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ARTICLE

A spatial age-structured model for describing sea lamprey (*Petromyzon marinus*) population dynamics

Jason M. Robinson, Michael J. Wilberg, Jean V. Adams, and Michael L. Jones

Abstract: The control of invasive sea lampreys (*Petromyzon marinus*) presents large-scale management challenges in the Laurentian Great Lakes. No modeling approach has been developed that describes spatial dynamics of lamprey populations. We developed and validated a spatial and age-structured model and applied it to a sea lamprey population in a large river in the Great Lakes basin. We considered 75 discrete spatial areas, included a stock–recruitment function, spatial recruitment patterns, natural mortality, chemical treatment mortality, and larval metamorphosis. Recruitment was variable, and an upstream shift in recruitment location was observed over time. From 1993 to 2011, recruitment, larval abundance, and the abundance of metamorphosing individuals decreased by 80%, 84%, and 86%, respectively. The model successfully identified areas of high larval abundance and showed that areas of low larval density contribute significantly to the population. Estimated treatment mortality was less than expected but had a large population-level impact. The results and general approach of this work have applications for sea lamprey control throughout the Great Lakes and for the restoration and conservation of native lamprey species globally.

Résumé : Le contrôle des lamproies marines (*Petromyzon marinus*), une espèce envahissante, pose des défis à grande échelle en ce qui concerne sa gestion dans les Grands Lacs laurentiens. Aucune approche de modélisation n'a encore été élaborée pour décrire la dynamique spatiale des populations de lamproies marines. Nous avons mis au point et validé un modèle spatial structuré selon l'âge et l'avons appliqué à une population de lamproies marines dans une grande rivière du bassin versant des Grands Lacs. Le modèle comprenait 75 aires discrètes et intégrait une fonction stock–recrutement, la distribution spatiale du recrutement, la mortalité naturelle, la mortalité par traitement chimique et la métamorphose des ammocètes. Le recrutement était variable, et un déplacement vers l'amont du lieu de recrutement a été observé dans le temps. De 1993 à 2011, le recrutement, l'abondance des ammocètes et l'abondance des individus en métamorphose ont diminué de 80 %, 84 % et 86 %, respectivement. Le modèle a cerné avec succès les zones de forte abondance d'ammocètes et démontré une contribution significative des zones de faible abondance d'ammocètes à la population. Si la mortalité par traitement estimée était plus faible que prévue, son impact à l'échelle de la population était considérable. Les résultats et l'approche générale de l'étude peuvent être appliqués au contrôle des lamproies marines à la grandeur des Grands Lacs et aux efforts de rétablissement et de conservation des lamproies indigènes partout dans le monde. [Traduit par la Rédaction]

Introduction

Once an invasive species becomes firmly established, detailed information about population dynamics and areas of aggregation and high abundance is often necessary for successful control (Simberloff 2003). Incorporating the spatial structure of populations into management programs has become increasingly prevalent (Pascoe et al. 2009; Struve et al. 2010) and is especially important for the management and control of invasive species (Kearney and Warren 2009; Gertzen and Leung 2011). Developing models that describe population dynamics, predict abundance or density of organisms, and reduce uncertainty around estimates is also an important component of management programs for many native terrestrial and aquatic species (Williams et al. 2002).

The invasion of sea lampreys (*Petromyzon marinus*) into the Laurentian Great Lakes has resulted in long-term ecological and economic impacts. Many fisheries in the Great Lakes collapsed in the 1950s and 1960s because of a combination of sea lamprey predation and overfishing (Coble et al. 1990). Sea lampreys are an anadromous, semelparous fish species native to the Atlantic coast of North America and Europe (Beamish 1980). In spring, following a parasitic phase in the lake, adults ascend streams to spawn. Adult sea lampreys select suitable streams based on the detection of a migratory pheromone released by larval lampreys (Sorensen and Vrieze 2003; Wagner et al. 2009). Evidence for natal homing in sea lamprey is lacking (Bergstedt and Seelye 1995; Waldman et al. 2008). After hatching, larvae drift downstream and settle in areas of fine sediment where they live in burrows as filter feeders for 3–8 years (Clemens et al. 2010). Larvae then metamorphose into the parasitic phase in a process called transformation. During the transformation phase, sea lampreys move downstream to the lake and develop eyes, a sucker-like mouth, and teeth. Parasitic phase sea lampreys are sanguivorous and prey on other fish species, sometimes resulting in the death of the host (Spangler et al. 1980). The parasitic phase spends from 12 to 18 months in the Great Lakes, and each lamprey has the potential to destroy approximately 19 kg of fish during that time (Swink 2003).

Sea lamprey control efforts have greatly reduced the numbers of parasitic phase sea lampreys in the Great Lakes, making the

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J.M. Robinson* and M.J. Wilberg. Chesapeake Biological Laboratory, University of Maryland Center for Environmental Science, P.O. Box 38, Solomons, MD 20688, USA.
J.V. Adams. US Geological Survey, Great Lakes Science Center, 1451 Green Road, Ann Arbor, MI 48105, USA.
M.L. Jones. Department of Fisheries and Wildlife, Michigan State University, 13 Natural Resources Building, East Lansing, MI 48824, USA.
Corresponding author: Jason M. Robinson (e-mail: jason.robinson@ferc.gov).
*Present address: Federal Energy Regulatory Commission, Division of Hydropower Licensing, 888 First Street NE, Washington, DC 20426, USA.

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rehabilitation of native piscivorous fish populations possible. The goal of the sea lamprey control program is to reduce the abundance of sea lampreys to so-called economic injury levels (Irwin et al. 2012), where the marginal cost of increased control begins to exceed the expected economic benefits. A large portion of the control efforts focus on the sedentary larval life stage. In small streams, TFM (3-trifluoromethyl-4-nitrophenol) is successfully used to control the larval stage through large-scale stream treatments. However, in large rivers and lentic areas, the application of TFM is not feasible, so spot treatments are carried out in areas of high density using a granular, bottom-release formulation of Bayluscide (2′,5-dichloro-4′-nitro-salicylanilide; Fodale et al. 2003). The spot treatment approach requires the estimation of larval abundances at relatively fine spatial scales to inform Bayluscide application (Fodale et al. 2003). In addition to chemical controls, adult trapping and sterile male release is also conducted on a subset of sea lamprey producing streams as a means of reducing reproductive potential (Bergstedt and Twohey 2007), although the sterile male release program was discontinued in 2012. The continued success of the sea lamprey control and native fish restoration programs, especially for lake trout (*Salvelinus namaycush*), relies on continued suppression of sea lamprey populations (Madenjian et al. 2003; Bronte et al. 2003; Dobiesz et al. 2005).

Developing a population process model that explicitly incorporates heterogeneous spatial distributions of sea lamprey larvae will allow estimation of spatially specific larval abundance and recruitment while also allowing the inclusion of critical aspects of sea lamprey life history and demographics such as natural mortality and transformation. This type of approach will also allow the effects of the chemical treatment program to be included in the model at a fine spatial scale. Data similar to those used to develop this model are currently being collected for sea lamprey populations in other areas of the Great Lakes and for native lamprey populations in the Pacific Northwest US (Jolley et al. 2010, 2011, 2012). The results and general approach of this work have applications for sea lamprey control efforts throughout the Great Lakes and for the restoration and conservation of native lamprey species, which are threatened globally (Renaud 1997; Close et al. 2002; OSPAR Commission 2009; Mateus et al. 2012). The long and detailed time series of data and history of control efforts available for the St. Marys River sea lamprey population make it an ideal system for which to develop and test this type of approach.

Here we develop a spatial age-structured model that explicitly incorporates a stock–recruitment function, spatial recruitment patterns, natural mortality, control actions, and larval metamorphosis for a sea lamprey population. We apply this model to a population of sea lampreys in a large river and inform management through the identification of areas of high larval sea lamprey abundance. We also compare some predictions of the model with independent data, a rarity for this type of model. To date, no models have been developed that account for spatial population dynamics of any lamprey species. The specific objective of this work was to develop a population model incorporating long-term data and critical aspects of sea lamprey life history that would (*i*) describe the long-term dynamics of sea lampreys in the St. Marys River (spawning through transformation), (*ii*) describe spatial and temporal trends at several life history stages, (*iii*) identify and project areas of high larval abundance, and (*iv*) estimate the effectiveness of Bayluscide applications. Objectives *iii* and *iv* are especially important in promoting cost-effective sea lamprey control by being able to predict the location of larvae concentrations, the number killed during each treatment event, and what the cumulative effect of the treatment program is at the population level.

Methods

Data

The St. Marys River is divided into 71 treatment plots (830 ha total, in-plot) ranging in size from 1.2 to 27.5 ha for the purposes of conducting deepwater electrofishing surveys for larval lampreys and applying Bayluscide (Fig. 1). Based on surveys conducted during 1993–1996, plots with high larval densities were defined (Fodale et al. 2003). A large area of the river (6980 ha) is characterized by low larval density (out-of-plot) in which Bayluscide treatment does not occur but electrofishing is conducted at a lower sampling intensity. For the purposes of our model, the out-of-plot portion of the river was separated into five areas. A single treatment plot (Plot 10) was included as part of the out-of-plot area because no sea lampreys were ever observed there, reducing the number of treatment plots in the analysis to 70.

Data were available on number and location of Bayluscide treatments, female spawner abundance, and larval density in the St. Marys River. Plot-specific Bayluscide treatment histories were available from 1998 through 2011 encompassing the entire duration of treatment efforts in the St. Marys River. The scale of the treatment efforts varied annually (Table 1) with large-scale treatment efforts (i.e., nearly all treatment plots) occurring in 1999, 2010, and 2011. Estimates of theoretical (i.e., effective) female spawner abundance were available from 1992 through 2011 (Bergstedt and Twohey 2007; Great Lakes Fishery Commission 2011; Table 1). Spawner abundance is estimated using a combination of mark recaptures and trap efficiency estimates. Female spawner abundance is calculated based on the annual sex ratio and is adjusted for removals by trapping and the estimated effect of the sterile male release program.

A 19-year time series (1993–2011) of plot-specific deepwater electrofishing data was available for larval sea lampreys in the St. Marys River. Electrofishing was conducted based on the methods described in Bergstedt and Genovese (1994), with each sample covering 2.44 m^2. In many years only a subset of plots was selected for sampling. The number of individual electrofishing samples taken for a treatment plot ranged from 1 to 76. Sampling was conducted based on a systematic, stratified sampling design, with higher sampling intensities occurring in treatment plots relative to the out-of-plot areas. All of the out-of-plot areas, with the exception of the shipping channel, were sampled periodically over the 19-year time period. Sampling density was not constant over time. Electrofishing data were classified as either pre-treatment or post-treatment depending on when sampling occurred relative to the timing of Bayluscide application (late spring or early summer) in a given year. Pre-treatment data collections occurred in spring just prior to a Bayluscide treatment in 1999, 2001, and 2003, with the number of plots sampled prior to treatment in each year ranging from 11 to 69 (total = 136). Post-treatment data collections occurred after a Bayluscide treatment or in years with no treatment. Post-treatment data were available in all years except 1997 and 1998, with the number of plots sampled annually ranging from 1 to 73 (including five out-of-plot areas, total = 778 plots sampled over 19 years). Density estimates (larvae·ha^{-1}) were based on the mean larval catch (corrected for gear selectivity) in an individual electrofishing sample (2.44 m^2) and were scaled up to an estimate of larval abundance by multiplying mean density in each plot by the plot area. Plot-specific larval density estimates (larvae·ha^{-1}) were calculated for each year in the pre- and post-treatment periods. Density estimates were calculated separately for age 1 (<47 mm) and ages 2+ (≥47 mm). The length cutoff between ages 1 and 2+ larvae was determined based on visual inspection of length frequency histograms.

The capture efficiency of the deepwater electrofishing gear is reduced as larval sea lamprey length increases, so a length-based gear selectivity correction was applied to all larval catch data:

Fig. 1. The St. Marys River from the navigational locks in Sault Ste. Marie, Michigan and Ontario, to the northern shore of Neebish Island. Coverage includes the entire portion of the river that is treated and assessed by the sea lamprey control program. Dark grey areas are treatment plots, and the white areas are considered out-of-plot (i.e., not treated). The river is separated into five areas by the solid black lines, which are used in the analysis to evaluate spatial changes in recruitment and to separate the out-of-plot areas into discrete units. Inset shows location in the Great Lakes Region. The major spawning area for sea lampreys in the river is located in the rapids north of the navigational locks.

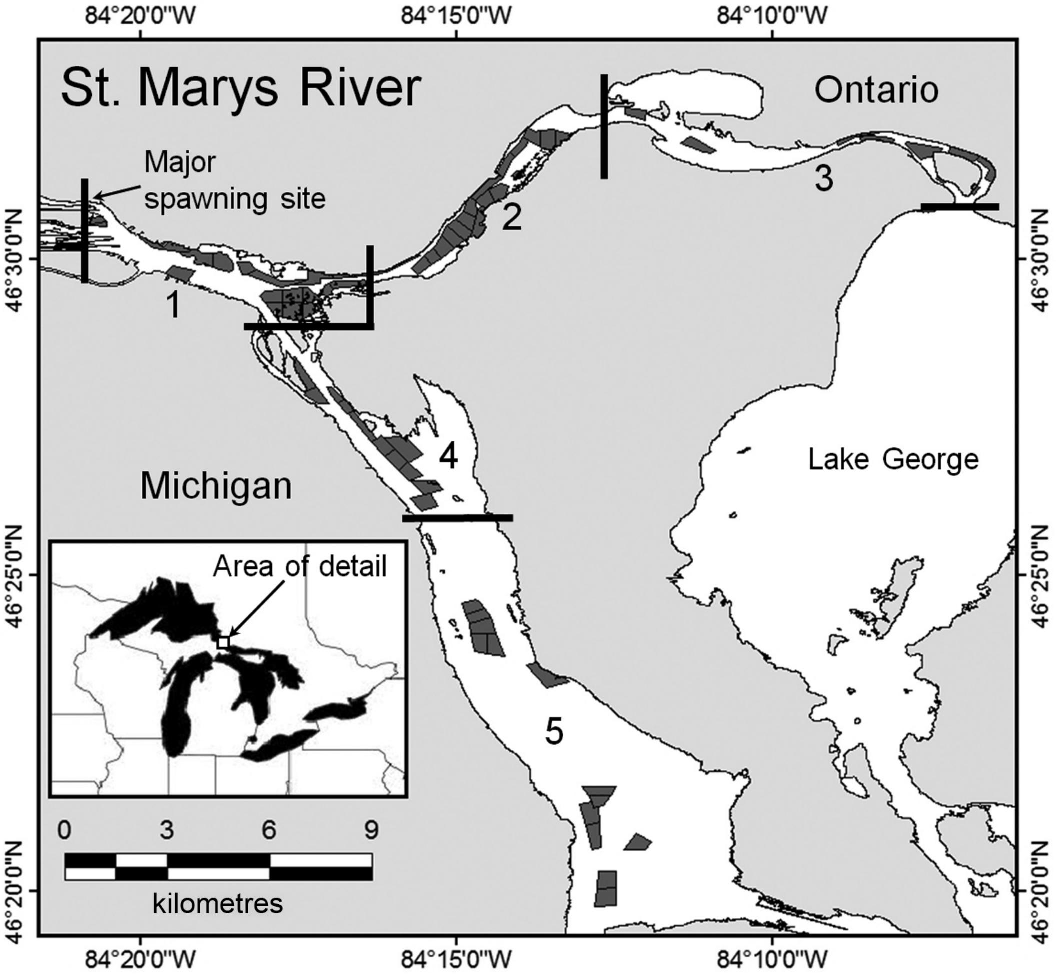


Table 1. The number of plots and hectares treated in each model year, and the effective female spawners (*S*) in each year.

Year	Plots treated	Hectares treated	S_{t-1}
1993	0	0	3 030
1994	0	0	12 500
1995	0	0	1 090
1996	0	0	2 870
1997	0	0	4 920
1998	6	81	402
1999	59	692	1 770
2000	0	0	638
2001	5	57	1 670
2002	0	0	1 110
2003	8	82	289
2004	8	60	1 860
2005	10	122	1 200
2006	8	106	673
2007	10	112	1 390
2008	9	121	1 560
2009	10	148	875
2010	70	829	643
2011	70	829	2 500

$$(1) \qquad C = \sum_{i} [1 + e^{(0.0229L_i - 1.732)}]$$

where C is the adjusted catch for an individual electrofishing sample, L is the length of a larvae (mm), and i is an index for the individual sea lampreys captured and measured in the sample (Great Lakes Fishery Commission, unpublished data).

Standard errors for the plot-specific density estimates were calculated when multiple electrofishing samples per plot were available and at least one of them was a positive observation. When a single sample was taken or no larvae were captured, standard errors were estimated across years with available data using a power function based on the average relationship between sample size and standard error estimates:

$$(2) \qquad \sigma_d = an^c$$

where n is the sample size for a given plot, and a and c are estimated parameters. Parameter a can be interpreted as the estimated standard error of a larval density estimate when $n = 1$. These relationships were developed separately for the pre-treatment and post-treatment density estimates and the age 1 and

Table 2. Parameter estimates, standard errors (SE) of parameter estimates, and P values associated with power functions describing the relationship between sample size and standard error of plot-level larval sea lamprey density estimates.

Time period and age	α	SE ($\log(\alpha)$)	c	SE (c)	P
Pre-treatment age 1	10 800	0.518	−0.855	0.194	<0.001
Pre-treatment age 2+	13 200	0.428	−0.853	0.159	<0.001
Post-treatment age 1	6 430	0.101	−0.840	0.035	<0.001
Post-treatment age 2+	10 000	0.122	−0.741	0.043	<0.001

Note: Estimates are reported to three significant digits.

age 2+ length bins (Table 2; Fig. 2). The power functions were used to estimate standard error instead of using a constant standard error (when the standard error could not be calculated), so that observations of zero larvae in plots where many samples were taken would carry greater weight in the model fitting than observations when only one sample was taken. This was necessary because of the high number of zeros in the data and the high variability in sample size. Standard errors associated with larval density (σ_d) in each plot were scaled up to the standard error of abundance (σ_N) by multiplying each standard error area by the plot area.

High-intensity pre-treatment deepwater electrofishing surveys were conducted in 2010 and 2011 to validate the ability of the model to project plot-specific larval abundance and to test the sensitivity of the model to inclusion of highly informative pre-treatment data. Prior to treatment in 2010, 16 plots were sampled using deepwater electrofishing at a much higher intensity (over six times as many samples in each plot, more than four samples per hectare) than would occur under normal sampling conditions. A similar sampling effort was undertaken in 2011, which intensively sampled 10 plots.

Population model

We developed a spatial age-structured model (Fournier and Archibald 1982) and applied it to sea lampreys in the St. Marys River. The model estimated parameters of a stock–recruitment relationship, spatial patterns in recruitment, natural mortality, treatment mortality, and plot-specific larval and transformer abundance. Within the model, plot-specific larval and transformer abundance changed because of variable recruitment, natural mortality, Bayluscide treatment mortality, and age-specific transformation rates (Fig. 3). We used a Bayesian approach for model fitting. Variables included in the model are described in Table 3.

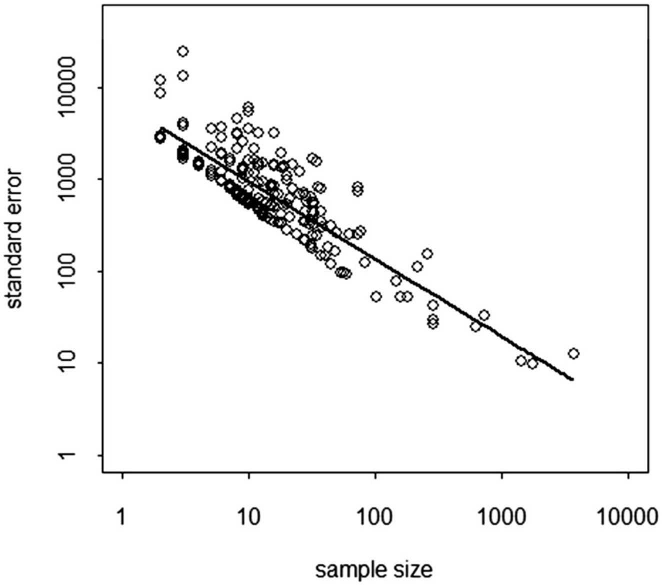
The model structure allowed for stochastic variability in recruitment at age 1 (Haeseker et al. 2003; Anderson 2006). Recruitment was estimated at age 1 because age 0 larvae are not vulnerable to the deepwater electrofishing gear. We assumed that the population was at equilibrium prior to the first year of the model with constant recruitment for 1993 and earlier. We assumed that recruitment of larvae to plots occurred prior to pre-treatment electrofishing (Fig. 3). Total (river-wide) recruitment was estimated using a Ricker stock–recruitment function with a year-specific process error:

$$R_t = \alpha S_{t-1} e^{-\beta S_{t-1} + \varepsilon_t} \tag{3}$$

The parameters of the Ricker function (α and β) were estimated within the model and were informed by the number of reproducing females with a 1-year time lag (e.g., 1993 females S_{1993} produce 1994 age 1 recruits R_{1994}). Recruitment process error was assumed to be normally distributed (on the log scale):

$$\varepsilon_t \sim N\left(0, \hat{\sigma}^2_{\mathrm{rec}}\right) \tag{4}$$

Fig. 2. Fitted power function describing the relationship between sample size and standard error of larval density estimates for post-treatment samples of age 1 sea lamprey larvae. See post-treatment age 1 row in Table 2 for parameter estimates. Open circles represent sampling events from individual plots in which multiple electrofishing samples per plot were available and at least one of them was a positive observation.



Recruits were apportioned among the plots as the product of total recruitment and the estimated proportion assigned to each plot:

$$\hat{N}\mathrm{pre}_{a=1,t,p} = R_t r_{t,p} \tag{5}$$

where Npre is the number of larvae prior to treatment in a given plot, R_t is the total number of recruits produced in a given year, and $r_{t,p}$ is the proportion of total recruitment assigned to each plot. The estimated proportion of total recruitment assigned to each plot ($r_{t,p}$) was allowed to change in 1999 so that the earlier data could inform the stock–recruitment relationship and the plot-specific recruitment proportions in recent years would not be dominated by the earlier data. Estimating the proportion of recruits assigned to each plot in two time periods ($r_{x,p}$, x = 1993–1998 and 1999–2011) also allowed for a shift in the spatial pattern of recruitment. Recruitment proportions for each plot were assumed to be constant within the two periods. The year 1999 was chosen as the change point in spatial recruitment because it was the year following the onset of treatment efforts, and it was preceded by 3 years of very sparse data collection. We did explore changing the year in which the change point occurred prior to implementing the MCMC and found that it had

Fig. 3. A basic representation of the recruitment dynamics and plot-specific population dynamics for larval sea lampreys in the St. Marys River as it is implemented within the age-structured population model. Arrows originating from the recruitment term indicate larval recruitment to different spatial areas (plots). The proportion of total age 1 recruitment that is assigned to each plot is allowed to change in 1999. Arrows originating on the right side of the age boxes indicate sources of larval mortality, and arrows originating from the left side of the age boxes indicate larval population loss due to transformation. The within-year dynamics box on the right represents the relative order of events within a single model year from top to bottom. However, sampling and treatment events do not occur in all plots and years. The parasitic phase is included in the box to represent transformers leaving the river, but is not included in the model.

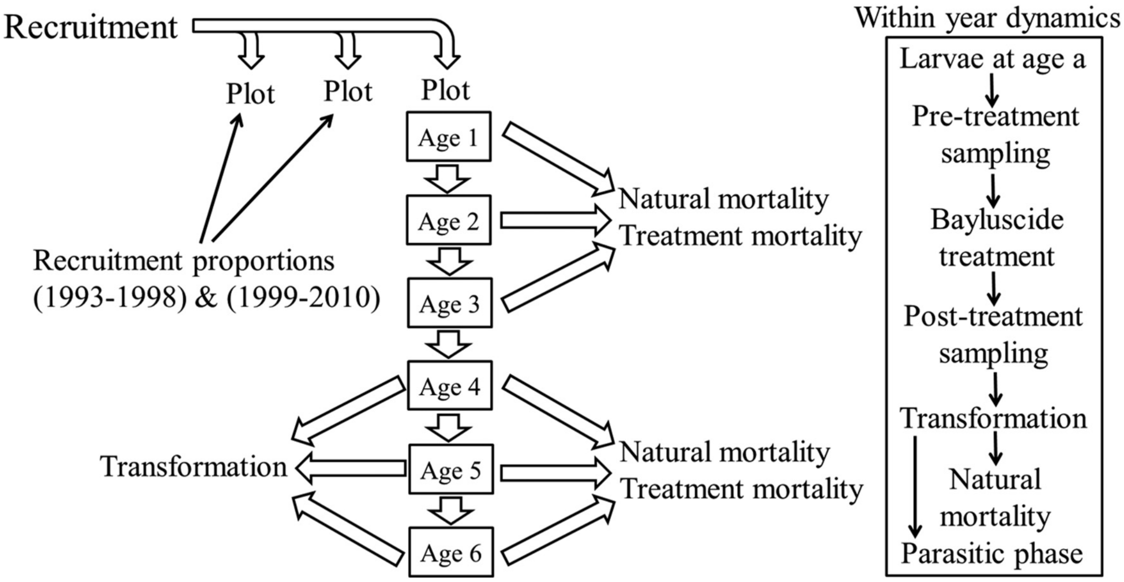


Table 3. Description of symbols used in model equations.

Symbol	Description	Type
a	Age class (age 1 through age 6)	i
t	Year (1993–2010)	i
p	Plots	i
n_p	Sample size for a given plot	d
S_t	Female spawner abundance	d
$N_{a,t,p}$	Plot-specific larval abundance estimates	d
$\sigma_{N_{t,p}}$	Standard error of plot-specific larval abundance estimates	d
σ_d	Standard error of plot-specific larval density estimates	d
Y	Number of years in the time series	d
ρ	Calculated priors on parameters	d
α	Ricker model alpha parameter (1)	p
β	Ricker model beta parameter (1)	p
ε_t	Normally distributed recruitment process error (19)	p
$\hat{\sigma}^2_{\mathrm{rec}}$	Variance of recruitment process error (1)	p
M	Instantaneous natural mortality rate (1)	p
B	Bayluscide treatment effectiveness (1)	p
$r_{t,p}$	Proportion of total recruits that settle in each plot (148)	p
τ_a	Age-specific transformation rate at age	c
β_p	Median prior for beta parameter	c
σ_β	Standard deviation for prior on the beta parameter	c
R_t	Total river age 1 recruitment	s
$\hat{N}\mathrm{pre}_{a,t,p}$	Larval lamprey abundance in each year prior to Bayluscide treatments	s
$\hat{N}\mathrm{post}_{a,t,p}$	Larval lamprey abundance in each year following Bayluscide treatments	s
T	Transformer abundance in the St. Marys River	s

Note: Numbers in parentheses indicate the number of estimated parameters. Symbol types are as follows: i, index; d, data; p, estimated parameters; c, constants; s, state variable.

little effect on the results in recent years. The model assumes no movement of larvae among plots after initial recruitment.

Six larval age classes were considered in the model (ages 1–6). The maximum larval age was set to six because less than 1% of larvae aged using statoliths from 1993 to 1996 were greater than 6 years old (Schleen et al. 2003). Plot-specific larval abundance following treatment in each year was calculated by multiplying the pre-treatment larval abundance by Bayluscide treatment survival:

$$(6)\quad \begin{aligned} \hat{N}\mathrm{post}_{a,t,p} &= \hat{N}\mathrm{pre}_{a,t,p} \quad \{\text{if no treatment occured}\} \\ \hat{N}\mathrm{post}_{a,t,p} &= (1 - B)\,\hat{N}\mathrm{pre}_{a,t,p} \quad \{\text{if treatment occured}\} \end{aligned}$$

B is the estimated larval mortality due to Bayluscide (Table 3). Pre-treatment larval abundance at the next year and age was calculated by decrementing post-treatment larval abundance in the previous year by transformation τ_a and natural mortality M:

$$\hat{N}\text{pre}_{a+1,t+1,p} = \hat{N}\text{post}_{a,t,p}(1 - \tau_a)e^{-M} \quad (7)$$

Estimated natural mortality was constant through time and was applied following larval transformation in all years. The natural mortality estimate is primarily informed by interannual plot-level changes in larval abundance for plots that were not subject to treatment in a given year.

Larval transformation was assumed to occur following post-treatment sampling (Fig. 3). Age-specific larval transformation rates (t_a: ages 1–3, $t_a = 0$; age 4, $t_a = 0.46$; age 5, $t_a = 0.57$; age 6, $t_a = 1.0$) were taken from the age-structured model developed by Haeseker et al. (2003) and were assumed to be constant through time. Transformer abundance (T) was calculated by multiplying the number of larvae that survive treatment by the expected proportion transformed at each age (τ_a):

$$T_{t,p} = \sum_{a} \hat{N}\text{post}_{a,t,p}\tau_a \quad (8)$$

An individual treatment event kills larvae that would have transformed in the year of the treatment and larvae that would have transformed in subsequent years. Therefore, plot-specific transformer abundance is influenced by the current year's Bayluscide treatment along with any treatments that have occurred in the previous 5 years. The number of transformers that would have been produced in the absence of the treatment program was calculated as a measure of the overall effect of treatment on the river-wide sea lamprey population. This was done by applying the plot-specific recruitment proportions to the estimated annual recruitment, then applying natural mortality and transformation rates to each cohort through time with no treatment mortality. Because sea lampreys do not exhibit natal homing behavior (Bergstedt and Twohey 2007; Waldman et al. 2008), there is no biological basis for using transformer production in the St. Marys River to inform future spawning stock size.

One-year projections of plot-specific pre-treatment larval abundance were produced using the population model equations and the resulting parameter estimates. Age 1 pre-treatment larval abundance (i.e., recruitment) was projected using the estimated stock–recruitment parameters and the abundance of females in the last model year. As such, the projected recruitment was estimated with no process error.

Model fitting

The model was developed in AD Model Builder, and parameters were estimated using Markov chain Monte Carlo (MCMC) using a Metropolis–Hastings algorithm (Fournier et al. 2012). A Bayesian approach to parameter estimation was used (Gelman et al. 2004), and the model was fitted to plot-specific abundance estimates from the deepwater electrofishing survey. We estimated 171 parameters simultaneously within the model (Table 3). Three parallel MCMC chains were run for 50 million steps and were thinned by saving every 10 000th step. The initial 100 000 steps were removed as a burn-in to reduce the effect of starting values on the chains (Gelman et al. 2004). Model convergence was determined using visual inspection of the chains of parameters and Gelman–Rubin plots (Brooks and Gelman 1998). Additionally, model fit was assessed by inspecting the standardized median residuals associated with larval abundance estimates for each plot. Residuals were standardized by dividing each residual by the observed standard error of each plot-specific larval abundance estimate. Uninformative uniform priors were placed on all parameters except the β parameter of the Ricker function (Table 4). A normal prior (ρ) was assumed for β based on Haeseker et al. (2003). The negative log-likelihood of the prior took the form

$$\rho_\beta = \log(\sigma_\beta) + \frac{(\beta_\rho - \beta)^2}{2\sigma_\beta^2} \quad (9)$$

where β_ρ (0.00018) is the mean prior for β, and σ_β (0.0001) is the standard deviation of the prior for β.

The objective function (L) was the sum of five negative log-likelihood components (LL) and the priors (ρ), where k is the number of priors.

$$L = \sum_{i=1}^{5} \text{LL}_i + \sum_{k=1}^{k} \rho_k \quad (10)$$

Likelihood components 1 and 2 were associated with observed numbers of pre- and post-treatment age 1 (<47 mm) larvae, and components 3 and 4 were associated with observed numbers of pre- and post-treatment ages 2–6 (≥47 mm) larvae. Normal distributions were used to describe the larval abundance estimates. The negative log-likelihood functions for the plot-specific larval abundance estimates took the form

$$\text{LL}_{1-4} = \sum_{t} \sum_{p} \left[\log(\sigma_{N_{t,p}}) + \frac{1}{2\sigma_{N_{t,p}}^2}(N_{t,p} - \hat{N}_{t,p})^2 \right] \quad (11)$$

where N is the empirical plot-specific abundance estimate from the deepwater electrofishing data, $\hat{N}$ is the model abundance estimate, and σ is the standard error of N. Asymptotically, the normal distribution is appropriate based on sampling theory. We also attempted lognormal and negative binomial likelihood functions to describe the larval abundance estimates, but these approaches performed poorly compared with the normal distribution based on residual patterns, model validation, and their ability to produce stable parameter estimates. A normal negative log-likelihood was assumed for the natural log of the recruitment process errors and took the form

$$\text{LL}_5 = 0.5Y \log \sum_{t} (\varepsilon_t)^2 \quad (12)$$

where ε is the estimated recruitment deviations, and Y is the number of years in the time series. The constants in the likelihood functions and the priors were ignored for simplicity. Ninety percent credible intervals (the Bayesian analog of confidence intervals) were constructed using the range between the 5th and the 95th percentiles of the posterior distributions (Gelman et al. 2004).

Model validation and sensitivity analysis

The ability of the model to project pre-treatment plot-specific larval abundance (i.e., model skill) was assessed by comparing projected larval abundance in 2010 and 2011 with independent estimates of pre-treatment larval abundance based on the intensive pre-treatment sampling efforts in those years that were not used in model fitting. The model was fitted to the 1993–2009 and 1993–2010 data to produce 2010 and 2011 projections, respectively. Observed and projected larval abundance were compared, and median error, median percent error, and median absolute error for the total plot-level larval density, age 1 larval density, and ages 2–6 larval density in 2010 and 2011 were compared. These metrics could not be calculated on a relative scale because the observed abundance estimates for some plots were zero.

We tested the sensitivity of the model to (*i*) the inclusion of the 2010 and 2011 pre-treatment validation data and (*ii*) an alternative selectivity relationship for the deepwater electrofishing gear

Table 4. Median model estimates, 90% credible intervals, and proportional differences in model estimates for the age-structured model without the 2010 and 2011 validation data included (primary model), with the validation data included, and using the Bergstedt and Genovese (1994) selectivity relationship.

Estimate	Prior	Model	Median	90% CI	Diff.*
Natural mortality (*M*)	$U(e^{-3}, e^{2})$	Primary model	0.092	0.053–0.177	
		Validation data included	0.109	0.055–0.203	0.16
		Bergstedt selectivity	0.144	0.031–0.245	0.36
Treatment mortality (*T*)	$U(e^{-5}, e^{0})$	Primary model	0.51	0.37–0.64	
		Validation data included	0.59	0.47–0.70	0.13
		Bergstedt selectivity	0.52	0.41–0.62	0.02
Alpha	$U(e^{-5}, e^{10})$	Primary model	268	177–379	
		Validation data included	291	193–415	0.08
		Bergstedt selectivity	355	161–355	0.25
Beta	$N(0.00018, 0.0001)$	Primary model	0.00018	0.00008–0.00028	
		Validation data included	0.00019	0.00008–0.00029	0.03
		Bergstedt selectivity	0.00018	0.00008–0.00027	0.00
1993 larval abundance estimate	—	Primary model	3 050 000	2 440 000–3 740 000	
		Validation data included	3 050 000	2 440 000–3 730 000	0.00
		Bergstedt selectivity	2 140 000	1 730 000–2 580 000	0.30
2011 larval abundance estimate	—	Primary model	500 000	292 000–767 000	
		Validation data included	424 000	245 000–646 000	0.15
		Bergstedt selectivity	452 000	278 000–763 000	0.10
1993 transformer abundance	—	Primary model	530 000	405 000–659 000	
		Validation data included	513 000	391 000–645 000	0.03
		Bergstedt selectivity	339 000	260 000–436 000	0.36
2011 transformer abundance	—	Primary model	72 900	37 300–126 000	
		Validation data included	66 300	30 800–114 000	0.09
		Bergstedt selectivity	141 000	33 200–103 000	0.48
1993 in-plot recruitment proportion	—	Primary model	0.58	0.51–0.65	
		Validation data included	0.58	0.51–0.65	0.00
		Bergstedt selectivity	0.59	0.53–0.66	0.01
2011 in-plot recruitment proportion	—	Primary model	0.63	0.50–0.78	
		Validation data included	0.66	0.54–0.80	0.05
		Bergstedt selectivity	0.63	0.51–0.77	0.00

*Proportional differences are relative to the estimates from the primary model.

(Bergstedt and Genovese 1994). The degree of sensitivity was evaluated by comparing the proportional difference of the model estimates of natural mortality (*M*), treatment mortality (*B*), alpha (α), beta (β), 1993 and 2011 larval abundance, 1993 and 2011 transformer abundance, and the proportion of recruitment assigned to the in-plot areas between model fits. Sampling directly before and after treatments provides information on treatment mortality that was relatively sparse in most years. Therefore, model sensitivity to the inclusion of the pre-treatment data from 2010 to 2011 was assessed by fitting the model with those data included.

Model sensitivity to potential changes in the gear selectivity relationship was tested by fitting the model to larval catch data that was corrected using the selectivity relationship developed by Bergstedt and Genovese (1994). Bergstedt and Genovese (1994) developed the original gear selectivity adjustment for the deepwater electrofishing gear in the Carp River, Michigan, USA:

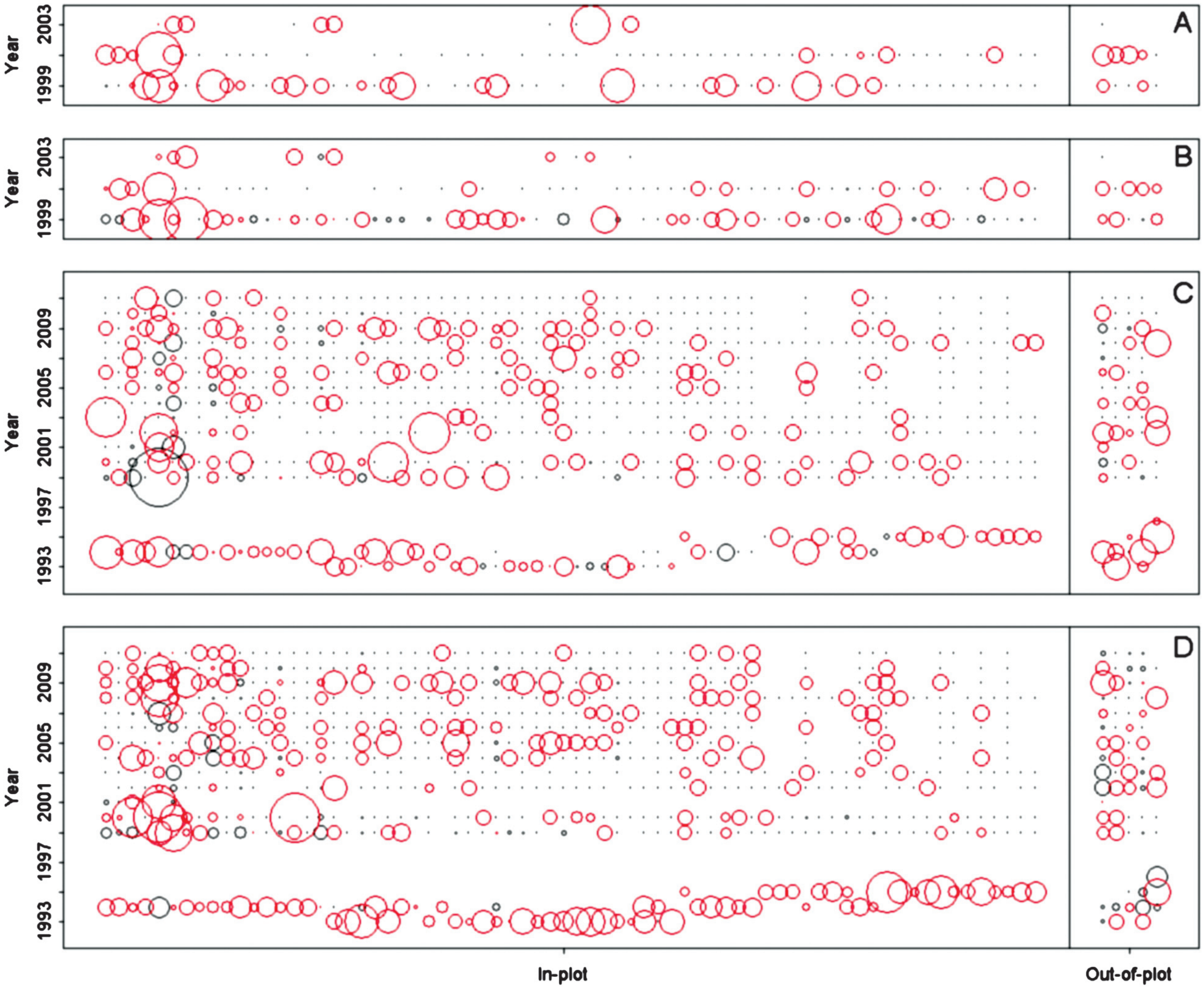
$$(13)\qquad C_{\text{Bergstedt}} = \sum_{i} 1 + e^{(0.0164L_i - 2.2429)}$$

where *C* is the adjusted catch value for each larvae, and *L* is the length of the larvae (mm). Following the development of the Bergstedt and Genovese (1994) selectivity relationship, a gear selectivity correction specific to the St. Marys River (eq. 1) was developed. The St. Marys River has a higher prevalence of clay-based substrates than the Carp River, which can affect the efficiency of the electrofishing gear (Michael Fodale, US Fish and Wildlife Service, personal communication). The Bergstedt and Genovese (1994) selectivity relationship suggests higher gear efficiency than the St. Marys River relationship, especially for larger larvae. The parameters of the power functions (eq. 2) used to determine the standard error of larval density estimates were estimated separately for the density estimates derived using the Bergstedt and Genovese (1994) relationship, prior to model fitting.

Results

The model fit the plot-specific estimates of larval abundance in the St. Marys River reasonably well (Figs. 4A–4D). The magnitude of the standardized residuals was small, with the largest residual (+3.7) occurring for a 1999 post-treatment age 1 estimate of larval abundance, but some patterns were observed. More positive residuals than negative residuals were present, and the positive residuals tended to be smaller. Most of the positive residuals were associated with observed larval abundances of zero. Zero larval abundances were numerous in the time series, and the model was constrained to estimate a positive larval abundance, therefore producing a small positive residual in these situations. Many of the larger negative residuals were associated with observations of very high larval abundance with low sample size. If a single electrofishing sample was taken and at least one larval sea lamprey was captured (especially a large larval sea lamprey), the resulting observed abundance estimate was extremely high. The magnitudes of the positive and negative residuals tended to be larger earlier in the time series and for areas of the river that were closest to the main spawning area. However, the model consistently identified plots that are known to have very high or low larval abundance.

Fig. 4. Standardized plot-specific larval abundance residuals for the pre-treatment age 1 samples (A), pre-treatment ages 2–6 samples (B), post-treatment age 1 samples (C), and the post-treatment ages 2–6 samples (D). Black and red circles represent positive and negative residuals, respectively. Areas of the figure with no circle indicate that no sample was taken. The size of each circle equates to the magnitude of each residual and is scaled relative to the largest residual, which was +3.7 and occurred in 1999 for an age 1 post-treatmet sample. Circles that appear as a single point on the figure represent residuals that are very close to zero. In-plot residuals are in the left box of each panel and are ordered from left to right based on each plot's distance from the main spawning area. Out-of-plot residuals for areas 1–5 are in the right box of each panel.



The credible intervals around the parameter estimates were all reasonable (Table 4), and the distributions of the parameter estimates differed from the priors in all cases except β. The median estimate of instantaneous natural mortality (M) for ages 1–6 larvae was 0.09 year^{-1}, and the estimated Bayluscide induced treatment mortality (B) was 0.51·treatment^{-1} (Table 4). The α and β parameters of the Ricker stock–recruitment relationship were 268 and 0.00018, respectively, and the standard deviation of the log-scale recruitment deviations was 0.78 (95% CI = 0.57, 1.04).

River-wide recruitment was highly variable over time, ranging from 61 400 in 2003 to 991 000 in 1995, and decreasing 80% during 1993–2011 (Fig. 5A). Recruitment was also highly variable at low spawning stock size and showed a moderate amount of compensation at higher spawning stock size that was largely driven by a single observation (Fig. 5B). Although the overall proportion of recruits that were assigned to out-of-plot areas changed little over time, there were major estimated shifts in where recruits were assigned within the river (Table 5). On average, more recruits settled in areas closer to the spawning area during 1999–2011 than 1993–1998. In recent years, 60% of recruits were assigned to area 1 (includes in- and out-of-plot) compared with 25% early in the time series. Conversely, area 5 received only 4% of recruitment in recent years compared with 36% earlier in the time series. More modest changes in recruitment proportions were estimated for areas 2, 3, and 4. The out-of-plot areas 1–4 have received a greater proportion of recruits in recent years, while out-of-plot recruitment to area 5 has decreased substantially.

River-wide larval and transformer abundance decreased over time in response to decreases in recruitment and the effects of the Bayluscide treatment program. Total post-treatment larval abundance decreased 84% from 1993 to 2011, while in-plot and out-of-plot larval abundance decreased 92% and 71%, respectively (Figs. 6A–6C). Transformer abundance decreased 86% from 1993 to 2011, while in-plot and out-of-plot transformer abundance decreased 96% and 72%, respectively (Figs. 6D–6F; Table 1).

When we removed the estimated effect of Bayluscide treatment on transformer abundance while holding other parameters constant, the estimated decrease in total river and in-plot transformer abundance from 1993 to 2011 dropped to 67% and 66%, respectively (Figs. 6D and 6E). If Bayluscide treatments had not

Fig. 5. Median model estimated temporal trend in total river age 1 recruits in millions (A) and the estimated Ricker stock–recruitment relationship with median estimates of annual recruitment in millions represented by the open circles (B). Solid black lines represent median model estimates, and the grey shading represents the 90% credible intervals. The dashed vertical line denotes the onset of treatment efforts in 1998.

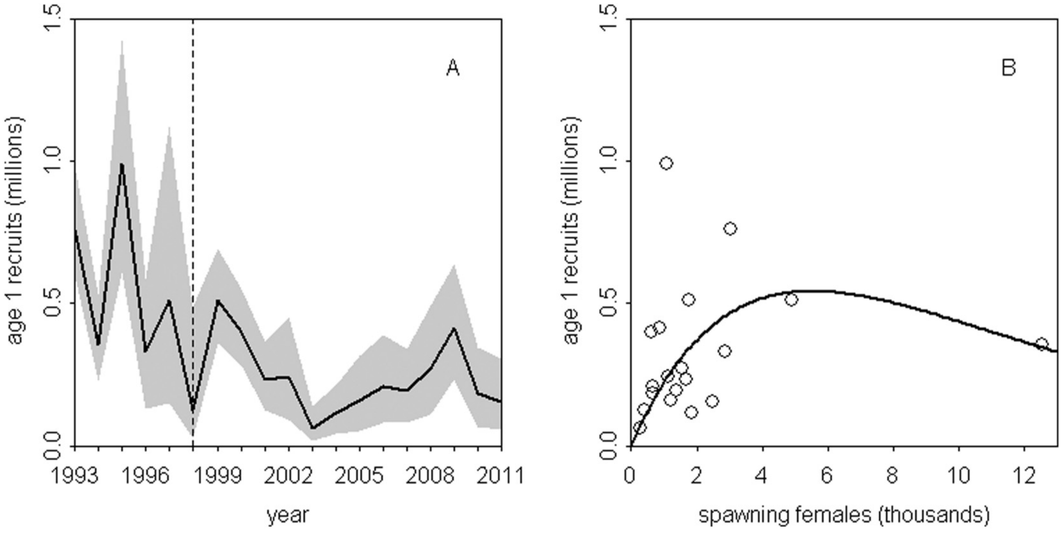


Table 5. Estimated proportions of total recruitment assigned to each of the five river areas, the in-plot portion of each area, the out-of-plot portion of each area, and the out-of-plot portion of the whole river for the 1993–1998 and 1999–2011 time periods.

Recruitment area	1993–1998	1999–2011
Area 1 total	0.25	0.60
Area 2 total	0.09	0.10
Area 3 total	0.08	0.12
Area 4 total	0.22	0.15
Area 5 total	0.36	0.04
Area 1 in-plot	0.22	0.45
Area 2 in-plot	0.08	0.05
Area 3 in-plot	0.04	0.03
Area 4 in-plot	0.16	0.06
Area 5 in-plot	0.08	0.04
Area 1 out-of-plot	0.03	0.14
Area 2 out-of-plot	0.01	0.04
Area 3 out-of-plot	0.04	0.09
Area 4 out-of-plot	0.06	0.09
Area 5 out-of-plot	0.28	<0.01
Total out-of-plot	0.42	0.37

Note: Locations of the five river areas are shown in Fig. 1.

occurred, we estimate that 2011 transformer abundance would have been 8.8 times higher than was estimated under the actual treatment program.

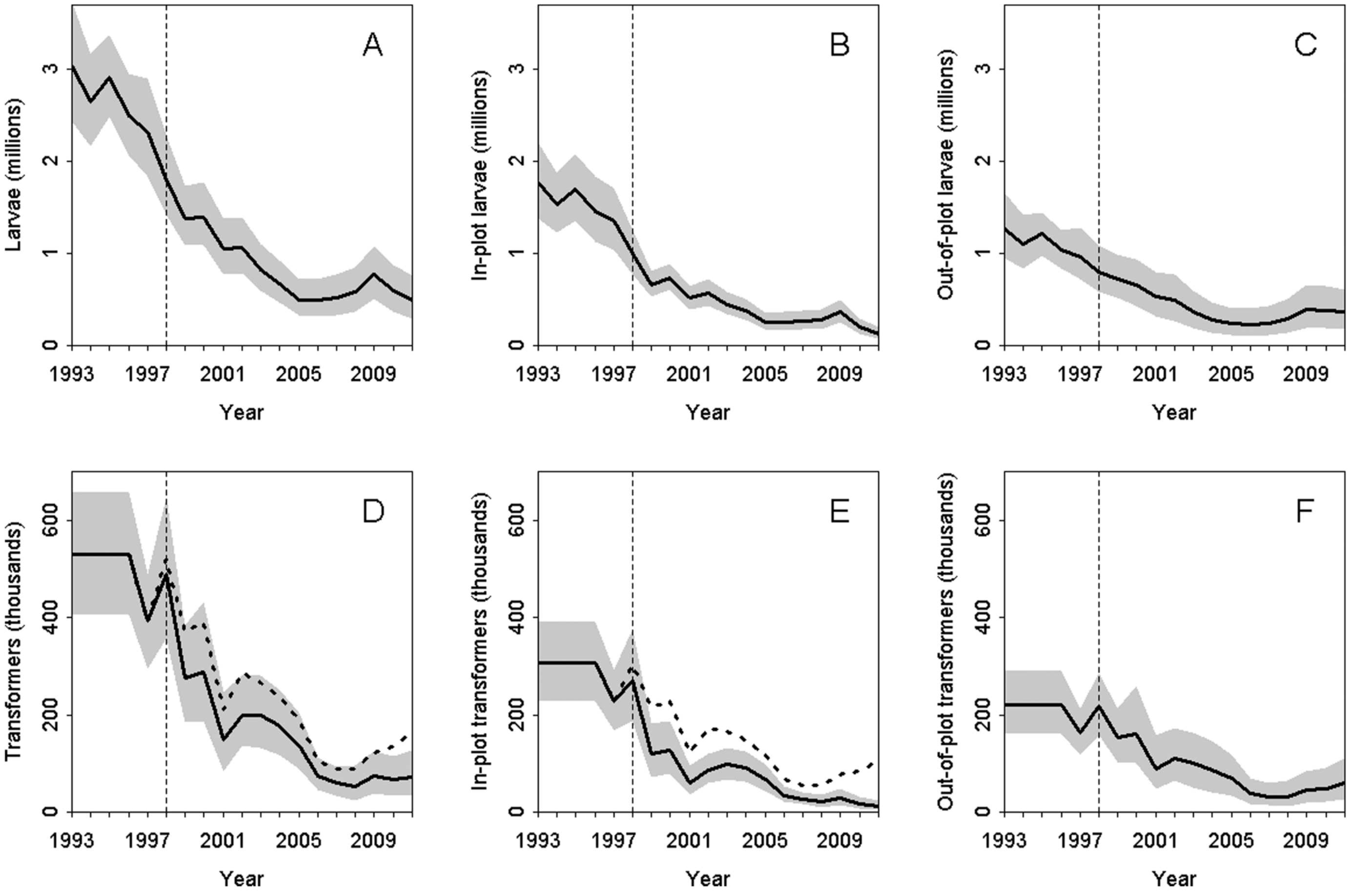
Projected larval density estimates in 2012 showed that only 10 of the 70 treatment plots had median estimates of larval density greater than 300 larvae·ha^{-1} and that all of these plots were within 10 km of the major spawning area at the rapids (Fig. 7). Pre-treatment deepwater electrofishing surveys on selected plots in 2010 and 2011 were used to validate the plot-specific projections of larval abundance for 2010 and 2011. Based on the validation comparisons, the 2010 projections of pre-treatment plot-level larval abundance tended to underestimate abundance compared with the sample-based estimates of abundance derived from the intensive electrofishing survey (Figs. 8A–8C; Table 6). This was especially true for older larvae in 2010. In 2011 the projected larval abundance estimates were very accurate, with the exception of two of the high abundance plots for which the projections overestimated the abundance of older larvae (Figs. 8D–8F; Table 6). The median error between the projected and observed total abundances in 2010 and 2011 was –7960 and 5800 larvae, respectively. Median error estimates were relatively small compared with the actual abundance estimates.

Some of the model parameters and predictions were sensitive to the inclusion of the data used for validation and changes in the assumed gear selectivity relationship (Table 4). Including the high sampling intensity pre-treatment data from 2010 and 2011 increased estimated natural and treatment mortality, but did not have a large effect on the estimates of α or β. Estimates of annual larval and transformer abundance early on in the time series were not affected. However, the larval and transformer abundance estimates in 2011 decreased. The proportion of larvae that were assigned to the in-plot area of the river was not sensitive to inclusion of the additional data. Increases in gear efficiency (i.e., Bergstedt and Genovese 1994 “selectivity”) increased the estimate of natural mortality and the α parameter of the Ricker function but had little effect on the estimate Bayluscide induced treatment mortality or the β parameter of the Ricker function. Sensitivity of annual estimates of larval and transformer abundance varied by year in both direction and magnitude. The estimated proportion of larvae that were assigned to the in-plot area of the river was not sensitive to a change in gear selectivity. We also tested the sensitivity of the model to a less restrictive prior on β by doubling the standard deviation of the beta prior (σ_β = 0.0001) and found that the model was not sensitive to this change.

Discussion

We documented substantial declines in abundance of larval sea lampreys and transformers that can be attributed to reductions in recruitment through time and the effects of the Bayluscide treatment program. We were able to specifically account for the acute effects of Bayluscide application on the population and estimate the overall effect of the larval control program in the river. A substantial effect of the Bayluscide treatment program on the transformer abundance in the River was evident. For example, in 2011 we estimated that the in-plot transformer abundance would have been 8.8 times greater if no treatment program had ever been implemented in the St. Marys River. Predicting the transformer abundance in the absence of a treatment program gives a minimum estimate of its impact. It is possible that the treatment program has other indirect effects on larval and transformer

Fig. 6. Model estimates of total river larval sea lamprey abundance (A), in-plot larval abundance (B), out-of-plot larval abundance (C), total river transformer abundance (D), in-plot transformer abundance (E), and out-of-plot transformer abundance (F) over time. All estimates are for the post-treatment period of each year. Larval abundance is in millions, and transformer abundance is in thousands. Solid black lines represent median model estimates, and grey shading represents the 90% credible intervals. Vertical dashed lines denote the onset of treatment efforts in 1998, and the dotted lines in panels D and E represent the median model estimates of the number of transformers that would have been produced if no Bayluscide treatments had ever occurred in the St. Marys River. The dotted lines are presented without credible intervals for the purposes of figure clarity.



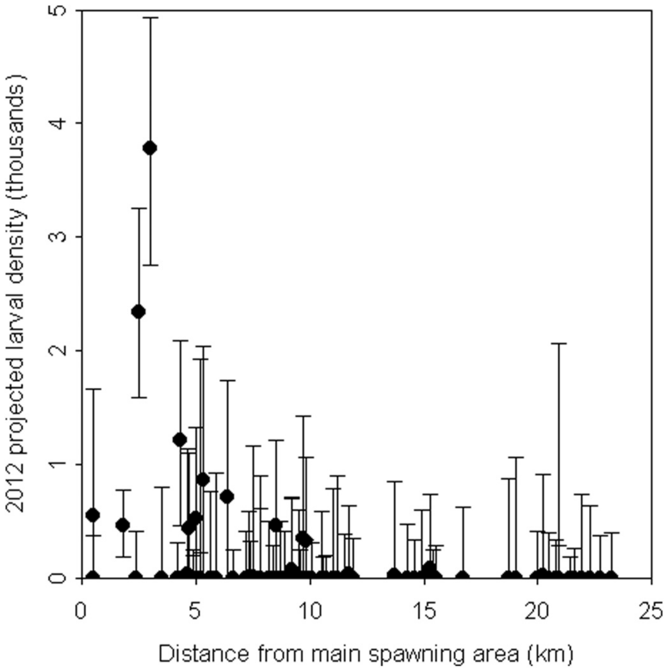
abundance through a reduction in the parasitic life stage in Lake Huron leading to reduced spawner biomass, although it was not explicitly accounted for in the model. Because sea lampreys do not exhibit natal homing behavior (Bergstedt and Twohey 2007; Waldman et al. 2008), decreases in the abundance of transformers from an individual river could have a much reduced impact on the number of returning adults and therefore future larval and transformer abundance from that river.

Understanding the dynamics and spatial structure of populations is an important component of successful management (Pascoe et al. 2009; Struve et al. 2010). To date there have been no efforts to quantitatively describe the spatial dynamics of either invasive or native larval lamprey populations. This work takes a data-driven modeling approach using a unique long-term data set for the St. Marys River to describe the dynamics of a lamprey population at a fine spatial scale while providing information to guide the management of invasive sea lampreys in the Great Lakes. This type of spatially specific assessment can improve our understanding of how invasive and native lamprey populations function and how approaches to control, conserve, or restore lamprey species might be changed to make them more effective.

The availability of the out-of-plot abundance data allowed us to examine the effects on the population that are not a direct result of Bayluscide applications. The time series of predicted out-of-plot transformer abundance highlights the potential importance of areas that are not currently treated (because of low larval density) to the total river transformer production and the parasitic population as a whole. The observed reductions in transformer and larval abundance in the St. Marys River are likely driven by a number of effects not directly related to the Bayluscide treatment program. These other effects could include a general decline in recruitment due to density-independent factors unrelated to chemical control, the consequence of the sterile male release program, trapping-derived reductions in spawner numbers, or even an intergenerational effect of the Bayluscide-derived reductions on returning adults.

Our model differed from previous approaches in that it explicitly incorporated the spatial structure of the population and the effects of management actions. Haeseker et al. (2003) developed an age-structured model for the St. Marys River with the goal of describing a stock–recruitment relationship and the uncertainty surrounding that relationship. The data used by Haeseker et al. (2003) were not the same as the data used in our study. Spatial structure was not explicitly incorporated, and the data used were collected before Bayluscide treatments began. As such, the Haeseker et al. (2003) model could not inform the larval sea lamprey control program at the scale of an individual Bayluscide treatment or describe spatiotemporal changes in abundance. Additionally, their model linked the larval population to an index of parasite abundance for Lake Huron. We chose not to link the

Fig. 7. Projected median 2012 larval density (larvae·ha^{-1}) estimates for each of the 70 treatment plots, ordered by their distance from the main spawning area at the rapids. Error bars represent 90% credible intervals. All estimates are greater than zero, and error bars do not extend into the negative range.



dynamics of the larvae to the population of parasites in Lake Huron to avoid assuming the proportion of Lake Huron parasites that originated in the St. Marys River. Instead, we focused on developing a model that could describe the long-term spatial dynamics of the in-river larval sea lamprey population to directly inform the Bayluscide portion of the control program, which costs twice as much as the combined adult trapping and sterile male release programs in some years (Haeseker et al. 2007). The Haeseker et al. (2003) model was also a fully age-structured model in that ages were assigned to all captured individuals based on length. Lamprey larvae are very difficult to age accurately using statoliths and exhibit high variability in length-at-age (Beamish and Medland 1988; Dawson et al. 2009). One of the strengths of our approach is that assigning length-based ages to sea lamprey larvae older than age 1 is not required. Our model is similar to other approaches such as catch–survey-type models (Collie and Sissenwine 1983), delay difference models (Deriso 1980; Schnute 1985), and some age-structured production models (e.g., Fenske et al 2011) in that it includes age-based dynamics, but fits the model to aggregated data (i.e., two age categories). However, the aggregation of age classes undoubtedly causes increased uncertainty in the estimates than would occur if data were available to implement a fully age-structured approach.

Our estimate of natural mortality was substantially lower than previously reported estimates (Haeseker et al. 2003; Fodale et al. 2003). Our estimate of instantaneous natural mortality for sea lamprey larvae from ages 1 to 6 (0.09 year^{-1}) is on the low end of reported mortality rates for fish stocks in general (Pauly 1980). Haeseker et al. (2003) estimated the natural mortality rate of the same St. Marys River larval sea lamprey population at 0.87 from age 0 to age 6. In our model the age 0 larval mortality is implicit within the stock–recruitment function, while Haeseker et al. (2003) included age 0 mortality in their estimate of natural mortality. During their first year of life, sea lamprey larvae are drifting downstream from the spawning area and locating suitable settlement habitat. It is likely that mortality during this life stage is substantially higher compared with mortality once the larvae have located suitable habitat and burrowed into the sediment. The difference between the α estimate with recruitment at age 0 included from Haeseker et al. (2003, $\alpha_{\text{age 0}}$ = 9410 larvae·spawner^{-1}) and our estimate with recruitment at age 1 ($\alpha_{\text{age 1}}$ = 268 larvae·spawner^{-1}) indicates an instantaneous natural mortality rate for age 0 larvae of about 3.56 year^{-1} (97%·year^{-1}). Therefore, Haeseker's estimates of higher (constant) mortality for age 0 through 6 larvae could be consistent with our much lower estimate because we do not include the apparently very high age 0 mortality in our larval mortality estimate.

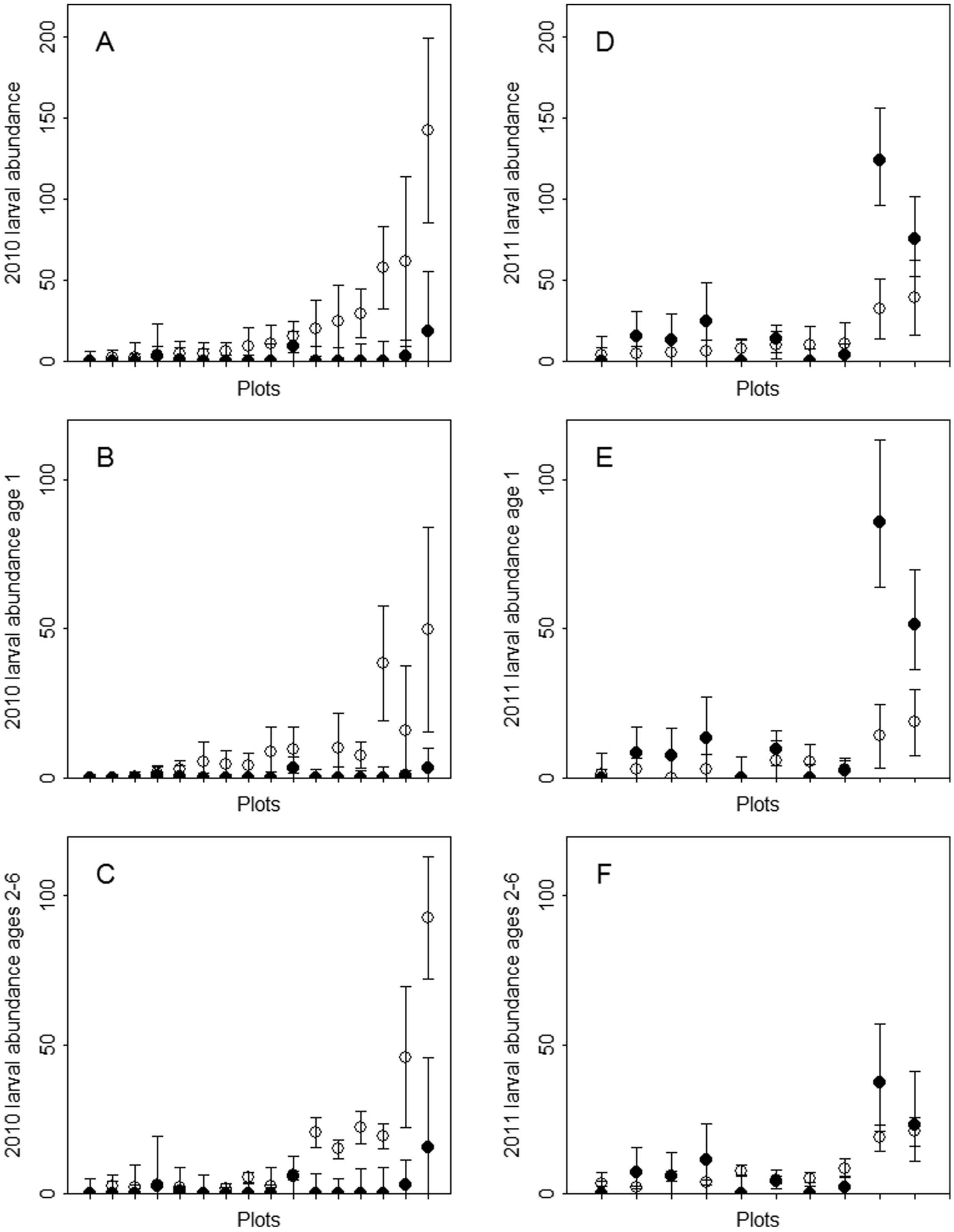
Table 6. Median error, median percent error, and median absolute error for the comparisons of pre-treatment model projected plot-level larval abundance and observed larval abundance in 2010 and 2011.

	Median error	Median percent error	Median absolute error
2010 all ages	−7960	100	7960
2010 age 1	−4940	38	4940
2010 ages 2–6	−2580	54	2580
2011 all ages	5800	100	9110
2011 age 1	4630	68	5360
2011 ages 2–6	−142	57	5130

Our estimate of Bayluscide-induced treatment mortality (0.51·treatment^{-1}) was also lower than the previous estimate (0.88·treatment^{-1}), which was estimated based on a single large-scale treatment event in 1999 (Fodale et al. 2003). Our estimate of Bayluscide-induced treatment mortality is likely more indicative of the effectiveness of individual treatment events over the entire range of the treatment program (1998–2011). Treating many adjoining plots over a short time frame may lead to synergistic effects of treatment resulting in higher overall treatment mortality. Evidence of such an effect may be implied by the higher estimate of treatment mortality by Fodale et al. (2003) during a large-scale treatment event (1999) and the higher estimate (0.59·treatment^{-1}) from our sensitivity analyses that included high-quality pre-treatment data for 2 years with large-scale treatments (2010 and 2011).

We observed an upstream shift in spatial recruitment patterns over time and a lack of larval recolonization of areas of previously high larval abundance (i.e., river area 5). Density-dependent larval settlement behavior coupled with chemical cues may play a role in these observed changes. Derosier et al. (2007) documented increased downstream movement of larval sea lampreys at high densities. In the early years of the time series, high larval densities were documented in the upstream portions of the St. Marys River. These high densities may have induced some larvae to seek suitable habitats farther downstream. In more recent years larval densities have been greatly reduced, potentially removing the pressure for larvae to seek out habitat far from the spawning site. Many benthic species also use chemical cues from conspecifics to govern larval settlement behavior (Rodriguez et al. 1993). Pheromones produced by lamprey larvae drive the selection of rivers for spawning by adults (Sorensen and Vrieze 2003; Wagner et al. 2009), and it is possible that larval settlement behavior is also affected by chemical cues of conspecifics. The potential chemical attraction coupled with lower larval densities in recent years may explain why larval recruitment has been concentrated in areas closest to the major spawning site. Further, this may explain why larvae have not recolonized the more downstream portions of the river even though these areas are no longer treated regularly with Bayluscide. These insights into density-dependent habitat use and colonization can help inform both control and conservation strategies for lamprey species. For example, it suggests that overall population declines could be masked if surveys are concentrated in higher density areas or in areas close to spawning habitats.

Fig. 8. Model projected median pre-treatment plot-specific larval abundance estimates in thousands (solid circles) and estimates of mean larval abundance from the intensive sampling effort in thousands (open circles) for 2010 all ages (A), 2010 age 1 (B), 2010 ages 2–6 (C), 2011 all ages (D), 2011 age 1 (E), and 2011 ages 2–6 (F). Error bars represent the 90% credible intervals for the model estimates and *t*-based 90% confidence intervals for the sampling-based estimates. Only plots in which pre-treatment samples were collected in 2010 or 2011 are shown, and the plots sampled are not consistent between years.



Model validation indicated that this model was able to successfully project plot-level larval abundance in many instances, although the results were not consistent among plots and years. In 2010, the model tended to underestimate larval abundance, especially for older larvae, while in 2011 the model performed well for most of the plot-level comparisons. For the purposes of making treatment decisions, making accurate projections of relative larval abundance is more important than getting the absolute estimate of abundance correct. In both 2010 and 2011, model projections were able to identify the plots with the highest larval abundance.

By using long-term data to inform spatial recruitment patterns and larval abundance estimates, our model can predict and project plot-specific abundances even given a paucity of data in some plots or years. We identified a substantial out-of-plot larval population that was previously thought to be unimportant to total river larval and transformer abundance. In light of this, options for controlling specific portions of the larval population located in out-of-plot areas should be explored. Given the sensitivity of aspects of this model to changes in length-based gear efficiency, we also recommend further research to establish and better characterize the uncertainty surrounding the gear selectivity relationship for the St. Marys River and other systems where deepwater electrofishing gear is used. Transformation rates are also important for model estimates and treatment program outcomes; different assumptions about transformation rates at age could alter our results. The high estimated productivity, low natural mortality of older larvae, and highly variable recruitment, coupled with the lower than expected estimate of Bayluscide-induced treatment mortality, highlights the challenges associated with controlling invasive sea lampreys, especially in large rivers and lentic areas.

Sea lamprey larvae are currently being assessed using the deepwater electrofishing approach in other Great Lakes tributaries (e.g., the St. Clair River), and native lamprey populations are being assessed using this technique in the Columbia River Basin in the northwestern US (Jolley et al. 2010, 2011, 2012). Little is known about the population dynamics and abundance of sea lamprey larvae in larger rivers in their native range, and there are no spatial population models available to describe the dynamics of native or introduced lamprey populations. Lamprey species are threatened or endangered throughout the Northern Hemisphere (Renaud 1997). In Europe, sea lampreys along with several other lamprey species are considered threatened, endangered, or extinct in the rivers they formerly occupied (OSPAR Commission 2009; Mateus et al. 2012). Pacific lamprey (*Lampetra tridentata*) populations on the west coast of North America are also threatened (Close et al. 2002). The nature of the catch data for this species and system allowed the development of a population model and abundance estimation using no fishery-specific data. The ability to project spatially specific larval density and abundance makes this model directly applicable to the annual decision-making process surrounding the application of Bayluscide in the St. Marys River and in other systems with invasive sea lampreys. The results of this work also yield valuable insights into the population dynamics of a family of organisms that are threatened globally and for which very little information on population dynamics exists.

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