MODELING EURASIAN WATERMILFOIL (*MYRIOPHYLLUM SPICATUM*) HABITAT WITH GEOGRAPHIC INFORMATION SYSTEMS

By

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Eurasian watermilfoil (*Myriophyllum spicatum*) habitat was predicted at multiple scales, including a lake, regional, and national level. This dissertation illustrates how habitat can be predicted for *M. spicatum* using publically-available data for both presence and environmental variables. Models were generated using statistical procedures and quantative methods to determine where the greatest likelihood of presence was located. For the single lake, presence and absence data were available, but the larger-scale models used presence-only methods of prediction. These models were paired with a Geographic Information System so that data could be visualized on a map. For the selected lake, Pend Oreille (Idaho), spatial analysis using general linear mixed models was used to show that depth and fetch could be used to predict habitat, although differences were seen in their importance between the littoral and pelagic zones. For the states of Minnesota and Wisconsin, Mahalanobis distance and maximum entropy methods were used to demonstrate that available habitat will not always mean presence of *M. spicatum*. The differing approaches to management in these states illustrated how an aggressive public education campaign can limit spread of *M. spicatum*, even when habitat is available. Bass habitat appeared to be the largest

predictor of *M. spicatum* in Minnesota, although this was due to the similar environmental preferences by these species. Using maximum entropy, on a national level, presence of *M. spicatum* appeared to be best predicted by annual precipitation. Again, results showed that habitat is colonized as time permits, and not necessarily as conditions permit.

DEDICATION

I would like to dedicate this dissertation to my parents, Mack and Donna Prince. God has blessed me beyond what I deserve, especially with my parents. I would not have wanted them to be any different and they could not have been better. While I am sure they would not call it a “sacrifice,” I know they have given much so that I could have the opportunities I have had. It can not be easy to tell people that your thirty-something daughter is “still in school”. I only hope that I have made my parents proud and that they will look at what we have done and say it was worth the cost.

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CHAPTER 1

INTRODUCTION

The abiotic components of the environment necessary for survival constitute the habitat requirements for a species (Gillenwater et al. 2006). Species habitat requirements are described by habitat factors, which cover the most essential characteristics of preferred habitats (Store and Jokimäki 2003). Geographic Information Systems (GIS) are well suited for studies involving habitat modeling and delineation, sometimes referred to as habitat suitability indexing (Gillenwater et al. 2006; Wang 1994). Geographic Information Systems also offer the advantage of being able to overlay layers representing the spatial distribution of different environmental variables related to habitat suitability and perform spatial operations on these layers (Gillenwater et al. 2006).

The majority of previous work in habitat modeling, with and without the use of GIS, focused on identifying and delineating potentially suitable habitats for desirable species. Less focus has been given to using predictive modeling for species control or proactive, preventative practices for nuisance species. Modeling such as this is necessary to provide natural resource managers and policy makers with predictions of the effects of a particular management practice (Valley et al. 2005). Morisette et al. (2006) developed a nationwide habitat map for tamarisk (*Tamarix* spp.). The habitat distribution map provided not only location information, but also helped guide containment boundaries, identify priority areas for early detection and rapid response,

and monitor control strategies and cost-effectiveness in different states. Ecological models can also be used as a forecasting tool to examine potential ecological impacts and prioritize needs (Rotenberry et al. 2006), and to evaluate the expected effects of a variety of landuse changes on a species or an ecological system (Romero-Calcerrada and Luque 2006).

Theoretical Background

Development of ecological models provides a simple, direct method by which to predict presence, absence, and spread of species in given environments. Levin (1992) calls the understanding of patterns and process the "essence of science" while acknowledging that complexity in nature forces modelers to make a trade-off between detail and generalization. Romero-Calcerrada and Luque (2006) urged a "need to develop indicators that simplify complexity in natural systems." Simpler models are often preferred to complex models because it is believed they have wider applicability and represent better overall prediction of species presence. Levin (1992) noted that models should contain "just enough" detail with the idea that the objective of the model build should ultimately be to ask how much detail can be ignored. This approach is useful because it limits the influence of peculiarities specific to a particular sample of species data (Elith et al. 2002).

Store and Jokimäki (2003) identified four steps to habitat suitability modeling: 1) constructing conceptual habitat suitability models; 2) producing the data needed for the models; 3) evaluating a target area based on habitat factors; and 4) combining the separate suitability indices. Empirical models in Store and Jokimäki (2003) were constructed based on investigated relationships between abundance of species and

appropriate background variables. For species lacking objective, data-driven models, habitat suitability models were based on expert knowledge of which factors determine the habitat for a species and the relative importance of these variables. Suitability was then determined by overlay analysis and cartographic modeling in a GIS using standardized and weighted layers for those factors which expert knowledge or objective models showed were foremost.

Several researchers (Baja et al. 2002; Carver 1991; Hall et al. 1992) reported that the use of Boolean operators was too limiting because areas must fall into one of two categories (suitable or unsuitable) when in reality, areas may be marginal in their classification into one of these two areas – an attribute which is ignored by a strict Boolean classification. Many felt that the use of fuzzy classification methods or suitability indices was more representative of the continuous nature of environmental variables (Baja et al. 2002; Carver 1991). Hall et al. (1992) contains a complete discussion of the use of fuzzy classification versus Boolean classification.

Habitat suitability is often quantified by means of a suitability index or probability (Store and Jokimäki 2003). A model may or may not encompass the additional step of identifying areas which are not only suitable, but which have a higher probability of site occupancy. This can, and probably should be, considered a separate research question, using separate models to estimate presence and suitability. A species may not act logically in that a species may not occupy the most suitable location for a variety of reasons; thus an area may have a high species density but limited contribution to long-term species persistence and vice versa (Elith et al. 2002).

In identifying those areas most likely to contain a species, it is often desirable to weight each criterion and develop levels of suitability such as was done by Joerin et al. (2001) and Wang (1994). It is important to note that weights can be either quantitative

or qualitative (Rohde et al. 2006). The consequence of qualitative weights is the impact on available statistical options and this should be a consideration when choosing to apply these types of weights.

Jensen et al. (1992) used GIS to predictively model dominant freshwater macrophytes. The GIS was used to store the spatial data, query the database, and employ Boolean logic to predict the spatial distribution of various aquatic macrophytes. The authors found it necessary to obtain spatially registered biophysical information; store the data using the appropriate GIS architecture; and specify and apply environmental constraint criteria rules. The basic assumption was that aquatic macrophytes would be present if all the environmental constraint criteria could be met. It was concluded that the techniques used in this study could predict the location of freshwater aquatic macrophytes and could also be used to predict where they would occur in the future. Narumalani et al. (1997) came to the same conclusion when using GIS to model aquatic macrophyte habitat.

Technical Aspects of Model Function

Overlay analysis using map algebra approaches have been used by other researchers working in habitat suitability modeling (Store and Jokimäki 2003) and related areas such as landuse planning (Millette et al. 1997). Map algebra is based on simple mathematical principles. If each environmental constraint (or predictor variable in statistical terms) is contained in an individual GIS layer, the intersection of those layers identifies areas which satisfy multiple constraints. Whether the approach taken is a strict Boolean approach (Joerin et al. 2001; Rohde et al. 2006; Romero-Calcerrada and Lunge 2006) or fuzzy classification (Baja et al. 2002; Carver 1991; Hall et al. 1992), there will be areas which meet all or most criteria and those which do not meet any. The most

efficient way to identify these areas in a GIS is to perform these types of overlay analyses.

Map algebra allows each raster cell (or vector grid cell) to be assigned a value and any mathematical model can then be applied to those values. For example, two layers can be "added" by adding cell values between layers for cells with corresponding geographic space. With either a Boolean or fuzzy classification approach, 0's and 1's can be utilized with multiplication operations to identify areas that are suitable and not suitable. Cells are assigned values of 0 or 1, with 0 being unsuitable and 1 being suitable. By multiplying the maps together, areas which meet both criteria return values of 1, and cells which meet one or zero criteria return values of 0. In a fuzzy classification system, layers can be added such that the overall magnitude of the output represents the level of suitability (Fig. 1.1). Cell values in individual GIS layers or the predictive output layer can be binned into ordinal categories to provide multiple levels of suitability.

Layers can also be combined in a more complex manner using a relationship developed through statistical procedures. Again, statistical procedures will differ depending on choices made regarding classification of layers. Unless actual values are used, categorical data analysis or nonparametric methods are more appropriate choices for developing algorithms for overlay. Boolean approaches require the use of statistical procedures designed for a 0/1 response variable.

Background for Conceptual Model

Currently Eurasian watermilfoil (*Myriophyllum spicatum*) is found in almost all fifty states and is one of the most troublesome submerged aquatic plants in North America

(Madsen 1998; Smith and Barko 1990). Among those factors which most impact presence of Eurasian watermilfoil, light availability, water movement, and sediment dynamics appear to be the major driving mechanisms. A discussion of the relationship between these factors is presented in Madsen et al. (2001).

Although many components of the aquatic environment influence presence, the complex interrelationship between the various components requires careful selection of model inputs to limit effects of multicollinearity between variables in the model. Smith and Barko (1990) present a thorough list of these components in their review of Eurasian watermilfoil ecology (Table 1.1).

Data on ecology of Eurasian watermilfoil are possibly of limited utility or may force choices (if lack of alternatives is truly considered choice) regarding model development in some instances. For example, it has been noted that the species is typically most abundant in one to four meters of water, but will occur in up to 10 m of water (Smith and Barko 1990). In a pure Boolean approach, an absolute limit may need to be decided on an individual case basis. Light intensity is also related to the growth of this species; however it has been found growing in a wide range of clarity and turbidity (Smith and Barko 1990). Again, it could be virtually impossible to assign clear demarcations between suitable and not suitable in this instance.

Store and Jokimäki (2003) advocated use of existing literature and expert knowledge in model development. A conceptual model was developed based on published scientific data (Madsen 1998; Madsen et al. 2001; Smith and Barko 1990, Fig. 1.2). The conceptual model acknowledges the influence only of elements of the physical environment which are non-anthropogenic. Buchan and Padilla (2000) used GIS and regression techniques to develop and test a model for predicting the likelihood of Eurasian watermilfoil in lakes. They included factors such as presence of boat ramps,

type of boat launch, and proximity to highways and residences. They determined that these factors were poorer predictors of milfoil presence than those which related to species growth directly.

Spatial Aspects of the Research Problem

The landmark paper by Levin (1992) on scale and pattern in ecology addresses the need for analyzing the problem on multiple scales. Levin proposes that variability only has meaning relative to scale, and prediction must operate at the scale relevant to the organism and process being examined. Many of the environmental factors thought to contribute to the presence Eurasian watermilfoil vary across geography and also in their importance between scales. The conceptual model (Fig. 1.2) shows an overview of interactions without regard for which are more important at specific scales (i.e., local, regional, national). Differences in importance among scales dictate which variables should be considered for corresponding models. For example, at a local level, fluctuations in mesoclimate and geology would likely not be significant because they would not vary greatly enough to be of any use. However, variability in depth, Secchi measurements, other species present, etc., is likely to be quite high and these variables should be initially considered for predictor variables in a local-scale model. For a national-scale model, temperature and climate should vary quite dramatically and would likely contribute greatly to a model, whereas Secchi measurements would provide an overabundance of data and detail which would only represent noise in a national scale model.

Utilization of GIS and a spatial approach allows these variations to be better visually represented in a model. The development of spatial statistics and the field of

landscape ecology serve as proof that many problems benefit from this method of inspection, and make a clear case for multi-scale analysis of spatial problems in predictive habitat modeling.

Model Uncertainty

Caswell (1976) suggests that the same model can and should be judged based on its intended purpose. The author makes a distinction in what validity means for models that predict outcomes versus models which recreate processes. Predictive models are validated by 1) determining the domain over which the model applies, and 2) attempting to refute the model to increase confidence. Duality of validity means that a single model might be a valid predictor despite being scientifically refuted (i.e., provides a good fit to the data but an illogical outcome).

Rykiel (1996) advocated a mechanistic approach to model evaluation as a frequently-missed next step, citing evidence that understanding underlying relationships is of crucial importance to resource managers who are often required to describe the influence of changing land use activities on species. Natural variation is unlikely to be fully-characterized by a model (Elith et al. 2002). As such, inaccuracy and imprecision of ecological data place limits on model testability (Rykiel 1996). General linear models are frequently used for habitat modeling, but relatively few publications exist in ecology literature which discuss uncertainty in these models (Elith et al. 2002).

Despite the push by several researchers (Levin 1992; Romero-Calcerrada and Luque 2006) to simplify ecological systems, Elith et al. (2002) argues that with general linear models uncertainty is created by simplifying assumptions and abstractions of ecological processes that must be made. Specific to GIS, layers are often interpolated,

creating uncertainty in the basedata which is propagated or compounded as the data are summarized, classified, modeled, and interpolated. Errors can also exist with field data due to sampling bias and observer error. Some of these represent systematic errors which may not be detrimental to the model if the overall relationship is intact. Non-systematic errors, particularly those in measurement and location can be hard to find and are frequently not identified in the metadata accompanying a GIS layer. Finally, spatio-temporal variability may not be fully captured by sampling protocols, which can skew results. Acknowledging that their list was not exhaustive, after examining a substantial number of potential error sources and their rectification, Regan et al. (2002) concluded that a single method to address model uncertainty did not exist.

It appears that model uncertainty cannot be fully quantified or qualified and many models may never be validated to levels acceptable for all purposes. A model must be judged based on its intended use, simplifying assumptions, and applicable domain without extension unless it can be shown that this extension is scientifically feasible and logical.

Project Objectives

- Objective 1: Develop a conceptual model and associated GIS framework for Eurasian watermilfoil (*Myriophyllum spicatum*) habitat suitability.
- Objective 2: Develop a local-scale model for *M. spicatum* presence in a single lake.
- Objective 3: Develop a regional-scale model for *M. spicatum* presence in a single state.
- Objective 4: Develop a national-scale model for *M. spicatum* presence.

Site location for the local-scale study was Pend Oreille Lake (Idaho). The regional-scale studies were performed for the States of Minnesota and Wisconsin.

Chapters 2, 3, and 4 present the methods, results, and conclusions for the local, regional, and national models, respectively. Chapter 5 serves as a summary and presents future directions for this area of research.

Project Contribution

An understanding of the factors which allow invasive species such as Eurasian watermilfoil to invade communities would improve the ability to eradicate these species. Even if the goal is not eradication, providing some level of control would ease the economic and ecological costs of Eurasian watermilfoil presence. As weed scientists, ecologists, wildlife managers, and water quality professionals work to maintain waterways, the GIS and GIS-modeling offers another tool in their arsenal. Predicting the location and spread of these species will allow them to prioritize financial and manpower resources, while simultaneously protecting many water resources.

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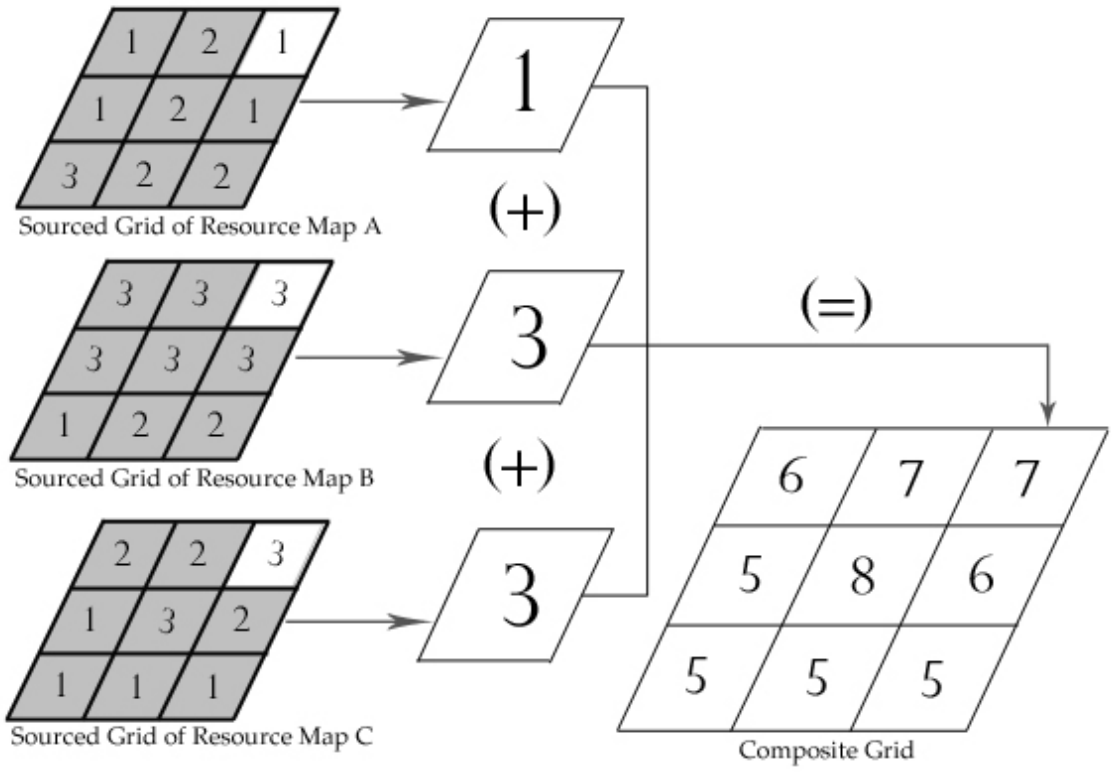

Figure 1.1. Example of a map algebra operation using addition (after Chrisman 2002).

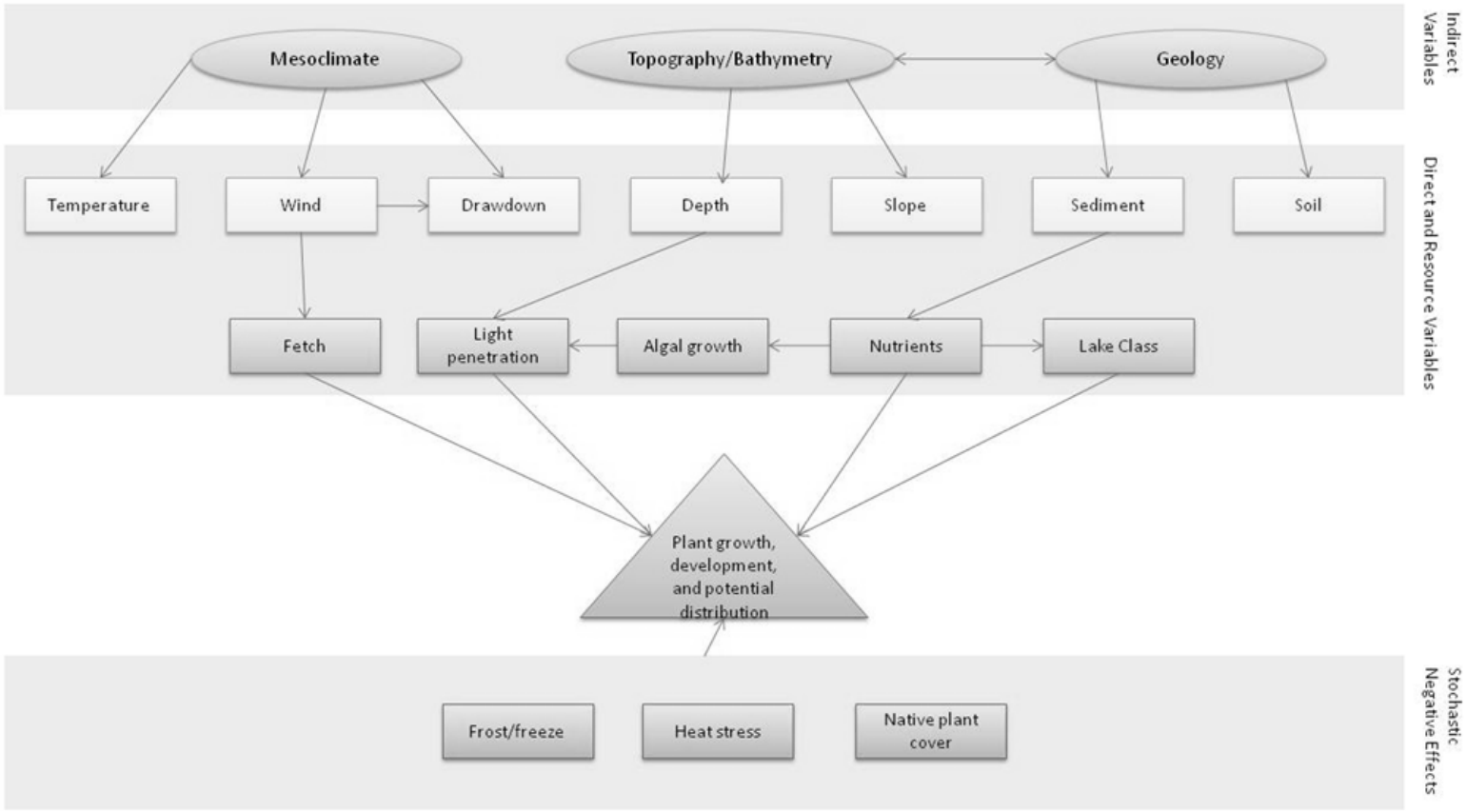

Figure 1.2. Conceptual model of proposed interactions between environmental variables affecting *Myriophyllum spicatum.*

Table 1.1. Factors influencing growth and morphology of Eurasian watermilfoil (Smith and Barko 1990).

Factor	Influence of Factor on Watermilfoil Growth
Water Clarity	1. Low water clarity limits watermilfoil to shallow rooting depths and leads to canopy formation. 2. High water clarity allows milfoil growth at greater depths.
Temperature	1. Plants photosynthesize and grow over a broad temperature range (ca. 15 to 35 C). 2. Maximum growth rates occur at relatively high water temperatures (ca. 30-35 C). 3. Growth is limited in the spring once the water temperature reaches approximately 15 C.
Inorganic Carbon	1. Plants grow best in relatively alkaline lakes. 2. Plants can grow in lakes of low alkalinity, but not as vigorously as elsewhere.
Mineral Nutrients	1. Nuisance growths of the plant are primarily restricted to moderately fertile lakes, or fertile locations in less fertile lakes. 2. Uptake of nutrients from sediments by roots is a very important source of mineral nutrients, particularly P and N. 3. Major cations and bicarbonate are taken predominately from the water.
Sediment Texture	1. Plants grow best on fine-textured inorganic sediments of intermediate density, because nutrient availability appears to be greatest there.
Water Movements	1. Vegetative spread of plant fragments is aided by water currents. 2. The plant does not usually occur in high energy environments.
Ice Scour	1. Ice scour may exclude the plant from shallow areas of lakes in cold climates.
Desiccation & Freezing	1. Desiccation during drawdown is a viable control measure particularly when accompanied by freezing during the wintertime.

CHAPTER 2

LOCAL-SCALE MODEL: PEND OREILLE (IDAHO)

The abiotic components of the environment necessary for survival constitute the habitat requirements for a species (Gillenwater et al. 2006). Species habitat requirements are described by habitat factors, which cover the most essential habitat characteristics of preferred habitats (Store and Jokimäki 2003). Geographic Information Systems (GIS) are well suited for studies involving habitat modeling and delineation, sometimes referred to as habitat suitability indexing (Gillenwater et al. 2006). Geographic Information Systems also offer the advantage of being able to overlay layers representing the spatial distribution of different environmental variables related to habitat suitability and perform spatial operations on these layers (Gillenwater et al. 2006). Linking habitat models with GIS represents a powerful tool in natural resource management and associated fields (Boyce et al. 2002).

Jensen and others (1992) and Narumalani and others (1997) used GIS to predictively model dominant freshwater macrophytes. They assumed that aquatic macrophytes would be present if all hypothesized environmental constraint criteria could be met. They concluded that the GIS techniques used could predict the current location of freshwater aquatic macrophytes.

The objective of this research is to develop a predictive model for Eurasian watermilfoil (*Myriophyllum spicatum* L.) that estimates presence of this species in a single lake ecosystem. *M. spicatum* is an invasive, aquatic weed, introduced into the

U.S. in the 1940s, currently occurring in almost every one of the United States. It is one of the most troublesome submerged aquatic plants in North America (Smith and Barko 1990).

A lengthy discussion on the dynamics of water quality and submerged macrophytes such as *M. spicatum*, is contained in Madsen et al. (2001). Water movement and light availability are major influences on the growth of submerged macrophytes. As a "canopy former," *M. spicatum* places the majority of its biomass disproportionally near the water surface. Research has shown that intermediate currents and wave action favor dispersal of *M. spicatum* because waves can break up canopy, spreading propagating fragments, without inducing plant mortality. A thorough review of *M. spicatum* ecology is in Smith and Barko (1990). A summary of their compiled data (Table 2.1) makes it is clear that *M. spicatum* has wide ranges of tolerance for a variety of influences, and that there are few clear cut decision rules which can be generalized about its preferences.

Methods and Materials

Site Description

The study site for this research is Pend Oreille Lake, and the outflowing Pend Oreille River. Glacially-formed Pend Oreille is located in northern Idaho and is an extremely deep, oligotrophic lake with more than 420 km^2 of surface water (including the river). It is fed by inflowing waters of the Clark Fork River. Approximately 27% of the lake is considered littoral zone habitat and can support the growth of aquatic plants (Madsen and Wersal 2008).

Conceptual Model

Based on published information, a conceptual model (Fig. 2.1) was built to show proposed predictor variables and interactions between variables. The conceptual model was used to focus data selection, but several proposed variables were not used because the data do not exist, were not easy to collect, or would not vary significantly in value across a single lake.

Major areas of mesoclimate and geology, labeled “indirect variables” in the conceptual model, would not be considerably different on a single lake, but would be of importance on a much larger scale, such as a national model. However, bathymetry/ topography would vary greatly in a single lake, and given the depths of Pend Oreille, are of immense importance in the model.

“Direct and resource variables” are of more immediate importance on a single-lake scale. However, for these are the variables, the risk of multicollinearity exists. For example, fetch is calculated from wind data. Thus both variables essentially yield the same information, and should not both be present as predictors in the same model. Certainly light availability, considered the most controlling factor, can be inferred from a variety of variables including depth and algal growth.

Some variables are simply not available. Many studies cite sediment nutrients as an important predictive mechanism. However, the expense both in time and money to collect sediment data often precludes its use for many studies. Unless a researcher makes a significant effort to obtain data for the specific project, it is not likely that the data can be found for use in a GIS or that the data will be sampled in accordance with the requirements of the project. Additionally, while drawdown has been shown to be a somewhat effective control, this method is associated more with reservoirs and waterbodies with water-level-control structures, making this impractical for many studies.

Pend Oreille, however, is a lake with a water control structure and is drawn down each winter. This affects the whole lake and thus would not be appropriate for a spatial analysis because the measured value would not change across the lake.

Negative effects (Fig. 2.1) such as freezing are avoided by the timing and location of the study. Information was recorded on native plant cover when the data set was collected. Preliminary analysis indicated that plant cover was not useful for this specific study, and thus was not included in further analysis.

Model Data Preparation

Spatial analysis using generalized linear models was conducted to estimate the predictive probability for the presence of *M. spicatum* in Pend Oreille Lake and the outflowing river. Predictor variables included water depth (hereafter depth), effective fetch length (hereafter fetch), and distance from nearest *M. spicatum* population (hereafter distance).

Data were split for separate analyses on Pend Oreille (Fig. 2.2). These areas have been named “littoral” and “pelagic” to reflect perceived differences in zones. The littoral zone contains the entire river and an upper portion of the lake where *M. spicatum* was visibly present and water depth was shallow. This area represents a large area of continous littoral zone. The majority of the lake is extremely deep and is thought to prohibit *M. spicatum* colonization; thus, that area has been labeled as the pelagic zone. Additionally, the littoral zone was grid-sampled, while the pelagic was not. It seems unwise to perform a unified analysis on what are clearly different systems with different sampling intensities, thus the division between zones for analyses. Hereafter, “littoral” refers to the geographic area shown in Figure 2.2 unless otherwise stated.

All interpolations performed on predictor variable data were done using ordinary kriging with ArcGIS Geostatistical Analyst[1]. In several studies designed to evaluate the various interpolation methods for aquatic ecosystem variables (e.g., kriging, spline, inverse distance weighted), kriging was generally regarded as the best option because it produced the lowest mean square error (Bello-Pineda and Hernandez-Stefanoni 2007; Valley et al. 2005). While this tool offers options for additional types of kriging, only ordinary was applicable to the research problem because no *a priori* information regarding the mean over the study area is required (Goovaerts 1997). Ordinary kriging produces a linear prediction based on weighted averages and is intrinsically stationary (i.e., assumes constant unknown mean and a semivariogram that is a function of distance apart only) (Waller and Gotway 2004). The ArcGIS Geostatistical Analyst contains options within ordinary kriging for anisotropy and specification of nugget. There was no evidence that depth and fetch changed with direction, thus anisotropy was not included. Further, in the areas investigated, due to the relative continuity of depth and fetch, no nugget was necessary.

Water depth for the pelagic zone was interpolated from NOAA sounding data. Bello-Pineda and Hernandez-Stefanoni (2007) noted that spherical models were found to best fit the experimental semi-variograms and to best explain the spatial autocorrelation present in the depth variable in their attempts to create a bathymetric map, and preliminary data analysis showed that this was also the best option for depth data from the NOAA sounding. Water depth for the littoral zone was collected in the field and then interpolated. It was not possible to get one complete depth data set for the entire study area.

[1] ESRI, 380 New York Street, Redlands, CA 92373-8100

Fetch length was determined using methods outlined in the Shore Protection Manual (USACE 1984). These methods were automated using Python scripts obtained from USGS (Rohweder et al. 2008). Effective fetch gives a more representative measure of how the wind governs the waves because it is a weighted distance of fetch around a specified wind direction (Lehmann 1998). Effective fetch is calculated as

$$L_f = \Sigma x_i * \cos \Upsilon_i / \Sigma \cos \Upsilon_i, \quad (2.1)$$

where L_f = effective fetch, x_i = distance to land, and Υ_i= deviation angle. Nine radials are used in the calculations for this study. In this instance the specified wind direction and speed were chosen to represent the dominant speed and direction such as was done by Narumalani et al. (1997) over the growing season of *M. spicatum* in Pend Oreille Lake.

Distance was used in two ways. First, distance was used as a Boolean variable which identified if the point was within 500 m of an existing population. The maximum separation of 500 m was chosen because it represented the smallest possible distance which could be used with a 250-m grid. Second, distance was used as an absolute variable measured from the closest observed *M. spicatum* presence point. Madsen and Smith (1997) noted that *M. spicatum*, although capable of spread by stolon and fragments, predominately (74%) propagated via stolon production, indicating a significant chance for localized spread.

Presence/absence data were obtained by field surveys conducted in summer 2007 (Madsen and Wersal 2008). Presence/absence data were collected using a plant rake with a point intercept sampling method developed by Madsen (1999).

Data were re-sampled to a 250-m point grid for analysis in SAS. This size was selected to match the point intercept sampling size, and was necessary to perform analysis within a unified framework. Re-sampling and grid generation were done with

Hawth's Analysis Tools in ArcGIS (Beyer 2004). To increase computational speed, only points where water depth was less than 10 m were considered for model use, representing the limit of preferred depth for *M. spicatum* reported in literature (Smith and Barko 1990) and the maximum depth observed during data collection (J. Madsen, personal communication).

Data Analysis

A wide range of statistical options for analysis exist, but the choice is driven primarily by known vs. unknown parameters, distribution, and model use. It is assumed that the location of each observation is thought to influence the outcome, making the problem inherently spatial. Tobler's First Law of Geography (Tobler 1970) is often cited in reference to spatial autocorrelation and postulates the level of correlation between observations decreases with increasing distance. In traditional statistics it is assumed that observations are independent and have normally distributed errors with mean zero and constant variance. The independence assumption is violated when spatial data are considered to be spatially autocorrelated. For this reason spatial statistical methods for spatial data analysis are correct, in contrast to traditional methods. The challenge is correctly modeling the spatial dependence so that it can be included in the analysis.

Initial models estimating the relationship between the presence of M. spicatum as a linear function of depth, fetch, and distance were fit using SAS Procs LOGISTIC and GLIMMIX[2]. From these models, residuals were computed. The residuals were then used to determine an appropriate class of semivariogram models using Procs VARIOGRAM and MEANS. Once it was determined a spherical semivariogram model was fit best by the residual empirical semivariogram, Proc NLIN was used to obtain parameter estimates for the semivariogram.

[2] SAS Institute Inc., 100 SAS Campus Drive, Cary, NC 27513-2414

Five statistical models were considered for estimating the predictive probability of the presence of *M. spicatum* in terms of the three predictors. The first was a traditional logistic regression model. This model did not include a spatial autocorrelation structure, but did include the distance variables. The remaining four models incorporated spatial autocorrelation via a spherical spatial covariance function, and did not require either distance variable. Specifically the four spatial models considered in this study were a (1) binomial regression model with overdispersion, (2) a random effects model, (3) a conditional spatial generalized linear mixed model (GLMM), and (4) a marginal spatial generalized linear model (GLM).

GIS Analysis

SAS results were exported as .dbf files and imported as XY Events in ArcGIS. Visual pattern analysis of the data was performed to determine if there were clear areas of growth and potential spread (or conversely, exclusionary areas) based on clustered areas of consistent probability. Boyce et al. (2002) suggested binning probabilities into categories following model development. To better identify patterns, probabilities were re-classified into two (low, high) and three (low, medium, high) ordinal categories of risk, based on natural breaks, and corresponding value ranges for depth and fetch were assigned to these categories so that *M. spicatum* habitat could be characterized.

Results

Disparate results between the littoral and pelagic zones are due to ecological differences between these systems. For the littoral zone, intercepts are always positive, while they are always negative for the pelagic zone. Depth was considerably different between these two systems. Results suggest that for a considerably more static, deeper body of water, location is the primary influencing factor. Specifically, proximity to

shoreline appears to increase probability of presence for *M. spicatum*. However, this is more likely a proxy for indicating those areas with shallow littoral zone, and necessarily proximity to shoreline per se.

Depth and fetch were highly significant in every model considered. Regardless of zone, depth had negative coefficients in every model, while fetch had positive coefficients for every model. The negative coefficient of depth indicates that the deeper the water, the less likely an occurrence of Eurasian Watermilfoil. On the other hand, the higher values of effective fetch indicated Eurasian Watermilfoil was more likely to occur. All four of the spatial models had a lower predictive probability error variance than the logistic regression model. However, the additional complexity of spatial models requires advanced computing algorithms for covariate parameter estimation. For this study, this additional complexity resulted in a lack of convergence in some cases. In the littoral zone, modeling efforts were enhanced by the added complexity introduced by these spatial models.

Model outputs indicate predictive probabilities for the presence of *M. spicatum* at each point in the study area. A spatial view of these probabilities created in ArcGIS illustrates areas where *M. spicatum* is likely to occur based on existing depth and fetch.

Littoral

Myriophyllum spicatum was present in 64% of the sample set and absent in 36% (Table 2.2). Despite repeated attempts, several models would not converge. For some models attempts were made to run models as bivariate with both depth and fetch, and as univariate models with depth or fetch. Convergence was never achieved for the random effects model (bivariate). While the univariate models for random effects did converge, alone, neither could explain the response variable sufficiently. Interaction between depth and fetch is likely present, and thus should not be used alone to model

response. The conditional spatial GLMM converged for both bivariate and univariate models. However, a standard error could not be calculated for the range despite using advanced techniques for estimating starting values and subsetting of data. Models for which convergence was obtained include the traditional logistic regression, the binomial regression model with overdispersion, and the marginal spatial GLM.

Logistic Regression

In this research problem, logistic models explain the trend in the probability of occurrence of *M. spicatum* through the covariates depth and fetch. In this research problem, response (Y) is binary (i.e., presence or absence), meaning that at any particular location, the data have a Bernoulli distribution with probability of occurrence $\mu(x_{i1}, x_{i2})$ in lieu of a normal distribution, where $\mu(x_{i1}, x_{i2})$ is also the mean of the Bernoulli distribution. It is also the case that, at a particular location, the variance of the process is $\mu(x_{i1}, x_{i2})[1 - \mu(x_{i1}x_{i2})]$.

The logistic regression model predicts the response variable (Y_i) without regard to any spatial location. This is the only model that does not have a spatial component. Our logistic model explains the trend in the probability of occurrence of *M. spicatum*, via the logit function, through the covariates depth and fetch. More specifically, Y_i is modeled with respect to depth $(x_{i,1})$ and fetch $(x_{i,2})$ by the relationship

$$\begin{aligned} Y_i &= \log\left\{\frac{\mu(x_{i,1},x_{i,2})}{1-\mu(x_{i,1},x_{i,2})}\right\} + \varepsilon_i \\ &= \beta_0 + \beta_{1,} x_{i,1} + \beta_2 x_{i,2} + \varepsilon_i, \qquad i = 1,2,\ldots,1343. \end{aligned} \tag{2.2}$$

A stepwise selection procedure was used, with depth entering the model first, and fetch second. The resulting fitted model was

$$\hat{Y}_i = 1.9182 - 0.3893x_{i,1} + 0.000297x_{i,2}, i = 1,2,\ldots 1343. \tag{2.3}$$

The summary of the fit for this model indicates that intercept, depth, and fetch were significant (Table 2.3). The Wald statistic reported represents the simplest and most commonly used interval estimate for a fitted value in a logistic regression for the logit function (Elith et al. 2002). Wald χ^2 values (167.7, 189.7, and 64.0, respectively) indicate that the full model explains the response variable markedly better than a random variable that does not depend on values of depth and fetch.

Measures of correlation indicate that the model did a reasonable job of correctly assigning predicted probabilities (Table 2.4). More frequently than not (c = 0.78), predicted probabilities were assigned by the model that corresponded to the observations (i.e., in any matched [0, 1] pair, the higher probability was predicted for the location with 1, and not 0).

Binomial Regression with Overdispersion

In the binomial regression model with overdispersion model, the trend in the probability of occurrence of *M. spicatum* is modeled via the logit function through the linear relationship between the covariates depth and fetch. The spatial component is indirectly modeled through the overdispersion parameter. Overdisperion refers to the situation whereby the data are more dispersed than is consistent with a standard mean-variance relationship. The addition of overdispersion is an attempt to quantify the inexactness of the mean-variance relationship (Schabenberger and Gotway 2005). The inexactness is thought to be due to spatial influence on the data.

For each location, s_i, the binomial regression model with overdispersion is described as

$$\begin{aligned} E[Y(\boldsymbol{s_i})] &= \mu(\boldsymbol{s_i}) \\ g\big(\mu(\boldsymbol{s_i})\big) &= \beta_o + \beta_1 x_1(\boldsymbol{s_i}) + \beta_2 x_2(\boldsymbol{s_i}) = logit\big[\mu\big(x_{i,1}, x_{i,2}\big)\big] \\ \mathrm{Var}[\mu(\boldsymbol{s_i})] &= \sigma^2 \mu(\boldsymbol{s_i})[1 - \mu(\boldsymbol{s_i})], \end{aligned} \qquad (2.4)$$

where σ^2 represents the overdispersion parameter. The fitted model for binomial regression with overdispersion was

$$logit\left[\mu\left(x_{i,1}, x_{i,2}\right)\right] = 1.9182 - 0.3893x_1(\boldsymbol{s_i}) + 0.000297x_2(\boldsymbol{s_i}). \quad (2.5)$$

The overdispersion model was fitted using restricted maximum likelihood (Table 2.5). A value of $\sigma^2 > 1$ indicates the presence of overdispersion. The large estimate of the overdispersion parameter of 1.8701 in this analysis indicates that the data likely is overdispersed. Thus the variability is not fully described by the predictors selected. It is possible this is due to underlying spatial variability. The inclusion of the overdispersion parameter should be an improvement over a traditional logistic model because there is clearly unexplained variability that needs to be accounted for, even if its cause is not identified.

Conditional Spatial GLMM

Spatial dependence can be explained partially or wholly by the proximity of environmental predictor variables. Randomness inherent in depth and fetch due to interpolation is accounted for through the normality assumption on the term S, having spatial covariance structure, ${\sigma_s}^2 R_s(\alpha_s)$. Any remaining spatial dependence can be due to underlying biotic processes or unobservable variables (Miller and Franklin 2006). The conditional approach models the unobserved spatial process through the use of random effects within the mean function and models the conditional mean and variance as a function of both fixed covariate effects and these random effects resulting from the unobserved spatial process. Variance is dependent on the mean with consideration for overdispersion. The data are conditionally independent and spatial dependence is addressed by a Gaussian random field (Schabenberger and Gotway 2005).

The conditional spatial GLMM is described as

$$
\begin{aligned}
Z(s_i)|\,\boldsymbol{S}(s_i) \;&\sim \text{Bernoulli}\big(\mu(s_i)\big), \text{independent} \\
\text{logit}[\mu(s_i)] &= \beta_0 + \beta_1 x_1(s_i) + \beta_2 x_2(s_i) + \boldsymbol{S}(s_i) \\
\text{Var}[Z(s)|\,\boldsymbol{S}(s)] &= \sigma^2 \boldsymbol{V}\mu \\
\boldsymbol{S} &\sim N\big(0, {\sigma_s}^2 R_s(\alpha_s)\big).
\end{aligned}
\tag{2.6}
$$

The fitted model for conditional spatial GLMM was

$$
\text{logit}[\mu(s_i)] = 9.1117 - 1.7061 x_1(s_i) + 0.001016 x_2(s_i) + \boldsymbol{S}(s_i). \tag{2.7}
$$

For this model, spatial autocorrelation was modeled using the spherical model given by

$$
R_3(h) = \begin{cases} 1 - \frac{3}{2}\left(\frac{h}{\alpha}\right) + \frac{1}{2}\left(\frac{h}{\alpha}\right)^3, h \le \alpha, \\ 0, \qquad \text{otherwise.} \end{cases} \tag{2.8}
$$

The spherical covariance function specifically modeled the spatial dependency in the data, partially due to kriging values of fetch and depth. The results of fitting this model indicate that intercept, depth, and fetch are all significant (Table 2.6). The fitted covariance structure was

$$
\boldsymbol{S} \sim N\big(0, 81.5731 R_s(1.0534)\big). \tag{2.9}
$$

Marginal Spatial GLM

The marginal spatial GLM incorporates a term which helps to describe the inexactness or random behavior in depth and fetch due to interpolation. The marginal spatial GLM differs from the conditional model in that the marginal mean is modeled as a function of unknown fixed, non-random parameters (i.e., β_0, β_1). It gives the same inference as a conditional model, but with differing interpretation (Schabenberger and Gotway 2005). The marginal spatial GLM is described as

$$
\begin{aligned}
\text{E}[Z(s)] &= \mu(s) \\
\text{logit}[\mu(s_i)] &= \beta_0 + \beta_1 x_1(s_i) + \beta_2 x_2(s_i) \\
\text{Var}[Z(s)] &= \sigma^2 \boldsymbol{V}\mu + \sigma^2 \boldsymbol{V}^{1/2} \mu R_s(\alpha_m) \boldsymbol{V}^{1/2} \mu.
\end{aligned}
\tag{2.10}
$$

The results of fitting this model indicate that intercept, depth, and fetch are all significant (Table 2.7). The fitted model was

$$\text{logit}[\mu(s_i)] = 1.9182 - 0.3893x_1(s_i) + 0.000297x_2(s_i). \quad (2.11)$$

GIS Analysis

Ordinal categories illustrated a clear trend (Fig. 2.3) with respect to depth and fetch. In general, probabilities were negatively related to depth and positively related to fetch. For many model outputs, in the 3-class system, high depth/high fetch was not always present. Predicted probabilities, when mapped, showed a clear increase with depth (Figs. 2.4, 2.5).

Pelagic

Myriophyllum spicatum was present in 9% of the sample set and absent in 91% (Table 2.8). Despite repeated attempts and robust methods for estimating starting parameter values, the conditional spatial GLM for the pelagic zone did not converge.

Logistic Regression

The logistic regression model predicts the response variable (Y_i) without regard for any spatial dependency. Y_i is modeled with respect to depth $(x_{i,1})$ and fetch $(x_{i,2})$ by Equation Set 2.2, with one exception: in the pelagic analysis, $i = 1,2,\ldots,930$.

As with the littoral analysis, a stepwise selection procedure was used, with depth entering the model first, and fetch second. The resulting fitted model was

$$\hat{Y}_i = -0.8995 - 0.3599x_{i,1} + 0.000179x_{i,2}. \quad (2.12)$$

The summary of the fit for this model indicates that intercept, depth, and fetch were significant (Table 2.9). Wald χ^2 values (5.3, 28.5, and 12.1, respectively) indicate that the full model explains the response variable markedly better than a random variable that does not depend on values of depth and fetch.

Measures of correlation indicate that the model did a reasonable job of correctly assigning predicted probabilities (Table 2.10). More frequently than not (c = 0.73), predicted probabilities were assigned by the model that corresponded to actual real-world observations (i.e., in any matched [0, 1] pair, the higher probability was predicted for the location with 1, and not 0).

Binomial Regression with Overdispersion

The binomial regression model with overdispersion was performed using Equation Set 2.4. As with the littoral analysis, the overdispersion model was fitted using maximum likelihood (Table 2.11). The fitted model was

$$logit\left[\mu\left(x_{i,1}, x_{i,2}\right)\right] = -0.8995 - 0.3599x_1(\boldsymbol{s_i}) + 0.000179x_2(\boldsymbol{s_i}). \quad (2.13)$$

The overdispersion parameter of 1.0320 in this analysis is likely not significantly greater than 1, and thus overdispersion may not be occurring. In this event, there would be no need to include this more complex model over the logistic regression model.

Random Effects

The random effects model is a standard bivariate binomial regression model that incorporates random effects to model the spatial dependence. The random effects model is described by

$$\begin{aligned} Y(s_i)|\,\boldsymbol{S}(s_i) &\sim \text{Bernoulli}\left(\mu(s_i)\right), \text{independent} \\ \text{logit}[\mu(s_i)] &= \beta_0 + \beta_1 x_1(s_i) + \beta_2 x_2(s_i) + \boldsymbol{S}(s_i) \\ \text{Var}[\text{Z(s)}|\,\mathbf{S}(\text{s})] &= \sigma^2\,\mathbf{V}\mu \\ \boldsymbol{S} &\sim N(0, \sigma^2{}_s\,\boldsymbol{I}) \end{aligned} \quad (2.14)$$

The results of fitting this model indicate that intercept, depth, and fetch are significant (Table 2.12). The fitted model was

$$\text{logit}[\mu(s_i)] = -8.1978 + -1.2530x_1(s_i) + 0.000680x_2(s_i) + \boldsymbol{S}(s_i). \quad (2.15)$$

Marginal Spatial GLM

The marginal spatial GLM is described by Equation Set 2.10. The results of fitting this model indicate that intercept, depth, and fetch are significant (Table 2.13). The fitted model was

$$\text{logit}[\mu(s_i)] = -1.3255 - 0.2329x_1(s_i) + 0.000112x_2(s_i) \quad (2.16)$$

GIS Analysis

Ordinal categories produced mixed results, and were deemed not valuable to data analysis. In general, probabilities were disparate and no clear patterns could be detected for any of the models with regard to both the two- and three-class systems. For many model outputs, the range of values was so small that graphs were of limited utility for illustration purposes, and thus they are not included. Predicted probabilities were low, except in the shallowest areas (Figs. 2.6, 2.7). When higher probabilities (> 0.50) were compared with the true, measured, littoral zone from Pend Oreille (Fig. 2.8) it appears that even when light, which is traditionally the most limiting factor, is available, depth and fetch will still control the ability of *M. spicatum* to establish.

Discussion

Multiple justifications can be made about which model is "best". It is improper to report traditionally-interpreted metrics like R^2 because R^2 is best interpreted in the context of linear models with independent errors – both naïve assumptions in our context. Consequently, it's not clearcut to compare a single reported value for each model and say which one is "best".

In this instance the most-defensible position is that the simplest model is best. This theory is called "Occam's Razor" or the "Principle of Parsimony." Rules of parsimony dictate that when two or more models are competitive, then the simplest

model should be used. Romero-Calcerrada and Luque (2006) reported that simpler models were preferred for their wider applicability and better overall prediction of species presence. Therefore the added complexity of a robust spatial model for the pelagic zone is not warranted, and the basic logistic model will suffice. For the littoral zone, the selection would be the overdispersion model. It did prove to be superior to the logistic regression, and when compared to the competing, more complex spatial models, it is the simplest choice.

The alternative argument is that it is irresponsible to recommend a model which knowingly omits information about a system, regardless of simplicity. The more explicit spatial models take into account variation due to location which is ignored in the logistic model. There is variability accounted for in the random effects model and conditional spatial GLMM due to random effects in the predictors. In this instance, added computational time and complexity are worth the added effort to produce a more "complete" model.

The amount of zeros (absence) in a dataset influences the failure rate for models relying on fixed effects. It is possible in this study, given the high percentage of zeros in the pelagic zone, that these models were limited in their usefulness from the onset, and might yield significantly different results in a study with a large percentage of presence points.

By definition a true pelagic zone would not contain aquatic plants. It is possible that trying to model presence in this habitat would not be possible in practice because the data create a situation for which a realistic model would never converge. Due to the lack of continuous true littoral zone, the model is never able to completely close around the pelagic zone.

Conclusions

Based on the results seen in this study, robust spatial models are more useful in modeling smaller, shallower, more dynamic systems. Depth and fetch were useful in predicting the presence of *M. spicatum*, but were not as significant in more robust models for the pelagic zone. In these systems, location only has more explanatory ability than spatial covariance structures. The littoral zone showed a clear trend of more frequent presence in low depth, high fetch areas. These trends were not as clear for the pelagic zone. However, the coefficients for the pelagic zone models indicate that the same trend should occur.

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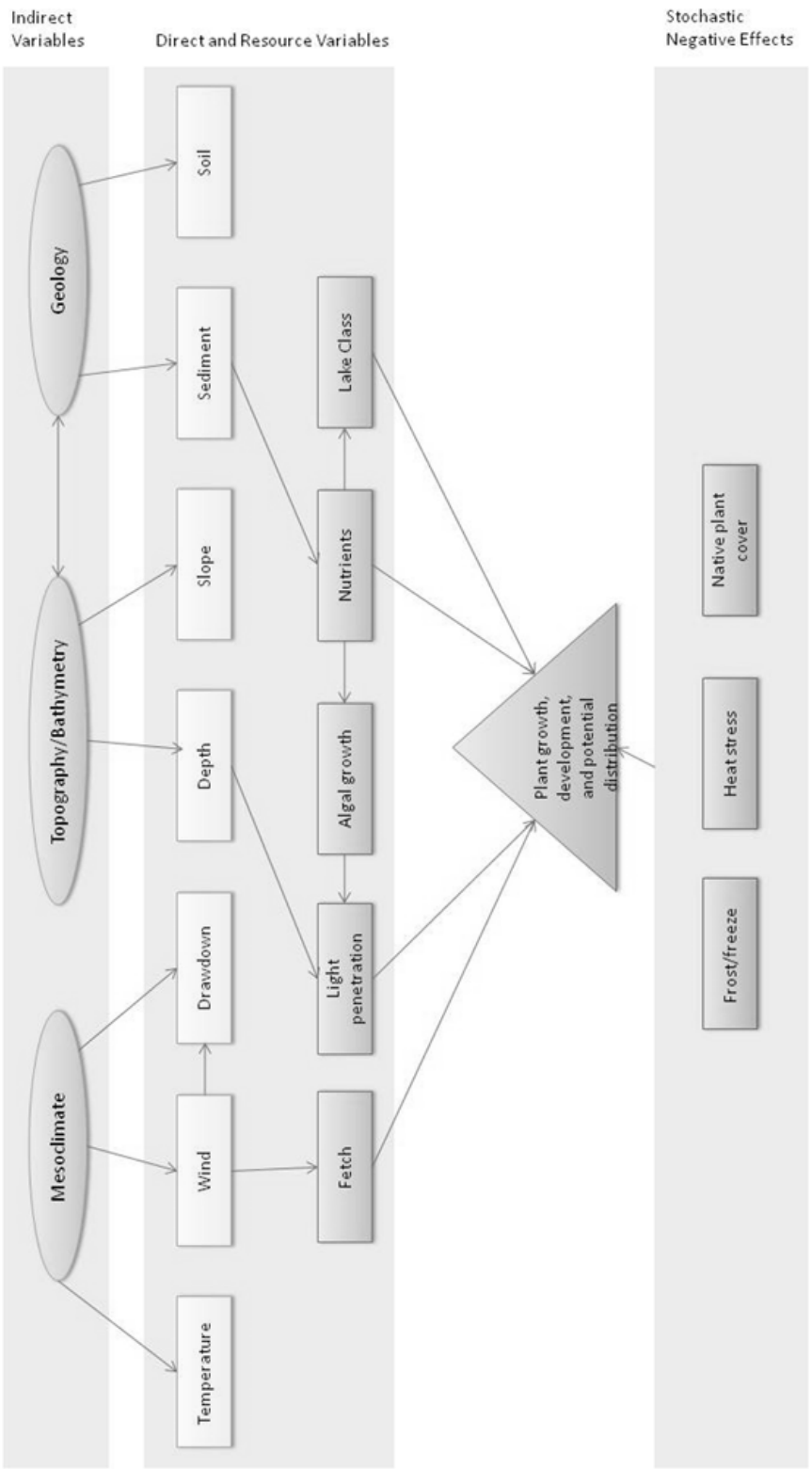


Figure 2.1. Conceptual model of proposed interactions between environmental variables affecting *Myriophyllum spicatum*.

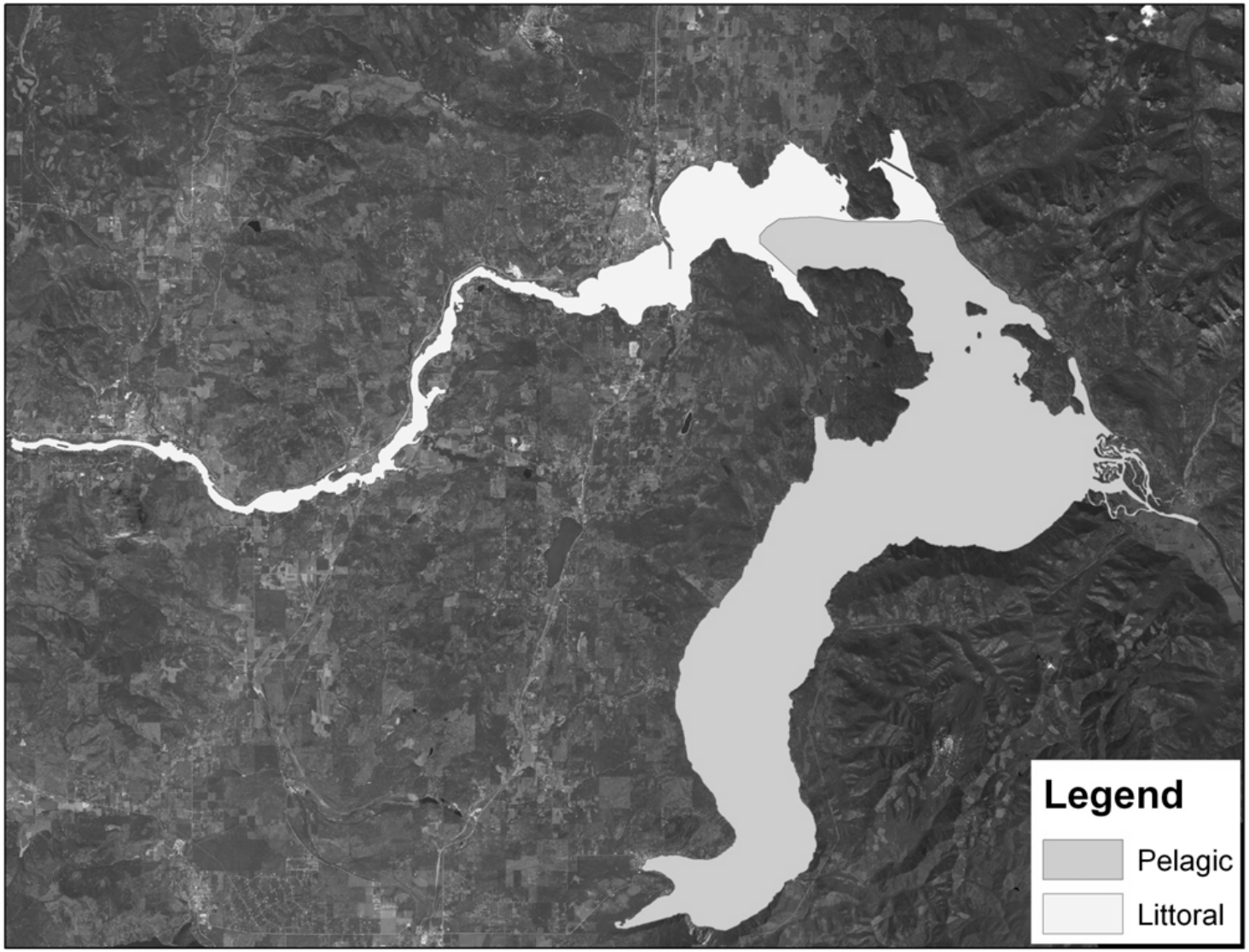
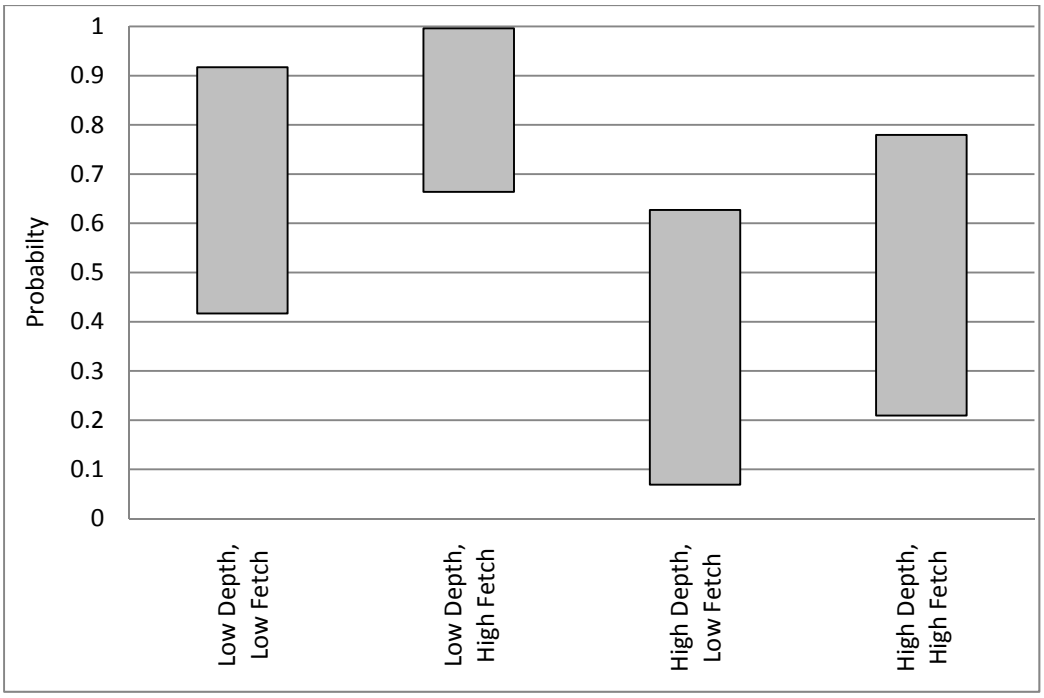


Figure 2.2. Separate analyses were conducted for the littoral and pelagic zones of Pend Oreille Lake (Idaho) and outflowing river.



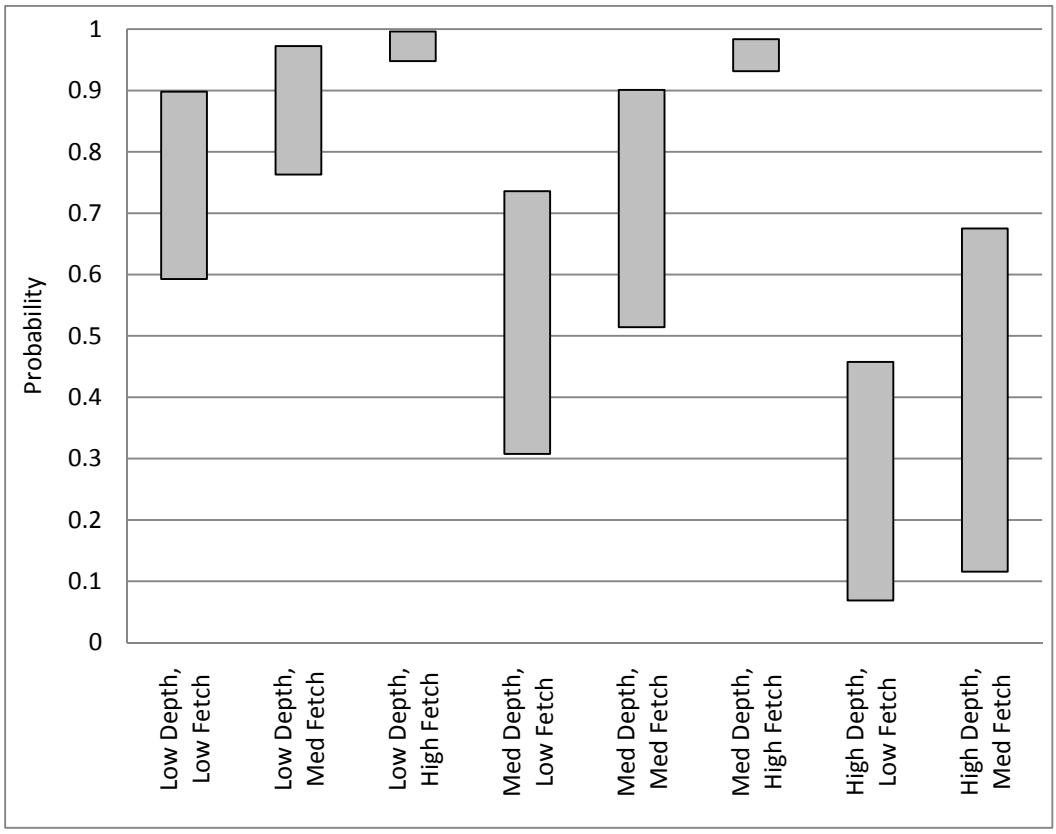


Figure 2.3. Summary of probabilities for marginal spatial GLMM on the littoral zone for two- and three-class ordinal categories (X-axis). Bar ranges run from the minimum to the maximum value for each ordinal category; values on the Y-axis reflect probability.

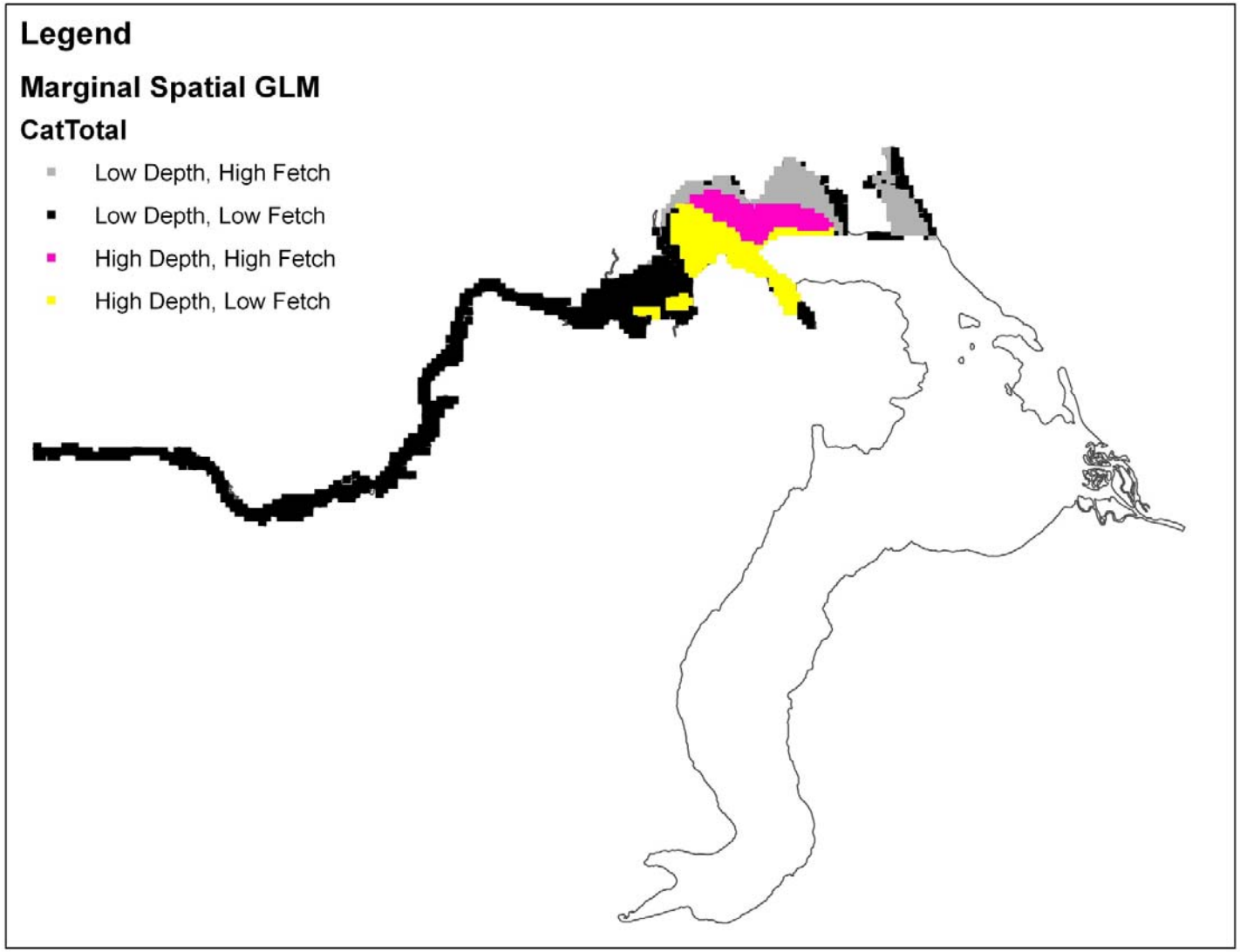


Figure 2.4. Map of paired ordinal categories for two-class marginal spatial GLM for Pend Oreille littoral zone.

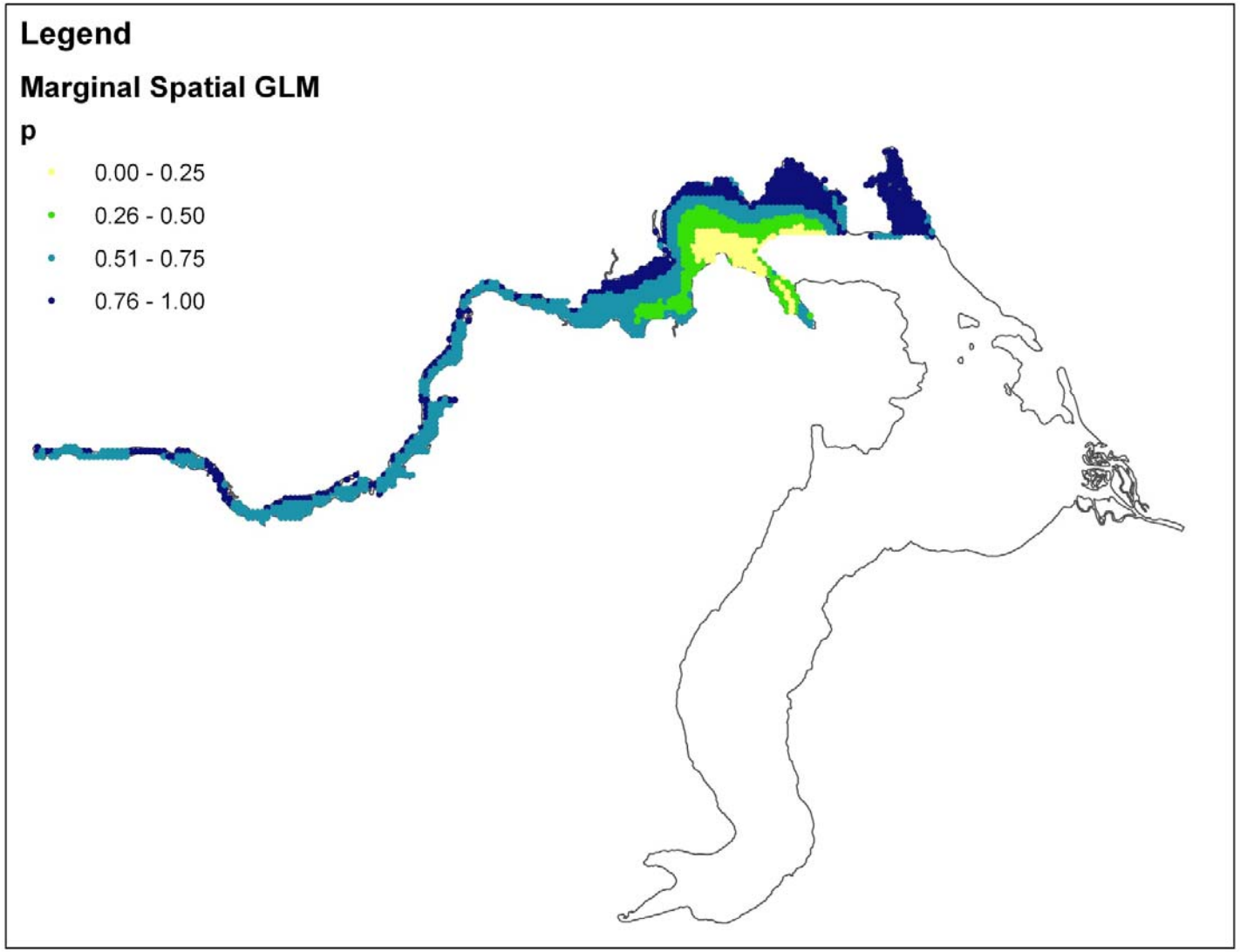


Figure 2.5. Predicted probabilities from marginal spatial GLM for Pend Oreille littoral zone.

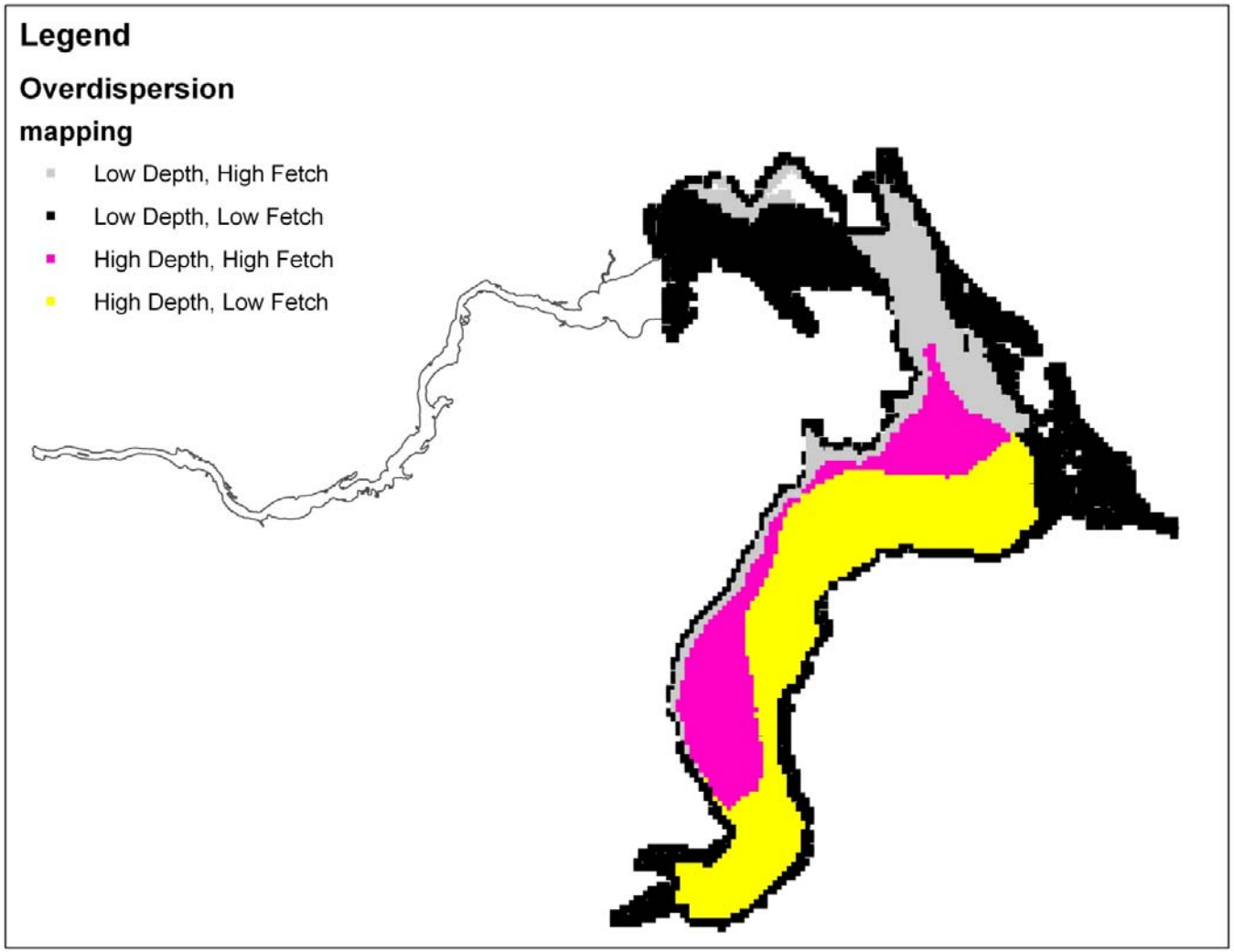


Figure 2.6. Map of paired ordinal categories for two-class binomial regression with overdispersion for Pend Oreille pelagic zone.

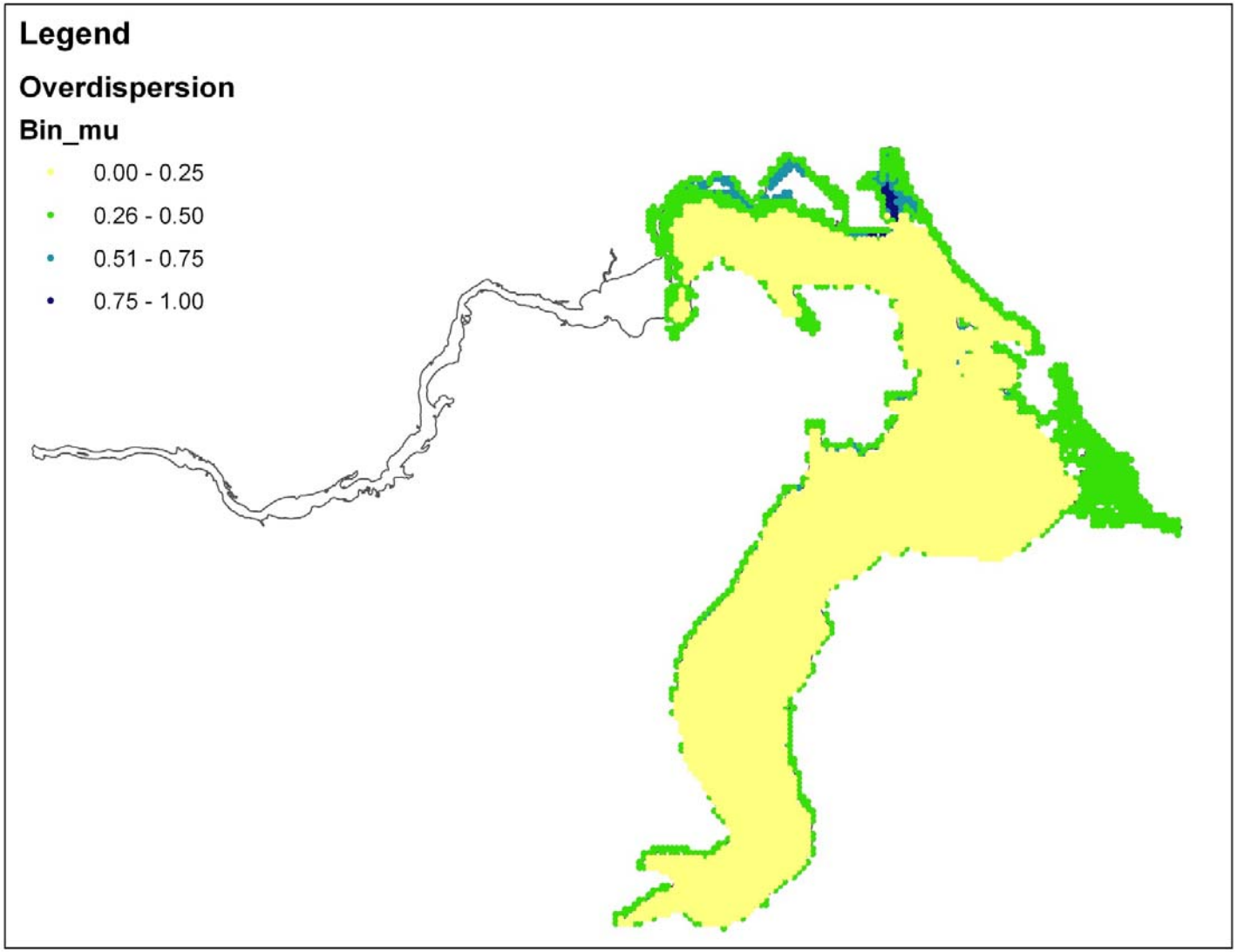


Figure 2.7. Predicted probabilities from binomial regression with overdispersion for Pend Oreille pelagic zone.

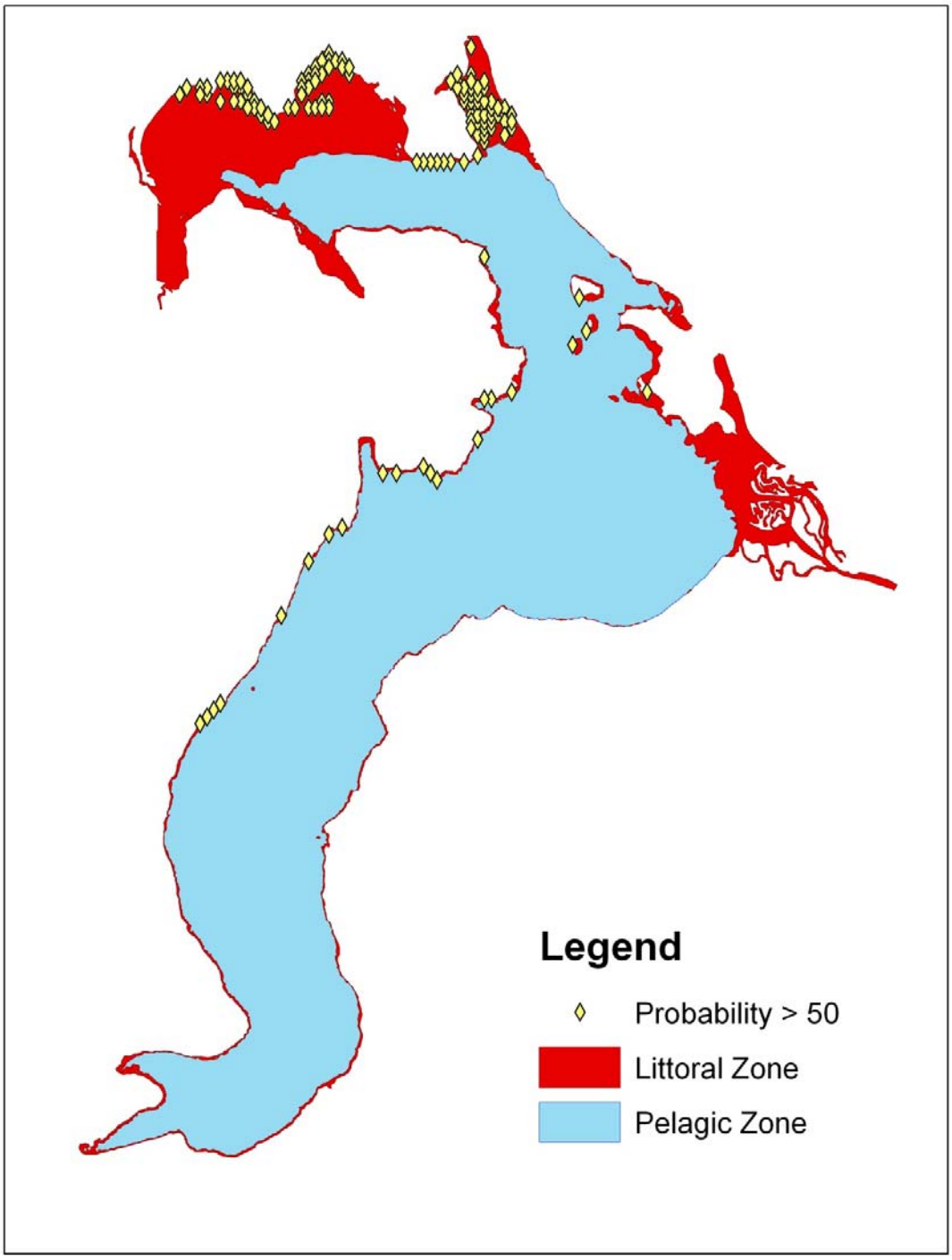


Figure 2.8. True littoral zone for Pend Oreille lake with points predicted at greater than or equal to 50% probability of being suitable *M. spicatum* habitat.

Table 2.1. Factors influencing growth and morphology of Eurasian watermilfoil (Smith and Barko 1990).

Factor	Influence of Factor on Watermilfoil Growth
Water Clarity	1.Low water clarity limits watermilfoil to shallow rooting depths and leads to canopy formation. 2.High water clarity allows milfoil growth at greater depths.
Temperature	1.Plants photosynthesize and grow over a broad temperature range (ca. 15 to 35 C). 2.Maximum growth rates occur at relatively high water temperatures (ca. 30-35 C). 3.Growth is limited in the spring once the water temperature reaches approximately 15 C.
Inorganic Carbon	1.Plants grow best in relatively alkaline lakes. 2.Plants can grow in lakes of low alkalinity, but not as vigorously as elsewhere.
Mineral Nutrients	1. Nuisance growths of the plant are primarily restricted to moderately fertile lakes, or fertile locations in less fertile lakes. 2. Uptake of nutrients from sediments by roots is a very important source of mineral nutrients, particularly P and N. 3. Major cations and bicarbonate are taken predominately from the water.
Sediment Texture	1.Plants grow best on fine-textured inorganic sediments of intermediate density, because nutrient availability appears to be greatest there.
Water Movements	1. Vegetative spread of plant fragments is aided by water currents. 2.The plant does not usually occur in high energy environments.
Ice Scour	1.Ice scour may exclude the plant from shallow areas of lakes in cold climates.
Desiccation & Freezing	1.Desiccation during drawdown is a viable control measure particularly when accompanied by freezing during the wintertime.

Table 2.2. Frequency table of presence of *M. spicatum* on Pend Oreille littoral zone.

M. spicatum Status	Frequency	Percent
Absent (0)	488	36.34
Present (1)	855	63.66

Table 2.3. Results of logistic regression model for *M. spicatum* on Pend Oreille littoral zone.

Parameter	Degrees of Freedom	Estimate	Standard Error	Wald χ^2	p-value
Intercept (β_0)	1	1.9182	0.1481	167.7057	< 0.0001
Depth (β_1)	1	-0.3893	0.0283	189.6671	< 0.0001
Fetch (β_2)	1	0.000297	0.000037	64.0487	< 0.0001

Table 2.4. Measures of correlation from logistic regression model for *M. spicatum* on Pend Oreille littoral zone.

Percent Concordant	77.5	Somers' *D*	0.555
Percent Discordant	22.0	Gamma	0.558
Percent Tied	0.5	τ_a	0.257
Pairs	417,240	c	0.778

Table 2.5. Results of binomial regression model with overdispersion for *M. spicatum* on Pend Oreille littoral zone.

Parameter	Estimate	Standard Error	t	p-value
Intercept (β_0)	1.9182	0.2026	9.47	< 0.0001
Depth (β_1)	-0.3893	0.03866	-10.07	< 0.0001
Fetch (β_2)	0.000297	0.000051	5.85	< 0.0001
Overdispersion (σ^2)	1.8701			

Table 2.6. Results of conditional spatial GLMM for *M. spicatum* on Pend Oreille littoral zone.

Parameter	Estimate	Standard Error	t	p-value
Intercept (β_0)	9.1117	0.6105	14.92	< 0.0001
Depth (β_1)	-1.7061	0.1064	-16.04	< 0.0001
Fetch (β_2)	0.001016	0.000132	7.72	< 0.0001
Variance (σ_s^2)	81.5731	3.2593		
Residual (σ^2)	0.000417	0.000046		
Range (α_m)	1.0534	.		

Table 2.7. Results of marginal spatial GLM for *M. spicatum* on Pend Oreille littoral zone.

Parameter	Estimate	Standard Error	t	p-value
Intercept (β_0)	1.9182	0.2026	9.47	< 0.0001
Depth (β_1)	-0.3893	0.03866	-10.07	< 0.0001
Fetch (β_2)	0.000297	0.000051	5.85	< 0.0001
Variance (σ_0^2)	1.8699	0.07228		
Residual (σ_1^2)	0.000187	0.002598		
Range (α_m)	.	.		

Table 2.8. Frequency table of presence of *M. spicatum* on Pend Oreille pelagic zone.

M. spicatum Status	Frequency	Percent
Absent (0)	843	90.65
Present (1)	87	9.35

Table 2.9. Results of logistic regression model for *M. spicatum* on Pend Oreille pelagic zone.

Parameter	Degrees of Freedom	Estimate	Standard Error	Wald χ^2	p-value
Intercept (β_0)	1	-0.8995	0.3923	5.2561	0.0219
Depth (β_1)	1	-0.3599	0.0674	28.5205	< 0.0001
Fetch (β_2)	1	0.000179	0.000052	12.0954	0.0005

Table 2.10. Measures of correlation from logistic regression model for *M. spicatum* on Pend Oreille pelagic zone.

Percent Concordant	72.1	Somers' *D*	0.451
Percent Discordant	27.1	Gamma	0.455
Percent Tied	0.8	τ_a	0.077
Pairs	73,341	c	0.725

Table 2.11. Results of binomial regression model with overdispersion for *M. spicatum* on Pend Oreille pelagic zone.

Parameter	Estimate	Standard Error	t	p-value
Intercept (β_0)	-0.8995	0.3986	-2.26	0.0243
Depth (β_1)	-0.3599	0.06846	-5.26	< 0.0001
Fetch (β_2)	0.000179	0.000052	3.42	0.0006
Overdispersion (σ^2)	1.0320			

Table 2.12. Results of random effects model for *M. spicatum* on Pend Oreille pelagic zone.

Parameter	Estimate	Standard Error	t	p-value
Intercept (β_0)	-8.1978	1.2516	-6.55	< 0.0001
Depth (β_1)	-1.2530	0.2097	-5.97	< 0.0001
Fetch (β_2)	0.000680	0.000166	4.10	< 0.0001
Variance (σ_s^2)	2.82×10^{-6}	.		
Residual (σ^2)	76.3477	3.5646		

Table 2.13. Results of marginal spatial GLM model for *M. spicatum* on Pend Oreille pelagic zone.

Parameter	Estimate	Standard Error	t	p-value
Intercept (β_0)	-1.3255	0.4874	-2.72	0.0067
Depth (β_1)	-0.2329	0.07844	-2.97	0.0031
Fetch (β_2)	0.000112	0.000069	1.63	0.1030
Variance (σ_0^2)	0.6775	0.05145		
Residual (σ_1^2)	0.2514	0.5866		
Range (α_m)	999.56	153.10		

CHAPTER 3

REGIONAL-SCALE MODEL: MINNESOTA

Development of ecological models provides a simple, direct method by which to predict presence, absence, and spread of species in given environments. Models can be used to highlight areas of concern with regard to invasive species such as Eurasian watermilfoil (*Myriophyllum spicatum* L.) because they can indicate areas susceptible to future invasion (Buchan and Padilla 2000). Roley and Newman (2008) reported that up to 4,700 lakes in Minnesota are uninfested but susceptible to invasion by *M. spicatum*. Invasions are often found providentially by state agencies or private citizens (Roley and Newman 2008). Thus a mechanism for directing scouting efforts could allow for better cataloging of current populations of this and other invasive species, which can mean better chances at early detection and eradication.

One method that can be used in modeling habitat is Mahalanobis distance. Mahalanobis distance is a dimensionless measure of the distance in multivariate space from the ideal ecological niche (Calenge et al. 2008; Knick and Rotenberry 1998). A special case of Mahalanobis distance can be used in a set of "presence only" methods for predictive habitat modeling. The majority of species data available tends to be presence only (Zaniewski et al. 2002). This is particularly true of invasive species as many data collection efforts are focused on detection. These data are often recorded without planned sampling schemes so that absences cannot be inferred (Elith et al.

2006). Regardless, Elith et al. (2006) reported that in many instances it was possible to achieve valid results using some presence-only methods.

In a maximum entropy analysis (hereafter "maxent"), areas without values are not automatically considered absences, which reduces bias from inclusion of false absences (Elith et al. 2006; Phillips et al. 2006). Maxent utilizes maximum entropy to make predictions from incomplete data, which in invasive species work could be unsampled areas. It can be used to estimate species distribution by finding the probability distribution that is closest to uniform (i.e., "maximum entropy") for a study area under a specified set of environmental constraints (Phillips et al. 2006). The maxent statistic weights each variable by a different constant where the value of each weight corresponds to the importance or the magnitude of the variable to the system's entropy. The probability distribution is estimated by iteratively altering one weight at a time to maximize the likelihood of the occurrence dataset. To avoid overfitting, the estimated distribution is constrained so that the average value for a given predictor is close to the empirical average rather than equal to it (Hernandez et al. 2006). In comparison studies, maxent outperformed other accepted quantitative methods for ecological modeling (Hernandez et al. 2006; Phillips et al. 2006).

An advantage of Mahalanobis, however, is that it assumes a species will distribute itself optimally within the available habitat. This method is thus ideal for spatial studies involving GIS because it partially accounts for the influences of spatial autocorrelation, interaction between variables, and covariance (Knick and Rotenberry 1998).

In general, most models assume that species distribution is a function of environmental conditions (Guisan and Zimmerman 2000). Some research (Cheruvelil and Soranno 2008) has reported that anthropogenic landscape features may outweigh

natural landscape influence in importance. In a study focusing specifically on detection of *M. spicatum* in Minnesota lakes, Roley and Newman (2008) found only physical habitat variables to be of significance despite including variables to serve as surrogates for human vectoring (i.e., boat ramps).

Cheruvelil and Soranno (2008) examined the ability of lake and landscape features to predict various metrics of macrophyte cover. They used combinations of variables including road density and lake hydrology, among other factors, in their determination that anthropogenic landscape features may outweigh natural landscape influence in importance. Conversely, Buchan and Padilla (2000) reported that anthropogenic variables were poorer predictors of *M. spicatum* presence. Both papers point to exceptions, however, that can explain these divergent conclusions. Cheruvelil and Soranno (2008) note that growth form affected variable selection, noting specifically that *M. spicatum* cover required the most complex model. Buchan and Padilla (2000) follow up their conclusions by stating that statistical significance of predictor variables may not equate to ecological significance. Thus anthropogenic variables may or may not be of use in a model, but intuitively are included because invasion ecology indicates these are key influences.

Methods and Materials

The states of Minnesota and Wisconsin were divided into a 500 m grid using ArcGIS[3] and Hawth's Tools (Beyer 2004). Non-water areas were removed from the sample. Data for analysis were obtained from the Minnesota Department of Natural Resources Data Deli[4] and researchers at the University of Minnesota (Roley and

[3] ESRI, 380 New York Street, Redlands, CA 92373-8100

[4] http://deli.dnr.state.mn.us/index.html.

Newman 2008). These included Secchi depth, total alkalinity, Carlson's Trophic State Index, lake size, distance from lake access (i.e., boat launch), distance from road, distance from reported bass habitat, and *M. spicatum* presence. Data were weighted for analysis using flow accumulation rates obtained from the National Hydrography Dataset Plus[5].

Mahalanobis

A Mahalanobis analysis was performed on the dataset using the Mahalanobis extension (Jenness 2003) for ArcView 3.x[6]. All variables were included in the analysis. The Mahalanobis extension calculates distance using the following equation (Jenness 2003)

$$D^2 = (\boldsymbol{x} - m)^T \boldsymbol{C}^{-1} (\boldsymbol{x} - m), \quad (3.1)$$

where x = vector of data, m = vector of mean values of x, C^{-1} = inverse covariance matrix of x, and T indicates transpose.

D^2 is approximately $x^2_{k-1.}$ It is only exactly if all x are N(M,Σ). P-values for a χ^2 distribution with k-1 degrees of freedom (where k = the number of predictor variables) were derived Mahalanobis distances and re-classed using cut-off values of 0.5 (Fig 3.1) and 0.4. The value of 0.5 is a standard choice, and 0.4 was selected because this was the natural break in the data. Values greater than or equal to 0.5 and 0.4, respectively, were considered presence when the data were re-classified, with values less than these thresholds considered absence. Re-classed output was compared to known values of presence and absence for validation. Validation included calculating Cohen's kappa, specificity, and sensitivity (Hirzel et al. 2006).

[5] Horizon Systems Corporation, P.O. Box 5084, Herndon, VA 20170
[6] ESRI, 380 New York Street, Redlands, CA 92373-8100

The Mahalanobis methods were repeated using combined data from Wisconsin and Minnesota. Data for Wisconsin were obtained from the Wisconsin Department of Natural Resources[7] and USGS Nonidigenous Aquatic Species database[8]. These included the same variables used for the Minnesota study.

Maxent

The maxent statistic (q_λ) was calculated using the Maxent software[9]. Only the state of Minnesota was considered. Maxent is defined by the following equation (Phillips and Dudik 2008)

$$q_\lambda(x) = \frac{1}{Z_\lambda} \exp\{\sum_{j=1}^{k} \lambda_j f_j(x)\}, \quad (3.2)$$

where for each $j, j = 1, \ldots k, \lambda_j$ represents the weight, f_j is the j^{th} feature at *x*, *x* is presence and Z_λ is a normalizing constant forcing the sum of the entropy components to one.

In addition to maps of predicted suitability, the Maxent software produces a receiver operating characteristic (ROC) curve, information regarding the relative contribution of each variables, jackknife tests of variable importance, and response curves. From a GIS standpoint, the map provides a useful tool in the production of a spatially-referenced continuous variable ranging from 0 to1 where higher values indicate higher relative suitability (Gibson et al. 2007). These values can be thresholded and binned into any number of ordinal categories for further analysis.

[7] http://dnr.wi.gov/

[8] http://nas.er.usgs.gov/

[9] http://www.cs.princeton.edu/~schapire/maxent/

Results

Mahalanobis

The Kappa statistic (K) measures the proportion of agreement between Mahalanobis predicted and the field observed presence and absence values, removing that part of agreement that is due to chance (Feuerman and Miller 2005). Despite repeated modifications to variable combinations, the results of K for Minnesota alone were below acceptable thresholds (typically 0.7 in literature). The highest K obtained was 0.1, which would not be considered a success under any circumstances. Calculated specificity and sensitivity were 0.75 and 0.55, respectively (Table 3.1). This indicates that there is high probability of correctly identifying an absence, but only a marginally better than random chance of correctly identifying a presence. Feuerman and Miller (2005) have shown that when both specificity and sensitivity are less than 0.875, it is not possible to obtain a K of 0.75 or greater (which indicates good to excellent agreement between model and observations).

The combined data for Minnesota and Wisconsin produced a K of 0.54, with specificity and sensitivity of 0.94 and 0.54, respectively (Fig. 3.2, Table 3.2). Again, K was below the standard threshold albeit substantially improved from the Minnesota alone analysis. Specificity and sensitivity values again indicate a high probability of correctly identifying an absence, but only a marginally better than random chance of correctly identifying a presence.

Maxent

An analysis based on maxent resulted in a highly predictive model for Minnesota. The ROC curve (Fig. 3.3) showed an area under the curve (AUC) of 0.968. AUC represents the probability that a randomly chosen presence site will be ranked more

suitable than a randomly chosen absence site (Phillips and Dudik 2008) and values > 0.9 are considered to be highly accurate (Manel et al. 2001).

The most useful variable in terms of explanatory power was bass habitat (45%) followed by Carlson's TSI (28%). Lake access was shown to be least useful (0.6%), which confirms what has been shown in other studies (Buchan and Padilla 2000; Roley and Newman 2008) with regard to anthropogenic contributions to presence. Spatially it appears the most suitable areas are clustered near the major metropolitan area of Minneapolis-St. Paul (Fig. 3.4).

A causal link may not exist between bass and *M. spicatum*, but empirically bass habitat would be an excellent predictor of *M. spicatum* presence. Both species prefer lakes dominated by a shallow littoral zone with abundant aquatic plant habitat. It is no secret on popular fishing press and natural resource agency websites that bass and *M. spicatum* are often co-located. This is particularly problematic because it creates friction between groups wishing to eliminate the threat posed by this invasive weed and bass fishing enthusiasts who equate *M. spicatum* mats with quality fishing. Guntersville Lake (Alabama) is a legendary bass fishing lake, largely due to its much-touted *M. spicatum* (Felsher 2007; Russow 2010). In other areas of the country many comments are made about how the bass fishing was better when *M. spicatum* was more prevalent (Anonymous 2002; Knapp 2004) or how the introduction of *M. spicatum* has been a positive step for the bass fishing community (Vick 2003). This problem is exacerbated by the disturbance (and subsequent fragmentation) caused by fishermen and their boats and also by the purposeful introduction of *M. spicatum* to a waterbody in the hopes of creating more bass habitat. Frequently the information given on forums does little to discourage spread and introduction. It is not difficult to find comments on forums (http://www.HotSpotOutdoors.com, accessed Jun 16, 2010) such as "Milfoil creates

awesome fish habitat while clearing up the water at the same time" and "I think people know what milfoil and zebra mussels are, but do we really know the true effects they can have -- both positive and negative? I know of the potential positive effects, and I have 'heard' of the potential negative effects." These comments illustrate that there is a definite culture that not only identifies bass habitat with *M. spicatum*, but encourages the growth of one species to support the other.

Discussion

Despite its prominence in ecology research, utility of Cohen's K is under some debate. A significant number of absences have been recorded for Minnesota. While the modeling methods used in these analyses do not rely on these data, the validation did utilize these figures. Therefore it seems fair to acknowledge potential limitations of these metrics.

Manel et al. (2001) reviewed published ecological literature and determined that many studies make no effort to evaluate the results, and when results are evaluated, performance metrics are potentially biased by the number of presence samples included in development of the model. Their findings indicated that specificity and sensitivity were influenced by prevalence, but that K was not. Vaughn and Ormerod (2005) raised concerns about K regarding the definition of "chance" and then pointed to specificity and sensitivity as better alternatives which are "independent of prevalence". However, McPherson et al. (2004) reported that changes in prevalence affected all three metrics. Changes in prevalence affected K, with deviations from optimum prevalence resulting in bias with low prevalence decreasing K values and high prevalence increasing K values. Higher prevalence also led to better sensitivity but poorer specificity. McPherson et al. (2004) cautioned that these biases made kappa inappropriate for comparisons between

models performed in varying regions of on varying species, stating that this issue had not been addressed by current (at that time) ecological literature.

In contrast, ROC curves are thought to be uninfluenced by prevalence (McPherson et al. 2004; Manel et al. 2001). Manel et al. (2001) reported that K was a more robust indicator of model performance, but they detected no prevalence bias in their analysis.

The dataset used in this analysis was considered to have sufficient sample points with more than reasonable spatial distribution. Although results from a Mahalanobis analysis may not be reasonably validated by chosen metrics, results from a maxent analysis indicate that a model can be formed for this dataset that is not influenced by prevalence bias because maxent analysis do not require absence data. Further, given the size and breadth of input data it is not likely the results are influenced by a "detection bias" which can sometimes be the case, particularly with invasive species.

Based on results from the Mahalanobis analysis, it appears possible the fundamental niche for *M. spicatum* is much larger than the realized niche. Roley and Newman (2008) reported that over 4,700 waterbodies were susceptible but not infested with *M. spicatum*. It is possible with more time that *M. spicatum* will spread to these areas if conditions are favorable. Roley and Newman (2008) also reported that infestations appeared to spread out from the point of initial introduction, with lakes closest to the initial invasion more likely to be positive for *M. spicatum*. This could be further support that proliferation in Minnesota is a function of time, and not a funcation of the natural characteristics of the waterbodies themselves precluding infestation by *M. spicatum*.

Additionally, the State of Minnesota's Department of Natural Resources has an active education campaign to prevent and limit spread of milfoil. These efforts include

billboards, radio and television advertising, public service announcements, printed materials, press releases, media contacts, newspaper ads, staffing at sports shows and other major events, educational displays and exhibits, informational signs at public water accesses, presentations to the public, and training all designed to increase awareness and limit introductions of *M. spicatum*. Surveys to quantify effectiveness indicate that these efforts are producing the desired results with 97% of boaters in one survey indicating they were aware of the State's invasive species laws, and 99% indicating the campaign had led them to action (Invasive Species Program 2010).

Unrelated to niche mechanics, this educational campaign could be artificially limiting the species' ability to spread, and would probably not be captured by the model input variables. Management strategies employed as a result of early detection and prevention campaigns could also limit *M. spicatum*'s ability to spread into some areas that are suitable habitat from a modeling standpoint.

The inclusion of Wisconsin in a second, combined Mahalanobis method was done to test which explanation was more likely. Wisconsin was selected more for its characteristics, not all of which are a function of its proximity to Minnesota. Wisconsin has a comparable environment; however, Wisconsin has had populations for *M. spicatum* for a much longer period of time. The earliest populations of *M. spicatum* in Wisconsin are from the late 1960's (Buchan and Padilla 2000), while the earliest population in Minnesota is from the late 1980's (Roley and Newman 2008). Wisconsin has also not had the aggressive education campaign of Minnesota.

Conclusion

From these results it may be concluded that (1) Mahalanobis is an inappropriate choice for modeling *M. spicatum* habitat, or (2) that the metrics used to evaluate the Mahalanobis model were inappropriate. Cohen's κ values indicate that the calculated

model would have no accuracy for predicting habitat. Perhaps this is due to bias from prevalence, which has been shown to be troublesome for Cohen's K, specificity, and sensitivity in previous research. Alternatively, and more likely, the Mahalanobis model could indicate that Eurasian watermilfoil may occupy only a small proportion of the habitat available in Minnesota. This conclusion is supported by results of the combined analysis of Minnesota and Wisconsin and results from the Mahalanobis analysis, in addition to other literature (Roley and Newman 2008).

Results of the maxent analysis indicate that *M. spicatum* habitat is correctly characterized by the maxent model or that *M. spicatum* has not reached all potential habitats due to some limiting factor, possibly time. *Myriophyllum spicatum* habitat is influenced primarily by bass habitat and trophic status. While it is true that *M. spicatum* does provide cover for bass, the coincidence in finding *M. spicatum* and bass is likely due to their favoring of similar conditions. Both prefer the shallow areas of highly productive lakes with similarly mesotrophic conditions.

Lack of *M. spicatum* spread into the fundamental niche may be a simple function of time for dispersal but it is not possible with current data to validate this hypothesis. Any data available would likely state the year *M. spicatum* was found, which may or may not be a valid indicator of when *M. spicatum* appeared given the aforementioned providential nature of species' discovery.

Based on the results seen from the joint analysis of Minnesota and Wisconsin, it appears the most likely scenario is that *M. spicatum* has not reached its maximum habitat potential in Minnesota, and in agreement with the findings of Roley and Newman (2008) will continue to find suitable habitat in Minnesota when allowed to spread to new areas.

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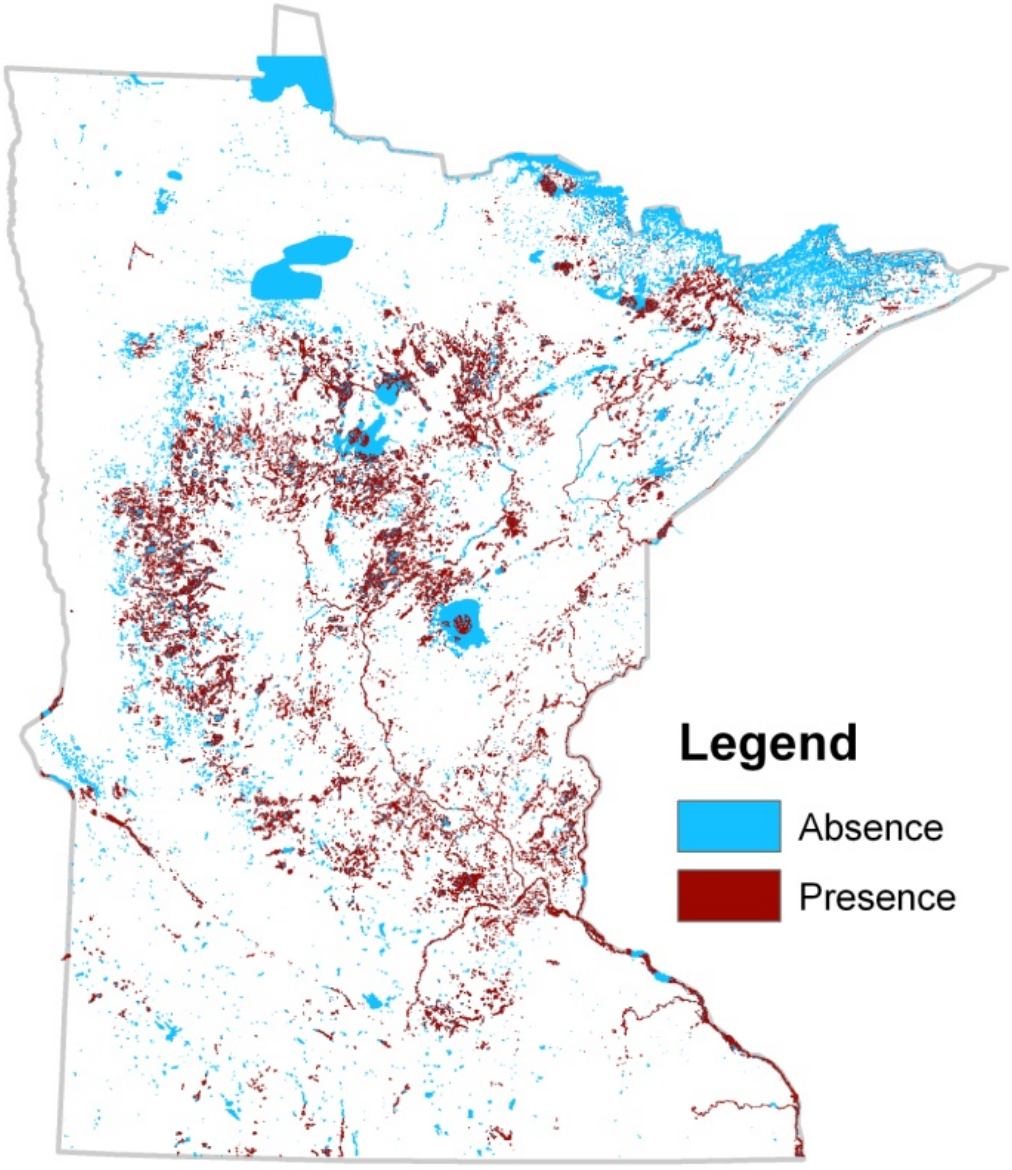

Figure 3.1. Results of Mahalanobis analysis using 0.5 as the threshold for presence/absence of *M. spicatum* in Minnesota.

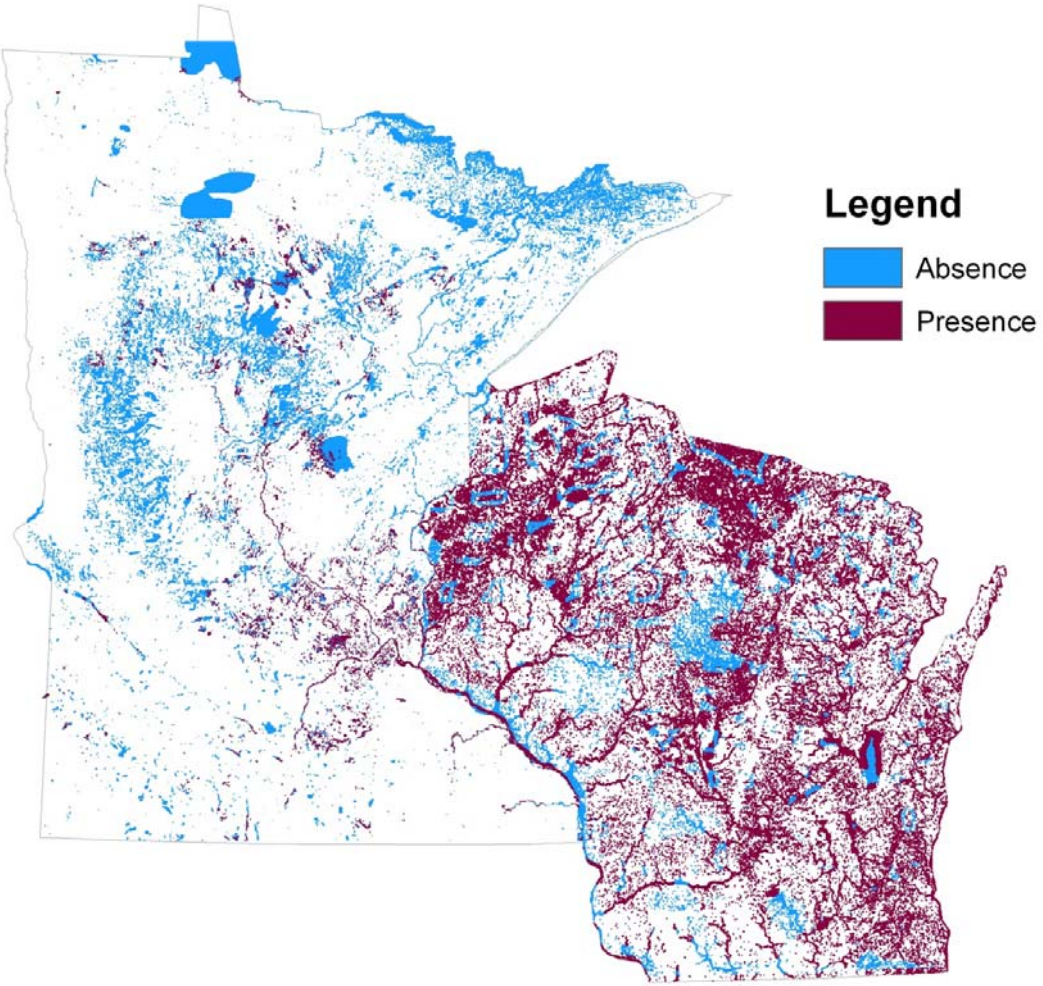

Figure 3.2. Results of Mahalanobis analysis using 0.5 as the threshold for presence/absence of *M. spicatum* in Minnesota and Wisconsin.

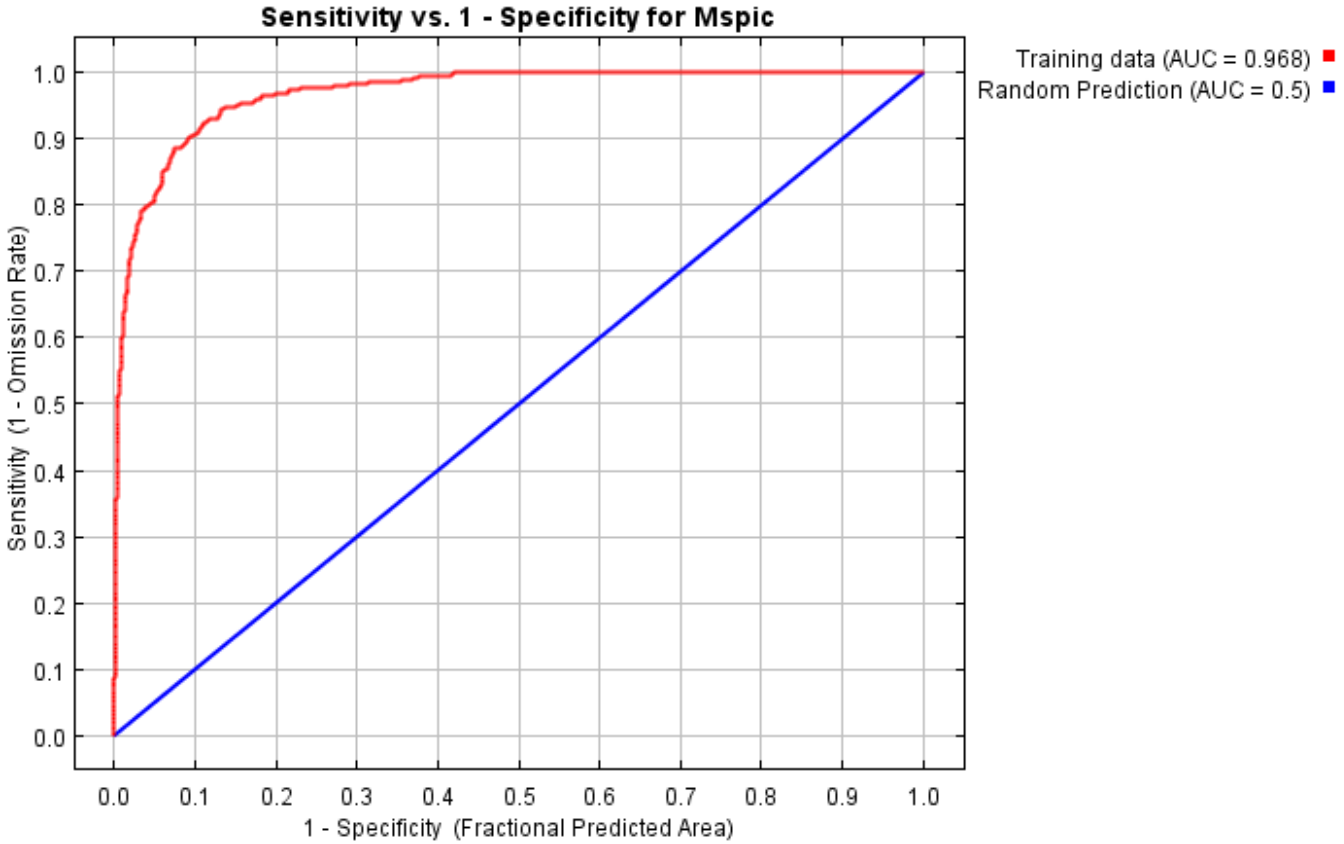

Figure 3.3. Receiver operating characteristic curve for maxent analysis of *M. spicatum* in Minnesota.

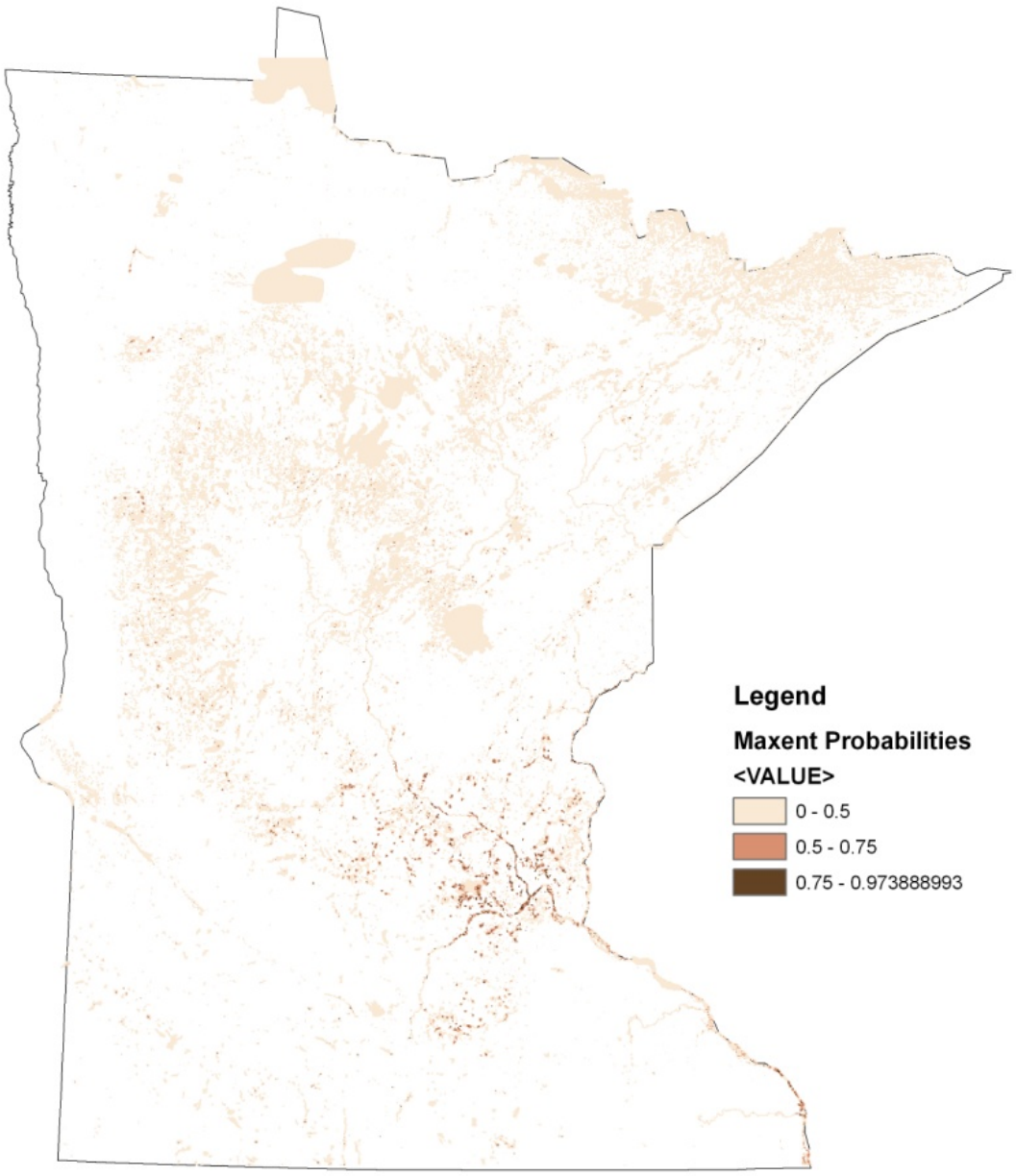

Figure 3.4. Results of maxent analysis for prediction of *M. spicatum* in Minnesota.

Table 3.1. Validation results comparing presence (P) and absence (A) for field (observed) and predicted from Mahalanobis model for prediction of *M. spicatum* in Minnesota.

		Field	
		P	A
Mahalanobis	P	244	1478
	A	81	1842

Table 3.2. Validation results comparing presence (P) and absence (A) for field (observed) and predicted from Mahalanobis model for prediction of *M. spicatum* in Minnesota and Wisconsin.

		Field	
		P	A
Mahalanobis	P	558	474
	A	172	2846

CHAPTER 4

NATIONAL-SCALE MODEL

Previous work in habitat modeling predominately focuses on identifying and delineating potentially suitable habitats for desirable species. Less focus has been given to using predictive modeling for species control or proactive, preventative practices for troublesome species, although interest in this area is increasing. Modeling of this sort could be especially useful for economically important invasive pest species (Peterson et al. 2003). Managers and researchers may find many benefits in large-scale solutions for identifying habitat that are neither labor intensive nor prohibitively time-consuming (Dettmers and Bart 1999) as these solutions may provide not only location information, but also help guide containment boundaries, identify priority areas for early detection and rapid response, and monitor control strategies and cost-effectiveness in different states. Large-scale national models could also be used to guide higher-resolution models for smaller extents (Morisette et al. 2006).

Morisette and others (2006) developed a nationwide habitat map for tamarisk (*Tamarix* spp.). Environmental layers used were those which covered large areas, including the land-cover component from NASA's MODIS instrument. Hirzel and Le Lay (2008) reported that land cover data have the most diverse influence on ecological niche, but were quick to add these data may not be well suited for ecological purposes because they are designed for a different purpose and suffer from poor spatial accuracy,

precluding their use in fine-scaled modeling. However a national model is not likely to be at the level of scale where slight locational accuracy is an issue.

Climate variables are also thought to drive species distribution, particularly at large extents. Climate is thought to affect plants in particular because, unlike animals, they cannot avoid adverse climates by sheltering or migrating (Hirzel and Le Lay 2008). Neilsen et al. (2008) constructed both national and regional models for the invasive ornamental, *Heracleum mantegazzianum*. Climate was shown to be significant in the national model for explaining distribution. Certainly the preponderance of studies on species range changes in response to climate change indicates that climate is a large driver in habitat determination.

Thuiller et al. (2004) assessed the influence of land cover and climate on species distribution in Europe. They concluded that climate was the major driver for both species distribution and land cover. However they also found that land cover inclusion improved the explanatory power of their models despite this. In larger-scale models, this effect was negligible unless the climate variables had poor predictive power. This was possibly due to correlation between climate and land cover, with exceptions occurring in specific classes where land cover was not as influenced by climatic conditions (i.e., inland water and arable land).

Many considerations go into developing a national-scale model covering a large geographic extent and requiring a large volume of data. In previous studies (Peterson et al. 2003) it has been noted that processing time was a bottleneck in model runs for predicting potential invasive distributions of plant species. Morisette and others (2006) produced their national map at a scale of 1 km, which was felt to be the resolution that fit both the available data and the practical constraints of computation.

Morisette et al. (2006) collected data for their tamarisk model from 45 disparate databases and additional geospatial information that was found via web search. In other studies (Peterson et al. 2003), another shortcoming of collecting data on-line was related to the availability of herbarium records and other forms of presence data in digital form on the web. This is applicable to many studies on invasive species, as the majority of available data is frequently presence-only and often comes from herbarium records.

The objective of this study is to develop a national model for the predicted habitat of Eurasian watermilfoil (*Myriophyllum spicatum* L.), an invasive, aquatic weed. This non-native weed was introduced into the U.S. in the 1940s, with the earliest herbarium records coming from Washington D.C. (1942), Arizona (1945), California (1948), Ohio (1949) (Couch and Nelson 1985). *Myriophyllum spicatum* currently occurs in almost every state, but some areas have more pronounced problems with this weed.

Methods and Materials

Each county in the United States was described by a set of predictor variables. These variables included those which were thought to vary across broad areas and influence suitability of habitat. Variables were hardiness zones, land cover, average precipitation, and percent water. All data were collected from publicly available sources of GIS data. Hardiness zones were obtained from the USDA (Cathey 1990). Land cover data was downloaded from the USGS National Land Cover Database (Homer et al. 2004). Precipitation data represented 30-yr average monthly precipitation and was compiled by the PRISM climate group at Oregon State University (PRISM climate group, 2006). Data on the percentage of water surface per county (hereafter “percent water”) were acquired from NOAA (Anonymous, 1999). Presence data were collected using several publicly available web databases. These included the Invasive Plant Atlas of

New England (IPANE)[10], the Invasive Plant Atlas of the Midsouth (IPAMS)[11], USGS Nonindigenous Aquatic Species (NAS) database[12], and USDA Plants database[13]. Presence data also came from unpublished field surveys.

Data were compiled in ArcGIS[14] so that each county had a value for each variable. These data were joined to county centroids so that (*x,y*) coordinates could be determined for input into maxent, which requires a latitude, longitude pair for each presence entry. Although a county-level analysis is not ideal, compiling data from various states showed a range of data assembly level, with many states reporting data on a county-level only. Thus a "lowest useable unit" of county was adopted for analysis.

The maxent statistic (q_λ) was calculated using the Maxent software[15]. Only the state of Minnesota was considered. Maxent is defined by the following equation (Phillips and Dudik 2008)

$$q_\lambda(x) = \frac{1}{Z_\lambda} \exp\left\{\sum_{j=1}^{k} \lambda_j f_j(x)\right\}, \qquad (4.1)$$

where for each $j, j = 1, \ldots k, \lambda_j$ represents the weight, f_j is the j^{th} feature at *x*, *x* is presence and Z_λ is a normalizing constant forcing the sum of the entropy components to one. Maxent allows for both categorical and continuous predictor variables. In the analysis hardiness zones and landcover are used as categorical, while precipitation and percent water are continuous variables.

[10] IPANE, http://nbii-nin.ciesin.columbia.edu/ipane

[11] IPAMS, http://www.gri.msstate.edu/ipams/

[12] USGS NAS database, http://nas.er.usgs.gov

[13] USDA PLANTS database, http://plants.usda.gov

[14] ESRI, 380 New York Street, Redlands, CA 92373-8100

[15] http://www.cs.princeton.edu/~schapire/maxent/

In addition to maps of predicted suitability, the Maxent software produces a receiver operating characteristic (ROC) curve, information regarding the relative contribution of each variables, jackknife tests of variable importance, and response curves. From a GIS standpoint, the map provides a useful tool in the production of a spatially-referenced continuous variable ranging from 0 to1 where higher values indicate higher relative suitability (Gibson et al. 2007). Another benefit is that these values can be thresholded and binned into any number of ordinal categories for further analysis.

Maxent utilizes maximum entropy to make predictions from incomplete data. It can be used to estimate species distribution by finding the probability distribution that is closest to uniform (i.e., “maximum entropy”) for a study area under a specified set of environmental constraints (Phillips et al. 2006). The maxent statistic weights each variable by a different constant where the value of each weight corresponds to the importance or the magnitude of the variable to the system’s entropy. The probability distribution is estimated by iteratively altering one weight at a time to maximize the likelihood of the occurrence dataset. To avoid overfitting, the estimated distribution is constrained so that the average value for a given predictor is close to the empirical average rather than equal to it (Hernandez et al. 2006). In comparison studies, maxent outperformed other accepted quantitative methods for ecological modeling (Hernandez et al. 2006; Phillips et al. 2006). A major advantage of maxent over many popular methods is that areas without values are not automatically considered absences, which reduces bias from inclusion of false absences (Elith et al. 2006; Phillips et al. 2006). Graham et al. (2007) concluded that maxent experienced no decline in performance due to errors in spatial accuracy when compared with other model techniques, also making it an appropriate choice for this study since data were not collected specifically for the

purpose of this study and it has been argued that landcover data suffered from spatial inaccuracy (Hirzel and Le Lay 2008).

Results and Discussion

The maxent analysis resulted in a highly predictive model. Maxent was run with different combinations of the selected variables until the highest area under the curve (AUC) for the ROC curve could be obtained. A ROC curve is plotted by placing all sensitivity values on the y-axis against their equivalent (1-specificity) values on the x-axis (Miller 2005). The AUC statistic represents the probability that a randomly chosen presence site will be ranked more suitable than a randomly chosen absence site (Phillips and Dudik 2008). AUC is a measure of overall accuracy and is independent of prevalence, making it well-suited for studies on vegetation modeling (Miller 2005). The model which produced the best ROC curve included all 4 variables. The ROC curve (Fig. 4.1) showed an area under the curve (AUC) of 0.792. AUC values > 0.7 indicate useful application (Manel et al. 2001), thus the model was considered to be good. The AUC of 0.792 indicates a reasonable likelihood of correctly predicting habitat.

The most useful variable in terms of explanatory power was precipitation (43%) followed by percent water (30%). Hardiness zone was shown to be least useful (10%). Jackknife analysis showed that land cover appears to have the most information by itself. Percent water was the variable with the most information not contained in the other variables.

It is hypothesized that hardiness zones were considered the least useful because the information that goes into the development of a hardiness zone is likely correlated with data already in the model. These zones are based on, among other things, rainfall, temperature, and day length (Cathey 1990), indicating that the precipitation data may have been adequate to describe the model without hardiness zones. It may also be that

hardiness zones are developed with additional data that are uninformative for *M. spicatum* distribution at this scale. It is possible percent water has the most explanatory power of a single variable solely since as an aquatic species, *M. spicatum* has greater likelihood of occurrence in areas where there is more available habitat (suitable or otherwise).

The geological processes which formed most lakes created lake districts, or groupings of lakes (Wetzel 2001). Soranno et al. (1999) found that annual climate was an important driver for synchrony – a measure of the degree to which lakes in a district behave similarly over time – in lake districts. This could explain why when precipitation is considered as the most useful explanatory variable, the resultant maxent output map appears to show clustering of probabilities within areas of high lake density (i.e., lake districts). Additionally, if it can be accepted that humans are the primary vector for *M. spicatum* as many authors suggest, the proximity of lakes in the district likely increases the number of chances for introductions from one lake to the next. Johnstone et al. (1985) reported that boaters had low probability of moving between lakes beyond 125 km apart, and around 0.25 probability of moving between lakes in a district. They concluded that boats provided a viable mechanism for interlake transport of plant fragments.

Neilsen et al. (2008) found that human population density was a driving force behind distribution of *H. mantegazzianum*. Although not considered in this study, the areas for which lower relative probabilities were determined are also areas for which populations are known to be limited (i.e., the Western U.S.). This could be an additional explanatory variable for consideration in future studies. Again, if humans can be considered a primary vector, the more populated areas pose more chances for introductions and increased likelihood of lake utilization.

Low probabilities in the areas for which density of lakes is smaller and populations are lower may also be explained by the arid nature of these areas. Chambers (1994) noticed a relationship between mean annual dew point temperature and *M. spicatum* range. Since by their nature aquatic plants must remain wet to remain viable, in an arid environment, fragments may have a harder time surviving transport on boat trailers, considered to be the primary means by which humans spread this weed. Additionally, with less dense distributions of lakes, the distance between lakes is greater, limiting the movement between lakes and increasing the time available for desiccation of plant fragments on boat trailers.

Specific to the model results, it is important not to equate availability with use (Dettmers and Bart 1999), as these are not the same thing for a species. Chambers (1994) reported no instance of *M. spicatum* in the Prairie Provinces of Canada despite no environmental constraint on its establishment. With few populations near these provinces, it was assumed that geographic restraints were likely one of the biggest mechanisms preventing presence of *M. spicatum,* with the nearest documented occurrence of *M. spicatum* over 300 km away. Additionally, depending on a state or county's protocols, *M. spicatum* may be aggressively managed, thus limiting its occurrence, despite high probability of habitat suitability. In Minnesota for example, Roley and Newman (2008) reported that over 4,700 waterbodies were susceptible but not infested with *M. spicatum*. This may be attributable to the State of Minnesota's Department of Natural Resources (MN DNR), which has an active education campaign to prevent and limit spread of *M. spicatum*. Multiple outlets are utilized by MN DNR in this endeavor including media outlets and other traditional forms of education and outreach all designed to increase awareness and limit introductions of *M. spicatum*. Ninety-seven percent of boaters in one survey conducted by MN DNR indicated they

were aware of the State's invasive species laws, and 99% indicated the campaign had led them to action (Invasive Species Program 2010).

Zaniewski et al. (2002) concluded that presence-only models were more likely to predict the fundamental niche, unless absences or even "pseudo" absences could be included. Phillips et al. (2006) stated that to the extent the model accurately predicts the fundamental niche, however, the projection to geographic space will represent the species' potential distribution. Even without absence data, concurrence with prior studies (Couch and Nelson 1985, Fig. 4.3) indicates that these results may accurately portray the fundamental niche, and thus the potential distribution of *M. spicatum*.

It should also be acknowledged several challenges are associated with use of presence-only data, specifically when the researcher is not the collector. Elith and others (2006) evaluated the capacity of presence-only data to predict species' distribution. They concluded that these data were useful for modeling distribution and that methods such as maxent were effective in these endeavors. Ideally presence and absence data would be used to create the model, particularly for a weed species that is as ubiquitous as *M. spicatum*. Unfortunately, data sources like IPANE log presence almost exclusively. The only way to obtain absence data would be to purposefully collect it, but this also presents many challenges. Because the analysis is done on a county level, it would be impossible to survey an entire county and guarantee absence. It wouls also be impossible to determine if this is truly absence or simply suitable area which has not been colonized by *M. spicatum*. Many states for which data are missing, Mississippi for example, do not have a severe enough problem with *M. spicatum* to warrant statewide surveys. Collecting these data would be prohibitive in terms of both cost and time.

Further, utilizing “volunteer” type databases such as IPANE introduces unknown sampling bias into the input data (Elith et al. 2006; Zaniewski et al. 2002). Often the data in these databases are collected without a sampling scheme, which can create data clustering in areas that are more accessible. Inputs in this case tended to be clustered in parts of the country where *M. spicatum* is problematic. Dependency on previously collected databases did limit the available inputs to the model, although it would be just as easy to argue that the prevalence is higher and the frequency greater in these areas because of the duration of *M. spicatum* in these areas, allowing for much more established populations.

Conclusion

While there are many considerations for presence-only models, the use of maxent overcomes many of the limitations these models present. Given the nature of data available on invasive species from public databases, it is more common to see these types of analysis. While it could be argued that more reliable results for a species’ potential distribution can be obtained when absence data are added, these studies are less feasible for large area models, particularly for ubiquitous invasive weed species like *M. spicatum*.

Invasive plants are known for their opportunistic traits. A large percentage of the U.S., particular in the Eastern half, appears to be available to *M. spicatum*, should it find an opportunity for introduction. Maxent produced a reasonable county-level national model of *M. spicatum* habitat based on land cover, precipitation, hardiness zone and percentage of water. Results indicated that percent water largely influences the probability of suitable habitat. Presence may be dictated by lake density, human population density, and dew point as reasonable justification can be made for each and all. These results closely resembled an introduction and spread pattern for *M. spicatum*,

perhaps indicating that habitat is colonized as time permits, and not necessarily as conditions permit.

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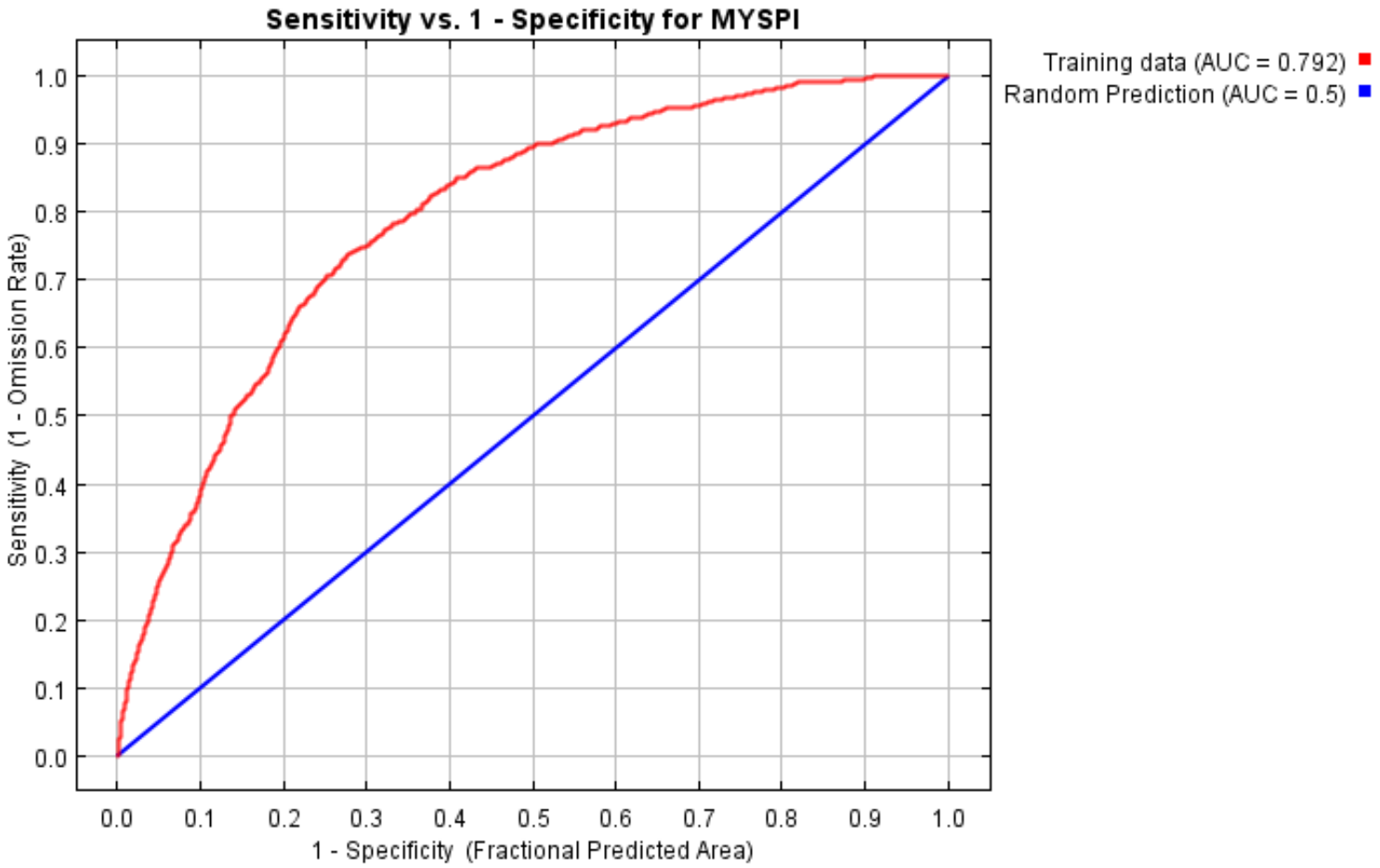


Figure 4.1. Receiver operating characteristic curve for maxent analysis of *M. spicatum* in the United States.

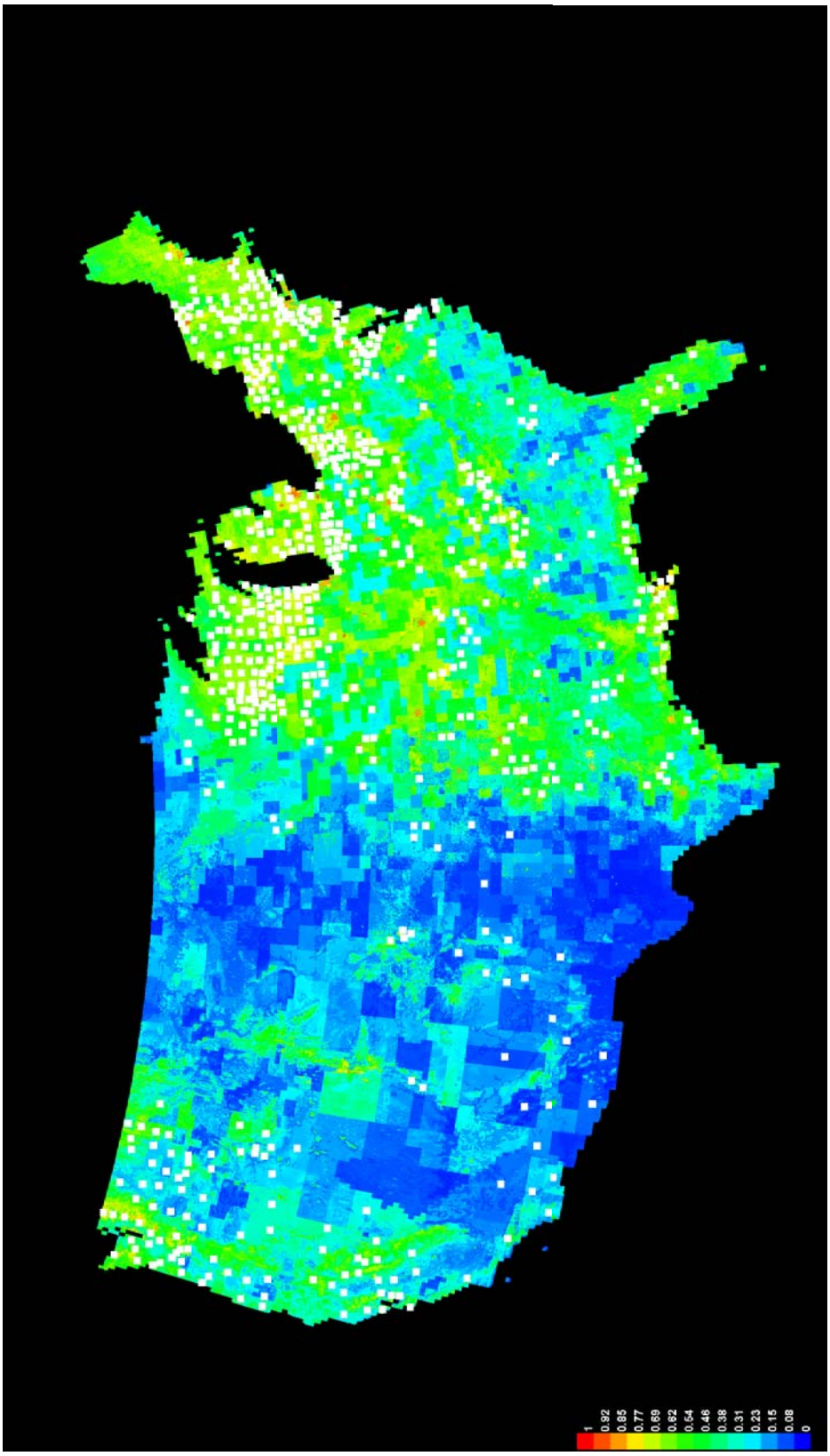
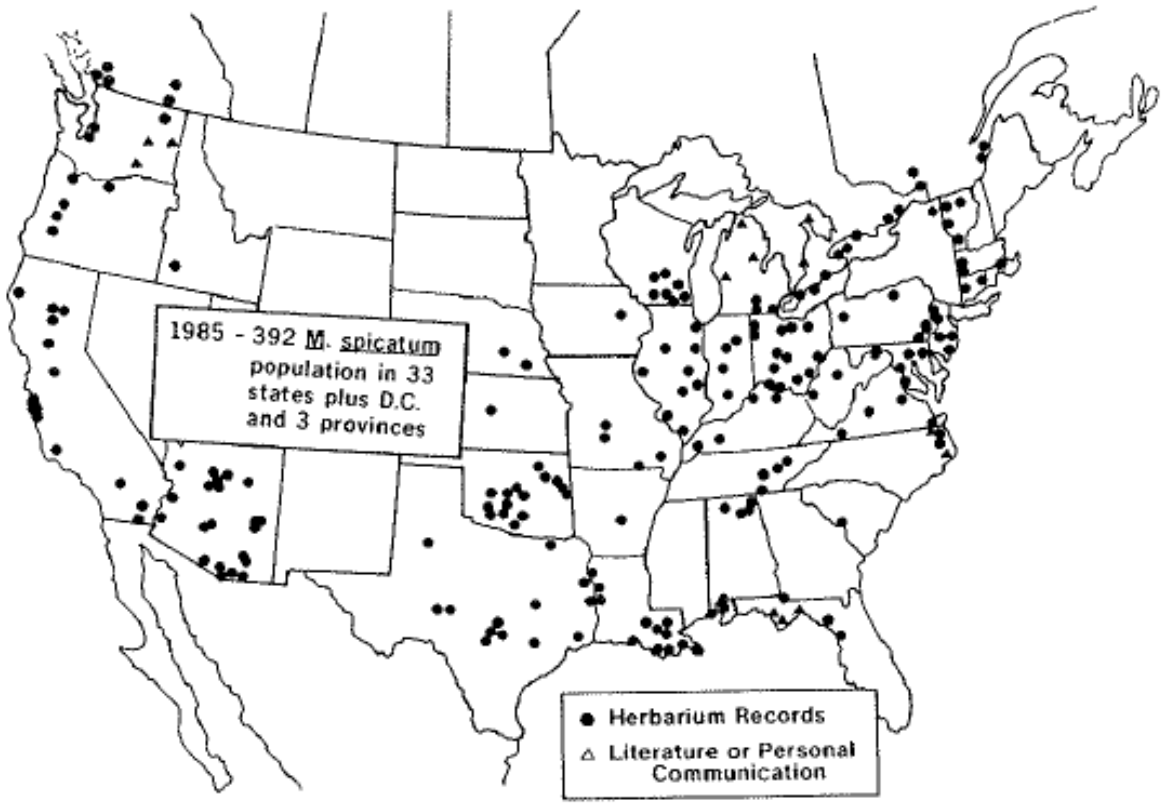


Figure 4.2. Maxent predictions for *M. spicatum* in the United States. Warmer colors show areas with better predicted conditions. White dots show the presence locations.



4.3. Distribution of *M. spicatum* records collected by Couch and Nelson (1985) for 1980.

CHAPTER 5

SUMMARY AND FUTURE RESEARCH

In their review paper, Guisan and Thuiller (2005) determined the earliest known example of modeling species was published in 1924 to predict the spread of cactus species in Australia. Computer-based modeling approaches for species distribution began in the mid-1970s, but it was not until the early 1990s when publications on predictive modeling of species distribution increased sharply (Guisan and Thuiller 2005). The area of predictive modeling in ecology and related fields continues to grow with new methods taken from other fields. These methods are then incorporated into a broader suite of tools which can be used to address issues related to invasive species.

For stakeholders and decision makers dealing with Eurasian watermilfoil (*Myriopyllum spicatum* L.), models can help direct limited financial and personnel resources aimed at prevention or containment. As pressure from tightening budgets at funding sources trickles down to front-line managers such as government agencies, water management districts, and university research programs, a targeted approach to invasion prevention will be key.

Using models can present a set of challenges. Many decisions, frequently subjective, go into building a model. Use of presence and/or absence data is frequently dictated by extent of the area of interest, economic considerations for data collection and processing, and the abundance of the species of interest. Methods exist for modeling

under both approaches and research supports positive outcomes for both presence/absence and presence-only modeling. When dealing with large areas, such as a national model, presence-only modeling is the most convenient option. Particular to invasive species, most available data is presence-only, so choices are dictated almost *a priori* by available data. Maxent is a very appealing option for presence-only modeling because it doesn't complicate a model by assuming unknown (i.e., unsurveyed or sampled) areas are absences. This assumption can be crucial when modeling invasive species.

Another decision which can not be ignored is the choice of scale. Levin (1992) posed that variability has meaning relative only to scale of observation. He added that it was more important to capture how a system changes across scales in lieu of trying to determine the correct scale. By using a three-scale approach in this study, it has been possible to use a variety of predictor variables to characterize *M. spicatum* habitat at different levels of observation. Given what is known about introduction, spread, and transport of Eurasian watermilfoil, it makes sense to examine all three scales in order to determine how spread is influenced: 1) in a single lake where stem elongation and fragments account for the majority of spread; 2) on a regional scale where spread is largely to due to transport among lakes by anthropogenic mechanisms; and 3) on a national scale where broader issues of climate and landcover influence habitat availability against the pressures from local and regional factors.

A comparison across scales of results from maximum entropy (hereafter "maxent") analysis yields AUCs of 0.771, 0.953, 0.968, and 0.792 for littoral, pelagic, Minnesota, and National models, respectively. It appears then, that the most useful scale is a regional-level model. Levin (1992) indicates that by increasing our scaling unit (i.e., going from local to regional) a model moves from "unpredictable, unrepeatable

individual cases" to a model which is more generalized, trading detail for predictability. This does not appear to extend to the case of the National model, for which the AUC decreases. It may be possible, however, that the AUC for the National model could be improved by increasing the number of samples. For a fixed number of predictor variables, increasing the sample size would increase ability to estimate coefficients, potentially increasing the AUC for this model.

The value of 0.953 for the pelagic seems extremely high and can likely be explained by the fact that for the largest part of the pelagic zone, predictions of absence or low probability are correct. Given the depths of the pelagic zone, intuitively *M. spicatum* would not be expected and thus if the model predicted the entire zone to be void of *M. spicatum*, the error rate for false positives would not be sufficiently high.

Positive Outcomes

Despite a fairly ubiquitous distribution, it is encouraging to see that when a concerted effort is made, Eurasian watermilfoil can successfully be prevented from overtaking habitat. *M. spicatum* spread appears to be largely time dependent, less than habitat dependent. When comparing the status of Eurasian watermilfoil in Wisconsin with Minnesota, it is possible to see the difference 20 years can make in establishment of Eurasian watermilfoil as a nuisance species. The experience of Minnesota proves that public education can be effective at limiting the spread of this invasive species. Even more promising is that this was true even when habitat was deemed suitable. For states where *M. spicatum* is still a non-nuisance species, this is extremely valuable, as these states can begin to think about approaches that can be undertaken to help ameliorate risks of widespread establishment and implement these measures early.

Public awareness and education programs, in addition to limiting spread, could provide added benefits to "volunteer" type databases such as IPANE[16] and IPAMS[17]. A more informed citizenry is resource that would be a boon to data collection and identification of invasives such as Eurasian watermilfoil. The economic and practical feasibilities of collecting both presence and absence data at large scales creates a need to focus on methods for presence-only prediction, and increases the dependency on these types of databases. While maybe not ideal, a sufficient amount of research supports the idea that presence-only data can be effectively used to predict habitat for many species. The development of methods specific to presence-only models will likely escalate, and public awareness of invasives can only benefit this type of work. A more informed citizenry is also much more likely to be supportive of control and prevention methods for Eurasian watermilfoil; something front-line managers can also appreciate.

Future Research

Macrophytes have traditionally been neglected in many water quality models including the most commonly used models such as WASP[18] and QUAL2K[19] (Park et al. 2003). Park and others (2003) were able to develop a non-GIS based, more "traditional" water quality model which also included the effect of macrophytes on environmental features such as dissolved oxygen and nutrient cycling. Another model, MILFO[20], models vegetative growth, but not location, of Eurasian watermilfoil based on

[16] IPANE, http://nbii-nin.ciesin.columbia.edu/ipane

[17] IPAMS, http://www.gri.msstate.edu/ipams/

[18] Water Analysis Simulation Program, U.S. Environmental Protection Agency, Washington, D.C., http://www.epa.gov

[19] U.S. Environmental Protection Agency, Washington, D.C., http://www.epa.gov

[20] U.S. Army Corps of Engineers, Washington, D.C., http://www.usace.army.mil

environment. Jensen and others (1992) were able to incorporate features such as fetch to determine not only presence, but density and spread of aquatic macrophytes. These successes represent pieces of a total modeling approach to Eurasian watermilfoil management. A logical next step is to incorporate existing mathematical-based water quality models into a GIS-based habitat suitability model for *M. spicatum*. A real world model requires the user to have pre-existing data which show the conditions present. Ideally it is desirable to link GIS-based habitat models for Eurasian watermilfoil with other existing water quality models so that this need not be the case.

Ultimately, incorporation of these models allows the user not only to predict probability of occurrence but also spread in response to user specified changes in environment variables. There is already considerable research underway about how climate change will affect the range of many species, including invasives.

Incorporation with water quality models would further allow the user to generate scenarios with simulated changes in water quality upstream or downstream, and also run models without measured field data on water quality. Not that it should be advocated, but it would be entirely possible for the user to run whole simulations from start to finish without leaving the desk.

Dependence on modeling will only increase as new methods and novel approaches are developed. Good science and a push for validation will help to ensure that modeling remains of value.

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APPENDIX A

DATA DEFINITIONS FOR ALL CHAPTERS

Data	Data type	Source	Number of records	Description
Chapter 2				
Field Survey – Pelagic	shapefile	Dr. John Madsen	1,071	Data from general 2007 field survey on Pend Oreille, contains presence absence data for *Myriophyllum spicatum*
Field Survey - Littoral	shapefile	Dr. John Madsen	606	Data from general 2007 field survey on Pend Oreille, contains presence absence data for *M. spicatum*
Boundary	shapefile	Dr. John Madsen	1	Boundary for research area
True Littoral Zone	shapefile	Dr. John Madsen	1	Boundary for the true littoral zone (as opposed to the portion of the study that was classified as littoral for analysis purposes)
Sounding	image	NOAA[a]	N/A	Image of NOAA sounding data collected over Pend Oreille lake
Wind	table	US Navy	101,201	Data from US Navy buoy on Pend Oreille contained wind speed and vector for 2007
Depth	shapefile	Dr. John Madsen	1,343	Data collected with a depth finding during a 2007 field survey on Pend Oreille
Chapter 3				
Field Survey	shapefile	Sarah Roley	3,446	Data collected on presence and absence of *M. spicatum*, total alkalinity, Secchi depth, and lake size
Field Survey	shapefile	MN DNR	199	Supplement data on presence of *M. spicatum*
MN basedata	shapefile	MN DNR		Boundary data for counties, lakes, and state, as well as road network, and boat access sites
Flow accumulation (30m)	image	NHD+[b]	N/A	Flow accumulation rates for MN and WI
Bass habitat data for MN	table	University of MN	19,966	Data from a fisheries survey where bass are identified

WI basedata	shapefile	WI DNR[c]		Boundary data for counties, lakes, and state, as well as road network, and boat access sites
Field Survey	shapefile	USGS NAS[d]	730	Data on presence of *M. spicatum*
Bass habitat data for WI	shapefile	WI DNR	4,385	Delineation of waters classified as bass habitat for the state
Chapter 4				
Hardiness zones	image	USDA[e]	N/A	Hardiness zones for the US
Land cover (30m)	image	USGS	N/A	Land cover classes from the National Land Cover database
Precipitation	table	PRISM Climate group	21,812,625	30-yr average monthly precipitation
Percent water	table	NOAA	3,141	Percent water by county
National basedata	shapefile	ESRI[f]		Boundaries for states, counties, lakes and rivers
Field survey	table	IPANE, IPAMS[g], USGS, USDA	2,563	Presence data from publicly available sources condensed into one table

[a]National Oceanic and Atmospheric Administration

[b]National Hydrography Dataset Plus

[c]Department of Natural Resources

[d]US Geologic Survey Nonindigenous Aquatic Species

[e]US Department of Agriculture

[f]Environmental Systems Research Institute

[g]Invasive Plant Atlas of New England, Invasive Plant Atlas of the Mid-South