The Response of Aquatic Macrophytes to Lake Management Practices and the Role of Light in the Germination of Macrophyte Propagules

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Dedication

This thesis is dedicated to my family and friends who have continued to support my love and curiosity for science and the natural world. My project would not have been possible without their support.

Comprehensive Abstract

Macrophytes are a vital component to functioning aquatic ecosystems. Specifically, macrophytes promote good water clarity by stabilizing sediments, sequestering nutrients, and reducing the abundance of phytoplankton in the water column. Also, macrophytes provide habitat for other aquatic organisms. Healthy, robust aquatic macrophyte communities are indicated by diverse, abundant stands in the littoral zones of lakes. Poor water clarity and invasive species are primary limiting factors that cause diminished aquatic plant communities. Poor water clarity reduces the light quantity, impeding the growth of macrophytes. Invasive fish, such as common carp (*Cyprinus carpio*), damage macrophyte communities by uprooting plants and suspending sediment and nutrients in the water column. Invasive plants, such as curlyleaf pondweed (*Potamogeton crispus*) and Eurasian watermilfoil (*Myriophyllum spicatum*), often outcompete native species creating dense monoculture stands.

To improve the growing conditions for macrophyte communities, several management actions can be pursued to limit the damage by invasive species and improve the water clarity. Common management practices in Midwestern lakes include invasive species control and nutrient sequestration. These practices have been documented to enhance native macrophyte communities. Lake management often requires several years of consistent, adaptive management to effectively restore the ecosystem. Adaptive management is the systematic process of learning from past management outcomes and subsequently incorporating that knowledge into current management decisions. I evaluated the change in the macrophyte community in Lake Riley, Chanhassen, MN over the course of 6 years of lake management actions using aquatic plant point-intercept

surveys from 2011 to 2016. The results of the surveys found that after a carp removal in 2010, curlyleaf pondweed dominated the littoral zone and water clarity did not greatly improve. Once invasive macrophytes were managed starting in 2013, incremental increases in the species richness of the macrophyte community occurred. However, native macrophyte expansion was limited because water clarity was still poor during the summer growing season.

In 2016, after an alum treatment, water clarity improved and the macrophyte community abundance and richness further increased. Species richness increased from 9 observed species in 2011 to 15 in 2016. During peak growth in August, the native species frequency of occurrence was 50% through 2013 and then increased up to 80% of sites in 2016. The August native macrophyte biomass increased from $30 g/m^2$ in 2011 to $600 g/m^2$ in 2016 ($p<0.05$). Prior to 2016, the average maximum depth of rooted native plant growth was 3.1m and in 2016 it increased to 4.1m. Overall, the density, coverage, and richness of the macrophyte community increased throughout the study period demonstrating that the macrophyte community had a positive response to the multi-year management practices on Lake Riley.

The specific mechanism of macrophyte recruitment following improved growing conditions, such as in Lake Riley, is an understudied area of macrophyte restoration. Macrophytes typically propagate through clonal growth and fragmentation. However, when macrophyte populations are reduced, the lake seed bank may contribute to the reestablishment of the population. In previous studies on temperate lake seed banks, seeds from vascular aquatic plants and spores from macroalgae have been found in varying densities and viability levels suggesting that recruitment from the seed bank is possible in some systems.

I conducted a controlled laboratory experiment using sediment from Lakes Ann and Riley located in Chanhassen, MN, to 1) evaluate the response of the seed banks to different treatments and 2) compare the observed taxa sprouting from the seed banks to the taxa observed growing in the lakes. The treatments included a maximum germination treatment using a germination promoter to evaluate the full extent of the viable seed bank, a treatment representative of a lake with good water clarity, and a treatment representative of a lake with poor water clarity. The good and low clarity treatments were designed to evaluate the response of seeds to two different light levels that were observed in lakes with high turbidity (low-light intensity) and low turbidity (high light intensity). It was hypothesized that the maximum germination treatment would have the highest amount of germination, the high clarity treatment would have the second highest amount, and the low clarity treatment would have the lowest amount of germination due to the low-light quantity.

The seed banks of both Lakes Riley and Ann were similar to the macrophyte community observed growing in the lake. In Lake Ann, 16 species were observed sprouting and every species observed in the experiment grew in the lake. In Lake Riley, 17 species were observed sprouting and all but two species were observed both in the lake and in the seed bank. The seed banks did not show any significant difference in response to the germination treatments. Chara, curlyleaf pondweed, and wild celery were the most frequent species observed. Under maximum germination conditions, Lake Riley had a viable vascular seed density of 2,916 ± 1,828 seeds/m^2 and a viable chara spore

density of 1,033 ± 698 spores/m^2. Lake Ann had a viable vascular seed density of 1,100 ± 440 seeds/m^2 and viable chara spore density of 13,833 ± 2,825 spores/m^2. The study demonstrated that germinating propagules from a lake seed bank can be a valuable tool for managers to evaluate the viable macrophyte taxa present and better understand the potential for recruitment from the seed bank. Overall, to restore native macrophyte communities, it requires several multi-year management actions and will likely include multiple forms of propagule recruitment.

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Prologue

There are four chapters in this thesis. Chapter I is a summary of the role of macrophytes in a lake ecosystem and common lake management actions to improve aquatic macrophyte communities. Chapter II assesses the response of the macrophyte community in Lake Riley, Chanhassen, MN, U.S.A. to several lake management actions including common carp (*Cyprinus carpio*) reduction, invasive macrophyte control, and an alum treatment. Using point-intercept surveys, I evaluated the change in species richness, abundance, and biomass over time using results from 2011 to 2016. Once data from the summer of 2017 are incorporated, the chapter will be submitted to a journal for publication.

In Chapter III, I evaluated the effect of water clarity and subsequently light quantity on the germination of propagules (seeds/spores) from lake sediments from Lakes Riley and Ann, Chanhassen, MN. I exposed seed bank samples to one of three treatments: maximum germination, high clarity, and low clarity. I also compared the viable seed bank to what was observed growing in the lakes during point-intercept surveys. This chapter will also be submitted to a journal for publication.

Chapter IV serves to summarize the entire thesis and link the main concepts between the chapters and compare these results to other similar studies. Overall, this thesis provides insight on the macrophyte response to lake management actions and the potential role of the lake seed bank in the revegetation of a lake after growing conditions are improved.

Chapter I

The Restoration of Aquatic Macrophyte Communities in Temperate Lakes

Introduction

Shallow lake restoration projects often begin with turbid, phytoplankton dominated lakes with the aim to flip the ecosystem to a clear-water, macrophyte dominated lake (Hupfer *et al*. 2016, Stroom and Kardinaal 2016). Aquatic macrophyte restoration is a multi-step process requiring adaptive management and long-term planning. Adaptive management is the systematic process of learning from past management outcomes and subsequently incorporating that knowledge into current management decisions (Westgate *et al.* 2013).

Currently, there are several methods used to improve the lake conditions for macrophyte regeneration. Improved water clarity is often pursued first as light is a primary limiting factor for plant growth (Bornette and Puijalon 2011, Verhofstad *et al.* 2016). Water clarity improvement is achieved by reducing nutrient concentrations within the lake because high nutrient concentrations sustain the growth of phytoplankton. Actions to minimize nutrients include decreasing the external loading of nutrients into the system and biomanipulation, such as reducing the benthivorous fish population or altering the trophic structure of the food web (Cooke *et al*. 2016). A reduction of internal phosphorus loading may also be needed if the total phosphorus within the system is still high (Hupfer *et al.* 2016).

Improved water clarity can aid in macrophyte expansion and may enhance propagule (seeds and spores) germination conditions for several species. However, it can also allow for exotic, low-light tolerant species to establish in high density before many native species. Therefore, as water clarity improvements are pursued, the active control of invasive species such as curlyleaf pondweed (*Potamogeton crispus*) and Eurasian watermilfoil (*Myriophyllum spicatum*) may also be necessary to allow for the expansion of the native macrophyte community.

The Role of Macrophytes in an Aquatic Ecosystem

Macrophytes include submersed and emergent aquatic vascular plants in addition to macroalgae such as those from the order Charales (Cooke *et al.* 2016). Macrophytes play an important role in maintaining the water clarity of a lake ecosystem. Aquatic macrophytes use nutrients such as nitrate and phosphate, limiting the amount of nutrients available for phytoplankton uptake (Dennison *et al.* 1993). Additionally, they can retain the sediment, which further sequesters nutrients and reduces turbidity (Dennison *et al.* 1993, Horppila and Nurminen 2003). As macrophytes effectively compete with phytoplankton for nutrients in the water column, algal blooms and the associated turbidity are limited, preventing decreases in water quality (Bakker *et al.* 2010).

A robust macrophyte community is an integral part of a functioning aquatic ecosystem as it also creates habitat for aquatic organisms. Zooplankton can thrive within stands of vegetation that act as a shelter and protects them from predation (Donk and Bund 2002). Zooplankton, such as *Daphnia spp.*, in turn also contribute to good water clarity by consuming phytoplankton, including blue-green algae species (Schoenberg and Carlson 1984). Juvenile fish rely on the complex structure provided by diverse stands of macrophytes as protection from piscivorous fish and as a food resource, consuming zooplankton and macroinvertebrates located in the plant beds (Valley *et al.* 2004, Cross and McInerny 2006). Moreover, mature piscivore populations have been shown to be effective at controlling planktivorous fish populations, which are known to consume zooplankters (Drenner and Hambright 2002). As a result, the piscivorous fish serve as a top down control and assist in maintaining high zooplankton populations, thus sustaining good water clarity (Drenner and Hambright 2002). Overall, a diverse macrophyte community increases the complexity of habitat and subsequently increases the diversity of present aquatic life.

These trophic relationships can result in a lake settling into one of two alternative stable states: a clear water, macrophyte dominated lake and a turbid water, phytoplankton dominated state (Scheffer *et al.* 1993). These ecosystem states are considered to be stable because lake systems tend to resist change due to reinforcing feedbacks within the ecosystem. Change to the other state occurs when perturbation to the ecosystem reaches a critical threshold disrupting the reinforcing feedbacks (Scheffer and Ness 2007). Common perturbations in lakes include large benthivorous fish populations and eutrophication (Scheffer *et al.* 2001).

Several studies have demonstrated that lake management can be successful in maintaining the clear-water stable state as opposed to the phytoplankton dominated, turbid stable state (Scheffer *et al.* 1993, Hansson *et al.* 1998). Macrophyte expansion is often necessary to maintain the clear-water alternative stable state due to their role in sequestering nutrients, suppressing sediment suspension and providing habitat for herbivorous zooplankters (Hansson *et al.* 1998, Hilt *et al.* 2006). To attain a clear-water state, a reduction in external loading of nutrients is essential. Excess nutrient loading into the system can fuel phytoplankton growth, which limits the water clarity and ability for macrophytes to grow within the littoral zone (Schindler 2006). To effectively shift the lake to a clear-water state following a reduction in external loading, several actions may be pursued to establish water clarity conditions that will allow for macrophyte growth and expansion in the littoral zone (Hilt *et al.* 2006). Potential actions include benthivorous fish reduction, decreasing internal nutrient loading, and invasive macrophyte control.

Impact of Common Carp on Macrophytes

The invasion of common carp (*Cyprinus carpio*) throughout the U.S. has greatly diminished water clarity and macrophyte assemblages in lakes across the country (Weber and Brown 2009). Common carp are a benthivorous fish that can have a myriad of cascading effects on lake ecosystems (Kloskowski 2011). Documented cases in Midwestern lakes have demonstrated that when carp reach a threshold biomass of approximately 100kg/ha, they can cause the switch to a phytoplankton dominated, turbid stable state (Bajer *et al.* 2009). Carp promote this condition through their feeding behavior. They consume benthic plants and sediment and as such cause the suspension of sediment and nutrients into the water column (Crivelli 1983). In addition, this behavior causes the uprooting of aquatic plants (Crivelli 1983). With the increase in nutrients and the decrease in macrophytes, algal blooms become common and phytoplankton can dominate the system (Zambrano *et al.* 2001). Some additional research has also demonstrated that carp may have a profound impact on the lake seed bank. Carp may consume seeds and spores, with complex outcomes for seed banks, inducing germination in some species while decreasing the viability of propagules in others (Pollux 2011). Overall, carp decrease water clarity and significantly reduce the ability of macrophytes to establish.

Carp Reduction and Invasive Macrophyte Response

In the Midwest region of the U.S., carp removals have been completed to reduce the biomass of the population and to begin the shift to the macrophyte dominated, clear-water stable state. Effective benthic fish removals have been documented to reduce sediment and nutrient suspension in the water column (Hanson and Butler 1994, Bajer and Sorensen 2015). Following reduction in carp biomass below the critical threshold, macrophytes have been documented to re-establish from intact source populations (De Backer *et al.* 2012). Also, the natural recruitment of vegetation from the seed bank has been documented to occur if the seed bank is still viable (De Backer *et al.* 2012, Knopik 2014). The extent of macrophyte recolonization following clarity improvement is variable among lakes, and macrophyte coverage in the years following fish removal ranged from 20% to 90% of the lake area (Reynolds 1994, Norlin *et al.* 2005, Knopik 2014).

Following reduction in external loading and fish removal, there is a risk of invasive vegetation proliferating under the new conditions before natives can expand or sprout from the seed bank. Low-light tolerant species can often dominate the system as water clarity slowly improves before most species are capable of germination and growth

(Lauridsen *et al.* 1993, Jeppsen *et al.* 2005, Søndergaard *et al.* 2008). Invasive macrophytes in North America, such as curlyleaf pondweed (*Potamogeton crispus*) and Eurasian watermilfoil (*Myriophyllum spicatum*), are adapted to grow under low-light conditions and in cold temperatures enabling them to establish early in the growing season and to grow in deeper locations (Nichols and Shaw 1986).

Curlyleaf pondweed often sprouts from vegetative buds called turions, which are deposited on the lake bed in mid-summer and store energy for the plant to grow under the ice in winter and early spring (Nichols and Shaw 1986). By the early summer, curlyleaf can form dense, monospecific stands that impede recreation and greatly alter the ecosystem (Bolduan *et al.* 1994). Due to this early season growth, many native species are unable to sprout from propagules or germinate from the seed bank at the appropriate time due to the shading imposed by the curlyleaf beds (Santos *et al.* 2011). Additionally, curlyleaf senesces in mid-summer providing a source of phosphorus for phytoplankton that can form algal blooms (Bolduan *et al.* 1994).

Eurasian watermilfoil can also form dense stands, matting out at the surface and shading other vegetation that may be growing below (Smith and Barko 1990, Madsen *et al.* 1991). Eurasian watermilfoil propagates largely through fragmentation and seeds are thought to play a minimal role in the spread of the species (Madsen *et al.* 1988). A low-light and cold tolerant species, Eurasian watermilfoil can also be observed growing under ice, shading out natives later in the growing season (Nichols and Shaw 1986).

Invasive macrophyte control

After the shift to the clear-water stable state has begun, through biomanipulation and external loading reduction, control of invasive macrophytes may be needed. Invasive aquatic macrophytes are easily spread and can occur in damaging abundances (Pimentel *et al.* 2005). There are several treatment methods that can be employed to control invasive or nuisance levels of macrophytes. Herbicide applications have been documented to effectively control, not eradicate, populations of curlyleaf pondweed and Eurasian watermilfoil. Specifically, early season endothall treatments have been demonstrated to target curlyleaf pondweed while it is actively growing and not significantly impair the growth of native macrophytes, mainly because they have not yet started to grow (Johnson *et al.* 2012, Jones *et al.* 2012, JaKa 2015). Similarly, Eurasian watermilfoil has been controlled by the use of 2,4-D and triclopyr herbicides, which primarily affect dicot species and not the majority of native macrophytes, which are monocots (Cooke *et al*. 2016). Therefore, selective control measures that target the prolific invasive species are highly useful in also maintaining an intact native plant community. The level of impact on native macrophytes is dependent on the dose concentration as well as the length of exposure. The use of herbicides is highly regulated and testing has determined limited impacts on non-targeted aquatic life (Cooke *et al.* 2016). Herbicide applications often require multiple years of treatment and the longevity of treatments is still an area of ongoing research (Nault *et al.* 2014, JaKa 2015, Netherland and Jones 2015).

Other methods used to control invasive macrophyte species include harvesting, dredging, and sheeting (Cooke *et al.* 2016). However, these methods tend to not be as species specific as the selective herbicide applications and they can affect the native plant community as well. Certain methods may work better than others depending on the lake system, therefore, the need for adaptive management and long-term planning are needed when managing invasive macrophytes.

Natural Revegetation of the Native Plant Community

Some cases have demonstrated that after biomanipulation and selective control of invasive macrophytes, native plants can increase in frequency and biomass due to the increases in clarity and reduced competition (Lauridsen *et al.* 1993, Getsinger *et al.* 2000, Jones *et al.* 2012, JaKa 2015). To establish a diverse aquatic plant community environmental conditions such as light, temperature, nutrients, and sediment characteristics must meet germination and growth demands (Arthaud *et al.* 2012). There are several ways for macrophyte communities to naturally reestablish before the need for further manipulation occurs.

Submersed aquatic vegetation often colonizes from a source population; fragmentation or clonal growth are the most common form of spread for aquatic vegetation (Boedeltje *et al.* 2002, Boedeltje *et al.* 2003). Sources of fragments may be from a small population that remained in the lake, from upstream drift, or via human or animal transport between lakes (De Winton *et al.* 2000, Figeroula and Green 2002). The role of the seed bank is relatively minimal compared to the spread of species by fragmentation or clonal growth (Santamaría 2002). However, when macrophyte species are eliminated from a lake system, through benthivorous fish disruption or competition with invasive plants, the seed bank may play an important role in recolonization (De Winton *et al.* 2000). Macrophyte propagules (seeds and spores) can also be spread between lake systems by wind-induced currents in a lake or by animal transport (Brochet *et al.* 2010).

There have been several studies assessing the role of the seed bank in revegetating wetland ecosystems, however few studies have been completed to assess the role of the seed bank in lake ecosystems (Haag 1983, McFarland and Schafer 2011). The studies that have occurred demonstrate that the present vegetation in a wetland or lake does not tend to correlate with the assemblage of seeds in the seed bank (Titus and Hoover 1991, Combroux and Bornette 2004). Lake sediments are also known to have lower propagule densities than wetland and riparian areas and the length of propagule viability is also highly variable among species and lake environments (Kleyer *et al.* 2008, De Backer *et al.* 2012). The timing of propagule germination in lake sediments has not been thoroughly investigated although it is thought to occur in late spring and early summer as water temperature and day length increases, likely triggers to break dormancy (Baskin and Baskin 2014).

The germination of propagules from the seed bank in a lake requires several environmental factors, including light (Sederias and Colman 2007). Light induced germination is common for macrophyte propagules and studies have demonstrated that burial reduces the germination, potentially due to lack of light (Dugdale *et al.* 2001, Baskin and Baskin 2014). In some systems, sediment disturbances are needed to suspend propagules to the top of the lake sediment to optimally induce germination in clear water systems where light can trigger germination cues. Other factors important to germination in some macrophyte taxa include temperature and dissolved oxygen (Dugdale *et al.* 2001, Arthaud *et al.* 2012).

Management Actions to Improve the Native Plant Community

When the return of native macrophyte species does not occur after a biomanipulation and reduction in external loading, low water clarity is often determined to be the cause impairing the ability of plants to grow and establish a robust population (van de Hatered *et al.* 2007). There are several reasons why water clarity may not improve enough for the establishment of a healthy macrophyte community. Internal phosphorus loading may still cause excessive phytoplankton blooms, maintaining a turbid state during the growing season. Alternatively, zooplankton may not recover quickly to high densities thus failing to control the phytoplankton growth. Additionally, the seed bank may be exhausted if carp have consumed a significant portion of propagules from the seed bank or there has been a lack of replenishment due to many years of suppressed macrophyte communities (Pollux *et al.* 2006, Vojtko *et al.* 2017). Even if clarity improves relative to the pre-carp removal levels, it may not be a sufficient amount to allow for substantial macrophyte growth or to induce germination in the seed bank and thus still be a limitation on the expansion of macrophytes throughout the lake and in deeper areas of the littoral zone (Chambers and Kalff 1985). When light conditions are not sufficient to allow for the recolonization of macrophytes after invasive species control, methods to improve the water clarity can be undertaken to improve the growing conditions.

A common tool used by lake managers to increase the water clarity is to reduce the internal loading of phosphorus in the lake. Internal loading of phosphorus is a common issue in lakes that stratify and become anoxic in the sediment for part of the year. Phosphorus is bound to ferric iron within the lake under oxygenated conditions (Cooke *et al.* 2016). When a stratified lake becomes anoxic, redox reactions in the sediment reduce iron, from the ferric to ferrous state, which no longer binds phosphorus. The phosphorus thus becomes mobilized again in the sediment and water column, available for uptake by organisms (Cooke *et al.* 2016). Thus, alternative approaches to bind phosphorus are used in eutrophic lakes such as an alum treatment.

Alum is an aluminum salt, which when added to water creates a floc that binds to phosphorus in the water column as it settles to the lake bottom and also binds to phosphorus in the sediment when it becomes mobilized again due to iron reduction (Barko *et al.* 1990). By conducting an alum treatment, the amount of available phosphorus due to internal loading is decreased and water clarity is improved due to a reduction in phytoplankton. Successful alum treatments have demonstrated an increase in water clarity and a decreased internal loading rate, total phosphorus concentration, and chlorophyll-*a* concentration within the system (Barko *et al.* 1990, Welch and Sherieve 1994, Welch and Cooke 1999, Huser *et al.* 2011).

The increase in water clarity after an alum treatment has been associated with an increase in macrophytes due to greater light availability. However, macrophytes can grow to nuisance levels and the increase is often due to exotic species (Welch and Shrive 1994, James 1996). One study in Minnesota demonstrated a successful alum treatment with an improvement in clarity however the vegetation increases were due to Eurasian watermilfoil (Huser *et al.* 2011). Currently, there are few studies that assess the capacity of the seed bank to respond to the increase in water clarity provided by an alum treatment. If seed bank sampling occurs and there appears to be viable propagules of desirable species, then one can monitor the effect of increased clarity and assess the extent of the propagule response. If sampling indicates few viable species, potentially due to benthivorous fish populations or poor sediment conditions, alternate measures will likely to be needed to aid in the recovery of the population if there is no source of recruitment for new species within the system.

The return of diverse macrophyte stands may be impeded by an impoverished regional pool of propagules, in this case there are additional restoration practices that can be implemented (Sand-Jensen 2008, Dudley *et al.* 2012). In this case transplanting of macrophytes from nearby systems may be a viable option (Smart *et al*. 1998). Following reintroduction, some species may establish and spread, called the founder colony approach (Smart *et al.* 1998, Cooke *et al.* 2016). However, several species do not survive transplanting experiments (Smart *et al*. 1998). The biggest factor attributed to limited success is poor water clarity (Knopik 2014). With limited light conditions macrophytes cannot expand. Therefore, improving water clarity still appears to be a vital step in the promulgation of a native plant community prior to beginning transplanting. One method of inducing native plant growth in a newly improved system that has not been investigated is transferring sediment and the seed bank from species rich systems to systems with a diminished seed bank. The propagules may be induced to germinate under the clear water conditions if spread over the current sediment, however there are concerns about unintentional species introductions. This is an area of research that requires further investigation.

Summary

Several environmental factors are important in the establishment or restoration of a native macrophyte community in lake ecosystems. In some cases, after reduction in external loading and biomanipulation, the clear water state is not improved to the degree that native macrophytes can repopulate the lake, leaving low-light tolerant species such as curlyleaf pondweed and Eurasian watermilfoil able to establish and become widespread at nuisance levels. Management of invasive macrophytes is common and often effective, however native plant communities still may not rebound. To aid in the restoration of a macrophyte community, further improvements in water clarity are often pursued next by the reduction of internal loading. Natural revegetation of some native plant species has been documented to occur from fragmentation and the seed bank. If the seed bank and available propagules are low, transplanting of species is a viable next step. Overall, the establishment of a stable, diverse submersed aquatic plant community requires several management actions to reduce nutrient loading, sediment suspension, and to control invasive macrophytes before revegetation efforts are made if they are not naturally occurring as the clarity improves. Once an established macrophyte population exists, the clear water state may become stabilized.

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Chapter II

The Restoration of Native Aquatic Macrophytes: Macrophyte Response to Carp Reduction, Invasive Macrophyte Control, and Alum Treatment

Summary

I evaluated the response of the aquatic vegetation community to several management actions in Lake Riley, Carver County, MN (MN DNR DOW ID 10-000200) using surveys from 2011 through 2016. Management actions included common carp (*Cyprinus carpio*) removal, selective control of invasive macrophytes, and an alum treatment. Using the point-intercept survey method, the frequency of occurrence and biomass of plants was assessed in June and August each year and the changes were evaluated using regression models. The changes in the native and invasive macrophyte species richness and abundance were also evaluated using regression models.

Following carp removal in 2010, the plant community was largely dominated by curlyleaf pondweed and water clarity did not greatly improve relative to pre-carp removal levels. Species richness increased gradually over the surveyed years as invasive species were managed with herbicide control starting in 2013. Water clarity significantly improved due to the alum treatment in May 2016 and the macrophyte community richness and abundance increased further. Species richness increased from 7 in 2011 to 15 in 2016. Additionally, throughout the study, the native species frequency of occurrence and biomass increased. During peak growth in August, native species frequency of occurrence was 50% in 2011 to 2013 and then steadily increased up to 80% of sites in 2016. The August native macrophyte biomass increased from 30g/m^2 in 2011 to 600g/m^2 in 2016 ($p<0.05$).

Following the alum treatment, the native plant community grew in deeper waters relative to pre-alum treatment observations. The maximum depth of rooted native plant

growth observed in 2016 was 4.1m, whereas prior to 2016 the average maximum depth of rooted native plant growth was 3.1m. Lastly, invasive macrophytes, curlyleaf pondweed and Eurasian watermilfoil, were controlled by the herbicide treatments and the frequency of occurrence and biomass of these taxa decreased relative to pre-control levels and remained low despite water clarity improvements. Overall, the management actions in Lake Riley resulted in a denser, more diverse macrophyte community. This case study demonstrates the need for adaptive, multi-year management when restoring macrophyte communities and lake ecosystems.

Introduction

Light availability is an environmental factor associated with the germination and survival of submersed aquatic macrophytes. When water clarity is poor many macrophyte species do not obtain enough light to efficiently photosynthesize (Binzer *et al.* 2006, Rodrigues and Thomaz. 2010). Often in low clarity lakes the macrophyte community has low species diversity and is dominated by low-light tolerant species (Binzer *et al.* 2006, Cooke *et al.* 2016). In central Minnesota lakes, poor water clarity is typically due to eutrophication and large populations of benthivorous fish. Eutrophication is caused by high nutrient concentrations resulting in the proliferation of phytoplankton in the water column (Schindler 2006). High phytoplankton abundance increases light attenuation and subsequently reduces the capacity for macrophytes photosynthesize (Binzer *et al.* 2006, Cooke *et al.* 2016). Additionally, common carp are widespread in Minnesota lakes, impairing water quality and macrophyte communities. Common carp suspend sediment and nutrients by spawning in macrophyte beds and uprooting macrophytes as they feed on macroinvertebrates in the sediment. (Bajer *et al.* 2009). These behaviors increase the turbidity and nutrient concentrations in the water column, subsequently also increasing the abundance of phytoplankton (Bajer *et al.* 2009).

Diminished macrophyte populations have significant impacts on other aquatic organisms as macrophytes play an integral role in the functioning of a lake ecosystem. Macrophytes sequester nutrients and sediment promoting water clarity (Dennison *et al.* 1993). Additionally, macrophytes provide rearing habitat for invertebrates and fish (Donk and Bund 2002, Cross and McInerny 2006). The lack of macrophytes in some Minnesota lakes have resulted in turbid water, higher nutrient concentrations, and a change in the composition of aquatic organisms as exotic species proliferate throughout the littoral zone (Hilt *et al.* 2006, Knopik 2014, JaKa 2015).

If the macrophyte population in a lake system is in low abundance and not diverse, lake managers can pursue several strategies to improve the growing conditions (Van de Hatered *et al.* 2007). Firstly, reducing the external loading of nutrients and sediment into the aquatic ecosystem is a critical management practice. This can be achieved by implementing riparian and upstream projects that aim to limit the amount of sediment and nutrient inputs into the system, such as reducing fertilizer use or planting riparian vegetation (Hilt *et al*. 2006). Secondly, if the benthivorous fish population is in high abundance, reduction of the population may be necessary to limit the damage to growing macrophytes and prevent the increased release of sediment and nutrients into the water column (Bajer *et al*. 2009).

If a reduction in external loading and benthivorous fish control do not yield an improvement in water clarity, a reduction in internal loading may be necessary to decrease the nutrient concentrations and phytoplankton abundance. This can be achieved by applying aluminum salts (alum) to the water, which bind to mobile phosphorus in the water column and sediment. Documented cases demonstrate that macrophyte colonization can increase following an alum treatment however, invasive macrophytes may respond more rapidly than native macrophytes (Newman *et al.* 2004, Spears *et al.* 2016). Therefore, management of invasive aquatic plants is often necessary as water clarity improves throughout the restoration process (Newman *et al*. 2004, JaKa 2015). Common management techniques for invasive macrophyte control include the use of mechanical removal such as a harvesting or the use of selective herbicides approved for aquatic use.

Several studies have evaluated the response of macrophyte communities to lake management actions. Some examples include the evaluation of the effects of endothall herbicide on macrophyte communities (Jones *et al*. 2012, JaKa 2015), the effect of reducing internal nutrient loading on macrophyte abundance (Newman *et al*. 2004, Spears *et al.* 2016), and the effect of carp reduction on the macrophyte community (Bajer *et al*. 2009). However, fewer studies evaluate the response of the macrophyte community to multiple management actions occurring over several years. Most studies have been three years or less in duration and do not evaluate long-term management strategies (Hilt *et al.* 2006, Johnson 2011, JaKa 2015, Cooke *et al.* 2016).

The purpose of this study was to assess the native and non-native submersed macrophyte community after carp removal from 2011 to 2016 in response to management actions. I assessed if selective invasive macrophyte control and an alum treatment can be used to increase the abundance and richness of a macrophyte community in a lake after successful carp reduction. After carp removal in 2010-2011, Lake Riley underwent curlyleaf pondweed control in early spring each year from 2013 through 2016 with endothall herbicide applied in delineated treatment blocks. Eurasian watermilfoil was treated in June of 2015 and 2016 using 2,4-D herbicide in delineated treatment blocks. A hypolimnetic alum treatment was conducted in May of 2016. Overall, this study assessed the change in abundance and diversity of the plant community in Lake Riley using point-intercept surveys that occurred each June and August from 2011 through 2016. Long-term, adaptive management is necessary for macrophyte restoration, and yet it is rarely assessed. This study provides insight into the key management factors that influence macrophyte communities.

Methods

Study Lake

Lake Riley (DOW 10-0002) is a eutrophic lake located within the Riley Purgatory Bluff Creek Watershed District (RPBCWD) in Chanhassen and Eden Prairie, Minnesota USA. Lake Riley has a maximum depth of 15m and is a dimictic lake, stratifying during the winter and summer. Lake Riley is 120 hectares in area and is within the Riley Creek drainage, with a watershed area of 2,590 hectares (Figure 1). The land use in the Riley

Creek watershed is suburban with a mixture of residential housing, commercial infrastructure, farmland and forested parks.

There were several management actions pursued on Lake Riley over the last 7 years. Common carp were removed from Lake Riley in 2010, as part of an attempt to improve water clarity and quality (Bajer *et al.* 2011). Following carp removal, water clarity marginally increased and limited native macrophyte expansion occurred (JaKa 2015). The invasive species curlyleaf pondweed and Eurasian watermilfoil were controlled in Lake Riley by multi-year, early season herbicide applications of endothall (2013-2016) and 2,4-D (2015-2016) respectively. In 2016, a hypolimnetic alum treatment was conducted to reduce internal nutrient loading and improve water clarity.

Invasive Species Control

To reduce the common carp population in Lake Riley, carp were removed in 2010 by winter seining. Prior to the removal, the estimated biomass of carp was 176.1 kg/ha in 2009. After the reduction occurred, the estimated biomass was reduced to 90.0 kg/ha (Bajer and Sorensen 2012). Throughout the study period, the carp population remained below 100 kg/ha in Lake Riley because of lack of recruitment and active control of the population after the initial removal.

To control curlyleaf pondweed, areas of dense growth were delineated in Lake Riley in early spring in 2013, 2014, 2015, and 2016. These areas were determined both visually and by throwing a double-headed garden rake over the boat to confirm presence or absence of curlyleaf pondweed. Treatment blocks were delineated using ArcGIS and when the water temperature reached 10 to 15 ˚C the delineated blocks were treated with Aquathol K ®, a 40.3% dipotassium salt of endothall herbicide (7-oxabicyclo[2,2,1]heptane-2,3-dicarboxylic acid) at a targeted concentration of 1.0mg/L. The herbicide application is selective for curlyleaf pondweed because most native plants are still dormant at this temperature and thus not affected (Johnson *et al.* 2012, Jones *et al.* 2012). Herbicide was applied to approximately 8 hectares in 2013, 13 hectares in 2014, 8 hectares in 2015 and 7hectares in 2016.

For control of Eurasian watermilfoil, the delineation of dense areas of growth occurred in late May in both 2015 and 2016 using the same methods as the curlyleaf pondweed delineation. Delineated treatment blocks were treated in mid-June in 2015 (14 hectares) and 2016 (13 hectares) with 2, 4- Dichlorophenoxyacetic acid (2, 4-D) herbicide at a targeted concentration of 2.0mg/L. The herbicide is selective for dicot plant species, therefore it is primarily selective for Eurasian watermilfoil.

Alum Treatment

Lake Riley received a hypolimnetic alum treatment (approximately 100 hectares) in early May 2016. The application occurred using a customized boat that followed GPS coordinates and released the alum (aluminum sulfate) into the water column. When applied, the alum creates a floc that binds to mobile phosphorus in the water column and in the sediment (Cooke *et al.* 2016). By sequestering the available phosphorus, the alum floc reduces the availability to phytoplankton thus decreasing the turbidity in the water column.

Aquatic Vegetation Surveys

Point-intercept surveys (Madsen 1999) were conducted to measure the frequency of occurrence of macrophyte species in Lake Riley in June and August between 2011 and 2016. Points were randomly created on a 50m grid in the littoral zone using ArcGIS. There were 185 survey points in the littoral zone sampled during each survey. The littoral zone is legally defined by the Minnesota Department of Natural Resources as depths less than or equal to 4.6m. The points were uploaded onto a Garmin GPSmap76 GPS. Once on the lake, a boat was navigated to each survey point using the GPS.

To obtain the macrophyte frequency of occurrence, at each survey point a double-headed metal garden rake connected to a rope was tossed and then allowed to sink to the lake bed. The rake was dragged along the lake bottom approximately 10 meters and then pulled to the surface when it reached the boat. The depth, species present, relative abundance, and overall rake density was observed. The rake density rating was on a scale of zero to five based on the extent that plants filled the rake, with five equating to a full, dense rake and one equating to a sparse rake. Empty rakes were given a rating of zero. The plants on the rake were identified to species and each species received an abundance rating from zero to five.

Plant biomass samples were also collected during point-intercept surveys. A subsample of 40 points were randomly selected for biomass sample collection. A single headed garden rake was used to sample an area of $0.09m^2$ (Johnson and Newman 2011). The 0.33m garden rake was lowered to the lake bottom and rotated three times and retrieved to obtain all the plants in the sampling area (Johnson and Newman 2011).

Biomass samples were placed in sealable plastic bags and stored in a cooler for transport to the laboratory. At the laboratory, samples were stored at 5 °C until they were processed and sorted. Samples were rinsed to remove sediment and excess debris and remaining roots were removed to obtain an estimate of above ground biomass. The separate species were spun in a salad spinner to remove excess water prior to drying and then weighed to obtain a wet biomass measurement. The separate species were then placed in pre-weighed brown paper bags. Plants were dried for at least 48 hours at 105°C and reweighed. Plant biomass was calculated as grams dry per square meter (g dry/m^2) by dividing the dry sample mass by the total sample area (0.09m^2). Mean lake-wide littoral plant biomass was calculated by averaging all samples from depths of ≤ 4.6m for each individual plant species and for total native biomass including points where plants were not present.

The results of the point-intercept surveys (frequency of occurrence) and biomass sampling are reported as an average from the June and August surveys.

Water Quality

A set of water quality measurements were recorded in Lake Riley at the deepest part of the lake at midday throughout the growing season from May through August and during the point-intercept surveys. Dissolved oxygen (DO), temperature, and photosynthetically active radiation (PAR) were measured at 0.5m increments until the hypolimnion was reached or until the cable ran out at 9.0m. DO and temperature were measured using a YSI ProODO electronic meter and measured in mg/L and °C respectively. Values for PAR were measured using a LiCor Li-189 Light Meter and a Li-Cor underwater quantum sensor and recorded in µmol photons/s/m^2. Secchi depths (nearest 0.1 m) were also recorded during water quality assessments and compared between years. Additionally, staff from the Riley Purgatory Bluff Creek Watershed District took water quality measurements every two weeks from April to October on Lake Riley during the study. The total phosphorus measurements obtained by the staff members from 2013 to 2016, were compared between years to evaluate the effectiveness of the alum treatment.

Statistical Analysis

All statistical analysis was conducted using R statistical software version 3.3.2 (The R Foundation for Statistical Computing, 2016). Results were considered statistically significant when p values were < 0.05. The frequency of occurrence data followed a Poisson distribution. Resultantly, Poisson regression models were used to evaluate significant factors affecting macrophyte frequency of occurrence for both June and August surveys. Factors included in the model to evaluate total native species abundance and individual native species abundance were year, month, exotic species frequency of occurrence, and pre- or post-alum treatment. Year was used to capture the climatic variability between survey years. Month was used to account for the difference in abundance in the early season (June) compared to the late season (August). To evaluate the change in the exotic species frequency of occurrence in both June and August (Eurasian watermilfoil and curlyleaf pondweed), Poisson regression models were also used and included the following parameters: year, month, native macrophyte frequency of occurrence, and pre- or post-herbicide treatment.

Multiple regression models were used to detect significant factors influencing total mean native species biomass and the mean biomass of each individual species in both the June and August surveys. Factors evaluated included year sampled, month, pre- or post-alum treatment, and mean exotic species biomass. Mean exotic species biomass (Eurasian watermilfoil and curlyleaf pondweed) were also evaluated for June and August surveys and the models included year, month, pre- or post- aquatic plant herbicide control, and total mean native species biomass. The log plus 1 of the biomass values was used to account for the non-normal distribution of the mean biomass values and also biomass values of zero.

Initially, mixed effects models were tested to account for the sampling point as the random effect and the alum treatment as the fixed effect. However, the mixed effect models resulted in a conservative estimate of variability and do not account for the fact that when we resampled points each year during point-intercept surveys, we did not precisely return to the same point due to GPS accuracy and human sampling error. Therefore, implementing multiple regression models allowed for a more precise assessment of the change in the plant community and accounts for other environmental factors such as year and the presence and density of other species.

To assess the significance in the change in August species richness, a Poisson regression model was used to assess the effect of the alum treatment, exotic species present, month, and year on the total August richness observed in the lake. Additionally, the change in the species richness per point in August was evaluated based on the number of exotic species at the site, alum treatment, month, and year. Only August richness was evaluated because that is the peak growth for native macrophyte species (Cooke *et al*. 2016). Lastly, a linear model was used to assess the change in the depth of rooted native macrophyte growth using alum treatment, exotic species biomass, month, and year to evaluate the change in colonization depth.

Overall, these statistical models were implemented to assess the change in the macrophyte community over the survey period due to the identified management factors of alum treatment and invasive macrophyte control. Carp biomass was not included as a factor because no pre-treatment data exists on the macrophyte community.

Results

Water quality

In May, the average Secchi depth was variable throughout all survey years. Prior to the 2016 alum treatment, the May Secchi depth varied between 1.1m and 3.5m from 2011 to 2015. After the alum treatment occurred on May 9th and 10th of 2016, the Secchi depth was 6.5m (Figure 2, Appendix Figure 1). Before the alum treatment, Secchi depths decreased to an average of 1.2m in July and 0.5m in August. After the alum treatment, the average August Secchi depth was 1.8m. During all years of monitoring, from 2011 through 2016, the dissolved oxygen and temperature profiles generally showed an anoxic hypolimnion below 5.0m in August (Appendix Figure 2). The August thermocline was consistently between 5.0m and 6.0m during all survey years (Appendix Figure 2). The

PAR was variable throughout the survey years due to different levels of cloud cover on survey days. The total phosphorus (TP) levels decreased following the alum treatment. August TP levels averaged at 0.055mg/L ± 0.012mg/L prior to the alum treatment. After the alum treatment, the TP levels decreased in August to 0.048mg/L ± 0.009mg/L.

Aquatic vegetation community

The native macrophyte community steadily increased in richness and abundance after the carp removal, exotic species treatments, and the alum treatment on Lake Riley. In 2011, immediately after carp removal, the August native species richness in Lake Riley was 7 species. Following the curlyleaf pondweed and Eurasian watermilfoil herbicide treatments the August native richness increased to 11 species in 2015, and after the alum treatment in 2016, 14 native species were observed in August (Table 1). The increase in lakewide August species richness was not significant (Appendix Table 1). However, the mean species richness per sampling point increased from 0.6 species in August of 2011 to 1.6 species in August of 2016 and this increase was significant ($p<0.01$). The results of the Poisson regression demonstrated that the August species richness per point was significantly related to alum treatment, year, and exotic species frequency of occurrence (Appendix Table 1).

Increases in species richness were observed throughout the study period (Table 2). The most commonly observed native species throughout all the survey years were coontail (*Ceratophyllum demersum*), Canada waterweed (*Elodea canadensis*), and sago pondweed (*Stuckenia pectinata*). Once exotic species were controlled, chara (*Chara spp.*) and narrowleaf pondweed (*Potamogeton pusillus*) were recruited to the lake. Following the increase in water clarity due to the alum treatment, wild celery (*Vallisneria americana*) and water stargrass (*Heteranthera dubia*) were observed in the lake (Figure 3, Table 2). The number of points in August with more than 3 species found at a point increased from 6 in 2011 to 42 in 2016. Additionally, the maximum depth of rooted native plant growth increased from 3.1m in 2011 to 4.1m in 2016, although the increase was not significant (Table 1).

The total native plant community (all native taxa combined) showed large increases over the study period in both frequency of occurrence and biomass. The total native plant frequency of occurrence increased from 49% in 2011 to 82% in 2016 ($p=0.08$) (Figure 4 and Appendix Table 2). The increase occurred steadily over the course of the survey years as growing conditions improved with exotic species control and water clarity improvement. The increases in native frequency of occurrence were significantly related to alum treatment, exotic species frequency, and month. (Appendix Table 2). The total biomass of all native species increased from 43.8g/m^2 ± 11.0g/m^2 in 2011 to 707.5g/m^2 ± 306.2g/m^2 in 2016 ($p<0.01$) (Figure 5). The native macrophyte biomass was significantly related to alum treatment, year, month and exotic species biomass ($p<0.01$) (Appendix Table 3). The August native plant biomass doubled between 2014 and 2015 and again between 2015 and 2016 (Figure 5). The total native plant biomass was composed mainly of coontail and Canada waterweed.

Exotic species curlyleaf pondweed and Eurasian watermilfoil also showed changes over the study period. The curlyleaf pondweed frequency of occurrence was high after carp removal; in June of 2011 the frequency of occurrence was 34% and in June of

2012 it was 28%. Following the herbicide treatments in early spring starting in 2013, the June curlyleaf pondweed frequency of occurrence remained at 35% or below in 2013 through 2016, the change in frequency was not significant (Figure 3 and Appendix Table 2). Although the June curlyleaf frequency of occurrence was still high, the biomass decreased greatly after herbicide treatments began in 2013. The June biomass was highest in 2012 at 120.0g/m^2 but never reached greater than 27.4 g/m^2 during the years when treatments occurred ($p<0.01$))(Figure 6 and Appendix Table 3). Curlyleaf pondeed biomass was significantly related to herbicide treatment and month (Appendix Table 3). The August curlyleaf pondweed frequency of occurrence and biomass was low throughout the survey years due to the life cycle of the plant in which it peaks its growth in June and senesces by August each year.

Eurasian watermilfoil frequency of occurrence was high in both June and August surveys after carp were removed (Figure 3). The treatment of Eurasian watermilfoil was successful in 2015 and 2016. Each year after treatment in June, the frequency of occurrence was reduced in August relative to the June frequency (Figure 3). The change in Eurasian watermilfoil frequency was significant over the study period ($p<0.05$) and was significantly related to native frequency of occurrence, year, and month (Appendix Table 2). Eurasian watermilfoil biomass also decreased in August relative to the June measurements after herbicide treatments occurred. The average biomass of Eurasian watermilfoil significantly decreased during the survey years ($p<0.01$). The Eurasian watermilfoil biomass was significantly related to native species biomass and month. The June biomass was highest in 2012 at 135.7 g/m^2 and decreased to 52.8 g/m^2 in 2015, and

11.7 g/m^2 in 2016. The August biomass was highest in 2014 at 43.2 g/m^2 and was 6.9g/m^2 in 2015 and 22.6g/m^2 in 2016 after treatments ($p<0.05$) (Figure 6, Appendix Table 3).

Coontail was the most commonly occurring native macrophyte throughout the survey years. The frequency of occurrence increased as growing conditions improved from 47% in 2011 to 72% in 2016, however the results were not significant (Figure 3, Appendix Table 2). Coontail biomass increased as a result of the management actions; the biomass was 41.7g/m^2 in 2011 and increased to 673.0g/m^2 in 2016 ($p<0.05$) (Figure 6). Coontail biomass was significantly related to alum treatment, year, month, and the exotic species biomass (Appendix Table 3). Coontail continued to make up the vast majority of the native aquatic plant biomass in Lake Riley, with little contribution of other native plants to total lake-wide native plant biomass.

Canada waterweed was commonly observed during surveys but not densely growing. The frequency of occurrence increased as growing conditions improved from 2% in 2011 to 38% in 2016 ($p<0.01$) (Figure 3). The frequency of occurrence was significantly related to year, month, alum treatment, and exotic species frequency of occurrence ($p<0.05$) (Appendix Table 2). The biomass also greatly increased as a result of the management actions. The biomass was 0.06g/m^2 in 2011 and 30.1g/m^2 in 2016 ($p<0.01$) (Figure 6). Similar to the frequency of occurrence analysis, the model for Canada waterweed biomass indicated that it was significantly related to year, month, exotic species biomass, and the alum treatment ($p<0.01$) (Appendix Table 3).

Sago pondweed was also regularly observed during surveys. The frequency of occurrence was stable during the survey period occurring between 0% and 6% occurrence, there was no significant change in the frequency of occurrence (Figure 3 and Appendix Table 2). The biomass fluctuated between 0g/m^2 and 3.4g/m^2 and there was no significant change (Figure 6 and Appendix Table 3).

Narrowleaf pondweed was also observed during surveys. The frequency of occurrence fluctuated between 0% and 10% throughout the study (Figure 3). The biomass fluctuated between 0g/m^2 and 0.4g/m^2 during the study. There was no significant change (Figure 6 and Appendix Tables 2 and 3).

Chara was recruited to Lake Riley in 2014. The frequency of occurrence was 0% for all survey years until 2014 when it was observed at 1% of sites. The frequency of occurrence in 2015 and 2016 ranged between 1% and 3% (Figure 3). The increase in frequency of occurrence was significant and was significantly related to exotic species frequency of occurrence, month, and year (Appendix Table 2). The biomass was 0.0g/m^2 until 2015 when it increased to 8.9g/m^2, but the biomass decreased to 3.1g/m^2 in 2016 (Figure 6). The change was not significant (Appendix Table 3).

Naiad species (*Najas flexilis* and *Najas guadalupensis*) also increased in frequency throughout the survey years. The frequency of occurrence was zero throughout all survey years until 2015 when it was observed at 6% in 2015 and 2% in 2016 (Figure 3). However, the increase in frequency of occurrence was not significant (Appendix Table 2). The naiad biomass was 0g/m^2 in all survey years until it reached 2.4g/m^2 in 2015 and 0.13g/m^2 in 2016 (Figure 6). The increase in biomass was significant and significantly related to exotic species biomass, month, and year ($p<0.05$) (Appendix Table 3)

Discussion

Overall, the Lake Riley macrophyte community increased in richness and abundance over the study period. The recruitment of new native species in Lake Riley was incremental as growing conditions improved throughout the study period. The comprehensive management on Lake Riley improved the native macrophyte community and demonstrated the importance of adaptive and multi-year management when attempting to restore aquatic macrophytes. This study on Lake Riley also emphasizes the importance of continuous exotic species control when simultaneously working to improve water clarity. A previous study on the effect of alum treatments in the Twin Cities metro area showed drastic increases in exotic species when the clarity improved and no control efforts were in place (Newman *et al.* 2004). Without the control of the invasive macrophytes, the alum treatment may have resulted in a dense monoculture of Eurasian watermilfoil or curlyleaf pondweed due to their rapid growth. However, this study demonstrated that with consistent, multi-year management of the exotic species population, the invasive species can be controlled as growing conditions are improved for native macrophyte species.

Prior to the carp removal, information on the Lake Riley plant community is sparse. Macrophyte data were gathered by UMN field technicians from 2007 through 2010 (P. G. Bajer and P. W. Sorensen, personal communication). Through a visual assessment, the only vegetation found were intermittent populations of Eurasian watermilfoil, coontail, curlyleaf pondweed, and Canada waterweed indicating that carp were limiting the expansion of vegetation in Lake Riley (P. G. Bajer, personal communication). Additionally, several studies have documented that macrophyte communities are greatly impaired by large populations of common carp (Bajer *et al.* 2009, Kloskowski 2011). Therefore, it is likely that if carp reduction did not occur on Lake Riley the macrophyte community would not have expanded as observed during the survey years. The July and August water clarity did not improve after carp reduction, likely due to high levels of phosphorus in the water column resulting in high phytoplankton abundances (see also Bajer and Sorensen 2015).

After the carp removal, the invasive species curlyleaf pondweed and Eurasian watermilfoil expanded rapidly in the lake as they can tolerate lower light conditions and outcompete native species (Bolduan *et al.* 1994, Chase and Knight 2006). Following herbicide control, the invasive macrophytes were still present but not at damaging levels. The curlyleaf pondweed frequency of occurrence and biomass was greatly reduced by the 2016 June survey and the Eurasian watermilfoil biomass was reduced by 2016 although the frequency of occurrence was still similar to pre-treatment years. After the exotic species curlyleaf pondweed and Eurasian watermilfoil were controlled, native plants slightly increased in frequency of occurrence and biomass. However, water clarity was still limiting the expansion and growth of native plants despite the reduced competition with the invasive species after herbicide control. After the water clarity improvement in 2016 the exotic species observations remained similar to previous years while native species were observed expanding, suggesting that the herbicide treatments were effective at controlling the invasives even after growing conditions improved.

After the alum treatment, the native species responded to the improved water clarity and the species richness further increased. The abundance and biomass also increased for several native macrophyte species as the growing conditions were enhanced throughout the survey years. For many species, the largest increases occurred between the years of 2015 and 2016 when water clarity was drastically improved. Similar to other studies on macrophyte community recovery, we found that water clarity is a significant driver in the abundance and diversity of the native plant community (Hilt *et al.* 2006). In many cases the observed increases in frequency of occurrence over the survey years were not significant. However, many species that had insignificant increases in frequency of occurrence significantly increased in biomass. This pattern may be due to increases in species density being more pronounced than increases in species expansion throughout the littoral zone.

Although the native macrophyte community increased in richness and abundance it was still largely dominated by coontail and Canada waterweed, two native species that can grow prolifically in the water column and in fact are highly invasive in other regions of the world (Heikkinen *et al*. 2009, Hyldgaard and Brix 2012). These taxa were the most abundant native species by far for both the frequency of occurrence and biomass. The remaining native macrophyte species all showed moderate to no increases in abundance, although as light availability increased new species were recruited to the lake during the survey years. Wild celery and water stargrass were observed in Lake Riley for the first time in 2016; indicative of a healthy plant community, these species are of high value to the lake ecosystem. Ideally, as water clarity and light conditions remain improved in the coming years these species will be observed expanding in the lake. Additionally, if the water clarity and light quality remain at this improved level, transplanting aquatic plants may be successful in Lake Riley which would further increase the abundance and diversity.

Overall, to restore a healthy macrophyte community there are several factors that must be managed in the lake system. Exotic species should be controlled if in high abundance as the results demonstrated that large populations of exotic species can lead to stunted native macrophyte populations. Additionally, water clarity appears to be the most important factor when trying to restore the native plant community. Native plant growth peaks in August when water clarity tends to be poorest in eutrophic lakes making it imperative to manage the lake to maintain good water clarity. Long-term planning for lake management and macrophyte restoration is imperative to ensure successful results that benefit the ecosystem and lake users.

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Tables Chapter II

Table 1. Summary of maximum depth of plant growth observed, the percent of points with native submersed taxa, the number of submersed native taxa, and the average Secchi depth obtained from point-intercept survey data in Lake Riley from 2011 through 2016. Maximum depth of growth is based on the 95th percentile of points where plants were observed growing.

Survey Date	Maximum Depth of Plant Growth Observed (95%) (m)	% of Points with Submersed Native Taxa	Number of Submersed Natives	Average Secchi Depth (m)
June 2011	4.0	50%	6	4.1
August 2011	3.8	49%	7	0.6
June 2012	4.0	55%	9	2.0
August 2012	3.9	55%	9	0.7
June 2013	3.8	53%	6	2.2
August 2013	3.8	42%	9	0.7
June 2014	3.2	46%	10	1.7
August 2014	3.5	53%	9	2.1
June 2015	3.1	62%	8	1.7
August 2015	3.2	67%	11	1.1
June 2016	4.0	81%	6	3.0
August 2016	4.0	87%	14	1.8

Table 2. Aquatic plants found in surveys conducted in Lake Riley 2011 through 2016.

Common Name	Scientific Name	Abbreviation	Year First Observed
Submerged species			
Coontail	*Ceratophyllum demersum*	Cdem	2011
Muskgrass	*Chara spp.*	Char	2012
Canada waterweed	*Elodea canadensis*	Ecan	2011
Water stargrass	*Heteranthera dubia*	Zdub	2016
Bushy Pondweed	*Najas flexilis*	Nfle	2011
Southern Naiad	*Najas guadalupensis*	Ngua	2015
Northern watermilfoil	*Myriophyllum sibiricum*	Msib	2011
Eurasian watermilfoil	*Myriophyllum spicatum*	Mspi	2011
Curlyleaf pondweed	*Potamogeton crispus*	Pcri	2011
Leafy pondweed	*Potamogeton foliosus*	Pfol	2015
Long-leaf pondweed	*Potamogeton nodosus*	Pnod	2015
Narrow leaf pondweed	*Potamogeton pusillus*	Ppus	2011
Flat-stem pondweed	*Potamogeton zosteriformis*	Pzos	2015
Sago pondweed	*Stuckenia pectinata*	Spec	2011
Wild celery	*Valliseneria americana*	Vame	2016
Horned pondweed	*Zannichellia palustris*	Zpal	2011
Floating-leaf Species			
Common duckweed	*Lemna minor*	Lmin	2014
White lily	*Nymphaea odorata*	Nodo	2011
Greater duckweed	*Spirodela polyrhiza*	Spol	2012

Figures Chapter II

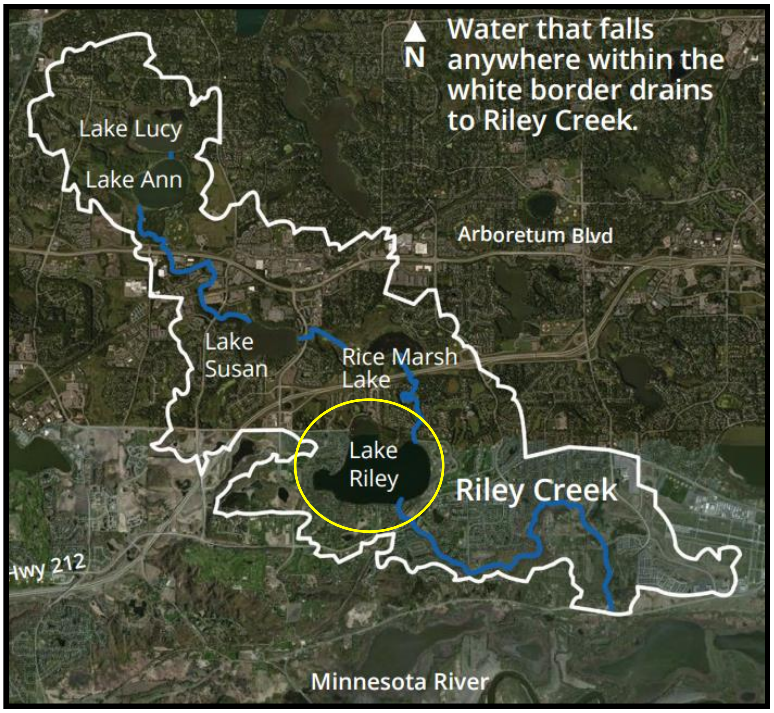


Figure 1. Riley Creek watershed with Lake Riley highlighted in yellow (source: Riley Purgatory Bluff Creek Watershed District, Chanhassen, MN).

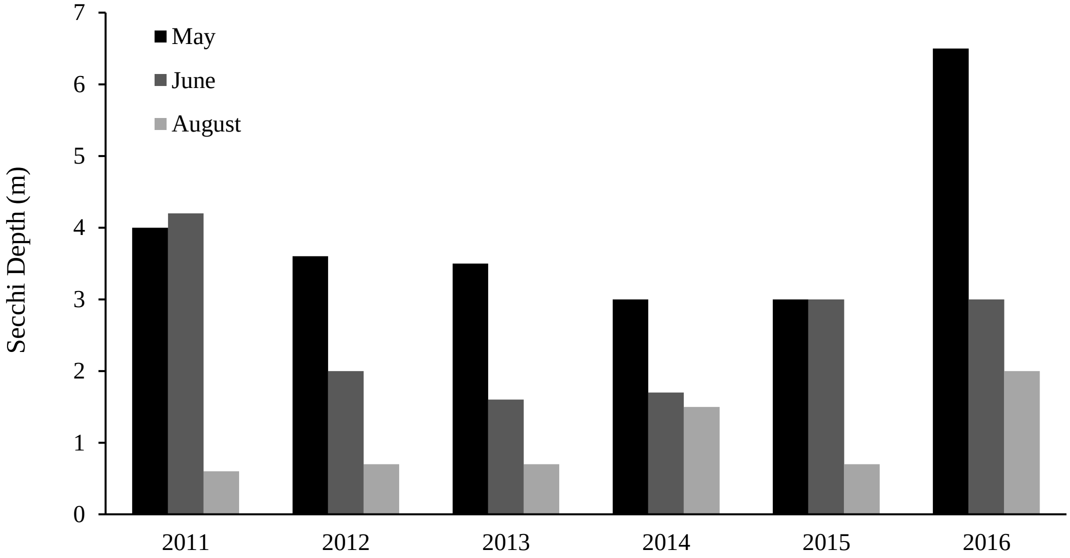
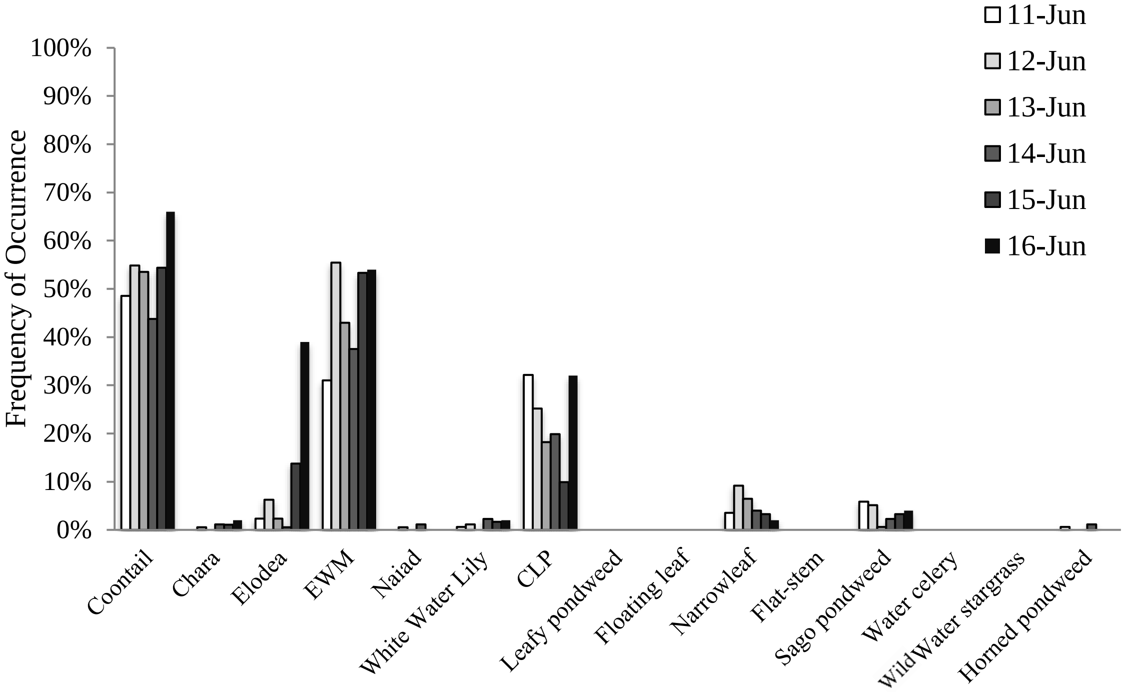


Figure 2. Lake Riley average Secchi depth (m) throughout the study period in spring (May), early summer (June), and late summer (August).



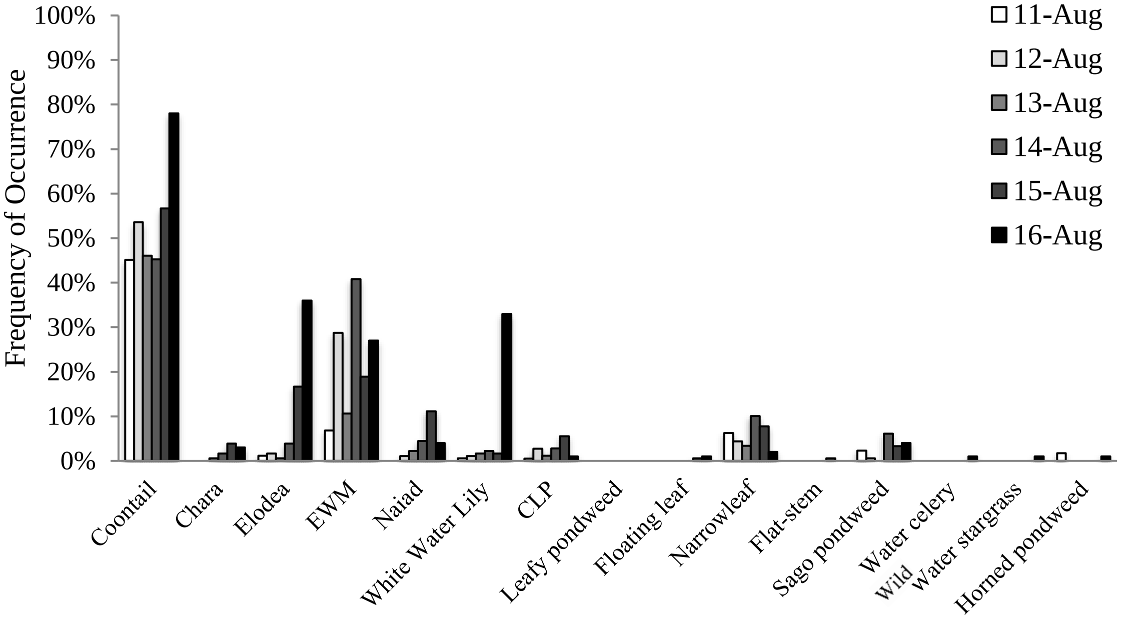


Figure 3. The frequency of occurrence of the most common species in Lake Riley in June and August surveys from 2011 to 2016. EWM stands for Eurasian watermilfoil, CLP stands for curlyleaf pondweed.

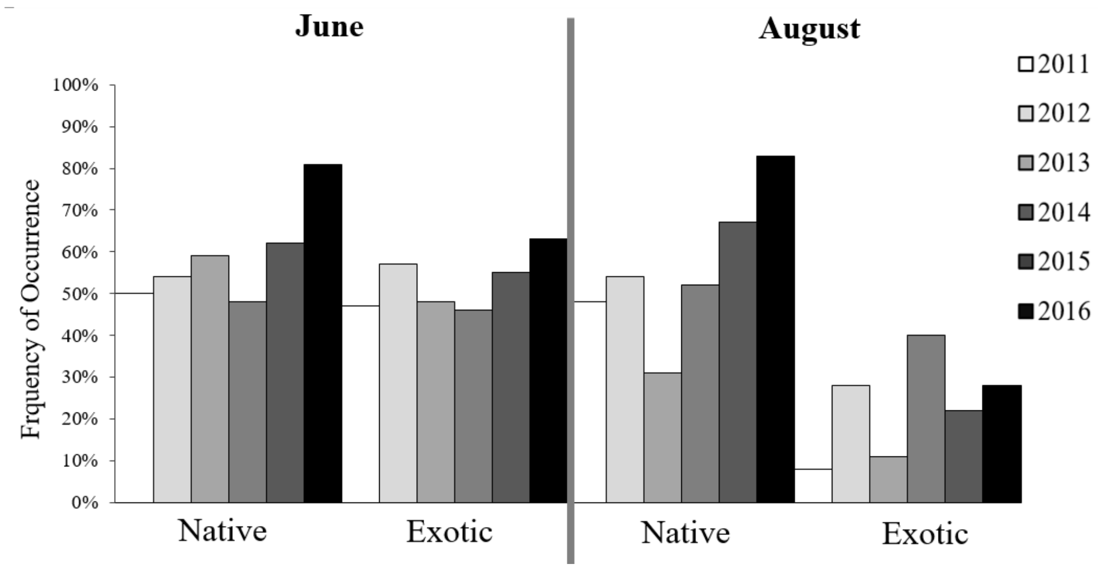


Figure 4. The frequency of occurrence for all native species combined and all exotic species combined in June and August surveys in the years of 2011 through 2016.

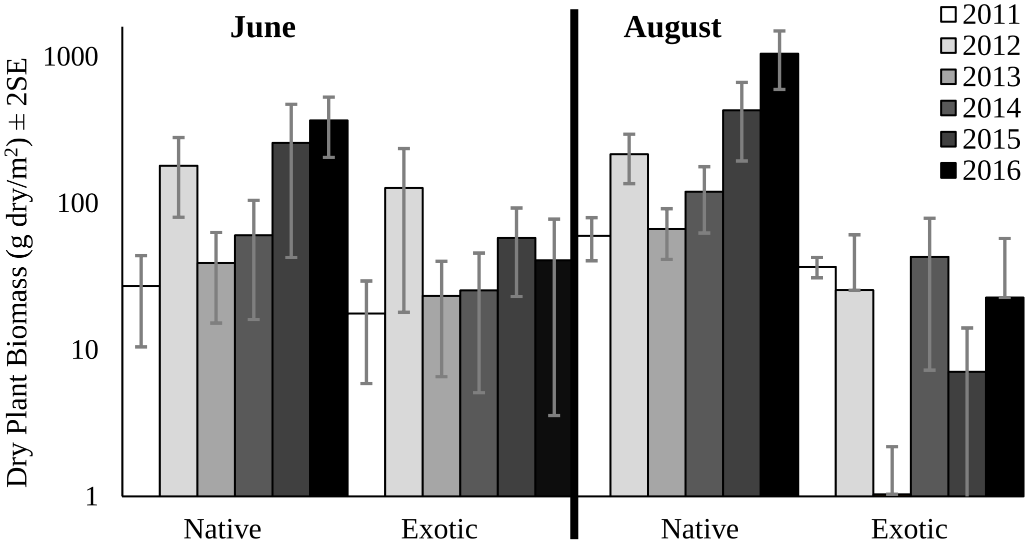
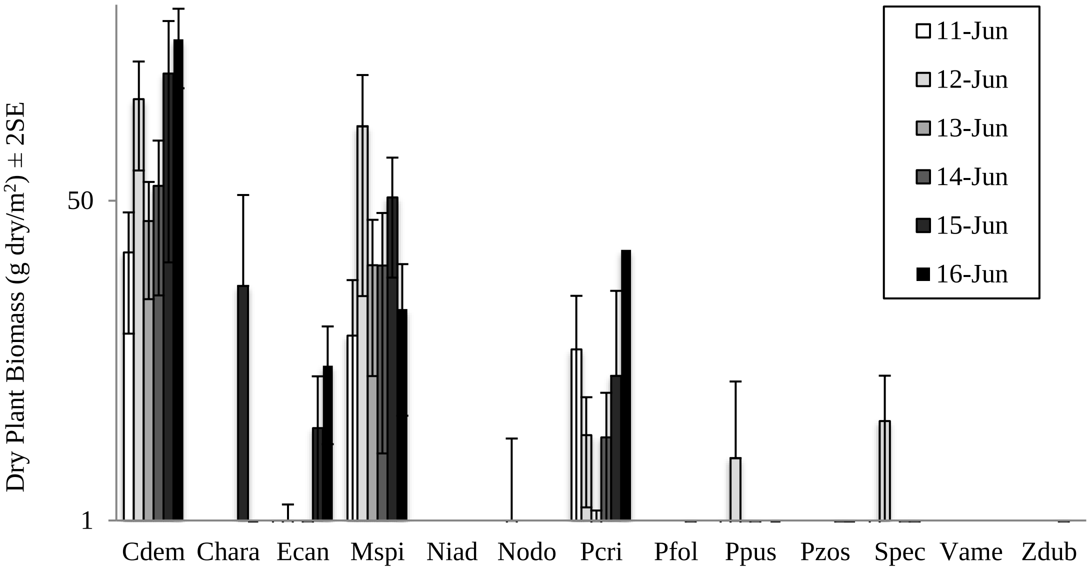


Figure 5. The biomass for all native species combined and all exotic species combined in the June and August surveys in the years of 2011 through 2016. Data are displayed on a log scale.



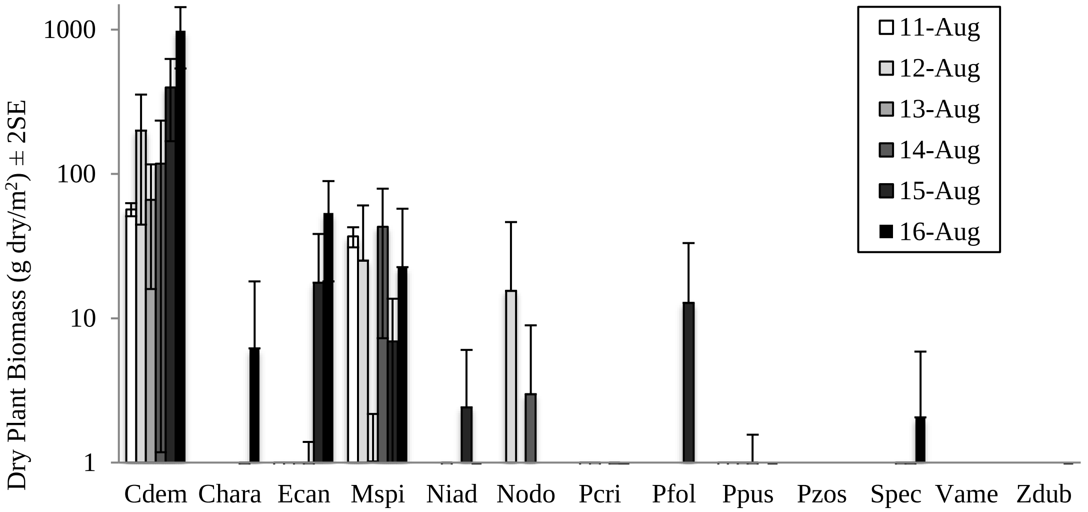


Figure 6. The biomass of the most commonly observed species in Lake Riley in the June and August surveys from 2011 through 2016. Species abbreviations are located in Table 2. Data are displayed on a log scale.

Chapter III

The Response of Macrophyte Propagules to Light Quantity and the Comparison of Viable Lake Seed Banks to the Existing Macrophyte Community

Summary

The importance of the aquatic macrophyte seed bank to sustaining macrophyte communities in lakes is an area in need of study. Although vegetative propagation is common, the seed bank may be contributing more to macrophyte recruitment than what is currently understood. This is potentially the case in eutrophic lakes that have had poor water clarity and few macrophytes for several years and then undergo management to improve clarity. Methods to enhance native macrophytes after improved water quality are needed. Moreover, the role of water clarity in recruitment from the seed bank is not understood.

I aimed to understand the role of the seed bank in the recruitment of macrophytes after water clarity improvement. A controlled laboratory experiment was conducted using sediment from Lakes Ann and Riley located in Chanhassen, MN, to 1) assess the germination response under different treatments and 2) compare the observed sprouting taxa to the taxa growing in the lakes. The treatments included a maximum germination treatment, a treatment representative of a lake with good water clarity, and a treatment representative of a lake with poor water clarity.

The observed viable seed banks of both Lakes Riley and Ann reflected the macrophyte community actively growing in the lake. In Lake Ann, every species observed in the experiment was observed growing in the lake. In Lake Riley, all but two species, Richardson’s pondweed and Robbins’ pondweed, observed in the seed bank were also found growing in the lake. The species observed in the seed bank were not, however, similar to the observed relative abundance in the lakes.

The seed banks did not show any significant difference in response to the germination treatments. The most frequent species observed in the seed banks were chara, curlyleaf pondweed, and wild celery. Seventeen species were observed in Lake Riley and 16 in Lake Ann. Under maximum germination conditions, Lake Riley had a viable vascular seed density of 2,916 ± 1,828 seeds/m^2 and a viable chara spore density of 1,033 ± 698 spores/m^2. Lake Ann had a viable vascular seed density of 1,100 ± 440 seeds/m^2 and viable chara spore density of 13,833 ± 2,825 spores/m^2. Overall, the study demonstrated that germinating propagules from a lake seed bank can be a valuable tool for managers to evaluate the viable macrophyte taxa present and the potential for recruitment from the seed bank.

Introduction

Macrophytes play an integral role in aquatic littoral zones. Macrophytes stabilize sediment and sequester nutrients, maintaining water clarity and reducing the potential for harmful algal blooms and other water quality impairments (Dennison *et al.* 1993, Horppila and Nurminen 2003, Bakker *et al.* 2010). Diverse, heterogeneous aquatic plant communities also provide habitat for invertebrates and fish communities in a lake (Valley *et al.* 2004, Cross and McInerny 2006). When large scale disturbances occur in a lake that affect macrophytes, such as benthivorous fish damage or high nutrient levels, the macrophyte community is often in low abundance and primarily a dense monoculture of an invasive plant due to poor water clarity and growing conditions (Chase and Knight 2006, Bajer *et al.* 2009). Subsequently, the reduced macrophyte population further impairs the functioning of the ecosystem and the water quality as they are no longer sequestering nutrients and sediment or providing habitat for other aquatic organisms (Scheffer *et al.* 1993, Hansson *et al.* 1998). As a result, these systems have poor recreational value for lake users and provide poor habitat for aquatic organisms.

Therefore, the management and restoration of aquatic macrophytes is often a primary goal when aiming to improve water quality and clarity in a lake (Scheffer *et al.* 1993). The restoration of native macrophyte communities is a dynamic process that regularly requires several steps and multiple years of active management. There are several disturbance factors that can be managed when attempting to improve the growing conditions for native macrophytes. In Minnesota lakes, eutrophication and invasive fish and macrophytes can reduce the abundance and diversity of native aquatic plant communities. Benthivorous fish, mainly common carp (*Cyprinus carpio*), disturb the sediment and uproot macrophytes during feeding and spawning (Bajer *et al.* 2009). Invasive macrophytes, such as curlyleaf pondweed (*Potamogeton crispus*) and Eurasian watermilfoil (*Myriophyllum spicatum*), can outcompete native species and subsequently reduce the diversity of the macrophyte community (Madsen *et al.* 1991, Johnson *et. al* 2012, Jones *et al.* 2012). Additionally, excess nutrients, including phosphorus and nitrogen, can cause the proliferation of planktonic algae and reduce water clarity, shading out macrophytes (Scheffer *et al.* 1993). Therefore, restorative actions often include nutrient reduction, nutrient sequestration, and invasive species control (Cooke *et al.* 2016). These mechanisms aim to improve the growing conditions for native macrophytes by decreasing competition with non-native macrophytes and by increasing the water clarity and subsequently the light availability allowing for efficient photosynthesis.

Often, when water clarity is improved through management actions, such as a benthivorous fish removal or alum treatment, the native macrophyte community increases in abundance and diversity. Specifically, in Midwestern lakes when common carp were reduced to a biomass of less than 100kg/hectare, the aquatic plant community was documented to improve (Bajer *et al.* 2009, Bajer and Sorensen 2015). The reduction of carp allows aquatic plant communities to improve due to the reduced sediment disturbance and improved water clarity that can occur when carp are reduced. Also, increases in macrophyte communities have been documented after water clarity improves due to alum or bentonite treatment (Spears *et al.* 2016). However, in some cases increases in macrophyte abundance can be largely due to an invasive species, such as Eurasian watermilfoil (*Myriophyllum spicatum*) (Jacocby *et al.* 1994, Newman *et al.* 2004). Therefore, actions to improve water clarity are often paired with invasive macrophyte control measures to allow for recovery of a diverse, heterogeneous native plant community, which improves overall lake ecosystem functioning (Hilt *et al.* 2006, Cooke *et al.* 2016).

When management of invasive fish and/or macrophytes occurs without an increase in water clarity, the native macrophyte community may show a marginal increase in abundance and species diversity (Knopik 2014, JaKa 2015). Therefore, it appears that to restore native macrophyte communities, water clarity must be maintained at a high enough level throughout the summer growing season to facilitate the recruitment of native macrophyte species to the lake (Chambers and Kalff 1985, Doyle and Smart 2001, Knopik 2014).

The recruitment of new species has been documented in lakes that have undergone a water clarity improvement. However, it is unknown if the recruitment is due to growth from existing source populations or the seed bank. Native macrophytes mainly propagate through clonal growth and fragmentation (Santamaría 2002). Many species can send out roots from which a new vegetative structure can sprout or they can grow a new plant from small fragments of a plant. Although most aquatic macrophytes propagate mainly through clonal growth they do still produce seeds or spores (Santamaría 2002, Boedeltje *et al.* 2003). However, the propagules that are produced are generally not thought be a large contributor to macrophyte community propagation and recruitment (Boedeltje *et al.* 2003).

Although propagation through clonal growth is most common, in some systems the source populations of submersed aquatic vegetation may be absent due to low clarity or benthivorous fish disturbance. This absence of a macrophyte community may lead to the role of the seed bank being more influential in the restoration of lake vegetation (De Winton *et al.* 2000, Pollux 2011). Overall, there are few studies that have assessed the relative role of the submersed macrophyte seed bank in the revegetation of a lake. Moreover, there is limited understanding on the extent that species rely on sexual and asexual modes of reproduction. Initial studies on submersed macrophyte species have found varying levels of asexual and sexual reproduction. For instance, *Najas minor* has been demonstrated to propagate mainly through seeds (Les *et al.* 2015), whereas Eurasian watermilfoil and water hyacynith have been demonstrated to rely more on propagation through clonal growth, and have low genetic diversity across their native range (Wu *et al*. 2015, Zhang *et al*. 2010). Overall, asexual versus sexual reproduction appears to vary by species and environmental conditions (Pollux *et al*. 2007). Specifically regarding sexual reproduction, several studies have evaluated the germination of submersed aquatic plant propagules but these studies have been focused on one or two species and not on the seed bank of a lake as a whole (Hartleb 1993, Jarvis and Moore 2008, Xiao 2010). Additionally, the majority of aquatic plant seed bank research has been conducted on emergent wetland species, which have different germination requirements than submersed aquatic vegetation (Baskin and Baskin 2014). These studies have found that light is an important factor in the germination process for some species (Coble and Vance 1987, Titus and Hoover 1991, Dugdale *et al.* 2001, Baskin and Baskin 2014).

My study aimed to assess the effect of improved water clarity and improved light quantity on the germination of macrophyte propagules from lake seed banks. Specifically, sediment was placed in one of three treatments, each with different environmental conditions, to evaluate the effect of water clarity on sprouting. The total number of sprouted propagules as well as number of sprouted propagules per species were counted to obtain an estimate of viable seed density. Propagule sprout counts were also separated into the total vascular seeds counted and the total macroalgae spores counted. Subsamples of sediment were also enumerated to estimate the number of seeds that did not germinate.

The aim of this study is twofold. Firstly, we were interested in estimating the seed bank in two Minnesota lakes, one with a diverse plant community and the other with a historically limited plant community due to low clarity and carp disturbance, to understand if the seed bank reflects the current occurrence of macrophytes in a lake. Secondly, we wanted to determine the role of light intensity on the germination of macrophyte propagules. Understanding how the seed bank of a lake responds to lake restoration actions, such as a water clarity/light intensity improvement, is key for a comprehensive macrophyte restoration project. Having an insight into what triggers germination from the seed bank is vital as lake managers plan for desired outcomes, such as a more stable, diverse macrophyte community.

Methods

Seed Bank Collection

Sediment was collected from Lake Ann (DOW ID 10001200) and Lake Riley (DOW ID 10000200). Both lakes are in Chanhassen, MN, in Carver County, west of the Twin Cities within the Riley Purgatory Bluff Creek Watershed District (Figure 1). Lake Ann is a dimictic, mesotrophic lake with a diverse macrophyte community and good water clarity (mean August Secchi depth: 1.8m). In Lake Ann, 17 to 21 species have been regularly observed in 2011 to 2014. The lake area is 48 hectares with a maximum depth of 12.2m. Lake Riley is a eutrophic lake with a historically diminished macrophyte population that has been steadily improving due to lake management actions over the last several years (carp reduction, invasive macrophyte control, and alum treatment). The lake area is 120 hectares with a maximum depth of 15.1m. The mean August Secchi depth was 0.5m prior to the 2016 alum treatment. In Lake Riley, 12-15 species have been regularly observed between the years of 2014 to 2016, previously 7 to 10 species were regularly observed in 2011 to 2013.

Sediment was collected at Lake Riley on May 5th and 6th, 2016 and at Lake Ann on May 19th, 2016. To collect the sediment for the treatments, seven transects were marked around each lake using ArcGIS. Transects were uploaded to a Garmin 76 GPS device and a boat was navigated to each site. At each transect, four sediment core samples were obtained at a 1.0m depth using a 10.0cm diameter PVC coring device; the top 5.0cm of the sediment core was collected. The sediment samples from each lake were homogenized to reduce the heterogeneity of seed bank distribution in lake and then stored in a dark refrigerator at 4 ˚C until the experiment was ready to begin.

Seed Bank Treatments

After sediment collection, the sediment from Lakes Ann and Riley was allocated into small trays. Sediment samples were washed with well water over a coarse sieve to remove large material, such as twigs and cobbles, and vegetative structures and buds, such as curlyleaf pondweed turions. After the material was removed, 200mL of sediment was spread in a layer over a medium of 200mL sterilized sand in 19.0cm x 19.0cm x 6.0cm trays (Galatowitsch 1994) and covered with 3.0cm of water (Boedeltje 2002, Baskin and Baskin 2014). A total of 45 trays were created for each lake. Fifteen additional trays were used as controls to ensure that contamination in the growing room did not occur. Control trays consisted of 200mL steam sterilized sand and 200mL sterilized lake sediment.

Trays were allocated to one of three germination treatments of varying light intensity and the experiment ran for sixteen weeks. Trays were illuminated with Helioscpectra lights. Heliospectra lights emit nine wavelengths of light that can each be individually adjusted to precisely control the light. The lights have 380nm, 400nm, 420nm, 450nm, 520nm, 630nm, 660nm, and 735nm wavelengths in addition to 5700K white LED lights that are similar to sunlight. Curtains were placed between different light treatments to eliminate the effect of other light sources on the propagules.

To assess the extent of the viable seed bank in Lakes Ann and Riley, 15 of the trays for each lake were used to assess the viability using the seedling emergence method to maximize germination (Boedeltje 2002). To maximize germination, the trays were exposed to a series of environmental conditions known to induce germination in aquatic plants. The photosynthetically active radiation (PAR) was set to 800 $\mu mol/m^2/s$ and a 15 hour light, 9 hour dark photoperiod (Coble and Vance 1987, Boedeltje 2002). All the wavelengths of light and white light were kept at equal intensity set to maintain the 800 $\mu mol/s/m^2$ PAR. The temperature ranged between 21°C and 23°C (Boedeltje 2002), and water levels remained at approximately 3.0cm in the trays throughout the testing period (Boedeltje 2002, Baskin and Baskin 2014). Gibberellic acid, to induce sprouting, was applied to the trays once at the onset of the experiment to reach a concentration of 0.3mM (Tuckett *et al*. 2010, Baskin and Baskin 2014).

In addition to assessing the total viability of the seed banks in Lakes Ann and Riley, the effect of water clarity and light quantity on submersed aquatic vegetation germination in lake seed banks was assessed by exposing the seed bank to one of two levels of light intensity. Fifteen trays were exposed to a light condition representative of a clear lake at 1.0m depth and the remaining fifteen trays were exposed to a light condition representative of a turbid lake at 1.0m depth. For this experiment, a “clear lake” was defined as having an August Secchi depth of 1.5m or greater and a “turbid lake” was defined as an August Secchi depth of less than 1.5m.

Field observations with a spectroradiometer were collected in 6 lakes of varying clarity in the Riley Purgatory Bluff Creek Watershed District at mid-day on a day with no cloud cover and little wind. These observations indicated that high clarity lakes had an average light intensity of 650 µmol/s/m^2 at 1.0m depth and low clarity lakes 125 µmol/s/m^2 at 1.0m. The light spectrum observed at 1.0m was very similar among the lakes and therefore the wavelengths remained at the same ratios for each treatment and only the overall intensity of the light was altered. Thus, in the high clarity treatment the Heliospectra lights were set at a PAR of 650µmol/s with an equal intensity of all nine wavelengths. In the low clarity treatment the lights were set at 125µmol/s PAR with an equal intensity of all nine wavelengths. For both treatments a 15 hour light: 9 hour dark photo period was used. In the good and low clarity treatments, the water temperature was consistently between 21.0°C to 23.0°C in the trays and the dissolved oxygen was consistently between 7.0 and 9.0 mg/L.

Trays were checked weekly and new propagule sprouts were identified to species and recorded. Any observed sprouting from the sediment was counted as germinated and was considered viable (Boedeltje 2002). Propagule sprouts were removed from the trays after being counted to prevent counting multiple times. If needed, propagules were transplanted into an environmental chamber for continued growth to confirm species identification. When trays were checked for sprouting, temperature and dissolved oxygen readings were made using a YSI ODO sensor every week at midday when the lights had been on for at least 5 hours.

After the experiment was concluded, a subsample of five trays from each treatment were examined to enumerate the seed bank to evaluate the number and species of propagules that did not germinate (Bernhardt *et al.* 2008). Sediment was sifted through 1.0mm, 0.5mm, 0.25mm, 0.125mm, and 0.053mm sieves stacked on each other to sort the sample by grain size and more easily find all ungerminated propagules. The sediment in each sieve was visually inspected and propagules were picked and identified to genus or species (depending on the morphological characteristics) using a Nikon stereo microscope.

Lastly, the viable seed bank was compared to the plants observed growing in the lake through point-intercept surveys to evaluate if the seed bank is representative of the existing plant community. The species observed sprouting were ranked by most abundant (rank=1) to least abundant and the species observed during the surveys were ranked by most abundant (rank=1) to least. These values were plotted on a scatterplot for each lake to evaluate if the most abundant sprouts were also the most abundant plants observed in the lake.

Sediment Analysis

Part of the homogenized sediment from Lakes Ann and Riley was used for analysis of the soil characteristics, specifically dry bulk density and organic matter content. To determine the dry bulk density and organic matter content, five 10.0mL subsamples of sediment from each lake were obtained using a modified syringe. The subsample was placed in a crucible that was weighed and recorded prior to the sediment being added. The subsamples were dried in an oven at 100°C for 48 hours. After drying, the samples were weighed and the dry bulk density was calculated as g dry/mL. The samples were then placed in a muffle furnace for 3 hours at 500°C to combust the organic content in the sediment. The samples were cooled and promptly weighed. The organic matter content was obtained by subtracting the mass of the sediment after the muffle furnace from the mass of the sediment after the drying oven; percent organic matter was then calculated as a percentage of the dry sediment mass. The five subsamples of dry bulk density and organic matter content for each lake were averaged to obtain a mean dry bulk density and organic matter content for the sediment.

Statistical Analysis

The study compared the germination of seeds from the seedling emergence method to the abundance and richness of propagule sprouts in the two light treatments. I also compared the viable seed bank to the observed species growing in the lakes. The

Lakes Riley and Ann seed banks were assessed for several metrics. The number of total propagule sprouts, number of propagules per species, number of species germinated, the average total viable seeds per tray and per square meter lake bottom, and the average viable seeds per tray and per square meter for each species was calculated. Additionally, the metrics of average viable propagule density per tray and per square meter was separated into vascular plants that produce seeds and the non-vascular plant spores from *Chara spp*. to better understand the composition of the lake seed banks as chara was a large contributor to the total propagule count in each lake. The average viable propagules per square meter of lake bottom was determined by taking the average of the count of propagules in each tray and dividing by 40cm^2 to obtain the average propagules per cm^2. The sediment core volume (10.0cm diameter and 5.0cm depth) was 395cm^3 representing a surface area of 79cm^2. Thus the 200cm^3 of sediment in each tray represents a surface area of 40cm^2. The propagules/cm^2 value was then multiplied by 10,000 to obtain the propagules/m^2.

All statistical analysis was conducted using R statistical software version 3.3.2 (The R Foundation for Statistical Computing, 2016). Results were considered statistically significant when p values were < 0.05. To assess the effect of the treatment on the number of propagules counted for both Lake Ann and Lake Riley samples, Poisson log-linear models were used as the data followed Poisson distributions. The models were used to evaluate the total count of propagules as well as the count of each species observed germinating. A Poisson log-linear model was also used to evaluate the significance of the difference between the species richness observed in each treatment.

Results

Lake Riley

Overall, in the Lake Riley samples the maximum germination and high clarity treatments had 13 taxa observed sprouting and the low clarity treatment had 10 taxa observed sprouting (Table 1). These differences were not significant ($p > 0.05$). The total number of propagules germinated was approached by week 8 and was reached by week 16 (Figure 2).

Under maximum germination conditions, the average number of propagules germinated per tray at the end of the experiment was 15.9 ± 6.24 propagules/tray (Figure 2). Therefore, the mean number of viable propagules was 3,950 ± 1,561 propagules/m^2. The mean number of vascular seeds germinated per tray was 11.6 ± 7.3 seeds/tray or 2,916 ± 1,828 seeds/m^2. The mean number of chara spores germinated per tray was 4.1 ± 2.8 spores/tray or 1,033 ± 698 spores/m^2 (Figure 3). In the maximum germination conditions, curlyleaf pondweed had the greatest number of viable seeds observed with an average of 6.3 ± 3.1 seeds/tray or 1,583 ± 776 seeds/m^2 (Figure 3, Table 1). We are confident that these were from seeds because all visible turions had been removed from the sediment. Chara was the second most common propagule (Figure 3, Table 1). Wild celery also had a high number of seeds, at an average of 2.6 ± 1.6 seeds/tray or 650 ± 399 seeds/m^2 (Figure 3, Table 1).

Relative to the maximum germination treatment, the Lake Riley sediment samples exposed to high clarity and low clarity treatments had a lower level of germination, but the differences were not significant. For the high clarity treatment, the average germination by 16 weeks was 9.3 ± 1.7 propagules/tray or 1,783 ± 444 propagules/m^2 (Figure 2). The mean number of vascular seeds germinated per tray was 4.5 ± 1.3 seeds/tray or 1,116 ± 312 seeds/m^2. The mean number of chara spores germinated per tray was 2.7 ± 1.4 spores/tray or 667 ± 341 spores/m^2. In the high clarity condition, chara was the most frequent species observed (Figure 3, Table 1). The second most abundant species was curlyleaf pondweed with an average germination of 1.7 ± 0.63 seeds/tray or 433 ± 158 seeds/m^2 (Figure 3, Table 1). Wild celery was also observed at an average 1.3 ± 0.6 seeds/tray or 333 ± 152 seeds/m^2 (Figure 3, Table 1). The remaining species were all observed in low frequencies.

The Lake Riley sediment samples exposed to the low clarity treatment had an average germination per tray of 7.1 ± 2.7 propagules/tray or 2,167 ± 683 propagules/m^2 (Figure 2). The mean number of vascular seeds germinated per tray was 5.4 ± 2.6 seeds/tray or 1,350 ± 653 seeds/m^2. The mean number of chara spores germinated per tray was 3.3 ± 2.3 spores/tray or 817 ± 574 spores/m^2. In the low clarity conditions, chara was the most abundant observed at an average of 3.3 ± 2.3 spores/tray or 816 ± 574 spores/m^2 (Figure 3, Table 1). Curlyleaf was also abundant with an average of 3.1 ± 2.1 seeds/tray or 767 ± 533 seeds/m^2 (Figure 2, Table 1). Wild celery was also abundant with an average of 1.47 ± 0.84 seeds/tray or 367 ± 212 seeds/m^2 (Figure 2, Table 1). The remaining species observed were in low abundance.

Overall, the results of the Poisson model indicated no significant difference between the different treatment types for the Lake Riley samples. Specifically, there was no difference in the total number of propagules, species diversity, or species abundance (all $p > 0.05$) (Appendix Table 4). All taxa were that were observed germinating in the maximum germination conditions, apart from two species (*Potamogeton richardsonii* and *Potamogeton robinsii*), were also observed growing in the lake during macrophyte surveys. Two taxa that were not present in previous years appeared in Lake Riley during the summer of 2016, wild celery (*Vallisneria americana)* and water stargrass (*Heteranthera dubia*).

The Lake Riley seed bank enumeration yielded few additional propagules that had not germinated in the maximum germination conditions. The maximum germination conditions yielded the fewest propagules that had not germinated while the good and low clarity conditions had a slightly higher abundance of propagules observed in each sub sample (Table 2). An average of 1.3 ± 0.42 propagules/tray for the maximum germination condition was counted. The good and low clarity treatments had a slightly higher number of remaining seeds with an average of 5.0 ± 2.3 propagules/tray and 6.1 ± 2.5 propagules/tray respectively. No species were found as propagules that had not also been observed germinating.

The average dry bulk density of the collected Lake Riley sediment was 0.53 ± 0.34 g/mL and the average organic matter content was 13% ± 4.5%.

Lake Ann

Lake Ann had a total propagule count that was much greater than Lake Riley, largely due to a high occurrence of chara spores. In the maximum germination conditions, 13 taxa were observed, in the good and low clarity treatments 10 taxa were observed. The maximum germination was approached by week 12 and was complete by week 16 in Lake Ann.

Under maximum germination conditions the average total germination after 16 weeks was 59.7 ± 11.1 propagules/tray or 14,933 ± 2,771 propagules/m^2 (Figure 4). The mean number of vascular seeds germinated per tray was 4.4 ± 1.6 seeds/tray or 1,100 ± 408 seeds/m^2. The mean number of chara spores germinated per tray was 55.3 ± 11.3 spores/tray or 13,833 ± 2,825 spores/m^2 (Figure 5, Table 3). The second most abundant species was wild celery, observed at an average of 2.1 ± 1.2 seeds/tray or 533 ± 296 seeds/m^2 (Figure 5, Table 3). Curlyleaf pondweed was observed at an average of 0.9 ± 0.45 seeds/tray or 233 ± 142 seeds/m^2 (Figure 5, Table 3). The remaining species observed were all at low abundances.

The Lake Ann sediment samples exposed to high clarity and low clarity conditions had a similar level of germination relative to the maximum germination conditions; the difference between treatments was not significant ($p>0.05$) For the high clarity treatment, the average germination per tray in each treatment was 58.6 ± 13.4 propagules/tray or 14,000 ± 3,351 propagules/m^2 (Figure 4). The mean number of vascular seeds germinated per tray was 4.5 ± 1.8 seeds/tray or 1,125 ± 446 seeds/m^2. The mean number of chara spores germinated per tray was 53.4 ± 12.6 spores/tray or 13,350 ± 3,149 spores/m^2 (Figure 5, Table 3). Chara was the most abundant taxa. The second most abundant species was wild celery with an average of 2.5 ± 1.1 seeds/tray or 633 ± 275 seeds/m^2 (Figure 5, Table 3). Curlyleaf was also present at high levels at an average of

1.3 ± 0.8 seeds/tray or 333 ± 193 seeds/m^2 (Figure 5, Table 3). The remaining species were all in low abundances.

For low clarity conditions, the total was an average of 58.1 ± 17.1 propagules/tray. The mean number of germinated propagules was 16,286 ± 4266 propagules/m^2 in the low clarity treatment (Figure 4). The mean number of vascular seeds germinated per tray was 4.0 ± 1.7 seeds/tray or 1,000 ± 428 seeds/m^2. The mean number of chara spores germinated per tray was 61.1 ± 16.9 spores/tray or 15,286 ± 4,218 spores/m^2. The most abundant species was chara (Figure 5, Table 3). The second most abundant species was wild celery 1.9 ± 0.8 seeds/tray with an average of 482 ± 210 seeds/m^2 (Figure 5, Table 3). Curlyleaf was also abundant with an average of 0.8 ± 0.1 seeds/tray or 286 ± 196 seeds/m^2 (Figure 5, Table 3).

The results of the Poisson model indicated no significant difference between the different treatment types for the Lake Ann samples. Specifically, there was no difference in the total number of sprouts, species diversity, or species abundance (Appendix Table 4). All taxa were that were observed germinating in the maximum germination conditions were also observed growing in the lake during macrophyte surveys.

The Lake Ann seed bank enumeration yielded few additional propagules that had not germinated. An average of 2.3 ± 1.4 propagules/tray remained from the maximum germination treatment (Table 2). An average of 1.3 ± 1.0 propagules/tray remained from the high clarity condition (Table 2). An average of 2.3 ± 1.7 propagules/tray were counted from the low clarity condition (Table 2). No species were found as propagules that had not also been observed as sprouts. Lastly, the average dry bulk density of the

Lake Ann sediment was 0.72 ± 0.12 g/mL and the average organic matter content was 21% ± 5%.

Overall, the seed banks of Lakes Ann and Riley were distinct despite being within the same watershed. The Lake Ann seed bank had a higher number of chara spores in all treatments relative to the Lake Riley seed bank and the difference was significant ($p<0.05$, t-test). The vascular seed count was similar among the two lakes for each treatment and there was no significant difference in the vascular seed counts between the two lakes or among the three treatments.

Discussion

Although germination was higher in the maximum germination treatment for both lakes, there was high variability and no significant increase in germination with that treatment for either lake relative to the good and low clarity treatments ($p>0.5$). Despite the findings in other studies (Dugdale *et al.* 2001, Sederias and Colman 2007), in this study light quantity did not appear to have a significant effect on the germination of propagules from a lake seed bank. Other studies have suggested that temperature and burial depth in the sediment are also key factors in dormancy breaking and germination (Baskin and Baskin 2014). In this experiment, these other factors may have been more critical to germination than light.

Interestingly, the timing of the germination was variable between the two lakes despite having similar compositions of taxa present (Figures 2, 4). Germination was observed in both lake sediments beginning at week two. However, the germination in the Lake Riley sediments leveled off roughly after 8 weeks whereas in Lake Ann germination continued through week 12. Overall, Lake Ann had a much higher viable propagule count in all treatments relative to Lake Riley, due to the many chara spores in the sediment in Lake Ann (Figure 5). However, there was no difference in the number or species of vascular seeds counted in the trays between both lakes despite Lake Ann having a greater level of macrophyte diversity. This study demonstrates that the seed banks of lakes, even within the same drainage, can be variable regarding the abundance of propagules such as is the case with chara.

These results provide important information that will guide future studies on macrophyte seed banks. Light intensity did not have an effect on germination, however it is likely an important factor promoting propagule growth and development into a mature plant (Jarvis and Moore 2008). Further evaluation of seedling survival in different light conditions is needed, such as evaluating responses in lower PAR conditions such as 25 µmol/s where the light may be under the compensation point for the plant.

Assessment of the seed bank also provides useful information to lake managers regarding invasive species management. Prior to the sediment collection in 2016, in Lake Riley, curlyleaf pondweed was treated with endothall herbicide for three consecutive years in May of 2014, 2015, and 2016 and the control efforts were successful at reducing the abundance of curlyleaf pondweed growth in Lake Riley. The fall turion densities in the sediment declined significantly from 61 ± 20 turions/m^2 in 2012 to to 2 ± 1.4 turions/m^2 in 2015 ($p<0.05$) (Dunne and Newman 2017). Suppression or depletion of turions is an important strategy for curlyleaf pondweed control but it is difficult to achieve (Crowell and Madsen 1988, Johnson *et al.* 2012). In the Lake Riley seed bank samples, curlyleaf pondweed was consistently one of the most abundant species sprouting, with an estimated viable seed density at 175 seeds/m^2 in the sediment as compared to the viable turion density of 2 turions/m^2 in 2016. There is clearly still an abundant and viable propagule source that managers will need to be aware of as they manage this plant over the next several years as recruitment from seed may be more common than generally thought.

Eurasian watermilfoil also occurs in Lakes Ann and Riley in relatively high abundances at certain locations in the lakes. However, this species had a low abundance in the seed bank based on sediment samples in both lakes. This finding is consistent with other studies on Eurasian watermilfoil propagation indicating that this species may rely mainly on fragmentation and clonal growth for its propagation (Coble and Vance 1987, Madsen and Smith 1997). However, viable seeds were present and did sprout in Lake Riley sediments at low levels.

In addition to aiding the understanding of invasive species populations, by employing a germination study, lake managers can also better understand the potential for native species recolonization from the seed bank in a lake. Specifically, lake managers can determine the extent of species diversity present in the lake and what taxa have the potential to recolonize. For example, in Lake Riley two species were observed sprouting in this experiment that had not been observed in Lake Riley during aquatic vegetation point-intercept surveys that occurred from 2011 to 2016. Richardson’s pondweed (*Potamogeton richardsonii*) and Robbins’ pondweed (*Potamogeton robinsii*) were observed as sprouts and this indicates that there may be the potential for recruitment from the seed bank in Lake Riley. Additionally, several species that were observed in the seed bank were only observed growing in Lake Riley after invasive species management and water clarity improvement, including floating leaf (*Potamogeton nodosus*) and flat stem pondweeds (*Potamogeton zosteriformis*) in 2015, and water stargrass (*Heteranthera dubia*) and wild celery (*Vallisneria americana*) in 2016. This study suggests that those species may have been recruited from seed due to the improvement in growing conditions. In Lake Ann, there was a high diversity of taxa observed during the 2011 through 2014 survey years. In the Lake Ann seed bank all species observed sprouting were also observed during point-intercept surveys. The scatterplots evaluating the relationship between seed bank abundance and lake abundance showed no relationship. If there were a relationship between abundance in the seed bank and the lake, one would expect the points to linearly align with a slope of one, however this is not the case in either lake. There was no clear pattern of sprout density and observed plant density indicating that high abundance in the seed bank does not equate to high abundance in the lake (Figures 6 and 7).

Overall, lake seed banks can be variable in abundance and richness and in this study the seed banks appear to reflect the existing macrophyte community in the lakes. Moreover, water clarity and ranges of high light intensity did not impact the propagule germination of macrophytes in our study but further investigation is warranted as to the effect of light on the survival of propagules to maturity.

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Tables Chapter III

Table 1. Total number of propagules germinating from Lake Riley sediment for the maximum germination, high clarity, and low clarity treatments based on 3.0L of collected sediment per treatment.

Species	Species Abbreviation	***Treatment Type*** Maximum Germination	High clarity	Low clarity
Ceratophyllum demersum	Cdem	10	8	3
Chara spp.	Char	62	40	49
Elodea canadensis	Ecan	3	5	1
Heteranthera dubia	Hdub	1	1	0
Lemna minor	Lmin	1	2	0
Lemna trisulca	Ltri	0	0	0
Myriophyllum spicatum	Mspi	1	1	0
Najas guadalupensis	Ngua	1	0	0
Nyphar varigaeta	Nvar	1	0	0
Potamogeton crispus	Pcri	95	26	46
Potamogeton pusillus	Ppus	13	8	5
Potamogeton nodosus	Pnod	9	1	3
Potamogeton robinsii	Prob	1	1	0
Potamogeton zosteriformis	Pzos	4	3	3
Ranunculus longirostris	Rlon	9	0	0
Stuckenia pectinata	Spec	39	4	1
Vallisneria americana	Vame	3	20	22

Table 2. Total ungerminated seeds enumerated from the subsample of five Lake Riley and five Ann trays.

	Lake Riley			***Lake Ann***		
Species	Max. Germination	High clarity	Low clarity	Max. Germination	High clarity	Low clarity
Mspi	1	0	0	3	0	2
Niad	1	2	2	1	2	0
Pamp	0	1	0	0	0	4
Pcri	0	2	1	0	2	1
Ppus	2	0	1	0	0	0
Prob	0	1	0	1	0	0
Pzos	0	0	1	2	0	0
Spec	0	0	0	0	0	0
Zpal	0	2	3	0	0	0

Table 3. Total germination of propagules from Lake Ann sediment for the maximum germination, high clarity, and low clarity treatments based on 3.0L of collected sediment per treatment.

Species	Species Abbreviation	***Treatment Type*** Maximum Germination	High clarity	Low clarity
Ceratophyllum demersum	Cdem	1	2	3
Chara spp.	Char	830	801	911
Lemna minor	Lmin	0	2	0
Lemna trisulca	Ltri	2	0	0
Najas guadalupensis	Ngua	2	0	0
Nutela lutembo	Nlut	1	0	0
Nyphar varigaeta	Nvar	1	0	0
Potamogeton crispus	Pcri	14	20	18
Potamogeton pusillus	Ppus	5	5	11
Potamogeton nodosus	Pnod	1	0	1
Potamogeton richardsonii	Pric	2	1	1
Potamogeton robinsii	Prob	0	1	0
Potamogeton zosteriformis	Pzos	1	2	0
Ranunculus longirostris	Rlon	1	0	0
Stuckenia pectinata	Spec	5	5	0
Vallisneria americana	Vame	32	38	29

Figures Chapter III

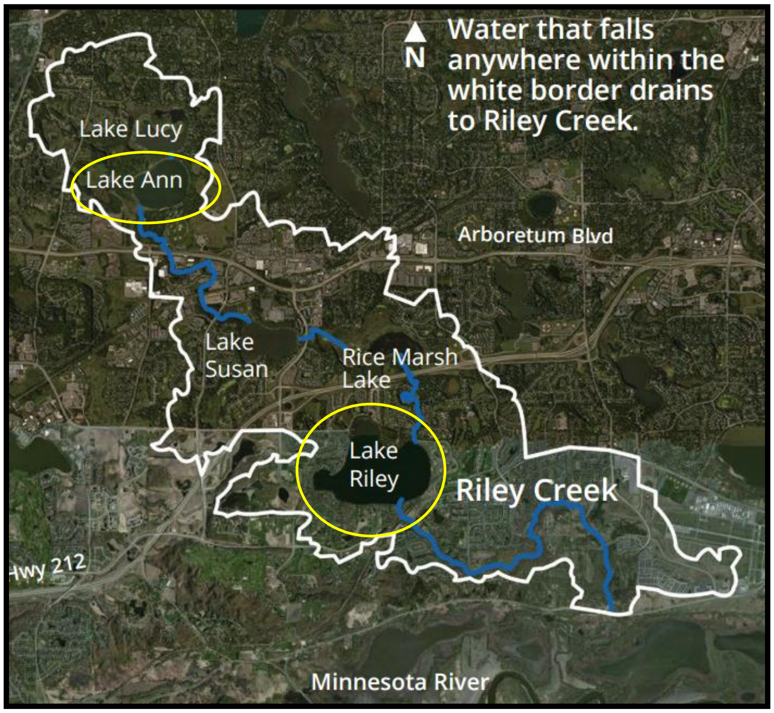

Figure 1. Riley Creek watershed with Lakes Ann and Riley highlighted in yellow (source: Riley Purgatory Bluff Creek Watershed District, Chanhassen, MN).

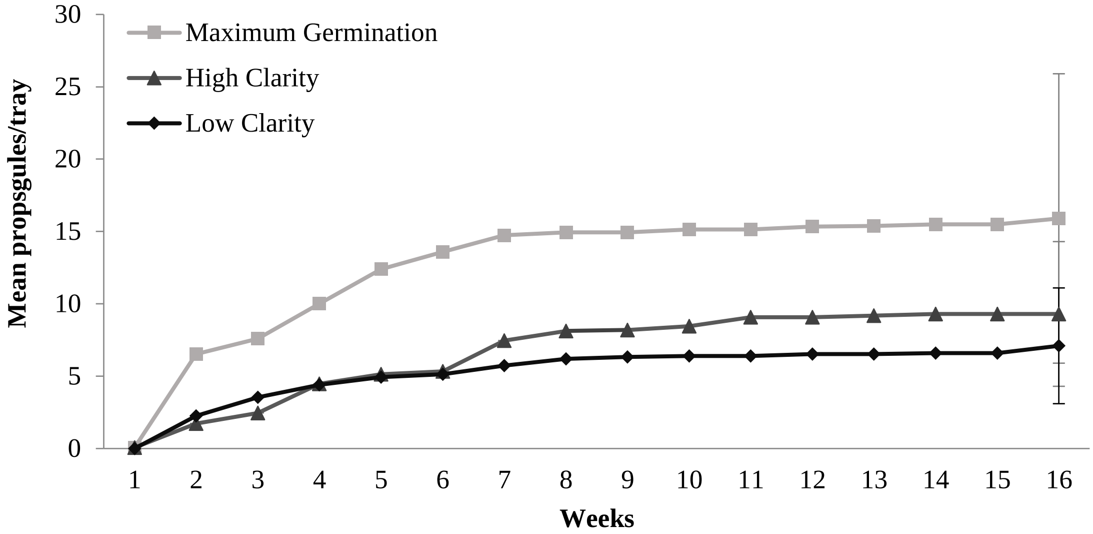

Figure 2. Lake Riley mean cumulative germination (propagules/tray) under the different treatment conditions.

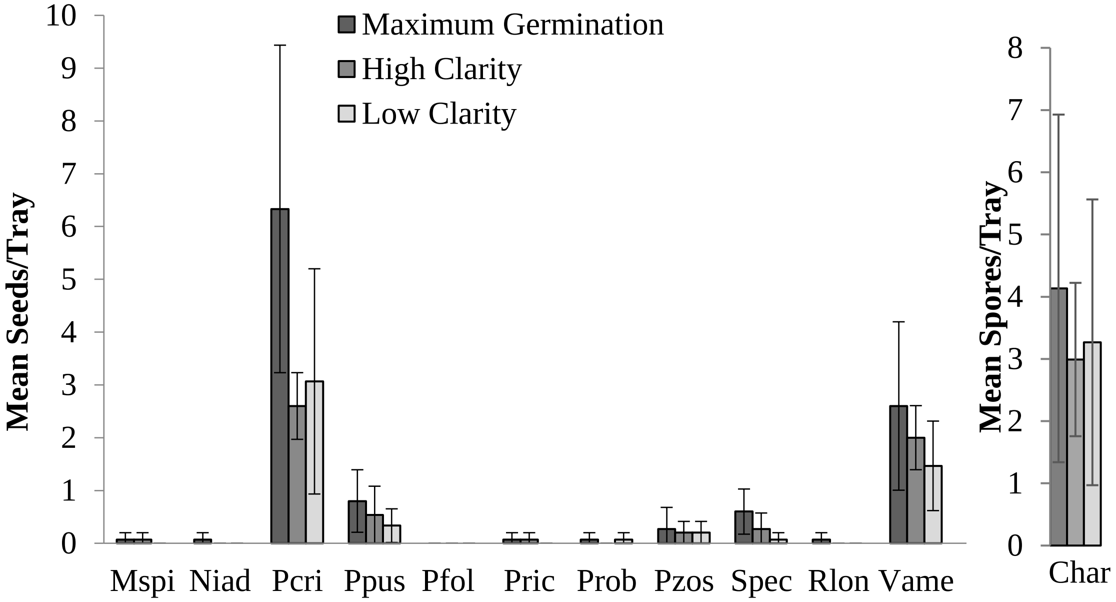

Figure 3. Lake Riley average germination (seeds/tray and spores/tray) under the maximum germination, high clarity and low clarity treatment conditions for the most abundant species observed. Abbreviations are located in Table 1.

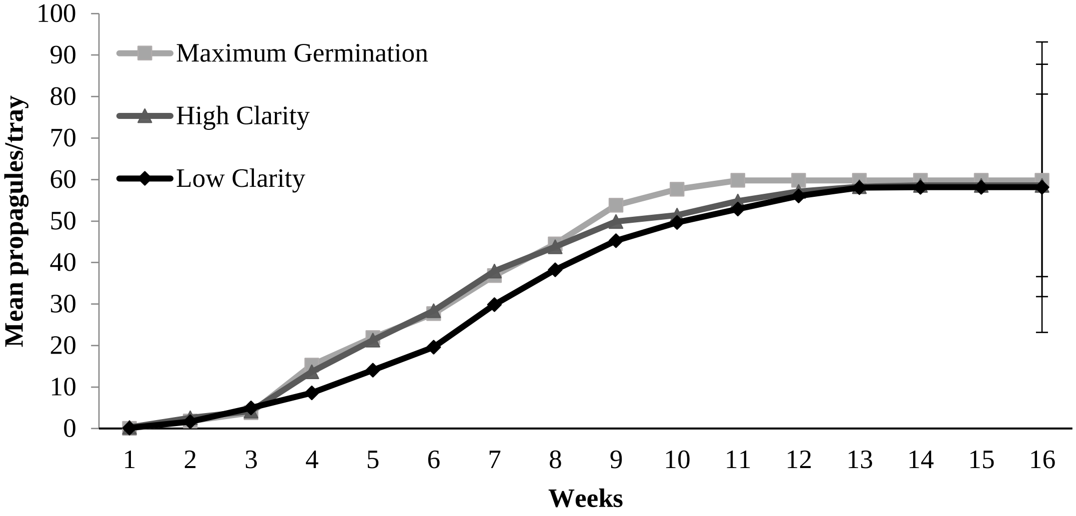

Figure 4. Lake Ann mean cumulative germination (propagules/tray) under the different treatments.

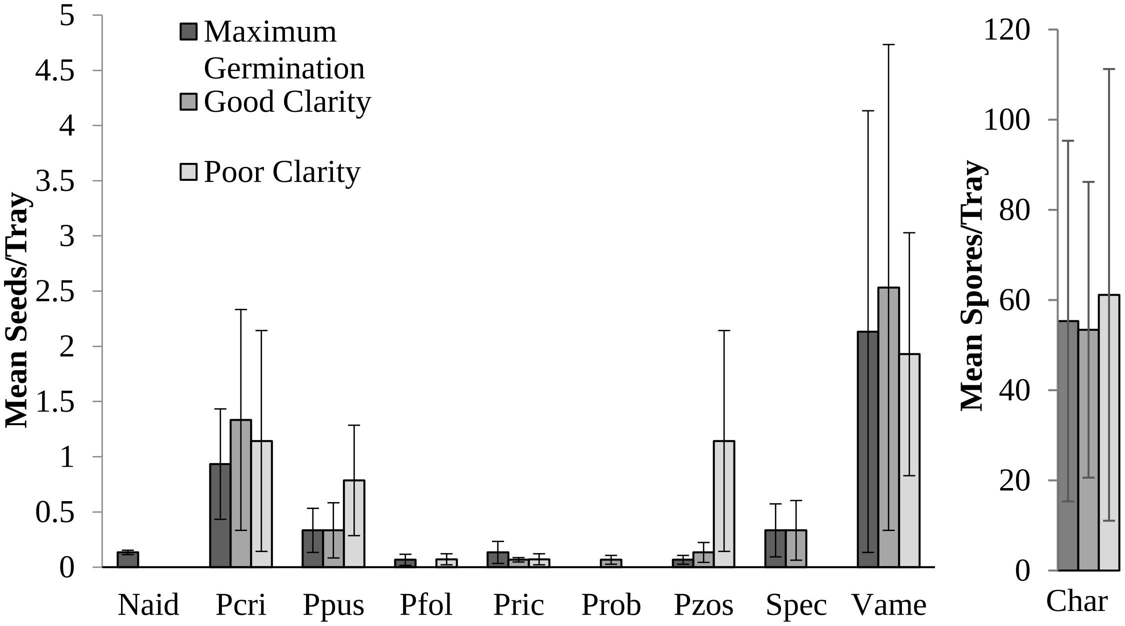

Figure 5. Lake Ann average germination (seeds/tray and spores/tray) under the maximum germination, high clarity and low clarity treatment conditions for the most abundant species observed. Abbreviations are located in Table 3.

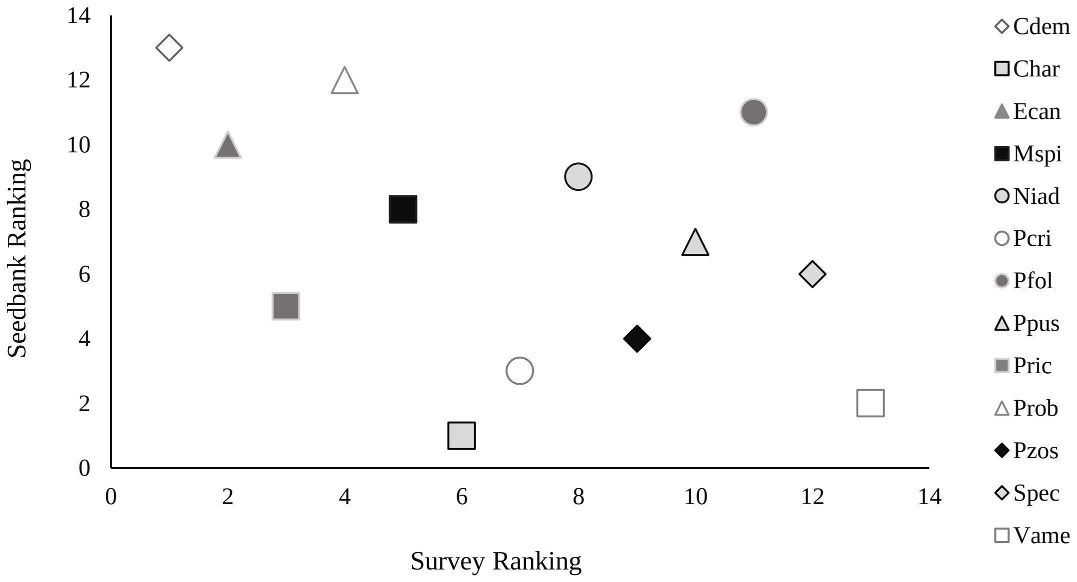

Figure 6. Lake Ann ranking of species sprouting from the seedbank compared to species observed during point intercept surveys. Species with a rating of 1 were the most abundant.

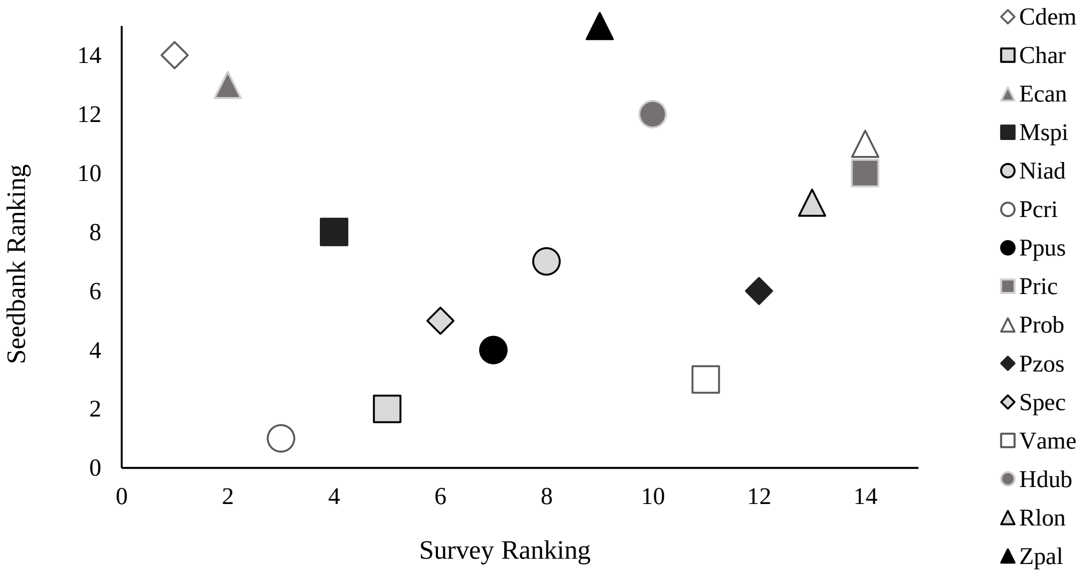

Figure 7. Lake Riley ranking of species sprouting from the seedbank compared to species observed during point intercept surveys. Species with a rating of 1 were the most abundant.

Chapter IV

Concluding Remarks

Macrophytes are a key component in lake ecosystems. They improve water clarity by sequestering nutrients and stabilizing sediment and provide habitat for aquatic organisms (Dennison *et al.* 1993, Donk and Bund 2002). Therefore, restoring aquatic macrophyte communities is an essential aspect of stabilizing a lake ecosystem to a clear water, macrophyte dominated stable state as opposed to a turbid water, phytoplankton dominated state (Scheffer *et al*. 1993). Often, macrophytes have been observed to increase following water clarity improvement through actions such as carp removal or nutrient reduction (Bajer *et al*. 2009, Spears *et al*. 2016). However, the mechanism of macrophyte recruitment is not often known. Additionally, it is uncommon to have long term observations on a macrophyte community as multi-year lake management actions are pursued such as invasive species control or nutrient reduction. It is imperative to understand how aquatic macrophytes, both native and invasive, respond to lake management actions and what actions serve to improve the macrophyte community richness and abundance.

In Chapter II, I showed that the restoration of macrophytes is possible with multi-year, adaptive management using Lake Riley in Chanhassen, MN as a case study. Over the course of the survey years the macrophyte community increased in abundance and richness as limiting factors were addressed. Limiting factors included high abundances of carp, high abundances of invasive macrophytes, and poor water clarity. Exotic species should be controlled if in high abundance as the results of this study and other studies have demonstrated that large populations of exotic species can lead to stunted native macrophyte growth (Bolduan 1994, Kloskowski 2011). Additionally, similar to other studies on macrophyte community recovery, we found that water clarity is a significant driver of the abundance and diversity of the native plant community (Hilt *et al.* 2006, Bajer *et al.* 2009, Knopik 2014). Generally, to restore a healthy macrophyte community, multiple limiting factors will need to be evaluated and it is imperative to plan for several years of management to ensure successful results that benefit the ecosystem and lake users.

Although the native macrophyte community increased in richness and abundance it was still largely dominated by coontail and Canada waterweed, two native species that can grow prolifically in the water column. The remaining native macrophyte species all showed moderate to no increases in abundance although as light availability increased new species were recruited in the lake during the survey years. As a next step, transplanting aquatic plants may be successful if water clarity and light quality remain at the improved levels observed in 2016.

In Chapter III, I demonstrated that recruitment from seed banks is possible although high levels of propagule viability and abundances in the seed bank are likely between different lakes. By employing a germination study, lake managers can better understand the potential for native and invasive species recolonization from the seed bank in a lake and can also determine the extent of species diversity present. Lake seed banks can be variable in abundance and richness and in this study the seed banks do appear to reflect the existing macrophyte community in the lakes. Moreover, ranges of high light intensity did not impact the propagule germination of macrophytes in this study but further investigation is warranted on the effect of light on the survival of propagules to maturity.

Overall, macrophyte restoration requires adaptive management that is aimed at identifying and addressing limiting factors to species recovery and abundance. It is crucial to understand the potential of both invasive and native macrophytes to respond to various lake management actions and the potential for propagule recruitment from the lake seed bank. This thesis has demonstrated that positive changes to macrophyte communities can be achieved through common lake management practices, improving the water quality for the ecosystem and lake users. This work has also furthered the understanding of lake seed banks and shown that there is potential in lake seed banks to aid in the recruitment and maintenance of macrophyte communities.

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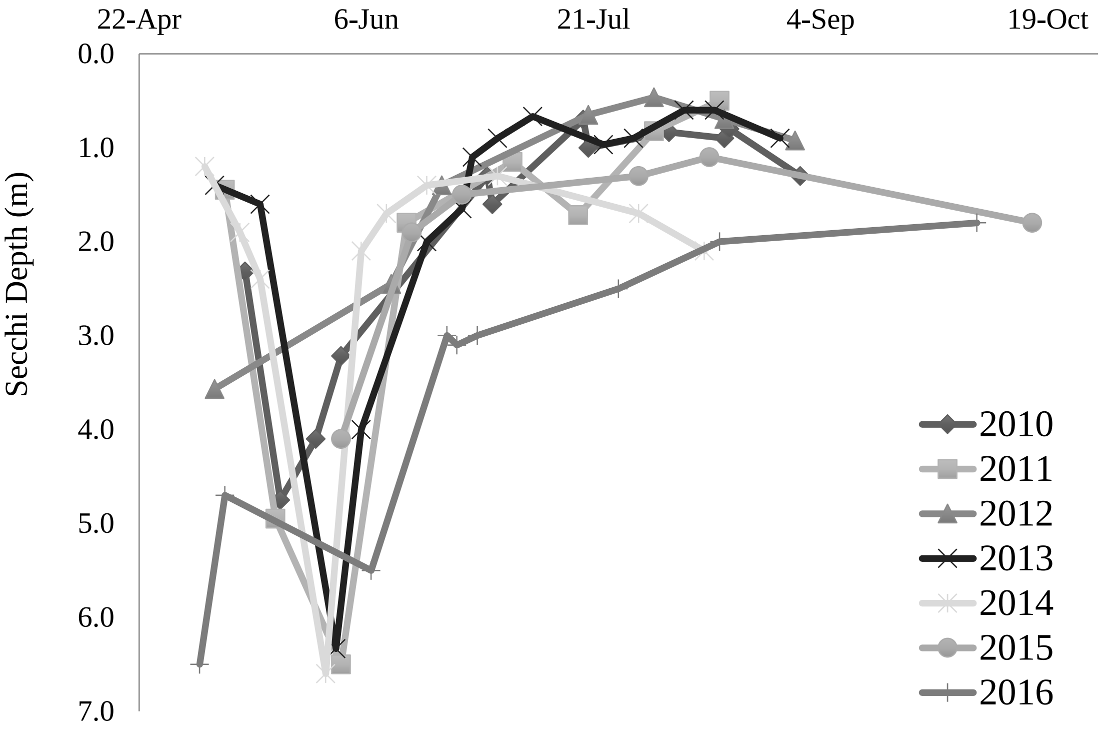
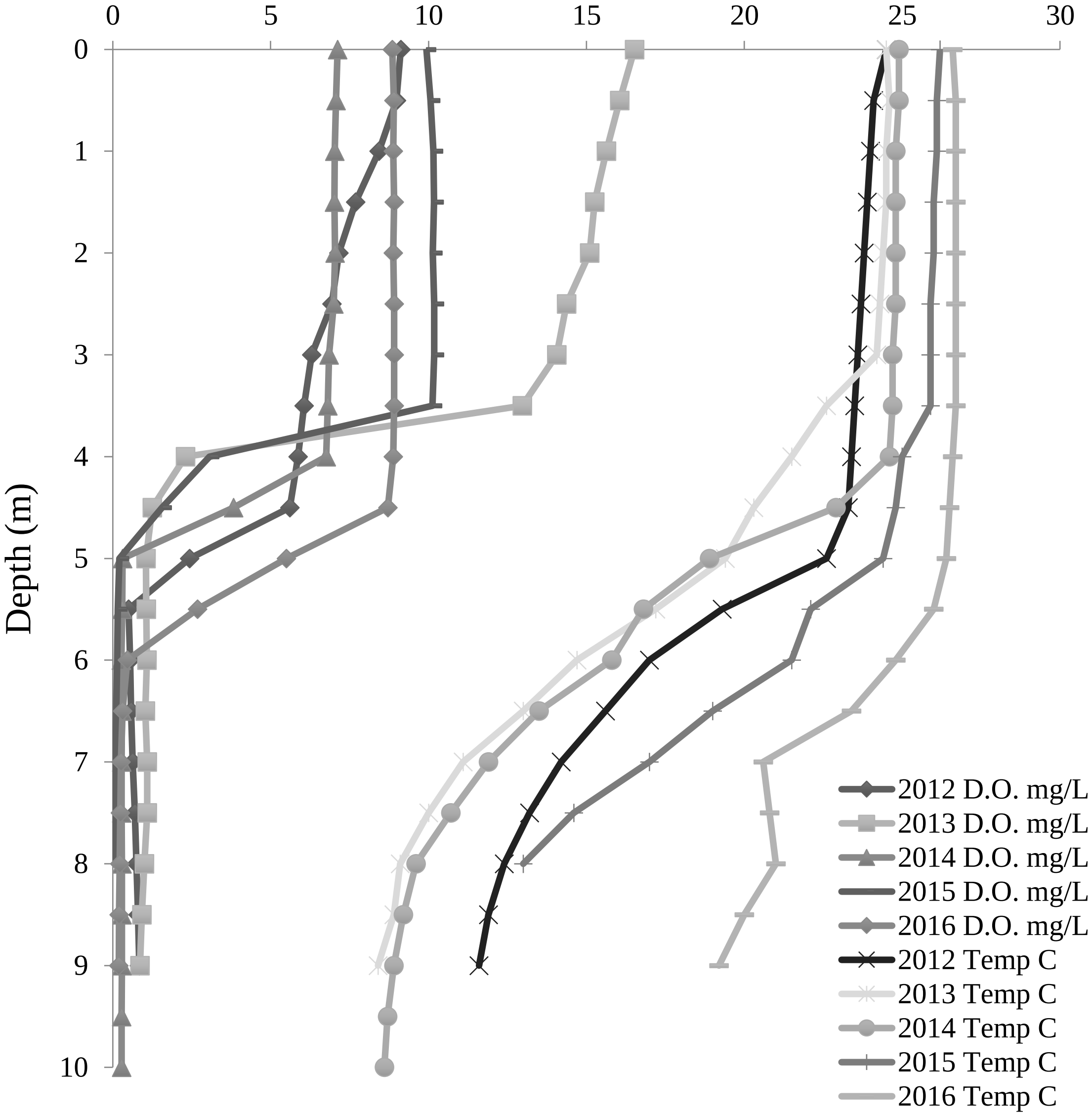
Appendix

Supplemental Information



Appendix Figure 1. All Secchi depths for the surveyed years of 2010 through 2016 on Lake Riley.



Appendix Figure 2. August dissolved oxygen (D.O.) and temperature for the surveyed years of 2012 through 2016 on Lake Riley.

Appendix Table 1. Chapter II results from the Poisson regression models from the Lake Riley species richness analysis which included both June and August survey data. The total native species richness counts from 2011 to 2016 and species richness per sampling point from 2011 to 2016 were assessed. The R code for the models is also included in the table.

	Estimate	SE	Z	P	AIC
Total native species richness	-177.2	154.2	-1.15	0.25	61.8
Pre-alum Treatment	0.10	0.33	0.31	0.76	
Exotics Freq.	0.34	0.95	0.36	0.72	
Year	0.09	0.08	1.16	0.24	
Month (June)	-0.26	0.20	-1.30	0.20	
R code: TotalRichness<-glm(Richness~ExoticFreq+AlumTrt +Year+Month , data=RileyRichness, family=poisson)					
Total native species richness per point	-80.3	32.7	-2.5	0.01	5306
Pre-alum Treatment	-0.30	0.06	-4.60	0	
Exotics Present	1.32	0.04	30.1	0	
Year	0.04	0.02	2.45	0.01	
Month (June)	-0.12	0.04	-2.98	0.003	
R code: RichnessPerPoint<-glm(RichnessPerPoint~NumExoticSpp +AlumTrt+Year+Month , data=RileyRichness, family=poisson)					

Appendix Table 2. Chapter II results from the Poisson regression models from the Lake Riley frequency of occurrence estimates for surveys from 2011 to 2016. Models evaluate the change in abundance in exotic species combined, native species combined, and the individual species with the highest biomass. The R code for the models is also included in the table.

	Estimate	SE	Z	P	AIC
Total native macrophyte frequency	-124.3	71.1	-1.75	0.08	2694
Pre-alum Treatment	-0.98	0.17	-5.6	0	
Exotics Freq.	1.69	0.11	15.4	0	
Year	0.06	0.04	1.76	0.8	
Month (June)	-0.52	0.10	-5.2	0	
R code: NativeFoC<-glm(Native~AlumTrt +Year+ExoticsFoC+Month, data=RileyFoC, family=binomial)					
Curlyleaf Frequency	150.1	172.0	0.87	0.38	1334
Post-herbicide	-9.7 e^{-4}	0.29	-3.0e^{-3}	0.99	
Natives Freq.	1.1	0.16	6.9	0	
Year	-0.08	0.09	-0.89	0.37	
Month (June)	2.6	0.23	11.4	0	
R code: CurlyeafFoC<-glm(Curlyleaf~HerbicideTrt+Year +NativeFoC+Month, data=RileyFoC, family=binomial)					
Eurasian watermilfoil Frequency	-267.4	114.7	-2.3	0.02	2375
Post-herbicide	-0.20	0.20	-0.99	0.32	
Natives Freq.	1.74	0.11	15.2	0	
Year	0.13	0.06	2.31	0.02	
Month (June)	1.18	0.12	10.9	0	
R code: EurasianFoC<-glm(Eurasian~HerbicideTrt+Year +NativeFoC+Month, data=RileyFoC, family=binomial)					
Coontail Frequency	-17.3	70.3	-0.25	0.8	2796
Pre-alum Treatment	-0.88	0.17	-5.3	0	
Exotics Freq.	1.51	0.1	14.5	0	
Year	0.008	0.03	0.25	0.8	
Month (June)	-0.5	0.10	-5.40	0	
R code: CoontailFoC<-glm(Coontail~AlumTrt +Year+ExoticsFoC+Month, data=RileyFoC, family=binomial)					

Appendix Table 2 Continued.

	Estimate	SE	Z	P	AIC
Canada waterweed frequency	-1.3 e^3	198.2	-6.38	0	1102
Pre-alum Treatment	-0.99	0.25	-3.9	0	
Exotics Freq.	1.2	0.17	7.03	0	
Year	0.63	0.10	6.38	0	
Month (June)	-0.35	0.17	-2.06	0.04	
R code: CanwaterweedFoC<-glm(Canwaterweed~AlumTrt +Year+ExoticsFoC+Month, data=RileyFoC, family=binomial)					
Sago Pondeed Frequency	39.4	204.7	0.19	0.19	0.85
Pre-alum Treatment	-0.38	0.43	-0.91	0.37	
Exotics Freq.	1.04	0.27	3.8	0	
Year	-0.02	0.10	-0.2	0.83	
Month (June)	-0.04	0.26	-0.17	0.86	
R code: SagoFoC<-glm(Sago~AlumTrt+Year +ExoticFoC+Month, data=RileyFoC, family=binomial)					
Narrowleaf pondweed Frequency	94.8	150.8	0.63	0.53	842
Pre-alum Treatment	0.8	0.44	1.82	0.07	
Exotics Freq.	0.4	0.22	1.9	0.06	
Year	-0.05	0.07	-0.65	0.51	
Month (June)	-0.46	0.21	-2.15	0.03	
R code: NarrowleafFoC<-glm(Narrowleaf~AlumTrt+Year +ExoticFoC+Month, data=RileyFoC, family=binomial)					
Chara Frequency	-1863	561.7	-3.3	0	246
Pre-alum Treatment	1.13	0.63	1.8	0.07	
Exotics Freq.	0.95	0.43	2.18	0.03	
Year	0.92	0.28	3.31	0	
Month (June)	-0.99	0.46	-2.18	0.03	
R code: CharaFoC<-glm(Chara~AlumTrt +Year+ExoticsFoC+Month, data=RileyFoC, family=binomial)					

Appendix Table 2 Continued.

	Estimate	SE	Z	P	AIC
Naiad frequency	$-3.8\ e^{4}$	$3.0\ e^{6}$	-0.01	0.99	159
Pre-alum Treatment	2.12	$1.5\ e^{3}$	0.014	0.99	
Exotics Freq.	0.26	0.54	0.48	0.63	
Year	1.88	$1.5\ e^{3}$	0.012	0.99	
Month (June)	-2.05	$3.2\ e^{3}$	-0.01	0.99	

R code: NaiadFoC<-glm(Naiad~AlumTrt
+Year+ExoticsFoC+Month, data=RileyFoC, family=binomial)

Appendix Table 3. Chapter II results from the multiple regression models from the Lake Riley mean biomass estimates for surveys from 2011 to 2016. Models evaluate the change in biomass in exotic species combined, native species combined, and the individual species with the highest biomass. The R code for the models is also included in the table.

	Estimate	SE	T	P	F	Df	P model	R^2	Adj-R^2
Total native macrophyte biomass	-432.7	163.1	-2.65	0.008	32	564	0	0.19	0.18
Pre-alum Treatment	-1.58	0.37	-4.3	0					
Log(Exotics+1)	0.44	0.06	7.7	0					
Year	0.21	0.08	2.68	0.007					
Month (June)	-0.55	0.21	-2.7	0.008					
R code: NativeBiomass<-lm((log(Natives+1))~AlumTrt+(log(Exotics+1))+Year+Month, data=RileyBiomass)									
Curlyleaf pondweed biomass	-115.4	72.8	-1.58	0.11	18.8	564	0	0.12	0.11
Post-herbicide	-0.30	0.12	-2.44	0.015					
Log(Natives+1)	$5.8 e^{-3}$	0.013	0.43	0.67					
Year	0.057	0.036	1.59	0.11					
Month (June)	0.54	0.066	8.25	0					
R code: CurlyleafBiomass<-lm((log(Curlyleaf+1))~HerbicideTrt+(log(Natives+1)) +Year+Month, data=RileyBiomass)									
Eurasian watermilfoil biomass	-42.1	156.1	-0.27	0.79	16.3	564	0	0.10	0.10
Post-herbicide	-0.44	0.27	-1.65	0.1					
Log(Natives+1)	0.17	0.03	5.96	0					
Year	0.02	0.078	0.27	0.79					
Month (June)	0.64	0.14	4.53	0					
R code: EurasianBiomass<-lm((log(Eurasian+1))~HerbicideTrt+(log(Natives+1)) +Year+Month, data=RileyBiomass)									
Coontail biomass	-330	166.7	-1.98	0.048	23.6	564	0	0.14	0.13
Pre-alum Treatment	-1.59	0.38	-4.2	0					
Log(Exotics+1)	0.36	0.06	6.24	0					
Year	0.16	0.08	2.004	0.05					
Month (June)	-0.47	0.21	-2.2	0.03					
R code: CoontailBiomass<-lm((log(Coontail+1))~AlumTrt+(log(Exotics+1)) +Year+Month, data=RileyBiomass)									

Appendix Table 3. Continued.

	Estimate	SE	T	P	F	Df	P_{model}	R^2	Adj-R^2
Canada waterweed biomass	-202.2	62.0	-3.26	0.001	48.2	564	0	0.25	0.25
Pre-alum Treatment	-1.06	0.14	-7.58	0					
Log(Exotics+1)	0.09	0.02	4.34	0					
Year	0.1	0.031	3.29	0.001					
Month (June)	-0.29	0.08	-3.66	0					
R code: CanwaterweedBiomass<-lm((log(Canwaterweed+1))~AlumTrt+(log(Exotics+1))+ Year+Month, data=RileyBiomass)									
Sago pondweed biomass	4.1	25.4	0.16	0.87	1.2	564	0.31	0.01	0.001
Pre-alum Treatment	-0.04	0.06	-0.7	0.48					
Log(Exotics+1)	0.02	0.009	1.98	0.05					
Year	-0.002	0.013	-0.16	0.87					
Month (June)	-0.002	0.03	-0.05	0.96					
R code: SagoBiomass<-lm((log(Sagol+1))~AlumTrt+(log(Exotics+1))+Year+Month, data=RileyBiomass)									
Narrowleaf pondweed biomass	40.2	27.8	1.45	0.15	1.54	564	0.19	0.01	0.004
Pre-alum Treatment	-0.007	0.06	-0.11	0.92					
Log(Exotics+1)	0.016	0.01	1.7	0.09					
Year	-0.02	0.014	-1.45	0.15					
Month (June)	-0.006	0.03	-0.17	0.87					
R code: NarrowleafBiomass<-lm((log(Narrowleaf+1))~AlumTrt+(log(Exotics+1))+Year +Month, data=RileyBiomass)									
Chara biomass	-44.5	26.9	-1.66	0.10	3.27	564	0.01	0.02	0.01
Pre-alum Treatment	-0.03	0.06	-0.46	0.65					
Log(Exotics+1)	0.02	0.01	2.5	0.01					
Year	0.02	0.01	1.67	0.09					
Month (June)	-0.03	0.03	-0.92	0.36					
R code: CharaBiomass<-lm((log(Chara+1))~AlumTrt+(log(Exotics+1))+Year +Month, data=RileyBiomass)									

Appendix Table 3. Continued.

	Estimate	SE	T	P	F	Df	P model	R^2	Adj-R^2
Naiad biomass	-48.4	18.25	-2.65	0.008	3.48	564	0.01	0.02	0.01
Pre-alum Treatment	0.07	0.04	1.8	0.07					
Log(Exotics+1)	0.007	0.006	1.16	0.24					
Year	0.024	0.009	2.66	0.008					
Month (June)	-0.59	0.023	-2.57	0.01					

R code: NaiadBiomass<-lm((log(Naiad+1))~AlumTrt+(log(Exotics+1))+Year+Month, data=RileyBiomass)

Appendix Table 4. Chapter III results from the Poisson regression models from the Lakes Riley and Ann seed bank total viable propagule counts in each germination treatment: maximum germination, high clarity, and low clarity. The R code for the models is also included in the table. Results from the species specific models were not included because they were also not significant.

	Estimate	SE	T	P
Lake Riley Total Propagules in each Trt.				
Intercept	1.96	0.16	11.9	0
Max. Germination	0.11	0.23	0.51	0.61
Low clarity	0.19	0.22	0.84	0.41
Week	-0.22	0.05	-4.83	0
R code: TotalRileyPropagules<glm(RileySeedbank$TotalSprouts ~1+RileySeedbank$Treatment, family=quasipoisson(link=log))				
Lake Ann Total Propagules in each Trt.				
Intercept	4.07	0.12	11.97	0
Max. Germination	0.02	0.16	0.14	0.89
Low clarity	0.10	0.16	0.64	0.52
Week	-0.02	0.03	-0.82	0.42
R code: TotalAnnPropagules<glm(AnnSeedbank$TotalSprouts ~1+AnnSeedbank$Treatment, family=quasipoisson(link=log))				