Title:

Forecasting the response of Great Lakes sea lamprey (*Petromyzon marinus*) to barrier removals

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Abstract

A key uncertainty surrounding barrier removals in the Great Lakes is the response of invasive sea lamprey populations to realized increases in available habitat for adfluvial species. We addressed this uncertainty by applying a management strategy evaluation model, originally developed to inform sea lamprey management in the Great Lakes, to forecast the effects of barrier removal on Lake Michigan sea lamprey abundances. We used this model to characterize the response to systematically increasing habitat availability and a specific proposed barrier removal. Our results suggest the removals allow novel production from newly opened habitat and, assuming a fixed budget for sea lamprey control, decrease the overall effectiveness of control, leading to disproportionate increases in abundance. The case study demonstrated that evaluating population effects only at the scale of watersheds directly affected by barrier removals would substantially underestimate effects at the scale of Lake Michigan. Similar population responses are possible when evaluating the effects on desired species. Our findings highlight the importance of considering trade-offs for barrier removals and selecting the appropriate scale for forecasting.

Introduction

Dams are ubiquitous features of watersheds throughout the world, and historically provided many societal benefits, but they also serve as significant barriers to migratory fish. Indeed, dams, hereafter referred to as stream barriers or simply barriers, have been implicated in the declines of numerous populations of diadromous species (Limburg and Waldman 2009). Thanks to growing public preference to increase lotic connectivity and benefit aquatic species, barrier removal in the U.S. is accelerating and many large-scale structures have been demolished in systems like the Penobscot, Carmel, and Elwha Rivers in Maine, California, and Washington, respectively. Observed ecological benefits from previous barrier removals include increased biological diversity, restoration of historical habitat, and enhanced passage (Bednarek 2001). Ecological trade-offs emerge, however, when improved river access eliminates impediments to the spread of unwanted species (McLaughlin et al. 2013). By restricting the range expansion of invasive species, stream barriers in select systems may actually provide an important conservation function by blocking fish migration (Sharov and Liebhold 1998; Vélez-Espino et al. 2011; Rahel 2013).

Sea lamprey have caused considerable ecological and economic damage within the Laurentian Great Lakes since their invasion in the early 20th century (Smith and Tibbles 1980). The parasitic juvenile stage of this species feeds on Great Lakes fish before maturing and migrating to Great Lakes tributaries to spawn; the resulting larvae live as burrowing filter-feeders in these streams for several years before metamorphosing and migrating back to the lakes to begin their parasitic stage (Applegate 1950). Sea lamprey are currently controlled to generally acceptable population levels in the Great Lakes using a combination of lamprey-specific pesticide (*i.e.*, lampricide) applications and intentional fragmentation (Smith and Tibbles 1980).

A limited budget is allocated annually to both elements of control. Stream barriers play an important role by preventing migratory adult sea lamprey from accessing high quality spawning habitat, and consequently eliminating the need for costly treatments of large sections of rivers (Hunn and Youngs 1980). The Great Lakes Fishery Commission (GLFC) Sea Lamprey Control Program (SLCP) uses both pre-existing and actively constructed stream barriers to block sea lamprey migration (Lavis et al. 2003).

In concert with the prospective benefits to resident fish species including various salmonids and lake sturgeon (*Acipenser fulvescens*), Great Lakes barrier removals have the potential to greatly reduce the effectiveness of sea lamprey control. In the Lake Michigan basin alone, barriers like the Sixth Street Dam, Union Street Dam, and Calkins Bridge Dam currently block hundreds of miles of viable spawning and larval habitat in the Grand River, Boardman River, and Kalamazoo River, respectively. If these structures were removed without construction of a replacement lamprey barrier or an increase in the lampricide control budget, there would be two options available to control agents: 1) ignore production from the newly available habitat, or 2) re-allocate lampricide application efforts to the newly available habitat as needed, at the expense of reducing the frequency of applications in other river systems. The first option is unlikely to be considered for large systems like the Grand River, while the second option requires a shift in control effort from existing stream systems to the new habitat, potentially decreasing treatment effectiveness across the basin as a whole. Although the qualitative risks of barrier removal for sea lamprey management in the Great Lakes are accepted by fishery management agencies, there is a need to better understand the actual magnitude of the sea lamprey response to barrier removals.

In addition to the ecological concerns surrounding barrier removals, decision-makers are faced with numerous competing objectives and pressures, including the maintenance of infrastructure condition and public safety, generation of power, and enhancement of recreational opportunities. The development of formal criteria, supported by the necessary scientific and social information, is one solution for managing these trade-offs (Pejchar and Warner 2001). With respect to the scientific information, researchers are specifically arguing for more careful, comprehensive consideration of the potential ecological consequences and an increased role for scientists in providing data on these consequences (Johnson and Graber 2002; Doyle et al. 2003). In the case of barrier removals in the Great Lakes, research that equips managers with a more explicit understanding of the effects of barrier removals on sea lamprey control can help formalize the balancing of trade-offs inherent in decision-making.

Evaluating the expected effects of barrier removals requires consideration for the appropriate spatial scale of modeling and relevant aspects of habitat quality upstream of barriers. Most previous studies have focused on river-specific impacts of barrier removals (Stanley et al. 2007; Burroughs et al. 2010). The effects of barrier removals on sea lamprey populations, however, are not restricted to river-specific production, as sea lamprey appear to exhibit a lack of natal homing when migrating to tributaries to spawn (Bergstedt and Seelye 1995). Sea lamprey production from a specific river can influence future spawner abundances in other rivers, so predicting the effects of barrier removals on Great Lakes requires a consideration of population dynamics on a larger scale than that of individual rivers. Furthermore, both the quality and quantity of habitat upstream of barriers needs to be evaluated. Sea lamprey recruitment is known to be limited by the availability of larval habitat, defined as substrate dominated by fine sediments (Slade et al. 2003), and the attractiveness of river systems to migrating spawners is partially driven by habitat quality and quantity (Morman et al. 1980; Mullett et al. 2003). Previous modeling efforts looking at the effect of changing habitat availability on other fish species have also emphasized the importance of habitat quality in predicting population responses (Cheng et al. 2006; van der Lee and Koops 2016).

Management strategy evaluation (MSE) modeling, using known information about sea lamprey life history and control in the Great Lakes, represents a feasible, realistic means to capture the expected effects of barrier removals on the long-term effectiveness of sea lamprey control. Management strategy evaluation models are powerful tools for research and management because they tie together biological, observational, and management processes, account for sources of uncertainty in each of these processes, and allow researchers to formally compare the ability of competing management strategies to achieve specified management objectives (Smith et al. 1999; Harwood and Stokes 2003). We have already developed an MSE model for sea lamprey, specific to the Great Lakes, to assess the effect of alternative management strategies (Jones et al. 2009). This model has been used to determine optimal control budgets to achieve target economic injury levels (Irwin et al. 2012) and to explicitly compare the effectiveness of alternative management strategies at a basin-wide scale (Dawson et al. 2016).

We modified the MSE model to evaluate the effects of barrier removals on the Lake Michigan sea lamprey population. Lake Michigan was selected as the focal spatial scale for this work due to the observed lack of natal homing for sea lamprey within lakes and the detailed understanding of sea lamprey population dynamics in this region (Dawson et al. 2016). We first assessed the system’s general response to increasing habitat availability through the incremental addition of discrete habitat units with varying attributes of habitat quality. We also modeled a specific Lake Michigan barrier removal scenario, using input data and management scenarios defined by sea lamprey control agents, to inform decision-making for a contentious, contemporary barrier removal scenario. Both approaches helped explain how a complex, intensively managed biological system would respond to anthropogenic changes in habitat availability.

Methods

Model Description

To evaluate the potential effect of barrier removals on sea lamprey production within an MSE framework, we modified the MSE operating model developed by Jones et al. (2009) and updated by Dawson et al. (2016). Briefly, this operating model includes interconnecting biological, observational, and management components, operates at the spatial scale of an entire Great Lake, and has an annual time step (Fig. 1). The biological model simulates the life history of sea lamprey: adult sea lamprey from the lake habitat are allocated to streams for spawning; these spawners produce stream-dwelling larvae according to a Ricker-type stock-recruitment function; the larvae experience growth and mortality before metamorphosing into the parasitic juvenile stages and migrating back to the lake. An observational model generates estimates of stream-specific larval abundances intended to reflect measurement uncertainty with existing sampling methods in the Great Lakes; these estimates are used to rank stream segments, called treatment units, for treatment on the basis of cost per expected larva killed in the entire segment. Treatment units are operationally defined as river sections treated with lampricides as a single unit. The number of annually selected treatment units is limited by the total available control budget. Treatment units selected for lampricide applications experience reductions in larval abundance; the actual proportional reduction in abundance due to a lampricide treatment is drawn from a beta distribution yielding average reductions of 93% and a CV of 0.10. Process uncertainty is also included in the model in the form of a stochastic reproduction function (Dawson and Jones 2009) and uncertainty in stream-specific larval growth rates. Further details of the model’s structure and parameterization are not repeated here; interested readers are referred to earlier papers.

In addition to incorporating the capacity to flexibly add new habitat, as described below, the model was altered to account for recent analyses of adult sea lamprey trapping data that re-assessed the rules for allocating adult sea lamprey to spawning habitats. These modifications included the following: 1) allocating 52% and 48% of all Lake Michigan spawners to northern and southern tributaries, respectively, prior to allocating spawners to individual streams based on drainage area and larval abundance, and 2) increasing the influence of drainage area, relative to larval abundance, in determining spawner allocation to individual tributaries. Tributaries were classified as northern or southern based on the location of their mouths relative to a dividing line stretching across Lake Michigan from Frankfort, MI, to just south of Manistique, MI (Mullett et al. 2003). These changes were made to match simulated spawner numbers with observed adult distributions in sixteen Lake Michigan rivers that have received previous spawner assessments (H. Dawson and M.L. Jones, Quantitative Fisheries Center, Michigan State University, East Lansing, Michigan, unpublished analysis), and to reflect an updated analysis of sea lamprey trapping data from throughout the Great Lakes that examined covariates affecting relative spawning run size (Mullett et al. 2003; M.L. Jones, Quantitative Fisheries Center, Michigan State University, East Lansing, Michigan, unpublished data).

Population Responses to Systematic Barrier Removals

We first characterized the general response of the Lake Michigan sea lamprey population to barrier removals by systematically adding standardized habitat blocks. Each block was assigned identical attributes, including areas of suitable larval sea lamprey habitat types as defined by the GLFC (*i.e.*, Type I and Type II; Slade et al. 2003), drainage area, treatment cost, and miscellaneous larval growth and mortality parameters; these are all attributes of existing treatment units within the original operating model. Block attributes were calculated as averages of all existing treatment units in Lake Michigan; each habitat block was assigned a total larval habitat area of 386,275 m^2, drainage area of 842.8 km^2, and treatment cost of \$127,864. These habitat additions were intended to simulate the effect of opening new river systems to sea lamprey (*i.e.*, removing barriers at the river mouths).

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

The influence of two categorical treatment unit attributes, namely recruitment potential and geographically-determined spawner allocation, on the sea lamprey response to barrier removals were formally evaluated by running increasing habitat addition simulations for each possible combination of attributes. New habitat areas were either characterized as having high or low recruitment potential, reflecting observed (Dawson et al. 2016) differences in Ricker stock-recruitment parameter estimates between streams classified by sea lamprey program control staff as regular versus irregular producers. Dawson et al. (2016) reported that recruitment potential (Ricker α estimates) was 3.4x greater in regular producers. Furthermore, habitat units were characterized as having elevated or reduced spawner allocation, based on whether they were assigned to northern or southern Lake Michigan, respectively. New habitat regions added to northern Lake Michigan were regarded as having elevated spawner allocations because 52% of all Lake Michigan spawners are assigned to this region, despite containing smaller rivers with smaller drainage areas and corresponding attractive flows for migrating sea lamprey compared to southern Lake Michigan.

For each removal scenario, we ran the model for 5 000 simulations, with a 100 year time horizon for each simulation; this was intended to capture the full range of stochasticity in model results and yield an equilibrium state for each simulation. For every simulation, the mean number of total lake-wide adult spawners across the last ten years was calculated to represent expected equilibrium conditions. The mean system response for each habitat addition scenario was summarized by calculating the percent change in mean abundance, across simulations, from status quo mean abundance using the equation below, in which the original value refers to mean status quo abundance unless otherwise stated:

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

The simulated range of variation for each scenario represented variability among the simulation-specific 10-year averages. We also took advantage of the stochastic nature of the simulations to calculate the proportion of the 5 000 simulations, for each habitat addition scenario, exceeding a high threshold relative to average status quo spawner abundance; we selected an abundance of 152 266 spawners based on the 90th percentile of simulated lamprey abundances under status quo conditions. This simulated threshold abundance is similar to the maximum estimated Lake Michigan adult abundance of 141 730 over a recent 10-year period (2005-2014). Finally, to calibrate the model at the current Lake Michigan control budget of $2.42 million, larval survival was adjusted until the base model (*i.e.*, no habitat additions) successfully projected the recently estimated average adult abundance of 72 200 (M. Siefkes, Great Lakes Fishery Commission, Ann Arbor, Michigan, personal communication, 2016).

Explaining Forecasted Population Trends

To explain the forecasted trends in adult sea lamprey abundance with increasing habitat availability, we ran additional simulations to characterize trends in the following model components: stream-specific parasitic sea lamprey production, control budget allocation among the newly added and original treatment units, and lampricide treatment frequency. Parasitic sea lamprey production reflected the total number of metamorphosed sea lamprey leaving streams in each year and simulation. Tracking stream-specific production facilitated comparison of the relative contribution of the new and original treatment units to lake-wide adult abundances. Additionally, looking at both control budget allocation and treatment frequency helped to explain why the relative contributions of sea lamprey production from new and original treatment units might change with increasing habitat availability.

We ran these additional simulations 1 000 times over the same 100 year timespan; consistent with other simulations, only the last ten years of data in each simulation were used to characterize trends. Simulations were run only for increasing habitat availability in which regular producing streams were added to northern Lake Michigan, as these attributes produced the strongest trends in sea lamprey abundance and were therefore more amenable for elucidating population drivers. These simulations were run for the full range of increasing habitat availability and for both the single large and multiple small river additions. We expect qualitative patterns to be similar for other scenarios, such as simulating increasing habitat availability in southern Lake Michigan streams.

Case Study: Simulating A Barrier Removal on Michigan's Grand River

We selected the potential removal of Michigan's Sixth Street Dam to demonstrate the utility of an MSE approach in informing a potentially high impact barrier removal scenario. The Sixth Street Dam is located in downtown Grand Rapids, MI, and has served as an important incidental lamprey barrier on the Grand River, Michigan's longest river system. Approximately 96 river km lies between the Sixth Street Dam and the Webber Dam, the next upstream barrier on the mainstem, and numerous large tributaries, including the Thornapple, Maple, and Rogue Rivers drain into the Grand River between the two barriers, in addition to many smaller streams (Fig. 2).

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

To simulate the removal of the Sixth Street Dam, we incorporated sixteen new treatment units between the Sixth Street Dam and Webber Dam, each representing distinct Grand River tributaries, into the model database. The mainstem of the Grand River was deemed likely to host relatively low densities of larvae, thereby making treatment prohibitive from a cost-effective standpoint (Fig. 2; J. Tews, U.S. Fish and Wildlife Service, Ludington, MI, personal communication, 2015). Each included treatment unit was known to contain viable habitat for spawning and larval sea lamprey, and had a uniquely estimable treatment cost. Additional attributes of the new treatment units were then estimated using all available data on the Grand River (supplementary data are available online).

Three primary management decisions were selected as the focus for modeling work: the decision to modify the Webber Dam to block sea lamprey, the decision to treat or ignore the newly available habitat upstream of the Sixth Street Dam, and the decision to maintain or increase the current lake-wide control budget (Table 1). Because the Webber Dam currently has the potential to pass sea lamprey but can be modified to block them, we simulated the influence of barrier modification by allowing or denying sea lamprey access to the Looking Glass River; this river is the only major tributary between the Webber Dam and the next mainstem barrier. The decision to treat or ignore habitat upstream of the Sixth Street Dam was intended to compare the effect of pulling treatment effort away from other Lake Michigan tributaries with the effect of allowing uninhibited lamprey production above the Sixth Street Dam, respectively. Finally, for the scenario in which the upstream system is treated and the Webber Dam blocks access to the Looking Glass River, we both evaluated the effect of treating the system under the current budget of $2.42 million and estimated the necessary budget increase to prevent a lake-wide increase in sea lamprey abundance above status quo levels.

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

The model was run and summarized in the same manner as for the systematic habitat additions (*i.e.*, 5 000 simulations, 100 year time horizon, ten year averages) for every scenario and assumption, and the proportions of simulation results above the same status quo threshold were again calculated.

Results

Population Responses to Systematic Barrier Removals

The simulated Lake Michigan sea lamprey population exhibited a nonlinear increase in abundance in response to systematically increasing habitat availability that varied in magnitude across the combinations of habitat addition attributes (Figs. 3, 4). The smallest percent increase in mean abundance from status quo conditions with a 20% increase in habitat availability was 161%; the greatest increase exceeded 800%. The type of barrier removal (*i.e.*, whether there is one large-scale barrier removal or multiple small-scale events) influenced the magnitude of the sea lamprey population's response to barrier removal, with the addition of a single large stream having the greater effect. The largest percent increase in abundance for the single stream addition was 885%, compared to 452% for multiple stream additions. This difference in abundance between the types of habitat addition held true across all combinations of recruitment potential and spawner allocation. Corresponding with the different trends in mean abundance, the proportion of simulations with forecasted abundances greater than the high threshold relative to status quo abundance (152 266) also approached one more rapidly, relative to the amount of added habitat, when additions were conducted as a single large river.

Whether the additional accessible habitat had high or low recruitment potential, as well as whether it experienced high or low spawner allocation, also had implications for the simulated effectiveness of sea lamprey control under barrier removal scenarios. Habitat additions with high recruitment potential and high spawner allocation, which would correspond to habitat assigned the status of regular producers and added to northern Lake Michigan, resulted in higher abundances than habitat additions with low recruitment potential and low spawner allocation (Figs. 3, 4). Between these two categorical factors, recruitment potential had the slightly greater effect on resulting adult sea lamprey abundances. With a 20% increase in habitat availability and the combination of spawner allocation and type of habitat addition held constant, high recruitment habitat additions resulted in 38.2% to 115% greater mean adult sea lamprey abundances relative to abundances arising from habitat additions with low recruitment potential. With the same 20% increase in habitat availability, high spawner allocation habitat resulted in mean abundances 23.3% to 92.2% greater than those achieved under habitat additions with low spawner allocation.

Explaining Forecasted Population Trends

A combination of novel sea lamprey production from newly added habitat and increasing production from the original treatment units, caused in part by a shifting allocation of treatment effort away from original units to new ones, underlie the disproportionate response of adult sea lamprey abundance to habitat increases. As expected, the average contribution of basin-wide sea lamprey production from new treatment units increased in response to increasing absolute amounts of new accessible habitat (Fig. 5a). Increasing habitat availability also caused a steep, concurrent increase in production within the original treatment units (Fig. 5b); the nature of the response was consistent across both types of habitat addition. This response may be explained in part by the reduced overall annual treatment frequency among original treatment units with increasing habitat additions (Fig. 5c). The average annual allocation of the control budget to original treatment units declined from $2.42 million to a median of $2.07 and $1.79 million for the single and multiple treatment unit additions, respectively, when 18 new habitat blocks were added to the Lake Michigan basin (Fig. 6).

Case Study

All management scenarios pertaining to the Sixth Street Dam removal forecasted large increases in adult sea lamprey abundance in Lake Michigan, assuming the control budget remains unchanged (Fig. 7). Among the simulations, the lowest mean percent increase in adult abundance from status quo conditions was 52%. This occurred when the Webber Dam was modified to block sea lamprey, new habitat units were treated, and sea lamprey used 10% of available habitat. For the same scenario, just over 24% of simulations resulted in abundances exceeding the status quo 90th percentile. The largest mean percent increase of 269% occurred when an unmodified Webber Dam allowed sea lamprey to infest the Looking Glass River, none of the new habitat units were treated, and sea lamprey used 50% of potentially available habitat. Approximately 87% of simulations for this scenario resulted in spawner abundances exceeding the status quo 90th percentile.

The decision to modify the Webber Dam, the decision to treat the upstream Grand River, and the assumed degree of habitat use each had substantial effects on equilibrium sea lamprey abundances, but the relative magnitude of effects differed. When the decision to treat and assumed habitat use were otherwise held constant among scenarios, the percent difference in mean lake-wide sea lamprey abundance between simulations including and excluding the Looking Glass River ranged between 13.1% and 19.6%, with higher simulated abundances for scenarios including the Looking Glass River. The decision whether or not to treat the upstream Grand River system had a larger effect on sea lamprey numbers than the decision to modify Webber Dam, with the decision to not treat these units resulting in a 40.4% to 52.1% increase in average adult abundance. Assuming greater habitat utilization in the new treatment units had a similarly large effect on equilibrium sea lamprey abundances (34.7% to 49.1% increase).

For the barrier removal scenario in which upstream habitat is treated and the Webber Dam is modified to block sea lamprey, substantial increases in the annual Lake Michigan control budget were needed to restore mean sea lamprey abundances to levels at or below status quo under the two assumptions of habitat use. Simulations suggested an annual control budget of $2.62 million per year, representing a $200 000 increase from the current budget, was needed to maintain mean abundances at or just below status quo levels when assumed habitat use was 10% (Fig. 8). A control budget of $2.78 million was required when assumed habitat use was 50%, representing an annual budget increase of $360 000.

Discussion

The systematic habitat addition simulations showed that a heavily-controlled invasive species, like sea lamprey, responds to the localized easing of key management-imposed constraints in a disproportionate manner. The primary constraints on sea lamprey population growth in the Great Lakes are habitat limitations created by barriers in large river systems and lampricide treatment-induced mortality at the larval stage (Christie et al. 2003; Lavis et al. 2003). When these two constraints were diminished by the addition of habitat and the subsequent shifting of treatment efforts to these new habitat blocks, simulated sea lamprey production increased in both the new and original river systems, leading to a large increase in forecasted adult abundance. Similarly strong responses in population abundance to changing top-down controls have been observed for mesopredators (*i.e.*, mesopredator release), where small reductions in the abundance of apex predators trigger disproportionate increases in mesopredator abundance (Ritchie and Johnson 2009). There is also evidence for sea lamprey of large population responses to barrier failures in Lake Michigan: unrestricted colonization of 220 km of the Manistique River above a degraded barrier in the late 1990s and early 2000s was associated with approximately a 100% increase in the estimated Lake Michigan sea lamprey abundance (Klar and Young 2004).

The forecasted disproportionate response can be explained in part by production of sea lamprey from newly available habitat and in part by dilution of control intensity across the basin. First, the simulated population increased due to an immediate contribution of sea lamprey production from new habitats. Second, shifts in control effort allocation to include new treatment units led to an overall simulated decrease in treatment frequency for the original treatment units, which led to increased production, on average, from the these units.

We further hypothesize that the lack of density-dependent controls on this already suppressed population compounded these shifts in treatment allocation and total sea lamprey producing habitat by giving rise to a positive feedback effect. The sea lamprey population in Lake Michigan has been reduced to abundances far below carrying capacity, defined at the lake-level by limits on the abundance of available hosts; contemporary abundances are believed to be at or below 10% of pre-control levels, and host abundances are much higher than they were at the start of the control program. Consequently, the modeled population is not regulated by density-dependent processes when management actions allow for increased recruitment except in rare instances when large recruitment events trigger density-dependent compensation at the individual stream level. In the near absence of density-dependent regulation, a positive feedback cycle allows the population to rise to a carrying capacity defined by the estimated stream-level stock-recruitment dynamics (Dawson and Jones 2009), subject to constraints imposed by a density-independent lampricide control program. It is possible that the size to which the lamprey population grows would be lower than forecasted in the more extreme scenarios modeled here, constrained by host dynamics. The abundances would, nevertheless, be large enough to inflict severe damage on host populations. Positive feedback effects have been predicted for other fisheries systems under changing predation pressure (Kirby et al. 2009; Audzijonyte et al. 2013).

In total, the simulated new production from new habitats, increased production from old habitats due to shifted control efforts, and the near absence of density-dependent compensation at current sea lamprey abundance levels drove the large forecasted response in sea lamprey abundance from a comparatively small increase in habitat. These results suggest that future evaluations of barrier removals focusing on potential fish responses should consider broader spatial scales, especially for systems in which species do not exhibit strict natal homing and control effort is necessarily balanced among many streams. Without considering lake-wide impacts of small-scale barrier removals, we would not have forecasted the disproportionate population response.

Similar types of population responses to increased accessible spawning and rearing habitat may occur for desirable fish species in the Great Lakes. Although many species relying on nearshore or riverine habitat for spawning are known to exhibit homing behavior, increased reproduction coupled with modest rates of straying from natal habitats could enhance future reproductive success across broader spatial scales. Lake sturgeon and lake trout (*Salvelinus namaycush*) were observed to exhibit overall straying rates of 0.105 and 0.60 in Lake Michigan, while walleye (*Sander vitreus*) in Lake Erie exhibit moderate gene flow among populations (Bronte et al. 2007; Strange and Stepien 2007; Homola et al. 2012). Although not assessed in the Great Lakes, the straying rates of Chinook salmon (*Oncorhyncus tshawytscha*) ranged from 0.01 to 1.0 among spawning tributaries in Washington’s Wenatchee River (Ford et al. 2015).

Our analysis also revealed that barrier removal decisions need to account for factors in addition to habitat quantity to accurately assess the effects of barrier removal. The difference between opening a single large river and multiple small river systems is due to the challenge of incorporating increasingly expensive single-system treatments into the stream ranking system; if there is insufficient budget remaining when a unit ranks for treatment, it will be passed over in favor of lower ranked, less expensive systems. Supporting this, simulated trends in budget expenditure and treatment frequency among original treatment units flatten with increasing habitat availability only for the single large river addition (Figs. 5c, 6), while lamprey production from this new habitat increases more steeply (Fig. 5a). Habitat attributes of recruitment potential and spawner allocation, the latter associated with geographic location, also played important roles in mediating the sea lamprey response to increasing barrier removals. Expected differences among these habitat attribute scenarios may be mitigated by more flexible management strategies (*e.g.*, based in part on professional judgment rather than a fixed algorithm) capable of accounting for higher sea lamprey output from larger, more productive systems.

The high degree of variability within each of the barrier removal scenarios reflects very real uncertainty in our understanding of sea lamprey dynamics and should be explicitly recognized in decision making. One of the strengths of the MSE approach is the incorporation of multiple sources of uncertainty (Bunnefeld et al. 2011); for our model, these sources included stochasticity in biological processes, larval abundance assessments, and control efforts. The resulting variability in model results implies that the forecasted mean responses in abundance are by no means guaranteed outcomes. Instead, the results indicate a wide range of plausible alternative outcomes. Reporting results as proportions of simulations with values above some management-relevant threshold value demonstrates the likelihood of an undesirable outcome, rather than simply focusing on a “best-guess”; decision-makers can use this information to assess the risk of key decisions.

Simulation results for the removal of the Sixth Street Dam confirmed trends forecasted in simulations of systematically increasing habitat availability. The case study also highlights the importance of treating the upstream Grand River in the case of barrier removal. To ignore the newly infested upstream habitat and continue a status quo treatment program resulted in markedly higher sea lamprey abundances, despite the dilution of basin-wide treatment effort that would have occurred if upstream habitat had been treated. The estimated increases in control budget necessary to maintain sea lamprey at status quo abundances provide decision makers with an estimate of the cost of a barrier removal. There are numerous other potential barrier removals under consideration in the Great Lakes, including those in Lake Michigan's Boardman River and Lake Superior's Black Sturgeon River, that could be evaluated with this MSE tool.

The case study simulations depended on several assumptions: that the Sixth Street Dam will not be replaced by a seasonal barrier, that migrating sea lamprey will eventually utilize all identified upstream tributary systems, and that the evaluated percent habitat use values (10%, 50%) bracket realistic values. Stakeholder groups have proposed the construction of a seasonally-adjusted structure, in place of the Sixth Street Dam, to operate as a barrier only during sea lamprey migrations (Adair and Sullivan 2015). We chose not to account for this possibility in simulating the removal due to the uncertainty surrounding its actual installation and potential success at blocking sea lamprey. If the goals of such a barrier are blocking sea lamprey and allowing passage of other non-jumping, migratory species, the overlapping migration phenologies of Great Lakes fish largely prevent the balancing of such objectives without installation of an effective fishway (Vélez-Espino et al. 2011). Even partial barrier failures can contribute to large increases in lake-wide sea lamprey abundances, as demonstrated by the historical failure of a barrier on Michigan's Manistique River (Klar and Young 2004). The assumption that sea lamprey can and will use all identified upstream tributaries for spawning has been largely supported by previous barrier removal studies and our understanding of sea lamprey migratory capacity. In coastal river systems smaller than the Grand River, sea lamprey have been observed to quickly re-colonize previously blocked upstream habitat (Hogg et al. 2013; Lasne et al. 2014). Sea lamprey also appeared to rapidly colonize upstream reaches of the Manistique River in northern Michigan, a river section over 220 km in length, following the partial failure of a blocking barrier, and access upstream tributary systems in Portugal's River Mondego, a river system draining a watershed slightly less than half the size of Michigan's

Grand River (Almeida et al. 2002; Klar and Young 2004). Finally, we assumed sea lamprey would likely use 10% of available river length in the upstream tributaries, and evaluated 50% habitat use as a worst-case scenario. Although the 10% assumption can be considered a reasonable estimate based on professional judgment and preliminary analyses, it remains a rough approximation. Identifying reliable habitat area estimates in future modeling endeavors will require more detailed GIS data integrating length and width information along streams, as well as an improved empirical understanding of habitat use by sea lamprey within tributaries.

Other modeling-based approaches have been used to inform barrier removal decisions and predict fish response to changing habitat availability, but none have matched both the extent and resolution of our modeling efforts for sea lamprey populations. At the broadest extent, barrier removal prioritization efforts synthesize multiple sources of information and strive to optimize barrier removals across varying spatial extents like the Great Lakes or Pacific Northwest, but often make simplifying assumptions in relating passability, stream length, and habitat quality to future fish production (Zheng et al. 2009; Kemp and O'Hanley 2010; Moody et al. 2017). At a smaller spatial extent, landscape models are increasingly used to predict indirect aspects of fish response to barrier removal, like spawning success; these models often fail to provide direct estimates of fish abundance (Steel et al. 2004; Spens et al. 2007). Finer resolution modeling has also occurred to predict scenario-specific fish responses to individual barrier removals using species-specific, population dynamics models for American shad (*Alosa sapidissima*), walleye, and American eels (*Anguilla rostrata*); (McCleave 2001; Cheng et al. 2006; Harris and Hightower 2012).

To our knowledge, no previous studies have assessed fish responses to barrier removal using a detailed, species-specific management strategy evaluation approach across a spatial extent comparable to Lake Michigan, nor have they explicitly considered the implications of barrier removals in a coupled management system with trade-offs. With sufficient demographic information, this approach could be applied to other species of migratory fishes where management is implemented at local scales but could potentially affect larger metapopulations. Protection of ecosystems from invasive species and restoration of ecological connectivity in lotic systems are two of the most important issues facing fishery managers in the Great Lakes and elsewhere. Although focused on the former, the approach detailed in this report illustrates a tool of potential utility for the challenge of reconciling these two issues.

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Tables

Table 1. Illustration of the simulated Grand River barrier removal scenarios (Fig. 7). The two habitat use alternatives (*i.e.*, 10%, 50%) were run for each of the four management scenarios below, while simulations evaluating the effect of an increasing control budget were run only for Scenario #1.

Scenario	Treat habitat above Sixth Street Dam?	Allow infestation of Looking Glass River?	Assumed habitat use
1	Yes	No	10%
			50%
2	No	No	10%
			50%
3	Yes	Yes	10%
			50%
4	No	Yes	10%
			50%

Figure Captions

Figure 1. Conceptual diagram for the sea lamprey MSE model. Solid and dashed lines indicate component linkages within and among the individual biological, observational, and management models, respectively.

Figure 2. Map of the Grand River mainstem (a) and the modeled Grand River system between the Sixth Street Dam and North Lansing Dam (b). Only those tributaries in (b) identified as “New Grand River Treatment Units” were explicitly considered in the simulations, and the numbers correspond to numbered treatment unit names in Table S1. River flowline data were obtained from the National Hydrography Dataset Plus (Bondelid et al. 2010) and state boundary lines were obtained from ESRI and TomTom North America, Inc.

Figure 3. Adult sea lamprey abundance trends with increasing habitat availability, assuming habitat is added within a single treatment unit. High and low spawner allocation and recruitment potential refer to the assignment of streams as northern or southern streams and regular or irregular producers, respectively. Boxes, whisker bars, and open circles represent the 25th and 75th, 10th and 90th, and 5th and 95th percentiles of simulated adult abundances, respectively. Solid horizontal lines and black circles represent corresponding median and mean values, respectively, and the gray squares indicate proportions of simulations with abundances greater than the status quo 90th percentile.

Figure 4. Adult sea lamprey abundance trends with increasing habitat availability, assuming habitat is added as independent treatment units. Boxes, whisker bars, and open circles represent

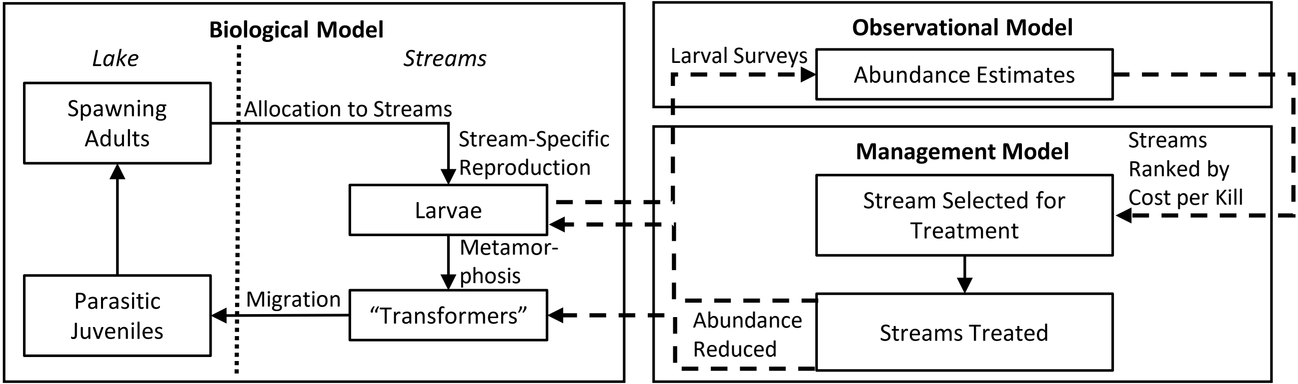
the 25th and 75th, 10th and 90th, and 5th and 95th percentiles of simulated adult abundances, respectively. Solid horizontal lines and black circles represent corresponding median and mean values, respectively, and the gray squares indicate proportions of simulations with abundances greater than the status quo 90th percentile. The asterisk indicates mean lamprey abundance from Scenario #1 of the Grand River case study, with an assumed 10% habitat use (see Figure 7).

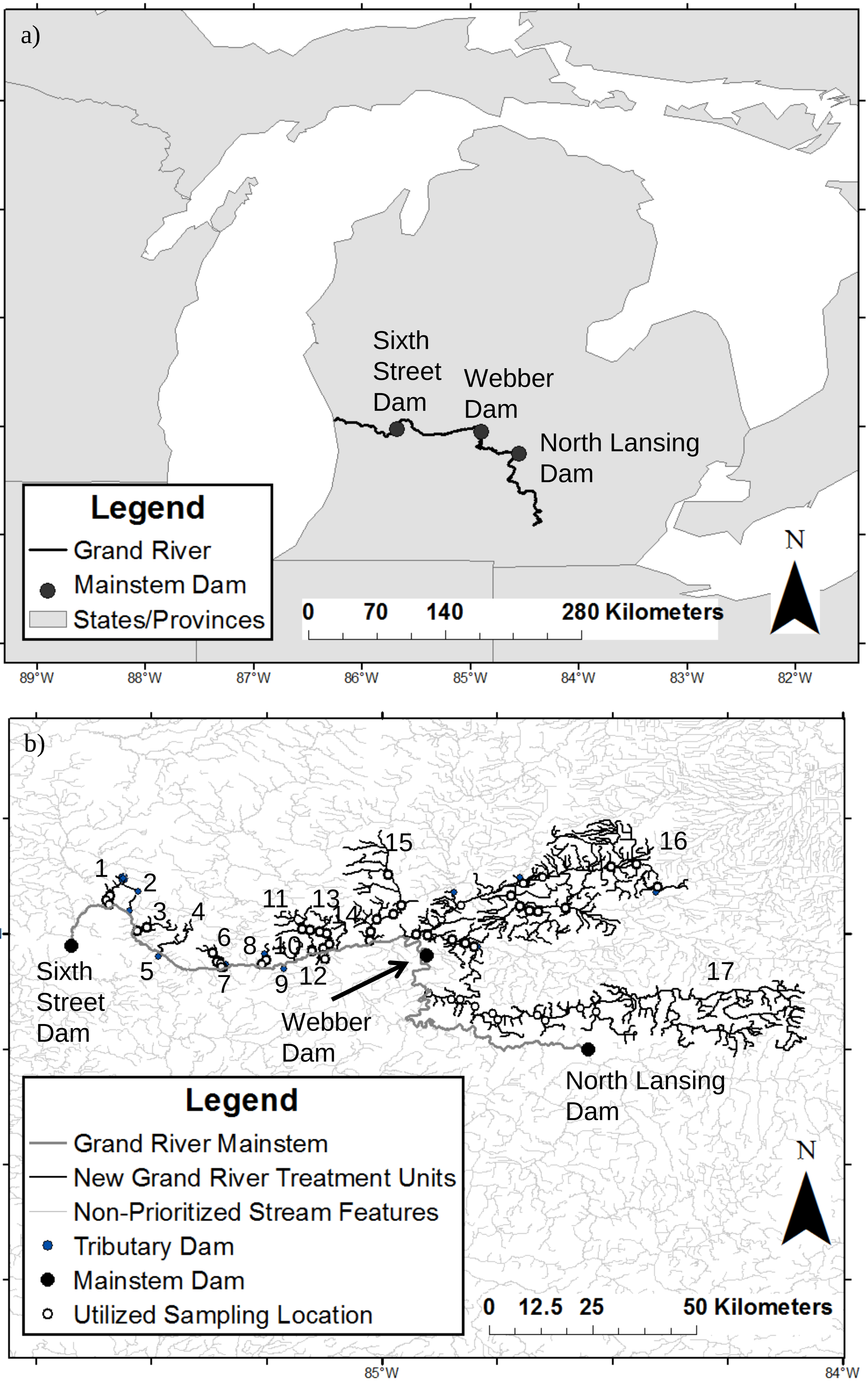
Figure 5. Changing model characteristics with increasing habitat. Lines and polygons represent the median and 10th and 90th percentiles, respectively, across all simulations (a, b) or treatment units (c). The dashed line and lighter polygon illustrate the effect of adding a single, large unit, and the solid line and darker polygon illustrate the addition of habitat as multiple, discrete treatment units, respectively.

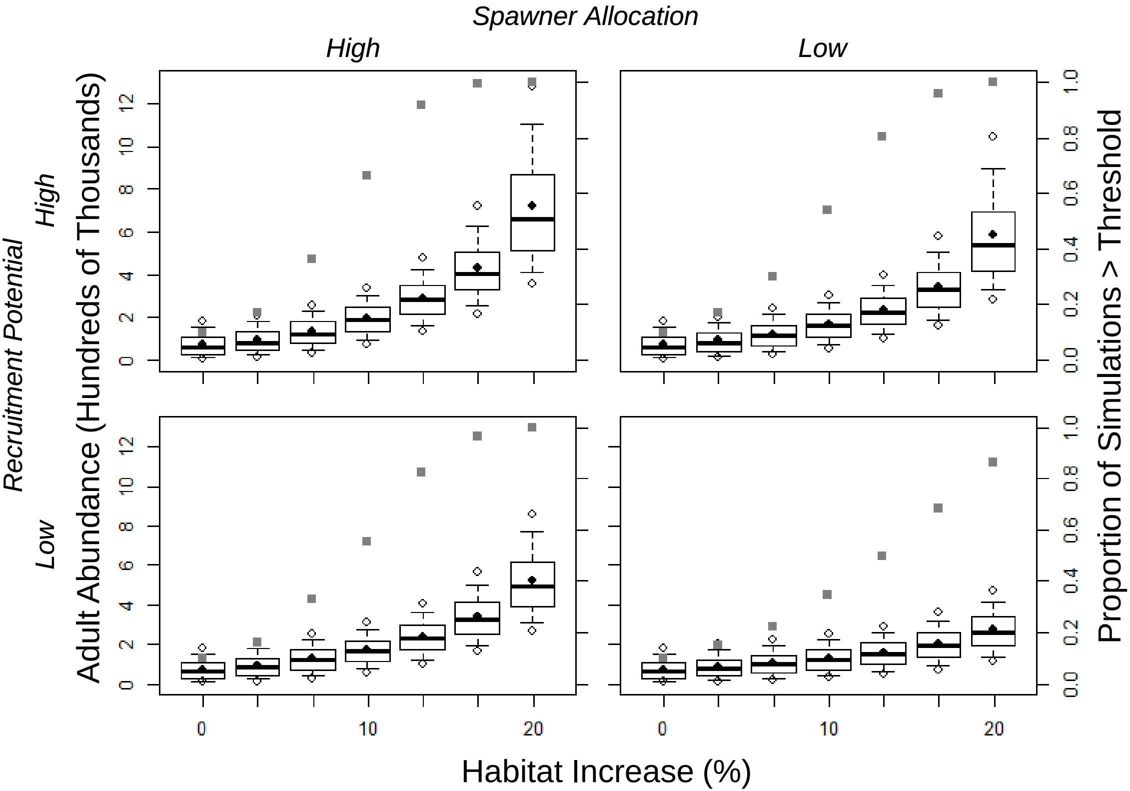
Figure 6. Average annual budget expenditure on the original treatment units with increasing habitat availability. The dashed and solid lines illustrate the response when habitat is added as a single, ever-larger system and multiple, discrete treatment units, respectively.

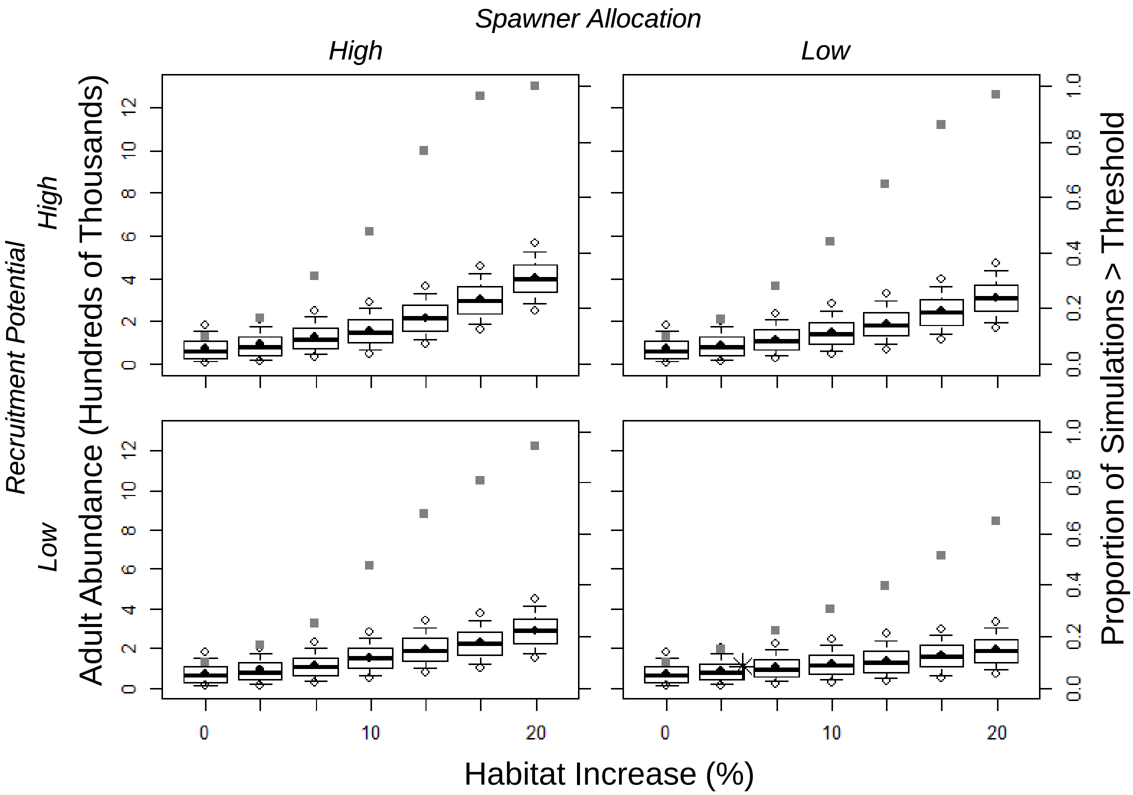
Figure 7. Expected sea lamprey abundances for each of the management scenarios. Scenarios #1 and #2 exclude the Looking Glass River, while Scenarios #3 and #4 account for its influence. New treatment units are treated by the SLCP in Scenarios #1 and #3, and ignored in Scenarios #2 and #4. Boxes, whisker bars, and open circles represent the 25th and 75th, 10th and 90th, and 5th and 95th percentiles of simulated adult abundances, respectively. The solid horizontal lines and black circles represent median and mean values, respectively. Numbers above the upper whisker bars indicate the proportion of simulations greater than the status quo 90th percentile.

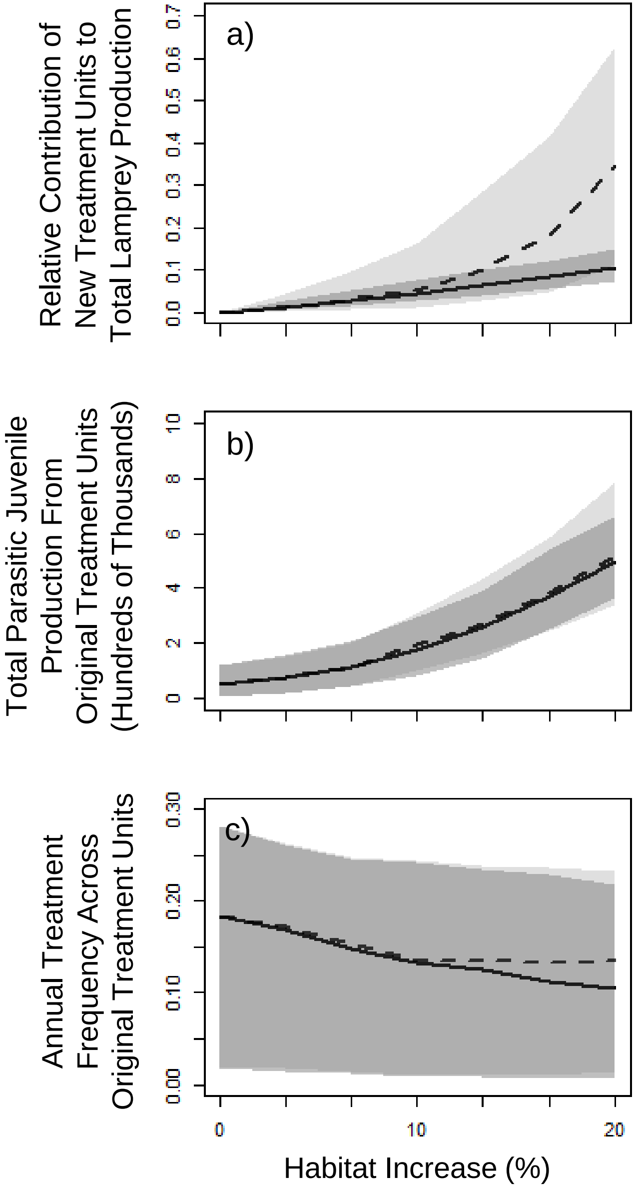
Figure 8. Expected sea lamprey abundances when the Sixth Street Dam is removed, the Webber Dam is modified to block sea lamprey, lamprey are assumed to use 10% (a) or 50% (b) of maximum potential river length, and the new treatment units are allocated control efforts with a steadily increasing Lake Michigan control budget. Boxes, whisker bars, and open circles represent the 25th and 75th, 10th and 90th, and 5th and 95th percentiles of simulated adult abundances, respectively. The solid horizontal lines and black circles represent median and mean values, respectively.

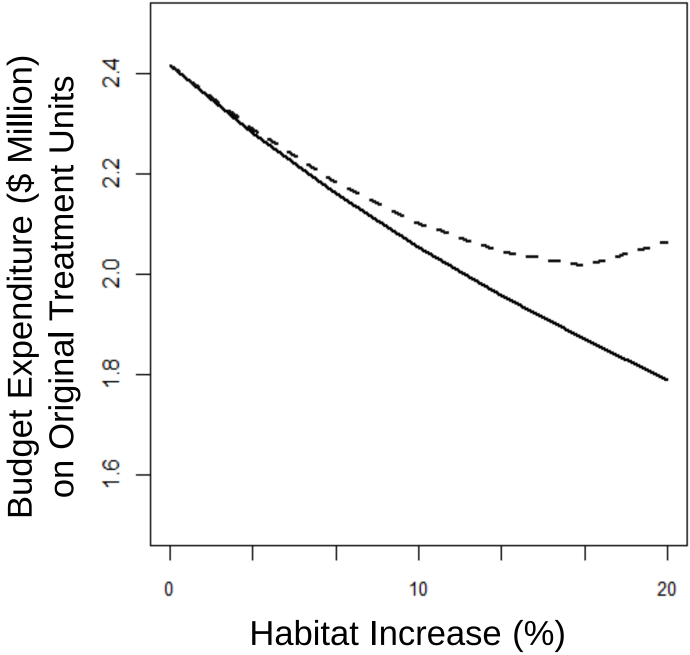

Biological Model
Lake
Streams
Spawning Adults
Allocation to Streams
Stream-Specific Reproduction
Larvae
Metamorphosis
Parasitic Juveniles
Migration
"Transformers"
Observational Model
Larval Surveys
Abundance Estimates
Management Model
Streams Ranked by Cost per Kill
Stream Selected for Treatment
Abundance Reduced
Streams Treated

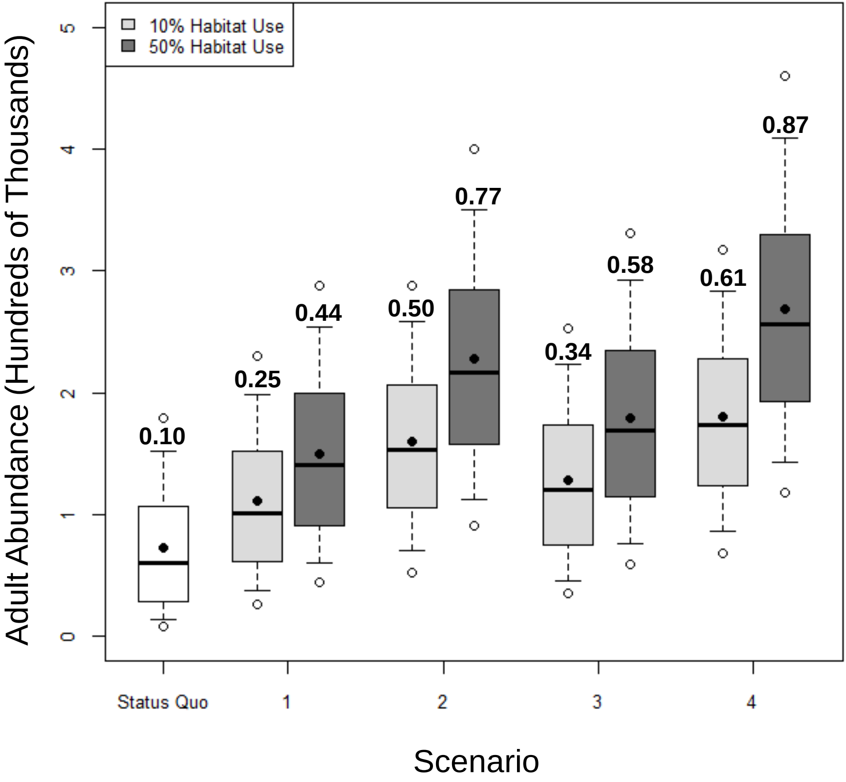

a)
46°N
45°N
44°N
43°N
42°N
41°N
89°W
88°W
87°W
86°W
85°W
84°W
83°W
82°W
Sixth Street Dam
Webber Dam
North Lansing Dam
Legend
Grand River
Mainstem Dam
States/Provinces
0 70 140 280 Kilometers
N
b)
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
43°N
85°W
84°W
Sixth Street Dam
Webber Dam
North Lansing Dam
Legend
Grand River Mainstem
New Grand River Treatment Units
Non-Prioritized Stream Features
Tributary Dam
Mainstem Dam
Utilized Sampling Location
0 12.5 25 50 Kilometers
N

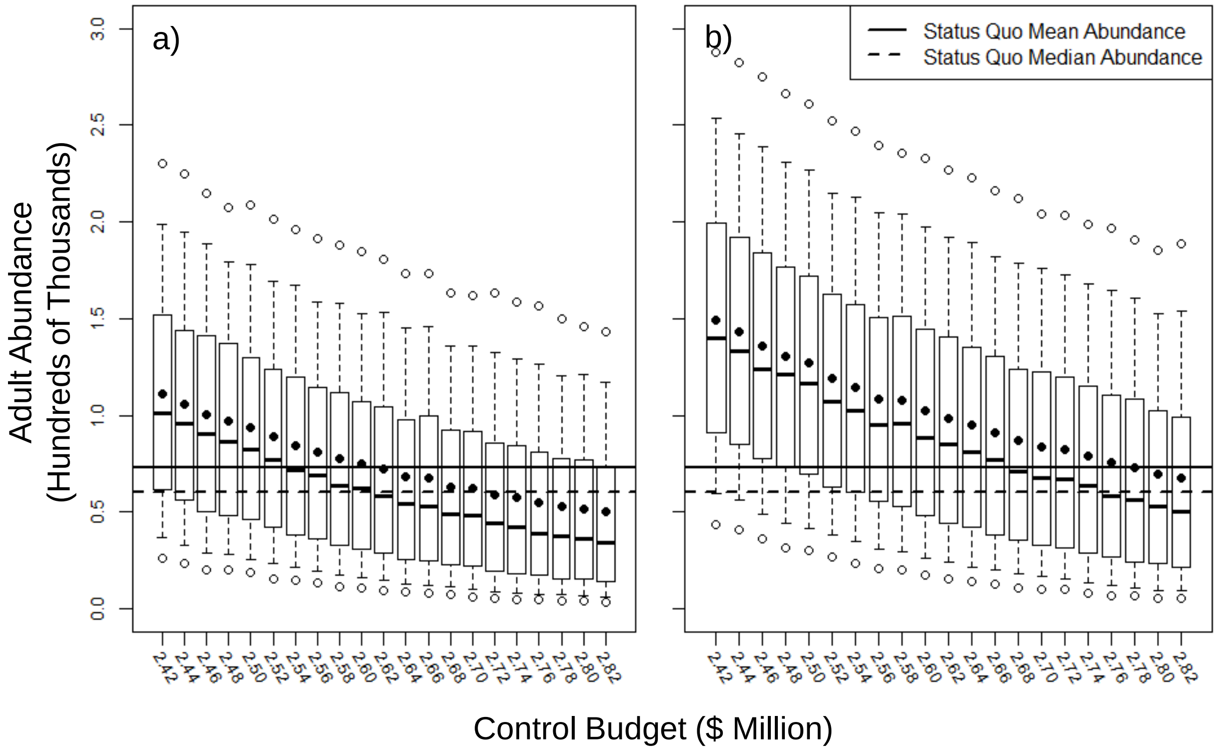

Spawner Allocation
High
Low
Recruitment Potential
High
Low
Adult Abundance (Hundreds of Thousands)
0
2
4
6
8
10
12
Proportion of Simulations > Threshold
0.0
0.2
0.4
0.6
0.8
1.0
0
10
20
Habitat Increase (%)


Spawner Allocation
High
Low
Recruitment Potential
High
Low
Adult Abundance (Hundreds of Thousands)
Proportion of Simulations > Threshold
0
2
4
6
8
10
12
0.0
0.2
0.4
0.6
0.8
1.0
0
10
20
Habitat Increase (%)


Relative Contribution of New Treatment Units to Total Lamprey Production
a)
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
Total Parasitic Juvenile Production From Original Treatment Units (Hundreds of Thousands)
b)
0
2
4
6
8
10
Annual Treatment Frequency Across Original Treatment Units
c)
0.00
0.10
0.20
0.30
0
10
20
Habitat Increase (%)


Budget Expenditure ($ Million)
on Original Treatment Units
2.4
2.2
2.0
1.8
1.6
0
10
20
Habitat Increase (%)


10% Habitat Use
50% Habitat Use
Adult Abundance (Hundreds of Thousands)
0
1
2
3
4
5
0.10
0.25
0.44
0.50
0.77
0.34
0.58
0.61
0.87
Status Quo
1
2
3
4
Scenario


a)
b)
Status Quo Mean Abundance
Status Quo Median Abundance
Adult Abundance
(Hundreds of Thousands)
0.0
0.5
1.0
1.5
2.0
2.5
3.0
2.42
2.44
2.46
2.48
2.50
2.52
2.54
2.56
2.58
2.60
2.62
2.64
2.66
2.68
2.70
2.72
2.74
2.76
2.78
2.80
2.82
Control Budget ($ Million)