INTEGRATING HETEROGENOUS SURVEY DATA TO CHARACTERIZE THE SUCCESS OF THE LAKE HURON SEA LAMPREY (*Petromyzon marinus*) CONTROL PROGRAM

By

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ABSTRACT

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Sea lamprey (*Petromyzon marinus*) induced mortality is perceived as a substantial impediment to the restoration of economically important commercial and sport fish species (e.g. (*Salvelinus namaycush*, *Coregonus clupeaformis*). A basin-wide management program has been in place to control and reduce lamprey abundance for the past 45 years. As part of this program, the abundance of juvenile and spawning lampreys has been assessed annually from lampreys collected using four trapping gears throughout the time series. In my first analysis, I integrated the information from the four trap types to characterize lamprey abundance from 1959-2000. Sea lamprey abundance declined dramatically following the start of the lampricide program in 1960 but increased again beginning in the 1980s. A stock recruitment (SR) model showed that recruitment of spawning phase lampreys was related to the spawning stock size, lampricide treatment history and mass of individual lampreys as spawners. Simulation models based on the SR model demonstrated that alternative control strategies that reduced reproduction in Lake Huron by 50%, coupled with an ongoing lampricide control program could reduce lamprey populations to levels necessary to rehabilitate native fish populations.

Since 1990, the lamprey control program has supplemented its spawning phase assessment program with mark-recapture (MR) studies of juvenile lampreys (migratory or transformer phases and lake-resident parasitic-phases). I used two analytical procedures to integrate the three sources of information into a single expression of lake-wide lamprey abundance. However, I observed substantial uncertainty in my estimate of lamprey abundance due to contradictory information regarding lamprey abundance from the transformer time series compared to the parasitic or spawner time series. I speculate that this contradiction stems from either large measurement error arising from low marking rates in the MR studies or substantial inter-annual variation in survival rates of transformer phase lampreys.

I recommend, based on simulation studies, that the number of spawning phase traps locations should be increased from 12 to approximately 16 with a commensurate decrease in the scope of the transformer MR studies. I also recommend future research to quantify the variation in transformer survival rates and the use of fish wounding data to supplement estimates of lamprey abundance.

DEDICATION

I dedicate this thesis to my family that has supported me throughout my education. First, my wife Margo and my children Caitlin, Heather and Jacob accepted the time away from them with great patience. My father Ken Young always let me know that he was proud of my accomplishments. Finally, my late mother, Winnifred Maud Young encouraged me to strive to reach my potential. Thank you.

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CHAPTER 1: INTRODUCTION

Sea lamprey *(Petromyzon marinus)* have been at the centre of fishery science and ecological debate in Lake Huron since they were first observed in 1937 (Applegate 1950; Smith and Tibbles 1980; Morse et al. 2003). The debate is fuelled by their deleterious effect on the fishery and because their inadvertent introduction highlighted the conflict between the economic benefits of commercialization and the effect on the biological integrity of the Great Lakes (Eshenroder and Burnham-Curtis 1999). Consequently, considerable effort has been expended to assess the abundance, ecological effect and the most appropriate management strategies for this species (Christie et al. 2003).

Sea lampreys are relatively primitive, cartilaginous (Petromyzontiformes; Petroymyzonidae) fish native to the Atlantic Ocean and its North American and European tributaries. Lampreys have an extended larval life stage (three to seven years) spent in burrows in the soft sediments of streams. They undergo a metamorphosis when larvae approach 120 mm and 3 g (Holmes and Youson 1997; Hollett 1998) to the sexually immature stage that are ectoparasites on large-bodied fishes. In the Atlantic Ocean where the body-size ratio between host and lamprey is relatively large, sea lamprey induced mortality in the fishery is likely small. In the Great Lakes lamprey induced mortality is much greater given the smaller relative size of prey (Christie and Kolenosky 1980). Laboratory studies indicate that roughly half of attacks on fish of sizes regularly attacked in the Great Lakes die (Swink 2003) and field studies have shown a relationship between mortality rates and sea lamprey marking (Koonce and Pycha 1985).

The geographic range of sea lampreys expanded following construction of ship canals that bypassed previous impediments to sea lamprey migrations. Sea lampreys gained access to Lake Champlain, the Finger Lakes and Lake Ontario in the nineteenth century following construction of the Erie Barge Canal and the other waterways in upstate New York. The potential range of sea lampreys was extended to all of the Great Lakes after 1839 (Applegate 1950) with the construction of the Welland Canal which allowed ship passage around Niagara Falls. However, Sullivan et al. (2003) contend that the invasion of the upper lakes probably did not occur until at least 1921 when Lake Erie water became the sole source of water for the Welland Canal.

Prior to the invasion of sea lamprey, Lake Huron hosted one of the world's largest freshwater commercial fisheries, focussing on lake trout (*Salvelinus namaycush)* and whitefish (*Coregonus clupeaformis;* Ebener 1995). A steep decline in lake trout abundance and other commercially significant species from occurred during 1930-1950. The decline in lake trout abundance has been attributed to sea lamprey induced mortality (Coble et al. 1990; Eshenroder 1992; Eshenroder and Burnham-Curtis 1999), although other factors, most notably overfishing, have also been implicated as major contributing factors to the decline (Eshenroder 1992). Eshenroder and Burnham-Curtis (1999) further contend that predation and competition pressure from today's exotic fish community in Lake Huron, especially alewife (*Alsoa pseudoharengus*) and sea lamprey, preclude the rehabilitation of endemic planktonic coregonids (chubs and herring), lake trout, and other members of the historic fish community.

The drastic decline in major commercial fish stocks in the mid-20th century spurred the creation of new management institutions, beginning with the Great Lakes

Fisheries Committee in 1950 and the establishment of the Great Lakes Fishery Commission (GLFC) in 1954 by treaty between the governments of the United States of America and Canada. The objective of these institutions was to pool scientific knowledge and coordinate research among federal, state, provincial and tribal governments with a stake in fishery management around the Great Lakes. The GLFC was given the responsibility for developing and implementing a management program to reduce or eradicate populations of sea lamprey.

Prior to 1958, sea lampreys were controlled in Lake Huron through a combination of mechanical and electrical weirs (Morse et al. 2003) placed in tributaries of the lake. The weirs were designed to block the spawning migration of sea lampreys. These structures were thought to be ineffective because spring and summer spates (mechanical weirs) and unreliable power supply (electrical barriers) enabled lampreys to pass.

Applegate et al. (1961) reported that 3-trifluromethyl-4-nitrophenol (TFM) was a relatively selective pesticide that could be used to kill sea lamprey larvae in streams. He observed in Lake Superior that TFM was effective at reducing larval populations, had relatively insignificant non-target effects and had a measurable effect on parasitic populations in the lake. Consequently the sea lamprey management strategy shifted from preventing reproduction to killing larvae in streams just prior to metamorphosis and downstream migration to the lakes. The TFM program began to replace the mechanical and electrical weir programs in Lake Huron in 1960 although some mechanical and electrical barriers were maintained as assessment structures.

TFM applications were introduced to Lake Michigan in 1960, Lake Ontario in 1971, and Lake Erie in 1986. In each lake, a precipitous decline in spawning runs was observed following the onset of TFM control (Smith and Tibbles 1980; Pearce et al. 1980). Additional control techniques were incorporated by the GLFC, including low-head barriers (Hunn and Youngs 1980) and the stocking of sterilized male lampreys into the St. Marys River in 1997 (Twohey et al. 2003). However, TFM has remained the mainstay of the management program because it is effective and lampreys have not evolved a resistance to the chemical.

The effectiveness of the sea lamprey management program has been assessed by monitoring spawning phase abundances. Prior to 1975, the assessment program measured the abundance of spawning-phase lampreys trapped at mechanical and electrical weirs. After 1975, the program changed its gear to a combination of portable assessment and dam traps (Mullett et al. 2003) and in Lake Huron the program experimented with transformer and parasitic-phase mark recapture studies to estimate lake wide populations. However, the design of the assessment program was *ad hoc* in nature compared across the Great Lakes in 1996. For example, only United States (US) tributaries of Lake Superior were to assess population trends but a set of three Canadian and US tributaries were used to assess trends in Lake Huron (Morse and Young 2000). The design and effectiveness of the program suffered because it did not have clear objectives with respect to evaluating specific hypotheses.

The GLFC faced a budgetary crisis in 1997. In order to balance its books, the GLFC was faced with either implementing a cut to its sea lamprey management program "across the board" or find a particular program element to cut to save the integrity of the other elements and implement new control measures. The GLFC considered dropping its spawning phase assessment program and thereby saving the integrity of other program elements. The GLFC convened an expert panel in 1997 to review the assessment program. The panel concluded that the adult assessment program was integral to the integrated pest management program but they did have a number of technical and policy level recommendations to improve the program. The three main recommendations of the panel were to;

- Focus the assessment program on evaluating the effects of changes in the treatment program
- Use the assessment program to evaluate current lampricide treatment effectiveness and the likely success of future treatment techniques
- Integrate the information from traditional assessment techniques (i.e., the spawning phase trapping) with new coded wire tagging techniques.

In this thesis, I take up the recommendations of the review panel. Chapter 2 reviews the history of assessment program to provide an integrated picture of spawning phase assessment from 1959 through 2000. I then use the time series to analyze stock and recruitment patterns of lampreys in Lake Huron and simulate the effect of new management strategies. In Chapters 3 and 4, I use two different techniques to integrate the traditional spawning phase assessment data with transformer and parasitic CWT data. I use the models developed in these chapters to simulate various allocations of sampling effort in order to optimize the assessment program.

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CHAPTER 2: THE RELATIONSHIP OF SEA LAMPREY (*PETROMYZON* MARINUS) SPAWNING STOCK TO RECRUITMENT IN LAKE HURON AND THE IMPLICATIONS FOR ALTERNATIVE CONTROL STRATEGIES.

ABSTRACT

Sea lamprey (*Petromyzon marinus*) populations in Lake Huron are controlled mainly through the application of the larvicide TFM (3-trifluromethyl-4-nitrophenol). However, the Great Lakes Fishery Commission (GLFC) has a goal of increasing the use of non-chemical tactics. An analysis of stock and recruitment from 1959-2000 and simulation modeling was used to evaluate the likelihood of this policy succeeding in meeting the Lake Huron fish community objective (75,000 – 100,000 spawning sea lampreys) for Lake Huron. The generalized Ricker stock-recruitment model was fit to data derived from integrating four fishing methods used to estimate the relative abundance of spawning lampreys. Additional explanatory variables related to TFM treatment effort and lamprey mass improved the fit of the stock recruitment model. Simulation models suggest that non-chemical alternatives could be successful in achieving the fish community objective if 50-60% of lamprey were removed prior to spawning. This level of fishing mortality could be achieved through a doubling of current trapping effort and relatively modest increases in trap efficiency.

INTRODUCTION

The abundance of Lake Huron sea lampreys (Petromyzon marinus) has been dynamic (Pearce et al. 1980; Morse et al. 2003) since they were inadvertently introduced in Lake Huron following the construction of canals and waterways in the Great Lakes during the 19th and 20th centuries. Lampreys are a significant concern in Great Lakes fishery management because lamprey feeding causes considerable mortality in economically significant fish species. Laboratory studies indicate that roughly half of attacks on fish of sizes regularly attacked in the Great Lakes die (Swink 2003) and field studies have shown a relationship between mortality rates and sea lamprey marking (Koonce and Pycha 1985). Since 1959, the lamprey control program has been based on stream applications of 3-trifluoro-nitrophenol (TFM) to kill larval lampreys before they transform to the open water parasitic life-stage. The TFM program has been successful because it has dramatically reduced lamprey abundance and mortality in most of the Great Lakes (Pearce et al 1980).

Despite the success of the TFM program, the GLFC's (2001) long term strategy is to reduce its use of TFM by 50% (based on the use pattern between 1986-2000) before 2010 and increase the use of non-pesticide based or "alternative control" tactics (not based on pesticides) to at least 50% of the management program. The GLFC embarked on this program due to:

- The high cost of the pesticide program;
- Concern that continued use of pesticides will become socially unacceptable; and,

- A broader spectrum of tactics would better ensure the long-term viability of the management program. Reliance on only one technique would make the program vulnerable if it was no longer available to be deployed.

A common characteristic of alternative control tactics is that they focus on reducing reproduction. Low-head barrier dams, stocking of sterilized male lampreys, and trapping all function by blocking or reducing the probability of successful reproduction. In addition, Sorensen and Vrieze (2003), Twohey et al. (2003) and Li et al. (2003) have reported the discovery of unique migratory and reproductive pheromones produced by sea lampreys. They suggest that these pheromones could be exploited by sea lamprey managers to interrupt communication among lampreys, divert their migrations, enhance trapping or be used in conjunction with the other control tactics.

The lamprey management program has recognized that the alternative control strategies may not be effective in reducing lamprey populations if decreasing spawning density triggers a compensatory response in some key population dynamic processes. Compensatory responses or mechanisms are population dynamic rates that increase population growth rates at lower population densities. While a strong compensatory response is desirable in managed fish stocks, it is counterproductive in sea lamprey management. If lamprey population dynamic rates are density dependent, then management strategies based on reducing spawning stock will not have a linear effect on the production of parasitic lampreys. These strategies will have to sufficiently “over-fish” these populations to overcome the compensatory changes in demographic processes. Control strategies based on lampricides may be more effective than alternative control strategies if compensatory responses are high and they are deployed after the compensation occurs. Jones et al. (2003) reviewed the literature for compensatory mechanisms in lampreys and found strong evidence for changes in sex ratios (e.g. Heinrich et al. 1980), weak and equivocal evidence for changes in larval growth rate (e.g. Weise and Pajos 1998) but weak evidence for other processes like time to metamorphosis. Jones et al. (2003) and Haeseker et al. (2003) both reported evidence of compensation based on recruitment of age 1+ larvae at various stock sizes. Importantly, both studies observed strong evidence for density independent effects in recruitment patterns that could potentially jeopardize the effectiveness of alternative control strategies because large year classes were observed even at very low spawning densities.

A wide array of environmental factors such as stream discharge, velocity and temperature has also been demonstrated to have a significant effect on the relative abundance of larval lamprey and their size at age (Malmquist et al. 1989; Young et al. 1990). The variation in important environmental factors could be important in understanding lamprey recruitment patterns. Young et al. (1996) proposed three habitat-based hypotheses to explain the apparent increased recruitment from the St. Marys River including:

- Changes to the quality and quantity of larval habitat from pollution abatement programs;
- Increased spawning habitat; and
- Increased density of lamprey forage available to recently metamorphosed larvae.

Their analysis supported the third hypothesis, by demonstrating that changes to the fish community were more strongly correlated with the changes in spawning lamprey abundance than changes in larval or spawning habitat.

The lamprey control program has undergone some significant changes in the past and recent policy changes initiated by the GLFC (see GLFC 2001) have the potential to radically change the future of this program. A systematic evaluation of past and future changes to the control program as well as the effect of changing environmental and biotic conditions depend on reliable parasitic or spawning stock assessment (Sawyer 1980). Stock assessment of these life stages provides the most information on the success of the lamprey control program because the abundance of the parasitic or spawning life stage represents that portion of the lamprey population that escaped treatment. To date, there has not been a systematic evaluation of lamprey abundance that covers the entire history of the control program. In studies of other semelparous fish, an analysis of the adult spawning stock has been used to determine the relationship between spawning stock and recruitment to the fishery and estimate management parameters such as maximum sustained yield (msy), effort at msy (u_{msy}) and stock size at msy (S_{msy}; e.g. Hilborn and Walters 1992). A similar stock assessment of sea lamprey would be useful to frame the policy discussion around changing the control strategy from one based on lampricides to a mix of lampricides and alternative technologies.

The GLFC has included some form of spawning run assessment throughout the history of the lamprey control program, albeit *ad hoc*. The changes in gear types and data analyses have had the effect of fragmenting the time series. The technology used to trap sea lampreys changed from electrical and mechanical weirs to portable assessment and dam traps (Mullett et al. 2003) beginning in 1975. However, no studies were conducted to evaluate the relative efficacies of the varying trapping gears, effectively severing the time series of spawning phase catches.

The recent trends in Lake Huron spawning abundance described by Morse et al. (1995) and Morse and Young (2005) used an index of the three largest runs. Johnson (1987) modified Schaeffer's (Ricker 1975) mark and recapture method to estimate lamprey spawning runs in individual tributaries. These spawning run estimates were used in a regression model that uses discharge, geographic region, and production potential to estimate runs in streams without assessment traps (Mullett et al 2003). The sum of the spawning run estimates has been used as an index of the spawning run and the time series of spawning run estimates has been used to evaluate lamprey "trends through time" (e.g. Klar and Young 2003).

Hilborn and Walters (1992) cautioned that stock and recruitment analyses can be unreliable because of uncertainty generated by short time series (<15 years) and a lack of contrast (< one order of magnitude between the smallest and largest stock sizes) in the spawning assessments. The current characterization of the lamprey abundance as a series of time blocks would fail to meet both of Hilborn and Walters' (1992) criteria for the analysis of lamprey recruitment. However, an integration of the assessment history into a single time series would enable an examination of the factors affecting sea lamprey recruitment. In addition, recruitment models could be used to predict the effect of proposed management strategies.

In this chapter, I unify the time series of spawning run estimates from 1959 – 2000 that form the basis of a stock-recruitment analysis. This analysis includes:

- An evaluation of the effect of stock size, lampricide treatment history and the condition of spawning lamprey on recruitment;
- Estimation of management parameters such as msy and S_{msy} to provide reference points for the scale of future alternative control strategies; and
- A model of the effect on recruitment of varying the effectiveness of alternative control strategies, measured as a reduction on the effective number of spawners.

The intent of this analysis is to provide a framework for evaluating the likelihood of the GLFC achieving the fish community objective for sea lamprey in Lake Huron given its policy objective of increasing the use of alternatives to TFM.

MATERIALS AND METHODS

This analysis has three components. First a model was developed that estimated the annual relative abundance or catch per effort (CPE) of sea lampreys in Lake Huron from 1959-2000 based on the catches of spawning-phase sea lamprey from four distinct gear types. The time series of CPE was then used to estimate the relationship between recruitment and three independent variables: spawning stock; the lake-wide level of lampricide control; and the mass of adult sea lampreys (Figure 2.1). Finally, I used the estimated stock-recruitment model to simulate the effects of varying the intensity of alternative control programs on the likelihood of achieving the objectives for sea lamprey management in Lake Huron.

Estimating CPE: The GLFC used four different gear types between 1959 and 2000 to assess spawning populations of sea lamprey. In most cases, the devices were fished throughout the spawning migration (April though June), catch was enumerated daily and summed to provide a total catch for the season. Mechanical and electrical weirs were used through the early portion of the time series. Mechanical weirs (MW) were temporary structures constructed of wood or steel mesh and acted as fish fences to lead lampreys to a trap where they were enumerated. An alternative device for blocking sea lampreys was the electrical weir (EW) that introduced an alternating current across the width of streams (Smith and Tibbles 1980). The current killed upstream migrating lampreys and the dead lampreys were speared or netted downstream of the weir. MWs and EWs were eventually replaced by portable assessment traps (PT) or low head barrier traps (BT; Table 2.1). PTs are wooden or steel and mesh boxes (~2.0 m x 0.5 m x 0.5 m) with funnels on either end that are typically fished at the surface of the water and along the face of dams. BTs are traps built into low-head sea lamprey barriers. They differ from PTs because some water from upstream of the dam is forced through the entrance funnel to act as an attractant to migrating sea lampreys.

In this analysis, trapping effort in each stream was defined as its watershed area. I made the assumption that the catch in each of the streams would be a function of stream size because Mullett et al. (2003) observed that sea lamprey spawning runs are proportional to stream discharge or watershed area. I used watershed area rather than discharge as the effort component because this data was available for all lamprey producing streams in the Lake Huron basin. Therefore, CPE for each stream fished was calculated as C/Q where C is the yearly catch and Q is watershed area. For each gear type j, I calculated the average annual CPE, $n_{i,j}$ (i=year) for use in analyses that follows.

The first objective in this analysis was to generate an annual estimate of the relative abundance of spawning lampreys, N_i, by integrating the estimates from each of the four sampling methodologies. Each method was assumed to have different catchability coefficients (a_j). The catchability coefficient for portable traps was fixed at $a_{pt}=1$ while the estimates of the remaining $a_j s$ and $N_i s$ (in years where the number of trap types was >1), was determined using weighted least squares (Rice 1995) by minimizing the following objective function:

$$O = \sum_{i=1}^{41} \sum_{j=1}^{4} k_{i,j} \left[\log(n_{i,j}) - \log(a_j) - \log(N_i) \right]^2 \qquad (1)$$

where $k_{i,j}$ is the number traps of type j fished in the ith year. For those years where only one gear was fished, the data provide no information on the relative catchabilities and these years are not included in the objective function. For these years, I estimated the CPE as $N_i=a_j n_i$.

Stock-Recruitment model: Two sources of data were used to estimate the stock and recruitment model. The primary data source, *P,* that I used was the relative abundance estimates (N_i) from the previous section. Second, Mullett et al. (2003) estimated an index, *I,* of the lake-wide abundance of spawners for a subset (1981-2000) of the years in this study. I used these data as supplementary information on lamprey recruitment in those years where the data was available and these data are denoted as $R_{I,i}$.

Spawning stock was defined as the number of female spawning lamprey available to spawn in Lake Huron in year *i,* after accounting for the catch in the assessment fishery in year *i*. I defined recruitment as the number of spawners returning to streams in year

$i+6$, the average time required to complete the life cycle in Lake Huron (see explanation below).

I defined the spawning stock as the abundance of female spawners because it may provide a more meaningful depiction of sea lamprey spawning activity. Sex ratio may be a density dependent parameter and the proportion of females varied considerably through the study period. At the beginning of the study period the percent of female spawners was approximately 40% (Figure 2.2). The proportion of females increased to a high of 66% as lake-wide populations declined in the mid-1970s. The proportion dropped to approximately 47% during the 1996-2000 periods.

My definition of recruitment infers that life span for Lake Huron lampreys is about six years from the egg stage to spawning. While the age of sea lamprey in Lake Huron is typically not estimated, I estimated the lag between spawning and recruitment to be six years based on three sources of information. First, Beamish and Medland (1988) described a method for aging larval lampreys by examining statoliths, a cartilaginous structure analogous to otoliths in teleost fishes. Steeves (1996; unpublished data) used this methodology to estimate the mean age of metamorphosing sea lamprey in the St. Marys River (perceived to be a largest source of parasitic sea lamprey in Lake Huron) at four years, implying the mean age of spawning lampreys to be six years since the parasitic stage can last up to 20 months. The Beamish and Medland aging method was also adapted to spawning sea lampreys (Hollett 2003; unpublished data). Statoliths were removed and examined from 90 spawning lampreys from six Lake Huron tributaries in 2002. Each statolith was examined on three occasions and results were accepted only if the same age was determined from each reading. These data indicated that >90% of Lake

Huron spawners were six years of age (Figure 2.3) and consequently that there was a six year differential between the spawning and recruitment years. Finally, the average treatment interval for primary sea lamprey streams in Lake Huron was been approximately four years (Morse et al. 2003), also implying an average sea lamprey life span of about six years. I also assumed that the differential between spawning and recruitment has remained fixed throughout the study period.

Two additional explanatory variables were used in the stock and recruitment analysis. I hypothesized that recruitment would be modified by the degree of effort in the lampricide control program. The GLFC maintains a database of Great Lakes tributaries with known sea lamprey populations. The database includes the estimated area of larval lamprey habitat (Christie et al. 2003; Slade et al. 2003) and a history of lampricide treatments. Based on the age of spawners, I assumed that most larval lampreys are stream-resident for four years and calculated the area of lamprey habitat treated in the previous four years. The history reflects the larval habitat treated in the four years prior to the transformation of each cohort. Second, I hypothesized that any change in the sea lamprey predator-prey ratio would be reflected in the size of spawning lamprey. I further speculated that there may be a relationship between lamprey mass and demographic factors like fecundity (Applegate 1950; Manion 1968) and survival that would ultimately affect recruitment.

The model evaluated was based on a Ricker stock-recruitment model with two environmental explanatory variables (Quinn and Deriso 1999),

$$
\begin{aligned}
S_i &= (qN_i - C_i) f_i \\
R_{P,i} &= qN_{i+6} \\
R_{P,i} &= \alpha S_i e^{-\beta S_i + \sum c_t X_{i,t} + \varepsilon}
\end{aligned}
\tag{2}
$$

Here, S_i was spawning stock (assumed known), q was the catchability coefficient parameter, C_i is the catch of lampreys in the assessment fishery that occurs prior to spawning (assumed known), f_i is the proportion of females (assumed known), $R_{P,i}$ was the recruitment of spawners from the primary data source (assumed known), α was a parameter that reflected recruits per spawner at small stock sizes, β was a parameter that described how quickly the recruits per spawners drop as stock sizes increases, $X_{i,t}$ are the environmental factors (assumed known), treatment history and lamprey weight, the coefficients c_t are parameters that describe the magnitude of their effects and ε are the process errors that were approximately normally distributed with mean 0 and variance σ_p^2. Equation 2 implies Equation 3 below, which is the form of model typically used to fit the parameters of the Ricker stock – recruitment model (Hilborn and Walters 1992).

$$
x_i = \log\left(\frac{R_{P,i}}{S_i}\right) = \log(\alpha) + \beta S_i + \sum c_t X_{i,t} + \varepsilon \tag{3}
$$

The maximum likelihood estimates of the parameters in equation 2 and 3 were obtained by minimizing the following objective function.

$$
\begin{aligned}
L_1 &= k_p[\log \sigma_p + \tfrac{1}{2}\log 2\pi] + \sum_{i=1}^{k_p} \frac{[x_i^{/} - \hat{x}_i]^2}{2\sigma_P^2} \\
L_2 &= k_I[\log \sigma_I + \tfrac{1}{2}\log 2\pi] + \sum_{i=1}^{k_I} \frac{[R_{I,i} - \hat{R}_{P,i}]^2}{2\sigma_I^2} \\
L &= L_1 + L_2
\end{aligned}
\tag{4}
$$

where L is the negative log likelihood that was comprised of two components. L_1 was based on the comparison of the observed recruitment from the primary data source and the predicted recruitment from the Ricker model and L_2 was based on the comparison of observed recruitment in the index data series and predicted recruitment from equation 2. Here, $x_i^{/}$ are the observed $\log\left(\frac{R_{P,i}}{S_i}\right)$, $\hat{x}_i$ are the predicted $\log\left(\frac{R_{P,i}}{S_i}\right)$ from equation 3, k_p is the number of observations in the primary data series, k_I is the number of observations in the index data set, $\hat{R}_{P,i}$ is the predicted recruitment from equation 2 and σ_I^2 was the variance associated with the process errors inferred by L_2. In those years where there was no data from the index data series, there wasn't any information to estimate the parameters and therefore those years were not included in the calculation of L_2. Models nested within the fully parameterized model (Table 2.2) were examined and the additional explanatory power of parameters was evaluated using the likelihood ratio test (Hilborn and Mangel 1997).

The uncertainty in model parameters was evaluated using two methods. First, the AD Model Builder software (Otter Research Ltd., 2001) produces asymptotic standard errors for each parameter estimated. These estimates of parameter uncertainty were compared with standard deviations derived from bootstrapped samples of the data (Hilborn and Mangel 1997). I randomly selected with replacement, $k_P=35$, observations from the primary data set along with the corresponding observations for the environmental variables and index data series, if applicable. I then estimated the parameters using the likelihood function, L. This procedure was repeated 1000 times.

Bias in parameters was estimated from Monte Carlo or stochastic simulations (Ripley 1987). For each model, 1000 simulated data sets were generated based on the parameter estimates generated from equation (2). The simulated data sets were developed using the model,

$$
\begin{aligned}
R_{P,i} &= \hat{\alpha} S_i e^{-\hat{\beta} S_i + \sum \hat{c}_t X_{i,t} + \omega \hat{\sigma}_P} \\
S_{i+6} &= f_i R_{i+6} - h_i \\
\hat{S}_{i+6} &= S_{i+6} e^{\omega \sigma_o}
\end{aligned}
\qquad (5)
$$

where $\hat{\alpha}$, $\hat{\beta}$, and $\hat{c}_t$ are the stock recruitment parameters estimated in equation (3), ω is a normally distributed random variable with mean zero and standard deviation of one, $\hat{\sigma}_P$ is the estimated stock recruitment process error standard deviation, and h_i was the fishing mortality rate calculated as $C_i / \hat{q} N_i$ and assumed to be known and σ_o, the standard deviation of the observation error that I varied from 0.0 to 0.3 (i.e. 1000 simulated data sets were created for each scenario of σ_o=0.0, 0.1, 0.2, 0.3). I estimated the stock and recruitment parameters for each simulated data set and then determined the average for each scenario.

Simulating the effect of alternative control: The stock – recruitment model developed in the previous section was used to examine two aspects of the GLFC vision and fish community objectives. First, how large an effect do alternative control measures need to be in order to achieve fish community objectives? Second, what is the effect of a 50% reduction in the lampricide treatment program on the performance of the alternative control program relative to achieving the fish community objectives? In addition, I examined the effect of both increasing and decreasing mass of spawners.

In these simulations, I assumed the initial population to be the average for the 1990s, approximately 200,000 recruits. I considered two possibilities for lampricide control effort – either the average during the 1990s or half of the 1990s average. For each of the lampricide control treatments, I simulated lamprey mass at the 1990s average or lamprey mass changing at rates of either -1.0 g*year^{-1} or 1.0 g*year^{-1}. For each of the six scenarios, I simulated annual "harvest" rates from 20 – 80% rates of the spawning population at 10% intervals using the following model,

$$\begin{aligned} R_{P,i} &= \hat{\alpha} S_i e^{-\hat{\beta} S_i + \sum \hat{c}_t X_{i,t} + \omega \hat{\sigma}_P} \\ S_{i+6} &= f_i R_{i+6} - h_i \end{aligned} \tag{6}$$

Simulations were run for 30 years and with 1000 repetitions of each fishing scenario.

The population trajectories were evaluated based on the following criteria. First, fishing programs that reduced populations below 100,000 were judged to have met the Lake Huron fish community objective. Final populations of 100-200,000 were considered to be approaching the target while simulated final populations greater than 200,000 were judged to be having no effect or an expanding population.

RESULTS

Estimating CPE: In general, model estimates of catch per effort reflected those observed in the four gear types (Figure 2.3). Estimated CPE was consistent with the observed EW data, reflecting the decline in abundance through the 1970s. Catchability at electrical weirs ($c_{ew}=0.35$) exceeded that of portable traps by approximately three fold. The observed MW data was generally consistent with model estimates with the exception of 1977 where the observed estimate of CPE was considerably greater than the predicted CPE. Mechanical weirs and portable assessment traps had similar catchability ($c_{mw}=1.16$). Estimated CPE was consistent with the CPE observed at portable assessment traps, reflecting the increase in spawner abundance through the 1980s. However, the observed CPE was not consistent with the observed CPE at dam traps in most years during the 1981-91 period, while the predicted and observed estimates were consistent during the 1994-2000 period. The large deviations in the dam trap time series likely reflects the small number of observations at dam traps relative to the number of observations at portable traps.

Based on the CPE index, the mean abundance of spawning sea lampreys in the first five years of the time series ($\bar{x}_{cpe} = 5.13; sd = 1.77$; Figure 2.4) was approximately 50% greater than the abundance during the last five years ($\bar{x}_{cpe} = 3.36; sd = 0.84$; Figure 2.4). As expected, relative abundance declined following the introduction of the TFM control program, with relatively low but variable estimates of abundance during the 1970s ($\bar{x}_{cpe} = 1.51; sd = 0.85$; Figure 4). Total assessment catch was greater in the later portion of the time series, reflecting greater trapping effort compared to the beginning of the time series.

Stock and recruitment model: Four stock and recruitment models were generated in the previous sections for the 1959-2000 time period. The "full model" consisted of the generalized Ricker model and two environmental variables, treatment history and lamprey weight. The three other models were nested within the full model (Table 2.2).

The area of habitat treated by the chemical treatment program varied considerably through the time series (Figure 2.5). The area treated through the early 1960s was relatively low because of a reduced treatment budget for Lake Huron during this era. However, the first peak in area treated occurred in 1972, followed by 25 years of relatively stable treatment effort. Area treated increased again in 1998 with granular Bayluscide treatments in the St. Marys River. Spawning weight of lamprey increased by more than 100 g during the study period, from <150 g in 1959 to >240 g in the 1990s (Figure 2.6). The greatest increase in weight occurred during the 1960s, corresponding to the increased treatment effort and decrease in the abundance index.

Figures 2.7 and 2.8 illustrate the linear relationship between log(R/S) and spawning stock and the model fit to the derived recruitment and spawning stock data for Model A. The negative slope of the relationship between log(R/S) and spawners suggests that significant density dependent survival occurred during the study period.

Model B (Ricker model with treatment area) did not increase the variance explained ($\chi^2 = 0.2, p > 0.10$) compared to Model A (Ricker model). Model C (Ricker model with spawning weight) provided a better model fit ($\chi^2 = 3.5, p = 0.06$) than the Ricker model. Model D (Ricker model with treatment area and lamprey weight) resulted in a better fit than Model A $\chi^2 = 6.1, p = 0.05$ but was not a better fit than Model C $\chi^2 = 2.7, p > 0.10$. Model C was deemed to be the "best fit" based on these comparisons although Models A and D were also considered in subsequent analyses.

The uncertainty in model parameters was characterized by the asymptotic standard deviations (SD) and by bootstrapping. Uncertainty of the parameter estimates for Model A were similar for both asymptotic SDs and bootstrap estimated SDs (Table 2.3; Figure 2.9) although bootstrap estimates underestimated asymptotic SDs for both log(α) and β. Results for Model C indicate similar estimates of parameter uncertainty among methods (Table 2.3; Figure 2.10) although bootstrapping estimated a higher SD for log(α). For Model D, estimates of parameter SDs were similar among methods (Table 2.3; Figure 2.11).

Correlation among model parameters is another indicator of the degree of uncertainty in parameter estimates because high correlation suggests that a wide range of parameter estimates can produce similar fits to the data. Parameter correlation was substantial in all models tested (Table 2.4). For example, the correlation between log(α) and β for Model A was $r_{\sigma,\beta}$=-0.93. The addition of lamprey weight as an explanatory variable in Model C reduced the correlation between log(α) and β parameters but not appreciably ($r_{\sigma,\beta}$=-.84) although the correlation between the "weight" parameter and the Ricker parameters was lower ($r_{\sigma,\mathrm{wt}}$= 0.01; $r_{\beta,\mathrm{wt}}$ = -0.40).

Potential biases in parameter estimates were examined through analysis of 1000 Monte Carlo simulations (MCS) for Models A, C and D (Table 2.5). In general, parameter estimates in all three models were consistently estimated over the range of observation error considered in the modelling (Table 2.5). The estimate of *log(α)* was underestimated by the MCSs in each model. The process error (σ_{sr}) was well estimated at low and moderate levels of recruitment observation error (0.0 – 0.2). However, in each model the estimate of σ_{sr} increased when modeled with increasing recruitment observation error.

Examination of residuals of Model A suggests a non-stationary stock and recruitment relationship (Figure 2.12a). Most residuals prior to the 1970 spawning year are negative followed by long periods of positive residuals after 1970. There are no significant autocorrelations (p>0.05) for any lag in the residuals except for lag 1 suggesting that recruitment events varied randomly around the average stock recruitment relationship. The addition of explanatory variables (Models C and D) "improved" the pattern of residuals with a more even distribution of residuals (Figure 2.12b, c). However, a pattern of strong negative residuals and strong positive residuals corresponding to spawning years in the late 1960s and 1970s, respectively, is evident in all models.

Figure 2.13 illustrates the change in the stock-recruitment relationship as lamprey as a function of changes in lamprey weight. As noted above, lamprey weight increased throughout the study period. Consequently, the maximum recruitment for Model C increased by 90,000 lamprey when comparing the first ten years of the time series with the last ten years.

Management parameters S_{msy} , u_{msy} and msy were calculated for Models A, C and D (Table 2.6). For models C and D, the a parameter was recast as $\tilde{a} = \log(\alpha) + c_{wt}wt$, $\tilde{a} = \log(\alpha) + c_{wt}wt + c_{tr}tr$ and $\alpha = \exp(\tilde{a})$ (Quinn and Deriso 1999), respectively, where wt and tr are the averages over the final ten years of the time series of weight and area treated. The addition of weight and treated area as explanatory variables had the effect of increasing the estimate of stock productivity compared to the mean over the entire time series (Figure 2.13). For example, u_{msy} increased from 0.58 to 0.69 while S_{msy} decreased from 89,300 to 80,800 with the addition of weight as an explanatory variable.

Simulating the effect of alternative control: The interaction of control effort, lamprey size and fishing effort affected the trajectory of simulated populations in Lake Huron (Figure 2.14, 2.15) and the likelihood of achieving fish community objectives (Table 2.7) although variation was substantial in all scenarios. In simulations with treatment effort similar to the 1990s and decreasing weight, F= 0.5 resulted in a >80% likelihood of achieving fish community objectives compared to F=0.6 and F=0.7 for no change in weight and increasing weight, respectively. With decreasing or stable lamprey weight, all fishing strategies, on average, resulted in decreasing lamprey populations (Figure 14a, b). However, if weight increased, F >0.4 on average resulted in declining recruitment (Figure 2.14c). In all weight and fishing strategies, recruitment did not exceed those observed in the 1990s.

In simulations where treatment effort is reduced by 50%, the fishing effort required to meet the fish community objectives increased substantially compared to the *status quo* treatment effort. In simulations of decreasing and static weight, fish community objective were met in 80% of simulations only when F=0.8. Fish community objectives were met in <80% in simulations of increasing weight regardless of the fishing strategy (Table 2.7). When lamprey weight decreased in the simulations, fishing intensities of 0.2 – 0.4 resulted, on average, in significant increases in recruitment while intensities of 0.5 and 0.6 resulted in stable recruitment (Figure 2.14a). Recruitment declined significantly with fishing intensities of 0.7 – 0.8. Results for simulations with stable weight were similar except that recruitment increased on average for fishing intensities ranging from 0.2 – 0.6 and only fishing intensities of 0.8 resulted in declining populations (Figure 2.15b). When lamprey weight increased, recruitment increased at a similar rate for all fishing intensities ranging from 0.2 - 0.6 and significant declines were not observed in the simulations until fishing intensity increased to 0.8. Simulations that assumed reduced lampricide treatments had a much wider range in recruitment compared to simulations assuming treatment simulations similar to the 1990s.

DISCUSSION

Observation model: These data indicate a pattern of abundance similar to that described by Morse et al. (1995). Lamprey abundance declined precipitously during the period 1965-72 which has been attributed to larval mortality caused by the TFM treatment program (Morse et al. 2003). Low abundance during the 1970s was followed by a doubling of the population in the 1980s. Young et al. (1996) suggest that production of larvae from the St. Marys River and increased survival of recently transformed larvae contributed to the increased abundance.

The estimation procedure used in this analysis assumed that CPE in each of the trapping techniques was an unbiased estimator of spawner abundance. However, it is unlikely that this assumption was met. None of the techniques used to assess spawning populations can be considered standard fishery techniques and each was developed specifically for the sea lamprey program. As a result, considerable "learning" likely occurred with the introduction of each technology resulting in a time varying catchability where the estimates of CPE at the introduction of a methodology would be underestimated relative to the end of a time series. This phenomenon may have exaggerated the difference between CPE at EW and PTs. For example, the proportionality constant for the EWs was developed between the overlap of the EWs at the end of their use and first use of PTs. If the CPE_{pt} was low at the beginning of the time series due to the introduction of a new methodology, then the population estimates would be exaggerated for those years with electrical weir trapping.

A second precaution stems from the non-random selection of streams used in the annual spawning run assessments. Moore and Schleen (1980) noted that spawning runs in some streams declined significantly following TFM treatments, likely because streams became less attractive due to the drop in migratory pheromone produced by larvae (Sorensen et al. 2003). While spawning runs in most streams returned to pre-treatment abundance, other spawning runs remained low. The response of the lamprey control agents was to not fish streams with consistently low spawning runs. For example, catches in the Still River were 554 in 1987 (immediately after the construction of the barrier dam) but declined to 34 in 1991 after which the trap was no longer fished. This form of "high grading" could have overestimated the CPE in all trap types, especially after the TFM treatment program stabilized post-1972.

Stock and recruitment: The models considered in this analysis indicated that a significant degree of compensatory survival was evident in the Lake Huron populations throughout the study period. The addition of mass and area treated with lampricides to model as explanatory variables significantly improved the fit of the Ricker model, indicating that environmental conditions experienced by lampreys in the parasitic life stage and the chemical treatment program were important determinants of recruitment in addition to spawning stock. In general, higher spawning mass increased recruitment while increases in area treated suppressed recruitment.

These conclusions are consistent with Jones et al. (2003) and Haseker et al. (2003) in that both of these studies reported significant compensatory survival. The significance of density independent factors was less pronounced in this study and persisted over the range of observed spawning populations. However, consistent with previous studies, the parameters of the stock – recruitment model was estimated with significant uncertainty in the parameter estimates and process error. The effect of this uncertainty in decision making was striking in the simulation modeling where a large range of outcomes was likely for all fishing strategies.

The magnitude of the compensatory response is important when considering whether to use alternative control tactics to further reduce populations in Lake Huron. Haseker et al. (2003) proposed a compensation ratio to describe the magnitude of compensation in recruitment. Populations with high compensation ratios were unlikely to decline due to reductions in recruitment. In this study, the expected compensation ratio was a relatively low (1.51) in the context of reducing Lake Huron populations from around 200,000 to 75,000.

Simulating the effect of alternative control: The GLFC's vision (GLFC 2001) is to reduce lamprey management program's dependency on the TFM program such that half of control is achieved using alternative control measures and half through traditional pesticide applications. In addition, the GLFC hopes to meet the Lake Huron Committee's fish community objective for the sea lamprey by reducing the population by at least 75% or approximately 75,000 spawning lampreys. All of the current options for alternative control involve removing or preventing spawning sea lampreys from completing their life cycle. I viewed each of these alternative control techniques as variants on fishing or harvest.

The management parameters used in maximum sustained yield strategies or $F_{0.0}$ indicate that sea lamprey have high rates of productivity relative to other fish populations. My results indicate lamprey harvest as a proportion of the population could be sustained at a relatively high level relative to other Lake Huron species. For example, lamprey $u_{msy}=0.59$ determined from the generalized Ricker model in this study is relatively high compared to the target total annual mortality for lake trout of 45% (Johnson et al. 1995). In the context of lamprey management, u_{msy} is a conservative target for fishing mortality because fishing plans based on this strategy often lead to declines in populations because of parameter and process uncertainties (Larkin 1977; Sissenwine 1978; Caddy and McGarvey 1996). The simulation modeling in this study indicate that, on average, declines in lamprey population size are likely at fishing rates much less than u_{msy}. Only in simulations involving increasing lamprey weight did fishing mortality rates approach u_{msy} for declines in population to approach the FCO objectives.

Does the GLFC policy of increasing the use of alternative control methods have a reasonable likelihood of success? Jones et al. (2003) indicated that density independent variation may compromise the effectiveness of alternative control methods. However, they contend that alternative control tactics could be effective supplements to the TFM program. The results of this analysis are consistent with their conclusion. Klar and Young (2003) report average trap efficiency in Lake Huron of 48% (22-80%). Their data indicate that approximately 41% of the discharge of primary sea lamprey producing streams is currently being trapped resulting in a "fish-up" of approximately 19% in Lake Huron. Increasing the trap effort to the 10 largest primary producing streams not currently fished would increase the stream discharge fished to >95% and an expected "fish-up" of ~42%. This magnitude of increase using traditional trapping procedures approaches the level of effort required to meet the Lake Huron FCOs if lampricide treatment effort remains at rates similar to those of the 1990s. Consequently, only modest increases in "fish-up" from new alternative control methods would be required to meet these objectives. However, if lampricide treatment effort is reduced to meet other program objectives (GLFC 2001), then alternative control strategies would need to Double current trapping efficiencies to meet fish community objectives.

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LIST OF TABLES

Table 2.1. Trap type (EB = electrical barrier; MW = mechanical weir; PT = portable trap; DT = low-head barrier trap), the years of service, and the range (*k*) in the number of streams fished in a season with each gear type.

Trap Type	Years in Service	*k*
EB	1959-80	1-9
MW	1965,1977-81	1
PT	1977-2000	3-13
DT	1981-2000	1-2

Table 2.2 Description of parameters included in each of the four stock-recruitment models considered (0=not included in the model; 1=included in the model.

Model	α	β	Weight	Treatment
A	1	1	0	0
B	1	1	1	0
C	1	1	0	1
D	1	1	1	1

Table 2.3. Parameter estimates, asymptotic standard deviations, standard deviations and 95% confidence intervals derived from 1000 bootstrap samples for Models A, C, and D.

Parameter	Model A	Model C	Model D
$\log(\alpha)$	1.359	1.374	2.301
$\sigma_{\log(\alpha)}$	0.230	0.213	0.592
$\sigma_{\log(\alpha)}$ (bootstrap)	0.192	0.242	0.544
lower 95% C.I.	1.058	1.065	1.288
upper 95% C.I.	1.832	1.893	3.453
B	-6.16E-06	-7.88E-06	-8.70E-06
σ_{β}	1.80E-06	2.31E-06	2.43E-06
σ_{β} (bootstrap)	1.49E-06	2.30E-06	2.92E-06
lower 95% C.I.	-1.05E-05	-1.35E-05	-1.49E-05
upper 95% C.I.	-4.48E-06	-5.67E-06	-6.25E-06
C_{wt}		0.006	0.012
σ_{C}		0.003	0.005
σ_{C} (bootstrap)		0.003	0.004
lower 95% C.I.		0.002	0.002
upper 95% C.I.		0.010	0.020
C_{tr}			-4.49E-08
σ_{tr}			2.68E-08
σ_{tr} (bootstrap)			2.55E-08
lower 95% C.I.			-9.16E-08
upper 95% C.I.			4.71E-09
q	1.286E-05	1.530E-05	1.554E-05
σ_{q}	2.291E-06	2.912E-06	2.840E-06
σ_{sr}	0.882	0.789	0.706
σ_{sdr}	0.465	0.484	0.516

Table 2.4. Stock-recruitment parameter correlation matrices for Models a) Model A, b) Model C, and, c) Model D.

Model A

	log(α)	β
log(α)	1	
B	-0.9285	1

Model C

	log(α)	β	C_{wt}
log(α)	1		
B	-0.8416	1	
C_{wt}	0.0065	-0.3985	1

Model D

	log(α)	β	C_{wt}	C_{tr}
log(α)	1			
β	-0.4835	1		
C_{wt}	0.7673	-0.3969	1	
C_{tr}	-0.9397	0.2222	-0.8169	1

Table 2.5 Parameter estimates derived from 1000 Monte Carlo simulations for a) Model A, b) Model C, and c) Model D. Parameter values were based on the results in Table 2.3.

Model A

σ_o	log(α)	β	σ_p
0.0	1.303	-5.58E-06	0.880
0.1	1.301	-5.57E-06	0.878
0.2	1.293	-5.52E-06	0.925
0.3	1.295	-5.49E-06	0.974

Model C

σ_o	log(α)	β	c_{wt}	σ_p
0.0	1.234	-6.66E-06	0.006	0.790
0.1	1.228	-6.62E-06	0.006	0.809
0.2	1.219	-6.56E-06	0.006	0.838
0.3	1.212	-6.46E-06	0.006	0.893

Model D

σ_o	log(α)	β	c_{wt}	c_{tr}	σ_p
0.0	1.906	-7.12E-06	0.010	-3.37E-08	0.708
0.1	1.878	-7.07E-06	0.010	-3.26E-08	0.715
0.2	1.839	-6.91E-06	0.010	-3.15E-08	0.766
0.3	1.794	-6.77E-06	0.010	-3.01E-08	0.831

Table 2.6 Estimates of management parameters (exploitation rate at msy (u_{msy}), stock size at msy (S_{msy}), and maximum sustained yield (msy)), asymptotic standard deviations, standard deviations and 95% confidence intervals derived from 1000 bootstrap samples for Models A, C, and D.

Parameter	Model A	Model C	Model D
u_{msy}	0.587	0.691	0.717
σ_u	0.084	0.086	0.081
σ_u (bootstrap)	0.074	0.082	0.067
lower 95% C.I.	0.448	0.571	0.596
upper 95% C.I.	0.662	0.851	0.857
S_{msy}	89331	80750	75497
σ_S	15947	15999	14835
σ_S (bootstrap)	11393	11496	10620
lower 95% C.I.	62303	56919	52680
upper 95% C.I.	93193	100523	93369
MSY	111230	143370	146460
σ_{msy}	20052	25553	25052
σ_{msy} (bootstrap)	18661	149660	22749
lower 95% C.I.	77882	109265	111560
upper 95% C.I.	151255	200555	202027

Table 2.7 The results of simulating the effect of varying the fishing mortality rate, *F*, from 0.2 to 0.8 for Model C for a) lamprey size decreases by 1.0 g annually from the 1990s mean weight and constant treatment effort, b) lamprey size remains static at 1990s mean size and constant treatment effort, c) lamprey size increase by 1.0 g from the 1990s mean size and constant treatment effort, d) lamprey size decreases by 1.0 g annually from the 1990s mean weight and 50% of treatment effort, e) lamprey size remains static at 1990s mean size and 50% treatment effort, and, f) lamprey size increase by 1.0 g from the 1990s mean size and 50% of treatment effort.

A

F	<100K	125K>p(N)<200K	200K
0.2	0.54	0.34	0.12
0.3	0.64	0.29	0.07
0.4	0.72	0.23	0.05
0.5	0.88	0.12	0.01
0.6	0.96	0.04	0.00
0.7	1.00	0.00	0.00
0.8	1.00	0.00	0.00

B

F	<100K	125>p(N)<200	200
0.2	0.38	0.39	0.23
0.3	0.48	0.36	0.16
0.4	0.58	0.30	0.12
0.5	0.72	0.22	0.06
0.6	0.87	0.12	0.01
0.7	0.99	0.01	0.00
0.8	1.00	0.00	0.00

C

F	<100K	125>p(N)<200	200
0.2	0.24	0.41	0.36
0.3	0.31	0.39	0.30
0.4	0.40	0.38	0.23
0.5	0.56	0.33	0.12
0.6	0.76	0.19	0.05
0.7	0.94	0.06	0.00
0.8	1.00	0.00	0.00

D

F	<100K	125K>p(N)<200K	200K
0.2	0.17	0.28	0.55
0.3	0.16	0.28	0.57
0.4	0.16	0.34	0.51
0.5	0.19	0.40	0.41
0.6	0.34	0.41	0.25
0.7	0.64	0.27	0.09
0.8	0.96	0.04	0.00

E

F	<100K	125K>p(N)<200K	200K
0.2	0.18	0.20	0.62
0.3	0.15	0.22	0.63
0.4	0.11	0.27	0.63
0.5	0.09	0.32	0.59
0.6	0.21	0.36	0.43
0.7	0.44	0.34	0.22
0.8	0.87	0.11	0.02

F

F	<100K	125K>p(N)<200K	200K
0.2	0.13	0.18	0.69
0.3	0.10	0.18	0.73
0.4	0.08	0.18	0.74
0.5	0.09	0.22	0.70
0.6	0.10	0.31	0.60
0.7	0.27	0.36	0.37
0.8	0.72	0.20	0.08

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Figure 2.1

Stock recruitment model

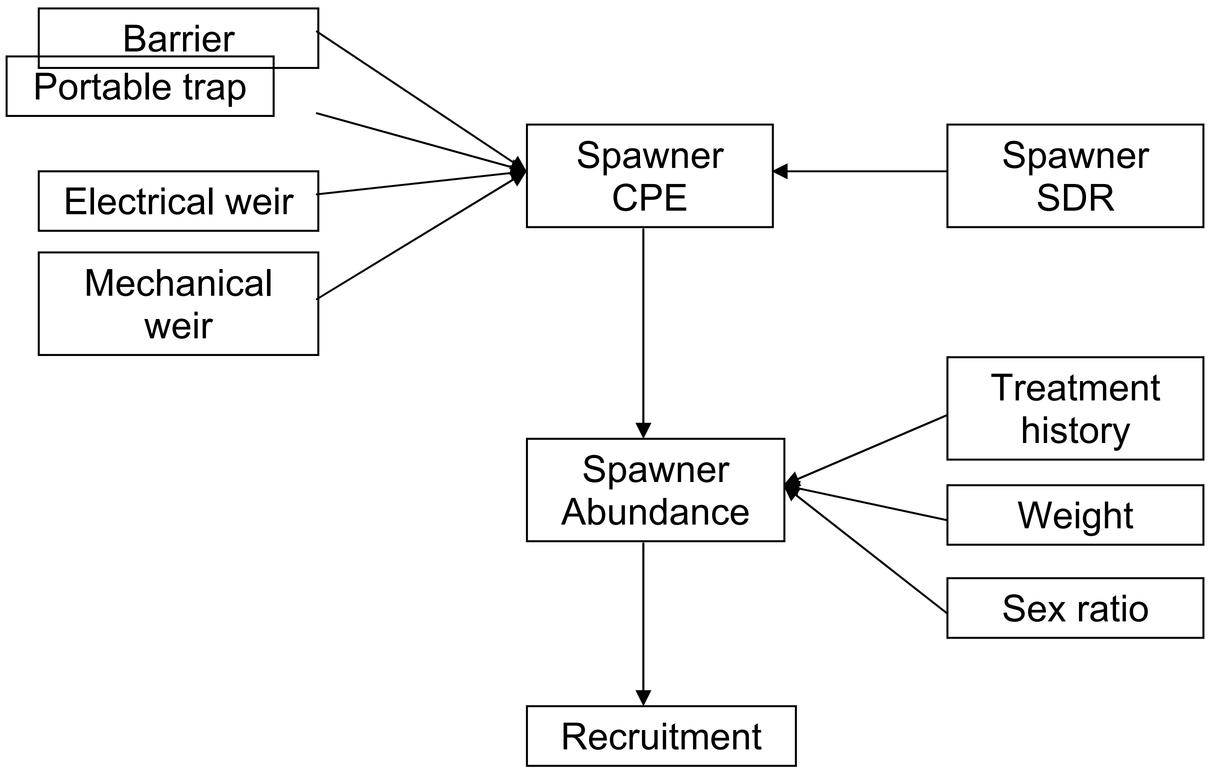


Figure 2.2.

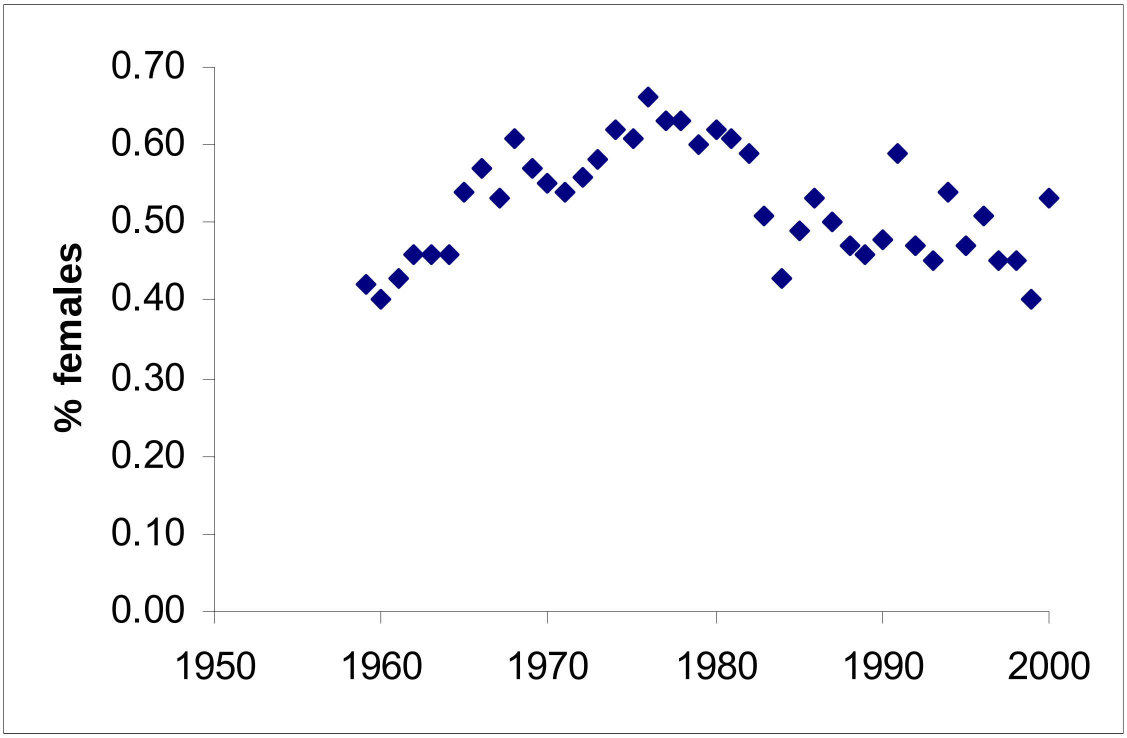

0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00
% females
1950
1960
1970
1980
1990
2000

Figure 2.3.

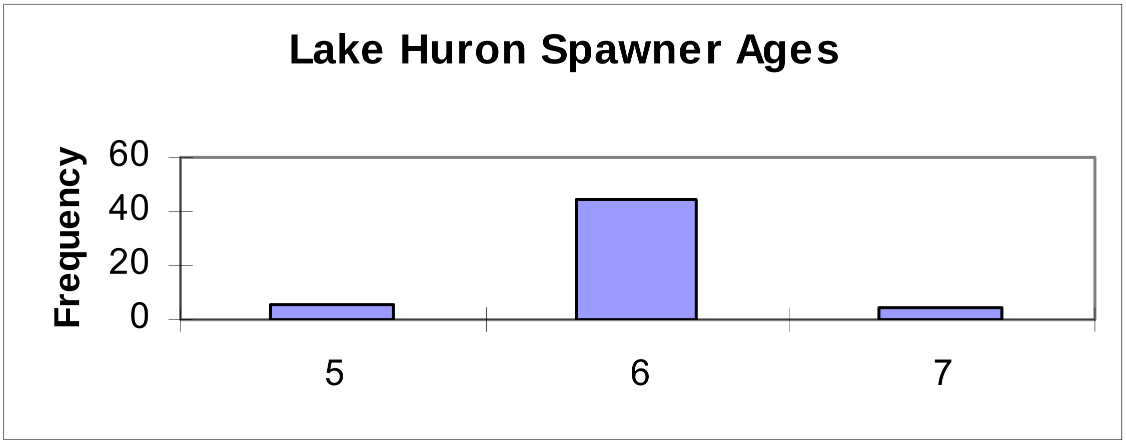


Figure 2.4.

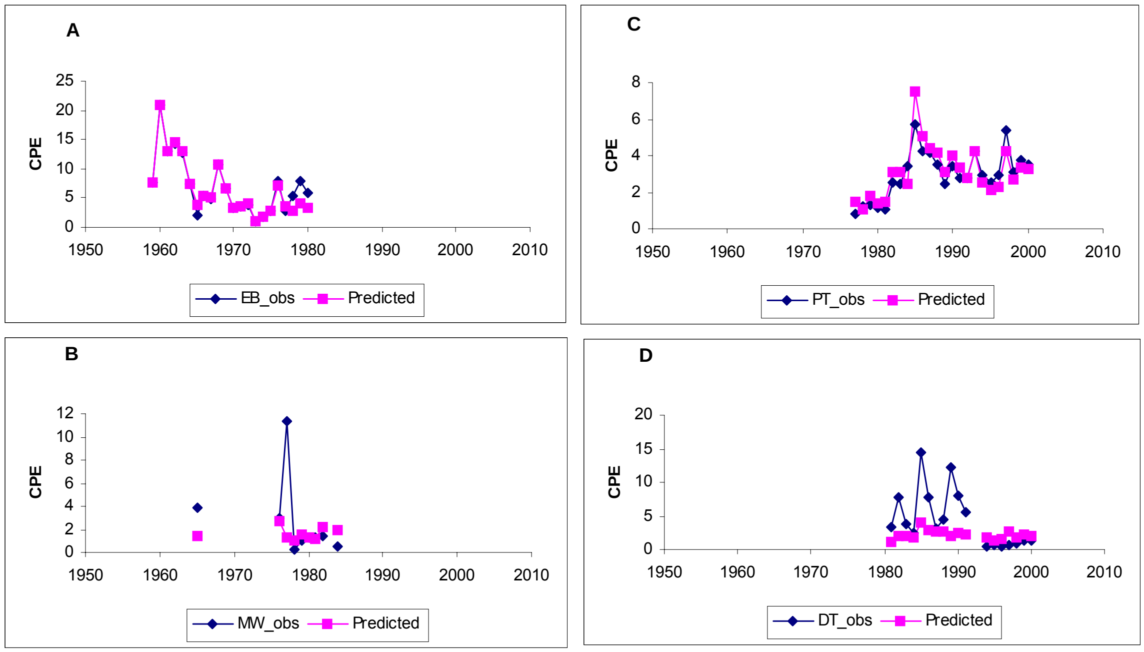
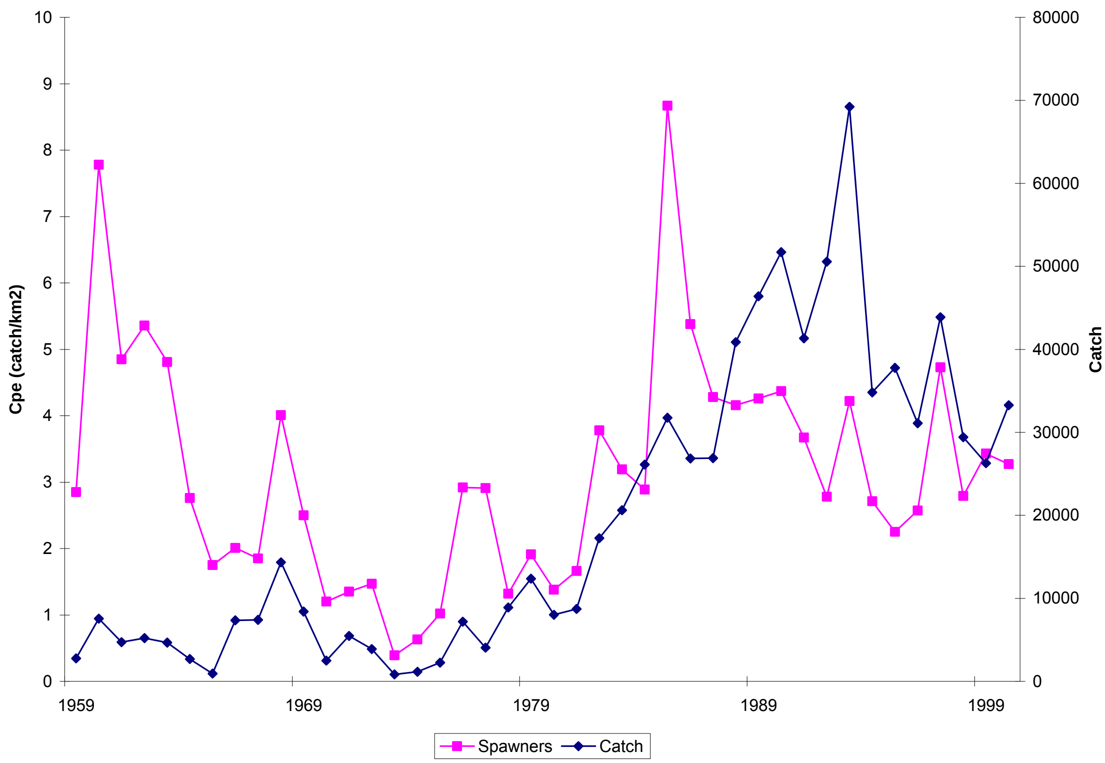
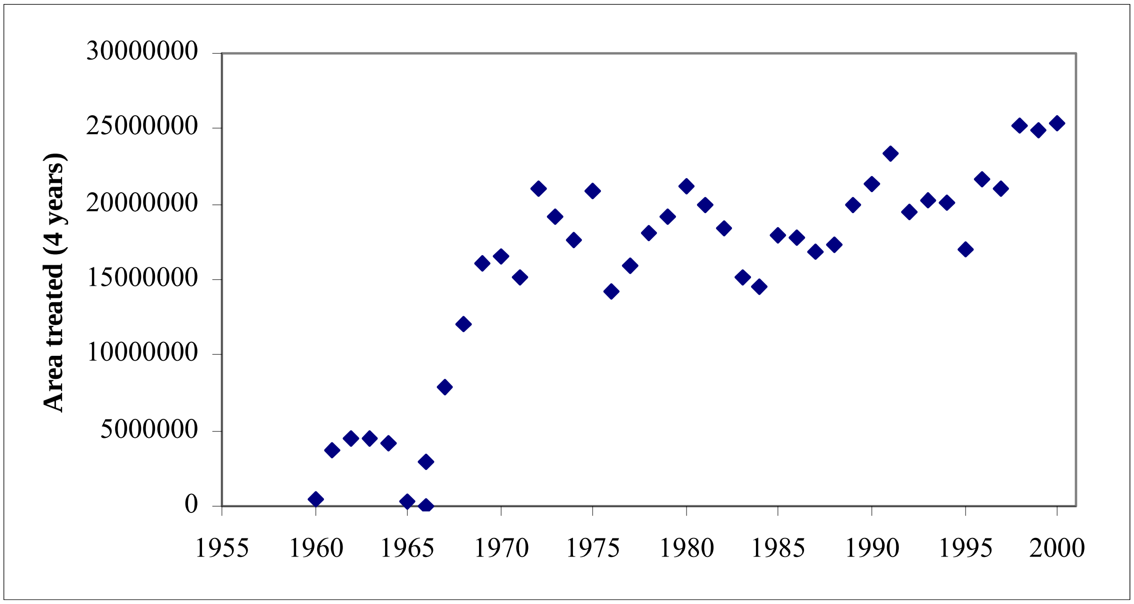

A
CPE
25
20
15
10
5
0
1950
1960
1970
1980
1990
2000
2010
EB_obs
Predicted
C
CPE
8
6
4
2
0
1950
1960
1970
1980
1990
2000
2010
PT_obs
Predicted
B
CPE
12
10
8
6
4
2
0
1950
1960
1970
1980
1990
2000
2010
MW_obs
Predicted
D
CPE
20
15
10
5
0
1950
1960
1970
1980
1990
2000
2010
DT_obs
Predicted

Figure 2.5.



Cpe (catch/km2)
Catch
10
9
8
7
6
5
4
3
2
1
0
80000
70000
60000
50000
40000
30000
20000
10000
0
1959
1969
1979
1989
1999
Spawners
Catch

Figure 2.6.



30000000
25000000
20000000
15000000
10000000
5000000
0
Area treated (4 years)
1955
1960
1965
1970
1975
1980
1985
1990
1995
2000

Figure 2.7.

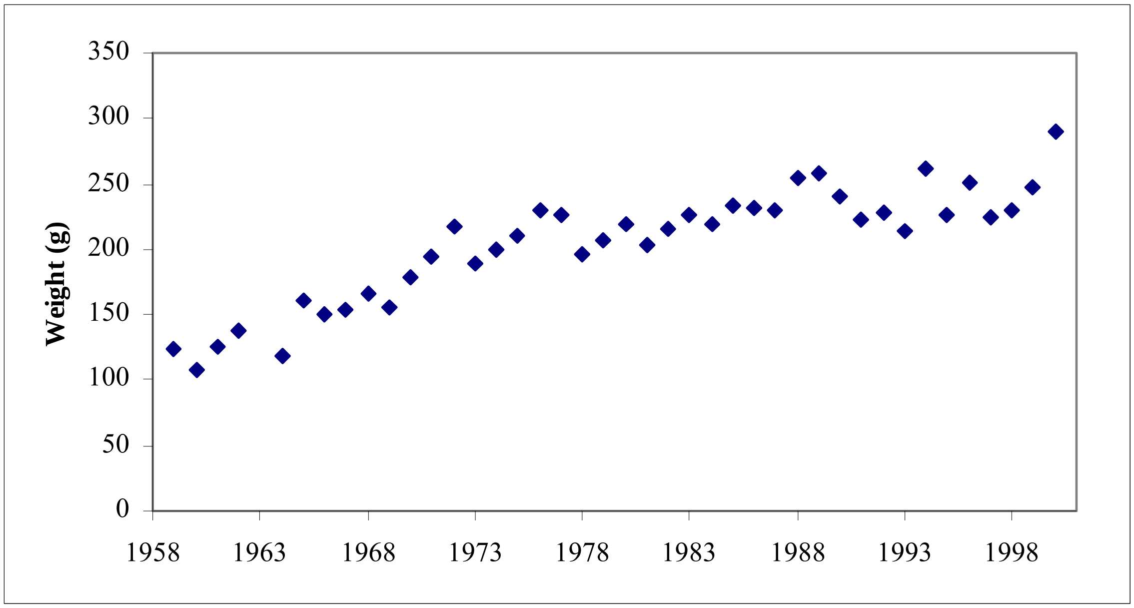

350
300
250
200
150
100
50
0
Weight (g)
1958
1963
1968
1973
1978
1983
1988
1993
1998

Figure 2.8.

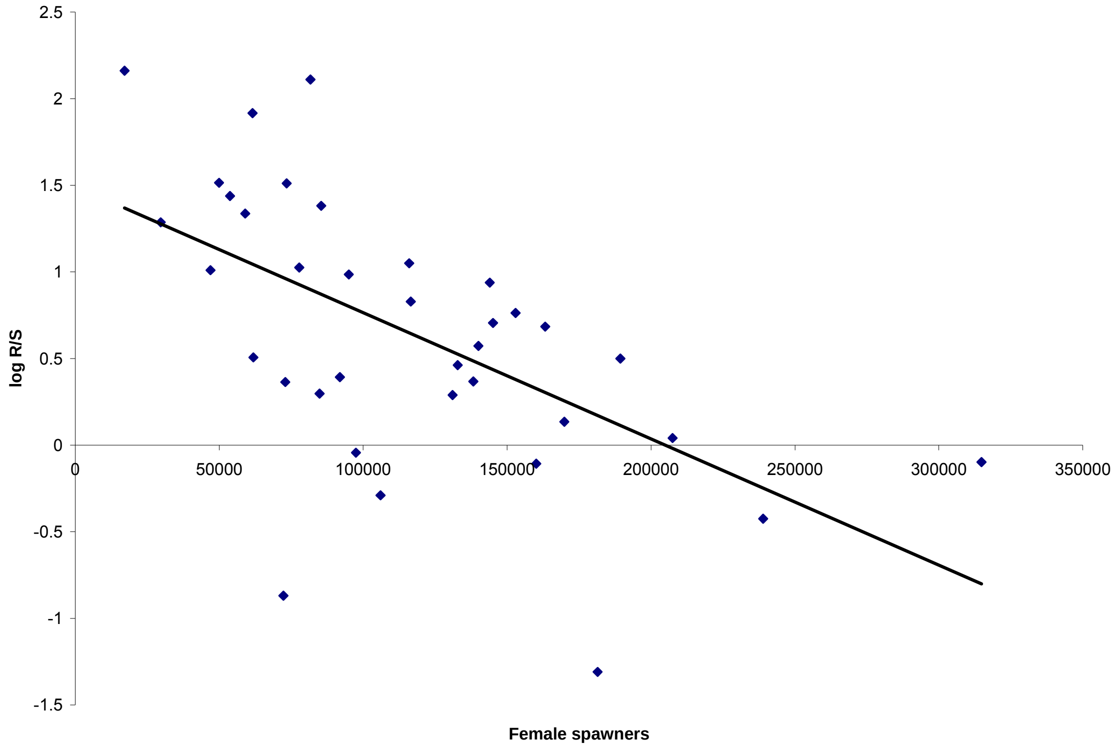

2.5
2
1.5
1
0.5
0
-0.5
-1
-1.5
log R/S
0
50000
100000
150000
200000
250000
300000
350000
Female spawners

Figure 2.9.

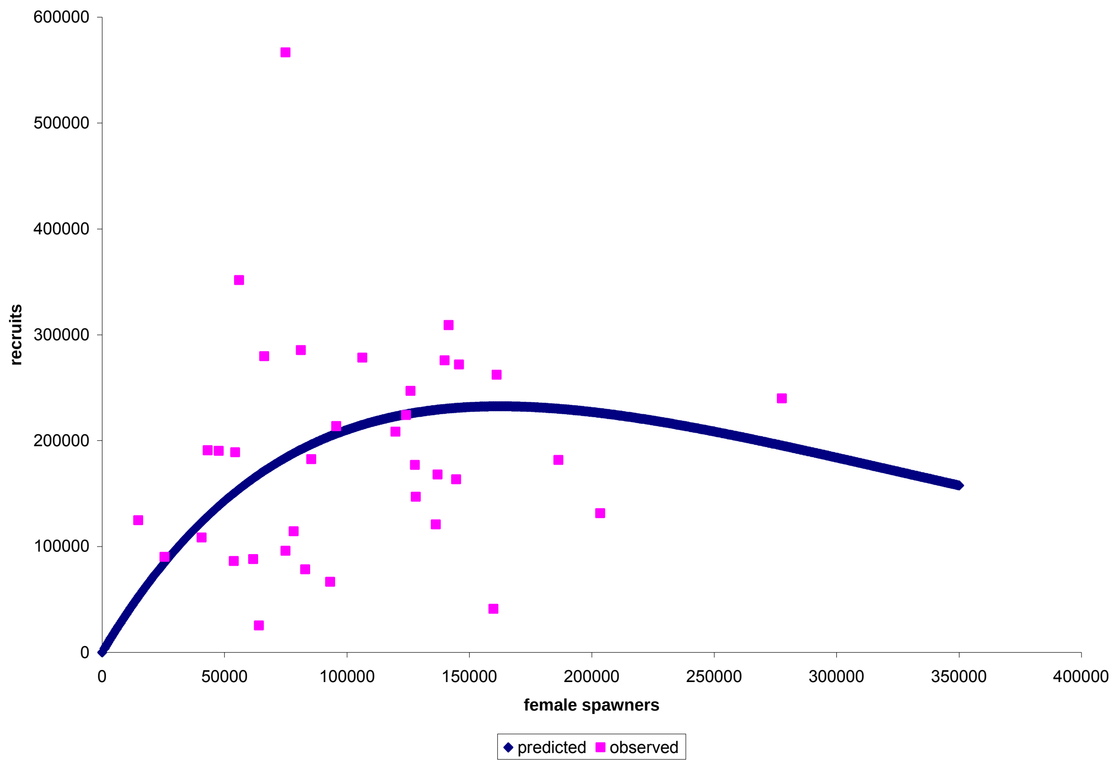

600000
500000
400000
300000
200000
100000
0
recruits
0
50000
100000
150000
200000
250000
300000
350000
400000
female spawners
predicted
observed

Figure 2.10.

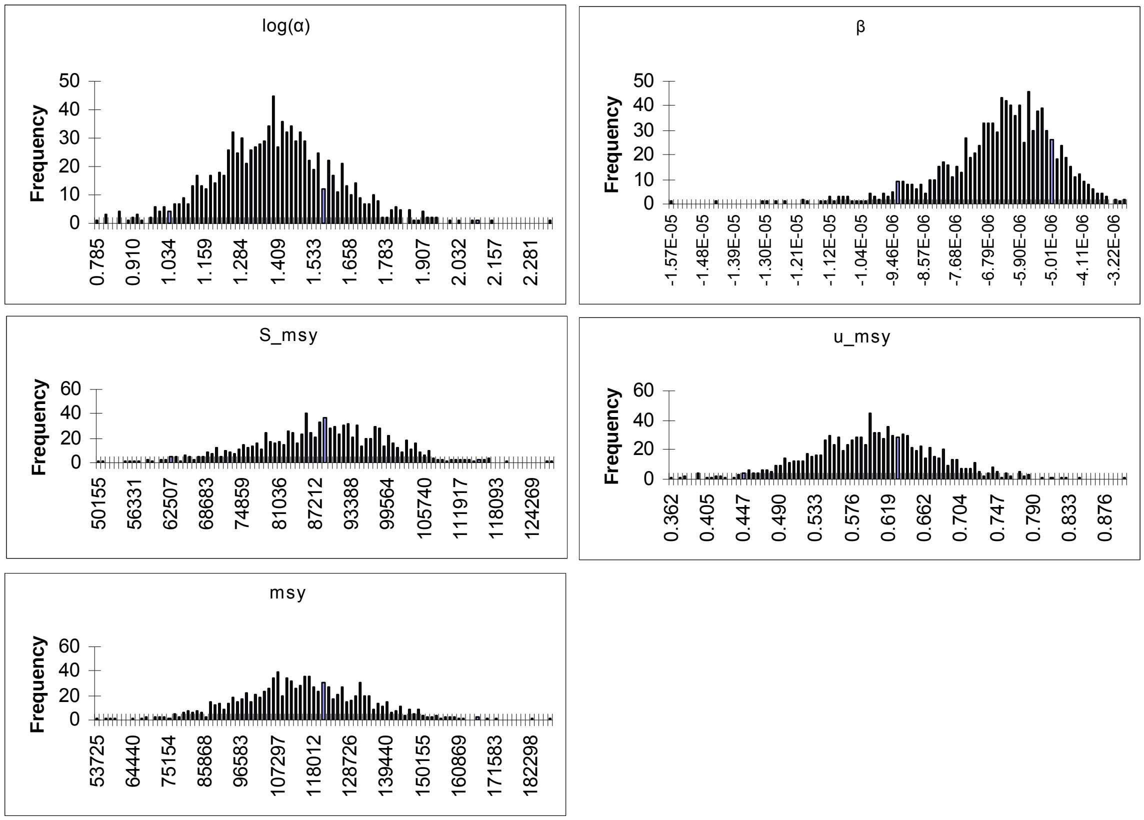
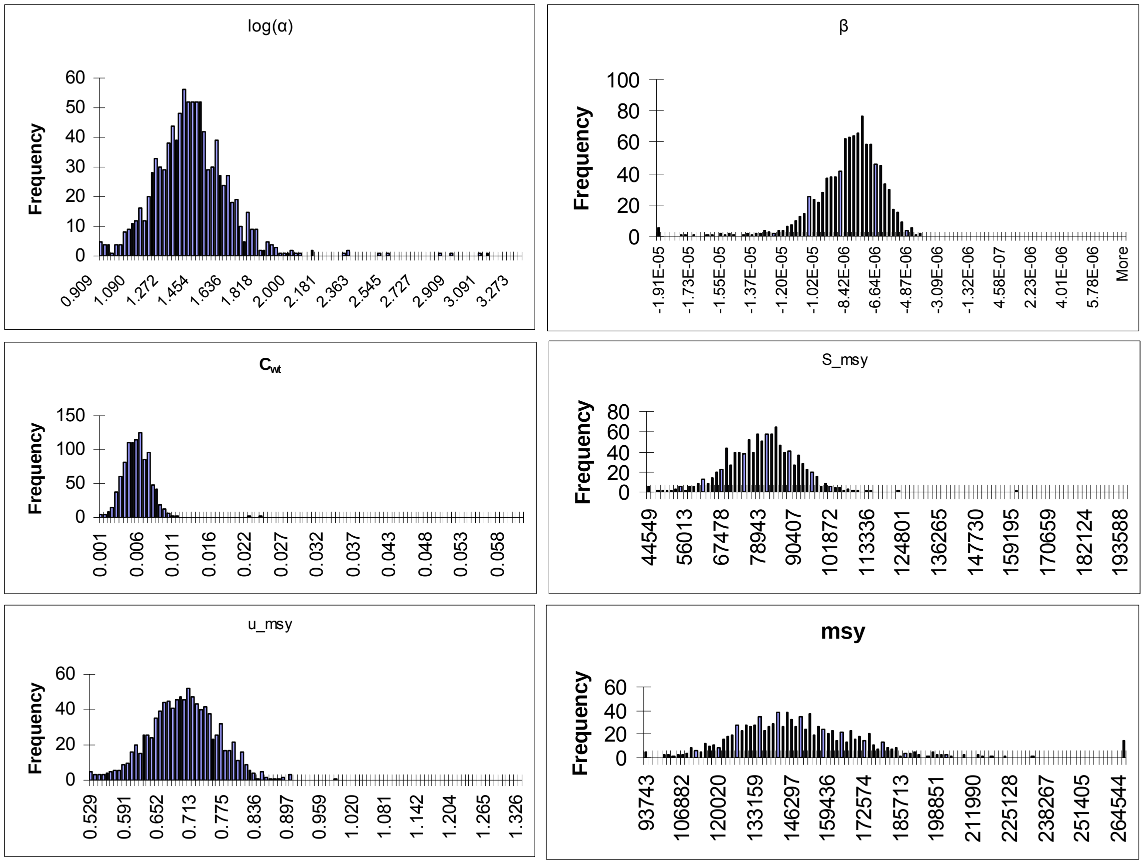

log(α)
Frequency
50
40
30
20
10
0
0.785
0.910
1.034
1.159
1.284
1.409
1.533
1.658
1.783
1.907
2.032
2.157
2.281
β
Frequency
-1.57E-05
-1.48E-05
-1.39E-05
-1.30E-05
-1.21E-05
-1.12E-05
-1.04E-05
-9.46E-06
-8.57E-06
-7.68E-06
-6.79E-06
-5.90E-06
-5.01E-06
-4.11E-06
-3.22E-06
S_msy
Frequency
60
40
20
0
50155
56331
62507
68683
74859
81036
87212
93388
99564
105740
111917
118093
124269
u_msy
Frequency
0.362
0.405
0.447
0.490
0.533
0.576
0.619
0.662
0.704
0.747
0.790
0.833
0.876
msy
Frequency
53725
64440
75154
85868
96583
107297
118012
128726
139440
150155
160869
171583
182298

Figure 2.11.



log(α)
Frequency
β
Frequency
C_{wt}
Frequency
S_msy
Frequency
u_msy
Frequency
msy
Frequency

Figure 2.12.

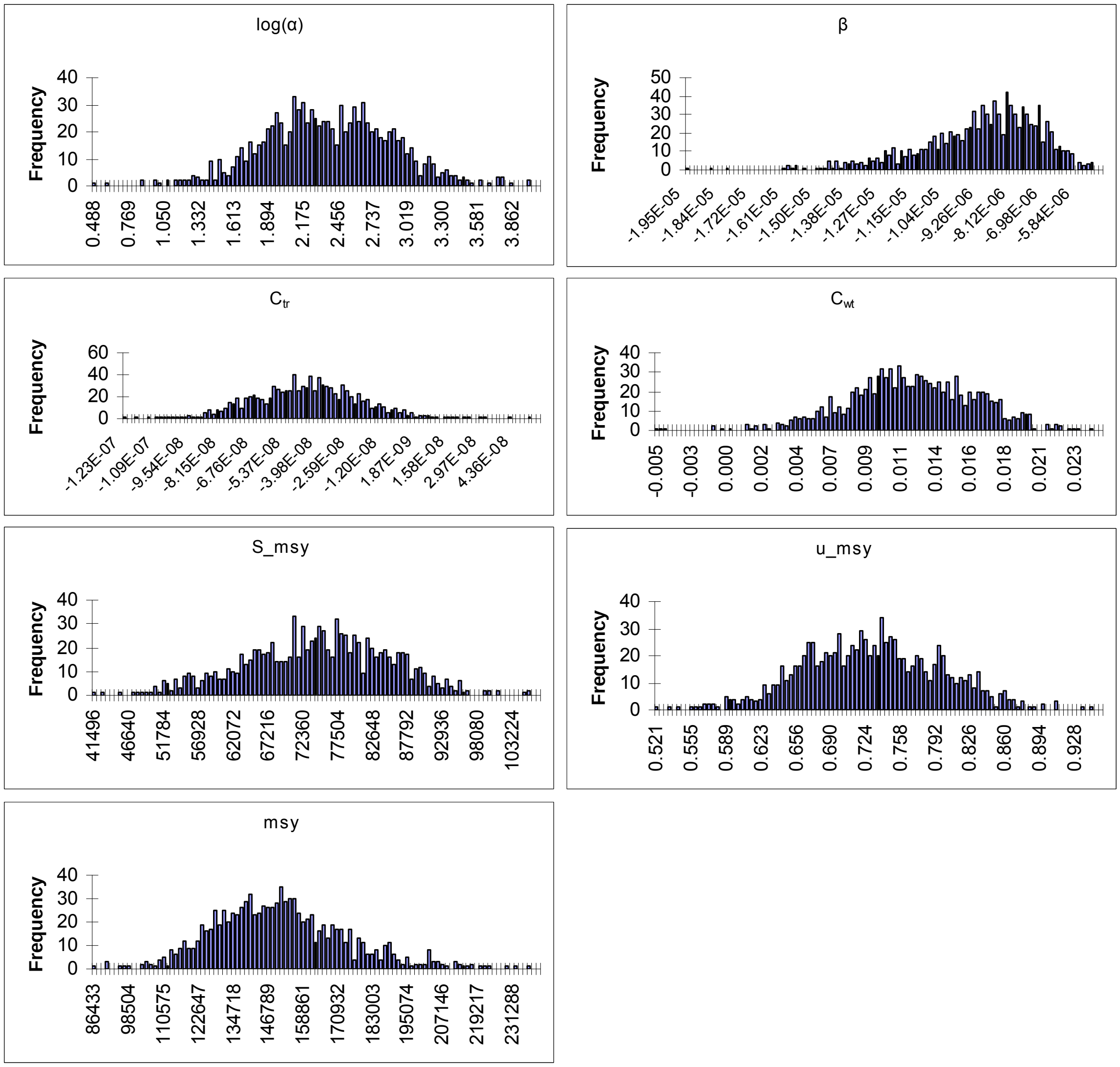
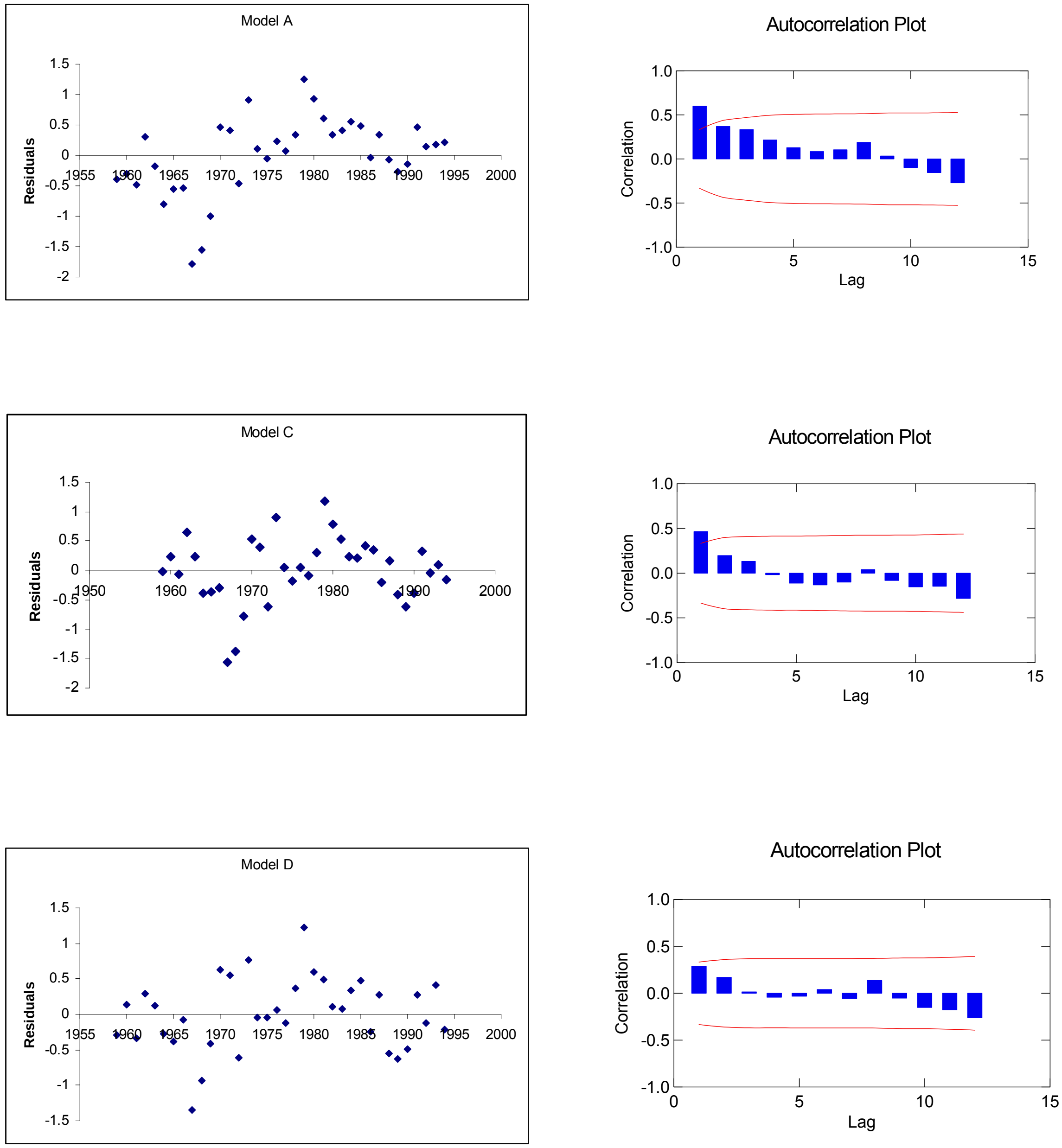

log(α)
Frequency
40
30
20
10
0
0.488
0.769
1.050
1.332
1.613
1.894
2.175
2.456
2.737
3.019
3.300
3.581
3.862
β
Frequency
50
40
30
20
10
0
-1.95E-05
-1.84E-05
-1.72E-05
-1.61E-05
-1.50E-05
-1.38E-05
-1.27E-05
-1.15E-05
-1.04E-05
-9.26E-06
-8.12E-06
-6.98E-06
-5.84E-06
C_{tr}
Frequency
60
40
20
0
-1.23E-07
-1.09E-07
-9.54E-08
-8.15E-08
-6.76E-08
-5.37E-08
-3.98E-08
-2.59E-08
-1.20E-08
1.87E-09
1.58E-08
2.97E-08
4.36E-08
C_{wt}
Frequency
40
30
20
10
0
-0.005
-0.003
0.000
0.002
0.004
0.007
0.009
0.011
0.014
0.016
0.018
0.021
0.023
S_msy
Frequency
40
30
20
10
0
41496
46640
51784
56928
62072
67216
72360
77504
82648
87792
92936
98080
103224
u_msy
Frequency
40
30
20
10
0
0.521
0.555
0.589
0.623
0.656
0.690
0.724
0.758
0.792
0.826
0.860
0.894
0.928
msy
Frequency
40
30
20
10
0
86433
98504
110575
122647
134718
146789
158861
170932
183003
195074
207146
219217
231288

Figure 2.13.



Model A
Residuals
Autocorrelation Plot
Correlation
Lag
Model C
Residuals
Autocorrelation Plot
Correlation
Lag
Model D
Residuals
Autocorrelation Plot
Correlation
Lag

Figure 2.14.

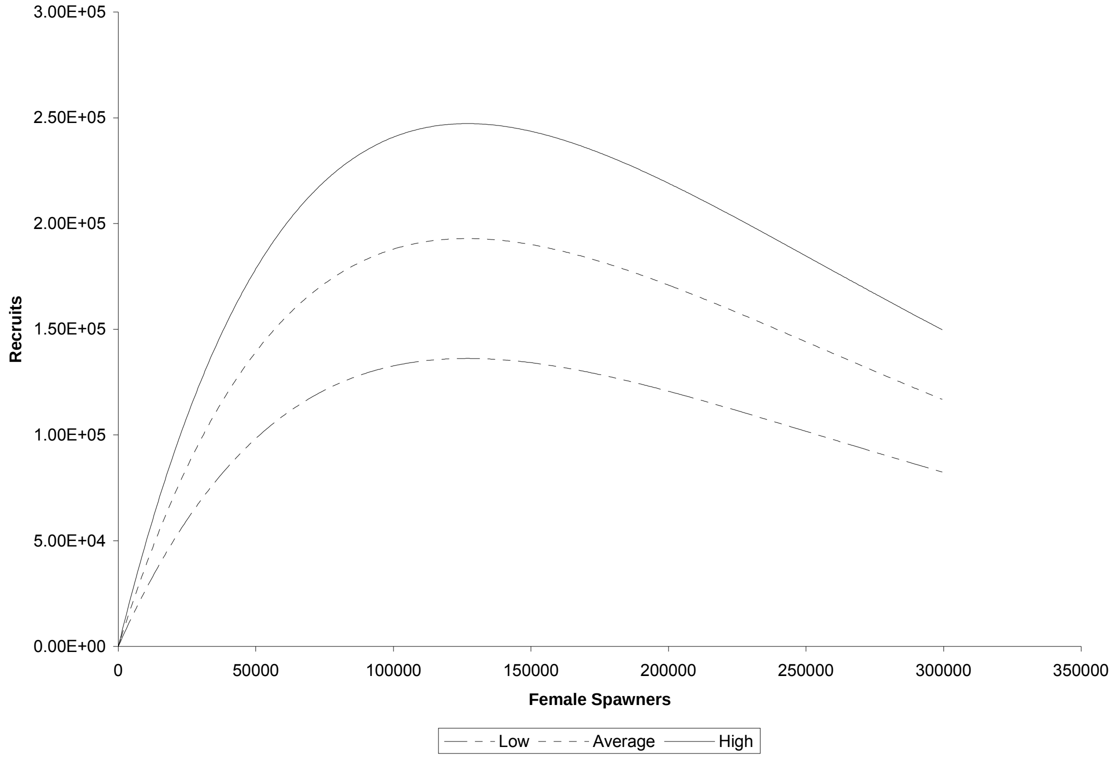
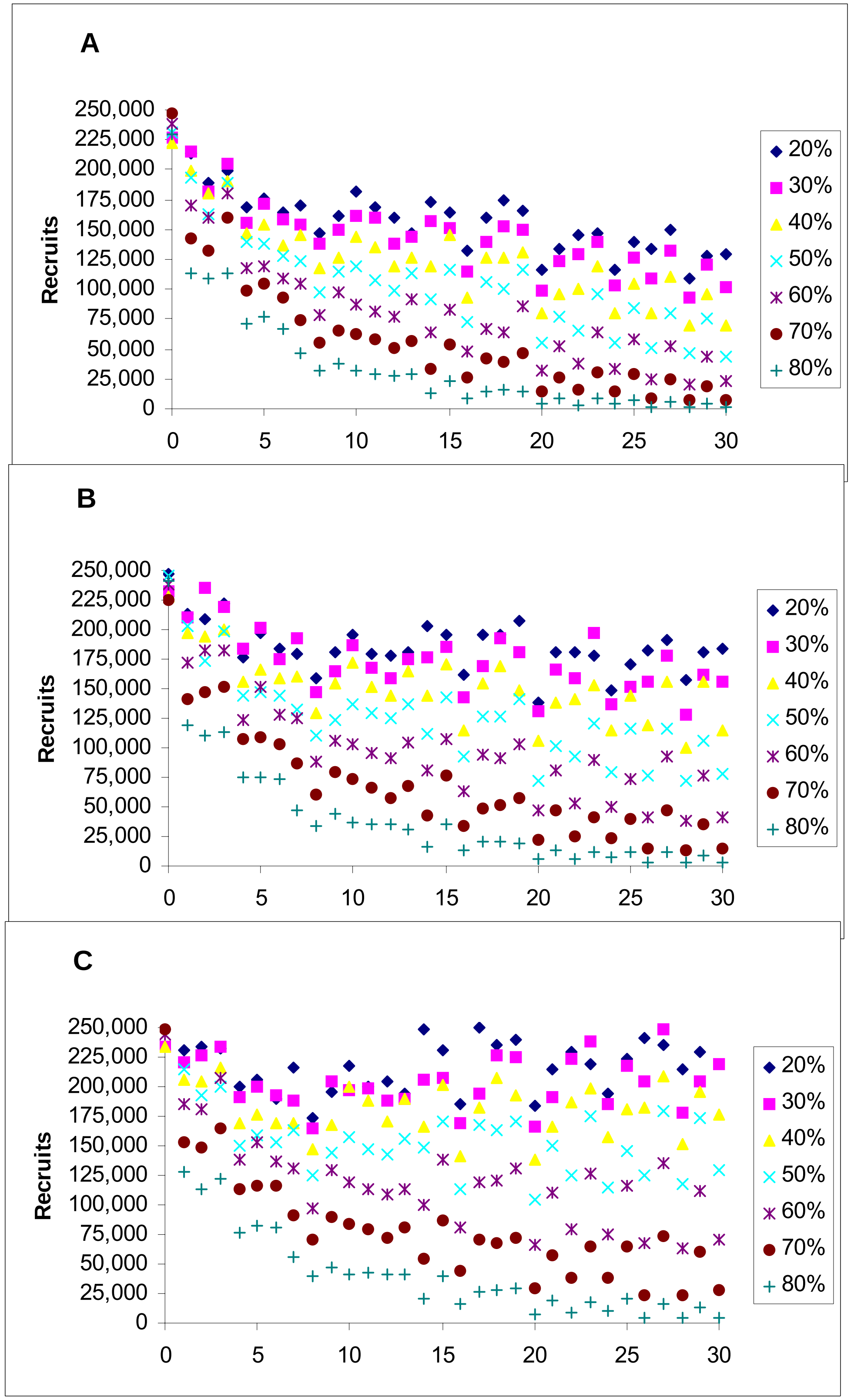
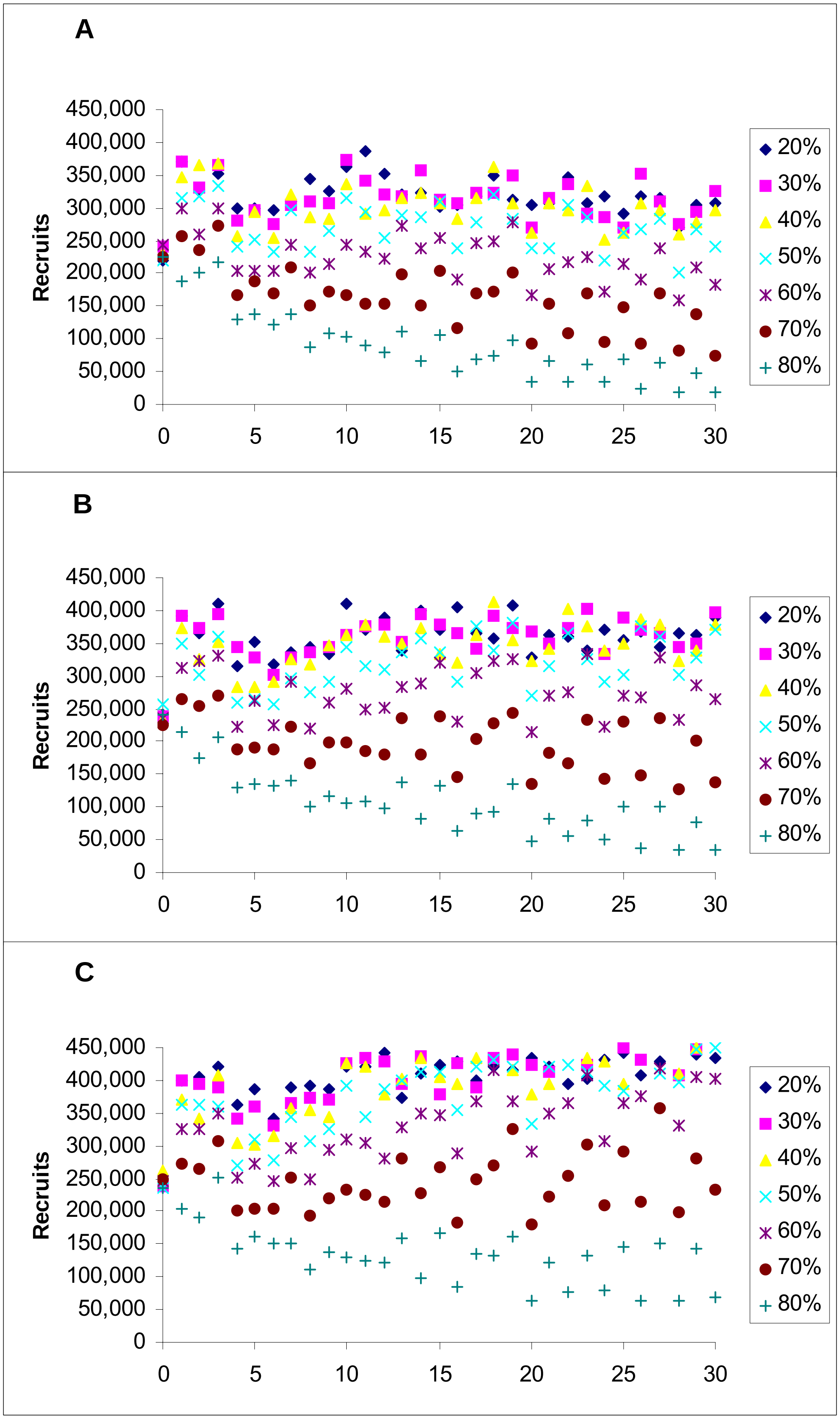

3.00E+05
2.50E+05
2.00E+05
1.50E+05
1.00E+05
5.00E+04
0.00E+00
Recruits
0
50000
100000
150000
200000
250000
300000
350000
Female Spawners
Low
Average
High

Figure 2.15.



A
B
C
Recruits
250,000
225,000
200,000
175,000
150,000
125,000
100,000
75,000
50,000
25,000
0
0
5
10
15
20
25
30
20%
30%
40%
50%
60%
70%
80%

Figure 2.16.



A
B
C
Recruits
450,000
400,000
350,000
300,000
250,000
200,000
150,000
100,000
50,000
0
0
5
10
15
20
25
30
20%
30%
40%
50%
60%
70%
80%

CHAPTER 3: ESTIMATING PARASITIC SEA LAMPREY ABUNDANCE IN LAKE HURON FROM HETEROGENEOUS DATA SOURCES

ABSTRACT

The Great Lakes Fishery Commission uses time series of transformer, parasitic, and adult population estimates to evaluate the effectiveness of its sea lamprey (*Petromyzon marinus*) control program. This study integrates Lake Huron sea lamprey population estimates derived from two estimation procedures: 1) prediction of the lake-wide spawning population from a regression model based on stream size and, 2) whole-lake mark and recapture estimates. In addition, I used a re-sampling procedure to evaluate the effect of trading off sampling effort between the regression and mark-recapture models. Population estimates derived from the regression model ranged from 132,000 to 377,000 while mark-recapture estimates of marked recently metamorphosed juveniles and parasitic sea lampreys ranged from 536,000 to 634,000 and 484,000 to 1,608,000, respectively. The precision of the estimates varied greatly among estimation procedures and years. The integrated estimate of the mark - recapture and spawner regression procedures ranged from 252,000 to 702,000 transformers. The re-sampling procedure indicated that the regression model is more sensitive to reduction in sampling effort than the mark-recapture model. Reliance on either the regression or mark-recapture model alone could produce misleading estimates of abundance of sea lampreys and the effect of the control program on sea lamprey abundance. These analyses indicate that the precision of the lake-wide population estimate can be maximized by re-allocating sampling effort from marking sea lampreys to trapping additional streams.

INTRODUCTION

Fishery managers are often confronted with choosing among two or more estimates of the same parameter that are derived from independent estimation procedures. Common examples are estimates of abundance (Kelso and Shuter 1989; Hilborn et al. 1994; Farrell and Werner 1999; Merritt and Quinn 2000) and harvest rates (Roach et al. 1999). The dilemma is in choosing which estimate to use. Estimates can differ greatly and their accuracy and bias are often unknown. The manager must choose whether to select the estimate with the lowest variance (Counihan et al. 1999), or integrate the information from all estimates using a variance weighting procedure (Merritt and Quinn 2000) or a Bayesian approach (Fried and Hilborn 1988). Furthermore, if the manager intends to spread the risk in estimation among more than one sampling procedure, a decision needs to be made regarding the relative amount of effort allocated to each method since precision of any method is related to sampling effort.

The Great Lakes Fishery Commission (GLFC) annually evaluates the success of its sea lamprey (*Petromyzon marinus)* management program in Lake Huron by trapping and estimating the abundance of spawning sea lampreys runs in selected streams. The relation of these spawning run estimates to stream size have been used to predict the spawning abundance in streams not trapped, but known to have populations of spawning sea lampreys (Mullett et al. 2003). The lake-wide abundance of sea lampreys is the sum of the individual estimates from all sea lamprey producing streams. A time-series of lake-wide estimates is used to evaluate major changes and determine the overall effectiveness of the sea lamprey control program. For example, Schleen et al. (2003)

considered the St. Marys River population as the largest source of sea lampreys in the Great Lakes prior to 1998. Evaluating the effect of applying granular bayluscide, enhanced trapping, and stocking sterilized spawning male sea lampreys in the St. Marys River in 1998-99, on the population of parasitic lamprey in Lake Huron will be based in large part on the time series of spawning population estimates (Adams et al. 2003).

The GLFC has periodically used mark and recapture studies of coded-wire tagged transformer and parasitic-phase sea lampreys as an experimental approach to study homing behavior and derive Lake Huron population estimates (Heinrich et al. 1985; Bergstedt and Seelye 1995; Bergstedt et al. 2003). Transforming sea lampreys were caught and released in Lake Huron tributaries and parasitic-phase sea lampreys were marked and released into the open water. The recaptures of both recently metamorphosed juveniles (transformers) and parasitic-phase sea lampreys were made at traps used to develop the annual regression models used to predict spawning-phase abundance.

The GLFC assembled an expert review panel in 1997 to evaluate the spawning-phase assessment program (Mullett et al. 2003). The panel concluded that the spawning-phase assessment was an important component of the integrated management of sea lamprey and the spawner regression model was a reasonable application of the trap data. However, they were critical of the reliance placed on lake-wide estimates based on an expansion of the spawner regression because a number of assumptions in the model had not been met. For example, the selection of trapping sites was non-random because there were relatively few suitable trapping locations. In addition, the prediction of spawning run size based on stream size was an extrapolation for some streams whose size exceeded the largest values used to build the model.

Given the challenges associated with the regression model, the panel encouraged greater use of mark and recapture studies as this technique enables direct population estimates with fewer assumptions than the regression procedure. However, the mark and recapture method tends to inflate both the estimate and its variance if the major assumptions (complete mixing of marked and unmarked fish, equal probability of collecting tagged and untagged individuals, no tag loss, detection of all tags, etc.) are not met.

The panel recommended incorporating both the regression model and mark-recapture studies into the assessment program with the understanding that additional resources would not be available to increase sampling effort. The precision of the techniques is generally a function of the sampling effort applied. When sampling resources are limited, any increase in effort for one method will necessitate a decrease in effort for the other methods and have a corresponding effect on the sampling precision. If integrating the estimation procedures derives the most reliable estimate of the population and additional sampling resources are not available then an optimal sampling program will allocate effort to the methods such that the variance of the integrated estimates will be minimized.

In this chapter, I integrate the lake-wide population estimates for Lake Huron from the spawner regression and the transformer and parasitic mark and recapture estimates. In addition, a re-sampling approach determined the optimal allocation of effort to trapping streams and marking sea lampreys to minimize the uncertainty of the integrated population estimate.

METHODS

Data sets: The U.S. Fish and Wildlife Service (FWS) and the Canadian Department of Fisheries and Oceans (DFO) annually (1977-1998) estimated spawning runs in up to 12 streams and the St. Marys River to derive lake-wide estimates for Lake Huron (Mullett et al. 2003; Figure 3. 1). Since 1991, FWS and DFO periodically tagged transformers in streams and parasitic-phase juveniles in the lake with coded wire micro-tags (Bergstedt et al. 2003). There were five marked cohorts that received relatively high recapture effort (spawners were checked for tags in most of the Lake Huron tributary traps): two transformer cohorts (1991 and 1998 feeding years), and three parasitic cohorts (1993, 1994, and 1998 feeding years). This study used these data sets with the corresponding spawning-phase trap data to derive integrated estimates and quantify the trade-off between trapping additional streams or marking additional transformers or parasitic-phase sea lampreys.

Spawner population estimates (N_S): Heinrich et al. (1985) and Mullett et al. (2003) describe the traps and techniques used in the Lake Huron spawning phase assessment program. In streams with assessment traps, a unique fin punch was applied to 5 to 100% of the lampreys captured to identify the week of release, usually spanning a 10 to 12 week spawning run. Lampreys were recaptured in subsequent weeks and examined for fin punches. Spawning-run estimates were derived using a mark-recapture method for migratory populations originally described by Schaefer (Ricker 1975):

$$N_{S,i,j} = \sum W_{m,r} = \sum_{mr} \left(\frac{R_{m,r} M_m C_r}{R_m R_r} \right) \tag{1}$$

where $N_{S_{i,j}}$ was the spawning run estimate in stream j in the year i, $W_{m,r}$ was the estimate of population available for marking in week m and available for recovery in week r, M_m was the number marked in marking period m, C_r was the number of lamprey captured in week of recovery r, $R_{m,r}$ was the number of lamprey marked in marking week m which are recaptured in recovery week r, R_m was the total number of lamprey recaptured which were marked in marking week m, and R_r was the total number of lamprey recaptured in the mth recovery week (Ricker 1975). The variance of the spawning run estimate was described by Chapman and Junge (1954):

$$\sigma^2 N_{S_{i,j}} = \sum \frac{W_{m,r} W_{m.} W_{.r}}{M_{m.} C_{.r}} \tag{2}$$

The assessment program did not conduct a MR in all streams in all years. For those with trap catch but no MR, $N_{S,i,j}$ was estimated from the ratio of trap catch in year i and average trap sampling efficiency from years when a MR was conducted in stream j (Mullett et al. 2003). In addition, the uncertainty in $N_{S,i,j}$ was estimated as the average CV from years with a MR estimate.

The estimates of the spawning runs did not in themselves provide information on the lake-wide spawning abundance. My approach was to assume a linear model that related the measurable spawning runs on a log scale to variables that were measured for every stream in the Lake Huron basin. I could then estimate the spawning run abundance in streams without spawning phase assessment traps based on the variables and parameter in the linear model. Heinrich et al. (1985) and Mullett et al. (2003) reported a significant relationship between sea lamprey spawning runs and stream discharge or watershed area. Based on those studies, I assumed a relationship between the spawning run estimates and watershed area and fit a weighted least squares regression for each year;

$$\ln N_{S_{i,j}} = a_i + b_i \ln X_j + \varepsilon_{i,j} \tag{3}$$

where a_i and b_i were estimated parameters and b_i described the effect of watershed area X for stream j, $e_{i,j}$ were normally distributed errors that had mean zero and variance $\sigma^2_{N_{S_i}.X}$ and the errors were weighted by the inverse of the CV of $N_{S,i,j}$.

The lamprey producing streams in the lake were assigned to either a "primary producer" or "secondary producer" category based on the stream's larval production history (Mullett et al. 2003). Streams that produced larval sea lampreys in sufficient quantity to require lampricide treatment on a cycle of every five or fewer years were considered primary producers and streams colonized less frequently were considered secondary producers. It was assumed that production in secondary streams was approximately 12% of primary stream production and the watershed area of these streams was adjusted by this rate. I could not test this assumption directly because no MR studies in secondary producers were conducted in the study period. The lake-wide abundance of spawners N_{S_i} and its variance was defined as:

$$N_{S_i} = \sum_{j=1}^{70} e^{a_i + b_i X_j + 0.5\sigma^2_{N_{S_i}.X}}$$

$$\sigma^2_{N_{S_i}} = \sum_{j=1}^{70} [\sigma_{N_{S_{i,j}}} e^{a_i + b_i X_j}]^2 \qquad (4)$$

where $\sigma_{N_{S_{i,j}}}$ is the SD of log $N_{S_{i,j}}$.

A non-parametric bootstrap procedure (Hilborn and Walters 1992) was used as an alternative method of estimating the parameters and their uncertainty in the regression model parameters because non-random stream selection procedure may have produced unreliable estimates of the model parameters or underestimated their variance. 2500 bootstrap data sets were generated from each year's data by randomly selecting, with replacement, n_i (sample size in year i) observations. The bootstrap parameter estimates and their standard deviation (SD) were determined by calculating the mean and SD of the 2500 sets of parameters generated by fitting equation 3.

Transformer and Parasitic Mark and Recapture (N_T and N_P): Parasitic-phase sea lampreys were collected as part of the by-catch from the commercial fishery and released with coded wire tags in 1993, 1994, and 1998. The number of release locations varied among years but I assumed this no effect on the portion of marked sea lampreys that were recaptured. Newly metamorphosed sea lampreys were collected in 1991 and 1998 by electrofishing or drift nets and released with coded wire tags. This analysis differed from Bergstedt et al. (2003) in that we included all recapture data rather than restricting the analysis to the main basin of Lake Huron.

The transformer MR population estimates and its variances were estimated using the modified Petersen method (Ricker 1975) to mark-recapture data

$$N_{T_i} = \frac{(M_{T_i}+1)(C_{T_i}+1)}{(R_{T_i}+1)} \tag{5}$$

$$\sigma^2_{N_{T_i}} = N^2_{T_i}\frac{C_{T_i}-R_{T_i}}{(C_{T_i}+1)(R_{T_i}+2)} \tag{6}$$

where C_{T_t} is the number of spawning sea lampreys examined for transformer CWTs in year *i*, M_{T_i} is the number of transformers sea lampreys implanted with CWTs in year *i*, and R_{T_i} is the number of spawning sea lampreys recovered in traps with transformer CWTs in year *i*. The parasitic phase MR estimates were derived from the same procedures used for the transformer estimates.

Integrated Population Estimate (N_i): The estimates of N_S, N_T, and N_P described above involve estimating the lake-wide sea lamprey population at three separate life stages, although the estimate at each life stage was assumed to provide information on the success of the control program and the parasitic activity in the lake. Integration of the information from the three estimates into a single expression of lamprey abundance in year *i* required me to translate the estimates into a common scale. If the annual survival rate was known, it could be applied to transform the population estimates to the same life stage units. I was unable to identify any published estimates of lamprey survival rates from the transformer to the spawner life stage and inspection of the estimates derived in this study were not informative about survival rates because parasitic MR estimates exceeded transformer MR estimates. However, I assumed that each of the life stage population estimates, N_{T_i}, N_{P_i}, and N_{S_i} were proportional to the overall estimate of abundance, N_i, by proportionality constant parameters c_T, $c_{P,}$ and c_S, respectively. The parameters N_i, c_T, $c_{P,}$ and c_S were estimated by minimizing the objective function;

$$L = \sum_{i=1}^{4} \left(\frac{(\ln N_i - \ln c_T - \ln N_{T_i})^2}{2\hat{\sigma}^2_{N_{P,i}}} \right) + \left(\frac{(\ln N_i - \ln c_P - \ln N_{P_i})^2}{2\hat{\sigma}^2_{N_{P,i}}} \right) + \left(\frac{(\ln N_i - \ln c_S - \ln N_{S_i})^2}{2\hat{\sigma}^2_{N_{S,i}}} \right) \tag{7}$$

where I fixed c_T equal to one thereby estimating N_i in transformer life stage units and $\hat{\sigma}_{N_{T,i}}$, $\hat{\sigma}_{N_{T,i}}$, and $\hat{\sigma}_{N_{T,i}}$ were the estimated SDs from the lake wide estimates.

Optimal Sample Allocation: The current distribution of sampling effort among the three life stage estimation procedures evolved through time in an *ad hoc* or opportunistic fashion. No formal power analysis was conducted to determine the sampling effort required for a precision level defined *a priori* for any of the methods. In this section, I present a simulation model to illustrate the trade off between increasing the number of assessment traps and marking additional transformer or parasitic with CWTs. I assumed a fixed budget for assessment and therefore any increase in sampling effort would require an equal reduction in another sampling method. I further assumed that the assessment program would include a mix of methods rather than focus all resources on a single assessment method and maximizing the precision of N_i could be achieved by optimally allocating the fixed resources among the two sampling procedures, trapping streams and marking sea lampreys.

Two further assumptions were made in this analysis. First, the marginal value of spawning phase assessment traps and marked sea lamprey was estimated based on the spending estimates generated by the GLFC Assessment Task Force in October 1999 (Cuddy, D. Department of Fisheries and Oceans, Sea Lamprey Control Centre, 2000, personal communication). Here, one trap site was estimated to be equivalent (in terms of effort available to the assessment program) to the collection and marking of 75 parasitic or transforming lampreys. As well, the St. Marys, Ocqueoc, and Cheboygan Rivers were always included in the mark and recapture procedure because typically more than 80% of marked sea lampreys recovered were harvested from these locations and therefore it is unlikely that any future sampling strategy would not include these three streams.

To illustrate this trade-off in sampling effort, I based my modeling on the 1993, 1994, and 1998 spawner regression and parasitic mark-recapture data. Table 3.1 outlines the various configurations of the assessment program considered by the modeling in relation to the numbers of streams trapped and CWTs released. In each simulation, the three fixed streams were selected and the remaining streams were randomly selected from the roster of streams sampled in that year according to the schedule in Table 3.1. The number of CWTs recovered at each stream was adjusted based on the number of CWTs released according to Table 3.1 where;

$$\hat{R}_{P,i,j} = rR_{P,i,j} \tag{8}$$

and r is the ratio of CWT released according to the schedule in Table 1 and $M_{P,i}$. For each simulation, N_S and N_P and their respective variances were determined and N_i, was estimated by inverse variance weighting,

$$N_i = \frac{c_S N_{S,i} w_{S,i} + c_P N_{P,i} w_{P,i}}{w_{S,i} + w_{P,i}} \tag{9}$$

where c_S and c_P were assumed known from equation 7 and $w_{S,i}$ and $w_{P,i}$ were the inverse of the variances of N_S and N_P in each simulation. 1000 simulations were conducted for each scenario in Table 3.1 and the coefficient of variation (CV) of the N_is for each scenario was determined. The optimal scenario from Table 3.1 was deemed to be the scenario that had the lowest CV.

RESULTS

Population Estimates: The estimate of spawning abundance, N_S, among the four years ranged from a low of 131,000 for 1993 feeding year to 380,000 for the 1991 feeding year. The parameters used in the regression model varied considerably within and among the four years used in this analysis. The intercept parameter a ranged from 1.2 in 1991 to 4.0 in 1998, while the slope parameter (b) varied from a 0.6 in 1998 to1.1 in 1991 (Table 3.2). The analysis also indicated that the regression parameters and the population estimates both were estimated with considerable uncertainty. The bootstrap estimates of uncertainty tended to underestimate those generated by the regression analysis's estimate of uncertainty in both the a_is and b_is. However, both methods suggest that a wide range in parameter values could explain the observed data.

On average, mark and recapture estimates were substantially greater than spawner regression estimates (Fig. 3.2). Mark and recapture estimates ranged from 484,000 to 1,608,000 for N_P and from 536,000 to 634,000 for N_T. In 1998, the estimate of N_P greatly exceeded the other parasitic population estimates in other years and was greater than N_T generated for the same feeding year. The SD of both the mark and recapture and the spawner regression estimates were similar among the four years (Fig. 3.3). However, the SD of each method varied across years (Fig. 3.3) and was not consistently different among methods, suggesting those specific sampling conditions in each year had an effect on sampling precision. For example, the rate of recovery of marked parasitic sea lamprey varied from a low of 3.3% in 1998 to 8.8% in 1994 feeding-year. Consequently, the contribution from the estimation procedures to the integrated population estimate varied considerably among years.

The integration procedure estimated the population abundance, N_i, (in terms of transformers) and the proportionality constants. The integrated population estimate (N_i) ranged from 252,000 in 1993 to 702,000 in 1991 (Fig. 3.2). The proportionality constant to convert spawners to transformer was 2.1, while the parasitic proportionality constant was 0.49. The small parasitic proportionality constant reflects the influence of the 1998 estimate, introducing considerable uncertainty in the estimate of this parameter.

Optimal Sample Allocation: The SD of mark-recapture and the spawner regression procedures were affected by trading off the number of streams trapped against number of marked sea lamprey released to the lake. In all years, increasing the sample size of the spawner regression decreased the SD and in two years decreasing the number of marked sea lamprey increased the SD of the parasitic mark-recapture. For example, the SD of the spawner regression for simulations of the 1993 feeding year decreased by 50% when the number of traps increased from 12 (original sample size) to 20 in the simulations (Fig. 3.4). Conversely, the SD of the mark-recapture estimate increased by 10% in the same simulations where the number of marked sea lampreys in the simulations declined from 907 to 307. However, when the number of traps in the simulations decreased to 12 from six, the SD of the spawner regression increased by over 250%.

The distribution of the regression parameters became increasingly diffuse and undefined as sample size decreased to six trapping sites. In these simulations, the number of marked sea lampreys increased to 1357 resulting in a decline of 10% in the mark-recapture SD. A similar pattern was observed in all years of increasing SD when the number of trap locations in the simulations was less than 14 and unreliable estimates were generated when there were fewer than 10 trap locations.

These data indicate that the precision of the spawner regression was more sensitive to changes in the number of streams trapped than the mark-recapture procedure is to changes in marked sea lamprey. This likely occurred because the variance of the mark and recapture procedure reflects the number of animals checked for tags and the number of tags recovered. For example, simulations using the 1994 data had the number of marked sea lampreys decline by 49%, but the number of marked sea lampreys recovered decreased by only 24% while the number of sea lampreys inspected for tags increased by 20%. A similar pattern was observed in simulations using the data from 1993 and 1998. While decreasing the number of tagged sea lampreys released increased variance, its effect was tempered by a greater number of sea lampreys checked for tags and an increase in the portion of tags recovered when additional trap sites are included in the simulations.

Similarly, the SD of the integrated population estimate was minimized when the number of trap sites increased from six to 22 locations (Fig. 3.5). The SD of the integrated population estimate decreased between 26 and 50% through the range of sample sizes used in these simulations. Increasing the number of trap locations to more than 18 sites had little effect, or increased the SD of the integrated population estimate. Decreasing the number of trap locations below 10 sites generally resulted in more imprecise estimates of the population.

DISCUSSION

Our mark-recapture methods likely over-estimated the sea lamprey populations in Lake Huron. These estimates depend in large part on the ratio between the number of marked animals recovered and those checked for tags. Bergstedt et al. (2003) stated that most violations in the usual assumptions for this technique (similar survival rates between mark and unmarked, equal catchability, no immigration or emigration) tend to decrease the numbers of marked animals captured relative to the unmarked animals, resulting in an over-estimation of the population. One exception to this phenomenon occurs if marked animals become conditioned to traps. However, in the case of trapping lampreys tagged as parasites, there is no expectation that this would occur. The re-capture traps are located over a wide geographic area (Figure 3.1) distant from the release sites (Bergstedt et al. 2003) and 8 – 18 months elapse between marking and recapture. Therefore, it’s unlikely that marked lampreys are preferentially recovered relative to unmarked lampreys. However, it is likely that some marked lamprey emigrated to Lake Michigan between the marking and recovery periods. Consequently, the estimates derived from either parasitic or transformer releases results to some degree in an overestimate of the population.

Alternatively, the regression model may derive underestimates of the population abundance for at least two reasons. First, the procedure used to estimate spawning runs in individual streams could result in an under-estimate of the population. Mullett et al. (2003) described the Schaefer model (Ricker 1975) used by DFO and the FWS to estimate the spawning runs in individual streams. In these studies, the release site of the marked animals is relatively close to the recapture site, ranging from 200 to10,000 m downstream of the trap. Consequently, this procedure could result in incomplete mixing of marked and unmarked spawning lampreys in the streams and over-representation of marked lamprey in the recovery periods. If the spawning run estimates were low, it would cause a subsequent underestimate of spawning populations in streams not fished and estimated by the regression model.

Second, there may be streams with unobserved sea lamprey spawning runs which are not used in the expansion of the regression model. Lake Huron has at least 1700 tributaries (Schleen and Klar 1999). We selected streams for this study based on either a recent history of lampricide treatment or records of larval lamprey collected during electrofishing surveys. However, there are records of significant lamprey runs in streams with no history of successful reproduction. For example, the largest spawning run estimates in Lake Ontario during the past 15 years have been from the Humber River (Schleen and Klar 1999). However, no larval lampreys have been collected from this stream because local conditions preclude successful reproduction. Given the large number of tributaries relative to the number with recently identified larval lamprey populations, it is likely that at least some streams with lamprey spawning runs that were not used in the regression estimate, resulting in an underestimate of the population.

In this analysis, we estimated proportionality constants as a surrogate for survival estimates from the transformer to spawner life stages. These constants were used to express both parasitic and spawner estimates in terms of transformers when estimating the integrated population estimate among all years. However, it is likely that lamprey survival is a dynamic parameter in Lake Huron. Young et al. (1996) speculated that the survival rate of transformers was correlated with changes in the Lake Huron fish community. In addition, the abundance and mortality rate of lake trout, the sea lamprey's preferred host, vary both spatially and temporally within Lake Huron, with mortality rates ranging from 27 to greater than 70% (Johnson et al. 1995). Based on the dynamic nature of the Lake Huron fish community, we expect the survival rate to vary considerably among years.

The magnitude of the parasitic proportionality constant was greatly influenced by the 1998 parasitic mark-recapture and its variance. The parasitic mark-recapture and its variance in 1998 greatly exceeded the estimates of these parameters in the other two years. In addition, these estimates were greater than both the transformer mark-recapture and spawner regression in the same year, suggesting that at least one of the population parameters was inaccurately estimated. It's likely that the 1998 parasitic mark-recapture exaggerated the parasitic population in that year, given the high variance associated with the estimate and its value relative to other estimates both within and among years. The effect on our model was to generate a parasitic proportionality constant that was significantly greater than we would have expected and likely inflated the integrated population estimate in all years. In addition, the 1998 parasitic mark-recapture highlighted the potential for inflating among year variation in population if monitoring of lamprey population was focused on a single estimation procedure.

The precision of the population estimates as measured by the mark and recapture and the regression model varied significantly (Figure 3.5). No method consistently outperformed the other in terms of minimizing the SD of the population estimate. Consequently, the relative weight assigned to the combined estimate varied among the data sets. Reliance on one technique would not consistently produce the most precise population estimate. The major advantage of using the integrated estimate is that it reduces the potential of producing an imprecise or inaccurate estimate of the population.

The sample size of traps used to calibrate the spawner regression model had a significant effect on both the magnitude and the precision of the population estimate. The precision of the population estimates declined significantly in our simulations when the sample size decreased below the 10 – 12 sites. As expected, the SD of the spawner regression increased as sample size declined. The distribution of both the slope and intercept parameters became diffuse as sample size decreased. Consequently, reducing the sample size also resulted in exaggerated and unreliable estimates of the population compared to simulations with larger sample sizes.

The precision of the mark and recapture method was not significantly affected by changes in the numbers of marked animals released. In these simulations, we included three streams that consistently accounted for the majority of recaptures each year and any future studies to recover marked lamprey would likely include these streams. Therefore, the proportion of the recaptures relative to the number of marked animals released was not greatly affected. A random selection of streams would likely have resulted in a greater decay in precision as the number of marked animals declined in the simulations. In addition, the proportion of marked animals recaptured in the simulation was enhanced by the addition of trapping sites caused by trading-off marked animals for trapping locations. Consequently, the combination of retaining the trapping sites that consistently generated the largest portion of recaptures and increasing the number of trapping opportunities resulted in minimal change in the proportion of animals recaptured. Thus, similar levels of precision for the mark and recapture estimates were observed over the range of trapping locations and numbers of marked animals released.

In these analyses, we used data from parasitic and transformer release of marked lamprey. Both release methods produced relatively high recapture rates (3 – 8%) and the cost of both study types was similar. However, the transformer releases have at least two advantages over parasitic releases. First, transformer releases enable a direct measure of the lamprey management programs success, i.e. the number of transformers escaping the control program. Second, marking at the transformer stage may enable us to more closely meet the usual assumptions for mark and recapture studies. For example, the transformer releases result in mixing of the marked and unmarked transformers throughout the entire feeding period for that cohort. In contrast, the parasitic marking occurs throughout the feeding period resulting in variable mixing times.

The effect of capture on the subsequent survival of tagged transformers and parasites is unknown but could have an important effect on the magnitude and reliability of population estimates. Parasitic lampreys are captured as by-catch in the commercial fishery for whitefish or lake trout. Lampreys are usually attached to a host when the host is caught thereby interrupting the lampreys feeding. Interrupting a feeding bout in this manner could have a deleterious effect on lamprey survival if locating and attaching to another suitable host fish is unlikely or metabolically expensive. Similarly, the magnitude of the effect on survival relative to unmarked lamprey of capturing transformers by electrofishing or fyke netting during the downstream migration to the lakes is unknown. However, it would result in over-estimates of transformer abundance if marking reduced survival.

Our analysis indicates that the decrease in SD observed by re-directing sampling resources from marking sea lampreys to fishing additional traps (Figure 3.5) decreased the coefficient of variation of the integrated population estimate from approximately 31% to 18%. The significance of improving this precision can be illustrated by examining an application of the assessment in determining the effect of changes in the sea lamprey management program on sea lamprey abundance. For example, fish managers could be asked to approve a change in the way streams are selected for TFM treatments (Slade et al., 2003) or change treatment protocols that could affect the parasitic population abundance. A likely application of the assessment data would be to ask how many years of data collection would be required to detect the change in abundance following the change in streams selection, given the measurement error and annual system variation that we observed (e.g. Adams et al. 2003). Power analysis (Hansen et al. 2003; Hilborn and Mangel 1997) using the integrated population estimate of the Lake Huron population provides the basis for answering questions of this nature. Increasing the trapping effort from 12 to 18 streams and reducing the number of lampreys marked would lower the coefficient of variation from 31 to 18%. The length of the time series required to detect a 30% change with 80% probability could be reduced from five to three years, assuming four years of pre-change data, without significantly affecting assessment costs.

In conclusion, integrating estimates from regression and mark – recapture estimation procedures will likely produce a more consistent and precise population compared with reliance on either methodology. I recommend that the number of code-wire tagged lampreys released be reduced to support an increase in the number of trapping locations.

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Table 3.1. Sample sizes used in the simulation to examine effects of sampling effort allocation on the variance of the integrated population estimate.

Trap Sites	Marked Lampreys		
	1993	1994	1998
6	1357	2157	1225
7	1282	2082	1150
8	1207	2007	1075
9	1132	1932	1000
10	1057	1857	925
11	982	1782	850
12	907	1707	775
13	832	1632	700
14	757	1557	625
15	682	1482	550
16	607	1407	475
17	532	1332	400
18	457	1257	325
19	382	1182	250
20	307	1107	175
21	232	1032	100
22	157	957	25

Table 3.2. Comparison of regression parameters and population estimates between regression model output and non-parametric bootstrap analysis. Figures in parentheses are the SD of the parameter and population estimates. N = 2500 for bootstrap analysis.

	Bootstrap			Regression		
Year	*a*	*b*	Estimate	*a*	*b*	Estimate
1991	1.129	0.629	365699	1.232	1.122	378640
	(0.629)	(1.126)	(93610)	(1.625)	(0.231)	(155660)
1993	1.421	0.860	116643	1.616	0.940	131500
	(0.860)	(0.941)	(46993)	(2.389)	(0.323)	(69908)
1994	3.137	0.614	155557	3.616	0.758	167430
	(0.614)	(0.762)	(23915)	(2.165)	(0.287)	(60829)
1998	4.007	0.317	157741	4.027	0.648	160670
	(0.317)	(0.647)	(15480)	(0.965)	(0.143)	(39110)

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Figure 3.1

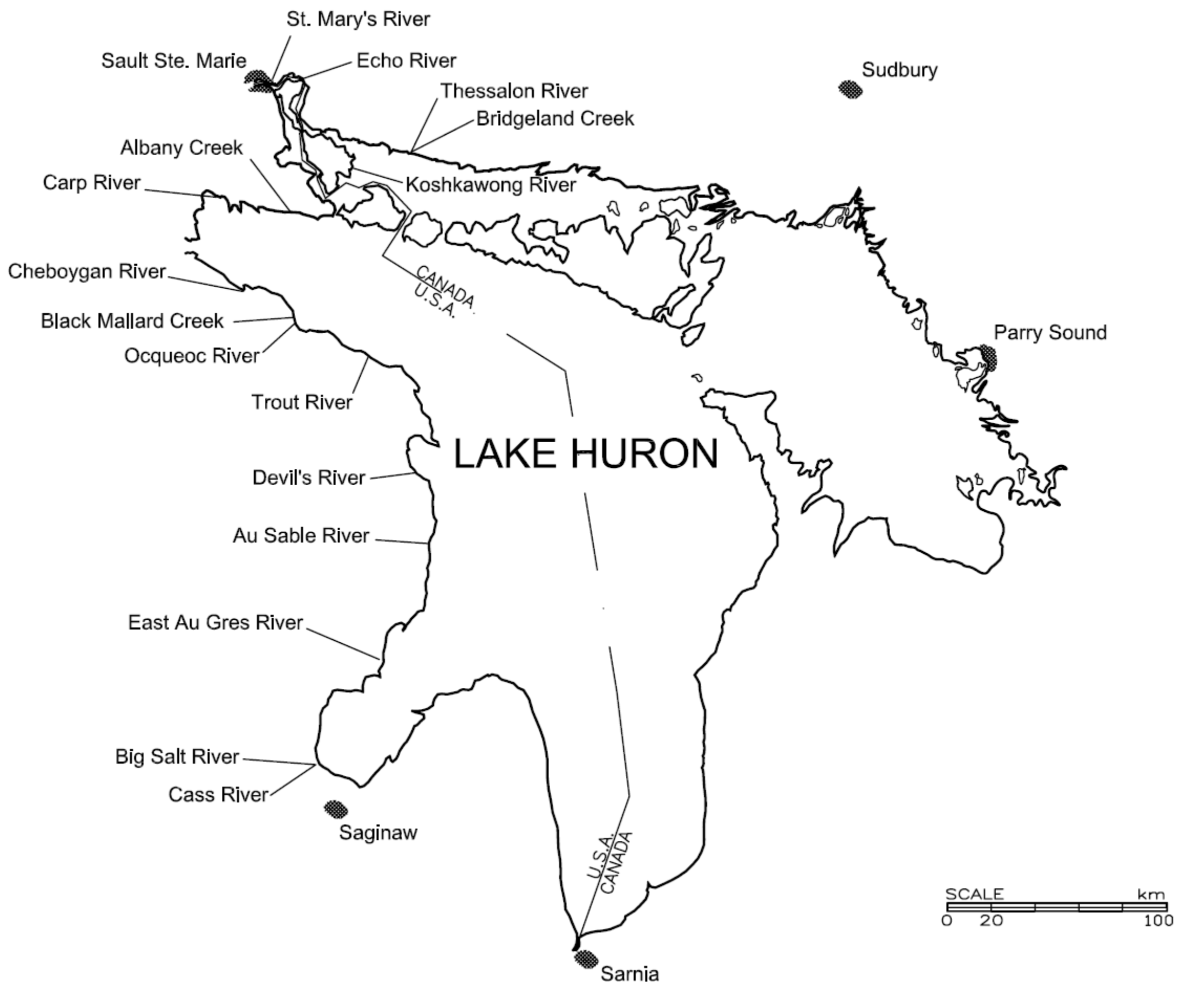

St. Mary's River
Sault Ste. Marie
Echo River
Sudbury
Thessalon River
Bridgeland Creek
Albany Creek
Koshkawong River
Carp River
Cheboygan River
CANADA
U.S.A.
Black Mallard Creek
Parry Sound
Ocqueoc River
Trout River
LAKE HURON
Devil's River
Au Sable River
East Au Gres River
Big Salt River
Cass River
Saginaw
U.S.A.
CANADA
SCALE
km
0
20
100
Sarnia

Figure 3.2.

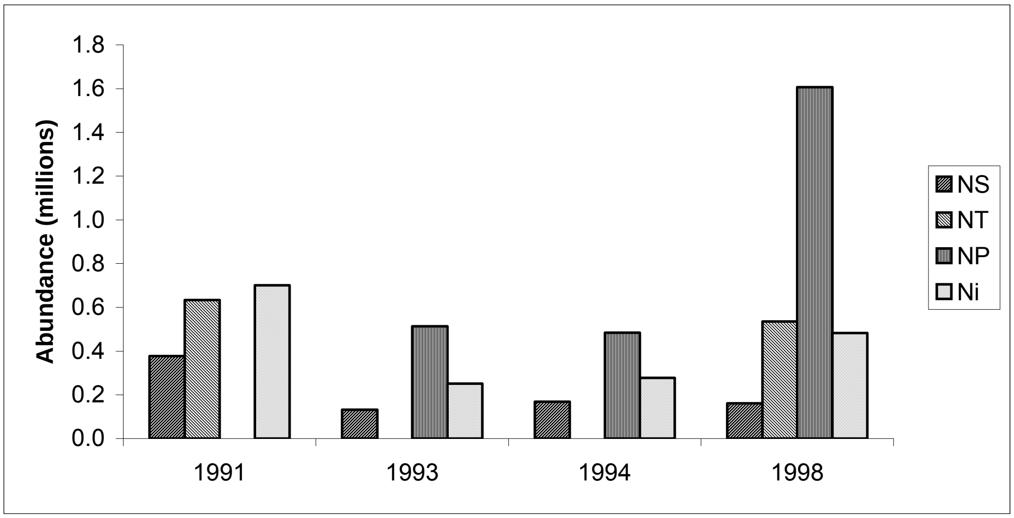

1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
Abundance (millions)
1991
1993
1994
1998
NS
NT
NP
Ni

Figure 3.3

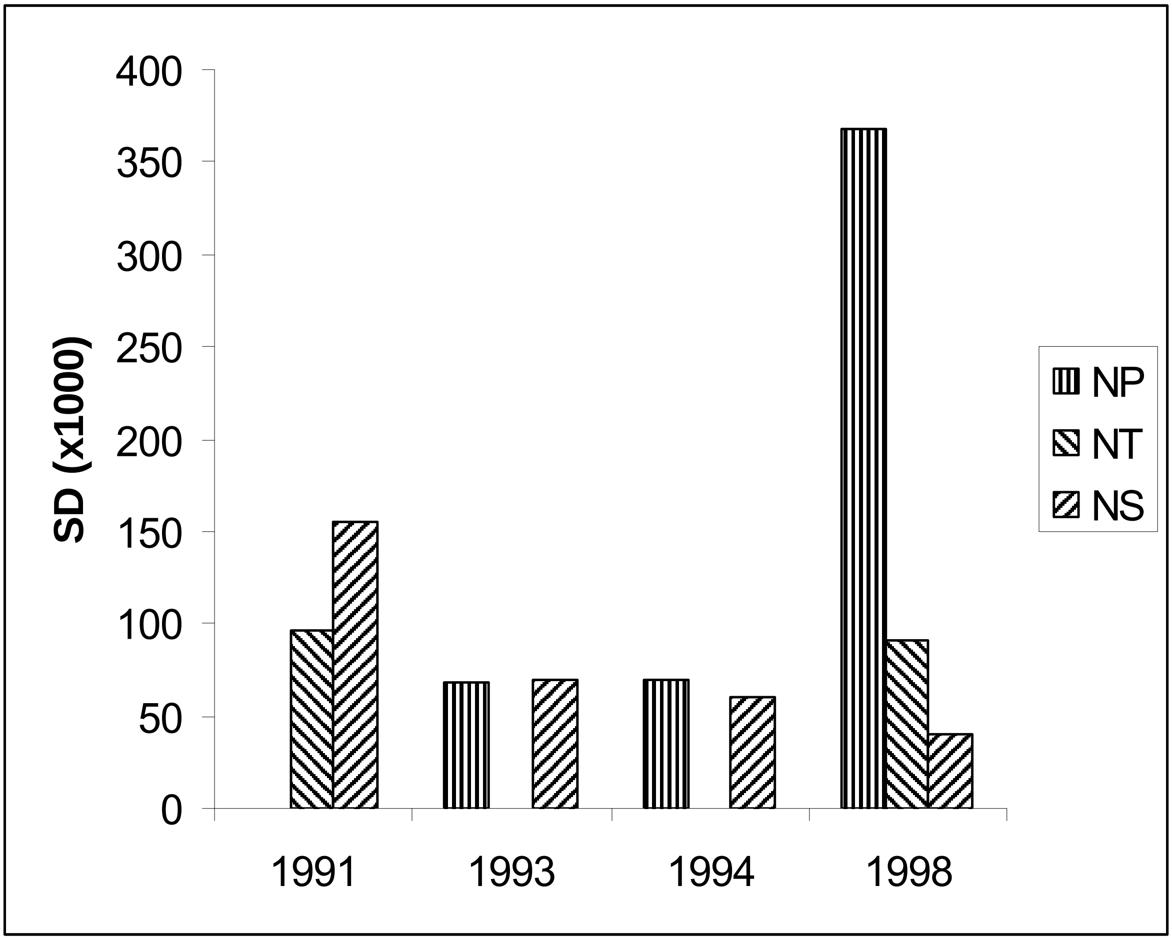

400
350
300
250
200
150
100
50
0
SD (x1000)
1991
1993
1994
1998
NP
NT
NS

Figure 3.4

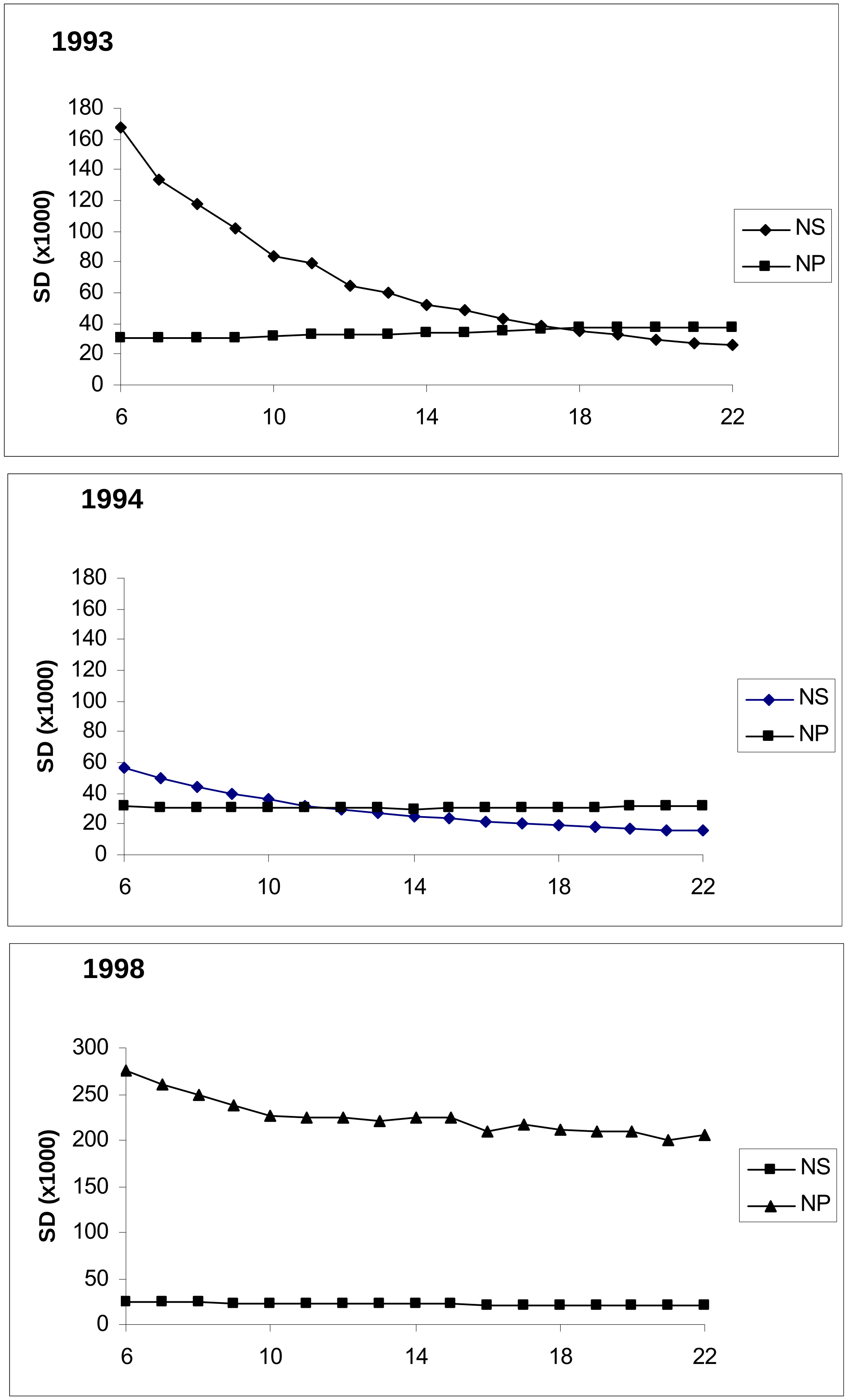
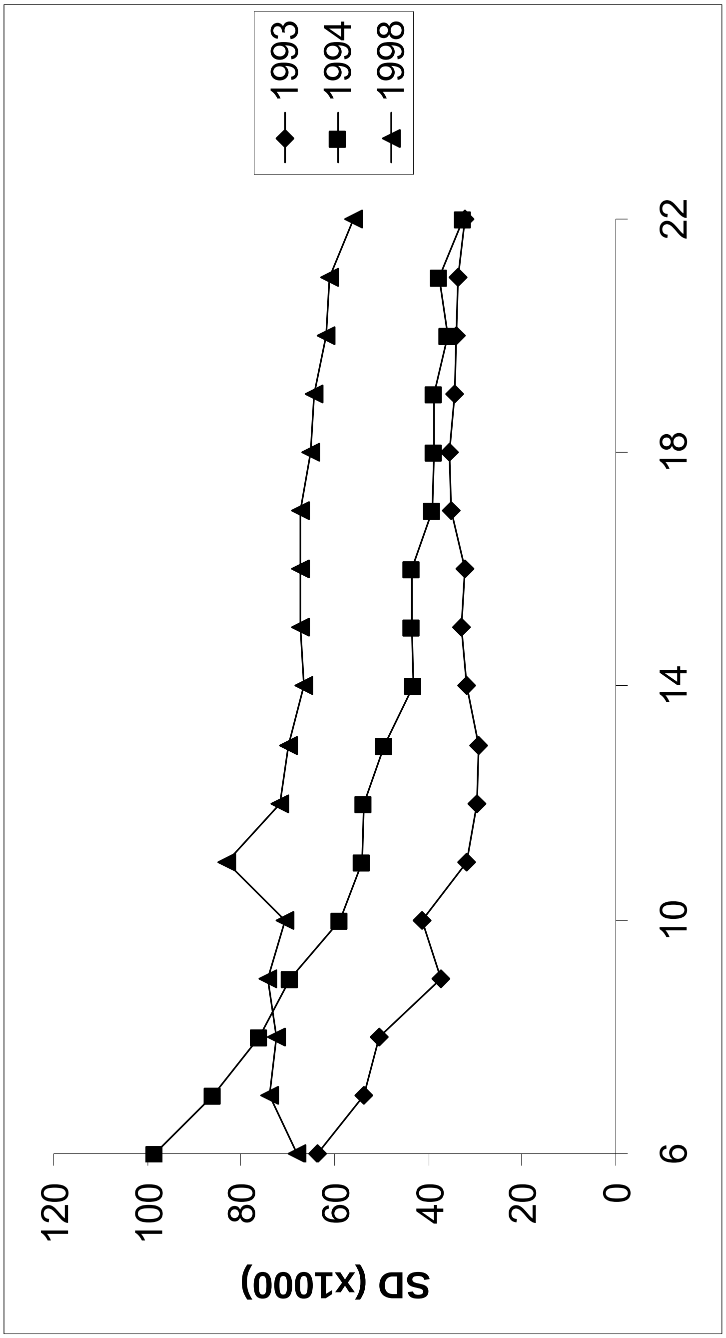

1993
SD (x1000)
180
160
140
120
100
80
60
40
20
0
6
10
14
18
22
NS
NP
1994
SD (x1000)
180
160
140
120
100
80
60
40
20
0
6
10
14
18
22
NS
NP
1998
SD (x1000)
300
250
200
150
100
50
0
6
10
14
18
22
NS
NP

Figure 3.5



CHAPTER 4: A MODEL BASED APPROACH TO ESTIMATING LAKE HURON SEA LAMPREY ABUNDANCE FROM HETEROGENEOUS DATA SOURCES AND OPTIMIZING THE SEA LAMPREY ASSESSMENT PROGRAM.

ABSTRACT

In this chapter, I estimated the abundance of spawning-phase sea lamprey in Lake Huron from 1990 – 2004 based on three heterogeneous sources of population assessment data – transformer and parasitic mark-recapture studies as well as regression-based estimates of spawning-phase sea lamprey. These methods are used by the sea lamprey management program to assess the success of the management program and degree of parasitic activity in Lake Huron. The model estimated that lamprey abundance declined from approximately 300,000 in 1990-92 to 285,000 in 1999-2000, immediately prior to an expansion of the control program to the St. Marys River. Lamprey populations declined by an average of 14% in 2001-2004 when the effects of the expanded control program were expected. However, the within- and among-year variability was substantial and I was unable to detect a clear change in abundance between these time periods. This uncertainty occurred because of contradictory information among the three data sources. In particular, the pattern of abundance for the transformers did not correspond with the parasitic or spawning phase patterns of abundance. I speculated that the lack of correspondence between the transformer and model estimate of abundance may have resulted from the variability associated with environmental factors affecting transformers survival or due to measurement error in the mark-recapture estimates that occurred when relatively few marked lamprey were released.

I also used a simulation model to evaluate the trade-off between marking lamprey and fishing spawning-phase traps and its affect on the precision of the annual abundance

estimate. The uncertainty in estimates of abundance was minimized in simulations that included more assessment traps and fewer CWT transformers compared to current practice.

INTRODUCTION

Sea lamprey (*Petromyzon marinus*) induced mortality in Lake Huron lake trout (*Salvenlinus namycush*) has been implicated as one of the primary factor in the collapse of the commercial fishery during the 1950's (Ebener 1995). Since 1960, the Great Lakes Fishery Commission (GLFC) has coordinated a program to reduce sea lamprey populations to enable the restoration of lake trout and other native species (Pearse et al. 1980 ; Morse et al. 2003). Since 1990, the effect of the management program on lamprey populations has been gauged by three sampling methods that estimate the population of lampreys at three different life stages; stream-dwelling recently metamorphosed juveniles (transformers), lake-dwelling parasitic juvenile, and spawning-phase adults. The time series generated from each method are used to assess whether lamprey populations have increased (i.e. the effectiveness of the management program is decreasing) or decreased (i.e. the effectiveness of the management program is increasing). The three estimates can produce contradictory evidence regarding trends in lamprey abundance in Lake Huron because of the inherent variability associated with sea lamprey population dynamics, particularly survival between the life stages being assessed due to sampling errors for each method. In this study, I integrate the information from these three methods to produce a single expression of lamprey abundance from 1990 - 2004. In addition, I use simulation modeling to optimize the allocation of resources among the three methods by minimizing the coefficient of variation of the integrated estimate of abundance.

The abundance of spawning phase lampreys has been monitored since the inception of the sea lamprey control program in 1959. Initially, spawning phase lampreys were collected at mechanical and electrical weirs and the yearly catch was used as an index of abundance (Smith and Tibbles 1980; Pearse et al. 1980). These traps were phased out in the 1970s and replaced with portable assessment and permanent dam traps. Since approximately 1990, mark and recapture studies have been conducted in most trapped streams to estimate the magnitude of the spawning runs (Mullett et al. 2003). The spawning runs in untrapped streams have been estimated using a regression model that relates the magnitude of the spawning run to stream discharge and other variables (e.g. relative productivity, larval abundance and the regional location; Mullett et al 2003). The sum of the spawning runs for all streams has been used as a lake wide estimate of spawning lamprey and is the most often cited indicator of the success of the management program (e.g. Klar and Young 2005).

Bergstedt et al. (2003) estimated the abundance of transformer and parasitic lampreys using mark and recapture (MR) experiments. They viewed these estimates as indicators of the success of the control program that were separate and independent of the spawning phase estimates. In 1998, the transformer and parasitic MR became a regular part of the GLFC's assessment program in Lake Huron.

The transformer and parasitic MR estimates may be preferable to regression estimates of spawner abundance (Mullett et al. 2003) because the MR method estimated fewer parameters, makes fewer statistical assumptions, and has been estimated with at least as much precision as the spawner estimates in most years. However, the transformer and parasitic MR estimate procedures were affected in some years by the limited availability of lampreys to mark or the possibility of differential morality between marked and unmarked lamprey induced by handling or changes in environmental conditions (Bergstedt et al. 2003). In some years, biologically inconsistent results have been obtained where the estimates of the parasitic phase exceeded those for transformers from the same year-class.

The purpose of the assessment program has been to judge the relative success of the management program and gauge the level of parasitic activity in the lake. For example, the spawning phase time series has been used to judge the success of the initial treatments in the 1960's (Pearse et al. 1980) and the resurgence of lamprey populations during the 1980's (Morse et al. 1995). Adams et al. (2003) used the spawning phase and parasitic abundance time series to detect the effect of enhanced sea lamprey control in the St. Marys River and they evaluated the statistical power to detect changes for each of these time series. In addition, estimates of lamprey abundance have been incorporated into models that predict length specific lake trout wounding rates (Rutter and Bence 2003) and used in models to predict sea lamprey induced lake trout mortality rates (Bence et al. 2003).

In Chapter 3 I integrated information derived from three estimates of abundance using inverse variance weighting and simulated various distributions of effort among the sampling programs that would maximize the precision of the integrated estimate. I concluded that most precise estimate could be achieved by redistributing effort from the MR program to trapping additional streams. In this chapter, I conducted a similar analysis of the assessment data but used a model based approach that integrated the spawning phase regression estimation procedure with the transformer and parasitic mark and recapture procedures to produce a time series of sea lamprey abundance from 1990 - 2004. In this approach, the uncertainty in the model parameters can be more thoroughly incorporated in the analysis, resulting in a more complete expression of the total uncertainty in the annual estimates. I use this model to simulate redistribution of sampling effort among the sampling methods to design an assessment program to minimize uncertainty in the integrated estimate of abundance relative to a fixed assessment budget.

METHODS

This analysis occurred in two stages. First, I derived a time series (1990-2004) of spawning-phase relative abundance from three independent sampling methodologies. Second, simulation modeling based on the preceding estimation procedure was used to compare various allocations of the total sampling effort among the three sampling methods in order maximize the precision of the estimate of lamprey relative abundance.

Assessment of Sea Lamprey Abundance: I used a model-based approach to integrating four sources of information, so as to estimate the relative abundance of sea lamprey in Lake Huron from 1990 through 2004. The sources of information I used are (1) stream-specific MR data of spawning run sea lamprey trapped in three to 13 streams annually; (2) information (stream size, geographic region, and years since the last lampricide treatment) from each stream or tributary in Lake Huron known to produce sea lamprey; (3) lake wide MR data for sea lamprey injected with coded wire tags (CWTs) at the transformer life stage prior to migration to the lake and (4) for sea lamprey injected with CWTs as parasites captured as by-catch in the lake trout or whitefish commercial fisheries. The first two data sources are used to obtain spawning-phase lamprey estiamates. Trapping of spawning run sea lamprey in streams is not only necessary for stream-specific mark recapture of spawners, but is also the source of recovery information on sea lamprey marked as transformers or parasites. The spawners recovered in traps are scanned for both transformer and parasitic CWTs.

The model underlying the analysis is illustrated in Figure 4. 1. The expected abundance measured as transformers, parasites, or spawners are assumed to be proportional to one another and to the target "overall" abundance of sea lamprey I seek to estimate. While the information collected on transformers, parasites, and spawners is intended to allow estimation of absolute abundances, past evaluations of these data indicate that their relative scaling cannot be explained simply by mortality that occurs between the times transformers, parasites, and spawners are assessed (Young et al. 2003). Consequently, I arbitrarily scaled N_i so that it was equal to the expected population measurable as spawners in year *i*. The transformer mark recapture data and the parasite mark recapture data each provide information on the lake-wide abundance for that stage. The spawner mark recapture data are available only for a subset of streams. Consequently use of these data in estimating lake-wide sea lamprey abundance requires information from all streams on characteristics that can be used to predict spawning runs.

I approached inferences from a Bayesian perspective. When point estimates were desired they were obtained for all parameters of the model illustrated in Figure 4. 1 by maximizing the posterior density:

$$p(\theta \mid y) = \frac{L(y \mid \theta) p(\theta)}{\int L(y \mid \theta) p(\theta) d\theta} \qquad (1)$$

Where θ is the set of parameters described in Table 4.1, y is the observed data, $p(\theta \mid y)$ is the posterior density, $L(y \mid \theta)$ is the likelihood of the observed data given the parameters, $p(\theta)$ is the prior probability density for the parameters before the data are considered, $\int L(y \mid \theta) p(\theta) d\theta$ is a normalizing constant that ensures that the posterior density defines a proper probability distribution. I chose modal parameters values as point estimates because they could be derived without estimating the full posterior distribution. While the full posterior distribution was estimated for the observed data, this was not practical in the simulation study. I did examine mean posterior values for quantities of interest, and they showed similar patterns to the modal estimates. I maximized this relationship by minimizing its negative log (ignoring the proportionality constant and some other constants):

$$L_{tot} = \ln(L(y \mid \theta) + \ln(p(\theta)) \tag{2}$$

I assume the data and priors consist of independent subsets so the objective function can be written as

$$L_{tot} = L_1 + L_2 + L_3 + L_4 + L_5 \tag{3}$$

where the five components are described below. I assumed uniform (uninformative) priors for all parameters on the scale they are estimated, unless otherwise indicated below. These uninformative priors are implemented by specifying bounds for those parameters and their priors drop out of the objective function because they are constants within the bounds and zero outside the bounds. AD Model Builder (Ver 5.2; Otter Research Ltd, 2001) was used to conduct the minimization.

Markov Chain Monte Carlo (MCMC) procedures within AD Model Builder were used to generate an estimate of the joint posterior distribution for model parameters. A chain of two million steps was “thinned” by saving every five hundredth step in the chain. Trace plots for the parameters were examined for trends. I also examined the autocorrelation among the saved samples, and autocorrelation was observed in up to lags of 20 samples. The effective sample size was at least 500 for the parameters and quantities examined based on the methods of Thiebaux and Zwiers (1984) . The resulting estimate of the posterior distribution for the parameters can be used to construct a posterior distribution for any quantity that can be calculated from the parameters. My focus was on describing the time series of parameters, N_i and the proportionality constants for the parasitic and transformer time series, a_P and a_T, respectively. In addition, the St. Marys River treatment was expected to affect lamprey populations beginning in 2001. I examined the differences between the log of average abundance of lamprey in 1999 and 2001 (prior to treatment) and the log of lamprey abundance during 2001 – 2004 to determine the likelihood of a treatment effect.

In the text below I describe each of the likelihood and prior components contributing to the posterior density. L_1 is calculated from a comparison between the estimated year specific abundance of sea lamprey that is potentially measurable by each method ($N_{T,i}$, $N_{P,i}$, and $N_{S,i}$) versus the abundance expected for that method given the overall abundance of sea lamprey (N_i) using data from ten years for which data from at least two sampling methods were available:

$$L_1 = \sum_{i=1}^{10} \left[\frac{(\ln N_{T,i} - \ln a_T - \ln N_i)^2 + (\ln N_{P,i} - \ln a_P - \ln N_i)^2 + (\ln N_{S,i} - \ln N_i)^2}{2\sigma_m^2} \right] \tag{4}$$

The abundance measurable for a method is assumed to deviate from direct proportionality to the overall abundance due to multiplicative process errors that come from independent and identical lognormal distributions. The variance (σ_m^2) was assumed to be known and not estimated during model fitting procedure. It was my intention to estimate to estimate σ_m^2 as a parameter in the model fitting process but the model did not converge for reasons given below.

The measurable abundances are calculated from one or more estimated parameters. In the case of the transformer and parasite mark recapture method this is a simple conversion. I estimated the probability of recovering a marked lamprey (which plays a direct role in L_2 and L_3 also) and therefore the estimated measurable abundance was the ratio of known marked lamprey to this probability. The N_i were estimated as parameters for the ten years used in equation 4.

Transformer and Parasite mark recapture data and associated likelihood components: The U.S. Fish and Wildlife Service (FWS) and Canada Department of Fisheries and Oceans (DFO) collect MR data for the transformer and parasitic life stages using injected coded-wire tag (CWT) marks and recapture during spawning runs (Bergstedt et al. 2003). Transformers were electrofished prior to their downstream migration or collected in fyke nets during the migration. The lampreys were injected with a sequentially numbered or a batch coded wire tag and then released (Bergstedt et al. 2003). This procedure was used in eight years (1992-93, 1999-2004 spawning years) during the study period and the number of transformers tagged ranged from 93 to 1953.

Transformers return to streams in spawning life stage approximately 12-18 months after migrating from the stream to the lake. The lamprey captured in the assessment traps were monitored for CWTs. I assumed a binomial process for each transformer life stage estimate but due to the large number of lampreys captured and tagged, used a normal approximation leading to the objective function components (a likelihood for the data) for the transformer mark recapture data:

$$L_2 = \sum_{i=1}^{8} \left[\ln \sigma_{T,i} + \frac{1}{2}\ln(2\pi) + \frac{(k_{T,i} - n_{T,i} p_{T,i} + 0.5)^2}{2\sigma_{T,i}^2} \right] \quad (5)$$

Where $n_{T,i}$ is the number of lampreys caught and examined for transformer tags throughout Lake Huron in year i, $k_{T,i}$ is the number of CWTs recovered, $p_{T,i}$ is the probability of capturing a tagged lamprey (estimated parameters) and $\sigma_{T,i}^2 = n_{T,i} p_{T,i} (1 - p_{T,i})$. As noted above, measurable transformer abundance can be calculated as $N_{T,i} = m_{T,i} / p_{T,i}$ where $m_{T,i}$ was the number of transforming lampreys marked with a CWT and released.

Parasitic lampreys were collected as by-catch from the whitefish and lake trout commercial fishery and the sport fishery in Lake Huron during eight years of the study period (1994-95, 1999-2004). Lampreys were marked with sequential CWTs, released and recaptured during the spawning phase assessment eight to 12 months after marking. Similar to the transformer MR likelihood component, I assumed a binomial process and estimated as parameters, $p_{P,\mathrm{i}}$, the probability of recapturing a spawner marked with a CWT during the parasitic stage using the normal approximation to the binomial. Thus the objective function component is:

$$L_3 = \sum_{i=1}^{8}\left[\ln\sigma_{P,i} + \frac{1}{2}\ln(2\pi) + \frac{(k_{P,i} - n_{P,i}p_{P,i} + 0.5)^2}{2\sigma_{P,i}^2}\right] \tag{6}$$

Where $n_{P,i}$ is the number of lampreys caught and examined for CWTs throughout Lake Huron spawning phase assessment in year i, $k_{P,i}$ is the number of parasitic CWTs recovered, and $\sigma_{P,i}^2 = n_{P,i}p_{P,i}(1 - p_{P,i})$. As for transformers, measurable abundance could be calculated from $N_{P,i} = m_{P,i}/p_{P,i}$ where mp_i was the number of parasitic lamprey tagged with a CWT and released.

Spawning run mark recapture data and associated objective function components: A total of 146 mark and recapture studies (stream and year combinations) of sea lamprey spawning runs were conducted (n = 3 to 13 streams each year). A unique fin punch was applied to 5 to 100% of lampreys captured during each week of release, usually spanning a 10 to 12 week spawning run. Lampreys were recaptured in subsequent weeks and examined for fin punches.

Spawning runs have previously been estimated using the Schaefer method (Ricker 1975; Mullet et al. 2003) assuming that these were open, migrating populations. For the purposes of this analysis, I treated these populations as closed so equations follow those used in simple Petersen mark and recapture estimation. I did this as an analytical convenience since the Schaefer and Petersen methods produced similar results (Figure 4.2) and use of the Petersen equations requires the estimation of only a single parameter for each stream. As for the other mark-recapture data I assumed a binomial distribution for recovery of marked sea lamprey, estimated the probability of recovering marked sea lamprey $p_{S,i,j}$ as parameters, and used the normal approximation because of large sample sizes. Thus, the objective function value (likelihood for data) is:

$$L_4 = \sum_{i=1}^{146} \left[\ln \sigma_{S,i,j} + \frac{1}{2}\ln(2\pi) + \frac{(k_{S,i,j} - n_{S,i,j}p_{S,i,j} + 0.5)^2}{2\sigma_{S,i,j}^2} \right] \tag{7}$$

Here, $n_{S,i,j}$ is the number of lampreys caught and examined for fin punches in stream j and year i, $k_{i,j}$ is the number of fin punched lampreys recovered, and $\sigma_{S,i,j}^2 = n_{S,i,jj}\, p_{S,i,j}(1-p_{S,i,j})$. In a similar fashion to how whole lake measurable populations were calculated for the transformer and parasitic mark-recapture data, measurable spawning runs were calculated as $N_{S,i,j} = m_{S,i,j}/p_{S,I,j}$ where $m_{S,I,j}$ was the number of lamprey fin punched released back into the stream.

Without further information and assumptions the individual stream spawning run information would not be informative about lake-wide sea lamprey abundance each year, the estimation target here. My approach was to assume a linear submodel that related the measurable spawning runs on a log scale to variables that were measured for every stream. Lake-wide measurable spawner abundance could then calculated based on those variables and the parameters of the submodel. In particular I assumed the following relationship between the magnitude of lamprey spawning runs and the explanatory variables average stream discharge (stream size), years since last lampricide treatment, and lake region:

$$N_{S,i,j} = \mu Q_j^{\alpha} T_{i,j}^{\beta} R_j^{\delta} (QR_j)^{\gamma} e^{\varepsilon_{i,j}} = \tilde{N}_{S,i,j}\, e^{\varepsilon_{i,j}} \tag{8}$$

where μ was a parameter describing the mean spawning abundance, α was a parameter relating the effect of stream size or average discharge Q_j, β was a parameter describing the effect of larval lamprey abundance $T_{i,j}$, δ was a parameter describing the difference between the two regions (R_j), γ was a parameter describing the interaction effect of stream size and region, λ_i was the year effect parameter ($\lambda_{2004}=0$) and $\varepsilon_{i,j}$*'s* represented the process errors that had mean zero and variance σ_S^2.

Stream size was included in the model because lampreys are more likely to encounter larger streams than small streams when migrating from the lake to streams (Sorensen and Vriesze 2003). Years since treatment was used as a surrogate for pheromone concentration and I included it because attractiveness of streams as potential spawning sites for lamprey may be proportional to the concentration of lamprey migratory pheromone present in those streams. I have assumed that larval biomass and hence pheromone concentration likely increased proportionate to the years since the last TFM treatment. Mullett et al. (2003) describe a regional difference in the regression between the northern and southern parts of the lake.

Taking the natural log of both sides of equation 8 results in the linear submodel

$$\ln N_{S,i,j} = \ln\mu + \alpha\ln Q_j + \beta\ln T_{i,j} + \delta\ln R_j + \gamma\ln Q_j R_j + \ln\lambda_i + \varepsilon_{i,j} \qquad (9)$$

Assuming the errors in equation 9 are independent and from a identically distributed normal distribution, the spawner discharge component of the objective function component becomes:

$$L_5 = k[\ln(\sigma_{\tilde{N}}) + \frac{1}{2}\ln(2\pi) + \left(\frac{\sum_i \sum_j (\ln N_{S,i,j} - \ln \tilde{N}_{S,i,j})^2}{2\sigma_{\tilde{N}}^2} \right) \tag{10}$$

In addition, the variance ($\sigma_{\tilde{N}}^2$) is also a parameter that is estimated during model fitting.

The measurable lake-wide population of spawners used in L_1 ($N_{S,i}$) is now defined as:

$$N_{S,i} = \sum_{j=1}^{70} \tilde{N}_{S,i,j} \tag{11}$$

Evaluation of alternative assessment strategies: I used simulated data to examine how varying effort among the estimation procedures affected the expected value and precision of the integrated population estimate, N_i. I assumed that assessment effort, defined as the budget available for assessment, was fixed but effort could be distributed among the three procedures in a fashion that could minimize the coefficient of variation of N_i,. However, the supply of parasitic phase lamprey is proportional to the effort in the commercial fishery and therefore is outside the influence of the control program. Consequently, I fixed the effort in the parasitic MR at the 2004 rate. The trade-off examined here was between the addition or deletion of traps used in the regression model used to predict spawning phase abundance and the corresponding decrease or increase in the number of CWT transformers released and recaptured. The marginal cost of adding or deleting a trapping location fluctuates as a function of the density of transformers available to be collected. In these simulations, costs for the spawning phase traps and the transformer mark and recapture were based on costs reported to the GLFC for the 2004 assessment program. The marginal savings accrued to the program by not trapping a stream and the cost of adding a stream for trapping was fixed at 90 CWTs, excluding capital costs for either method. Consequently the effect of deleting a stream from trapping in these simulations will result in the addition of 90 CWTs.

For the purpose of these simulations, the Lake Huron lamprey population was fixed at the 2004 level for ten years. Table 4.2 outlines the various configurations of the assessment program considered by the modeling in relation to the numbers of streams trapped and CWTs released. For each scenario, I randomly selected with replacement streams sampled during 2004.

For each stream selected, the number of lampreys trapped each year and the number of fin punched lampreys released were fixed at 2004 values. The number of recaptures observed in the model for each year of the simulation was determined by sampling the distribution of $p_{S,2004,j}$. First, a random number, u, was drawn from a uniform distribution $F(u)$ ranging between zero and one. Next, the number of recaptures was allowed to be any integer value ranging from $k_{i,j}=0$ to $k_{i,j}=n_{S,2004,,j}$. The value used in the simulation, k_u, was selected such that,

$$\frac{1}{\sqrt{2\pi}}\int_0^{k_u+1}\exp\left(\frac{-((k_u+0.5)-p_{S,2004,j}n_{S,2004,j})^2}{2\sigma^2_{S,2004,j}}\right)\le u$$
$$\text{and} \qquad (12)$$
$$\frac{1}{\sqrt{2\pi}}\int_0^{k_u+1}\exp\left(\frac{-((k_u+0.5)-p_{S,2004,j}n_{S,2004,j})^2}{2\sigma^2_{S,2004,j}}\right)> u$$

where $p_{S,2004,j}$ and $\sigma^2_{S,2004,j}$ were determined from equation (7).

The number of transformer *CWTs* observed at each stream in the simulation was determined in a similar manner. First, the value p_T was set based on $p_{T,2004}$ estimated in the previous section. For each stream in each year of the simulation, a value, $\tilde{p}_{T,i}$, was drawn from the distribution of $p_{T,2004}$ in a manner similar to that used to the simulated recoveries of spawners with the exception that a Poisson distribution was used instead of the normal approximation. This distinction was made because relatively few transformer CWTs were recovered in each stream. The value of $\tilde{p}_{T,i}$ was adjusted based on the number of transformer CWTs released in the simulation where

$$\overset{*}{p}_{T,i} = \tilde{p}_{T,i} r \tag{13}$$

where *r* is the ratio of transformer cwt released in the according to the schedule in Table 4.2 and $m_{T,2004}$. The number of parasitic *CWTs* recaptured in each stream was determined in the same manner as transformer *CWTs*.

I ran 100 trials for each scenario described in Table 4.2 and each trial consisted of 10 years of simulated data. For each simulated dataset I obtained point estimates using AD Model Builder to maximize the posterior distribution for the model defined by equations 1-11 (i.e., the same model used for inferences on the actual data, and based on these point estimates calculated the N_i and the average abundance in each trial, $\overline{N_i}$ and the coefficient of variation (CV) for each trial. The average CV was determined for each scenario in Table 4.2 to assess the scenario's performance relative to the other scenarios.

RESULTS

Integrating the population estimates: My analysis indicates that modal estimates of Lake Huron sea lamprey populations were measured with considerable uncertainty even though they declined by approximately 20% from approximately 300,000 spawners in 1990-92 to 240,000 in 2002-04 (Figure 4.3). The combination of enhanced trapping and sterile male release in St. Marys River began in 1997 and the initial granular Bayluscide treatments occurred during the summers of 1998-99. If the St. Marys treatment program had a significant effect on the Lake Huron lamprey populations, the effects of that program would have been observed in 2001 and later. The sea lamprey population declined from approximately 290,000 during 1999-2000 to 240,000 in 2001-04. However, the modal estimates of lamprey abundance were highly variable in years preceding the St. Marys treatment program ranging from 120,000 to 370,000. In addition, the annual estimates (N_i) were highly variable based on their marginal distributions (Figure 4.4).

Each of the sampling methods generally produced estimates with a relatively high degree of precision. The high degree of uncertainty in the estimates of N_i occurred because the three time series produced contradictory information. Figure 4.5 illustrates the marginal posterior distribution of the difference between the average population ($\log N$) in 1999-2000 and 2001-2004. Negative scores indicate that the population increased while positive values indicate that the population decreased during this period. 56% of samples indicated that the population declined but values ranged widely. The marginal posterior distribution for the difference derived from each of the three sampling methods are quite different (Figure 4.6). Approximately 94% of N_S samples and 99% of N_P

samples indicate that the population declined following the St. Marys treatment but 78% of N_T samples reflect an increase in the population.

The three estimation procedures and the N_is produced similar estimates of lamprey abundance in most years. However, Figure 4.7(a-c) illustrates that despite the joint estimation procedure, each of the sampling procedures produced significant deviations from the integrated estimate at different points in the time series. For example, $N_{S,1995}$ was 30% greater than N_{1995}, $N_{P,2001}$ deviated from N_{2002} by 65% while $N_{T,2002}$ exceeded N_{2002} by 120%. The largest deviations from the integrated estimates corresponded with low sample size for the corresponding sampling method. Only six spawning run MR were conducted in 1995 and the fewest parasitic and transformers CWTs were released for the 2001 and 2002 spawning years, respectively. $N_{T,2000}$,$N_{T,2001}$ and $N_{P,2002}$ were at least 30% less than the integrated abundance in those years but the numbers released were near the average released through the time series. I observed a positive correlation between $N_{P,i}$ and N_i (r=0.86; Figure 4.8a) while $N_{T,i}$ was uncorrelated (r=0.10; Figure 4.8b) with N_i. These data indicate the assumption of equal process errors between the three sampling procedures and N_i may not be valid. It appears that the transformer process errors are substantially different from the parasitic and spawning phase process errors. The effect of fixing σ_m^2 likely overestimated the importance of the transformer data in some years.

The marginal posterior distributions for the parasitic and transformer proportionality constants parameters are depicted in the histograms in Figure 4.9. They indicate that these parameters were poorly defined and that a wide range of values were nearly equally likely.

Evaluation of alternative assessment strategies: Figure 4.10 illustrates the effect of trading off transformer CWTs and trapping more streams. The CV of N in the simulation ranged from a low of 13.2% when 16 traps were fished and 480 transformer CWTs were released to a high of 29.1% when six traps and 1290 CWTs were released. Assessment strategies ranging from 11 to 17 traps and 840 to 300 CWTs preformed well relative to the "optimum" strategy of 16 trap sites and 480 transformer CWTs.

The estimates of the proportionality constants from the simulations were much better defined than those generated from the 1990-2004 data (Figure 4.10) in most simulations. The simulations were based on the 2004 data and therefore a more consistent process error among sampling methods was implied in the simulations over most scenarios. However, the proportionality constants were poorly estimated when few CWTs were released. For example, c_p and c_T in Scenerio 14 ranged from -2.1 to 0.5 and -1.8 to 0.1 respectively.

DISCUSSION

In this analysis, Lake Huron sea lamprey abundance during 2002-04 was not significantly less than the abundance at the beginning of the time series or prior to initiation of bayluscide treatments in the St. Marys River. However, there was a large degree of uncertainty in the estimates of abundance, N_i, resulting in little or no ability to detect differences in abundance between time periods and the effect of new management strategies. In contrast, the assessment program's current method of reporting the status of sea lamprey abundance is based on the spawning phase time series (e.g. Mullett et al. 2003) and Klar and Young (2005) used this time series to show that lamprey abundance in Lake Huron declined significantly since the start of the bayluscide treatments in the St. Marys River and that annual population estimates were measured with relatively high precision compared to N_i generated in this study. While the estimates of the transformer and parasitic MR are reported, these estimates generally have been ignored in the analysis of sea lamprey status (Klar and Young 2005).

The uncertainty in the integrated estimate of abundance generated in this study stemmed from the contradictory information generated from the three time series. The lack of correspondence between the time series may have resulted from at least two sources. First, the survival of transformers to the parasitic and spawner life stages may be highly variable among years due to the effect of dynamic fish community and environmental factors (Young et al. 1996 ; Bence 2003; Haeseker et al. 2003). For example, transformer survival to the parasitic stage is affected by stream temperature and discharge in the fall, density of predators and availability of suitable initial hosts following their migration from the streams to the lakes (Applegate 1950 ; Potter 1980; Purvis 1980). Consequently, the pattern of recruitment to the parasitic stage could be subjected to the same pattern of uncertainty that Jones et al. (2003) observed for recruitment of age 1 larvae. They observed a broad range in recruitment throughout the range of spawning lampreys densities used in Great Lakes tributaries. If this pattern is applied to the survival of transformers, I would expect that in general, a positive correlation between transformer and parasite or spawning phase abundance would be observed. However, a large degree of annual variability in the survival of transformers could lead to a wide range of parasitic abundance from any year class of transformers even if escapement of transformers from the control program was relatively constant.

On the other hand, I would expect that the differences between the parasitic and spawning phase assessments would be less variable and my analysis indicated that these time series were generally consistent with one another. The time elapsed between the marking of parasitic lampreys and the subsequent trapping of spawners was roughly half of the time elapsed between the marking of transformers and spawning phase trapping. In addition, the lake environment is likely more consistent than the stream environment. This could result in a less variable annual survival rate between the parasitic and spawning life stages compared to the transformer to parasitic life stages. However, the availability of suitable hosts for the parasitic life stage could also affect the survival rate to the spawning life stage.

A second limitation in the estimation of the probability of recapture was the combination of low contrast in the abundance through the time series and high measurement error in the transformer and parasitic estimates when few CWTs were released. The estimates of $N_{P,2001}$ and $N_{T,2002}$ were based on the release of low numbers of CWTs. The large deviations from N_i observed in these two years relative to most other years could represent outliers that have large influence on the parameter estimates. In addition, the relationship between transformer and spawning phase abundance could be a non-linear function (Schnute 1987) if transformer survival was density dependent. However, the data were not informative enough to explore this hypothesis. Density dependent relationships are best defined when there is strong contrast of at least an order of magnitude in the observed abundance and an a number of observations over a broad range of population sizes (Walters and Ludwig 1981; Hilborn & Walters 1992). This data set had approximately a three fold difference between the lowest and highest estimates of abundance through the time series (Figure 4.3) and only eight releases of transformer and parasitic CWTs.

The management of sea lampreys relies on its assessment program to scale the management effort on a lake by lake basis (Sawyer 1980). When lamprey abundance increases in a lake, the general response is to increase the effort to control the population (e.g Sullivan et al. 2003). Generally, sea lamprey management along with stocking and harvest management are considered the primary tools for managing native fish stocks in the Great Lakes. For example, expectations of future catch rates of Lake Huron lake trout were tied to the prospect of fewer lamprey and lower sea lamprey induced mortality in lake trout stemming from the integrated treatment program to reduce larvae and reproduction of parasites from the St. Marys River. However, the marginal costs of treatments significantly increase as populations decrease without a commensurate increase in benefits (Christie et al. 2003). In addition, I have argued that the annual survival rate of transformer may vary considerably and that changes in transformer survival could substantially affect the size of the parasitic populations that damage the fishery. Therefore in the short term, relatively small changes in treatment effort may not have a measurable impact on parasitic activity in the lake because the factors affecting survival between the transformer and parasitic life stages are poorly understood. Therefore, I recommend research to explore factors affecting transformer survival in order to better understand the expected marginal benefits of increased treatment effort.

A better understanding of how transformer survival rates may affect how the Great Lakes Fishery Commission views its assessment program. The current assessment program (transformer and parasitic MR and spawning-phase assessment) is predicated on the hypothesis that each sampling strategy provides information on both the success of the management program at killing transformers and the relative size of the parasitic phase population feeding on the fish community. If future research demonstrates that annual transformer survival rate varies substantially, then the transformer MR could be viewed as an indicator of escapement from the management program while the parasitic MR and spawner assessment would be viewed as joint measure of parasitic activity. On the other hand, the low release rates in some years likely contributed to the uncertainty in the transformer and parasitic proportionality constants. Years where the fewest numbers of CWTs were released resulted in the highest deviations from the integrated estimate of abundance. The results from the simulations modeling suggest that release rates below 300 transformers substantially increased the uncertainty in the overall estimate of lamprey abundance even with a commensurate increase in recapture effort. Consequently, I recommend a reallocation of assessment effort to fish 16 assessment traps and reducing the number of transformer CWTs released to 300-400, given that assessment resources are fixed and limited to 2004 levels. In future, the estimates of transformer abundance could be used as an indicator of the control program's effectiveness if future studies conclude that annual survival varies substantially. On the other hand, transformer estimates could be included as a measure of parasitic activity if the deviations from parasitic and spawning phase abundance observed in this study resulted from measurement error stemming for the release of few CWTs. My recommendation would provide adequate sampling effort to test either of these scenarios.

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LIST OF TABLES

Table 4.1. Description of nominal parameters directly estimated by numerical search using AD Model builder. These parameters are used in equations 4 -11.

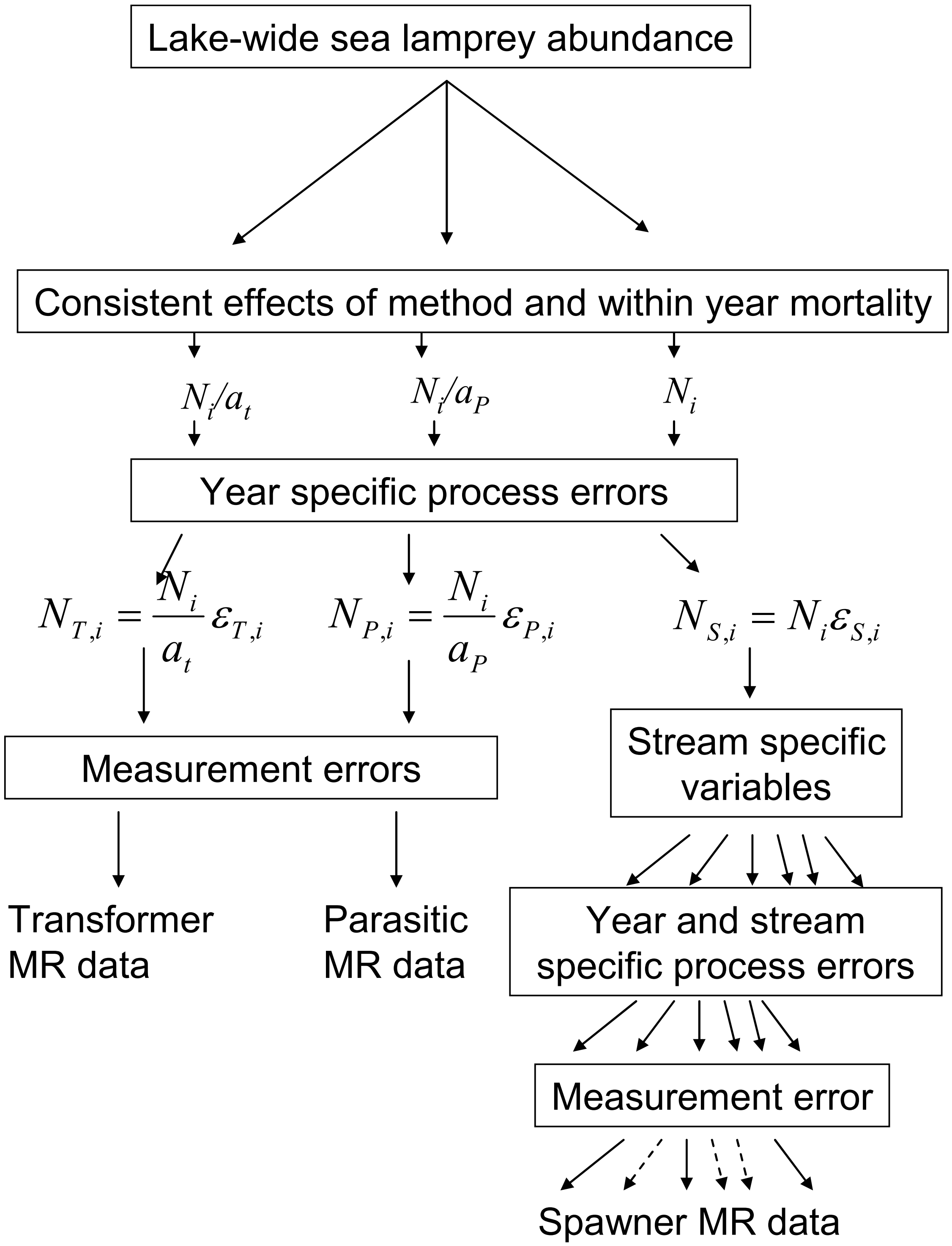
Symbol	**Description**	**Number of parameters**	**Bounds used during estimation**
N_i	Log abundance in year *i*	10	8.0 – 18.0
a_T	Transformer proportionality constant	1	-10.0 – 10.0
a_P	Parasitic proportionality Constant	1	-10.0 – 10.0
$p_{T,i}$	Probability of capturing a transformer CWT in year *i*	8	0.0 -1.0
$P_{P,i}$	Probability of capturing a Parasitic CWT in year *i*	8	0.0 -1.0
μ	Mean spawner abundance	1	0.0 – 18.0
α	stream discharge effect	1	-20.0 – 20.0
β	larval abundance effect	1	-20.0 – 20.0
δ	Regional effect	1	-20.0 – 20.0
γ	Discharge x Region interaction	1	-20.0 – 20.0
λ_i	Year effect	14	-20.0 – 20.0
$Ln(\sigma)$	Regression process error	1	-20.0 – 20.0
$p_{S,i,j}$	Probability of capturing a marked spawner in year *i,* stream *j*.	146	0.0 -1.0

Table 4.2. The number of spawning run estimates and transformer coded wire tags used in the simulation modeling scenarios.

Scenario	Assessment Traps	Transformer CWTs
1	6	1290
2	7	1200
3	8	1110
4	9	1020
5	10	930
6	11	840
7	12	750
8	13	660
9	14	570
10	15	480
11	16	390
12	17	300
13	18	210
14	19	120

LIST OF FIGURES

Figure 4.1.



Lake-wide sea lamprey abundance
Consistent effects of method and within year mortality
N_i/a_t
N_i/a_P
N_i
Year specific process errors
$N_{T,i} = \frac{N_i}{a_t}\varepsilon_{T,i}$
$N_{P,i} = \frac{N_i}{a_P}\varepsilon_{P,i}$
$N_{S,i} = N_i\varepsilon_{S,i}$
Measurement errors
Stream specific variables
Transformer MR data
Parasitic MR data
Year and stream specific process errors
Measurement error
Spawner MR data

Figure 4.2.

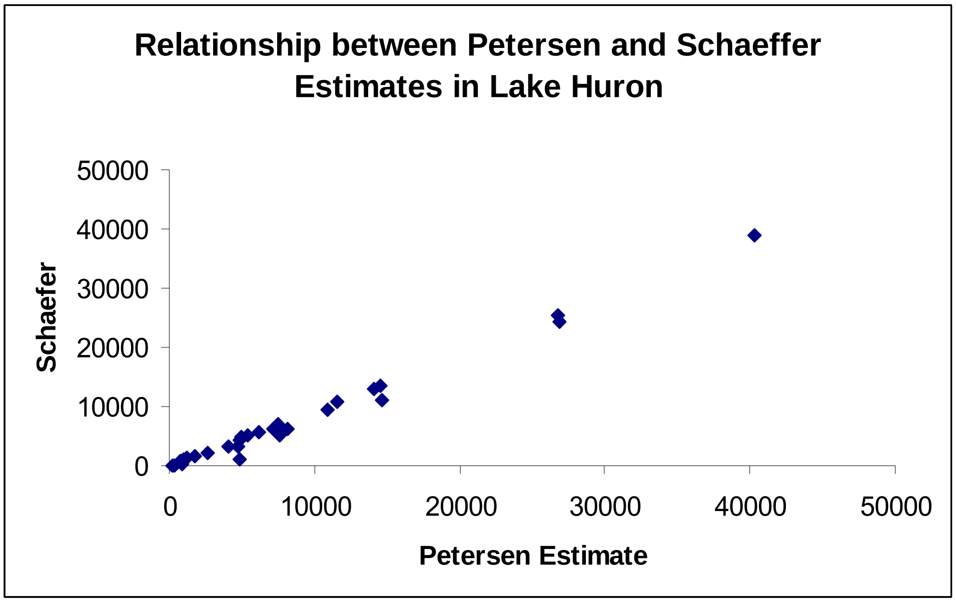

Relationship between Petersen and Schaeffer Estimates in Lake Huron
Schaefer
50000
40000
30000
20000
10000
0
0
10000
20000
30000
40000
50000
Petersen Estimate

Figure 4.3

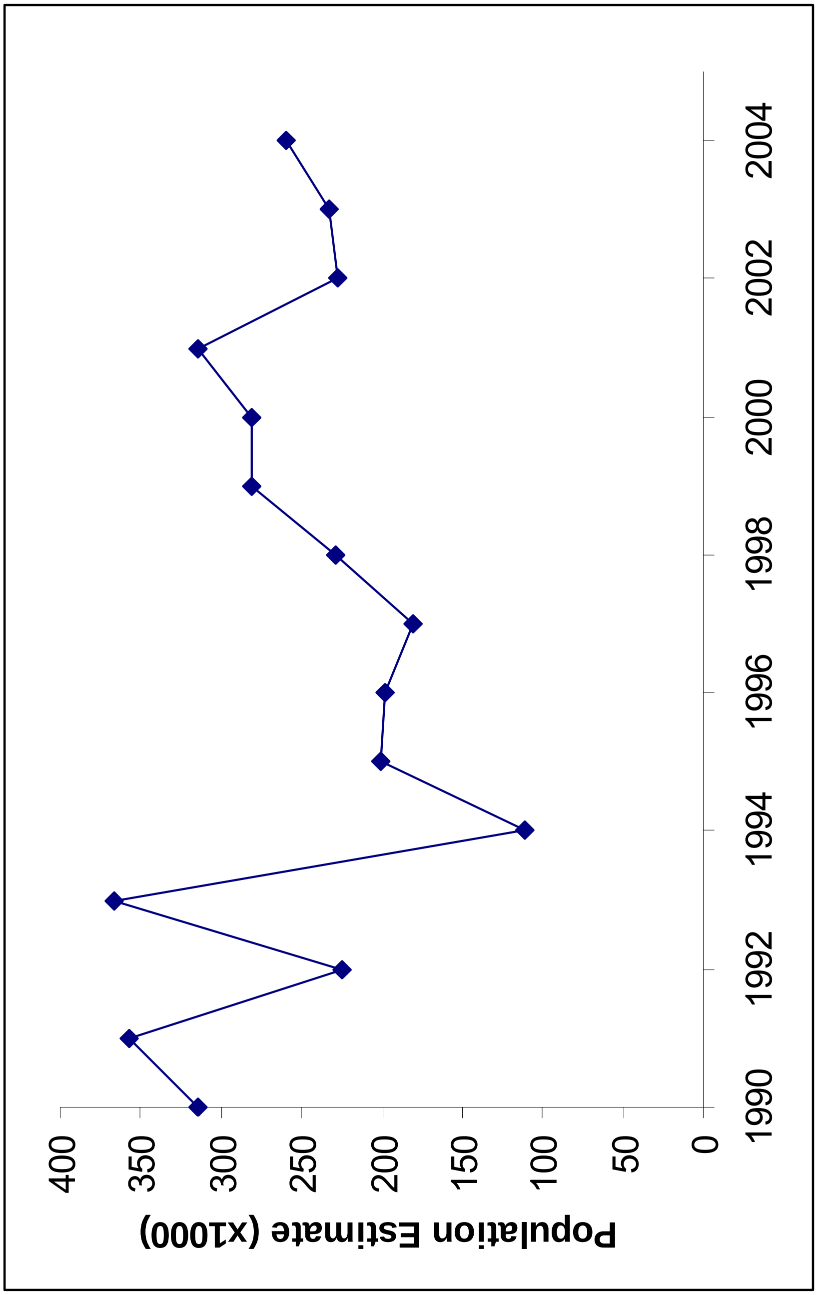

Population Estimate (x1000)
0
50
100
150
200
250
300
350
400
1990
1992
1994
1996
1998
2000
2002
2004

Figure 4.4

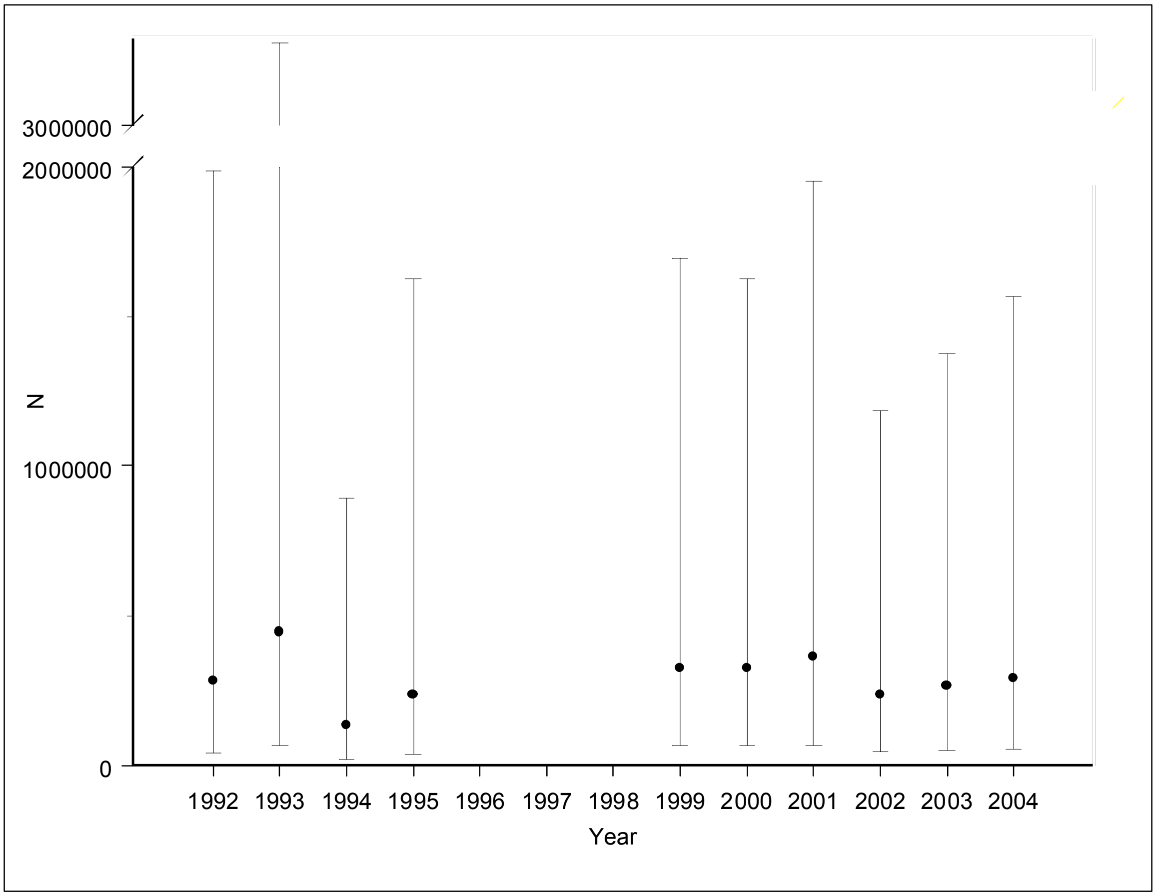

3000000
2000000
1000000
0
N
1992 1993 1994 1995 1996 1997 1998 1999 2000 2001 2002 2003 2004
Year

Figure 4.5

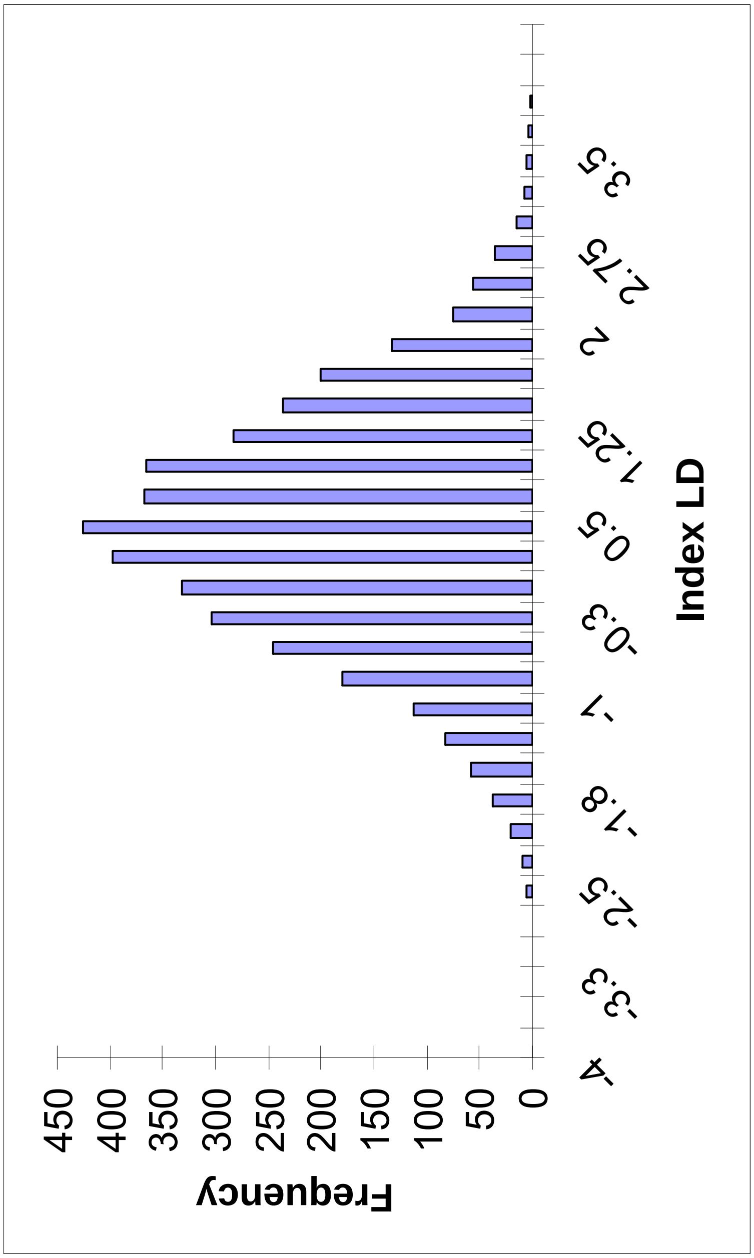

Frequency
450
400
350
300
250
200
150
100
50
0
-4
-3.3
-2.5
-1.8
-1
-0.3
0.5
1.25
2
2.75
3.5
Index LD

Figure 4.6

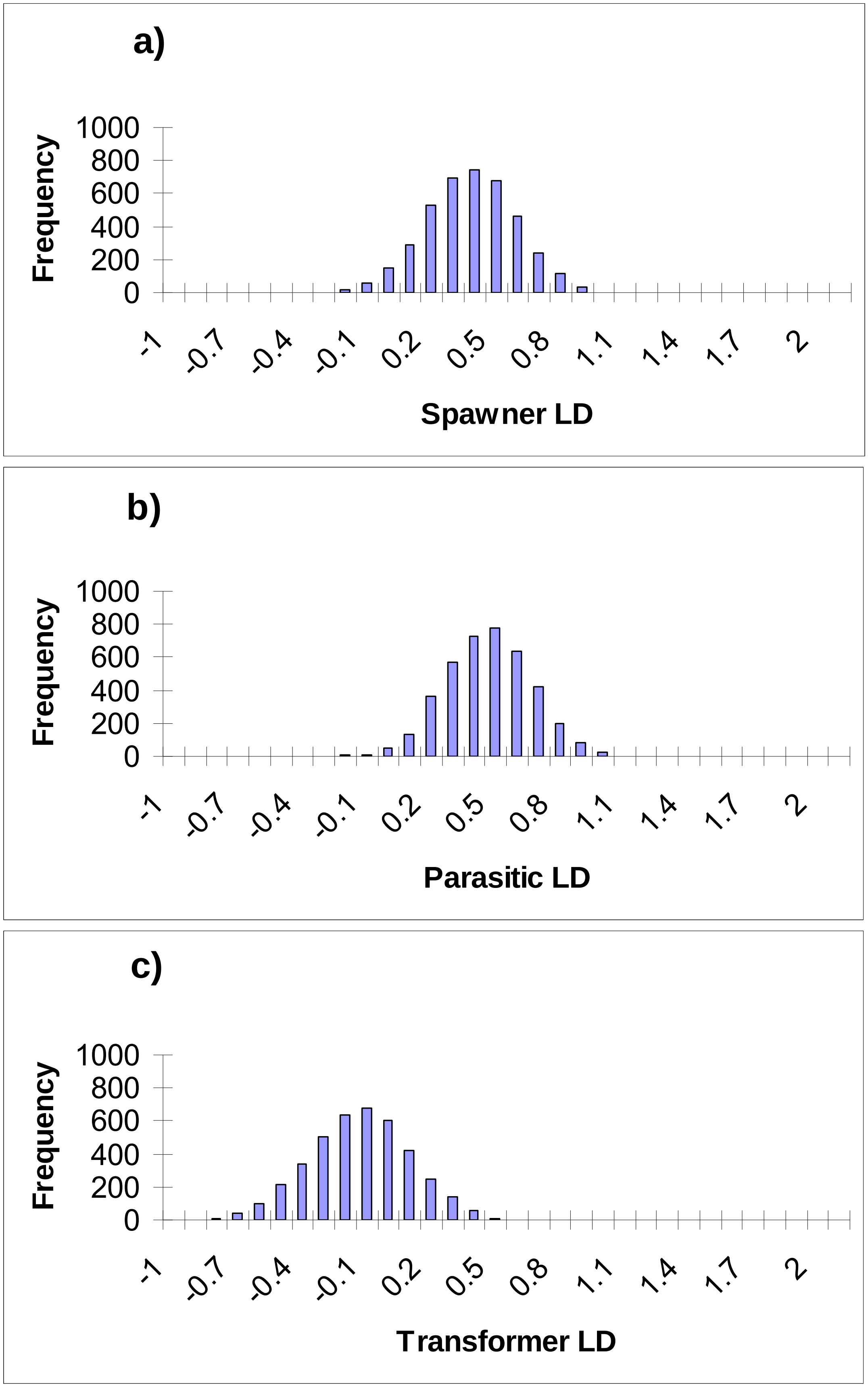
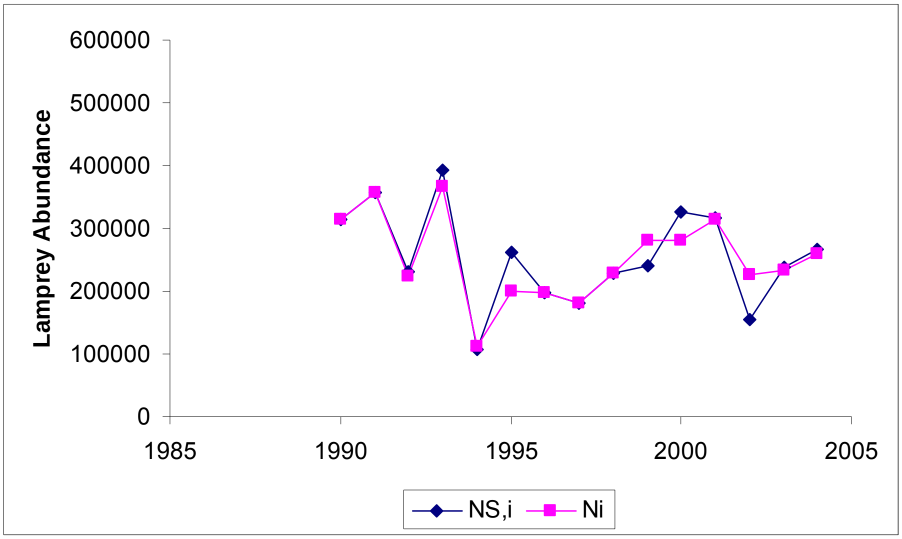
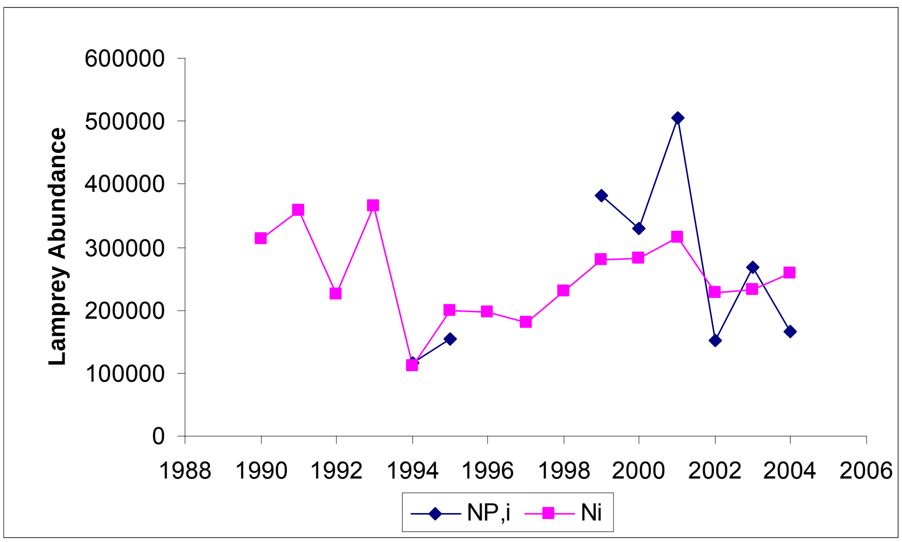

a)
Frequency
1000
800
600
400
200
0
-1
-0.7
-0.4
-0.1
0.2
0.5
0.8
1.1
1.4
1.7
2
Spawner LD
b)
Frequency
1000
800
600
400
200
0
-1
-0.7
-0.4
-0.1
0.2
0.5
0.8
1.1
1.4
1.7
2
Parasitic LD
c)
Frequency
1000
800
600
400
200
0
-1
-0.7
-0.4
-0.1
0.2
0.5
0.8
1.1
1.4
1.7
2
Transformer LD

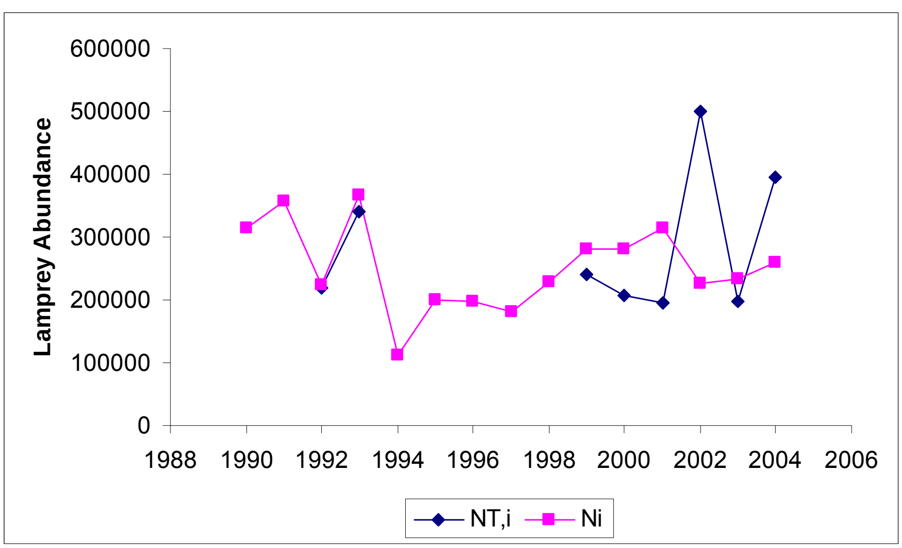
Figure 4.7



Lamprey Abundance
600000
500000
400000
300000
200000
100000
0
1985
1990
1995
2000
2005
NS,i
Ni

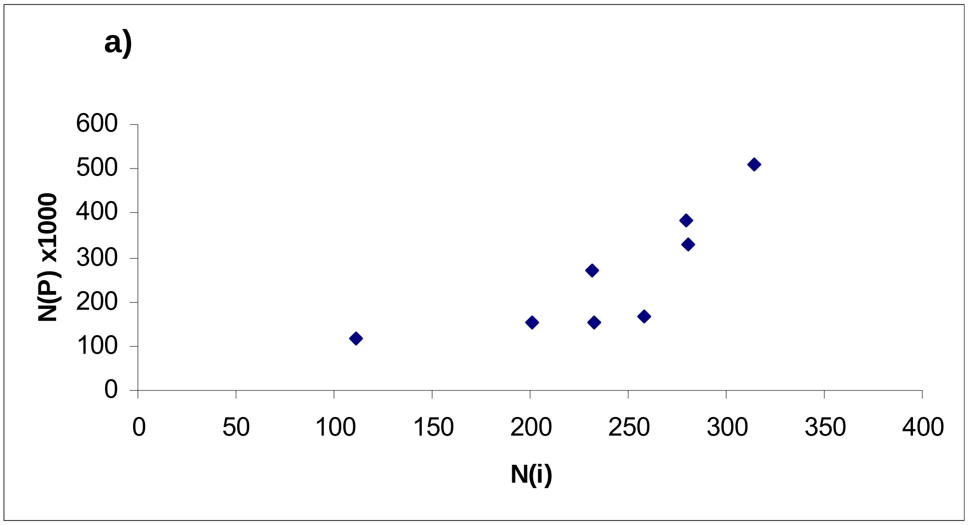


Lamprey Abundance
600000
500000
400000
300000
200000
100000
0
1988
1990
1992
1994
1996
1998
2000
2002
2004
2006
NP,i
Ni



Lamprey Abundance
600000
500000
400000
300000
200000
100000
0
1988
1990
1992
1994
1996
1998
2000
2002
2004
2006
NT,i
Ni

Figure 4.8


a)
N(P) x1000
600
500
400
300
200
100
0
0 50 100 150 200 250 300 350 400
N(i)

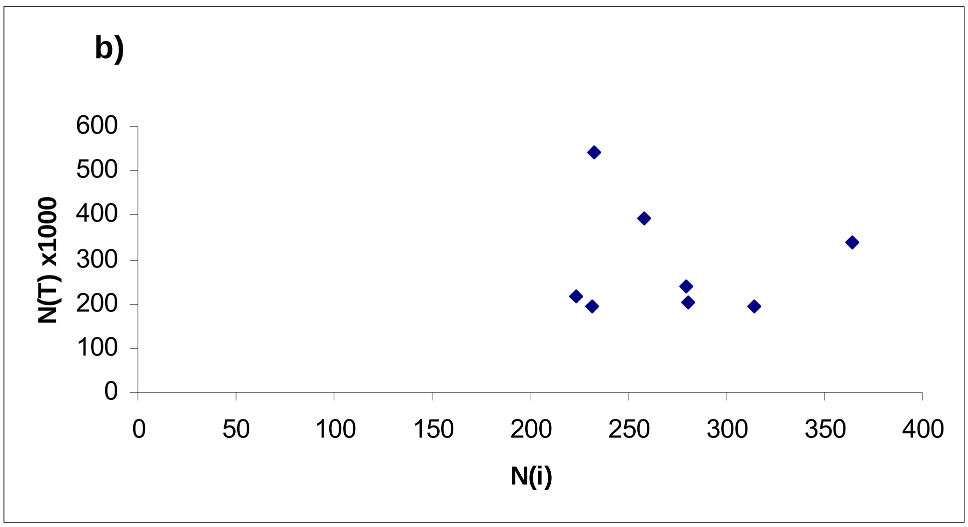

b)
N(T) x1000
600
500
400
300
200
100
0
0 50 100 150 200 250 300 350 400
N(i)

Figure 4.9

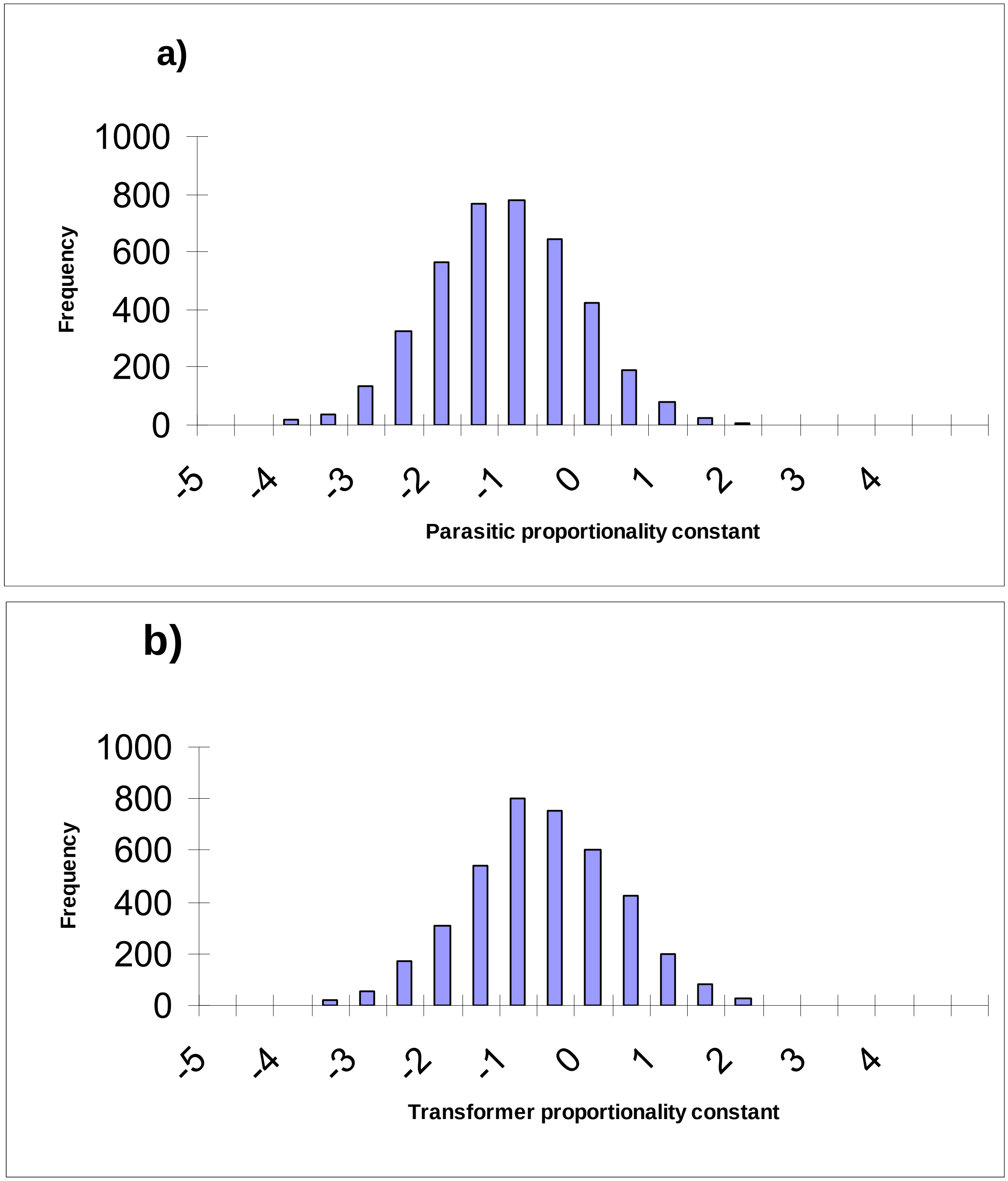
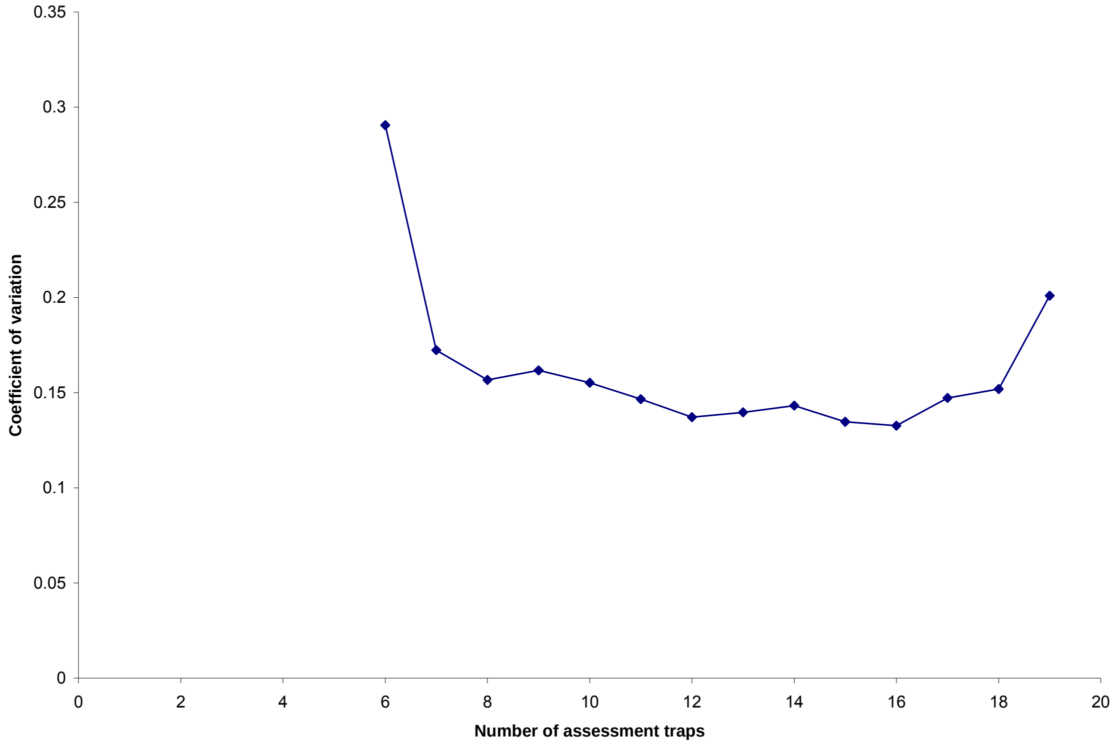
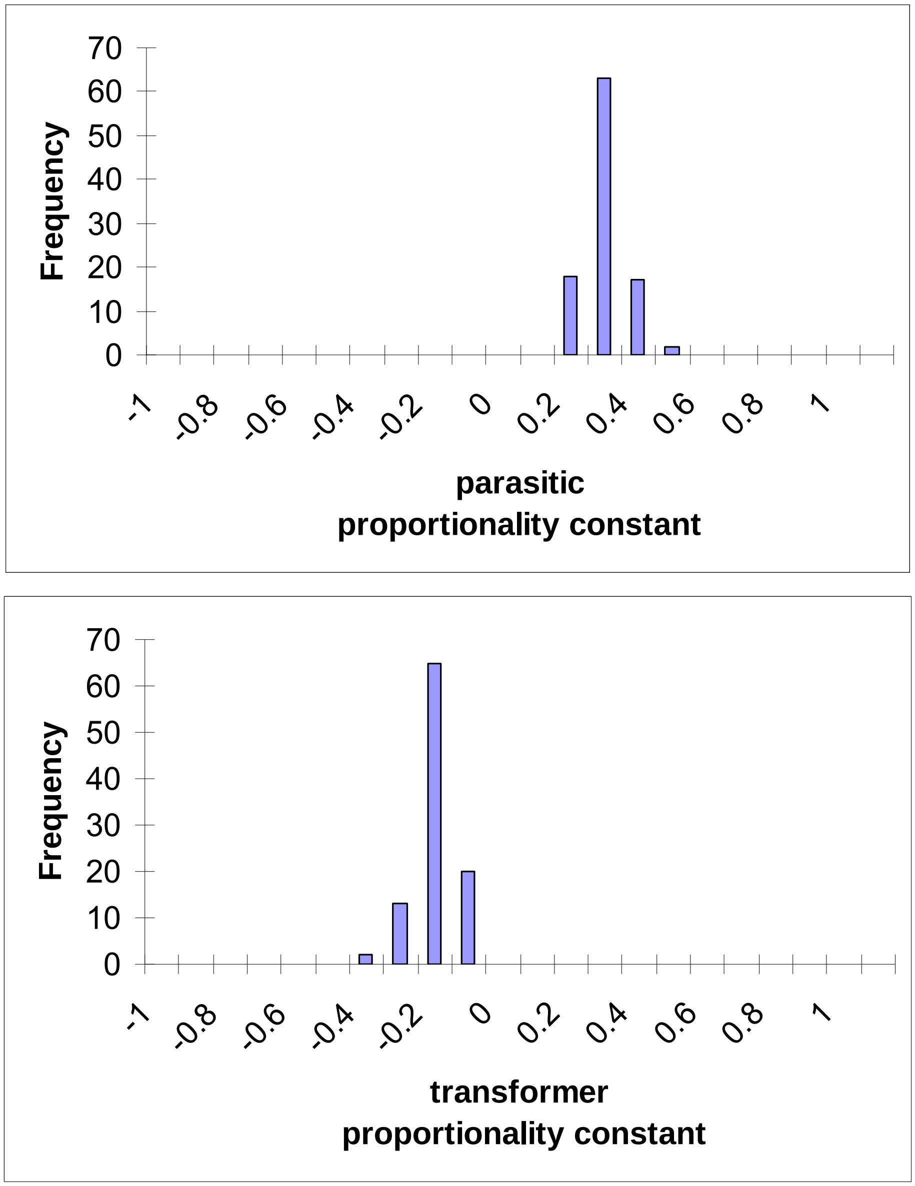

a)
1000
800
600
400
200
0
Frequency
-5
-4
-3
-2
-1
0
1
2
3
4
Parasitic proportionality constant
b)
1000
800
600
400
200
0
Frequency
-5
-4
-3
-2
-1
0
1
2
3
4
Transformer proportionality constant

Figure 4.10



0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
Coefficient of variation
0
2
4
6
8
10
12
14
16
18
20
Number of assessment traps

Figure 4.11


70
60
50
40
30
20
10
0
Frequency
-1
-0.8
-0.6
-0.4
-0.2
0
0.2
0.4
0.6
0.8
1
parasitic
proportionality constant
70
60
50
40
30
20
10
0
Frequency
-1
-0.8
-0.6
-0.4
-0.2
0
0.2
0.4
0.6
0.8
1
transformer
proportionality constant

CHAPTER 5: RECOMMENDATIONS

In 1997, the GLFC convened an expert panel to review the relevance and technical merit of its spawning phase assessment program. The panel concluded that spawning-phase was an integral part of the sea lamprey integrated pest management program because it enabled managers to assess the effectiveness of the control program. The panel also made a number of important technical recommendations as well as some broader scale recommendations including:

- The assessment program should focus on evaluating the effectiveness of the control program and evaluating the likelihood of detecting the impact of changes in the control program;
- Integrating all of the information generated from the various data collection methodologies, and:
- Optimize the allocation of effort among these collection methods to maximize the precision of the population estimates.

The purpose of this thesis was to take up the recommendations of the review panel. What follows are my recommendations for changes in the Lake Huron assessment program.

1. *Increase the number of streams fished with spawning phase assessment traps by four to ten traps from the current effort:* Increasing the number of streams trapped would benefit both the assessment and control programs. The analyses in chapters two and three show that increasing trapping effort resulted in a more precise estimate of abundance. In addition, based on simulations using the stock-recruitment model, I concluded that fishing lampreys in the ten largest streams currently without assessment

traps would approach the level of fishing necessary to impart significant downward pressure on lake wide population abundances. Equally important, additional trap locations would provide opportunities for the application of future alternative control method. For example, the male lampreys fished could be used in the sterile-male release program in the St. Marys River management program. In addition, new trapping locations could be used in both experimental and operational deployment of pheromone based control strategies.

2. Annually tag and release at least 300 – 400 transformers with CWTs: A number of previous publications (e.g. Young et al. 1996; Haeseker et al. 2003) have recognized that studies directed at understanding the factors influencing transformers survival would be important in improving our understanding of lamprey population dynamics. In this study, the transformer MR time series was an enigma because the transformer time series appeared to be poorly correlated with the population estimate procedure that integrated separated time series. I speculated that this result could be due to measurement error associated with not releasing an adequate number of CWTs, or that the transformer time series varied from the parasitic and spawning-phase time series because of density dependent or independent factors. Therefore, I recommend that transformer releases of at least 300 – 400 CWTs, coupled with increased spawning phase assessment effort, in order to adequately assess the transformer population. In addition, I recommend that studies be initiated to evaluate the potential impact of environmental, fish community and density dependant factors affecting transformer survival.

3. *Integrate fish wounding data into the assessment of parasitic abundance:* The integration of the three time series is based on the hypothesis that combining all of the

data provides a more reliable indicator of both the effectiveness of the treatment program and the parasitic activity in the fish community. Fishery management agencies routinely collect information on lake trout wounding rates in Lake Huron (Rutter and Bence 2003) but this information has not been integrated into lamprey population estimates. This time series generally reflects the wounding rate of a specific length (~500 mm) but would be more useful if it reflected the total wounding across all length classes and incorporated all important host species including pacific salmon species, lake whitefish, burbot and sturgeon. A community wounding index (Mark Ebener, Chippewa-Ottawa Resource Authority, personal communications) combined with a better understanding of foraging behaviour at varying fish densities may prove to be another important source of information on parasitic lamprey activity.

The GLFC's spawning-phase assessment program has undergone fundamental change since the "expert panel review" in 1997. A program that was once *ad hoc* in nature now has design and purpose. Prior to the review, the methods of estimating lake wide sea lamprey populations among the Great Lakes did not enable comparison among lakes or provide any consistent framework for establishing target abundances for sea lampreys. Today the methods to generate spawning-phase abundance is consistently applied across the lakes (Mullett et al. 2003), target abundances have been established and the population estimates are annually used to judge the status of lamprey populations against these targets (e.g. Klar and Young 2005). Adopting the recommendations I have provided will further improve the effectiveness of the assessment program.

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