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INCORPORATING UNCERTAINTY INTO ST. MARYS RIVER SEA LAMPREY MANAGEMENT THROUGH DECISION ANALYSIS

By

Steven Lewis Haeseker

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ABSTRACT

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Steven L. Haeseker

Methods used to control St. Marys River sea lampreys (*Petromyzon marinus*) include trapping adults, releasing sterilized males into the spawning population, and applying lampricide to kill larvae living within the streambed. Future control activities will require some, or all of, these methods. In addition to the costs and logistical challenges associated with implementing control options, considerable uncertainty exists about lamprey population dynamics and about control option effectiveness. These uncertainties hinder the ability of scientists to accurately forecast management option performance and thus limit the ability of decision-makers to arrive at well-informed decisions about which control methods to use. I use the method of decision analysis to evaluate the performance of a set of management options for controlling the St. Marys River sea lamprey population while explicitly accounting for uncertainty. I considered two main sources of uncertainty: uncertainty in the stock-recruitment relationship and uncertainty in larval distribution within the St. Marys River. To characterize the first of these, I developed a statistically-based, age-structured population model to estimate the parameters of a Ricker stock-recruitment relationship for St. Marys River sea lampreys and the uncertainty associated with these parameters. To characterize the second main uncertainty, I developed a stochastic model that predicts the abundance of larvae at a location in the next year based on the abundance in the current year. I applied the model

to forecast a variety of possible larval abundance maps for the lampricide treatment that took place in 1999 to estimate the uncertainty in treatment effectiveness resulting from spatial and temporal uncertainty in larval distribution. By combining these sources of uncertainty into a stochastic simulation model that forecasted parasitic lamprey abundance over time, I was able to examine the performance of a variety of management options. I found that uncertainty in lamprey population dynamics and in treatment option effectiveness can have large effects on the forecasts of lamprey abundance. In addition, the relative ranking of management options depended on the performance indicator used to evaluate them. Important tradeoffs exist between achieving management objectives and the cost associated with achieving the management objective. Decision-makers should evaluate option performance by considering several performance indicators. Incorporating uncertainty into St. Marys River sea lamprey management decisions through decision analysis should improve the quality of the decisions and increase the probability of achieving management objectives.

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INTRODUCTION

Controlling the St. Marys River sea lamprey (*Petromyzon marinus*) population is a major challenge facing fishery managers in the Great Lakes. The sea lamprey is an exotic fish species that has decimated fisheries in the Great Lakes through parasitism, and the St. Marys River is the largest remaining source of sea lampreys in the Great Lakes basin (Schleen 1992, Eshenroder et al. 1995). Because of the large number of lampreys that are produced, mortality rates for several species (e.g., lake trout *Salvelinus namaycush* and lake whitefish *Coregonus clupeaformis*) have risen above target levels set by management agencies (Sitar et al. 1999). Thus, reducing the number of sea lampreys in northern Lakes Huron and Michigan has become a high priority for fisheries managers in the region.

Methods used to control St. Marys River sea lampreys include trapping adults, releasing sterilized males into the spawning population, and applying lampricide to kill larvae living within the streambed. In addition to the costs and logistical challenges associated with implementing a lamprey control program for the St. Marys River, considerable uncertainties exist in lamprey population dynamics and in control option effectiveness. These uncertainties hinder the ability of scientists to accurately forecast management option performance and thus limit the ability of decision-makers to arrive at well-informed decisions.

Uncertainty is inherent in natural resource management decisions. Within the field of fisheries, there is a growing trend towards incorporating uncertainty and risk in the decision-making process (Hilborn et al. 1993). Rosenberg and Restrepo (1994) stress the importance of estimating and communicating uncertainty to fishery managers, who must weigh the benefits, costs, and risks of various management options. They note that while many managed fisheries have incorporated elements of uncertainty and risk analysis, the advice resulting from these analyses needs to be expressed to decision-makers in an effective manner. Providing fishery managers with a quantitative evaluation of the potential consequences of alternative management actions is one of the primary roles of stock assessment scientists (National Research Council Committee on Fish Stock Assessment Methods 1998). Because fisheries management problems typically involve a complex system of biological and socio-economic objectives and constraints, Lane and Stephenson (1998) contend that a conceptual change is necessary, and fisheries management needs to move toward implementing integrated decision-making systems where uncertainty is incorporated. When uncertainty is ignored, or accounted for in an arbitrary fashion, sub-optimal decision options may be selected, leading to outcomes such as unnecessary losses in yields or stock collapse (Frederick and Peterman 1994). Achieving fisheries management goals is more likely when uncertainties are acknowledged, quantified, and accounted for (Peterman et al. 1998).

The method of decision analysis is specifically designed to quantitatively deal with management problems in the presence of uncertainty (Raiffa and Schlaifer 1961, Morgan and Henrion 1990, Clemen 1996). Decision analysis is the application of statistical decision theory to a management decision problem, generally with the following components: a defined set of management options available to the decision-maker, a listing of the alternative states of nature and their associated probabilities which characterize the uncertainty in the problem, a listing of possible outcomes resulting from the management options, and a representation of the decision-maker's utility for the outcomes. The relative merit of each management option is determined by the decision-maker's utility for the expected outcomes.

Several researchers have applied the method of decision analysis to fisheries management problems and found that uncertainty can affect both forecasts and optimal decision-making. McAllister and Peterman (1992) used decision analysis to evaluate the performance of experimental and status quo management strategies for pink salmon (*Oncorhynchus gorbuscha*), while accounting for uncertainty in the cause of decreased mean body weight. They concluded that the expected value of the experimental management strategy was higher than that of the status quo under most conditions. Robb and Peterman (1997) examined uncertainties in the stock-recruitment relationship, annual recruitment, run timing, and catchability for a sockeye salmon (*Oncorhynchus nerka*) fishery through a decision analysis. They found that the shape of the stock-recruitment relationship had a large effect in determining the optimal management option. Hilborn et al. (1994) use decision analysis to examine the performance of different quotas in the presence of uncertainty in virgin stock size. Peterman et al. (1998) summarize three case studies where decision analysis has been applied to fisheries management and recommend that uncertainty be included in the decision making process whenever possible to improve the quality of management decisions.

There are several reasons why decision analysis represents a valuable tool to assist managers who wish to control St. Marys River sea lampreys. First, managing the St. Marys River sea lamprey population is one of the most important problems challenging fisheries managers in the Great Lakes. As a result of the high number of sea lampreys in northern Lakes Huron and Michigan, rehabilitation of lake trout (*Salvelinus namaycush*) has been difficult due to the predation mortality imposed by lamprey in these areas (Sitar *et al.* 1999, Sitar *et al.* 1997, Eshenroder *et al.* 1995). Thus, the management problem is important enough to justify a concerted effort in evaluating management options through decision analysis. Second, major uncertainties exist regarding lamprey population dynamics and the effectiveness of available management options. As noted above, decision analysis is specifically designed to incorporate uncertainty into the decision-making process. Third, economic constraints demand careful evaluation of all lamprey management decisions in the Great Lakes. Spending too little on control of the St. Marys may result in foregone recovery of lake trout in northern Lake Huron. Conversely, spending too much on the St. Marys takes money away from assessment and control needs of other lamprey populations in the Great Lakes basin. Decision makers want and need to know the expected benefits of directing funds at controlling the St. Marys population in order to properly allocate funds available for control and assessment throughout the basin. Fourth, several well-defined management options are and will be considered as alternatives, effectively bounding the number of options available for consideration. Fifth, specific targets exist for lake trout recovery and sea lamprey suppression in Lake Huron that provide indicators against which the performance of management options can be judged. Each of these issues argues for the application of decision analysis to the problem of managing St. Marys River sea lampreys.

In this dissertation, I applied the method of decision analysis to the problem of controlling St. Marys River sea lampreys. I considered two main sources of uncertainty: uncertainty in the stock-recruitment relationship and uncertainty in larval distribution within the St. Marys River. I incorporated these two sources of uncertainty into a stochastic simulation model that forecast parasitic lamprey abundance over time. By using the simulation model within a decision analytic framework, I was able to examine the performance of a set of management options for controlling the St. Marys River sea lamprey population.

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CHAPTER 1

ESTIMATING UNCERTAINTY IN THE STOCK-RECRUITMENT RELATIONSHIP FOR ST. MARYS RIVER SEA LAMPREYS

Abstract

For successful control of the St. Marys River sea lamprey population, one critical uncertainty that needs to be characterized is uncertainty in the stock-recruit relationship. In this paper I develop a statistically-based, age-structured population model to estimate the parameters of a Ricker stock-recruit relationship for St. Marys River sea lamprey and the associated uncertainty in these parameters. My analysis indicates that there is considerable stock-independent variability in recruitment across a range of stock sizes, potentially limiting the effectiveness of control options that reduce spawning population abundance in comparison to control options that reduce the abundance of larvae. I found evidence of negligible- to low compensation levels, which would result in nearly proportional reductions in recruitment with spawning stock. However, I also found evidence of strong compensation, which may reduce the effectiveness of treatment options that attempt to reduce the size of the spawning stock. Through characterizing these uncertainties and incorporating the results into a decision analytic framework, the effects of compensation and stock-recruit uncertainty can be evaluated in reference to the management options available for this system.

Introduction

Connecting Lake Superior to Lake Huron, the St. Marys River has been a primary focus area for sea lamprey (*Petromyzon marinus*) management efforts since 1990. The main reason for this focus has been the recent increase of parasitic lampreys in northern Lakes Huron and Michigan, hindering lake trout (*Salvelinus namaycush*) rehabilitation (Sitar et al. 1999). Several studies have concluded that the St. Marys River is the primary source of these lampreys (Johnson 1988, Schleen et al. 1992). However, because of its large size and high flow, the primary method for reducing lamprey populations (i.e., the lampricide TFM) is infeasible for both practical and financial reasons.

During 1998-99 the Great Lakes Fishery Commission (GLFC) initiated a program to reduce the production of St. Marys River lampreys using a combination of adult trapping, sterile male release, and the application of granular Bayluscide (a lampricide) (Schleen et al., *in review*). The decision to treat the St. Marys River, and which treatment option to select, was heavily based on models used to forecast the future abundance of lamprey in Lake Huron. Although initial indications suggest that the treatment was successful in reducing lamprey abundance (Fodale et al., *in review*), future control actions will almost certainly be necessary.

Forecasting population dynamics is a common task in fisheries management. Forecasting models by definition are critically dependent upon the characterization of system dynamics. Consequently, models that forecast lamprey abundance require the formulation of a stock-recruit relationship, as well as other important demographic parameters that determine sea lamprey population dynamics. Although lamprey biology has been studied extensively, comparatively little attention has been paid to the factors and processes that govern lamprey population dynamics.

The effectiveness of control methods that alter the number of effective spawners (e.g., adult trapping, releasing sterilized males) depends on the reproduction and recruitment dynamics of sea lamprey populations. Specifically, the shape of the stock-recruitment relationship and the variability around it (process error) will determine the degree to which reductions in spawner numbers will consistently result in reductions in recruitment. Conversely, control methods that target the larval population after year-class strength is determined (e.g., application of lampricides) are not affected by the stock-recruitment relationship. For these reasons, knowledge of the stock-recruitment relationship is key to assessing the trade-off between these control strategies.

Although estimates of recent spawner abundance for St. Marys River sea lampreys are available, estimates of larval recruitment are not. Without estimates of larval production, directly estimating a stock-recruit relationship was impossible. However, six separate data sets provided information on the relative abundance and age-composition of lamprey at various stages of their life history. This information was combined by developing an age-structured population model describing the lamprey life cycle and fitting model parameters to the observed data using likelihood techniques. Through this process I was able to estimate a series of historical recruitment and other demographic parameters consistent with the observed data sets. This approach is similar to that described by Fournier and Archibald (1982) and Methot (1989) whereby several sources of data are incorporated into a single, statistically-based framework. To describe the uncertainty in the stock-recruit relationship parameters, I utilize Bayesian methods to obtain samples from the joint posterior density of key parameters.

Methods

Data sources

Since 1967, the Canada Department of Fisheries and Oceans (DFO) has paid Lake Huron commercial fishermen for lamprey captured while attached to host species caught in gillnets. In addition, the Ontario Ministry of Natural Resources (OMNR) collected effort data for Lake Huron commercial fisheries, recording the fisherman, location, and km of gillnet associated with landed fish. I combined the catch and effort data to develop a catch-per-unit-effort (CPUE) index that can be used to track the relative abundance of parasitic-phase lamprey over time. I modeled CPUE using the relationship

$$CPUE_{t,j,k} = \alpha_t \beta_j \delta_k \mu \cdot e^{\varepsilon_{t,j,k}} \qquad (1)$$

where α_t is the effect of year t = 1967,...,1999, β_j is the effect of fisherman j = 1,...,8, δ_k is the effect of location k = North Channel or Main Basin of Lake Huron, μ is the overall mean CPUE and $\varepsilon_{t,j,k} \sim N(0,\sigma^2)$. Taking the natural log of both sides of the equation resulted in a general linear model of the form

$$\log_e(CPUE_{t,j,k}) = \log_e(\alpha_t) + \log_e(\beta_j) + \log_e(\delta_k) + \log_e(\mu) + \varepsilon_{t,j,k} \qquad (2)$$

A total of 251 observations were used to estimate the parameters of equation 2 and their associated standard errors using SAS (SAS 1997). By convention within the SAS procedure, the last effect value for each of the effect types is set to 0 and the remaining effects are scaled relative to this value. For example, $\log_e(\hat{\alpha}_{1999})$ is set to 0 and the remaining $\log_e(\hat{\alpha}_t)$ are scaled relative to 0. These estimates for $\log_e(\hat{\alpha}_t)$ were used as an annual relative abundance index for lamprey in Lake Huron. The linear model only contained main effects because I had no *a priori* information suggesting higher order (interaction) effects.

The United States Fish and Wildlife Service (USFWS) and the DFO have calculated mark-recapture population estimates of spawning-phase St. Marys River sea lampreys annually since 1986. These data provide a direct estimate of the spawning stock size within the St. Marys River. Adult lampreys migrating upstream in the St. Marys River are collected using traps, marked, released, and a portion is subsequently recaptured using traps. These data were used to annually estimate St. Marys River lamprey spawning population sizes and their associated variances (Mullet et al., *in review*). In addition to the spawning-phase population estimate, data on the number of lamprey removed by trapping, the sex ratio, and the expected reduction in successful female spawners due to the release of sterilized males were recorded. I combined the mark-recapture population estimates with the trapping, sex ratio, and sterile male effectiveness data to estimate the effective number of female spawners in the St. Marys River 1985-2000.

Mark-recapture parasitic-phase population estimates have been conducted for Lake Huron sea lamprey intermittently since 1982. Animals were marked as newly-metamorphosed individuals leaving their natal streams. Two years later, adults migrating upstream to spawn were captured using traps and investigated for marks. Bergstedt et al. (*in review*) describe the methods used to estimate population sizes and their associated variance. Because the animals were marked as metamorphosing larvae, the population estimate refers to the population of metamorphosing larvae (juvenile lampreys) entering Lake Huron (Bergstedt et al., *in review*). Individuals that metamorphose in the fall of year t and winter of year $t + 1$ constitute the summer parasitic feeding yearclass of year $t + 1$. I will refer to these data as the parasitic-phase data set. The sea lamprey parasitic population sizes in Lake Huron have been estimated for 1982, 1991, 1992, 1998, and 1999.

Intermittently since 1971, sea lamprey larvae in the St. Marys River have been sampled using Bayluscide. The chemical is applied to the water surface, and larvae respond by swimming to the surface where they are captured using dip nets and measured for length. I used these data to estimate an annual length-frequency distribution for years when the survey was conducted. An analysis of data on the size-selectivity of Bayluscide in the St. Marys River revealed no pattern in selectivity over larval length (Michael Fodale (USFWS), unpublished data). Therefore these distributions were assumed to be representative of the length-frequency distributions for larvae in the river. These surveys ended in 1989.

During 1993-1998, a deepwater electrofishing boat was used to sample St. Marys River larvae. Information on the size selectivity of the deepwater electrofishing gear is available (Bergstedt and Genovese 1994). Using the Bergstedt and Genoveese (1994) gear selectivity function, I estimated annual selectivity-adjusted length-frequency distributions for St. Marys River larval lamprey.

During 1993-96, sea lamprey larvae from the St. Marys River were aged using statoliths, a structure analogous to otoliths in teleosts (T.B. Steeves, unpublished data). I used these data and an inverse age-length key method (Hoenig and Heisey 1987) to estimate annual age compositions from the annual length-frequency data. This method makes the assumption that the growth pattern is constant, but recruitment can vary over time. Because fluctuations in temperature and flow in the St. Marys River are buffered by the immense volume of Lake Superior, I believe that inter-annual variation in growth should be limited, especially relative to inter-annual variation in recruitment for a highly fecund species such as the sea lamprey. Therefore I believe that the constant growth pattern assumption is reasonable. By using this method, I were able to apply a recently developed age-length key to historical data, assuming that larval growth rates in the St. Marys River have remained similar during 1971-1998. I used this method to estimate the annual age-compositions of larvae ages 2-5 from the Bayluscide and deepwater electrofishing length-frequencies.

During 1995 and 1996, metamorphosing sea lamprey larvae from the St. Marys River were collected and aged using statoliths (T.B. Steeves, unpublished data). I summarized these data to estimate the age-compositions of metamorphosing sea lamprey larvae ages 4-6 during 1995 and 1996.

Age-Structured Population Model

I constructed an age-structured population model to describe the full lamprey life cycle from age-0 recruitment through spawning, and fit this model to the six data sources. The modeled life cycle consisted of a larval (riverine) population ages 0 through 6 subject to natural mortality constant across ages and years. A maximum larval age of 6 was used because over 99% of the larvae aged during 1993-1996 were estimated to be ≤ 6 years old (T.B. Steeves, unpublished data). As the model larvae age, they undergo a process of metamorphosis from larval to parasitic form. I modeled the probability of metamorphosis as an increasing function of age for larvae ages 4 though 6. Of the metamorphosing larvae that were aged in 1995 and 1996, 89% were 4-6 years old (T.B. Steeves, unpublished data). Metamorphosed larvae enter the parasitic-phase population in Lake Huron. After 18 months in the parasitic form, a portion of the parasitic-phase population in Lake Huron returns to the St. Marys River to reproduce.

The overall model required 39 parameters to be estimated. These included the number of age-0 recruits from 1967 through 1996 ($N_{0,t}$, $t = 1967, 1970, \ldots 1996$), the initial numbers-at-age for ages 0 through 4 during 1966 ($N_{i,1966}$, $i = 0, 2, \ldots 4$), a natural mortality rate (M) assumed to be constant across years and ages in the larval population, two parameters describing the probability of metamorphosis for larvae age 4 and 5, and the proportion (λ) of the parasitic-phase population in Lake Huron that migrates to the St. Marys River during spawning. The λ parameter represents a combination of two processes: the survival from metarhorphosis to spawner and the fraction of parasites in Lake Huron that migrate into the St. Marys River.

Given the initial age- and year-specific abundance estimates, subsequent larval abundances were calculated using the equation

$$N_{i+1,t+1} = N_{i,t} * e^{-M} * \left[1 - P(met. \mid age = i)\right] \qquad (3)$$

where $P(met. \mid age = i)$ is a larvae's probability of metamorphosis given that it is age i. This formulation of the equation essentially assumes that lamprey are removed from the larval population due to mortality and metamorphosis occurring fall through winter, and maintain constant abundance over the rest of the year. The formulation of this equation is consistent with observations on the timing of mortality and metamorphosis (Youson, *in review*).

Although researchers have estimated the probability of larval metamorphosis as an increasing function of length for various tributaries to the Great Lakes, there are no estimates of these probabilities as a function of age and no estimates for the St. Marys River. Nearly all of the metamorphosed larvae collected from the St. Marys River have been assigned ages 4 through 6. To reflect this auxiliary information, I constructed the model such that the probability of metamorphosis increases with age by assuming that the probability was zero at age 3 and 1.0 at age 6 and estimating as parameters the increase from age 3 to age 4 and the increase from age 4 to age 5.

The number of metamorphosed lamprey produced in a particular year was calculated using the equation

$$n_{metamorphosed,t} = \sum_{i=4}^{6} P(met. \mid age = i) * N_{i,t} \qquad (4)$$

Because of the timing of the metamorphosis process relative to the operation of the commercial fishery, the metamorphosed larvae produced in the fall and early winter of year t would not show up in the commercial catch until year $t + 1$. Similarly, parasitic lampreys feeding in Lake Huron during the summer of year t do not spawn until the spring and summer of year $t + 1$.

The St. Marys River is not the only river producing parasitic lamprey in Lake Huron. At this time the river-specific contribution to Lake Huron parasitic-phase lamprey population is largely unknown. The parasitic-phase CPUE and the parasitic-phase mark-recapture data sets can only be used to provide information on the overall abundance of lamprey in Lake Huron, not on how much the St. Marys River population contributes to the overall population. To properly describe the overall system, I needed an estimate of the contribution of the St. Marys River to the Lake Huron parasitic-phase population.

The St. Marys River Assessment Plan (Bergstedt et al. 1998) estimated that the St. Marys River produces 88% of the total parasites in Lake Huron. I used this estimate in my model to scale the production of the St. Marys River relative to the other sources in Lake Huron. By using this estimate I am essentially assuming that number of lamprey in Lake Huron is a function of the amount of larval habitat, the number of spawners, and the number of hosts available. Of these three factors, I assume that only the amount and quality of larval habitat remains constant over time. The number of spawners and hosts is assumed to vary over time, causing the observed variability in recruitment and parasite densities. This assumption is supported by Young et al. (1996) who concluded that habitat quantity and quality have remained relatively constant in the St. Marys River and that host availability was likely a more important factor in ultimately determining parasite abundance.

To estimate parameters, the overall model was fit to the six data sets by specifying the assumed statistical distribution of each data set and then constructing the likelihood function. For the parasitic-phase CPUE data set, a lognormal distribution was assumed and the corresponding log-likelihood (ignoring constants) was

$$L_1 = -\sum_t 0.5\left[\left(\log_e\left(\frac{n_t}{n_{1999}}\right) - \log_e(\hat{\alpha}_t)\right)\Big/\hat{\sigma}_t\right]^2 \qquad (5)$$

where n_t is the estimated number of parasitic-phase lamprey in year *t*, n_{1999} is the estimated number of parasitic-phase lamprey in year 1999, $\hat{\alpha}_t$ is the relative parasitic-phase CPUE in year *t*, $\hat{\sigma}_t$ is the standard error estimate associated with each $\hat{\alpha}_t$. This form for the likelihood was used because it mirrored the CPUE outputs from the linear model used to estimate the $\hat{\alpha}_t$. The $\hat{\sigma}_t$ were estimated using a separate linear model, were treated as known values, and were not estimated within the lamprey population model.

The parasitic-phase mark-recapture data set and the spawning-phase mark-recapture data set were assumed to be described by lognormal distributions. The log-likelihoods (ignoring constants) for these data sets were of the form

$$L_i = -\sum_t 0.5\left[\left(\log_e(\hat{x}_{i,t}) - \log_e(x'_{i,t})\right)/\hat{\sigma}_{i,t}\right]^2 \qquad (6)$$

where L_i is the log-likelihood for data set *i*, $\hat{x}_{i,t}$ is the empirical estimate of the population size for data set *i* in year *t*, $x'_{i,t}$ is the model prediction of population size for data set *i* in year *t*, and $\hat{\sigma}_{i,t}$ is the estimated standard deviation for data set *i* in year *t*. As for the CPUE data, the $\hat{\sigma}_{i,t}$ were estimated in separate analyses (i.e., mark-recapture studies). In the population model, they were treated as known values and were not estimated during model fitting.

For the Bayer survey data set, the deepwater electrofishing data set, and the transforming larvae data set, a multinomial distribution was assumed to describe the proportions-at-age. The corresponding log-likelihoods (ignoring constants) were of the form

$$L_i = \sum_t J_{i,t} \sum_a P'_{i,a,t} \log_e(P_{i,a,t}) \qquad (7)$$

where L_i is the log-likelihood for data set *i*, $J_{i,t}$ is the sample size in year *t* for data set *i*, $P_{i,a,t}$ is the model prediction of the proportion age-*a* in year *t*, and $P'_{i,a,t}$ is the empirical estimate of the proportion age-*a* in year *t*. To prevent large sample sizes from overwhelming the log-likelihood, a maximum effective sample size for the combined Bayluscide and deepwater electrofishing data sets was determined using the iterative method outlined in the appendix of McAllister and Ianelli (1997). If the number sampled in a year was greater than the maximum sample size calculated, then $J_{i,t}$ was set to the calculated maximum effective sample size. For the Bayluscide and deepwater electrofishing data sets, $J_{\max} = 30$. Because the number of samples in the metamorphosing larvae data set were only 34 in 1995 and 43 in 1996, a maximum effective sample size was not estimated and instead the observed number of samples were used for the $J_{i,t}$.

Combining the six log-likelihoods, the overall log-likelihood objective function used to estimate model parameters was

$$L = L_1 + L_2 + L_3 + L_4 + L_5 + L_6 \qquad (8)$$

I used AD Model Builder software (Otter Research Ltd. 1994) to estimate model parameters.

Estimating Stock-Recruit Function Uncertainty

The primary objective of this study was to estimate the stock-recruit function for St. Marys River sea lamprey and its associated uncertainty. An additional objective was to estimate demographic parameters (M, λ, and $P(met. | age = i)$) and their uncertainty for forecasting future population dynamics. To accomplish these objectives I adopted a Bayesian estimation framework, placing bounded, uniform priors on each of the estimated parameters. The priors were bounded to avoid implausible parameter estimates, such as a negative survival rate. I used a Monte Carlo Markov Chain (MCMC) procedure to obtain samples from the joint posterior distribution of the estimated parameters. These samples from the joint posterior distribution served to characterize the uncertainty in the estimated parameters.

I assumed that lamprey recruitment was governed by a Ricker-type stock-recruit function of the form

$$R = S\exp(\alpha - \beta S + \varepsilon) \qquad (9)$$

where R is the number of age-0 larvae produced, S is the number of female spawners that produced R, α and β are parameters determining the productivity and compensation, respectively, and $\log(\varepsilon)$ is distributed N (0, σ^2). Let θ be defined as a vector of the 39 parameters estimated in the population model. θ contains the initial numbers-at-age for 1966, the number of age-0 larvae from 1967-1996, M, λ, and the two parameters describing $P(met. | age = i)$. If I denote the information contained in the six data sets as Z, then my primary objective is to approximate the joint posterior density

$$p(\alpha, \beta, \sigma^2, \theta \mid Z)$$

I accomplished this objective using a two-stage approach. For the first stage I utilized the MCMC procedure within AD Model Builder (a version of the Metropolis Hastings algorithm) to obtain 12,000 samples from the posterior density of $\theta(p(\theta \mid Z))$. I generated a total of 12 million samples and saved every thousandth sample (to arrive at a set of 12,000 samples) in order to reduce the degree of autocorrelation in the chain. Each sample (θ_i, i = 1...12,000) determines a set of stock sizes and associated number of age-0 recruits that were produced, which are completely determined by θ. I denote these stock-recruit sets as Y_i, i = 1...12,000.

The second stage consisted of obtaining samples from the joint posterior density,

$$p(\alpha, \beta, \sigma^2 \mid Y)$$

To accomplish this, first I converted the Ricker model above into its linear form,

$$\ln(R / S) = \alpha - \beta S + \varepsilon \qquad (10)$$

Then for each stock-recruit set (Y_i), I drew a single sample of α_i, β_i, and σ_i^2 from the joint posterior density $p(\alpha_i, \beta_i, \sigma_i^2 \mid Y_i)$ (Gelman et al. 1995, p. 236).

Combining the results from the two stages resulted in samples from an approximation to the posterior density,

$$p(\alpha, \beta, \sigma^2, \theta \mid Z).$$

This two-stage approach is not unique, as my approach is analogous to sampling from the joint posterior distribution for hierarchical models (Gelman et al. 1995, p 129). I used this approach to quantify the joint uncertainty in the parameters of the stock-recruit function as well as the demographic parameters for use in forecasting models.

Trace plots (i.e., plots of the ordered, saved sample values) for the parameters show no trends or burn-in period. However, time series analyses revealed that there was autocorrelation among the samples up to lags of 40 saved samples (or 40,000 among the originally-generated 12 million samples) for some of the parameters. Using the methods described by Thiebaux and Zwiers (1984), I estimated the effective number of independent samples among the 12,000 samples for each parameter. Based on these methods, there were 1300 to 2000 effectively independent samples among the 12,000 for each of the parameters.

One of my objectives was to examine the degree that compensation exhibited by St. Marys River sea lamprey could reduce the effectiveness of the trapping and sterile male release control options. During 1985-1990 (a time of relatively high lamprey abundance), the estimated average number of spawning females in the St. Marys River was ~9700. With a trapping rate of 45% and a 3:1 ratio of sterile:fertile males (both reasonable target levels for future control, Michael Twohey (USFWS), personal communication), the expected number of successful female spawners would be reduced from ~9700 to ~1100. To investigate the degree of compensation, I calculated a compensation ratio (Figure 1.1). First I calculated the expected number of recruits (R^*) at low spawning stock size (~1100, S^*=1100 in Figure 1) based on a set of stock-recruit relationship parameters. The same parameters were also used to compute the expected number of recruits (R') at high stock size (S'=9700 in Figure 1). Linear interpolation between zero and R' defines the expected number of recruits (R_0) that would be produced if proportional stock reductions from S' to S* resulted in the same proportional recruit reduction (i.e., no compensation). The compensation ratio is given by R^*/R_0. For each set of α_i and β_i ($i = 1,\ldots 12{,}000$), I calculated the compensation ratio and defined negligible compensation as ratios less than 1, low compensation as ratios between 1 and 2, moderate compensation as ratios between 2 and 5, and high compensation as ratios over 5.

Results

Overall, the modal estimates of CPUE, spawner abundance, parasitic abundance, and age-composition were consistent with observed data. The modal posterior density estimates for CPUE followed the observed pattern of low CPUE during the 1970's, increasing CPUE during the 1980's, and high CPUE during the 1990's (Figure 1.2). The modal posterior density estimates for spawner abundance closely matched observed data, with the possible exceptions of 1991 and 1992 (Figure 1.3). The modal posterior density estimates of parasitic abundance were relatively close to the observed data, although there were some departures from the observations during 1992 and 1993 (Figure 1.4).

The degree to which the model fit each of the data sets is largely a reflection of the number of observations in each data set and their associated variance estimates. The CPUE data set contained 31 observations and the average coefficient of variation (C.V.) was 45% (Appendix Table A.1). The spawner data set contained 16 observations and average C.V. was 0.6%. The parasitic data set only contained 5 observations with an average C.V. of 1.3%. Because the average C.V. for the spawner data set is so low and the number of observations is fairly high, it is not surprising that the modal estimates were so close to the observed data. The objective function (equation 8) is penalized more by parameter estimates that fail to fit data sets with many observations or small measurement error estimates. Because each data set may suggest a slightly different state of the system, simultaneously obtaining a tight fit to all of the data sets may be impossible and suggests model error.

The modal estimates for age-composition also matched observed data (Figure 1.5, Appendix Tables A.2 and A.3). I did not detect any consistent patterns in the larval age-composition residuals over time or across ages. Because larval lampreys are difficult to age, I believe that the information contained in the age-composition data sets is rather limited. The modal estimates of the metamorphosing larvae age-composition data were generally poor. With only two years of data, this outcome is not surprising. However, the metamorphosing larval age-composition data did allow for the estimation of the parameters describing the probability of metamorphosis: 0.46 for age-4 larvae, 0.57 for age-5 larvae, and the assumed value of 1 for age-6 larvae.

The modal estimate for the larval natural mortality rate (M) was 0.82. The histogram in Figure 1.6 depicts the marginal posterior distribution of this parameter, with an approximate 95% posterior probability interval of (0.73, 0.92). The modal posterior estimate for the proportion of the parasitic population migrating to the St. Marys River (λ) was 0.045, and the histogram in Figure 1.7 depicts the marginal posterior distribution of this parameter.

As mentioned earlier, λ represents a combination of the survival from metamorphosis to spawning and the fraction that migrates to the St. Marys River. Because I was unable to estimate the survival from metamorphosis to the parasitic stage, I have implicitly assumed that it was 100% and therefore my estimates for λ are likely biased low. However, survival during this period may be low, especially when small hosts are unavailable (Young et al. 1996).

My modal estimates of historical stock sizes and the number of age-0 recruits that were produced suggest that variation in recruitment is substantial across stock sizes (Figure 1.8). The least squares fit of the Ricker stock-recruit function to these point estimates resulted in estimates of $\hat{\alpha} = 9.15$, $\hat{\beta} = 0.00018$, and $\hat{\sigma}^2 = 1.16$. The marginal posterior distributions for these parameters can be seen in Figure 1.9. There is considerable uncertainty in each of these parameters. Marginal posterior density values for α were generally between 7 and 10. The marginal posterior density for σ^2 has most of its mass between 0 and 10, suggesting that there is considerable variation in recruitment.

A histogram of compensation ratios suggests that high compensation may be possible (Figure 1.10). Overall, 24.5% of the ratios showed negligible compensation, 15.1% showed low compensation, 27.6% showed moderate compensation, and 32.8% showed high compensation.

Discussion

Understanding fish population dynamics is a difficult task. Often the data available for fitting models do not come from rigorously designed population surveys and is of questionable quality. Data sets collected from the same population often seem to support different hypotheses on the state of the system or the parameters governing the population's dynamics. However, management decisions have to be made, and will be made, regardless of the quality of the data or the sophistication of the analyses conducted.

In this paper I have attempted to gather all relevant data sources that could help me to make inferences about St. Marys River sea lamprey population dynamics. None of the data sets were collected with the idea that they would be used to estimate a stock-recruit relationship. However, I combined these data sets into a single, statistically-based, age-structured population model for the purpose of estimating the parameters of a stock-recruit relationship and the associated uncertainty in these and other demographic parameters. Much of the model fitting process involved balancing the information suggested by each data set. I used estimates of the variances associated with each data set (both empirical estimates and effective sample size estimates derived through iteratively fitting the model) to provide a basis for this balancing process. In so doing, I was able to avoid attaching "emphasis factors" (Methot 1990), representing my degree of belief in the individual data sets and their likelihood components. However, because systematic errors (e.g., temporal trends in catchability) were not accounted for, the estimated variances likely represent lower bounds for the true uncertainties in these data sets.

The model that I developed attributed the increase in parasitic-phase abundance over time to increased age-0 recruitment to the larval population. An alternative and equally plausible mechanism, which I did not incorporate into my model, is that larval- or parasitic-phase survival rates increased. Young et al. (1996) suggested that increased survival for newly metamorphosed parasites was a better explanation for the increase in parasitic-phase abundance than changes in the quality or quantity of larval habitat in the

St. Marys River. To examine this increased survival hypothesis, I compared my modal estimates of the number of parasites ($\hat{P}$) with the estimates of parasites based on the least-squares fit of a Ricker stock-recruit function to the modal estimates ($\hat{P}_{SR}$). Figure 1.11 shows the residuals ($\hat{P}$ minus $\hat{P}_{SR}$) plotted over time. This graph suggests that there were a lower number of parasites in the 1970's and early 1980's than expected based on the least-squares stock-recruit relationship parameters. The graph also suggests that the number of parasites in 1992 and 1999 was much higher than expected based on the stock-recruit parameters. This pattern in the residuals indicates that survival rates may have changed over time (Peterman et al. 1998). Unfortunately, I was unable to estimate time-varying survival rates due to a lack of the appropriate data. However, my analyses support the conclusions of Young et al. (1996) that newly metamorphosed parasitic survival rates may have increased over time. Potential reasons for this change may be increased prey fish abundance or biomass. Further investigations into the factors that determine lamprey survival rates would be beneficial and could improve the accuracy of my model.

Fisheries management agencies have long recognized uncertainty, but until recently it has generally been ignored or treated qualitatively in the decision-making process. The GLFC, which oversees the sea lamprey management program in the Great Lakes, has accepted that uncertainty needs to be more formally incorporated into the decision-making process, especially when decisions have to be made at considerable public expense, as is the case with the St. Marys River. The decision to treat the St. Marys River with Bayluscide in 1998 and 1999 had an associated cost of over $5 million dollars, a substantial fraction of the total operating budget for the GLFC. Estimating a single stock-recruit relationship for St. Marys River sea lamprey certainly would have improved the understanding of this system's population dynamics. However, it would have overstated the certainty about the processes and demographic parameters that govern the system dynamics. Therefore the objective of this study was to characterize the uncertainties in the stock-recruit relationship and demographic parameters.

Examining the uncertainty in the stock-recruit function parameters yielded several important findings. First, it is apparent that there is considerable variability in recruitment over a range of stock sizes. The stock-recruit data set presented in Figure 1.7 represented a data set with comparatively low variability ($\hat{\sigma}^2 = 1.16$), but much higher values ($5 < \hat{\sigma}^2 < 15$) might be possible (Figure 1.9). Second, the amount of compensation operating in this population may be substantial. Although the majority of the ratios were classified as negligible, low, or moderate, the potential for high compensation remains. If this population has low amounts of compensation, reducing the number of spawning individuals should result in a nearly proportional reduction in the number of recruits. But if high compensation is operating in this population then management options that reduce the number of spawners will not result in proportional reductions in recruitment. However, the probability of high compensation levels suggested in this study may be overly pessimistic. Jones et al. (*in review*) found only slight compensation in a meta-analysis of sea lamprey stock-recruit data from Great Lakes tributary streams. The scale of the St. Marys River system is much larger than those systems examined by Jones et al. (*in review*). If scaling issues are unimportant in determining population compensation levels, then compensation levels should not significantly differ.

Extreme recruitment variation does not bode well for control options that aim to reduce the number of effective spawners (e.g., trapping and releasing sterilized males). Even if stock sizes are reduced through these control techniques, there is a high probability that a large year-class could be produced. On the other hand, the evidence against high compensation suggests that, on average, reducing the number of spawners will result in a lower number of recruits. My results imply that trapping and releasing sterilized males can be effective treatment options resulting in lower production on average, but that strong year-classes may still result on occasion.

When the effectiveness of control options that reduce the number of effective spawners is highly uncertain, control options that target the larval population may be preferred. In smaller streams and rivers, TFM is still the main method for controlling sea lamprey populations and its success has clearly been demonstrated. The uncertainty in its effectiveness is relatively low. However, conditions in the St. Marys River make a TFM treatment impractical, expensive, and ineffective (Shen et al., *in review*). Because Bayluscide can be applied to localized areas with high larval densities, it represents an opportunity to suppress the larval population in large systems with patchy larval distributions like the St. Marys River. High recruitment variability at low stock sizes may make the Bayluscide treatment option preferable in the St. Marys River compared to trapping and sterilized male releases.

The St. Marys River will continue to pose a major challenge for the integrated management of sea lamprey in Lake Huron. Future management decisions will be required as to which treatment options to use and how much control is necessary to achieve management goals. In this paper I have attempted to characterize the uncertainty in St. Marys River sea lamprey population dynamics, specifically the stock-recruit relationship. This information can serve as a valuable input to models that forecast and evaluate the expected results of different treatment combinations, given the uncertainty present in the system. When these models are incorporated into a formal decision analysis, they can provide a valuable tool for decision-makers and managers alike and should result in improved management of the system.

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Table A.1 Data used in fitting the sea lamprey population model

Year	Ln(CPUE)	S.E. of Ln(CPUE)	Ln(S)	Variance of Ln(S)	Ln(P)	Variance of Ln(P)
1967	-1.30	0.64				
1968	-1.39	0.55				
1969	-1.36	0.55				
1970	-2.46	0.60				
1971	-2.50	0.64				
1972	-3.57	0.60				
1973						
1974	-2.76	0.53				
1975	-2.63	0.51				
1976	-2.28	0.51				
1977	-2.62	0.51				
1978						
1979	-2.18	0.54				
1980	-1.39	0.54				
1981	-1.97	0.64				
1982	-2.53	0.54			12.43	0.0177
1983	-1.54	0.50				
1984	-0.66	0.49				
1985	-1.17	0.50	10.08	0.0007		
1986	-1.15	0.50	9.73	0.0015		
1987	-0.99	0.50	9.94	0.0013		
1988	-1.02	0.50	9.96	0.0014		
1989	-0.36	0.50	10.20	0.0013		
1990	-0.84	0.50	10.05	0.0021		
1991	-0.94	0.50	10.48	0.0020	13.36	0.0293
1992	-0.04	0.51	9.88	0.0020	13.46	0.0778
1993	-0.62	0.50	10.73	0.0153	13.19	0.0206
1994	-1.19	0.51	9.27	0.0043	13.15	0.0112
1995	-1.10	0.52	9.88	0.0032		
1996	-0.72	0.51	10.01	0.0144		
1997	-1.48	0.52	9.01	0.0147		
1998	-0.66	0.52	9.92	0.0046		
1999	0.00	.	9.90	0.0021		
2000			10.57	0.0027	12.55	0.0174

Table A.2 Estimated age composition for St. Marys River sea lampreys.

Year	Age-2	Age-3	Age-4	Age-5	n
1971	0.34	0.47	0.18	0.01	306
1972	0.40	0.38	0.20	0.02	1147
1978	0.92	0.08	< 0.01	< 0.01	62
1980	0.56	0.39	0.05	< 0.01	298
1981	0.76	0.22	0.02	< 0.01	2033
1982	0.30	0.64	0.06	< 0.01	44
1984	0.71	0.25	0.04	< 0.01	95
1985	0.58	0.28	0.13	0.01	779
1986	0.86	0.10	0.04	< 0.01	442
1987	0.42	0.50	0.08	< 0.01	660
1988	0.91	0.07	0.01	0.01	257
1989	0.81	0.11	0.08	< 0.01	32
1993	0.44	0.19	0.29	0.07	421
1994	0.43	0.28	0.24	0.05	898
1995	0.46	0.30	0.24	< 0.01	933
1996	0.65	0.26	0.09	< 0.01	1175
1997	0.61	0.34	< 0.01	0.06	407
1998	0.52	0.27	0.17	0.04	809

Table A.3 Estimated transformer age composition.

Year	Age-4	Age-5	Age-6	n
1995	0.53	0.38	0.09	34
1996	0.3	0.44	0.26	43

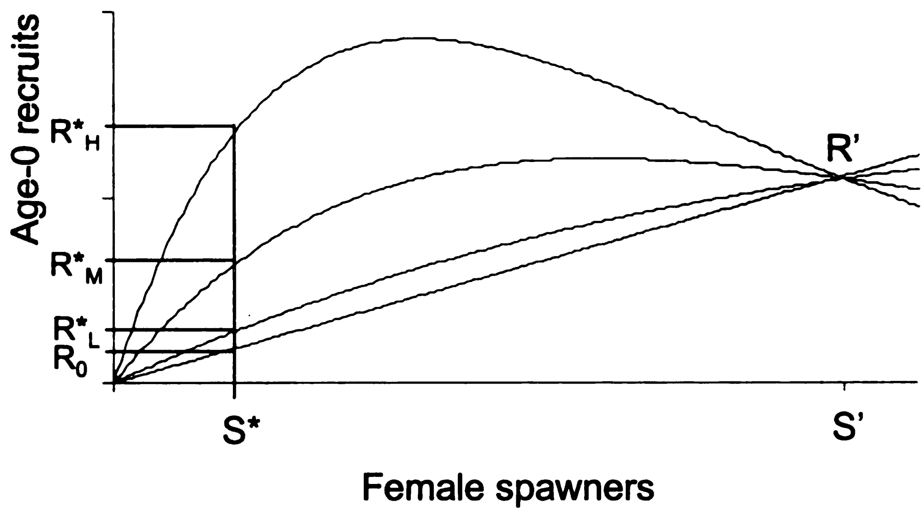

Figure 1.1 Stock-recruit relationships depicting high (R^*_H), moderate (R^*_M), and low (R^*_L) values for the compensation ratio (R^*/R_0) at a low stock size (S*). Recruitment at low spawning stock size with zero compensation is denoted by R_0 and recruitment at high spawning stock size (S') is denoted by R'.

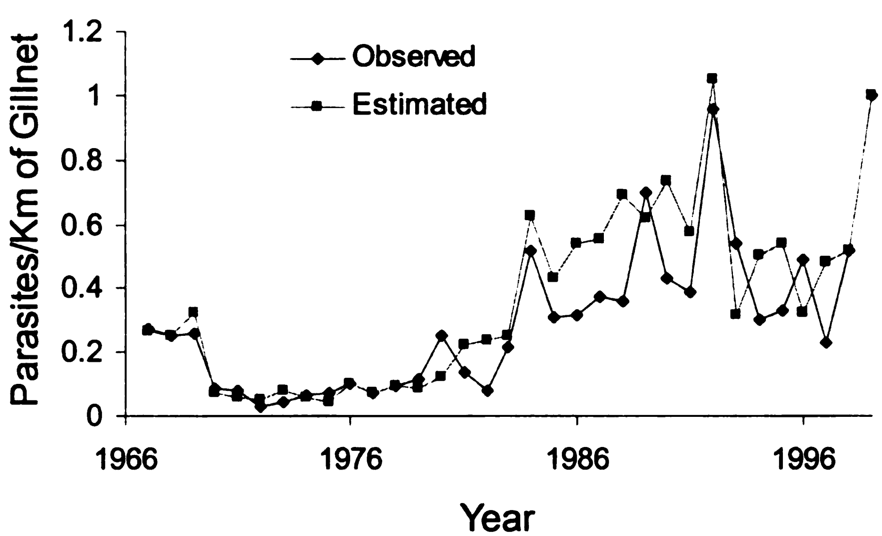

Figure 1.2 MPD (modal posterior density) model estimates and observed commercial fishery catch-per-unit-effort (number of lamprey per km of gillnet) estimates, 1967-1999.

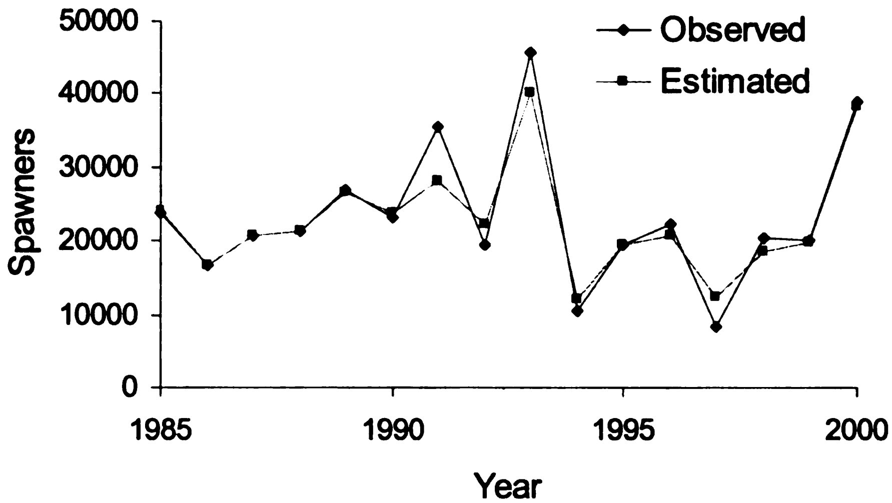

Figure 1.3 MPD (modal posterior density) model estimates and observed spawning-phase population estimates based on mark-recapture, 1985-2000.

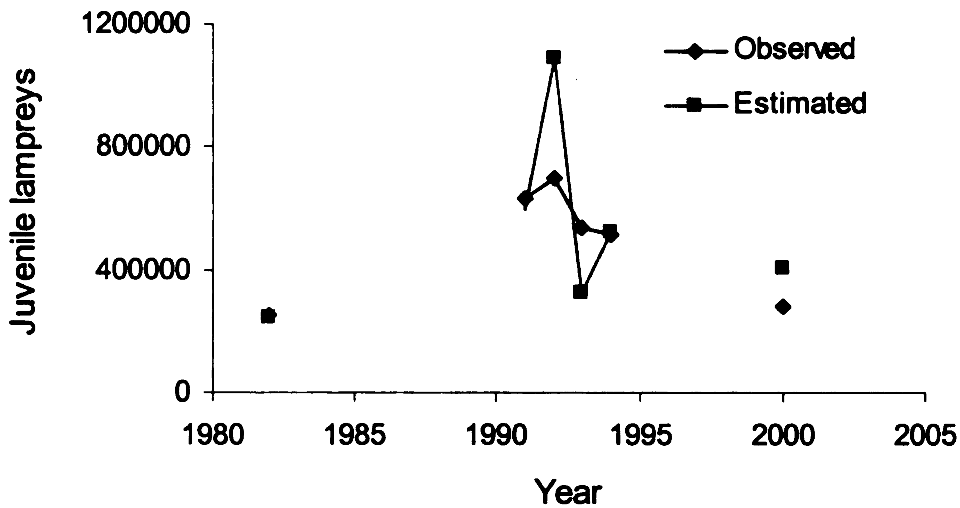

Figure 1.4 MPD (modal posterior density) model estimates and observed parasitic-phase mark-recapture population estimates for juvenile lampreys, 1982, 1991-1994, and 2000.

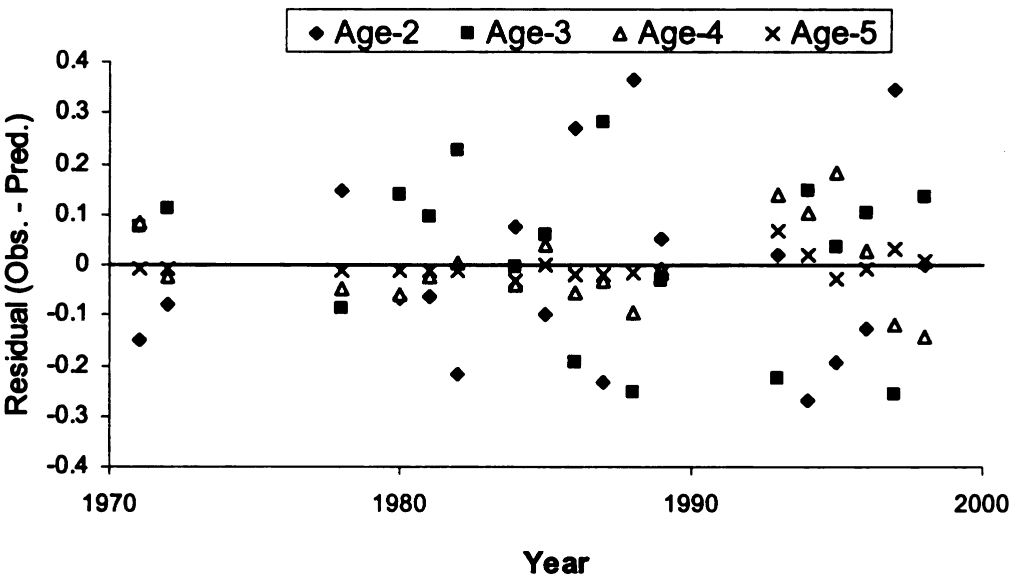

Figure 1.5 Residuals (observed minus predicted value) of proportions-at-age for larval lamprey ages 2-5, 1971-1998.

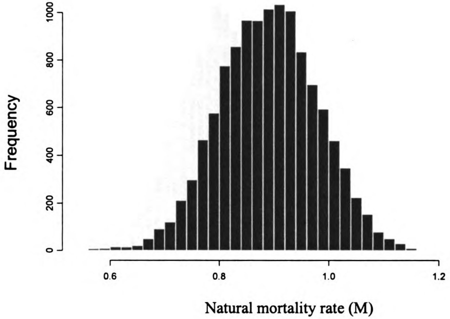

Figure 1.6 Frequency histogram of 12,000 MCMC samples of the larval natural mortality rate (M).

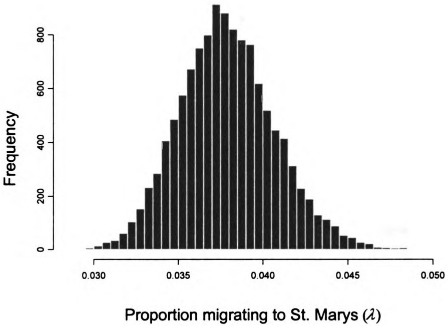

Figure 1.7 Frequency histogram of 12,000 MCMC samples of the proportion of the parasitic-phase population that migrates to the St. Marys River to spawn (λ).

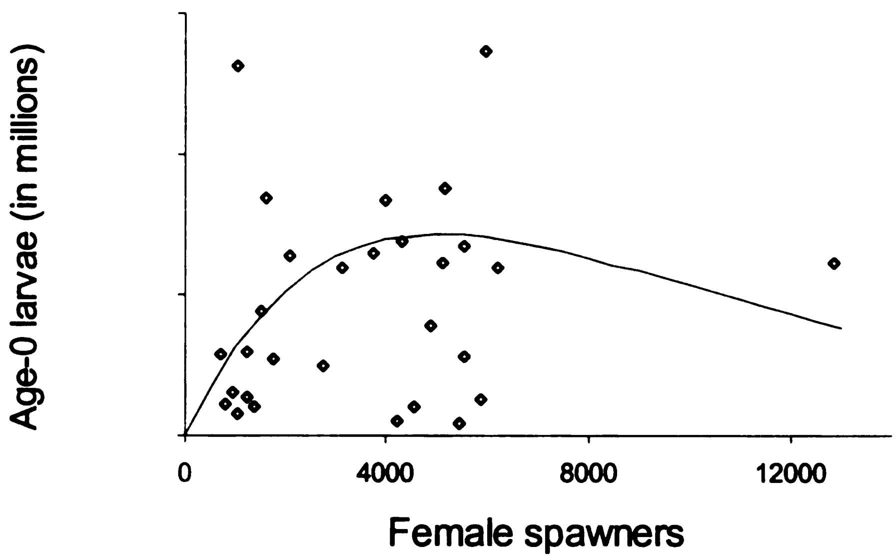

Figure 1.8 MPD model estimates of the number of female spawners and age-0 recruits for the St. Marys River sea lamprey population, 1968-1996. The least-squares fit of a Ricker stock-recruitment function is also plotted.

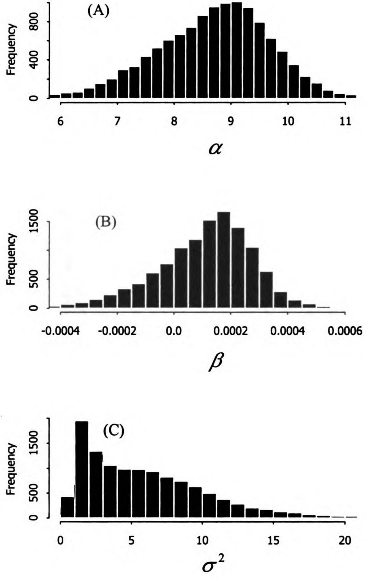

Figure 1.9 Marginal frequency histogram of 12,000 MCMC samples of the α (panel A), β (panel B), and σ^2 (panel C) parameters from a Ricker stock-recruitment function.

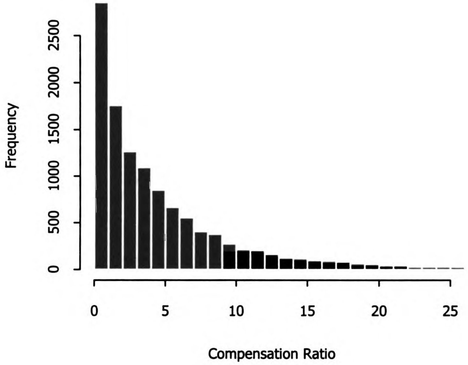

Figure 1.10 Frequency histogram of 12,000 estimates of the compensation ratio, R^*/R_0, based on the MCMC samples from the joint distribution of α and β.

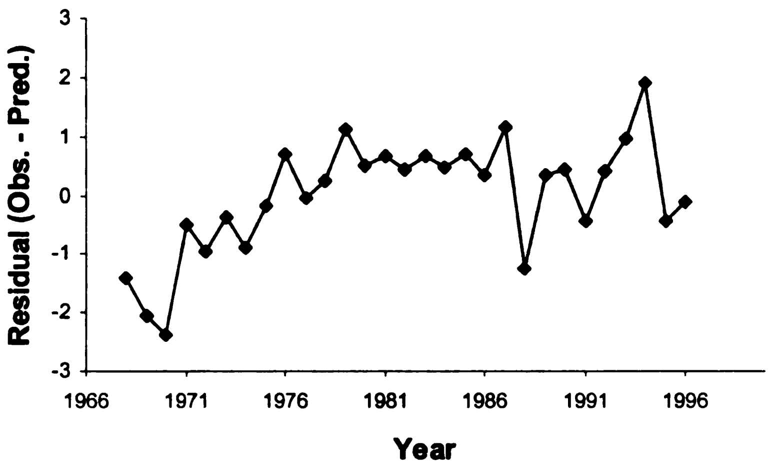

Figure 1.11 Residuals ($\hat{P}_{MPD}$ minus $\hat{P}_{SR}$) of the MPD estimates of the number of parasites ($\hat{P}_{MPD}$) minus the estimated number of parasites based on the least-squares stock-recruit relationship parameters ($\hat{P}_{SR}$) plotted over time

CHAPTER 2

QUANTIFYING SPATIAL AND TEMPORAL UNCERTAINTY IN LARVAL LAMPREY ABUNDANCE AND ITS EFFECT ON CHEMICAL TREATMENT SUCCESS IN THE ST. MARYS RIVER

Abstract

Effective chemical treatment of sea lamprey (*Petromyzon marinus*) larvae in the St. Marys River requires reliable knowledge of their spatial distribution. However, surveys to adequately characterize the distribution cannot be conducted in the same year as the chemical treatment, thus raising questions about the accuracy of using historical survey data to delineate treatment areas. In this project I developed stochastic models that predict the abundance of larvae at a location in the next year based on data collected in the current year. Recursive application of these models can allow for stochastic forecasts at locations in space and time, simulating how population abundance may have changed from the time each location was originally mapped (1993-1996) until the time that the main treatment took place (1999). My approach to modeling was to develop two generalized linear models (GLMs). The first GLM model estimates the probability that larvae would be present at a location. The second GLM model estimates parameters defining the probability distribution for larval abundance at that point, given that larvae were present. I applied these models to forecast a variety of possible abundance maps for the lampricide treatment that took place in 1999 to estimate the uncertainty in treatment effectiveness resulting from spatial and temporal uncertainty in larval distribution. The results suggest that expected treatment effectiveness did not differ from previous predictions of treatment effectiveness at the level of treatment implemented in 1999. However, if less area of the river had been targeted for treatment, then expected treatment

effectiveness would have been lower than predicted treatment effectiveness. The large scale of the 1999 treatment may have compensated for the spatial and temporal uncertainty by targeting the majority of the high density areas in the river, leaving few areas with larval lamprey untreated.

Introduction

A combination of adult trapping, sterilized male releases, and chemical applications is used to control the St. Marys River sea lamprey (*Petromyzon marinus*) population. However, the large size and flow patterns of the St. Marys River inhibit the effective use of the lampricide 3-triflouromethyl-4-nitrophenol (TFM), the predominant method for controlling sea lampreys in the Great Lakes region. In other rivers and streams, TFM is applied at a rate that saturates the water column with a lethal dosage to kill the majority of larvae in the riverbed. With typical TFM treatments, the spatial distribution of larvae in the river is unimportant because it is assumed that virtually all larvae in the stream are exposed to a lethal dose of the lampricide.

Although a substantial population exists in limited areas of the river, most of the St. Marys riverbed area contains few larval lampreys. So TFM is not cost-effective (Schleen et al., *in review*). To control the larval population in a cost-effective manner, managers have chosen to use granular Bayluscide, an alternative lampricide that can be applied locally to discrete patches of larval habitat rather than saturating the entire river with TFM. With Bayluscide, managers can achieve effective population control by targeting local areas of high larval density. However, cost-effective control of sea lamprey larvae in the St. Marys River using Bayluscide requires a reliable knowledge of their spatial distribution.

During 1993-1996, nearly 12,000 locations throughout the St. Marys River were sampled using deepwater electrofishing to determine the distribution and abundance of larval sea lamprey (Fodale et al., *in review*). Based on maps generated using these data, researchers and managers delineated areas with the highest larval densities as candidates for possible treatment with Bayluscide. The larval population within each treatment area was estimated and areas were ranked according to the number that would be killed per dollar spent on Bayluscide. Combining these estimates resulted in a graph depicting the proportion of the total population that would be removed as a function of the amount of Bayluscide applied. Given this information, decision-makers chose to spend approximately $5 million on an aggressive treatment of the St. Marys River lamprey population that included a combination of applying Bayluscide, trapping, and releasing sterilized males into the spawning population during 1998-1999. While a small portion of the river was treated during pilot studies in 1998, the majority of the treatment effort took place during 1999. Biologists predicted that 55% of the larval population would be killed using the level of Bayluscide that was selected.

The actual distribution of larvae in the river at the time of Bayluscide treatment affects the performance of these lampricide applications. The data used to describe larval distribution were collected during 1993-1996. The treatment took place 2-3 years later. This raises questions about the degree to which larval distributions are spatially and temporally stable. If the distribution changes substantially from year to year, treatment areas delineated from data collected in one year may substantially deviate from the optimal treatment areas based on data collected in other years. Managers recognized that this could be an important uncertainty, and set up a series of index stations in the St. Marys that were sampled annually 1994-1998 to assess the degree of spatial and temporal stability.

In this study I utilized these index site data to parameterize and develop stochastic models that predict the abundance of larvae at a location in the next year based on data collected in the current year. Recursive application of these models allows for simulating how population abundance changed from the time each location was originally mapped (1993-1996) until the time of the main treatment (1999). My approach to modeling was to develop two generalized linear models (GLMs). The first model estimates the probability that larvae would be present at a location in the next year. The second model estimates parameters that define the probability distribution for larval abundance at that point in the next year, given that larvae were present. This general approach to modeling population change over time and space has been applied quite successfully in other contexts (Augustin et al. 1998a, Augustin *et al.* 1998b, Welsh et al. 1996, Augustin et al. 1996, Lindenmayer et al. 1991, Osborne and Tigar 1992).

I used the index site data to parameterize the GLMs and then recursively apply the resulting models to the areas delineated for the 1999 lampricide treatment. I applied these models to forecast a variety of possible abundance maps for the lampricide treatment that took place in 1999 in order to estimate the uncertainty in treatment effectiveness resulting from the spatial and temporal uncertainty in larval distribution. Understanding how the spatial and temporal uncertainties in larval distribution affect lampricide effectiveness is essential for assessing the trade-offs among the management options available for controlling St. Marys River sea lampreys.

Methods

My overall approach was to develop a stochastic simulation model that could predict population abundance at each point given the population abundance at that point and other information observed in the previous time step. I then applied that simulation model to evaluate how well the procedure used to decide on areas for Bayluscide treatment was likely to have performed. This was done by repeatedly simulating the spatial patterns of larval catches in 1999 that might have arisen from those points mapped during 1993-1996. As a preliminary step, prior to developing the stochastic simulation model, I explored the spatial and temporal variability in the data. In part this guided my choice of variables to include in forecasting the next year's map of larval catches.

The data on larval distribution and catch within the St. Marys River were collected using the boat-mounted deepwater electrofishing gear developed by Bergstedt and Genovese (1994). The gear consists of a covered, electrified grid connected to an onboard suction pump. The covered grid is lowered onto the river substrate and an electric current is initiated using a DC backpack electrofishing unit (Weisser and Klar 1990). The electrical field causes larval lamprey to emerge from the substrate whereupon they are pumped to the surface and collected in a basket, measured for length, and enumerated. Because efficiency of the deepwater electrofishing gear varies as a function of length, each larva was assigned an efficiency-adjusted catch (adjusted catch) equal to the inverse of the capture probability calculated at its length (e.g., a larva with a capture probability of 0.5 would be assigned an efficiency-adjusted catch of 2) (Bergstedt and Genovese 1994, Fodale et al., *in review*). At each sampled location, a differentially corrected global positioning system was used to determine position coordinates and a Ponar dredge was used to categorize habitat quality as preferred, acceptable, or unacceptable. An area of approximately 2.44 m^2 was sampled at each location.

During 1993-1996, biologists under the direction of the St. Marys River Task Force (Task Force) sampled nearly 12,000 locations spanning the St. Marys River using the deepwater electrofishing gear (Fodale et al., *in review*). The biologists used a combination of systematic and adaptive sampling. Systematic sample locations were 65-140 m apart, while the adaptive samples were 35 m from systematic sample locations where more than four animals were caught. The majority of the sampled locations had catches of zero (94.4%).

In addition to the full river survey, the Task Force also established a set of thirteen index sites that were sampled repeatedly during 1994-1998 (Fodale et al., *in review*), prior to the Bayluscide treatment. Each site consisted of a grid of 22 m x 32 m cells, with between 48 and 244 cells per index site. Biologists sampled each cell in each index site annually. Sites 1-4 were sampled all five years, while sites 5-9 were only sampled 1995-1998 and sites 10-13 were only sampled 1996-1997. The index sites were established in areas with medium to high larval densities to monitor trends in abundance and treatment effectiveness. Figure 2.1 shows the adjusted catch (mean +/- 1 S.E.) across years for index sites 1-9.

I used geostatistical methods to characterize the spatial and temporal variability in the index site data. Based on initial data summaries, I observed that the variance in adjusted catch increased with the mean and the data had a high proportion of zero values (~75%) (Figure 2.2). Therefore I performed a $\log_e$(adjusted catch + 1) transformation (hereafter referred to as transformed catch) to help stabilize the variance and better approximate normality. To characterize the spatial correlation, I calculated an empirical, omnidirectional semivariogram combining all five years of index site adjusted catch data. Because preliminary analyses did not reveal anisotropy, omnidirectional semivariograms were used (Isaaks and Srivastava 1989). To characterize the spatial and temporal correlation, I calculated an empirical, omnidirectional cross-semivariogram, using a one-year lag as the crossing variable. I used this cross-semivariogram to describe the correlation in transformed catch between points as a function of distance at one-year lags. I estimated the range (i.e., the distance up to which the data are spatially correlated) for both the semivariogram and the cross-semivariogram to aid in developing the GLMs.

Using the index site data, I modeled the pointwise inter-annual changes in adjusted catch of larval lamprey in two stages. The first stage was a logistic GLM whereby I estimated the probability of larvae being present at each point *i* as a function of the previous year's adjusted catch ($catch_i$) at that point, a weighted average of the adjusted catches at neighboring points ($autocov_i$) (Augustin et al. 1996), and the habitat type ($habtype_i$). The model took the form

$$\log\left(\frac{p_i}{1-p_i}\right) = \beta_0 + \beta_1 catch_i + \beta_2 autocov_i + \beta_3 habtype_i \qquad (1)$$

where the β's are estimated parameters and

$$autocov_i = \frac{\sum_{j=1}^{n_{ij}} w_{ij} catch_j}{\sum_{j=1}^{n_{ij}} w_{ij}} \qquad (2)$$

is a weighted average of the adjusted catch values ($catch_j$) among the set of n_{ij} neighbors within 120 m of point *i*. The weight applied to $catch_j$ is $w_{ij} = 1/h_{ij}$, where h_{ij} is the Euclidean distance between points *i* and *j*. This autocovariate is intended to help account for the fine scale (< 120 m) spatial autocorrelation between points (Augustin et al. 1996). However, it is only one of many methods available for incorporating this information. The influence of habitat quality was incorporated through the $habtype_i$ term where

$$habtype_i = \begin{cases} 0, & \text{if} \quad \text{preferred} \\ 1, & \text{if} \quad \text{acceptable} \end{cases} \qquad (3)$$

By definition, if a location is classified as having unsuitable habitat, then no lamprey are present at that location.

The second stage of the model consisted of a second GLM that fit a gamma distribution to the adjusted catch data at each point *i*, conditional on the presence of lamprey at point *i*. The model took the form

$$\frac{1}{\mu_i} = \alpha_0 + \alpha_1 catch_i \qquad (4)$$

where the $\alpha's$ are estimated parameters, $catch_i$ is the previous year's adjusted catch at point *i*, and $\frac{1}{\mu_i}$ is the link function for the mean (μ_i) of the gamma distribution describing the adjusted catch data, fit at point *i* (McCullagh and Nelder 1989). The adjusted catch data showed a high proportion of zero values and a continuous, right-skewed distribution of positive catch values that resembled a gamma distribution or perhaps a Poisson distribution (Figure 2). However, residual plots and histogram plots revealed that a gamma distribution provided a better approximation to the distribution of the positive adjusted catch data than did the Poisson distribution. The gamma distributions were fit with an assumed constant variance (shape). Because parameter estimates for the weighted average of the adjusted catches at neighboring points ($autocov_i$) and habitat quality ($habtype_i$) terms were not significantly different from zero

(χ^2 test, p-value > 0.05), these terms were left out of the second stage model. A total of 1814 observations were available for fitting the first stage model and 474 observations were available for fitting the second stage model. I limited the data to observations where the recorded habitat quality was the same between years at each point to avoid incorporating habitat measurement error in the estimation process.

Using the index site data set with its known transitions, I examined the ability of the first stage model to correctly predict inter-annual transitions through calculation of a matching coefficient (Buckland and Elston 1993). I applied the model to each point in the index site data set and predicted whether lamprey would be present at each point the following year. I generated a total of 1000 stochastic realizations of the model and calculated the mean matching coefficient resulting from these simulations. As a comparison, I also calculated the mean matching coefficient for 1000 simulations where the predicted transitions were bootstrap samples (with replacement) from a population with the same proportion of presences and absences as the index site data set.

As mentioned earlier, the overall river sampling occurred 1993-1996 and the treatment took place in 1998-1999. To generate a larval distribution map for 1999 I had to recursively apply the models, starting with the most historic data. The data from each stochastic forecast became the data set used for generating the next year's forecast until a map was generated for 1999 (Buckland and Elston 1993). The algorithm that I used is described in Table 2.1. I generated a total of 100 distribution maps. Each simulated map consisted of adjusted catches during 1999 at each of the 2042 points within the treatment sites areas. At this point in the analysis, I switched from a spatially explicit characterization of the population (i.e., modeling the point data) to a spatially implicit characterization of the population (i.e., modeling the total abundance in each treatment area). For each map I calculated the mean density (number of larvae/m^2) within each of the 46 ranked treatment areas. By multiplying the mean density of each treatment plot by the plot area, I estimated the number of larval lampreys within each treatment plot. I then examined the effects of selecting the ranked treatment areas (based on the original ranking analysis performed by the Task Force) by calculating the total population that would be targeted for each map and for each set of treatment areas.

The data used to calibrate the models came from index sites with relatively high larval densities, similar to the treatment areas to which the models were applied. Because the remaining portions of the river generally had much lower densities, I believed that it would be inappropriate to apply the models to these low-density areas. Preliminary applications of the models to these areas resulted in forecasted larval densities an order of magnitude higher than observed densities. However, I was interested in incorporating variability in the number of larvae outside the treatment areas in our calculations of the percent of the total population targeted by the treatment. To do this I estimated the coefficient of variation (CV) for the mean density in the index sites between years. I assumed that points outside the treatment area would have the same CV for mean density. Using the empirical estimate for the mean density outside the treatment area ($\hat{\mu}_{outside}$) and the estimate of the total area outside the treatment areas, I estimated the number of larval lampreys outside the treatment areas. I allowed this number to vary between simulations by generating a random normal variable for the mean density ($\mu^{*}_{outside}$) for each simulation with mean = $\hat{\mu}_{outside}$ and standard deviation = CV $\cdot$ $\hat{\mu}_{outside}$. To calculate treatment effectiveness (i.e., the proportion of the total population that would be removed for a given amount spent on Bayluscide), I divided the cumulative population in the ranked treatment areas by the sum of the populations within all treatment areas and the population outside the treatment areas. All estimates reflect an empirical estimate for Bayluscide efficiency of 75% (i.e., 75% of the larvae within an area are killed when Bayluscide is applied to that area).

The variability in treatment effectiveness has two components: variation in the number of larvae predicted in the treatment areas due to the stochastic nature of the models and variation in the number of larvae predicted in the non-treated areas. To examine the degree that these two sources affected the overall treatment effectiveness estimates, I also calculated treatment effectiveness holding the number of larvae in the non-treated areas constant across simulations.

Results

Although the annual means for the adjusted catch data in index sites 1-9 varied among years, a consistent trend was not evident (Figure 2.1). A linear regression of adjusted catch versus year did reveal a slightly negative slope, but the slope parameter estimate was not significantly different from zero (p-value = 0.63). This result suggests that a consistent trend in abundance was not present in the index site data during 1994-1998 and thus that parameters estimated in the model should not impose a negative trend in abundance over time.

Calculation of the empirical semivariograms elucidated some of the spatial autocorrelation patterns present within the data (Figures 2.3 and 2.4). Spherical models fit to the data generally had the lowest error sum of squares compared to exponential, linear, or Gaussian models (Isaaks and Shirvistrana 1989). The estimate of the range for the semivariogram (within years) was 124 m, with a sill of 0.19 and a nugget of 0.31. The estimate of the range for the cross-semivariogram (1-year lag) was 129 m, with a sill of 0.21 and a nugget of 0.39. The variation among points reached an asymptote of 0.50 for the semivariogram and 0.60 for the cross-semivariogram. Because spatial autocorrelation was present in the cross-semivariogram up to a distance of 129 m, we believe that our use of a weighted average for catches within 120 m was appropriate in our logistic model fitting.

The results of the two GLMs are presented in Tables 2.2 and 2.3. For the logistic GLM, all three variables (e.g., *catch*, *autocov*, and *habtype*) reduced the residual deviance and were significantly different from zero (χ^2 test, $p < 0.01$). The highest probability of presence at a point in the next year came when the previous year's catch was high, the distance-weighted average catch was high, and the habitat was classified as preferred. For the gamma GLM, only the previous year's catch variable was significantly different from zero (χ^2 test, $p < 0.01$). The estimated mean of the gamma distribution increased as a function of the previous year's catch.

Using the parameter estimates from the two-stage GLM and the data from index site 6 (the largest index site), I simulated a series of abundance maps to illustrate the observed variability in larval distribution and to demonstrate an execution of our model (Figure 2.5). Each simulated abundance map is based on the previous year's observed data (i.e., the simulated map for 1996 is based on the observed data from 1995, the map for 1997 is based on 1996 observed data, and the map for 1998 is based on 1997 observed data) and represents a possible realization of the distribution of larvae in site 6 during the specified year. Within both the observed and simulated maps, there were considerable differences between years at individual points.

Based on the results of 1000 simulations applying the logistic model to the index site data, the mean matching coefficient was 65.1% (standard deviation = 0.95%). The mean matching coefficient for the bootstrap procedure was 60.7% (standard deviation = 1.1%). Using a t-test, I confirmed that the matching coefficient from the logistic model was significantly higher than the matching coefficient from the bootstrap procedure ($p < 0.01$). This result does not constitute a formal test or calibration of the model because the same data that were used to estimate model parameters were used to evaluate its performance using the matching coefficient. However, I believe that the matching coefficient does provide a relative measure of model fit. Based on the matching coefficient results, the logistic model did improve predictions of the inter-annual transitions between presences and absences.

By sequentially applying the two-stage GLM to the treatment site areas, I was able to simulate the pointwise adjusted catch of larval lamprey in 1999, the year of the main treatment of the St. Marys River. I generated a total of 100 maps and calculated the efficiency associated with various expenditures on Bayluscide. Plotting the cumulative proportion killed versus cumulative cost for these 100 maps, I quantified the effects of spatial and temporal uncertainty in larval distribution on treatment effectiveness (Figure 2.6). Also plotted is the expected percent killed based on the mapping data assuming that the historical (1993-1996) data represent the actual values in 1999 (i.e., assuming no uncertainty in larval distribution). Our simulation results suggest that the proportion killed is generally lower than when uncertainty is ignored. This difference is most pronounced when smaller portions of the river are selected for treatment. However, as the amount of area treated increases, which is proportional to the amount spent on chemical treatment, this difference becomes less apparent. When the largest amount of area is treated, the mean proportion killed for the estimates that include uncertainty is 0.57 (standard deviation = 0.04) as compared to 0.55 predicted when uncertainty is ignored.

The total simulated variability in treatment effectiveness is due to the variability in abundance both within the treatment areas and within the non-treated areas. Figure 2.7 shows the simulated variability in treatment effectiveness when the total abundance in the non-treated areas is held constant. When less of the river is selected for treatment, the variability in treatment effectiveness is similar to that shown in Figure 2.6. However, when the largest amount of area is selected for treatment, the variability in treatment effectiveness is less (standard deviation = 0.01).

Discussion

Effective control of sea lamprey larvae in the St. Marys River using Bayluscide requires a reliable knowledge of their spatial distribution. However, determining the distribution and abundance of larval lampreys immediately prior to the application of Bayluscide in a system as large as the St. Marys River would be prohibitively expensive. Likewise, financial constraints make treating the entire river with lampricide impossible. Some sort of compromise between the limitations of assessment and treatment is necessary.

Managers and scientists involved in the management and assessment of sea lamprey have long recognized spatial and temporal uncertainty in larval abundance within the St. Marys and other rivers. When delineating the treatment areas in the St. Marys, the Task Force attempted to compensate for this uncertainty by delineating low-density buffers around the core areas of high larval density. Final treatment areas consisted of both the high-density core areas and the buffers. While this approach was somewhat subjective, our analysis suggests that it may have performed well.

The scale of the treatment that took place in 1999 appears to have been large enough to counteract the effects of the spatial and temporal uncertainty. Intuitively, this should be the case, as increasing the area treated will result in a greater proportion of the population being killed regardless of the degree of spatial and temporal uncertainty. Conversely, as the scale of treatment decreases, the effects of these uncertainties become more profound, resulting in reduced effectiveness. The larval population in individual treatment areas varies from year to year, and the optimal treatment area ranking based on data from one year may not be optimal when data from other years is considered. This ranking effect is most apparent when fewer areas are selected for treatment. A preferable treatment ranking approach might be to utilize these models to rank areas for treatment based on the frequency with which they are ranked highly.

One of the advantages of using GLMs to model changes in the spatial and temporal distribution and abundance is that data patterns can be described without having to model the specific processes (e.g., mortality, density dependence, emigration, immigration, and recruitment) that generate the patterns. Spatially explicit population models have been used to describe changes in animal distribution and abundance, but they typically require a large number of parameters to be estimated (Dunning et al. 1995). Many of these parameters are difficult or nearly impossible to estimate empirically (Conroy et al. 1995). In contrast, GLMs take advantage of the correlations between covariates and the independent variable to statistically reproduce the patterns in the data. However, the variable selection process requires special attention to avoid the inclusion of irrelevant variables (Buckland and Elston 1993) and applications of the model to different systems may result in poor performance. Because of the limited number of variables available for modeling lamprey in the St. Marys River, the likelihood that irrelevant variables were included in our model is small.

One of the shortcomings of my analysis was an inability to correctly model the pointwise inter-annual changes in the non-treated portions of the river. The data used to estimate the parameters of the GLMs came from index sites that have relatively high larval densities. Data summarizing inter-annual changes in areas of low larval density were not available. An implicit assumption of the way I modeled these non-treated areas of the river was that mean adjusted catch in these areas did not increase or decrease over time. Mean adjusted catch these areas may vary temporally around a mean, as I have modeled, or may follow a trend over time (i.e., either increasing or decreasing) with some noise. If the latter is true, then my results (Figure 2.6) should be considered minimum estimates of the variability in treatment effectiveness. To address this issue, index sites need to be established in low-density areas of the river and sampled annually. These data would provide a starting point for better describing how low-density areas behave over time and could easily be incorporated into the model described here.

Related to the problem of applying the model to non-treated areas are the issues of future assessment and treatment decision needs. An ongoing monitoring program is in place to monitor trends in overall larval abundance within the river. However, redoing the detailed, extensive surveys that took place during 1993-1996 would be an expensive and difficult task. To map the distribution and abundance of larvae in the river and provide decision-makers with appropriate estimates of treatment effectiveness, a version of our model could be applied to surveys conducted within a limited portion of the river or to simulated maps that incorporate the reductions due to the treatment that took place in 1999. Another alternative would be to survey a limited portion of the river and use Gibbs sampling to estimate the abundance at non-sampled locations (Weir and Pettitt 2000, Augustin et al. 1996). Despite having samples for only 20% of the total area, Augustin et al. (1996) was able to effectively predict presence/absence at non-sampled locations by using Gibbs sampling. Given the rich data available in the St. Marys, this type of approach may be feasible.

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Table 2.1 Algorithm for generating a single abundance map.

1. Starting with the data collected in 1993 and the logistic GLM, estimate the probability of larval presence at each point for 1994.
2. Conduct a Bernoulli trial at each point using the probability calculated in step 1.
    - If the trial results in larval presence predicted at that point, estimate the abundance at that point by generating a random sample from a gamma distribution with the parameters given by the gamma GLM.
3. Append the location and habitat data from 1993 to the abundance map simulated in step 2.
4. Append the data collected in 1994 to the data from step 3.
5. Repeat steps 1-4, sequentially adding the location and habitat data that was collected in each year, to generate abundance maps for 1995, 1996, 1997, 1998, and 1999.

Table 2.2 Logistic GLM results.

Parameter	DF	Estimate	S.E.	Pr > χ^2	Residual Deviance	Residual DF
β_0		-1.5165	0.0842		2083.97	1813
β_1	1	0.0686	0.0164	< 0.0001	2001.71	1812
β_2	1	0.3130	0.0401	< 0.0001	1941.40	1811
β_3	1	-0.7624	0.1687	< 0.0001	1918.55	1810

Table 2.3 Gamma GLM results.

Parameter	DF	Estimate	S.E.	Pr > χ^2	Residual Deviance	Residual DF
α_0		0.2019	0.0113		354.92	473
α_1	1	-0.0031	0.0010	0.0063	347.46	472

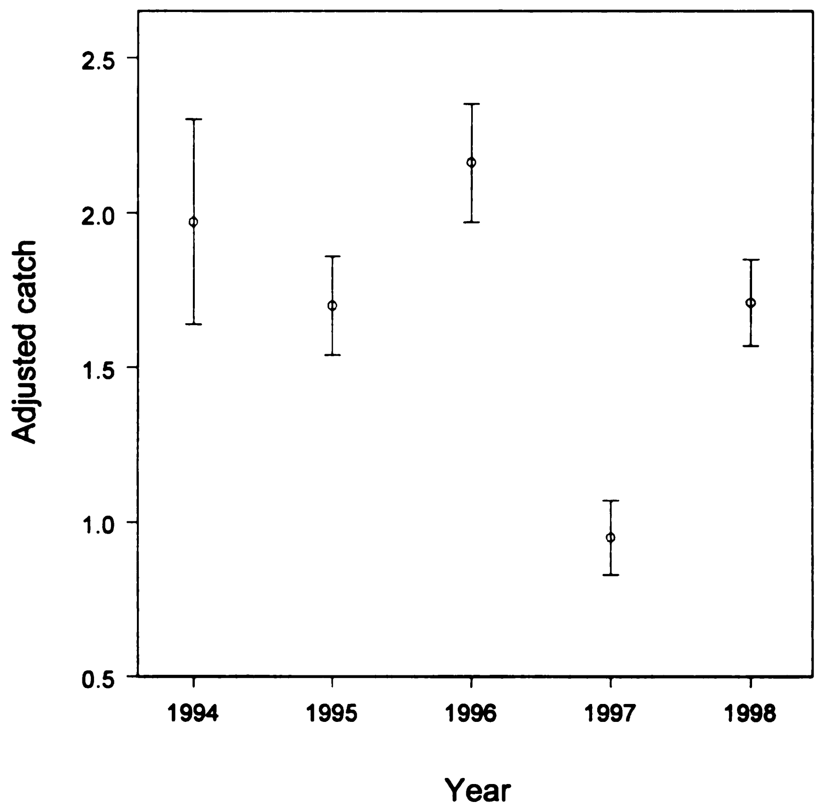

Figure 2.1 Annual means (+/- 1 S.E.) of adjusted larval catches from index sites 1-9.

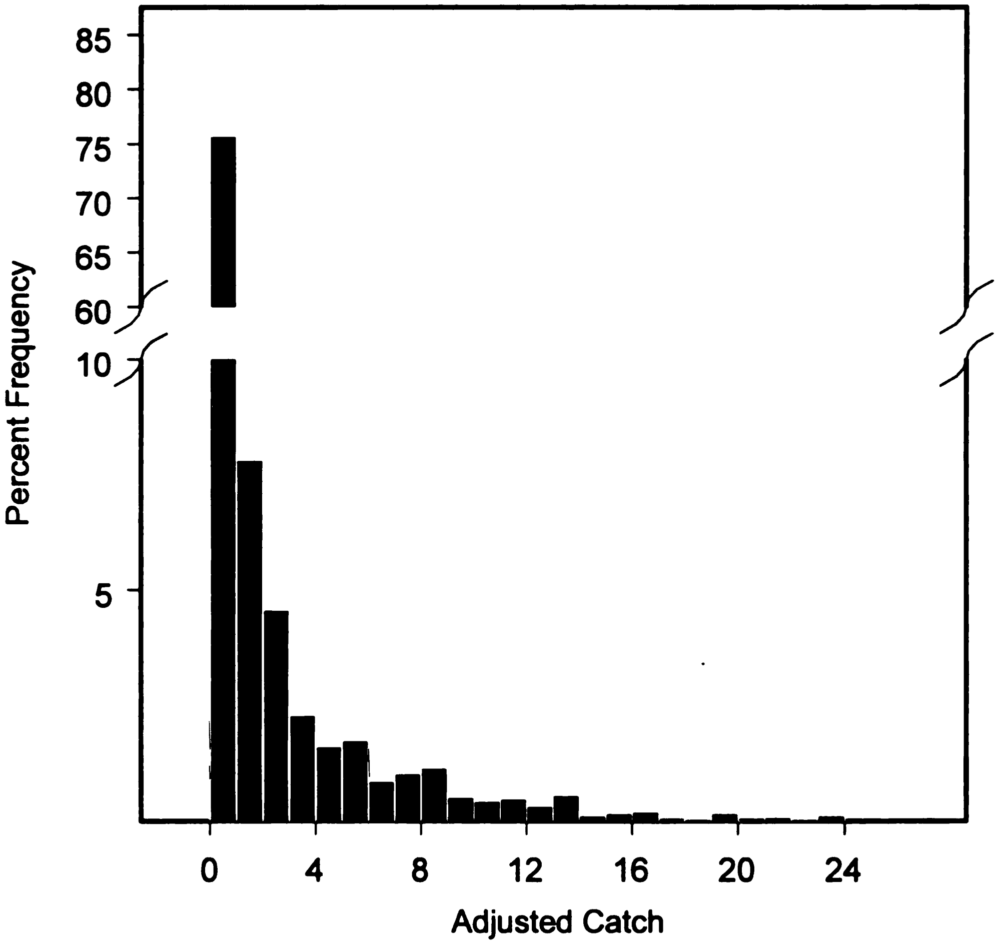

Figure 2.2 Percent frequency histogram of adjusted larval catches from index sites 1-9.

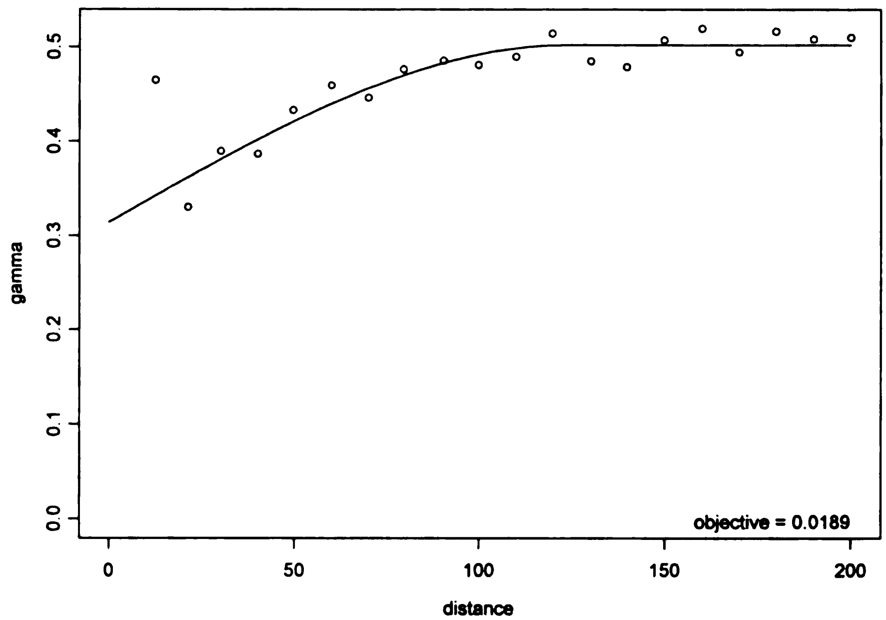

Figure 2.3 Empirical semivariogram and fitted spherical semivariogram function based on transformed larval catches from index sites 1-13.

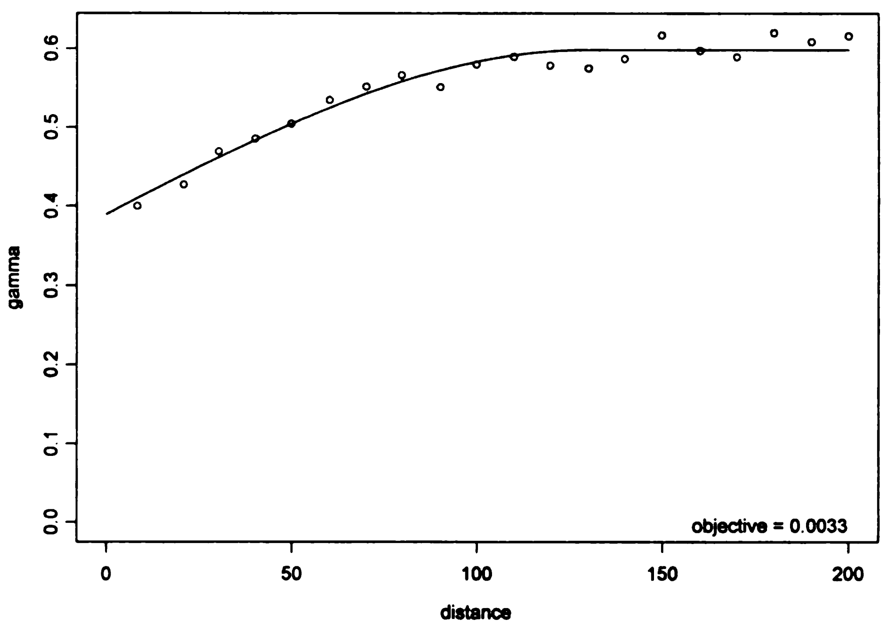

Figure 2.4 Empirical cross-semivariogram and fitted spherical semivariogram function based on transformed larval catches from index sites 1-13.

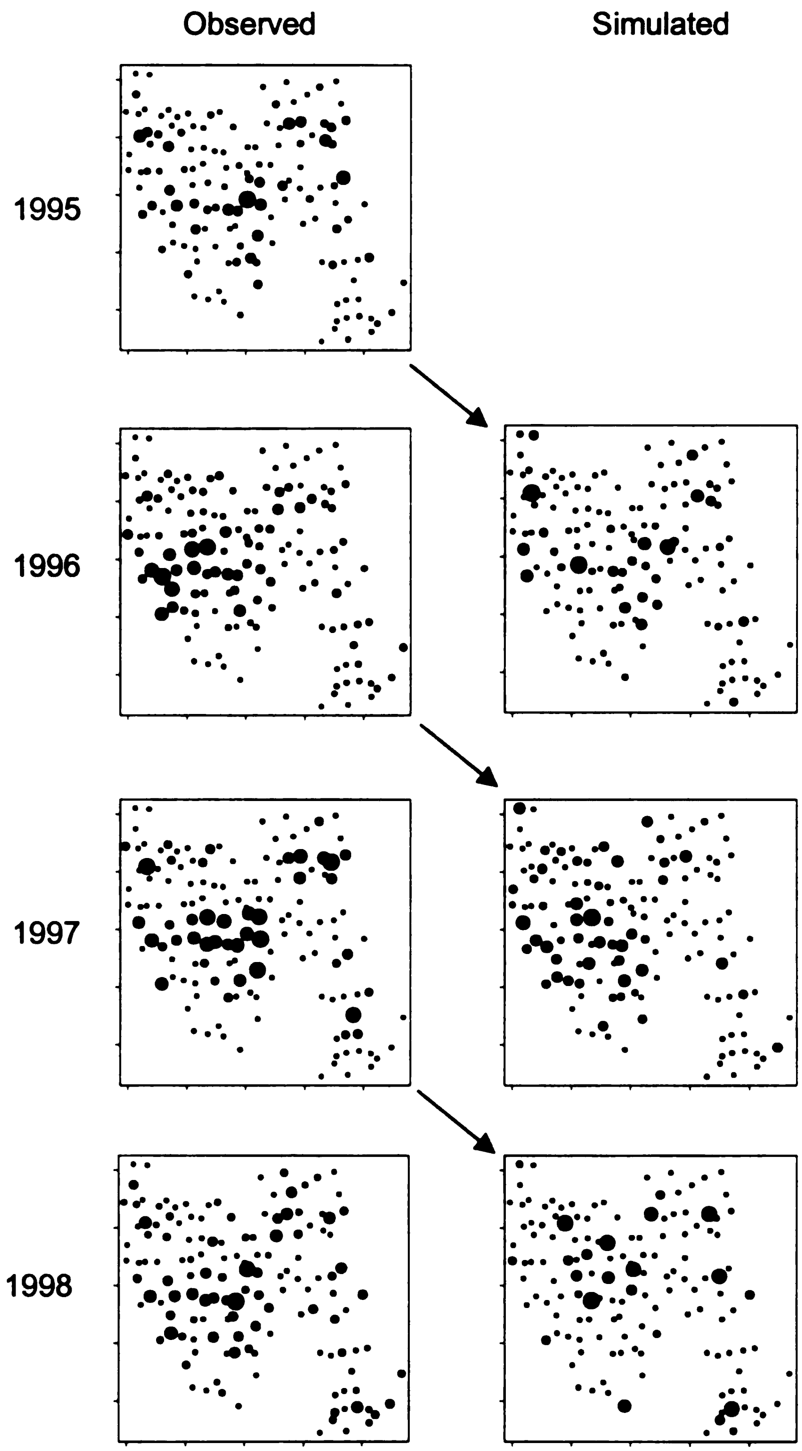

Figure 2.5 Observed and simulated annual distribution and abundance of larvae in index site 6. Dot diameters are proportional to abundance with the largest dots representing adjusted catches of approximately 30 and the smallest dots representing zeros.

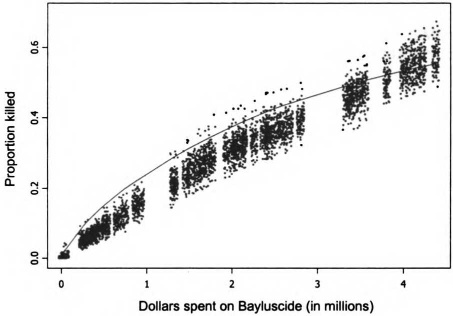

Figure 2.6 Results of one hundred simulations of the percent of larval population targeted versus dollars spent on Bayluscide (dots). Also plotted is the predicted percent targeted versus dollars spent assuming temporal stationarity in larval distribution and abundance.

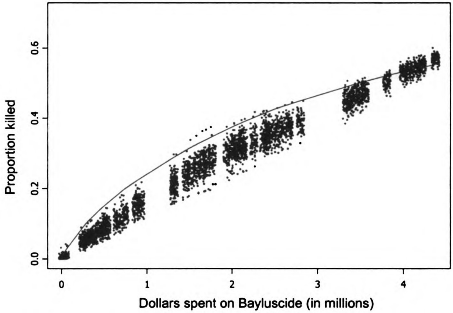

Figure 2.7 Results of one hundred simulations of the percent of larval population targeted versus dollars spent on Bayluscide (dots), holding the total abundance in non-treated areas constant. Also plotted is the predicted percent targeted versus dollars spent assuming temporal stationarity in larval distribution and abundance.

CHAPTER 3

AN APPLICATION OF DECISION ANALYSIS TO THE MANAGEMENT OF ST. MARYS RIVER SEA LAMPREYS (PETROMYZON MARINUS)

Abstract

Controlling the St. Marys River sea lamprey population is one of the most challenging and important problems facing fishery managers in the Great Lakes. In addition to the costs and logistical challenges associated with implementing control options, considerable uncertainties exist in lamprey population dynamics and in control option effectiveness. These uncertainties hinder the ability of scientists to forecast management option performance and thus limit the ability of decision-makers to arrive at well-informed decisions. In this paper, three methods for controlling the St. Marys River sea lamprey population are considered: trapping, releasing sterilized males, and applying Bayluscide. Performance of the management options is measured using forecasts of future lamprey abundance, an economic net benefit statistic, and risk tolerance measures. I found that uncertainty in lamprey population dynamics and in treatment option effectiveness can have large effects on the forecasts of lamprey abundance. In addition, the relative ranking of a particular management option depends on the performance indicator used to evaluate it. Important tradeoffs exist between achieving management objectives and the cost associated with achieving the management objective. Therefore decision-makers will have to evaluate option performance in light of several performance indicators. Incorporating uncertainty into St. Marys River sea lamprey management decisions through decision analysis should improve the quality of the decisions used to manage the system and increase the probability of achieving management objectives.

Introduction

The field of statistical decision theory merges the concepts of utility and subjective probability to quantitatively deal with management problems in the presence of uncertainty (Raiffa and Schlaifer 1961, Morgan and Henrion 1990, Clemen 1996). The method of decision analysis is the application of statistical decision theory to a management decision problem, generally with the following components: a defined set of management options available to the decision-maker, a listing of the alternative states of nature and their associated probabilities which characterize the uncertainty in the problem, a listing of possible outcomes resulting from the management options, and a representation of the decision-maker's utility for the outcomes. The relative merit of each management option is determined by the decision-maker's utility for the expected outcomes.

Uncertainty is inherent in natural resource management decisions. Within the field of fisheries, there is a growing trend towards incorporating uncertainty and risk in the decision-making process (Hilborn et al. 1993). Rosenberg and Restrepo (1994) stress the importance of estimating and communicating uncertainty to fishery managers, who must weigh the benefits, costs, and risks of various management options. They note that while many managed fisheries have incorporated elements of uncertainty and risk analysis, the advice resulting from these analyses needs to be expressed to decision-makers in an effective manner. Providing fishery managers with a quantitative evaluation of the potential consequences of alternative management actions is one of the primary roles of stock assessment scientists (National Research Council Committee on Fish Stock Assessment Methods 1998). Because fisheries management problems typically involve a complex system of biological and socio-economic objectives and constraints, Lane and Stephenson (1998) contend that a conceptual change is necessary, and fisheries management needs to move toward implementing integrated decision-making systems where uncertainty is incorporated. When uncertainty is ignored, or accounted for in an arbitrary fashion, sub-optimal decision options may be selected, leading to outcomes such as unnecessary losses in yields or stock collapse (Frederick and Peterman 1994). Achieving fisheries management goals is more likely when uncertainties are acknowledged, quantified, and accounted for (Peterman et al. 1998).

Several researchers have applied the method of decision analysis to fisheries management problems and found that uncertainty can affect both forecasts and optimal decision-making. McAllister and Peterman (1992) used decision analysis to evaluate the performance of experimental and status quo management strategies for pink salmon (*Oncorhynchus gorbuscha*), while accounting for uncertainty in the cause of decreased mean body weight. They concluded that the expected value of the experimental management strategy was higher than that of the status quo under most conditions. Robb and Peterman (1997) examined uncertainties in the stock-recruitment relationship, annual recruitment, run timing, and catchability for a sockeye salmon (*Oncorhynchus nerka*) fishery through a decision analysis. They found that the shape of the stock-recruitment relationship had a large effect in determining the optimal management option. Hilborn et al. (1994) use decision analysis to examine the performance of different quotas in the presence of uncertainty in virgin stock size. Peterman et al. (1998) summarize three case studies where decision analysis has been applied to fisheries management and recommend that uncertainty be included in the decision making process whenever possible to improve the quality of management decisions.

In this paper I apply decision analysis to one of the major problems confronting fishery managers in the Great Lakes region: controlling sea lampreys (*Petromyzon marinus*) originating from the St. Marys River. The sea lamprey is an exotic fish specie that has decimated fisheries in the Great Lakes through parasitism. The St. Marys River is the primary source of sea lampreys in the Great Lakes. Because of the large number of lampreys that are produced, mortality rates for several managed species (e.g., lake trout and lake whitefish) have risen above target levels. Although a substantial and effective program exists for controlling sea lampreys in other tributaries to Great Lakes, the unique characteristics of the St. Marys make the typical approaches for control inadequate. Reducing the number of sea lampreys in northern Lakes Huron and Michigan is a high priority for fisheries managers in the region.

There are several reasons why decision analysis represents a valuable tool to assist managers who wish to control St. Marys River sea lampreys. First, managing the St. Marys River sea lamprey population is one of the most important problems challenging fisheries managers in the Great Lakes. Connecting Lake Superior to Lake Huron, the St. Marys River has become the largest source of parasitic sea lampreys in the Great Lakes (Schleen 1992, Eshenroder *et al.* 1995). The St. Marys is believed to produce more lampreys than all other tributaries to the Great Lakes combined. As a result of the high number of sea lampreys in northern Lakes Huron and Michigan, rehabilitation of lake trout (*Salvelinus namaycush*) has been difficult due to the predation mortality imposed by lamprey in these areas (Sitar *et al.* 1999, Sitar *et al.* 1997, Eshenroder *et al.* 1995). Thus, the management problem is important enough to justify a concerted effort in evaluating management options through decision analysis. Second, major uncertainties exist regarding lamprey population dynamics and the effectiveness of available management options. As noted above, decision analysis is specifically designed to incorporate uncertainty into the decision-making process. Third, economic constraints demand careful evaluation of all lamprey management decisions in the Great Lakes. Spending too little on control of the St. Marys may result in foregone recovery of lake trout in northern Lake Huron. Conversely, spending too much on the St. Marys takes money away from assessment and control needs of other lamprey populations in the Great Lakes basin. Decision makers want and need to know the expected benefits of directing funds at controlling the St. Marys population in order to properly allocate funds available for control and assessment throughout the basin. Fourth, several well-defined management options are and will be considered as alternatives, effectively bounding the number of options available for consideration. Fifth, specific targets exist for lake trout recovery and sea lamprey suppression in Lake Huron that provide indicators against which the performance of management options can be judged. Each of these issues argues for the application of decision analysis to the problem of managing St. Marys River sea lampreys.

In this paper we summarize our efforts to conduct a decision analysis on the St. Marys River sea lamprey management problem. Our summary follows the main steps in conducting a decision analysis: (1) Identifying alternative management actions; (2) Specifying management objectives; (3) Identifying the uncertain states of nature; (4) Assigning probabilities to the states of nature; (5) Calculating outcomes with a simulation of the fishery; and (6) Using a decision analysis framework to evaluate management options in terms of performance indicators.

Description of the System and Sea Lamprey Control

The St. Marys River is believed to be the primary source of parasitic sea lampreys in northern Lake Huron (Schleen 1992, Eshenroder *et al.* 1995). The St. Marys River is the outflow of Lake Superior, beginning at the lake's eastern tip. After a distance of roughly 40 km, the river flows into an area known as the North Channel of Lake Huron. The river's mean annual discharge is 2,140 m^3/s, over 20 times the largest flow previously treated with the chemical 3-trifluoromethyl-4-nitrophenol (TFM), the primary method for controlling sea lampreys in the Great Lakes. The large size and high flow of the St. Marys rendered conventional control methods inappropriate and new approaches needed to be developed.

Anadromous in their original range, sea lampreys have a life history adapted to living in the Great Lakes (Lawrie 1970). In late spring-early summer, adult sea lampreys move up Great Lakes tributaries to spawn. During spawning, eggs are deposited into nests. Viable eggs develop into larvae, which leave the nests but remain in the streambed for a period of 3-17 years. Once they obtain sufficient size and energy reserves, they undergo a process of metamorphosis from detrital to a parasitic feeding form. Following metamorphosis, juvenile lampreys leave their natal stream to parasitically feed in the Great Lakes. During this time they parasitize host species (e.g., lake trout, lake whitefish, salmonids) for a period of approximately 18 months, often causing death of the host.

Sea lamprey life history characteristics are exploited to achieve population control in the Great Lakes. Barrier dams and weirs are control methods designed to block lamprey access to suitable spawning locations. Trapping of adults moving upstream is also used to help control the number of spawning individuals. Releasing chemically sterilized males into spawning populations is a control method used to interfere with reproductive success. However, the primary method used to control lamprey populations in the Great Lakes is the lampricide, TFM. This liquid chemical is applied to Great Lakes tributaries to kill larval lampreys in the streambeds and has been very effective in controlling lamprey populations. Another lampricide, the 2-aminoethanol salt of 2',5-dichloro-4'-nitrosalicylanilde (Bayluscide), achieves the same effect of killing larval lampreys, but can be applied in the form of dry granules. Because of this, Bayluscide can be applied to small, specific areas of high larval density, whereas TFM is applied at the whole tributary level.

The sea lamprey control program in the Great Lakes is directed and coordinated by the Great Lakes Fishery Commission (GLFC), a bi-national governmental organization. In 1997 the GLFC adopted a control strategy for the St. Marys River that included trapping adults, releasing sterilized males, and applying Bayluscide to approximately 1000 ha of high-density larval habitat in the river during 1998 and 1999. The decision to adopt this strategy was based on deterministic models presented to the GLFC Commissioners that forecasted the effects of various management options along with a cost-benefit analysis of those management options. An ongoing assessment program is in place to evaluate the effects of this control strategy, but regardless of the outcome, future control decisions will be necessary. The decision analysis presented here is intended to help inform decision-makers with these future decisions.

Conducting the Decision Analysis

Identifying alternative management actions

In May 1998, we convened a meeting of scientists, agency management personnel, and other stakeholders to explain our decision analysis approach and identify a list of alternative management actions that could be used to control St. Marys River sea lampreys in the future. The group identified trapping, sterile male releases, and the application of Bayluscide as the primary actions that could be used. There was considerable interest in examining the effects of various levels of use and timing of these actions. The sterile male option relies on obtaining trapped animals from the St. Marys and other Great Lakes tributaries. Because a large portion of the animals used in the sterile male program comes from the St. Marys, the intensity of the sterile male release technique (SMRT) is not independent of the intensity of trapping. Therefore the group believed that different intensity levels of trapping and SMRT should be examined in concert with each other. The group also argued that trapping (and therefore SMRT) should be considered as a management action regardless of whether Bayluscide applications are considered because of the relatively low costs associated with trapping and the large capital investment of the traps currently in place. The intensity and timing of Bayluscide applications are independent of both trapping and SMRT, and therefore could be investigated at various intensity levels without defining a relationship between Bayluscide and the other control actions. The option of treating the river with TFM was briefly discussed, but the group concluded that this potential action was cost prohibitive and not likely to be effective as a future control technique.

Specifying management objectives

Defining the set of management objectives proved a more difficult challenge for the group. Ultimately, they agreed that the goal of controlling lamprey populations in the Great Lakes is to provide the opportunity for a healthy, productive fish community. Restoring lake trout in northern Lakes Huron and Michigan is a particular concern, and therefore some believed that creating self-sustaining lake trout populations should be a management objective. However, issues of commercial and recreational fishing levels, stocking levels, and the lack of natural spawning populations all affect lake trout restoration separate from the issue of lamprey control. As a result of discussions on this topic, the group agreed that while restoring lake trout was indeed a management goal, it was too broad a topic to serve as a management objective in this particular instance.

Eventually, the group agreed on an objective of reducing the number of parasitic sea lampreys in Lake Huron. Setting this as the objective implied that reducing the number of lampreys would aid lake trout recovery efforts in Lake Huron. The group discussed several ways to measure achievement of the objective by various management options. The timing and magnitude of the reductions were regarded as important components of measuring performance, as well as the probability that a particular management action will be successful in achieving the objective. Recent agreements between the State of Michigan and several Native American tribes have implicitly established target levels for future lamprey abundance in Lakes Huron and Michigan.

The group expressed an interest in using these targets as a measure of option performance. Because greater reductions are generally associated with greater control costs, some expressed an interest in incorporating economic factors such as the economic injury level approach described by Koonce et al. (1993). We describe the specific details of our methods for evaluating management option performance in light of the general objective of lamprey suppression below.

Identifying the uncertain states of nature

After discussing the uncertainties that could have effects on the St. Marys River lamprey population, the group identified a set of critical uncertainties that needed to be incorporated into the decision analysis. This exercise was important for narrowing the large number of potential uncertainties down to a number manageable in a decision analysis. The group identified two principal uncertainties. The first was uncertainty in St. Marys River lamprey population dynamics, particularly the stock-recruitment relationship. The group recognized that little is known about lamprey demographic rates, their productivity, and their degree of compensation (i.e., larval density-dependence). These uncertainties limit the ability to forecast the effects of implementing different treatment options, especially those options that affect adults attempting to spawn (e.g., trapping and SMRT). The second major uncertainty identified by the group was uncertainty in larval distribution. During 1993-1996, nearly 12,000 locations in the St. Marys River were sampled to determine the distribution of larvae. The Bayluscide treatment that took place in 1998 and 1999 only targeted areas identified as having high larval densities based on the historical survey. The effectiveness of any Bayluscide treatment depends on the distribution of larvae in the river just prior to treatment, and any differences due to spatial or temporal variability may reduce treatment effectiveness. The group agreed that a characterization of this uncertainty would be critical for evaluating the likely effects of Bayluscide treatments. To be consistent, the group agreed that uncertainty in trapping and SMRT effectiveness should also be included in the decision analysis. Similar to the larval distribution uncertainty, trapping and SMRT uncertainties deal with implementation error. That is, how well will a control method actually perform if it is selected? Thus, four uncertainties were identified to be included in the decision analysis: demographic and stock-recruitment uncertainty, larval distribution uncertainty, trapping uncertainty, and SMRT uncertainty.

Assigning probabilities to the states of nature

My first analytical task was to characterize the uncertainty in demographics and the stock-recruit relationship for St. Marys River sea lampreys. In doing this, my first objective was to develop sets of parameter values that span the range of values possibly underlying the population dynamics of St. Marys River sea lampreys. In the terminology of decision analysis, these sets of parameter values are known as "alternative states of nature." From an ecological perspective, these sets represent alternative hypotheses about the abundance and vital rates of this sea lamprey population.

The methods describing the quantification of the demographic and stock-recruit uncertainty are presented in Chapter 1 of this dissertation. To summarize, I built an age-structured population model that reflects the life history of St. Marys River sea lampreys, utilizing six sources of data to fit demographic parameters. These demographic parameters included time series of age-0 abundance from 1967 to 1996, initial age composition in 1966, a constant larval natural mortality rate, two parameters describing the probability of larval metamorphosis as a function of age, and a parameter describing the proportion of metamorphosed juvenile lampreys that survive to maturity and return to the St. Marys River to spawn. Using a nonlinear optimization program, I obtained the parameter estimates that maximized the objective function (i.e., the set of parameter estimates that best fit the six data sources). I refer to this set of parameters values as the modal posterior density (MPD) estimates.

To characterize demographic uncertainty, I used Monte Carlo Markov Chain (MCMC) methods to obtain 1000 samples (each sample containing the full set of demographic parameters) from the approximate joint posterior distribution of the demographic parameters. The 1000 samples were independent random samples from the autocorrelated chain of 12,000 samples described in Chapter 1. With the resulting parameter estimates, I reconstructed 1000 stock and recruitment data sets. The stock-recruit data sets could be determined because the age-0 recruitments were estimated parameters and the stock sizes could be calculated from the recruitment time series and the demographic parameters. I characterized the stock-recruit uncertainty by estimating parameters of a stock-recruit function for each data set. I then obtained estimates of α_i, β_i, and σ^2_i ($i = 1, 2, \ldots, 1000$) for a Ricker model of the form

$$R = S\exp(\alpha - \beta S + \varepsilon) \qquad (1)$$

where R is the number of age-0 larvae produced, S is the number of female spawners that produced R, and log (ε) is distributed N (0, σ^2). I used the set of 1000 demographic parameter estimates and the associated stock-recruit parameter estimates to characterize the uncertainty in St. Marys River lamprey population dynamics. The MPD combined estimates represented the most likely state of nature, while the other sets represented alternative (possible) states of nature. Because the HPD estimates are biased estimates of the expected value for each of the parameters, I also consider a set of estimates that are the means from each distribution of parameter values (termed "average parameters"). While the average parameters do not maintain the full covariance structure of the joint posterior distribution, they may better approximate the central tendency of the joint posterior than the maximum likelihood (HPD) estimates.

The second source of uncertainty to be characterized was the spatial and temporal uncertainty in larval lamprey distribution and abundance. The principal objective in the estimation of this uncertainty was to characterize the implementation uncertainty associated with Bayluscide applications. In other words, how well will a Bayluscide treatment perform if it is chosen as a management option in the future, given the spatial and temporal variability in larval distribution and abundance?

The methods used to describe this uncertainty are presented in Chapter 2. I used two spatially-referenced data sets containing information on larval distribution and abundance. One data set contained the results of annual samples collected from small index sites in the river. The other data set contained the results of an extensive, complete sampling of the river that took place 1993-1996. Using the index site data, I estimated a model that described the annual changes in abundance at individual sample locations based on habitat quality at those locations, the measured abundance at those locations the previous year, and the inverse distance-weighted average of abundance at neighboring locations. I applied this model to the historic survey of the whole river to generate a series of maps representing the possible distribution and abundance of larvae in 1999, the year of the major treatment of the St. Marys with Bayluscide. I then simulated the application of Bayluscide to the simulated maps, and calculated the proportion of larvae that would have been killed (i.e., treatment effectiveness) for each map. The distribution of effectiveness values for a given level of treatment characterizes the implementation uncertainty associated with different levels of Bayluscide applications.

The simulated values of the proportion killed at the highest level of Bayluscide treatment appeared to be normally distributed with a mean of 0.57 and a standard deviation of 0.04. Biologists with the St. Marys River Task Force separately estimated the proportion killed at the level of Bayluscide treatment that was selected by the decision-makers (i.e., a large-scale treatment) to be 0.55 (Bergstedt et al. 1998). The empirical estimate for the actual proportion killed was 0.45 (Fodale et al., *in review*). I assume that the variability about the mean proportion killed at the large-scale treatment level would be similar to the variability about the realized proportion killed. Therefore I characterize the implementation uncertainty associated with large-scale Bayluscide treatments to be normally distributed with a mean of 0.45 and a standard deviation of 0.04.

The third source of uncertainty to be characterized was the implementation uncertainty associated with trapping efficiency. During 1991-2000 the average trapping efficiency (i.e., the proportion of the spawning population removed by trapping) in the St. Marys River was nearly 40% (Figure 3.1). Annually, efficiencies ranged from 20% to 54%. Based on a histogram plot of these values, they appeared to come from a uniform distribution. Therefore I characterize the implementation errors associated with trapping as uniformly distributed from –18% to +18%. To characterize the implementation uncertainty associated with a particular level of trapping, I take the target level and add a randomly selected implementation error from the uniform distribution specified above. In the decision analysis I only examine trapping levels of 40% and 70%. Because the errors come from a uniform distribution, each alternative state of nature (i.e., combination of target efficiency and implementation error) has equal probability.

The fourth source of uncertainty to be characterized was the implementation uncertainty associated with SMRT effectiveness. Biologists with the St. Marys River Task Force have collected data on SMRT effectiveness in the St. Marys River 1992-2000. Complications associated with estimating the number of spawners in 1997 resulted in an unreliable estimate of SMRT effectiveness (Mike Twohey, personal communication). Therefore, this year's data was excluded from my analyses. The data include an estimate of the ratio of sterile:fertile males in the spawning population based on mark-recapture methods. For example, a sterile:fertile ratio of 3 implies that there are 3 sterilized males for every one fertile male in the spawning population. The theoretical proportion of viable eggs in a population where sterilized males compete with fertile males can be estimated using the equation

$$PV = \frac{1}{1 + SFR} \qquad (2)$$

where PV is the proportion of eggs that is viable and SFR is the sterile:fertile ratio. Using the example above, a sterile:fertile ratio of 3 would result in only 25% of the eggs being viable.

In addition to the estimated SMRT ratio in the river, biologists with the Task Force empirically estimated the annual PV by sampling spawning nests and comparing the number of viable eggs to the total number of eggs in the nests. Even in the absence of sterilized males, nests showed viabilities of considerably less than 100% (43.4% is the estimate for incomplete viability in the St. Marys River nests not visited by sterile males). After adjusting for incomplete viability, for each year I calculated the SMRT ratio that would have resulted in the empirical estimates for *PV* based on the nest sampling. Combining the two sources of data resulted in an estimated SMRT ratio based on mark-recapture and an estimated SMRT ratio based on the egg viability sampling (Figure 3.2). I then calculated the percent deviation of the SMRT ratio based on nest sampling from the SMRT ratio based on mark-recapture (Figure 3.3). Essentially these values form an estimate of the deviations from the assumed relationship (Equation 2) and form the implementation error associated with SMRT. The mark-recapture SMRT ratio provides an estimate of theoretical performance, while the egg viability SMRT ratio provides an estimate of actual performance (i.e., the reduction in viability). A regression of the percent deviation versus the mark-recapture ratio did not reveal a slope significantly different from zero, indicating that the errors did not follow a trend over the range of the mark-recapture ratios. However, I was unable to determine the distribution of the errors. Therefore I assumed that the observed errors define the distribution and rely on bootstrapping to quantify the implementation uncertainty associated with a target level for SMRT. Operationally, I would take the target ratio and multiply it by a randomly sampled percent deviation (sampled using bootstrapping with replacement) to calculate the *PV* associated with a given target for the SMRT ratio.

Calculating outcomes with a simulation of the fishery

I used a simulation model, similar to the demographic parameter estimation model, to forecast future abundance of parasitic sea lamprey in Lake Huron. Whereas the parameter estimation model (Chapter 1) was utilized for reconstructing historic population dynamics, the simulation model was used to forecast future population dynamics in light of the uncertainties identified above and the effects of different control options.

The simulation model shared the same age-structure characteristics and life-history basis as the parameter estimation model. I modeled larvae ages 0-6 in the St. Marys River with age-specific abundance determined by the previous year's abundance minus losses due to natural mortality and emigration (i.e., metamorphosis). Larvae ages 4-6 underwent the process of metamorphosis according to the estimated parameters that define the probability of metamorphosis as a function of age. Juvenile (newly metamorphosed) lampreys that leave the river in any particular year form the parasitic population the following year, plus an addition of 30,000 parasites from other Lake Huron tributaries. In the next year, a proportion of the total Lake Huron parasitic population migrates to the St. Marys River to spawn. Trapping reduces the number of female spawners, which produce age-0 recruits according to the parameters of the Ricker stock-recruit relationship. The number of viable age-0 recruits is determined by the SMRT ratio, if SMRT is selected as a treatment option. If Bayluscide is selected as a treatment option, then a portion (45% +/- the Bayluscide implementation error) of the larval population is removed during the year of application.

Some calculations were necessary to set up the initial conditions, defined as the abundance of lampreys in the river and Lake Huron in 2000. The initial conditions were calculated for each of the 1000 demographic parameter sets, termed "demographic models." Each demographic model was associated with an estimate of the larval age composition in 1996. The numbers of age-0 recruits for 1997-2000 were determined by the stock-recruit parameters for each demographic model and the empirical estimates of the number of spawning lamprey present in each of those years. The stock-recruit parameters and the forecasted number of spawners determined recruitment subsequent to 2000. In setting up the initial conditions, I incorporated the estimated effects of the Bayluscide treatments that took place during 1998 and 1999.

As mentioned earlier, one of the 1000 demographic models represented the modal posterior density estimates for the demographic parameters underlying sea lamprey population dynamics. I designed the simulation model in such a way that forecasts could be generated using only this model or using all 1000 demographic models. The timeframe considered in the simulation model forecasts was year 2001 through 2030.

Using a decision analysis framework to evaluate management options

To evaluate the performance of management options under uncertainty, I incorporated the four uncertainties described above into a decision analysis framework. Figure 3.4 offers a depiction of this framework in the form of a decision tree. Uncertainties are represented by the circular "uncertainty nodes" while alternative management options arise out of the square management options box. Outcomes (defined here as abundance of lamprey in Lake Huron 2001-2030) are calculated for each branch arising from the uncertainty nodes and for each management option. A Monte Carlo approach is used to obtain sample values at each of the uncertainty nodes. Values at these nodes are sampled according to their probability distribution defined above.

Based on the management options under consideration, individual uncertainties may or may not be included in the outcome calculations. For example, to implement no control is one potential management option. To calculate the range of possible outcomes associated with no control, I simply calculate lamprey trajectories sampling the demographic model uncertainty distribution. When trapping and SMRT options are under consideration, I calculate lamprey trajectories sampling the range of trapping uncertainty, SMRT uncertainty, and demographic model uncertainty. Likewise, all four uncertainties are sampled for management options that consider trapping, SMRT, and Bayluscide applications.

Measuring the performance of any management option depends critically upon the utility decision-makers have for the various performance indicators provided. Different performance indicators will be more meaningful to individual decision-makers than other performance indicators. Determining which management option is "optimal" may depend on which performance indicator is chosen. A management options that maximizes one performance indicator may minimize other performance measures. The decision to choose a particular management option will almost invariably involve trade-offs in the performance measures. In this decision analysis, the management objective was to reduce the number of parasitic sea lamprey in Lake Huron. I attempted to provide a suite of performance indicators from which individual decision-makers could choose indicators that they believed to be most meaningful. The indicators fall into three general categories: abundance trajectories, economic cost/benefit rankings, and risk-tolerance measures.

Abundance trajectories represent trends in the abundance of parasitic sea lamprey in Lake Huron over time. The principal type of abundance trajectory that I used was the average parasitic abundance. To calculate this trajectory, I averaged, by year, the individual outcomes across realizations of the uncertain states of nature for each management option under consideration. The values in this trajectory represent how many parasitic lampreys would be present in Lake Huron in any particular year, on average. The second type of abundance trajectory that I used was the median parasitic abundance. To calculate this trajectory, I estimated the median abundance, by year, across realizations of the uncertain states of nature for each management option under consideration. By definition, half of the outcomes associated with the management option were above the year-specific median value and half were below. Differences exist between the implications associated with using the median versus using the average abundance. Individual decision-makers may prefer one over the other in evaluating management option performance.

For sea lamprey management, there will always be a tradeoff between the benefits and costs of control. The most effective management options, in terms of suppressing the population by the greatest amount, are also the most expensive. Following the tenets of integrated pest management, the aim of the sea lamprey control program has been to achieve a level of control that maximizes the difference between benefits and costs. My second type of performance indicator attempts to examine this tradeoff between benefits and costs.

When the GLFC Commissioners chose the control strategy for the St. Marys River, they were supplied with graphs that depicted the relative abundance of lamprey over time for each management option, along with its associated cost (Figure 3.5). In the end, they chose to go with the most effective option (in terms of reducing lamprey by the greatest amount in the shortest period of time), but it was also the most expensive option available. I contend that this decision provides insight to the value the decision-makers held for reducing lamprey. A simple way to look at benefits is through the equation

$$\text{Net benefit} = \text{Outcome} * \text{Value} - \text{Cost} \qquad (3)$$

I assume that the decision-makers implicitly evaluated the net benefits associated with each of the different treatment options, and chose the option with the greatest net benefit. In this case, the outcome was the relative reduction in parasitic abundance and the cost was the amount of money that the option required for implementation. The only unknown is the value that the decision-makers held for reductions in lamprey.

One way to solve for this unknown is to examine the problem using the concept of implied value. Because the decision-makers chose the most expensive option presented for consideration over options that were also effective (albeit to a lesser degree), this suggests that the decision-makers associated a high value with lamprey reductions. By substituting different dollar amounts for the value unknown in the net benefit equation above, we can estimate the minimum dollar value where the net benefit for the most expensive treatment option exceeds the net benefit for the next most expensive treatment option. The value at which this occurs is termed the implied value. Values higher than the implied value increase the difference in net benefit between the most expensive and next best treatment options. Therefore the implied value represents a minimum value that the decision-makers held for lamprey reductions in order to justify choosing the most expensive treatment option.

Discussions with the decision-makers revealed that they were mainly concerned with the performance of the management options over a 15 year period (Gavin Christie, personal communication). In addition, they preferred options that reduced lamprey faster over options that reduced lamprey by the same amount, but over a longer period of time. This difference in preference as a function of timing implies that the decision-makers were employing some sort of discounting. That is, immediate benefits were valued higher than benefits deferred into the future.

To calculate an implied value that the decision-makers may have used, I estimated the net benefits associated with the two most expensive treatment options considered in 1997. The more expensive option consisted of a 40% rate of trapping, a 2.8 SMRT ratio, and removing 55% of the larval population with Bayluscide. The next most expensive option consisted of a 40% rate of trapping and a 2.8 SMRT ratio (Figure 3.5). Using the same graph as was presented to the decision-makers in 1997 (Figure 3.5) and my estimate of the number of parasites present in 1997, I calculated the discounted, 15-year total reduction in parasitic lamprey for both treatment options as compared to no control. I used a discount rate of 6% and a 1997 parasitic abundance of 500,000 lampreys (a reasonable number based on my model estimates). By substitution, I determined that the implied value was $15.65 per additional lamprey removed by control. Values greater than this amount had a higher net benefit for the most expensive treatment option (trapping, SMRT, and Bayluscide application) than the alternative treatment option (trapping and SMRT). With an estimate of the implied value, net benefits of future management options can be estimated in a similar fashion. The net benefit calculation forms my cost/benefit performance indicator for the different treatment options.

The final group of performance indicators is risk-tolerance measures. As a result of the negations between the State of Michigan and several Native American tribes regarding treaty-related fishing rights (termed the "Consent Agreement"), there are implied targets for reductions in lamprey abundance in Lake Huron for the years 2006 and 2012. These targets are proportional to the average abundance of lamprey in Lake Huron during 1998-2000. My estimate for average abundance during this time period is 658,000. The Consent Agreement implies lamprey abundance targets of 183,000 in 2006 and 114,000 in 2012. As a performance indicator, for each management option I calculate the proportion of cases where the outcomes are at or below the Consent Agreement targets established for 2006 and 2012. These proportions represent an estimate of the probability that the targets will be achieved by the management options under consideration. In a related measure of risk-tolerance, I graph the probability of being below a range of parasitic abundances in the years 2012 and 2030. These graphs provide indications of performance based on the risk of exceeding various levels of parasitic abundance for the management options under consideration.

<u>Simulation details and management option notation</u>

Within the simulation model, a standard run consisted of 100,000 30-year forecasts for each management option. This total number is the result of 100 realizations of the stock-recruit process error term for each of the 1,000 demographic models (100 *

1,000 = 100,000). Each forecast randomly samples the distributions of the implementation uncertainties defined above when applicable.

Three options are available for controlling sea lampreys from the St. Marys River: trapping, SMRT, and Bayluscide applications. The objective of this decision analysis is to compare different levels of use and timing for these control options. I considered nine options and use a shorthand notation to refer to these options (Table 3.1). The notation consists of the proportion removed by trapping followed by a "/", the target SMRT ratio followed by a "/", and the proportion of the larval population removed by Bayluscide followed by the timing of the Bayluscide applications.

Costs for the various treatment options were estimated using the data contained in Bergstedt et al. (1998). A linear regression was fit to the costs for three levels of SMRT (0.67, 2.77, and 3.8) and was extended to predict the costs associated with SMRT ratios of 4:1 and 7:1. The cost of a high level of trapping (70%) was based on expert opinions (St. Marys River Decision Analysis Workshop, April 24-25, 2001). To provide a relative measure of the total costs associated with the treatment options, costs were annualized over the thirty-year period considered in this study. When estimating net benefits for the treatment options, both the costs and benefits (the reduction in the number of lamprey compared to no control) were discounted. I used a discount rate of 6%.

Results

The results of the simulations that included all of the defined uncertainties and all of the treatment options revealed several interesting patterns (Figure 3.6). As expected, maximum population suppression was associated with the most expensive treatment option (0.7 / 7 / 0.45 every 4, 2004-2030). However, options that included trapping at 70% and a SMRT ratio of 7 performed nearly as well, even without the application of Bayluscide (e.g., 0.7 / 7 / 0). Options that included trapping at 40% and a SMRT ratio of 4 displayed relatively poor performance, with the exception of the 0.4 / 4 / 0.45 every 4, 2004-2030 option. But even the worst option (0.4 / 4 / 0) was able to achieve suppression levels that were, on average, 50% of the no control levels.

The results presented in Figure 3.6 incorporate the effects of all the uncertainties that were considered in this decision analysis. When I examined the uncertainties individually, I found that not all uncertainties affect the average number of parasites over time. Average trajectories for treatment options where uncertainties were characterized using symmetrical distributions (i.e., the trapping uncertainty and the Bayluscide uncertainty) did not differ from average trajectories where these uncertainties were ignored. However, uncertainty did make a difference in the average trajectories when an asymmetric distribution was used to characterize the uncertainty (i.e., the demographic uncertainty and the SMRT uncertainty).

Figure 3.7 shows the forecasted trajectories for no control and low levels of trapping and SMRT, with and without uncertainty in trapping and SMRT. The differences between those simulations with uncertainty and those without are due to the asymmetric distribution that was used to characterize SMRT effectiveness (Frederick and Peterman 1994). The asymmetry is due to the differences between observed and theoretical SMRT effectives, and is a combination of process error and model error. The process error is a result of natural variability in the underlying relationship while the model error is a result of not having the correct model describing how SMRT ratios translate into reductions in viable eggs. Of the seven estimates of the SMRT percent deviation, five are negative (Figure 3.3). When these negative deviations are randomly selected through bootstrapping, the predicted effectiveness of SMRT is reduced and therefore greater lamprey abundances would be forecasted.

Figure 3.8 shows the forecasted trajectories for the no control management option, using various descriptions of the demographic uncertainty. When I assume that only the maximum likelihood model (the MPD model) describes the stock-recruitment relationship and the associated demographic rates, trajectories are lower than when I consider all models. Using the "average parameters" set is a better approximation to the full uncertainty (all models) results, but is biased low beyond year 2015. These effects are due to a complex asymmetry in the parameters describing the demographic uncertainty. Allowing for demographic uncertainty results in less optimistic forecasts of lamprey abundance than if the MPD or average parameters models are used.

The results of the simulations are also dependent upon the statistic used to measure central tendency. The distribution of abundance forecasts within most years showed positive skewness. This observation is reflected in Figure 3.9, where the mean and median forecasts are compared for a no control option and a 0.4 / 4 / 0 option. The mean forecasts for the no control option approach 570,000 whereas the median forecasts approach 270,000. Similarly, the mean of the 0.4 / 4 / 0 option forecasts is around 490,000 whereas the median forecast values lie around 130,000. With positively skewed distributions, the mean is greater than the median. The median may be a more useful indicator of performance than the mean for decision-makers concerned with the frequency of high and low abundances, but not so much concerned with the average abundance across simulations.

By calculating the mean net benefits associated with each option, I was able to rank the options and examine the sensitivity of this ranking to alternative assumptions of the implied value, the time horizon, and the discount rate (Table 3.2). Option 5 was generally ranked highest over the range of assumptions examined within the sensitivity analysis. Option 6 was also ranked highly and was ranked highest for my approximation of the values, time horizon, and discount rate associated with the 1997 decision by the GLFC Commissioners. The 0.4 / 4 / 0 option ranked lowest across all assumptions. However, there is considerable variation and overlap in the net benefits across simulations for the treatment options (Figure 3.10). While there are slight differences in the mean net benefits for each treatment option (Table 3.2), the variation in net benefits across simulations is large, making the differences in mean option performance negligible.

In terms of achieving the Consent Agreement targets for lamprey abundance, several of the options show a high probability of success (Table 3.3). While option 7 had the highest chance of meeting both targets, option 6 also showed a high probability of success. With no control, there is a 50% chance of meeting the 2006 target, but only a 18% chance of meeting the 2012 target. Option 4 had a high probability of meeting the 2006 target at relatively low cost. Interestingly, option 9 (the most expensive option) did not perform much better (in terms of meeting the Consent Agreement goals) than option 5, at half the cost.

Another way to view these same results is presented in Figure 3.11. The x-axis represents the number of parasites in 2012 while the y-axis represents the proportion of simulation cases where the parasitic abundance was less than the values on the x-axis. The vertical arrow marks the location of the Consent Agreement target for 2012. For example, there is a 60% chance of less than 200,000 parasites in 2012 when the 0.4 / 4 / 0 option is selected. The y-values at the intersections of the vertical arrow with the lines representing the treatment options are the same as those values listed in Table 3.3. Similarly, Figure 3.12 shows the chances of exceeding parasite abundances in 2030 for the different treatment options. Notice that over a longer time frame, the performance of a Bayluscide application in 2004 does not differ from relying only on trapping and SMRT at the same levels.

Discussion

Over the last decade the sea lamprey control program has moved towards incorporating greater quantitative rigor into their assessment and treatment activities. The St. Marys River provides an excellent example of the use of quantitative methods and assessment tools to address the problems confronting natural resource management. When it became apparent that something needed to be done about sea lampreys in the St. Marys River, a Task Force was formed and began the long process of identifying and addressing the most critical knowledge gaps about the system. Through the studies that followed, knowledge about the system grew tremendously. When the time arrived for decision-makers to evaluate alternative control strategies, scientists and agency personnel were well prepared to communicate their best estimates of treatment option performance (Bergstedt et al. 1998).

This decision analysis represents the next logical step along the road of providing decision-makers with the information necessary to make good decisions. The problem of the St. Marys River will persist and future strategic decisions will be necessary. The decision analysis that I have presented in this paper serves as a tool that can be used to investigate the expected performance of alternative control strategies in the presence of uncertainties in demographic rates and in management option implementation. Although the GLFC did consider uncertainty when evaluating the decision options in 1997, it was done subjectively (Bergstedt et al. 1998). In the presentation of each management option, the GLFC provided a qualitative assessment of the uncertainty associated with it. This uncertainty assessment likely influenced the decision-maker's evaluation of the treatment options under consideration. The decision analysis that I present formalizes and quantifies that uncertainty assessment. I have also presented several indicators that can be used by decision-makers to evaluate the performance of alternative management options. Both of these features of a decision analysis should help decision-makers to consider the trade-offs when choosing a strategy that best meets their objectives.

One important issue to be recognized when using this decision analysis is the feasibility of achieving the targeted levels for the control methods. In the analyses, I assumed that the control agents would be able to achieve the specified levels and timing of trapping, SMRT, and Bayluscide applications. Based on the recommendations and knowledge of management personnel, I limited the range of control effort to that which realistically could be achieved. However, up to this point in time, the control program has not been able to trap 70% of the spawning population, or implement a 7:1 SMRT ratio. Likewise, removing 45% of the larvae with Bayluscide every two years may be difficult to achieve. As the number of larvae in the river is reduced, more area may need to be treated to achieve the target control level. Issues such as this are not reflected in the analysis because I assume that the specified treatment levels and timing are achieved, albeit with some measure of error, when evaluating option performance.

Another important issue is the limitation of the net benefit calculations. The implied value that I calculated was based on the 1997 decision. It is not the same as the economic injury level proposed by Koonce et al. (1993) and should not be construed as a true economic value for lamprey suppression. It served as a first approximation for the values that decision-makers apparently held for comparisons among a limited set of management options. A more comprehensive analysis of the economic values associated with sea lamprey reductions (and lake trout restoration) is ultimately needed to properly examinine management option performance.

One important finding of this study was the degree of overlap in the range of estimated net benefits among treatment options. While certain treatment options may perform better on average (in terms of maximizing the average net benefit), the high amount of overlap in net benefits among decision options suggests that these differences are small relative to their variability. The variability in net benefits may itself be an important consideration for decision-makers, however. An option that has less variability in net benefits but a lower average value may be preferable to an option with more variability and a higher average value. Preferences regarding this variation around the mean values relate to the economic risk tolerances of the decision-maker. In spite of this, economic considerations may not strongly influence decision-maker choices.

The parameter estimates and model relationships that I used in this project represent a summary of our current understanding of lamprey demographics and control method effectiveness. However, the decision analysis model that I developed is a flexible one that can be re-parameterized as new information becomes available. Each of the uncertainties that I considered includes a combination of process error, model error, and measurement error. Of these three types, both model error and measurement error can be reduced by scientific investigations. If the costs and benefits of these investigations can be estimated, then this decision analysis model can be used for prioritizing future studies aimed at reducing uncertainty using "value of information" calculations (Morgan and Henrion 1990). This model could also be used for examining adaptive management opportunities (Walters 1986). By altering the number of spawners through trapping and SMRT and observing the effects on recruitment, it may be possible to learn about the shape of the underlying stock-recruitment relationship for St. Marys River sea lampreys (Smith and Walters 1980). However, the high variability in recruitment for sea lamprey (see Chapter 1) may hinder learning about the stock-recruitment relationship for this population (Hinrichsen 2001).

Similar to the findings of Robb and Peterman (1997), I found that uncertainty in the stock-recruit relationship affected the forecasts of parasitic abundance. In addition, I found that uncertainty in SMRT effectiveness affected forecasts. Ignoring these two uncertainties would have resulted in more optimistic forecasts of parasitic abundance than forecasts that ignored these uncertainties. As a general recommendation, it appears that stock-recruitment uncertainty should routinely be included in the evaluations of fishery management options. When other asymmetric uncertainties affect forecasts (as with SMRT), then these uncertainties should be incorporated as well.

The sea lamprey population of the St. Marys River will continue to present challenges for Great Lakes fishery managers. The analysis presented in this dissertation should help managers as they consider the risks associated with alternative control strategies. The development of these decision and simulation models represents an incremental step forward. As knowledge about the system and the processes that govern its dynamics advances, these models can and should be revised to reflect changes in understanding. Hopefully, as the models improve, decision-making will also improve, and a healthier Great Lakes ecosystem will be the result.

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Table 3.1 A listing of the nine management options under consideration in the decision analysis along with the specific levels and timing associated with each control method.

Option Number	Management Option	Trapping rate	SMRT ratio	Proportion killed with Bayluscide	Timing of Bayluscide applications
1	No control	0.00	0.0	0.00	N/A
2	0.4 / 4 / 0	0.40	4.0	0.00	N/A
3	0.7 / 7 / 0	0.70	7.0	0.00	N/A
4	0.4 / 4 / 0.45 once in 2004	0.40	4.0	0.45	once in 2004
5	0.7 / 7 / 0.45 once in 2004	0.70	7.0	0.45	once in 2004
6	0.4 / 4 / 0.45 every 2, 2003-2009	0.40	4.0	0.45	every 2 years, 2003-2009
7	0.7 / 7 / 0.45 every 2, 2003-2009	0.70	7.0	0.45	every 2 years, 2003-2009
8	0.4 / 4 / 0.45 every 4, 2004-2030	0.40	4.0	0.45	every 4 years, 2004-2030
9	0.7 / 7 / 0.45 every 4, 2004-2030	0.70	7.0	0.45	every 4 years, 2004-2030

Table 3.2. Average net benefits (over all simulations) associated with the eight active treatment options across a range of assumed values for the implied value, the time horizon, and the discount rate. The rank for each treatment option is listed in superscript next to the calculated average net benefit for each set of assumptions.

		Implied value:	\$15.65	\$15.65	\$15.65	\$15.65	\$12.65	\$18.65
		Time horizon (yrs):	15	30	15	30	15	15
		Discount rate:	0.06	0.06	0	0	0.06	0.06
Option Number	Management Option	Annualized cost (over 30 yrs.)	Net Benefit (in millions \$)					
2	0.4 / 4 / 0	\$400,000	13.4^{8}	29.4^{8}	25.1^{8}	86.5^{8}	10.1^{7}	16.8^{8}
3	0.7 / 7 / 0	\$851,000	16.0^{7}	38.0^{4}	31.6^{7}	116.2^{4}	11.3^{5}	20.7^{7}
4	0.4 / 4 / 0.45 once 2004	\$539,000	16.9^{4}	33.6^{7}	31.6^{6}	95.6^{7}	12.2^{2}	21.6^{6}
5	0.7 / 7 / 0.45 once 2004	\$990,000	18.3^{2}	40.7^{1}	36.1^{2}	121.9^{2}	12.4^{1}	24.1^{2}
6	0.4 / 4 / 0.45 every 2, 2003-2009	\$956,000	18.3^{1}	37.6^{6}	36.8^{1}	109.5^{6}	11.6^{4}	24.9^{1}
7	0.7 / 7 / 0.45 every 2, 2003-2009	\$1,407,000	16.4^{6}	40.2^{2}	35.4^{3}	125.3^{1}	9.3^{8}	23.6^{3}
8	0.4 / 4 / 0.45 every 4, 2004-2030	\$1,373,000	17.7^{3}	38.0^{5}	34.3^{4}	113.4^{5}	11.9^{3}	23.4^{4}
9	0.7 / 7 / 0.45 every 4, 2004-2030	\$1,824,000	16.7^{5}	38.4^{3}	34.2^{5}	118.0^{3}	10.3^{6}	23.2^{5}

Table 3.3 Proportion of simulation cases that meet Consent Agreement implied lamprey abundance targets of 183,000 in 2006 and 114,000 in 2012 for each of the nine management options. Also listed is the cost associated with each option.

Option Number	Management Option	Annual cost (over 30 yrs.)	Proportion of cases with parasites < 183,000 in 2006	Proportion of cases with parasites < 114,000 in 2012
1	No control	$0	0.50	0.18
2	0.4 / 4 / 0	$400,000	0.50	0.41
3	0.7 / 7 / 0	$851,000	0.50	0.60
4	0.4 / 4 / 0.45 once 2004	$539,000	0.69	0.48
5	0.7 / 7 / 0.45 once 2004	$990,000	0.70	0.67
6	0.4 / 4 / 0.45 every 2, 2003-2009	$956,000	0.84	0.75
7	0.7 / 7 / 0.45 every 2, 2003-2009	$1,407,000	0.84	0.86
8	0.4 / 4 / 0.45 every 4, 2004-2030	$1,373,000	0.70	0.63
9	0.7 / 7 / 0.45 every 4, 2004-2030	$1,824,000	0.70	0.78

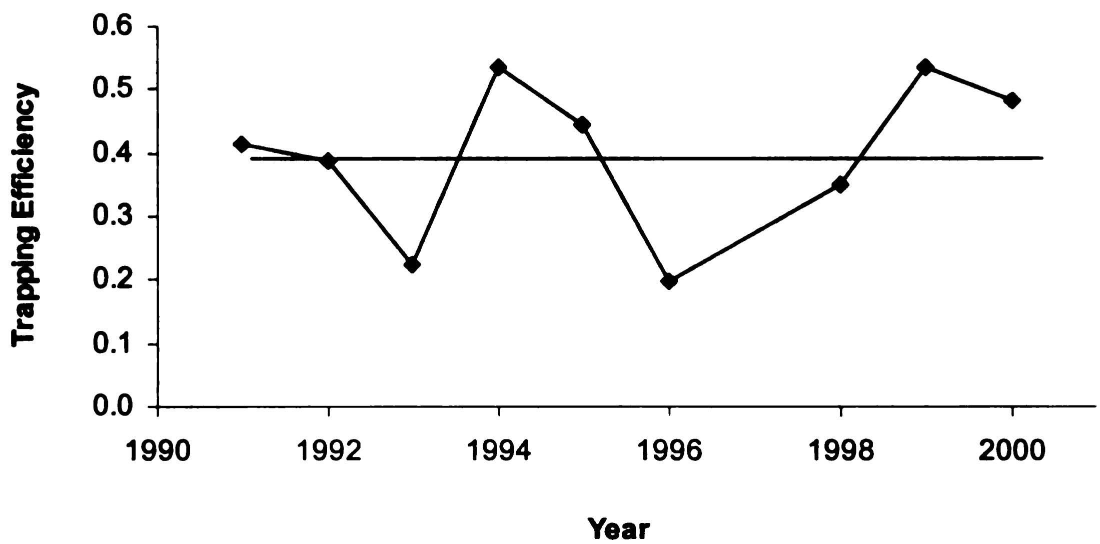

Figure 3.1 Trapping efficiency in the St. Marys River 1991-2000. The horizontal line represents the average efficiency for this period.

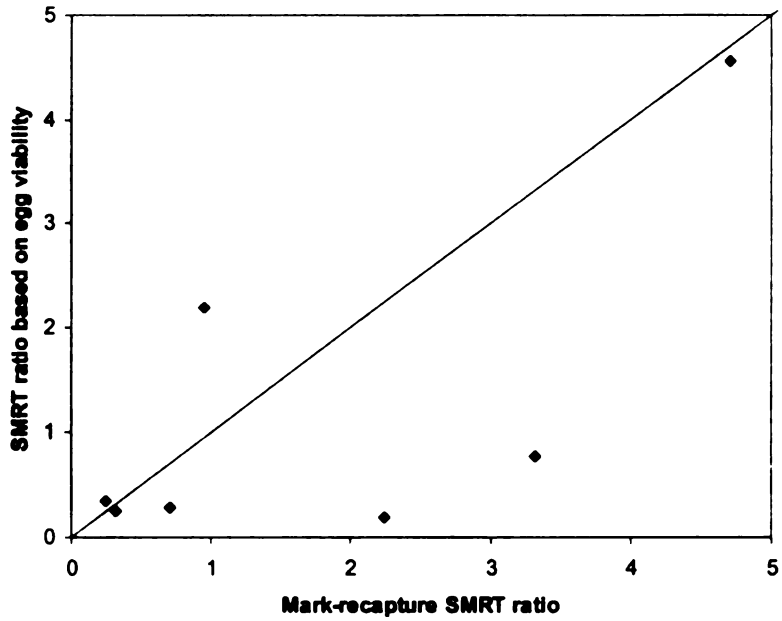

Figure 3.2 SMRT ratio based on mark recapture versus the SMRT ratio calculated based on egg viability assessments. The diagonal line represents a 1:1 relationship between the two variables.

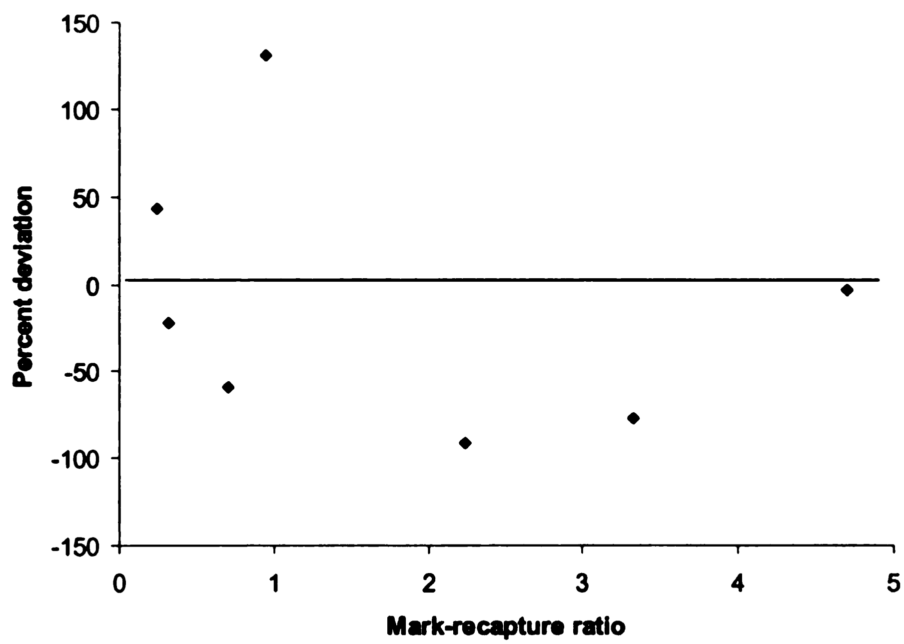

Figure 3.3 Percent deviation of the predicted SMRT ratio based on egg viabilities from the SMRT ratio based on mark-recapture, over the range observed for SMRT mark-recapture ratios.

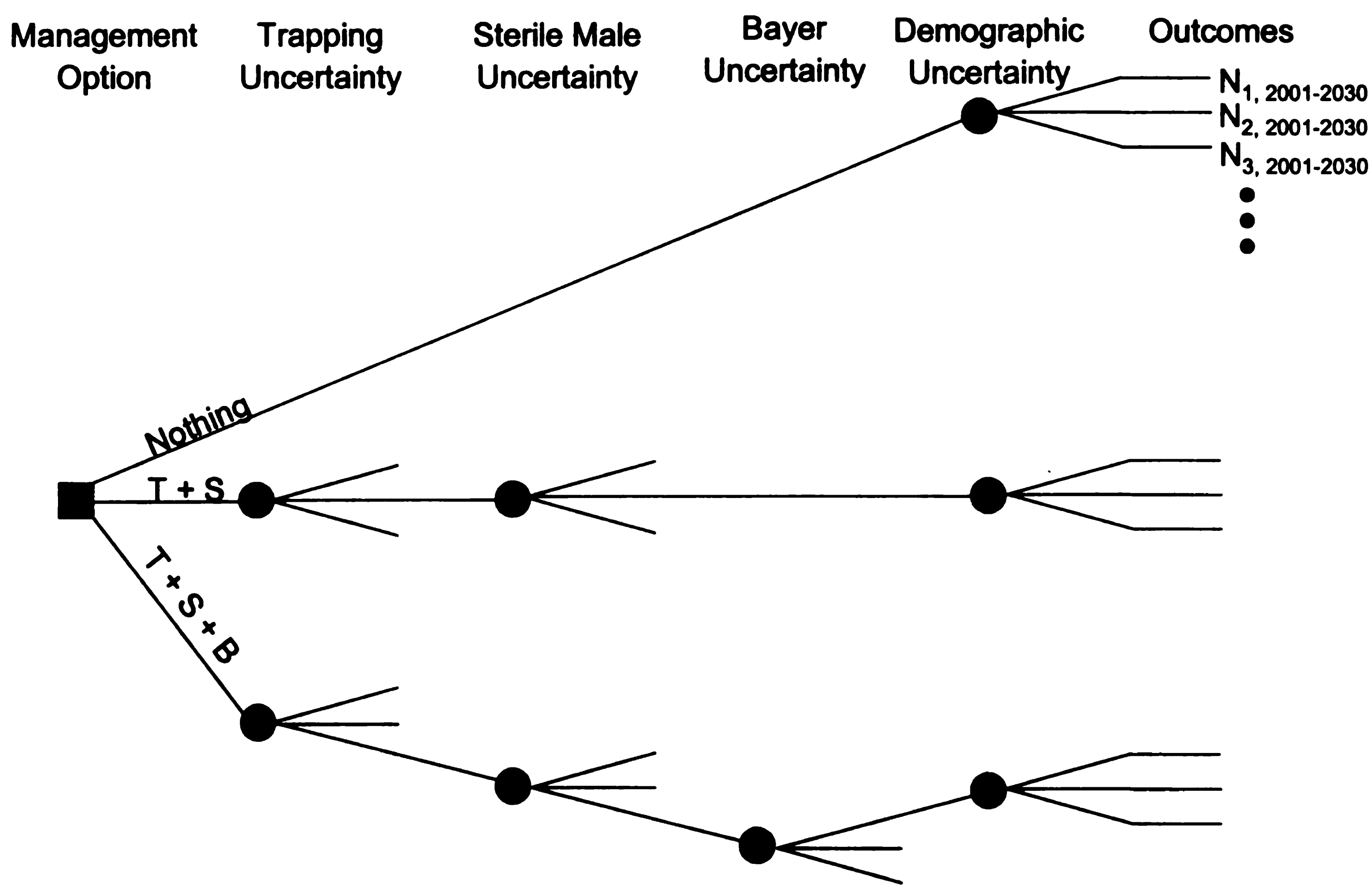

Figure 3.4 Decision tree representing the management options, key uncertainties and outcomes used in the decision analysis.

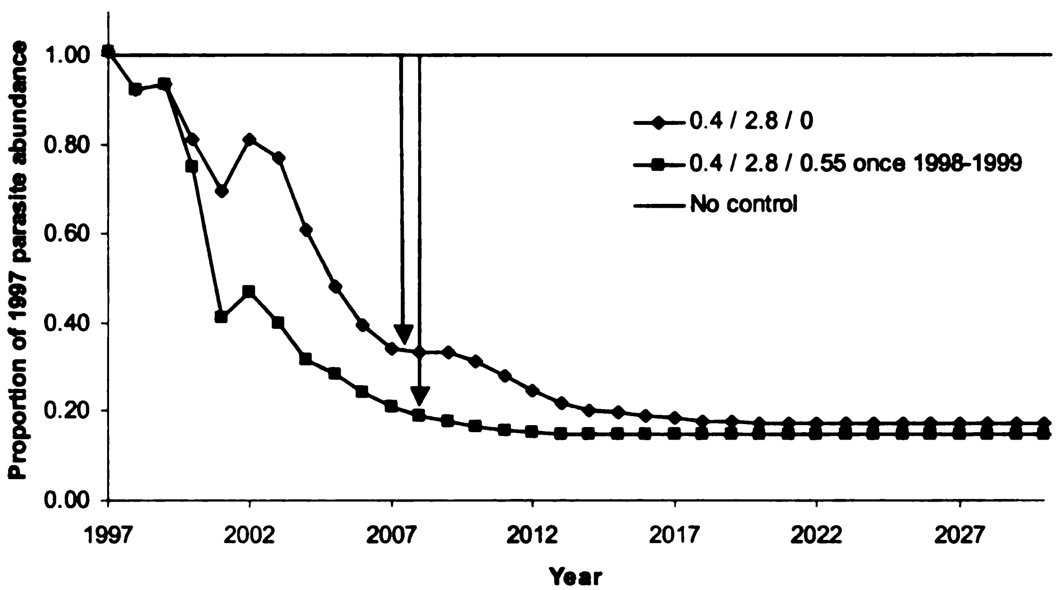

Figure 3.5 Deterministic forecasts of reductions in sea lampreys of two control options that were presented to GLFC Commissioners in 1997. Vertical arrows represent the reduction in lampreys compared to no control.

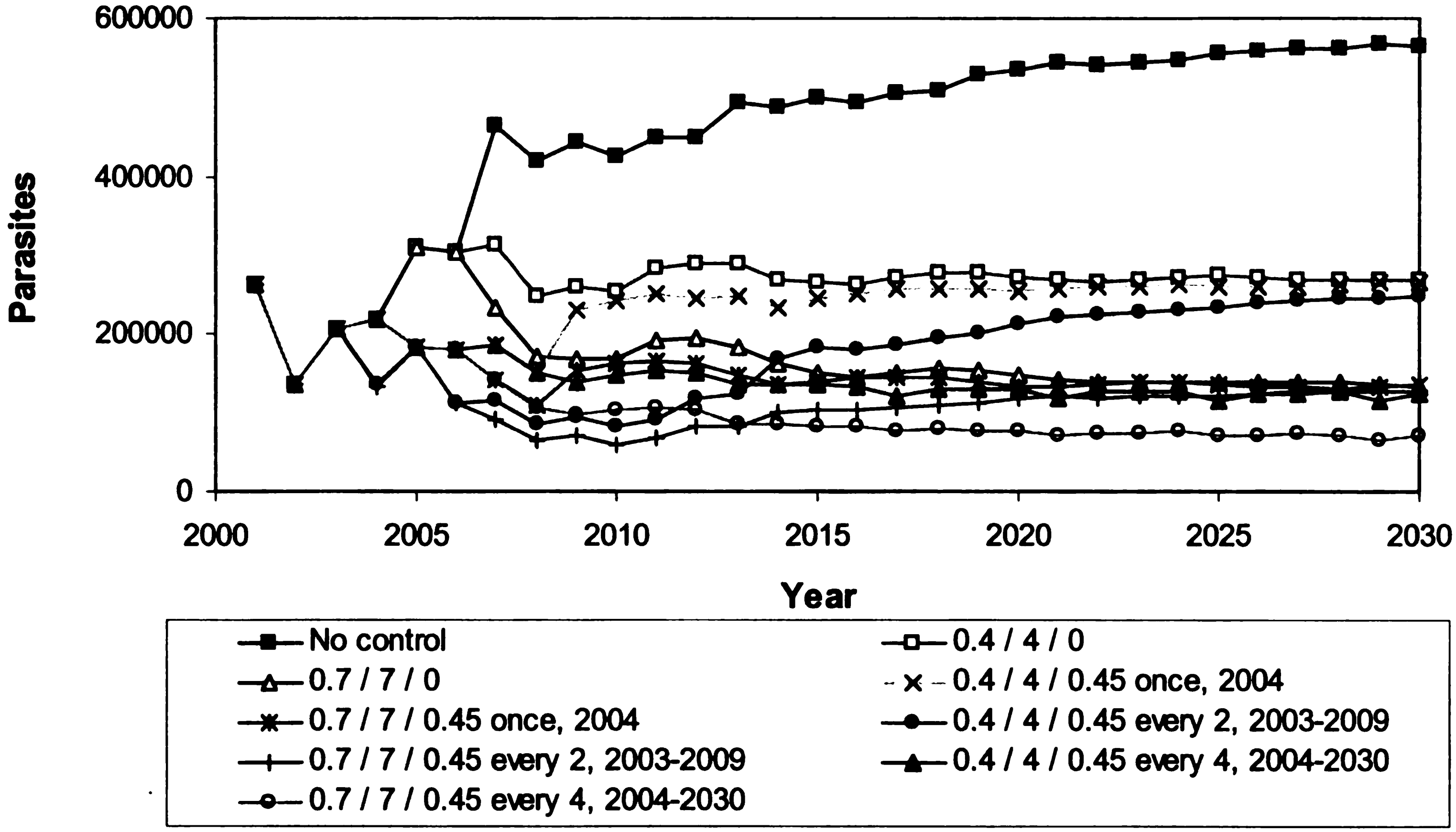

Figure 3.6 Forecasts of average parasitic lamprey abundance in northern Lake Huron, incorporating all uncertainties, for decision options 1-9.

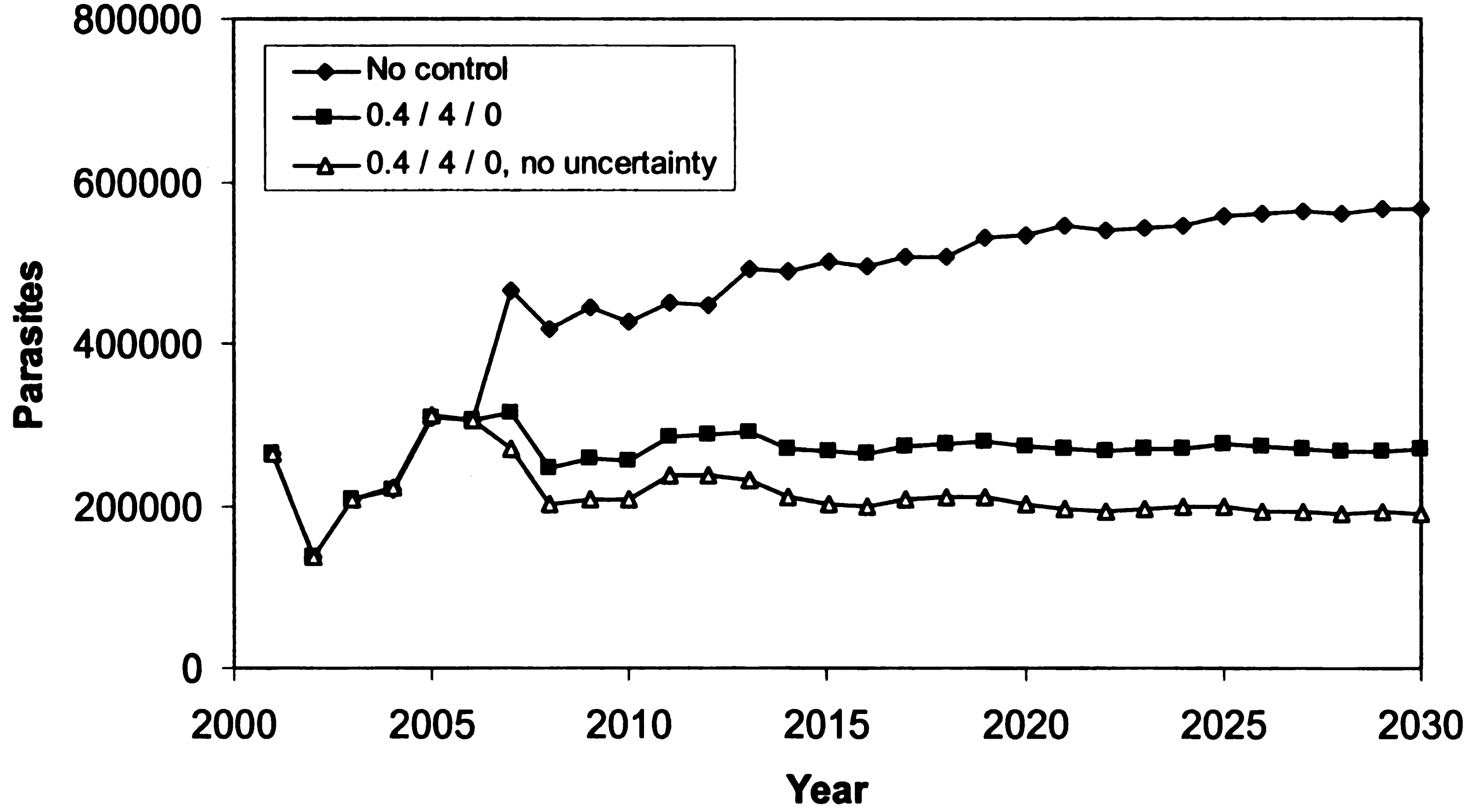

Figure 3.7 Forecasts of average parasitic lamprey abundance in northern Lake Huron associated with using no control, and using decision option 2, with and without uncertainty in trapping and SMRT effectiveness.

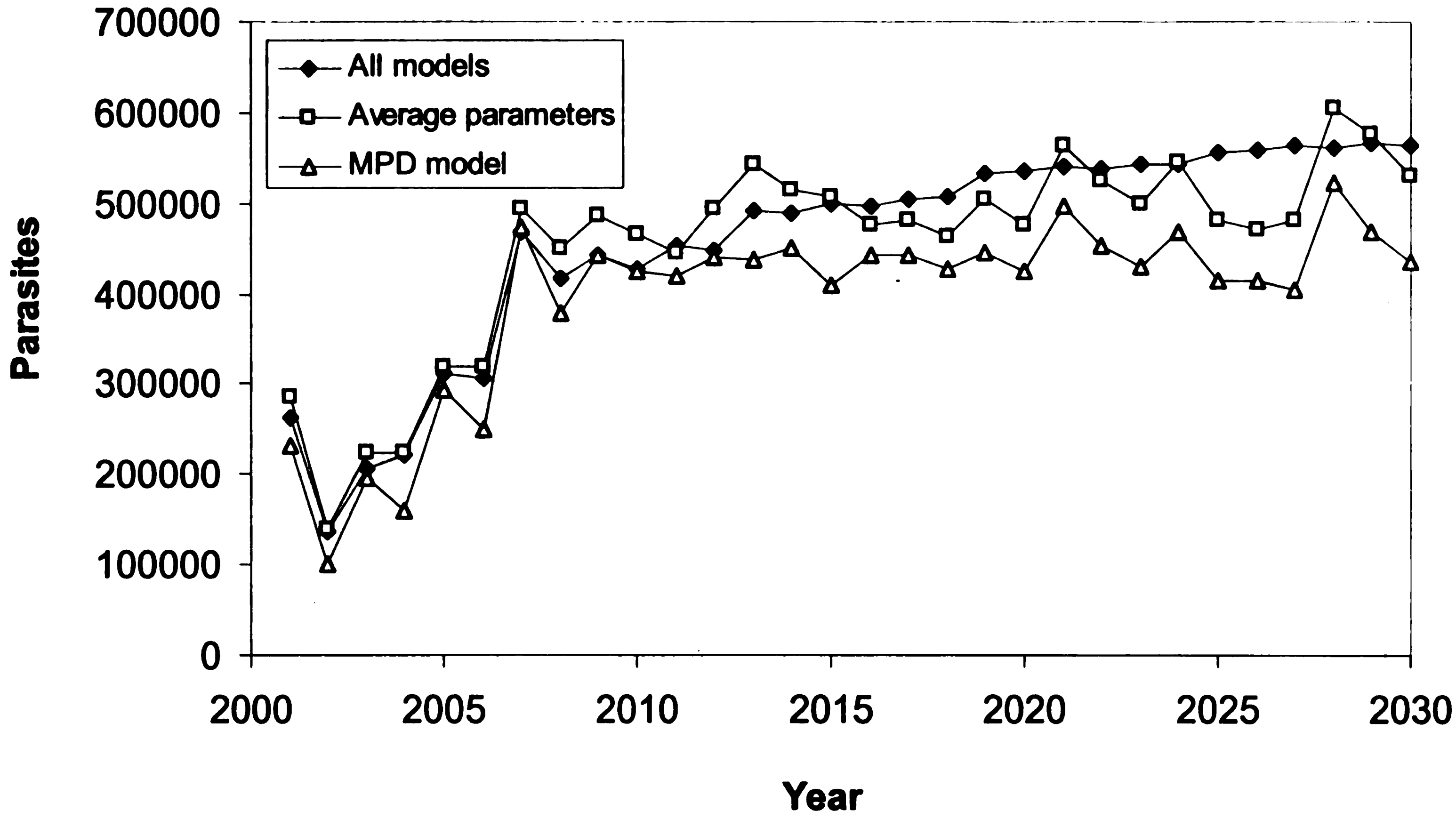

Figure 3.8 Forecasts of average parasitic lamprey abundance in northern Lake Huron associated with using no control, with full demographic uncertainty (All models), using only the average parameters set of demographic parameters (average parameters), and only using the MPD set of demographic parameters (MPD model).

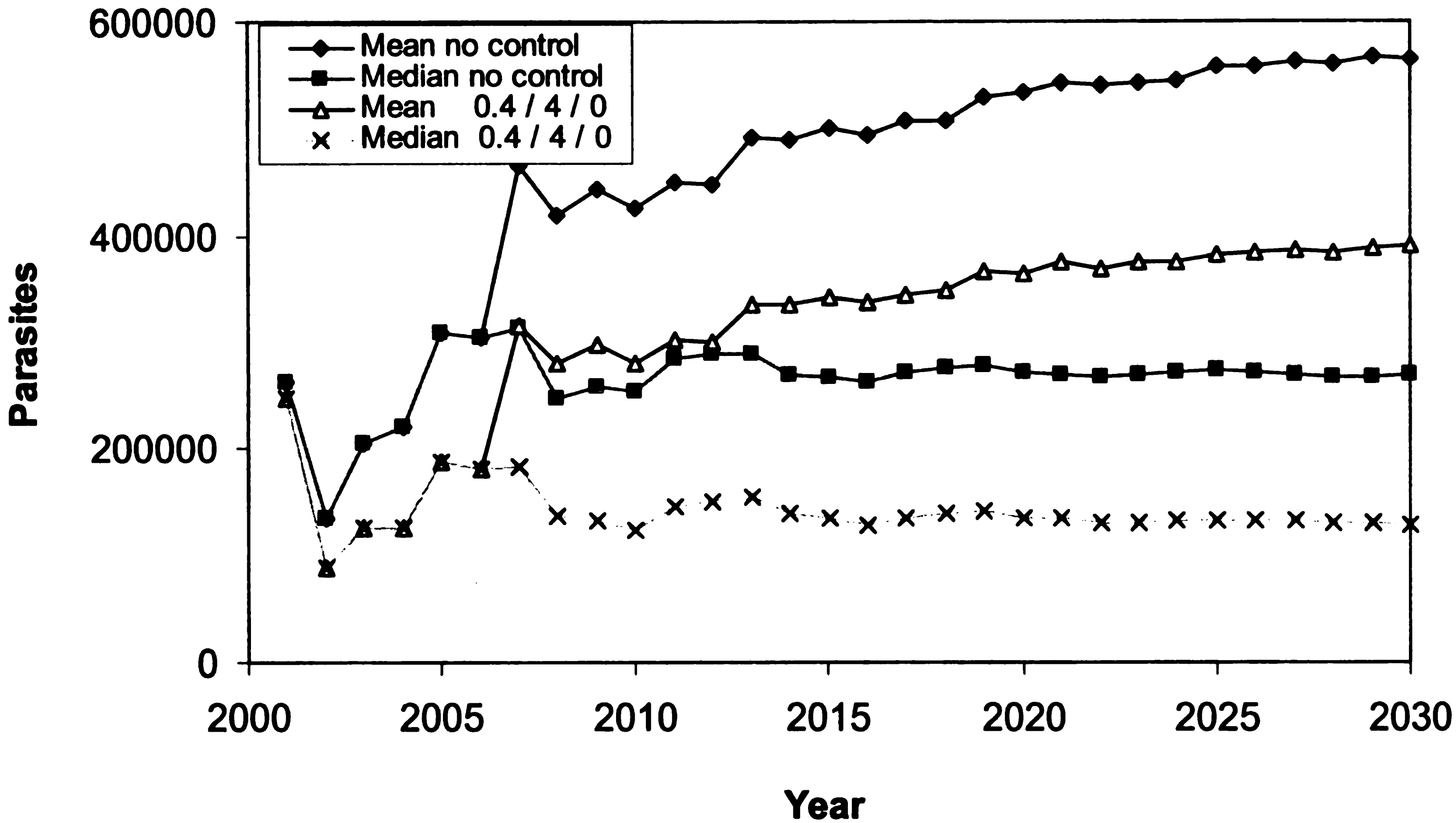

Figure 3.9 Forecasts of mean and median parasitic lamprey abundance in northern Lake Huron associated with using no control and with using decision option 2.

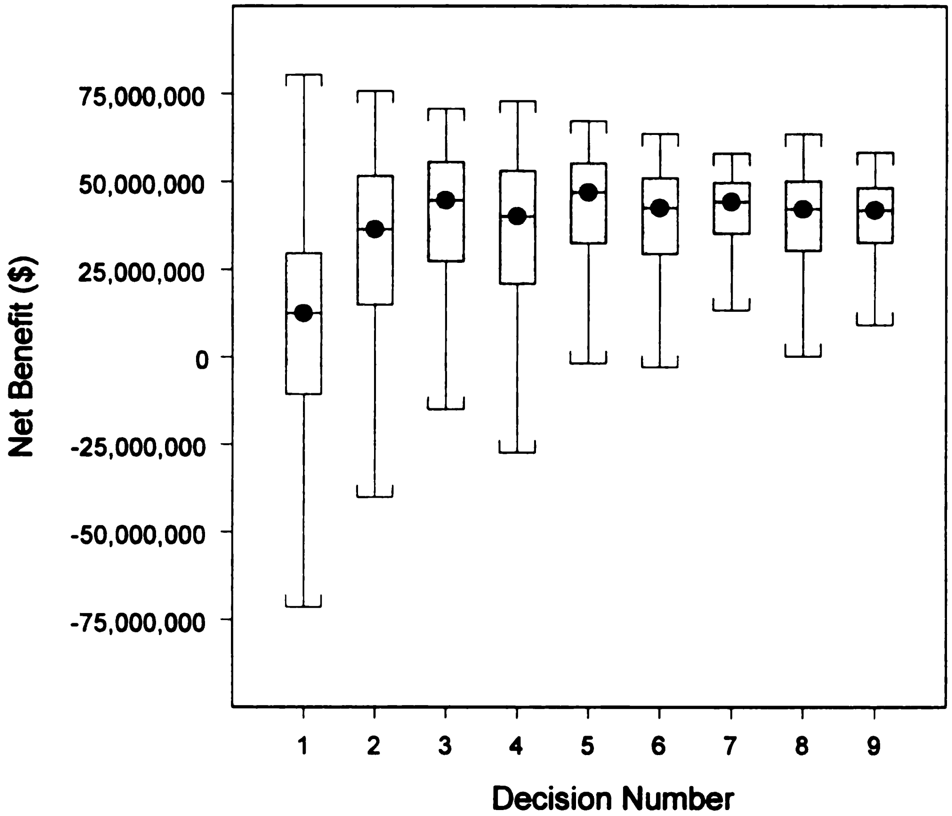

Figure 3.10 Box and whisker plots of the net benefits across all simulations for decision options 1-9. The dot represents the median net benefit and the box ends represent the 25th and 75th percentiles of the distribution.

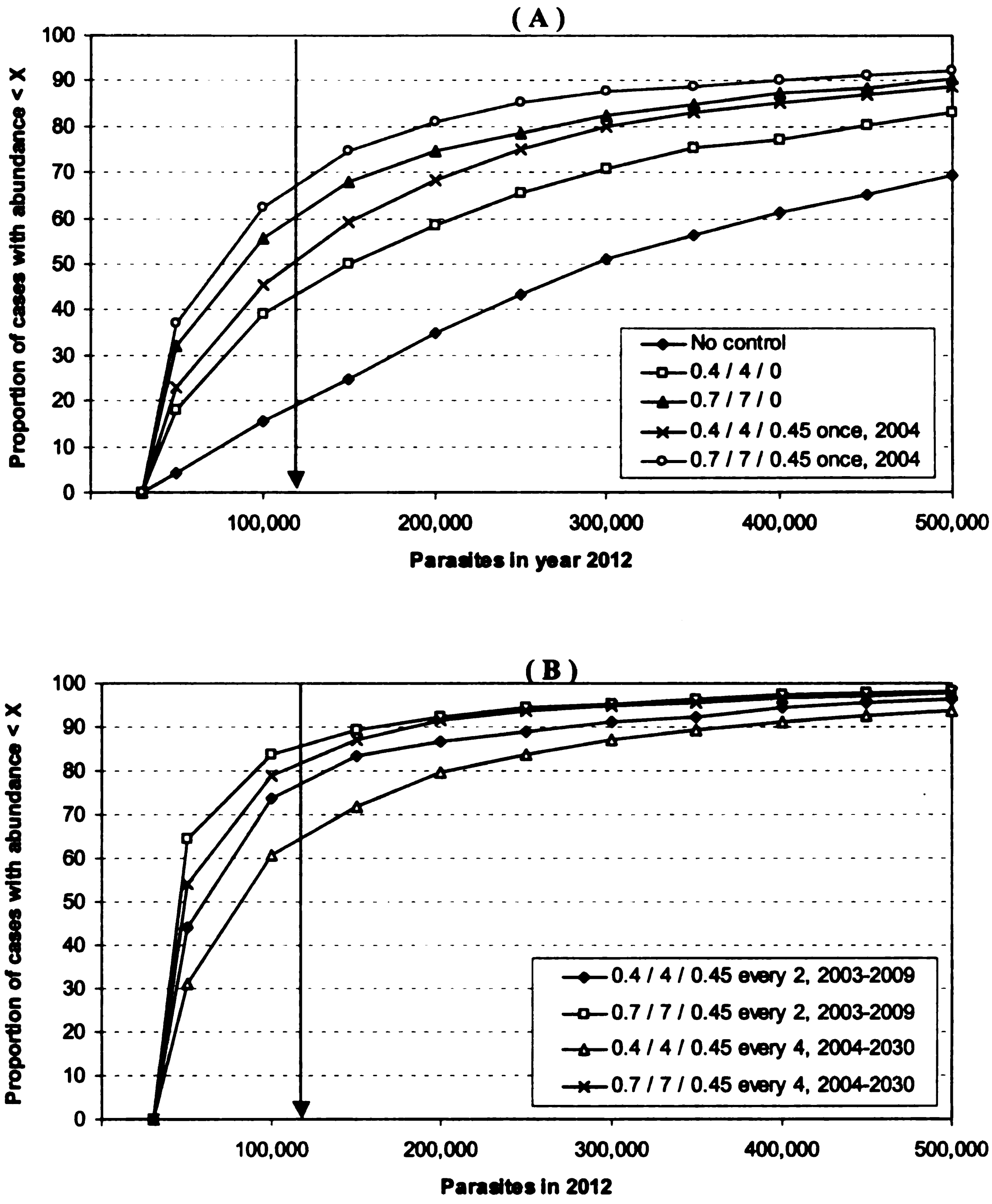

Figure 3.11 Cumulative probability of being below specified parasitic abundance (on x-axis) in year 2012 for options 1-5 (panel A) and options 6-9 (panel B). The vertical arrows denote the parasitic abundance target implied by the Consent Agreement.

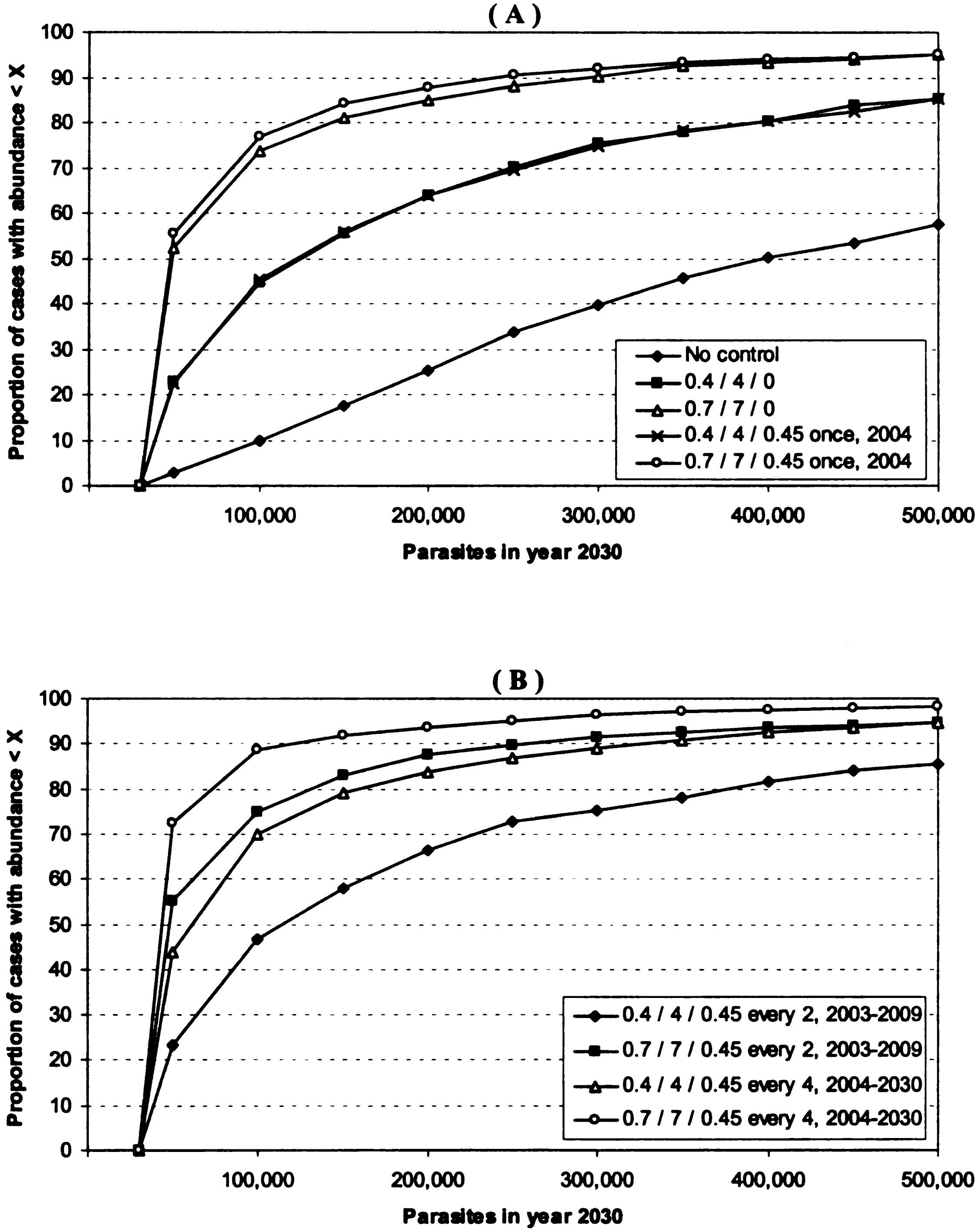

Figure 3.12 Cumulative probability of being below specified parasitic abundance (on x-axis) in year 2030 for options 1-5 (panel A) and options 6-9 (panel B).