Abiotic Factors That Affect The Distribution of Aquatic Macrophytes In Shallow Lakes Located In Sibley County, Minnesota, USA: 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 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 quantified by determining soil particle size and percent organic matter. 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. Water depth and distance from shore were negatively related to mean species richness, and silt was either negatively or positively related to species richness depending on the lake and macrophytes present. All species richness models had *pseudo*-R^2 values between 0.25 and 0.40. Curlyleaf pondweed (*Potamogeton crispus*) was related to with water depth, percent silt, and percent sediment organic matter during early season surveys.

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 & Giovanni, 2002; Wersal et al., 2005; Dibble & Pelicice, 2010). In addition to supporting animal communities, aquatic macrophytes inhibit the growth of phytoplankton allopathically, and provide habitat for important filter feeders that graze on phytoplankton; which 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). 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 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 (Chambers & Kaiff, 1985; Barko et al., 1986; 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). Light regime is the primary driver for the niche partitioning of aquatic macrophytes throughout the littoral zones of lakes (Barko et al., 1986). 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 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 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. Overall, water depth has been found to have a negative relationship between the density and abundance of aquatic macrophytes (Barko et al., 1986; Cheruvelil & Soranno, 2008).

One of the major factors that limits the growth of aquatic macrophytes is water turbidity. Light availability in aquatic systems is primarily a function of turbidity and water depth (Barko et al., 1986; 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

Another important factor that affects the abundance and distribution of aquatic macrophytes is the fetch, the distance wind can travel unimpeded. 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. Macrophytes may respond to high wave action by changing their morphology, and moderate wave action may increase nutrient availability for the macrophyte community (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).

A lake's sediment is highly influential on the macrophyte community, and interactions between sediment and macrophyte communities are highly complex (Barko & Smart, 1986; Barko et al., 1991). 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, MN, 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 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.

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. State-wide, shallow lakes (max depth ≤ 4.5) are more common than deep lakes (max depth > 4.5m) (Radomski & Perleberg, 2012). In Minnesota, regions with deeper and more oligothrophic lakes, have lakes with much greater macrophyte 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 typical 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 community. 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, MN, USA.

Materials And Methods

Study site

The current 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 soil series include Lester soil series and Canisteo soil series, both of which are fine loams with relatively 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 1, Fig. 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 Co. 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. 2–6). These point grids were used to conduct macrophyte community and sediment surveys during the early season (May and June) of 2019. 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 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 5cm 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 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). A pick list of aquatic macrophytes was constructed for these surveys that allowed for the recording of macrophyte species in a database template. 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

Prior to all sediment analysis, stored sediment cores were homogenized and dried in a forced-air drying oven for 48hrs 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 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 24hrs before it was mixed for another 2 min in the mixer. The mixture was then added to a 1,000mL sedimentation cylinder and distilled water was added to bring the final volume to 1,000 mL. A blank cylinder was prepared by combining 100mL of dispersal agent and 900mL 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 40s and 2hrs 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 40s reading was represented as hydrometer 1 (H_1) and the corrected 2hrs 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 were 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 16hrs and the samples were re-weighed (m_{post}). The proportion 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

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. 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 & Wersal, 2021). To assess this shift the relationships between macrophytes and the 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 the corrected Akaike's information criterion (AICc) values, where a lower AICc is considered a stronger model (Fleming et al., 2021). Candidate 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 considered the best-fit model for the dependent variable. After the best-fit 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. Statistical significance for all analyses were determined with $\alpha = 0.05$.

Results

Mean species richness at High Island Lake was 0.62. The best-fit model for the species richness in High Island Lake consisted of water depth as the only explanatory variable. The candidate model had a *pseudo*-R^2 of 0.281 (table 2). Water depth was negatively related to species richness with a slope coefficient of -1.5416 (table 3). Global Moran's I found that the residuals of the candidate model were significantly clumped ($Z = 4.498$, $P < 0.001$) (table 3) 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.

Mean species richness at Titlow Lake was 0.16. 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 2). According to Moran's I, the residuals for this GLR were clumped ($Z = 1.837$, $P = 0.066$) (table 3), However, 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 at Schilling Lake was 0.69. 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 2). Slope coefficients for the explanatory variables were – 0.8854 and – 0.0284 for water depth and silt respectively (table 3). Residuals for this best-fit model were also clumped ($Z = 3.708$, $P < 0.001$) (table 3) and so a GWR was performed on these variables. *Pseudo*-R^2 for the global model with these variable 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. 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 4). In the early season both water depth and silt were negatively related to presence and absence of curlyleaf pondweed, with slope coefficients of -1.4582 and – 0.0613 respectively (table 5). Conversely, early season presence and absence of curlyleaf pondweed was positively related to SOM with a slope coefficient of 0.0367 (table 5). Residuals from this model were clumped according the Moran's I ($Z = 3.959$, $P < 0.001$) (table 5). 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 the early season presence and absence of sago pondweed found no significant explanatory variables (table 5). The strongest explanatory variable for the presence/absence of sago pondweed was percent silt, which had a P-value of 0.544 (table 5). Residuals of this model were randomly distributed ($Z=-1.086$, $P = 0.278$) (table 5). 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 (table 6&7). Water depth was negatively related to curlyleaf pondweed presence during the late season survey, and the residuals for the best-fit model were clumped (table 7). 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 (table 6&7). 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 7). The best-fit model had a *pseudo*-R^2 of 0.082 and the residuals were randomly distributed (table 6&7).

Mean species richness at Silver Lake was 0.30. 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 2). 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 3). In the best-fit model, silt was positively related to species richness and had a slope coefficient of 0.0510 (table 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).

Mean species richness at Clear Lake was 0.08. 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 2). Distance from shore was negatively related to the species richness, with a slope coefficient of -0.0424 (table 3). Residuals of the best-fit model were randomly distributed according Moran's I ($Z=-1.383$, $P = 0.167$) (table 3).

Discussion

The 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 (table 2&3), and selected explanatory variables accounted for between 25% and 40% of the variation in species richenss in all significant models.

Water depth was related to mean species richness in three of the five lakes in Sibley County (table 3). In all three models, water depth was 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., 1986; Lacoul & Freedman, 2006; Bornette & 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 2m of the surface in both lakes. Silver Lake also had depth as a significant variable (table 3), however, Silver Lake was dominated by *Nymphaea odorata* Aiton (fragrant waterlily), a floating-leaf macrophyte, whereas Schilling lake and High Island Lake were dominated by submersed aquatic vegetation (curlyleaf pondweed and sago pondweed). The dominance of fragrant waterlily in Silver Lake is likely due to the lakes's high turbidity (table 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 were 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). 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). 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 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 (table 3). 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 contribute significantly to turbidity which limits light availability for submersed macrophytes (Zhu et al., 2015). However, higher silt content can improve 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, the 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 fragrant waterlily dominated Silver Lake, mean species richness was positively related to percent silt in the sediment (table 3). Fragrant waterlily produces thick rhizomes that support large floating leaves. Once the floating leave reach the surface of the water, fragrant waterlily no longer experiences 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 that not only is fragrant waterlily not inhibited by suspended silt, but it benefits from higher sediment nutrient availability caused by silts greater cation exchange capasity (Gerbersdorf et al., 2007). Similarly, late season presence and absence of sago pondweed was positively related to silt (table 7). This relationship was also observed in previous research in southern MN lakes (Case & 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 & 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 fragrant 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 5). 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 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 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 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.

Declarations

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Conflict of interest

There are no conflict of interests.

Data availability

Data that support the findings of this study are available from the corresponding author, upon reasonable request.

Code availability

Not applicable

Ethics approval

Not applicable

Consent to participate

Not applicable

Consent for publication

The authors consent to have this manuscript published if accepted.

Authors' Contributions

SS – conducted the research as part of his MS degree, analyzed data, and was the primary writer of the manuscript.

RW – was the chair of the graduate committee, assisted in field data collection, and was a major contributor in data analysis and manuscript preparation.

JF – was a major contributor in spatial model creation and data analysis, he was also a major contributor in manuscript preparation.

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Tables

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

Table 2. 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

Table 3. 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. Best-fit models were determined via GLR model selection.

	Explanatory variable statistics				Moran's I	
Lake	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

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

Table 4. 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 5. 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. Best-fit models were determined via GLR model selection.

	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	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

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

Table 6. 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 7. 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. Best-fit models were determined via GLR model selection.

	Explanatory variable statistics				Moran's I	
Species	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		

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

Figures

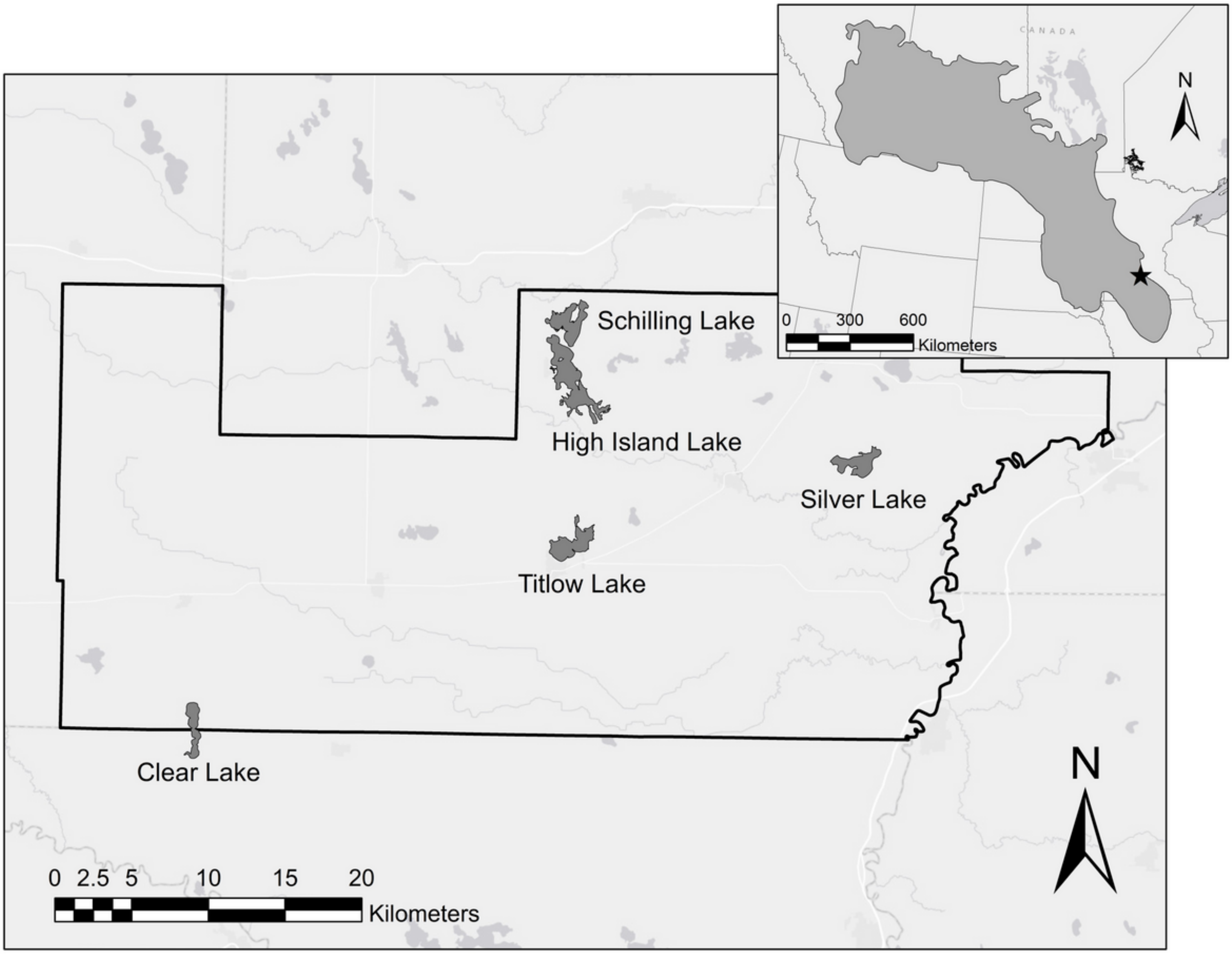

Figure 1

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.

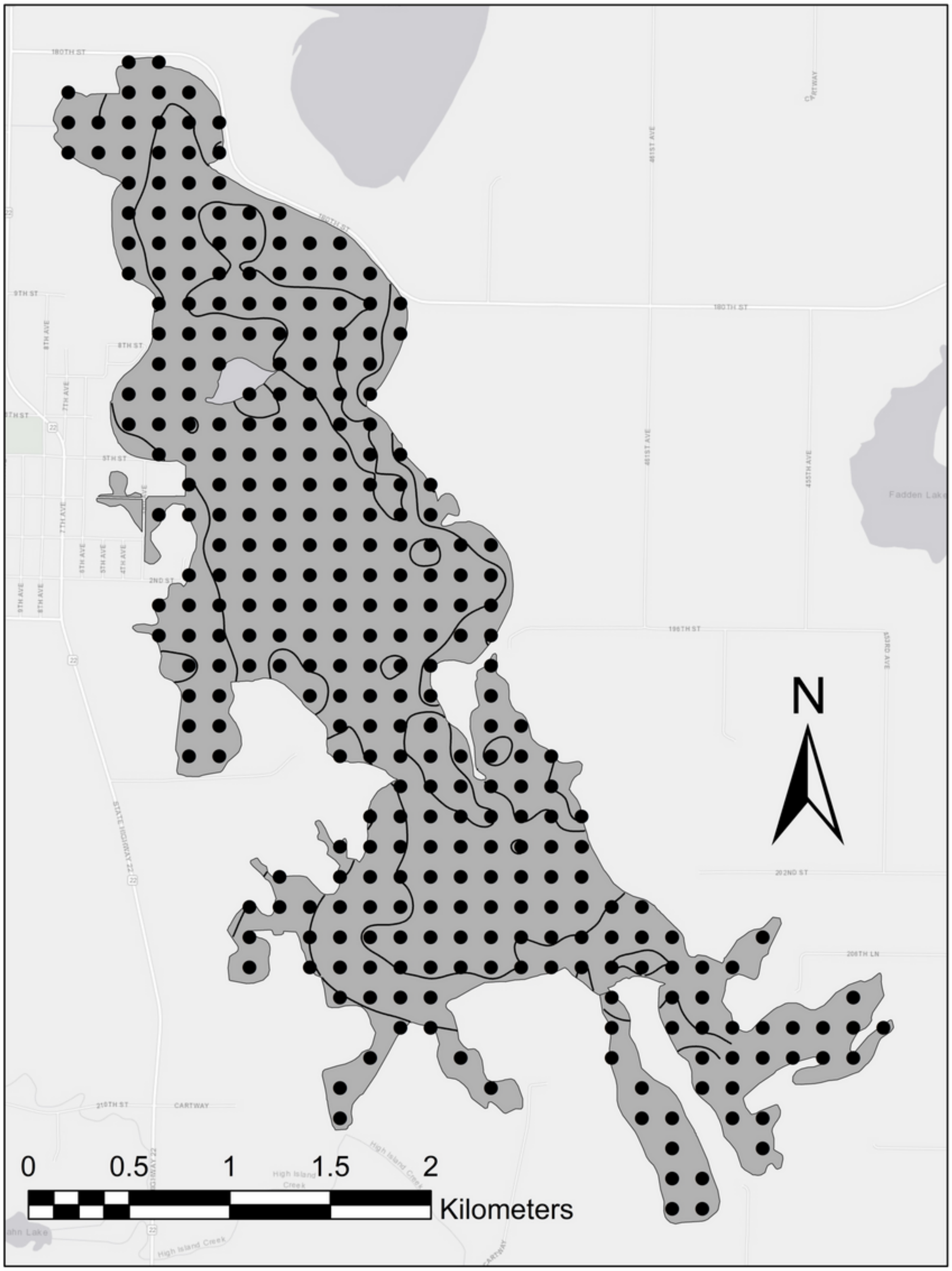

Figure 2

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

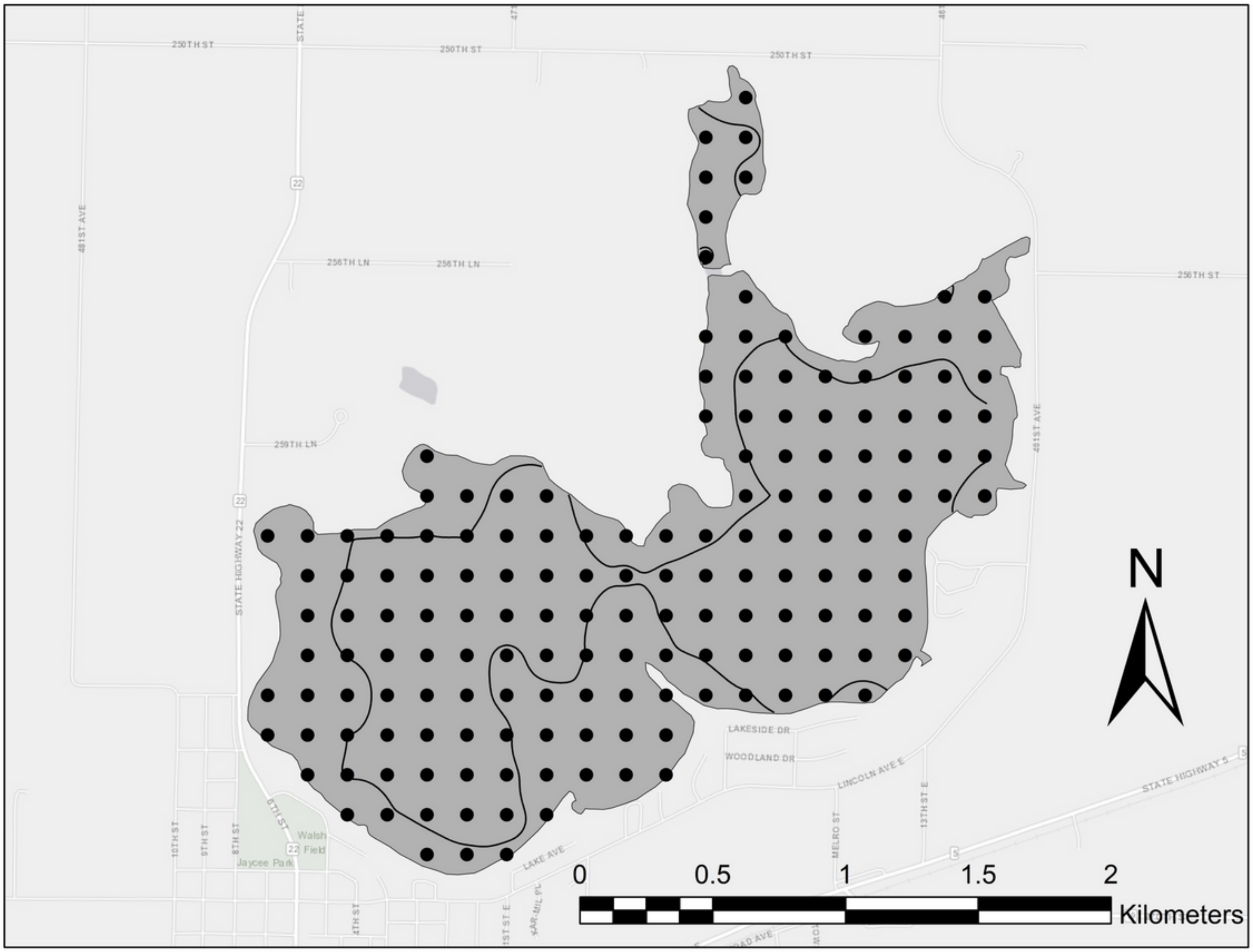

Figure 3

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

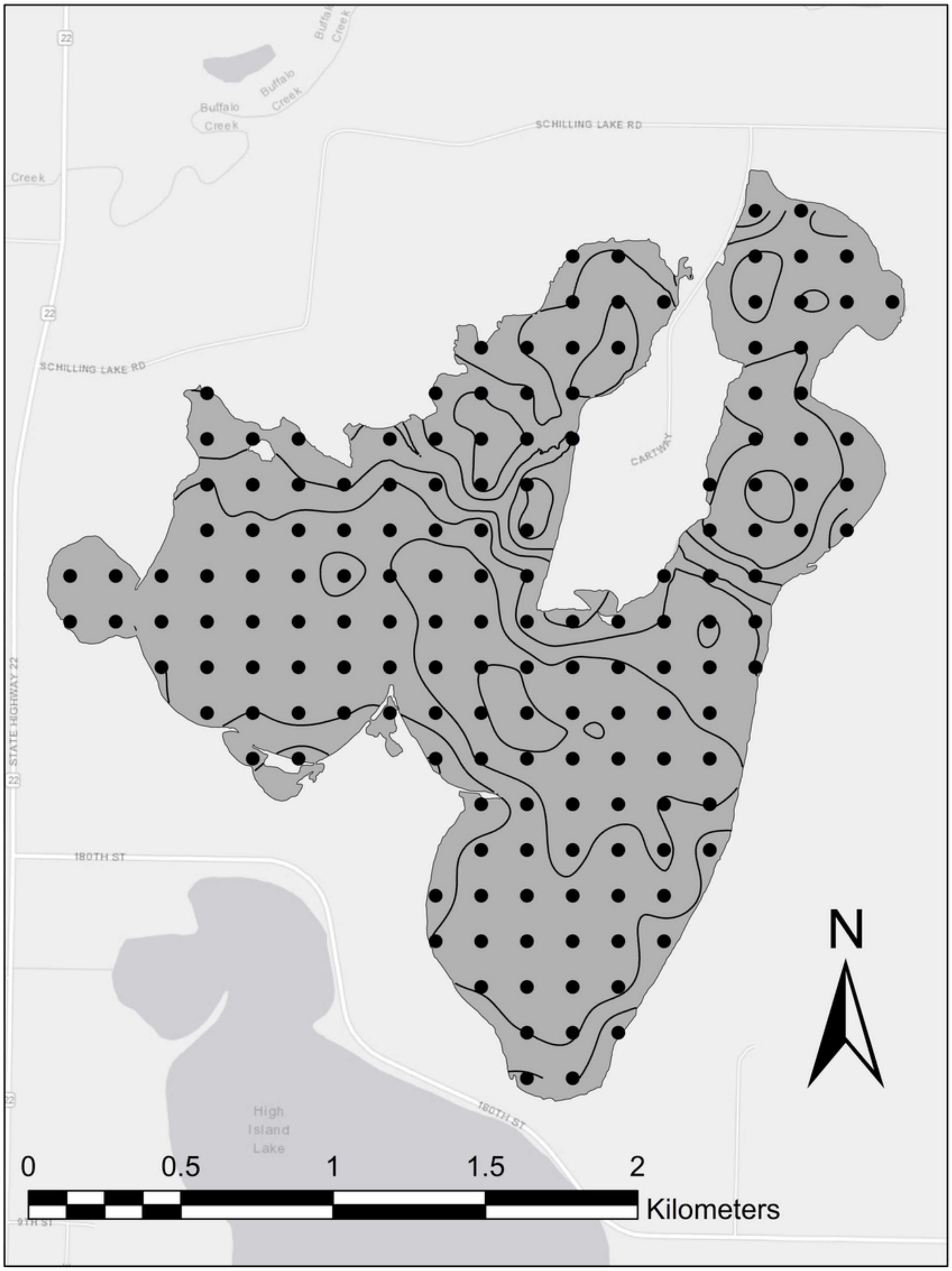

Figure 4

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

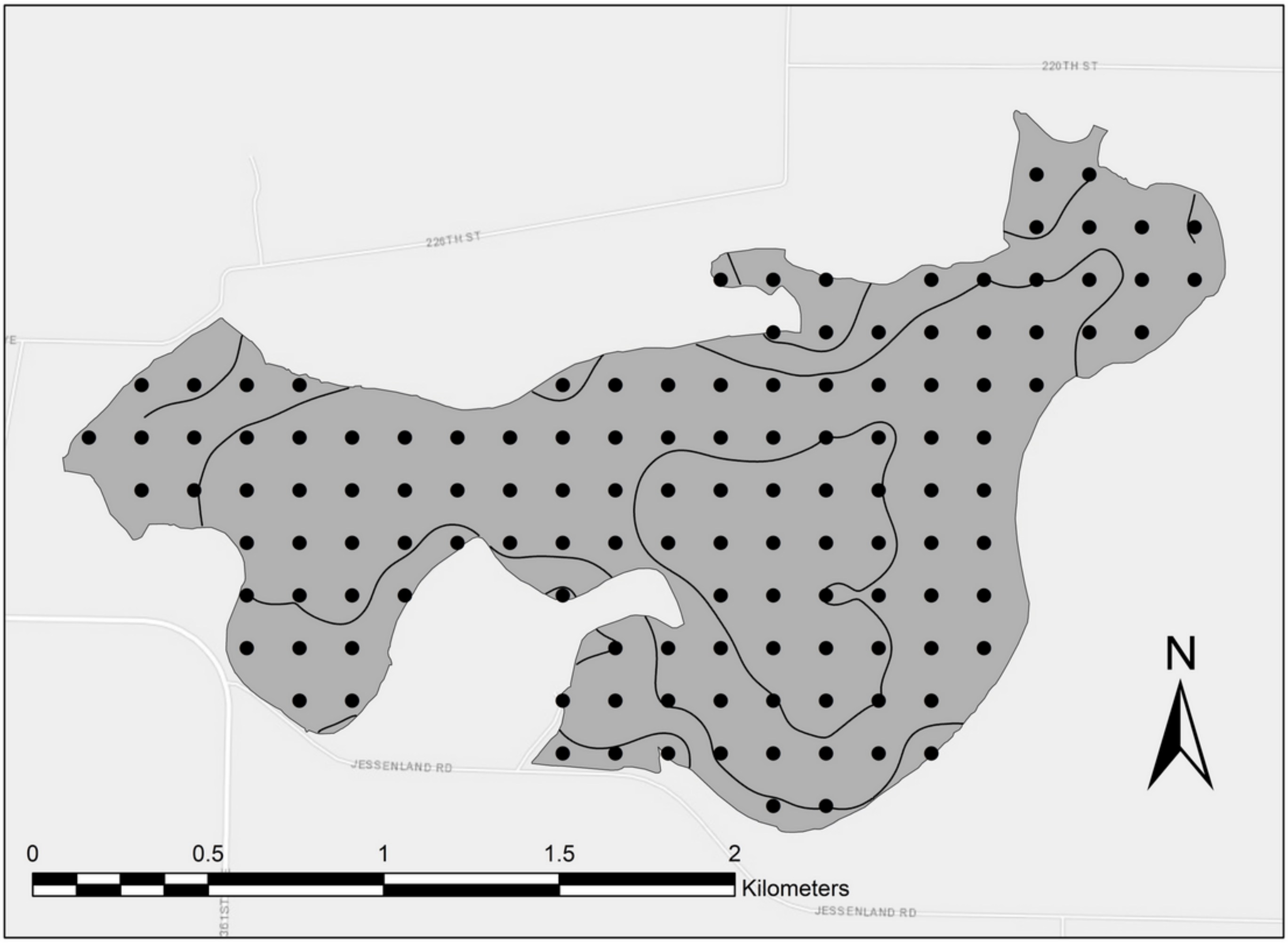

Figure 5

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

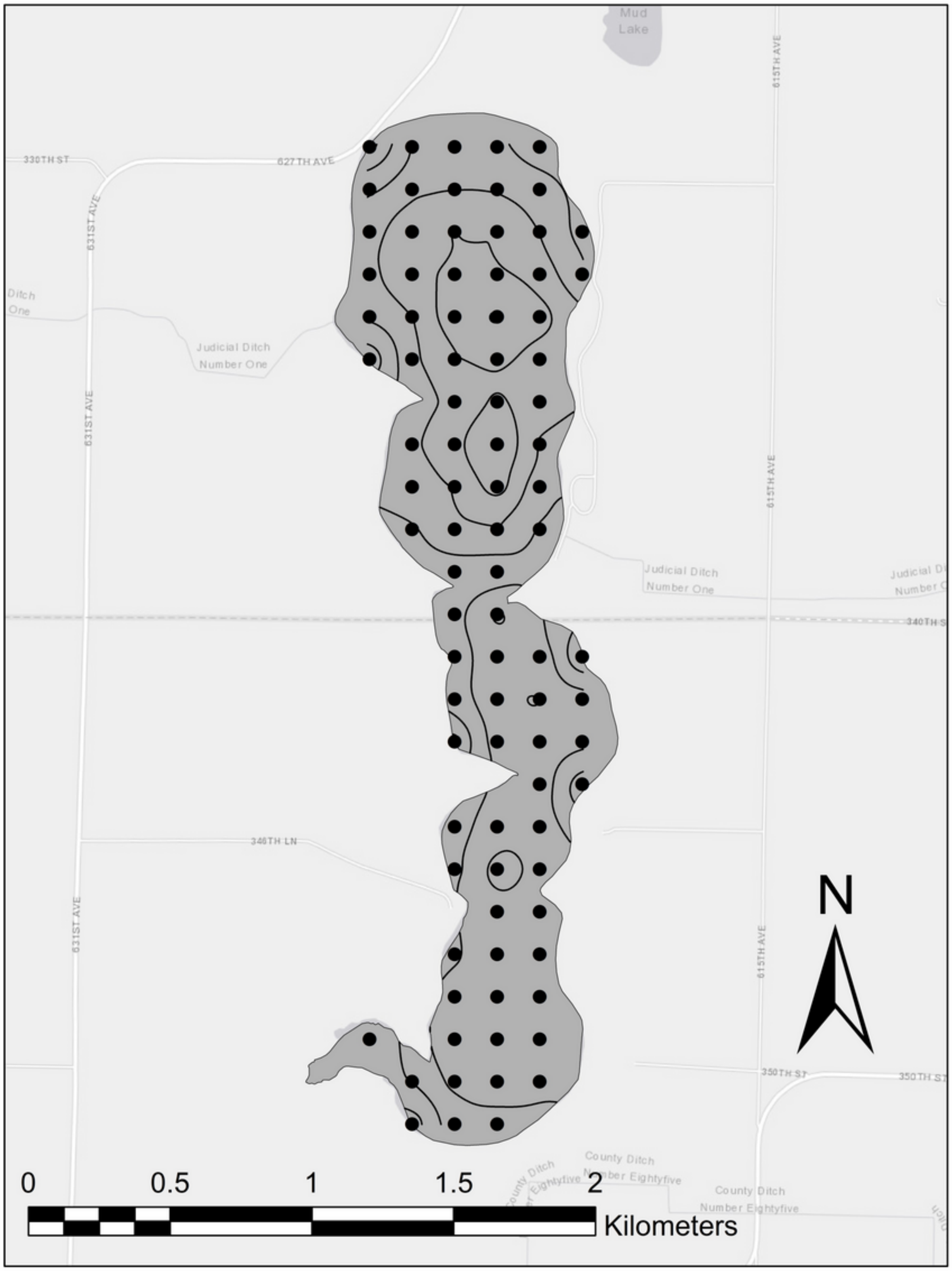

Figure 6

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