A MODEL OF SEA LAMPREY FEEDING WITH IMPLICATIONS FOR LAKE TROUT DYNAMICS IN LAKE HURON

By

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ABSTRACT

A MODEL OF SEA LAMPREY FEEDING WITH IMPLICATIONS FOR LAKE TROUT DYNAMICS IN LAKE HURON

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The dynamics of sea lamprey (*Petromyzon marinus*) and lake trout (*Salvelinus namaycush*) in Lake Huron were investigated and a population model for lake trout in the main basin of Lake Huron was parameterized. I also examined the implications of uncertainty in these dynamics on the outcomes of sea lamprey control programs and lake trout stocking strategies using a stochastic model.

To better estimate wounding rates on hosts of sea lamprey in the Great Lakes, I developed a method to fit a logistic model for the mean number of wounds per host as a function of host length. Wounds per fish were assumed to follow a Poisson distribution, and a number of alternative models were considered using maximum likelihood techniques. Parameters were allowed to vary spatially and temporally, and my results suggest that the asymptote, or wounding rate on the largest lake trout, varied over years and among lake regions. In addition, the inflection point (where wounding rates increased most rapidly toward the asymptote) varied among regions, shifting toward smaller lake trout lengths further north in Lake Huron.

Using a statistical catch-at-age model as a framework, I parameterized a population model for lake trout in the main basin of Lake Huron. Natural, commercial fishing, and recreational fishing mortality were estimated separately for each of the three regions. Sea lamprey-induced mortality was determined by a multi-species Type II functional response model parameterized across three regions in the main basin of Lake

Huron. The functional response parameters were estimated during the model fitting process using observed wounding rates on lake trout as one important measure of goodness of fit. The effective search rate of sea lamprey, a key component of the functional response model, was modeled as a logistic function of prey length and was shown to vary spatially across the regions of Lake Huron. I used the functional response model to estimate sea lamprey-induced mortality as a function of sea lamprey density, lake trout density, and the density of alternative prey. Sea lamprey-induced mortality was the largest component of annual lake trout mortality rates in central and southern Lake Huron, while commercial fishing was the largest component of lake trout annual mortality in the north.

To assess the impacts of sea lamprey control and lake trout restoration programs, I used a stochastic model to forecast future lake trout population dynamics. This model was based on the catch-at-age model, and incorporated the parameterized type II functional response. A variety of possible lake trout and sea lamprey management scenarios were forecast for Lake Huron. A Markov Chain Monte Carlo analysis of the catch-at-age model accounted for uncertainty in model parameters and I allowed for stochastic temporal variation in model inputs such as sea lamprey abundance and lake trout stocking when assessing the uncertainty of the forecasts. In northern Lake Huron, reducing sea lamprey abundance 90% and increasing lake trout stocking 200% reduced sea lamprey-induced mortality on large lake trout 85%. Reduced commercial fishing mortality rates in northern Lake Huron will allow sea lamprey-induced morality rates to decease as lake trout density increases when lamprey populations are reduced 90%, indicating that sea lamprey are partially saturated with prey hosts under these conditions.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

Rutter, M.A. and Bence, J.R.. 2003. An improved method to estimate sea lamprey wounding rate on hosts with application to lake trout in Lake Huron. J. Great Lakes Res. **29** (Supplement 1): 320-331.

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An Improved Method to Estimate Sea Lamprey Wounding Rate on Hosts with Application to Lake Trout in Lake Huron

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ABSTRACT. *To better estimate wounding rates on hosts of sea lamprey* (Petromyzon marinus) *in the Great Lakes, methods were developed to fit a logistic model for the mean number of wounds per host as a function of host length. These methods were applied to the number of wounds (the sum of type A-I to A-III marks on hosts collected in spring) on individual lake trout* (Salvelinus namaycush) *collected by surveys and by a commercial fishery in three regions of U.S. waters of Lake Huron from 1984 to 2000. Wounds per fish were assumed to follow a Poisson distribution, and a number of models were examined using maximum likelihood techniques. Parameters were allowed to vary spatially and temporally, and Markov Chain Monte Carlo techniques were used to evaluate uncertainty in parameter values. By using data for individual hosts and modeling the effect of host length as a continuous function, this method makes more complete use of available data, increases precision, and removes biases in comparison with widely used approaches for estimating wounding rates. In this application, the asymptote, or wounding rate on the largest lake trout, varied over years and among lake regions. In addition, the inflection point (where wounding rates increased most rapidly toward the asymptote) varied among regions, shifting toward smaller lake trout lengths further north in Lake Huron. This change in shape suggests some complexity in the sea lamprey-lake trout interaction. For a 500-mm lake trout, a host size observed in all areas, estimated wounding rates were highest in the north.*

INDEX WORDS: *Lake trout, sea lamprey, wounding, Markov Chain Monte Carlo, Lake Huron.*

INTRODUCTION

Wounds on host fish that survive sea lamprey (*Petromyzon marinus*) attacks provide an important source of information to fishery managers and scientists in the Great Lakes. Although attacks by sea lamprey often lead to host death, many fish survive and bear marks resulting from the attacks (King 1980). “Wounds” are marks made by lamprey on hosts that heal to “scars” within a period of a year. There is evidence that mortality experienced by the host population can be positively correlated with frequency of wounds (Bence *et al.* 2003), and the mean number of wounds per fish is used to assess the success of the sea lamprey management program (Adams *et al.* 2003), estimate host mortality rates (Eshenroder *et al.* 1995, Sitar *et al.* 1999), and to calibrate sea lamprey-host models that provide guidance to the sea lamprey management program (Koonce *et al.* 1993, Larson *et al.* 2003). The host species emphasized in all these applications is lake trout (*Salvelinus namaycush*).

The incidence of and characteristics of sea lamprey marks vary seasonally (Spangler *et al.* 1980, Jacobson 1989) and with host size (Wigley 1959, Pycha and King 1975, Sitar 1996). Most parasitic-phase sea lamprey leave streams and enter the Great Lakes during fall and spring but do not begin to grow rapidly until the summer after they enter the lake. Most potentially lethal attacks on larger hosts such as lake trout or lake whitefish (*Coregonus clapeaformis*) are by rapidly growing sea lamprey in the autumn (Spangler *et al.* 1980, Bergstedt and Schneider 1988, Bence *et al.* 2003) following one summer’s growth. The King (1980) system for refer-

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ring to marks was used. In this system, type A marks result from attacks where the skin has been broken and stages I to IV represent progressive stages of healing. For hosts collected and observed in the autumn, A-I marks unquestionably are the result of attacks by the currently feeding cohort of sea lamprey, whereas marks in later stages of healing may represent a mix of attacks by the current and prior year's cohort (Eshenroder and Koonce 1984, Schneider *et al.* 1996, Ebener *et al.* 2003). When observed in the spring, larger type A-I, A-II, and A-III marks are most likely the result of the cohort that was responsible for lethal attacks the previous autumn (Eshenroder and Koonce 1984). Virtually all A-I to A-III marks observed on lake trout in the upper Great Lakes in the spring are larger marks (Mark Ebener, Chippewa-Ottawa Resource Authority, and James Johnson, Michigan Department of Natural Resources, personal communication). Thus, for lake trout, A-I marks in the autumn and the sum of A-I to A-III marks in the spring provide two ways to assess wounding on lake trout for the same cohort of sea lamprey. The frequency of wounds generally increases with host size (Wigley 1959, Pycha and King 1975, Sitar 1996). Examination of patterns reported in the literature, observations from laboratory experiments (Farmer and Beamish 1973, Swink 1991), and unpublished data from Lakes Michigan, Huron, and Superior all suggest a general pattern where the mean wounds per fish increases with fish size up to an asymptote (Bence *et al.* 2003).

Current practice for recording and reporting sea lamprey marks in the Great Lakes generally follows recommendations made by Eshenroder and Koonce (1984). They recommended reporting marks of the year (what are called wounds) on lake trout from either autumn or spring surveys. They assumed that A-I to A-III marks would qualify as marks of the year at both times of year, but fall A-III marks in Lake Ontario were found to be better correlated with A-I marks from the previous year (Schneider *et al.* 1996). More recently Ebener *et al.* (2003) recommend only including A-I marks when fish are observed in the autumn. Eshenroder and Koonce (1984) also recommended that marks be summarized as the mean number of wounds per lake trout (wounding rate) for each of several broad length categories or bins (432 to 533 mm, 534 to 635 mm, 636 to 737 mm, > 737 mm).

The common practice for estimating mean wounds has several substantial limitations and does not make full use of available data. First, it treats each year and region independently, and thus makes no use of any regularity among regions or years. Second, it does not take advantage of the fact that the expected number of wounds is related to host length in a predictable way. Finally, the use of broad host length bins can produce biases that will vary depending upon the length-composition of hosts within each bin. Because sample sizes are often small for the largest length bin of hosts, estimated wounding rates for such bins often vary wildly from year to year.

In this paper, an approach for estimating mean wounds per fish was developed by fitting a model based on a logistic function to observed wounding data, and applying this approach to spring wounding data for lake trout in Lake Huron. The logistic equation allows wounding rates to increase as a continuous function of host length, eventually leveling off at an asymptotic rate for large hosts. This model is only applicable to wounds, since scars can accumulate over the life of the host and the number of scars per fish is not expected to reach an upper asymptote with increasing fish size. The basic idea was to encapsulate the relationship between wounding rate and host size through a limited number of parameters, while allowing for wounding rates that vary from region to region and year to year.

This approach differs from conventional methods by making use of individual observations on the number of wounds and the size of each fish, and makes the reasonable assumption that the distribution of wounds among fish of a given length is Poisson (Bence *et al.* 2003). This approach makes more complete use of the available information than conventional approaches, provides wounding rates for any length of host, and circumvents some of the problems associated with small sample sizes and bias by assuming a functional form for the relationship between wounds per host and host length.

METHODS

Data Used in Analysis

Data used in the analysis came from spring lake trout surveys and sampling of tribal commercial harvest during the spring (April through June) in U.S. waters of the main basin of Lake Huron during 1984 to 2000. Marking data were recorded using the protocol developed by King (1980), and A-I, A-II, and A-III marks were considered to be wounds. Earlier marking data exist, but were not used because they were not recorded using the King (1980) protocol. Only data collected in the spring were analyzed, as this is the one time period consistently sampled for lake trout in all regions of U.S. waters of the main basin of Lake Huron. In addition, spring wounding was of special interest because estimated spring wounding rates have been transformed into estimated per capita host mortality, based on an assumed direct proportionality that depends on the lethality of an attack (Eshenroder *et al.* 1995, Sitar *et al.* 1999, Bence *et al.* 2003). Surveys were conducted using gill nets by both the Michigan Department of Natural Resources (MDNR) and the Chippewa-Ottawa Resource Authority (CORA), and were done during April to June of each year. The MDNR gill nets were graded mesh in 125-cm intervals ranging from 5 to 15 cm, typically 3,000 m in length (Merena *et al.* 1981, Johnson and VanAmberg 1995). Survey sites were fixed stations in U.S. waters of Lake Huron. Survey data were collected near Drummond Island in northern Lake Huron by CORA using similar methods. Commercial samples came from sampling by CORA of a tribal fishery in the northern part of the lake during April through June, and fish were collected by trap nets, small-mesh (6.35 cm and 7.6 cm) gillnets, and large-mesh (11.4 cm and larger) gillnets (Mark Ebener, CORA, Sault Ste. Maire, MI, personal communication).

Data were pooled spatially into three regions: north, central, and south (Fig. 1). Only fish greater in total length (TL) than 430 mm were considered in this study, which is consistent with current methods and low wounding rates on smaller lake trout. Only 0.5% of sampled lake trout 430 mm and smaller had wounds. Wounding data were available for 18,284 individual fish greater than 430 mm, TL, in length.

FIG. 1. Lake Huron with the regions used in this study demarcated. The north, central and south regions correspond to regions used in lake trout assessments (Sitar* et al. *1999). Following the statistical districts devised by Smith* et al. *(1961), U.S. waters of the north region corresponds to MH-1, U.S. waters of the central region corresponds to MH-2 and U.S. waters of the southern region corresponds to MH-3, MH-4 and MH-5 combined. The international boundary is denoted by a dashed line.

Models for Observed Wounding Rates

The logistic function is a simple model that allows wounding rates to increase gradually with host length, eventually reaching an asymptote, in the same way actual wounding rates typically do (see Introduction). This three parameter function:

$$\hat{w}(l) = \frac{\theta}{1 + e^{-\alpha(l-\beta)}} \tag{1}$$

describes the average wounding rate per fish, $\hat{w}$, observed on a fish of length l. The parameter θ describes the average wounding rate for large fish (the asymptotic wounding rate), while α and β affect the steepness and position of the curve, respectively (Fig. 2). The length at which lake trout wounding reaches 50% of the asymptote is given by β and is the inflection point. The rate at which the wounding rate approaches the asymptote while passing through the inflection point is determined by α, with the slope at the inflection point being $\alpha\theta/4$. As described below, a range of model variants were explored in which the parameters of the logistic function were allowed to vary among regions and years.

The model was fit to the observed data using maximum likelihood techniques. The observed number of wounds for a lake trout of a given length was assumed to follow a Poisson distribution (Bence *et al.* 2003). The mean of the Poisson varies as a function of length, and is described by the logistic wounding model (eq. 1). Parameters were estimated by maximizing the log-likelihood:

$$L(\theta,\alpha,\beta) = \sum_{i=1}^{n} \left(w_{obs,i} \ln(\hat{w}_i) - \hat{w}_i \right) \tag{2}$$

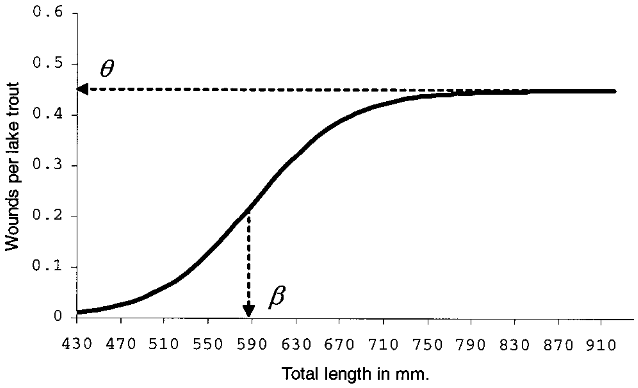


FIG. 2. An example of a logistic function relating expected or average wounds per fish (wounding rate) to total fish length, with the asymptote indicated by θ and the inflection point indicated by β.

where n is the number of fish sampled, $w_{obs,i}$ is the observed number of wounds on fish i, and $\hat{w}_i$ is the predicted number of wounds for fish i from equation 1. The maximum likelihood approach allows the use of data available for each individual fish, including length and number of observed wounds. Parameter estimation was done using the optimization software Admodel Builder (Otter Research 2000). Akakie's Information Criteria (AIC) (Akaike 1973) was used to determine which model variant provided the best fit to the data.

It was originally hypothesized that the shape of the logistic curve would be constant, and that only the asymptote (θ) potentially varied temporally and spatially. This premise was initially used because foraging models where both sea lamprey size selection and the lethality of their attacks are constant produce this pattern (Bence *et al.* 2003). Following this approach, year-to-year (1984 to 2000) and region-to-region (north, central and south) differences in wounding rates can be estimated through differences in the asymptote parameter. Within this class of models, the simplest case where a common asymptote was shared among all regions and years was fit first (Table 1, model A). Models where the asymptote varied among regions but not years (model B), among years but not regions (model C), as an additive sum of region and year effects (model D), and freely among regions and years (i.e., with 51 values of θ representing each combination of year and region, model E) were then considered.

The shape of the logistic model was explored next to determine if it varied among regions. It was expected that changes in the logistic shape would largely reflect changes in sea lamprey behavioral responses to host populations (Bence *et al.* 2003), and would thus change gradually in response to gradual changes in the host community. This contrasts with the expectation for the overall level of wounding, which was expected to reflect both large year to year variations in sea lamprey abundance (Morse *et al.* 2003, Young *et al.* 2003) and possible variations in how wounds were recorded (Ebener *et al.* 2003). Regional rather than temporal effects were focused on first because over the study period spatial differences in the lake trout stocks appear more substantial than temporal ones (Eshenroder *et al.* 1995, Sitar 1996, Sitar *et al.* 1999, Wilberg *et al.* 2002). The set of models considered allowed α or β to vary among regions with the other shape parameter fixed (Table 1, models F and G, respectively), and for both shape parameters to vary among regions at the same time (model H). This exploration of regional variation in the logistic shape was viewed as building upon the previous analysis of variation in the asymptote, so the approach was to add these variants in the shape parameters to the best model obtained when the shape parameters were assumed constant. In addition, these three treatments of spatial variation in α and β were added to each of the four other treatments for spatial and temporal variation in θ (as in models A through D), to check that none of these alternatives had a better fit (lower AIC).

Next, the shape parameters α and β were allowed to vary temporally. Initial attempts to fit models that allowed these parameters to vary freely from year to year were unsuccessful, either because the resulting AIC was large or because not all parameters were estimable (convergence to a solution was not achieved). Therefore, an approach was implemented that reflected the premise that temporal changes in the shape parameters would result from responses to changes in host populations, and that these changes would occur gradually over time. Gradual temporal changes in α and β were estimated by modeling them using a random walk model (Gudmundsson 1998). A single set of random walk variations were applied to all regions (Table 1, models I and J) and independent random walks for each region were also considered (models K and L). In the former case, the random walk effects were added to regional differences, if any (essentially additive year and region effects), using both the best model with fixed shape parameters

TABLE 1. Description of models used in estimating sea lamprey wounding rates on lake trout. Subscripts N, C, and S refer to the northern (MH-1), central (MH-2) and southern (MH-3,MH-4, and MH-5) regions (Fig. 1) respectively. Subscripts 1984, . . . , 2000 refer to the year lake trout were collected.

Model	θ	α and β	Random effects
A	Constant across years and regions	Constant across years and regions	none
B	Region effects (θ_N,θ_C, θ_S), constant across years	Constant across years and regions	none
C	Year effects ($\theta_{1984}, \ldots, \theta_{2000}$)	Constant across years and regions	none
D	Additive region and year effects (θ_N, θ_C, θ_S, $\theta_{1984}, \ldots, \theta_{2000}$)	Constant across years and regions	none
E	Asymptote for each year and region ($\theta_{N,1984}$,$\theta_{C,1984}, \ldots, \theta_{S,2000}$)	Constant across years and regions	none
F	Asymptote for each year and region	α: Region effects, constant across years; β: constant across regions and years	none
G	Asymptote for each year and region	α: Constant across regions and years; β: Region effects, constant across years	none
H	Asymptote for each year and region	Region effects for both α and β, both constant across years	none
I	Asymptote for each year and region	α: One random walk across years for all regions. β: region effects, constant across years.	none
J	Asymptote for each year and region	α: Constant across years and regions. β: region effects and one random walk across years for all regions.	none
K	Asymptote for each year and region	α: Independent random walks across years for each region. β: region effects and constant across years.	none
L	Asymptote for each year and region	α: Constant across years and regions. β: independent random walks across years for each region	none
M	Asymptote for each year and region	α: Constant across regions and years; β: Region effects, constant across years	site by year
N	Asymptote for each year and region	α: Constant across regions and years; β: Region effects, constant across years	net set

and the best model that allowed regional differences in the shape parameters. In the latter case, the separate random walks were added to the best model with a constant shape, as this way of using the random walk for the shape parameters already incorporates regional effects, temporal effects, and interactions. When considering α and β separately, the random walk year effects did not improve model fit, so variants where both α and β varied temporally at the same time were not considered.

All the previous models treat each observed lake trout within a given year and region as an independent observation. In reality, multiple lake trout are collected from within a given year and region at each fixed site, and within a fixed site multiple lake trout are taken from individual sets of gill nets. It is conceivable that lake trout taken together either at the level of a site or at the level of an individual net set would have different average wounding rates than one might expect on average for the region and year. Ignoring such "random-cluster effects" if they exist would lead to underestimating uncertainty associated with the parameter estimates. This possibility was explored by adding to the best model without random effects (model G, Table 1) random effects in θ, first for site by year combinations and then for individual net sets (models M and N, respectively). Mixed models, that combine fixed and random effects, are increasingly being used in fisheries to address such "cluster sampling" and correlations among observations (Conover *et al.* 1997, Sitar *et al.* 1999, Bergstedt *et al.* 2003).

For the overall best model (model G, table 1), overdispersion was tested for using the T-test described by Dean and Lawless (1989). Substantial overdispersion could compromise the use of AIC for model choice or otherwise influence conclusions. The assumption in the model that the observed wounding frequency follows a Poisson distribution means that the variance of the observed wounds is equal to the mean wounding rate. If wounding rates are overdispersed, then the variance would be greater than assumed, and there would be more fish with multiple wounds than is expected for the Poisson distribution.

Assessment of Uncertainty

A Bayesian approach was adopted to assess uncertainty through posterior distributions for the parameters. Given the nonlinear model, correlation among parameters, and small sample sizes for some year and region combinations, more familiar asymptotic standard errors would provide a less reliable assessment of uncertainty. The joint posterior distribution of the parameters was estimated using Markov Chain Monte Carlo (MCMC) methods (Brooks 1998). It is possible to calculate a posterior distribution for any quantity of interest that can be calculated as a function of the parameters. This was done for the mean number of wounds on a 500-mm fish as a basis for comparison among areas. This length was chosen as it represents fish that are observed commonly in all three regions of Lake Huron.

Assuring that calculated posterior distributions are valid is not an automatic nor simple task (Cowles and Carlin 1996), and care was taken in this area. To ensure that the posterior distribution was a proper one, all parameters were bounded during estimation, which effectively gave each parameter a uniform prior distribution between the bounds (set to be well above or below what was viewed as possible values for the parameters). Thus, the priors were only weakly informative, as *a priori* all values within the bounds were considered equally likely. To ensure the MCMC chains converged to the posterior distributions, a number of methods were used, including visual inspection of trace plots. The effective sample size, or the number of independent samples contained within the correlated MCMC chain, for each parameter of interest was also calculated. This was done using the methods outlined in Thiebaux and Zwiers (1984), estimating the autocorrelation function for lags up to 150 steps and insuring the autocorrelation function converged to zero. The length of the MCMC chain was chosen with a goal of achieving an effective sample size of at least 1,000. Diagnostics of the MCMC chains showed that convergence was satisfactory, and that effective sample sizes were greater than 1,000 for all parameters.

RESULTS

Model Selection and Evaluation

Model G was selected as the best model (Tables 1 and 2). This model allowed the average wounding rate on large fish (θ) to vary freely among years and regions, and allowed for regional differences in β (the lake trout length at which 50% of the asymptotic rate was reached). Among models with fixed shape parameters, model E, which allowed θ to vary freely over years and regions (Table 1), had a substantially lower AIC than the alternatives and was selected as best (Table 2). When possible regional differences in the shape parameter were considered, model G was selected, which added a regional effect to β. Models that include regional effects on α (which would alter the rate at which wounding rate approached the asymptote), either alone or in combination with regional effects for β, had higher AIC values (Table 2). The attempts to include annual effects on the shape parameters (α and β) led to very small year effects and no improvement in goodness-of-fit. None of the mixed effects were significant when added to model G, thus there was no evidence that lake trout sampled together tended to have a common wounding rate that differed from the overall value for the region and year.

In general, comparison of model predictions with observed wounding data indicated the model fit

TABLE 2. Akakie's Information Criteria (AIC) values for wounding models A through H (Table 1). The lower the AIC value, the better the model fit the data.

Model	Number of Parameters	Akakie's Information Criteria
A	3	16674
B	5	16538
C	19	16560
D	23	16383
E	53	16326
F	55	16291
G	55	16283
H	57	16286

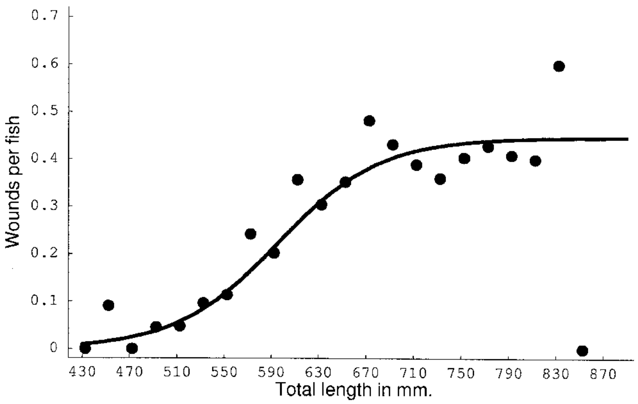


FIG. 3. An example of wounds per lake trout as a function of lake trout length (southern Lake Huron in 1985). Solid circles represent observed data grouped by 20-mm length bins for visual clarity, and the solid line is the model estimated mean wounds per lake trout.

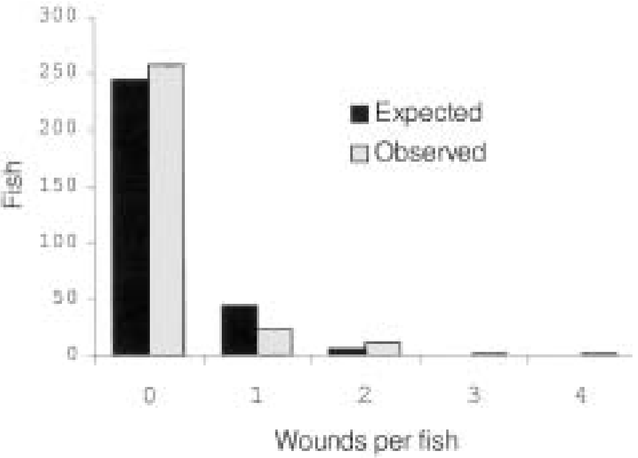


FIG. 4. Expected and observed number of wounds per fish on lake trout for northern Lake Huron in 1995.

well (Fig. 3). In graphically comparing observed and predicted values, the data were summarized into 20-mm length bins, but even so, large deviations between observed and predicted wounding rates for large fish were typical because few lake trout were observed for the larger length bins.

The t-test for overdispersion using the entire data set suggests that there was overdispersion (t = 9.02, p-value < 0.01). These results imply that the variance of the distribution of wounds is greater than the Poisson model predicts. The year and area with the greatest level of overdispersion was northern Lake Huron in 1995. Closer examination of the data for this extreme case showed that the model failed to predict accurately the number of fish with three wounds per fish or greater (Fig. 4), indicating a larger variance than assumed by the Poisson distribution. For model G, the deviance was determined to be 1.08, indicating that no adjustments to the AIC values in Table 2 are needed. (McCullagh and Nelder 1989). This, together with the fact that very few fish are causing the overdispersion, suggests that overdispersion had little influence on parameter estimates and model choice, although this could be explored further through simulation.

Patterns in Estimated Wounding Parameters and Rates

The estimated asymptotic wounding rates (θ) fluctuated significantly from year to year (Table 3). While there is a fairly large amount of temporal variation in the estimates for each region, central Lake Huron had the highest estimated asymptotic wounding rates. Yearly fluctuations in θ did not track across regions (Table 3). For example, asymptotic wounding rates were low during 1990 and 1991 in northern Lake Huron, whereas they were high at the same time in central Lake Huron. The lake trout length at which 50% of the asymptotic rate was reached (β) was smallest in the north and largest in southern Lake Huron (Table 4).

A consequence of the fact that β varies spatially is that asymptotic wounding rates cannot be interpreted in a simple way. This is evident when considering the fact that estimates of θ for northern Lake Huron tended to be less than the estimates for cental Lake Huron (Table 3), a result that at first appears to contradict observations that sea lamprey attacks are greatest in the northern portions of Lake Huron (Rakoczy and Rogers 1991a, 1991b; Rakoczy 1992; Rakoczy and Svboda 1993, 1994; Sitar 1996). However, as the inflection point β occurred at progressively lower lengths when moving from the southern to northern region, the resulting rates of sea lamprey wounding for lake trout of the same length were greater in the north than in either central or southern Lake Huron. For example, the expected wounding rate was higher in northern Lake Huron than in central Lake Huron in 1992 for the size range that includes most of the fish sampled, even though θ was estimated to be lower in the north (Fig. 5).

To compare wounding rates across regions and

TABLE 3. Maximum likelihood estimates and 95% probability intervals of asymptotic wounding rate, θ, for northern (MH-1), central (MH-2), and southern (MH-3,MH-4, and MH-5) Lake Huron from 1984 to 2000. Results based on model G (Table 1).

Region	Year	θ	MCMC 95% Prob. Interval
North	1984	0.235	[0.226,0.385]
	1985	0.306	[0.265,0.592]
	1986	0.338	[0.313,0.598]
	1987	0.524	[0.489,0.921]
	1988	0.269	[0.214,0.587]
	1989	0.167	[0.102,0.512]
	1990	0.064	[0.033,0.259]
	1991	0.089	[0.055,0.266]
	1992	0.361	[0.297,0.755]
	1993	0.327	[0.286,0.598]
	1994	0.333	[0.282,0.582]
	1995	0.547	[0.516,0.909]
	1996	0.390	[0.363,0.682]
	1997	0.580	[0.538,0.915]
	1998	0.523	[0.493,0.859]
	1999	0.181	[0.155,0.313]
	2000	0.278	[0.236,0.485]
Central	1984	0.816	[0.720,1.200]
	1985	0.955	[0.878,1.367]
	1986	0.527	[0.460,0.808]
	1987	0.277	[0.226,0.453]
	1988	0.217	[0.117,0.547]
	1989	0.470	[0.406,0.724]
	1990	0.666	[0.487,1.221]
	1991	0.259	[0.210,0.408]
	1992	0.424	[0.369,0.620]
	1993	0.450	[0.361,0.779]
	1994	0.443	[0.386,0.665]
	1995	0.866	[0.767,1.291]
	1996	0.337	[0.295,0.514]
	1997	0.323	[0.259,0.540]
	1998	0.561	[0.529,0.812]
	1999	0.386	[0.356,0.572]
	2000	0.497	[0.467,0.708]
South	1984	0.272	[0.249,0.330]
	1985	0.448	[0.425,0.528]
	1986	0.238	[0.213,0.304]
	1987	0.400	[0.367,0.492]
	1988	0.255	[0.227,0.321]
	1989	0.273	[0.242,0.348]
	1990	0.456	[0.421,0.551]
	1991	0.323	[0.270,0.421]
	1992	0.301	[0.264,0.374]
	1993	0.521	[0.458,0.652]
	1994	0.432	[0.385,0.539]
	1995	0.355	[0.302,0.461]
	1996	0.524	[0.465,0.668]
	1997	0.486	[0.430,0.627]
	1998	0.450	[0.393,0.596]
	1999	0.361	[0.328,0.466]
	2000	0.313	[0.285,0.400]

TABLE 4. Maximum likelihood estimates of the shape parameters. Results based on model G (Table 1). Subscripts N, C, S refer to northern, central and southern regions (Fig. 1) respectively.

Parameter	MLE Estimate
α	0.0231
β_N	528.825
β_C	576.088
β_S	595.897

years, given the differences in inflection points of the logistic function for different regions, the estimated sea lamprey wounding rate for 500-mm lake trout was focused on. Wounds per 500-mm lake trout are highest in the north and lowest in the south (Fig. 6). Following the patterns seen in θ, temporal fluctuations in the wounds per fish did not track across regions. Due to the variability in year-to-year wounding rates, there did not appear to be a trend of increasing or decreasing wounding rates on 500-mm lake trout over the past fifteen years in any of the regions.

DISCUSSION

The model based on the logistic function was successfully fit to wounding data from Lake Huron, thereby estimating how sea lamprey wounding rates on lake trout varied among regions, years, and as a function of lake trout size. In this application, sepa-

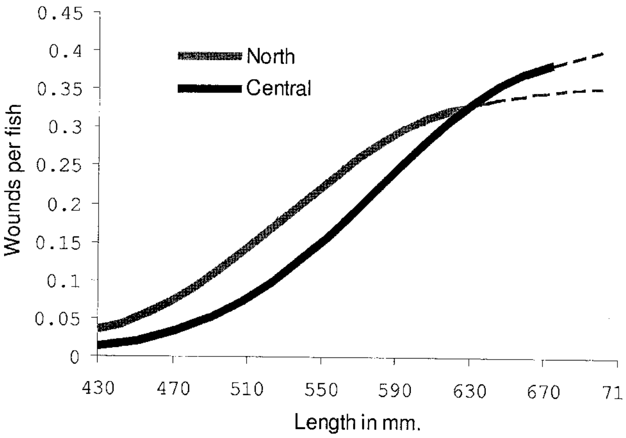


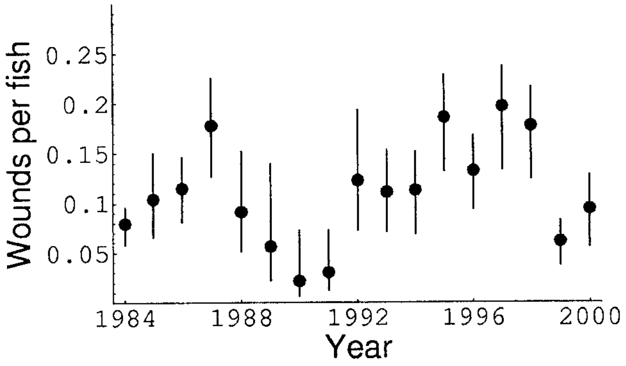
FIG. 5. Predicted wounds on lake trout in northern and central Lake Huron in 1992. The solid line extends to a length below which 95% of the observed lake trout lengths occurred, and the dashed line continues the plot for larger lake trout sizes.

rate wounding rates for large lake trout (θ) for each region and year combination needed to be estimated, but the shape of the logistic function only varied through region-specific inflection points (β).

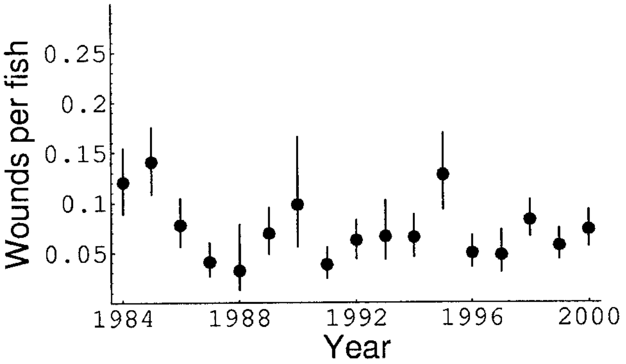
The initial expectation was that the wounding rate on large lake trout (θ) would vary among regions and years, but it was expected that the shape of the logistic function would be fairly constant. Large temporal and regional variations in parasitic-phase sea lamprey density (Young *et al.* 2003) are one reason large temporal variations in wounding rates were expected. Although wounding rates varied spatially and temporally, the temporal correspondence between wounding rates and independent estimates of sea lamprey abundance (Young *et al.* 2003) is not a tight one. For example, the large number of sea lamprey estimated to be present in Lake Huron in 1993 was not followed by an increase in wounding rates on lake trout sampled in the spring of 1994.

Variations in the density of host populations can also cause variations in wounds per fish, as there is an upper limit to the total number of attacks a sea lamprey can make in a year (Koonce *et al.* 1993, Bence *et al.* 2003). Wounding rates can also vary if the procedures followed when recording wounds vary over time or geographically (Ebener *et al.* 2003). In addition, any other factor that influences either the feeding activity of sea lamprey or the healing of the resulting marks could cause variations in observed wounding rates.

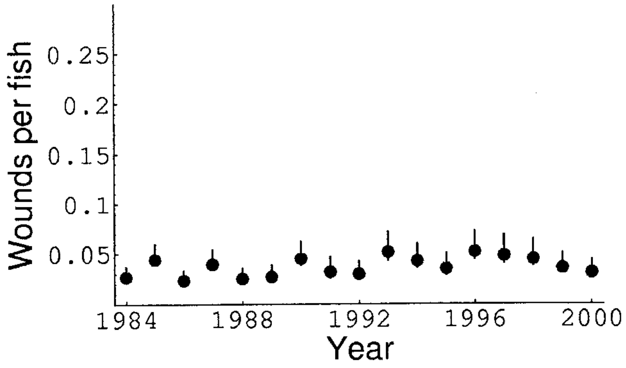
The shift of the logistic function to the right along the lake trout length axis when going from north to south in Lake Huron (as indicated by increasing value of β) can not be as easily explained. The shape was originally expected to remain constant because foraging models based on a type-2 functional response predict that the relative magnitude of attack rates on different categories of hosts should not change as host or parasitic-phase sea lamprey densities change (Bence *et al.* 2003). For differences in procedures for recording marks to produce such an artifactual pattern, the method by which wounds are recorded would need to change differently as a function of host size in the different regions. This seems very unlikely, especially since all the data for the central and southern region were collected by the same personnel. One possible explanation stems from the fact that in the northern part of the main basin of Lake Huron large lake trout have been at low abundance. Given the low abundance of large lake trout, sea lamprey might direct more attacks toward smaller fish, causing the



Northern Lake Huron



Central Lake Huron



Southern Lake Huron

FIG. 6. Maximum likelihood estimates of wounds per fish for a 500-mm lake trout in northern (MH-1), central (MH-2), and southern (MH-3,MH-4, and MH-5) Lake Huron from 1984 to 2000. Solid line indicates 95% probability interval determined by MCMC methods.

inflection point to shift towards a smaller host size in the north. Such a broadening of diets to include lower ranked prey when high quality prey are scarce is a qualitative prediction of optimal diet theory (Pulliam 1974) and has been observed in many other systems (Dill 1983, Sih and Christensen 2001). The failure to see temporal variations in the shape of the logistic function is not inconsistent with this explanation, because temporal changes in lake trout densities and size compositions during the 1980s and 1990s have been less pronounced than the regional differences (Eshenroder *et al.* 1995). This hypothesis to explain regional differences in shape of the logistic function needs to be explored further along with any other potential explanations for the pattern.

The approach suggested herein avoids biases caused by grouping hosts into arbitrary length bins and better accounts for the effects of host size and other sources of variation. Previous efforts to compare annual wounding rates in Lake Huron have been challenged by low sample sizes for many region and size-bin combinations and differences in size compositions within size bins between regions (Sitar *et al.* 1997). These problems were encountered even though Sitar *et al.* (1997) attempted to share information among regions and years by estimating wounding rates of lake trout in Lake Huron using a general linear model that included effects for length bin, region, year, and associated interactions. They attributed some of the patterns in their results to exactly the kind of bias this approach avoids. For example, they estimated lower mean wounds per fish in MH-1 (north) than in MH-2 (central) for the 534 to 635 mm bin, and attributed this to the fact that most of the lake trout in this bin in MH-1 had lengths below the midpoint of the bin. It is instructive to compare the 95% probability interval for wounding rate on 500-mm fish in central Lake Huron in 1994 (0.046,0.089) with a 95% confidence interval (0, 0.215) for the wounding rate for the 432 to 533 mm size bin of lake trout reported by Sitar (1996) based on these same data. The probability interval is a Bayesian version of a confidence interval and should approximate a confidence interval given the diffuse nature of the priors. While the development of a comprehensive model that allows information to be shared among years and regions is certainly partly responsible for the tighter interval, it is clear that the ability of the model to account for effects of host size within the broader size categories used in the conventional approach provides a huge advantage.

The approach of Jacobson (1989) is related to the approach described herein in that he modeled either the proportion wounded or wounding rate for a monthly collection of fish as continuous function of time of year, treating time of year in much the same way as fish size was dealt with here. Therefore, in his model he accounted for seasonal changes using a restricted size range of fish, while for the approach applied herein effects of size were accounted for using data collected from a restricted set of dates. In a situation where wounding data are available from a number of times during the year, it might be possible to improve on both approaches by modeling the joint effects of host size and season. Eshenroder and Koonce (1984) also discussed the possibility of summarizing wounding in the form of parameters of linear regressions of wounding rates versus host size. This analysis can be viewed as the further exploration and refinement of the approach they called for.

The lack of significant random effects in this application indicates that sea lamprey wounding rates on lake trout were homogenous within each region for a given year. Although the actual process of sea lamprey attacks on lake trout almost certainly varies spatially within regions, because both the sea lamprey and lake trout move extensively (Bergstedt and Seeleye 1995, Ebener 1998) there appears to be sufficient mixing to eliminate strong correlations that could potentially be induced by the sampling scheme. Thus, while the amount of wounding varies from year to year and region to region, this analysis indicates that the estimated rates can be applied to different locations or samples within a region.

In conclusion, this approach can be strongly recommended to be broadly applied as a method for summarizing wounding data. As experience with this approach is gained, it is suggested that this technique should replace the reporting of mean wounding rates for broad size bins, which is currently the accepted standard in the Great Lakes (Eshenroder and Koonce 1984). Some movement in this direction has already occurred, as lake trout wounding rates used in lake trout assessment models for Michigan's waters of Lakes Huron and Superior are already estimated using this approach (Bence and Ebener 2002), and wounding rates estimated through this approach have been used to design how to assess the success of sea lamprey control on the St. Marys River (Adams *et al.* 2003). As this approach is extended into other areas, and applied to different host species and/or ranges of years, the assumed logistic relationship and how the parameters of logistic function vary regionally and temporally will need to continue to be checked. Examination of many data sets with this approach may reveal new insights regarding sea lamprey parasite-host interactions.

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CHAPTER 2

PARAMETER ESTIMATION OF A FUNCTIONAL RESPONSE MODEL TO IMPROVE ESTIMATES OF SEA LAMPREY-INDUCED MORTALITY ON LAKE TROUT IN LAKE HURON

Introduction

Prior to the 1950s, the lake trout (*Salvelinus namaycush*) fishery in the Great Lakes represented one of the largest freshwater fisheries in the world. Annual commercial yield varied over time and among the Great Lakes, and on Lake Huron ranged from 1.3 to 3.0 million kg from 1912 through 1940 (Baldwin et al. 2002). This peak period was quickly followed by a drastic decrease in yield to the point that lake trout were considered commercially extinct in Lake Huron in the 1950s (Eshenroder et al. 1995).

Before the collapse of lake trout, they were an important top level predator in the Great Lakes' ecosystem. The rapid decline in lake trout abundance created large perturbations throughout the ecosystem and heightened the detrimental influence of other nonindigenous species. For example, the lack of abundant top level piscivores may have contributed to the spread and population explosion of alewife (*Alosa pseudoharengus*) in the Great Lakes (Smith 1970). Alewife in turn have had negative effects on other native species (Smith 1970).

The cause of this decline in lake trout sparked a debate in the 1950s that has continued well into the 1990s. Possible explanations for the drastic decline in lake trout include intense overfishing (Eshenroder et al. 1995), predation by the nonindigenous parasitic sea lamprey (*Petromyzon marinus*) (Coble et al. 1990), or the combination of overfishing and the sea lamprey predation (Hansen 1999). Soon after the collapse of the lake trout fishery, efforts began to reestablish self-sustaining lake trout populations. Lake trout restoration remains a major goal of fishery management on the Great Lakes. Ongoing restoration efforts include extensive stocking of lake trout and control of fishing effort and sea lamprey populations.

While the role of sea lamprey in the collapse of lake trout populations has been debated, there remains little doubt that sea lamprey are now a major impediment to lake trout restoration efforts (Bence et al. 2003; Morse et al. 2003). After the modifications to the Welland Canal in 1919, sea lamprey began colonizing the Upper Great Lakes and were established by 1947. Sea lamprey predation in the Great Lakes is the result of “parasitic” juvenile stage sea lamprey that have migrated from rearing habitats in streams into the lakes where they generally spend up to 18 months feeding before maturing and returning to Great Lakes tributaries to spawn. These juveniles preferentially attack large fish, attach to and gnaw through the prey’s skin and feed on body fluids. These attacks frequently result in the death of the fish that is attacked. Sea lamprey negatively impact species other than lake trout, including burbot (*Lota lota*) and lake whitefish (*Coregonus clupeaformis*).

In 1958, the Great Lakes Fishery Commission (GLFC) began efforts to control sea lamprey populations in the Great Lakes. Control methods have included both chemical and biological approaches (see Morse et al. 2003 for details), and the results of sea lamprey control have been somewhat successful in terms of lake trout restoration. Self-sustaining populations of lake trout have been restored in Lake Superior, and reduced sea lamprey abundance has increased the amount of lake trout spawning stock produced due to stocking in other areas of the Great Lakes. While stocked lake trout have contributed to a resurgence in recreational fishing throughout Lake Huron, self sustaining populations have not been observed in Lake Huron outside of an isolated embayment of Georgian Bay (Reid et al. 2001). However, there has been evidence of natural reproduction of lake trout in the main basin at the Six Fathom Bank Refuge since 1992 (Ebener 1998).

Currently, the GLFC takes the lead in planning sea lamprey management, with facilities and support provided by the U.S. Fish and Wildlife Service and the Department of Fisheries and Oceans, Canada. The approach, referred to as Integrated Management of Sea Lamprey (IMSL) (Greig et al. 1992), is based on the philosophy of integrated pest management (Sawyer 1980). The GLFC has worked with state and provincial fishery management agencies to develop lake trout restoration plans and lake trout mortality limits, with the aim of reestablishing self-sustaining lake trout populations. In the upper Great Lakes, current estimates of sea lamprey-induced mortality are based primarily upon observed wounds per lake trout of fish sampled in the spring of each year (Eshenroder et al. 1995, Sitar et al. 1999, Rutter and Bence 2003). In order to predict future levels of sea lamprey-induced mortality, another key component of IMSL, a sea lamprey/lake trout functional response model is needed to predict the number of attacks on lake trout.

A functional response model predicts the number of attacks per predator as a function of prey densities (Holling 1966). Recent models used to predict the number of sea lamprey attacks on lake trout on the upper Great Lakes have assumed implicitly or explicitly a Type I functional response (Sitar 1996; Sitar et al. 1999; Lupi et al. 2003; Stewart et al. 2003). A Type I functional response assumes that the number of attacks per sea lamprey increases in direct proportion to lake trout density. Under this type of functional response, the number of sea lamprey attacks per lake trout, and therefore the per capita sea lamprey-induced mortality rate, remains constant regardless of lake trout density. A more realistic model of attack rates is a Type II functional response (Holling 1966) in which attacks are assumed to take a known amount of time, therefore limiting the number of attacks that can occur during a feeding season. As the density of lake trout increases, sea lamprey become saturated with possible hosts, and the number of attacks per lamprey reaches an asymptote, the maximum number of attacks per feeding season. The per capita sea lamprey-induced mortality rate will decrease as lake trout density increases due to the limited number of attacks per predator being distributed among a greater number of hosts.

Sea lamprey-induced mortality rates will decrease as sea lamprey densities are reduced, regardless of which functional response model is used to predict attack rates. To include the effects of increased lake trout densities and saturation on sea lamprey-induced mortality rate projections, a Type II functional is needed. This type of functional response is being used for this purpose on Lake Ontario, and although such a model had previously been used on Lake Superior, no such models are currently in use or up to date on the upper Great Lakes (Bence et al. 2003).

In this paper, we develop and parameterize an age-structured population model that utilizes available fishery, survey, and sea lamprey-related data to estimate lake trout population and mortality levels for the main basin of Lake Huron. This approach is an extension of previous statistical catch-at-age approaches to lake trout in southern Lake Huron (Sitar et al. 1999) and includes parameterization of a sea lamprey/lake trout Type II functional response model (Holling 1966), similar to one developed as part of the IMSL process (Greig et al. 1992; Koonce et al. 1993; Bence et al. 2003). By accurately describing the predator-prey relationship of sea lamprey and lake trout, we can better model lake trout population dynamics and evaluate the current and future success of lake trout restoration plans. Our work is unique in the integration of the parameterization of the lake trout assessment model and the sea lamprey functional response in a unified procedure.

Methods

Our statistical catch-at-age model (Megrey 1989) includes a lake trout population submodel and an observation submodel. The population submodel describes lake trout dynamics over the observation period (1984-1998), whereas the observation submodel predicts observed data given those dynamics. We developed an age-structured population submodel for lake trout and estimated model parameters that maximized the agreement between observed and predicted values for survey indices of abundance, fishery harvest, fishery effort, and sea lamprey wounding. In this section we describe the data and annual inputs used in fitting the model, the population submodel, and the observation submodel.

The main basin of Lake Huron, excluding Saginaw Bay, was broken into three regions based on statistical districts (Figure 1). Separate lake trout populations were assumed for Northern Lake Huron (MH-1 and portions of OH-1), Central Lake Huron (MH-2, portions of OH-1, and OH-2) and Southern Lake Huron (MH-3, MH-4, MH-5, MH-6, OH-3, OH-4, and OH-5). The estimation/assessment model presented here includes a model of lake trout dynamics and fishing similar to that used by Sitar et al. (1999) and described in Bence and Ebener (2002). Our model expands on that work by simultaneously considering the entire main basin of Lake Huron while including parameters used to estimate sea lamprey-induced mortality.

We fit the statistical catch-at-age model using a likelihood-based objective function (Fournier and Archibald 1982; Methot 1990; Methot 2000). Formally, our point estimates maximized the Bayesian posterior density because we made use of prior information on key model parameters (see below). Our catch-at-age model covered 1984 through 1998 and recognized lake trout ages 1-14 and an age-15 and older "plus" group.

The population submodel was developed so as to take advantage of the available data sets while providing insight to key ecological quantities such as sea lamprey-induced mortality rates. Based on the spatial sampling design and reporting of the data used, we modeled the main basin of Lake Huron as consisting of three areas: north, central, and south (see above and Figure 1). Most parameters were estimated separately for each region (exceptions are noted) and, subsequent to a redistribution of stocked fish (see below), there was no migration of lake trout between the areas. The areas were linked by several shared parameters and the division of a common total population of sea lamprey among the areas.

Observed data and annual inputs

As noted above, the model was fit by comparing observed and predicted indices of abundance from surveys, fishery harvest and effort values, and sea lamprey wounding on lake trout and alternative prey. Survey data were collected by the Michigan Department of Natural Resources (MIDNR) in the spring from 1984-1998. The surveys were conducted at fixed stations from April through June using graded-mesh gill nets. Each sampling unit consisted of nine panels that were 30.5 m long, ranging in stretched-mesh sizes from 51 mm to 152 mm in 13 mm increments (Merna et al. 1981; Johnson and VanAmberg 1995). All fish sampled in the survey were aged and measured in length. Since virtually all lake trout in Lake Huron are stocked, there is very little aging error due to the use of fin clips. Estimates of the mean log-scale survey catch-per-unit effort (CPUE) and associated standard error were generated for each year and area using a mixed-effect linear model (see Sitar et. al. 1999 and Bence and Ebener 2002 for details). Age compositions (proportions at age) for each year of the survey data was compiled for each of the three regions in the model, including the number of aged fish used to determine the age composition.

Fishery related data used in the model included (separately for the recreational and commercial fisheries) total harvest, fishery effort, and fishery age-composition. The MIDNR, Chippewa Ottawa Resource Authority (CORA), and the Ontario Ministry of Natural Resources (OMNR) all supplied data on commercial and recreational harvest and effort for the main basin of Lake Huron. Commercial fisheries included tribal large-mesh and small-mesh gill nets on northern Lake Huron, and a gill-net fishery in Ontario. Reported harvest from these sources was combined to obtain the recreational and commercial totals. The tribal fisheries primarily target lake whitefish, salmon, and bloater chubs (*Coregonus hoyi*), but significant numbers of lake trout are caught also. In Canadian waters, there is a substantial large-mesh gill-net harvest of lake trout. Harvest information collected from the northern Canadian statistical district, OH-1, was divided, based on location of harvest, among northern and central Lake Huron for modeling purposes. Effort data for the commercial fishery was determined in feet of large-mesh gill-net set per year (the primary source of commercial fishing mortality). Recreational fisheries in the main basin consisted of both charter and non-charter fishermen. The total number of fish caught, as well as angling hours of effort, were determined from mandatory charter boat reports and creel surveys. For details on which years of data were collected for the commercial and recreational fisheries in each region, see Table 1.

The model was also fit to data on sea lamprey wounding of lake trout and alternative prey: lake whitefish and Chinook salmon (*Oncorhynchus tshawytscha*). Wounding data for lake trout was based on data collected as part of the spring surveys by the MIDNR and tribal harvest data (see above). Rutter and Bence (2003) summarized the number of A1-A3 sea lamprey wounds observed per fish in the spring using a logistic function of lake trout length, and estimated asymptotic wounding rates (observed wounds per fish on the largest lake trout) as well as the logistic curve's shape parameters. These logistic model parameter estimates and the associated variance-covariance matrix were used as data here for fitting the catch-at-age model. Observed sea lamprey wounds-per-fish for all lengths of Chinook salmon and lake whitefish in northern Lake Huron were obtained from Bence et al. (2003) and from unpublished data provided by Mark Ebener (CORA), and the average number of observed wounds per Chinook salmon and lake whitefish were determined (averaged over all years).

In addition to data directly compared with model predictions, our modeling required other annual inputs. These were the number of lake trout stocked each year, the abundance of sea lamprey each year, and the abundance of alternative prey. These annual inputs were assumed known without error. The number of lake trout stocked provided an indication of the abundance of each year class of lake trout, whereas the abundance of sea lamprey and alternative prey for sea lampreys was needed for the sea lamprey functional response, a key feature of our model.

Our use of stocking as an indicator of recruitment is justified because almost all of the lake trout harvested in the main basin are stocked fish. From data for both the number of fingerlings and yearlings stocked in each region in each year, the total number of “yearling equivalents” stocked was obtained by adding to the number of yearlings stocked to 0.4 times the number of fingerlings stocked for the same year class (i.e., in the previous year). A “migration matrix” was used to reassign the yearling equivalents stocked for each region and year to a recruitment location based on tagging information on where stocked lake trout were recovered (see Bence and Ebener 2002 for more details). We obtained the needed stocking information from the United States Fish and Wildlife Service (USFWS), coordinators of data collection for lake trout stocking in both the United States and Canada.

We assumed that the abundance of parasitic phase sea lamprey was equal to values estimated by Mullet et al. (2003) for the main basin of Lake Huron from trap catches of adult sea lamprey during their spawning migration. Population level estimates of Chinook salmon (total for ages 3 and older) in the main basin of Lake Huron for each year were taken from Dobiesz and Bence (in review); population abundances of lake whitefish stocks (total for ages 4 and older) for each year were based on statistical catch-at-age assessments conducted for 1836 treaty waters (Ebener et al. in press).

Population model

Detailed equations for our population model are provided in Table 2, and individual equations therein are referenced as equation T2.Y, and symbols are defined in Table 4. Numbers at age (*a*) and year (*y*) for the population model are given by:

$$N_{a+1,y+1,r} = N_{a,y,r} S_{a,y,r} \qquad (1)$$

where $S_{a,y,r}$ is the survival for age *a* fish over year *y* in region *r*. This survival is modeled as a function of natural mortality, fishing mortality and sea lamprey induced mortality. For each region, the lake trout population was estimated for ages 1 to 14, and a plus group including ages 15 and above, from 1984 to 1998. Age 1 lake trout for each year and region were determined by taking the results of the stocking analysis (see above) and multiplying it by a year and region specific post-stocking survivability ($\gamma_{y,r}$). The year was modeled as consisting of two periods during which fishing and natural (not including sea lamprey mortality) occurred, separated by a fall pulse of sea lamprey mortality which was assumed to occur after the first nine months of fishing and natural mortality. Equations T2.1, T2.2, and T2.3 provide the modeled number of lake trout of each age surviving immediately before the pulse of sea lamprey mortality, immediately after the pulse of sea lamprey mortality, and to the start of the next year.

Natural mortality was assumed constant over time, with one rate for age-1 fish and another that applied to all other ages of lake trout. Prior information was provided on these natural mortality rates and they were estimated during model fitting (see *Fitting the catch-at-age model* below).

We included distinct commercial and recreational fisheries in each region of Lake Huron. The instantaneous fishing mortality rates for each region and fishery were modeled as the product of an age-specific selectivity and a year specific fishery intensity (eqs. T2.4 and T2.5). In their basic forms (which we modified below to allow for time-varying selectivity), commercial fishing was modeled as a four-parameter double logistic function of age (eq. T2.6, Figure 2) and recreational selectivity was modeled as a two parameter logistic function of age (eq. T2.7). The double logistic functional form of the selectivity curve was chosen because gill net selectivity is known to generally decrease for the oldest and largest fish. We used a logistic function for the recreational fishery because preliminary attempts using the double logistic function produced selectivity patterns that reached an asymptote with age over the age range we were modeling. The fishing intensities for each of the two fisheries for each region of the lake and year modeled were parameters estimated as part of the procedure of fitting the statistical catch-at-age model to the data.

A variety of factors, such as changes in length at age, can act to cause selectivity to change over time. We therefore modified the double logistic and logistic functions to allow such variation without unduly increasing the number of parameters that were estimated. Our approach here was to model the inflection point parameters of the selectivity functions for each fishery and region which were modeled as random walks to allow selectivity to vary over time (eq. T2.8). This approach allows selectivity to change over time but penalizes solutions where selectivity changes sharply from year to year. For the commercial selectivity function, there were two inflection points for each region (one for the increasing portion of the function and one for the decreasing portion) and thus two random walks for each region, whereas for the recreational fishery there was just one random walk per region. For each random walk a vector of n-1 parameters were estimated during the fitting of the statistical catch-at-age model where $n=15$ is the number of years used in the model.

Sea lamprey-induced mortality on a given age of fish was modeled as proportional to the expected number of attacks by sea lamprey per lake trout over the feeding season with the proportionality constant being the complement of the probability of a lake trout surviving a given attack (eq. T2.9, Eshenroder and Koonce 1984, Bence et al. 2003). We assumed the probability of surviving a sea lamprey attack was a logistic function of lake trout weight (one function for the entire lake) based on laboratory work by Swink (2003) (eq. T2.10). For a given age lake trout, weight at age was determined from region-specific weight at age keys generated by applying a von Bertalanffy growth model to data collected during spring lake trout surveys (Bence and Ebener 2002).

The number of sea lamprey attacks ($A_{a,y,r}$) per lake trout for a given age, year, and region was predicted from the density of sea lamprey and the density of each type of sea lamprey prey (each age of lake trout, Chinook salmon and whitefish) in that region using a multi-species type II functional response model (Holling 1959, eq. T2.11). This is a saturating function that reaches an asymptote as prey become dense. The handling time (or times if they vary among prey types) determines the maximum possible attack rates, whereas the effective search rate (or rates if they vary among prey types) determines how fast attack rates increase with prey densities. See Bence et al. (2003) for extensive discussion of application of this functional response to sea lamprey. Current modeled values of lake trout population abundance at age in each region, just prior to the pulse of sea lamprey mortality, were divided by lake trout habitat area for that region to determine the lake trout densities used in these calculations. The abundance of alternative host species, specifically Chinook salmon and lake whitefish, were assumed known based on species specific population models (see *Observed data and annual inputs*) above. Densities of Chinook salmon were determined by dividing the lake wide estimate by the amount of lake wide lake trout habitat, while whitefish densities were determined on a region-by-region basis. Lake trout habitat (in square kilometers) that is shared by sea lamprey and lake trout is defined as depths less than 40 fathoms, and were taken from Ebener (1998) (see Table 5).

The annual sea lamprey population abundances derived by Mullet et al. (2003) were treated as known and provided spawning run estimates associated with northern and central streams (sea lamprey production in the south is negligible). We assumed that some of the sea lamprey that contributed to northern or central spawning runs fed further south. During fitting of the statistical catch-at-age model we estimated two parameters that allocated the observed spawning runs of sea lamprey to obtain numbers feeding in each of our modeled regions. First we estimated a proportion of sea lamprey observed in northern spawning runs that fed in either the central or southern region (ML_{NtoC}), which was assumed to apply to all years. The total number of sea lamprey feeding in the central and southern main basin was taken as the sum of these sea lamprey allocated from the northern streams and the spawning run for the central streams. The second parameter (also assumed to apply to all years) allocated a proportion of these sea lamprey to southern Lake Huron (ML_S). The sea lamprey density was determined after this allocation by taking the estimated sea lamprey population for each region and dividing it by the area of lake trout habitat in each region (Table 5).

We attempted to estimate several parameters of the functional response during the model fitting process, whereas other parameters were assumed known. The length of the feeding season (S), was assumed to be 150 days, or 0.41 years (Koonce and Loci-Hernandez 1989). We attempted to estimate handling time by taking advantage of prior information (see *Fitting the catch-at-age model* below). In order to obtain handling times for alternative host species, the lake trout handling time was multiplied by an adjustment factor for lake whitefish (H_w **)** that was estimated during model fitting, while Chinook salmon were assumed to have the same handling time as lake trout (H). We assumed that similar sized lake trout and Chinook salmon would have nearly identical handling times, while smaller lake whitefish would have shorter handling times.

Parameters determining effective search rate were also estimated during model fitting. We assumed that the effective search rate would be a logistic function of host length, similar to patterns in observed wounding rates (Rutter and Bence 2003, eq. T2.12). Based on results reported by Rutter and Bence (2003), we allowed the inflection point of this function to vary among regions but assumed other parameters applied to the entire lake. A logistic form of the effective search rate was chosen to best match results from summarizing observed wounding rates and to fit predicted wounding rates to observed wounding rates (see *Fitting the catch-at-age model* below).

Submodels for predicting observed quantities

Baranov's catch equation was used to predict harvest-at-age for the commercial and recreational fisheries (Ricker 1975). Due to the fact sea lamprey-induced mortality is applied as a pulse after nine months, the catch equations need to be applied separately to the two periods to determine annual catch of each fishery ($C^C_{a,y,r}$ and $C^R_{a,y,r}$, eqs. T2.13 and T2.14). Total harvest and proportions at age for each fishery, region and year were calculated based on the predicted catch-at-age.

For each source of harvest information, commercial and recreational, predicted fishery effort in a given year and region was calculated. As described in *Population model* above, for each fishery in each region and year, fishing intensity was estimated during model fitting. Predicted fishery effort was determined by dividing the appropriate fishing intensity by catchability, q^C_r for commercial and q^R_r recreational, which were also estimated during model fitting for each fishery in each region. This approach effectively assumes that fishing mortality will be proportional (up to a multiplicative error, see *Fitting the catch-at-age model*) to fishing effort.

In order to match CPUE (K) data collected during spring surveys, the predicted CPUE was calculated for each age, year and region assuming CPUE would be proportional to actual abundance (equation T2.15). Our approach here allowed survey catchability for "fully selected fish" to vary among regions. In addition, we modeled relative catchability of different ages by a double logistic function (as for the commercial fishery selectivity above but with parameters that remained constant over years), with parameters specific to each region. As with harvest, spring survey proportions at age was calculated in a similar way for comparison with the observed values.

Parameter estimates describing how wounding rates varied as a function of lake trout size, and how this relationship varied by region and year (from Rutter and Bence 2003) were treated as input data. In their analysis, Rutter and Bence (2003) modeled wounding as a logistic function of host length. For the period we are modeling, they estimated 45 year and region specific asymptotic wounding rates ($\theta_{y,r}$), three area-specific inflection points (β_r) and one overall logistic slope parameter (α), and we generated predictions corresponding to these "observations". We used predicted wounding rates on arbitrarily large (1200 mm) lake trout (eq. T2.16), as our predictions for the asymptotic rates. Calculations of the predicted shape parameters was more involved.

Although our predicted wounding rates do not exactly follow a logistic function of length, because the predictions result from the product of two logistic functions (one for effective search rate and the other for survival), the resulting function is similar in form to a logistic function. However, the resulting "logistic - like" function does not have an inflection point that can be found algebraically. Assuming the probability of survival is nearly linear with length in the region of the inflection point, we approximated the inflection point for each region by taking a Taylor series expansion around the inflection point of the effective search rate and solving for the lake trout length for which the second derivative is equal to zero for each region (eq. T2.17). The predicted value of the slope of the "logistic-like" function of predicted observable wounding rates, $\hat{\alpha}$, was determined by averaging the slope of the predicted observable wounding rate function at $\hat{\beta}_r$ in each of the three regions.

For alternative prey, the number of predicted observable wounds on lake whitefish and Chinook salmon is calculated from the same functional response model used for lake trout (eq. T2.11). Since length based wounding information is not available for alternative prey, we assumed that the average length of whitefish is 500 mm and 600 mm for Chinook salmon. In addition, we assumed that the effective search rate for these species would be equal to the product of what the effective search rate would be for lake trout of this length in the region ($\lambda_{500,r}$ or $\lambda_{600,r}$) and a species-specific adjustment factor (τ_s, estimated during model fitting) that is applied to all regions (eq. T2.18). The predicted number of observable wounds on alternative prey is the product of the predicted attack rate and the probability of surviving an attack (eq. T2.10) where mass was assumed to be 1.5 kg for lake whitefish and 4.0 kg for a Chinook salmon.

Fitting the catch-at-age model

Detailed equations for fitting the catch-at-age model are provided in Table 3, and individual equations therein are referenced as equation T3.Y, and symbol definitions are continued in Table 4. We followed the likelihood based Bayesian approach of McAllister and Ianelli (1997) and Sitar et al. (1999). Following this approach, the point estimates of parameters maximize the likelihood given by the Bayesian posterior distribution of the parameters given the observed data. Such estimates were termed joint posterior modal (JPM) estimates (e.g., Tempelman 1998) and are the mode of the posterior distribution of the parameters. The general form of the likelihood, up to a proportional constant, is

$$f(\theta | X) \propto f(X | \theta) p(\theta) \qquad (2)$$

where $f(\theta | X)$ is the posterior likelihood for parameters given the data, $f(x | \theta)$ is the probability density of the data given the parameters, and $p(\theta)$ is the prior distribution of the parameters. In this application, there are a number of independent data sources used to estimate the model: commercial fishery harvest and effort, recreational fishery harvest and effort, survey CPUE, age compositions from harvests and surveys, and sea lamprey-induced marking data. Given their independence, it is possible to write the likelihood of the data given the parameters ($f(X|\theta)$) as the product of the densities for each component. A similar approach can be used when the prior distributions of model parameters for natural mortality are assumed to be independent, allowing for $p(\theta)$ to be a product of the prior distribution of each parameter. By taking the natural log of the likelihood, we obtain the log-likelihood (*L*), up to an ignored constant, for the model as:

$$L = L_1 + L_2 + L_3 + L_4 + L_5 + L_6 + L_7 + L_8 + L_9 + L_{10} + L_{11} + L_{12} + L_{13} \quad (3)$$

where L_1 to L_{13} were the log-likelihood components associated with the commercial fishery harvest, the recreational fishery harvest, the index of commercial fishing effort, the index of recreational fishing effort, the index of survey CPUE, the commercial fishery age composition, the recreational fishery age composition, the survey age composition, observed sea lamprey-induced wounding rates on lake trout, observed sea lamprey-induced wounding rates on alternative prey, post-stocking survivability of yearlings, commercial selectivity random walk, and Bayesian prior distributions, respectively.

The first five likelihood components (ignoring some constants) are based on the log-normal distribution (eq. T3.1) where observed and predicted values for components 1 through 5 are the annual commercial fishery harvests, annual recreational fishery harvests, index of commercial fishing effort, index of recreational fishing effort, and survey CPUE. For each information source, the number of years of data ($T_{i,r}$, Table 1) and assumed variability (log-scale standard deviations, $\sigma_{i,y,r}$, Tables 6 and 7) varies by source and region, and by year for survey CPUE. The inverse of the log-scale standard deviation acts as a weight controlling how much each type of data contributes to the overall likelihood.

Age compositions were determined for the commercial fishery harvest (L_6), recreation fishery harvest (L_7), and survey catches (L_8), and were assumed to follow a multinomial likelihood distribution. Likelihoods assume that observed proportions behave as though they were calculated from multinomial samples with specified effective samples sizes (eq. T3.2). Similar to the inverse of log-scale standard deviations for the log normal distributions, the effective sample size acts as a weighting factor for each component of the log-likelihood. In order to prevent certain years from dominating the likelihood function (Fournier and Archibald 1982), the maximum effective sample ($J_{i,y,r}$) was set to 200. In cases where the sample size was less than 200, the actual sample size was used.

The likelihood component used to compare observed to predicted wounding rate parameters (the $\theta_{y,r}$, the β_r and α) was based on the multivariate normal distribution (eq. T3.3), with the variance-covariance matrix treated as known based on the asymptotic estimate obtained by Rutter and Bence (2003).

An additional component of the log-likelihood (L_{10}) for observed wounding rates includes wounds observed on alternative prey in northern Lake Huron. Based on observed data in northern Lake Huron, the average wounds per alternative prey species was determined for the time period 1984-1998 (0.102 wounds per fish for Chinook, 0.169 for lake whitefish), and compared to the same calculation of predicted wounds per alternative prey over the same time period. Wounds on alternative prey were considered to be normally distributed with a coefficient of variation of 35% (eq. T3.4).

While fitting the statistical catch-at-age model, we estimated post-stocking survivability parameters to allow variation in the survival among year classes of stocked lake trout. We penalized the model for deviations in post-stocking survivability from 100% by treating the deviations as log-normally distributed with a median of 1.0 and an estimated standard deviation for each region of Lake Huron (eq. T3.5). The model was also penalized for large variations in the random walks in the inflection points for commercial and recreational selectivity functions. We treated the deviations for each random walk coming from a normal distribution with mean zero and a standard deviation estimated during the model fitting process (eq. T3.6).

Informative prior distributions for natural mortality of age 1 fish for the entire lake, natural mortality of age 2+ lake trout for each region of Lake Huron, and (for our initial variant of the model) the handling time were included in likelihood component L_{13} to account for available information on these difficult to estimate quantities For these priors, we used independent log-normal distributions (eq. T3.7). Final parameter estimates represent a compromise between these priors and fit to the data since the posterior likelihood includes a "penalty" when parameters deviate from the prior medians. For age 1 natural mortality (M_1), the mean of the prior was chosen such that the median of the log-normal distribution was 0.8, a value based on estimates in Grand Traverse Bay, Lake Michigan by Rybicki (1990). Under a log-normal distribution, choosing σ_{M_1} to be 0.175 ensures that M will fall between 0.53 and 1.20 99% of the time, and creating a large likelihood penalty if the value of M_1 exceeds these bounds. For age 2+ natural mortality in each region, the median of the log-normal prior was 0.162 with a standard deviation of 0.21. These values are based on previous estimates of natural mortality for older lake trout in the Great Lakes (Sakagawa and Pycha 1971; Pycha 1980). Handling time was assumed to have a median of 13.4 days with a standard deviation of 0.21, and in this case the handling time range of 7.8 to 23.0 days encompasses 99% percent of the prior probability. We did not specify informative priors for other parameters, although parameters were bounded during the model fitting process. This implies that all plausible values (e.g. positive abundance estimates, yet not biologically unreasonable) of these other parameters on the scale they were estimated were considered equally likely a priori.

In this chapter we express uncertainty in the form of marginal distributions of the parameters of interest taken from the joint posterior distribution of all parameters calculated using Markov Chain Monte Carlo (MCMC) analysis (Brooks 1998). The MCMC chain was created using AdModel builder. This software starts chains at parameter values that produce the maximum posterior density, and takes multivariate normal steps based on the asymptotic variance-covariance matrix (Otter Research 2000). After an initial burn-in was conducted, every subsequent 2,000th realization was saved until a chain of length 100,000 was created. The MCMC analysis creates a posterior distribution of all the parameters estimated during the model fitting process in the form of a long, multivariate Markov Chain (100,000 saved vectors of parameters for this study). In addition to providing a check on inferences based on asymptotic standard errors, these posterior distributions can also provide the basis for random draws of parameter values for use in stochastic forecasting simulations of lake trout dynamics. While we do not present the MCMC results for all estimated parameters in this chapter, these are central to our approach to stochastic forecasting, and will be discussed further in chapter three.

Results

In a preliminary attempt to fit the estimation model to the data, the model did a good job of matching the observed data, but failed to produce results that would allow estimation of the asymptotic standard errors to begin the MCMC process (the Hessian was not invertible). After examining parameter estimates and residuals, we determined that in some instances, there was not enough information available to estimate certain parameters. Given the lack of information on the number of young (ages 1-3) fish in the lake, the model was unable to estimate both age 1 natural mortality (M_1), and post-stocking survivability. By assuming age 1 natural mortality to be known and equal to the median of the prior distribution on M_1, the estimation process behaved better. The model also showed no evidence for a random walk in the commercial fishery inflection points for central and southern Lake Huron. The random walks were omitted in these two areas, mainly due to the lack of age composition data for the first five years in the central region and ten years in the southern region.

We were not able to estimate plausible values for handling time (*H*), and ultimately fixed the value of *H* at an assumed known 11 days (see below for explanation), and the objective function was modified by removing the component for the prior distribution for handling time. Our difficulties with estimating handling time were associated with difficulties in matching observed wounding on alternate prey in northern Lake Huron. When attempting to estimate handling time, predicted wounding on the alternate prey did not approach the observed levels until handling time approached the smallest allowable value. The resulting estimate of handling time was determined by the bound of what was meant to be an uninformative prior. When handling time is as low as five days, the number of attacks per lamprey over the feeding season was very high. These results greatly contradict lab results (Swink 2003) from both a handling time and growth perspective, as lamprey with such a high number of attacks would be larger than observed in the lake.

To explore how handling times influenced estimates of other quantities, we fixed handling time at three different assumed known values (6.8 days, 11 days, and 20 days) and fit the statistical catch-at-age model for each assumed value. We summarized the results of these analyses by total number of attacks per sea lamprey on each prey species, and by age-specific sea lamprey-induced mortality on lake trout. While the total number of attacks on lake trout varies with the assumed handling time, the greatest impact of the assumed handling time was on attack rates for alternative prey (Table 8). In particular, attack rates were substantially lower for lake whitefish in the north and Chinook salmon in the south when handling time was assumed to be longer. Apparently, when estimating handling time, the model is able to match predicted wounding rates on lake whitefish in northern Lake Huron and produces a “better” model fit in terms of maximizing the likelihood (eq. 3). It should be noted that in contrast with the results for lake whitefish, wounding rates on Chinook salmon are not matched as well with shorter rather than longer handling times. As handling time increases, sea lamprey-induced mortality will decrease as the total number of sea lamprey attacks decreases. Assumed handling time only had modest effects on estimates of sea lamprey-induced mortality of lake trout (Table 9). The effect of handling time on estimated sea lamprey-induced mortality on lake trout was the most pronounced in the northern and central regions. In northern Lake Huron, there was a modest decrease in sea lamprey induced mortality on age 4 and 9 lake trout as handling time was increased from 11 to 20 days, and a similar effect is observed for age 9 lake trout in the central region. Combining the results from this sensitivity analysis with current beliefs that indicate handling times are long but can vary (Koonce and Locci-Hernandez 1989, Bence et al. 2003), led to our decision to assume a known handling time of 11 days in our final model. This choice represents a compromise between the handling time estimated by the model (5 days) and the maximum assumed value of 20 days (Koonce and Locci-Hernandez 1989).

The quality of the model's predictions of the observed harvest and survey data was acceptable. Predicted total commercial harvest matched observed levels in northern and central Lake Huron well (Figure 3), while results in the south were slightly worse. Total predicted recreational harvests were consistent across the entire lake (Figure 4), with central Lake Huron producing the best results. Given the fact that four sources of mortality were estimated by the model, the temporal trends in harvest were matched fairly well. The model had a more difficult time matching effort data for the commercial harvest (Figure 5) while the observed recreational harvest (Figure 6) was matched fairly well by model predictions.

In order to summarize the ability of the model to match observed age composition data in the fisheries and the survey, average age at harvest was determined for both the observed and predicted values. Model predictions of average age at harvest for both the commercial (Figure 7) and recreational (Figure 8) fisheries matched observed quantities quite well, save for the commercial harvest in central Lake Huron. For some years, observed age composition was not available, but the predicted values are shown for reference. The model was unable to match the average age of surveyed fish (Figure 9), especially in central and southern Lake Huron.

Comparing observed sea lamprey-induced wounding rates to predicted wounding rates is difficult, given the changing wounding patterns and age composition of lake trout in Lake Huron. One method to quantify the results of the model fitting process is to compare observed and predicted values of the parameters of the logistic wounding model as described by Rutter and Bence (2003). Initial examination of observed and predicted asymptotic wounding rates indicated some substantial lack of fit (Figure 10). The model was unable to fit the temporal patterns in wounding, but the overall level of wounding for each region was matched with some success. Goodness of fit can also be assessed by comparing observed and predicted wounding rates in a given year by length. Example results for 1987 show that while the asymptotic wounding rate has not been matched, the pattern of wounding as a function of length has been estimated with some success (Figure 11).

We estimated that lake trout abundance was highest in southern Lake Huron, averaging 3.6 million lake trout (Figure 12). However, the southern region also has the largest area and the density of lake trout was actually lowest in this region (242 per square kilometer), with northern Lake Huron containing the highest density, with an average of 270 lake trout per square kilometer. Average density in central Lake Huron was lower than in the other regions (181 lake trout/square kilometer). While northern and southern Lake Huron have similar densities of lake trout, the age composition varies among regions, as seen by the levels of spawning stock biomass (here calculated as age 7+ fish assuming a 1:1 male to female ratio) (Figure 13). Northern Lake Huron average spawning stock biomass density (kg/sq km) is 2.30, with an average density of **7**.19 and 29.54 in central and southern Lake Huron, respectively. Spawning stock biomass is increasing in all regions of Lake Huron during the final years of the model, 1994-1998.

Average recreational fishing mortality rates for age 5-10 lake trout are low in all regions of Lake Huron (Figure 14), as are commercial fishing mortality rates in central and southern Lake Huron. In northern Lake Huron, tribal gill-net fisheries and a commercial gill-net fishery in Ontario account for the high average commercial fishing mortality rates. Commercial fishing mortality rates are higher in the north then average sea-lamprey induced mortality rates, except in 1991 and 1992. The model estimated a spike in sea lamprey lamprey-induced mortality in 1992 in all regions of Lake Huron (Figure 15). This increase is associated with a large estimate of spawning run sea lamprey (Mullett et al. 2003).

The overall yearly trends in sea lamprey-induced mortality, including the spike in 1992, can be seen in the average total annual mortality of age 5-10 lake trout for central and southern Lake Huron (Figure 16). In northern Lake Huron, where average total annual mortality is the highest, the high levels of commercial fishing mask year-to-year trends in sea lamprey-induced mortality. Total annual mortality includes the model estimate of background natural mortality for age 2+ lake trout (Table 10). These model estimates of natural mortality are higher than the median of the log normal prior 0.162, which was based on previous estimates of natural mortality on older lake trout (Sakagawa and Pycha 1971; Pycha 1980).

The estimated effective search rate (eq. T2.12 and Figure 17) differs greatly from the effective search rate proposed in IMSL (Greig et al. 1992). While the IMSL model was based on a mechanistic model, the functional form of our effective search rate was chosen to match the observed patterns in the wounding data for lake trout (Rutter and Bence 2003). The inflection point of the effective search was allowed to vary for each region, with the smallest inflection point estimated for northern Lake Huron (Table 11). The inflection point increased in central and southern Lake Huron, although these results indicate little difference between the two regions. These results match patterns observed in the wounding data for lake trout in which the inflection point for the function describing the average number of observed wounds per lake trout as a function of length was smallest in the north and increased in central and southern Lake Huron.

Discussion

In this study, we incorporated a sea lamprey/lake trout functional response model into a lake trout population model for the main basin of Lake Huron. The population model was parameterized using statistical catch-at-age techniques that were extended to include a functional response model. We were able to model commercial fishing mortality, recreational fishing mortality, sea lamprey-induced mortality and natural mortality. Expanding on previous efforts to model Lake Huron lake trout (Sitar et al. 1999), the population model utilized data from the entire main basin of Lake Huron and estimated lake trout populations in northern, central, and southern Lake Huron.

Improvements in the summarization of sea lamprey-induced wounding rates on lake trout (Rutter and Bence 2003) allowed us to parameterize a multi-species functional response model describing attack rates on lake trout by sea lamprey. This functional response model can be used to predict sea lamprey-induced mortality as a function of sea lamprey and host prey densities. This contrasts with previous lake trout assessments that calculated sea lamprey mortality from observed wounding rates and did not allow for such predictions without additional assumptions about the functional response. This functional response model can be used by managers to predict effects of fishery management and lamprey control programs on sea lamprey-induced mortality and future lake trout population levels (Ebener 1998).

Fishery stock assessment models have become increasingly more sophisticated in using observed fishery data by utilizing such techniques as virtual population analysis and stock-synthesis approaches (Quinn and Deriso 1999). In order to separate sources of natural (non-fishing related) mortality, there is active research in incorporating functional response models into population models in an effort to estimate predator-induced mortality. Initial attempts at incorporating these types of functional response models centered on virtual population analysis (VPA) based fishery models (Mohn and Bowen 1996; Livingston and Jurado-Molina 2000; Tsou and Collie 2001) utilizing consumption rate information based on stomach content analysis. Functional response models have been parameterized using a stock synthesis, statistical catch-at-age approach (Hollowed et al. 2000; Szalai et al. in review) by comparing predicted consumption to observed consumption of prey, again based on stomach content analysis. In our approach, we took advantage of the parasitic nature of sea lamprey coupled with the quantifiable evidence of sea lamprey attacks via observed wounding rates to parameterize the functional response model.

Patterns in the observed wounding rates (Rutter and Bence 2003) suggested a shift in the predatory response of sea lamprey when there is a lack of large trout, especially in the north. In the estimation model we were able to emulate this, while retaining a type two functional response, by allowing the inflection point of the function relating effective search rate to prey size to vary among regions. In northern Lake Huron, the inflection point was at the lowest prey size, in association with the greatest scarcity of larger prey. We strongly suspect the difference in inflection points between the northern and other regions results from sea lamprey responding to a scarcity of large prey by increasing their search for smaller prey.

An increase in search activity due to an increase in prey density can lead to Type III functional response (Holling 1966) and is sometimes seen for a particular prey type when predators switch between types that reside in different areas or require different search strategies (Akre and Johnson 1979; Dale et al. 1994). Essentially, time spent searching for one type reduces time spent searching for the other. This may be occurring for sea lamprey feeding on larger lake trout, with effective search rates on large lake trout increasing with the density of large lake trout over some range of densities. For smaller lake trout the number of attacks will actually decrease as the density of large lake trout increases.

The parameterization of the functional response model, combined with the estimated population levels of lake trout and alternative prey in each region in 1998, indicates that each region of Lake Huron will respond differently to an increase in lake trout populations. In northern Lake Huron, sea lampreys are saturated with available prey, mainly in the form of lake whitefish. If the lake trout population were to increase (assuming constant sea lamprey densities), the total attacks per sea lamprey will decrease as the sea lamprey switch from lake whitefish to their preferred host, lake trout. The handling time on lake trout is longer than the handling time for lake whitefish, and therefore fewer lake trout can be attacked by a single lamprey during the feeding season compared to lake whitefish. Under this scenario, sea lamprey-induced mortality in the north will decrease slowly as the lake trout population increases (Figure 18). In central and southern Lake Huron, the average number of attacks per lamprey in 1998 was 9.8 and 10.1, respectively. Assuming a handling time of 11 days, the maximum number of attacks per lamprey is 11.4. Therefore, sea lamprey in central and southern Lake Huron are not yet saturated with available hosts, and the total number of attacks per lamprey will increase as lake trout densities increase. However, due to the Type II functional response, the increase in attacks per lamprey is not linear, and sea lamprey-induced mortality rates on lake trout will decrease as lake trout abundance increases in central and southern Lake Huron.

As is often the case when fitting fishery models to data, lack of critical data imposed limitations on what could be estimated. This was particularly true here for the functional response parameters. As shown above, handling time plays an important role in determining the number of attacks per lamprey. We were unable to estimate a plausible handling time based solely on data used to fit the statistical catch-at-age model, and a handling time of 11 days was assumed instead. As described above, an important aspect of determining handling time is how attacks are allocated to alternative prey, Chinook salmon and lake whitefish. The limited data for wounding rates on alternative prey is a concern, as the number of sea lamprey attacks absorbed by Chinook salmon and lake whitefish are quite high. In order to effectively understand the role of alternative prey, yearly surveys designed to collect wounding data on alternative prey are needed, as well as more laboratory research that emulates the current work being done on lake trout with regards to handling time and probability of survival (Swink 2003). This lack of data makes it difficult to accurately model the distribution of sea lamprey attacks across all prey types, including lake trout. The lack of fit associated with some functional response related quantities may also be attributed to the assumption that sea lamprey and alternative prey populations were assumed known. By incorporating into the model fitting process estimates of uncertainty about these population estimates, it may be possible to better match observed wounding data.

The estimation process did an adequate job of matching observed quantities to values predicted by the population model. Predicted quantities that are based on parameters that are estimated separately for each region of Lake Huron, such as annual commercial and recreational harvest, matched observed data reasonably well. The model had a more difficult time matching predicted quantities based on parameters linked across the entire lake, such as those based on observed sea lamprey wounding rates. Many of the parameters associated with the functional response model are estimated lake wide, including the asymptote of the effective search rate and adjustments for alternative prey. The model was forced to match wounding rates under a variety of predator and prey densities, and did not match observed data as well as those predicted quantities that were based on region specific parameters. However, we feel that we have parameterized a functional response model that is applicable under a wide range of sea lamprey and lake trout densities.

We believe that our study has provided a valuable tool for assessing the future of lake trout rehabilitation in Lake Huron. The parameterized functional response model could allow managers to determine sea lamprey-induced mortality rates under a variety of management scenarios. The main factors in these scenarios are future lake trout and sea lamprey populations, and, to a lesser extent, the populations of alternative prey. For example, it would be possible to explore how changes in lake trout stocking levels influence the mortality they suffer from sea lamprey, and their future spawning stock size, given status quo control levels for sea lamprey or alternative levels of control.

Table 1: Years in which data sources are available for the commercial and recreational harvest in Lake Huron for each region.

Data	Region	Years
Commercial yield	North	1984-1998
	Central	1984-1998
	South	1984-1998
Commercial effort	North	1984-1998
	Central	1984-1998
	South	1984-1998
Commercial age composition	North	1984-1998
	Central	1990-1998
	South	1994-1998
Recreation yield	North	1985-1998
	Central	1985-1988,1991-1998
	South	1986-1998
Recreation effort	North	1985-1998
	Central	1985-1988,1991-1998
	South	1986-1998
Recreational age composition	North	1985-1989,1991-1992,1994-1998
	Central	1985-1988,1991-1998
	South	1985-1997

Table 2: Model equations describing the catch-at-age model.

$$N^{9}_{a,y,r} = N_{a,y,r}e^{-(M_{a,y,r}+F^{C}_{a,y,r}+F^{R}_{a,y,r})\frac{9}{12}} \tag{T2.1}$$

$$N^{9*}_{a,y,r} = N^{9}_{a,y,r}e^{-M^{L}_{a,y,r}} \tag{T2.2}$$

$$N_{a+1,y+1,r} = N^{9*}_{a,y,r}e^{-(M_{a,y,r}+F^{C}_{a,y,r}+F^{R}_{a,y,r})\frac{3}{12}} \tag{T2.3}$$

$$F^{C}_{a,y,r} = S^{C}_{a,r}f^{C}_{y,r} \tag{T2.4}$$

$$F^{R}_{a,y,r} = S^{R}_{a,r}f^{R}_{y,r} \tag{T2.5}$$

$$S^{C}_{a,r} = \frac{1}{1+e^{-\omega_{1,r}\left(a+\omega_{2,r}\right)}}\left(1-\frac{1}{1+e^{-\omega_{3,r}\left(a+\omega_{4,r}\right)}}\right) \tag{T2.6}$$

$$S^{R}_{a,r} = \frac{1}{1+e^{-\alpha_{R,r}\left(a-\beta_{R,r}\right)}} \tag{T2.7}$$

$$\beta^{i}_{y,r} = \beta^{i}_{y-1,r} + \delta^{i}_{y,r} \tag{T2.8}$$

$$M^{L}_{a,y,r} = A_{a,y,r}\left(1-P_{s}\left(a\right)\right) \tag{T2.9}$$

$$P_{s}\left(a\right) = \frac{1}{1+e^{1.462-.00041w\left(a\right)}} \tag{T2.10}$$

$$A_{host,y,r} = \frac{S\lambda_{host,r}L_{y,r}}{1+\sum_{i}^{all\ hosts}H_{i}\lambda_{i,r}N_{i,y,r}} \tag{T2.11}$$

$$\lambda_{l,r} = \frac{\theta_{\lambda}}{1+e^{-\alpha_{\lambda}\left(l-\beta_{\lambda,r}\right)}} \tag{T2.12}$$

$$C^{C9}_{a,y,r} = \frac{F^{C}_{a,y,r}}{Z'_{a,y,r}}\left(1-e^{-Z'_{a,y,r}\frac{9}{12}}\right)N_{a,y,r} \tag{T2.13}$$

Table 2 (cont'd)

$$C^{C}_{a,y,r} = C^{C9}_{a,y,r} + \frac{F^{C}_{a,y,r}}{Z'_{a,y,r}}\left(1 - e^{-Z'_{a,y,r}\frac{3}{12}}\right)N^{9*}_{a,y,r} \tag{T2.14}$$

$$K_{a,y,r} = q^{S}_{r} S^{S}_{a,y,r} N_{a,y,r} \tag{T2.15}$$

$$w_{1200,\ y,r} = \frac{S\lambda_{1200,\ r} L_{y,r}}{1 + \sum_{i}^{allhosts} H_i \lambda_{i,r} N_{i,y,r}} \tag{T2.16}$$

$$\hat{\beta}_r = -\frac{-4b_{ps} - \alpha_{ps}\alpha_{\lambda}{}^{2}\beta_{\lambda,r} - b_{ps}\alpha_{\lambda}{}^{2}\beta^{2}_{\lambda,r}}{\alpha_{\lambda}{}^{2}\left(\alpha_{ps} + b_{ps}\beta_{\lambda,r}\right)} \tag{T2.17}$$

$$\lambda_{s,r} = \tau_s \lambda_{l,r} \tag{T2.18}$$

Table 3: Likelihood equations used to fit the catch-at-age model.

$$L_i = \sum_r \left(T_{i,r} \ln\left(\frac{1}{\sqrt{2\pi\sigma^2_{i,y,r}}} \right) - \sum_y .5 \left[\frac{\ln\left(\frac{X_{i,y,r}}{X'_{i,y,r}} \right)}{\sigma_{i,y,r}} \right]^2 \right) \tag{T3.1}$$

$$L_i = \sum_r \left[\sum_y J_{i,y,r} \sum_a P'_{i,a,y,r} \ln\left(P_{i,a,y,r}\right) \right] \tag{T3.2}$$

$$L_9 = \ln\left((2\pi)^{-m/2} \Sigma^{-1/2} e^{-\frac{1}{2}(\bar{x}-\bar{\mu})^T \Sigma^{-1} (\bar{x}-\bar{\mu})} \right) \tag{T3.3}$$

$$L_{10} = \sum_i \ln\left(\frac{1}{\sqrt{2\pi\sigma^2_{10,i}}} e^{-\frac{1}{2\sigma^2_{10,i}}\left(w_i - w'_i \right)^2} \right) \tag{T3.4}$$

$$L_{11} = \sum_{y,r} \left(\ln\left(\frac{1}{\sqrt{2\pi\hat{s}^2_{11,r}}} \right) - .5 \left[\frac{\ln\left(\frac{\gamma_{y,r}}{1} \right)}{\hat{s}_{11,r}} \right]^2 \right) \tag{T3.5}$$

$$L_{12} = \sum_{y,r,i} \ln\left(\left(2\pi\hat{s}^2_{12,r}\right)^{-1/2} e^{-\frac{1}{2s^2_{12,r}}\left(\delta^i_{y,r} \right)^2} \right) \tag{T3.6}$$

$$L_{13} = \sum_i \ln\left(\frac{1}{\sigma_{\theta i}\sqrt{2\pi}} \right) - .5 \left[\frac{\ln\left(\frac{\theta_i}{\theta'_i} \right)}{\sigma_{\theta i}} \right]^2 \tag{T3.7}$$

Table 4**:** List of variables and parameters used in the model

y	Year (1984-1998)
r	Region of Lake Huron (north, central or south)
a	Age of fish (1-15)
$N_{a,y,r}$	Number of fish of age a in year y and region r
$S_{a,y,r}$	Survival rate for a fish of age a in year y and region r
$\gamma_{y,r}$	Post stocking survivability for year y and region r
$N^{9}_{a,y,r}$	Number of age a fish after nine months in year y and region r
$M_{a,y,r}$	Natural mortality rate for a fish of age a in year y and region r
$F^{C}_{a,y,r}$	Commercial fishing mortality for a fish of age a in year y and region r
$F^{R}_{a,y,r}$	Recreational fishing mortality for a fish of age a in year y and region r
$N^{9*}_{a,y,r}$	Number of age a fish after nine months and a pulse of sea lamprey-induced mortality in year y and region r
$M^{L}_{a,y,r}$	Sea lamprey-induced mortality rate for a fish of age a in year y and region r
$s^{C}_{a,r}$	Commercial fishing selectivity for a fish of age a in region r
$f^{C}_{y,r}$	Commercial fishing intensity for a fish in year y and region r
$s^{R}_{a,r}$	Recreational fishing selectivity for a fish of age a in region r
$f^{R}_{y,r}$	Recreational fishing intensity for a fish in year y and region r
$\omega_{\mathrm{n},r}$	One of four (n=1,2,3,4) shape parameters for model of commercial fishing selectivity in region r
$\alpha_{R,r}$, $\beta_{R,r}$	Shape parameters for model of recreational fishing selectivity in region r
$\beta^{i}_{y,r}$	Inflection point of selectivity for fishery i (commercial or recreational) in year y and region r
$\delta^{i}_{y,r}$	Random walk component for inflection points in selectivity models for fishery i (commercial or recreational) in year y and region r
$A_{a,y,r}$	Number of sea lamprey attacks on a fish of age a in year y and region r
$P_s(a)$	Probability of a fish of age a surviving a sea lamprey attack
$w(a)$	Weight of a fish of age a in grams
S	Length of the feeding season in years
$\lambda_{i,r}$	Effective search rate of sea lamprey for the host species i of interest in region r
$L_{y,r}$	Sea lamprey density for a given year y and region r
H	Handling time in years for lake trout and Chinook salmon
ML_{NtoC}	Percent of sea lamprey that migrate from Northern to Central/Southern Lake Huron
ML_{S}	Percentage of sea lamprey in Central/Southern Lake Huron located in the South

Table 4 (cont’d)

H_w	Handling time in years for lake whitefish
l	Length of fish in mm
θ_λ	Asymptotic effective search rate
α_λ	Shape parameter for logistic function of effective search rate
$\beta_{\lambda,r}$	Inflection point for logistic function of effective search rate in region *r*
$C_{a,y,r}^{C9}$	Commercial catch in the first nine months of the year for age *a* fish in year *y* and region *r*
$Z'_{a,y,r}$	Summation of natural, commercial and fishing mortality for age *a* fish in year *y* and region *r*
$C_{a,y,r}^{C}$	Total commercial catch for age *a* fish in year *y* and region *r*
q_r^C , q_r^R	Catchability for commercial and recreational fisheries, respectively, in region *r*
$K_{a,y,r}$	Catch per unit effort for spring surveys for age *a* fish in year *y* and region *r*
q_r^S	Catchability for spring surveys in region *r*
$S_{a,y,r}^S$	Selectivity for spring surveys for age *a* fish in year *y* and region *r*
$\theta_{y,r}$	Observed asymptotic wounding rates in year *y* and region *r*
β_r	Observed inflection point for wounding rates in region *r*
α	Observed slope parameter for wounding rates
$w_{1200,y,r}$	Predicted number of wounds on a 1200mm lake trout
$\hat{\beta}_r$	Predicted inflection point of the wounding rate in region *r*
a_{ps}	Intercept of the linear approximation of the probability of survival function
b_{ps}	Slope of the linear approximation of the probability of survival function
$\lambda_{s,r}$	Effective search rate for alternative prey species *s* in region *r*
τ_s	Adjustment to the effective search rate for alternative prey species *s*
L_i	Likelihood component *i*
$T_{i,r}$	Number of years of data for data source *i* in year *y*
$\sigma_{i,y,r}$	Variability of data source *i* in year *y* and region *r*
$X'_{i,y,r}$	Observed value of interest for data source *i* in year *y* and region *r*
$X_{i,y,r}$	Predicted value of interest for data source *i* in year *y* and region *r*
$J_{i,y,r}$	Sample size of data source *i* in year *y* and region *r*
$P'_{i,a,y,r}$	Observed proportion at age *a* for data source *i* in year *y* and region *r*
$P_{i,a,y,r}$	Predicted proportion at age *a* for data source *i* in year *y* and region *r*
$\vec{\mu}$	Vector of observed wounding rate parameters
$\vec{x}$	Vector of predicted wounding rate parameters

Table 4 (cont'd)

Σ	Covariance matrix for observed wounding rate parameters
w'_i	Predicted number of sea lamprey wounds on alternative prey *i*
w_i	Observed number of sea lamprey wounds on alternative prey *i*
$\hat{s}_{i,r}$	Predicted standard deviation for data source *i* in region *r*
θ'_i	Prior mean on parameter *i*
θ_i	Estimated value of parameter *i*
$\sigma_{\theta i}$	Prior standard deviation on parameter *i*

Table 5: Area of lake trout habitat (<40 fathoms) in km^2 for each region of Lake Huron (Ebener 1998).

Region	km^2
North	3,432
Central	4,575
South	15,210

Table 6: Variability ($\sigma_{i,y,r}$) of data for log-normal likelihood components (assumed constant across all year) estimated from the data.

Data	Region	Standard Deviation
Commercial Harvest	North	0.15
	Central	0.15
	South	0.15
Recreational Harvest	North	0.3
	Central	0.14916
	South	0.15
Commercial Harvest Effort	North	0.15
	Central	0.15
	South	0.15
Recreational Harvest Effort	North	0.13
	Central	0.06991
	South	0.15

Table 7: Yearly variability ($\sigma_{i,y,r}$) of the log-normal likelihood component of survey CPUE based on mixed-effect linear model analysis. An entry of zero indicates no data for that year.

	Region		
Year	North	Central	South
1984	0.84	0.96	0.40
1985	0.84	0.96	0.43
1986	1.37	0.96	0.42
1987	1.37	0.85	0.42
1988	1.87	1.01	0.40
1989	1.37	1.04	0.38
1990	0.00	1.01	0.42
1991	1.37	0.90	0.43
1992	0.60	0.91	0.45
1993	0.82	1.03	0.45
1994	0.91	0.92	0.45
1995	0.81	0.83	0.34
1996	1.08	0.80	0.34
1997	0.91	0.83	0.43
1998	0.82	0.83	0.37

Table 8: Predicted average number of attacks per lamprey (1997-1998) for assumed handling times of 6.8, 11, and 20 days.

	Handling Time		
Region	6.8 Days	11 Days	20 Days
North			
Lake Trout	1.11	1.19	1.89
Whitefish	26.60	14.46	1.66
Chinook	3.29	3.14	3.63
Total	31.00	18.80	7.19
Central			
Lake Trout	5.46	4.41	3.04
Whitefish	0.09	0.04	0.00
Chinook	7.00	5.45	3.36
Total	12.55	9.90	6.40
South			
Lake Trout	7.53	5.33	3.41
Whitefish	0.05	0.02	0.00
Chinook	6.21	4.96	3.10
Total	13.79	10.31	6.51

Table 9: Predicted average sea lamprey-induced mortality rates (1997-1998) for age 4 and age 10 lake trout for assumed handling times of 6.8, 11, and 20 days.

	Handling Time		
Region	6.8 Days	11 Days	20 Days
North			
Zl-4	0.135	0.126	0.085
Zl-9	0.428	0.420	0.348
Central			
Zl-4	0.000	0.000	0.000
Zl-9	0.317	0.275	0.234
South			
Zl-4	0.027	0.024	0.021
Zl-9	0.236	0.218	0.203

Table 10: Estimated background natural mortality rates for age 2+ lake trout for each region of Lake Huron.

Region	Natural Mortality
North	0.24
Central	0.21
South	0.20

Table 11: Estimated parameters for the effective search rate for sea lamprey (eq. 12). 95% Bayesian prediction interval based on MCMC analysis.

Parameter	Estimate	95% Prediction Interval
θ_λ	0.70	(0.43,1.66)
α_λ	0.0983	(0.0810,0.1151)
$\beta_{\lambda,North}$	498.67	(492.32,503.39)
$\beta_{\lambda,Central}$	562.32	(556.15,566.26)
$\beta_{\lambda,South}$	548.62	(537.34,555.87)

FIGURES

Figure 1: Map of Lake Huron with model regions based on the statistical districts listed (Smith et al. 1961). Northern Lake Huron consists of MH-1 and portions of OH-1. Central Lake Huron consists of MH-2, portions of OH-1, and OH-2. Southern Lake Huron consists of MH-3, MH-4, MH-5, MH-6, OH-3, OH-4, and OH-5. Dotted line indicates boundary between Canada and United States.

Figure 2: Example of a double logistic selectivity curve estimated by the model for commercial fishery selectivity and spring survey selectivity.

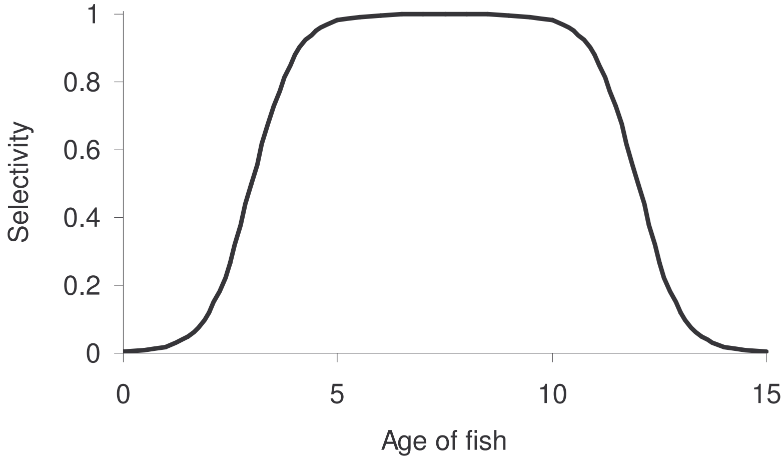
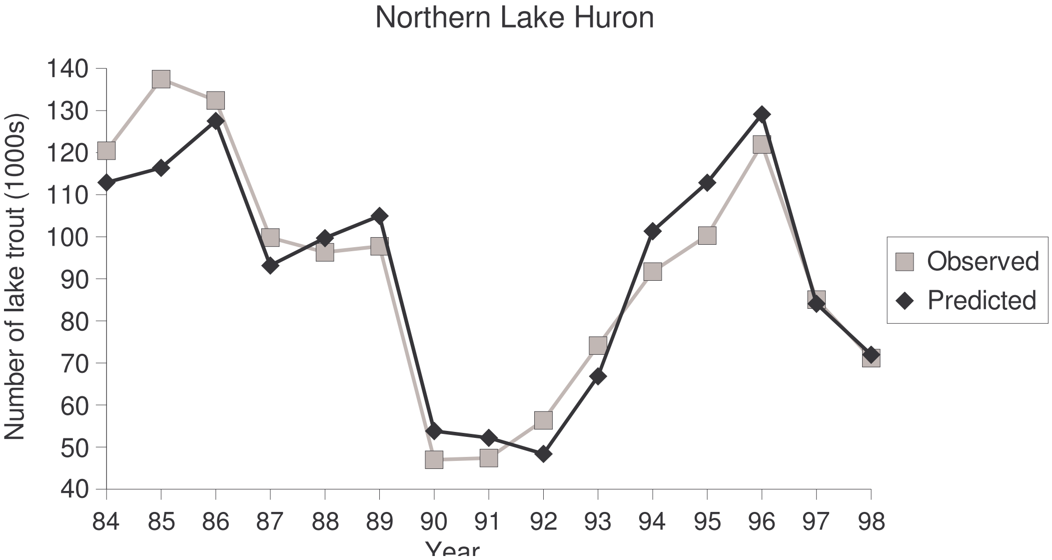


Figure 3: Total commercial harvest (in 1000s of lake trout) for Lake Huron comparing observed harvest to harvest predicted by the model for each region of Lake Huron for 1984-1998. Note the difference in scale for each region.



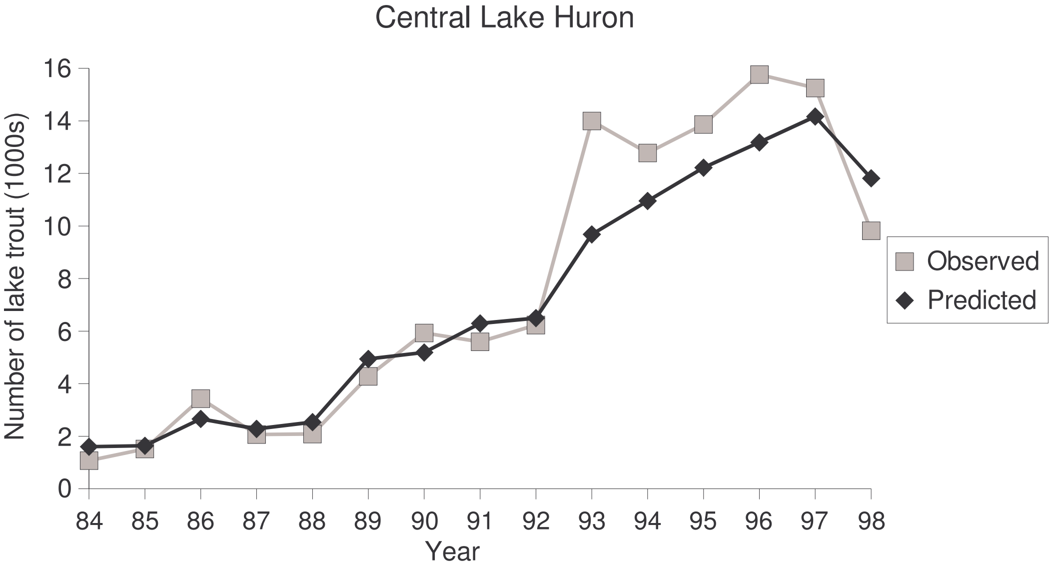


Figure 3 (cont'd)

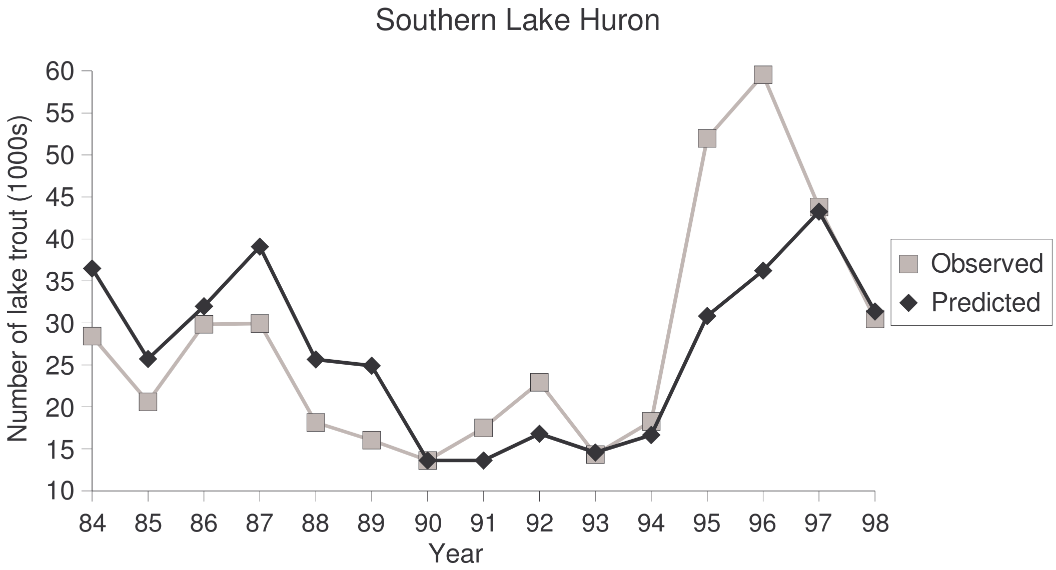
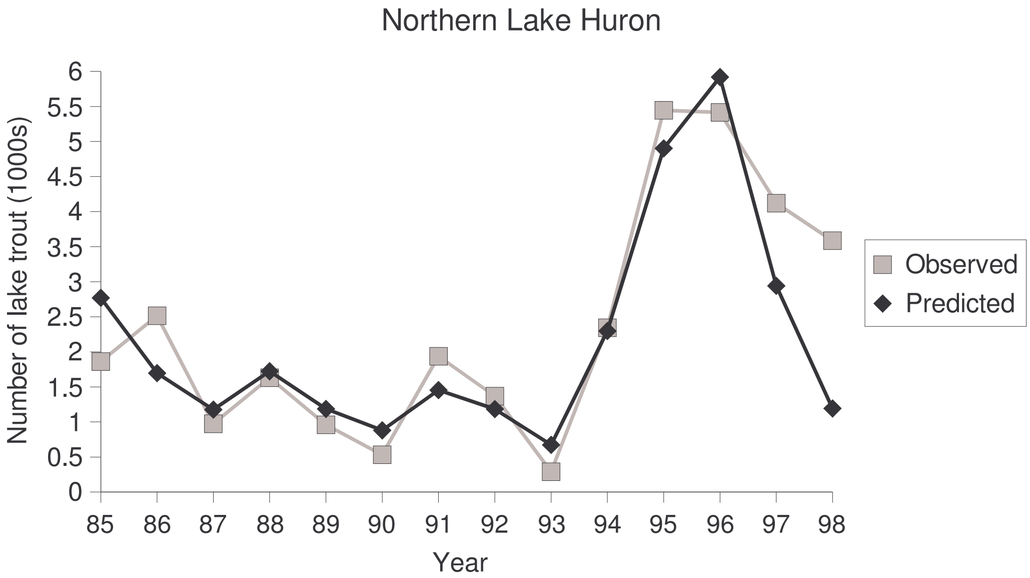


Figure 4: Total recreational harvest (in 1000s of lake trout) for Lake Huron comparing observed harvest to harvest predicted by the model for each region of Lake Huron for 1985-1998. Note the difference in scale for each region.



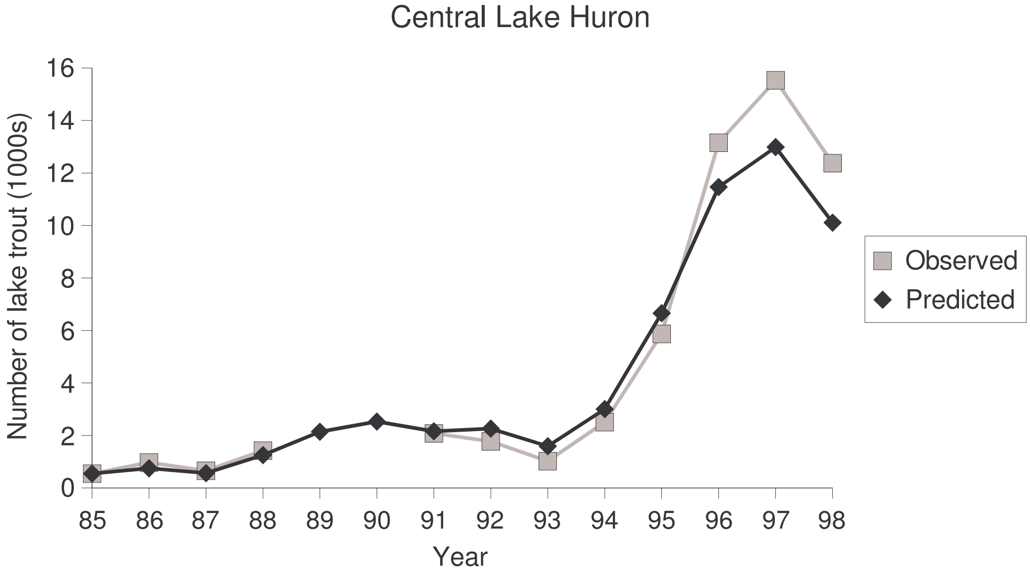


Figure 4 (cont'd)

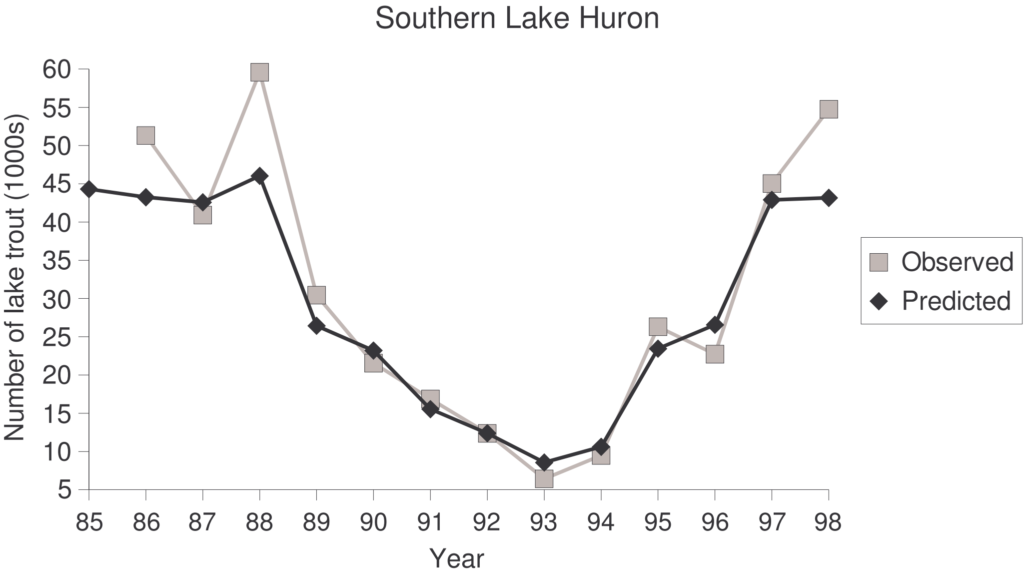


Figure 5: Commercial effort for Lake Huron in 1000s of meters of large-mesh gill-net set per year comparing observed effort to effort predicted by the model for each region of Lake Huron for 1984-1998. Note the difference in scale for each region.

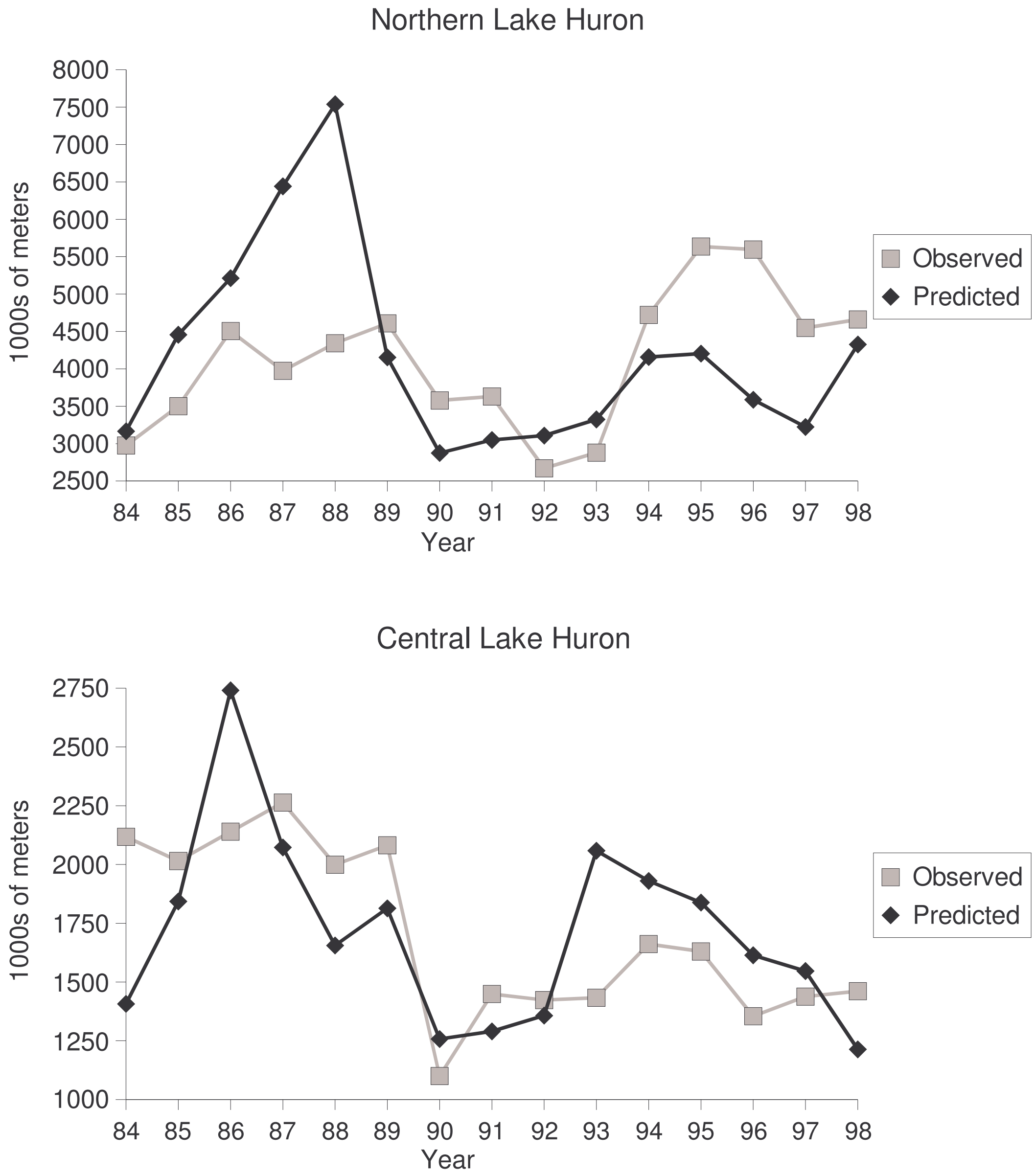


Figure 5 (cont'd)

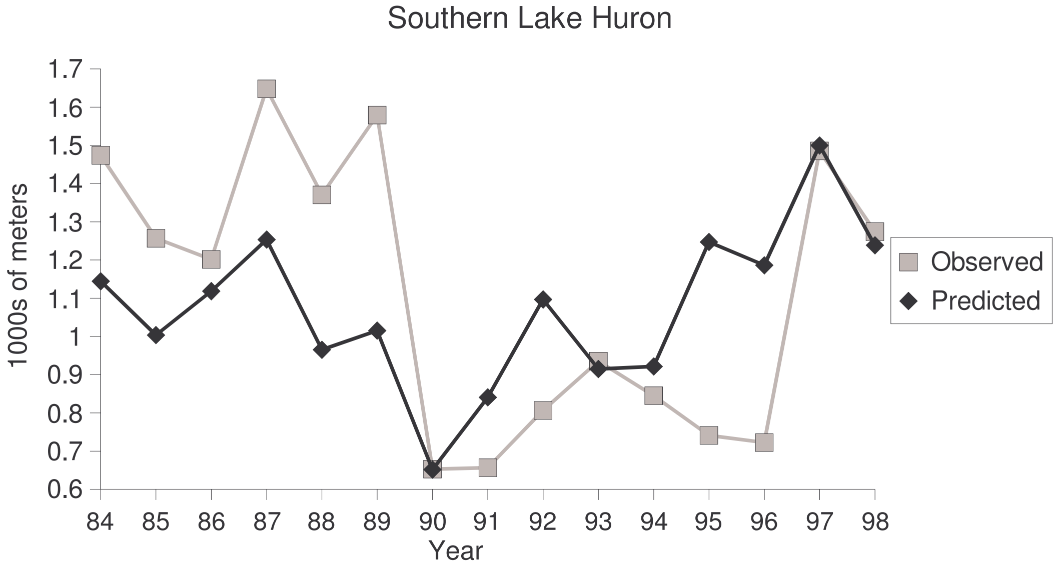
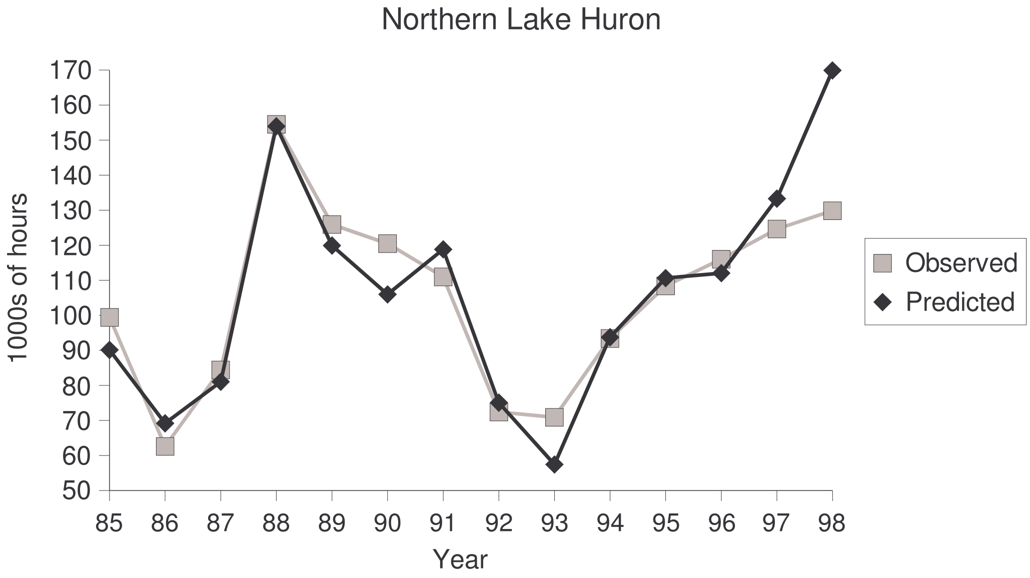
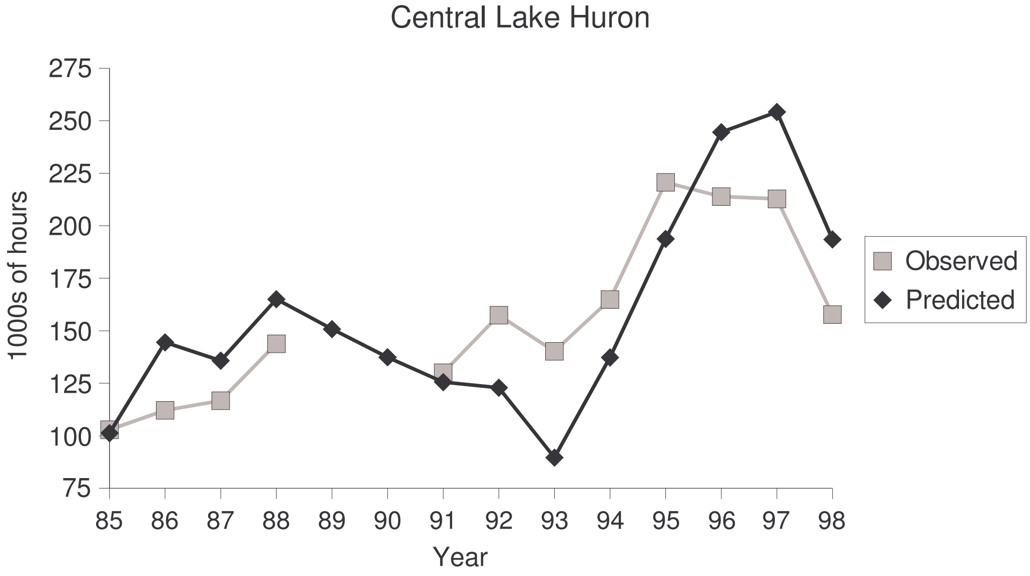


Figure 6: Recreational effort for Lake Huron in 1000s of angling hours comparing observed effort to effort predicted by the model for each region of Lake Huron for 1985-1998. Note the difference in scale for each region.





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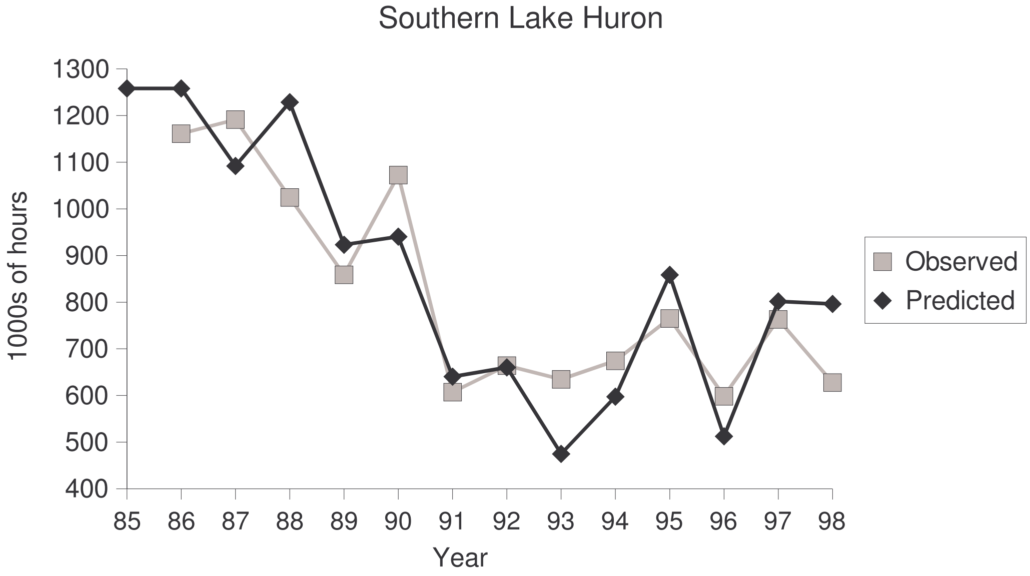
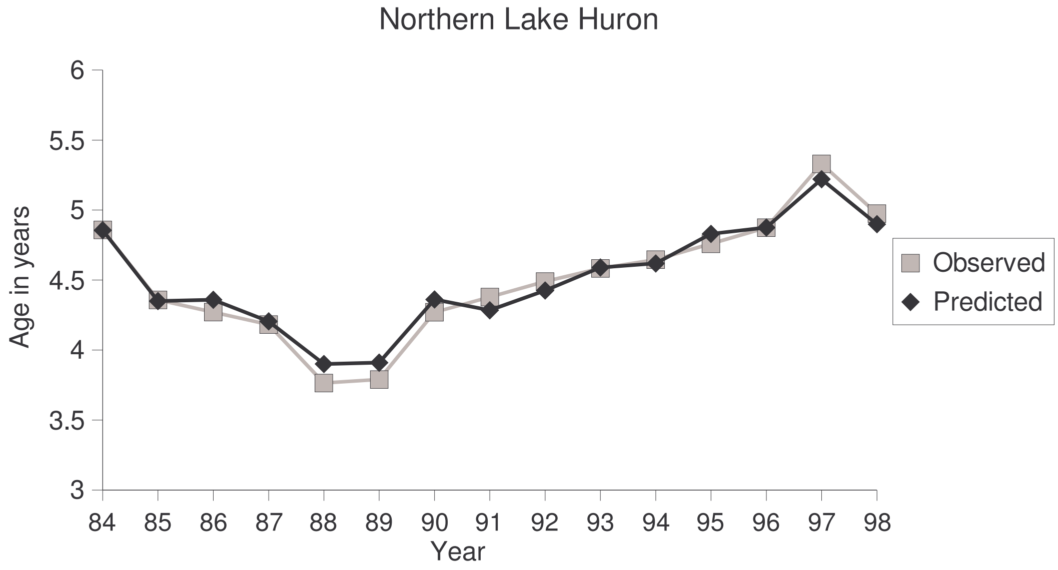
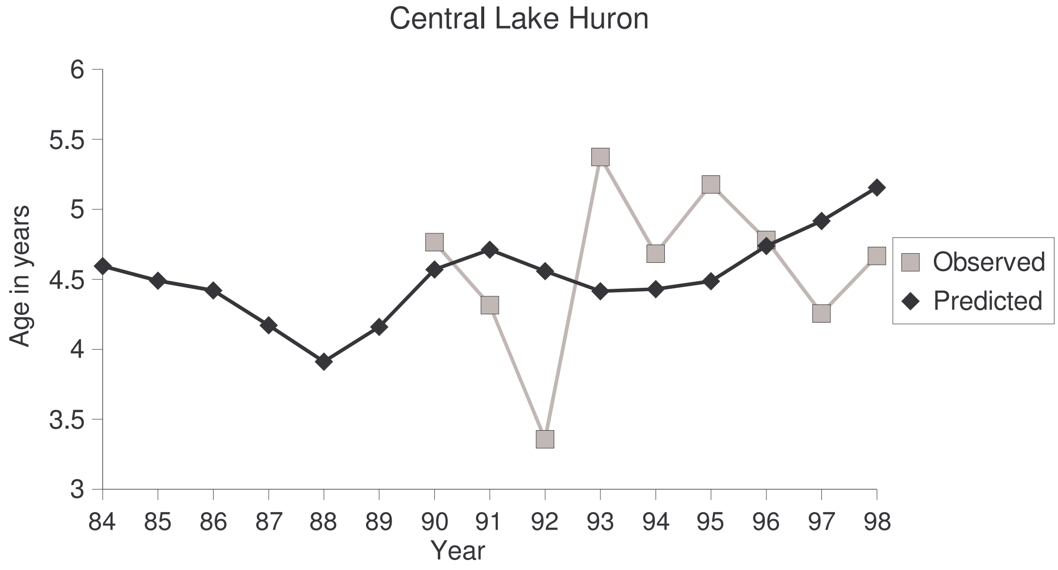


Figure 7: Average age at harvest in the commercial fishery for Lake Huron comparing observed average age to average age predicted by the model for each region of Lake Huron for 1984-1998.





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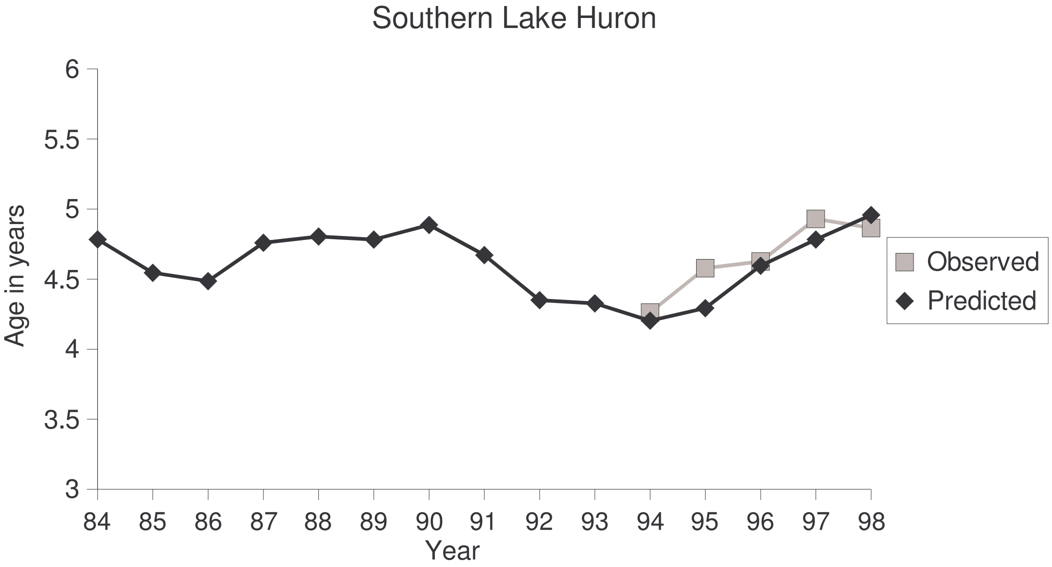
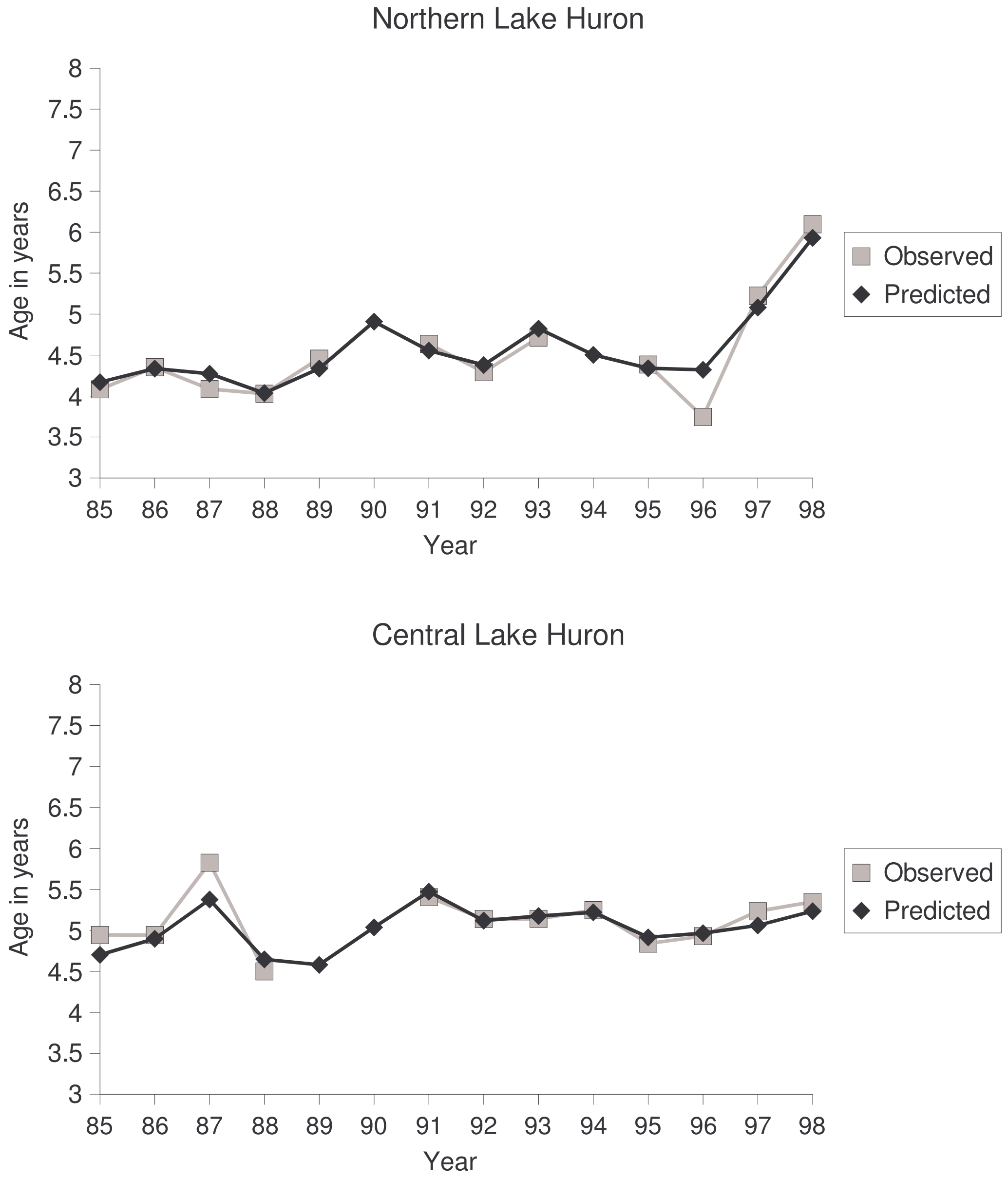


Figure 8: Average age at harvest in the recreational fishery for Lake Huron comparing observed average age to average age predicted by the model for each region of Lake Huron for 1985-1998.



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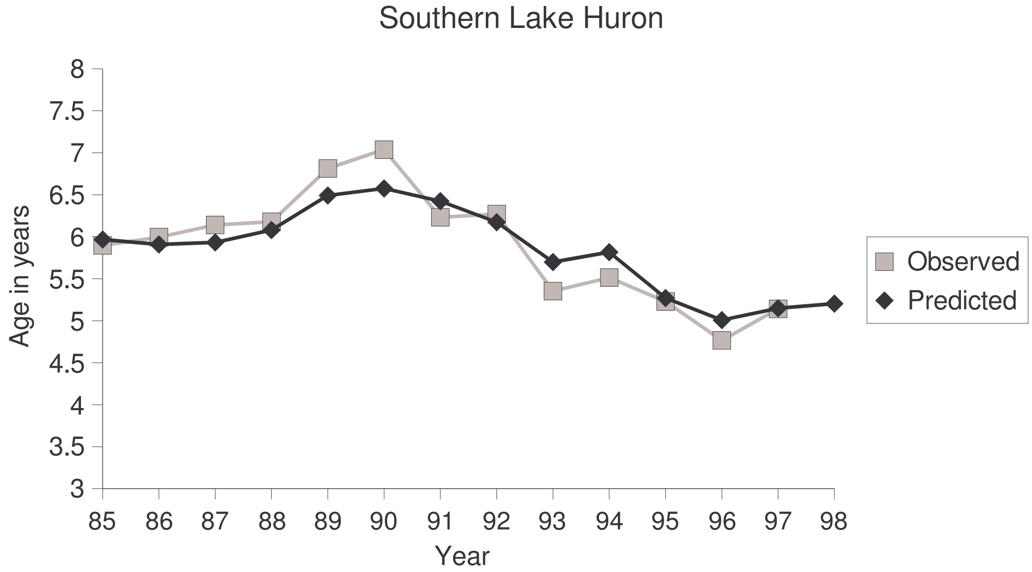
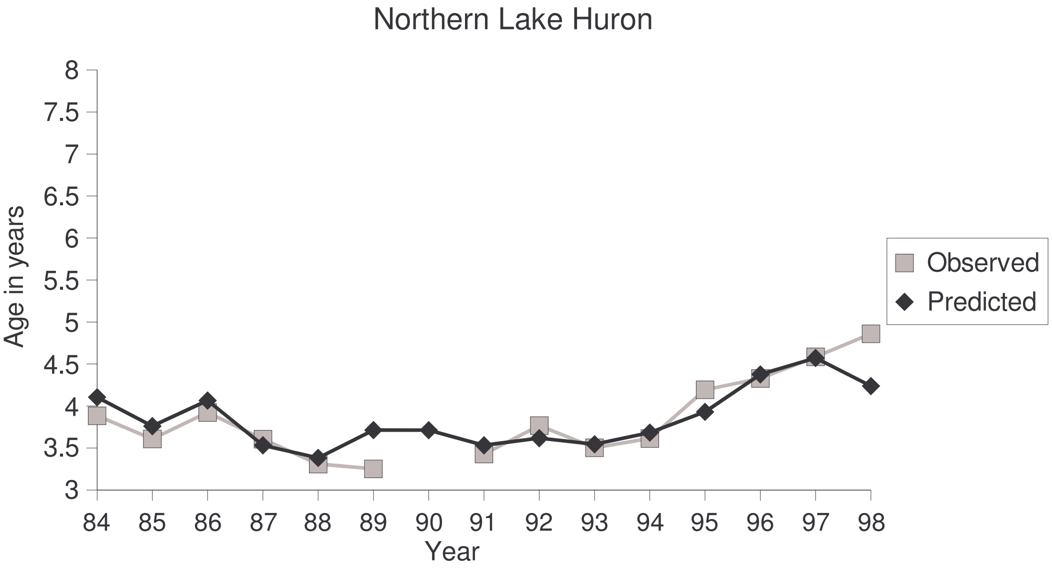
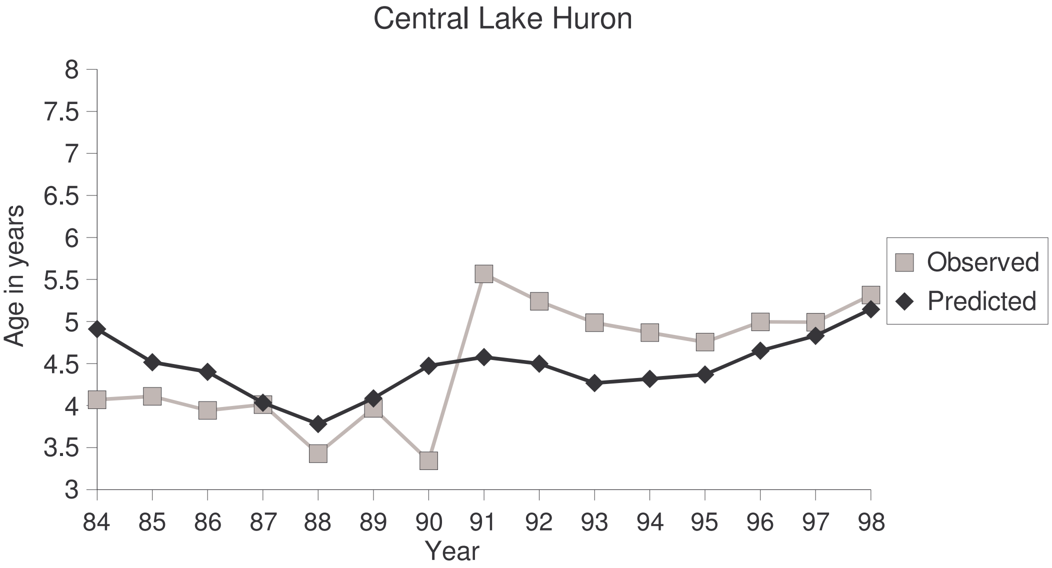


Figure 9: Average age in the spring graded-mesh gill-net survey for Lake Huron comparing observed average age to average age predicted by the model for each region of Lake Huron for 1984-1998.





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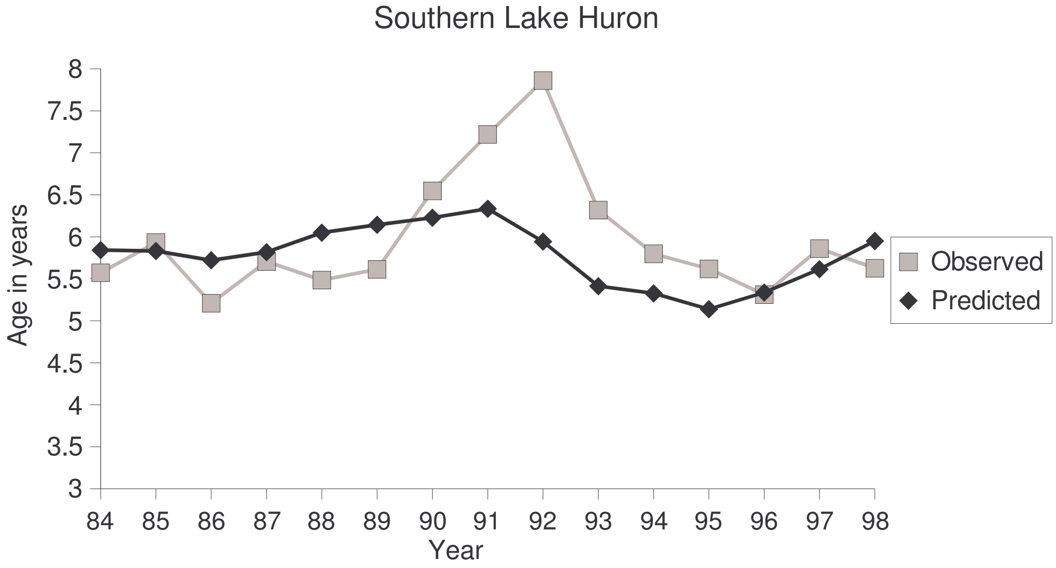
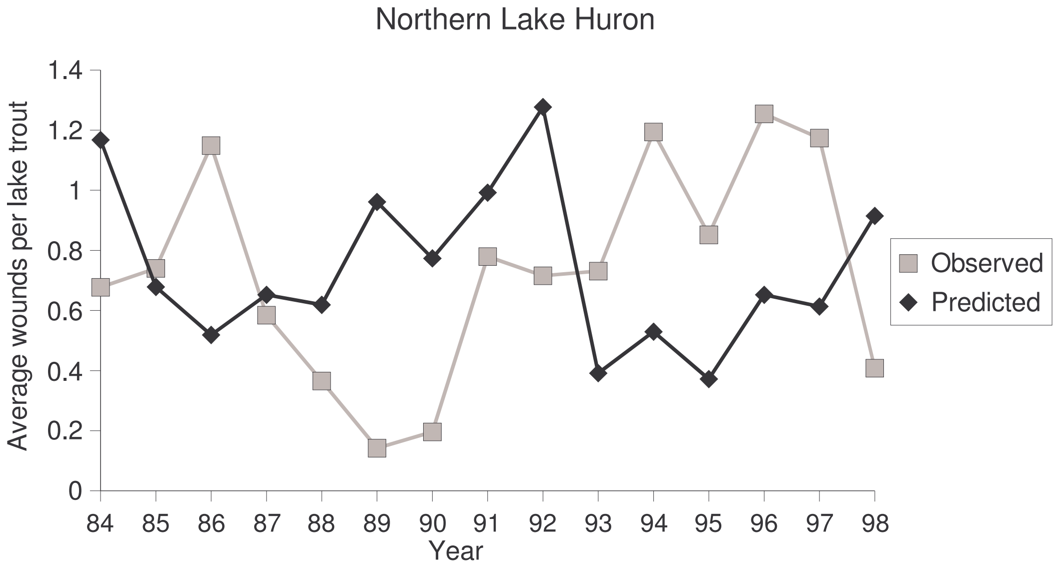
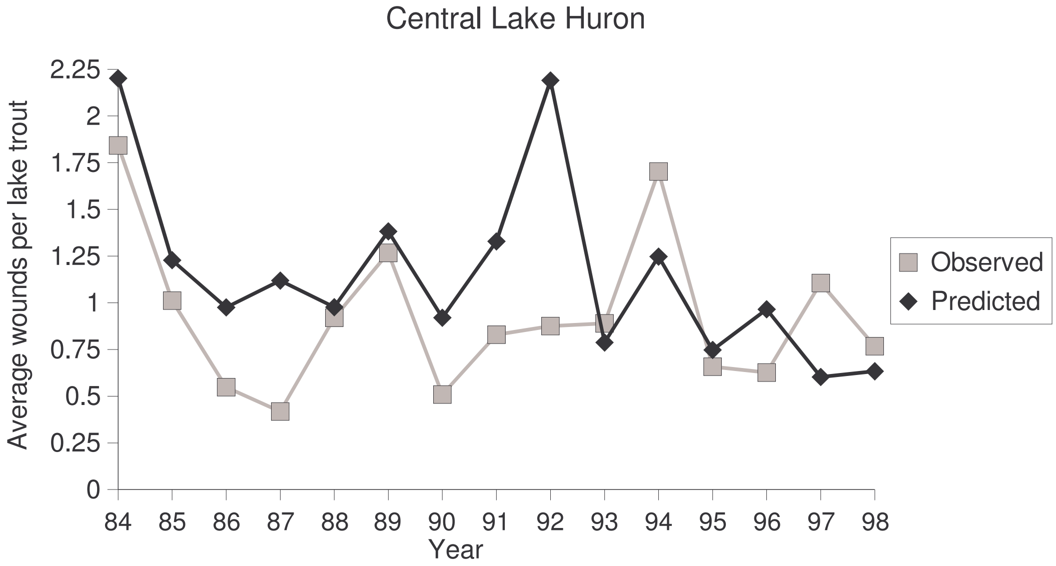


Figure 10: Observed asymptotic wounding rates from Rutter and Bence (2003) compared to the asymptotic wounding rates predicted by the model for each region of Lake Huron for 1984-1998.





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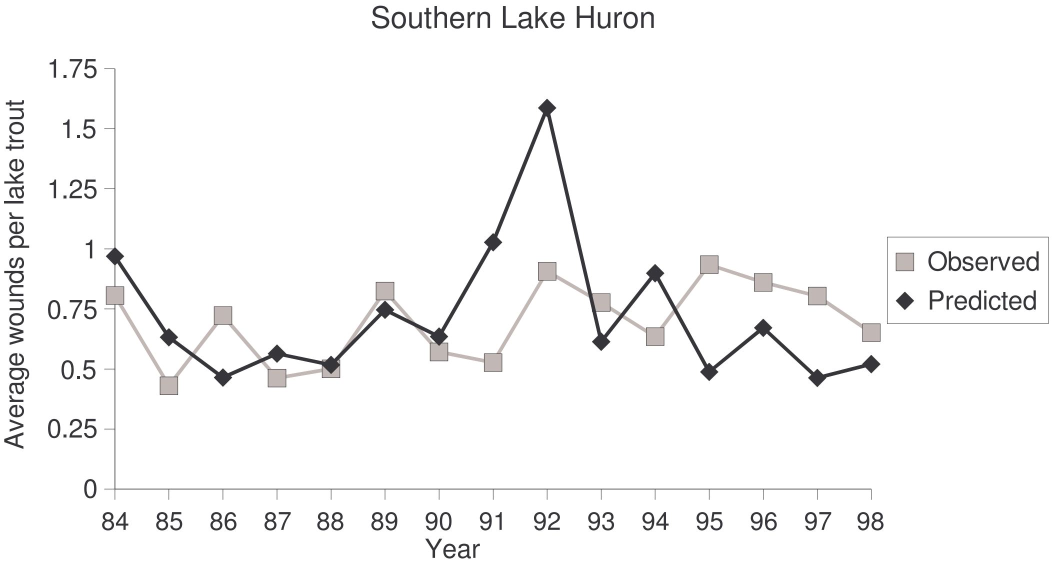
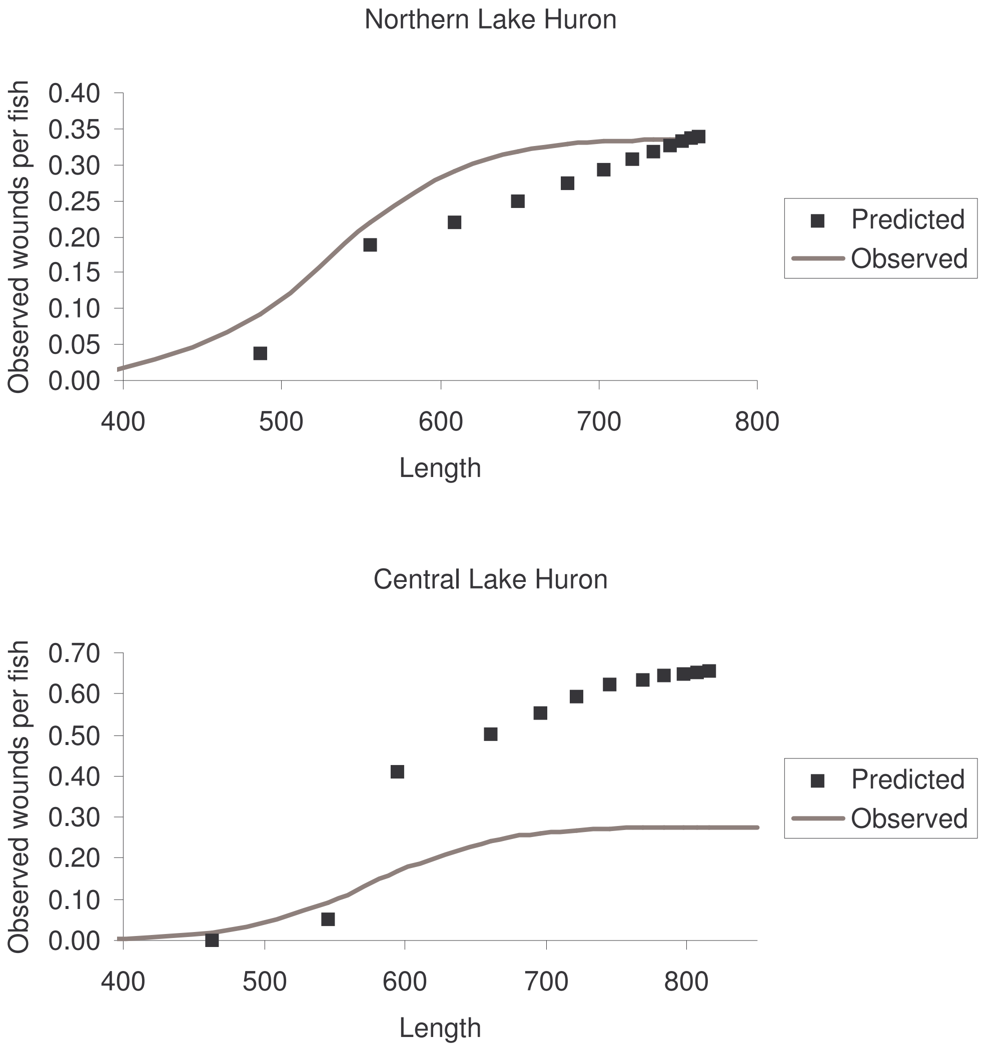


Figure 11: Observed wounding rates from Rutter and Bence (2003) for 1987 in each region of Lake Huron compared to wounding rates predicted by the model for 1987. Note the difference in scale for each region.



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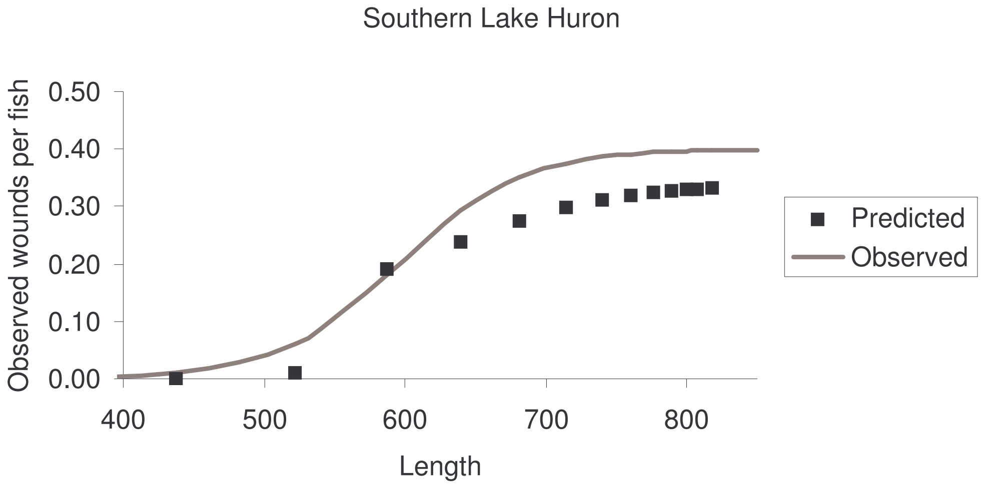


Figure 12: Total number of lake trout (in 1000s) age 1 to age 15 predicted by the model for the three regions of Lake Huron from 1984-1998.

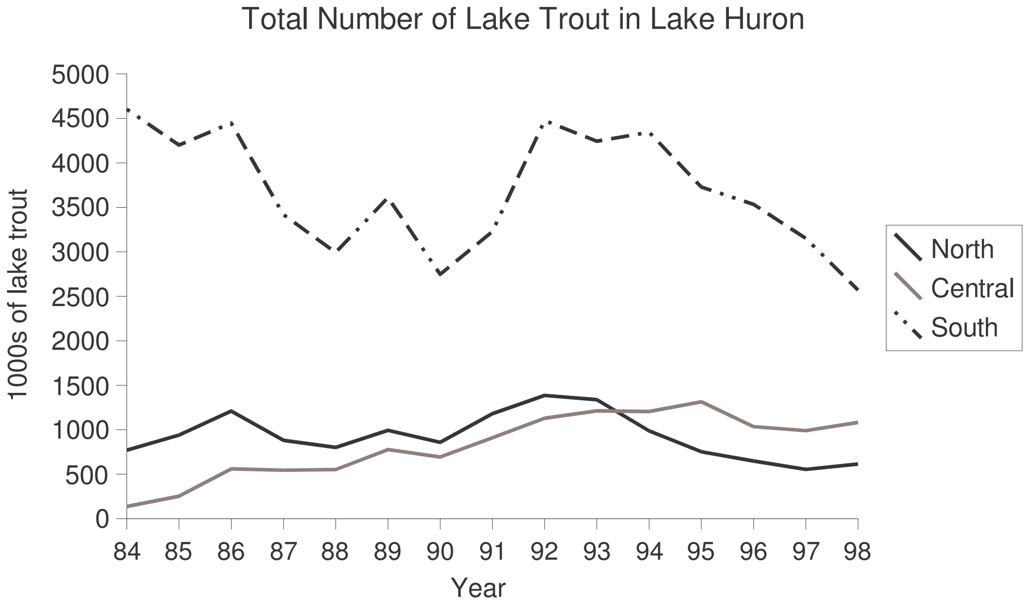


Figure 13: Predicted spawning stock biomass (biomass of age 7+ female lake trout assuming 50% gender ratio) in 1000s of kg of lake trout in three regions of Lake Huron from 1984-1998.

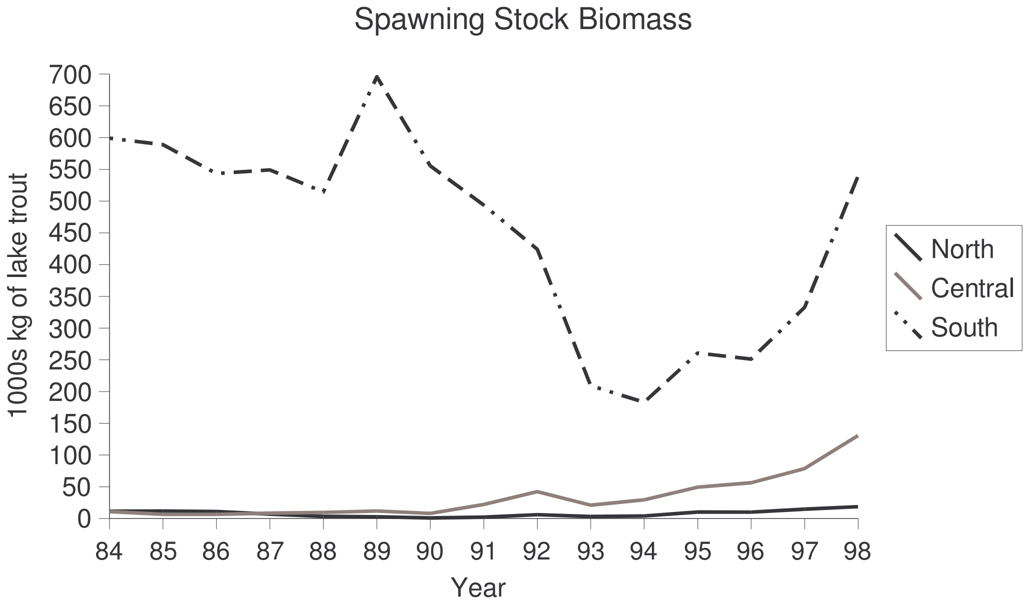
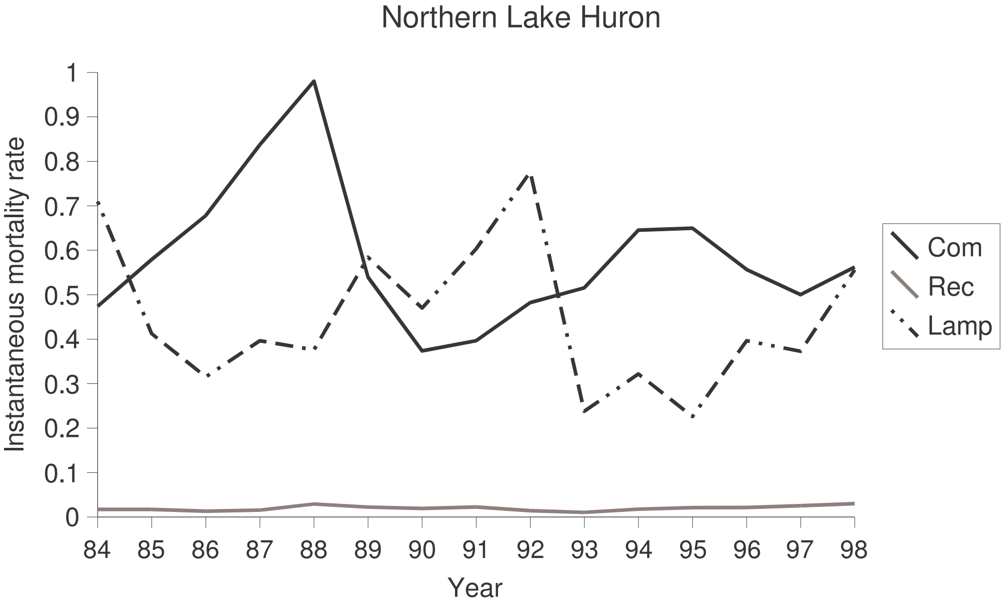
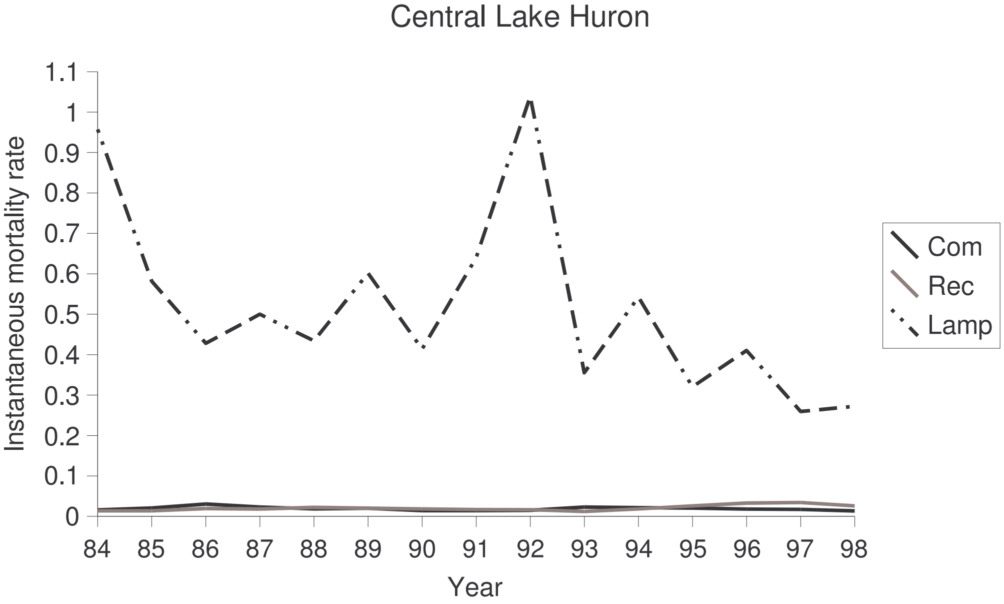


Figure 14: Predicted average instantaneous mortality rates due to commercial fishing, recreational fishing, and sea lamprey on age 5-10 lake trout in each region of Lake Huron from 1984-1998. Note the difference in scale for each region.





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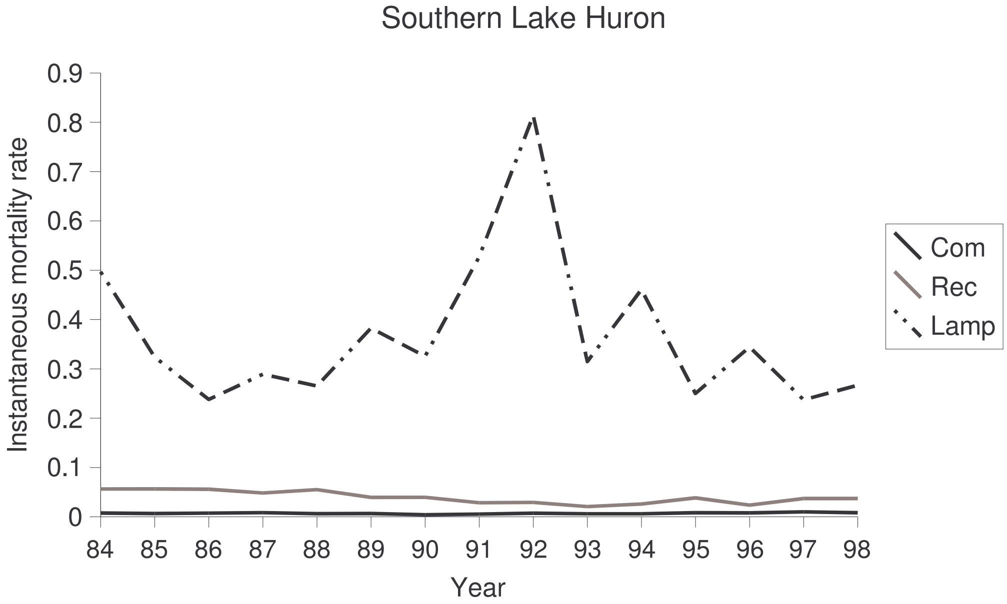
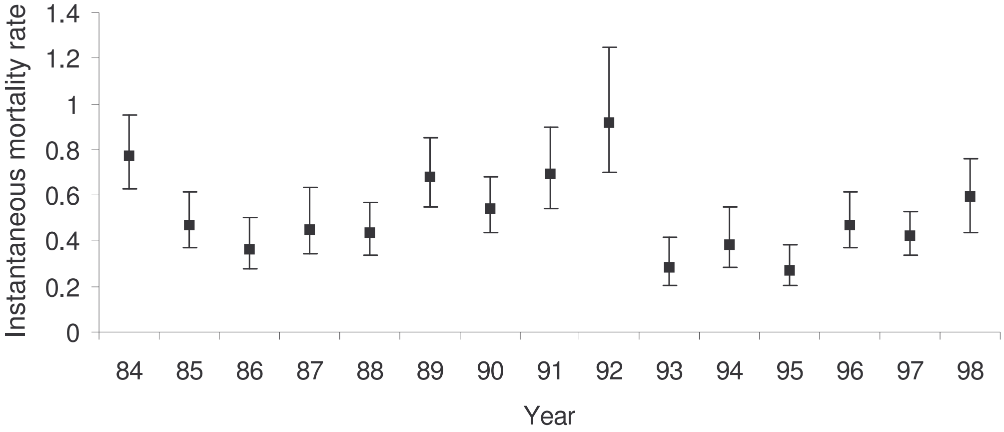
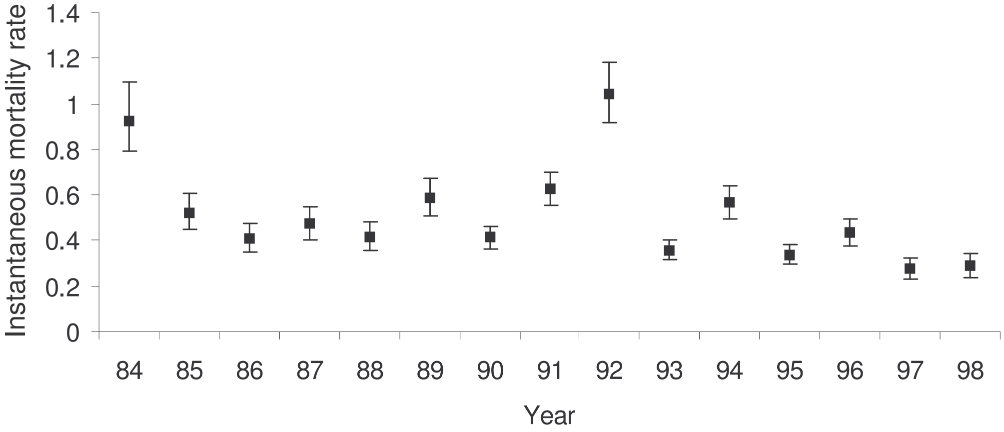


Figure 15: Predicted average sea lamprey-induced mortality rates on age 5-10 lake trout for each region of Lake Huron from 1984-1998. The 95% Bayesian prediction interval of the marginal distribution is shown, with the median of the marginal indicated by the square.

Northern Lake Huron



Central Lake Huron



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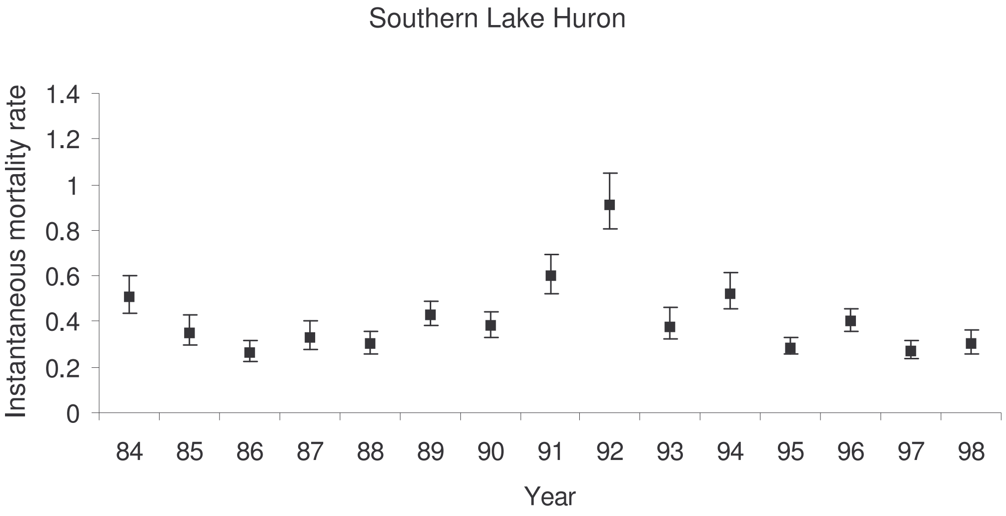


Figure 16: Predicted average total (natural, sea lamprey, commercial and recreational fishing) annual mortality on age 5-10 lake trout for each region of Lake Huron from 1984-1998.

Figure 17: Estimated effective search rate (eq. 12) for central Lake Huron as a function of lake trout length with the IMSL effective search (Greig et al. 1992) given for reference.

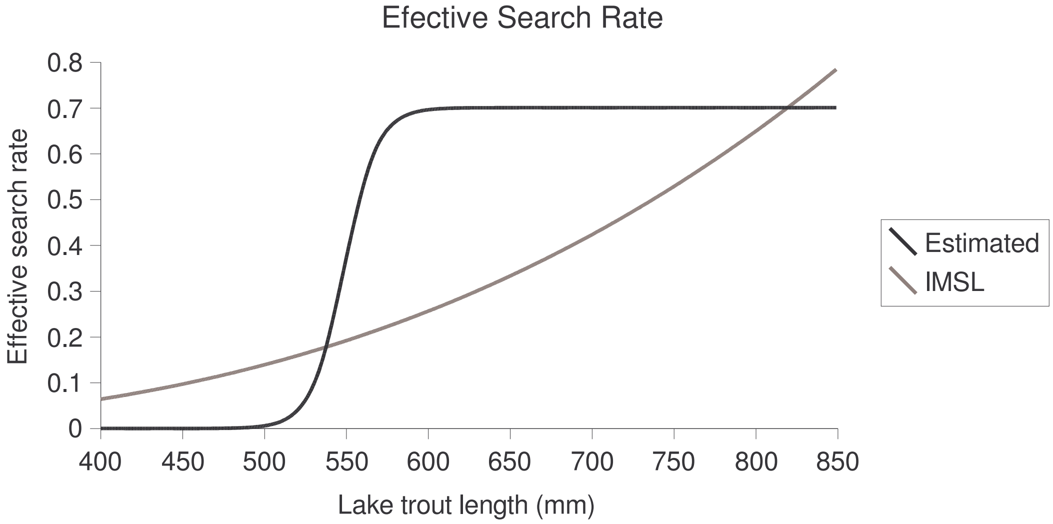
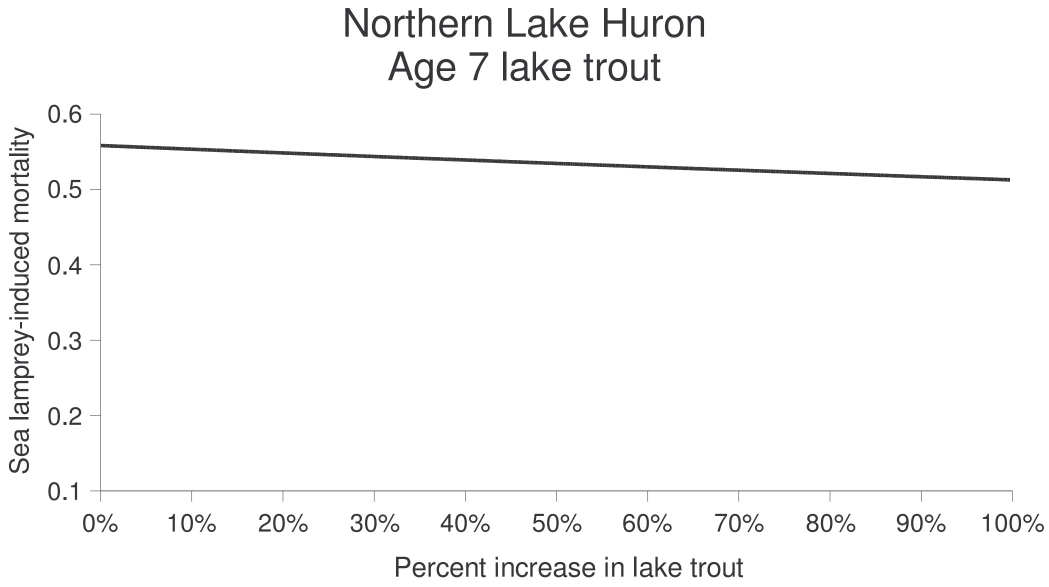


Figure 18: Sea lamprey induced-mortality rates as a function of the percent increase in lake trout population based on 1998 levels of sea lamprey, lake trout and alternative prey.


Northern Lake Huron
Age 7 lake trout

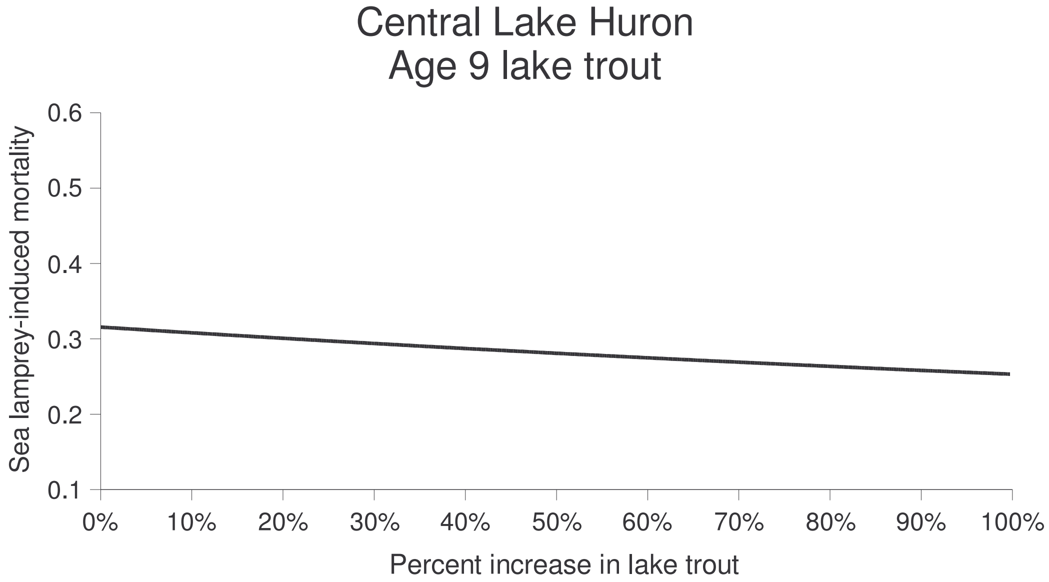
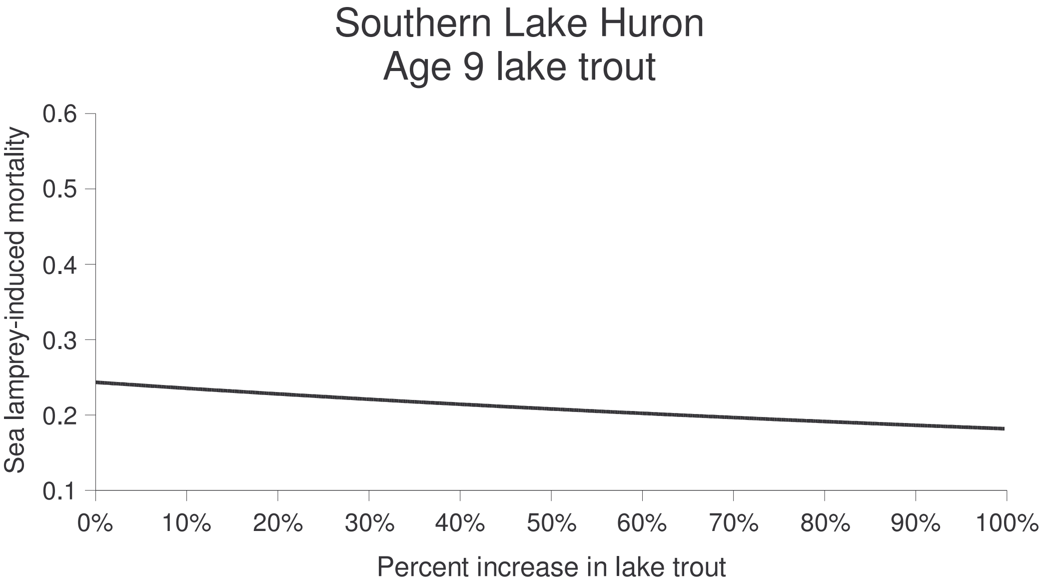

Central Lake Huron
Age 9 lake trout

Figure 18 (cont'd)



CHAPTER 3

PROJECTING THE OUTCOMES OF LAKE TROUT RESTORATION EFFORTS IN LAKE HURON: INCORPORATING A SEA LAMPREY FUNCTIONAL RESPONSE AND ACCOUNTING FOR UNCERTAINTY

Introduction

Lake trout (*Salvelinus namaycush*) historically were an important top level predator of the Lake Huron fish community, and supported the largest commercial fishery in the Great Lakes. Following their collapse in the 1950s, lake trout were considered commercially extinct in Lake Huron (Eshenroder et al. 1995) and lake trout restoration became a goal in Lake Huron and throughout the Great Lakes. Possible explanations for the rapid decline of lake trout include overfishing (Eshenroder et al. 1995), predation from the nonindigenous sea lamprey (*Petromyzon marinus*) (Coble et al. 1990), or a combination of both factors (Hansen 1999). Sea lamprey colonized the upper Great Lakes by 1947 after migrating through the St. Lawrence River and the Welland Canal. Following the collapse of lake trout populations, a large scale program of stocking hatchery-reared lake trout was undertaken, combined with programs to control sea lamprey, in an effort to restore self-sustaining populations.

Although the sea lamprey control program began in 1958, control efforts are still ongoing and sea lamprey predation continues to be a hindrance to successful lake rehabilitation in Lake Huron (Morse et al. 2003, Bence et al. 2003). Lake trout populations in the main basin of Lake Huron are subject to predation by “parasitic” juvenile stage sea lamprey that spend up to 18 months feeding before maturing and returning to Great Lakes' tributaries to spawn. Juvenile sea lamprey prey on larger fishes by attaching to and gnawing through their skin to feed on body fluids. Such attacks frequently result in the death of the prey. Efforts to control sea lamprey by the U.S. Fish and Wildlife Service and the Department of Fisheries and Oceans, Canada are coordinated by the Great Lakes Fishery Commission. Control options have concentrated on preventing larval sea lamprey, called ammocetes, from transforming to their parasitic phase. In some tributaries, chemicals are used to destroy the ammocetes, and in the St. Marys River sterile males are released to reduce the percentage of eggs that are fertilized (see Morse et al. 2003 for details). Other methods of control include placing barriers and traps on tributaries in order to prevent adult sea lamprey from spawning in the tributaries. These control programs have been successful in some of the Great Lakes. Lake Superior currently has self-sustaining lake trout populations, and reduced sea lamprey abundance has increased the number of larger and older stocked lake trout in Lake Huron.

Cost-effective implementation of sea lamprey control requires an ability to predict future levels of sea lamprey-induced mortality resulting from different sea lamprey and lake trout management approaches. In order to forecast sea lamprey-induced mortality rates, a sea lamprey functional response model is needed to predict the number of attacks on lake trout (and other prey fish species). An important aspect of sea lamprey attack behavior that is likely to be important to predictions from a functional response is the time it takes for the attack to occur. Since the duration of a sea lamprey attack is on the order of days, and not instantaneous, there is a maximum number of attacks that occur during a feeding season. If the duration of an attack is ignored the resulting Type I functional response predicts that the number of attacks per sea lamprey will be directly proportional to host density (Holling 1966). As a consequence, attack rates per host and resulting per capita sea lamprey-induced mortality will be independent of host density. To incorporate the duration of an attack, a Type II functional response is needed (Holling 1966; chapter two). With this type of response the number of attacks per host and the associated per capita sea lamprey-induced mortality will decrease as sea lamprey become saturated with possible hosts and the maximum number of attacks is approached. While this type of functional response model was parameterized for the Integrated Management of Sea Lamprey (IMSL) (Greig et al. 1992) program, it was based on assumed mechanistic relationships and limited empirical information. Recent work (see chapter two) has resulted in a multi-species functional response model parameterized within the framework of a statistical catch-at-age model. This work provides information on the probable values of parameters for a lake trout population dynamics model including those controlling the sea lamprey functional response.

It is now clear that management strategies based on models using point estimates of parameters, acting as though these are known, can often lead to poor results (Smith et al. 1993, Megrey et al. 1994). One method for addressing this concern is by evaluating management responses using models based upon Bayesian stock assessments. In this context, model parameters are reported as posterior distributions (Gelman et al. 2004), and quantities of interest to managers that are functions of the model parameters can be expressed as marginal probability distributions. These probability distributions allow managers to examine the wide range of possible outcomes under different management scenarios and determine the probability of meeting management goals (McAllister and Kirkwood 1998a and 1998b).

Here we evaluate alternative management scenarios with regard to lake trout stocking and sea lamprey control taking into account both parameter uncertainty and stochastic temporal variation in system dynamics. The projection model uses the results from chapter two in a Bayesian stock assessment context. The stock assessment model fit in chapter two did not make explicit assumptions regarding how sea lamprey size-selection would vary in response to lake trout density. However, the differences among lake regions suggested an intriguing relationship, whereby sea lamprey prey selection shifted toward larger lake trout when large lake trout were more abundant. Likewise, although the assessment model did not make explicit assumptions about stochastic variation in fishing mortality or effective numbers of fish stocked (recruitment), the results can be used to determine likely levels of future variability. The full model presented here for evaluating management scenarios incorporated assumptions about dynamic shifts in prey size selection and stochastic variations in fishing mortality and stocking. We contrast the predictions of this full model to models without dynamic prey size selection and stochastic temporal variability to evaluate the importance of these features. The management scenarios simulated here (see *Methods* below) were chosen to represent possible levels of sea lamprey control in Lake Huron as well as changes in lake stocking regimes in response to successful sea lamprey control and increased lake trout survival rates.

While self-sustaining populations of lake trout have not been observed in Lake Huron outside of an isolated embayment of Georgian Bay (Reid et al. 2001), such lakewide stocks are the goal of the rehabilitation program. A variety of milestones have been developed for lake trout rehabilitation efforts, a number of which are centered on measures thought to be related to the abundance of mature fish, or factors that would promote increased spawning stocks (Ebener 1998). Of particular interest here is the recognition that sea lamprey-induced mortality rates must be reduced in order to rehabilitate self-sustaining lake trout populations (Ebener 1998). Tied to this is the objective to maintain total annual mortality for lake trout in rehabilitation zones in Lake Huron below 45% (DesJardine et al. 1995). We evaluate the consequences of different scenarios both in terms of lake trout abundance and in terms of mortality caused by sea lamprey.

Methods

Overview

Our simulations were based on the population model and the parameters described in chapter two. For a given set of parameters a population model was used to forecast population dynamics over a fifty-year time-horizon. As described below, parameter values were drawn from a multivariate posterior probability distribution derived using Markov Chain Monte Carlo methods. By running simulations over the distribution of parameters we obtained a distribution of outcomes that reflects the likelihood of different parameter values.

Forecasts from three different models are presented. Models I and II are preliminary versions, and their results are contrasted with each other and our third “final” model as a means for evaluating the influence of the differences among the models. Models I and II are deterministic, in the sense that once a set of parameter values is selected the dynamics are determined. Model I is based most directly on the results of the population model created in chapter two. Of particular importance is that the relationship between sea lamprey attack rate and host size is assumed to be fixed for each area based on the relationships estimated for each area in chapter two. Numbers of age-1 recruits, sea lamprey abundance, and abundance of alternative (other than lake trout) prey are assumed constant over time, and are based on average values observed for the 1984-1998 period used to parameterize the model in chapter two. Model II differed from model I only in that the assumed relationship between sea lamprey attack rate and prey size was modeled as a dynamic function of large lake trout density. Model III retains the dynamic prey size selection of model II, but allows fishing mortality rates, sea lamprey abundance, and alternative prey abundance to vary stochastically over time, based on observed variation during the 1984-1998 period.

Population model

The population model used in the simulations describes numbers of age *a* lake trout at the start of year *y* and region *r* by

$$N_{a+1,y+1,r} = N_{a,y,r} S_{a,y,r}$$

where $S_{a,y,r}$ is the survival for age *a* lake trout over year *y* in region *r*. This survival is modeled (following chapter two) as a function of natural mortality, fishing mortality and sea lamprey induced mortality. For each region, the model recognizes lake trout ages 1-14 and a plus group including ages 15 and above. In order to approximate mortality events in the lake, the year is separated into two periods in which natural (not including sea lamprey-induced mortality) and fishing morality occur, separated by a fall pulse of sea lamprey-induced mortality.

The lake trout population abundance nine months from the start of the year is modeled as:

$$N^{9}_{a,y,r} = N_{a,y,r} e^{-(M_{a,y,r}+F^{C}_{a,y,r}+F^{R}_{a,y,r})\frac{9}{12}}$$

where $M_{a,y,r}$ is the natural mortality rate for age *a* lake trout in year *y* and region *r*, $F^{C}_{a,y,r}$ is commercial fishing mortality rate, and $F^{R}_{a,y,r}$ is the recreational fishing mortality rate. Sea lamprey-induced mortality is then applied and the post sea lamprey mortality population is given by:

$$N^{9*}_{a,y,r} = N^{9}_{a,y,r} e^{-M^{L}_{a,y,r}} .$$

The number of lake trout at the end of year *y* (which equals the number at the start of the next year incremented by one year in age) is then determined by applying the last three months of natural and fishing mortality:

$$N_{a+1,y+1,r} = N^{9*}_{a,y,r} e^{-(M_{a,y,r}+F^{C}_{a,y,r}+F^{R}_{a,y,r})\frac{3}{12}} .$$

Natural mortality for age 2+ lake trout is based upon a single parameter estimated during the model fitting process for each region of the lake, while mortality on age 1 lake trout was assumed to be 0.81 (see chapter two). Both commercial and recreational fishing mortality are determined as the product of an age-specific selectivity component and a year specific fishery intensity component:

$$F^{i}_{a,y,r} = S^{i}_{a,r} f^{i}_{y,r}$$

where $S^{i}_{a,r}$ is the selectivity for either the commercial (*i*=*C*) or recreational fishery (*i*=*R*) on age *a* in region *r* and $f^{i}_{y,r}$ is the commercial or recreational fishing intensity in year *y* in region *r*. Commercial selectivity is determined by a four-parameter double logistic model

$$S^{C}_{a,r} = \frac{1}{1+e^{-\omega_{1,r}\left(a+\omega_{2,r}\right)}}\left(1-\frac{1}{1+e^{-\omega_{3,r}\left(a+\omega_{4,r}\right)}}\right)$$

where $\omega_{2,r}$ and $\omega_{4,r}$ are the inflection points of the double logistic for each region *r*, and $\omega_{1,r}$ and $\omega_{3,r}$ and the slopes at the respective inflection points. Selectivity for the recreational fishery was assumed to follow the logistic curve:

$$S^{R}_{a,r} = \frac{1}{1+e^{-\alpha_{R,r}\left(a-\beta_{R,r}\right)}}$$

where $\beta_{R,r}$ is the inflection point of the logistic curve and $\alpha_{R,r}$ describes the slope at the inflection point. The parameterization of the curve starts with a selectivity of zero for age 1 fish and asymptotes to one for older fish. In the simulations fishing intensity was either set to a region specific constant for both fisheries or allowed to vary over time (see below).

Sea lamprey-induced mortality is determined by

$$M_{a,y,r}^{L} = A_{a,y,r}\left(1 - P_s\left(a\right)\right)$$

where $A_{a,y,r}$ was the number of attacks by sea lamprey on age *a* lake trout over the feeding season in year *y* and region *r*, and $P_s\left(a\right)$ is the probability of an age *a* lake trout surviving a sea lamprey attack (Eshenroder and Koonce 1984, Bence et al. 2003). The probability of surviving a sea lamprey attack was a function of lake trout weight based on laboratory work by Swink (2003), and this same function applied to all three lake regions:

$$P_s\left(a\right) = \frac{1}{1 + e^{1.462 - .00041 w\left(a\right)}}$$

where $w\left(a\right)$ is the lake trout weight in grams at age *a*. Weight at age differed among the three regions and thus the probability of surviving a sea lamprey attack varied at the same age among the lake regions. For each region, the weight at age was based on data collected during spring lake trout surveys and calculated following procedures described by Bence and Ebener (2002).

The number of sea lamprey attacks ($A_{a,y,r}$) per lake trout for a given age, year, and region is determined by a multi-species type II functional response model (Holling

1959). As reviewed in Bence et al. (2003), the number of attacks per host (A_{host}) is predicted by

$$A_{host} = \frac{S\lambda_{host} L_{y,r}}{1 + \sum_{i}^{allhosts} H\lambda_i D_{i,y,r}}$$

where S is the length of the feeding season (in years), λ_{host} is the effective search rate of sea lamprey for the host species of interest, $L_{y,r}$ is the sea lamprey density for a given year and region, H is the handling time (in years), and $D_{i,y,r}$ is the host density in the year and region of interest. Host density is determined by dividing the host abundance ($N_{host,y,r}$) by the area of lake trout habitat in each region (Table 12). The catch-at-age model treats each age of lake trout as a separate host type, and in order to incorporate the affects of alternative host species, estimates of Chinook salmon (*Oncorhynchus tshawytscha*) and lake whitefish (*Coregonus clupeaformis*) density were included along with each age of lake trout in the denominator of the functional response. Lake trout population estimates at nine months, prior to the pulse of sea lamprey-induced mortality, were used in these calculations. Sea lamprey, Chinook salmon, and lake whitefish populations used in the deterministic population model are averages (over years) calculated from data used to estimate model parameters (see chapter two).

Simulations

Simulations begin with initial numbers at age for the stocks representing each region of the main basin of Lake Huron and run for 50 years. These initial abundances were taken from the results of chapter two, using the values estimated for 1998. These initial age compositions had little effect on the age composition at the end of the 50 year simulations. Projections after the first year require a value for the number of lake trout that recruited at age-1. For the two preliminary models, recruitment at age one was based on the 1984-1998 average of “yearling equivalents” stocked multiplied by a post-stocking survivability of 0.968, the mean post-stocking survivability estimated in chapter two. The stochastic model allowed for varying recruitment by sampling from normal distributions centered around the 1984-1998 averages (see Table 13). These are essentially empirical estimates of “effective stocking” of yearling lake trout, taking into account the numbers of yearling equivalents stocked, an assumed probability fish stocked in one region will move to another immediately after stocking and the level of mortality that occurred immediately after stocking (see chapter two).

The parameters used in each simulation represent one vector of parameter values from the Markov Chain Monte Carlo (MCMC) (Brooks 1998). The MCMC analysis results in a joint posterior distribution for all the estimated parameters in the form of a long, multivariate Markov Chain (100,000 saved vectors of parameters for this study), with each member of the chain representing a realization from the joint posterior. By running the lake trout population simulation using parameter estimates from each realization of the posterior, the distribution of simulation results reflects the variation in the probability distribution for the parameters.

The MCMC chain was created using AdModel builder. This software starts chains at parameter values that produce the maximum posterior density, and takes multivariate normal steps based on the asymptotic variance-covariance matrix (Otter Research 2000). After an initial burn-in was conducted, every subsequent 2,000th realization was saved until a chain of length 100,000 was created. Posterior distributions of all estimated parameters were created, as well as marginal distributions of functions of estimated parameters that represent quantities of interest to managers. Key model quantities of interest calculated from the MCMC analysis include the number of age 2+ lake trout, the number of age 7+ trout, and the sea lamprey-induced mortality rates on age 5, 8, and 9 lake trout.

To assure that the posterior distribution was a proper one, all parameters were restricted between upper and lower bounds during estimation. Unless otherwise noted in chapter two, these bounds effectively served as weakly informative flat prior distributions between the bounds. All bounds were set to well above and below what was viewed as possible values for the parameters. Convergence of the MCMC to the posterior distributions was determined by visual inspection of trace plots and by calculating the effective sample size. Effective sample size was determined by the methods outlined in Thiebaux and Zwiers (1984), estimating the autocorrelation function for lags up to 150 steps to insure the autocorrelation function converged to zero.

Comparisons among models

To compare and contrast forecasts from the three models we considered three scenarios. The first assumed sea lamprey abundance equal to that of the average of the 1984-1998 period (scenario A). The other two scenarios assumed that average sea lamprey abundance was lowered from this baseline by either 50% (scenario B) or 90% (scenario C). For comparative purposes we also used model I to make projections based on point estimates for the model’s parameters. These point estimates were the joint posterior modal (JPM) estimates (Tempelman 1998) from chapter two.

For models I and II, stocking rates were kept constant for all 50 years (see Table 13), as were sea lamprey, lake whitefish, and Chinook salmon densities (see Table 14). In chapter two, we assumed that attack rates by sea lamprey would increase with host size following a logistic function, and based on our analysis of wounding rates (chapter one), we allowed the inflection point of this function to vary among regions of Lake Huron. The estimated inflection points were lower in northern Lake Huron than in southern Lake Huron. A possible explanation for this phenomenon is that there are very few large lake trout in northern Lake Huron, and sea lamprey responded by increasing their attack rates on smaller fish. This explanation argues that the observed patterns in wounding reflects behavioral responses by sea lamprey to lake trout population characteristics, and that the absence of similar changes in wounding patterns over time merely reflects a lack of contrast over the period used to parameterize the model. Therefore, in model II we allowed the inflection point to vary in response to changes in the age-composition of the lake trout population in a region. This was done because large changes in lake trout populations did occur in some of our simulations. Our approach was to make the inflection point depend upon the density of lake trout longer than 700 mm in the previous year. The form of this function is

$$\hat{\beta}_{r,y+1,i} = 0.0052\left(d_{r,y,i} - d_{r,i}\right) + \beta_{r,i}$$

where $\hat{\beta}_{r,y+1,i}$ is the inflection point that applied to region *r* during year *y+1* for simulation *i*, $d_{r,y,i}$ is the density of lake trout greater than 700 mm in length in year *y* and region *r* for simulation *i*, $d_{r,i}$ is the density based on the initial age composition at the start of the simulation for region r, and $\beta_{r,i}$ is the initial value of the inflection point at the start of the simulation for region *r*. Both the $\beta_{r,i}$ and $d_{r,i}$ are determined directly by the parameters drawn from the MCMC chain for a particular simulation. The maximum value of the $\beta_{r,y+1,i}$ was restricted to 700 mm, to ensure that sea lamprey continue to attack lake trout greater than that length, regardless of lake trout densities. This formulation ensures that the initial inflection point is consistent with the both the initial age composition of large lake trout and the dynamic equation for updating this parameter. The proportionality constant between the inflection point and density (0.052) was determined by regressing the maximum likelihood estimate for the inflection point for each region versus the maximum likelihood estimate of density from 1996-1998 (i.e., nine data points used in this regression).

Model III allowed for stochastic temporal variation in fishing mortality, sea lamprey abundance, lake trout stocking, and in the densities of alternative prey species. In this model, quantities that had been assumed constant were drawn anew each year from normal distributions, with means and variances based on inputs and estimates for the 1984-1998 period (see chapter two). The equivalent number of yearlings stocked for each region, sea lamprey populations for northern and central/southern Lake Huron, lake wide Chinook salmon populations, and lake whitefish population for each region were randomly generated for each year of the simulation (see Table 15). Additionally, commercial and recreational fishing intensities were randomly generated for each year in the simulation (see Table 15). The mean and standard deviations were determined from the estimated values for 1984-1998 in each region of Lake Huron.

Scenarios varying lake trout stocking

As described above, we considered scenarios with different levels of sea lamprey abundance for all three models. In addition to these scenarios, we used our final model III to explore how changes in lake trout recruitment (stocking) or densities of alternative prey influenced forecasts. To examine the influence of lake trout stocking we considered a 50% decrease, a 100% increase and a 200% increase in average stocking under conditions of a 90% reduction in sea lamprey abundance and a 50% reduction in sea lamprey abundance (see Table 16). All eight scenarios were repeated with commercial fishing effort in northern Lake Huron reduced by 56%, corresponding to levels recommended as necessary for reaching target mortality rates in that region (Bence and Ebener 2002).

Sea lamprey saturation in northern Lake Huron

Our use of a multi-species type II functional response model implies that the number of attacks per sea lamprey will be a decelerating function of prey density, with saturation effects eventually limiting attacks to an upper asymptote at high prey densities. At relatively low prey densities, saturation effects are minimal and attacks will increase nearly in proportion with prey density. When saturation effects are evident, sea lamprey-induced mortality rates will decrease with increases in lake trout density, even without a decrease in sea lamprey abundance. Lake trout densities, particularly for older fish, had been extremely low in northern Lake Huron and other scenarios did not suggest substantial effects of lake trout density on sea lamprey-induced mortality for this region. We explored the potential for saturation further in northern Lake Huron using model III. We did this by varying lake trout stocking from baseline levels through a 700% increase, with commercial fishing effort set to zero. This set of scenarios was done using the baseline sea lamprey abundances (corresponding to Scenario A) and a 90% reduction in sea lamprey abundance (corresponding to Scenario C) Results were summarized by the marginal distribution for sea lamprey induced-mortality on age 9 lake trout.

Lake trout damage goals

One possible way to assess the success of the eight simulated management scenarios is by examining the probability that the scenario reduces sea lamprey-induced mortality on large lake trout below a target level. The Great Lakes Fishery Commission, based on existing Fish Community Objectives for the Great Lakes, has proposed a goal of 5 marks per 100 fish as a target for sea lamprey abundance (Mark Ebener, personal communication). This level of marking corresponds to a mortality rate of approximately 0.05 on large lake trout longer than 700 mm, referred hereafter as large lake trout. Using model III for each management scenario, the marginal distribution was used to determine the probability that sea lamprey-induced mortality rates would be less than 0.10 and 0.05 on large lake trout.

Marginal distributions for parameters of interest

For simulations using models I and II, the marginal distribution of the number of age 2+ and 7+ lake trout corresponds to the stable age structure of the population after 50 years. Sea lamprey-induced mortality marginal distributions were determined for age 5 lake trout and for the first age class of lake trout larger than 700 mm. For northern and central Lake Huron, age 9 lake trout were considered large, while age 8 lake trout were reported for southern Lake Huron. For model III, the same marginal distributions are based on the average of the quantities of interest over the last five years of the simulation.

For each marginal distribution presented, the 95% Bayesian prediction interval is given, as well as the median.

Results

Comparisons among models

The greatest number of age 2+ (Figure 19) and age 7+ (Figure 21) lake trout under model I are in southern Lake Huron. Lake trout densities however, were highest in central Lake Huron (Figures 20 and 22). Commercial fishing mortality rates are much higher in northern Lake Huron (see chapter two), contributing to lower densities of older lake trout in the north. Densities of age 2+ lake trout in southern Lake Huron were lower than in the central region because lower stocking rates were assumed for the simulations. The number of lake trout yearlings recruiting per square km of lake trout habitat in southern Lake Huron is approximately half of the levels recruiting in the rest of Lake Huron (Table 13). Lake trout population levels increased when sea lamprey population levels were reduced (scenarios B and C). Under scenario C, the number of age 7+ lake trout in southern Lake Huron increased 117% (Figure 21). Similar results can be seen in northern (571% increase) and central (711% increase) Lake Huron. Increases in the densities of age 2+ lake trout (Figure 20) were not as pronounced, as sea lamprey rarely feed on the smaller lake trout that represent the majority of age 2+ lake trout. Sea lamprey-induced morality rates on age 5 lake trout (Figure 23) and large lake trout (Figure 24) decreased sharply in all regions with lake wide decreases in sea lamprey. Averaged across the lake, a 90% reduction in sea lamprey reduces sea lamprey-induced mortality 91% on large lake trout under model I.

Trends in the lake trout populations and sea lamprey-induced mortality rates for simulations based on the JPM estimates are similar to the results based on simulations using the MCMC results. The width of the 95% Bayesian prediction interval is an indication of the level of uncertainty that is unaccounted when only the JPM estimates are used to simulate lake trout populations. The point estimates based on simulations using the JPM estimates typically fell near the center of the 95% Bayesian prediction interval for model I (Figures 19-24).

For Model II, which allows the relationship between attack rate and prey size to respond to the density of large lake trout, the effects of reducing sea lamprey are similar to those under Model I, for both numbers (Figures 25 and 27) and density (Figures 26 and 28). There were important differences between model II and model I predictions of sea lamprey-induced mortality of age 5 lake trout (Figure 29). In central Lake Huron, for baseline (scenario A) sea lamprey abundance, the median sea lamprey-induced mortality was 64% higher under model II compared to model I. In this region, the density of fish larger than 700 mm (after 50 years) was lower than that estimated by the catch-at-age model for 1996-1998. This causes the inflection point of the effective search rate to shift towards smaller fish in model II, increasing the mortality rate on younger lake trout. The opposite effect can be seen in southern Lake Huron under scenario C. The increase in the density of large lake trout causes the inflection point of the effective search rate to increase for model II. The shift in the inflection point results in lower sea lamprey-induced mortality rates on age 5 lake trout (Figure 29) and slightly higher mortality rates on large lake trout (Figure 30). The same effect is observed in central Lake Huron under scenarios B and C. In contrast, in northern Lake Huron the density of large lake trout does not increase enough to lower mortality rates on age 5 lake trout noticeably.

The effects of the stochastic components of Model III, especially the variation in year to year stocking, are apparent in Figures 7-12. For all three regions, the number of age 2+ lake trout was greater under model III (Figures 25 and 26) than under model II, and the width of the 95% Bayesian prediction intervals was greater for model III. In northern Lake Huron, the increase in age 2+ lake trout abundance does not lead to a equivalent increase in age 7+ lake trout abundance (Figures 27 and 28), as high commercial fishing and sea lamprey-induced mortality rates reduce older lake trout populations to model II levels. For central and southern Lake Huron, which have limited commercial fishing and lower sea lamprey densities, the increase in age 2+ lake trout is accompanied by an increase in the predicted abundance of age 7+ lake trout. In southern Lake Huron, the increase in the density of larger lake trout is sufficient to cause sea lamprey-induced mortality on age 5 lake trout to approach zero under management scenarios assuming a 50% or greater decrease in sea lamprey density (scenarios B and C), with the median number of age 7+ lake trout being 230% greater for model III than model II under a 50% reduction in sea lamprey density.

Scenarios varying lake trout stocking

When various management scenarios combining different levels of sea lamprey control and lake trout stocking strategies are examined, the effects of reducing lamprey densities are apparent. The number and density of age 2+ lake trout (Figures 31 and 32) depends largely on the stocking scenario. Scenarios with the largest increase in stocking (F and H) produce the largest number of age 2+ lake trout, regardless of the level of sea lamprey population control. This result is not surprising since younger fish make up the bulk of total abundance and they suffer very low sea lamprey mortality under all conditions. Changes in age 7+ lake trout numbers are influenced by both the level of sea lamprey control and stocking regime (Figures 33 and 34). In northern Lake Huron, a 90% reduction in sea lamprey combined with a 200% increase in stocking (scenario F) results in a 1940% increase in the median number of age 7+ lake trout over scenario A (Figure 33). Similar results are demonstrated in central (2622% increase) and southern (3442% increase) Lake Huron. Densities of age 7+ lake trout are still highest in the central region, however, and the absolute gains in the north seem negligible by comparison (Figure 34). Scenario D demonstrates that a 50% decrease in stocking offsets the gains of reducing sea lamprey from 50% to 90% of current values in all regions of Lake Huron. In southern Lake Huron, the difference between a 50% reduction in sea lamprey (scenarios G and H) and a 90% reduction (scenarios E and F) are minimal in terms of the number of age 7+ lake trout. This reflects low sea lamprey induced-mortality rates in southern Lake Huron (Figures 35 and 36).

Sea lamprey-induced mortality on age 5 lake trout approaches zero in southern Lake Huron for all scenarios involving a 50% or greater reduction in sea lamprey density (scenarios B-H) (Figure 35). In these cases, the density of older lake trout became large enough to shift the inflection point of the effective search rate to its maximum value of 700 mm. In northern Lake Huron, sea lamprey-induced mortality rates for age 5 lake trout did decline with decreases in density of sea lamprey. In this case, however, the change was approximately proportional to the density of sea lamprey, reflecting a direct predator density effect rather than a change in size-specific attack rates. In central and southern Lake Huron, when lake trout stocking is increased from current levels to 200% of current levels, median sea lamprey-induced mortality on older lake trout decreases

(Figure 36), when comparing the same scenarios with the same sea lamprey densities (Scenarios B,G, and H for a 50% reduction in sea lamprey, Scenarios C,E, and F for a 90% reduction). This indicates a saturation effect for these regions. In the northern region, sea lamprey are not saturated under these scenarios, and median sea lamprey-induced mortality is not appreciably altered over the range of lake trout stocking rates considered here.

When commercial fishing effort in the north is reduced 56%, the median number of age 2+ lake trout increases, on average, 15% across all eight management scenarios (Figures 37 and 38), while age 7+ lake trout median abundance increases 335% on average (Figures 39 and 40). Somewhat surprisingly, under these commercial fishing conditions, median sea lamprey-induced mortality rates on both age 5 and on older (age 9) lake trout for each scenario are higher than those forecast under historical commercial fishing effort (compare Figures 41 and 42 with Figures 35 and 36). This increase in mortality rates as the number of lake trout increases reflects a shift in the inflection point for the effective search rate function. As densities of large lake trout increased from very low abundances, the effective search rate on small lake trout (ages 4 and younger) decreased and these attacks were redirected toward age-5 and older lake trout. Given the low densities of hosts, saturation effects did not counterbalance the change in effective search rates. No reduction in sea lamprey-induced mortality was evident with increases in lake trout stocking for the scenarios with sea lamprey density reduced 90% (scenarios C,E, and F) and commercial fishing effort is reduced. Similar to the response to reduced commercial fishing, median sea-lamprey induced mortality rates on age 9 lake trout actually increase slightly as stocking rates increased for these scenarios. Again this reflects a shift in the inflection point of the effective search rate, with attacks being further concentrated on older lake trout.

Sea lamprey saturation in northern Lake Huron

When commercial fishing is eliminated in northern Lake Huron, and sea lamprey mortality is reduced by 90%, model III predicted a decrease in median sea lamprey-induced mortality with increases in lake trout stocking (Figure 43). In contrast, without the reduction in sea lamprey abundance, lake trout stocking had little apparent effect on median sea lamprey-induced mortality (Figure 44).

Lake trout damage goals

We do not believe that changes in sea lamprey-induced mortality rates on older lake trout are meaningful measures of success when commercial fishing mortality is sustained at historical levels seen in northern Lake Huron. Under these conditions we sometimes saw increases in sea lamprey-induced mortality as lake trout density increased. However, these shifts in mortality are occurring when the density of older lake trout are undesirably low. However, we do note that under these conditions, decreases in sea lamprey density of 90% (scenarios C-F) suggest a probability ~100% of sea lamprey-induced mortality on age 9 lake trout being below 0.10 (Table 17). Similar results are shown when commercial fishing effort is reduced 56%, as the probability of reducing sea lamprey-induced mortality on age 9 lake trout below 0.10 ranges from 85% to ~100% for the same scenarios (C-F). When the probability of reducing sea lamprey-induced mortality to below 0.05 is examined (Table 18), simulations conducted with a 56% reduction in commercial effort have a much lower probability of reaching 0.05 or below than those conducted with historical levels of commercial fishing. The counterintuitive result of apparently higher success when commercial fishing is high in northern Lake Huron is based on a sea lamprey-induced mortality rate for the very few fish that survive to these older ages. Since few old fish are present, this mortality rate has little import to the population. Under these conditions, even a decline in sea lamprey density of 90% still allows few lake trout to survive to large size. The reason sea lamprey-induced mortality rates on old lake trout are lower in the face of higher commercial fishing mortality is because attacks are shifted toward smaller lake trout.

The results for northern Lake Huron with a 56% reduction in fishing effort are more indicative of the effects of sea lamprey control under proposed reductions of commercial fishing effort (Bence and Ebener 2002), as densities of large lake trout reach levels observed in other parts of the lake (see Figure 40). These results indicate that management scenarios (C-F) with a 90% reduction in sea lamprey have a high probability of lowering sea lamprey-induced mortality rates on large lake trout to below 0.10. Under these conditions, the probability of reducing sea lamprey-induced mortality in northern Lake Huron to below 0.05 varies between 5% and 12% (Table 18). When stocking is reduced 50% (scenario D), the highest probability of achieving mortality rates below 0.05 is indicated. However, the density of older lake trout under this scenario is similar to scenarios without a 90% reductions in sea lamprey (Figure 40) and is undesirable in terms of potential spawning stock biomass. Scenarios with lower levels of sea lamprey reduction have probabilities approaching 0% for reducing sea lamprey-induced mortality rates to 0.10 or below.

When sea lamprey densities are reduced by 90% in central Lake Huron the probability of sea lamprey mortality rates being below 0.10 is ~0% with baseline and

~100% with substantial increases in stocking. Under these conditions the probability of mortality rates being below the 0.10 threshold is substantially decreased when stocking was decreased to 50% of baseline levels. With only a 50% reduction in sea lamprey density, it appears improbable that the 0.10 level can be reached even with a 200% increase in lake trout stocking. In central Lake Huron, even a 200% increase in stocking combined with a 90% reduction is sea lamprey density (scenario F) may be insufficient for reaching the more stringent sea lamprey mortality target, as the probability of reaching the 0.05 target was 12% under these conditions.

In southern Lake Huron, where sea lamprey densities are very low, a 90% reduction in sea lamprey density combined with a 200% increase in lake trout stocking produces a probability of 61% for meeting a sea lamprey-induced mortality target rate of 0.05 (Table 18). A 50% reduction in sea lamprey, under a 200% increase stocking scenario in the south, leads to a 87% probability of sea lamprey-induced mortality rates being below 0.10 for large lake trout. Thus, the southern region has the highest probability of reaching acceptable sea lamprey mortality through a combination of sea lamprey control and increased lake trout stocking.

Discussion

Effective management of lake trout in the Great Lakes requires projections of how lake trout dynamics change in response to sea lamprey control and lake trout stocking. In Lake Huron, previous models used for making these projections implicitly assumed a type I functional response, with sea lamprey-induced mortality a linear function of sea lamprey abundance, regardless of lake trout density (Sitar 1996; Sitar et al. 1999; Lupi et al. 2003; Stewart et al. 2003). Given the time sea lamprey spend feeding on a single prey item, it seems likely that they would become partially saturated at high prey densities, with sea lamprey-induced mortality rates declining as prey densities increase (see Bence et al. 2003 for a review). The extent to which this actually would occur under feasible management conditions clearly has important management implications (Walters et al. 1980; Stewart et al. 2003). The results presented in this chapter suggest that saturation would likely become a factor in Lake Huron if sea lamprey densities decline by 90% from abundances seen from the mid-1980s through the late 1990s. This is especially true in central and southern Lake Huron, as sea lamprey-induced mortality rates on lake trout decrease as lake trout stocking rates increase and sea lamprey populations are reduced 90% from 1984-1998 levels. In northern Lake Huron clear saturation effects were not evident unless lake trout stocking is substantially increased and fishing mortality was substantially decreased from the levels of the 1980s and 1990s. Overall, our results confirm the need to incorporate a sea lamprey saturation component into lake trout projection models for Lake Huron.

Previous explicit models of the sea lamprey functional response (reviewed in Bence et al. 2003) have been Type II (sensu Holling 1966). Such models assume constant effective attack rates while sea lamprey search for prey, with saturation occurring because less time is spent searching for prey (and more time handling prey) as prey density increases. To a large extent, previous applications of these models in the Great Lakes (Greig et al. 1992) set effective attack rates based on assumed mechanisms of feeding (e.g., based on values for swimming speed and reactive distances). The resulting effective attack rates were not only constant with respect to prey density, but increased at an accelerating rate with increases in prey size. Our investigation of the data suggested that attack rates would be sigmoid functions of prey length, and that the inflection point of these sigmoid functions respond to changes in the abundance of large prey (chapter two). This result is similar to a Type III functional response (Holling 1966), which is characterized by increases in prey density resulting in an increase in search activity, and is sometimes an indication that predators switch between prey types that require different search strategies (Akre and Johnson 1979; Dale et al. 1994). Here we show that tying changes in the inflection point of the sigmoid function to the density of large lake trout has important consequences (by contrasting model I and model II), with projected sea lamprey-induced mortality and lake trout densities being altered. These results need to be interpreted in light of the fact that our understanding of sea lamprey feeding behavior is very uncertain, however they clearly emphasize the need for an improved understanding of how sea lamprey feeding may be responding to prey densities.

As noted above, our functional response model, with the dynamic sigmoid attack rate, are no longer pure type II functional responses. In many cases, sea lamprey-induced mortality rates on smaller prey decreased with increases in prey densities while mortality rates on larger prey remained relatively constant, increased, or decreased. For smaller prey this represented a combination of saturation and a shifting of attacks toward larger prey (i.e., the change in the inflection point of the sigmoid function, Figure 45). For larger prey, these patterns reflected the complex relationship between shifts in the sigmoid attack function, increasing large prey density (Figure 45), and saturation (Figure 46). While the saturation effect built into the type II functional response generally produces depensatory mortality (Figure 46), our modification allowed for compensatory mortality on larger prey (Figure 45). The full dynamic consequences of our modeled functional response on self-sustaining lake trout populations is an area warranting future study.

We incorporated uncertainty of two forms into our final model. First, rather than using point estimates, we used estimated probability distributions for the model parameters. Each simulation represented a draw from the underlying distribution of model parameters. Second we allowed for stochastic temporal variability in quantities that were not dynamically modeled, such as recruitment of young lake trout, abundance of alternative prey species, and sea lamprey abundances. Our inclusion of probability distributions for the parameters allowed us to consider probabilities of different outcomes, rather than being forced to rely on point estimates. Our experiences reinforce current fisheries management ideas that managers need to know the probability that a management plan will yield the desired effect (Gavaris and Sinclair 1998). However, we found that probability distributions for forecast quantities were substantially altered when we acknowledged that some of the unmodeled “constants” actually varied over time. Ignoring this variation would produce unrealistically tight distributions of our forecasts.

We emphasize that our incorporation of both types of uncertainty did more than place a distribution around the quantity forecast by a point estimate and a deterministic model. The median or other central measures were also altered. One example of this was the increase in median sea lamprey-induced mortality rates in northern Lake Huron when temporal stochasticity was incorporated into the final model. This results from a well known phenomenon (Jensen's inequality), whereby a nonlinear function applied to an expected value produces a different value than the expected value obtained by applying the same function to each individual input. The potential for this phenomenon is noted in decision theory literature (Boyce 1992). Here we found that the effects were large enough to alter point estimates of management quantities in significant ways, underestimating the density of age 7+ lake trout for example (Figure 8).

Our results indicate that meeting a sea lamprey-induced mortality target of 0.05 in southern Lake Huron may be possible. However, in northern and central Lake Huron, reaching this target is a greater challenge. While reductions in commercial fishing (northern region) combined with increases in lake trout stocking can increase the probability, the likelihood of reaching the target sea lamprey mortality still remain low. However, a shift in the overall probability distribution toward lower sea lamprey-induced mortality rates can be achieved. In order to reduce sea lamprey-induced mortality rates, our results show that reducing sea lamprey populations has the greatest effect on the probability of reaching sea lamprey-induced mortality rate goals. Once sea lamprey populations are lowered, increasing lake trout populations, by either stocking more lake trout or reducing fishing effort, can lead to additional reductions in sea lamprey-induced mortality, if a type II functional response, like the one proposed here, is assumed. Since planned sea lamprey control and lake trout management efforts appear unlikely to meet the existing target, we believe that a cost-benefit analysis is called for (see also Stewart et al. 2003) to evaluate the ongoing management efforts.

More generally, our modeling and stochastic forecasts provide valuable insight on the probability of successfully rehabilitating lake trout in Lake Huron. We predicted probability distributions for sea lamprey induced mortality rates and lake trout stock sizes based on a population model that incorporated a parameterized functional response model. Managers could use this same model to evaluate additional management scenarios and measures of success. Following this approach it is possible to estimate the probability of meeting quantifiable management goals, and this should help guide lake trout managers toward actions more likely to facilitate lake trout rehabilitation in Lake Huron.

Table 12: Area of lake trout habitat (<40 fathoms) in square km for each region of Lake Huron (Ebener 1998).

Region	km^2
North	3,432
Central	4,575
South	15,210

Table 13: The average number of yearling equivalents recruiting in each region of Lake Huron for models I and II. This is based on the average number of yearling equivalents stocked from 1984-1998, and takes into account an assumed probability fish stocked in one region will move to another immediately after stocking (see chapter two).

Region	Yearling Equivalents
North	357,164
Central	321,635
South	594,639

Table 14: Assumed abundances (numbers of fish) assumed constant in the simulation models based on the average values estimated from 1984-1998 (see chapter two). For sea lamprey these represent the baseline values, which were adjusted by stated percentages for different scenarios.

Quantity	Region	Value
Chinook salmon	All	674048
Whitefish	North	6219133
Whitefish	Central	1034461
Whitefish	South	1284019
Sea Lamprey	North	212152
Sea Lamprey	Central/South	15320

Table 15: Means of the normal distribution used to randomly generated simulation model inputs for each year in model III. Chinook salmon, whitefish, sea lamprey and yearling equivalents are numbers as defined in Table 14. Fishing intensity represents the instantaneous fishing mortality rate on a fully selected age . The mean and coefficient of variation (CV) are based on the values estimated from 1984-1998 (see chapter two). Coefficient of variation is reported for each quantity because the CV was held constant when sea lamprey abundance and stocked yearling equivalents were changed from baseline values.

Quantity	Region	Mean	CV
Chinook salmon	All	674048	0.32
Whitefish	North	6219133	0.28
Whitefish	Central	1034461	0.53
Whitefish	South	1284019	0.20
Sea Lamprey	North	212152	0.32
Sea Lamprey	Central/South	15320	0.46
Yearling Equivalents	North	357164	0.35
Yearling Equivalents	Central	321633	0.29
Yearling Equivalents	South	594640	0.42
Commercial Fishing Intensity	North	0.63	0.32
Commercial Fishing Intensity	Central	0.03	0.24
Commercial Fishing Intensity	South	0.04	0.20
Recreational Fishing Intensity	North	0.02	0.29
Recreational Fishing Intensity	Central	0.02	0.32
Recreational Fishing Intensity	South	0.04	0.28

Table 16: Descriptions of management scenarios simulated in terms of changes in sea lamprey abundance and lake trout stocking.

Scenario	Percent Change in Lamprey	Percent Change in Lake Trout Stocking
A	0%	0%
B	-50%	0%
C	-90%	0%
D	-90%	-50%
E	-90%	100%
F	-90%	200%
G	-50%	100%
H	-50%	200%

Table 17: Probability of reducing sea lamprey-induced mortality on age 9 lake trout in northern Lake Huron below 0.10 based on marginal distribution determined under model III for each management scenario described in Table 16.

Scenario	Region			
	North Historical commercial effort	North 56% reduction in commercial effort	Central	South
A	0%	0%	0%	0%
B	0%	0%	0%	33%
C	99%	97%	76%	56%
D	99%	98%	94%	32%
E	100%	92%	93%	84%
F	99%	85%	99%	97%
G	0%	0%	0%	62%
H	0%	0%	0%	87%

Table 18: Probability of reducing sea lamprey-induced mortality on age 9 lake trout in northern Lake Huron below 0.05 based on marginal distribution determined under model III for each management scenario described in Table 16.

Scenario	Region			
	North Historical commercial effort	North 56% reduction in commercial effort	Central	South
A	0%	0%	0%	0%
B	0%	0%	0%	6%
C	26%	5%	0%	16%
D	95%	12%	0%	6%
E	32%	6%	0%	35%
F	40%	10%	12%	61%
G	0%	0%	0%	16%
H	0%	0%	0%	33%

Figure 19: Number of age 2+ lake trout in northern, central, and southern Lake Huron for model I. The 95% Bayesian prediction interval of the marginal distribution of age 2+ lake trout is shown, with the median of the marginal indicated by the square. The point estimate of age 2+ lake trout based on the joint posterior modal estimates from chapter two is indicated by the gray circle. For information on scenarios, see Table 16. Note the difference in scale between regions.

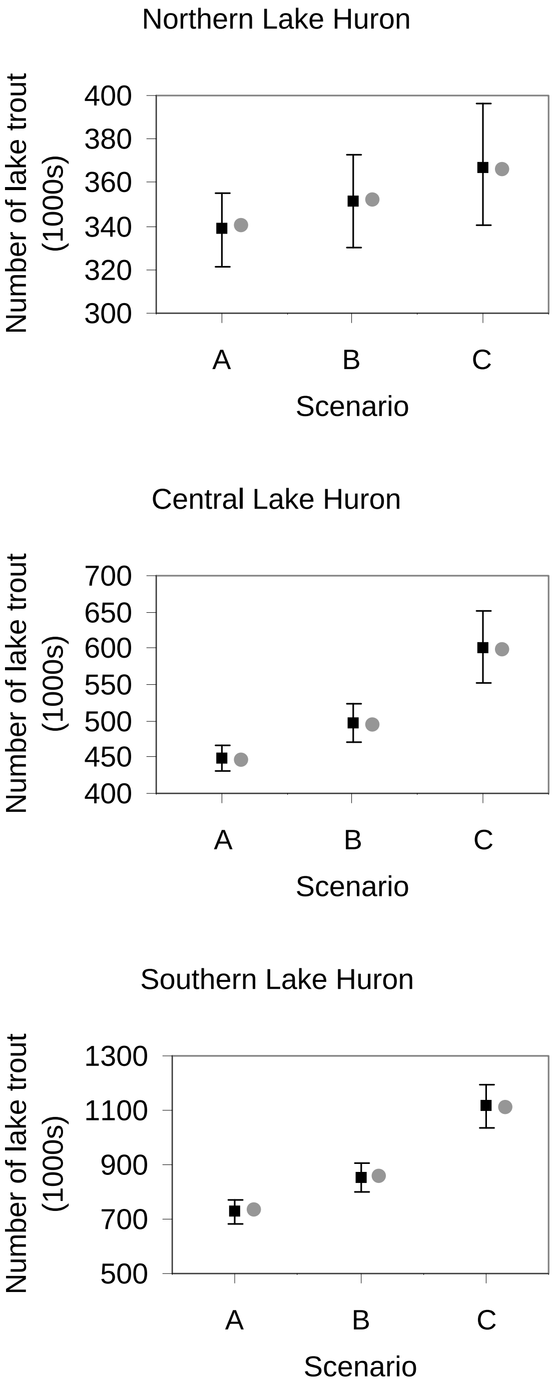


Figure 20: Density of age 2+ lake trout in northern, central, and southern Lake Huron for model I. The 95% Bayesian prediction interval of the marginal distribution for age 2+ lake trout density is shown, with the median of the marginal indicated by the square. The point estimate of the age 2+ lake trout density based on the joint posterior modal estimates from chapter two is indicated by the gray circle. For information on scenarios, see Table 16.

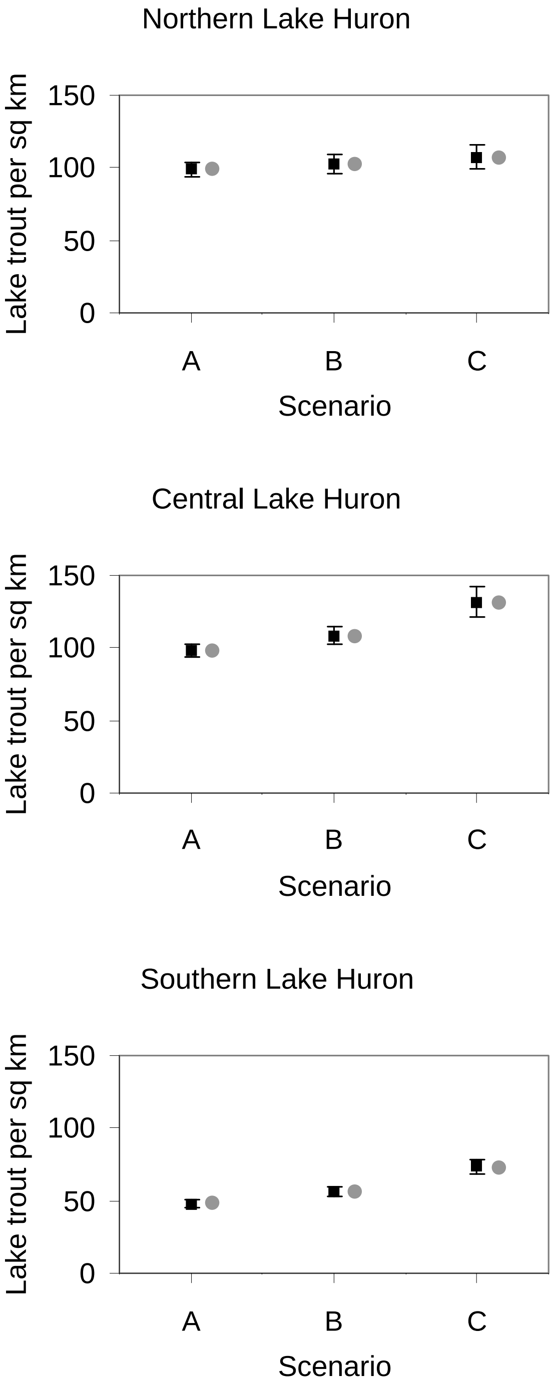
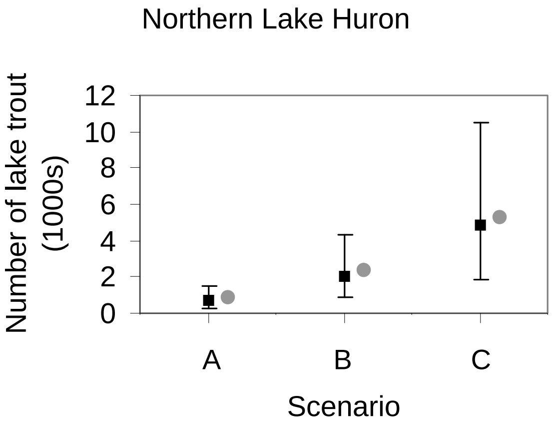
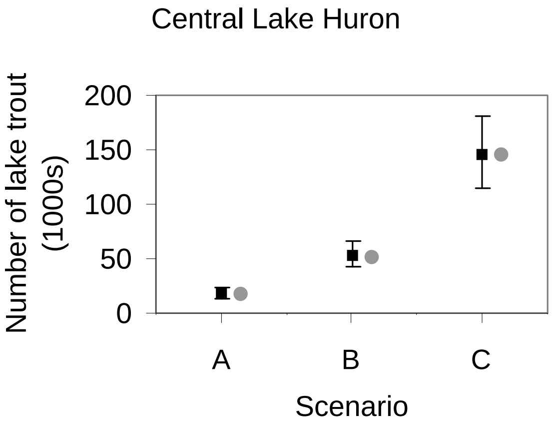


Figure 21: Number of age 7+ lake trout in northern, central, and southern Lake Huron for model I. The 95% Bayesian prediction interval of the marginal distribution of age 7+ lake trout is shown, with the median of the marginal indicated by the square. The point estimate of age 7+ lake trout based on the joint posterior modal estimates from chapter two is indicated by the gray circle. For information on scenarios, see Table 16. Note the difference in scale between regions.


Northern Lake Huron


Central Lake Huron

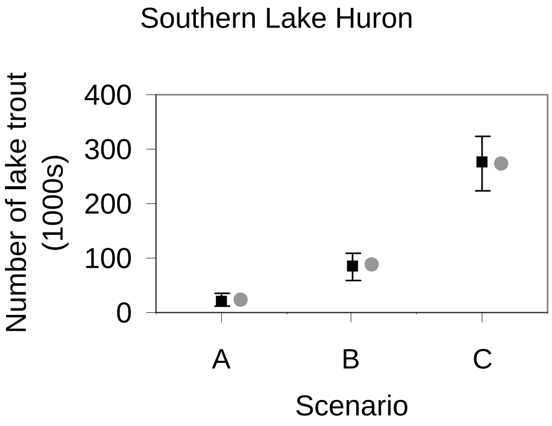
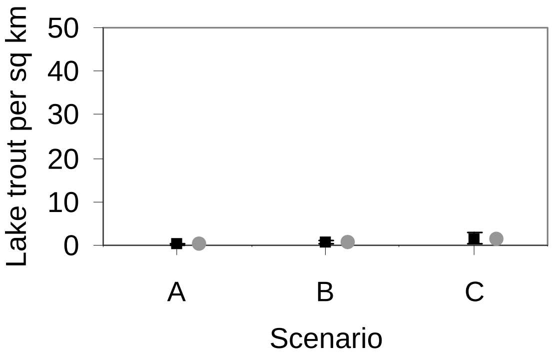
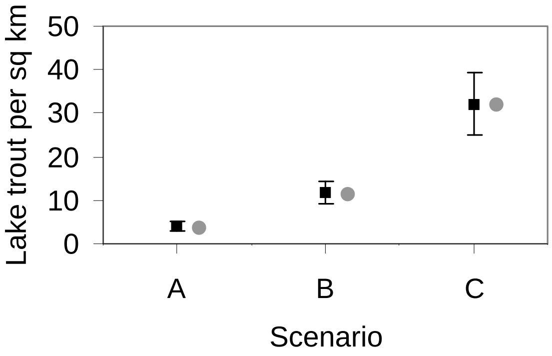

Southern Lake Huron

Figure 22: Density of age 7+ lake trout in northern, central, and southern Lake Huron for model I. The 95% Bayesian prediction interval of the marginal distribution for age 7+ lake trout density is shown, with the median of the marginal indicated by the square. The point estimate of the age 7+ lake trout density based on the joint posterior modal estimates from chapter two is indicated by the gray circle. For information on scenarios, see Table 16.

Northern Lake Huron



Central Lake Huron



Southern Lake Huron

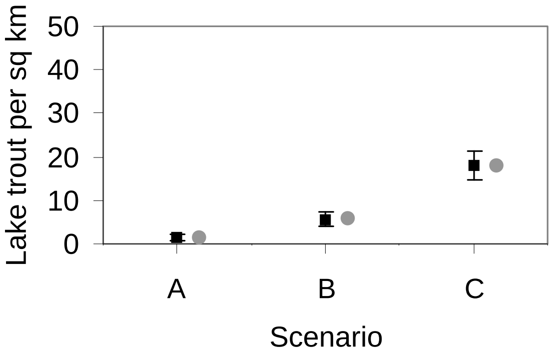


Figure 23: Sea lamprey-induced mortality on age 5 lake trout in northern, central, and southern Lake Huron for model I. The 95% Bayesian prediction interval of the marginal distribution of mortality is shown, with the median of the marginal indicated by the square. The point estimate of mortality based on the joint posterior modal estimates from chapter two is indicated by the gray circle. For information on scenarios, see Table 16. Note the difference in scale between regions.

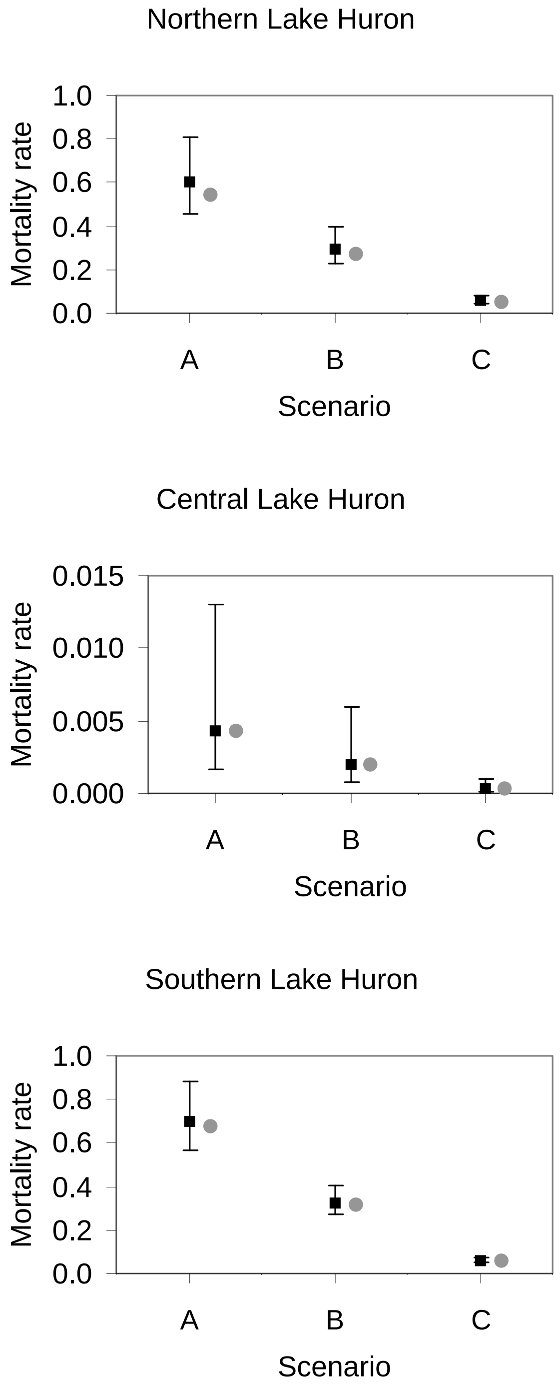
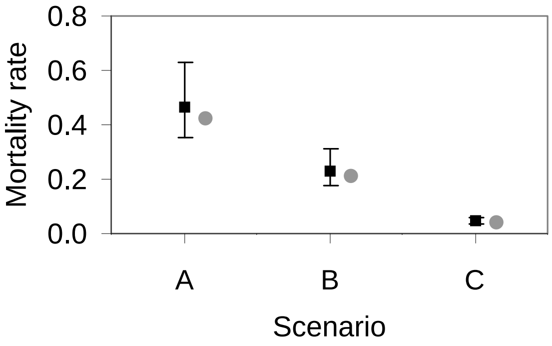
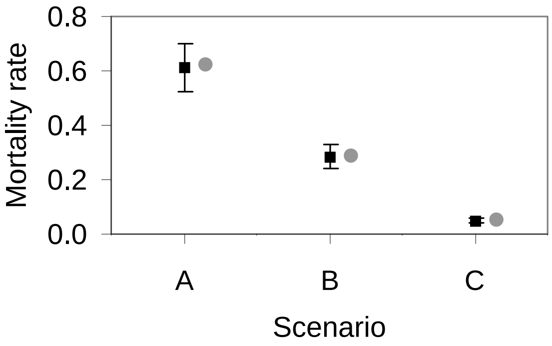


Figure 24: Sea lamprey-induced mortality on lake trout for the youngest age lake trout with mean length exceeding 700 mm in northern (age 9), central (age 9), and southern (age 8) Lake Huron for model I. The 95% Bayesian prediction interval of the marginal distribution of mortality is shown, with the median of the marginal indicated by the square. The point estimate of mortality based on the joint posterior modal estimates from chapter two is indicated by the gray circle. For information on scenarios, see Table 16. Note the difference in scale between regions.

Northern Lake Huron



Central Lake Huron



Southern Lake Huron

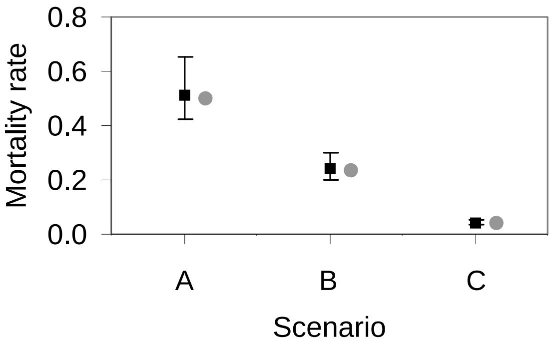
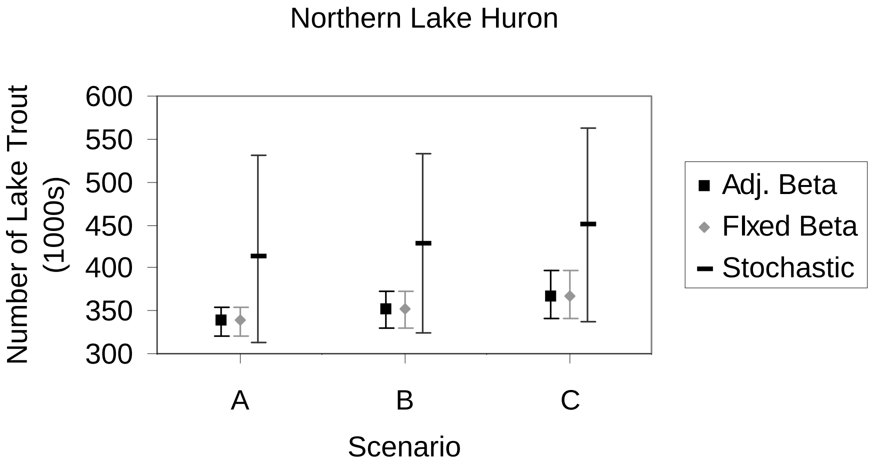


Figure 25: Number of age 2+ lake trout in northern, central, and southern Lake Huron for three different models. The 95% Bayesian prediction interval of the marginal distribution of age 2+ lake trout is shown, with the median of the marginal indicated. The models with an adjusting β (model II), a fixed β (model I), and the stochastic simulations with an adjusting β (model III) are shown. For information on scenarios, see Table 16. Note the difference in scale between regions.



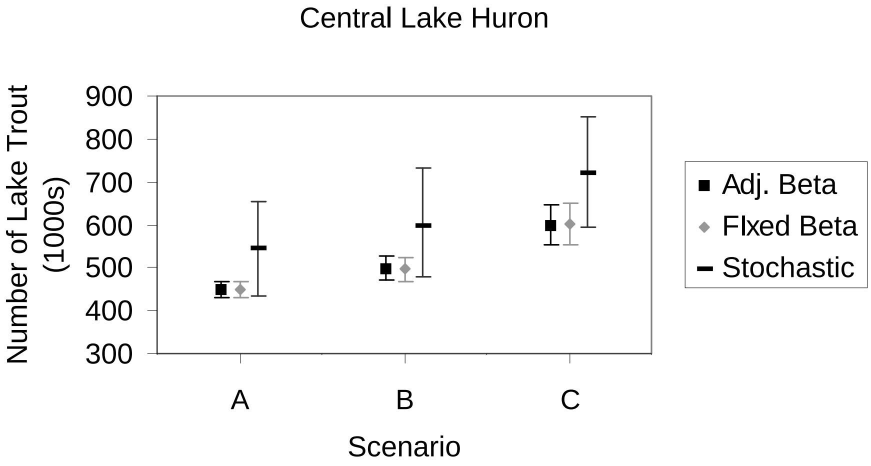


Figure 25 (cont'd)

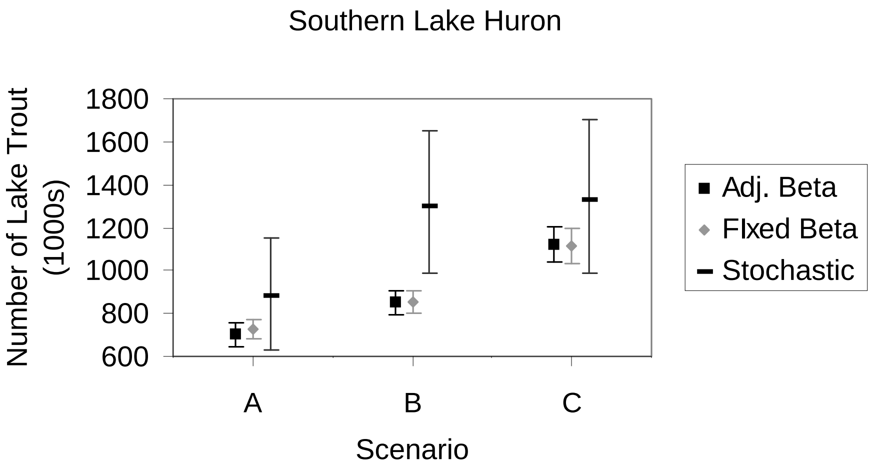
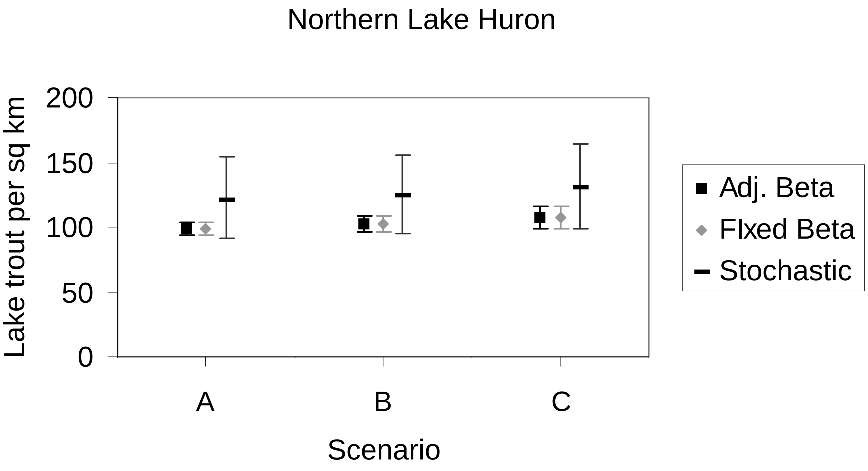
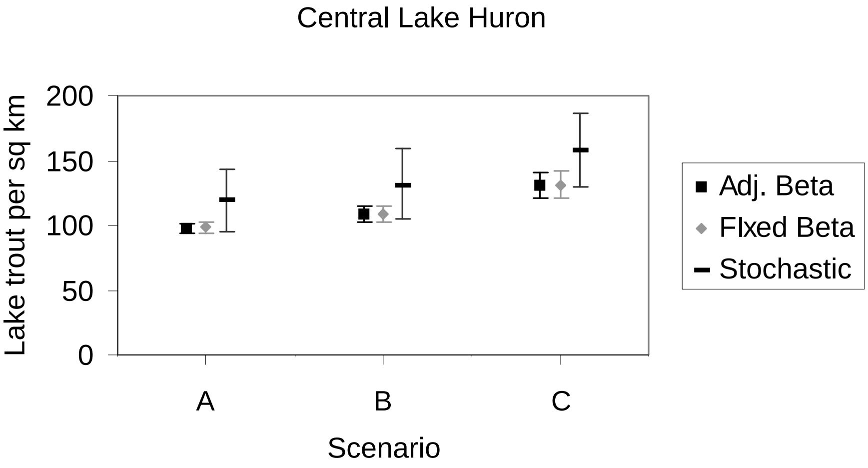


Figure 26: Density of age 2+ lake trout in northern, central, and southern Lake Huron for three different models. The 95% Bayesian prediction interval of the marginal distribution for age 2+ lake trout density is shown, with the median of the marginal indicated. The models with an adjusting β (model II), a fixed β (model I), and the stochastic simulations with an adjusting β (model III) are shown. For information on scenarios, see Table 16.



Northern Lake Huron



Central Lake Huron

Figure 26 (cont'd)

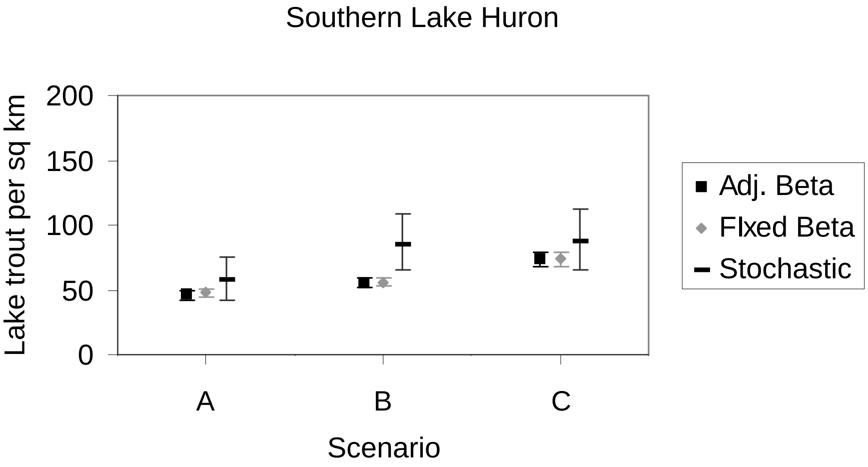
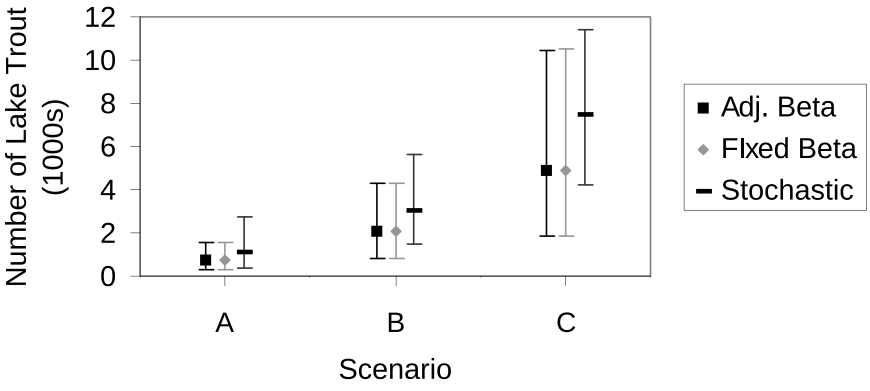


Figure 27: Number of age 7+ lake trout in northern, central, and southern Lake Huron for three different models. The 95% Bayesian prediction interval of the marginal distribution of age 7+ lake trout is shown, with the median of the marginal indicated. The models with an adjusting β (model II), a fixed β (model I), and the stochastic simulations with an adjusting β (model III) are shown. For information on scenarios, see Table 16. Note the difference in scale between regions.

Northern Lake Huron



Central Lake Huron

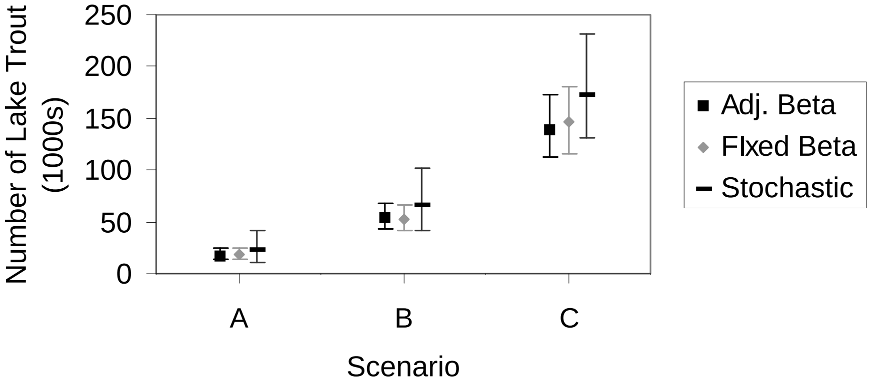


Figure 27 (cont'd)

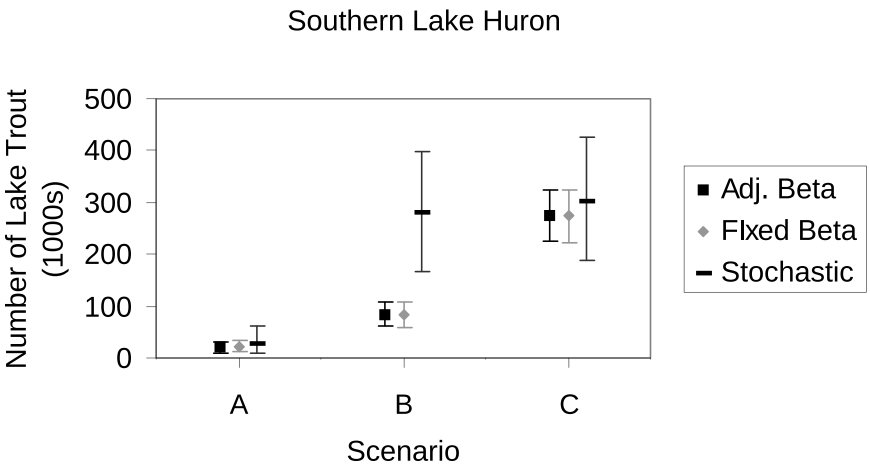
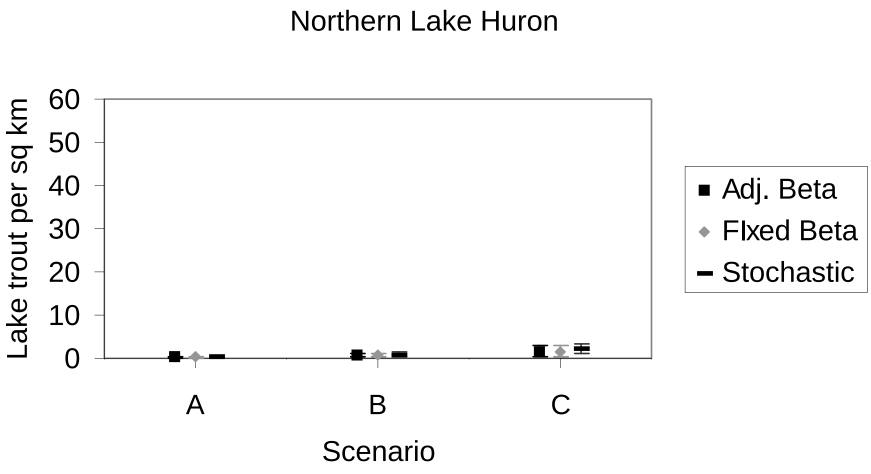


Figure 28: Density of age 7+ lake trout in northern, central, and southern Lake Huron for three different models. The 95% Bayesian prediction interval of the marginal distribution for age 7+ lake trout density is shown, with the median of the marginal indicated. The models with an adjusting β (model II), a fixed β (model I), and the stochastic simulations with an adjusting β (model III) are shown. For information on scenarios, see Table 16.


Northern Lake Huron

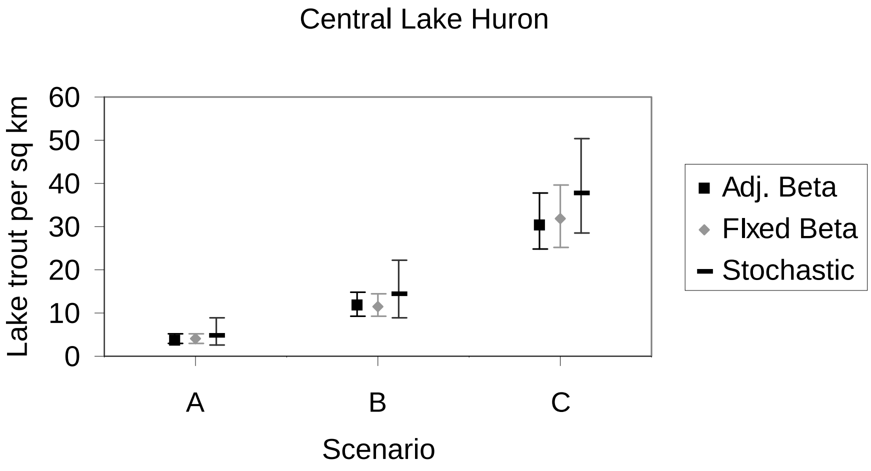

Central Lake Huron

Figure 28 (cont'd)

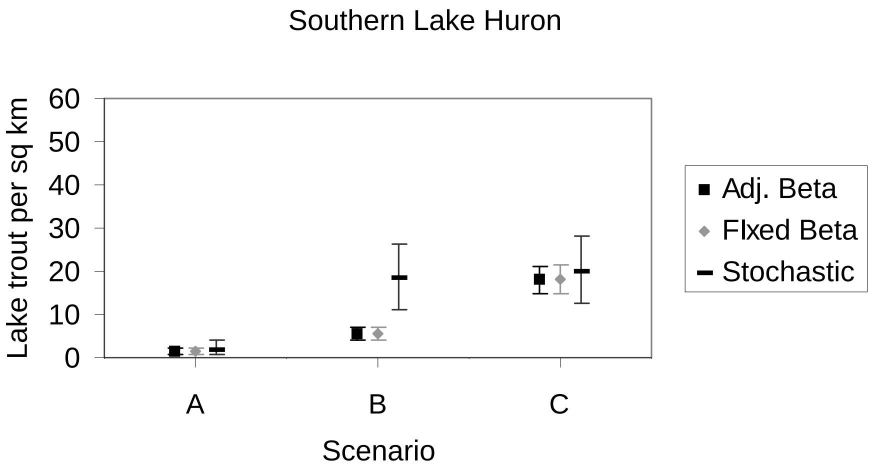
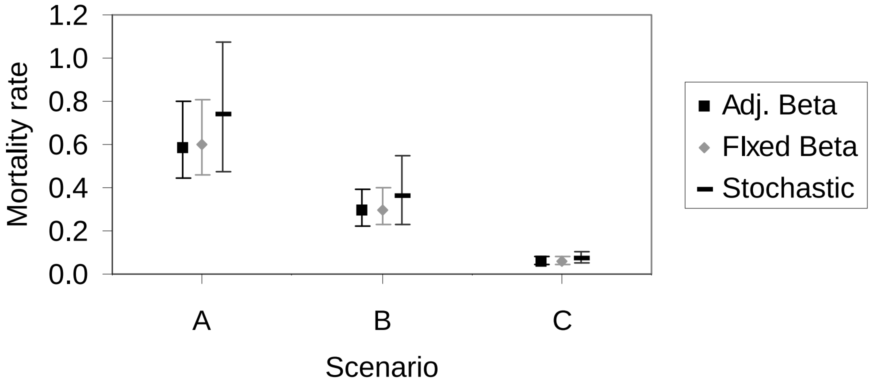


Figure 29: Sea lamprey-induced mortality on age 5 lake trout in northern, central, and southern Lake Huron for three different models. The 95% Bayesian prediction interval of the marginal distribution of mortality is shown, with the median of the marginal indicated. The models with an adjusting β (model II), a fixed β (model I), and the stochastic simulations with an adjusting β (model III) are shown. For information on scenarios, see Table 16. Note the difference in scale between regions.

Northern Lake Huron



Central Lake Huron

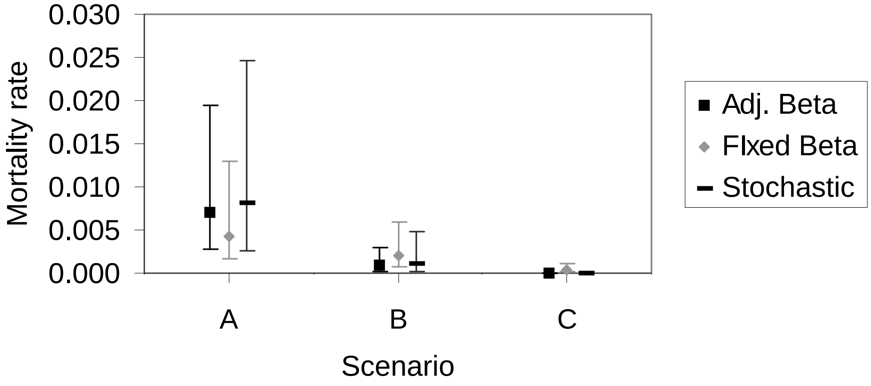


Figure 29 (cont’d)

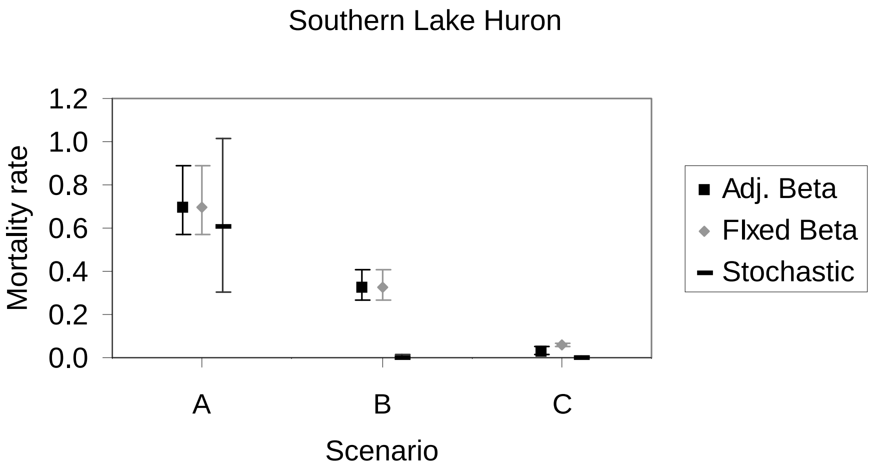
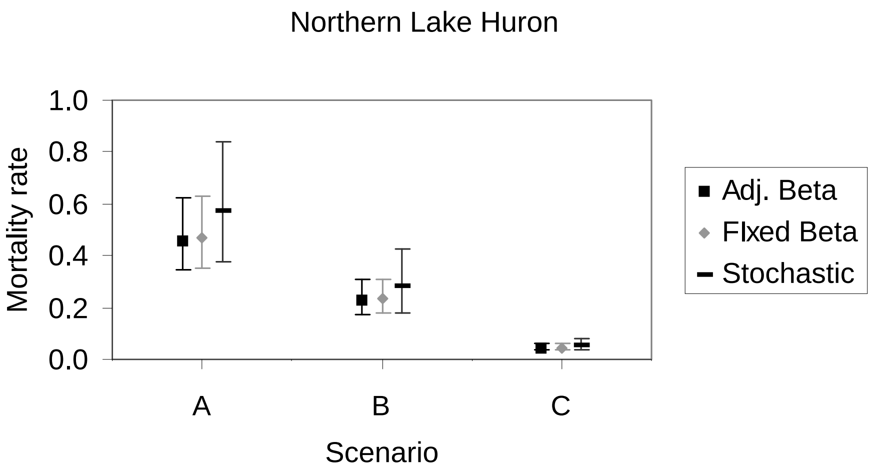


Figure 30: Sea lamprey-induced mortality for the youngest age lake trout with mean length exceeding 700 mm in northern (age 9), central (age 9), and southern (age 8) Lake Huron for three different models. The 95% Bayesian prediction interval of the marginal distribution of mortality is shown, with the median of the marginal indicated. The models with an adjusting β (model II), a fixed β (model I), and the stochastic simulations with an adjusting β (model III) are shown. For information on scenarios, see Table 16. Note the difference in scale between regions.


Northern Lake Huron

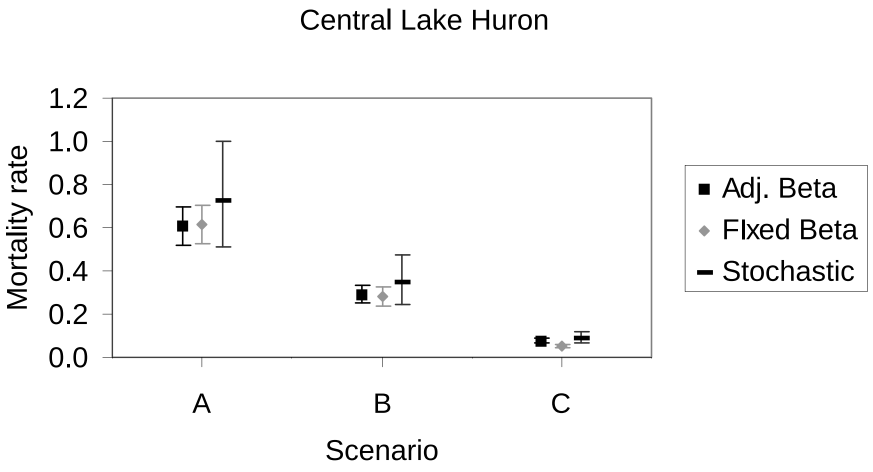

Central Lake Huron

Figure 30 (cont'd)

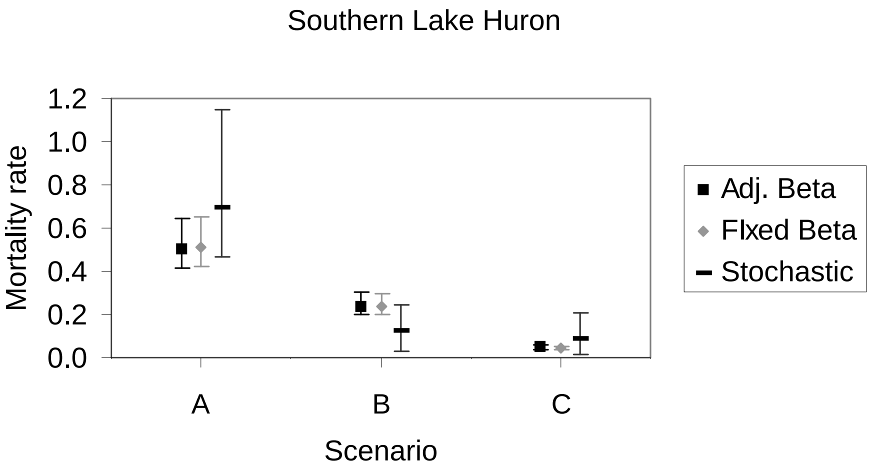
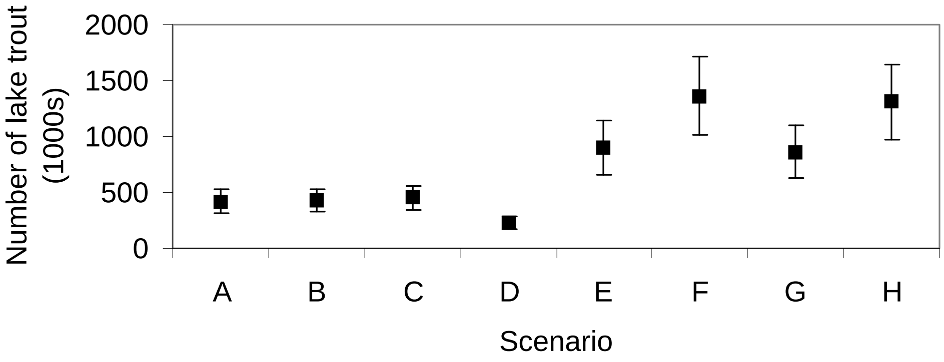
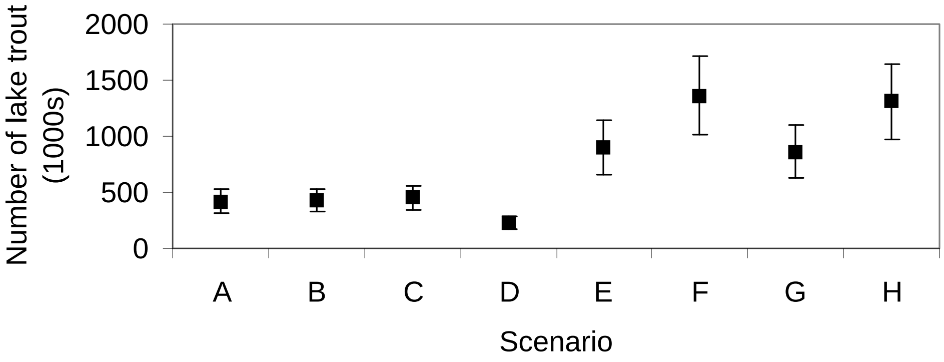


Figure 31: Number of age 2+ lake trout in northern, central, and southern Lake Huron for model III under a series of proposed lake trout management scenarios. The 95% Bayesian prediction interval of the marginal distribution of age 2+ lake trout is shown, with the median of the marginal indicated by the square. For information on scenarios, see Table 16. Note the difference in scale between regions.

Northern Lake Huron



Central Lake Huron



Southern Lake Huron

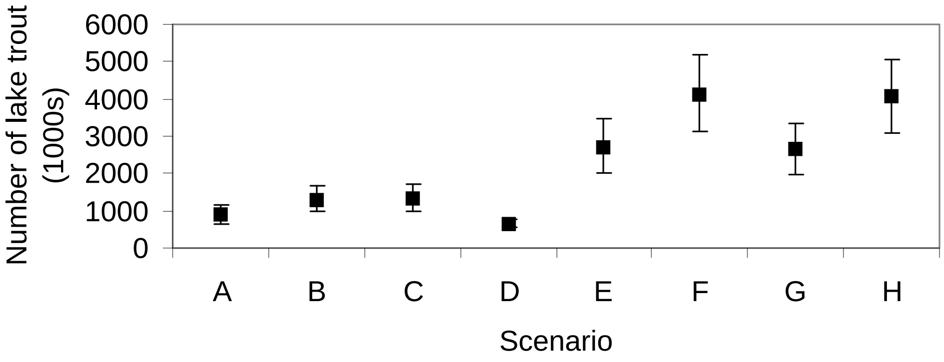
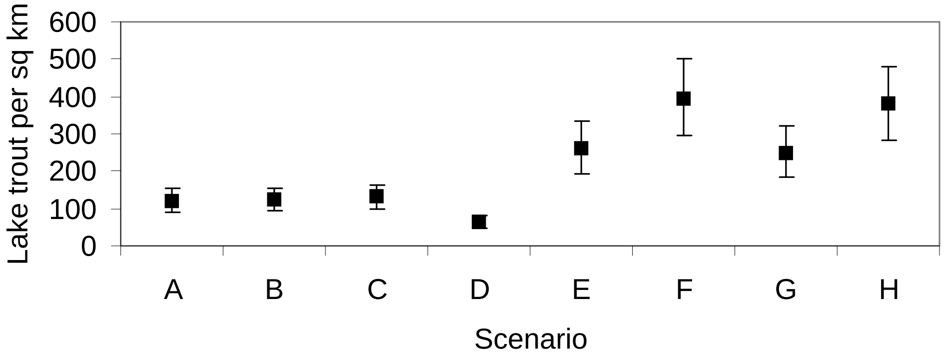
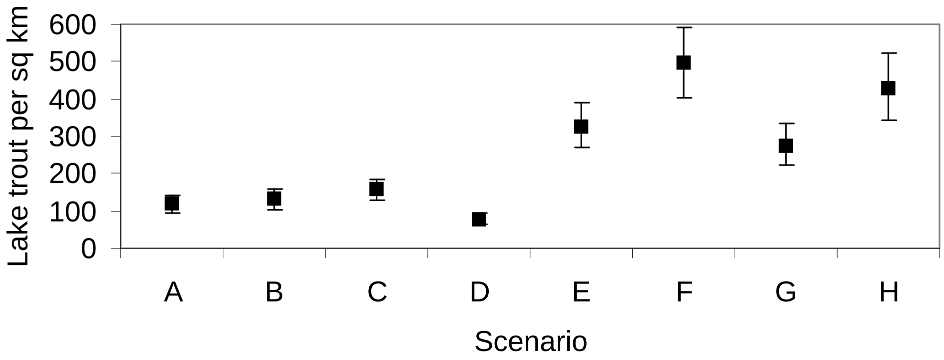


Figure 32: Density of age 2+ lake trout in northern, central, and southern Lake Huron for model III under a series of proposed lake trout management scenarios. The 95% Bayesian prediction interval of the marginal distribution for age 2+ lake trout density is shown, with the median of the marginal indicated by the square. For information on scenarios, see Table 16.

Northern Lake Huron



Central Lake Huron



Southern Lake Huron

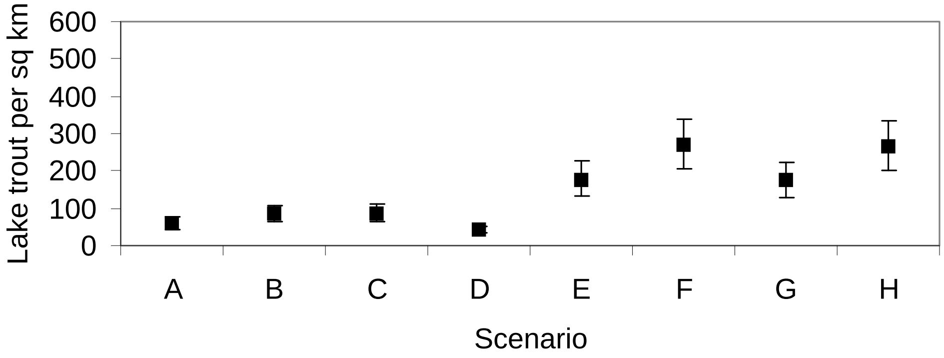


Figure 33: Number of age 7+ lake trout in northern, central, and southern Lake Huron for model III under a series of proposed lake trout management scenarios. The 95% Bayesian prediction interval of the marginal distribution of age 7+ lake trout is shown, with the median of the marginal indicated by the square. For information on scenarios, see Table 16. Note the difference in scale between regions.

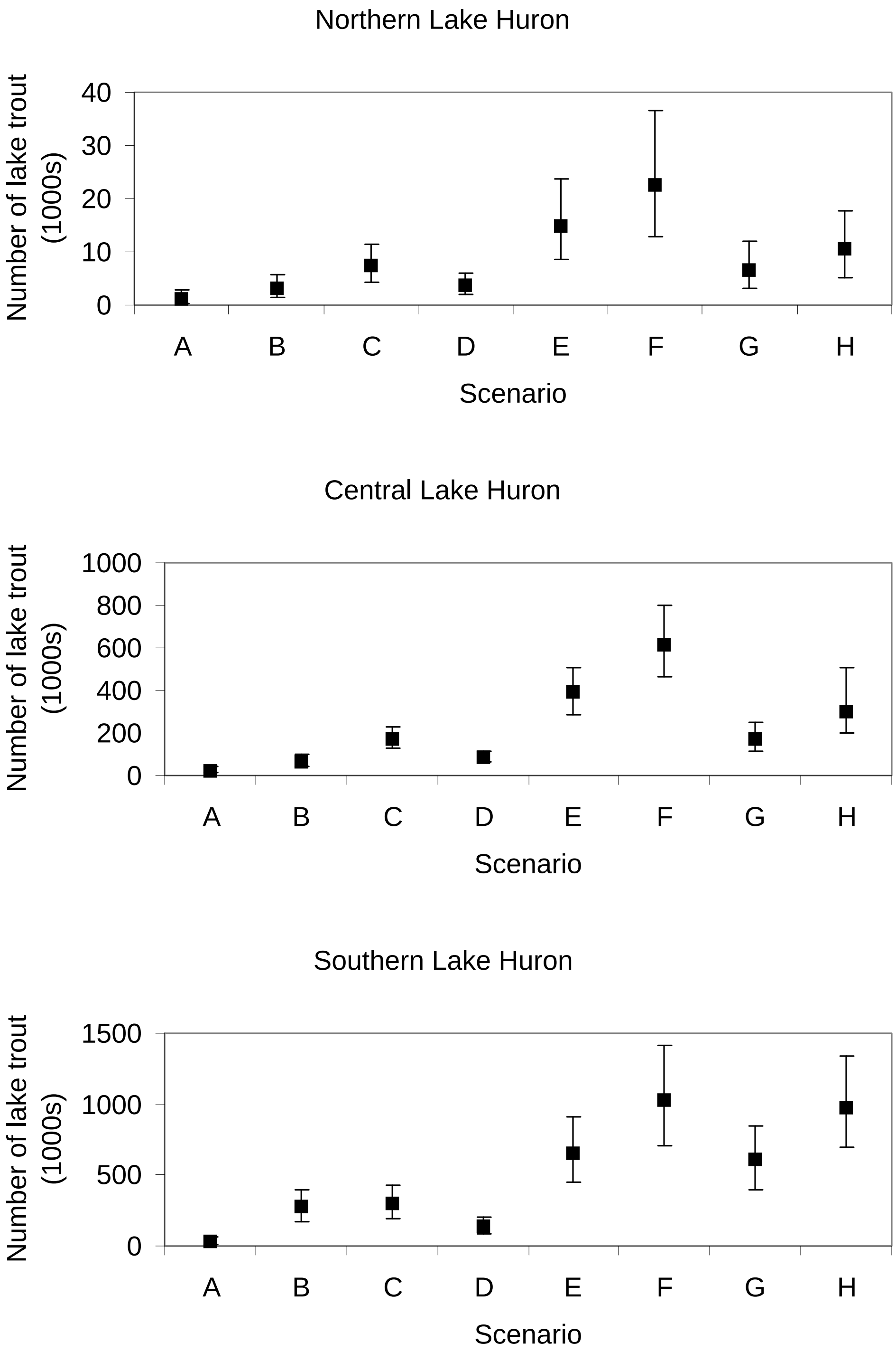
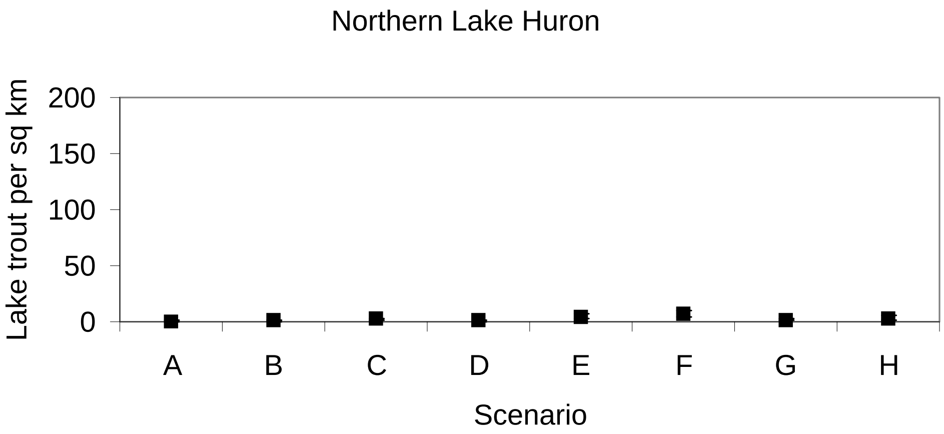
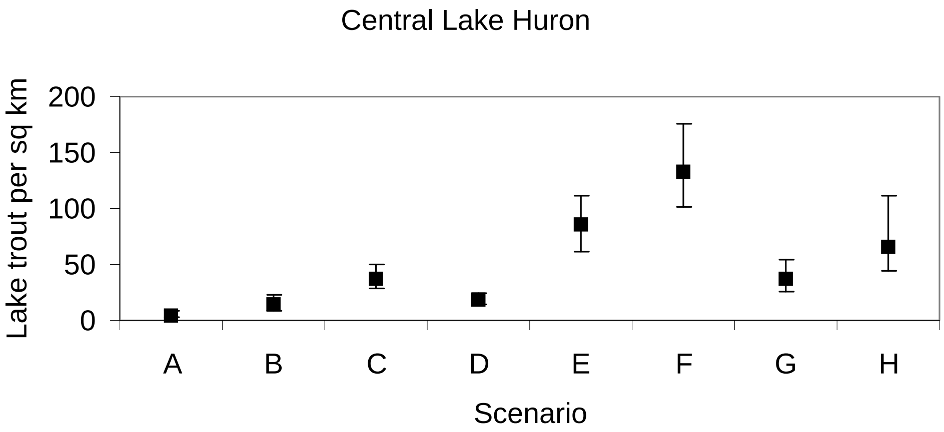


Figure 34: Density of age 7+ lake trout in northern, central, and southern Lake Huron for model III under a series of proposed lake trout management scenarios The 95% Bayesian prediction interval of the marginal distribution for age 7+ lake trout density is shown, with the median of the marginal indicated by the square. For information on scenarios, see Table 16.





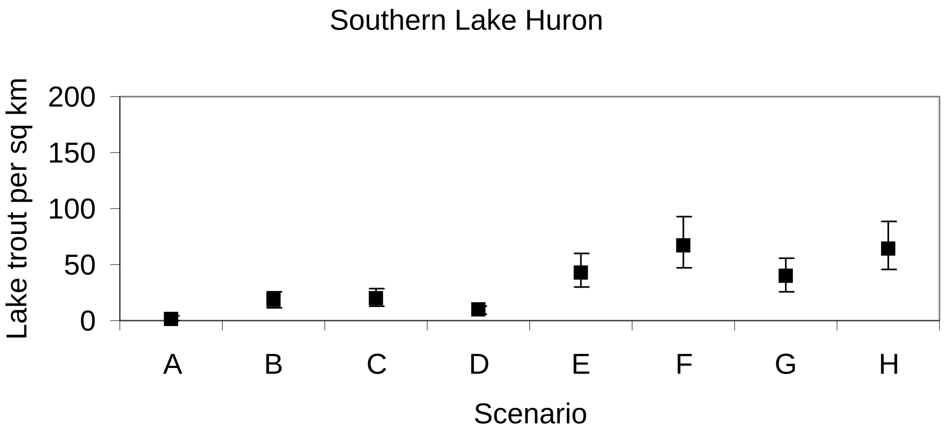
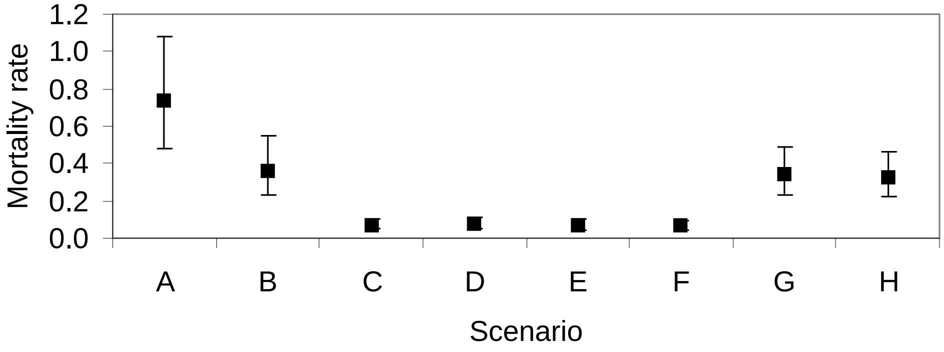
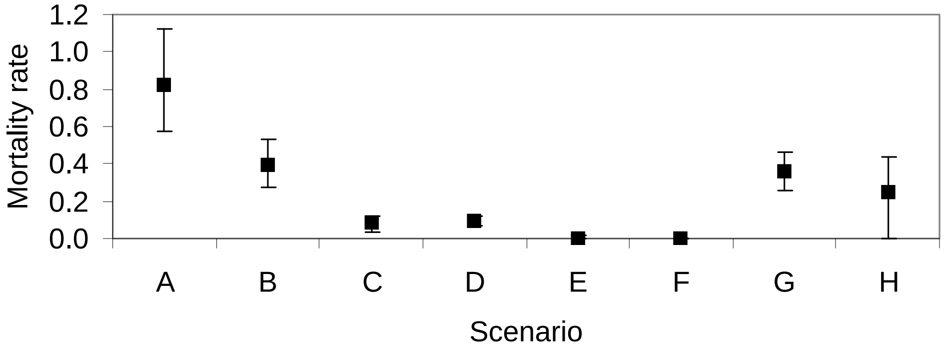


Figure 35: Sea lamprey-induced mortality on age 5 lake trout in northern, central, and southern Lake Huron for model III under a series of proposed lake trout management scenarios. The 95% Bayesian prediction interval of the marginal distribution of mortality is shown, with the median of the marginal indicated by the square. For information on scenarios, see Table 16. Note the difference in scale between regions.

Northern Lake Huron



Central Lake Huron



Southern Lake Huron

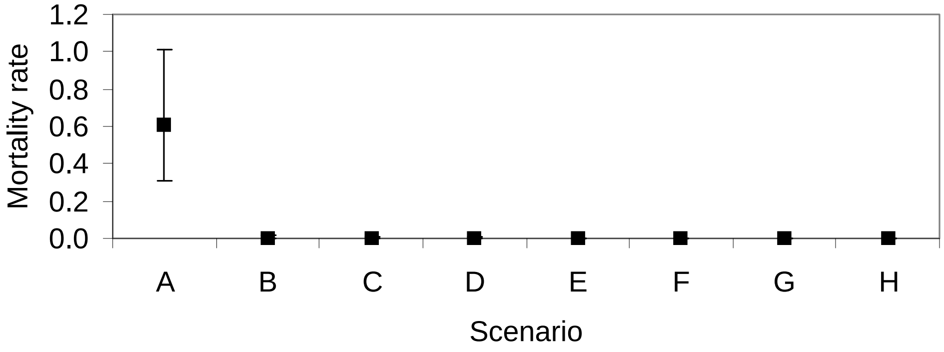
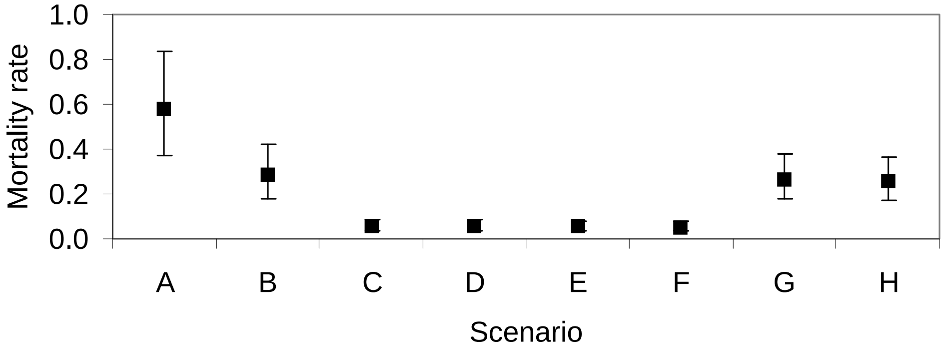


Figure 36: Sea lamprey-induced mortality for the youngest age lake trout with mean length exceeding 700 mm in northern (age 9), central (age 9), and southern (age 8) Lake Huron for model III under a series of proposed lake trout management scenarios. The 95% Bayesian prediction interval of the marginal distribution of mortality is shown, with the median of the marginal indicated by the square. For information on scenarios, see Table 16. Note the difference in scale between regions.

Northern Lake Huron



Central Lake Huron

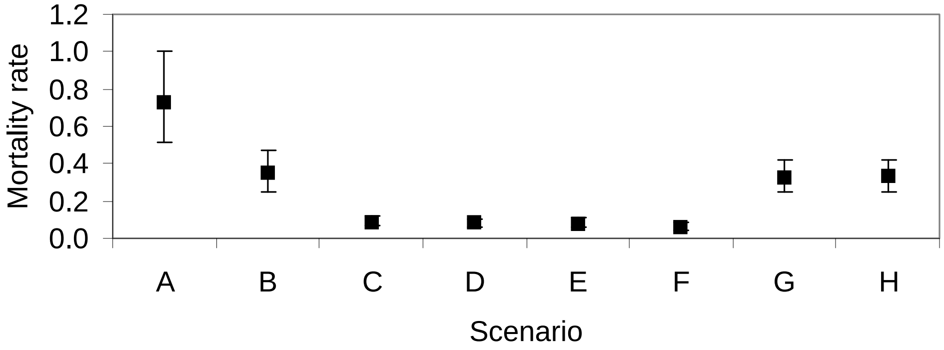


Figure 36 (cont’d)

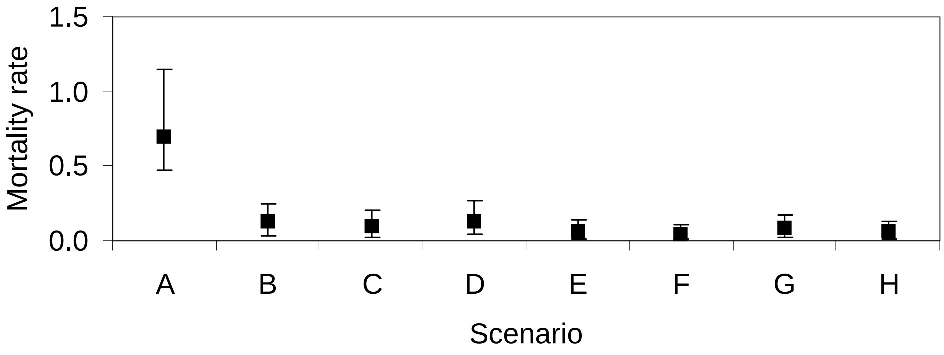

Southern Lake Huron

Figure 37: Number of age 2+ lake trout in northern Lake Huron for model III under a series of proposed lake trout management scenarios. Commercial fishing rates are reduced 56%. The 95% Bayesian prediction interval of the marginal distribution of age 2+ lake trout is shown, with the median of the marginal indicated by the square. For information on scenarios, see Table 16.

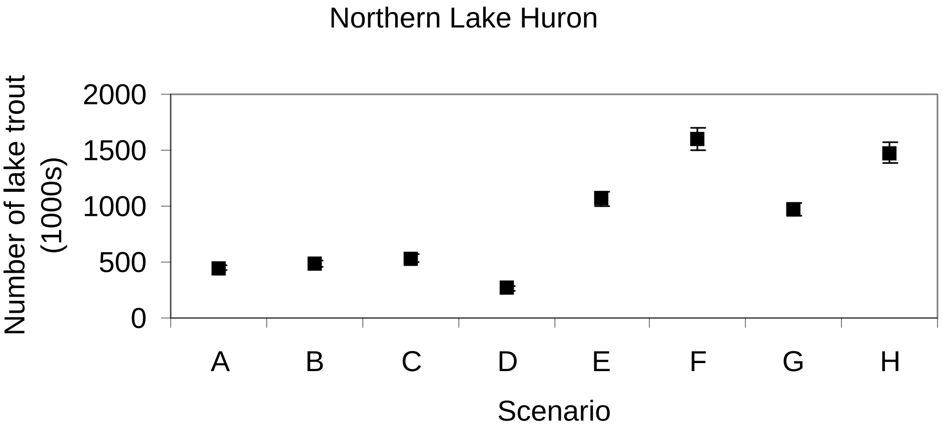


Figure 38: Density of age 2+ lake trout in northern Lake Huron for model III under a series of proposed lake trout management scenarios. Commercial fishing rates are reduced 56%. The 95% Bayesian prediction interval of the marginal distribution for age 2+ lake trout density is shown, with the median of the marginal indicated by the square. For information on scenarios, see Table 16.

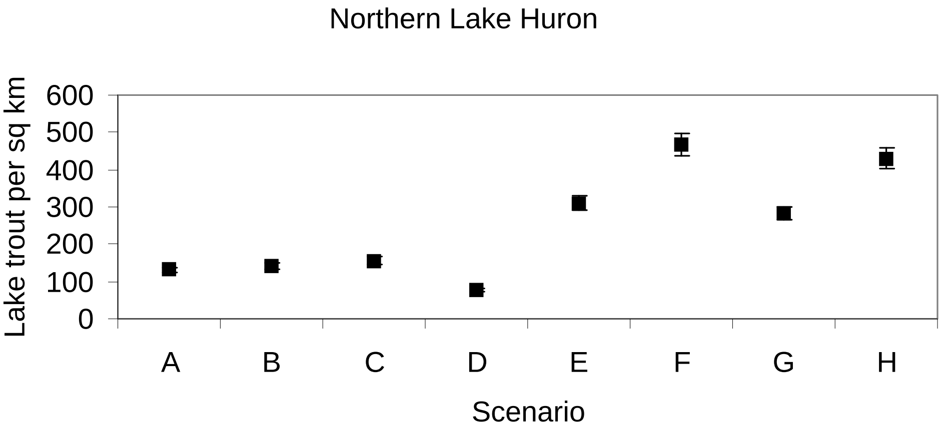


Figure 39: Number of age 7+ lake trout in northern Lake Huron for model III under a series of proposed lake trout management scenarios. Commercial fishing rates are reduced 56%. The 95% Bayesian prediction interval of the marginal distribution of age 7+ lake trout is shown, with the median of the marginal indicated by the square. For information on scenarios, see Table 16.

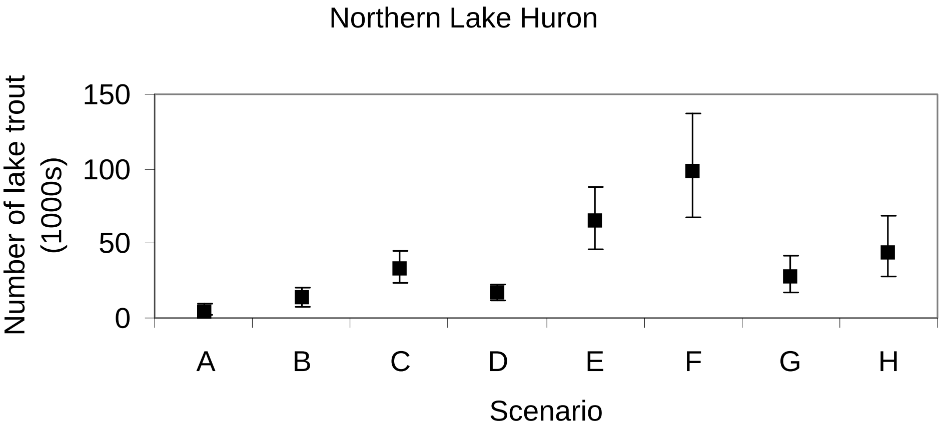


Figure 40: Density of age 7+ lake trout in northern Lake Huron for model III under a series of proposed lake trout management scenarios. Commercial fishing rates are reduced 56%. The 95% Bayesian prediction interval of the marginal distribution for age 7+ lake trout density is shown, with the median of the marginal indicated by the square. For information on scenarios, see Table 16.

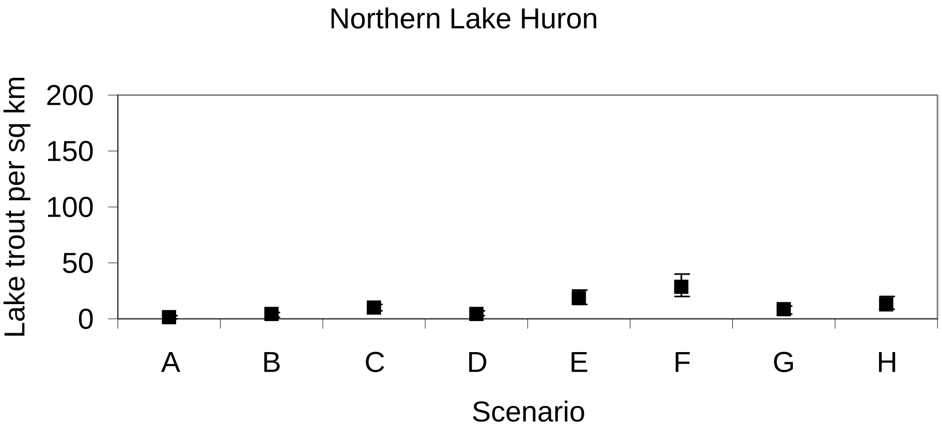


Figure 41: Sea lamprey-induced mortality on age 5 lake trout in northern Lake Huron for model III under a series of proposed lake trout management scenarios. Commercial fishing rates are reduced 56%. The 95% Bayesian prediction interval of the marginal distribution of mortality is shown, with the median of the marginal indicated by the square. For information on scenarios, see Table 16.

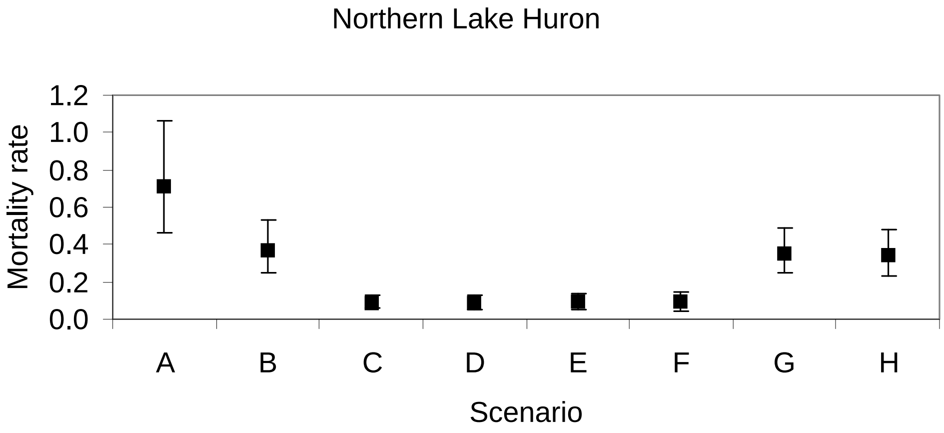


Figure 42: Sea lamprey-induced mortality on age-9 lake trout in northern Lake Huron for model III under a series of proposed lake trout management scenarios. Commercial fishing rates are reduced 56%. The 95% Bayesian prediction interval of the marginal distribution of mortality is shown, with the median of the marginal indicated by the square. For information on scenarios, see Table 16.

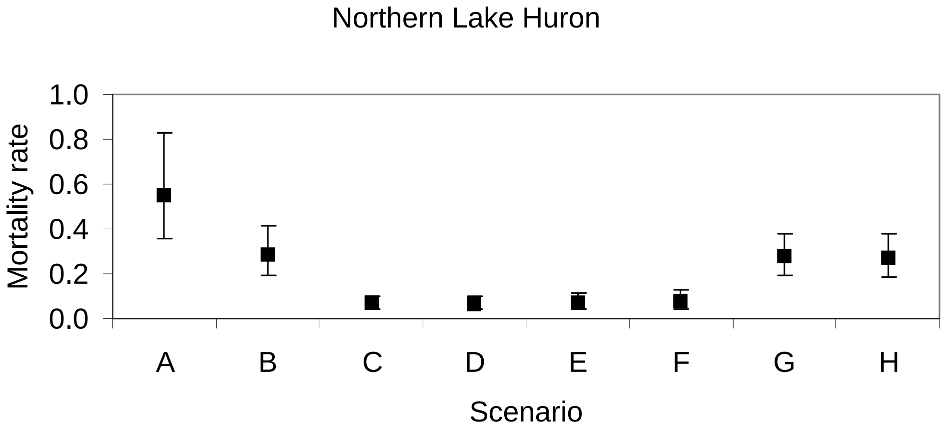


Figure 43: Sea lamprey-induced mortality on age 9 lake trout in northern Lake Huron for model III as the number of lake trout stocked is increased. Sea lamprey populations are based on a 90% reduction in the average value observed in Lake Huron from 1984-1998.

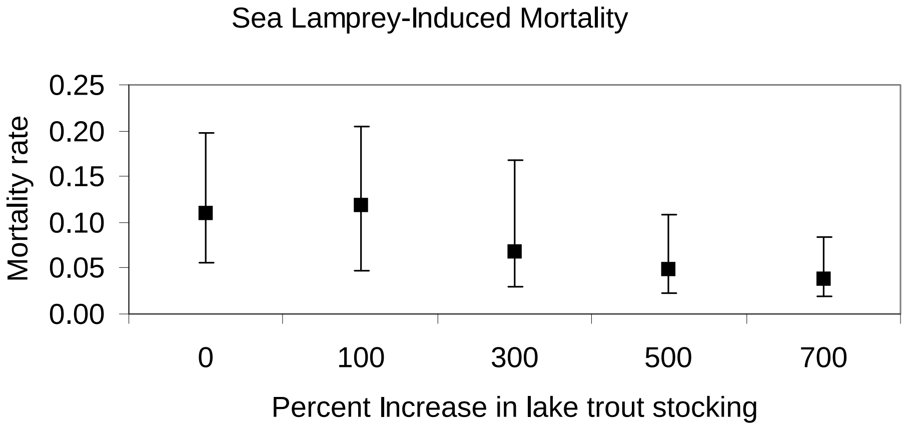


Figure 44: Sea lamprey-induced mortality on age 9 lake trout in northern Lake Huron for model III as the number of lake trout stocked is increased. Sea lamprey populations are based on the average value observed in Lake Huron from 1984-1998.

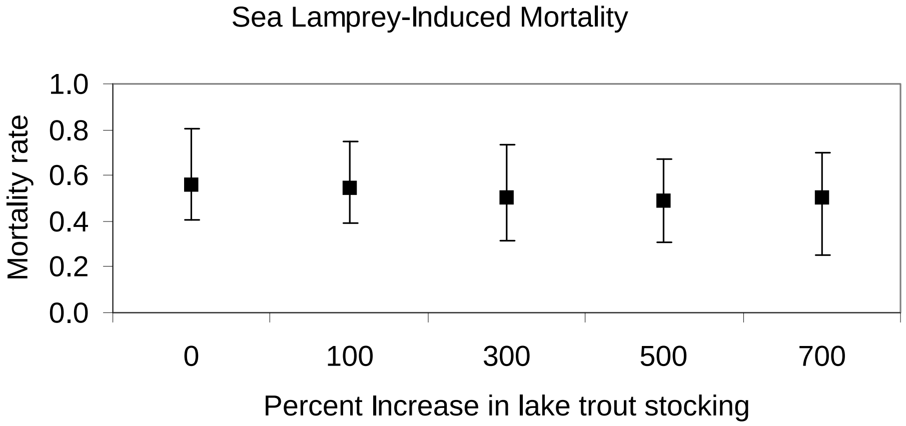


Figure 45: Age specific sea lamprey-induced mortality rates for lake trout in northern Lake Huron under scenario C (90% reduction in sea lamprey) and scenario F (90% reduction in sea lamprey and a 200% increase in stocking) using model III. The median of the marginal distribution of mortality is shown.

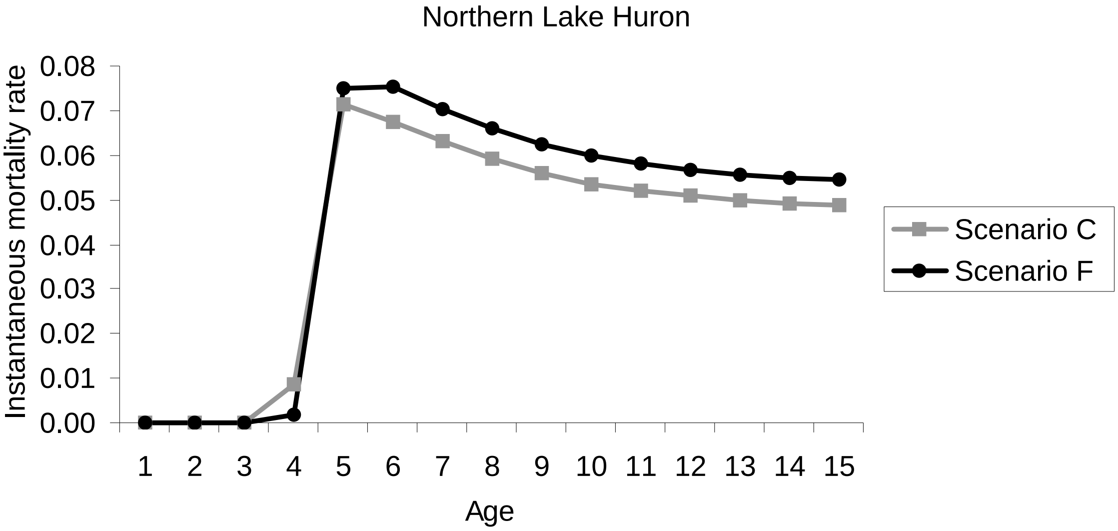
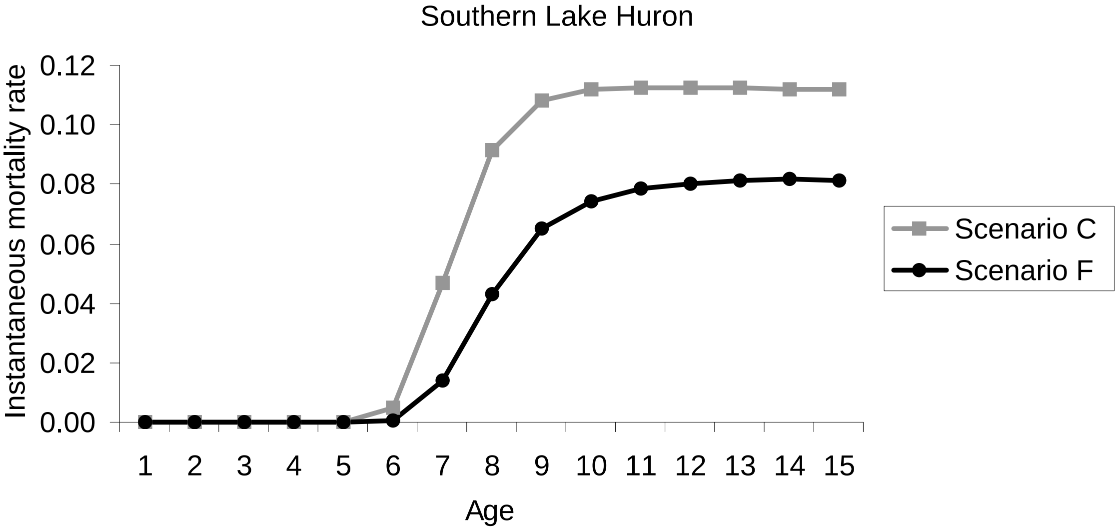


Figure 46: Age specific sea lamprey-induced mortality rates for lake trout in southern Lake Huron under scenario C (90% reduction in sea lamprey) and scenario F (90% reduction in sea lamprey and a 200% increase in stocking) using model III. The median of the marginal distribution of mortality is shown.



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