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Milt, A. and Diebel, M. and Doran, P. and Ferris, M. and Herbert, M. and Khoury, M. and Moody, A. and Neeson, T. and Ross, J. and Treska, T. and O'Hanley, J.R. and Walter, L. and Wangen, S. and Yacobson, E. and McIntyre, P. (2018) Minimizing opportunity costs to aquatic connectivity restoration while controlling an invasive species. *Conservation Biology*, 32 (4). pp. 894-904.

DOI

<https://doi.org/10.1111/cobi.13105>

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1 **Title**

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

4 **Abstract**

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

23 **Key-words**

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

26 **Introduction**

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

38 Both species invasions and river fragmentation are key conservation challenges from
39 local to global scales but are generally considered separately. Human-mediated biological
40 invasions are a leading contributor to species declines and extinctions in aquatic ecosystems
41 (Harrison & Stiassny 2004) and also alter ecosystem processes (Vander Zanden et al. 2016) and
42 service provisioning (Pejchar & Mooney 2017). Mitigating the effects of invasive species can be
43 costly (Zavaleta 2000; Olson & Roy 2002), so controlling them preemptively is ideal. As dams
44 and road culverts have proliferated worldwide (Laurance et al. 2014; Grill et al. 2015), these

45 barriers have sometimes fostered species invasions by shifting water temperatures and creating
46 standing water habitats (Closs et al. 2015). Barriers fragment river networks, alter flow
47 dynamics, sediment transport, and nutrient cycling (Closs et al. 2015) and hinder animal
48 movement (Fuller et al. 2015). Man-made barriers that inhibit dispersal of native species within
49 river networks also inhibit expansion of harmful invaders, thereby protecting economically
50 valuable or endangered native species (Fausch et al. 2006; Scott et al. 2010). Concerns about
51 both connectivity and infrastructure degradation have spurred efforts to remove barriers from
52 rivers (Doyle et al. 2008), but consequent increased invasion risk is rarely considered
53 simultaneously.

54 Tradeoffs between connectivity restoration and invasion control are exemplified by
55 management of thousands of tributary rivers flowing into the North American Great Lakes. Of
56 42 native and commercial migratory fishes (McLaughlin et al. 2006; Landsman et al. 2011;
57 Moody et al. 2017), many have suffered from overfishing, habitat degradation, and loss of access
58 to breeding habitat. Species invasions, most prominently the parasitic sea lamprey (Limburg &
59 Waldman 2009), have further pressured desirable fishes. Sea lamprey (*Petromyzon marinus*)
60 were introduced to the Great Lakes in the early 1900s and subsequently contributed to the
61 collapse of several fisheries, including lake trout (*Salvelinus namaycush*), whitefish (*Coregonus*
62 *clupeaformis*), and cisco (*Coregonus* spp.) and reduction of burbot (*Lota lota*), walleye (*Sander*
63 *vitreus*), and rainbow trout (*Oncorhynchus mykiss*) populations in all five Great Lakes (Hubbs &
64 Pope 1937; Smith & Tibbles 1980). Consequently, Great Lakes sea lamprey are the focus of one
65 of the world's largest and oldest invasive species control programs. To suppress sea lamprey
66 populations to a fraction of historical levels (Sullivan et al. 2015; Hansen et al. 2016), annually
67 this program spends millions of dollars on chemical lampricides (Great Lakes Fishery

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

75 Over recent decades, interest in connectivity restoration has led to removal of dozens of
76 dams and replacement of hundreds of road culverts. Some such projects were paid for by the
77 \$1.7B U.S. Great Lakes Restoration Initiative between 2010-2017 (Great Lakes Restoration
78 Initiative 2017), with the specific goal of restoring aquatic organism passage (Burroughs et al.
79 2010; Bunt et al. 2012). These underscore the need to strategically assess potential barrier
80 removals in a way that maximizes habitat available to desirable species while also minimizing
81 habitat available to harmful sea lamprey (McLaughlin et al. 2007). A few previous studies have
82 addressed this balance, but without explicitly accounting for the biogeography and diversity of
83 beneficiary species (Zheng et al. 2009; Vélez-Espino et al. 2011).

84 In this paper, we quantify the tradeoffs between habitat gains for desirable migratory
85 fishes versus sea lamprey during connectivity restoration in Great Lakes tributaries. Specifically,
86 we first assess the degree to which limiting access for sea lamprey to spawning habitat affects the
87 ability to restore access for 37 desirable species. Second, we evaluate whether such opportunity
88 costs can be overcome by paying a premium for removals that avoid sea lamprey habitats. We
89 use a basin-wide barrier removal optimization model that maximizes accessibility-weighted
90 habitat for individual desirable species while limiting access for sea lamprey. We conclude with

91 recommendations for decision makers faced with situations where restoration has both positive
92 and negative consequences for conservation.

93 **Materials and methods**

94 Great Lakes Tributary Connectivity

95 This analysis was conducted with the same 1:100,000-scale tributary hydrography and
96 barrier datasets described in Moody et al. (2017). Historical access to Great Lakes tributaries is
97 limited by an estimated 4,417 dams and 99,936 road crossings, resulting in only 15% of potential
98 stream habitat (2,082 km²) being accessible to migratory fishes after accounting for partially-
99 passable barriers (Neeson et al. 2015). We defined the gain in habitat access resulting from
100 barrier removal as the increase in accessibility-weighted tributary area for fish migrating
101 upstream from the Great Lakes (O’Hanley & Tomberlin 2005; Zheng et al. 2009). Cumulative
102 accessibility of a stream reach for a fish was defined as the probability that a fish can bypass all
103 downstream barriers and calculated as the product of passabilities of those barriers (O’Hanley &
104 Tomberlin 2005). Consequently, it also reflects the expected fraction of a migrating population
105 that can access the full reach beyond the barrier. For example, a 1-km² section of stream above a
106 series of two road culverts that each has passability 0.5 for species X would have an
107 accessibility-weighted area of 0.25 km² – 25% of fish species X would be able to use 100% of
108 the habitat - which would increase to 0.5 km² (and 50% of fish species X) if one of these two
109 culverts were replaced. The intent is to approximate the total potential use of upstream habitat
110 given a set of downstream barriers. Since most dams lack specialized fish-passage structures –
111 though see Hatry et al. (2013) for a treatment of Canadian structures - and have either unknown
112 height or exceed the height that desirable fish can jump, all dams were assigned a passability of

113 zero. Culvert passability was calculated as the product of (1) the probability that a culvert's
114 downstream end is perched above the receiving stream level (and is thus impassable to most,
115 non-jumping fish), and (2) the probability that the water velocity in the culvert exceeds a fish's
116 sustainable swimming speed (Januchowski-Hartley et al. 2014). Moody et al. (2017) assigned
117 each species to one of three guilds based on adult sustained swimming speed, so every culvert
118 has three guild-associated passability values. Removing a dam or replacing a culvert increases
119 access to upstream habitat by changing that barrier's passability to one, which also increases the
120 cumulative passability of upstream barriers.

121 We focused on 37 native or introduced desirable migratory fish species that vary in their
122 historical range as well as their overlap with sea lamprey (Figure 1 and Figure 2). Species ranges
123 were estimated at the watershed scale using historical point observations collated from over
124 thirty data sources including fishery surveys, bioassessments, and museum records for every
125 state and province in the basin (Khoury et al. 2018). Data points further than 100 m from a
126 channel were verified. Any tributary in which ≥ 1 -point observations of a species occurred was
127 considered potential habitat for that species. No species will spawn in all accessible parts of a
128 tributary, so our potential habitat estimates are liberal but must suffice given the lack of
129 systematic assessment of migration patterns and microhabitat needs. The tributary habitat area
130 affected by a particular barrier was calculated by summing the area of all reaches (Moody et al.
131 2017) beyond the focal barrier weighted by the estimated passability of each upstream barrier
132 until reaching the river terminus. This includes both mainstem and all tributary reaches. Reach
133 area was calculated as reach length multiplied by bankfull width estimated from a drainage area
134 regression (Wilkerson et al. 2014).

135 Costs of replacing culverts with ‘fish friendly’ structures were based on estimates of
136 replacement materials (e.g., culvert structure, fill, road resurfacing) and labor (Neeson et al.
137 unpublished). Cost components were derived from the Michigan Department of Transportation’s
138 2015 schedule of pay items (Michigan Department of Transportation 2017). The width of each
139 structure was derived by estimating bankfull width from a drainage area regression (Wilkerson et
140 al. 2014). Road crossing structure type was determined by road type and stream bankfull width.
141 Interstate, highway, and urban roads use concrete structures, rural roads use metal structures, and
142 all crossings use the lowest cost structure that meets material and size requirements. Dam
143 removal costs were modeled using a height-cost relationship fitted using inflation-adjusted data
144 for 108 recent removals (Neeson et al. 2015). Dams without height data (23%) were assigned the
145 median cost of all dams in the basin for which empirical cost data were available.

146 Barrier Removal Optimization

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

$$152 \quad H(X) = \sum_{j=1}^{|J|} h_j \pi_j(X) \leq u$$

153
154 where J is the set of all barriers, indexed by j , $\pi_j(X)$ is the cumulative passability for sea lamprey
155 at barrier j , which is a function of the binary vector of barrier removal decisions X , h_j is the net
156 amount of habitat (km²) above barrier j (to the next set of upstream barriers), and u is the cap –

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

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

170 Policy scenarios

171 We explored several scenarios to understand the opportunity costs from capping sea lamprey
172 access to tributary habitat. Two idealized scenarios illustrate the range of opportunity costs. The
173 first is a “no-cap” scenario that allows any level of sea lamprey access and reflects the maximum
174 amount of habitat that could be restored for a species and budget. While this scenario represents
175 an unrealistic policy, it serves as an important reference point. The second, “no-increase”
176 scenario places a strict limit of no new sea lamprey access. This is a best-case scenario for sea
177 lamprey control when focusing exclusively on barrier removals, and most closely reflects the
178 current policy of the Great Lakes Fishery Commission. Between these two extremes, we
179 explored a range of compromise scenarios, including 5, 10, 15, 20, and 25% increases in sea

180 lamprey access over current, basin-wide accessibility-weighted habitat. These scenarios
181 represent a spectrum of potential options that could guide management of connectivity in the
182 future. Scenarios were analyzed over a range of removal budgets: 1, 3, 6, 10, 15, 21, 28, 36, 45,
183 55, 66, 78, 91, and 105 million US\$. Non-uniform budget increments were chosen to resolve the
184 shapes of return-on-investment curves at low budgets.

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

193 **Results**

194 Opportunities for restoring habitat access for desirable migratory fish are strongly controlled by
195 both the barrier removal budget and sea lamprey access cap (Figure 3). Currently, each migratory
196 fish species can access an average of 115 km² (95% CI = 10 km²) of tributary habitat across the
197 basin. Under a no-cap scenario, this access could be tripled for \$14M. However, barrier removals
198 offer diminishing returns. For instance, further increasing accessible habitat to 550 km² would
199 cost a total of \$80M. Individual species vary in both current habitat access and relative gains
200 from barrier removals (Table S1). At one extreme, mooneye (*Hiodon tergisus*) currently has 19
201 km² of accessibility-weighted habitat in the basin. For \$15M, access to 96 km² of its 235 km²

202 potential range could be restored under a no-cap scenario. At the other extreme, yellow perch
203 (*Perca flavescens*) would require \$65M for a proportionally similar increase beyond its current
204 228 km².

205 Opportunity costs of a sea lamprey access cap

206 Capping sea lamprey access imposes limits on opportunities for restoring habitat access
207 across species. Doubling current average access per species (115 km²) would cost \$8-16M
208 depending on the strictness of the cap (Figure 3). Tripling access, achievable for \$14M under a
209 no-cap scenario, would require both a $\geq 20\%$ increase in sea lamprey access and a budget of at
210 least \$78M. Incremental cap increases can enhance access for most desirable species. Interactive
211 effects of budget level and lamprey constraints diminished at larger budgets; for instance, any
212 two scenarios with a cap are equidistant beyond \$20M budget (Figure 3). Except for three
213 species – mooneye, bigmouth buffalo (*Ictiobus cyprinellus*), and river darter (*Percina shumardi*)
214 – individual species results were qualitatively like the average. For these three species, $\geq 5\%$ -cap
215 scenarios would boost their access close to the no-cap scenario (Table S1).

216 Comparing the no-cap to other scenarios revealed that average opportunity costs to
217 desirable species of capping sea lamprey access increased disproportionately fast as the strictness
218 of the lamprey cap tightened (Figure 3). At relatively low budgets ($< \$5M$), this opportunity cost
219 grew quickly to 10-30% beyond the no-cap scenario. This growth slowed at larger budgets; at
220 \$105M, a no-increase cap on sea lamprey access resulted in an opportunity cost of 53% relative
221 to the no-cap scenario. Conversely, incrementally relaxing the cap from a no-increase starting
222 point led to reduced opportunity cost, but relaxation beyond the initial 5% had a constant effect
223 (i.e., in Figure 3 distances between curves above 5% are constant). This is likely due to the high
224 spatial overlap of species with sea lamprey, such that an increase in sea lamprey access beyond

225 5% results in a similar increase in desirable species access. However, some species exhibited
226 qualitative differences from the average. For example, river darter exhibited an opportunity cost
227 of 80% at \$20M under a no-increase scenario, but that could be reduced to 30% under a 5%-
228 increase scenario (Table S1).

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

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

242 Between the no-cap and no-increase scenarios, the geography and number of barriers
243 recommended for removal shifted (Figure S1). At \$105M, more barriers were removed in the no-
244 cap scenario (average \pm 95%-CI over species = 339 ± 14) versus the no-increase scenario ($298 \pm$
245 33). Barrier removals were more spatially concentrated in the no-increase scenario (number of
246 watersheds with ≥ 1 removal: 30.8 ± 6.9 versus 44.1 ± 5.9) as the model avoided watersheds

247 known to be used by sea lamprey. Under the no-cap, \$105M scenario, barrier removals were
248 concentrated in the Fox (Lake Michigan) and Trent (Lake Ontario) river watersheds (averaged
249 20% of removals across species). Under the no-increase scenario, barrier removals shifted to Fox
250 and French (Lake Huron) river watersheds (31%).

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

252 Species varied in the cost of and degree to which supplementing the removal budget could offset
253 opportunity costs from capping sea lamprey access (Figure 5). Two distinct patterns emerged.
254 First, for seven study species with modest ranges (<1000 km²; Figure 2), including American eel
255 (*Anguilla rostrata*), mooneye, bigmouth buffalo, white bass (*Morone chrysops*), pink salmon
256 (*Onchorynchus gorboscha*), channel darter (*Percina copelandi*), and river darter, an additional
257 investment of <\$10M with some sea lamprey access cap could boost habitat access to 50% of
258 that range of habitat access achieved in the no-cap scenario (e.g. Figure 5, top). For most of those
259 species, the sea lamprey access cap would also need to be increased to 25%. For these seven
260 species, it was costly or impossible to achieve much higher habitat access regardless of further
261 spending, especially under the no-increase scenario.

262 Most of the remaining 30 species exhibited less potential to offset the effect of capping
263 sea lamprey access, and high cost of doing so (Figure 5, bottom). For the state-listed lake
264 sturgeon (*Acipenser fulvescens*), 250 km² habitat access could be achieved under the no-increase
265 scenario at an additional \$5M beyond the no-cap scenario. However, to reach 350 km² would
266 cost an additional \$20M-80M and require ≥5%-increase cap. Further increases in tributary access
267 for lake sturgeon could not be achieved for any cost. Similar patterns were applicable to many
268 broadly-distributed species.

269 **Discussion**

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

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

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

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

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

305 Restoring connectivity is expensive, may not increase resilience or population size
306 (McLaughlin et al. 2013), and consequences are neither uniformly positive nor certain (Smyth
307 2011) for all fishes. This is true even without accounting for complex interactions with species
308 invasions. Moreover, maintaining fragmentation can separate hatchery from wild populations,
309 prevent the spread of disease, and help fish avoid ecological traps (Rahel 2013). Some of these
310 factors are surely at play for Great Lakes migratory fishes, resulting in overestimation of the
311 aggregate benefits of increasing connectivity in our model. Though such complexities have been
312 explored for certain well-studied species in specific tributaries (e.g. Smyth, 2011), it is unknown

313 if this generalizes to other species and places. We have elected to focus on benefits for lack of
314 information to guide a more refined approach.

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

327 Including sea lamprey control strategies other than barrier management (Jones et al.
328 2015) were beyond the scope of this analysis but could improve outcomes. For instance,
329 lampricide – lamprey-specific pesticide - application has helped reduce sea lamprey populations
330 by >85% in most areas of the Great Lakes basin (Great Lakes Fishery Commission 2008).
331 Complete eradication of sea lamprey from the Great Lakes is implausible (Mullett & Sullivan
332 2016), but the combination of existing dams, strategic application of lampricides, and selective
333 passage structures that stop sea lamprey has proven effective in suppressing them (McLaughlin
334 et al. 2007). Increased access for sea lamprey could trigger demographic feedback mechanisms
335 leading to explosive population growth (Jones et al. 2003), making other controls more

336 necessary. We are unable to account for demographic consequences on commercial and other
337 desirable species from additional sea lamprey production. In addition, it is beyond the scope of
338 this study to estimate potential lampricide application costs that might be used to suppress sea
339 lamprey following barrier removals. Instead, we focus on locating sites where gains for desirable
340 species can be accomplished while minimizing increases in sea lamprey without additional
341 controls.

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

357 **Supporting Information**

358

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

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538

539 **Figure Legends**

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

543 Figure 2. Species range data and example results of imposing a limit on sea lamprey access in the
544 Great Lakes basin. From left to right: (1) “Range” is total potential accessible habitat if all
545 barriers were removed, (2) “Overlap with sea lamprey” is percent of range shared by *Petromyzon*
546 *marinus*, (3) “Unrealized potential gain” is opportunity cost to habitat access restoration incurred
547 from a no-increase cap on sea lamprey access beyond the effect of budget given a \$105M
548 removal budget, and (4) “Cost to double access” describes the necessary removal budget beyond
549 a no-cap scenario to double habitat access while limiting sea lamprey increase to 10%.

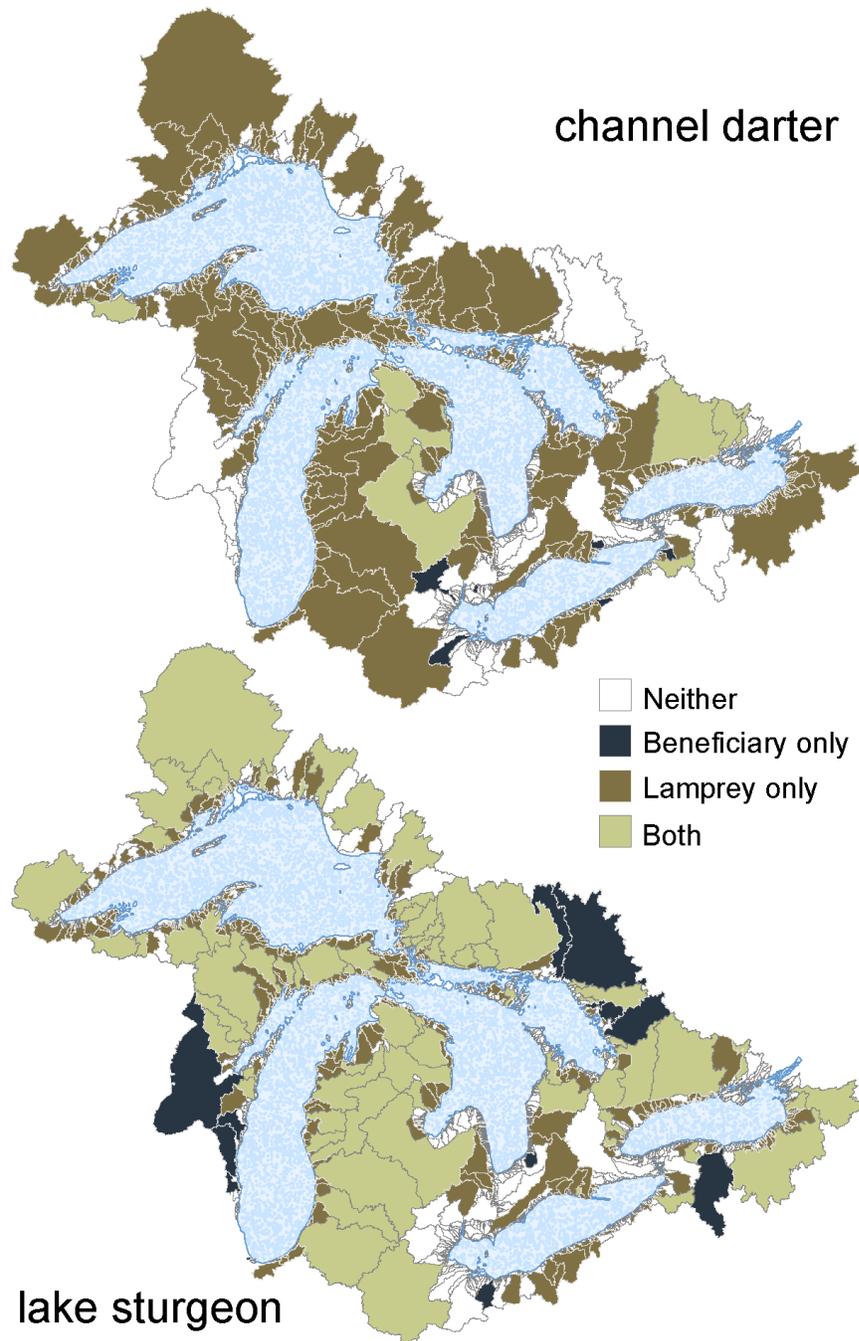
550 *Petromyzon marinus* is bold to emphasize it is invasive and no optimizations were run to
551 maximize its habitat access. Species preceded by * are non-native. Species with “Not Possible”
552 were found to have no level of spending under the 10%-increase scenario that could offset the
553 effect of a cap to double current habitat access.

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

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

561 Figure 5. Example species-specific costs of offsetting opportunity costs to desirable habitat
562 access from capping sea lamprey access. Horizontal axis is target level of habitat access for
563 species named in the upper-right. Vertical axis is additional budget required to achieve the same
564 level of habitat access as the no-cap scenario. No-cap scenario is drawn for reference to show
565 both zero additional cost and range of habitat access achieved for that species in our analyses
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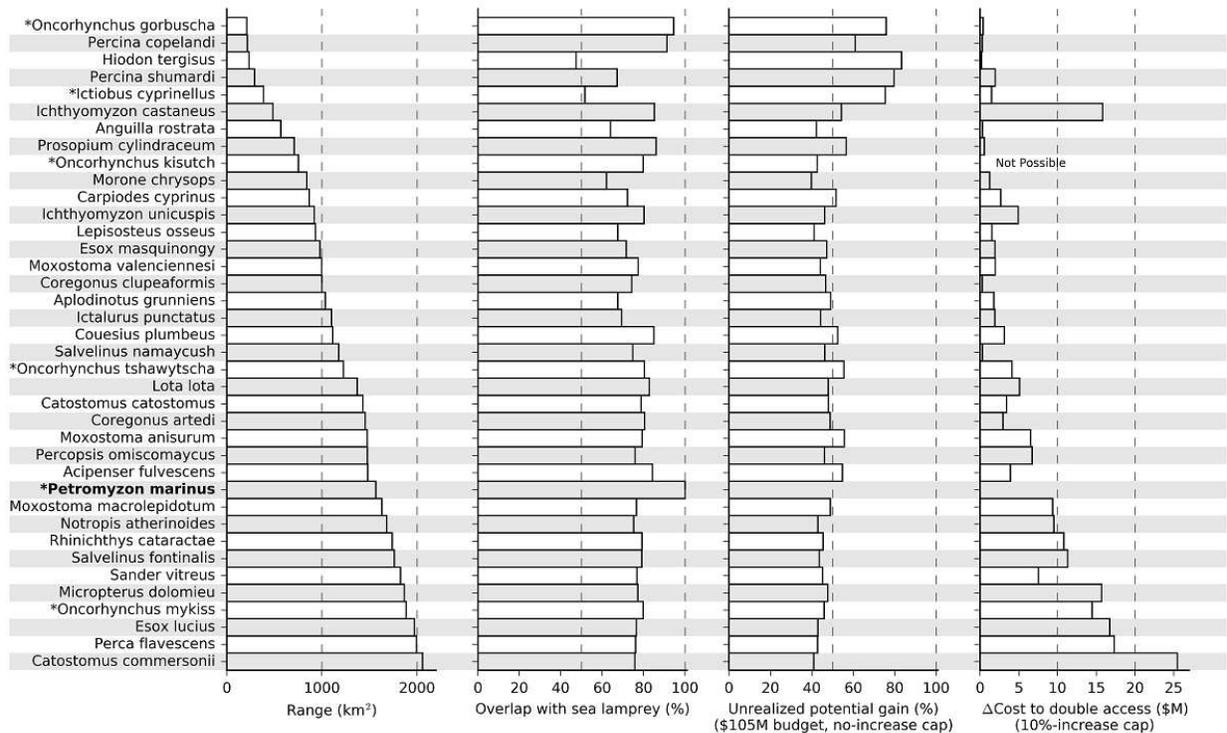


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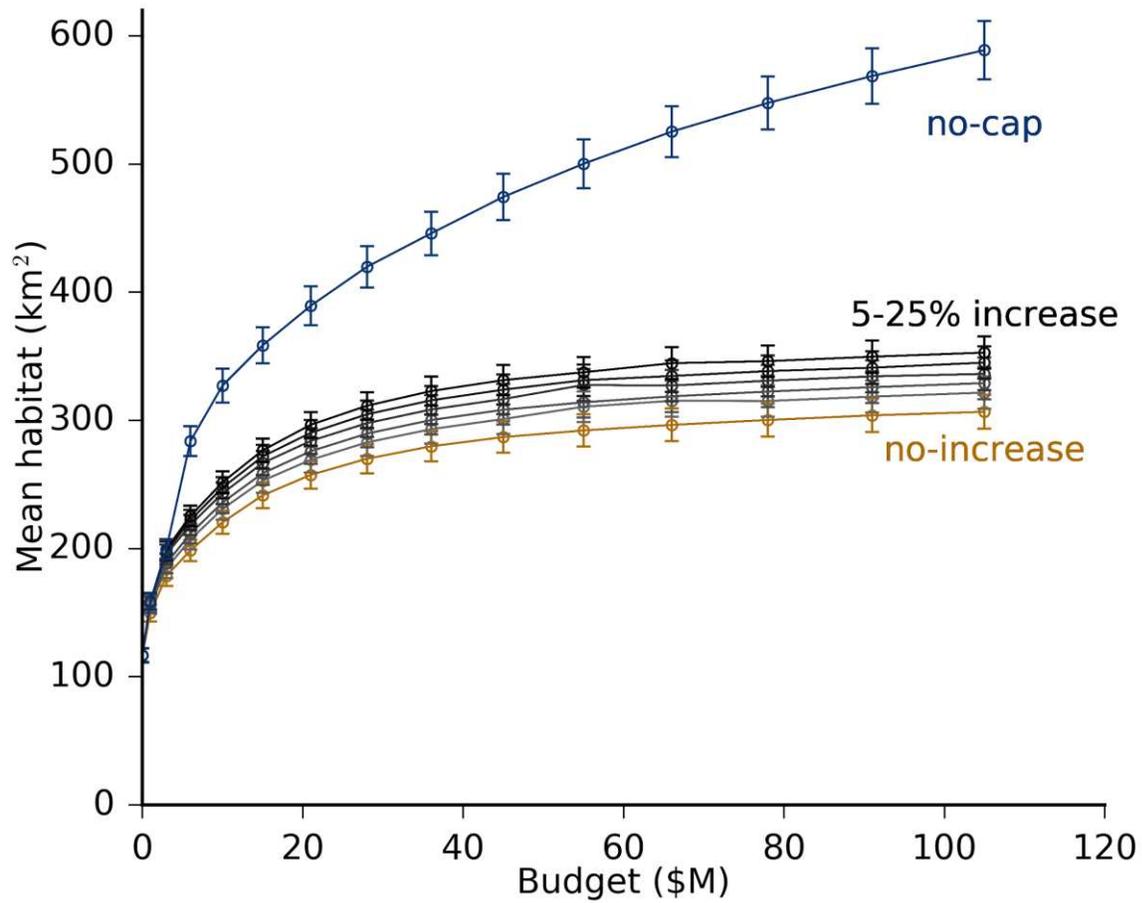
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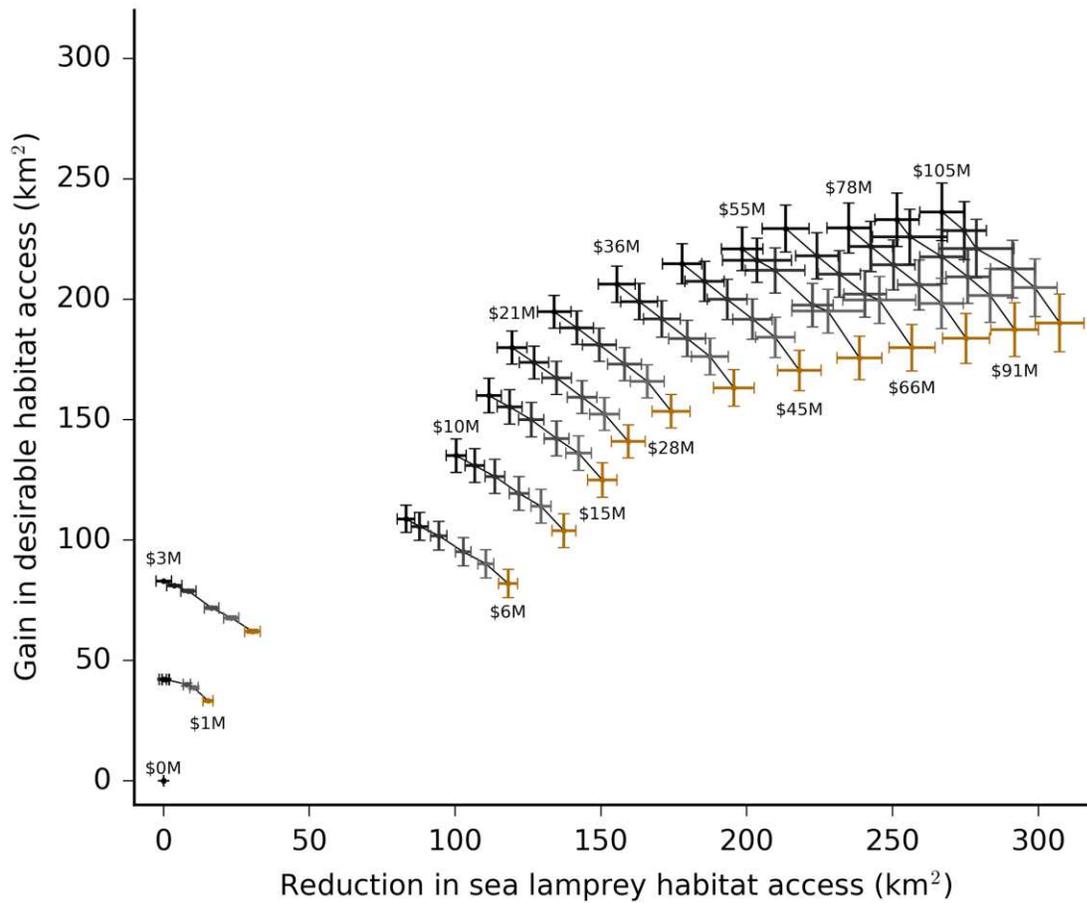
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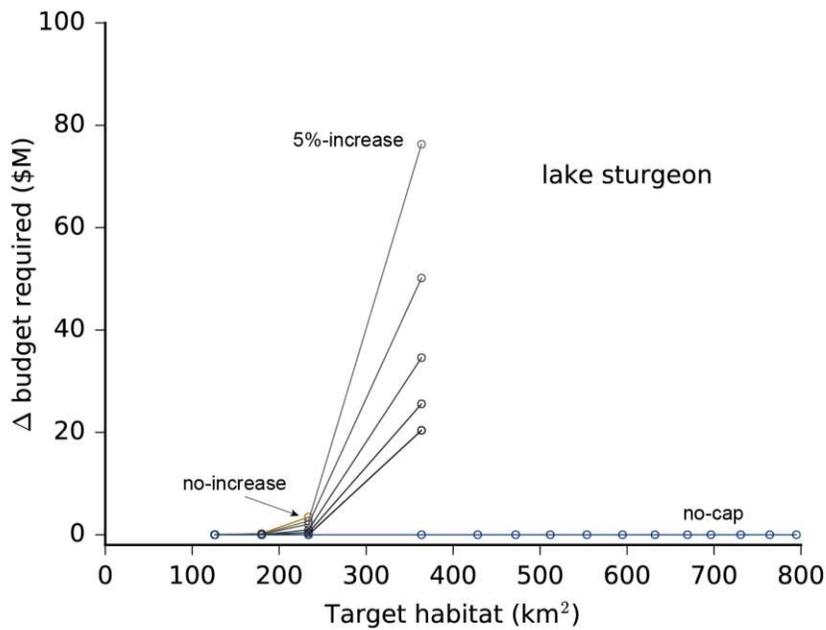
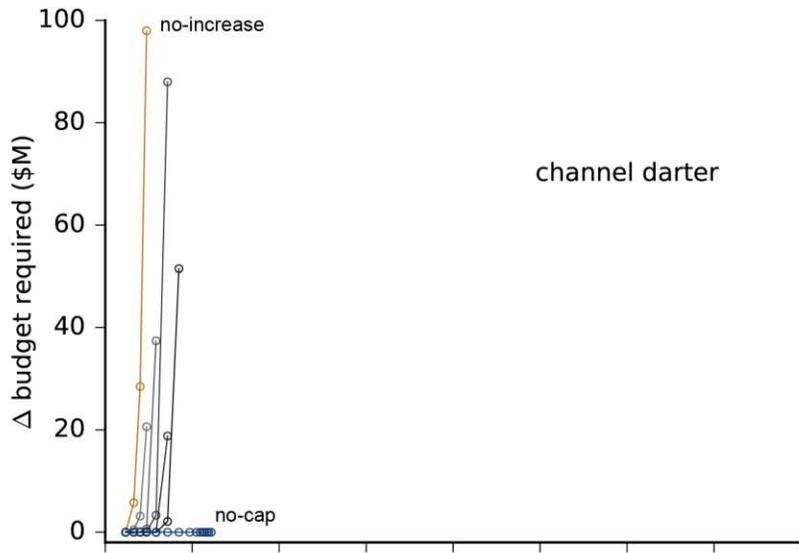


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