Evaluating Integrated Pest Management in the St. Marys River

by:

Michael L. Jones\textsuperscript{2}, Travis O. Brenden\textsuperscript{2}, Brian J. Irwin\textsuperscript{3}

\textsuperscript{2} Quantitative Fisheries Center  
Department of Fisheries and Wildlife  
480 Wilson Road  
Michigan State University  
East Lansing, MI 48824-1222

\textsuperscript{3} USGS Georgia Cooperative Fish and Wildlife Research Unit  
Warnell School of Forestry and Natural Resources  
University of Georgia  
Athens, GA 30602

December 2012

\textsuperscript{1} Project completion reports of Commission-sponsored research are made available to the Commission’s Cooperators in the interest of rapid dissemination of information that may be useful in Great Lakes fishery management, research, or administration. The reader should be aware that project completion reports have not been through a peer-review process and that sponsorship of the project by the Commission does not necessarily imply that the findings or conclusions are endorsed by the Commission. Do not cite findings without permission of the author.
ABSTRACT:

The St. Marys River (SMR) historically has been and continues to be an important source of parasitic sea lampreys (*Petromyzon marinus*) for lakes Huron and Michigan. A decision analysis (DA) project was conducted in the early 2000s to help inform management decisions regarding ongoing integrated control of SMR sea lampreys; the results from this project suggested that a program of enhanced trapping and release of sterile males, and moderate levels of annual Bayluscide applications would provide the greatest net economic benefits. In light of persistent challenges in achieving enhanced trapping effectiveness, we conducted an updated DA project to explore integrated management options for the river. An integrated assessment model similar to what was used in the first DA project but which incorporated an additional 10 years of data was used to estimate demographic and control parameters for SMR sea lampreys, including survival and metamorphosis rates, contributions of juvenile sea lampreys to Lake Huron from other sources, contributions of Lake Huron adult sea lampreys to the SMR, Ricker stock-recruitment parameters, and the area-specific mortality caused by applications of Bayluscide. A Bayesian estimation procedure was used to successfully generate a stable joint posterior probability distribution for all estimated parameters, thereby allowing characterization of the uncertainty of each estimated parameter or derived variable. We used a model similar in structure to the integrated assessment model to forecast SMR and Lake Huron sea lamprey abundances conditional on a range of potential management scenarios. To account for demographic and control uncertainty, simulations were repeated 1000 times. For each iteration, an independent random sample of parameters and initial conditions was drawn from the estimated joint posterior probability distribution. We compared a reference strategy of no control to scenarios with increasing areas treated annually with Bayluscide (100-400 ha) and to a scenario with 200 ha treated and the annual release of 25,000 sterile male sea lampreys. We repeated these scenarios for two models, one in which we assumed average trapping effectiveness in the SMR was 40%, based on historical evidence, and a second in which we assumed trapping effectiveness was 8%, based on recent acoustic telemetry findings. The simulation results suggested that with annual Bayluscide treatment of 400 ha, the adult sea lamprey population returning to the SMR was largely derived from juvenile production from other sources as SMR juvenile production was reduced by over 90% relative to the “no-control” treatment strategy. Releases of sterile males had only a small effect on juvenile production in the scenarios we examined, and in fact resulted in slight increases in juvenile production under the 8% trapping effectiveness scenario. Our stock-recruitment analysis suggested that recent sea lamprey spawner abundance was near (40% model) or somewhat above (8% model) the abundance expected to result in peak recruitment. The implication is that adult control tactics (trapping and sterile male releases) will only be effective in the SMR if overall adult abundance can be reduced to levels substantially below that associated with peak recruitment.
INTRODUCTION:

The St. Marys River (SMR) is well known to be a major source of parasitic sea lampreys to lakes Huron and Michigan. Since the mid 1990s, the Great Lakes Fishery Commission has utilized an integrated approach to controlling production of SMR sea lampreys. The approach has included trapping of adult sea lampreys during the spawning migration, release of sterilized male sea lampreys onto spawning grounds and, since 1999, application of granular Bayluscide to selected larval rearing habitats in the river.

In 2000, the Great Lakes Fishery Commission and Michigan Sea Grant College Program funded a research project with the goal of developing a Decision Analysis (DA) model to help guide future integrated pest management in the SMR. This project yielded estimates of important demographic parameters for SMR sea lampreys (Haeseker et al. 2003) and an analysis that compared alternative management strategies (Haeseker et al. 2007). The results from this project were used to support continued efforts to suppress sea lamprey production through a combination of trapping, sterile male releases, and moderate levels of Bayluscide control. One of the main conclusions of the project was that there would be increased net economic benefits from an enhanced trapping and sterile male release program.

Since completion of this initial DA project, considerable additional data have been collected, adding to our knowledge of sea lamprey demographics in the SMR. Perhaps most important, since 1999 annual quantitative assessments of larval abundance have been conducted, providing valuable information on recruitment rates over time, as well as data to inform decisions about where to apply Bayluscide control. As well, efforts to increase trapping rates and, consequently, sterile male releases, have largely proven unsuccessful. This accumulation of new information, together with growing realization that one of the options favored in the earlier analysis might not be practically achievable, provided strong impetus to update the DA.

This report documents the results of the updated DA project. With assistance from sea lamprey control agents, we assembled contemporary data on SMR and Lake Huron sea lamprey abundances and age composition and control activities. We revised the assessment model used to estimate sea lamprey demographic parameters to accommodate the new information and changes in how population dynamics and control are conceptualized. We then incorporated our estimates of sea lamprey demographic parameters and control effectiveness, and the uncertainty associated with these estimates, into a forecasting model that permitted the projection of the effects on sea lamprey abundance at various life stages for a range of possible management options. During the project, it became evident that two alternative hypotheses about SMR trapping effectiveness have emerged. In our analyses, we accounted for both hypotheses so that the sensitivity of the control strategies to trapping effectiveness could be
OBJECTIVES:

1. Update the integrated assessment model developed for the initial SMR DA project with data collected since project completion.
2. Revise the integrated assessment and DA models to reflect changes in conceptualization of SMR sea lamprey population dynamics and control tactics.
3. Conduct DA simulations to forecast the relative performance of alternative management strategies that vary in the use of trapping, sterile male releases, and Bayluscide treatment area as control tactics.

These objectives were not stated in the study proposal, which was limited to a two-page description of the work to be completed. However these were the implied task objectives of the study. We were able to meet each of these objectives, as detailed below. The assessment model (objectives 1 and 2) and the forecasting model (objectives 2 and 3) are deliverables for the project and can be provided to the GLFC or sea lamprey program committees if requested.

METHODS:

Integrated Assessment Model

The integrated assessment that was conducted to estimate the population demographics and stock-recruitment relationships for the SMR sea lamprey population was conceptually similar to that of Haeseker et al. (2003). An age-structured population model was constructed and fit to abundance and age composition measurements from several data sources. Among the estimated parameters and derived variables were time series of age-0 larval and effective spawning female abundances. These abundances were used to estimate a stock-recruitment relationship and quantify the uncertainty associated with the estimated recruitment function. Our assessment differed from that of Haeseker et al. (2003) in terms of the data sources that were used to fit the age-structured population model, the time-frames associated with the data sources, and some aspects of the population model that were updated to reflect improvements in understanding of SMR sea lamprey demographics or conceptual advancements in conducting integrated analyses.

Data Sources

Data sources that were used in conducting the integrated assessment included larval abundances and age compositions in the SMR, recently metamorphosed juvenile abundances in Lake Huron, age-
compositions of recently metamorphosed juvenile sea lampreys in the SMR, adult abundances in the SMR, and adult abundances in Lake Huron. With the exception of SMR larval abundances, these data sources were also incorporated in the integrated assessment conducted by Haeseker et al. (2003), although the time frames covered by the data sources differed between the studies. Unlike Haeseker et al. (2003), we did not include a catch-per-unit effort index of juvenile abundance based on bycatch from Lake Huron commercial fisheries as these data were not consistently recorded. Other data sources that were used as inputs for constructing the age-structured population model included the total area treated with Bayluscide in each year, the number of sterile males released each year as part of the sterile male release program, and the ratio of male:female sea lampreys observed as part of the trapping conducted to estimate adult abundance in the SMR.

The larval abundance and age composition measurements in the SMR were from annual assessments conducted cooperatively by the U.S. Fish and Wildlife Service and Canada Department of Fisheries and Oceans. The assessments were stratified, systematic sampling efforts consisting of multiple deepwater electrofishing drops (Bergstedt and Genovese 1994) to measure larval density throughout the river. Stratification was by two categories of historic larval density: high and low. Areas identified as having high larval density (those that have been targeted for treatment with Bayluscide since 1998) were sampled at a rate of 1 sample per ha while those identified as having low densities were sampled at a rate of 1 sample per 30 ha (J. Adams, USGS, personal communication). Lengths of collected sea lampreys were measured, with observed length frequencies subsequently adjusted based on the assessed sampling efficiency of deepwater electrofishing using an updated version of the Bergstedt and Genovese (1994) adjustment. Densities were estimated from the adjusted catch and expanded to the whole river for a population estimate. Age composition was estimated using an inverse age length key (Hoenig and Heisey 1987) developed from statolith age and length estimates of previously sampled SMR sea lampreys (Haeseker et al. 2003). Larval population estimates from this assessment post-Bayluscide treatment were available from 1999 to 2011, while larval age-composition estimates were available from 1993 to 2011. Additionally, larval population and age-composition estimates prior to Bayluscide treatment were available for 1999, 2001, and 2003.

Annual abundances of recently metamorphosed juvenile sea lampreys in Lake Huron were estimated via tag-recovery studies (Bergstedt et al. 2003). Prior to migration, recently metamorphosed sea lampreys were collected by stream electrofishing, tagged with coded wire tags near the dorsal fin, and released back into the streams (Bergstedt et al. 2003). Tagged sea lampreys were recovered during spring spawning runs, with abundances of recently metamorphosed juveniles estimated using the Lincoln-Peterson method (Seber 2002). Juvenile abundance estimates were available for 1990, 1991, 1997 to
2002, and 2007. For additional description of how juvenile abundances were estimated see Bergstedt et al. (2003).

Recently metamorphosed sea lampreys in the SMR were collected by surface trawling. Statoliths from collected individuals were removed and aged using methods described in Beamish and Medland (1988). Age compositions of recently metamorphosed sea lampreys were available from 1995 to 2001.

Annual adult (i.e., spawning stage) abundances of sea lampreys in the SMR used in fitting the population model were estimated using mark-recapture studies (Mullett et al. 2003). The mark-recapture studies entailed trapping adult sea lampreys during an approximate 8 to 10 week period during the spawning run, marking a subset of trapped fish via dorsal fin notches, and transporting and releasing marked fish downstream from the trapping site. Adult abundances were then estimated based on the number of marked fish subsequently recaptured at the original trapping site using a modified Schaeffer (1951) estimation approach. These estimates were available from 1993 to 2011. There is uncertainty concerning the trapping effectiveness estimated from this approach, based on preliminary results from a recent acoustic telemetry study (C. Holbrook, USGS Hammond Bay, unpublished data). We formally considered this uncertainty in a sensitivity analysis, discussed below.

Annual adult abundances for all of Lake Huron were estimated using a combination of mark-recapture studies and model predictions (Mullet et al. 2003). For a subset of sea lamprey producing Lake Huron tributaries, mark-recapture studies were used to estimate adult abundances similar to what was described above for estimating SMR adult abundances. For those sea lamprey producing tributaries where mark-recapture studies were not conducted, adult abundances were predicted by multiplying observed trap catches by assumed sampling efficiencies for streams where trapping was conducted or else through a weighted least-squares linear regression model described in Mullett et al. (2003). Total Lake Huron adult abundance was estimated by summing the mark-recapture and predicted abundance estimates for all sea lamprey producing tributaries. Total Lake Huron adult abundances were available from 1992 to 2011.

Population Model

The age-structured population model that was constructed covered the time period from 1990 to 2011 and encompassed the full sea lamprey life cycle (i.e., larval, juvenile, and adult stages). The larval stage lasted up to 6 years, with a model-estimated proportion of age-4 and age-5 larvae assumed to metamorphose into juveniles in each year. After metamorphosis, juvenile sea lampreys were assumed to migrate to Lake Huron where they remained for approximately 18 to 24 months, before maturing into adults and migrating to tributaries to spawn and ultimately die.

Annual age-0 larval abundances (i.e., recruitment) were estimated as the product of a mean recruitment level and multiplicative annual deviation terms
Recruitment in 2010 and 2011 was assumed equal to the mean of the 2006 to 2009 levels. Larval abundances for ages 1 to 6 in the first modeled year were similarly predicted.

Mortality stemming from Bayluscide treatment of the SMR was assumed to occur prior to natural mortality or larval metamorphosis. Bayluscide mortality was modeled as a function of the total area treated in each year and a time-invariant treatment area-mortality relationship scalar

\[ B_y = 1.0 - \exp(-qT_y). \]  

Post-treatment larval abundances were predicted as the product of larval abundances at the beginning of the year and the associated Bayluscide treatment survival rate

\[ \tilde{N}_{y,a} = N_{y,a}(1 - B_y). \]  

Larval abundances in subsequent years and ages were projected as the product of post-treatment larval abundances, an annual larval survival rate, and an age-specific probability of larvae not metamorphosing into juveniles

\[ N_{y+1,a+1} = \tilde{N}_{y,a}S_{\text{larval}}(1.0 - m_a). \]  

The annual survival rate of larval sea lampreys was estimated on a logit scale

\[ S_{\text{larval}} = \frac{\exp(y_{\text{larval}})}{1.0 + \exp(y_{\text{larval}})}, \]  

which constrained survival to values between 0.0 and 1.0 while allowing the estimated parameter to occur on the real number line. Probability of metamorphosis for individuals between ages 0 and 3 was assumed to be 0.0, while the metamorphosis probability for age-6 larvae was assumed to be 1.0. Like larval survival, the metamorphosis probabilities for age-4 and age-5 larvae were estimated on a logit scale

\[ m_a = \frac{\exp(\theta_a)}{1.0 + \exp(\theta_a)} \quad \text{for } a = 4 \text{ and } 5. \]  

Age composition of larval sea lampreys in the SMR prior to Bayluscide treatment was calculated by dividing larval abundance at age by total larval abundance and using matrix multiplication to multiply the resulting quotient by an aging error matrix.
Larval age composition post Bayluscide treatment was similarly calculated

\[ p_{y,a} = \frac{N_{y,a}}{\sum_a N_{y,a}} \Gamma_{a,a}. \]  

(8)

The aging error matrix (Table 2) that we assumed was based on statolith aging error estimates presented in Dawson et al. (2009).

The total abundance of juvenile sea lampreys from the SMR that contributed to the overall Lake Huron population in each year was calculated as

\[ J_y^{SMR} = \sum_a \tilde{N}_{y,a} m_a \Gamma_{a,a}. \]  

(10)

Like larval age compositions, age composition of recently metamorphosed sea lampreys from the SMR incorporated an aging error component

\[ q_{y,a} = \frac{\tilde{N}_{y,a} m_a}{\sum_a \tilde{N}_{y,a} m_a} \Gamma_{a,a}. \]  

(11)

The contribution of juvenile sea lampreys from other Lake Huron tributaries was a time-invariant, model-estimated parameter, with the total annual contribution of newly metamorphosed juvenile sea lampreys to Lake Huron equal to

\[ J_y^{LH} = J_y^{SMR} + J_y^{other}. \]  

(12)

Juvenile sea lampreys spend no more than two years in the Great Lakes prior to maturing and migrating to streams and rivers to spawn, thus the total abundance of adult (i.e., spawning phase) sea lampreys in Lake Huron prior to migration equaled

\[ A_y^{LH} = S_{juvenile} J_y^{SMR} + J_y^{other}. \]  

(13)

As with larval survival and metamorphosis rates, the juvenile survival rate was estimated on a logit scale

\[ S_{juvenile} = \frac{\exp(y_{juvenile})}{1.0 + \exp(y_{juvenile})}. \]  

(14)

Multiple studies have found that sea lampreys do not home to natal streams, either within the Great Lakes (Bergstedt and Seelye 1995) or their native range (Waldman et al. 2008). Thus, the total abundance of adult sea lampreys migrating to the SMR to spawn was the product of the total adult abundance of sea lampreys in Lake Huron and a model-estimated proportion of those adults that migrate to the SMR.
with the proportion migrating to the river estimated on a logit scale

\[ \rho = \frac{\exp(\phi)}{1.0 + \exp(\phi)}. \]  

To estimate the stock-recruitment relationship for SMR sea lampreys, annual abundances of spawning females was required as this is how spawning stock size traditionally has been indexed (Haeseker et al. 2003; Jones et al. 2003). Annual abundances of adult females returning to the SMR was calculated as the product of total adult abundances and the proportion of returning adults that were females as measured during the trapping conducted to estimate adult abundances

\[ F_{y}^{SMR} = A_{y}^{SMR} f_{y}. \]  

Because of the trapping program conducted on the SMR, some adjustment of the adult female abundances was necessary. As previously described, the mark-recapture studies used to estimate total abundance of adult sea lamprey involves dorsal fin marking of trapped individuals, and transport and release of marked fish downstream from the trapping site. After the release of marked individuals, all adult sea lamprey (both marked and unmarked) subsequently captured in traps are destroyed (L. Walters, USFWS, personal communication) so the abundance of adult female sea lamprey was reduced by the number of females captured after initial marking

\[ \widetilde{F}_{y}^{SMR} = F_{y}^{SMR} - \widetilde{F}_{y}^{SMR}. \]  

The effect of releasing sterile males onto SMR spawning grounds (Twohey et al. 2003) also needed to be accounted for in determining the effective number of spawning females. In short, released sterile male sea lampreys are presumed to compete with fertile males so that the effective number of spawning females depends in part on the relative abundances of sterile and fertile males (Bergstedt and Twohey 2007). The proportion of SMR adult females expected to breed with sterile males was calculated as

\[ r_{y} = \frac{\frac{U_{y}^{SMR}}{M_{y}^{SMR}}}{\frac{1}{M_{y}^{SMR}} + 1}, \]  

with the number of adult fertile males calculated as

\[ M_{y}^{SMR} = A_{y}^{SMR}(1 - f_{y}) \]
\[ \widetilde{M}_{y}^{SMR} = M_{y}^{SMR} - \widetilde{M}_{y}^{SMR}. \]  

Thus, the effective number of reproducing adult females in the SMR was equal to

\[ \widetilde{F}_{y}^{SMR} = F_{y}^{SMR}(1.0 - r_{y}). \]
Model Fitting

Integrated assessment model parameters were estimated using AD model Builder (Fournier et al. 2012). We used a Bayesian-based approach, whereby the point estimates of the model parameters were the highest posterior density estimates (Schnute 1994). Operationally this was accomplished by defining an objective function equal to the negative log-posterior density (ignoring some constants) and using a quasi-Newton optimization algorithm to numerically search for the parameters that minimized the function. The model was considered to have converged on a solution when the maximum gradient of the parameters with respect to the objective function was less than $1.0 \times 10^{-5}$. Uncertainty was characterized by the full posterior probability distributions for the estimated parameters and derived variables (see below).

The objective function consisted of the sum of eleven negative log-likelihood or negative log-prior components (Table 3). Lognormal distributions were assumed for the negative log likelihoods for pre- (equation T.3.1) and post- (equation T.3.2) Bayluscide treatment total larval abundances in the SMR, pre- (equation T.3.3) and post- (equation T.3.4) Bayluscide treatment age-1 larval abundances in the SMR, total contribution of recently metamorphosed juvenile sea lampreys to Lake Huron (equation T.3.5), total abundance of adult sea lamprey in the SMR (equation T.3.6), and total abundance of adult sea lamprey in Lake Huron prior to their migrating to streams to spawn (equation T.3.7). Multinomial distributions were assumed for the negative log likelihoods for pre- (equation T.3.8) and post- (equation T.3.9) Bayluscide treatment larval age composition in the SMR, and for the age composition of recently metamorphosed juvenile sea lamprey in the SMR (equation T.3.10). Finally, a lognormal distribution was used as the negative log prior for the model-estimated abundance of juvenile sea lampreys contributed from other Lake Huron tributaries (equation T.3.11). The hyperparameters for this prior were derived as follows. First, we obtained for each sea lamprey producing tributary to Lake Huron an estimate of the maximum juvenile production given current treatment scheduling (J.W. Slade, USFWS, unpublished data). For each tributary, a random variate from a lognormal distribution with a mean equal to the natural log of the maximum juvenile production value for that stream and a dispersion corresponding to a coefficient of variation (CV) of 0.30, which is similar to the CV for sea lamprey recruitment found by Jones et al. (2003). We then summed the random variates across all streams. We repeated this process 10,000 times to generate a distribution of abundance of juvenile sea lamprey from other Lake Huron tributaries. A lognormal distribution was then fit to the distribution of abundances, with these parameter estimates composing the hyperparameters for the prior for the abundance of juvenile sea lampreys contributed from other Lake Huron tributaries.
When fitting the integrated assessment model, the “standard” dispersion for the lognormal distributions assumed for the negative log-likelihood and negative log-prior components listed in Table 3 was among the estimated parameters. The $\lambda$ terms are weighting factors that represent how far the dispersion parameter for a particular data source deviates from this “standard”. We used an iterative approach for setting the $\lambda$ values. The initial weighting factors were designated based on the perceived reliability of the data sources. The assumed dispersions were then compared to the integrated assessment model mean-squared error for the different sources. The $\lambda$ values were then adjusted based on the differences between the assumed dispersions and the fitted assessment model residual estimates, until the assumed dispersions and fitted model residual estimates were approximately equal or were reasonable given the data source (Table 4). Negative log-likelihood components for the age composition of pre- and post-Baylusclide treatment larvae and recently metamorphosed juvenile sea lampreys in the SMR were weighted by the effective sample size, which was the number of fish for which ages were determined each year up to a maximum of 10 for larvae and 35 for juveniles. The effective sample sizes were set to fairly low values because of the considerable uncertainty associated with using statoliths to age sea lampreys (Dawson et al. 2009). Haeseker et al. (2003) similarly assumed low (< 35) effective sample size for age composition negative log-likelihood components in their integrated assessment, although in their case effective sample sizes were determined iteratively using the process described in McAllister and Ianelli (1997).

Characterization of Parameter Estimate and Derived Variable Uncertainty

To assess the uncertainty associated with the parameter estimates and derived variables from the integrated assessment model, posterior probability distributions were obtained by Markov Chain Monte Carlo (MCMC) simulations through a Metropolis Hastings algorithm (Fournier et al. 2012). Parameters and derived variables for which posterior probability distributions were obtained included larval and juvenile annual survival rates, the abundance of juvenile sea lampreys contributed from other Lake Huron tributaries, the Baylusclide mortality-treatment area relationship scalar, the proportion of adult Lake Huron sea lampreys that migrate to the SMR to spawn, the probabilities of metamorphosing for age-4 and age-5 larvae, larval and juvenile abundances in the penultimate year of the assessment model, and the time series (1992 to 2010) of abundances of age-0 larvae and effective reproducing females. The MCMC chain was run for 10 million steps sampling every 2,000th step. The initial 2,500 saved steps were discarded as a burn-in period. Convergence of the MCMC chain was evaluated by constructing trace plots for each estimated parameter and derived variable as a visual check to ensure the chain was well-mixed, and by using a Z-score test to evaluate differences between the means of the first 20% and last 50% of the saved chain (Geweke 1992). Additionally, we compared the effective sample size of the saved MCMC chain
with the actual chain sample size as a method for evaluating autocorrelation among the saved MCMC samples. All MCMC diagnostic measures were conducted in R (R Core Team 2012) using the “coda” package (Plummer et al. 2006).

Stock Recruitment Relationship Estimation and Uncertainty

A linearized Ricker stock-recruit function was fit to the highest posterior density estimate of the time series of age-0 larval and effective reproducing female abundances

\[
\log_e \left( \frac{N_{y,0}}{F_{y,SMR}} \right) = \alpha - \beta \frac{\hat{F}_{y,SMR}}{1.0 \times 10^3}.
\]  

(22)

Determination of the uncertainty associated with the fitted stock-recruitment relationship followed the two-stage approach described in Haeseker et al. (2003), which in turn was based on a method developed for sampling from joint posterior probability distributions for hierarchical models (Gelman et al. 2004). The first stage was using the MCMC simulations described above to obtain the time series of age-0 larval and effective reproducing female abundances. For the second stage, linearized Ricker stock-recruit functions were fit to the time series samples from the MCMC simulations. For each sample, this yielded point estimates of the parameters of the stock-recruit function (i.e., \( \alpha \), \( \beta \), and \( \sigma_R^2 \)), as well as the variance-covariance matrix for \( \alpha \) and \( \beta \). Random samples of stock recruitment relationship parameters were then drawn from either a bivariate normal distribution defined by the point estimates of \( \alpha \), \( \beta \), and the variance-covariance matrix for \( \alpha \) and \( \beta \), or from a scaled inverse chi-squared distribution with a scale parameter equal to the point estimate of \( \sigma_R^2 \) and degrees of freedom equal to two less than the number of stock-recruit observations (Haeseker et al. 2003). MCMC chain diagnostics for the randomly generated samples of the stock-recruitment relationship parameters was assessed using the same approaches previously described (i.e., trace plots, Z-score tests, determination of effective sample sizes). The degree of compensation in estimated stock-recruitment relationships was determined by calculating compensation ratios at spawning stock abundances of 1,000 and 7,000 effective spawning females (Haeseker et al. 2003). Compensation ratios less than one were characterized as negligible compensation, between one and two as low compensation between two and seven as moderate compensation, and more than seven as high compensation.

Sensitivity analysis

One of the data sources for which there is some uncertainty regarding measurement accuracy is the annual adult abundances of sea lampreys in the SMR. In particular, there is concern that the mark-recapture method that is used to estimate adult abundance may be biased low given preliminary acoustic-
array determination of efficiency of sea lamprey traps in the SMR (C. Holbrook, USGS, unpublished data). To address this, we refit the integrated assessment model and estimated a new stock-recruit relationship under an assumption that the adult abundances of sea lampreys in the SMR were five-times larger than the mark-recapture estimates (i.e., trapping effectiveness was assumed to be one-fifth as high as estimated from the mark-recapture study). Increasing the adult abundances in the SMR also necessitated increasing the adult abundances in Lake Huron as the latter encompasses the former. When assessing compensation for the stock-recruitment relationships estimated as part of the sensitivity analyses, compensation ratios were calculated at spawning stock abundances of 10,000 and 70,000 effective spawning females.

Forecasting Model

We used an age-structured population model with essentially the same structure as the integrated assessment model to simulate future sea lamprey population dynamics under a range of management scenarios. The model was used to generate 25-year projections of sea lamprey abundance at various life stages, beginning with estimates of abundance from the final year of the fitted integrated assessment model. The total abundance of adult SMR sea lampreys was calculated as the product of Lake Huron adult abundances, the proportion of Lake Huron adults migrating to the SMR, and the proportion of SMR adults that escape the trapping operation

$$A_y^{SMR} = A_y^{LH} \rho (1.0 - \tau), \quad (23)$$

where $\tau$ was assumed equal to either 0.4 or 0.08. The effective abundance of reproducing adult female sea lamprey in the SMR was calculated as the product of the total abundance of adult SMR sea lamprey, the proportion of adults that were females, and the proportion of adult females expected to breed with fertile males

$$F_y^{SMR} = A_y^{SMR} \beta (1 - r). \quad (24)$$

For the forecasting model, the female: male ratio was assumed to be 50:50, with the proportion of adult females expected to breed with fertile males depending on the number of sterile males released as part of the management scenario being evaluated. Annual recruitment in the forecasting model was calculated assuming a Ricker stock-recruitment function

$$N_{y,0} = 1.0 \times 10^0 \left[ \alpha \left( F_y^{SMR} / 1.0 \times 10^3 \right) \exp \left( - \beta \left( F_y^{SMR} / 1.0 \times 10^3 \right) + \epsilon_y \right) \right], \quad \epsilon_y \sim N(0, \sigma_R^2). \quad (25)$$

Post-Bayluscide treatment larval abundances were calculated using equations 3 and 4, where the total area of the SMR treated was part of the management scenario being evaluated. Larval abundances in subsequent years and ages were projected using equation 6, with annual contribution of newly metamorphosed juvenile sea lampreys from the SMR to Lake Huron calculated using equation 10. The
total contribution of newly metamorphosed juvenile sea lampreys to Lake Huron from all sources was calculated using equation 12. The total abundance of adult (i.e., spawning phase) sea lampreys in Lake Huron prior to migration was calculated using equation 13.

For this report, five management scenarios were evaluated (Table 5), with an individual scenario consisting of different levels of sterile male releases, and the total area of the SMR treated with Bayluscide. Each management scenario was repeated under the assumption that trapping effectiveness was either 40% (base model) or 8% (sensitivity model). To account for uncertainty in estimates of model parameters and initial abundances, we repeated each scenario simulation 1000 times, drawing a new set of parameters and initial abundances for each simulation randomly from the joint posterior distribution of these estimated and derived values. Simulation results are reported as the distribution of mean abundances, averaged over years 10-25 of each simulation, of juvenile sea lamprey \( \frac{\sum_{y=10}^{25} J_{y}^{SMR}}{16} \) produced from the SMR, and the effective number of adult female sea lamprey returning to the SMR \( \frac{\sum_{y=10}^{25} F_{y}^{SMR}}{16} \).

**RESULTS:**

**Integrated Assessment Model**

The integrated assessment model successfully converged on a solution. As well, the MCMC chain for the model was judged to have converged on a stationary distribution. Examination of trace plots indicated that the chain was well mixed, and the Z-score test statistics for comparing means of the first 20% and last 50% of the saved chain for the parameters and derived variables for which posterior probability distributions were obtained ranged from -0.68 to 1.84, suggesting there were not significant differences between means at Type-I error rates of 0.05. The effective sample sizes for most parameters and derived variables were greater than 1,900, although a few derived variables had effective sample sizes ranging between 1,400 and 1,500. Even at the low effective sample sizes, we felt the information in the saved chains was suitable for constructing 95% Bayesian credible intervals for parameter and derived variable estimates and for selecting a random subset of the saved chain to use in the decision analysis model for evaluating sea lamprey control techniques.

**Model fits**

For the most part, the predictions from the integrated assessment model were similar to observed values. For all larvae and for age-1 larvae, predicted and observed abundances post-Bayluscide treatment
closely aligned (Figure 2). As well, pre-Bayluscide treatment predicted abundances were similar to observed abundances for age-1 larvae (Figure 2). There was some discrepancy between predicted and observed pre-treatment larval abundances for all age classes of larvae, with predicted abundances generally less than observed abundances (Figure 2). This likely was due at least in part to the lower weighting assigned to this data source, relative to the other data sources (Table 4). For larval age composition, predicted mean age was generally greater by a slight amount than observed mean age post-Bayluscide treatment, but predicted and observed mean ages pre-Bayluscide treatment were quite similar (Figure 2). The discrepancy between observed and predicted mean ages post-Bayluscide treatment may be a consequence of several factors, including the low maximum effective sample sizes assumed for larval age compositions, actual statolith aging errors differing from our assumed aging error matrix, or possible differences in age-specific vulnerabilities to Bayluscide treatment.

Both predicted and observed abundances of recently metamorphosed juveniles in Lake Huron exhibited considerable inter-annual fluctuations during the modeled time period, although the assessment model did appear to have some difficulty in reproducing the observed fluctuations. The assessment model predicted a sharp increase in juvenile abundances a couple of years earlier than an observed increase (Figure 2). Further, the assessment model had a tendency to be positively biased early in the time series and negatively biased later in the time series. Despite this difficulty in matching observed juvenile abundances in Lake Huron, the mean age predictions for juvenile sea lamprey from the SMR were similar to observed mean ages (Figure 2).

In terms of adult abundances, the predictions from the integrated assessment model matched closely to observed data sources for both the SMR and Lake Huron (Figure 2). For the Lake Huron adult abundances, the assessment model had difficulty predicting an increase in abundance from 1992 to 1993, but otherwise values were closely aligned.

Model estimates

The highest posterior density estimate of larval annual survival was approximately 0.80 with a 95% Bayesian credible interval of 0.66 to 0.91 (Figure 3). Conversely, the estimated juvenile annual survival rate was 0.55 (95% Bayesian credible interval: 0.50–0.64). The Bayluscide treatment area-mortality relationship scalar was 0.0017 (95% Bayesian credible interval: 0.0012–0.0021), which meant that the estimated finite mortality rate for a treatment area of 100 ha was approximately 0.15 and for 800 ha was approximately 0.74. The estimated probability of metamorphosis for age-4 and age-5 larvae was 0.49 (95% Bayesian credible interval: 0.38 to 0.61) and 0.73 (95% Bayesian credible interval: 0.61 to 0.80), respectively. The annual contribution of juvenile sea lamprey from Lake Huron tributaries other than the SMR was estimated at approximately 290 thousand fish (95% Bayesian credible interval: 235
thousand–366 thousand), which meant that the SMR accounted for between 26 and 69% of the total contribution of juvenile sea lamprey to Lake Huron in any given year. The proportion of Lake Huron adult sea lamprey that migrated to the SMR was approximately 0.12 (95% Bayesian credible interval: 0.09–0.15).

A Ricker stock-recruit function fitted to the highest posterior density estimates of the time series of age-0 larval and effective reproducing female abundances exhibited a moderate level of compensation (Figure 4). As is generally the case when estimating stock-recruitment functions, there was considerable uncertainty associated with the fitted relationship. The Ricker stock-recruitment relationships estimated from the two stage joint posterior probability distribution sampling procedure had compensation levels ranging from low to high, with the vast majority of relationships exhibiting either moderate (55%) or high (45%) levels of compensation.

**Sensitivity model**

The integrated assessment model that was fit under the assumption that the SMR sea lamprey adult abundance was 5-times greater than measured values (hereafter referred to as the sensitivity model) also successfully converged on a solution. Although examination of trace plots and Z-score tests comparing the means of the first 20% and last 50% of the saved chain for the parameters and derived variables for which posterior probability distributions were obtained indicated that the MCMC chain had converged on a stationary distribution, determination of effective sample sizes suggested possible autocorrelation problems with the MCMC chain. Most parameters and derived variables had effective sample sizes in excess of 1,400, although a few derived variables had effective sample sizes as low as 800. Despite the low effective sample sizes, we felt that the estimates were sufficient for exploring the sensitivity of the integrated assessment and decision analysis management models to assumptions concerning SMR adult abundances.

The fits for the sensitivity model were very similar to that of the baseline model. With the exception of the SMR and Lake Huron adult abundances, the fits from the sensitive model were largely indistinguishable from those of the baseline model (Figure 2). As with the baseline model, the sensitivity model had some difficulty in predicting early increases in adult abundances, but overall predictions of both SMR and Lake Huron adult abundances closely matched observed values despite the increases that were assumed for the data sources (Figure 2).

For several parameters and derived variables, including larval annual survival, age-4 and age-5 metamorphosis probabilities, Bayluscide treatment area-mortality relationship scalars, and contribution of juvenile sea lamprey from other Lake Huron tributaries, the highest posterior density estimates and 95% Bayesian credible intervals from the sensitivity model were very similar to those of the baseline model.
Conversely, the highest posterior density estimates for juvenile annual survival and the proportion of Lake Huron adult sea lamprey that migrated to the SMR were greater for the sensitivity model than for the baseline model. Juvenile annual survival for the sensitivity model increased to 0.68 (95% Bayesian credible interval: 0.61–0.79), while the proportion of adults migrating from Lake Huron to the SMR increased to 0.40 (95% Bayesian credible interval: 0.31–0.51). The higher assumed and predicted adult abundances for the SMR did affect the fitted stock-recruitment relationship for the sensitivity model. The fitted model still exhibited a moderate level of compensation, although the compensation level was lower than that of the baseline model. The Ricker stock-recruitment relationships estimated from the two stage joint posterior probability distribution sampling procedure for the sensitivity model also had compensation levels ranging from low to high, with approximately 3% of the relationships exhibiting low compensation, 60% moderate compensation, and 37% high compensation.

**Forecasting Model**

When no control was applied to the SMR sea lamprey population, abundance of effective females increased to 10,100, with 75% of simulations resulting in abundances between 8,700 and 11,800 females (Figure 5). Production of juvenile sea lampreys from the SMR increased to 222,000 with an interquartile range of 163,000 to 312,000 (Figure 5). Annual treatment of 200 ha of the river with Bayluscide combined with a 40% trapping rate reduced the effective female abundance by 50% to 4,800 (interquartile range: 4,400-5,300), and juvenile production by a similar proportion to 117,000 (interquartile range: 89,600-153,000). Release of 25,000 sterile males along with 40% trapping and 200 ha of Bayluscide treatment substantially reduced the abundance of effective females to 700 (interquartile range: 600-800) but resulted in only modest reductions in juvenile production (median: 84,600, interquartile range 64,900-112,000).

Increasing the area treated annually with Bayluscide from 100 to 200 to 400 ha resulted in moderate reductions in the forecasted abundance of effective females, but sharper reductions in the production of juvenile sea lamprey from the SMR (Figure 6). When 400 ha were treated, juvenile production dropped to 23,800 (> 89% below the no control level), with little variation among simulations. At this high level of chemical control, adult returns to the SMR were largely derived from other source populations, maintaining the spawning population above 3,500 effective females.

When trapping effectiveness was assumed to be only 8%, the results were qualitatively similar for the abundance of effective females, but scaled much higher (Figure 5, 6). Median abundance ranged from 63,500 for no control down to 20,900 for the scenario where 25,000 sterile males were released. The effect of increasing the area treated with Bayluscide on juvenile production was also similar for this
model (Figure 6), but adding the release of sterile males actually resulted in a slight increase in juvenile production compared to the same management strategy without sterile male releases (Figure 5).

**DISCUSSION:**

There were some notable differences in the demographic parameters estimated for the SMR and Lake Huron sea lamprey populations between our study and that of Haeseker et al. (2003). In particular, Haeseker et al. (2003) estimated a more productive stock recruitment relationship for the SMR. In Haeseker et al. (2003), the highest posterior density estimate for the Ricker stock-recruitment productivity parameter ($a$) was 9.15, with a 95% Bayesian credible interval of 6.45 – 10.47. Conversely, our highest posterior density estimate (assuming a 40% trapping efficiency) was 3.15, with a 95% Bayesian credible interval of 1.85 – 7.49. Part of this discrepancy in the recruitment productivity estimates between the studies likely stemmed from our incorporating in our integrated assessment a SMR larval abundance dataset, which provided a reference point for estimating recruitment levels. Despite the higher productivity level estimated as part of their study, Haeseker et al. (2003) also found the stock recruitment relationship for SMR sea lampreys to exhibit a moderate level of compensation.

Although Haeseker et al. (2003) estimated a more productive stock-recruitment relationship for SMR sea lampreys, the effect of this was partially offset by our estimation of a higher larval survival rate. In Haeseker et al. (2003), the highest posterior density estimate for the larval annual survival rate was 0.42, with a 95% Bayesian credible interval of 0.35 – 0.49, which was approximately half the survival rate estimated as part of this study. A consequence of our estimating a higher survival rate for larval sea lampreys was that there was not a large difference in the effective abundance of spawning females between the studies, with estimated abundance levels generally ranging between 500 and 8000 spawning females.

In the integrated assessment model fit by Haeseker et al. (2003), juvenile survival rates and proportion of Lake Huron adults migrating to the SMR to spawn were not separately estimated, rather a parameter representing a combination of these rates was estimated. The highest posterior density estimate for this combined parameter in Haeseker et al. (2003) was 0.037, with a 95% Bayesian credible interval of 0.033 – 0.044. Using our estimates of juvenile survival and proportion of Lake Huron adult migrating to the SMR to spawn to calculate a similar joint quantity, there was actually close agreement the studies with regards to this variable. Our highest posterior density estimate for the joint quantity was 0.036, with a 95% Bayesian credible interval of 0.029 – 0.050. As well, there was pretty close agreement between the studies with regards to the age-4 age-5 metamorphosis probabilities. Haeseker et al. (2003) estimated that in any given year, 46% of age-4 larvae, which was slightly lower than the probability (49%) we estimated. There was a slightly larger discrepancy between the studies in the metamorphosis probabilities...
for age-5 larvae, with Haeseker et al. (2003) estimating a 57% metamorphosis probability, which was about 15% lower than what we estimated.

We focused comparison of our results with the earlier Haeseker et al. (2003) analysis on the model for which trapping effectiveness was assumed to be 40%, which was approximately the trapping effectiveness assumed in the earlier study. The results for the 8% effectiveness model were similar, except for the estimates of SMR spawner abundance and the proportion of Lake Huron sea lampreys returning to the SMR. The much higher estimated SMR spawner abundance also resulted in substantial differences in estimated stock-recruitment parameters, because these much larger abundances are associated with similar estimates of recruitment for both models, constrained by the observed larval abundances. Consequently the stock-recruitment productivity parameter estimated for the 8% effectiveness model was much lower than for the 40% effectiveness model.

The forecasting model suggests that maintaining Bayluscide treatment at intermediate levels (~200 ha) can provide a moderate level of control (nearly 50% reduction relative to no control) of juvenile sea lamprey production from the SMR, but a greater extent of annual treatment will be required to achieve reductions (~90%) comparable to those typically achieved from chemical treatment of smaller Great Lakes streams with TFM. Our results also suggest that at current levels of adult sea lamprey abundance in Lake Huron, addition of sterile males to the spawning population at practically achievable levels is not likely to provide for additional control, and may in fact lead to increased recruitment, on average. This forecast is especially likely if trapping effectiveness is actually much lower than has historically been assumed. Our findings suggest that research aimed at reducing uncertainty about trapping effectiveness in the SMR should be a top priority. They also suggest that management of the SMR should be formally integrated with management of other rivers that produce Lake Huron parasitic sea lampreys. Because sea lampreys recruiting from anywhere in the Lake Huron watershed can potentially return to the SMR to spawn, the long-term effectiveness of control strategies that target the SMR, especially those that rely on reducing reproduction, will depend critically on the production of sea lampreys from these other sources.

REFERENCES:


ACKNOWLEDGEMENTS:

We wish to acknowledge members of the former Assessment and Lampricide Control Task Forces for their engagement throughout this study, especially Jean Adams, Jessica Barber, Gale Bravener, Mike Fodale, and Jeff Slade. We are especially grateful to Lisa Walter for assistance with obtaining data, arranging meetings, and helping to report on our findings to the Sea Lamprey Control Board.
**Table 1. Description of equation symbols used in the model and text for describing the integrated assessment and decision analysis models for SMR sea lamprey.**

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>$y$</td>
<td>Year (1990-2011)</td>
</tr>
<tr>
<td>$a$</td>
<td>Larval age class (0-6)</td>
</tr>
</tbody>
</table>

**Indicator variables**

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\bar{R}$</td>
<td>Mean age-0 larval abundance</td>
</tr>
<tr>
<td>$\delta$</td>
<td>Annual deviations in age-0 larval abundances</td>
</tr>
<tr>
<td>$\bar{N}$</td>
<td>Mean age-1 to age-6 larval abundance in 1990</td>
</tr>
<tr>
<td>$\xi$</td>
<td>Age-specific deviations in larval abundances in 1990</td>
</tr>
<tr>
<td>$q$</td>
<td>Bayluscide mortality-treatment area relationship scalar</td>
</tr>
<tr>
<td>$\gamma^{\text{larval}}$</td>
<td>Logit-scale parameter for estimating larval annual survival rate</td>
</tr>
<tr>
<td>$\theta$</td>
<td>Logit-scale parameter for estimating probability of metamorphosis</td>
</tr>
<tr>
<td>$J^{\text{other}}$</td>
<td>Annual contribution of newly metamorphosed juvenile sea lamprey from all other Lake Huron tributaries</td>
</tr>
<tr>
<td>$\gamma^{\text{juvenile}}$</td>
<td>Logit-scale parameter for estimating juvenile annual survival rate</td>
</tr>
<tr>
<td>$\phi$</td>
<td>Logit-scale parameter for estimating proportion of Lake Huron adult sea lamprey migrating to the SMR to spawn</td>
</tr>
<tr>
<td>$s$</td>
<td>Standard dispersion parameter for lognormal objective function components</td>
</tr>
<tr>
<td>$a$</td>
<td>Ricker stock-recruitment function parameter</td>
</tr>
<tr>
<td>$b$</td>
<td>Ricker stock-recruitment function parameter</td>
</tr>
<tr>
<td>$\sigma_R$</td>
<td>Ricker stock-recruitment function standard deviation</td>
</tr>
</tbody>
</table>

**Estimated parameters**

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>$N$</td>
<td>Larval abundance prior to Bayluscide treatment</td>
</tr>
<tr>
<td>$B$</td>
<td>Bayluscide mortality</td>
</tr>
<tr>
<td>$\tilde{N}$</td>
<td>Larval abundance post Bayluscide treatment</td>
</tr>
<tr>
<td>$S^{\text{larval}}$</td>
<td>Larval annual survival rate</td>
</tr>
<tr>
<td>$m$</td>
<td>Probability of metamorphosis</td>
</tr>
<tr>
<td>$p$</td>
<td>Larval age composition prior to Bayluscide treatment</td>
</tr>
</tbody>
</table>
\( \tilde{p} \) Larval age composition post Bayluscide treatment

\( J^{SMR} \) Annual contribution of newly metamorphosed juveniles from the SMR to Lake Huron

\( S_{juvenile} \) Juvenile annual survival rate

\( q \) Age composition of recently metamorphosed juveniles in the SMR

\( J^{LH} \) Total contribution of newly metamorphosed juveniles to Lake Huron

\( A^{LH} \) Lake Huron adult abundances

\( A^{SMR} \) SMR adult abundances

\( \rho \) Proportion of Lake Huron adults migrating to the SMR to spawn

\( \tau \) Proportion of adults removed from the SMR spawning population through trapping

\( F^{SMR} \) SMR adult female abundances

\( \tilde{F}^{SMR} \) SMR adult female abundances after trapping operations

\( r \) Proportion of SMR adult females expected to breed with sterile males

\( M^{SMR} \) SMR adult male abundances

\( \tilde{M}^{SMR} \) SMR adult male abundances after trapping operations

\( \tilde{F}^{SMR} \) SMR effective spawning female abundances

\( \lambda \) Weighting factor for lognormal objective function components

\( E \) Maximum effective sample sizes for multinomial objective function components

**Data**

\( T \) Total area (ha) of the SMR treated with Bayluscide.

\( \Gamma \) Statolith aging-error matrix

\( f \) Proportion of returning adults to the SMR that were females

\( \tilde{F}^{SMR} \) Number of female adults captured after initial marking as part of trapping operations conducted on the SMR

\( U \) Number of released sterile males

\( \tilde{M}^{SMR} \) Number of male adults captured after initial marking as part of trapping operations conducted on the SMR

\( N^* \) Measured larval abundances prior to Bayluscide treatment

\( \tilde{N}^* \) Measured larval abundances post Bayluscide treatment
<table>
<thead>
<tr>
<th>Symbol</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>$J^{LH^*}$</td>
<td>Measured total contribution of newly metamorphosed juveniles to Lake Huron</td>
</tr>
<tr>
<td>$A^{SMR^*}$</td>
<td>Measured abundance of SMR adults</td>
</tr>
<tr>
<td>$A^{LH^*}$</td>
<td>Measured abundance of Lake Huron adults</td>
</tr>
<tr>
<td>$p^*$</td>
<td>Measured SMR larval age composition prior to Bayluscide treatment</td>
</tr>
<tr>
<td>$\tilde{p}^*$</td>
<td>Measured SMR larval age composition post Bayluscide treatment</td>
</tr>
<tr>
<td>$q^*$</td>
<td>Measured age composition of recently metamorphosed juveniles in the SMR</td>
</tr>
<tr>
<td>$n$</td>
<td>Data source sample sizes</td>
</tr>
</tbody>
</table>
Table 2. Assumed aging error matrix for sea lampreys aged with statolths based on the results from Dawson et al. (2009).

<table>
<thead>
<tr>
<th>Estimated Age</th>
<th>0</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>1.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>1</td>
<td>0.00</td>
<td>0.65</td>
<td>0.20</td>
<td>0.15</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>2</td>
<td>0.00</td>
<td>0.15</td>
<td>0.50</td>
<td>0.35</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>3</td>
<td>0.00</td>
<td>0.00</td>
<td>0.30</td>
<td>0.30</td>
<td>0.40</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>4</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.30</td>
<td>0.30</td>
<td>0.40</td>
<td>0.00</td>
</tr>
<tr>
<td>5</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.30</td>
<td>0.30</td>
<td>0.40</td>
</tr>
<tr>
<td>6</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.50</td>
<td>0.50</td>
</tr>
</tbody>
</table>
Table 3. Equations and descriptions of the negative log-likelihood and negative log-prior components for the St. Marys River sea lamprey integrated assessment model. The objective function of the integrated assessment model, which consisted of the sum of these components, was minimized during the model fitting process.

<table>
<thead>
<tr>
<th>Equation</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>[ \ell_N = n_N \log \left( \frac{\sigma}{\sqrt{\lambda_N}} \right) + 0.5 \left( \frac{\sqrt{\lambda_N}}{\sigma} \right) \sum_y \log \left( \frac{\sum_a N_{y,a}^s}{\sum_a N_{y,a}} \right)^2 ]</td>
<td>Total SMR larval abundance prior to Bayluscide treatment T.3.1</td>
</tr>
<tr>
<td>[ \ell_N = n_N \log e \left( \frac{\sigma}{\sqrt{\lambda_N}} \right) + 0.5 \left( \frac{\sqrt{\lambda_N}}{\sigma} \right) \sum_y \log \left( \frac{\sum_a \tilde{N}<em>{y,a}^s}{\sum_a \tilde{N}</em>{y,a}} \right)^2 ]</td>
<td>Total SMR larval abundance post Bayluscide treatment T.3.2</td>
</tr>
<tr>
<td>[ \ell_{N_0} = n_{N_0} \log e \left( \frac{\sigma}{\sqrt{\lambda_{N_0}}} \right) + 0.5 \left( \frac{\sqrt{\lambda_{N_0}}}{\sigma} \right) \sum_y \log \left( \frac{N_{y,1}^1}{N_{y,1}} \right)^2 ]</td>
<td>Age-1 SMR larval abundance prior to Bayluscide treatment T.3.3</td>
</tr>
<tr>
<td>[ \ell_{\tilde{N}<em>0} = n</em>{\tilde{N}<em>0} \log e \left( \frac{\sigma}{\sqrt{\lambda</em>{\tilde{N}<em>0}}} \right) + 0.5 \left( \frac{\sqrt{\lambda</em>{\tilde{N}<em>0}}}{\sigma} \right) \sum_y \log \left( \frac{\tilde{N}</em>{y,1}^1}{\tilde{N}_{y,1}} \right)^2 ]</td>
<td>Age-1 SMR larval abundance post Bayluscide treatment T.3.4</td>
</tr>
<tr>
<td>[ \ell_J = n_J \log \left( \frac{\sigma}{\sqrt{\lambda_J}} \right) + 0.5 \left( \frac{\sqrt{\lambda_J}}{\sigma} \right) \sum_y \log \left( \frac{J_{y,1}^{LH*}}{J_y} \right)^2 ]</td>
<td>Total contribution of newly metamorphosed juveniles lamprey to Lake Huron T.3.5</td>
</tr>
<tr>
<td>[ \ell_{A_{SMR}} = n_{A_{SMR}} \log e \left( \frac{\sigma}{\sqrt{\lambda_{A_{SMR}}}} \right) + 0.5 \left( \frac{\sqrt{\lambda_{A_{SMR}}}}{\sigma} \right) \sum_y \log e \left( \frac{A_{y,SMR}^{SMR}}{A_{y,SMR}} \right)^2 ]</td>
<td>Abundance of SMR adults T.3.6</td>
</tr>
<tr>
<td>[ \ell_{A_{LH}} = n_{A_{LH}} \log e \left( \frac{\sigma}{\sqrt{\lambda_{A_{LH}}}} \right) + 0.5 \left( \frac{\sqrt{\lambda_{A_{LH}}}}{\sigma} \right) \sum_y \log e \left( \frac{A_{y,LH}^{LH*}}{A_{y,LH}} \right)^2 ]</td>
<td>Abundance of Lake Huron adults T.3.7</td>
</tr>
<tr>
<td>[ \ell_p = - \sum_y E_y \sum_a \left( p_{y,a}^* \log e p_{y,a} \right) ]</td>
<td>Age composition of SMR larvae prior to Bayluscide treatment T.3.8</td>
</tr>
<tr>
<td>[ \ell_{\tilde{p}} = - \sum_y E_{\tilde{y}} \sum_a \left( \tilde{p}<em>{y,a}^* \log e \tilde{p}</em>{y,a} \right) ]</td>
<td>Age composition of SMR larvae post Bayluscide treatment T.3.9</td>
</tr>
<tr>
<td>[ \ell_q = - \sum_y E_q \sum_a \left( q_{y,a}^* \log e q_{y,a} \right) ]</td>
<td>Age composition of recently metamorphosed SMR juveniles T.3.10</td>
</tr>
<tr>
<td>[ \ell_{J_{other}} = \log e (0.1165) + 0.5 \left( \frac{0.1165}{12.445} \right) \log e \left( \frac{J_{other}}{12.445} \right)^2 ]</td>
<td>Prior for the contribution of juveniles from other Lake Huron tributaries T.3.11</td>
</tr>
</tbody>
</table>
Table 4. Weighting factors and maximum effective sample sizes for negative log-likelihood and negative log-prior components.

<table>
<thead>
<tr>
<th>Weight. Factor/Max.</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Effect. Sample Size</td>
<td></td>
</tr>
<tr>
<td>( \lambda_N )</td>
<td>0.15</td>
</tr>
<tr>
<td>( \lambda_{\bar{N}} )</td>
<td>0.50</td>
</tr>
<tr>
<td>( \lambda_{N_1} )</td>
<td>1.00</td>
</tr>
<tr>
<td>( \lambda_{\bar{N}_1} )</td>
<td>1.00</td>
</tr>
<tr>
<td>( \lambda_J )</td>
<td>1.00</td>
</tr>
<tr>
<td>( \lambda_{ASMRE} )</td>
<td>1.00</td>
</tr>
<tr>
<td>( \lambda_{ASLN} )</td>
<td>1.00</td>
</tr>
<tr>
<td>( E_p )</td>
<td>10</td>
</tr>
<tr>
<td>( E_{\bar{p}} )</td>
<td>10</td>
</tr>
<tr>
<td>( E_q )</td>
<td>35</td>
</tr>
</tbody>
</table>
Table 5. Management scenarios simulated for this report

<table>
<thead>
<tr>
<th>Scenario</th>
<th>Trapping rate</th>
<th>Sterile males released</th>
<th>Area treated with Bayluscide</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 (no control)</td>
<td>0%</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>2 (200 ha + 40%)</td>
<td>40% (or 8%)</td>
<td>0</td>
<td>200</td>
</tr>
<tr>
<td>3 (200 ha + 40%+ 25K SMRT)</td>
<td>40% (or 8%)</td>
<td>25,000</td>
<td>200</td>
</tr>
<tr>
<td>4 (100 ha + 40%)</td>
<td>40% (or 8%)</td>
<td>0</td>
<td>100</td>
</tr>
<tr>
<td>5 (400 ha + 40%)</td>
<td>40% (or 8%)</td>
<td>0</td>
<td>400</td>
</tr>
</tbody>
</table>
Figure 1. Map of the St. Marys River, which serves as a connection between lakes Superior and Huron via the North Channel.
Figure 2. Integrated assessment model fits to St. Marys River (SMR) age-1 and older larval abundance (pre- and post-Bayluscide treatment), SMR age-1 larval abundance (pre- and post-Bayluscide treatment), Lake Huron juvenile abundance, SMR adult abundance, Lake Huron adult abundance, SMR larval age composition (pre- and post-Bayluscide treatment), SMR larval mean age, and SMR juvenile mean age. Model estimates are highest posterior density estimates and are represented by solid lines; observed values are represented by symbols. Solid lines are predictions from the base model; dashed lines are the predictions from the sensitivity model. For most data sources, the base and sensitivity model predictions were very similar making the lines indistinguishable.
Figure 3. Integrated assessment model highest posterior density estimates (symbols) and 95% Bayesian credible intervals (error bars) for larval survival ($S_{\text{larval}}$), juvenile survival ($S_{\text{juvenile}}$), age-4 metamorphosis probability ($m_4$), age-5 metamorphosis probability ($m_5$), proportion of adult Lake Huron sea lampreys migrating to the St. Marys River ($\rho$), Bayluscide treatment area-mortality relationship scalar ($q$), and contribution of newly metamorphosed juvenile sea lampreys from all other Lake Huron tributaries ($J_{\text{other}}$). Closed symbols are for the baseline model; open symbols are for the sensitivity model.
Figure 4. Integrated assessment model highest posterior density estimates (symbols) of age-0 larval and effective reproducing adult female abundances. Also, shown are the predictions from the Ricker stock-recruitment relationship estimated from the highest posterior density estimates (solid black lines), and predictions from a sample of Ricker stock-recruitment relationships estimated from the two stage joint posterior probability distribution sampling procedure for hierarchical models (solid gray lines).
Figure 5. Forecasting model results for scenarios 1-3, shown from left to right in each panel. The upper panels summarize the effective number of female sea lampreys spawning in the St. Marys River for the 40% (left) and 8% (right) trapping effectiveness assumptions. The lower panels summarize the forecasted number of juvenile sea lampreys produced from the St. Marys River for the same two assumptions. The thick horizontal line is the median of 1000 simulations, the box represents the interquartile range, and the whiskers represent the 2.5th and 97.5th percentiles. Extreme values are plotted as open circles.
Figure 6. Forecasting model results for scenarios 4, 2 and 5, shown from left to right in each panel. The upper panels summarize the effective number of female sea lampreys spawning in the St. Marys River for the 40% (left) and 8% (right) trapping effectiveness assumptions. The lower panels summarize the forecasted number of juvenile sea lampreys produced from the St. Marys River for the same two assumptions. The thick horizontal line is the median of 1000 simulations, the box represents the interquartile range, and the whiskers represent the 2.5th and 97.5th percentiles. Extreme values are plotted as open circles.
DELIVERABLES:

We met on several occasions during this project with sea lamprey program staff to discuss early results and seek input on modeling strategies, data sources, and assumptions. We presented preliminary findings to the Sea Lamprey Integration Committee (now Sea Lamprey Control Board) on two occasions, most recently in spring 2012, and provided input to a report on this work at the fall 2012 meeting. The assessment and forecasting models can be made available to the GLFC or sea lamprey program staff upon request. We anticipate preparing a manuscript for submission to a peer-reviewed journal (likely the Journal of Great Lakes Research) during 2013 to describe this work and report on its findings.