Devil’s Advocate: An Assessment of Housing Density on Littoral Macrophyte Composition in Devil Lake, ON

Abbie-Rose Forde

Affiliated with the Arnott Lab and Devil Lake Association

A thesis submitted to the Department of Biology

in partial fulfilment of the requirements for

the degree of Bachelor of Science (Honours)

Queen's University

Kingston, Ontario, Canada

April 2025

ABSTRACT

Preservation of our freshwater lakes is important for mitigating loss of native biodiversity and for promoting longevity of these critical habitats. With numerous stressors acting on them, it's important we understand how they are impacted and the mechanisms involved, by monitoring changes in the aquatic environment over time. The aim of this study is to understand the impact of increasing lakeshore residential development on Devil Lake, by estimating the abundance and species composition of macrophytes in the littoral zone based on density type. A map of the shoreline residential density was plotted based on the presence, or lack thereof at least one building, allowing us to quantify areas as: high or low housing density, with contrasting protected zones. A total of 60 sites, with 20 from each housing category were randomly selected for analysis. Transects were 100m long and set up at a distance to shore where depth was ~2m. Sites were not considered if they had too steep an incline or had a primarily rocky shoreline, in which event another transect was randomly selected. At each transect, a macrophyte hoop was lowered onto the lake floor 4 times (~25m). Species were identified and percent composition within each hoop was recorded. Macrophyte cover was higher in protected regions than in the high or low densities, suggesting a significant effect of housing density on the abundance of aquatic plants. Macrophyte species composition varied among sites and no significant difference in community composition was observed, however some change in species type (emergent, submergent) was observed, with more emergent species in low density sites. Future studies should continue to explore the effect of stressors on species characteristics to determine if other factors play a role in shaping these communities. With this information, we hope to gain insight into the impacts of human activities on the vulnerable littoral regions to inform best long-term management practices.

ACKNOWLEDGMENTS

I would like to give a huge thank you to my supervisor Dr. Shelley Arnott for allowing me to do this project and her continued guidance and support along the way. I would like to thank Dr. Brian Cumming for his support as my committee member. I would like to thank Tim, Nancy, Jim, Jana and the rest of the Devil Lake Association for the use of their property/equipment, time, and their unwavering dedication towards the project – none of this would have been possible without you! A thank you to my associates in the Arnott lab and friends at QUBS for all their assistance during the field season. Lastly, I would like to thank my coworker Sophie Mably for her hard work and support throughout the field season, I had such an amazing time working with you!

TABLE OF CONTENTS

LIST OF FIGURES:

LIST OF TABLES

INTRODUCTION:

Stressors that Affect Aquatic Habitats

Anthropogenic stressors that affect freshwater ecosystems are numerous and well known but the ways in which each one impacts the biodiversity and functionality of a lake, either exclusively or associatively with other factors, are of growing interest in the field (Madzivanzira et al., 2023). Some studies have explored nutrient pollution and eutrophication as they relate to agricultural runoff, sewage waste, and industrial waste runoff, with their potential to introduce harmful algal blooms and fish kills (Akinnawo, 2023; Neijnens et al., 2024). Others have explored chemical and microplastic pollution and the harmful effects that excess toxins can have on the environment (Pinheiro et al., 2021). Overfishing and recreational boating activities are also known disruptors to the food web because they can introduce invasive species. This can directly affect population counts, shifting community dynamics of many aquatic species, increasing within habitat pressures (Smith et al., 2021). Shoreline development (i.e. houses, docks, boathouses, roads, parks, etc.) was the focus of this study, and it is a form of habitat alteration that directly affects the environment surrounding a lake. When studying pre-disturbance land-use against current trajectories of shoreline development, this allows us to track any significant and potentially harmful changes in the aquatic environment (Sass et al., 2010). With such a broad range of environmental influences from lakeshore development alone, we decided to narrow in on the impacts of this stressor on the aquatic environment closest to the shore; not only due to its importance to ecosystem health and its susceptibility to rapid and profound changes from land use, but also to fill in the gaps in literature where it has otherwise been lacking (France, 1995).

The Importance of the Littoral Zone

Lakes are made up of two primary zones, the pelagic zone and the littoral zone. The littoral habitat is classified as the nearest to shore aquatic environment. A littoral community is typically made up of sediment, macrophytes, aquatic species and coarse woody habitat (CWH). In comparison to the rest of the lake area, the littoral zone is quite small, but it has the most in terms of productivity and complexity (Dustin & Vondracek, 2017). It's an important component of lake ecosystems critical for promoting biodiversity and providing structure to aquatic organisms including fish, benthic and macro invertebrates (Mayo & Jackson, 2006). A study by Vadeboncoeur et al. (2011) on the great lakes found that the littoral zone played host to 93% of species found within the lakes and 72% of the species were restricted to this area for survival (Vadeboncoeur et al., 2011). Moreover, results from a study by Vander Zanden et al. (2011), showed that it took less primary production to support a fish species in littoral than pelagic zone, consistent with the importance for prioritizing this region.

Importance of Macrophytes in the Littoral Zone

The macrophytes found within this region are often diverse (floating, free-floating, emergent, and submergent), with a wide range of uses and functions to the organisms that live there. They are an essential part of the complexity of the littoral community, with each type of macrophyte providing food and shelter to aquatic organisms in different ways. As primary producers, they have the unique ability to provide the energy that is sent up the food web; and alongside algae they help oxygenate the surrounding environment (Madzivanzira, 2023); Importantly, they also provide structure for fish communities and their prey; thereby influencing the spawning rate, refuge, and feeding opportunities for nearshore fishes, as well as the abundances, growth rates, mean lengths, and trophic interactions of their young (Dustin and Vondracek, 2017).

With high biodiversity and structural complexity, this gives way for complex predator-prey and other species interactions between and amongst communities within the littoral zone and lake wide. Studies show that many fish species rely heavily on littoral-benthic resources, which help promote fish species diversity (Vadeboncouer, 2011). With decreasing vegetation, fish species have been declining with both a loss of a primary food source (benthic invertebrates) and increased risk of predation from loss of habitat and shelter (Czarnecka, 2016; Dustin & Vondracek, 2017; Mushet et al., 2023). In the study by Dustin & Vondracek (2017), they assessed macrophyte cover nearshore versus lake-wide IBI (index of biotic integrity) across gradients of lakeshore development, using docks as a proxy. They found that not only did macrophyte abundance decline, but nearshore fish IBI decreased; but lake-wide (open water) IBI showed no significant change. Other studies have found similar evidence that human activities can reduce food chain length. A study by Ziegler et al. in 2015, showed that shallow lakes with higher macrophyte biomass, support longer food chains, independent of ecosystem size and nutrient concentration – when this is at stake, there are potential consequences for overall ecosystem function.

This comes back to the idea that a loss of macrophytes could cause cascading effects throughout the littoral community because of the heavy reliance on these species. They have also been known to play host to certain vegetation dwelling species, that rely on these species not only as habitat but as a source of nutrients (Dustin & Vondracek, 2017).This extends to larger animals such as waterfowl (ducks, geese, etc.) that like to graze on the larger emergent and submergent plants. Additionally, macrophytes act as major sinks for essential nutrients (P, C, N) and help with the flow of nutrients between terrestrial and aquatic ecosystems, and throughout the food web (Kufel & Kufel, 2002). Through structure in their leaves and roots, they can absorb nutrients stored in the sediment, incorporating them into their biomass, preventing nutrients from fueling harmful algal blooms. Submergent plants such as Canadian waterweed and tape grass, are known for being particularly useful because they take up dissolved nitrogen and phosphorus directly from the water column (Gosselin et al., 2018). Despite their many uses in lake systems, their susceptibility to stressors risks the health and longevity of the littoral zone (K. S. Cheruvelil & Soranno, 2008).

The effect of Anthropogenic Stressors on Macrophyte Communities

Previous studies have looked at how environmental stressors such as biotic (herbivory, invasive species, competition, pathogens, and diseases) and abiotic (water chemistry, temperature, substrate composition, and hydrological conditions) affect macrophytes within the littoral zone (Madzivanzira et al., 2023); and these help us understand the types of relationships and trends observed when plant communities are under stress. Nutrient addition is a major contributor to the stress placed on aquatic systems and over time can cause shifts in plant community abundance. A study done in the south-central region of Ontario looked at plant communities' nutrient stoichiometry across several lakes to determine if there was an impact from increased land use (Frost & Hicks, 2012). The researchers found that C:N and C:P nutrient ratios were lower in plant communities found in the littoral zones near areas of high land-use, impacting their functional health. Physical alteration of the littoral zone, such as macrophyte removal or the addition of a biological or chemical control, is another significant stressor placed on these ecosystems. Directly altering the ecological environment by destroying or removing macrophytes, leaves less habitat for fish to nest, less places for benthic invertebrates to inhabit, and can create loose sedimentation impacting water clarity among other issues (Frost & Hicks, 2012). Land-use change is one of the major stressors that plays a role in shaping nearshore environments. Studies have linked a decrease in plant biomass to dock installation and have shown that aquatic species will tend towards areas that have more macrophyte cover, especially those in crucial stages of their development (Dustin & Vondracek, 2017). Residential housing development will be the proxy of focus in this study, but it's important to keep in mind that lakeshore development cannot be thought of exclusively from other metrics of lakeshore development (manicured properties, gardens, increased road construction and subsequent salt runoff, potentially faulty septic systems, recreational/commercial boating, etc.) it's simply one factor.

Studies that have explored metrics of lakeshore development on macrophytes have found that littoral macrophyte abundance is influenced by residential development. Many were large-scale, looking at multiple lakes within a similar geographic area; lakes that ranged in size, water chemistry, clarity, and depth (Alexander et al., 2008; K. S. Cheruvelil & Soranno, 2008; Hicks & Frost, 2011a; Radomski et al., 2010). Most of these studies were based in the US and looked at macrophytes across different metrics of lakeshore development. The consensus was that macrophyte cover decreases with more development; and for those studies that examined multiple metrics and not just housing density, they found abundance varied based on the type of development and the surrounding landscape (Alexander et al., 2008; K. S. Cheruvelil & Soranno, 2008). Radomski & Goeman (2001) took a similar approach to this study by focusing on emergent and floating vegetation characteristics in response to housing density and they found a 66% reduction in vegetative cover. They also went beyond the scope of this study and identified a correlation between loss of macrophytes and their northern pike species which has interesting implications for littoral community studies. Alexander et al. (2008) tracked changes in both abundance and community composition in response to many metrics (manicured lawns, buildings, docks, roads, etc.). An interesting find of this study showed shifts in community composition, depending on the landscape position of the lake. They showed that elodeids, a type of fast growing submergent macrophyte that can outcompete isoetids, were found in the low-lying landscape lakes, whereas the isoetids, a slower growing macrophyte, were found more in the lakes with a high landscape position. This shows that nutrient level as a mechanism of lakeshore development can affect water quality, changing based on landscape and this influences the type of macrophyte community found there, with invasive like plants having more success where alkalinity increases.

Hicks & Frost (2011) was based in Canada, and they assessed biomass and species composition of littoral macrophytes across cottage densities (0-23 cottages/km shoreline). A unique feature of this study was that they sampled at different depths (0.5m and 1.5m) to determine if that plays a role in macrophyte composition. They found that not only did biomass decrease with increasing housing density, but the shallower depth was more vulnerable and showed higher rates of changes in species richness in relation to cottage development. Like Alexander et al. (2008), they also observed shifts in aquatic plant structure, but they saw a clear shift from floating and emergent species on undeveloped lakes to submergent and low lying on developed lakes. One thing not explored by these studies, however, was the presence of invasive species from increased boating activity presence on the lake.

Invasive species are an important metric of lakeshore development that due to their nature to outcompete native species, can completely change the community composition in a lake if conditions are ideal and trends favor their proliferation. Studies show that when monitored over decades, invasive macrophytes have caused changes to littoral community abundance and species composition (Ranta & Toivonen, 2008). Boating, agriculture, and aquarium trade are particularly important contributors to the introduction of alien species because they facilitate the transport of invasives across water systems (Strayer, 2010). Research has shown that when alien species are introduced to an environment they can dominate over other species and risk homogeneity within the aquatic plant community (Havel et al., 2015). Research on invasive species as a biproduct of human activity and land-use (recreational watersports, boating, fishing, etc.) is of growing concern – as it pertains to the health and functional diversity of communities within and across lakes (Twardochleb & Olden, 2016). Invasive species can also be linked to housing development as it pertains to increased dock construction and higher than pre-disturbance activity, increasing the risk of species being introduced to the environment. Invasive species and their abundance in the littoral community of Devil Lake will be explored further in this study with housing density as the primary metric of development.

Preserving the biodiversity and ecological health of large lakes will elicit a stronger focus on integrating littoral zones into our understanding of lake ecosystems and targeted efforts to reduce human impacts along the shoreline (Vadeboncoeur et al., 2011). Notable gaps in our understanding of how these ecosystems function lies in our understanding of the independent mechanisms behind a decline in macrophyte richness and abundance in relation to lakeshore development. Studies that address these issues are a great way to quantify the scope of the issue and represent macrophytes in literature where they may be lacking. Understanding even the slightest shift in littoral macrophyte structure or a shift from native to more dominant to invasive species (Radomski et al., 2010), is very important in our predictions of the projected health and stability of freshwater lakes. Especially when we consider that fewer studies have been done in Canada and those that have focus mainly on the Kawartha Lakes region, many of which are impacted differently by nutrients and water-level variations (KLSA, 2023), comparatively to Devil Lake. In this study, I have assessed changes in macrophyte abundance and composition associated with housing development. With this information my study will aim to answer the question *"does lakeshore development have a significant impact on littoral macrophyte abundance and species composition in a large oligotrophic lake?"* (CRCA, 2017). I will address this question by examining two hypotheses; **H1: does lakeshore residential development decrease macrophyte abundanc**e and **H2: does lakeshore residential development cause shifts in community composition of macrophytes**. I predict that with high density, we expect to see a significant decrease in macrophyte species abundance and richness, with low density having slightly more cover and diversity, and baseline conditions (protected habitat) being most abundant and diverse. I also predict that with increasing lakeshore development we will see more invasive species than native species because developed areas have a higher risk of being sites where invasive species are introduced. I predict that we will see shifts community composition towards submergent macrophytes away from emergent species because with increased exposure (surface and underwater) to pollutants that enter the system, this could drive community composition towards tolerant species. I also see emergent species as being at higher risk of being extracted because they are visually or physically a deterrent to cottagers who want a clear environment around their dock.

METHODS

Study Site

With a lake circumference of 58km and an area of 10 sq km, Devil Lake is one of the largest, oligotrophic, lakes in Frontenac Provincial Park (CRCA, 2017). In the 1850s, the Devil Lake watershed experienced logging and the construction of a local sawmill increased lakeshore housing developments. Later this became an issue when a lack of zoning laws saw many properties built near one another (Frontenac Provincial Park, 2021). West-end Devil and the houses closest to Bedford Mills are the primary areas of high development (APPENDIX E), with low gradients scattered around the lake. Devil Lake also has a significant portion of its shoreline on the outskirts of Frontenac Provincial Park, setting the protected sites apart from the rest of the developed land. Devil Lake's development status is now listed as high on the Cataraqui Region Lake Report, making it in the top 25% of developed lakes within this region, that are at a higher risk of habitat change and introduction of invasive species (Cataraqui Conservation, 2024). Devil Lake's current invasive species status is classified as low, with only 13 listed invasive species, partially due to their lower level of boat access. There is a major roadway that runs between Kingston and Perth, and this is where the primary boat ramp exists, increasing activity in this region, allowing us to add it to the high-density classification. These clear designations between areas of high and low density of cottages presented us with an ideal situation to test density patterns within a lake system.

Identifying Areas of Interest and Mapping Transects

Using the 'plot layer' on ArcGIS; we mapped the hot and cold spots of residential housing along the nearshore plots of Devil Lake, ON (APPENDIX E). Hot spots were all areas around the lake with significant clustering of housing and cold spots existed where there were no significant density clusters. Sites were included based on the presence of at least one building on a plot of land along the shoreline. With this, 3 classifications of density were created: high, low, and protected areas. High-density regions have 12-28 houses per km, low density regions have 1-11/km and protected areas had 0/km.

Sixty transects were selected for observation. Sites were selected by subdividing the shoreline into 100m transects based on housing density type. Using a random number generator, 20 transects were selected from each density category (Figure 1). In the event a transect had a nearshore environment that was too steep (>45°) and therefore was not proper representation of the impact of residential development, randomly selected backup transects were used. This was assessed on a site per site basis as we arrived on each sampling day. A few of the transects were specifically chosen to ensure that the potential sites met a few requirements – a broad distribution along the shoreline to account for different wind exposures and to include sites of interest to the Devil Lake Association (boat launch, islands, and campgrounds). These areas were of particular interest for their unique activity, associated with higher-than-normal human disturbance and possible introduction of invasive species.

Setting Up Sampling Equipment and Sampling Macrophytes

Black PVC tubing (~2.60m length) was filled with sand and made into a ring so that an equal circular transect (0.75 m diameter) could be used to observe and sample. The Aquatic Plants Guide (KLSA, 2023) is an identification book for macrophytes in the Kawartha Lakes region; this was used to ID the plants found in Devil Lake. On each sampling day, once a desired transect was reached, the transect rope was unravelled and laid out along 50m of the shoreline. The rope was placed roughly 2-3m depth offshore. This distance was swum twice at each site to observe 100m of shoreline. 2-4 transects were swam each day. At each site - shoreline characteristics, cottage density, coordinates, weather, and substrate type (sandy/rocky/vegetated/woody/other) were recorded. The PVC ring was lowered onto the lake bottom 4 times (roughly every ~25m) along the 100m transect, at anywhere up to a metre on either side of the transect (2m wide). Total cover of macrophytes and individual species composition was estimated within the hoop through visual inspection. Species composition at each site was estimated by percent cover. We identified plants to species level and recorded whether the plant was native or invasive. If we were not able to identify species in situ, small samples were cut and transported back to Queen's University Biological Station, in 1L Rubbermaid containers for further identification. This study was conducted over an 8-week study period, from July 3rd – August 19th, 2024.

Analysis and Statistics

Analyses for total percent cover and species composition between sites was assessed using 'R' (R Core Team, 2024). To test for correlation between lakeshore development and macrophyte abundance, I ran a Kruskal-Wallis test on a linear model; with housing density level (high, low, protected) as the categorical predictor and percent cover as the response variable. The results of the linear model were verified using a non-parametric post-hoc test ('Dunn's statistical test'), and normality assumption checks using 'autoplot' on the residuals. The results were placed into a boxplot using the 'ggplot2' package.

To analyze any differences in species composition across the housing density levels, I applied a PCA to a matrix of the data, standardizing using a scaling factor of 10, to account for differences in abundances amongst species. A criterion was applied to the species included in the matrix so that only species present in at least 4 samples (1.5% of all samples). This ensures all unique species are included, while excluding any outliers found only once that are not representative of the larger lake community. A ‘scree plot’ was created to address which principal components were responsible for explaining the most variation in species composition across the sites. PC1 and PC2 were analyzed in a biplot to observe if variation showed clustering amongst the density categories. Species loadings were placed over the biplot to determine community structure trends. Kruskal-Wallis tests was run on the linear models for PC1 and PC2, with habitat type as the categorical predictor. The results of these tests were verified by ‘Dunn’s statistical test’ and plotting the residuals. To further analyze changes in species characteristics (species type and status) between the density categories, a ‘bar plot’ was used to demonstrate total counts of invasive, native, emergent, and submergent species across the transects. Kruskal-Wallis and Dunn’s tests were run on linear models, one for each species characteristic, to determine any significant shift in community composition.

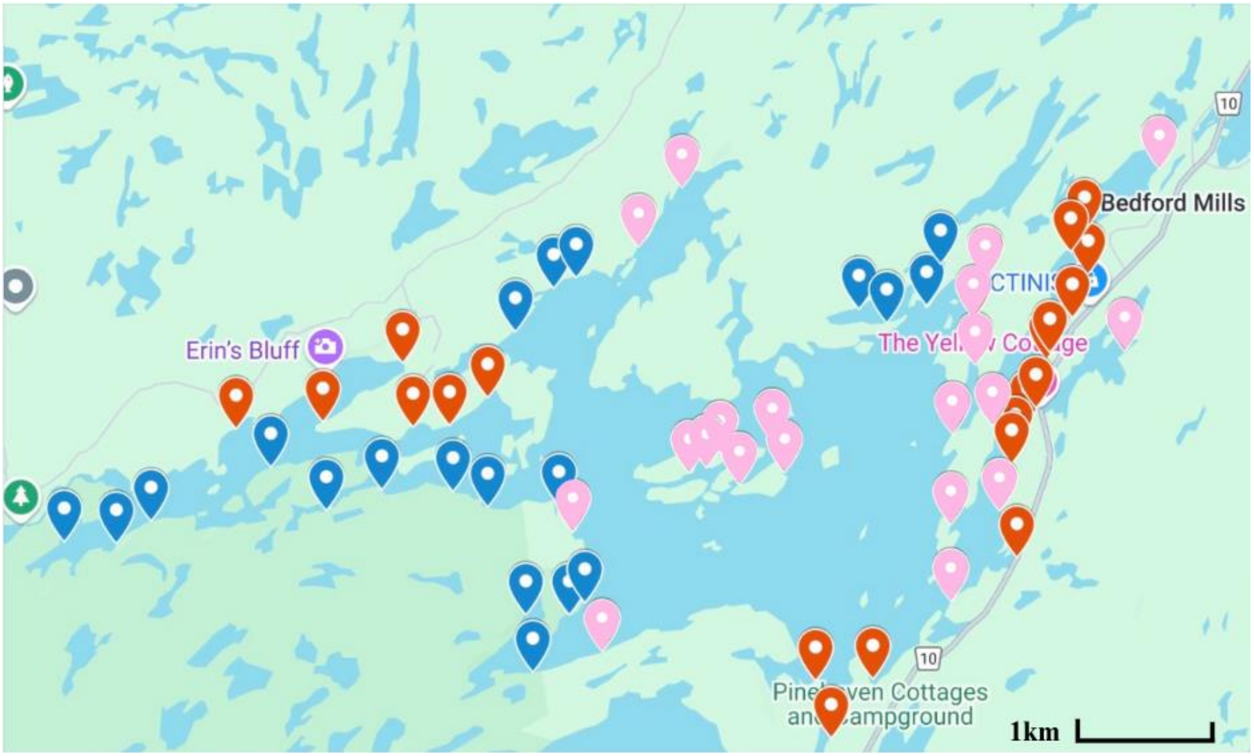


Figure 1. Map showing the designations of randomized transects across Devil Lake, ON. Red markers indicate areas of 'high density' residential housing (Bedford mills/Green Bay campground/West end Devil Lake). Blue markers indicate 'protected' areas, with no residential housing (Frontenac Park/crown land). Pink markers indicate areas of 'low density' residential housing (Buce Bay/Parkers Bay/Pine Haven campground/Islands/Hardwood Bay).

RESULTS

Invasive Species Counts:

The following table represents the cover and areas in which rare invasive species were found, including starry stonewort and curly-leaved pondweed. Starry stonewort was observed 7 times across 6 transects. Curly-leaved pondweed was observed 4 times across 3 transects. We also observed Eurasian milfoil 87 times and water nymph 112 times, across most transects around the lake.

Table 1: Invasive Species Counts

Invasive Species	Percent Cover	Density Type	Transect Location
Starry Stonewort	10%	low	Buce bay (44.60037°N, 76.45648°W)
	10%	low	Loon Song Island (44.58169°N, 76.45266°W)
	75%	low	Vanderbilts Island (44.57660°N, 76.42978°W)
	15%	protected	Buce Bay crown land (44.59406°N, 76.46696°W)
	85%	high	Boat ramp (44.57364°N, 76.42383°W)
	3%	high	Boat ramp (44.57438°N, 76.42330°W)
	5%	high	Boat ramp (44.57438°N, 76.42330°W)
Curly-leaved Pondweed	20%	high	(44.59737°N, 76.41665°W)
	2.5%	protected	Lost Bay (44.59232°N, 76.43798°W)
	5%	high	West end (44.58390°N, 76.49198°W)

Boxplots and Non-Parametric Tests:

To determine if macrophyte cover was reduced in regions with higher housing density compared to protected areas I analyzed percent cover trends within 4 replicates (hoops) of each transect across all habitat types. This helps answer the question “does housing density as a metric of lakeshore development have a significant effect on the abundance of macrophytes within a given littoral community?". I found that percent macrophyte cover was highest on average in the protected habitat type, with high and low housing density environments having significantly less cover (Kruskal-Wallis's test, X^2= 7.51, p=0.023). The protected habitat had higher macrophyte cover compared to the high-density area (Dunn's test p=0.004) and the low-density habitat (p=0.023) (Table 2). The protected habitat type was 19% higher in cover than the high-density habitat type and 15% higher than the low-density habitat type (Table 3).

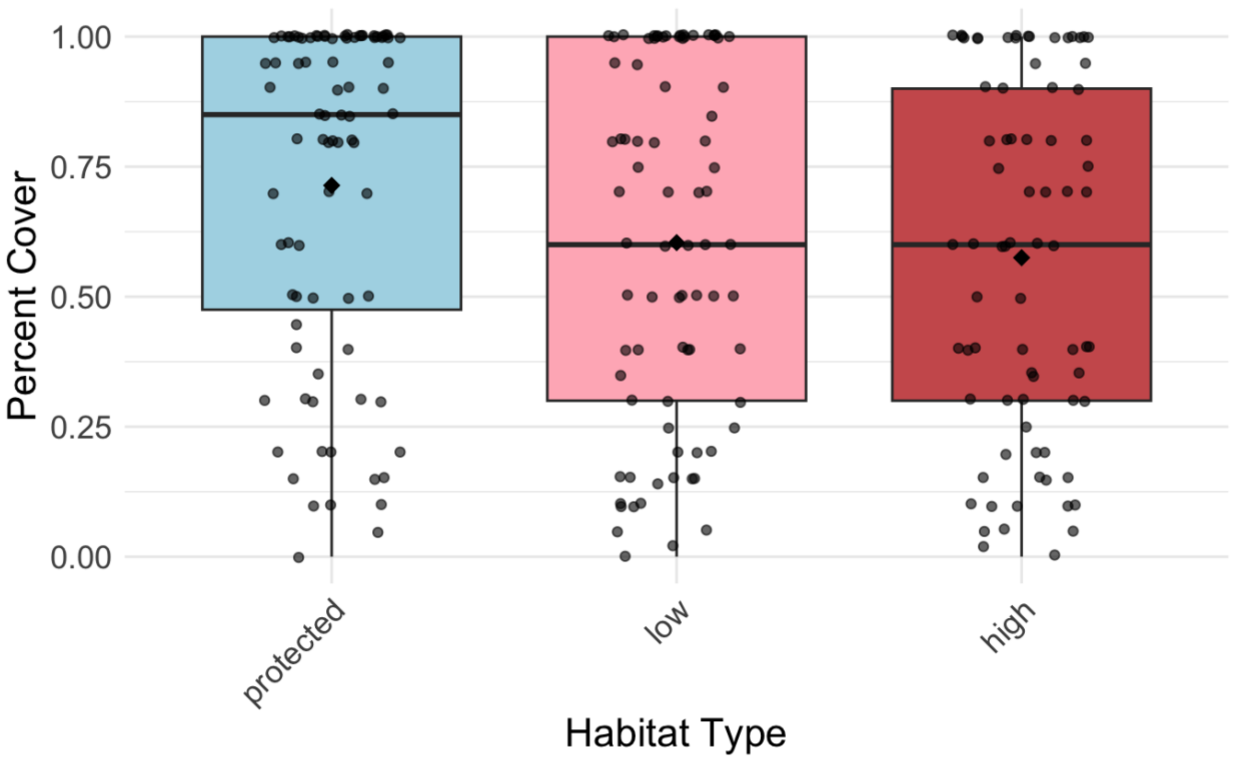


Figure 2. Percent macrophyte cover found within each sampling hoop across the three habitat/density types (protected-blue, high-red, and low-pink). Circles represent individual observations collected from Devil, Lake, ON. Percent cover is reported as a proportion, with 1 equal to 100% cover.

Table 2. Kruskal-Wallis Rank Sum Test for Percent Cover and Dunn's Comparison Test

Data: Percent Cover by Habitat Type				
Kruskal-Wallis Rank Sum	chi-squared = 7.510	df = 2	p-value = 0.023	
Dunn's Test		High-Low	High-Protected	Low-Protected
Z score		-0.620	-2.609	-2.0017
p-value		0.267	0.0045*	0.0227*

Table 3. Percent Cover Difference Calculations

Equation: (high - protected)/protected * 100
High density and Protected -> (0.575 - 0.714) / 0.714 * 100 = 19.47%
Low Density and Protected -> (0.604 - 0.714) / 0.714 * 100 = 15.41%

Sampling Criterion and PCA Analysis:

To analyze the second hypothesis, I tested the percent cover of each macrophyte species found within each hoop, across all density categories to see if there was a difference in macrophyte type or status from housing density pressures. I visualized the composition of each sample using a PCA biplot. I didn't observe any clear clustering in the points (by housing density) indicating that habitat type does not influence a shift in community composition (see figure 2). A scree plot (APPENDIX A) was used to determine which principal components explained the highest proportions of variation. It was determined that PC1 explains 8.1% of variation and PC2 explains 7.2% of variation. Therefore, there is a relationship that exists between PCA components and housing density, but when accompanied by an insignificant Kruskal-Wallis test for PC1 (p=0.471) and PC2 (p=0.0895) (Table 5), this tells us the relationship is not strong, and we fail to reject the null hypothesis. The arrows on the biplot give an indication of which species may fall within similar habitats as explained by the relative component. Figure 2 shows that Richardson's pondweed, muskgrass, baby pondweed, shining pondweed, and water nymph tend to exist in similar transects, as do Sago pondweed, watermilfoil, tape grass, slender pondweed, and Canadian waterweed. Trends that show species loadings facing in opposite directions indicate that when one species is present, the species on the opposing side is likely not present. These results will give us insight into how species composition may be influenced by other species that co-occur in similar regions.

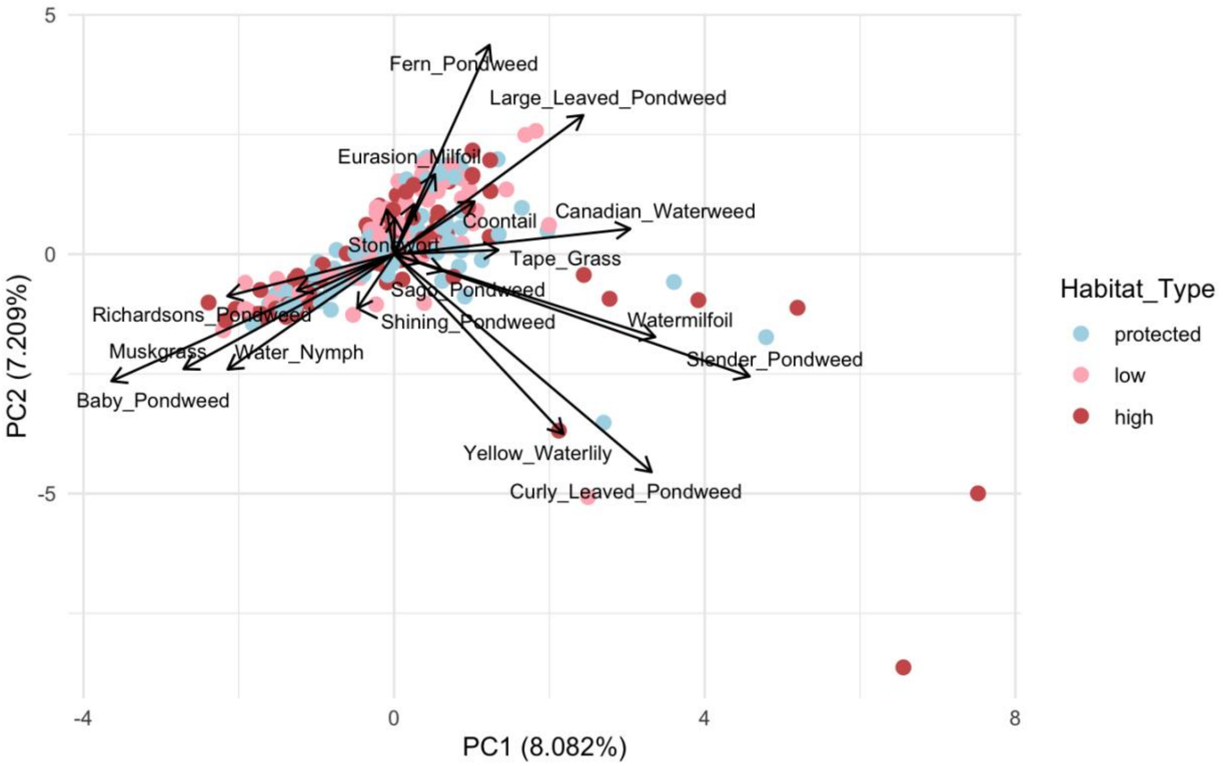


Figure 3. PCA biplot with species loadings (arrows) based on the density categories (protected, low, high). PC1 represents 8.1% of the variation explained and PC2 represents 7.2% of the variation explained by habitat type.

Table 4. Kruskal-Wallis Rank Sum Test for PC1 and PC2

Data: PCA components by Habitat Type			
PC1	Kruskal-Wallis chi-squared = 1.507	df = 2	p-value = 0.4708
PC2	Kruskal-Wallis chi-squared = 4.8267	df = 2	p-value = 0.0895

Species Counts by Characteristic and Habitat Type

To continue analyzing the effect of housing density on species composition, count data was used to observe the presence of invasive species and native species as well as emergent and submergent species in across all densities to give a better scope of how density can influence species characteristics (type and status). Protected sites had the highest number of both invasive species and native species (88 and 349 respectively) (APPENDIX D). Eurasian milfoil and water nymph were present in most sites (in 87 and 112 respectively, out of 240 samples) (Table 1), indicating that their presence across habitat types coupled with a higher abundance in the protected sites gives this high abundance. Emergent species were highest in the low-density sites (21) and submergent species were highest in the protected sites (424) (APPENDIX C). This indicates that housing density may see some shift in species type between the density categories, but insignificant Kruskal Wallis tests (p-values=0.386) (Table 6), suggest that we must fail to reject the null hypothesis and re-examine reasons for this shift in species dynamics.

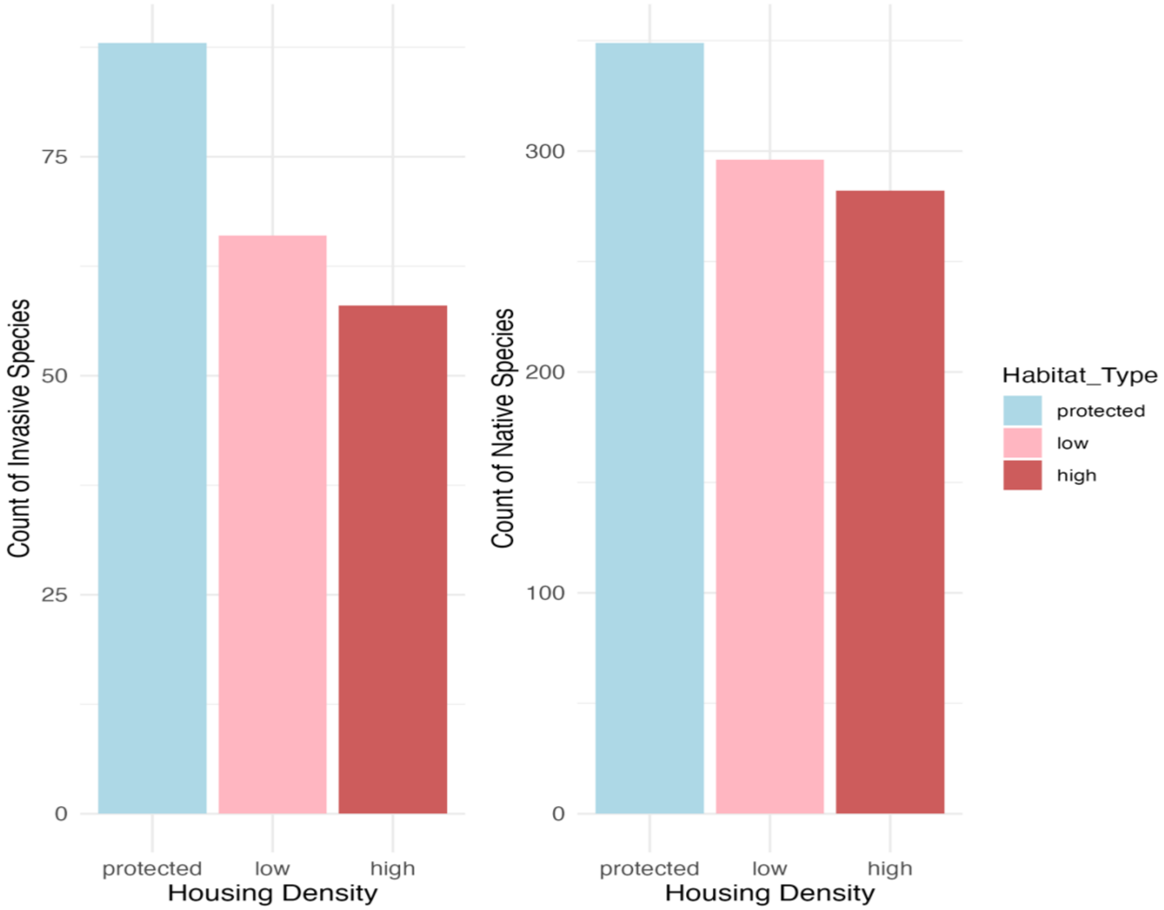


Figure 4. Counts of Invasive and Native species between the density categories (protected, low, and high). All samples were collected from Devil Lake, ON. Species were included if they existed in at least 4 samples (>1.5%).

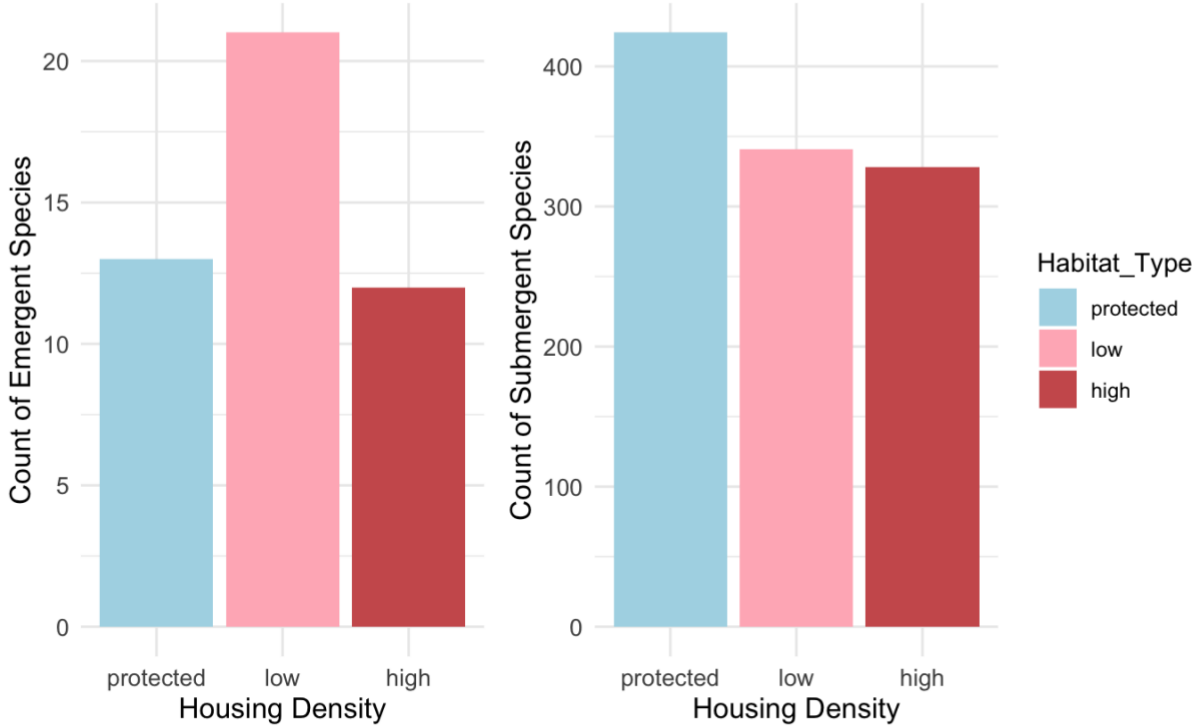


Figure 5. Counts of Emergent and Submergent species between the density categories (protected, low, and high). All samples were collected from Devil Lake, ON. Species were included if they existed in at least 4 samples (>1.5%).

Table 5: Kruskal-Wallis Rank Sum Test for Species Type and Status

Data: Species models by Habitat Type			
Invasive ~ Habitat_Type	Kruskal-Wallis chi-squared = 2	df = 2	p-value = 0.368
Native ~ Habitat_Type	Kruskal-Wallis chi-squared = 2	df = 2	p-value = 0.368
Emergent ~ Habitat_Type	Kruskal-Wallis chi-squared = 2	df = 2	p-value = 0.368
Submergent ~ Habitat_Type	Kruskal-Wallis chi-squared = 2	df = 2	p-value = 0.368

DISCUSSION:

Influence of Housing Density on Macrophytes:

I found that lakeshore housing development reduces littoral macrophyte cover. Macrophyte percent cover in the high-density housing areas (12-28 houses/km) and intermediate/low housing areas (1-11 houses/km) were found to be lower than the abundance of macrophytes in the protected habitat (0 houses/km). Since no significant difference was observed between high and low-density habitat types (p = 0.267), this indicates that any level of cottage development has a similar decreasing effect on macrophyte abundance. When calculated, percent cover was found to be 19.5% less in the high density and 15.4% less in the low-density sites than in the baseline conditions. This tells us that cottage density should be considered a significant player in shaping littoral communities and should be considered a prominent player in the larger metric of lakeshore development.

The second hypothesis examined whether housing density can shift littoral macrophyte composition. Upon classifying all the species observed within the transects as invasive or native (species status), and submergent or emergent (species type), this allowed us to track the distribution of the aquatic plants by their important ecological properties. PCA analysis showed no distinct clustering between the ecological properties of macrophytes and housing density. There is however some variation in species composition being explained by the trends in the data. PC1 and PC2 together explain 15% of the data, indicating some confidence in housing density as a predictor for influencing species composition. Species loadings on the biplot of PC1 and PC2 showed certain species tend to exist in communities together (figure 3). Many of the native species found in Devil Lake tended to co-occur in groups but interestingly, many of the invasive species occurred apart from one another. Species arrows indicate that water nymph (invasive) occurred with richardson's pondweed, muskgrass, baby pondweed and shining pondweed (native), but was primarily separate from the other identified invasive species, Eurasian milfoil and curly-leaved pondweed. Although the tests for PC1 and PC2 by habitat type were not significant (Table 4), the trends observed in these species, particularly when related to the separation of invasives are similar to what other studies have observed (Herkül et al., 2023) and should encourage further analysis.

The bar plots for species counts across the habitat types, show that both native and invasive species were the most abundant in the protected sites and least abundant in the high-density sites (figure 4). This does not match my earlier prediction, that invasive species would be highest in the high-density sites because of increased human and boating activity in those regions. Since Eurasian milfoil and water nymph proliferated in many transects across the lake in all habitat types, this suggests the introduction of these species are not novel and the increased boating activity on the lake has only helped spread them around to all reaches. Submergent species were most abundant in protected sites and least abundant in high density sites, while emergent species were most abundant in the low-density sites (figure 5). These findings were contrary to previous predictions as studies have often demonstrated that macrophyte community composition tends to shift away from emergent on developed shorelines (Hicks & Frost, 2011a; Radomski & Goeman, 2001). The Kruskal-Wallis tests on linear models for species type and status do not confirm any significant shifts in species composition by housing density however (p=0.368), by examining how these trends relate to other studies we will gain an encompassing view of the impact of housing density as it applies to Canadian freshwater lakes.

Significance of Decreased Macrophyte Cover:

The implications of decreased macrophyte cover on the functional ecology of the littoral zone are numerous due to the significant reliance of species on this area and the important contributions of this region to the lake as whole. With less macrophytes to help filter nutrients from the land, nutrient loading is a known risk, which can lead to eutrophication and impact overall lake water quality (Kufel & Kufel, 2002). Nutrients play a role in algae formation as well and with less macrophyte cover, zooplankton community dynamics could shift. Increased nutrients suggests the zooplankton could become more abundant in the water column initially, but changes in their diversity and abundance could decrease over time and this is just one example that parallels can be drawn for many aquatic species (Dodson et al., 2009). Decreased cover also invites unprotected habitat, exposing the lake bottom and the species that live there to their predators creating significant changes in fish and benthic predator-prey dynamics (K. S. N. Cheruvelil, 2005; Vander Zanden et al., 2011). Additionally, when food availability is scarce, fish and waterfowl species may be forced to shift to another food source or rely on other regions of the lake (Dustin & Vondracek, 2017). This suggests that micro-regional shifts in food-prey dynamics could be evident under these conditions, many of which may be difficult to predict.

Some other factors that may influence macrophyte cover include water clarity, nutrient availability, substrate type, water temperature, and hydrology. Water clarity will determine light availability and if the water is turbid, submergent macrophyte abundance may decrease because of low light penetration (Skovsholt et al., 2024). Low nutrient availability as previously mentioned is a limiting growth factor for all macrophytes types, especially when macrophyte abundance is high. Moreover, climate change as it relates to increasing water temperatures could also influence macrophyte growth, especially in terms of the cascading effects on the survival of Devil Lake’s native cold-water species (trout, pike, bass). Hydrological patterns are also important to consider, as stronger currents have the potential to uproot plants and carry them to catchment regions of the lake. Substrate is another significant factor that influences macrophyte growth, with rocky or sandy substrates typically yielding less macrophyte growth than nutrient rich soil that has the proper density to support root growth (Li et al., 2012). In the context of this study, substrate and light penetration likely had the largest influence on the macrophyte growth seen across the transects. We observed far less substrate macrophyte growth on rocky and sandy sediment compared to the other regions of the lake. Light penetration also varied based on shade/dock cover which may have highly influenced macrophyte abundance totals.

With housing density studies many looked at different types of structures that cause this kind of stress on the littoral zone (roads, houses, docks) (Hicks & Frost, 2011; Radomski et al., 2010; Radomski

& Goeman, 2001). The type of development structure chosen could influence the results based on its contact/impact with the shoreline therefore this is an important thing to consider when running these studies. Moreover, many studies looked at changes between lakes when clear density categories around the lake perimeter could not be identified and this could be a useful strategy that works well for large-scale studies. Despite these differences, many of these studies did find similar results to what was observed on Devil Lake, that macrophyte abundance decreased with increasing development (Hicks & Frost, 2011; Radomski et al., 2010; Radomski & Goeman, 2001). Other studies that looked at macrophyte abundance under varying gradients of development, found similar findings but many had additional reasons for why abundance was low in high density areas. Some mentioned variation in substrate, fetch, and slope (Li et al., 2012), others mentioned depth in addition to these factors (Ojdanič et al., 2023). Another relevant factor considered was the physical removal of macrophytes, especially floating ones that could take away from the aesthetics of a property (Olden et al., 2022). Devil Lake could be influenced by one of these factors or all these factors, but future studies should consider them all where possible and potentially gather take survey data from cottagers to gain a full scope of the issue.

Significance of Shifts in Species Composition:

Understanding which species are present within a community is no less important than abundance for understanding the way that community will grow, i.e. it informs the presence of any competition dynamics between species within the littoral community and how much a given species is contributing to the overall ecosystem function (Ness, 2006). Invasive species have been known to outcompete native species, and if serious enough could lead to complete extirpation of ecologically valuable species (Smith et al., 2021). There is no evidence of this occurring yet in Devil Lake, however the invasive species were observed roughly 1/5 of the time in all transects showing that their presence is already verry high, across all transect types. Since Eurasian milfoil and water nymph were the most abundant of the invasive species they may be showing signs of outcompeting native species. Long-term studies on invasive species are important for helping to track changes over time. Since trends are similar in the baseline conditions as there are everywhere else on the lake, it is difficult to discern which species are being outcompeted, but by continuing studies on Devil Lake that will allow us to see which macrophyte species are decreasing in abundance and this will allow us to track novel invasive species (Starry Stonewort) and any growth patterns to determine the potential impact.

The risk of a shift to invasive species is not a new concept and many studies have linked widespread distribution to various metrics of human disturbance like boating and fishing which can introduce and transport these species across a lake (Hicks & Frost, 2011; Radomski et al., 2010). Invasive species can proliferate fast, and these trends should be continuously monitored over time to observe any shifts in dominant community composition. Moreover, native species like the ones observed in Devil Lake (i.e. Muskgrass, Coontail, and Pondweeds) have ecological importance such as providing food for the fauna of the lake, particularly waterfowl and fish species. Trends in the data demonstrated that invasive species abundance was high across all transects of the lake, leaving the possibility of outcompeting important native faunae, and this could have resulting effects throughout trophic web (Skovsholt et al., 2024). As previously mentioned, species that lack sufficient food sources will shift elsewhere. For Devil Lake and many other lakes this means aquatic wildlife may feel forced to shift away from areas of high stress towards other healthier areas of the lake or to a whole different lake; and the resulting effects of that shift could throw off population dynamics and ecosystem function depending on the severity of the issue and the importance of the species lost. Ideally, waterfowl and other species may find uses for the invasive plant species, helping to mitigate their proliferation but not all species adapt in the same way, and not all invasive species are sufficient replacements for the plants they outcompete.

Additionally, if the cover of invasive macrophytes were to increase to a level where sunlight penetration is affected, other flora in the community may become redundant, impacting native species survival and the functional ecology of the littoral zone (Tan et al., 2019). In Devil Lake, the average cover of a singular invasive species in the protected sites was lower than in the low- and high-density sites (APPENDIX F). Interestingly, the average cover of native species was lower across all density types (APPENDIX G). This is likely because species diversity was higher amongst the native species than the invasive species. These results suggest that invasive species are spreading, especially in the high density transects and there is the potential for increased competition and lowering native species diversity.

The type of aquatic plant (emergent or submergent) is also relevant to the function of the littoral community because their structure plays in role in their relationship with filtering nutrients that enter from the shore. Nitrogen and phosphorus are typical nutrients that enter through runoff, and often become dissolved in the water column. Aquatic plants tend to absorb these nutrients through their leaves or submerged stems, assisting in their growth and development. Both emergent and submergent plants are beneficial over free-floating plants because their roots anchor them into the sediment, allowing them to absorb nutrients that are stored in the soil. In oligotrophic lakes such as Devil, where nutrient availability is much lower, this process is very important because many aquatic species rely on these nutrients and can't directly absorb them from the sediment. Because submergent plants lie entirely under water, their leaves filter a large portion of dissolved nutrients in the water column, whereas emergent plants do all this, and they have the added ability to absorb CO_2 from the air through their leaves to carry out photosynthesis. In both cases, the nutrients contained within the sediment are responsible for providing a stable source of nutrient availability to assist with growth, especially with seasonal fluctuations, limiting nutrient availability within the water column (Chomicki et al., 2022). In Devil Lake, submergent plants were far more common with the highest number in the protected sites. Interestingly, although emergent plants were less common across the lake, they were most abundant in the low-density sites. As previously mentioned, with increased density we tend to see macrophyte composition shift towards submergent species (Radomski & Goeman, 2001). This was contrary to what was found in Devil Lake, although the counts were too low to gain any statistical significance, the trends support that emergent species thrived in areas with low levels of development. This has implications for the way we might see nutrient run off filtered from the nearshore environments (Liu et al., 2021). These changes have outward consequences for the littoral zone, which could increase the risk of seeing wider whole-lake ecological changes (Dubey et al., 2022).

Conclusion:

One limitation was that despite housing density being an easy metric to define and calculate, its exact effect on invasive species is harder to define than overall abundance. When discussing invasive species, aquatic vessel abundance is directly correlated with dock abundance and often with housing density, which is why we tend to draw these parallels. One issue is, with a popular lake such as this one, the presence of individuals on the lake far exceeds the number of houses, especially when considering annual fishing tournaments and easy boat ramp access increase the likelihood of individuals on the lake. The nature in which invasive species spread is often on boat motors, which do not confine themselves to the density categories. Within the scope of this study, twelve houses within 1 km of land represent a high-density area. Hypothetically, if only two of those owners have boats, they are the ones that contribute to a higher risk of spreading invasive species, but the strength of their effect and the areas of the lake they travel to will both influence the results.

On Devil Lake non-native species likely entered the aquatic habitat near the boat ramp or through other smaller access sites like portage trails in Frontenac Park. The Devil Lake fishing events also occur commonly in the west end, increasing the boating activity on that end of the lake where the Frontenac Park perimeter is. The boat ramp did show trends that matched this, with a high abundance of Starry Stonewort. Furthermore, common native fish species, desired for fishing have also been linked to increased macrophyte cover, and we see evidence that invasive species were highest where cover was also highest. This trend suggests that boating activity may have been higher in these regions and introduced non-native species to the area. This makes tracking baseline conditions more difficult, therefore long-term studies that track changes in invasive species and other types of macrophytes are recommended for Devil Lake.

Future studies should continue to examine the roles of anthropogenic stressors and the role they play in shaping aquatic environments, with a focus on isolating the metrics of residential development (i.e. nutrient loading, road development, dock abundance, etc.). Species composition studies are a great way to monitor community shifts over time, and a particular emphasis on invasive species should be examined in relation to boating activity/boat ramp access across multiple lakes with the Cataraqui region. Additionally, studies could explore the stressors that affect submergent and emergent plant types and discover if trends based on housing density on other developed lakes in the area match those seen in Devil; where submergent species were dominant lake-wide, emergent macrophytes were popular in low-density sites, invasive species and native species were more common in protected sites, and invasive species decreased native species richness across all density categories. During our study, we identified a new invasive macrophyte species not previously listed on the Devil Lake Fact Sheet (CRCA, 2017) called starry stonewort. It can reach heights of up to 10 m and create dense mats which have been known to displace aquatic plants and animals and replace native macroalgae (Invasive Species Centre, 2022). It will be very important moving forward to monitor its abundance and track long-term changes in community dynamics to understand its impact and do our best to minimize this. Studies in past have had some success with invasive species reduction using methods such as mechanical removal (dredging, manual hand-removal), biological controls (herbivorous fish, insects, or shading), mesocosm studies that have tested herbicides which successfully targeted invasive species and preserved native communities, and lastly habitat restoration efforts which promoted native species growth and good water clarity (Echo-Hawk et al., n.d.; Kleindl & Steinman, 2021; Kovalenko et al., 2010; Thiemer et al., 2021).

Reversing the effects cottage density on these ecosystems entirely is not realistic, but by demonstrating the relationship between baseline conditions and increased development we can deconstructing the relationship between stressors and the fragile nature of the environment. By using adaptive management strategies for invasive as previously listed we can work to alleviate some of the pressures placed on aquatic systems like Devil Lake and promote longevity of ecosystem and littoral health. With this, I suggest that local and provincial government also enforce greater restriction on boat access, ensuring the vessel has been confirmed properly cleaned to mitigate the introduction and spreading of invasive species. I also suggest that the Devil Lake Association continue to inform those on the lake of how their actions can shape littoral communities. This includes encouraging the installation low impact/floating docks over other styles, encourage no native macrophyte removal, being mindful of where they fish/boat, and taking proper precautions with lawn maintenance and tree clearing to maintain the natural riparian zone and minimize nutrient runoff. I also encourage them to be mindful of fishing events hosted on the lake. Devil Lake has a longstanding history with fishing on the lake (Frontenac Provincial Park, 2021) so this may be difficult to cut back wide-scale fishing practices (tournaments) entirely but understanding one’s own impact is essential. If you are visiting from another country or different region in Canada, consider what the local flora is where you originate from, “are there invasive species there?”, “what is the risk you are unintentionally transporting any?”, and “are you taking proper precautions?”. Cottagers and visitors should be encouraged to avoiding protected shorelines where macrophyte abundance is still quite high and is susceptible to decreases in species diversity and shifts in composition. Therefore, conservation of littoral habitats, encouraging freshwater research, providing landowner education, and altering government policy will all be crucial moving forward to help mitigate the loss of biomass and species richness of aquatic plants, and the cascading negative effects on the littoral zone and larger lake ecosystem (Hicks & Frost, 2011).

LITERATURE CITED

Akinnawo, S. O. (2023). Eutrophication: Causes, consequences, physical, chemical and biological techniques for mitigation strategies. *Environmental Challenges*, *12*, 100733. https://doi.org/10.1016/j.envc.2023.100733

Alexander, M. L., Woodford, M. P., & Hotchkiss, S. C. (2008). Freshwater macrophyte communities in lakes of variable landscape position and development in northern Wisconsin, U.S.A. *Aquatic Botany*, *88*(1), 77–86. doi:10.1016/j.aquabot.2007.08.010

Kawartha Lake Stewards Association (2023). Aquatic Plants Guide 2nd edition. Retrieved from https://klsa.ca/wp-content/uploads/2023/11/klsa-aquatic-plant-guide-2023_web.pdf

Kawartha Lake Stewards Association (2023). Lake Health: A Delicate Balance – Annual Lake Water Quality Report. Retrieved from https://klsa.ca/annual-lake-water-quality-report-directory/

Cataraqui Region Conservation (2024). Cataraqui Region Lake Reporting Dashboard. Retrieved from https://storymaps.arcgis.com/collections/451629f9fa7e4f328a4a9a21fd7ffc0a?item=9

Cataraqui Region Conservation Authority (2017). Devil Lake Fact Sheet - Cataraqui Region Lake Assessment Report. Retrieved from https://cataraquiconservation.ca/pages/lakes

Cheruvelil, K. S. N. (2005). Lack of a unimodal relationship between fish growth and macrophyte cover in 45 north temperate lakes. *Archiv Für Hydrobiologie*, 193–215. https://doi.org/10.1127/0003-9136/2005/0164-0193

Cheruvelil, K. S., & Soranno, P. A. (2008). Relationships between lake macrophyte cover and lake and landscape features. *Aquatic Botany*, *88*(3), 219–227. https://doi.org/10.1016/j.aquabot.2007.10.005

Chomicki, K. M., Taylor, W. D., Brown, C. J. M., Dove, A., Bowen, G. S., & Mohamed, M. N. (2022). Seasonal variation in the influence of environmental drivers on nearshore water quality along an urban northern Lake Ontario shoreline. *Journal of Great Lakes Research*, *48*(4), 914–926. https://doi.org/10.1016/j.jglr.2022.04.011

Czarnecka, M. (2016). Coarse woody debris in temperate littoral zones: Implications for biodiversity, food webs and lake management. *Hydrobiologia*, *767*(1), 13–25.

Dodson, S. I., Newman, A. L., Will-Wolf, S., Alexander, M. L., Woodford, M. P., & Van Egeren, S. (2009). The relationship between zooplankton community structure and lake characteristics in temperate lakes (Northern Wisconsin, USA). *Journal of Plankton Research*, *31*(1), 93–100. https://doi.org/10.1093/plankt/fbn095

Dubey, D., Kumar, S., & Dutta, V. (2022). Impact of nutrient enrichment on habitat heterogeneity and species richness of aquatic macrophytes: Evidence from freshwater tropical lakes of Central Ganga Plain, India. *International Journal of Environmental Science and Technology*, *19*(6), 5529–5546. https://doi.org/10.1007/s13762-021-03438-4

Dustin, D. L., & Vondracek, B. (2017). Nearshore Habitat and Fish Assemblages along a Gradient of Shoreline Development. *North American Journal of Fisheries Management*, *37*(2), 432–444. https://doi.org/10.1080/02755947.2017.1280567

Echo-Hawk, P. D., Oxley, F. M., Williamson, P. S., & Cantu, V. (n.d.). *Integrated management of an invasive macrophyte*.

France, R. L. (1995). Differentiation between littoral and pelagic food webs in lakes using stable carbon isotopes. *Limnology and Oceanography*, *40*(7), 1310–1313. https://doi.org/10.4319/lo.1995.40.7.1310

Frontenac Provincial Park. (2021, June 4). *Devil Lake Association.* https://devillake.org/frontenac-provincial-park/

Frost, P. C., & Hicks, A. L. (2012). Human shoreline development and the nutrient stoichiometry of aquatic plant communities in Canadian Shield lakes. *Canadian Journal of Fisheries and Aquatic Sciences*, *69*(10), 1642–1650. https://doi.org/10.1139/f2012-080

Gosselin, J. R., Haller, W. T., Gettys, L. A., Griffin, T., & Crawford, E. S. (2018). *Effects of substrate nutrients on growth of three submersed aquatic plants*.

Havel, J. E., Kovalenko, K. E., Thomaz, S. M., Amalfitano, S., & Kats, L. B. (2015). Aquatic invasive species: Challenges for the future. *Hydrobiologia*, *750*(1), 147–170. https://doi.org/10.1007/s10750-014-2166-0

Herkül, K., Torn, K., Möller-Raid, T., & Martin, G. (2023). Distribution and co-occurrence patterns of charophytes and angiosperms in the northern Baltic Sea. *Scientific Reports*, *13*(1), 20096. https://doi.org/10.1038/s41598-023-47176-8

Hicks, A. L., & Frost, P. C. (2011). Shifts in aquatic macrophyte abundance and community composition in cottage developed lakes of the Canadian Shield. *Aquatic Botany*, *94*(1), 9–16. https://doi.org/10.1016/j.aquabot.2010.09.005

Invasive Species Center (2022). Starry Stonewort. Retrieved from https://www.invasivespeciescentre.ca/invasive-species/meet-the-species/invasive-aquatic-plants/starry-stonewort/

Kefford, B. J., Nichols, S. J., & Duncan, R. P. (2023). The cumulative impacts of anthropogenic stressors vary markedly along environmental gradients. *Global Change Biology*, *29*(3), 590–602. https://doi.org/10.1111/gcb.16435

Kleindl, P. M., & Steinman, A. D. (2021). Contrasting trajectories in macrophyte community development after shoreline restoration: Water level obscures trends. *Aquatic Botany*, *169*, 103327. https://doi.org/10.1016/j.aquabot.2020.103327

Kovalenko, K. E., Dibble, E. D., & Slade, J. G. (2010). Community effects of invasive macrophyte control: Role of invasive plant abundance and habitat complexity. *Journal of Applied Ecology*, *47*(2), 318–328. https://doi.org/10.1111/j.1365-2664.2009.01768.x

Kufel, L., & Kufel, I. (2002). *Chara* beds acting as nutrient sinks in shallow lakes—A review. *Aquatic Botany*, *72*(3), 249–260. https://doi.org/10.1016/S0304-3770(01)00204-2

Lacoul, P., & Freedman, B. (2006). Environmental influences on aquatic plants in freshwater ecosystems. *Environmental Reviews*, *14*(2), 89–136. https://doi.org/10.1139/a06-001

Li, Z. Q., Kong, L. Y., Yang, L. F., Zhang, M., Cao, T., Xu, J., Wang, Z. X., & Lei, Y. (2012). Effect of substrate grain size on the growth and morphology of the submersed macrophyte *Vallisneria natans* L. *Limnologica*, *42*(1), 81–85. https://doi.org/10.1016/j.limno.2011.09.003

Liu, H., Liu, G., & Xing, W. (2021). Functional traits of submerged macrophytes in eutrophic shallow lakes affect their ecological functions. *Science of The Total Environment*, *760*, 143332. https://doi.org/10.1016/j.scitotenv.2020.143332

Madzivanzira, T. C., Coetzee, J. A., & Dalu, T. (2023). Factors Structuring Aquatic Macrophytes. In S. Kumar, K. Bauddh, R. Singh, N. Kumar, & R. Kumar (Eds.), *Aquatic Macrophytes: Ecology, Functions and Services* (pp. 21–52). Springer Nature. https://doi.org/10.1007/978-981-99-3822-3_2

Mayo, J. S., & Jackson, D. A. (2006). Quantifying Littoral Vertical Habitat Structure and Fish Community Associations using Underwater Visual Census. *Environmental Biology of Fishes*, *75*(4), 395–407. https://doi.org/10.1007/s10641-005-5150-8

Mushet, G. R., Yee, C., Bergson, S., & Blanchfield, P. J. (2023). Abundance and movement of fishes among nearshore habitat types in small boreal shield lakes. *Hydrobiologia*, *850*(9), 1985–2003. https://doi.org/10.1007/s10750-023-05205-7

Neijnens, F. K., Moreira, H., de Jonge, M. M. J., Linssen, B. B. H. P., Huijbregts, M. A. J., Geerling, G. W., & Schipper, A. M. (2024). Effects of nutrient enrichment on freshwater macrophyte and invertebrate abundance: A meta-analysis. *Global Change Biology*, *30*(1), e17094. https://doi.org/10.1111/gcb.17094

Ness, K. L. (2006). *The Effects of Shoreline Development on Lake Littoral and Riparian Habitats: Are Shoreline Protection Regulations Enough?* Retrieved April 3, 2025, from https://digitalcommons.library.umaine.edu/etd/1236

Ojdanič, N., Germ, M., Andlovic, M., Černela, D., & Zelnik, I. (2023). Distribution of Aquatic Macrophytes in the Littoral of Lake Bohinj (Slovenia). *Diversity*, *15*(11), Article 11. https://doi.org/10.3390/d15111115

Olden, J. D., Miler, O., & Bijaye, A. (2022). Lake-wide mapping of littoral habitat using underwater videography. *Knowledge & Management of Aquatic Ecosystems*, *423*, 18. https://doi.org/10.1051/kmae/2022018

Pinheiro, J. P. S., Windsor, F. M., Wilson, R. W., & Tyler, C. R. (2021). Global variation in freshwater physico-chemistry and its influence on chemical toxicity in aquatic wildlife. *Biological Reviews of the Cambridge Philosophical Society*, *96*(4), 1528–1546. https://doi.org/10.1111/brv.12711

R Core Team (2024). _R: A Language and Environment for Statistical Computing_. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.

Radomski, P., Bergquist, L. A., Duval, M., & Williquett, A. (2010). Potential Impacts of Docks on Littoral Habitats in Minnesota Lakes. *Fisheries*, *35*(10), 489–495. https://doi.org/10.1577/1548-8446-35.10.489

Radomski, P., & Goeman, T. J. (2001). Consequences of Human Lakeshore Development on Emergent and Floating-Leaf Vegetation Abundance. *North American Journal of Fisheries Management*, *21*(1), 46–61. https://doi.org/10.1577/1548-8675(2001)021<0046:COHLDO>2.0.CO;2

Ranta, P., & Toivonen, H. (2008). Changes in Aquatic Macrophytes Since 1933 in an Urban Lake, Iidesjärvi, SW Finland. *Annales Botanici Fennici*, *45*(5), 359–371. https://doi.org/10.5735/085.045.0503

Sass, L. L., Bozek, M. A., Hauxwell, J. A., Wagner, K., & Knight, S. (2010). Response of aquatic macrophytes to human land use perturbations in the watersheds of Wisconsin lakes, U.S.A. *Aquatic Botany*, *93*(1), 1–8. https://doi.org/10.1016/j.aquabot.2010.02.001

Skovsholt, L. J., Matheson, F., Riis, T., & Hawes, I. (2024). Trait-specific groups of aquatic macrophytes respond differently to eutrophication of unshaded lowland streams. *Science of The Total Environment*, *954*, 176724. https://doi.org/10.1016/j.scitotenv.2024.176724

Smith, S., Küpper, F. C., Trinder, C., & Louca, V. (2021). Assessing watermilfoil invasion effects on native macrophyte communities in North American lakes using a novel approach for macrophyte sampling. *Knowledge & Management of Aquatic Ecosystems*, *422*, Article 422. https://doi.org/10.1051/kmae/2020043

Strayer, D. L. (2010). Alien species in fresh waters: Ecological effects, interactions with other stressors, and prospects for the future. *Freshwater Biology*, *55*(s1), 152–174. https://doi.org/10.1111/j.1365-2427.2009.02380.x

Tan, B.-C., He, H., Gu, J., & Li, K.-Y. (2019). Effects of nutrient levels and light intensity on aquatic macrophyte (Myriophyllum aquaticum) grown in floating-bed platform. *Ecological Engineering*, *128*, 27–32. https://doi.org/10.1016/j.ecoleng.2018.12.011

Thiemer, K., Schneider, S. C., & Demars, B. O. L. (2021). Mechanical removal of macrophytes in freshwater ecosystems: Implications for ecosystem structure and function. *Science of The Total Environment*, *782*, 146671. https://doi.org/10.1016/j.scitotenv.2021.146671

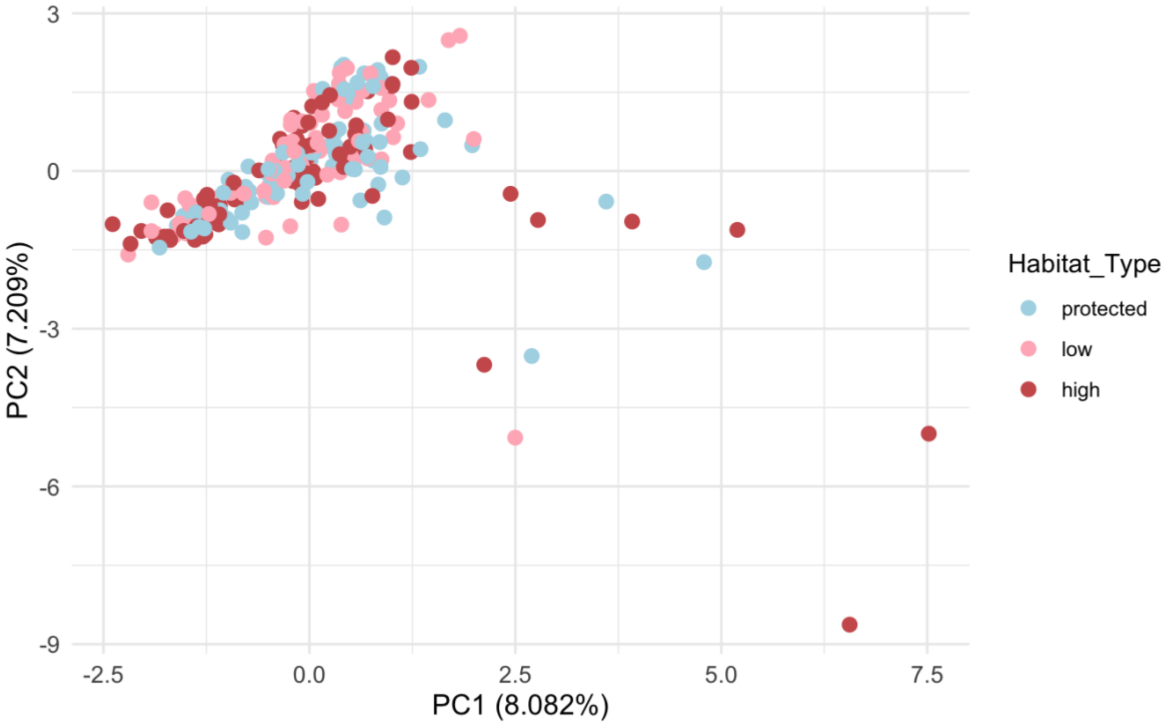
Twardochleb, L. A., & Olden, J. D. (2016). Human development modifies the functional composition of lake littoral invertebrate communities. *Hydrobiologia*, *775*(1), 167–184. https://doi.org/10.1007/s10750-016-2727-5

Vadeboncoeur, Y., McIntyre, P. B., & Vander Zanden, M. J. (2011). Borders of Biodiversity: Life at the Edge of the World’s Large Lakes. *BioScience*, *61*(7), 526–537. https://doi.org/10.1525/bio.2011.61.7.7

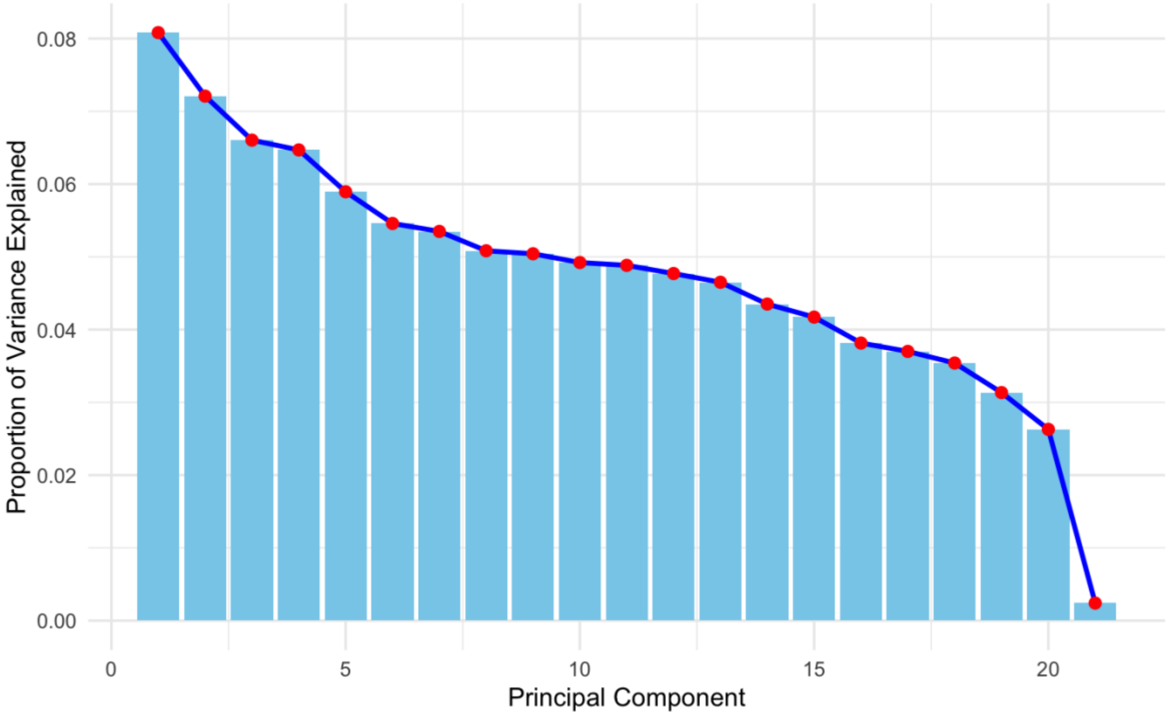
Vander Zanden, M. J., Vadeboncoeur, Y., & Chandra, S. (2011). Fish Reliance on Littoral–Benthic Resources and the Distribution of Primary Production in Lakes. *Ecosystems*, *14*(6), 894–903. https://doi.org/10.1007/s10021-011-9454-6

APPENDICES

APPENDIX (A) - Scaled biplot demonstrating the variation explained by PC1 and PC2 on habitat type. Axes represent the principal components responsible for variation in individual macrophyte species cover within a sampling hoop that meets the criterion (>1.5%), across habitat density types. Density categories represented by the various colors (high-red, low-pink, protected-blue).



APPENDIX (B) - Scree plot showing the proportion of variance explained by all principal components. PC1 and PC2 have the two highest components explaining variation in the data.



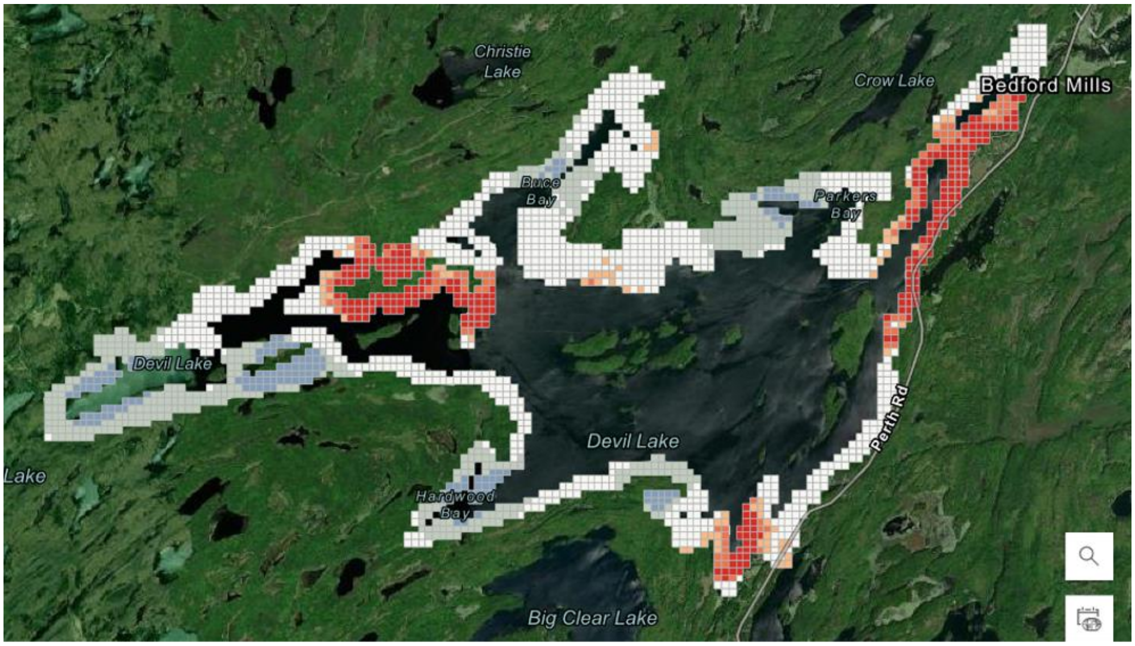
APPENDIX (C) - Count data for all emergent and submergent species that met the criterion (>1.5%) across all habitat types.

Habitat Type	**Species Type**	**Count/times observed**
protected	Emergent	13
protected	Submergent	424
low	Emergent	21
low	Submergent	341
high	Emergent	12
high	Submergent	328

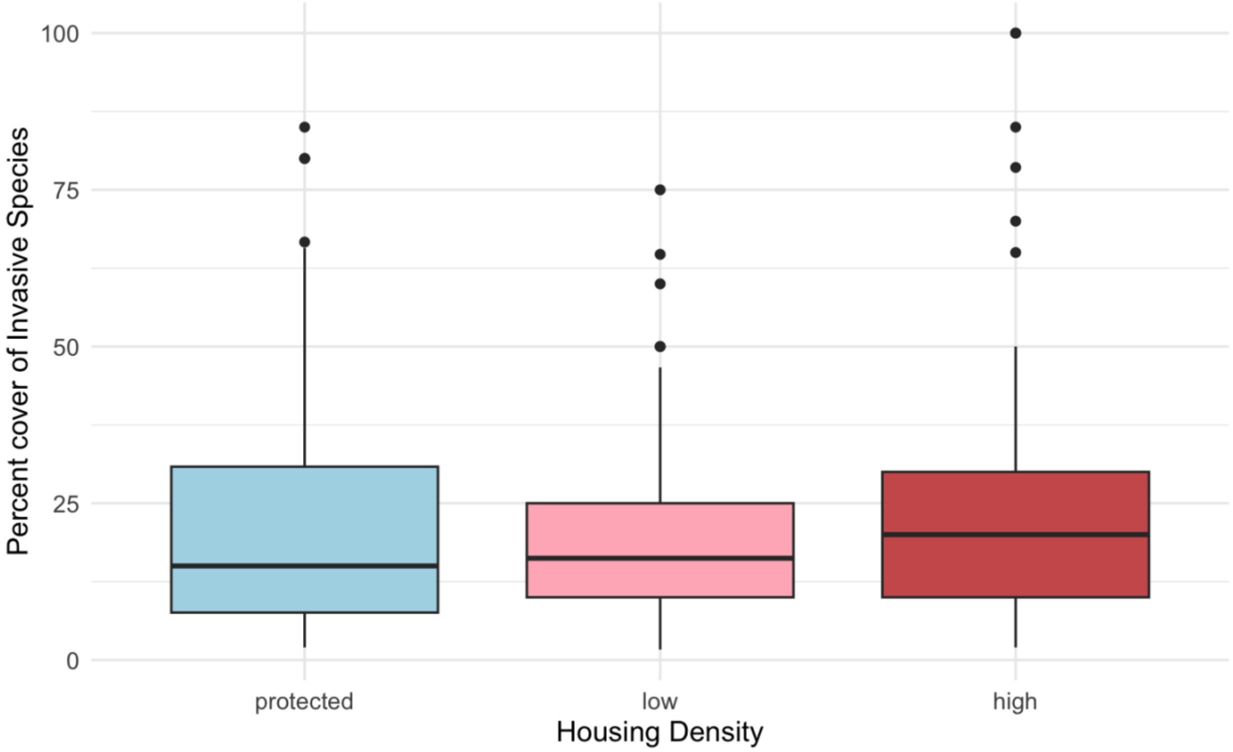
APPENDIX (D) - Count data for all Invasive and Native species that met the criterion (>1.5%) across all habitat types.

Habitat Type	**Species Status**	**Count/times observed**
protected	Invasive	88
protected	Native	349
low	Invasive	66
low	Native	296
high	Invasive	58
high	Native	282

APPENDIX (E) - Devil Lake Housing Density Map. Red points represent areas of high housing density. Blue points indicate areas with a significant lack of density, also known as the protected areas. White areas are not significant (there’s no low density or high density of cottages).



APPENDIX (F) – Boxplot of the percent cover of invasive species across the different transects types (high, low, protected). Average cover of an invasive species in the protected site was 14%, low was 15%, and high density was around 20%. Note: these averages do not represent total cover of invasive species but rather the cover of each invasive species found within a transect, therefore the cover of all invasive species within a transect could be higher.



APPENDIX (G) – Boxplot of the percent cover of native species across the different transects types (high, low, protected). Average cover of a native species in the protected site was 11%, low was and high density was around 13%. Note: these averages do not represent total cover of invasive species but rather the cover of each native species found within a transect, therefore the cover of all native species within a transect could be higher.