A Thesis

entitled

Potential Spread of Hydrilla verticillata in the Great Lakes Basin

by

Kristen M Hebebrand

Submitted to the Graduate Faculty as partial fulfillment of the requirements for the

Masters of Science Degree in

Biology

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May 2019

An Abstract of

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Hydrilla *(Hydrilla verticillata*), an aquatic invasive plant, threatens to invade the Great Lakes Basin. Hydrilla creates dense webs that out competes native vegetation, reduces flow in canals, clogs intakes, and interferes with navigation of watercraft. Recreational boating has acted as a primary vector of spread for other aquatic invasive species and is expected be a primary vector for hydrilla spread. The goal of this project was to analyze the current distribution of hydrilla and identify the risk of introduction in the Great Lakes Basin via overland recreational boat transport. This goal was achieved by 1) assessing the current distribution of hydrilla to determine likely vectors of spread and 2) predicting the potential spread of hydrilla to the Great Lakes Basin via recreational watercraft and boat trailers and 3) identifying high risk areas for introduction. This analysis will aid in predicting and detecting the spread of invasive hydrilla into new waterways in the Great Lakes Basin.

Acknowledgements

I would like to thank my advisor Dr. Jon Bossenbroek for all his guidance, knowledge, and patients that have helped me through this process. I would also like to thank the other members of my committee Dr. Richard Becker and Dr. Daryl Moorhead, for all their expertise and input. Thank you to all the partners I have worked with on the Hydrilla Collaborative for their input. Thank you to Jessica Collier, Sara Guiher, Jake Kvistad, and Stephanie Nummer for their input, support, and friendship. I could not have asked for a better lab! A special thanks to Rachel Johnson for her friendship and support. I would like to thank my family. Mom and Dad thank you for all the support and encouragement throughout my life and this process. Stephanie thank you for your support and friendship. Matthew thank you for your encouragement, friendship, and comic relief! Lastly, thank you to all my other family and friends who have supported me throughout this process.

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Chapter 1

Introduction

The Great Lakes are now home to over 180 invasive species with the majority of them being aquatic plants (GLRI Task Force 2010, Mills et al. 1993, Ricciardi 2006). Pathways responsible for the spread of invasive species in the Great Lakes include unintentional and intentional release, entry through canals, shipping, and hitch-hiking on overland transport such as recreational boats (Mills et al. 1994). The Great Lakes economy and ecosystem have been negatively impacted by the introduction of invasive species (Mills et al. 1993) at an estimated annual cost of $138.3 million (Rothlisberger et al. 2012). The costs incurred by invasive species (OTA 1993) justify resources spent on prevention and methods for early detection (Ricciardi & Rasmussen 1998). Effectiveness of early detection and monitoring rely on knowledge of invasive threats, including the invasive species' life history, biological needs, and dispersal patterns (Ricciardi & Rasmussen 1998). One invasive species that currently threatens the Great Lakes Basin both ecologically and economically is *Hydrilla verticillata* (hereafter referred to as hydrilla).

Hydrilla is native to warmer regions of Asia, but is invasive in parts of Europe, Australia, New Zealand, Africa, the Pacific Islands, South America, and North America. Hydrilla was first discovered in the USA in 1960 in two waterbodies in Florida: a canal near Miami and in the Crystal River. In its first decade in the USA, hydrilla spread rapidly and invaded major water bodies in every drainage basin in Florida. By 1995 hydrilla was established in 43% of public lakes in Florida, infesting 40,000 ha (Langeland 1996). As hydrilla spreads to northern latitudes, spread rates decrease, but hydrilla has established at 50 degrees N. latitude in Poland and Russia, which is climatically similar to Southern Canada (Langeland 1996). Therefore, spread and establishment of hydrilla in the Great Lakes Basin is a possibility.

Hydrilla can survive with limited nutrients and rapidly grows at a rate of one inch per day, which allows it to be an effective competitor for space and sunlight against native species (Langeland 1996). Hydrilla typically grows as a straight stem until it nears the waters' surface where it can then branch extensively, creating dense webs that can exclude native vegetation and consequently adversely affect native fish and invertebrates (Langeland 1996). Hydrilla also survives in a free-floating state, which facilitates its spread through waterways. When hydrilla breaks from its stem about 50% of those fragments are capable of forming new plants (Langeland and Sutton 1980). Thus, fragmented hydrilla can be carried on watercrafts, boat trailers, and bait buckets, which serve as potential vectors for infesting new areas (Langeland and Sutton 1980).

Hydrilla's biological characteristics allow it to be an adaptable plant and an effective invader (Langeland 1996). Binimelis et al. (2007), documented hydrilla's ecological impacts on Lake Izabal in Guatemala and found that hydrilla can lower sediment resuspension and compartmentalize nutrients, which can reduce phytoplankton and change soil substrates of the lake shore by accumulating organic matter. Hydrilla also displaced native aquatic plant communities in Lake Izabal such as *Pistia stratiotes* and *Chara phoetida* (Binimelis et al. 2007). These ecological impacts can alter the species composition and habitat characteristics of ecosystems (Posey et al. 1993).

Hydrilla can also have negative economic impacts. Dense webs of hydrilla can reduce flow in canals and clog intakes, increasing flooding and damage to structures. Hydrilla interferes with navigation of watercraft and displacing native aquatic plants negatively impacts sportfish populations (Langeland 1996). An economic study of Orange Lake, FL during a year when hydrilla was aggressive estimated a loss of $11 million in profit (Milon et al 1986). In order to manage hydrilla in Florida public waters ~ $14.5 million was spent in 1995. These economic losses and management costs are motivators to prevent the spread of hydrilla (Langeland 1996).

The research presented in this thesis was completed as a part of a risk assessment on the introduction and spread of hydrilla in the Great Lakes Basin funded by United States Army Corps of Engineers- Buffalo District (USACE Buffalo) and USACE Engineering Research and Development Center (ERDC) and led by Ecology and Environment, Inc. (E & E). Table 1.1 shows the partners and their roles in the hydrilla collaborative. The main goal of the risk assessment was to identify locations most vulnerable to hydrilla invasion based on the likelihood of introduction and habitat suitability. Other outcomes of the risk assessment included providing recommendations for early detection and how to reduce the risk of spread.

The University of Toledo component of this project had two main objectives: 1) assessing the current distribution of hydrilla to determine likely vectors of spread and 2) predicting the potential spread of hydrilla to the Great Lakes Basin via recreational watercraft and boat trailers and identifying high risk areas for introduction.

Chapter 2 focuses on assessing the distribution of hydrilla in the continental United States to determine likely vectors of spread in addition to recreational watercraft and boat trailers. This chapter focuses on natural dispersal via hydrologic pathways, which was determined to be one of the more likely vectors of hydrilla spread based on available data and literature. A proximity and connectedness analysis was performed to evaluate hydrilla dispersal via hydrologic pathways using occurrence data from 2015 and hydrography data for the United States.

Chapter 3 focuses on modeling the potential spread of hydrilla in the Great Lakes Basin via recreational watercraft and boat trailers and identifying high-risk areas for introduction. A gravity model predicting the movement of boaters was also constructed to predict the spread of hydrilla in the continental United States.

Table 1.1: Great Lakes Risk Assessment Collaborative: The partners and their roles in the hydrilla collaborative. The University of Toledo's role for this risk assessment was to construct a gravity model to identify vulnerable areas to hydrilla invasion.

Team Member	**Project Role**
USACE, Buffalo District	Project Management and Technical Oversight
USACE, Engineer Research Development Center	Technical Guidance and Oversight
Ecology and Environment, Inc. (E&E Inc.)	Project Management, Risk Assessment Lead
Texas Tech University	Distributional Modeling
University of Toledo	**Dispersal Modeling**
North Carolina State University	Hydrilla Growth Studies

Chapter 2

Assessing Hydrilla Distribution – Identifying the Risk of Introduction in the Great Lakes Basin

2.1 Introduction

Invasive species spread naturally by various mechanisms including hydrologic pathways, animal mediated dispersal, and aerial dispersal (Keller 2009). A study performed in Mystic, Connecticut suggests that hydrilla fragments and stem tubers may spread by waterfowl from waterbody to waterbody (Langeland 1996). Hydrologic pathways, such as rivers and streams, are also a potential dispersal mechanism into connected waterbodies (Keller 2009). In a similar study, Bobeldyk et al. (2005) examined the importance of stream connectivity and the proximity to infested sources in explaining the distribution of zebra mussel infested lakes. The results showed that the probability of invasion decreased with distance between lakes and that understanding streams as dispersal pathways is critical to directing management efforts (Bobeldyk et al, 2005). To evaluate the natural dispersal of hydrilla, connectedness and proximity of infested lakes within watersheds were analyzed as in Bobeldyk et al. (2005).

2.2 Methods

The data needed for these analyses included hydrilla locations, date of infestation, hydrography data for the United States, and lake and stream data including size and location. The hydrilla occurrence data were compiled by Ecology and Environment, Inc., from multiple databases, including Early Detection and Distribution Mapping System (EDDMapS) and the Global Biodiversity Information Facility (GBIF). The waterbody data, which includes surface areas and locations of lakes, ponds, rivers, and streams area, were acquired from the National Hydrography Dataset (USGS, 2013). All known hydrilla invaded USA lakes that had an outflowing stream were assessed using ArcMaps 10.3. For each infested lake, the distance downstream to the next connected lake was measured and then determined if that lake was infested based on the hydrilla occurrence data. The distances of infested waterbodies connected to downstream infested waterbodies and the distances of infested waterbodies connected to downstream not infested/not detected waterbodies were compared using a two-sample t-test to determine if there was a pattern between the likelihood of potential hydrilla presence and lake proximity.

2.3 Results

Twenty-two hydrilla invaded continental U.S. lakes were studied to evaluate the role streams play in hydrilla dispersal. 11 waterbodies were connected to downstream infested waterbodies. There was no evidence that proximity to an infested lake increased the likelihood of a downstream lake being infested ($p = 0.5$, two sample t-test). The mean distance to infested waterbodies was 23.66±stdev km. The mean distance to a not infested/not detected waterbody was 13.52±stdev km. For this analysis, it was hypothesized that connected lakes that were closer in proximity to each other would be more likely to be infested. However, the results from the analysis refuted this hypothesis (Table 2.1).

2.4 Discussion

Our analysis suggests that lakes that are closer to a lake with hydrilla do not necessarily have a higher chance of becoming infested. This analysis could be limited to the small sample size. In the regions where hydrilla is currently established the connections between lakes are infrequent and little evidence of the importance of downstream flow as a major vector of dispersal was found. However, in areas surrounding the Great Lakes, particularly in Michigan, Wisconsin, and Minnesota, lakes are often highly connected. Based on previous studies on similar aquatic species, such as zebra mussels, with fuller datasets, lakes in close proximity to infested lakes were expected to have a higher probability of becoming infested due to downstream connections (Bobeldyk, 2005).

Table 2.1: Natural Dispersal Results: Results from natural dispersal analysis.

Watershed	Infested Lake	First Downstream Lake	Distance (km)	Infestation Status
Susquehanna	Highland Lake	NA	0.01	not infested
Merrimack	South Meadow Pond	NA	0.04	not infested
Cape Fear	Lake Kennedy	NA	0.13	not infested
Edisto-Santee	Lake Johnson	Lake Edwin Johnson	0.14	not infested
St Johns	Lake Virginia	Lake Osceola	0.22	infested
Massachusetts-Rhode Island Coastal.	Oakman Pond	Hatch Pond	0.29	not infested
Massachusetts-Rhode Island Coastal.	Long Pond	Seine Pond	0.97	not infested
Saco	Pickerel Pond	Lake Arrowhead	2.35	not infested
St Johns	Puzzle Lake	Lake Harney	3.31	infested
Southern Flroida	Cypress Lake	Lake Hatchineha	3.83	infested
Ochlockonee	Lake Munson	NA	4.74	not infested
St Johns	Sawgrass Lake	Lake Washington	5.11	infested
Susquehanna	Harveys Lake	NA	5.17	not infested
Ogeechee-Savannah	Lake Keowee	NA	7.26	not infested
Edisto-Santee	Lake Norman	Mountain Island Lake	11.77	infested
Kanawha	Claytor Lake	Bluestone Lake	12.90	infested
Lower Tennesee/ Middle Tennesee Elk	Pickwick Lake	Kentucky Lake	14.00	infested
St Johns	Lake Washington	Lake Winder	14.24	infested
Edisto-Santee	Buzzard Roost	Lake Murray	35.13	infested
Chowan-Roanoke	John H. Kerr Reservoir	Roanoke Rapids Lake	54.78	infested
Apalachicola	Walter F George Reservoir	Lake Seminole	105.00	infested
Alabama	Allatoona Lake	Weiss Lake	127.66	not infested

Chapter 3

Modeling the Potential Spread of Hydrilla to the Great Lakes Basin via Recreational Watercraft and Boat Trailers

3.1 Introduction

Hauling recreational boats over land from an infested waterbody to a non-infested body of water will likely contribute to the spread of hydrilla in the Great Lakes Basin (Anderson et al, 2015). Recreational boating has already been a pathway between lakes and rivers in the U.S. for zebra mussels (*Dreissena polymorpha*) and other invasive macrophytes (Anderson et al, 2015). Overland transport of recreational boating also has been linked with the spread of species such as spiny waterflea (*Bythotrephes longimanus*; MacIsaac et al. 2004; Muirhead and MacIsaac 2005), Eurasian watermilfoil (*Myriophyllum spicatum*; Buchan and Padilla 2000), and zebra and quagga mussels (*Dreissena* spp.; Schneider et al. 1998; Leung et al. 2004; Stokstad 2007).

Modeling overland dispersal via recreational boating has been an effective tool for early detection of other aquatic invasive species. In particular, gravity models have been used to model overland dispersal via boats of other aquatic invasive species such as zebra mussels (Bossenbroek, 2006) and Eurasion watermilfoil (Rothlisberger and Lodge, 2010). A gravity model uses spatial interactions to predict spread based on attraction; it is useful for predicting which waterbodies will most likely attract recreational boaters. In turn it will identify which recreational boating vectors pose the greatest threat as pathways for hydrilla in the Great Lakes Basin. By accurately predicting the vectors and pathways, Great Lakes Basin management efforts can place focus in areas where they will be most effective in containing and reducing spread (Keller 2009).

The most effective way to reduce impacts of invasive species is to prevent their movement into uninvaded areas (Simberloff, 2003). Monitoring for early detection is necessary to effectively manage invasive species before they are able to establish populations (Keller 2009). Because an uninvaded area surrounded by established populations of invasive species is considered an area at high risk for invasion, the Great Lakes Basin is considered a high risk area for hydrilla (Balciunas & Chen 1993). The spread and establishment of hydrilla in the Great Lakes Basin may be slowed or stopped with proper management techniques, monitoring programs, and a better understanding of hydrilla's present and future dispersal patterns. Being able to identify watersheds at high risk for hydrilla infestation will focus monitoring efforts. The objectives for Chapter 3 is to predict the potential spread of hydrilla to the Great Lakes Basin via recreational watercraft and boat trailers, and identify high risk areas for introduction.

3.2 Methods

3.2.1 Data and Study Area

To address my objective, a gravity model was used to predict hydrilla dispersal in the continental US and Great Lakes Basin via trailered boater movement. The model was built based on 4-digit Hydrological Unit Codes (HUC), which divides the continental US into 210 watersheds. At this scale, the model gave a broader, more generalized look at recreational boater spread and predictions for the entire continental United States.

The data needed to construct the model included county boater registrations, watershed boundaries and locations, and known hydrilla occurrences. County boater registration data from Morandi (2013) for the continental United States was used to provide the number of registered boats per watershed. The National Hydrologic Database provided the waterbody data, i.e., the NHDPlusV2 data (USGS, 2013) including major lakes, reservoirs, rivers, and streams. US Highway data were retrieved from the Federal Highway Administration (HEP, 2015). Hydrilla occurrence data was compiled by Ecology and Environment, Inc (unpublished data) displayed in Figure 1. All data were managed using ArcGIS 10.3 (ESRI, 2011) and R (R Studio Team, 2015). The gravity model was constructed using R (R Studio Team, 2015). Using ArcGIS 10.3 the hydrilla occurrence points were joined to the waterbodies they infest, using a 50m buffer to account for occurrence coordinates that do not fall directly within an NHD waterbody. These waterbody areas were then assigned as infested and were used as the current infested areas for the model.

Suitable habitat of hydrilla was modeled using hydrilla distributions, the results of this model were incorporated in the gravity model. This model was a MaxEnt model from Barnes and Soto (unpublished niche model results). This model was based on species occurrence data and favorable environmental conditions across landscapes. The output of MaxEnt results range from zero to one on a scale of 10 x 10 km grid cells across the modeling area. A score near one suggests high confidence that an area can support a population of the target species. A score near zero indicates low confidence that an area can support the modeled species. Barnes and Soto's MaxEnt output was based on the environmental conditions where hydrilla is currently established (Unpublished niche model results). The MaxEnt results are displayed in Figure 2. Incorporating habitat suitability into the dispersal model may allow for more accurate model predictions since it will be incorporating habitat suitability as well as dispersal.

3.2.2 Model Development

To predict the spread of hydrilla in the United States, a gravity model was developed using the following steps: 1) estimate number of boaters traveling from each watershed, 2) estimate the proportion of those boats that will travel from watersheds infested with hydrilla to another watershed, 3) assign new infestations based on the watershed's habitat suitability and the number of boaters traveling from infested locations, and 4) estimate the area of lakes and rivers that are newly infested in each watershed each year.

The gravity model was based on Bossenbroek et al. (2007) and predicts the movement of recreational boaters. The base of the model is Equation 1:

$$T_{ij} = A_i O_i W_j c_{ij}^{-\propto}, \qquad \text{(Eq 1)}$$

where T_{ij} represents the number of boaters that travel from watershed i to watershed j. O_i is the number of boats that travel from watershed i. The attractiveness of each watershed, W_j, was based on the total surface area of lakes, reservoirs, rivers, and length of Great Lakes coastlines (Equation 2):

$$W_j = I_j + xS_j, \qquad \text{(Eq 2)}$$

where I_j is the surface area (ha) of lakes, reservoirs, and rivers, S_j is the length of oceanic and/or Great Lakes shoreline (km) and x is a scalar to equate the "attractiveness" of shorelines to the "attractiveness" of lakes, which was an estimated parameter (see below and Table 3.1). This parameter is used for shoreline and coasts of likes that cannot be accounted for by area. The distance matrix (c_{ij}) was developed to estimate the movement of recreational boaters from a series of origins to a series of destinations (Thomas and Hugget, 1980) and $\propto$ defines the deterrent effect of distance estimated from empirical data and previous studies to reflect the likelihood of travel based on distance (Fotheringham 1981). The origins and destinations used in this model were calculated for each watershed by finding the centroid of attraction (Wj) using highway data and waterbody data within each watershed. The waterbodies with the largest surface area and closest to highways were considered to have a high attraction when determining this. Distances between watersheds were based on highway distances. Transient recreational boaters traveling from waterbodies within a watershed can further infest that watershed. Therefore, it is important to account for boats whose origin watershed is also their destination watershed. Travel within a watershed (i.e. for c_{ij}, $i = j$) was estimated as a proportion of the minimum distance from each watershed to its nearest neighboring watershed (m). A_i is the balancing factor that ensures all boats leaving watershed i will reach watershed j, and is defined by Equation 3:

$$A_i = \frac{1}{\sum_{j=1}^{N} W_j c_{ij}^{-\propto}} \qquad \text{(Eq 3)}$$

where N is the total number of waterbodies.

Once the basic gravity model structure was constructed, a dynamic model was developed that began with a pre-determined infestation of hydrilla and then predicted the spread and increase of hydrilla in range through time. For each model iteration representing one year, an infestation probability, P_j, for each watershed was estimated. The probability of a new infestation event is a function of the number of boats leaving an infested watershed (s) and the proportion of a watershed that is already infested (Q_j). Thus Equation 4,

$$P_j = BQ_j \sum_{i=1}^{s} T_{ij} \qquad \text{(Eq 4)}$$

where s is the number of watersheds currently infested with hydrilla. B is the probability that an individual boater will infest a watershed.

To incorporated the habitat suitability results of each destination watershed into the equation, parameter Z_j was included in the infestation probability (P_j) equation resulting in equation 5,

$$P_j = BQ_j Z_j \sum_{j=1}^{s} T_{ij} \qquad \text{(Eq 5)}$$

The probability of a destination watershed becoming infested was also influenced by the habitat suitability of the watershed (Z_j) as per Barnes and Soto (Unpublished niche model results). The niche model results were at a finer resolution than the HUC 4 watersheds used for this model. w_i is the average habitat suitability probability calculated for each watershed from the niche model results. A scalar, y, was estimated to adjust the habitat suitability model values to be taken into consideration in the dispersal model while ensuring that the habitat suitability results were not outweighing the dispersal model results. The fitted habitat suitability probability for each watershed is Z_j (Equation 6).

$$Z_j = w_i y \tag{Eq 6}$$

At the end of each iteration, each destination watershed was assigned a probability of colonization, P_j, and then subjected to a Bernoulli trial where a result of one designated the watershed as colonized and a result of zero designated the watershed as not colonized during that iteration.

For those watersheds determined to have a colonization event, the model predicted the amount of new area, or proportion of the waterbodies within the watershed, that was newly infested with hydrilla. The new area infested per year in each watershed (k_i) was drawn from a normal distribution, $k_i \sim N(\mu, \sigma 2)$, where μ and $\sigma 2$ were calculated using the estimated parameter (k_i) infested area per watershed. This area (k_j) was added to the area of already infested area within a watershed and thus updating Q_j, the area within a watershed infested with hydrilla.

To predict the spread of hydrilla over the next 10 years the gravity model was run using the best-fit parameters calculated from a parameterization routine. The model was initiated using the current occurrence data (2015) and ran for ten iterations (2025) and 1,000 trials.

3.2.3 Gravity Model Parameterization

The parameterization methodology for this gravity model was adapted from Bossenbroek et al. 2001. The goal was to select parameter values that mimic actual spread patterns and replicate current hydrilla distribution by running the model from the first known infested watershed in 1953 to 2015. Six model parameters were assessed using least sum-of-squares (LSS): a distance coefficient (α), a distance multiplier (m), a scalar to estimate the "attractiveness" of shoreline in terms of the "attractiveness" of lakes (x), a scalar to adjust habitat suitability for this model (y), the probability that an individual boater will infest a waterbody (B), and area infested per year (k_j; see Table 3.1 for more details). The LSS was calculated by taking the squared sum of the difference of the current infested area for each watershed and the predicted infested area for each watershed allowing a comparison between the current infested area to the predicted. In the parameterization routine, α ranged from 0.01 to 10, m from 0.01 to 0.99, x from 0.1 to 50, y from 0.1 to 10, B from 0.0001 to 0.01, and k_j from 100 to 10,000. These ranges were determined by LSS patterns when running the model at 25,000 trials for each parameter set at a wide range. Each trial randomly selected a value for the parameter within that range. The LSS results for each parameter were graphed, when a defined dip, representing the lowest LSS, appeared within the graph the range of values for that parameter were refined. The final ranges were then used in increments to perform the parameterization. 1,000 LSS comparisons of models using the hydrilla occurrence data were used to determine best-fit parameter values of each parameter.

3.2.4 Gravity Model Sensitivity Analysis

A sensitivity analysis of model parameters was performed based on Bossenbroek et al. 2007. To analyze the sensitivity of the model to changes in parameter values the model was run while changing the best-fit parameter values from - 25% and + 25%. Each parameter value variation was run for 1,000 trials. The proportion (P_j) of the average colonization for each watershed was calculated for each iteration (Equation 7).

$$P_j = B\mathrm{Q}_j Z_j \sum_{j=1}^{s} T_{ij} \qquad \text{(Eq 7)}$$

P_j was calculated taking the average of 1,000 trials with the best-fit parameter values as inputs. This result was used to compare to the results from P_j with the manipulated parameter values to gauge the models sensitivity the change in each parameter.

3.2.5 Gravity Model Validation

The validation method used for the parameterization routine and model was adapted from Rothlisberger and Lodge (2010). The full data set included 743 infestation points for which the year of infestation was unknown years and 1,583 with known year. The data set was split into two temporal subsets in order to compare the best fit parameter results for each subset to the full data set to justify whether or not using the same parameters from the full data set (1953-2015) to run the model 10 years past 2015 is appropriate. The full data set (1953-2015) was split into two subsets: training data (1953-1999) and test data (2000-2015).

Since there were so many data points with unknown years these points were assigned either 2010 or 1990 based on a probability. The probability used was calculated by using the proportion of infestation points that occurred after 1999 to the total number of infestation points with known years (L) for each watershed. The proportion (L) was used as well as one minus proportion (L) to designate the unknown infestation points for that watershed. This process was repeated for all the watersheds with infestations with unknown years. In the case where there were infestations with unknown years in a watershed without known years the unknown infestation received a designation based on the nearest known infestation point. The best-fit parameters were then calculated for the two subsets, training data (1953-1999) and test data (2000-2015), using the parameterization methodology used for the full data set (1953-2015).

The gravity model was also validated by comparing the current distribution results (1953-2015) to the results of the parameterized gravity model run from 1953 to 2015. This comparison shows the model's ability to recreate current distribution patterns.

3.3 Results

3.3.1 Gravity Model Parameterization

Based on results of the 1,000 trials of the parameterization routine the best fit results for each parameter were estimated (Table 3.2) and those values were used to mimic the 63 year spread in the current distribution data from 1953-2015. The current area of hydrilla infestation in the continental USA is 1,553,643 ha based on the hydrilla occurrence data from 1953 to 2015. On average, the model over estimated that 1,766,683 ha would be infested by 2015. The actual observed value of 1,553,643 ha is within the 1st and 3rd quartiles of the distribution (1st - 1,515,150 ha 3rd – 1,964,775 ha) of the model results. The overall range of infested area over 1,000 trials was 875,214 ha to 3,445,601 ha. The gravity model uses these estimated best-fit values (Table 3.2) for subsequent simulations.

3.3.2 Gravity Model Sensitivity Analysis

The sensitivity analysis showed that the model was effected most to changes in the distance coefficient parameter (α), area infested per year per watershed (k_i), the probability that an individual boater will infest a waterbody (B), and the habitat suitability scalar parameter (y) (Table 3.3). The model was the most sensitive to changes to the distance coefficient parameter. A 25% decrease in α increased the proportion (P_j) of the average colonization for each watershed by 83%. An increase of 25% in α decreased the proportion (P_j) by 77% (Table 3).

3.3.3 Gravity Model Validation

Table 3.2 shows the best-fit parameterization results for thetraining data (1953-1999). The average area predicted to be infested for the training data was 940,962 ha compared to 868,105 ha of actual infestation in 1999. The overall range of infested area for the training data was 354,782 ha to 1,780,793 ha. The average results are within the 1st and 3rd quartiles of the distribution (1st – 800,166 ha 3rd – 1,056, 892 ha) of our results.

Table 3.2 shows the best-fit parameterization results for the test data (2000-2015). The average area predicted to be infested for the test data was 1,607,058 ha compared to the actual area of infestation in 2015, 1,553,643 ha. The overall range for the results of the test data was 1,548,634 ha to 1,714,631 ha. The average results are within the 1st and 3rd quartiles of the distribution (1st – 1,587,645 ha 3rd – 1,621,652 ha) of the results.

3.3.4 Gravity Model

The area of reported infestation for 2015 was 1,553,642 ha; on average the model predicts an increase to 2,866,937 ha from 2015 to 2025. Occurrence data from 1953 to 2015 hydrilla had an average spread of 117 ha per infested watershed per year. The model predicts an infestation rate of about 625 ha per watershed per year (2015-2025). The average of the 1,000 trials for all 210 watershed are displayed in Figure 3.

The primary objective of this study was to predict the potential spread of hydrilla in the Great Lakes Basin via recreational watercraft and boat trailers and to identify high-risk areas for introduction. Table 3.4 shows the Great Lakes Basin watersheds results in order of the overall proportion of water expected to be infested with hydrilla within that watershed by 2025.all of the Great Lakes Basin watersheds. The five watersheds surrounding the Great Lakes Basin watersheds that are at highest risk for overall hydrilla infestation based on the model results are Upper Ohio, Scioto, Muskingum, Great Miami, and Upper Hudson (Figure 4). The Upper Ohio, Scioto, Muskingum, and the Upper Hudson watersheds all have current infestations based on the occurrence data. The Great Miami watershed was at 0 hectares infested and is predicted to have an infested proportion of 67% by 2025.

We ranked watersheds throughout the continental US by new infestation areas and the top ten watersheds that have the largest new infestation proportions are presented in Table 3.5. Knowing which infested watersheds are at risk for further infestation may be useful for managers attempting to prevent further spread in already infested watersheds. Seven of the top ten in this ranking are watersheds that are currently infested with hydrilla. Table 3.6 shows the top ten watersheds that have the largest increase in infestation proportions per watershed including those with and without current infestations.

3.4 Discussion

3.4.1 Continental United States

Hydrilla has been established in the U.S. since 1953 and is likely to continue spreading, particularly to the non-infested waterbodies within and surrounding infected watersheds. The gravity model I developed quantifies that pattern of spread and enables predictions to be made of regions most susceptible to new infestations. Of the top ten watersheds predicted to have the highest increase in infestation proportions, seven already have hydrilla infestations. Watersheds with large areas of water and high boater registration and are in or near watersheds with established hydrilla populations are also at high risk for hydrilla infestation.

Although hydrilla will spread most in watersheds already infested, we predict it will spread further throughout the continental United States and in the Great Lakes Basin over the next 10 years. The watersheds in the Great Lakes Basin were most likely to increase overall proportion of infestation were the St. Clair-Detroit, Southwestern Lake Huron-Lake Huron, Southeastern Lake Ontario, Western Lake Erie, and Southern Lake Erie watersheds (Figure 5). Thus, it is important to monitor for hydrilla within these watersheds and in the surrounding watersheds in order to prevent the establishment of hydrilla in the Great Lakes.

The watersheds in the Ohio River Valley are predicted to have a much higher proportion of each watershed infested over the next 10 years than surrounding watersheds. These watersheds either have current infestations or are surrounded by watersheds that have infestations. Taking these factors into account along with the model results it is likely that these watersheds will have new or increased hydrilla infestation within the next ten years. Because these watersheds have less than 1,000 ha total waterbody area their proportion of infestation is likely to increase rapidly.

Our model also predicts that the rate of infestation of hydrilla in the U.S. will increase over the next 10 years. There are two primary explanations for this. First, as sources of hydrilla increase, more boats will likely transport hydrilla to new areas that are not yet infested. Second, the observed distribution of hydrilla may be a low estimate as hydrilla may exist in locations and be unreported, particularly in areas such as the southeastern United States where hydrilla has been established for many years. In these areas where hydrilla is common less monitoring and reporting of hydrilla may have been done. Therefore, the model will continue to infest watersheds where hydrilla has been established such as watersheds in the southeast region of the United States.

3.4.3 Model Limitations

When modeling at the scale of the continental United States, there are logistical and data limitations that constrain the accuracy or specificity of the model results. As expected the model showed that watersheds with high boater registration and those surrounding watersheds with high boater registration have higher risk of infestation. However, the methodology did not distinguish between different types of boats. Resident boats for instance that stay in one body of water are not likely to transport hydrilla to other waterbodies. The model focuses on transient boats; therefore, if a watershed has a high number of resident boats then model results may overestimate the risk of infestation in that watershed or surrounding watersheds. It was assumed that boaters in the Midwest and Northeastern states behave the same as they do in Florida and the Southeastern United States. Another assumption made was that despite varying human behavior and geography throughout the United States, distance had the same impact in decision making for transient recreational boaters.

The waterbody data that was used does not include minor waterways (USGS, 2013). As a result, not all infestations will be reflected in the model. For example, the current Tonawanda creek infestation in western New York is not reflected in the model. If a finer scale is used, minor waterways could potentially be included as well as more specific attraction parameters, such as boat ramps. Nonetheless, current results provide regional guidance as to where to monitor and prioritize additional modeling or analyses to provide further refinement of the predictions.

The model may have overpredicted the increased rate of infestation if current estimates of infection are low because waterbodies in close proximity to those with established populations of hydrilla will most likely have hydrilla despite not accounted in occurrence data. The model will predict that these waterbodies will become infested within the densely infested regions as well as predict spread in areas where hydrilla has not yet been established. It is important to remember that the observed distribution of hydrilla is the result of a dynamic and stochastic process that has occurred for over 50 years. The range of potential outcomes is likely very broad and the best-fit parameters suggest that the current distribution is lower than would be expected on average.

Another limitation of this model is that desiccation rates of hydrilla were not incorporated for the model. Vegetative fragments as well as tubers likely have different desiccation rates (Langeland, 1996). The rate of desiccation would also vary with length of travel and changes in environmental conditions per individual boat. This was not incorporated into the model due to availability of data and scale, but should be taken into consideration in further hydrilla dispersal studies (Barnes et al., 2013).

3.4.4 Model Validation

No independent data sets were available to validate the model. For this study splitting the available data into two subsets revealed differences in parameter values for the two subsets. This was expected as hydrilla infestation rates should change over time due to differential spreading into new areas and within already infested areas. The data set did not have enough points with known year data to break into more than two subsets. In future studies with fuller data sets estimating parameters for multiple temporal subsets may allow for predicting how the parameter values may change over time and using identified trends to adjust parameter values. The sensitivity analysis did show that parameters, which differed between the two subsets, would not have a significant effect on model outcome giving confidence to use the original parameterization method (Bossenbroek et al. 2007).

3.4.5 Hydrilla Management

These model results were combined with other results from the hydrilla risk assessment collaboration partners to provide management recommendations for prevention, detection, and response. These recommendations include public education campaigns on how aquatic invasive species can spread via transient recreational boating and how to prevent hitchhikers in the watersheds. It is recommended that these efforts are focused in the watersheds that were identified by the model to have high probability for hydrilla infestation as well as in areas of known infestations.

3.5 Conclusion

Through this thesis work, a gravity model incorporating habitat suitability was constructed that was able to replicate current conditions, giving confidence that the model predicts what watersheds may be vulnerable for hydrilla infestation. The model identified watersheds surrounding and in the Great Lakes Basin that are at high risk for future hydrilla infestation. Based on the model results, waterbodies that are in watersheds with current hydrilla infestations are at high risk for hydrilla infestation. Monitoring efforts to prevent further hydrilla infestation should be focused on these high-risk watersheds.

Table 3.1: Gravity Model Parameters: Description of each parameter and how each value was determined.

Parameter	Description	How value was determined
T_{ij}	Number of boaters that travel from watershed i to watershed j	Equation 1
A_i	Balancing factor that ensures all boaters leaving watershed i reach a destination j	Equation 2
O_i	Number of boats traveling from watershed i	Estimated from data
W_j	Attractiveness of watershed j	Estimated from data
c_{ij}	Distance from watershed i to watershed j using US road data (Centroid of watershed based on waterbody surface area)	Estimated from data
α	Distance coefficient	Fit parameter
I	Area of surface water of lakes, reservoirs, and rivers (ha)	Estimated from data
S_j	Length of oceanic and great lakes shoreline	Estimated from data
x	Scalar to estimate the "attractiveness" of shoreline in terms of the "attractiveness" of lakes	Fit parameter
m	Parameter to estimate the distance traveled within a watershed	Fit parameter
w_i	Habitat suitability probability for each watershed	Estimated from data (provided from MaxEnt)
y	Scalar to adjust habitat suitability	Fit parameter
B	*P*robability that an individual boater will infest a waterbody	Fit parameter
k_i	Area infested per year per watershed	Fit parameter

Table 3.2 Parameterization Routines: Results from parameterization routines.

Parameters	Range Tested	Best Fit Value	Best Fit Value Train	Best Fit Value Test
m	0.01-0.99	0.75	0.7	0.1
x	0.1-50	5.5	5.9	1.25
B	0.0001-0.01	1/650	1/600	1/300
k	100-10000	2500	2250	1000
α	0.01-10	4	4	4
y	0.1-10	1.64	1.64	1.64

Table 3.3: Sensitivity Analysis: Results from the sensitivity analysis.

Trial	Parameter Value	Percentage adjusted from best fit	Results (Pj)
Best fit			0.27
m	0.56	(- 25%)	0.26
m	0.94	(+ 25%)	0.27
x	4.1	(- 25%)	0.27
x	6.9	(+ 25%)	0.27
B	1/488	(- 25%)	0.27
B	1/813	(+ 25%)	0.26
k	1875	(- 25%)	0.24
k	3125	(+ 25%)	0.31
α	3	(- 25%)	0.49
α	5	(+ 25%)	0.06
y	1.23	(- 25%)	0.25
y	2.05	(+ 25%)	0.28

Table 3.4: Great Lakes Basin Watersheds Gravity Model Results: The watersheds are in order of the overall proportion of water expected to be infested with hydrilla by 2025. Current Infested Area (ha) is the current infested area of water within that watershed. Current proportion of infested waterbodies per watershed is the current infested area of water to the overall area of water within that watershed. 2025 Area (ha) is predicted area of infestation based on the10 year model results per watershed. 2025 Proportion is the proportion of the predicted area of infestation to the total the overall area of water within that watershed.

Watershed Name	Current Area(ha)	Current Proportion	2025 Area (ha)	2025 Proportion
St. Clair-Detroit	0	0	12162.53	0.1733
Southwestern Lake Huron-Lake Huron	0	0	7032.47	0.0578
Southeastern Lake Ontario	17166.9	0.03	28009.44	0.0489
Western Lake Erie	0	0	15547.46	0.0382
Southern Lake Erie	15.7	0.00003	21120.76	0.0342
Eastern Lake Erie-Lake Erie	0	0	11482.54	0.0220
Northeastern Lake Michigan-Lake Michigan 2	0	0	3954.93	0.0177
Southwestern Lake Michigan 2	0	0	9679.97	0.0173
Southwestern Lake Ontario	0	0	4140.00	0.0127
Southeastern Lake Michigan	0	0	10489.92	0.0105
Southwestern Lake Michigan 1	0	0	805.00	0.0040
Northwestern Lake Michigan	0	0	332.51	0.0010
Northwestern Lake Huron 2	0	0	887.48	0.0010
Northeastern Lake Ontario-Lake Ontario-St. Lawrence	0	0	150.00	0.0004
Southern Lake Superior-Lake Superior	0	0	97.50	0.0004
Southern Lake Superior-Lake Superior	0	0	97.50	0.0004
Northwestern Lake Huron 1	0	0	200.00	0.0004
Northeastern Lake Michigan-Lake Michigan 1	0	0	225.02	0.0002

Table 3.5: Largest New Infestations: The top ten watersheds that have the largest new infestation proportions of infested area to total hectares per watershed.

Watershed Name	Current Infested Area (ha)	Predicted Infested Area (ha)	Proportion Infested
Kentucky-Licking	0	13581.51	0.93
Great Miami	0	9364.52	0.67
Pascagoula	0	22222.36	0.59
Green	0	12585.10	0.48
Lower Missouri	0	11262.47	0.27
Upper Tennessee	0	18137.36	0.19
St. Clair-Detroit	0	12162.53	0.17
Lower Mississippi-Hatchie	0	12504.97	0.12
Central California Coastal	0	1078.81	0.10
Upper Mississippi-Salt	0	4790.00	0.09

Table 3.6: Largest Increase to Infestation Proportion: The top ten watersheds that have the largest increase to infestation proportions of infested area to total area per watershed for current and new infestations.

Watershed Name	Current Infested Area(ha)	Current Infested Proportion	Predicted Infested Area(ha)	Predicted Infested Proportion
Kentucky-Licking	0	0	13581.5	0.93
Muskingum	3671.4	0.17	21403.0	0.99
Choctawhatchee-Escambia	2202.9	0.08	25413.0	0.89
Great Miami	0	0	9364.5	0.67
Scioto	5805.7	0.37	15695.2	1.00
Middle Ohio	14450.1	0.40	35843.9	1.00
Pee Dee	3587.1	0.09	28587.0	0.68
Cape Fear	7562.9	0.18	32562.9	0.76
Pascagoula	0	0	22222.4	0.59
Middle Tennessee-Hiwassee	10390.4	0.35	27079.7	0.91

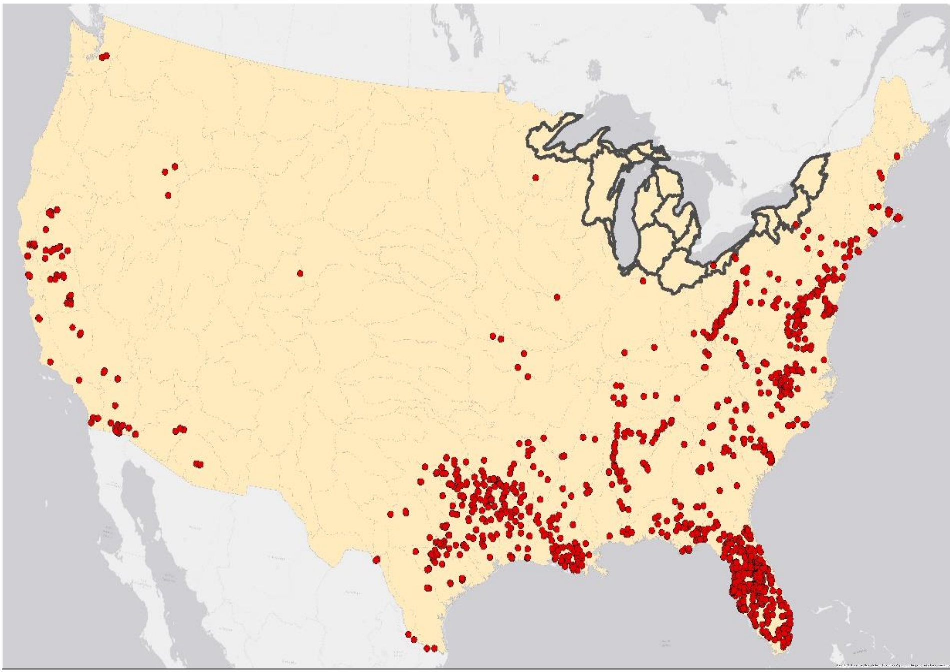

Figure 1. Map of current distribution of hydrilla in the continental United States.

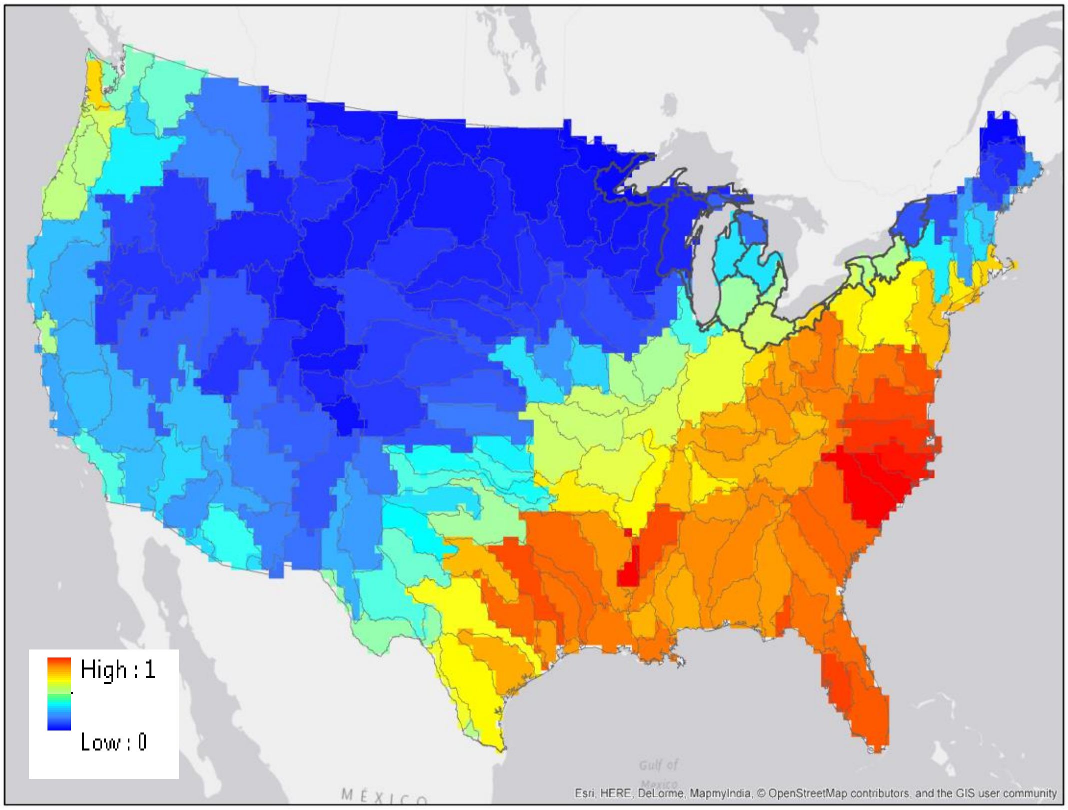

Figure 2. MaxEnt habitat suitability results (Barnes & Soto, Unpublished).

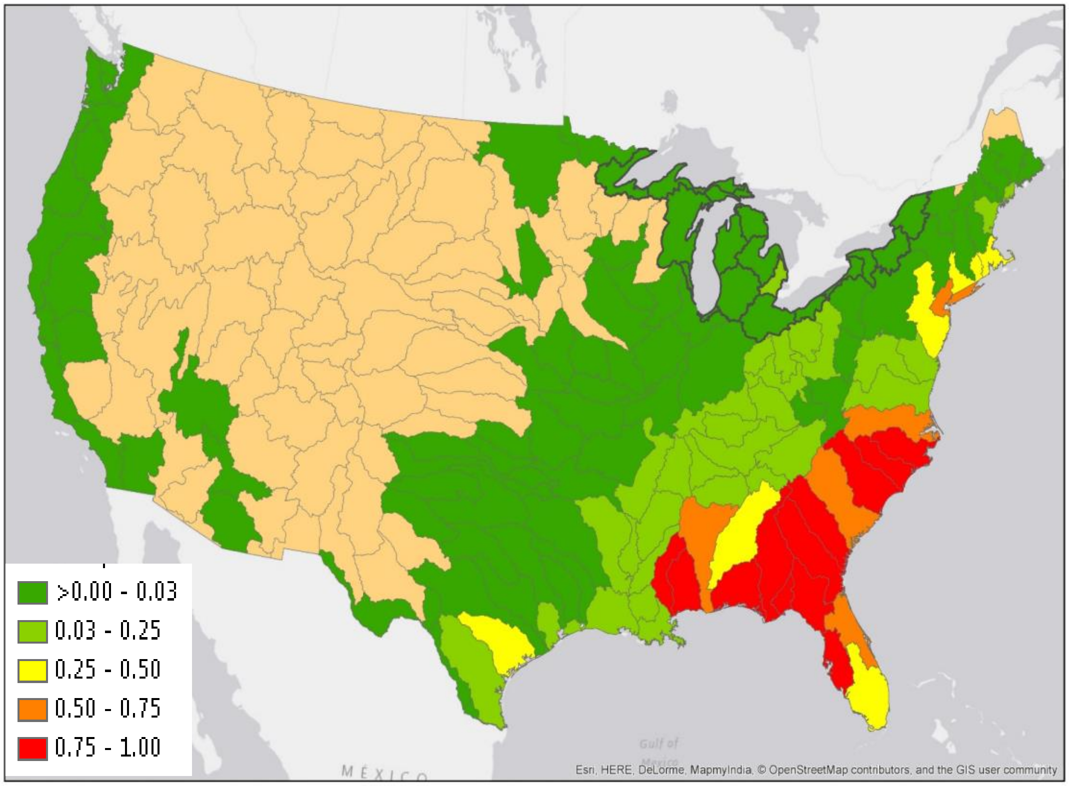

Figure 3. Map of predicted infested proportion distribution (1953-2015) from parameterization.

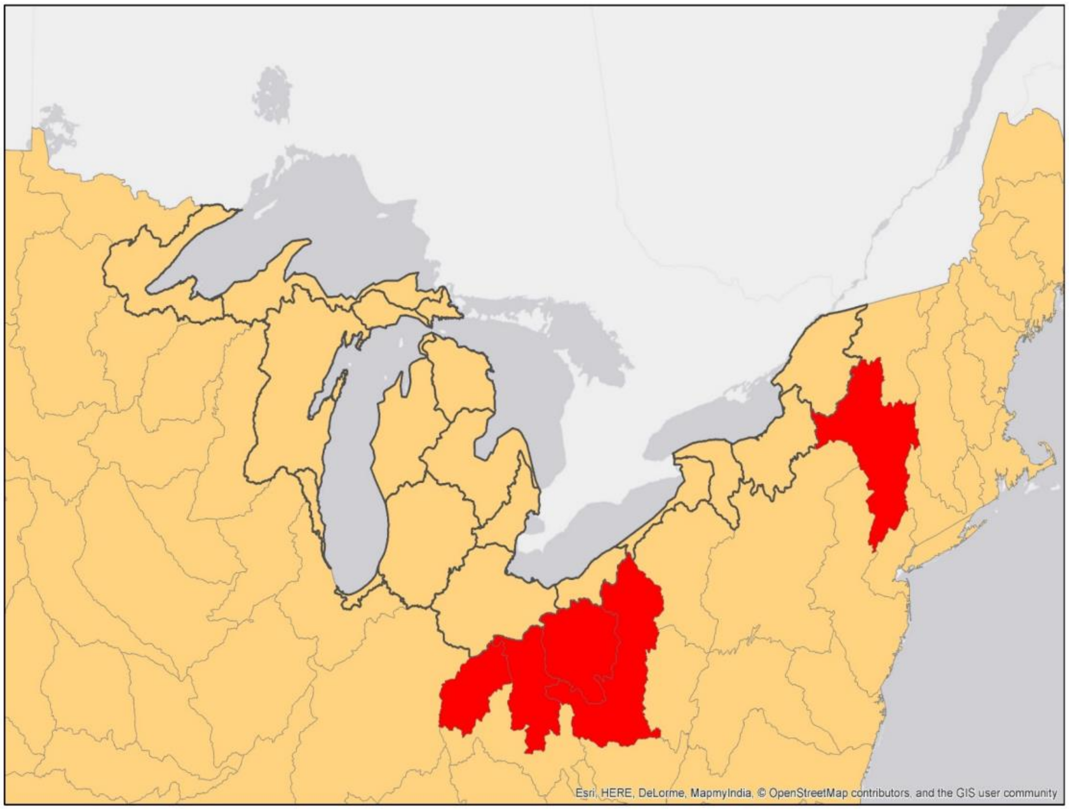

Figure 4. The top five watersheds surrounding the Great Lakes Basin Upper Ohio, Scioto, Muskingum, Great Miami, and Upper Hudson.

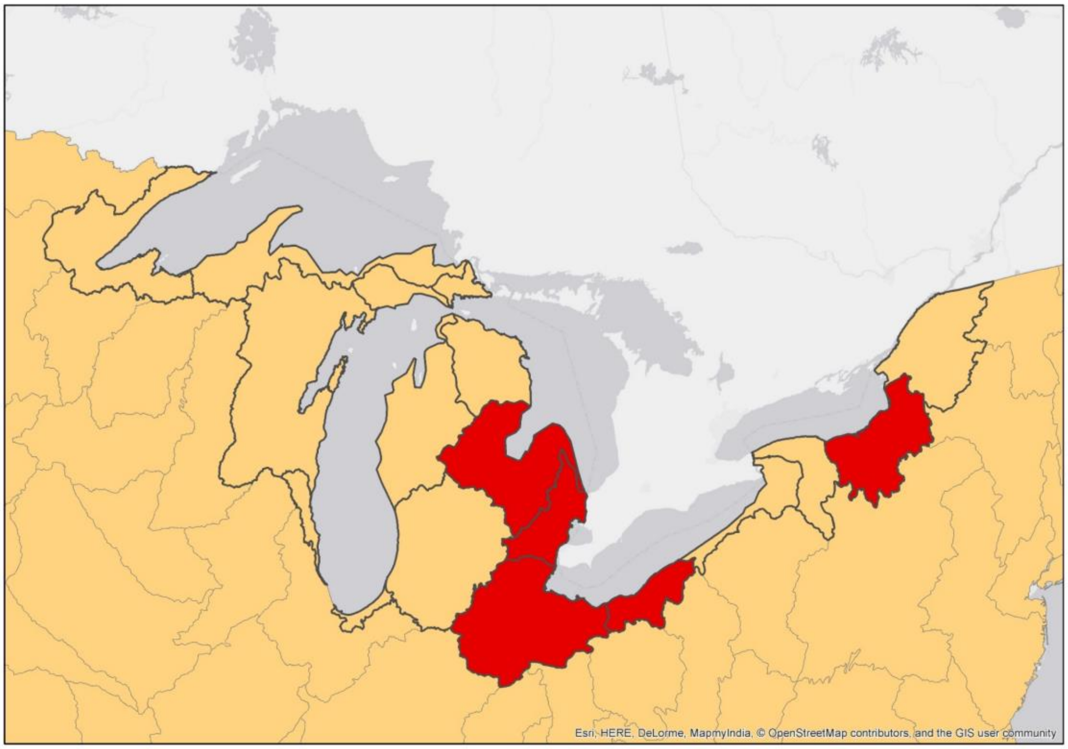

Figure 5. High risk watersheds in the Great Lakes Basin watersheds. St. Clair-Detroit, Southwestern Lake Huron-Lake Huron, Southeastern Lake Ontario, Western Lake Erie, and Southern Lake Erie.

References

Anderson, L. G., Rocliffe, S., Haddaway, N. R., & Dunn, A. M. (2015). The Role of Tourism and Recreation in the Spread of Non-Native Species: A Systematic Review and Meta-Analysis. PloS one, 10(10), e0140833.

Barnes, M., Jerde, C., Keller, D., Chadderton, W., Howeth, J., & Lodge, D. (2013). Viability of Aquatic Plant Fragments following Desiccation. *Invasive Plant Science and Management,6*(2), 320-325. doi:10.1614/IPSM-D-12-00060.1

Binimelis, R., Monterroso, I., & Rodríguez-Labajos, B. (2007). A social analysis of the bioinvasions of Dreissena polymorpha in Spain and Hydrilla verticillata in Guatemala. Environmental Management, 40(4), 555-566.

Bobeldyk, A. M., Bossenbroek, J. M., Evans-White, M. A., Lodge, D. M., & Lamberti, G. A. (2005). Secondary spread of zebra mussels (Dreissena polymorpha) in coupled lake-stream systems. Ecoscience, 12(3), 339-346.

Bossenbroek, J. M., Johnson, L. E., Peters, B., & Lodge, D. M. (2007). Forecasting the expansion of zebra mussels in the United States. Conservation Biology, 21(3), 800-810.

Bossenbroek, J. M., Kraft, C.E., & Nekola, J.C. (2001). Prediction of long-distance dispersal using gravity models: zebra mussel invasion of inland lakes. Ecological Applications, 11(6), 1778-1788.

Buchan, L. A. J., and D. K. Padilla. 2000. Predicting the likelihood of Eurasian watermilfoil presence in lakes, a macrophyte monitoring tool. Ecological Applications 10:1442-1455.

ESRI. 2011. ArcGIS Desktop: Release10. Environmental Systems Research Institute. Redlands, CA.

Fotheringham, A. S. (1981). Spatial structure and distance-decay parameters. Annals of the Association of American Geographers, 71(3), 425-436.

Great Lakes Restoration Initiative (GLRI) Task Force. GLRI Action Plan FY2010-FY2014. (2010) http://greatlakesrestoration.us/action/wp-content/uploads/glri_actionplan.pdf

Keller, R. P. (2009). Bioeconomics of invasive species: integrating ecology, economics, policy, and management. Oxford University Press.

Kraft, C.E., Sullivan, P.J., Karatayev, A.Y., Burlakova, L.E., Nekola, J.C., Johnson, L.E., & Padilla, D.K. (2002). Landscape Patterns of an Aquatic Invader: Assessing Dispersal Extent from Spatial Distributions. Ecological Applications 12(3), 749-759.

Langeland, K. A. (1996). Hydrilla verticillata (LF) Royle (Hydrocharitaceae)," The Perfect Aquatic Weed". Castanea, 293-304.

Langeland, K. A., & Sutton, D. L. (1980). Regrowth of Hydrilla from Axillary Buds1.

Les, D. H., Mehrhoff, L. J., Cleland, M. A., & Gabel, J. D. (1997). Hydrilla verticillata (Hydrocharitaceae) in Connecticut. Journal of Aquatic Plant Management, 35, 10-14.

Leung, B., J. M. Drake, and D. M. Lodge. 2004. Predicting invasions: propagule pressure and the gravity of allee effects. Ecology 85:1651- 1660.

Mills, E. L., Leach, J. H., Carlton, J. T., & Secor, C. L. (1993). Exotic species in the Great Lakes: a history of biotic crises and anthropogenic introductions. Journal of Great Lakes Research, 19(1), 1-54.

Mills, E. L., Leach, J. H., Carlton, J. T., & Secor, C. L. (1994). Exotic species and the integrity of the Great Lakes. BioScience, 666-676.

Milon, J. W., J. Yingling and J. E. Reynolds. 1986. An economic analysis of the benefits of aquatic weed control in North-Central Florida, Economics Report No. 113, Food and Resource Economics, Agricultural Experiment Station, Institute of Food and Agricultural Sciences, University of Florida, Gainesville 32611. 52 pp.

Morandi, M. J., "Assessing the influence of different inland lake management strategies on human-mediated invasive species spread" (2013). *Theses and Dissertations*. Paper 156.

MacIsaac, H. J., J. V. M. Borbely, J. R. Muirhead, and P. A. Graniero. 2004. Backcasting and forecasting biological invasions of inland lakes. Ecological Applications 14:773-783.

Muirhead, J. R., and H. J. MacIsaac. 2005. Development of inland lakes as hubs in an invasion network. Journal of Applied Ecology 42:80-90.

Office of Planning, Environment, & Realty (HEP). 2015. National Highway Planning Network Version 14.05 (NHPN). Available from https://www.fhwa.dot.gov/planning/processes/tools/nhpn/index.cfm? [Accessed 15 January 2016].

Office of Technology Assessment (OTA). 1993. Harmful non-indigenous species in the United States. OTA-F-565. US Government Printing Office, Washington, DC.

Posey, M. H., Wigand, C., & Stevenson, J. C. (1993). Effects of an introduced aquatic plant, Hydrilla verticillata, on benthic communities in the upper Chesapeake Bay. Estuarine, Coastal and Shelf Science, 37(5), 539-555.

RStudio Team (2015). RStudio: Integrated Development for R. RStudio, Inc., Boston, MA URL http://www.rstudio.com/.

Ricciardi, A. Patterns of invasion in the Laurentian Great Lakes in relation to changes in vector activity. Diversity and Distributions 12(4):425-433 (2006).

Ricciardi, A., & Rasmussen, J. B. (1998). Predicting the identity and impact of future biological invaders: a priority for aquatic resource management. Canadian Journal of Fisheries and Aquatic Sciences, 55(7), 1759-1765.

Rothlisberger, J.D., Chadderton, William, McNulty, Joanna & Lodge, David. (2010). Aquatic Invasive Species Transport via Trailered Boats: What Is Being Moved, Who Is Moving It, and What Can Be Done. Fishereis. 35. 121-132. 10.1577/1548-8446-35.3.121.

Rothlisberger, J. D., Finnoff, D. C., Cooke, R. M., & Lodge, D. M. (2012). Ship-borne nonindigenous species diminish Great Lakes ecosystem services.

Ecosystems, *15*(3), 1-15. Rothlisberger, J. D., & Lodge, D. M. (2010). Limitations of Gravity Models in Predicting the spread of Eurasion Watermilfoil. *Society for Conservation Biology*, 25(1), 64-72.

Schneider, D. W., C. D. Ellis, and K. S. Cummings. 1998. A transportation model assessment of the risk to native mussel communities from zebra mussel spread. Conservation Biology 12:788-800.

Simberloff, D. 2003. How much information on population biology is needed to manage introduced species? Conservation Biology 17:83-92.

Stokstad, E. 2007. Feared quagga mussel turns up in western United States. Science 315:453-453.

Thomas, R. W., and R. J. Hugget. 1980. Modeling in geography. Barnes and Noble Books, Totowa, New Jersey.

Unpublished niche model results from Texas Tech University, Dr. Matthew Barnes and Sasha Soto

U.S. Geological Survey, 2013, National Hydrography Geodatabase: The National Map viewer available on the World Wide Web (https://viewer.nationalmap.gov/viewer/nhd.html?p=nhd), accessed 2015.