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Comparing methods for estimating larval sea lamprey (*Petromyzon marinus*) density in the St. Marys River for the purposes of control

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ABSTRACT

The St. Marys River is a major producer of parasitic sea lampreys (*Petromyzon marinus*) to Lake Huron making it an important area for larval control. Bayluscide treatments are conducted in areas of high larval density requiring density estimation at fine spatial scales to inform treatment decisions. We evaluated six methods of estimating spatially specific density including the currently used sampling-based estimates, a generalized linear model (GLM) based on mean larval density per plot, a GLM based on larval density per sample, a generalized additive model based on mean larval density per plot, a spatial age-structured population model, and a hybrid approach, which averaged the best performing sampling- and model-based methods. Methods were evaluated based on accuracy in matching independent validation data. Specifically, the methods were evaluated based on their ability to project plot-level larval density, identify high density plots for treatment, and rank plots in order based on density resulting in high numbers of sea lampreys killed per hectare treated. Performance was variable, and no single method outperformed the others for all metrics. Although the sampling-based estimation method and the GLM based on catch data performed adequately for estimating density and identifying high density plots, the hybrid approach was identified as the best method to inform sea lamprey control decisions in the St. Marys River due to its consistent performance. Incorporating model-based approaches should lead to a more efficient and effective treatment program in the St. Marys River and aid in making decisions about the allocation of control resources.

Introduction

Sea lamprey (*Petromyzon marinus*) invaded the upper Laurentian Great Lakes (Lakes Superior, Huron, and Michigan) in the early 20th century resulting in long term ecological changes and economic impacts (Christie and Goddard, 2003; Lupi et al., 2003; Smith, 1971). Many fisheries in the Great Lakes collapsed in the 1950s and 60s due to a combination of sea lamprey predation and overfishing (Coble et al., 1990). Since that time sea lamprey control efforts have greatly reduced the numbers of parasitic sea lampreys in the Great Lakes making the rehabilitation of native piscivorous fish populations possible. The continued success of the sea lamprey control and native fish restoration programs relies on continued suppression of sea lamprey populations (Bronte et al., 2003; Dobiesz et al., 2005; Madenjian et al., 2003).

A large portion of the sea lamprey control efforts in the Great Lakes focuses on the sedentary larval life stage. TFM (3-trifluoromethyl-4-nitrophenol) is successfully used to control the larval stage through treatments in streams and rivers. However, TFM application is not feasible in connecting channels and lentic areas (e.g., the St. Marys River), so spot treatments are carried out in areas of high larval 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 density at relatively fine spatial scales to identify areas for Bayluscide application (Fodale et al., 2003). Treating areas with the highest larval density ensures greater potential treatment efficiency and effectiveness in terms of larvae killed per hectare treated. Accurately estimating larval abundance can also be important because decisions about the allocation of treatment resources among streams depend on how many total sea lamprey larvae are expected to be killed by a treatment event using either TFM or Bayluscide (Slade et al., 2003).

The St. Marys River is one of the major producers of parasitic sea lampreys in Lake Huron and northern Lake Michigan making it an important area for sea lamprey assessment and control (Fodale et al., 2003; Schleen et al., 2003). Starting in 1998, targeted Bayluscide applications have

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been performed to control the larval life stage in the St. Marys River (Fodale et al., 2003). Although large scale Bayluscide applications have occurred in 1999, 2010, and 2011, only a small fraction of the suitable larval sea lamprey habitat is treated in most years (Robinson et al., 2013). These targeted treatments occur in areas thought to have high densities of larvae greater than 100 mm, which are likely to metamorphose into parasitic juveniles. Decisions about which plots to treat are based on spatially specific density estimates of larvae greater than 100 mm from deepwater electrofishing surveys that occur following Bayluscide treatment in the previous year and on expert judgment. For example, if the sea lamprey control agents think a plot has a high density of sea lamprey larvae greater than 100 mm based on previous experience, but the deepwater electrofishing survey fails to identify that plot as high density, the plot could still be treated. The overall approach is limited by sample size, the subjectivity of expert judgment, and the small number of larvae greater than 100 mm observed in any given year. Out of the 541 deepwater electrofishing sampling events on the St. Marys River in 2011, only 6 sea lamprey larvae greater than 100 mm were captured. In many cases, the correction for length-specific capture efficiency of the deepwater electrofishing gear, which decreases as larval sea lamprey length increases (Bergstedt and Genovese, 1994), causes plots to be treated based on the observation of only one larva greater than 100 mm. A model based approach that quantitatively incorporates the entire 19 year time series of data, instead of just the most recent year's data, may provide an alternative to the current method of selecting plots for treatment and has the added benefits of being testable, transparent, and repeatable. The objective of this work was to identify a statistical method, or methods that would lead to better estimation of spatially specific density and abundance, resulting in an increase in the potential effectiveness and efficiency of the Bayluscide-based treatment program for larval sea lampreys in the in the St. Marys River.

Methods

We evaluated six methods of estimating spatially specific density based on each method's ability to (1) accurately project plot-level density, (2) identify high density plots for treatment, and (3) rank plots based on density in an order that most closely matched rankings based on independent validation data. The six density estimation methods included the currently used sampling-based estimates, two generalized linear models (GLMs), a generalized additive model (GAM), a spatial age-structured population model recently developed by Robinson et al. (2013) for the St. Marys River, and a hybrid approach, which used the mean density from the sampling-based estimation method and the best performing model-based method. Initially, a model-averaging approach was tried in which the results of all five methods were averaged (with equal weighting), but this approach performed poorly. The hybrid approach was then developed as a way to combine the results of the sample-based approach and the best model-based approach. These methods represent three levels of analytical complexity with the sampling-based estimates being easiest to implement, followed by the GLMs and GAM, and finally the population model. Performance of each estimation method was compared to independent estimates of spatially specific density and abundance, based on an intensive sampling effort (validation data).

Data

The upper St. Marys River contains 71 plots (830 ha. total), ranging in size from 1.2 to 27.5 ha, for the purpose of applying Bayluscide and conducting deepwater-electrofishing surveys for larval sea lampreys (Fig. 1). These plots were defined as areas of high larval density based on deepwater electrofishing surveys conducted during 1993–1996 (Fodale et al., 2003). A single treatment plot (Plot 10) was excluded from all analysis because no sea lampreys were ever observed there, reducing the number of treatment plots to 70. Plot-specific Bayluscide treatment histories were available from 1998 through 2011 encompassing the entire duration of treatment efforts in the St. Marys River.

A 19 year time series (1993–2011) of spatially referenced 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), and the total length of each captured larval sea lamprey was recorded. Adaptive sampling was also conducted in a number of years, but was not included in the analysis. Electrofishing data were classified as either pre-treatment or post-treatment, depending on the timing of sampling relative to annual treatment events. Pre-treatment surveys are those conducted just prior to the onset of treatment efforts in a given year and were conducted on a limited basis in 1999, 2001, and 2003. Post-treatment surveys are conducted annually following treatment efforts. Survey data were also available from the period prior to the onset of Bayluscide treatments (1993–1997).

With the exception of the population model, only post-treatment data and data collected prior to the onset of Bayluscide applications (1993–1997) were included in our analysis. Pre-treatment sampling was excluded because it was only available in 1999, 2001, and 2003. Post-treatment sampling was conducted in all years except 1997 and 1998, with the number of plots sampled annually ranging from 1 to 67 (total = 764 plots sampled over 19 years). The number of individual electrofishing samples taken when a treatment plot was sampled ranged from 1 to 76. Capture efficiency of the deepwater electrofishing gear is reduced as larval sea lamprey length increases (Bergstedt and Genovese, 1994), so a length-based gear selectivity correction was applied to all larval catch data:

$$C = \sum_i \left[1 + e^{(L_i * 0.0229 - 1.732)}\right], \tag{1}$$

where C is the adjusted catch for an individual electrofishing sample, and L is the length of a larva i in mm (U.S. Fish and Wildlife Service unpublished data).

Plot-specific larval density estimates (larvae ha^{-1}) were calculated for each year using the mean adjusted catch in a sample multiplied by the area sampled (2.44×10^{-4} ha). 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 using a power function based on the average relationship between sample size and standard error estimates:

$$\sigma_d = aN^c, \tag{2}$$

where N is the sample size for a given plot and a and c are estimated parameters ($a = 9080$, $c = -0.703$, $R^2 = 0.40$, $p < 0.001$) (Robinson, 2013; Robinson et al., 2013). Parameter a can be interpreted as the estimated standard error of a larval density estimate when $N = 1$. Power functions were used to estimate standard errors 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.

High intensity pre-treatment deepwater electrofishing surveys were conducted in 2010 and 2011 as a means to validate the ability of each estimation method to rank plots for treatment and project plot-specific larval abundance. 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, >4 samples per ha) than would occur under normal sampling conditions (0.66 samples per ha in 2011). Sampling areas were randomly selected within each plot. A similar sampling effort was undertaken in 2011, where 10 plots

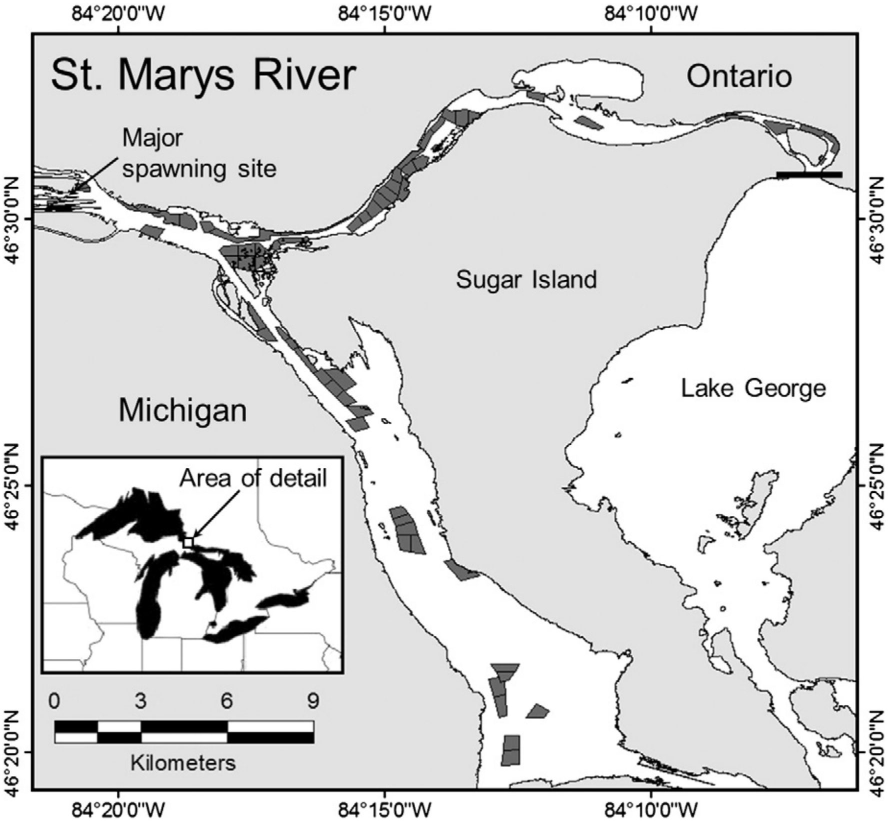

Fig. 1. The St. Marys River from the navigational locks in Sault Ste. Marie, Michigan and Ontario, to the southern end of Sugar Island. Coverage includes all plots that are assessed and considered for treatment. Dark gray areas are treatment plots and the white areas are considered out-of-plot (i.e., not treated). A portion of the out-of-plot areas that appear in the figure are never surveyed (Lake George) and a small area that is surveyed is not included in the figure (near the southern end of Sugar Island). 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.

were intensively sampled. These sampling efforts were designed to include a range of high, medium and low density plots across two years, and were separate from the annual sampling used to inform treatment decisions. The increased sampling intensity and closer temporal proximity to the timing of potential treatment events for the validation data provided density and abundance estimates with substantially greater precision (mean CV 54%) than those from the normal sampling intensity (mean CV 94%). Therefore, the density estimates from the high intensity sampling data were considered the best possible estimates (i.e., closest to the true density) and mean density per plot was used to assess the performance of each estimation method.

Estimation methods

Six estimation methods were tested for predicting plot level density and abundance (Fig. 2). The first method simply used the plot-specific density estimates from the previous year's electrofishing sampling. Next, two GLMs and one GAM were fit to the 1993–2009 and 1993–2010 data to produce 2010 and 2011 projections respectively. The spatial age-structured population model developed by Robinson et al. (2013) was also used to produce plot-specific projections of density and abundance in 2010 and 2011. Because none of the methods tested were the best at predicting larval abundance for both 2010 and 2011, we developed an additional hybrid approach for estimating plot-level density by averaging the two methods with the best performance in each year.

The GLMs and the GAM included plot as a categorical effect and years-since-treatment as a covariate. A number of other potential explanatory variables were initially considered in model development (e.g., depth, habitat, and date). However, effects of additional explanatory variables were not estimable due to the limitations of the available data and their redundancy with the categorical plot variable. The first GLM used the natural log transformed plot-level mean larval density estimates as the response variable, a Gaussian error structure and an identity link function,

$$\log\left(D_{p,y}+c\right)=\beta_0+\beta_1 P+\beta_2 T_{p,y}+\varepsilon_{p,y}, \tag{3}$$

where $D_{p,y}$ are the density estimates for each plot p and year y, c is a constant, P is a categorical plot variable, T is the number of years since last treatment for each plot and year, and the βs are estimated parameters. If a plot had never been treated, the years-since-treatment was set at 20 (length of the time series + 1). As with many other fisheries data, standard errors of density estimates increased proportionally with density, and thus the coefficient of variation was approximately constant (Punt et al., 2000). Therefore, a variance stabilizing log transformation was applied to the density estimates (Venables and Dichmont, 2004). A constant ($c = 24.7$), half of the lowest plot-level non-zero density estimate, was added to each density estimate to avoid taking the log of zero. Each observed plot-level density estimate was weighted based on the calculated variance of the natural logarithm of the plot specific density estimates, so estimates with greater precision and higher sample size would carry greater weight in the model. The variance of the natural logarithm of the plot specific density estimates, σ^2_{LN}, can be calculated as,

$$\sigma^2_{LN}=\log\left[\left(\frac{\sigma^2_N}{D_{p,y}+c}\right)^2+1\right], \tag{4}$$

where σ^2_N the variance of each density estimate. The second GLM used catch data at the scale of an individual electrofishing sample ($C_{p,y}$), a negative binomial error structure, and a log link function, and was performed using the glm.nb function in package MASS (Venables and Ripley, 2002) of the program R (R Development Core Team, 2012).

$$C_{p,y} = \log\left(\beta_0 + \beta_1 P + \beta_2 T_{p,y} + \varepsilon_{p,y}\right). \tag{5}$$

The negative binomial distribution is often used to describe catches of benthic organisms because it accommodates highly variable catches that include many zeros (Elliott, 1977) and avoids the need for data transformation or the addition of a constant (Maunder and Punt, 2004).

A GAM may be used in situations where a GLM would be appropriate and can incorporate possible nonlinear effects of continuous covariates such as years since treatment (Hastie and Tibshirani, 1990). The GAM was implemented with the log transformed mean plot-level larval density estimates as the response variable, a Gaussian error structure and identity link function,

$$\log\left(D_{p,y} + c\right) = \beta_0 + \beta_1 P + f_1 T_{p,y} + \varepsilon_{p,y}, \tag{6}$$

where the βs are estimated parameters and f_1 is an estimated non-parametric regression spline curve. The flexibility of the regression spline curve was optimized using an iterative method that rewards model fit and penalizes model complexity (Wood, 2004). As with the GLM based on density, the variance of the natural log of the plot specific density estimates σ_{LN}^2 as used to weight the plot-level density estimates in the model fitting. The GAM analysis was performed using the gam function in package mgcv (Wood, 2011) of the program R (R Development Core Team, 2012).

Robinson et al. (2013) developed and validated a spatial age-structured model (Fournier and Archibald, 1982) for sea lampreys and applied it to the sea lamprey population 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 abundance of larval and metamorphosing sea lampreys. Plot-specific larval abundance changed due to recruitment, natural mortality, Bayluscide treatment mortality, and age-specific larval metamorphosis rates. 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 fit to mean plot-specific abundance estimates from the entire 19-year deepwater electrofishing survey dataset. One year projections of plot-specific larval abundance were produced using the model equations and the resulting parameter estimates. The model was fit to the 1993–2009 and 1993–2010 data to produce 2010 and 2011 projections respectively. A more detailed description of the model can be found in Robinson et al. (2013).

The hybrid approach involved calculating the mean density from the sampling-based estimation method and the GLM based on catch data for each plot. Both estimation methods were given equal weight in the averaging process. The resulting plot-level density estimates were evaluated based on the same criteria and process as the other five estimation methods. Traditional model averaging approaches, such as those based on AIC, could not be applied because the models use data aggregated at different levels; and AIC-based model averaging requires that all models use the same data.

Comparisons

The six methods of estimating plot level density of larval sea lampreys were evaluated based on three criteria (Fig. 2): the ability to (1) accurately project plot-level density, (2) identify high density plots for treatment, and (3) rank plots based on density in an order that most closely matched the ranking for the validation data. The three criteria have subtle but important differences and were designed to measure outcomes for different objectives. Criterion 1 is a course, aggregated metric that could be used if estimating abundance across all plots was the primary objective. Criteria 2 and 3 deal with actually making treatment decisions when resources are limited and only a subset plots can be treated, which is often the case. For example, if a method has high accuracy in low-density plots, but not in the highest density plots, then criterion 1 could be misleading with respect to making treatment decisions. Therefore, criterion 2 measures a methods ability to identify the plots with the highest abundance. Likewise, criterion 3 is not automatically satisfied by satisfying criterion 1 when resources to treat all plots are not available, and some intermediate level of treatment effort is desired. Estimates, rankings, and relationships from each method were compared to those based on the intensive pre-treatment electrofishing surveys (validation data) from 2010 and 2011, which were assumed to represent the best possible estimates. Methods with estimates that were closer to those from the validation data were considered more accurate than those with greater discrepancy from the

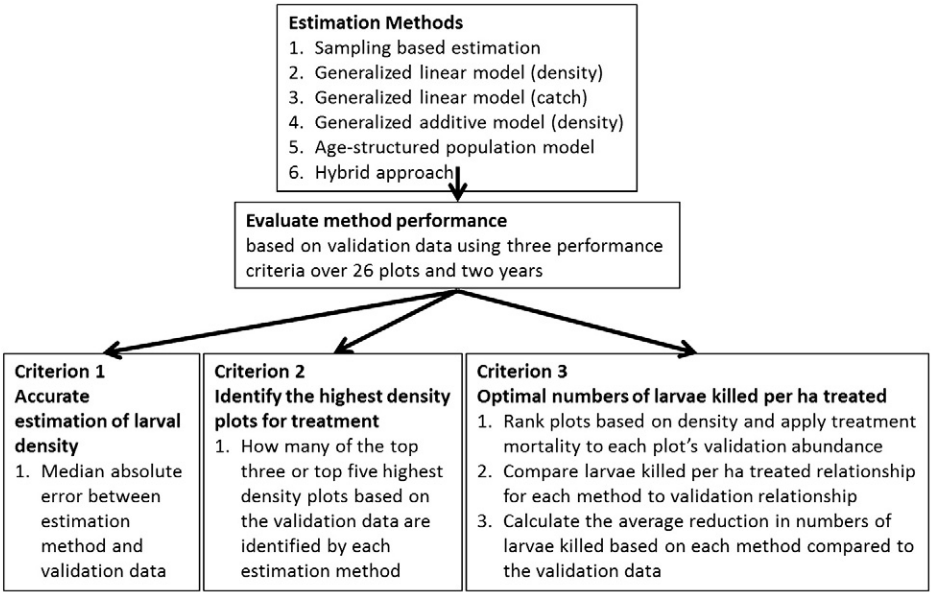

Fig. 2. Flow chart describing the estimation methods, performance criteria, and the steps and metrics associated with each criterion.

validation data. This allowed for 26 plot level comparisons for each method, spanning two years.

We used median absolute error between the estimates from the validation data and the six estimation methods for 2010 and 2011 to assess the ability of each method to accurately project estimates of plot-level larval density and abundance (criterion 1). The median errors and median absolute errors were calculated as follows,

$$\text{median absolute error} = \text{median}\left|D_p - V_p\right|, \quad (7)$$

where D_p are the plot level density estimates from one of the six estimation methods from a specific year and V_p are the density estimates based on the validation sampling.

The ability of each estimation method to identify the highest density plots (criterion 2) was assessed by comparing how many of the top three or top five highest density plots in the validation data set were also identified by each estimation method. This approach simulates a three and a five plot treatment event.

The expected numbers of larvae killed per hectare treated was compared to the number expected to be killed based on the validation data for each method (criterion 3). First the plots were ranked in descending order based on the estimates of larval density. Then a Bayluscide treatment was simulated by applying the estimated percent mortality from an individual treatment event (51%, Robinson et al., 2013) to the validation estimate of larval abundance for each plot, with treatments being applied to the plots with the highest projected density first for each estimation method. Larvae killed per hectare treated relationships were developed for each estimation method and the validation data for 2010 and 2011. Estimation methods whose larvae killed per hectare treated relationship was closest to the validation relationship were considered better at rankings plots for treatment. The area between the larvae killed per ha treated relationship based on the validation data and the relationship for each estimation method was calculated to characterize the overall similarity between each estimation method and the validation data. This area also represents the potential loss in treatment effectiveness based on each estimation method relative to the validation data. Average reduction in larvae killed per ha treated was calculated for each estimation method by dividing the area between the validation curve and the curve for each estimation method by the total area of all plots.

Results

Estimates of plot-level density (larvae $\cdot$ ha^{-1}) produced using the validation data ranged from 0 to 18,700 in 2010, and from 523 to 4730 in 2011. Plot-level abundance estimates ranged from 0 to 142,000 in 2010, and from 4510 to 39,400 in 2011. Density estimates produced using the validation data had moderate precision (mean CV 54%) but represented a substantial improvement in precision relative to density estimates produced based on the data from the annual electrofishing survey (mean CV 94%).

The GLMs and GAM fit the data reasonably well although they did not explain a large percentage of the deviance (Table 1). Years since treatment (YST) effects were significant for each model with the density of larvae increasing as the number of years since treatment increased. Back-transformed YST effects for the GLM based on density data and the GLM based on catch data were 1.17 and 1.10 respectively (Table 1). This indicates a 17% increase in density or abundance for each year a plot goes untreated based on the density data and a 10% increase based on the catch data. The population model also fit reasonably well (Robinson, 2013; Robinson et al., 2013).

The method that produced the most accurate estimates of larval sea lamprey density varied by year. The GLM based on catch data performed the best over most performance metrics for 2010 and 2011 and was therefore used, along with the sample-based approach, to develop the hybrid approach. In 2010 the hybrid approach produced density estimates with the highest accuracy (median absolute error = 697 larvae per ha) followed by the GLM based on catch (median absolute error = 857 larvae per ha; Table 2, Fig. 3A). The other four estimation methods had larger median absolute errors (>1300 larvae per ha). In 2011 the GLM and GAM based on density produced the most accurate estimates of larval density (median absolute errors: GLM density = 681, GAM density = 605) while the other four methods produced density estimates with larger median absolute errors ranging from 1320 to 1620 larvae per ha in (Table 2, Fig. 3B).

The ability of each estimation method to identify plots with the highest density varied between 2010 and 2011 (Table 3). The sampling data identified the three plots with the highest larval density correctly, followed by the GAM, the population model, and the hybrid approach, all of which identified two of the top three plots based on density in 2010. The GLM based on density identified four of the top five plots while the other five methods all identified three of the top five plots in 2010. The sampling data, the GLM based on catch data, and the hybrid approach, all identified two of the top three plots while the other three methods only identified one of the top three based on density in 2011. The GLM based on catch data and the hybrid approach identified four of the top five plots while the other four methods identified three or fewer in 2011.

In 2010 the plot-level density rankings based on the sampling data resulted in a larva killed per ha treated relationship that was the same as the validation data for very high density plots (Fig. 4A) and the hybrid approach was very similar to the relationship based on the sampling data. The GLMs based on density and catch data performed similarly, producing a relationship that was close to the validation relationship for high and medium density plots while the GAM and the population model deviated from the validation relationship for all but the highest density plots in 2010. The sampling-based method resulted in the smallest reduction difference in the average number of larvae killed per ha (7500 larvae per ha) relative to the validation data, followed by the hybrid approach (8620 larvae per ha) in 2010 (Table 2). The reduction in the number of larvae killed based on the other four methods ranged from 14,200 to 22,000 larvae per ha. In 2011 the hybrid approach represented an improvement upon the other methods, being very close to the validation relationship (Fig. 4B). The GLM based on catch data also performed well, producing a larva killed per ha treated relationship that was close to the validation relationship for high, medium and low density plots. The other four methods performed similarly

Table 1
Percent deviance explained, parameter estimates, standard errors, test statistics, and *P* values associated with the generalized linear models (GLM) and generalized additive models (GAM). The YST smoothed term is the regression spline fit of the years since treatment (YST) effect of the GAM and the test statistic for that term is an *F* value not a *z* value. The 70 categorical plot effects associated with each model are not reported.

Model type	Dependent variable	Deviance explained	Parameter	Estimate	Std. err	*z* Value	$P(>\|z\|)$
GLM	Log(density + *c*)	35.60%	Intercept	5.059	0.550	9.19	<0.001
			YST	0.158	0.013	12.59	<0.001
GLM	Catch	22.40%	Intercept	0.305	0.765	0.40	0.690
			YST	0.100	0.006	17.44	<0.001
GAM	Log(density + *c*)	37.50%	Intercept	5.961	0.545	10.94	<0.001
			YST (smooth)			35.23	<0.001

Table 2
Median absolute error of density estimates and reduction in the average number of larvae killed per ha in 2010 and 2011. Median absolute error is the median of the absolute value of the difference between the density estimates based on each estimation method and those based on the validation data. Reduction in larval kill per ha is the reduction in larvae killed based on each density estimation method compared to the validation data. Density estimation methods include previous year's sample-based estimates (Sampling), the generalized linear model based on density data (GLM density), the generalized linear model based on catch data (GLM catch), the generalized additive model based on density data (GAM density), the spatial age-structured population model (Population model), and the average of the density estimates produced using the sampling data and the GLM based on catch data (Hybrid approach).

	Median abs. error		Kill reduction per ha	
Method	2010	2011	2010	2011
Sampling data	1460	1610	7500	6390
GLM density	1300	681	15,700	8240
GLM catch	857	1620	14,200	3630
GAM density	1300	605	22,000	8370
Population model	1380	1150	14400	9150
Hybrid approach	697	1320	8620	1780

to each other, producing a larva killed per ha treated relationship that was close to the validation data for only the high density plots in 2011. The hybrid approach resulted in the smallest reduction in average number of larvae killed per ha (1780 larvae per ha), followed by the GLM based on catch data (3630 larvae per ha) in 2011. The reduction in the number of larvae killed based on the other four methods ranged from 6390 to 9150 larvae per ha.

Discussion

Our results suggest that model-based methods could be used to replace expert judgment in the process to select plots for sea lamprey control in the St. Marys River. Alternative model-based approaches have been developed to inform sea lamprey control decisions in the St. Marys River (Haeseker et al., 2003, 2007) and for other streams (Christie et al., 2003; Hansen and Jones, 2008a). However, the previous model-based approaches specific to the St. Marys River did not provide spatially specific larval density estimates necessary to drive annual treatment decisions and did not make use of the long time series of available deepwater electrofishing data (Haeseker et al., 2003, 2007). Currently, treatment decisions in the St. Marys River are driven by the previous year's deepwater electrofishing survey combined with expert judgment. This approach is limited by sample size, the subjectivity of expert judgment, and the small number of larvae greater than 100 mm observed in any given year. The GLM based on catch data for spatially specific density estimation can use the available long-term data set, as well as the most recent data, to inform treatment decisions for sea lamprey control and replace expert judgment. A hybrid approach that averages both the sampling data in the most recent year with a GLM based on catch data performed well in our study and combines the benefits of using the whole time series to inform control decisions while also relying on the most recent year's data. It is important to note that none of the model-based approaches we considered incorporates the potential for temporal changes in larval sea lamprey habitat.

For model comparison purposes, the validation data represent the best data available for estimating larval density and abundance because of the increased sampling intensity and closer temporal proximity to the timing of potential treatment events. However, the validation data produced density estimates with only moderate precision given the high sample size (mean CV of density = 54%). This is likely a consequence of highly aggregated spatial distributions of larval sea lampreys even at the scale of a treatment plot (Schleen et al., 2003) and of correcting for the selectivity of the deepwater electrofishing gear (Bergstedt and

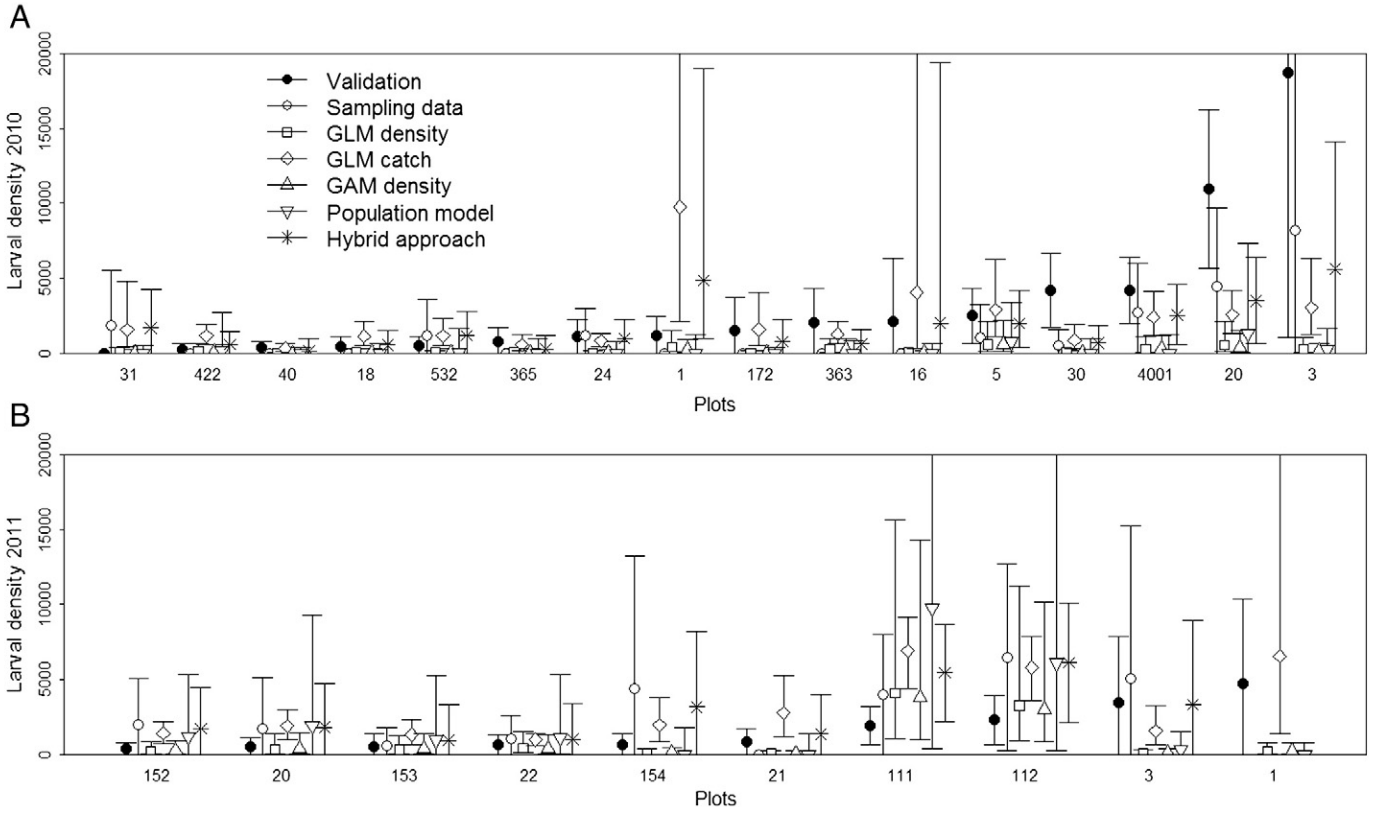

Fig. 3. Plot-level larval density projections for 2010 (A) and 2011 (B) based on pre-treatment validation data, sampling-based estimates from the previous year, a generalized linear model based on density data (GLM density), a generalized linear model based on catch data (GLM catch), a generalized additive model based on density data (GAM density), a population model, and the hybrid approach. The hybrid approach is produced by averaging the density estimates from the sampling data and the GLM based on catch data. Error bars represent two standard errors with the exception of the population model where they represent 90% credible intervals. Sample based estimates of zero have no error bars. Numbers listed on x axis are plot identification numbers and are listed from the lowest to the highest based on validation density estimates.

Table 3

Plots listed in descending order based on estimated density for each method in 2010 and 2011, and compared with the priority order based on the validation rank. Numbers listed are plot identification numbers. Density estimation methods include previous year's sample-based estimates (Sampling), the generalized linear model based on density data (GLM density), the generalized linear model based on catch data (GLM catch), the generalized additive model based on density data (GAM density), the spatial age-structured population model (Population model), and the average of the density estimates produced using the sampling data and the GLM based on catch data (Hybrid approach). A single asterisk indicates a sample based estimate of zero larvae. When this occurred, plots were ranked in numerical order. A double asterisk indicated no sampling occurred. The top five highest density plots based on the validation data are in bold text, and the top three are in bold italics.

Year	Rank	Validation	Sampling data	GLM density	GLM catch	GAM density	Population model	Hybrid approach
2010	1	***3***	***3***	**5**	1	**5**	***20***	***3***
	2	***20***	***20***	***20***	16	***20***	**5**	1
	3	***4001***	***4001***	1	***3***	***4001***	***3***	***20***
	4	**30**	31	***3***	**5**	363	422	***4001***
	5	**5**	532	***4001***	***20***	1	532	16
	6	16	24	363	***4001***	***3***	363	**5**
	7	363	**5**	422	172	422	1	31
	8	172	**30**	31	31	532	**30**	634
	9	1	1*	18	363	18	24	24
	10	24	16*	16	422	31	365	172
	11	365	18*	365	532	365	***4001***	**30**
	12	532	40*	**30**	18	24	18	363
	13	18	172*	532	**30**	**30**	16	422
	14	40	363*	172	24	16	31	18
	15	422	365*	24	365	172	172	365
	16	31	422*	40	40	40	40	40
2011	1	***1***	***112***	**111**	**111**	**111**	**111**	***1***
	2	***3***	***3***	***112***	***1***	***112***	***112***	***112***
	3	***112***	154	22	***112***	20	20	**111**
	4	**111**	111	20	**21**	22	152	***3***
	5	**21**	152	153	154	153	22	154
	6	154	20	152	20	152	153	20
	7	22	22	***1***	***3***	***1***	***3***	162
	8	153	153	154	152	154	154	**21**
	9	20	**21***	***3***	153	***3***	**21**	22
	10	152	***1*****	**21**	22	**21**	***1***	153

Genovese, 1994). However, density estimates from the validation data had substantially improved precision compared to those produced using the annual electrofishing survey in recent years (mean CV of density = 94%). Recent simulation results by Robinson (2013) also indicated that increased sampling intensity associated with the validation data yield more precise density estimates and a better ability to properly identify plots for treatment based on density. However, the moderate precision of the density estimates produced using the validation data adds additional uncertainty about the performance of the estimation methods because our analyses treated the validation data as known with no uncertainty.

Sampling-based estimates under the current level of sampling intensity appear adequate to inform treatment decisions within the St. Marys River. However, in some years not all plots are sampled, and occasionally no sampling is conducted (Robinson, 2013). If some or all plots are not sampled, a model-based method must be used to inform treatment efforts the following year. In most situations the GLM based on catch data performed well. The consistent performance of this estimation method across years and criteria makes it a good choice to fill in gaps in the sampling data, replace the sample based estimates entirely if sampling is not conducted, or to use in conjunction with the sampling-based estimates by averaging the results of the two (i.e., the hybrid approach). The GLM based on catch data has the added benefit of being the simplest of the model-based methods to implement because it uses data at the level of an individual sample and requires no weighting in the model fitting process.

Even given the adequate performance of the sampling-based estimates, there are several potential issues associated with using the sampling-based estimates from the previous year alone to inform treatment decisions. At the current sampling intensity many of the plots have density and abundance estimates of zero. This occurred in eight of the 16 plots in 2010 and in one of the ten plots in 2011 for which validation data were collected. In the absence of model-based approaches there is no way of ranking those plots for treatment other than to use additional information such as density estimates from a year earlier. Sometimes even high density plots are not sampled for a variety of reasons. For example, in 2011 plot one (one of the smallest plots in the river) was not sampled but was identified as a high density plot based on our validation data and the GLM based on catch data. The probability of catching no sea lampreys in a high density plot can be substantial for small plots, because the number of samples taken in each plot is based on plot area, with some plots having only one sample in a given year. Limited sampling of small plots leads to a risk of small high density plots going untreated, resulting in a missed opportunity to kill a relatively large number of sea lampreys with a small-scale treatment.

The method that performs best also depends on the level of treatment that occurs in each year (Robinson, 2013). During some years there are limited resources available for treatment and only the highest density plots can be treated, while in other years all plots are treated. If only high density plots are to be treated, sample-based estimates are likely adequate to inform treatment. However, if resources are available to treat medium and low density plots, incorporating the GLM based on catch data as part of the hybrid approach will likely be beneficial. The opportunity cost associated with sampling and modeling efforts must also be taken in account because money spent on sampling and modeling cannot be spent on treatment (Fenichel and Hansen, 2010; Hansen and Jones, 2008b).

Two major differences in the approach presented here and the approach currently used to select plots for treatment are 1) we considered the density of all larvae in a plot while the current approach considers only larvae greater than 100 mm, and 2) we do not include expert judgment as part of our analysis. The 100 mm treatment strategy is predicated upon the assumption that a treatment will kill a large majority of individuals just prior to transformation. The effectiveness of plot-level Bayluscide applications may be less than previously thought; 51% mortality per treatment (Robinson et al., 2013), compared to 88% effective (Fodale et al., 2003). Strategies that consider the entire larval length structure when selecting plots for treatment may be beneficial given the uncertainty surrounding Bayluscide based treatment effectiveness and the infrequency with which larvae greater than 100 mm are

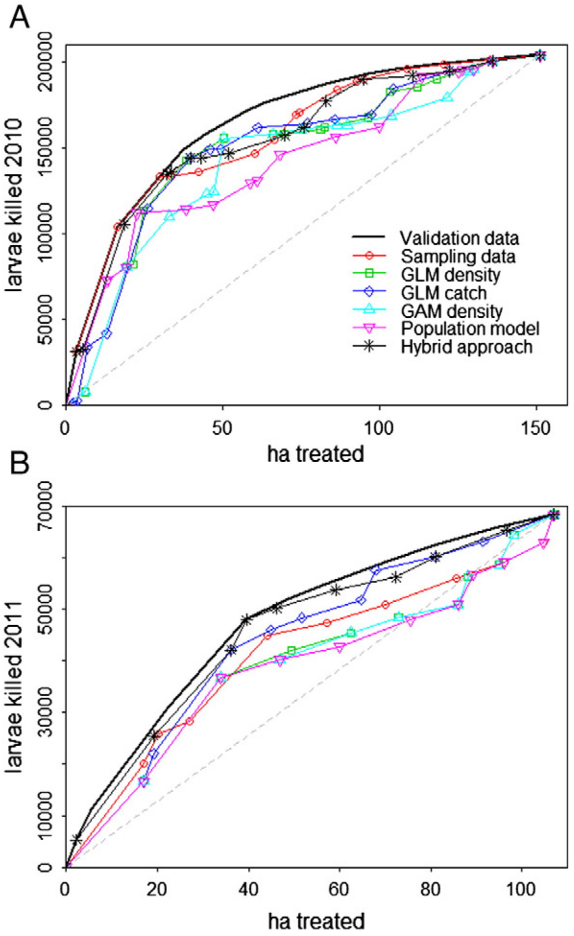

Fig. 4. The expected number of larvae killed in 2010 (A) and 2011 (B) as plots are treated based on rankings in order of decreasing density for each method. The expected number of larvae killed is based on the density from the pre-treatment validation data and the estimate of treatment effectiveness from Robinson et al. (2013). The hybrid approach is the relationship produced by averaging the density estimates from the sampling data and the GLM based on catch data. The gray dashed line is the average expected relationship if plots were treated in random order.

actually observed in the electrofishing catch. If only larvae larger than 100 mm are used, the sample sizes are too small for the model-based methods to produce reliable estimates. For example, in 2010 and 2011, the most recent years incorporated in the time series, there were only five and six larvae greater than 100 mm captured respectively, and only one instance in which more than one larva greater the 100 mm was captured in a single plot. In contrast, using all sizes of larvae increases the number of observations to 20 and 18 in 2010 and 2011, respectively. The rationale behind the expert judgment approach is to be able to treat “known” high density plots when the previous year's sampling fails to identify them as such. Combining the sample-based and model-based approaches in the hybrid-method approximates the current combination of the sample-based approach and expert judgment in a quantitative framework. The hybrid approach, which combines the entire available dataset along with the most recent year's density estimates, provides a way to explicitly consider two decades of prior information about where high densities of larval sea lampreys will occur while still relying on the most up to date information.

Choosing between the sample and model-based estimation methods presents a tradeoff. The model-based methods can incorporate the entire 19-year data set in the estimation process, but lack the flexibility to identify anomalous high density plots because plot effects and the influence of years-since-treatment cannot vary annually. The sample-based estimation method may identify anomalous high density plots, but is limited by the intensity and coverage of the sampling which varies annually. Because of these limitations, it is likely wise to incorporate both the flexibility of the sampling-based estimation and the more long term information incorporated in the model-based methods. The consistent performance across criteria and years of the hybrid approach, which combined the sample based method and the best model-based method, suggests that it is a viable option to guide treatment decisions for sea lamprey larvae in the St. Marys River. This approach should lead to a more efficient and effective Bayluscide treatment program in the St. Marys River and should aid in the decision making process surrounding the allocation of resources to sea lamprey control efforts within and among systems.

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