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# Abiotic factors that affect the distribution of aquatic macrophytes in shallow north temperate Minnesota lakes: a spatial modeling approach

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**Abstract** Macrophytes are an integral component of lake communities; therefore, understanding the factors that affect macrophyte community structure is important for conservation and management of lakes. In Sibley County, Minnesota, USA, five of the largest and most recreationally important lakes 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 partitioned by determining sand, silt, clay, and organic matter fractions. The richness of macrophytes in all lakes were modeled via generalized linear regression with six explanatory variables: water depth, distance from shore, percent sand, percent silt, percent clay, and percent sediment organic matter. If model residuals were spatially autocorrelated, then a geographically weighted regression was used. Mean species richness (N point$^{-1}$) was negatively related to depth and distance from shore and either positively or negatively related to silt depending on the lake and which macrophytes were present. All species richness models had *pseudo*-$R^2$ values between 0.25 and 0.40. Curlyleaf pondweed (*Potamogeton crispus*) was found at 44% of all sampling points in one lake, and its presence was related to water depth, percent silt, and percent sediment organic matter during early season surveys. Results from this study exhibit the inhibitory relationship between water depth and macrophyte growth. The results from these models suggest interactions are complex between macrophytes, environmental factors, and sediment texture; and that these interactions are species and site specific. A single landscape scale model would not be appropriate to capture the in-lake processes driving macrophyte distribution and abundance; and management strategies will need to be developed on a lake-by-lake basis.

**Keywords** Submersed aquatic vegetation · Sediment texture · Sediment organic matter · Generalized linear regression · Water depth · Distance from shore

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## 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 (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 and Giovanni 2002; Wersal et al. 2005; Dibble and Pelicice 2010). Additionally, aquatic macrophytes inhibit the growth of phytoplankton allopathically, and provide habitat for important filter feeders that graze on phytoplankton; which can then mitigate the frequency and intensity of algal blooms (Scheffer 1999; Körner and Nicklisch 2002; Takamura et al. 2003; Bakker et al. 2010). Aquatic vegetation can also improve water clarity by promoting the settling of suspended sediment and inhibiting the resuspension of settled sediment by reducing wave action in the water column (Barko and Smart 1986; James et al. 2004). Aquatic vegetation promotes sedimentation of suspended particles, but macrophyte roots are also essential for maintaining benthos stability (Wang et al. 2015). The benefits of a diverse aquatic plant community affirm its value as an integral constituent of the freshwater lake system. Understanding the factors that affect composition of aquatic macrophyte communities 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. 1986; Lacoul and Freedman 2006; O'Hare et al. 2018). Light is a rate limiting factor for the primary productivity of plants in aquatic systems, as light availability is often limited by the attenuation of light in the water column (Lacoul and Freedman 2006; Bornette and Puijalon 2011). Light availability is the primary driver for competition and niche partitioning of aquatic macrophytes in the littoral zone of lakes (Barko et al. 1986; van Gerven et al. 2015). Typical structure of the littoral zone consists of angiosperms at shallow depths and bryophytes and charophytes at deeper depths (Chambers and Kaiff 1985; Blindow 1992; Azzella et al. 2014). This zonation is primarily driven by the availability of light and the adaptations of plants to those light conditions (van Gerven et al. 2015). 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 and Freedman 2006). Conversely, submersed macrophytes are generally more abundant in lakes where there is more light available in the water column (Lacoul and Freedman 2006).

Water depth is also an important factor that affects 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 and Kaiff 1985; Rooney and Kalff 2000; Azzella et al. 2014). When water depths in a 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 an inhibiter of macrophyte growth because the water column attenuates more light as depth increases. This also explains why submersed macrophytes at lower depths are often better adapted to lower light conditions than macrophytes at shallower depths. Overall, water depth has been found to have a negative relationship between the density and abundance of aquatic macrophytes (Barko et al. 1986; Cheruvelil and Soranno 2008).

Light availability in aquatic systems is primarily a function of turbidity and water depth (Barko et al. 1986; Lacoul and Freedman 2006; Bornette and 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 turbidity in lake systems. Many studies have found presence of aquatic macrophytes reduces wave energy and, consequently, reduces suspension and resuspension of fine sediments that contribute to turbidity (Barko et al. 1991; Madsen et al. 2001; Wu and Hua 2014). Reductions in turbidity could improve light availability and promote further expansion of vegetation. Relationship between turbidity and aquatic macrophytes are complex, but turbidity is a major limiting factor for plant growth by limiting light availability.

In shallow lakes, wave energy can have a profound effect on macrophyte distribution both spatially and temporally (Andersson 2001; Lacoul and Freedman 2006). Depending on the intensity of wave energy, macrophytes may respond by changing their morphology, or increase growth rate due to the availability of nutrients released from re-suspended sediments (Madsen et al. 2001; Lacoul and Freedman 2006; Bornette and Puijalon 2011). Wave energy that reaches bottom sediments in shallow lakes will contribute to suspension and resuspension of fine textured sediment that will affect community structure by limiting light availability and increasing nutrient availability in the water column (Madsen et al. 2001; Schallenberg and Burns 2004; James et al. 2004).

In lakes, sediment is defined as a combination of decaying organic matter and mineral parent material; it is an essential component of nutrient cycling in aquatic systems (Barko et al. 1991; Wetzel 2001; Reverey et al. 2016). Lake sediment is highly influential on the macrophyte community, and interactions between sediment and macrophyte communities are complex (Barko and Smart 1986; Barko et al. 1991; Wang et al. 2015). 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 and Madsen 2004). A study of Swan Lake and Middle Lake in Nicollet County, MN, USA showed sediment clay fraction 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 activity, which improves cation exchange capacity (CEC), elevating nutrient availability. However, reduced porosity of finer sediments can inhibit root growth as bulk density is greater and generally results in more hypoxic sediments (Koch 2001; Gerbersdorf et al. 2007). Evidence from numerous studies suggests that the interface between macrophytes and sediment is a major factor that affects macrophyte community structure (Madsen et al. 1996, 2006; Bini et al. 1999; Salgado et al. 2009; Liu et al. 2017).

Lakes of Minnesota are very diverse, and this is largely due to landscape complexity across the state. State-wide, shallow lakes (max depth $\leq$ 4.5 m) are more common than deep lakes (max depth > 4.5 m) (Radomski and Perleberg 2012). Deeper, oligotrophic lakes have greater macrophyte species richness than shallow, eutrophic lakes (Radomski and Perleberg 2012). Much of southern Minnesota is situated in the Prairie Pothole Region, where lakes are much smaller, shallower, and more species poor than most other regions of Minnesota (Guntenspergen et al. 2002; Radomski and Perleberg 2012). The Prairie Pothole Region is critical habitat for migratory waterfowl; providing over half of North America's waterfowl production (Guntenspergen et al. 2002). Since wetland primary productivity is so high, the wetland-rich landscape of this region is preferred breeding ground for many species of North American waterfowl (Naugle et al. 2001; Rivera-Monroy et al. 2019). Aquatic and wetland systems in this region are currently threatened by pollution and habitat fragmentation as a result of high agriculture intensity and ongoing changes to land use (Naugle et al. 2001; Wright and Wimberly 2013; Johnston and McIntyre 2019). Despite the importance and vulnerability of this region, it is relatively understudied. Understanding the factors that affect macrophyte community composition in prairie potholes is not only important locally but can be applied to similar depressional systems globally, as small lakes make up the majority of the planet's freshwater area (Downing et al. 2006). The ecology and management of shallow lakes are fundamentally different from deep lakes as they are generally warmer, more turbid, and more productive than deep lakes (Scheffer 2004). Additionally, prairie lakes are often subject to eutrophication as intense agriculture is common in the surrounding landscape (Salm et al. 2009; Gascoigne et al. 2011). Managing these lakes requires an understanding of how certain physical and geographic factors affect the aquatic macrophyte community. The purpose of this study was to establish relationships between mean species richness, lake sediment, and geographic factors in five major lakes in Sibley County, MN, USA.

## Materials and methods

### Study site

The study took place in Sibley County, MN which is located in the Prairie Pothole Region of North America (Guntenspergen et al. 2002) (Fig. 1). Cultivated land makes up ~ 79% of Sibley County's total land area (Sibley County 2018). Dominant

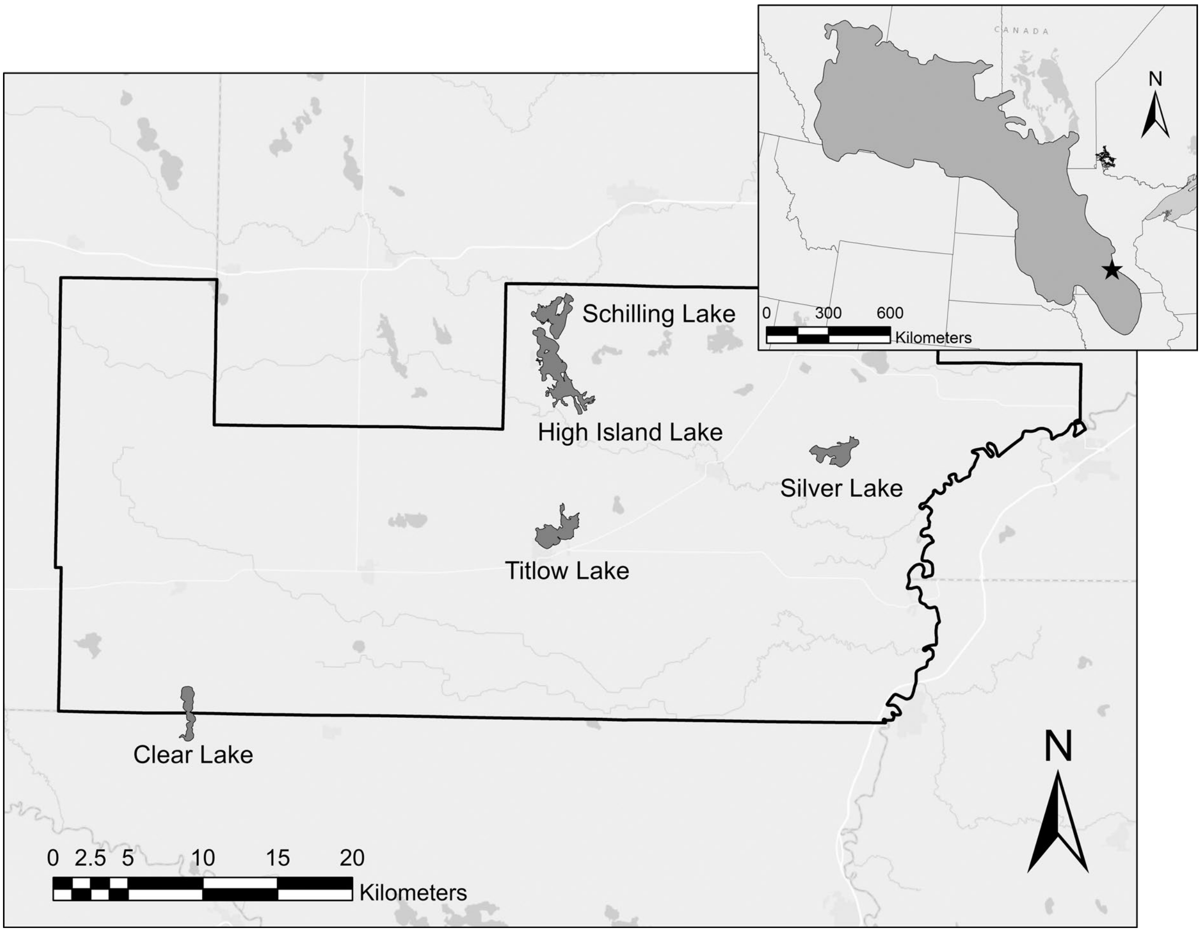


**Fig. 1** The five lakes in Sibley Co., MN that were surveyed during the 2019 growing season. Black line indicates the border of Sibley Co. Inset shows position of Sibley Co. (black star) in the Prairie Pothole Region located in Midwestern North America

soil series includes the Lester soil and Canisteo soil series, both of which are fine loams with relatively high CEC (National Resource Conservation Service 1997). Both of these soils have mesic temperature regimes and the Lester soil series has an udic moisture regime, whereas Canisteo soil series has an aquic moisture regime (National Resource Conservation Service 2008, 2015). For this study, five natural, shallow lakes were surveyed: High Island Lake, Titlow Lake, Schilling Lake, Silver Lake, and Clear Lake (Table 1, Fig. 1). These lakes are shallow, 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 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 *Stuckenia pectinata* (L.) Böerner (sago pondweed), with *Typha spp.* L. (cattails) being the dominant shoreline macrophytes in 2019 (Schmid and Wersal 2021).

## Lake surveys

Similar to other studies in southern Minnesota, all five lakes were surveyed using point-intercept surveys (Woolf and Madsen 2003; Case and Madsen 2004; Madsen et al. 2006; Wersal et al. 2006). For all five lakes, survey points were arranged in a 150 m grid (Figs. 2, 3, 4, 5, 6). These point grids were used to conduct macrophyte community and sediment

**Table 1** Physical and geographic properties of the five lakes in Sibley Co., MN, 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 |

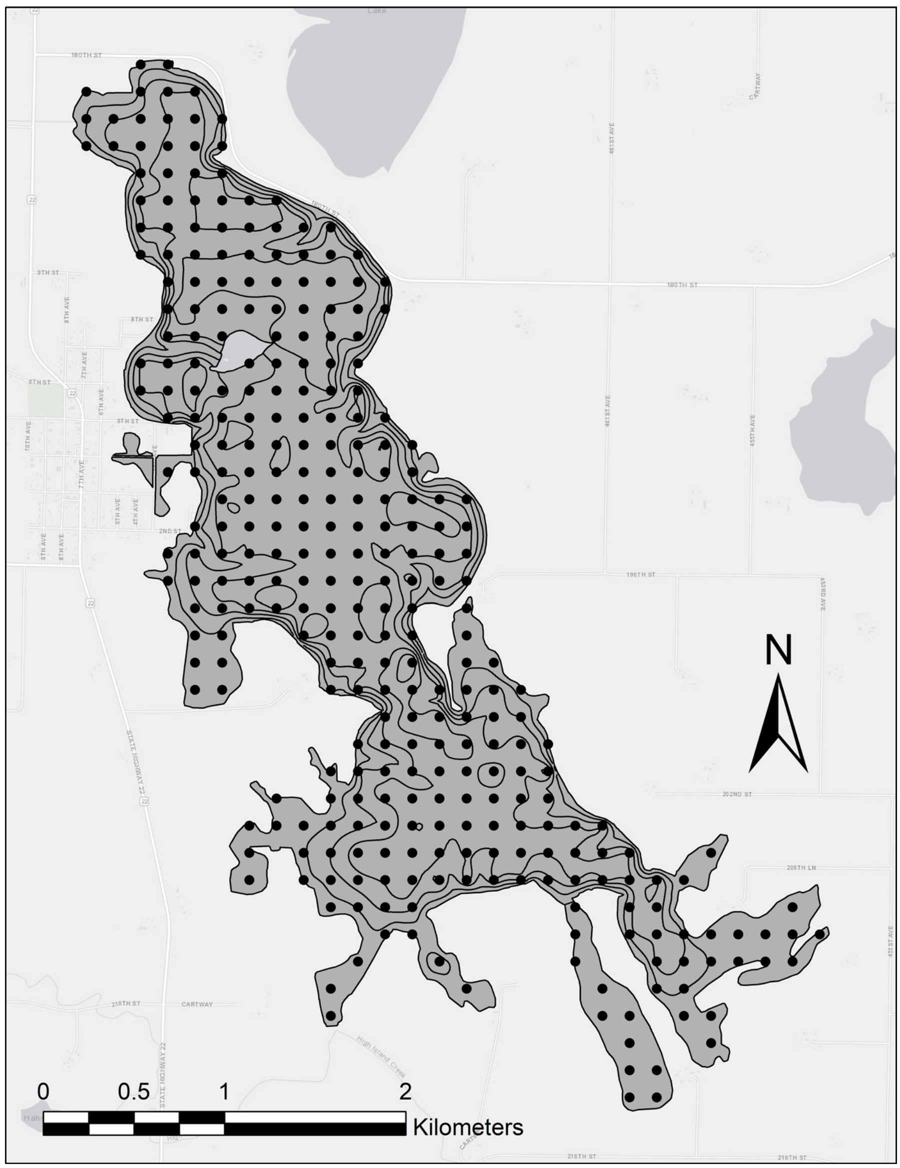


**Fig. 2** Grid of survey points in High Island Lake for surveys during the 2019 growing season in Sibley Co., MN. Contour lines represent changes in depth by 0.5 m intervals. Contour lines derived from depth data at sample points ($n = 318$)

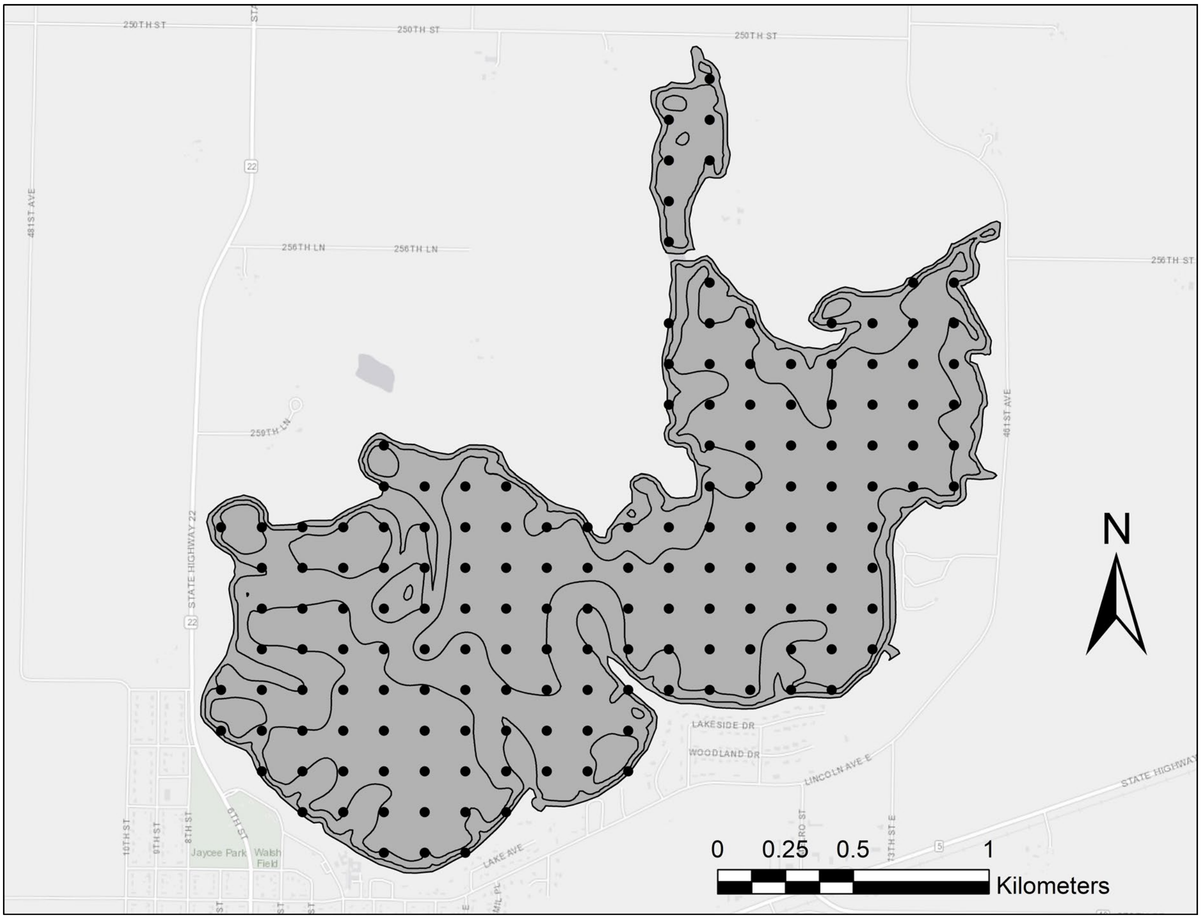


**Fig. 3** Grid of survey points in Titlow Lake for surveys during the 2019 growing season in Sibley Co., MN. Contour lines represent changes in depth by 0.5 m intervals. Contour lines derived from depth data at sample points ($n = 163$)

surveys during the early season (May and June) of 2019. A late season survey was conducted in August or September for each lake. During the surveys, these points were navigated to by watercraft under the direction of a GPS enabled ruggedized tablet with a spatial accuracy 1–2 m (Trimble Navigation Limited, Sunnyvale, California, USA). At each point, a plant rake tide to a rope 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 and 30 cm deep to collect an adequate sediment volume. Sediment samples were stored in a cooler for transport to the laboratory. Once in the laboratory, sediment samples were frozen. 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 recorded geospatial data and allowed for the entry of geospatial attributes in the field, which reduced data entry errors and post-processing time (Wersal et al. 2010; Cox et al. 2014; Madsen et al. 2015). Frequency of occurrence for macrophytes were calculated for each lake. 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. For a complete description of the macrophyte community composition in these lakes see Schmid and Wersal (2021).

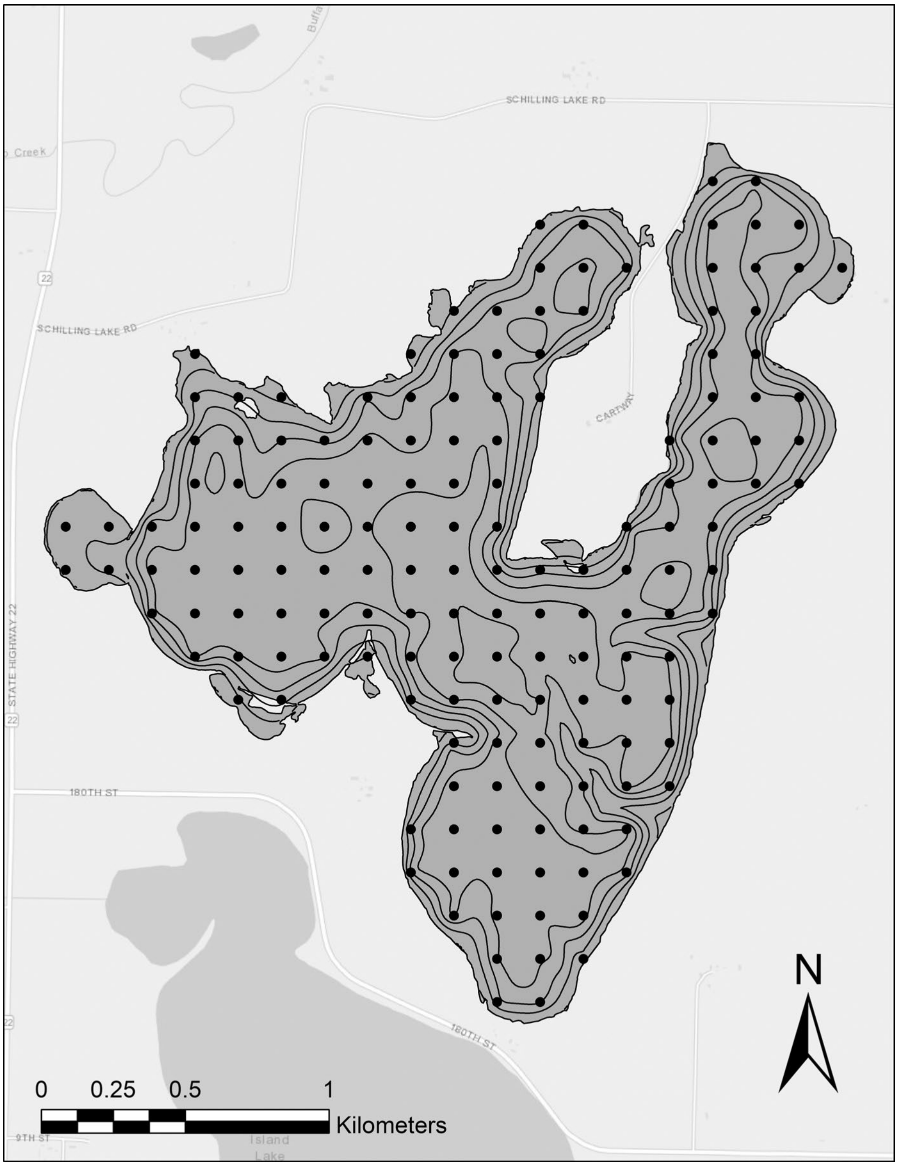


**Fig. 4** Grid of survey points in Schilling Lake for surveys during the 2019 growing season in Sibley Co., MN. Contour lines represent changes in depth by 0.5 m intervals. Contour lines derived from depth data at sample points ($n = 160$)

Sediment analyses

Prior to all sediment analysis, stored sediment cores were homogenized and dried in a forced-air drying oven for 48 h at 105 °C. Composition of the fine-grained fraction (particle size) and percent organic matter were both estimated for all oven-dried samples. A minimum of 60 g of oven-dried sediment per sample was used for both analyses.

Particle size fractions of oven-dried sediment samples were estimated using the Bouyoucos hydrometer method (Bouyoucos 1962). A 50 g portion of oven-dried sediment was weighed to the nearest hundredth of a gram 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 100 mL of a dispersal agent, which was a solution of 50 g of sodium hexametaphosphate dissolved in 1 L 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 h before it was mixed

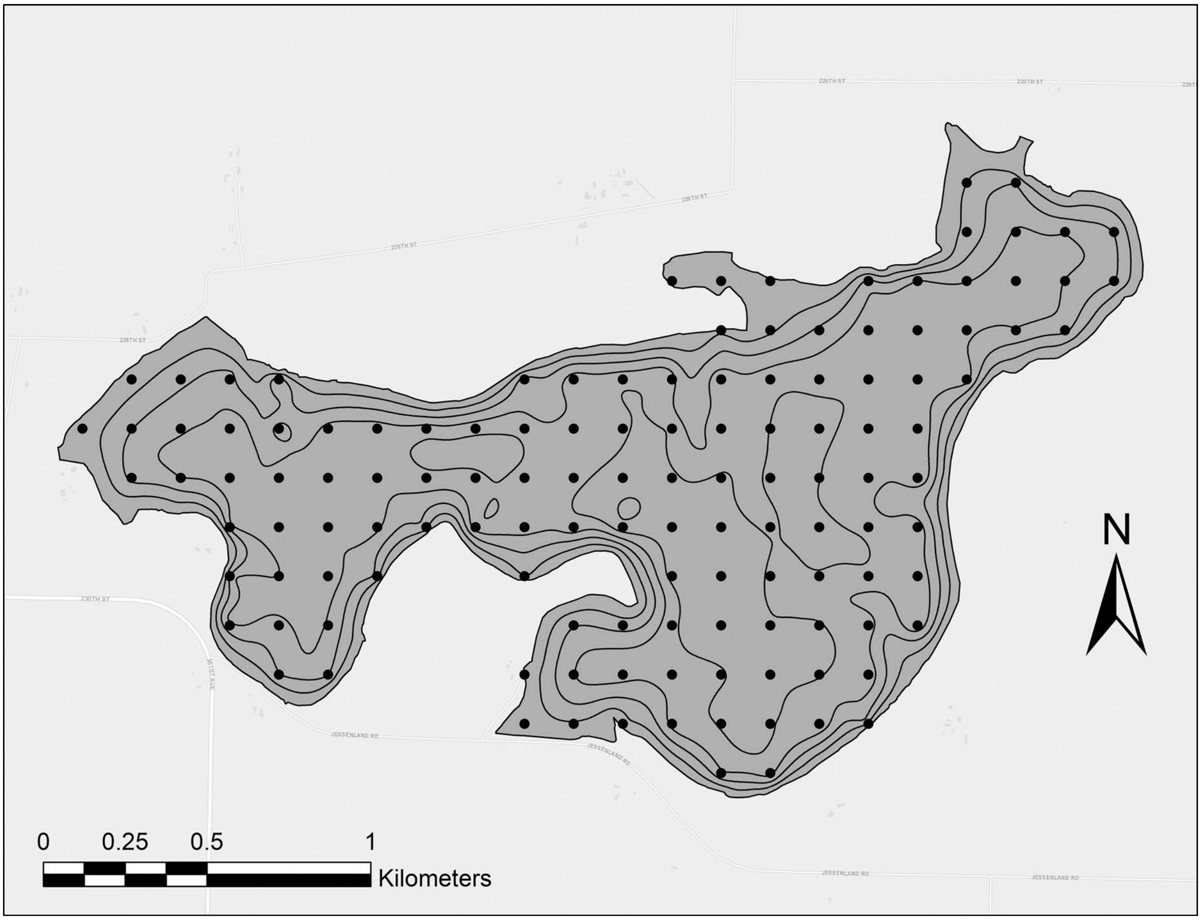


**Fig. 5** Grid of survey points in Silver Lake for surveys during the 2019 growing season in Sibley Co., MN. Contour lines represent changes in depth by 0.5 m intervals. Contour lines derived from depth data at sample points ($n = 129$)

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 each test by capping the cylinder with a bung and inverting it multiple times. A hydrometer reading (specific gravity of the soil suspension) was taken at 40 s and 2 h after start time. Hydrometer readings were taken from blank cylinders after each test reading and the 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 h reading was represented as hydrometer 2 ($H_2$). Sediment fractions of sand ($P_{sand}$), silt ($P_{silt}$), and clay ($P_{clay}$) in the sediment samples were estimated using the following formulae:

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

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

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

In these formulae, m represents dry weight of the sediment sample.

The sediment organic matter (SOM) of sediment samples was estimated using the loss on ignition

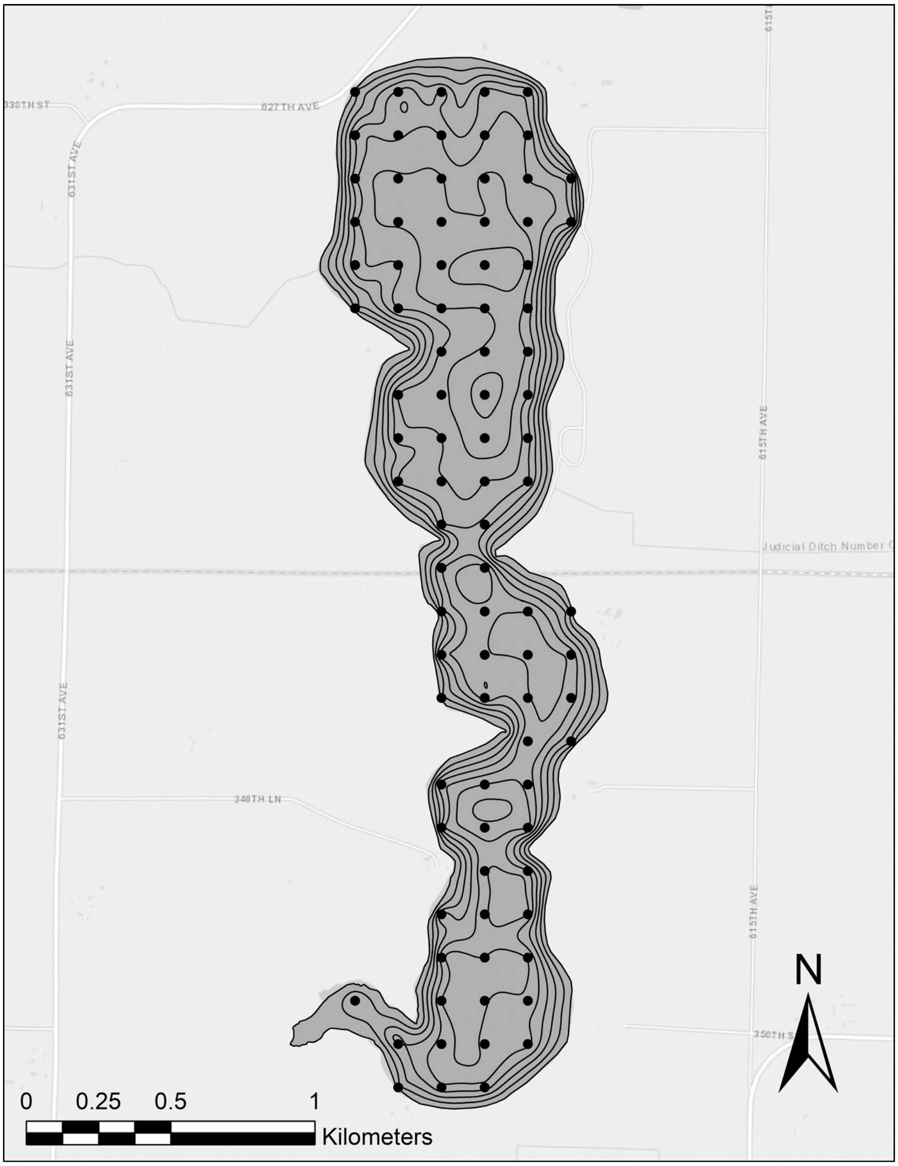


**Fig. 6** Grid of survey points in Clear Lake for surveys during the 2019 growing season in Sibley Co., MN. Contour lines represent changes in depth by 0.5 m intervals. Contour lines derived from depth data at sample points ($n = 90$)

(LOI) method (Dean 1974; Heiri et al. 2001). Of the oven-dried sediment samples, 5 g was measured and recorded which represented the pre-ignition weight ($m_{pre}$). Samples were baked at 550 °C in a muffle furnace for 16 h to ignite the organic carbon fraction, after which the samples were re-weighed ($m_{post}$). Fraction of SOM ($P_{SOM}$) in the samples was calculated using the following formula:

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

Spatial modeling and statistical analyses

All geoprocessing and geospatial analyses were conducted using ArcMap and ArcGIS Pro (Environmental Systems Research Institute, Redlands, California, USA). 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 using the point distance tool in ArcMap. Generalized linear regressions (GLR) were performed on survey data to determine relationships between macrophyte species richness and water depth, distance from shore, percent sand, percent silt, percent clay, and percent SOM within lakes (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. All mean species richness models were performed using macrophyte data from the early season surveys. However, Schilling Lake's macrophyte community shifted from curlyleaf pondweed dominated in the early season, to sago pondweed dominated in the late season (Schmid and Wersal 2021). To assess this shift, relationships between macrophytes and explanatory variables in Schilling Lake, GLR's were performed on macrophyte data from late season surveys (August–September) in 2019, using the same explanatory variables. Model performance was determined principally by corrected Akaike's information criterion (AICc) values, where a lower AICc was considered a better performing model (Fleming et al. 2021). Candidate models with AICc values that were within $\pm 2$ 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 considered the best-fit model for the dependent variable. To control for spatial autocorrelation after the best-fit model was determined, a Moran's I test for spatial autocorrelation was conducted on residuals of that model (Chen 2016). If the Moran's I test determined 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. The golden search tool in ArcGIS Pro finds maximum and minimum distances within the data set and tests the AICc at various distances incrementally and then choses the best distance values for each model. Model performance was assessed based on appropriate pseudo-$R^2$ values provided in regression outputs. Statistical significance for all analyses were determined with $\alpha = 0.05$.

## Results

Curlyleaf pondweed was the only invasive species observed in this study and it was only found in Schilling Lake. The most common native macrophyte was sago pondweed which was observed in all five lakes and had a frequency of occurrence of 49.0%, 14.8%, 6.2%, 8.4%, and 7.7% for High Island Lake, Titlow Lake, Schilling Lake, Silver Lake, and Clear Lake, respectively (Table 2). Silver Lake was the only lake where *Nymphaea odorata* Aiton (white waterlily) was the dominant macrophyte where it occurred at 10.0% of the sample points (Table 2). Mean species richness values for High Island Lake, Titlow Lake, Schilling Lake, Silver Lake, and Clear Lake were 0.62, 0.16, 0.69, 0.30, and 0.08 species per sample point, respectively.

Sediment texture in High Island Lake consisted of 67.1% sand, 18.7% silt, and 13.6% clay. Sediment in High Island Lake contained 26.4% SOM. In Titlow Lake, average sediment texture consisted of 40.9% sand, 26.9% silt, and 32.1% clay. Sediment in Titlow Lake contained 14.0% SOM. Schilling Lake sediment texture consisted of 65.6% sand, 19.6% silt, and 14.6% clay. Schilling Lake sediments contained 27.7% SOM. Sediment texture in Silver Lake consisted of 65.9% sand, 18.4% silt, and 15.5% clay. Silver Lake sediments were composed of 38.8% SOM. Clear Lake sediment texture consisted of 47.0% sand, 28.7% silt, and 24.1% clay. Clear Lake sediments contained 17.5% SOM. Factors that affected mean species richness were water depth, sample distance from shore, and percent silt. All mean species richness models with significant results had relatively high *pseudo*-$R^2$ values (Tables 3, 4), and selected explanatory variables accounted for between 25 and 40% of the variation in species richness in all significant models.

The best-fit model for the species richness in High Island Lake consisted of water depth as the only explanatory variable. The best-fit model had a *pseudo*-$R^2$ of 0.281 (Table 3). Species richness was negatively related to water depth with a slope coefficient of -1.5416 (Table 4). Global Moran's I found that the residuals of the candidate model were

**Table 2** Mean species richness and frequency of macrophytes sampled at all Sibley Co. lakes surveyed during the early 2019 growing season

| Species | Common name | High Island Lake | Titlow Lake | Schilling Lake | Silver Lake | Clear Lake |
|---|---|---|---|---|---|---|
| *Carex* spp. L. | True sedge | | | 2.78 | 1.68 | |
| *Ceratophyllum demersum* L. | Coontail | 2.00 | | | | |
| *Lemna minor* L. | Lesser duckweed | 2.80 | 0.62 | 2.08 | 2.52 | |
| *Lemna trisulca* L. | Star duckweed | 0.80 | | | | |
| *Nympheae odorata* Ait | White waterlily | | | | 10.08 | |
| *Phragmites australis* (Cav.) Trin. ex Steud. | Common Reed | | 0.60 | 0.69 | | |
| *Potamogeton crispus* L. | Curly pondweed | | | 44.44 | | |
| *Sagittaria latifolia* Willd. | Broadleaf arrowhead | | | | 0.84 | |
| *Schoenoplectus tabernaemontani* (C.C.Gmel.) Palla | Softstem bulrush | 0.40 | | | | |
| *Stuckenia pectinata* (L.) Böerner | Sago pondweed | 49.00 | 14.81 | 6.25 | 8.40 | 7.78 |
| *Typha spp.* L | Cattail | 4.80 | 0.62 | 15.28 | 6.72 | |
| *Wolffia columbiana* H. Karst | Columbian Watermeal | 0.80 | | | | |
| Mean species richness | | 0.62 | 0.16 | 0.69 | 0.30 | 0.08 |

significantly clumped ($Z = 4.498$, $P < 0.001$) (Table 4) and so a GWR was performed on the best-fit model. GWR had an improved *pseudo*-$R^2$ of 0.374 when compared to the global model which had a *pseudo*-$R^2$ of 0.278.

There were no significant explanatory variables for species richness in Titlow Lake according to the GLR. GLR with clay as the sole explanatory variable had the highest performance, but the *pseudo*-$R^2$ value was 0.010 (Table 3). According to Moran's I, the residuals for this GLR were clumped ($Z = 1.837$, $P = 0.066$) (Table 4). The GWR was unable to find enough variation in species richness across at least one of the neighborhoods and was therefore unable to execute.

Mean species richness for Schilling Lake was negatively related water depth and silt. *Pseudo*-$R^2$ for this best-fit model was 0.285 (Table 3). Slope coefficients for the explanatory variables were − 0.8854 and − 0.0284 for water depth and silt, respectively (Table 4). Residuals for this best-fit model were also clumped ($Z = 3.708$, $P < 0.001$) (Table 4) and so a GWR was performed on these variables. *Pseudo*-$R^2$ for the global model with these variables was 0.2679 and the GWR had a *pseudo*-$R^2$ of 0.4169. Early season frequency of occurrence for sago pondweed and curlyleaf pondweed in Schilling Lake was 6.25 and 44.44, respectively (Table 2). Early season presence and absence of curlyleaf pondweed was modeled with water depth, silt, and SOM as explanatory variables. *Pseudo*-$R^2$ of the best-fit model was 0.143 (Table 5). In the early season presence and absence of curlyleaf pondweed was negatively related to both water depth and silt, with slope coefficients of − 1.4582 and − 0.0613, respectively (Table 6). Conversely, early season presence and absence of curlyleaf pondweed was positively related to SOM with a slope coefficient of 0.0367 (Table 6). Residuals from this model were clumped according to the Moran's I ($Z = 3.959$, $P < 0.001$) (Table 6). 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. The model on early season presence/absence of sago pondweed found no significant explanatory variables (Table 6). The strongest explanatory variable for presence/absence of sago pondweed was percent silt, which had a $P$ value of 0.544 (Table 6). Residuals of this model were randomly distributed ($Z = -1.086$, $P = 0.278$) (Table 6). During the late season survey, frequency of occurrence was 63.89 for sago pondweed and 13.89 for curlyleaf pondweed in Schilling Lake. The best-fit model for late season presence and absence of curlyleaf pondweed had a *pseudo*-$R^2$ of 0.070 and included water depth as the sole explanatory variable (Tables 7, 8). Water depth was negatively related to curlyleaf pondweed presence during

**Table 3** GLR results for factors that affect mean species richness in the five survey lakes, Sibley Co., MN, 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

the late season survey, and the residuals for the best-fit model were clumped (Table 8). A GWR on the relationship between curlyleaf pondweed late season presence and absence and water depth provided an improved *pseudo-R*$^2$ of 0.162 over 0.070 from the global model. Late season presence and absence of sago pondweed was explained by water depth and silt according to the best-fit model (Tables 7, 8). Water depth was negatively related to the late season sago pondweed presence and absence, whereas silt was positively related to sago pondweed presence and absence (Table 8). The best-fit model had a *pseudo-R*$^2$ of 0.082 and the residuals were randomly distributed (Tables 7, 8).

Regarding mean 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 was 0.357 (Table 3). Both water depth and distance from shore were negatively related to the species richness in Silver Lake. GLR's slope coefficient was − 2.8882 for water depth and − 0.0085 for distance from shore (Table 4). In the best-fit model, silt was positively related to species richness and

**Table 4** Statistics for explanatory variables and Moran's I results on residuals of the best-fit models for factors that affect mean species richness in the five study lakes, Sibley Co., MN, USA 2019

| Lake | Explanatory variable statistics | | | | Moran's I | |
|---|---|---|---|---|---|---|
| | Variable[a] | 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 |

Best-fit models were determined via GLR model selection

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

**Table 5** GLR results for the factors that affect early season presence/absence of curlyleaf pondweed and sago pondweed in Schilling Lake, Sibley Co., MN, 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 6** Statistics for explanatory variables and Moran's I results on residuals of the best-fit models for factors that affect early season presence/absence of curlyleaf pondweed and sago pondweed in Schilling Lake, Sibley Co., MN, USA 2019

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

Best-fit models were determined via GLR model selection

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

**Table 7** GLR results for the factors that affect late season presence/absence of curlyleaf pondweed and sago pondweed in Schilling Lake, Sibley Co., MN, USA 2019

| Species | Model[a] | AICc[b] | ΔAICc[c] | *Pseudo-$R^2$* | Rank |
|---|---|---|---|---|---|
| Curlyleaf pondweed | DEPTH | 118.56 | 0.00 | 0.070 | 1 |
| | DEPTH + DISTANCE | 119.62 | 1.06 | 0.079 | 2 |
| | DEPTH + DISTANCE + SAND | 120.99 | 2.43 | 0.085 | 3 |
| | DEPTH + DISTANCE + SAND + SOM | 122.97 | 4.40 | 0.086 | 4 |
| | DEPTH + DISTANCE + SAND + SILT + SOM | 125.03 | 6.46 | 0.087 | 5 |
| | DEPTH + DISTANCE + SAND + SILT + CLAY + SOM | 127.23 | 8.67 | 0.087 | 6 |
| Sago pondweed | DEPTH + SILT | 175.66 | 0.00 | 0.082 | 1 |
| | DEPTH | 179.50 | 3.83 | 0.050 | 2 |
| | DEPTH + DISTANCE + SILT | 177.63 | 1.97 | 0.083 | 3 |
| | DEPTH + DISTANCE + SILT + CLAY | 179.69 | 4.03 | 0.083 | 4 |
| | DEPTH + DISTANCE + SILT + CLAY + SOM | 181.78 | 6.12 | 0.084 | 5 |
| | DEPTH + DISTANCE + SAND + SILT + CLAY + SOM | 183.98 | 8.32 | 0.084 | 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 8** Statistics for explanatory variables and Moran's I results on residuals of the best-fit models for factors that affect late season presence/absence of curlyleaf pondweed and sago pondweed in Schilling Lake, Sibley Co., MN, USA 2019

| Species | Explanatory variable statistics | | | | Moran's I | |
|---|---|---|---|---|---|---|
| | Variable[a] | Slope coefficient | Standard error | *P* value | *Z* score | *P* value |
| Curlyleaf pondweed | DEPTH | − 0.595 | 0.211 | 0.005 | 4.618 | < 0.001 |
| Sago pondweed | DEPTH | − 0.585 | 0.174 | 0.018 | 0.014 | 0.989 |
| | SILT | 0.037 | 0.015 | < 0.001 | | |

Best-fit models were determined via GLR model selection

[a]Model variables are water depth (DEPTH) and percent silt (SILT)

had a slope coefficient of 0.0510 (Table 4). Residuals of the GLR were found to be randomly distributed by the Moran's I test ($Z = 0.580$, $P = 0.562$) (Table 4).

The best-fit model for mean species richness in Clear Lake consisted of distance from shore as the only significant explanatory variable. This model had a *pseudo-$R^2$* of 0.313 (Table 3). Distance from shore was negatively related to the species richness, with a slope coefficient of − 0.0424 (Table 4). Residuals of the best-fit model were randomly distributed according to Moran's I ($Z = -1.383$, $P = 0.167$) (Table 4).

## Discussion

Water depth significantly predicted mean species richness in three of the five lakes in Sibley County. In all three models, mean species richness was negatively related to water depth. Negative relationships between mean species richness and water depth are primarily driven by the reduction of light availability at increasing depths in turbid lakes (Barko et al. 1986; Lacoul and Freedman 2006; Bornette and Puijalon 2011). In both Schilling Lake and High Island Lake, mean species richness declined as depth increased. 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 had relatively deep secchi depths (Table 1), and ~ 95% of all macrophytes were found growing within 2 m of the surface in both lakes. Silver Lake also had depth as a significant variable; however, Silver Lake was dominated by white waterlily, a floating-leaf macrophyte, whereas Schilling Lake and High Island Lake were dominated by submersed aquatic vegetation (curlyleaf pondweed and sago pondweed). Dominance of white waterlily in Silver Lake was likely due to high turbidity. Floating-leaf macrophytes are able to attenuate light at the surface of the water, which negates the growth inhibition of turbidity (Lacoul and Freedman 2006). Prior to the production of floating leaves, white waterlily produces submersed growth that is subject to the effects of turbidity, which is probably a reason why white waterlily is usually relegated to shallow water (Lacoul and Freedman 2006). This zonation of floating leaf macrophytes was observed in Silver Lake, as nearly all macrophytes surveyed were found at depths shallower than 1.5 m. 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 4). This is likely because white 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 was a significant predictor for mean species richness in Silver Lake (Lacoul and Freedman, 2006). In the Clear Lake model, distance from shore was the only significant variable that affects the richness of macrophytes. Distance from shore was highly influential in Clear Lake's mean species richness because its bottom was deeper than any other lakes in the study, and water clarity was low. Additionally, water depth deepened dramatically very close to the shore. This steep slope in combination with turbid waters greatly limited the distance from shore that rooted macrophytes could grow in Clear Lake.

The only sediment factor related to mean species richness was percent silt in Schilling Lake and Silver Lake. 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 increase the 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 percent silt is positively or negatively related to sediment silt is largely species-specific (Koch 2001). Both relationships were observed in this study. Silt percent was negatively related to the species richness in Schilling Lake, which was dominated by curlyleaf pondweed. Additionally, presence of curlyleaf pondweed in Schilling Lake was negatively related to silt percent. Data from these models suggest that silt in the sediment inhibits the growth of curlyleaf pondweed, because it contributes to turbidity as it is suspended in the water column. Conversely, in the white waterlily dominated Silver Lake, mean species richness was positively related to percent silt in the sediment. White waterlily produces thick rhizomes that support large floating leaves. Once the floating leave reach the surface of the water, white waterlily no longer experiences the detrimental effects of turbidity, which is why white waterlily and other morphologically similar species often dominate shallow, turbid lakes (Lacoul and Freedman 2006). The positive relationship observed in Silver Lake suggests that not only is white waterlily not inhibited by suspended silt, but it benefits from higher sediment nutrient availability caused by silts greater cation exchange capacity (Gerbersdorf et al. 2007). Additionally, higher turbidity caused by finer sediments may provide a competitive advantage for the floating leaves of white waterlily over SAV. Similar to white waterlily, late season presence and absence of sago pondweed was positively related to silt. This relationship was also observed in previous research in southern MN lakes (Case and Madsen 2004; Madsen et al. 2006).

In Heron Lake (Jackson County, MN, USA) researchers found that the frequency of sago pondweed was positively related to percent silt in the sediment (Case and 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). In Swan Lake (Nicollet County, MN, USA) researchers 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 white waterlily, sago pondweed and American eelgrass are likely benefitting from higher CEC of silt rich soils, which is beneficial for plants with high root biomass. Ultimately, evidence from this study and previous studies suggest 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 in the early season. The model for factors that affect early season 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 6). However, the early season 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 6). This relationship contradicts the literature, which consistently cites SOM as an inhibitor of rooted macrophyte growth as SOM contains many phytoinhibitory compounds (Barko and Smart 1986; Koch 2001; Hechmi et al. 2020). However, previous studies have found that the inhibitory effects of SOM plateau after about 20% SOM (Barko and 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 and Thomaz 2015). It is possible that curlyleaf pondweed is not as susceptible to growth inhibition by SOM. Future research should assess relationships between curlyleaf pondweed and SOM in greater detail.

## 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 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 the 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 in mean species richness and frequency as distance from shore increased. This study determined that the only sediment factor that was a significant predictor of macrophyte distribution was silt. However, whether silt promotes or inhibits its macrophyte frequency and richness depends on species composition. Silt contributes to turbidity in some systems which can negatively affect submersed macrophytes. Results from these models suggest interactions are complex between macrophytes, environmental factors, and sediment texture and that these interactions are species and site specific. A single landscape scale model would not be appropriate to capture the in-lake processes driving macrophyte distribution and abundance, and management strategies will need to be developed on a lake-by-lake basis. Our findings highlight the complexity inherent in relationships between aquatic macrophyte communities and the abiotic factors that act on them. Further investigation into these interactions will allow researchers and managers to better understand and preserve aquatic macrophyte communities in this highly important region.

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**Declarations**

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