**Michigan
Technological
University**

Michigan Technological University
Digital Commons @ Michigan Tech

Dissertations, Master's Theses and Master's Reports

2017

ASSOCIATIONS BETWEEN INVASIVE EURASIAN WATERMILFOIL AND LITTORAL FISH AND INVERTEBRATE COMMUNITIES IN THE KEWEENAW WATERWAY OF LAKE SUPERIOR

Carmen Leguizamon
Michigan Technological University, cmleguiz@mtu.edu

Copyright 2017 Carmen Leguizamon

Recommended Citation

Leguizamon, Carmen, "ASSOCIATIONS BETWEEN INVASIVE EURASIAN WATERMILFOIL AND LITTORAL FISH AND INVERTEBRATE COMMUNITIES IN THE KEWEENAW WATERWAY OF LAKE SUPERIOR", Open Access Master's Thesis, Michigan Technological University, 2017.
<https://doi.org/10.37099/mtu.dc.etdr/519>

Follow this and additional works at: <https://digitalcommons.mtu.edu/etdr>

Part of the [Other Ecology and Evolutionary Biology Commons](#)

ASSOCIATIONS BETWEEN INVASIVE EURASIAN WATERMILFOIL AND
LITTORAL FISH AND INVERTEBRATE COMMUNITIES IN THE KEWEENAW
WATERWAY OF LAKE SUPERIOR

By

Carmen M. Leguizamon

A THESIS

Submitted in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

In Biological Sciences

MICHIGAN TECHNOLOGICAL UNIVERSITY

2017

© 2017 Carmen M. Leguizamon

This thesis has been approved in partial fulfillment of the requirements for the Degree of Master of Science in Biological Sciences.

Department of Biological Sciences

Thesis Advisor: *Dr. Casey Huckins*

Committee Member: *Dr. Amy Marcarelli*

Committee Member: *Dr. Christopher Webster*

Department Chair: *Dr. Chandrashekhhar P. Joshi*

Table of Contents

Acknowledgements.....	iv
Abstract.....	v
Introduction.....	1
Chapter 1: Macrophytes.....	4
<i>1.1 Background</i>	4
<i>1.2 Methods</i>	4
<i>1.3 Results</i>	7
<i>1.4 Discussion</i>	9
Chapter 2: Fish and invertebrates.....	11
<i>2.1 Background</i>	11
<i>2.2 Methods</i>	14
<i>2.3 Results</i>	18
<i>2.4 Discussion</i>	24
References.....	28
Tables.....	37
Figures.....	51
Appendix I.....	65

Acknowledgements

This research was supported by the Michigan Department of Natural Resources Invasive Species Grant (#IS14-2005), which was awarded to Drs. Casey Huckins, Amy Marcarelli, and Erika Hersch-Green at Michigan Technological University.

I would like to thank my advisor, Dr. Casey Huckins, for his guidance and patience throughout my graduate education. In addition, thank you to Drs. Amy Marcarelli and Christopher Webster for lending their time and expertise as committee members and teachers.

This work would not have been possible without the help of many others that contributed time to this project. In particular, I would like to acknowledge Christopher Adams and Bradley Wells for their many hours spent in the field. Thank you also to Addaline Huckins and Sunflower Wilson for their help in collecting these data.

Lastly, I want to thank my family and friends. Thank you to my mom and my siblings, Marissa and Luis, for their years of encouragement. To my father, the person that inspired my love of nature and learning, this thesis is dedicated in your memory. And of course, my husband, John. Thank you for supporting me throughout this process and beyond, and for keeping me sane. This is also dedicated to you.

Abstract

The invasion of Eurasian watermilfoil (*Myriophyllum spicatum*) can influence littoral zone communities within lakes. Its formation of dense mats at the water surface can suppress native macrophyte growth and impact fish diets and community structure, as well as invertebrate assemblages. However, in the colder waters of the upper Great Lakes region, Eurasian watermilfoil is patchily distributed and integrates more with the native macrophyte community. In order to identify the associations of invasive Eurasian watermilfoil and the littoral communities of the Keweenaw Waterway of Michigan's Upper Peninsula, we sampled invertebrates, fish, and macrophytes at sites that represented a gradient of Eurasian watermilfoil abundance, as well as habitats with dense and sparse native vegetation. We hypothesized that areas dominated by Eurasian watermilfoil would exhibit less rich and diverse communities of native macrophytes, fish, and invertebrates. We also hypothesized that invertebrate abundances would be greatest in more invaded habitats as a result of reduced predation, but that fish would be more abundant at moderate invasion levels due to optimal foraging efficiency. Our results indicate that, overall, the more vegetated habitats supported more abundant and rich fish and invertebrate communities. However, while habitats with more abundant Eurasian watermilfoil tended to support more abundant fish communities, the most invaded habitats supported fewer fish, and reduced species richness and diversity. While invertebrate abundance also increased along with Eurasian watermilfoil abundance, more of the variation in invertebrate abundance was explained by native macrophytes. At the abundances observed in the Keweenaw Waterway, Eurasian watermilfoil appears to have little impact on invertebrate taxa richness and diversity. Overall, Eurasian watermilfoil appears to provide useful habitat to fish and invertebrates where it integrates more with the native macrophyte community. Yet, if Eurasian watermilfoil is left unmanaged and continues to spread, these effects may intensify over time, leading to reductions in fish abundance and biomass.

1. Introduction

Eurasian watermilfoil (*Myriophyllum spicatum*) is an aquatic macrophyte that since the 1940s has become a pervasive invasive species throughout the contiguous United States (Madsen 2005) and much of the Great Lakes region (EDDMapS 2017). When established in the littoral zone of lakes, its structural complexity and formation of dense canopies at the water's surface can outcompete native macrophytes (Madsen et al. 1991, Boylen et al. 1999), stunt fish foraging efficiency (Valley and Bremigan 2002a) and growth (Unmuth et al. 1999, Parsons et al. 2011), as well as support less taxa rich invertebrate communities (Cheruvilil et al. 2002). In Michigan's Upper Peninsula, Eurasian watermilfoil was first detected in 2002 in Gogebic County, with the first detection in the Keweenaw Waterway occurring a decade later in Pike Bay, Houghton County (EDDMapS 2017) (Figure 1.1). Macrophyte surveys have been conducted in Pike Bay since 2014, and treatment for Eurasian watermilfoil has consisted of annual applications of herbicide (Juneau et al. in prep, Huckins et al., http://www.mtri.org/eurasian_watermilfoil.html). Much of the research in Michigan on the interactions between invasive Eurasian watermilfoil and littoral fish and invertebrates has been concentrated in the Lower Peninsula (i.e. Cheruvilil et al. 2001, Cheruvilil et al. 2002, Valley and Bremigan 2002a, Valley and Bremigan 2002b, Cheruvilil et al. 2005, Bremigan et al. 2005), with comparatively less work focused on the cold waters of the Upper Great Lakes region.

Littoral zones serve as important habitat for fish and invertebrates (see reviews by Diehl and Kornijow 1998, Winfield 2004, and Valley et al. 2004), and are used by the majority of lentic fish species in some or all life stages (Vadeboncoeur et al. 2011). These shallower nearshore areas support the establishment of submerged aquatic macrophytes, which provide more habitat complexity than deeper waters (Rea et al. 1998). Fish and invertebrates are often more abundant in these vegetated habitats relative to non-vegetated sites (Beckett et al. 1992, Duffy and Baltz 1998, Theel et al. 2008) due to the provision of food resources (Rozas and Odum 1988, Cattaneo et al. 1998, Grenouillet and Pont 2001), refuge from predators (Werner et al. 1983, Gilinsky 1984, Rozas and Odum 1988, Beckett et al. 1992), and reproductive habitat (Trebitz et al. 2009).

The establishment of non-native aquatic macrophytes can negatively impact the littoral communities of recipient ecosystems (see review by Schultz and Dibble 2012). Invasive macrophytes can reduce native plant richness and abundance (Madsen et al. 1991, Boylen et al. 1999) by forming dense canopies (Smith and Barko 1990), limiting light penetration (Bowes et al. 1979, Titus and Adams 1979) and making it less available to the surrounding native macrophytes (Madsen et al. 1991, Boylen et al. 1999). This can ultimately shift macrophyte community assemblages toward species, such as pondweeds, that are better competitors in low-light environments (Spence and Chrystal 1970).

However, the Keweenaw Waterway of Michigan's Upper Peninsula is a unique system because it bisects the Keweenaw Peninsula and connects with Lake Superior on each end, thus receiving substantial mixing with the cold Lake Superior waters. The dense canopies of Eurasian watermilfoil often observed in southern Michigan (e.g. Cheruvilil et al. 2001) and in inland lakes at similar northern latitudes (e.g. Getsinger et al. 1997 in northern Washington State) are less common in this region. Rather, Eurasian watermilfoil appears as either smaller dense patches or is integrated into the native macrophyte community (Juneau et al. in Prep., Huckins et al. unpublished data). Nevertheless, the increased structural complexity of Eurasian watermilfoil may still influence the native littoral faunal communities.

Eurasian watermilfoil has a complex architecture composed of many finely dissected leaves with small interstitial spaces that are oriented in whorls around the stem (Thomaz and da Cunha 2010). This complex architecture is associated with greater surface area (Sher-Kaul 1995), which generally supports more invertebrates than broad undissected plant structures (Krecker 1939, Cheruvilil et al. 2000, Cheruvilil et al. 2002) due to the accumulation of epiphytic food sources (Balci and Kennedy 2003, Strimaitis and Sheldon 2011) and its refuge value (Valinoti et al. 2011). However, greater canopy cover of Eurasian watermilfoil has also been found to support fewer invertebrates (Cheruvilil et al. 2001), likely due to its allelopathic traits creating an unfavorable chemical environment (Unmuth et al. 2000, Linden and Lehtiniemi 2005). Additionally, while structurally complex invasive macrophytes, such as *Hydrilla verticillata*, often support more fish than native macrophytes (Troutman et al. 2007), this has not been supported in studies focused

on Eurasian watermilfoil (Valley et al. 2004). However, habitats with abundant and patchily distributed Eurasian watermilfoil have been found to support more bluegill of smaller size classes (Weaver et al. 1997), which could be attributed to reduced fish foraging efficiency (Valley and Bremigan 2002) and growth (Unmuth et al. 1999, Parsons et al. 2011).

Treatment with herbicides has been found to be an effective method for controlling Eurasian watermilfoil (Westerdahl and Hall 1983, Getsinger et al. 1997, Bremigan et al. 2005, Kovalenko et al. 2010, Wersal et al. 2010, Cason and Roost 2011), while also promoting native macrophyte growth (Getsinger et al. 1997, Pedlow et al. 2006, Webb et al. 2016). The commonly used herbicides 2,4-dichlorophenoxy acetic acid (2,4-D) and triclopyr selectively target macrophytes, like Eurasian watermilfoil (Skogerboe and Getsinger 2006, Madsen et al. 2002, Madsen et al. 2015), and are preferred in habitats where the native macrophyte community is dominated by monocots. However, 2,4-D has also been found to reduce the abundance of certain native monocot species, including Canadian waterweed (*Elodea canadensis*), watershield (*Brasenia schreberi*), coontail (*Ceratophyllum demersum*), small pondweed (*Potamogeton pusillus*), and variable pondweed (*P. gramineus*) (Westerdahl and Hall 1983, Cason and Roost 2011, Nault et al. 2014), all of which are found in the Keweenaw Waterway. At the rates commonly used for treatment, herbicides have not been found to have a significant negative effect on fish or invertebrates (Hiltibran 1967, Hamelink et al. 1986, Kreutzweiser et al. 1994, Relyea 2005).

This study has two primary objectives: 1) to determine if and how abundance of native macrophytes vary along an increasing gradient of invasion, as well as to 2) assess the fish and invertebrate communities in habitats across a gradient of macrophyte abundance and community type (i.e. native vs. Eurasian watermilfoil).

Chapter 1: Associations between invasive Eurasian watermilfoil and native macrophytes

1.1 Background and Hypotheses

The establishment of invasive Eurasian watermilfoil has been found to alter native macrophyte community dynamics by reducing overall macrophyte abundance (Madsen et al. 1991, Boylen et al. 1999, Webb et al. 2016) and species richness (Madsen et al. 1991, Boylen et al. 1996, Boylen et al. 1999, Parsons et al. 2009, Wersal et al. 2010). The greater dissected structure and small interstitial spaces of Eurasian watermilfoil (Lillie and Budd 1992) can increase habitat complexity and surface area relative to some native macrophytes (i.e. sago pondweed (*Potamogeton pectinatus*) and clasping leaf pondweed (*P. richardsonii*)) (Sher-Kaul et al. 1995). However, overall habitat heterogeneity may decrease under dense monotypic canopies (Cheruvilil et al. 2001).

Herbicide treatment is considered an effective control method for Eurasian watermilfoil (Westerdahl and Hall 1983, Getsinger et al. 1997, Bremigan et al. 2005, Kovalenko et al. 2010, Wersal et al. 2010, Cason and Roost 2011). Herbicide reduces the invasive canopy cover and increases light availability (Pedlow et al. 2006), thereby promoting native macrophyte growth (Getsinger et al. 1997, Pedlow et al. 2006, Wersal et al. 2010, Cason and Roost 2011, Webb et al. 2016). Furthermore, selective herbicide applications has been shown to increase native macrophyte richness (Getsinger et al. 1997, Wersal et al. 2010, Webb et al. 2016).

While in the Keweenaw Waterway of Michigan's Upper Peninsula, Eurasian watermilfoil is patchily distributed and integrates more with the native macrophyte community (Juneau et al. in prep), we still hypothesized that the more invaded habitats would outcompete native macrophytes, and thereby, would support less abundant and less species rich native macrophyte communities.

1.2 Methods

Study Area

This study was conducted in the summer of 2016 within the Keweenaw Waterway of the Upper Peninsula of Michigan. Study areas were selected based on their suitability for conducting fish trap sampling (see Chapter 2). From June through August, we sampled for macrophytes at all fish sampling sites except Marsin (Figure 1.2, Table 1.1). Sampling sites were determined based on macrophyte surveys conducted in the summer of 2015, and were selected in order to represent a range of macrophyte abundance and community composition (i.e. natives, Eurasian watermilfoil, and no/sparse vegetation). However, Eurasian watermilfoil failed to establish at some of these sites in the summer of 2016, leading us to identify alternative sampling areas. This addition of survey sites resulted in uneven sampling effort across the complete set of sites over time.

As part of the management efforts for Eurasian Watermilfoil, two sites, Pike Bay 1 and 2, were treated by an independent contractor (contracted by the local Township) on June 22 with granular triclopyr (SePro Renovate OTF), liquid triclopyr (Renovate 3), and granular 2,4-D (SePro Sculpin G). These sites were also treated the previous summer with Renovate OTF, SePro Sculpin G, and a granular triclopyr/2,4-D combination (Renovate Max G). To our knowledge, no other sampling sites received herbicide treatment during this sampling period.

Sampling Methods

Categorical assessments of plant presence and abundance were completed at sampling sites based on a modified point-transect method (Madsen 1999) using twist and toss rake sampling, which has been found to be an accurate technique for assessing vegetation biomass (Kenow et al. 2007). The rakes were constructed of two metal rakes attached back-to-back and to a braided rope or an extendable handle for the toss and twist rake, respectively. The twist rake was made from two 0.34m wide rakes with 14 tines and the toss rake was constructed using two 0.39m wide rakes with 16 tines. Typically, macrophytes were sampled at 4 points within the vicinity of each fish survey area, 3 points nearshore and 1 point offshore. Twist and toss rake samples were each collected 3 times at each sample point. Twist rake samples were collected by placing the rake at the lake bottom and rotating the rake 3 complete rotations. For toss samples, the rake was thrown

approximately 4-5 m from the boat and dragged along the lake bottom, collecting macrophytes in the tines. Plant species were identified (Skawinski 2011) and abundance was visually assessed based on rake fullness using a gradient from low to high abundance on a numeric categorical scale of 1 to 4 (Figure 1.3).

Data Analysis Methods

To determine if estimates of relative macrophyte abundances from twist and toss rake samples differed from each other, the categorical rake abundances of Eurasian watermilfoil and the five most common native macrophytes were averaged together within each individual rake sample and analyzed relative to sampling month and rake type using a two-way factorial ANOVA (JMP Pro13). Species were considered common if they were detected in $\geq 76\%$ of surveys. These species included chara (*Chara* sp.), *Ceratophyllum demersum*, *Elodea canadensis*, naiad (*Najas* sp.), and eel grass (*Vallisneria americana*), which were detected in 82% to 100% of toss rakes in all surveys. The next most commonly detected native macrophytes were bladderwort (*Utricularia* sp.) and water marigold (*Bidens beckii*), both of which were detected in 53% of all surveys. Toss rakes collected a greater abundance of macrophytes (ANOVA, $F_{1,430} = 6.97$, $p = 0.009$) and number of species (ANOVA, $F_{1,430} = 8.49$, $p = 0.004$), and therefore, toss rake results were exclusively used for further analyses.

The macrophyte community was analyzed using two-way factorial ANOVAs, where abundance of Eurasian watermilfoil represents the categorical abundance per toss rake in a survey, while native macrophyte abundance represents the mean categorical abundance of all common native species per toss rake. To account for uneven sampling across sites across sampling dates, survey results were analyzed based on means for each sampling month, as well as with and without post-treatment sites to isolate any possible herbicide effect. The two-way factorial ANOVAs analyzed the toss rake results of Eurasian watermilfoil abundance, native macrophyte abundance (mean categorical abundance per rake), and number of species detected per toss rake relative to site and sampling month (Table 1.2), as well as to identify the interaction between the macrophyte types over sampling month. Likely due to uneven sampling, there were not sufficient degrees of

freedom to run three-way factorial ANOVAs to analyze interaction effects between macrophyte types, site, and month. Correlations between the mean abundances of Eurasian watermilfoil and native macrophytes (averaged from all toss rake results in a survey), as well as species richness (total number of unique species detected in a survey from toss rakes) were analyzed across all surveys and within each sampling month using Pearson correlations.

Further analysis included a nonmetric multidimensional scaling (NMS) ordination conducted to analyze macrophyte community assemblages. The main matrix was the species matrix, representing the mean categorical abundance of each macrophyte species in a survey (Table 1.3). The secondary matrix was the environmental matrix and consisted of the averaged water depth (m) of macrophyte sampling points within a survey (Table 1.2). Dissolved oxygen (DO) was not included in the secondary matrix because meter measurements were determined to be inaccurate due to improper calibration. Surveys where water depth was not recorded were not included in the analysis (i.e. North Slough on July 24), nor were the species that were not detected within these surveys (i.e. grass-leaved arrowhead (*Sagittaria graminea*), longleaf pondweed (*Potamogeton nodosus*), and Oakes' pondweed (*Potamogeton oakesianus*). This analysis was performed using Sorenson distance measure, and the “slow and thorough” autopilot mode of PC-ORD with 250 runs. The ordination of macrophyte surveys across sites and sampling dates were grouped and analyzed based on categorical designations of Eurasian watermilfoil and native macrophyte abundance, where “low” abundance represented the 25th percentile of relative abundance across surveys, “moderate” represented the next group up to the 50th percentile, and any sites with greater milfoil abundances were considered “high” abundance (Table 1.2). A multi-response permutation procedure (MRPP) using Sorensen distance measure was conducted to determine if sites significantly varied relative to categorical abundance of Eurasian watermilfoil and native macrophytes. Due to only one survey having moderate Eurasian watermilfoil abundance (i.e. Pike Bay 1 on August 16), this site was excluded from the MRPP analysis.

1.3 Results

Our sites varied in their macrophyte communities, as expected to represent a gradient of macrophyte abundance and invasion. Yet, macrophyte assemblages also exhibited temporal variation. There was a significant interaction effect of site and month on the abundances of both Eurasian watermilfoil (ANOVA, $F_{14,201} = 2.30$, $p = 0.04$) and native macrophytes (ANOVA, $F_{14,201} = 2.13$, $p = 0.05$) (Figure 1.4 a-b), indicating that macrophyte abundance at sites changed over time. Furthermore, the positive relationship between Eurasian watermilfoil and native macrophyte abundance across surveys ($r = 0.45$, $p = 0.07$) (Figure 1.5), while only marginally non-significant, supports prior observations in the Keweenaw Waterway that Eurasian watermilfoil integrates with the native macrophyte community. When data from sites surveyed post-treatment were excluded from analysis, this relationship was significant ($r = 0.62$, $p = 0.03$), suggesting a confounding treatment effect. Nevertheless, this positive relationship indicates that Eurasian watermilfoil is more abundant in habitats that support macrophyte communities in general. However, at the highest abundance of Eurasian watermilfoil (i.e. Portage), there was a notable decline in native macrophyte abundance, suggesting that as the invasive spreads it may suppress native macrophytes.

There was a significant interaction between site and sampling month on the number of species detected in toss rake samples (ANOVA, $F_{14,201} = 3.46$, $p = 0.003$), corresponding with changes in macrophyte abundance. Across all sites, species richness was greater in sites with greater native macrophyte abundance ($r = 0.53$, $p = 0.03$) (Figure 1.6a), supporting our predictions. We also had hypothesized that species richness would decrease with increasing Eurasian watermilfoil abundance; however, our results found no significant relationship between these two variables ($r = 0.27$, $p = 0.30$) (Figure 1.6b). Yet, species richness tended to be greatest at the moderately invaded sites, but the habitats with a low abundance of Eurasian watermilfoil supported the least rich macrophyte communities (Table 1.2).

Macrophyte Community Assemblages

The NMS ordination produced a two-dimensional solution (final stress = 9.93, instability < 0.0001, number of iterations = 95) that explained a cumulative 89.1% of the

variation. Water depth was most strongly correlated with axis 1 ($r = -0.455$, $\tau = -0.43$), which explained 77.8% of the variation, while Axis 2 explained 11.2% ($r = 0.355$, $\tau = 0.262$). The macrophyte surveys (across sites and sampling dates) separated across a gradient of Eurasian watermilfoil abundance (Figure 1.7a, Table 1.4). This was determined to be significant based on results from the MRPP ($A = 0.07$, $p = 0.007$) and indicates that Eurasian watermilfoil invasion may support different species of native macrophyte. Yet, sites were more significantly separated across the categorical gradient of native macrophyte categorical abundance ($A = 0.17$, $p = 0.00004$) (Figure 1.7b). Overall, this suggests that the more densely vegetated and invaded habitats supported disparate macrophyte community assemblages.

Relative abundance of Eurasian watermilfoil was negatively correlated with axis 1 ($r = -0.516$) (Figure 1.8), and had only a moderately negative correlation with axis 2 ($r = 0.381$) (Table 1.5). The mean relative abundance of most macrophyte species observed in our surveys also exhibited a stronger association with axis 1 than axis 2, which supports our previous results that indicated that Eurasian watermilfoil was more abundant in habitats that supported more species rich macrophyte communities. The species that grouped away from Eurasian watermilfoil within the NMS ordination were primarily species that were rarely detected and generally low in abundance. More specifically, these species included alpine pondweed (*Potamogeton alpinus*), bulrush (*Scirpus* sp.), quillwort (*Isoetes* sp.), small pondweed (*Potamogeton pusillus*), spearwort (*Ranunculus* sp.), floating bur-reed (*Sparganium fluctuans*), and variable watermilfoil (*Myriophyllum heterophyllum*). However, chara (*Chara* sp.), which was also strongly associated with axis 1, was one of the most common species detected across our sampling surveys, but was generally at low relative abundances, rarely exceeding a categorical abundance of 2 in rake samples.

1.4 Discussion

While the formation of dense mats by Eurasian watermilfoil has been observed at similar northern latitudes (e.g. Getsinger et al. 1997 in northern Washington state) and in the more southern Great Lakes region (e.g. Titus and Adams in Wisconsin 1979 and Cheruvilil et al. 2001 in southern Michigan), we found that in the Keweenaw Waterway,

Eurasian watermilfoil integrated with the native macrophyte community. Sites that supported more native macrophytes also supported more Eurasian watermilfoil, and Eurasian watermilfoil also tended to occupy more plant species-rich habitats, which has also been supported in other studies (Keast 1984). This suggests that Eurasian watermilfoil is growing in quality habitats that support greater macrophyte growth, and that the more species-rich macrophyte communities in the Keweenaw Waterway may not be more resistant to invasion. However, the integration of Eurasian watermilfoil into the native community is likely attributed to the mixing with the cold Lake Superior waters.

Prior theoretical research in the field of invasion ecology has suggested that diverse habitats are more resistant to invasion (Elton 1958, MacArthur and Wilson 1967, Case 1990). However, in field studies the relationship between habitat diversity and invasibility has been found to be both positive (Robinson et al. 1995, Knops et al. 1995) and negative (Naeem et al. 2000, Kennedy et al. 2002, Tilman 1997), and is often dependent on spatial scale (Lonsdale 1999) or community composition of the recipient ecosystem (Meiners et al. 2004). Furthermore, most studies exploring this topic are focused on terrestrial systems (e.g. Robinson et al. 1995, Knops et al. 1995, Tilman 1997, Naeem et al. 2000, Kennedy et al. 2002). Yet, in surveys of lentic habitats in Connecticut, species richness of macrophytes was not found to contribute to invasion resistance (Capers et al. 2007), and in fact, invasive Parrotfeather (*Myriophyllum aquaticum*) was more abundant in communities with greater macrophyte diversity in the Chehalis River in southwest Washington state (Kuehne et al. 2016).

Based on our results, in the Upper Great Lakes region, the more species rich habitats may be more susceptible to invasion. Furthermore, while Capers et al (2007) observed that greater densities of native macrophytes were more resistant to invasive species, this did not apply to our sites. Eurasian watermilfoil was more abundant in the more species rich and abundant native macrophyte communities within this region. However, at the most invaded site (i.e. Portage) there was a notable decline in native macrophyte abundance. This suggests that further spread of Eurasian watermilfoil could suppress native macrophyte growth. The herbicide application was effective at controlling Eurasian watermilfoil. Yet, late season emergence of Eurasian watermilfoil was detected

in some of our post-treatment surveys. Boylen et al. (1996) observed that no one management approach completely eliminated Eurasian watermilfoil, and advocated for the use of multiple combined approaches. Therefore, further management efforts in this region should incorporate multiple techniques for better long-term management.

Chapter 2: Associations for Eurasian watermilfoil with fish and invertebrate communities

2.1 Background and Hypotheses

A primary objective of this study was to identify if and how aquatic faunal communities vary across a gradient of native macrophyte abundance and Eurasian watermilfoil (*Myriophyllum spicatum*) invasion. The nearshore areas of lakes that support macrophytes, known as the littoral zone, serve as important habitat for fish and invertebrates (see reviews by Diehl and Kornijow 1998, Winfield 2004, and Valley et al. 2004). These vegetated habitats support more abundant and taxa rich fish and invertebrate communities relative to non-vegetated sites (Randall et al. 1996, Weaver et al. 1997, Duffy and Baltz 1998, Theel et al. 2008, Collingsworth and Kohler 2010). While invertebrate abundance has been found to increase along a gradient of increasing macrophyte abundance (Crowder and Cooper 1982, Beckett et al. 1992, Savino et al. 1992), the relationship between macrophyte density and fish abundance tends to vary depending on the size class of fish. Small fish often utilize the more densely vegetated habitats as refuge from predators (Werner et al. 1983, Savino and Stein 1989a, Massicotte et al. 2015), while larger size classes occupy more moderately vegetated sites due to greater foraging efficiency (Crowder and Cooper 1982, Savino and Stein 1989a, Savino and Stein 1989b, Valley and Bremigan 2002a, Collingsworth and Kohler 2010).

The establishment of invasive Eurasian watermilfoil in littoral zones can alter local communities by forming dense canopies at the water's surface, reducing native macrophyte abundance (Madsen et al. 1991, Boylen et al. 1999, Webb et al. 2016) and richness (Boylen et al. 1996, Boylen et al. 1999, Madsen et al. 1991, Parsons et al. 2009, Wersal et al. 2010).

This can ultimately influence littoral faunal communities, depending on the native macrophyte assemblage of the recipient ecosystem. Eurasian watermilfoil has a complex architecture composed of many finely dissected leaves (Thomaz and da Cunha 2010) and is associated with greater surface area (Sher-Kaul 1995). This complexity has been found to support a greater abundance of invertebrates relative to less-dissected native macrophytes, including American pondweed (*Potamogeton nodosus*) (Collingsworth and Kohler 2010), water stargrass (*Heteranthera dubia*) (Balci and Kennedy 2003), Canadian waterweed (*Elodea canadensis*), and sago pondweed (*P. pectinatus*) (Krecker 1939). However, variation in invertebrate abundance can be less driven by vegetation type than by the availability of epiphytic algae (Strimaitis and Sheldon 2011, Balci and Kennedy 2003). The greater surface area of Eurasian watermilfoil (Sher-Kaul 1995) can accumulate more epiphytic food sources for invertebrates (Cattaneo and Kalff 1980, Balci and Kennedy 2003), and provide refuge from predators (Gilinsky 1984, Valinoti et al. 2011). When compared to the similarly complex native species variable watermilfoil (*Myriophyllum heterophyllum*) and alternate watermilfoil (*M. alterniflorum*) in southern Quebec and upstate New York, Eurasian watermilfoil supported less abundant and less diverse invertebrate communities relative to native watermilfoils (i.e. *M. sibericum* and *M. alterniflorum*) (Wilson and Ricciardi 2009). Yet, in inland lakes of southern Michigan, dense cover of Eurasian watermilfoil was negatively correlated to invertebrate biomass and taxa richness relative to plant communities composed of other dissected native macrophytes (Cheruvelil et al. 2002), but invertebrate taxa richness was similar between Eurasian watermilfoil and the broad-leaved claspingleaf pondweed (*Potamogeton richardsonii*) in Lake Erie (Phillips 2008).

Most studies that address the associations of Eurasian watermilfoil and the fish community are focused on common littoral species, specifically sunfish (e.g. Unmuth et al. 1999, Collingsworth and Kohler 2010, Webb et al. 2016) and largemouth bass (e.g. Dibble and Harrel 1997, Unmuth et al. 1999, Valley and Bremigan 2002a, Valley and Bremigan 2002b, Bremigan et al. 2005), likely because these species were the most abundant. Yet, in Minnesota, following annual herbicide application and subsequent decline in Eurasian watermilfoil, overall fish abundance and biomass remained similar over

a three year period (Kovalenko et al. 2010), but total macrophyte abundance and complexity also exhibited no significant change due to the early season treatment efforts when most native macrophytes were dormant. Where total macrophyte abundance decreased significantly due to eradication of Eurasian watermilfoil, a reduction in abundance of small fish size classes was detected (Parsons et al. 2009). Small fish have been found to be more abundant in habitats that are more structurally complex (Troutman et al. 2007) and densely vegetated (Randall et al. 1996), which provide these fish with refuge from predators (Johnson et al. 1988, Collingsworth and Kohler 2010). But, dense vegetation can also negatively affect fish foraging behavior by serving as a visual barrier (Savino and Stein 1982), increasing search times (Valley and Bremigan 2002a) and decreasing prey encounters and consumption rates (Crowder and Cooper 1982, Miranda and Pugh 1997). Thus, exceptionally thick vegetation ultimately can lead to stunted growth of the predators despite greater prey abundances (Crowder and Cooper 1982, Unmuth et al. 1999, Bremigan et al. 2005, Parsons et al. 2009). In the southern United States, Eurasian watermilfoil was also found to support less diverse and species rich fish communities relative to native *V. americana* (Duffy and Baltz 1998), a common species in the Keweenaw Waterway (Juneau et al. in prep., personal observation). Additionally, reduced fish species richness has also been observed in habitats dominated by other invasive macrophytes (Arrivillaga 2003 with *Hydrilla verticillata*).

Our study area, the Keweenaw Waterway of Michigan's Upper Peninsula, connects with Lake Superior on each end, experiencing substantial mixing with the cold Lake Superior waters (Figure 1.1). While formation of dense Eurasian watermilfoil canopies at the water's surface has been observed in southern Michigan (e.g. Cheruvilil et al. 2001) and in inland lakes at northern latitudes (e.g. Getsinger et al. 1997 in northern Washington State), Eurasian watermilfoil in the Keweenaw Waterway appears is patchily distributed and integrates more into the native macrophyte community (Juneau et al. in Prep., Huckins et al. unpublished data). Nevertheless, the increased structural complexity of Eurasian watermilfoil may still have a significant impact on the native littoral faunal communities.

In this study, we hypothesized that: 1) sites of low macrophyte abundance would support fewer fish than more vegetated sites. We also hypothesized that 2) fish abundance

and biomass would be greatest at moderate levels of Eurasian watermilfoil invasion as smaller size classes of fish gain refuge from predators and thus are more abundant within dense vegetation, but larger fish occupy moderately vegetated habitats for optimal foraging efficiency and productivity. Furthermore, we hypothesized that 3) fish species richness and diversity would be lower in sites with more Eurasian watermilfoil abundance.

We also hypothesized that 4) invertebrate abundance would be greater at sites with the most abundant Eurasian watermilfoil, and Eurasian watermilfoil would have an additive effect as these sites provide more epiphytic food sources and surface area, but that 5) invertebrate richness and diversity would decrease with increasing invasion.

2.2 Methods

Study Area

We sampled for fish and invertebrates in the littoral zone of 8 sites (Figure 1.2 a-c, Table 1.1) in the Keweenaw Waterway from June through July in 2016. Sampling sites were determined based on macrophyte surveys conducted during the prior summer, and were selected to represent a range of macrophyte abundance and community composition (i.e. natives, Eurasian watermilfoil, and no/sparse vegetation). Eurasian watermilfoil failed to establish at some of these sites in the summer of 2016, leading us to seek out alternative sampling areas and resulting in uneven sampling effort across sites over time.

Two sites, Pike Bay 1 and 2, were treated for Eurasian watermilfoil with herbicide applied by certified application (contracted by Chassell Township, Michigan) on June 22 with granular triclopyr (SePro Renovate OTF), liquid triclopyr (Renovate 3), and granular 2,4-D (SePro Sculpin G). To our knowledge, no other sampling sites received herbicide treatment during this sampling period. Previous research suggests that herbicides do not have significantly negative biological effects on fish or invertebrates when applied at the application rates suggested for macrophyte control (Hiltibran 1967, Hamelink et al. 1986, Kreutzweiser et al. 1994, Relyea 2005), and thus we assumed this to remain true in our study.

Sampling Methods

Fish Sampling: Fyke nets were used to survey fish communities because of their effectiveness at sampling in complex and often turbulent littoral habitats (Hubert et al. 2012, Clark et al. 2007) that are common in this waterway of Lake Superior. When conditions allowed (i.e. where the water was not too deep), three fyke nets were used to capture fish movements along the shore and between inshore and offshore habitats, as suggested by Hubert et al. (2012) (Figure 2.1). Two nets (3x4-foot frames, 3/16-inch mesh, 50-foot lead, 5-foot wings) were situated with leads running parallel to shore and facing each other, and another net (4x5-foot frame, 3/16-inch mesh, 50-foot lead, no wings) was set perpendicular to shore with lead facing into open water. Nets, wings, and leads were anchored to the lake bottom, and buoys were placed in the cod end of each net to provide air pockets for captured air-breathing organisms. Nets were deployed overnight and checked after approximately 24 hours. At the Portage site, the water depth was too deep to accommodate our smaller fyke nets, and therefore, two 4x5-ft nets were set with leads facing each other and running perpendicular to the adjacent bed of emergent reeds. Additionally, early season net arrays had the lead of the larger 4x5-ft net facing into shore, but was rotated 180° beginning on June 17 so that the lead extended into deeper waters (with the exception of the June 23 survey at the North Sturgeon Slough). Initially, fyke net sampling was supplemented with underwater cameras deployed to face the opening of the net and capture a time-lapse series in 5-min intervals. However, this effort was deemed unsuccessful and was discontinued after July 20 due to low fish detections in the images relative to fish observed in the traps. Species, length, and weight were recorded for all captured fish. Small sunfish (≤ 40 mm) that could not be identified to species in the field were labeled as “juvenile sunfish” (approximately 92% of sunfish were ≤ 40 mm, mean length (mm) of approximately 28 ± 4.22), but were most likely pumpkinseed (*Lepomis gibbosus*).

Conductivity, pH, and water temperature were measured approximately 5-10cm below the water’s surface at the time nets were set, as well as when the nets were pulled. At each net, water depth was measured at the center of the throat, and distance to shore was measured as the distance from the center of throat to the shoreline.

Invertebrate Sampling: Invertebrate samples were collected at several points (usually 6 points per site per survey date) at each trap-net site. Samples were collected by making a 1-m linear sweep of a 500-micron mesh D-frame dip net along the lake bottom and through vegetation (when present) to collect both benthic and water column invertebrates (Cheal et al. 1993). Samples were only collected at survey sites in the southern region of the Keweenaw Waterway (i.e. Pike Bay, North Pike, North Slough, South Slough, Portage). Additional pre-treatment invertebrate samples were collected throughout Pike Bay at an array of sites representing the various macrophyte communities observed in the bay (specifically Eurasian watermilfoil, and native coontail and pondweed communities). Fine particles were removed from the sample by rinsing each sample through a 500-micron sieve, and the remaining material was preserved using 100% ethyl alcohol for later analysis. In the laboratory, specimens were sorted under a dissecting scope and identified to the lowest classification possible (Bouchard 2004), typically to family.

Data Analysis Methods

Fish surveys were conducted more often than macrophyte surveys based on the assumption that the fish community would vary at a faster rate relative to the macrophyte community. To identify associations between the macrophyte and fish communities, categorical designations of abundance for Eurasian watermilfoil and native macrophytes were assigned to each fish sampling date based on visual observations and mean abundances from macrophyte surveys (i.e. low, moderate, or high abundance) (Table 2.1). Categorical abundances for the respective macrophyte groups were based on the mean toss rake abundances of Eurasian watermilfoil and the five common native macrophytes. The five common native species were chara (*Chara* sp.), coontail (*Ceratophyllum demersum*), *E. canadensis*, naiad (*Najas* sp.), and *V. americana*, which were detected in $\geq 76\%$ of macrophyte surveys. A “low” macrophyte abundance represented the 25th percentile of relative abundance across surveys, “moderate” represented the next group up to the 50th percentile, and any sites with greater abundances were considered “high” abundance. Categorical abundances of macrophytes at invertebrate sampling points was determined

based on visual observations at that specific sampling point (Table 2.2), and did not necessarily coincide with the categorical abundances of fish surveys that were sampled over a larger spatial scale.

Fish abundance and biomass were analyzed based on the average per net at a site to account for differences in the number of fyke nets set at each site and date. Both fish abundance and fish biomass were highly right-skewed and were log-transformed in order to fit assumptions of normality. When fish length or weight was not recorded (i.e. when a fish was dropped or in windy conditions), these data were estimated based on species length-weight regressions (Table 2.3). For individuals identified as pumpkinseed x bluegill hybrid or juvenile sunfish, length-weight regressions were generated with pumpkinseed and bluegill in combination.

Fish diversity was calculated based on Simpson's Index of Diversity

$$(D = \sum n(n-1)/N(N-1)) \quad \text{eq. 1}$$

where n is the number of individuals within a species and N is the total number of individuals within the sample. Fish abundance, biomass (g), mean total length (mm), mean individual weight (g) (log-transformed), richness (number of unique species detected at a site), and diversity for each site were analyzed relative to the categorical abundances of Eurasian watermilfoil and native macrophytes using two-way factorial ANOVAs, where time represents sampling month (Appendix, Table 1). Due to uneven sampling effort, three-way factorial ANOVAS incorporating month and categorical abundances of native macrophytes and Eurasian watermilfoil) relative to fish abundance or biomass did not yield sufficient degrees of freedom (JMP Pro13). In addition, data for fish abundance, biomass, mean length (mm) , mean weight (g) (log-transformed), species richness, and diversity were averaged per site, and analyzed relative to mean macrophyte species richness (total # of species detected in a survey), Eurasian watermilfoil relative abundance, and native macrophyte relative abundance using Pearson's correlation (Table 2.4).

A nonmetric multidimensional scaling (NMS) ordination was conducted to analyze how fish surveys group across a gradient of categorical Eurasian watermilfoil invasion, and to identify the associated community assemblages within these groupings. The main matrix was the species matrix, representing the mean abundance of each species (# / net) per

survey (Table 2.5). The secondary matrix consisted of the averaged environmental variables (i.e. catch time (the number of hours nets were set, rounded to the nearest quarter hour), conductivity (μS) at time of setting nets and pulling nets, water temperature ($^{\circ}\text{C}$) at set and pull, pH at set and pull, and water depth (m)), as well as the categorical abundances of Eurasian watermilfoil and native macrophytes (Table 2.6). This analysis was performed using Sorensen distance measure, and “slow and thorough” autopilot mode of PC-ORD with 250 runs. A multi-response permutation procedure (MRPP) using Sorensen distance measure was conducted to determine if sites significantly varied relative to categorical abundance of Eurasian watermilfoil.

A sub-sample of invertebrate specimens was analyzed (from 3 sampling points at each site/sampling date), as well as all samples obtained from Pike Bay prior to treatment at representative macrophyte beds outside of our fish survey areas (designated as “Pike Bay”) (Table 2.2). Invertebrate abundances was right-skewed and thus log-transformed to fit normality assumptions. Two-way factorial ANOVAs were conducted to examine taxa richness (# of unique taxa / sample), diversity (Simpson’s Index of Diversity / sample) total invertebrate abundance (# / sampling point), as well as the abundances of benthic macroinvertebrates relative to categorical abundance of each macrophyte type and sampling month. Pearson’s correlation analysis was used to analyze the mean abundances of Eurasian watermilfoil and native macrophytes per site, as well as mean macrophyte species richness, relative to mean monthly invertebrate abundance (# / sampling point), taxa richness (total # of unique taxa at a sampling point), and diversity (Table 2.4).

2.3 Results

Fish Community Structure

Over the course of the summer, we captured a total of 6,253 fish in our nets, representing 22 species, with a total recorded biomass of approximately 282,130 g. The most abundant species was pumpkinseed, which accounted for 29% of the total fish abundance and 36% of the total biomass (g). Unidentified juvenile sunfish (*Lepomis* sp.) were equally abundant, yet made up <1% of the biomass. Bullheads (*Ameiurus* sp.) made up 11% of total fish abundance and accounted for 21.5% of the total fish biomass. While

rock bass (*Ambloplites rupestris*) accounted for just 4% of fish abundance, they made up nearly 11% of the total fish biomass. Collectively, the other 19 species accounted for 23% of abundance and approximately 32% of the biomass.

Overall, fish abundance was similar across the gradients of macrophyte abundance and invasion. Fish abundance did not significantly vary relative to Eurasian watermilfoil relative abundance (ANOVA, $F_{2,29} = 2.24$, $p = 0.12$) (Figure 2.2a), nor native macrophyte relative abundance (ANOVA, $F_{2,29} = 0.68$, $p = 0.52$) (Figure 2.2b). Sampling month also did not explain a significant amount of the variation in fish abundance (ANOVA, $F_{2,29} = 0.95$, $p = 0.40$). For fish biomass, however, there was a significant interaction effect between the relative abundances of Eurasian watermilfoil and native macrophytes (ANOVA, $F_{8,23} = 3.48$, $p = 0.02$) (Figure 2.3a), where habitats of moderate to high native macrophyte relative abundance together with moderate to high Eurasian watermilfoil relative abundance tended to support more fish biomass than habitats of low Eurasian watermilfoil invasion. Yet, habitats of high invasion and high native macrophyte relative abundance generally supported less biomass of fish in comparison to the more moderately invaded and vegetated habitats. Furthermore, on average, fish biomass decreased over sampling month (Figure 2.3b), although this was only marginally non-significant (ANOVA, $F_{2,29} = 2.5$, $p = 0.10$). This indicates that the moderately vegetated habitats with more Eurasian watermilfoil are supporting larger size classes of fish.

Overall, the more vegetated and invaded habitats supported greater fish abundance and biomass, and the more species-rich macrophyte communities also supported more abundant fish communities. While, our correlation analysis did not identify significant relationships of mean fish abundance and biomass per site with the mean relative abundance of Eurasian watermilfoil ($r = 0.31$, $p = 0.50$ and $r = -0.25$, $p = 0.59$, respectively) (Figure 2.4a-b), both fish abundance and biomass exhibited a general unimodal relationship with Eurasian watermilfoil relative abundance. However, this relationship was largely driven by one site (i.e. Portage) that was determined to be an outlier. When this site was excluded from analysis, mean fish abundance exhibited a positive linear correlation with mean Eurasian watermilfoil relative abundance ($r = 0.92$, $p = 0.01$), as did mean fish biomass ($r = 0.83$, $p = 0.04$). This site was not an outlier in the analysis of mean fish

abundance and biomass with mean native macrophyte relative abundance. While mean fish abundance had a positive correlation with mean native macrophyte relative abundance ($r = 0.92$, $p = 0.003$) (Figure 2.5c), there was no significant relationship between mean fish biomass and mean native macrophyte relative abundance ($r = 0.54$, $p = 0.22$) (Figure 2.5d). Furthermore, the most macrophyte species rich habitats supported the most abundant fish communities, on average ($r = 0.85$, $p = 0.02$) (Figure 2.4e). The greater mean macrophyte species rich habitats also generally supported greater fish biomass, although this was only marginally non-significant ($r = 0.74$, $p = 0.06$) (Figure 2.5f). Overall, at most of our sites, those that supported more Eurasian watermilfoil also supported more fish relative to sites where Eurasian watermilfoil was not present or low in abundance. Furthermore, those sites with more native macrophytes supported more abundant fish communities relative to sites of low vegetation.

Our early season surveys generally supported larger size classes of fish, coinciding with our observations of spawning sunfish in June and juvenile recruitment late in the sampling season. Fish length and weight both varied significantly over sampling month (ANOVA, $F_{2,29} = 11.41$, $p = 0.0002$ and $F_{2,29} = 7.14$, $p = 0.003$, respectively) (Figure 2.6a, Figure 2.7a). Fish length also varied significantly relative native macrophyte relative abundance (ANOVA, $F_{2,29} = 10.03$, $p = 0.0005$) (Figure 2.6c), as did fish weight (ANOVA, $F_{2,29} = 9.62$, $p = 0.0006$), where the sparsely vegetated habitats supported greater fish lengths and weights relative to moderate or high vegetated sites. Fish length did not significantly vary relative to Eurasian watermilfoil (ANOVA, $F_{2,29} = 0.22$, $p = 0.80$) (Figure 2.6b), nor did fish weight (ANOVA, $F_{2,29} = 1.14$, $p = 0.33$) (Figure 2.7b).

In general, the more invaded sites supported smaller size classes of fish, while relative to native macrophyte habitats, the more moderately vegetated habitats supported the largest size classes of fish. Based on correlation analysis, mean fish length was significantly and negatively related to mean native macrophyte relative abundance ($r = -0.80$, $p = 0.03$) (Figure 2.8c), and exhibited a marginally non-significant negative relationship with mean Eurasian watermilfoil relative abundance ($r = -0.71$, $p = 0.07$) (Figure 2.8a). Yet, mean fish weight was not correlated to native macrophyte relative abundance ($r = -0.66$, $p = 0.11$) (Figure 2.8d) or Eurasian watermilfoil relative abundance

($r = -0.43$, $p = 0.34$) (Figure 2.8b). Yet, both mean fish length and weight both exhibited a general unimodal relationship with mean native macrophyte relative abundance, where the moderately vegetated habitats appeared to support the largest size classes of fish. Relative to Eurasian watermilfoil, mean fish length and weight tended to be greatest at habitats of low invasion. Mean macrophyte species richness did not explain a significant amount of variation in mean fish length ($r = -0.48$, $p = 0.28$) or mean fish weight ($r = -0.41$, $p = 0.36$).

There was a marginally non-significant interaction between the relative abundances of Eurasian watermilfoil and native macrophytes on fish species richness (ANOVA, $F_{8,23} = 2.33$, $p = 0.09$) (Figure 2.9), where the more vegetated habitats tended to support less species rich fish communities. On average, habitats of low native macrophytes and moderate Eurasian watermilfoil relative abundance supported the most species rich fish communities, but generally decreased with increased invasion and native macrophyte abundance. Species richness did not vary significantly over sampling month (ANOVA, $F_{2,29} = 1.55$, $p = 0.23$). Fish diversity, however, did not vary relative to month (ANOVA, $F_{2,29} = 2.15$, $p = 0.14$), Eurasian watermilfoil relative abundance (ANOVA, $F_{2,29} = 2.47$, $p = 0.10$), or native macrophyte relative abundance (ANOVA, $F_{2,29} = 1.19$, $p = 0.32$). Correlation analysis of mean fish species richness per site identified no significant correlation with either mean Eurasian watermilfoil relative abundance ($r = -0.38$, $p = 0.52$) or native macrophyte relative abundance ($r = -0.23$, $p = 0.62$). Mean fish diversity also exhibited no significant relationship with mean relative abundances of Eurasian watermilfoil ($r = 0.51$, $p = 0.24$) or native macrophytes ($r = 0.39$, $p = 0.39$). Mean macrophyte species richness also did not explain a significant amount of the variation in mean fish species richness ($r = -0.36$, $p = 0.43$) or diversity ($r = 0.29$, $p = 0.53$).

Fish Community Assemblages

The NMS ordination produced a two-dimensional solution (final stress = 11.06, instability < 0.0001, number of iterations = 64) that explained a cumulative 84% of the variation. Axis 1 explained most of the variation (65%), while axis 2 explained 18.9% of the variation. The environmental variable that was most strongly correlated with axis 1 was the conductivity of the water measured at the time when nets were pulled ($r = -0.439$)

(Table 2.7), as well as pH at the time the nets were pulled ($r = -0.338$) and total catch time (in hours) ($r = -0.302$).

Relative to categorical abundance of Eurasian watermilfoil, the macrophyte surveys (across sites and sampling dates) separated across a gradient of Eurasian watermilfoil abundance (Figure 2.10, Table 2.8). These groupings were determined to be significantly different based on the results from the MRPP ($A = 0.07$, $p = 0.0002$). More specifically, sites of high abundance of Eurasian watermilfoil were generally more positively associated with axis 1, while low invasion sites typically had a negative association with axis 1. This indicates that habitats along a gradient of Eurasian watermilfoil invasion support disparate fish community assemblages.

The fish species that also exhibited strong positive correlations with axis 1 were black crappie (*Pomoxis nigromaculatus*) ($r = 0.502$), bluegill (*Lepomis macrochirus*) ($r = 0.227$), bullhead (*Ameiurus* sp.) ($r = 0.523$), golden shiner (*Notemigonus crysoleucas*) ($r = 0.335$), largemouth bass (*Micropterus salmoides*) ($r = 0.317$), pumpkinseed (*Lepomis gibbosus*) ($r = 0.565$), and juvenile sunfish ($r = 0.488$) (Figure 2.11, Table 2.9). This suggests that these species were more abundant in habitats with more Eurasian watermilfoil. The fish species that were associated with the least invaded habitats were blacknose shiner (*Notropis heterolepis*) ($r = -0.310$), Eurasian ruffe (*Gymnocephalus cernua*) ($r = -0.234$), johnny darter (*Boleosoma nigrum*) ($r = -0.458$), rock bass (*Ambloplites rupestris*) ($r = -0.352$), sculpin (*Cottus* sp.) ($r = -0.336$), smallmouth bass (*Micropterus dolomieu*) ($r = -0.349$), spottail shiner (*Notropis hudsonicus*) ($r = -0.411$), and troutperch (*Percopsis omiscomaycus*) ($r = -0.246$).

Invertebrate Community Structure

Of the samples that were sorted and identified, we documented a total of 15,484 invertebrates, representing a 21 taxonomic orders. Overall, the most abundant taxa was Order Cladocera (specifically, the Families Bosminidae, Chydoridae, Daphniidae, Onychopoda, Sididae and Superfamily Macrothricoidea), which accounted for nearly 60% of the total invertebrate abundance. Of the benthic macroinvertebrates, amphipods were most abundant, making up 13% of the total invertebrate abundance, and nearly 36% of the

macroinvertebrate abundance. Gastropods and oligochaetes accounted for approximately 18% and 11% of the macroinvertebrate abundance, respectively. Other taxa contributed to no more than 6% of the total invertebrate abundance, and 9% of the macroinvertebrate abundance.

There was a significant interaction between site and sampling month on total invertebrate abundance (ANOVA, $F_{11,31} = 3.32$, $p = 0.03$). While this was expected based on the gradient of macrophyte abundance and temporal trends of emergence in certain invertebrate taxa, this interaction is likely confounded by the uneven sampling over sampling month at representative macrophyte habitats. Yet, on average, total invertebrate abundance tended to be greater in August than in June. Total invertebrate abundance varied relative to both Eurasian watermilfoil (ANOVA, $F_{2,40} = 4.01$, $p = 0.03$) (Figure 2.12a) and native macrophyte abundance (ANOVA, $F_{2,40} = 25.87$, $p < 0.0001$) (Figure 2.12b), where the most vegetated or invaded habitats tended to support more invertebrates. This was also supported by our correlation analysis, mean total abundance of invertebrates per site was positively related to mean Eurasian watermilfoil relative abundance ($r = 0.80$, $p = 0.06$) (Figure 2.13a), although marginally non-significant, and was significantly correlated to mean native macrophyte abundance ($r = 0.92$, $p = 0.01$) (Figure 2.13b).

Benthic macroinvertebrate abundance varied between sites (ANOVA, $F_{6,36} = 3.43$, $p = 0.01$), as expected based on the gradient of macrophyte abundance represented across sites. Benthic abundance also varied between sampling months (ANOVA, $F_{2,40} = 4.39$, $p = 0.02$) with June and August supporting similar abundances of benthic macroinvertebrates, and the lowest abundance occurring in July. However, this temporal variation is likely confounded by uneven sampling over time. There was a marginally non-significant interaction between the abundances of native macrophyte abundance and Eurasian watermilfoil on benthic macroinvertebrate abundance (ANOVA, $F_{7,35} = 2.25$, $p = 0.10$) (Figure 2.14). Moderate to high abundances of native macrophytes tended to support similar abundances of benthic macroinvertebrate, regardless of Eurasian watermilfoil abundance. Mean benthic macroinvertebrate abundance per site was not related to mean Eurasian watermilfoil relative abundance ($r = 0.63$, $p = 0.18$) (Figure 2.15a), based on correlation analysis, but increased significantly along with mean native macrophyte

relative abundance ($r = 0.99$, $p = 0.0001$) (Figure 2.15b). These results suggest that despite the greater surface area and habitat complexity provided by Eurasian watermilfoil, benthic macroinvertebrate abundance was more driven by abundance of native macrophytes.

We had hypothesized that native macrophyte habitats would support the most taxa rich and diverse invertebrate communities, and that Eurasian watermilfoil invasion would reduce invertebrate taxa richness and diversity. Variation in invertebrate taxa richness was significantly related to Eurasian watermilfoil abundance (ANOVA, $F_{2,40} = 7.14$, $p = 0.002$) (Figure 2.16a), as well as native macrophyte abundance (ANOVA, $F_{2,40} = 9.35$, $p = 0.0005$) (Figure 2.16b), where invertebrate taxa richness tended to be greatest at the more vegetated habitats, including those with high Eurasian watermilfoil invasion. While invertebrate diversity did not vary relative to Eurasian watermilfoil abundance (ANOVA, $F_{2,40} = 0.25$, $p = 0.78$) (Figure 2.17a), native macrophyte abundance did explain a significant amount of the variation in invertebrate diversity (ANOVA, $F_{2,40} = 8.75$, $p = 0.0007$) (Figure 2.17b).

The mean invertebrate taxa richness (total # of unique species per survey) was not correlated with mean Eurasian watermilfoil relative abundance ($r = 0.66$, $p = 0.15$) (Figure 2.18a), based on our correlation analysis, but did exhibit a general unimodal relationship where moderately invaded habitats supported the most taxa rich invertebrate communities. Mean invertebrate diversity (per survey) also was not correlated to mean Eurasian watermilfoil relative abundance ($r = 0.43$, $p = 0.40$) (Figure 2.18b). Mean taxa richness was positively correlated with mean native macrophyte relative abundance ($r = 0.95$, $p = 0.003$) (Figure 2.18c), but mean invertebrate diversity was not ($r = 0.57$, $p = 0.24$) (Figure 2.18d). Macrophyte species richness did not explain a significant amount of variation in invertebrate taxa richness ($r = 0.57$, $p = 0.24$) or diversity ($r = 0.26$, $p = 0.62$).

2.4 Discussion

While other studies have found that Eurasian watermilfoil did not significantly impact fish abundance (e.g. Pothoven et al. 1999, Unmuth et al. 1999, Kovalenko et al. 2010), we hypothesized that moderate levels of invasion in the Keweenaw Waterway would support more fish and thus greater fish biomass. These predictions were based on previous research that found that habitats of dense macrophytes would provide refuge to

smaller size classes of fish (Werner et al. 1983, Savino and Stein 1989a, Massicotte et al. 2015), but more and larger fish would occupy moderately invaded habitats for optimal foraging efficiency and productivity (Crowder and Cooper 1982, Savino and Stein 1989a, Savino and Stein 1989b, Valley and Bremigan 2002a, Collingsworth and Kohler 2010). This was generally supported by our findings, where fish abundance tended to increase along with Eurasian watermilfoil invasion.

We also had predicted that habitats dominated by native macrophytes would support the most species rich and diverse fish communities, while more invaded habitats would decrease fish richness and diversity, as has been observed with other invasive macrophytes (Arrivillaga 2002). In our study, while fish species richness and diversity tended to be greater at habitats of greater native macrophyte abundance, as well as the more invaded sites, neither macrophyte type significantly explained variation in richness or diversity per month. Overall, richness and diversity, on average, varied relatively little between sites. The lack of a significant correlation between Eurasian watermilfoil and fish richness and diversity could be attributed to the integration of Eurasian watermilfoil with the native macrophyte community. Yet, similar results have been observed in central Minnesota following treatment and subsequent reduction in Eurasian watermilfoil (Kovalenko et al. 2010), as well as with invasive *H. verticillata* (Barrientos and Allen 2008, Cunha et al. 2011), and thus could be explained by the frequent movements of fish species in and out of the littoral zone (Hall and Werner 1977).

However, while fish abundance, biomass, richness, and diversity tended to increase with increasing invasion, the site where Eurasian watermilfoil was most abundant (i.e. Portage) supported a fish community that was less abundant, rich, and diverse. This suggests that in the Keeweenaw Waterway, at lower invaded sites where Eurasian watermilfoil integrates more with the native macrophyte community, this invasive macrophyte may provide useful habitat for fish. Yet, continued spread of Eurasian watermilfoil may have detrimental impacts on the littoral fish community if left unmanaged.

Additionally, we had hypothesized that the more moderately vegetated and invaded habitats would support larger size classes of fish due to optimal foraging efficiency, and

that smaller size classes would occupy the more densely vegetated sites as refuge from predators. For Eurasian watermilfoil, this was generally supported by our findings, where fish mean fish length and weight tended to be greatest at moderately invaded habitats. However, where Eurasian watermilfoil was most abundant, both mean length and weight were notably reduced. Thus, further spread of Eurasian watermilfoil could lead to a shift in fish community size structure towards smaller, more stunted individuals. Relative to native macrophytes, mean fish length decreased significantly along an increasing gradient of macrophyte abundance, where larger fish generally occupied the least vegetated sites. However, this is likely skewed by the spawning patterns of larger sunfish, where adults were observed spawning in sparsely vegetated nearshore habitats early in the season (namely, Pike Bay 2).

We also had hypothesized that more vegetated habitats would support a greater abundance of invertebrates. Based on our results, both Eurasian watermilfoil and native macrophyte abundance had a positive correlation with invertebrate abundance. While it was expected that the greater surface area and dissected structure of Eurasian watermilfoil (Sher-Kaul 1995) would support more invertebrates relative to the generally more abundant simple-structured native macrophytes in the Keweenaw Waterway (e.g. *V. americana*, *Najas* sp., *E. canadensis*), native macrophyte abundance explained more of the variation in invertebrate abundance. This could also be attributed to a more favorable chemical environment, as Eurasian watermilfoil can have lethal allelopathic effects on certain invertebrates (Linden and Lehtiniemi 2005). Furthermore, *C. demersum*, has a complex architecture relative to most of our other common native macrophytes, and thus may have provided habitat to support more invertebrates. Benthic macroinvertebrate abundance tended to be similar along moderate to high abundances of native macrophytes, regardless of Eurasian watermilfoil invasion. Yet, habitats where native macrophytes were sparse generally supported the less macroinvertebrates, on average. Except, at sites where native macrophytes were sparse and Eurasian watermilfoil was abundant, Eurasian watermilfoil appeared to provide valuable habitat by supporting more macroinvertebrates.

Invertebrate taxa richness and diversity increased along with native macrophyte abundance, as we had hypothesized. Yet, in contrast to our predictions, taxa richness also

increased along with Eurasian watermilfoil invasion, but had no significant correlation with diversity. This suggests that at the levels of invasion observed in the Keweenaw Waterway, Eurasian watermilfoil does not appear to have a negative impact on invertebrate taxa richness or diversity.

Based on our research, it appears that the integrated communities of native macrophytes and Eurasian watermilfoil provide habitat to support more fish and invertebrates. However, without continued treatment for Eurasian watermilfoil, this invasive macrophyte may reduce fish abundance and potentially stunt fish growth as the dense habitats would reduce foraging efficiency, despite greater abundance of food sources. Furthermore, while Eurasian watermilfoil currently integrates into the native community in the Keweenaw Waterway, the continual rise of Lake Superior water temperatures (Austin and Colman 2007) could create stressful conditions for the cold-adapted native macrophytes but provide more more favorable water conditions for the highly thermal tolerant Eurasian watermilfoil (Madsen and Smith 1997).

References

- Arrivillaga, A. 2003. Estudio de impacto ambiental para la aplicación de medidas de control y mitigación de la especie invasora *Hydrilla verticillata* en Izabel. Ciudad de Guatemala, Guatemala, Ministerio de Ambiente y Recursos Naturales, pp. 120.
- Austin, J.A., and S.M. Coleman. 2007. Lake Superior summer water temperatures are increasing more rapidly than regional air temperatures: A positive ice-albedo feedback. *Geophysical Research Letters* **34**(6), L06604.
- Balci, P., and J.H. Kennedy. 2003. Comparison of chironomids and other macroinvertebrates associated with *Myriophyllum spicatum* and *Heteranthera dubia*. *Journal of Freshwater Ecology* **18**(2):235-247.
- Beckett, D.C., T.P. Aartila, and A.C. Miller. 1992. Contrasts in density of benthic invertebrates between macrophyte beds and open littoral patches in Eau Galle Lake, Wisconsin. *American Midland Naturalist* **127**(1):77-90.
- Bouchard Jr., R.W. 2004. Guide to Aquatic Macroinvertebrates of the Upper Midwest. Water Research Center University of Minnesota, St. Paul, MN 208.
- Bowes, G., A.S. Holaday, and W.T. Haller. 1979. Seasonal variation in the biomass, tuber density, and photosynthetic metabolism of hydrilla in three Florida lakes. *Journal of Aquatic Plant Management* **17**:61-65.
- Boyle, T.P. 1980. Effects of the aquatic herbicide 2,4-D DMA on the ecology of experimental ponds. *Environmental Pollution* **21**: 35-49.
- Boylen, C.W., L.W. Eichler, and J.W. Sutherland. 1996. Physical control of Eurasian watermilfoil in an oligotrophic lake. *Hydrobiologia* **340**:213-218.
- Boylen, C.W., L.W. Eichler, and J.D. Madsen. 1999. Loss of native aquatic plant species in a community dominated by Eurasian watermilfoil. *Hydrobiologia* **415**:207-211.
- Bremigan, M.T., S.M. Hanson, P.A. Soranno, K.S. Cheruvilil, and R.D. Valley. 2005. Aquatic vegetation, largemouth bass and water quality responses to low-dose fluridone two years post treatment. *Journal of Aquatic Plant Management* **43**:65-75.
- Capers, R.S. R. Selsky, G.J. Bugbee, and J.C. White. 2007. Aquatic plant community invisibility and scale-dependent patterns in native and invasive species-richness. *Ecology* **88**(12):3135-3143.
- Case, T.J. 1990. Invasion resistance arises in strongly interacting species-rich model competition communities. *Proceedings of the National Academy of Sciences* **87**:9610-9614.

Cason, C., and B.A. Roost. 2011. Species selectivity of granular 2,4-D herbicide when used to control Eurasian watermilfoil (*Myriophyllum spicatum*) in Wisconsin lakes. *Invasive Plant Science and Management* **4**(2):251-259.

Cattaneo, A., and J. Kalff. 1980. The relative contribution of aquatic macrophytes and their epiphytes to the production of macrophyte beds. *Limnology and Oceanography* **25**(2): 280-289.

Cattaneo, A., G. Galanti, S. Gentinetta, and S. Romo. 1998. Epiphytic algae and macroinvertebrates on submerged and floating-leaved macrophytes in an Italian Lake. *Freshwater Biology* **39**:725-740.

Cheal, F., J.A. Davis, J.E. Growns, J.S. Bradley, and F.H. Whittles. 1993. The influence of sampling method on the classification of wetland macroinvertebrate communities. *Hydrobiologia* **257**:47-56.

Cheruvilil, K.S., P.A. Soranno, and R.D. Serbin. 2000. Macroinvertebrates associated with submerged macrophytes: sample size and power to detect effects. *Hydrobiologia* **441**:133-139.

Cheruvilil, K.S., P.A. Soranno, and J.D. Madsen. 2001. Epiphytic macroinvertebrates along a gradient of Eurasian watermilfoil cover. *Journal of Aquatic Plant Management* **39**:67-72.

Cheruvilil, K.S., P.A. Soranno, J.D. Madsen, and M.J. Roberson. 2002. Plant architecture and epiphytic macroinvertebrate communities: the role of an exotic dissected macrophyte. *Journal of North American Benthological Society* **21**(2):261-277.

Cheruvilil, K.S., N.A. Nate, P.A. Soranno, and M.T. Bremigan. 2005. Lack of a unimodal relationship between fish growth and macrophyte cover in 45 north temperate lakes. *Archiv fur Hydrobiologie* **164**(2):193-215.

Chick, J.H., and C.C. McIvor. 1994. Patterns in the abundance and composition of fishes among beds of different macrophytes: viewing a littoral zone as a landscape. *Canadian Journal of Fisheries and Aquatic Sciences* **51**:2873-2882.

Collingsworth, P.D., and C.C. Kohler. 2010. Abundance and habitat use of juvenile sunfish among different macrophyte stands. *Lake and Reservoir Management* **26**:35-42.

Crowder, L.B., and W.E. Cooper. 1982. Habitat structural complexity and the interaction between bluegills and their prey. *Ecology* **63**:1802-1813.

Dibble, E.D., and S.L. Harrel. 1997. Largemouth bass diets in two aquatic plant communities. *Journal of Aquatic Plant Management* **35**:74-78.

Dibble, E.D., K.J. Killgore, and G.O. Dick. 1996. Measurement of plant architecture in seven aquatic plants. *Journal of Freshwater Ecology* **11**(3):311-318.

Diehl, S., and R. Kornijów. 1998. Influence of submerged macrophytes on trophic interactions among fish and macroinvertebrates. In: *The Structuring Role of Submerged Macrophytes in Lakes* (Eds E. Jeppesen, Ma. Søndergaard, Mo. Søndergaard and K. Christoffersen), pp. 24-26. Springer Verlag, New York.

Duffy, K.C., and D.M. Baltz. 1998. Comparison of fish assemblages associated with native and exotic submerged macrophytes in Lake Pontchartrain estuary, USA. *Journal of Experimental Marine Biology and Ecology* **223**:199-221.

Dvořák, J., and E.P.H. Best. 1982. Macro-invertebrate communities associated with the macrophytes of Lake Vechten: structural and functional relationships. *Hydrobiologia* **95**:115-126.

EDDMapS. 2017. Early Detection and Distribution Mapping System. The University of Georgia – Center for Invasive Species and Ecosystem Health. Available online at <http://www.eddmaps.org/>.

Elton, C. 1958. *The ecology of invasions by plants and animals*. Methuen, London, UK.

George, E.L., and W.F. Hadley. 1979. Food and habitat partitioning between rock bass (*Ambloplites rupestris*) and smallmouth bass (*Micropterus dolomieu*) young of the year. *Transactions of the American Fisheries Society* **108**(3):253-261.

Getsinger, K.D., E.G. Turner, J.D. Madsen, and M.D. Netherland. 1997. Restoring native vegetation in a Eurasian water milfoil-dominated plant community using the herbicide triclopyr. *Regulated Rivers: Research and Management* **13**:357-375.

Gilinsky, E. 1984. Fish predation and spatial heterogeneity in determining benthic community structure. *Ecology* **65**(2):455-468.

Grenouillet, G., and D. Pont. 2001. Juvenile fishes in macrophyte beds: influence of food resources, habitat structure and body size. *Journal of Fish Biology* **59**(4):939-959.

Hall, D.J., and E.E. Werner. 1977. Seasonal distribution and abundance of fishes in the littoral zone of a Michigan lake. *Transactions of the American Fisheries Society* **106**(6):545-555.

Hamelink, J.L., D.R. Buckler, F.L. Mayer, D.U. Palawski, and H.O. Sanders. 1986. Toxicity of fluridone to aquatic invertebrates and fish. *Environmental Toxicology and Chemistry* **5**(1):87-94.

- Hiltibran, R.C. 1967. Effects of some herbicides on fertilized fish eggs and fry. *Transactions of the American Fisheries Society* **96**(4):414-416.
- Hubert, W.A., K.L. Pope, and J.M. Dettmers. 2012. Passive capture techniques. Pages 223-265 in A.V. Zale, D.L. Parrish, and T.M. Sutton, editors. *Fisheries techniques*, 3rd edition. American Fisheries Society, Bethesda, Maryland.
- Huckins, C.J.F. 1997. Linkages between morphology, feeding performance, diet, and competitive ability of molluscivorous sunfish. *Ecology* **78**: 2401-2414.
- Huckins, C. J et al. http://www.mtri.org/eurasian_watermilfoil.html
- Johnson, D.L., R.A. Beaumier, and W.E. Lynch Jr. 1988. Selection of habitat structure interstice size by bluegills and largemouth bass in ponds. *Transactions of the American Fisheries Society* **117**:171-179.
- Kennedy, T.A., S. Naeem, K.M. Howe, J.M.H. Knops, D. Tilman, and P. Reich. 2002. Biodiversity as a barrier to ecological invasion. *Nature* **417**:636-638.
- Kenow, K.P., J.E. Lyon, R.K. Hines, and A. Elfessi. 2007. Estimating biomass of submersed vegetation using a rake sampling technique. *Hydrobiologia* **575**:447-454.
- Kirby, L.J., and N.H. Ringler. 2015. Associations of epiphytic macroinvertebrates within four assemblages of submerged aquatic vegetation in a recovering urban lake. *Northeastern Naturalist* **22**(4): 672-689.
- Knops, J.M.H., J.R. Griffin, and A.C. Royalty. 1995. Introduced and native plants of the Hastings reservation central coastal California: a comparison. *Conservation Biology* **71**:115-123.
- Kovalenko, K.E., E.D. Dibble, and J.G. Slade. 2010. Community effects of invasive macrophyte control: role of invasive plant abundance and habitat complexity. *Journal of Applied Ecology* **47**:318-328.
- Krecker, F.H. 1939. A comparative study of the animal population of certain submerged aquatic plants. *Ecology* **20**(4):553-562.
- Kreutzweiser, D.P., S.B. Holmes, and D.C. Eichenberg. 1994. Influence of exposure duration on the toxicity of triclopyr ester to fish and aquatic insects. *Archives of Environmental Contamination and Toxicology* **26**:124-129.
- Kuehne, L.M., J.D. Olden, and E.S. Rubenson. 2016. Multi-trophic impacts of invasive aquatic plant. *Freshwater Biology* **61**:1846-1861.

Lillie, R.A., and J. Budd. 1992. Habitat architecture of *Myriophyllum spicatum* L. as an index to habitat quality for fish and macroinvertebrates. *Journal of Freshwater Ecology* **7**:113-125.

Lindén, E., and M. Lehtiniemi. 2005. The lethal and sublethal effects of the aquatic macrophyte *Myriophyllum spicatum* on Baltic littoral planktivores. *Limnology and Oceanography* **50**(2):405-411.

Lonsdale, W.M. 1999. Global patterns of plant invasions and the concept of invisibility. *Ecology* **80**:1522-1536.

MacArthur, R.H., and E.O. Wilson. 1967. *The theory of island biogeography*. Princeton University Press, Princeton, New Jersey, USA.

Madsen, J.D. 1999. Point intercept and line intercept methods for aquatic plant management. APCRP Technical Notes Collection (TN APCRP-M1-02). U.S. Army Engineer Research and Development Center, Vicksburg, MS.

Madsen, J.D. 2005. Eurasian watermilfoil invasions and management across the United States. *The Journal of Marine Education* **21**(2):21-26.

Madsen, J.D., and D.H. Smith. 1997. Vegetative spread of Eurasian watermilfoil colonies. *Journal of Aquatic Plant Management* **35**:63-68.

Madsen, J.D., J.W. Sutherland, J.A. Bloomfield, L.W. Eichler, and C.W. Boylen. 1991. The decline of native vegetation under dense Eurasian watermilfoil canopies. *Journal of Aquatic Plant Management* **29**:94-99.

Madsen, J.D., K.D. Getsinger, R.M. Stewart, and C.S. Owens. 2002. Whole lake fluridone treatments for selective control of Eurasian watermilfoil: II. Impacts on Submersed Plant Communities **18**(3):191-200.

Madsen, J.D., R.M. Wersal, and T.E. Woolf. 2015. Operational control of Eurasian watermilfoil (*Myriophyllum spicatum*) and impacts to the native submersed aquatic macrophyte community in Lake Pend Oreille, Idaho. *Invasive Plant Science and Management* **8**(2):219-232.

Massicotte, P., A. Bertolo, P. Brodeur, C. Hudon, M. Mingelbier, and P. Magnan. 2015. Influence of the aquatic vegetation landscape on larval fish abundance. *Journal of Great Lakes Research* **41**: 873-880.

Meiners, S.J., M.L. Cadenasso, and S.T.A. Pickett. 2004. Beyond biodiversity: individualistic controls of invasion in a self-assembled community. *Ecology Letters* **7**:121-126.

- Miranda, L.E., and L.L. Pugh. 1997. Relationship between vegetation coverage and abundance, size, and diet of juvenile largemouth bass during winter. *North American Journal of Fisheries Management* **17**: 601-610.
- Naeem, S., J.M.H. Knops, D. Tilman, K.M. Howe, T. Kennedy, and S. Gale. 2000. Plant diversity increases resistance to invasion in the absence of covarying extrinsic factors. *Oikos* **91**:97-108.
- Nault, M.E., M.D. Netherland, A. Mikulyuk, J.G. Skogerboe, T. Asplund, J. Hauxwell, and P. Toshner. 2014. Efficacy, selectivity, and herbicide concentrations following a whole-lake 2,4-D application targeting Eurasian watermilfoil in two adjacent northern Wisconsin lakes. *Lake and Reservoir Management* **30**(1):1-10.
- Pardue, W.J., and D.H. Webb. 1985. A comparison of aquatic macroinvertebrates occurring in association with Eurasian watermilfoil (*Myriophyllum spicatum* L.) with those found in the open littoral zone. *Journal of Freshwater Ecology* **3**(1): 69-79.
- Parsons, J.K., A. Couto, K.S. Hamel, and G.E. Marx. 2009. Effect of fluridone on macrophytes and fish in a coastal Washington lake. *Journal of Aquatic Plant Management* **47**:31-40.
- Pedlow, C.L., E.D. Dibble, and K.D. Getsinger. 2006. Littoral habitat heterogeneity and shifts in plant composition relative to a fall whole-lake fluridone application in Perch Lake, Michigan. *Journal of Aquatic Plant Management* **44**:26-31.
- Phillips, E.C. 2008. Invertebrate colonization of native and invasive aquatic macrophytes in Presque Isle Bay, Lake Erie. *Journal of Freshwater ecology* **23**:451-457.
- Pothoven, S.A., B. Vondracek, D.L. Pereira. 1999. Effects of vegetation removal on bluegill and largemouth bass in two Minnesota lakes. *North American Journal of Fisheries Management* **19**(3):748-757.
- Randall, R.G., C.K. Minns, V.W. Cairns, and J.E. Moore. 1996. The relationship between an index of fish production and submerged macrophytes and other habitat features at three littoral areas in the Great Lakes. *Canadian journal of Fisheries and Aquatic Sciences* **53**(1):35-44.
- Rea, T.E., D.J. Karapatakis, K.K. Guy, J.E. Pinder III, and H.E. Mackey Jr. 1998. The relative effects of water depth, fetch and other physical factors on the development of macrophytes in a small southeastern US pond. *Aquatic Botany* **61**:289-299.
- Relyea, R.A. 2005. The impact of insecticides and herbicides on the biodiversity and productivity of aquatic communities. *Ecological Applications* **15**(2):618-627.

Robinson, G.R., J.F. Quinn, and M.L. Stanton. 1995. Invasibility of experimental habitat islands in a California winter annual grassland. *Ecology* **76**(3):786-794.

Rozas, L.P., and W.E. Odum. 1988. Occupation of submerged aquatic vegetation by fishes: testing the roles of good and refuge. *Oecologia* **77**(1):101-106.

Savino, J.F., and R.A. Stein. 1982. Predator-prey interactions between largemouth bass and bluegills as influenced by simulated, submersed vegetation. *Transactions of the American Fisheries Society* **111**: 255-266.

Savino, J.F., and R.A. Stein. 1989a. Behavior of fish predators and their prey: habitat choice between open water and dense vegetation. *Environmental Biology of Fishes* **24**:287-293.

Savino, J.F., and R.A. Stein. 1989b. Behavioural interactions between fish predators and their prey: effects of plant density. *Animal Behaviour* **37**(2): 311-321.

Savino, J.F., E.A. Marschall, and R.A. Stein. 1992. Bluegill growth as modified by plant density: an exploration of underlying mechanisms. *Oecologia* **89**(2): 153-160.

Schultz, R., and E. Dibble. 2012. Effects of invasive macrophytes on freshwater fish and macroinvertebrate communities: the role of invasive plant traits. *Hydrobiologia* **684**:1-14.

Sher-Kaul, S., B. Oertli, E. Castella, J.B. Lachavanne. 1995. Relationship between biomass and surface area of six submerged aquatic plant species. *Aquatic Botany* **51**:147-154.

Skawinski, P.M. 2014. *Aquatic Plants of the Upper Midwest: A photographic guide to our underwater forests*. 2nd edition. P. Skawinski.

Skogerboe, J.G., and K.D. Getsinger. 2002. Endothall species selectivity evaluation: Northern latitude aquatic plant community. *Journal of Aquatic Plant Management* **40**:1-5.

Skogerboe, J.G., and K.D. Getsinger. 2006. Selective control of Eurasian watermilfoil and curlyleaf pondweed using low doses of endothall combined with 2,4-D. No. ERDC/TN-APCRP-CC-05. Engineer Research and Development Center, Vicksburg, MS.

Smith, C.S., and J.W. Barko. 1990. Ecology of Eurasian watermilfoil. *Journal of Aquatic Plant Management* **28**:55-64.

Spence, D.H.N., and J. Chrystal. 1970. Photosynthesis and zonation of freshwater macrophytes. *New Phytologist* **69**:206-215.

Strimaitis, A.M., and S.P. Sheldon. 2011. A comparison of macroinvertebrate and epiphyte density and diversity on native and exotic complex macrophytes in three Vermont lakes. *Northeastern Naturalist* **18**(2):149-160.

Theel, H.J., E.D. Dibble, and J.D. Madsen. 2008. Differential influence of a monotypic and diverse native aquatic plant bed on a macroinvertebrate assemblage; an experimental implication of exotic plant induced habitat. *Hydrobiologia* **600**:77-87.

Thomaz, S.M., and E.R. da Cunha. 2010. The role of macrophytes in habitat structuring in aquatic ecosystems: methods of measurement, causes and consequences on animal assemblages' composition and biodiversity. *Acta Limnologica Brasiliensia* **22**(2):218-236.

Tilman, D. 1997. Invasibility, recruitment limitation, and grassland biodiversity. *Ecology* **78**(1):81-92.

Titus, J.E., and M.S. Adams. 1979. Coexistence and the comparative light relations of the submersed macrophytes *Myriophyllum spicatum* L. and *Vallisneria Americana* Michx. *Oecologia* **40**:273-286.

Trebitz, A.S., J.C. Brazner, M.S. Pearson, G.S. Peterson, D.K. Tanner, and D.L. Taylor. 2009. Patterns in habitat and fish assemblages within Great Lakes coastal wetlands and implications for sampling design. *Canadian Journal of Fisheries and Aquatic Sciences* **66**:1343-1354.

Troutman, J.P., D.A. Rutherford, and W.E. Kelso. 2007. Patterns of habitat use among vegetation-dwelling littoral fishes in the Atchafalaya River Basin, Louisiana. *Transaction of the American Fisheries Society* **136**(4):1063-1075.

Unmuth, J.M.L., M.J. Hansen, and T.D. Pellet. 1999. Effects of mechanical harvesting on Eurasian watermilfoil on largemouth bass and bluegill populations in Fish Lake, Wisconsin. *North American Journal of Fisheries Management* **19**:1089-1098.

Unmuth, J.M.L., R.A. Lillie, D.S. Dreikosen, and D.W. Marshall. 2000. Influence of dense growth of Eurasian watermilfoil on lake temperature and dissolved oxygen. *Journal of Freshwater Ecology* **15**(4):497-503.

Vadeboncoeur, Y., P.B. McIntyre, and M.J. Vander Zanden. 2011. Borders of biodiversity : life at the edge of the world's large lakes. *BioScience* **61**(7):526-537.

Valinoti, C.E., C.K. Ho, and A.R. Armitage. 2011. Native and exotic submerged aquatic vegetation provide differential nutritional and refuge values for macroinvertebrates. *Journal of Experimental Marine Biology and Ecology* **409**(1-2):42-47.

Valley, R.D., and M.T. Bremigan. 2002a. Effects of macrophyte bed architecture on largemouth bass foraging: implications of exotic macrophyte invasions. *Transactions of the American Fisheries Society* **131**(2):234-244.

Valley, R.D., and M.T. Bremigan. 2002b. Effects of selective removal of Eurasian watermilfoil on age-0 largemouth bass piscivory and growth in southern Michigan lakes. *Journal of Aquatic Plant Management* **40**:79-87.

Valley, R.D., T.K. Cross, and P. Radomski. 2004. The role of submersed aquatic vegetation as habitat for fish in Minnesota lakes, including the implications of non-native plant invasions and their management. Minnesota Department of Natural Resources, Division of Fish and Wildlife, Special Publication 160. St. Paul, MN 55155. 25 pp.

Wagner, K.I., J. Hauxwell, P.W. Rasmussen, F. Koshere, P. Toshner, K. Aron, D.R. Helsel, S. Toshner, S. Provost, M. Gansberg, J. Masterson, and S. Warwick. 2007. Whole-lake herbicide treatments for Eurasian watermilfoil in four Wisconsin lakes: effects on vegetation and water clarity. *Lake and Reservoir Management* **23**: 83-94.

Warfe, D.M., and L.A. Barmuta. 2006. Habitat structural complexity mediates food web dynamics in a freshwater macrophyte community. *Oecologia* **150**:141-154.

Weaver, M.J., J.J. Magnuson, and M.K. Clayton. 1997. Distribution of littoral fishes in structurally complex macrophytes. *Canadian Journal of Fisheries and Aquatic Sciences* **54**(10):2277-2289.

Webb, K.M., R.E. Schultz, and E.D. Dibble. 2016. The influence of invasive aquatic plant removal on diets of bluegill in Minnesota lakes. *Journal of Aquatic Plant Management* **54**:37-45.

Werner, E.E., J.F. Gilliam, D.J. Hall, and G.G. Mittelbach. 1983. An experimental test of the effects of predation risk on habitat use in fish. *Ecology* **64**(6):540-1548.

Wersal, R.M., J.D. Madsen, T.E. Woolf, and N. Eckberg. 2010. Assessment of herbicide efficacy on Eurasian watermilfoil and impacts to the native submersed plant community in Hayden Lake, Idaho, USA. *Journal of Aquatic Plant Management* **48**:5-11.

Westerdahl, H.E., and J.F. Hall. 1983. Threshold 2,4-D concentrations for control of Eurasian watermilfoil and sago pondweed. *Journal of Aquatic Plant Management* **21**:22-25.

Wilson, S.J., and A. Ricciardi. 2009. Epiphytic macroinvertebrate communities on Eurasian watermilfoil (*Myriophyllum spicatum*) and native milfoils *Myriophyllum sibiricum* and *Myriophyllum alterniflorum* in eastern North America. *Canadian Journal of Fisheries and Aquatic Sciences* **66**:18-30.

Winfield, I.J. 2004. Fish in the littoral zone: ecology, threats and management. *Limnologia* **34**(1-2):124-131.

Tables

Table 1.1. Sampling dates for fish (○ circles), invertebrates (□ squares), and macrophytes (△ triangles) across all sites in the Keweenaw Waterway. “Pike Bay” site refers to invertebrate sampling that was conducted in areas outside of our fish trap sites within Pike Bay prior to herbicide treatment.

	Sampling Date																																	
Site	13-Jun	14-Jun	16-Jun	17-Jun	18-Jun	21-Jun	23-Jun	27-Jun	28-Jun	30-Jun	1-Jul	5-Jul	6-Jul	7-Jul	8-Jul	11-Jul	20-Jul	24-Jul	25-Jul	26-Jul	27-Jul	28-Jul	1-Aug	3-Aug	4-Aug	5-Aug	9-Aug	13-Aug	14-Aug	15-Aug	16-Aug	18-Aug	26-Aug	
Pike Bay 1		○	○	□	△			●			●								●	▲				●				●		▲		■		
Pike Bay 2		○	○	□	△		●				●				▲					●				●				●			■	▲		
Oskar Bay	○																					○	△											
Marsin		○																					○											
North Pike										○	□	△					○							○				○	□		△			
North Slough						○	□		△			○						○	△							○						□	△	
South Slough														○	□	△			○	△							○					□	△	
Portage																										○	○	□		○	△			
Pike Bay				□																														

Table 1.2. Results of macrophyte surveys across all sites and sampling dates. Native macrophyte abundance indicates the averaged categorical abundances of the common native macrophytes (i.e. *Chara* sp., *C. demersum*, *E. canadensis*, *Najas* sp., and *V. americana*). Categorical designations are based on quartiles of toss rake results only. "Low" abundance refers to values within the 25th percentile of their respective macrophyte type, while "moderate" represents the 50th percentile. Values greater than the 50th percentile are considered "high" abundance. Species richness represents the total number of unique macrophyte species collected within a survey. "-" indicates that that information was not collected at that time.

Site	Date	Treatment	# of Rake Samples	Rake Type	Mean Water Depth (m)	EWM Abundance	EWM Category	Native Macrophyte Abundance	Native Category	Species Richness
Pike Bay 1	21-Jun	Pre-Treatment	12	Twist	0.93	0.08		0.13		10
			12	Toss		0.42	High	0.32	Moderate	16
Pike Bay 1	27-Jul	Post-Treatment	12	Twist	1.08	0.08		0.78		14
			12	Toss		0.00	Low	0.78	High	14
Pike Bay 1	16-Aug	Post-Treatment	12	Twist	0.98	0.17		0.78		16
			12	Toss		0.17	Moderate	0.93	High	14
Pike Bay 2	21-Jun	Pre-Treatment	24	Twist	0.93	0.25		0.13		9
			24	Toss		0.54	High	0.19	Low	15
Pike Bay 2	11-Jul	Post-Treatment	15	Twist	1.06	0.40		0.44		7
			15	Toss		0.00	Low	0.48	Moderate	12
Pike Bay 2	28-Jul	Post-Treatment	12	Twist	0.95	0.00		0.22		6
			12	Toss		0.00	Low	0.38	Moderate	10
Pike Bay 2	18-Aug	Post-Treatment	12	Twist	0.93	0.00		0.30		7
			12	Toss		0.00	Low	0.52	Moderate	6
Oskar Bay	28-Jul	Reference	12	Twist	1.15	0.00		0.05		5
			12	Toss		0.00	Low	0.08	Low	6
North Pike	5-Jul	Reference	12	Twist	1.11	0.42		0.67		15
			12	Toss		0.33	High	0.60	High	20
North Pike	16-Aug	Reference	12	Twist	1.18	0.67		0.62		14
			12	Toss		0.67	High	0.75	High	15
North Slough	28-Jun	Reference	12	Twist	1.02	0.33		0.53		13
			12	Toss		0.50	High	0.78	High	16
North Slough	24-Jul	Reference	12	Twist	-	0.25		0.92		9
			12	Toss		0.83	High	0.98	High	11
North Slough	18-Aug	Reference	12	Twist	1.07	0.17		0.75		11
			12	Toss		0.42	High	0.82	High	14
South Slough	8-Jul	Reference	12	Twist	0.84	0.00		0.07		2
			12	Toss		0.00	Low	0.08	Low	4
South Slough	26-Jul	Reference	12	Twist	0.92	0.00		0.03		3
			12	Toss		0.00	Low	0.13	Low	3
South Slough	18-Aug	Reference	12	Twist	1.05	0.00		0.12		7
			12	Toss		0.00	Low	0.25	Moderate	10
Portage	16-Aug	Reference	9	Twist	1.60	1.44		0.78		8
			9	Toss		2.11	High	0.78	High	11

Table 1.3. Mean categorical abundances of each macrophyte species detected in toss rakes across surveys. AGPW = algal-leaved pondweed (*Potamogeton confervoides*), AM = aquatic moss (*Drepanocladus* sp.), APW = alpine pondweed (*P. alpinus*), BHL = bull-head pond lily (*Nuphar variegata*), BLP = blunt-leaved pondweed (*P. obtusifolius*), BNS = bird's nest stonewort (*Tolypella intricata*), BR = bulrush (*Scirpus* sp.), BW = bladderwort (*Utricularia* sp.), CHA = *Chara* sp., CNT = coontail (*Ceratophyllum demersum*), CPW = clasping pondweed (*P. richardsonii*), CRA = crested arrowhead (*Sagittaria cristata*), ELO = Canadian waterweed (*Elodea canadensis*), EWM = Eurasian watermilfoil (*Myriophyllum spicatum*), FBR = floating bur reed (*Sparganium fluctuans*), FPW = Fries' pondweed (*P. friesii*), FRPW = fern pondweed (*P. robbinsii*), FSPW = flat-stem pondweed (*P. zosteriformis*), GRA = grass-leaved pondweed (*S. graminea*), IPL = intermediate pond lily (*Nuphar x rubrodisca*), IPW = Illinois pondweed (*P. illinoensis*).

Site	Date	AGPW	AM	APW	BHL	BLP	BNS	BR	BW	CHA	CNT	CPW	CRA	ELO	EWM	FBR	FPW	FRPW	FSPW	GLA	IPL	IPW
Pike Bay 1	21-Jun	0.00	0.00	0.25	0.08	0.25	0.00	0.00	0.08	0.25	0.17	0.17	0.08	0.58	0.42	0.00	0.00	0.00	0.17	0.00	0.00	0.00
Pike Bay 1	27-Jul	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.08	0.58	0.75	0.17	0.00	1.17	0.00	0.00	0.00	0.00	0.17	0.00	0.00	0.00
Pike Bay 1	16-Aug	0.00	0.00	0.00	0.00	0.08	0.33	0.00	1.17	0.92	0.75	0.00	0.00	1.00	0.17	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Pike Bay 2	21-Jun	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.13	0.21	0.21	0.00	0.33	0.54	0.00	0.04	0.04	0.04	0.00	0.00	0.00
Pike Bay 2	11-Jul	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.07	1.47	0.07	0.00	0.33	0.33	0.00	0.00	0.07	0.13	0.00	0.00	0.00
Pike Bay 2	28-Jul	0.00	0.00	0.00	0.00	0.00	0.00	0.08	0.00	0.33	0.58	0.00	0.00	0.50	0.00	0.00	0.00	0.08	0.08	0.00	0.00	0.00
Pike Bay 2	18-Aug	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.17	0.58	0.00	0.00	0.75	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Oskar Bay	28-Jul	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.08	0.00	0.08	0.00	0.00	0.00	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.00
North Pike	5-Jul	0.00	0.33	0.08	0.00	0.08	0.00	0.00	0.50	0.25	0.83	0.08	0.00	0.83	0.33	0.00	0.00	0.08	0.25	0.00	0.00	0.08
North Pike	16-Aug	0.08	0.00	0.00	0.08	0.17	0.00	0.00	0.67	0.17	1.17	0.00	0.00	0.83	0.67	0.08	0.00	0.00	0.00	0.00	0.50	0.00
North Slough	28-Jun	0.00	0.00	0.08	0.25	0.00	0.00	0.00	1.08	0.75	0.83	0.08	0.00	1.67	0.50	0.00	0.00	0.00	0.08	0.00	0.00	0.00
North Slough	24-Jul	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.08	0.58	0.50	0.17	0.00	2.25	0.83	0.00	0.00	0.00	0.00	0.00	0.00	0.00
North Slough	18-Aug	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.17	0.33	0.08	0.00	1.83	0.42	0.00	0.00	0.17	0.00	0.00	0.00	0.00
South Slough	8-Jul	0.00	0.00	0.08	0.08	0.00	0.00	0.00	0.00	0.17	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
South Slough	26-Jul	0.00	0.00	0.00	0.00	0.00	0.00	0.08	0.00	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
South Slough	18-Aug	0.08	0.00	0.00	0.00	0.00	0.00	0.08	0.00	0.67	0.25	0.00	0.00	0.08	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Portage	16-Aug	0.00	0.00	0.00	0.00	0.11	0.00	0.00	0.00	0.11	1.00	0.00	0.00	0.44	2.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Table 1.3 (continued). Mean categorical abundances of each macrophyte species detected in toss rakes across surveys. LLPW = longleaf pondweed (*P. nodosus*), LPW = leafy pondweed (*P. foliosus*), MAR = water-marigold (*Bidens beckii*), NAI = naiad (*Najas* sp.), NMF = northern watermilfoil (*M. sibiricum*), NSR = needle spikerush (*Eleocharis acicularis*), PPW = perfoliate pondweed (*P. perfoliatus*), QW = quillwort (*Isoetes* sp.), SHPW = sheathed pondweed (*Stuckenia vaginata*), SMPW = small pondweed (*P. pusillus*), SPRW = spearwort (*Ranunculus* sp.), SPW = stiff pondweed (*P. strictifolius*), VAL = eel grass (*Vallisneria americana*), VPW = variable pondweed (*P. gramineus*), WCF = water crowfoot (*Ranunculus* sp), WSG = water stargrass (*Heteranthera dubia*), WSPW = white-stem pondweed (*P. praelongus*), WWL = white water lily (*Nymphaea odorata*), YWL = yellow water lily (*Nuphar lutea*).

Site	Date	LLPW	LPW	MAR	NAI	NMF	NSR	OPW	PPW	QW	SHPW	SLPW	SMPW	SPRW	SPW	VAL	VMF	VPW	WCF	WSG	WSPW	WWL	YWL
Pike Bay 1	21-Jun	0.00	0.00	0.08	0.17	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.42	0.00	0.08	0.00	0.08	0.00	0.00	0.00
Pike Bay 1	27-Jul	0.00	1.25	0.00	0.58	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.83	0.08	0.25	0.08	0.00	0.17	0.00	0.33
Pike Bay 1	16-Aug	0.00	0.25	0.25	1.25	0.00	0.00	0.00	0.33	0.00	0.00	0.00	0.00	0.00	1.33	0.75	0.00	0.25	0.00	0.00	0.00	0.00	0.00
Pike Bay 2	21-Jun	0.00	0.00	0.08	0.08	0.00	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.21	0.00	0.13	0.00	0.04	0.04	0.00	0.00
Pike Bay 2	11-Jul	0.00	0.00	0.13	0.07	0.00	0.00	0.00	0.00	0.00	0.07	0.00	0.07	0.00	0.00	0.47	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Pike Bay 2	28-Jul	0.00	0.08	0.00	0.08	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.42	0.00	0.08	0.00	0.00	0.00	0.00	0.00
Pike Bay 2	18-Aug	0.00	0.00	0.17	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.83	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Oskar Bay	28-Jul	0.00	0.00	0.00	0.08	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.25	0.25	0.00	0.00	0.00	0.00	0.00	0.00
North Pike	5-Jul	0.00	0.08	0.17	0.50	0.00	0.00	0.00	0.08	0.00	0.00	0.00	0.00	0.00	0.08	0.92	0.00	0.00	0.00	0.00	0.00	0.08	0.00
North Pike	16-Aug	0.00	0.42	0.33	0.42	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.17	0.00	0.17	0.00	0.00	0.00	0.00	0.00
North Slough	28-Jun	0.00	0.00	0.25	0.25	0.25	0.00	0.00	0.00	0.00	0.00	0.58	0.00	0.00	0.00	0.42	0.00	0.00	0.00	0.08	0.00	0.08	0.00
North Slough	24-Jul	0.00	0.00	0.00	0.42	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.17	0.00	0.00	1.17	0.17	0.00	0.00	0.00	0.00	0.58	0.00
North Slough	18-Aug	0.00	0.00	0.00	0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.25	0.25	0.00	0.17	0.00	0.25	0.42	0.00
South Slough	8-Jul	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00
South Slough	26-Jul	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.42	0.00	0.00	0.00	0.00	0.00	0.00	0.00
South Slough	18-Aug	0.00	0.00	0.00	0.08	0.00	0.00	0.00	0.00	0.17	0.00	0.00	0.08	0.08	0.00	0.17	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Portage	16-Aug	0.00	0.22	0.56	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.33	2.00	0.11	0.00	0.00	0.00	0.00	0.00	0.00

Table 1.4. Summary of NMS ordination results for macrophyte surveys across sites and sampling dates.

Site	Site Code	Date	Treatment	Axis 1	Axis 2	EWM	Native
Pike Bay 1	PB1	21-Jun	Pre	0.11542	0.17435	High	Moderate
Pike Bay 1	PB1	27-Jul	Post	-0.63128	-0.39872	Low	High
Pike Bay 1	PB1	16-Aug	Post	-1.05182	-0.46166	Moderate	High
Pike Bay 2	PB2	21-Jun	Pre	0.19215	0.53053	High	Low
Pike Bay 2	PB2	11-Jul	Post	-0.17418	0.39188	Low	Moderate
Pike Bay 2	PB2	28-Jul	Post	0.15388	-0.17106	Low	Moderate
Pike Bay 2	PB2	18-Aug	Post	-0.16665	-0.10918	Low	Moderate
Oskar Bay	OB	28-Jul	Reference	1.54365	0.99486	Low	Low
North Pike	NP	5-Jul	Reference	-0.55024	0.00235	High	High
North Pike	NP	16-Aug	Reference	-0.79414	0.09924	High	High
North Slough	NS	28-Jun	Reference	-0.76399	-0.21222	High	High
North Slough	NS	18-Aug	Reference	-0.67872	0.32583	High	High
South Slough	SS	8-Jul	Reference	1.76184	-0.21268	Low	Low
South Slough	SS	26-Jul	Reference	1.34622	-0.46848	Low	Low
South Slough	SS	18-Aug	Reference	0.77848	-0.91353	Low	Low
Portage	P	16-Aug	Reference	-1.08061	0.42848	High	High

Table 1.5. Summary of NMS ordination results for all macrophyte species. For species codes see description of Table 1.3.

Species	Axis 1		Axis 2	
	r	tau	r	tau
AGPW	-0.189	-0.128	0.035	-0.043
AM	-0.160	-0.071	0.001	0.024
APW	0.700	0.089	0.021	-0.038
BHL	-0.113	-0.038	-0.103	-0.064
BLP	-0.337	-0.411	0.132	0.160
BNS	-0.305	-0.306	-0.262	-0.259
BR	0.410	0.365	-0.547	-0.453
BW	-0.548	-0.493	-0.190	-0.068
CHA	-0.321	-0.147	-0.737	-0.667
CNT	-0.738	-0.627	0.077	0.119
CPW	-0.218	-0.082	0.214	0.204
CRA	0.034	0.071	0.099	0.118
ELO	-0.747	-0.655	-0.063	-0.094
EWM	-0.516	-0.510	0.381	0.417
FBR	0.387	0.051	0.571	0.322
FPW	0.056	0.165	0.301	0.306
FRPW	-0.224	-0.068	0.262	0.251
FSPW	-0.258	-0.101	0.007	0.060
IPL	-0.230	-0.259	0.056	0.071
IPW	-0.160	-0.071	0.001	0.024
LPW	-0.375	-0.467	-0.218	-0.106
MAR	-0.656	-0.652	0.172	0.149
NAI	-0.682	-0.633	-0.200	-0.043
NMF	-0.222	-0.212	-0.120	-0.118
NSR	0.056	0.165	0.301	0.306
PPW	-0.339	-0.288	-0.258	-0.186
QW	0.226	0.212	-0.518	-0.354
SHPW	-0.050	-0.024	0.222	0.212
SLPW	-0.222	-0.212	-0.120	-0.118
SMPW	0.142	0.153	-0.252	-0.119
SPRW	0.226	0.212	-0.518	-0.354
SPW	-0.388	-0.451	-0.199	0.000
VAL	-0.686	-0.638	0.193	0.224
VMF	0.039	-0.163	0.563	0.339
VPW	-0.403	-0.224	-0.200	-0.096
WCF	-0.263	-0.220	0.073	-0.017
WSG	-0.114	-0.014	0.092	0.157
WSPW	-0.268	-0.113	0.068	0.141
WWL	-0.267	-0.271	0.161	0.071
YWL	-0.183	-0.118	-0.226	-0.212

Table 2.1. Summary of abiotic data collected from all fish surveys. “-” indicates that that information was not recorded during that survey.

Site	Date	Treatment Type	Catch Time (H:M)	Water Temp (°C) at Set	Water Temp (°C) at Pull	Conductivity (µS) at Set	Conductivity (µS) at Pull	pH at Set	pH at Pull	EWM Abundance	Native Macrophyte Abundance
Pike Bay 1	16-Jun	Pre-Treatment	23:30	20.0	22.0	107.8	109.9	8.02	8.18	High	Moderate
	17-Jun	Pre-Treatment	20:15	22.0	23.0	109.9	110.7	8.18	8.40	High	Moderate
	28-Jun	Post-Treatment	21:06	20.3	18.2	124.9	117.2	7.26	7.16	Moderate	Moderate
	5-Jul	Post-Treatment	21:30	23.7	23.5	123.2	122.0	7.28	6.90	Low	Moderate
	26-Jul	Post-Treatment	22:20	24.9	25.0	135.3	129.4	7.04	6.81	Low	High
	4-Aug	Post-Treatment	21:50	-	23.9	133.8	133.9	6.93	6.85	Low	High
Pike Bay 2	14-Aug	Post-Treatment	20:45	23.1	22.4	130.7	123.2	4.50	4.46	Moderate	High
	16-Jun	Pre-Treatment	19:15	20.0	21.0	115.2	107.8	8.31	8.27	High	Low
	17-Jun	Pre-Treatment	20:40	30.0	21.7	107.8	108.0	8.27	8.22	High	Low
	27-Jun	Post-Treatment	20:45	20.5	19.6	117.5	125.1	7.41	6.69	Moderate	Low
	5-Jul	Post-Treatment	20:30	23.0	22.8	120.6	117.3	7.47	7.11	Low	Moderate
	27-Jul	Post-Treatment	22:30	24.5	22.8	134.8	129.0	7.13	7.24	Low	Moderate
Oskar Bay	4-Aug	Post-Treatment	21:35	30.0	23.2	133.5	131.0	6.95	6.63	Low	Moderate
	14-Aug	Post-Treatment	23:30	23.9	23.5	130.2	132.8	4.48	4.48	Low	Moderate
	13-Jun	Reference	20:20	13.0	13.0	120.5	132	7.75	7.75	Low	Low
	28-Jul	Reference	19:35	21.8	20.5	117.4	115.5	7.01	6.69	Low	Low
	14-Jun	Reference	21:00	15.7	14.5	121.3	121.3	7.90	8.04	Low	Low
	1-Aug	Reference	23:25	23.4	24.1	120.7	121.4	7.18	6.09	Low	Low
North Pike	30-Jun	Reference	18:45	20.6	17.3	115.8	116.0	6.86	7.02	High	High
	20-Jul	Reference	23:46	23.4	24.3	126.6	118.6	6.81	6.60	High	High
	3-Aug	Reference	26:45	24.5	26.3	-	127.8	-	6.81	High	High
	13-Aug	Reference	23:15	21.3	22.4	118.9	119.4	4.46	7.17	High	High
North Slough	23-Jun	Reference	21:30	20.5	21.0	114.8	117.0	7.72	7.72	High	High
	6-Jul	Reference	16:45	24.8	23.4	122.6	122.5	7.07	6.60	High	High
	24-Jul	Reference	26:00	24.6	26.0	125.1	139.2	6.55	6.54	High	High
	5-Aug	Reference	-	22.4	-	124.9	-	6.98	-	High	High
South Slough	7-Jul	Reference	19:30	22.7	19.5	115.8	116.1	7.54	6.84	Low	Low
	25-Jul	Reference	17:50	25.7	23.5	115.2	120.5	6.95	6.92	Low	Low
	9-Aug	Reference	23:15	24.5	23.0	123.6	121.7	6.71	4.55	Low	Moderate
Portage	9-Aug	Reference	23:15	23.4	-	124.9	124.6	6.79	4.42	High	High
	13-Aug	Reference	23:20	21.5	22.0	126.8	121.0	6.47	6.79	High	High
	15-Aug	Reference	20:20	24.5	23.1	123.6	121.9	4.57	4.42	High	High

Table 2.2. Summary of invertebrate survey results. “-” indicates that that information was not recorded during that survey. Oskar Bay and Marsin were not surveyed for invertebrates. Diversity represents Simpsons Diversity Index, and taxa richness represents the number of unique taxa detected in the sample.

Site	Date	Treatment	Sampling Point	Water Depth (m)	EWM Abundance	Native Macrophyte Abundance	Total Invertebrate Abundance	Benthic Macro-invertebrate Abundance	Amphipod Abundance	Diversity	Taxa Richness
Pike Bay 1	18-Jun	Pre-Treatment	1	0.95	Moderate	Moderate	140	92	16	0.14	17
			2	0.93	Low	Low	52	42	2	0.31	11
			3	0.91	High	Moderate	178	90	22	0.15	16
Pike Bay 1	26-Aug	Post-Treatment	1	1.10	Low	High	1012	318	205	0.36	19
			2	0.85	Low	High	691	83	30	0.57	18
			3	1.05	Low	High	500	138	29	0.42	17
Pike Bay 2	17-Jun	Pre-Treatment	1	1.22	High	Low	250	175	11	0.10	22
			2	1.03	Low	Low	19	16	1	0.13	9
			3	1.01	Low	Low	32	32	0	0.14	9
Pike Bay 2	18-Aug	Post-Treatment	1	0.80	Low	Moderate	20	13	1	0.09	8
			2	0.97	Low	Moderate	53	47	1	0.14	11
			3	1.50	Low	Moderate	380	350	40	0.12	18
North Pike	1-Jul	Control	1	1.20	Moderate	Moderate	84	67	15	0.07	18
			2	0.80	Low	Moderate	126	84	23	0.07	19
			3	0.95	Low	Moderate	72	34	6	0.17	15
North Pike	13-Aug	Control	1	1.35	Moderate	High	1779	302	90	0.21	22
			2	-	Moderate	High	745	116	17	0.38	16
			3	-	Low	High	815	202	4	0.21	18
North Slough	23-Jun	Control	1	-	High	High	513	152	84	0.23	20
			2	0.95	High	High	1407	238	39	0.29	24
			3	0.82	High	High	416	210	118	0.13	23
North Slough	18-Aug	Control	1	1.02	Moderate	High	277	169	46	0.10	22
			2	1.20	Moderate	High	208	95	10	0.25	14
			3	1.05	Moderate	High	353	140	27	0.26	20
South Slough	8-Jul	Control	1	0.95	Low	Low	94	16	2	0.22	10
			2	0.75	Low	Low	15	8	0	0.17	8
			3	1.05	Low	Low	68	42	2	0.16	11
South Slough	18-Aug	Control	1	0.70	Low	Moderate	500	291	147	0.13	24
			2	0.98	Low	Moderate	51	36	1	0.11	12
			3	1.10	Low	Moderate	14	7	0	0.23	5
Portage	13-Aug	Control	1	1.50	High	High	3384	311	28	0.31	20
			2	1.50	High	High	658	127	12	0.22	20
			3	1.17	High	High	459	99	7	0.30	20
Pike Bay	17-Jun	Pre-Treatment	1	2.05	Low	High	725	705	506	0.43	20
			2	1.90	Low	High	411	396	270	0.37	15
			3	0.95	Low	High	97	97	5	0.12	20
			4	2.00	Low	High	572	559	324	0.28	20
			5	0.91	Low	Moderate	183	183	43	0.10	19
			6	0.85	Low	Moderate	112	112	3	0.42	13
			7	0.90	Low	Low	75	75	7	0.22	12
			8	1.33	High	Low	163	84	28	0.17	18
			9	1.25	High	Low	155	155	37	0.20	17
			10	1.45	High	Low	128	76	29	0.13	18

Table 2.3. Length-weight regression parameters for all fish species for which length-data had to be extrapolated for some individuals.

Species	N	Slope	Intercept
Black crappie	221	3.20	-5.29
Bluegill	106	3.25	-5.25
Bullhead	423	2.98	-4.83
Golden shiner	189	3.10	-5.27
Johnny darter	18	2.22	-3.81
Largemouth bass	106	3.13	-5.16
Pumpkinseed	1143	3.19	-5.07
Rock bass	235	3.14	-4.98
Smallmouth bass	111	2.94	-4.76
Spottail shiner	10	2.44	-4.16
White sucker	21	2.11	-2.67
Yellow perch	194	3.24	-5.45
PS x BG/ juvenile sunfish	1252	3.19	-5.07

Table 2.4. Summary of fish, invertebrate, and macrophyte data averaged per survey sites. “-” indicates that a given survey was not conducted during that sampling month.

Site	Mean EWM Relative Abundance	Mean Native Macrophyte Relative Abundance	Mean Fish Abundance	Mean Fish Biomass (g)	Mean Macrophyte Species Richness	Mean Fish Length (mm)	Mean Fish Weight (g)	Mean Fish Species Richness	Mean Fish Diversity	Mean Invertebrate Abundance	Mean Benthic Invertebrate Abundance	Mean Invertebrate Taxa Richness	Mean Invertebrate Diversity
Pike Bay 1	0.19	0.68	76	3339.8	15	115	1.2	9	0.34	429	127	16	0.32
Pike Bay 2	0.21	0.36	33	2749.5	11	135	1.4	10	0.28	126	106	13	0.12
Oskar Bay	0.00	0.08	15	1072.5	6	120	1.1	9	0.36	-	-	-	-
Marsin	-	-	14	1965.7	-	140	1.2	10	0.46	-	-	-	-
North Pike	0.50	0.71	62	2560.7	18	105	0.9	7	0.33	604	134	18	0.18
North Slough	0.58	0.86	236	5070.0	14	97	0.7	10	0.31	529	167	21	0.21
South Slough	0.00	0.16	11	702.5	6	125	1.2	9	0.23	124	67	12	0.17
Portage	2.11	0.78	34	870.6	11	95	1.0	8	0.37	1500	179	20	0.28

Table 2.5. Mean abundances of all fish species captured across sites and sampling dates. AW = alewife (*Alosa pseudoharengus*), BC = black crappie (*Pomoxis nigromaculatus*), BG = bluegill (*Lepomis macrochirus*), BNS = blacknose shiner (*Notropis heterolepis*), BH = bullhead (*Ameiurus* spp.), ER = Eurasian ruffe (*Gymnocephalus cernua*), GS = golden shiner (*Notemigonus crysoleucas*), JD = Johnny darter (*Etheostoma nigrum*), LMB = largemouth bass (*Micropterus salmoides*), NOP = northern pike (*Esox lucius*), PS = pumpkinseed (*L. gibbosus*), PSBG = pumpkinseed X bluegill hybrid, ROB = rock bass (*Ambloplites rupestris*), SCU = sculpin (*Cottus* sp.), SLR = silver redhorse (*Moxostoma anisurum*), TP = trout perch (*Percopsis omisomaycus*), WAL = walleye (*Sander vitreus*), WSU = white sucker (*Catostomus commersonii*), YP = yellow perch (*Perca flavescens*), JSF = juvenile sunfish (pumpkinseed or bluegill ≤ 75 mm).

	Mean Abundance / Net																									
	Nets																									
	Site	Date	Set	AW	BC	BG	BNS	BH	ER	GS	JD	LMB	NOP	NPD	PS	PSBG	ROB	SCU	SLR	SMB	STS	TP	WAL	WSU	YP	JSF
47	Pike Bay 1	16-Jun	3	0.00	1.33	0.00	0.00	12.00	0.00	27.67	0.00	0.00	0.00	0.00	79.00	0.00	2.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.33	0.00
	Pike Bay 1	17-Jun	3	0.00	1.67	1.67	0.00	7.00	0.00	40.00	0.00	0.00	0.00	0.00	87.67	0.33	3.67	0.00	0.33	0.00	0.33	0.00	0.33	0.33	5.33	0.00
	Pike Bay 1	28-Jun	3	0.00	0.67	0.00	0.00	3.00	0.00	10.67	0.00	0.33	0.67	0.00	30.33	0.00	1.67	0.00	0.00	0.00	0.00	0.00	0.00	0.33	20.67	0.00
	Pike Bay 1	5-Jul	3	0.00	2.33	0.33	0.00	2.33	0.00	1.33	0.00	0.33	0.00	0.00	25.33	0.00	2.67	0.00	0.00	0.33	0.00	0.00	0.00	1.00	1.33	0.67
	Pike Bay 1	26-Jul	3	0.00	2.67	1.00	0.00	9.00	0.00	0.00	0.00	6.00	0.00	0.00	10.33	0.00	1.00	0.00	0.00	0.33	0.00	0.00	0.00	0.00	1.00	0.00
	Pike Bay 1	4-Aug	3	0.00	2.67	0.33	0.00	8.00	0.33	0.00	0.00	2.67	0.00	0.00	10.67	0.00	2.67	0.00	0.00	0.33	0.00	0.00	0.00	0.67	1.00	0.00
	Pike Bay 1	14-Aug	3	0.00	6.00	3.67	0.00	10.33	0.00	0.33	0.00	2.67	0.67	0.00	6.67	0.00	1.00	0.00	0.00	1.67	0.00	0.00	0.00	0.33	1.67	54.67
	Pike Bay 2	16-Jun	3	0.67	0.00	6.67	0.00	1.33	0.00	2.00	0.33	0.67	0.00	0.33	9.00	0.00	2.00	0.00	1.33	0.00	0.33	0.00	0.00	0.33	0.67	0.00
	Pike Bay 2	17-Jun	3	0.33	0.00	3.00	0.00	1.00	0.00	1.00	0.00	0.33	0.00	0.00	24.00	0.00	3.67	0.00	0.67	1.00	0.00	0.33	0.00	0.33	2.00	0.00
	Pike Bay 2	27-Jun	3	0.00	1.00	2.00	0.00	3.33	0.00	0.00	0.33	0.00	0.00	0.00	14.00	0.00	2.33	0.00	1.33	0.33	0.00	0.00	0.00	0.33	12.00	0.00
	Pike Bay 2	5-Jul	3	0.00	4.67	3.33	0.00	1.33	0.00	0.33	1.00	0.00	0.33	0.00	15.33	0.00	1.67	0.00	0.67	2.33	0.33	0.00	0.00	0.00	6.67	0.00
	Pike Bay 2	27-Jul	3	0.00	0.00	0.67	0.00	5.33	0.00	0.00	1.00	0.67	0.00	0.00	4.33	0.00	0.33	0.00	0.67	4.67	0.00	0.00	0.33	1.00	0.33	0.00
	Pike Bay 2	4-Aug	3	0.00	24.33	0.33	0.00	4.67	0.00	0.00	0.00	3.33	0.00	0.00	9.67	0.00	1.00	0.00	0.00	3.33	0.33	0.00	0.00	1.33	2.67	0.00
	Pike Bay 2	14-Aug	3	0.00	3.00	1.00	0.00	0.00	0.00	0.00	0.00	0.67	0.00	0.00	4.33	0.00	0.33	0.00	0.33	8.33	0.00	0.00	0.00	1.00	0.00	0.00
	Oskar Bay	13-Jun	3	0.00	0.00	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	6.00	0.00	0.33	0.00	0.00	0.00	0.00	0.00	2.67	0.00
	Oskar Bay	28-Jul	3	0.00	0.00	1.33	0.00	0.00	0.00	1.00	0.33	0.00	0.00	0.00	1.00	0.00	6.67	0.00	0.00	2.33	1.33	0.00	0.00	0.33	7.00	0.00
	Marsin	14-Jun	3	0.00	0.00	0.00	0.00	0.33	0.00	0.00	2.33	0.00	0.67	0.00	0.00	0.00	8.33	0.67	0.33	0.67	0.00	0.00	0.00	0.67	0.67	0.00
	Marsin	1-Aug	3	0.00	0.00	0.00	0.00	1.67	0.00	0.00	1.67	0.00	0.00	0.00	0.00	0.00	3.67	0.00	0.00	5.33	0.33	0.00	0.00	0.00	1.33	0.00
	North Pike	30-Jun	3	0.00	3.33	0.33	0.00	4.67	0.00	1.33	0.00	0.00	0.00	0.00	42.00	0.67	8.33	0.00	0.33	0.00	0.00	0.00	0.00	0.00	3.00	0.00
	North Pike	20-Jul	3	0.00	4.33	6.67	0.00	8.00	0.00	0.67	0.00	36.00	0.33	0.00	30.00	0.00	5.67	0.00	0.33	0.67	0.00	0.00	0.00	0.00	2.67	0.00
	North Pike	3-Aug	3	0.00	0.33	0.00	0.00	4.00	0.00	0.33	0.00	4.33	0.00	0.00	34.67	0.00	3.33	0.00	0.00	1.67	0.00	0.00	0.00	0.00	1.00	0.33
	North Pike	13-Aug	3	0.00	1.67	0.00	0.00	5.33	0.00	0.00	0.00	4.00	0.00	0.00	19.33	0.00	2.33	0.00	0.00	0.67	0.00	0.00	0.00	0.00	3.33	2.33
	North Slough	23-Jun	3	0.00	2.67	0.67	0.00	34.67	0.00	61.33	0.00	0.00	0.33	0.00	40.00	0.00	4.00	0.00	0.67	0.00	0.00	0.00	0.00	0.33	2.33	9.33
	North Slough	6-Jul	3	0.00	1.33	0.33	0.00	8.67	0.00	12.33	0.00	0.00	0.00	0.00	23.67	0.00	3.00	0.00	0.67	0.00	0.00	0.00	0.00	0.00	0.00	0.33
	North Slough	24-Jul	3	0.00	20.33	6.00	0.00	66.33	0.00	0.33	0.33	1.33	0.67	0.00	36.67	0.00	1.67	0.00	0.00	1.67	0.00	0.00	0.00	0.00	0.67	0.00
	North Slough	5-Aug	3	0.00	15.67	0.00	0.00	18.00	0.00	0.00	0.00	11.00	0.33	0.00	14.33	0.00	1.33	0.00	0.00	1.33	0.00	0.00	0.00	0.33	1.33	539.00
	South Slough	7-Jul	3	0.00	0.00	0.00	0.00	0.33	0.33	0.00	0.00	0.00	0.33	0.00	0.67	0.33	1.33	0.00	0.00	1.00	1.00	0.33	0.00	0.00	0.67	0.00
	South Slough	25-Jul	2	0.00	1.50	0.50	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	3.00	0.00	2.50	0.00	0.00	1.50	0.00	0.00	0.00	0.00	1.00	0.00
	South Slough	9-Aug	3	0.00	0.33	0.00	0.00	1.33	0.00	0.00	0.00	0.00	0.00	0.00	0.67	0.00	3.67	0.00	0.00	8.00	1.00	0.00	0.00	0.00	0.67	0.00
	Portage	9-Aug	1	0.00	1.00	2.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	37.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	2.00	0.00
	Portage	13-Aug	1	0.00	8.00	0.00	0.00	6.00	0.00	1.00	0.00	4.00	0.00	0.00	5.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	2.00	0.00	1.00
	Portage	15-Aug	2	0.00	8.00	1.00	0.00	2.50	0.00	1.50	0.00	3.50	0.00	0.00	9.50	0.00	0.50	0.00	0.00	2.00	0.00	0.00	0.00	0.00	2.00	0.50

Table 2.6. Summary of abiotic data and categorical abundances of Eurasian watermilfoil and native macrophytes across fish survey sites and dates. “-” indicates that that data was not recorded during that survey.

Site	Date	Treatment Type	EWM Abundance	Native Macrophyte Abundance	Catch Time (H)	Water Temp (°C) at Set	Water Temp (°C) at Pull	Conductivity (µS) at Set	Conductivity (µS) at Pull	pH at Set	pH at Pull
Pike Bay 1	16-Jun	Pre-Treatment	High	Moderate	23.50	20.0	22.0	107.8	109.9	8.02	8.18
Pike Bay 1	17-Jun	Pre-Treatment	High	Moderate	20.25	22.0	23.0	109.9	110.7	8.18	8.40
Pike Bay 1	28-Jun	Post-Treatment	Moderate	Moderate	21.00	20.3	18.2	124.9	117.2	7.26	7.16
Pike Bay 1	5-Jul	Post-Treatment	Low	Moderate	21.50	23.7	23.5	123.2	122.0	7.28	6.90
Pike Bay 1	26-Jul	Post-Treatment	Low	High	22.25	24.9	25.0	135.3	129.4	7.04	6.81
Pike Bay 1	4-Aug	Post-Treatment	Low	High	22.00	-	23.9	133.8	133.9	6.93	6.85
Pike Bay 1	14-Aug	Post-Treatment	Moderate	High	20.75	23.1	22.4	130.7	123.2	4.50	4.46
Pike Bay 2	16-Jun	Pre-Treatment	High	Low	19.25	20.0	21.0	115.2	107.8	8.31	8.27
Pike Bay 2	17-Jun	Pre-Treatment	High	Low	20.75	30.0	21.7	107.8	108.0	8.27	8.22
Pike Bay 2	27-Jun	Post-Treatment	Moderate	Low	20.75	20.5	19.6	117.5	125.1	7.41	6.69
Pike Bay 2	5-Jul	Post-Treatment	Low	Moderate	20.50	23.0	22.8	120.6	117.3	7.47	7.11
Pike Bay 2	27-Jul	Post-Treatment	Low	Moderate	22.50	24.5	22.8	134.8	129.0	7.13	7.24
Pike Bay 2	4-Aug	Post-Treatment	Low	Moderate	21.50	30.0	23.2	133.5	131.0	6.95	6.63
Pike Bay 2	14-Aug	Post-Treatment	Low	Moderate	24.00	23.9	23.5	130.2	132.8	4.48	4.48
Oskar Bay	13-Jun	Reference	Low	Low	20.25	13.0	13.0	120.5	132	7.75	7.75
Oskar Bay	28-Jul	Control	Low	Low	19.50	21.8	20.5	117.4	115.5	7.01	6.69
Marsin	14-Jun	Control	Low	Low	21.00	15.7	14.5	121.3	121.3	7.90	8.04
Marsin	1-Aug	Control	Low	Low	23.75	23.4	24.1	120.7	121.4	7.18	6.09
North Pike	30-Jun	Control	High	High	18.75	20.6	17.3	115.8	116.0	6.86	7.02
North Pike	20-Jul	Control	High	High	23.75	23.4	24.3	126.6	118.6	6.81	6.60
North Pike	3-Aug	Control	High	High	26.75	24.5	26.3	-	127.8	-	6.81
North Pike	13-Aug	Control	High	High	23.25	21.3	22.4	118.9	119.4	4.46	7.17
North Slough	23-Jun	Control	High	High	21.50	20.5	21.0	114.8	117.0	7.72	7.72
North Slough	6-Jul	Control	High	High	16.75	24.8	23.4	122.6	122.5	7.07	6.60
North Slough	24-Jul	Control	High	High	26.00	24.6	26.0	125.1	139.2	6.55	6.54
North Slough	5-Aug	Control	High	High	-	22.4	-	124.9	-	6.98	
South Slough	7-Jul	Control	Low	Low	19.50	22.7	19.5	115.8	116.1	7.54	6.84
South Slough	25-Jul	Control	Low	Low	18.00	25.7	23.5	115.2	120.5	6.95	6.92
South Slough	9-Aug	Control	Low	Moderate	23.25	24.5	23.0	123.6	121.7	6.71	4.55
Portage	9-Aug	Control	High	High	23.25	23.4	-	124.9	124.6	6.79	4.42
Portage	13-Aug	Control	High	High	23.25	21.5	22.0	126.8	121.0	6.47	6.79
Portage	15-Aug	Control	High	High	20.25	24.5	23.1	123.6	121.9	4.57	4.42

Table 2.7. Summary of NMS ordination results of environmental variables from fish surveys.

Variable	Axis 1		Axis 2	
	r	tau	r	tau
Catch Time (H)	-0.302	0.127	0.216	-0.045
Water Temp (°C) at Set	0.138	0.029	-0.203	-0.237
Water Temp (°C) at Pull	-0.175	0.063	-0.074	-0.153
Conductivity (µS) at Set	-0.028	0.079	-0.27	-0.388
Conductivity (µS) at Pull	-0.439	-0.077	0.187	-0.165
pH at Set	-0.144	-0.159	0.277	0.329
pH at Pull	-0.338	-0.146	0.576	0.372

Table 2.8. Summary of NMS ordination results for fish surveys across sites and sampling dates.

Site	Site Code	Date	Axis 1	Axis 2	EWM Abundance	Native Macrophyte Abundance
Pike Bay 1	PB1	16-Jun	0.83335	0.82408	High	Moderate
Pike Bay 1	PB1	17-Jun	0.67853	0.95944	High	Moderate
Pike Bay 1	PB1	28-Jun	0.32177	0.66344	Moderate	Moderate
Pike Bay 1	PB1	5-Jul	0.15425	0.18373	Low	Moderate
Pike Bay 1	PB1	26-Jul	0.26996	-0.34926	Low	High
Pike Bay 1	PB1	4-Aug	0.05732	-0.22376	Low	High
Pike Bay 1	PB1	14-Aug	0.83322	-0.81718	Moderate	High
Pike Bay 2	PB2	16-Jun	-0.27940	-0.15637	High	Low
Pike Bay 2	PB2	17-Jun	-0.02116	0.32383	High	Low
Pike Bay 2	PB2	27-Jun	-0.13529	0.18947	Moderate	Low
Pike Bay 2	PB2	5-Jul	-0.10916	0.01763	Low	Moderate
Pike Bay 2	PB2	27-Jul	-0.37199	-0.74819	Low	Moderate
Pike Bay 2	PB2	4-Aug	0.26100	-0.56186	Low	Moderate
Pike Bay 2	PB2	14-Aug	-0.39719	-1.00716	Low	Moderate
Oskar Bay	OB	13-Jun	-1.44322	0.86104	Low	Low
Oskar Bay	OB	28-Jul	-1.09381	0.37179	Low	Low
Marsin	M	14-Jun	-1.56274	0.42523	Low	Low
Marsin	M	1-Aug	-1.32476	-0.16007	Low	Low
North Pike	NP	30-Jun	0.25439	0.47836	High	High
North Pike	NP	20-Jul	0.57701	0.17957	High	High
North Pike	NP	3-Aug	0.30275	0.25715	High	High
North Pike	NP	13-Aug	0.18619	0.01436	High	High
North Slough	NS	23-Jun	0.97113	0.70527	High	High
North Slough	NS	6-Jul	0.38894	0.35328	High	High
North Slough	NS	24-Jul	1.03600	0.21091	High	High
North Slough	NS	5-Aug	2.17279	-0.95702	High	High
South Slough	SS	7-Jul	-1.57133	-0.51506	Low	Low
South Slough	SS	25-Jul	-0.73803	-0.35025	Low	Low
South Slough	SS	9-Aug	-1.23939	-0.41072	Low	Moderate
Portage	P	9-Aug	0.53745	-0.48000	High	High
Portage	P	13-Aug	0.34850	-0.83503	High	High
Portage	P	15-Aug	0.10291	-0.40666	High	High

Table 2.9. Summary of NMS ordination results for all fish species.

Species	Species Code	Axis 1		Axis 2	
		r	tau	r	tau
Alewife	AW	-0.057	-0.121	-0.001	-0.029
Black crappie	BC	0.502	0.460	0.347	0.238
Bluegill	BG	0.227	0.137	-0.030	0.007
Blacknose shiner	BNS	-0.310	-0.218	-0.282	-0.234
Bullhead sp.	BH	0.523	0.634	-0.098	0.049
Eurasian ruffe	ER	-0.234	-0.209	0.174	0.162
Golden shiner	GS	0.335	0.370	-0.500	-0.398
Johnny darter	JD	-0.458	-0.329	-0.021	-0.015
Largemouth bass	LMB	0.317	0.354	0.129	0.354
Northern pike	NOP	0.175	0.212	-0.033	-0.015
Northern pearl dace	NPD	-0.060	-0.105	0.051	0.040
Pumpkinseed	PS	0.565	0.622	-0.632	-0.428
Pumpkinseed x Bluegill hybrid	PSBG	-0.034	-0.033	-0.193	-0.148
Rock bass	ROB	-0.352	-0.154	-0.559	-0.463
Sculpin sp.	SCU	-0.336	-0.234	-0.139	-0.137
Silver redhorse	SLR	-0.060	-0.106	-0.170	-0.184
Smallmouth bass	SMB	-0.349	-0.264	0.555	0.516
Spottail shiner	STS	-0.411	-0.255	-0.013	0.006
Trout perch	TP	-0.246	-0.220	0.045	0.046
Walleye	WAL	0.047	0.035	-0.050	-0.046
White sucker	WSU	0.044	0.000	0.415	0.196
Yellow perch	YP	0.051	0.094	-0.384	-0.376
Juvenile sunfish	JSF	0.488	0.381	0.337	0.185

Figures

Figure 1.1. Map of the Keweenaw Waterway. Image source: Google Earth.

Figure 1.2. Sampling sites in the Keweenaw Waterway. Sites treated with herbicide (Pike Bay 1 and 2) are represented by closed triangles, while open circles represent non-treatment sites. Image source: Google Earth.

Figure 1.3. Macrophyte numeric categorical gradient for rake samples. Image source: Many Waters LLC, USFS Ottawa National Forest.

Figure 1.4. Mean abundance of a) Eurasian watermilfoil (EWM) (ANOVA, $F_{14,201} = 2.30$, $p = 0.04$) and b) native macrophytes (ANOVA, $F_{14,201} = 2.13$, $p = 0.05$) from toss rakes across site and sampling month. “NS” indicates site was not surveying during that sampling period. Error bars represent standard error of the mean for each month. Darker bars of Pike Bay 1 and 2 are treatment sites, for which the July and August results represent post-treatment surveys. Marsin was not surveyed for macrophytes.

Figure 1.5. Mean native macrophyte abundance as a function of Eurasian watermilfoil (EWM) abundance across all macrophyte surveys with ($R = 0.45$, $p = 0.07$) and without post-treatment results ($R = 0.62$, $p = 0.03$). Reference sites are represented by open circles, while treatment sites are represented by triangles (gray = pre-treatment, black = post-treatment). Linear trendline of all surveys is dashed, and solid when post-treatment surveys were excluded. Error bars represent standard error.

Figure 1.6. Species richness (total # of unique species detected in a survey) relative to a) mean native macrophyte relative abundance ($r = 0.53$, $p = 0.03$) and b) mean Eurasian watermilfoil (EWM) relative abundance ($r = 0.27$, $p = 0.30$). Error bars represent standard error. Reference sites are represented by open circles, pre-treatment sites by black triangles, and post-treatment sites by gray triangles.

Figure 1.7. Scatter plot of macrophyte survey sites across sampling dates relative to categorical abundance of a) Eurasian watermilfoil (EWM) and b) native macrophytes using nonmetric multidimensional scaling (NMS). Closed symbols represent sites with low abundance of EWM, gray symbols are moderate abundance of EWM, and open symbols represent sites of high EWM abundance. Circles are reference sites, treatment sites are designated with triangles. For site codes see description for Table 1.4.

Figure 1.8. Scatter plot of macrophyte species using nonmetric multidimensional scaling. Arrow represents water depth (m). For species codes see description for Table 1.3.

Figure 2.1. Orientation of fyke nets in littoral zone.

Figure 2.2. Mean fish abundance (log-transformed) relative to the categorical abundances of a) Eurasian watermilfoil (EWM) (ANOVA, $F_{2,29} = 2.25$, $p = 0.12$) and b) native macrophytes (ANOVA, $F_{2,29} = 0.68$, $p = 0.52$). Error bars represent standard error.

Figure 2.3. Mean fish biomass (g) (log-transformed) relative to a) Eurasian watermilfoil (EWM) and native macrophyte relative abundances (ANOVA, $F_{2,23} = 3.48$, $p = 0.02$) and b) sampling month (ANOVA, $F_{2,29} = 2.5$, $p = 0.10$). Error bars represent standard error.

Figure 2.4. Mean fish abundance and biomass (g) relative to mean Eurasian watermilfoil (EWM) relative abundance (a-b), mean native macrophyte relative abundance (c-d), and mean macrophyte species richness (e-f). Error bars represent standard error. Each point represents a survey site.

Figure 2.6. Mean fish length (mm) relative to the abundance of a) sampling month (ANOVA, $F_{2,29} = 11.41$, $p = 0.0003$), b) Eurasian watermilfoil (EWM) relative abundance (ANOVA, $F_{2,29} = 0.22$, $p = 0.80$), and c) native macrophyte relative abundance (ANOVA, $F_{2,29} = 10.03$, $p = 0.0005$). Error bars represent standard error.

Figure 2.7. Mean fish weight (g) (log-transformed) relative to a) sampling month (ANOVA, $F_{2,29} = 7.14$, $p = 0.003$), b) Eurasian watermilfoil (EWM) relative abundance (ANOVA, $F_{2,29} = 1.14$, $p = 0.33$), and c) native macrophyte relative abundance (ANOVA, $F_{2,29} = 9.62$, $p = 0.0006$). Error bars represent standard error.

Figure 2.8. Mean fish length (mm) and fish weight relative to mean relative abundances of a) Eurasian watermilfoil (a-b) and native macrophytes (c-d). Error bars represent standard error. Each point represents a survey site.

Figure 2.9. Mean fish species richness (# of species averaged per net) relative to Eurasian watermilfoil and native macrophyte relative abundance (ANOVA, $F_{8,23} = 2.33$, $p = 0.09$). Error bars represent standard error.

Figure 2.10. Scatter plot of fish survey sites across sampling dates relative to categorical abundance of Eurasian watermilfoil (EWM) using nonmetric multidimensional scaling (NMS). For site codes see description for Table 2.8.

Figure 2.11. Scatter plot of fish species and environmental variables (arrows) using nonmetric multidimensional scaling. For fish species codes see description for Table 2.9.

Figure 2.12. Mean invertebrate abundance (# / sampling point) (log-transformed) relative to the relative abundance of a) Eurasian watermilfoil (EWM) (ANOVA, $F_{2,40} = 2.31$, $p = 0.03$) and b) native macrophytes (ANOVA, $F_{2,40} = 25.87$, $p < 0.0001$). Error bars represent standard error.

Figure 2.13. Mean monthly invertebrate abundance (# of individuals per sampling point) (log-transformed) relative to a) mean Eurasian watermilfoil relative abundance (EWM) and b) mean native macrophyte relative abundance. Error bars represent standard error. Each point represents a survey site.

Figure 2.14. Mean benthic macroinvertebrate abundance (# / sampling point) (log-transformed) relative to the relative abundances of native macrophytes and Eurasian watermilfoil (EWM) (ANOVA, $F_{7,35} = 2.25$, $p = 0.09$). “NR” indicates that that habitat type was not represented during our sampling period. Error bars represent standard error.

Figure 2.15. Mean benthic macroinvertebrate abundance (# of individuals per sampling point) (log-transformed) relative to a) mean Eurasian watermilfoil (EWM) relative abundance, and b) mean native macrophyte relative abundance. Error bars represent standard error. Each point represents a sampling month at a survey site.

Figure 2.16. Mean taxa richness (# of taxa / sample) relative to abundance of a) Eurasian watermilfoil (EWM) (ANOVA, $F_{2,40} = 7.14$, $p = 0.002$) and b) native macrophytes (ANOVA, $F_{2,40} = 9.35$, $p = 0.0005$). Error bars represent standard error.

Figure 2.17. Mean invertebrate diversity (per sample) relative to abundance of a) Eurasian watermilfoil (EWM) (ANOVA, $F_{2,40} = 0.25$, $p = 0.78$) and b) native macrophytes (ANOVA, $F_{2,40} = 8.75$, $p = 0.0007$). Error bars represent standard error.

Figure 2.18. Mean invertebrate taxa richness and diversity relative to mean Eurasian watermilfoil (EWM) relative abundance (a-b) and mean native macrophyte relative abundance (c-d). Error bars represent standard error. Each point represents a survey site.

Appendix

Table 1. Summary of fish survey results per net.

Site	Date	# of Nets	Mean Fish Abund/Net	Mean Fish Biomass/Net	Mean Fish Length (mm)	Mean Fish Weight (g)	Species Richness	Diversity	EWM	Native
Pike Bay 1	6/16/2016	3	124	6927.9	132	55.9	6	0.46	High	Moderate
Pike Bay 1	6/17/2016	3	149	7831.8	124	52.7	12	0.42	High	Moderate
Pike Bay 1	6/28/2016	3	68	3453.9	106	50.5	9	0.31	Moderate	Moderate
Pike Bay 1	7/5/2016	3	38	1830.5	115	49.0	10	0.46	Low	Moderate
Pike Bay 1	7/26/2016	3	31	778.9	78	24.9	8	0.23	Low	High
Pike Bay 1	8/4/2016	3	29	1340.7	108	45.7	10	0.22	Low	High
Pike Bay 1	8/14/2016	3	90	1215.1	83	25.0	11	0.40	Moderate	High
Pike Bay 2	6/16/2016	3	26	3643.0	180	141.9	13	0.20	High	Low
Pike Bay 2	6/17/2016	3	38	3745.7	157	100.3	12	0.42	High	Low
Pike Bay 2	6/27/2016	3	37	3649.2	142	98.6	10	0.26	Moderate	Low
Pike Bay 2	7/5/2016	3	38	2521.9	119	66.4	12	0.22	Low	Moderate
Pike Bay 2	7/27/2016	3	19	2382.2	118	123.2	11	0.18	Low	Moderate
Pike Bay 2	8/4/2016	3	51	1715.7	79	33.6	10	0.28	Low	Moderate
Pike Bay 2	8/14/2016	3	19	1588.6	111	83.6	8	0.26	Low	Moderate
Oskar Bay	6/13/2016	3	9	1294.3	181	138.7	4	0.48	Low	Low
Oskar Bay	7/28/2016	3	21	850.7	94	39.9	9	0.22	Low	Low
Marsin	6/14/2016	3	15	3316.6	184	226.1	9	0.34	Low	Low
Marsin	8/1/2016	3	14	614.8	94	43.9	6	0.23	Low	Low
North Pike	6/30/2016	3	64	3179.1	108	49.7	9	0.46	High	High
North Pike	7/20/2016	3	95	4768.6	100	51.1	11	0.26	High	High
North Pike	8/3/2016	3	50	1232.8	91	24.7	8	0.50	High	High
North Pike	8/13/2016	3	39	1062.3	97	27.5	7	0.29	High	High
North Slough	6/23/2016	3	156	12519.8	142	80.4	10	0.27	High	High
North Slough	7/6/2016	3	50	4293.4	145	85.9	7	0.31	High	High
North Slough	7/24/2016	3	136	1886.0	70	13.9	11	0.33	High	High
North Slough	8/5/2016	3	603	1580.9	51	12.6	9	0.80	High	High
South Slough	7/7/2016	3	6	586.6	154	92.6	10	0.08	Low	Low
South Slough	7/25/2016	2	11	970.5	150	88.2	7	0.14	Low	Low
South Slough	8/9/2016	3	16	639.8	101	40.8	7	0.32	Low	Moderate
Portage	8/9/2016	1	44	309.8	71	7.0	6	0.71	High	High
Portage	8/13/2016	1	28	1831.3	125	67.8	7	0.16	High	High
Portage	8/15/2016	2	31	670.6	98	21.6	9	0.18	High	High