MODELING THE IMPACTS OF BARRIER REMOVAL ON GREAT LAKES SEA LAMPREY

By

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ABSTRACT

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Barriers in the Great Lakes represent an effective form of control for the invasive sea
lamprey (*Petromyzon marinus*) by blocking large extents of river habitat and subsequently
eliminating the need for the lampricide treatments in these upstream areas. With increasing
pressure for barrier removals, the availability of suitable sea lamprey habitat above these barriers
and the expected population response to dam removals represent key uncertainties in decision-
making. The development and evaluation of models to predict larval habitat quantities using
readily-available, reach-scale landscape predictors improved our understanding of common
influences on stream habitat, but failed to reliably predict habitat proportions upstream of
barriers in the Lake Michigan drainage basin. Subsequent simulation-based modeling of the
Lake Michigan sea lamprey population revealed a disproportionate, exponential response to
increasing habitat availability, driven in part by decreasing overall lampricide treatment
frequencies under a fixed control budget. The same modeling approach was used to generate sea
lamprey population predictions associated with projected removal of Grand River's Sixth Street
Dam under a suite of alternative management actions and biological assumptions. Based on all
simulation results, barrier removals appear to necessitate a substantial increase in annual
lampricide control costs to prevent disproportionate increases in sea lamprey abundance across
the Lake Michigan basin.

ACKNOWLEDGMENTS

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THESIS INTRODUCTION

The parasitic sea lamprey (*Petromyzon marinus*) has played an important contributing role in the ecology and economics of the Great Lakes since its invasion in the early 20th century. In conjunction to high fishing pressure and fish habitat loss, peak sea lamprey abundances in the 1950s and 1960s contributed to the declines of numerous fish populations and commercial fisheries across the Great Lakes; the commercial catch of lake trout (*Salvelinus namaycush*) catch declined from 2268 t to 76 t between 1938 and 1954 in Lake Huron, and similar declines were reported in both Lakes Michigan and Superior (Smith and Tibbles 1980). Other species, including burbot (*Lota lota*), lake whitefish (*Coregonus clupeaformis*), walleye (*Sander vitreus*), and rainbow trout (*Oncorhynchus mykiss*) also experienced declines during this time period (Smith 1972). In addition to the co-occurring rise and fall of sea lamprey and teleost abundances, respectively, evidence for the effect of sea lampreys on Great Lakes fish includes the explicit linking of lamprey wounding rates, mortality rates, and abundance for multiple species of Great Lakes fish, including lake whitefish and lake trout (Moore and Lychwick 1980; Spangler et al. 1980; Wells 1980). The removal of top predators also led to longer-term, persistent changes in lake-wide ecology. Released from predation pressure, multiple species of native ciscoes (*Coregonus* spp.) experienced a temporary surge in abundance before shifting parasitic pressure by sea lamprey caused subsequent depletions in both Lakes Michigan and Huron (Smith 1968).

The sea lamprey, native to the northern Atlantic Ocean, invaded the upper Great Lakes in the early 20th century after the creation of the Welland Canal. This artificial waterway presumably allowed sea lampreys, previously constrained to Lake Ontario, to bypass Niagara

Falls and begin spreading throughout the Great Lakes (Hubbs and Pope 1937). The first evidence of sea lamprey spawning in Lake Erie was confirmed in 1932, and subsequent observations of sea lamprey in Lakes Huron and Michigan followed in 1937 and 1936, respectively (Hubbs and Pope 1937; Applegate 1950). The earliest potential observed sea lamprey in Lake Superior was reported in 1938, with subsequent observations in 1946 (Applegate 1950; Smith and Tibbles 1980). By 1948, sea lampreys were firmly established, with confirmed spawning runs in 34, 68, and 4 tributaries in Lakes Huron, Michigan, and Superior, respectively (Applegate 1950).

Sea lampreys are an anadromous species in their native range, and their pattern of migrating to coastal rivers for spawning persists in the Great Lakes. After the parasitic juvenile stage finishes feeding within one of the Great Lakes, individuals commence migration to find suitable rivers for spawning (Applegate 1950). Unlike many anadromous species, sea lampreys appear to exhibit a lack of natal homing (Bergstedt and Seelye 1995). Stream selection is instead based on river-specific cues including discharge and the concentration of pheromone-based larval cues (Moore and Schleen 1980; Morman et al. 1980; Mullett et al. 2003; Sorensen and Vrieze 2003). Higher river discharge presumably helps migrating individuals sense and orient to river plumes, while larval cues indicate suitable habitat based on the occurrence of previous successful spawning (Wagner et al. 2009; Meckley et al. 2014). Upon selecting a river and moving upstream, adults find suitable gravel habitat for spawning, construct mounded nests, deposit and fertilize eggs in the nests, and subsequently die (Applegate 1950; Manion and Hanson 1980). Successfully hatched sea lamprey larvae from these eggs will leave the nest approximately three weeks after spawning, drift downstream, and locate suitable burrowing habitat (Applegate 1950).

Sea lamprey ammocoetes, or larvae, are largely sedentary and possess a different morphology from their subsequent life stages. Ammocoetes are relatively unselective filter-feeders that live in fine substrate sediments (Beamish 1980). They lack any semblance of the oral disc found in the parasitic juvenile stage, and instead use an oral hood to direct water into the pharynx for respiration and filter feeding (Youson and Potter 1979). Larvae prefer fine substrate habitat, like silt and sand, for burrowing, and will live and grow within these habitats for an average of approximately 5 years (Potter 1980). Over the course of their larval stage, ammocoetes can disperse widely from their original spawning sites; full siblings can be found more than 1 km apart within one year after hatch (Derosier et al. 2007). Once larvae reach a threshold length and lipid content, they undergo metamorphosis, in which they develop larger and more complex eyes, a toothed-oral disc, a rasping tongue, and more prominent dorsal fins, among other features (Youson and Potter 1979; Potter 1980). Sea lampreys then migrate downstream to the Great Lakes, where they typically spend 12 to 20 months feeding on teleosts using their newly developed oral disc and piston-like rasping tongue (Applegate 1950). The commencement of the spawning migration, after feeding stage is done, then marks the start of a new cycle.

Since their invasion in the early 20th century, sea lamprey abundances have been controlled to less than 10% of peak abundances due primarily to the application of sea lamprey-specific pesticides ("lampricides"). Thousands of chemicals were tested by the Great Lakes Fishery Commission (GLFC) for their selective effects on larval sea lampreys since 1953, and two chemicals were eventually selected: 3-trifluoromethyl-4-nitrophenol (TFM) and 5,2'-dichloro-4'nitrosalicylaniiide (Bayluscide) (Howell et al. 1980). These two chemicals were applied in conjunction to Great Lakes rivers, starting in 1958, to reduce numbers of larval sea

lampreys and subsequently decrease the number of out-migrating parasites. The application of lampricides has had an observable effect on sea lamprey populations: spawning runs have become smaller, wounding rates on teleosts have dropped, and abundance of important fish stocks have rebounded (Smith and Tibbles 1980). Currently, rivers typically are selected annually for lampricide application based on treatment efficiency; this system is otherwise known as the Empiric Stream Treatment Ranking (ESTR) system (Christie et al. 2003).

Decisions to treat specific river systems around each Great Lakes basin are guided by assessment surveys to characterize larval densities and habitat quality. Streams are regularly surveyed for relative measures of sea lamprey abundance, using the rapid assessment approach, to rank streams for treatment (Hansen and Jones 2008). Backpack electrofishers are used to sample optimal larval habitat, and the number of expected larvae greater than 100 mm in length ("large" larvae) at the end of the growing season is calculated from sampled larvae quantities using known length frequencies and growth rates. Streams are then ranked according to cost per expected large larva killed, and the highest ranked streams are selected for lampricide applications. Larval habitat quantity is also irregularly sampled alongside these surveys. Habitat is sampled by measuring the proportion of larval sea lamprey-specific habitat types along stream transects collected around fixed access points and aggregating these habitat measures to the spatial scale of treatment units (Slade et al. 2003). These measures of habitat can help extrapolate sampled larval densities to total larval quantities across stream reaches.

Dams play a complementary and well-recognized role in sea lamprey control within the Great Lakes. Incidental barriers (*i.e.*, those in place before the invasion of sea lamprey) block sea lamprey from accessing abundant quantities of both spawning and larval habitat in tributaries (Lavis et al. 2003). The presence of effective barriers has a two-fold benefit for sea lamprey

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control by reducing their production from streams and eliminating the need for lampricide

treatment in select systems (*i.e.*, freeing up resources for use in other tributaries). An explicit

strategy of the GLFC in sea lamprey control is the construction of new, purpose-built barriers

and maintenance of existing dams in Great Lakes tributaries (Great Lakes Fishery Commission

2011).

Intentional fragmentation in river systems also plays a useful conservation role in systems

other than the Great Lakes. Purposefully restricting aquatic connectivity within watersheds can

yield multiple benefits, including limiting the spread of invasive species, restricting the dispersal

of new diseases, blocking hybridization between wild and hatchery populations, and stopping

organisms from accessing suboptimal habitats (Rahel 2013). Barriers have been modified or

constructed to specifically block the spread of nonnative species like lake trout, brown trout

(*Salmo trutta*), and rainbow trout in Montana, California, and Arizona, respectively (Avenetti et

al. 2006; D'Angelo et al. 2010; Pister 2010).

Despite these examples for the positive role of barriers, dams can cause more harm than

good to aquatic ecosystems and increasingly are being considered for removal. Correspondingly,

there is growing opportunity and interest in barrier removals across the United States for a

multitude of reasons. First, there is widespread concern over the public safety of existing dam

infrastructure. Approximately 80% of dams identified by the National Inventory of Dams will

be older than the average life expectancy of dams (*i.e.*, 50 years) by 2020 (NRC 1992; ASDSO

2016). Furthermore, hundreds of hydroelectric dams will require relicensing from the Federal

Energy Regulatory Commission, which necessitates the decision to retain or remove the dam

(Pejchar and Warner 2001). Concurrently, there is increasing motivation to increase aquatic

connectivity and restore fish populations, as the declines of several migratory fish populations

have been linked to dams (Limburg and Waldman 2009). These opportunities and motivations, among numerous others, have driven dam removals efforts in Great Lakes states, including Michigan. The Michigan Department of Natural Resources has granted millions of dollars to aid in dam repair and removal, and otherwise assisted in the removal of numerous additional barriers (Michigan Department of Natural Resources 2016)

Both the benefits and costs of barrier removals in regions like the Great Lakes have to be considered in decision-making, and these aspects can be informed by fisheries research. Dams have both positive and negative effects on Great Lakes fisheries due to their role in simultaneously blocking sea lamprey and other desirable, migratory species fish species (*e.g.*, salmonids). The relative magnitudes of these effects, and the expected response of fish populations upon barrier removals, need to be understood before making dam removal decisions. The effects of barrier removals on sea lamprey populations represents an especially pertinent aspect to understand due to their known effects on numerous Great Lakes fish species and a detailed understanding of their population dynamics. An operating model, incorporating both sea lamprey population dynamics and control efficacy, has already been developed to formalize our understanding of this system and represents a potentially useful tool to inform barrier removal decisions (Jones et al. 2009).

This thesis is intended to characterize the likely response of sea lamprey populations, including the future effectiveness of sea lamprey control, to barrier removals in Lake Michigan. Lake Michigan was selected as the focal representative of the Great Lakes based on the detailed population dynamics information available for the system. In chapter 1, I compare the performance of multiple modeling approaches in predicting the quantity of sea lamprey larval habitat upstream of barriers in Lake Michigan tributaries using predominantly catchment-scale

landscape attributes. The availability of larval habitat is an important determinant of recruitment success but is resource-intensive to measure across large spatial extents. Habitat modeling efforts shed light on dominant influences of substrate-based stream habitat in Michigan and may inform future population dynamics modeling. In chapter 2, I apply a modified version of a sea lamprey operating model to evaluate the quantitative response of the Lake Michigan sea lamprey population to both systematic increases in habitat availability and a specific barrier removal case study. In doing so, I assess the influence of modeling assumptions, including habitat quality, habitat use, and alternative management actions, on the expected response, and identify driving factors behind simulated changes in abundance. Population modeling results revealed unexpected influences of life history traits and spatial scale on a species' response to barrier removals and demonstrate the utility of similar modeling efforts to inform future barrier removal decisions.

CHAPTER 1: COMPARISON OF MODEL PERFORMANCE IN PREDICTING REACH-SCALE LARVAL SEA LAMPREY HABITAT ABOVE LAKE MICHIGAN BARRIERS

INTRODUCTION

Quantitative measures of stream habitat features, such as those describing substrate characteristics, are often necessary for estimating potential fish production within rivers. For example, the amount of larval habitat, physically defined as substrate dominated by fine particles, is an established driver of Great Lakes sea lamprey (*Petromyzon marinus*) recruitment success (Jones et al. 2003; Dawson and Jones 2009; Jones et al. 2009). However, physical habitat measurements are often unavailable and difficult to collect at the appropriate extent and resolution for management application, so an alternative is to develop predictive models capable of estimating habitat quantities in streams.

The use of predictive models to estimate measures of stream habitat can save resources that otherwise would be required for physical sampling. Stream habitat modeling typically draws upon the hierarchy theory of streams, in which large-scale catchment characteristics constrain local physical, chemical, and biotic components of stream, to predict fine-scale habitat features relevant to aquatic resource management (Curry 1972; Hynes 1975). These established hierarchies can be very useful in predicting local stream habitat because it can be difficult to measure fine-resolution habitat features, like sea lamprey larval habitat, across broad spatial extents (Brenden et al. 2007). Conversely, large-scale catchment predictors, including predictors like land use and topography, are often readily available in databases like the National Land Cover Database (Multi-Resolution Land Characteristics Consortium 2015). Many studies have successfully applied hierarchy theory for local stream habitat predictions, including substrate composition, using various catchment-scale predictors (Jeffers 1998; Mugodo et al. 2006; Frappier and Eckert 2007; Brenden et al. 2007; Wang et al. 2013).

The quantification of sea lamprey larval habitat in stream reaches above dams in the Great Lakes basin is a particularly important issue that can be informed by predictive modeling. Sea lampreys in the Great Lakes are an invasive species predominantly controlled by the application of selective pesticides, specifically 3-trifluoromethyl- 4'-nitrophenol (TFM) and 2', 5-dichloro-4'- nitrosalicylanilide (Bayluscide), to streams to kill the resident larval sea lamprey (Smith and Tibbles 1980). Dams also play a key role in sea lamprey control by blocking lampreys from sections of stream that would otherwise provide additional spawning and larval habitat area (Hunn and Youngs 1980). These same dams, however, are being considered for removal to improve public safety and enhance fishery resources. Removal of dams could greatly increase the amount of available habitat (Lavis et al. 2003) and possibly decrease the effectiveness of current control efforts if funds available for lampricide treatments are constrained. Knowledge of sea lamprey population responses to dam removals is needed to allow more explicit cost-benefit analyses to inform decisions on barrier removals. Quantifying the amount of available larval habitat above dams, as an important driver of recruitment success, is needed to predict the overall response of sea lamprey populations to dam removals.

The Great Lakes Fishery Commission (GLFC) has conducted habitat sampling for larval sea lamprey in currently infested stream reaches, in which they quantify the proportion of different habitat categories based on substrate composition along stream transects (Larval Assessment Work Group 2013). Larval habitat is divided into three primary categories (Type I, II, and III), among which only Type I and II habitat are considered suitable for larvae due to the presence of fine sediments for burrowing. More specifically, Type I, II, and III habitat are defined as mixtures of fine sands and organic matter, medium to coarse shifting sands, and hard-packed surfaces (*e.g.*, bedrock, gravel, hardpan clay), respectively (Applegate 1950; Slade et al.

2003). Type I habitat was observed to contain 93% of sampled sea lamprey larvae in Great

Lakes tributaries and has been found to supports significantly higher larval densities than Type II

(Mullett 1997). Because sea lamprey are not present in stream reaches above effective lamprey

barriers, little sampling has been conducted by the GLFC to characterize larval habitat in these

areas. Although previous studies have attempted to predict larval sea lamprey habitat using a

combination of river and landscape features (Neeson et al. 2007; Neeson et al. 2012), none have

developed models with the intent to predict habitat in new spatial extents, using landscape-scale,

widely available GIS-derived covariates.

Large-scale landscape predictors and fine-scale habitat elements are measured at very

different scales; hierarchical models are particularly well-suited to handling these spatial

discrepancies. Hierarchical models, also known as multilevel models, are a generalization of

linear regressions, in which model coefficients themselves are modeled with distinct parameters

(Gelman 2006a). The incorporation of random effects in these models, in which spatial scales

can be treated as nested levels, allow for prediction outside of the existing spatial units or levels;

this is a valuable feature for predicting habitat in areas outside of the data extent. Random

effects represent "a random sample of a larger set of potential effects" instead of representing

"all possible levels of a factor" (Wagner et al. 2006). These hierarchical models can be flexibly

implemented in a Bayesian framework, which also allow for probabilistic interpretation of

results (Midway et al. 2014). Multilevel models are therefore suitable for modeling transect-

level sea lamprey habitat features based on reach-level landscape predictors.

Proportional data can also be difficult to model using traditional modeling techniques.

Sea lamprey habitat data are reported as proportions; a logit transformation is commonly used to

re-scale proportion data to allow estimation within a linear modeling framework (Warton and

Hui 2011). An extension of the logit transformation is beta regression, based on the beta distribution; this approach is suited to model response variables that take values between 0 and 1 (Ferrari and Cribari-Neto 2004). With a beta regression, a link function (typically logit, but sometimes probit or cloglog) connects the response data to the explanatory variable, which are then modeled assuming a beta distribution (Liu and Kong 2015) An extension of the beta regression, namely zero/one inflated beta regression, is useful for cases where zeroes and ones are common in the response variable data.

Additional problems in predictive modeling include incorrectly assuming linear relationships exist between dependent and independent variables and overfitting from an excess of predictor variables. Nonlinearity and thresholds can be expected in fluvial geomorphology, wherein stream features are simultaneously affected by interacting factors at a multitude of spatial and temporal scales (Shreve 1979). Generalized additive modeling using component-wise gradient boosting is an emerging method to avoid overfitting data and allow nonlinear relationships among predictor and response variables (Hofner et al. 2014). Additive models, introduced by Hastie and Tibshirani (1986), allow for smooth, nonlinear, component-wise fitting of predictors to response data using specified linear components. Pairing additive modeling with component-wise gradient boosting further allows for implicit variable selection by iteratively improving the model one predictor variable at a time (Friedman 2001; Hofner et al. 2014). This modeling approach was successfully applied in Wang et al. (2013) to predict multiple facets of fine-scale stream habitat, including substrate composition.

I used larval habitat data collected by the GLFC between 2004 and 2008 and a wide range of potential landscape-scale covariates attributed to stream reaches to predict the amount of Type I and Type II larval habitat (*i.e.*, suitable burrowing habitats) in stream reaches upstream

of existing dams. I first evaluated the ability of three modeling approaches, fit independently to the original Type I and Type II habitat proportion response data, to predict both habitat types by comparing their model fit, important predictor variables, and predictive capacity: 1) hierarchical linear regression in a Bayesian framework using logit-transformed response variables, 2) hierarchical zero/one inflated beta regression in a Bayesian framework using the raw proportional response variables, and 3) generalized additive modeling, in a Gaussian likelihood framework, with component-wise gradient boosting using the logit-transformed response variables.   The predictive capacity of each modeling approach was assessed using independent, out-of-sample data collected in Lake Michigan tributaries, upstream of existing dams, in the summer of 2016. Following these comparisons, I then evaluated the ability of the generalized additive model to predict Type I and Type II habitat when the model was fit to two new, derived response variables: the total larval habitat proportion (*i.e.*, the sum of Type I and Type II habitat proportions) and the ratio between the two habitat types. Combining the two new predicted response variables represents a unique way to predict individual habitat quantities, in which information is shared across the two response variable datasets.

The successful quantification of larval habitat in stream reaches upstream of relevant barriers can inform simulations of sea lamprey response to dam removals and has the potential to subsequently improve barrier removal decisions. Furthermore, an improved understanding of the driving landscape influences on sea lamprey habitat can guide future habitat sampling and estimation.

METHODS

Historical Data

Larval habitat data were collected by GLFC field crews between 2004 and 2008 according to their current larval assessment sampling protocol (Larval Assessment Work Group 2013). Within each treatment unit, defined by the GLFC as a section of stream where a unified lampricide treatment can be applied, field crews sampled up to six access points, which were simply points along the river where crews could physically access the water. Sampling locations were broadly distributed around sea lamprey-infested watersheds in the Lake Michigan drainage basin (Fig. 1.1). At each access point, control agents sampled two upstream and two downstream cross-sectional transects, and divided the total transect length of each into segments of one of the following three aquatic habitat types, identified using visual and tactile assessment: Type I, Type II, and Type III. The proportion of Type I and Type II habitat along each transect was calculated from these distances and used as the primary response variable in this analysis. The GLFC uses total larval habitat areas, calculated from these surveys as the product of treatment unit length, average width, and average habitat proportions, in combination with larval abundance surveys to estimate total larval abundance within treatment units and inform control efforts.
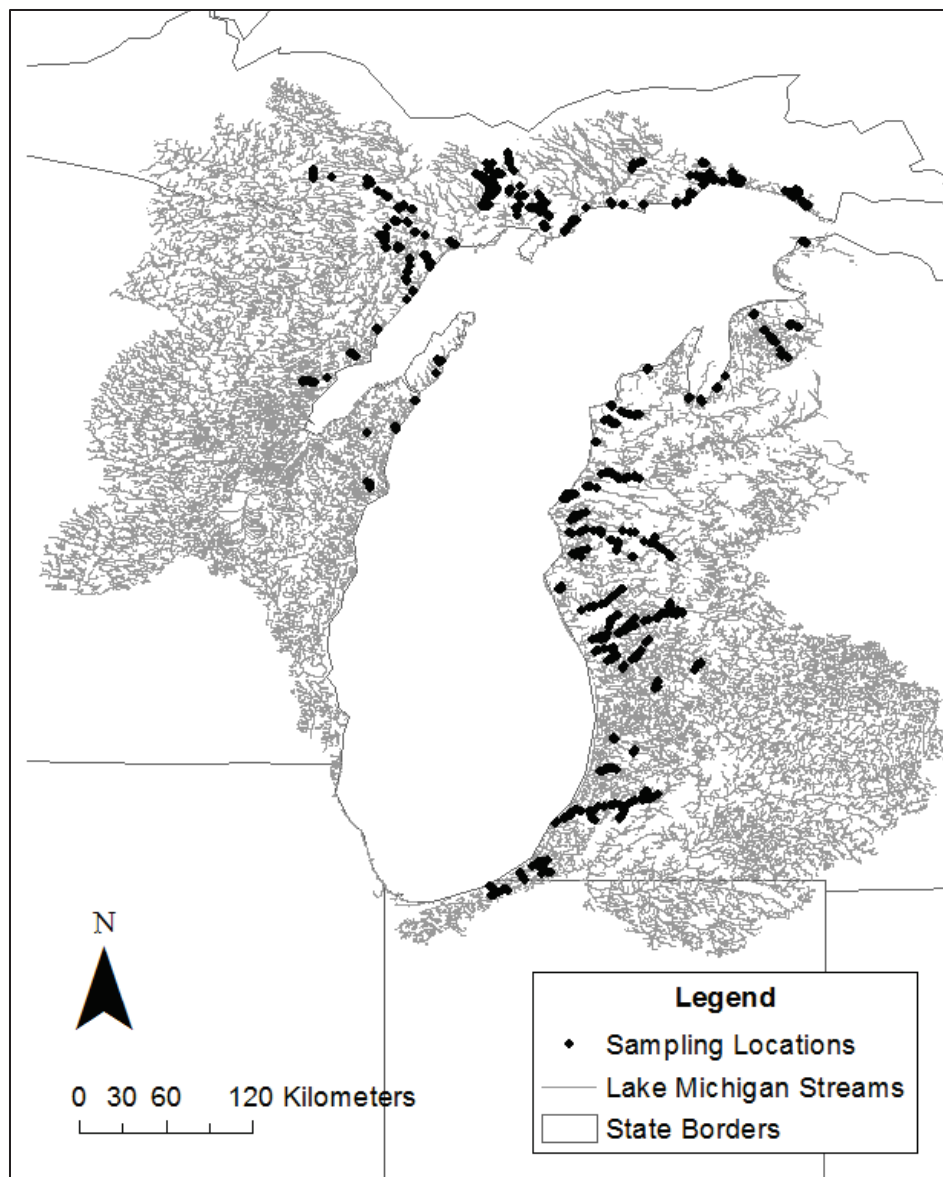
Figure 1.1: Distribution of GLFC sampling locations around the Lake Michigan drainage basin for the 2004-2008 time period.

All landscape covariate data were obtained from a spatial framework developed by Wang et al. (2011), in which landscape and stream network variables were assigned to stream reaches, as well as their associated catchments and buffers, across the conterminous United States using the National Hydrography Dataset Plus (1:100,000 scale; http://www.horizon-systems.com/nhdplus). A wide range of variables were selected to capture aspects of climate, elevation, geology, soil, land cover, groundwater contribution, as well as river size and connectivity. These variables were attributed to five possible spatial scales: the reach, local buffer (LB), network buffer (NB), local catchment (LC), and network catchment (NC). Within this spatial framework, a reach is defined as an inter-confluence section of a stream, a buffer as the portion of the landscape within a set distance of the reach (90 m in this case), and a catchment as the entirety of upstream land draining into the lowermost portion of a reach (Brenden et al. 2006). Local and network refer to how the buffers and catchments are bounded; local buffers and catchments only extend to the boundaries with the nearest neighboring reaches, and network buffers and catchments are the totality of all buffer or catchment area upstream of the reach in question (Brenden et al. 2006).

Because measures of the predictor variables were attributed to NHDPlus-defined reaches and not those defined by the GLFC, the habitat measurements associated with transects were re-assigned to NHDPlus-defined reaches using GPS coordinates recorded for each downstream/upstream transect pair. This work was performed in ArcMap (PC ARC/GIS Version 10.0. Environmental System Research Institute, Redlands, California, http://www.esri.com/software/arcgis).

Landscape Variable Reduction Techniques

Variable reduction of the initial candidate set of approximately 300 variables included the following steps: 1) remove variables with no observed variation, 2) aggregate detailed categorical variables (*e.g.*, attributes like land cover, surficial lithology) into more commonly-used, functional predictors, 3) remove variables with no proposed mechanistic relationship to stream sediment composition, 4) choose just one spatial scale per variable where applicable (LB, NB, LC, NC), and 5) remove collinear variables. The selection of combined variable categories, removal of variables with no proposed relationships to sediment composition, and choice of spatial scale were based on available scientific literature, professional judgment by experts in the field of ecohydrology, and best personal judgment. Assessment of collinearity was conducted using a generalized variance inflation factor (GVIF) analysis applied to the logit-transformed Type I and Type II response variables (Fox and Monette 1992), where modified GVIF values ($GVIF^{1/2p}$) greater than 3, as a proxy for VIF, indicated the presence of troublesome collinearity (Zuur et al. 2010). GVIF was used in place of the more traditional VIF due to the presence of categorical variables in the analysis. The goal of variable reduction was to obtain a manageable set of uncorrelated covariates, supported by personal and professional judgment, to predict sea lamprey habitat.

Pre-Modeling Data Transformations

Prior to fitting the hierarchical logit regression and generalized additive models to the individual Type I and Type II responses, I transformed the proportion data for both habitat types using the logit-transformation recommended by Warton and Hui (2011). Because the log-based

transformation cannot inherently handle the presence of zeroes and ones in the dataset, the

following modified logit-transformation was used:

$$log \frac{(x+M)}{(1-x+M)}$$

where x is the proportional response data and M is the minimum non-zero value in the response

dataset being transformed. In contrast, untransformed proportion data were used in fitting the

zero/one-inflated beta regression model.

The same modified logit-transformation was applied to the transect-specific total larval

habitat proportions, which were simply the sum of transect-specific Type I and Type II habitat

proportions. The ratio of Type II to Type I habitat proportions was calculated using a similar

modification to handle zeroes and ones; the minimum non-zero value in each response dataset

was added to the Type I and Type II habitat proportions before the quotient calculation.

All landscape covariates were centered and scaled to increase the ease of model

convergence and to facilitate coefficient comparison within and among models (Kéry 2010).

Fitting the Original Type I and Type II Response Data

Hierarchical Logit Regression Model

I constructed this model with three levels in the hierarchy: transect-scale habitat

proportion measurements, the random effect of access point, and the random effect of reach. I

included the effect of access point to account for the fact that transects were not randomly

sampled throughout each reach; instead, transects were systematically sampled within "clusters"

(*i.e.*, around the access points). The random effect of access point helps accounts for the

expected higher similarity among transects within these "clusters" than among transects from

separate clusters. Access point was nested within reach to match the spatial scale of the

landscape covariates, and the linear regression of the thirteen covariates was applied to the

random effect of reach (variables are defined in Table 1.1):

Hierarchy Level 1 (Transect):

$$y_{ijk} \sim Normal\ (\alpha_{1_{jk}}, \sigma_1{}^2)$$

Hierarchy Level 2 (Access Point):

$$\alpha_{1_{jk}} \sim Normal(\alpha_{2_k}, \sigma_2{}^2)$$

Hierarchy Level 3 (Reach):

$$\alpha_{2_k} \sim Normal(\mu_{1_k}, \sigma_3{}^2)$$

$$\mu_{1_k} = \beta_1 * P_{1_k} + \beta_2 * P_{2_k} + \ldots + \beta_n * P_{n_k} + \alpha_p + \alpha_3$$

The model was constructed in WinBUGS (Lunn et al. 2000) and run from R (R Core

Team 2016) using the R2WinBUGS package (Sturtz et al. 2005, Running 'WinBUGS' and

'OpenBUGS' from 'R' / 'S-PLUS', version 2.1-21, https://cran.r-project.org/package=coda).

The full WinBUGS script for hierarchical Bayesian model used to predict Type I habitat is

provided in Appendix A.

Table 1.1: Descriptive key of model parameters describing the Bayesian hierarchical logit regression and beta regression models.

Variable	Description
	Logit Regression
i	Transect-scale
j	Access point-scale
k	Reach-scale
y	Logit-transformed transect-scale habitat measurement
α_1	Random effect of access point, nested within reach
α_2	Random effect of reach
α_3	Linear regression intercept
μ_1	Mean reach effect
β	Slope coefficient for continuous predictor n
P	Value for continuous predictor
n	Number of continuous predictors
α_p	Coefficient for dam presence
p	Categorical predictor levels
σ_1^2	Unexplained model variance
σ_2^2	Within access point variance
σ_3^2	Within reach variance
	Beta Regression
i	Transect-scale
j	Reach-scale
y	Transect-scale habitat measurement
p_{ij}	Probability $y_{ij}=0$
q_{ij}	Conditional probability $y_{ij}=1|y_{ij}\neq0$
$\alpha_{ij1}, \alpha_{ij2}$	Beta distribution shape parameters
μ_{ij}	Beta distribution mean
v_{ij}	Beta distribution variance
β	Slope coefficient for continuous predictor n
P	Value for continuous predictor
n	Number of continuous predictors
α_p	Coefficient for categorical predictor
p	Categorical predictor levels
$\alpha_1, \alpha_3, \alpha_4$	Regression intercept values
α_{2j}	Random effect of reach
μ_1	Mean reach effect
σ_1^2	Within reach variance

In running this model, I used uninformative normal priors (N ~ [0, 1000]) for all slope, fixed effect, and intercept terms. Similar priors have been used in other hierarchical, linear modeling approaches (Thomas et al. 2006; Midway et al. 2015). Vague uniform priors were applied for the three standard variance terms (Unif ~ [0, 20]), as recommended by Gelman (2006b) for hierarchical models.

Recommended chain length was assessed by running a 1000 iteration chain with no burn-in and applying Raftery and Lewis' diagnostics. Raftery and Lewis' convergence diagnostics indicated the necessary chain and burn-in length for each evaluated model parameter to achieve a certain probability of obtaining a model estimate within some margin of error around a set quantile; I specified a 95% probability, 5% margin of error, and 50% quantile in my analyses (Cowles and Carlin 1996). Following the burn-in and chain length recommendations from the Raftery and Lewis' diagnostics, I ran the full model and assessed model convergence using Geweke's criterion, in which the absolute value of a z score greater than 1.96, from the comparison between the means of the first 10% and last 50% of the MCMC chain for every evaluated parameter, indicated a failure to converge at the p=0.05 level of significance (Geweke 1992). I also performed visual examinations of the parameter trace and autocorrelation plots. I evaluated the posterior probability distribution for every intercept, fixed effect, and slope parameter, in addition to all variance terms and reach-scale model predictions. MCMC chain diagnostics were assessed using the coda package (Plummer et al. 2015, Output Analysis and Diagnostics for MCMC, version 0.18-1, https://cran.r-project.org/package=coda).

Hierarchical Zero/One Inflated Beta Regression Model

I intended the hierarchical zero/one inflated beta regression to account for the influence of extreme response variable values (*i.e.*, zeroes and ones), model the response using a non-

normal distribution, and account for the random effect of reach. In fitting the zero/one inflated

beta regression for the untransformed proportion data, I included the same set of covariates as

those applied in the hierarchical logit regression model, as well as the random effect of reach. I

also allowed for separate intercept terms to account for the zeroes and ones via zero/one

inflation. Unlike the logit regression, the random effect of access point was not accounted for

and predictors were fit to response data at the transect scale; these changes were due to inherent

limitations in the R package used to fit the model. The model equations for this beta regression

with zero/one inflation and the random effect of reach, modified from Liu and Kong (2015), are

provided below (variables are defined in Table 1.1):

<p style="text-align:center"><u>Hierarchy Level 1 (Transect):</u></p>

$$y_{ij} = \begin{cases} p_{ij} & if\ y_{ij} = 0 \\ (1 - p_{ij})q_{ij} & if\ y_{ij} = 1 \\ (1 - p_{ij})(1 - q_{ij})Beta(\alpha_{ij1}, \alpha_{ij2}) & if\ y_{ij} \in (0,1) \end{cases}$$

$$\mu_{ij}^{(0,1)} = \alpha_{ij1}(\alpha_{ij1} + \alpha_{ij2})^{-1}$$

$$v_{ij} = \alpha_{ij1} + \alpha_{ij2}$$

$$logit(\mu_{ij}^{(0,1)}) = \beta_1 * P_{1j} + \beta_2 * P_{2j} + \dots + \beta_n * P_{jn} + \alpha_1 + \alpha_{jp} + \alpha_{2j}$$

$$logit(p_{ij}) = \alpha_3$$

$$logit(q_{ij}) = \alpha_4$$

<p style="text-align:center"><u>Hierarchy Level 2 (Reach):</u></p>

$$\alpha_{2j} \sim Normal(\mu_1, \sigma_1^2)$$

Default diffuse normal priors (N ~ [0,1000]) were used for all model parameters except

for the variance terms; uniform priors with the model's default distribution (Unif ~ [0, 20]) were

used for the variance parameters. Recommended chain length and initial convergence were

<p style="text-align:center">22</p>

again assessed using Raftery and Lewis' convergence diagnostics run on two separate 1000 iteration chains with no burn-in. Following the burn-in and chain length recommendations from the Raftery and Lewis' diagnostics, I assessed final model convergence using Geweke's criterion and examination of the trace and autocorrelation plots.

The model was run from R (R Core Team 2016) using the zoib package (Liu and Kong 2015, Bayesian Inference for Beta Regression and Zero-or One Inflated Beta Regression, version 1.3.3, https://cran.r-project.org/package=zoib), which runs the MCMC chain using JAGS software (Plummer 2014).

Boosted Generalized Additive Model

For this model, I assumed a Normal distribution for the logit-transformed habitat values, and correspondingly applied a normal negative log-likelihood loss function within the model framework. The same landscape predictors as in the previous models were applied in the boosted generalized additive model; all variable reduction was conducted during the iterative model fitting. No random effects were included due to the model's inability to separate random and fixed effects in the implicit variable reduction. The continuous covariate effects were incorporated using additive P-spline base-learners (typical in generalized additive modeling) with the default 4 degrees of freedom and 20 interior knots; categorical effects were modeled using ordinary least squares base-learners (Schmid and Hothorn 2008; Wang et al. 2013). Following the recommendations of Hofner et al. (2014), I determined the optimal number of boosting iterations (m_{stop}) in model fitting by fitting the full model ($m_{stop}=100$), applying 10-fold cross-validation, and identifying the m_{stop} value that minimized predictive risk. The model was run from R (R Core Team 2016) using the mboost package (Hofner et al. 2016, Model-Based Boosting, version 2.6-0, https://cran.r-project.org/package=mboost).

Fitting the Derived Response Variables

I fit the same landscape predictors for Type I habitat models to the total larval habitat

proportions and ratio response variables within a generalized additive model framework. For the

total larval habitat response, I again assumed a Normal distribution for the logit-transformed

values and applied a normal negative log-likelihood loss function. Based on the observed

distribution of the ratio between the two habitat types, I decided to fit a Laplace (*i.e.*, double

exponential) loss function to best characterize the ratio-based response variable. The Laplace

distribution exhibits exponential decline moving away from zero in a positive direction and, as

such, can be successfully applied to long-tailed error distributions (Hofner et al. 2014).   The

same base-learners and procedure to identify an optimal number of boosting operations, as

described for fitting the individual habitat response data, were applied in these two models.

After fitting the model and generated predictions for derived quantities, individual predictions

for Type I and Type II habitat were calculated by dividing the predicted total larval habitat

proportion by the appropriate Type II to Type I ratio estimate.

Assessing Variable Influence and Model Fit

Variable importance and direction of covariate influence for the logit regression and

zero/one inflated beta regression models were assessed by examining the coefficient posterior

distribution, and specifically the 95% highest posterior densities (HPD). Highest posterior

density intervals reflect the smallest range of coefficient values that contains a specified

percentage of the coefficient estimates generated from the MCMC chain, and can be applied to

determine variable importance in a similar manner to frequentist confidence intervals. I chose to

interpret coefficients with a 95% HPD that did not overlap zero as a strong predictor of larval

habitat. The coefficient sign (positive/negative) determined the direction of variable influence.

For the boosted generalized additive models, I assessed each variable's relative importance in driving model fit using selection frequencies, representing the number of iterations in the model fitting process in which each variable was selected as the best predictor. The direction of variable influence was assessed through the use of partial effects plots, which illustrate the nonlinear effect of each variable on the response with all other variables held at a constant value.

Model fit was assessed by comparing observed and predicted habitat values, on both the transect- and reach-scale larval habitat proportions. The transect scale is the original scale of our models' response variables, and assessing model fit on this scale reflects the realized amount of variation among transects within each reach. Model fit was also assessed on the reach scale, as this the scale of interest for future habitat predictions; observed reach-scale habitat proportions were obtained by calculating the simple average of all available transect-scale observations within each reach. For the hierarchical logit regression and zero/one inflated beta regression models, habitat predictions were generated using just the mean of the model-estimated coefficients and the original model data. Random effects were not incorporated because future habitat predictions, in stream access points or reaches outside of those used to fit the models, can only be calculated using these fixed coefficients. Habitat predictions for the boosted generalized additive model were obtained using the package's built-in prediction functionality.

Quantification of model fit for both habitat types was achieved by fitting a linear regression model between observed and predicted values, and calculating the intercept, slope, and model fit (R^2; equivalent to the squared Pearson's correlation coefficient between the two datasets). I also performed regression-based equivalence tests to assess whether intercept and

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slope terms from a linear regression fit to the observed and predicted data fell within some specified range around the expected value (Robinson et al. 2005). The intercept test specifically assessed whether the means of the observations and predictions are equivalent; the slope test assesses whether the slope term is equal to the expected value of 1. I chose a relatively broad equivalence range of 50% due to the large degree of stochasticity and dynamism typical in in-stream habitat features; a similar value was applied in Wang et al. (2013). Finally, based on the recommendation of Piñeiro et al. (2008), I calculated the root mean squared deviation (RMSD) for the association between the observed and predicted larval habitat proportions; lower RMSD values indicate better model fit. The RMSD correctly assessed the deviation of predicted values from the expected 1:1 line between observed and predicted values, as opposed to similar measures like mean squared error (MSE).

Evaluating Model Predictive Ability on Out-of-Sample Data

As the modeling results of this study were intended to predict habitat quantities in stream reaches upstream of dams, and more generally in spatial extents not included in the model building dataset, I conducted habitat sampling in stream reaches upstream of existing dams in order to create a dataset for external model validation. This dataset allowed me to assess whether the models can successfully predict in these upstream systems, the habitats of interest for this study. Sampling occurred between July 18, 2016 and August 11, 2016.

Sampling sites were determined by first selecting river systems in the Lake Michigan with the following characteristics: (a) contained a sea lamprey barrier blocking an extensive amount of potential lamprey habitat, (b) were previously sampled sometime between 2004-2008 downstream of the dam, (c) were listed as a high priority by sea lamprey control agents in the

GLFC's Barrier and Larval Control Task Forces, and (d) represented the diverse spatial extent captured by the original model dataset. A diverse spatial extent was crucial to capture the full range of covariate variability within the model training dataset. Six streams were eventually selected for sampling: Twin River, Peshtigo River, Whitefish River, Boardman River, Pentwater River, and Kalamazoo River. The Twin and Peshtigo Rivers are in Wisconsin, the Whitefish River is in Michigan's Upper Peninsula, and the remaining three are in Michigan's Lower Peninsula (Fig. 1.2).
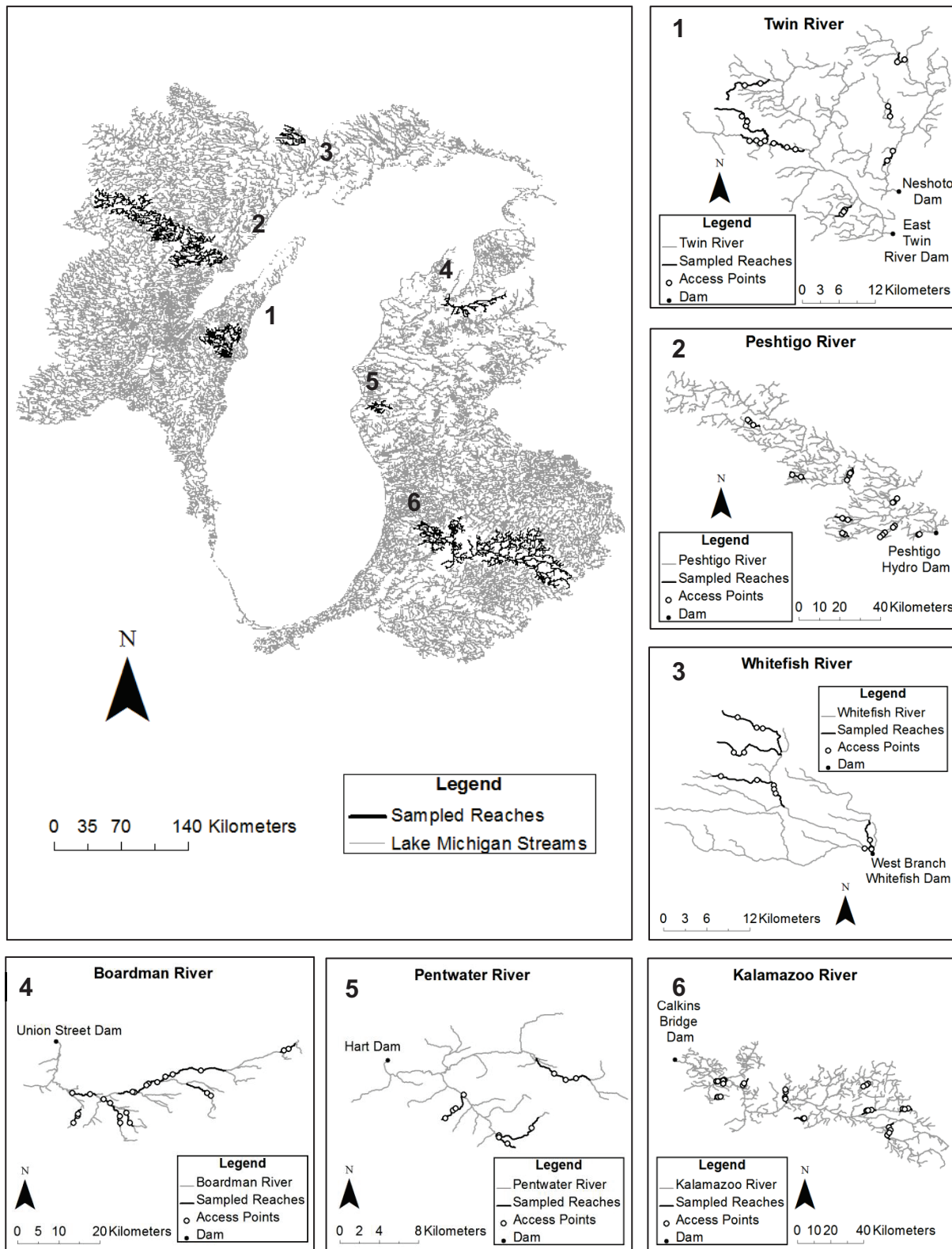
Figure 1.2: Distribution of 2016 sampling effort across the Lake Michigan basin, and within each of the sampled river systems.

Based on resampling simulations of the 2004-2008 transect data (A. Jensen, Michigan State University, East Lansing, Michigan, unpublished analysis), four access points were determined to be desirable to capture the true expected amount of Type I and Type II habitat within a given reach. This desired number of access points was selected by qualitatively assessing the trade-off between minimizing the observed coefficient of variation for observed reach-scale Type I and Type II habitat quantities, assuming that four transects were taken at each access point, and sampling a maximum number of stream reaches.

For each of the six river systems, I aimed to sample a minimum of eight randomly selected NHD reaches, upstream of the first effective lamprey barrier, with each reach having at least four accessible road crossings. Low crossing densities and inaccessible stream crossings in some systems necessarily resulted in stream reaches with less than four access points; a minimum of two access points and eight transects were required to include reach data in model validation. Furthermore, some reaches, when examined in the field, were stagnant (lentic), dry, or otherwise inaccessible; when feasible, these reaches were replaced by opportunistic sampling of nearby stream reaches.

The in-stream sampling protocol followed that of the GLFC Sea Lamprey Control Board (Larval Assessment Work Group 2013), with one primary exception. If either upstream or downstream transects could not be measured at an access point, compensatory additional transects were collected in the accessible direction; a maximum of four transects were collected at any one access point. I then used these data to assess the ability of each modeling approach to predict reach-scale Type I and Type II habitat quantities using available landscape covariate data. The same metrics used to evaluate model fit (*e.g.*, RMSD, equivalence testing, R^2) were used to compare predictive capacity.

RESULTS

Data Transformations

The logit transformation established approximately normal distributions in the larval habitat quantity variables between extreme high and low values, but did not account for the dominance of these extreme values on both ends of the distribution (*e.g.*, zeroes and ones in the original proportional data) (Fig. 1.3). The habitat ratio response had a strongly right-skewed distribution (Fig. 1.3d).

Variable Reduction

At each of the four covariate spatial scales, I aggregated 15 land cover and surficial lithology variables into just 5 covariates following recommendations of local experts in Lake Michigan limnology (Table 1.2; D. Infante, Michigan State University, East Lansing, MI, personal communication, 2015; D. Lusch, Michigan State University, East Lansing, MI, personal communication, 2015). Following all other variable reductions, sixteen variables were finally considered for model inclusion prior to analysis of collinearity; this analysis resulted in the removal of three covariates for each habitat type (Table 1.3). The final variable set for each habitat type therefore consisted of the following thirteen variables: agriculture land cover, impervious land cover, natural vegetation land cover, wetland land cover, catchment area, catchment elevation, catchment slope, lithology (fine or coarse for Type I and II habitat, respectively), precipitation, soil permeability, groundwater index, road crossing density, and dam presence.
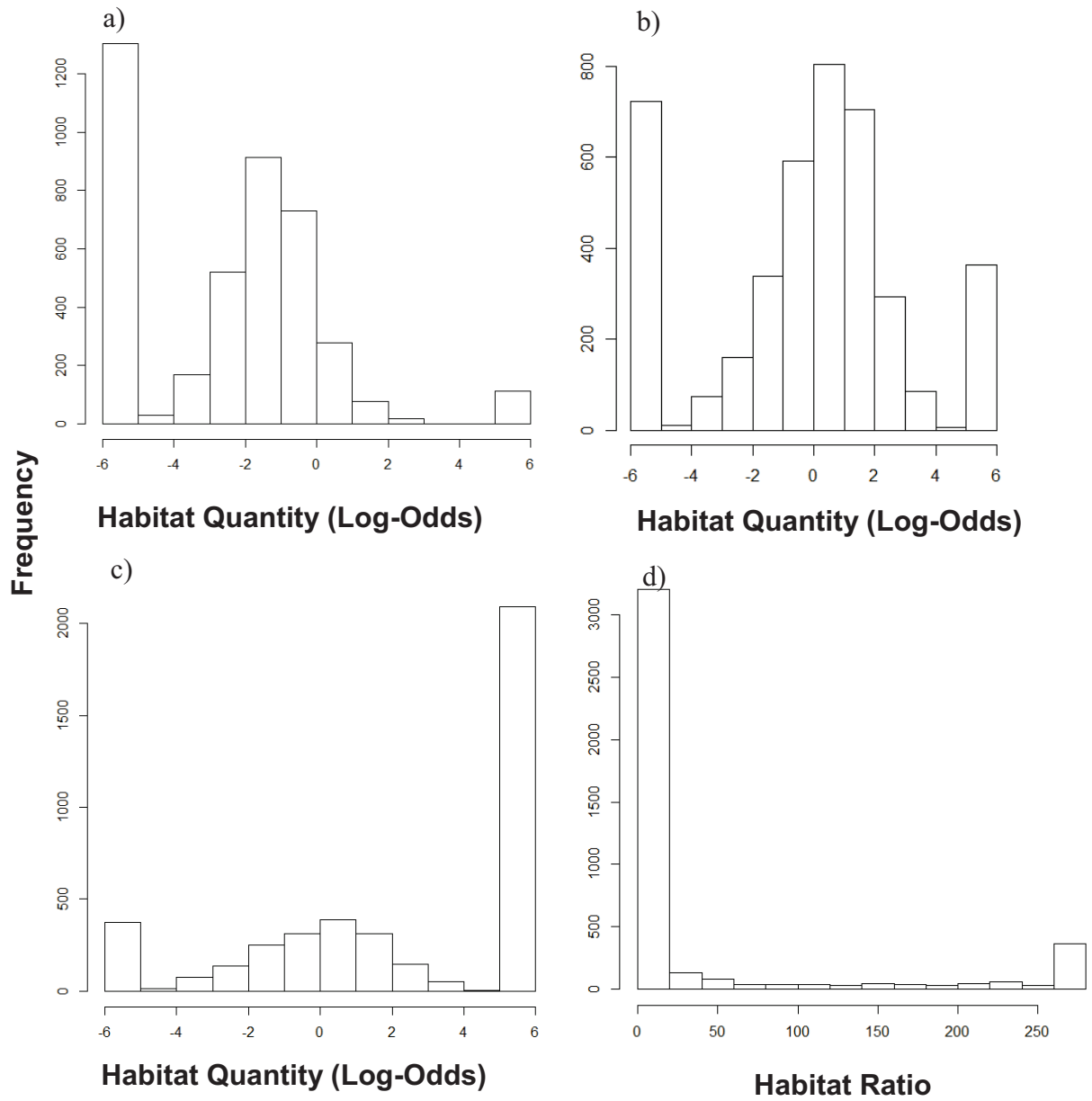
Figure 1.3: Distributions of transect-scale values of logit-transformed Type I (a), Type II (b), and total larval habitat (c) proportions, in addition to the distribution of Type II to Type I habitat proportion ratios (d).

Table 1.2: Summary of aggregated class-based predictor variables considered for model inclusion.

Aggregated Variable	Constituent Variables	Justification
% Agriculture	Pasture/Hay Cultivated Crops	Agricultural land is expected to serve as source of fine sediments
% Natural Vegetation	Deciduous Forest Evergreen Forest Mixed Forest Shrubland - Shrub/Scrub Herbaceous / Grassland	Riparian buffer zones are known to filter run-off, including sediments
% Wetland	Woody Wetlands Emergent Herbaceous Wetlands	Wetlands, similar to riparian zones, can filter run-off and serve as a sediment trap
% Fine Lithology	Glacial Till - Clayey Glacial Till - Loamy Glacial Lake Sediment - Fine	Small substrate lithology is expected to serve as a source of fine sediments and inhibit groundwater loading
% Coarse Lithology	Glacial Outwash - Coarse Glacial Lake Sediment - Coarse Eolian Sediment - Coarse	Coarse substrates are expected to serve as a source of coarser sediments and promote groundwater loading

Table 1.3: Final set of predictors considered for modeling. Bolded terms indicate those variables not considered collinear according to the GVIF analysis, and therefore included in the final modeling efforts. LB, NB, LC, NC, and reach refer to local buffer, network buffer, local catchment, network catchment, and reach scales, respectively. Further details on the resolution and year of creation for these predictor datasets can be obtained in Wang et al. 2011.

Variable	Unit	Scale
Agricultural Land Cover	%	NC
Impervious Surface Land Cover	%	NC
Urban Land Cover	%	NC
Wetland Land Cover	%	NC
Catchment Area	km^2	NC
Mean Annual Precipitation	$mm\ yr^{-1}$	NC
Upstream Dam Presence within 100 km	Binary (Y / N)	NC
Catchment Slope	°	LC
Mean Elevation	m	LC
Coarse Surficial Lithology (Type II)	%	LC
Fine Surficial Lithology (Type I)	%	LC
Soil Permeability Rate	$100*(inches\ hr^{-1})$	LC
Groundwater Contribution to Baseflow	%	LC
Road Crossing Density by Stream Length	$\#\ km^{-1}$	LC
Natural Vegetation Land Cover	%	LB
Stream Order	Categorical	Reach
Stream Type	Categorical	Reach

Final Dataset Size

Only response data with corresponding data for all thirteen independent variables were included in the final modeling efforts. This resulted in 4153 transect-scale measurements for both Type I and Type II habitat. These 4153 transects represented a total of 941 unique access points and 428 NHD stream reaches; these groupings were used in the hierarchical modeling and the assessment of model fit at the stream reach-scale.

Convergence Diagnostics

Based on both the initial and final convergence diagnostics, the logit and beta regression models for both habitat types appeared to converge satisfactorily. The Raftery and Lewis' diagnostics suggested varying chain lengths across the habitat types and models, but consistently low recommended burn-in values. To ensure adequate model convergence, I applied the same 10,000 iteration chain with a 1,000 iteration burn-for Type I and Type II habitat in the logit regression model. Because model computation took significantly more computing power and time, I was less liberal in total chain length for the zero/one inflated beta regression model: I chose to run a 5,000 iteration, 500 burn-in model for Type I habitat and an 8,000 iteration, 500 burn-in model for Type II habitat.

For the resulting final models, Geweke's convergence diagnostics for all intercepts, slope coefficients, and variance terms indicated that all parameters converged satisfactorily; the worst value across both modeling approaches and habitat types was -1.764, safely below the threshold value of 1.96. There were no apparent issues with autocorrelation, as the observed degree of autocorrelation for all model variables decreased either immediately or regularly with increasing

lag; examinations of parameter trace plots also revealed reasonably consistent mixing for all parameters over the chain length.

Variable Coefficients

I used the distribution mean and 95% highest posterior density (HPD) intervals to evaluate the relative influence of each covariate coefficient among the logit and beta regression modeling approaches and two habitat types (Fig. 1.4). I selected the mean as the measure of central tendency based on the highly symmetric parameter distributions and associated 95% HPD intervals. Among the coefficients for both Type I and Type II habitat, there was a noticeable difference between those generated from the logit and beta linear regressions; coefficients generated from the beta regressions tended to have less extreme mean values and narrower 95% HPD intervals (Fig. 1.4). This difference resulted in different predictors considered important from each modeling approach. For Type I habitat, based on the 95% HPD intervals, the logit linear regression indicated that six covariates (agriculture land cover, natural vegetation land cover, catchment area, fine lithology, groundwater index, and dam presence) were strong predictors; only four (natural vegetation land cover, catchment area, fine lithology, and dam presence) had 95% HPD intervals that did not overlap with zero for the beta regression. For Type II habitat, logit regression indicated that eight covariates (agriculture land cover, wetland land cover, catchment area, catchment slope, coarse lithology, precipitation, groundwater index, and road crossing density) were important predictors; beta regression indicated that seven covariates (catchment area, catchment elevation, catchment slope, coarse lithology, precipitation, soil permeability, and groundwater index) were strong predictors. The directions of covariate influence, however, were highly similar between the two modeling approaches.

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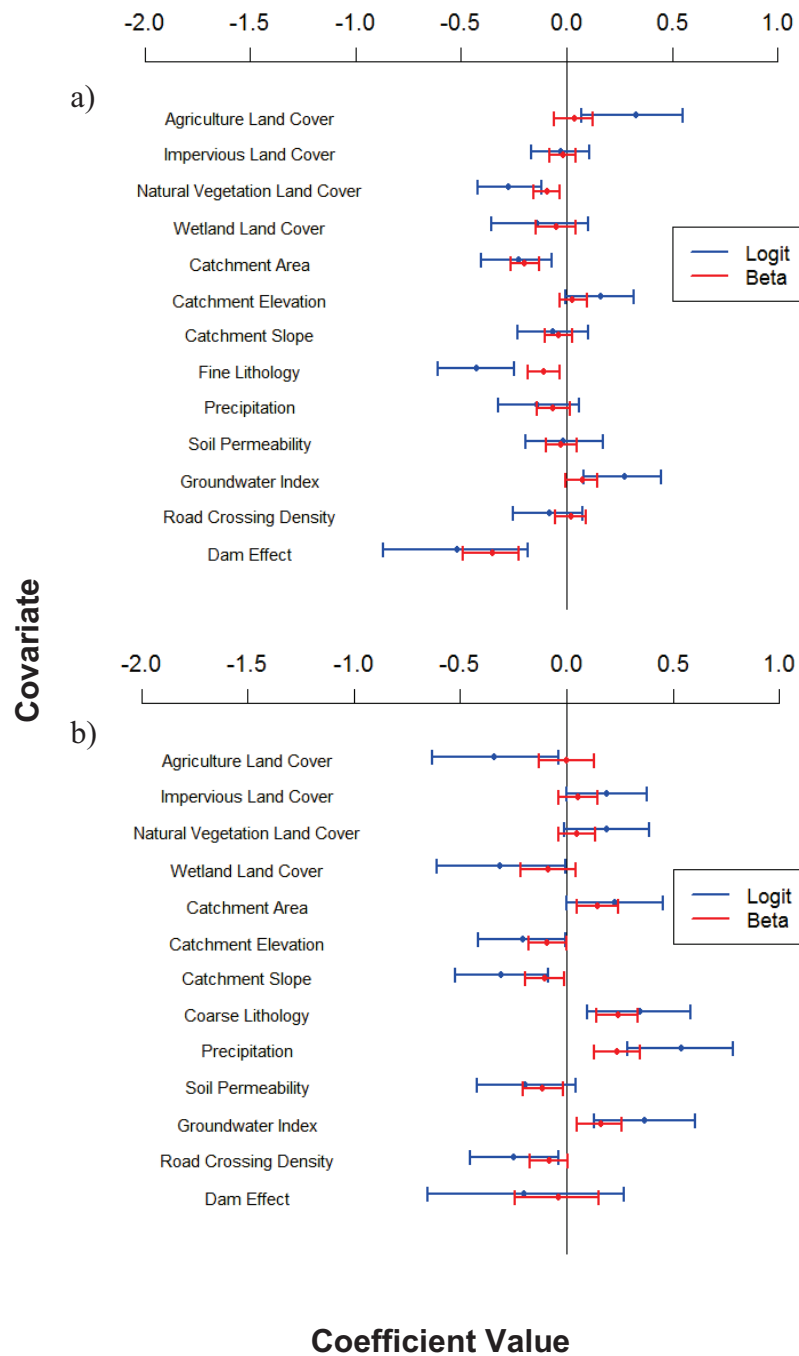
Figure 1.4: Plots of the coefficient mean values (points) and 95% HPD intervals (bars), generated from both the logit and beta linear regressions, for Type I (a) and Type II (b) habitat.

Selection frequencies, which served as the best available measure of variable importance for the boosted additive model, indicated that catchment elevation and mean precipitation were the most utilized predictors for Type I and Type II habitat, respectively (Table 1.4). Catchment area and precipitation were the most influential predictors for the derived response variables of total larval habitat and Type II to Type I habitat ratios, respectively. The directional influence of the landscape covariates for both habitat types were predominantly nonlinear, with the apparent exceptions being natural vegetation land cover and fine lithology for Type I habitat and wetland land cover, impervious land cover, and coarse lithology for Type II habitat (Figs. 1.5, 1.6). Similar nonlinear trends were observed for the two derived response variables (Appendix B).

Table 1.4: Variable selection frequency in the boosted generalized additive model fit to Type I habitat, Type II habitat, total larval habitat, and the Type II to Type I habitat ratio. The bolded values indicate the three most frequently selected predictor variables for each response.

Variable	Selection Frequency			
	Type I	Type II	Total Habitat	Ratio
Agriculture Land Cover	0.068	0.124	0.108	0.006
Impervious Land Cover	0.058	0.050	0.028	0.038
Natural Vegetation Land Cover	0.038	0.024	0.026	0.052
Wetland Land Cover	**0.135**	0.074	0.092	0.032
Catchment Area	0.100	**0.144**	**0.176**	**0.200**
Catchment Elevation	**0.171**	0.036	0.034	0.110
Catchment Slope	**0.118**	0.030	**0.128**	0
Coarse Lithology	N/A	0.012	N/A	N/A
Fine Lithology	0.058	N/A	0.048	0.018
Precipitation	0.086	**0.208**	**0.144**	**0.318**
Soil Permeability	0.048	0.122	0.108	0.010
Groundwater Index	0.028	**0.126**	0.050	**0.182**
Road Crossing Density	0.078	0.050	0.046	0
Dam Presence	0.012	0	0.012	0.034
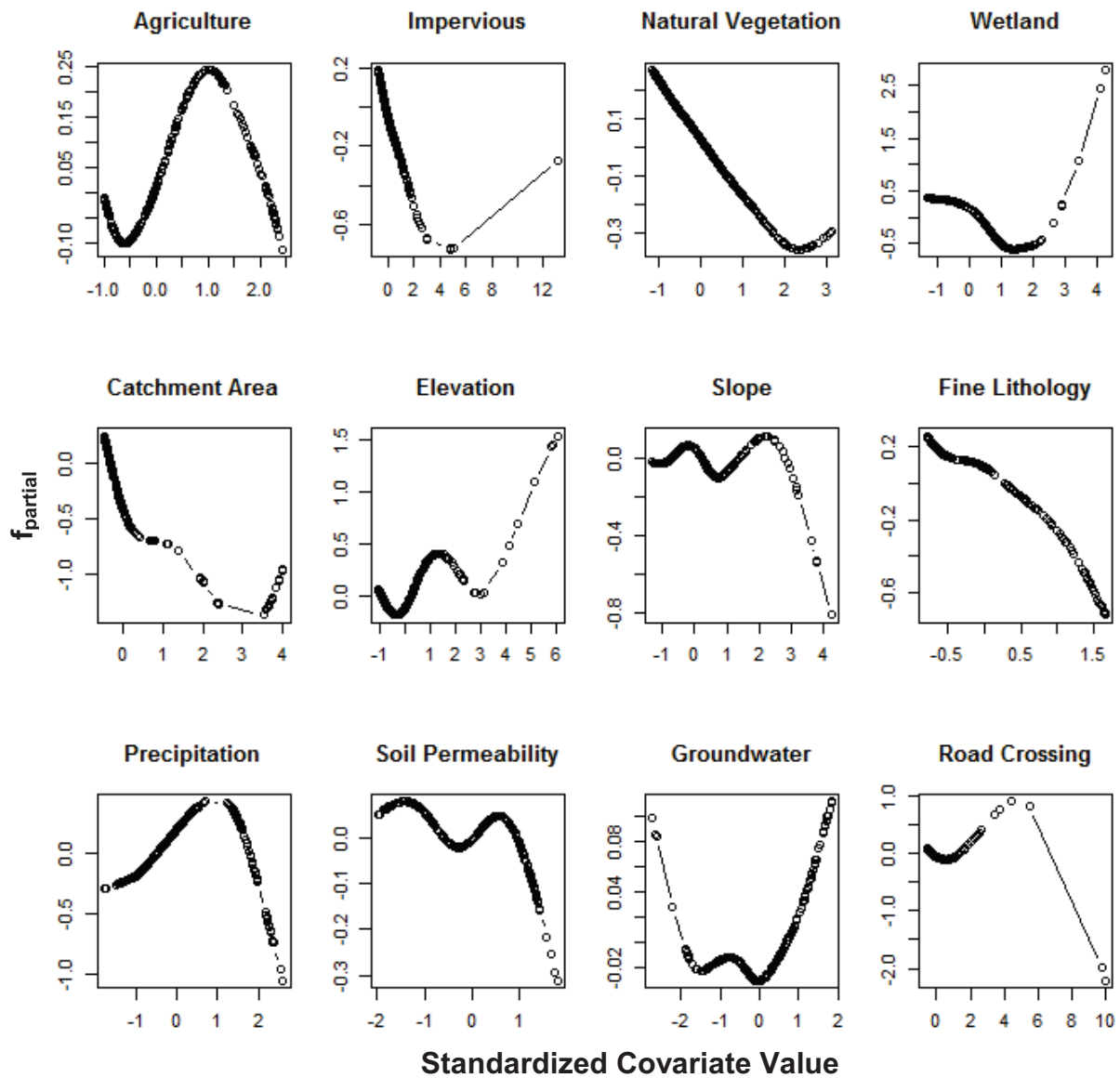
Figure 1.5: Partial effects plots, generated from the generalized additive model for Type I habitat, showing the marginal, nonlinear influence of each continuous covariate on the response.
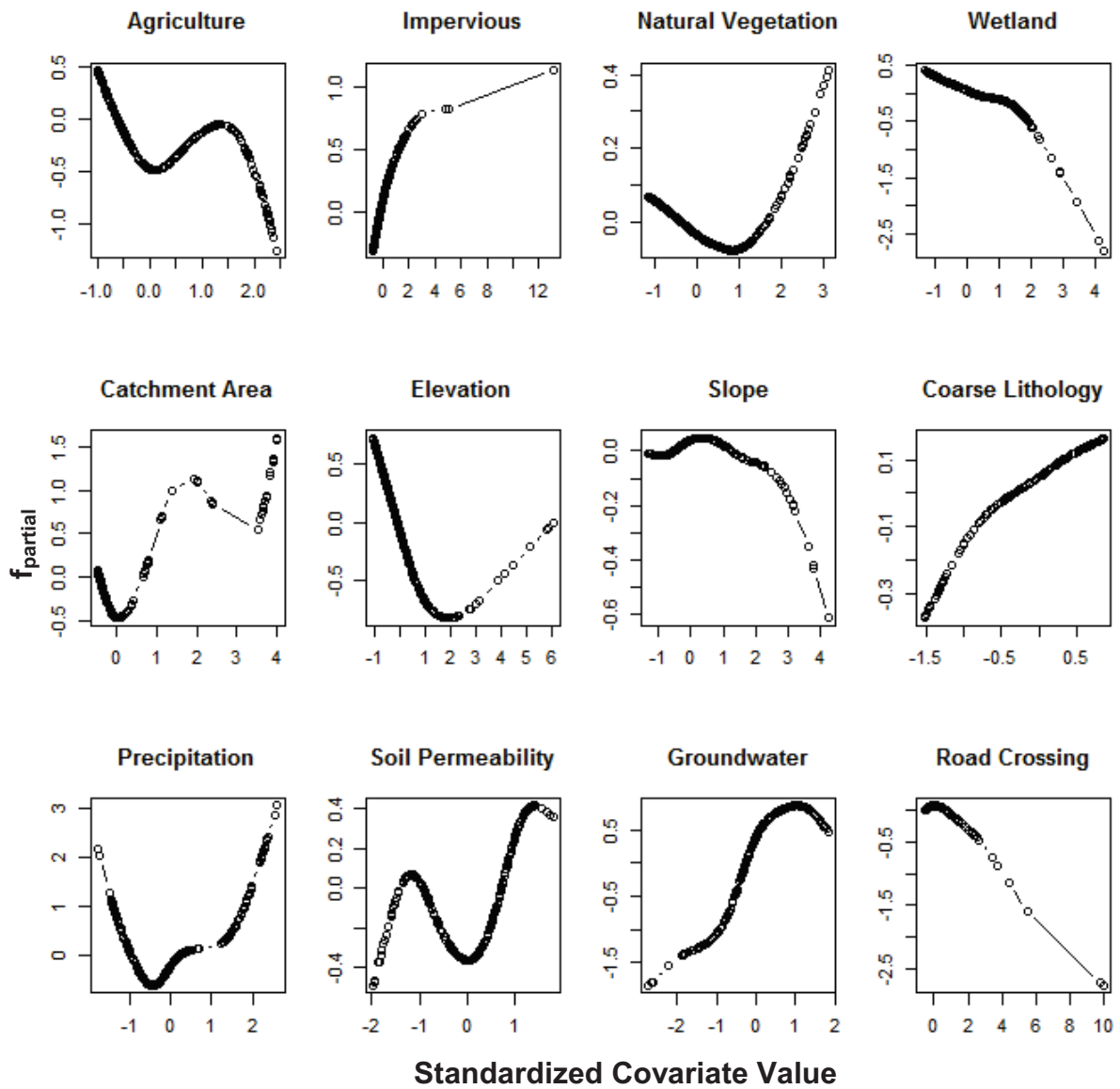
Figure 1.6: Partial effects plots, generated from the generalized additive model for Type II habitat, showing the marginal, nonlinear influence of each continuous covariate on the response.

Model Fit

Across the three models fitting the original Type I and Type II habitat data, none of the approaches predicted Type I habitat proportions well (Table 1.5; Fig. 1.7). Focusing on the reach-scale as the scale of interest, the logit regression, beta regression, and additive model explained just 14.1%, 14.4%, and 16.2% of variation in the observed habitat proportions, respectively, and none of the models had both their slope and intercept terms fall within expected equivalence regions. Although the intercepts and slopes of the linear fits between observed and predicted values differed noticeably, none of the three models distinguished themselves from one another in the other measures of model fit; all three had similar R^2 and RMSD values. All three models performed better in fitting Type II habitat observations (Table 1.5; Fig. 1.7). The additive model explained the most variation at the reach-scale (37.0%), followed by the logit and beta regressions at 26.0% and 24.1%, respectively. Although there was little difference among the model's RMSD values, equivalence test results suggested that both the logit regression and additive model outperformed the beta regression; this is supported by the strong deviation of the beta regression's slope between observed and predicted values from the expected 1:1 line (Fig. 1.7d). All three models had higher observed model fits at the reach-scale than for individual transect-scale observations.

Table 1.5: Summary of model fit metrics across the different modeling approaches and habitat types. The root mean squared deviation (RMSD) is the observed average deviation of the predicted values from the observed. Intercept (a), slope (b), and R^2 were calculated from a linear regression of observed against predicted values. (D) indicates the model was fit using derived response variables, and * indicates the intercept/slope parameter fell within the expected range based on equivalence testing.

Model	Transect-Scale Model Fit			Reach-Scale Model Fit			
	RMSD	a	b	RMSD	a	b	R^2
Type I Habitat							
Logit Regression	0.273	0.165	0.469	0.184	0.088	1.103*	0.141
Beta Regression	0.240	-0.144*	1.725	0.156	-0.123*	1.644	0.144
Boosted Additive	0.257	0.110	0.954*	0.182	0.116	0.826*	0.162
Boosted Additive (D)	0.234	-0.006*	0.984*	0.150	0.010*	0.966*	0.193
Type II Habitat							
Logit Regression	0.338	0.213*	0.641*	0.251	0.199*	0.658*	0.260
Beta Regression	0.331	-0.274*	1.627	0.249	-0.214*	1.450	0.241
Boosted Additive	0.315	0.174*	0.704*	0.240	0.206*	0.659*	0.370
Boosted Additive (D)	0.328	-0.014*	0.851*	0.257	0.059*	0.751*	0.307
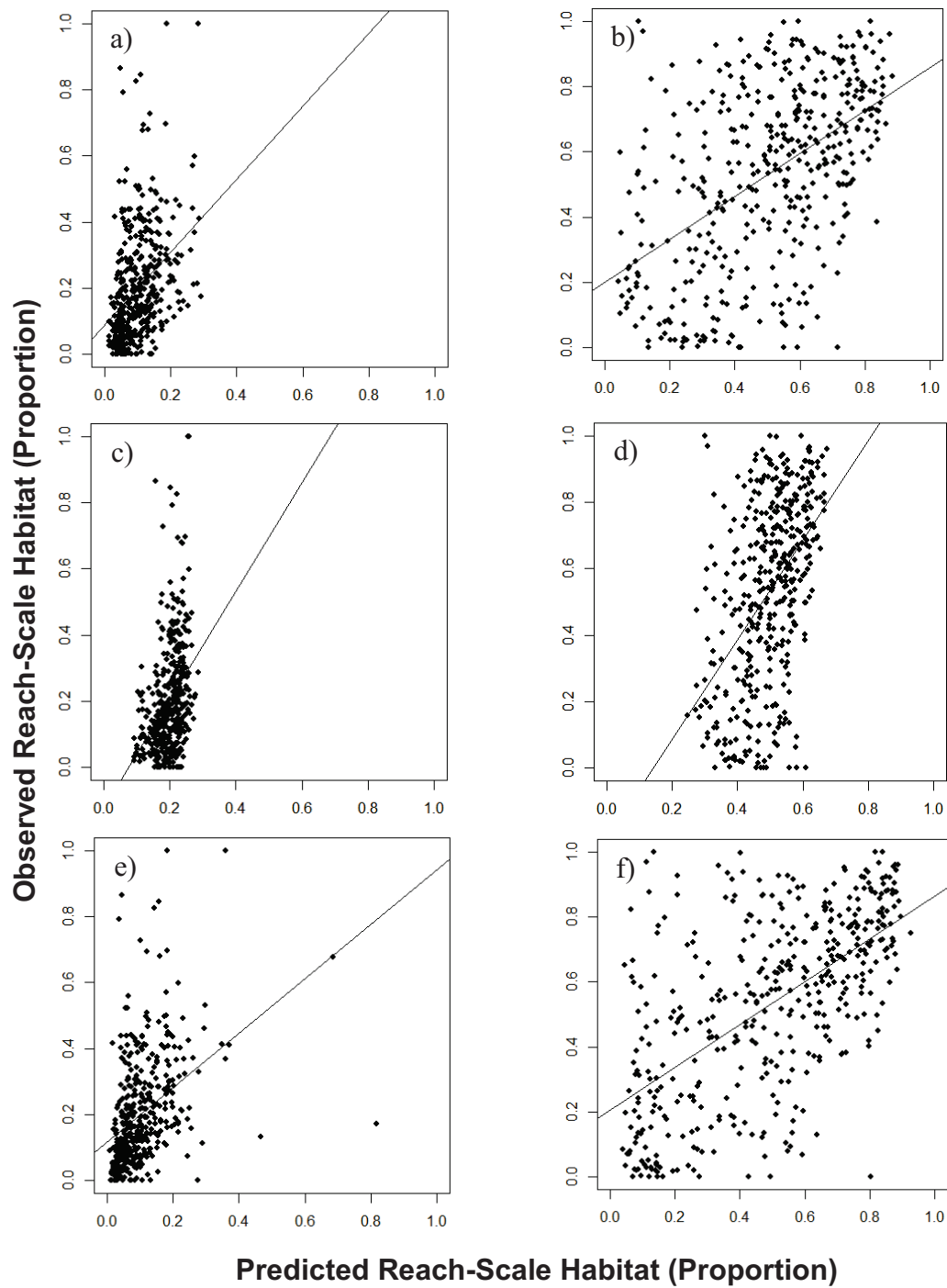
Figure 1.7: Observed model fit for the Type I (a, c, e) and Type II (b, d, f) habitat values generated from the logit regression (a, b), beta regression (c, d), and boosted additive model (e, f). The line represents the linear fit between observed and predicted values.

Among all modeling approaches, the additive model fit to the derived quantities of total larval habitat and habitat ratio had the greatest observed model fit for Type I habitat predictions and second best fit for Type II habitat (Table 1.5). This model explained 19.3% of variation in observed, reach-scale Type I habitat, had the lowest observed RMSD among modeling approaches, and had the nearest fit to the expected 1:1 line between observed and predicted values (Fig. 1.8). For reach-scale Type II habitat, the model explained 30.7% of variation, and had the second lowest RMSD value of 0.257. Again, there was a clear difference in the model fit between the transect-scale and reach-scale observations, with noticeably more variation among transects than reaches (Fig. 1.8).
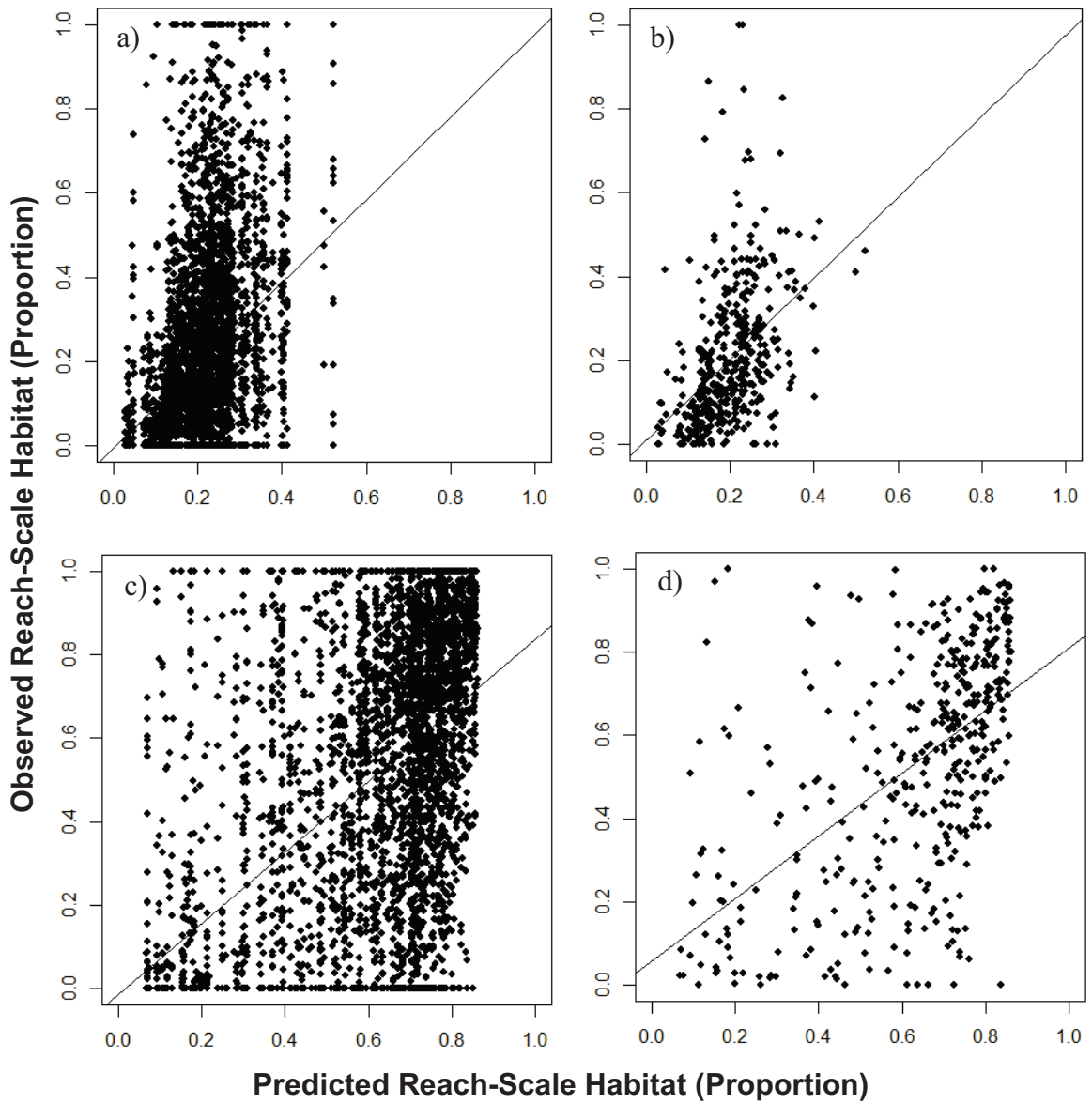
Figure 1.8: Observed model fit for Type I (a, b) and Type II (c, b) transect-scale (a, c) and reach-scale (b, d) habitat values generated by the boosted generalized additive model fit to the two derived response variables. The line represents the linear fit between observed and predicted values.

Sampling Success and Model Predictive Ability

All six streams were sampled with varying degrees of success; between 4 and 10 reaches were sampled within any given stream, with an average sampling intensity of 2.8 access points and 10.3 transects per reach (Fig. 1.2). Sampling resulted in a total of 47 reaches, 130 access points, and 483 transects, composing a dataset over 10% of the size of the model training datasest (11.0%, 13.8%, and 11.6% for reaches, access points, and transects, respectively). Drought conditions in late July and early August contributed to the difficulty of habitat sampling. The distribution of sampling effort across the basin and among reaches within each stream system, however, effectively captured the range of covariate variation within the original model training dataset (Fig. 1.9).

Similar to the model fitting evaluation results, none of the three models fit to the original response variables experienced particular success in predicting Type I habitat (Table 1.6; Fig. 1.10); all models were similar in explaining less than one percent of variation in the response. Predictive performance was noticeably higher and variable among models for Type II habitat, however. The boosted additive model performed best by explaining 24.6% of variation in the response, followed by the logit and beta regression at 11.7% and 3.8%, respectively.

The model fit to derived habitat quantities had similarly limited success in predicting Type I and Type II habitat quantities in the new spatial extents. The additive model explained less than one percent of variation in Type I habitat and just 18.0% of variation in Type II habitat (Table 1.6; Fig. 1.10).
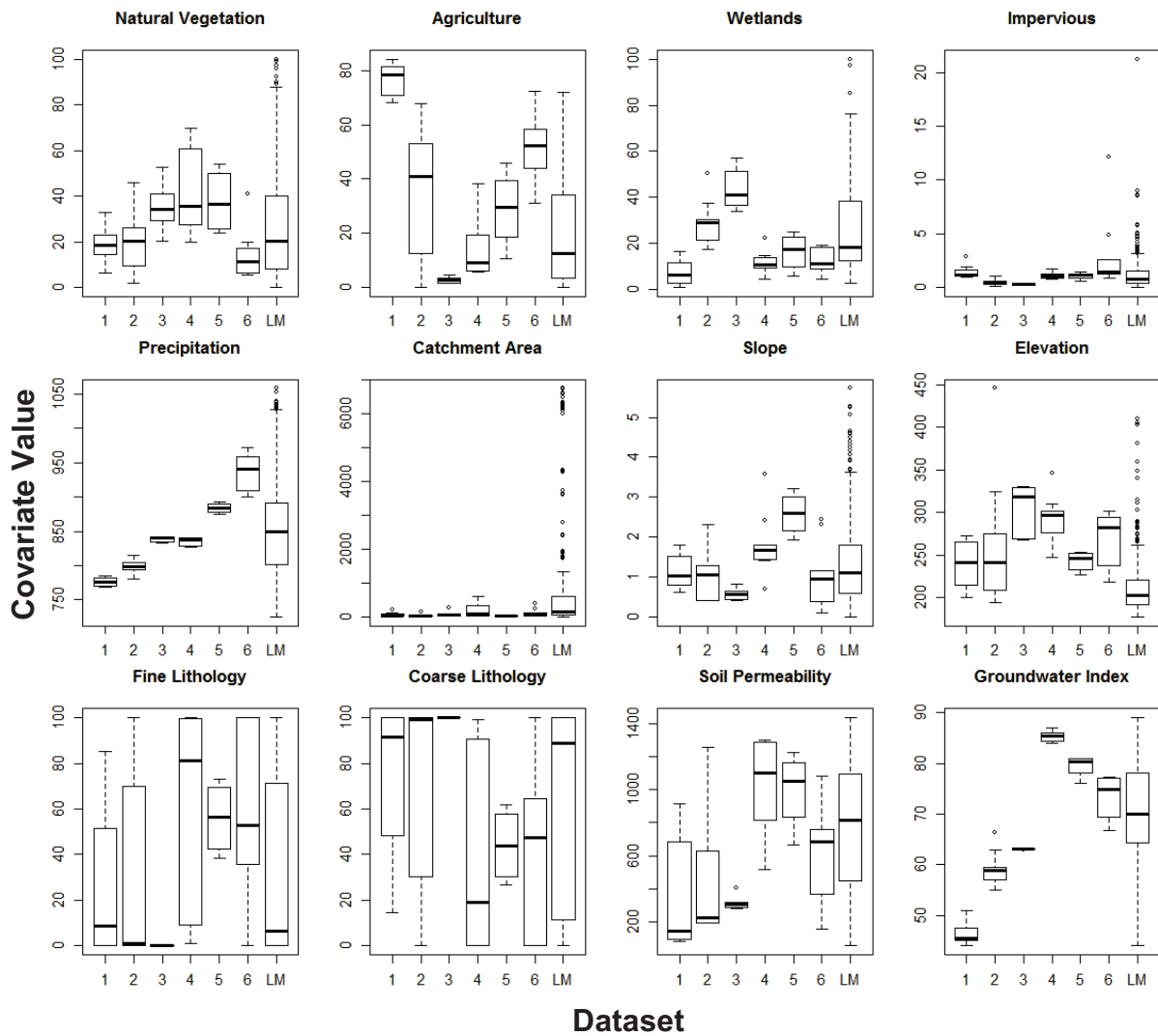
Figure 1.9: Boxplots of observed covariate variation among reaches sampled in each river system, where 1 through 6 correspond to the Twin, Peshtigo, Whitefish, Boardman, Pentwater, and Kalamazoo River, respectively. LM refers to covariate variation in the original model training dataset.

Table 1.6: Model predictive fit for Type I and Type II habitat, among each of the modeling approaches. (D) indicates the model was fit to derived response variables, and * indicates the intercept/slope parameter fell within the expected range based on equivalence testing.

| Model | Reach-Scale Model Fit | | | |
	RMSD	a	b	R^2
	Type I Habitat			
Logit Regression	0.159	0.139*	0.031	0.000
Beta Regression	0.160	0.210	-0.280	0.003
Boosted Additive	0.145	0.154*	-0.073	0.001
Boosted Additive (D)	0.201	0.160	-0.056	0.001
	Type II Habitat			
Logit Regression	0.254	0.130*	0.500	0.118
Beta Regression	0.289	-0.057*	0.793	0.040
Boosted Additive	0.235	0.143*	0.626	0.242
Boosted Additive (D)	0.301	0.066	0.503*	0.181
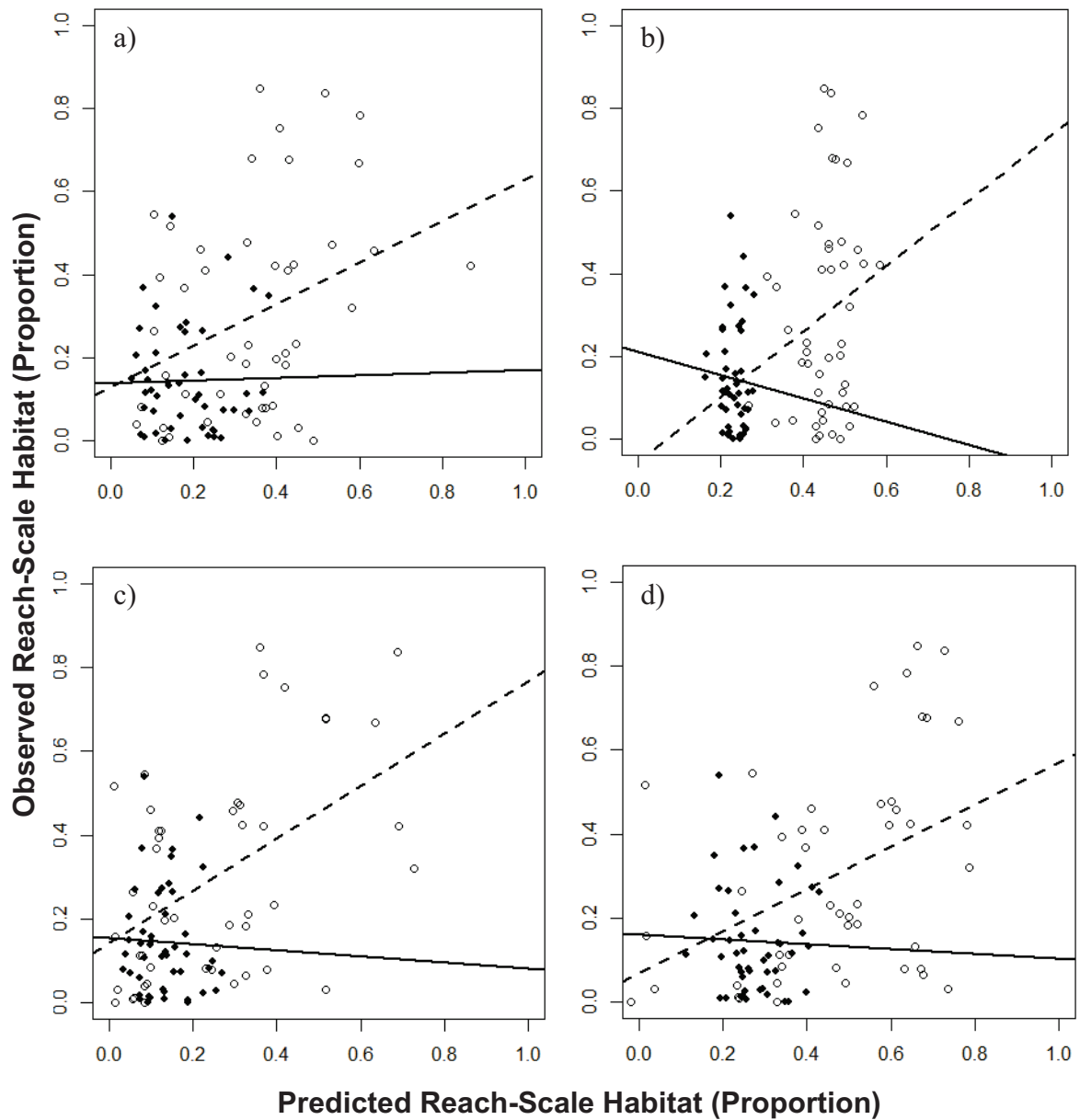
Figure 1.10: Plots of predictive fit for the logit regression model (a), beta regression model (b), boosted additive model (c), and boosted additive model fit to the derived habitat quantities (d). Closed circles and solid lines represent data points and linear fits, respectively, between observed and predicted values for Type I habitat; open circles and dotted lines represent the same for Type II habitat.

DISCUSSION

Among models fit to original habitat data, the boosted additive model clearly performed best among the evaluated approaches, followed by the logit regression. The boosted model explained the most variation in the training dataset for both habitat types, and was the most accurate in predicting Type II habitat quantities. Despite the still significant amount of variation left unexplained by the model, the ability of the boosted additive model to account for 24.2% of variation in the out-of-sample data for Type II dataset supports its potential future utility for predicting habitat quantities above barriers. The markedly greater performance of this approach can be attributed to both its application of implicit variable reduction, through the use of iterative model fitting, and built-in cross-validation techniques to decrease model size, as well as its nonlinear nature. In fact, the improved ability of the nonlinear model to predict habitat supports the theorized predominance of nonlinearities and thresholds in fluvial geomorphology and complex river-landscape systems (Shreve 1979; Phillips 2003; Phillips 2006). Accounting for the random effects of access point and reach in the logit and beta regressions did not appear to overcome the restrictions imposed by the assumption of linearity. Furthermore, the use of a beta distribution in the beta regression, even with zero-one inflation, did not improve model performance; model predictions appeared to be condensed towards observed habitat averages, resulting in low model and predictive fits.

The boosted generalized additive model fit to the derived habitat quantities, representing an attempt to work around possible limitations of the individual Type I and Type II datasets, did not improve the predictive fit for either habitat type. I primarily selected this modeling approach to avoid the limited variation, lack of normality, and preponderance of zeroes or similarly small

values in modeling Type I habitat. The derived quantities of total larval habitat and ratio between habitat types were meant to uniquely combine Type I and Type II information, fit new models, and subsequently back-calculate improved predictions for the two habitat types. Instead of improving predictive performance, this model resulted in model predictions equivalent or worse than those for the additive model fit to the original habitat datasets. These results are not entirely surprising, as the distribution of the habitat ratios and log-odds total habitat quantities did not readily conform to standard statistical distributions and exhibited a continued dominance of extreme values.

The apparent mismatch between the assessed model fit and predictive capacity, across both habitat types and all four modeling approaches, speaks to the difficulty of predicting across new spatial extents. The intent of this modeling effort, in essence, is simple extrapolation; I built a model from habitat data collected downstream of dams in order to predict upstream habitat quantities. The model fit values, especially those for Type II habitat, do compare favorably to those reported in past studies attempting to predict substrate habitat, with observed R^2 ranging from 0.22 (Mugodo et al. 2006) and 0.32 (Neeson et al. 2012) all the way to 0.50 (Wang et al. 2013). However, the predictive ability for Type I habitat was non-existent and the observed correlation between observed and predicted Type II habitat quantities declined when moving from the training to validation datasets. The failure to predict above dams, by itself, might indicate a complete inability to extrapolate Type I habitat quantity predictions to any new spatial extents, or simply the inability to predict in river headwaters specifically; regardless, the models are not useful for predicting Type I habitat in the context of barrier removal scenarios, and only the boosted additive model appears able to predict Type II habitat in upstream regions.

The mismatch between predictive capacity and model fit also reinforces the importance of out-of-sample data collection for model validation. If the validation results on the out-of-sample data are excluded from these analyses, a different story would have emerged: the logit and beta regressions appear to perform similarly and all three models appear to explain some degree of variation in Type I habitat. Instead, the zero/one inflated beta regression performs exceptionally poorly in predicting both habitat types, and none of the models can predict Type I habitat quantity above dams reliably, especially compared to the habitat variation explained by similar studies. This example provides compelling motivation for testing models' capacity for spatial extrapolation when evaluating predictive methods against new data (Miller et al. 2004).

The differences in selected important predictors for predicting Type I habitat among the three modeling approaches reflect the difficulty of predicting stream habitat quantities using only landscape-scale covariates in a complex, fluvial system, as well as the importance of accounting for nonlinear relationships in modeling efforts. The two regression models both agreed natural vegetation land cover, catchment area, fine lithology, and dam effect were statistically important in influencing fine-substrate habitat quantities   However, the boosted additive model identified catchment elevation, wetland land cover, and catchment slope as the strongest predictors for Type I habitat. The apparent lack of consistency between the variables selected by modeling approaches may reflect a preponderance of purely correlative (*i.e.*, not mechanistic) relationships and explain the poor predictive capacity upstream of barriers. Given that low velocity regions in streams, often created by fine-scale channel characteristics, are required for the deposition of the fine sedimentary materials, exclusively catchment-scale characteristics may be insufficient to explain trends in this habitat feature (Charlton 2008). Alternatively, simple nonlinearity within the system may explain the difference between the modeling approaches; natural vegetation land

cover and fine lithology, both selected as important by the linear modeling approaches, were the only two covariates with primarily linear relationships to the response (Fig. 1.5). Rather than emphasizing real drivers of habitat, linear models may ignore important non-linear effects that drive habitat variation.

The more consistent identification of important covariates across models for Type II habitat seems to reflect the increased capacity to predict these habitat quantities and may help researchers understand dominant influences on stream habitat features. The two linear models identified catchment area, catchment slope, coarse lithology, precipitation, and groundwater index as important predictors for Type II habitat, and the boosted additive model used precipitation, catchment area, and groundwater index most frequently. Furthermore, it is worthwhile to note that five of the six top predictors for total larval habitat and habitat ratio response variables, representing related but unique measures of stream habitat, were also catchment area, precipitation, and groundwater index. Past studies have also identified both catchment area and catchment slope as strong predictors of stream substrate habitat (Jeffers 1998; Davies et al. 2000; Frappier and Eckert 2007). Indeed, the selection of these landscape features reinforces our understanding of these characteristics' influence on stream flow. The medium- to coarse-grained sands comprising Type II habitat are typically transported as bedload, and are more frequently transport limited rather than supply limited (Charlton 2008). Subsequently, stream power, calculated as a function of catchment area and slope, both regulates the capacity of a river to transport sediment and influences median substrate size (Bagnold 1980; Whiting et al. 1999). In the case of these analyses, Type II habitat quantities appear to respond positively to high catchment areas and negatively to high catchment slopes. Furthermore, groundwater contribution to base flow is known to play a role in regulating extreme flow events

in rivers, and particularly in watersheds with limited anthropogenic disturbances like urbanization or agricultural development (Resh et al. 1988; Allan 2004). It is possible that increased flow stability in some Lake Michigan systems, indicated by high surficial drainage rates related to coarse lithology and subsequently high groundwater contributions, promotes the local accumulation of medium- to coarse-grain sand. Indeed, the direction of groundwater influence, across all modeling approaches, is positive. Finally, although multiple landscape attributes likely interact to influence river habitat features, it is worth noting that interactions among variables were not explicitly considered in my modeling efforts due to a lack of prior knowledge regarding the form these interactions might take.

This study reflects a unique attempt to predict GLFC-defined, sea lamprey larval habitat quantities in new spatial extents, using only readily-available, landscape-scale, GIS-derived covariates and a convenient predictive spatial scale for management. Past attempts to model to model sea lamprey habitat have either been limited to very fine-scale spatial extents (Neeson et al. 2007) or focused on evaluating model fit only within the spatial extent used to train the models (Neeson et al. 2012). By building the predictive models using only landscape-scale covariates, the models have the capability to predict anywhere within the Lake Michigan basin, and perhaps beyond if fundamental landscape-stream relationships happen to hold. Field sampling-based "ground-truthing" is a newly applied methodology in the prediction of sea lamprey habitat that assesses this broader modeling utility. Moreover, many previous stream habitat modeling efforts have focused on strictly linear approaches, which have been shown by this study's inclusion of multiple modeling approaches to potentially produce spurious correlations (Davies et al. 2000; Neeson et al. 2007). Finally, this study's predictions are made at the spatial scale of NHDPlus stream reaches; this base scale better facilitates the scaling of

predictions to larger extents for the purpose of management (Wang et al. 2013). Sea lamprey assessment and control efforts are coordinated across Great Lakes basins, and habitat data have to be accessible on similar scales.

Regrettably, the failure of the assessed modeling approaches to capably predict both Type I and Type II habitat limits their utility in informing sea lamprey management. Given the differing production potential among habitat types, the quantity of both habitat types should be known in order to predict future lamprey production with established modeling approaches, like the SLaMSE model for the Great Lakes (Jones et al. 2009; Dawson et al. 2016; see chapter 2). Depending on the desired scale of analysis, predicting sea lamprey production in new rivers without accompanying larval habitat data or subsequent model improvements may require locally measured or region-specific average habitat quantities with some realistic measure of uncertainty. This removes the need to rely on potentially unreliable habitat predictions, and instead directly incorporates some measure of uncertainty around habitat quantities into model predictions.

Limitations in the extent, accuracy, and utility of the available response and predictor variable data can help explain the observed inadequate predictive capabilities, especially for Type I habitat. First, the observed data forming the basis of modeling efforts may have been collected with a significant amount of measurement error, typical in the sampling of local-scale stream habitats (Wang et al. 2013). Second, the available data and selected spatial scale of model fitting could have led to inaccurate estimates of observed reach-scale habitat quantities, as over 50% of training dataset's stream reaches were characterized by four or fewer transects. Despite findings that a single sampling site on a confluence-to-confluence stream reach can represent general conditions throughout the reach (Wang et al. 2006), the heterogeneous nature

of stream habitat conditions seems to require a greater intensity of sampling effort than four transects. Furthermore, the lower model fit and much higher degree of scatter for the transect-scale observations, relative to the reach-scale observations, for both habitat types reflects the large amount of variation within reaches and the resulting difficulty in effectively capturing reach-scale dynamics. Temporal stochasticity and disconnects may have played a significant role in influencing model and predictive performance. Although utilized predictor data were ideally summarized within a similar time frame as the initial larval habitat data collection (*i.e.,* 2004-2008), localized land use disturbances on short-time scales, characteristic in stream systems with a strong anthropogenic influence, may have added further unexplained variation in the dataset; these anthropogenic disturbances can temporarily overwhelm natural catchment characteristics in stream influence (Johnson et al. 1997; Allan 2004). Historical, large-scale land use changes and climatic conditions, again uncaptured by my chosen variables, may also be exerting remnant influences on localized stream habitat (Langbein and Schumm 1958). Finally, the greater temporal mismatch between the predictors and the larval habitat data collected in 2016 may help explain the reduced predictive fit, as I did not account for the potential change in predictive features like land cover between the collection of the two response datasets.

Despite these limitations, there remains room for improvement in future modeling endeavors. Modeling systems without well-established mechanistic relationships can result in purely correlative habitat relationships (Miller et al. 2004), and subsequently produce spurious predictions. Given the observed low predictive ability of the evaluated models, especially for Type I habitat, it is certainly possible this occurred in these analyses. This source of error translates directly into model improvement, as simpler models with proven mechanistically-supported landscape covariates may have resulted in improved fit. Further empirical work

should be done to more closely evaluate driving factors of stream habitat in Michigan streams, with a focus on untangling linkages among spatial and temporal scales. Exploring additional variable reduction and nonlinear modeling techniques also has the potential to improve modeling utility in the future.

These modeling efforts to predict upstream larval habitat quantities represented a unique effort to generate habitat estimates in Lake Michigan tributaries at a scale useful to management and inform future sea lamprey control efforts. The results have the potential to inform future sampling by identifying dominant influences on habitat quantity, but have limited utility in generating accurate predictions. The insights provided from evaluating model predictive capacity on out-of-sample data also highlight the importance of "ground-truthing" model performance. Moving forward, the reliability of future habitat predictions can be improved with a better understanding of landscape-scale drivers and further work in identifying new variable reduction or nonlinear modeling techniques.

APPENDICES

WinBUGS SCRIPT FOR THE TYPE 1 HABITAT LOGIT REGRESSION

```
model{
#Introducing Observed Data and the Random Effect of Access Point (AP)
        for (i in 1:Num_Transects) {
                T1_Logit[i]~dnorm(mu[i],tau)
                mu[i]<-AP_effect[AP [i]]
        }
#Modeling the Random Effect of Access Point
        for (i in 1:Num_Access_Points){
                AP_effect[i]~dnorm(mean_AP[i],tau_AP)
                mean_AP[i]<-reach_effect[reachID[i]]
        }
#Modeling the Random Effect of Reach
        for (i in 1:Num_Reaches){
                reach_effect[i]~dnorm(mean_reach[i],tau_reach)
                mean_reach[i]<-beta_Precip*Precip[i]+beta_NatVeg*NatVeg[i]+
                        beta_Agr*Agr[i]+beta_Wetl*Wetl[i]+beta_Imperv*Imperv[i]+
                        beta_CatchmentArea*Catchment_Area[i]+beta_Slope*Slope[i]+
                        beta_Elev*Elev[i]+beta_GWIndex*GW_Index[i]+
                        beta_FineLith*FineLith[i]+beta_SoilPerm*SoilPerm[i]+
                        beta_StrXing*Str_Xing[i]+alpha_Dam[Dam_Presence[i]]
        }
#Prior Specification
        sigma~dunif(0,20)
        sigma_AP~dunif(0,20)
        sigma_reach~dunif(0,20)
        beta_Precip~dnorm(0,0.001)
        beta_NatVeg~dnorm(0,0.001)
        beta_Agr~dnorm(0,0.001)
        beta_Wetl~dnorm(0,0.001)
        beta_Imperv~dnorm(0,0.001)
        beta_CatchmentArea~dnorm(0,0.001)
        beta_Slope~dnorm(0,0.001)
        beta_Elev~dnorm(0,0.001)
        beta_GWIndex~dnorm(0,0.001)
        beta_FineLith~dnorm(0,0.001)
        beta_SoilPerm~dnorm(0,0.001)
        beta_StrXing~dnorm(0,0.001)
        for(i in 1:2){
                alpha_Dam[i]~dnorm(0,0.001)

#Additional Parameters to Track
        tau<-1/(sigma * sigma)
```

```
tau_AP<-1/(sigma_AP * sigma_AP)
tau_reach<-1/(sigma_reach * sigma_reach)
```

PARTIAL EFFECTS PLOTS FOR DERIVED RESPONSE VARIABLES
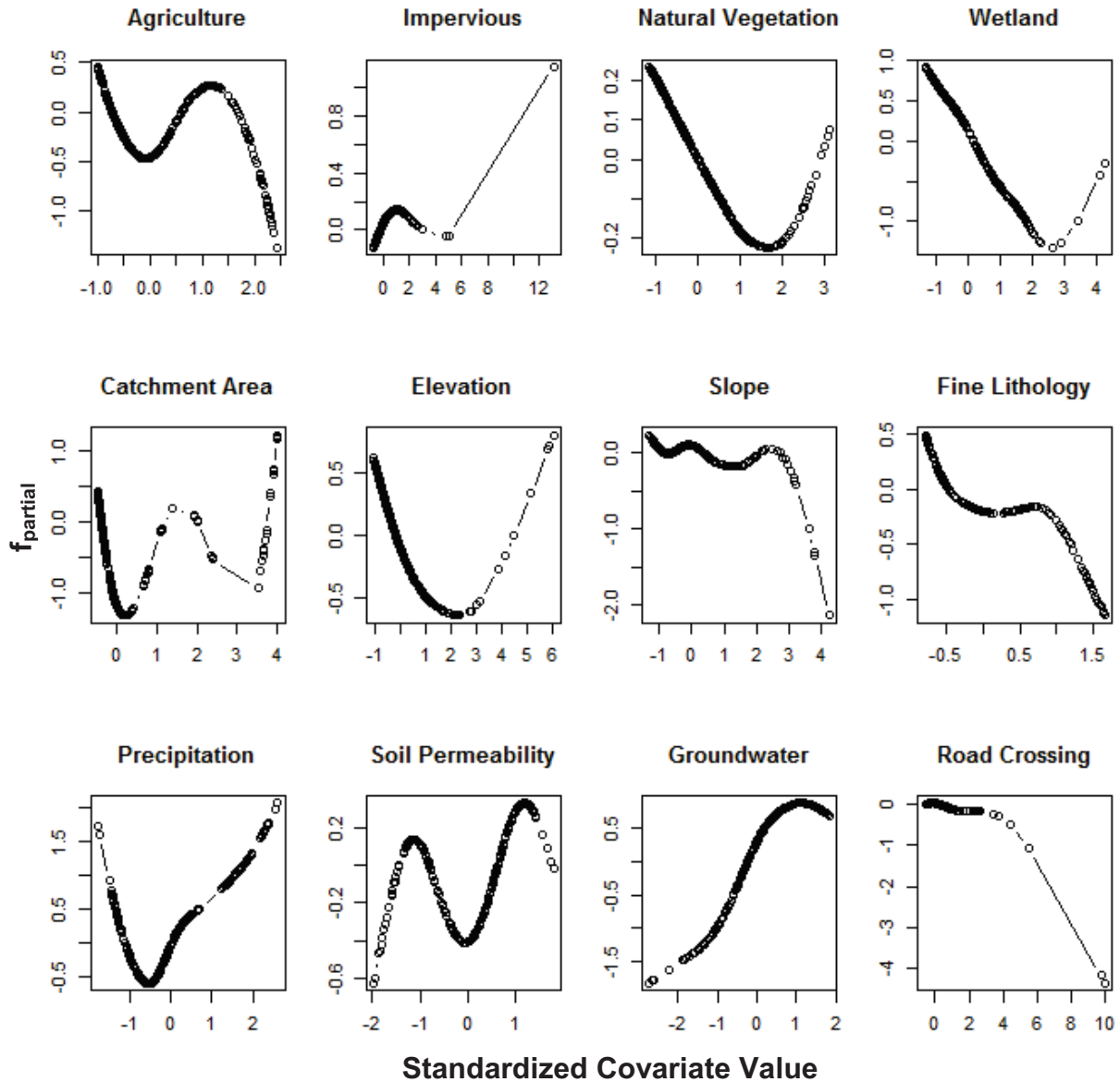
Figure 1.11: Partial effects plots, generated from the generalized additive model for total larval habitat, showing the marginal, nonlinear influence of each continuous covariate on the response.
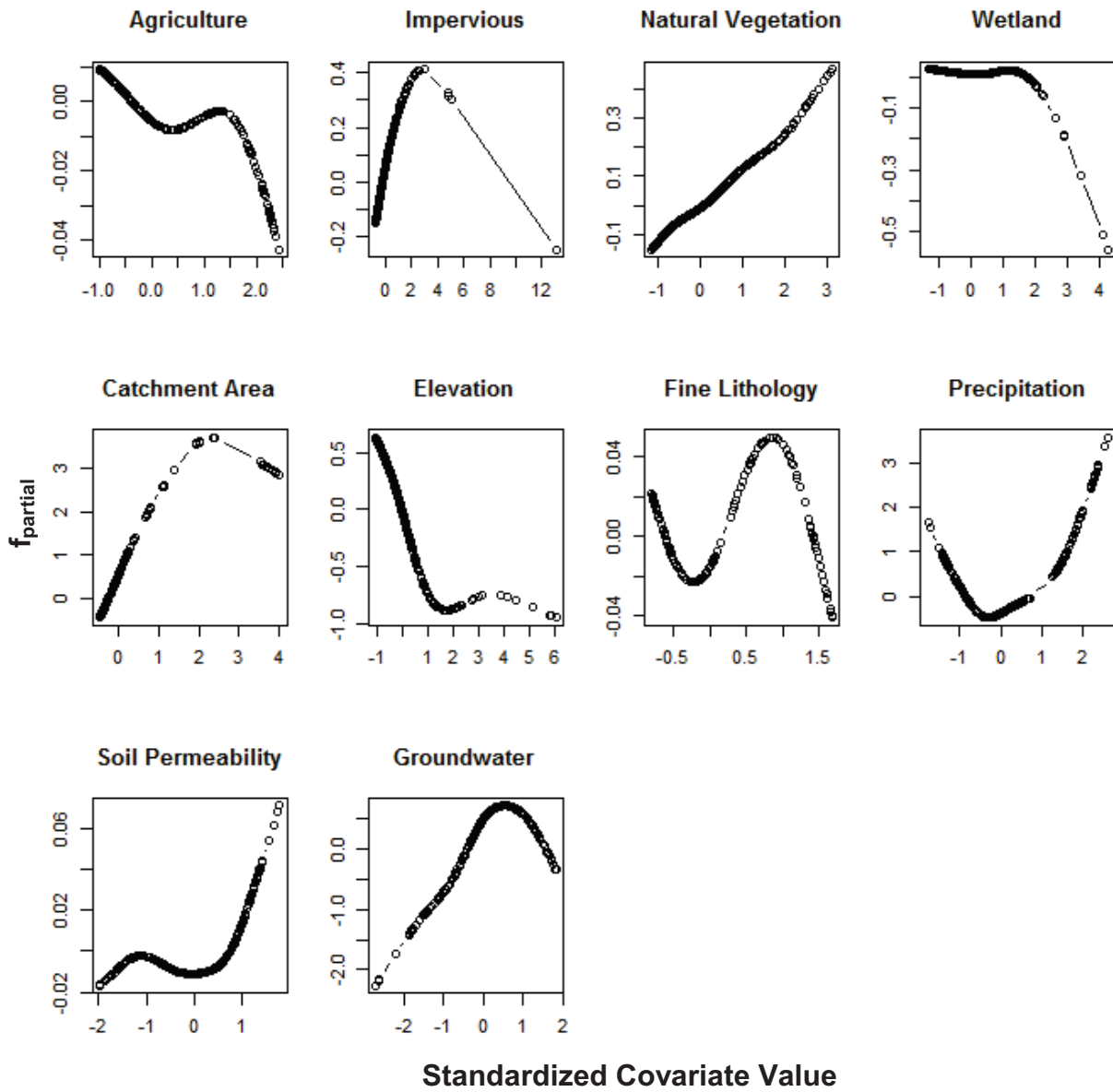
Figure 1.12: Partial effects plots, generated from the generalized additive model for Type II to Type I habitat ratios, showing the marginal, nonlinear influence of each continuous covariate on the response.

CHAPTER 2: SIMULATING THE SEA LAMPREY RESPONSE TO DAM REMOVALS IN
THE LAKE MICHIGAN DRAINAGE BASIN

INTRODUCTION

Although dams are globally pervasive and can provide many societal benefits, they can be significant barriers to migratory fish. Indeed, dams have been implicated in the declines of numerous populations of diadromous species (Limburg and Waldman 2009). Thanks to growing public preference to increase lotic connectivity and benefit aquatic species, dam removal in the U.S. is accelerating and numerous large-scale dams have been demolished in systems like the Penobscot, Carmel, and Elwha Rivers in Maine, California, and Washington, respectively. In numerous regions of the world, however, stream barriers can actually provide an ecosystem service by blocking fish migration, specifically in impeding the spread and success of invasive species (Sharov and Liebhold 1998; Vélez-Espino et al. 2011; Rahel 2013).

Sea lampreys have been major parasites within the Laurentian Great Lakes since their invasion in the early 20th century, and their arrival and subsequent increase in population abundance are associated with historic declines in commercially important fish populations, including lake whitefish (*Coregonus clupeaformis*) and lake trout (*Salvelinus namaycush*) (Smith and Tibbles 1980). The parasitic juvenile stage of this species feeds on Great Lakes fish before maturing and migrating to Great Lakes tributaries to spawn; the resulting larvae live as burrowing filter-feeders in these streams for several years before metamorphosing and migrating back to the lakes to begin their parasitic stage (Applegate 1950). Sea lampreys are currently controlled to more acceptable population levels in the Great Lakes using a combination of lampricide application and intentional fragmentation (Smith and Tibbles 1980). A generally fixed budget is spent annually to treat Great Lakes tributaries, typically selected by expected treatment effect relative to other tributaries, using lampricides to kill the burrowing larval stages

before metamorphosis (Christie et al 2003). Stream barriers play a significant complementary role by preventing migratory spawners from accessing high quality spawning and larval habitat, and consequently eliminating the need to treat large sections of rivers for larval sea lampreys (Hunn and Youngs 1980). Indeed, in addition to pre-existing dams, the Great Lakes Fishery Commission (GLFC) Sea Lamprey Control Program (SLCP) has actively constructed stream barriers with the express purpose of blocking sea lamprey migration (Lavis et al. 2003).

Due to the complementary roles of lampricide application and barrier presence, barrier removals have the potential to drastically reduce the effectiveness of sea lamprey control. In the Lake Michigan basin alone, dams like the Sixth Street Dam, Union Street Dam, and Calkins Bridge Dam currently block hundreds of miles of viable spawning and larval habitat in the Grand River, Boardman River, and Kalamazoo River, respectively, and consequently eliminate the need for costly control efforts in the form of lampricide applications. If any of these dams were removed without the construction of a replacement lamprey barrier or an increase in the lampricide control budget, there would be two options available to control agents: 1) ignore the newly available habitat and do not allocate any treatment efforts, or 2) allocate lampricide application efforts to the newly available habitat as needed, at the possible expense of neglecting other river systems. The first option is unlikely to be considered for large systems like the Grand River, especially in light of a real-life scenario in Lake Michigan's Manistique River; an initially unrecognized barrier failure in this system has been linked to unexpected increases in the lake's total sea lamprey population in the late 1990's (Schleen and Klar 1999; Klar and Young 2004). Assuming a fixed lake-wide control budget for lampricide applications, the second option requires a shift in control effort from existing stream systems to the newly available habitat, potentially decreasing treatment effectiveness across the basin as a whole.

Although the general risks of barrier removal in the Great Lakes are accepted by fishery management agencies, there is a need to better understand the actual magnitude of the sea lamprey response to barrier removal, as well as implications for the long-term effectiveness of sea lamprey control. Dam removals are often driven by political and stakeholder considerations or advocated under the assumption that removals are inherently positive, despite a historical dearth of studies documenting the effect of removals (Born et al. 1998; Doyle et al. 2003). In response to the divisive and sometimes arbitrary nature of past dam removal decisions, researchers are increasingly arguing for more careful, comprehensive consideration of the potential ecological consequences and an increased role for scientists in providing data on these consequences (Johnson and Graber 2002; Doyle et al. 2003). Barrier managers are also faced with many competing objectives and pressures, in addition to ecological ones, that include the maintenance of public safety and enhancement of recreational opportunities. The development of formal criteria, supported by the necessary scientific and social information, is one solution for managing these trade-offs (Pejchar and Warner 2001). In the case of barrier removals in the Great Lakes, research that equips managers with a more explicit understanding of the effect of barrier removals on sea lamprey control can help formalize the balancing of trade-offs inherent in decision-making; this, in turn, can lead to more informed barrier removal decisions and increasingly positive consequences for society and the environment.

Management strategy evaluation (MSE) modeling, using known information about sea lamprey life history and control in the Great Lakes, represents a feasible, realistic means to capture the expected effects of barrier removals on the long-term effectiveness of sea lamprey control. Management strategy evaluation models are powerful tools for research and management because they tie together biological, observational, and management (including

control) processes, account for sources of uncertainty in each of these processes, and allow researchers to formally compare the ability of competing management strategies to achieve specified management objectives (Smith et al. 1999; Harwood and Stokes 2003). Researchers have already developed a MSE model for sea lamprey, specific to the Great Lakes, incorporating biological, observational, and management models, each with simulated uncertainty, to assess the effect of alternative management strategies (Jones et al. 2009). Moreover, each model component is informed by years or decades of data on life history processes, sampling accuracy, and control effectiveness. This Sea Lamprey Management Strategy Evaluation (SLaMSE) model has been used to determine optimal control budgets to achieve target economic injury levels (Irwin et al. 2012) and to explicitly compare the effectiveness of alternative management strategies at a basin-wide scale (Dawson et al. 2016). Most importantly, this model can be modified to simulate barrier removal by creating new artificial habitat units, each representing newly opened sections of streams, and forecasting the effect of the increased habitat availability on the equilibrium, lake-wide sea lamprey abundances.

Given the established strengths of MSE models and the breadth of information incorporated into the existing model for Great Lakes sea lamprey, I used a modified version of the SLaMSE model to evaluate the effects of barrier removals on the response of the Lake Michigan sea lamprey population. Lake Michigan was selected as the area of focus for this work due to the detailed understanding of sea lamprey dynamics in this region (Dawson et al. 2016). I first assessed the system's general response to increasing habitat availability through the systematic, incremental addition of discrete habitat units. This approach allowed me to evaluate basic trends in the sea lamprey population response under varying habitat perturbations and characterize the drivers of changing population abundances. I also modeled a specific Lake

Michigan barrier removal scenario, using relevant input data and management scenarios prioritized by sea lamprey control agents, to provide useful information for a contentious, contemporary barrier removal decision. Both approaches helped explain how a complex, heavily controlled biological system responds to fundamental changes in habitat availability and illustrated the ability of an MSE approach to provide applicable predictions of ecological responses to barrier removals. The success of these modeling efforts further supports the use of the SLaMSE model in informing future barrier removal scenarios in the Great Lakes.

METHODS

Modifying the SLaMSE Model

In modifying the SLaMSE model to accommodate habitat additions and unique management scenarios, I started with the model used by Dawson et al. (2016). In addition to the original SLaMSE model structure (Jones et al. 2009), the updated model accounted for historical trapping effort on 16 Lake Michigan tributaries and assigned streams as regular or irregular producers, based on expert professional judgment, with different corresponding Ricker recruitment curves (Dawson and Jones 2009). Regular producers are attributed a more productive Ricker curve (*i.e.*, a larger Ricker α value) than irregular producers.

New model modifications were also included to match recent analyses of historical data. These modifications included the following: 1) allocating 52% and 48% of all Lake Michigan spawners to northern and southern tributaries, respectively, prior to assigning spawners to individual streams based on drainage area and larval abundance, and 2) increasing the influence of drainage area, relative to larval abundance, in determining spawner allocation to individual tributaries. These changes were made to match simulated spawner numbers with observed adult distributions in Lake Michigan rivers that received previous spawner assessments (Mullett et al. 2003; H. Dawson and M.L. Jones, Michigan State University, East Lansing, Michigan, unpublished analysis).

I made two further modifications to the SLaMSE model to accomplish barrier removal simulation objectives: 1) I enabled the flexible addition of new habitat units depending on editable data inputs, and 2) I allowed sea lamprey to infest treatment units that were not treated

with lampricides. The second modification allows for estimation of maximum potential parasitic

sea lamprey production, for a given number of allocated spawners, from selected treatment units.

Assessing Population Responses to Systematically Increasing Habitat Availability

I first characterized the general response of the Lake Michigan sea lamprey population to

barrier removals by systematically adding standardized habitat blocks. Each block was assigned

identical attributes, including areas of suitable larval sea lamprey habitat types as defined by the

GLFC (*i.e.*, Type I and Type II; Slade et al. 2003), drainage area, treatment cost, and

miscellaneous larval growth and mortality parameters; these are all attributes of existing

treatment units within the original SLaMSE model. Block attributes were calculated as averages

of all existing treatment units in Lake Michigan (Table 2.1). These habitat additions were

intended to simulate the effect of opening new river systems to sea lamprey (*e.g.*, removing

barriers at the river mouths).

Table 2.1: Base model inputs for a single standardized habitat block in the systematic habitat additions.

Type I Habitat (m^2)	Type II Habitat (m^2)	Drainage Area (km^2)	Treatment Cost ($)
72,872	313,403	842.8	127,864

The systematic addition of treatment units was conducted in two ways: 1) combine new habitat blocks into an ever larger single treatment unit or 2) add habitat blocks as multiple, discrete treatment units. These two approaches were intended to contrast the effect of opening a single large river with the effect of opening numerous small tributaries, with the same overall increase in total habitat area. When additional habitat blocks were combined to form a single treatment unit, the total habitat area, drainage area, and treatment cost were correspondingly increased in a 1:1 relationship; a treatment unit composed of six habitat blocks would therefore have twice the drainage area, treatment cost, and habitat area as one composed of three such blocks. I systematically assessed the effect of increased habitat availability by adding three habitat blocks at a time. This was a convenient scale of analysis because nine additional habitat units represent a 10% increase in total habitat availability across Lake Michigan. In the end, I chose to evaluate increasing habitat availability up to an additional 18 habitat units, representing a 20% increase in habitat availability across the basin.

The influence of two categorical treatment unit attributes, namely producer status and geographic region, on the sea lamprey response to barrier removals were formally evaluated by running increasing habitat addition simulations for each possible combination of attributes. New habitat areas were either assigned the status of regular or irregular producers and the geographic location of northern or southern Lake Michigan, with the corresponding Ricker recruitment curves and spawner allocations, respectively. The range of outcomes observed across each of these attribute scenarios reflected the range of variation expected with future dam removals, especially as new river systems cannot be readily identified as regular or irregular producers *a priori*.

For each dam removal scenario, I ran the SLaMSE model for 5000 simulations, with a 100 year time horizon for each simulation; this was intended to capture the full range of stochasticity in model results. For every simulation, the mean number of total lake-wide adult spawners across the last ten years was calculated to represent expected equilibrium conditions. This mean system response was summarized by calculating the percent change in mean abundance from status quo mean abundance using the equation below, in which the original value refers to mean status quo abundance unless otherwise stated:

$$\frac{(New\,Value - Original\,Value)}{Original\,Value} \times 100$$

The observed range of variation for each model run represented variability among the simulation-specific 10-year averages. I also took advantage of the stochastic nature of the simulations to calculate the proportion of the 5000 simulations, for each habitat addition scenario, exceeding a high threshold relative to average status quo spawner abundance; I selected an abundance of 152,266 based on the 90th percentile of simulated lamprey abundances under status quo conditions. This simulated threshold abundance is similar to the maximum observed Lake Michigan adult abundance of 141,730 over a recent 10-year period (2005-2014). Finally, to calibrate the model at the current Lake Michigan control budget of $2.42 million, larval survival was adjusted until the base model (*i.e.*, no habitat additions) successfully projected the recent observed average adult abundance of 72,200 (M. Siefkes, Great Lakes Fishery Commission, Ann Arbor, Michigan, personal communication, 2016).

To explain the observed trends in sea lamprey abundance with increasing habitat availability, I ran additional simulations to characterize trends in the following model components: stream-specific parasite production, control budget allocation among the newly added and original treatment units, and lampricide treatment frequency. Parasitic sea lamprey

production reflected the total number of metamorphosed sea lampreys leaving streams in each year and iteration. Tracking stream-specific parasite production facilitated comparison of the relative contribution of the new and original treatment units to lake-wide adult abundances. Additionally, looking at both control budget allocation and treatment frequency helped to explain why the relative contributions of parasite production from new and original treatment units might change with increasing habitat availability.

I ran these additional simulations 1000 times over the same 100 year timespan; consistent with other simulations, only the last ten years of data in each simulation were used to characterize trends. Simulations were run only for increasing habitat availability in which regular producing streams were added to northern Lake Michigan, as these attributes produced the strongest trends in sea lamprey abundance and were therefore more amenable for elucidating population drivers. I ran these simulations across the full range of increasing habitat availability and for both the single large and multiple small river additions.

Modeling Barrier Removal on the Grand River

I selected the potential removal of the Sixth Street Dam to demonstrate the utility of SLaMSE in informing a relevant, potentially high impact barrier removal scenario. The Sixth Street Dam is located in downtown Grand Rapids, MI, and has served as an incidental lamprey barrier on the Grand River, Michigan's longest river system. This barrier currently blocks a large extent of potential lamprey habitat from access by migrating spawners. Approximately 96 km lies between the Sixth Street Dam and the Webber Dam, the next upstream barrier on the mainstem, and numerous large tributaries, including the Thornapple, Maple, and Rogue Rivers drain into the Grand River between the two dams, in addition to many smaller streams (Fig. 2.1).
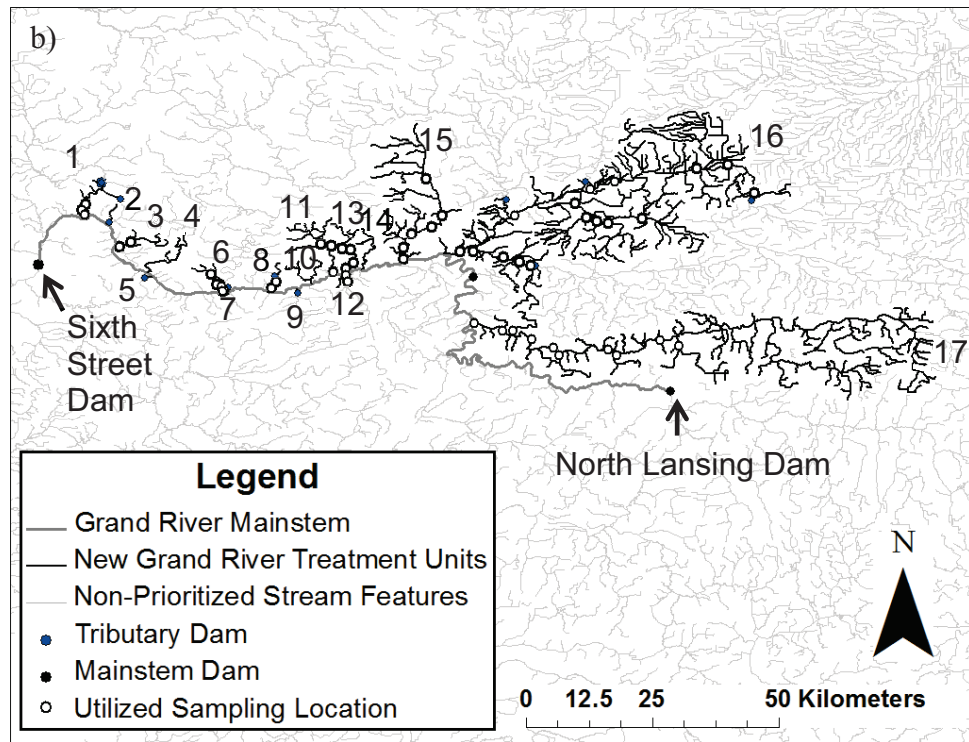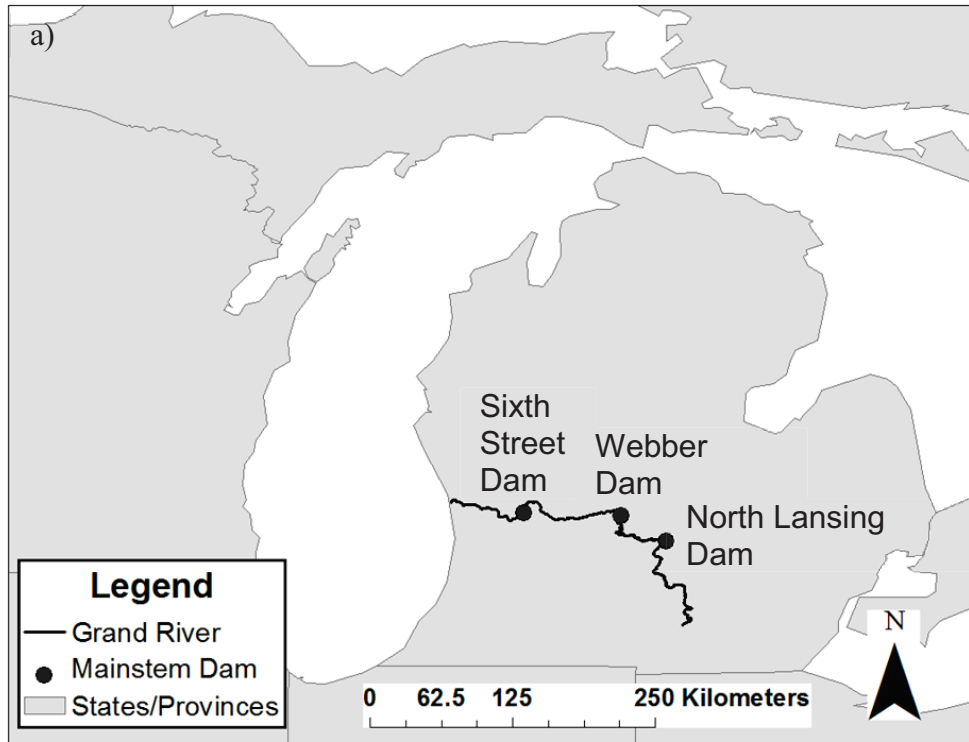
Figure 2.1: Map of the Grand River mainstem (a) and the modeled Grand River system between the Sixth Street Dam and North Lansing Dam (b). Numbers in (b) correspond to numbered treatment unit names in Table 2.2.

Recently, there has been pressure by stakeholders to remove this dam, with the primary goal of recreating the historical rapids and establishing new recreational boating opportunities (Adair and Sullivan 2015). Thanks in large part to the current relevance and extent of protected upstream habitat, the Sixth Street Dam removal scenario was listed a high priority for modeling by SLCP managers (P. Hrodey and M. Siefkes, Great Lakes Fishery Commission, Ann Arbor, Michigan, personal communication, 2015). Furthermore, this system can also be modeled with some degree of accuracy given the quantity of compiled data; SLCP surveys for larval habitat quantities and native lamprey densities were conducted in 2014 and 2015 (Adair and Sullivan 2015), in addition to the recent development of treatment cost estimates for the area.

To simulate the removal of the Sixth Street Dam, I incorporated sixteen new treatment units between the Sixth Street Dam and Webber Dam, each representing distinct Grand River tributaries, to the SLaMSE database. The mainstem of the Grand River was deemed unlikely to host significant larval quantities or require treatment (Fig. 2.1; J. Tews, U.S. Fish and Wildlife Service, Ludington, MI, personal communication, 2015). Each included treatment unit was known to contain viable habitat for spawning and larval sea lamprey, and had a uniquely estimable treatment cost.

Additional attributes of the new treatment units were then estimated using all available data on the Grand River. The following inputs were estimated for each treatment unit using available data sources from the SLCP: total stream length, average stream width, the proportion of Type I and Type II habitat, and treatment cost (Table 2.2). Total stream length was calculated using the Sea Lamprey Control Map, a decision-support tool developed by the SLCP to help quantify and visualize the extent of potential sea lamprey habitat blocked by barriers in the Great Lakes (Great Lakes Fishery Commission 2016). Average stream width and the proportion of

Type I and Type II habitat for each treatment unit were estimated by calculating the mean of all transect data within the system (D. Keffer, U.S. Fish and Wildlife Service, Ludington, MI, unpublished data). If transect data were absent, the mean width from a similarly-sized, nearby treatment unit and average habitat proportions across all other treatment units served as replacements; this was required for six of the sixteen units. Treatment unit length, width, and habitat proportion data were used in concert to calculate total Type I and Type II habitat area values. Treatment cost estimates were obtained for all sixteen tributary units from SLCP agents. Drainage area estimates for each treatment unit, obtained from the National Hydrography Dataset Plus (1:100,000 scale; http://www.horizon-systems.com/nhdplus), were calculated then scaled to match the total drainage area of the Grand River. In the case of independent treatment units within a single watershed, like the Grand River, treatment units are assigned a proportional fraction of the entire watershed's drainage area, based on the relative size of their drainage areas compared to that of all other units. The drainage areas of the new treatment units, in addition to existing units downstream of the Sixth Street Dam, therefore were appropriately adjusted based on their individual drainage area estimates. Other inputs, including river-specific features describing sea lamprey growth and mortality rates, could not be estimated using external databases and were assigned the same values as existing Grand River treatment units downstream of the Sixth Street Dam.

Table 2.2: Base model inputs for the new treatment units in the Grand River, upstream of the Sixth Street Dam. Treatment units are ordered top to bottom by increasing upstream distance from the Sixth Street Dam.

Treatment Unit Tributary	Length (m)	Width (m)	Type I Habitat (Proportion)	Type II Habitat (Proportion)	Treatment Cost ($)
1. Rogue River	4122	25.79	0.0633	0.1302	131125
2. Bear Creek	1631	6.86	0.1675	0.3503	49230
3. Egypt Creek	7093	2.73	0.3013	0.2989	90440
4. Honey Creek	5659	4.31	0.2329	0.3566	97110
5. Thornapple River	479	16.70	0.1675	0.3503	387840
6. Lowell Creek	4172	3.21	0.2407	0.4824	73170
7. Flat River	412	16.70	0.1675	0.3503	245870
8. Toles Creek	4544	2.93	0.1324	0.4532	171800
9. Lake Creek	3359	5.25	0.1675	0.3503	83870
10. Red Creek	6438	2.99	0.1675	0.3503	196700
11. Timberlin Creek	2842	2.85	0.2277	0.4010	64485
12. Sessions Creek	1962	5.25	0.0763	0.1529	73385
13. Bellamy Creek	13536	6.86	0.1096	0.3468	164700
14. Trestle Creek	3473	5.25	0.1675	0.3503	68085
15. Prairie Creek	29846	11.80	0.1320	0.1658	196700
16. Maple River	133946	18.56	0.1526	0.3838	503161
17. Looking Glass River*	93979	20.86	0.1195	0.1306	471201

I also accounted for the potential influence of numerous small tributaries along the Grand River mainstem, deemed too small or otherwise insignificant to merit consideration as an independent treatment unit, on future sea lamprey production. Using estimates of the expected influence of these small tributaries in attracting sea lamprey spawners, based on their observed drainage areas, I calculated the probable, proportional increase in available habitat in the upstream Grand River that might result if lampreys used these small tributaries. This increase in available habitat was then spread equally among the sixteen new treatment units by artificially increasing stream lengths; a similar adjustment was made for relative drainage area. The total cost of treating these small tributaries for larval sea lamprey, again estimated by control agents, was also spread equally among the sixteen explicit treatment units. Across all new treatment units, these adjustments resulted in a 2.6% inflation in stream area and drainage area and a 20.0% increase in total treatment cost.

Relevant dam removal scenarios and assumptions for the Sixth Street Dam case study were identified following a meeting with SLCP and Michigan Department of Natural Resources managers. Three primary management decisions were selected as the focus for modeling work: the decision to modify the Webber Dam to block sea lamprey, the decision to treat or ignore the newly available habitat upstream of the Sixth Street Dam, and the decision to maintain or increase the current lake-wide control budget (Fig. 2.2). Because the Webber Dam currently has the potential to pass sea lamprey but can be appropriately modified with sufficient justification, I evaluated the decision to modify the dam by simulating the effect of including the Looking Glass River; the Looking Glass River is the only major tributary system between the Webber Dam and the next mainstem barrier. To include this system, I estimated the necessary inputs using the steps outlined for the sixteen new units downstream of Webber Dam (Table 2.2). The decision

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to treat or ignore habitat upstream of the Sixth Street Dam is intended to compare the effect of

potentially pulling treatment effort away from other Lake Michigan tributaries with the effect of

allowing uninhibited lamprey production above the Sixth Street Dam, respectively. Finally, if

the system is in fact treated, I both evaluated the effect of treating the system under the current

budget of $2.42 million and estimated the necessary budget increase to prevent a lake-wide

increase in sea lamprey abundance from status quo. I only evaluated the necessary budget

increase for the scenario in which the Webber Dam was modified to block sea lamprey.
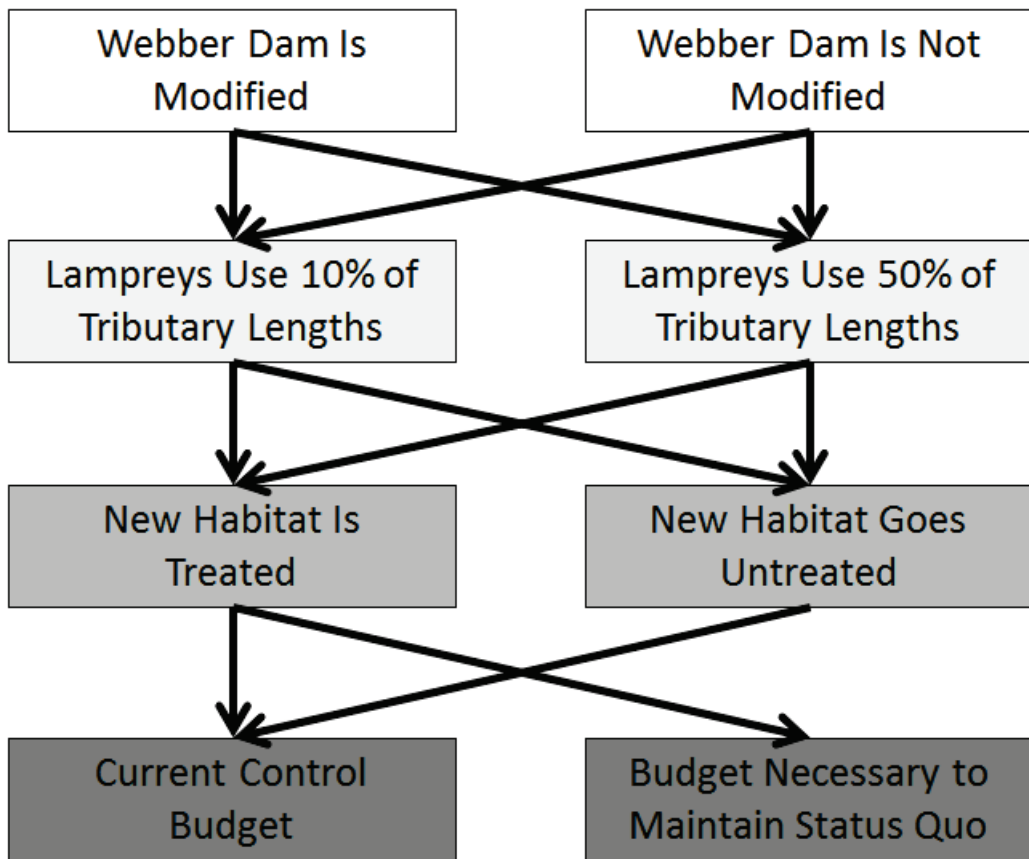
Figure 2.2: Visual representation of the modeling scenario combinations considered in simulating the Sixth Street Dam removal.

I also formally assessed the influence of the assumed degree to which sea lampreys utilize the newly available larval habitat upstream of the Sixth Street Dam. Among all inputs, larval habitat quantity is especially important to evaluate given its observed role in influencing recruitment success (Jones et al. 2003) and explicit incorporation into the SLaMSE model (Jones et al. 2009). I therefore assessed the response of sea lampreys to two levels of assumed habitat use within added tributaries for each of the control scenario combinations: 10% and 50% habitat use. The 10% habitat use represents a reasonable approximation of expected lamprey use of total river length based on professional judgment (A. Jubar, U.S. Fish and Wildlife Service, Ludington, Michigan, personal communication, 2016) and preliminary analyses indicating that the observed lengths of existing Grand River treatment units (obtained from the SLCP's database) averaged just 10% of the total tributary lengths calculated from the Sea Lamprey Control Map (A. Jensen, Michigan State University, East Lansing, Michigan, unpublished analysis). Expected use of total river length is as low as 10% because linear referencing, in which even marginal lotic habitats unsuitable for larval sea lamprey (*e.g.*, drainage ditches, ephemeral headwater creeks) are digitized to form stream GIS datasets, can produce overestimates of total river lengths. I chose to assess the influence of 50% habitat use on the sea lamprey response in order to evaluate a presumed worst-case scenario for extent of habitat use.

The SLaMSE model was run and summarized in the same manner as for the systematic habitat additions (*i.e.*, 5000 simulations, 100 year time horizon, ten year averages) for every scenario and assumption, and the proportions of simulation results above the same status quo threshold were again calculated.

RESULTS

Systematic Habitat Increases

There was a nonlinear increase in the adult sea lamprey population in response to systematically increasing habitat availability (Figs. 2.3, 2.4). The smallest percent increase in mean abundance from status quo conditions with a 20% increase in habitat availability was 161%; the greatest increase exceeded 800%. This nonlinear response with increasing habitat appeared to be adequately characterized by an exponential function across all combinations of types of habitat addition, producer status, and geographic location (Figs. 2.3, 2.4).

The type of barrier removal (*i.e.*, whether there is one large-scale barrier removal or multiple small-scale events) influenced the sea lamprey population's response to barrier removal, with the addition of a single large stream having the greater effect. The largest percent increase in abundance for the single stream addition was 885%, in comparison to 452% for multiple stream additions. This difference in abundance between the types of habitat addition held true across all combinations of producer status and geographic location. Corresponding with the different trends in mean abundance, the proportion of simulations with forecasted abundances greater than the high threshold relative to status quo abundance (152,266) also approached one more rapidly, relative to the amount of added habitat, when additions were conducted as a single large river.
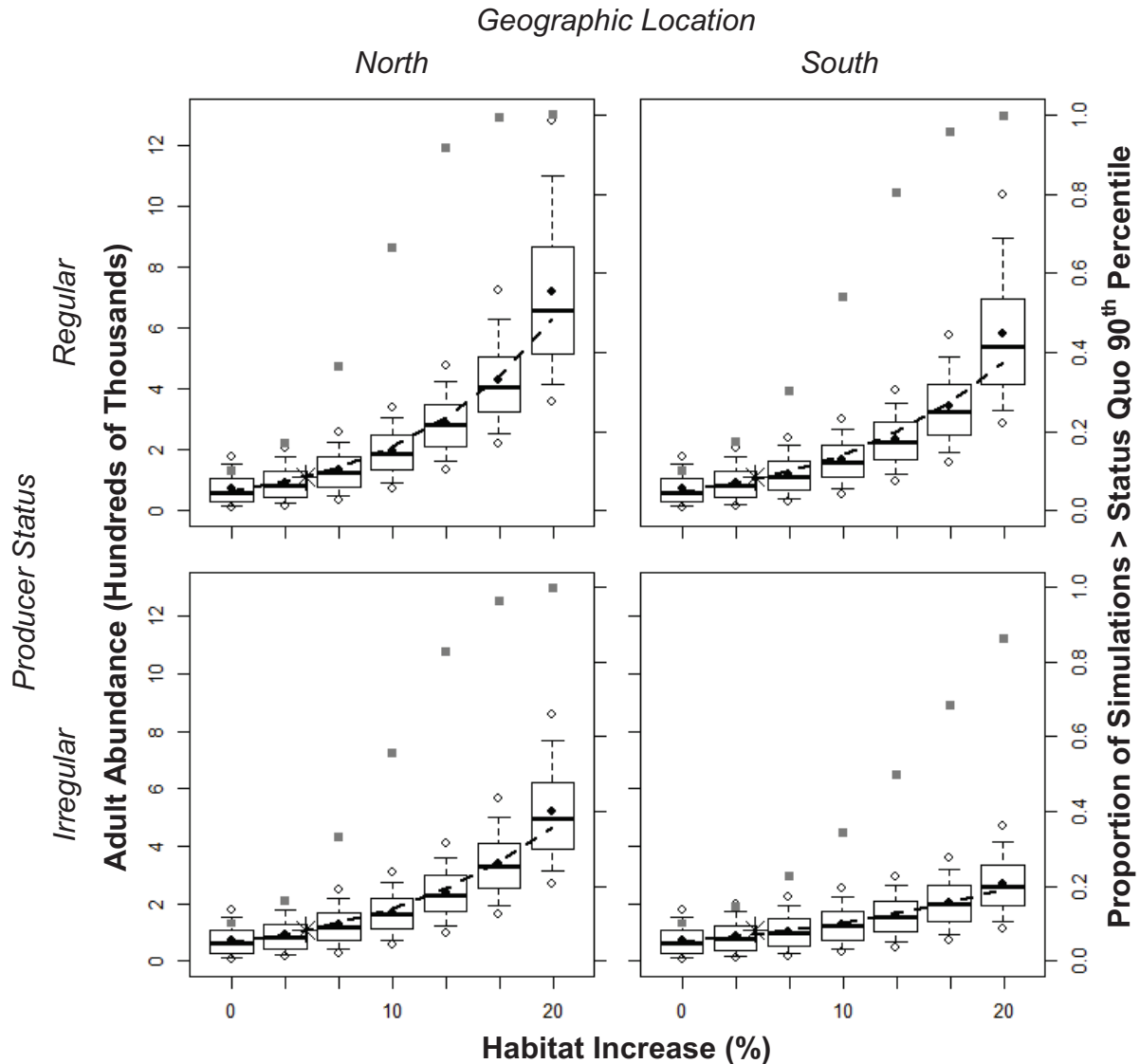
Figure 2.3: Adult sea lamprey abundance trends with increasing habitat availability, assuming habitat units are added within a single stream unit. Boxes, whisker bars, and open circles represent the 25th and 75th, 10th and 90th, and 5th and 95th percentiles of simulated adult abundances, respectively. Solid horizontal lines and black circles represent corresponding median and mean values, respectively, and the dashed line represents the exponential model fit to the mean abundance values. The asterisk indicates mean lamprey abundance from Scenario #1 of the Grand River case study, with an assumed 10% habitat use (see Figure 2.7). Gray squares indicate proportions of simulations with abundances greater than the status quo 90th percentile.
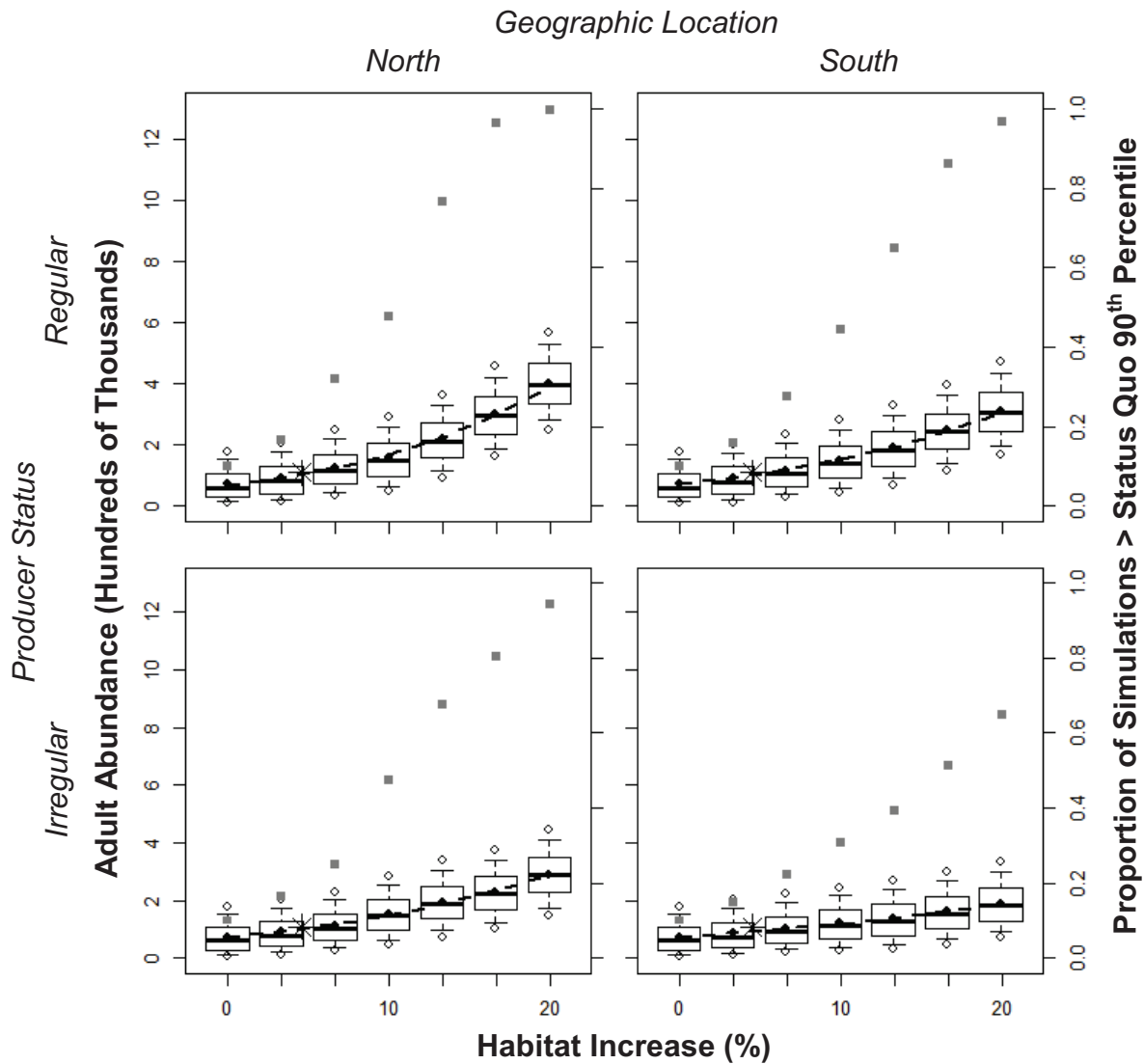
Figure 2.4: Adult sea lamprey abundance trends with increasing habitat availability, assuming habitat units are added as independent stream units. Boxes, whisker bars, and open circles represent the 25th and 75th, 10th and 90th, and 5th and 95th percentiles of simulated adult abundances, respectively. Solid horizontal lines and black circles represent corresponding median and mean values, respectively, and the dashed line represents the exponential model fit to the mean abundance values. The asterisk indicates mean lamprey abundance from Scenario #1 of the Grand River case study, with an assumed 10% habitat use (see Figure 2.7). Gray squares indicate proportions of simulations with abundances greater than the status quo 90th percentile.

The status of opened river systems as regular or irregular producers, as well as their geographical location, also had implications for the effectiveness of sea lamprey control under dam removal scenarios. Habitat additions to northern Lake Michigan resulted in higher abundances than habitat additions in southern Lake Michigan, and new treatment units assigned as regular producers produced greater overall abundances than habitat additions assigned as irregular producers (Figs. 2.3, 2.4). Among the two categorical factors of producer status and geographic location, producer status of the newly added habitat had a slightly greater effect on resulting adult sea lamprey abundances. With a 20% increase in habitat availability and the combination of geographic region and type of habitat addition held constant, regular producer habitat additions resulted in 38.2% to 115% greater mean adult sea lamprey abundances relative to abundances arising from habitat additions assigned as irregular producers. With the same 20% increase in habitat availability, habitat added to northern Lake Michigan resulted in mean abundances 23.3% to 92.2% greater than those achieved with habitat added to southern Lake Michigan.

A combination of novel parasite production from newly added habitat and exponentially increasing parasite production from the original treatment units, caused in part by a shifting allocation of treatment effort away from original units to new ones, appeared to drive the exponential response of adult sea lamprey abundance to habitat increases. There was a trend of increasing average contribution of new treatment units to basin-wide parasite production with increasing habitat availability (Fig. 2.5a). This increasing relative contribution from new habitat constituted novel production of parasites due to barrier removals, but did not completely explain the magnitude of the sea lamprey response to habitat change, especially if we assume the production of parasites from the original Lake Michigan treatment units remained unchanged.

Perhaps more importantly, increasing habitat availability also caused a steep, concurrent increase in parasite production within the original treatment units (Fig. 2.5b); the nature of the response was consistent across both types of habitat addition. This response may be explained in part by the reduced overall annual treatment frequency among original treatment units with increasing habitat additions (Fig 2.5c). Concurrently, the average annual allocation of the control budget to original treatment units declined from $2.42 million to a median of $2.07 and $1.79 million for the single and multiple treatment unit additions, respectively, when 18 habitat units were added to the Lake Michigan basin (Fig. 2.6).
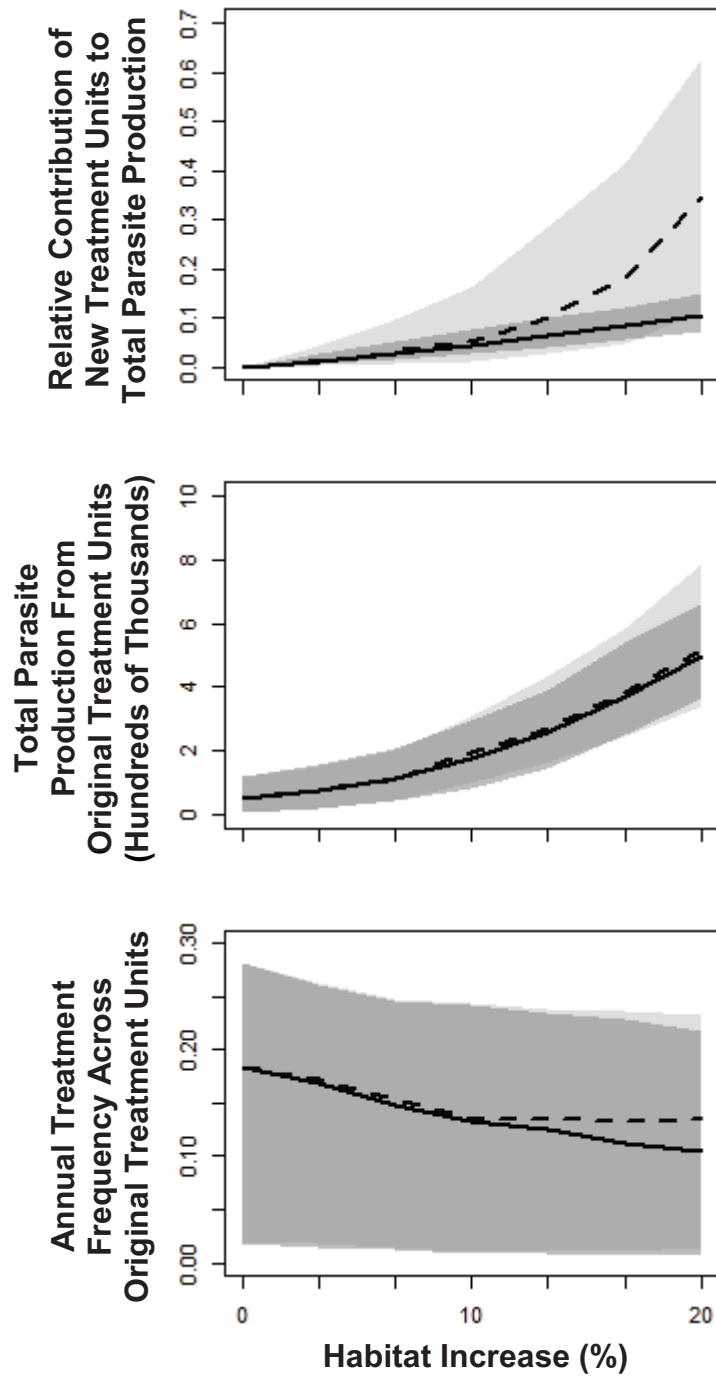
Figure 2.5: Changing model characteristics with increasing habitat. Lines and polygons represent the median and 10th and 90th percentiles, respectively, across all simulations (a, b) or treatment units (c). The dotted line and lighter polygon illustrate the effect of adding a single, large unit, and the solid line and darker polygon illustrate the addition of habitat units as multiple, discrete treatment units, respectively.
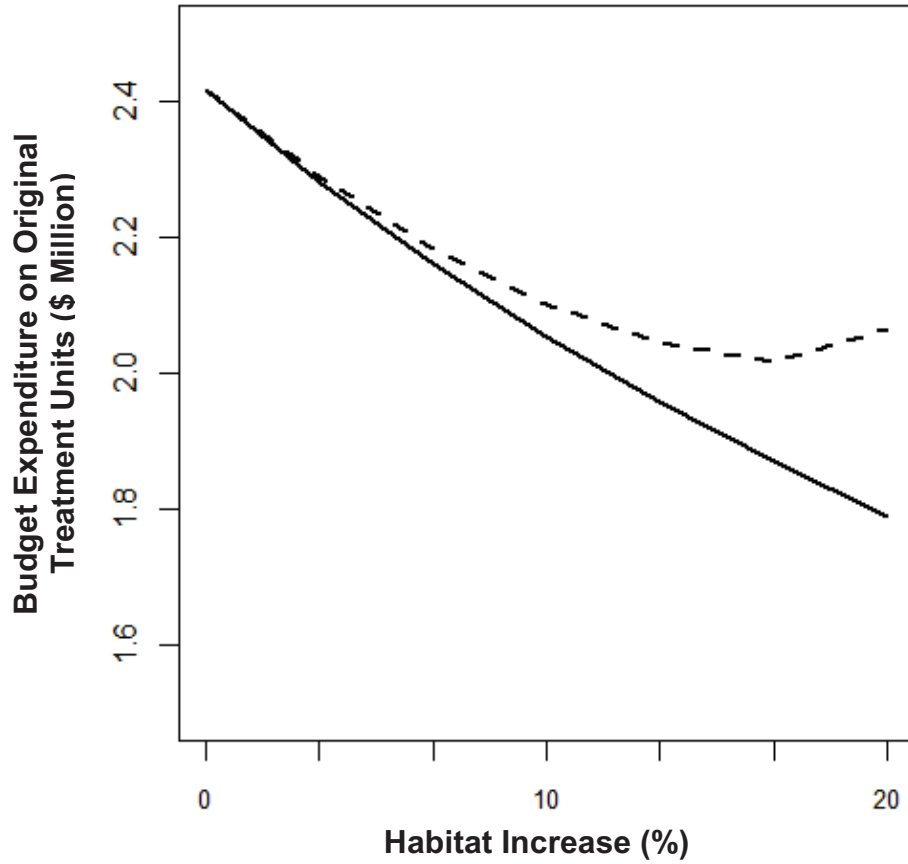
Figure 2.6: Average annual budget expenditure on the original treatment units with increasing habitat availability. The dotted and solid lines illustrate the response when habitat is added as a single, ever-larger system and multiple, discrete treatment units, respectively.

Case Study: Barrier Removal on the Grand River

Treatment unit attributes were successfully estimated for all 17 potential new treatment units (Table 2.2). The length measurements represent values expected for 10% habitat utilization; stream length was subsequently adjusted upwards to accommodate the 50% habitat use assumption. Drainage area values are not listed as they varied depending on the simulation scenario; the decision to exclude or include the Looking Glass River necessarily altered drainage area values for all other Grand River treatment units, as they are expressed relative to the Grand River's total drainage area.

All management scenarios pertaining to the dam removal forecasted large increases in adult sea lamprey abundance in Lake Michigan, assuming the control budget remains unchanged (Fig. 2.7). Among the simulations, the lowest mean percent increase in adult abundance, over that observed under status quo conditions, was 52%. It occurred when the Webber Dam was modified to block sea lamprey, new habitat units were treated, and sea lampreys used 10% of available habitat. For the same scenario, just over 24% of simulations produced abundances exceeding the status quo 90th percentile. The largest mean increase of 269% occurred when an unmodified Webber Dam allowed sea lamprey to infest the Looking Glass River, none of the new habitat units were treated, and sea lampreys used 50% of potentially available habitat. Approximately 87% of simulations resulted in spawner abundances exceeding the threshold for this worst case scenario.
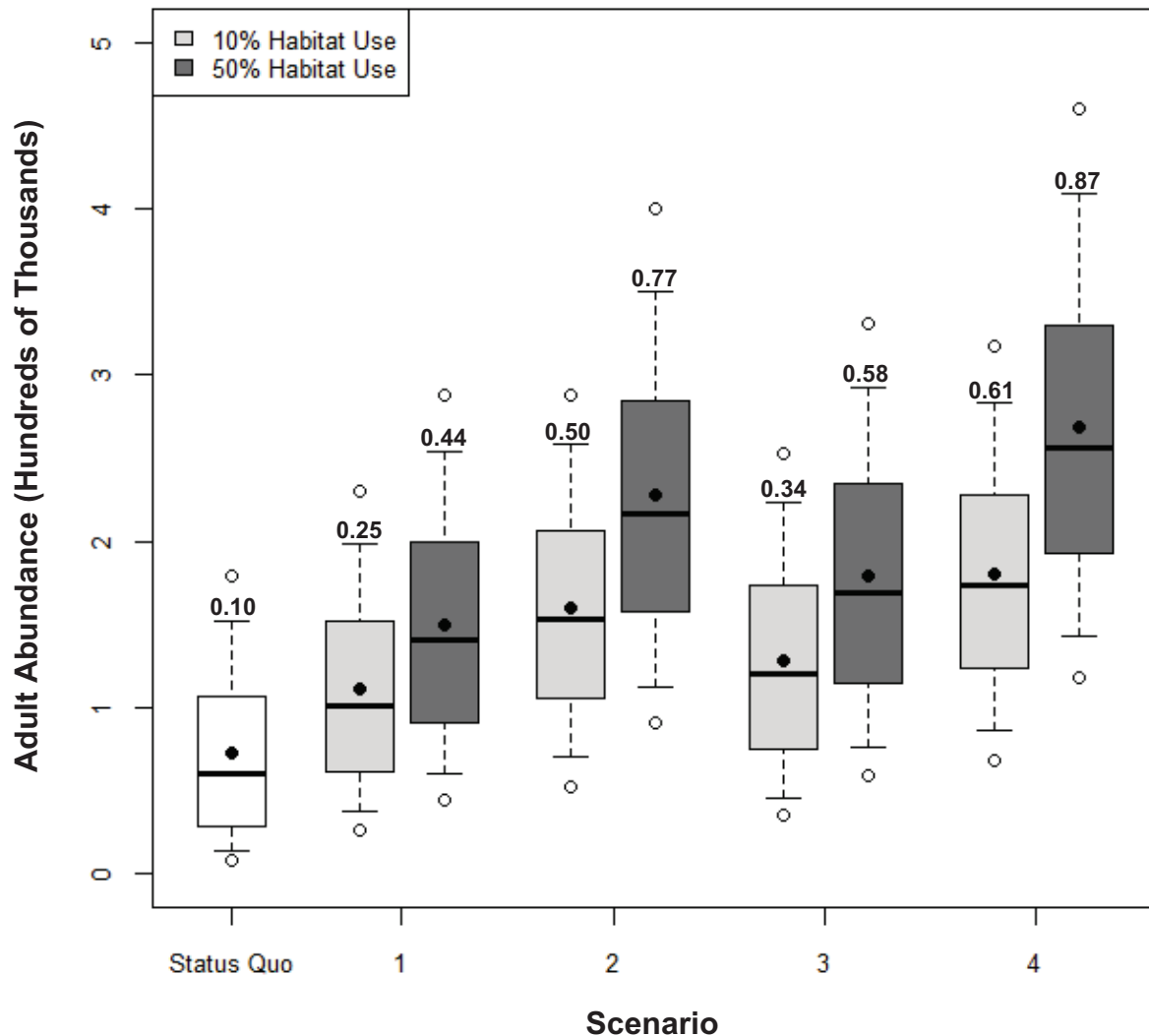
Figure 2.7: Expected sea lamprey abundances for each of the management scenarios. Scenarios #1 and #2 exclude the Looking Glass River, while Scenarios #3 and #4 account for its influence. New treatment units are treated by the SLCP in Scenarios #1 and #3, and ignored in Scenarios #2 and #4. Boxes, whisker bars, and open circles represent the 25th and 75th, 10th and 90th, and 5th and 95th percentiles of simulated adult abundances, respectively. The solid horizontal lines and black circles represent median and mean values, respectively. Numbers above the upper whisker bars indicate the proportion of simulations greater than the status quo 90th percentile.

The decision to modify the Webber Dam, the decision to treat the upstream Grand River, and the assumed degree of habitat use each had substantial effects on equilibrium sea lamprey abundances, but the relative magnitude of effects differed. When the decision to treat and assumed habitat use were otherwise held constant among scenarios, the percent difference in mean lake-wide sea lamprey abundance between simulations including and excluding the Looking Glass River ranged between 13.1% and 19.6%, with higher simulated abundances for scenarios including the Looking Glass River. The decision whether or not to treat the upstream Grand River system had a larger effect on sea lamprey numbers than the decision to modify Webber Dam. Compared to simulation scenarios with the new habitat units considered for treatment, again assuming that all other factors are held constant, the decision to not treat these units resulted in a 40.4% to 52.1% increase in average adult abundance. Assuming increased habitat utilization in the new treatment units had a similarly dramatic effect on equilibrium sea lamprey abundances. With management decisions held constant, the increase in assumed habitat utilization from 10% to 50% caused the percent differences in abundances between these habitat use assumptions to range from 34.7% to 49.1%.

For the dam removal scenario in which the Webber Dam is modified to block sea lamprey, substantial increases in the annual Lake Michigan control budget were needed to restore mean sea lamprey abundances to levels at or below status quo under the two assumptions of habitat use. Simulations suggested an annual control budget of $2.62 million per year, representing a $200,000 increase from the current $2.42 million budget, was needed to decrease mean abundances to levels at or just below status quo when assumed habitat use was 10% (Fig. 2.8). In comparison, a control budget of $2.78 million was required to accomplish the same

objective when assumed habitat use was 50%, representing an annual budget increase of
$360,000.
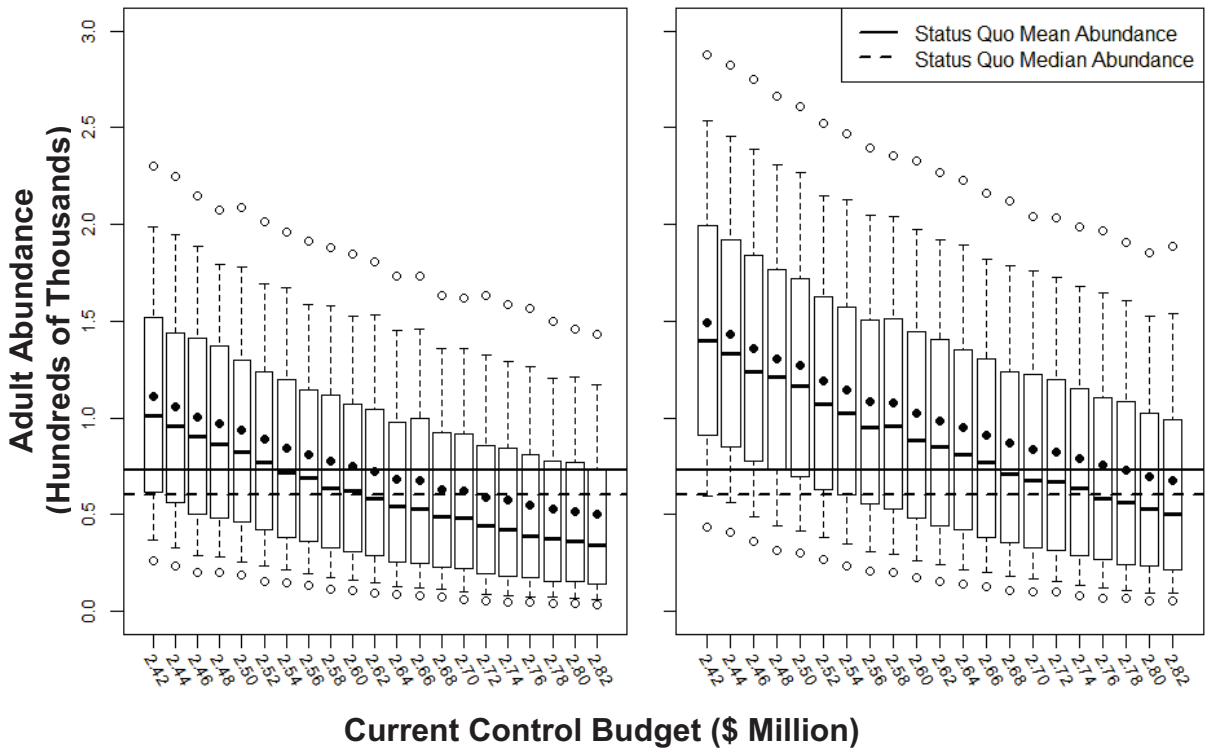
Figure 2.8: Expected sea lamprey abundances when the Sixth Street Dam is removed, the
Webber Dam is modified to block sea lamprey, lampreys are assumed to use 10% (a) or 50% (b)
of maximum potential river length, and the new treatment units are allocated control efforts with
a steadily increasing Lake Michigan control budget. Boxes, whisker bars, and open circles
represent the 25th and 75th, 10th and 90th, and 5th and 95th percentiles of simulated adult
abundances, respectively. The solid horizontal lines and black circles represent median and
mean values, respectively.

DISCUSSION

This analysis quantitatively characterized the probable response of the Lake Michigan sea lamprey population to increasing habitat availability associated with future barrier removals. Simulations of systematic habitat additions resulted in an exponential population response to changing habitat, revealed causative drivers of this change within the tightly-controlled biological system, and illustrated sensitivity to habitat quality attributes. The simulated influence of alternative management actions and expected cost of maintaining status quo sea lamprey abundance after removal of the Sixth Street Dam can inform future conservation actions within the Grand River watershed. More broadly, modeling results revealed complex dynamic behavior of an intensively managed biological system.

The systematic habitat addition simulations showed that a heavily-controlled invasive species, like sea lamprey, responds to the localized easing of key management-imposed constraints in a complex, disproportionate manner. The primary constraints on sea lamprey population growth in the Great Lakes are habitat limitations created by barriers in large river systems and lampricide treatment-induced mortality at the larval stage (Christie et al. 2003; Lavis et al. 2003). When these two constraints were diminished by the addition of habitat and the subsequent shifting of treatment efforts to these new habitat patches, sea lamprey production increased in both the new and original river systems and Lake Michigan adult abundances exhibited a sharp, exponential increase. The population responded to the new habitat through the immediate contribution of additional parasite production from the new treatment unit(s). Additionally, the simulated shifts in control effort allocation, following established management procedures, seemed to drive a more complex response from the original treatment units. The

necessity to treat new habitat in a zero-sum control system caused an overall decrease in treatment frequency across original treatment units, which contributed to increased production from the these units and helped drive the overall population response. The inter-connected relaxation of the two critical constraints of habitat and lampricide control determined the sea lamprey response to increasing habitat availability. Similarly complex responses in population abundance to changing top-down controls have been observed in outbreaks of mesopredators ("mesopredator release"), in which small reductions in the abundance of apex predators trigger disproportion increases in mesopredator abundance (Ritchie and Johnson 2009).

Compounding these shifts in treatment allocation and parasite production is the likely presence of positive feedback. Positive feedback effects are often observed in complex fisheries systems under changing predation pressure or habitat conditions (Rose and Cowan Jr 2000; Walters and Kitchell 2001; Kirby et al. 2009; Audzijonyte et al. 2013). In the Lake Michigan system, positive feedback refers to increased recruitment and subsequent parasite production from previously spawner-limited river systems due to increased lake-wide production of parasites from newly added habitat. Great Lakes sea lampreys seem to exhibit density-dependent recruitment with a large degree of density-independent variation (Jones et al. 2003; Dawson and Jones 2009). Great Lakes sea lamprey populations are currently suppressed to abundances less than 10% of historical abundances by the combination of lampricides and barriers, and this suppression of adult numbers likely results in spawner-limited tributaries. Increased spawner allocations to each Lake Michigan tributary, driven by elevated spawner abundances across Lake Michigan from the addition of habitat, should produce greater future recruitment in these rivers, and contribute to increasing lamprey production across the basin. Of course, the magnitude of

this effect will eventually be limited by compensation (*i.e.*, spawner over-saturation), but this likely does not occur until after some positive feedback effects are observed.

In total, the combined new production from new habitats, increased production from old habitats due to shifted control efforts, and positive feedback drove a large response of sea lamprey abundance from a comparatively small increase in habitat. There is evidence for such a population response from historical barrier failures in Lake Michigan, as unrestricted colonization of 220 km of the Manistique River in the late 1990s and early 2000s was associated with approximately a 100% increase in the estimated Lake Michigan sea lamprey abundance (Klar and Young 2004). Although the example represents uncontrolled production from a river system, it suggests that increased habitat availability for a controlled species can have disproportionate consequences.

The simulated effects of positive feedbacks and shifting treatment efforts in driving the Lake Michigan sea lamprey population response underscore the importance of explicitly considering linked impacts when evaluating barrier removal decisions. For species that exhibit natal homing for spawning, increased spawning and larval habitat in a single stream will typically translate into increased productivity for that stream. Sea lampreys, however, do not exhibit natal homing, and the allocation of spawners to rivers in the SLaMSE model reflects this reality (Bergstedt and Seelye 1995; Jones et al. 2009). The effects of increased production from a single river for a non-homing species, like sea lamprey, are spread throughout the basin in the form of broad, but more modest, increases in spawners in multiple streams, with a corresponding increase in average recruitment success. Furthermore, the need to treat new regions of habitat made accessible by barrier removals disrupts the finely tuned balance of control effort among the linked river systems and leads to escalating production from pre-existing treatment units. These

results suggest that evaluations of barrier removals focusing on potential fish responses must consider broader scale, linked implications of increased fish production, especially for systems in which species do not exhibit strict natal homing and control effort is necessarily balanced among many streams.

My analysis also revealed that barrier removal decisions need to account for factors in addition to habitat quantity to accurately assess the effects of barrier removal. Specifically, the decision to remove a dam from a single large river system versus multiple small rivers, while providing access to the same overall amount of additional habitat, had a large influence on lamprey response, as adding ever-larger single river systems produced much greater increases in lake-wide lamprey abundance than adding multiple discrete units. The difference is due to the challenge of incorporating increasingly expensive single-system treatments into an annual stream ranking system; in the current scheme, streams in a given year are treated in descending order based on the projected cost per expected larva killed until the available budget is exhausted (Slade et al. 2003). As a system becomes more expensive to treat, the probability that there would be sufficient budget remaining by the time it ranks for treatment decreases; if there is insufficient budget remaining at the point a treatment unit is selected, the unit will be passed over and lower ranked, less expensive systems will instead be treated. There is evidence for this occurring in the model results: trends in budget expenditure and treatment frequency among original treatment units appeared to flatten and even rise slightly as increasing habitat availability in a single large river approaches the final value of 20% (Figs. 2.5c, 2.6). Furthermore, consistent with the differing treatment frequencies for the types of habitat addition, parasite production from new habitat for the single river dam removal increased more steeply with increasing habitat additions than that for multiple dam removals (Fig. 2.5a). Within the existing

model framework, an increasingly large single river system is simply more difficult to treat than multiple, smaller river systems, and ends up producing more parasites than the same amount of added habitat spread over several smaller rivers.

The geographic location and production potential (*i.e.*, regular or irregular producers) of affected areas also played important roles in mediating the sea lamprey response to increasing barrier removals. The geographic location of barrier removals regulates the sea lamprey response by dictating spawner allocation to new habitat units. Given that a fixed 52% of lake-wide spawners are allocated to northern Lake Michigan tributaries, with smaller overall drainage areas relative to the southern tributaries, habitat additions in northern Lake Michigan will result in relatively greater spawner allocations to these new habitat units, which in turn increases the production potential and required treatment frequency in the new habitat units. In comparison, inherent production potential regulates the response by affecting recruitment dynamics; regular producers produce more recruits per spawner, on average, than irregular ones. This has the same effect of increasing production potential and required treatment effort in the new habitat areas. In a similar vein, the influence of dams and fragmentation on indicator fish species has been shown to be mediated by river attributes including stream size and thermal regime (Cooper et al. 2016). The variability in projected abundances among these scenarios, dependent on the attributes of the newly available habitat, therefore should be considered when making barrier removal decisions.

Furthermore, the high degree of variability across simulations for each of the barrier removal scenarios reflects very real uncertainty in our understanding of sea lamprey dynamics and should be explicitly recognized in decision making. One of the strengths of the MSE approach is the incorporation of multiple sources of uncertainty (Bunnefeld et al. 2011); for the

SLaMSE model, these sources included stochasticity in biological processes, larval abundance assessments, and control efforts. The resulting variability in model results indicates that the calculated mean responses in abundance are by no means guaranteed outcomes. Instead, the results indicate expected trends in the sea lamprey response to barrier removals, with a correspondingly wide range of plausible alternative outcomes. Reporting results as proportions of simulations with values above some threshold value, selected in this paper as the upper limit of expected status quo conditions, is one useful means of capturing uncertainty in the simulated outcomes; decision-makers can then use information like this to assess the risk of key decisions. In some cases, precautionary approaches are used to deal with uncertainty over management actions (Kell et al. 1999); in others, uncertainty can be formally accounted for using a decision analysis process (Irwin et al. 2008). Modeling approaches like that of SLaMSE are not intended to make decisions (Sharov and Liebhold 1998). Instead, these models provide information on the best current understanding of the influence of management actions on biological processes, and the uncertainty around this understanding is a critical component of the simulation results whenever decisions involve risks.

Simulating the removal of the Sixth Street dam can inform decision making efforts on the Grand River. The difference between the treated and untreated habitat scenarios points to the value of treating the upstream Grand River in the case of barrier removal. The decision to ignore the upstream habitat resulted in higher sea lamprey abundances, despite the dilution of basin-wide treatment effort that would have occurred if upstream habitat were to be treated. The decision to modify the Webber Dam also appeared to be secondary in importance to that regarding treatment, as the decision to include upstream habitat in treatment efforts had the relatively bigger effect on the sea lamprey response. Finally, the modest control budget

increases required to suppress sea lamprey to status quo abundances, relative to the percent

increases in abundance with no change in budget, seem to justify the recommended increases in

annual control spending.   Similar to this application of management strategy evaluation to the

Sixth Street Dam removal, MSE has guided other fisheries-based decisions in the face of

biological and management uncertainty (Kell et al. 1999; Smith et al. 1999; Irwin et al. 2012;

Dawson et al. 2016). Additional SLaMSE-based analyses around the Great Lakes could be used

to inform management decisions for future barrier removal scenarios.

The responsiveness of model results to uncertainty about habitat use by colonizing sea

lampreys underscores the importance of identifying accurate input values. Moving from a 10%

to 50% habitat use assumption, for each of the four evaluated management scenarios,

meaningfully increased expected mean lamprey abundances. Although the 10% assumption can

be considered a reasonable estimate based on professional judgment and preliminary analyses, it

remains a rough approximation, as does the worst case scenario of 50% habitat use. Identifying

reliable habitat area estimates in future modeling endeavors will require both more detailed GIS

data integrating length and width information along streams and improved empirical

understanding of habitat use by spawning sea lamprey within tributary systems. Although not

utilized in these simulation efforts, results from habitat modeling for sea lamprey-specific

attributes like larval habitat quality also have the potential to improve future population

dynamics work (see chapter 1).

An important, implicit assumption of all case study simulations is my assumption that

migrating sea lampreys would utilize all selected upstream tributary systems after the dam

removal.   This assumption has been largely supported by dam removal studies on coastal river

systems smaller than the Grand River, in which lampreys were observed to quickly re-colonize

previously blocked upstream habitat (Hogg et al. 2013; Lasne et al. 2014). Additionally, sea lampreys appeared to rapidly colonize upstream reaches of the Manistique River in northern Michigan, a river section over 220 km in length (Klar and Young 2004). Upstream migration rates for land-locked sea lamprey have been observed to exceed 3 km/d (Wigley 1959) and appear to increase with increasing stream size (Kelso and Gardner 2000). There is also evidence that lampreys can access and utilize upstream tributaries on larger river systems. Tagged and released anadromous sea lamprey were observed to travel over 18 km to access upstream tributary systems in Portugal's River Mondego, a river system draining a watershed slightly less than half the size of Michigan's Grand River (Almeida et al. 2002).

I also did not simulate the effect of a seasonal barrier on sea lamprey populations. Stakeholder groups have proposed the construction of a seasonally-adjusted structure, in place of the Sixth Street Dam, to operate as a barrier only during sea lamprey migrations (Adair and Sullivan 2015). I chose not to account for this possibility in simulating the dam removal due to the uncertainty surrounding its actual installation and potential success at blocking sea lamprey. If the goals of such a barrier are blocking sea lamprey and allowing passage of other non-jumping, migratory species, the overlapping migration phenologies of Great Lakes fish have been demonstrated to prevent the successful balancing of such objectives without the installation of an effective fishway (Vélez-Espino et al. 2011). While certainly not inclusive of all possibilities, the simulation scenarios and assumptions selected for model analysis reflected best judgment based on the current understanding of the Grand River system and lamprey migratory capacities.

As with most modeling approaches, there are key limitations with the SLaMSE model structure that deserve mentioning. First, the SLaMSE model is concerned with a single species,

and does not take any multi-species interactions within the Great Lakes into account. Related to this, our models assume that sea lampreys in Lake Michigan do not become limited by the availability of hosts, even at projected abundances exceeding observed historical levels in the 1950's and 1960's (Smith and Tibbles 1980). It is reasonable to expect that prey limitation would occur at some of the higher forecasted abundances and restrict further production (LaRue 1980). The current SLaMSE model also lacks the ability to flexibly treat large treatment units, with correspondingly high production potential, outside of the annual stream ranking system. The SLCP sometimes selects high-profile river systems for preferential or consecutive treatments based on professional judgment, independent of the stream ranking system (Adair and Sullivan 2015). It is possible that a more flexible treatment strategy might reduce the effect of adding single large habitat units, in both the systematic habitat additions and Grand River case study, by reducing parasite production from these larger systems. Both modeling limitations have the potential to forecast future sea lamprey abundances above those which might be observed following a real-world barrier removal.

Although other modeling-based approaches have been used to inform barrier removal decisions and predict fish response to changing habitat availability, few, if any, have matched both the extent and resolution of the reported MSE modeling efforts for sea lamprey populations. At the broadest extent, barrier removal prioritization efforts, using information like existing barrier passability, blocked stream length, and estimated cost of removal, are being advocated to optimize barrier removals across varying spatial extents like the coastal rivers of the Pacific Northwest (Kemp and O'Hanley 2010). These models help synthesize multiple sources of information and coordinate decisions at scales similar to the Great Lakes, but often make simplifying assumptions in relating passability, stream length, and habitat quality to future fish

production (Kuby et al. 2005; O'Hanley and Tomberlin 2005; Zheng et al. 2009). At a smaller spatial extent, landscape models are increasingly used to predict some aspect of fish response to barrier removal , including projected steelhead (*Onchorhynchus mykiss*) redd density in the Pacific Northwest (Steel et al. 2004) and northern pike (*Esox lucius*) incidence in northern Sweden (Spens et al. 2007). This type of work also has the potential to inform decision-making at a broad scale using indirect measures of productivity, but does not directly inform fish abundance. Finer resolution modeling has occurred to predict fish response to individual barrier removals using species-specific, population dynamics models for American shad (*Alosa sapidissima*), walleye (*Sander vitreus*), and American eels (*Anguilla rostrata*) (McCleave 2001; Cheng et al. 2006; Harris and Hightower 2012). While these models successfully predicted fish production from systems under different barrier removal scenarios, they did not connect stream-specific production to larger population effects or extrapolate findings to other river systems. To our knowledge, no previous studies have assessed fish responses to barrier removal using a detailed, species-specific management strategy evaluation approach across a spatial extent comparable to Lake Michigan, nor have they explicitly considered the implications of barrier removals in a coupled management system with trade-offs. Results from these analyses therefore represent unique, spatially explicit, and comprehensive population predictions for a suppressed invasive species.

The MSE modeling efforts for the Lake Michigan sea lamprey population represent a useful quantification of the sea lamprey response to barrier removal and can be used to guide future barrier decisions. Modeling results revealed new insights into interactions and feedbacks among the different system components, and highlighted the high degree of uncertainty in the expected responses to habitat additions. This type of MSE approach has the potential to be

replicated in other biological systems similar to that of Great Lakes sea lamprey, in which a detailed understanding of a controlled species' population dynamics is already established and there is a readily manipulated environmental constraint. Future SLaMSE-based analyses of barrier removals can be improved by implementing some form of prey-based limitation in population growth, continuing to increase the quality of input data, and clarifying our understanding of sea lamprey migratory capacity in the Great Lakes.

MANAGEMENT RECOMMENDATIONS

The limited success in predicting the quantity of Type I and Type II data in stream

reaches in the Lake Michigan basin, due in part due to sampling methods and inconsistent

sample sizes among reaches, reveals an opportunity to improve the utility of future habitat data

collection for research use. Designing future sampling efforts to capture habitat dynamics at the

scale of natural river features like stream reaches and linking collected data to a common spatial

framework (*e.g.*, National Hydrography Dataset) can facilitate modeling efforts similar to those

reported in chapter 1. Furthermore, changing the sampling protocol to identify more detailed

measures of substrate type (*i.e.*, classify habitat by objective grain size) in place of the current

habitat types can lead to more effective modeling, as Type I and II habitat refer to observed

functional habitat types for sea lamprey rather than sharply defined measures of substrate

composition. Sampling protocols similar to those used in the U.S. EPA's Wadeable Stream

Assessment program may serve as a useful guide for such changes (USEPA 2004; USEPA

2006). Finally, in the case of sampling new potential habitats for sea lamprey (*e.g.*, river

sections upstream of dams), protocols should incorporate sampling the upstream extent of

spawning habitat and ultimately frame larval habitat quantity relative to this distribution. Given

the inability of larvae to disperse upstream of nest sites, actual potential larval habitat only exists

downstream of the furthest upstream spawning habitat patches.

The most important, and simplest, recommendation from the population simulations is

that an increase in the annual control budget is necessary to avoid a disproportionate sea lamprey

population response with Great Lakes barrier removals. The increases in budget required for

barrier removals like the Grand River represent a small proportional increase in cost relative to

the proportional increase in sea lamprey abundance that would otherwise result. Furthermore, decision makers should account for river attributes other than sheer available habitat when considering possible effects of barrier removals on sea lamprey populations. The different spawner allocations and simulated effect of adding habitat in northern and southern Lake Michigan support the recommendation that expected implications of barrier removals between these two regions should vary. Additionally, the implications of opening multiple small rivers or a single large river system for the effectiveness of sea lamprey control need to be carefully considered on a case-by-case basis. Modeling results suggest addition of a single, expensive river system can be more difficult to accommodate in the existing ranking system than several small additions. On the other hand, widely spaced small rivers may be more logistically challenging to sample and treat, given required travel times between sites.

In addition to the projected costs of barrier removals associated with sea lamprey control, all relevant objectives of barrier removals should be considered with a similar level of scrutiny. Sea lamprey control comprises just one aspect of the numerous biological objectives associated with barrier removal, which range from aquatic ecosystem restoration to the enhancement of desirable diadromous fish populations. Beyond these biological objectives are equally pressing social and economic concerns, including public safety, recreation, and power generation. Researchers are increasingly urging that all of these objectives are formally accounted for and compared to formal criteria (Pejchar and Warner 2001; Johnson and Graber 2002).

To this end, improving our understanding of the population-level processes influencing the abundance of desirable fish species represents a major next step to achieve a formal comparison of biological objectives with dam removals. Simulations of the sea lamprey population response to increasing habitat were facilitated by decades of persistent research on

life history processes for this species. Equivalent levels of understanding regarding population

dynamics processes, or similarly developed simulation-based models, are lacking for desirable

fish species like lake sturgeon (*Acipenser fulvescens*) and walleye (*Sander vitreus*).

Incorporating an improved understanding of desirable fish dynamics into comparable models is

critical if we want to explicitly compare the competing objectives of helping certain species and

inhibiting the success of others.

Further research needs include developing an improved mechanistic understanding of

drivers on sea lamprey habitat and incorporating predator-prey dynamics into our understanding

of sea lamprey population processes. Purely modeling-based attempts to predict fine-scale river

habitat rarely explain more than 50% of variation (Wang et al. 2013); *in situ* observations and

manipulative experiments on fine substrate habitat distribution in the Great Lakes basin can

improve our mechanistic understanding of landscape processes and improve predictive

performance. Finally, time-series analyses that explicitly link the abundances of sea lamprey and

prominent host species should be conducted to inform future population analyses. An improved

understanding of population responses at the simulated extremes will improve the utility of

generated model predictions, particularly in the case of large-scale barrier removals.

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