Estimating Sea Lamprey Damage to Fish Populations in Lakes Michigan and Huron

Emily B. Szalai, James R. Bence, and Michael L. Jones

Department of Fisheries and Wildlife
Michigan State University
13 Natural Resources Building
East Lansing, Michigan 48824

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Abstract

Integrated management of sea lampreys calls for the Great Lakes Fishery commission to deliver sea lamprey control in the Great Lakes that provides the optimum benefits to the fish community. One approach to assessing optimal control of sea lampreys is the economic injury level (EIL, Koonce et al. 1993), where the costs of sea lamprey control are balanced with the benefits to the fishery of reduced host deaths caused by sea lampreys. Here, we apply the EIL approach to sea lamprey control in Lakes Michigan and Huron to calculate the EIL for both lake trout and lake whitefish using improved estimates of sea lamprey-host functional response parameters and sea lamprey population dynamics. The resulting EILs suggest that the current level of control in both lakes is below optimal, and that current levels of control imply values of \$0.74 and \$2.12 for a lake trout harvested in Lake Michigan and Huron, respectively. We discuss the substantial uncertainties regarding both sea lamprey dynamics and sea lamprey-host interactions, which in turn lead to uncertainty in our estimates of EILs. Our results suggest that the EILs for Lake Huron are strongly influenced by the presence of a source of parasitic sea lampreys in the St. Marys River and future investigations of the optimal control of sea lampreys in Lake Huron should explicitly include control of the St Marys River population. We also present dynamic short-term projection models of the effects of sea lampreys on lake trout population dynamics for both lakes. These models predict the effects of changes in lake trout management and sea lamprey control on the damages caused by sea lampreys under current conditions and may offer guidance to managers in decisions regarding sea lamprey control and lake trout restoration.

Introduction

The effects of the invasion of parasitic sea lampreys (*Petromyzon marinus*) on the fish communities and, in particular, the native lake trout (*Salvelinus namaycush*) populations of the Great Lakes has led to the need to (a) justify the overall level of investment in sea lamprey control, and (b) design a pest control strategy that is able to allocate limited control resources equitably across the Great Lakes (Stewart et al. 2003). One of the goals of current sea lamprey control program is to balance on each Great Lake the economic costs of the control program with the economic value gained by avoiding the fishery damages caused by the sea lampreys. Currently, the Great Lakes Fishery Commission uses a stream ranking procedure, the Empiric Stream Treatment Ranking (ESTR) system, which allows them to rank streams for treatment based on the estimated number of metamorphosing sea lampreys killed per unit cost of treatment (Christie et al. 2003). This allows treatments to be allocated to streams where cost effectiveness will be greatest. This approach is useful for selecting streams given a control budget, but it cannot offer guidance on the optimal budget for any given lake nor can it estimate the additional benefits that would result from an increase in spending on sea lamprey control. To achieve these goals, a decision model is needed that predicts both the numbers of parasitic sea lampreys that result from a given budget and the damage caused by sea lampreys on economically important fish populations.

One approach to developing a decision technique to address these needs was described by Koonce et al. (1993) in developing an economic injury level for the control of sea lampreys in Lake Ontario. This approach utilizes information on the equilibrium abundance of parasitic sea lampreys produced for a range of control budgets. This information is then paired with a model that predicts the number of fish killed at a given level of parasitic sea lamprey abundance. By assuming that the host populations are at equilibrium, there is a direct tradeoff such that any reduction in the number of hosts killed by sea lamprey corresponds to an increase in the number of hosts harvested. Therefore, after specifying a target total mortality rate for the host population and the economic value of a harvested host, we can find the economic injury level (EIL). This is defined as the control level above which additional control of sea lamprey populations costs more than the economic value of the resulting increase in harvest (Koonce et al. 1993). In practice, control efforts can only be applied in discrete amounts corresponding to streams or stream reaches. If control efforts and benefits were continuous, the EIL for a given lake would be the control budget where the marginal costs of control are equal to the marginal benefits (Koonce et al. 1993). This EIL provides both an economic justification for sea lamprey control and a benchmark to compare current levels of control to.

The EIL approach has been applied in Lake Ontario, considering the application of trifluormethyl nitrophenol (TFM) as the primary mode of control, but its application to the other Great Lakes has been limited by the availability of quantitative models to predict both equilibrium sea lamprey abundance given a level of control and the damage caused by these sea lampreys (Stewart et al. 2003). The prediction of damage caused by a parasitic sea lamprey requires understanding of the interaction between a sea lamprey and their hosts and how this interaction leads to host mortality. Quantitatively describing this process depends on models that predict functional, numerical and developmental responses of the sea lamprey-host interaction (Bence et al. 2003). While our knowledge of these interactions is limited (Bence et al. 2003), models to predict damage in Lake

Ontario exist as part of the integrated management of sea lamprey (IMSL) parasitic sea lamprey submodel and include a multi-species type-2 functional response for predicting sea lamprey marking rates where the number of attacks per sea lamprey saturates to an asymptote as host abundance increases.

Here, we have applied the EIL approach to Lake Michigan and Huron to generate economic injury levels for both lakes. By using the framework provided by the existing Lake Ontario IMSL model and updated estimates of the parameters of the functional response (Rutter 2004), we constructed damage models for Lakes Huron and Michigan to be used in the calculation of the EILs for these lakes. Additionally, the development of models of sea lamprey population dynamics for Lakes Huron and Michigan allowed us to develop the predictions of the equilibrium abundance of parasitic sea lampreys for a range of control budgets necessary to calculate EIL values. In Lake Huron and Lake Michigan, both lake trout and lake whitefish (*Coregonus clupeaformis*) populations are impacted by sea lamprey attacks and support economically important fisheries. Furthermore, rehabilitation of self-sustaining stocks of lake trout is not certain for either lake. For these reasons, it is important to consider both lake trout and lake whitefish when calculating economic injury levels for the lakes. Because the EIL approach is based on equilibrium conditions, an EIL calculated for each species represents a different interpretation for the assumed steady-state fish community. The EIL based solely on lake trout assumes that the equilibrium status of the lake is one in which large lake trout are abundant, and, sea lamprey attacks (during the feeding season when attacks are potentially lethal to lake trout) are almost entirely concentrated on large lake trout, their preferred prey (Bence et al. 2003). Such conditions reflect the success of lake trout restoration. An EIL based solely on lake whitefish assumes that these sea lamprey attacks are concentrated on lake whitefish and may reflect conditions in the lake if lake trout restoration attempts are abandoned. Either EIL can provide useful information in guiding future management decisions and objectives.

While the EIL approach can provide useful benchmarks for sea lamprey control, its reliance on steady-state conditions limits its applicability to current conditions in the Great Lakes, where conditions are far from the desired fish community. For this reason, Stewart et al. (2003) communicated the need for projection models that predict the response of system in its current state to changes in sea lamprey control. These projection models share a similar framework as the equilibrium models but rely on information about the current or projected state of the system rather than the desired equilibrium conditions. Here we combine specified initial conditions and recruitment of host populations, trajectories of sea lamprey abundance, along with our current knowledge of the sea lamprey-host interaction, to produce dynamic projections of sea lamprey damage for the main basin of Lake Huron and Lake Michigan. (We illustrate the application of the short-term projection models based on initial conditions that reflect recent assessment of host fish communities along with assumed future recruitment and abundances of parasitic sea lampreys.) For the main basin of Lake Huron, recent work has improved estimated abundances of lake trout, Chinook salmon, and lake whitefish (Dobiesz and Bence *in review*) and provided improved estimates of functional response parameters from wounding data on lake trout (Rutter 2004). Furthermore, sea lamprey abundance has been estimated based on expansion to the entire lake of mark-recapture estimates of spawners from selected streams, and by whole lake estimates based on marking of transformers and parasites (Mullet et al. 2003, Young et al. 2003). By combining these updated sources of information, along with current estimates of sea lamprey abundance, we constructed a projection model for the damage caused by sea lamprey in the main basin of Lake Huron. For Lake Michigan, recent improvements in the estimates of host abundance, particularly lake trout, Chinook salmon, coho salmon, brown trout, and steelhead, as part of on going stock assessments (Madenjian et al. 2002), help specify the initial host community and expansion of stream specific sea lamprey spawner numbers provides an estimate of recent sea lamprey abundances (Mullet et al. 2003).

Methods

Economic Injury Levels

Koonce et al. (1993) showed that the economic injury level (EIL) for sea lamprey control in a given lake can be calculated from information on the cost of sea lamprey control treatments using TFM, the effect of these treatment on sea lamprey population size, the management goal for total lake trout (or lake whitefish) mortality, the number of lake trout (or lake whitefish) killed by sea lampreys, and the economic value of lake trout (or lake whitefish) harvested in the fishery. All parameters are defined in Table 1. As in Koonce et al. (1993), total cost (C_T) is defined as the sum of management costs and damages:

$$C_T = C_S + C_C + C_D. \qquad (1)$$

We then expressed the equilibrium level of sea lamprey abundance (L^*) as a function of control budget:

$$L^* = L_{\min} + \alpha e^{-\beta C_c} \quad . \qquad (2)$$

The cost of stocking and fishery management and cost of damage is expressed as in Koonce et al. (1993), using the Type II functional response model. Following the original derivation of Koonce et al. (1993), we took the derivative of total costs with respect to control costs and solved the equation for the optimal control costs leading to

$$\hat{C}_C = -\frac{1}{\beta}\log_e\left(\frac{1}{V}\frac{1+ahN^*}{Ta}\frac{Z}{1-e^{-Z}}\frac{1}{\alpha\beta}\frac{1}{N^*(1-p)}\right) \qquad (3)$$

where all parameters are defined as in Table 1. Assuming sea lampreys are not search limited due to the high densities of hosts at equilibrium, eq. 3, simplifies to

$$\hat{C}_C \approx -\frac{1}{\beta}\log_e\left(\frac{1}{V}\frac{h}{T}\frac{Z}{1-e^{-Z}}\frac{1}{\alpha\beta}\frac{1}{(1-p)}\right) \qquad (4)$$

Target total mortality rates for lake trout and lake whitefish were based on stated management objectives for lake trout and lake whitefish in lake trout rehabilitation plans and evaluations (Healy 1978, LMLTTC 1985, Ebener 1998, Bronte et al. 2003) and in a negotiated settlement governing fishing in the 1836 Treaty waters (U.S. vs. Michigan 2000) (Table 1). We chose to use a total annual mortality rate (A) of 0.45 for lake trout, corresponding to an instantaneous total mortality rate of 0.6, rather than the lower value of 0.4 specified for some areas in some documents because our intent is to evaluate conditions at equilibrium after rehabilitation has occurred.

Equilibrium parasitic sea lamprey abundance

We used a stochastic age-structured population model to forecast equilibrium parasitic sea lamprey abundance for a range of control budgets for Lake Michigan and Huron. The model was derived from the whole-life cycle model described in Jones et al. (2003) but with a number of important modifications:

- The complete set of sea lamprey producing streams for each lake is explicitly represented in the model, following the data structure used in the ESTR system, which divides large streams into reaches for which independent lampricide treatment decisions can be made. Each reach is characterized by its length, average width, and the area of habitat suitable for larval sea lamprey production;
- The model is still age-structured, but each cohort of larval sea lamprey is subdivided into a set of nine length bins, with the proportion of the cohort in each length bin characterized by a normal distribution with a fixed mean and coefficient of variation. This change was made to enable application of a length-dependent logistic model of metamorphosis, as is used in the ESTR system for forecasting future production of metamorphosing sea lampreys;
- Each year the whole-lake population of adult sea lampreys is allocated to stream reaches for spawning based on two rules: (1) the area of larval habitat in each reach, and (2) the abundance of larvae in each reach. In all of the simulations used in this analysis, the two rules were given equal weight;
- Both lakes include an additional source of parasitic sea lampreys, called the “untreatable pool” which is intended to represent production of sea lampreys from sources that are not presently vulnerable to lampricide control (e.g., lentic areas). Population dynamics (reproduction, larval growth and survival, etc.) in the untreatable pool follows the same rules as for the treatable stream reaches, as does the allocation of spawning sea lamprey to this compartment. The size (larval habitat area) of the untreatable pool was defined as a proportion of the overall area of larval habitat in the entire lake.
- For the Lake Huron model, we simulated an additional pool to represent the St. Marys River. The St. Marys River is not amenable to TFM treatment, yet produces considerable numbers of parasitic sea lamprey and is subject to alternative treatment tactics. The model allows exploration of the effect of varying levels of control for the St. Marys River pool, but for the analyses reported here, we fixed the size of this pool and the level of control (proportional reduction in larval, and thus parasitic, production) at a constant value. Thus, for Lake Huron, our EIL calculations apply only to expenditures directed at TFM treatment of streams other than the St. Marys River, assuming a fixed level of control for the latter.

We calibrated the models for each lake using recent observations of adult sea lamprey abundance and recent control expenditures, and by assuming that the adult sea lamprey population in each lake is roughly in equilibrium with control expenditures. We set the size of the untreatable pools (and the treatable pool for Lake Huron) to give plausible sea lamprey abundances at very high control expenditures. Then we adjusted the survival rate of larval sea lampreys until the median forecasted adult sea lamprey abundance for long-term (250 year) simulations using a budget corresponding to recent control expenditures reasonably matched observed adult abundance for recent years.

Simulations using control budgets that ranged from the minimum budget necessary to treat the largest stream ($1.31 million in Lake Michigan, $834,000 in Lake Huron) to a maximum budget of $3.3 million in Lake Michigan and $2.8 million in Lake Huron were run. These maximum budgets were those for which the estimated equilibrium abundance of sea lamprey was similar (with only slight variations due to the stochasticity in the population model) for three consecutive increasing budgets that differed by $250,000. Because the population model is stochastic, we needed to determine how to define the equilibrium abundance of parasitic sea lampreys. First, because Rutter (2004) used the lakewide abundance of spawning sea lampreys as the measure of sea lamprey abundance is the estimation of the functional response parameters for Lake Huron, we also used the abundance of spawning sea lampreys as our measure of sea lamprey abundance. Preliminary simulations showed that the distribution of spawning sea lampreys in a given year for all budgets considered was skewed with a heavy right tail. For this reason, we chose to represent the spawner abundance by the median rather than the mean of the simulations. These initial simulations also showed that 500 trials of each budget were necessary to adequately represent the distribution of potential spawner abundances. We then investigated through a series of simulations how to determine if the sea lamprey population was in steady-state conditions. We graphically assessed if the median spawner abundance in each year appeared to be increasing or decreasing for a wide range of budgets. We found that for most budgets the median spawner abundance by year in the last ten years of the simulations did not vary with trend for simulations run for 150 years. For some larger budgets, a longer simulation time of 250 years was needed to achieve this condition. We then defined the equilibrium sea lamprey abundance as the median of the spawner abundances for the last ten years of the simulated time period.

We represent the control costs for each specified budget as the mean of the actual amount of spending across years and trials. This differs from the budget we specified because treatment is allocated in discrete units corresponding to stream or stream reaches starting with the highest ranking stream unit (according to kill per cost) until no additional stream units could be added without exceeding the budget. Thus the actual control cost is always less than the specified budget. We needed to use mean cost because the population model was stochastic and thus the actual amount of money spent on control varied among years in a given trial and between trials in a given budget.

The pairs of estimated equilibrium sea lamprey abundance and control costs were then used to estimate the parameters of equation 2. For Lake Huron, we used nonlinear regression (SAS Version 8.2, Proc NLIN) to estimate the three needed parameters. For Lake Michigan, we found that for large budgets (greater than $2.8 million), the sea lamprey populations were extinct by the time steady-state conditions were achieved. For this reason, we simplified equation 2 to:

$$L^* = \alpha e^{-\beta C_c} \tag{5}$$

and estimated the parameters using nonlinear regression (SAS Version 8.2, Proc NLIN).

Functional response parameters

Values for the handling time, *h*, and the duration of the attack season, *T*, for lake trout and lake whitefish were obtained from Rutter (2004) (Table 2). While these parameters were estimated only for the main basin of Lake Huron, we believe they are the best estimates of these parameters available and since functional response was based on densities of host and sea lampreys, not absolute abundances, the results may be applicable to both lakes. Additionally, our work with short-term projection models for Lake Michigan (see below) using these parameters values produce reasonable sea lamprey mortality rates for lake trout.

The probability of surviving an attack for lake trout and lake whitefish was based on the logistic regression of the probability of survival as a function of weight from laboratory studies by Swink (2003). Lake trout at equilibrium were assumed to have a weight of 6 kg for both lakes. Lake whitefish at equilibrium were assumed to have a weight of 1.5 kg for both lakes. The resulting probability of surviving an attack for these weights is shown in Table 2.

Lake trout and lake whitefish value

The economic injury level for a lake can be expressed as a function of the perceived value of a harvested lake trout or lake whitefish. For illustrative purposes, we have chosen several possible values for lake trout derived from different sources. First we calculated the economic injury level for Lake Huron and Michigan using the value assumed by Koonce et al (1993) ($12) for comparative purposes between Lake Ontario and these two Lakes. We also adjusted the $12 value to account for the inflation of the value of the dollar to the year 2004 (referred to as the Adjusted Koonce et al. (1993) value). The original value utilized in Koonce et al. (1993) was based on catch records from 1985-1986 (Eshenroder at al. 1987). So we adjusted the $12 value to 2004 dollars by the ratio of the Consumer Price Index (CPI) from 2004 to that of 1985.

$$V_{2004} = \frac{CPI_{2004}}{CPI_{1985}} V_{1985} \tag{6}$$

Consumer Price Indexes for the Midwest region of all goods for 1985 and 2004 were obtained from the Bureau of Labor statistics website (http://data.bls.gov). We also estimated the value of lake trout in each lake by its value to the sport fishery. This value was calculated from the price of a half day charter boat expedition for four people. We then divided this by the jurisdictional bag limit for lake trout to get a per person, per lake trout cost. Average per person, per lake trout cost for each lake was assumed to be the recreational value of a harvested lake trout. Charter boat rates were obtained for several charter boat companies located in different regions of each lake from www.micharterboats.com and www.great-lakes.org , which both list links to charter boat services by state and port. A total of 10 companies were used from each lake. The value of lake trout estimated by the Ludington Pump Damage assessment could not be used because they were calculated using a travel cost model, which assumes that value changes with changes in catch rate unlike EIL calculations that assume a constant value independent of catch rates (Lupi and Jester 2002).

Short-term Projection Models

Population models for lake trout and other alternative hosts for Lake Michigan and Lake Huron were constructed to forecast the effects of changes in stocking and changes in sea lamprey abundances on the population of lake trout in each lake. The population models are deterministic and age-structured for lake trout and are similar in nature to Rutter (2004) for Lake Huron and Szalai (2003) for Lake Michigan

For Lake Huron, the main basin, excluding Saginaw Bay, was divided into three regions based on statistical districts as in Rutter (2004) with Northern Lake Huron composed of MH-1 and portions of OH-1, Central Lake Huron of MH-2, portions of OH-1, and OH-2, and Southern Lake Huron of MH-3, MH-4, MH-5, MH-6, OH-3, OH-4, and OH-5. One lakewide model of Lake Michigan, excluding Green Bay, was constructed.

In addition to lake trout, several alternative host species were included for both lakes. In Lake Huron, Chinook salmon (*Oncorhynchus tshawytscha*) and lake whitefish were included as alternative host species. Their abundance in each year was assumed known, that is they were not modeled dynamically, as in Rutter (2004) with a single host category for each species. Lakewide abundances of Chinook salmon were assumed constant at the abundance in 1998 from Dobiesz and Bence (*in review*) and were distributed equally across all three regions. The abundance of lake whitefish (ages 4 and older) in each region was also assumed constant at the abundance in 1998 from Ebener et al. (*in press*). The length, weight, and natural mortality rates of Chinook salmon and lake whitefish were obtained from Rutter (2004). For Lake Michigan, Chinook salmon, coho salmon, brown trout and steelhead were included as alternative host species. An age-structured population model for each species was constructed following Szalai (2003). Length and weight at age were assumed constant over time and were obtained from Szalai (2003). For Chinook salmon, the weight and length at age in 1998 was used. The symbols used in all equations are defined in Table 3.

The population models for lake trout for each region in Lake Huron and for all species in Lake Michigan were age-structured and

$$N_{i,a+1,r,y+1} = N_{i,a,r,y}S_{i,a,y,r} \tag{7}$$

Age categories ranged from 1 to 15 and older for lake trout in Lake Huron and from 1 to 10 and older in Lake Michigan. Ages ranged from 1 to 5 for Chinook salmon, 1 to 5 and older for brown trout and steelhead and 1 to 2 for coho salmon in Lake Michigan. Abundances of each species at age 1 was obtained by multiplying the numbers of yearling equivalents stocked by a post-stocking survival rate. Stocking for all species in Lake Michigan was assumed constant at 1998 levels and both stocking and post-stocking survival estimates were obtained from Szalai (2003). For Lake Huron, the number of yearling equivalents stocked in each statistical district was assumed constant over time at the average level from 1994-1998 (Rutter 2004). Stocked fish were then distributed to each region of the lake by a migration matrix (see Rutter 2004 for details). Region specific post-stocking survival rates were obtained from Rutter (2004) by taking the average of the 1996-1998 year-specific post-stocking rates estimated.

Survival (S) over the entire year was modeled a function of background natural mortality, sea lamprey mortality and fishing mortality. In calculating survival over the entire year, the year was assumed to be composed of two distinct periods separated by a pulse of sea lamprey mortality occurring at the end of the ninth month. During the first nine months and the last three months, background natural mortality and fishing mortality were assumed to be operating at constant (instantaneous per capita) rates. At the end of the second period of constant mortality, some species experience mortality associated with reproduction (see below). Survival was simply the ratio of the numbers of a given age at the end of the year (after any mortality associated with reproduction) to the numbers at the start of the year. Background natural mortality rates were age-specific and assumed constant over time for all species in both lakes and were obtained from Rutter (2004) for Lake Huron and Szalai (2003) for Lake Michigan. In Lake Michigan, Chinook salmon have experienced large episodic mortality events, thought to be associated with periods of nutritional stress (Holey et al. 1998). The potential for these mortality events was not included in the Lake Michigan projection model. Fishing mortality rates were modeled as a function of effort, age-specific selectivity, and catchability. Age-specific selectivity and catchability was assumed constant over time for all species in both lakes. For Lake Michigan, only one fishery was assumed to operate on all species and values for effort (at 1998 levels), age-specific selectivity and catchability were obtained from Szalai (2003). In Lake Huron, a recreational and commercial fishery was assumed to operate on lake trout in all regions and catchability coefficients and effort levels for 1998 were obtained from Rutter (2004). As age-specific selectivity was allowed to vary across years in Rutter (2004), we averaged used the age-specific selectivity for 1994-1998.

The numbers of fish at the end of the ninth month are

$$N^{9}_{i,a,r,y} = N_{i,a,r,y} e^{-\frac{9}{12}(M_{i,a} + \sum_{t} F^{t}_{i,a,r,y})} \qquad (8)$$

For Chinook salmon, coho salmon, brown trout, and steelhead, a pulse of maturation mortality was assumed to occur at the end of the year and maturation mortality rates were obtained from Szalai (2003). The timing of the pulses of sea lamprey mortality and maturation mortality in Lake Michigan for all species except for lake trout is an area of difficulty since in reality these processes are occurring concurrently. We retained the original timing used in Szalai (2003) for maturation mortality and Rutter (2004) for sea lamprey mortality since the parameter values from each source were to tuned to match existing data using this timing.

Sea lamprey mortality rates were approximated by a pulse of mortality at the start of the tenth month of the year. It is calculated from the sea lamprey attacks by

$$M^{L}_{i,a,r,y} = A^{host}_{a,r,y} * (1 - P^{s}_{i,a}) \qquad (9)$$

The probability of surviving a sea lamprey attack was assumed to follow the logistic function of weight estimated by Swink (2003).

Sea lamprey attacks on their hosts were modeled using a multi-species Type II functional response.

$$A_{host,r,y} = \frac{T\lambda_{host,r}L_{y,r}}{1+\sum_{i}^{allhosts} h_i \lambda_{i,r} D^{9}_{i,r,y}} \tag{10}$$

Although the population effect is approximated as a pulse, the number of attacks depends on the feeding season length as well as handling times. Season length and handling times for lake trout, lake whitefish, and Chinook salmon for both Lakes Huron and Michigan were taken from Rutter (2004). Handling times for steelhead, coho salmon, and brown trout for Lake Michigan were assumed to be the same as Chinook salmon. Status quo sea lamprey abundances for both lakes were obtained from Mullet et al. (2003) as the number of spawning sea lampreys and were divided by the volume of lake trout habitat (Szalai 2003, Rutter 2004) to obtain a density. For the main basin of Lake Huron, spawning sea lampreys were assumed to migrate from northern Lake Huron to central and southern Lake Huron using the migration parameters estimated by Rutter (2004).

Effective search rates were assumed to follow the logistic function of host length estimated by Rutter (2004) for the main basin of Lake Huron. The parameters of this logistic function varied by region in the main basin of Lake Huron and the values of the parameters from southern main basin of Lake Huron were used in Lake Michigan, as the size structure of lake trout in this part of Lake Huron is most similar to the size structure in Lake Michigan. For the northern main basin of Lake Huron, the low inflection point estimate of this function is thought to reflect the lack of large lake trout hosts in this region. To account for the possibility that the size structure of lake trout in the northern main basin of Lake Huron may shift towards larger lake trout in some projection scenarios, the inflection point of the logistic function was allowed to vary with the abundance of large lake trout (over 700 mm) as in Rutter (2004). In the main basin of Lake Huron, the effective search rates of lake whitefish and Chinook salmon were adjusted from the values predicted by the logistic function of length by the adjustment factor estimated by Rutter (2004). In Lake Michigan, we did not use these adjustment factors as we felt they might be correcting for the lack of age-structure in the alternative prey populations in the Lake Huron model rather than reflecting only the effect of differences in characteristics of the species on effective search rates. To account for differences between species in Lake Michigan, we adjusted the effective search rates of the alternative prey by multiplying by the habitat overlap values for these species from the Lake Ontario IMSL model (Koonce and Locci-Hernandez 1989).

The numbers at age after the pulse of sea lamprey mortality was calculated by

$$N^{*9}_{i,a,r,y} = N^{9}_{i,a,r,y} e^{-M^{L}_{i,a,y,r}}\,. \tag{11}$$

Yield of fish from each fishery is calculated by applying the Baranov catch equation to both pre- and post-sea lamprey mortality periods.

The models project damages (number of lake trout killed by sea lamprey), lake trout abundance, total number of lake trout deaths from all sources and fishery yield. The user can alter year-specific stocking rates, sea lamprey abundance, and year-specific effort values to project the effect of a variety of management policies on lake trout damages in either lake. The time period simulated can be specified by the user from 2 to

50 years. For illustrative purposes, we have included the results of 4 different scenarios forecasting lake trout damages from 1998 to 2010. The four scenarios presented are:

1. Status quo, where stocking and sea lamprey abundance are left at their current values
2. A 1/3 reduction in lakewide lake trout stocking from status quo for all years
3. A 3-fold increase in lakewide lake trout stocking for all years
4. A ½ reduction in lakewide sea lamprey abundances for all years.

Results

The EIL for lake whitefish and lake trout is an asymptotically increasing function of host value for both Lake Michigan and Huron (Figs. 1,2). The resulting functions generally predict a higher EIL for Lake Michigan than for Lake Huron and a higher EIL for an equilibrium system dominated by lake whitefish than for an equilibrium system dominated by lake trout (Table 4). The higher EIL for Lake Michigan than for Lake Huron results from the shape of the sea lamprey spawner abundance versus control spending curve (Fig. 3). For Lake Huron, higher levels of control spending do not lead to as large a decrease in sea lamprey spawner abundance because of the larger sea lamprey spawner abundance that persists (due to the St. Marys River source) at high levels of control effort.

For recent years, spending on TFM treatments (including both the cost of TFM and effort costs) have been well below the EIL level for lake trout, using either adjusted Koonce et al. (1993) value or the recreational harvest value for both lakes (Table 5, Figure 4). Current average levels of spending on sea lamprey control for Lake Michigan ($1.90 million) and Lake Huron ($1.63 million) imply a value for lake trout of approximately $0.74 and $2.12 respectively.

The short-term projection models for Lakes Michigan and Huron predict that the biomass of age 3 and older lake trout can be increased relative to status quo conditions by increasing lake trout stocking or decreasing sea lamprey abundance (Figures 5a and 6). Average sea lamprey mortality rates on age 5 and older fish can also be reduced from the status quo condition by decreasing sea lamprey abundance or increasing lake trout stocking (Figures 5b and 7). A decrease in lake trout stocking by one third is predicted to cause an increase in sea lamprey mortality rates and a decrease lake trout biomass in both lakes (Figures 5, 6, and 7).

Discussion

Integrated management of sea lamprey (IMSL) requires managers to balance the cost in controlling adult sea lamprey populations with the damages these populations causes to the Great Lakes ecosystem (Koonce et al. 1993, Christie and Goddard 2003). One of the key components of this approach is to identify the tradeoffs between increased control and other fisheries management objectives. Additionally, the Great Lakes Fishery Commission (GLFC) is called upon to allocate limited control resources among the Great Lakes (Stewart et al. 2003). The economic injury level approach, as implemented by Koonce et al. (1993), provides one means to balance the tradeoff between the cost of increased control and the benefit of reduced damages, as measured by reductions in host deaths caused by sea lampreys under equilibrium conditions. By combining knowledge on the response of the sea lamprey population to varying levels of control effort and the number of hosts deaths that result for a given sea lamprey population, the level at which increased spending on control does not lead to an commensurate increased harvest of hosts can be found. Previously, the application of this approach has been limited to lake trout in Lake Ontario (Koonce et al. 1993). Here, we have extended the application of this approach to Lakes Michigan and Huron for lake trout and lake whitefish by combining models of sea lamprey population dynamics in both lakes with the improved estimates of the parameters describing the link between sea lamprey populations and host deaths, in particular lake trout (Rutter 2004).

Our results suggest that in both Lakes Michigan and Huron, the level of control currently being applied is well below the level justifiable by two potential measures of lake trout value (adjusted Koonce et al. (1993) value and recreational harvest value) and further investments in control for both lakes could be warranted. While both of these value measures are imperfect and fail to capture the full economic value of lake trout, current levels of spending on control in both lakes imply a low value of lake trout, less than $1 in Lake Michigan and about $2.12 in Lake Huron.

The difference in EILs for Lake Michigan and Lake Huron are a direct consequence of the shape of the predicted response of the sea lamprey population to control efforts. In Lake Huron, unlike Lake Michigan, the sea lamprey population includes a large pool of sea lampreys (St. Marys River) that are treatable (Morse et al. 2003) but not with TFM; in this analysis we have not included this pool in the population of sea lampreys that are directly vulnerable to an increase in control budget – it acts as a source of sea lampreys that sustains the population even at high levels of lampricide treatment. The consequence of this feature is that higher levels of treatment are not justified in Lake Huron because of the proportionally smaller reductions in sea lamprey populations they would cause. This suggests that the control of sea lampreys in the St. Marys River may potentially have a large impact on the level of control justified for the rest of Lake Huron; reductions in the pool of sea lampreys available from the St. Marys River may lead to a higher EIL for Lake Huron. Future work on EIL calculations for Lake Huron should attempt to explicitly include control of the St. Marys River component of the population.

The calculation of EILs relies on the populations of hosts and sea lampreys being at equilibrium. Here, we have presented two extreme possibilities for the composition of the fish communities in Lakes Michigan and Huron at equilibrium. At one extreme, the fish community is dominated by large abundant lake trout that are the primary preferred hosts of the parasitic sea lampreys. At the other extreme is a system where the sea lamprey attacks are concentrated on the smaller lake whitefish. In the latter case, the predicted EIL for both lakes is higher than that based on a lake trout dominated system. Because lake whitefish have a shorter handling time by sea lampreys and are smaller, and therefore have a lower probability of surviving an attack, they suffer higher sea lamprey mortality rates. This combined with the larger target total mortality rates leads to larger benefits to reducing sea lamprey populations to lower levels assuming that a harvested lake whitefish and lake trout have the same value. While neither of these extremes represents the Lake Michigan or Lake Huron fish community currently, in both cases, the EIL for plausible values of harvested fish exceeds the current levels of control. Therefore justification for increasing sea lamprey control in both lakes does not depend solely on assuming that lake trout restoration efforts will be successful.

The EIL approach depends critically upon our ability to quantitatively describe how changes in the control of sea lamprey lead to changes in the number of hosts killed by parasitic sea lampreys. While our calculations of the EILs for Lake Huron and Lake Michigan reflect our current level of understanding, substantial uncertainty remains. In our calculations, parameters of the sea lamprey-host functional response influence EILs through the expected number of deaths caused per sea lamprey at high host densities: $T(1-p)/h$. Thus both handling time (*h*) and the probability of surviving an attack (*p*) are critical. Handling time remains difficult to estimate from observed sea lamprey wounding patterns and more detailed information on the wounding patterns in alternative hosts, such as Chinook salmon and lake whitefish, are needed to improve estimates of sea lamprey handling times (Rutter 2004). Our current estimates of the probability of surviving an attack are based on laboratory experiments (Swink 2003), but there remains disagreement between laboratory estimated probabilities and those predicted by bioenergetics modeling (Bence et al. 2003). In addition to the functional response parameters, the relationship between equilibrium sea lamprey abundance and expenditures on control efforts is central to determination of EILs. This relationship depends upon our depiction of sea lamprey population dynamics and treatment effectiveness, and both remain areas for future investigation (Jones et al. 2003).

Here we have also presented a dynamic, short-term projection model for sea lamprey-lake trout interactions reflecting current conditions in both Lake Michigan and Lake Huron. The projections produced by these models predict the effects of changes in lake trout management (e.g. stocking rates) or sea lamprey control on the damages to lake trout caused by sea lampreys using a multispecies Type II functional response. These models can be used to guide management decisions regarding lake trout and sea lamprey control and also could be used in formal economic valuation studies (e.g. Lupi et al. 2003). Our projection models are based upon Rutter's (2004) point estimates of functional response parameters. Although he showed that mean projections for lake trout abundance and mortality were similar to projections based upon the mean parameters, he also emphasized that projecting distributions of outcomes based on parameter distributions provided useful information regarding risk. This is an area for future work.

Sea lamprey control in the Great Lakes depends upon the ability of mangers to allocate limited control resources across all systems. While EILs for Lake Ontario were produced over a decade ago, EILs have not been subsequently established for other Great Lakes (Koonce et al. 1993, Stewart et al. 2003). Here we have presented EILs for two other Great Lakes, suggesting that current control levels are below the optimal levels, just as was concluded by Koonce et al. (1993). We reached this same qualitative conclusion even though we assumed that sea lamprey attacks were substantially less lethal to lake trout. We believe that our results are an important part of evaluating the basis for sea lamprey control expenditures and that similar efforts to examine EILs for all the Great Lakes could help provide useful guidance to decision makers regarding overall investment in sea lamprey control and the allocation of sea lamprey control resources among the lakes.

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Table 1. Definition of parameters used in the calculation of the Economic Injury Level for Lakes Michigan and Huron

Parameter	Definition
C_T	Total cost of integrated sea lamprey management (dollars)
C_C	Cost of sea lamprey TFM control (dollars)
C_S	Cost of stocking and fishery management (dollars)
C_D	Cost of damage due to adult sea lamprey (dollars)
L^*	Equilibrium abundance of parasitic sea lamprey (number)
$L_{\min}$	Asymptotic minimum abundance of parasitic sea lamprey (number)
α	Constant of lamprey versus cost relationship (number)
β	Slope of lamprey versus cost relationship (dollars^{-1})
V	Value of lake trout or lake whitefish (dollars)
a	Coefficient for effective search rate of sea lamprey
h	Handling time of sea lamprey (year)
T	Duration of attack season (year)
N^*	Equilibrium abundance of hosts (number)
Z	Target instantaneous mortality rate for lake trout or lake whitefish (year^{-1})
p	Probability of host surviving an attack (unitless)

Table 2. Values of parameters used in calculating Economic Injury Level for lake trout and lake whitefish in Lakes Michigan and Huron

Parameter	Value	
T	0.41	
	Lake Michigan	Lake Huron
α	1.50E10	9.96E6
β	6.20E-6	3.21E-6
	Lake trout	Lake whitefish
h	0.030137	0.015068
Z	0.6	1.05
p	0.73	0.3

Table 3. Definition of parameters used in short-term projection models for Lakes Michigan and Huron.

Parameter	Definition
y	year
r	region
a	age
i	species
$N_{i,a,r,y}$	Number of fish at the beginning of the year
$S_{i,a,r,y}$	Survival
$\gamma_{i,r}$	Post-stocking survival
$N^{9}_{i,a,r,y}$	Number of fish after 9 months of mortality
$D^{9}_{i,a,r,y}$	Density of fish after 9 months of mortality
$M_{i,a,r}$	Instantaneous natural mortality rate
$F^{t}_{i,a,r,y}$	Instantaneous fishing mortality of type *t*
$N^{*9}_{i,a,r,y}$	Number of fish after 9 months of mortality and a pulse of sea lamprey mortality
$M^{L}_{i,a,r,y}$	Sea lamprey mortality rate
$A^{i}_{a,r,y}$	Number of sea lamprey attacks on a fish
$P^{s}_{i,a}$	Probability of survival of sea lamprey attack
T	Length of feeding season in years
$\lambda_{j,r}$	Effective search rate of sea lamprey for host type *j*
$L_{r,y}$	Sea lamprey density
h_i	Handling time in years

Table 4. The Economic Injury Level (millions of dollars) for lake trout and lake whitefish in Lakes Michigan and Huron at a variety of host values.

Value	Michigan		Huron	
	Lake trout	Lake whitefish	Lake trout	Lake whitefish
$10.00	2.66	2.80	2.11	2.21
$25.00	2.92	3.07	2.40	2.48
$50.00	3.12	3.27	2.62	2.69

Table 5. Economic Injury Level for lake trout in Lakes Michigan and Huron using three illustrative values.

Source	Value	EIL (millions of U.S. dollars)	
		Lake Michigan	Lake Huron
Koonce et al. (1993)	$12.00	2.71	2.17
Adjusted Koonce et al.(1993)	$20.52	2.87	2.34
Recreational Fishery	$40.00	3.06	n/a
	$30.00	n/a	2.46

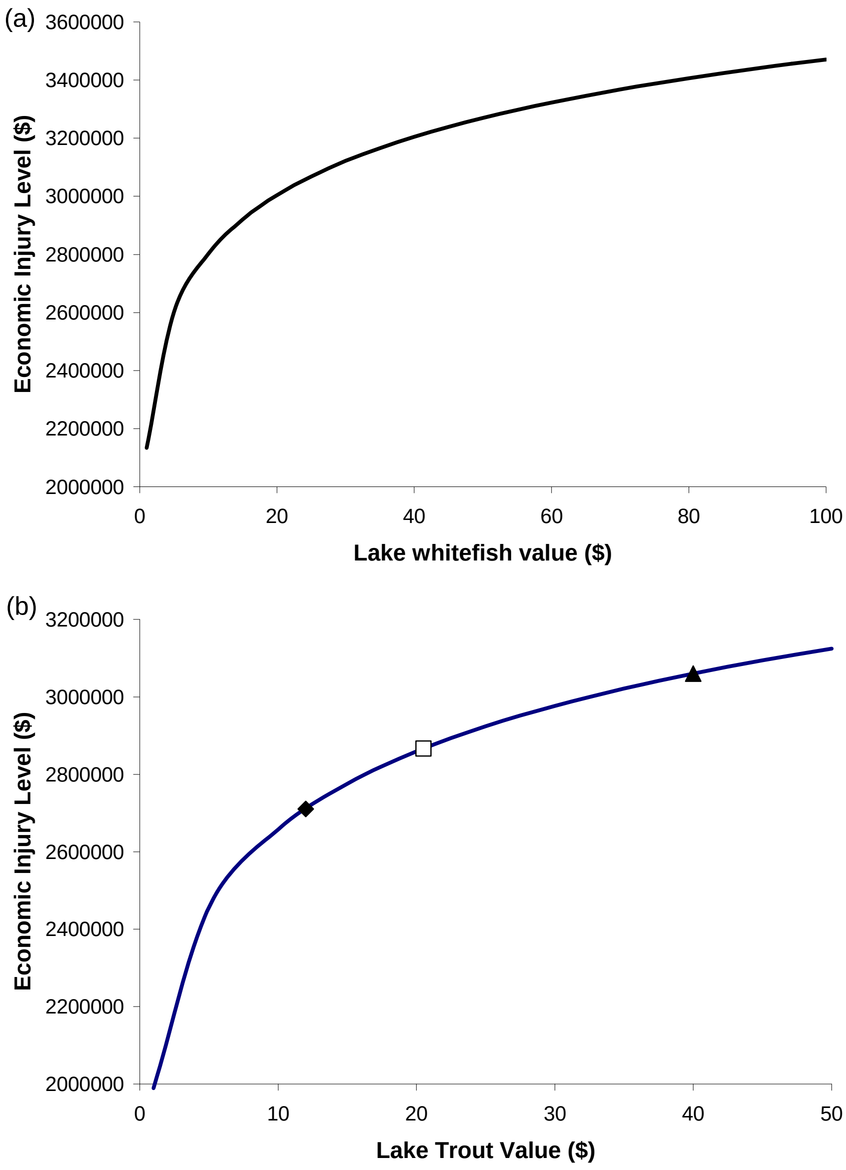

Figure 1. Economic Injury Level (solid line) for Lake Michigan as a function of (a) lake whitefish value and (b) lake trout value. For lake trout, three illustrative values are shown: Koonce et al. (1993) value (diamond), adjusted Koonce et al. (1993) value (open square), and recreational fishery value (triangle).

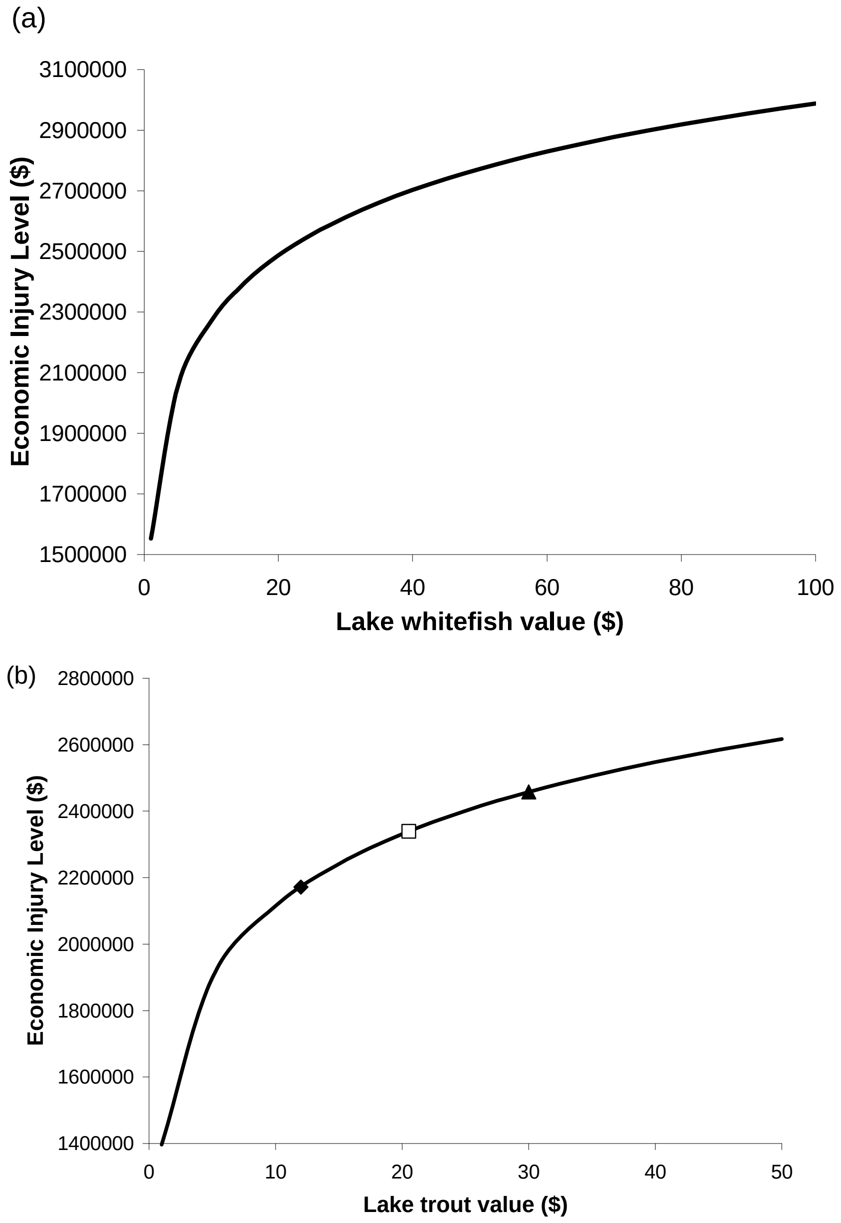

Figure 2. Economic Injury Level (solid line) for Lake Huron as a function of (a) lake whitefish value and (b) lake trout value. For lake trout, three illustrative values are shown: Koonce et al. (1993) value (diamond), adjusted Koonce et al. (1993) value (open square), and recreational fishery value (triangle).

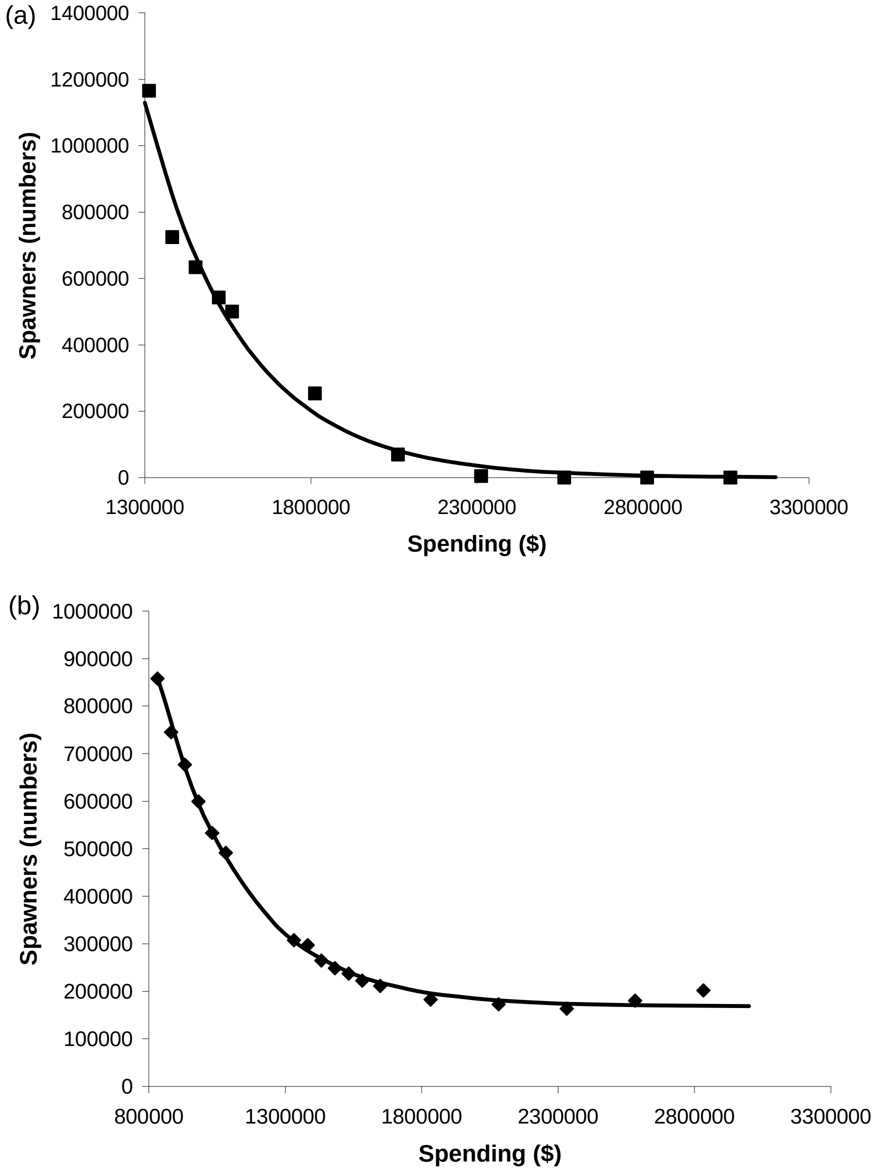

Figure 3. Sea lamprey median spawner abundance observed (diamond) from the ESTR model and predicted (line) from equation 2 versus average simulated spending on sea lamprey TFM control for (a) Lake Michigan and (b) Lake Huron.

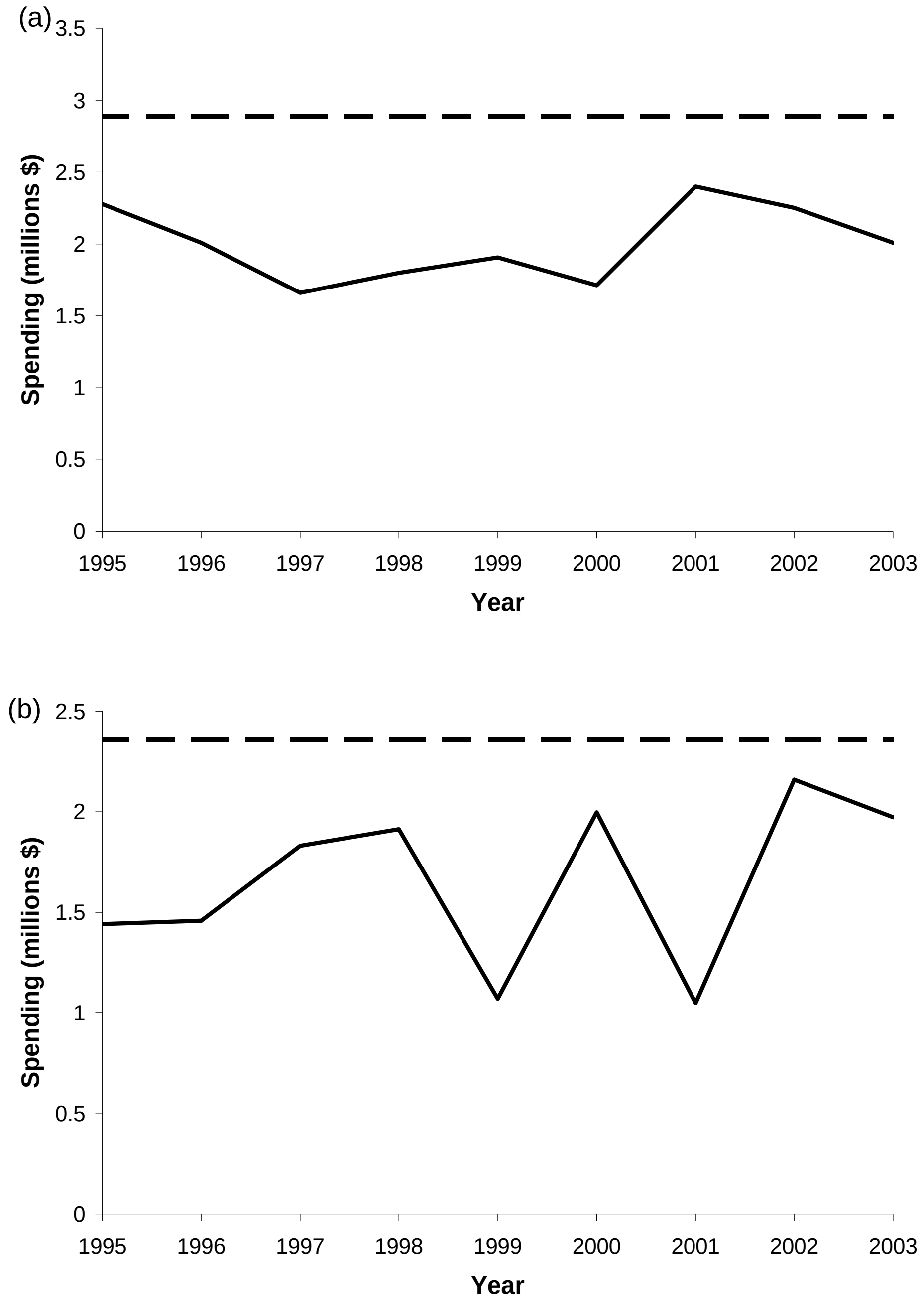

Figure 4. Recent spending (1995-2003) on TFM control (solid line) and economic injury level (dashed line) for lake trout using the adjusted Koonce et al. (1993) value for (a) Lake Michigan and (b) Lake Huron.

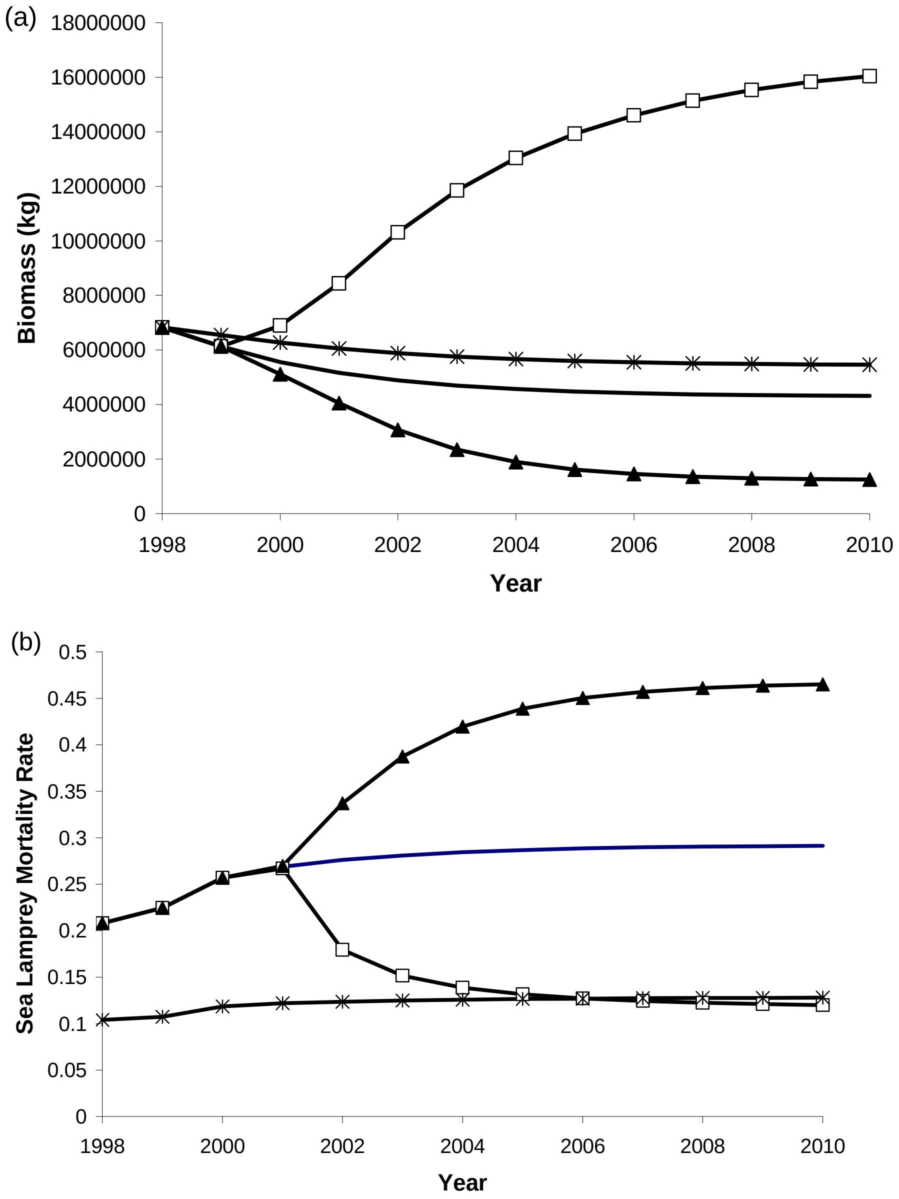

Figure 5. (a) Predicted biomass (kg) of age 3+ lake trout in Lake Michigan, 1998-2010, for status quo stocking (solid line), 3 times status quo stocking (open squares), and 1/3 status quo stocking (triangles), and a 50% reduction in sea lamprey abundance (stars). (b) Predicted average instantaneous sea lamprey mortality for age 5+ lake trout in Lake Michigan, 1998-2010, for status quo stocking (solid line), 3 times status quo stocking (open squares), 1/3 status quo stocking (triangles), and a 50% reduction in sea lamprey abundance (stars).

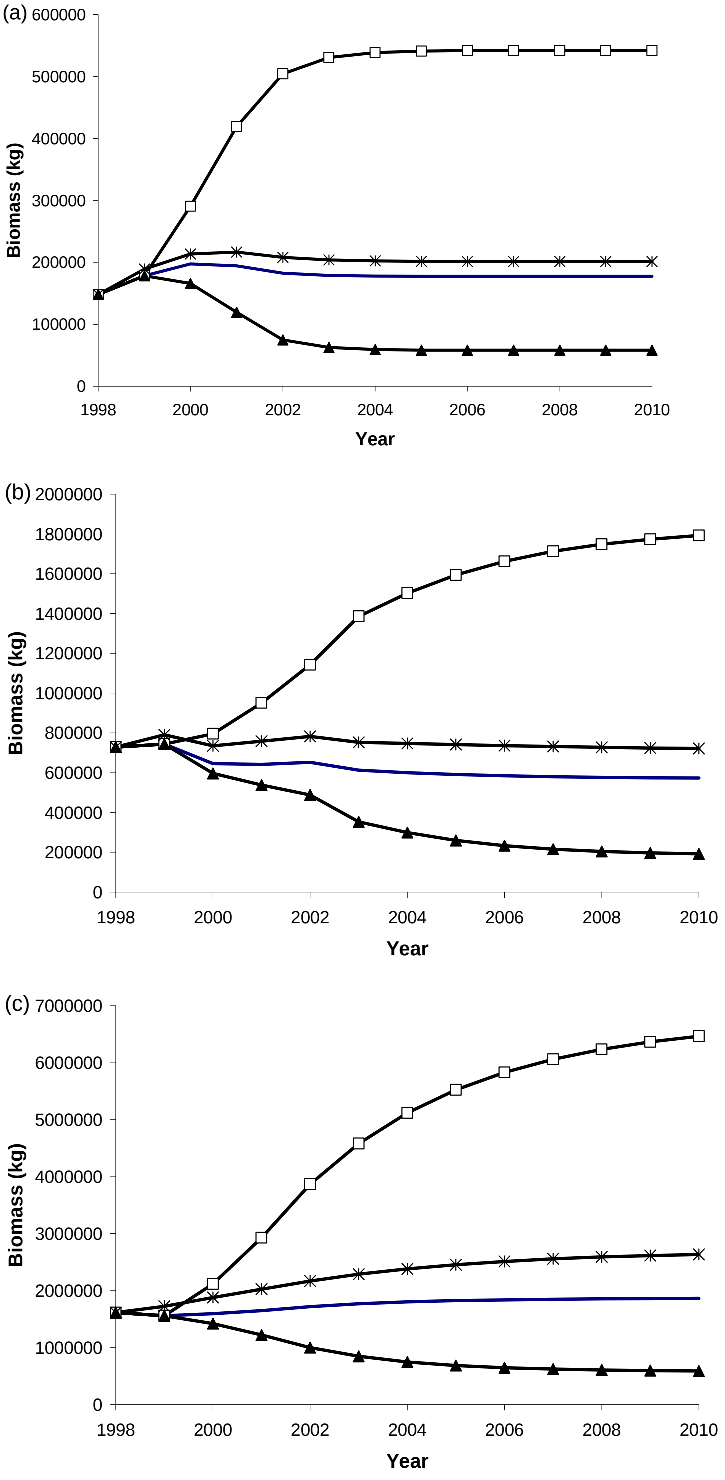

Figure 6. Predicted biomass (kg) of age 3+ lake trout in (a) North, (b) Central, and (c) Southern Lake Huron, 1998-2010, for status quo stocking (solid line), 3 times status quo stocking (open squares), and 1/3 status quo stocking (triangles), and a 50% reduction in sea lamprey abundance (stars).

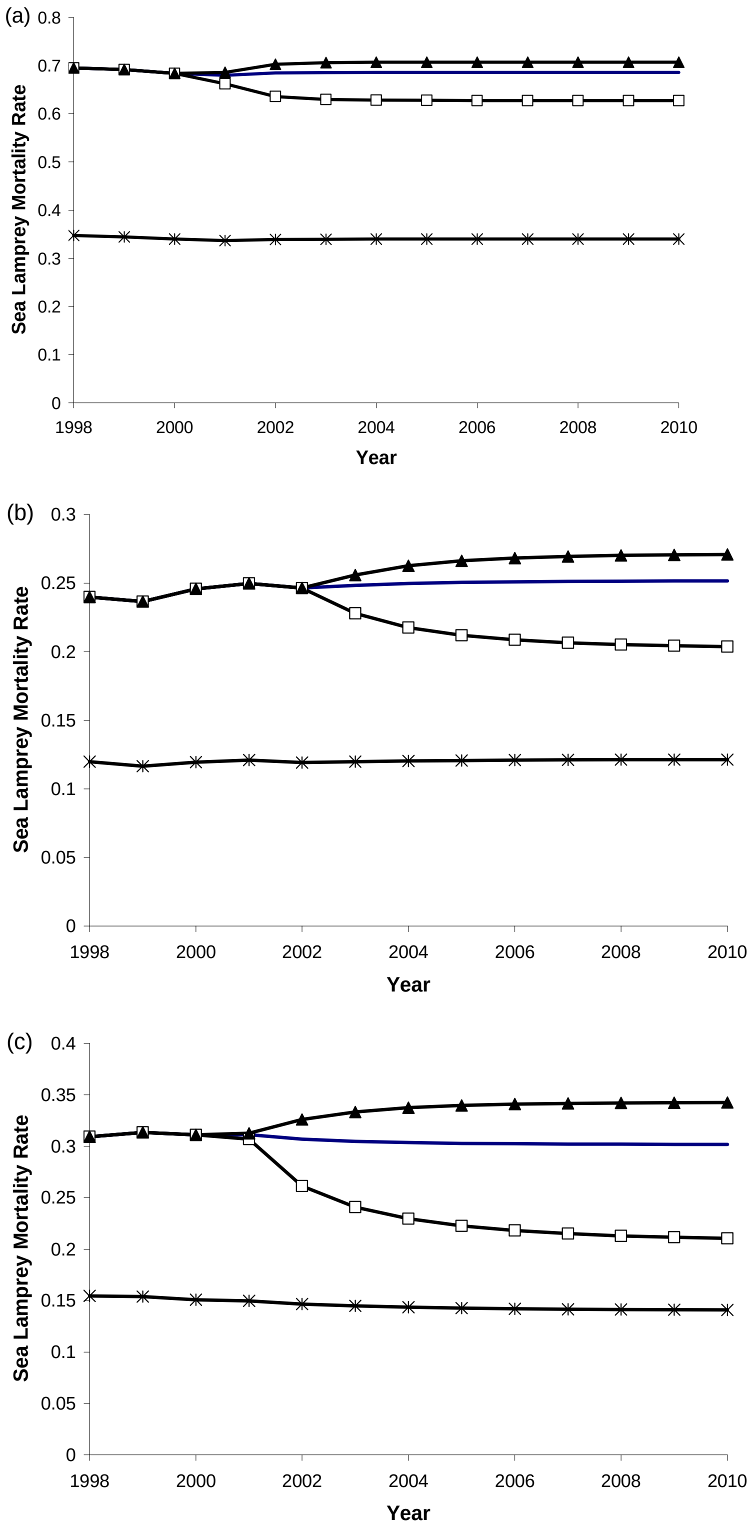

Figure 7. Predicted average instantaneous sea lamprey mortality rate of age 5+ lake trout in (a) North, (b) Central, and (c) Southern Lake Huron, 1998-2010, for status quo stocking (solid line), 3 times status quo stocking (open squares), and 1/3 status quo stocking (triangles), and a 50% reduction in sea lamprey abundance (stars).