Defining Targets for Sea Lamprey Control in the Great Lakes: Economic Injury Levels and Fish Community Goal-based Targets

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[1] This technical report is identical in content to a project completion report submitted to the Great Lakes Fishery Commission.

ABSTRACT:

We estimated economic injury levels (EILs) and the associated treatment budgets for sea lamprey (*Petromyzon marinus*) control for each of the Great Lakes using common assumptions and methods. EILs are sea lamprey abundances below which incremental increases in control expenditures do not pay for themselves in terms of fishery benefits (in the form of increased harvest of desired host species). We assume that sea lamprey control efforts result in an increase in the availability of additional adult hosts for fishery harvest, which provides additional economic value to society. For each of the Great Lakes separately, we used a stochastic population model to simulate the entire sea lamprey life cycle as well as management actions that can affect multiple generations (e.g., treatment of streams with lampricide) over a range of potential control budgets. Model simulations relied on input data (e.g., stream-specific measures of larval habitat and growth), which were provided by the Great Lakes Fishery Commission (GLFC) and by sea lamprey biologists and managers at a project workshop and through later correspondence. In response to recommendations from these interactions with sea lamprey control agents, various modifications to the simulation model (inclusion of drainage-area information, incorporation of a non-linear larval growth model, variable treatment effectiveness, inclusion of treatable lentic habitats) were made during this project. Prior to running simulations, the model was calibrated for each Great Lake so that it replicated recent observed spawning-phase sea lamprey abundance given recent control budgets. We also compared our calculated EILs with current GLFC/Lake Committee accepted interim damage targets for spawning-phase sea lamprey abundance. Current damage targets suggest that a substantial reduction of sea lampreys across the Great Lakes is desired. Our EILs suggest that even lower average levels of sea lamprey abundance are justifiable, and may be obtainable, with a sufficient sustained increase in expenditures on control. This conclusion relies on the assumptions that lentic area treatments could successfully reduce some previously untreated sources of sea lampreys and remaining “untreatable” areas would produce few sea lampreys.

INTRODUCTION:

Sea lampreys (*Petromyzon marinus*) are considered exotic throughout much of the Great Lakes region, and their parasitism is detrimental to native fishes (Hubbs and Pope 1937; Lawrie 1970). In particular, dramatic declines in abundance of native lake trout (*Salvelinus namaycush*) occurred coincident with increases in sea lamprey numbers in the Great Lakes (Coble et al. 1990), although over-fishing also may have contributed to declines in some fish stocks (Wilberg et al. 2003). Due to the undesired negative effects on desired host species, much effort is routinely expended in an attempt to control sea lamprey populations. Currently, the Great Lakes Fishery Commission (GLFC) oversees a multifaceted treatment program that includes annual application of chemical lampricides, including TFM (3-trifluormethyl-4-nitrophenol; Hubert 2003) and various formulations of Bayluscide (Dawson 2003), which are used to reduce the number of larval sea lampreys. For each of the Great Lakes, individual streams are identified for treatment using the Empiric Stream Treatment Ranking (ESTR) system, in an effort to select streams in a way that maximizes the reduction of larval sea lampreys per unit treatment cost (Christie et al. 2003). Even though the costs associated with reduction of larval sea lampreys through lampricide treatments are substantial, insufficient reduction of the sea lamprey population also induces costs through the loss of desirable fish species. Therefore, an overall goal of the current sea lamprey control program is to balance the economic costs of control efforts with the economic value gained by avoiding fishery damages caused by sea lampreys in each of the Great Lakes.

Identifying lake-specific optimal control levels is important because such levels would provide an economic rationale for the desired total investment in sea lamprey control and its allocation across the Great Lakes. While more control will generally lead to the benefit of a less afflicted host population, an optimal level of control needs to balance this benefit with the cost. Here, we contribute information towards achieving the objective of lake-specific optimal control targets by assessing the costs and benefits of control treatments using a combination of economic and ecological analyses. Specifically, we present economic injury levels (EILs; e.g., Koonce et al. 1993) and associated budgets related to steady-state or average abundance of spawning-phase sea lampreys exposed to sustained control efforts for each of the five Great Lakes. For this study, an EIL is identified as the point (sea lamprey abundance level) where additional control expenditure would exceed the corresponding economic value of additional host fish that survive due to reduced exposure to sea lampreys (see Methods for description of calculations). On a plot of net profits, the EIL would be the inflection point where profits no longer increase at increasing treatment levels.

Previous efforts have generated EILs of sea lamprey abundance for Lakes Ontario (Koonce et al. 1993; Larson et al. 2003) and Erie (Sullivan et al. 2003) based on TFM applications, and preliminary EILs have been developed for Lakes Michigan and Huron (Szalai et al. 2005) based on control expenditures. Because these previous calculations of EILs did not use consistent assumptions and methods across lakes, their comparability is limited. Further, an EIL calculation has not been presented for Lake Superior. Here, we used common methods and assumptions with lake-specific information and a recently modified version of a stochastic simulation model to calculate updated EIL budgets and new EIL values for all five Great Lakes. Moreover, our basin-wide comparison of EILs provides managers with the opportunity to evaluate allocation of resources among all five lakes and whether additional basin-wide investment in sea lamprey control can be justified. A synopsis of the major findings of this study is provided in Appendix 1.

OBJECTIVES:

Here, we list project objectives and provide a brief summary for each:

1) To develop EIL estimates for all five Great Lakes based on a common method and set of assumptions.

> This objective was met by calibrating a stochastic-simulation model to each Great Lake and using it to forecast average abundance of spawning-phase sea lampreys as well as the control process (e.g., selection of treatment areas). Parameters describing relationships between sea lamprey abundance and control costs were then fit to each simulation, and these

parameters were used to calculate distributions of optimal control budgets and EILs for each lake. We also performed sensitivity analyses related to assumptions of host value and probability of surviving a sea lamprey attack. Results from this objective suggest that increased annual investment in sea lamprey control is economically justifiable.

2) To review the assumptions, strengths, and limitations of alternative methods for determining appropriate targets for sea lamprey control in the Great Lakes.

In this report, we completed a synthesis of the details associated with the EIL approach and compared these values with interim damage targets, currently accepted by the GLFC and Lake Committees, and the approach used to derive those values. Assumptions, strengths, and limitations of EILs as targets for sea lamprey control were also presented through various project updates (Appendix 1). Certain assumptions were needed to mathematically represent the sea lamprey life cycle (e.g., growth and recruitment models) as well as sea lamprey control (e.g., potential range in treatment effectiveness, amount of "untreatable" areas that support production of sea lampreys). The explicit linkage between control efforts and predicted consequences and detailing of the assumptions underlying this linkage are strengths of the EIL approach. An additional strength of the EIL approach is that it explicitly balances economic benefits and costs. Furthermore, it provides economic benchmarks that can be compared among all five Great Lakes and can aid decisions about allocation of management resources among locations. These economic benchmarks can also be compared with current control levels. These comparisons benefit from using consistent assumptions across the lakes. Some limitations of the EIL work arise from various uncertainties about both the sea lamprey life cycle (e.g., larval survival rate) and control efforts (e.g., sources of larval lamprey that survive to spawning-phase). These uncertainties increase the number of assumptions that are required to perform simulations. Likewise, EIL calculations also require specification of values that retain some subjectivity, such as the monetary value of a host species. In this case, we can simply calculate optimal treatment budgets across a range of plausible host values. An additional limitation of the EIL approach is that it assumes that fish community objectives, in terms of species composition and abundance of lake trout, will be achieved and that extractions from that community can be reallocated from sea lamprey to human use. Such an approach cannot be used to decide on an appropriate mortality rate target for a host species or whether that mortality rate should be reduced during rehabilitation. Thus, the EIL approach cannot directly address whether higher levels of control should be implemented during rehabilitation than can be justified once the fish community has reached a desired state. We argue it is likely that higher levels of expenditures are warranted during rehabilitation but formal analysis of this claim would require alternative economic approaches.

The interim damage targets are based on a view that marking rates can be used to identify a tolerable level of sea-lamprey induced mortality rates that are consistent with efforts to achieve fish community objectives. An advantage of this approach is that it is applicable when fish community objectives are not met, and the process of developing them has explicitly incorporated Lake Committee views about what level of mortality would allow acceptable progress in achieving the objectives. Like the EILs, interim damage targets take the fish community objectives as given. A significant limitation is that these targets do not explicitly account for a tradeoff between benefits from sea lamprey control and the costs of the program. Thus although they might reflect an acceptable level of marking and associated sea lamprey abundance from the perspective of fishery resource managers, they do not address whether higher investment in control and lower sea lamprey abundances might be justified. The target marking rates are partly based on the same uncertain information on lethality of sea lamprey attacks used in EIL calculations as well as additional assumptions on how marks made by sea lamprey heal. Furthermore, the translation of marking targets into a target for sea lamprey abundance presumes that in the future the same relationship between target sea lamprey abundance and target marking rates will apply as did during a historical reference period.

3) To evaluate how sea lamprey abundances corresponding to the GLFC damage target of five A1-3 marks per 100 lake trout compare with EIL sea lamprey abundances.

We used common methods and assumptions to calculate EILs for each Great Lake and compared these values to abundance levels corresponding to the interim damage targets currently in use. The GLFC interim marking targets are actually five A1-3 marks per 100 fish on all lakes except Lake Ontario, where the marking target is two A1 marks per 100 fish. For most plausible host values, EILs were less than these current damage targets for all five Great Lakes. Only at the lowest highlighted host value did EILs approximate or exceed the interim damage targets for sea lamprey abundance. Both interim damage targets and EILs suggest that a substantial reduction in recent sea lamprey levels is warranted. EILs were associated with sustained, long-term treatment control expenditures which were higher than current levels of actual expenditure. Given that host populations have not necessarily reached desired long-term average levels, control levels during rehabilitation from low lake trout stock sizes likely warrant even higher investments in treatment.

METHODS:

General overview

We used a stochastic age-structured operating model to simulate sea lamprey population dynamics and perform numerous projections of control efforts for each of the Great Lakes: Superior, Michigan, Huron, Erie, and Ontario. For each lake, the model operated using stream-reach specific information derived from quantitative assessment surveys (QAS) recorded in the Great Lakes Fishery Commission's ESTR database (Christie et al. 2003). Over the course of the project, we used an interactive format in project workshops with biologists and sea lamprey managers to present preliminary results and identify areas that would improve realism through model refinement

(Appendix 2). Here, we provide only a brief overview of the operating model's structure related to the calculations of EIL budgets and EILs. For additional details about numerous submodel components of the operating model (e.g., growth, recruitment, metamorphosis, population assessment and treatment) see Jones et al. (2003), Dawson (2006), and Jones et al. (*in prep.*)[1]. In addition to modeling the entire life cycle of sea lamprey, the operating model also simulates lamprey-control treatments of individual streams as well as lentic areas that can contribute to the production of sea lampreys (e.g., Wagner and Stauffer 1962; Haeseker et al. 2007). Because uncertainty was explicitly incorporated in several sub-models (e.g., recruitment, assessment of larval abundance, variation in effectiveness of treatment), these stochastic forecasts were repeated 500 times for each control budget considered. Each simulation was a 250-year projection to allow the simulated population to reach an average steady state relative to the imposed control measures.

Projection of the sea lamprey population and control treatments

Multiple habitat types were spatially represented in the operating model, including: individual streams, a river pool, an untreated pool, and a lentic pool. For each Great Lake, the individual simulated streams represented actual streams assessed and treated by sea lamprey biologists, and these streams were defined based on empiric data from ESTR. For most lamprey-supporting streams, QAS surveys have provided information (e.g., amount of larval habitat, estimates of larval growth rate) at the level of individual reaches. Each individual stream reach had a known cost-to-treat and an expected achievable level of treatment effectiveness, which were also included in the empiric database. The river pool was implemented to more realistically represent the treatment of the St. Marys River and was active only for the Lake Huron simulations. Unlike the streams and the river pool, the untreated pool was not intended to represent specific locations. Rather, it was included in the model to represent sources contributing to production of larval sea lampreys that are unaffected by current control efforts. Based on discussions with sea lamprey control agents, the untreated area was

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[1] Jones, M. L., H. A. Dawson, B. J. Irwin, A. J. Treble, W. Liu, W. Dai, and J. R. Bence. (*in prep*.). An operating model for Great Lakes sea lamprey integrated pest management.

set to 2% of the larval habitat area for each lake (i.e., the amount of untreated area then varied among lakes). Lastly, the lentic pool represents lentic areas (typically located at the mouths of infested streams) which are able to support larval sea lampreys and are currently available, at a cost, for lampricide (e.g., Bayluscide) treatments.

Each simulation began with an initial population size of 75,000 spawning-phase sea lampreys and an age-0 larval density of 1 m^{-2} based on specified larval habitat areas. In all subsequent years, the allocation of returning spawning-phase sea lampreys to individual streams occurred through a combination of the stream's drainage area and the stream reach's current larval abundance and larval habitat area. These two differing parts of the allocation rule were intended to represent 1) high-discharge streams that can accommodate large numbers of returning spawning-phase sea lampreys (Mullett et al. 2003) and 2) olfactory cues related to con-specific larval abundance that likely help attract spawning-phase sea lampreys to particular stream reaches (Li et al. 1995; Sorensen and Vrieze 2003). Likewise, spawning-phase sea lampreys were allocated to either the river pool or the untreated pool based on the similar rules as for streams (larval habitat area and larval abundance). However, the river pool differed from the untreated pool in that it also included alternative control options in the form of direct removal of returning spawning-phase sea lampreys (trapping) or through use of the sterile-male-release technique (SMRT; Twohey et al. 2003). Trapping directly reduces the number of returning females through their removal and contributes males for use in SMRT. Captured spawning-phase males are sterilized and then returned to the St. Marys in an attempt to lessen the production from the remaining mature females. To represent these alternative controls in the Lake Huron model, a 40% reduction was imposed on returning spawning-phase sea lampreys allocated to the river pool. In each of these habitat areas, spawning-phase sea lampreys produced recruits (age-0 larvae) assuming a Ricker stock-recruitment relationship (Jones et al. *in prep.*).

Both the river pool and lentic pool contained individual spatial sub-units that were on the scale of the chemical applications applied to individual stream sections so that units for each of these areas could be ranked and considered for treatment. The rule for ranking and selecting an area for treatment was constant across habitat types and was based on the anticipated number of transformers that could be killed given associated treatment costs. Treatment costs for stream sections were included in the lake-specific databases provided by the GLFC. For treatment of lentic areas, we assumed a \$5000 ha^{-1} expense based on actual recent lentic treatment costs for plots in the St. Marys River (GLFC, unpublished data) to calculate the cost-to-treat for individual lentic units. Also, the same methods were used to allocate larvae into these individual spatial sub-units for both the river pool and the lentic pool (Appendix 3); however the methods that determined the total number of age-0 larvae designated to either pool for a particular year differed between pools. For the river pool, age-0 larvae were determined using stock-recruitment relationships, as indicated above. Alternatively, an "outflow scalar" was used to transfer a proportion of age-0 larvae produced in streams and the untreated pool to the lentic pool. This outflow scalar was modified during the calibration process (described below). For the remainder of the sea lamprey life cycle, each of the "pool" habitat areas followed the same rules as the stream habitats using lake-specific averages determined by the stream-specific database values.

Sources of uncertainty

The operating model incorporated several sources of uncertainty related to recruitment and treatment of sea lampreys. For example, recruitment was modeled using a stochastic Ricker stock-recruitment function so that reoccurrences of similar stock sizes over time or among stream reaches did not necessarily produce similar levels of recruitment (see Jones et al. *in prep*. for more details). In addition, assessment uncertainty was simulated by adding error to the actual abundance of larvae in a stream reach prior to the ranking and selection of areas for treatment. This error term was drawn from a gamma distribution with a CV of 1.71 (Steeves 2002) and mimicked the uncertainty associated with real-world selection of streams for treatment. Likewise, we simulated population assessments for individual units of both the treatable lentic habitat and St. Marys River using the same uncertainty assumptions as described for the stream reaches because there is no reason to expect that larval density surveys in these habitats would be any more precise than stream surveys. Because each stream reach represented a known location, an anticipated treatment effectiveness value was specified in the empiric database. The treatment effectiveness of lampricide in lentic habitats is generally less than in streams (Bills and Genovese 1990). For ranking of lentic units for treatment selection, we assumed a treatment effectiveness of 75% for all lentic units. Using the population assessments combined with anticipated treatment effectiveness and control costs, the anticipated number of transformers that could be killed through treatment per control dollar spent was calculated for each stream reach and lentic unit for each year. Based on this selection rule, individual lentic units were then ranked together with stream treatment units. Once a stream section was selected for treatment in the simulation model, the actual treatment effectiveness applied was modeled as variable over time (drawn from a highly-skewed Beta distribution; see Appendix 4). Little is known about the variability of treatment effectiveness in lentic areas; therefore, we assumed that actual treatment effectiveness of a lentic unit would vary about a mean 75% according to a normal distribution with a CV of 0.10. Therefore, reselection of a habitat unit over time for lampricide treatment did not necessarily produce identical levels of larval lamprey reduction.

Calibration of the operating model for each Great Lake and summary of simulations

Prior to running the simulations, we calibrated the model for each Great Lake using the lake-specific databases as well as information on both recent control expenditures (7-year mean of recent annual lampricide budgets, 1998-2004) and recent observed values of abundance for spawning-phase sea lampreys (7-year mean, 2000-2006; Table 1; Fig. 1). For each lake, the calculations of target calibration abundance and control budget values were offset by a two-year lag to approximate an expected delay between treatments targeting larval lamprey and measures of the adult population. The goal of the calibration process was for the simulation model to approximate spawning-phase sea lamprey abundances close to recent observations when using control budgets that correspond to actual recent expenditures. The lake-specific calibration budgets were the combined costs associated with TFM and treatment staff (effort). The calibration budget for Lake Huron also included costs associated with Bayluscide treatments because the effects of these extra treatments could not be removed from the corresponding estimates of sea lamprey abundance. Except for Lake Huron, lentic areas were not treated during the calibration process to correspond more closely to control efforts summarized for the calibration budgets. Larval survival was the primary adjusted parameter during these calibrations based upon earlier work (e.g., Szalai et al. 2005) and because it remains an important demographic parameter for which we presently have very limited information about its true value. In addition to the larval survival rate, we adjusted an outflow scalar which determined the movement of age-0 larvae from streams and the untreated pool into lentic areas. This outflow scalar was adjusted so that density of larvae in lentic areas was approximately one quarter of the average density in streams during the calibration runs. This target ratio was based on observed densities from a lentic inventory survey where larval lamprey densities were measured in both natal lotic areas and associated lentic habitats (Mike Steeves, unpublished data; Appendix 5).

To compare simulated sea lamprey abundance to the calibration target abundance, we defined the equilibrium level as mean abundance of spawning-phase sea lampreys resulting from sustained treatment. For each simulation (i) of a given control budget (C; in this case the calibration control budget), the simulated abundance of spawning-phase sea lampreys was averaged across final 10 years of the simulations $\left(\bar{x}_{i,C}\right)$. Then, a grand mean $\left(\bar{\bar{x}}_{C}\right)$ was also calculated by averaging $\bar{x}_{i,C}$ across the 500 simulations. The larval survival rate was adjusted until these lake-specific grand means were approximately equal to the calibration target abundances.

Once the lake-specific calibrations were complete, 500 replications of the 250-year simulations were performed using the lake- and stream-specific databases and calibrated parameter values across a range of potential control budgets. Specifically, we evaluated 20 potential control budgets for each lake (Appendix 6). For each lake, the minimum control budget considered was calculated as 75% of the calibration budget. Then additional budgets were determined by applying a lake-specific increment equal to 5% of the lake's calibration budget. These increments varied from $13k for Lake Erie to $114k for Lake Huron. All economic values are presented in U.S. dollars. For each potential control budget and for each lake, we used the operating model to repeatedly simulate sea lamprey dynamics based on the entire sea lamprey life cycle as well as the control program (as described above), and summarized the results of each simulation by the average abundance of spawning-phase sea lampreys during the final 10 years of each simulation. The objective of these simulations was to develop a relationship between various potential levels of sustained control expenditures and the resulting expected abundances of spawning-phase sea lamprey.

EIL calculations

EIL calculations involve comparing pest-control related costs against the economic benefits provided by a desirable host species. Our first step in calculating EILs was to use the simulation outputs to generate curves of average long-term sea lamprey abundance versus amount of money spent annually on sea lamprey control for all five Great Lakes. Economic benefits are then calculated based on assumptions about sea lamprey feeding, host survival of attacks, and value of fish harvested by fisheries. Because 500 simulations were performed for each of the 20 lake-specific control budgets, the simulations provided 10,000 “observed” values $\left(\bar{x}_{i,C}\right)$ for each lake. For each simulation and control budget, the predicted average abundances of spawning-phase sea lampreys after sustained control $\left(L_C^*\right)$ was expressed as a function of control expenditures:

$$L_C^* = L_{\min} + \alpha e^{-\beta C},$$

where $L_{\min}$ is the asymptotic minimum abundance of spawning-phase sea lamprey, α and β are estimated shape parameters, and C represents a sustained level of control expenditures. The parameters $L_{\min}$, α, and β were estimated for each set of simulations that shared common stochastic errors (500 per lake) by minimizing the sum of weighted squared residuals, with weights set to $\left(\frac{1}{\sigma_C^2}\right)$, where σ_C^2 was the assumed relative variance of means at each control level. For each lake, these weights were calculated from the standard deviation of the 500 average abundance measures:

$$\sigma_C = \sqrt{\frac{\sum_{i=1}^{500} \left(\bar{x}_{i,C} - \bar{\bar{x}}_C \right)^2}{500 - 1}} .$$

During estimation, $L_{\min}$ was constrained to be positive as this parameter represents a minimum abundance value.

We implemented our estimation method using Solver in Microsoft Excel. Solver uses a quasi-Newton nonlinear search routine to iteratively update parameters, and we needed to specify starting values for parameters prior to the initiation of this search for the weighted least squares parameter estimates for each simulation. We did this by first specifying a common set of starting parameter values ($L_{\min} = 0.01,\ \alpha = 10,\ \text{and}\ \beta = 10$), and finding the unweighted least squares estimates for each simulation. These simulation–specific unweighted parameter estimates were then used as the starting values for the weighted least-squares fitting. We adopted this approach because we found that the approach of using the same set of starting values for every simulation for the weighted-fitting process occasionally could lead to convergence failure.

Once α and β were estimated for every set of simulation for each lake, they were combined with basin-wide parameters to calculate optimal control costs for each set of simulations, which were then averaged for each lake. Following the derivation of Koonce et al. (1993), the optimal control budget is:

$$\hat{C} = -\frac{1}{\beta} \log_e \left(\frac{1}{V} \frac{1 + ahN^*}{Ta} \frac{Z}{1 - e^{-Z}} \frac{1}{\alpha\beta} \frac{1}{N^*(1-p)} \right),$$

where V is the value of an individual of the host species (in dollars), a is a coefficient representing the effective search rate for a parasitic sea lamprey, h is the handling time of a sea lamprey (year^{-1}), T is the duration of the attack season for sea lamprey (as % of year), N^* is the abundance of the host species (number) associated with the sustained optimal control budget, Z is the target instantaneous mortality rate for the host species (year^{-1}), and p is the probability of a host surviving a sea lamprey attack. Here the optimal budget is defined as the budget for which marginal increase in the value of hosts saved for the fishery equals the incremental increase in the budget. At this point further increases or decreases in control expenditures lead to net losses. This equation simplifies with the assumption that parasitic sea lampreys are not search limited when hosts are at a high-density (a host-population goal of effective sea lamprey control; Koonce et al. 1993):

$$\hat{C} \approx -\frac{1}{\beta}\log_e\left(\frac{1}{V}\frac{h}{T}\frac{Z}{1-e^{-Z}}\frac{1}{\alpha\beta}\frac{1}{(1-p)}\right).$$

Henceforth, we refer to this calculated optimal treatment budget as the EIL budget. The host-species related parameters are not produced by the operating model, rather they were set to assumed values based on stated management objectives for lake trout, published estimates of sea lamprey feeding rates, and the probability of host mortality due to a sea lamprey attack.

Specification of a monetary value for individuals of the host species (e.g., lake trout) involves some subjectivity. Therefore, we highlight three potential economic values for an individual from the selected host species, including an arbitrary low-end value for lake trout of \$2.00. The lowest value reported by Szalai et al. (2005) was \$10, and we use that value for the graphical reporting of EIL budgets and EILs. Koonce et al. (1993) assumed a host value of \$12.00 using sport angling metrics based on an estimate reported by Eshenroder et al. (1987), which was derived from a value of angling days (Talhelm 1988) and sport angling information for Chinook salmon (*Oncorhynchus tshawytscha*) in the mid-1980s. We adjusted this value for inflation using the Consumer Price Index (www.bls.gov/data) to approximate this value in 2007 dollars and highlight this value (\$25) as a higher-end value for an individual lake trout. Beyond these three selected potential host values, we also performed a sensitivity analysis by calculating EIL budgets and EILs across a much wider range of plausible *V*.

We used the same values as Szalai et al. (2005) for h, T, Z, and p. The values for h (0.030137) and T (0.41) are from Rutter (2004). The choice of Z was based on the assumption that the population had reached equilibrium conditions (after rehabilitation), and a value of 0.6

(corresponding annual mortality of 0.45) was used for all lakes and is close to mortality rates of exploited lake trout population that are not declining (Healey 1978). For the primary presentation of EIL budgets and EILs, *p* was held constant (0.73). This value of *p* was based on calculations presented by Swink (2003) for a lake trout weight of 6 kg and previous work (Szalai et al. 2005) but was later evaluated as part of a sensitivity analysis. As for *V*, we also show how EIL budgets and EILs would change over a wide range of values for *p* (range: 0.25-0.93; e.g., Bence et al. 2003).

Once the EIL budget was determined for each simulation, the corresponding EIL was calculated as:

$$\hat{L}^{*} = L_{\min} + \alpha e^{\left(-\beta\hat{C}\right)}.$$

By calculating $\hat{L}^{*}$ for each of the 500 individual simulations for each lake across the 20 control budgets considered, it was possible to examine the distribution of potential EILs corresponding to the uncertainty included in the stochastic simulation model.

Interim damage targets

Currently, success of the sea lamprey control program is judged against interim damage targets established by comparing sea lamprey abundance estimates with benchmark sea lamprey marking rates on lake trout. We refer to these targets as interim because the GLFC and Lake Committees acknowledged that additional analysis considering both costs and benefits of sea lamprey control was needed. Thus, it is useful to compare EILs to these lake specific sea lamprey abundance targets. The interim damage targets reported here were provided by the Great Lakes Fishery Commission (G. Christie, unpublished data). The GLFC adopted the interim damage targets for each Great Lake to define the degree to which sea lamprey control is achieving fish community objectives. These interim damage targets were accepted by all Lake Committees as adequate reflections of the amount of sea lamprey suppression needed to achieve their fish community objectives. The interim damage targets for sea lamprey abundance are based on a benchmark marking rate chosen to correspond to tolerable levels of sea lamprey-induced mortality (additional detail given below).

Interim damage targets were estimated as the abundance of spawning-phase sea lampreys during a five-year period when the average observed marking rates indicated a tolerable rate of mortality on lake trout. Benchmark rates of sea lamprey marking on standardized sizes of lake trout were used to define periods of tolerable mortality. Sea lamprey marks on wounded lake trout were classified following the criteria established by King and Edsall (1979), King (1980), and Ebener et al. (2006). A type A mark indicates that a wound is open, and the healing stage is categorized from 1 (recent detachment, no healing) to 4 (skin nearly unbroken, near complete healing). Based on published relationships (see review in Bence et al. 2003), A1-3 marking rates of five marks per 100 fish were assumed to correspond to a instantaneous mortality rate due to sea lamprey of about 0.05 y^{-1}. For Lake Superior, the Lake Committee explicitly identified this mortality rate as defining a "tolerable rate of mortality" and that rate to define the fish community objective for sea lamprey (Horns et al. 2003). These benchmark rates of morality and marking were extended to Lakes Michigan, Huron, and Erie because they were considered to be consistent with achieving progress toward fish community objectives. While full time series of marking rates were available during spring for Lakes Superior and Huron, only fall time series were available for Lakes Michigan and Erie, but analysis indicated overall spring and fall marking rates were comparable. Thus, comparable benchmarks for tolerable marking rates were set to five A1-3 marks per 100 fish based on either fall or spring data for Lakes Superior, Michigan, Huron, and Erie. For Lake Ontario, the standard index of marking was A1 marks based on a late summer survey and relationships with carcass surveys (Bence et al. 2003). Fish community objectives for Lake Ontario specified a target marking rate of two marks per 100 fish (Stewart et al. 1999) based on empiric observations of survival of lake trout during periods when marking rates were at or below that level. This level of A1 marks was adopted as the benchmark for Lake Ontario, although this corresponds to a higher A1-3 marking rate than the target used on other lakes (ratio was 6.4:1 for A1-3 versus A1 during 1983-2002; Mark Ebener, unpublished analysis). Sea lamprey marking rates generally increase with host size (Bence et al.

2003), and thus marking rate targets were based on lake trout 53.3 cm (21 inches) or larger for each lake.

Interim damage targets for sea lamprey abundance were calculated by comparing the time series of marking rates to the time series of abundance estimates for spawning-phase sea lampreys. For each lake, abundance of spawning-phase sea lampreys was the total from all streams thought to contribute to lamprey production (Mullett et al. 2003). On rivers with traps, the spawning-run abundances were estimated with mark and recapture. On rivers without traps, spawning-run abundances were estimated from a regression model relating run size to stream discharge (i.e. drainage area) and larval abundance (i.e. years since last treatment). The time series of marking rates was used to establish the most recent five-year period during which marking rates were less than or equal to the benchmark rate for each lake. The interim damage target for sea lamprey abundance was estimated as the average abundance of spawning-phase sea lampreys corresponding to that five-year period. For Lake Huron, this was not possible because there was no historical period when the benchmark marking rate was achieved. In this case, the sea lamprey abundance target was calculated based on an explicit fish community objective for a percentage reduction in sea lamprey abundance and the estimate of sea lamprey abundance during a reference period from which this desired reduction was derived.

RESULTS:

Calibration results

For each lake, calibration targets were well approximated by the simulation model (Table 2). Important uncertainties (e.g., larval survival, outmigration of larvae from streams to lentic areas) were adjusted to calibrate the model, and values that approximated calibration targets varied among lakes (Table 2). The calibration process indicated that average abundance of spawning-phase sea lampreys was strongly positively related to changes in the larval survival rate, although the selected annual survival rates only ranged from 40-52%. Likewise, the outflow scalar required to approximate a lentic to lotic ratio for larval density of 25% varied among lakes (Table 2) because of differences in areas of both habitats. Based upon expert advice from sea lamprey assessment biologists, the largest amount of lentic areas represented in our simulations was the St. Marys River (700 ha; in Lake Huron model); whereas, no lentic areas were included in the Lake Erie model (and thus no outflow scalar was used).

Following calibration steps, we simulated and summarized spawning-phase sea lamprey abundance for 500 simulations for each of 20 potential control budgets for each lake (Appendix 6). For every simulation, we predicted an average abundance of spawning-phase sea lampreys corresponding to the sustained control budget used for that simulation by summarizing across the final 10 years of each simulation (illustrated for the calibration budget in Appendix 7). Average abundance of spawning-phase sea lampreys (across final 10 years and over 500 simulations) declined exponentially with increases in control expenditures (as illustrated for Lake Ontario in Fig. 2).

EIL budgets and EILs

EIL budgets varied widely across lakes. For each Great Lake, we highlighted EIL budgets for three selected host values ($2, $10, and $25; Table 3). For these selected host values, the average EIL budgets for Lakes Michigan and Huron were always greater than 2.2 million dollars; whereas, the average EIL budgets for Lakes Erie and Ontario were less than 1 million dollars for these same host values. The average EIL budget for Lake Superior was intermediate, ranging from 1.2 to almost 1.7 million dollars over three host values. At V = $10, the basin-wide optimal annual expenditure was nearly $8.5 million dollars, nearly a 35% increase above recent control expenditures. By lake, justifiable increases in control expenditure ranged from 25 (Lake Erie) to nearly 50% (Superior) at this selected host value (V = $10). EIL budgets also varied among the 500 sets of simulations within a lake due to demographic and assessment uncertainty, but the majority of the sets of simulations produced EILs close to the mean (Fig. 3).

Correspondingly, the EILs varied widely among lakes. For each lake, EILs were reduced by an increase in host value and larger justifiable EIL budget. As host value increased from $2 to $25, the largest proportional decrease in the EIL was seen for Lake Superior (nearly 89%), while Lake Ontario's EIL decreased by only about half. Recent estimates of spawning-phase sea lampreys suggest basin-wide abundance levels in excess of 400,000 individuals (Table 1; Fig. 1). Current interim damage targets suggest that an approximately 50% reduction in abundance of spawning-phase sea lampreys is desired across the basin. EILs, totaled across lakes at V = \$10, suggest that long-term sustained treatments at optimal EIL budgets could produce targets closer to 100,000 individuals. At V = \$10, EILs were below interim damage targets for each Great Lake. Only when host value was reduced to the lowest highlighted value (\$2 per individual host harvested) did EILs approximate or exceed interim damage targets. Taken in reverse, if it was decided to sustain sea lamprey control so as to achieve the current interim damage targets on average, this would only be optimal in the context of EIL calculations for a very low host value. Even at the lowest highlighted value for hosts, EILs were considerably below recent population estimates. Variation in EIL budgets across simulations (Fig. 3) produced a proportionally large variation in EILs (Fig. 4).

We further evaluated the sensitivities of calculated EIL budgets and EILs to changes in two poorly determined quantities relating to the host population by varying V and p across a wide range of plausible values of each and then recalculating the EIL budgets and EILs. Therefore, even though we highlight values relative to selected quantities, we also show that these results can be produced across a continuum of potential values (Figs. 5 – 6). Average EIL budgets and EILs were highly sensitive of changes across lower-end V (Fig. 5), with substantially less variation at larger V. Conversely, average EIL budgets decreased (and hence EILs increased) as p increased (Fig. 6). Therefore, if a less optimistic value were assumed for p than used in Table 3, larger EIL budgets would be justified. Increasing the expected probability of survival from 0.73 to 0.93 would have the opposite effect. For example, the average EIL budget for Lake Ontario (at V = \$10) would drop from 0.86 to 0.74 million dollars due to this change in p (Fig. 6).

DISCUSSION:

A basin-wide comparison of EILs, such as the one we present here, provides managers with the opportunity to evaluate allocation of resources among all five Great Lakes and whether additional investment in sea lamprey control can be justified. Our EIL budgets were consistently larger than current control expenditures across a wide range of plausible host-species values, suggesting that recent levels of control expenditure do not produce the maximum benefits obtainable from a host-species population. These EIL budgets are for a sustained steady state when lake trout have reached a desirable (rehabilitated) abundance. In general, we believe that during rehabilitation from low lake trout stock sizes even higher levels of control could be justified, so as to reach the optimal conditions sooner. Thus, we think that our EIL budget estimates should be viewed as minimum justifiable investments in control. Likewise, current damage targets indicate that reducing spawning-phase sea lamprey abundance to about half of recent levels is desirable. EIL estimates were lower than these interim damage targets for all five Great Lakes, suggesting that it can be economically justified to increase budgets for sea lamprey control above levels that would over the long-term achieve, on average, the interim targets for sea lamprey abundance. Combined, these metrics argue for sustained, long-term control expenditures that are higher than current levels of actual expenditure and that these higher levels of control expenditure are economically justifiable. The management implications of our work include supporting sustained, increased expenditure on sea lamprey control for each of the Great Lakes.

Consistent with the objectives of the sea lamprey control program in the Great Lakes, Pedigo and Higley (1996) describe the goals of integrated pest management as reducing pest status, accepting the presence of a tolerable pest density, conserving environmental quality, and improving user profits. When deciding to manage a pest population with the goal of avoiding future economic losses, it may be preferable to keep pest densities below EILs rather than at target. Peterson and Higley (2002) describe this economic threshold as a management target that “provides a window of time to take action before the pest density or injury increases to produce economic damage”. Unfortunately, sea lamprey abundance in the Great Lakes has long since passed the point where economic damage is occurring. More relevant to current management of sea lampreys is determining the appropriate level of sustained control to implement given the value provided by a host fishery.

Our results suggest that the optimal control budget can be sensitive to the determination of a value of a harvested host, especially across a range of low-end values. Determination of host value is one of the most contentious measures to quantify when calculating EILs. Our approach simply assumes that an individual host that is captured by the fishery rather than killed by a sea lamprey has a constant quantifiable economic value. We highlighted the same host values for each of the Great Lakes, but host value may vary across systems. Because some lake trout are of hatchery origin, different values may be attributed to naturally born versus stocked individuals. While “existence” value and differences among values of individual hosts do not play a role in EIL calculations, this idea could translate into different values being placed on different types of harvested lake trout, which would influence EILs. For example, market value of a host may be influenced by its aesthetic appeal (Peterson and Higley 2002), or anglers might much prefer to catch a wild fish. In addition to assuming all hosts have the same value, we assumed that value would remain constant across control budgets. This assumption might be violated if, for instance, a wound-free lake trout could be considered more valuable than a host that has survived a lamprey attack and is disfigured. The latter would be more common at low control budgets. Alternatively, host value might decline with increases in control budget if demand for lake trout harvest becomes saturated at high population levels. The largest highlighted host value ($25) represented an inflation adjustment applied to the host value used by Koonce et al. (1993), even though these authors reported this as a conservative value. As stated by Koonce et al. (1993) and shown by our results, larger host values would lead to even higher justifiable levels of control. Because the determination of such designations of value retains some subjectivity and because different values may be plausible under different management situations, we also presented EIL budgets and associated EILs across a range of plausible host values.

By providing a range of potential host values, interpretations may be made by others who might not agree with the host values that we selected to highlight.

As for host value, we also calculated lake-specific EIL budgets and EILs across a range of potential values for the probability of surviving a sea lamprey attack. We chose to highlight EIL budgets and EILs based on a relatively high probability of survival ($p = 0.73$), as did Szalai et al. (2005). This value is within the range described by Madenjian et al. (2008), but others have suggested much lower survivorship (Heinrich et al. 2003). For example, Koonce et al. (1993) used $p = 0.25$ when calculating an EIL for Lake Ontario, and Eshenroder et al. (1987) also report this low survival probability. In reality, p is likely influenced by the host's size, the size of the parasite, water temperature, attack location, duration of attachment, number of previous attacks, among other factors (e.g., Bence et al. 2003; Swink 2003). Our results show how, for all lakes, EIL budgets would be even higher if the p was reduced (higher lethality).

For the Great Lakes, many challenges exist for designing effective management programs to reduce sea lampreys so that host populations experience benefits (e.g., fewer parasites) but undesired effects of treatment do not exceed acceptable levels (McLaughlin et al. 2003). Although chemical treatments are highly selective for larval sea lampreys, they can also affect non-target species (Applegate and King 1962; Smith 1967). As such, widespread use of chemicals may induce costs beyond those directly related to their application. Further, even effective lampricide treatments can have limits to their ultimate benefits due to factors separate from the treatments themselves, such as potentially insufficient forage for recovering host populations (Koonce et al. 1993). We did not incorporate potential negative effects of sea lamprey control on non-target species nor directly include food web complexities related to host recovery into the economic considerations presented here.

For some lakes, our EIL budgets and EILs are comparable to previous studies. Szalai et al. (2005) presented EIL budgets for Lakes Michigan and Huron. At a $V = \$10$, the EIL budget presented here for Lake Michigan was very close to that presented by Szalai et al. (2005), while our EIL budget for Lake Huron was higher. This difference in optimal budgets for Lake Huron is likely due to our representation of the costs and effectiveness of lentic-area treatments associated with the St. Marys River. Other previous studies of optimal levels of sea lamprey treatment in the Great Lakes were presented in terms of the quantity of TFM applications (i.e. control staff effort not included) and therefore are not directly compared to the optimal EIL budgets presented here. However, we can compare our EILs to these studies. In general, the EILs highlighted here were close to those previously published for some of the Great Lakes. For Lake Ontario, Koonce et al. (1993) calculated an EIL of 30,000 adult sea lampreys, and later Larson et al. (2003) reported an EIL range of 14,100 to 19,100 adult sea lampreys for that lake. Both of these previous studies assumed that the majority of these adults were produced by untreated sources, primarily the Niagara River. To do so, Koonce et al. (1993) used an L_{min} = 25,000; whereas, Larson et al. (2003) assumed that a range of 10,000 to 15,000 adult sea lampreys were derived from untreated sources. Although, neither of these previous studies nor our current simulation model have explicitly included the Niagara River, our simulation model did include a general representation of untreated areas as well as indentified lentic areas that can be treated for a cost and are associated with outflow of larvae from lotic areas. The EILs presented here for Lake Ontario were generally within the range of Larson et al. (2003) but less than presented by Koonce et al. (1993). For Lake Erie, Sullivan et al. (2003) estimated a treatment residual of 1,500 sea lampreys, and the EILs that we present for Lake Eire were only slightly higher. These similarities among the EILs, given fairly substantial differences in models and parameter values (e.g., survival from a sea lamprey attack), suggest that the qualitative conclusions reported here are quite robust.

Calibrating the simulation model for each Great Lake was an important initial step, where we used actual treatment expenditures and match simulated outcomes to a calibration target abundance. This calibration effort produced the estimates of larval survival used in the simulations to produce parameters required for calculating EIL budgets and EILs. The calibration process relied on valuable input from sea lamprey biologists and control agents. As a result, we performed multiple model modifications during this project to improve biological realism and incorporate critical uncertainties.

Even so, the calibration process relied on certain assumptions. For example, we assumed the amount of area unsusceptible to lamprey control efforts yet able to support larval sea lampreys was equal to 2% of the amount of larval habitat in a lake's stream. If large untreated sources of sea lampreys were to be identified in the future, then the calibration process detailed here would likely need to be updated to reflect such a large change in the perception of the system. Likewise, we modeled treatment effectiveness as variable across locations and over time in response to control agents indicating that actual lampricide treatments sometimes vary from anticipated levels. Although this uncertainty was explicitly included in our simulation model, treatment effectiveness was generally applied at levels that produced substantial mortality (e.g., >90%) of larval sea lampreys in the treated area. If future studies were to suggest that the effectiveness of treatments were to be much lower or perhaps trend downward over time, then an alternate set of assumptions should be considered.

The strengths of the current interim damage targets are that they are based on direct estimates of marking rates and sea lamprey abundance, that they have been accepted by the Lake Committees, and that they are applicable whether or not the fish community has reached a desired state. Limitations include the reliance on an assumption about the lethality of sea lamprey attacks as is the case for the EIL calculations. The interim damage targets also rely on assumptions regarding healing time and on consistency in how marks are classified (Bence et al. 2003, Ebener et al. 2003). The approach also assumes that the relationship between marking rates and sea lamprey abundance will not change over time, as target marking rates are approached. This either requires direct proportionality between mortality and sea lamprey abundance or that factors that would cause a lack of proportionality will be similar when the abundance targets are used as during the reference periods when they were established. Predation theory actually suggests that a lack of proportionality between mortality and parasite abundance would be expected because of a saturating functional response, which would lead to a fixed sea lamprey abundance producing a lower mortality rate as hosts become more abundant (Bence et al. 2003).

A major strength of EILs is that they explicitly consider both costs and benefits of sea lamprey control and seek the control budget and sea lamprey abundance that balances these. EILs are fundamentally different from the interim damage targets because they should not be used in the short-term to evaluate whether or not the objectives of the control program are achieved. The EIL calculations are primarily aimed at determining appropriate amounts of investment in control and how that control should be allocated among lakes. Managers and stakeholders may argue that host value differs among lakes, which would further influence the allocation of control effort based on an EIL calculation. Regardless, the EIL approach provides a sound, scientific basis for accounting for the costs of control on each lake, something that is absent from the interim damage targets.

Given a control budget that matches our estimates of the EIL budget for each lake, why might sea lamprey abundance in a given year exceed the expected EIL? Three possible explanations for this are: (1) because the actual control program has not been at the level of the EIL budget for a sustained period and sea lamprey populations are still adjusting to the new control budget; (2) because of short term fluctuations in sea lamprey abundance due to environmental variation; or (3) because the operating model we used to derive the EILs is not correctly predicting mean sea lamprey abundance for a given sustained control effort. In the first of these, the failure to reach the EIL is due not to a problem with the control program given the budget, but that the resources needed for an EIL budget have not been available for long enough. Secondly, simple random excursions of sea lamprey abundance above (and below) the EIL would obviously not be a failure of the program; stochastic variation in sea lamprey abundance will invariably be a part of their population dynamics. In the last case, where a sustained budget equal to the estimated EIL budget did not produce the corresponding average sea lamprey abundance, reasons for this failure would need to be carefully considered. It may be that the control program is not operating with the efficiency (i.e., treatment effectiveness) assumed in our operating model, or it might be that other parameters in the operating model (e.g., sea lamprey larval survival rates) are inaccurate and need to be modified. In such cases, the appropriate action would not be to increase control efforts in an attempt to achieve the current EIL target for sea lamprey abundance, but rather to make appropriate revisions to the operating model, followed by new EIL calculations.

The many assumptions and complexity of the calculations (e.g., specification of larval survival rate and larval sources of lamprey that survive to spawning-phase) is a weakness or limitation of the EIL approach, in that it makes understanding the results more difficult and apparently subject to a larger array of uncertainties and assumptions than other approaches. We believe that, in contrast with alternatives, this approach does not make more assumptions but instead is more explicit about them. Some additional assumptions are required to allow the model to connect control efforts to the desired benefits, but this connection itself is a strength of the approach. Another limitation of the EIL approach is that it assumes in its calculations that the host population has reached a desired abundance level or more generally that the fish community is rehabilitated. Thus, the benefits resulting from sea lamprey control are those that come from reallocating fish-community extractions from sea lampreys to humans.

We strongly suspect that when away from equilibrium, higher levels of control would be optimal, because this would allow the optimal long term strategy to be pursued sooner. However, an explicit economic evaluation of how fishery extractions and sea lamprey control should be jointly and optimally managed when away from the desired fish community would require fundamentally different approaches and, in fact, would likely imply a different set of fish community objectives than is currently in place (Stewart et al. 2003). Lupi et al. (2003) considered, for sea lamprey control in the St. Marys River, how investments in sea lamprey control that lead to changes in lake trout abundance over time translate into economic benefits accrued by recreational anglers. This work emphasized, as do EIL calculations, the sea lamprey control program. Instead of assuming achievement of a target total mortality as given, they assumed an unregulated behavioral response on the part of anglers. Their work has the advantage of directly evaluating the economic benefits of increases in lake trout abundance away from the long-term desired steady state. This approach did not incorporate non-fishery benefits such as “existence” value.

Both the EIL and interim damage targets presume that existence value is of such importance that they impose reaching a desired fish community as either a constraint assumed during calculations (EILs) or the fundamental objective (interim damage target). This has the disadvantage of not providing insight on how valuable sea lamprey control efforts are in terms of allowing more fish or a different fish, above and beyond simply what the value of fishery experience is. Such values might include reduced management costs for hatcheries, and perhaps more importantly the possibility that the non-fishing public would assign a high value to rehabilitated fish stocks. There are well established non-market valuation techniques that could be used assign values to different fish communities, which would be essential for considering the sea lamprey control program in such a broader context. Stewart et al. (2003) provided more details on this topic and make recommendations. While we endorse those recommendations, we note here that such a program would be ambitious and goes far beyond the immediate goal of specifying target or benchmark budgets and sea lamprey abundances. Such an endeavor would necessarily require jointly considering sea lamprey control with other management actions such as stocking of hatchery-raised fish and harvest regulation.

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Table 1. Mean observed control expenditures for recent years (1998-2004; Recent expenditure) and mean observed abundance of spawning-phase sea lampreys based on a two-year lag from treatment years (2000-2006) used to calibrate lake-specific models.

	Superior	Michigan	Huron	Erie	Ontario
Recent expenditures (millions)	\$1.01	\$2.03	\$2.28[1]	\$0.27	\$0.68
Observed abundance	107,400	113,200	159,800	9,700	40,500

NOTE: [1] Contains costs associated with Bayluscide treatments (see text for additional information).

Table 2. Calibration values for annual larval survival and lake-specific estimates of untreated-pool size (as percent of total larval habitat in streams), treated-pool size, number of lentic units in each treated pool, and the proportion of age-0 larvae that migrate into lentic areas (Outflow scalar).

	Superior	Michigan	Huron	Erie	Ontario
Larval survival	0.498	0.438	0.505	0.400	0.521
Untreated pool size (%)	2	2	2	2	2
Treated pool size (ha)	161	67	12	0	28
Lentic units (#)	13	5	1	0	2
Outflow scalar	0.026	0.0077	0.0015	0	0.02

Table 3. Comparison of recent control expenditures (Recent budget; all dollar values shown in millions, from Table 1) with EIL budgets as well as lake-specific interim damage targets with EILs (values are rounded) for three plausible host values for an individual lake trout. For host values, \$2.00 is an arbitrary low-end value, \$10 is the lowest value presented for lake trout by Szalai et al. (2005), and \$25.00 corresponds to an inflation-adjusted value originally derived for sport angling of Chinook salmon and then reported for lake trout by Eshenroder et al. (1987) and was the basis for the host value used by Koonce et al. (1993) and others (see text for additional details).

		Superior	Michigan	Huron	Erie	Ontario
Host Value ($)	Recent budget ($)	1.01	2.03	2.28[1]	0.27	0.68
2	EIL budget ($)	1.20	2.21	2.39	0.28	0.68
10	EIL budget ($)	1.50	2.69	3.08	0.34	0.86
25	EIL budget ($)	1.67	2.97	3.48	0.38	0.97
	Damage target	35,000	61,000	74,000	4,000	30,000
2	EIL	35,000	62,000	121,000	9,000	33,000
10	EIL	8,000	19,000	59,000	3,000	16,000
25	EIL	4,000	12,000	50,000	2,000	14,000

NOTE: [1] Contains costs associated with Bayluscide treatments (see text for additional information).

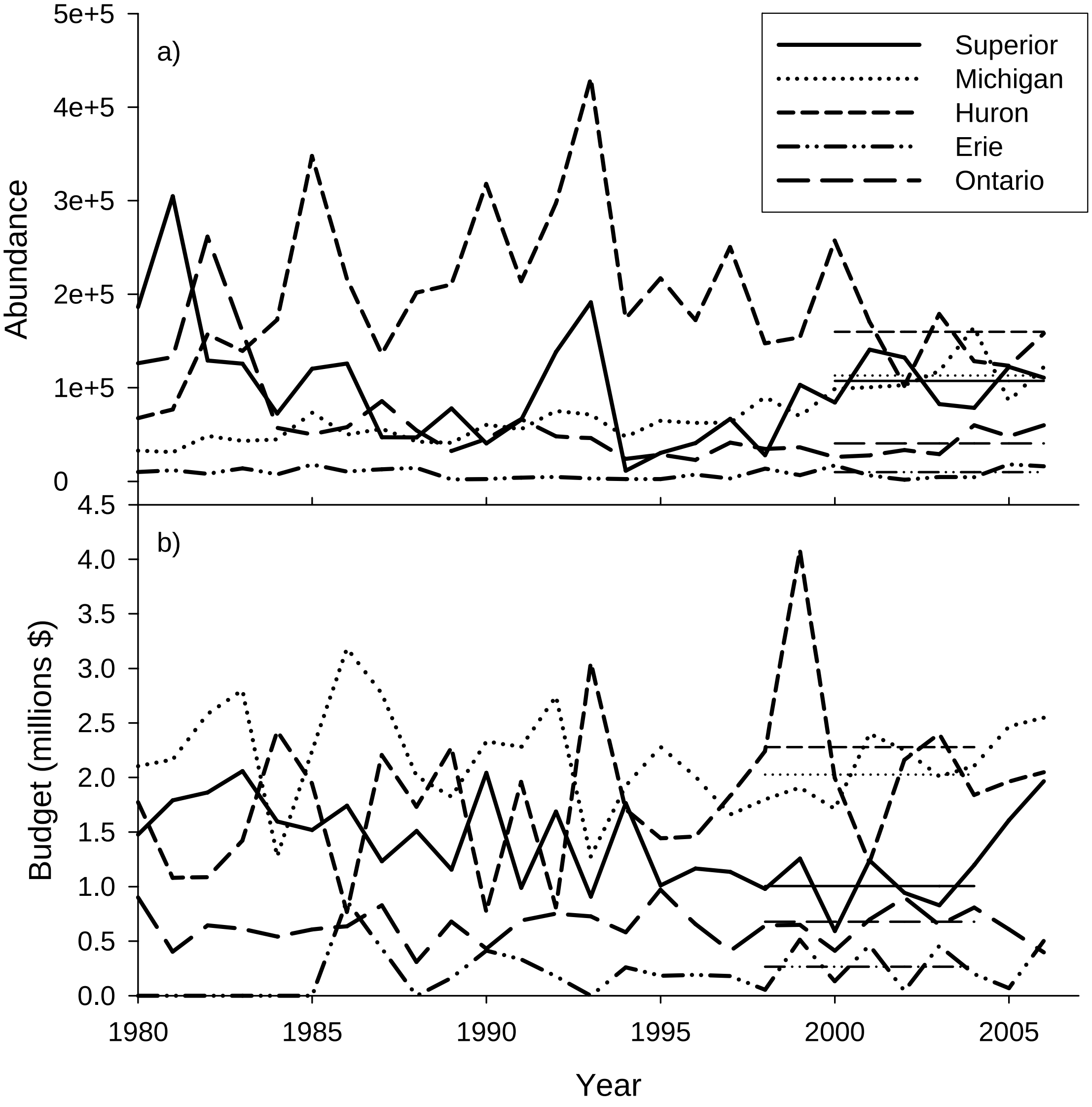


Figure 1. (a) Lake-specific abundance estimates of spawning-phase sea lamprey. Mean abundance values (2000-2006) are shown with thinner horizontal lines and were used as a calibration target. (b) Control expenditures each of the Great Lakes (Bayluscide costs included for Lake Huron). Mean expenditure values (1998-2004) are shown with thinner horizontal lines and were used as calibration budgets.

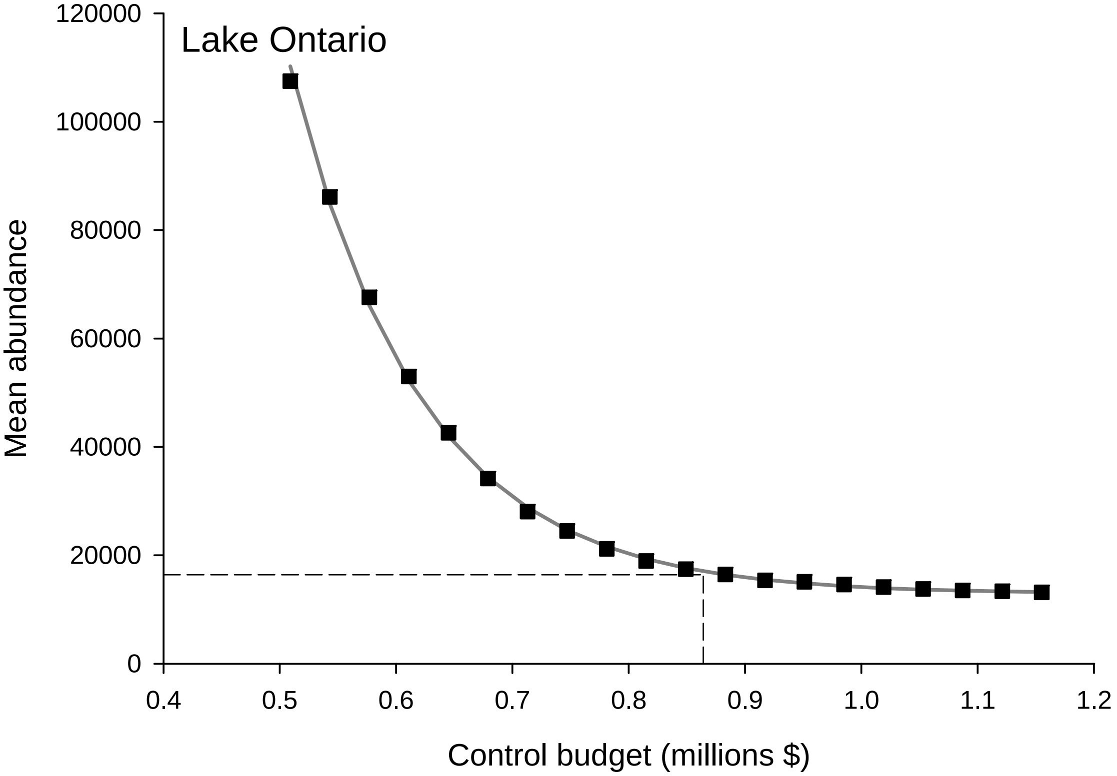


Figure 2. Illustration of relationship between mean abundance of spawning-phase sea lampreys and sustained control budgets. In this example, each point (■) represents the grand mean from 500 simulations of a 250-year projection (mean abundance during final 10 years). Solid grey line is predicted values of fitted relationship. Dashed line indicates EIL budget and corresponding EIL abundance value, based on a host value of $10 and *p* = 0.73.

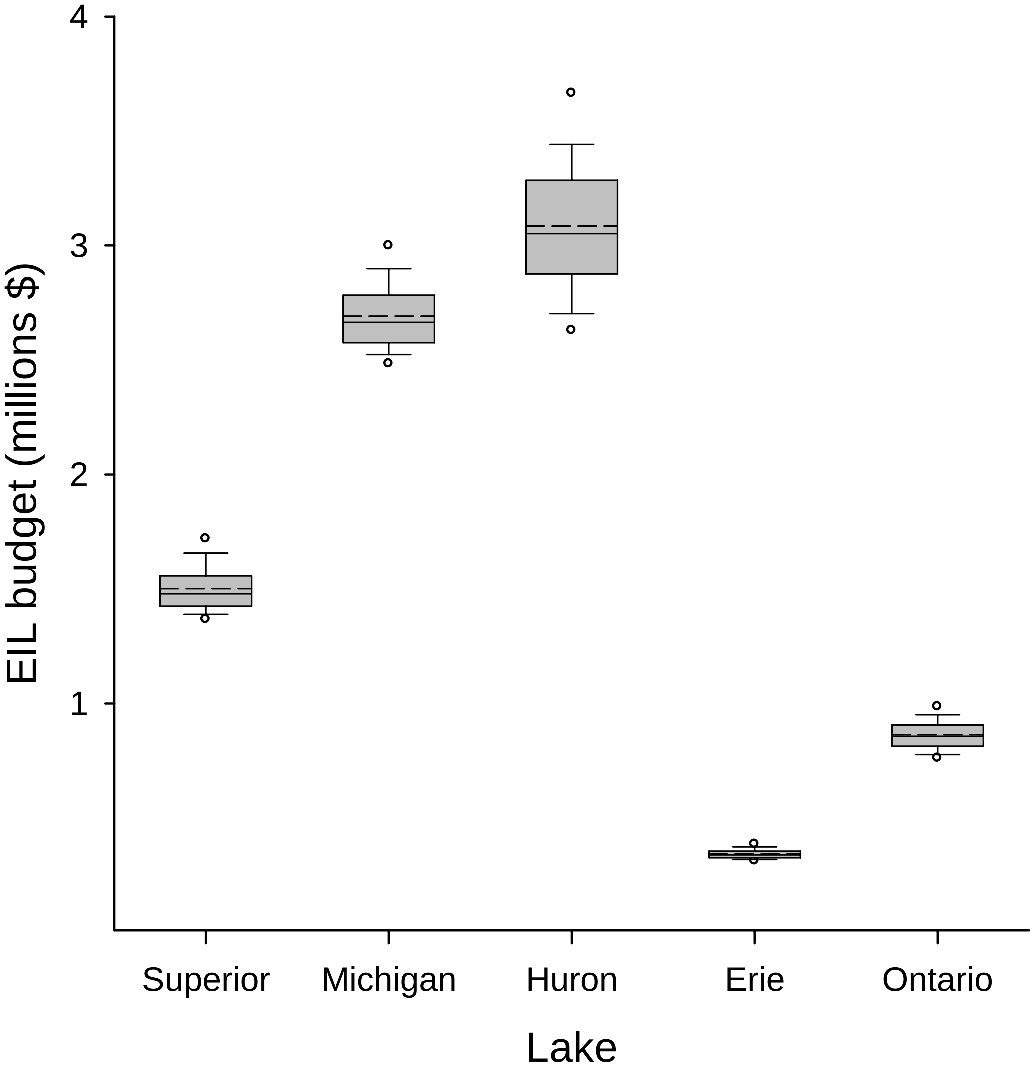


Figure 3. Distribution of EIL budgets based on 500 sets of simulations for each Great Lake, assuming a host value of $10 and *p* = 0.73. Boxes contain the 25th and 75th percentiles, the median value is identified with a solid horizontal line, whisker bars are the 10th and 90th percentiles, open circles are the 5th and 95th percentiles, and mean values are shown with a dashed horizontal line.

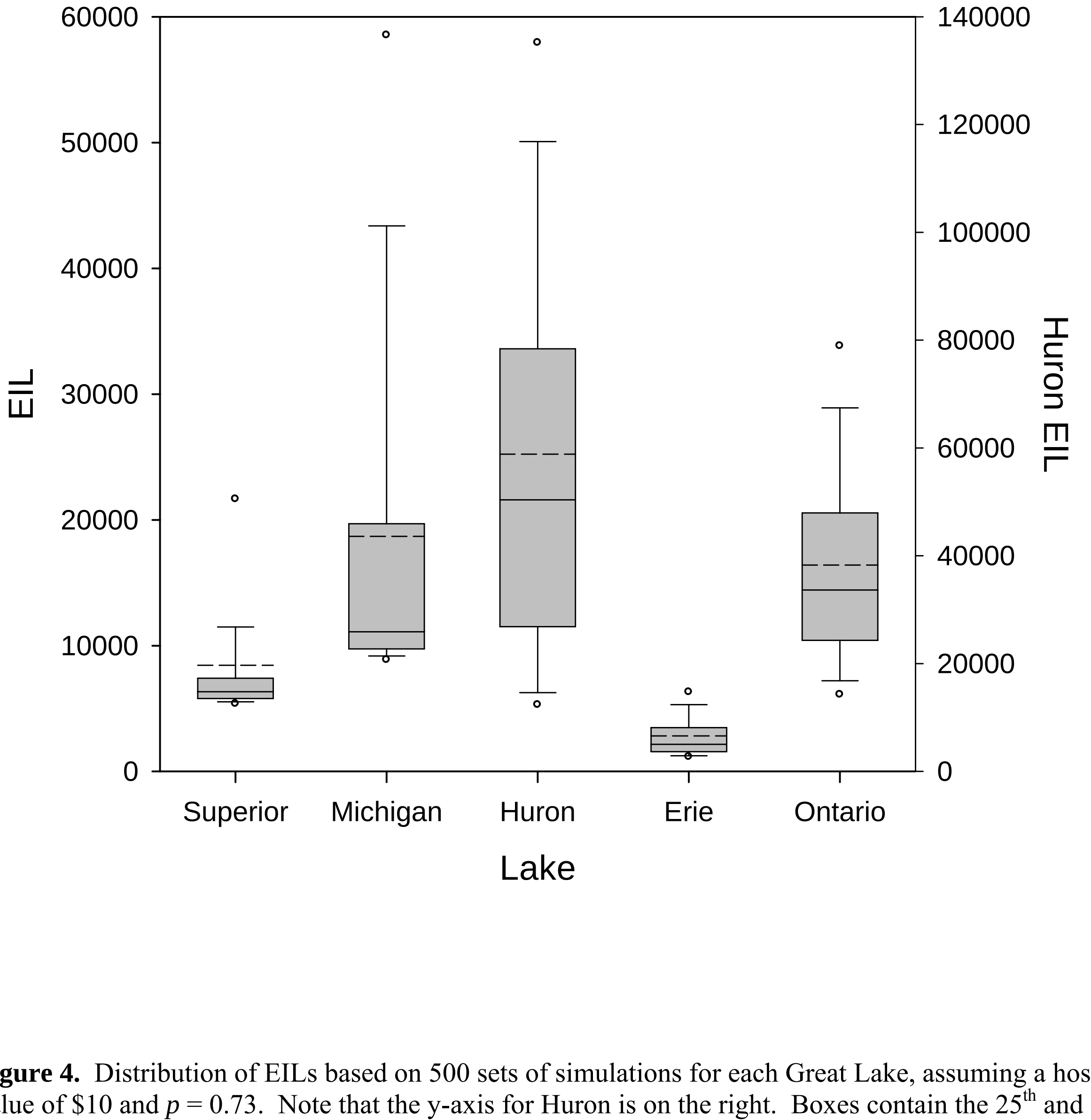


Figure 4. Distribution of EILs based on 500 sets of simulations for each Great Lake, assuming a host value of $10 and p = 0.73. Note that the y-axis for Huron is on the right. Boxes contain the 25th and 75th percentiles, medians are identified with a solid horizontal line, whisker bars are the 10th and 90th percentiles, open circles are the 5th and 95th percentiles, and mean values are shown with a dashed horizontal line.

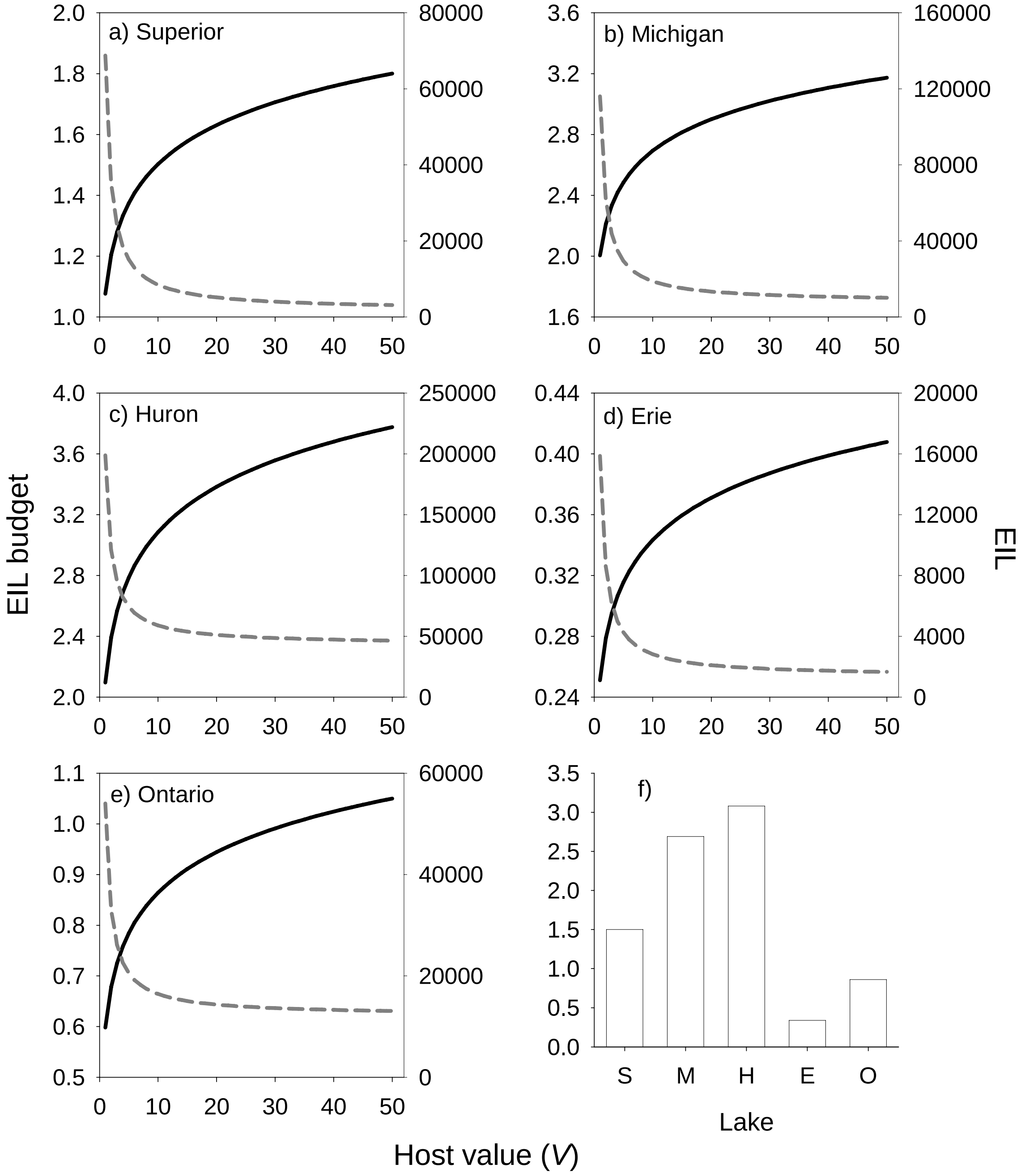


Figure 5. (a-e) Comparison of calculated EIL budgets (solid line) and EILs (dashed line) across a range ($1 to $50) of plausible host values (*V*) for each of the five Great Lakes. (f) EIL budgets for each Great Lake assuming a *V* of $10 and other parameters as defined in the text.

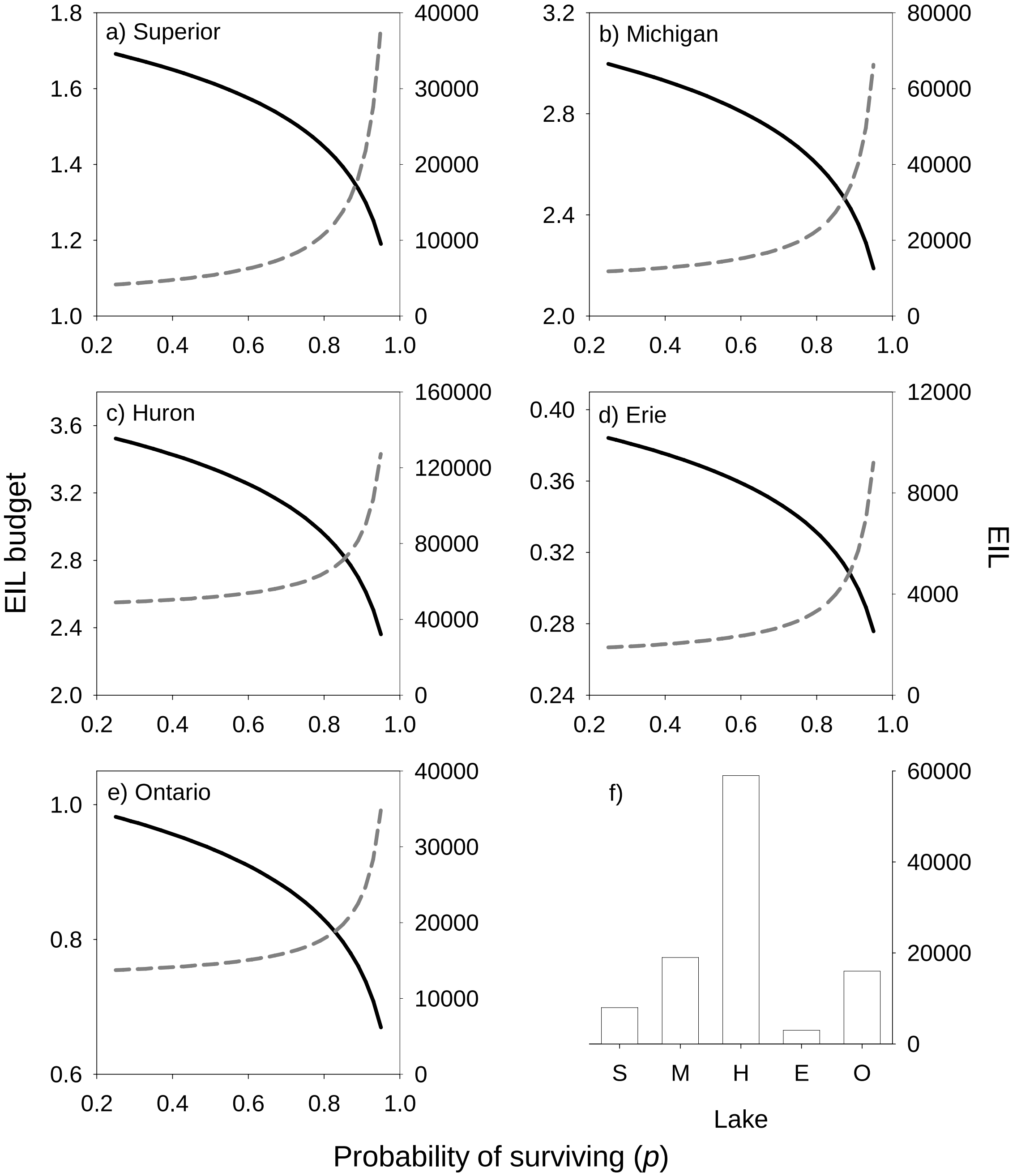


Figure 6. (a-e) Comparison of calculated EIL budgets (solid line) and EILs (dashed line) across a wide range of values (0.25 to 0.93) for the probability of surviving a sea lamprey attack (*p*) for each of the five Great Lakes. (f) EILs for each Great Lake assuming a *p* of 0.73 and other parameters as defined in the text.

DELIVERABLES:

1) A project workshop (see Appendix 2)

2) Several scientific presentations (see Appendix 2)

3) An updated stochastic projection model that simulates both the entire sea lamprey life cycle and treatment control efforts (described in Jones et al. *in prep*.)

4) EIL values calculated for each of the Great Lakes using common methods and assumptions

5) A project progress report
    - Irwin, B. J., J. R. Bence, M. L. Jones, and W. Liu. 2007. Defining targets for sea lamprey control in the Great Lakes: economic injury levels and fish community goal-based targets. Great Lakes Fishery Commission Project Progress Report, July.

6) A final completion report

7) Manuscripts in preparation
    - Jones, M. L., H. A. Dawson, B. J. Irwin, A. J. Treble, W. Liu, W. Dai, and J. R. Bence. (*in prep.*). An operating model for Great Lakes sea lamprey integrated pest management.

    - Irwin, B. J., J. R. Bence, M. L. Jones, and W. Liu. (*in prep.*). Economic injury levels for sea lampreys in the Great Lakes.

PRESS RELEASE:

A study, funded by the Great Lakes Fishery Commission, has provided estimates of optimal control budgets and associated sea lamprey abundances for each of the Great Lakes. These levels of sea lamprey abundance are called economic injury levels (EILs) and are the abundance level of spawning-phase sea lampreys where additional control expenditure would exceed the corresponding economic value of additional host fish that survive due to reduced exposure to sea lamprey predation. Because investment in sea lamprey control relies on limited resources, the need arises to both justify the overall level of treatment as well as appropriately allocate these resources among the Great Lakes. Although EILs have been calculated for sea lamprey in the past, this project was the first to generate EILs for each of the Great Lakes using common assumptions and methods. The resulting EILs offer a benchmark to compare with current control levels and allocation of treatment resources across the Great Lakes, as well as identifying levels of sustained long-term treatment procedures that can be justified based on economic benefits from resource use.

Calculations of EILs relied on a series of ecological and economic analyses. An operating model was calibrated to each Great Lake and then used to project how sea lamprey abundance varied given specified management actions. Numerous simulations were conducted to capture several sources of uncertainty (e.g., recruitment dynamics and effectiveness of treatments). Critical uncertainties were identified through a project workshop and subsequent interactions with sea lamprey biologists and managers. These interactions facilitated identification of critical uncertainties and led to model modifications. Results from the stochastic simulations were then used to develop relationships between the equilibrium abundance of spawning-phase sea lampreys and changes in control budgets. Syntheses of the simulation outputs were communicated through a series of presentations to sea lamprey biologists and decision makers. EILs were also compared to current damage targets, which are used to gauge whether sea lamprey abundances have been reduced to levels consistent with fish community objectives of the management agencies. This comparison suggests that it would be justified to reduce average sea lamprey abundance below these current targets. This project has contributed information to one of the primary goals of the sea lamprey control program – balancing the economic costs of sea lamprey control with the economic benefits gained by avoiding sea lamprey induced damages to the fishery.

Appendix 1. Synopsis of major findings.

- Current damage targets suggest that reducing spawning-phase sea lamprey abundance to about half of recent levels is desirable.
- EILs were consistently lower than damage targets at all but the lowest assumed host values, suggesting that reduction of average sea lamprey abundance to even lower levels than the current targets is justified.
- Achieving EILs would likely require increased and sustained treatment expenditures (>25% per lake) and successful lentic-area control.
- EIL budgets were consistently larger than current expenditure for several plausible host-species values.
- These calculations assume some lamprey originating from untreated areas could remain but that these areas are small.
- Interactive workshops with sea lamprey biologists and managers facilitated identification of critical uncertainties.
- This project has provided information that is relevant to ultimate goals of the sea lamprey control program – balancing the economic costs of control efforts with the economic value gained by avoiding fishery damages caused by sea lamprey in each of the Great Lakes.

Appendix 2. Workshops and presentations.

The proposal called for one project workshop, which was held at Weber's Inn, Ann Arbor, MI, October 2006.

In attendance: Jessica Doemel, Paul Sullivan, Brian Irwin, Weihai Liu, Jim Bence, Fraser Neave, Andy Treble, Mike Steeves, Brian Stephens, Rod McDonald, Bob Adair, Michael Twohey, Sara Adlerstein, Jeff Slade, Kasia Mullett, Michael Fodale, Miro Kuc, Jean Adams, Dale Burkett, Gavin Christie, Mike Jones.

- At this workshop, three presentations were given about the operating model (referred to as the MUSTR model):

  Bence, J. 2006. An introduction to and overview of the economic injury level project. MUSTR Model – Sea Lamprey EIL workshop, Ann Arbor, MI.

  Jones, M. 2006. Description of the MUSTR model. MUSTR Model – Sea Lamprey EIL workshop, Ann Arbor, MI.

  Irwin, B. 2006. Calibration of MUSTR. MUSTR Model – Sea Lamprey EIL workshop, Ann Arbor, MI.

In addition to the above project workshop, several project updates and a mini-workshop were conducted as part of this project.

- An update on modifications to the MUSTR model resulting from recommendations from the first workshop was presented at the 2007 Assessment Task Force meeting in Gaylord, MI, February 2007.

  Irwin, B., W. Liu, M. Jones, and J. Bence. 2007. An update on MUSTR modification and the EIL project. Assessment Task Force meeting, Gaylord, MI.

- An update on EIL calculations was presented at the spring 2007 Sea Lamprey Integration Committee Meeting in Ann Arbor, MI, April 2007.

  Irwin, B., J. Bence, M. Jones, and W. Liu. 2007. An update on the EIL project. Sea Lamprey Integration Committee meeting, Ann Arbor, MI.

- An update on EIL calculations and preliminary EILs was presented at the 2007 Great Lakes Fishery Commission meeting in Sault Ste. Marie, ON, Canada, June 2007.

  Irwin, B., J. Bence, M. Jones, and W. Liu. 2007. Economic Injury Levels for Sea Lampreys in the Great Lakes. 52nd Annual Meeting of the Great Lakes Fishery Commission Meeting, Sault Ste Marie, ON, Canada.

- A half-day mini-workshop to review the MUSTR model and EIL assumptions was held at the Quantitative Fisheries Center, Michigan State University, East Lansing, MI, July 2007. In attendance: Mike Jones, Rob Young, Jim Bence, Dennis Lavis, Mike Steeves, Brian Irwin.

- An update on modifications to the MUSTR model was presented by Mike Jones at the 2007 Assessment Task Force meeting in Gaylord, MI, February 2007.

  Jones, M., B. Irwin, J. Bence, and W. Liu. 2007. Economic Injury Levels for Sea Lampreys in the Great Lakes. Assessment Task Force meeting, Gaylord, MI

- An update on EIL calculations was presented at the fall 2007 Sea Lamprey Integration Committee meeting in Ann Arbor, MI, October 2007

  Jones, M., B. Irwin, J. Bence, and W. Liu. 2007. Economic injury levels: how should this work affect targets and what is next? Sea Lamprey Integration Committee meeting, Ann Arbor, MI.

Appendix 3. Summary of 2006 St. Marys treatment information used to allocate age-0 larvae among individual lentic units.

Using observed values based on 25 lentic blocks from the St. Marys River during 2006 (points), we defined a relationship (line) between the cumulative area of plots (*x*) and the cumulative proportion of the total larval population (*y*) in all plots and fitted the following function to these data:

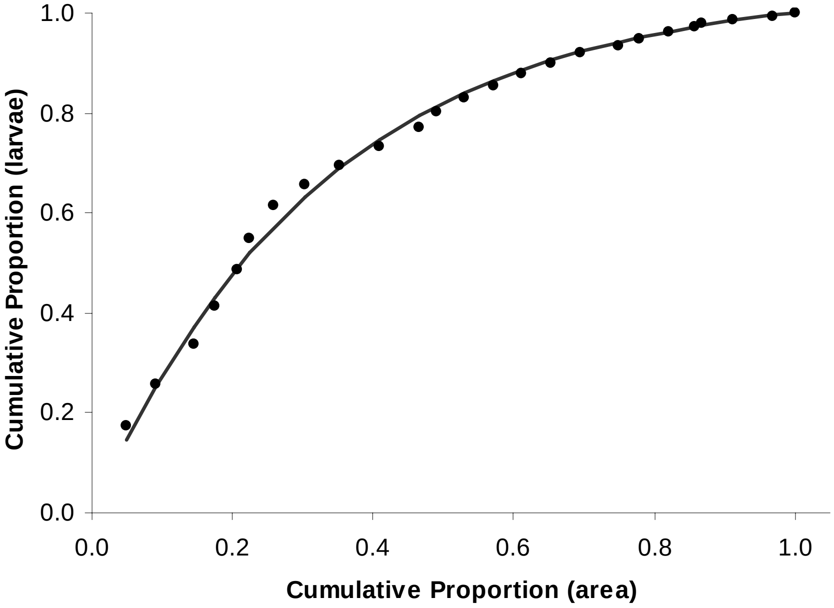
$$y = \frac{\left(1 - e^{-\lambda x}\right)}{\left(1 - e^{-\lambda}\right)},$$

where λ describes the extent to which the majority of the larvae are in a small proportion of the total area, with larger values implying a less uniform distribution among units. For the St. Marys River data, λ was estimated to be 3.02. Approximately 1.27 million larval sea lampreys were estimated to inhabit these 25 St. Marys units. The range (minimum and maximum) of area, treatment costs, staff days between the treated units with larval abundance estimates were relatively similar to other units without larval abundance estimates.

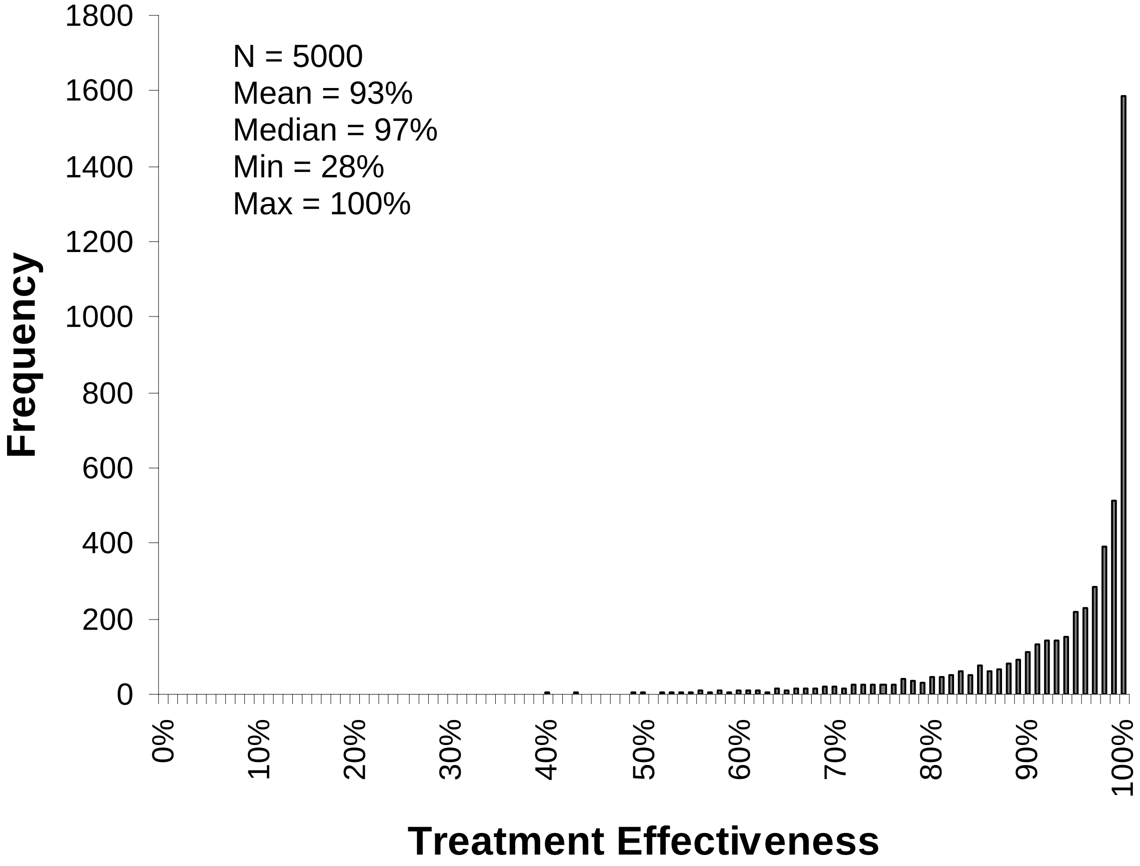
In the operating model, age-0 larvae were then allocated to treatable lentic habitat among the *N* individual lentic units using the equations:

$$\begin{aligned} L_i &= \overline{L} \cdot \frac{(1 - e^{-\lambda x_i})}{(1 - e^{-\lambda})}, i = 1 \\ L_i &= \overline{L} \cdot \frac{(1 - e^{-\lambda x_i})}{(1 - e^{-\lambda})} - \sum_{j=1}^{i-1} L_j, i = 2, N \end{aligned},$$

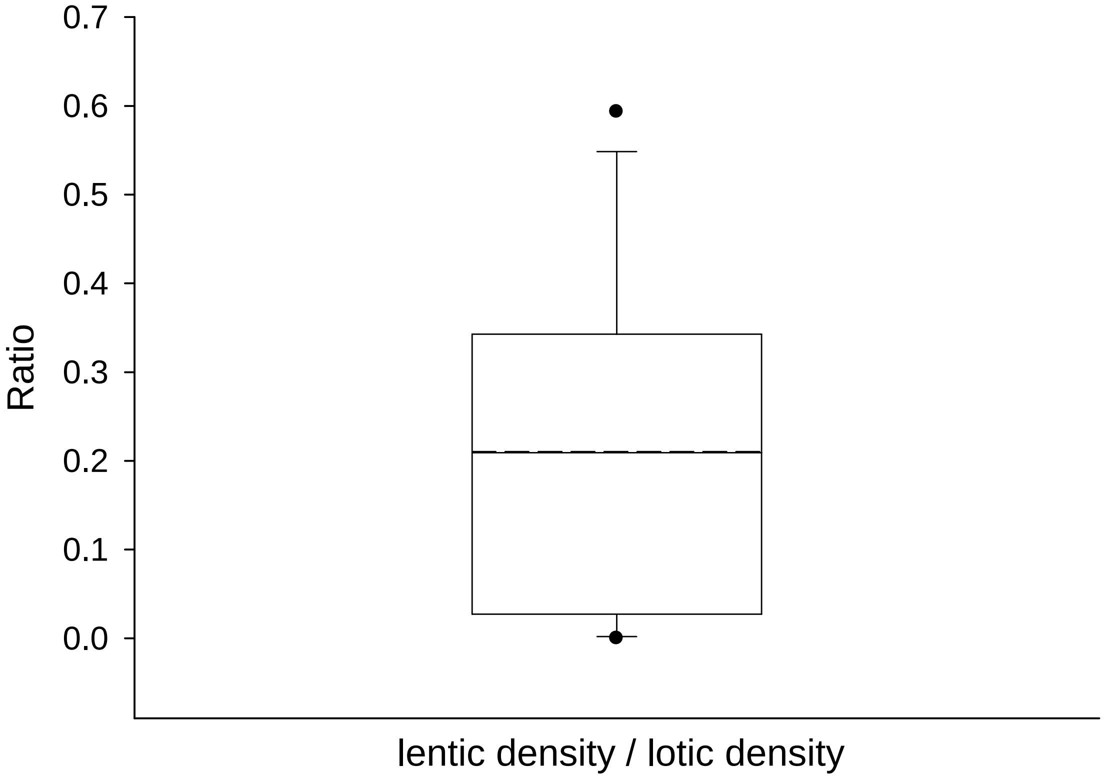
where $\overline{L}$ is the total number of age-0 larvae in lentic areas, and x_i is the cumulative proportion of total lentic area in units 1 through *i*,and λ was estimated from the St. Marys relationship described above.



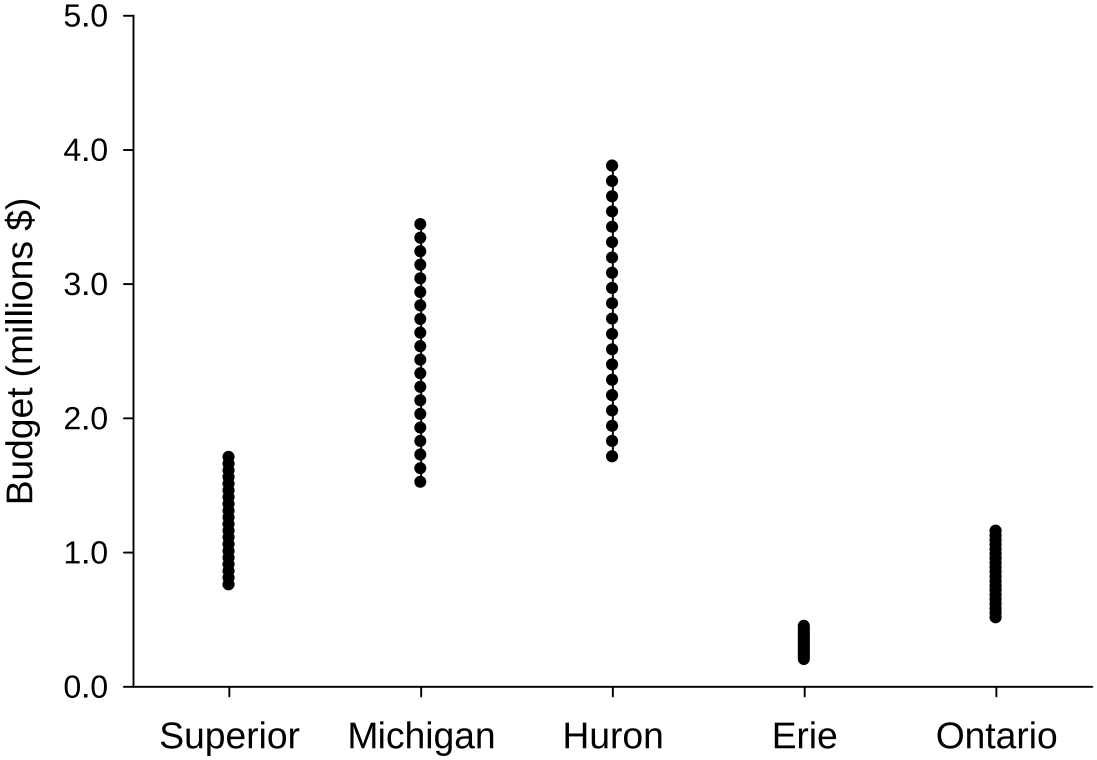
Appendix 4. Example of 5000 treatment effectiveness values from the distribution used in the operating model to simulate the reduction of larval sea lamprey in a stream area exposed to TFM treatment. Some descriptive statistics are also shown on the figure. The parameters used in the Beta distribution were α = 5.42 and β = 0.41.



Appendix 5. Box plot of 11 observed ratios of lentic to lotic densities of larval sea lamprey based on locations in Lakes Superior and Huron (data from Mike Steeves). Box contains the 25th and 75th percentiles, the median is identified with a solid horizontal line, whisker bars are the 10th and 90th percentiles, closed circles are points beyond these percentiles, and the mean value is shown with a dashed horizontal line.



Appendix 6. Range of 20 control budgets explored through simulations for each of the Great Lakes.



Appendix 7. Histograms of average abundance of spawning-phase sea lampreys $\left(\bar{x}_{i,C}\right)$ during the last 10 years of 500 simulations and the calibration control budget for each Great Lake. Panel d shows 497 of the values shown in panel c, after removing the 3 largest values.