Estimating the Relationship between Sea Lamprey-Induced Mortality on Lake Trout and Observed Marking Rates

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ABSTRACT:

We modified existing stock-assessment models for lake trout to evaluate the relationship between sea lamprey-induced mortality and observed marking rates on lake trout in the upper Great Lakes. The overall objective of the project was to evaluate the ability to estimate the proportionality between sea lamprey-induced mortality and wounding marking rates used in lake trout assessment models. We considered models for the following assessment units: Lake Huron MH1, MH2, and MH3456; Lake Michigan MM123, MM4, MM5, and MM67; and Lake Superior MI5 and MI7. The primary method used to estimate the new scaling parameter was to estimate this parameter simultaneous to other assessment-model parameters, but we also considered an iterative approach to estimation where the scaling parameter was estimated separately from other model parameters. We considered models at the scale of individual assessment units (listed above), for each lake separately (combining across assessment units – "combined-by-lake" model variants), and by combining across lakes ("combined-across-lake" model variants). The combined-by-lake approach was intended to take advantage of contrast in patterns in marking rates among areas. Prior to combining, individual models were adjusted to a consistent compiler format and given assessment-unit-specific naming conventions. Reflecting the high degree of model complexity and large number of included parameters, several attempted alternative models could not be fit either because of convergence issues or because standard errors for estimated parameters could not be calculated. For example, we were unable to estimate a lake-specific scaling parameter for Lake Superior. Such problems persisted despite our efforts to modify the models to reduce the number of parameters to be estimated. We were able to generate estimates of a scaling parameter for four model variants, spanning different levels of spatial aggregation. The point estimates of the scaling parameter for the combined-by-lake versions for both Lake Huron and Lake Michigan and for the combined-across-lake model variant were greater than 1, suggesting that model fit could be improved by increasing the mortality rate associated with a given level of observed marks from sea lamprey parasitism. We further estimated a weighting factor to allow the estimated scaling parameter to change monotonically over ages for one variant of the combined-by-lake model for Lake Huron. This weighting factor suggested that the influence of the scaling parameter was largest for the youngest ages of lake trout in Lake Huron, despite the marking data being essentially pre-adjusted to account for laboratory-based estimates of how size influences lethality of sea lamprey attacks.

INTRODUCTION:

A fundamental goal of the sea lamprey (*Petromyzon marinus*) management program in the Great Lakes is to reduce sea lamprey-induced damages on host fish populations (Larson et al. 2003). As such, understanding fishery damages caused by sea lamprey is critical to the overall assessment of the sea lamprey control program. A principal fishery concern in the Great Lakes is that abundances of the native lake trout (*Salvelinus namaycush*) stocks are reduced by sea lamprey parasitism that causes mortality (Lawrie 1970). When an individual host survives a sea lamprey attack, observable "wounds" remain visible throughout a prolonged but variable healing duration (King and Edsall 1979; King 1980; Ebener et al. 2003). Currently, the Lake Committee for each of the Great Lakes uses information on observed wounds per lake trout to assess whether sea lamprey populations have been suppressed by the control program to levels consistent with specified fish community objectives. It is generally believed and assumed that sea lamprey-induced mortality is positively correlated with these observed wounding rates (Bence et al. 2003). Identifying target levels of wounding rates (e.g., number of wounds per lake trout) depends critically on the relationship between wounding rates and the realized mortality experienced by a host population. To date, much uncertainty remains regarding damages caused by individual parasitic sea lamprey, and improved understanding of the relationship between sea lamprey-induced mortality and the observed marking data would greatly assist management (Bence et al. 2003).

Changes in mortality of host fish have been linked to the frequency of sea lamprey wounds, the rate at which sea lamprey scars accumulate, and estimates of the abundance of sea lamprey (Budd et al. 1969; Pycha 1980; Spangler et al. 1980; Eshenroder et al. 1995). Although correlations between marking statistics and estimates of sea lamprey abundance also provide evidence that marking data are useful (Smith et al. 1974), the most compelling evidence for the relationship between marking and host mortality comes from an innovative study on Lake Ontario, in which lake trout carcasses were collected by trawling (Bergstedt and Schneider 1988; Schneider et al. 1996). From 1982 through 1992, trawl samples collected between 1 October and 15 November from U.S. waters were assessed for dead lake trout. Additional trawl sampling was done during spring and summer and after 15 November in some years, but few dead lake trout were recovered, even though substantial effort was expended (Bergstedt and Schneider 1988). Live lake trout were sampled by gillnet during September for the same years. Schneider et al. (1996) found a strong positive correlation between the density of dead lake trout with relatively fresh sea lamprey wounds (A1 or A2 marks according to the system of King (1980)) and total number of fresh (A1) marks observed on live lake trout (summed over all live lake trout collected with a standard amount of gillnet effort). Nearly all dead lake trout had recent sea lamprey marks, whereas a relatively small fraction of live lake trout had such marks.

In all of the current stock-assessment models for lake trout in the 1836 treaty waters of the Great Lakes, sea lamprey-induced mortality rates are treated as known quantities based on an assumed proportionality between observed wounding rates (sum of A1-A3 marks) and sea lamprey-induced mortality, and the assumed proportionality is influenced by an assumed healing time, the presumed observability of wounds on all hosts that survived potentially lethal attacks, and a lab-based estimate of the probability of surviving an attack. The lab-based estimates are quite uncertain (Bence et al. 2003), and recently Madenjian et al. (2008) argued that the actual probability of surviving an attack is higher than that assumed in the assessment models, based on those lab experiments. The stock-assessment approaches can be viewed as something akin to nonlinear regression, where the observed dependent variables are fishery and survey catch rates, independent variables include fishery and survey effort, and estimated parameters include recruitment levels, mortality rates, and fishery and survey catchability. In principle, the sea lamprey wounding data could be used in the assessment models as an indicator of sea lamprey-induced mortality rather than treated as providing known values for this mortality source. This would be similar to treating sea lamprey wounding in the same fashion as how fishing effort is used to provide an index of fishing mortality, and the proportionality between sea lamprey-induced mortality and wounds per fish would represent a new parameter to be estimated when fitting the stock-assessment model. Here, we describe efforts to modify and combine existing stock-assessment models for lake trout in order to better evaluate quantitative relationships between observed sea lamprey wounding information and sea lamprey-induced mortality.

OBJECTIVES:

The objectives articulated in the project proposal and some comments related to our activities to accomplish each objective are:

1. Determine the strength of evidence, for lean lake trout in lakes Huron, Michigan, and Superior, that natural mortality rate is positively associated with wounds (spring data, sum of A1-A3 marks) per lake trout caused by sea lamprey.

This objective was met by combining estimation models for multiple assessment units across lakes (i.e., the "combined-across-lake" model variant) and introducing a newly estimated parameter, which was shared across assessment units and lakes, and quantifies the proportionality between the nominal sea lamprey mortality rates directly calculated from A1-A3 marking and actual mortality rates caused by sea lamprey parasitism. When Lake Superior's assessment units were included with those from lakes Huron and Michigan, we were unable to identify an unambiguous estimate for various reasons, such as the models did not converge or standard errors could not be produced. Therefore, the estimation of a scaling parameter shared across lakes was conducted using models from seven assessment units from lakes Huron and Michigan.

2. Evaluate whether the natural mortality rate versus wounding relationship differs among lakes or regions within lakes.

This objective was met by combining estimation models for multiple assessment units within each lake (i.e., the "combined-by-lake" model variants) and introducing an estimated scaling parameter, shared across assessment units, which, as for objective one, quantifies the proportionality between mortality rates and the nominal mortality rates. As was the case for objective one, we were unable to satisfactorily fit the model when Lake Superior's two available assessment units were combined together, even though alternative model structures (e.g., gamma selectivities) were incorporated in the model. A scaling parameter was estimable for both a combined Lake Huron model and a combined Lake Michigan model, although both cases required additional modifications to the lake-specific models (described in more detail below). Two alternative cases of combined-by-lake models were evaluated for Lake Huron, with each reflecting different restrictive assumptions related to time-varying gear selectivity.

3. Evaluate whether the relationship between natural mortality rate and marking diverges from linearity. The overall objective is to better establish the quantitative relationship between mortality caused by sea lamprey and sea lamprey marking.

This objective was met by introducing an additional estimated parameter to allow the influence of the scaling parameter to be age dependent. We evaluated this using one of the combined-by-lake model variants for Lake Huron. Additional attempts to estimate a parameter affecting the scaling parameter for other model variants were made, but these attempts did not result in estimable parameters.

METHODS:

General overview

We modified and combined existing statistical catch-at-age models used to assess lake trout abundance and mortality, using assessments from eight regions that constituted one or more lake trout management units in 1836 treaty waters of lakes Huron, Michigan, and Superior, and one additional region from southern Lake Huron outside the treaty waters that used a similar assessment approach. We excluded one additional treaty water assessment unit (MI-6 in Lake Superior) from consideration both because we were not provided access to the most recent assessment in time to use it and because the assessment is acknowledged as producing problematic results (MSC 2007). The purpose of combining the assessments was to allow an estimated parameter or parameters associated with the scaling of nominal sea lamprey mortality to be shared across assessment units, and thus to be estimated by taking advantage of all the data simultaneously. Before we combined the models, they all assumed a known direct proportionality between observed marking rates and the sea lamprey component of natural mortality. The sea lamprey mortality rates used in these models were calculated outside the assessment models (i.e., prior to fitting of the models) and assumed known. This was done by first estimating year-specific relationships between marking rates and size, converting these to size-specific mortality rates based on information on how survival of a sea lamprey attack scales with size, and then converting these to age-specific rates based on an age-length key (Sitar et al. 1999; Bence et al. 2003; Rutter and Bence 2003). In this study, we used these nominal age-specific sea lamprey mortality rates, and replaced the assumption that these rates were correct on an absolute scale with various assumptions on how actual mortality was related to these nominal rates. Below, we describe how we prepared the models for individual assessment units for this analysis, the construction of different variants of new multi-unit estimation models that simultaneously estimated parameters across various assessment units ("combined" model variants), and the inclusion of new parameters within the combined models to address the project's objectives.

In all our analyses, we used information based on the sum of A1-A3 wounds per fish according to the system of King (1980), which we refer to as the wounding rate. The visual appearance of a lamprey wound at the time it is observed is influenced by several factors (e.g., the size of the parasite, the duration of attachment to the host; King 1980). Observed lamprey wounds are classified following a criteria that recognizes two types of marks, each with different stages of healing (King 1980; Ebener et al. 2003). Type-A marks are those where the skin at the attachment site is broken, exposing the underlying musculature, and type-B marks appear as abrasions or elongated scrapes with no visible break through the integument. Each type of mark can be in stages 1 to 4 of healing, where stage 1 indicates the most recent attack with the least healing (e.g., "A3" is a type-A mark in stage 3 of healing). Current assessment practice across lakes Huron, Michigan, and Superior is to treat the sum of A1-A3 marks as wounds that reflect the level of sea lamprey-induced mortality that occurred over the previous year. On Lake Ontario A1 marks are used; however, these marks are thought to heal much faster than one year, and their use most likely requires survey data collected in late summer when most lethal attacks are occurring. Such data are not generally available for the areas with existing lake trout stock assessments. While there may be other measures of wounding that are better correlated with mortality than the wounding rate currently used in assessments and used in this report, we did not pursue this because of the more challenging than expected programming challenges we experienced.

Models for individual assessment units

We considered estimation models for lake trout from nine separate assessment units in lakes Huron (MH1, MH2, and MH3456), Michigan (MM123, MM4, MM5, and MM67), and Superior (MI5 and MI7). Assessment units with a single digit number correspond to one specific lake trout management unit. For example, MH1 and MI5 represent assessments for the management units MH-1 and MI-5 respectively. Multiple digits represent assessments that combine management units. For example, MM123 combines MM-1, MM-2, and MM-3, while MH3456 combines MH-3, MH-4, MH-5, and MH-6. Furthermore, Lake Huron assessment units are meant to represent lake trout in adjacent Canadian waters of the Lake Huron Main Basin. Each of the lake trout models for the individual assessment units was coded using AD Model Builder software; however, different compilers were used originally and coding styles varied due to individual preferences of the programmers who maintained the computer code for these assessments. Therefore, several models required coding adjustments in order for them to be run individually on our compiling systems, which included using a gnu C++ compiler as well as a Linux based system on our server (a multiprocessor Dell PowerEdge 6850 server with four 3.66 GHz Intel Xeon Processors and 16 GB RAM, housed in a ventilated computer cabinet and running AD Model Builder Software).

Description of a new scaling parameter

In the existing stock-assessment models for the individual assessment units, sea lamprey-induced mortality is pre-calculated (i.e., not estimated) for each modeled year and lake trout age and is then combined with estimated parameters to determine instantaneous mortality rates $\left(Z_{m,a,y}\right)$ for each assessment unit-*m*, age-*a*, and year-*y*:

(1) $$Z_{m,a,y} = F_{Cm,a,y} + F_{Rm,a,y} + M_{m,a} + M_{Lm,a,y} ,$$

where $F_{Cm,a,y}$ is the age- and year-specific commercial fishing mortality, $F_{Rm,a,y}$ is the age- and year-specific recreational fishing mortality, $M_{m,a}$ is other natural mortality (sometimes by age), and $M_{Lm,a,y}$ is the age- and year-specific sea lamprey-induced mortality. The instantaneous mortality rates are used to determine the annual proportion of fish surviving from one age to the next:

(2) $$S_{m,a,y} = e^{-Z_{m,a,y}} ,$$

and this survival rate is used to determine age- and year-specific abundances $\left(N_{m,a,y}\right)$:

(3) $$N_{m,a+1,y+1} = N_{m,a,y} S_{m,a,y} .$$

In order to initialize this abundance matrix, most of the individual assessment units also estimate abundance-at-age during the first year as well as recruitment at the youngest age in subsequent years or initial natural mortality rates for each year. Numerous additional computations are conducted for each stock to predict the effects of the fishery components (commercial and recreational) as well as survey catch per unit effort (CPUE) for comparison with observed data. Additional description of the existing stock-assessment models and their parameterization is provided by MSC (2007).

We evaluated new parameters associated with sea lamprey-induced mortality. First, we applied a new estimated parameter that scaled nominal pre-calculated sea lamprey-induced mortality rates such that the equation for the age- and year-specific instantaneous mortality rate became:

(4) $$Z_{m,a,y} = F_{C m,a,y} + F_{R m,a,y} + M_{m,a} + \alpha M_{L m,a,y},$$

where the scaling parameter, α, was estimated on the $\log_e$ scale. In subsequent sections, we describe specific application of the scaling parameter as it was applied across assessment units within lakes as well as across lakes (see objectives 1 and 2).

Our approach of applying a proportionality parameter to the nominal age-specific sea lamprey mortality rate is equivalent to applying the proportionality parameter to the observed wounding rates, while retaining the relative size-specific values among the nominal size-specific rates. Calculation of the nominal sea lamprey-induced mortality rates (for the original assessment models) followed an overall approach similar to that of Sitar et al. (1999). First, length-specific wounding rates for each year were estimated based on fitting a logistic function of length to the wounding data following Rutter and Bence (2003). This use of Rutter and Bence's (2003) approach to summarizing wounding data is the primary divergence from how Sitar et al. (1999) calculated sea lamprey mortality. Second, these length-specific wounding rates were converted to length-specific sea lamprey mortality rates by:

(5) $$M_L = \overline{w}\frac{(1-P_S)}{P_S},$$

where $\overline{w}$ is the mean observed wounds per fish of a specific length and P_S is a length-specific estimate of the probability of surviving an attack, as based on laboratory experiments (Swink 2003). Then the length-specific rates are converted to age-specific rates using an age-length key. It should be evident from equations 4 and 5 that our approach is equivalent to assuming:

(6) $$\widetilde{M}_L = \alpha\overline{w}\frac{(1-P_S)}{P_S},$$

where $\widetilde{M}_L$ is the estimated actual sea lamprey-induced mortality rate for a specific length, verifying our prior claim that our approach corresponds to assuming proportionality between sea lamprey-induced mortality and observed wounding. Thus after our revision, the sea lamprey mortality rate applied in the assessment model is assumed to be proportional to a nominal rate $\left(\text{i.e., } \widetilde{M}_{L\,m,a,y} = \alpha M_{L\,m,a,y}\right)$. To address objective 3, we further evaluated if there was evidence that the relationship between sea lamprey mortality and nominal mortality diverged from the same direct proportionality over all ages. In this case, we considered an additional parameter (λ) that allowed the proportionality to change monotonically over ages (a):

(7)
$$Z_{m,a,y} = F_{C\,m,a,y} + F_{R\,m,a,y} + M_{m,a} + e^{(-\lambda a)} \alpha M_{L\,m,a,y}.$$

The parameter λ was estimated as a free parameter such that it could take either positive or negative values.

<u>*Combined-by-lake model variants*</u>

Each model for the individual assessment units for each lake was assigned an assessment-unit-specific prefix prior to combining with other assessment units. This prefix was added to parameters, index variables, and calculated quantities for each respective assessment unit. This time-consuming step was necessary given that many parameters, constants, and calculated variables needed to retain assessment-unit specificity once the combined models were constructed. Attempts to simply combine assessment units to form larger lake-specific models while simultaneously estimating the scaling parameter were not successful, and each combined-by-lake model could not be fitted once the scaling parameter was added as an estimated parameter. We believed that the difficulty in fitting these combined models was due to over-parameterization of the models; therefore, we modified the combined-by-lake models so that they shared additional selected parameters across assessment units. Additionally, for some of the lakes, we modified the gear selectivity function because we believed it was sometimes difficult to find unique parameters for the pre-existing function that produce a desired selectivity pattern. We describe the more substantial modifications for each lake below. In addition to these modifications, some minor adjustments were made to the bounds of certain parameters as well as to the estimation phases to which some parameters were assigned. We do not detail these minor adjustments here. The combined-by-lake models were constructed to allow a single set of sea lamprey mortality parameters to be shared across assessment units in different lakes, and lake-specific values were compared to evaluate whether there was evidence that the mortality-wounding relationship differed among lakes (see objective 2).

The first suite of modifications for the combined-by-lake model for Lake Huron was to share natural mortality parameters across assessment units. For example, the parameters representing initial natural mortality over time were shared among MH1, MH2, and MH3456. However, the initial models for the three separate assessment units previously included different assumptions for determining initial natural mortality for the last few years. Thus, a slight additional modification was made to the calculation of initial natural mortality of the last three years in MH1 such that the value estimated for 2004 was held constant through 2007. This change increased consistency in mortality assumptions between MH1 and other assessment units for Lake Huron. We retained other existing assumptions about recent initial natural mortality so that, in the end, estimated values for initial mortality parameters were the same across assessment units in Lake Huron for years 1984-2002. In addition, a single parameter for age-2 and older natural mortality was modified to be shared across Lake Huron assessment units in the combined-by-lake model.

The second suite of modifications for the combined-by-lake model for Lake Huron was to change the gear selectivity functions from double logistic to gamma selectivities. Age-based selectivities in the individual assessment units for Lake Huron were initially estimated as a double-logistic function:

(8) $$S_{y,m,f,a} = \left(\frac{1}{1 + e^{\left(-p_{2_{m,f}}\left(a - p_{1_{y,m,f}}\right)\right)}} \right) \left(1 - \frac{1}{1 + e^{\left(-p_{4_{m,f}}\left(a - p_{3_{m,f}}\right)\right)}} \right),$$

where up to four parameters $\left(p_{1_{y,m,f}}, p_{2_{m,f}}, p_{3_{m,f}}, p_{4_{m,f}}\right)$ were estimated for each fishery or survey (f) in each assessment unit (m). In some assessment units for Lake Huron, a random walk was applied to allow $p_{1_{y,m,f}}$ to vary over time:

(9) $$p_{1_{y+1,m,f}} = p_{1_{y,m,f}} e^{\zeta_{y,m}},$$

where $\zeta_{y,m}$ represents annual deviations that were estimated for each assessment unit.

For Lake Huron, we changed the age-based selectivity model for each fishery or survey to follow a gamma function:

(10) $$S_{y,f,a} = \left(a - \phi_{y,f}\right)^{p_{1_f}} e^{\left(-p_{2_f}\left(a - \phi_{y,f}\right)\right)},$$

where p_{1_f} and p_{2_f} are estimated parameters that define the overall shape of the selectivity pattern and $\phi_{y,f}$ is an estimated offset parameter that determines the age of entry to the fishery or survey. During estimation, the parameters p_{1f} and p_{2f} were shared across assessment units for each fishery separately, and this modification reduced the number of parameters associated with estimating selectivity. The offset parameter can be thought of as adjusting for the effects of changes in growth over time. We constructed two cases for the offset parameter in Lake Huron. First, the offset parameter was allowed to vary over time but was shared across both assessment units and fisheries.

(11) $$\phi_{y+1} = \phi_y e^{\delta_y},$$

where δ_y represents annual deviations ("case 1") that are assumed to be normally distributed with a mean of 0 and variance of σ_δ^2. Second, a less restrictive case increased the number of estimated parameters to allow the offset parameter to vary over time and to be estimated separately for each fishery (i.e., a gear-specific, time-varying offset; "case 2"):

(12) $$\phi_{y+1,f} = \phi_{y,f} e^{\delta_{y,f}},$$

where $\delta_{y,f}$ represents annual deviations that affected the age of entry of each fishery separately and that also are assumed to be normally distributed with means of 0 and variances of $\sigma_{\delta_f}^2$. Using case 2 (eq. 12), we further allowed the scaling parameter to vary across ages in Lake Huron by introducing a weighting factor as an additional parameter (eq. 7).

For Lake Michigan, models for individual assessment units were compiled and executed separately in order to determine starting values for all parameters included in the combined-by-lake model, but with α not estimated and assumed to equal 1.0. This was necessary to obtain reasonable parameter values to initiate the search in the more parameter-rich combined model. The double logistic selectivity function (eq. 8) was retained for each assessment unit included in the combined-by-lake variant for Lake Michigan. In the model for the individual assessment unit of MM4 of Lake Michigan, $p_{1y,m,f}$ for the commercial fishery was allowed to vary over time as a function of two additional estimated parameters (b_1, b_2) that produced an additive quadratic increment:

(13) $$p_{1y+1,m,f} = p_{1m,f} + b_1(i) + b_2(i)^2,$$

where i = 1 to n-1 years and the estimate of $p_{1m,f}$ was used during year 1. However, these two additional parameters related to time-varying selectivity for the commercial fishery in MM4 were not estimated in the combined models but were rather left fixed at the values estimated by the model for the individual assessment unit. Then, we assumed that the natural mortality of age-2 and older lake trout was constant across assessment units within Lake Michigan. The prior information for natural mortality for assessment units in Lake Michigan was different for one of the units; therefore, we retained the likelihood function component for natural mortality for each area.

For Lake Superior, we combined models for assessment units MI5 and MI7, but this combined model could not be satisfactorily fitted for any of the various model variants we attempted. In our efforts to seek a combined model that could be fitted, we modified the original combined-by-lake model for Lake Superior to share one natural mortality rate for age-4 and older fish across assessment units and the selectivity model was adjusted to follow a gamma function, as described above for Lake Huron. None of these changes resulted in an estimable scaling parameter. Given our inability to fit the combined-by-lake model even without estimating sea lamprey parameters, we did not attempt to further modify Lake Superior's stock-assessment models for the purposes of this exercise.

Combined-across-lakes model variants

As was the case for the combined-by-lake model variants, attempts to simply combine assessment units to form a larger combined-across-lakes model that would simultaneously estimate a scaling parameter was not successful. This extremely large model (over 1,200 parameters; see Table 1) failed to converge when all nine assessment units were incorporated into a single estimation procedure. This across-lake model had over 8,500 lines of model code and required several hours to compile and had a much longer run time than the combined-by-lake models, which caused unexpected and real limitations for the number of alternative configurations that could be considered because most changes to the model's structure required recompiling the model. In this case, we provided initial values for parameters that were based on the values estimated when the models were run individually for the separate assessment units. However, providing these starting values for estimated parameters did not lead to adequate model fitting. Due to the difficulties that we confronted in fitting the model for the combination of Lake Superior assessment units, we chose to focus our subsequent efforts on fitting a combined-across-lakes model variant using only assessment units for lakes Huron and Michigan (see description of modifications to those combined-by-lake variants above). Once models for lakes Huron (case 2) and Michigan were modified and then recombined, a single proportionality parameter was applied across their seven assessment units (i.e., shared across lakes; the “7-model” variant; see objective 1).

An iterative approach to estimating the scaling parameter

Above, we described a variety of model combinations and modifications that were used to estimate a scaling parameter simultaneous to other model parameters. Here, we briefly describe an additional attempt to estimate the scaling parameter using an iterative estimation approach. This approach was attempted due to the difficulties in estimating the scaling parameter for the larger combined-model variants and the expectation that it might allow the estimation process to avoid some confounded parameter combinations. This iterative estimation approach basically separated the estimation of the scaling parameter from the estimation of all other stock-assessment parameters. The first step of the iterative approach was to perform parameter estimation for the seven assessment units of Lake Huron and Lake Michigan separately from one another and without including the scaling parameter as an additional estimated parameter. The resulting estimated parameter values were then used as fixed values in a combined-across-lakes model that included only the scaling parameter as an estimated parameter. These steps were then repeated across multiple iterations until a user-defined convergence criterion was satisfied. Overall, the outcomes of this iterative approach appeared sensitive to the choice of the convergence criteria and did not appear to produce stable estimates. Therefore, we refocused our efforts on estimating the scaling parameter simultaneous to other stock-assessment parameters (as described above). We do not describe the iterative approach further in this report, but this alternative attempt to estimate the scaling parameter for large, complex models required development of new code to perform the iterative cycle. Estimating the scaling parameter simultaneously with other model parameters is likely preferable to using such an iterative approach.

RESULTS:

Models for individual assessment units

The number of estimated parameters ranged from 82 to 196 across the nine individual assessment unit models, totaling more than 1,200 parameters (Table 1). The models for the nine individual assessment units differed in amount and type of input data. Assessment units from Lake Superior had the longest time series of data, with some sources of information spanning from 1975 through 2007 (e.g., a large-mesh survey), but only included data for ages-4 and older lake trout. The age structure incorporated in the models for both Lake Huron and Lake Michigan ranged from age 1 to age 15. Population calculations for Lake Huron began in 1977 for MH1 and in 1984 for MH2 and MH3456. Not all data sources were available continuously starting with the first year of the population calculations. Population calculations for Lake Michigan began in 1981. Model structure related to initial mortality and time varying selectivity also varied among individual assessment units, namely across lakes. The constant natural mortality rates estimated separately for individual assessment units were fairly similar for older ages of lake trout (Table 2).

Combined-by-lake model variants

Each of the two alternative cases for the combined-by-lake models for Lake Huron had fewer parameters than the total implemented in the models for the three assessment units. For case 1 of the combined-by-lake Lake Huron model variant, 241 parameters were estimated, which is fewer than half of the total number originally included in the three assessment units. This substantial reduction was in large part due to sharing the annual values for estimated initial natural mortality rates among the three assessment units and reducing the parameters associated with variation over time in selectivity. These modifications resulted in deviations from previous values of lake trout natural mortality and abundance that were determined by models for the individual assessment units, but we did not detect large-scale differences in these quantities (Tables 2 – 4). For example, MH2 had the largest estimate of initial natural mortality and MH1 had the lowest estimate in both the individual assessment unit models and in case 2 of the combined-by-lake model variant for Lake Huron. However, the estimate of initial natural mortality for MH2 was lower than for the other assessment units in the case 1 model variant. For case 2 of the combined-by-lake Lake Huron model variant, 296 parameters were estimated, with all of the additional parameters to case 1 being associated with allowing the offset parameter of the gamma selectivity function to vary over time separately for each fishery.

We compared the resulting estimated values (averaged over time) for fishery selectivity for the previous double logistic selectivity function, where values were estimated independently for each assessment unit, and for our modified version using a gamma function (case 2), where parameters were shared across assessment units within Lake Huron (Figures 1 – 3). The original double-logistic selectivity estimates were similar in shape across assessment units for both the commercial fishery and the recreational fishery (black lines; Figures 1 – 3). However, the pattern for survey selectivity in MH3456 differed from those seen in either MH1 or MH2 (black lines; Figures 1 – 3). The fishery-specific parameters associated with the gamma function were shared across assessment units in Lake Huron resulting in the same annual values for selectivity for a particular fishery across Lake Huron's assessment units, although the overall time duration included in the estimation did vary among assessment units and fisheries (grey lines; Figures 1 – 3). As a result, the difference between selectivity models (double logistic vs. gamma function) was greatest for the estimated survey selectivity in Lake Huron (Figures 1 – 3).

For Lake Michigan, a total of 392 parameters were estimated across the four combined assessment units. This is slightly fewer parameters than the total of the individual assessment units because the natural mortality rate for age-2 and older fish was shared across assessment units in our combined-by-lake model variant for Lake Michigan (Table 3) and the time-varying selectivity of the commercial fishery in MM4 was no longer estimated. As was the case for the combined-by-lake model variants of Lake Huron, the Michigan model produced somewhat different estimates of natural mortality as a result of sharing the value for ages-2 and older across assessment units (Tables 2 and 3). When the models for the individual assessment units for Lake Michigan were run separately, MM67 had a slightly greater estimate of natural mortality prior to age-2 than did MM4 (Table 2); however, this pattern was reversed in the combined-by-lake model (Table 3). We expect that assumptions related to modeling natural mortality are potentially important to the estimation procedures, particularly those that combine across areas, and we are interested in pursuing future sensitivity analyses connected to altering some of these assumptions.

Combined-across-lake model variants

The 7-model version (named because the seven Lake Huron and Lake Michigan units were included) that was produced during this study included both the case 2 variant of the combined-by-lake Lake Huron model and the combined-by-lake Lake Michigan model. The total number of parameters estimated by the 7-model version was

687. This was a large, highly parameterized model that required longer compiling and run times than any of the individual assessment unit models or any of the combined-by-lake model variants. The relative patterns across assessment units in natural mortality rates determined by the 7-model variant were the same as those of the two combined-by-lake model variants that it contained (Table 3). The 7-model variant produced the lowest total estimate of average abundance for age-5 and older lake trout in Lake Huron, although patterns across assessment units remained similar to those of other model variants (Table 4).

Estimated values for the scaling parameter

In total, we produced four model variants capable of estimating a scaling parameter (Figure 4). Interestingly, the highest point estimate for the scaling parameter (1.40) was associated with case 1 of the combined-by-lake Lake Huron model, while the lowest point estimate (1.04) was associated with case 2 of the combined-by-lake Lake Huron model (Figure 4). The case 2 Lake Huron model variant produced the only lower bound (point estimate -2 SE) that was less than 1 (Figure 4). The point estimate for the scaling parameter from the combined-by-lake Lake Michigan model variant (1.35) was close to that for case 1 of Lake Huron and had a larger standard error, which resulted in the highest value at the upper bound (point estimate +2 SE; Figure 4). The point estimate (1.16) and the range of values for the 7-model variant were roughly intermediate to the values of the variants for case 2 of Lake Huron and the Lake Michigan combined-by-lake models (Figure 4).

Lastly, we used case 2 of the combined-by-lake Lake Huron model variant to evaluate if there was evidence that the relationship between sea lamprey-induced mortality and wounding diverged from linearity by including an additional parameter (λ) that allowed the influence of the scaling parameter to vary across ages. Thus, the total number of parameters for this evaluation was 297. This modified version of the case 2 Lake Huron variant produced a range of scaling parameters across ages that was greater than the intervals calculated for the other model variants (Figures 4 and 5). The combination of the estimates of the scaling parameter (1.90) and λ (0.073) from this modified version produced an effective scaling parameter at approximately age 8 that was similar to the scaling parameter estimated in the case 2 combined-by-lake Lake Huron model variant (Figure 5). Including the λ parameter in the case 2 Lake Huron model variant produced a total estimate of average abundance for age-5 and older lake trout that was closer to the total from the individual assessment units run separately than did the other model variants that also included these assessment units (Table 4). Additional attempts were made to estimate a λ parameter for both the combined-by-lake Lake Michigan model variant and for the combined-across-lake 7-model variant, but in both cases the models could not be fitted.

DISCUSSION:

The assumed proportionality between observed sea lamprey wounding rates and sea lamprey-induced mortality currently used in lake trout assessment models in the upper Great Lakes makes strong assumptions about healing time and the time-averaged probability of surviving an attack. The actual probability that a host survives a sea lamprey attack is likely influenced by several biotic and abiotic factors (e.g., the host's size, duration of attachment, number of previous attacks, water temperature; Bence et al. 2003; Swink 2003). Estimates of the probability of surviving a sea lamprey attack are critical not only for the current lake trout assessments but also in other models that are used either to develop economic injury levels ("EILs"; Koonce et al. 1993, Szalai et al. 2005; Irwin et al. 2008) or project the consequences of changes in sea lamprey abundance to the fish community. While our estimates of the proportionality between sea lamprey-induced mortality and wounds per fish do not fully define the probability of surviving a sea lamprey attack, they are informative about plausible values of this probability. This improved understanding will aid in consideration of how sea lamprey control efforts influence damages experienced by important fish communities in the Great Lakes.

We estimated a scaling parameter with a value greater than 1 for four different model variants based on assessments for Lake Michigan, Lake Huron, or both lakes. These values imply an increase in the sea lamprey-induced mortality rate associated with a given level of observed marks from sea lamprey parasitism from that currently assumed in lake trout assessment models. Our point estimates of the scaling parameter suggest that current assumptions about the magnitude of sea lamprey-induced mortality used in the stock-assessment models appear reasonable and even on the low side. Bence et al. (2003) previously highlighted the wide range of estimates of the probability of surviving an attack for lake trout that have been published, ranging from 0.14 to over 0.6 for large hosts. More recently, Madenjian et al. (2008) suggested that the probability of surviving a sea lamprey attack is higher for Lake Champlain (0.74) and Lake Huron (0.66) than the value assumed in the assessment models (0.55). Some previous calculations of EILs have also used a relatively high probability of survival for large fish (0.73; Szalai et al. 2005; Irwin et al. 2008) based on the regression models developed from lab data by Swink (2003), within the range described by Madenjian et al. (2008). Others have suggested much lower survivorship (Heinrich et al. 2003). For example, Koonce et al. (1993) used a low probability of survival (0.25) when calculating an EIL for Lake Ontario, as was also reported by Eshenroder et al. (1987). Irwin et al. (2008) further considered a range of plausible values for the probability of surviving an attack, indicating that EIL budgets would be higher if the probability of surviving a sea lamprey attack was reduced (i.e., higher lethality). Some of the different values that have been used, such as 0.55 in the assessment models versus 0.66 of Madenjian et al. (2008), may appear similar on first consideration and indeed may not be distinguishable given the existing lab data. However, replacing the currently assumed value of 0.55 by 0.66 without any other changes would correspond to a proportionality of 0.63 (at least on older ages) between new and previously assumed sea lamprey-induced mortality in the lake trout assessment models, which our analysis suggests is implausible.

The apparent discrepancy between our results and those of Madenjian et al. (2008) could reflect other influences on the proportionality between mortality and wounding rates, besides the probability of surviving an attack. For example, if wounds from potentially lethal attacks heal or are not included in the marks classified as wounds (A1-A3 marks), then this would lead to a higher proportionality between mortality and observed wounds (Bence et al. 2003). For Lake Champlain, Madenjian et al. (2008) estimated sea lamprey-induced mortality by subtracting out estimates of other natural mortality and fishing mortality from a catch curve estimate of total mortality. They then used information on wounding rates to solve for the probability of surviving an attack (our eq. 5). This approach essentially estimates the proportionality between mortality and wounds, and other variables that might influence the relationship are incorporated into the estimate of the probability of surviving an attack. Madenjian et al. (2008) also estimated a ratio of the total number of deaths due to sea lamprey (based on field data from Lake Champlain) to those directly attributable to blood loss (predicted from an individual based model [IBM] for Lake Champlain). This ratio was assumed constant across lakes and applied to the IBM predictions for Lake Huron to estimate the probability of surviving an attack in Lake Huron. They interpreted the need to scale-up the IBM results by a factor somewhat larger than 2 as being due to the fact that the IBM accounts for deaths directly attributable to blood loss but not those deaths that occur subsequent to detachment by sea lamprey. Other alternatives involved in the need to scale-up the IBM results could include actual underestimation of directly lethal attacks in the IBM (given they involve an extrapolation from lab results based on sea lamprey feeding on smaller hosts), as well as not all survivors of potentially lethal attacks in the previous year being classified as wounded in the survey data (see above). We see no obvious reason why the estimated relationship between sea lamprey-induced mortality and wounding for Lake Champlain would be a substantial underestimate for that lake. This said, the range of values for the probability of surviving a sea lamprey attack presented in Madenjian et al. (2008) are based on several point estimates rather than a full propagation of error through the calculations such that this range may not be statistically distinguishable from 0.55. Most importantly, even if the relationship between sea lamprey-induced mortality and wounding for Lake Champlain estimated by Madenjian et al. were exactly correct, we believe the extrapolation to Lake Huron is likely biased. Our results, like theirs for Lake Champlain, are based on patterns in the survey and fishery data and indicate that the scaling between the IBM and actual sea lamprey-induced mortality in Lake Huron is likely different than their assumed value based on Lake Champlain.

Both the original configurations of the stock-assessment models and the modified versions used in the current study make assumptions related to various uncertainties that ultimately contribute to the parameter values that are estimated. If certain model assumptions differ dramatically from reality, then it is likely that inaccuracies or biases exist in the modeling outputs, as is the case with any estimation procedure. One major uncertainty that was assumed here was that natural mortality is constant across older ages and over time, and that the prior information on the level of natural mortality used in the assessment models is valid. Total mortality has a strong influence on model predictions of observed data and a mistake in assumptions about other sources of natural mortality could be confounded with what is estimated as due to sea lamprey. When we introduced a weighting factor to alter the influence of the scaling parameter across ages for case 2 of the combined-by-lake model for Lake Huron, our results suggested that the proportionality between mortality and age may decrease more with age than is currently assumed in the assessment models. If, however, older fish experience reduced natural mortality due to factors other than sea lamprey, then this relationship might be mistaken for one due to sea lamprey. Likewise, if our prior values for natural mortality are centered on too high a value, then this could lead to an underestimate of the proportionality between sea lamprey-induced mortality and wounding. In this regard we note that the means of the priors for other natural mortality assumed in the assessments are substantially higher than the value of other natural mortality assumed for Lake Champlain lake trout by Madenjian et al. (2008).

Some technical challenges arose during this project, and we offer some thoughts on how some impediments might be circumvented in the future. Simply combining models for the individual assessment units in an additive fashion did not allow for successful estimation of the new scaling parameter. One potential challenge faced by the estimation software is the need to produce covariances among all parameter estimates included in the model. The stock-assessment models include a large number of estimated parameters (see Table 1), and when the different assessment units are run independently, the covariances of parameters from separate units are not calculated and are implicitly assumed to be zero. However, when models are combined but parameters remain unique to particular assessment units, the parameters from different units still should have zero covariances, but the estimation procedure used by the software does not take advantage of that fact. It may be possible to take advantage of such known structure if the software were modified or if options and programming choices could be defined in the context of the current software to allow this. An as yet unexplored modeling alternative would be to keep the stock-assessment models for the individual assessment units separate (as opposed to combining as was done here) with proportionality (or other shared parameters) fixed. Then a "control" program could be used to fit each of the stock-assessment models sequentially, in each case using the same shared scaling parameter. The overall log likelihood for that value of the scaling parameter would then be obtained based on the sum of the log likelihoods for that value for each individual model. The control program would then evaluate a sequence or profile of different values of the shared parameter and the fit for different values could be compared. This approach would retain the assumption of uncorrelated parameters among assessment units that is present when individual assessment units are fit independently from one another.

Secondly, an unexpected technical challenge that occurred was the substantial increase in compile and run times required by the larger models. This outcome stresses the importance of simplifying code whenever possible to gain efficiency. The existing stock-assessment models were initially coded without the intention of being combined with other models; however, reduction of some redundancies in the large combined models would likely be possible and allow for shorter compile and run times if standardization and use of common functions for repeated tasks were introduced to the coding for all assessment units. This is not a trivial coding task, in the case of the complex lake trout assessment models, but one that could be accomplished if the necessary resources were available.

The overall principle of combining models across assessment units that was applied in this study could also be beneficial to other types of analyses. For example, the estimation of stock-recruitment parameters could be performed where some estimated parameters are shared across assessment units while others are retained as independent among units. Stock-recruitment analyses based on stock size and recruitment time series estimated from stock-assessment models are common. Meta-analyses of such time series have been used to develop knowledge about the stock-recruitment relationship, given that many such time-series have limited information on the relationship when considered alone (Myers et al. 1999). However, such stock-recruitment analyses and meta-analyses treat the estimated stock sizes as known and assume that the recruitment estimates given stock size are independent. Furthermore, most interpretations treat the variation about the estimated stock recruitment relationship as due to process variation and not due to uncertainty in the recruitment estimates. It is clear these assumptions will be violated and in some cases such violations could have substantial effects (e.g., Hilborn and Walters 1992; Quinn and Deriso 1999). Likewise, the construction of larger models that contain multiple assessment units could allow for movement of fish among spatial areas (Sibert et al. 1999). In either case, the combination of models may also be able to contribute improved biological realism without requiring increases in the total number of estimated parameters. In addition, the sharing of some estimated parameters (e.g., natural mortality) across areas might substantially increase the ability to perform estimation procedures that include assessment units that are relatively data poor. At a policy level, the construction of models that span jurisdictional boundaries often helps facilitate sharing of information while also creating conduits for communication during the management decision-making process.

In addition to providing information related to a scaling parameter for sea lamprey-induced mortality, this study is providing additional benefits to stock-assessment efforts in the Great Lakes. The project provided staff at the Quantitative Fisheries Center the opportunity to become familiar with the current details of multiple stock-assessment models for lake trout in lakes Huron, Michigan, and Superior. Through this research, we have already informed the Modeling Subcommittee of model behavior in response to recent modifications and made suggestions on how assessments could be improved. Further, our consideration of alternative selectivity functions should be informative to future decisions about the structure of the stock-assessment models used in the Great Lakes.

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Table 1. Summary of the number of estimated parameters for nine individual assessment units.

Lake	Management unit	Number of estimated parameters
Superior	MI5	196
	MI7	118
Huron	MH1	194
	MH2	161
	MH3456	168
Michigan	MM123	111
	MM4	105
	MM5	82
	MM67	98

Table 2. Estimates of natural mortality for age 1 (Age-1 *M*) and for older ages (*M*) for nine individual assessment units.

Lake	Management unit	Age-1 *M*	*M*
Superior	MI5	NA	0.170[i]
	MI7	NA	0.201[i]
Huron	MH1	0.646[ii]	0.202
	MH2	0.691[ii]	0.264
	MH3456	0.661[ii]	0.206
Michigan	MM123	0.338	0.233
	MM4	0.556	0.290
	MM5	0.779	0.288
	MM67	0.575	0.199

[i] The *M* values reported for Lake Superior are for age-4 and older, all other areas are for age-2 and older.
[ii] Average across years.

Table 3. Estimates of natural mortality for age 1 (Age-1 *M*) and for older ages (*M*) for combined-by-lake and combined-across-lake model variants.

Model variant	Management unit	Age-1 *M*	*M*
Huron (case 1)	MH1	0.789[i]	0.189
	MH2	0.687[i]	0.189
	MH3456	0.708[i]	0.189
Huron (case 2)	MH1	0.699[i]	0.211
	MH2	0.740[i]	0.211
	MH3456	0.723[i]	0.211
Michigan	MM123	0.312	0.243
	MM4	0.658	0.243
	MM5	0.808	0.243
	MM67	0.469	0.243
7-model	MH1	0.696[i]	0.204
	MH2	0.733[i]	0.204
	MH3456	0.712[i]	0.204
	MM123	0.315	0.249
	MM4	0.688	0.249
	MM5	0.858	0.249
	MM67	0.477	0.249
Case 2 with λ	MH1	0.649[i]	0.183
	MH2	0.683[i]	0.183
	MH3456	0.667[i]	0.183

[i] Average across years.

Table 4. Estimated abundance of age-5 and older lake trout during the final 15 years (1993-2007) in Lake Huron. Values are rounded. Individual = estimates from individual assessment units run separately; Case 1 = case 1 of the combined-by-lake Lake Huron model variant; Case 2 = case 2 of the combined-by-lake Lake Huron model variant; 7-model = estimates for Lake Huron based on the 7-model combined-across-lake model variant; Case 2 with λ = case 2 of the combined-by-lake Lake Huron model variant with one additional parameter; see text for additional details.

Model variant	MH1	MH2	MH3456	Total
Individual	185,000	214,000	482,000	881,000
Case 1	148,000	234,000	432,000	814,000
Case 2	149,000	233,000	429,000	811,000
7-model	149,000	230,000	424,000	803,000
Case 2 with λ	157,000	253,000	467,000	877,000

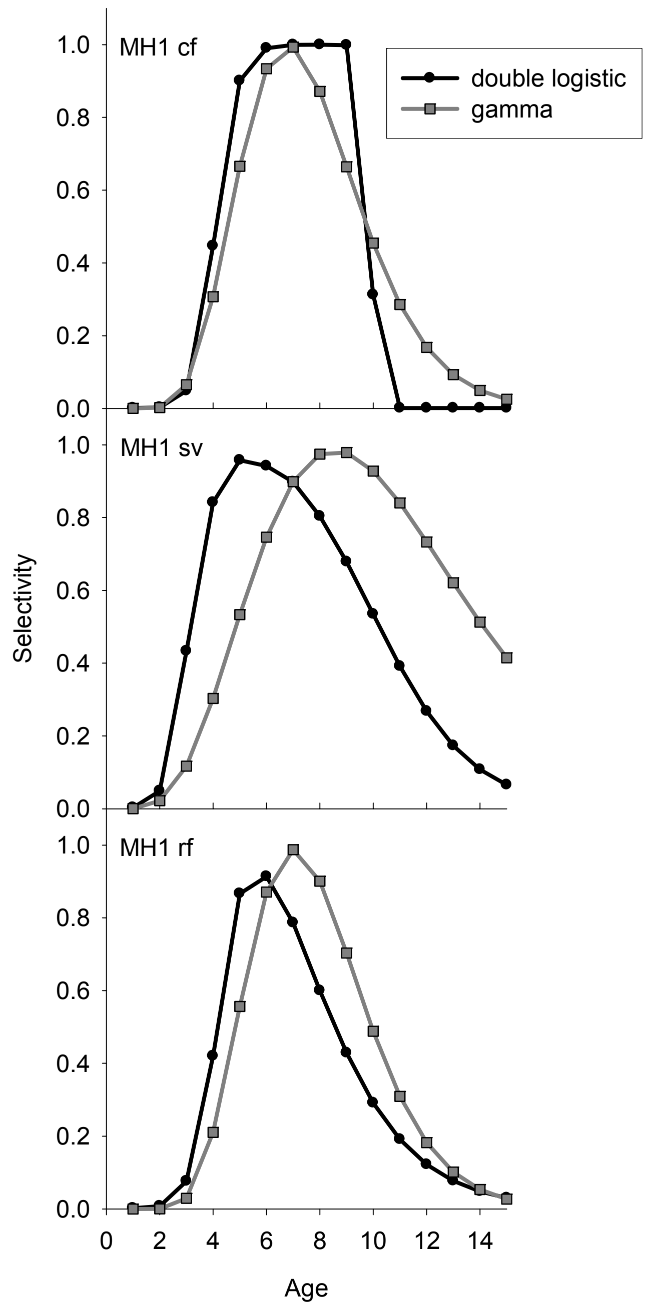

Figure 1. Average selectivity curves over time for the commercial fishery (cf), the fishery-independent survey (sv), and the recreational fishery (rf) in an assessment unit (MH1) of Lake Huron based on a double logistic model where parameters were estimated at the level of the individual assessment unit and based on a gamma model where the estimated selectivity parameters were shared across assessment units.

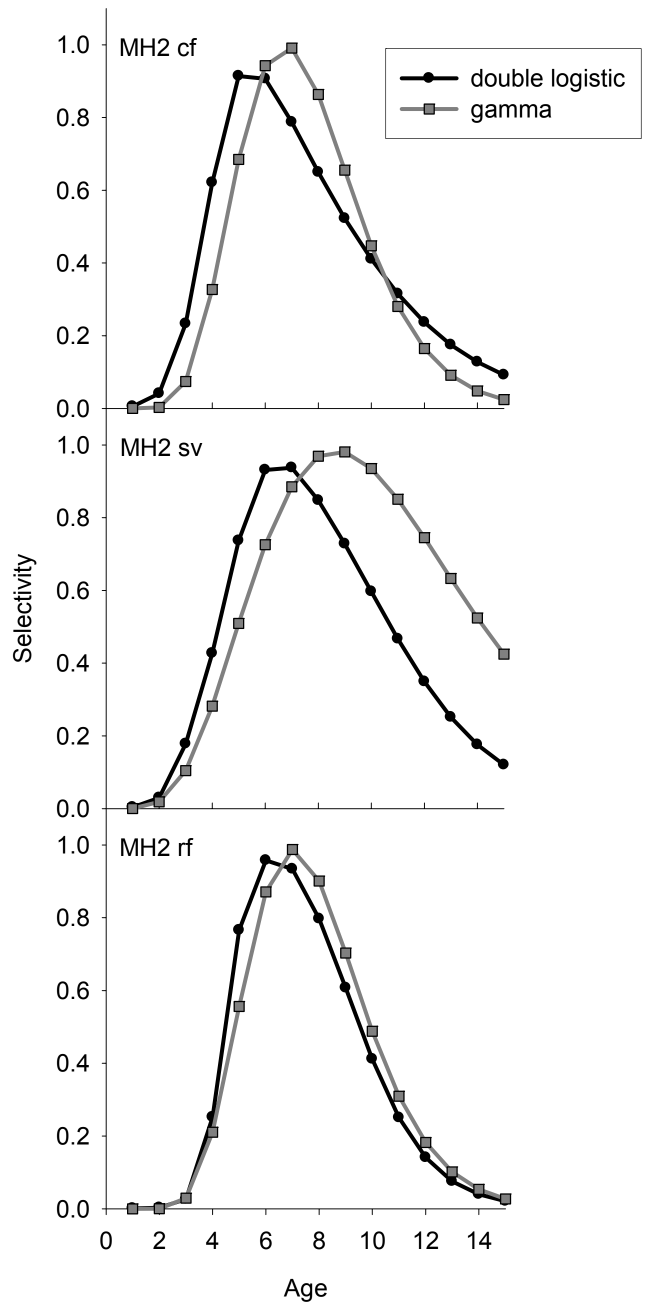

Figure 2. Average selectivity curves over time for the commercial fishery (cf), the fishery-independent survey (sv), and the recreational fishery (rf) in an assessment unit (MH2) of Lake Huron based on a double logistic model where parameters were estimated at the level of the individual assessment unit and based on a gamma model where the estimated selectivity parameters were shared across assessment units.

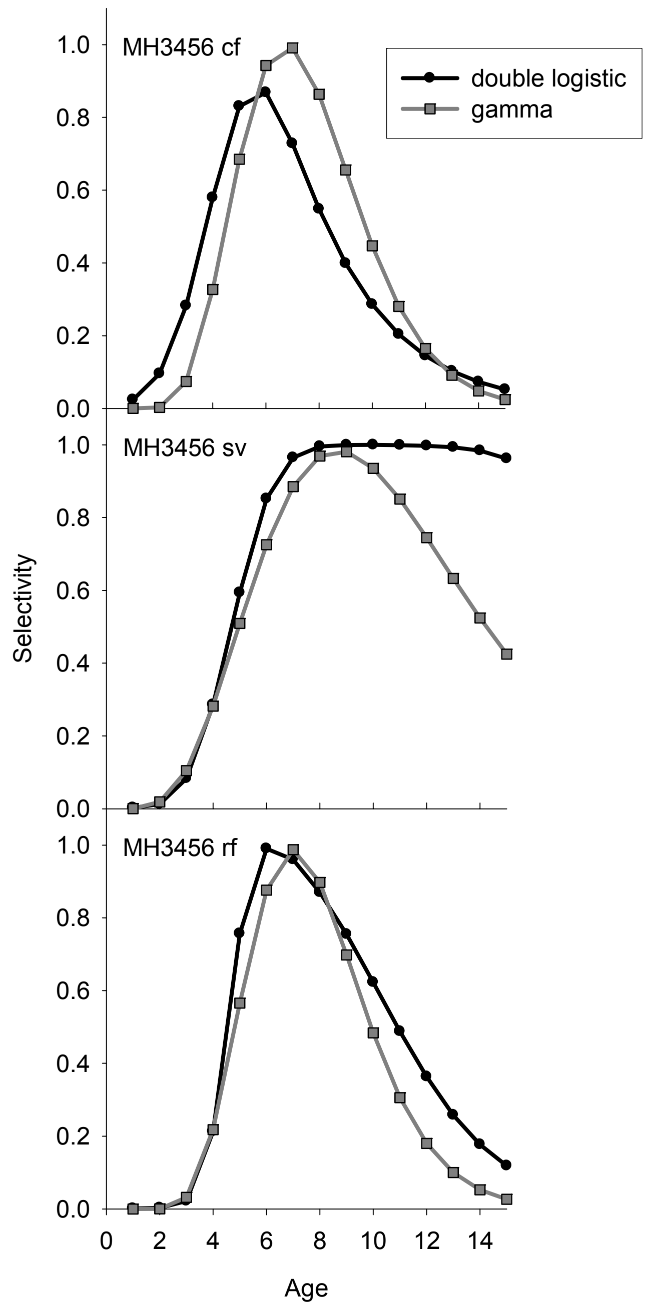

Figure 3. Average selectivity curves over time for the commercial fishery (cf), the fishery-independent survey (sv), and the recreational fishery (rf) in an assessment unit (MH3456) of Lake Huron based on a double logistic model where parameters were estimated at the level of the individual assessment unit and based on a gamma model where the estimated selectivity parameters were shared across assessment units.

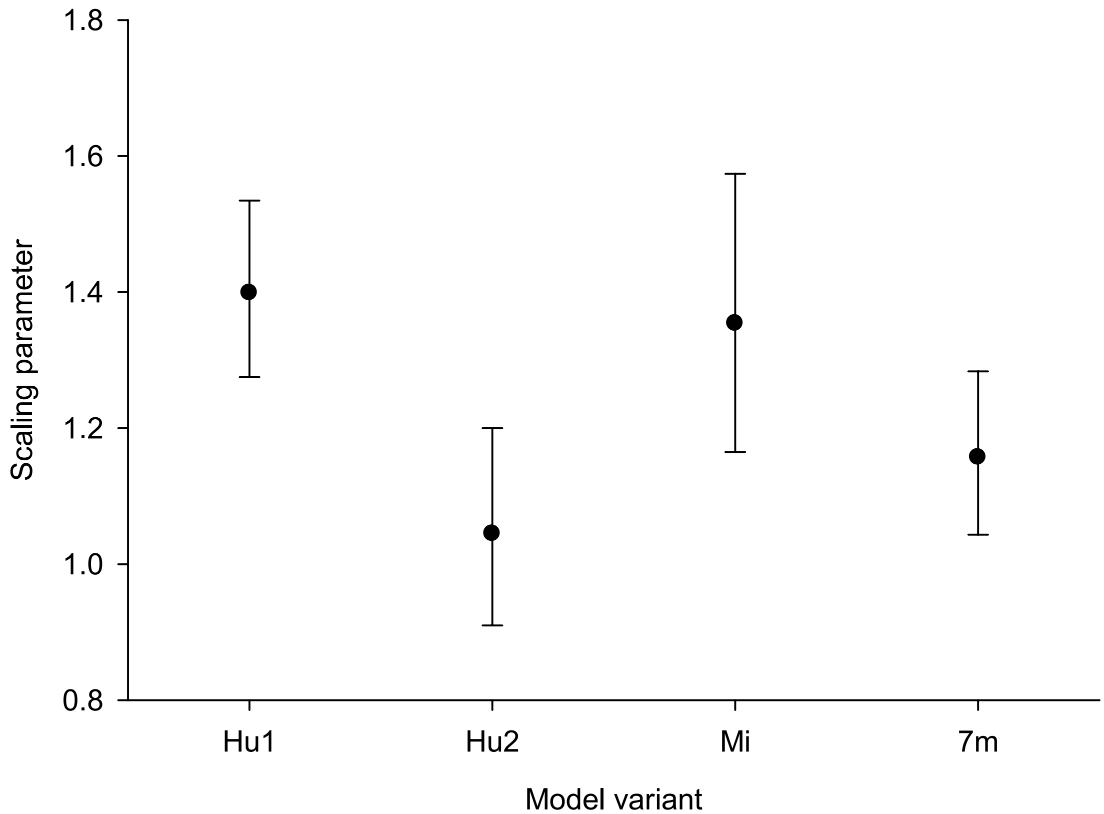

Figure 4. Estimates of the scaling parameter (± 2 SE) for different model variants. Hu1 = combined-by-lake Lake Huron case 1; Hu2 = combined-by-lake Lake Huron case 2; Mi = combined-by-lake Lake Michigan; 7m = combined-across-lake 7-model variant (see text for additional details).

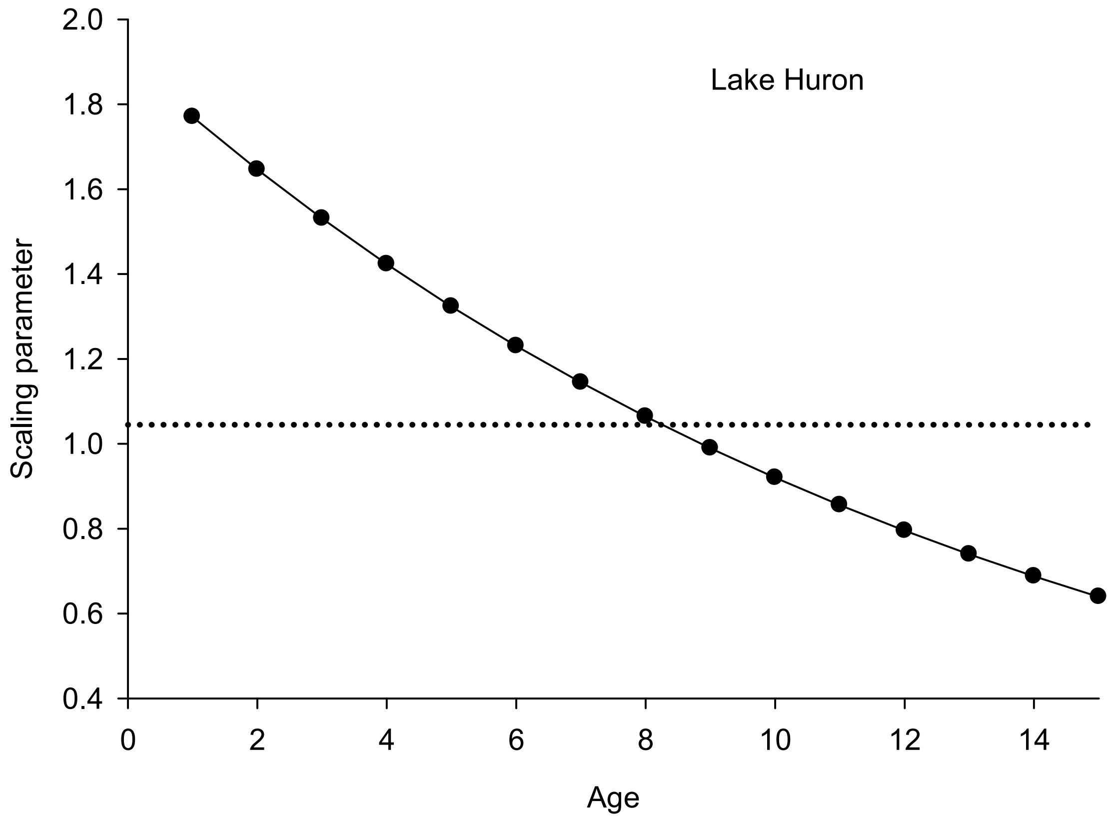

Figure 5. Estimated influence of the scaling parameter for the combined-by-lake Lake Huron case 2 model variant where an additional parameter (lambda) suggested lower values for older lake trout. The horizontal dotted line represents the scaling parameter estimate when lambda was not included as an additional estimated parameter.

DELIVERABLES:

1) A progress report was submitted in June 2008: Bence, J. R., B. J. Irwin, and T. O. Brenden. 2008. Estimating the relationship between sea lamprey-induced mortality on lake trout and observed marking rates. Great Lakes Fishery Commission Annual Project Progress Report.

2) This completion report is submitted as the final report.

3) Estimation models were modified for 9 lake trout assessment units.

4) Multiple versions of combined-by-lake estimation models were produced.

5) A combined-across-lake estimation model was produced.

6) An iterative approach to estimating the scaling parameter was developed.

7) Updates based on this research have been communicated to the Modeling Subcommittee.

PRESS RELEASE:

In all of the Great Lakes, sea lampreys attack and kill fishes that are targeted by recreational and commercial fisheries. Fish that survive a sea lamprey attack bear visible wounds that are classified by scientists when these fish are collected in samples. These observed rates of sea lamprey wounds are used to inform stock-assessment models about levels of mortality of lake trout and other desired species that are caused by sea lamprey. The information on observed wounds per lake trout is also used to determine if sea lamprey populations have been suppressed to levels consistent with fish community objectives for the Great Lakes. It is generally believed that a positive relationship exists between observed wounds on desirable fish and sea lamprey-induced mortality, meaning that if sea lamprey wounds are observed frequently, then sea lamprey are killing a higher fraction of the populations of desired fish. Nevertheless, the true relationship between observable wounds and the actual level of mortality experienced by the desired fish population remains poorly understood.

A recent study, funded by the Great Lakes Fishery Commission, supports current assumptions and interpretation of sea lamprey wounding data. This study provided results in agreement with the view that nearly half of the lake trout attacked by sea lamprey will die, although larger lake trout likely have a greater chance of surviving a sea lamprey attack. The quantitative models that were produced through this study are now being used to inform the assessments of lake trout populations in the upper Great Lakes.