# Eradication of Sea Lampreys from the Laurentian Great Lakes is Possible

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## Abstract

Eradication has been achieved for many vertebrate pest control programs, primarily on small, isolated islands, but has never been considered a practical goal for invasive sea lampreys in the Laurentian Great Lakes. Our objective was to examine evidence relevant to the feasibility of setting eradication as a management goal for Great Lakes sea lampreys. Bomford and O'Brien (1995) listed six conditions for successful eradication of a vertebrate pest; here we examine evidence that these conditions are likely to be met for Great Lakes sea lampreys, with a focus on the first condition: that removal of the pest through control can exceed their rate of replenishment. We analyzed two data sets – one empirical and one synthetic – to estimate stock-recruitment relationships and calculate the exploitation rate necessary for extinction. The empirical data set included the effect of existing lampricide control and suggested an exploitation rate of 59%, in addition to lampricide control, would be sufficient for eventual eradication. The synthetic data set, derived from a simulation of stream-level recruitment dynamics in the absence of lampricide control, suggested that an overall exploitation rate of 90% would be sufficient. We suggest that both of these targets could be achieved. Meeting the other conditions will depend on the scale of the eradication effort, and on development of an exploitation strategy, such as genetic biocontrol, that can target sea lampreys in presently invulnerable habitats. Overall, we concluded that eradication of sea lampreys from the Great Lakes should not be dismissed as a prospective goal.

Keywords: sea lampreys, stock-recruitment, eradication

## Introduction

Invasive species have been responsible for enormous economic and ecological consequences, on a global scale, and represent one of the greatest threats to future sustainability (Bellard et al., 2016; Millenium Ecosystem Assessment, 2005). Interest in and progress with prevention of future invasions has greatly increased in recent decades (Simberloff et al. 2013, Ricciardi et al., 2017) but for invasive species whose impacts have already been felt, the primary management objective is to reduce their abundance to levels where the damage they cause is tolerable. Most often this involves exactly that – suppression of abundance to reduce damage – but another option sometimes considered is eradication: complete removal of the pest species from its non-native habitat.

Eradication has been the goal of many vertebrate pest control efforts, particularly on New Zealand and Australian islands, and success rates for invasive rodent control on small islands has been very high (581 successes out of 650 documented attempts to eradicate *Rattus* sp.: Russell and Holmes 2015). However, small, uninhabited islands represent ideal circumstances for a pest eradication program, whereas eradication has proven much more challenging in most other situations (Glen et al. 2013).

In the Laurentian Great Lakes, sea lampreys (*Petromyzon marinus*) have been the object of an active program of invasive species control since the late 1950s. Even prior to the signing of the Convention on Great Lakes Fisheries by Canada and the United States in 1954, creating the Great Lakes Fishery Commission, experts expressed conviction that control (i.e, suppression), not eradication, of sea lampreys should be the goal of any pest management program targeting this species. For example, Albert Day, Director of the Fish and Wildlife Service in 1951, stated, “I still do not know what it will cost to devise workable, practicable methods for controlling the sea lamprey.  Please note that I say ‘control’ because I do not honestly believe that we can eliminate the animal. I think the best that we can hope for is to reduce the numbers so that they will not constitute any serious handicap to the application of whatever other measures may be necessary to restore and maintain the fisheries of the Great Lakes" (U.S. Congress, House, 1951). At this time, mechanical and electrical weirs were the only known means of control; consequently it is not surprising that this was the prevalent view among experts and decision makers.

The successful introduction of lampricide control in the late 1950s greatly increased optimism about prospects for successful suppression of sea lampreys and motivated further debate about prospects for eradication of the pest. Nevertheless, during the 60 years since sea lamprey control efforts began, most decision makers, scientists, and stakeholders have continued to assume that eradication is likely not an achievable outcome. As a consequence the control program has focused its efforts on achieving target levels of population suppression that are presumed to be consistent with other fishery management objectives defined for each of the Great Lakes. For example, the 2017 Lake Ontario Fish Community Objectives (Stewart et al. 2017, p.15) list as an objective: "suppress abundance of Sea Lamprey to levels that will not impede achievement of objectives for Lake Trout and other fish".

Sea lamprey populations are far less abundant than they were before control began (Heinrich et al. 2003), and populations of host species such as lake trout (*Salvelinus namaycush*) and lake whitefish (*Coregonus clupeaformis*) suffer much lower sea lamprey-induced mortality today than in the 1960s when sea lampreys were more abundant. On the other hand, at no time has a formal analysis been conducted to objectively evaluate whether eradication of sea lampreys in the Great Lakes would be possible, and if so under what circumstances.

In this paper we consider this question, using knowledge accumulated since the previous Sea Lamprey International Symposium (II in 2000) on the population dynamics of Great Lakes sea lampreys. Bomford and O'Brien (1995) proposed six criteria as necessary conditions for a successful eradication effort (Table 1). The first of these criteria is that it is possible to remove individuals from the population at a greater rate than they are replenished through reproduction. Our primary objective for this paper is to determine, using population dynamics data for sea lampreys, the rate of sea lamprey exploitation or removal that would meet this criterion. Additionally, we will discuss evidence that the other five criteria presented in Table 1 likely can be met for Great Lakes sea lamprey control, and on this basis offer some conclusions about the prospects for future eradication of this invasive species.

## Methods

We investigated sea lamprey population dynamics by fitting data to the Ricker stock-recruitment model:

$$R = \alpha S e^{-\beta S} \quad , \qquad (1)$$

where $R$ is recruits, $S$ is stock (spawning adults), and $\alpha$ and $\beta$ are fitted parameters, accurately, if not precisely, describes the dynamics of sea lamprey reproduction (Ricker 1975). The Ricker model is widely used to describe stock-recruitment dynamics, particularly for anadromous, semelparous species, and was used by Dawson and Jones (2009) to describe stream-level recruitment dynamics for sea lampreys. From parameters estimated for the Ricker model, and assuming the units of $R$ are the same as the units of $S$, it is possible to calculate the lowest exploitation rate[1] that is unsustainable – that is, will eventually result in the population declining to zero,

$$u_{ext} = 1 - \frac{1}{\alpha} \quad . \tag{2}$$

*Empirical Model*

We analyzed two sets of data to obtain estimates of $u_{ext}$ and its uncertainty. The first is an empirical data set of adult sea lamprey abundance estimates from 1994-2019 for all five Great Lakes (Great Lakes Fishery Commission, unpublished data, http://glfc.org/status.php). Estimates were not available for all years for all lakes (Table 2). We defined recruitment as the numbers of adults produced from an individual year of reproduction (brood year). Sea lampreys are semelparous, and have a variable age of metamorphosis from larva to juvenile parasite, which implies that the recruits from a given brood year will be spread across multiple spawning years. Normally the reconstruction of a brood table (recruits, by age, originating from individual brood years) would be informed by adult age composition data, but no validated age estimation method exists for sea lampreys (Dawson et al. 2009). As a consequence, we fitted the adult abundance data to the following model:

$$A_t = \sum_{a=5}^{7} R_{t-a}\, p_a, \tag{3}$$

where $A_t$ is the abundance of returning adults in year $t$, $R_{t-a}$ are recruits from three contributing brood years ($t$-$a$), calculated from equation 1, and $p_a$ is the proportion of recruits that mature at age $a$. We assumed that all lampreys matured at age 5, 6, 7, or 8 (or arguably that a negligible proportion mature at other ages), and estimated $\alpha$,$\beta$, $u_{ext}$. We estimated lake-specific $\beta$ values and

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[1] For lamprey control the exploitation rate would be equivalent to the fraction of the sea lamprey population in a given lake that is removed by control actions prior to spawning.

a single $\alpha$ value for all lakes. The $p_a$ were assumed known and derived from estimates of growth rates and length-based metamorphosis rates used for the synthetic model (see below). We used $p_a$ values calculated for Lake Michigan for comparison to the synthetic model, but evaluated sensitivity of our conclusions to an alternative maturation schedule based on Lake Superior growth data.

The adult abundance data used for this analysis include the effect of lampricide treatment on recruitment. We were interested in the recruitment that would result from a range of adult abundances in the absence of lampricide treatments, so we needed to estimate the effect of treatment separately from the effect of adult abundance. To do this we used data on lampricide control effort (TFM – 3-trifluormethyl-4-nitrophenol – in kg of active ingredient used) in year *t-2* which corresponds to the year when adults returning in year *t* would be completing metamorphosis and entering the lake. We normalized the effort by dividing each year's effort value for each lake by the mean level of effort over the entire time series for that lake. The overall model was:

$$A_t = \alpha \sum_{a=5}^{7} \left( S_{t-a} e^{-\beta S_{t-a}} p_a \right) e^{\gamma T_{t-2}}, \qquad (4)$$

where *T* is the treatment effort index and γ is the estimated effect of treatment on adult abundance. We assumed a log-normal residual error (Hilborn and Walters 1982), and used uninformative priors for all estimated parameters. Parameters were estimated using WinBugs (Spiegelhalter et al. 2004) and the R2WinBugs package in R (Sturtz et al. 2005).

*Synthetic Model*

The second data set was generated from simulation output, using the Sea Lamprey Management Strategy Evaluation (SLaMSE) model (Jones et al. 2009). This model simulates sea lamprey population dynamics and management for each Great Lake. Sea lamprey recruitment is simulated at the spatial scale of individual spawning streams, and the annual production of juvenile sea lampreys from all streams tributary to a lake are combined into a single whole-lake population. Sea lampreys do not home (Bergstedt and Seelye 1995) so we assumed juvenile sea lampreys occupying a lake comprised a single panmictic population which distribute themselves among spawning streams when they mature. In the SLaMSE model, allocation of adults to streams is informed by relative stream size and the abundance of larval sea lampreys, the latter representing an assumed migratory pheromone effect (Jones et al. 2009). The SLaMSE model has been modified since 2009 – major changes from the Jones et al. (2009) version are detailed in Miehls et al. (This volume: Supplemental Materials).

Recruitment in the SLaMSE model is informed by empirical evidence of stock-recruitment patterns from individual Great Lakes streams (Dawson and Jones 2009). These data describe the density-dependent relationship between the number of spawning adults and the abundance of age 1 larval sea lampreys the following year in a single stream. For this analysis we needed to determine the emergent relationship between lake-scale stock and recruitment by aggregating the effects of stream-scale stock and recruitment.

To accomplish this, we ran simulations of SLaMSE for a single Great Lake (Michigan) and recorded the total annual production of age 1 recruits in each year, summed across all streams. Then we created a brood table and calculated the subsequent abundance of age 2, 3, etc larvae, and the production of juveniles according to averaged empirical estimates of growth rates and the size-dependence of metamorphosis (see Jones et al 2009 for an explanation of how growth and metamorphosis are modeled in SLaMSE). We used data on larval growth rates and the length-based probability metamorphosis for Lake Michigan to determine expected proportions of larvae transforming to parasites across larval ages ranging from 3 to 6. From the brood table we could calculate the total recruitment of adult sea lampreys from each brood year, by summing across the ages at which the recruits from each brood year would have matured (see Supplemental Materials – S1).

The SLaMSE model explicitly includes lampricide control, so we were able to run simulations with no control, and thus avoid the confounding influence of control effort on recruitment. This is equivalent to assessing recruitment to the adult population in the absence of fishing for an exploited fish population. However, simulations with no control quickly result in large populations of sea lampreys with relatively little contrast among years or simulations (analogous to an unfished equilibrium state). To introduce contrast into adult abundance we repeated simulations with four levels of simulated trapping removals of adult sea lampreys (0%, 50%, 80%, and 90%). Stock was recorded as adults after trapping; recruits were recorded as adults before trapping. These trapping removal levels were not intended to simulate currently realistic trapping-for-control scenarios, but rather to introduce contrast into adult abundances for our purpose of estimating a whole-lake stock-recruitment relationship informed by empirical evidence of a stream-level stock-recruitment relationship and the other demographic assumptions incorporated in the SLaMSE model.

To generate the simulated whole-lake stock recruitment data we ran 10, 100-year simulations for each trapping level, and sampled brood years 85-90 for each simulation, which yielded 60 stock-recruit pairs for each trapping level. Examination of larger numbers of simulations indicated the 10 simulations was sufficient to capture model-generated variability in the simulated stock-recruitment relationship (i.e., no appreciable increase in estimated process uncertainty with larger sample sizes). We fit the simulated data to a simple Ricker model (equation 1) using WinBugs in R and uninformative priors, and estimated $\alpha$, $\beta$, and $u_{ext}$.

## Results

### *Empirical Model*

Sea lamprey adult abundances varied widely across the time series for each lake (Figure 1), ranging from 5-fold variation for Lake Ontario to 20-fold variation for Lake Erie. The model to estimate stock-recruitment parameters from the empirical adult abundance data set converged successfully, using a Markov Chain Monte Carlo (MCMC) chain length of 30,000, a burn in of 500 samples and a thinning rate of 10. Brooks-Gelman-Rubin statistic values for all estimated parameters were between 0.99 and 1.01, well within the range defined as acceptable by Gelman and Hill (2007). Estimated equilibrium population sizes ($\ln(\alpha)/\beta$) varied among lakes as expected, with median values ranging from 16,700 for Lake Erie to 263,200 for Lake Superior (Table 3, Figure 2). The estimated posterior median value of $\alpha$ (2.43) corresponded to a posterior median value of 0.588 for $u_{ext}$, implying an exploitation rate of 58.8% to achieve eradication. The estimated effect of lampricide treatment ($\Upsilon$, Table 3) was small (0.26), but the 95% credible intervals for this parameter did not overlap zero, implying a modest effect of treatment on adult abundance (i.e., a 23% reduction in recruitment for an average treatment relative to no treatment). When we used an alternative maturation schedule ($p_a$), based on Lake Superior growth data, the resulting estimates of $\alpha$, and $u_{ext}$ were very similar (2.49 vs 2.43 for $\alpha$, .599 vs .588 for $u_{ext}$).

### *Synthetic Model*

The model to estimate stock-recruitment parameters for Lake Michigan from the synthetic data set generated from output from the SLaMSE model (Figure 3) also converged easily, with shorter chain lengths (1200), burn in (200), and no thinning. The estimate of $\alpha$ was about four times that of the empirical model (9.92 vs. 2.43, Table 3), while the estimate of $\beta$ was much smaller ($4.2 \times 10^{-7}$) than the corresponding empirical model value for Lake Michigan ($6.69 \times 10^{-6}$). These estimates suggest a much more productive (maximum recruits per adult) population with a much larger uncontrolled population size (5,491,000 vs. 132,800, Table 3). The higher $\alpha$ estimate implies a much larger $u_{ext}$ estimate (90% vs. 59%).

## Discussion

Stock-recruitment analyses for the two models considered here yielded sharply contrasting results. Estimates of population productivity ($\alpha$), equilibrium abundance in the absence of control ($\ln(\alpha)/\beta$), and the exploitation rate needed for eradication ($u_{ext}$) were all much lower for the empirical model – where the estimates were derived from adult abundance estimates for each of the Great Lakes. These data include the effect of ongoing lampricide control on adult abundance. We attempted to estimate this effect from data on lampricide effort but the estimate suggested a relatively modest effect (23% lower recruitment for an average level of lampricide effort relative to no effort). It is widely believed (e.g., Heinrich et al. 2003) that lampricide control has reduced the abundance of adult lampreys by far more than 23% relative to what would be expected in the absence of control, which would suggest these data underestimate the effect of treatment. We suspect this is due to a lack of contrast in the independent variable (treatment effort) that we used in our analysis – during the time periods for which we have data for each of the lakes the variation in treatment effort was modest relative to a possible range that would include little or no control effort.

Our inability to accurately estimate a lampricide treatment effect for the empirical model implies that our estimates of productivity, equilibrium abundance, and $u_{ext}$ reflect conditions for a sea lamprey population experiencing levels of lampricide control consistent with the recent history of control effort in each lake. The lower value for $\alpha$ compared to that for the second data set (2.56 vs. 9.92) reflects a reduction in observed productivity due to lampricide treatment of stream populations of roughly 74%. The values for equilibrium abundance for each lake can be interpreted as estimates of the expected long-term average abundance of adult sea lampreys in each lake, given no change in the average level of lampricide effort (or in other factors affecting sea lamprey abundance such as barriers). Finally, the estimate of $u_{ext}$ (58.8%) is an indication of the amount of *additional exploitation*, beyond that resulting from current levels of lampricide effort, required to achieve a 50% chance of eradication (or 76% additional exploitation to achieve a 97.5% chance of eradication, Table 3). These findings compare favorably with those of Velez et al. (2008), who used a matrix population model informed by empirical sea lamprey abundance data to conclude that additional reductions in population fecundity (proportional to adult abundance) ranging from 72-88% across the Great Lakes would be needed to ensure persistent population declines. This could be accomplished by supplemental controls, or by a combination of supplemental controls and additional lampricide control.

Our second stock-recruitment analysis (synthetic model) resulted in much higher estimates of all the parameters of interest for Lake Michigan (Table 3). The difference in results would likely be similar for other lakes, as the life history parameters used in the SLaMSE model are largely similar for all five Great Lakes. The data generated to inform this analysis do not include the effect of lampricide control because our SLaMSE simulations turned off this management option. The stock-recruitment dynamics that emerged represent the predicted consequence at the whole lake scale, of observed stream-level stock recruitment dynamics and plausible assumptions about sea lamprey growth, metamorphosis, and survival rates from age 1 to adult life stages. The estimated equilibrium abundance for Lake Michigan in the absence of control was 5.5 million adults. It is unlikely that sea lamprey populations would reach this level of abundance in the absence of lampricide control because this estimate did not allow for density-dependent effects on growth, metamorphosis, or survival of juvenile sea lampreys at these high abundance levels. In all likelihood sea lamprey populations this large would experience density-dependent effects at the juvenile stage due to the extremely large number of hosts needed to support this large a population. On the other hand, Heinrich et al. (2003) estimated pre-control abundances of sea lampreys of at least 1.3 million.

For the synthetic model, the estimated exploitation rate required to achieve a 50% chance of eradication was 89.9% (or 90.3% to achieve a 97.5% chance of eradication, Table 3). In contrast to the previous analysis, this estimate represents an exploitation rate that *includes* the current level of sea lamprey control. In this regard, consider the difference between our estimate of the uncontrolled adult abundance estimate (5.5 million) and current adult abundance levels (on the order of 100,000) in Lake Michigan. This difference implies a 98.2% reduction in adult sea lamprey abundance in Lake Michigan, relative to what stream-level stock-recruitment dynamics suggest would be possible in the absence of control. This magnitude of reduction is well above our estimate of the exploitation rate required for eradication, prompting the following question: given this estimated magnitude of population reduction due to lampricide control, why haven’t we already achieved eradication of sea lampreys in Lake Michigan? Even if the pre-control abundance was only 1.3 million (Heinrich et al. 2003) the reduction to current levels is in excess of 92%. We offer a potential explanation for this in our discussion of Bomford and O'Brien's third and fourth criteria (Table 1) for successful eradication below.

These two stock-recruitment analyses yielded contrasting results, but the differences can be explained by differences in the data used to model the relationship, as discussed above. Our estimates of exploitation rates needed to eradicate sea lampreys, either in relation to existing control efforts (61-75%) or relative to no control (90%), do not seem unattainable. It is plausible that enhanced lampricide effort combined with supplemental controls could target over 60% of the sea lamprey population residual to existing control. As noted above, an overall level of suppression of 90%, inclusive of lampricide control at current levels, seems even more attainable. So a reasonable answer to the first criterion listed by Bomford and O'Brien (Table 1): "The rate of removal of the pest can exceed the rate of increase" is YES. What about the other criteria?

The second criterion is that "immigration of the pest into the target area for eradication is prevented". For Great Lakes sea lampreys the prospects for meeting this condition almost certainly depend on the scale of the eradication effort. Sea lampreys were first observed in Lake Erie in 1921 (Sullivan et al. 2003) and within at most two decades had established large populations in all five Great Lakes. This suggests that any eradication effort undertaken at a scale smaller than the entire Great Lakes basin is unlikely to meet this criterion.

On the other hand, there is little evidence to suggest that there continues to be movement of sea lampreys between the Great Lakes and their native range in the northeastern U.S. Whether there is currently any immigration from outside the basin remains an important source of uncertainty, but it is reasonably likely that this criterion can be met if eradication efforts target the entire Great Lakes. Informative research about gene flow between Atlantic sea lamprey populations and the Great Lakes is currently ongoing (M. Docker, University of Manitoba, personal communication).

The third (all reproductive animals at risk) and fourth (pest can be detected at low densities) criteria are related. Sea lamprey managers have long considered the detection of populations of larval sea lampreys that are not currently exposed to lampricide control as a priority research topic. Are there habitats, either within streams currently targeted with lampricides (e.g., upwelling areas where lampricide is not effective due to groundwater influences), or in regions not vulnerable to conventional control (e.g,. some lentic areas or the St. Clair River) that would continue to act as sources for sea lamprey recruitment even if all vulnerable habitats are effectively targeted. Such habitats would provide a refuge for sea lamprey reproduction as production from other habitats is suppressed, and our understanding of the contribution made by these areas to current populations of sea lampreys is very limited, because assessment of populations in these habitats is a challenge, although emerging techniques using genetic analysis methods such as eDNA or larval sea lamprey pheromone bioassays may improve assessment capabilities.

The results from the synthetic model reported above also provide evidence that there is a component of the sea lamprey population in Lake Michigan that is not vulnerable to lampricide control. The results suggest that the exploitation rate necessary to achieve eradication is about 90%, but the comparison of current adult abundance levels to those that would be expected in the absence of lampricide control suggests a much higher degree of suppression (about 98%), raising the question noted earlier of why eradication has not already been achieved. One explanation for this discrepancy might be that there is a component of the sea lamprey population that is not vulnerable to lampricide control and that this allows the population as a whole to persist despite removal rates that appear sufficient to achieve eradication. For example, larval populations have recently been identified in the St. Clair River upstream of Lake Erie that will prove costly or even impossible to effectively treat with lampricide because of their widespread, low density distribution. The implication of this is that eradication success will depend on our ability to find a control strategy that can effectively target the component of the population that is less vulnerable to lampricide. One possibility that is of growing interest to sea lamprey managers is genetic biocontrol (Thresher et al. 2019a). A genetic construct that, for example, distorted sex ratios, if introduced into a sea lamprey population would be expected to spread to all components of the population, given the panmictic nature of the sea lamprey population in individual lakes (Bergstedt and Seelye 1995).

The fifth criterion reflects the practical notion that eradication, however feasible it might be, is only justified if the costs can be justified relative to the expected benefits – when compared to other decision options such as controlling the population to target levels of abundance. The existence of a sea lamprey control program that for the last few decades has been guided by the objective of "meeting targets" suggests that this benefit-cost comparison has at least implicitly favoured control over eradication. However, we are not aware of any formal analysis that has led to this conclusion. Certainly any serious effort to determine whether an eradication strategy is wise to pursue should include a careful examination of this criterion – eradication may be possible, but still not worth doing. Uncertainty about the costs of strategies aimed at eradication will need to be reduced before strong conclusions can be reached about cost-benefit trade-offs. As well, the answer to this question will depend on what decision makers assume the discount rate to be, because the greatest benefits of an eradication strategy will accrue many years into the future. Finally, if sea lamprey abundance falls to very low levels due to successful control, the marginal cost of further control effort (i.e., cost per sea lamprey killed) will increase, and the benefits of further reductions may be small, which may affect the socio-political will for eradication.

Finally, the sixth criterion is that the socio-political environment would not be an impediment to implementation of the tactics necessary for eradication. Generally speaking the interested public has been highly supportive of sea lamprey control, despite the use of tactics (lampricides, barriers) that have the potential to raise socio-ecological concerns. If an eradication strategy were to be based on increased deployment of existing primary (lampricides, barriers) and supplemental (sterile male release, trapping, behavioural modification) control tactics it is reasonable to presume the socio-political license would be there. On the other hand, if the strategy requires deployment of new methods, such as genetic biocontrol techniques, the prospects for public support are less certain. Early evidence suggests that engaged Great Lakes fishery stakeholders are supportive of research and development of genetic biocontrols (Thresher et al. 2019b) but the degree to which the broader public would support such tactics is less clear, although there is emerging evidence for broader public support for the use of genetic biocontrols in agricultural systems (Jones et al. 2019).

Our analysis suggests that eradication of sea lampreys should not be considered “an impossible dream”. This analysis presents the first empirically-based examination of the lake-scale stock-recruitment dynamics for Great Lakes sea lampreys, an analysis which was not possible until empirical data on stream-level recruitment dynamics or adequate time-series of adult abundance became available. Our estimates of $u_{ext}$ from both analyses imply exploitation levels for eradication that are plausibly achievable. An eradication strategy would only likely be effective if it targeted all five Great Lakes, and if a tactic can be deployed that is able to target currently invulnerable components of the population. If these criteria can be met, at a reasonable cost relative to the alternatives, and without undermining public support for sea lamprey control, eradication of sea lampreys should be a part of the discussion about the future of sea lamprey management in the Great Lakes.

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## References

Bellard, C., Casey, P., and Blackburn, T.M. 2016. Alien species as a driver of recent extinctions. Biol. Lett. 12: 20150623. http://dx.doi.org/10.1098/rsbl.2015.0623

Bergstedt, R.A. and Seelye, J.G., 1995. Evidence for lack of homing by sea lampreys. Trans. Am. Fish. Soc. 124:235-239.

Bomford, M. and O'Brien, P. 1995. Eradication or control for vertebrate pests. Wildl. Soc. Bull. 23:249-255.

Dawson, H.A., Jones, M.L., Scribner, K.T., and Gilmore, S.A. 2009. An assessment of age determination methods for Great Lakes larval sea lampreys. N. Am. J. Fish. Manag. 29:914-927.

Dawson, H.A. and Jones, M.L. 2009. Factors affecting recruitment dynamics of Great Lakes sea lamprey (*Petromyzon marinus*) populations. J. Great Lakes Res. 35:353-360.

Gelman, A., Hill, J. 2007. Data Analysis Using Regression and Multilevel/Hierarchical Models. Cambridge University Press, Cambridge.

Glen, A.S., Atkinson, R., Campbell, K.J., Hagen, E., Holmes, N.D., Keitt, B.S., Parkes, J.P., Sanders, A., Sawyer, J., Torres, H., 2013. Eradicating multiple invasive species on inhabited islands: the next big step in island restoration? Biol. Invasions 15:2589–2603.

Jones, M.L., Irwin, B.J., Hansen, G.J.A., Dawson, H.A., Treble, A.J., Lui, W., Dai, W., and Bence, J.R. 2009. An Operating Model for the Integrated Pest Management of Great Lakes Sea Lampreys. Open Fish. Sci. J. 2:59-73.

Jones, M.S., Delborne, J.A., Elsensohn, J., Mitchell, P.D., and Brown, Z.S. 2019. Does the U.S. public support using gene drives in agriculture? And what do they want to know? Science Advances 5:eaau8462.

Millennium Ecosystem Assessment. 2005. Ecosystems and Human Well-Being: Current State and Trends: Findings of the Condition and Trends Working Group, Island Press

Ricciardi, A., Blackburn, T. M., Carlton, J. T., Dick, J. T. A., Hulme, P. E., Iacarella, J. C., Jeschke, J.M., Liebold, A.M., Lockwood, J.L.,MacIsaac, H.J., Pyšek, P., Richardson, D.M., Ruiz, G.M., Simberloff, D., Sutherland, W.J., Wardle, D.A., and Aldridge, D. C. 2017. Invasion science: A horizon scan of emerging challenges and opportunities. Trends in Ecology & Evolution, 32( 6), 464– 474.

Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. Bulletin of the Fisheries Research Board of Canada, Bulletin 191, Ottawa. http://www.dfo-mpo.gc.ca/Library/1485.pdf

Russell, J.C., Holmes, N.D. 2015. Tropical island conservation: rat eradication for species recovery. Biol. Conserv. 185. 1-7.

Simberloff, D., Martin, J.-L., Genovesi, P., Maris, V., Wardle, D. A., Aronson, J., Courchamp, F., Galil, B., Garcia-Berthou, E., Pascal, M., Pyšek, P., Sousa, R., Tabacchi, E., and Vilà, M. 2013. Impacts of biological invasions: What's what and the way forward. Trends in Ecology & Evolution, 28( 1), 58– 66.

Spiegelhalter, D.J., Thomas, A., Best, N.G., and Lunn, D. 2004. "WinBUGS Version 2.0 Users Manual." MRC Biostatistics Unit, Cambridge. URL http://mathstat.helsinki.fi/openbugs/.

Stewart, T.J., Todd, A., and LaPan, S. 2017. Fish community objectives for Lake Ontario [online]. Available from: www.glfc.org/pubs/FisheryMgmtDocs/Fmd17-01.pdf [accessed 27 July 2017].

Sturtz, S., Ligges, U., and Gelman, A. 2005. R2WinBUGS: a package for running WinBUGS from R. J. Stat. Softw. 12:1-16.

Sullivan, W.P., Christie, G.C., Cornelius, F.C., Fodale, M.F., Johnson, D.A., Koonce, J.F., Larson, G.L., McDonald, R.B., Mullett, K.M., Murray, C.K., and Ryan, P.A. 2003. The Sea Lamprey in Lake Erie: a Case History. J. Great Lakes Res. 29 (Supplement 1):615–636.

Vélez-Espino, L.A., McLaughlin, R.L., and Pratt, T.C. 2008. Management inferences from a demographic analysis of sea lamprey (*Petromyzon marinus*) in the Laurentian Great Lakes. Canadian Journal of Fisheries and Aquatic Sciences 65: 227-244.

Thresher, R.E., Jones, M.L. and Drake, A.R. 2018. Evaluating active genetic options for the control of sea lampreys (Petromyzon marinus) in the upper Laurentian Great Lakes. Canadian Journal of Fisheries and Aquatic Sciences https://doi-org.proxy2.cl.msu.edu/10.1139/cjfas-2018-0153

U.S. Congress, House. (1951). Further research and control of sea lampreys of the Great Lakes area. Merchant Marine and Fisheries, Subcommittee on Fisheries and Wildlife Conservation. Washington, U.S. Government Printing Office p. 4.

## Tables

Table 1. Six criteria required for a successful pest eradication program (after Bomford and O'Brien 1995).

1. The rate of removal of the pest can exceed the rate of increase.
2. Immigration of the pest into the target area for eradication is prevented.
3. All reproductive animals must be at risk.
4. The pest can be detected at low densities.
5. A discounted cost-benefit analysis favours eradication over control.
6. There is a suitable socio-political environment.

Table 2. Years for which adult abundance data were available for both the recruitment year (*t*) and the three brood years (*t*-5, *t*-6, *t*-7) that produced those recruits, for each of the Great Lakes.

| Lake | Available years |
|---|---|
| Superior | 1994-1996, 2001-2019 |
| Michigan | 2003-2019 |
| Huron | 1994-1995, 2000-2019 |
| Erie | 2006-2007, 2017-2019 |
| Ontario | 1995-2019 |

Table 3. Posterior median estimates and 95% credible intervals for parameters estimated for the empirical and synthetic models.

| Parameter | | Empirical model | | | Synthetic model | | |
|---|---|---|---|---|---|---|---|
| | Lake | median | 2.5% | 97.5% | median | 2.5% | 97.5% |
| $\alpha$ | | 2.43 | 1.56 | 4.09 | 9.92 | 9.31 | 10.61 |
| $N_0$[†] | Superior | 263,850 | 141,020 | 1,810,775 | | | |
| | Michigan | 132,800 | 83,810 | 221,750 | 5,491,000 | 5,260,000 | 5,770,000 |
| | Huron | 261,850 | 168,920 | 508,080 | | | |
| | Erie | 16,780 | 8,880 | 58,510 | | | |
| | Ontario | 67,030 | 42,370 | 186,100 | | | |
| $\Upsilon$[*] | | 0.261 | 0.001 | 0.520 | | | |
| $u_{ext}$ | | 0.588 | 0.339 | 0.762 | 0.899 | 0.893 | 0.906 |

[†] Uncontrolled equilibrium adult abundance estimates (= ln($\alpha$)/$\beta$).

[*] Estimate of the effect of lampricide treatment on adult abundance.

Figure Captions

Figure 1. Assessed abundances for adult sea lampreys in each of the Great Lakes between 1993 and 2019. See Table 2 for the years included in these time series.

Figure 2. The fitted stock recruitment relationships inferred from adult abundance data for each of the five Great Lakes.

Figure 3. A sample of 240 stock-recruit pairs generated from the SLaMSE model for Lake Michigan, with lampricide control set to zero and four levels of lake-wide trapping exploitation rates.

Figures as separate file(s)

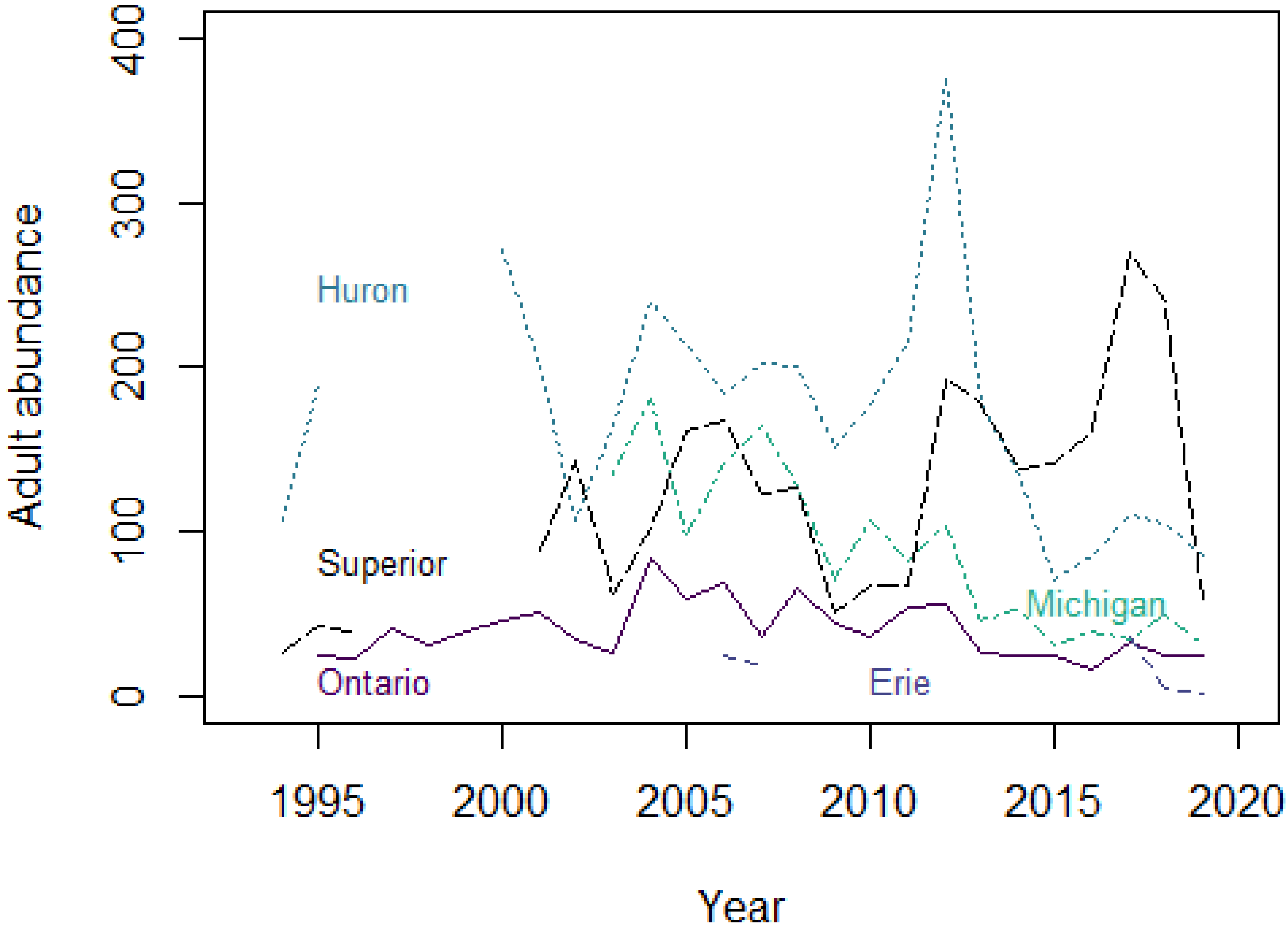

Figure 1. Assessed abundances for adult sea lampreys in each of the Great Lakes between 1993 and 2019. See Table 2 for the years included in these time series.

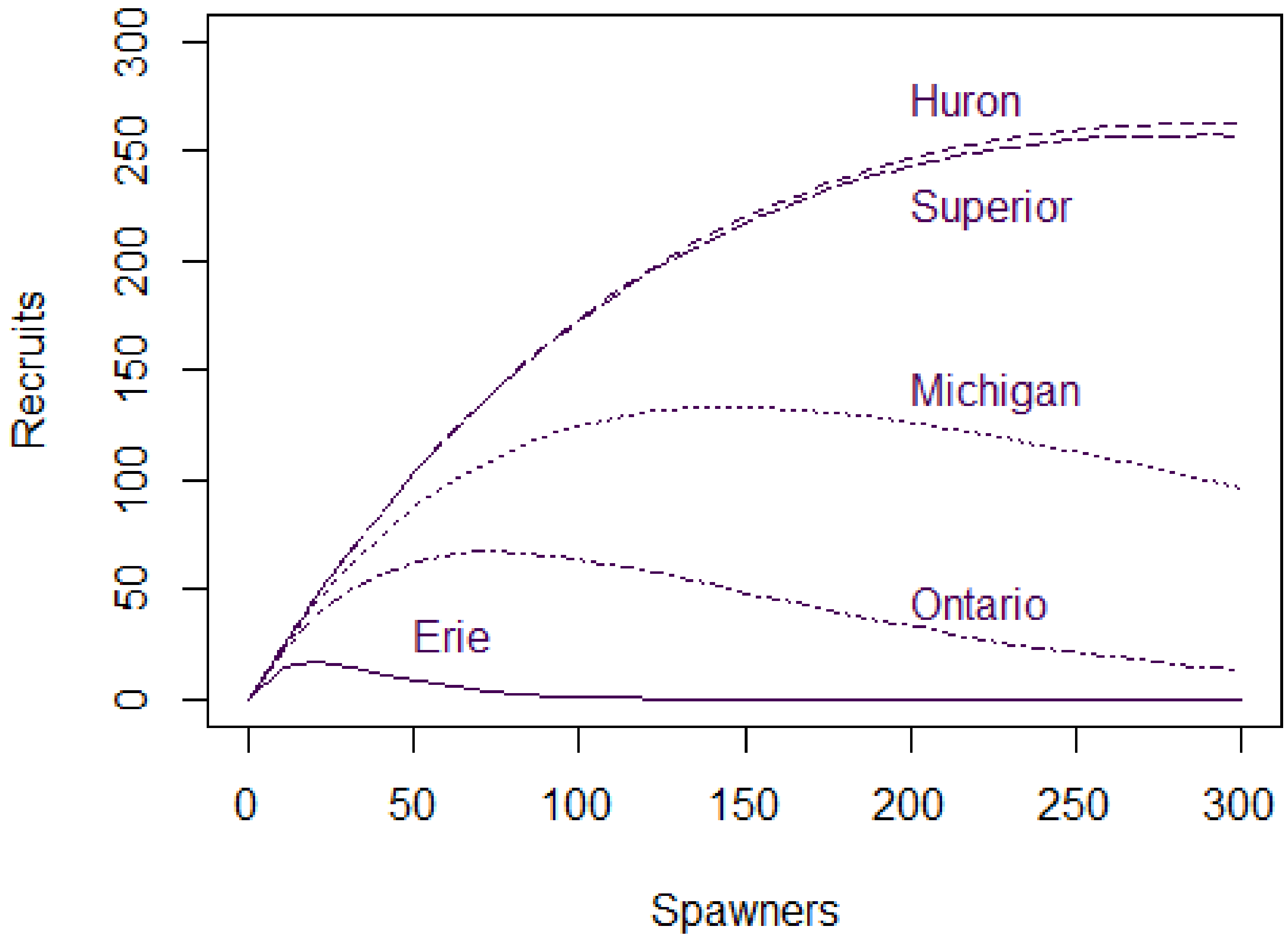

Figure 2. The fitted stock recruitment relationships inferred from adult abundance data for each of the five Great Lakes.

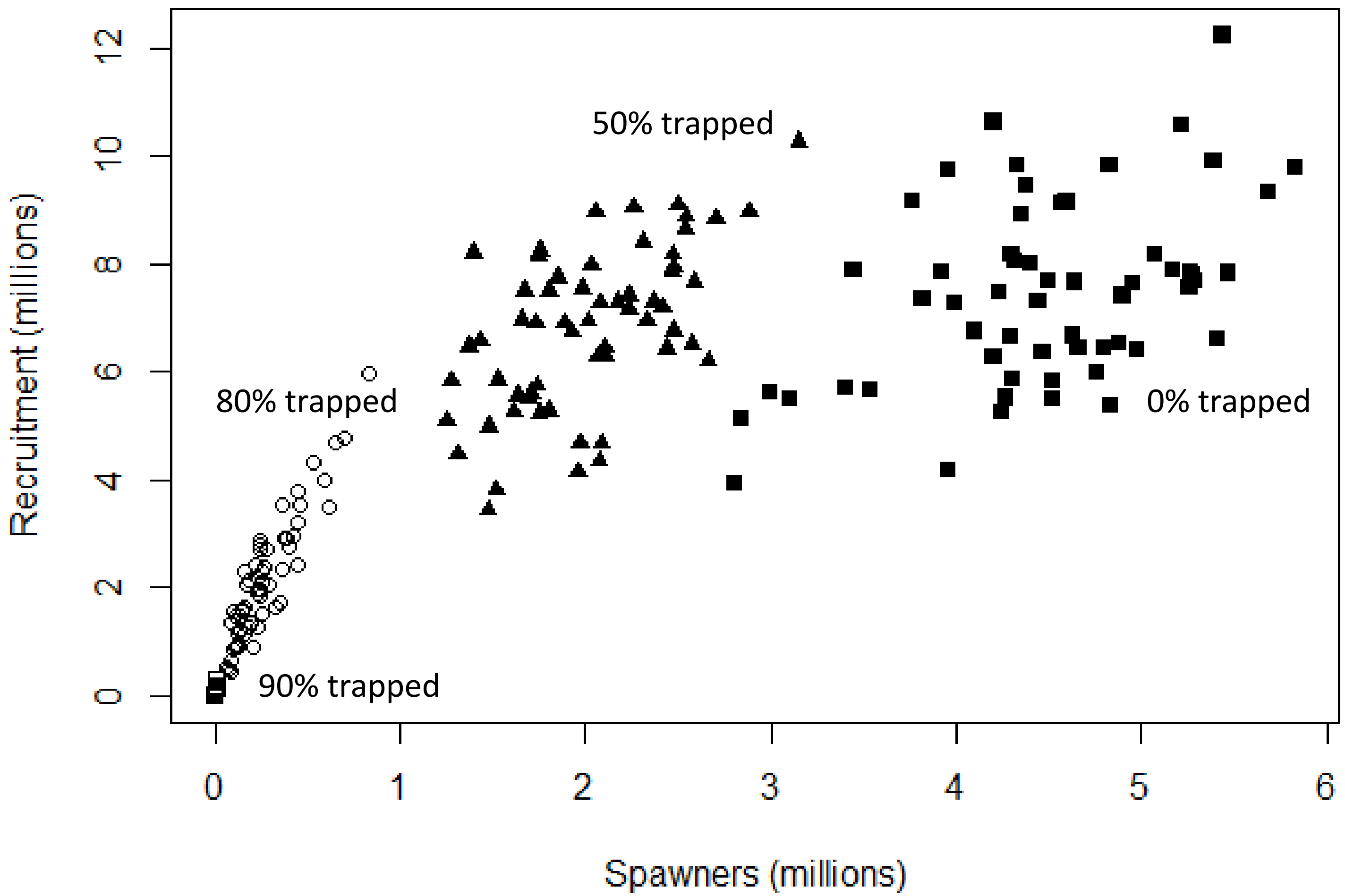

Figure 3. A sample of 240 spawner-recruit pairs generated from the SLaMSE model for Lake Michigan, with lampricide control set to zero and four levels of lake-wide trapping exploitation rates.