Title

Minimizing opportunity costs to aquatic connectivity restoration while controlling an invasive species

Abstract

Controlling invasive species is critical for conservation but can have unintended consequences for native species and divert resources away from other efforts. This dilemma occurs on a grand scale in the North American Great Lakes, where dams and culverts block tributary habitat access for desirable fish species and are also a lynchpin of long-standing efforts to limit ecological damage inflicted by invasive, parasitic sea lamprey. Habitat restoration and sea lamprey control create conflicting goals for managing aging infrastructure. Here, we use optimization to minimize opportunity costs to habitat gains for 37 desirable migratory fishes that arise from restricting sea lamprey access (0-25% increase) when selecting barriers for removal under a limited budget ($1-105M). Imposing limits on sea lamprey habitat reduces gains in tributary access for desirable species by 15-50% relative to an unconstrained scenario. Working around a sea lamprey access cap is costly for 30 of 37 species (e.g., an additional $20-80M for lake sturgeon), and often requires ≥5% increase in sea lamprey access to be feasible. Narrowly distributed species exhibit the highest opportunity costs, but also benefit more at lower cost from allowing small increases in sea lamprey access. Our results illustrate the value of optimization for limiting opportunity costs when balancing invasion control against restoration benefits for diverse desirable species. Such tradeoff analyses are essential for expanded efforts in the conservation community to restore connectivity within fragmented rivers without unleashing invaders.

Key-words

culverts, dams, spawning, invasive species control, spatial conservation planning, optimization, sea lamprey

Introduction

Construction of dams and road crossing structures is widely viewed as a profound threat to riverine animals. These barriers can prevent fish and other species from accessing critical habitat for breeding or feeding (Fuller et al. 2015), leading to growing desire to remove barriers. However, these same barriers can be important to blocking the spread of aquatic invasive species (Fausch et al. 2009; Vélez-Espino et al. 2011). Thus, removing barriers can give rise to conflicts between conservation goals (Peterson et al. 2008; Kopf et al. 2017). Identifying balanced sets of barrier removals is further complicated by variation in the life history needs and conservation status of affected species, the configuration of river networks and barriers, and funding constraints. In any river network with more than a few dozen barriers, such a problem requires sophisticated optimization techniques that can assist decision making by quantitatively comparing the consequences of barrier removal combinations (King et al. 2017).

Both species invasions and river fragmentation are key conservation challenges from local to global scales but are generally considered separately. Human-mediated biological invasions are a leading contributor to species declines and extinctions in aquatic ecosystems (Harrison & Stiassny 2004) and also alter ecosystem processes (Vander Zanden et al. 2016) and service provisioning (Pejchar & Mooney 2017). Mitigating the effects of invasive species can be costly (Zavaleta 2000; Olson & Roy 2002), so controlling them preemptively is ideal. As dams and road culverts have proliferated worldwide (Laurance et al. 2014; Grill et al. 2015), these barriers have sometimes fostered species invasions by shifting water temperatures and creating standing water habitats (Closs et al. 2015). Barriers fragment river networks, alter flow dynamics, sediment transport, and nutrient cycling (Closs et al. 2015) and hinder animal movement (Fuller et al. 2015). Man-made barriers that inhibit dispersal of native species within river networks also inhibit expansion of harmful invaders, thereby protecting economically valuable or endangered native species (Fausch et al. 2006; Scott et al. 2010). Concerns about both connectivity and infrastructure degradation have spurred efforts to remove barriers from rivers (Doyle et al. 2008), but consequent increased invasion risk is rarely considered simultaneously.

Tradeoffs between connectivity restoration and invasion control are exemplified by management of thousands of tributary rivers flowing into the North American Great Lakes. Of 42 native and commercial migratory fishes (McLaughlin et al. 2006; Landsman et al. 2011; Moody et al. 2017), many have suffered from overfishing, habitat degradation, and loss of access to breeding habitat. Species invasions, most prominently the parasitic sea lamprey(Limburg & Waldman 2009), have further pressured desirable fishes. Sea lamprey (*Petromyzon marinus*) were introduced to the Great Lakes in the early 1900s and subsequently contributed to the collapse of several fisheries, including lake trout (*Salvelinus namaycush*), whitefish (*Coregonus clupeaformis*), and cisco (*Coregonus* spp.) and reduction of burbot (*Lota lota*), walleye (*Sander vitreus*), and rainbow trout (*Oncorhynchus mykiss*) populations in all five Great Lakes (Hubbs & Pope 1937; Smith & Tibbles 1980). Consequently, Great Lakes sea lamprey are the focus of one of the world’s largest and oldest invasive species control programs. To suppress sea lamprey populations to a fraction of historical levels (Sullivan et al. 2015; Hansen et al. 2016), annually this program spends millions of dollars on chemical lampricides (Great Lakes Fishery

Commission 2008) and construction and maintenance of barriers (Lavis et al. 2003). Seasonal trapping is used to assess spawning-phase sea lampreys while also reducing reproductive success in trapped streams (Heinrich et al. 2003; Jones et al. 2009), and researchers continue to work on pheromone attractants and repellents and selective fish passage structures. These experimental technologies may one day enable full removal of tributary barriers without enhancing sea lamprey populations but are not currently viable alternatives to migration barriers and lampricides.

Over recent decades, interest in connectivity restoration has led to removal of dozens of dams and replacement of hundreds of road culverts. Some such projects were paid for by the $1.7B U.S. Great Lakes Restoration Initiative between 2010-2017 (Great Lakes Restoration Initiative 2017), with the specific goal of restoring aquatic organism passage (Burroughs et al. 2010; Bunt et al. 2012). These underscore the need to strategically assess potential barrier removals in a way that maximizes habitat available to desirable species while also minimizing habitat available to harmful sea lamprey (McLaughlin et al. 2007). A few previous studies have addressed this balance, but without explicitly accounting for the biogeography and diversity of beneficiary species (Zheng et al. 2009; Vélez-Espino et al. 2011).

In this paper, we quantify the tradeoffs between habitat gains for desirable migratory fishes versus sea lamprey during connectivity restoration in Great Lakes tributaries. Specifically, we first assess the degree to which limiting access for sea lamprey to spawning habitat affects the ability to restore access for 37 desirable species. Second, we evaluate whether such opportunity costs can be overcome by paying a premium for removals that avoid sea lamprey habitats. We use a basin-wide barrier removal optimization model that maximizes accessibility-weighted habitat for individual desirable species while limiting access for sea lamprey. We conclude with recommendations for decision makers faced with situations where restoration has both positive and negative consequences for conservation.

Materials and methods

Great Lakes Tributary Connectivity

This analysis was conducted with the same 1:100,000-scale tributary hydrography and barrier datasets described in Moody et al. (2017). Historical access to Great Lakes tributaries is limited by an estimated 4,417 dams and 99,936 road crossings, resulting in only 15% of potential stream habitat (2,082 km^2) being accessible to migratory fishes after accounting for partially-passable barriers (Neeson et al. 2015). We defined the gain in habitat access resulting from barrier removal as the increase in accessibility-weighted tributary area for fish migrating upstream from the Great Lakes (O'Hanley & Tomberlin 2005; Zheng et al. 2009). Cumulative accessibility of a stream reach for a fish was defined as the probability that a fish can bypass all downstream barriers and calculated as the product of passabilities of those barriers (O'Hanley & Tomberlin 2005). Consequently, it also reflects the expected fraction of a migrating population that can access the full reach beyond the barrier. For example, a 1-km^2 section of stream above a series of two road culverts that each has passability 0.5 for species X would have an accessibility-weighted area of 0.25 km^2 – 25% of fish species X would be able to use 100% of the habitat - which would increase to 0.5 km^2 (and 50% of fish species X) if one of these two culverts were replaced. The intent is to approximate the total potential use of upstream habitat given a set of downstream barriers. Since most dams lack specialized fish-passage structures – though see Hatry et al. (2013) for a treatment of Canadian structures - and have either unknown height or exceed the height that desirable fish can jump, all dams were assigned a passability of zero. Culvert passability was calculated as the product of (1) the probability that a culvert's downstream end is perched above the receiving stream level (and is thus impassable to most, non-jumping fish), and (2) the probability that the water velocity in the culvert exceeds a fish's sustainable swimming speed (Januchowski-Hartley et al. 2014). Moody et al. (2017) assigned each species to one of three guilds based on adult sustained swimming speed, so every culvert has three guild-associated passability values. Removing a dam or replacing a culvert increases access to upstream habitat by changing that barrier's passability to one, which also increases the cumulative passability of upstream barriers.

We focused on 37 native or introduced desirable migratory fish species that vary in their historical range as well as their overlap with sea lamprey (Figure 1 and Figure 2). Species ranges were estimated at the watershed scale using historical point observations collated from over thirty data sources including fishery surveys, bioassessments, and museum records for every state and province in the basin (Khoury et al. 2018). Data points further than 100 m from a channel were verified. Any tributary in which ≥1-point observations of a species occurred was considered potential habitat for that species. No species will spawn in all accessible parts of a tributary, so our potential habitat estimates are liberal but must suffice given the lack of systematic assessment of migration patterns and microhabitat needs. The tributary habitat area affected by a particular barrier was calculated by summing the area of all reaches (Moody et al. 2017) beyond the focal barrier weighted by the estimated passability of each upstream barrier until reaching the river terminus. This includes both mainstem and all tributary reaches. Reach area was calculated as reach length multiplied by bankfull width estimated from a drainage area regression (Wilkerson *et al.* 2014).

Costs of replacing culverts with 'fish friendly' structures were based on estimates of replacement materials (e.g., culvert structure, fill, road resurfacing) and labor (Neeson *et al. unpublished*). Cost components were derived from the Michigan Department of Transportation's 2015 schedule of pay items (Michigan Department of Transportation 2017). The width of each structure was derived by estimating bankfull width from a drainage area regression (Wilkerson et al. 2014). Road crossing structure type was determined by road type and stream bankfull width. Interstate, highway, and urban roads use concrete structures, rural roads use metal structures, and all crossings use the lowest cost structure that meets material and size requirements. Dam removal costs were modeled using a height-cost relationship fitted using inflation-adjusted data for 108 recent removals (Neeson et al. 2015). Dams without height data (23%) were assigned the median cost of all dams in the basin for which empirical cost data were available.

Barrier Removal Optimization

To maximize habitat access for desirable species while limiting access for sea lamprey, we modified the optimization presented in Neeson et al. (2015), in which barriers are chosen for "removal" to maximize the accessibility-weighted habitat for a single target species, subject to a removal budget constraint. Here we add a constraint on the total accessibility-weighted habitat for sea lamprey, of the form

$$H(X) = \sum_{j=1}^{|J|} h_j \pi_j(X) \leq u$$

where J is the set of all barriers, indexed by j, $\pi_j(X)$ is the cumulative passability for sea lamprey at barrier j, which is a function of the binary vector of barrier removal decisions X, h_j is the net amount of habitat (km^2) above barrier j (to the next set of upstream barriers), and u is the cap –

an upper bound – on accessibility-weighted habitat for sea lamprey. In this way, accessibility-weighted habitat for both sea lamprey and desirable species changes with every proposed barrier removal. The algorithm searches over all feasible sets of removals to find the one that maximizes accessibility-weighted habitat for desirable species while satisfying the cap on accessibility-weighted habitat for sea lamprey. The optimization model was coded using General Algebraic Modeling System (GAMS) v24.7.3 and solved using the CPLEX mixed integer linear programming solver with an optimality tolerance of 1%.

To avoid excessive memory usage, the addition of a cap on sea lamprey access required us to add a pre-analysis filtering process to the optimization workflow (Supporting Information, SI). Barriers that had little potential to increase desirable access, were expensive to remove, or resulted in large increases for sea lamprey access relative to the cap were excluded as candidates for removal. Preliminary models indicated that this filtering did not affect the ability of the model to discover a near-optimal set of barrier removals.

Policy scenarios

We explored several scenarios to understand the opportunity costs from capping sea lamprey access to tributary habitat. Two idealized scenarios illustrate the range of opportunity costs. The first is a "no-cap" scenario that allows any level of sea lamprey access and reflects the maximum amount of habitat that could be restored for a species and budget. While this scenario represents an unrealistic policy, it serves as an important reference point. The second, "no-increase" scenario places a strict limit of no new sea lamprey access. This is a best-case scenario for sea lamprey control when focusing exclusively on barrier removals, and most closely reflects the current policy of the Great Lakes Fishery Commission. Between these two extremes, we explored a range of compromise scenarios, including 5, 10, 15, 20, and 25% increases in sea lamprey access over current, basin-wide accessibility-weighted habitat. These scenarios represent a spectrum of potential options that could guide management of connectivity in the future. Scenarios were analyzed over a range of removal budgets: 1, 3, 6, 10, 15, 21, 28, 36, 45, 55, 66, 78, 91, and 105 million US$. Non-uniform budget increments were chosen to resolve the shapes of return-on-investment curves at low budgets.

Additional metrics were derived from core results. First, we estimated opportunity cost by calculating the difference in accessibility-weighted habitat between the no-cap scenario and each of the sea lamprey access-cap scenarios. This value represents the reduced potential to restore habitat access for a desirable species imposed by the sea lamprey cap beyond that imposed by budget constraints. Second, we estimated Pareto-style tradeoffs between increased access for desirable species and limits on sea lamprey access. Third, we estimated the additional budget required to overcome the opportunity cost by calculating the difference in budget to achieve a target accessibility-weighted habitat under no-cap versus sea lamprey cap scenarios.

Results

Opportunities for restoring habitat access for desirable migratory fish are strongly controlled by both the barrier removal budget and sea lamprey access cap (Figure 3). Currently, each migratory fish species can access an average of 115 km^2 (95% CI = 10 km^2) of tributary habitat across the basin. Under a no-cap scenario, this access could be tripled for $14M. However, barrier removals offer diminishing returns. For instance, further increasing accessible habitat to 550 km^2 would cost a total of $80M. Individual species vary in both current habitat access and relative gains from barrier removals (Table S1). At one extreme, mooneye (*Hiodon tergisus*) currently has 19 km^2 of accessibility-weighted habitat in the basin. For $15M, access to 96 km^2 of its 235 km^2

potential range could be restored under a no-cap scenario. At the other extreme, yellow perch (*Perca flavescens*) would require $65M for a proportionally similar increase beyond its current 228 km^2.

Opportunity costs of a sea lamprey access cap

Capping sea lamprey access imposes limits on opportunities for restoring habitat access across species. Doubling current average access per species (115 km^2) would cost $8-16M depending on the strictness of the cap (Figure 3). Tripling access, achievable for $14M under a no-cap scenario, would require both a ≥20% increase in sea lamprey access and a budget of at least $78M. Incremental cap increases can enhance access for most desirable species. Interactive effects of budget level and lamprey constraints diminished at larger budgets; for instance, any two scenarios with a cap are equidistant beyond $20M budget (Figure 3). Except for three species – mooneye, bigmouth buffalo (*Ictiobus cyprinellus*), and river darter (*Percina shumardi*) – individual species results were qualitatively like the average. For these three species, ≥5%-cap scenarios would boost their access close to the no-cap scenario (Table S1).

Comparing the no-cap to other scenarios revealed that average opportunity costs to desirable species of capping sea lamprey access increased disproportionately fast as the strictness of the lamprey cap tightened (Figure 3). At relatively low budgets (<$5M), this opportunity cost grew quickly to 10-30% beyond the no-cap scenario. This growth slowed at larger budgets; at $105M, a no-increase cap on sea lamprey access resulted in an opportunity cost of 53% relative to the no-cap scenario. Conversely, incrementally relaxing the cap from a no-increase starting point led to reduced opportunity cost, but relaxation beyond the initial 5% had a constant effect (i.e., in Figure 3 distances between curves above 5% are constant). This is likely due to the high spatial overlap of species with sea lamprey, such that an increase in sea lamprey access beyond

5% results in a similar increase in desirable species access. However, some species exhibited qualitative differences from the average. For example, river darter exhibited an opportunity cost of 80% at $20M under a no-increase scenario, but that could be reduced to 30% under a 5%-increase scenario (Table S1).

Importantly, narrowly distributed species exhibited higher opportunity costs from limiting sea lamprey access, and conversely gained proportionally more from relaxing the cap (Figure 2 fourth chart, Table S1). At one extreme, mooneye exhibited an opportunity cost of 83% at $105M under a no-increase scenario, while relaxing the cap to 15%-increase would reduce the opportunity cost to 2%. At the other extreme, white sucker's opportunity cost under the same scenarios only would change from 40% to 37%, respectively.

There were clear tradeoffs between the goals of increasing access for desirable species relative to current (at $0) levels versus reducing sea lamprey access relative to the no-cap scenario (Figure 4). At any budget, relaxing the cap benefitted desirable species and sea lampreys roughly proportionately (Figure 4, curves have slopes near -1). Spending more improved the relative efficiency of achieving both goals (Figure 4, increasing values with budget), but gains in habitat access for desirable species were achieved more quickly (Figure 4, slopes of curves are more negative at larger budgets).

Between the no-cap and no-increase scenarios, the geography and number of barriers recommended for removal shifted (Figure S1). At $105M, more barriers were removed in the no-cap scenario (average ± 95%-CI over species = 339 ± 14) versus the no-increase scenario (298 ± 33). Barrier removals were more spatially concentrated in the no-increase scenario (number of watersheds with ≥1 removal: 30.8 ± 6.9 versus 44.1 ± 5.9) as the model avoided watersheds known to be used by sea lamprey. Under the no-cap, $105M scenario, barrier removals were concentrated in the Fox (Lake Michigan) and Trent (Lake Ontario) river watersheds (averaged 20% of removals across species). Under the no-increase scenario, barrier removals shifted to Fox and French (Lake Huron) river watersheds (31%).

Additional investment required to offset opportunity costs of a sea lamprey cap

Species varied in the cost of and degree to which supplementing the removal budget could offset opportunity costs from capping sea lamprey access (Figure 5). Two distinct patterns emerged. First, for seven study species with modest ranges (<1000 km^2; Figure 2), including American eel (*Anguilla rostrata*), mooneye, bigmouth buffalo, white bass (*Morone chrysops*), pink salmon (*Onchorynchus gorbuscha*), channel darter (*Percina copelandi*), and river darter, an additional investment of <$10M with some sea lamprey access cap could boost habitat access to 50% of that range of habitat access achieved in the no-cap scenario (e.g. Figure 5, top). For most of those species, the sea lamprey access cap would also need to be increased to 25%. For these seven species, it was costly or impossible to achieve much higher habitat access regardless of further spending, especially under the no-increase scenario.

Most of the remaining 30 species exhibited less potential to offset the effect of capping sea lamprey access, and high cost of doing so (Figure 5, bottom). For the state-listed lake sturgeon (*Acipenser fulvescens*), 250 km^2 habitat access could be achieved under the no-increase scenario at an additional $5M beyond the no-cap scenario. However, to reach 350 km^2 would cost an additional $20M-80M and require ≥5%-increase cap. Further increases in tributary access for lake sturgeon could not be achieved for any cost. Similar patterns were applicable to many broadly-distributed species.

Discussion

Ours is among the first studies to evaluate the collateral damage to numerous desirable species of controlling invasions at a large spatial scale. Controlling sea lamprey to protect desirable species has limited opportunities for cost-efficient restoration of habitat access for desirable migratory fish (Vélez-Espino et al. 2011). We found this approach resulted in an average 15-50% lower habitat gains for budgets ≥\$5M (Figure 3). Gains of desirable habitat access traded-off with reductions in sea lamprey access relative to a no-cap scenario at every budget and cap level, but this compromise could be reduced by spending more (Figure 4). For seven narrowly distributed species (Figure 2), >50% of this reduced restoration could be regained for <\$10M and increased sea lamprey access. In contrast, we found relatively little scope to offset opportunity costs for the other 30 species (Figure 5).

Many important Great Lakes fishes benefit from blocking sea lamprey access to tributaries (Landsman et al. 2011), but more species are impacted by lost access to tributary spawning grounds (Cheng et al. 2006; Burroughs et al. 2010). Our analyses are a step toward accounting for impacts of connectivity management on a broad range of migratory species, yet a comprehensive assessment would require demographic models based on current distributions of target species – we were limited to historical presence/absence data, value weightings of species, and accounting for other current (round goby, *Neogobius melanostomus*) and potential (silver carp, *Hypophthalmichthys molitrix*; bighead carp, *Hypophthalmichthys nobilis*) invaders of Great Lakes tributaries. Such a comprehensive approach is not possible because even the best-studied species' demographics are insufficiently understood. Thus, we assume that every species present benefits equally per additional unit of access anywhere in a tributary, even though we recognize that species' needs differ along tributary penetration, substrate, temperature, and other factors.

Summing benefits across all species in this study buffers against inability to use demographic models.

Our findings help to frame barrier removal decisions around questions of societal values. For example, is a 10% increase in habitat access for dozens of migratory fishes worth an accompanying 5% increase in sea lamprey access (Figure 4)? Resolving such issues will require difficult dialogue among parties with conflicting mandates. Our optimization models show that win-win solutions do exist but are limited in location and scope.

A no-increase scenario for sea lamprey access, a goal of the Great Lakes Fishery Commission and other fisheries agencies, would concentrate more removals in fewer watersheds. Such a strategy should boost local populations of desirable species that breed in those watersheds and could benefit recreational fishing. However, concentrating removals might cushion species less against environmental variation, stochastic demographic events, and overfishing (e.g. Schindler et al. 2010).

Restoring connectivity is expensive, may not increase resilience or population size (Mclaughlin et al. 2013), and consequences are neither uniformly positive nor certain (Smyth 2011) for all fishes. This is true even without accounting for complex interactions with species invasions. Moreover, maintaining fragmentation can separate hatchery from wild populations, prevent the spread of disease, and help fish avoid ecological traps (Rahel 2013). Some of these factors are surely at play for Great Lakes migratory fishes, resulting in overestimation of the aggregate benefits of increasing connectivity in our model. Though such complexities have been explored for certain well-studied species in specific tributaries (e.g. Smyth, 2011), it is unknown if this generalizes to other species and places. We have elected to focus on benefits for lack of information to guide a more refined approach.

Future studies could expand upon our approach by performing simultaneous planning across species. We focused on barrier removal optimizations to benefit a single species while capping sea lamprey access. Simultaneously planning across all 37 desirable species would suggest removals that maximize restoration of access for the entire group. Solving such models is computationally challenging and requires difficult decisions about weighting each species. Our approach informs conservation of particular priority species and offers a precursor to multispecies optimization if recommendations are compared or aggregated across species. We found sufficient disparities in species distributions to create complex trade-offs when maximizing restoration of habitat access (see also Vélez-Espino et al. 2011), such that one could achieve greater gains for any single species alone than the average of a joint-optimization. Such tradeoffs are unavoidable when the overall goal is to improve habitat access for all desirable species.

Including sea lamprey control strategies other than barrier management (Jones et al. 2015) were beyond the scope of this analysis but could improve outcomes. For instance, lampricide – lamprey-specific pesticide - application has helped reduce sea lamprey populations by >85% in most areas of the Great Lakes basin (Great Lakes Fishery Commission 2008). Complete eradication of sea lamprey from the Great Lakes is implausible (Mullett & Sullivan 2016), but the combination of existing dams, strategic application of lampricides, and selective passage structures that stop sea lamprey has proven effective in suppressing them (McLaughlin et al. 2007). Increased access for sea lamprey could trigger demographic feedback mechanisms leading to explosive population growth (Jones et al. 2003), making other controls more necessary. We are unable to account for demographic consequences on commercial and other desirable species from additional sea lamprey production. In addition, it is beyond the scope of this study to estimate potential lampricide application costs that might be used to suppress sea lamprey following barrier removals. Instead, we focus on locating sites where gains for desirable species can be accomplished while minimizing increases in sea lamprey without additional controls.

Species invasions will continue to threaten native biodiversity and desirable species for the foreseeable future. Our findings show how and why we must assess collateral damage from control. This consideration extends beyond aquatic connectivity in the Great Lakes, for instance to predator exclusions which may not be complete barriers and may prevent movement of non-target species (Hayward & Kerley 2009), or in myriad examples where biological or chemical control affects non-target species (Kettenring & Adams 2011; Kopf et al. 2017). Opportunity costs to restoration for desirable species are not trivial; there are few win-win options available in Great Lakes tributary connectivity management. We expect this to be the case generally when harmful invaders substantially overlap with beneficiaries. Great Lakes sea lamprey control will likely have to become increasingly reliant on non-barrier strategies, since aging infrastructure (Doyle et al. 2008), increased storm flows under a changing climate (Cherkauer & Sinha 2010), and benefits of aquatic connectivity (Moody et al. 2017) all favor barrier removal. Thus, systematic analyses of restoration options are more important than ever for balancing invasive species control with these other priorities to achieve ecologically and economically efficient outcomes.

Supporting Information

Details on barrier removal candidate filtering and spatial distribution of removals (Appendix S1) and table of species-level results (Table S1) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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Figure Legends

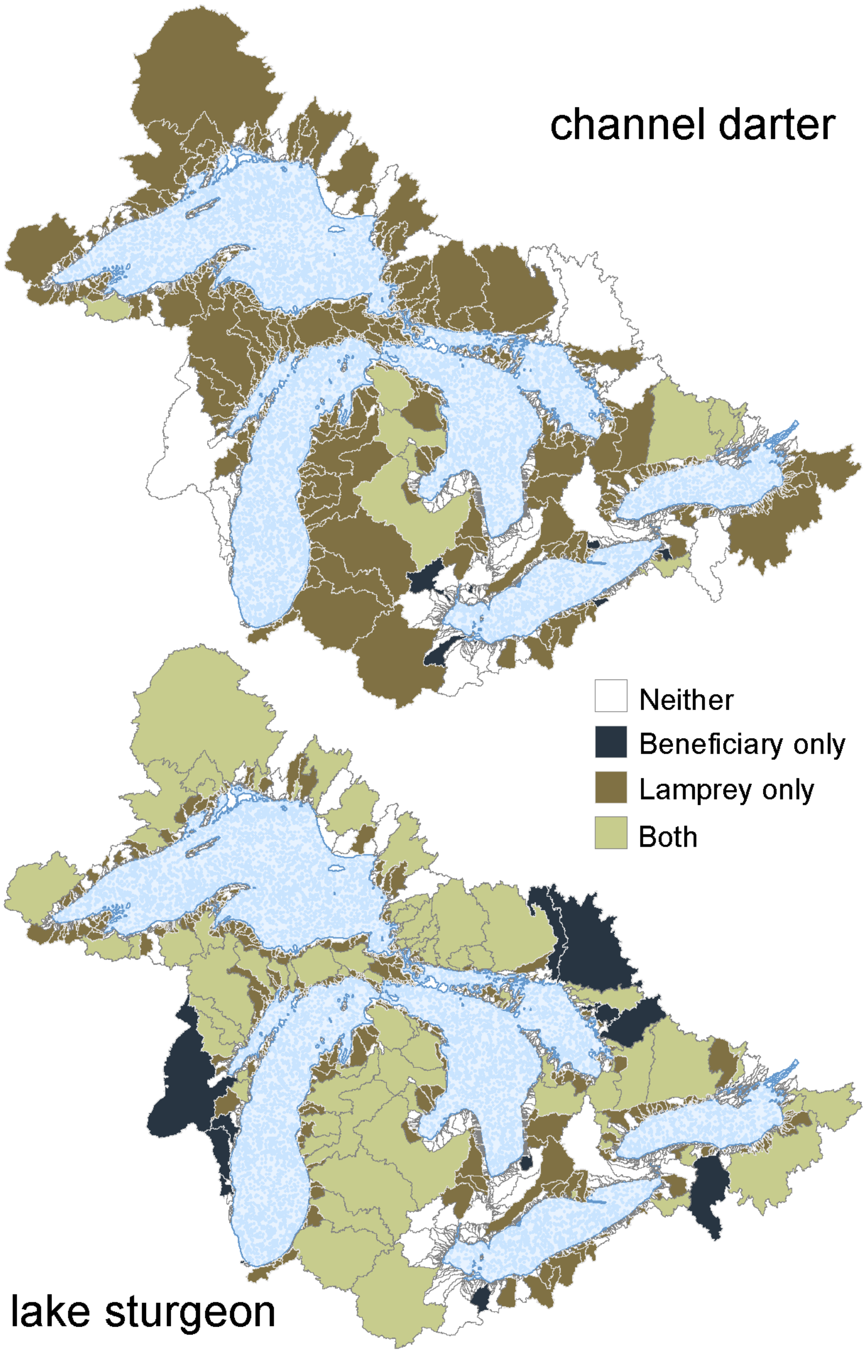
Figure 1. Ranges of two study species relative to sea lamprey. Ranges for all species, including sea lamprey, were derived from historical point observations and propagated to the entire catchment of the tributary of observation.

Figure 2. Species range data and example results of imposing a limit on sea lamprey access in the Great Lakes basin. From left to right: (1) "Range" is total potential accessible habitat if all barriers were removed, (2) "Overlap with sea lamprey" is percent of range shared by *Petromyzon marinus*, (3) "Unrealized potential gain" is opportunity cost to habitat access restoration incurred from a no-increase cap on sea lamprey access beyond the effect of budget given a $105M removal budget, and (4) "Cost to double access" describes the necessary removal budget beyond a no-cap scenario to double habitat access while limiting sea lamprey increase to 10%. *Petromyzon marinus* is bold to emphasize it is invasive and no optimizations were run to maximize its habitat access. Species preceded by * are non-native. Species with "Not Possible" were found to have no level of spending under the 10%-increase scenario that could offset the effect of a cap to double current habitat access.

Figure 3. Return-on-investment, averaged across species and 95%-CI. Curves between the extremes increase the sea lamprey access cap in increments of 5% over current levels. Circles are averages over all 37 single-species barrier-removal optimizations.

Figure 4. Tradeoff between (1) increasing desirable habitat access and (2) reducing sea lamprey access relative to no-cap scenario. Points are averaged (±95%-CI) over individual species results and joined along lines of the same budget. Right-most point on a curve is no-increase, and advancing left are 5% incremental increases in the cap.

Figure 5. Example species-specific costs of offsetting opportunity costs to desirable habitat access from capping sea lamprey access. Horizontal axis is target level of habitat access for species named in the upper-right. Vertical axis is additional budget required to achieve the same level of habitat access as the no-cap scenario. No-cap scenario is drawn for reference to show both zero additional cost and range of habitat access achieved for that species in our analyses (ranges from current access to no-cap access at $105M). Other curves, from left-to-right and top-to-bottom are 5%-increments of increasing caps on sea lamprey access. Curves are truncated to the left of the no-cap scenario since under various caps species could only achieve a fraction of the no-cap scenario's habitat access regardless of cost.



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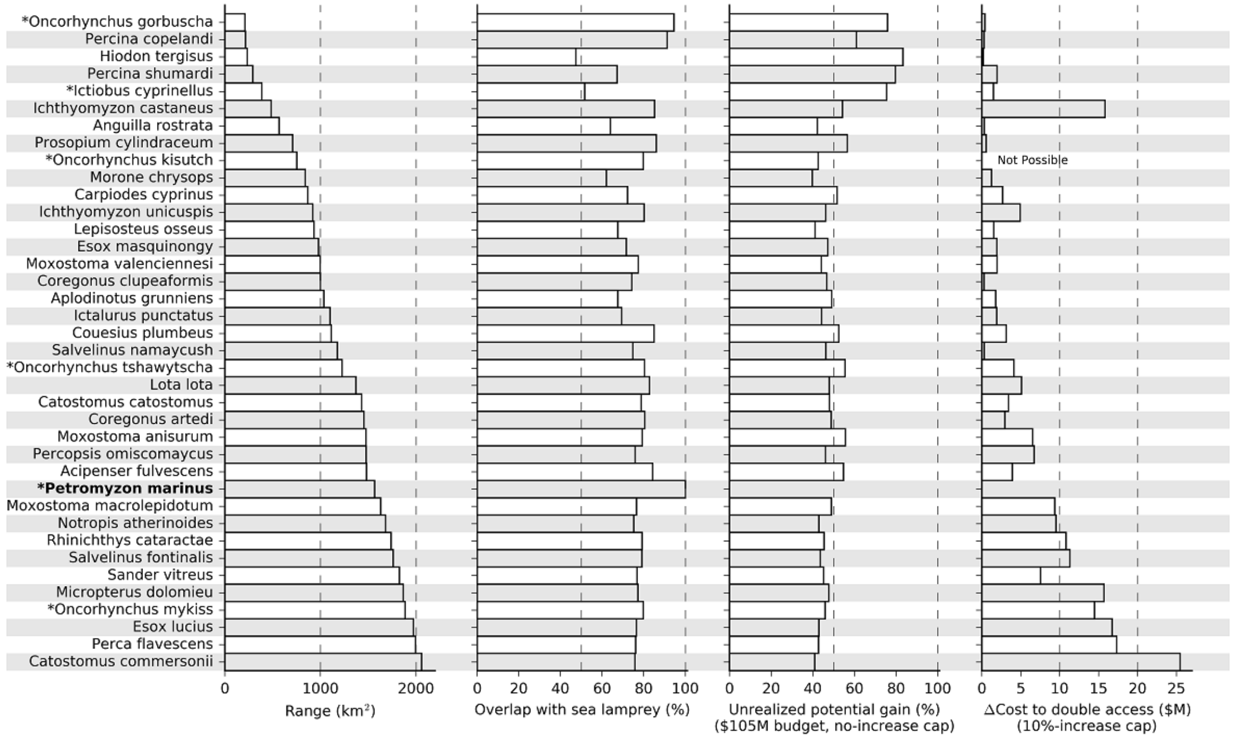

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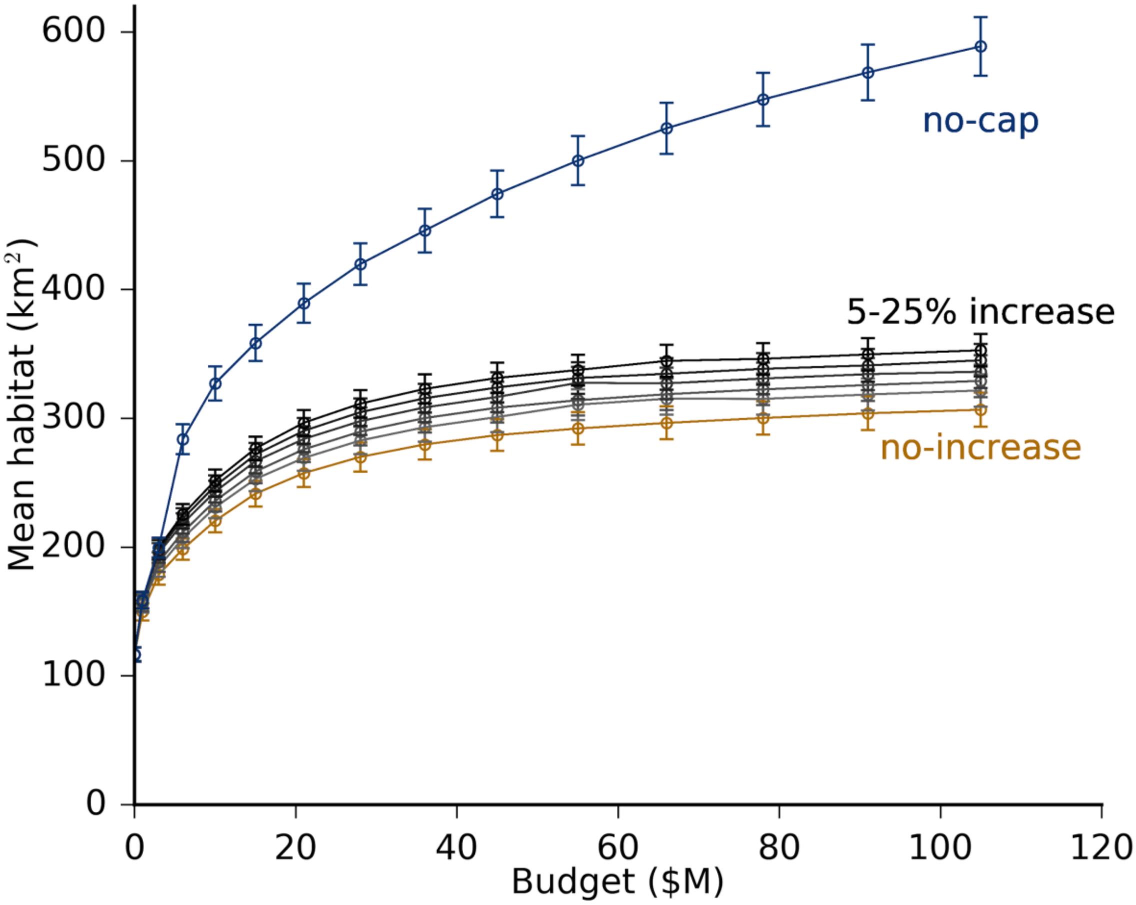

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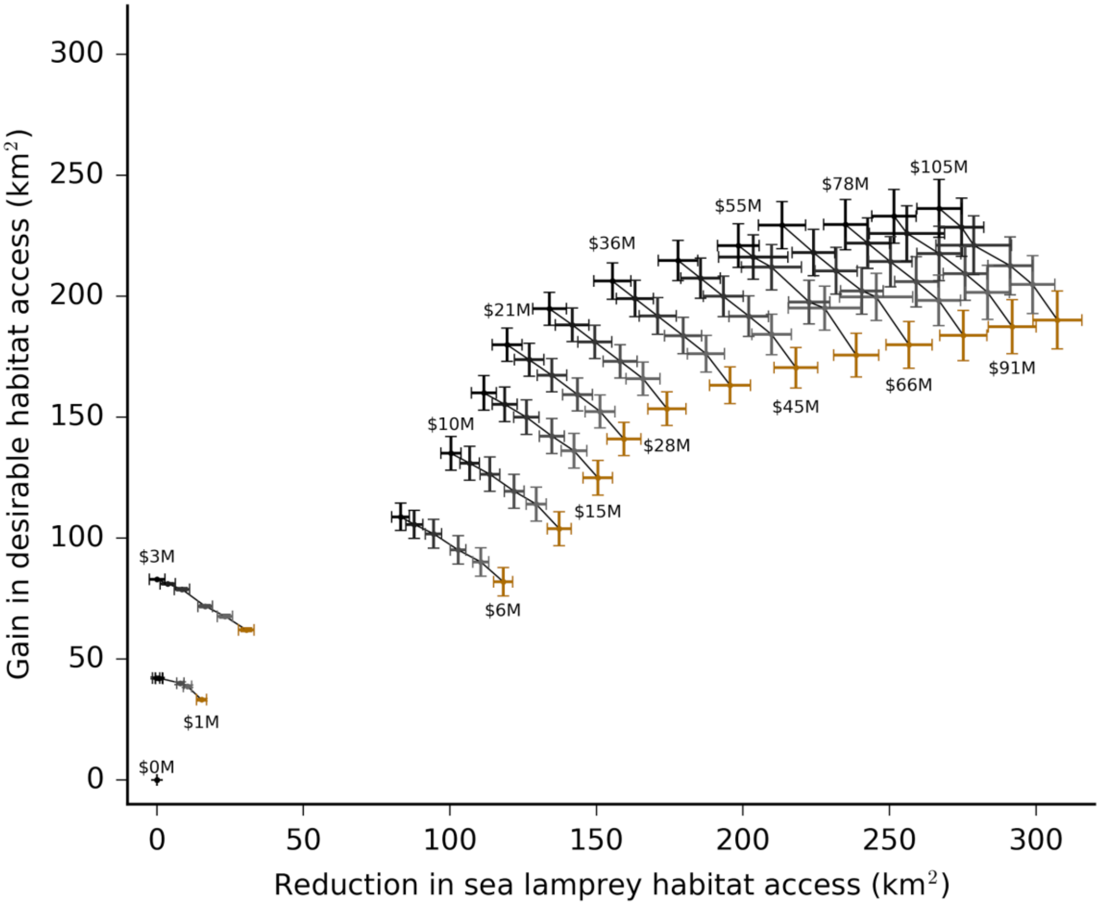

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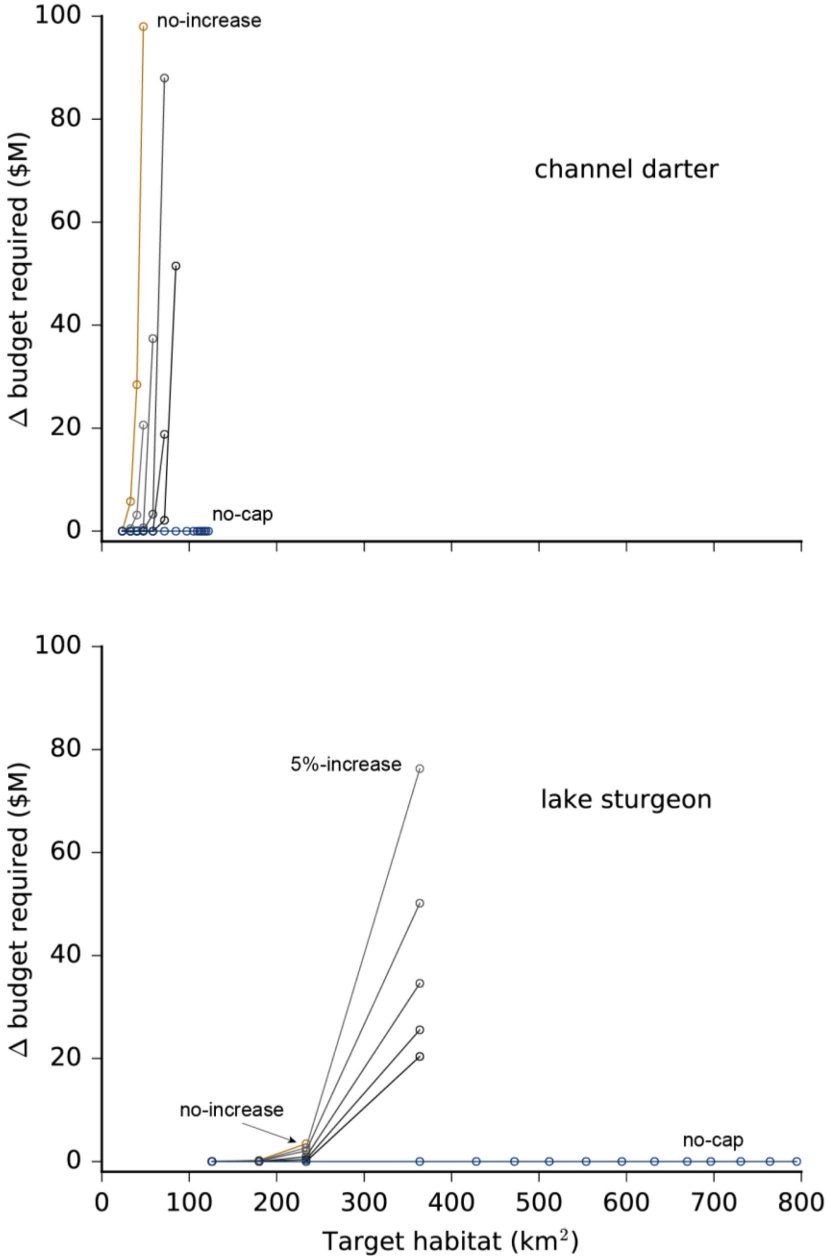

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