

## ABSTRACT

Title of Document: SEA LAMPREY (PETROMYZON MARINUS)  
POPULATION DYNAMICS, ASSESSMENT,  
AND CONTROL STRATEGY EVALUATION  
IN THE ST. MARYS RIVER, MICHIGAN

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The St. Marys River is a major producer of invasive parasitic sea lampreys (*Petromyzon marinus*) to Lake Huron. My dissertation seeks to inform the management process for sea lamprey through a combination of statistical and simulation modeling. In Chapter 1, I developed a spatial age-structured model and applied it to the sea lamprey population in the St. Marys River. The model 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. During 1993–2011, transformer escapement decreased by 86%. The model successfully identified areas of high larval abundance and showed that areas of low larval density contribute significantly to the population. In Chapter 2, I evaluated six methods of estimating sea lamprey density and abundance including the currently used sampling-based estimates, generalized linear and additive models, the population model from Chapter

1, and a hybrid approach. Methods were evaluated based on accuracy in matching independent validation data. The hybrid method was identified as the best method to inform sea lamprey control decisions in the St. Marys River due to its consistent performance. In Chapter 3, I used a resampling approach to estimate the effect of sampling intensity on the success of sea lamprey control and examined the economic tradeoff between assessment and control efforts. Sea lamprey control actions based on assessment outperformed those implemented with no assessment under all budget scenarios. The sampling intensity that maximized the number of larvae killed depended on the overall budget, with increased sampling intensities maximizing effectiveness under medium to large budgets. In Chapter 4, I conducted a management strategy evaluation using a stochastic simulation model to evaluate several fixed and survey-based Bayluscide-based treatment strategies for sea lamprey. The model incorporated population dynamics, sampling and assessment, and larval control actions. Treatment options with higher cost resulted in larger long-term reductions in transformer escapement, but increasing treatment effort did not result in a proportional decrease in transformer escapement. Survey-based treatment scenarios were the most desirable from both an economic and population control perspective.

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MARYS RIVER, MICHIGAN

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I dedicate this dissertation to my wife Beth and daughter Nora.

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## Introduction

Non-native species introductions can have negative ecological and economic impacts on systems in which they occur (Pimentel 2005). Ideally invasion should be prevented. However, when nascent invasions are identified, rapid control efforts can sometimes be successful at preventing establishment and are usually implemented without detailed biological information (Simberloff 2003a). Once an invasive species becomes firmly established, detailed information about the species life history in the new environment, population dynamics, and areas of aggregation and high abundance, is necessary for successful control (Simberloff 2003b). The control program in place for sea lamprey (*Petromyzon marinus*) populations in the Great Lakes is one of largest and longest running control efforts ever implemented for an invasive fish species. Management and control programs for larval sea lamprey populations in the Great Lakes face many challenges common among other invasive species control programs, such as patchy spatial distributions, low detection probabilities, incomplete knowledge of important life history characteristics, and limited financial resources. Development and testing of approaches for effective control are required for successful management of invasive species.

Sea lampreys are a parasitic fish native to the Atlantic coast of North America and Europe, and are invasive in the Great Lakes. In spring adult sea lampreys ascend streams to spawn in fast flowing areas of gravel substrate and subsequently die. After hatching, larvae drift downstream and settle in areas of fine sediment where they live in burrows as filter feeders. Following the larval phase, larvae metamorphose into the parasitic phase in a process known as transformation. During the transformation

phase sea lamprey develop eyes, a sucker-like mouth, and teeth. The parasitic phase spends from 12 to 18 months in the Great Lakes and each lamprey has the potential to destroy 19 kg of fish before spawning occurs (Swink 2003).

Sea lamprey invaded the upper Great Lakes (Lakes Superior, Huron, and Michigan) following improvements to the Welland Canal in 1919 and were considered abundant by the 1950s. Many fisheries in the upper 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, especially for lake trout (*Salvelinus namaycush*), relies on continued suppression of sea lamprey populations (Madenjian et al. 2002; Bronte et al. 2003; Dobiesz et al. 2005).

A lake-wide sea lamprey control program was initiated in Lake Huron in 1970 resulting in a reduction of the sea lamprey population by about 85% (Smith and Tibbles 1980). Following the initial success of the control program in Lake Huron, sea lamprey numbers began to increase because of the uncontrolled sea lamprey population in the St. Marys River (Young et al. 1996). By 1994, the abundance of sea lampreys in Lake Huron was greater than in all of the other lakes combined (Morse et al. 2003), resulting in high lake trout mortality and the suspension of the lake trout stocking program in the northern part of Lake Huron (Wilberg et al. 2002; Morse et al. 2003). In response to high sea lamprey abundance, the Great Lakes Fishery Commission (GLFC) developed and implemented an integrated program for the

control of sea lampreys in the St. Marys River (Schleen et al. 2003). The program seeks to reduce sea lamprey abundance through a combination of treatment of areas of high larval abundance with granular Bayluscide, adult trapping, and sterile male release technique (SMRT). Bayluscide treatments target the larval population, and trapping and SMRT target the spawning population with the goal of reducing recruitment. Bayluscide application is the largest component of the integrated control program in the St. Marys River, costing twice as much as the combined trapping and SMRT program in some years (Haeseker et al. 2007).

Larval density estimates that inform treatment decisions in the Saint Marys River are currently produced using deepwater electrofishing and a stratified systematic sampling design based on 71 pre-established treatment plots (Figure 2). Treatment plots were delineated prior to the start of the treatment program based on areas of high larval density during 1993-1996. Treatment began in 1998, and from 2003 to 2009 high density plots were treated based on density estimates obtained using a post-treatment survey. In 2010 and 2011 all plots were treated in an attempt to further reduce the recruitment of parasitic phase sea lampreys from the St. Marys River into Lake Huron. Bayluscide treatments will continue to be an important component of control in the St. Marys River, and a strategy for selecting treatment locations will have to be readopted after 2011 because economic considerations make it very unlikely that treating all plots in every year can be continued indefinitely. Due to the highly variable nature of sea lamprey recruitment (Haeseker et al. 2007; Dawson and Jones 2009; Wilberg et al. unpublished data) some amount of chemical control will be needed for the foreseeable future in the St. Marys River. My

dissertation aims to provide information that will allow more effective and efficient chemical control of the larval sea lamprey population in the St. Marys River through the development of spatially specific modeling techniques designed to inform Bayluscide application, and through management strategy evaluation to guide sampling and treatment decisions. My dissertation also addresses questions that are applicable to invasive species management and control in general.

My dissertation addresses four main objectives: (1) to develop and validate a spatially specific population model to describe the population dynamics of sea lampreys in the St. Marys River, (2) to compare and validate sample-based and model-based methods of ranking areas for control efforts and predicting spatially-specific larval lamprey abundance, (3) to quantify the influence of resource allocation between sampling and control efforts on the effectiveness of the sea lamprey control program, and (4) to identify Bayluscide-based control strategies that will result in the greatest long-term reductions in sea lamprey production. Each chapter of my dissertation addresses an objective. Chapter 1 arose from a management need to describe the long term dynamics of the St. Marys River sea lamprey population and incorporate long-term data to inform annual Bayluscide applications. Chapter 2 also seeks to inform annual Bayluscide applications by comparing the relative performance of several assessment approaches. Chapter 3 addresses the tradeoff in the allocation of resources between the sampling program and the treatment efforts that are driven by the sampling program. Chapter 4 builds on the results of Chapters 1–3 by developing a simulation modeling framework to evaluate control strategies prior to their implementation.

## **Objective 1**

Developing models that describe population dynamics, predict abundance or density of organisms, and reduce uncertainty around estimates is an important component of management programs for many species (Williams et al. 2002). Incorporating the spatial structure of populations into management programs has also 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). In Chapter 1 I developed and validated a spatial and age-structured model and applied it to the sea lamprey population in the St. Marys River. The model considered 75 discrete spatial areas, estimated parameters of a stock-recruitment relationship, spatial patterns in recruitment, natural mortality, treatment mortality, and plot-specific larval abundance and transformer abundance. I used a Bayesian approach for model fitting.

## **Objective 2**

In Chapter 2, I evaluated six methods of estimating spatially specific density and abundance including the currently used sampling-based estimates, a generalized linear model (GLM) based on larval density, a GLM based on larval catch, a generalized additive model based on larval density, a spatial age-structured population model (Chapter 1), and a hybrid approach. Methods were evaluated based on accuracy in matching independent validation data. Specifically, the methods were evaluated based on their ability to accurately 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.

### **Objective 3**

Management of natural resources should ideally seek to maximize the effectiveness of an action (*e.g.*, pests killed, fish stocked, ecosystem services provided) while minimizing costs. Economic costs play a fundamental role in natural resource management (Clark 2005, Fenichel and Hansen 2010), and the need to formally incorporate these costs into the decision making process has become increasingly important (Shogren et al. 1999, Hansen and Jones 2008a, Fenichel and Hansen 2010). An inherent economic tradeoff exists between the gathering of information (assessment or sampling) to guide management actions and implementation of those actions (Mehta et al. 2007). Such a tradeoff is particularly evident for sea lamprey control in the St. Marys River, a major source of parasitic sea lampreys (*Petromyzon marinus*) to Lake Huron and northern Lake Michigan. In Chapter 3, I took a resampling approach to determine the effect of sampling intensity on the success of the larval sea lamprey control program and explicitly incorporated the economic tradeoff between assessment and control efforts to maximize numbers of larvae killed in the St. Marys River.

### **Objective 4**

Management strategy evaluation (MSE) is becoming increasingly prevalent in the field of resource management (Cooke 1999, Sainsbury 1998). While MSE has

been used to inform the control of invasive species (Dunstan and Bax 2008, Jones et. al 2009), it is more commonly employed in traditional management settings involving harvest (Cooke 1999, Mapstone et. al. 2008). In Chapter 4, I built upon the results of Chapters 1–3 to develop evaluation MSE. The MSE employs a stochastic, spatially specific, age-structured simulation model to evaluate the performance of several fixed and survey-based Bayluscide-based treatment strategies for the control of sea lamprey (*Petromyzon marinus*) in the St. Marys River. The model considered 75 discrete spatial units (plots), incorporated annual larval recruitment, spatial recruitment patterns, natural mortality, larval metamorphosis, sampling and assessment, and larval control actions.

## Chapter 1: A spatial age-structured model for describing sea lamprey (Petromyzon marinus) population dynamics

### **Abstract**

The control of invasive sea lamprey (*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. I 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. The model 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 1993–2011 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.

## 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 lamprey (*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 60s due to 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 lamprey (Sorensen and Vrieze 2003; Wagner et al. 2009). There is no evidence for natal homing in sea lamprey (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 lamprey move downstream to the lake and develop eyes, a sucker-like mouth, and teeth. Parasitic phase sea lamprey 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 lamprey in the Great Lakes making the 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). 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 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 metamorphosis. 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 United States (Jolley et al. 2010, 2011, 2012). The results and general approach of this work have applications for sea lamprey control efforts throughout 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, makes it an ideal system for which to develop and test this type of approach.

Here I develop a spatial age-structured model that is statistically fitted to observed data. The model explicitly incorporates a stock recruitment function, spatial recruitment patterns, natural mortality, management actions, and larval metamorphosis for a lamprey population. I apply this model to a population of sea lamprey in a large river, and inform management through the identification of areas of high larval lamprey abundance. I 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 lamprey 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 to lamprey management because they will promote cost-effective control by being able to predict where concentrations of larvae are likely to be found, how many will be 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, MI, 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 lamprey and applying Bayluscide (Fig. 1.1). Based on surveys conducted 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 my model, the out-of-plot portion of the River was separated into 5 areas. A single treatment plot (Plot 10) was included as part of the out-of-plot area because no sea

lamprey 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 (Great Lakes Fishery Commission unpublished data). 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 1.1) with large-scale treatment efforts (*i.e.*, nearly all treatment plots) occurring in 1999, 2010, and 2011. Estimates of female spawner abundance were available from 1992 through 2011 (Table 1.1), and were corrected for the effects of trapping and the estimated effects of the sterile male release program (Bergstedt and Twohey 2007).

A 19-year time series (1993-2011) of plot-specific deepwater electrofishing data were available for larval sea lamprey in the St. Marys River. Electrofishing was conducted based on the methods described in Bergstedt and Genovese (1994). 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 collection 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 5 out-of-plot areas, total=778 plots sampled over 19 years). The number of individual electrofishing samples taken when a treatment-plot was sampled ranged from 1 to 76. The capture efficiency of the deepwater electrofishing gear is reduced as larval lamprey length increases so a length-based gear selectivity correction was applied to all larval catch data:

$$C = \sum_i \left[ 1 + e^{(L_i * 0.0229 - 1.732)} \right] \quad (1.1)$$

where  $C$  is the adjusted catch for an individual electrofishing sample,  $L$  is the length of a larvae in mm, and  $i$  is an index for the individual sea lampreys captured and measured in the sample (U.S. Fish and Wildlife Service unpublished data).

Plot-specific larval density estimates (larvae·ha<sup>-1</sup>) were calculated for each year in the pre- and post-treatment periods. Density estimates were calculated separately for age-1 (< 47mm) and ages-2+ (≥ 47mm). The length cutoff between ages 1 and 2+ larvae was determined based on visual inspection of length frequency histograms. Density estimates (larvae ha<sup>-1</sup>) were based on the mean larval catch in an individual electrofishing sample (2.44 m<sup>2</sup>) and were scaled up to an estimate of larval abundance by multiplying plot specific densities by the plot area.

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:

$$\sigma_d = aN^c \quad (1.2)$$

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 age 2+ length bins (pre-treatment age 1:  $a = 10,800$ ,  $c = -0.855$ ,  $r^2 = 0.32$ ,  $df = 42$ ,  $p < 0.001$ ; pre-treatment age 2+:  $a = 13,200$ ,  $c = -0.853$ ,  $r^2 = 0.33$ ,  $df = 59$ ,  $p < 0.001$ ; post-treatment age 1:  $a = 6430$ ,  $c = -0.840$ ,  $r^2 = 0.72$ ,  $df = 228$ ,  $p < 0.001$ ; post-treatment age 2+:  $a = 10,000$ ,  $c = -0.741$ ,  $r^2 = 0.51$ ,  $df = 288$ ,  $p < 0.001$ ). 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 due to the high number of zeros in the data and the high variability in sample size.

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,  $> 4$  samples per ha) than would occur under normal sampling conditions. A similar sampling effort was undertaken in 2011, which intensively sampled 10 plots. Data associated with the high intensity pre-treatment deepwater electrofishing surveys can be found in Appendix A.

### *Population model*

I developed a spatial, age-structured model (e.g., Fournier and Archibald 1992) and applied it to sea lamprey in the St. Marys River, MI. The model estimated parameters of a stock-recruitment relationship, spatial patterns in recruitment, natural mortality, treatment mortality, and plot-specific larval abundance and transformer abundance. Within the model, plot-specific larval and transformer abundance changed due to variable recruitment, natural mortality, Bayluscide treatment mortality, and age specific transformation rates (Fig. 1.2). I used a Bayesian approach for model fitting. Variables included in the model are described in Table 1.2. It is important to note that the model describes an open population and does not describe the complete sea lamprey life cycle, as it does not incorporate the parasitic phase. This approach was adopted because sea lampreys do not exhibit natal homing behavior (Bergstedt and Twohey 2007, Waldman et al. 2008).

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. I assumed that recruitment of larvae to plots occurred prior to pre-treatment electrofishing (Fig. 1.2). Total (river-wide) recruitment was estimated using a Ricker stock-recruitment function with a year-specific process error:

$$R_t = \alpha S_{t-1} e^{-\beta S_{t-1} + \epsilon_t}. \quad (1.3)$$

The parameters of the Ricker function ( $\alpha$  and  $\beta$ ) were estimated within the model and were informed by the number of reproducing females with a one 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):

$$\varepsilon \sim N(0, \sigma_{rec}^2). \quad (1.4)$$

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

$$\hat{N} pre_{a=1, t, p} = R_t r_{t,p} \quad (1.5)$$

where  $Npre$  is the number of age 1 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 (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. 1999 was chosen as the change-point in spatial recruitment because it was the year following the onset of treatment efforts and because it was preceded by three years of very sparse data collection. The model assumed no movement of larvae among plots after initial recruitment.

Plot-specific larval abundance following treatment in each year was calculated by multiplying the pre-treatment larval abundance by Bayluscide treatment survival:

$$\hat{N} post_{a, t, p} = \hat{N} pre_{a, t, p} (1 - b_{t,p} B) \quad (1.6)$$

where  $b$  is a binary indicator variable that describes whether treatment occurred in a plot in each year, and upper case  $B$  is the estimated larval mortality due to Bayluscide (Table 1.2). Pre-treatment larval abundance was calculated by decrementing post-treatment larval abundance in the previous year by natural mortality,  $M$ , and transformation,  $t$ ,

$$\hat{N} pre_{a+1, t+1, p} = \hat{N} post_{a, t, p} e^{-M} (1 - t_a) \quad (1.7)$$

where  $t_a$  is the probability of transformation at age. Estimated natural mortality was constant through time and was applied following larval transformation in all years.

Larval transformation was assumed to occur following post-treatment sampling (Fig. 1.2). Age-specific larval transformation rates ( $t_a$ : age 1-3, 0; age 4, 0.46; age 5, 0.57; age 6, 1.0) were taken from Haeseker et al. (2003) and were assumed to be time-invariant. The maximum larval age was set to six because less than 1% of larvae aged from 1993 to 1996 were greater than 6 years old (Schleen et al. 2003). Transformer abundance ( $T$ ) was calculated by multiplying the number of larvae that survive treatment by the expected proportion that transformed at each age ( $t_a$ ),

$$T_{t, p} = \sum_a \hat{N} post_{a, t, p} t_a. \quad (1.8)$$

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 five 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), using transformer production in the St. Marys River to inform future spawning stock size would require an assumption that parasites from the rest of Lake Huron either do not contribute to the St. Marys River or that they contribute in a small constant proportion.

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. 171 parameters were estimated simultaneously within the model (Table 1.2). 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 & 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  $\beta$  parameter of the Ricker function. A normal prior ( $\rho$ ) was assumed for  $\beta$  based on Haeseker et al. (2003) and took the form:

$$\rho_{\beta} = \log(\sigma_{\beta}) + \frac{(\beta_p - \beta)^2}{2\sigma_{\beta}^2} \quad (1.9)$$

where  $\beta_p$  (0.00018) is the mean prior for  $\beta$ , and  $\sigma_{\beta}$  (0.0001) is the standard deviation of the prior for  $\beta$ .

The objective function ( $L$ ), was the sum of five log likelihood components ( $LL$ ), and the priors ( $\rho$ ),

$$L = \sum_{i=1}^5 LL_i + \sum_{k=1}^j \rho_k. \quad (1.10)$$

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

$$LL_{1-4} = \sum_t \sum_p \left[ \log(\sigma_N) + \frac{1}{2\sigma_N^2} \left( N_{t,p} - \hat{N}_{t,p} \right)^2 \right] \quad (1.11)$$

where  $N$  is the empirical plot-specific abundance estimate from the deepwater

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

$$LL_s = 0.5Y \log \sum_t (\varepsilon_t)^2 \quad (1.12)$$

where  $\varepsilon$  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. 90% credible intervals (the Bayesian analog of confidence intervals) were constructed using the range between the 5<sup>th</sup> and the 95<sup>th</sup> 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 to 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 and median absolute error for the total plot-level larval density, age 1 larval density, and age 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.

I tested the sensitivity of the model to (1) the inclusion of the 2010 and 2011 pre-treatment validation data, and (2) an alternative selectivity relationship for the deepwater electrofishing gear (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 ( $\alpha$ ), beta ( $\beta$ ), 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 2010-2011 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, MI:

$$C_{Bergstedt} = 1 + e^{(L * 0.0164 - 2.2429)} \quad (1.13)$$

where  $C$  is the adjusted catch value for each larvae and  $L$  is the length of the larvae in mm. Following the development of the Bergstedt and Genovese (1994) selectivity relationship a gear selectivity correction specific to the St. Marys River (equation 1.1) 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 (Fig. 1.3A-D). 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. There were more positive residuals than negative residuals and the positive residuals tended to be smaller. Most of the positive residuals were associated with observed larval abundances of zero. There were many of these 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 lamprey was captured (especially a large 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.

The credible intervals around the parameter estimates were all reasonable (Table 1.3) and the distributions of the parameter estimates differed from the priors in all cases except  $\beta$ . The median estimate of instantaneous natural mortality ( $M$ ) for age 1-6 larvae was  $0.09 \text{ yr}^{-1}$ , and the estimated Bayluscide induced treatment mortality ( $B$ ) was  $0.51 \text{ treatment}^{-1}$  (Table 1.3). The  $\alpha$  and  $\beta$  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 decreased 80% during 1993-2011 (Fig. 1.4A, Table 1.1). Recruitment was also highly variable at low spawning stock size and showed a moderate amount of compensation at higher spawning stock size (Fig. 1.4B). 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 1.4). 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 to 25% early in the time series. Conversely, area 5 received only 4% of recruitment in recent years compared to 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 (Fig. 1.5A-C, Table 1.1). Transformer abundance decreased 86% from 1993 to 2011 while in-plot and out-of-plot transformer abundance decreased 96% and 72%, respectively (Fig. 1.5D-F, Table 1.1).

When I removed the estimated effect of Bayluscide treatment on transformer abundance, the estimated decrease in total-river and in-plot transformer abundance from 1993-2011 dropped to 67% and 66%, respectively, (Fig. 1.5D and E). If Bayluscide treatments had not occurred, I 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<sup>-1</sup> and that all of these plots were within 10 km of the major spawning area at the rapids (Fig. 1.6). 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 to the sample based estimates of abundance derived from the intensive electrofishing survey (Fig. 1.7A-C, Table 1.5). 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 overestimate the abundance of older larvae (Fig. 1.7D-F, Table 1.5). The median error between the projected and observed total abundances in 2010 and 2011, was -7920 and 5800 larvae respectively. Median error estimates were relatively small compared to 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 1.3). 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  $\alpha$  or  $\beta$ . Estimates of annual larval and transformer abundance early on in the time series were not affected. However, the larval abundance estimate in 2011 increased and the estimate of transformer abundance 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  $\alpha$  parameter of the Ricker function but had little effect on the estimate Bayluscide induced treatment mortality or the  $\beta$  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.

## **Discussion**

I documented substantial declines in abundance of sea lamprey larvae and transformers that can be attributed to reductions in recruitment through time and the effects of the Bayluscide treatment program. The model was 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 I 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 abundance through 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 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 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 lamprey 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, conservation, or restoration of 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 (due to 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 in addition to those 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 sterile male release program, trapping-derived reductions in spawner numbers, or even an intergenerational effect of the Bayluscide-derived reductions on returning adults.

My 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. 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. I chose not to link the dynamics of the larval to the population of parasites in Lake Huron to avoid having to assume the proportion of Lake Huron parasites that originated in the St. Marys River. Instead, I focused on developing a model that could describe the long term spatial dynamics of the in-river lamprey population and 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 my approach is that assigning length based ages to lamprey larvae older than age-1 is not required.

My estimates of both natural mortality and Bayluscide treatment mortality are substantially lower than previously reported estimates (Haeseker et al. 2003; Fodale et al. 2003). The estimate of instantaneous natural mortality for sea lamprey larvae from ages 1-6 ( $0.09 \text{ yr}^{-1}$ ) is on the low end of reported mortality rates for fish stocks in general (Pauley 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 my 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 spawning area and locating suitable settlement habitat. It is likely that mortality during this life stage is substantially higher compared to mortality once the larvae have located suitable habitat and burrowed into the sediment. The difference between the  $\alpha$  estimate with recruitment at age 0 included ( $\alpha_{\text{age } 0} = 9410$  larvae) from Haeseker et al. (2003) and my estimate with recruitment at age 1 ( $\alpha_{\text{age } 1} = 268$  larvae) indicates an instantaneous natural mortality rate for age-0 larvae of about  $3.56 \text{ yr}^{-1}$  (97%  $\text{yr}^{-1}$ ). Therefore, Haeseker's estimates of higher (constant) mortality for age 0 through 6 larvae could be consistent with my much lower estimate because I do not include the apparently very high age-0 mortality in my larval mortality estimate.

My estimate of Bayluscide induced treatment mortality ( $0.51 \text{ treatment}^{-1}$ ) was also lower than the previous estimate ( $0.88 \text{ treatment}^{-1}$ ), which was estimated based on a single large scale treatment event in 1999 (Fodale et al. 2003). My 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 ( $0.59 \text{ treatment}^{-1}$ ) from my sensitivity analyses that included high quality pre-treatment data for two years with large scale treatments (2010 and 2011).

I 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 lamprey 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 the 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 and 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 areas close to spawning habitats.

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, my model can predict and project plot-specific abundances even given a paucity of data in some plots or years. I identified a substantial out-of-plot larval population which 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, I 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 the deepwater electrofishing gear is used. 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 lamprey, especially in large rivers and lentic areas.

Sea lampreys are currently being assessed using the deepwater electrofishing approach in other Great Lakes tributaries (*e.g.*, the St. Clair River) and native lamprey population 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 lamprey 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 make 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 lamprey. 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.

Table 1.1. The number of plots and hectares treated in each model year, the effective female spawners (S) in each year, and the model estimates of recruits (R), post-treatment larval abundance (Npost), and transformer abundance (Tt) in each year.

Year	Plots treated	ha. treated	$S_{t-1}$	R	Npost <sub>y</sub>	T <sub>y</sub>
1993	0	0	3,030	761,000	3,050,000	530,000
1994	0	0	12,500	357,000	2,640,000	530,000
1995	0	0	1,090	991,000	2,910,000	530,000
1996	0	0	2,870	330,000	2,500,000	530,000
1997	0	0	4,920	510,000	2,330,000	394,000
1998	6	81	402	124,000	1,800,000	489,000
1999	59	692	1,770	511,000	1,380,000	275,000
2000	0	0	638	399,000	1,400,000	288,000
2001	5	57	1,670	232,000	1,060,000	149,000
2002	0	0	1,110	243,000	1,070,000	200,000
2003	8	82	289	61,400	826,000	198,000
2004	8	60	1,860	114,000	676,000	179,000
2005	10	122	1,200	159,000	502,000	137,000
2006	8	106	673	210,000	493,000	73,900
2007	10	112	1,390	193,000	521,000	59,500
2008	9	121	1,560	275,000	578,000	53,900
2009	10	148	875	413,000	768,000	73,800
2010	70	829	643	183,000	597,000	66,400
2011	70	829	2,500	156,000	500,000	72,900

Table 1.2. Description of symbols used in model equations. 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.

Symbol	Description	Type
$a$	Age class (age-1 through age-6)	i
$t$	Year (1993-2010)	i
$p$	plots	i
$S$	Female spawner abundance	d
$N$	Plot-specific larval abundance estimates	d
$\sigma_N$	Standard error of plot-specific larval abundance estimates	d
$\sigma_d$	Standard error of plot-specific larval density estimates	d
$\sigma_{LN}$	Standard error of the natural log of larval abundance estimates	d
$b$	Binary variable indicating Bayluscide treatment	d
$Y$	Number of years in the time series	d
$\rho$	Calculated priors on parameters	d
$\alpha$	Ricker model alpha parameter (1)	p
$\beta$	Ricker model beta parameter (1)	p
$\varepsilon$	Normally distributed recruitment process error (19)	p
$\sigma_{rec}^2$	Variance of recruitment process error (1)	p
$M$	Instantaneous natural mortality rate (1)	p
$B$	Bayluscide treatment effectiveness (1)	p
$r$	Proportion of total recruits that settle in each plot (148)	p
$t$	Age-specific transformation rate at age	c
$A$	plot area	c
$\beta_p$	Median prior for beta parameter	c
$\sigma_\beta$	Standard deviation of for prior on the beta parameter	c
$R$	Total river age-1recruitment	s
$N_{pre}$	Larval abundance in each year prior to treatment	s
$N_{post}$	Larval abundance in each year following treatment	s
$T$	Transformer abundance in the St. Marys River	s

Table 1.3. 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, using the Bergstedt and Genovese (1994) selectivity relationship, and using lognormal likelihood functions to describe larval abundance. Proportional differences are relative to the estimates from the primary model.

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

Table 1.4. 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. Locations of the five river areas are shown in Fig. 1.1.

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

Table 1.5. Median 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 absolute error
2010 all ages	-7960	7960
2010 age 1	-4940	4940
2010 age 2-6	-2580	2580
2011 all ages	5800	9110
2011 age 1	4630	5360
2011 age 2-6	-142	5130

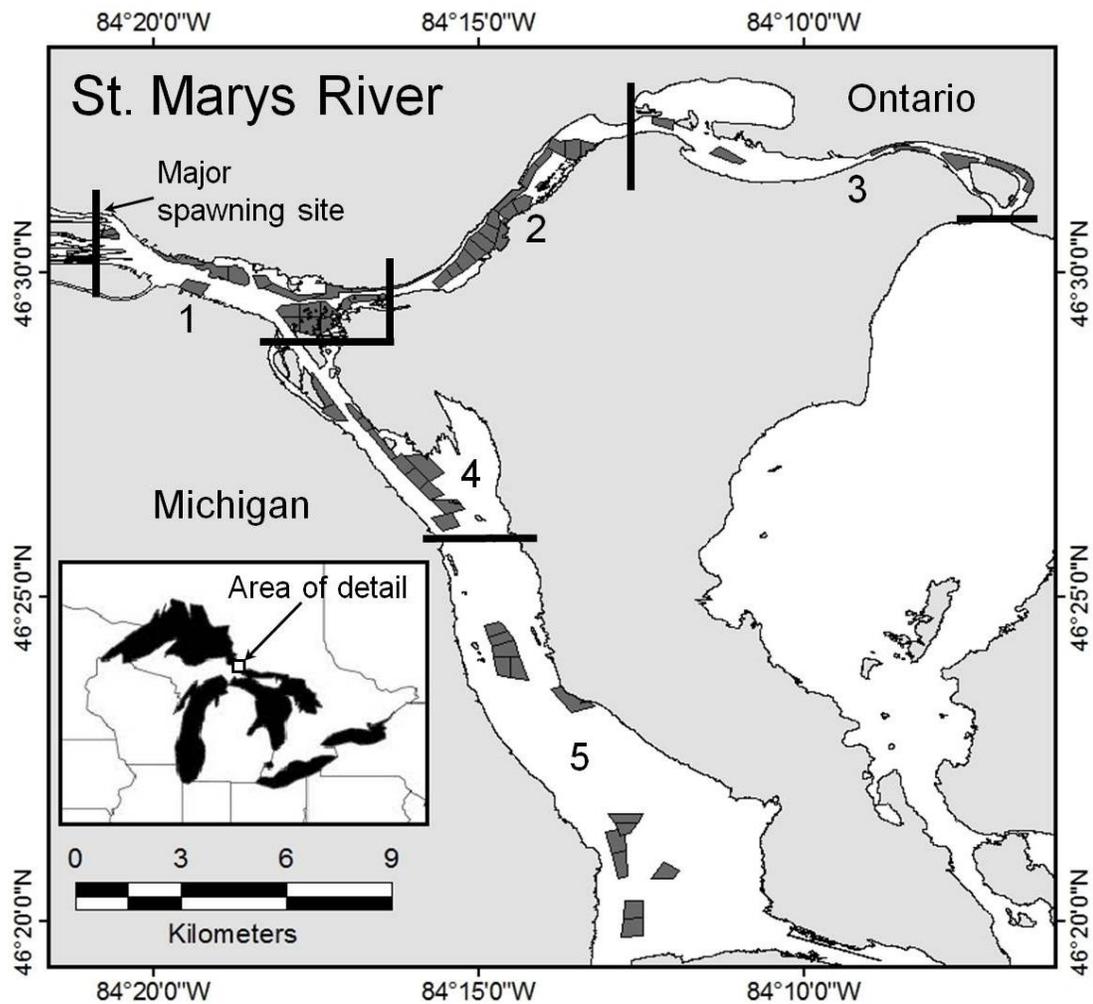


Figure 1.1. The St. Marys River from the navigational locks in Sault Ste. Marie, Michigan and Ontario, to the northern shore of Neebish Island. Coverage includes the entire portion of the river that is treated and assessed by the sea lamprey control program. Dark grey areas are treatment plots and the 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.

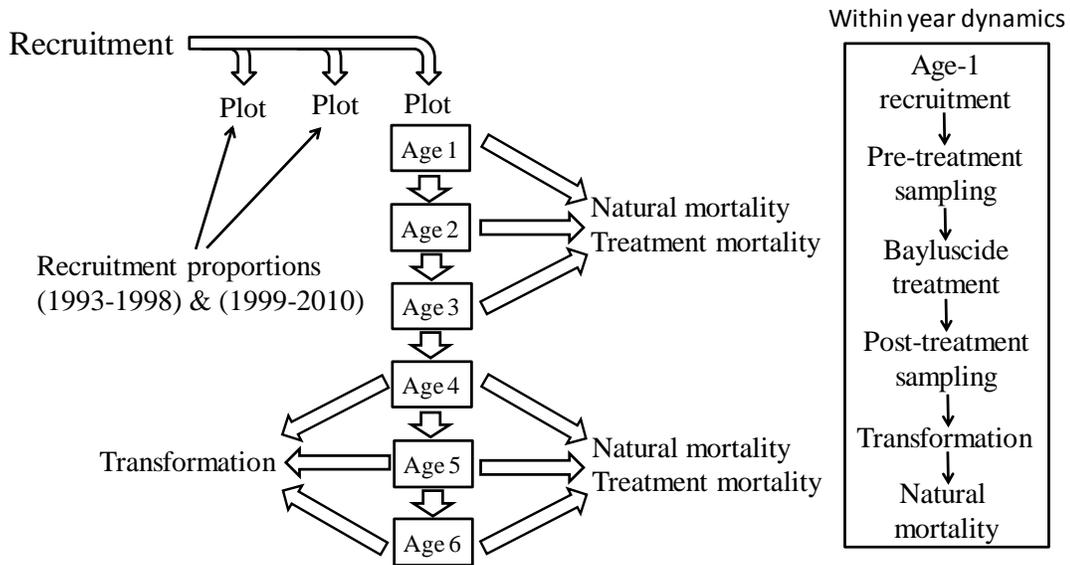


Figure 1.2. A basic representation of the recruitment dynamics and plot-specific population dynamics for larval lamprey in the St. Marys River as it is implemented within the age-structured population model. Arrows originating from the recruitment term indicate larval recruitment to different spatial 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 box on the right represents the relative order of events within a single model year from top to bottom.

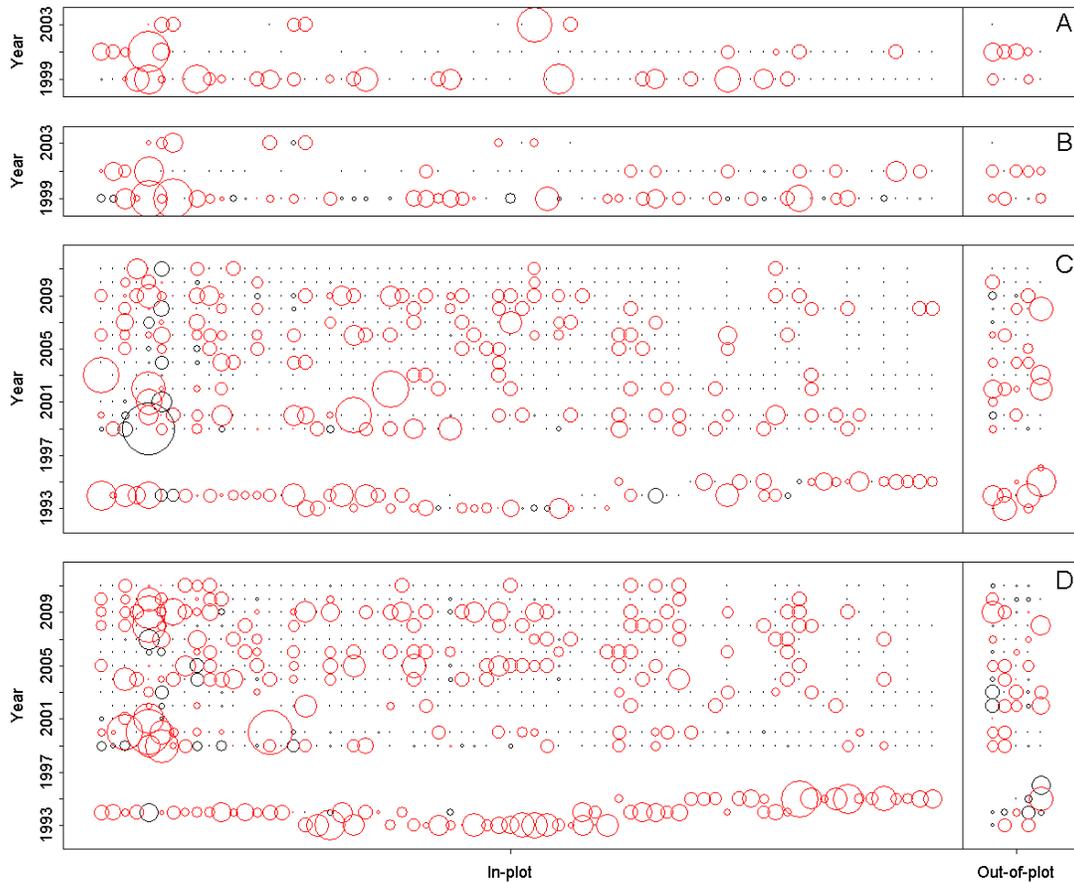


Figure 1.3. Standardized plot-specific larval abundance residuals for the pre-treatment age 1 samples (A), pre treatment age 2-6 samples (B), post-treatment age 1 samples (C), and the post-treatment age 2-6 samples (D). Black and red circles represent positive and negative residuals respectively. Areas 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-treatment sample. In-plot residuals are in the left box of each figure 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 figure.

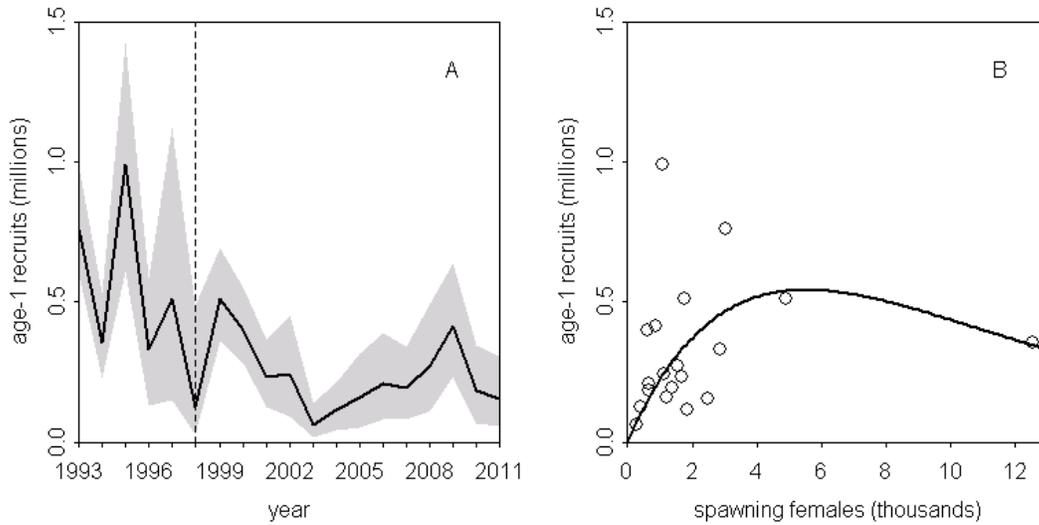


Figure 1.4. Median model estimated temporal trend in total river age 1 recruits in millions (A), and the estimated Ricker stock-recruitment relationship with median estimates of annual recruitment in millions represented by the open circles (B). Solid black lines represent median model estimates and the grey shading represents the 90% credible interval. The dashed vertical line denotes the onset of treatment efforts in 1998.

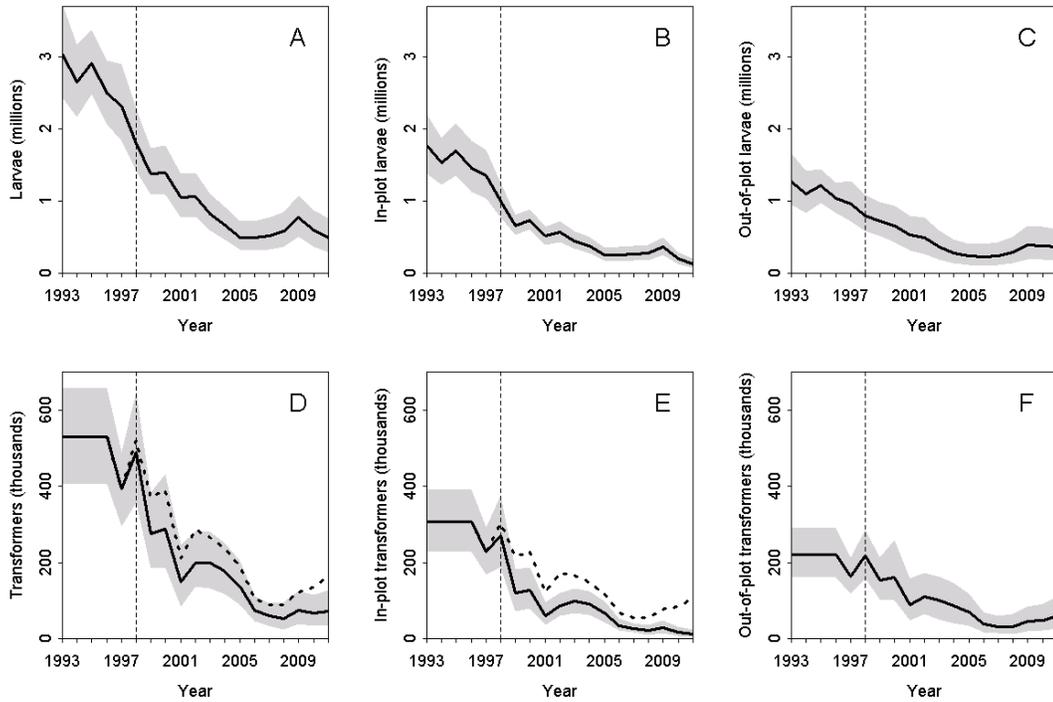


Figure 1.5. Model estimates of total river larval sea lamprey abundance (A), in-plot larval abundance (B), out-of-plot larval abundance (C), total river transformer abundance (D), in-plot transformer abundance (E), and out-of-plot transformer abundance (F) over time. All estimates are for the post-treatment 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 interval. Vertical dashed lines denote the onset of treatment efforts in 1998 and the dotted lines 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.

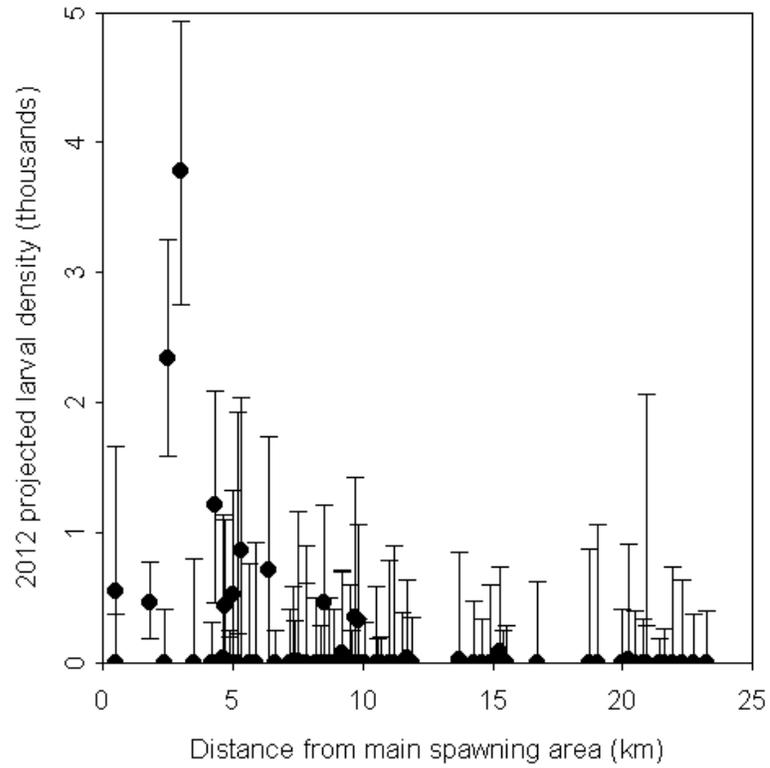


Figure 1.6. Projected median 2012 larval density (larvae ha<sup>-1</sup>) estimates for each of the 70 treatment plots, ordered by their distance from the main spawning area at the rapids. Error bars represent 90% credible intervals. All estimates are greater than zero and error bars do not extend into the negative range.

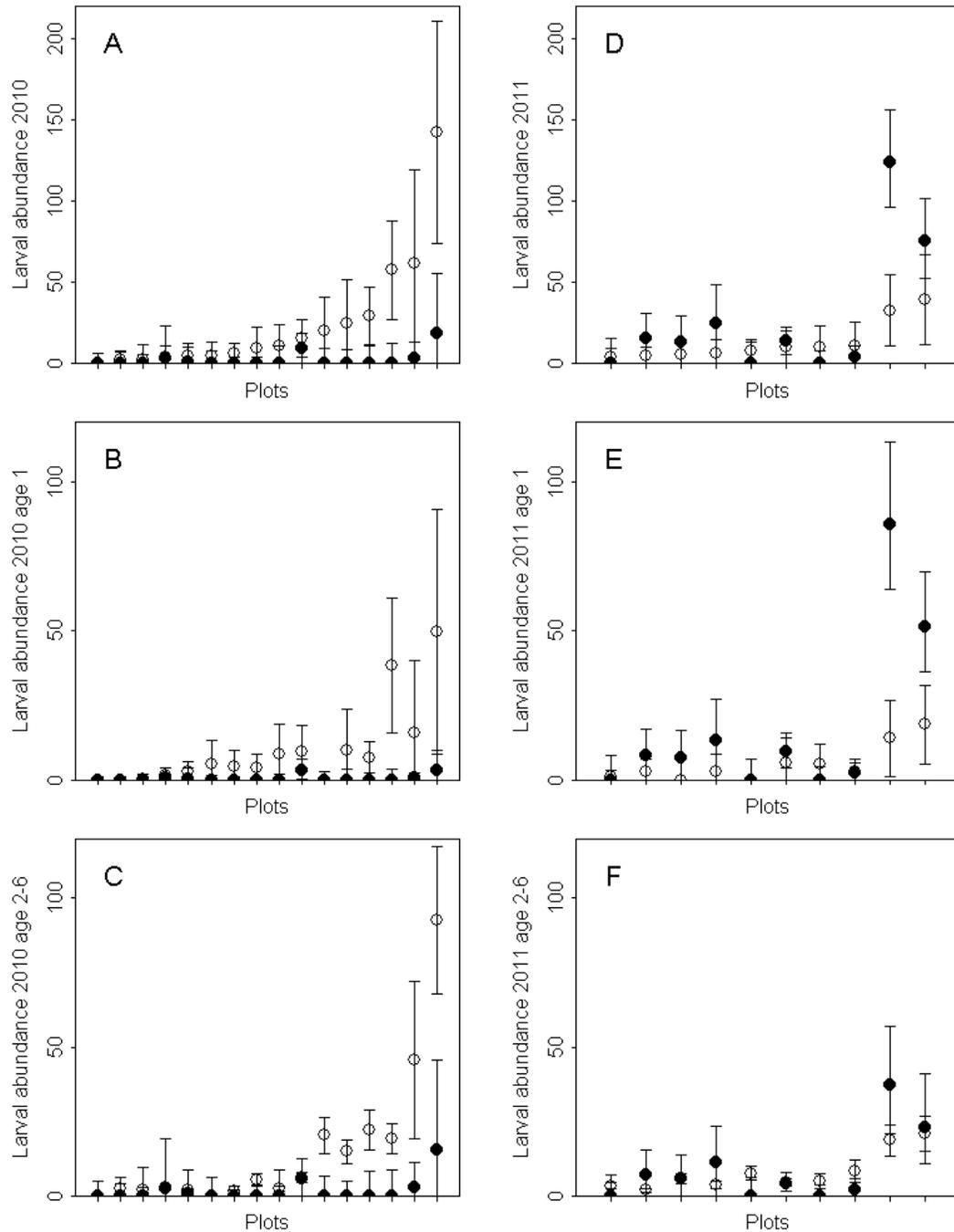


Figure 1.7. Model projected median pre-treatment plot-specific larval abundance estimates in thousands (black circles) and estimates of mean larval abundance from the intensive sampling effort in thousands (open circles) for 2010 all ages (A), 2010 age 1 (B), 2010 ages 2-6 (C), 2011 all ages (D), 2011 age 1 (E), and 2011 ages 2-6 (F). Error bars represent the 90% credible interval for the model estimates and two standard errors 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.

## Chapter 2: Comparing methods for estimating larval sea lamprey (*Petromyzon marinus*) density and abundance for the purposes of control

### **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 relatively fine spatial scales to inform treatment decisions. I evaluated six methods of estimating spatially specific density and abundance including the currently used sampling-based estimates, a generalized linear model (GLM) based on larval density, a GLM based on larval catch, a generalized additive model based on larval density, a spatial age-structured population model, and a hybrid approach. Methods were evaluated based on accuracy in matching independent validation data. Specifically, the methods were evaluated based on their ability to accurately 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 in terms of estimating density and identifying high density plots, the hybrid method 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 20<sup>th</sup> century resulting in long term ecological changes and economic impacts (Smith 1971, Christie and Goddard 2003, Lupi et al. 2003). 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 (Madenjian et al. 2002; Bronte et al. 2003; Dobiesz et al. 2005).

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 large-scale treatments in small streams. However, TFM application is not feasible in large rivers and lentic areas, 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 treatment efficiency and effectiveness in terms of larvae killed per hectare treated and cost per kill. 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.

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 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 (Chapter 1). These targeted treatments occur in areas of high larval density and are based on spatially specific density estimates from deepwater electrofishing surveys that occur following Bayluscide treatment in the previous year. This approach is limited by the intensity and coverage of the sampling, which is variable. I hypothesized that taking a model-based approach to spatially specific density estimation that incorporates the entire 19 year deepwater electrofishing dataset instead of just the most recent year's data would lead to more accurate selection of sites for treatment, and a more efficient and effective Bayluscide treatment program in the St. Marys River.

I evaluated six methods of estimating spatially specific density including the currently used sampling-based estimates, two generalized linear models (GLMs), a generalized additive model (GAM), a spatial age-structured population model (Chapter 1) for the St. Marys River, and a hybrid approach in which the sample-based method and the best performing model-based method were averaged. These methods represent three levels of 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) with the goal of identifying a method or methods that would lead to better estimation of spatially specific density and abundance, and an increase in the effectiveness of the larval treatment program in the St. Marys River.

## **Methods**

### *Data*

The portion of the St. Marys River considered good larval sea lamprey habitat is divided into 71 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 sea lampreys and applying Bayluscide (Fig. 2). These plots were defined as areas of high larval density based on deepwater electrofishing surveys conducted from 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 were 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, post-treatment, or no-treatment depending on whether a treatment event occurred and the timing of sampling relative to the treatment event. Only no-treatment and post-treatment data were included in my analysis because the collection of these data occurred roughly simultaneously in the post-treatment period, and are hereafter referred to as post-treatment data. Post-treatment data were available 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 in the post-treatment period 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:

$$C = \sum_i \left[ 1 + e^{(L_i * 0.0229 - 1.732)} \right] \quad (2.1)$$

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

Plot-specific larval density estimates (larvae·ha<sup>-1</sup>) were calculated for each year in the post-treatment period. Density estimates were based on the mean larval catch in an individual electrofishing sample (2.44 m<sup>2</sup>) and were scaled up to larval density per hectare. 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 (Chapter 1):

$$\sigma_d = aN^c \quad (2.2)$$

where  $N$  is the sample size for a given plot and  $a$  and  $c$  are estimated parameters ( $a = 9080$ ,  $c = -0.703$ ,  $r^2 = 0.40$ ,  $p < 0.001$ ). 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, which intensively sampled 10 plots. These sampling efforts were designed to include a range of high, medium and low density plots across two years. Data associated with the high intensity pre-treatment deepwater electrofishing surveys can be found in Appendix A. The increased sampling intensity and closer temporal proximity to the timing of potential treatment events for the validation data should translate into density and abundance estimates that are closer to the true value

than would be expected for the other estimation methods. However, it must be noted that several factors such as, gear selectivity, inconsistent habitat, flow, depth, or sampling error, will cause the validation estimates to differ from true larval sea lamprey abundance.

### *Estimation methods*

Six estimation methods were tested for predicting plot level density and abundance (Fig. 2.2). The first method simply used the plot-specific density estimates from the previous year's post-treatment electrofishing sampling. Two GLMs and one GAM were implemented. The GLMs and GAM were fitted to the 1993-2009 and 1993-2010 data to produce 2010 and 2011 projections respectively. The spatial age-structured population model developed in Chapter 1 was also used to produce plot-specific projections of density and abundance in 2010 and 2011. Due to the inconsistency in the performance of the first five density estimation methods tested, I included an additional approach for estimating plot-level density by averaging the two methods with the most consistent performance.

Only post-treatment data were considered in the GLMs and GAM. The GLMs and the GAM included plot as a categorical effect and years-since-treatment as a covariate. Effects of additional explanatory variables (e.g. depth and habitat) were not estimable and were not included. The first GLM used the log transformed plot-level larval density estimates as the response variable, a Gaussian error structure and an identity link function,

$$\log(D_{p,y} + c) = \beta_0 + \beta_1 P + \beta_2 T_{p,y} + \varepsilon_{p,y} \quad (2.3)$$

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  $\beta$ s 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 Ripley 2002). 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,  $\sigma_{LN}^2$ , can be calculated as,

$$\sigma_{LN}^2 = \log \left[ \left( \frac{\sigma_N^2}{D_{p,y} + c} \right)^2 + 1 \right] \quad (2.4)$$

where  $\sigma_N^2$  the variance of each density estimate. The second GLM used selectivity corrected 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 program R (R Development Core Team 2012), and package MASS:

$$C_{p,y} = \log(\beta_0 + \beta_1 P + \beta_2 T_{p,y} + \varepsilon_{p,y}). \quad (2.5)$$

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), avoiding 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 plot-level larval density estimates as the response variable, a Gaussian error structure and identity link function,

$$\log(D_{p,y} + c) = \beta_0 + \beta_1 P + f_1 T_{p,y} + \varepsilon_{p,y} \quad (2.6)$$

where the  $\beta$ s 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  $\sigma_{LN}^2$  as used to weight the plot-level density estimates in the model fitting. The GAM analysis was performed using program R (R Development Core Team 2012) using package mgcv (Wood 2011).

In chapter 1, I 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 larval abundance and transformer abundance. Plot-specific larval abundance changed due to recruitment, natural mortality, Bayluscide treatment mortality, and age specific larval transformation 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 fitted to plot-specific abundance estimates from the 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 fitted 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 Chapter 1.

The hybrid approach involved calculating the mean density from sampling-based estimation method and the GLM based on catch data. 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. Initially, a modeling 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.

### *Comparisons*

The five methods of estimating plot level density of larval sea lampreys were evaluated based on 3 criteria (Fig. 2.2): 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 resulting in effective larval control. 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. This allowed for 26 plot level comparisons for each method, spanning two years.

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

$$\text{median absolute error} = \text{median} |D_p - V_p| \quad (2.7)$$

where  $D_p$  are the plot level density estimates from one of the five estimation methods from a specific year and  $V_p$  are the density estimates based in 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. In terms of informing treatment events, obtaining accurate rankings is more important than obtaining unbiased density estimates.

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%, Chapter 1) 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**

The GLMs and GAM fit the data reasonably well although they did not explain a large percentage of the deviance (Table 2.1). 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 2.1). 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 (Chapter 1).

Estimates of plot-level density (larvae·ha<sup>-1</sup>) produced using the validation data ranged from 0 to 18,700 in 2010, and from 523 to 4,730 in 2011. Abundance

estimates ranged from 0 to 142,000 in 2010, and from 4,510 to 39,400 in 2011.

Density estimates produced using the validation data had moderate precision (mean CV 54%) but represented an improvement in precision relative to density estimates produced based on the data from the annual electrofishing survey (mean CV 94%).

The method that produced the most accurate estimates of larval sea lamprey density varied by year. 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 2.2, Fig. 2.3A). The other four estimation methods had larger median absolute errors (>1,300 larvae per ha). In 2011 the GLM and GAM based on density produced the most accurate estimates of larval density (median absolute error = approximately 640 larvae per ha) while the other four methods produced density estimates with larger median absolute errors ranging from 1,320 to 1,620 larvae per ha in (Table 2.2, Fig. 2.3B).

The ability of each estimation method to identify plots with the highest density varied between 2010 and 2011 (Table 2.3). 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 larvae killed per ha treated relationship that was the same as the validation data for very high density plots (Fig. 2.4A) and 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 smallest reduction in average number of larvae killed per ha (7,500 larvae per ha) relative to the validation data, followed by hybrid approach (8,620 larvae per ha) in 2010 (Table 2.2). 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 2.4B). The GLM based on catch data also performed well, producing a larvae 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 to each other, producing a larvae 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 (1,780 larvae per ha), followed by the GLM based on catch data (3,630 larvae per ha) in 2011. The

reduction in the number of larvae killed based on the other four methods ranged from 6,390 to 9,150 larvae per ha.

## **Discussion**

The performance of the estimation methods was variable, and comparisons did not identify a single method that outperformed the others for all performance criteria or years. In 2010 the hybrid approach produced the most accurate density estimates, while in 2011 the GLM and GAM based on density produced the best estimates. In 2010 the GLM and the sampling data performed best in terms of identifying the three plots with the highest larval density, but the GLM based on density performed best when the top five plots were considered. In 2011 the GLM based on catch and the hybrid approach performed best at identifying high density plots for both the three and five plot treatment scenarios. On average, conducting treatment based on the sampling data would have resulted in numbers of larvae killed per ha treated that was closest to the validation data in 2010, followed closely by the hybrid approach. In 2011 conducting treatment based density estimated from the hybrid approach would have resulted in numbers of larvae killed per ha treated that was closest to the validation data.

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 lamprey even at the

scale of a treatment plot and an effect of correcting for the selectivity of the deepwater electrofishing gear. 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%). The moderate precision of the density estimates produced using the validation data adds additional uncertainty about the performance of the estimation methods because my 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 in more rare instances no sampling is conducted. When this occurs a model-based method must be used to inform treatment efforts in the following year. In most situations the GLM based on catch data performed well. The consistent performance of this estimation method 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. The GLM based on the catch data has the added benefit of being the simplest of the model-based methods to implement because it uses catch 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 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 my validation data and the GLM based on catch data. There is also some probability of catching no sea lampreys in a high density plot by random chance, a possibility which increases for small plots because the number of samples that occur in each plot is based on plot area, with some small 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.

Detailed information about population dynamics can aid in the control of invasive species (Simberloff 2003). Although the spatial age-structured population model did not perform as well as some of the other methods for tactical treatment decisions, the approach provides insights that the other methods do not. Because the population model is based on sea lamprey life history, it allows the description of long term sea lamprey population dynamics, the estimation of treatment and natural mortality rates, and the evaluation of the treatment program that other methods do not. The population model has additional utility in that it could be used in a simulation context to evaluate the potential performance of new treatment strategies in the St. Marys River (i.e., management strategy evaluation). The GLM and GAM

approach are of limited utility for describing the dynamics of the population but allow the estimation of years since treatment effect that is equivalent to estimating the proportional increase in density for every year that a plot goes untreated.

There is an inherent tradeoff between the sample and model-based estimation methods. 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.

Table 2.1. 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	Est.	Std. err	z value	P(> z )
GLM	log(den + 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(den + c)	37.50%	Intercept	5.961	0.545	10.94	<0.001
			YST (smooth)			35.23	<0.001

Table 2.2. Median absolute error of density estimates and mean reduction in larval kill per ha treated in 2010 and 2011. 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 post-treatment sampling in the previous year (Sampling), the generalized linear model based on density data (GLM den.), the generalized linear model based on catch data (GLM catch), the generalized additive model based on density data (GAM den.), the spatial age-structured population model (Pop. model), and the average of the density estimates produced using the sampling data and the GLM based on catch data (hybrid approach).

Method	Median abs. error		Kill reduction per ha	
	2010	2011	2010	2011
Sampling data	1,460	1,610	7,500	6,390
GLM density norm	1,300	681	15,700	8,240
GLM catch neg bin	857	1,620	14,200	3,630
GAM density norm	1,300	605	22,000	8,370
Population model	1,380	1,150	14,400	9,150
Hybrid approach	697	1,320	8,620	1,780

Table 2.3. Plots listed in descending order based on estimated density for each method in 2010 and 2011. Numbers listed are plot identification numbers. Density estimates were based on pre-treatment sampling (Validation) , Post treatment sampling in the previous year (Sampling), the linear model (LM), the generalized linear model (GLiM), the generalized additive model (GAM), the spatial age-structured population model (Pop. 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 arbitrary order. A double asterisk indicated no sampling occurred.

Year	Rank	Validation	Sampling data	GLM den.	GLM catch	GAM den.	Pop. 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
Year	Rank	Validation	Sampling data	GLM den.	GLM catch.	GAM den.	Pop. model	Hybrid mean
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

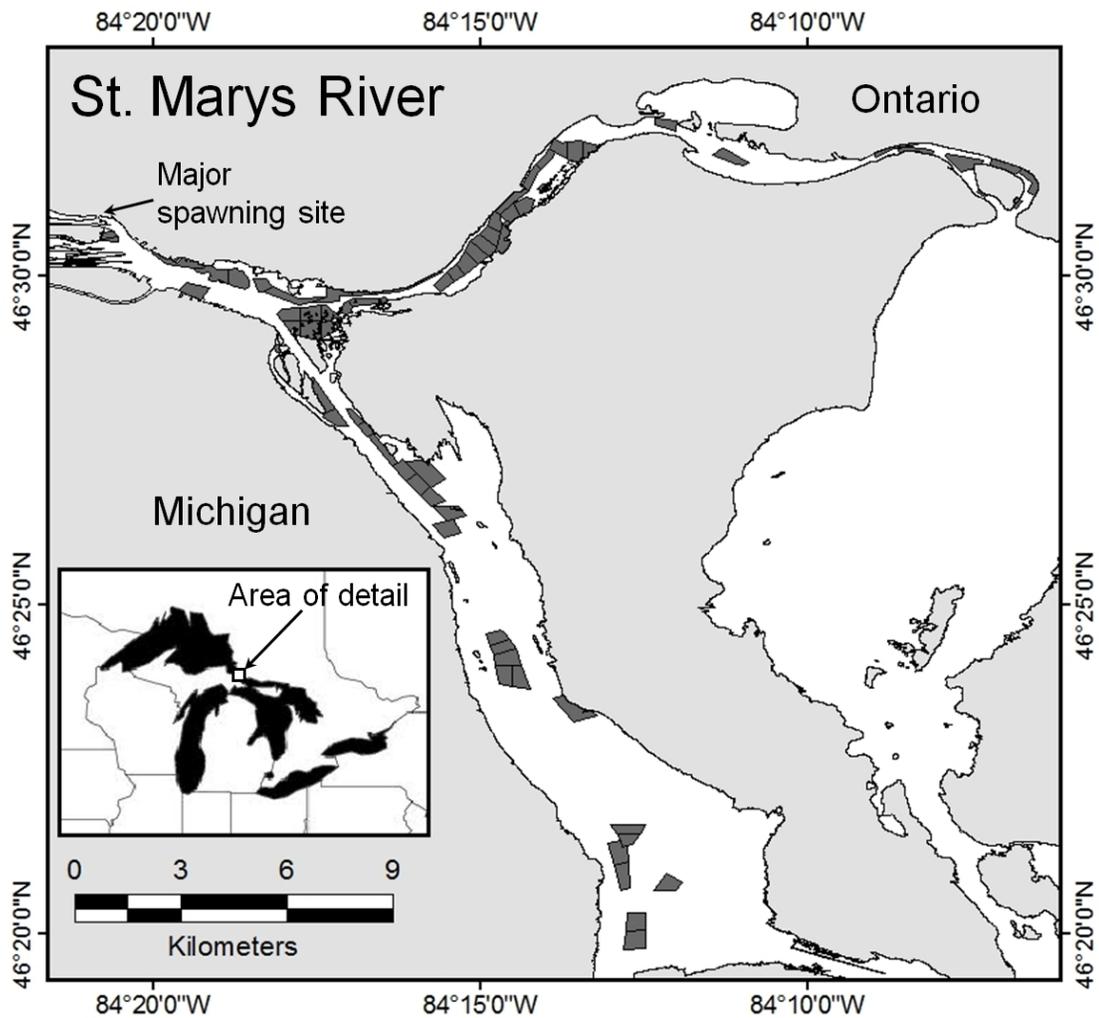


Figure 2.1. The St. Marys River from the navigational locks in Sault Ste. Marie, Michigan and Ontario, to the northern shore of Neebish Island. Coverage includes all plots that are assessed and considered for treatment. Dark gray areas are treatment plots and the white areas are considered out-of-plot (i.e., not treated). A portion of the out-of-plot areas that appear in the figure are never surveyed (large easternmost lentic area) and a small area that is surveyed is not included (Neebish channels to the south). 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.

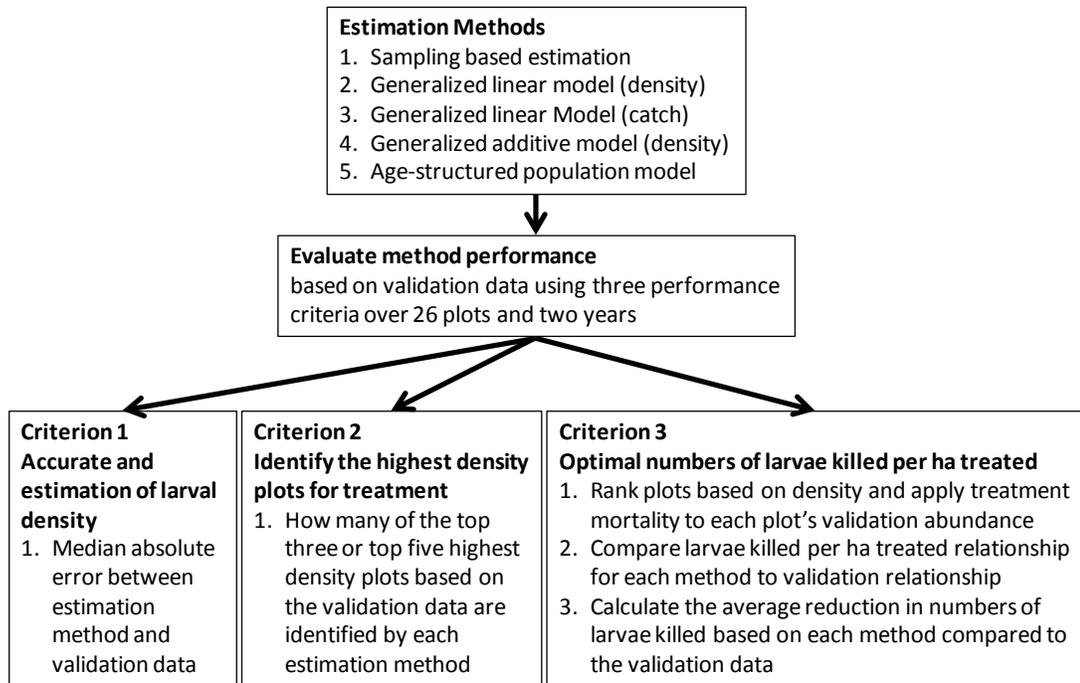


Figure 2.2. Flow chart describing the estimation methods, performance criteria, and the steps and metrics associated with each criterion.

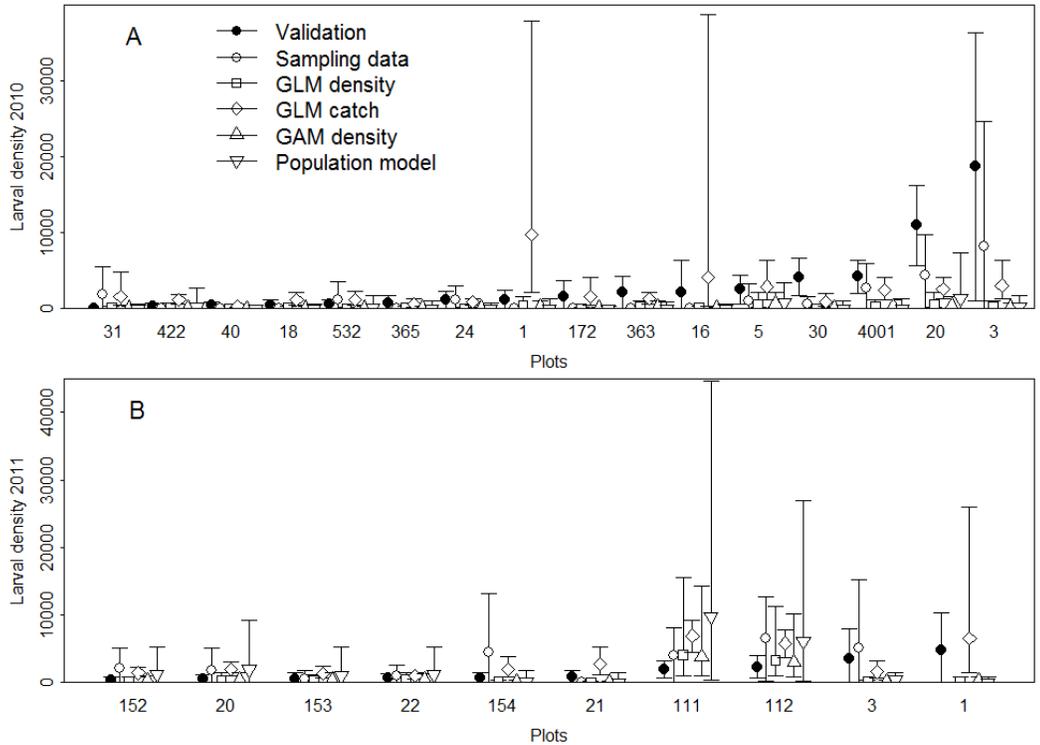


Figure 2.3. Plot-level larval density projections for 2010 (A) and 2011 (B) based on pre-treatment validation data, post-treatment sampling-based estimates from the previous year, generalized linear model based on density data (GLM density), generalized linear model based on catch data (GLM catch), generalized additive model projections based on density data (GAM density), and the population model. The hybrid approach was not included to prevent crowding. 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.

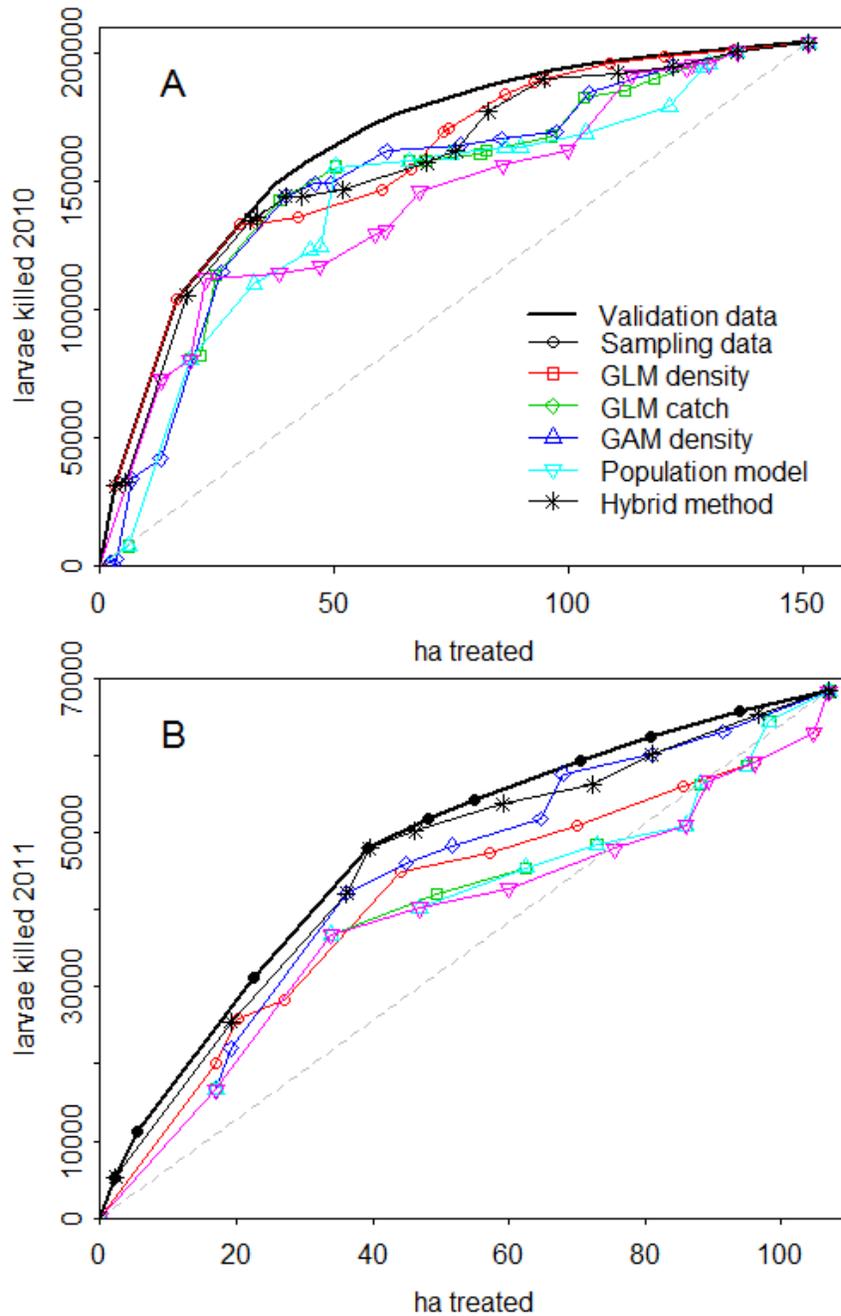


Figure 2.4. The expected number of larvae killed in 2010 (A) and 2011(B) as plots are treated based on rankings in order of decreasing density for each method. The expected number of larvae killed is based on the density from the pre-treatment validation data and the estimate of treatment effectiveness from Chapter 1. The hybrid is the relationship produced by averaging the density estimates from the sampling data and the GLM based on catch data. The grey dashed line is the average expected relationship if plots were treated in random order.

## Chapter 3: Maximizing sea lamprey (*Petromyzon marinus*) control by optimizing assessment and treatment decisions

### **Abstract**

Allocating resources between the gathering of information to guide management actions and implementing those actions presents an inherent tradeoff. Such a tradeoff is particularly evident for sea lamprey control in the St. Marys River, a major source of parasitic sea lampreys (*Petromyzon marinus*) to Lake Huron and northern Lake Michigan. Bayluscide treatments are carried out in areas of high larval density requiring abundance estimation at relatively fine spatial scales to inform treatment decisions. I took a resampling approach to consider the effect of sampling intensity on the success of the larval sea lamprey control program and explicitly incorporated the economic tradeoff between assessment and control efforts to maximize numbers of larvae killed in the St. Marys River. As expected, when no tradeoff between assessment and control was incorporated, increasing assessment always led to more control for the same treatment budget. When the tradeoff was incorporated, the sampling intensity that maximized the number of larvae killed depended on the overall budget available, with increased sampling intensities maximizing effectiveness under medium to large budgets (\$0.4 to \$2.0 million). Sea lamprey control actions based on assessment information outperformed those that were implemented with no assessment under all budget scenarios.

## **Introduction**

Management of natural resources should ideally seek to maximize the effectiveness an action (*e.g.*, pests killed, fish stocked, ecosystem services provided) while minimizing costs. Costs play a fundamental role in natural resource management (Fenichel and Hansen 2010, Clark 2005), and the need to formally incorporate these costs into the decision making process has become increasingly important (Shogren et al. 1999, Hansen and Jones 2008a, Fenichel and Hansen 2010). An inherent tradeoff exists between the gathering of information (assessment or sampling) to guide a management actions and implementing those actions (Mehta et al. 2007). Costs associated with gathering information to advise management include the cost of data collection and the opportunity costs: resources used to gather information that could be used in some other way to improve the management (Hansen and Jones 2008b). While many authors note the importance of incorporating this tradeoff into the management process, in most instances the tradeoff is not explicitly considered (Mehta et al 2007, Hansen and Jones 2008a, Fenichel and Hansen 2010). Explicitly considering the effect of resource allocation on the success of management actions should make the management process more effective and efficient.

Determining the appropriate level of sampling is an important consideration for management programs that assess populations and is especially important for invasive species control (Nally 1997, Mehta et al. 2007). Data collected via sampling programs are often the basis on which control decisions are made, and the intensity at which sampling is conducted can influence the success of a control program. If two

few samples are collected, the ability to differentiate between areas of high and low abundance may be reduced, and areas of high abundance may be missed. This is especially true when species distributions are patchy and zero catches are common, even in high density areas. Conversely, intensive sampling programs are costly, and there may be a point of diminishing returns, at which adding more samples will not lead to an increased ability to identify areas of high abundance. Consideration of appropriate sampling intensities is also important when the resources allocated to sampling reduce resources available for control. The sea lamprey (*Petromyzon marinus*) assessment and control program in the Laurentian Great Lakes is an example of a management program for which sampling has a direct impact on the effectiveness of control efforts through both the influence of sampling intensity on accuracy and the opportunity cost associated with data collection.

The invasion of sea lampreys into the upper Laurentian Great Lakes (Lakes Superior, Huron, and Michigan) in the early 20<sup>th</sup> century has resulted in major ecological and economic impacts (Smith 1971, Christie and Goddard 2003, Lupi et al. 2003). The U.S. portion of the Great Lakes' sport fishery is worth over \$7 billion USD to the U.S. regional economy each year (U.S. Fish and Wildlife Service 2006, Southwick Associates 2008) and the successful control of sea lampreys is a major reason for that economic value (Great Lakes Fishery Commission 2012). As a result, large scale efforts to control sea lampreys have been implemented throughout the Great Lakes with an annual budget of over \$15 million US (Hansen and Jones 2008b). The majority of these control efforts target the sedentary larval life stage in stream sediments using chemical control. In most streams, the lampricide TFM (3-

trifluoromethyl-4-nitrophenol) is used to control the larval stage (Christie and Goddard 2003). In lentic areas and extremely large rivers, TFM application is not feasible, 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 St. Marys River is one of the largest producers of sea lampreys to Lake Huron and northern Lake Michigan due to good spawning habitat and a large amount of high quality larval habitat, making it an important system for larval control (Fodale et al. 2003, Schleen et al. 2003). Sea lamprey control efforts in the St. Marys River have a positive net value in terms of economic benefits to recreational angling in Lake Huron (Lupi et al. 2003). TFM applications are impractical for the St. Marys River, because of its large size (depth and flow), so sea lampreys there are controlled through Bayluscide applications in areas of high larval density. Within river treatment decisions must be made on an annual basis, and are analogous to the among river treatment decisions associated with sea lamprey control in streams treated with TFM (Hansen and Jones 2008a). Seventy-one areas (plots) of good larval habitat have been identified within the river and are considered annually for Bayluscide application. In most years treating all plots in the river is impractical, and annual variation in the magnitude and spatial distribution of larval recruitment make plot-specific estimates of larval density necessary to guide treatment decisions. Therefore, annual assessments are conducted to inform treatment decisions in an attempt to achieve the highest number of larvae killed per ha treated. The larval sea lamprey assessment program in the St. Marys River is costly and resources allocated to

assessment effectively reduce the resources available for larval control in the river.

Hansen and Jones (2008a) showed that reduced assessment (*i.e.*, lower accuracy) in smaller sea lamprey producing streams could lead to increases in the number of sea lampreys killed by reallocating resources to control efforts. A similar tradeoff between assessment and control resources may also exist in the St. Marys River. The likelihood of ranking plots in the correct order based on larval density should increase as sampling intensity increases, resulting in higher numbers of larvae killed per ha treated. Given nearly perfect knowledge of larval density (*i.e.*, very high sampling intensity), the expectation is that the number of larvae killed per hectare treated would be very high at first and would slowly level off as areas with lower larval densities were treated. However, catches of larval sea lampreys in the survey are highly variable because of their heterogeneous spatial distributions and the relatively small area covered by each sampling event (2.44 m<sup>2</sup>); at low sampling intensities accurately ranking plots by density would likely be very inaccurate, resulting in a sub-optimal number of larvae killed per ha treated. When the economic tradeoff between resource allocation to assessment and control is considered there is likely to be a point of diminishing returns, where more assessment data will not increase the number of larvae killed because of the loss of control resources – leading to an optimal level of sampling effort. It is also likely that this optimal level of sampling effort will change with changing overall budget levels.

The continued suppression of the sea lamprey population in the Great Lakes is critical to achieving future fish management and restoration goals (Madenjian et al. 2003; Bronte et al. 2003; Dobiesz et al. 2005), and the success of the larval control

program in the Saint Marys River depends on the ability to successfully prioritize plots for treatment. Identifying sampling intensities that maximize the number of larval sea lampreys killed by the control program and explicitly incorporating economic tradeoffs between assessment and control should result in a more effective and efficient larval sea lamprey control program in the St. Marys River. I used a resampling approach using intensive deepwater electrofishing survey data to determine the effect of sampling intensity on the efficiency of the sea lamprey control program in the St. Marys River. I explicitly incorporated the tradeoff between the costs of assessment and control to maximize kill of larval sea lampreys in the St. Marys River. The specific objectives of this work were to (1) develop larvae killed per ha treated relationships for varying levels of sampling intensity and examine the potential for increased sampling to increase the efficiency of the treatment program, and (2) to explicitly consider the tradeoff between resource allocation to assessment versus control efforts to identify sampling intensities that will maximize the number of larvae killed under different overall budgets.

## **Methods**

The St. Marys River contains 71 treatment plots (830 ha total, in-plot) ranging in size from 1.2 to 27.5 ha for the purposes of conducting the deepwater-electrofishing surveys for larval sea lamprey assessment and applying Bayluscide for larval control (Fig. 3.1). Bayluscide application occurs in late spring and early summer, and is followed by annual post-treatment deepwater-electrofishing surveys that drive treatment decisions in the following year. Treatment plots were defined based on areas observed with high larval density during 1993–1996 (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 where electrofishing is conducted at a reduced intensity ( $0.02 \text{ samples} \cdot \text{ha}^{-1}$ , Chapter 1).

### *Field data*

High intensity pre-treatment deepwater electrofishing surveys were conducted in 2010 (16 plots) and 2011(10 plots) based on the methods described in Bergstedt and Genovese (1994). Surveys were conducted prior to treatment at a much higher intensity (mean intensity =  $5.2 \text{ samples} \cdot \text{ha}^{-1}$ , 8 fold increase) than would occur under normal sampling conditions ( $0.66 \text{ samples per ha}$  in 2011). Sampling areas were randomly selected within each plot, and a range of high, medium and low density plots were included to approximate the range of larval densities in the St. Marys River. The capture efficiency of the deepwater electrofishing gear decreases as larval sea lamprey length increases (Bergstedt and Genovese 1994), so a length-based gear selectivity correction was applied to all larval catch data:

$$C = \sum_i \left[ 1 + e^{(L_i * 0.0229 - 1.732)} \right] \quad (3.1)$$

where  $C$  is the adjusted catch for an individual electrofishing sample,  $L$  is the length of a larvae in mm, and  $i$  is an index for the individual sea lampreys captured and measured in the sample (U.S. Fish and Wildlife Service unpublished data).

The cost and time associated with intensively sampling all 71 plots in the St. Marys River was prohibitive, so I chose to represent the population based on a subsample of plots. Data from the 2010 and 2011 intensive surveys were combined to create a 26 plot pseudo-population, based on the assumption that the range of larval

densities and plot sizes in the St. Marys River was represented in the 26 plots sampled (Table 1.3). The pseudo-population was contained in an area 31% the size of the in-plot portion of the St. Marys River. Selectivity adjusted catch data from the intensive survey were used to calculate plot-level larval density estimates (larvae·ha<sup>-1</sup>) for the pseudo-population:

$$D_p = \frac{10,000}{n_p \cdot 2.44} \sum_{i=1}^{n_p} C_{i,p} \quad (3.2)$$

where  $D$  is the density and  $n$  is the sample size in each plot  $p$ , and 2.44 m<sup>2</sup> is the area of each sample. Plot-level larval abundance was calculated by multiplying the density estimates by plot areas. The density and abundance estimates calculated using all the field data from the intensive deepwater electrofishing survey are considered the best possible estimates.

A larvae killed per ha treated relationship was developed for the pseudo-population to represent the best possible treatment efficiency under the maximum available sampling intensity. This relationship offered a best case scenario to which relationships derived from lower sampling intensities could be compared. To develop the larvae killed per ha treated relationship, plots were ranked in descending order based on larval density estimates. Then a Bayluscide treatment was simulated by applying the percent mortality from an individual treatment event (51%, Chapter 1) to the estimated larval abundance for each plot, starting with the highest density plot. Treatment mortality was applied without error. Cumulative number of larvae killed, and cumulative area treated were calculated following the simulated treatment of each additional plot.

### *Resampling*

Five deepwater electrofishing sampling intensities were simulated by resampling the selectivity corrected catch data from each plot in the pseudo-population 1,000 times at each sampling intensity. In-plot sampling intensity used during the 2011 annual deepwater electrofishing survey conducted by the Department of Fisheries and Oceans Canada (DFO) are indicative of the sampling intensity in recent years, and were used to inform the simulated sampling intensities. I simulated five sampling intensities at 25, 50, 100, 150, and 200% of the average 2011 sampling intensity ( $0.66 \text{ samples} \cdot \text{ha}^{-1}$ ), resulting in sampling intensities of 0.15, 0.33, 0.66, 0.99, and  $1.32 \text{ samples} \cdot \text{ha}^{-1}$ . All of the simulated sampling intensities were considerably lower than those used to develop the pseudo-population (Table 1.3). The number of samples collected from each plot was calculated for each level of sampling intensity, by multiplying the plot area in ha by the desired sampling intensity ( $\text{samples} \cdot \text{ha}^{-1}$ ) and rounding to the nearest integer. The minimum number of samples that could be collected in each plot was set at one, ensuring that every plot received at least one sample under each sampling intensity.

Estimates of plot-level larval density were calculated for each simulated sampling event, providing 1,000 density estimates for each plot, at each sampling intensity. The 26 plots were ranked in descending order based on density for each of the 1,000 simulated sampling events. Larvae killed per ha treated relationships were then developed based on each simulated sampling event and by applying treatment mortality (51%, Chapter 1) to the abundance estimate for each plot calculated using all field data (Table 1.3). Cumulative larvae killed and cumulative ha treated were

then calculated following the simulated treatment of each additional plot. Larvae killed per ha treated relationships were also developed for a “no information” scenario, which was designed to simulate the random treatment of plots in the river with no sampling information. Plots were randomly selected and a simulated treatment event was applied. As with the other sampling intensities, this process was repeated 1,000 times.

Mean larvae killed per ha treated relationships were characterized for each sampling intensity and for the no information scenario using locally weighted regression scatter plot smoothing (loess curves, Neter et al. 1996). Loess curves were estimated with cumulative larvae killed in each plot as the dependent variable and cumulative ha treated as the independent variable, resulting in 26,000 data points for each loess curve. The loess method is nonparametric and fits successive linear regression functions from predetermined data point neighborhoods into a single curved line. To prevent the loss of information, loess curves were fitted with relatively small neighborhoods (20% of data points per neighborhood).

#### *Optimizing resource allocation*

I assumed that the overall budget for sea lamprey control in the St. Marys River was exclusive, such that resources spent on assessment reduced the funds available for control. The cost of collecting an electrofishing sample in the St. Marys River is \$80.11 USD, and the cost of treating one ha of river bottom with Bayluscide is \$4,395.50 USD, which includes staff time, equipment costs, and the cost of Bayluscide (Mike Steeves, Great Lakes Fishery Commission, personal communication). These values were used to describe the effect of the tradeoff

between assessment and control resources on numbers of sea lampreys killed under different budgets. I considered realistic total annual control budgets for the St. Marys River ranging from \$100,000 to \$2,000,000 USD. \$2 million USD would be enough to treat roughly half the plots in the St. Marys River if no resources were allocated to assessment. Total river budget levels corresponded to pseudo-population budget levels ranging from \$31,000 to \$622,000, because the area of the pseudo-population was 31% of St. Marys River in-plot population.

The cost of assessment for each sampling intensity was calculated by multiplying the cost of a single sample by the number of samples required to achieve the desired simulated sampling intensities for the 26 plot pseudo-population. The cost of collecting 50 (31% of the five year out-of-plot average sample size) additional samples was added to every assessment budget to account for the out-of-plot sampling that occurs in the river each year. The out-of-plot sampling level did not change with the in-plot sampling intensities based on the assumption that the out-of-plot areas would continue to be sampled at their present intensity, regardless of in-plot assessment decisions. The number of hectares that could be treated under each budget was calculated by subtracting the assessment budget from the total budget and dividing by the cost to treat one ha.

The loess curves for each sampling intensity were used to predict the mean number of larvae that would be killed as a result of treating a given number of ha. Numbers of larvae killed in the pseudo-population were predicted for each sampling intensity, under each budget. I approximated a 90% confidence interval around the estimated number of larvae killed by calculating the 0.05 and 0.95 quantiles for the

number of larvae killed for a given area treated ( $\pm 5$  ha) from the resampling data. The 10 ha range was necessary to ensure that enough data points were available to properly calculate the quantiles. For example, if 100 ha were treated the quantiles were calculated based on the number of larvae killed from 95 to 105 ha treated. Assessment: control cost ratios were also calculated for each budget and sampling intensity. All data analyses were performed using the statistical software R (R Development Core Team 2012).

## Results

High intensity pre-treatment deepwater electrofishing surveys ranged in sampling intensity from 2.6 to 14.2 samples $\cdot$ ha<sup>-1</sup> (Table 3.1). Estimates of plot-level larval sea lamprey density (larvae $\cdot$ ha<sup>-1</sup>) ranged from 0 to 18,700, and larval abundance estimates ranged from 0 to 142,000 (Table 3.1). The larvae killed per ha treated relationship developed using the intensive field data predicted a rapid increase in the number of larvae killed as very high density plots are treated, followed by a gradual reduction in larvae killed per ha as medium and low density plots are treated (Fig. 3.2).

Mean larvae killed per ha treated curves for each simulated sampling intensity fell below the curve based on the intensive field data, indicating a less efficient treatment application in terms of larvae killed for each additional ha treated (Fig. 3.2). The distance between larvae killed per ha treated curves based on the resampling data and the curve based on the intensive field data increased as simulated sampling intensity decreased, indicating increasing treatment efficiency with increasing sampling intensity. The kill per ha treated curve for the no information scenario was

approximately linear and was the most inefficient. Areas of greatest distance between the resampling-based curves and the field-based curve occurred at medium levels of treatment effort and were smallest at the extremes of treatment effort (*i.e.*, few or all plots treated). Variability in the number of larvae predicted to be killed by a simulated treatment event increased as the sampling intensity decreased for the survey data upon which treatment decisions were based (Fig. 3.3A-E). The no information scenario, in which plot-level treatment events were simulated in random order, produced the greatest variability (Fig. 3.3F).

Explicitly including a budgetary tradeoff between assessment and control efforts caused changes to the shape of the relationship between number of larvae killed and the sampling intensity upon which treatment decisions were based, depending on the overall size of the budget (Fig. 3.4A). As a result, the sampling intensity that maximized numbers of larvae killed changed as the overall budget changed. Larvae killed was never maximized under a no information scenario and the greatest change in the number of larvae killed occurred between the no information scenario and the lowest sampling intensity scenario ( $0.15 \text{ larvae} \cdot \text{ha}^{-1}$ ) at all budget levels. Under very small budgets (\$0.1 – \$0.2 million) larval kill was maximized from 0.15 to  $0.66 \text{ samples} \cdot \text{ha}^{-1}$ . As the overall budget increased, larval kill was maximized at the highest sampling intensity included in the analyses ( $1.32 \text{ samples} \cdot \text{ha}^{-1}$ ). However, the difference between larval kill at low versus high sampling intensities was relatively small especially under the largest budgets. Differences between numbers of larvae killed for each incremental increase in the overall budget also decreased as the size of the budget increased. Uncertainty around

the number of larvae killed decreases as the sampling intensity increased at all budget levels (Fig. 3.4B). At medium and high budget levels, the minimum number of lamprey larvae expected to be killed increases as sampling intensity increases. For example, at a budget of \$0.4 million and a sampling intensity  $0.15 \text{ samples} \cdot \text{ha}^{-1}$  there was a 95% chance of killing at least 21,400 lamprey larvae compared to 66,600 lamprey at a sampling intensity of  $1.32 \text{ samples} \cdot \text{ha}^{-1}$ . At a budget of \$1.8 million and a sampling intensity  $0.15 \text{ samples} \cdot \text{ha}^{-1}$  there was a 95% chance of killing at least 145,000 lamprey larvae compared to 205,000 lamprey at a sampling intensity of  $1.32 \text{ samples} \cdot \text{ha}^{-1}$ .

Assessment:control cost ratios at each sampling intensity decreased as the overall budget increased, and ratios for each budget increased with increasing sampling intensity. Assessment:control cost ratios exceeded one only for the lowest budget at sampling intensities of  $0.66 \text{ samples} \cdot \text{ha}^{-1}$  or above.

## **Discussion**

The tradeoff between resource allocation to data collection versus management actions has important implications for the cost effectiveness of management. I explicitly incorporated the economic tradeoff between assessment and control efforts to maximize the effectiveness of larval sea lamprey control in the St. Marys River. The sampling intensity that maximized the number of sea lampreys killed depended on the budget available, with higher sampling effort being beneficial under larger overall budgets. Additionally, simulated sea lamprey control actions based on sampling outperformed those that were implemented without sampling under all scenarios. Explicitly incorporating the economic tradeoff between resource

allocation to assessment and control in the St. Marys River and elsewhere should result in more efficient and effective control of sea lampreys in the Great Lakes, given the economic resources available.

Although the resources available for assessment and control in the St. Marys River are linked, it is worthwhile to consider a scenario under which resources allocated to assessment are separate from control. When no tradeoff between assessment and control is incorporated, increasing assessment always leads to more effective control, but approaches a point of diminishing returns as sampling intensity becomes high. The benefit of increased sampling is additionally diminished at very high or low treatment levels (*i.e.*, treatment of only a small area or treatment of the entire river). This occurs because the few areas of very high larval density can be identified with relatively low levels of sampling; therefore, a high sampling intensity is not necessary to effectively identify high density plots. Conversely, if a very large portion of the river is to be treated, the number of larvae killed will necessarily be maximized, greatly reducing the benefits of high sampling intensity.

Explicitly including the economic tradeoff between resource allocation to assessment and control changes how sampling intensity impacts the success of the treatment program. The effectiveness of treatment efforts does not necessarily increase with increasing sampling intensity if the tradeoff is included. If the budget is small, low sampling intensity frees up resources for treatment while still identifying high density plots. Under very large budgets low sampling intensity is also adequate because differentiating between high, medium, and low density plots becomes unnecessary. Increasing sampling intensity is most beneficial at intermediate budget

levels when differentiating between medium and low density plots becomes necessary to avoid wasting treatment resources in areas containing few sea lamprey larvae. At higher budget levels the estimated number of lamprey larvae killed was similar for all nonzero sampling intensities. However, there is still a benefit to high sampling intensities under high budgets because the minimum number of lamprey larvae expected to be killed increases as sampling intensity increases. Regardless of the budget level, collecting some information rather than none resulted in greater numbers of lamprey larvae killed.

Maximizing the number of larval sea lampreys killed is the primary goal of the sea lamprey control program, but it is not the only benefit of the sampling program and is therefore not the only consideration when determining appropriate sampling intensity. Defining goals in terms of population thresholds and sampling at intensities that will allow the detections of the desired changes if they occur is also an important consideration. Although a low level of sampling may maximize the number of larvae killed it may also be important to accurately estimate the number of sea lampreys killed as well as the current population level. Without this knowledge it is difficult to know when to suspend or scale back the control program in the Saint Marys River and allocate resources to some other sea lamprey producing area in the Great Lakes. The sampling program may also identify areas of high larval density outside the current plots, or in-plot areas that have consistently low larval populations, resulting in necessary changes in the plot structure. These issues represent opportunity costs that could result from inadequate sampling, but were not explicitly included in the analysis.

My analyses have several potential sources of uncertainty that are important to consider. Ideally the analyses would have included all of the treatment plots in the St. Marys River to ensure that the larval sea lamprey population was accurately characterized. However, the cost of sampling the entire population at a very high intensity was prohibitive, so I chose to represent the population based on a subsample of plots. The most likely potential issue with using a subsample of plots is that the frequency of high, medium, and low density plots in the pseudo-population is different than the actual St. Marys River population. If this is the case, it is most likely that very low density plots are underrepresented in the pseudo-population. Chapter 1 showed that there were a high number of very low density plots in the St. Marys River in recent years. I compared the frequency distributions of the plot densities in the pseudo-population to that of Chapter 1 and found them to be very similar. However, underrepresenting low density plots in the pseudo-population would result in underestimating the potential benefit of increasing sampling intensity at higher budget levels. Variability in the effectiveness of individual treatment events is also a source of uncertainty that was not accounted for in my analysis. Chapter 1 estimated a Bayluscide induced treatment mortality of 51% with a 90% credible interval of 0.37–0.64. As a result, the variability around simulated larval kill underestimates the true variability.

I considered the tradeoff between assessment and control for a single year's treatment event, which reflects the current method of assessment and treatment. If the information gained in assessment can help inform decisions in future years, the value of assessment would be higher than presented in my analyses. Prior

information could be used to inform the plot selection or assessment process, although prior information is not formally incorporated into the sea lamprey control program in the Saint Marys River currently. One potential method for including information from previous years is to include plots for treatment that have been identified as having very high larval sea lamprey density in past years (*i.e.*, expert judgment). However, my analysis indicates that low sampling intensities are successful in identifying plots with the highest densities, so this method is unlikely to significantly alter the relationship between sampling intensity and the success of the control program. A model based approach that incorporates previous years' data could also be used to identify plots for treatment. In Chapter 2 I found that averaging plot-level density estimates produced using a generalized linear model with those based on the survey data, would result in more effective treatment program for sea lampreys in the Saint Marys River.

The effect of sampling and assessment practices and the tradeoff between resource allocation to assessment and control have been considered in smaller sea lamprey producing streams (Hansen et al. 2003, Hansen and Jones 2008a). Hansen et al. (2003) recommended that sampling in smaller sea lamprey producing streams (*i.e.*, TFM treated streams) should be expanded to include suboptimal habitats and that reducing uncertainty surrounding stream-specific sea lamprey production could improve control efforts. In contrast, Hansen and Jones (2008a) showed that reducing effort allocation to assessment in smaller sea lamprey producing streams would result in a reduction in the accuracy of population estimate, but that the resulting increase in resources available for stream treatment would result in more larval sea lampreys

killed overall. My results agree with those of Hansen and Jones (2008a) for small St. Marys River control budgets, but the benefit of reducing sampling intensity was not apparent as budget size increased.

My work quantifies the tradeoff between assessment and control of an invasive species, and supports previous theoretical and empirical evidence demonstrating the importance of including economic tradeoffs in invasive species management (Mehta et al. 2007, Hansen and Jones 2008b, Fenichel and Hansen 2010). Additionally, this study illustrates the potential for budget constraints to change the optimal assessment or sampling strategy. Explicitly incorporating tradeoffs between assessment and control into invasive species management will help to identify the optimal allocation of resources to achieve desired objectives. The approach, and patterns I observed likely apply to spatially targeted control efforts for other invasive or nuisance species.

Table 3.1. St. Marys River plots sampled in 2010 and 2011, including plot identification number, plot areas (ha), number of samples, sample density (samples·ha<sup>-1</sup>), larval sea lamprey density estimates (larvae·ha<sup>-1</sup>), and larval abundance estimates for each plot.

year	plot	plot area	no. samples	sample density	larval density	larval abundance
2010	1	2.2	32	14.4	1,211	2,684
	3	3.3	12	3.6	18,702	61,510
	5	6.2	50	8.1	2,518	15,558
	16	1.2	9	7.3	2,111	2,591
	18	11.7	59	5.0	447	5,227
	20	13.0	56	4.3	10,961	142,356
	24	17.9	46	2.6	1,140	20,393
	30	7.1	44	6.2	4,189	29,757
	31	3.5	27	7.8	0	0
	40	15.2	59	3.9	419	6,360
	172	6.1	35	5.7	1,556	9,567
	363	11.9	60	5.0	2,101	25,042
	365	13.8	57	4.1	807	11,153
	422	15.7	60	3.8	279	4,383
	532	8.7	50	5.7	557	4,868
	4001	13.7	60	4.4	4,206	57,765
2011	1	2.2	15	6.8	4,727	10,473
	3	3.3	21	6.4	3,469	11,408
	20	13.0	47	3.6	523	6,789
	21	8.7	44	5.0	880	7,679
	22	15.6	47	3.0	657	10,212
	111	17.0	49	2.9	1,925	32,704
	112	17.0	50	2.9	2,322	39,382
	152	13.1	49	3.7	379	4,960
	153	10.4	40	3.8	561	5,858
	154	6.8	40	5.9	665	4,510

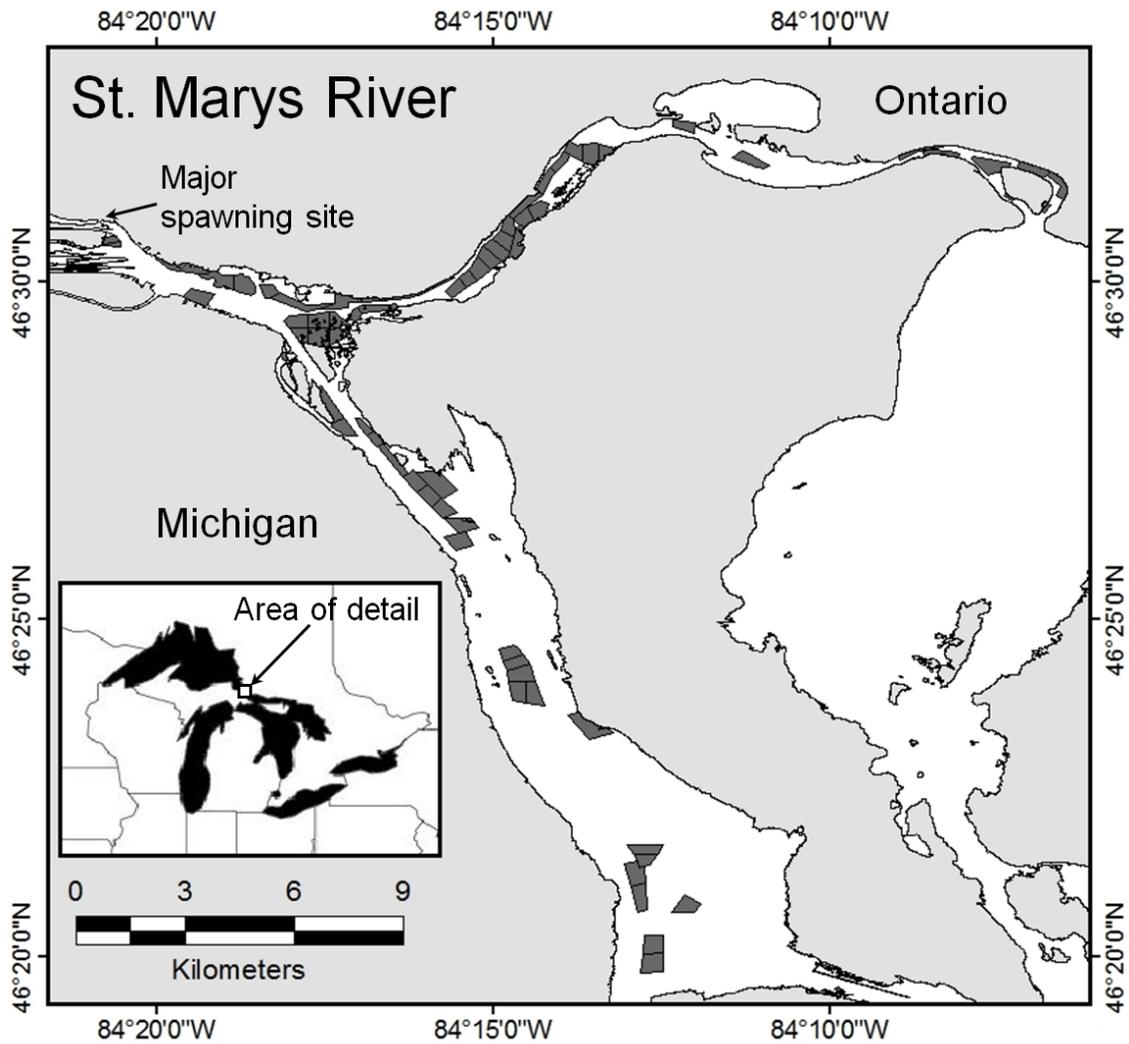


Figure 3.1. The St. Marys River from the navigational locks in Sault Ste. Marie, Michigan and Ontario, to the northern shore of Neebish Island. Coverage includes all plots that are assessed and considered for treatment. Dark gray areas are treatment plots and the white areas are considered out-of-plot (*i.e.*, not treated). A portion of the out-of-plot areas that appear in the figure are never surveyed (large easternmost lentic area) and a small area that is surveyed is not included (Neebish channels to the south). 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.

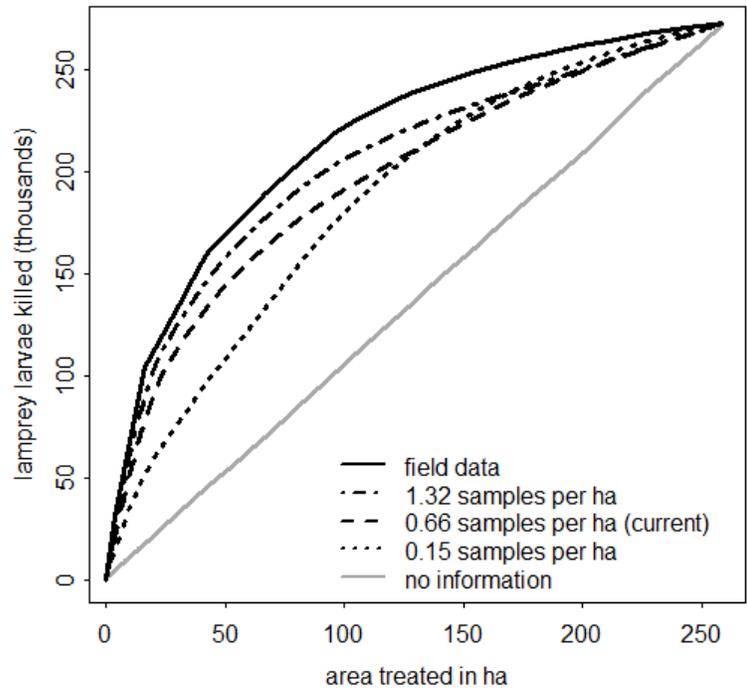


Figure 3.2. Loess curves fitted to larval sea lampreys killed per ha treated data from resampling at three sampling intensities and under a no information scenario. The solid black line is the larvae killed per ha treated relationship based on the high intensity field sampling and represents the most efficient kill per ha treated relationship. Only four of the six loess curves are shown, to prevent crowding.

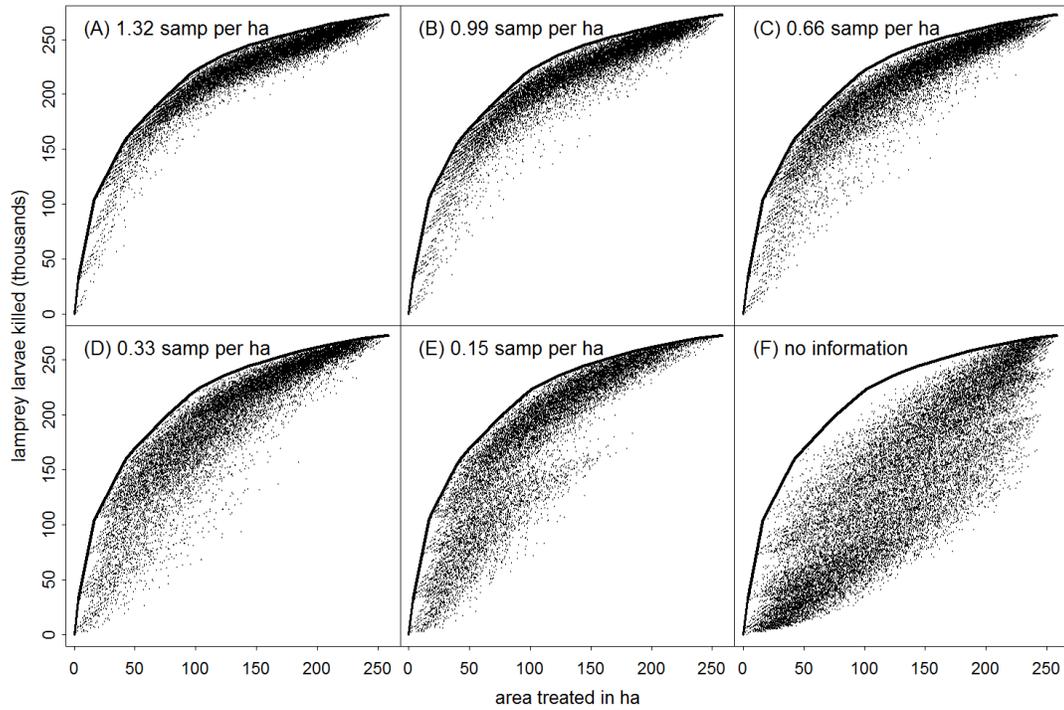


Figure 3.3. Larvae killed per ha treated estimates based on resampling of field data at five sampling intensities and a no information scenario (black points). The solid black line is the larvae killed per ha treated relationship based on the high intensity field sampling. The expected number of larvae killed is based on abundance estimates from the field data and the estimate of treatment effectiveness from Chapter 1.

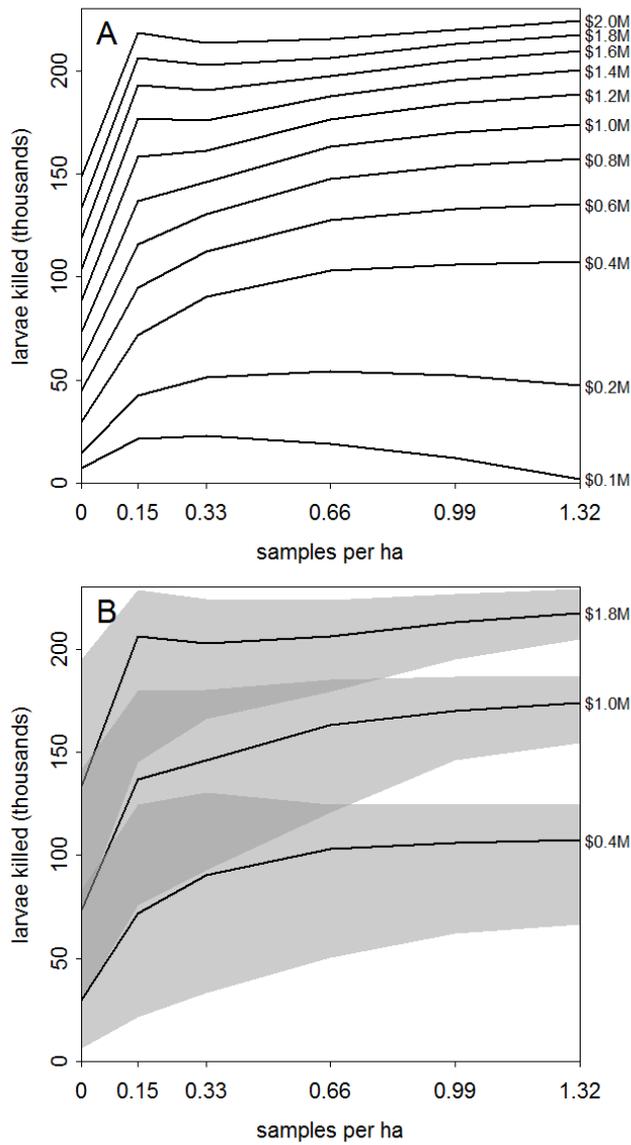


Figure 3.4. Larval kill isopleths at several budget levels (panel A). Estimated numbers of larvae killed applies only to the 26 plot pseudo-population at one point in time, but the budget levels are labeled at the scale of the Saint Marys River. Each line represents a fixed budget for treatment and assessment: as assessment increases the number of ha treated decreases. Grey shaded areas in panel B represent the range between the 5<sup>th</sup> and 95<sup>th</sup> percentiles around larval kill estimates for three budgets.

## Chapter 4: Evaluating Bayluscide-based control strategies for sea lamprey (*Petromyzon marinus*) in the St. Marys River, Michigan

### **Abstract**

The St. Marys River is one of the largest contributors of parasitic sea lamprey to Lake Huron and northern Lake Michigan making it an important area for larval control efforts. I developed a management strategy evaluation using a stochastic, spatially specific, age-structured simulation model to evaluate the performance of several fixed and survey-based Bayluscide-based treatment strategies for the control of sea lamprey (*Petromyzon marinus*) in the St. Marys River. The model considered 75 discrete spatial units (plots), incorporated annual larval recruitment, spatial recruitment patterns, natural mortality, larval metamorphosis, sampling and assessment, and larval control actions. The simulation results indicated that treatment options with higher cost (i.e. greater area of the river treated with higher frequency) resulted in larger long-term reductions in transformer abundance. However, as the level of treatment increased to a point at which all plots were being treated on an annual basis, increasing treatment effort did not result in a proportional decrease in the transformer population. In addition, survey-based treatment scenarios in which the location of treatment efforts was informed by annual deepwater electrofishing surveys, resulted in smaller transformer populations relative to fixed treatment scenarios of comparable cost. Therefore, survey-based treatment scenarios emerge as the most desirable from both an economic perspective and population control perspective. This approach provides a flexible framework to evaluate proposed changes in treatment strategy, and should be used in the future to identify treatment

strategies most likely to achieve cost-effective sea lamprey control goals in the St. Marys River.

## **Introduction**

Management strategy evaluation is becoming increasingly prevalent in the field of resource management (Cooke 1999, Sainsbury 1998). In a broad sense, management strategy evaluation seeks to identify management actions that are likely to achieve management objectives (Smith 1994). In practice, there are several factors that must be taken into consideration, such as the cost of implementing management actions, or uncertainty in population dynamics and effectiveness of management actions. This approach usually consists of identifying a management objective or objectives, a set of informative performance criteria, a set of realistic management actions, and a means of forecasting outcomes in terms of performance criteria (Smith 1994). In many cases the means of forecasting outcomes consist of a population model that can incorporate species specific life history and the effects of management and/or exploitation on the population (Sainsbury et. al 2000). There are many examples of management strategy evaluation improving the management of biological resources and resulting in the implementation of management actions that may not have been seen as optimal prior to the evaluation (Sainsbury et. al 2000).

While management strategy evaluation has been used to inform the control of invasive species (Dunstan and Bax 2008, Jones et. al 2009), it is more commonly employed in traditional management settings involving harvest (Cooke 1999, Mapstone et. al. 2008). Using management strategy evaluation to inform invasive species control holds promise for a number of reasons. In many cases the

management objectives for invasive species are more straightforward than for recreationally or commercially valuable species. In a typical resource management setting there are usually several stakeholder groups with different resource objectives. For example recreational anglers, commercial fisherman, and conservation groups may have very different management objectives in mind (Miller et al. 2010). In the case of invasive species management, the eradication or control of populations is the primary goal, with cost as the chief limitation. In these situations management strategy evaluation can offer a powerful approach to evaluate the costs and benefits of control strategies for invasive or nuisance species prior to implementation.

The invasion of sea lampreys into the upper Laurentian Great Lakes (Lakes Superior, Huron, and Michigan) in the early 20<sup>th</sup> century has resulted in major ecological and economic impacts (Smith 1971, Christie and Goddard 2003, Lupi et al. 2003). 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 Great Lakes, adults ascend streams to spawn. Adult sea lampreys select suitable streams based on the detection of a migratory pheromone released by larval lamprey (Sorensen and Vrieze 2003; Wagner et al. 2009). There is no evidence for natal homing in sea lamprey (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 lamprey 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). Irwin et al (2012) estimated that each parasitic phase sea lamprey causes approximately \$37 in damages, in terms of fishery value.

Sea lamprey control efforts have greatly reduced the numbers of parasitic phase sea lamprey in the Great Lakes making the rehabilitation of native piscivorous fish populations possible. 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). 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).

The St. Marys River is one of the largest producers of sea lampreys to Lake Huron and northern Lake Michigan due to good spawning habitat and a large amount of high quality larval habitat, making it an important system for larval control (Fodale et al. 2003, Schleen et al. 2003). Sea lamprey control efforts in the St. Marys River

have a positive net value in terms of economic benefits to recreational angling in Lake Huron (Lupi et al. 2003). TFM applications are impractical for the St. Marys River, because of its large size (depth and flow), so sea lampreys there are controlled through Bayluscide applications in areas of high larval density. Seventy-one areas (plots) of good larval habitat have been identified within the river and are considered annually for Bayluscide application. In most years treating all plots in the river has been impractical, and annual variation in the magnitude and spatial distribution of larval recruitment make plot-specific estimates of larval density necessary to guide treatment decisions. Therefore, annual assessments are conducted to inform treatment decisions in an attempt to achieve the highest number of larvae killed per ha treated. The objective of the sea lamprey control program in the St. Marys River is to reduce the number of metamorphosing sea lamprey (transformers) by as much as possible with the available resources.

Although the sea lamprey population in the St. Marys River is reported to be approximately 15 percent of its former abundance, the chemical treatment program in the river will continue into the foreseeable future (Chapter 1). In this study I develop a stochastic, spatially specific age-structured simulation model to evaluate the performance of several fixed and survey-based Bayluscide-based treatment strategies for the Control of sea lamprey in the St. Marys River. The model incorporates annual larval recruitment, spatial recruitment patterns, natural mortality, larval metamorphosis, sampling and assessment, and larval control actions. I then used this model to evaluate the long-term performance of several potential larval control scenarios. I also evaluate the sensitivity of each of these treatment scenarios to

uncertainty surrounding the effectiveness of control measures, gaps in the understanding of sea lamprey life history, and potential changes in the assessment program in the St. Marys River. The specific objectives of this work were to: (i) identify Bayluscide-specific treatment options that have the best long-term performance and that are robust to uncertainty, and (ii) to quantify the expected long-term impacts of each treatment option on the larval sea lamprey population.

## **Methods**

The St. Marys River, MI, 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 lamprey and applying Bayluscide (Fig. 4.1). Based on surveys conducted 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 ( $0.02 \text{ ha}^{-1}$ , Chapter 3). For the purposes of the simulation model, the out-of-plot portion of the St. Marys River was separated into 5 areas (Chapter 1). A single treatment plot (Plot 10) was included as part of the out-of-plot area because no sea lamprey were ever observed there, reducing the number of treatment plots in the analysis to 70. Application of Bayluscide to plots in the St. Marys River has occurred since 1998. The scale of the treatment efforts has varied annually with no plots being treated in some years and large-scale treatment efforts (*i.e.*, nearly all treatment plots) occurring in 1999, 2010, and 2011 (Chapter 1). Deepwater electrofishing surveys are conducted following

treatment efforts in each year. Larval density estimates produced using these surveys are used to drive treatment decisions in the following year, with only the highest density plots being treated in most years (Chapter 1)

High intensity pre-treatment deepwater electrofishing surveys were conducted in 2010 and 2011 as a means to validate the results of Chapter 1 and 2, and were used to inform the sampling portion of the simulation in this study. 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. A similar sampling effort was undertaken in 2011, which intensively sampled 10 plots. Data associated with the high intensity pre-treatment deepwater electrofishing surveys can be found in Appendix A. The capture efficiency of the deepwater electrofishing gear is reduced as larval lamprey length increases so a length-based gear selectivity correction was applied to all larval catch data:

$$C = \sum_i \left[ 1 + e^{(L_i * 0.0229 - 1.732)} \right] \quad (4.1)$$

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

### *Simulation model*

I simulated the population dynamics of sea lamprey in the Saint Marys River using a stochastic, spatially specific, age-structured model. The model structure and parameter distributions were based on the model structure and results of the model

developed in Chapter 1. The model incorporated annual recruitment, spatial patterns in recruitment, Bayluscide treatment mortality, and natural mortality to describe the long term dynamics of sea lamprey larvae and transformers under several hypothetical Bayluscide-based treatment scenarios (Fig. 4.2). Simulated treatment options included fixed treatment scenarios in which a fixed area of the river was treated on a fixed schedule, and survey-based treatment scenarios in which the areas treated changed annually based on a simulated sampling program designed to approximate the current sampling program in the St. Marys River. The simulation model was run 1000 times for each treatment scenario, and each simulation ran for fifty years using an annual time step. The sea lamprey population was allowed to stabilize for 14 time steps prior to any treatment program being simulated. Variables included in the simulation model are described in Table 1.4. All simulations and analyses analyses were performed using program R (R Development Core Team 2012).

The model structure allowed for stochastic variability in total river 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. I assumed that recruitment of larvae to plots occurred prior to treatment events (Fig. 4.2). A traditional stock-recruitment relationship was not used to inform larval sea lamprey recruitment in the simulation. Rather, total river annual recruitment ( $R$ ) at age-1 was drawn from a log normal distribution ( $\log N(\mu = 12.18, \sigma^2 = 0.56)$ ), the parameters of which were estimated using the posterior distribution of total river recruitment estimates from Chapter 1. Recruits were apportioned among the plots as

the product of total recruitment and the proportion of total recruitment,  $r$ , assigned to each plot:

$$N_{a=1, t, p} = R_t r_{t, p} \quad (4.2)$$

Recruitment proportions were produced using a multinomial distribution in each simulation year. The distribution was informed using the mean of the posterior distributions of estimated recruitment proportions from Chapter 1. Using those probabilities 1000 objects were assigned to the treatment plots. Annual recruitment proportions for each plot were then produced by normalizing the vector of plot-level objects to sum to one. Recruitment proportions were determined for each model year independently.

Plot-specific larval abundance following treatment in each year,  $N$ , was calculated by decrementing post-treatment larval abundance in the previous year by natural mortality,  $M$ , larval transformation rates at age,  $t$ , and Bayluscide treatment mortality,  $B$ :

$$N_{a+1, t+1, p} = N_{a, t, p} e^{-M} (1 - t_a) (1 - B)^{b_{t+1, p}} \quad (4.3)$$

where  $b$  is an indicator variable that describes the number of times a plot should be treated in each year. Natural mortality values for each plot and year were drawn from a log-normal distribution ( $\log N(\mu = -2.37, \sigma^2 = 0.14)$ ). Bayluscide treatment mortality values for each plot and year were drawn from a normal distribution ( $N(\mu = 0.51, \sigma^2 = 0.0065)$ ). The parameters of the distributions for  $M$  and  $B$  were estimated using the posterior distributions of  $M$ , and  $B$  from estimates from Chapter 1. Larval transformation was assumed to occur following post-treatment sampling (Fig. 4.2). Age-specific larval transformation rates ( $t_a$ : age 1-3, 0; age 4, 0.46; age 5, 0.57; age 6,

1.0) were taken from Haeseker et al. (2003) and were assumed to be constant through time. The maximum larval age was set to six because less than 1% of larvae aged from 1993 to 1996 were greater than 6 years old (Schleen et al. 2003). Transformer abundance ( $T$ ) was calculated by multiplying the number of larvae that survive treatment and natural mortality by the expected proportion that transformed at each age:

$$T_{a,t,p} = \sum_a N e^{-M} t_a (1-B)^{b_{t,p}}. \quad (4.4)$$

Numbers of larvae killed ( $Nkill$ ) was calculated by multiplying the number of larvae surviving in the previous year by treatment mortality:

$$Nkill_{a+1,t+1,p} = N e^{-M} (1-t_a) [1 - (1-B)^{b_{t+1,p}}]. \quad (4.5)$$

#### *Simulated sampling and treatment*

Sampling was simulated to approximate the sampling program in the St. Marys River in recent years, which occurs at an intensity of 0.66 samples·ha<sup>-1</sup> and 0.02 samples·ha<sup>-1</sup> for in- and out-of-plot areas respectively (Chapter 3). Negative binomial distributions were fitted to gear selectivity adjusted catch data from each plot sampled during the 2010 and 2011 intensive sampling surveys. Simple linear models were used to describe the relationship between plot-level larval density and the parameters of the negative binomial distribution. The linear regression parameters were then used to estimate the parameters of a negative binomial distribution for each plot and year based on the simulated plot-level densities. Larval lamprey catch was simulated for each individual electrofishing sample by using simulated density to inform the parameters of the negative binomial distributions.

Sample size in each plot was calculated by multiplying the plot area by the desired sampling intensity. Larval density estimates for each plot were calculated using the simulated catch data, and were used to inform treatment decisions.

Several fixed and survey-based treatment scenarios were simulated. Fixed treatment scenarios were those in which all plots (829 ha) or a subset of plots were treated on a set time interval. These scenarios include no treatment, all plots being treated annually, every two years, every three years, or every four years. An additional fixed interval scenario was included in which the in- and out-of-plot areas contained in river area one (541 ha, Fig. 4.1) were treated annually. This scenario was based the results of Chapter 1, which indicated that river area one received 60% of the total river age-1 recruitment. Survey-based treatment scenarios used density estimates from the simulated sampling program to drive treatment decisions, and included a 100 ha treatment and a 200 ha treatment. These treatment scenarios are realistic given the cost of treatment and the size of the in-plot area of the St. Marys River. Plots were treated in descending order based on estimated density until the desired number of ha were treated. Partial plot treatments were not considered and the desired number of ha to be treated could not be exceeded. A scenario under which some plots could be treated twice in one model year was also considered for the 100 and 200 ha treatment scenarios. Under this scenario plots were treated twice if they still had a higher estimated larval lamprey density than other plots after the mean expected treatment mortality was applied.

### *Metrics of performance*

Two metrics of treatment program performance were considered. For the purposes of calculating treatment program performance, the population was considered stable during model years 10-14 (pre-treatment implementation), and 30-50 (treatment period). Metrics of treatment program performance were: (1) mean transformer abundance from year 30-50, and (2) the mean of the standard deviation of transformer abundance from year 30-50. The percent reduction in transformer abundance from the pre-treatment period to the treatment period was also calculated along with the cost of treatment under each treatment scenario. The relationship between the percent reduction in transformer escapement and the cost of each treatment scenario was considered as way to objectively compare the overall performance of each scenario. The cost of collecting an electrofishing sample in the St. Marys River is \$80.11 USD, and the cost of treating one ha of river bottom with Bayluscide is \$4,395.50 USD, which includes staff time, equipment costs, and the cost of Bayluscide (Mike Steeves, Great Lakes Fishery Commission, personal communication).

### *Sensitivity analysis*

We tested the sensitivity of the model to (1) changes in the effectiveness of Bayluscide treatments, (2) changes in the amount of spatial variability in recruitment, and (3) changes in the intensity of the sampling program that informs survey-based treatment decisions. The degree of sensitivity was evaluated by comparing the proportional difference in the metrics of treatment program performance relative to the base simulation. Sensitivity to the effectiveness of Bayluscide treatments was

tested by increasing the mean and decreasing the variance (of the normal distribution from which Bayluscide treatment effectiveness was drawn in the simulation ( $N(\mu = 0.88, \sigma^2 = 0.0025)$ ). This mean and variance was based on an estimate of Bayluscide treatment mortality from a single large scale treatment event in 1999 (Fodale et al. 2003). The distribution was constrained so the treatment effectiveness could not exceed one. Sensitivity to spatial variability in recruitment was tested by changing the number of objects assigned to each plot (500 and 1500) based on the multinomial distribution. Decreasing the number of objects increases the spatial recruitment variability and vice versa. Sensitivity to the intensity of the sampling program that informs treatment was tested by assuming realistic sampling intensities that were higher and lower than the intensity used for the base model (0.33 and 0.99 samples·ha<sup>-1</sup>, Chapter 3). Sensitivity to sampling intensity was only considered for survey-based treatment scenarios.

## Results

There were significant positive relationships between the dispersion and the mean parameters of the negative binomial distributions and the plot specific density estimates associated with the deepwater electrofishing survey catch data (Fig. 4.3). Linear models fit the data well, and larval density explained a large amount of the variability in the dispersion and mean parameters of the negative binomial distributions (dispersion parameter:  $\beta_0 = 0.007, \beta_1 = .000019, R^2 = 0.69$ ; mean parameter:  $\beta_0 = 0, \beta_1 = 0.00024, R^2 = 1$ )

All simulated treatment scenarios resulted in rapid decreases in larval lamprey and transformer abundance, with larval and transformer abundance stabilizing

approximately five years after the onset of treatment (Fig. 4.4). Fixed treatment scenarios in which treatment did not occur every year resulted in a saw tooth pattern in larval and transformer abundance. All treatment scenarios in which treatment occurred annually resulted in large numbers of lamprey killed by the initial treatment followed by a rapid decrease and stabilization in the number of lamprey killed in subsequent years (Fig. 4.5A and 4.5E-I). Treatment scenarios in which treatment was not conducted every year resulted in large numbers of lamprey killed in treatment years (Fig. 4.5B-D).

Treating all plots annually resulted in the lowest mean long term transformer abundance and mean standard deviation in transformer abundance (63,300 and 30,400 respectively) followed closely by treating the entirety of area one annually (68,100 and 32,800 respectively, Table 4.1). Treating all plots every 4 years resulted in the largest long term transformer abundance and standard deviation in abundance transformers (105,000 and 51,600 respectively). Survey-based treatment scenarios in which treated plots changed annually based on the results of sampling resulted in intermediate levels of transformer abundance (Table 4.1). Survey-based treatment scenarios in which double treatments were considered did not reduce transformer abundance relative to the survey-based scenarios with single treatments.

Variability surrounding the simulation estimates was very high (Fig. 4.6) and there was a positive relationship between the mean transformer abundance under each treatment scenario and the mean standard deviation of transformer abundance for each scenario (Fig. 4.7A). However, there was no obvious trend between transformer abundance and the coefficient of variation (CV) for each scenario, with all CVs

ranging from 46.5-50.1. Percent transformer reduction from the untreated conditions to the treated condition increased as the cost of treatment increased (*i.e.* larger areas of the river were treated, Fig 4.7B). However, survey-based treatment scenarios resulted in a greater percent reduction in transformer abundance than fixed treatment scenarios that had similar treatment costs.

Performance metrics and treatment scenarios were moderately sensitive to increases in Bayluscide treatment mortality (Table 4.2). Increasing mean treatment mortality from 0.51 to 0.88 decreased estimates of transformer abundance and the variability around those estimates for all treatment scenarios, but had the highest impact on fixed scenarios in which plots were not treated annually. Increasing treatment mortality also altered the order of performance for the nine treatment scenarios relative to each other. Annual variability in spatial recruitment patterns of larvae had little to no impact on the simulation results regardless of the direction of that variability. Sensitivity to changing sampling intensities was only considered for survey-based treatment scenarios which are driven by sampling-based density estimates. Increasing sampling intensity from 0.66 to 0.99 samples·ha<sup>-1</sup> had almost no impact on the simulation results. However, decreasing sampling intensity to 0.33 samples·ha<sup>-1</sup> did cause a slight decrease in the effectiveness of survey-based treatment scenarios.

## **Discussion**

I developed a stochastic, spatially specific, age-structured simulation model that incorporated critical aspects of sea lamprey life history, the annual larval assessment program, and larval control actions in the St. Marys River, Michigan. The

model was designed to simulate the long term performance of several fixed and survey-based treatment programs for sea lamprey larvae based on predicted long-term reduction in transformer abundance. Initial treatments killed large numbers of larvae followed by a rapid decrease in the number of larvae killed by subsequent treatment under all scenarios. The simulation results indicate that treatment options with higher cost (i.e. greater area of the river treated with higher frequency) resulted in larger long-term reductions in transformer abundance. However, as the level of treatment increased to a point at which all plots were being treated on an annual basis, increasing treatment effort did not result in a proportional decrease in the transformer population. In addition, survey-based treatment scenarios in which the location of treatment efforts was informed by annual deepwater electrofishing surveys, resulted in smaller transformer populations relative to fixed treatment scenarios of comparable cost.

Increasing the effectiveness of Bayluscide treatment within the simulation resulted in substantial decreases in the transformer abundance and changes in the relative performance of each treatment scenario. The model-based estimate of Bayluscide induced treatment mortality from Chapter 1 ( $0.51 \text{ treatment}^{-1}$ ) was lower than the previous estimate ( $0.88 \text{ treatment}^{-1}$ ), which was estimated based on a single large scale treatment event in 1999 (Fodale et al. 2003). The sensitivity of the simulation results to uncertainty surrounding Bayluscide effectiveness, and the disparity in the estimates of Bayluscide mortality produced using different methods, underscores the need for targeted efforts to improve estimates of Bayluscide effectiveness in a field environment.

Changes in spatial recruitment patterns had very little impact on the performance of treatment scenarios. However, major changes in underlying drivers of spatial recruitment were not considered because high density plot locations have been quite stable over time (Chapter 1). If large changes in spatial recruitment were to occur, fixed treatment scenarios that focus only on one area of the river (*e.g.* treating area 1 only) would be highly sensitive to these changes. This simulation was based on recent recruitment conditions, but the results, in terms of the relative size of the transformer population resulting from each scenario, should be robust to modest changes in future larval recruitment levels.

Increasing sampling intensity from 0.66 to 0.99 samples·ha<sup>-1</sup> also had very little impact on the estimated transformer population for the survey-based treatment scenarios. However, decreasing sampling intensity to 0.33 samples·ha<sup>-1</sup> did cause a slight decrease in the effectiveness of survey-based treatment scenarios. This supports the results of Chapter 3 in which increasing sampling intensity was shown to reach a point of diminishing returns because it does not increase the ability identify high density plots. In contrast, decreasing sampling intensity was shown to reduce the ability to identify high density plots resulting in failure to treat those areas under a survey-based treatment scenario.

The directionality and magnitude of the sensitivity of standard deviation of transformer abundance estimates was very similar to that of the actual transformer abundance estimates. This was due to the fact that variability in estimates of transformer abundance was reduced as the transformer population decreased. Similarly, Chapters 1 and 2 showed that variability in sample-based estimates of

larval density tended to decrease as larval density decreased, a phenomenon common in fisheries data (Punt et al. 2000).

The evaluation of treatment strategies indicates that if treatment resources are limited (e.g., not all plots can be treated), a survey-based, assessment driven approach is preferable to treating a fixed area of the river every year. The superiority of the survey-based approach is largely driven by the low cost of sampling relative to treatment. The survey-based scenarios have the added benefit of being able to adjust to unexpected changes in spatial recruitment patterns. The estimated reduction in transformer abundance that can be achieved using a survey-based treatment approach occurs at a reduced cost relative to fixed treatment scenarios with similar performance. For example: the 200 ha survey-based treatment scenario and the fixed treatment scenario under which all plots were treated every four years had similar long term costs, but the survey-based scenario resulted in 20,000 fewer transformers being produced annually. Fixed treatment scenarios that did not occur annually also resulted in pulses of transformer abundance which could cause higher year to year variation in lake trout wounding and mortality rates. The results of this study also indicate that treating the entire in-plot portion of river at current population levels, as was done in 2011 and 2012, will almost certainly result in a large amount of wasted resources given the number of plots that contain very few lamprey larvae.

Haeseker et al. (2007) conducted a similar study in which they used decision analysis to rank management options for controlling sea lamprey in the St. Marys River. In some ways their approach was more complex in that they considered combinations of three treatment methods (i.e., Bayluscide, adult trapping, and sterile

male release), and linked the simulated dynamics of the sea lamprey population in the St. Marys River to that of Lake Huron. As a consequence of that broad complexity, their simulation model did not include spatial variation in lamprey density in the St. Marys River, or the potential for annual sampling to drive treatment decisions. In contrast, my approach focused on directly informing Bayluscide application decisions in the St. Marys River, including the location of treatment and the sampling that informs that treatment application. Relative to my conclusions, Haeseker et al. (2007) downplay the effectiveness of Bayluscide treatment. It is likely that their analysis underestimates the potential for Bayluscide treatments to reduce lamprey abundance relative to other approaches because they only consider fixed treatment events occurring every 4 years, an approach which my results show to be inferior to survey-based treatments and many fixed treatment scenarios. Although they did not consider survey-based Bayluscide applications, Haeseker et al. (2007) posited that treatment events driven by larval density data (i.e., sampling) will almost certainly be superior to those conducted on a four year cycle. It is also important to note that Bayluscide is increasingly becoming the primary tool for controlling the sea lamprey population in the St. Marys River, with large scale treatment events having occurred in 2010 and 2011 and the sterile male release program in the river being discontinued.

Uncertainty surrounding the movement of organisms in habitats to which they are not native is likely because movement patterns and other life history traits of invasive species may differ from their native habitats (Moony and Cleland 2001). Although including post-settlement larval sea lamprey movement in the simulation model and management strategy evaluation was beyond the scope of Chapter 4,

movement has the potential to negatively impact the effectiveness of control efforts if larvae are moving into low density areas that are not likely to be selected for chemical treatment. The age and timing of movement, coupled with the direction and magnitude of that movement will affect the optimal timing, location, and magnitude of control efforts. Data do not currently exist to directly inform movement of larval lampreys in the St. Marys River, and conducting field based studies to assess movement would be logistically challenging and costly due to low detection probabilities, a large area of suitable habitat, difficulty in tagging small individuals, and large numbers of individuals. Given this lack of information, future simulation studies should be conducted to identify optimal control strategies that are robust to uncertainties surrounding larval sea lamprey movement in the St. Marys River.

Continuing to increase the effectiveness and efficiency of the sea lamprey control program has benefits that apply to the entire Great Lakes ecosystem. Decreasing the amount of area that has to be treated to obtain a given reduction in transformer escapement would result in a reduction in both the cost of treatment and the amount of Bayluscide that must be applied. A reduction in the amount of Bayluscide applied is desirable from an ecosystem health perspective, given the documented lethal and sublethal effects of Bayluscide on non-target organisms (Dawson 2003).

This study includes only a small fraction of the Bayluscide-based treatment options that could be applied to control sea lamprey in the St. Marys River, but provides a flexible framework to evaluate proposed changes in treatment strategy or the larval sampling program. An approach such as this should be used in the future to

identify treatment strategies most likely to achieve sea lamprey control goals in the St. Marys River without wasting financial resources that could be applied to other lamprey producing streams. This approach shows promise for improving decisions associated with invasive species control in general, and is currently being underutilized.

Table 4.1. Description of symbols used in simulation equations and values associated with each symbol where applicable.

Symbol	Description	Value if applicable
$a$	Age class (age-1 through age-6)	
$t$	Time 1-50	
$p$	Plots (75 river areas, see Fig. 4.1)	
$N$	Plot-specific larval abundance	
$R$	Total river age-1recruitment	$\log N(\mu = 12.18, \sigma^2 = 0.56)$
$r$	Recruitment proportions	
$M$	Instantaneous natural mortality (1)	$\log N(\mu = -2.37, \sigma^2 = 0.14)$
$t$	Age-specific transformation rate	age-4 = 0.46, age-5 = 0.57 age 6 = 1
$B$	Bayluscide effectiveness (1)	$N(\mu = 0.51, \sigma^2 = 0.0065)$
$b$	Bayluscide treatment indicator	
$T$	Transformer abundance	
$N_{kill}$	Number of larvae killed	

Table 4.2. Mean estimates of performance metrics and proportional differences in estimates (in parentheses) from the primary simulation, and the simulations with increased treatment effectiveness, increased recruitment variability, decreased recruitment variability, increased sampling intensity, and decreased sampling intensity. Simulations were performed under each of the nine treatment scenarios. Proportional differences in performance metrics are relative to the estimates from the primary model.

Performance metric	treatment scenario	Primary simulation	Increased treatment efficiency	Increased recruitment variability	Decreased recruitment variability	Increased sampling intensity	Decreased sampling intensity
mean	all plots every year	63.3	59.0 (0.07)	63.2 (0.00)	62.9 (0.01)		
transformer	all plots 2 year	79.5	60.1 (0.24)	78.6 (0.01)	78.3 (0.02)		
abundance	all plots 3 year	93.9	65.2 (0.31)	94.9 (0.01)	93.6 (0.00)		
in thousands	all plots 4 year	105	70.1 (0.33)	104.2 (0.01)	105.6 (0.00)		
	area one annually	68.1	63.8 (0.06)	67.7 (0.01)	68.2 (0.00)		
	survey 100 ha	95.6	81.6 (0.15)	96.6 (0.01)	97.0 (0.01)	94.9 (0.01)	100.8 (0.05)
	survey 200 ha	84.5	70.6 (0.16)	83.6 (0.01)	84.6 (0.00)	83.1 (0.02)	89.5 (0.06)
	survey 100 ha double	96.3	82.6 (0.14)	96.5 (0.00)	97.7 (0.01)	95 (0.01)	100.9 (0.05)
	survey 200 ha double	83.8	72.5 (0.13)	84.0 (0.00)	84.7 (0.01)	83.2 (0.01)	87.8 (0.05)
standard	all plots every year	30.4	28.1 (0.08)	30.4 (0.00)	30.0 (0.01)		
deviation of	all plots 2 year	38.5	28.8 (0.25)	38.3 (0.01)	37.3 (0.03)		
transformer	all plots 3 year	47.0	31.7 (0.33)	48.5 (0.03)	46.4 (0.01)		
abundance	all plots 4 year	51.6	34.1 (0.34)	50.8 (0.02)	52.8 (0.02)		
in thousands	area one annually	32.8	30.3 (0.08)	32.9 (0.00)	32.7 (0.00)		
	survey 100 ha	44.5	37.8 (0.15)	46.4 (0.04)	45.6 (0.02)	45.5 (0.02)	47.7 (0.07)
	survey 200 ha	40.1	33.3 (0.17)	39 (0.03)	39.8 (0.01)	39.6 (0.01)	40.7 (0.01)
	survey 100 ha double	45.6	39.0 (0.14)	44.9 (0.02)	46.3 (0.02)	44.7 (0.02)	48.2 (0.05)
	survey 200 ha double	39.9	33.1 (0.17)	39.2 (0.02)	40.8 (0.02)	39.1 (0.02)	41.1 (0.03)

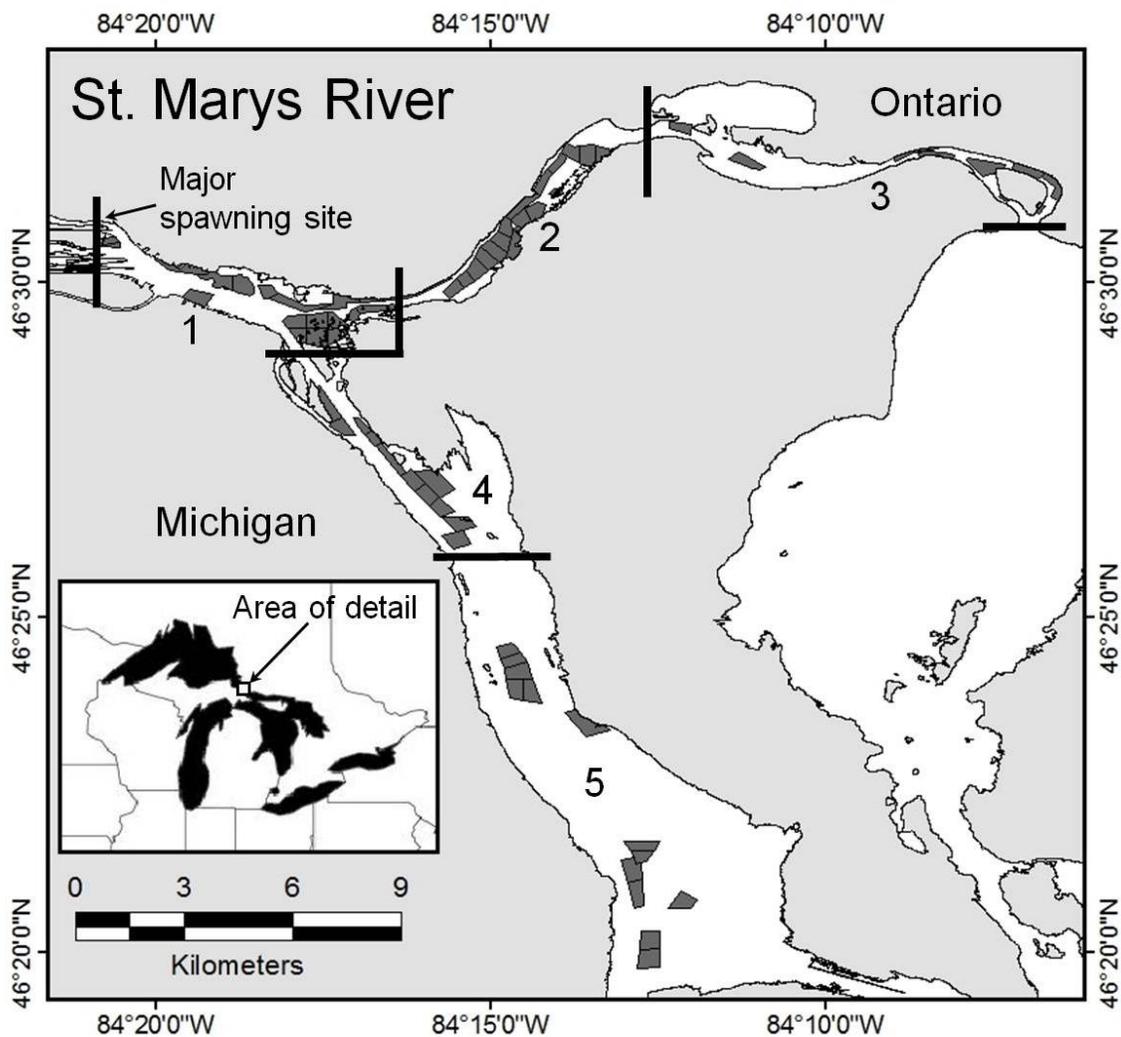


Figure 4.1. The St. Marys River from the navigational locks in Sault Ste. Marie, Michigan and Ontario, to the northern shore of Neebish Island. Coverage includes the entire portion of the river that is treated and assessed by the sea lamprey control program. Dark grey areas are treatment plots and the 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.

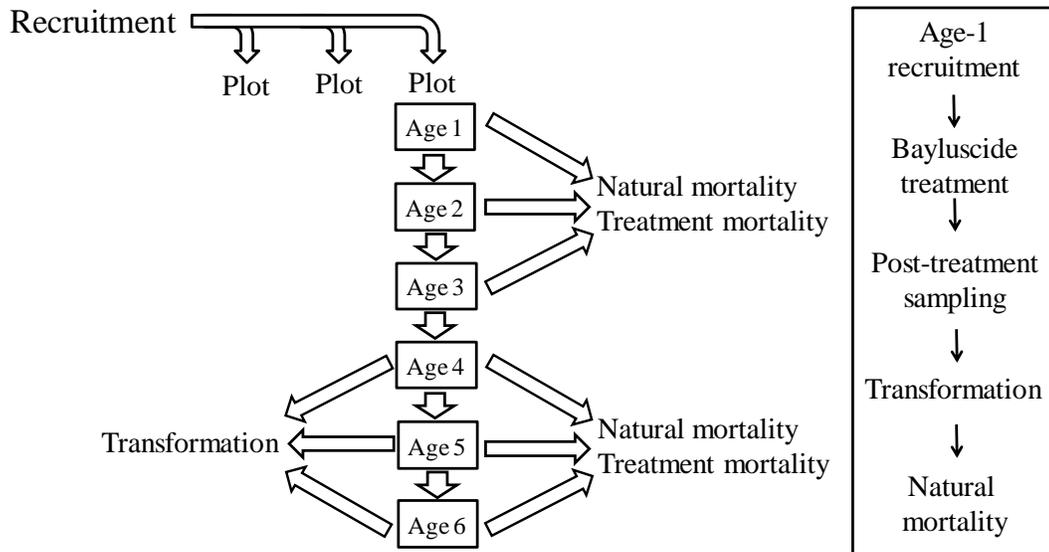


Figure 4.2. A basic representation of the recruitment dynamics and plot-specific population dynamics for larval lamprey in the St. Marys River as it is implemented within simulation. Arrows originating from the recruitment term indicate larval recruitment to different spatial areas (plots). The proportion of total recruitment that is assigned to each plot is allowed vary. 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 box on the right represents the relative order of events within a single model year from top to bottom.

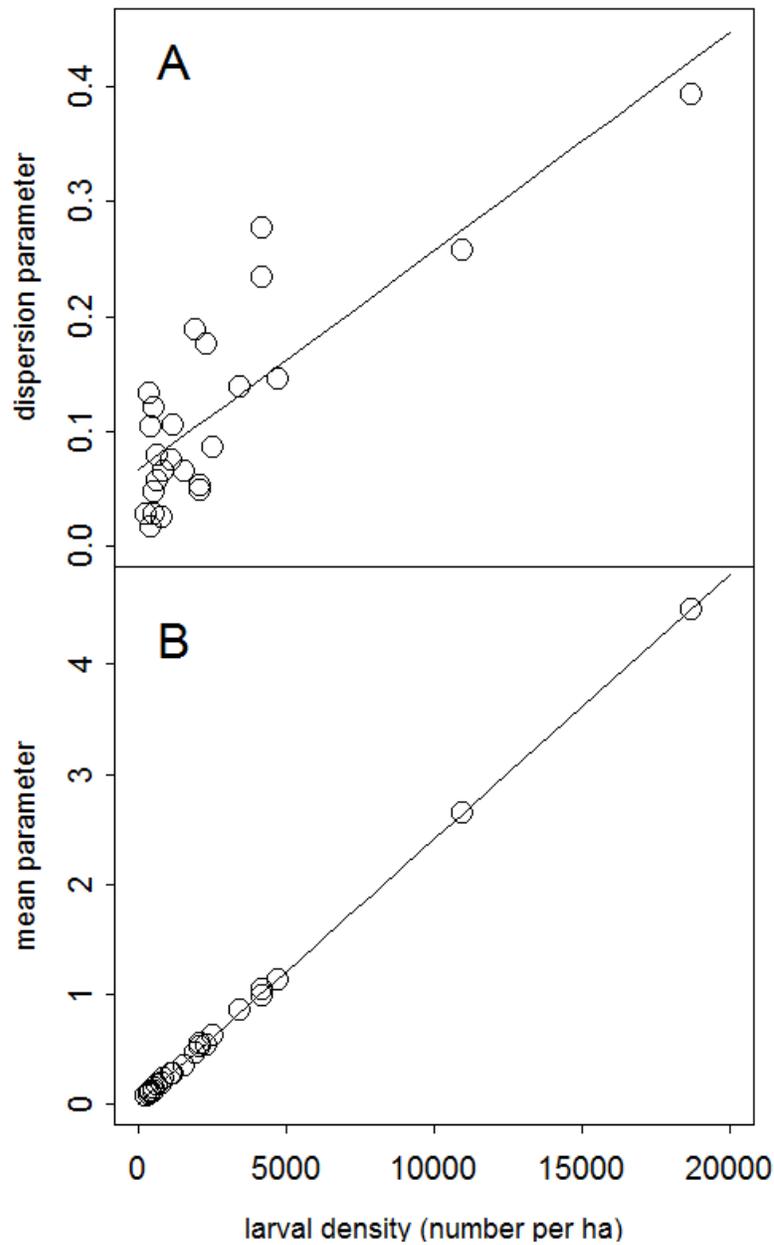


Figure 4.3. Fitted linear relationship between estimated larval density (number per ha) and the dispersion (panel A) and mean (panel B) parameters of a negative binomial distribution. Negative binomial distributions were fit to the plot-specific gear selectivity corrected catch data from the 2011 and 2012 intensive deepwater electrofishing surveys in the St. Marys River.

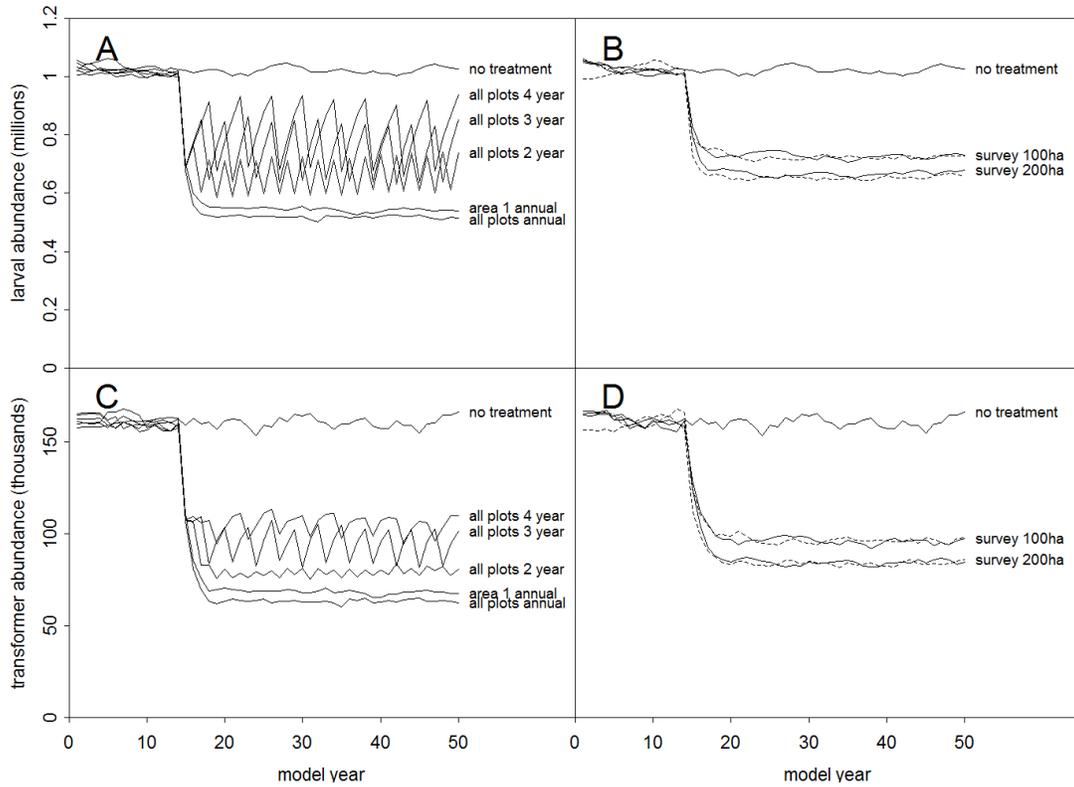


Figure 4.4. Mean estimates of larval abundance (panel A and B), and transformer abundance (panel C and D) for each treatment scenario. Dashed lines represent survey-based treatment scenarios under which double treatment of plots is possible.

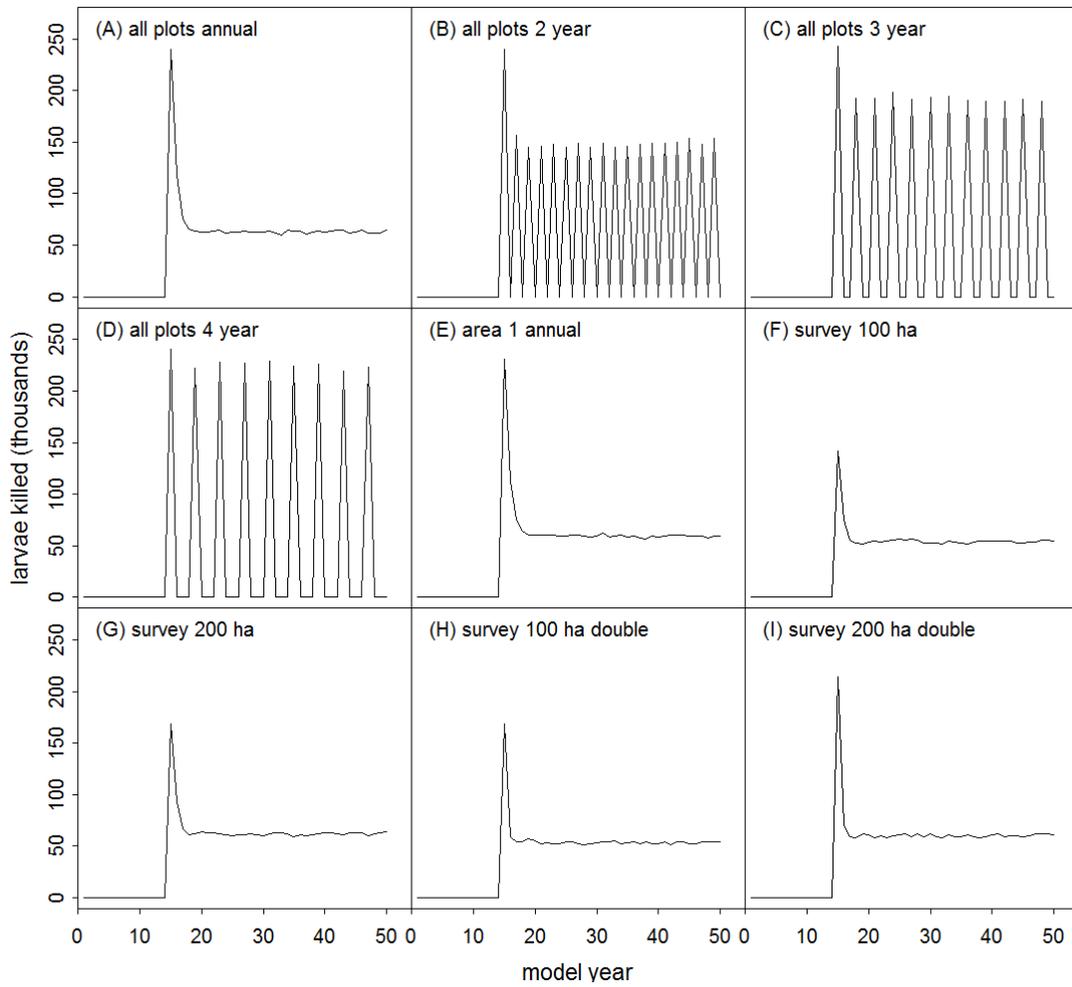


Figure 4.5. Mean estimates of annual lamprey killed under each treatment scenario.

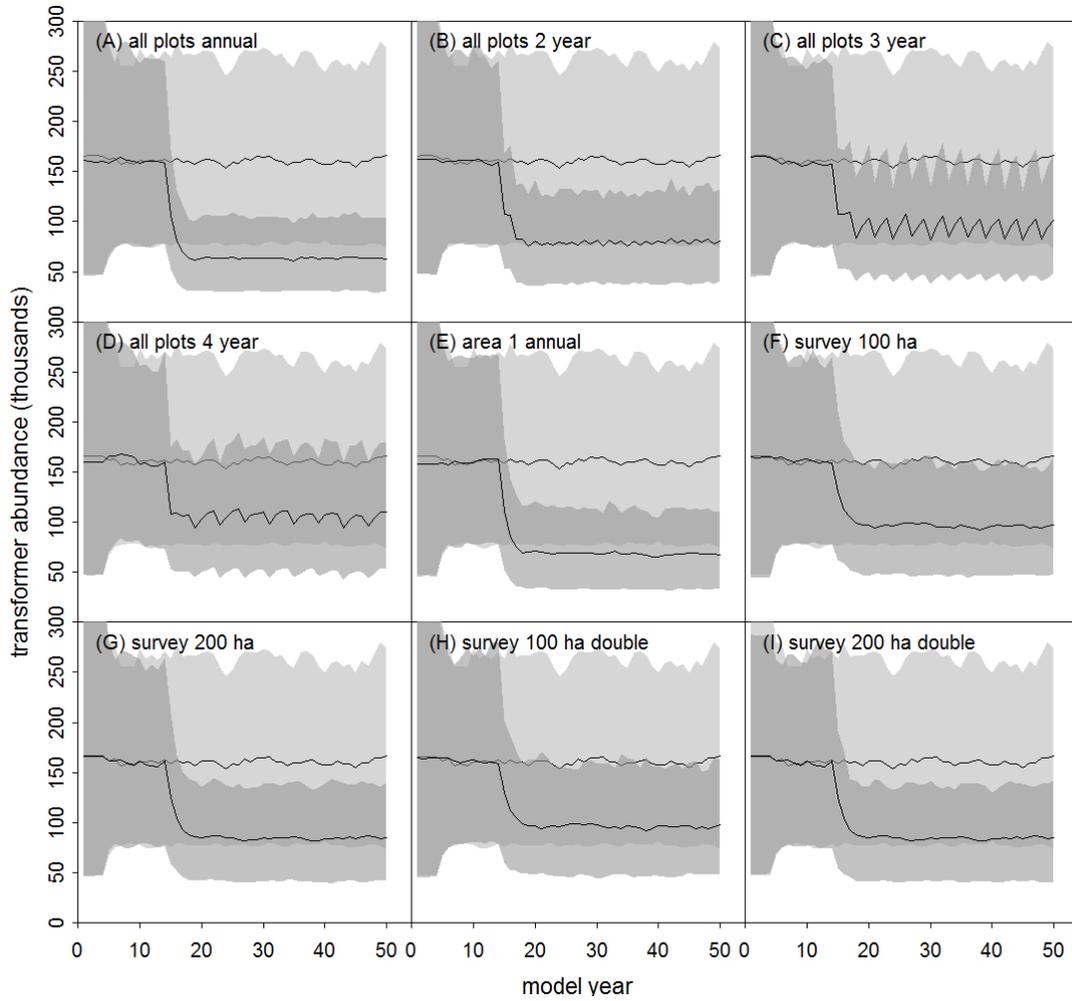


Figure 4.6. Mean estimates of transformer abundance under each treatment scenario. The upper line in each pannel represent a scenario under wh ich no treatment occurs. Shaded areas represent 80% quantiles.

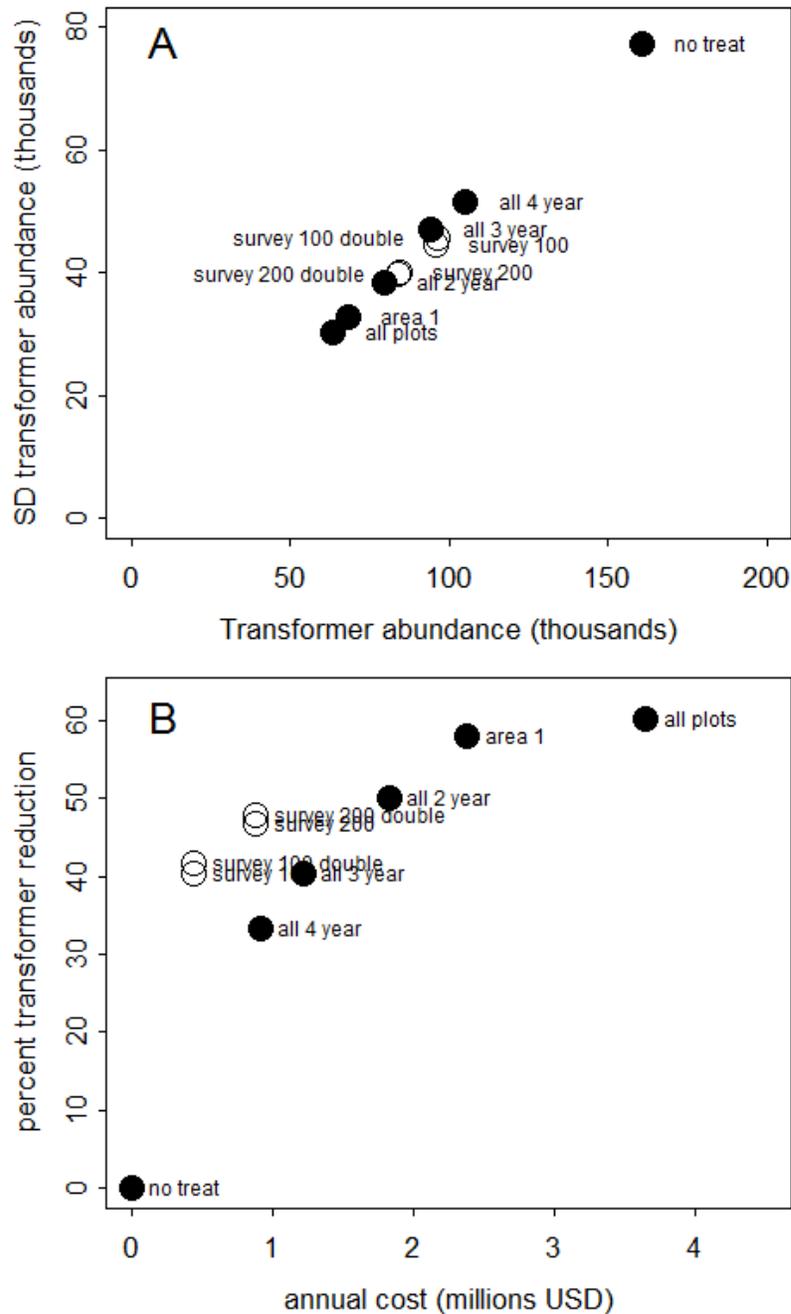


Figure 4.7. Panel A represents the mean transformer abundance in the last 30 years of the simulation and the mean of standard deviation of transformer abundance over that time for each treatment scenario. Panel B represents the relationship between annual treatment cost and the mean percent reduction in transformers for each treatment scenario. Solid and open points represent fixed and survey-based treatment scenarios respectively.



## Summary and Conclusions

The goal of the control program for invasive sea lamprey (*Petromyzon marinus*) in the St. Marys River is to obtain the largest reduction in annual transformer escapement possible with the financial resources available. My dissertation seeks to improve the Bayluscide-based portion of the St. Marys River control program using two primary approaches. Chapters 1 and 2 use a statistical modeling and validation approach to improve the current understanding of sea lamprey population dynamics, and inform the annual application of Bayluscide. Chapters 3 and 4 take a simulation approach and seek to improve future treatment and assessment decisions by considering budget constraints, resource tradeoffs, and sources of uncertainty in the management process. In addition to the sea lamprey management and control program in the Great Lakes, this work has implications for the management and restoration of lamprey species globally, and the control of invasive species in general.

### **Population dynamics**

In Chapter 1 I developed a spatially specific, age-structured model, to describe the dynamics of the sea lamprey population in the St. Marys River. This study yielded several insights that have implications for sea lamprey management. I documented substantial declines in abundance of sea lamprey larvae and transformers that can be attributed to reductions in recruitment through time and the effects of the Bayluscide treatment program. Recruitment was highly variable at low spawning stock size and showed a moderate amount of compensation at higher spawning stock

size. I also documented an upstream shift in the spatial distribution of larval recruitment over time. The model successfully identified areas of high larval abundance and showed that areas of low larval density contribute significantly to the population. The model also provided an estimate of Bayluscide treatment mortality ( $0.51 \text{ treatment}^{-1}$ ), natural mortality ( $0.09 \text{ yr}^{-1}$ ), and the parameters of a Ricker stock recruitment function ( $\alpha = 268$ , and  $\beta = 0.00018$ ).

Chapter 1 yielded several results and insights regarding the control program and sea lamprey population dynamics in the St. Marys River that do not coincide with conventional wisdom or the results of previous studies including the effect of out-of-plot areas on transformer production and the lethality of Bayluscide treatments. In the past it has been assumed that the out-of-plot areas of the river did not contribute significantly to total transformer escapement in the St. Marys River (Haeseker et al. 2003). My results indicated that the out-of-plot areas of the St. Marys River receive 37% of the total larval recruitment, but produce approximately 87% of the total river transformer escapement in 2011. This result reflects the effectiveness of controlling abundance by the in-plot treatment program, but also illustrates the current importance of the out-of-plot areas.

The estimated mortality associated with Bayluscide treatment ( $0.51 \text{ treatment}^{-1}$ ) was substantially lower than the previously reported estimate ( $0.88 \text{ treatment}^{-1}$ ), which was estimated based on a single large scale treatment event in 1999 (Fodale et al. 2003). The results of the Chapter 4 showed that increasing the effectiveness of Bayluscide treatment resulted in substantial decreases in the transformer escapement and changes in the relative performance of each treatment scenario considered. The

sensitivity of treatment performance to uncertainty surrounding Bayluscide effectiveness, and the disparity in the estimates of Bayluscide mortality produced using different methods, underscores the need for targeted efforts to improve both effectiveness of Bayluscide treatment and estimates of Bayluscide effectiveness in a field setting.

During the first two years of the Bayluscide-based control program (1998-1999) every plot in the river was treated. At that time large scale treatment caused a large decrease in total river larval abundance and transformer production because the larval lamprey population was at a higher abundance and was more evenly distributed over many treatment plots relative to the current state of the population. Chapter 1 indicated that in recent years, a large portion of the larval lamprey population was contained in a relatively small number of plots. However, in 2010 and 2011 all plots were treated in each year in an effort to have a major impact on the population. These large scale treatments likely had a marginal increase in effectiveness over more a more targeted treatment because sea lamprey were concentrated in relatively few areas (Chapter 4). Further, the expected performance of treating the entire in-plot portion of the river on a frequent basis will almost certainly result in resources not being used to their full potential given the number of plots that contain very low abundance.

### **Model comparison**

The age-structured population model developed in Chapter 1 has increased the understanding of sea lamprey population dynamics in the St. Marys River. The results of Chapter 2, however, indicate that a simpler approach may be better able to

inform annual treatment decisions. My goal in Chapter 2 was to identify a method that would lead to better estimation of spatially specific density and abundance, and an increase in the effectiveness of the larval treatment program in the St. Marys River. There is an inherent tradeoff between the currently used sample-based estimation method, and model-based estimation methods. 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 and treatment effects cannot vary annually. The sample-based method can identify anomalous high density plots, but is limited by high uncertainty because the level of sampling for any plot is fairly low and the intensity and coverage of the sampling 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. I used a hybrid approach that involved calculating the mean density from sampling-based estimation method and the generalized linear model based on catch data. The consistent performance across criteria and years of the hybrid approach, which combined the sample based method and the best model-based method (generalized linear model based on catch), suggests that it is a viable option to guide treatment decisions for sea lamprey larvae in the St. Marys River.

### **Resource allocation**

An inherent economic tradeoff exists between the gathering of information (assessment or sampling) to guide a management actions and implementing those actions (Mehta et al. 2007). I used a resampling approach to consider the effect of sampling intensity on the success of the larval sea lamprey control program by

explicitly incorporated the economic tradeoff between assessment and control efforts in Chapter 3. As expected, when no tradeoff between assessment and control was incorporated, increasing assessment always led to more control for the same treatment budget. When the tradeoff was incorporated, the sampling intensity that maximized the number of larvae killed depended on the overall budget available, with increased sampling intensities maximizing effectiveness under medium to large budgets (\$0.4 to \$2.0 million year<sup>-1</sup>). Sea lamprey control actions based on assessment information outperformed those that were implemented with no assessment under all budget scenarios. The results of Chapter 3 support previous theoretical and empirical evidence demonstrating the importance of including economic tradeoffs in invasive species management (Mehta et al. 2007, Hansen and Jones 2008, Fenichel and Hansen 2010). Additionally, my results illustrate the potential for budget constraints to change the optimal assessment or sampling strategy. The approach and patterns I observed likely apply to spatially targeted control efforts for other invasive or nuisance species.

### **Management strategy evaluation**

Management strategy evaluation (MSE) is becoming increasingly prevalent in the field of resource management (Sainsbury 1998, Cooke 1999). For invasive species management the eradication or control of populations is the primary goal, with cost as the chief limitation. In these situations MSE can offer a powerful approach to evaluate the costs and benefits of control strategies for invasive or nuisance species prior to implementation. Chapter 4 used the results from Chapters 1–3 to develop an MSE using a stochastic, spatially specific, age-structured

simulation model to evaluate the performance of several fixed and survey-based Bayluscide-based treatment strategies for the control of sea lamprey in the St. Marys River. If treatment resources are limited, a survey-based, assessment driven approach is preferable to treating a fixed area of the river every year (Chapter 4). The superiority of the survey-based approach is largely driven by the low cost of sampling relative to treatment. The survey-based scenarios have the added benefit of being able to adjust to unexpected changes in spatial recruitment patterns. The estimated reduction in transformer escapement that can be achieved using a survey-based treatment approach occurs at a reduced cost relative to fixed treatment scenarios with similar performance. The MSE also indicated that treating the entire in-plot portion of river at current population levels, as was done in 2010 and 2011, will almost certainly result in a resources not being used to their full potential given the number of plots that contain very few larval sea lamprey. This MSE provides a flexible framework to evaluate proposed changes in treatment strategy or the larval sampling program and should be used to identify treatment strategies that are most likely to achieve sea lamprey control goals in the St. Marys River.

### **Improving larval control efforts**

The chemical treatment program for sea lampreys in the St. Marys River has been in place in its current form for long enough to reach a kind of equilibrium state. That is, while the current control program has been a success in terms of reducing transformer escapement from the St. Marys River, maintaining the chemical control program in its current form is not likely to result in major reductions in transformer escapement in the future. My work has identified aspects of the control program, and

the sampling program that drives it, that could be changed with the goal of increasing efficiency and effectiveness.

My results indicated that the out-of-plot areas of the St. Marys River receive 37% of the total larval recruitment, but produced approximately 87% of the total river transformer escapement in 2011. This result illustrates the current importance of the out-of-plot areas and identifies an opportunity to increase the effectiveness of treatment efforts by developing ways to target the out-of-plot areas. Broadly, there are two options for accomplishing this. The first is to treat large contiguous areas of the out-of-plot and in-plot habitat that have high larval densities. One such approach, treating all of area one (Fig. 4.1), was described and simulated in Chapter 4. The results of Chapter 4 indicate that this approach would result in a greater reduction in transformer escapement per dollar spent than treating all in-plot areas in a single year, an approach which has been implemented in the past. The second approach would consist of fine-scale changes to the plot structure that would exclude areas of current plots with low larval density, and include out-of-plot areas adjacent to plot margins if they have larval densities higher than the surrounding out-of-plot areas. These adjacent areas of high larval density are not currently included in treatment efforts. Implementing this approach would likely require additional field sampling, the incorporation of historic data, and spatial interpolation.

Continuing to increase the effectiveness and efficiency of the sea lamprey control program has benefits that apply to the entire Great Lakes ecosystem. The results of Chapter 4 indicate that changes in the location of Bayluscide application in the river could decrease the amount of area that has to be treated to obtain similar

reductions in transformer escapement. This would result in a reduction in both the cost of treatment and the amount of Bayluscide that must be applied. Given the documented lethal and sublethal effects of Balyuscide on non-target organisms (Dawson 2003), a reduction in the amount of Bayluscide applied is desirable from an ecosystem health perspective.

The goal of the sea lamprey control program is to reduce the abundance of sea lampreys to Economic Injury Levels where the marginal cost of increased control begins to exceed the expected economic benefits (Irwin et al, 2012). However, increasing the effectiveness of the chemical treatment program for sea lampreys also has positive implications for ecosystem restoration. Reducing the impact of high trophic position, non-native fish species can lead to food web shifts that help to restore trophic pathways to a less disturbed state and can lead to systemic momentum that can aid in restoration efforts (Lepak et al. 2006, Bunnell et al 2006, Weidel et al. 2007).

### **Global lamprey management**

Little is known about the population dynamics and abundance of larval sea lamprey in larger rivers in their native range, and no models are 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 lamprey 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).

In addition to providing information relevant to the control program for sea lamprey in the St. Marys River, Chapter 1 also yielded valuable insights into modeling the population dynamics of a family of organisms that are threatened globally and for which very little information on population dynamics exists. Chapter 1 demonstrated that natural mortality of the larval stage was very low relative to the larval life stages of most other fishes. This low natural mortality rate indicates that the sedentary larvae are likely the least vulnerable of the lamprey life stages if good larval habitat is available. Therefore, if good larval habitat exists, imperiled lamprey populations are likely limited during other life stages. Barriers to upstream migration such as dams, sources of mortality in the adult or parasitic life stages, or limited spawning habitat may all be likely areas to focus restoration efforts if adequate larval habitat is present. Many of these causes of species decline are not unique to lamprey, as many diadromous species are imperiled globally (Limberg and Waldman 2009). However, knowledge about the relative vulnerability of life stages may help focus restoration efforts and financial resources.

### **Implications for invasive species control**

The concept of propagule pressure is important to the understanding the process of species invasion and for developing control strategies for many groups of invasive species such as plants (Rouget and Richardson 2003), and insects (Suarez et al. 2005). Propagule pressure can be defined as the quality, quantity, and frequency of invading organisms (Groom, 2006) and is an important factor influencing the

persistence of invaders (Lockwood, 2005). Annual recruitment of larval sea lamprey to discrete areas of the St. Marys River is analogous to propagule pressure associated with species introductions/invasions, in that each discrete spatial area receives different recruitment densities and the quality of habitat in each area plays a role in survival. Essentially, each area functions as an independent population for a time. Over time there have been changes in the number of larval sea lamprey recruits (i.e., propagules) that arrive at each area of the river (Chapter 1). These changes have warranted altering the treatment program to adapt to changing conditions. The models and approaches developed in Chapters 1 and 2 quantify this relationship and identify the relative importance of each area of the river to sea lamprey control. Additionally, the approach developed in Chapter 4, simulates this process to test the effect of variable spatial recruitment on the performance of potential treatment strategies.

The approaches developed in my dissertation have applications for other invasive species that exhibit dynamics similar to sea lamprey, and for situations in which quantifying propagule pressure-like effects can inform invasive species control programs. The general, predicting areas likely to be invaded based on hypothetical propagule pressure has been applied in the past (Rouget and Richardson 2003). However, using a modeling or simulation-based approach to predict where secondary generations of invasive species may emerge or will be most abundant, allows flexible control programs to be put in place that can adapt as conditions change.

## Appendix A

High intensity pre-treatment deepwater electrofishing surveys were conducted in 2010 and 2011 as a means to validate the results of chapters one and two.

Sampling was conducted with the participation of Department of Fisheries and Oceans Canada staff to ensure that the intensive sampling methodology conformed to their sampling methodology. 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, which intensively sampled 10 plots. These sampling efforts were designed to include a range of high, medium and low density plots across two years. Table A.1 contains data associated with the timing, location, habitat, and catch for each electrofishing sample. Table A.2 lists the length of each sea lamprey larvae collected during the intensive sampling effort. Data in Tables A.1 and A.2 can be linked using the Samp\_ID column. For more information regarding the deepwater electrofishing gear, habitat designations, and sampling methodology, see Bergstedt and Genovese (1994) and Slade et al. (2003).

Table A.1. Data associated with timing, location, habitat, and larval lamprey catch for the intensive pre-treatment electrofishing sampling that occurred in 2010 and 2011. Data in tables A.1 and A.2 can be linked using the Samp\_ID column.

Samp_ID	Date	Time	Latitude	Longitude	Depth (m)	Plot	Hab.	Catch	Comment
201140379	6/28/2011	10:42	46.4935500	-84.2778010	4.88	21	NA	0	Unnatural substrate
201140364	6/28/2011	9:00	46.4940960	-84.2767930	3.66	21	3	0	
201140365	6/28/2011	9:03	46.4941010	-84.2771950	4.27	21	3	0	
201140366	6/28/2011	9:07	46.4940800	-84.2776660	5.49	21	3	0	
201140367	6/28/2011	9:10	46.4940900	-84.2779710	4.57	21	3	0	
201140368	6/28/2011	9:13	46.4940810	-84.2787680	6.40	21	3	0	
201140369	6/28/2011	9:16	46.4940860	-84.2795850	8.84	21	3	0	
201140374	6/28/2011	10:04	46.4939380	-84.2766080	0.91	21	3	0	
201140376	6/28/2011	10:20	46.4937830	-84.2783880	5.79	21	3	0	
201140378	6/28/2011	10:31	46.4936580	-84.2766330	0.91	21	3	0	
201140384	6/28/2011	11:33	46.4933660	-84.2766230	0.91	21	3	0	
201140385	6/28/2011	11:35	46.4933210	-84.2769850	0.91	21	3	0	
201140392	6/28/2011	13:11	46.4934110	-84.2804450	0.91	21	3	0	
201140396	6/28/2011	13:39	46.4930230	-84.2784980	0.91	21	3	0	
201140400	6/28/2011	14:05	46.4927680	-84.2802210	1.52	21	3	0	
201140401	6/28/2011	14:08	46.4926930	-84.2805060	1.22	21	3	0	
201140402	6/28/2011	14:11	46.4926660	-84.2808150	2.44	21	3	0	
201140403	6/28/2011	14:13	46.4926450	-84.2812600	2.13	21	3	0	
201140404	6/28/2011	14:18	46.4927530	-84.2817550	0.91	21	3	0	
201140405	6/28/2011	14:20	46.4927150	-84.2819430	1.22	21	3	0	
201140406	6/28/2011	14:29	46.4936760	-84.2833060	2.44	21	3	0	
201140408	6/28/2011	14:38	46.4929730	-84.2813750	2.13	21	3	0	
201140409	6/28/2011	14:40	46.4929850	-84.2815700	2.44	21	3	0	
201140370	6/28/2011	9:19	46.4938880	-84.2803530	3.66	21	1	1	Dense vegetation
201140382	6/28/2011	11:12	46.4935810	-84.2797660	1.83	21	1	1	Dense vegetation
201140391	6/28/2011	12:54	46.4933310	-84.2796880	2.74	21	1	1	Dense vegetation
201140395	6/28/2011	13:30	46.4929510	-84.2775810	2.74	21	1	0	Dense vegetation
201140399	6/28/2011	13:56	46.4927830	-84.2788080	1.83	21	1	1	Dense vegetation
201140371	6/28/2011	9:35	46.4938610	-84.2808730	1.52	21	1	0	
201140372	6/28/2011	9:43	46.4938950	-84.2813500	1.83	21	1	0	
201140373	6/28/2011	9:56	46.4939550	-84.2762150	1.22	21	2	0	
201140375	6/28/2011	10:08	46.4939410	-84.2769680	1.83	21	1	0	
201140377	6/28/2011	10:23	46.4936780	-84.2762010	0.91	21	2	0	
201140380	6/28/2011	10:51	46.4936150	-84.2780050	3.05	21	1	0	
201140381	6/28/2011	11:05	46.4936230	-84.2792980	2.13	21	1	0	
201140383	6/28/2011	11:23	46.4936210	-84.2802460	1.52	21	2	0	
201140386	6/28/2011	11:38	46.4932850	-84.2777900	0.91	21	2	0	
201140387	6/28/2011	11:46	46.4933600	-84.2781910	0.61	21	2	0	
201140388	6/28/2011	11:53	46.4933200	-84.2786130	1.22	21	1	0	
201140389	6/28/2011	12:36	46.4932760	-84.2790000	1.22	21	2	0	
201140393	6/28/2011	13:16	46.4929960	-84.2762950	0.91	21	1	0	
201140394	6/28/2011	13:23	46.4929830	-84.2768960	1.22	21	2	0	
201140398	6/28/2011	13:48	46.4930160	-84.2791830	1.22	21	1	0	
201140332	6/27/2011	9:02	46.4880380	-84.2989700	0.91	154	3	0	
201140333	6/27/2011	9:09	46.4880710	-84.2986200	0.91	154	3	0	
201140343	6/27/2011	10:36	46.4883780	-84.2963260	0.91	154	3	0	
201140348	6/27/2011	11:40	46.4872050	-84.2959330	0.91	154	3	0	
201140350	6/27/2011	12:10	46.4862750	-84.2961410	0.30	154	3	0	
201140356	6/27/2011	13:33	46.4870150	-84.2973850	0.61	154	3	0	
201140357	6/27/2011	13:36	46.4870180	-84.2969380	0.61	154	3	0	
201140358	6/27/2011	13:39	46.4869750	-84.2965650	0.30	154	3	0	
201140359	6/27/2011	13:48	46.4870410	-84.2961210	0.61	154	3	0	
201140361	6/27/2011	14:09	46.4872930	-84.2989560	0.61	154	3	0	
201140362	6/27/2011	14:14	46.4867950	-84.2981680	0.61	154	3	0	
201140341	6/27/2011	10:15	46.4880900	-84.2967560	1.22	154	1	0	Dense vegetation
201140363	6/27/2011	14:32	46.4941280	-84.2759780	3.05	21	1	0	Dense vegetation
201140334	6/27/2011	9:12	46.4881400	-84.2981860	0.91	154	2	0	
201140335	6/27/2011	9:20	46.4881330	-84.2978360	0.91	154	2	0	
201140336	6/27/2011	9:27	46.4884380	-84.2978310	0.91	154	2	1	
201140337	6/27/2011	9:36	46.4884660	-84.2973680	0.61	154	2	1	
201140338	6/27/2011	9:50	46.4881860	-84.2974410	0.91	154	2	0	
201140339	6/27/2011	9:57	46.4881850	-84.2970710	1.22	154	2	0	
201140340	6/27/2011	10:05	46.4884850	-84.2970930	0.91	154	2	0	

201140342	6/27/2011	10:26	46.4877730	-84.2967750	1.22	154	1	0	
201140344	6/27/2011	10:44	46.4880400	-84.2962330	1.22	154	2	0	
201140345	6/27/2011	10:59	46.4878730	-84.2979850	0.61	154	2	0	
201140346	6/27/2011	11:12	46.4874410	-84.2973480	0.61	154	2	0	
201140347	6/27/2011	11:30	46.4875850	-84.2959010	1.22	154	2	0	
201140349	6/27/2011	11:46	46.4866260	-84.2958230	0.61	154	2	0	
201140351	6/27/2011	12:49	46.4860050	-84.2963480	0.61	154	3	0	
201140352	6/27/2011	12:56	46.4854510	-84.2962350	0.91	154	2	0	
201140353	6/27/2011	13:06	46.4854310	-84.2958280	0.61	154	2	0	
201140354	6/27/2011	13:15	46.4858010	-84.2961930	0.91	154	2	0	
201140355	6/27/2011	13:22	46.4857430	-84.2958930	1.22	154	2	0	
201140360	6/27/2011	14:03	46.4865730	-84.2985300	0.61	154	3	0	
201140311	6/24/2011	10:35	46.4912080	-84.2954850	0.61	152	3	0	
201140325	6/24/2011	13:59	46.4877650	-84.2993480	0.91	154	3	0	
201140326	6/24/2011	14:06	46.4883750	-84.2998410	2.13	154	3	0	
201140328	6/24/2011	14:27	46.4875880	-84.2978050	0.30	154	3	0	
201140310	6/24/2011	10:12	46.4895250	-84.2905900	3.35	152	1	1	Dense vegetation
201140315	6/24/2011	11:25	46.4892260	-84.2955250	0.91	152	2	0	Dense vegetation
201140316	6/24/2011	11:36	46.4895860	-84.2946850	6.10	152	1	0	Dense vegetation
201140331	6/24/2011	14:55	46.4872260	-84.2977730	0.61	154	2	1	Dense vegetation
201140305	6/24/2011	8:59	46.4903210	-84.2907900	8.84	152	1	0	
201140306	6/24/2011	9:17	46.4900380	-84.2912130	3.05	152	1	0	
201140307	6/24/2011	9:31	46.4893250	-84.2912680	0.91	152	1	0	
201140308	6/24/2011	9:44	46.4895730	-84.2916010	0.91	152	1	0	
201140309	6/24/2011	10:02	46.4887380	-84.2907030	0.91	152	2	0	
201140312	6/24/2011	10:51	46.4886750	-84.2944080	1.22	152	2	0	
201140313	6/24/2011	11:02	46.4889530	-84.2947100	3.66	152	1	0	
201140314	6/24/2011	11:15	46.4886260	-84.2955330	1.22	152	2	0	
201140317	6/24/2011	11:47	46.4897260	-84.2951310	3.96	152	1	0	
201140318	6/24/2011	11:59	46.4901960	-84.2955810	0.61	152	2	0	
201140319	6/24/2011	12:06	46.4903900	-84.2956210	0.30	152	2	0	
201140320	6/24/2011	13:03	46.4904080	-84.2947660	1.22	152	2	0	
201140321	6/24/2011	13:06	46.4904780	-84.2949850	0.30	152	3	0	
201140322	6/24/2011	13:12	46.4909500	-84.2956410	0.61	152	2	1	
201140323	6/24/2011	13:36	46.4874500	-84.2986710	0.61	154	2	0	
201140324	6/24/2011	13:47	46.4881650	-84.2994800	0.91	154	2	0	
201140327	6/24/2011	14:11	46.4877980	-84.2990030	0.91	154	2	0	
201140329	6/24/2011	14:32	46.4872560	-84.2983930	1.22	154	2	0	
201140330	6/24/2011	14:45	46.4869250	-84.2982550	1.22	154	2	0	
201140281	6/23/2011	9:23	46.4916550	-84.2945850	3.96	152	3	0	
201140282	6/23/2011	9:33	46.4916000	-84.2943280	0.61	152	3	0	
201140284	6/23/2011	10:59	46.4913030	-84.2942310	0.61	152	3	0	
201140292	6/23/2011	12:56	46.4909650	-84.2925910	0.91	152	3	0	
201140293	6/23/2011	13:06	46.4909350	-84.2912200	7.01	152	3	0	
201140285	6/23/2011	11:04	46.4918910	-84.2915860	11.58	152	NA	0	Too deep
201140299	6/23/2011	14:14	46.4895480	-84.2923550	2.13	152	1	0	Dense vegetation
201140300	6/23/2011	14:25	46.4892650	-84.2930700	2.44	152	1	0	Dense vegetation
201140304	6/23/2011	15:13	46.4893230	-84.2917930	2.13	152	1	0	Dense vegetation
201140283	6/23/2011	9:42	46.4910680	-84.2941950	0.91	152	2	0	
201140286	6/23/2011	11:08	46.4915960	-84.2916110	8.84	152	1	0	
201140287	6/23/2011	11:23	46.4913480	-84.2920900	2.44	152	1	0	
201140288	6/23/2011	11:33	46.4913030	-84.2908950	2.74	152	1	1	
201140289	6/23/2011	11:46	46.4913480	-84.2926430	1.22	152	2	0	
201140290	6/23/2011	12:02	46.4909700	-84.2934500	1.22	152	2	0	
201140291	6/23/2011	12:47	46.4909560	-84.2929850	1.22	152	2	0	
201140294	6/23/2011	13:10	46.4907450	-84.2918480	0.91	152	2	0	
201140295	6/23/2011	13:21	46.4904210	-84.2921780	3.05	152	1	0	
201140296	6/23/2011	13:39	46.4900850	-84.2934110	0.61	152	1	0	
201140297	6/23/2011	13:54	46.4901430	-84.2930150	0.91	152	1	0	
201140298	6/23/2011	14:06	46.4897710	-84.2921810	1.22	152	1	0	
201140301	6/23/2011	14:35	46.4892030	-84.2927000	7.32	152	1	0	
201140302	6/23/2011	14:45	46.4889630	-84.2918450	7.32	152	1	0	
201140303	6/23/2011	15:01	46.4887160	-84.2918180	4.57	152	1	0	
201140270	6/21/2011	12:43	46.4891800	-84.2879380	0.91	153	3	0	
201140276	6/21/2011	13:45	46.4917600	-84.2935580	6.40	152	3	0	
201140279	6/21/2011	14:23	46.4917630	-84.2918630	6.71	152	3	0	
201140274	6/21/2011	13:32	46.4922180	-84.2918550	12.19	152	NA	0	Too deep
201140275	6/21/2011	13:34	46.4921480	-84.2906560	12.80	152	NA	0	Too deep
201140264	6/21/2011	11:13	46.4898330	-84.2883860	2.74	153	1	0	Dense vegetation
201140267	6/21/2011	12:08	46.4896110	-84.2883130	3.05	153	1	0	Dense vegetation

201140255	6/21/2011	9:38	46.4909850	-84.2879150	0.91	153	2	0	
201140256	6/21/2011	9:49	46.4909600	-84.2875130	0.91	153	2	0	
201140257	6/21/2011	10:00	46.4903330	-84.2876010	0.91	153	1	0	
201140258	6/21/2011	10:09	46.4906800	-84.2880010	0.61	153	2	0	
201140259	6/21/2011	10:25	46.4907330	-84.2876810	0.91	153	2	0	
201140260	6/21/2011	10:34	46.4901280	-84.2880880	1.22	153	2	0	
201140261	6/21/2011	10:42	46.4900400	-84.2884010	0.91	153	2	0	
201140262	6/21/2011	10:50	46.4901430	-84.2888900	1.22	153	1	0	
201140263	6/21/2011	10:59	46.4898360	-84.2886100	0.91	153	1	0	
201140265	6/21/2011	11:22	46.4897500	-84.2875360	0.61	153	2	0	
201140266	6/21/2011	11:55	46.4895130	-84.2887360	0.61	153	1	0	
201140268	6/21/2011	12:18	46.4892560	-84.2887900	0.91	153	1	0	
201140269	6/21/2011	12:29	46.4891880	-84.2882430	1.83	153	2	0	
201140271	6/21/2011	12:46	46.4889730	-84.2887980	1.52	153	1	0	
201140272	6/21/2011	12:58	46.4886510	-84.2882350	2.13	153	1	0	
201140273	6/21/2011	13:12	46.4895850	-84.2869210	1.22	153	2	0	
201140277	6/21/2011	13:49	46.4918750	-84.2927430	6.10	152	2	0	
201140278	6/21/2011	14:05	46.4918610	-84.2925060	5.18	152	2	0	
201140280	6/21/2011	14:25	46.4915930	-84.2921150	3.05	152	1	0	
201140234	6/20/2011	10:42	46.4924110	-84.2894960	3.05	153	3	0	
201140235	6/20/2011	10:53	46.4922050	-84.2892800	2.74	153	3	0	
201140237	6/20/2011	11:04	46.4918610	-84.2902830	3.05	153	3	0	
201140238	6/20/2011	11:07	46.4918550	-84.2900480	2.74	153	3	0	
201140239	6/20/2011	11:09	46.4918750	-84.2895060	1.83	153	3	0	
201140240	6/20/2011	11:18	46.4917910	-84.2884210	0.30	153	3	0	
201140236	6/20/2011	10:58	46.4921100	-84.2903460	3.35	153	NA	0	Too deep
201140243	6/20/2011	11:55	46.4909710	-84.2900500	0.30	153	2	0	Dense vegetation
201140246	6/20/2011	13:22	46.4901400	-84.2895960	0.61	153	1	0	Dense vegetation
201140247	6/20/2011	13:41	46.4895410	-84.2904510	0.91	153	1	0	Dense vegetation
201140241	6/20/2011	11:24	46.4915000	-84.2901130	0.30	153	1	0	
201140242	6/20/2011	11:43	46.4912810	-84.2899710	0.30	153	2	0	
201140244	6/20/2011	12:43	46.4907200	-84.2902400	0.91	153	1	0	
201140245	6/20/2011	13:02	46.4905150	-84.2902360	1.83	153	1	1	
201140248	6/20/2011	13:54	46.4892400	-84.2902860	0.61	153	1	0	
201140249	6/20/2011	14:06	46.4889360	-84.2904530	0.30	153	1	0	
201140250	6/20/2011	14:20	46.4916600	-84.2897080	0.30	153	2	0	
201140251	6/20/2011	14:32	46.4915580	-84.2890380	0.00	153	2	0	
201140252	6/20/2011	14:42	46.4911780	-84.2886910	0.61	153	1	1	
201140253	6/20/2011	14:54	46.4909630	-84.2884480	0.30	153	1	0	
201140254	6/20/2011	15:03	46.4912860	-84.2878900	0.30	153	2	0	
201140185	6/17/2011	9:42	46.5091330	-84.3442010	1.52	3	3	0	
201140186	6/17/2011	9:48	46.5094150	-84.3441760	1.52	3	3	0	
201140196	6/17/2011	11:12	46.4990110	-84.2634550	3.96	20	3	0	
201140198	6/17/2011	11:33	46.4983780	-84.2651350	2.13	20	3	0	
201140201	6/17/2011	11:50	46.4976260	-84.2663110	7.92	20	3	0	
201140203	6/17/2011	12:45	46.4972760	-84.2673950	8.84	20	3	0	
201140206	6/17/2011	12:59	46.4963860	-84.2697610	7.92	20	3	0	
201140207	6/17/2011	13:04	46.4964850	-84.2694180	7.62	20	3	0	
201140208	6/17/2011	13:09	46.4962330	-84.2701830	7.62	20	3	0	
201140209	6/17/2011	13:13	46.4961230	-84.2710680	7.01	20	3	0	
201140217	6/17/2011	14:06	46.4956010	-84.2753010	1.83	20	3	0	
201140221	6/17/2011	14:27	46.4953030	-84.2773280	2.13	20	3	0	
201140222	6/17/2011	14:29	46.4954700	-84.2780830	3.96	20	3	0	
201140223	6/17/2011	14:32	46.4952430	-84.2781210	4.57	20	3	0	
201140224	6/17/2011	14:34	46.4952930	-84.2785180	2.74	20	3	0	
201140225	6/17/2011	14:36	46.4952130	-84.2788950	6.40	20	3	0	
201140183	6/17/2011	9:29	46.5094530	-84.3450080	0.30	3	1	0	Dense vegetation
201140184	6/17/2011	9:36	46.5095110	-84.3446380	1.22	3	1	0	Dense vegetation
201140194	6/17/2011	11:02	46.4993400	-84.2632200	2.74	20	1	0	Dense vegetation
201140197	6/17/2011	11:18	46.4987210	-84.2642580	3.05	20	1	2	Dense vegetation
201140199	6/17/2011	11:35	46.4985280	-84.2647280	2.44	20	1	0	Dense vegetation
201140218	6/17/2011	14:11	46.4955280	-84.2763880	3.05	20	1	0	Dense vegetation
201140187	6/17/2011	10:15	46.5007080	-84.2599210	3.96	20	1	0	
201140188	6/17/2011	10:21	46.5007260	-84.2601330	1.22	20	2	0	
201140189	6/17/2011	10:29	46.5003980	-84.2609830	0.91	20	1	0	
201140190	6/17/2011	10:34	46.4999850	-84.2615000	3.96	20	1	0	
201140191	6/17/2011	10:42	46.5000050	-84.2618830	3.66	20	2	1	
201140192	6/17/2011	10:50	46.4995850	-84.2626360	3.66	20	1	1	
201140193	6/17/2011	10:58	46.4992400	-84.2634080	2.74	20	1	0	
201140195	6/17/2011	11:06	46.4994360	-84.2628050	2.44	20	1	0	

201140200	6/17/2011	11:41	46.4978510	-84.2658800	7.92	20	1	0
201140202	6/17/2011	11:54	46.4976250	-84.2666510	9.45	20	2	0
201140204	6/17/2011	12:49	46.4972130	-84.2678410	5.49	20	1	0
201140205	6/17/2011	12:56	46.4966910	-84.2685560	7.01	20	3	0
201140210	6/17/2011	13:18	46.4961360	-84.2724230	3.66	20	1	0
201140211	6/17/2011	13:31	46.4961610	-84.2722850	5.79	20	1	0
201140212	6/17/2011	13:34	46.4958300	-84.2725410	6.71	20	2	0
201140213	6/17/2011	13:44	46.4961150	-84.2732000	1.22	20	1	0
201140214	6/17/2011	13:49	46.4961300	-84.2731000	0.91	20	1	0
201140215	6/17/2011	13:56	46.4958660	-84.2737280	5.18	20	3	0
201140216	6/17/2011	13:59	46.4957900	-84.2749400	3.96	20	1	0
201140219	6/17/2011	14:16	46.4955080	-84.2762160	4.88	20	1	0
201140220	6/17/2011	14:23	46.4955030	-84.2770460	3.66	20	2	0
201140226	6/17/2011	14:41	46.4955300	-84.2789010	3.96	20	2	0
201140227	6/17/2011	14:48	46.4955880	-84.2796300	3.05	20	1	0
201140228	6/17/2011	14:53	46.4957750	-84.2796400	0.61	20	1	0
201140229	6/17/2011	14:59	46.4953330	-84.2804130	3.35	20	2	0
201140230	6/17/2011	15:06	46.4955380	-84.2809630	1.22	20	1	0
201140231	6/17/2011	15:13	46.4955330	-84.2819280	1.52	20	1	0
201140232	6/17/2011	15:17	46.4955500	-84.2818130	1.22	20	1	0
201140233	6/17/2011	15:22	46.4953260	-84.2823200	4.57	20	1	0
201140173	6/16/2011	13:47	46.5090400	-84.3431760	0.61	3	3	0
201140180	6/16/2011	9:15	46.5090660	-84.3450710	0.91	3	3	0
201140166	6/16/2011	11:33	46.5091310	-84.3426060	3.05	3	1	1
201140167	6/16/2011	11:35	46.5090650	-84.3428550	1.22	3	1	0
201140168	6/16/2011	11:41	46.5094180	-84.3432300	0.61	3	1	0
201140169	6/16/2011	12:02	46.5087760	-84.3428780	3.66	3	2	1
201140170	6/16/2011	13:02	46.5088960	-84.3427250	3.96	3	1	7
201140171	6/16/2011	13:08	46.5093750	-84.3425360	3.35	3	1	0
201140172	6/16/2011	13:21	46.5096630	-84.3426080	3.66	3	1	1
201140174	6/16/2011	13:50	46.5089230	-84.3433430	0.61	3	3	0
201140175	6/16/2011	13:52	46.5093700	-84.3430850	1.22	3	1	1
201140176	6/16/2011	14:10	46.5095900	-84.3433300	0.61	3	1	0
201140177	6/16/2011	14:14	46.5096230	-84.3429030	0.61	3	1	0
201140178	6/16/2011	14:24	46.5093710	-84.3435710	0.91	3	2	0
201140179	6/16/2011	9:10	46.5090630	-84.3447130	1.22	3	1	0
201140181	6/16/2011	9:16	46.5092580	-84.3452730	0.61	3	1	0
201140182	6/16/2011	9:23	46.5092230	-84.3455410	0.91	3	1	0
201140139	6/15/2011	9:27	46.5027810	-84.3259850	5.49	22	2	0
201140140	6/15/2011	9:46	46.5031230	-84.3260600	6.10	22	2	0
201140141	6/15/2011	9:58	46.5030950	-84.3263630	8.23	22	2	0
201140142	6/15/2011	10:06	46.5031210	-84.3252010	0.61	22	1	0
201140143	6/15/2011	10:23	46.5033530	-84.3243060	0.30	22	1	0
201140144	6/15/2011	10:33	46.5036550	-84.3243310	0.30	22	1	0
201140145	6/15/2011	10:37	46.5035900	-84.3247230	0.30	22	1	0
201140146	6/15/2011	10:42	46.5034260	-84.3249260	0.30	22	1	0
201140147	6/15/2011	10:55	46.5027460	-84.3274530	7.62	22	2	0
201140148	6/15/2011	11:02	46.5028980	-84.3277430	7.62	22	2	0
201140149	6/15/2011	11:21	46.5031030	-84.3281700	7.32	22	2	2
201140150	6/15/2011	11:32	46.5036880	-84.3282260	5.49	22	1	0
201140151	6/15/2011	13:13	46.5037130	-84.3287310	5.49	22	1	0
201140152	6/15/2011	13:20	46.5038880	-84.3290550	5.79	22	1	0
201140153	6/15/2011	13:29	46.5051350	-84.3321910	3.66	22	1	0
201140154	6/15/2011	13:37	46.5050980	-84.3318380	3.96	22	1	0
201140155	6/15/2011	13:45	46.5047600	-84.3313950	4.88	22	1	1
201140156	6/15/2011	13:56	46.5045130	-84.3311150	5.49	22	1	1
201140157	6/15/2011	14:04	46.5042450	-84.3309680	6.10	22	2	0
201140158	6/15/2011	14:14	46.5039230	-84.3306260	6.40	22	1	0
201140159	6/15/2011	14:21	46.5036560	-84.3301030	6.10	22	2	0
201140161	6/15/2011	14:32	46.5033950	-84.3298260	6.40	22	2	0
201140162	6/15/2011	14:42	46.5029910	-84.3294160	7.01	22	2	0
201140163	6/15/2011	14:53	46.5039060	-84.3295680	6.10	22	1	0
201140164	6/15/2011	15:02	46.5040410	-84.3297080	6.40	22	1	0
201140165	6/15/2011	15:11	46.5036280	-84.3290900	6.10	22	1	0
201140125	6/14/2011	10:28	46.5034130	-84.3235150	3.35	22	1	0
201140123	6/14/2011	10:12	46.5030460	-84.3229360	1.83	22	1	0
201140118	6/14/2011	9:30	46.5022310	-84.3204710	2.13	22	1	0
201140119	6/14/2011	9:42	46.5021730	-84.3210800	4.88	22	1	0
201140120	6/14/2011	9:51	46.5021350	-84.3227780	3.66	22	1	0
201140121	6/14/2011	9:58	46.5025510	-84.3223980	2.74	22	1	0

Unnatural substrate  
Dense vegetation

201140122	6/14/2011	10:06	46.5028430	-84.3224260	2.74	22	1	0	
201140124	6/14/2011	10:21	46.5034100	-84.3228810	0.91	22	1	0	
201140126	6/14/2011	10:35	46.5028810	-84.3234980	1.83	22	1	1	
201140127	6/14/2011	11:04	46.5027730	-84.3232280	1.83	22	1	0	
201140128	6/14/2011	11:13	46.5025750	-84.3230410	2.74	22	1	0	
201140129	6/14/2011	11:21	46.5022710	-84.3231450	3.05	22	1	0	
201140130	6/14/2011	11:31	46.5028130	-84.3240060	1.52	22	1	0	
201140131	6/14/2011	11:39	46.5033150	-84.3240000	0.91	22	1	0	
201140132	6/14/2011	14:28	46.5024330	-84.3247430	4.88	22	1	0	
201140133	6/14/2011	14:37	46.5025730	-84.3250580	4.57	22	1	0	
201140134	6/14/2011	14:45	46.5028010	-84.3242280	1.52	22	1	0	
201140135	6/14/2011	14:51	46.5031280	-84.3242880	0.61	22	1	0	
201140136	6/14/2011	14:57	46.5030800	-84.3246780	0.61	22	1	0	
201140137	6/14/2011	15:03	46.5028810	-84.3246550	0.91	22	2	0	
201140138	6/14/2011	15:12	46.5027150	-84.3251360	3.35	22	1	0	
201140101	6/13/2011	10:58	46.4986760	-84.3180060	9.14	112	NA	0	Too deep
201140097	6/13/2011	9:29	46.4996730	-84.3175310	5.18	112	1	3	Dense vegetation
201140098	6/13/2011	9:52	46.4993400	-84.3175900	5.49	112	1	1	Dense vegetation
201140099	6/13/2011	10:28	46.4995450	-84.3183450	6.10	112	1	1	
201140100	6/13/2011	10:47	46.4990680	-84.3174900	5.49	112	1	0	
201140102	6/13/2011	11:04	46.4993410	-84.3186580	7.62	112	1	1	
201140103	6/13/2011	11:26	46.4821310	-84.3014030	2.74	1	2	3	
201140104	6/13/2011	11:38	46.4823260	-84.3016010	2.74	1	1	0	
201140105	6/13/2011	11:47	46.4819650	-84.3018800	4.88	1	2	0	
201140106	6/13/2011	11:53	46.4818280	-84.3019360	4.27	1	1	5	
201140107	6/13/2011	12:05	46.4813460	-84.3018860	0.30	1	1	0	
201140108	6/13/2011	12:53	46.4811900	-84.3019600	0.00	1	1	0	
201140109	6/13/2011	13:01	46.4815850	-84.3021230	4.27	1	1	0	
201140110	6/13/2011	13:10	46.4824510	-84.3017980	0.61	1	1	0	
201140111	6/13/2011	13:18	46.4820680	-84.3022060	0.91	1	1	0	
201140112	6/13/2011	13:24	46.4817650	-84.3023160	2.13	1	1	0	
201140113	6/13/2011	14:25	46.4810050	-84.3017150	0.30	1	1	0	
201140114	6/13/2011	14:34	46.4809750	-84.3014830	0.61	1	1	0	
201140115	6/13/2011	14:41	46.4810760	-84.3016000	0.30	1	1	0	
201140116	6/13/2011	14:48	46.4806460	-84.3013430	0.30	1	2	1	
201140117	6/13/2011	14:59	46.4805880	-84.3008980	1.83	1	1	1	
201140080	6/10/2011	11:10	46.4992600	-84.3167350	2.13	112	3	0	
201140081	6/10/2011	11:24	46.4999150	-84.3164700	5.49	112	1	0	
201140082	6/10/2011	11:36	46.5001160	-84.3177630	5.18	112	1	0	
201140083	6/10/2011	11:44	46.5005450	-84.3171360	6.40	112	1	1	
201140084	6/10/2011	11:54	46.5007760	-84.3176180	5.49	112	1	0	
201140085	6/10/2011	12:32	46.5016060	-84.3192360	4.57	112	1	0	
201140086	6/10/2011	12:42	46.5011530	-84.3204060	5.79	112	2	0	
201140087	6/10/2011	12:49	46.5010130	-84.3210860	6.10	112	1	1	
201140088	6/10/2011	12:59	46.5012730	-84.3214130	6.10	112	1	0	
201140089	6/10/2011	13:08	46.5015930	-84.3224280	6.40	112	1	0	
201140090	6/10/2011	13:17	46.5010910	-84.3191650	5.18	112	1	0	
201140091	6/10/2011	13:27	46.5013850	-84.3191280	4.27	112	1	0	
201140092	6/10/2011	13:34	46.5010600	-84.3188330	4.88	112	1	0	
201140093	6/10/2011	13:41	46.5007700	-84.3188110	5.49	112	1	0	
201140094	6/10/2011	13:49	46.5010500	-84.3183280	4.88	112	1	0	
201140095	6/10/2011	13:59	46.5013560	-84.3179700	3.66	112	1	0	
201140096	6/10/2011	14:09	46.5008000	-84.3184080	5.18	112	1	0	
201140053	6/9/2011	9:43	46.4986810	-84.3154300	3.05	112	1	1	
201140054	6/9/2011	10:00	46.4990950	-84.3148630	5.49	112	1	0	
201140055	6/9/2011	10:16	46.4993930	-84.3151980	4.57	112	1	2	
201140056	6/9/2011	10:27	46.4996400	-84.3152310	5.49	112	3	0	
201140057	6/9/2011	10:32	46.4993260	-84.3150250	2.44	112	1	0	
201140058	6/9/2011	10:41	46.4993200	-84.3146500	5.49	112	1	0	
201140059	6/9/2011	10:51	46.5002610	-84.3144830	5.18	112	1	0	
201140060	6/9/2011	11:00	46.5007780	-84.3145510	5.18	112	1	1	
201140061	6/9/2011	11:11	46.5008610	-84.3147280	5.18	112	1	0	
201140062	6/9/2011	11:18	46.5010400	-84.3144750	5.18	112	1	0	
201140063	6/9/2011	11:25	46.5010100	-84.3150300	5.49	112	1	0	
201140064	6/9/2011	11:33	46.5008360	-84.3151360	5.49	112	1	0	
201140065	6/9/2011	11:41	46.5010760	-84.3151300	5.49	112	1	0	
201140066	6/9/2011	11:49	46.5013080	-84.3156680	4.57	112	1	1	
201140067	6/9/2011	13:26	46.4993980	-84.3160280	3.66	112	1	0	
201140068	6/9/2011	13:41	46.4996230	-84.3160460	5.79	112	3	0	
201140069	6/9/2011	13:45	46.5001630	-84.3155250	5.49	112	1	3	

201140070	6/9/2011	13:56	46.5007310	-84.3157410	5.49	112	2	0
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201140072	6/9/2011	14:14	46.5012910	-84.3169050	3.96	112	1	0
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201140075	6/9/2011	14:39	46.5022660	-84.3184550	2.74	112	1	0
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201140077	6/9/2011	15:12	46.5022950	-84.3195260	2.13	112	1	0
201140078	6/9/2011	15:21	46.5016760	-84.3199980	4.27	112	1	0
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201140037	6/8/2011	10:56	46.4984280	-84.3128730	1.52	111	1	0
201140038	6/8/2011	11:04	46.4987660	-84.3137660	2.13	111	1	0
201140039	6/8/2011	11:11	46.4993860	-84.3134110	2.74	111	2	1
201140040	6/8/2011	11:19	46.4996500	-84.3126350	3.96	111	1	0
201140041	6/8/2011	11:28	46.5005450	-84.3123700	3.96	111	1	0
201140042	6/8/2011	11:34	46.5008160	-84.3115980	5.49	111	1	0
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201140045	6/8/2011	12:47	46.5005260	-84.3136450	3.96	111	1	0
201140046	6/8/2011	12:55	46.5008310	-84.3135200	3.96	111	1	0
201140047	6/8/2011	13:05	46.5007560	-84.3141000	4.57	111	1	1
201140048	6/8/2011	13:19	46.5010880	-84.3140860	5.49	111	1	0
201140049	6/8/2011	13:32	46.4995360	-84.3129900	1.83	111	3	0
201140050	6/8/2011	13:40	46.4993130	-84.3127160	2.74	111	3	0
201140051	6/8/2011	13:44	46.4992930	-84.3137350	3.66	111	3	0
201140052	6/8/2011	13:55	46.4984410	-84.3143430	3.66	112	1	0
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201140004	6/7/2011	9:58	46.4977150	-84.3091600	3.96	111	1	0
201140005	6/7/2011	10:07	46.4980230	-84.3092600	5.18	111	1	0
201140006	6/7/2011	10:15	46.4982400	-84.3094500	5.79	111	1	1
201140007	6/7/2011	10:33	46.4985400	-84.3089550	2.13	111	1	0
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201140009	6/7/2011	10:57	46.4983780	-84.3098560	5.79	111	1	0
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201140011	6/7/2011	11:15	46.4993010	-84.3093100	4.88	111	1	0
201140012	6/7/2011	11:27	46.4999000	-84.3096450	4.57	111	2	2
201140013	6/7/2011	11:38	46.5004780	-84.3100460	5.79	111	2	1
201140014	6/7/2011	13:26	46.4974680	-84.3113350	5.18	111	1	0
201140015	6/7/2011	13:34	46.4973580	-84.3120780	3.35	111	1	1
201140016	6/7/2011	13:42	46.4979560	-84.3127760	1.52	111	1	0
201140017	6/7/2011	13:48	46.4979710	-84.3125380	1.22	111	2	0
201140018	6/7/2011	13:54	46.4984530	-84.3123830	1.22	111	2	0
201140019	6/7/2011	14:13	46.4988680	-84.3122160	3.05	111	2	1
201140020	6/7/2011	14:17	46.4985710	-84.3116180	2.44	111	1	0
201140021	6/7/2011	14:25	46.4989560	-84.3116900	2.74	111	1	0
201140022	6/7/2011	14:31	46.4993250	-84.3113600	4.27	111	1	3
201140023	6/7/2011	14:39	46.4996700	-84.3112300	5.49	111	1	1
201140024	6/7/2011	14:48	46.4997410	-84.3110380	6.40	111	1	0
201140025	6/7/2011	14:57	46.4998850	-84.3106330	7.01	111	1	0
201140026	6/7/2011	15:05	46.5001210	-84.3108110	6.10	111	2	1
201140027	6/7/2011	15:14	46.4999710	-84.3116700	4.27	111	1	0
201140028	6/7/2011	15:20	46.5001530	-84.3120950	3.96	111	1	0
201140029	6/7/2011	15:27	46.5004460	-84.3119280	4.57	111	1	0
201040680	6/4/2010	09:29	46.5251983	-84.1094233	0.61	18	2	0
201040681	6/4/2010	09:34	46.5249567	-84.1093150	0.61	18	1	0
201040682	6/4/2010	09:40	46.5244883	-84.1101083	0.91	18	1	0
201040683	6/4/2010	09:44	46.5243767	-84.1097217	0.61	18	2	0
201040684	6/4/2010	09:50	46.5241583	-84.1096833	0.61	18	2	0
201040685	6/4/2010	09:54	46.5241917	-84.1094183	0.91	18	2	0
201040686	6/4/2010	09:59	46.5241633	-84.1092017	0.91	18	2	0
201040687	6/4/2010	10:03	46.5241617	-84.1089133	0.91	18	2	0
201040688	6/4/2010	10:08	46.5238783	-84.1084317	0.30	18	2	0
201040689	6/4/2010	10:12	46.5235733	-84.1092650	0.91	18	2	0
201040690	6/4/2010	10:18	46.5227417	-84.1085667	0.61	18	2	0

201040691	6/4/2010	10:23	46.5229217	-84.1085817	0.91	18	2	0
201040692	6/4/2010	10:27	46.5229050	-84.1083967	0.91	18	1	0
201040693	6/4/2010	10:58	46.5228817	-84.1088933	0.91	18	2	0
201040694	6/4/2010	11:02	46.5229150	-84.1092683	0.91	18	2	0
201040695	6/4/2010	11:06	46.5226933	-84.1096350	0.91	18	1	0
201040696	6/4/2010	11:10	46.5224033	-84.1097117	1.52	18	1	0
201040697	6/4/2010	11:16	46.5220167	-84.1100600	1.83	18	2	0
201040698	6/4/2010	11:20	46.5216217	-84.1100783	1.83	18	2	0
201040699	6/4/2010	11:25	46.5214550	-84.1100783	1.83	18	2	0
201040700	6/4/2010	11:29	46.5218333	-84.1096267	1.52	18	2	0
201040701	6/4/2010	11:34	46.5215117	-84.1095900	1.52	18	2	0
201040702	6/4/2010	11:40	46.5209833	-84.1096533	1.52	18	2	0
201040703	6/4/2010	11:44	46.5207500	-84.1096367	1.52	18	2	0
201040704	6/4/2010	11:49	46.5205817	-84.1096100	1.83	18	2	0
201040705	6/4/2010	11:54	46.5209167	-84.1092967	1.83	18	2	0
201040706	6/4/2010	11:59	46.5214383	-84.1092900	1.52	18	2	0
201040707	6/4/2010	12:03	46.5216000	-84.1092450	1.52	18	2	0
201040708	6/4/2010	12:07	46.5218100	-84.1092733	1.22	18	2	0
201040709	6/4/2010	12:12	46.5215483	-84.1088800	0.61	18	2	0
201040710	6/4/2010	12:16	46.5209967	-84.1088317	0.91	18	2	0
201040711	6/4/2010	12:21	46.5206717	-84.1088267	0.91	18	2	0
201040712	6/4/2010	12:25	46.5204067	-84.1089400	1.52	18	2	0
201040713	6/4/2010	12:30	46.5212317	-84.1084500	0.61	18	2	0
201040714	6/4/2010	12:36	46.5217517	-84.1082000	0.61	18	2	0
201040715	6/4/2010	12:44	46.5218683	-84.1081150	0.30	18	2	0
201040716	6/4/2010	12:49	46.5220633	-84.1084800	0.61	18	2	0
201040631	6/3/2010	08:47	46.5036433	-84.2520967	6.71	363	2	0
201040632	6/3/2010	08:52	46.5035783	-84.2525417	4.27	363	2	0
201040633	6/3/2010	08:59	46.5039883	-84.2520033	4.88	363	2	0
201040634	6/3/2010	09:05	46.5042933	-84.2524550	3.96	363	2	0
201040635	6/3/2010	09:10	46.5048000	-84.2524583	1.52	363	1	0
201040636	6/3/2010	09:15	46.5046150	-84.2529300	0.91	363	2	0
201040637	6/3/2010	09:20	46.5043250	-84.2529250	0.91	363	1	0
201040638	6/3/2010	09:29	46.5036717	-84.2549917	0.30	363	2	0
201040639	6/3/2010	09:34	46.5036950	-84.2548333	0.61	363	1	0
201040640	6/3/2010	09:38	46.5037333	-84.2546083	0.30	363	2	0
201040641	6/3/2010	09:43	46.5039233	-84.2551750	0.61	363	2	2
201040642	6/3/2010	09:48	46.5039583	-84.2550017	0.30	363	2	0
201040643	6/3/2010	09:54	46.5037750	-84.2543767	0.30	363	2	0
201040644	6/3/2010	10:00	46.5037467	-84.2539317	1.22	363	2	0
201040645	6/3/2010	10:04	46.5037550	-84.2540383	0.91	363	2	0
201040646	6/3/2010	10:09	46.5040067	-84.2538867	0.30	363	2	0
201040647	6/3/2010	10:13	46.5040283	-84.2535683	0.30	363	2	0
201040648	6/3/2010	10:18	46.5039717	-84.2530567	3.35	363	2	0
201040649	6/3/2010	10:44	46.5045517	-84.2541350	0.30	363	2	0
201040650	6/3/2010	10:49	46.5044550	-84.2537950	0.30	363	1	0
201040651	6/3/2010	10:54	46.5045683	-84.2542950	0.30	363	1	0
201040652	6/3/2010	11:03	46.5043183	-84.2539283	0.30	363	2	0
201040653	6/3/2010	11:06	46.5050300	-84.2532150	0.61	363	1	0
201040654	6/3/2010	11:11	46.5051817	-84.2530983	0.61	363	1	0
201040655	6/3/2010	11:16	46.5052917	-84.2541900	0.30	363	2	0
201040656	6/3/2010	11:23	46.5057050	-84.2539217	0.30	363	1	0
201040657	6/3/2010	11:27	46.5057283	-84.2541083	0.30	363	1	0
201040658	6/3/2010	12:39	46.5261533	-84.1123817	0.61	18	2	0
201040659	6/3/2010	12:44	46.5263250	-84.1123583	1.22	18	1	0
201040660	6/3/2010	12:50	46.5264400	-84.1123183	1.52	18	1	0
201040661	6/3/2010	12:56	46.5267083	-84.1119717	0.91	18	2	0
201040662	6/3/2010	13:00	46.5264383	-84.1115850	0.30	18	2	1
201040663	6/3/2010	13:05	46.5261467	-84.1112650	0.30	18	2	0
201040664	6/3/2010	13:10	46.5258817	-84.1108783	0.91	18	2	0
201040665	6/3/2010	13:15	46.5258650	-84.1112300	1.22	18	1	0
201040666	6/3/2010	13:20	46.5258267	-84.1116633	0.91	18	1	0
201040667	6/3/2010	13:25	46.5258100	-84.1120033	0.91	18	2	0
201040668	6/3/2010	13:29	46.5256500	-84.1121533	1.83	18	1	0
201040669	6/3/2010	13:35	46.5252317	-84.1110950	0.61	18	2	0
201040670	6/3/2010	13:42	46.5257117	-84.1102367	0.91	18	2	0
201040671	6/3/2010	13:48	46.5258300	-84.1101933	0.61	18	1	1
201040672	6/3/2010	13:56	46.5258050	-84.1105250	0.61	18	2	0
201040673	6/3/2010	14:00	46.5258417	-84.1103467	0.91	18	1	0
201040674	6/3/2010	14:05	46.5261500	-84.1106083	0.30	18	2	0

201040675	6/3/2010	14:11	46.5252267	-84.1105017	0.91	18	1	0	
201040676	6/3/2010	14:16	46.5246550	-84.1103300	0.61	18	1	0	
201040677	6/3/2010	14:21	46.5249317	-84.1099933	0.91	18	2	0	
201040678	6/3/2010	14:26	46.5249367	-84.1104600	0.61	18	2	0	
201040679	6/3/2010	14:31	46.5247117	-84.1109317	1.22	18	2	0	
201040608	6/2/2010	12:11	46.5008283	-84.2536967	3.96	363	1	0	Dense vegetation
201040598	6/2/2010	11:06	46.5037633	-84.2513700	8.53	363	2	0	
201040599	6/2/2010	11:13	46.5027717	-84.2512733	7.32	363	2	0	
201040600	6/2/2010	11:20	46.5025267	-84.2512817	8.53	363	2	0	
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201040602	6/2/2010	11:33	46.5021883	-84.2521017	7.92	363	2	0	
201040603	6/2/2010	11:39	46.5022700	-84.2519133	7.92	363	2	1	
201040604	6/2/2010	11:47	46.5017217	-84.2527267	6.10	363	2	0	
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201040607	6/2/2010	12:05	46.5013733	-84.2532933	4.27	363	2	0	
201040609	6/2/2010	12:17	46.5005450	-84.2540417	1.22	363	2	0	
201040610	6/2/2010	12:59	46.5013517	-84.2540317	6.10	363	2	0	
201040611	6/2/2010	13:04	46.5011700	-84.2543717	4.57	363	2	6	
201040612	6/2/2010	13:13	46.5013117	-84.2546017	4.88	363	2	0	
201040613	6/2/2010	13:20	46.5022000	-84.2525583	4.57	363	2	0	
201040614	6/2/2010	13:28	46.5018967	-84.2539900	5.18	363	2	0	
201040615	6/2/2010	13:36	46.5028233	-84.2524483	6.71	363	3	0	
201040616	6/2/2010	13:42	46.5028783	-84.2527467	6.10	363	2	4	
201040617	6/2/2010	13:49	46.5029017	-84.2530967	4.88	363	3	0	
201040618	6/2/2010	13:53	46.5027800	-84.2530083	5.49	363	3	0	
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201040623	6/2/2010	14:22	46.5025300	-84.2538717	4.57	363	2	0	
201040624	6/2/2010	14:30	46.5028150	-84.2548117	3.96	363	2	0	
201040625	6/2/2010	14:35	46.5030817	-84.2548867	2.74	363	1	1	
201040626	6/2/2010	14:41	46.5030417	-84.2555183	0.61	363	1	0	
201040627	6/2/2010	14:45	46.5030667	-84.2558850	0.30	363	2	0	
201040628	6/2/2010	14:55	46.5033850	-84.2531800	4.27	363	2	1	
201040629	6/2/2010	15:01	46.5034483	-84.2526733	5.18	363	2	0	
201040630	6/2/2010	15:07	46.5032150	-84.2527367	4.88	363	2	0	
201040553	6/1/2010	10:31	46.5063067	-84.2483533	11.28	365	NA	0	Too deep
201040554	6/1/2010	10:32	46.5065467	-84.2481933	11.58	365	NA	0	Too deep
201040555	6/1/2010	10:35	46.5074383	-84.2465683	10.97	365	NA	0	Too deep
201040556	6/1/2010	11:05	46.5073917	-84.2468250	11.89	365	NA	0	Too deep
201040557	6/1/2010	11:06	46.5076133	-84.2472717	12.19	365	NA	0	Too deep
201040558	6/1/2010	11:08	46.5080700	-84.2471967	11.28	365	NA	0	Too deep
201040559	6/1/2010	11:09	46.5077967	-84.2476983	11.89	365	NA	0	Too deep
201040560	6/1/2010	11:11	46.5074717	-84.2480967	10.97	365	NA	0	Too deep
201040561	6/1/2010	11:12	46.5072067	-84.2473600	11.58	365	NA	0	Too deep
201040562	6/1/2010	11:13	46.5070183	-84.2470383	11.58	365	NA	0	Too deep
201040563	6/1/2010	11:15	46.5071017	-84.2475867	11.58	365	NA	0	Too deep
201040564	6/1/2010	11:16	46.5074067	-84.2484267	10.67	365	NA	0	Too deep
201040566	6/1/2010	11:25	46.5076983	-84.2493233	1.83	365	1	0	Dense vegetation
201040570	6/1/2010	11:48	46.5071617	-84.2501483	2.13	365	1	0	Dense vegetation
201040571	6/1/2010	11:53	46.5076467	-84.2499800	0.91	365	1	0	Dense vegetation
201040572	6/1/2010	11:59	46.5079733	-84.2501217	1.22	365	1	0	Dense vegetation
201040577	6/1/2010	12:35	46.5088950	-84.2485600	2.13	365	1	0	Dense vegetation
201040579	6/1/2010	13:25	46.5088950	-84.2493133	1.22	365	1	0	Dense vegetation
201040580	6/1/2010	13:30	46.5088033	-84.2496700	0.91	365	1	0	Dense vegetation
201040581	6/1/2010	13:35	46.5085233	-84.2499850	0.91	365	1	0	Dense vegetation
201040582	6/1/2010	13:41	46.5085517	-84.2500833	1.22	365	1	0	Dense vegetation
201040583	6/1/2010	13:54	46.5088267	-84.2499683	0.91	365	1	0	Dense vegetation
201040584	6/1/2010	14:01	46.5082633	-84.2508167	1.52	365	1	0	Dense vegetation
201040585	6/1/2010	14:08	46.5082517	-84.2509583	1.22	365	1	0	Dense vegetation
201040588	6/1/2010	14:26	46.5092167	-84.2496850	0.91	365	1	0	Dense vegetation
201040591	6/1/2010	14:40	46.5095417	-84.2500183	1.22	365	2	0	Dense vegetation
201040594	6/1/2010	14:55	46.5097833	-84.2500650	0.91	365	1	0	Dense vegetation
201040541	6/1/2010	09:08	46.5060283	-84.2469083	5.18	365	1	0	
201040542	6/1/2010	09:14	46.5060483	-84.2464517	1.52	365	2	0	
201040543	6/1/2010	09:20	46.5056400	-84.2472300	4.57	365	3	0	
201040544	6/1/2010	09:25	46.5054117	-84.2475917	7.01	365	1	0	
201040545	6/1/2010	09:32	46.5056450	-84.2480700	6.40	365	2	0	

201040546	6/1/2010	09:39	46.5059817	-84.2485433	10.36	365	2	0
201040547	6/1/2010	09:48	46.5059733	-84.2484100	9.14	365	2	1
201040548	6/1/2010	09:56	46.5060717	-84.2488400	10.67	365	2	0
201040549	6/1/2010	10:06	46.5065300	-84.2472167	10.06	365	2	0
201040550	6/1/2010	10:13	46.5063017	-84.2473150	10.06	365	1	0
201040551	6/1/2010	10:21	46.5062683	-84.2478117	7.62	365	3	0
201040552	6/1/2010	10:26	46.5062667	-84.2481033	10.67	365	2	0
201040565	6/1/2010	11:20	46.5077233	-84.2489883	3.96	365	1	0
201040567	6/1/2010	11:31	46.5074517	-84.2492683	3.66	365	1	0
201040568	6/1/2010	11:35	46.5075117	-84.2490883	4.27	365	1	0
201040569	6/1/2010	11:42	46.5068533	-84.2496450	3.66	365	1	0
201040573	6/1/2010	12:06	46.5080467	-84.2488600	3.05	365	1	0
201040574	6/1/2010	12:11	46.5079350	-84.2487700	3.96	365	1	0
201040575	6/1/2010	12:18	46.5086383	-84.2481650	5.79	365	1	2
201040576	6/1/2010	12:26	46.5085800	-84.2480817	7.01	365	1	3
201040578	6/1/2010	13:17	46.5093917	-84.2488917	1.52	365	1	0
201040586	6/1/2010	14:13	46.5081833	-84.2512433	0.61	365	1	0
201040587	6/1/2010	14:19	46.5091017	-84.2517100	0.30	365	2	0
201040589	6/1/2010	14:30	46.5092333	-84.2495367	1.22	365	1	0
201040590	6/1/2010	14:36	46.5094267	-84.2501267	1.22	365	2	0
201040592	6/1/2010	14:47	46.5095083	-84.2497450	1.83	365	1	0
201040593	6/1/2010	14:50	46.5095683	-84.2497117	1.52	365	1	0
201040595	6/1/2010	15:00	46.5099217	-84.2504333	0.30	365	2	0
201040596	6/1/2010	15:04	46.5097467	-84.2507833	0.30	365	2	0
201040597	6/1/2010	15:10	46.5095100	-84.2508867	0.30	365	2	0
201040506	5/31/2010	08:50	46.4662533	-84.2838783	0.61	172	2	0
201040507	5/31/2010	08:55	46.4660033	-84.2835900	0.30	172	2	0
201040508	5/31/2010	08:59	46.4658100	-84.2835167	0.61	172	2	1
201040509	5/31/2010	09:05	46.4658517	-84.2833033	0.30	172	2	0
201040510	5/31/2010	09:10	46.4655983	-84.2832467	0.30	172	2	0
201040511	5/31/2010	09:15	46.4655567	-84.2835100	0.91	172	2	0
201040512	5/31/2010	09:25	46.4656817	-84.2835350	0.61	172	2	1
201040513	5/31/2010	09:34	46.4651033	-84.2828950	0.30	172	2	0
201040514	5/31/2010	09:38	46.4650567	-84.2830967	0.61	172	2	0
201040515	5/31/2010	09:46	46.4648200	-84.2829250	0.61	172	2	0
201040516	5/31/2010	09:48	46.4650767	-84.2825133	0.30	172	2	0
201040517	5/31/2010	09:52	46.4653317	-84.2825283	0.30	172	2	0
201040518	5/31/2010	09:56	46.4656017	-84.2825017	0.30	172	2	0
201040519	5/31/2010	10:01	46.4648050	-84.2825117	0.30	172	2	0
201040520	5/31/2010	10:06	46.4644567	-84.2825233	0.61	172	2	0
201040521	5/31/2010	10:10	46.4645833	-84.2823483	0.30	172	2	0
201040522	5/31/2010	10:14	46.4642267	-84.2823833	0.61	172	2	5
201040523	5/31/2010	10:25	46.4642583	-84.2819200	0.30	172	2	0
201040524	5/31/2010	10:30	46.4645683	-84.2815633	0.30	172	2	0
201040525	5/31/2010	10:49	46.4648250	-84.2818083	0.30	172	2	0
201040526	5/31/2010	10:57	46.4649917	-84.2819800	0.30	172	2	0
201040527	5/31/2010	11:00	46.4651717	-84.2816800	0.30	172	2	1
201040528	5/31/2010	11:07	46.4642867	-84.2816683	0.30	172	2	0
201040529	5/31/2010	11:11	46.4639650	-84.2815117	0.30	172	2	0
201040530	5/31/2010	11:16	46.4643183	-84.2813200	0.30	172	2	0
201040531	5/31/2010	11:21	46.4642167	-84.2811483	0.30	172	2	0
201040532	5/31/2010	11:29	46.4633833	-84.2815350	2.13	172	2	0
201040533	5/31/2010	11:34	46.4636283	-84.2812467	0.61	172	2	0
201040534	5/31/2010	11:38	46.4639133	-84.2813017	0.30	172	2	0
201040535	5/31/2010	11:43	46.4634317	-84.2813133	0.30	172	3	0
201040536	5/31/2010	11:45	46.4631350	-84.2810967	0.30	172	2	0
201040537	5/31/2010	11:52	46.4634033	-84.2808667	0.61	172	3	0
201040538	5/31/2010	11:57	46.4633483	-84.2803233	0.30	172	3	0
201040539	5/31/2010	12:01	46.4628167	-84.2809050	0.30	172	2	0
201040540	5/31/2010	12:06	46.4627333	-84.2807067	0.30	172	2	0
201040447	5/30/2010	08:47	46.4411367	-84.2615000	2.13	40	2	0
201040448	5/30/2010	08:53	46.4410617	-84.2611500	2.13	40	2	0
201040449	5/30/2010	08:58	46.4411317	-84.2609517	2.13	40	2	0
201040450	5/30/2010	09:02	46.4411567	-84.2606650	1.52	40	2	0
201040451	5/30/2010	09:07	46.4413183	-84.2610833	2.13	40	2	0
201040452	5/30/2010	09:15	46.4408383	-84.2614067	5.49	40	2	1
201040453	5/30/2010	09:21	46.4407850	-84.2611817	1.83	40	2	0
201040454	5/30/2010	09:26	46.4408350	-84.2609467	1.83	40	2	0
201040455	5/30/2010	09:32	46.4405300	-84.2610350	2.74	40	2	0
201040456	5/30/2010	09:38	46.4405233	-84.2603583	2.13	40	2	1

201040457	5/30/2010	09:43	46.4402050	-84.2602550	1.83	40	2	0
201040458	5/30/2010	09:49	46.4402050	-84.2595833	2.13	40	2	0
201040459	5/30/2010	09:52	46.4402800	-84.2593733	2.13	40	2	0
201040460	5/30/2010	09:56	46.4405233	-84.2594800	2.13	40	2	0
201040461	5/30/2010	10:01	46.4406367	-84.2590517	2.44	40	2	0
201040462	5/30/2010	10:06	46.4403750	-84.2586067	2.13	40	2	0
201040463	5/30/2010	10:11	46.4413467	-84.2595083	2.13	40	2	0
201040464	5/30/2010	10:16	46.4413200	-84.2598617	2.13	40	1	0
201040465	5/30/2010	10:21	46.4413983	-84.2600567	2.13	40	2	0
201040466	5/30/2010	10:51	46.4394917	-84.2594567	1.83	40	2	0
201040467	5/30/2010	10:55	46.4396467	-84.2591467	1.22	40	2	0
201040468	5/30/2010	11:00	46.4397000	-84.2587883	2.44	40	2	0
201040469	5/30/2010	11:04	46.4397783	-84.2585850	2.13	40	2	0
201040470	5/30/2010	11:08	46.4394567	-84.2582367	2.74	40	2	0
201040471	5/30/2010	11:13	46.4390950	-84.2582167	3.05	40	2	0
201040472	5/30/2010	11:19	46.4388150	-84.2585967	5.18	40	2	0
201040473	5/30/2010	11:24	46.4387483	-84.2590317	5.49	40	2	0
201040474	5/30/2010	11:30	46.4385117	-84.2589317	8.84	40	2	0
201040475	5/30/2010	11:36	46.4384983	-84.2585567	5.79	40	2	0
201040476	5/30/2010	11:43	46.4382917	-84.2582950	3.96	40	2	1
201040477	5/30/2010	11:49	46.4388450	-84.2579983	4.27	40	2	0
201040478	5/30/2010	11:53	46.4391400	-84.2575467	3.05	40	2	0
201040479	5/30/2010	11:58	46.4388400	-84.2574867	3.96	40	2	0
201040480	5/30/2010	12:33	46.4385767	-84.2574917	3.05	40	2	0
201040481	5/30/2010	12:38	46.4384500	-84.2568283	3.35	40	2	0
201040482	5/30/2010	12:43	46.4385950	-84.2566000	3.05	40	2	0
201040483	5/30/2010	12:47	46.4387750	-84.2571967	3.35	40	2	0
201040484	5/30/2010	12:52	46.4389283	-84.2572833	3.35	40	2	0
201040485	5/30/2010	12:56	46.4390650	-84.2571367	3.05	40	2	0
201040486	5/30/2010	13:01	46.4392233	-84.2570283	2.74	40	2	0
201040487	5/30/2010	13:06	46.4394367	-84.2572300	2.74	40	2	0
201040488	5/30/2010	13:10	46.4396283	-84.2575817	3.05	40	2	0
201040489	5/30/2010	13:15	46.4397533	-84.2568617	0.30	40	2	0
201040490	5/30/2010	13:19	46.4399117	-84.2564800	0.30	40	2	0
201040491	5/30/2010	13:24	46.4399783	-84.2562083	0.30	40	2	0
201040492	5/30/2010	13:29	46.4400767	-84.2559067	0.30	40	2	0
201040493	5/30/2010	13:34	46.4397767	-84.2556883	0.30	40	2	0
201040494	5/30/2010	13:38	46.4396933	-84.2554933	0.30	40	2	0
201040495	5/30/2010	13:42	46.4400067	-84.2550767	0.91	40	2	0
201040496	5/30/2010	13:47	46.4402983	-84.2552383	0.30	40	2	0
201040497	5/30/2010	13:52	46.4404450	-84.2559600	0.30	40	2	0
201040498	5/30/2010	13:57	46.4404733	-84.2566683	0.30	40	2	0
201040499	5/30/2010	14:01	46.4403333	-84.2570967	0.30	40	2	0
201040500	5/30/2010	14:05	46.4404917	-84.2575433	0.91	40	2	0
201040501	5/30/2010	14:13	46.4407917	-84.2579900	2.74	40	1	1
201040502	5/30/2010	14:15	46.4409050	-84.2577017	0.30	40	2	0
201040503	5/30/2010	14:20	46.4408483	-84.2583367	2.13	40	2	0
201040504	5/30/2010	14:25	46.4411383	-84.2583683	2.44	40	1	0
201040505	5/30/2010	14:29	46.4413717	-84.2583683	2.74	40	2	0
201040387	5/29/2010	09:06	46.4483617	-84.2689067	2.44	4001	2	0
201040388	5/29/2010	09:12	46.4494467	-84.2700083	2.74	4001	2	0
201040389	5/29/2010	09:18	46.4492800	-84.2692883	0.91	4001	2	0
201040390	5/29/2010	09:23	46.4492517	-84.2689267	0.30	4001	2	1
201040391	5/29/2010	09:30	46.4494617	-84.2688633	0.30	4001	2	2
201040392	5/29/2010	09:35	46.4495083	-84.2686667	0.30	4001	2	1
201040393	5/29/2010	09:40	46.4497283	-84.2686417	0.61	4001	3	0
201040394	5/29/2010	09:42	46.4497967	-84.2689500	0.30	4001	2	0
201040395	5/29/2010	09:46	46.4497983	-84.2683650	0.30	4001	3	0
201040396	5/29/2010	09:49	46.4497983	-84.2681383	0.30	4001	3	0
201040397	5/29/2010	09:51	46.4498217	-84.2678533	0.30	4001	2	0
201040398	5/29/2010	09:55	46.4498367	-84.2674883	0.30	4001	2	0
201040399	5/29/2010	09:58	46.4498050	-84.2672933	0.30	4001	2	0
201040400	5/29/2010	10:02	46.4494683	-84.2673150	0.30	4001	2	0
201040401	5/29/2010	10:06	46.4492050	-84.2676783	0.30	4001	3	0
201040402	5/29/2010	10:07	46.4492050	-84.2678283	0.30	4001	3	0
201040403	5/29/2010	10:08	46.4492050	-84.2683533	0.30	4001	2	2
201040404	5/29/2010	10:41	46.4500450	-84.2667283	0.30	4001	2	0
201040405	5/29/2010	10:45	46.4500683	-84.2669850	0.30	4001	3	0
201040406	5/29/2010	10:48	46.4502450	-84.2678167	0.30	4001	2	0
201040407	5/29/2010	10:53	46.4505600	-84.2670733	0.61	4001	2	0

201040408	5/29/2010	10:57	46.4508300	-84.2674050	0.91	4001	2	0
201040409	5/29/2010	11:02	46.4509217	-84.2675783	0.91	4001	2	0
201040410	5/29/2010	11:06	46.4509033	-84.2678433	1.22	4001	2	1
201040411	5/29/2010	11:11	46.4511817	-84.2673900	0.61	4001	2	0
201040412	5/29/2010	11:16	46.4514433	-84.2678100	0.30	4001	2	1
201040413	5/29/2010	11:22	46.4503550	-84.2685367	0.61	4001	2	0
201040414	5/29/2010	11:29	46.4502650	-84.2688600	0.30	4001	1	2
201040415	5/29/2010	11:34	46.4503317	-84.2690533	0.30	4001	2	1
201040416	5/29/2010	11:40	46.4505983	-84.2694700	0.30	4001	3	0
201040417	5/29/2010	11:42	46.4508583	-84.2689950	0.30	4001	3	0
201040418	5/29/2010	11:45	46.4514150	-84.2686183	0.30	4001	2	1
201040419	5/29/2010	11:49	46.4515783	-84.2685550	0.61	4001	2	0
201040420	5/29/2010	11:53	46.4514800	-84.2689533	0.30	4001	2	2
201040421	5/29/2010	12:00	46.4509550	-84.2697667	0.30	4001	2	0
201040422	5/29/2010	12:46	46.4511650	-84.2698133	0.30	4001	2	0
201040423	5/29/2010	12:49	46.4511433	-84.2700767	0.30	4001	2	0
201040424	5/29/2010	12:54	46.4512117	-84.2702850	0.30	4001	2	0
201040425	5/29/2010	12:57	46.4509967	-84.2704250	0.30	4001	2	1
201040426	5/29/2010	13:03	46.4509083	-84.2708567	0.61	4001	2	1
201040427	5/29/2010	13:14	46.4501583	-84.2700583	3.05	4001	2	3
201040428	5/29/2010	13:23	46.4499600	-84.2704433	3.35	4001	2	0
201040429	5/29/2010	13:32	46.4517383	-84.2721217	3.35	4001	2	6
201040430	5/29/2010	13:42	46.4518600	-84.2717667	0.30	4001	2	0
201040431	5/29/2010	13:46	46.4518750	-84.2714317	0.30	4001	2	0
201040432	5/29/2010	13:51	46.4518117	-84.2712600	0.30	4001	2	0
201040433	5/29/2010	13:55	46.4515483	-84.2709517	0.30	4001	2	3
201040434	5/29/2010	14:01	46.4515350	-84.2706767	0.30	4001	2	1
201040435	5/29/2010	14:06	46.4515417	-84.2704800	0.30	4001	2	1
201040436	5/29/2010	14:13	46.4517683	-84.2704950	0.30	4001	2	0
201040437	5/29/2010	14:18	46.4520567	-84.2709700	0.30	4001	2	0
201040438	5/29/2010	14:23	46.4523783	-84.2710483	0.30	4001	3	0
201040439	5/29/2010	14:24	46.4523067	-84.2712050	0.30	4001	3	0
201040440	5/29/2010	14:28	46.4529300	-84.2698767	0.30	4001	2	0
201040441	5/29/2010	14:33	46.4524317	-84.2690050	0.30	4001	2	1
201040442	5/29/2010	14:40	46.4523867	-84.2697017	0.30	4001	2	0
201040443	5/29/2010	14:45	46.4518833	-84.2693000	0.30	4001	3	0
201040444	5/29/2010	14:46	46.4517500	-84.2694650	0.30	4001	3	0
201040445	5/29/2010	14:47	46.4517433	-84.2698183	0.30	4001	3	0
201040446	5/29/2010	14:49	46.4514950	-84.2702817	0.30	4001	2	1
201040355	5/28/2010	09:06	46.5327600	-84.1437050	3.05	30	2	0
201040356	5/28/2010	09:11	46.5326983	-84.1441150	3.05	30	1	1
201040357	5/28/2010	09:21	46.5325033	-84.1435783	8.23	30	2	1
201040358	5/28/2010	09:29	46.5324300	-84.1436967	8.53	30	2	0
201040359	5/28/2010	09:37	46.5325467	-84.1441250	8.23	30	2	0
201040360	5/28/2010	09:45	46.5324883	-84.1445717	4.88	30	2	0
201040361	5/28/2010	09:51	46.5324500	-84.1449783	3.66	30	1	0
201040362	5/28/2010	09:56	46.5323917	-84.1453750	3.96	30	2	0
201040363	5/28/2010	10:06	46.5322717	-84.1447733	7.92	30	2	0
201040364	5/28/2010	10:13	46.5319283	-84.1450883	6.71	30	2	0
201040365	5/28/2010	10:22	46.5317333	-84.1455567	7.01	30	2	1
201040366	5/28/2010	10:32	46.5316983	-84.1456950	7.01	30	2	0
201040367	5/28/2010	11:05	46.5319867	-84.1460833	6.40	30	2	1
201040368	5/28/2010	11:11	46.5320183	-84.1459117	6.71	30	2	1
201040369	5/28/2010	11:22	46.5321683	-84.1461117	4.27	30	2	0
201040370	5/28/2010	11:28	46.5314567	-84.1463883	7.92	30	2	0
201040371	5/28/2010	11:37	46.5314450	-84.1466767	7.01	30	2	0
201040372	5/28/2010	11:46	46.5316450	-84.1469050	5.49	30	2	0
201040373	5/28/2010	11:52	46.5316600	-84.1467217	6.10	30	2	0
201040374	5/28/2010	11:59	46.5316750	-84.1473800	3.05	30	1	2
201040375	5/28/2010	12:07	46.5314317	-84.1472867	5.49	30	2	0
201040376	5/28/2010	12:13	46.5311950	-84.1476900	5.49	30	2	0
201040377	5/28/2010	12:21	46.5312883	-84.1481517	3.05	30	1	0
201040378	5/28/2010	12:26	46.5313483	-84.1479733	3.35	30	1	1
201040379	5/28/2010	12:33	46.5315167	-84.1479067	1.83	30	1	1
201040380	5/28/2010	13:18	46.5308767	-84.1481283	6.40	30	2	0
201040381	5/28/2010	13:28	46.5308650	-84.1485000	6.40	30	2	2
201040382	5/28/2010	13:38	46.5310483	-84.1489250	1.83	30	1	1
201040383	5/28/2010	13:45	46.5308283	-84.1491667	5.18	30	2	0
201040384	5/28/2010	13:55	46.5307183	-84.1496733	2.44	30	1	1
201040385	5/28/2010	14:00	46.5305350	-84.1496067	6.10	30	2	0

201040386	5/28/2010	14:05	46.5305767	-84.1494700	6.40	30	2	0	
201040312	5/27/2010	08:56	46.5289450	-84.1282100	1.83	24	1	0	
201040313	5/27/2010	09:02	46.5290283	-84.1282583	1.83	24	2	0	
201040314	5/27/2010	09:07	46.5287783	-84.1280900	0.91	24	2	0	
201040315	5/27/2010	09:12	46.5287150	-84.1283400	0.30	24	2	0	
201040316	5/27/2010	09:16	46.5283383	-84.1279183	0.30	24	1	0	
201040317	5/27/2010	09:27	46.5283267	-84.1274117	3.66	24	2	0	
201040318	5/27/2010	09:33	46.5280433	-84.1266633	5.18	24	2	0	
201040319	5/27/2010	09:43	46.5287367	-84.1261017	4.57	24	2	0	
201040320	5/27/2010	09:52	46.5292800	-84.1266717	4.27	24	2	0	
201040321	5/27/2010	10:00	46.5298033	-84.1266633	0.91	24	2	0	
201040322	5/27/2010	10:09	46.5280917	-84.1257250	5.49	24	2	0	
201040323	5/27/2010	10:20	46.5281000	-84.1254400	0.61	24	2	0	
201040324	5/27/2010	10:26	46.5268767	-84.1254733	5.49	24	2	0	
201040325	5/27/2010	10:33	46.5271767	-84.1257850	5.49	24	2	0	
201040326	5/27/2010	10:33	46.5272967	-84.1258333	5.49	24	2	0	
201040327	5/27/2010	10:34	46.5275700	-84.1261883	5.49	24	2	0	
201040328	5/27/2010	10:37	46.5275817	-84.1270167	1.83	24	2	0	
201040329	5/27/2010	10:42	46.5271133	-84.1267200	2.44	24	2	1	
201040330	5/27/2010	11:08	46.5269267	-84.1265917	3.35	24	1	0	
201040331	5/27/2010	11:14	46.5267067	-84.1266150	2.74	24	1	0	
201040332	5/27/2010	11:18	46.5268283	-84.1271050	0.30	24	1	0	
201040333	5/27/2010	11:25	46.5272967	-84.1277883	0.30	24	1	0	
201040334	5/27/2010	11:45	46.5206800	-84.1215667	1.83	16	1	0	
201040335	5/27/2010	11:50	46.5205883	-84.1213933	3.35	16	1	0	
201040336	5/27/2010	11:57	46.5210417	-84.1222483	1.52	16	2	0	
201040337	5/27/2010	12:04	46.5215217	-84.1228567	3.35	16	2	0	
201040338	5/27/2010	12:11	46.5214117	-84.1227050	4.57	16	2	0	
201040339	5/27/2010	12:19	46.5212533	-84.1224750	3.05	16	1	0	
201040340	5/27/2010	12:26	46.5208817	-84.1219150	1.83	16	2	0	
201040341	5/27/2010	12:32	46.5204833	-84.1211383	1.83	16	2	1	
201040342	5/27/2010	12:41	46.5203833	-84.1209717	3.35	16	2	0	
201040343	5/27/2010	13:30	46.5332983	-84.1388750	6.40	30	1	0	
201040344	5/27/2010	13:40	46.533217	-84.1402300	2.74	30	2	0	
201040345	5/27/2010	13:48	46.5331350	-84.1403367	7.01	30	1	0	
201040346	5/27/2010	13:55	46.5330900	-84.1405883	7.62	30	2	2	
201040347	5/27/2010	14:03	46.5332300	-84.1409100	1.52	30	2	0	
201040348	5/27/2010	14:11	46.5331150	-84.1412833	5.18	30	2	0	
201040349	5/27/2010	14:17	46.5330667	-84.1422250	0.91	30	1	1	
201040350	5/27/2010	14:23	46.5330000	-84.1425250	1.22	30	2	0	
201040351	5/27/2010	14:28	46.5329850	-84.1424233	2.44	30	2	0	
201040352	5/27/2010	14:34	46.5328633	-84.1421100	6.40	30	2	0	
201040353	5/27/2010	14:40	46.5328550	-84.1424900	6.10	30	2	0	
201040354	5/27/2010	14:48	46.5328033	-84.1427283	7.32	30	2	1	
201040262	5/26/2010	09:15	46.5293400	-84.2342350	2.13	532	1	0	Dense vegetation
201040263	5/26/2010	09:20	46.5291283	-84.2345167	1.83	532	1	0	Dense vegetation
201040264	5/26/2010	09:25	46.5291133	-84.2343333	2.74	532	1	0	Dense vegetation
201040272	5/26/2010	10:08	46.5288517	-84.2341033	3.35	532	1	0	Dense vegetation
201040273	5/26/2010	10:13	46.5287750	-84.2343617	3.35	532	1	0	Dense vegetation
201040274	5/26/2010	10:17	46.5285467	-84.2347650	2.74	532	1	0	Dense vegetation
201040275	5/26/2010	10:35	46.5285417	-84.2353517	0.91	532	1	0	Dense vegetation
201040276	5/26/2010	10:40	46.5284200	-84.2354150	1.22	532	1	0	Dense vegetation
201040277	5/26/2010	10:44	46.5281983	-84.2354033	1.22	532	1	0	Dense vegetation
201040278	5/26/2010	10:48	46.5278867	-84.2354450	1.52	532	1	0	Dense vegetation
201040279	5/26/2010	10:53	46.5278233	-84.2350933	3.05	532	1	0	Dense vegetation
201040280	5/26/2010	10:57	46.5278117	-84.2348267	3.05	532	1	0	Dense vegetation
201040281	5/26/2010	11:01	46.5278150	-84.2345383	3.35	532	1	0	Dense vegetation
201040258	5/26/2010	08:51	46.5295950	-84.2322333	6.10	532	2	0	
201040259	5/26/2010	08:57	46.5296667	-84.2320433	5.49	532	2	0	
201040260	5/26/2010	09:02	46.5293900	-84.2328767	6.71	532	1	0	
201040261	5/26/2010	09:10	46.5293867	-84.2334017	4.27	532	1	0	
201040265	5/26/2010	09:30	46.5289867	-84.2341117	3.66	532	1	0	
201040266	5/26/2010	09:35	46.5290217	-84.2333150	5.18	532	1	0	
201040267	5/26/2010	09:41	46.5290583	-84.2329383	6.40	532	2	0	
201040268	5/26/2010	09:47	46.5290833	-84.2325183	5.18	532	2	0	
201040269	5/26/2010	09:53	46.5287683	-84.2329333	6.10	532	1	0	
201040270	5/26/2010	09:58	46.5287717	-84.2334067	4.57	532	1	0	
201040271	5/26/2010	10:04	46.5287367	-84.2338033	3.66	532	1	0	
201040282	5/26/2010	11:07	46.5273350	-84.2346200	4.27	532	1	0	
201040283	5/26/2010	11:13	46.5271917	-84.2346050	4.57	532	2	1	

201040284	5/26/2010	11:21	46.5284400	-84.2334567	5.79	532	2	0	
201040285	5/26/2010	11:27	46.5284383	-84.2338400	4.57	532	2	0	
201040286	5/26/2010	11:32	46.5281467	-84.2338817	5.18	532	2	1	
201040287	5/26/2010	11:38	46.5279017	-84.2339200	5.49	532	2	1	
201040288	5/26/2010	12:14	46.5307083	-84.1307767	4.88	24	2	0	
201040289	5/26/2010	12:22	46.5304883	-84.1310283	4.27	24	2	0	
201040290	5/26/2010	12:28	46.5303883	-84.1305700	4.57	24	2	0	
201040291	5/26/2010	12:34	46.5298233	-84.1301150	0.91	24	2	0	
201040292	5/26/2010	12:39	46.5298683	-84.1305017	2.44	24	2	0	
201040293	5/26/2010	12:45	46.5298417	-84.1306333	1.22	24	1	2	
201040294	5/26/2010	12:52	46.5298083	-84.1309767	1.22	24	1	0	
201040295	5/26/2010	12:57	46.5286367	-84.1297183	0.91	24	2	0	
201040296	5/26/2010	13:04	46.5290333	-84.1296983	0.91	24	1	0	
201040297	5/26/2010	13:09	46.5292717	-84.1297750	0.61	24	2	0	
201040298	5/26/2010	13:14	46.5292550	-84.1301833	1.22	24	1	0	
201040299	5/26/2010	13:24	46.5275350	-84.1285400	1.52	24	1	1	
201040300	5/26/2010	13:31	46.5279050	-84.1285850	0.30	24	1	0	
201040301	5/26/2010	13:35	46.5283467	-84.1287050	0.30	24	2	1	
201040302	5/26/2010	13:54	46.5286583	-84.1289650	0.30	24	2	0	
201040303	5/26/2010	14:00	46.5292167	-84.1285300	1.83	24	2	0	
201040304	5/26/2010	14:05	46.5292700	-84.1289383	0.61	24	2	0	
201040305	5/26/2010	14:11	46.5295383	-84.1285633	4.27	24	2	1	
201040306	5/26/2010	14:18	46.5297883	-84.1290817	3.96	24	2	0	
201040307	5/26/2010	14:23	46.5300833	-84.1292650	4.88	24	2	0	
201040308	5/26/2010	14:28	46.5300533	-84.1280917	5.18	24	2	0	
201040309	5/26/2010	14:34	46.5301500	-84.1282483	4.88	24	2	0	
201040310	5/26/2010	14:40	46.5295817	-84.1280467	5.18	24	2	0	
201040311	5/26/2010	14:45	46.5295300	-84.1282450	4.57	24	2	0	
201040211	5/25/2010	09:40	46.5328183	-84.2274433	10.67	422	NA	0	Too deep
201040212	5/25/2010	09:45	46.5330500	-84.2271200	10.67	422	NA	0	Too deep
201040224	5/25/2010	11:12	46.5322350	-84.2246317	10.97	422	NA	0	Too deep
201040225	5/25/2010	11:13	46.5322717	-84.2250100	10.36	422	NA	0	Too deep
201040229	5/25/2010	11:33	46.5328517	-84.2242333	10.97	422	NA	0	Too deep
201040241	5/25/2010	13:19	46.5310533	-84.2313817	5.18	532	1	0	Dense vegetation
201040244	5/25/2010	13:37	46.5307933	-84.2329417	3.35	532	1	0	Dense vegetation
201040245	5/25/2010	13:42	46.5306517	-84.2329733	3.35	532	1	0	Dense vegetation
201040246	5/25/2010	13:48	46.5304133	-84.2334467	2.13	532	1	0	Dense vegetation
201040247	5/25/2010	13:54	46.5301450	-84.2326300	4.27	532	1	0	Dense vegetation
201040253	5/25/2010	14:33	46.5296550	-84.2340500	1.83	532	1	0	Dense vegetation
201040254	5/25/2010	14:38	46.5295717	-84.2338917	2.44	532	1	0	Dense vegetation
201040255	5/25/2010	14:44	46.5295833	-84.2336633	2.74	532	1	0	Dense vegetation
201040256	5/25/2010	14:49	46.5296967	-84.2332817	3.35	532	1	0	Dense vegetation
201040207	5/25/2010	09:12	46.5316317	-84.2273833	7.01	422	1	0	
201040208	5/25/2010	09:20	46.5317400	-84.2275733	7.01	422	1	0	
201040209	5/25/2010	09:25	46.5322583	-84.2273767	6.71	422	1	0	
201040210	5/25/2010	09:31	46.5322900	-84.2276417	6.71	422	2	0	
201040213	5/25/2010	09:47	46.5336817	-84.2271733	7.32	422	1	0	
201040214	5/25/2010	09:54	46.5322350	-84.2266817	7.01	422	2	0	
201040215	5/25/2010	10:00	46.5319000	-84.2263100	6.10	422	1	1	
201040216	5/25/2010	10:10	46.5319317	-84.2255083	7.92	422	1	0	
201040217	5/25/2010	10:16	46.5324567	-84.2253667	7.01	422	2	0	
201040218	5/25/2010	10:22	46.5324950	-84.2258100	6.71	422	2	0	
201040219	5/25/2010	10:28	46.5325633	-84.2262033	7.01	422	2	0	
201040220	5/25/2010	10:36	46.5325083	-84.2263150	7.32	422	2	0	
201040221	5/25/2010	10:41	46.5330167	-84.2258217	7.01	422	2	0	
201040222	5/25/2010	10:48	46.5330633	-84.2259883	6.71	422	2	0	
201040223	5/25/2010	11:05	46.5319050	-84.2245717	7.32	422	1	0	
201040226	5/25/2010	11:15	46.5324933	-84.2252183	7.32	422	2	0	
201040227	5/25/2010	11:20	46.5325667	-84.2249567	7.62	422	2	0	
201040228	5/25/2010	11:26	46.5327517	-84.2246067	7.92	422	1	0	
201040230	5/25/2010	11:34	46.5331633	-84.2245817	7.32	422	2	0	
201040231	5/25/2010	11:41	46.5331467	-84.2250967	7.01	422	2	0	
201040232	5/25/2010	11:49	46.5332983	-84.2246817	7.32	422	2	0	
201040233	5/25/2010	11:54	46.5334183	-84.2243183	7.32	422	1	0	
201040234	5/25/2010	12:00	46.5337083	-84.2243983	7.32	422	1	0	
201040235	5/25/2010	12:09	46.5336817	-84.2254183	6.71	422	2	0	
201040236	5/25/2010	12:14	46.5339417	-84.2257733	6.40	422	2	0	
201040237	5/25/2010	12:19	46.5338617	-84.2260067	6.71	422	2	0	
201040238	5/25/2010	12:58	46.5316350	-84.2323767	3.66	532	1	0	
201040239	5/25/2010	13:05	46.5313700	-84.2317517	4.88	532	1	0	

201040240	5/25/2010	13:11	46.5313933	-84.2314117	4.88	532	1	0
201040242	5/25/2010	13:25	46.5308167	-84.2317567	4.88	532	1	0
201040243	5/25/2010	13:29	46.5305083	-84.2314283	5.49	532	2	0
201040248	5/25/2010	14:00	46.5301650	-84.2324617	4.88	532	1	0
201040249	5/25/2010	14:05	46.5301933	-84.2322383	5.18	532	2	0
201040250	5/25/2010	14:09	46.5301033	-84.2320567	5.49	532	2	0
201040251	5/25/2010	14:16	46.5303117	-84.2318800	5.18	532	2	1
201040252	5/25/2010	14:25	46.5299967	-84.2317983	6.10	532	2	0
201040257	5/25/2010	14:56	46.5296883	-84.2325683	6.10	532	2	0
201040160	5/23/2010	08:56	46.5229433	-84.2334250	2.13	31	1	0
201040161	5/23/2010	09:04	46.5230083	-84.2337550	6.40	31	1	0
201040162	5/23/2010	09:14	46.5229783	-84.2341850	9.14	31	2	0
201040163	5/23/2010	09:20	46.5229200	-84.2340500	9.14	31	1	0
201040164	5/23/2010	09:31	46.5227150	-84.2341333	9.75	31	1	0
201040165	5/23/2010	09:39	46.5231383	-84.2337567	9.14	31	1	0
201040166	5/23/2010	09:50	46.5231517	-84.2332883	2.44	31	1	0
201040167	5/23/2010	10:13	46.5226667	-84.2321900	0.61	31	1	0
201040168	5/23/2010	10:18	46.5225867	-84.2325483	0.30	31	1	0
201040169	5/23/2010	10:25	46.5224150	-84.2325683	0.61	31	1	0
201040170	5/23/2010	10:30	46.5223433	-84.2320583	0.61	31	1	0
201040171	5/23/2010	10:35	46.5221617	-84.2323033	0.61	31	1	0
201040172	5/23/2010	10:40	46.5221967	-84.2325117	0.30	31	1	0
201040173	5/23/2010	10:46	46.5220583	-84.2325133	0.61	31	1	0
201040174	5/23/2010	10:52	46.5218600	-84.2323050	0.61	31	1	0
201040175	5/23/2010	10:56	46.5217183	-84.2322017	0.61	31	1	0
201040176	5/23/2010	11:02	46.5214817	-84.2330467	0.91	31	1	0
201040177	5/23/2010	11:07	46.5215567	-84.2332550	0.30	31	1	0
201040178	5/23/2010	11:30	46.5307950	-84.2273950	5.18	422	2	0
201040179	5/23/2010	11:38	46.5302450	-84.2266117	5.49	422	1	0
201040180	5/23/2010	11:43	46.5300450	-84.2261883	1.22	422	1	0
201040181	5/23/2010	11:51	46.5302383	-84.2257933	1.22	422	1	0
201040182	5/23/2010	12:28	46.5305450	-84.2262350	6.71	422	2	0
201040183	5/23/2010	12:33	46.5303800	-84.2258433	3.05	422	1	0
201040184	5/23/2010	12:39	46.5305250	-84.2257767	4.57	422	1	0
201040185	5/23/2010	12:46	46.5293550	-84.2269633	2.74	422	1	2
201040186	5/23/2010	12:53	46.5292700	-84.2266433	0.61	422	1	0
201040187	5/23/2010	12:57	46.5294200	-84.2266383	0.91	422	1	0
201040188	5/23/2010	13:02	46.5297217	-84.2262267	1.22	422	1	0
201040189	5/23/2010	13:07	46.5295300	-84.2259883	1.22	422	1	0
201040190	5/23/2010	13:12	46.5293017	-84.2259400	2.74	422	1	0
201040191	5/23/2010	13:18	46.5290133	-84.2256000	3.35	422	2	0
201040192	5/23/2010	13:23	46.5289750	-84.2254067	3.35	422	2	0
201040193	5/23/2010	13:29	46.5292483	-84.2246117	2.74	422	1	0
201040194	5/23/2010	13:33	46.5291733	-84.2244167	1.22	422	3	0
201040195	5/23/2010	13:36	46.5295817	-84.2248167	3.96	422	2	0
201040196	5/23/2010	13:40	46.5299933	-84.2245850	3.96	422	2	0
201040197	5/23/2010	13:48	46.5303000	-84.2250500	3.66	422	1	0
201040198	5/23/2010	13:56	46.5310133	-84.2257467	8.53	422	1	0
201040199	5/23/2010	14:07	46.5310667	-84.2254033	8.53	422	1	0
201040200	5/23/2010	14:14	46.5307533	-84.2249500	2.44	422	1	0
201040201	5/23/2010	14:19	46.5309650	-84.2242533	1.83	422	3	0
201040202	5/23/2010	14:22	46.5313883	-84.2243900	2.74	422	1	0
201040203	5/23/2010	14:28	46.5316867	-84.2241950	3.35	422	1	0
201040204	5/23/2010	14:40	46.5314033	-84.2275000	7.32	422	1	0
201040205	5/23/2010	14:48	46.5312983	-84.2270067	5.79	422	1	0
201040206	5/23/2010	14:53	46.5314350	-84.2270183	6.10	422	1	0
201040151	5/22/2010	13:52	46.5220333	-84.2345617	6.10	31	1	0
201040152	5/22/2010	14:02	46.5222233	-84.2345617	7.62	31	1	0
201040153	5/22/2010	14:09	46.5220867	-84.2342000	3.05	31	1	0
201040154	5/22/2010	14:16	46.5217900	-84.2343417	1.22	31	1	0
201040155	5/22/2010	14:23	46.5218283	-84.2345700	1.22	31	1	0
201040156	5/22/2010	14:28	46.5217917	-84.2338233	0.61	31	1	0
201040157	5/22/2010	14:37	46.5223867	-84.2338433	1.22	31	1	0
201040158	5/22/2010	14:46	46.5224533	-84.2341917	5.49	31	1	0
201040159	5/22/2010	14:51	46.5226700	-84.2336833	3.05	31	1	0
201040088	5/20/2010	08:58	46.4964617	-84.2697183	6.71	20	1	0
201040089	5/20/2010	09:08	46.4964650	-84.2698400	6.71	20	1	0
201040090	5/20/2010	09:18	46.4964850	-84.2701933	3.96	20	2	0
201040091	5/20/2010	09:27	46.4962500	-84.2702850	5.49	20	3	0
201040092	5/20/2010	09:35	46.4964383	-84.2711383	0.91	20	1	2

201040093	5/20/2010	09:39	46.4963683	-84.2714583	0.91	20	1	1
201040094	5/20/2010	09:48	46.4961433	-84.2713433	7.01	20	3	0
201040095	5/20/2010	09:53	46.4962250	-84.2718367	3.35	20	3	0
201040096	5/20/2010	09:55	46.4963483	-84.2718683	0.61	20	1	0
201040097	5/20/2010	10:07	46.4960517	-84.2741083	0.61	20	1	0
201040098	5/20/2010	10:21	46.4956250	-84.2745850	1.22	20	3	0
201040099	5/20/2010	10:23	46.4956150	-84.2750317	5.49	20	1	2
201040100	5/20/2010	10:34	46.4957867	-84.2753433	0.91	20	2	1
201040101	5/20/2010	10:41	46.4958233	-84.2751683	2.44	20	1	1
201040102	5/20/2010	10:50	46.4953483	-84.2768383	2.13	20	3	0
201040103	5/20/2010	10:54	46.4955267	-84.2773383	2.44	20	1	2
201040104	5/20/2010	11:04	46.4955817	-84.2781733	1.22	20	1	2
201040105	5/20/2010	11:12	46.4955367	-84.2779533	3.05	20	1	2
201040106	5/20/2010	11:22	46.4956333	-84.2785700	0.91	20	1	0
201040107	5/20/2010	11:28	46.4953133	-84.2783583	1.83	20	3	0
201040108	5/20/2010	11:30	46.4956167	-84.2789850	0.91	20	3	0
201040109	5/20/2010	11:32	46.4956133	-84.2792933	1.83	20	1	0
201040110	5/20/2010	11:40	46.4958117	-84.2798317	0.61	20	1	0
201040111	5/20/2010	11:47	46.4953400	-84.2804633	2.74	20	1	3
201040112	5/20/2010	12:25	46.4955417	-84.2804733	0.61	20	2	0
201040113	5/20/2010	12:29	46.4955400	-84.2808350	0.30	20	2	1
201040114	5/20/2010	12:35	46.4955333	-84.2810000	0.91	20	1	0
201040115	5/20/2010	12:43	46.4953450	-84.2815683	3.96	20	2	5
201040116	5/20/2010	12:53	46.4953183	-84.2817350	4.57	20	2	0
201040117	5/20/2010	13:00	46.4953083	-84.2823467	4.88	20	2	1
201040118	5/20/2010	13:08	46.4955283	-84.2823850	1.22	20	2	0
201040119	5/20/2010	13:33	46.4808300	-84.3017983	0.30	1	1	1
201040120	5/20/2010	13:42	46.4809117	-84.3017783	0.30	1	2	0
201040121	5/20/2010	13:49	46.4806967	-84.3010350	1.83	1	1	1
201040122	5/20/2010	13:55	46.4806000	-84.3009283	3.35	1	1	0
201040123	5/20/2010	14:17	46.4805783	-84.3013283	0.30	1	1	0
201040124	5/20/2010	14:23	46.4805550	-84.3015633	0.30	1	3	0
201040125	5/20/2010	14:25	46.4808883	-84.3013750	0.61	1	1	0
201040126	5/20/2010	14:30	46.4809433	-84.3015217	0.61	1	2	0
201040127	5/20/2010	14:34	46.4811067	-84.3014350	0.61	1	2	0
201040128	5/20/2010	14:38	46.4812383	-84.3014683	0.61	1	2	0
201040129	5/20/2010	14:43	46.4812200	-84.3017750	0.61	1	2	0
201040130	5/20/2010	14:49	46.4812650	-84.3019517	0.61	1	2	0
201040131	5/20/2010	14:54	46.4815517	-84.3016550	0.30	1	2	0
201040132	5/20/2010	15:00	46.4815717	-84.3018667	1.52	1	1	2
201040133	5/20/2010	15:10	46.4817233	-84.3019100	4.27	1	3	0
201040134	5/20/2010	15:14	46.4817817	-84.3016733	2.44	1	1	2
201040135	5/20/2010	08:52	46.4814467	-84.3021700	2.44	1	2	0
201040136	5/20/2010	08:57	46.4814650	-84.3020450	1.52	1	1	0
201040137	5/20/2010	09:08	46.4817233	-84.3021583	3.96	1	1	0
201040138	5/20/2010	09:14	46.4817983	-84.3022617	2.44	1	1	0
201040139	5/20/2010	09:19	46.4819917	-84.3022567	0.91	1	1	0
201040140	5/20/2010	09:23	46.4819633	-84.3020617	1.22	1	1	0
201040141	5/20/2010	09:28	46.4819533	-84.3018983	4.88	1	3	0
201040142	5/20/2010	09:33	46.4820983	-84.3017683	3.66	1	3	0
201040143	5/20/2010	09:35	46.4819233	-84.3013467	2.44	1	1	0
201040144	5/20/2010	09:41	46.4820617	-84.3014967	4.57	1	3	0
201040145	5/20/2010	09:44	46.4822767	-84.3013783	3.35	1	3	0
201040146	5/20/2010	09:45	46.4824150	-84.3013633	1.52	1	1	0
201040147	5/20/2010	09:50	46.4823400	-84.3017550	0.61	1	1	0
201040148	5/20/2010	09:56	46.4824333	-84.3019133	0.91	1	1	0
201040149	5/20/2010	10:00	46.4826483	-84.3018383	1.83	1	1	0
201040150	5/20/2010	10:05	46.4825333	-84.3018533	1.22	1	1	0
201040063	5/19/2010	11:13	46.5007517	-84.2599533	3.05	20	1	8
201040064	5/19/2010	11:26	46.5007383	-84.2600567	2.74	20	1	2
201040065	5/19/2010	11:36	46.5005383	-84.2602917	4.88	20	1	1
201040066	5/19/2010	11:45	46.5003200	-84.2612150	3.05	20	1	0
201040067	5/19/2010	12:29	46.4997200	-84.2618617	3.66	20	3	0
201040068	5/19/2010	12:40	46.4995517	-84.2628200	1.83	20	1	3
201040069	5/19/2010	12:49	46.4996083	-84.2626017	3.05	20	1	3
201040070	5/19/2010	13:01	46.4991083	-84.2630750	2.74	20	3	0
201040071	5/19/2010	13:06	46.4992517	-84.2636367	1.22	20	1	1
201040072	5/19/2010	13:13	46.4990650	-84.2638583	1.83	20	1	2
201040073	5/19/2010	13:27	46.4986967	-84.2646350	0.61	20	1	1
201040074	5/19/2010	13:33	46.4986250	-84.2647983	0.61	20	2	0

201040075	5/19/2010	13:40	46.4984900	-84.2644750	6.10	20	3	0
201040076	5/19/2010	13:46	46.4983867	-84.2650967	2.13	20	1	8
201040077	5/19/2010	13:56	46.4981717	-84.2654700	3.96	20	2	10
201040078	5/19/2010	14:07	46.4977767	-84.2663183	3.66	20	2	2
201040079	5/19/2010	14:19	46.4974000	-84.2670350	9.75	20	2	0
201040080	5/19/2010	14:28	46.4972017	-84.2679967	0.61	20	2	0
201040081	5/19/2010	14:35	46.4972850	-84.2677367	3.35	20	2	0
201040082	5/19/2010	14:42	46.4970183	-84.2682617	3.35	20	2	1
201040083	5/19/2010	14:49	46.4968683	-84.2681567	9.14	20	2	0
201040084	5/19/2010	15:00	46.4968033	-84.2684883	7.62	20	3	0
201040085	5/19/2010	15:03	46.4968533	-84.2686733	6.10	20	2	0
201040086	5/19/2010	15:13	46.4967317	-84.2695000	3.66	20	1	1
201040087	5/19/2010	15:21	46.4965000	-84.2692367	7.01	20	3	0
201040013	5/18/2010	09:13	46.4933417	-84.2842583	0.91	5	3	0
201040014	5/18/2010	09:17	46.4933200	-84.2839750	0.91	5	3	0
201040015	5/18/2010	09:31	46.4924067	-84.2828433	2.74	5	1	1
201040016	5/18/2010	09:44	46.4924267	-84.2832500	2.13	5	1	0
201040017	5/18/2010	10:38	46.4930083	-84.2834083	1.83	5	2	0
201040018	5/18/2010	10:45	46.4930267	-84.2840483	4.57	5	2	0
201040019	5/18/2010	10:55	46.4927233	-84.2836083	4.57	5	2	0
201040020	5/18/2010	11:00	46.4927150	-84.2840817	5.49	5	2	0
201040021	5/18/2010	11:08	46.4927017	-84.2844233	5.18	5	1	0
201040022	5/18/2010	11:17	46.4923983	-84.2844650	6.10	5	1	0
201040023	5/18/2010	11:27	46.4920550	-84.2836633	3.35	5	1	2
201040024	5/18/2010	11:37	46.4920733	-84.2840450	3.66	5	1	2
201040025	5/18/2010	11:48	46.4921050	-84.2842383	4.88	5	1	0
201040026	5/18/2010	11:58	46.4921133	-84.2844000	5.79	5	1	0
201040027	5/18/2010	12:42	46.4921100	-84.2847767	4.88	5	1	3
201040028	5/18/2010	12:52	46.4920950	-84.2849217	3.66	5	1	4
201040029	5/18/2010	13:01	46.4920917	-84.2852183	1.52	5	1	0
201040030	5/18/2010	13:06	46.4918800	-84.2847983	2.44	5	1	0
201040031	5/18/2010	13:12	46.4918083	-84.2846917	2.74	5	1	0
201040032	5/18/2010	13:22	46.4918183	-84.2831600	2.74	5	1	1
201040033	5/18/2010	13:32	46.4918950	-84.2833117	3.35	5	1	2
201040034	5/18/2010	13:42	46.4916550	-84.2828550	1.83	5	1	0
201040035	5/18/2010	13:48	46.4915850	-84.2833117	3.66	5	1	0
201040036	5/18/2010	13:55	46.4916083	-84.2835300	4.88	5	1	1
201040037	5/18/2010	14:04	46.4916183	-84.2837733	4.88	5	1	0
201040038	5/18/2010	14:12	46.4916367	-84.2840983	3.96	5	1	0
201040039	5/18/2010	14:19	46.4916250	-84.2843350	3.96	5	1	0
201040040	5/18/2010	14:25	46.4916083	-84.2845367	3.35	5	1	0
201040041	5/18/2010	14:31	46.4916083	-84.2847783	1.83	5	1	0
201040042	5/18/2010	14:37	46.4915950	-84.2851000	0.61	5	1	0
201040043	5/18/2010	14:44	46.4910517	-84.2849383	5.49	5	1	0
201040044	5/18/2010	14:49	46.4909933	-84.2852350	1.52	5	1	0
201040045	5/18/2010	14:54	46.4912333	-84.2851017	0.61	5	1	0
201040046	5/18/2010	09:10	46.4906983	-84.2855150	1.22	5	2	0
201040047	5/18/2010	09:15	46.4906667	-84.2848250	3.35	5	1	0
201040048	5/18/2010	09:20	46.4906650	-84.2846800	7.62	5	1	0
201040049	5/18/2010	09:28	46.4904783	-84.2849450	1.83	5	1	0
201040050	5/18/2010	09:34	46.4905267	-84.2846817	1.52	5	1	0
201040051	5/18/2010	09:39	46.4904417	-84.2843133	1.22	5	1	0
201040052	5/18/2010	09:44	46.4904217	-84.2840183	2.13	5	1	0
201040053	5/18/2010	09:51	46.4904450	-84.2836367	4.27	5	1	0
201040054	5/18/2010	09:57	46.4906450	-84.2835017	3.66	5	1	0
201040055	5/18/2010	10:02	46.4907683	-84.2837233	3.05	5	1	0
201040056	5/18/2010	10:09	46.4909267	-84.2836217	2.44	5	1	0
201040057	5/18/2010	10:14	46.4909083	-84.2839183	4.27	5	1	0
201040058	5/18/2010	10:23	46.4908967	-84.2841750	7.01	5	1	0
201040059	5/18/2010	10:30	46.4912217	-84.2839817	4.27	5	1	0
201040060	5/18/2010	10:38	46.4912900	-84.2836517	4.27	5	1	0
201040061	5/18/2010	10:45	46.4913017	-84.2832450	2.13	5	1	0
201040062	5/18/2010	10:50	46.4909883	-84.2832917	2.13	5	1	0
201040001	5/17/2010	12:20	46.5090950	-84.3429417	3.05	3	1	2
201040002	5/17/2010	12:53	46.5088067	-84.3429700	3.96	3	2	12
201040003	5/17/2010	13:05	46.5088083	-84.3425633	3.66	3	1	13
201040004	5/17/2010	13:16	46.5088750	-84.3426100	3.66	3	1	1
201040005	5/17/2010	13:24	46.5085767	-84.3425633	4.27	3	2	1
201040006	5/17/2010	13:34	46.5091550	-84.3425350	3.35	3	1	1
201040007	5/17/2010	13:42	46.5094417	-84.3426033	3.66	3	1	1

201040008	5/17/2010	13:49	46.5093250	-84.3425333	3.96	3	1	0
201040009	5/17/2010	13:56	46.5097467	-84.3426133	4.27	3	1	1
201040010	5/17/2010	14:04	46.5096500	-84.3428700	2.74	3	1	0
201040011	5/17/2010	14:11	46.5095883	-84.3429667	2.74	3	1	0
201040012	5/17/2010	14:17	46.5094417	-84.3429133	3.05	3	1	0

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Table A.2. Individual larval lamprey length data associated with the intensive pre-treatment electrofishing sampling that occurred in 2010 and 2011. Adjusted catch represents the gear selectivity adjusted catch data for each sea lamprey larva captured. Adjustments for gear efficiency were performed using equation 1.1. Data in Tables A.1 and A.2 can be linked using the Samp\_ID column.

Samp_ID	Date	Length	Adjusted Catch
201040001	5/17/2010	34	1.75
201040001	5/17/2010	55	1.77
201040002	5/17/2010	47	1.77
201040002	5/17/2010	54	1.88
201040002	5/17/2010	57	1.92
201040002	5/17/2010	58	1.92
201040002	5/17/2010	63	1.94
201040002	5/17/2010	64	2.11
201040002	5/17/2010	64	1.36
201040002	5/17/2010	70	1.46
201040002	5/17/2010	72	1.47
201040002	5/17/2010	72	1.47
201040002	5/17/2010	73	1.48
201040002	5/17/2010	80	1.48
201040003	5/17/2010	31	1.50
201040003	5/17/2010	42	1.52
201040003	5/17/2010	43	1.53
201040003	5/17/2010	43	1.56
201040003	5/17/2010	44	1.58
201040003	5/17/2010	44	1.58
201040003	5/17/2010	45	1.61
201040003	5/17/2010	47	1.60
201040003	5/17/2010	48	1.56
201040003	5/17/2010	50	1.52
201040003	5/17/2010	52	1.73
201040003	5/17/2010	52	1.40
201040003	5/17/2010	54	1.39
201040004	5/17/2010	53	1.39
201040005	5/17/2010	50	5.08
201040006	5/17/2010	47	1.41
201040007	5/17/2010	62	1.64
201040009	5/17/2010	36	1.38
201040015	5/18/2010	35	1.40
201040023	5/18/2010	35	1.44
201040023	5/18/2010	137	1.39
201040024	5/18/2010	37	1.39
201040024	5/18/2010	56	1.41
201040027	5/18/2010	33	1.47
201040027	5/18/2010	36	2.87
201040027	5/18/2010	40	1.34
201040028	5/18/2010	34	2.11
201040028	5/18/2010	35	1.68
201040028	5/18/2010	37	1.29
201040028	5/18/2010	43	1.54
201040032	5/18/2010	103	1.70
201040033	5/18/2010	28	1.84
201040033	5/18/2010	80	3.52
201040036	5/18/2010	59	4.32
201040063	5/19/2010	21	6.37
201040063	5/19/2010	49	1.39
201040063	5/19/2010	60	1.94
201040063	5/19/2010	68	3.30
201040063	5/19/2010	116	4.72
201040063	5/19/2010	128	1.31
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201140149	6/15/2011	31	1.36
201140149	6/15/2011	33	1.38
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201140170	6/16/2011	52	1.58

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201140170	6/16/2011	58	1.67
201140170	6/16/2011	65	1.78
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201140175	6/16/2011	45	1.50
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201140331	6/24/2011	96	2.59
201140336	6/27/2011	46	1.51
201140337	6/27/2011	90	2.39
201140370	6/28/2011	95	2.56
201140382	6/28/2011	83	2.18
201140391	6/28/2011	77	2.03
201140399	6/28/2011	98	2.67

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## Bibliography

- Anderson, G. 2006. Optimizing larval sea lamprey assessment in the Great Lakes through the use of adaptive management and historical records. Master's Thesis. Michigan State University.
- Beamish, F.W.H. 1980. Biology of the North American anadromous sea lamprey, *Petromyzon marinus*. Can. J. Fish. Aquat. Sci. 37:1924–1943.
- Beamish, F.W.H., and T.E. Medland. 1988. Age determination in lampreys. Trans. Am. Fish. Soc. 117:63–71.
- Bergstedt, R.A., and J.H. Genovese. 1994. New technique for sampling sea lamprey larvae in deepwater habitats. N. Am. J. Fish. Manage. 14:449–452.
- Bergstedt, R.A., and J.G. Seelye. 1995. Evidence for lack of homing by sea lampreys. Trans. Am. Fish. Soc. 124:235–239.
- Bergstedt, R.A., and M.B. Twohey. 2007. Research to support sterile-male-release and genetic alteration techniques for sea lamprey control. J. Great Lakes Res. 33(Special Issue 2):48–69.
- Bunnell, D.B., C.P. Madenjian, and R.M. Claramunt. 2006. Long-term changes of the Lake Michigan fish community following the reduction of exotic alewife (*Alosa pseudoharengus*). Can. J. Fish. Aquat. Sci. 63:2434–2446.
- Bronte, C.R., M.P. Ebener, D.R. Schreiner, D.S. DeVault, M.M. Petzold, D.A. Jensen, C. Richards, and S.J. Lozano 2003. Fish community changes in Lake Superior, 1970–2000. Can. J. Fish. Aquat. Sci. 60:1552–1574.
- Brooks, S.P., and A. Gelman. 1998. General methods for monitoring convergence of iterative simulations. J Comput. Graph. Statist. 7:434–455.

- Christie, G.C., and C.I. Goddard. 2003. Sea Lamprey International Symposium (SLISII): advances in the integrated management of sea lampreys in the Great Lakes. *J. Great Lakes Res.* 29 (Suppl. 1):1–14.
- Clark, C.W. 2005. *Mathematical bioeconomics optimal management of renewable resources*. 2<sup>nd</sup> ed. John Wiley and Sons , Hoboken, New Jersey.
- Clemens, B.J., T.R. Binder, M.F. Docker, M.L. Moser, and S.A. Sower. 2010. Similarities, differences, and unknowns in biology and management of three parasitic lampreys of north America. *Fisheries*. 35:580–594.
- Close, D.A., M.S. Fitzpatrick, and H.W. Li. 2002. The ecological and cultural importance of a species at risk of extinction, Pacific lamprey. *Fisheries*. 27:19–25.
- Coble, D.W., R.E. Bruesewitz, T.W. Fratt, and J.W. Scheirer. 1990. Lake trout, sea lamprey, and overfishing in the upper Great Lakes: a review and reanalysis. *T. Am. Fish. Soc.* 119:985-995.
- Cooke, J.G. 1999. Improvement of fishery-management advice through simulation testing of harvest algorithms. *ICES J. Mar. Sci.* 56:797–810.
- Derosier, A.L., M.L. Jones, and K.T. Scribner. 2007. Dispersal of sea lamprey larvae during early life: relevance for recruitment dynamics. *Environ. Biol. Fish.* 78:271–284.
- Dawson, V.K. 2003. Environmental fate and effects of the lampricide Bayluscide: a review. *J. Great Lakes Res.* 29(Suppl. 1): 475–492.

- Dawson, H.A., M.L. Jones, K.T. Scribner, and S.A. Gilmore, 2009. An assessment of age determination methods for Great Lakes larval sea lampreys. *N. Am. J. Fish. Manage.* 29:914–927
- Dobiesz, N.E., D.A. McLeish, R.L. Eshenroder, J.R. Bence, L.C. Mohr, B.A. Henderson, M.P. Ebener, T.F. Nalepa, A.P. Woldt, J.E. Johnson, R.L. Argyle, and J.C. Makarewicz. 2005. Ecology of the Lake Huron fish community, 1970–1999. *Can. J. Fish. Aquat. Sci.* 62:1432–1451.
- Dunstan, P.K., and N.J. Bax. 2008. Management of an invasive marine species: defining and testing the effectiveness of ballast-water management options using management strategy evaluation. *ICES J. Mar. Sci.* 65:841–850.
- Elliott, J.M. 1977. *Statistical analysis of samples of benthic invertebrates*, 2nd ed. Freshwater Biological Association, Scientific Publication No. 25.
- Fenichel, E.P., and G.J.A. Hansen. 2010. The opportunity cost of information: an economic framework for understanding the balance between assessment and control in sea lamprey (*Petromyzon marinus*) management. *Can. J. Fish. Aquat. Sci.* 67:209–216.
- Fodale, M.F., R.A. Bergstedt, D.W. Cuddy, J.V. Adams, and D.A. Stolyarenko. 2003. Planning and executing a lampricide treatment of the St. Marys River using georeferenced data. *J. Great Lakes Res.* 29(Supp. 1):706–716.
- Fournier, D.A., and C.P. Archibald. 1982. A general theory for analyzing catch at age data. *Can. J. Fish. Aquat. Sci.* 39:1195–1207.
- Fournier, D.A., H.J. Skaug, J. Ancheta, J. Ianelli, A. Magnusson, M.N. Maunder, A. Nielsen, and J. Sibert. 2012. AD Model Builder: using automatic

differentiation for statistical inference of highly parameterized complex nonlinear models. *Optim. Methods Softw.* 27:233-249.

Gelman, A, J.B. Carlin, H.S. Stern, and D.B. Rubin. 2004. *Bayesian data analysis*. Chapman & Hall/CRC, New York, NY.

Gertzen, E.L., and B. Leung. 2011. Predicting the spread of invasive species in an uncertain world: accommodating multiple vectors and gaps in temporal and spatial data for *Bythotrephes longimanus*. *Biol. invasions.* 13:2433–2444.

Great Lakes Fishery Commission (GLFC). 2011. *Sea lamprey control in the Great Lakes, Annual report to the Great Lakes Fishery Commission*. Great Lakes Fishery Commission, Ann Arbor, MI.

Great Lakes Fishery Commission. 2012. *Great Lakes Fishery Commission, budget summary, fiscal year 2012*.

Groom, M.J., G.K. Meffe, and C.R. Carroll. *Principles of Conservation Biology*. 3rd ed. Sunderland: Sinauer Associates, Inc., 2006.

Haeseker, S.L., M.L. Jones, and J.R. Bence. 2003. Estimating uncertainty in the stock-recruitment relationship for St. Marys River sea lampreys. *J. Great Lakes Res.* 29 (Supp. 1):728–741.

Haeseker, S.L., M.L. Jones, R.M. Peterman, J.R. Bence, W. Dai, and G.C. Christie. 2007. Explicit consideration of uncertainty in Great Lakes fishery management: decision analysis of sea lamprey control in the St. Marys River. *Can. J. Fish. Aquat. Sci.* 64:1456–1468.

- Hansen, G.J.A., and M.L. Jones. 2008a. A rapid assessment approach to prioritizing streams for control of Great Lakes sea lampreys (*Petromyzon marinus*): a case study in adaptive management. *Can. J. Fish. Aquat. Sci.* 65:2471–2484.
- Hansen, G.J.A., and M.L. Jones. 2008b. The value of information in fisheries management. *Fisheries*. 33:340–348.
- Hastie T. and R. Tibshirani. 1990. *Generalized Additive Models*. Chapman and Hall.
- Irwin, B.J., W. Liu, J.R. Bence, and M.L. Jones. 2012. Defining economic injury levels for sea lamprey control in the great lakes basin. *N. Am. J. Fish. Manage.* 32:760–771.
- Jolley, J.C., G.S. Silver, and T.A. Whitesel. 2010. Occurrence, Detection, and Habitat Use of Larval Lamprey in Columbia River Mainstem Environments: Bonneville Reservoir and Tailwater. Annual Report U.S. Fish and Wildlife Service.
- Jolley, J.C., G.S. Silver, and T.A. Whitesel. 2011. Occurrence, Detection, and Habitat Use of Larval Lamprey in the White Salmon River Basin: Pre-Condit Dam Removal. Annual Report U.S. Fish and Wildlife Service.
- Jolley, J.C., G.S. Silver, and T.A. Whitesel. 2012. Occupancy and Detection of Larval Pacific Lampreys and *Lampetra* spp. in a Large River: the Lower Willamette River. *Trans. Am. Fish. Soc.* 141:305–312.
- Jones, M.L., B.J. Irwin, G.J.A. Hansen, H.A. Dawson, A.J. Treble, W. Liu, W. Dai, and J.R. Bence. 2009. An operating model for the integrated pest management of Great Lakes sea lamprey.

- Kearney, M., and P. Warren. 2009. Mechanistic niche modeling: combining physiological and spatial data to predict species' ranges. *Ecol. Lett.* 12:334–350.
- Lepak, J.M., C.E. Kraft and B.C. Weidel. 2006. Rapid food web recovery in response to removal of an introduced apex predator. *Can. J. Fish. Aquat. Sci.* 63:569–575.
- Limburg, K.E., and J.R. Waldman. 2009. Dramatic declines in North Atlantic diadromous fishes. *BioScience.* 59:955–965.
- Lockwood, J.L, P. Cassey, and T. Blackburn. 2005. The role of propagule pressure in explaining species invasions. *Trends Ecol. Evol.* 20:223–228.
- Lupi, F., J.P. Hoehn, and G.C. Christie. 2003. Using an economic model of recreational fishing to evaluate the benefits of sea lamprey (*Petromyzon marinus*) control on the St. Marys River. *J. Great Lakes Res.* 29 (Suppl.1):742–754.
- Madenjian, C.P., G.L. Fahnenstiel, T.H. Johengen, T.F. Nalepa, H.A. Vanderploeg, G.W. Fleischer, P.J. Schneeberger, D.M. Benjamin, E.B. Smith, J.R. Bence, E.S. Rutherford, D.S. Lavis, D.M. Robertson, D.J. Jude, and M.P. Ebener. 2003. Dynamics of the Lake Michigan food web, 1970-2000. *Can. J. Fish. Aquat. Sci.* 59:736–753.
- Mapstone, B.D., L.R. Little, A.E. Punt, C.R. Davies, A.D.M. Smith, F. Pantus, A.D. McDonald, A.J. Williams, and A. Jones. 2008. Management strategy evaluation for line fishing in the Great Barrier Reef: Balancing conservation and multi-sector fishery objectives. *Fish. Res.* 94:315–329.

- Mateus, C.S., R. Rodríguez-Muñoz, B.R. Quintella, M.J. Alves, and P.R. Almeida. 2012. Lampreys of the Iberian Peninsula: distribution, population status and conservation. *Endang. Species. Res.* 16:183–198.
- Maunder, M.N., and A.E. Punt. 2004. Standardizing catch and effort data: a review of recent approaches. *Fish. Res.* 70:141–159.
- Mehta, S.V., R.G. Haight, F.R. Homans, S. Polasky, and R.C. Venett. 2007. Optimal detection and control strategies for invasive species management. *Ecol. Econ.* 61:237–245.
- Miller, T.J., J. Blair, T.F. Ihde, R.M. Jones, D.H. Secor, and M.J. Wilberg. 2010. FishSmart: an innovative role for science in stakeholder-centered approaches to fisheries management. *Fisheries.* 35:242–433.
- Mooney, H.A. and E.E. Cleland. 2001. The evolutionary impact of invasive species. *Proc. Natl. Acad. Sci. USA.* 98:5446–5451
- Morse, T.J., M.P. Ebener, E.M. Koon, S.B. Morkert, D.A. Johnson, D.W. Cuddy, J.W. Weisser, K.M. Mullett, and J.H. Genovese. 2003. A case history of sea lamprey control in Lake Huron: 1979 to 1999. *J. Great Lakes Res.* 29(Supp. 1):599-614.
- Nally, R.M. 1997. Monitoring forest bird communities for impact assessment: the influence of sampling intensity and spatial scale. *Biological Conservation.* 82:355–367.
- Neter, J., M. H. Kutner, C. J. Nachtsheim, and W. Wasserman. 1996. *Applied linear statistical models*, 4th edition. Irwin, New York.

- OSPAR Commission. 2009. Background Document for Sea lamprey *Petromyzon marinus*. OSPAR Commission.
- Pascoe, S., R. Bustamante, C. Wilcox, and M. Gibbs. 2009. Spatial fisheries management: a framework for multi-objective qualitative assessment. *Ocean Coast. Manage.* 52:130–138.
- Pauly, D. 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. *ICES J. Mar. Sci.* 39:175–192.
- Pimentel, D., R. Zuniga, and D. Morrison. 2005. Update on the environmental and economic costs associated with alien–invasive species in the United States. *Ecol. Econ.* 52:273–88.
- Punt, A.E., T.I. Walker, B.L. Taylor, and F. Pribac. 2000. Standardization of catch and effort data in a spatially-structured shark fishery. *Fish. Res.* 45:129–145.
- R Development Core Team. 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org/>.
- Renaud, C.B. 1997. Conservation status of Northern hemisphere lampreys (Petromyzontidae). *J. Appl. Ichthyol.* 13:143–148.
- Rodriguez, S.R., F.P. Ojeda, and N.C. Inestrosa. 1993. Settlement of benthic marine invertebrates. *Mar. Ecol. Prog. Ser.* 97:193–207.
- Rouget, M. and D.M. Richardson. 2003. Inferring process from pattern in plant invasions: A semimechanistic model incorporating propagule pressure and environmental factors. *Am. Nat.* 162:713–724.

- Sainsbury, K.J. 1998. Living marine resource assessment for the 21<sup>st</sup> Century: What will be needed and how will it be provided. *In* Fishery Stock Assessment Models, pp. 1–40. Ed. by: Heifetz, J., J.N. Ianelli, J.E. Powers, J.F. Schweigert, P.J. Sullivan and C.-I. Zhang. Alaska Sea Grant College Program Report No. AK–SG–98–01, University of Alaska Fairbanks, USA.
- Sainsbury, K.J., A.E. Punt, and A.D.M. Smith. 2000. Design of operational management strategies for achieving fishery ecosystem objectives. *ICES J. Mar. Sci.* 57:731–741.
- Suarez, A.V., D.A. Holway, and P.S. Ward. 2005. The role of opportunity in the unintentional introduction of nonnative ants. *Proc. Natl. Acad. Sci.* 102:17032–17035.
- Schleen, L.P., G.C. Christie, J.W. Heinrich, R.A. Bergstedt, R.J. Young, T.L. Morse, D.S. Lavis, T.D. Bills, J.E. Johnson, and M.P. Ebener. 2003. Development and implementation of an integrated program for control of sea lampreys in the St. Marys River. *J. Great Lakes Res.* 29(Suppl. 1):677–693.
- Shogren, J.F., J. Tschirhart, T. Anderson, A.W. Ando, S.R. Beissinger, D. Brookshire, G.M. Brown, D. Coursey, R. Innes, S.M. Meyer, and S. Polasky. 1999. Why economics matters for endangered species protection. *Conserv. Biol.* 13:1257–1261.
- Simberloff, D. 2003a. Eradication – preventing invasion at the outset. *Weed Sci.* 51:274–253.
- Simberloff, D. 2003b. How much information on population biology is needed to manage introduced species? *Conserv. Biol.* 17:83–92.

- Slade, J.W., Adams, J.V., Christie, G.C., Cuddy, D.W., Fodale, M.F., Heinrich, J.W., Quinlan, H.R., Weise, J.G., Weisser, J.W., and Young, R.J. 2003. Techniques and methods for estimating abundance of larval and metamorphosed sea lampreys in Great Lakes tributaries, 1995 to 2002. *J. Great Lakes Res.* 29 (Suppl. 1):137–151.
- Smith, A.D.M. 1994. Management Strategy Evaluation – The Light on the Hill. *In: Population Dynamics for Fisheries Management, Australian Society for Fish Biology Workshop Proceedings, Perth 24–25 August 1993.* D. A. Hancock (ed.), p. 249–253.
- Smith, B.R. 1971. Sea lampreys in the Great Lakes of North America. *In The Biology of Lampreys, Vol. 1., eds. M. W. Hardisty and I. C. Potter.* New York: Academic Press.
- Smith, B.R., and J.J. Tibbles 1980. Sea lamprey (*Petromyzon marinus*) in Lake Huron, Michigan, and Superior: history of invasion and control, 1936-78. *Can. J. Fish. Aquat. Sci.* 37:1780-1801.
- Spangler, G.R., Robson, D.S., and Regier, H.A. 1980. Estimates of lamprey-induced mortality in whitefish, *Coregonus clupeaformis*. *Can. J. Fish. Aquat. Sci.* 37: 2146–2150,
- Sorensen, P.W., and L.A. Vrieze. 2003. The chemical ecology and potential application of the sea lamprey migratory pheromone. *J. Great Lakes Res.* 29(Suppl. 1):66–84.

- Southwick Associates. 2008. Sportfishing in America: an economic engine and conservation powerhouse. Produced for the American Sportfishing Association with funding from the Multistate Conservation Grand Program.
- Spangler, G.R., D.S. Robson, and H.A. Regier. 1980. Estimates of lamprey-induced mortality in whitefish, *Coregonus clupeaformis*. *Can. J. Fish. Aquat. Sci.* 37:2146–2150.
- Struve, J., K. Lorenzen, J. Blanchard, L. Börger, N. Bunnefeld, C. Edwards, J. Hortal, A. MacCall, J. Matthiopoulos, B. Van Moorter, A. Ozgul, F. Royer, N. Singh, C. Yesson, and R. Bernard. 2010. Lost in space? Searching for directions in the spatial modelling of individuals, populations and species ranges. *Biolo. Lett.* 6:575–578.
- Swink, W.D. 2003. Host selection and lethality of attacks by sea lampreys (*Petromyzon marinus*) in laboratory studies. *J. of Great Lakes Res.* 29:307–319.
- U.S. Fish and Wildlife Service. 2006. 2006 National Survey of Fishing, Hunting, and Wildlife-Associated Recreation.
- Venables, W.N., and C.M. Dichmont. 2004. GLMs, GAMS, and GLMMs: an overview of theory for applications in fisheries research. *Fish. Res.* 70:319–337.
- Wagner, C.M., M.B. Twohey, and J.M. Fine. 2009. Conspecific cueing in the sea lamprey: do reproductive migrations consistently follow the most intense larval odour? *Anim. Behav.* 78:593–599.

- Waldman, J., C. Grunwald, and I. Wirgin. 2008. Sea lamprey *Petromyzon marinus*: an exception to the rule of homing in anadromous fishes. *Biol. Lett.* 4:659–662
- Weidel, B.C., D.C. Josephson and C.E. Kraft. 2007. Littoral fish community response to smallmouth bass removal from an Adirondack lake. *Trans. Am. Fish. Soc.* 136:778–789.
- Wilberg, M.J., J.R. Bence, and J.E. Johnson. 2002. Survival of juvenile lake trout stocked in Wilberg, M.J., J.R. Bence, and J.E. Johnson. 2002. Survival of juvenile lake trout stocked in western Lake Huron during 1974-1992. *N. Am. J. Fisheries Manage.* 22:213–218.
- Williams, B.K., J.D. Nichols, and M.J. Conroy. 2002. Analysis and management of animal populations: modeling, estimation, and decision making. Academic Press, New York.
- Wood, S.N. 2004. Stable and efficient multiple smoothing parameter estimation for generalized additive models. *J Am Stat Assoc* 99:673-686.
- Wood, S.N. 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *J Royal Stat Soc (B)* 73:3-36.
- Young, R.J., G.C. Christie, R.B. McDonald, D.W. Cuddy, T.J. Morse, and N.R. Payne. 1996. Effects of habitat change in the St. Marys River and northern Lake Huron on sea lamprey (*Petromyzon marinus*) populations. *Can. J. Fish. Aquat. Sci.* 53(Suppl.1):99–104.