al., 2001). Of the oven-dried sediment samples, 5g was measured and recorded and represented the pre-ignition weight (m_{pre}). The samples were

placed in crucibles and set in a muffle furnace. The muffle furnace cycled at 550°C for

16 hrs and the samples were re-weighed (m_{post}). The percentage of SOM (P_{SOM}) in the

samples was calculated using the following formula:

$$P_{SOM} = \frac{m_{pre} - m_{post}}{m_{pre}}$$

The P_{SOM} was then multiplied by 100 to represent the percent of the sediment that

consisted of SOM.

Spatial modeling and statistical analyses

In order to assess the effects of abiotic factors on the macrophyte communities all

geoprocessing and geospatial analyses were conducted using ArcMap and ArcGIS Pro

(Environmental Systems Research Institute, Redlands, California, USA) using a P≤0.05

significance level. Data from lake surveys consisted of presence and absence of

macrophyte species, water depth, and geographic coordinates. Species richness and

distance from shore of each point was calculated and added as an attribute. A point's

distance from shore was determined by calculating the shortest distance from that point to

the edge of the lake polygon, which was based on the lake's historic boundary.

Generalized linear regressions (GLR) were performed on survey data to determine

relationships between mean species richness and water depth, distance from shore,

percent sand, percent silt, percent clay, and percent SOM within lakes (Fleming et al.,

2015; Fleming et al., 2021). Additionally, relationships between these same independent

variables and the presence and absence of both curlyleaf pondweed and sago pondweed

in Schilling Lake were analyzed using a GLR. The best models were determined

principally by the corrected Akaike's information criterion (AICc) values, where a lower

AICc is considered a stronger model (Fleming et al., 2015; Fleming et al., 2021). Models

with AICc values that were within ±2 of each other were considered not significantly

different. In cases where the strongest models were not significantly different, the most

parsimonious model was considered the strongest model. The strongest model was then

used as a candidate model for the dependent variable. After the candidate model was

determined, a Moran's I test for spatial autocorrelation was conducted on the residuals of

that model (Chen, 2016). If the Moran's I test determined the residuals to be non-

randomly distributed, then a geographically weighted regression (GWR) was executed

using the same variables as the GLR. Neighborhoods for the GWR were produced using

the golden search function. Model performance was assessed based on the appropriate

pseudo-R^2 values provided in regression outputs.

RESULTS

Mean species richness at High Island Lake was 0.61 (Appendix B&C). The

candidate model for species richness in High Island Lake consists of water depth as the

only explanatory variable. The candidate model has a *pseudo*-R^2 of 0.281 (Table 3.2).

Water depth is negatively related to species richness with a slope coefficient of -1.5416

(Table 3.3). The global Moran's I found that the residuals of the candidate model are

significantly clumped (Z=4.498, P<0.001) (Table 3.3), so a GWR was performed on the

candidate model. The GWR has an improved *pseudo*-R^2 of 0.374 when compared to the

global model, which has a *pseudo*-R^2 of 0.278.

Mean species richness at Titlow Lake was 0.16 (Appendix B&C). There is no significant explanatory variables for species richness in Titlow Lake according to the GLR. The GLR with clay as the sole explanatory variable has the highest performance, but the *pseudo*-R^2 value is 0.010 (Table 3.2). According to the Moran's I, residuals for this GLR are clumped (Z=1.837, P=0.066) (Table 3.3). However, the GWR is unable to find enough variation in species richness across at least one of the neighborhoods and is unable to execute.

Mean species richness at Schilling Lake is 0.71 (Appendix B&C). Species richness for Schilling Lake is negatively related water depth and silt. The *pseudo*-R^2 for this candidate model is 0.285 (Table 3.2). Slope coefficients for the explanatory variables are -0.8854 and -0.0284 for water depth and silt, respectively (Table 3.3). The residuals for this candidate model are also clumped (Z=3.708, P<0.001) (Table 3.3), so a GWR was performed. The *pseudo*-R^2 for the global model with these variables is 0.2679, and the GWR has a *pseudo*-R^2 of 0.4169. Frequency of occurrence for sago pondweed and curlyleaf pondweed in Schilling Lake is 6.25 and 44.44 respectively. Presence and absence of curlyleaf pondweed was modeled with water depth, silt, and SOM as explanatory variables. The *pseudo*-R^2 of the candidate model is 0.143 (Table 3.4). Both water depth and silt are negatively related to the presence and absence of curlyleaf pondweed, with slope coefficients of -1.4582 and -0.0613 respectively (Table 3.5). Conversely, presence and absence of curlyleaf pondweed is positively related to SOM with a slope coefficient of 0.0367 (Table 3.5). Residuals from this model are clumped according to Moran's I (Z=3.959, P<0.001) (Table 3.5). The GWR on these

variables produced a *pseudo*-R^2 of 0.341, which is greater than the global model's *pseudo*-R^2 of 0.116. Presence and absence of sago pondweed was also modeled, but the GLR shows there is no significant explanatory variables and produced no *pseudo*-R^2 values greater than zero. The strongest explanatory variable for the presence/absence of sago pondweed is percent silt, which had a P-value of 0.544 (Table 3.5). The residuals of the model are randomly distributed (Z=-1.086, P=0.278) (Table 3.5).

Mean species richness at Silver Lake is 0.30 (Appendix B&C). Regarding species richness in Silver Lake, the model with the highest performance consisted of water depth, distance from shore, and silt as the explanatory variables; the *pseudo*-R^2 for this model is 0.357 (Table 3.2). Both water depth and distance from shore are negatively related to species richness in Silver Lake. The GLR's slope coefficient was -2.8882 for water depth and -0.0085 for distance from shore (Table 3.3). In the candidate model, silt is positively related to species richness and has a slope coefficient of 0.0510 (Table 3.3). Residuals of the GLR were found to be randomly distributed by the Moran's I test (Z=0.580, P=0.562) (Table 3.3).

Mean species richness at Clear Lake is 0.08 (Appendix B&C). The candidate model for species richness in Clear Lake consists of distance from shore as the only significant explanatory variable. This model had a *pseudo*-R^2 of 0.313 (Table 3.2). Distance from shore is negatively related to the species richness, with a slope coefficient of -0.0424 (Table 3.3). The residuals of the candidate model are randomly distributed according to Moran's I (Z=-1.383, P=0.167) (Table 3.3).

DISCUSSION

The factors that affected mean species richness the most are water depth, sample distance from shore, and percent silt. All mean species richness models with significant results have relatively high *pseudo*-R^2 values (Table 3.2), and selected explanatory variables account for between 25% and 40% of the variation in species richness in all significant models.

Water depth is related to mean species richness in three of the five lakes in Sibley County (Table 3.3; Appendix B&C). In all three models, water depth is negatively related to mean species richness. Negative relationships between water depth and mean species richness are primarily driven by the reduction of light availability at increasing depths (Barko et al., 1985; Lacoul & Freedman, 2006; Bornette & Puijalon, 2011). In both Schilling Lake and High Island Lake, mean species richness decreases as depth increases. This supports the hypothesis that light attenuation increases as depth increases, which inhibits the richness and frequency of macrophytes at greater depth. Both Schilling Lake and High Island Lake have relatively deep secchi depths (Table 3.1), and ~95% of all macrophytes were found growing within 2m of the surface in both lakes. Silver Lake also has depth as a significant variable (Table 3.3), however, Silver Lake is dominated by *Nymphaea odorata* Aiton (fragrant waterlily), a floating-leaf macrophyte, whereas Schilling lake and High Island Lake are dominated by submersed aquatic vegetation (curlyleaf pondweed and sago pondweed). The dominance of fragrant waterlily in Silver Lake is likely due to the lake's high turbidity (Table 3.1). Floating-leaf macrophytes are able to attenuate light at the surface of the water, which negates the

growth inhibition of turbidity (Lacoul & Freedman, 2006). Prior to the production of floating leaves, fragrant waterlily produces submersed growth that is subject to the effects of turbidity, which is probably a reason why fragrant waterlily is usually relegated to shallow water (Lacoul & Freedman, 2006). This zonation of floating leaf macrophytes was observed in Silver Lake, as nearly all macrophytes surveyed are found at depths shallower than 1.5m. This evidence suggests that water depth is a major limiting factor for mean species richness in Silver Lake.

Similar to how depth limits mean species richness of Silver Lake, there is also a significant negative relationship between distance from shore and mean species richness in Silver Lake (Table 3.3, Appendix B&C). This is likely because fragrant waterlily is the dominant macrophyte. Floating leaf macrophytes are usually distributed much closer to shore than submersed macrophytes, which would explain why distance from shore is a significant predictor in Silver Lake mean species richness (Lacoul & Freedman, 2006). Additionally, submersed macrophytes can inhabit areas that are deeper and further from shore than free-floating macrophytes, which would explain why distance from shore is not a significant variable in Schilling and High Island lake (Lacoul & Freedman, 2006). In the Clear Lake model, distance from shore is the only significant variable that affects the richness of macrophtyes (Table 3.3, Appendix B&C). Distance from shore is highly influential in Clear Lake's mean species richness because its bottom is deeper than the other lakes in the study, and the water clarity is low. Additionally, water depth deepens dramatically very close to the shore. This steep slope in combination with turbid waters greatly limits the distance from shore that rooted macrophytes could grow in Clear Lake.

The only sediment factor related to mean species richness is percent silt in

Schilling Lake and Silver Lake (Table 3.3, Appendix B&C). Silt consists of fine-grained

particles that readily re-suspend when significant wave action is present (Barko et al.,

1991; Koch, 2001). When suspended in the water column, silt contributes significantly to

turbidity, which limits light availability for submersed macrophytes (Zhu et al., 2015).

However, higher silt content can improve nutrient availability of the sediment by raising

the CEC (Gerbersdorf et al., 2007). This tradeoff causes silt content of the sediment to

exhibit both facultative and inhibitory effects on the abundance and distribution of

aquatic macrophytes and whether precent silt is positively or negatively related to

sediment silt is largely species-specific (Koch, 2001). Both relationships were observed

in this study. Silt percent is negatively related to the species richness in Schilling Lake,

which is dominated by curlyleaf pondweed. Additionally, the presence of curlyleaf

pondweed in Schilling Lake is negatively related to silt percent. Data from these models

suggest that silt in the sediment inhibits growth of curlyleaf pondweed because it

contributes to turbidity as it is suspended in the water column. Conversely, in the

fragrant waterlily dominated Silver Lake, species richness is positively related to percent

silt in the sediment. Fragrant waterlily produces thick rhizomes that support large

floating leaves. Once the floating leaves reach the surface of the water, fragrant waterlily

can offset the detrimental effects of turbidity, which is why fragrant waterlily and other

morphologically similar species often dominate shallow, turbid lakes (Lacoul &

Freedman, 2006). The positive relationship observed in Silver Lake suggests not only is

fragrant waterlily not inhibited by suspended silt, but it benefits from the higher sediment

nutrient availability caused by silts greater CEC (Gerbersdorf et al., 2007).

A similar study in Heron Lake (Jackson County, Minnesota, USA) found that the

frequency of sago pondweed was positively related to percent silt in the sediment (Case

& Madsen, 2004). Although sago pondweed is a submersed aquatic macrophyte, like

curlyleaf pondweed, unlike curlyleaf pondweed, it is a prolific tuber producer (Kantrud,

1990; Wersal et al., 2006). Researchers conducting a study in Swan Lake (Nicollet

County, Minnesota, USA) observed a preference for siltier sediment exhibited by

Vallisneria americana Michx. (American eelgrass), another species with high root

biomass (Madsen et al., 2006). Similar to fragrant waterlily, sago pondweed and

American eelgrass are likely benefitting from the higher CEC of silt rich soils, which is

beneficial for plants with high root biomass. Ultimately, evidence from this study and

previous studies show that the effect silt has on the abundance and distribution of aquatic

macrophytes is highly species-specific.

In Schilling Lake, the dominant submersed macrophyte was curlyleaf pondweed.

The model for factors that affect the presence and absence of curlyleaf pondweed in

Schilling Lake had water depth and percent silt as significant, explanatory variables, just

like the model for mean species richness in Schilling Lake (Table 3.5). However, the

curlyleaf pondweed model also had percent SOM as a significant explanatory variable,

which was a positive predictor of the presence of curlyleaf pondweed in Schilling Lake

(Table 3.5). This relationship contradicts the literature, which consistently cites SOM as

an inhibitor of rooted macrophyte growth (Barko & Smart, 1986; Koch, 2001). However,

previous studies have found that the inhibitory effects of SOM plateau after about 20% SOM (Barko & Smart, 1986), and in Schilling Lake, the mean percent SOM was 27.77% (s=10.02%). Additionally, a mesocosm study found that different species of submersed macrophytes express differential susceptibility to the inhibitory effects of SOM (Silveira & Thomaz, 2015). It could be that curlyleaf pondweed is not as susceptible to growth inhibition by SOM.

CONCLUSIONS

Overall, model results for factors that affect mean species richness in the study lakes show depth as the primary factor. However, in lakes with high turbidity, the effect of water depth on mean species richness is diminished and distance from shore was instead found to be a significant variable. Sediment silt also had significant, negative effects on mean species richness in Schilling Lake, however, in Silver Lake, which was dominated by a floating-leaf macrophyte, silty sediments promoted mean species richness. When predicting the distribution of macrophytes in shallow lake systems, water depth should be the principal factor accounted for. Lakes in which depth was a significant predictor had frequency of macrophytes greatly diminish at depths greater than 2 m due to the reduced light availability. Distance from shore will also need to be accounted for as some of the lakes showed a reduction of mean species richness and frequency as distance from shore increased. This study determined that the only sediment factor that was a significant predictor of macrophtye distribution was silt.

However, whether silt promotes or inhibits macrophyte frequency and richness depends on species composition. Silt contributes to turbidity in some systems, which can negatively affect submersed macrophytes. However, in systems where floating leaf macrophytes are dominant, the distribution of macrophytes may be positively related silt content, with the higher CEC of the silt as a possible explanation.

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TABLES

Table 3.1 Physical and geographic properties of the five study lakes in Sibley County, Minnesota, USA during the 2019 growing season.

	Latitude (°)	Longitude (°)	Total area (km^2)	Average depth (cm)	Secchi depth (cm)	mean species richness
High Island Lake	44.6678	-94.2103	6.99	167.6	149	0.61($\pm$0.05)
Titlow Lake	44.5696	-94.2000	3.60	149.4	22	0.16($\pm$0.03)
Schilling Lake	44.6959	-94.2103	3.55	167.6	86	0.71($\pm$0.07)
Silver Lake	44.6185	-93.9710	2.92	164.6	10	0.30($\pm$0.08)
Clear Lake	44.4566	-94.5147	2.04	228.6	29	0.08($\pm$0.03)

Table 3.2 Model selection for the factors that affect the species richness in the five study lakes, Sibley County, Minnesota, USA 2019.

Lake	Model[a]	AICc[b]	ΔAICc[c]	Pseudo-R^2	Rank
High Island Lake	DEPTH	439.18	0.00	0.281	1
	DEPTH+DISTANCE	440.59	1.41	0.272	2
	DEPTH+DISTANCE+SAND	442.22	3.04	0.275	3
	DEPTH+DISTANCE+SAND+CLAY	444.09	4.91	0.271	4
	DEPTH+DISTANCE+SAND+SILT+CLAY	445.90	6.72	0.270	5
	DEPTH+DISTANCE+SAND+SILT+CLAY+SOM	447.88	8.70	0.267	6
Titlow Lake	CLAY	150.48	0.00	0.010	1
	SILT+CLAY	151.67	1.19	0.007	2
	DEPTH+SILT+CLAY	153.23	2.75	0.004	3
	DEPTH+SAND+SILT+CLAY	154.79	4.31	-0.001	4
	DEPTH+DISTANCE+SAND+SILT+CLAY	156.70	6.22	-0.004	5
	DEPTH+DISTANCE+SAND+SILT+CLAY+SOM	158.14	7.66	-0.003	6
Schilling Lake	DEPTH+SILT	280.53	0.05	0.285	1
	DEPTH+DISTANCE+SILT	280.48	0.00	0.315	2
	DEPTH+DISTANCE+SILT+SOM	281.15	0.67	0.328	3
	DEPTH+DISTANCE+SILT+CLAY+SOM	282.47	1.99	0.314	4
	DEPTH+DISTANCE+SAND+SILT+CLAY+SOM	285.27	4.79	0.306	5
Silver Lake	DEPTH+DISTANCE+SILT	111.03	1.08	0.357	1
	DEPTH+DISTANCE+SILT+CLAY	109.95	0.00	0.408	2
	DEPTH+DISTANCE+SILT+CLAY+SOM	111.07	1.12	0.402	3
	DEPTH+SILT	113.60	3.65	0.400	4
	DEPTH+DISTANCE+SAND+SILT+CLAY+SOM	112.36	2.41	0.389	5
Clear Lake	DISTANCE	36.80	0.00	0.313	1
	DISTANCE+SILT	36.97	0.17	0.298	2
	DEPTH+DISTANCE+SILT	37.86	1.06	0.273	3
	DEPTH+DISTANCE+SILT+SOM	40.38	3.58	0.278	4
	DEPTH+DISTANCE+SILT+CLAY+SOM	42.83	6.03	0.270	5
	DEPTH+DISTANCE+SAND+SILT+CLAY+SOM	44.82	8.02	0.262	6

[a]Model variables are water depth (DEPTH), distance from shore (DISTANCE), percent sand (SAND), percent silt (SILT), percent clay (CLAY), and percent sediment organic matter (SOM).
[b]Corrected Akaike's Information Criterion
[c]The difference between the lowest AICc value and the respective AICc value

Table 3.3 Statistics for the explanatory variables and Moran's I results on the residuals of the candidate models for the factors that affect the species richness in the five study lakes, Sibley County, Minnesota, USA 2019. Candidate models were determined via GLR.

Lake	Variable[a]	Explanatory variable statistics			Moran's I	
		Slope coefficient	Standard error	P-value	Z-score	P-value
High Island Lake	DEPTH	-1.5416	0.1883	<0.001	4.498	<0.001
Titlow Lake	CLAY	-0.0242	0.0163	0.137	1.837	0.066
Schilling Lake	DEPTH	-0.8854	0.2005	<0.001	3.708	<0.001
	SILT	-0.0284	0.0083	<0.001		
Silver Lake	DEPTH	-2.8882	0.4929	<0.001	0.580	0.562
	DISTANCE	-0.0085	0.0043	0.047		
	SILT	0.0510	0.0153	<0.001		
Clear Lake	DISTANCE	-0.0424	0.0156	0.007	-1.383	0.167

[a]Model variables are water depth (DEPTH), distance from shore (DISTANCE), percent silt (SILT), and percent clay (CLAY).

Table 3.4 Model selection for factors that affect presence/absence of curlyleaf pondweed and sago pondweed in Schilling Lake, Sibley County, Minnesota, USA 2019.

Species	Model[a]	AICc[b]	ΔAICc[c]	*Pseudo*-R^2	Rank
Curlyleaf pondweed	DEPTH+SILT+SOM	181.45	0.00	0.143	1
	DEPTH+SILT	183.59	2.14	0.122	2
	DEPTH+DISTANCE+SILT+SOM	181.67	0.22	0.145	3
	DEPTH+DISTANCE+SAND+SILT+SOM	183.41	1.96	0.141	4
	DEPTH+DISTANCE+SAND+SILT+CLAY+SOM	185.23	3.78	0.135	5
Sago pondweed	SILT	70.96	0.00	-0.003	1
	SILT+CLAY	72.19	1.23	-0.005	2
	DISTANCE+SILT+CLAY	73.71	2.75	-0.012	3
	DISTANCE+SILT+CLAY+SOM	75.54	4.58	-0.017	4
	DEPTH+DISTANCE+SILT+CLAY+SOM	77.51	6.55	-0.023	5
	DEPTH+DISTANCE+SAND+SILT+CLAY+SOM	80.5	9.54	-0.030	6

[a]Model variables are water depth (DEPTH), distance from shore (DISTANCE), percent sand (SAND), percent silt (SILT), percent clay (CLAY), and percent sediment organic matter (SOM).
[b]Corrected Akaike's Information Criterion
[c]The difference between the lowest AICc value and the respective AICc value

Table 3.5 Statistics for explanatory variables and Moran's I results on residuals of the candidate models for factors that affect presence/absence of curlyleaf pondweed and sago pondweed in Schilling Lake, Sibley County, Minnesota, USA 2019. Candidate models were determined via GLR.

| Species | | Explanatory variable statistics | | | Moran's I | |
Species	Variable[a]	Slope coefficient	Standard Error	P-value	z-score	P-value
Curlyleaf pondweed	DEPTH	-1.4582	0.5127	0.004		
	SILT	-0.0613	0.0170	<0.001	3.959	<0.001
	SOM	0.0367	0.0186	0.048		
Sago pondweed	SILT	0.0167	0.0275	0.544	-1.085	0.278

[a]Model variables are water depth (DEPTH), percent silt (SILT), and percent sediment organic matter (SOM).
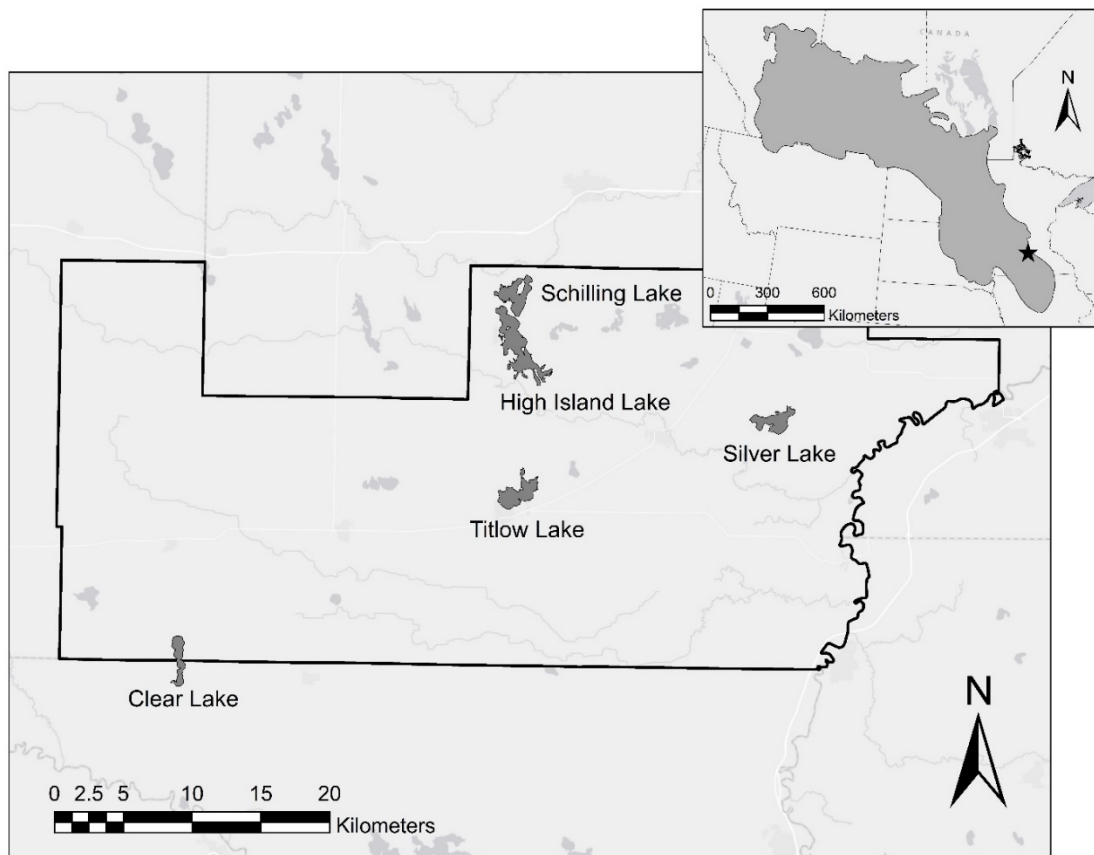
FIGURES

Fig 3.1 Five lakes in Sibley County, Minnesota that were surveyed during the 2019 growing season. Black line indicates the border of Sibley County. Inset shows the position of Sibley County (black star) in the Prairie Pothole Region located in Midwestern North America.
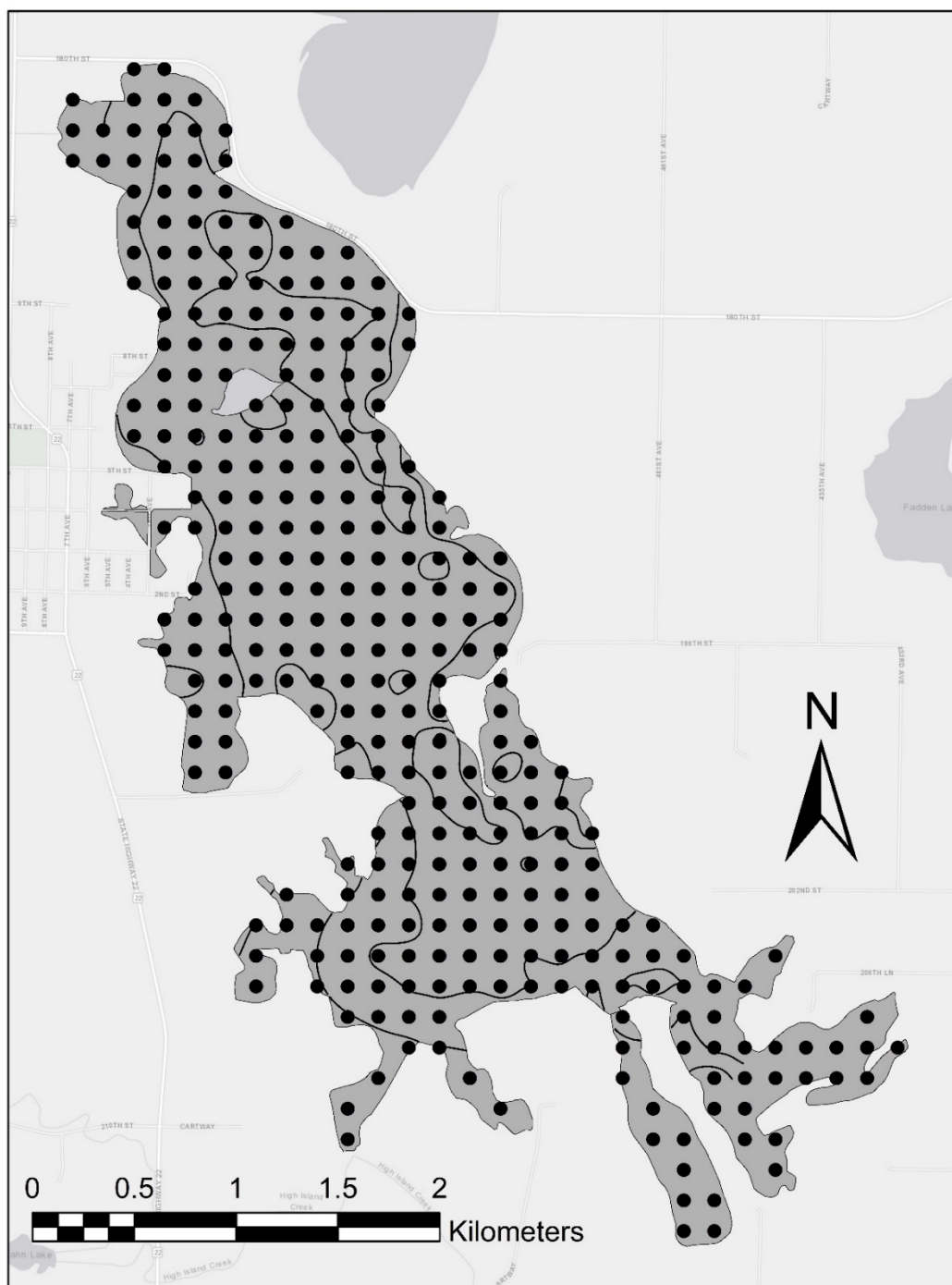
Fig 3.2 The grid of survey points in High Island Lake for the surveys during the 2019 growing season in Sibley County, Minnesota. Contour lines represent changes of depth by 0.5m intervals. Contour lines derived from depth data at sample points (n=318).

Fig 3.3 The grid of survey points in Titlow Lake for the surveys during the 2019 growing season in Sibley County, Minnesota. Contour lines represent changes of depth by 0.5m intervals. Contour lines derived from depth data at sample points (n=163).

Fig 3.4 The grid of survey points in Schilling Lake for the surveys during the 2019 growing season in Sibley County, Minnesota. Contour lines represent changes of depth by 0.5m intervals. Contour lines derived from depth data at sample points (n=160).
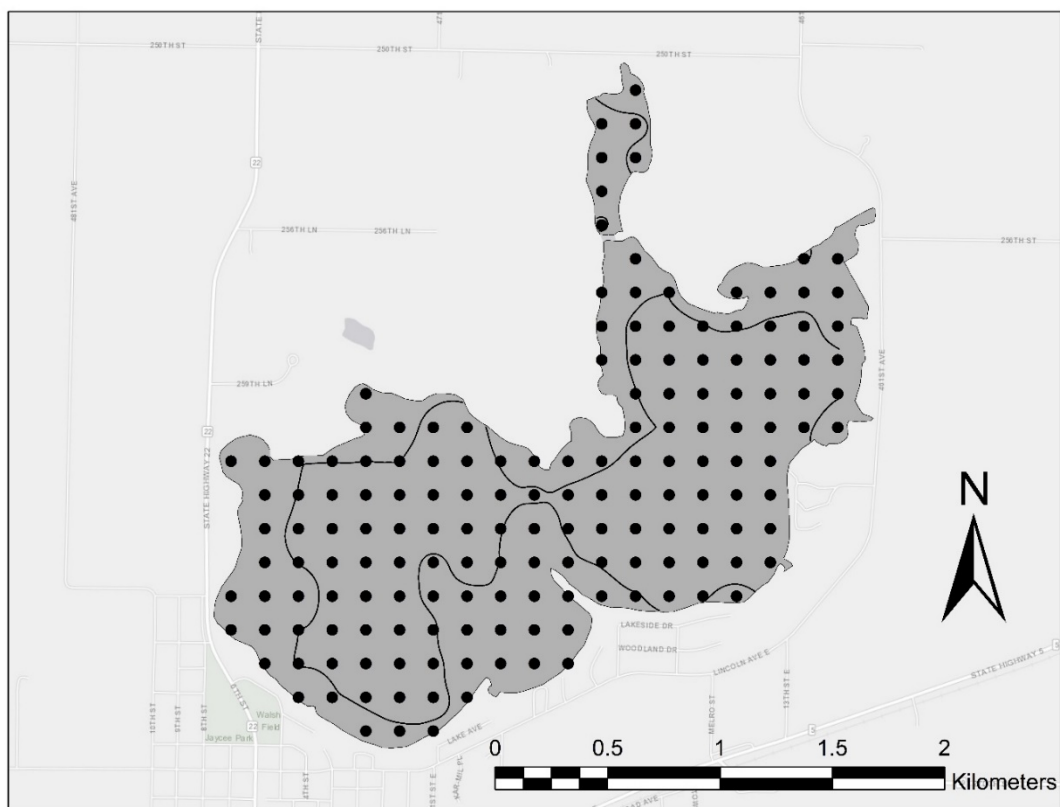
Fig 3.5 The grid of survey points in Silver Lake for the surveys during the 2019 growing season in Sibley County, Minnesota. Contour lines represent changes of depth by 0.5m intervals. Contour lines derived from depth data at sample points (n=129).

Fig 3.6 The grid of survey points in Clear Lake for the surveys during the 2019 growing season in Sibley County, Minnesota. Contour lines represent changes of depth by 0.5m intervals. Contour lines derived from depth data at sample points (n=90).
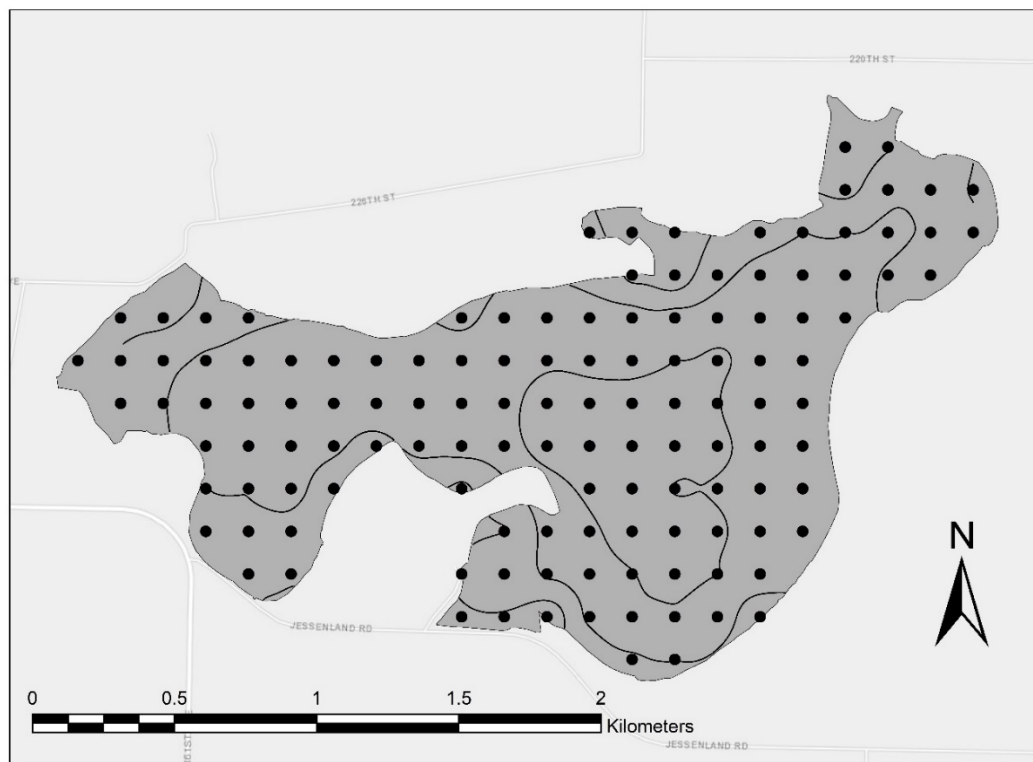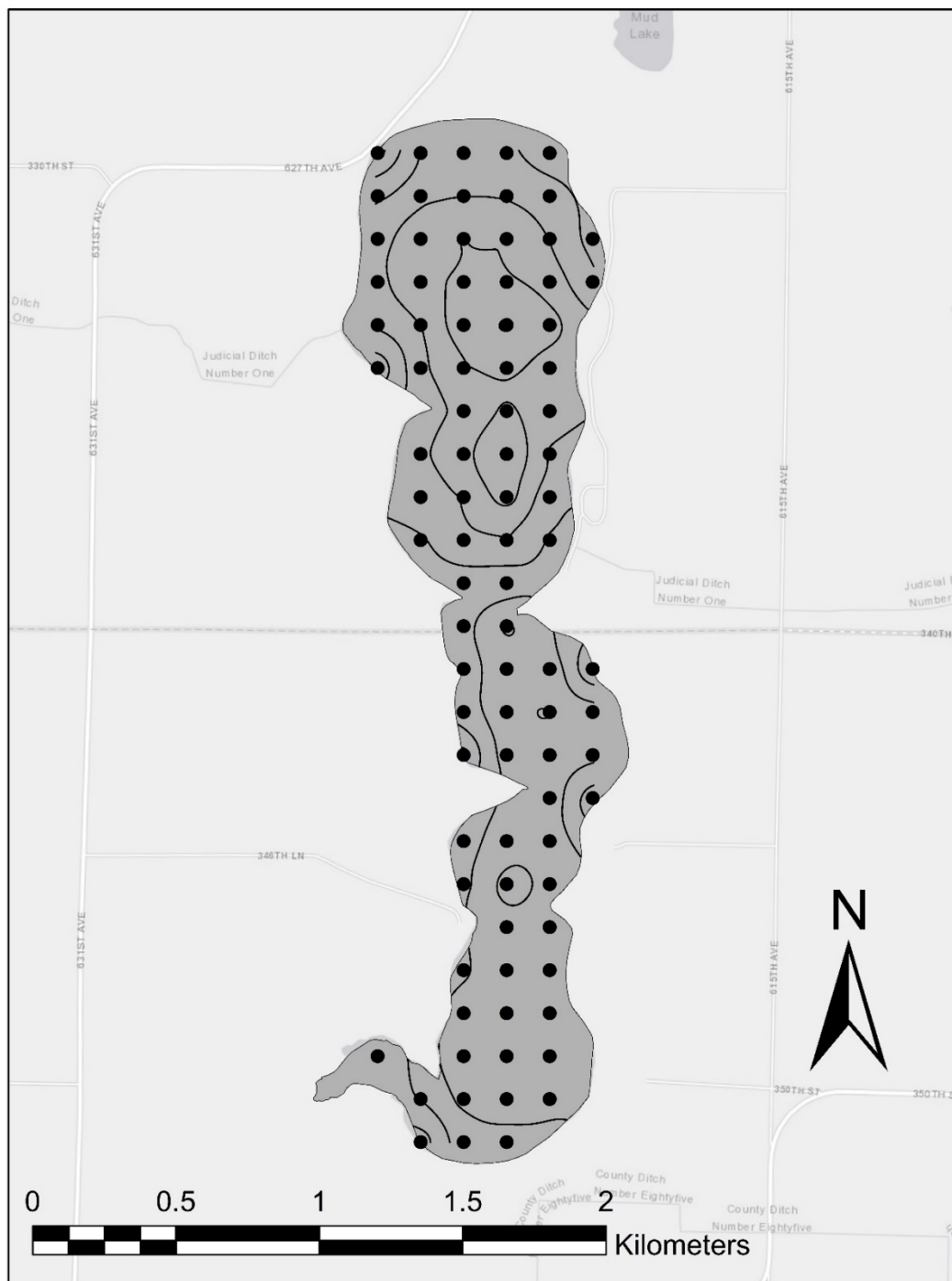
CHAPTER 4 – CONCLUSIONS

Seasonal macrophyte community shifts

Sago pondweed was the dominant macrophyte in High Island Lake and Titlow Lake. Sago pondweed is an herbaceous perennial that can form dense canopies during the mid to late growing season (Wersal et al., 2006). Sago pondweed also produces tubers that overwinter in the sediment and supports shoot growth the following year (Wersal et al., 2006). Water temperature is a major driver of the seasonal growth of sago pondweed (and many other submersed macrophytes), which explains why there was an increase in species richness in many of the study lakes from early to late season (Lacoul & Freedman, 2006; Wersal et al., 2006; Bornette & Puijalon, 2011). Titlow Lake exhibited an increase in mean species richness from the early season survey (0.16) to the late season survey (0.28), which was driven by the presence of sago pondweed. This increase in mean species richness was consistent with the phenology of sago pondweed, which generally exhibits maximum shoot growth in mid to late summer and starts dying back in the fall (Case & Madsen, 2004; Wersal et al., 2006).

In Silver Lake, there was a decline in mean mean species richness from early season (0.30) to late season (0.20), however this is primarily attributed to the absence of submersed aquatic vegetation in the late season, caused by a dense algal bloom. The dominant macrophyte in Silver Lake (fragrant waterlily) and the primary emergent macrophyte (cattails) exhibited no discernable change in frequency from early season to late season. This is primarily because growth forms of these macrophytes leave them

largely unaffected by the increase in turbidity from an algal bloom (Lacoul & Freedman, 2006).

Schilling Lake exhibited the most dramatic shifts in community composition from early season to late season. This shift was driven by the infestation of curlyleaf pondweed, which exhibits a unique winter annual phenology in the northern latitudes of North America (Turnage et al., 2018). During the early part of the season, curlyleaf pondweed formed dense mats that out-competed other submersed macrophytes for light and limited mean species richness. However, by midsummer, curlyleaf pondweed had produced turions and died back. Sago pondweed became the dominant submersed macrophyte in Schilling Lake after the senescence of curlyleaf pondweed. This is expected, since the phenology of sago pondweed does not exhibit maximum biomass until well after curlyleaf pondweed senesces (Wersal et al., 2006). However, sago pondweed was not the only species that benefitted, as species that were absent in the early season (like slender naiad and muskgrasses) were recorded in the late season as the competitive pressure from curlyleaf pondweed was released. The decline in curlyleaf pondweed ultimately resulted in an increase in Schilling Lake's species richness from early season (0.69) to late season (1.11) even though it may have displaced native species in the early season. Overall, the shifts in macrophyte communities in Sibley County lakes varied by lake.

Relationships between macrophytes and abiotic factors

Abiotic factors in Sibley County lakes exhibited strong relationships with the abundance and distribution of macrophtyes. The best predictors of mean species richness were water depth, distance from shore, and percent silt. Although all three variables were related to mean species richness in multiple lakes, only Silver Lake had all three variables in the final candidate model, and none of these variables were significant across all five lakes. This variability in significant explanatory variables suggests that the relationships between these abiotic factors and macrophyte communities are highly complex.

Water depth was the most common predictor of mean species richness, and in High Island Lake, Schilling Lake, and Silver Lake, water depth was negatively related to mean species richness. This relationship is primarily driven by the reduction in light availability at increasing depths. As water depth increases, light that is attenuated by the water column increases, causing light to be a limiting factor for macrophyte abundance (Barko et al., 1985; Lacoul & Freedman, 2006; Bornette & Puijalon, 2011). The variation in water depth is the principal factor that causes the zonation of macrophyte growth forms in the littoral zone (Wetzel, 2001).

In both Silver Lake and Clear Lake, the distance from shore was a significant negative predictor of mean species richness. This relationship is similar to how depth affects macrophyte abundance and distribution, as depth generally increases as the distance from shore increases. Specifically, in Clear Lake, water depth increased dramatically near the shoreline, but in the middle of the lake, depth had low variability. This caused all of the macrophytes to be recorded in close proximity (<100m) to the shore. In the case of Silver Lake, the dominant macrophyte was fragrant waterlily, a

floating leaf macrophyte that most often grows in close proximity to the shore (Lacoul & Freedman, 2006).

The only sediment factor that was a significant predictor of mean species richness was percent silt in Schilling Lake and Silver Lake. However, macrophyte communities responded differently; species richness in Schilling Lake was negatively related to silt, whereas species richness in in Silver Lake was positively related to silt. Sediment with high silt content introduces an ecological tradeoff for aquatic macrophytes. Silty sediment has higher nutrient availability than coarser sediments caused by a greater cation exchange capacity; however, silty sediment also has a greater bulk density that hinders root growth (Gerbersdorf et al., 2007). In Schilling Lake, the primary macrophyte was curlyleaf pondweed, which produces a relatively limited root system. This suggests that siltier sediments impeded the growth and limited the abundance of curlyleaf pondweed. Conversely, Silver Lake was dominated by fragrant waterlily, which is a prolific producer of large, persistent rhizomes. The large rhizomes of fragrant waterlily could benefit from the greater nutrient availability of silty sediments and cause them to be more abundant. Ultimately, the response of a macrophyte community to silt seems to be largely dependent on the community structure.

Data applications

These data show that life history strategy is a major factor that influences seasonal species composition and needs to be accounted for when managing lakes. In the instance of curlyleaf pondweed, management needs to occur in the spring when native species

growth is low and curlyleaf pondweed has not yet produced turions (Poovey et al., 2002; Turnage et al., 2018). Additionally, of all the lakes in this study, the only lake infested with an invasive macrophyte was Schilling Lake, which was also the most species rich lake. This supports the "rich get richer" hypothesis; aquatic invasive species are more often found in systems with greater species richness (Stohlgren et al., 2003).

While silt content may be beneficial for some native macrophytes, high turbidity caused by fine suspended sediments can greatly limit the growth of submersed aquatic vegetation and contribute to algal blooms (James et al., 2004; Valipour et al., 2017). Many factors can affect turbidity, and controlling turbidity in lakes can be difficult. There are documented turbidity reductions and macrophyte diversity improvements from biomanipulation in a Minnesota lake (Hansel-Welch et al., 2003). This study showed that draw-downs can remove excess fine sediment, stabilize sediment with rooted macrophytes, and ultimately promote a clear water column with higher light availability and macrophyte growth (Hansel-Welch et al., 2003).

Based on spatial models, water depth is the best predictor of mean species richness in shallow lakes, in that it will be a main driver of light limitation. Light is the most limiting factor for aquatic plant growth, because light availability is primarily a factor of water depth and turbidity (Barko et al., 1985; Lacoul & Freedman, 2006; Bornette & Puijalon, 2011). When depth was a significant predictor of mean species richness, more than 95% of all macrophytes were found at depths shallower than 2 m. These data could be applied to surveys of similar lakes. When surveying other shallow lakes in southern Minnesota, managers and researchers can focus resources and survey

time to areas with depths shallower than 2m and capture the majority of the littoral zone. This will improve the efficiency of surveys by reducing time and labor costs for managers and researchers.

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APPENDICES

Appendix A Pick-list fields used for point-intercept surveys. Field names were used as
column headings for survey datasets.

	Field name	Definition
	ObjectID	
Geophraphic data	Speed	Speed (m/s)
	Heading	Heading (°)
	Elevation	Elevation (m)
	Depth	Water depth (ft)
	Date	
	SampleID	
Macrophyte species	B_schreber	*Brasenia schreberi*
	C_demersum	*Ceratophyllum demersum*
	Carex	*Carex spp.*
	E_canadens	*Elodea canadensis*
	L_minor	*Lemna minor*
	M_sibiricu	*Myriophyllum sibiricum*
	M_spicatum	*Myriophyllum spicatum*
	N_obtusa	*Nitellopsis obtusa*
	N_lutea	*Nuphar lutea*
	N_odorata	*Nymphaea odorata*
	P_crispus	*Potamogeton crispus*
	P_foliosus	*Potamogeton foliosus*
	P_richards	*Potamogeton richardsonii*
	P_zosterif	*Potamogeton zosteriformis*
	R_aquatili	*Ranunculus aquatilis*
	S_latifoli	*Sagittaria latifolia*
	S_acutus	*Schoenoplectus acutus*
	S_tabernae	*Schoenoplectus tabernaemontani*
	S_fluviati	*Scirpus fluviatilis*
	S_eurycarp	*Scirpus eurycarpus*
	S_pectinat	*Stuckenia pectinata*
	Typha	*Typha spp.*
	U_purpurea	*Utricularia pupurea*
	U_vulgaris	*Utricularia vulgaris*
	V_american	*Vallisneria americana*
	W_columbia	*Wolffia columbiana*
	Z_palustri	*Zizania palustris*
	Note1	
	Note2	
	Note3	

Appendix B Mean values of dependent and explanatory variables from all five lakes used in GLR analysis. Mean species richness displayed with ± 1 standard error. Model variables are water depth (DEPTH), distance from shore (DISTANCE), percent sand (SAND), percent silt (SILT), percent clay (CLAY), and percent sediment organic matter (SOM). DEPTH and DISTANCE are measured in meters.

	mean species richness	DEPTH (m)	DISTANCE (m)	SAND	SILT	CLAY	SOM
High Island Lake	0.61(±0.05)	1.67	185.17	67.18	18.77	13.61	26.33
Titlow Lake	0.16(±0.03)	1.49	181.15	40.93	26.94	32.12	14.07
Schilling Lake	0.71(±0.07)	1.67	154.55	65.65	19.69	14.65	27.56
Silver Lake	0.30(±0.08)	1.65	166.61	65.99	18.43	15.59	38.23
Clear Lake	0.08(±0.03)	2.28	121.63	47.09	28.76	24.15	17.52

Appendix C Maximum and minimum values of dependent and explanatory variables from all five lakes used in GLR analysis. Model variables are water depth (DEPTH), distance from shore (DISTANCE), percent sand (SAND), percent silt (SILT), percent clay (CLAY), and percent sediment organic matter (SOM). DEPTH and DISTANCE are measured in meters.

	species richness	DEPTH (m)	DISTANCE (m)	SAND	SILT	CLAY	SOM
High Island Lake	5	2.90	557.94	98.20	36.58	36.18	49.70
	0	0.61	3.34	40.64	0.60	0.80	1.20
Titlow Lake	2	0.79	585.52	89.60	55.99	50.63	35.69
	0	1.83	4.40	3.22	4.00	6.40	1.41
Schilling Lake	4	2.59	404.24	99.60	45.99	43.61	48.89
	0	0.58	13.25	36.20	0.60	0.79	0.60
Silver Lake	5	2.38	457.92	91.20	47.02	35.19	60.00
	0	0.46	7.22	23.23	2.00	2.80	1.81
Clear Lake	1	3.66	367.56	91.20	49.62	39.42	23.02
	0	0.64	3.34	15.17	1.60	3.80	1.40