CHARACTERIZING THE INFLUENCE OF STREAM FRAGMENTATION ON FRESHWATER MIGRATORY FISHES ACROSS LARGE SPATIAL EXTENTS: INFORMATION TO CONSERVE MIGRATORY SPECIES FROM CURRENT AND FUTURE THREATS

By

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ABSTRACT

Migrations of fishes throughout stream networks support natural and human communities globally. Despite their importance, freshwater migratory fishes are increasingly under threat from stream habitat degradation due to land use and climate change and stream habitat fragmentation from barriers, with the latter being especially threatening to migratory species. This is because barriers can block migratory fishes from accessing the distinct stream habitats located throughout networks needed to complete their life cycles. Strategies to conserve freshwater migratory fishes are needed, including identifying specific threats and, in some cases, opportunities for barrier removals. Because barriers can also benefit human communities and protect native species from species invasions, fishery managers must attempt to balance the benefits and costs for migratory fishes, natural systems, and people when making barrier removal decisions. To make effective decisions, fishery managers need to know the diversity of migratory life histories in stream fish assemblages. Additionally, fishery managers need to know the relative influence of barriers and additional threats to migratory fish assemblages across the large spatial extents in which barriers and migratory fish habitat are distributed. The goal of my dissertation is to address these needs. I aim to increase our understanding of distributions and abundances of migratory fishes along with the ways in which steam fragmentation by barriers affects those fishes over large regions. In my first chapter, I characterize the migratory life histories of 1,250 fish species across the continent of North America. This information supports analyses of my second chapter, in which I characterize regional migratory fish assemblages and the relative influences of natural factors, human land uses, and stream fragmentation by barriers on those assemblages in the conterminous United States. I then focus my research within the Great Lakes region, an area where fishery managers must balance restoring connectivity for

migratory fishes while controlling for invasive Sea Lamprey *Petromyzon marinus*. In my third chapter, I evaluate habitat suitability in streams above barriers for six migratory fish species, including Sea Lamprey, across the state of Michigan and a portion of Wisconsin. I use these habitat suitability estimates in my fourth chapter along with costs of barrier removal and an alternative method to control Sea Lamprey, lampricide, in an optimization analysis to prioritize barriers for removal in Great Lakes tributaries. Collectively, my dissertation emphasizes the prominence and variation in migratory fish life histories in stream fish assemblages, identifies the relative importance of barriers and other landscape-scale threats on migratory fish assemblages, and demonstrates the value and challenges associated with barrier removal decision-making across large spatial extents. In addition, the approaches developed and implemented in my dissertation can be applied in other regions that require similar information for barrier removal decision-making to improve the conservation and management of freshwater migratory fish species in fragmented stream networks.

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INTRODUCTION

Migrations of fishes throughout stream networks contribute to the structure and function of natural ecosystems and support human populations across the globe (McDowall, 1988; Lucas & Baras, 2001; Brink et al., 2018). In spite of their importance, freshwater migratory fishes and their stream habitats are increasingly under threat from overfishing and exploitation (e.g., Allan et al., 2005; Hupfield et al., 2016; Prestes et al., 2022), stream habitat degradation from land use and climate change (e.g., Fièvet et al., 2005; Lin et al., 2017; Bailly et al., 2021), and stream habitat fragmentation from barriers (Liermann et al., 2012; Barbarossa et al., 2020), with fragmentation by barriers being especially threatening to migratory species. This is because barriers in stream networks block migratory species from accessing the multiple, distinct habitats needed to complete their life cycles (Larinier, 2000; McIntyre et al., 2016). Deinet et al. (2020) estimated that populations of freshwater migratory fish species globally have decreased by an average of 76%, with barriers in stream networks being a primary driver. Because freshwater migratory fishes are important to natural and human systems globally (Holmlund & Hammer, 1999; Freeman et al., 2003; Flecker et al., 2010), strategies to mitigate the impacts of barriers and stream fragmentation are needed to conserve migratory species (Lennox et al., 2019).

Globally, millions of barriers in stream networks support irrigation, hydroelectric power, flood protection, navigation, and recreation for people (WCD, 2000; Lehner et al., 2011). Barriers also serve to control the spread of invasive species (Jones et al., 2021), an additional and pervasive threat to freshwater biodiversity and the economy on a global scale (Cuthbert et al., 2021; Duenas et al., 2021). Despite benefits that barriers provide, efforts to call attention to the ecological consequences of barriers and the need for investments in barrier removals are occurring across the world (i.e., World Fish Migration Day, Twardek et al., 2020; Global

Swimways Program, Worthington et al., 2022). Consequently, when barrier removals are being considered, fishery managers must attempt to balance benefits and costs for migratory species, natural ecosystems, and human communities (King & O'Hanley, 2016).

Fishery managers are often charged with identifying barrier removal options across large areas in which barriers and migratory fish habitats are distributed, including entire drainage basins, states, or regions (e.g., Kraft et al., 2019; Walter et al., 2021). Several pieces of information are needed to make effective barrier removal decisions over such large spatial extents. One piece of information is an understanding of the variation in migratory life histories of fishes in stream assemblages (Cooke et al., 2012; Tamario et al., 2019). This information is necessary to characterize migratory assemblages, the habitats they require, and the influence of barrier-driven fragmentation on those assemblages and habitats in stream networks. Another important piece of information is an accounting of other threats to migratory fishes and their stream habitats such as human land use in stream catchments (e.g., Wang et al., 2011) and the spread of invasive species that would result from a barrier removal (Rahel, 2013; Rahel & McLaughin, 2018). Such information can help managers pinpoint possible locations for barrier removals across large regions and identify local mechanisms that underpin population loss (Fausch et al., 2002; Lin & Robinson, 2019).

My dissertation research will help address those needs. My overarching goal is to increase our understanding of distributions and abundances of migratory fishes along with the ways in which steam fragmentation by barriers affects those fishes over large regions. In my first chapter, I characterize freshwater fishes that are migratory across North America. To do this, I develop a database describing the migratory statuses, patterns, and behaviors of 1,250 North American freshwater fish species, which has not been done before in a comprehensive manner for North American species. This information supports analyses conducted as part of my second chapter, in which I couple the database with fish sample data from streams across the conterminous United States to characterize migratory assemblages. Using this information and environmental data, I use an ordination technique to understand the key natural influences and the relative influences of human land uses and stream fragmentation by barriers on migratory assemblages. I then focus my research within the Great Lakes region, an area inhabited by numerous migratory fishes important to natural ecosystems and fisheries that is also an area where barriers are used by managers to control the spread of invasive Sea Lamprey *Petromyzon marinus*. In my third chapter, I evaluate habitat suitability in streams above barriers for the invasive Sea Lamprey along with five desirable migratory fish species across the state of Michigan and a portion of Wisconsin. Because records are generally not available for these species above barriers in this region to support species distribution modelling, I instead use an approach to characterize species habitat preferences from various landscape factors important to habitat to evaluate stream suitability. In my fourth chapter, I use these habitat suitability estimates along with barrier removal cost estimates and cost estimates of an alternative method to control Sea Lamprey, lampricide, in an optimization analysis to prioritize barriers for removal in Great Lakes tributaries. Collectively, my dissertation underscores the prominence and variation of migratory fishes in assemblages across large spatial extents and provides information that will aid in decision-making to conserve freshwater migratory fishes from current and future threats.

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CHAPTER 1:

THE NORTH AMERICAN FRESHWATER MIGRATORY FISH DATABASE (NAFMFD): CHARACTERIZING THE MIGRATORY LIFE HISTORIES OF FRESHWATER FISHES OF CANADA, THE UNITED STATES, AND MEXICO

Summary

A limiting factor to successfully conserve freshwater migratory fishes is that the migratory life histories of many species are unknown or only partially described. To address this limitation, I created the North American Freshwater Migratory Fish Database (NAFMFD) to provide researchers and managers with comprehensive migratory life history information to help improve the conservation and management of freshwater migratory fish species. This database was developed through an intensive literature review and was reviewed by fish experts from across North America. A summary of the database reveals that many more freshwater fish species are migratory than previously appreciated, and that the migratory life histories of freshwater fishes can vary substantially over the large region. For the full text, go to:

Dean, E. M., Cooper, A. R., Wang, L., Daniel, W., David, S., Ernzen, C., Gido, K. B., Hale, E., Haxton, T. J., Kelso, W., Leonard, N., Lido, C., Margraf, J., Porter, M., Pennock, C., Propst, D., Ross, J., Staudinger, M. D., Whelan, G., & Infante, D. M. (2022). The North American Freshwater Migratory Fish Database (NAFMFD): Characterizing the migratory life histories of freshwater fishes of Canada, the United States and Mexico. Journal of Biogeography, 49, 1193-1203 https://doi.org/10.1111/jbi.14367.

CHAPTER 2:

CUMULATIVE EFFECTS OF DAMS ON MIGRATORY FISHES ACROSS THE CONTERMINOUS UNITED STATES: REGIONAL PATTERNS IN FISH RESPONSES TO RIVER NETWORK FRAGMENTATION

Summary

Efforts to understand how cumulative effects of multiple dams affect freshwater migratory fishes across large regions are needed to identify locations for connectivity-enhancing actions to conserve freshwater migratory fish species. To address this need, I evaluated the cumulative effects of dams on migratory fish assemblages in river networks across nine ecoregions of the conterminous United States (U. S.). I first characterized ecoregional patterns in freshwater migratory fish assemblages. I then compared the importance of a set of river network fragmentation metrics representing influences of multiple dams in networks versus other anthropogenic landscape stressors and natural factors on those assemblages using Canonical Correspondence Analysis. I used Boosted Regression Tree modelling to understand the specific environmental effects on migratory fish assemblages in the eastern conterminous U. S. Key natural influences on migratory assemblages included catchment area, river baseflow, and air temperature, suggesting that migratory fishes may be affected by changing climate. Downstream dams were more influential than other human stressors to potamodromous fishes, underscoring the importance of enhancing connectivity within river networks to conserve these species. The full text was recommended for publication in River Research and Applications as of April 25, 2023, and was re-submitted to the journal with addressed revisions as of May 24, 2023:

Dean, E. M., Infante, D. M., Yu, H., Cooper, A., Wang, L., & Ross, J. (In Review). Cumulative effects of dams on migratory fishes across the conterminous United States: Regional patterns in fish response to river network fragmentation. River Research & Applications.

CHAPTER 3:

ASSESSING HABITAT SUITABILITY FOR MIGRATORY FISHES ACROSS LARGE REGIONS: SUPPORTING BARRIER REMOVAL DECISION-MAKING IN GREAT LAKES TRIBUTARIES

Abstract

Millions of barriers fragment stream habitats and contribute to declines in freshwater fish species globally. Migratory freshwater fishes are especially vulnerable to barriers because they must access discrete habitats in stream networks to complete their life cycles. Worldwide, barrier removals are being considered to improve production and conservation of desirable migratory fishes by restoring access to habitats, but removals can also benefit undesirable or invasive species by providing access. Because of this, understanding the suitability of stream habitat above barriers for both desirable and undesirable fishes is key for evaluating trade-offs in barrier removals. While species distribution models can predict habitat suitability, such an approach may be inapplicable when species records are limited, which is often the case for migratory species with restricted distributions above barriers. To overcome this challenge, I developed an approach to discriminate habitat suitability for migratory species among stream reaches in the Laurentian Great Lakes region, including reaches above barriers where species records are limited. My first objective was to document stream habitat preferences of six migratory fishes of interest by reviewing the literature. Species included Lake Sturgeon *Acipenser fulvescens*, Walleye *Sander vitreus*, White Sucker *Catostomus commersonii*, Brook Trout *Salvelinus fontinalis*, Steelhead *Oncorhynchus mykiss*, and Sea Lamprey *Petromyzon marinus*. My second objective was to assess stream habitat suitability for these species by identifying mappable stream habitat factors or surrogate landscape variables of stream habitat factors. I identified different values in factors or variables reflecting differences in suitability for a species of

interest, and I assigned discrete scores to ranges in values to indicate suitability. My third objective was to map stream habitat suitability scores above barriers for the migratory fishes. Collectively, my results characterize stream habitat suitability for migratory fishes that will aid in barrier removal decision-making, and my approach serves to estimate habitat suitability in streams for aquatic species lacking occurrence records.

Introduction

Freshwater migratory fishes support natural ecosystems and human communities in stream networks globally (Holmlund & Hammer, 1999; Flecker et al., 2010). While migration patterns and behaviors vary widely, freshwater migratory fishes move among habitats at different life stages, and these habitats frequently include streams (as reviewed by McDowall, 1988; Lucas & Baras, 2001 and Morais & Daverat, 2016). Stream habitats, however, are fragmented globally by millions of barriers, contributing to a world-wide decline in migratory fishes (Barbarossa et al., 2020; Deinet et al., 2020). In the Laurentian Great Lakes region, hundreds of barriers occurring near river mouths directly separate stream habitats from a Great Lake (referred to as terminal barriers). Production of migratory fish species including Lake Sturgeon *Acipenser fulvescens*, Walleye *Sander vitreus*, White Sucker *Catostomus commersonii*, Brook Trout *Salvelinus fontinalis*, and Steelhead *Oncorhynchus mykiss* is prioritized by management in the region, and terminal barriers limit access of these fishes to priority stream habitats, potentially limiting production (Walter et al., 2021; Zielinski & Freiburger, 2021). Consequently, terminal barrier removals are being considered to improve production and conservation of these desirable migratory fishes by restoring access to otherwise inaccessible stream habitats.

Terminal barrier removals can also provide undesirable fish species with access to stream habitats (Rahel, 2013; Rahel & McLaughlin, 2018; Jones et al., 2021). The Sea Lamprey

Petromyzon marinus is an invasive migratory fish species responsible for severe declines in Great Lakes fisheries since its introduction to the region in the early 1900s (Christie & Goddard, 2003; Brant, 2019; Robinson et al., 2021). Great Lakes fishery managers control the production and spread of the Sea Lamprey using various techniques such as lampricide treatment of tributaries to eradicate larvae (Sullivan et al., 2021), release of sterile males (Siefkes et al., 2021), and trapping of migratory juveniles and adults (Miehls et al., 2020; Miehls et al., 2021), yet terminal barriers are the primary method of control (Hrodey et al., 2021). Because terminal barrier removals can have positive management implications for desirable fishes and negative management implications for Sea Lamprey, trade-offs in these outcomes should be clearly understood before terminal barrier removals occur (Walter et al., 2021). Characterizing the suitability of stream habitat above terminal barriers for both desirable and undesirable migratory fishes can contribute to this understanding.

Species occurrence or abundance data are often absent or limited for migratory fishes with restricted distributions in stream networks. When species occurrence data are lacking, the efficiency of species distribution models (SDMs; Soberón, 2007; Elith et al., 2008; Elith & Leathwick, 2009) to assess habitat suitability for specific species across large geographic areas is greatly reduced (Lozier et al., 2009; Lee-Yaw et al., 2020). In such instances, a second approach for assessing species habitat suitability could be applied using just stream habitat or landscape data to identify locations where migratory species might be expected to occur. Such an approach was applied by Quist et al. (2005) who used landscape factors (i.e., elevation, stream size) and habitat characteristics (e.g., stream temperature) to identify a potential set of suitable streams for minnow (Cyprinidae), darter (Percidae) and sucker (Catostomidae) in Wyoming. Landscape and habitat factors were used to filter out unsuitable streams from the study region although the authors had fish species occurrence data to help evaluate their predictions. Tingley et al. (2022) used a similar approach in streams across the state of Michigan to evaluate habitat suitability for an extirpated fish species, the Arctic Grayling *Thymallus arcticus*. Tingley et al. (2022) determined stream habitat preferences of Arctic Grayling from an extensive literature review. Using known habitat preferences along with measured and modeled stream habitat features for select systems and catchment landscape factors available for all streams in the region, Tingley et al. (2022) assessed stream habitat suitability for Arctic Grayling under current conditions and a changing climate. Given the effectiveness of this overall approach for discriminating among streams for this species' suitability, a similar approach could be applied for migratory fishes to aid in understanding habitat suitability above terminal barriers where species records may be lacking.

My study helps to meet that need by evaluating stream habitat suitability above terminal barriers for migratory populations of Lake Sturgeon *Acipenser fulvescens,* Walleye *Sander vitreus*, White Sucker *Catostomus commersonii,* Brook Trout *Salvelinus fontinalis*, Steelhead *Oncorhynchus mykiss*, and Sea Lamprey *Petromyzon marinus* in Great Lakes tributaries. Because records are generally not available for these species above terminal barriers in the region, I instead use data characterizing known habitat preferences of species along with landscape factors important to those habitat features following Tingley et al. (2022). My first objective was to document stream habitat preferences of the six migratory fishes of interest by reviewing literature focused within the Great Lakes. My second objective was to assess stream habitat suitability for all species in the study region by identifying mappable stream habitat factors or catchment landscape variables important to stream habitat factors (i.e., surrogates). I identified different values in factors or variables reflecting differences in suitability for a species of interest (i.e., value at which suitability changes, termed a “break”), and I assigned discrete scores to ranges in values separated by breaks to indicate suitability. My third objective was to summarize and map stream habitat suitability scores above terminal barriers for the migratory fishes. Collectively, my results characterize stream habitat suitability for migratory fishes that will aid in informing fishery managers of the trade-offs of terminal barrier removals in Great Lakes tributaries.

Methods

Study region

Terminal barrier removals are being considered by fishery managers to restore access to Great Lakes tributary habitat for desirable migratory fish species, but such decisions must also be balanced with invasion of migratory Sea Lamprey in those tributaries (Walter et al., 2021). My study region includes all streams in the Upper and Lower Peninsulas of Michigan and the Bayfield Peninsula, Wisconsin that could be used by migratory Great Lakes fishes (Figure 3.1). Stream catchments across the region vary greatly in terms of their hydraulic conductivity. Historical glaciation and lacustrine deposition contribute to varying amounts of groundwater delivery versus surface runoff regionally and within individual stream networks (Zorn et al., 2002; Lyons et al., 2009; Wehrly et al., 2009; Zorn et al., 2012). Stream reaches receiving substantial groundwater are generally colder in summer with stable flows, while reaches that receive more surface run-off are warmer with more variable flow regimes. Landscape features of stream catchments also vary. Natural land cover in the study region is characterized by deciduous, coniferous, and dry-mixed forests and woody and emergent herbaceous wetlands. Intensity of agricultural land uses, and water withdrawals, generally increases from north to south, with many areas of the southern Lower Peninsula used extensively for agriculture.

Urbanization is also more common in the southern Lower Peninsula, including large cities and suburbs associated with Detroit and Grand Rapids. Across the study region, at least 346 barriers are terminal, with an additional 1,251 barriers located above terminal barriers (Figure 3.1). Barriers were obtained from the 2012 National Anthropogenic Barrier Database (NABD; Ostroff et al. 2013), the Michigan Department of Environment, Great Lakes, and Energy (EGLE; https://gis-egle.hub.arcgis.com/datasets/egle::michigan-dam-inventory), and the Wisconsin Department of Natural Resources (https://data-wi-dnr.opendata.arcgis.com/datasets/wi-dnr::wisconsin-repository-of-dams/). Non-terminal barriers were included in this study to account for the availability of connected stream habitat above terminal barriers.

Stream habitat suitability approach

Overview

My approach for assessing stream habitat suitability for migratory fishes above terminal barriers followed five steps (Figure 3.2). Step 1 of the approach was to identify habitat preferences of species through a literature review focused within the Great Lakes region. Stream habitat preferences of fishes were organized into groups including channel morphology, geomorphic units, substrate, fish cover, temperature, and overall habitat condition. In Step 2, mappable stream habitat factors or landscape variables serving as surrogates for stream habitat factors were identified to represent stream habitat preferences of the migratory fishes. Surrogates were identified based on relationships between landscape factors and sampled habitat variables and with support from the literature. In Step 3, five options were used to identify differences in suitability of a stream habitat factor or surrogate landscape variable, with the values that discriminate differences referred to as “breaks.” I assigned different suitability values to ranges of each habitat and surrogate landscape variable separated by breaks. Next, in Steps 4 and 5, stream habitat suitability scores were summarized within two spatial scales to generate two stream habitat suitability maps for each migratory fish species. Below, I describe each step in my approach in more detail.

Step 1. Identify species habitat preferences

I identified stream habitat preferences of the migratory fishes through an intensive literature review focused within the Great Lakes region. If Great Lakes-specific information was unavailable, I reviewed literature from other locations within the species' native range to identify habitat preferences. I reviewed published books, journal articles, conference proceedings, research reports, technical reports, theses, and dissertations. For each species, I included information for all life stages.

Step 2. Identify mappable habitat factors or surrogate landscape variables

Overview. Step 2 involved the assembly of a variety of spatial information and its attribution to the spatial framework. I identified previously modeled stream habitat data available over the entire study region that represent stream habitat factors important to migratory fishes. I also identified landscape data available across the study region to use as surrogates for stream habitat factors. To select landscape variables as surrogates for stream habitat factors, I used relationships identified in the literature or quantified relationships between habitat data sampled from stream sites across the study region and landscape factors.

Spatial framework. I used the 1:100,000 scale National Hydrography Dataset Plus Version 2 (NHDPlusV2; USEPA & USGS, 2012) to characterize streams in the study region. The smallest spatial unit, the stream reach, is defined as an interconfluence section of water, with confluences occurring at stream junctions and inlets or outlets of lakes and impoundments. Each stream reach in the NHDPlusV2 is associated with a local catchment, or an area of land that drains directly to the reach (USEPA & USGS, 2012) and a network catchment that includes the cumulative upstream land area draining to a reach (including the local catchment; Wang et al., 2011). Each stream reach is also associated with a local buffer, or 90 m of land on either side of a reach, to characterize riparian landscape influences on stream habitat (Brenden et al., 2006; Cooper et al., 2019). Habitat suitability is summarized for each fish species within stream reaches. Also, I developed an additional spatial unit, a stream segment, which is a contiguous, connected set of stream reaches bounded by barriers, headwaters, or terminal outlets. This unit serves to account for suitable habitat connectivity (Cooper et al., 2017).

Landscape data. I assembled natural and anthropogenic landscape variables from various sources based on known influences on stream habitat characteristics in the study region (Table C3.1; e.g., Allan et al., 1997; Allan & Johnson, 1997; Johnson et al., 1997; Wang et al., 2003). Landscape variables were attributed to local catchments and buffers and then aggregated to summarize conditions within network catchments and buffers. I included five landscape variables summarized in network catchments: drainage area (km^2; USEPA & USGS, 2012), regional estimates of groundwater velocity (mm/day; Baker et al., 2003), percent fine geology which included landforms with hydraulic conductivity of less than 0.005 m/day (Farrand & Bell, 1982; Soller et al., 2009), and a cumulative fish habitat condition index (CHCI; Crawford et al., 2016). The CHCI scores were produced based on statistically significant declines in numbers of stream fishes with various levels of human land uses and stream network fragmentation by barriers (Crawford et al., 2016). I included two landscape variables summarized in network buffers: percent forest cover (a composite variable of percent deciduous forest, evergreen forest, and mixed forest data) and percent wetland cover (a composite variable of percent woody wetland and emergent herbaceous wetland data; Homer et al., 2012). Stream reach gradient (m/m) was obtained from the NHDPlusV2 (USEPA & USGS, 2012). All landscape data were available for streams throughout the study region except for the groundwater velocity variable which was not available for Wisconsin streams.

Modeled stream habitat data. I used modeled data to characterize stream flow and temperature regimes at the reach scale from the FishVis geodatabase (Stewart et al., 2016; Table C3.1) which provides monthly temperature and annual flow estimates for all stream reaches in Michigan and Wisconsin. I used modeled July mean temperature (°C) to assess each reach's suitability for growth of larval and juvenile stages considering that rivers serve as nursery habitat for species (Figure D3.1). To estimate the stability of streamflow in a reach, I calculated an annual 10/90 ratio flow metric (Knighton, 2014) using modeled annual 10-percent and 90-percent exceedance discharge metrics, and I calculated an annual 90/50 flow metric to estimate stream baseflow (Caissie & Robichaud, 2009) using the annual 50-percent and 90-percent exceedance discharge metrics.

Measured stream habitat data. I sampled streams across the state of Michigan and the Bayfield Peninsula to summarize habitat variables that could be used to identify surrogate landscape variables. I sampled 71 stream reaches across the study region, with 60 sites in the Upper and Lower Peninsulas of Michigan and 11 sites in the Bayfield Peninsula, Wisconsin (Figure 3.1). Stream habitat data were collected between May and September of 2019 and included measures of channel morphology, geomorphic units, substrate, riparian condition, and fish cover using sampling methods following Wills et al. (2009) and the Larval Assessment Task Force of the Sea Lamprey Control Program (LATF SLCP, 2019). I sampled habitat at least 10 m upstream of a stream access point, and the length of the reach sampled varied according to the stream's drainage area. Each reach was divided into 13 transects with stream habitat data assessed within transects or throughout the entire reach. I also measured stream water temperature data in 37 of the 71 sites following Wills et al. (2009), with data collected in hourly increments from July 1, 2019, to August 31, 2019, using Onset HOBO Water Temperature Pro V2 data loggers. Monthly average daily mean temperature and seasonal average daily temperature were calculated for each site using the Stream Thermal package (Tsang et al., 2014) in the R program (R Core Team, 2022).

At each transect, channel morphology dimensions including wetted and bankfull widths were measured to the nearest 0.1 m. Presence and width of islands were recorded, and island width was included in calculating total width but not wetted width (Wills et al., 2009). Bankfull height (i.e., the difference between the elevation of the stream surface and the point at which the stream would enter the floodplain) and bank undercut length were measured on the left and right banks for each transect. Depth measurements were taken at five points across each transect, with the space between sampling points occurring at 1/5, 2/5, 3/5, and 4/5 across the channel and at the thalweg. Dominant geomorphic units were visually estimated at each transect and categorized as a riffle, pool, or run.

Dominant substrate was visually estimated within a 0.3 m diameter circle at the same five sampling points across the transect where depth measurements were taken. Substrate types included silt and detritus, sand, gravel, small cobble, large cobble, boulder, bedrock, and clay. I combined measures of silt/detritus and sand into a fine material variable and measures of gravel, small cobble, and large cobble into a coarse material variable to broadly characterize substrate surfaces important to fish reproductive and feeding guilds (Balon, 1975; Frimpong & Angermeier, 2009). Substrate types specific to larval and adult Sea Lamprey were estimated across the transect to the nearest meter from left bank to right bank (LATF SLCP, 2019).

Substrate types for the larval stage were categorized by their suitability for burrowing. Optimal or “Type 1” substrate consists primarily of silt, sub-optimal or “Type 2” substrate is primarily sand with some shifting gravel, and poor or “Type 3” substrate includes clay, bedrock, gravel, small and large cobble, and boulders (Slade et al., 2003). Substrate of spawning adult Sea Lamprey consists of coarse material (>9 mm diameter) with sand as a minor component among interstitial spaces (LATF SLCP, 2019).

On both banks of a transect, dominant riparian vegetation type within 9 m downstream, upstream, and perpendicular to the channel was visually categorized as yard/lawn, pasture or row crop agriculture, grassland/forbs, tag alders, small or large coniferous trees, and small or large deciduous trees. Because some types were infrequently detected, I combined some measures into composite variables. Yard/lawn, pasture, and row crop agriculture were summarized into an anthropogenic disturbance variable, and grassland/forbs, tag alders, and small and large coniferous and deciduous trees were combined into a natural cover variable. Bank stability, describing the percent of the stream bank that was bare soil, was visually ranked on a scale of one to four on both the left and right banks of a transect, where a score of 1 indicates good stability (<25% bare), 2 is fair stability (25%-50% bare), 3 is poor stability (50%-75% bare), and 4 is very poor stability (>75% bare).

The proportions of woody material and submerged aquatic vegetation were measured at five sampling points across the transect and visually estimated within a 0.3 m diameter circle around a sampling point. Upon completion of data collection at the final transect, lineal and areal measures of large woody debris (LWD) were estimated throughout the entire length of the site. Lineal measures included the number of full 1.8 m lengths of individual logs in contact with the water at least 15 cm deep by diameter classes (15-30 cm; 30-45 cm; 45-60 cm; >60 cm). I summed the number of logs of each diameter class into a composite variable to estimate the total number of single logs providing cover throughout a reach. Areal measures (m^2) were recorded for natural structures including log jams, beaver dams, and brush deposits and artificial structures including human-made log jams, lunker structures, rip-rap, rafts, stump-clumps, and wing deflectors. Some of these structures were infrequently detected so I combined the natural and artificial areal measures to broadly characterize the total area of cover provided by LWD structures within each reach.

Measured stream habitat variable reduction. I summarized the sampled stream habitat data into 60 variables (Table C3.2). Variables were transformed using arcsine square root for percentage data, square root for count data, and natural log for continuous data to achieve linearity. I evaluated distributions of the 60 variables and removed those that did not vary substantially across sites. I used Pearson's correlation to evaluate the relationships of pairs of variables within groups (i.e., channel morphology, geomorphic units, substrate, riparian condition, fish cover, and temperature). When a pair of variables were correlated by an absolute value of r greater than 0.6, I removed one of the variables based on ecological interpretability. The initial 60 habitat variables were reduced to a subset of 14 variables (Table C3.3) that best characterize different aspects of stream habitat important to fishes to aid in identifying surrogate landscape variables for stream habitat factors.

Surrogate landscape variables. I identified landscape variables as surrogates for some stream habitat factors using Pearson's correlation. To choose a landscape variable as a surrogate for a stream habitat factor, I associated the set of landscape variables (Table C3.1) to the subset of sampled stream habitat variables (Table C3.3) and evaluated the strength of their associations. To also help in choosing surrogate landscape variables, I used established associations or relationships from the literature (see Dean et al., 2020 for additional details).

Sensitivity analysis. The robustness of an approach is often contingent upon the uncertainty that may be introduced through the approach itself (Caswell, 2019). In my approach, surrogate landscape variables used to represent key habitat preferences were selected based on the strength of their associations with sampled habitat factors (Figure 3.2). To gauge the uncertainty of these relationships, I used a simple outlier analysis technique to evaluate the robustness of the strength of those associations. Broadly, outlier analysis involves identifying and then removing or adjusting outliers and observing the change in the significance or strength of a relationship to identify potential factors contributing to uncertainty in results. I used a 90% Winsorization method on my dataset, in which I identified the values that were greater than or equal to the 95th percentile of the dataset, and the values that were less than or equal to the 5th percentile of the dataset. Any values outside of this range were replaced with the next highest or lowest value within the range. I report differences in the strength and significance of correlation coefficients of pairs of landscape variables and sampled habitat variables to characterize some of the uncertainty introduced into my results.

Step 3. Identify breaks in variables that indicate differences in suitability

I identified breaks in mappable stream habitat factors or surrogate landscape variables to indicate differences in suitability for fish species using options that varied depending on best available information (Options A-E; Figure 3.2). I assigned discrete scores to ranges in values (i.e., 0, less suitable; 1, suitable; 2, more suitable). First, whenever possible, I used Option A, which included identifying breaks derived from laboratory or field observations defined in the literature. I expected to find breaks for temperature widely available in the literature, as the relationship between temperature and fish growth and tolerance is relatively easy to test in a laboratory setting.

When values from the literature were unavailable, I next attempted Option B, which was to identify breaks based on characteristics of locations in the study region where stream resident populations of a species were documented to occur. Stream residents were identified using an existing dataset characterizing stream fish assemblages compiled from state and federal programs that were collected from 1990 to 2019 (additional details of data described in Daniel et al., 2015), with species occurrence records spatially referenced to corresponding stream reaches of the NHDPlusV2 (USGS & USEPA, 2012). In my study, I consider stream residents to be fishes that do not require access to a Great Lake to complete a life stage (Figure D3.1). Therefore, occurrences of fish species in streams above barriers are assumed to belong to populations that are stream resident. Because spawning adults, larvae, and juveniles of adfluvial fishes (i.e., Great Lakes-run migratory species) and stream resident fishes use similar habitats in my study region (e.g., Ivan, 2009), I assumed that locations with stream resident species were likely suitable for adfluvial fish, too. If stream resident occurrences were too limited (i.e., total number of records above barriers is less than 100 across the study region), I used Option C, which included identifying breaks based on characteristics of locations in the study region within species ranges. I used range maps developed by the USGS Non-indigenous Aquatic Species database (https://nas.er.usgs.gov/) to identify those locations and characteristics.

If the above three options could not be used to determine breaks, I used Option D which was to visually evaluate the approximate value of a landscape variable associated with the approximate value of sampled stream habitat variable. For example, Tingley et al. (2022) visually determined a threshold of Brook Trout abundance with stream drainage area, assuming that habitat would be more suitable for Brook Trout in smaller systems where re-establishment of

Arctic Grayling may be less likely to succeed. They assigned streams with drainage areas as suitable (score of 2) and marginal (score of 1), given evidence of limited negative effects of Brook Trout on Arctic Grayling in overlapping habitats (Byroth & Magee, 1998; McCollough, 2017). Finally, while not used in my study, Option E, or expert opinion, can be used to determine breaks if other options are not possible.

Step 4. Score habitat suitability within stream reaches

To produce a single stream habitat suitability score for each reach for each migratory fish species, I summed the scores assigned for each mappable stream habitat factor and surrogate landscape variable. For the Sea Lamprey, I scored the larval and adult stages separately because methods to control the species depends on life stage (Siefkes et al., 2021). Any reach where the modeled July mean temperature (°C) exceeded the upper thermal limit for a species was scored a 0. After reaches in the study region were scored, I divided the reach scores that were greater than 1 into quartiles, with scores indicating relative (vs. absolute) suitability. I used a quantile classification because my data are ordinal and a defined distance between the categories doesn't exist (Campbell & Shin, 2011). I then mapped stream reach scores for species using ArcGIS 10.7.1 desktop software (https://www.esri.com/en-us/arcgis/products/arcgis-desktop/resources).

Step 5. Score habitat suitability within stream segments

To score stream habitat suitability of migratory fishes within segments, I calculated a length-weighted average score from reach scores calculated in Step 4 and then assigned that score to all reaches in that segment. Watersheds with stream segments draining multiple states (e.g., St. Joseph and Menominee watersheds; Figure D3.2) and segments comprised entirely of waterways that were not classified as reaches in the NHDPlusV2 (e.g., artificial paths) were not scored. I divided the scores into quartiles with scores indicating relative suitability and mapped the stream segment scores for migratory fishes using ArcGIS 10.7.1 desktop software.

Mapping stream habitat suitability above terminal barriers

I first summarized the number of reaches and segments within suitability ranges (i.e., most suitable, suitable, moderately suitable, least suitable, and unsuitable) for species stratified by geographic area (Michigan, Bayfield Peninsula). I then mapped the reaches and segments and their suitability categories for each species using ArcGIS 10.7.1 desktop software. I combined reach and segment maps to summarize the number of desirable migratory fishes with suitable habitat in reaches or segments. I also identified reaches and segments that scored as least suitable for larval Sea Lamprey. I flagged reaches and segments that were suitable for migratory fish species and least suitable for Sea Lamprey above terminal barriers.

Results

Stream habitat suitability assessment

Step 1. Species habitat preferences

I summarized the life histories (Figure D3.1) and stream habitat preferences (Tables C3.4-C3.9) of the six migratory fish species using numerous literature sources (Appendix 3.E), finding some similarities among species as well as distinct habitat preferences to discriminate stream habitat suitability for different fishes. For example, Lake Sturgeon and Walleye prefer streams with large volumes of water and inhabit depths greater than 0.5 m, while remaining species can be found in shallower streams at least 0.1 m deep. Compared to other fishes, Walleye inhabit streams of lower gradients, slower water velocities, and variable flow conditions. Lake Sturgeon, White Sucker, Steelhead, and Brook Trout prefer streams with relatively stable flows and greater baseflows. Brook Trout and Steelhead inhabit cold water streams (summer water temperature <18°C), Lake Sturgeon and White Sucker prefer cool water streams (18-22°) and

Walleye and Sea Lamprey prefer cool to warm water streams (>22°; Wills et al., 2009). Lake Sturgeon, White Sucker, and Sea Lamprey use fine material for feeding and rearing habitat, yet excessive fine material can negatively affect salmonids. Adults of all species use riffle habitat and coarse material in streams for spawning, and most species use pool habitat for refuge.

Step 2. Mappable habitat factors and surrogate landscape variables

I identified 10 total stream habitat factors and surrogate landscape variables that could be used to map habitat suitability of species. Three modeled stream habitat variables were available for every reach in the entire study region: the 10/90 flow ratio, the 90/50 flow ratio, and July mean temperature, which represented flow stability, baseflow, and water temperature conditions, respectively. I used associations established in the literature to identify three landscape variables as surrogates for stream habitat factors. Stream gradient was selected as a surrogate for water velocity because higher gradients indicate steeper slopes and more rapid flow of water than in channels with lower slopes (Knighton, 1998). Catchment groundwater velocity was a surrogate for groundwater input because I assumed that a higher velocity of groundwater movement in catchments would likely result in more groundwater delivery to stream channels (Baker et al., 2003). The CHCI variable was a surrogate for habitat quality because the variable captures the response of whole stream fish assemblages to anthropogenic land uses and in-stream barriers (Crawford et al., 2016).

Four surrogate landscape variables were identified by evaluating the strength of their associations with sampled stream habitat variables using Pearson's correlation (Table C3.10). Catchment drainage area was selected as a surrogate for stream size because of its significant, positive relationships with sampled stream width ($r = 0.92$, $p < 0.01$) and depth ($r = 0.73$, $p < 0.01$). Additionally, wetland cover (%) in network buffers was selected as a surrogate for fine substrate because it was significantly, positively related to amount of fine material ($r = 0.34$; $p < 0.01$) in sampled streams. Forest cover (%) was selected as a surrogate for riffles and coarse substrate because it was significantly, positively related to amount of riffle habitat ($r = 0.29$, $p < 0.05$) and coarse material ($r = 0.30$; $p < 0.05$) in sampled streams. Catchment fine geology (%) was selected as a surrogate for pools because it was significantly and positively related to the amount of pools in sampled streams ($r = 0.32$, $p < 0.05$).

I used a 90% Winsorization method to test the sensitivity of the relationships of pairs of landscape variables and habitat factors. According to the results, two relationships were not significant after running the test: the relationship between forest cover (%) in network buffers and coarse material (count in reach) in streams and the relationship between fine geology (%) in network catchments and pool habitat (% of reach) in streams. However, because the test showed that the relationship between forest cover in the network buffer was positively, significantly correlated with riffle habitat, this suggests the landscape variable has utility as a surrogate for habitat factors. While the relationship between fine geology in the network catchment and pools could be better understood if a higher resolution geology dataset was available, this was not an option and I chose to keep the fine geology variable in my rating system.

Step 3. Breaks in variables that indicate differences in suitability

I assigned scores to ranges in values (i.e., 2, 1, or 0) for species where a score of 2 is highly suitable, 1 is suitable, and 0 is relatively less suitable. I used the literature (Option A; Figure 3.2) to define suitability ranges and associated break values for the CHCI, July mean temperature, drainage area, gradient, and 90/50 flow ratio variables for species (Table 3.1). CHCI break values were obtained from Crawford et al. (2016) and were the same for all fishes (Table 3.1). July mean temperature (°C) break values were obtained from various studies on fish thermal tolerances and optimal growth experiments (Table 3.1). I used Wills et al. (2009) to establish break values in drainage area (km^2; Table 3.1). According to Wills et al. (2009), stream reaches draining less than 103.6 km2 are small, 103.6 to 466.2 km^2 are medium, 466.2 to 1605.7 km^2 are large, and greater than 1605.7 km^2 are very large. Gradient (m/m) break values for Lake Sturgeon were obtained from Hay-Chmielewski and Whelan (1997), for Walleye from Hamilton (2009), for Sea Lamprey from Dawson et al. (2015), for Brook Trout from Raleigh (1982), and for Steelhead from Raleigh (1984). The 90/50 flow ratio values for Steelhead and Brook Trout were also obtained from Raleigh (1982; 1984).

I defined suitability ranges in gradient, the 90/50 flow ratio, and 10/90 flow ratio for White Sucker by evaluating the range of values for the variables in stream reaches where stream resident populations of a species were documented to occur (Option B; Figure 3.2). I determined a break value at 75% of sites where species were found. Break values for White Sucker (Table 3.1) reflected this species' tolerance of stream gradients (75th percentile = 0.003 m/m; Figure 3.3), use of deeper habitats as refuge for multiple life stages (75th percentile of 90/50 ratio = 0.20; Figure 3.4), and preference for stable flows (75th percentile of 10/90 flow ratio = 0.40; Figure 3.5A). Similar to White Sucker, I needed to use Option B (Figure 3.2) to define suitability ranges in the 10/90 flow ratio and groundwater input variable for salmonids. Break values (Table 3.1) reflected preference of stable flows for Steelhead (75th percentile of 10/90 flow ratio = 0.40; Figure 3.5B) and Brook Trout (75th percentile of 10/90 flow ratio = 0.30; Figure 3.5C), and preference of higher groundwater input for Steelhead (75th percentile of groundwater velocity = 40 mm/day; Figure3.6A) and Brook Trout (75th percentile of groundwater velocity = 60 mm/day; Figure 3.6B). Lake Sturgeon lacked sufficient records (<100 occurrences) to apply Option B to determine a break value. Therefore, I applied Option C (Figure 3.2), which involved evaluating the range of values in reaches within the Lake Sturgeon's range. I determined a break in the 10/90 flow ratio at 0.20 because 75% of reaches within the native range of the Lake Sturgeon had that value or less (Table 3.1; Figure 3.7).

Using associations between landscape variables and sampled habitat data (Option D; Figure 3.2), I determined break values in the drainage area, fine geology (%), forest cover (%), and wetland cover (%) variables for all species (Table 3.1; Table C3.10). I visually determined additional break values in the drainage area variable because I assumed that some streams would be too small to support fishes being considered. I identified break values at 25 km^2 and 50 km^2 (Figure 3.8). I did this because streams with less than these drainage areas are associated with depths that are shallower than the minimum depth preferences of 0.1 m for White Sucker, Sea Lamprey, and salmonids and 0.5 m for Lake Sturgeon and Walleye, respectively (Table 3.1; Figure 3.8). I could not visibly establish break values when examining plots of geology or land cover variables with stream habitat factors due to variable relationships with the sampled habitat data. Therefore, I broadly determined a break value at 50% for each of the fine geology, forest cover, and wetland cover variables, with more or less than 50% of each of these variables suggestive of more or less amounts of pool habitat, riffle habitat and coarse material, and fine material, respectively. Expert opinion (Option E; Figure 3.2) to determine breaks in variables was not required in my study.

Step 4. Habitat suitability scores within stream reaches

By summing scores assigned for each mappable stream habitat factor and surrogate landscape variable, I scored 31,965 reaches in watersheds of Michigan (Figure D3.2) and 1,175 reaches in watersheds of the Bayfield Peninsula, Wisconsin (Figure D3.3) for each species (Table C3.12). Suitable reaches for Lake Sturgeon (Figure D3.4A) and White Sucker (Figure

D3.5A) were in catchments north of the Grand and Shiawassee watersheds, portions of the Huron, Kalamazoo, and St. Joseph watersheds in the Lower Peninsula of Michigan (Figure D3.2) and east of the Balsam watershed in the Bayfield Peninsula of Wisconsin (Figure D3.3). Because July mean temperatures (°C) exceeded upper thermal limits, approximately 0.4% of reaches in Michigan scored as unsuitable (i.e., total score of 0) for Steelhead (Figure D3.6A), and 1.0% scored as unsuitable for Brook Trout (Figure D3.7A). Otherwise, the distribution of suitable reaches for both salmonids reflect that of Lake Sturgeon and White Sucker. Suitable habitat for Walleye (Figure D3.8A) and adult Sea Lamprey (Figure D3.9A) were well-distributed throughout Michigan. Suitable reaches for larval Sea Lamprey were more patchily distributed across the study region in comparison to the other species and its adult stage, with suitable reaches concentrated in the Menominee, Escanaba, Fishdam-Sturgeon, Manistique, and St. Mary's watersheds in the Upper Peninsula of Michigan (Figure D3.2; Figure D3.10A). I also synthesized reach-scale habitat suitability maps of desirable species (Figures D3.4A-D3.8A) and larval Sea Lamprey (Figure D3.10A), which indicated that suitable reaches for many desirable species and least suitable reaches for larval Sea Lamprey overlap in watersheds of the western Upper Peninsula (Figure D3.2; Figure D3.11A).

Step 5. Habitat suitability scores within stream segments

By summarizing reach scores within segments, I assigned scores to 1,053 segments in Michigan and 82 segments in the Bayfield Peninsula, Wisconsin (Table C3.13). Suitable segments for Lake Sturgeon (Figure D3.4B), White Sucker (Figure D3.5B), Steelhead (Figure D3.6B), and Brook Trout (Figure D3.7B) were in catchments north of the Grand and Shiawassee watersheds, portions of the Kalamazoo watershed in the Lower Peninsula of Michigan (Figure D3.2) and east of the Balsam watershed in the Bayfield Peninsula of Wisconsin (Figure D3.3).

For Walleye, suitable segments were well distributed in watersheds throughout the study region (Figure 3.8B). Unlike other desirable species, suitable habitat for Walleye was common in watersheds of the Lower and Upper Grand and Saginaw Bay (i.e., Cass, Kawkawlin, Pine, Shiawassee, Tittabawassee; Figure D3.2; Figure D3.87B). Suitable segments for adult Sea Lamprey (Figure D3.9B) and larval Sea Lamprey (Figure D3.10B) were similarly distributed to Walleye. I synthesized segment-scale habitat suitability maps of species (Figures D3.4B-D3.8B) to identify overlapping suitable habitat for most desirable fishes, which were concentrated in watersheds of the Upper and northern Lower Peninsulas of Michigan (Figure 3.9A). Synthesis of this map (Figure 3.9A) with the larval Sea Lamprey segment habitat suitability map (Figure D3.10B) highlighted locations of segments that also were least suitable for larval Sea Lamprey. These included segments in the Keewenaw Peninsula and Dead-Kelsey watersheds in the Upper Peninsula and in the Au Sable, Platte, Pere Marquette-White, Kalamazoo, and the Tittabawassee watersheds the Lower Peninsula (Figure 3.9B; Figure D3.2).

Discussion

Overview

I used a multi-step approach to identify potential locations of suitable habitat for six migratory fishes above terminal barriers over a large portion of the Great Lakes region. My approach could extrapolate habitat suitability in streams lacking species occurrence data, including above terminal barriers. To do this, I used species habitat preferences identified from literature and other means, and assigned relative suitability values for modeled habitat factors and surrogate landscape variables available for all reaches in the region. I then incorporated this information into reach-specific scores and then summarized scores within segments to account for connected sets of suitable streams occurring between barriers. Variation in flow and temperature conditions across the study region limited the number of suitable streams for Lake Sturgeon, White Sucker, and salmonids to cooler, stabler streams of northern Michigan and Wisconsin river systems. In contrast, warmer temperature in streams of southern Michigan resulted in more favorable habitat for Walleye and Sea Lamprey. My synthesis of species habitat suitability maps indicated that suitable streams for all five desirable species and least suitable streams for larval Sea Lamprey overlapped in river systems of the northern Lower and western Upper Peninsulas of Michigan. This information can aid fishery managers in evaluating trade-offs of barrier removals in tributaries of the Great Lakes region. My approach can be applied to inform trade-offs in other regions with similar barrier management problems and where desirable and invasive species data are lacking in streams of interest (e.g., Jones et al., 2021). Additionally, the results of my approach supplemented with additional information such as socioeconomic factors (e.g., cost of removal, cost of alternative strategies to control invasive species) can be used in a barrier prioritization scheme (e.g., optimization; McKay et al., 2017) or structured decision-making (Lin et al., 2019) to further enhance trade-off evaluations for fishery managers.

Amount and type of information on species habitat preferences influences assessment of stream suitability

The amount and type of information on species habitat preferences were influential on my overall ability to assess stream suitability for fishes. Some species are habitat generalists with fewer preferences described than other species. For example, Walleye are considered habitat generalists (Bozek et al., 2011) and therefore had fewer habitat preferences described than the other species in the study, including information on geomorphic units, flow stability, and baseflow, which were all described for salmonid species. Additionally, habitat preferences for some migratory species are better described than others because of their socioeconomic importance (McDowall, 1988; Lucas & Baras, 2001; Morais & Daverat, 2016). For example, salmonids support numerous recreational fisheries in the region (Lauer & Pyron, 2014) and because of this have been intensively studied in comparison to non-game species like White Sucker (Cooke et al., 2005). Additionally, some habitat preferences are easier to measure and associate with species than other preferences. For example, stream temperature has defined numerical suitability ranges for all fishes because the relationship between temperature and fish mortality and growth can be tested in a laboratory setting (Beitinger et al., 2000). In contrast, preferences regarding mesohabitat, substrate, and riparian conditions tended to be qualitatively described in the literature (e.g., "salmonids prefer abundant gravel") because the relationships between these habitat factors and fishes are comparatively less easy to test. Thus, I had to use different options to determine suitability ranges as part of my approach. Consequently, the suitability of some habitat factors, like availability of mesohabitat or substrate, were more coarsely captured in my suitability assessment than factors like temperature. Broadly, the amount and type of information available for a species controls the ability of my approach to discriminate among suitable streams for the species and likely is more robust for species with well-documented habitat preferences to aid in their conservation.

Landscape variables and modeled habitat factors can identify suitable streams over a large region

My integration of landscape and local habitat data in my approach identified suitable habitat for species over all streams in a large region. First, my use of landscape data (i.e., geology, drainage area, land cover, gradient) summarized in stream catchments and buffers helped identify potential sets of suitable streams for species across my large study region. Similarly, Quist et al. (2005) and Tingley et al. (2022) found geology, land cover and use, drainage area, and topography to be important landscape variables filtering the potential set of suitable streams for fish species in the Rocky Mountain and Michigan, respectively (e.g., Poff, 1997). Second, my use of modeled habitat data in reaches distinguished stream habitat suitability more finely for species. Tingley et al. (2022) found reach flow and temperature markedly refined the potential set of suitable re-introduction sites of Arctic Grayling in Michigan. In my study, geographic variation in flow and temperature conditions limited suitable streams for Lake Sturgeon, White Sucker, and salmonids to cooler, stabler streams of northern Michigan and Wisconsin river systems. Warmer temperatures in streams of southern Michigan contributed to more favorable habitat for Walleye and Sea Lamprey. Flow conditions, however, did not limit Walleye and Sea Lamprey in my assessment because I could not find enough information to distinguish their preferences in flow conditions. As a result, Walleye and Sea Lamprey have a greater range of suitable habitats across the study region.

Utility of approach for barrier removal decision-making

My approach can be applied to investigate habitat suitability for any aquatic species lacking occurrence data in streams across a large region. I demonstrated how results can be used to inform management and conservation of migratory fish species lacking occurrence records above barriers. I also showed how results can be used to limit the spread of invasive species, another threat to freshwater biodiversity (Dudgeon et al., 2006; Dudgeon, 2017). My approach is useful to Great Lakes fishery managers as well as to managers focused on restoring connectivity and limiting invasive species in river systems globally (Jones et al., 2021), or perhaps anticipating changes in stream suitability due to climate change, another threat to freshwater biodiversity (Strayer & Dudgeon, 2010; Tingley et al., 2022).

Besides species habitat suitability, another important concern to fishery managers is project cost, which includes the cost of mitigating barriers (e.g., removal, fish passage installation) and the cost of an alternative strategy to control invasive species. In the Great Lakes region, streams lacking barriers are treated with lampricide. Application of lampricide is dependent on larval life history, expense, and labor, requiring treatment of tributaries in cycles (e.g., three to four years) due to budget constraints (Lavis et al., 2003; Jubar et al., 2017). In addition, there is some uncertainty about Sea Lamprey response to barrier removal, where novel production from newly available stream habitat has been forecasted to decrease the overall effectiveness of control leading to disproportionate increases in Sea Lamprey abundance (Jensen & Jones, 2018). Thus, fishery managers must balance project costs with restoring connectivity for species to effectively manage sustainable fisheries and limit the spread of invasive species.

An optimization approach can balance species habitat suitability estimates and barrier mitigation costs, identifying the most cost-effective solutions among many barrier removal options in the context of invasive species management (McKay et al., 2017; 2020). For example, Cooper et al. (2021) coupled SDMs of native fishes and invasive carps with barrier mitigation costs (e.g., barrier removal, fish passage installation) in an optimization model to identify cost-effective opportunities to restore connectivity in the Upper Mississippi River Basin. In the Great Lakes, Neeson et al. (2015) and Milt et al. (2018) applied a similar approach using total channel length gained with barrier removals as a proxy for suitable habitat. However, channel length treats all stream habitat accessible to fishes to be equally suitable (McKay et al., 2017) potentially resulting in less efficient and more costly solutions (Sethi et al., 2017; Rodeles et al., 2020). My results suggest that stream habitats are not equally suitable for species considered. Using the habitat suitability results in an optimization approach provides a unique opportunity to re-examine the most cost-effective solutions among the barrier removal options in the Great

Lakes region.

Limitations of the approach and opportunities for refinement

I identified limitations to my approach along with opportunities for refinement to improve overall results. One limitation is that I was unable to capture all habitat preferences described for species in my study such as turbidity and dissolved oxygen that were defined for some fishes in the literature and known to be especially important to Lake Sturgeon, White Sucker, and salmonids (documented in Dean et al., 2020). While identification of datasets to represent those habitat preferences across the large scale of my study would improve overall results, these factors can change daily, and it is difficult to adequately capture that amount of variation over such a large spatial extent. Another limitation in my approach is that some habitat preferences are likely more important than others, and I lacked information to effectively weight that importance. With sufficient information, landscape variables or habitat factors could be weighted to adjust their relative importance in evaluating overall habitat suitability. I also did not account for biotic interactions in my study, although predation of and competition with other species, especially when a species is in its larval or juvenile stages (Fausch & White 1981; Fausch & White, 1986) influences overall habitat suitability (Mills et al., 2004). In the assessment of Rocky Mountain streams, Quist et al. (2005) used the abundance of non-native piscivores to further refine the potential set of suitable streams identified for species that were predicted from habitat characteristics and landscape features. A similar biotic measure could be used in my approach to further refine habitat suitability results. Another limitation is that stream habitat conditions, as well as habitat preferences of species, vary throughout the year. In my study, I only considered summer stream temperatures. Integration of seasonal stream habitat factors into the approach, like stream temperature during spring and fall spawning migrations, would also improve estimates of habitat suitability. A final limitation of my study is that in a previous study, landscape variables did not predict Type I or Type II habitat well in Lake Michigan tributaries (Jensen, 2017). This could imply that the landscape variables used in my study may not fully capture the most critical habitat component for Sea Lamprey production, substrate. Integration of additional sampled Sea Lamprey habitat data, such as from the Great Lakes Fishery Commission that has collected such information in tributaries across the Great Lakes region for many years, could help ground-truth and improve accuracy of my results.

Conclusion

I used an approach to identify suitable habitat for migratory fishes above barriers where approaches like SDMs were not an option due to a lack of species occurrence records. I considered six Great Lakes migratory species with distributions limited below barriers in my stream habitat suitability assessment to aid fishery managers in evaluating trade-offs of barrier mitigation. My results coupled with costs of barrier mitigation and invasive species control in an optimization approach can further enhance trade-off evaluations at barrier locations for Great Lakes fishery managers. Managers of river systems around the world struggle with balancing connectivity restoration and invasive species control like fishery managers in the Great Lakes. My approach provides an opportunity to inform trade-offs in these other regions to aid managers and contribute to the conservation of species threatened by barriers, including migratory fish species.

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APPENDIX A: CHAPTER 3 TABLES

Table 3.1. Species habitat preferences along with representative habitat factors and surrogate landscape variables and associated defined suitability ranges used to generate reach scores. Options refer to approaches from Figure 3.2.

Habitat preference	Factor or variable	Species	Option	Suitability range and score		
				2	1	0
Stream size	Drainage area (km^2)	Lake Sturgeon	A, D	≥466.2	50.0-466.2	<50.0
		White Sucker	A, D	≥25.0	<25.0	-
		Walleye	A, D	466.2-1605.7	50.0-466.2; ≥1605.7	<50.0
		Steelhead	A, D	25.0-1605.7	≥1605.7	<25.0
		Brook Trout	A, D	25.0-103.6	≥103.6	<25.0
		Sea Lamprey				
		-Larval	A, D	≥103.6	25.0-103.6	<25.0
		-Adult	A, D	≥103.6	25.0-103.6	<25.0
Riffle habitat, coarse material	Forest cover (%)	Lake Sturgeon	D	≥50	<50	-
		White Sucker	D	≥50	<50	-
		Walleye	D	≥50	<50	-
		Steelhead	D	≥50	<50	-
		Brook Trout	D	≥50	<50	-
		Sea Lamprey				
		-Larval	-	-	-	-
		-Adult	D	≥50	<50	-

Table 3.1. (cont'd)

Habitat preference	Factor or variable	Species	Option	Suitability range and score		
				2	1	0
Pool habitat	Fine geology (%)	Lake Sturgeon	D	≥50	<50	-
		White Sucker	D	≥50	<50	-
		Walleye	D	≥50	<50	-
		Steelhead	D	≥50	<50	-
		Brook Trout	D	≥50	<50	-
		Sea Lamprey				
		-Larval	D	≥50	<50	-
		-Adult	-	-	-	-
Fine material	Wetland cover (%)	Lake Sturgeon	D	≥50	<50	-
		White Sucker	D	≥50	<50	-
		Walleye	-	-	-	-
		Steelhead	D	≤50	>50	-
		Brook Trout	D	≤50	>50	-
		Sea Lamprey				
		-Larval	D	≥50	<50	-
		-Adult	-	-	-	-

Table 3.1. (cont'd)

Habitat preference	Factor or variable	Species	Option	Suitability range and score		
				2	1	0
Flow stability	10/90 flow ratio	Lake Sturgeon	C	≤20	>20	-
		White Sucker	B	≤40	>40	-
		Walleye	-	-	-	-
		Steelhead	B	≤40	<40	-
		Brook Trout	B	≤30	>30	-
		Sea Lamprey				
		-Larval	-	-	-	-
		-Adult	-	-	-	-
Baseflow	90/50 flow ratio	Lake Sturgeon	-	-	-	-
		White Sucker	B	≥0.20	<0.20	-
		Walleye	-	-	-	-
		Steelhead	A	≥0.55	0.25-0.55	<0.25
		Brook Trout	A	≥0.55	0.25-0.55	<0.25
		Sea Lamprey				
		-Larval	-	-	-	-
		-Adult	-	-	-	-

Table 3.1. (cont'd)

Habitat preference	Factor or variable	Species	Option	Suitability range and score		
				2	1	0
Velocity	Gradient (m/m)	Lake Sturgeon	A	≥0.0009	<0.0009	-
		White Sucker	B	≤0.003	>0.003	-
		Walleye	A	≤0.0003	>0.0003	-
		Steelhead	A	≥0.0009	<0.0009	-
		Brook Trout	A	≥0.0009	<0.0009	-
		Sea Lamprey				
		-Larval	A	≤0.005	>0.005	-
		-Adult	A	≤0.005	>0.005	-
Groundwater input	Groundwater velocity (m/m)	Lake Sturgeon	-	-	-	-
		White Sucker	-	-	-	-
		Walleye	-	-	-	-
		Steelhead	B	≥40	<40	-
		Brook Trout	B	≥60	<60	-
		Sea Lamprey				
		-Larval	-	-	-	-
		-Adult	-	-	-	-

Table 3.1. (cont'd)

Habitat preferences	Factor or variable	Species	Option	Suitability range and score		
				2	1	0
Stream temperature	July mean temperature (°C)	Lake Sturgeon	A	13-20	≤13; 20-30	≥30
		White Sucker	A	15-23	≤15; 23-27	≥27
		Walleye	A	18-24	≤18; 24-32	≥32
		Steelhead	A	13-20	≤13; 20-24	≥24
		Brook Trout	A	11-15	≤11; 15-22	≥22
		Sea Lamprey				
		-Larval	A	18-23	≤18; 23-31	≥31
		-Adult	A	18-23	≤18; 23-31	≥31
Habitat condition	CHCI	Lake Sturgeon	A	≥3.60	2.75-3.60	≤2.75
		White Sucker	A	≥3.60	2.75-3.60	≤2.75
		Walleye	A	≥3.60	2.75-3.60	≤2.75
		Steelhead	A	≥3.60	2.75-3.60	≤2.75
		Brook Trout	A	≥3.60	2.75-3.60	≤2.75
		Sea Lamprey				
		-Larval	A	≥3.60	2.75-3.60	≤2.75
		-Adult	A	≥3.60	2.75-3.60	≤2.75

APPENDIX B: CHAPTER 3 FIGURES

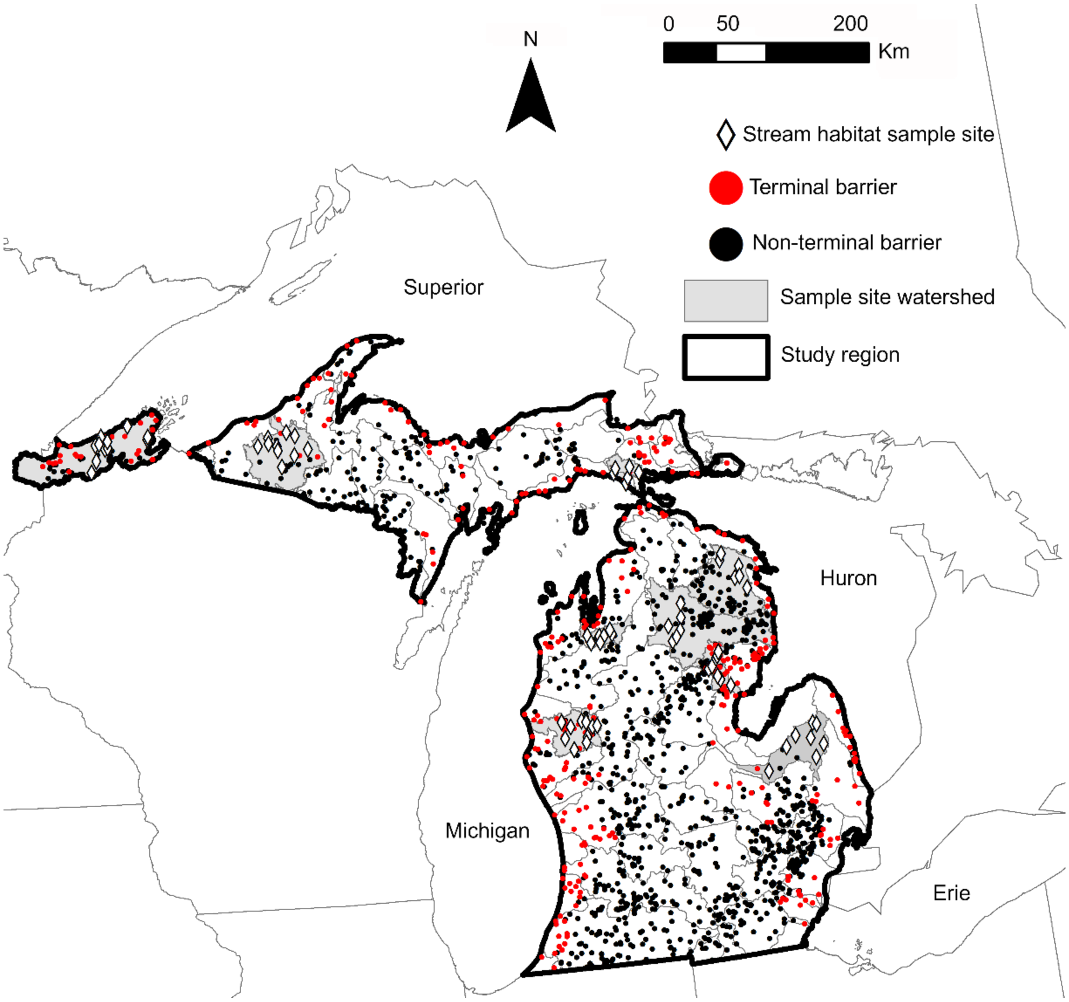

Figure 3.1. Map of the study region including the distribution of terminal (N = 346) and non-terminal (N = 1,251) barriers and stream habitat sample sites (N = 71).

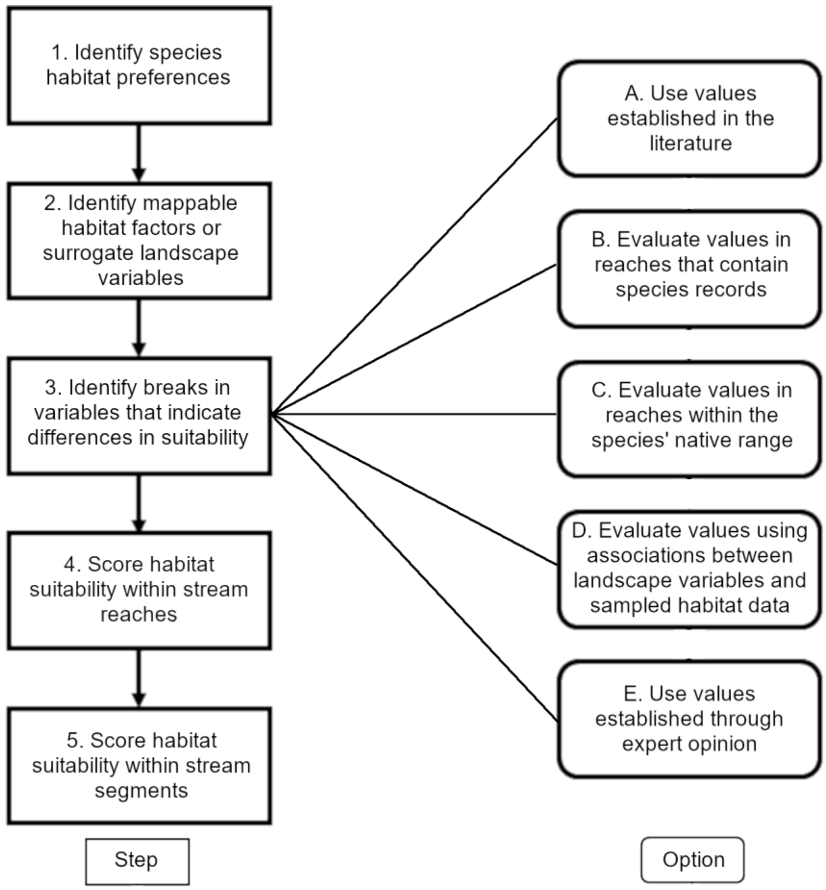

Figure 3.2. Approach to assess stream habitat suitability for migratory fish species above barriers.

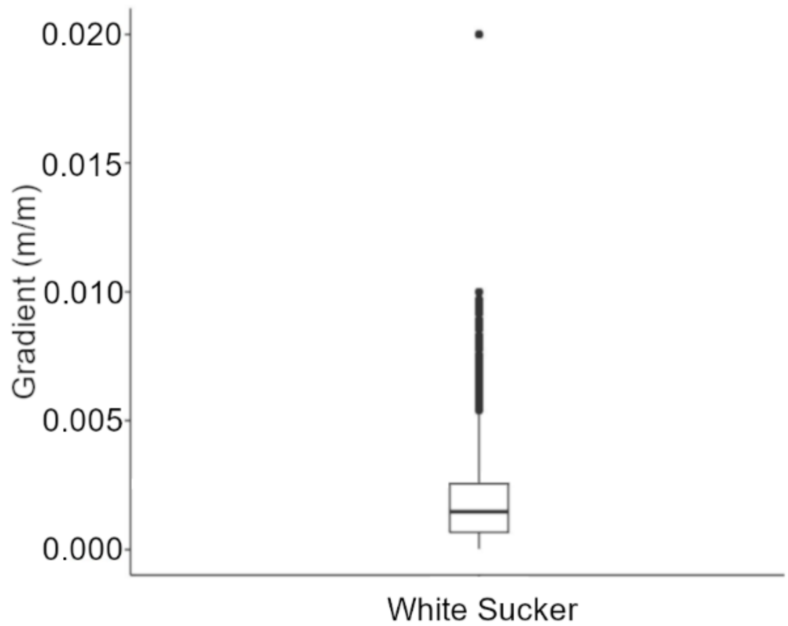

Figure 3.3. Distribution of gradient values in stream reaches with stream resident White Sucker occurrence records (N = 2,471) above barriers in the study region. The associated break value is 0.003 m/m (75th percentile; Table 3.1).

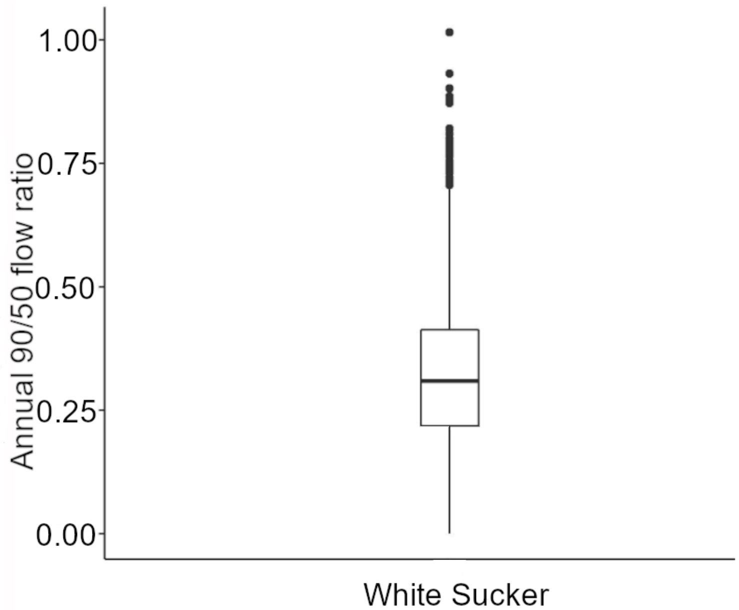

Figure 3.4. Distribution of the 90/50 flow ratio in stream reaches with stream resident White Sucker occurrence records (N = 2,471) above barriers in the study region. The associated break value is 0.20 (75th percentile; Table 3.1).

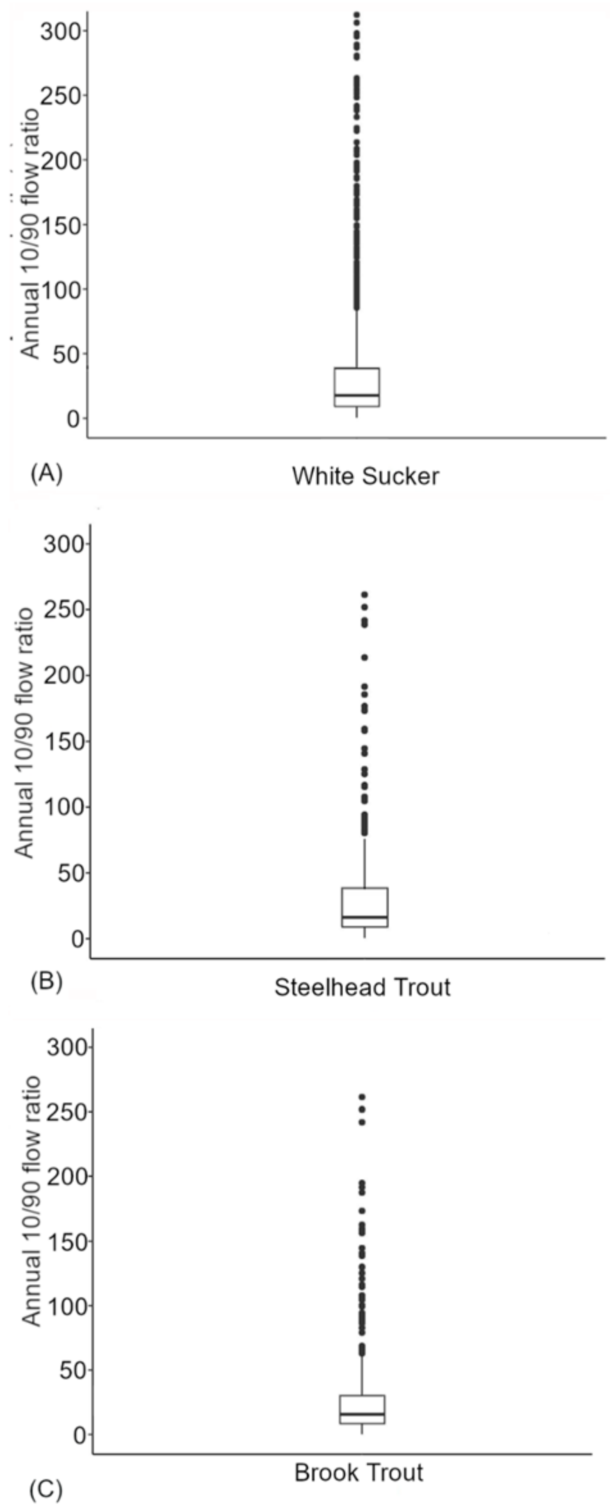

Figure 3.5. Distribution of the 10/90 flow ratio in stream reaches with stream resident (A) White Sucker, (B) Steelhead, and (C) Brook Trout occurrence records. The associated break values are 0.40 for White Sucker and Steelhead and 0.30 for Brook Trout (Table 3.1).

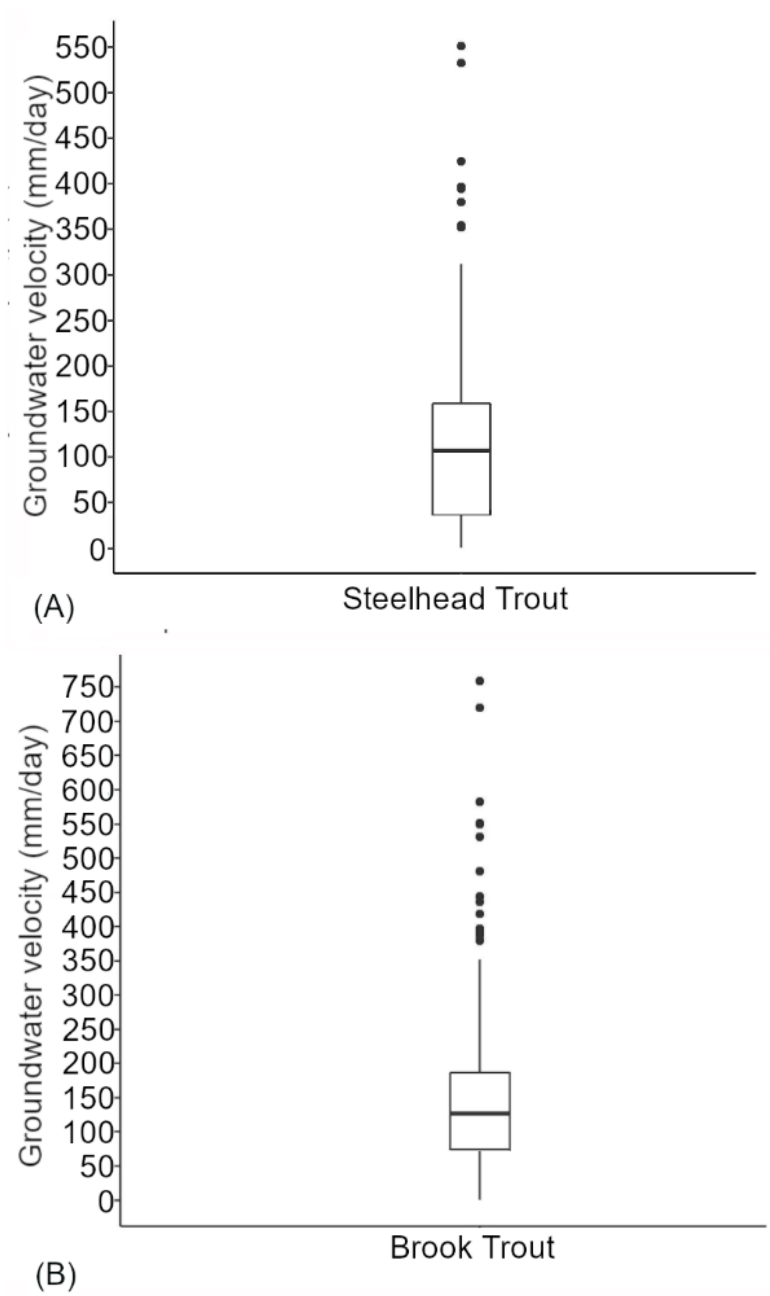

Figure 3.6. Boxplot of the values of groundwater velocity (mm/day) in reaches with stream resident (A) Steelhead and (B) Brook Trout occurrence records. The associated break values are 40 mm/day for Steelhead and 60 mm/day for Brook Trout (Table 3.1).

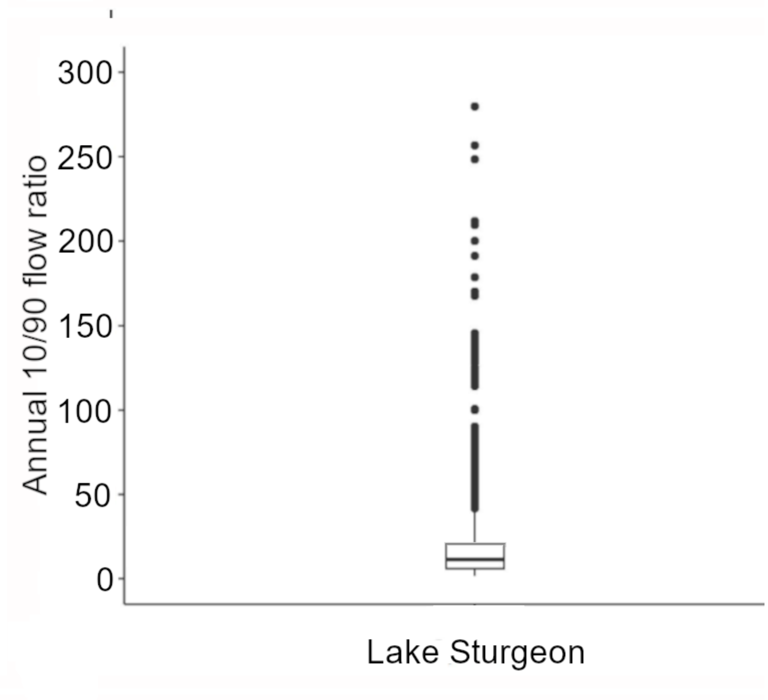

Figure 3.7. Boxplot of the 10/90 flow ratio values in reaches within the Lake Sturgeon's native range.

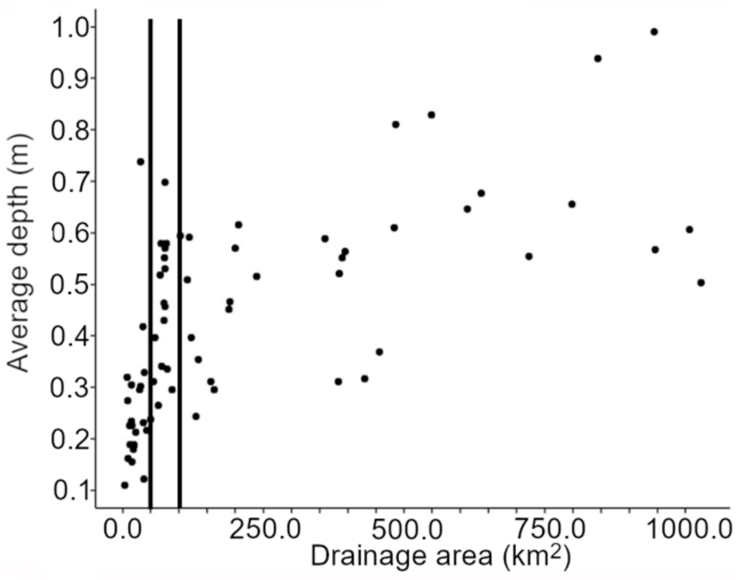

Figure 3.8. Scatterplot of average depth (m) from sampled streams and their respective drainage area (km^2). The first black line represents a break at 25.0 km^2 (0.1 m) and the second black line represents a break at 50.0 km^2 (0.5m; Table 3.1).

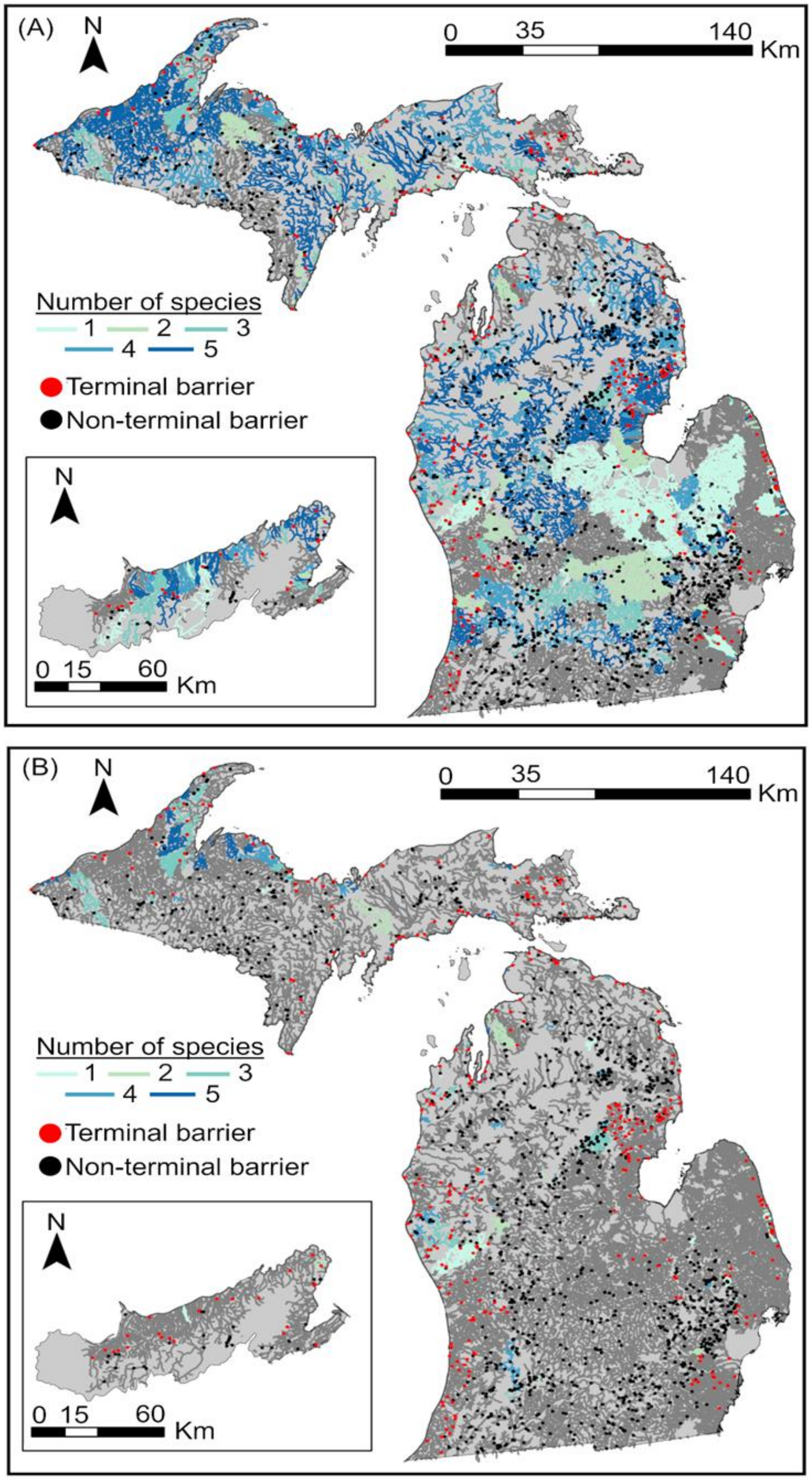

Figure 3.9. Map of the study region (Bayfield Peninsula shown in the inset map) with Panel (A) showing the distribution of suitable segments for one, two, three, four, or all five desirable fishes and Panel (B) showing the distribution of these suitable segments if they were also least suitable for larval Sea Lamprey.

APPENDIX C: CHAPTER 3 SUPPLEMENTARY TABLES

Table C3.1. Landscape and modeled stream habitat data used in the study along with minimum, mean, and maximum values summarized across 71 sampled streams in the study region.

Variable or factor	Variable or factor, scale (unit)	Dataset (scale/resolution)	Minimum	Mean	Maximum
Landscape	Drainage area, network catchment (km^2)	National Hydrography Dataset Plus V2 (1:100,000)	3.5	219.8	1027.9
	Michigan groundwater velocity, network catchment (mm/day; N = 60)	MRI-DARCY (30 m)	0.0	106.5	530.6
	Michigan fine geology, network catchment (%; N = 60)	National Geologic Map Database (1:250,000)	0.0	20.5	100.0
	Wisconsin fine geology, network catchment (%; N = 11)	Geologic Map of North America (1:5,000,000)	0.0	43.8	100.0
	Cumulative habitat condition index, network catchment	National Fish Habitat Partnership 2015 Cumulative Habitat Condition Indices (1:100,000)	1.0	3.9	5.0
	Forest cover, network buffer (%)	2011 National Land Cover Database (30 m)	2.0	34.5	87.0
	Wetland cover, network buffer (%)	2011 National Land Cover Database (30 m)	1.0	36.1	85.0
	Gradient, reach (m/m)	National Hydrography Dataset Plus V2 (1:100,000)	0.00001	0.00300	0.02000
Habitat	Annual 10/90 flow ratio, reach	FishVis	0.6	60.2	686.0
	Annual 90/50 flow ratio, reach	FishVis	<0.1	0.3	0.8
	July mean temperature, reach (°C)	FishVis	10.5	17.9	22.1

Table C3.2. List of 60 habitat variables sampled from 71 stream sites and the minimum, mean, and maximum values of the variables.

Group	Variable	Minimum	Mean	Maximum
Channel morphology	Wetted width (m)	0.39	9.91	41.15
	Bankfull width (m)	0.40	10.64	42.52
	Islands (# in reach)	0.00	0.29	3.00
	Island width (m)	0.91	6.57	24.99
	Bankfull height (m)	0.00	0.33	2.74
	Undercuts (# in transects)	0.00	4.63	22.00
	Undercut length (m)	0.03	0.28	3.41
	Depth (m)	0.03	0.43	1.82
	Thalweg depth (m)	0.03	0.61	1.83
Geomorphic units (% of reach)	Pools	0.00	21.99	92.31
	Riffles	0.00	14.84	76.92
	Runs	0.08	63.16	100.00
Substrate (# of points in reach)	Clay	0.00	2.28	26.00
	Silt/detritus	0.00	10.71	65.00
	Sand	0.00	22.35	63.00
	Fine material (silt/detritus and sand)	0.00	33.07	65.00
	Gravel	0.00	16.20	53.00
	Small and large cobble	0.00	11.96	55.00
	Coarse material (gravel and cobble)	0.00	28.15	61.00
	Boulder	0.00	0.70	10.00
	Bedrock	0.00	0.45	32.00
	Embedded coarse substrate	0.00	13.39	57.00
	Non-embedded coarse substrate	0.00	16.34	64.00

Table C3.2. (cont'd)

Group	Variable	Minimum	Mean	Maximum
Substrate (% of reach)	Type 1 (silt/detritus)	0.00	17.95	100.00
	Type 2 (sand)	0.00	33.54	97.70
	Type 3 (gravel, cobble, boulder, hardpan clay, bedrock)	0.00	48.50	100.00
	Coarse spawning material (>9 mm diameter)	0.00	43.07	100.00
Riparian condition (# of points in reach)	Yard/lawn	0.00	1.10	14.00
	Pasture	0.00	0.22	13.00
	Row crop	0.00	0.89	26.00
	Yard, pasture, and row crop	0.00	2.21	26.00
	Grassland/forb	0.00	5.00	26.00
	Tag alder	0.00	7.91	25.00
	Small coniferous trees	0.00	0.49	6.00
	Large coniferous trees	0.00	3.66	24.00
	Small deciduous trees	0.00	4.06	24.00
	Large deciduous trees	0.00	2.65	26.00
	Natural cover (grassland/forb, tag alder, small coniferous trees, large coniferous trees, small deciduous trees, and large deciduous trees)	0.00	23.77	26.00
	Bank stability score (# in reach)	1.00	2.53	4.00

Table C3.2. (cont'd)

Group	Variable	Minimum	Mean	Maximum
Fish cover	Woody material (% in reach)*	0.00	6.71	100.00
	Submerged aquatic vegetation (% in reach)	0.00	9.03	100.00
	15-30 cm diameter logs (# in reach)	0.00	22.44	100.00
	30-45 cm diameter logs (# in reach)	0.00	9.34	61.00
	45-60 cm diameter logs (# in reach)	0.00	1.07	6.00
	>60 cm diameter logs (# in reach)	0.00	0.58	6.00
	15-30 cm, 30-45 cm, 45-60 cm, and >60 cm diameter logs (# in reach)	0.00	33.42	145.00
	Natural jog jam area (m^2)	0.00	235.17	2392.00
	Beaver dam area (m^2)	0.00	44.04	1529.00
	Brush deposit area (m^2)	0.00	275.94	1803.00
	Artificial log jam area (m^2)	0.00	270.59	7332.00
	Lunker structure area (m^2)	0.00	0.34	12.00
	Rip-rap area (m^2)	0.00	0.17	12.00
	Rafts area (m^2)	0.00	0.00	0.00
	Stump clumps (m^2)	0.00	13.86	984.00
	Wing deflectors (m^2)	0.00	0.56	40.00
	Artificially-placed logs (m^2)	0.00	8.14	510.00
	Total LWD structure (m^2)	0.00	862.30	8801.00
Temperature (°C)	July mean temperature	12.44	19.31	28.20
	August mean temperature	10.39	17.46	26.95
	Seasonal (July-August) mean temperature	10.07	18.39	26.95

Table C3.3. List of 14 sampled habitat variables identified from variable reduction that characterize aspects of stream habitat important to migratory fishes.

Group	Habitat variable (unit)	Code	Minimum	Mean	Maximum
Channel morphology (m)	Wetted width	WID	0.4	9.9	41.1
	Bankfull height	BH	0.0	0.3	2.7
	Depth	DEP	<0.1	0.4	1.8
Geomorphic units (% of reach)	Pool	POOL	0.0	21.9	92.3
	Riffle	RIFF	0.0	14.8	76.9
Substrate (# of points in reach)	Fine substrate	FINE	0.0	33.0	65.0
	Coarse substrate	COAR	0.00	28.15	61.00
Riparian condition (# of points in reach)	Natural cover	COV	0.0	23.7	26.0
	Bank stability score	BST	1.0	2.5	4.0
Fish cover	Woody material (% of reach)	WOOD	0.0	6.7	100.0
	Submerged aquatic vegetation (% of reach)	PLT	0.0	9.0	100.0
	Total single logs (# in reach)	LOG	0.0	33.4	145.0
	Total LWD structures (m^2)	LWD	0.0	862.3	8801.0
Stream temperature (°C)	Measured July mean temperature	TEMP	12.4	19.3	28.2

Table C3.4. Stream habitat preferences of the Lake Sturgeon *Acipenser fulvescens* with literature sources.

Group	Habitat preference	Description	Literature source
Channel morphology	Stream size	Fish observed in large streams. Spawning adults found at various depths (e.g., < 1 m to > 10 m). Larvae and juveniles require minimum depth of 0.5 m to rear.	Harkness & Dymond, 1961; Goodyear et al., 1982; Kempinger, 1996; Hay-Chmielewski & Whelan, 1997; Threader, 1998; Auer, 1999; Auer & Baker, 2002; Manny & Kennedy, 2002; Benson et al., 2005; Friday, 2006; Adams et al., 2006; Barth et al., 2009; Daugherty et al., 2009; Haxton, 2011; Boase et al., 2014; Bruch et al., 2016; Krieger & Diana, 2017; Baril et al., 2018; Roseman et al., 2020
	Gradient	Spawning adults require gradients greater than $\geq$ 0.0009 m/m while larvae and juveniles prefer lower gradients between 0.0003 m/m and 0.0006 m/m.	Hay-Chmielewski & Whelan, 1997; Threader, 1998; Benson et al., 2005; Daugherty et al., 2008; Daugherty et al., 2009; Krieger & Diana, 2017
Geomorphic units	Riffle	Spawning adults prefer rapids or riffles.	Harkness & Dymond, 1961; Goodyear et al., 1982; Hay-Chmielewski & Whelan, 1997; Peterson et al., 2007; Chiotti et al., 2008; Roseman et al., 2020
	Pool	Larval, juvenile, and non-spawning adult fish use pools for refuge.	Harkness & Dymond, 1961; Hay-Chmielewski & Whelan, 1997
	Run	Larval, juvenile, and non-spawning adult fish use runs for feeding.	Becker, 1983; Auer, 1996a; Lyons & Stewart, 2014

Table C3.4. (cont'd)

Group	Habitat requirement	Description	Literature source
Flow regime	Flow stability	Larval and juvenile fish are weak swimmers and require stable flows to maintain orientation.	Kempinger, 1988; Kempinger, 1996; Auer, 1996b; Hay-Chmielewski & Whelan, 1997; Peake et al., 1997
	Velocity	Spawning adults prefer streams with 'swift' velocities ($\geq$5.5 m/s) but have been observed to spawn in velocities less than 5.5 m/s. Larval and juvenile fish prefer streams with relatively slower velocities ranging from 0.6-1.0 m/s.	Harkness & Dymond, 1961; LaHaye et al., 1992; Auer & Baker, 2002; Manny & Kennedy, 2002; Benson et al., 2005; Dittman & Zollweg, 2006; Johnson et al., 2006; Chiotti et al., 2008; Barth et al., 2009; Daugherty et al., 2008; Daugherty et al., 2009; Kerr et al., 2010; Dumont et al., 2011; Bruch et al., 2016; Krieger & Diana, 2017; Baril et al., 2018; Krieger et al., 2018; Roseman et al., 2020
Substrate	Coarse material	Spawning adults require gravel, cobble, rubble, boulder, or cinder.	Goodyear et al., 1982; Kempinger, 1988; Auer, 1990; Lane et al., 1996; Hay-Chmielewski & Whelan, 1997; Auer, 1999; Bruch & Binkowski, 2002; Caswell et al., 2002; Manny & Kennedy, 2002; Johnson et al., 2006; Peterson et al., 2007; Daugherty et al., 2008; Haxton & Findlay, 2008; Haxton et al., 2008; Daugherty et al., 2009; Kerr et al., 2010; Dumont et al., 2011; Roseman et al., 2011; Bruch et al., 2016; Baril et al., 2018; Roseman et al., 2020

Table C3.4. (cont'd)

Group	Habitat requirement	Description	Literature source
Substrate	Fine material	Larvae and juveniles prefer to feed in areas with fine substrate lacking aquatic vegetation; non-spawning adults feed in areas with sand and mud.	Kempinger, 1988; Lane et al., 1996; Peake et al., 1997; Peake, 1999; Holtgren & Auer, 2004; Benson et al., 2005; Daugherty et al., 2008; Haxton & Findlay, 2008; Haxton et al., 2008; Daugherty et al., 2009; Krieger & Diana, 2017; Krieger et al., 2018
Temperature	Cool water	Spawning migrations occur in spring with optimal temperatures between 12°C and 17°C. Optimal embryo incubation occurs between 14°C and 17°C. Downstream drift of larval fish occurs at 16°C. Optimal summer growth of larval and juvenile fish occurs between 13°C and 20°C. Upper thermal lethal limit for the species is $\geq$30°C.	Harkness & Dymond, 1961; Scott & Crossman, 1973; Goodyear et al., 1982; Wang et al., 1985; Hay-Chmielewski & Whelan, 1997; Bruch & Binkowski, 2002; Cech & Doroshov, 2004; Wilson & McKinley, 2004; Smith & King, 2005; Kerr et al., 2010; Wilkes, 2011; Lyons & Stewart, 2014; Bruch et al., 2016
Habitat condition	Connectivity	Adults can migrate between 1,000 and 1,800 km to spawning habitat. Larvae drift between 10 to 30 km to nursery habitat, but some have been observed to drift farther than 60 km.	Auer, 1996a; Rusak & Mosindy, 1997; Auer & Baker, 2002; Bruch & Binkowski, 2002; Smith & King, 2005; Benson et al., 2005; Daugherty et al., 2008; Daugherty et al., 2009; Gerig et al., 2011; Kuhadja, 2014; Lyons & Stewart, 2014
	Quality	Spawning and nursery habitats are negatively affected by land uses and in-stream barriers.	Baker, 1980; Knights et al., 2002; Nichols et al., 2003; Peterson et al., 2007; Hayes & Carrofino, 2012; Bouckert et al., 2014; Pratt et al., 2014

Table C3.5. Stream habitat preferences of the Walleye *Sander vitreus* with literature sources.

Group	Habitat preference	Description	Literature source
Channel morphology	Stream size	Fish prefer large to very large rivers and stream depths of greater than 0.3 m.	Eschmeyer, 1950; Regier et al., 1969; Priegel, 1970; Ryder & Kerr, 1978; McMahon et al., 1984; Sternberg, 1986; Eshenroder, 2003; Manny et al., 2010; Bozek et al., 2011
	Gradient	Fish prefer streams with gradients $\leq$0.0003 m/m.	Kitchell et al., 1977; Hamilton, 2009
Geomorphic units	Riffle	Spawning adults prefer riffles.	McMahon et al., 1984; Corbett & Powles, 1986
Flow regime	Flow stability	Spawning success and larval survival are related to stable discharge, however, species can tolerate a range of flow conditions.	Busch et al., 1975; Groen & Schroeder, 1978; McMahon et al., 1984; Mion et al., 1998; Jones et al., 2003; Gillenwater et al., 2006; Bozek et al., 2011
	Velocity	Spawning adults prefer streams with water velocities less than 2 m/s.	McMahon et al., 1984; Cheng et al., 2006; Jones et al., 2003; Hartman, 2009; Bozek et al., 2011
Substrate	Coarse material	Spawning adults require gravel, cobble, and rubble.	Eschmeyer, 1950; McMahon et al., 1984; Jones et al., 2003; Gillenwater et al., 2006; Hartman, 2009; Ivan et al., 2010

Table C3.5. (cont'd)

Group	Habitat preference	Description	Literature source
Temperature	Cool water	Spawning migrations occur in spring, triggered at 1°C. Optimal egg incubation and hatching occur between 9°C and 15°C. Optimal growth of larval, juvenile, and non-spawning adult fish occurs between 20°C and 24°C. Upper thermal lethal limit for the species is greater than 32°C.	Eschmeyer, 1950; Scott & Crossman, 1973; Koenst & Smith, 1976; Hokanson, 1977; McMahon et al., 1984; Jones et al., 2003; Hartman, 2009; Manny et al., 2010; Hasnain et al., 2010; Bozek et al., 2011; Rutherford et al., 2016
Fish cover	Large woody debris	Provides cover habitat for larvae and juveniles especially in light intense situations.	McMahon et al., 1984
	Submerged aquatic vegetation	Provides cover habitat for larvae and juveniles.	McMahon et al., 1984
Habitat condition	Connectivity	Fish can migrate between 50 to 300 km to spawning habitat. Larvae drift many kilometers downstream.	Ferguson & Derksen, 1971; Colby et al., 1979; DePhilip et al., 2005; Bozek et al., 2011; Hayden et al., 2018
	Quality	Spawning habitats are negatively affected by land uses and in-stream barriers.	Bunt et al. 2000; Cheng et al. 2006; MacDougall et al., 2007; Vandergoot et al., 2010

Table C3.6. Stream habitat preferences of White Sucker *Catostomus commersoniii* with literature sources.

Group	Habitat preference	Description	Literature source
Channel morphology	Stream size	Fish common in streams of various sizes; observed in stream depths greater than 0.10 m.	Becker, 1983; Goodyear et al., 1982; Curry & Spacie, 1984; Twomey et al., 1984; Moody, 1989; Lane et al., 1996
	Gradient	Spawning adults observed in streams with gradients between 0.001 m/m to 0.003 m/m although these values were reported for fish in mountainous streams of western U.S.	Curry & Spacie, 1984; Twomey et al., 1984
Geomorphic units	Riffle	Spawning adults prefer riffles.	Goodyear et al., 1982; Twomey et al., 1984; Corbett & Powles, 1986; Hubert & Rahel, 1989
	Pool	Larval, juvenile, and non-spawning adult fish prefer deep pools (0.7-1.0 m) for refuge; streams that are 40% to 60% pools are optimal.	Curry & Spacie, 1984; Twomey et al., 1984; Hubert & Rahel, 1989
	Run	Larval, juvenile, and non-spawning adult fish use runs for feeding.	Twomey et al., 1984
Flow regime	Flow stability	Optimal habitat conditions associated with stable flow because fish are weak swimmers.	Curry & Spacie, 1984; McManamay et al., 2012
	Baseflow	Higher baseflows yield greater depths to support refuge habitat.	Curry & Spacie, 1984; Twomey et al., 1984; McManamay et al., 2012
	Velocity	Spawning adults prefer slow water velocities ($\leq$0.9 m/s).	Twomey et al., 1984; Aadland, 1993
Substrate	Coarse material	Larval, juvenile, and non-spawning adult fish prefer streams with a mixture of sand and gravel.	Twomey et al., 1984; Lane et al., 1996
	Fine material	Larval, juvenile, and non-spawning adult fish prefer streams with a mixture of sand and gravel.	Twomey et al., 1984; Lane et al., 1996

Table C3.6. (cont'd)

Group	Habitat preference	Description	Literature source
Temperature	Cool water	Spawning migrations occur in spring and begin when water temperatures reach 3°C. Optimal spawning occurs between 6°C and 23°C. Optimal embryo incubation occurs between 11°C and 16°C. Optimal summer growth of larval, juvenile, and non-spawning adult fish occurs between 15°C and 23°C. Upper thermal lethal limit is greater than 27°C.	Goodyear et al., 1982; Becker, 1983; Twomey et al., 1984; Castleberry & Cech, 1992; Smale & Rabeni, 1995
Fish cover	Large woody debris	Serves as cover habitat for all life stages.	Twomey et al., 1984; Hubert & Rahel, 1989
	Submerged aquatic vegetation	Fish prefer low amounts of submerged aquatic vegetation.	Lane et al., 1996
	Overhead bank vegetation	Serves as cover habitat for all life stages.	Twomey et al., 1984
Habitat condition	Connectivity	Can migrate between 40 to 50 km to spawning habitat.	Scott & Crossman, 1973; Werner, 1979; Becker, 1983; Doherty et al., 2010
	Quality	Spawning and nursery habitats are negatively affected by land uses and in-stream barriers.	Cooke et al., 2005

Table C3.7. Stream habitat preferences of Steelhead *Oncorhynchus mykiss* with literature sources.

Group	Habitat preference	Description	Literature source
Channel morphology	Stream size	Fish prefer small to very large rivers. Spawning adult, larval, and juvenile fish prefer depths greater than 0.10 m.	Scott & Crossman, 1973; Goodyear et al., 1982; Raleigh, 1984; Sheppard & Johnson, 1985; Bjornn & Reiser, 1991; Workman et al., 2004
	Gradient	Fish prefer streams with gradients >0.0009 m/m.	Seelbach et al., 1994; Zorn et al., 2018
Geomorphic units	Riffle	Spawning adults prefer riffles.	Raleigh, 1984
	Pool	Pools serve as refuge for all life stages.	Raleigh, 1984; Studdert & Johnson, 2015
Flow regime	Flow stability	Optimal spawning habitat conditions related to stable flows.	Raleigh, 1984
	Baseflow	Baseflow >55% of the average annual daily flow is excellent, between 25 and 55% is fair, and less than 25% is poor habitat.	Raleigh, 1984
	Velocity	Spawning adults prefer velocities between 0.1 and 0.9 m/s. Optimal embryo development occurs between 0.3 and 0.7 m/s. Larval fish prefer velocities <0.3 m/s, and juvenile and non-spawning adult fish observed in velocities <0.2 m/s.	Raleigh, 1984; Sheppard & Johnson, 1985; Bjornn & Reiser, 1991; Kocik & Taylor, 1996; Workman et al., 2004
	Groundwater input	Important for stabilizing flow and maintaining cooler stream temperature for the species.	Sowder & Power, 1985; Seelbach, 1993; Woldt & Rutherford, 2002
Substrate	Coarse material	Spawning adults require gravel, cobble, and rubble.	Raleigh, 1984; Sheppard & Johnson, 1985; Bjornn & Reiser, 1991; Workman et al., 2004
	Fine material	Excess fines can negatively affect growth, abundance, survival, and reproduction.	Raleigh, 1984; Chapman, 1988; Bjornn & Reiser, 1991

Table C3.7. (cont'd)

Group	Habitat preference	Description	Literature source
Temperature	Cold water	Species can spawn in all seasons. Spring or fall migrations occur between 4°C and 10°C, and summer migrations occur at higher temperatures but below 21°C. For fall or spring run fish, optimal embryo incubation and hatching occurs between 4°C and 12°C, and optimal growth of larvae and juveniles occurs between 12°C and 20°C. Optimal incubation and growth of summer-run fish assumed to be similar to fall or spring run fish. Upper thermal lethal limit is greater than 24°C.	Fielder, 1948; Goodyear et al., 1982; Raleigh, 1984; Bell, 1986; Velsen, 1987; Rombough, 1988; Bell, 1991; Nielsen et al., 1994; Seelbach et al., 1994; Haynes et al., 1986; Hicks, 2000; Richter & Kolmes, 2005; Workman et al., 2004; Godby et al., 2007
Fish cover	Large woody debris	Cover for all life stages.	Bjornn & Reiser, 1991
	Overhead bank vegetation	Cover for all life stages.	Wesche et al., 1987
	Undercut banks	Cover for all life stages.	Raleigh, 1984
Habitat condition	Connectivity	Species migrate thousands of kilometers to spawning habitat in its native range. In the Great Lakes region, migrations over 300 km to spawning habitat have been observed.	Becker, 1983; Northcote, 1997; Cramer & Ackerman, 2009a; Cramer & Ackerman, 2009b; Zorn et al., 2018; Roni et al., 2019
	Quality	Spawning and nursery habitats are negatively affected by land uses and in-stream barriers.	Zorn et al., 2018

Table C3.8. Stream habitat preferences of the Brook Trout *Salvelinus fontinalis* with literature sources.

Group	Habitat preference	Description	Literature source
Channel morphology	Stream size	Species inhabits small to medium-sized streams. Spawning adult, larval, juvenile, and non-spawning adult fish prefer depths >0.10 m.	Scott & Crossman, 1973; Fausch & White, 1981; Raleigh, 1982; Baker & Coon, 1997; Curry et al., 1997; Zorn et al., 2018
	Gradient	Prefer streams with gradients >0.0009 m/m.	Zorn et al., 2018
Geomorphic units	Riffle	Spawning adults prefer riffles.	Raleigh, 1982
	Pool	Cover habitat for all life stages.	Raleigh, 1982
	Flow stability	Optimal spawning for adults and survival of larval fish occurs in streams with stable flow.	Raleigh, 1982; Curry et al., 1994; Zorn et al., 2018
	Baseflow	Baseflow >55% of the average annual daily flow is excellent, between 25 and 55% is fair, and less than 25% is poor habitat.	Raleigh, 1982
	Velocity	Adult fish observed spawning in velocities between 0.01 and 0.9 m/s. Optimal embryo development between 0.3 and 0.7 m/s. Larval fish prefer velocities <0.1 m/s, and juvenile and non-spawning adult fish prefer velocities <0.2 m/s.	Raleigh, 1982; Nuhfer et al., 1994; Baker & Coon, 1997; Zorn & Nuhfer, 2007
	Groundwater input	Important for stabilizing flow and maintaining cooler stream temperature for the species.	Benson, 1953; Witzel & MacCrimmon, 1983; Curry et al., 1994; McRae & Edwards, 1994; Curry et al., 1995; Zorn et al., 2018
Substrate	Coarse material	Spawning adults require gravel, cobble, and rubble.	Raleigh, 1982; Workman et al., 2004
	Fine material	Excess fines can negatively affect growth, abundance, survival, and reproduction.	Raleigh, 1982; Alexander & Hansen, 1943; Waters, 1995; Nuhfer, 2004

Table C3.8. (cont'd)

Group	Habitat preference	Description	Literature source
Temperature	Cold water	Spawning occurs in fall and migrations occur between 4.5°C and 10°C. Optimal embryo incubation is between 4°C and 11°C. Optimal growth of larvae and juveniles occurs between 11°C and 15°C. Upper thermal lethal limit is $\geq$22°C.	Creaser, 1930; Raleigh, 1982; McRae & Edwards, 1994; Eaton et al., 1995; Mucha & Mackereth, 2008; Zorn et al., 2018
Fish cover	Large woody debris	Cover habitat for all life stages.	Fausch & Northcote, 1992; Zorn & Nuhfer, 2007; Cordova et al., 2007; Wills & Dexter, 2011
	Overhead bank vegetation	Cover habitat for all life stages.	Wesche et al., 1987
	Undercut banks	Cover habitat for all life stages.	Raleigh, 1982
Habitat condition	Connectivity	Fish can migrate between 1 and 20 km. Coaster Brook Trout observed migrating between 20 and 70 km among lake and stream habitat.	Shetter, 1968; O'Connor & Power, 1973; Fausch & White, 1981 Fausch & White, 1986; Northcote, 1997; Fraser & Bernatchez, 2008; Huckins et al., 2008; Zorn & Wiley, 2010; Cross, 2013; Evans et al., 2015; Fausch, 2018; Zorn et al., 2018; Zorn et al., 2020
	Quality	Spawning and nursery habitats are negatively affected by land uses and in-stream barriers.	Zorn et al., 2018

Table C3.9. Stream habitat preferences of the Sea Lamprey *Petromyzon marinus* with literature sources.

Group	Habitat preference	Description	Literature source
Channel morphology	Stream size	Larval fish inhabit a variety of stream sizes, including tributaries to large inter-lake channels (e.g., St. Mary's River; Criger et al., 2021). Largest streams in a watershed attract and accommodate largest spawning runs of adult fish. Spawning adult and larval fish prefer depths > 0.1 m. Larval fish can be found in deep water habitat including inter-lake channels and river mouths.	Applegate, 1950; Manion & Hanson, 1980; Morman et al., 1980; Dawson et al., 2015; Criger et al., 2021
	Gradient	Spawning adult and larval fish tolerate a wide range of stream gradients (<0.005 m/).	Neeson et al., 2007; Dawson et al., 2015
Geomorphic units	Riffle	Spawning adults prefer riffles.	Johnson et al., 2015
	Pool	Larvae prefer burrowing in sections of river with pools.	Dawson et al., 2015
	Flow stability	Larval fish do not prefer low or unstable flows have been found in streams with these conditions.	Morman et al., 1980
	Velocity	Spawning adult fish and embryos prefer water velocities between 0.5 and 1.5 m/s. Larval fish prefer water velocities <0.8 m/s.	Applegate, 1950; Schleen et al., 2003; Dawson et al., 2015
Substrate	Coarse material	Spawning adults require gravel, cobble, and rubble.	Applegate, 1950; Morman et al., 1980; Slade et al., 2003; Gardner et al., 2012
	Fine material	Larval fish prefer silt substrate for burrowing; sand may also provide habitat.	Bowen et al., 1998; Slade et al., 2003; Dawson et al., 2015

Table C3.9. (cont'd)

Group	Habitat requirements	Description	Literature source
Temperature	Cool water	Spawning occurs in spring and migrations are triggered between 3°C and 4°C. Spawning occurs between 10°C and 18°C. Optimal embryo incubation is between 15°C and 25°C. Optimal growth of larval fish is between 18°C and 23°C. Optimal metamorphosis is between 21°C and 25°C. Upper thermal lethal limit is greater than 31°C.	Applegate, 1950; Piavis, 1961; McCauley, 1963; Piavis, 1971; Farmer et al., 1977; Manion & Hanson, 1980; Morman et al., 1980; Holmes & Linn, 1994; Holmes et al., 1994; Holmes & Youson, 1998; Binder et al., 2010
Fish cover	Submerged aquatic vegetation	Preferred by larval fish.	Applegate, 1950; Bowen et al., 1998; Slade et al., 2003; Dawson et al., 2015
Habitat condition	Connectivity	Fish can migrate between 100 to 300 km to spawning habitat in the Great Lakes.	Applegate, 1950; Applegate et al., 1952; Morman et al., 1980; Kelso & Gardner, 2000; Gardner et al., 2012; Dawson et al., 2015
	Quality	Species negatively affected by habitat degradation and fragmentation from anthropogenic disturbances.	Dawson et al., 2015

Table C3.10. Pearson's correlation values between sampled stream habitat variables and landscape variables. Codes for sampled stream habitat variables are in Table C3.3.

Variable, scale	WID	DEP	BH	POOL	RIFF	FINE	COAR	COV	BST	WOOD	PLT	LOG	LWD
Drainage area, network catchment	0.92‡	0.73†	0.02	-0.12	0.08	-0.31‡	0.33†	0.06	-0.34†	-0.15	0.09	0.37†	0.30†
Fine geology, network catchment (N=60)	-0.29‡	-0.42†	0.13	0.32‡	0.17	-0.06	-0.09	0.19	0.44†	-0.14	-0.09	-0.31‡	-0.06
Forest cover, network buffer	-0.07	-0.22	0.11	0.22	0.29‡	-0.14	0.30‡	0.37†	0.22	-0.06	-0.25‡	-0.15	0.04
Wetland cover, network buffer	0.11	0.31†	-0.08	0.18	-0.14	0.34†	-0.21	0.27†	-0.15	0.47†	0.00	0.45†	0.34†

†Correlation is significant at the 0.01 level (two tailed)
‡Correlation is significant at the 0.05 level (two tailed)

Table C3.11. Pearson's correlation values between sampled stream habitat variables and landscape variables when outliers were adjusted using a 90% Winsorization method. Change from significant to non-significant relationships are indicated in bold.

Variable, scale	WID	DEP	BH	POOL	RIFF	FINE	COAR	COV	BST	WOOD	PLT	LOG	LWD
Drainage area, network catchment	0.93[†]	0.72[†]	0.02	-0.16	0.04	-0.32[†]	0.35[†]	-0.01	-0.34[†]	-0.14	-0.06	0.37[†]	0.35[†]
Fine geology, network catchment (N = 60)	-0.31[‡]	-0.43[†]	0.13	**0.20**	0.15	-0.07	0.12	0.21	0.45[†]	-0.14	-0.08	-0.31[‡]	-0.08
Forest cover, network buffer	-0.08	-0.21	0.12	0.13	0.33[†]	-0.16	**0.13**	0.29[‡]	0.22	-0.06	-0.21	-0.18	-0.01
Wetland cover, network buffer	0.12	0.31[†]	-0.09	0.22	-0.16	0.33[†]	-0.18	0.18	-0.15	0.44[†]	0.03	0.45[†]	0.30[†]

[†]Correlation is significant at the 0.01 level (two tailed)
[‡]Correlation is significant at the 0.05 level (two tailed)

Table C3.12. Suitability ranges and associated number (N) of stream reaches for the six fish species in the study region.

Species	Location	Most suitable		Suitable		Moderately suitable		Least suitable		Unsuitable		Total
		Score	N	Score	N	Score	N	Score	N	Score	N	N
Lake Sturgeon	Michigan	12-15	6667	11	8213	10	6421	6-9	10665	0	0	31965
	Wisconsin	13-14	108	12	595	11	295	8-10	179	0	0	1175
Walleye	Michigan	5-9	18391	4.5	3607	3.5-4	9413	3	284	0	0	31965
	Wisconsin	5.5-8	342	5	648	4.5	65	3-4	123	0	0	1175
White Sucker	Michigan	16-17	2964	15	4119	14	5470	9-13	19412	0	0	31965
	Wisconsin	16-17	82	14-15	541	13	345	10-12	206	0	0	1175
Steelhead	Michigan	16-19	3558	14-15	7830	12-13	10524	7-11	9912	0	141	31965
	Wisconsin	15-17	177	13-14	612	12	217	8-11	168	0	0	1175
Brook Trout	Michigan	15-19	3504	13-14	7909	11-12	11186	7-10	8795	0	571	31965
	Wisconsin	15-17	86	13-14	234	12	505	8-11	371	0	0	1175
Larval Sea Lamprey	Michigan	10-12	3931	9	5230	8	8150	4-7	14654	0	0	31965
	Wisconsin	10-12	103	9	142	8	220	5-7	709	0	0	1175
Adult Sea Lamprey	Michigan	8-12	16543	7	9637	6	4818	4-5	967	0	0	31965
	Wisconsin	9-12	375	8	576	7	161	5-6	62	0	0	1175

Table C3.13. Suitability ranges and associated number (N) of stream segments for the six fish species in the study region.

Species	Location	Most suitable		Suitable		Moderately suitable		Least suitable		Unsuitable		Total
		Score	N	Score	N	Score	N	Score	N	Score	N	N
Lake Sturgeon	Michigan	10.33-13.28	305	9.17-10.33	212	8.49-9.17	140	0.04-8.49	396	0.00	0	1053
	Wisconsin	11.91-12.99	40	10.88-11.91	21	9.95-10.88	12	0.02-9.95	12	0.00	0	82
Walleye	Michigan	4.74-8.06	255	4.54-4.74	75	4.16-4.54	201	0.02-4.16	522	0.00	0	1053
	Wisconsin	5.31-5.99	11	4.93-5.31	38	4.37-4.93	18	0.01-4.37	15	0.00	0	82
White Sucker	Michigan	12.83-18.09	288	11.60-12.83	206	10.95-11.60	131	0.06-10.95	428	0.00	0	1053
	Wisconsin	13.76-15.23	22	12.99-13.76	14	12.03-12.99	28	0.03-12.03	18	0.00	0	82
Steelhead	Michigan	12.95-18.86	284	11.47-12.95	209	10.43-11.47	179	0.06-10.43	381	0.00	0	1053
	Wisconsin	13.00-14.53	20	12.18-13.00	37	11.35-12.18	9	0.03-11.35	16	0.00	0	82
Brook Trout	Michigan	11.85-17.64	275	10.47-11.85	221	9.48-10.47	219	0.05-9.48	338	0.00	0	1053
	Wisconsin	12.00-14.00	19	11.37-12.00	34	10.45-11.37	10	0.02-10.45	19	0.00	0	82
Larval Sea Lamprey	Michigan	7.69-10.83	200	7.12-7.69	140	6.65-7.12	180	0.04-6.65	531	0.00	0	1053
	Wisconsin	7.37-8.27	12	7.04-7.37	9	6.44-7.04	47	0.02-6.44	13	0.00	0	82
Adult Sea Lamprey	Michigan	7.46-10.95	244	7.08-7.46	101	6.63-7.08	190	0.04-6.63	516	0.00	0	1053
	Wisconsin	8.10-9.08	10	7.90-8.10	36	6.89-7.90	19	0.02-6.89	12	0.00	0	82

APPENDIX D: CHAPTER 3 SUPPLEMENTARY FIGURES

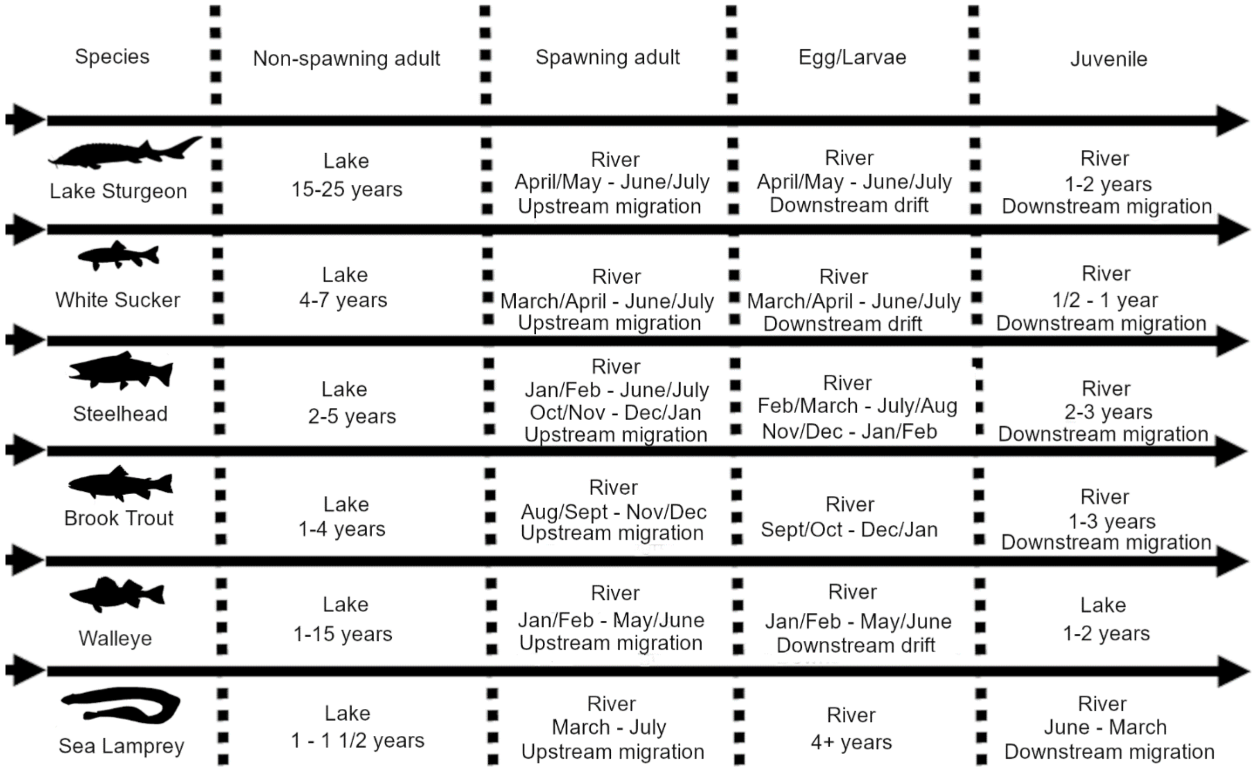

Figure D3.1. Life history of migratory (i.e., adfluvial) populations of the six fish species across the Great Lakes basins constructed from various accounts. References are documented in Appendix 3.E. Figure indicates the habitat and amount of time each life stage of each fish accesses the habitat.

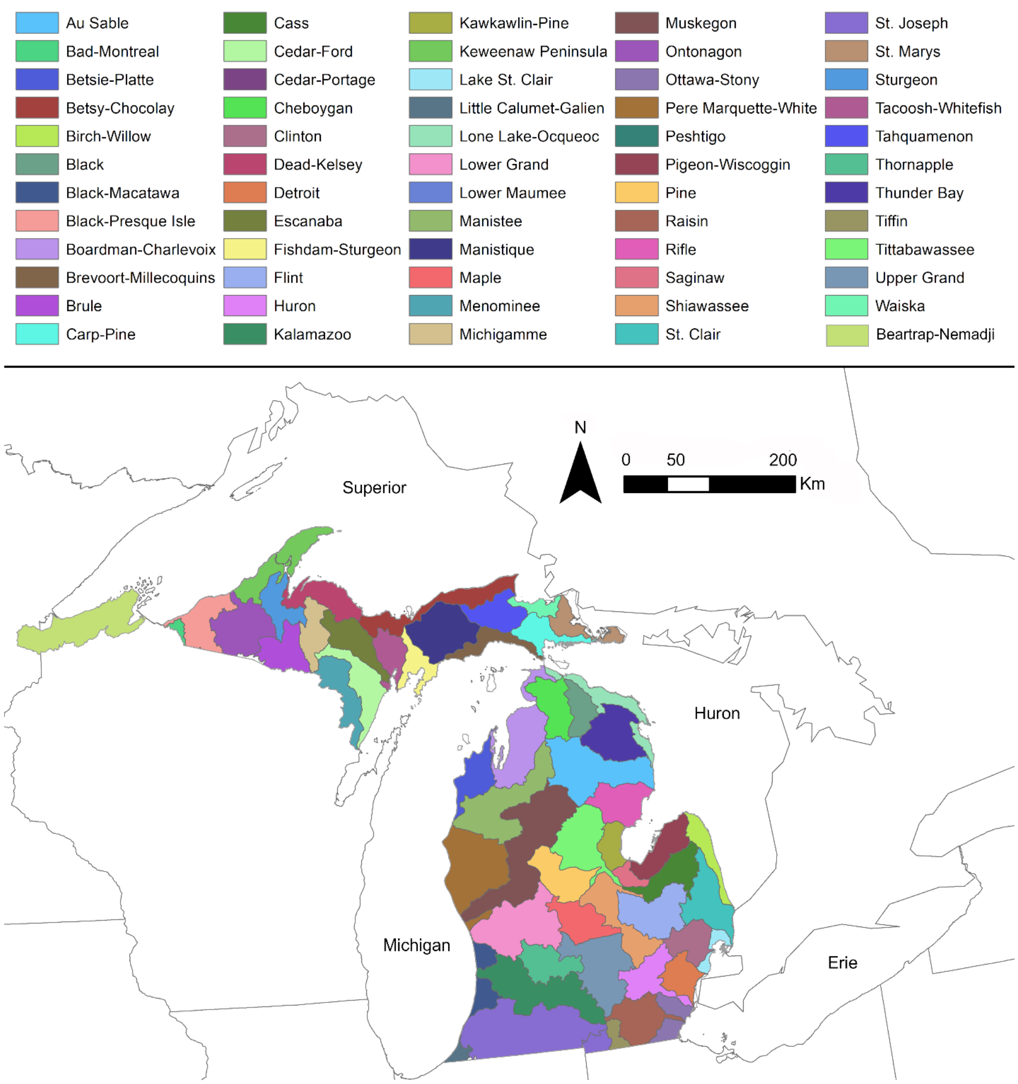

Figure D3.2. Location of watersheds in Michigan and Wisconsin.

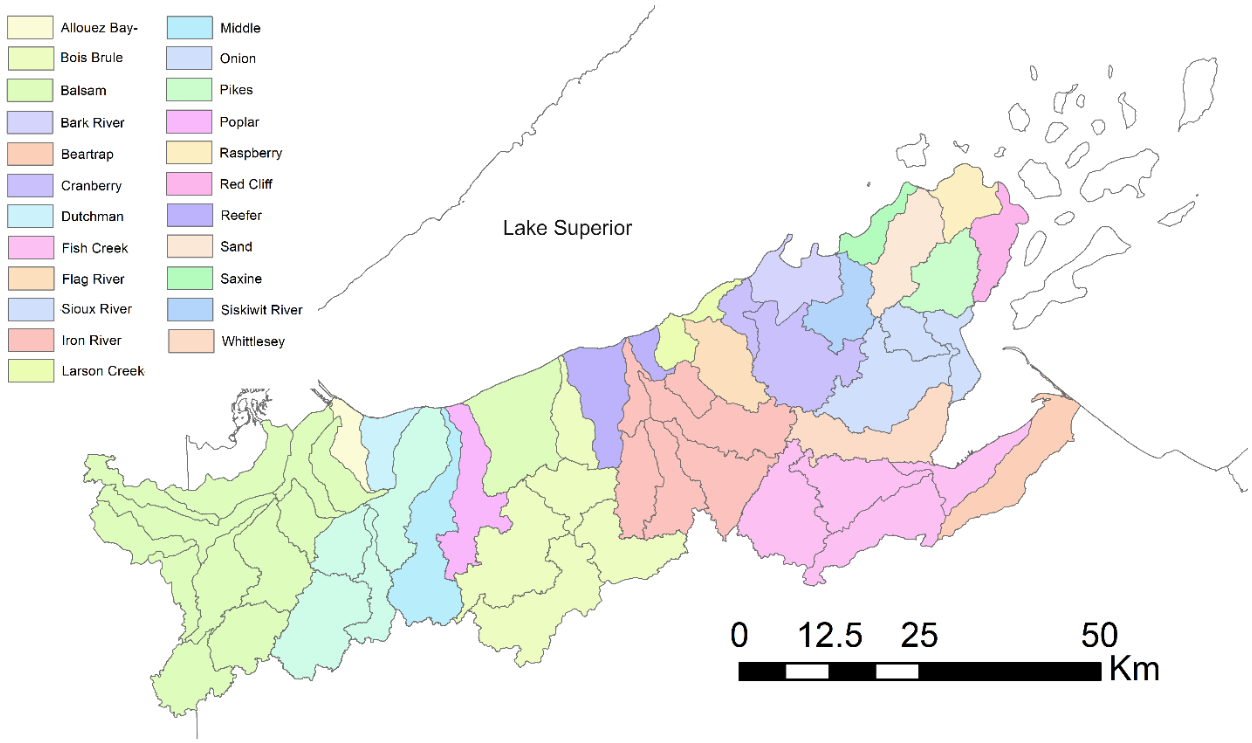

Figure D3.3. Location of watersheds in the Beartrap-Nemadji basin of Lake Superior in the Bayfield Peninsula, Wisconsin.

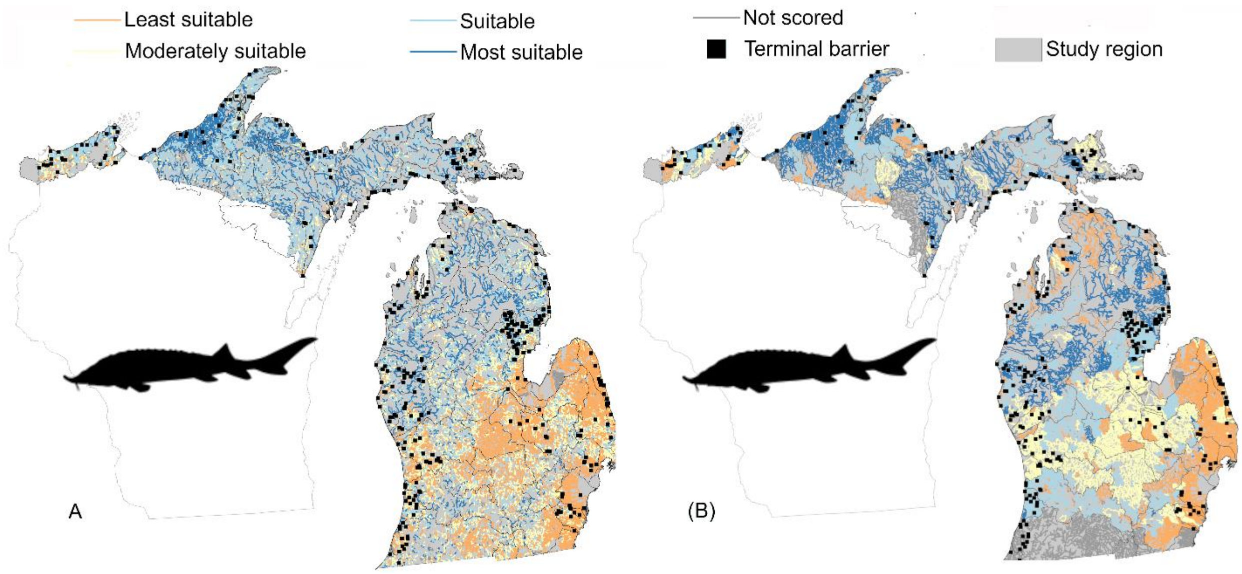

Figure D3.4. Lake Sturgeon (A) reach-scale habitat suitability map and (B) segment-scale habitat suitability map in Michigan and the Bayfield Peninsula, Wisconsin.

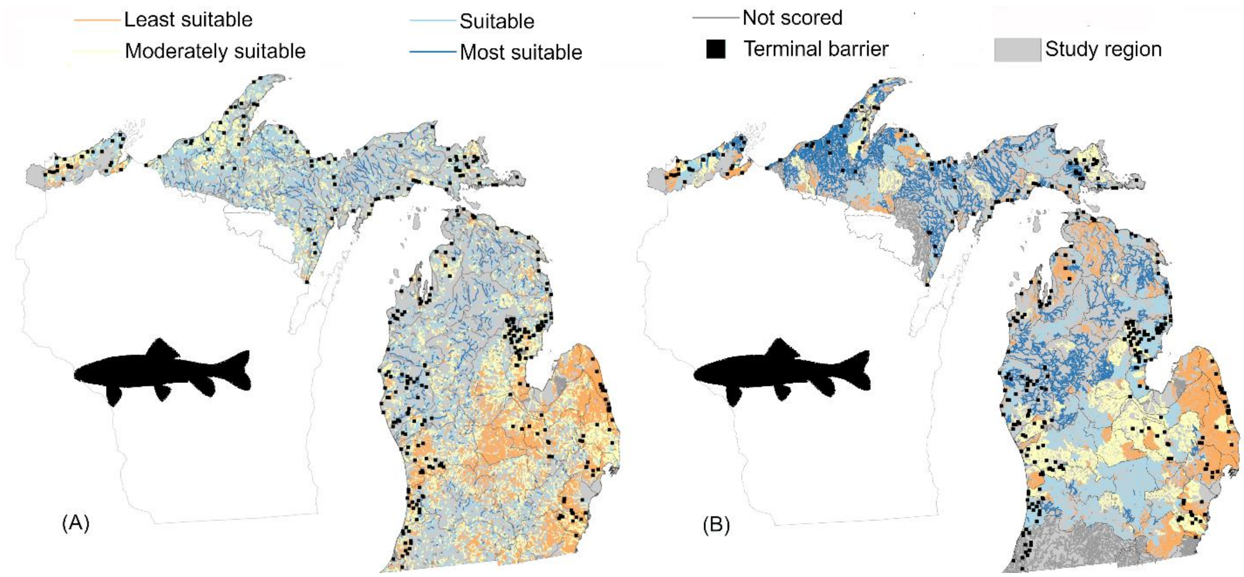

Figure D3.5. White Sucker (A) reach-scale habitat suitability map and (B) segment-scale habitat suitability map in Michigan and the Bayfield Peninsula, Wisconsin.

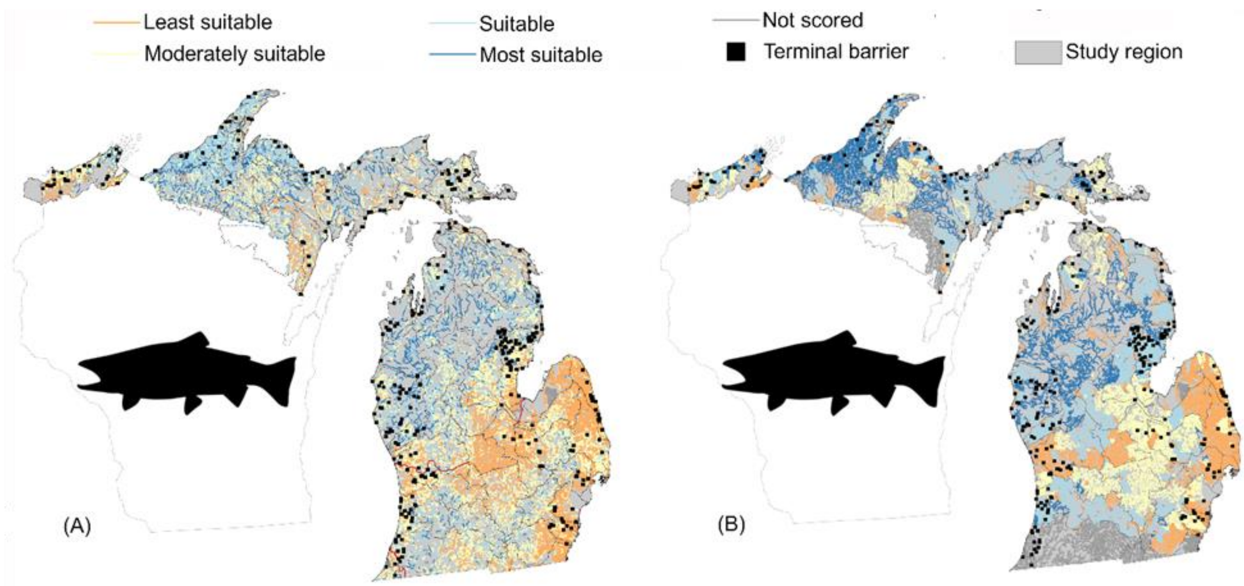

Figure D3.6. Steelhead (A) reach-scale habitat suitability map and (B) segment-scale habitat suitability map in Michigan and the Bayfield Peninsula, Wisconsin.

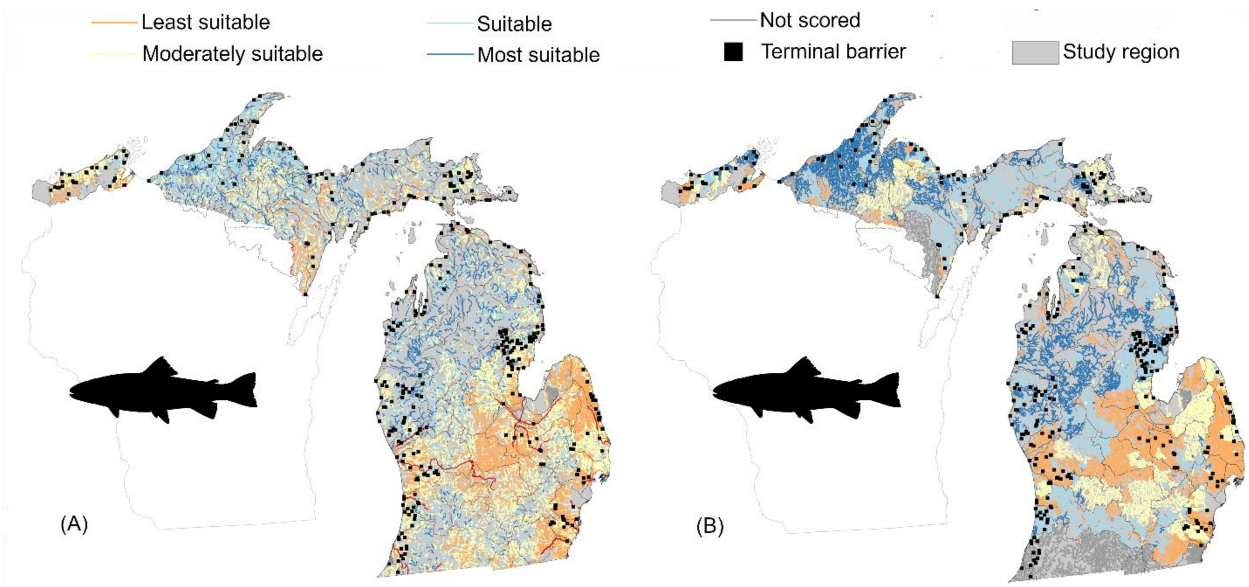

Figure D3.7. Brook Trout (A) reach-scale habitat suitability map and (B) segment-scale habitat suitability map in Michigan and the Bayfield Peninsula, Wisconsin.

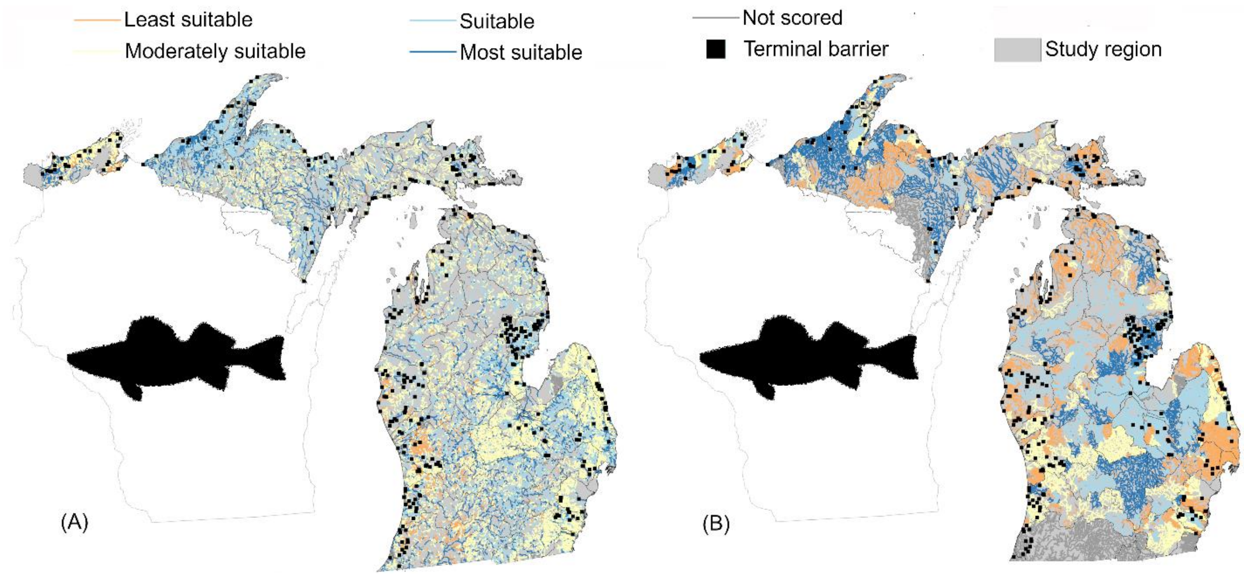

Figure D3.8. Walleye (A) reach-scale habitat suitability map and (B) segment-scale habitat suitability map in Michigan and the Bayfield Peninsula, Wisconsin.

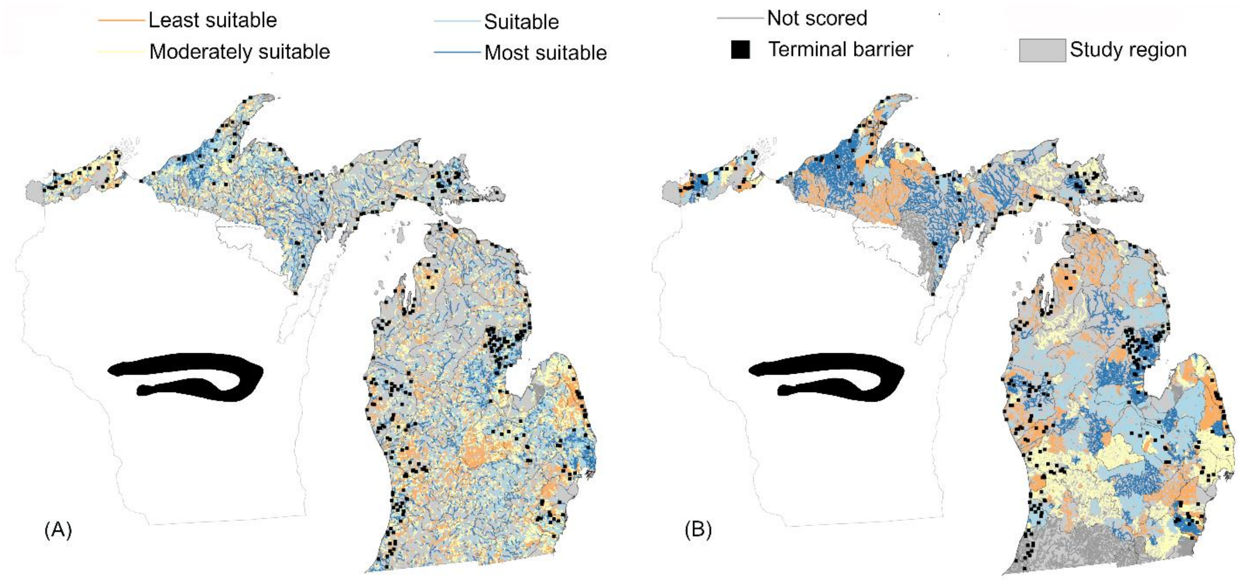

Figure D3.9. Adult Sea Lamprey (A) reach-scale habitat suitability map and (B) segment-scale habitat suitability map in Michigan and the Bayfield Peninsula, Wisconsin.

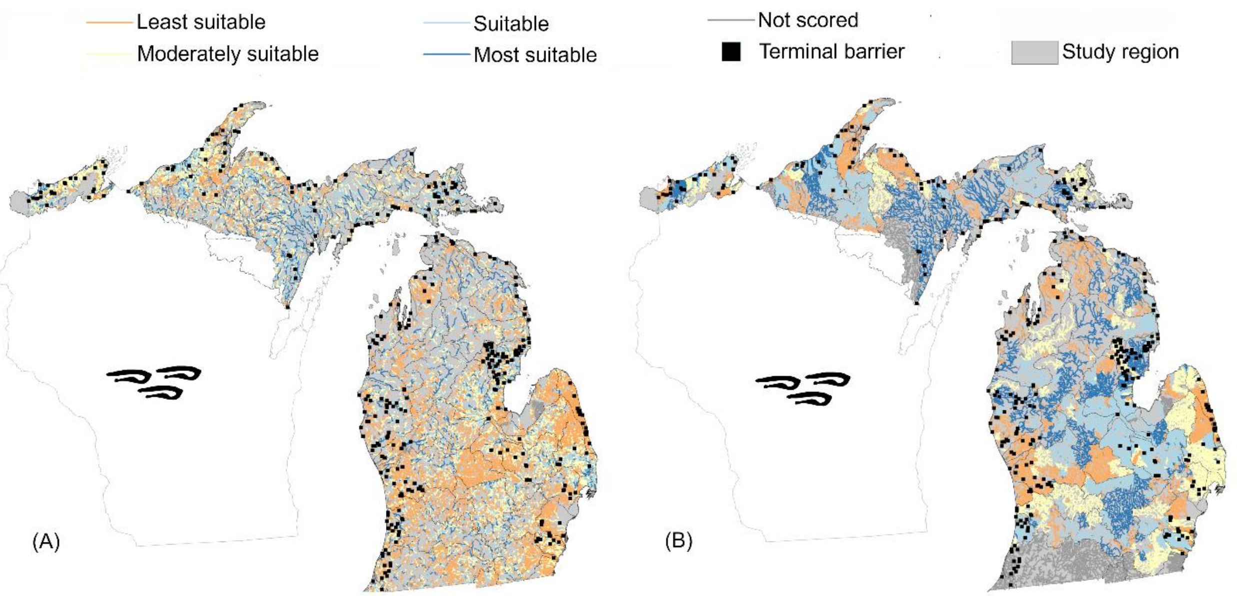

Figure D3.10. Larval Sea Lamprey (A) reach-scale habitat suitability map and (B) segment-scale habitat suitability map in Michigan and the Bayfield Peninsula, Wisconsin.

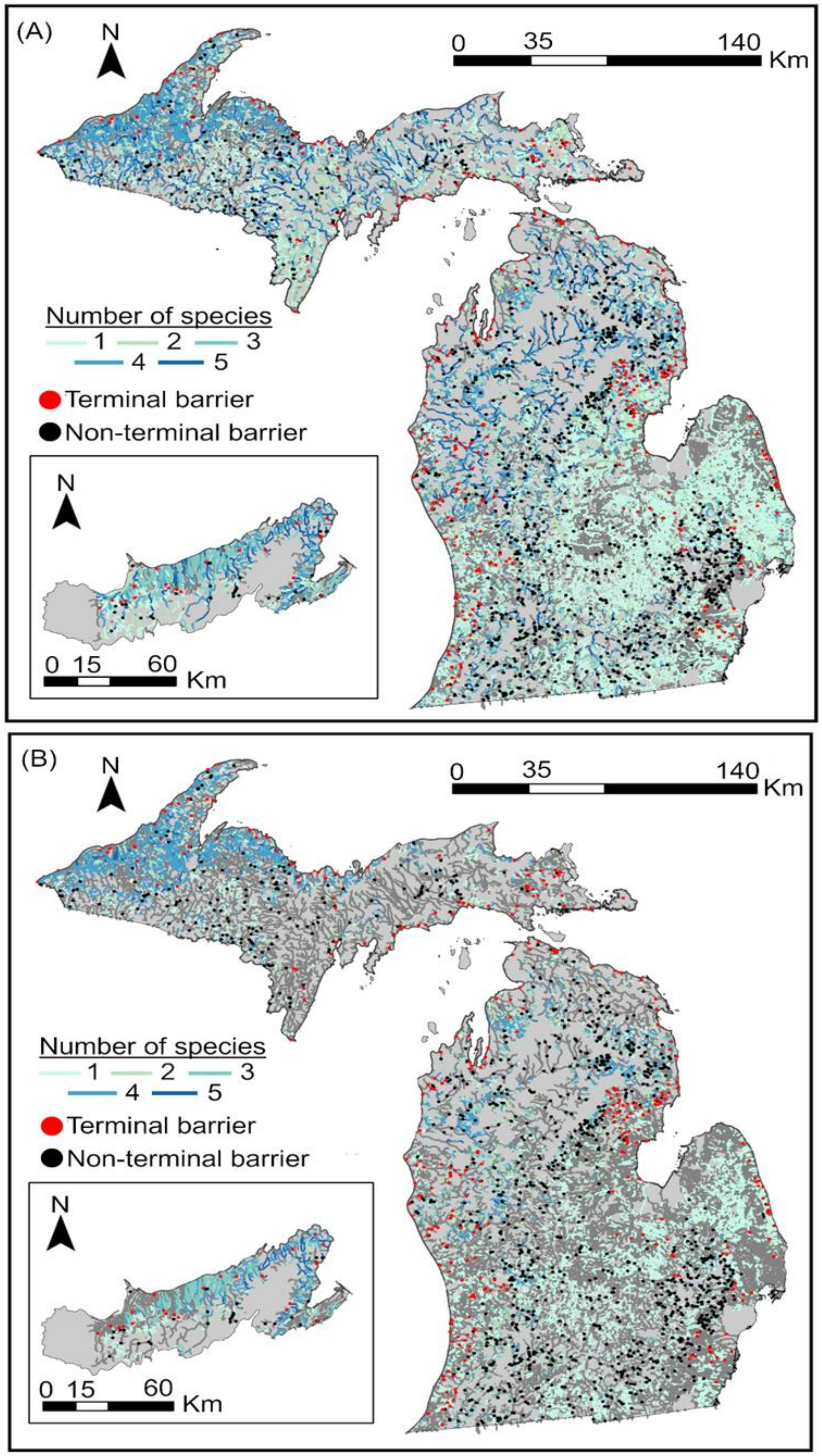

Figure D3.11. Map of the study region (Bayfield Peninsula shown in the inset map) with Panel (A) showing the distribution of suitable reaches for one, two, three, four, or all five desirable fishes and Panel (B) showing the distribution of these suitable reaches if they were also least suitable for larval Sea Lamprey.

CHAPTER 4:

BALANCING CONNECTIVITY RESTORATION AND INVASIVE SPECIES MANAGEMENT: PRIORITIZING BARRIER REMOVAL OPPORTUNITIES IN GREAT LAKES TRIBUTARIES

Abstract

Barriers are pervasive in stream networks, fragmenting stream habitat and threatening the persistence of many freshwater migratory fishes globally. In river systems worldwide, managers are increasingly being tasked with deciding which barriers to remove in streams to improve migratory fish populations. These efforts are tempered with the fact that barriers are also an effective method to control the spread of aquatic invasive species, another threat to freshwater biodiversity. To address this problem, approaches that identify barrier removal opportunities by evaluating trade-offs between restoring connectivity for desirable species and managing species invasions are needed. I address this need by prioritizing barriers for removal in tributaries within the Great Lakes region using an optimization analysis. My first objective was to quantify the amount of suitable habitat available above barriers for six migratory fishes including one invasive species, the Sea Lamprey *Petromyzon marinus*. My second objective was to estimate project costs at barrier locations, which included costs of barrier removal and lampricide application, an alternative method to control Sea Lamprey that would be required in the absence of barriers. My third objective was to input estimates of habitat suitability and project costs at barrier locations into an optimization model. The results provide cost-benefit curves (i.e., total gain in suitable habitat across budgets) for the five desirable fish species and a barrier prioritization list for removal in the state of Michigan. My approach serves as a way to inform barrier removal decisions by highlighting trade-offs between restoring connectivity for desirable species and managing species invasions in the Great Lakes and more broadly.

Introduction

Barriers occur throughout stream networks globally, fragmenting habitats and threatening the persistence of many freshwater fish species, including migratory fishes (Gido et al., 2016; Barbarossa et al., 2020; Deinet et al., 2020). Barriers are especially threatening to migratory species because these fishes require access to multiple distinct stream habitats to complete their life cycles (McDowall, 1988; Lucas & Baras, 2001; McIntyre et al., 2016). Worldwide, removing barriers to restore access to stream habitats for migratory fishes is a growing focus of management (e.g., Brink et al., 2018; Twardek et al., 2020). However, barriers can also function as management tools to prevent the spread of aquatic invasive species in stream networks in many parts of the world (Jones et al., 2021). In these cases, restoring access to habitat for migratory fishes can conflict with the need to prevent the spread of aquatic invasive species (Rahel, 2013; Zielinski et al., 2021). To address this problem, approaches that can inform barrier removal decisions by highlighting trade-offs between restoring connectivity for desirable species and managing species invasions are needed.

The Great Lakes region is one area where restoring connectivity for migratory fishes is a focus of management. Over 160 fish species inhabit the Great Lakes (Hubbs & Lagler, 1941), and many of these species are migratory, with populations accessing habitats located in a Great Lake and its tributaries to support critical life stages (Landsman et al. 2011). Migratory native Lake Sturgeon *Acipenser fulvescens*, Walleye *Sander vitreus*, Brook Trout *Salvelinus fontinalis* and stocked Steelhead *Oncorhynchus mykiss* support numerous recreational fisheries (Lauer, 2015), and migratory native White Sucker *Catostomus commersoniii* is an important vector of lake-derived nutrients and energy in river systems (e.g., Childress & McIntyre et al., 2016). Restoring connectivity would lead to more habitat for these desirable fishes, however, this goal is tempered with the fact that the spread of several invasive aquatic species is controlled by barriers in the region (Walter et al., 2021). Migratory populations of invasive Sea Lamprey *Petromyzon marinus* target many of the same stream habitats as desirable native and stocked migratory fishes (Lavis et al., 2003), and its parasitic feeding strategy limits production of many of those species. Therefore, controlling Sea Lamprey spread and production is a focus of management in the region (Gaden et al., 2021). Currently, reducing the spread of Sea Lamprey is central to their control. One control method is to limit Sea Lamprey access from the Great Lakes to tributary habitat using terminal barriers, or the first barrier to fish migration in a tributary (Hrodey et al., 2021). Sea Lamprey production can also be reduced using lampricide (i.e., 2', 5-dichloro-4'-nitrosalicylanilide or nicolsamide or Bayluscide; 3-trifluoromethyl-4-nitrophenol or TFM). Lampricide is applied in tributaries that kills the larval stage of the species (Sullivan et al., 2021). Lampricide application, however, is labor-intensive and expensive. Terminal barriers are recognized as a more efficient method of control (Hrodey et al., 2021), even while they are recognized as limiting production of desirable migratory fishes in the region. Solving this 'connectivity conundrum' (Zielinkski et al., 2020) requires an approach to balance these incompatible management objectives: restoring tributary connectivity for desirable migratory fishes while limiting the spread and production of the Sea Lamprey.

A strategy that aids in highlighting gains in suitable habitat for desirable fishes while minimizing gains in suitable habitats for Sea Lamprey is essential, and one way to achieve this could be through an optimization analysis. Optimization analysis can prioritize barriers to remove based on available habitat for species upstream of individual barriers as well as project costs that would result from barrier removals (McKay et al., 2017). Project costs could include those associated with removals, installation of fish passage structures, and/or the cost of other mitigation options required in the absence of the barrier, such as control strategies for invasive species. Such costs have been accounted for in the Great Lakes by considering the cost of lampricide treatment required after barrier removal. Milt et al. (2018) used an optimization analysis (modified from Neeson et al., 2015) to identify barriers for mitigation in the Great Lakes region. In their efforts, potential gain in stream habitat for migratory fish species was represented as an increase in the length of accessible tributary habitat. These gains were balanced with costs characterized by potential increase in length of accessible tributary habitat for Sea Lamprey as well as barrier removal costs. While this analysis provided important information to support decision making, one limitation with using length of accessible habitat as a proxy for habitat gains, however, is that it assumes that all stream habitat that becomes accessible to fishes is suitable (McKay et al., 2017). Additionally, Milt et al. (2018) did not address the cost of lampricide treatment in areas upstream of barrier removals, which is a major project cost to be accounted for in the Great Lakes region. Thus, an optimization analysis that incorporates measures of habitat suitability for species under consideration as well as the cost of lampricide treatment would further enhance the ability to identify barrier removal opportunities to aid Great Lakes fishery managers.

My goal is to address that need. I use an optimization approach to prioritize barriers for removal in Great Lakes tributaries in the state of Michigan. My first objective is to quantify the amount of suitable habitat available above barriers for migratory Lake Sturgeon, Walleye, White Sucker, Brook Trout, Steelhead, and Sea Lamprey. My second objective is to estimate project costs at barrier locations, which includes costs of barrier removal and of lampricide treatment upstream. My final objective is to integrate measures of habitat suitability and project costs at barrier locations into an optimization model to prioritize barriers to remove. Results include cost-benefit curves depicting gain in suitable habitat across varying budgets for the desirable fish species and a list prioritizing barriers for removal across the study region. This information enhances the ability of Great Lakes fishery managers to restore connectivity for desirable migratory fishes while managing Sea Lamprey and potentially other aquatic invasive species. Additionally, my approach to optimization analysis can be applied in river networks across the world where restoring connecting for desirable species while minimizing access for invasive species are priorities.

Methods

Study region

My study region includes all streams draining to Lake Huron, Lake Michigan, and Lake Superior in the state of Michigan (Figure 4.1). The region's stream habitats are diverse due to different hydrologic and thermal regimes resulting from historical glaciation and lacustrine deposition (Zorn et al., 2002; Wehrly et al., 2009). Streams receiving large amounts of groundwater are typically colder in summer with stable flows, while streams that receive more run-off are warmer with more variable flow regimes. Natural land cover in the study region is characterized by deciduous, coniferous, and dry-mixed forests and woody and emergent herbaceous wetlands, with greater amounts of forest and wetland cover in stream catchments in the Upper Peninsula and the northern Lower Peninsula (NLCD, https://www.mrlc.gov/data/nlcd-2011-land-cover-conus). Intensity of agricultural land use and water withdrawals generally increases from north to south, and urbanization is more common in the southern Lower Peninsula of Michigan. Barriers have caused extensive fragmentation of stream networks throughout the state (Cooper, 2013; Januchowski-Hartley et al., 2013). In my study, large dam data were obtained from the 2012 National Anthropogenic Barrier Database (NABD; Ostroff et al. 2013) and included 517 barriers distributed across the study region, with 108 barriers being terminal (Figure 4.1). Non-terminal barriers were also incorporated into my analyses to account for the availability of connected stream habitat above terminal barriers.

Spatial framework

I used the 1:100,000 scale National Hydrography Dataset Plus Version 2 (NHDPlusV2, USEPA & USGS, 2012) to define my spatial framework. The smallest spatial unit, the stream reach, is defined as an interconfluence section of water, with confluences occurring at stream junctions and inlets or outlets of lakes and impoundments. Each stream reach in the NHDPlusV2 is associated with a local catchment, or an area of land that drains directly to the reach (USEPA & USGS, 2012) and a network catchment that includes the cumulative upstream land area draining to a reach (including the local catchment; Wang et al., 2011). Each stream reach is also associated with a local buffer, or 90 m of land on either side of a reach to characterize riparian landscape influences on stream habitat (Brenden et al. 2006; Cooper et al. 2019). An additional spatial unit, a stream segment, represents contiguous, connected sets of stream reaches bounded by barriers, headwaters, or terminal outlets to account for stream habitat connectivity in my study (Cooper et al., 2017). Stream segments are the unit in which suitable habitat and lampricide treatment are quantified to use in the optimization analysis (described below).

Overview

In my optimization analysis, I first obtained habitat suitability data for desirable species and invasive species as well as project cost data, which included barrier removal cost and the cost of lampricide (Figure 4.2). In this study, I obtained habitat suitability data for five desirable fishes and larval Sea Lamprey. I calculated the amount of suitable habitat available for the species within segments. I modeled barrier removal cost, and I used the amount of suitable habitat available for larval Sea Lamprey and lampricide cost per stream kilometer to calculate lamprey treatment cost within segments. I input the habitat suitability and project cost information at barrier locations into an optimization model to prioritize barriers to remove (Figure 4.2).

Quantifying suitable habitat above barriers for individual species

I obtained estimates of habitat suitability summarized in stream reaches across the study region for Lake Sturgeon, Walleye, White Sucker, Brook Trout, Steelhead, and larval Sea Lamprey from Dean (this volume; Table C4.1; Figure 4.2) using local and landscape-scale data. In that study, suitability of various in-stream habitat factors such as size, geomorphic units, substrate, flow and water temperature, and habitat condition measures were used to develop an overall assessment of suitability of streams specific to each priority species. Stream reaches were scored as highly suitable, suitable, or unsuitable, with rankings indicating relative suitability levels for each species. In this study, I used that information to calculate the total length (km) of most suitable and suitable reaches (termed suitable stream reaches hereafter) within segments for Lake Sturgeon, Walleye, White Sucker, Brook Trout, and Steelhead to later use as inputs in the optimization analysis. Information on suitable segments for larval Sea Lamprey were also used to calculate the cost of lampricide treatment upstream of barriers (described below).

Estimating project costs at barrier locations

I used a generalized linear model (GLM) developed by Cooper et al. (2021) to estimate barrier removal cost ($USD) in the study region (N = 571 barriers). I obtained barrier height, age, and type from NABD (Ostroff et al., 2013) and estimated mean annual stream discharge from the NHDPlusV2 (USEPA & USGS, 2012). I then used these variables in the GLM to predict removal cost at barrier locations. To estimate the cost of lampricide treatment in segments between barriers, I first calculated a median cost of lampricide per stream kilometer in each Great Lake basin using data collected from 2010-2021 provided by the Great Lakes Fishery Commission Larval Assessment Task Force (Personal communication, P. Hrodey, 2022). I adjusted for inflation using an inflation calculator (https://www.bls.gov/data/inflation_calculator.htm) to convert lampricide cost per stream kilometer to 2021 $USD. To produce an estimate of cost of lampricide treatment within a segment, I multiplied the median cost of lampricide treatment per stream kilometer by the total length of suitable habitat of larval Sea Lamprey within a segment. I accounted for the cost of lampricide treatment over approximately 20 years post-barrier removal by multiplying the segment-level cost by the average periodic treatment cycle of tributaries, which was three years in tributaries of Lakes Michigan and Huron and four years in tributaries of Lake Superior (Personal communication, P. Hrodey, 2022, Great Lakes Fishery Commission). Estimates of barrier removal and lampricide treatment costs were then used as inputs in the optimization analysis (Figure 4.2).

Optimizing barriers for removal with habitat suitability estimates and project costs

I used a mixed linear integer linear programming model (Cooper et al., 2021) based on the Optimization Programming Language (OPL) operated using CPLEX Studio v12.10 software (IBM, 2020) to evaluate barrier removal options to increase suitable habitat availability for Lake Sturgeon, Walleye, White Sucker, Brook Trout, and Steelhead while minimizing costs of barrier removal and upstream lampricide treatment. Inputs to the optimization included the length of suitable habitat within segments for the five desirable species, lampricide treatment cost within segments, and removal cost at barrier locations. Because I aimed to increase suitable tributary habitat access for these species migrating from the Great Lakes, I ran optimizations based on an anadromous pattern, which refers to movement between tributary habitat and a large waterbody, which typically includes the ocean but, in this case, includes the Great Lakes (McDowall, 1988; Morais & Daverat, 2016). I ran optimizations to generate cost-benefit curves for each of the five species that compares gains in suitable habitat for species across a range of budgets ($1M-$500M USD at intervals of $1M). I calculated the percentage of times terminal and non-terminal barriers were selected as the most cost-effective solution across all budgets in each Great Lake basin and mapped the geographic distribution of these barriers. I also developed a list of the names and locations of these terminal barriers and the percentage of times they were selected as the most cost-effective solution in the model.

Results

Optimization model inputs

I calculated the amount of suitable habitat for Lake Sturgeon, Walleye, White Sucker, Brook Trout, Steelhead, and larval Sea Lamprey in 1,337 stream segments across the study region, including 492 segments in the Lake Huron basin, 539 segments in the Lake Michigan basin, and 305 segments in the Lake Superior basin (Figure 4.1). The model I used from Cooper et al. (2021) to estimate the cost of barrier removal at barrier locations (N = 571) performed well, with the percent deviance explained being 70.5% ($R^2 = 0.64$; Figure D4.1). I also calculated the median cost of lampricide treatment per stream kilometer in Great Lake basins, which was $7,611.7/km in the Lake Huron basin; $5,718.4/km in the Lake Michigan basin, and $5,876.6/km in the Lake Superior basin (Figure D4.2).

Optimization model outcomes

Gains in suitable habitat for Lake Sturgeon, Walleye, White Sucker, Brook Trout, and Steelhead at a given budget varied across basins and species (Figure 4.3; Figure D4.3). In tributaries of Lake Huron (Figure 4.3A) and Michigan (Figure 4.3C), Walleye have the largest amount of suitable habitat available while salmonids have the least amount of suitable habitat currently available. At a budget of approximately $175M, all species can gain access to 100% of the total suitable habitat in tributaries of Lake Huron (Figure 4.3B). The same budget would result in access to only 50% of total suitable habitat in tributaries of Lake Michigan (Figure 4.3D). In tributaries of Lake Superior (Figure 4.3E), Lake Sturgeon have the largest amount while White Sucker have the least amount of suitable habitat currently available. According to model results, all species can gain access to 100% of total suitable habitat at a budget of $150M (Figure 4.3F).

The number of times barriers were selected as the most cost-effective solution in optimization modelling varied between 0 and 99.8% (Figure 4.4A; Table C4.2). Nine terminal barriers were selected more than 99% of the time (Figure 4.4B; Table 4.4). In tributaries of Lake Huron, this included Rodman Dam (99.8%) located on the Tawas River in the Au Gres-Rifle basin, Dolbee Dam (99.2%) on the Pine River in the Kawkawlin sub-basin, and the Van Etten Dam (99.2%) on the Pine River in the Au Sable basin (Table 4.1; Figure D4.4). In tributaries of Lake Michigan, this included the Union Street Dam (99.6%) on the Boardman River in the Boardman-Charlevoix basin and the Hamilton Dam on the Rabbit River in the Kalamazoo basin (99.4%; Table 4.1; Figure D4.4). Finally, in tributaries of Lake Superior, this included Lower Dam (99.6%) on the East Branch Ontonagon River in the Ontonagon basin, Lake Independence Dam (99.4%) on the Iron River in the Dead-Kelsey basin, and Otter Lake Dam (99.4%) on the Sturgeon River in the Sturgeon basin (Table 4.1; Figure D4.4).

Discussion

Overview

I used an optimization analysis to prioritize barriers for removal that would restore access to suitable stream habitat for Lake Sturgeon, Walleye, White Sucker, Brook Trout, and Steelhead while minimizing costs of barrier removal and lampricide treatment in Great Lakes tributaries. My results build on our understanding of previous efforts (i.e., Neeson et al., 2015; Milt et al., 2018) by explicitly accounting for stream habitat suitability and the cost of controlling Sea Lamprey using lampricide. My analysis identified a list of barriers that can be considered for removal which can aid managers in reducing a large set of potential projects to a smaller, more manageable list of projects for consideration. The list from my study combined with additional site-specific information can help managers evaluate trade-offs of barrier removals ranging in scale from individual to multiple barriers in stream networks.

Benefits of using explicit measures of habitat suitability in barrier optimization

Using explicit measures of habitat suitability provided two major benefits, one being that it can contribute to more efficient solutions in optimization modelling. One challenge with using just the length of accessible tributary habitat in optimization modelling is that it can lead to sub-optimal solutions by overestimating habitat availability for species of interest because the measure leads to all accessible habitat being considered equally suitable (McKay et al., 2017). Another benefit of using explicit habitat suitability estimates is that I was able to account for other anthropogenic stressors (e.g., land use) to stream habitat in addition to barriers. Failure to consider the full extent of anthropogenic disturbance to streams in barrier removal decision-making can promote species use of poorer quality habitats and subsequently less productive populations (McLaughlin et al., 2013).

Connectivity for desirable fishes can be improved in watersheds under invasion

The results of this study showed that connectivity to suitable habitat can be enhanced for desirable fishes while still controlling for Sea Lamprey spread in all three of the lake basins. In Lake Superior, barriers were selected for removal in streams in the western Upper Peninsula. Streams in this area are relatively more suitable for desirable fishes than streams in the eastern Upper Peninsula and Lower Peninsula (Dean, this volume), but the amount of suitable habitat to be gained in Lake Superior is less than in the Lake Huron or Michigan basins. In the Lake Huron basin, barriers were selected for removal in streams of the Au Sable and Au Gres that are relatively more suitable than streams to the southeast (e.g., Flint) which are relatively more disturbed by human stressors including agriculture and urbanization in catchments (Dean, this volume). In the Lake Michigan basin, barriers were selected for removal in a stream of a northern watershed, the Boardman, and a stream of a southern watershed, the Kalamazoo. Streams in the Kalamazoo and Boardman are relatively more suitable than streams in other river systems draining to Lake Michigan in the Lower Peninsula (Dean, this volume). The barrier selected for removal in the Boardman watershed, Union Dam, has an on-going project to install a fish-pass at the location (www.glfc.org/fishpass.php); my results with support from local expertise and site-specific information (e.g., Bingham & Kinnell, 2012; Fausch, 2018; Diedrich et al., 2022) could aid in understanding trade-offs of the fish-pass.

My results also identify accessible suitable habitat for individual desirable species that can be useful for managers in prioritizing among species in a particular basin. For example, species with the least access to suitable stream habitat include Lake Sturgeon and salmonid species in Lakes Huron and Michigan. Using my barrier list, local expertise, and site-specific information, managers could prioritize barriers to improve populations of Lake Sturgeon and salmonids in Lakes Huron and Michigan, specifically. Additionally, my results are useful for prioritizing suitable habitat access for multiple desirable species simultaneously. Considering the five desirable fishes together, barrier removals could be more beneficial in one lake basin over another. For example, a budget of $150M could result in a 25% increase in access to suitable habitat for desirable fishes in Lakes Superior and Michigan basins. Comparatively, the same budget would result in a 50% increase in accessible suitable habitat for the species in Lake Huron. Thus, Lake Huron could be a basin to prioritize for barrier removal projects if a manager is tasked with managing multiple desirable migratory fishes.

Limitations

One limitation of this study is that barriers considered in the optimization analysis only included large dams (Ostroff et al., 2013), which were the only data available consistently across the entire study region. However, numerous other types of barriers, including culverts, can change suitable habitat accessibility and barrier removal selection in optimizations, and a consistently-developed coverage for the entire study region would allow for a richer optimization analysis (Januchowski-Hartley et al., 2013; Neeson et al., 2015; Milt et al., 2018). Another limitation is that I lacked a consistent information documenting locations and types of fish-passage structures which could change optimization results, although the analysis could be run again with an updated barrier dataset accounting for fish-passages and with passability values for species incorporated (Neeson et al., 2015; Milt et al., 2018; Cooper et al., 2021). Another limitation is that I also used barrier and stream attributes to model removal costs which can be imprecise considering the wide variety of conditions that can exist among barrier locations. An additional limitation is that some streams had no suitable habitat for larval Sea Lamprey which would cost zero USD in lampricide treatment, which is an unlikely scenario. This was because of how I calculated lampricide cost in segments (length of suitable habitat multiplied by lampricide treatment cost per stream kilometer). A final limitation is that I did not account for the cost of controlling the spread of other aquatic invasive species in the region which could target stream habitat similar to desirable fishes. Suitability can be estimated for additional invasive species above barriers using the stream habitat suitability assessment approach described previously (Dean, this volume).

Conclusion

Freshwater migratory fish species are important in the Great Lakes region as well as globally, and their conservation requires approaches that improve connectivity in critical habitats while also managing for the spread of aquatic invasive species. In this study, I used optimization analysis to identify barriers for removal over a very large spatial extent to support desirable fishes while limiting the cost of controlling invasive Sea Lamprey and barrier removal. My results along with local knowledge and site-specific information could help managers with barrier decision-making in the Great Lakes region. Additionally, my approach to optimization analysis can be applied in other regions challenged with restoring connectivity for desirable species while managing the spread of aquatic invasive species.

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APPENDIX A: CHAPTER 4 TABLES

Table 4.1. List of terminal barriers where the number of times a barrier was selected as the most cost-effective solution was greater than 99% in optimization runs, along with the associated cost of barrier removal at the location and lampricide treatment of the upstream segment.

			Cost ($USD)		Times selected
Basin	Name	Stream	Removal	Lampricide treatment	(%)
Huron	Rodman	Tawas R.	128,125	0	99.8
	Dolbee	Pine (Kawkawlin) R.	38,609	31,147	99.2
	Van Etten	Pine (Au Sable) R.	440,000	2,787,453	99.0
Michigan	Union Street	Boardman R.	1,338,593	20,483	99.6
	Hamilton	Rabbit R.	710,872	408,187	99.4
Superior	Lower	Ontonagon R.	176,719	0	99.6
	Lake Independence	Iron R.	575,431	551,045	99.4
	Otter Lake	Sturgeon R.	675,782	1,464,556	99.4

APPENDIX B: CHAPTER 4 FIGURES

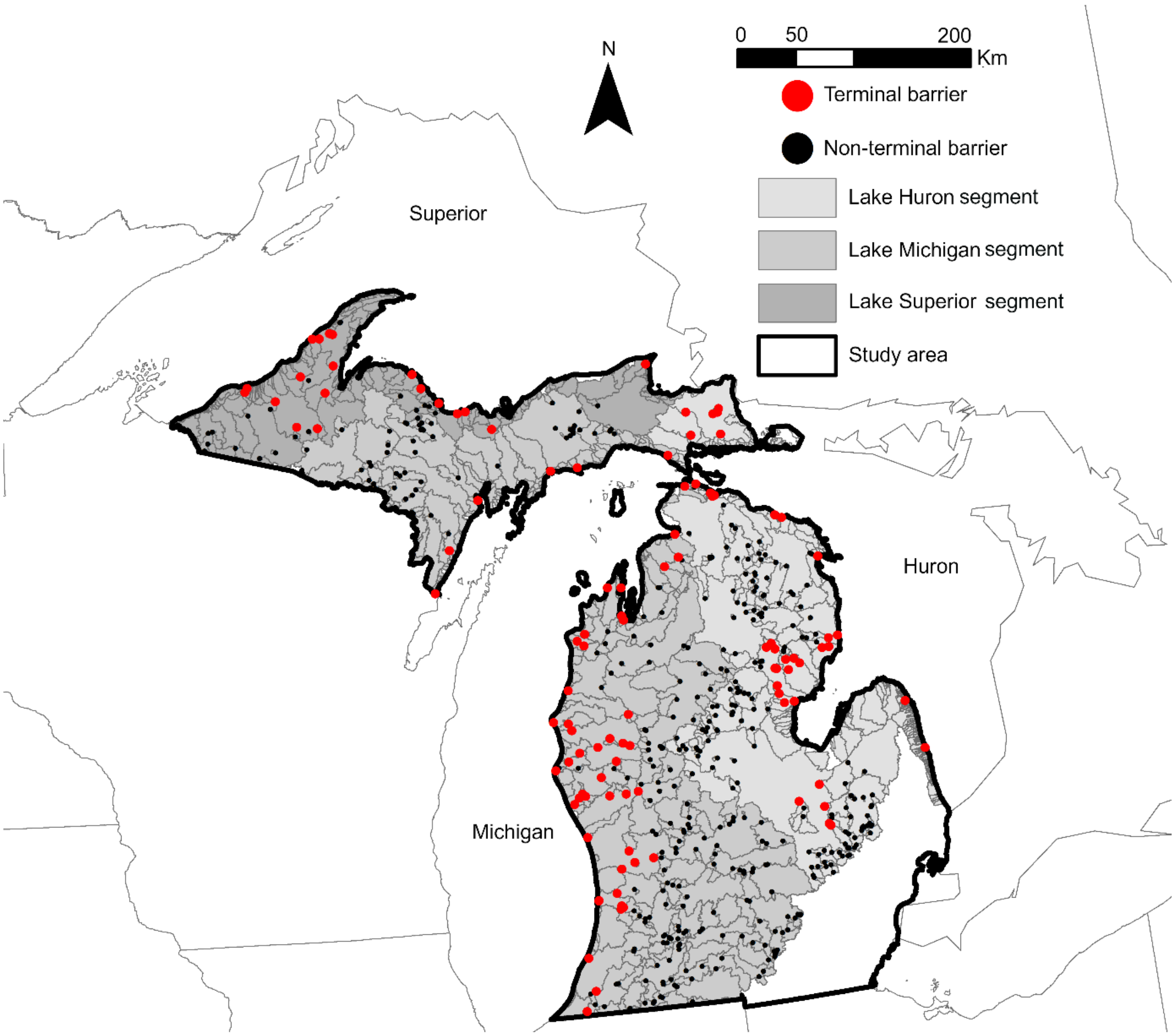

Figure 4.1. Map of the study area and locations of terminal and non-terminal barriers and segments in the Lake Huron, Lake Michigan, and Lake Superior basins of Michigan.

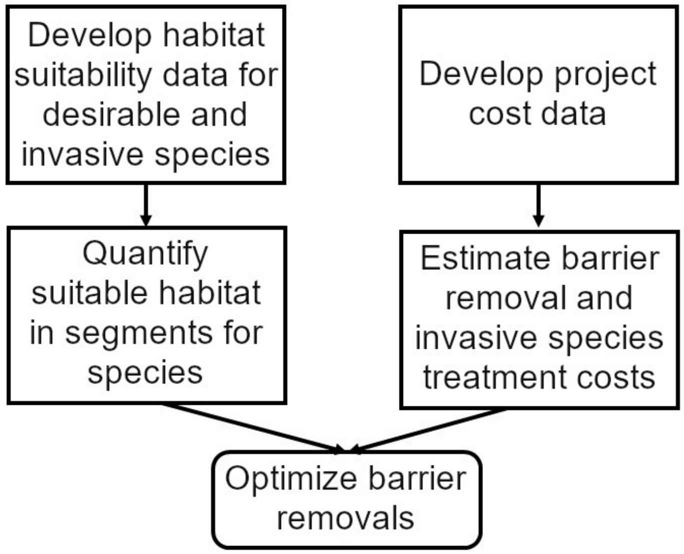

Figure 4.2. Approach to optimization analysis applied in this study.

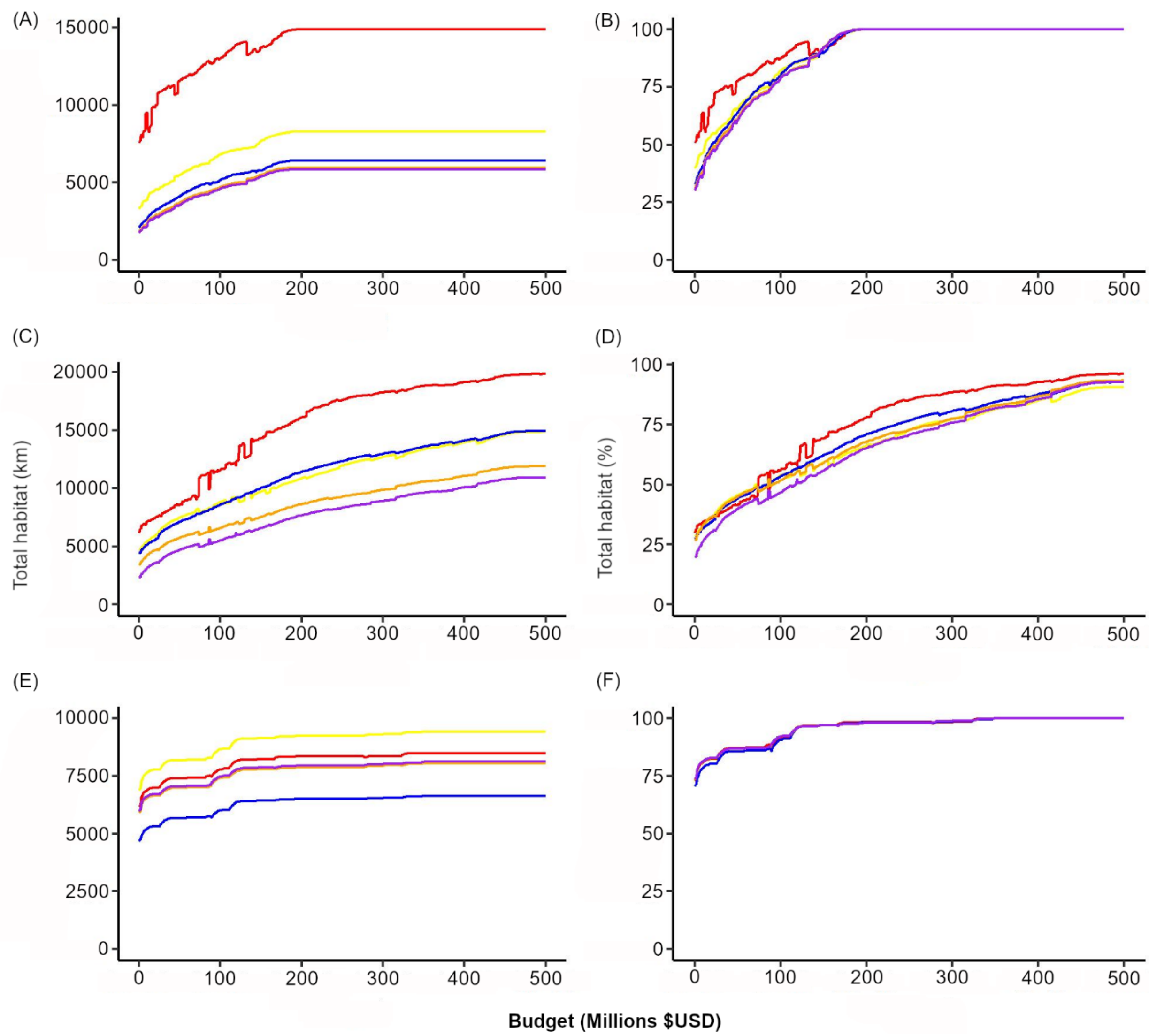

Figure 4.3. Cost-benefit curves for Lake Sturgeon (yellow), Walleye (red), White Sucker (blue), Brook Trout (orange) and Steelhead (purple) in tributaries of Lake Huron (A, B), Lake Michigan (C, D), and Lake Superior (E, F). Total habitat (%) for individual species does not necessarily monotonically increase with budget due to tradeoffs among species (see Cooper et al., 2021).

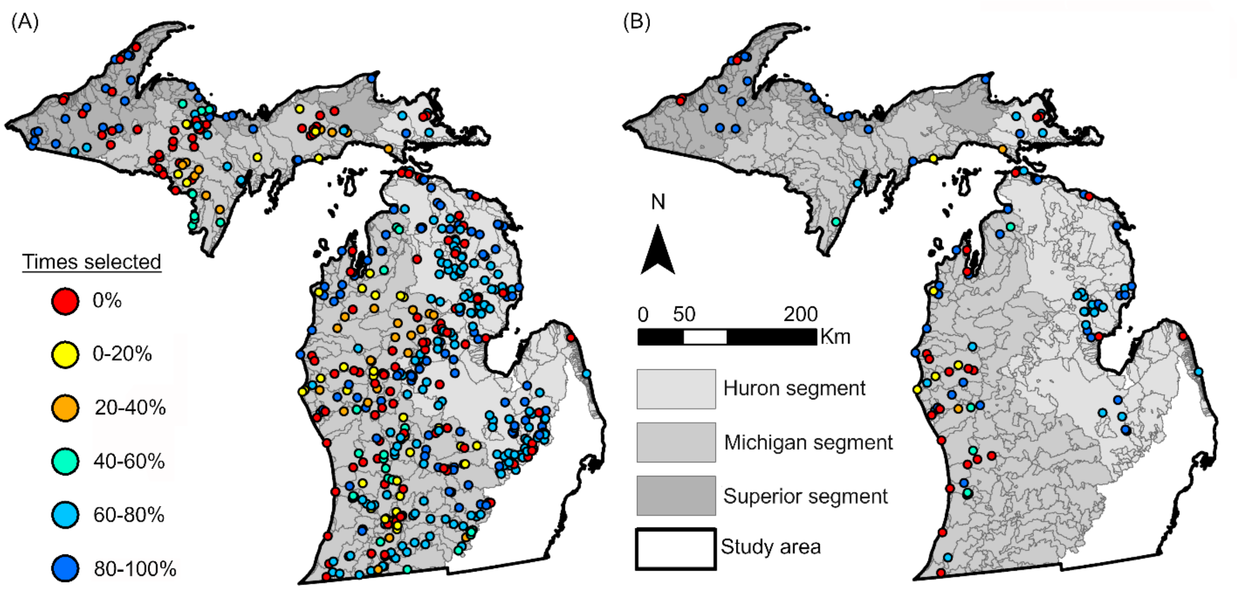

Figure 4.4. The percentage of times any barrier (terminal and non-terminal, A) and terminal barriers (B) were selected for removal in tributaries of Lakes Huron, Michigan, and Superior.

APPENDIX C: CHAPTER 4 SUPPLEMENTARY TABLES

Table C4.1. Number of reaches (N) scored within suitability ranges in Michigan for migratory fishes from Dean (this volume).

	Most suitable		Suitable		Moderately suitable		Least suitable		Unsuitable		Total
Species	Score	N	Score	N	Score	N	Score	N	Score	N	N
Lake Sturgeon	12-15	6667	11	8213	10	6421	6-9	10665	0	0	31965
Walleye	5-9	18391	4.5	3607	3.5-4	9413	3	284	0	0	31965
White Sucker	16-17	2964	15	4119	14	5470	9-13	19412	0	0	31965
Steelhead	16-19	3558	14-15	7830	12-13	10524	7-11	9912	0	141	31965
Brook Trout	15-19	3504	13-14	7909	11-12	11186	7-10	8795	0	571	31965
Larval Sea Lamprey	10-12	3931	9	5230	8	8150	4-7	14654	0	0	31965

Table C4.2. Comprehensive list of terminal barriers, the associated costs of removal and upstream lampricide treatment, and the number of times a barrier was selected as the most-cost effective solution in optimization modelling. Table includes the NABD barrier identification number (ID), barrier name, the name of the associated river, and some attributes from NABD (2012) including the year built, owner type, and the dam's general purpose.

			Cost ($USD)					
Basin	Name	Stream	Removal	Lampricide	Times selected (%)	Year Built	Owner	Purpose
Huron	Rodman	Silver Cr.	128,125	0	99.8	1957	Private	Recreation
	Dolbee	Mid. Br. Pine R.	38,609	31,147	99.2	1962	Private	Recreation
	Van Etten	Pine R.	440,000	2,787,453	99.0	1947	Private	Recreation
	Tuttle Marsh	Kalamazoo R.	35,784	0	98.8	1989	Federal	Fish and Wildlife Pond
	Thread Lake	Thread Cr.	287,410	220,908	98.6	1973	Local	Recreation
	Cheboygan	Cheboygan R.	1,513,743	6,587,696	97.8	1922	Private	Hydroelectric
	Trout Cr.	Trout Cr.	183,750	0	96.8	1971	Private	Recreation
	Elmhirst Cr.	Elmhirst Cr.	21,959	0	94.8	1990	Federal	Recreation
	Hamilton	Flint R.	1,498,922	0	94.6	1920	Local	Water supply
	Ninth Street	Thunder Bay	1,621,543	198,210	91.2	1910	Public	Hydroelectric
	Charlyle	Parmalee Cr.	73,914	0	88.4	1957	Private	Recreation
	Barnes	Hope Cr.	71,336	130,160	80.6	1964	Private	Recreation

Table C4.2. (cont'd)

	Name		Cost ($USD)					
Basin	Name	Stream	Removal	Lampricide	Times selected (%)	Year Built	Owner	Purpose
Huron	Sylvester Cr.	Sylvester Cr.	74,407	0	79.2	1968	Federal	Recreation
	Foote	Au Sable R.	13,428,691	0	73.5	1918	Public	Hydroelectric
	Lake Ogemaw	Peterson Cr.	150,523	0	71.9	1964	Private	Recreation
	Bay Land	Trib. to Whitney Cr.	89,840	0	71.3	1967	Private	Recreation
	Misteguay Cr. #4	Misteguay Cr.	578,645	0	69.9	1967	Private	Flood control
	Devoe Lake	Rifle R.	35,481	0	66.9	1963	State	Recreation
	Christian Service Brigade Camp	Rapson Cr.	93,172	0	66.5	1960	Private	Recreation
	Mill Cr.	Mill Cr.	94,482	0	65.3	1984	State	Water supply
	Forest Lake	Wells Cr.	976,574	0	65.1	1971	Private	Recreation
	Stylus Lake	Au Gres R.	170,796	204,512	63.7	1954	Private	Recreation
	Latter Cr.	Latter Cr.	308,458	0	63.3	1973	Private	Recreation
	Lewis Dr.	Lewis Dr.	175,613	0	63.3	1969	Private	Recreation

Table C4.2. (cont'd)

Basin	Name	Stream	Cost ($USD)		Times selected (%)	Year Built	Owner	Purpose
			Removal	Lampricide				
Huron	Rose Valley Gun Club	Oyster Cr.	364,228	0	63.1	1946	Private	Recreation
	Armstrong #2	School Cr.	68,286	0	62.7	1954	Private	Recreation
	Sanback	Beach Cr.	453,408	0	62.3	1857	Private	Other
	Little Black R. Structure C	Trib to S. Br. Little Black R.	89,398	0	62.1	1962	Local gov.	Flood control
	Fawn Lake	Stoney Cr.	257,083	0	61.9	1971	Private	Recreation

Table C4.2. (cont'd)

Basin	Name	Stream	Cost ($USD) Removal	Cost ($USD) Lampricide	Times selected (%)	Year Built	Owner	Purpose
Huron	Lionel Wensley	Forester Cr.	408,328	0	60.7	1971	Private	Recreation
	Clymers Basin	Trib. to Lake Huron	180,576	0	0.0	1999	Private	Tailings
	Tanny Armstrong	Trib. to Little Munuscong R.	492,535	0	0.0	1978	Private	Recreation
	Fletcher Cr.	Trib. to Little Munuscong R.	115,464	0	0.0	1955	Private	Recreation
	Little Black R. Structure B	Litle Black R.	203,537	0	0.0	1962	Local	Flood control
	Little Black R. Structure D	S. Br. Little Black R.	122,992	0	0.0	1964	Local	Flood control
	Senske	Trib. to Pine R.	45,983	0	0.0	1960	Private	Recreation
	Schmucker Cr.	Schmucker Cr.	178,243	0	0.0	1967	Private	Recreation

Table C4.2. (cont'd)

Basin	Name	Stream	Cost ($USD) Removal	Lampricide	Times selected (%)	Year Built	Owner	Purpose
Michigan	Union Street	Boardman R.	1,338,593	20,483	99.6	1867	Local	Recreation
	Hamilton	Rabbit R.	710,872	408,187	99.4	1900	Local	Other
	Peters Bayou	Manistee R.	421,520	2,799,636	98.4	1969	State	Other
	Lake Street	Bear R.	419,178	334,489	97.6	1895	Local	Other
	East Jordan	Deer Cr.	850,646	0	97.0	1900	Private	Other
	Little Platte Lake Control	N. Br. Platte R.	143,511	48,514	96.8	1969	Local	Recreation; Other
	Hesperia	White R.	597,370	1,054,830	96.2	1977	Local	Other
	Leland	Trib. to Lake Michigan	775,761	26,658	95.6	1910	Private	Other
	Manistique Papers	Manistique R.	2,063,261	14,648,663	95.2	1919	Private	Other
	Hamlin Lake	Big Sable R.	1,027,595	1,397,039	95.0	1913	State	Recreation

Table C4.2. (cont'd)

Basin	Name	Stream	Cost ($USD)		Times selected (%)	Year Built	Owner	Purpose
			Removal	Lampricide				
Michigan	Homestead	Betsie R.	828,176	448,535	93.4	1979	State	Other
	Croton	Muskegon R.	3,400,945	3,054,388	90.4	1907	Public utility	Hydroelectric; Recreation
	Browns Pond	Sand Cr.	341,079	0	84.8	1844	Local	Recreation
	Clayton Dam	Michigan Cr.	58,638	0	83.0	1955	Private	Recreation
	Escanaba #1	Escanaba R.	2,446,112	41,824	78.2	1907	Private	Hydroelectric
	Berrien Springs	Saint Joseph R.	3,556,846	0	74.5	1908	Private	Hydroelectric
	Luther Pond	Little Manistee R.	469,615	0	72.9	1910	Local	Recreation

Table C4.2. (cont'd)

Basin	Name	Stream	Cost ($USD)		Times selected (%)	Year Built	Owner	Purpose
			Removal	Lampricide				
Michigan	Allegan	Kalamazoo R.	5,110,307	0	71.7	1936	Public utility	Hydroelectric
	Silver Cr. Pond	Silver Cr.	152,786	0	68.5	1950	Private	Recreation
	Hart Lake	S. Br. Pentwater	1,913,536	0	67.3	1927	Local	Hydroelectric
	Boyne R.	Boyne R.	1,559,706	67,796	56.5	1904	Private	Hydroelectric; Recreation
	Palmer Bayou	Trib. to Kalamazoo R.	163,456	0	51.9	1952	State	Other
	Swan Cr.	Swan Cr.	1,532,676	556,544	51.9	1937	State	Recreation
	Hayward Lake	Walton R.	136,205	1,088,042	48.5	1952	State	Recreation
	Rowe #1	Penoyer Cr.	475,355	0	43.7	1888	Private	Recreation
	Root	Sand Cr.	643,876	385,885	41.3	1860	Private	Other
	Peterson	Brooks Cr.	277,521	0	36.9	-	Private	Recreation

Table C4.2. (cont'd)

Basin	Name	Stream	Cost ($USD) Removal	Cost ($USD) Lampricide	Times selected (%)	Year Built	Owner	Purpose
Michigan	Brevoort Lake	Brevoort R.	1,065,854	0	26.3	1936	Federal	Recreation
	Danaher Lake	Danaher Cr.	861,607	0	18.8	1931	Private	Recreation
	Crystal Lake Level Control	Crystal Lake Outlet	1,002,526	0	8.6	1976	Private	Recreation; Other
	Crystal Valley	Crystal Cr.	760,376	0	7.4	1937	Local	Recreation
	Silver Lake Level Control	Silver Cr.	11,754	0	6.4	1995	Private	Recreation; Other
	McDonald Lake	Bulldog Cr.	950,658	43,951	5.4	1945	Local	Recreation

Table C4.2. (cont'd)

Basin	Name	Stream	Cost ($USD)		Times selected (%)	Year Built	Owner	Purpose
			Removal	Lampricide				
Michigan	Beren's	Trib. to Macatawa R.	28,901	0	0.0	1993	Private	Flood control
	Kenowa Lake Level Control	Huizeinga Dr. trib to Rush Cr	308,767	0	0.0	1975	Private	Recreation
	Eastbrook Lake Level Control	Whiskey Cr.	66,002	0	0.0	1965	Private	Recreation
	Pease Cr.	Pease Cr.	116,387	0	0.0	1965	Private	Recreation
	Whitehall Millpond	Mill Pond Cr.	453,199	0	0.0	1940	Private	Recreation
	Lake Connamara	Baker Cr.	254,656	0	0.0	1970	Private	Recreation
	Welch	Trib. to Paw Paw R.	131,906	0	0.0	-	Private	Unknown
	Cleveland Lake	Cleveland Cr.	111,378	0	0.0	1960	Private	Recreation

Table C4.2. (cont'd)

Basin	Name	Stream	Cost ($USD		Times selected (%)	Year Built	Owner	Purpose
			Removal	Lampricide				
Michigan	Dayton Lake	Galien R.	177,148	0	0.0	1833	Private	Recreation
	West Shore Community College	Trib. to S. Br. Lincoln R.	258,279	0	0.0	1972	Private	Recreation
	French Farm Lake	French Farm Cr.	236,816	0	0.0	1949	State	Recreation
	Belanger	Belangers Cr.	642,692	0	0.0	1864	Private	Other
	Silver Valley Ponds Dam	Tannery Cr.	88,609	0	0.0	1963	Private	Other

Table C4.2. (cont'd)

Basin	Name	Stream	Cost ($USD) Removal	Lampricide	Times selected (%)	Year Built	Owner	Purpose
Michigan	Van Dragt's	Tannery Cr.	96,556	0	0.0	1963	Private	Recreation; Irrigation
	Foster Lake	Trib to Big S. Br. Pere Marquette R.	207,544	0	0.0	1973	Private	Recreation
	Cedar Lake	Cedar Lake Outlet	433,253	0	0.0	1856	Local	Recreation
	Brookside Cemetery	Trib. to Pere Marquette R.	75,698	0	0.0	1951	Local	Other
	Little Black Lake	Little Black Cr.	239,284	0	0.0	1927	Local	Recreation; Other

Table C4.2. (cont'd)

Basin	Name	Stream	Cost ($USD)		Times selected (%)	Year Built	Owner	Purpose
			Removal	Lampricide				
Superior	Lower	E. Br. Ontonagon R.	176,719	0	99.6	1965	Federal	Recreation
	Lake Independence	Iron R.	575,431	551,045	99.4	1913	Private	Other
	Otter Lake	Sturgeon R.	675,782	1,464,556	99.4	1978	Private	Other
	Au Train South Levee	Au Train R.	625,237	404,277	98.2	1910	Public utility	Hydroelectric; Recreation
	Sand R. Wildlife Flooding	Sand R.	318,484	128,931	98.0	1981	State	Other
	Trout Cr.	Trout Cr.	297,079	0	96.2	1899	Local	Recreation
	Shelldrake	Betsy R.	121,217	733,482	94.8	1964	State	Recreation
	Lake Le Vasseur	Le Vassuer Cr.	122,749	99,108	93.6	1953	State	Recreation
	Redridge	Salmon Trout R.	1,925,515	27,678	93.4	1902	Local	Recreation

Table C4.2. (cont'd)

Basin	Name	Stream	Cost ($USD) Removal	Lampricide	Times selected (%)	Year Built	Owner	Purpose
Superior	Prickett	Sturgeon R.	19,121,739	2,996,605	90.4	1931	Public utility	Hydroelectric; Recreation
	Varvil	Sawmill Cr.	112,436	0	90.4	1966	Private	Recreation
	Sleepy	Sleepy Cr.	905,974	0	86.6	-	State	Other
	Boston Pond	Boston Cr.	108,055	0	84.0	1968	State	Recreation
	Vitton	Boston Cr.	38,472	0	84.0	1960	Private	Irrigation
	Victoria	W. Br. Ontonagon	76,878,626	7,806,540	82.2	1930	Public utility	Hydroelectric; Recreation

Table C4.2. (cont'd)

Basin	Name	Stream	Cost ($USD)		Times selected (%)	Year Built	Owner	Purpose
			Removal	Lampricide				
Superior	Marquette Tourist Park	Dead R.	2,073,625	0	80.4	1924	Local government	Hydroelectric; Recreation
	White Pine Mine North Tailings #2	Native Cr.	1,816,481	0	0.0	1971	Private	Tailings
	White Pine Mine North Tailings #1	Bedell Cr.	303,942	0	0.0	1970	Private	Tailings
	Kissam	Trib. to Schlot Cr.	70,088	0	0.0	1966	Private	Recreation

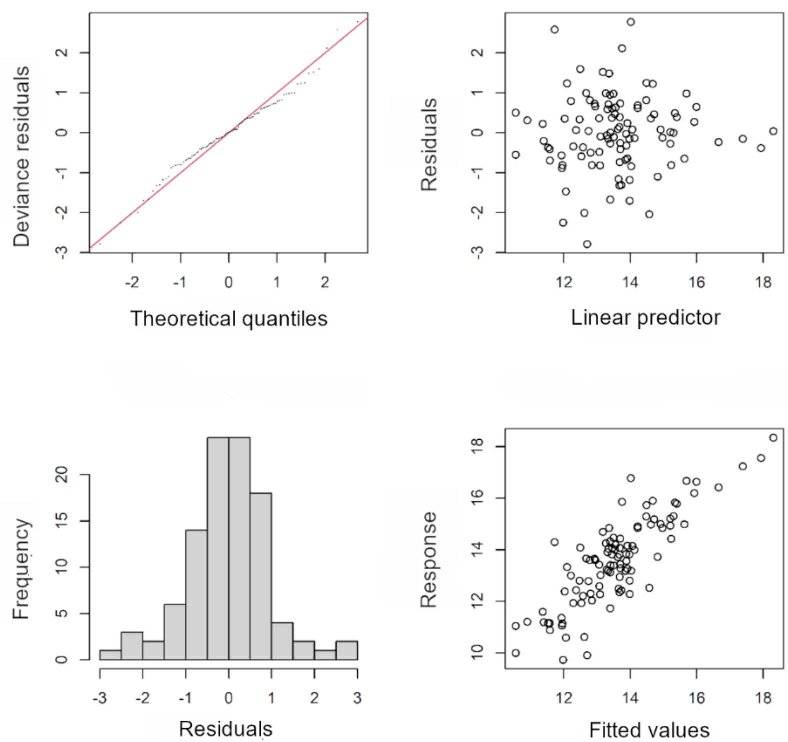

Figure D4.1. Diagnostic plots for the barrier removal cost model.

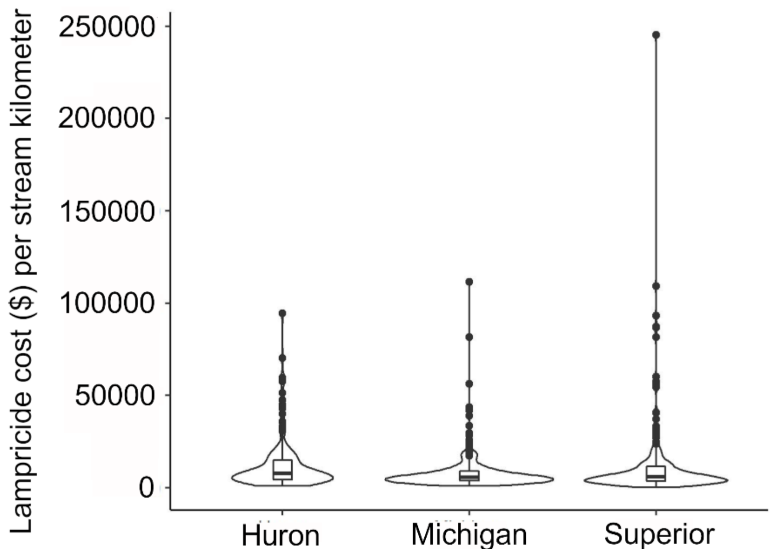

Figure D4.2. Distribution of lampricide treatment cost in streams of Lakes Huron, Michigan, and Superior from 2010-2020.

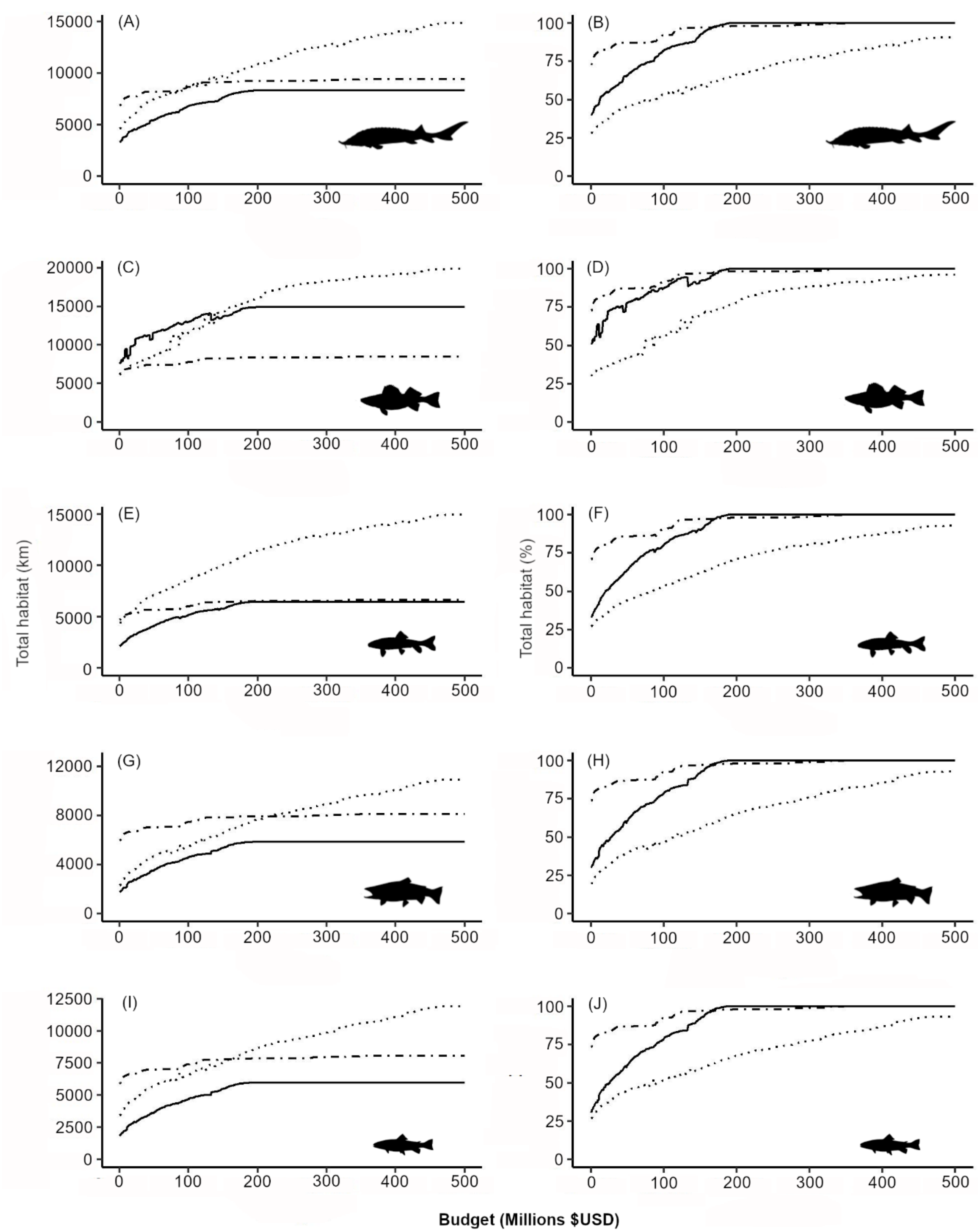

Figure D4.3. Species-specific cost-benefit curves of Lake Sturgeon (A, B), Walleye (C, D), White Sucker (E, F), Steelhead (G, H), and Brook Trout (I, J) in basins of Lakes Huron (solid), Michigan (dotted), and Superior (dot-dash). Total habitatfor individual species does not necessarily monotonically increase with budget due to tradeoffs among species (see Cooper et al., 2021).

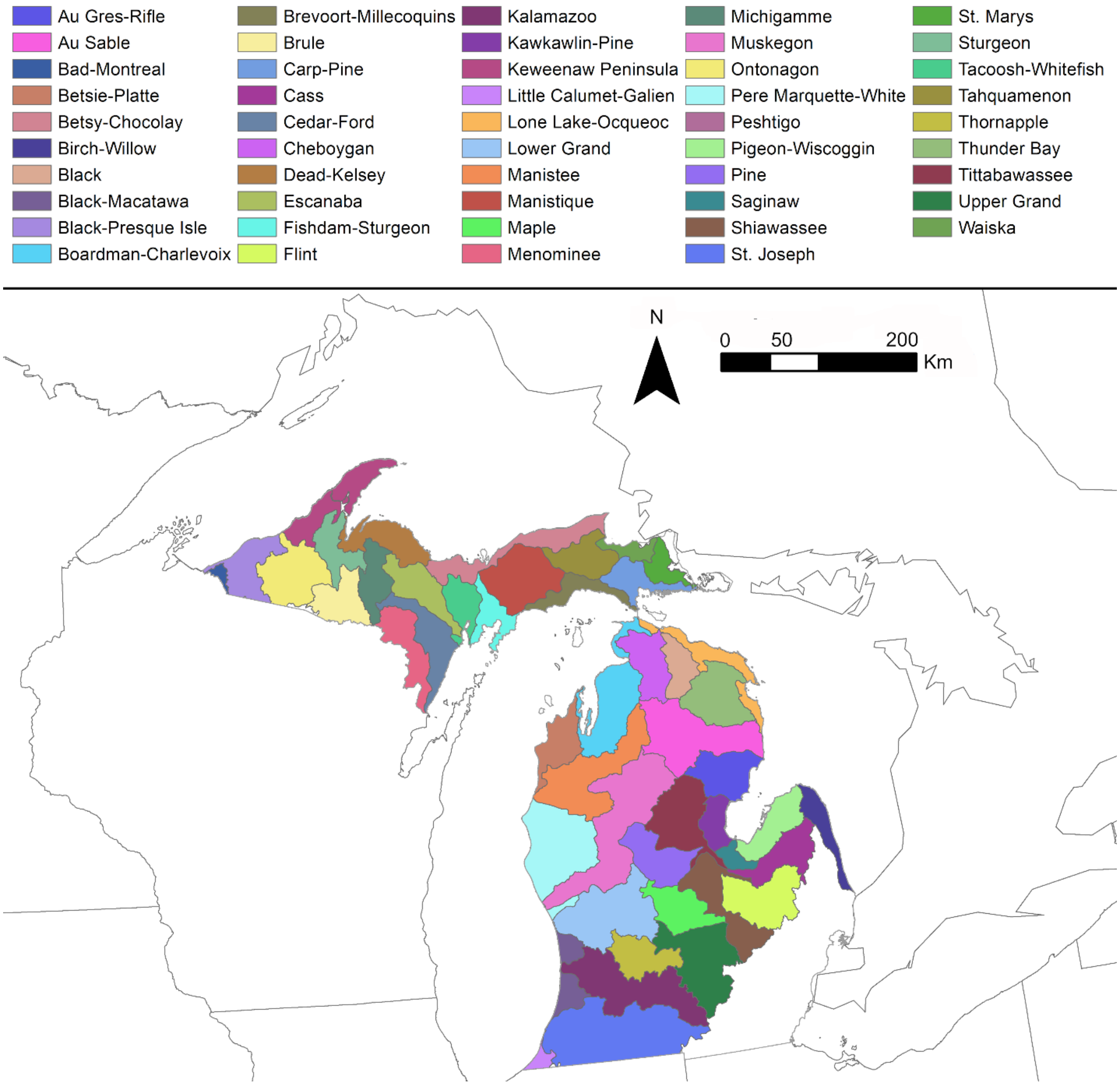

Figure D4.4. Locations and names of watersheds of Lakes Huron, Michigan, and Superior in the state of Michigan.

CHAPTER 5:

PRINCIPAL FINDINGS AND MANAGEMENT IMPLICATIONS

Chapter 1

I developed the North American Freshwater Migratory Fish Database (NAFMFD) synthesizing current knowledge of the migratory statuses, patterns, and behaviors of 1,250 native and non-native freshwater fishes throughout North America. My results suggest that at least 25% of the North American freshwater fish assemblage is migratory. Some fish families have more than 50% of species considered migratory (Catostomidae, Gobiidae, Salmonidae), while others are entirely migratory (e.g., Acipenseridae, Anguillidae, Eleotridae). Potamodromous species (i.e., migratory fishes that use wholly freshwater habitats) comprise more than 66% of freshwater migratory fish species. Multiple species exhibit a wide diversity in their migratory life histories throughout their ranges, including populations with different patterns (e.g., diadromous vs. potamodromous) or statuses (i.e., migratory vs. non-migratory).

When I coupled NAFMFD information with conservation data from the International Union of Conservation Network (IUCN; https://www.iucnredlist.org/), I showed that 25% of the North American freshwater migratory fish assemblage is imperiled. This information is critical for managers to prioritize migratory species for conservation, such as designating imperiled migratory fishes as Species of Greatest Conservation Need in U. S. State Wildlife Action Plans (https://www1.usgs.gov/csas/swap/). My work emphasized that freshwater fishes vary in their migratory life histories across the continent, so managers will need to invest in research to understand that variation in the streams they manage. This information is essential to understand the migratory species and habitats that must be conserved and protected from threats, including stream fragmentation by barriers.

Chapter 2

Using existing datasets including the NAFMFD, sampled stream fish assemblages, fragmentation in stream networks, and anthropogenic and natural conditions in stream catchments, I determined the relative influences of barriers compared to human land uses and natural factors on freshwater migratory fish assemblages in nine ecoregions of the conterminous U. S. I found that many species comprising fish assemblages are migratory in each ecoregion, emphasizing the prominence of migratory fishes in stream networks across the country. Ecoregional differences in the relative influence of barriers, human land uses, and natural factors on migratory assemblages in stream networks implies that barrier removal in one region may not have similar outcomes in another region for freshwater migratory fish populations. My results also suggest that the key natural influences on migratory fishes included catchment area, river baseflow, and air temperature, implying that migratory fishes may be affected by changing climate. I also found that downstream dams were more influential than other human stressors to potamodromous fishes in the eastern conterminous U. S.

Managers will need to invest in research to understand the full suite of migratory species in freshwater fish assemblages occurring throughout the year to improve mitigation opportunities involving barriers. By knowing the relative influence of barriers, human land uses, and natural factors on migratory assemblages across large regions, managers can use this information to better understand the response of populations to barrier removal and local mechanisms underpinning population loss in smaller areas with less variability. In rivers of the eastern conterminous U.S., my results suggest that managers could prioritize locations to mitigate effects of barriers and climate change on freshwater migratory fishes. One strategy could be to remove barriers where migratory fish species will have access to more thermally suitable stream habitats.

Chapter 3

In tributaries of the Great Lakes region, I used a landscape-based approach to discriminate suitability among streams for six migratory fish species above barriers where species records were too limited to support species distribution modelling. The amount and type of information on species habitat preferences were influential on my overall ability to assess stream suitability for fishes using my approach. Nevertheless, I was able to integrate landscape and local habitat data to identify suitable habitat in streams for six migratory fish species across a large area. My results suggest that segments of streams that are suitable for desirable migratory fish species while also least suitable for invasive, larval Sea Lamprey are located above barriers in the Keweenaw Peninsula and Dead-Kelsey watersheds in the Upper Peninsula of Michigan and the Au Sable, Platte, Pere Marquette-White, Kalamazoo, and the Tittabawassee watersheds in the Lower Peninsula of Michigan.

Managers can use my approach to understand suitability in streams for migratory fishes or any aquatic species in which occurrence data are lacking. Additionally, the approach can be incorporated into broader decision-making processes, like anticipating changes in stream suitability due to changing climate. The outcomes of the approach help managers reduce a large set of potential streams to a more targeted list to consider for restoring connectivity. Because my approach generates relative estimates of suitability, managers can use the approach to further understand habitat suitability at smaller spatial scales, such as within a single watershed. Managers could then target specific reaches to consider for barrier removal using local expertise and site-specific information.

Chapter 4

In the state of Michigan, I used estimates of stream habitat suitability for five desirable migratory fish species, barrier removal cost, and cost of lampricide treatment in an optimization analysis to prioritize barriers removals in tributaries draining to Lakes Superior, Huron, and Michigan. I explicitly distinguished the suitability of accessible habitat in contrast to previous optimization efforts that used just accessible tributary length which treats all streams as equally suitable and can result in less optimal solutions. My results suggest that connectivity to suitable habitat can be enhanced for desirable migratory fishes while controlling for Sea Lamprey spread in the Great Lakes region. Barrier removals could be more beneficial in the Lake Huron basin than Lake Superior or Michigan basins when desirable species are considered all together. Additionally, I generated a prioritized list of barriers to consider for removal in the three lake basins.

The cost-benefit curves generated by the optimization analysis helps managers to prioritize barrier removal actions among basins or species. The prioritized list generated from this study is also useful for managers to reduce a large set of potential barrier projects to a smaller list in basins. Managers can use the prioritized list along with local knowledge and site-specific information to identify candidate barriers to remove. My approach to optimization analysis can be applied to any region struggling to restore stream connectivity while managing the spread of invasive species, aiding managers on a global scale.