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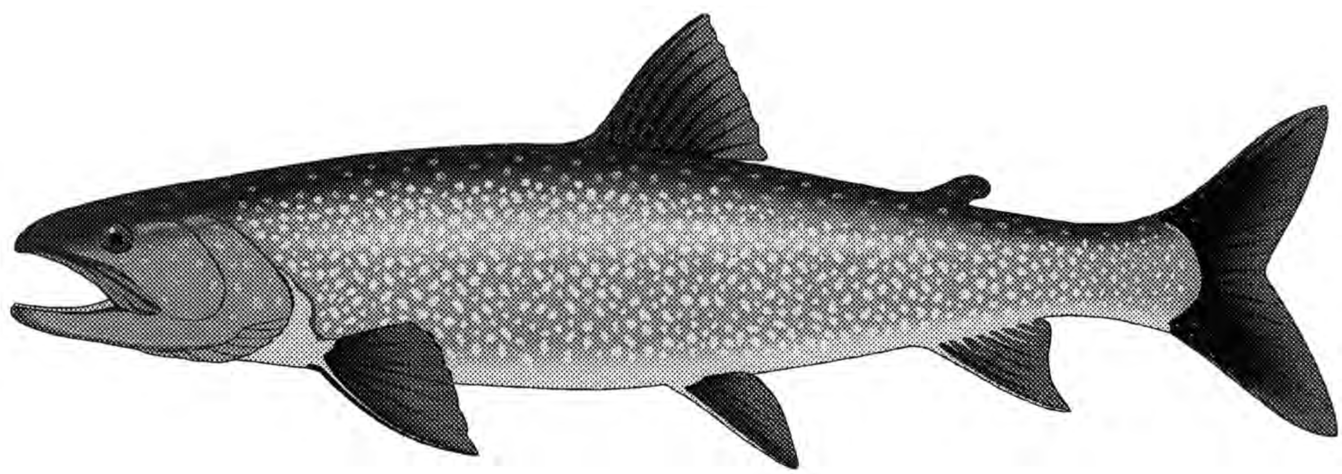
Shawn Paul Sitar



FISHERIES DIVISION

RESEARCH REPORT

MICHIGAN DEPARTMENT OF NATURAL RESOURCES
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By

Shawn Paul Sitar

A THESIS

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ABSTRACT

ESTIMATION OF LAKE TROUT (*Salvelinus namaycush*) ABUNDANCE AND MORTALITY DUE TO SEA LAMPEYS (*Petromyzon marinus*) AND FISHING IN THE MAIN BASIN OF LAKE HURON, 1984-1993

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Sea lamprey (*Petromyzon marinus*) parasitism and overfishing have been cited as the causes of the collapse of lake trout (*Salvelinus namaycush*) populations in Lake Huron during the 1950s. The goal of the ongoing lake trout rehabilitation program is aimed at reducing sea lamprey abundance, controlling fishing mortality, and restocking lake trout to establish self-sustaining populations. In order to rehabilitate lake trout, the magnitude of sea lamprey parasitism and fishing mortality must be determined in order to gauge progress towards the goal. With reliable estimates of lake trout deaths due to sea lampreys and fishery harvest, managers can adjust sea lamprey control programs and fishing regulations to reach rehabilitation objectives. I analyzed data on sea lamprey wounding of lake trout, from 1984-1994, to assess patterns in sea lamprey parasitism according to length of lake trout, geographic distribution, and year. Lake trout population models, calibrated by statistical catch-at-age analysis, were constructed to estimate abundance, fishery harvest, and numbers killed by sea lamprey during 1984-1993 for the main basin of Lake Huron.

Sea lamprey wounding rates on lake trout increased with length of lake trout and were higher in central Lake Huron than in the south for lake trout >533 mm. Although sea lamprey wounding of lake trout varied by year, no overall temporal trends were observed during 1984-1994 in the central and southern main basin of Lake Huron. Comparisons with northern Lake Huron were not possible because of insufficient data.

Abundance of mature lake trout, an index of potential natural recruitment, was estimated to be highest in southern Lake Huron and lowest in the north. For lake trout ages most selected by sea lampreys and fishing (ages 3-10), total annual mortality rates were highest in northern Lake Huron and have exceeded the Great Lakes Fishery Commission (GLFC) target maximum total annual mortality rate of 45% in all years from 1984-1993. Total annual mortality rates in central and southern main basin of Lake Huron were below the GLFC target maximum during the same time period. Sea lamprey-induced mortality accounted for most lake trout deaths in central and southern Lake Huron, whereas commercial fishing and sea lamprey parasitism both were responsible for the high number of lake trout deaths in the north. Recreational fishing was not a significant source of lake trout mortality in the main basin of Lake Huron.

The lack of success in re-establishing self-sustaining populations of lake trout in the main basin of Lake Huron was due in part to the mismatching of reproductive biomass and spawning habitat. In central and southern Lake Huron, lack of sufficient spawners and insufficient spawning habitat are possible reasons that rehabilitation has not progressed in these areas. In northern Lake Huron, where the amount of spawning habitat is greatest, excessive sea lamprey-induced and commercial fishing mortality at premature ages has limited the abundance of spawners. In order to successfully rehabilitate lake trout, total mortality rates must be reduced in northern Lake Huron.

This work is dedicated to

my loving wife, Kristie,

my parents, Dania and Steve,

and my brother, Robert.

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INTRODUCTION

Lake trout (*Salvelinus namaycush*) is a long-lived species that functions as a dominant predator in the fish communities of the Great Lakes of North America (Smith 1972). Historically, lake trout populations supported important commercial and recreational fisheries in these lakes (Berst and Spangler 1973). In Lake Huron, the commercial fishery averaged annual yields of 2.4 million kg from 1912 through 1940 (Baldwin et al. 1979).

In the 1940s, lake trout abundance in Lake Huron declined, and stocks collapsed in the 1950s (Figure 1; Hile 1949; Baldwin et al. 1979; Coble et al. 1990). The decline of lake trout stocks in Lake Huron has been attributed to commercial exploitation, environmental degradation, and sea lamprey (*Petromyzon marinus*) parasitism (Christie 1974). Sea lampreys invaded the upper Great Lakes by circumventing Niagara Falls via the Welland Canal (Lawrie 1970). Sea lampreys were first observed in Lake Huron in 1937 (Shetter 1949), and then colonized most of the lake with the highest abundance in northern waters (Lawrie 1970; Morman 1979). Although there is debate about whether the initial decline in lake trout stocks was due to fishing, sea lamprey parasitism, or a combination of the two (Coble et al. 1990; Eshenroder et al. 1992), it is recognized that sea lampreys were responsible for the final demise of lake trout in Lake Huron (Berst and Spangler 1973; Coble et al. 1990; Eshenroder et al. 1995).

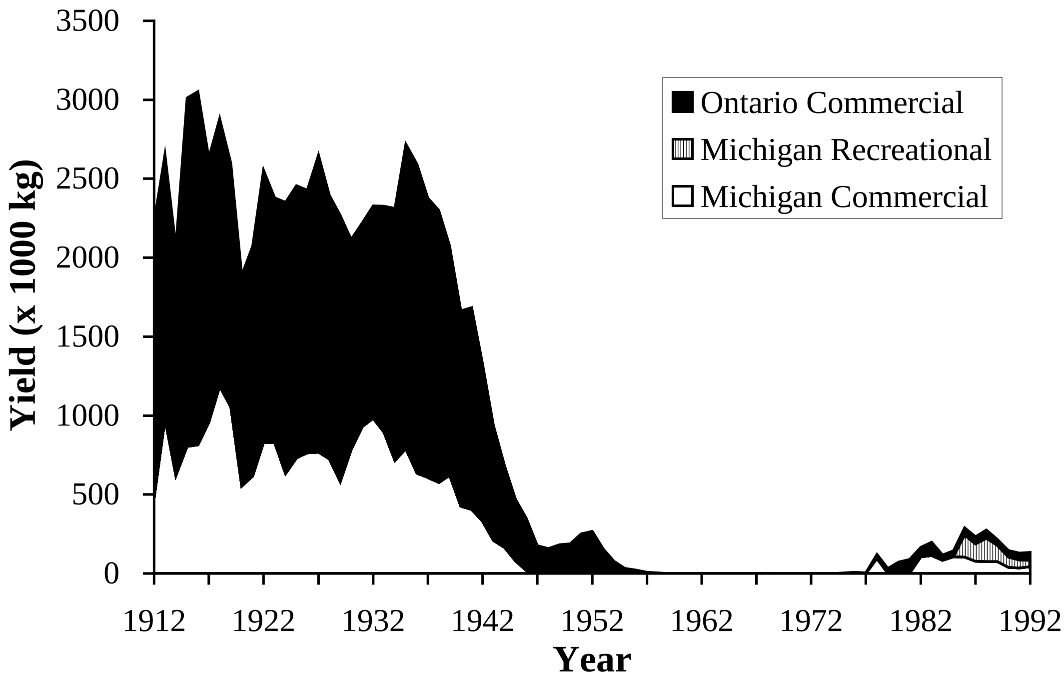

Figure 1. Lake trout commercial and recreational yield in Lake Huron from 1912-1992. Data from Baldwin et al. (1979) and Johnson et al. (1995). Recreational harvest data were not available prior to 1985.

Subsequent to the collapse of lake trout populations, a rehabilitation program was implemented with emphasis on sea lamprey suppression combined with stocking of hatchery produced lake trout, and restrictions on commercial and recreational fishing (Francis et al. 1979; Smith and Tibbles 1980; Koonce et al. 1993). Initial efforts at controlling sea lampreys were in the form of mechanical and electrical barriers that prevented upstream migration of spawning adults. Subsequently, selective chemical toxicants were used in streams to kill ammocoetes (Smith and Tibbles 1980). This efficacious technique helped to significantly reduce sea lamprey abundance and continues to be implemented in Lake Huron tributaries (Morse et al. 1995). Stocking of lake trout in Lake Huron began in 1973 (Smith and Tibbles 1980) and continues today with current populations supported almost entirely by these hatchery fish (Johnson et al. 1995).

Since the collapse of lake trout stocks, no commercial fishing for lake trout in Michigan waters has been allowed except for a tribal fishery in the northern region (Smith and Tibbles 1980). These restrictions on harvest have contributed to an increased abundance in Lake Huron, though it is less evident in the northern areas of the lake. Although some progress has been made in reducing the high mortality experienced by lake trout, sea lampreys are still one of the main factors in inhibiting the rehabilitation of lake trout (Eshenroder et al. 1995; Johnson et al. 1995).

Various studies reporting the negative effects of sea lamprey on lake trout populations have been reviewed by Coble et al. (1990). Some of these studies investigated the relationship between decreasing lake trout abundance and the incidence of sea lamprey wounds and showed that they were correlated (Fry 1953; Budd et al. 1969). Wounding rates have been reported to increase with length of lake trout (Eschmeyer 1957; Farmer and Beamish 1973; Pycha and King 1975; Swink 1991), vary temporally (Pycha and King 1975; Jacobson 1985) and geographically. Hypotheses for explaining why wounding rates increase with length of lake trout include: 1) lower wounding rates on smaller hosts are due to higher lethality of sea lamprey attacks on smaller fish than larger fish (Eschmeyer 1957; Swink 1990); and 2) sea lampreys select for larger hosts (Budd and Fry 1960; Farmer and Beamish 1973; Pycha and King 1975; Cochran 1985; Swink 1991). These studies indicate that mortality caused by sea lampreys is likely to differ according to size of lake trout- which also implies that sea lamprey-induced mortality varies by age of lake trout.

Sea lamprey wounds on lake trout are a record of sea lamprey attacks and an index of sea lamprey abundance (King 1980). Eshenroder and Koonce (1984) reported a protocol for quantifying and translating sea lamprey wounding data to lamprey-induced mortality rates. This procedure is dependent on an estimate of the probability of surviving a sea lamprey attack. Current estimates of this parameter for various lengths of lake trout have been reported from laboratory experiments conducted by Swink (1990). A standardized classification of wounds inflicted by sea lampreys on lake trout (King 1980) is used by most of the U.S. fisheries agencies in the Great Lakes, and has led to a substantial database on lake trout wounding rates. Sea lamprey-induced mortality estimates from this procedure can be used in population models to evaluate the effects of sea lampreys on lake trout abundance.

The goal of lake trout restoration for Lake Huron is to re-establish self-sustaining populations that can produce a yield of 1.4 to 1.8 million kg annually (DesJardine et al. 1995). Due to the low abundance of lake trout, recent (1986-1992) annual recreational and commercial harvest of lake trout averaged 204,000 kg, which is less than 15% of the goal, and less than 10% of historic yield (Johnson et al. 1995). The success of lake trout rehabilitation has been limited by low spawner abundance and excessive mortality rates (Hatch 1983; Johnson et al. 1995). Healey (1978) reported that in order for a lake trout population to sustain itself, total annual mortality should not exceed 50%. The desired maximum for total annual mortality for lake trout restoration has been set at 45% (equal to an instantaneous rate, Z of 0.59 year^{-1}) by the Great Lakes Fishery Commission (GLFC) as an attempt to increase spawner abundance (Johnson et al. 1995).

The lack of progress in the rehabilitation program in northern Lake Huron has been attributed to the high abundance of sea lampreys over the past decade in conjunction with exploitation by the tribal fishery (Johnson et al. 1995; Eshenroder et al. 1987). Estimates of total annual mortality for lake trout in U.S. waters of Lake Huron, based on catch curves applied to data from spring assessments (1982-1992), have been reported to be greater than 70% in the north, with sea lampreys accounting for at least 33% of annual losses of lake trout larger than 630 mm in that region (Johnson et al. 1995). However, these reports do not address the age-selective effects or the relative magnitude of sea lamprey-induced and fishing mortality.

In order to rehabilitate lake trout, overall effects of sea lamprey parasitism and fishing mortality must be determined in order to gauge progress toward the goals. However, it is important to take into account the dynamics of each mortality source by understanding the age-selectivity of each mortality source in relation to temporal variations in fishing or sea lamprey abundance. It is important to assess which ages are suffering the highest mortality and how this affects spawning stock abundance. Catch curve approaches are not robust in this respect. Catch curve techniques rely on unrealistic assumptions of age-independent mortality rates, equal vulnerability to the sampling gear for ages used in the analysis, and equal recruitment for all cohorts (Ricker 1975). With reliable estimates of lake trout deaths due to sea lampreys and fishery harvest, managers can adjust lamprey control programs or fishing regulations to reach rehabilitation objectives.

Stock assessments have been performed for lake trout using an age-structured, deterministic Total Allowable Catch (TAC) model in U.S. waters of Lake Superior (Wisconsin State/Tribal Technical Committee 1984; Ebener et al. 1989) and for parts of northern Lake Huron (Technical Fisheries Review Committee 1992). This model projects levels of allowable harvest based on estimates of sea lamprey-induced mortality from wounding data, fishing mortality, and desired maximum for total mortality.

The goal of this study was to evaluate the effects of sea lamprey parasitism and fishing on lake trout populations the main basin of Lake Huron. The specific objectives were to:

1. Analyze patterns in sea lamprey-induced mortality, as indexed by wounds, for lake trout in the main basin of Lake Huron. These results were used as a guide in accomplishing other specific objectives.
2. Estimate abundance, sea lamprey-induced, and fishing mortality for lake trout by constructing age-structured population models for the main basin of Lake Huron.
3. Evaluate changes in future spawning stock size according to decreases in sea lamprey-induced and fishing mortality.

To accomplish objectives 2 and 3 of this study, lake trout population models were developed for the main basin of Lake Huron that integrated sea lamprey-induced mortality estimates from standardized wounding data (collected by the Chippewa-Ottawa Treaty Fishery Management Authority (COTFMA) and Michigan Department of Natural Resources (MDNR)) along with estimates of fishing mortality based on commercial and recreational harvest and effort data supplied by COTFMA, MDNR, and Ontario Ministry of Natural Resources. Model calibrations were performed using statistical catch-at-age approaches that used auxiliary information to estimate model parameters (Megrey 1989). Auxiliary information included fishery harvest-at-age, fishery effort, and standardized research survey indices of abundance.

METHODS

The methods are described in five subsections, I first describe how I assessed patterns in sea lamprey wounding to determine how sea lamprey-induced mortality experienced by lake trout populations varied over time, among geographic regions, or among lake trout size categories. In part two, I then describe how the results from these analyses were used to guide the development of models to estimate wounding rates for years or geographic regions where few or no lake trout were examined. In part three, I describe the lake trout population model. The fourth part of the methods describes the calibration of the model using statistical catch-at-age analysis. In the last part, I describe simulation runs for the population models.

Patterns in sea lamprey wounding

I used sea lamprey wounding data for lake trout in Lake Huron, collected in spring gill net surveys from 1984-1994 by COTFMA and MDNR. These surveys were conducted from April through June at various fixed stations in Michigan waters of Lake Huron using graded-mesh multifilament, nylon gill nets that were 1.8 m deep and consisted of nine panels that were 30.5 m long with mesh sizes (stretch measure) ranging from 51 mm to 152 mm in 13 mm increments (Merna et al. 1981; Johnson and VanAmberg 1995). Wounding data were recorded using the protocol developed by King (1980). I used only recent, potentially lethal wounds (type a, stages 1-3 (King 1980)) based on the recommendations of Eshenroder and Koonce (1984). Potentially lethal, recent wounds were characterized as wounds that have penetrated through the scales and epidermis exposing the underlying musculature (King 1980). Eshenroder and Koonce (1984) also recommended that spring wounding rates should be used because these wounding rates were correlated with catches of spawning sea lampreys at stream barriers, which was used as an index of lamprey abundance. Standardization of sea lamprey wounding data began in 1984, and I used data from 1984-1994.

Wounding rates were calculated by length class of lake trout, geographic region, and year. I established four length categories (432-533, 534-635, 636-737, >737 mm) in accordance with conventions used by COTFMA, Great Lakes Fishery Commission (GLFC), and MDNR. These length classes matched those for which estimates of lethality of sea lamprey attacks were available (Greig et al. 1992). I focused on three areas in Lake Huron: northern (MH-1), central (MH-2), and southern (MH-3/4/5)(Figure 2). These geographic regions were thought to represent discrete lake trout populations based on previous surveys (J. Johnson, Alpena Fisheries Research Station, MDNR, pers. comm.). Regions MH-3, MH-4, and MH-5 were pooled based on the same reasoning. Lake trout populations in these three geographic regions of the main basin of Lake Huron are exposed to different levels of fishery harvest and are reported to be exposed to differing levels of sea lamprey parasitism (Johnson et al. 1995).

Low sample sizes and complete absence of data for some strata in the wounding database prevented the use of one statistical analysis to simultaneously examine the effects of lake trout length, geographic region, time, and their interactions on wounding rates (Table 1). Therefore, I used different subsets of the database in a suite of analyses, each aimed at evaluating one or more of these main factors. Subsets were selected so that a wide range of

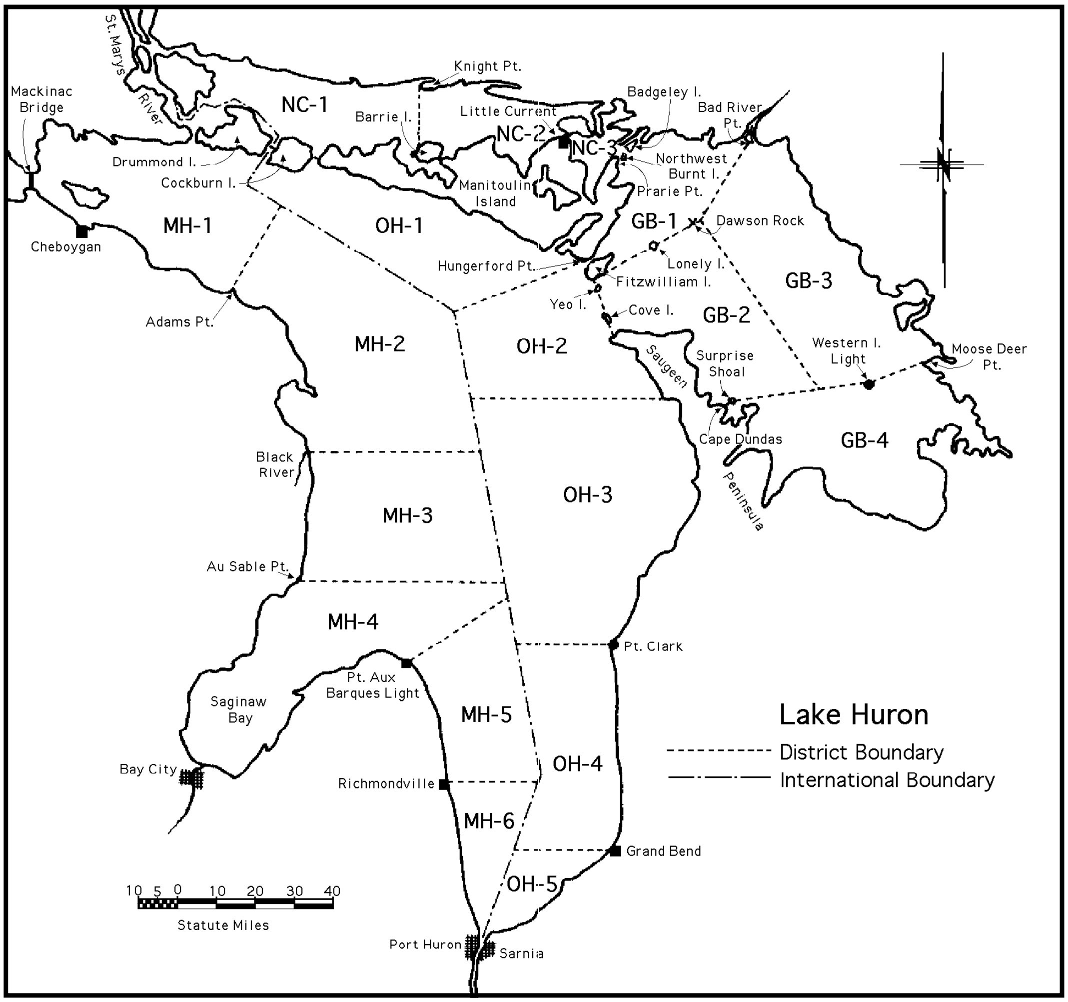

Figure 2. Statistical districts of Lake Huron (Smith et al. 1961).

Table 1. Numbers of lake trout examined for sea lamprey wounds in Michigan waters of Lake Huron in spring gill net surveys and subsampling of tribal gill net and trap net catches. Observations are stratified by lake trout length class. Data provided by the Chippewa-Ottawa Treaty Management Authority, and Michigan Department of Natural Resources. Region: MH-1= north, MH-2= central, and MH-3/4/5= south.

Region	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994
432-533 mm											
MH-1	457	134	380	257	143	71	63	130	202	279	78
MH-2	181	206	181	89	44	123	31	34	87	62	61
MH-3/4/5	247	127	240	118	159	126	38	18	38	83	100
534-635 mm											
MH-1	171	30	53	45	14	11	20	23	31	55	18
MH-2	61	74	80	82	15	83	23	66	81	52	82
MH-3/4/5	217	363	265	219	203	139	149	39	77	140	116
636-737 mm											
MH-1	19	0	2	4	1	1	0	1	1	9	3
MH-2	19	27	22	37	8	28	6	59	47	12	43
MH-3/4/5	359	450	241	220	244	233	281	98	135	66	137
>737 mm											
MH-1	2	1	0	0	0	0	0	0	1	0	0
MH-2	6	5	5	2	1	4	1	7	7	1	2
MH-3/4/5	82	149	65	72	70	45	85	72	153	68	65

one or more factors could be included to provide contrast for those factors, while other factors were necessarily represented by fewer levels. This was done so that all combinations of the factors used in an analysis contained some data. A variety of subsets were analyzed so that each factor and potential interactions could be evaluated. These analyses were restricted to subsets of levels that did not include missing cells. Data were square root transformed to approximate normality (Miller 1984) based on previous indications that frequencies of sea lamprey wounds on fish were Poisson distributed (Eshenroder and Koonce 1984).

Analysis of variance (ANOVA) models were constructed using subsets of the transformed data to test for effects of main factors: length class (α_i), geographic region (β_j), and year (δ_k) on sea lamprey wounding rates. The full model was:

$$W_{ijk} = \mu + \alpha_i + \beta_j + \delta_k + \alpha\beta_{ij} + \alpha\delta_{ik} + \beta\delta_{jk} + \alpha\beta\delta_{ijk} + \varepsilon_{ijk} \qquad (1)$$

where W_{ijk} was estimated mean wounds per fish for ith length class, jth geographic region, and kth year; $\alpha\beta_{ij}$ was the interaction of length class and geographic region, $\alpha\delta_{ik}$ was the interaction term for length class and year, $\beta\delta_{jk}$ was the interaction of geographic region and year, and $\alpha\beta\delta_{ijk}$ was the interaction term for all three main factors. For some subsets of the data, one or more of the main effects and its associated interactions were not included because only one level of those factors were represented. ANOVA models were fit using the General Linear Models procedure (SAS Institute 1985).

Estimation of sea lamprey-induced mortality

In order to estimate sea lamprey-induced mortality for all age classes in each year and geographic area, estimates of wounding rates were needed for each combination of these factors. As indicated in the previous section, attempts were made to estimate wounding rates that were not available for all levels for each of the main factors. Although the initial analyses provided information about how sea lamprey wounding rates were influenced by lake trout size and geographic location (see *Patterns in sea lamprey wounding* in Results section), the approach led to biased estimates of wounding rates after back-transformation. This was true even after attempts at bias correction following procedures suggested by Miller (1984). This was determined by comparisons between least-square means with original mean wounding rates, when available. Thus, results from these analyses were not suitable for estimating absolute wounding rates and corresponding sea lamprey-induced mortality rates.

My objectives here were first to systematically estimate mean wounding rates for specific year by length class by geographic region combinations where data were not sufficient or absent with the least amount of extrapolation. The second objective was to compute age-specific lamprey-induced mortality rates for each region and year for use in the lake trout population models. The first objective was approached by constructing another set of ANOVA models based on the information found in the analysis of patterns in sea lamprey wounding. The patterns observed were that wounding rates increased with length class of lake trout, and were higher in the central region of Lake Huron than in the south for fish >533 mm. Therefore as an example, in order to estimate a wounding rate for a missing year in the central area for the 534-635 mm length class, a model can be constructed based on the relationship between the central and southern areas for all fish >533 mm using the available data for all other years. Overall, this second set of ANOVA models used the available data to estimate effects of year, length class, and geographic region on mean wounds per fish. These estimated effects were then used to predict mean wounding rates for specific combinations without data. However, in northern Lake Huron there were insufficient data for lake trout >533 mm to reliably estimate wounding rates using these ANOVA models. Thus, ANOVA models constructed to estimate wounding rates were only used for central and southern Lake Huron and for the smallest length class in the north. Sea lamprey-induced mortality for lake trout >533 mm in northern Lake Huron was estimated using a different approach described later in the methods section (see *Calibration of the northern and central lake trout population models*).

The second set of ANOVA models were constructed using untransformed mean wounds per fish as observations to estimate wounding rates for each combination of main factors in which data were absent. In these analyses, the models assumed no interactions since replicate observations were not available. Although unlikely to be strictly true, I attempted to restrict the extent to which I extrapolated across very different size classes or distant geographic areas to minimize problems due to interactions. Mean wounds per fish for length class i, region j, and year k were calculated for each combination of main factors by:

$$\overline{W}_{ijk} = \frac{\Sigma w_{ijk}}{n_{ijk}} \tag{2}$$

where w was number of observed wounds and n was number of fish. Mean wounds per fish were only calculated when data from 40 or more fish were available. This sample size criteria was established because of the inability to reliably estimate wounding rates such as 0.1 wounds per fish when less than 40 fish were examined. For example, the coefficient of variation for a mean of 0.1 wounds per fish and a sample size of 40 fish was about 50%. The means were weighted in the ANOVA by the inverse of the estimated variance of the mean to reduce bias from lower sample sizes.

Relationships between main factors, guided by the results from the analyses of sea lamprey wounding patterns, were used to develop models to estimate wounding rates for missing cells. The basic form of the model was:

$$W_{ijk} = \mu + \alpha_i + \beta_j + \delta_k + \varepsilon_{ijk} \tag{3}$$

where α_i , β_j, and δ_k were as defined in equation 1. Based on review of the estimates of the variance of the means, estimated variances less than 0.0009 were set to 0.0009 when weighting was done so that observations with extremely low variance estimates did not dominate solutions. My estimates of variance did not account for some sources of variability, such as process error, therefore this procedure was implemented so that any one observation would not completely control the solution.

The size- and year-specific instantaneous rate of sea lamprey-induced mortality (Z_L) for each geographic area of Lake Huron was estimated using Eshenroder and Koonce’s (1984) procedure:

$$Z_{L\,i,k} = \overline{W}_{i,k}\left(\frac{1-P_{S,i}}{P_{S,i}}\right) \tag{4}$$

where $\overline{W}_{i,k}$ was the mean wounds per fish for the ith length class in year k, and $P_{S,i}$ was the probability of surviving a sea lamprey attack for the ith length class of lake trout. Assumptions in using this model included: 1) $P_{S,i}$ was independent of prior attacks, and 2) $\overline{W}_{i,k}$ was representative of the wounds accumulated over a year (see Eshenroder and Koonce (1984) for further discussion). Estimates of the probability of survival from a sea lamprey attack were reported by Swink (1990) based on laboratory studies using lake trout. Summarized values of the survival probabilities were: 0.35 for 432-533 mm, 0.45 for 534-635 mm, 0.55 for 636-737 mm, and 0.55 for >737 mm lake trout (Greig et al. 1992). These values were used in this study since no in situ estimates of $P_{S,i}$ were available.

Since this study used an age-structured model, the length-based estimates of lamprey-induced mortality had to be converted to age-specific values. This was accomplished using an age-length key (Tables 15-17, Appendix) and the equation:

$$Z_{L,a} = \sum_j \frac{n_{a,j}}{\sum_i n_{a,i}} Z_{L,j} \tag{5}$$

where $n_{a,j}$ was the number of fish of age class a and in length class j, and $Z_{L,j}$ was the instantaneous rate of lamprey-induced mortality for length class j. For a specific age, this equation multiplies the proportion of fish in each length class by the appropriate rate of lamprey-induced mortality and then sums over all length classes for that age. Virtually all lake trout sampled in research surveys were of hatchery origin, thus age of fish were determined from fin clip patterns. Scales were used to age unclipped lake trout (J. Johnson, Alpena Fisheries Research Station, MDNR, pers. comm.). Age-length keys for each of the regional populations used in this study were tabulated from unpublished data collected in spring gill net surveys of lake trout provided by the MDNR (Tables 15-17, Appendix). These keys were based on data pooled from 1984-1994.

An assumption made in the above procedure was that mean wounds per fish, which are sampled in the spring of year $y+1$, were representative of attacks that occurred in year y. The length at which a lake trout suffered its attacks may be shorter than when sampled in the spring survey. Therefore, fish growing into a larger length class, which has a different $P_{S,i}$, could potentially bias the mortality estimate. However, sea lamprey attacks are most prevalent in the late summer and fall (Jacobson 1989) and this is after much of the year's growth has occurred in lake trout (Martin and Olver 1980). Hence, the effect of the violating this assumption, though not estimated, is likely to be small.

Lake trout population model

The model used in this study was based upon a total allowable catch (TAC) model developed for lake trout in Lake Superior (Wisconsin State/Tribal Technical Committee 1984; Ebener et al. 1989). Initial efforts at construction and parameterization of the Lake Huron models were performed by M. Ebener (COTFMA) and J. Johnson (MDNR) of the Lake Huron Technical Committee, Great Lakes Fishery Commission (GLFC). This study was initiated, in part, to complete and calibrate lake trout TAC models for Lake Huron. The major advance presented here was the use of statistical catch-at-age procedures so that better parameter estimates could be obtained based on more of the available data.

The lake trout TAC model integrates age-specific estimates of sea lamprey-induced, natural, and fishing mortality to estimate abundance and projections of allowable harvest. The idea underlying the model is that stocks can be managed by adjusting fishing mortality based on information on recruitment, harvest, and the other sources of mortality (i.e., sea lamprey-induced mortality). Regulation of fishing mortality can be in the form of harvest quotas or effort restrictions.

Population models were constructed for each of the three regional stocks of lake trout: northern (MH-1 and northwest part of OH-1), central (MH-2, most of OH-1, OH-2), and southern (MH-3, MH-4, MH-5, MH-6, OH-3, OH-4, OH-5)(see Figure 2). The time series modeled in each area was from 1984-1993. Prior to 1984, recreational harvest data were unavailable and wounding data were not recorded following the same protocol. Model parameters, variables, and constraints that were available for use in this study are listed in Table 2.

In the main basin of Lake Huron, essentially all lake trout were derived from hatchery-stockings in Michigan waters. Canada has not stocked lake trout in the main basin, and there were insignificant immigrations of fish from the North Channel, and Georgian Bay (L. Mohr, Lake Huron Management Unit, Ontario Ministry of Natural Resources, pers. comm.). Thus, all lake trout in Canadian waters of the main basin were assumed to be immigrants from the adjacent populations in U.S. waters.

Models for northern and central Lake Huron were similar in that both areas have recreational and commercial fisheries. All lake trout harvests in statistical districts OH-1 and OH-2 of Canada (Figure 2) were incorporated into the harvests of the northern and central models. Southern Lake Huron was considered to have only recreational fishing, though there was some commercial harvest of lake trout in adjacent Canadian waters. All this commercial harvest of lake trout in OH-3, OH-4, and OH-5 (Figure 2) was incorporated into the sport harvest of the southern model since no accompanying biological information was available (see later section titled *Statistical catch-at-age analysis of the southern Lake Huron lake trout population model*).

Table 2. Previously reported parameter values for estimating mortality rates of lake trout in the main basin of Lake Huron. COTFMA= Chippewa-Ottawa Treaty Fishery Management Authority, MDNR= Michigan Department of Natural Resources.

Parameter (units)	Description	Source	Values (age or length-class)
$f_{C,\,y}$ (year^{-1})	Commercial fishing intensity	COTFMA	Proportional to effort in harvest reports
$f_{R,\,y}$ (year^{-1})	Recreational fishing intensity in year *y*	MDNR	Proportional to effort in creel survey reports
M_a (year^{-1})	Natural mortality rate (excluding sea lamprey-induced mortality), assumed temporally constant	Rybicki (1990), MDNR	0.799 (1), 0.25 (2,3), 0.20 (4), 0.15 (>4)
$P_{S,\,i}$	Probability of surviving a sea lamprey attack for length class *i*	Swink (1990)	0.35 (432-533 mm), 0.45 (534-635 mm), 0.55 (636-737 mm), 0.55 (>737 mm)
$S_{C,\,a}$	Commercial fishery selectivity	COTFMA	0 (1), 0.01 (2), 0.10 (3), 0.75 (4), 1 (5), 0.86 (6), 0.55 (7), 0.49 (8), 0.39 (9), 0.2 (>9)
$S_{R,\,a}$	Recreational fishery selectivity	MDNR	0 (1), 0.01 (2), 0.10 (3), 0.75 (4), 0.85 (5), 1 (>5)
$\overline{W}_{i,y}$	Mean number of sea lamprey wounds per fish in length class *i*, in year *y*	COTFMA, MDNR	From annual spring surveys

Substantial migration between geographic areas was thought to occur only between northern and central Lake Huron, with movement being unidirectional northward. The proportion of stocked fish that emigrate to the north has been approximated at 60% based on coded-wire tag results (J. Johnson, Alpena Fisheries Research Station, MDNR, pers. comm.). The northern and central models account for this migration by adjusting the age-1 recruitment numbers. Sixty percent of the age-1 fish in the central area were subtracted and then added to the age-1 abundance in the north.

Lake trout abundance

Lake trout numbers (N) at age *a+1*, and year *y+1* were computed using an exponential mortality equation:

$$N_{a+1,y+1} = N_{a,y} e^{-Z_{a,y}} = N_{a,y} e^{-(Z_{L,a,y}+F_{a,y}+M_a)} \qquad (6)$$

where Z was the total instantaneous mortality rate, Z_L was the lamprey-induced mortality rate, F was the rate of fishing mortality, and M was the natural mortality rate excluding sea lamprey-induced mortality. Since there is no significant natural reproduction of lake trout in Lake Huron, recruitment was a direct function of hatchery stockings. Lake trout are stocked as yearlings and fall fingerlings, therefore age-1 abundance was equal to the numbers of stocked yearlings and the survivors of fall stocked fingerlings. Based on values used by Ebener et al. (1989), forty percent of the number of fall fingerlings stocked were assumed to survive to yearlings, thus the abundance at age-1 was the sum of the number of yearlings stocked in year *y* and 40% of fall fingerings stocked in year *y-1*(Table 18, Appendix).

Natural mortality

Available values of natural mortality rates (M_a), excluding sea lamprey-induced mortality, for hatchery stocked lake trout ages 1-3 were reported by Rybicki (1990) in a study conducted in Grand Traverse Bay, Lake Michigan. For lake trout age-4 and older, unpublished estimates of natural mortality rates were provided by the MDNR (J. Johnson, Alpena Fisheries Research Station, MDNR, pers. comm.). These values for M_a are listed in Table 2. Natural mortality rates were also estimated by statistical catch-at-age analysis (CAA) of the lake trout population model using information on age-specific harvest and effort from the fishery and research surveys (see later in section titled *Statistical catch-at-age analysis of the southern Lake Huron lake trout population model*).

Fishing mortality

The fishing mortality rate of the recreational fishery ($F_{R,a,y}$) was modeled as being separable into age- and year-specific components by:

$$F_{R,a,y} = S_{R,a}\, f_{R,y} \qquad (7)$$

where $S_{R,a}$ was the recreational fishery selectivity on age *a*, and $f_{R,y}$ was fishing intensity which scales the overall recreational fishing mortality for year *y*. In the southern region, both $f_{R,y}$ and $S_{R,a}$ were estimated as parameters by CAA. Prior estimates of the recreational selectivity pattern assumed it to be asymptotic because larger fish tend to be targeted by anglers (Figure 3; Table 2). In this study, I assumed that recreational selectivity was constant for ages 9+ and estimated the specific values for ages 2-8 rather than using the values in Table 2. To obtain an unique parameterization (Doubleday 1976), $S_{R,a}$ was set to 1 for ages 9+ fish, and thus $f_{R,y}$ was an estimate of the actual fishing mortality rate for those ages. The recreational selectivity values estimated by CAA of the southern model were used to estimate recreational fishing mortality rates in the northern and central population models.

In the northern and central regions, a commercial gill net fishery exists in addition to a recreational fishery, therefore an additional fishing mortality component was added to those models with:

$$F_{C,a,y} = S_{C,a} f_{C,y} \tag{8}$$

Values for commercial fishery selectivity were based on studies conducted by tribal biologists in Lake Superior (M. Ebener, COTFMA, pers. comm.). The selectivity pattern for this gear was dome shaped (Figure 3; Table 2).

Recreational fishing intensity ($f_{R,y}$) for the northern and central regions was estimated by:

$$f_{R,y} = q_R E_{R,y} \tag{9}$$

where q_R was the proportionality constant (catchability coefficient), and $E_{R,y}$ was the reported recreational fishing effort in year y in units of angler hours. Since fluctuations in recreational harvest matched the patterns in recreational effort, this procedure worked well for estimating recreational fishing intensity.

Initial attempts to estimate commercial fishing intensities ($f_{C,y}$) were approached by adjusting q_C to scale the reported effort so that predicted annual harvest would be equal to

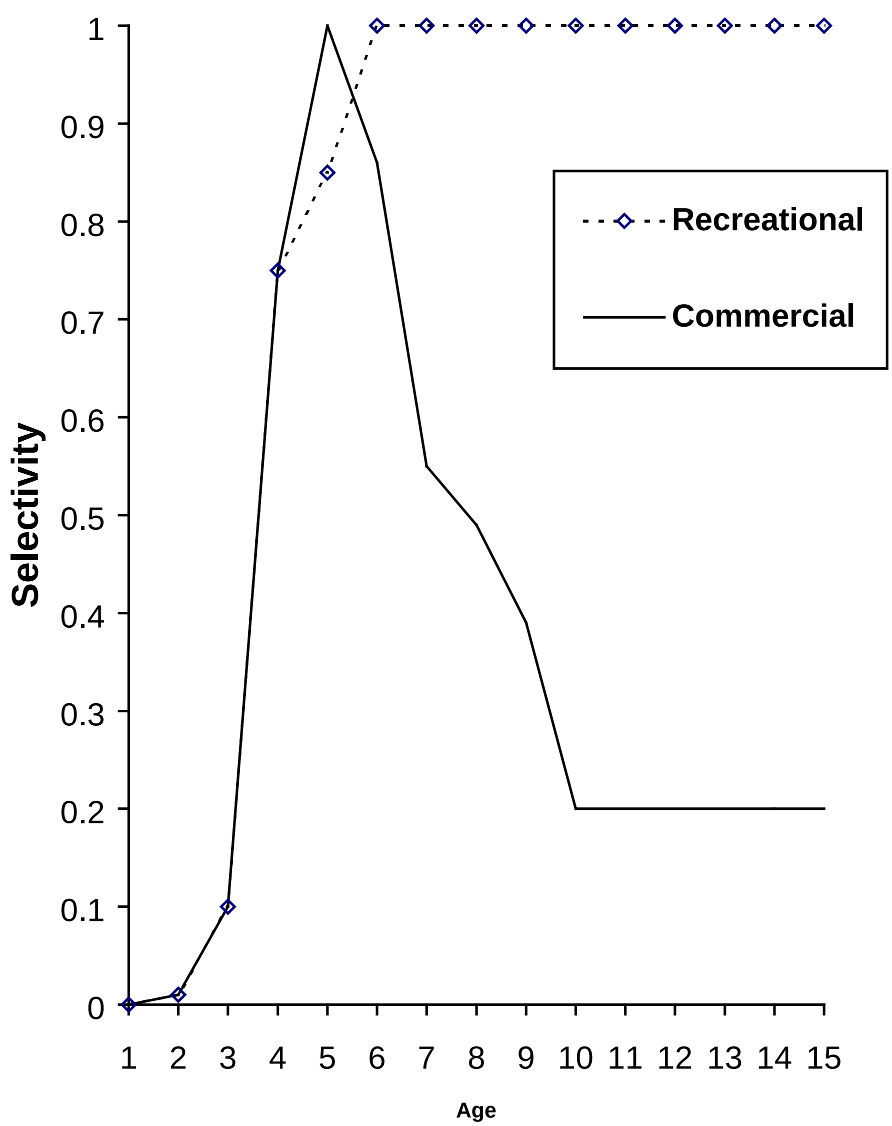

Figure 3. Selectivity patterns of the recreational and commercial gill net fisheries in Michigan waters of Lake Huron assumed by the lake trout total allowable catch (TAC) model.

observed values from harvest reports. This procedure was unsuccessful due to inconsistencies between the patterns in reported commercial effort and the patterns in reported commercial harvest. Therefore, year-specific commercial fishing intensities were estimated as parameters to match the model's predicted harvest to observed values using equation 8. Fishing intensities for MH-3/4/5 were estimated by CAA.

Fishery harvest ($C_{a,y}$) for age *a*, in year *y* was calculated using the Baranov catch equation (Ricker 1975):

$$C_{a,y} = N_{a,y} F_{a,y} \left[\frac{1 - e^{-(Z_{L,a,y} + F_{a,y} + M_a)}}{(Z_{L,a,y} + F_{a,y} + M_a)} \right] \tag{10}$$

where $F_{a,y} = F_{R,a,y} + F_{C,a,y}$ in northern and central Lake Huron. In the southern region, only a recreational fishery exists so $F_{a,\,y} = F_{R,\,a,\,y}$. For the northern and central area, the recreational or commercial harvest was estimated by:

$$C_{X,a,y} = N_{a,y} F_{X,a,y} \left[\frac{1 - e^{-(Z_{L,a,y} + F_{a,y} + M_a)}}{(Z_{L,a,y} + F_{a,y} + M_a)} \right] \tag{11}$$

where *X* was either *R* (recreational) or *C* (commercial). Similarly, numbers of lake trout killed by sea lampreys ($C_{L\,,\,a,y}$) were estimated using:

$$C_{L,a,y} = N_{a,y} Z_{L,a,y} \left[\frac{1 - e^{-(Z_{L,a,y} + F_{a,y} + M_a)}}{(Z_{L,a,y} + F_{a,y} + M_a)} \right] \tag{12}$$

Biomass of the population was calculated using mass-at-age information by:

$$B_y = \sum_a N_{a,y} m_a \tag{13}$$

where B_y was the biomass in year *y*, and $N_{a,y}$ was the numbers at age *a* in year *y* calculated by the model, and m_a was the mass at age *a*. The yield or biomass of the harvest was calculated in a similar fashion:

$$Y_y = \sum_a C_{a,y} m_a \tag{14}$$

Average mass-at-age used in this model were based on the compilation of MDNR survey data from 1984-1994 (Table 3). A von Bertalanffy model was used to estimate average mass for missing ages (C.P. Ferreri, Pennsylvania State University, unpublished).

Statistical catch-at-age analysis of the southern Lake Huron lake trout population model

Based on the availability of harvest-at-age information from MDNR creel and research surveys of Lake Huron, statistical catch-at-age (CAA) analysis was implemented to calibrate the lake trout population model. This was only performed for the southern stock because there were insufficient data for the other regions (e.g., recreational harvest and fishery age-composition not available). The CAA approach integrates information on fishery harvest, age composition of the fishery harvest, fishery effort, survey catch per unit effort (CPUE), and age composition of the survey CPUE to estimate parameter values of the lake trout population model. Some of the reported parameter values listed in Table 2 were re-estimated by CAA. Model parameters that were estimated by the CAA analysis are listed in Table 4.

In addition to estimating fishing mortality related parameters, CAA analysis was also used to assess the sensitivity of parameters used to estimate sea lamprey-induced mortality (Z_L) by including a proportionality coefficient (μ') to equation 4 as follows:

$$Z_{Li,k} = \mu' \overline{W}_{i,k} \left(\frac{1 - P_{S,i}}{P_{S,i}} \right) \tag{15}$$

The proportionality coefficient would equal 1 if $\overline{W}_{i,k}$, and $P_{S,i}$ were accurate, and the

Table 3. Average mass-at-age of lake trout in Michigan waters of Lake Huron. Data provided by Michigan Department of Natural Resources and C.P. Ferreri, Pennsylvania State University.

Age	North (MH-1)	Central (MH-2)	South (MH-3/4/5)
1	0.09	0.09	0.09
2	0.157	0.179	0.223
3	0.365	0.458	0.593
4	0.731	1.041	1.293
5	1.140	1.712	2.123
6	1.539	2.474	2.931
7	1.878	2.861	3.467
8	2.264*	3.419	3.964
9	2.610*	3.928*	4.390
10	2.947*	4.386*	4.765
11	3.276*	4.816*	5.141
12	3.597*	5.220*	5.388
13	3.910*	5.599*	5.451
14	4.216*	5.956*	5.486
15	4.514*	6.290*	6.056
16	4.804*	6.605*	6.291*
17	5.088*	6.900*	6.453*
18	5.364*	7.178*	6.596*
19	5.634*	7.439*	6.722*
20	5.897*	7.684*	6.833*
>20	6.154*	7.914*	6.930*

* estimated by von Bertalanffy procedure (C.P. Ferreri, Pennsylvania State University, unpublished)

Table 4. Parameters of the southern Lake Huron (MH-3/4/5) lake trout population model estimated by statistical catch-at-age analysis.

Parameter	Description	Units
μ'	Proportionality coefficient for sea lamprey-induced mortality	unitless
c	Proportionality coefficient for natural mortality	unitless
$f_{R, y}$	Recreational fishing intensity for year *y*	$year^{-1}$
M_1	Natural mortality (excluding sea lamprey-induced mortality) for age-1 lake trout	$year^{-1}$
$N_{2, 1984} \ldots N_{20+, 1984}$	Initial abundance-at-age in 1984	numbers
$S_{R, 2} \ldots S_{R, 8}$	Recreational fishery selectivity	unitless
$S^*_2 \ldots S^*_4$, $S^*_6 \ldots S^*_{10+}$	Survey selectivity, S^*_5 assumed to equal 1	unitless
τ	Rate of decrease in natural mortality (excluding sea lamprey-induced mortality) for lake trout	$year^{-1}$ age^{-1}
q_R	Recreational fishery catchability coefficient	angler $hours^{-1}$
q*	Survey catchability coefficient	meters of gill net^{-1}

assumptions used to relate these to Z_L were met. Thus any such deviations from these assumptions would be indicated by the departure of the CAA estimate of μ' from unity.

Natural mortality excluding sea lamprey-induced mortality (M_a) was estimated using two approaches. It was possible to estimate M_a in this study because recruitment was known and there were data to estimate sea lamprey-induced mortality. The first approach was based on the assumption that the relative differences in natural mortality across ages from the reported estimates (Table 2) were accurate, but the specific values may be incorrect. Hence, $M_a = c(M_a^*)$, where M_a^* were the reported natural mortality rates. The value of *c* would equal 1 if the current vector of natural mortality rates were accurate. Otherwise, any variations in natural mortality from the current rates would be indicated by the CAA estimate of *c*. The second approach estimated natural mortality as a type 3 exponential survivorship function since it reasonably describes the age-specific pattern of mortality in lake trout. The equation was:

$$M_a = M_1 e^{-\tau(a-1)} + 0.1 \qquad (16)$$

where M_1 was the instantaneous rate of natural mortality for age-1 lake trout, τ was the rate of decrease, and *a* was age. M_1 and τ were estimated by catch-at-age analysis as parameters. This procedure facilitated the solution process by allowing only two parameters to be estimated for natural mortality. The minimum natural mortality rate was set at 0.1 so that the function did not underestimate natural mortality rates for older fish. This minimum value was set just below the natural mortality rate used in the Lake Superior lake trout models, which is based on a catch curve applied to a refuge population in that lake, as described by J. Selgeby (National Biological Service, Ashland, WI) at the July 1995 Lake Superior Technical

Committee Meeting (J. Bence, Michigan State University, pers. comm.).

Following Methot (1990), differences between model predictions and observed values were quantified using a specified error model cast in terms of a log-likelihood function. Optimum parameter values were ones that maximized the log-likelihood. The maximum likelihood solution was found numerically using a quasi-Newton search algorithm, central differencing to estimate the partial derivatives of the objective and constraint functions, and quadratic extrapolation to obtain estimates of the parameters. More specific details of the maximum likelihood approach for analyzing catch-at-age data are explained by Fournier and Archibald (1982), Methot (1990), and Bence et al. (1993).

The log-likelihood (L) equation was:

$$L = L_1 + L_2 + L_3 + L_4 + L_5 \tag{17}$$

where L_1 was the log-likelihood of the fit to the fishery harvest, L_2 was the log-likelihood associated with the survey index of abundance, L_3 was the log-likelihood of the fit to the fishery age composition, L_4 was the log-likelihood associated with the fit to the survey age composition data, and L_5 was the log-likelihood of the fit to the fishery effort data. The individual components were:

$$L_1 = \left(-\sum_y \left\{ 0.5 \left[\frac{\ln\left(\frac{C_y}{C'_y}\right)}{\sigma_f} \right]^2 \right\} \right) + \ln\left[\left(\frac{1}{\sigma_f \sqrt{2\pi}} \right)^N \right] \tag{18}$$

$$L_2 = \left(-\sum_y \left\{ 0.5 \left[\frac{\ln\left(\frac{K_y}{K'_y}\right)}{\sigma_s} \right]^2 \right\} \right) + \ln\left[\left(\frac{1}{\sigma_s \sqrt{2\pi}} \right)^N \right] \tag{19}$$

$$L_3 = \left[\sum_y J_y \sum_a P'_{a,y} \ln(P_{a,y}) \right] + \left[\sum_y \ln\left(\frac{J_y!}{n_a! n_{a+1}! \ldots n_k!} \right) \right] \tag{20}$$

$$L_4 = \left[\sum_y j_y \sum_a p'_{a,y} \ln(p_{a,y}) \right] + \left[\sum_y \ln\left(\frac{j_y!}{u_a! u_{a+1}! \ldots u_k!} \right) \right] \tag{21}$$

$$L_5 = \left(-\sum_y \left\{ 0.5 \left[\frac{\ln\left(\frac{E_y}{E'_y}\right)}{\sigma_E} \right]^2 \right\} \right) + \ln\left[\left(\frac{1}{\sigma_E \sqrt{2\pi}} \right)^N \right] \tag{22}$$

where C_y was the model predicted fishery harvest (equation 10), C'_y was the observed fishery harvest, K was the predicted survey CPUE, K'_y was the observed survey CPUE, N was the total number of years of data, $P_{a,y}$ was the proportion-at-age of the predicted fishery harvest, $P'_{a,y}$ was the observed proportion-at-age of the fishery harvest, J_y was the sample size for the fishery age composition with maximum values set to 200, n_a was the fishery harvest for age a, $p_{a,y}$ was the predicted survey proportion-at-age, $p'_{a,y}$ was the observed proportion-at-age of the survey catch, j_y was the sample size for the survey age composition, u_a was the survey CPUE for age a, E_y was the predicted fishery effort, E'_y was the observed fishery effort, σ_f was the standard error (s.e.) of the log of harvest, σ_s was the s.e. of the $\log_e$ of the survey CPUE, and σ_E was the s.e. of the log of fishery effort.

The predicted survey CPUE ($K_{a,y}$) was calculated by

$$K_{a,y} = q^{*}S_{a}^{*}N_{a,y} \tag{23}$$

where q^* was the survey proportionality constant, S_a^* was the survey selectivity at age a, and $N_{a,y}$ was the number of lake trout at age a, and in year y (from equation 6). K_y was the sum of all $K_{a,y}$ for year y.

The predicted fishery effort (E_y) was calculated using

$$E_y = \frac{f_y}{q} \tag{24}$$

where f_y was the fishing intensity in year y, and q was the proportionality constant.

Estimates of total recreational harvest (C'_y) of lake trout from 1984-1993 were calculated for use by the catch-at-age procedures (Table 19, Appendix). These data were from MDNR creel surveys conducted at ports in Lake Huron and represents all recreational harvest of lake trout in Michigan waters of Lake Huron. For southern Lake Huron, the ports with significant harvest were Oscoda, Harrisville, Tawas, Port Austin, and Harbor Beach (Figure 4). Harvest data were not available for all ports in all years. Missing harvest data were estimated based on the ratio of the harvest in ports without data to the harvest in ports with data from the other years where data on all ports were available (Table 19, Appendix).

Recreational fishery age composition information was derived from subsamples of the recreational harvest by MDNR creel clerks. These subsamples were usually collected monthly in each year from May through September. Recreational fishery age composition ($P'_{a,y}$) information was only available for 1985-1988 and 1991-1992 and were not available for all months (Table 20, Appendix). Fortunately, catch-at-age analysis does not require age

Figure 4. Lake trout sport harvest ports surveyed by the Michigan Department of Natural Resources in Michigan waters of Lake Huron (Rakoczy and Svoboda 1994a).

composition data for every year to calibrate the population model. The harvest-at-age information for each year with data available was estimated by pooling the harvest subsamples across all months by ports and estimating the proportions for each age and then multiplying these values by the total harvest.

Estimates of an index of recreational fishery effort (E'_y) were available for 1984-1993 from MDNR creel surveys (Table 19, Appendix). Effort was assumed to be proportional to fishing mortality for lake trout. At Harbor Beach, the effort of the sport fishery shifted during this time period from the targeting of salmonines to walleye (*Stizostedion vitreum*), which was also reflected in the harvest (J. Johnson, Alpena Fisheries Research Station, MDNR, pers. comm.). Hence, this port was not included since trends in effort there would not be proportional to fishing mortality of lake trout. As with recreational harvest, effort data were not available for all ports in all years and were estimated in the same manner as for harvest.

Commercial harvest data for lake trout in Canadian waters of southern Lake Huron were also included in the total fishery harvest to account for all removals from the population (Table 21, Appendix). Nearly all of the lake trout harvested in Canadian waters were immigrants from adjacent Michigan waters, because there has been no stocking of lake trout by Canada in the southern main basin of Lake Huron. In addition, natural recruitment was thought to be insignificant or non-existent (L. Mohr, Lake Huron Management Unit, Ontario Ministry of Natural Resources, pers. comm.). Lake trout commercial harvest, from 1984-1993, in regions OH-3, OH-4, and OH-5 (Figure 2) were available only as total mass in kilograms. No biological information was available for the commercial harvest to estimate harvest in numbers or catch-at-age. Thereupon, total numbers of lake trout harvested in the commercial yield each year were estimated by dividing the annual yield by the mean mass of a recreationally harvested fish for the corresponding year. This harvest was pooled with the recreational harvest and assumed to have the same age composition. A separate commercial fishing mortality was not estimable due to the lack of information on factors such as effort and selectivity.

Observed survey CPUE ($K'_{a,y}$) were collected from MDNR spring gill net surveys conducted from 1984-1993 (Tables 22-24, Appendix). The observed proportion-at-age of the survey CPUE ($p'_{a,y}$) was simply the total numbers at each age *a* in year *y* divided by the total number of fish caught in year *y* (K'_y). σ_f , σ_s , and σ_E , which are estimates of the variability of the data, function as weighting factors in the log-likelihood function and were estimated from the MDNR creel and gill net surveys. The standard error on the log-normal scale (σ) of fishery harvest, fishery effort, and survey CPUE were calculated from the coefficient of variation (C.V.) of each data type (Law and Kelton 1982) using:

$$\sigma = \sqrt{\ln\left[(\mathrm{C.V.})^2 + 1\right]} \tag{25}$$

The C.V. of the fishery harvest was 0.502 ($\sigma_f = 0.474$), fishery effort C.V. was 0.251 (σ_E = 0.247), and survey CPUE C.V. was 0.433 ($\sigma_s = 0.415$).

The error structure of L_3 and L_4 was based on the multinomial distribution. A maximum sample size of 200 was established so that large samples would not dominate the model's fit (e.g., Fournier and Archibald 1982). The rationale for the multinomial model as opposed to the log-normal approach used by models such as CAGEAN (Deriso et al. 1985) was that the log-normal model essentially assumes that the coefficient of variation of the numbers caught at each age was constant. However, the multinomial model allows for higher C.V.s for ages that are less frequently observed (Methot 1990).

Sensitivity of the southern model to calibration data

The model's sensitivity to each of the data sources that were used to estimate model parameters by catch-at-age analysis was evaluated by multiplying of each log-likelihood component with an emphasis or weighting factor (λ_i). These weighting factors were used to explore the implications of over- or de-emphasizing the fit of one type of data in comparison to that of another. If the assumed error structures were accurate, and the separability assumption was correct, the λ for each of the components (i.e., L_1 , L_2 , L_3 , L_4 , L_5) should equal 1 to provide the maximum likelihood solution for the total log-likelihood (Methot 1990). Sensitivity of the model to each data source (i.e., fishery harvest, fishery age composition, fishery effort, survey CPUE, and survey age composition) was evaluated by setting λ_i to 0.1, 0.5, and 5. High sensitivity would be indicated by large changes in the likelihood values.

<u>Calibration of the northern and central lake trout population models</u>

Statistical catch-at-age analysis of the northern and central population models was not possible due to incomplete catch-at-age information in these regions. Some parameters of the lake trout population models for these areas were calibrated using a maximum likelihood approach, while having other parameters fixed at values obtained by the statistical catch-at-age analysis of the southern model. These fixed parameters included natural mortality rates and recreational fishery selectivity. Models for northern and central Lake Huron were calibrated by matching the model's prediction of harvest to observed values by estimating year-specific commercial fishing intensities ($f_{C,\,y}$), catchability coefficient for the recreational fishery (q_R), and the survival rates for cohorts before 1984 (ρ_a). ρ_a was the proportion surviving from age *a* to *a+1* and were needed to estimate the age-specific abundance in 1984 ($N_{a,\,1984}$), the starting year of the model. For ages >1, $N_{a,1984}$ was estimated by:

$$N_{a,1984} = [N_{1,\,1984-(a-1)}]\,(\rho_1\,\rho_2 \ldots \rho_{a-1}) \qquad (26)$$

where $N_{1,\,1984-(a-1)}$ was the age-1 abundance of a cohort as determined from stocking data.

The "optimum" set of commercial fishing intensities ($f_{C,y}$) and q_R were those that minimized the difference in the log sum of squared residuals for total harvest (Deriso et al. 1985; Megrey 1989). The objective function (ϕ) was written as:

$$\phi(f_{C,y}[y = 1984 - 1993], q_R) = \sum_y \left[(\log_e C'_{C,y}) - (\log_e C_{C,y})\right]^2 + \sum_y \left[(\log_e C'_{R,y}) - (\log_e C_{R,y})\right]^2 \qquad (27)$$

where $C'_{C,y}$ was observed commercial harvest in year *y*, $C_{C,y}$ was predicted commercial harvest, $C'_{R,y}$ was observed recreational harvest, and $C_{R,y}$ was predicted recreational harvest. Reported recreational harvest from MDNR creel reports are listed in Table 19 of the Appendix.

For the central region, commercial harvest was only in Canadian waters (OH-1, OH-2) and was reported as total biomass. No biological information was available from the commercial harvest to estimate harvest in numbers. Thereupon, total numbers of lake trout harvested in the commercial yield each year were estimated by dividing the total annual yield by the mean mass of a recreationally harvested fish for the corresponding year (Table 25, Appendix).

In northern Lake Huron, there were both a tribal commercial fishery in U.S. waters and a commercial fishery in adjacent Canadian waters. Since commercial harvest was only available as total biomass, the commercial harvest portion of the objective function was expressed in terms of yield. The observed commercial harvest values used in the calibration process were scaled 20% higher than actual reported values because of suspected under-reporting of harvest by commercial fishers (M. Ebener, Chippewa-Ottawa Treaty Fishery Management Authority, pers. comm.). Reported annual commercial harvest for northern Lake Huron are listed in Tables 25-26 of the Appendix. Due to the lack of sufficient sea lamprey wounding data for lake trout >533 mm in northern Lake Huron, sea lamprey-induced mortality rates for these sizes of fish were assumed to be at least equal to central Lake Huron rates. However, this assumption was likely to be conservative based on reports that sea lamprey abundance is highest in northern Lake Huron (Eshenroder at al. 1987). As an alternative, I estimated sea lamprey-induced mortality rates for lake trout >533 mm in northern Lake Huron by attempting to find the level of Z_L that was consistent with harvest levels and age compositions in the surveys. I did this by estimating the parameter μ' in the objective function of the northern model. The parameter μ' was the proportionality coefficient for sea lamprey-induced mortality, which was defined in equation 15 of the Methods section. This parameter scaled Z_L to allow the model predictions to match the age distribution of the survey index of abundance and the observed values for commercial harvest. This was done only for lake trout >533 mm since there were sufficient data for wounding rates for the 432-533 mm length class. Thus, for the calibration of the northern Lake Huron model, the following term was added to the objective function in equation 27:

$$L_4 = \left[\sum_y j_y \sum_a p'_{a,y} \ln(p_{a,y})\right] + \left[\sum_y \ln\left(\frac{j_y!}{u_a!u_{a+1}!\ldots u_k!}\right)\right]$$

where $p'_{a,y}$ was the observed survey proportion-at-age a in year y and $p_{a,y}$ was the model's predicted value for survey proportion-at-age, n_a was the fishery harvest for age a, j_y was the sample size for the survey age composition, and u_a was the survey CPUE for age a.

Model projections

Three fishery management scenarios were run to evaluate the effects of decreasing the sea lamprey wounding rates on lake trout by model projections of abundance of ages 8 and older fish and total harvest from 1994-2010. In order to view the effects of the management scenarios in the mature portion of the population, ages 8+ were evaluated rather than total abundance of all ages. These projections were evaluated under three fishery conditions: 1) total allowable catch (TAC) with Z at the GLFC lake trout rehabilitation target maximum of 0.59 year^{-1}; 2) constant fishing mortality rate equal to average of f_y during 1991-1993; and 3) No fishing. The TAC plan is a management strategy that establishes harvest quotas based on estimates of mortality rates for all sources in relation to an established target maximum total mortality rate (e.g., A=0.45, Z=0.59 year^{-1}). A quota will be possible only if natural and sea lamprey-induced mortality rates are below the established target maximum total mortality rate.

Age-specific natural mortality rates were assumed to be constant, as were the base sea lamprey-induced mortality and stocking numbers (recruitment), which were set equal to the average of current rates (1991-1993). Total abundance and harvest were projected for five levels of sea lamprey-induced mortality: current rates, 75%, 50%, 25%, and 0% of current rates. TAC was computed by estimating the maximum fishing intensity (f_{max}) that would match harvest and limit the instantaneous rate of total mortality to 0.59 year^{-1} for ages 5 and older. In northern and central Lake Huron, where there were both commercial and recreational fishing, the fishing intensity of the recreational fishery ($f_{R,\ max}$) was estimated by the following:

$$f_{R,\ max} = \alpha\ f_{C,\ max} \qquad (28)$$

where α was the ratio of $f_{R,\ max}$ to $f_{C,\ max}$ averaged from 1991-1993. For the north, $\alpha = 0.0095$ and in the central area, $\alpha = 0.2526$.

RESULTS

The results are reported in five subsections. First, I present the findings from the analysis of sea lamprey wounding patterns on lake trout according to length of lake trout, geographic region, and year. Secondly, I discuss the ANOVA models constructed to estimate mean wounding rates for specific length class, geographic region, and year combinations where data were missing in central and southern Lake Huron. Furthermore, I report age- and year-specific rates of lamprey induced mortality for these regions. In the third part, I present results from statistical catch-at-age analysis of the southern lake trout population model. In part four, I describe results from the calibration of the northern and central Lake Huron models. Lastly, I report simulation results from the population models for northern, central, and southern Lake Huron.

Patterns in sea lamprey wounding

ANOVA models constructed to assess patterns in wounding rates are listed in Table 5 and included as factors lake trout size, geographic region, and year. Significance levels for main effects and interactions for each model are listed in Table 6. In all models, there were significant interactions between year and geographic region, and year and length class. However, these year effects and their interactions do not seem to reflect either overall or length class specific long-term trends. Analyses presented below suggest that the significant results

Table 5. Levels for each factor in analysis of variance models used to evaluate patterns in sea lamprey wounding of lake trout in Michigan waters of Lake Huron.

	Factor		
Model	Year	Geographic Region†	Length Class
1	1984, 1985, 1986, 1987, 1988, 1989, 1990, 1991, 1992, 1993, 1994	central, south	432-533 mm, 534-635 mm, 636-737 mm, >737 mm
2	1984, 1985, 1986, 1987, 1988, 1989, 1990, 1991, 1992, 1993, 1994	central	432-533 mm, 534-635 mm, 636-737 mm, >737 mm
3	1984, 1985, 1986, 1987, 1988, 1989, 1990, 1991, 1992, 1993, 1994	south	432-533 mm, 534-635 mm, 636-737 mm, >737 mm
4	1984, 1985, 1986, 1987, 1988, 1989, 1990, 1991, 1992, 1993, 1994	north, central , south	432-533 mm, 534-635 mm
5	1984, 1985, 1986, 1987, 1988, 1989, 1990, 1991, 1992, 1993, 1994	central, south	534-635 mm, 636-737 mm, >737 mm
6	1984, 1985, 1986, 1987, 1988, 1989, 1990, 1991, 1992, 1993, 1994	central, south	534-635 mm, 636-737 mm

† North= MH-1, central= MH-2, and south= MH-3/4/5.

Table 6. Significance levels (attained *P*-value) for main effects and interactions in analysis of variance models of sea lamprey wounding rates on lake trout in Michigan waters of Lake Huron, 1984-1994. Further information on data used with these models is given in Table 5.

	Main Effect			Interaction		
Model	Year (Y)	Geographic Region (GR)	Length Class (LC)	Y x GR	Y x LC	GR x LC
1	0.0001	0.0148	0.0001	0.0042	0.0001	0.0527
2	0.0001	------	0.0001	-----	0.0001	------
3	0.0001	------	0.0001	-----	0.0001	------
4	0.0001	0.0169	0.0001	0.0001	0.0001	0.1484
5	0.0001	0.0397	0.0001	0.0132	0.0001	0.3142
6	0.0001	0.0001	0.0001	0.0093	0.0033	0.1316

were from short-term fluctuations in the true wounding rates from year to year. Wounding rates are presented as least-square means of square root transformed wounds per fish due to biases in back-transformation. However, the overall patterns in wounding rates were similar between transformed and untransformed wounding rates.

Patterns in wounding according to length of lake trout

In central and southern Lake Huron, wounding rates increased significantly with length class of lake trout (Table 6; Figure 5). The estimated wounding rates for the 636-737 mm, and >737 mm length classes were not significantly different, possibly due to the low sample sizes for the largest length class. Northern Lake Huron (MH-1) was not included in this model because no fish of these sizes were collected in this region in most years. The ANOVA model for this analysis was designated as Model 1 (Table 5). Because near significant interaction between geographic region and length class was detected (Table 6), models 2 and 3 were constructed to test the effects of length class on wounding rates independent of geographic region. Model 2 contains only the central area (MH-2), and model 3 contains only the south (Table 5). For these additional models wounding rates increased significantly with length of lake trout (Table 6; Figure 6).

Geographic patterns in wounding rates

Analysis of wounding rates across all three geographic areas was only possible for the two smaller length classes of lake trout (432-533, and 534-635 mm) because few large lake trout were collected in the northern region for the 636-737 mm, and >737 mm length

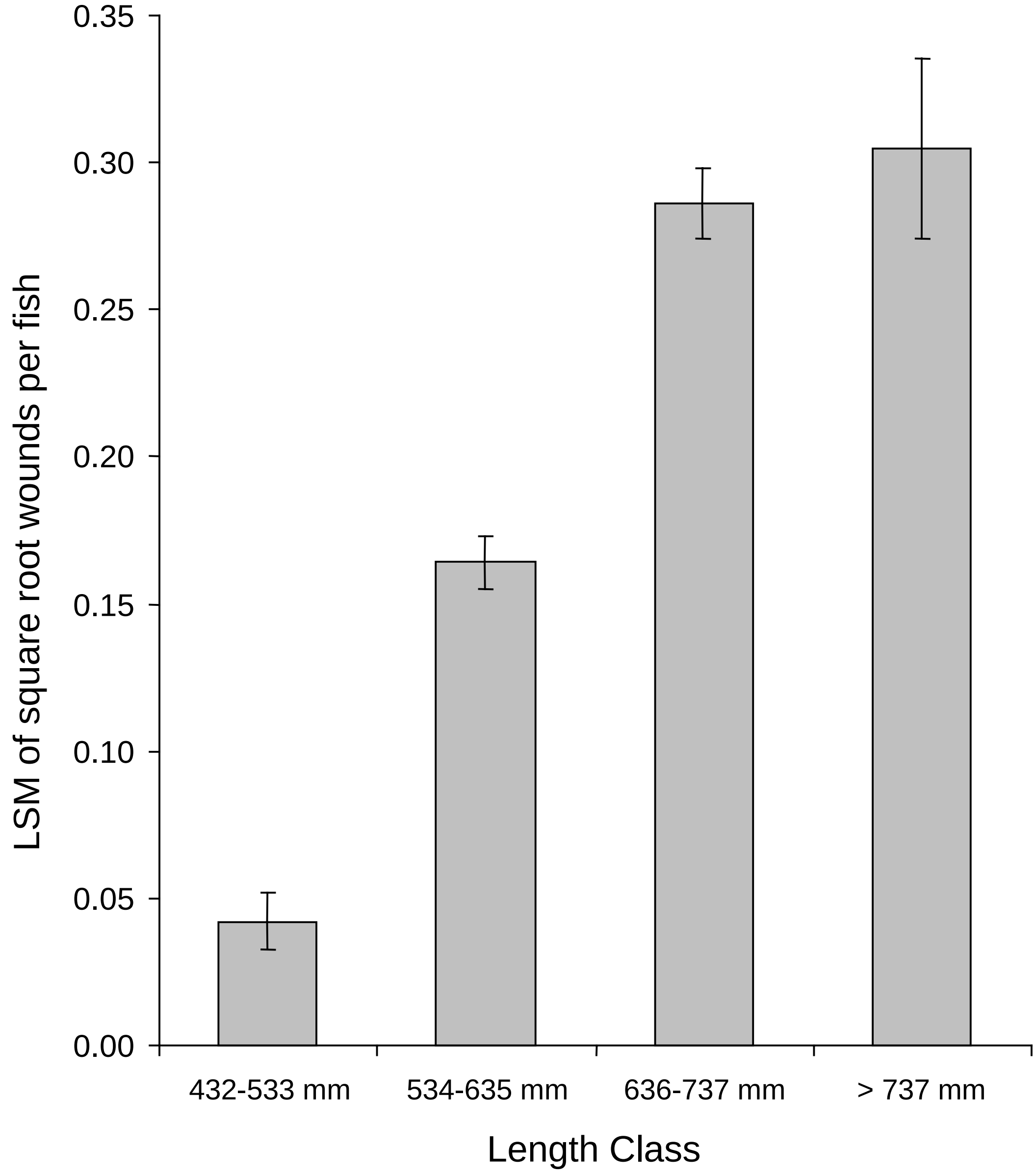

Figure 5. Sea lamprey wounding patterns by length class of lake trout for central (MH-2) and southern (MH-3/4/5) Lake Huron, 1984-1994. Least-square means (LSM) of square root transformed wounds per fish calculated from analysis of variance with length class, geographic region, and year as treatment factors. Estimated means for length class, adjusted for all other effects and interactions, reported with one standard error.

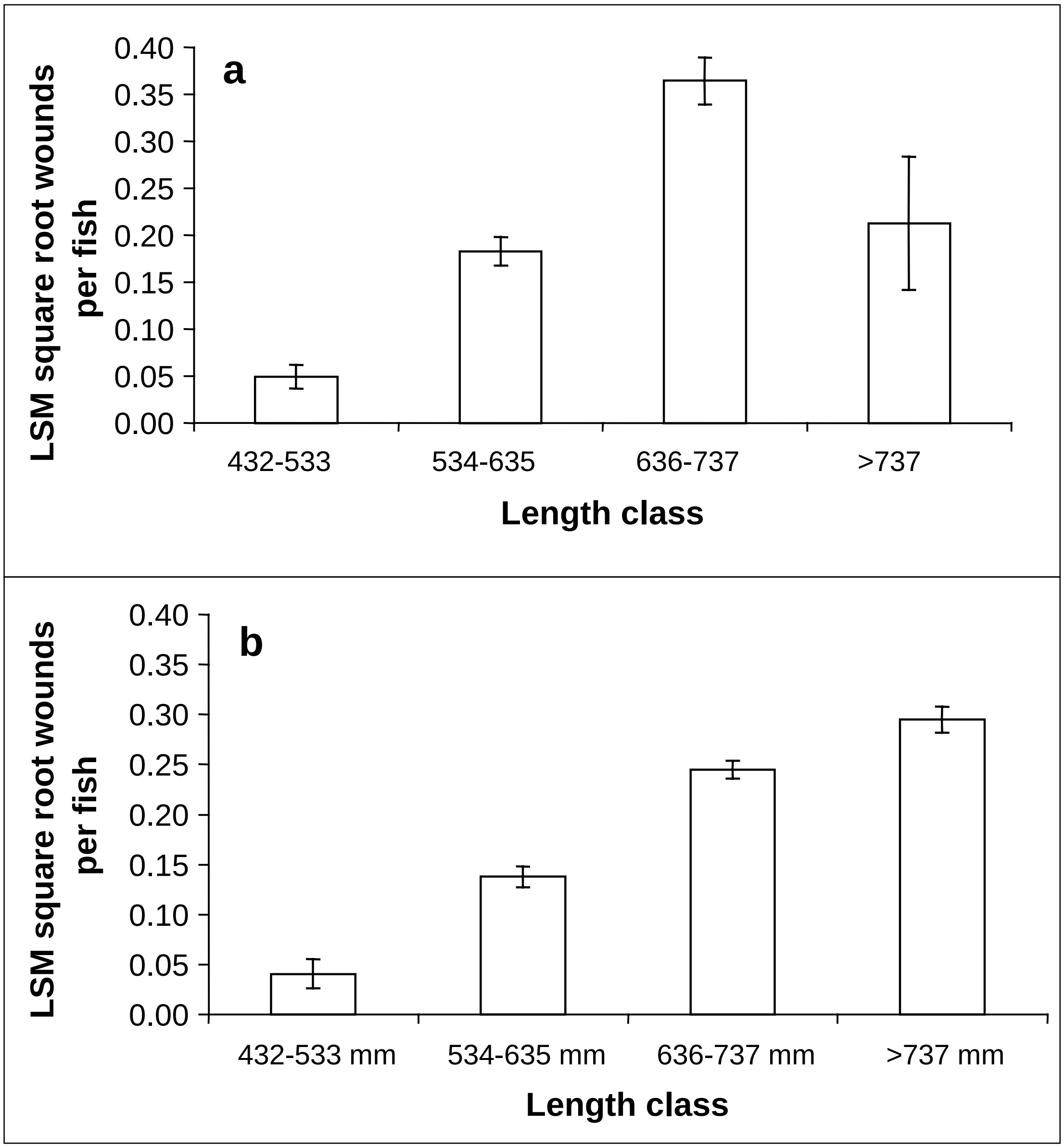

Figure 6. Sea lamprey wounding of lake trout in Michigan waters of Lake Huron, 1984-1994. (a) Central region (MH-2). (b) Southern region (MH-3/4/5). Least-square means (LSM) of square root transformed wounds per fish calculated from analysis of variance with length class and year as treatment factors. Estimated means for length class, adjusted for all other effects and interactions, reported with one standard error.

categories (see Table 1). The smallest length class (432-533 mm) of lake trout had relatively low wounding rates (<0.08), and did not differ geographically, while differences in wounding rates were significantly higher in central than in southern Lake Huron for 534-635 mm lake trout (Model 4, Table 5; Figure 7).

Wounding rates for the north did not differ significantly from the other two areas for the 432-533 mm length class (Figure 7). However, the results for the 534-635 mm length class in the north were biased. Further review of the 534-635 mm data revealed that most fish in this length category in northern Lake Huron were distributed towards the smaller size ranges, while in central and southern Lake Huron the observations were evenly distributed across all lengths. Consequently, the wounding rates for 534-635 mm lake trout in northern Lake Huron were not accurately represented. Thus, the only valid comparisons with northern Lake Huron were for the 432-533 mm lake trout, which did not differ geographically.

Although I was not able to evaluate how sea lamprey-induced mortality rates (as indexed from wounding data) for lake trout >533 mm in northern Lake Huron compared with the other areas of the main basin, other sources of information indicated that sea lamprey abundance was highest in the north. One source of information was the observations of the number of sea lampreys attached to lake trout and chinook salmon (*Oncorhynchus tshawytscha*) caught aboard sport fishing charter boats (Rakoczy and Rogers 1991a, 1991b; Rakoczy 1992; Rakoczy and Svboda 1993, 1994b). In the main basin of Lake Huron from 1989-1993, the mean number of sea lampreys attached to both lake trout and chinook salmon were significantly higher in the north compared to the other regions (Figure 8). This implies that sea lamprey abundance and attack rates were highest in northern Lake Huron.

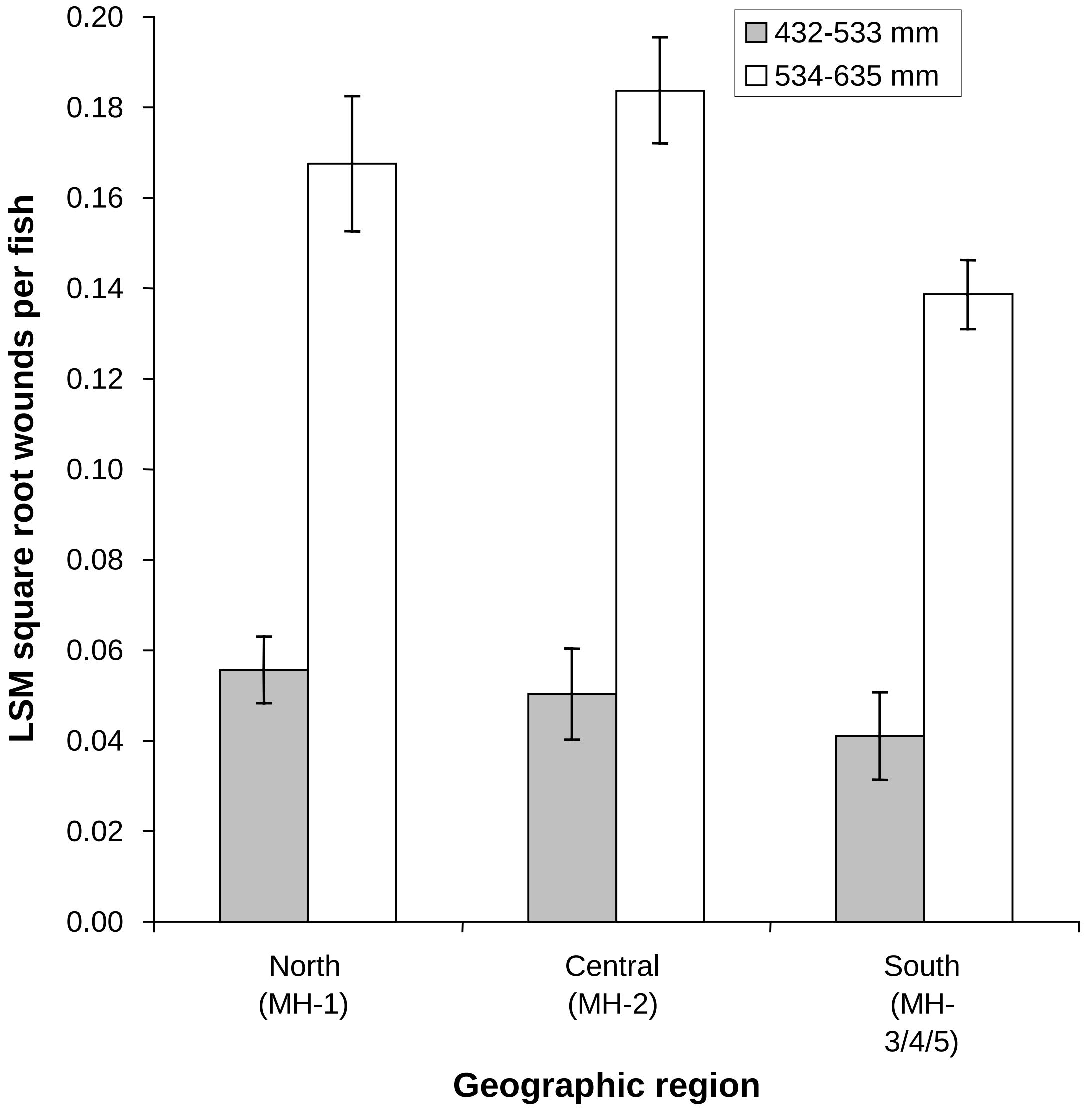

Figure 7. Geographic patterns in sea lamprey wounding of lake trout less than 636 mm in Lake Huron, Michigan for 1984-1994. Least-square means (LSM) of square root transformed wounds per fish calculated from analysis of variance with length class, geographic region, and year as treatment factors. Estimated means for length class and geographic region, adjusted for all other effects and interactions, reported with one standard error.

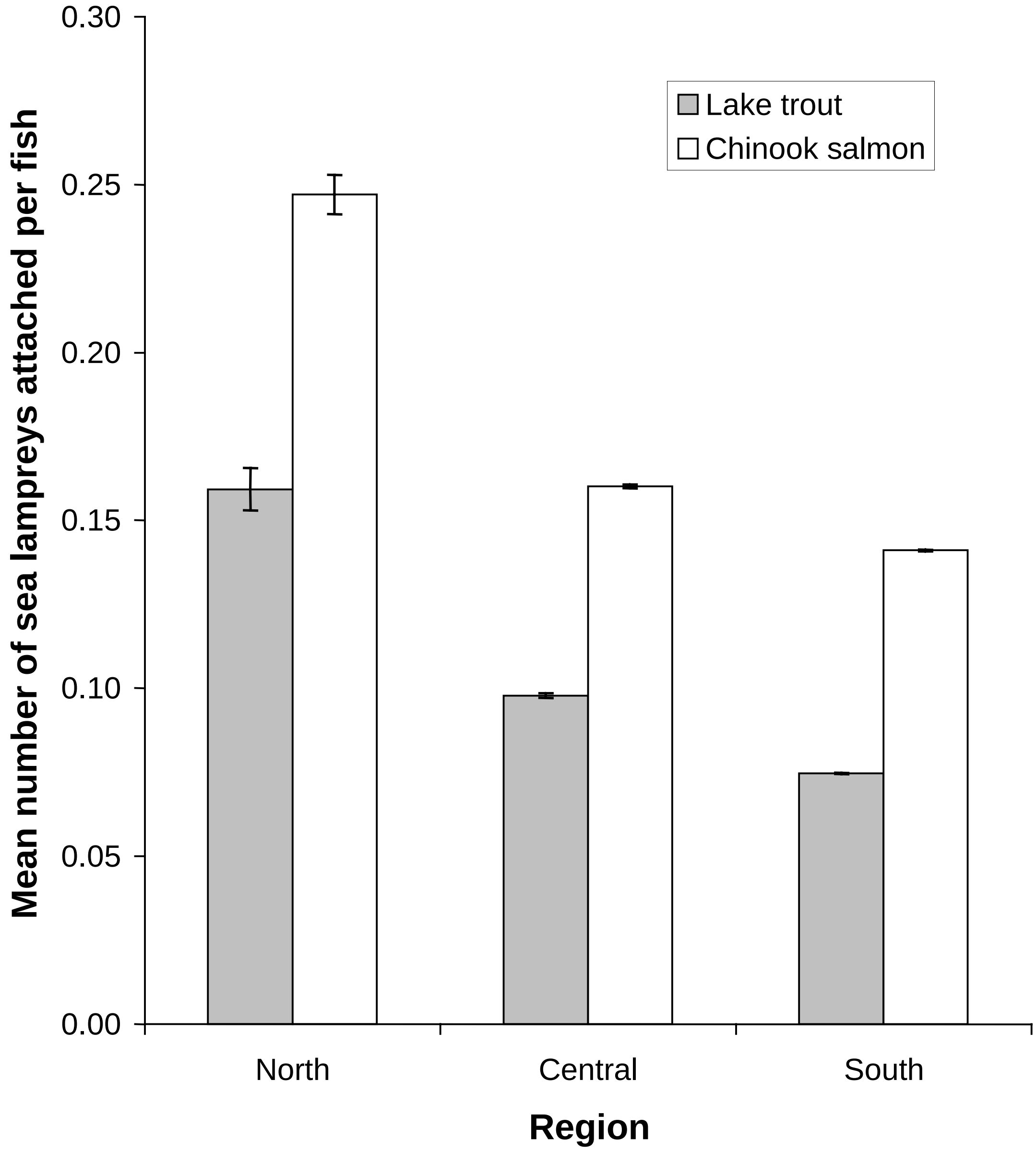

Figure 8. Mean number of sea lampreys attached to lake trout and chinook salmon caught aboard sport fishing charter boats in Michigan waters of Lake Huron, 1989-1993. Data from Michigan Department of Natural Resources. Error bars represent two standard errors.

Another data source that indicates that sea lamprey abundance was highest in northern waters were assessment catches of spawning phase and larval sea lampreys conducted by the Canadian Department of Fisheries and Oceans and the U.S. Fish and Wildlife Service. In the tributaries monitored in the main basin of Lake Huron, the highest catches of spawning phase were in the St. Mary's, Cheboygan, and Ocqueoc Rivers which are located in northern waters. Likewise, assessment catches of sea lamprey larvae were also highest in northern waters of Lake Huron (J. Heinrich, Sea Lamprey Control, U.S. Fish and Wildlife Service, Marquette, MI, pers. comm.). Lastly, Mormon (1979) reported that abundance of sea lamprey larvae were higher in the northern than in the southern regions of Lake Huron due to habitat preferences. Overall, there is sufficient evidence indicating that sea lamprey abundance is highest in the northern waters of Lake Huron, implying that sea lamprey-induced mortality is also likely to be highest in the north.

For lake trout larger than 533 mm, wounding rates were significantly higher in the central area than in the south (Model 5, Table 5; Figure 9). Due to the predominance of extremely low sample sizes for the >737 mm length class in the central area (see Table 1), differences in wounding rates between central and southern Lake Huron were further evaluated using only the 534-635 mm and 636-737 mm length classes (Model 6, Table 5). For these length classes, wounding rates were found to be significantly higher in the central region than in the south (Figure 10).

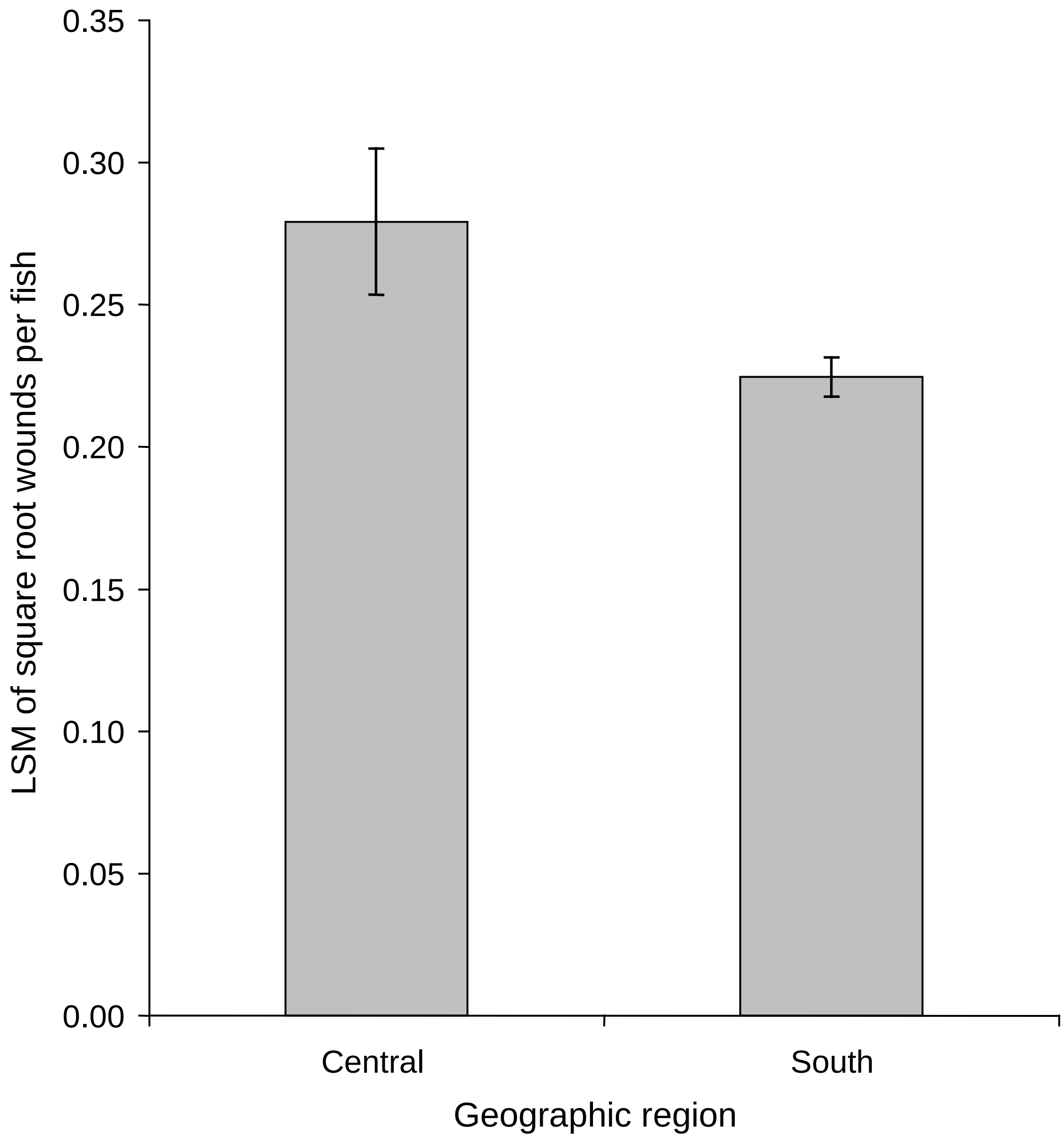

Figure 9. Geographic patterns in sea lamprey wounding of lake trout larger than 533 mm in central (MH-2) and southern (MH-3/4/5) regions of Lake Huron, 1984-1994. Least-square means (LSM) of square root transformed wounds per fish calculated from analysis of variance with length class, geographic region, and year as treatment factors. Estimated means for geographic region, adjusted for all other effects and interactions, reported with one standard error.

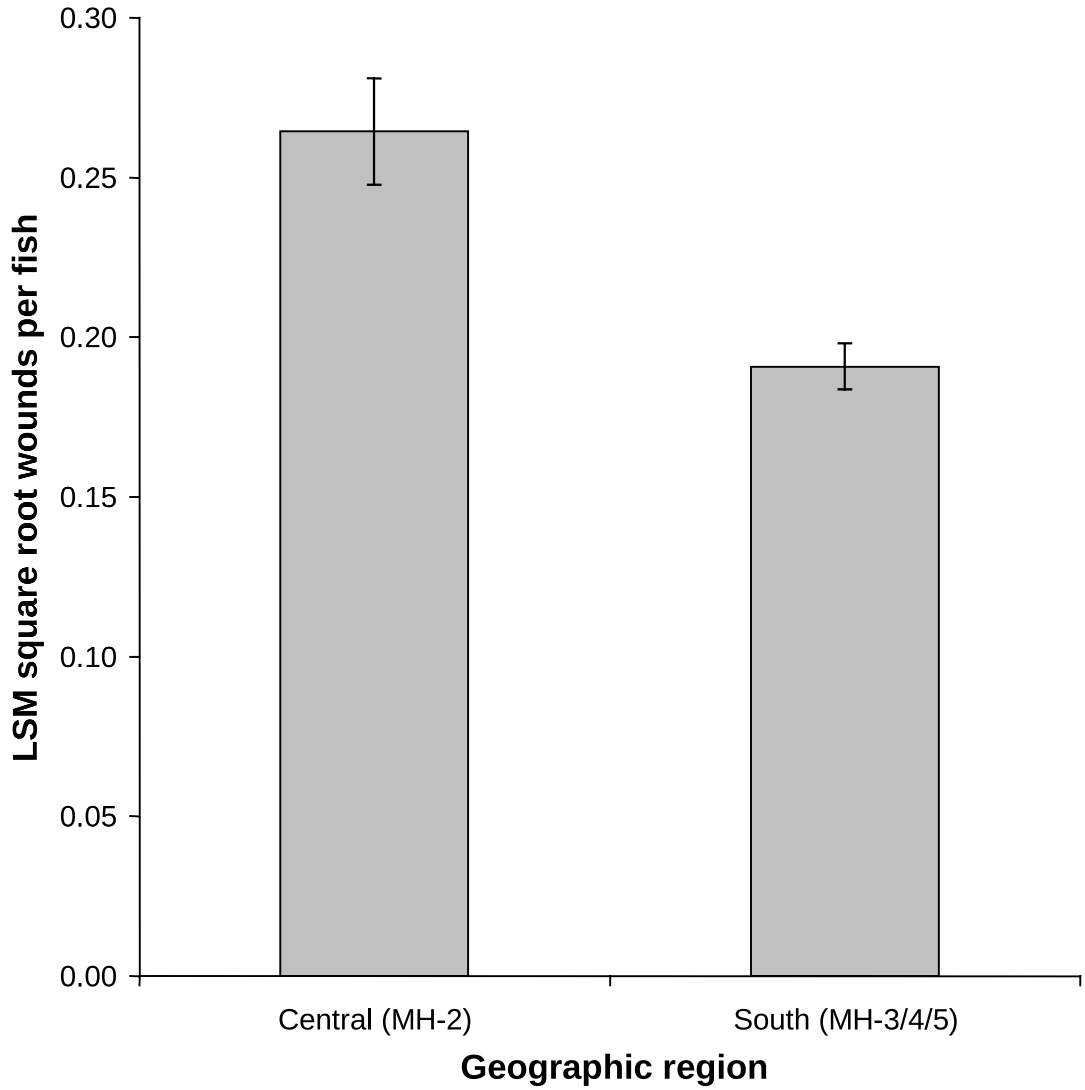

Figure 10. Geographic patterns in sea lamprey wounding of 534-737 mm lake trout in central (MH-2) and southern (MH-3/4/5) regions of Lake Huron, 1984-1994. Least-square means (LSM) of square root transformed wounds per fish calculated from analysis of variance with length class, geographic region, and year as treatment factors. Estimated means for geographic region, adjusted for all other effects and interactions, reported with one standard error.

Temporal trends in wounding rates

Overall, there were annual differences in wounding rates for lake trout in the central and southern regions of the main basin of Lake Huron. However, no obvious long-term temporal trends in wounding were observed from 1984-1994, although there seemed to be a cyclic pattern (model 1, Table 5; Figure 11). Peaks in wounding rates were observed in 1985, 1987, 1990, and 1993. These high wounding years were evident in lake trout >533 mm (Figure 12). Wounding rates were lowest in 1984. No temporal trends were evident in wounding rates for each of the length classes when the central and southern regions were combined (Model 1, Table 5; Figure 12), nor were there trends over time in these areas when all length classes were pooled (Model 1, Table 5; Figure 13). Again, northern Lake Huron was excluded from these analyses due to many years without data.

Estimation of sea lamprey-induced mortality

My objectives here were first to systematically estimate mean wounding rates for central and southern Lake Huron where data were not sufficient or absent with the least amount of extrapolation. The second objective was to compute age-specific sea lamprey-induced mortality rates for the central and southern lake trout population models. The models constructed and the data points they predict are listed in Table 7.

For the 432-533 mm length class, it was not possible to directly calculate mean wounds per fish for the central area in years 1990 and 1991, or for the southern area in 1990-1992 because sufficient data were lacking. Hence, mean wounds per fish were estimated for these locations based on data collected in other regions and years. Model A was constructed

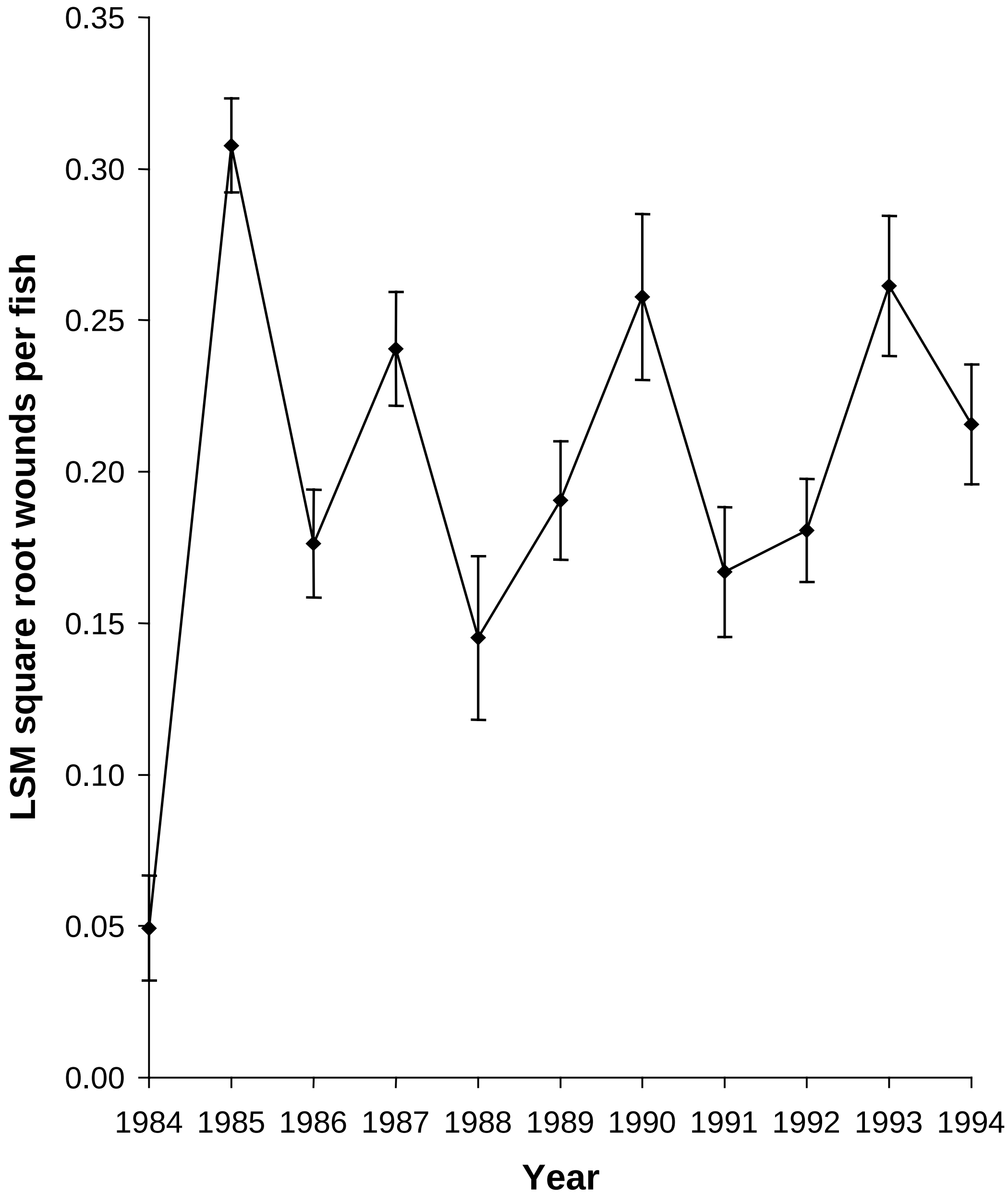

Figure 11. Sea lamprey wounding of lake trout ≥432 mm in central (MH-2) and southern (MH-3/4/5) Lake Huron, 1984-1994. Least-square means (LSM) of square root transformed wounds per fish calculated from analysis of variance with length class, geographic region, and year as treatment factors. Estimated means for year, adjusted for all other effects and interactions, reported with one standard error.

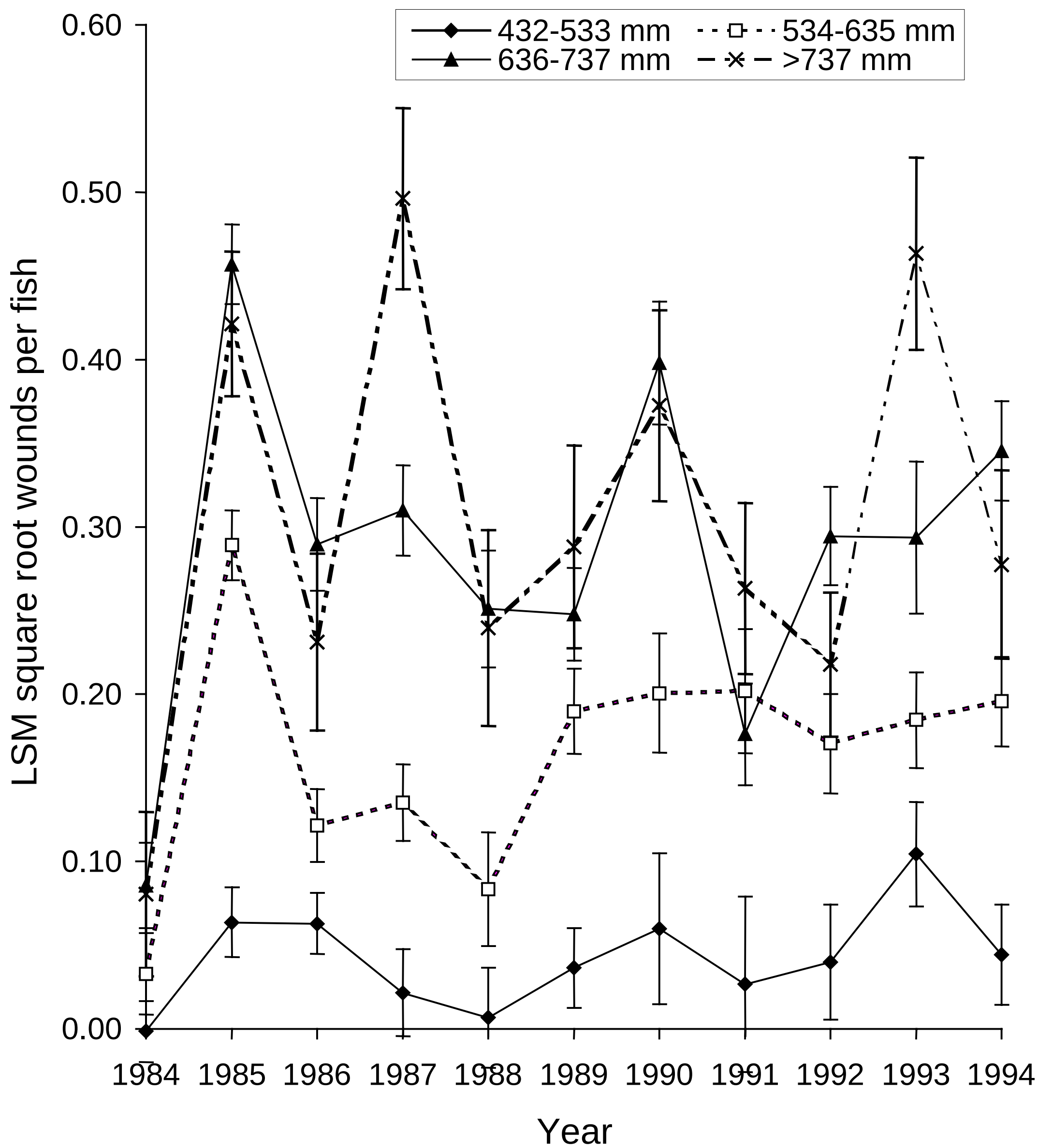

Figure 12. Sea lamprey wounding of lake trout in central (MH-2) and southern (MH-3/4/5) Lake Huron, 1984-1994. Least-square means (LSM) of square root transformed wounds per fish calculated from analysis of variance with length class, geographic region, and year as treatment factors. Estimated means for length class and year, adjusted for all other effects and interactions, reported with one standard error.

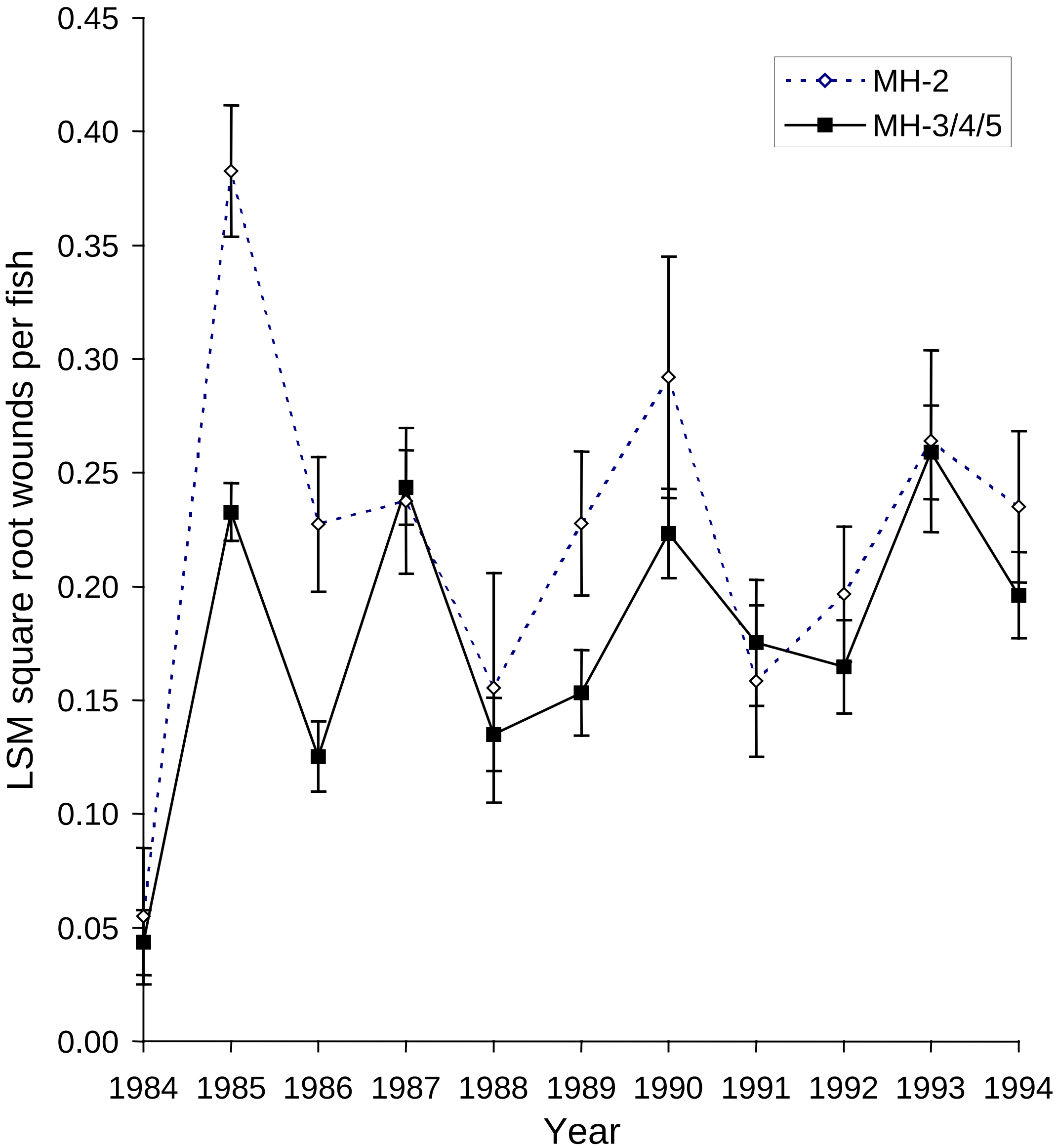

Figure 13. Sea lamprey wounding of lake trout ≥432 mm in central (MH-2) and southern (MH-3/4/5) Lake Huron, 1984-1994. Least-square means (LSM) of square root transformed wounds per fish calculated from analysis of variance with length class, geographic region, and year as treatment factors. Estimated means for geographic region and year, adjusted for all other effects and interactions, reported with one standard error.

Table 7. Levels for each factor in analysis of variance models used to estimate mean wounds per fish when an insufficient number of observations (less than 40 lake trout) were available in Michigan waters of Lake Huron. MH-1= north, MH-2= central, and MH-3/4/5= south.

Model	Factor			Data points estimated by model
	Year	Geographic Region	Length Class	
A	1984, 1985, 1986, 1987, 1988, 1989, 1990, 1991, 1992, 1993, 1994	MH-1, MH-2, MH-3/4/5	432-533 mm	[1990, MH-2, 432-533 mm] [1991, MH-2, 432-533 mm] [1990, MH-3/4/5, 432-533 mm] [1991, MH-3/4/5, 432-533 mm] [1992, MH-3/4/5, 432-533 mm]
B	1984, 1985, 1986, 1987, 1988, 1989, 1990, 1991, 1992, 1993, 1994	MH-2, MH-3/4/5	534-635 mm	[1988, MH-2, 534-635 mm] [1990, MH-2, 534-635 mm] [1991, MH-3/4/5, 534-635 mm]
C	1984, 1985, 1986, 1987, 1988, 1989, 1990, 1991, 1992, 1993, 1994	MH-2, MH-3/4/5	534-635 mm, 636-737 mm, >737 mm	[1984, MH-2, 636-737 mm] [1985, MH-2, 636-737 mm] [1986, MH-2, 636-737 mm] [1987, MH-2, 636-737 mm] [1988, MH-2, 636-737 mm] [1989, MH-2, 636-737 mm] [1990, MH-2, 636-737 mm] [1993, MH-2, 636-737 mm]
D	1984, 1985, 1986, 1987, 1988, 1989, 1990, 1991, 1992, 1993, 1994	MH-2, MH-3/4/5	534-635 mm, >737 mm	[all years, MH-2, >737 mm]

with year and geographic region as main factors by using the available data for all three geographic regions for the 432-533 mm length class with information from 1984-1994 (Table 7). Model B was constructed to predict wounding rates for the 534-635 mm length class in the central region for 1988 and 1990, and in the southern region for 1991 (Table 7). This was done using wounding rates from the other years in both years for the 534-635 mm length class.

For lake trout in the 636-737, and >737 mm length classes, the only data that were available were for the southern region (see Table 1). Therefore, ANOVA models to predict wounding rates for these length classes in the central region were dependent on the observed differences in wounding rates among length classes in the south for estimating the length class effect, and geographic differences for fish <636 mm to estimate area effects. Wounding rates for 636-737 mm lake trout in central Lake Huron were estimated using the effects from lake trout >533 mm in the central and southern regions in all years (Model C, Table 7).

For the >737 mm length class in the central region, there were no samples with 40 or more lake trout. Therefore, model D was constructed to project wounding rates for this length class in relation to the 534-635 mm lake trout in the central area based on the differences in wounding rates between the 534-635 mm and the >737 mm length groups in the south (Table 7). These estimated wounding rates for >737 mm fish in the central area are unimportant in terms of model output since so few fish survive to these sizes. Never-the-less, in order to run the population model, wounding rates were needed to estimate sea lamprey-induced mortality for old lake trout; otherwise, the model could not be used to make projections for scenarios with lower mortality rates (and hence have large, older fish).

For central and southern main basin of Lake Huron, mean wounds per fish for lake trout are listed by length class in Tables 8 and 9. For samples with more than 40 lake trout, raw mean wounds per fish were used, whereas mean wounds per fish were estimated by ANOVA models (Table 7) for strata in the database with observations with less than 40 fish. Age-specific lamprey-induced mortality rates, computed using equations 4 and 5, are listed in Tables 10 and 11.

The only wounding data with sufficient sample sizes for northern Lake Huron were for the 432-533 mm fish and mean wounding rates ranged from 0.01 to 0.15 wounds per fish during 1984-1994. Due to the lack to of wounding data for lake trout >533 mm for northern Lake Huron, an alternative approach was used to estimate sea lamprey-induced mortality based on fitting the parameter μ' as described in the Methods section (see section titled *Calibration of the northern and central lake trout population models* in Methods). Estimates of sea lamprey-induced mortality for northern Lake Huron using this procedure are presented later in the results (see *Calibration of the northern and central lake trout population models* in Results).

Patterns in estimated sea lamprey-induced mortality were directly related to patterns in wounding rates. In general, sea lamprey-induced mortality increased with length of lake trout, and tended to be higher in the central regions than in the south.

Statistical catch-at-age analysis of the southern Lake Huron lake trout population model

Parameters values for the southern model estimated by CAA analyses and corresponding log-likelihood components are listed in Tables 12 and 13. Several versions of

Table 8. Sea lamprey wounding rates by length class for lake trout in central Lake Huron (MH-2). Wounding rates expressed as mean wounds per fish. Data from Michigan Department of Natural Resources spring surveys.

	Length Class			
Year	432-533 mm	534-635 mm	636-737 mm	>737 mm
1984	0.00000	0.01639	0.14316*	0.19024*
1985	0.10194	0.41892	0.42141*	0.44562*
1986	0.10497	0.18750	0.26890*	0.29141*
1987	0.03371	0.12195	0.32829*	0.34299*
1988	0.00000	0.11639*	0.27194*	0.29125*
1989	0.05691	0.25301	0.30010*	0.38313*
1990	0.01019*	0.25905*	0.42716*	0.43605*
1991	0.00000*	0.21212	0.18644	0.38853*
1992	0.02299	0.19753	0.36170	0.31612*
1993	0.08065	0.25000	0.38572*	0.41371*
1994	0.09836	0.24390	0.39535	0.39113*

* Estimated by analysis of variance model.

Table 9. Sea lamprey wounding rates by length class for lake trout in southern Lake Huron (MH-3/4/5). Wounding rates expressed as mean wounds per fish. Data from Michigan Department of Natural Resources spring surveys.

	Length Class			
Year	432-533 mm	534-635 mm	636-737 mm	>737 mm
1984	0.00000	0.03226	0.05571	0.09756
1985	0.04724	0.22865	0.38444	0.39597
1986	0.02500	0.07170	0.24066	0.23077
1987	0.01695	0.14612	0.33636	0.58333
1988	0.01258	0.07882	0.24180	0.31429
1989	0.01587	0.17986	0.20601	0.28889
1990	0.00000*	0.22148	0.40569	0.42353
1991	0.00000*	0.17455*	0.19388	0.38889
1992	0.03076*	0.18182	0.31111	0.21569
1993	0.13253	0.17857	0.36364	0.55882
1994	0.02000	0.17241	0.38686	0.41538

* Estimated by analysis of variance model.

Table 10. Estimated instantaneous rates of sea lamprey-induced mortality ($year^{-1}$) for lake trout in central Lake Huron (MH-2) during 1984-1993.

	Year									
Age	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993
1	0	0	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0	0	0
3	0.203	0.196	0.066	0.006	0.114	0.032	0.011	0.051	0.157	0.188
4	0.236	0.200	0.076	0.021	0.136	0.063	0.038	0.072	0.173	0.200
5	0.367	0.214	0.121	0.088	0.221	0.195	0.145	0.162	0.242	0.252
6	0.418	0.223	0.196	0.168	0.269	0.311	0.198	0.252	0.300	0.302
7	0.391	0.222	0.218	0.183	0.261	0.319	0.186	0.261	0.303	0.306
8	0.368	0.225	0.241	0.201	0.265	0.328	0.202	0.264	0.311	0.311
9	0.353	0.228	0.274	0.229	0.274	0.353	0.222	0.280	0.325	0.322
10	0.357	0.232	0.276	0.232	0.288	0.354	0.256	0.273	0.330	0.321
11	0.351	0.226	0.273	0.228	0.268	0.352	0.208	0.284	0.323	0.322
12	0.360	0.234	0.278	0.234	0.297	0.355	0.277	0.268	0.333	0.321
13	0.355	0.229	0.275	0.230	0.280	0.353	0.235	0.277	0.327	0.322
14	0.365	0.238	0.281	0.238	0.314	0.357	0.318	0.259	0.339	0.320
15	0.365	0.238	0.281	0.238	0.314	0.357	0.318	0.259	0.339	0.320
16	0.365	0.238	0.281	0.238	0.314	0.357	0.318	0.259	0.339	0.320
17	0.365	0.238	0.281	0.238	0.314	0.357	0.318	0.259	0.339	0.320
18	0.365	0.238	0.281	0.238	0.314	0.357	0.318	0.259	0.339	0.320
19	0.365	0.238	0.281	0.238	0.314	0.357	0.318	0.259	0.339	0.320
20	0.365	0.238	0.281	0.238	0.314	0.357	0.318	0.259	0.339	0.320
>20	0.365	0.238	0.281	0.238	0.314	0.357	0.318	0.259	0.339	0.320

Table 11. Estimated instantaneous rates of sea lamprey-induced mortality ($year^{-1}$) for lake trout in southern Lake Huron (MH-3/4/5) during 1984-1993.

	Year									
Age	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993
1	0	0	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0	0	0
3	0.105	0.050	0.045	0.030	0.047	0.114	0.113	0.072	0.244	0.053
4	0.141	0.059	0.073	0.044	0.082	0.146	0.133	0.103	0.239	0.086
5	0.247	0.099	0.166	0.100	0.172	0.247	0.181	0.194	0.238	0.194
6	0.299	0.159	0.242	0.163	0.184	0.308	0.177	0.240	0.273	0.278
7	0.309	0.184	0.282	0.192	0.178	0.325	0.178	0.242	0.305	0.305
8	0.316	0.190	0.339	0.214	0.193	0.334	0.214	0.227	0.348	0.321
9	0.319	0.191	0.388	0.230	0.207	0.339	0.249	0.210	0.387	0.328
10	0.320	0.190	0.415	0.238	0.216	0.341	0.271	0.199	0.408	0.331
11	0.322	0.189	0.438	0.245	0.224	0.343	0.288	0.191	0.426	0.334
12	0.323	0.189	0.462	0.253	0.231	0.345	0.306	0.182	0.445	0.338
13	0.323	0.190	0.457	0.251	0.230	0.345	0.302	0.184	0.441	0.338
14	0.322	0.190	0.445	0.248	0.226	0.344	0.293	0.189	0.432	0.336
15	0.323	0.189	0.463	0.253	0.232	0.345	0.307	0.182	0.446	0.338
16	0.322	0.190	0.437	0.245	0.223	0.344	0.286	0.192	0.425	0.335
17	0.324	0.189	0.477	0.257	0.236	0.347	0.318	0.176	0.457	0.340
18	0.324	0.189	0.477	0.257	0.236	0.347	0.318	0.176	0.457	0.340
19	0.324	0.189	0.477	0.257	0.236	0.347	0.318	0.176	0.457	0.340
20	0.324	0.189	0.477	0.257	0.236	0.347	0.318	0.176	0.457	0.340
>20	0.324	0.189	0.477	0.257	0.236	0.347	0.318	0.176	0.457	0.340

Table 12. Estimated parameter values from catch-at-age analyses of the southern Lake Huron lake trout population model, 1984-1993. Recreational fishery parameters: q_R= catchability (angler hours^{-1}), $S_{R,\,a}$= selectivity at age *a*, and $f_{R,\,y}$= fishing intensity (year^{-1}). μ'= proportionality coefficient for sea lamprey-induced mortality. Research survey parameters: q*= catchability (meters of gill net^{-1}), S^*_a= selectivity at age *a*. Population parameters: $N_{a,1984}$= abundance at age *a* in 1984, c= proportionality coefficient for natural mortality, M_1= age-1 instantaneous natural mortality (year^{-1}), and τ= rate of decrease in natural mortality rate (year^{-1} age^{-1}). $^{\#}$= parameter not estimated by catch-at-age analysis.

	Catch-at-age model:				
Parameters	CAA1	CAA2	CAA3	CAA4	CAA5
Fishery					
q_R	1.82081 x10^{-07}	1.35120 x10^{-07}	1.32557 x10^{-07}	1.66248 x10^{-07}	1.56302 x10^{-07}
$S_{R,\,1}$	0$^{\#}$	0$^{\#}$	0$^{\#}$	0$^{\#}$	0$^{\#}$
$S_{R,\,2}$	0.000064	0.000033	0.000044	0.000022	0.000043
$S_{R,\,3}$	0.023185	0.048057	0.030697	0.040342	0.033187
$S_{R,\,4}$	0.247836	0.494797	0.307270	0.421826	0.331398
$S_{R,\,5}$	0.683335	1.348836	0.833276	1.162254	0.911426
$S_{R,\,6}$	0.731383	1.336467	0.880659	1.166437	0.992864
$S_{R,\,7}$	0.751762	1.204770	0.854484	1.071924	0.975735
$S_{R,\,8}$	0.998337	1.124553	0.996947	1.014570	0.998220
$S_{R,\,9+}$	1$^{\#}$	1$^{\#}$	1$^{\#}$	1$^{\#}$	1$^{\#}$
$f_{R,\,1984}$	0.142549	0.091657	0.096037	0.117867	0.109834
$f_{R,\,1985}$	0.148104	0.105439	0.103115	0.133211	0.122809
$f_{R,\,1986}$	0.216524	0.156968	0.155994	0.196289	0.183475
$f_{R,\,987}$	0.178980	0.119329	0.129193	0.147928	0.149416
$f_{R,\,1988}$	0.174794	0.119498	0.131549	0.144713	0.146812
$f_{R,\,1989}$	0.124317	0.090034	0.092790	0.109261	0.105413
$f_{R,\,1990}$	0.208954	0.230527	0.172152	0.268877	0.214931
$f_{R,\,1991}$	0.113067	0.084671	0.080215	0.104765	0.097112
$f_{R,\,1992}$	0.115043	0.075162	0.076347	0.095023	0.091895
$f_{R,\,1993}$	0.115995	0.035917	0.049671	0.049123	0.060918
Lamprey					
μ'	1$^{\#}$	0.048894	1$^{\#}$	0.000349	1$^{\#}$

Table 12 (cont'd).

Parameters	Catch-at-age model: CAA1	CAA2	CAA3	CAA4	CAA5
Survey					
q^*	0.001134	0.001051	0.000709	0.001225	0.000947
S^*_1	0[#]	0[#]	0[#]	0[#]	0[#]
S^*_2	0.024729	0.026910	0.030937	0.025261	0.026284
S^*_3	0.180430	0.200711	0.211788	0.192967	0.208198
S^*_4	0.507441	0.523947	0.550043	0.512957	0.541355
S^*_5	1[#]	1[#]	1[#]	1[#]	1[#]
S^*_6	0.990297	0.952700	0.996646	0.958498	1.011189
S^*_7	0.943763	0.813802	1.000256	0.830414	1.000370
S^*_8	1.206543	0.906150	1.116072	0.945295	1.122270
S^*_9	1.449042	0.890466	1.236359	0.958673	1.181630
S^*_{10+}	2.625431	0.982813	1.968542	1.136801	1.679869
Population					
$N_{2,\ 1984}$	426861.982	381721.967	488286.153	358963.125	434857.682
$N_{3,\ 1984}$	139172.149	112566.865	165328.627	103814.264	127660.333
$N_{4,\ 1984}$	140175.860	114038.703	174114.800	103423.934	134857.190
$N_{5,\ 1984}$	119144.898	92941.040	151666.465	82863.397	117584.339
$N_{6,\ 1984}$	101295.205	81900.967	130255.278	72053.946	98613.080
$N_{7,\ 1984}$	42293.469	38300.960	54906.096	33300.385	40918.423
$N_{8,\ 1984}$	25281.895	25219.011	35039.038	21187.430	26166.310
$N_{9,\ 1984}$	14216.299	18774.859	22715.026	15290.472	18064.430
$N_{10,1984}$	349.826	5026.792	989.877	2918.870	985.216
$N_{11+,\ 1984}$	3669.679[#]	3669.679[#]	3669.679[#]	3669.679[#]	3669.679[#]
c	1[#]	1[#]	0.676613	1.114583	[#]
M_1	[#]	[#]	[#]	[#]	0.666290
τ	[#]	[#]	[#]	[#]	1.115309

Table 13. Maximum $\log_e$-likelihood components from statistical catch-at-age analyses of the southern Lake Huron lake trout population model, 1984-1993.

Likelihood Component	Catch-at-age model: CAA1	CAA2	CAA3	CAA4	CAA5
Fishery harvest (L_1)	-4.4457	-3.9535	-2.6376	-3.3275	-2.7533
Survey CPUE (L_2)	-1.8072	-1.4892	-1.3296	-1.4883	-1.3362
Fishery age composition (L_3)	7.0330	11.7392	7.5129	11.9857	9.3428
Survey age composition (L_4)	-169.4730	-159.7915	-162.7454	-160.4057	-162.1344
Fishery effort (L_5)	2.8447	1.3453	3.1637	1.5008	2.7207
Total ($L = \Sigma L_i$)	-165.8482	-152.1497	-156.0359	-151.7351	-154.1604

the catch-at-age analysis were run based on restrictions set to particular parameters that were thought to heavily influence the calibration process. For example, the proportionality coefficient for sea lamprey-induced mortality (μ') and natural mortality proportionality coefficient (c) were either fixed as 1 or estimated by CAA analysis. In preliminary analyses, survey selectivity was fixed with values that followed an asymptotic relationship to length. This reduced the number of parameters estimated. However, for these preliminary analyses, harvest was consistently either underpredicted or overpredicted. The total log-likelihood (L) for these analyses, which ranged from -270.48 to -299.20, indicated a poorer fit than subsequent CAA analyses. In addition, trends were observed in both predicted fishery and survey age compositions. Thus, survey selectivity values were estimated as parameters in all ensuing analyses.

In CAA1, parameters μ' and *c* were fixed at 1. This was designated as the baseline CAA model since this implies that I have correctly defined the relationship between sea lamprey-induced mortality and wounding data and also have correctly assigned the level of natural mortality from other sources. The parameters estimated for this analysis are listed in Table 12 and $\log_e$- likelihood components are listed in Table 13. Predicted harvest was consistently below observed harvest (Figure 14a). A decreasing trend in residuals for survey total CPUE was observed (Figure 14b). Predicted total survey CPUEs were higher than observed values in 1984-1987, while they were lower in most of the later years. This analysis was based on a stringent model that assumed the current, baseline values for natural mortality (see Table 2) and sea lamprey-induced mortality were correct. However, the consistent underprediction of harvest indicates that either natural or lamprey-induced mortality was

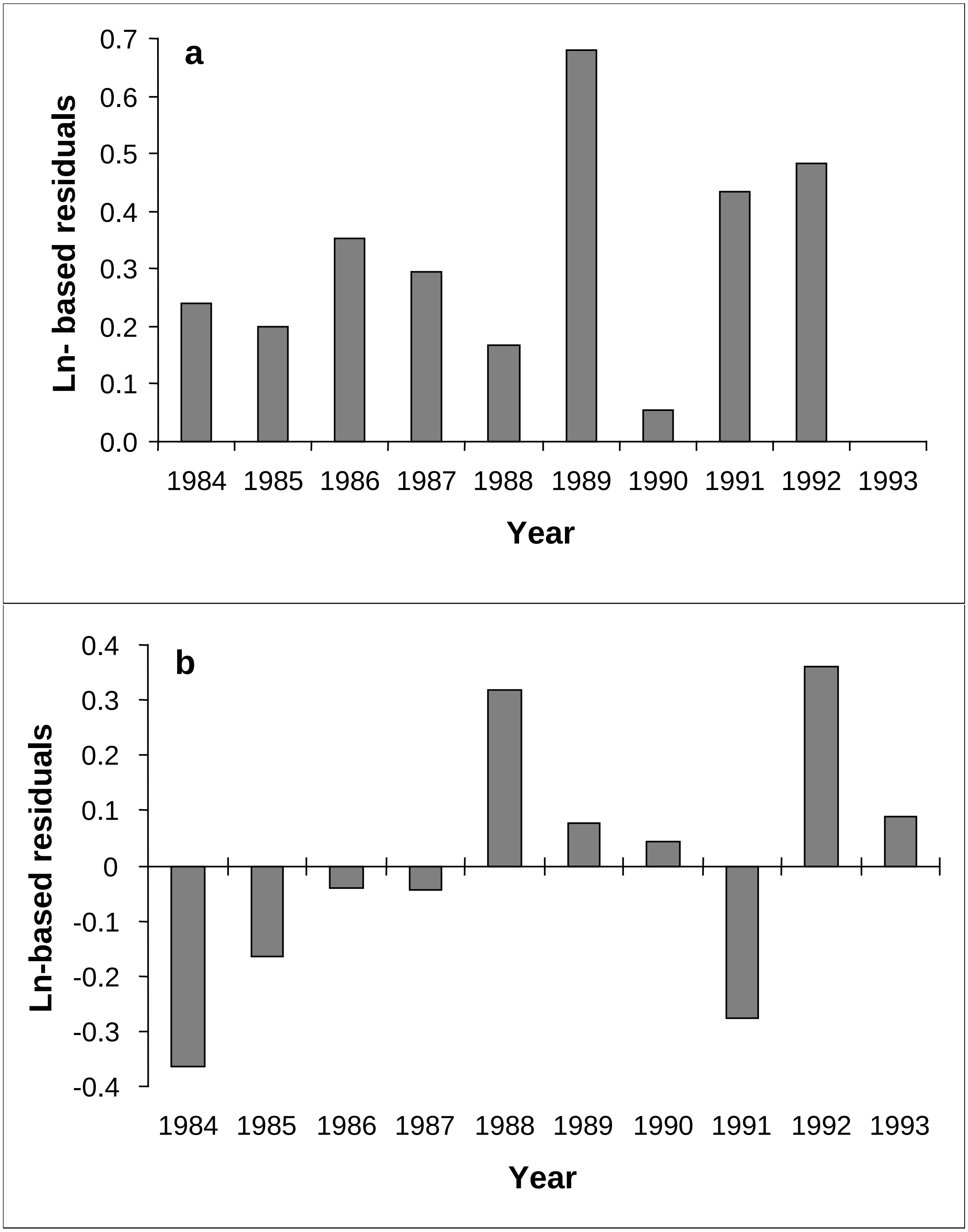

Figure 14. Log_e-based residuals from catch-at-age analysis CAA1 of the southern Lake Huron lake trout population model. (a) fishery harvest. (b) survey total CPUE.

overestimated by this set of parameter values. Subsequent CAA analyses were structured to assess which one of these sources of mortality (natural or lamprey-induced) was set too high.

In CAA2, *c* was fixed to 1, while μ' was estimated. This analysis produced a better model fit as indicated by the matching of model predicted harvest with observed values, and by the total $\log_e$-likelihood (L) which was maximized to -152.15, and higher than the value of -165.85 for CAA1 (Table 13). I did not detect patterns in fishery harvest residuals, survey CPUE residuals, or in residuals for fishery or survey age compositions. However, μ' was estimated to be 0.0489, and if we accept the results of CAA2, the lethality of sea lamprey attacks on lake trout would be significantly lower than previously thought. I concluded that this was unrealistic based on other sources of information indicating that lethality of attacks and mortality caused by sea lamprey are significant for lake trout populations in the Great Lakes.

For example, Bergstedt and Schneider (1988) compared the wounding rates on live lake trout captured in assessment gill nets to recovered dead lake trout using bottom trawls in Lake Ontario and found that nearly all (99%) of the carcasses had recent sea lamprey wounds, whereas the live fish had much lower wounding rates. They concluded that sea lamprey attack was the primary cause of death of the lake trout carcasses they collected and natural mortality other than that cause by sea lampreys was insignificant. Similar results were reported by Schneider et al. (in press) which was based on the continuation of Bergstedt and Schneider's (1988) study. Furthermore, laboratory studies evaluating the lethality of attacks on lake trout from sea lampreys indicate that approximately 50% of attacks result in death of the host (Swink and Hanson 1989; Swink 1990).

CAA 3 was used to evaluate whether adjustment of natural mortality could produce an adequate model. Parameter *c* was estimated while μ' was fixed to 1 (Table 12). The total $\log_e$-likelihood value converged at -156.04 (Table 13). There were no trends in fishery harvest or survey total CPUE residuals (Figure 15). Likewise, no patterns in residuals were observed for fishery or survey age compositions (Figures 16, 17). Parameter *c* was estimated to be 0.6766, indicating that natural mortality was 67.7% of baseline rates.

Parameters μ' and *c* were both estimated in CAA4 (Table 12). The total $\log_e$-likelihood was -151.74. Since this model had an additional parameter estimated, it is not surprising that the total log-likelihood value was maximized at a value higher than the other catch-at-age analyses (Table 13). Again, no trends in residuals were observed. The parameter μ' was estimated to be 0.0003, 0.03% of baseline rates, while parameter *c* was estimated to be 1.1146. Although the results of CAA4 indicated a relatively good fit, other evidence indicates that the estimated value for μ' was unrealistic (see results for CAA2) and sea lamprey-induced mortality is not trivial as these results would seem to indicate.

CAA5 estimated natural mortality using the second approach of fitting a type 3 survivorship function. Parameters estimated by CAA5 are listed in Table 12. The total $\log_e$-likelihood was maximized to -154.16. No patterns in residuals were observed for fishery harvest or survey CPUE (Figure 18). Likewise, no trends were observed in the residuals for fishery age composition (Figure 19) or survey age composition (Figure 20). The instantaneous rate of natural mortality for age-1 lake trout (M_1) was estimated to be 0.6663 year^{-1} and τ was estimated to be 1.115 $\text{age}^{-1}\ \text{year}^{-1}$.

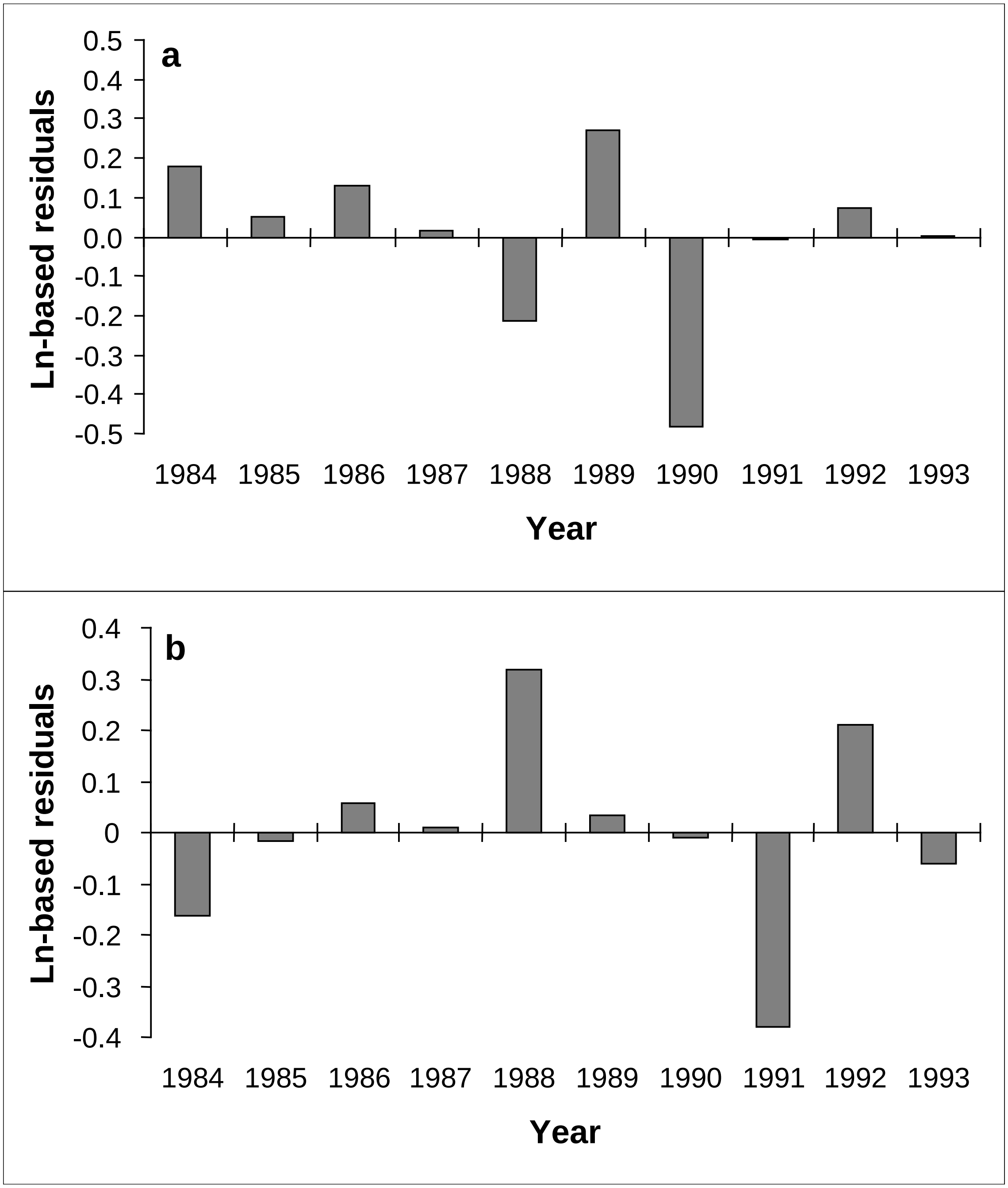

Figure 15. Log_e-based residuals from catch-at-age analysis CAA3 of the southern Lake Huron lake trout population model. (a) fishery harvest. (b) survey total CPUE.

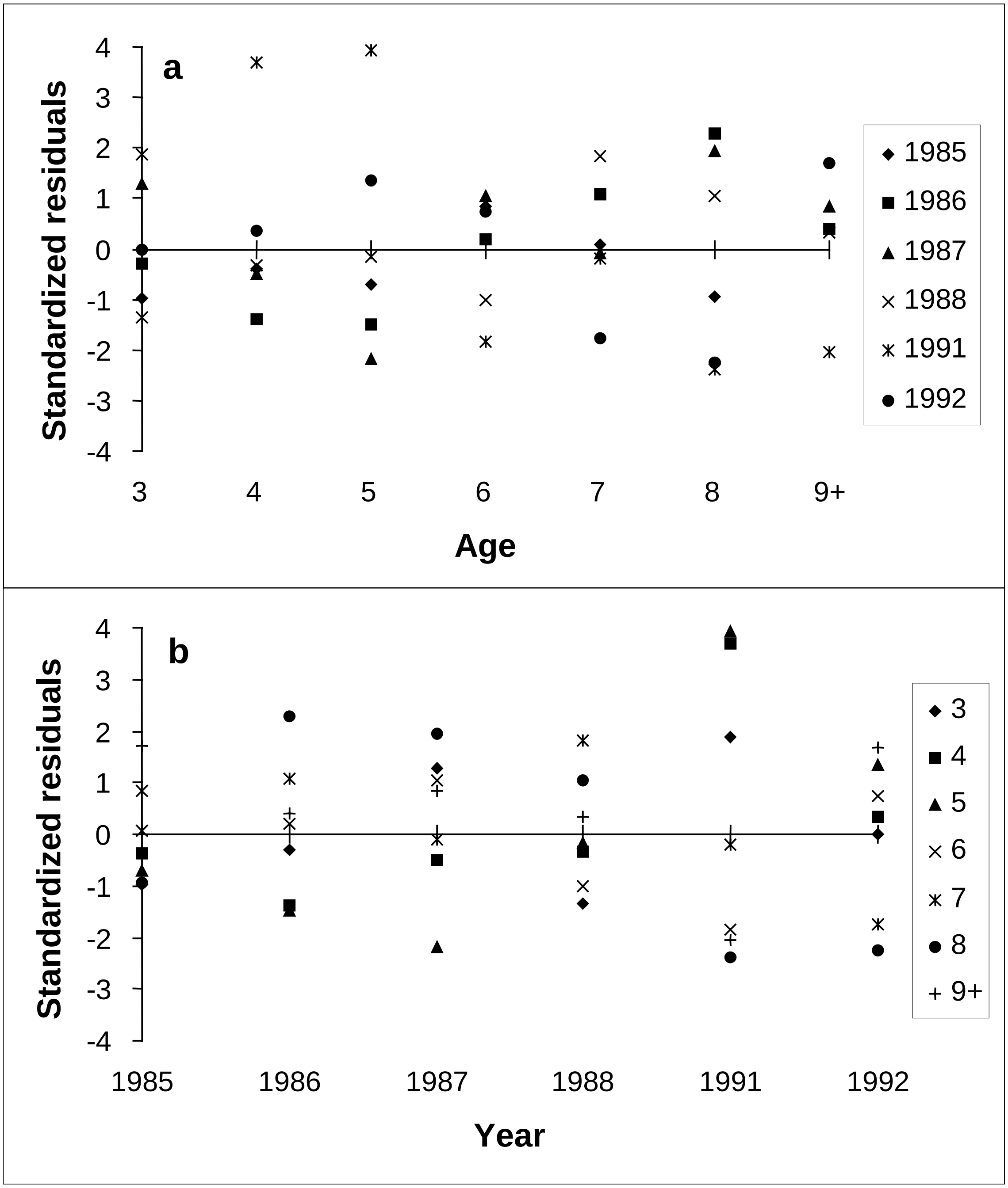

Figure 16. Standardized residuals for fishery age composition from CAA3. (a) across years. (b) across ages. Standardized residuals= observed minus predicted proportions at age divided by estimated standard deviation.

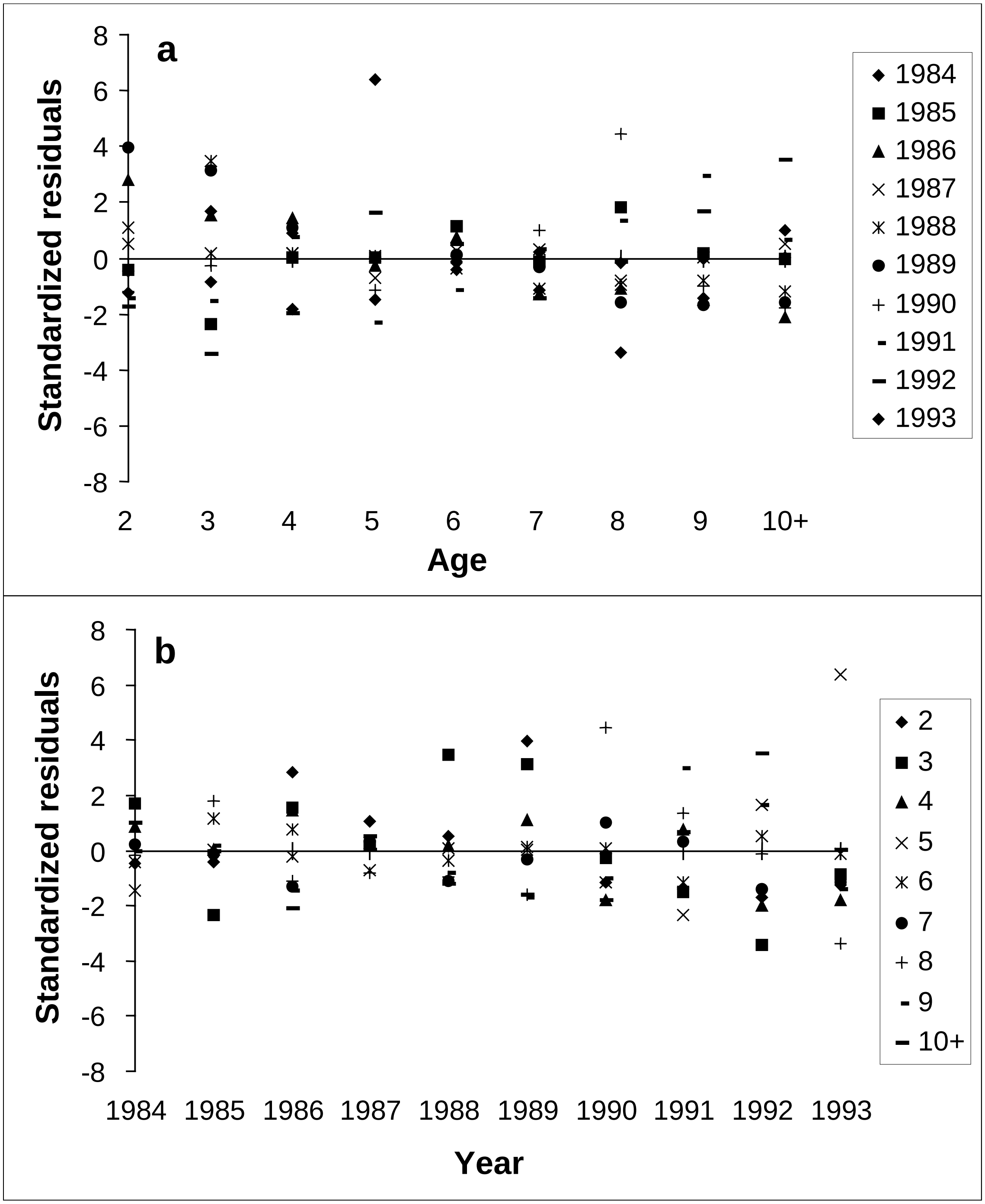

Figure 17. Standardized residuals for survey age composition from CAA3. (a) across years. (b) across ages. Standardized residuals= observed minus predicted proportions at age divided by estimated standard deviation.

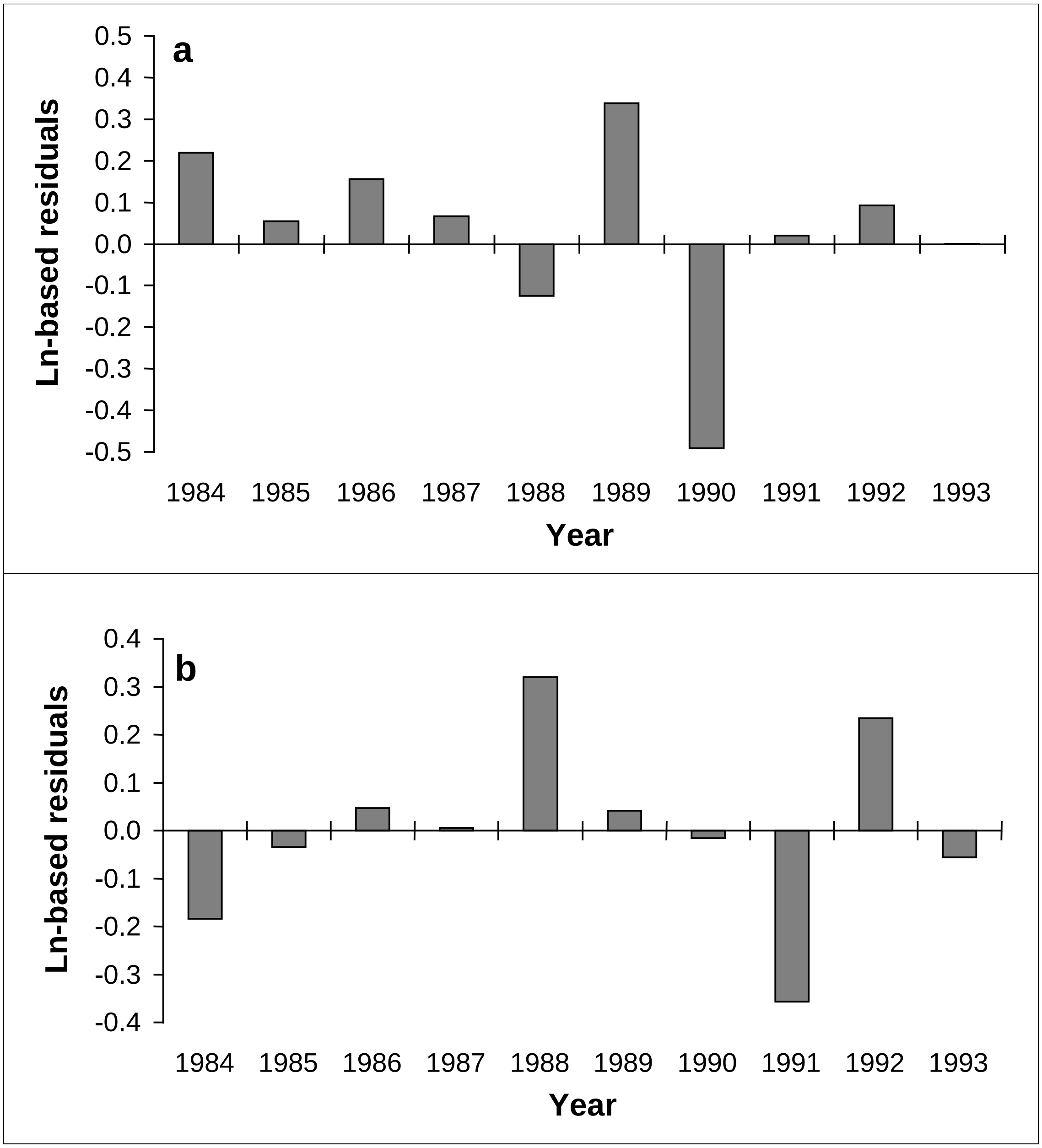

Figure 18. Log_e-based residuals from catch-at-age analysis CAA5 of the southern Lake Huron lake trout population model. (a) fishery harvest. (b) survey total CPUE.

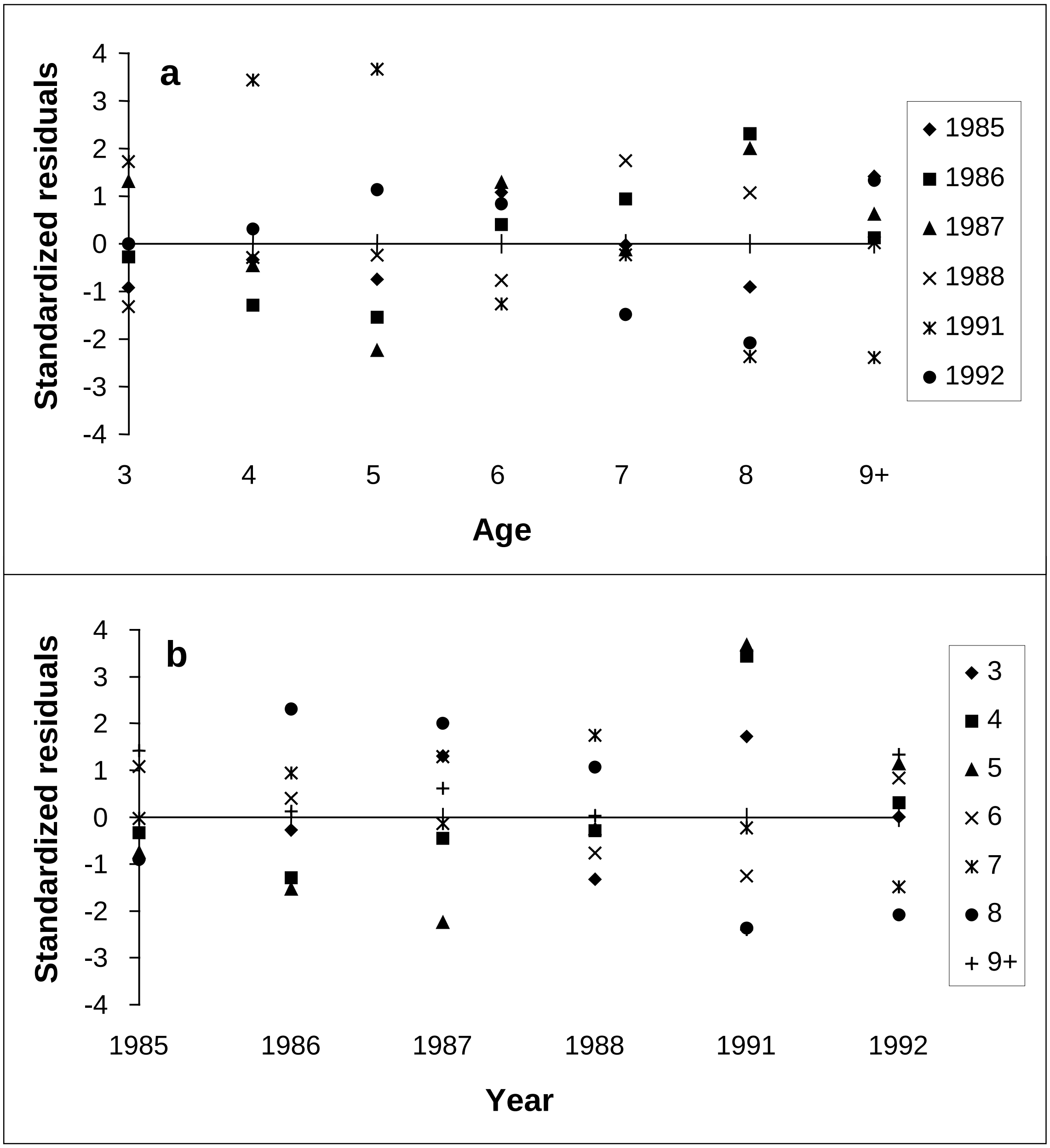

Figure 19. Standardized residuals for fishery age composition from CAA5. (a) across years. (b) across ages. Standardized residuals= observed minus predicted proportions at age divided by estimated standard deviation.

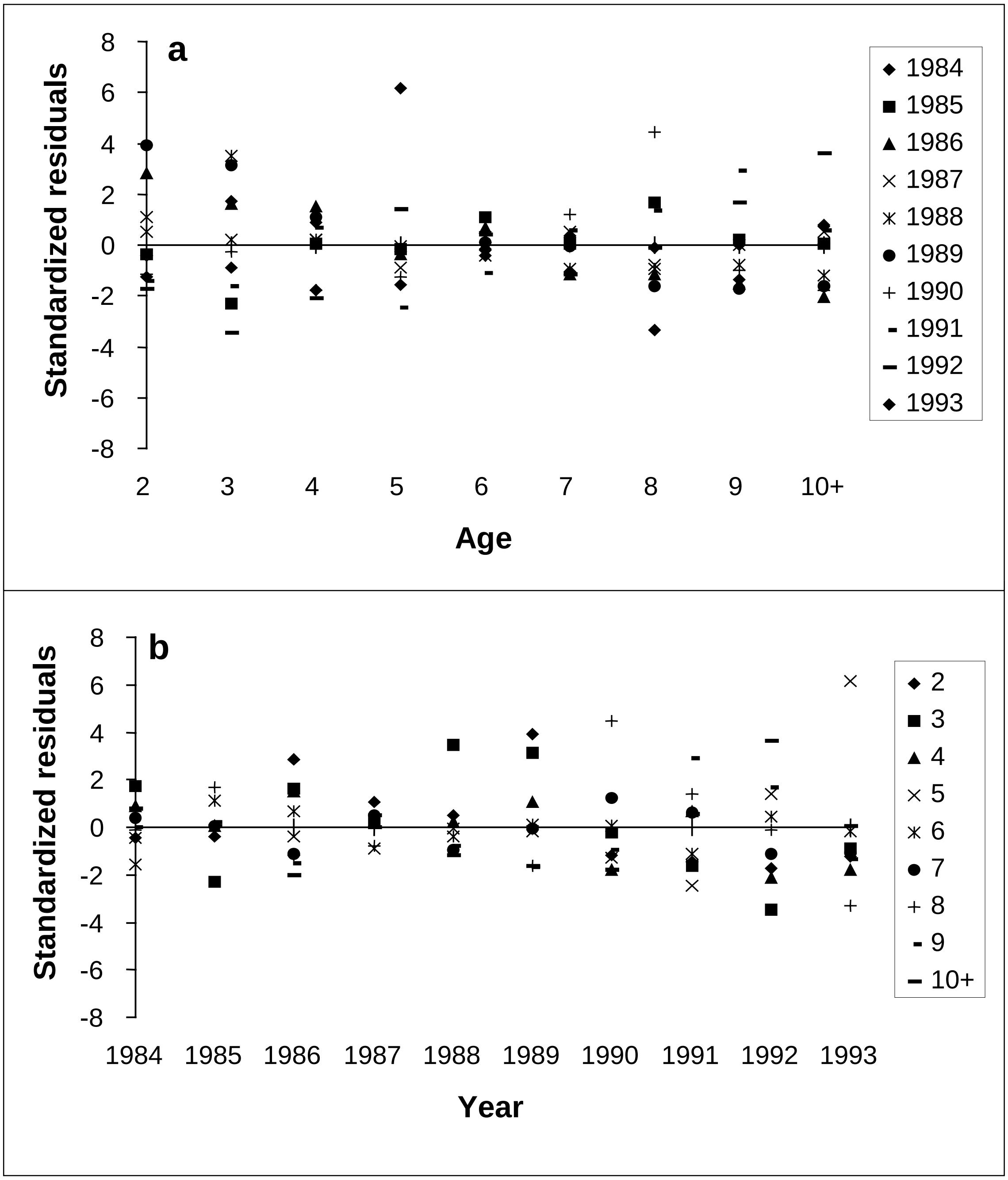

Figure 20. Standardized residuals for survey age composition from CAA5. (a) across years. (b) across ages. Standardized residuals= observed minus predicted proportions at age divided by estimated standard deviation.

In order to test whether a CAA model had a significantly better fit than the baseline model (CAA1), a likelihood ratio test was used (Seber and Wild 1989). Significant difference in total log-likelihoods was tested against the Chi-square distribution using the likelihood ratio test statistic: $2\left[L(\hat{\theta}) - L(\theta_o)\right]$, where $L(\hat{\theta})$ was the total log-likelihood for a CAA analysis with either μ*'*, *c*, both μ*'* and *c*, or both M_1 and τ estimated, while $L(\theta_o)$ was total log-likelihood for the baseline CAA model (CAA1). Degrees of freedom were equal to the number of parameters (i.e., μ*'*, *c*, M_1, τ) estimated in $L(\hat{\theta})$ minus the number of parameters estimated by $L(\theta_o)$. All CAA models in which the parameters μ*'*, *c*, M_1, or τ were estimated had significantly higher total log-likelihood values than the baseline CAA model (CAA2, $P<0.00001$; CAA3, $P<0.0001$; CAA4, $P<0.00001$; CAA5, $P<0.0001$). Furthermore, the estimation of natural mortality by the parameters M_1 and τ in CAA5 seemed to fit better than the estimation of *c* in CAA3 ($P<0.054$), although not significant at the conventional $\alpha=0.05$ level.

Based on the results from the likelihood ratio test and review of the parameters estimated by the various analyses; CAA5 was considered to be the best model. In models CAA2 and CAA4, the estimates of μ*'* did not realistically reflect the lethality of sea lamprey attacks (see results for CAA2). In retrospect, it appears that there was not enough contrast in wounding rates during 1984-1993 in southern Lake Huron to adequately estimate μ*'* (see Figures 11-13). Even a very large change in wounding rates to unrealistic levels produced little change in model fit. Moreover, CAA3 had a poorer fit than model CAA5. Based on the parameters estimated by CAA5, predicted values of southern Lake Huron fishery harvest, effort, and survey CPUE matched the observed values well. The parameters estimated were based on the assumption that each type of observed data used in the calibration process was reliable (i.e., fishery harvest, age composition, effort, and survey CPUE and age composition). This was evaluated by measuring the sensitivity of the model to each of the data sources (see below).

Sensitivity of the southern model to calibration data

Figures 21-25 illustrate changes in log-likelihood values according to various weightings (λ_i) that changed how much data source *i* was emphasized in the fit using catch-at-age model CAA5 (see Methods). Positive changes in log-likelihood indicated improvements in model fit for particular likelihood components, whereas negative values denoted worse fit. The lake trout population model was relatively insensitive to reducing or increasing the emphasis of λ_1, the emphasis factor for fishery harvest data (Figure 21). The total log-likelihood (L) did not decrease more than one unit. Similarly, altering λ_2 (the emphasis factor for survey CPUE data) did not result in notable changes in overall model fit (Figure 22). However, down-weighting of λ_3 (the emphasis factor for fishery age composition data) yielded large decreases in L and L_3 (likelihood component for fishery age composition) and large increases in L_4 (likelihood component for survey age composition). This indicates that model fit was strongly influenced by fishery age composition information (Figure 23). The greatest change in L resulted from the de-emphasis of λ_4 (Figure 24). Model fit was highly sensitive to survey age composition data.

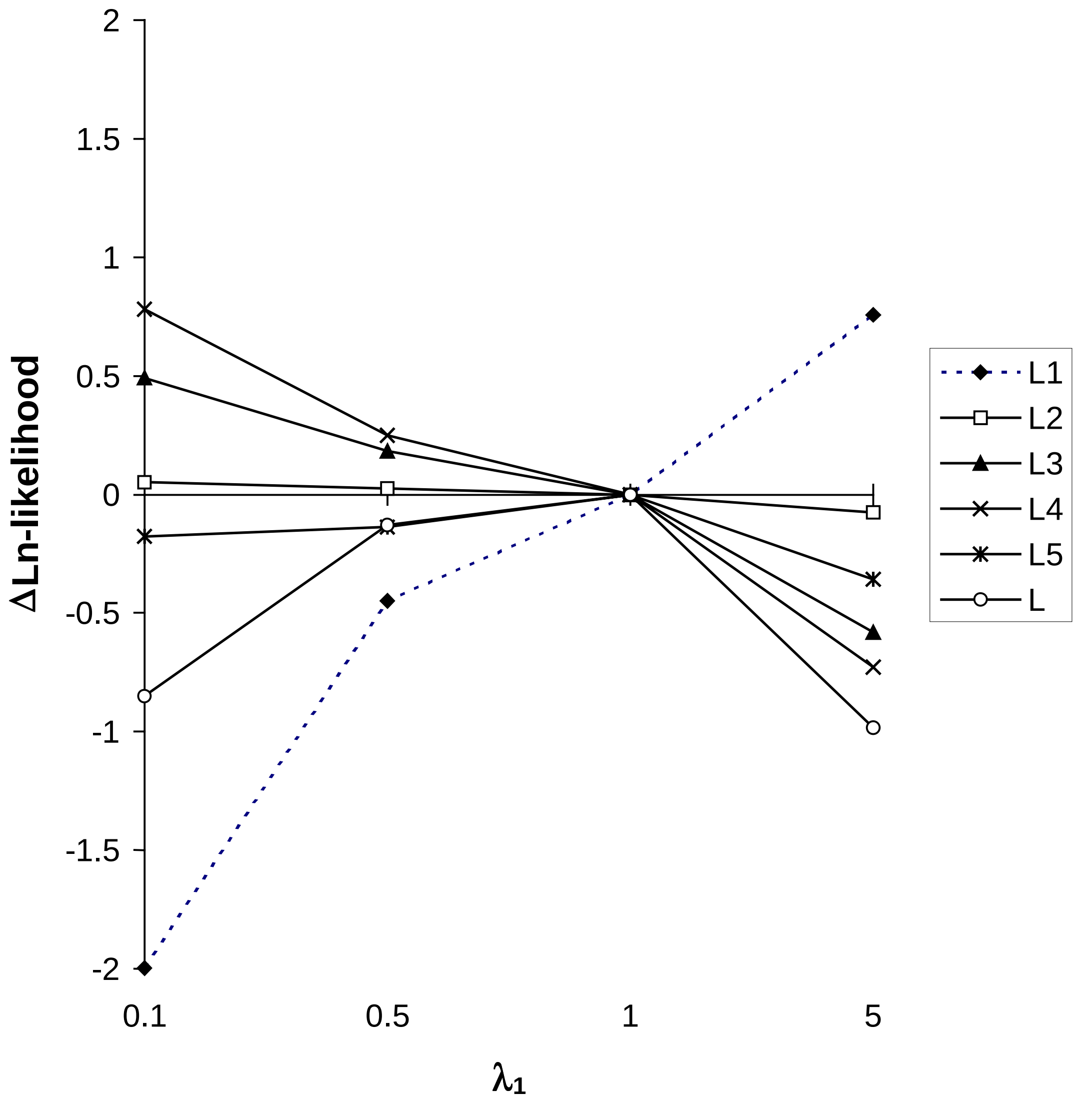

Figure 21. Changes in $\log_e$-likelihood components for catch-at-age model fit due to varying emphasis of fishery harvest data (λ_1). Likelihood components: L1= fishery harvest, L2= survey CPUE, L3= fishery age composition, L4= survey age composition, L5= fishery effort, L= total.

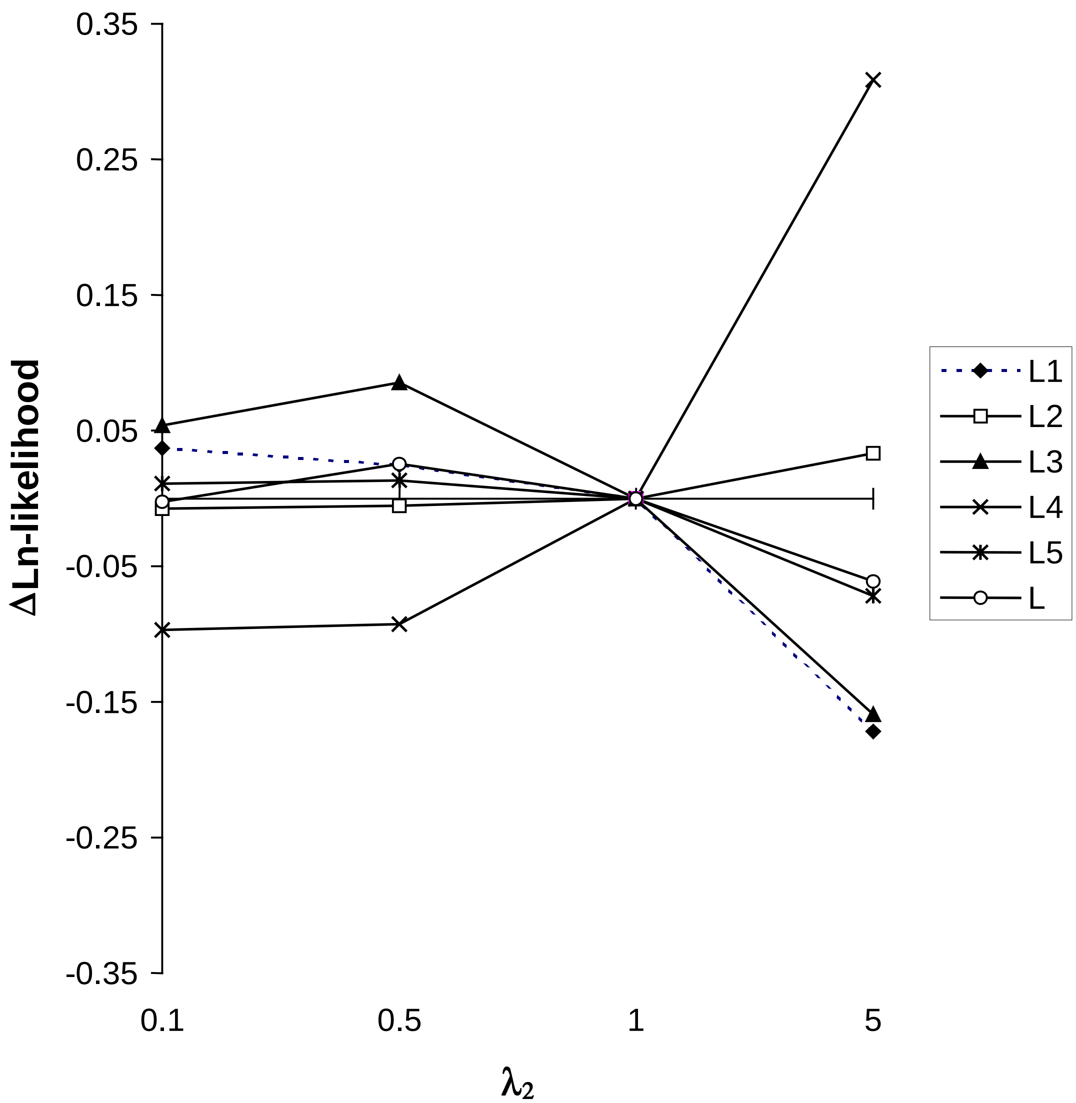

Figure 22. Changes in $\log_e$-likelihood components for catch-at-age model fit due to varying emphasis of survey CPUE data (λ_2). Likelihood components: L1= fishery harvest, L2= survey CPUE, L3= fishery age composition, L4= survey age composition, L5= fishery effort, L= total.

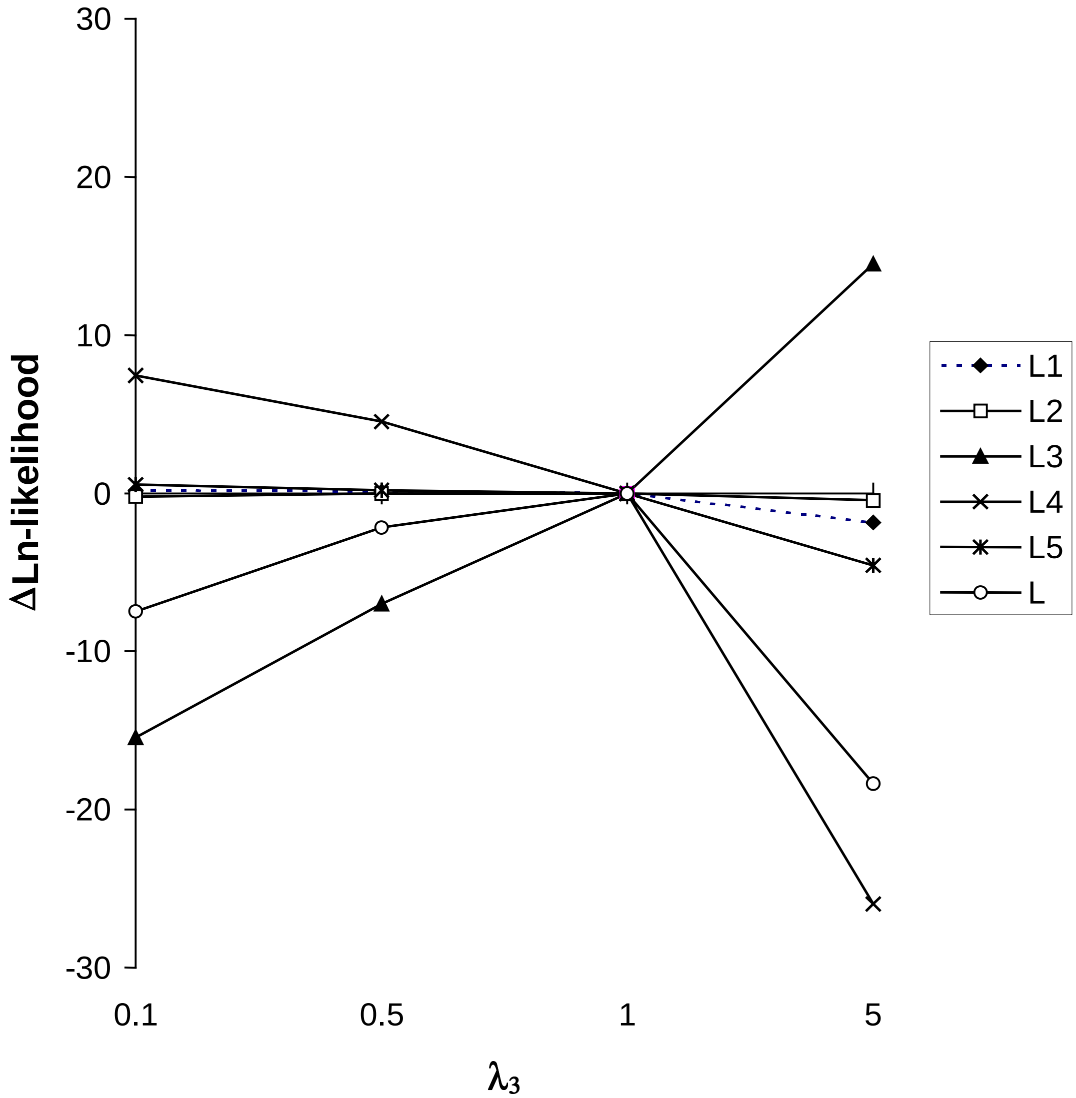

Figure 23. Changes in $\log_e$-likelihood components for catch-at-age model fit due to varying emphasis of fishery age composition data (λ_3). Likelihood components: L1= fishery harvest, L2= survey CPUE, L3= fishery age composition, L4= survey age composition, L5= fishery effort, L= total.

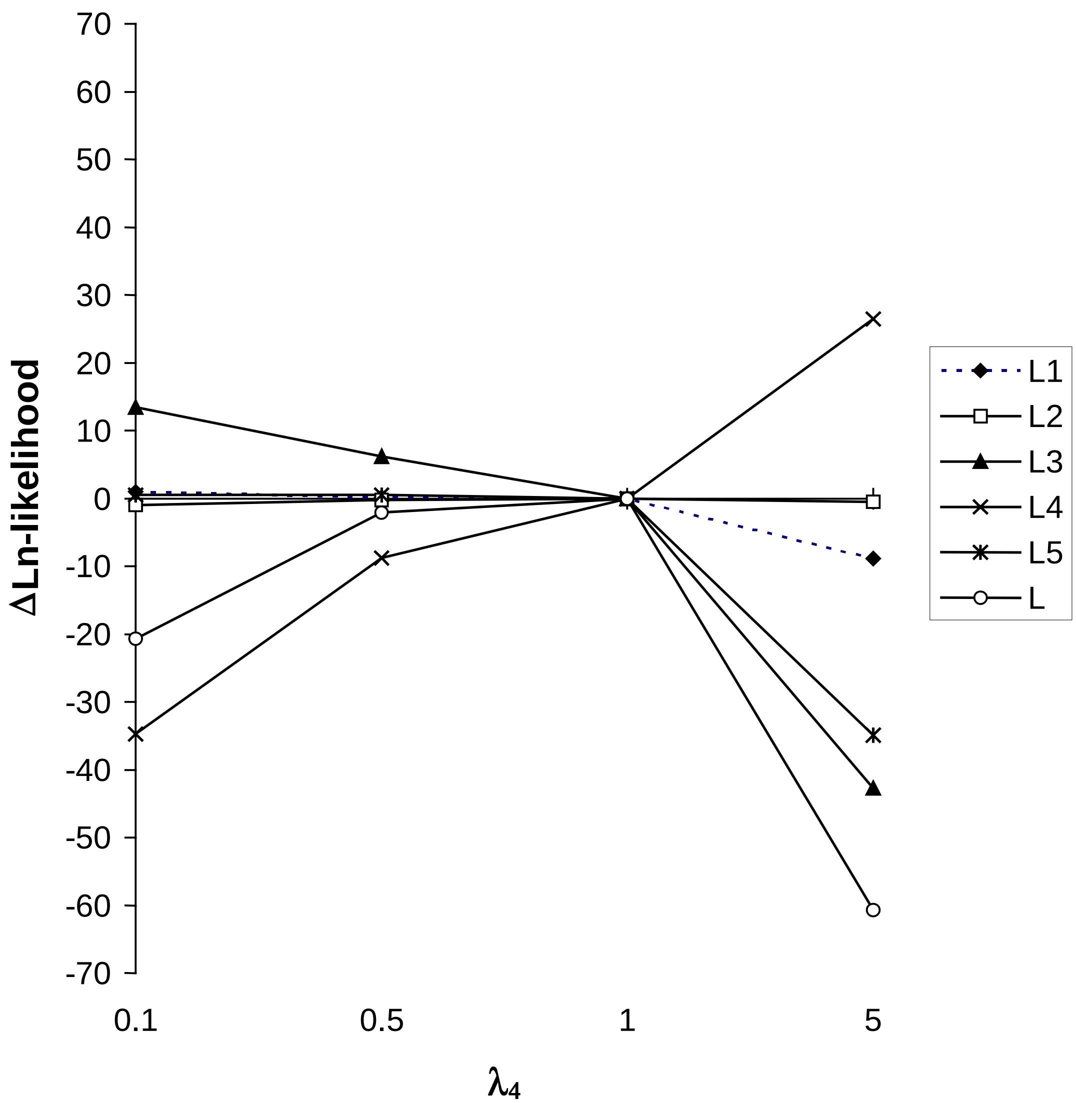

Figure 24. Changes in $\log_e$-likelihood components for catch-at-age model fit due to varying emphasis of survey age composition data (λ_4). Likelihood components: L1= fishery harvest, L2= survey CPUE, L3= fishery age composition, L4= survey age composition, L5= fishery effort, L= total.

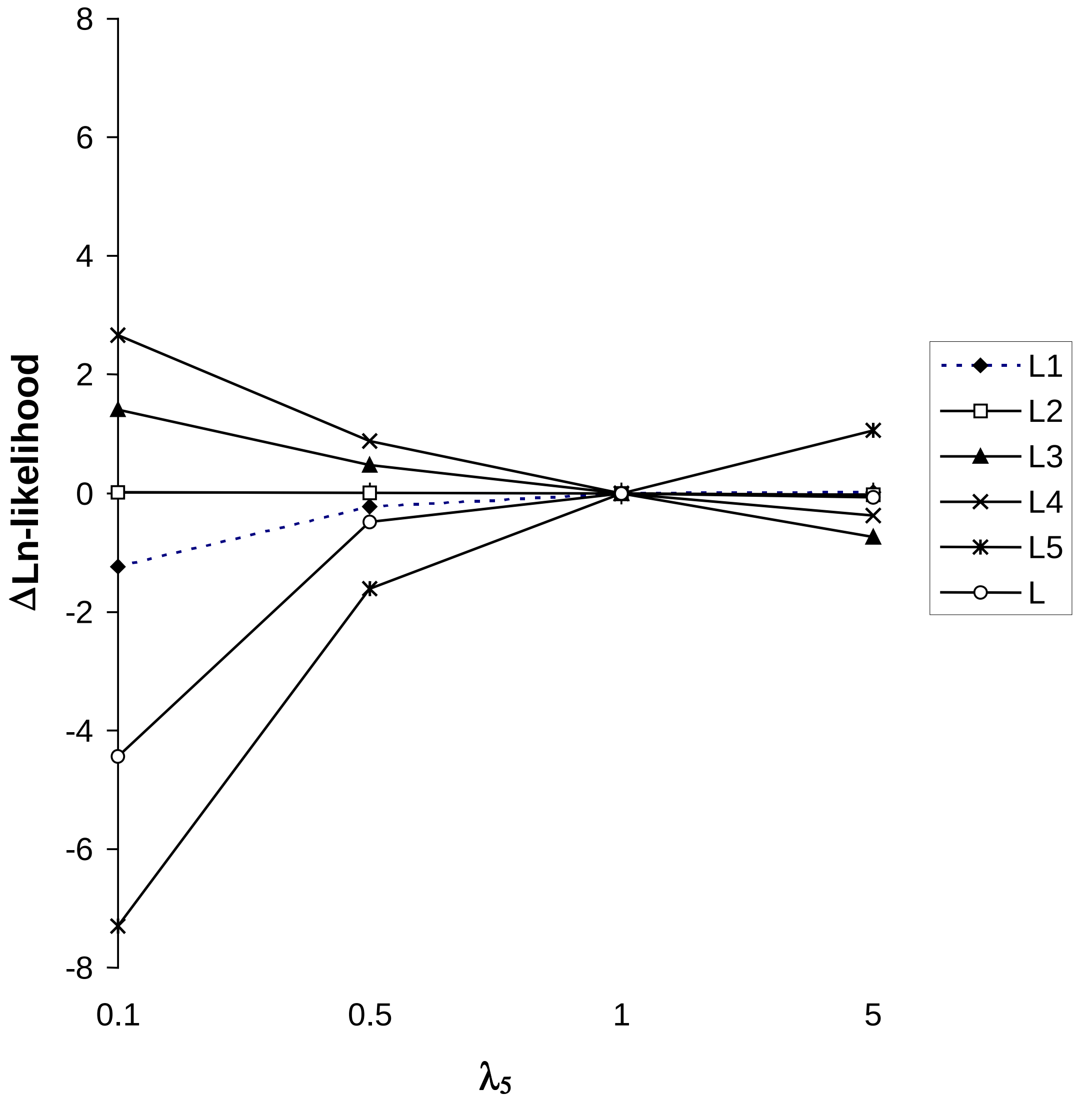

Figure 25. Changes in $\log_e$-likelihood components for catch-at-age model fit due to varying emphasis of fishery effort data (λ_5). Likelihood components: L1= fishery harvest, L2= survey CPUE, L3= fishery age composition, L4= survey age composition, L5= fishery effort, L= total.

Reduced emphasis of λ_5 resulted in higher likelihood values for L_3 and L_4 (Figure 25). Fishery effort information is usually the most questionable source of data in fishery models (Hilborn and Walters 1992). Since the fishery effort information used in CAA was based on effort targeted at all salmonines (e.g., *Oncorhynchus tshawytscha, O. kisutch, and O. mykiss*), trends in lake trout CPUE may be biased. This may be due to differences in habitat preferences or angler targeting of lake trout and other salmonines. Thus, another catch-at-age analysis was performed to explore the fit of the MH-3/4/5 model without the use of any effort information (CAA6). Since there is one less component in this model without effort data, it was not directly comparable to model CAA5 using the total $\log_e$-likelihoods (L). However, one can compare the individual likelihood components common to both models. The parameter values estimated by the two models were similar (Table 14; see Tables 12, 13). Predicted harvest based on parameters estimated by CAA6 (L_1 = -5.110188) did not match observed values as well as those of CAA5 (L_1 = -2.753300). The other likelihood component values for CAA6 were: L_2=-1.329959, L_3=10.552618, and L_4=-158.107641. The age-specific mortality rates averaged from 1984-1993 were similar between CAA5 and CAA6 (Figure 26). Total mortality was slightly higher for CAA6, which is primarily due to higher recreational fishing mortality rates. Based on these results, omission of fishery effort data did not significantly improve model fit to other data sources or dramatically alter estimated mortality rates.

Testing the model's sensitivity to each data source revealed that survey and fishery age composition information were important in determining the set of parameters for optimum fit. Changing the emphasis of survey age composition data contributed the largest

Table 14. Estimated parameter values from catch-at-age analysis model CAA6. Recreational fishery parameters: q_R= catchability (angler hours^{-1}), $S_{R,a}$= selectivity at age *a*, and $f_{R,y}$= fishing intensity (year^{-1}). μ'= proportionality coefficient for sea lamprey-induced mortality. Research survey parameters: q^*= catchability (meters of gill net^{-1}), S^*_a= selectivity at age *a*. Population parameters: $N_{a,1984}$= abundance at age *a* in 1984, M_1= age-1 instantaneous natural mortality (year^{-1}), and τ= rate of decrease in natural mortality rate (year^{-1} age^{-1}). $^{\#}$= parameter not estimated by catch-at-age analysis.

Fishery Parameters	Value	Survey Parameters	Value	Sea Lamprey and Population Parameters	Value
q_R	1.56302 x10^{-07}	q^*	0.001030	μ'	1$^{\#}$
$S_{R,1}$	0$^{\#}$	S^*_1	0$^{\#}$	$N_{2,1984}$	403756.464
$S_{R,2}$	0.000043	S^*_2	0.025174	$N_{3,1984}$	118621.889
$S_{R,3}$	0.031078	S^*_3	0.202199	$N_{4,1984}$	126903.823
$S_{R,4}$	0.310250	S^*_4	0.530940	$N_{5,1984}$	110246.361
$S_{R,5}$	0.887269	S^*_5	1$^{\#}$	$N_{6,1984}$	92275.104
$S_{R,6}$	0.993080	S^*_6	1.011411	$N_{7,1984}$	38053.854
$S_{R,7}$	0.975843	S^*_7	1.000369	$N_{8,1984}$	23906.748
$S_{R,8}$	0.998185	S^*_8	1.163516	$N_{9,1984}$	16092.736
$S_{R,9+}$	1$^{\#}$	S^*_9	1.230265	$N_{10,1984}$	985.310
$f_{R,1984}$	0.117562	S^*_{10+}	1.781492	$N_{11+,1984}$	3669.679$^{\#}$
$f_{R,1985}$	0.189955			M_1	0.707333
$f_{R,1986}$	0.197934			τ	1.116077
$f_{R,1987}$	0.132127				
$f_{R,1988}$	0.086388				
$f_{R,1989}$	0.098662				
$f_{R,1990}$	0.333537				
$f_{R,1991}$	0.122551				
$f_{R,1992}$	0.168678				
$f_{R,1993}$	0.072327				

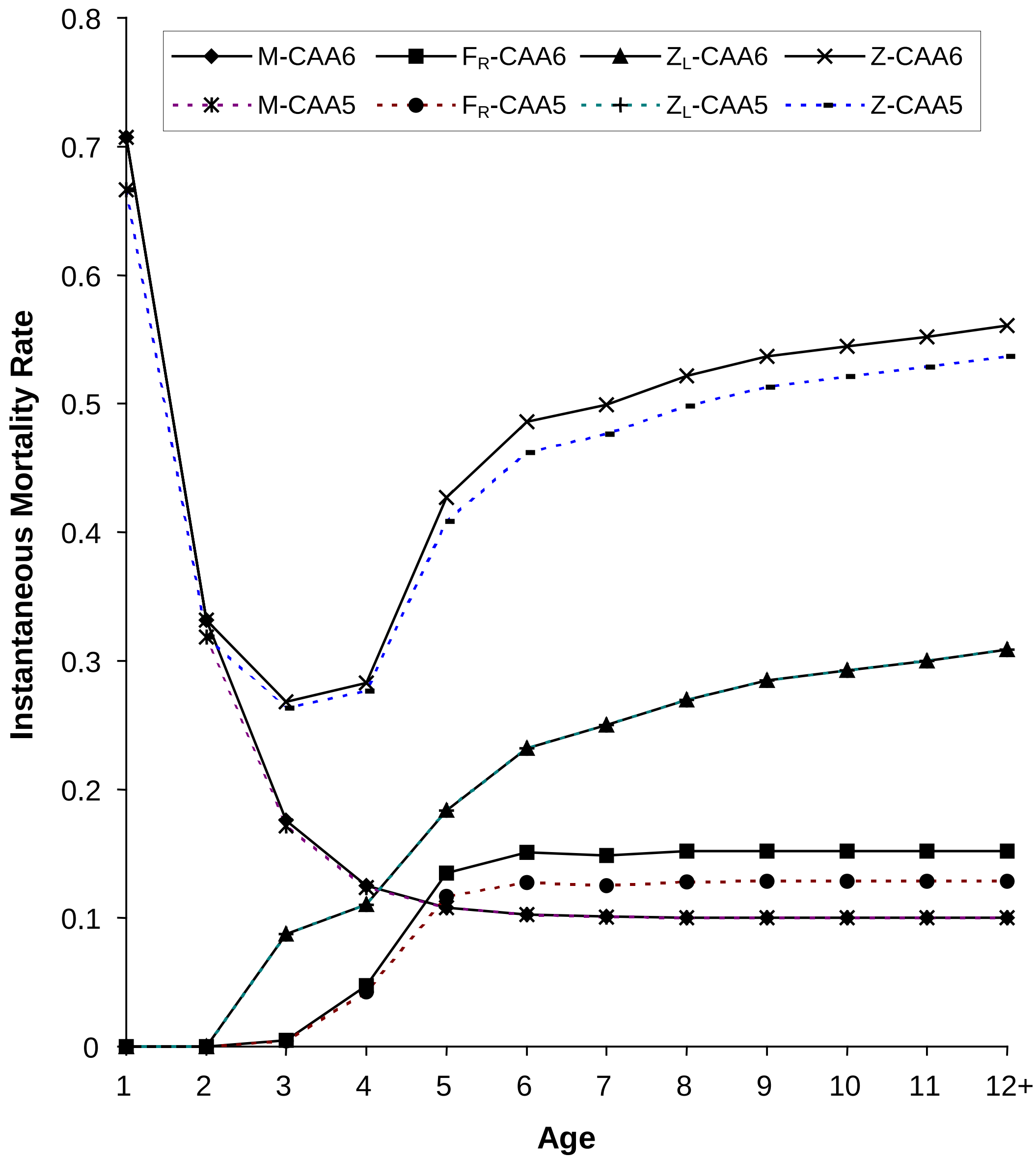

Figure 26. Age-specific instantaneous mortality rates (year^{-1}) for lake trout in southern Lake Huron as estimated by statistical catch-at-age analysis models CAA5 and CAA6. Mortality rates averaged from 1984-1993. M= natural mortality, F_R= recreational fishing mortality, Z_L= sea lamprey-induced mortality, and Z= total mortality.

fluctuations in the total log-likelihood. This indicated that model predictions of lake trout abundance were heavily influenced by survey data. The research survey data were collected in a systematic and consistent manner, and were considered the most reliable data source. Since virtually all lake trout collected in surveys had fin clips, aging errors were insignificant because each cohort had a distinguishing fin clip pattern. Furthermore, identical fin clip patterns between cohorts were validated by scale analysis of age (J. Johnson, Alpena Fisheries Research Station, MDNR, pers. comm.).

Fishery age composition data also strongly influenced model fit. However, fishery data were considered less reliable in comparison to research survey data. Specifically, fishery age composition data were collected in a less rigorous manner and were subject to biases associated with angler behavior. Fishery harvest and age composition data were not available for all years, and were not collected in all months for each year. In addition, age composition of fishery harvest were derived from subsamples, which may be biased due to an inconsistent sampling regime. As indicated in the methods section, some of these measurement errors were accounted for by limiting maximum sample size in a particular year to 200 fish in the $\log_e$-likelihood equation for fishery age composition data (L_3).

Based on the considerations discussed above, model predictions of mortality rates were evaluated by de-emphasizing fishery age composition data (L_3). When λ_3 was set to 0.1, age-specific total mortality rates were lower than when λ_3 was set at 1 (Figure 27). This was primarily due to reductions in natural mortality for ages 1-4 and reductions in fishing mortality for ages 5 and older. However, the proportion of lake trout killed in southern Lake Huron by sea lamprey and fishing averaged from 1984- 1993 remained roughly the same with

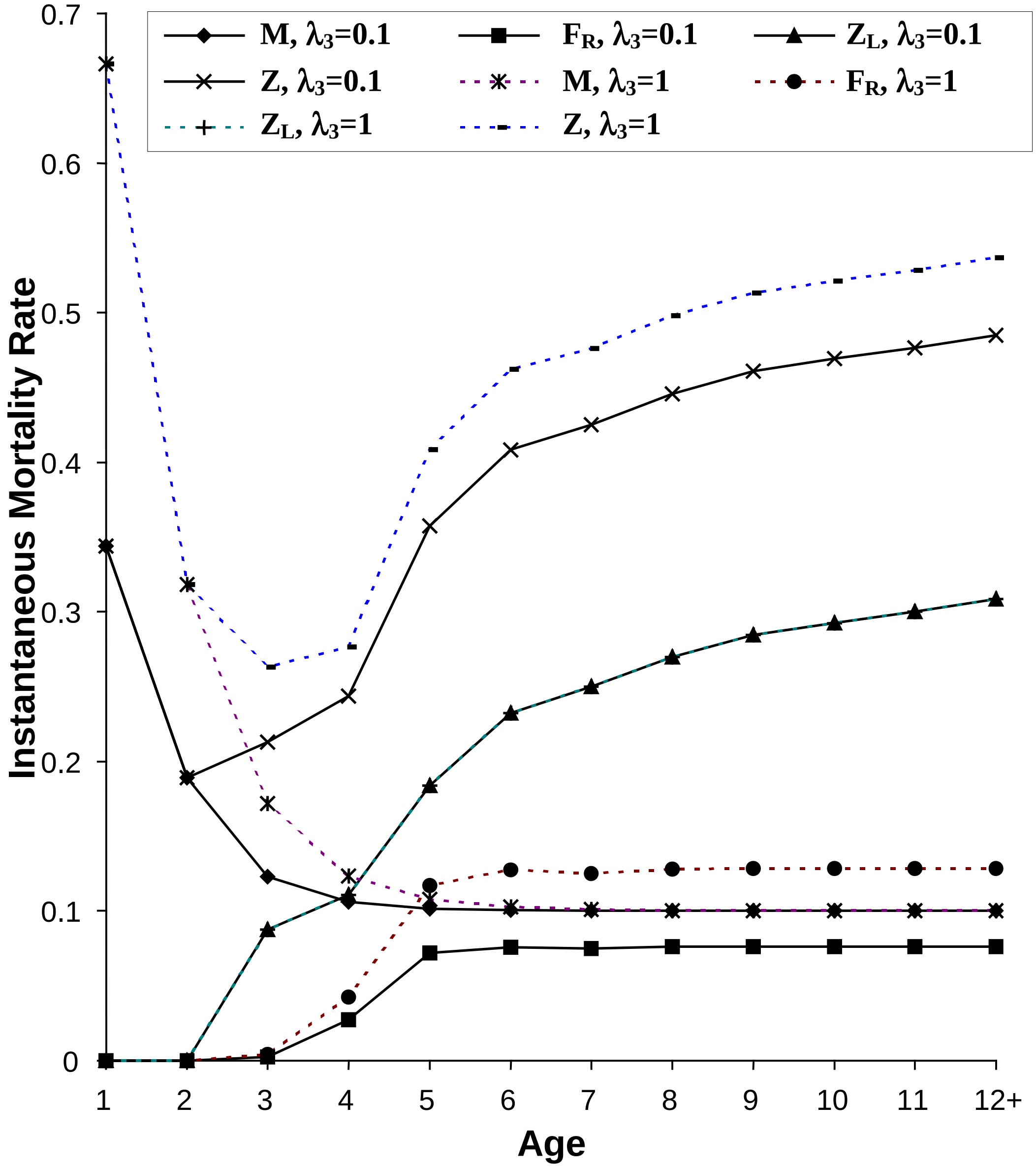

Figure 27. Differences in estimated age-specific instantaneous mortality rates ($year^{-1}$) with emphasis factor for fishery age composition data (λ_3) set at 0.1 and 1. Mortality rates averaged from 1984-1993. M=natural mortality, F_R= recreational fishing mortality, Z_L= sea lamprey-induced mortality, and Z= total mortality.

λ_3 =0.1 and λ_3 =1. When λ_3 =1, fishing accounted for 2.8% of the deaths on average, while sea lamprey parasitism killed 5.9%. For λ_3 =0.1, fishing removed 2.1% of the population and sea lampreys killed 7.2% of lake trout. Average total annual abundance of lake trout in southern Lake Huron from 1984-1993 was estimated to be 1.2 million fish per year for λ_3 =1 and 1.6 million fish per year for λ_3= 0.1. Overall, de-emphasizing fishery age composition data did not qualitatively change model predictions. Presumably, this is because predicted fishery age composition poorly matched the observed data--and it is those data and the estimates of their reliability that is questioned.

Based on the evaluations of model sensitivity to data sources, changing the emphasis factors did not significantly alter qualitative patterns and usually did not alter quantitative estimates by large amounts. As a result of these analyses, the emphasis factors for each data source were maintained at 1.

Uncertainty in estimated abundance

In order to evaluate the uncertainty in model estimates of abundance, the confidence bounds of parameter estimates must be determined. However, for multi-dimensional and highly non-linear problems such as the case in this study where there were 38 parameters estimated, conventional methods are often not robust (Seber and Wild 1989). Therefore, I used a one-dimensional approach aimed at a critical parameter linked to population abundance, namely recreational fishing intensity in 1993 ($f_{R,\,1993}$). I found the values (confidence bounds) of this parameter that had 5% of the total likelihood below the lower bound and had 5% of the total likelihood above the upper bound (Hilborn and Walters 1992).

I calculated this 90% confidence interval using a likelihood ratio test (see *Statistical catch-at-age analysis of the southern Lake Huron lake trout population model* in Results section). I then evaluated the corresponding abundance values for 1993 at the limits of this confidence interval and took this as approximate confidence bounds for abundance for that year. For 1993, these bounds for abundance of ages 3+ lake trout from the southern model were 20% below and 24% above the estimated value. Thus, the model's estimate of the mean abundance of ages 3+ lake trout in 1993 was 377,000 fish with a 90% confidence interval of 301,000 to 467,000 fish. This confidence interval probably underestimates uncertainty since it is conditional on the values of quantities such as sea lamprey-induced mortality, which were assumed known.

Calibration of the northern and central lake trout population models

Year-specific commercial fishing intensities and recreational fishery catchability coefficients for the northern and central regions estimated by the calibration procedure are listed in Table 27 of the Appendix. The central area model was successfully calibrated with the objective function minimized to match predicted commercial harvest to observed values (scaled 20% higher to account for under-reporting). The northern area model was successfully calibrated to both survey age composition and commercial harvest (adjusted for under-reporting). The parameter μ' in the northern model was estimated to be 4.06 (Table 14) indicating that sea lamprey-induced mortality rates for lake trout >533 mm were substantially underestimated using the wounding rates from central Lake Huron. Sea lamprey-induced mortality rates for lake trout in northern Lake Huron are in Table 44 of the Appendix.

Model output

Southern Lake Huron (MH-3/4/5), 1984-1993

Based on the results of statistical catch-at-age analysis of the southern Lake Huron population model, the estimated mean annual abundance of lake trout from 1984-1993 was 1.1 million (Table 28, Appendix). Mean annual abundance for mature lake trout (ages 8+) was estimated at about 70,000 fish. Total annual abundance was estimated to be lower during 1990-1993 than 1984-1989. This was due to lower stocking rates in 1987, 1988, and 1990 (Table 18, Appendix). Estimated mortality rates were relatively constant during this time period. On average, sea lamprey-induced mortality was estimated to be higher than all other sources of mortality (Figure 27, λ_3=1; Table 11; also see Tables 29-30 in Appendix). For lake trout ages most selected by sea lampreys and recreational fishing (ages 3-10), it was estimated that 43% of lake trout deaths were caused by sea lamprey parasitism, recreational fishing accounted for 21% of the deaths, while natural mortality killed 36% (Figure 28). Estimates of annual deaths due to each mortality source for each age are listed in Tables 31-33 of the Appendix.

Central Lake Huron (MH-2), 1984-1993

During 1984-1993, estimated mean annual abundance of lake trout in region MH-2 was about 385,000 (Table 34, Appendix). Mean abundance estimated for ages 8+ was

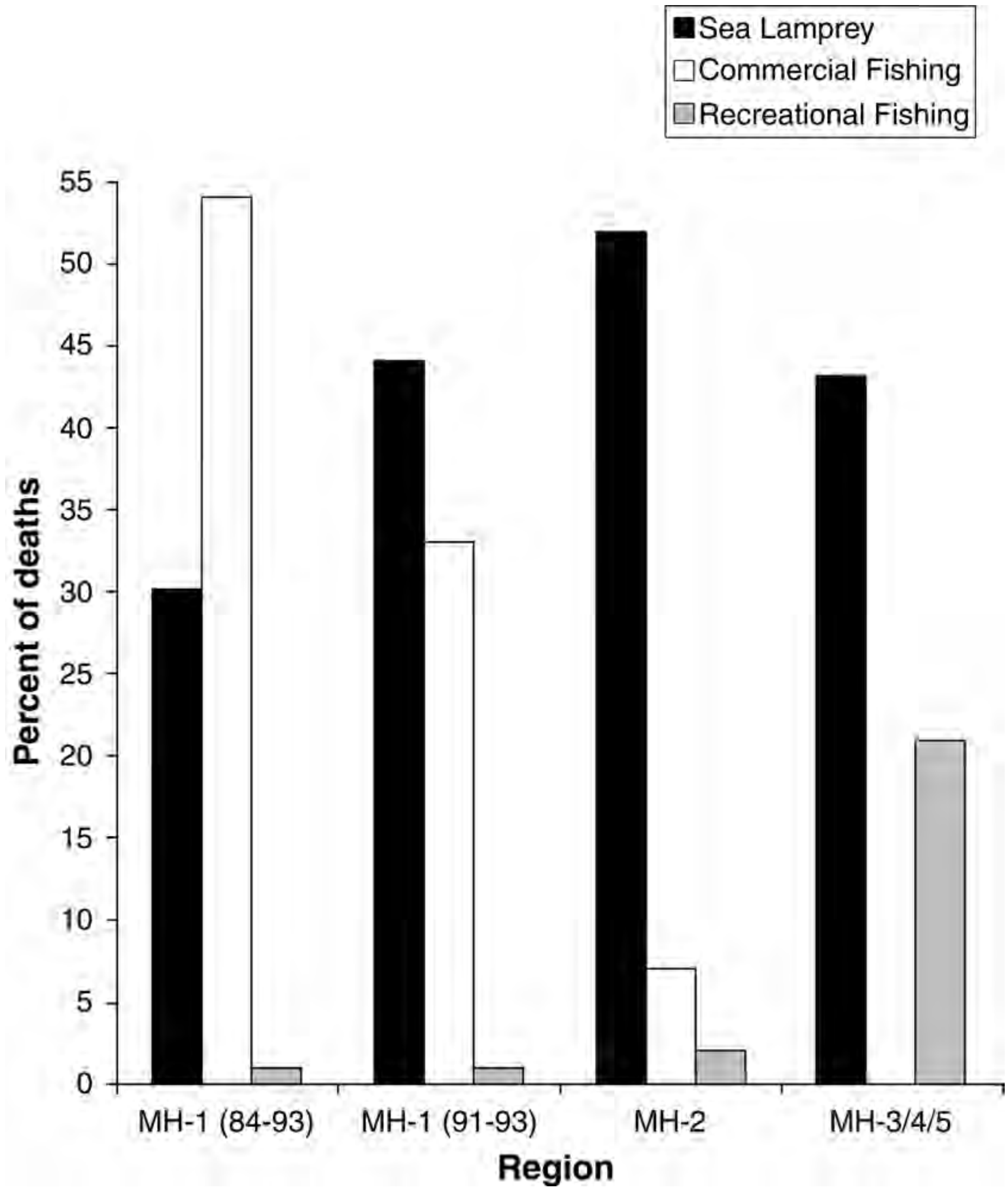

Figure 28. Allocation of estimated lake trout deaths (ages 3-10) in the main basin of Lake Huron from 1984-1993. MH-1= north, MH-2= central, and MH-3/4/5= south.

approximately 26,000 fish. An increasing trend in total abundance can be attributed to higher stocking rates over time (Table 18, Appendix). Overall recruitment in central Lake Huron, as indexed by age-1 abundance, was lower than southern Lake Huron. This was due to lower stocking rates and the high emigration rate (60%) from central to northern Lake Huron assumed in the population models. This was reflected in the lower mean annual abundance estimated in the central region as compared to the south. Sea lamprey-induced mortality was overwhelmingly the dominant source of lake trout death in central Lake Huron (Figure 29; Table 10; also see Tables 29, 35-36 in Appendix). In contrast, commercial and recreational fishing mortality were minor. In relation to numbers of ages 3-10 lake trout killed in the central area from 1984-1993, sea lamprey parasitism was estimated to account for more than half of all deaths (Figure 28). Recreational fishing accounted for 2%, commercial fishing accounted for 7%, and natural mortality 39% of ages 3-10 lake trout deaths. Estimates of total deaths by year and age are in Tables 37-40 of the Appendix.

Northern Lake Huron (MH-1), 1984-1993

Estimated abundance of lake trout in northern Lake Huron averaged 1.4 million fish per year from 1984-1993 (Table 41, Appendix). However, estimated mean abundance of mature lake trout (ages 8+) was about 3,000 fish per year. Total lake trout abundance was estimated to be highest in the north compared with the rest of the main basin of Lake Huron, and was dominated by immature fish. This was due to the higher stocking rates in the north and the high immigration from central Lake Huron (Table 18, Appendix). An increasing

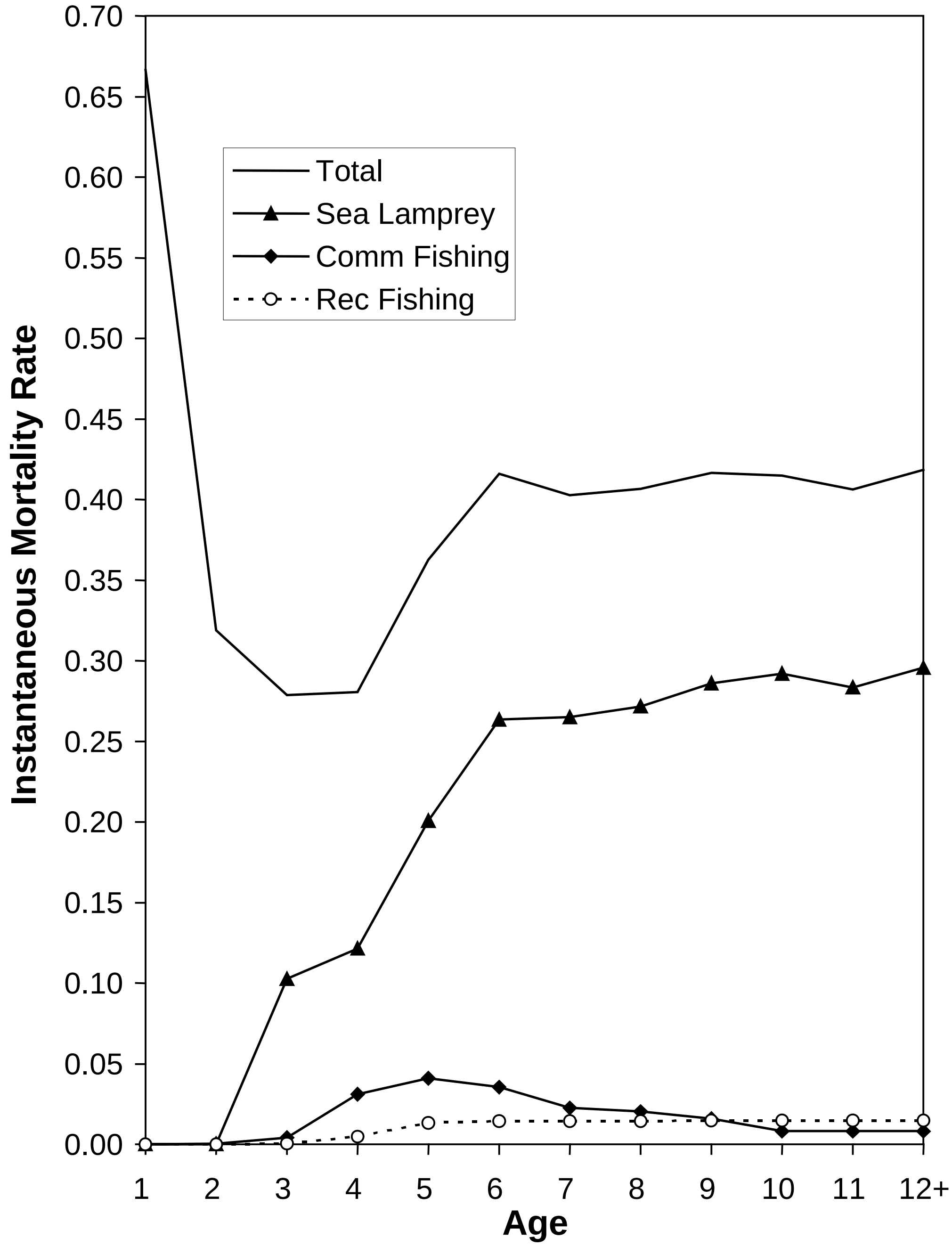

Figure 29. Age-specific estimates of instantaneous mortality rates ($year^{-1}$) for lake trout in central Lake Huron. Mortality rates averaged from 1984-1993.

trend in estimated total annual abundance was observed over the time series. This trend reflects recruitment as indicated by age-1 abundance (Tables 41, 18, Appendix).

Mortality rates changed dramatically from 1984-1994. Commercial fishing mortality for ages 3-10 lake trout was the highest source of death during 1987-1989, whereas sea lamprey-induced mortality was the dominant source during 1984-1985 and 1991-1993 (Figure 30; Tables 29, 42-44, Appendix). For ages 4-7 lake trout during 1987-1988, estimated instantaneous mortality rates due to commercial fishing ranged from 3.81 to 9.15 year^{-1}. Lake trout are not a target species in the commercial fishery, and are harvested as bycatch in the lake whitefish (*Coregonus clupeaformis*) large-mesh gill net fishery (M. Ebener, Chippewa-Ottawa Treaty Fishery Management Authority, pers. comm.). The high commercial fishing mortality rates estimated correspond to the highest levels of tribal gill net effort for lake whitefish during 1984-1993 (Table 26, Appendix). From 1991-1993, when mortality rates were relatively constant, the dominant source of mortality for lake trout in northern Lake Huron was due to sea lampreys (Figure 31; Tables 29, 42-44, Appendix). Commercial fishing was also a significant source of lake trout mortality starting at age-4. In contrast, recreational fishing was an insignificant source of mortality for lake trout in the north. Although total mortality was estimated to be extremely high for the older lake trout, there were very few fish older than age-8 in the population, because most fish were killed at earlier ages (Table 41, Appendix).

In terms of the average number of ages 3-10 lake trout killed in the northern region, from 1984-1993 commercial fishing caused 54%, sea lamprey parasitism 30%, recreational fishing less than 1%, and natural mortality 16% of deaths (Figure 28; Tables 45-48,

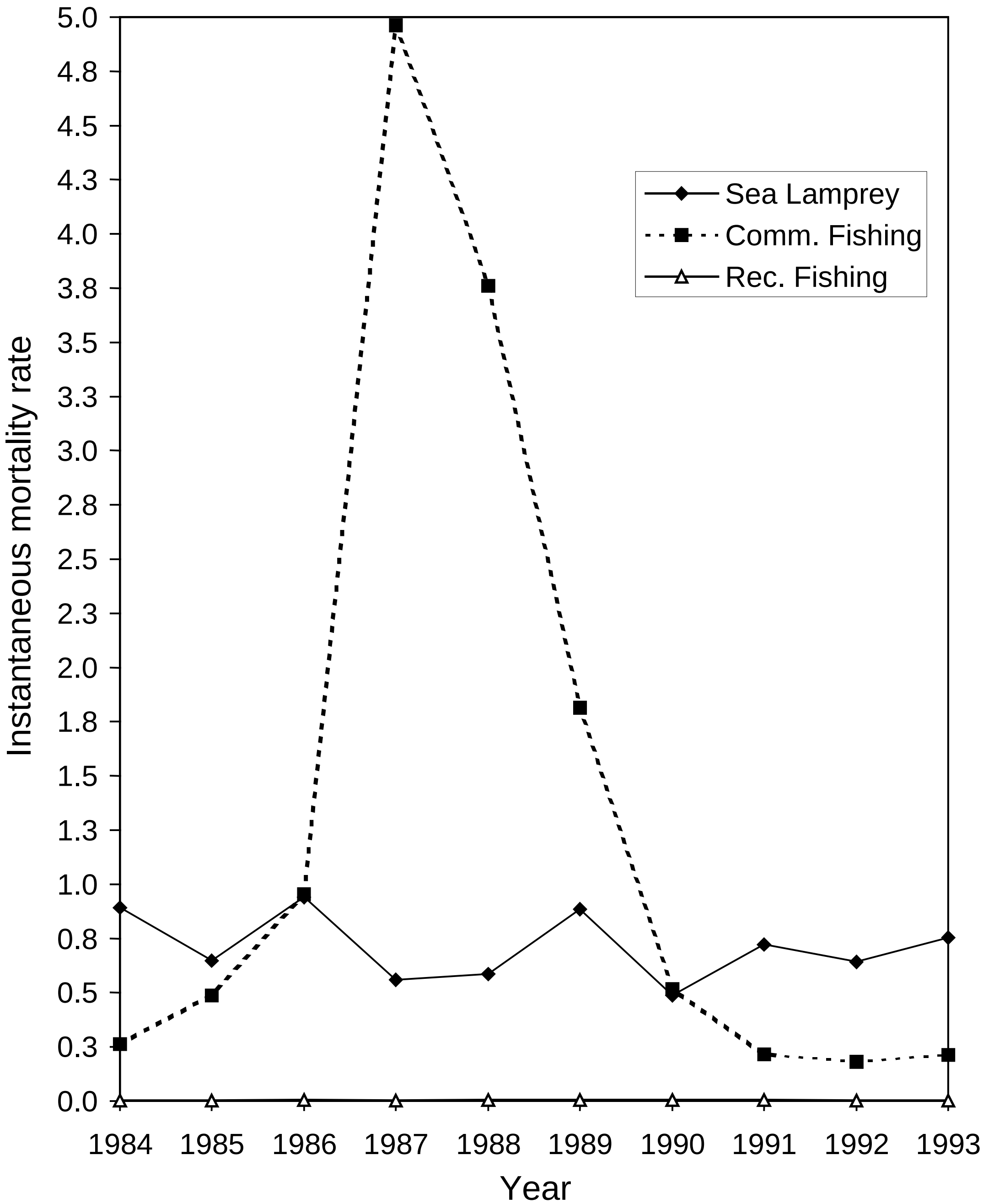

Figure 30. Temporal patterns in estimated instantaneous mortality rates (year^{-1}) averaged for ages 3-10 lake trout in northern Lake Huron.

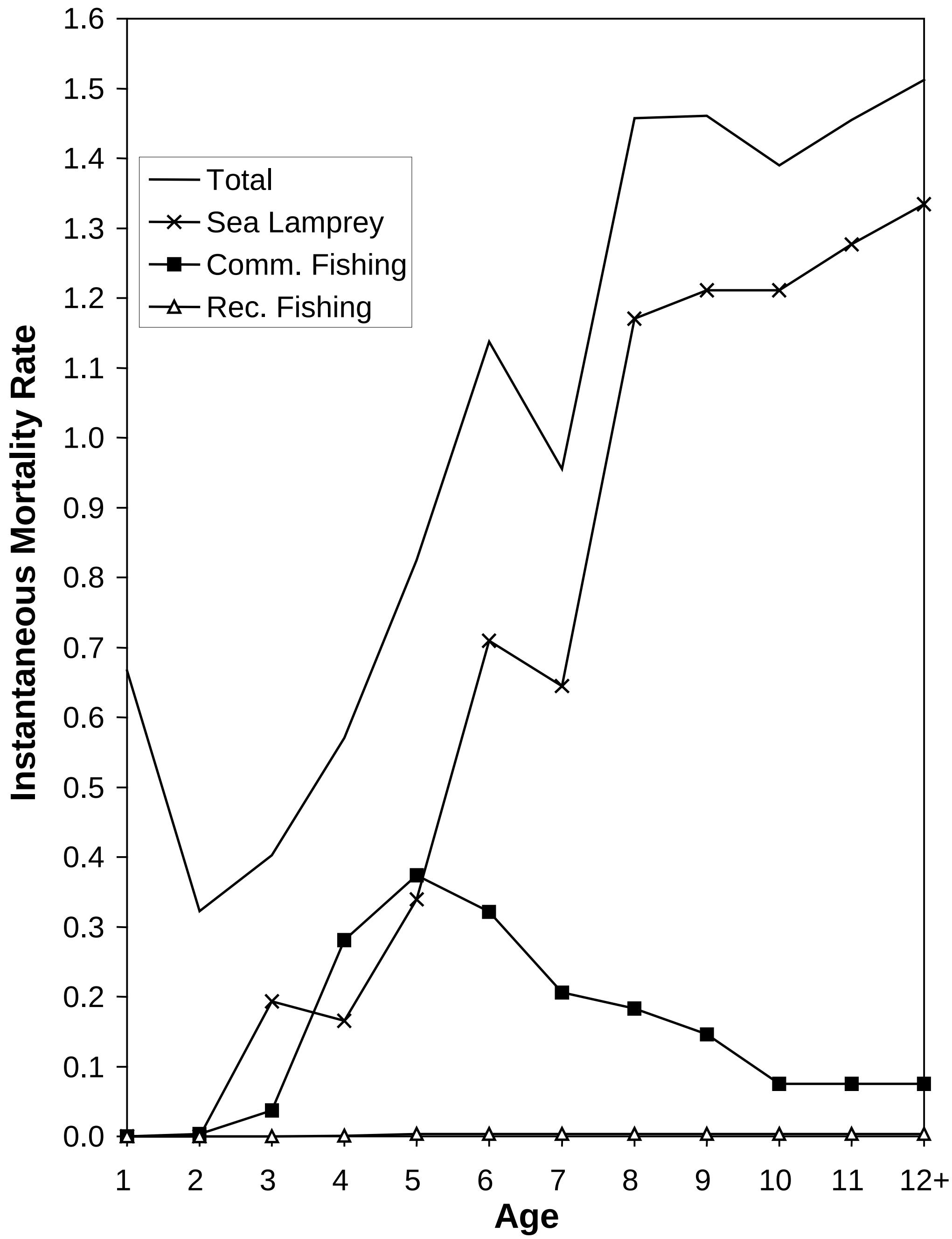

Figure 31. Estimates of age-specific instantaneous mortality rates ($year^{-1}$) for lake trout in northern Lake Huron. Mortality rates averaged from 1991-1993.

Appendix). However, during the most recent period (1991-1993), sea lampreys caused 44% of deaths for ages 3-10 lake trout, while commercial fishing accounted for 33% (Figure 28).

Total mortality rates in Lake Huron

In southern Lake Huron, estimated instantaneous rates of total mortality (Z) for lake trout ages 5 and older were above the GLFC lake trout rehabilitation target maximum of 0.59 $year^{-1}$ during 1987, 1990, and 1993(Table 49, Appendix). Overall, total mortality rates in southern Lake Huron were below the lake trout rehabilitation target. For central Lake Huron, estimates of Z were below the GLFC target maximum in all years from 1984-1993 (Table 50, Appendix). The total mortality rates estimated for lake trout ages 5+ in northern Lake Huron exceeded the rehabilitation target maximum in all years from 1984-1993 (Table 51, Appendix).

Model projections

Southern Lake Huron (MH-3/4/5)

Scenario 1: Total Allowable Catch (TAC) with maximum Z=0.59 $year^{-1}$

Under the TAC scenario, abundance of lake trout ages 8 and older in southern Lake Huron is projected to decrease 56% by the year 2010 if sea lamprey-induced mortality was equal to current estimated rates (Figure 32a). If sea lamprey-induced mortality was eliminated, total abundance of lake trout ages 8+ is projected to still decrease 54% by the year 2010. TAC is projected to increase 194% by the year 2010 under current conditions and is projected to increase 783% if sea lamprey-induced mortality was reduced to 0 (Figure 32b).

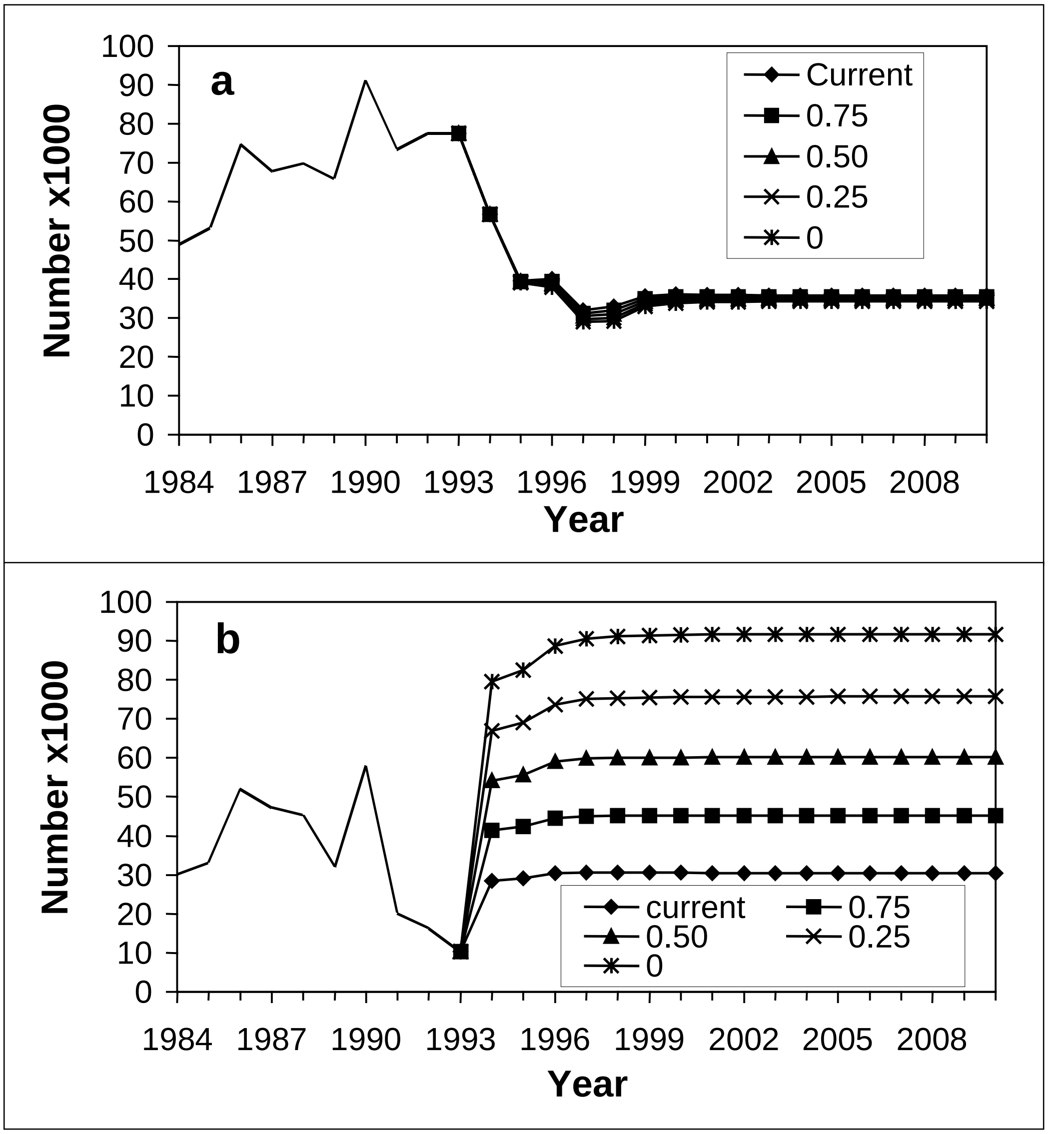

Figure 32. Model estimates of lake trout (a) abundance for ages 8+, and (b) total harvest under a total allowable catch (TAC) management scenario in southern Lake Huron from 1984-2010. Maximum total instantaneous mortality for projections was 0.59 $year^{-1}$. Projections (1994-2010) were according to varying levels of sea lamprey-induced mortality (Z_L): Current= average Z_L for 1991-1993; 0.75= 75% of current; 0.50= 50% of current; 0.25= 25% of current; 0.0= Z_L is 0.

These results were based under the assumption that fishing mortality could be increased to make total mortality equal to the target rate of 0.59 year^{-1}.

Scenario 2: Current fishing mortality rate

If fishing mortality remained constant during the projection period (equal to average of 1991-1993), total abundance of ages 8+ lake trout is projected to decrease 29% under current sea lamprey-induced mortality rates (Figure 33a). However, if Z_L was reduced to 0, abundance would increase 318% by 2010 (Figure 33a). Under this management regime, harvest would increase 66% by the year 2010 with current sea lamprey-induced mortality rates and would increase 353% if $Z_L=0$ (Figure 33b).

Scenario 3: No fishing

Under this scenario, total abundance of lake trout older than age-7 are projected to increase 7% under current sea lamprey-induced mortality rates and to increase 678% by the year 2010 if Z_L was 0 (Figure 34). This management option provides the highest projected spawner population increase under current stocking, natural mortality, and sea lamprey-induced mortality rates.

Central Lake Huron (MH-2)

Scenario 1: Total Allowable Catch (TAC) with maximum Z=0.59 year^{-1}

Total abundance of ages 8+ lake trout in the central region is projected to decrease 15% by 2010 under this management plan with current sea lamprey-induced mortality rates

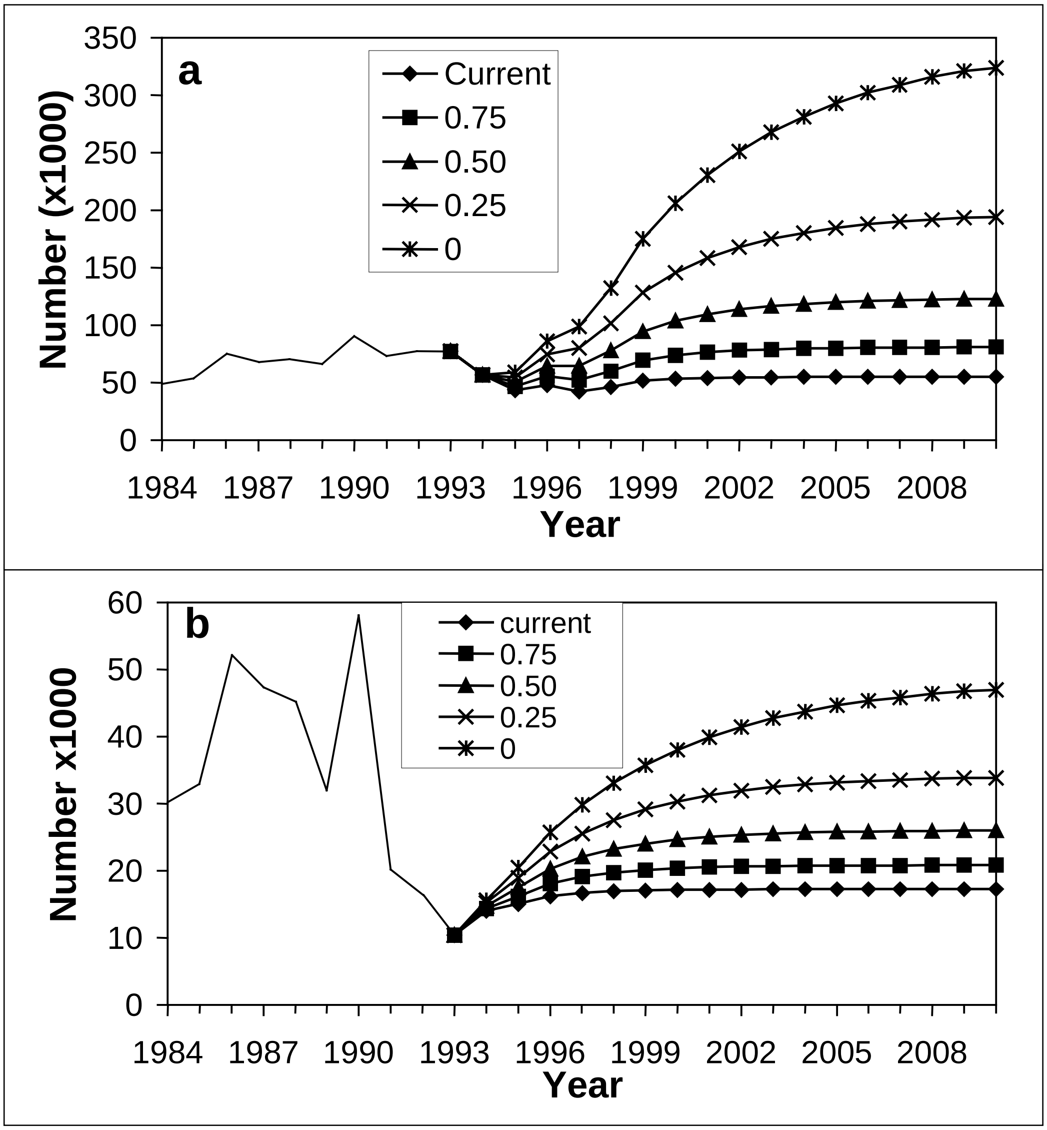

Figure 33. Model estimates of lake trout (a) abundance for ages 8+ and, (b) total harvest under a constant fishing mortality management scenario in southern Lake Huron from 1984-2010. Fishing mortality rates for projections were based on the average of 1991-1993 rates. Projections (1994-2010) were according to varying levels of sea lamprey-induced mortality (Z_L): Current= average Z_L for 1991-1993; 0.75= 75% of current; 0.50= 50% of current; 0.25= 25% of current; 0.0= Z_L is 0.

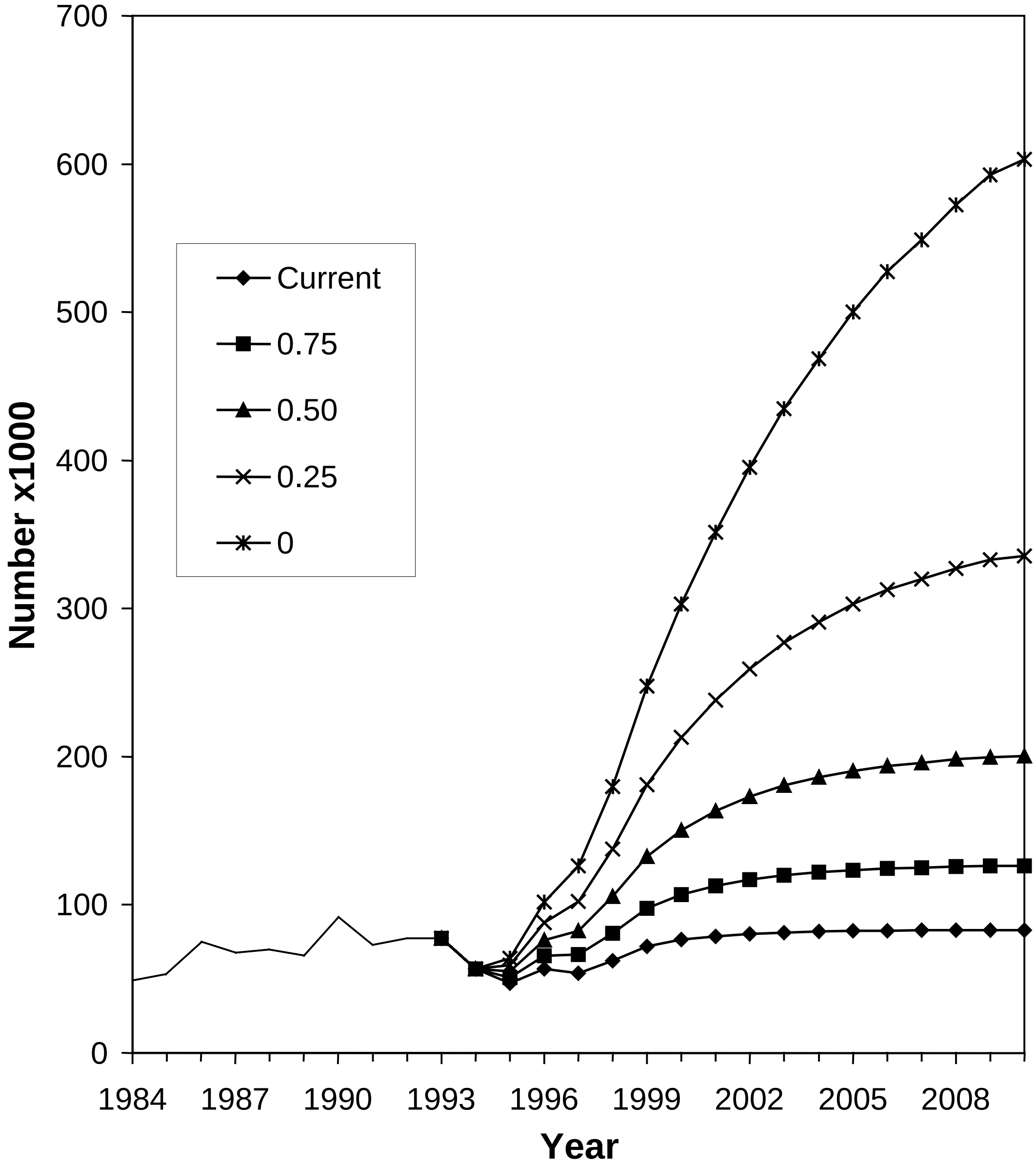

Figure 34. Model estimates of ages 8+ lake trout abundance in southern Lake Huron from 1984-2010. Projections were based on a no fishing management scenario according to varying levels of sea lamprey-induced mortality (Z_L): Current= average Z_L for 1991-1993; 0.75= 75% of current; 0.50= 50% of current; 0.25= 25% of current; 0.0= Z_L is 0.

(Figure 35). If sea lamprey-induced mortality was reduced to zero, ages 8+ abundance is projected to increase 51% by 2010. This is because of the differential age-selectivity of sea lamprey-induced and fishing mortality rates. Thus, it is more beneficial to allocate the maximum mortality rate to fishing than to sea lampreys because fishing tends to target a smaller range of ages than sea lampreys. If Z_L was equal to current rates, commercial harvest is projected to increase 157% under the TAC plan (Figure 36a). If Z_L was zero, TAC is projected to increase 500% by 2010. Similar increases in projected recreational harvest were observed (Figure 36b).

Scenario 2: Current fishing mortality rate

Under current fishing and sea lamprey-induced mortality levels, total abundance of ages 8+ lake trout is projected to increase 50% by the year 2010 (Figure 37). If Z_L was reduced to zero, abundance of ages 8+ in central Lake Huron is projected to increase 924% by 2010. Commercial harvest of lake trout is projected to increase 27% with current sea lamprey conditions, and to increase 134% when Z_L was zero (Figure 38a). Recreational harvest had a higher level of projected increase than commercial harvest. Under current sea lamprey-induced mortality rates, recreational harvest is projected to increase 49% by 2010 (Figure 38b). If Z_L was reduced to zero, projected harvest increases 357% by 2010.

Scenario 3: No fishing

Under this management plan, ages 8+ lake trout abundance is projected to increase 124% by the year 2010 given current sea lamprey-induced mortality rates (Figure 39). Total

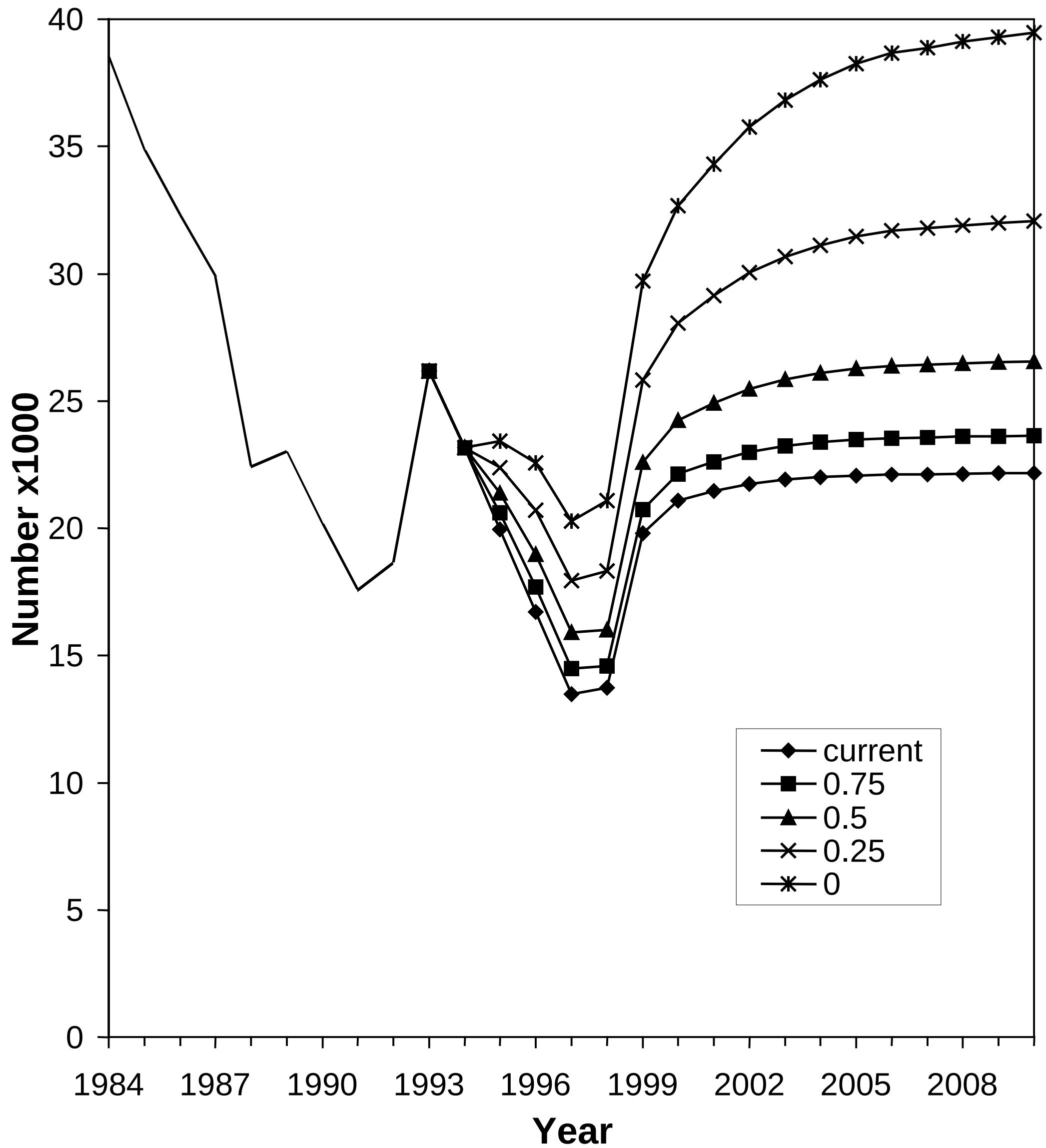

Figure 35. Model estimates of ages 8+ lake trout abundance under a total allowable catch (TAC) management scenario in central Lake Huron from 1984-2010. Maximum total instantaneous mortality for projections was 0.59 year^{-1}. Projections (1994-2010) were according to varying levels of sea lamprey-induced mortality (Z_L): Current= average Z_L for 1991-1993; 0.75= 75% of current; 0.50= 50% of current; 0.25= 25% of current; 0.0= Z_L is 0.

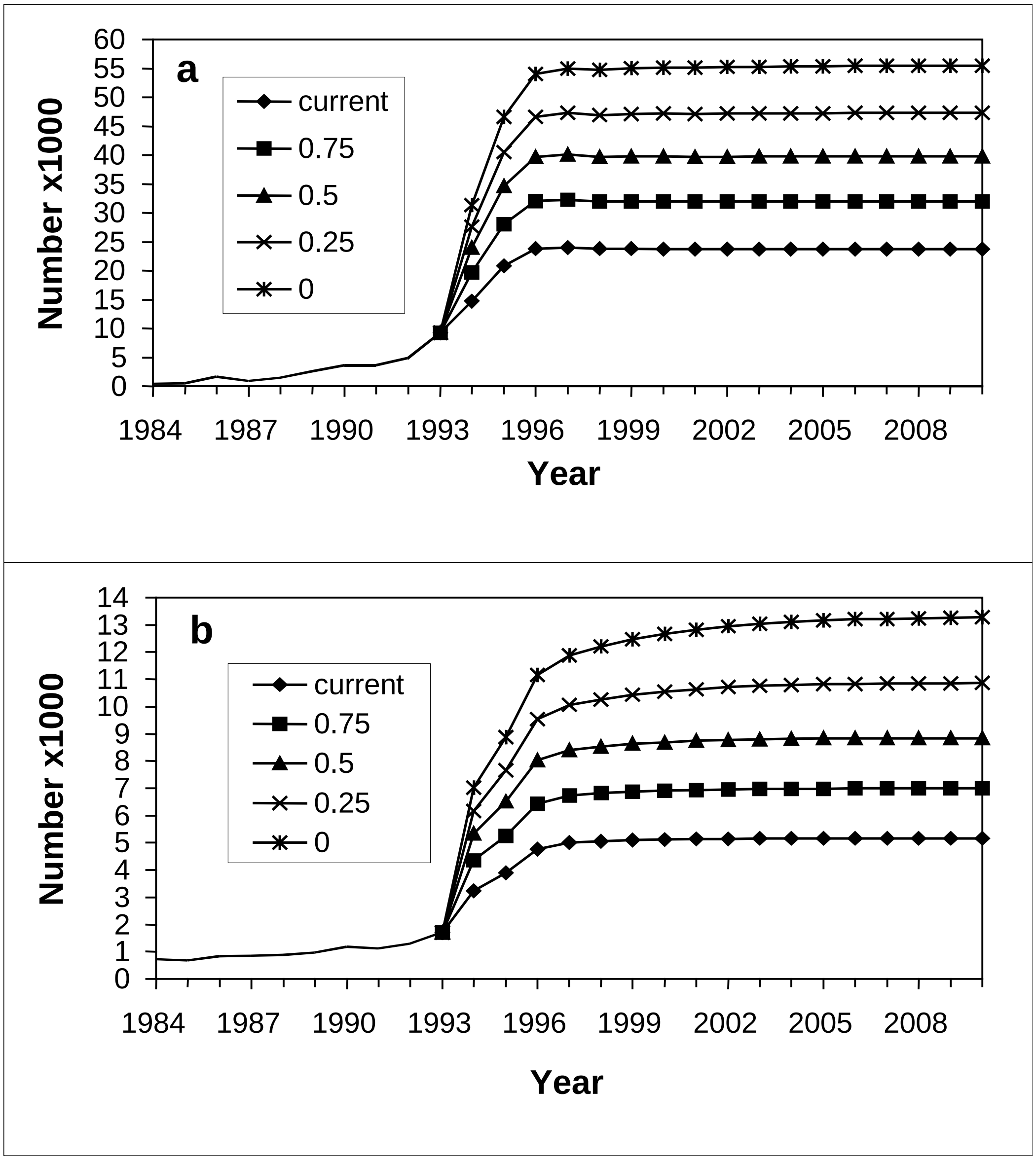

Figure 36. Model estimates of lake trout (a) commercial harvest, and (b) recreational harvest in central Lake Huron from 1984-2010. Projections were based on a total allowable catch (TAC) management scenario according to varying levels of sea lamprey-induced mortality (Z_L): Current= average Z_L for 1991-1993; 0.75= 75% of current; 0.50= 50% of current; 0.25= 25% of current; 0.0= Z_L is 0. Maximum total instantaneous mortality for projections was 0.59 year^{-1}.

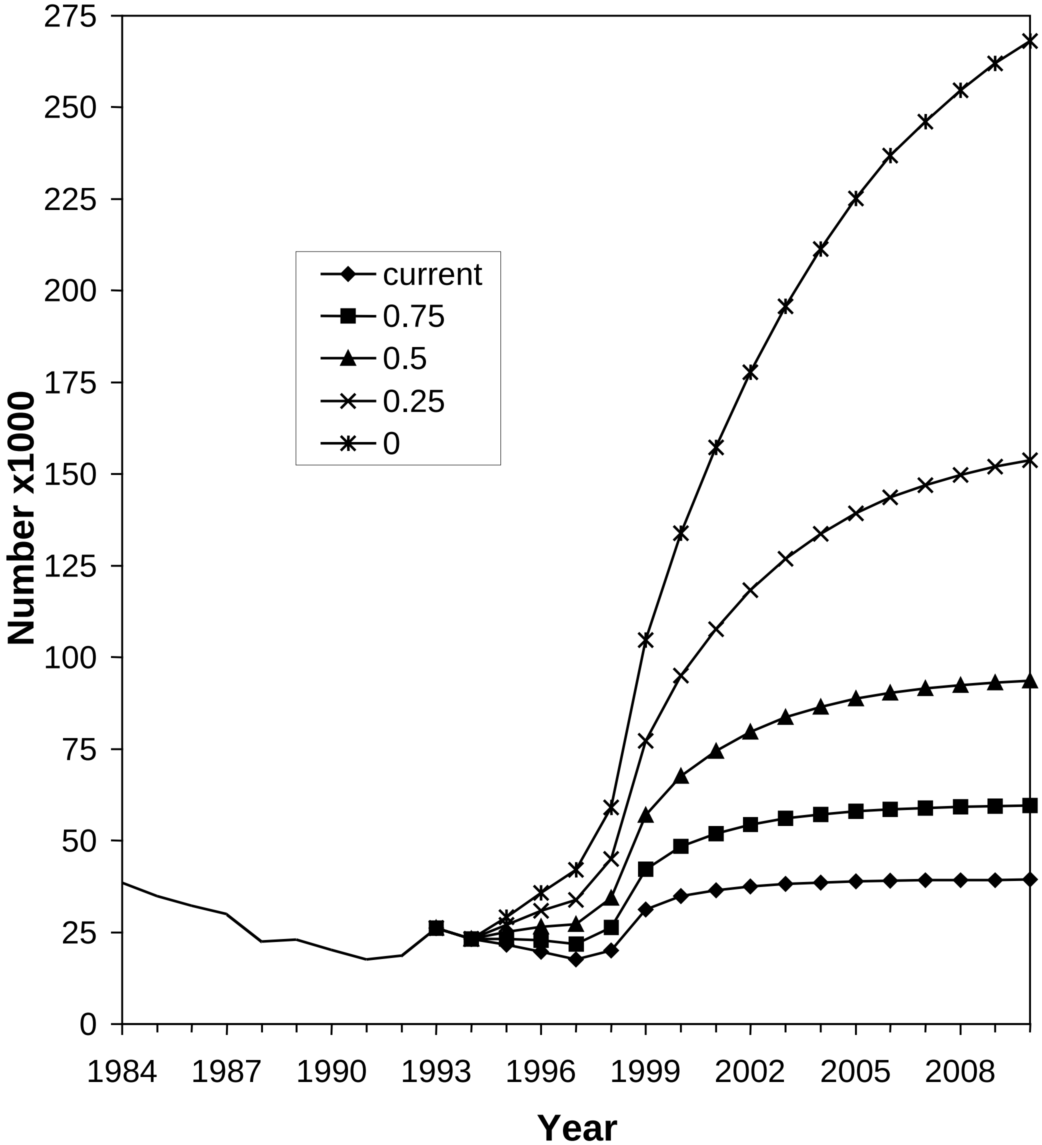

Figure 37. Model estimates of ages 8+ lake trout abundance under a constant fishing mortality management scenario in central Lake Huron from 1984-2010. Fishing mortality rates for projections were based on the average of 1991-1993 rates. Projections (1994-2010) were according to varying levels of sea lamprey-induced mortality (Z_L): Current= average Z_L for 1991-1993; 0.75= 75% of current; 0.50= 50% of current; 0.25= 25% of current; 0.0= Z_L is 0.

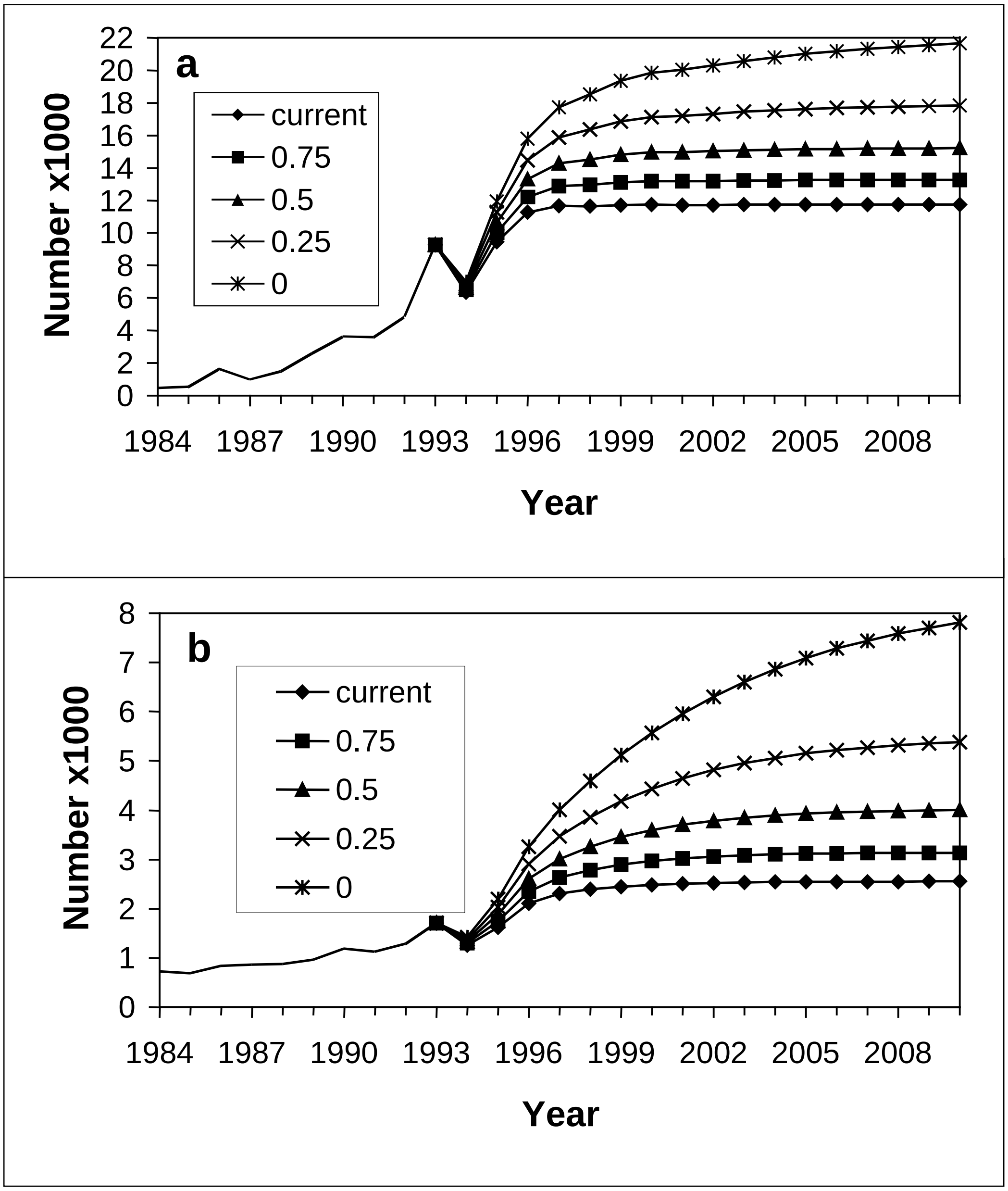

Figure 38. Model estimates of lake trout (a) commercial harvest, and (b) recreational harvest in central Lake Huron from 1984-2010. Projections were based on a constant fishing mortality management scenario according to varying levels of sea lamprey-induced mortality (Z_L): Current= average Z_L for 1991-1993; 0.75= 75% of current; 0.50= 50% of current; 0.25= 25% of current; 0.0= Z_L is 0. Fishing mortality rates for projections were based on the average of 1991-1993 rates.

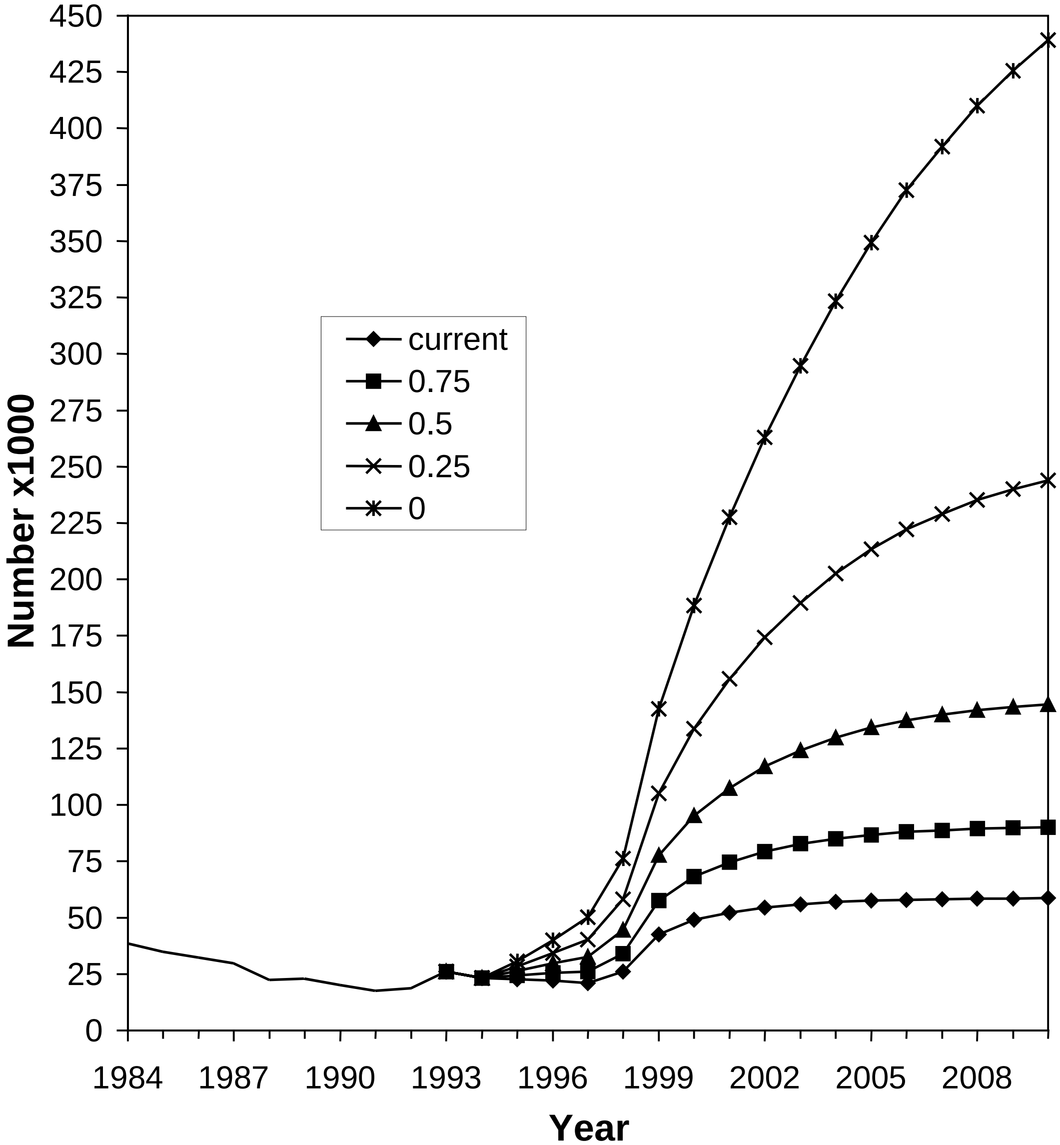

Figure 39. Model estimates of ages 8+ lake trout abundance in central Lake Huron from 1984-2010. Projections were based on a zero fishing management scenario according to varying levels of sea lamprey-induced mortality (Z_L): Current= average Z_L for 1991-1993; 0.75= 75% of current; 0.50= 50% of current; 0.25= 25% of current; 0.0= Z_L is 0.

abundance is projected to increase 1,578% if Z_L was zero. Compared to the other two plans, zero fishing would allow for maximum spawner population regeneration in central Lake Huron.

Northern Lake Huron (MH-1)

Scenario 1: Total Allowable Catch (TAC) with maximum Z=0.59 year^{-1}

Following the TAC management plan, total abundance of ages 8+ lake trout in northern Lake Huron is projected to increase 10,784% by the year 2010 (Figure 40). However, no harvest would be allowed since sea lamprey-induced and natural mortality rates exceeded the target maximum rate (Figure 41). This enormous increase in ages 8+ abundance in the projections was due to low fishing mortality rates in comparison with the extremely high rates during 1987-1989. This high fishing mortality period essentially eliminated fish that would be ages 8+ (see Tables 41-44, Appendix). Moreover, under the TAC plan, no harvest was allowed until sea lamprey-induced mortality was reduced to 25% of current rates. The highest increase in ages 8+ lake trout abundance (52,976%) is projected to occur if sea lamprey-induced mortality was reduced to zero (Figure 40). Furthermore, when sea lamprey-induced mortality was reduced to 25% of current rates, the projected increase in ages 8+ abundance was less than when Z_L was reduced only by 50%. This lower increase in abundance was due to the increase in fishing mortality to scale total mortality to the target of 0.59 year^{-1}.

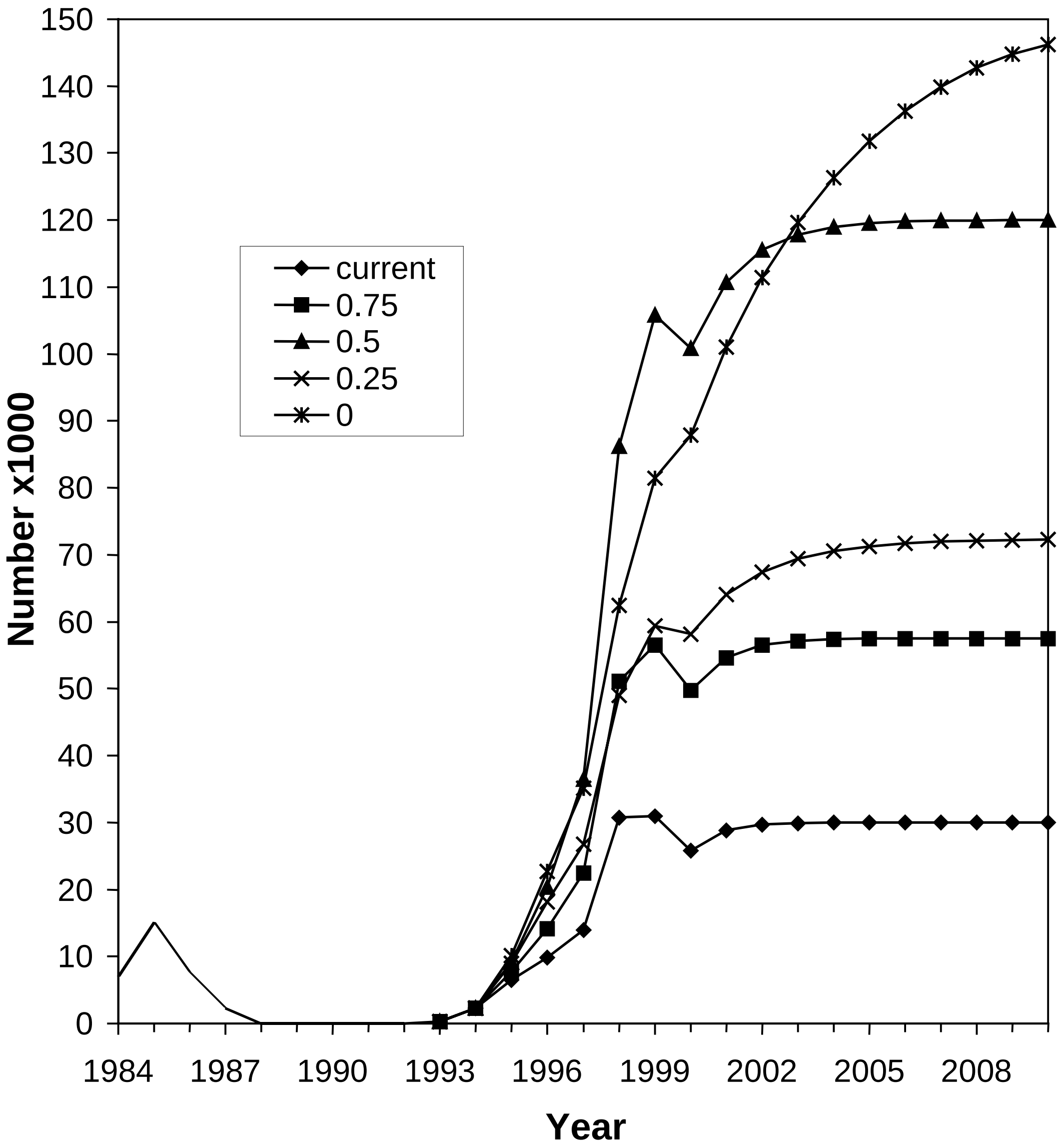

Figure 40. Model estimates of ages 8+ lake trout abundance under a total allowable catch (TAC) management scenario in northern Lake Huron from 1984-2010. Maximum total instantaneous mortality for projections was 0.59 year^{-1}. Projections (1994-2010) were according to varying levels of sea lamprey-induced mortality (Z_L): Current= average Z_L for 1991-1993; 0.75= 75% of current; 0.50= 50% of current; 0.25= 25% of current; 0.0= Z_L is 0.

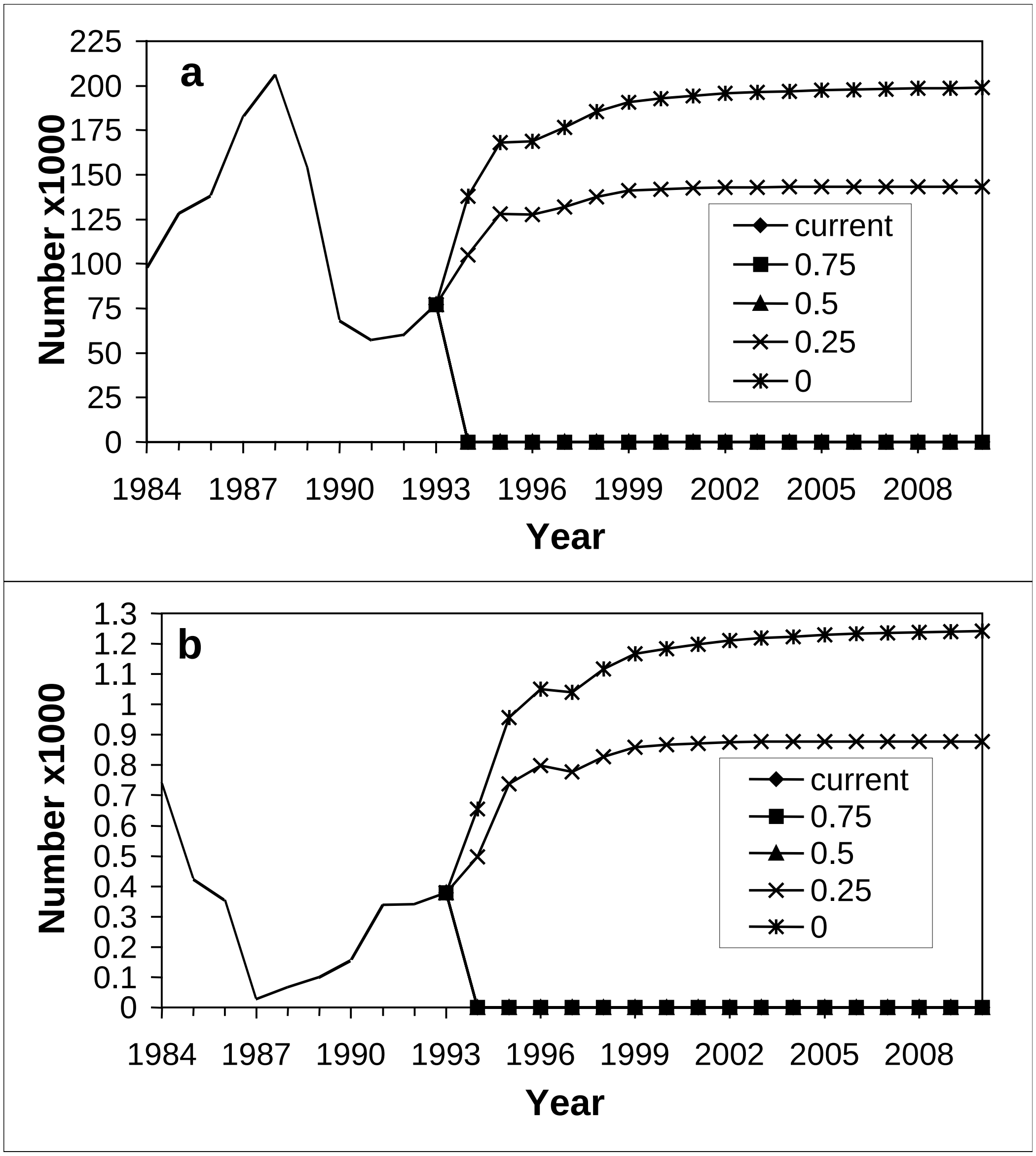

Figure 41. Model estimates of lake trout (a) commercial harvest, and (b) recreational harvest in northern Lake Huron from 1984-2010. Projections were based on a total allowable catch (TAC) management scenario according to varying levels of sea lamprey-induced mortality (Z_L): Current= average Z_L for 1991-1993; 0.75= 75% of current; 0.50= 50% of current; 0.25= 25% of current; 0.0= Z_L is 0. Maximum total instantaneous mortality for projections was 0.59 year^{-1}.

Scenario 2: Current fishing mortality rate

Under current (1991-1993) fishing mortality rates, ages 8+ abundance in northern Lake Huron is projected to increase under all levels of sea lamprey-induced mortality (Figure 42). Under current Z_L, projected abundance of ages 8+ lake trout would increase 2,885% by 2010, and increase 86,305% if Z_L was zero. This high increase was due to the current fishing mortality rates being significantly lower than the mortality rates during 1987-1989, which in turn allowed for the resurgence of older fish in the projection period even with similar sea lamprey-induced mortality rates. During 1989-1993, there were very few fish older than age-8 in the population (Tables 22, 41, Appendix). Natural mortality was estimated to be highest for ages 1-3, commercial fishing mortality impacted the population at age-3 and was most selective for ages 4-6, while sea lampreys started to impact lake trout at age-5 and increased with age. When fishing mortality rates from 1987-1989 were used instead of 1991-1993 rates in this scenario, ages 8+ abundance is projected to decrease by 99.9% or more by the year 2010 under all levels of sea lamprey-induced mortality.

Increases in projected commercial harvest by the year 2010 ranged from 26% under current sea lamprey conditions to 135% increase when Z_L was zero (Figure 43a). Similarly, recreational harvest is also projected to increase, although in higher proportions (Figure 43b). Recreational harvest is projected to increase 67% by the year 2010 under current sea lamprey-induced mortality rates and by 418% if Z_L was zero.

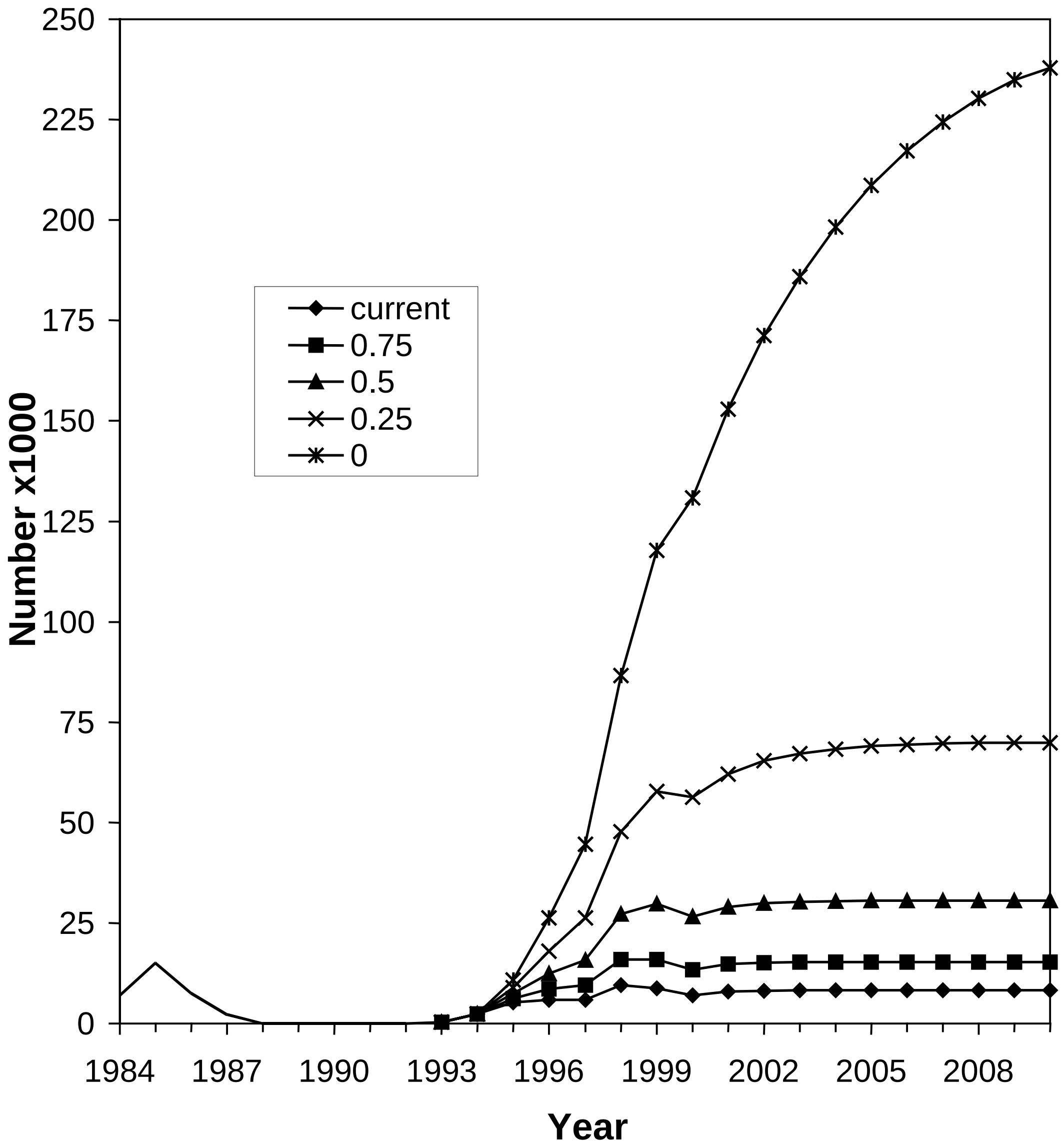

Figure 42. Model estimates of ages 8+ lake trout abundance under a constant fishing mortality management scenario in northern Lake Huron from 1984-2010. Fishing mortality rates for projections were based on the average of 1991-1993 rates. Projections (1994-2010) were according to varying levels of sea lamprey-induced mortality (Z_L): Current= average Z_L for 1991-1993; 0.75= 75% of current; 0.50= 50% of current; 0.25= 25% of current; 0.0= Z_L is 0.

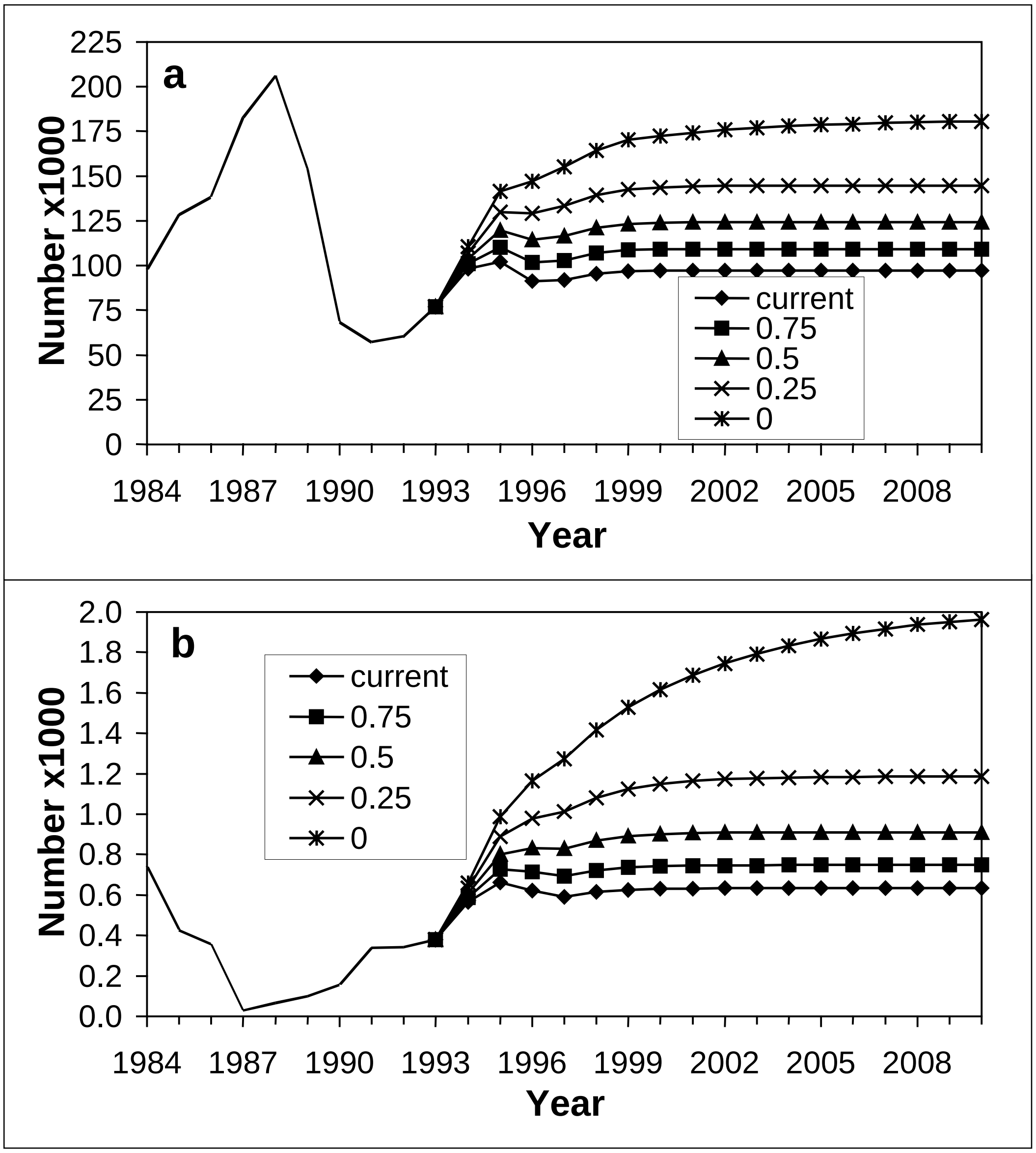

Figure 43. Model estimates of lake trout (a) commercial harvest, and (b) recreational harvest in northern Lake Huron from 1984-2010. Projections were based on a constant fishing mortality management scenario according to varying levels of sea lamprey-induced mortality (Z_L): Current= average Z_L for 1991-1993; 0.75= 75% of current; 0.50= 50% of current; 0.25= 25% of current; 0.0= Z_L is 0. Fishing mortality rates for projections were based on the average of 1991-1993 rates.

Scenario 3: No fishing

The maximum increase in ages 8+ abundance in northern Lake Huron is projected to occur under this strict management plan (Figure 44). With current sea lamprey-induced mortality rates, abundance of ages 8+ lake trout is projected to exceed 30,900 fish by 2010, an increase of greater than 10,700%. If sea lamprey-induced mortality was reduced to zero, ages 8+ lake trout would increase more than 470,000% or reach an abundance of 1.3 million fish.

Mortality trade-off: sea lamprey-induced vs. fishing mortality

Under 1991-1993 sea lamprey and fishing conditions in the main basin of Lake Huron, decreases in sea lamprey-induced mortality yield a larger increase in projected ages 8+ abundance than equivalent percentage decreases in fishing mortality. However, this was not true over the entire period for northern Lake Huron. Assuming current sea lamprey-induced mortality rates and the much higher fishing mortality rates from 1987-1989, decreases in fishing mortality are projected to yield greater gains in ages 8+ lake trout abundance than equivalent decreases in sea lamprey-induced mortality (Figure 45).

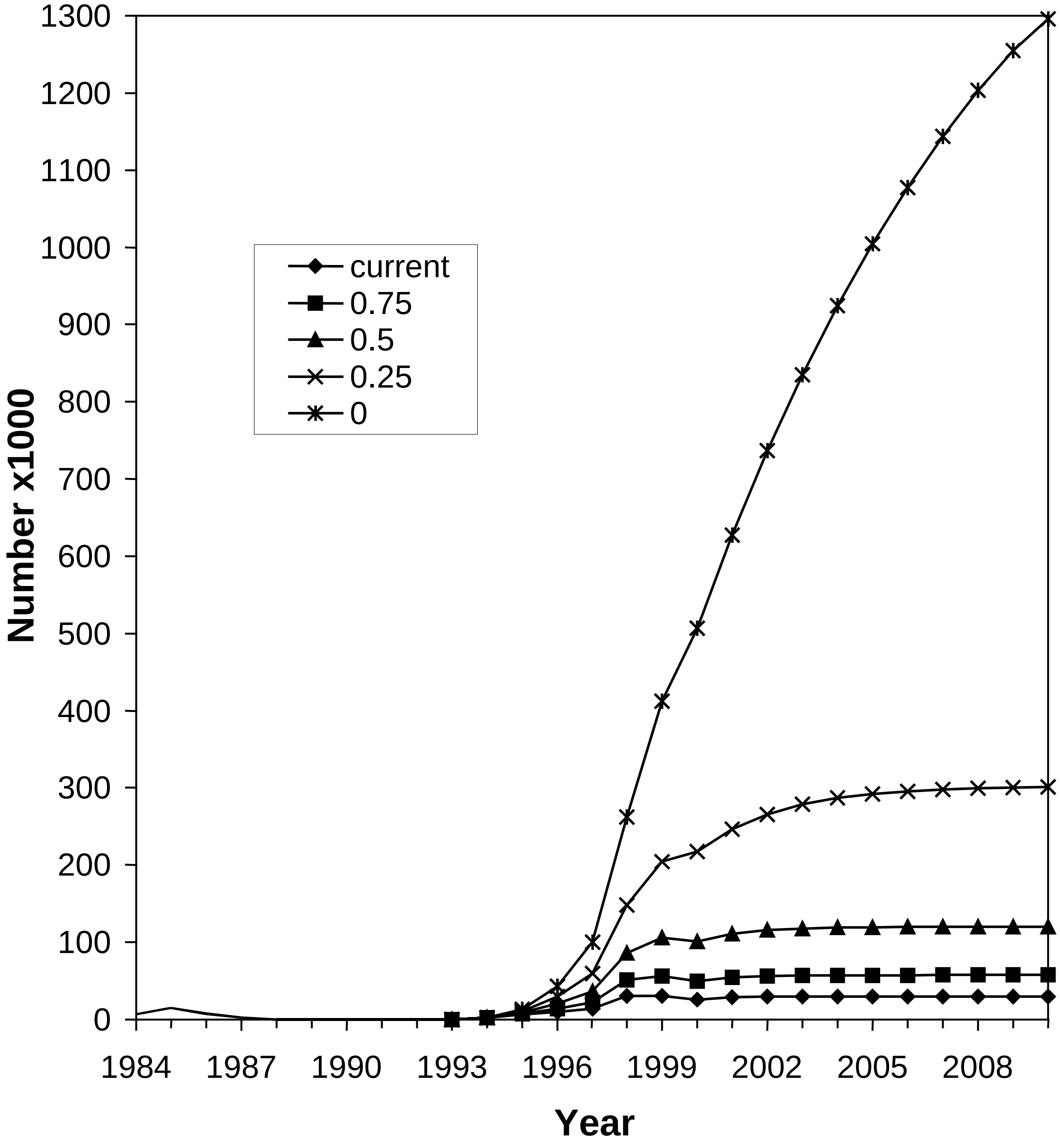

Figure 44. Model estimates of ages 8+ lake trout abundance in northern Lake Huron from 1984-2010. Projections were based on a zero fishing management scenario according to varying levels of sea lamprey-induced mortality (Z_L): Current= average Z_L for 1991-1993; 0.75= 75% of current; 0.50= 50% of current; 0.25= 25% of current; 0.0= Z_L is 0.

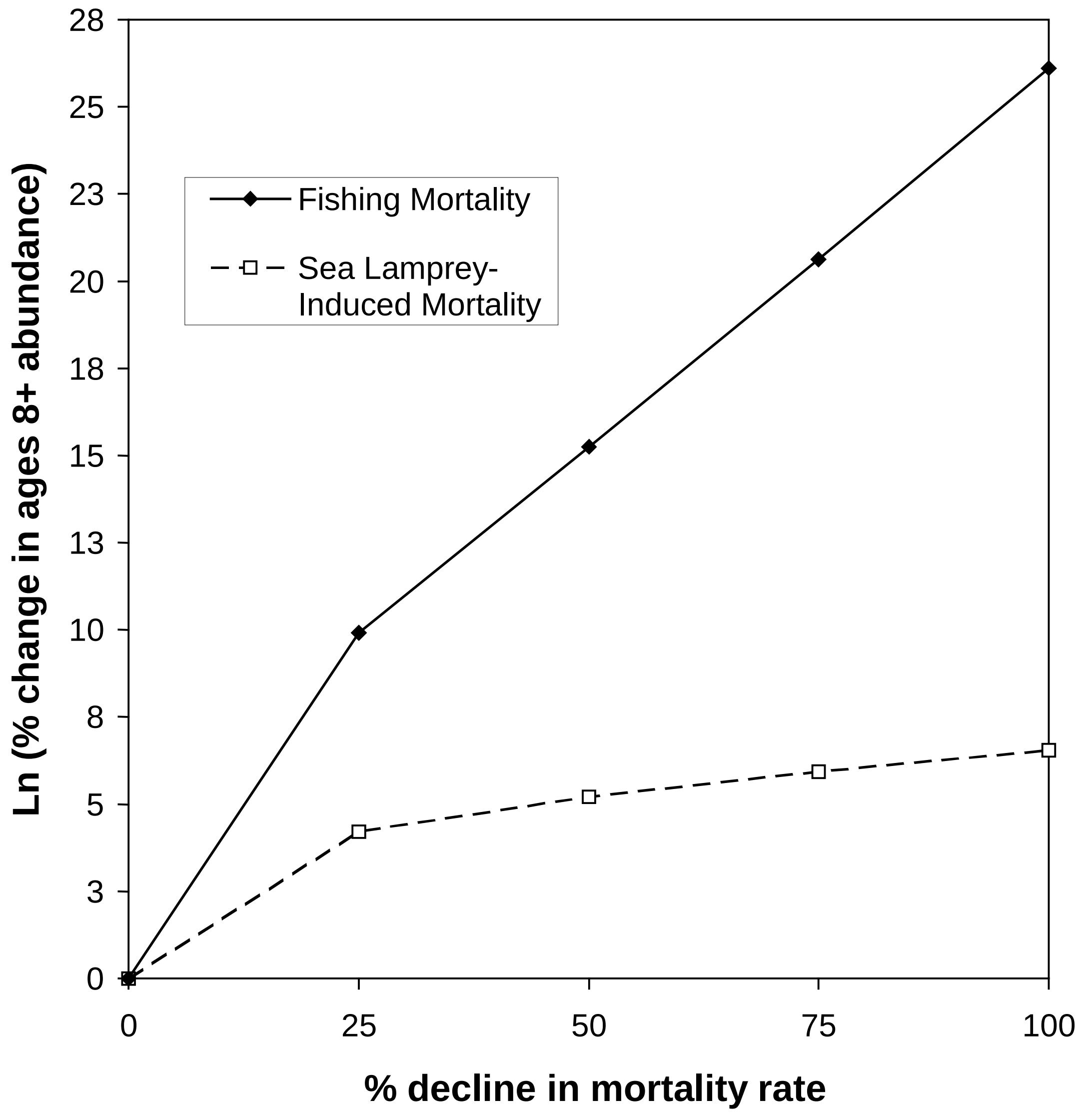

Figure 45. Change in projected abundance of ages 8+ lake trout in the year 2010 due to decreases in fishing and sea lamprey-induced mortality rates for northern Lake Huron. Fishing mortality was based on the average of 1987-1989 rates, sea lamprey-induced mortality was based on the average of 1991-1993 rates.

DISCUSSION

The primary goal of lake trout rehabilitation in Lake Huron is to re-establish self-sustaining populations that are capable of supporting harvest (DesJardine et al. 1995). In addition, the rehabilitation plan states that total annual mortality rates should not exceed 45% to facilitate the achievement of the primary goal. Although the rehabilitation efforts in Lake Huron have been ongoing since the late 1960s, progress has been limited by the fact that lake trout populations in the main basin are still totally dependent on hatchery stockings. The lack of significant natural recruitment may be due to spawning habitat deficiencies, poor spawning site homing ability, poor genetic fitness of hatchery lake trout, insufficient spawning stock biomass, or a combination of these factors. The failure of lake trout to re-establish self-sustaining populations is likely due to several of these factors, however, high mortality rates have played an important role in limiting population growth, especially for populations that were starting from near extinction levels, as in the case with lake trout in the main basin of Lake Huron. This study examined the effects of fishing and sea lamprey parasitism on lake trout abundance and showed that temporal variations and age-selectivity of these mortality sources have greatly affected population growth in Lake Huron, particularly in northern waters.

Role of sea lampreys in lake trout rehabilitation

Based on the evaluations of the patterns in sea lamprey wounding rates on lake trout, my results indicated that sea lampreys target larger lake trout in Lake Huron, and thus inflict higher mortality rates on older fish. This finding has been previously documented, but has not been reported for the main basin of Lake Huron. Although I did not detect any overall temporal trends in wounding rates from 1984-1993, there did appear to be a cyclic pattern. This cyclic phenomenon may be related to variations in sea lamprey year-class strength associated with treatment of streams and rivers with chemical toxicants by sea lamprey control programs. I also detected a geographic gradient in sea lamprey-induced mortality rates with the highest rates in northern Lake Huron. This was based on the results from ANOVA models that compared the rates between central and southern Lake Huron, and the calibration of the northern population model which estimated sea lamprey-induced mortality rates much higher than the other regions. These sea lamprey-induced mortality rates were based on the assumption that the laboratory values for the probability of survival from a sea lamprey attack reported by Swink (1990) were realistic values. An attempt was made to evaluate these probabilities using statistical catch-at-age analysis, but due to the lack of sufficient contrast in wounding rates in the time series, no conclusions could be made as to the accuracy of these values. Future research should focus on validating these survival probabilities in natural systems.

Overall, the analyses of the patterns in wounding rates showed that sea lamprey-induced mortality rates were not constant across age, time, or geographic area. The implications for lake trout rehabilitation are that lake trout population growth is highly dependent on sea lamprey dynamics. The high mortality rates caused by sea lamprey parasitism in northern Lake Huron was one of the most influential factors in inhibiting lake trout population increase.

Survival and abundance of lake trout during 1984-1993

Lake trout total mortality rates were lower in the central region of the main basin of Lake Huron than in the other regions during 1984-1993. Total instantaneous mortality in the central region was below the rehabilitation target of 0.59 $year^{-1}$ (A=0.45). In southern Lake Huron, total mortality was higher than the central region mostly due to higher fishing mortality rates. Similar to central Lake Huron, total mortality rates in the south were usually below the target maximum mortality rate during 1984-1993. In northern Lake Huron, total mortality has exceeded the target rate in every year with instantaneous rates reaching values up to 9.5 $year^{-1}$. During the late 1980s, high commercial fishing mortality, combined with high levels of sea lamprey parasitism caused the age structure of the population to be truncated with virtually no fish older than age-8 from 1988 to the present. These mortality rates do not provide promise for lake trout re-establishment, particularly for a population that is recovering from virtual extinction.

Abundance of mature lake trout, an index of potential natural recruitment, was highest in southern Lake Huron and lowest in northern Lake Huron. There was approximately a twenty-fold difference in mean abundance of ages 8+ lake trout between the two regions during 1984-1993. This was not due to differential stocking rates, but can be attributed to the lower sea lamprey-induced and fishing mortality rates in the south. The lack of commercial exploitation has contributed in allowing the high abundance of mature lake trout in southern Lake Huron. There were eight times as many mature lake trout in central Lake Huron than in the north. Even with 60% immigration from central Lake Huron, abundance of ages 8+ lake trout in the north only averaged about 3,200 fish during 1984-1993. Such low spawning stock biomass probably explains why there has been no natural recruitment in northern Lake Huron. Similarly, low spawning stock biomass in central Lake Huron, which is likely due to the high emigration (60%) to northern Lake Huron, is also precluding natural recruitment, while lack of sufficient suitable spawning substrate is also an important factor. Although there are reports of some natural recruitment in central Lake Huron in Thunder Bay (Johnson and VanAmberg 1995) and on the mid-lake Six Fathom-Yankee Reef complex (C. Bowen, II, National Biological Service, pers. comm.), these observations were localized and are probably not contributing significantly to the regional population at this time.

Despite the high numbers of mature lake trout in southern Lake Huron (annual mean of approximately 70,000 fish), lack of suitable spawning habitat has probably reduced the likelihood for natural reproduction (Hansen 1994; Eshenroder et al. 1995). Ironically, spawning habitat has been reported to be abundant in northern Lake Huron (Eshenroder et al. 1995), but the low abundance of mature fish there due to high mortality rates has diminished the potential for natural recruitment. This is despite immigration of lake trout from central Lake Huron. Unless mortality rates are reduced in northern Lake Huron, rehabilitation will not be achieved under current conditions.

Management trade-off: fishing vs. sea lamprey-induced mortality

Northern Lake Huron

Progress towards lake trout rehabilitation, as indicated by changes in spawner abundance (ages 8 and older), was evaluated through a series of trade-off analyses between the management of fishing and sea lamprey-induced mortality. In northern Lake Huron (MH-1), there has been concern about the high influx of parasitic phase sea lampreys from the St. Mary's River, and mortality caused by the tribal gill net fishery. Under 1991-1993 fishing and sea lamprey-induced mortality rates, there is the potential for increase in mature lake trout abundance. However, the amount of increase may not produce sufficient spawning stock biomass to allow natural recruitment. Currently, there is no quantitative reference to what spawning stock biomass must be for natural recruitment, which is the first step towards self-sustainability.

Commercial fishing mortality has fluctuated temporally and drastically affected the age structure of the population in concert with sea lamprey-induced mortality. For example, fishing intensities during 1987-1989, which were the highest in the time series, resulted in a highly truncated age structure with very few fish in the population older than age-8. If fishing mortality were allowed to reach those high rates again, spawning stock biomass will decrease. Under current sea lamprey-induced mortality rates, model simulations indicated that the maximum abundance of ages 8+ lake trout would be 9,500 fish under current fishing mortality rates, and 31,000 fish under a zero fishing scenario. Given the large spatial area of northern Lake Huron and the ongoing high mortality rates due to sea lampreys, these results suggest that re-establishment of self-sustaining lake trout populations is unlikely until sea lamprey abundance is reduced.

Although optimal levels of fishing and sea lamprey control depend upon economic costs of reducing mortality due to each source, the trade-off analysis suggests that a percentage drop in sea lamprey-induced mortality produces more mature lake trout than a similar decrease in fishing mortality. However, it is imperative that both sea lamprey-induced and commercial fishing mortality be managed closely so that total mortality rates do not reach the levels comparable to 1987-1989. If mortality rates are to remain high in northern Lake Huron, the only way to increase the abundance of mature lake trout would be to significantly increase hatchery stockings. This is not a wise option since it is financially costly and does not account for possible depensatory responses from sea lampreys and fishing.

Central Lake Huron

Results from trade-off analyses indicated that reductions in sea lamprey-induced mortality would produce a higher increase in mature lake trout abundance than equivalent reductions in fishing mortality. Overall, fishery exploitation has been low on this population when compared to sea lamprey-induced mortality and to the situation in northern Lake Huron. Under current conditions, there is promise for population growth in central Lake Huron. Simulation results indicated that total abundance of mature lake trout would increase 50% by the year 2010 with current fishing and sea lamprey-induced mortality rates. If fishing mortality was to be regulated, the TAC management plan with a target of A=0.45 would not be a logical choice. Under current conditions, simulations indicate that adoption of the TAC plan would result in a 15.4% decrease in ages 8+ abundance by the year 2010. No increase in ages 8+ abundance would be observed unless sea lamprey-induced mortality was reduced to 50% of current rates. The TAC management strategy does not seem appropriate for populations that are recovering from extinction levels and are not self-sustaining.

Maintaining current mortality levels in central Lake Huron will lead to an increase in abundance of mature lake trout. Higher stocking rates would accelerate this increase, however the issue of successful spawning still needs to be investigated. The ongoing research at the mid-lake Six Fathom Bank-Yankee Reef complex (C. Bowen, II, National Biological Service, pers. comm.) may provide a quantitative measure for the potential for natural recruitment in central Lake Huron. There has been low levels of natural recruitment detected on this reef complex. In addition, there are indications that mortality rates are lower in this region than in other parts of central Lake Huron and that certain genetic strains of lake trout suffer lower sea lamprey wounding rates (C. Bowen, II, National Biological Service, pers. comm.).

Southern Lake Huron

Current fishing and sea lamprey-induced mortality rates are at levels that do not allow increases in mature lake trout abundance. Under current conditions, abundance of ages 8+ lake trout are projected to decrease 29%. Sea lamprey-induced mortality accounts for most of the lake trout deaths in southern Lake Huron. Therefore, similar to central Lake Huron, adoption of a TAC management strategy would inhibit the increase in the numbers of mature lake trout in southern Lake Huron. In fact, under current sea lamprey wounding rates, the TAC plan would decrease ages 8+ abundance approximately 50% by the year 2010. Based on model simulation results, more emphasis should be placed on reducing sea lamprey-induced mortality than reducing fishing mortality. However, this assumes that recreational fishing mortality remains constant at current rates and does not take into account the relative economic costs to control each source of mortality.

Status and potentials of lake trout rehabilitation

If sufficient suitable spawning sites are available and sufficient numbers of hatchery lake trout are being stocked, significant progress towards lake trout rehabilitation can occur as exhibited by lake trout populations in Lake Superior (Hansen 1994). The results of this study partly answers why the goals of lake trout rehabilitation have not been attained in the main basin of Lake Huron. In northern Lake Huron, commercial fishing and sea lamprey-induced mortality rates were too high to allow sufficient accumulation of mature fish, despite sufficient spawning habitat. Although mortality rates were not excessive in central Lake Huron, low population size due to high emigration to the north, and moderate levels of sea lamprey parasitism, as well as lack of sufficient spawning habitat are factors that have precluded the existence of a self-sustaining population in this region. In southern Lake Huron, sea lamprey-induced mortality has reduced the rate of population growth. Although abundance of mature lake trout is highest in this region of the main basin, lack of natural recruitment is likely due to insufficient spawning habitat. However, the failure may be also be partly due to insufficient spawning stock biomass.

In order to rehabilitate lake trout in the main basin of Lake Huron, mortality rates must be effectively reduced and managed. This means that sea lamprey control must be increased and the commercial gill net fishery must be managed. Current research on the St. Mary's River, a major source of sea lampreys in the main basin, indicates that localized application of lampricides in areas where ammocoetes are highly concentrated may be highly efficacious (Lake Huron Technical Committee, Great Lakes Fishery Commission, pers. comm.). This strategy is currently being pursued by the Great Lakes Fishery Commission. Commercial fishing mortality on lake trout must be reduced for rehabilitation to proceed. The high lake trout harvest is a result of incidental harvest in the lake whitefish gill net fishery. A promising management strategy is to convert the lake whitefish fishery gear from gill nets to trap nets. In comparison to gill nets, trap nets have been reported to dramatically reduce capture and mortality of non-target species such as lake trout (Schorfhaar and Peck 1993). Further research on gear conversion from gill to trap nets should be pursued with emphasis on the social, economic, and biological impacts.

Stocking of hatchery-raised lake trout should continue as a management tool to increase population size. Stocked lake trout have contributed significantly to the successful re-establishment of populations in Lake Superior (Hansen 1994). However, this tool can only be effective if total mortality rates are reduced and effectively managed in northern Lake Huron, where there is high potential for natural recruitment. Furthermore, criteria, based on quantitative analyses, must be established as to when stocking should cease. Results from the ongoing genetic research on the differential fitness of various lake trout strains should also be applied to the stocking program.

Lake trout mortality rates in Lake Huron appear to vary over time and depend upon age. The statistical catch-at-age method used here allowed me to estimate these rates without the acceptance of unrealistic assumptions. In contrast, catch curve techniques, which have been used in the past to estimate mortality rates of lake trout, are based on the assumption of age-independent mortality rates, equal vulnerability to the sampling gear for the ages used in the analysis, and equal recruitment for all cohorts (Ricker 1975). The results of this study exemplify the utility of approaches such as statistical catch-at-age analysis in describing the dynamics of Great Lakes fish populations such as lake trout. My results showed that mortality rates were age- and year dependent, which had important implications to population growth and age structure of lake trout in the main basin of Lake Huron. However, these results also caused some difficulty in applying the 45% target rate, since in any given year, there was no single mortality rate.

A goal of this study was to gauge progress towards rehabilitation by reference to the GLFC target maximum mortality rate (A=0.45, Z=0.59 year^{-1}). The fact that mortality rates vary with lake trout age brings forward a question of interpretation: to what ages should the target of 45% annual losses apply? In the model projections, I assumed that total annual mortality should not exceed this level for lake trout ages 5 and older. However, this was in some sense an arbitrary choice, and if the age-specific patterns were different, very different dynamics could occur for populations experiencing the same peak mortality rate. This could even be the case when mortality rates had the same average over a broad range of ages. Furthermore, gauging rehabilitation progress using a target mortality rate seems more pertinent to self-sustaining populations, which is not the situation in the main basin of Lake

Huron. Since a preliminary step towards rehabilitation is the establishment of self-sustaining lake trout populations, it would be more logical to set goals in terms of spawning stock biomass produced per fish rather than a mortality rate. Moreover, as populations become self-reproducing, stock-recruitment relationships, harvest allocations, and hatchery stocking should be evaluated in terms of population stability and rehabilitation objectives and goals.

In closing, lake trout populations in the main basin of Lake Huron face a difficult path towards self-sustainability due to sea lamprey parasitism and commercial fishing. If successful rehabilitation is to be achieved, total mortality in northern Lake Huron will have to be limited through coordinated multi-agency management of fishery harvest and sea lamprey control.

APPENDIX- ADDITIONAL TABLES

Table 15. Joint age-length distribution for lake trout in northern Lake Huron (MH-1). Data from Michigan Department of Natural Resources annual spring gill net surveys from 1984-1994.

	Length Class (mm)				
Age	432-533	534-635	636-737	>737	Total
1	0	0	0	0	0
2	0	0	0	0	0
3	18	1	0	0	19
4	222	5	0	0	227
5	128	34	0	0	162
6	15	22	1	0	38
7	6	3	3	0	12
8	0	1	2	0	3
9	0	1	2	1	4
10	0	1	2	1	4
11	0	0	1	1	2
12	0	0	0	1	1
13	0	0	0	1	1
14	0	0	0	1	1
15	0	0	0	1	1
16	0	0	0	1	1
17	0	0	0	1	1
18	0	0	0	1	1
19	0	0	0	1	1
20	0	0	0	1	1
>20	0	0	0	1	1
Total	389	68	11	13	481

Table 16. Joint age-length distribution for lake trout in central Lake Huron (MH-2). Data from Michigan Department of Natural Resources annual spring gill net surveys from 1984-1994.

	Length Class (mm)				
Age	432-533	534-635	636-737	>737	Total
1	0	0	0	0	0
2	0	0	0	0	0
3	67	3	0	0	70
4	682	115	3	0	800
5	271	339	42	0	652
6	21	158	135	4	318
7	8	42	73	6	129
8	2	6	20	9	37
9	0	0	11	8	19
10	0	0	3	5	8
11	0	0	2	1	3
12	0	0	1	3	4
13	0	0	2	2	4
14	0	0	0	1	1
15	0	0	0	1	1
16	0	0	0	1	1
17	0	0	0	1	1
18	0	0	0	1	1
19	0	0	0	1	1
20	0	0	0	1	1
>20	0	0	0	1	1
Total	1,051	663	292	47	2,053

Table 17. Joint age-length distribution for lake trout in southern Lake Huron (MH-3/4/5). Data from Michigan Department of Natural Resources annual spring gill net surveys from 1984-1994.

Age	Length Class (mm)				
	432-533	534-635	636-737	>737	Total
1	0	0	0	0	0
2	0	0	0	0	0
3	89	9	0	0	98
4	808	299	8	1	1,116
5	335	1,025	292	2	1,654
6	25	454	903	18	1,400
7	9	73	614	73	769
8	1	18	362	192	573
9	1	3	135	180	319
10	1	2	68	166	237
11	0	1	18	80	99
12	0	0	6	74	80
13	0	0	4	36	40
14	0	0	6	32	38
15	0	0	1	13	14
16	0	0	1	4	5
17	0	0	0	6	6
18	0	0	0	9	9
19	0	0	0	2	2
20	0	0	0	2	2
>20	0	0	0	2	2
Total	1,269	1,884	2,418	892	6,463

Table 18. Assumed age-1 abundance (x 1000) of lake trout in the main basin of Lake Huron. Data, adjusted for migration, were based on number of yearlings and fall fingerlings (age-0) stocked. Fall fingerlings were converted to yearling-equivalents based on the assumption that 40% of fingerlings survived to the yearling stage. Sixty percent of lake trout stocked in MH-2 were assumed to migrate to MH-1 (J. Johnson, Alpena Fisheries Research Station, Michigan Department of Natural Resources, pers. comm.).

	Region			
Year	North (MH-1)	Central (MH-2)	South (MH-3/4/5)	Basin total
1972	0	0	0	0
1973	384.6	0	100.0	484.6
1974	850.9	71.6	187.0	1,109.5
1975	707.4	72.8	331.0	1,111.2
1976	659.5	82.8	395.5	1,137.8
1977	713.0	81.2	361.0	1,155.2
1978	654.4	88.0	550.0	1,292.4
1979	555.0	75.2	777.8	1,408.0
1980	751.8	95.2	605.0	1,452.0
1981	245.3	15.2	555.0	815.5
1982	634.3	115.4	612.8	1,362.5
1983	529.1	84.0	650.4	1,263.5
1984	136.8	45.2	360.0	542.0
1985	489.8	87.6	482.1	1,059.5
1986	943.2	205.5	638.9	1,787.5
1987	480.1	105.2	169.6	754.9
1988	645.7	114.8	157.0	917.5
1989	658.6	120.4	390.8	1,169.8
1990	565.6	110.8	240.0	916.4
1991	967.1	185.9	339.0	1,492.0
1992	859.7	362.7	416.8	1,639.2
1993	657.3	293.0	389.5	1,339.8

Table 19. Sport harvest and effort of lake trout in Michigan waters of Lake Huron. Harvest reported in numbers of fish and effort expressed as angler hours. Data from Michigan Department of Natural Resources.

	Region					
	North (MH-1)		Central (MH-2)		South (MH-3/4/5)	
Year	Harvest	Effort	Harvest	Effort	Harvest	Effort†
1984	1,861*	99,413*	381**	86,337**	27,827*	723,572.7*
1985	1,861	99,413	454	102,860	27,827***	723,572.7***
1986	3,410	160,634	283	55,590	50,993	1,169,127
1987	974	82,698	380	72,306	40,255	1,059,693
1988	1,631	153,954	1,188	143,814	34,162	1,248,123
1989	869	130,019	67	4,627	38,615	685,205
1990	444	119,390	167	6,467	30,698	1,176,035
1991	1,968	108,959	1,689	129,022	14,351	581,542.5
1992	1,216	70,318	1,443	153,210	10,581	535,071
1993	264	69,408	424	142,517	5,450	410,962.5

† = Does not include data from Harbor Beach, MI.

* No data available, assumed to equal 1985 values.

** Estimated value based on ratio of 1984 to 1985 Canadian harvest in MH-2, 1984 sport harvest and effort = 0.8394 of 1985 harvest and effort.

*** Estimated value based on ratio of 1985 to 1986 in MH-1, 1985 harvest = 0.5457 of 1986 harvest, 1985 effort = 0.6189 of 1986 effort.

Table 20. Age composition of sport fishery harvest of lake trout in Michigan waters of Lake Huron. Data, expressed as proportions at age, were from Michigan Department of Natural Resources sport harvest monitoring program. n= sample size.

		Year					
Region	Age	1985	1986	1987	1988	1991	1992
North (MH-1)	2	0.09412	0	0.02344	0	0.04545	0
	3	0.24706	0.04310	0.34375	0.29710	0.13636	0.10989
	4	0.35294	0.64655	0.25781	0.52899	0.31818	0.53846
	5	0.15294	0.25862	0.28125	0.06522	0.22727	0.30769
	6	0.11765	0.03448	0.08594	0.07246	0.18182	0.03297
	7	0.02353	0.00862	0.00781	0.02899	0.09091	0.01099
	8	0	0	0	0.00725	0	0
	9+	0.01176	0.00862	0	0	0	0
	n	85	116	128	138	22	91
Central (MH-2)	3	0.13699	0.03004	0.02362	0.05000	0	0
	4	0.30822	0.40343	0.12598	0.65000	0.13514	0.44318
	5	0.23288	0.32618	0.29921	0.10000	0.37838	0.15909
	6	0.19178	0.12446	0.22047	0.15000	0.43243	0.19318
	7	0.06849	0.03433	0.24409	0.05000	0.05405	0.20455
	8	0.02055	0.05150	0.03150	0	0	0
	9+	0.04110	0.03004	0.05512	0	0	0
	n	146	233	127	20	37	88
South (MH-3/4/5)	3	0.02443	0.01081	0.02779	0.00946	0.03483	0.01233
	4	0.10860	0.21364	0.09458	0.13061	0.11946	0.20834
	5	0.26489	0.16902	0.40052	0.21991	0.23611	0.17703
	6	0.25795	0.20798	0.16079	0.33218	0.30978	0.12040
	7	0.17480	0.15676	0.10236	0.11108	0.14613	0.19017
	8	0.05737	0.14963	0.10381	0.08627	0.03142	0.06506
	9+	0.11196	0.09216	0.11015	0.11050	0.12227	0.22667
	n	375	458	323	220	189	202

Table 21. Canadian harvest of lake trout in southern Lake Huron (OH-3, OH-4 and OH-5). Annual yield data from Ontario Ministry of Natural Resources. Harvest in numbers estimated by dividing yield by average mass per fish of Michigan sport harvest for each year.

	OH-3		OH-4/5		OH-3 + OH-4/5	
Year	Yield (kg)	Numbers	Yield (kg)	Numbers	Yield (kg)	Numbers
1984	1,309	445	27,117	9,226	28,426	9,672
1985	368	125	20,235	6,885	20,603	7,010
1986	109	36	29,724	9,768	29,833	9,804
1987	107	36	29,829	10,154	29,936	10,191
1988	191	61	17,956	5741	18,147	5,802
1989	901	346	15,134	5,820	16,035	6,166
1990	1,625	572	11,985	4,221	13,610	4,793
1991	2,006	748	14,736	5,495	16,742	6,244
1992	1,564	510	21,355	6,959	22,919	7,469
1993	3,980	1,370	10,354	3,565	14,334	4,935
1994	7,769	2,675	10,393	3,578	18,162	6,253

Table 22. Catch and effort of lake trout from Michigan Department of Natural Resources annual spring gill net surveys in northern Lake Huron (MH-1). Effort expressed as meters of gill net per day. No data available for 1990.

	Year									
Age	1984	1985	1986	1987	1988	1989	1991	1992	1993	1994
1	0	0	0	0	2	0	0	0	0	0
2	12	4	22	5	1	31	2	6	5	1
3	124	82	17	40	81	28	33	42	68	73
4	187	76	91	8	29	34	17	65	34	33
5	87	21	24	11	2	5	3	5	8	22
6	16	3	10	5	1	2	1	0	2	0
7	9	1	1	1	0	0	0	0	0	0
8	3	0	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0	0	0
10	0	0	0	0	0	0	0	0	0	0
11	1	1	0	0	0	0	0	0	0	0
12	0	0	0	0	0	0	0	0	0	0
13	0	0	0	0	0	0	0	0	0	0
14	0	0	0	0	0	0	0	0	0	0
15	0	0	0	0	0	0	0	0	0	0
16	0	0	0	0	0	0	0	0	0	0
17	0	0	0	0	0	0	0	0	0	0
18	0	0	0	0	0	0	0	0	0	0
19	0	0	0	0	0	0	0	0	0	0
20	0	0	0	0	0	0	0	0	0	0
>20	0	0	0	0	0	0	0	0	0	0
Total	439	188	165	70	116	100	56	118	117	129
Effort	3,018	3,018	3,018	3,018	3,018	3,018	3,018	3,018	3,018	3,018

Table 23. Catch and effort of lake trout from Michigan Department of Natural Resources annual spring gill net surveys in central Lake Huron (MH-2). Effort expressed as meters of gill net per day.

	Year										
Age	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994
1	0	0	0	0	0	0	0	0	0	0	0
2	35	12	76	23	15	24	68	0	0	2	4
3	150	157	57	173	187	119	98	11	3	9	33
4	156	195	185	56	65	203	53	25	91	22	51
5	90	51	84	99	11	71	33	33	59	91	45
6	29	37	5	47	7	11	5	89	29	9	50
7	21	17	12	4	4	12	2	4	43	5	5
8	3	7	7	1	0	4	2	7	0	5	1
9	3	0	2	2	1	0	1	6	2	0	2
10	2	2	1	0	1	0	0	0	2	0	0
11	0	0	0	0	0	1	0	1	1	0	0
12	1	2	0	0	0	0	0	0	1	0	0
13	0	1	2	0	0	0	0	0	0	1	0
14	0	0	0	0	0	0	0	0	0	0	0
15	0	0	0	0	0	0	0	0	0	0	0
16	0	0	0	0	0	0	0	0	0	0	0
17	0	0	0	0	0	0	0	0	1	0	0
18	0	0	0	0	0	0	0	0	1	0	0
19	0	0	0	0	0	0	0	0	0	0	0
20	0	0	0	0	0	0	0	0	0	0	0
>20	0	0	0	0	0	0	0	0	0	0	0
Total	490	481	431	405	291	445	262	176	233	144	191
Effort	3,018	3,018	3,018	3,018	3,018	2,012	3,018	1,372	1,372	1,554	1,852

Table 24. Catch and effort of lake trout from Michigan Department of Natural Resources annual spring gill net surveys in southern Lake Huron (MH-3/4/5). Effort expressed as meters of gill net per day.

	Year										
Age	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994
1	0	0	0	0	13	11	18	0	0	0	1
2	22	10	35	20	6	14	2	0	0	3	6
3	93	113	81	58	146	39	15	15	1	30	35
4	198	146	318	90	139	152	18	21	57	29	96
5	229	270	145	267	146	143	168	13	57	185	39
6	224	243	163	79	227	76	101	58	34	30	166
7	105	165	78	71	42	115	60	37	61	14	21
8	68	110	66	38	39	16	143	24	41	22	6
9	51	54	18	37	27	12	13	44	32	18	10
10	26	31	10	29	24	8	23	6	55	14	9
11	0	16	5	8	9	14	4	4	10	24	5
12	0	16	6	8	3	8	7	7	16	5	4
13	0	0	8	1	4	4	1	12	3	7	0
14	0	0	1	4	7	2	2	0	12	6	4
15	0	0	0	0	2	1	0	1	6	3	1
16	0	0	0	0	0	0	0	0	0	4	1
17	0	0	0	0	0	0	0	0	4	1	1
18	0	0	0	0	0	0	0	0	8	0	1
19	0	0	0	0	0	0	0	0	1	0	0
20	0	0	0	0	0	0	0	0	3	0	0
>20	0	0	0	0	0	0	0	0	0	0	0
Total	1,016	1,174	934	710	834	615	575	242	401	395	406
Effort	3,018	3,018	2,012	1,555	1,303	1,303	1,463	1,143	1,097	1,573	1,481

Table 25. Canadian harvest of lake trout in OH-1 and OH-2 in northern and central Lake Huron. Forty percent of the harvest from zone 4-1 in district OH-1 were assumed to be from the northern area. Sixty percent of lake trout harvested in zone 4-1 of OH-1, and all harvest in OH-2 were assumed to be from the central area. Annual yield data from Ontario Ministry of Natural Resources. Harvest in numbers for Canadian removals from the MH-1 stock estimated by dividing reported yield by average mass per fish of tribal gill net harvest in MH-1 for each year. Harvest in numbers for Canadian removals from the MH-2 stock estimated by dividing reported yield by average mass per fish of Michigan sport harvest for each year.

	Northern OH-1 (MH-1)		Central OH-1 + OH-2 (MH-2)	
Year	Yield (kg)	Numbers	Yield (kg)	Numbers
1984	249.2	207	737.8	381
1985	116.0	93	879.0	453
1986	112.8	115	2,484.2	1,361
1987	435.6	376	1,903.4	810
1988	506.0	771	2,104.0	1,222
1989	588.8	1,039	3,884.2	2,160
1990	613.6	697	5,409.4	3,008
1991	886.8	831	5,633.2	3,004
1992	1,386.8	1,211	7,041.2	4,029
1993	2,150.4	5,532	14,817.6	7,710

Table 26. Reported tribal commercial harvest and effort of lake trout in northern Lake Huron (MH-1). Data provided by Chippewa-Ottawa Treaty Fishery Management Authority. Effort expressed as meters of large-mesh gill net targeted at lake whitefish and lake trout.

Year	Yield (kg)	Effort (m)
1984	89,151.45	2,239,579
1985	102,468.24	2,782,824
1986	105,370.37	3,822,680
1987	78,583.02	3,310,555
1988	75,575.20	3,702,863
1989	76,512.34	4,122,511
1990	35,945.53	3,296,442
1991	35,557.25	3,386,999
1992	43,579.62	2,334,097
1993	56,659.63	2,362,779

Table 27. Parameters estimated to calibrate the northern and central lake trout population models. $f_{C,\,y}$ =commercial fishing intensity (year^{-1}) in year *y*, μ' = proportionality coefficient for sea lamprey-induced mortality, and q_R= catchability coefficient for the recreational fishery (angler hours^{-1}) , ρ_a = survival proportion for age *a* for cohorts before 1984 to estimate abundance in 1984 for ages>1.

	Modeled Region	
Parameter	MH-1	MH-2
$f_{C,\,1984}$	0.485177	0.007804
$f_{C,\,1985}$	0.897677	0.010657
$f_{C,\,1986}$	1.760810	0.032434
$f_{C,\,1987}$	9.148661	0.019773
$f_{C,\,1988}$	6.931023	0.026980
$f_{C,\,1989}$	3.344381	0.034468
$f_{C,\,1990}$	0.953025	0.042784
$f_{C,\,1991}$	0.398272	0.043089
$f_{C,\,1992}$	0.331953	0.062046
$f_{C,\,1993}$	0.392221	0.130979
q_R	4.29318 x10^{-08}	1.05413 x10^{-07}
μ'	4.059982	not estimated
ρ_1	0.513611	0.513611
ρ_2	0.725195	0.727298
ρ_3	0.781318	0.841338
ρ_4	0.683716	0.878265
ρ_5	0.614042	0.874634
ρ_6	0.575742	0.840974
ρ_7	0.125603	0.827164
ρ_8	0.099222	0.807527
ρ_9	0.096822	0.784633
ρ_{10}	0.102303	0.778539
ρ_{11}	0.092245	0.787351
ρ_{12}	0.087107	0.774820
ρ_{13}	0.087107	0.782319
ρ_{14+}	0.087107	0.767396

Table 28. Model estimates of lake trout abundance in southern main basin of Lake Huron (MH-3/4/5).

	Year									
Age	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993
1	360,000	482,100	638,900	169,600	157,000	390,800	240,000	339,000	416,800	389,500
2	434,858	184,900	247,612	328,146	87,108	80,637	200,719	123,267	174,114	214,073
3	127,660	316,270	134,477	180,086	238,658	63,353	58,647	145,981	89,651	126,632
4	134,857	96,427	252,322	107,631	146,469	190,872	47,465	43,794	114,019	59,010
5	117,584	99,824	77,165	195,076	86,604	113,639	140,783	34,193	33,817	76,955
6	98,613	74,625	72,609	49,641	138,358	57,260	72,435	86,672	23,136	22,006
7	40,918	59,169	50,874	42,874	32,831	89,836	34,204	44,227	55,905	14,507
8	26,166	24,389	39,478	28,995	27,657	21,522	52,961	20,978	28,560	34,077
9	18,064	15,462	16,131	21,176	18,238	17,821	12,542	31,219	13,725	16,636
10	985	10,646	10,223	8,245	13,112	11,585	10,340	7,135	20,785	7,695
11	2,758	580	7,048	5,085	5,065	8,255	6,710	5,757	4,803	11,402
12	912	1,620	384	3,427	3,102	3,164	4,770	3,671	3,905	2,590
13	0	535	1,073	182	2,074	1,923	1,824	2,563	2,512	2,065
14	0	0	354	512	110	1,288	1,109	984	1,750	1,334
15	0	0	0	171	311	69	743	604	669	938
16	0	0	0	0	103	193	40	399	413	353
17	0	0	0	0	0	65	111	22	271	223
18	0	0	0	0	0	0	37	59	15	141
19	0	0	0	0	0	0	0	20	41	8
20	0	0	0	0	0	0	0	0	14	21
>20	0	0	0	0	0	0	0	0	0	7
Total	1,363,377	1,366,547	1,548,648	1,140,848	956,802	1,052,283	885,440	890,545	984,904	980,174

Table 29. Estimates of instantaneous rates of natural mortality (M) for lake trout in main basin of Lake Huron based on statistical catch-at-age analysis of the southern Lake Huron population model. Rates were assumed constant from 1984-1993.

Age	M ($year^{-1}$)
1	0.666
2	0.318
3	0.172
4	0.123
5	0.108
6	0.103
7	0.101
8	0.100
9	0.100
10	0.100
11	0.100
12	0.100
13	0.100
14	0.100
15	0.100
16	0.100
17	0.100
18	0.100
19	0.100
20	0.100
>20	0.100

Table 30. Model estimates of instantaneous rates of recreational fishing mortality (year^{-1}) for lake trout in southern Lake Huron (MH-3/4/5).

	Year									
Age	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993
1	0	0	0	0	0	0	0	0	0	0
2	4.77×10^{-6}	5.33×10^{-6}	7.96×10^{-6}	6.48×10^{-6}	6.37×10^{-6}	4.57×10^{-6}	9.33×10^{-6}	4.21×10^{-6}	3.99×10^{-6}	2.64×10^{-6}
3	0.004	0.004	0.006	0.005	0.005	0.003	0.007	0.003	0.003	0.002
4	0.036	0.041	0.061	0.050	0.049	0.035	0.071	0.032	0.030	0.020
5	0.100	0.112	0.167	0.136	0.134	0.096	0.196	0.089	0.084	0.056
6	0.109	0.122	0.182	0.148	0.146	0.105	0.213	0.096	0.091	0.060
7	0.107	0.120	0.179	0.146	0.143	0.103	0.210	0.095	0.090	0.059
8	0.110	0.123	0.183	0.149	0.147	0.105	0.215	0.097	0.092	0.061
9	0.110	0.123	0.183	0.149	0.147	0.105	0.215	0.097	0.092	0.061
10	0.110	0.123	0.183	0.149	0.147	0.105	0.215	0.097	0.092	0.061
11	0.110	0.123	0.183	0.149	0.147	0.105	0.215	0.097	0.092	0.061
12	0.110	0.123	0.183	0.149	0.147	0.105	0.215	0.097	0.092	0.061
13	0.110	0.123	0.183	0.149	0.147	0.105	0.215	0.097	0.092	0.061
14	0.110	0.123	0.183	0.149	0.147	0.105	0.215	0.097	0.092	0.061
15	0.110	0.123	0.183	0.149	0.147	0.105	0.215	0.097	0.092	0.061
16	0.110	0.123	0.183	0.149	0.147	0.105	0.215	0.097	0.092	0.061
17	0.110	0.123	0.183	0.149	0.147	0.105	0.215	0.097	0.092	0.061
18	0.110	0.123	0.183	0.149	0.147	0.105	0.215	0.097	0.092	0.061
19	0.110	0.123	0.183	0.149	0.147	0.105	0.215	0.097	0.092	0.061
20	0.110	0.123	0.183	0.149	0.147	0.105	0.215	0.097	0.092	0.061
>20	0.110	0.123	0.183	0.149	0.147	0.105	0.215	0.097	0.092	0.061

Table 31. Model estimates of number of lake trout deaths (x1000) due to natural mortality in region southern Lake Huron (MH-3/4/5).

	Year									
Age	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993
1	175.100	234.488	310.754	82.492	76.363	190.081	116.733	164.886	202.727	189.449
2	118.586	50.422	67.524	89.486	23.755	21.990	54.736	33.615	47.481	58.378
3	19.102	48.579	20.688	27.919	36.701	9.443	8.728	22.195	12.572	19.443
4	14.380	10.673	27.469	11.944	15.972	20.318	4.997	4.765	11.640	6.510
5	10.175	9.207	6.720	17.780	7.638	9.854	12.013	3.048	2.961	6.968
6	7.917	6.356	5.787	4.168	11.519	4.588	5.862	7.194	1.895	1.825
7	3.221	4.906	3.924	3.500	2.700	7.036	2.728	3.612	4.446	1.169
8	2.040	2.003	2.946	2.327	2.244	1.667	4.125	1.714	2.212	2.712
9	1.404	1.267	1.176	1.684	1.467	1.376	0.959	2.567	1.043	1.317
10	0.077	0.873	0.736	0.653	1.050	0.893	0.783	0.589	1.563	0.608
11	0.214	0.048	0.502	0.401	0.404	0.635	0.504	0.477	0.358	0.899
12	0.071	0.133	0.027	0.269	0.247	0.243	0.355	0.306	0.289	0.204
13	0	0.044	0.076	0.014	0.165	0.148	0.136	0.213	0.186	0.163
14	0	0	0.025	0.040	0.009	0.099	0.083	0.082	0.130	0.105
15	0	0	0	0.013	0.025	0.005	0.055	0.050	0.049	0.074
16	0	0	0	0	0.008	0.015	0.003	0.033	0.031	0.028
17	0	0	0	0	0	0.005	0.008	0.002	0.020	0.018
18	0	0	0	0	0	0	0.003	0.005	0.001	0.011
19	0	0	0	0	0	0	0	0.002	0.003	0.001
20	0	0	0	0	0	0	0	0	0.001	0.002
>20	0	0	0	0	0	0	0	0	0	0.001
Total	352.287	368.999	448.353	242.691	180.268	268.396	212.811	245.355	289.610	289.883

Table 32. Model estimates of number of lake trout deaths (x1000) due to recreational fishing mortality in southern Lake Huron (MH-3/4/5).

	Year									
Age	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993
1	0	0	0	0	0	0	0	0	0	0
2	0.002	0.001	0.002	0.002	0	0	0.002	0	0.001	0
3	0.406	1.154	0.734	0.807	1.042	0.193	0.363	0.417	0.223	0.229
4	4.239	3.518	13.527	4.790	6.294	5.749	2.882	1.242	2.871	1.064
5	9.458	9.570	10.434	22.483	9.490	8.791	21.852	2.505	2.302	3.592
6	8.421	7.559	10.282	6.032	16.378	4.683	12.201	6.766	1.687	1.077
7	3.423	5.831	6.967	5.061	3.836	7.177	5.674	3.395	3.954	0.689
8	2.231	2.449	5.381	3.461	3.280	1.750	8.826	1.657	2.024	1.645
9	1.541	1.555	2.156	2.514	2.152	1.449	2.060	2.491	0.958	0.802
10	0.084	1.071	1.350	0.975	1.541	0.941	1.682	0.572	1.436	0.370
11	0.235	0.058	0.921	0.599	0.593	0.670	1.083	0.463	0.329	0.548
12	0.078	0.163	0.050	0.403	0.362	0.256	0.764	0.297	0.265	0.124
13	0	0.054	0.139	0.021	0.242	0.156	0.292	0.207	0.171	0.099
14	0	0	0.046	0.060	0.013	0.104	0.179	0.079	0.120	0.064
15	0	0	0	0.020	0.036	0.006	0.119	0.049	0.045	0.045
16	0	0	0	0	0.012	0.016	0.006	0.032	0.028	0.017
17	0	0	0	0	0	0.005	0.018	0.002	0.018	0.011
18	0	0	0	0	0	0	0.006	0.005	0.001	0.007
19	0	0	0	0	0	0	0	0.002	0.003	0
20	0	0	0	0	0	0	0	0	0.001	0.001
>20	0	0	0	0	0	0	0	0	0	0
Total	30.117	32.983	51.989	47.227	45.272	31.945	58.008	20.180	16.438	10.385

Table 33. Model estimates of number of lake trout deaths (x1000) due to sea lamprey-induced mortality in southern Lake Huron (MH-3/4/5).

	Year									
Age	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993
1	0	0	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0	0	0
3	11.726	14.215	5.424	4.891	10.042	6.253	5.762	9.350	17.845	6.015
4	16.414	5.072	16.249	4.293	10.563	24.023	5.394	3.970	22.552	4.530
5	23.325	8.438	10.371	16.455	12.216	22.560	20.246	5.504	6.548	12.577
6	23.107	9.837	13.666	6.610	20.625	13.785	10.145	16.808	5.046	4.940
7	9.885	8.954	10.988	6.657	4.773	22.662	4.824	8.661	13.429	3.542
8	6.434	3.805	9.974	4.970	4.311	5.562	8.791	3.881	7.688	8.668
9	4.473	2.416	4.554	3.866	3.033	4.657	2.387	5.375	4.030	4.314
10	0.245	1.655	3.052	1.552	2.266	3.041	2.118	1.171	6.384	2.011
11	0.688	0.090	2.197	0.982	0.904	2.180	1.452	0.912	1.525	3.006
12	0.229	0.252	0.125	0.681	0.570	0.840	1.088	0.557	1.286	0.689
13	0	0.083	0.346	0.036	0.379	0.510	0.411	0.393	0.821	0.549
14	0	0	0.112	0.100	0.020	0.341	0.243	0.154	0.563	0.353
15	0	0	0	0.034	0.057	0.018	0.170	0.091	0.220	0.250
16	0	0	0	0	0.018	0.051	0.009	0.064	0.131	0.093
17	0	0	0	0	0	0.017	0.026	0.003	0.091	0.060
18	0	0	0	0	0	0	0.009	0.009	0.005	0.038
19	0	0	0	0	0	0	0	0.003	0.014	0.002
20	0	0	0	0	0	0	0	0	0.005	0.006
>20	0	0	0	0	0	0	0	0	0	0.002
Total	96.526	54.817	77.059	51.127	69.779	106.502	63.075	56.905	88.183	51.645

Table 34. Model estimates of lake trout abundance in central main basin of Lake Huron (MH-2).

	Year									
Age	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993
1	45,200	87,600	205,472	105,200	114,800	120,400	110,800	185,920	362,720	293,040
2	43,143	23,215	44,992	105,533	54,032	58,962	61,839	56,908	95,490	186,297
3	43,122	31,376	16,883	32,712	76,738	39,287	42,868	44,956	41,371	69,407
4	4,777	29,613	21,684	13,259	27,319	57,466	31,934	35,540	35,806	29,600
5	26,277	3,304	21,183	17,262	11,249	20,561	46,251	26,190	28,167	25,279
6	18,155	16,084	2,346	16,118	13,730	7,778	14,483	33,973	18,913	18,398
7	17,866	10,621	11,384	1,670	11,917	9,116	4,920	10,191	22,665	11,799
8	13,636	10,788	7,563	8,028	1,226	8,058	5,797	3,557	6,841	14,397
9	11,229	8,425	7,671	5,221	5,796	827	5,089	4,136	2,386	4,330
10	7,746	7,051	5,980	5,143	3,674	3,886	512	3,573	2,743	1,498
11	5,931	4,852	4,996	4,024	3,621	2,442	2,415	350	2,407	1,734
12	0	3,737	3,456	3,374	2,846	2,455	1,521	1,735	233	1,532
13	0	0	2,642	2,322	2,371	1,876	1,524	1,020	1,174	147
14	0	0	0	1,780	1,639	1,589	1,167	1,065	684	745
15	0	0	0	0	1,246	1,062	985	751	728	429
16	0	0	0	0	0	807	658	634	513	456
17	0	0	0	0	0	0	501	423	433	322
18	0	0	0	0	0	0	0	322	289	271
19	0	0	0	0	0	0	0	0	220	181
20	0	0	0	0	0	0	0	0	0	138
>20	0	0	0	0	0	0	0	0	0	0
Total	237,084	236,664	356,251	321,646	332,205	336,571	333,264	411,243	623,784	659,999

Table 35. Model estimates of instantaneous rates of recreational fishing mortality (year^{-1}) for lake trout in central Lake Huron (MH-2).

	Year									
Age	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993
1	0	0	0	0	0	0	0	0	0	0
2	3.95×10^{-7}	4.71×10^{-7}	5.85×10^{-7}	6.28×10^{-7}	6.58×10^{-7}	6.31×10^{-7}	6.39×10^{-7}	5.90×10^{-7}	7.01×10^{-7}	1.03×10^{-6}
3	3.02×10^{-4}	3.60×10^{-4}	4.47×10^{-4}	4.80×10^{-4}	5.03×10^{-4}	4.82×10^{-4}	4.89×10^{-4}	4.51×10^{-4}	5.36×10^{-4}	7.91×10^{-4}
4	0.003	0.004	0.004	0.005	0.005	0.005	0.005	0.005	0.005	0.008
5	0.008	0.010	0.012	0.013	0.014	0.013	0.013	0.012	0.015	0.022
6	0.009	0.011	0.013	0.014	0.015	0.014	0.015	0.014	0.016	0.024
7	0.009	0.011	0.013	0.014	0.015	0.014	0.014	0.013	0.016	0.023
8	0.009	0.011	0.013	0.014	0.015	0.015	0.015	0.014	0.016	0.024
9	0.009	0.011	0.013	0.014	0.015	0.015	0.015	0.014	0.016	0.024
10	0.009	0.011	0.013	0.014	0.015	0.015	0.015	0.014	0.016	0.024
11	0.009	0.011	0.013	0.014	0.015	0.015	0.015	0.014	0.016	0.024
12	0.009	0.011	0.013	0.014	0.015	0.015	0.015	0.014	0.016	0.024
13	0.009	0.011	0.013	0.014	0.015	0.015	0.015	0.014	0.016	0.024
14	0.009	0.011	0.013	0.014	0.015	0.015	0.015	0.014	0.016	0.024
15	0.009	0.011	0.013	0.014	0.015	0.015	0.015	0.014	0.016	0.024
16	0.009	0.011	0.013	0.014	0.015	0.015	0.015	0.014	0.016	0.024
17	0.009	0.011	0.013	0.014	0.015	0.015	0.015	0.014	0.016	0.024
18	0.009	0.011	0.013	0.014	0.015	0.015	0.015	0.014	0.016	0.024
19	0.009	0.011	0.013	0.014	0.015	0.015	0.015	0.014	0.016	0.024
20	0.009	0.011	0.013	0.014	0.015	0.015	0.015	0.014	0.016	0.024
>20	0.009	0.011	0.013	0.014	0.015	0.015	0.015	0.014	0.016	0.024

Table 36. Model estimates of instantaneous rates of commercial fishing mortality (year^{-1}) for lake trout in central Lake Huron (MH-2).

	Year									
Age	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993
1	0	0	0	0	0	0	0	0	0	0
2	7.80×10^{-5}	1.07×10^{-4}	3.24×10^{-4}	1.98×10^{-4}	2.70×10^{-4}	3.45×10^{-4}	4.28×10^{-4}	4.31×10^{-4}	0.001	0.001
3	7.80×10^{-4}	1.07×10^{-3}	3.24×10^{-3}	1.98×10^{-3}	2.70×10^{-3}	3.45×10^{-3}	4.28×10^{-3}	4.31×10^{-3}	6.20×10^{-3}	0.010
4	0.006	0.008	0.024	0.015	0.020	0.026	0.032	0.032	0.047	0.098
5	0.008	0.011	0.032	0.020	0.027	0.034	0.043	0.043	0.062	0.131
6	0.007	0.009	0.028	0.017	0.023	0.030	0.037	0.037	0.053	0.113
7	0.004	0.006	0.018	0.011	0.015	0.019	0.024	0.024	0.034	0.072
8	0.004	0.005	0.016	0.010	0.013	0.017	0.021	0.021	0.030	0.064
9	0.003	0.004	0.013	0.008	0.011	0.013	0.017	0.017	0.024	0.051
10	0.002	0.002	0.006	0.004	0.005	0.007	0.009	0.009	0.012	0.026
11	0.002	0.002	0.006	0.004	0.005	0.007	0.009	0.009	0.012	0.026
12	0.002	0.002	0.006	0.004	0.005	0.007	0.009	0.009	0.012	0.026
13	0.002	0.002	0.006	0.004	0.005	0.007	0.009	0.009	0.012	0.026
14	0.002	0.002	0.006	0.004	0.005	0.007	0.009	0.009	0.012	0.026
15	0.002	0.002	0.006	0.004	0.005	0.007	0.009	0.009	0.012	0.026
16	0.002	0.002	0.006	0.004	0.005	0.007	0.009	0.009	0.012	0.026
17	0.002	0.002	0.006	0.004	0.005	0.007	0.009	0.009	0.012	0.026
18	0.002	0.002	0.006	0.004	0.005	0.007	0.009	0.009	0.012	0.026
19	0.002	0.002	0.006	0.004	0.005	0.007	0.009	0.009	0.012	0.026
20	0.002	0.002	0.006	0.004	0.005	0.007	0.009	0.009	0.012	0.026
>20	0.002	0.002	0.006	0.004	0.005	0.007	0.009	0.009	0.012	0.026

Table 37. Model estimates of number of lake trout deaths (x1000) due to natural mortality in central Lake Huron (MH-2).

	Year									
Age	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993
1	21.985	42.608	99.939	51.168	55.838	58.561	53.892	90.430	176.423	142.532
2	11.765	6.331	12.268	28.776	14.733	16.077	16.860	15.516	26.033	50.772
3	6.168	4.501	2.574	5.137	11.435	6.089	6.708	6.900	6.033	9.941
4	0.493	3.107	2.394	1.510	2.936	6.378	3.577	3.915	3.733	2.971
5	2.236	0.301	1.996	1.662	1.013	1.868	4.286	2.407	2.470	2.130
6	1.441	1.394	0.204	1.426	1.155	0.640	1.252	2.864	1.546	1.457
7	1.415	0.908	0.969	0.145	0.994	0.739	0.424	0.847	1.837	0.935
8	1.085	0.917	0.634	0.687	0.102	0.648	0.493	0.294	0.550	1.136
9	0.899	0.714	0.633	0.441	0.478	0.066	0.429	0.339	0.191	0.342
10	0.619	0.597	0.494	0.434	0.302	0.309	0.043	0.295	0.220	0.119
11	0.475	0.412	0.413	0.340	0.300	0.195	0.206	0.029	0.194	0.138
12	0	0.316	0.285	0.284	0.233	0.195	0.125	0.144	0.019	0.122
13	0	0.000	0.218	0.196	0.195	0.149	0.128	0.084	0.094	0.012
14	0	0.000	0.000	0.150	0.133	0.126	0.094	0.089	0.055	0.059
15	0	0	0	0	0.101	0.084	0.080	0.062	0.058	0.034
16	0	0	0	0	0	0.064	0.053	0.053	0.041	0.036
17	0	0	0	0	0	0	0.040	0.035	0.035	0.026
18	0	0	0	0	0	0	0	0.027	0.023	0.022
19	0	0	0	0	0	0	0	0	0.018	0.014
20	0	0	0	0	0	0	0	0	0	0.011
>20	0	0	0	0	0	0	0	0	0	0
Total	48.581	62.104	123.021	92.355	89.948	92.189	88.690	124.331	219.573	212.811

Table 38. Model estimates of number of lake trout deaths (x1000) due to recreational fishing mortality in central Lake Huron (MH-2).

	Year									
Age	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993
1	0	0	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0	0	0
3	0.011	0.009	0.007	0.014	0.034	0.017	0.019	0.018	0.019	0.046
4	0.012	0.090	0.087	0.059	0.119	0.249	0.141	0.143	0.162	0.190
5	0.172	0.028	0.228	0.203	0.130	0.230	0.534	0.277	0.338	0.430
6	0.127	0.146	0.027	0.200	0.170	0.090	0.179	0.377	0.242	0.336
7	0.125	0.095	0.126	0.020	0.146	0.104	0.060	0.112	0.287	0.216
8	0.098	0.099	0.085	0.099	0.015	0.094	0.072	0.040	0.089	0.270
9	0.082	0.077	0.085	0.064	0.072	0.010	0.063	0.046	0.031	0.081
10	0.056	0.065	0.067	0.063	0.046	0.045	0.006	0.040	0.036	0.028
11	0.043	0.045	0.056	0.049	0.045	0.028	0.030	0.004	0.031	0.033
12	0	0.034	0.038	0.041	0.035	0.028	0.018	0.020	0.003	0.029
13	0	0	0.029	0.028	0.030	0.022	0.019	0.011	0.015	0.003
14	0	0	0	0.022	0.020	0.018	0.014	0.012	0.009	0.014
15	0	0	0	0	0.015	0.012	0.012	0.008	0.009	0.008
16	0	0	0	0	0	0.009	0.008	0.007	0.007	0.009
17	0	0	0	0	0	0	0.006	0.005	0.006	0.006
18	0	0	0	0	0	0	0	0.004	0.004	0.005
19	0	0	0	0	0	0	0	0	0.003	0.003
20	0	0	0	0	0	0	0	0	0	0.003
>20	0	0	0	0	0	0	0	0	0	0
Total	0.726	0.689	0.835	0.862	0.878	0.956	1.182	1.124	1.289	1.710

Table 39. Model estimates of number of lake trout deaths (x1000) due to commercial fishing mortality in central Lake Huron (MH-2).

	Year									
Age	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993
1	0	0	0	0	0	0	0	0	0	0
2	0.003	0.002	0.012	0.018	0.012	0.017	0.023	0.021	0.051	0.209
3	0.028	0.028	0.049	0.059	0.180	0.122	0.167	0.173	0.218	0.759
4	0.023	0.201	0.472	0.181	0.481	1.335	0.929	1.025	1.407	2.364
5	0.162	0.030	0.601	0.305	0.254	0.598	1.703	0.963	1.423	2.591
6	0.094	0.125	0.055	0.237	0.261	0.185	0.449	1.035	0.805	1.601
7	0.060	0.053	0.171	0.016	0.146	0.139	0.099	0.199	0.622	0.668
8	0.041	0.048	0.100	0.066	0.013	0.109	0.103	0.062	0.167	0.727
9	0.027	0.030	0.080	0.034	0.050	0.009	0.072	0.057	0.046	0.174
10	0.010	0.013	0.032	0.017	0.016	0.021	0.004	0.025	0.027	0.031
11	0.007	0.009	0.027	0.013	0.016	0.013	0.018	0.002	0.024	0.036
12	0	0.007	0.019	0.011	0.013	0.013	0.011	0.012	0.002	0.032
13	0	0	0.014	0.008	0.011	0.010	0.011	0.007	0.012	0.003
14	0	0	0	0.006	0.007	0.009	0.008	0.008	0.007	0.016
15	0	0	0	0	0.005	0.006	0.007	0.005	0.007	0.009
16	0	0	0	0	0	0.004	0.005	0.005	0.005	0.010
17	0	0	0	0	0	0	0.003	0.003	0.004	0.007
18	0	0	0	0	0	0	0	0.002	0.003	0.006
19	0	0	0	0	0	0	0	0	0.002	0.004
20	0	0	0	0	0	0	0	0	0.0	0.003
>20	0	0	0	0	0	0	0	0	0.0	0
Total	0.457	0.544	1.633	0.972	1.467	2.592	3.611	3.606	4.832	9.249

Table 40. Model estimates of number of lake trout deaths (x1000) due to sea lamprey-induced mortality in central Lake Huron (MH-2).

	Year									
Age	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993
1	0	0	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0	0	0
3	7.302	5.152	0.994	0.183	7.624	1.124	0.434	2.059	5.501	10.868
4	0.944	5.032	1.470	0.260	3.222	3.252	1.096	2.290	5.225	4.808
5	7.623	0.600	2.239	1.362	2.075	3.382	5.756	3.629	5.538	4.980
6	5.872	3.034	0.389	2.339	3.028	1.943	2.413	7.031	4.522	4.286
7	5.479	2.002	2.089	0.263	2.572	2.336	0.780	2.192	5.522	2.841
8	3.986	2.053	1.523	1.379	0.268	2.119	0.993	0.775	1.705	3.524
9	3.170	1.625	1.730	1.009	1.310	0.232	0.952	0.950	0.620	1.099
10	2.210	1.381	1.363	1.008	0.869	1.095	0.109	0.805	0.726	0.384
11	1.669	0.931	1.126	0.775	0.805	0.684	0.427	0.082	0.626	0.445
12	0	0.738	0.792	0.666	0.690	0.693	0.347	0.385	0.062	0.392
13	0	0	0.599	0.452	0.546	0.527	0.301	0.233	0.308	0.038
14	0	0	0	0.357	0.417	0.451	0.300	0.229	0.185	0.190
15	0	0	0	0	0.317	0.301	0.253	0.161	0.197	0.109
16	0	0	0	0	0	0.229	0.169	0.136	0.139	0.116
17	0	0	0	0	0	0	0.129	0.091	0.117	0.082
18	0	0	0	0	0	0	0	0.069	0.078	0.069
19	0	0	0	0	0	0	0	0	0.059	0.046
20	0	0	0	0	0	0	0	0	0	0.035
>20	0	0	0	0	0	0	0	0	0	0.000
Total	38.256	22.547	14.317	10.053	23.741	18.369	14.458	21.118	31.132	34.314

Table 41. Model estimates of lake trout abundance in northern main basin of Lake Huron (MH-1).

	Year									
Age	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993
1	136,800	489,840	943,176	480,060	645,720	658,580	565,620	967,100	859,680	657,260
2	271,751	70,262	251,587	484,425	246,564	331,649	338,254	290,508	496,713	441,541
3	236,241	196,688	50,645	179,785	321,519	167,317	233,274	243,678	210,446	360,061
4	71,386	155,194	124,798	24,929	52,655	119,788	87,679	172,419	155,096	133,847
5	149,587	37,455	59,333	21,354	20	233	7,840	37,301	91,720	84,383
6	67,808	53,868	9,642	5,118	2	0	5	2,348	14,883	43,163
7	46,032	14,958	10,754	629	1	0	0	1	655	6,182
8	6,300	13,978	4,511	1,511	2	0	0	0	0	275
9	578	996	2,877	411	6	0	0	0	0	0
10	60	94	220	312	4	0	0	0	0	0
11	7	11	25	33	17	0	0	0	0	0
12	0	1	3	4	2	1	0	0	0	0
13	0	0	0	0	0	0	0	0	0	0
14	0	0	0	0	0	0	0	0	0	0
15	0	0	0	0	0	0	0	0	0	0
16	0	0	0	0	0	0	0	0	0	0
17	0	0	0	0	0	0	0	0	0	0
18	0	0	0	0	0	0	0	0	0	0
19	0	0	0	0	0	0	0	0	0	0
20	0	0	0	0	0	0	0	0	0	0
>20	0	0	0	0	0	0	0	0	0	0
Total	986,552	1,033,344	1,457,570	1,198,572	1,266,512	1,277,569	1,232,672	1,713,355	1,829,193	1,726,712

Table 42. Model estimates of instantaneous rates of recreational fishing mortality (year^{-1}) for lake trout in northern Lake Huron (MH-1).

	Year									
Age	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993
1	0	0	0	0	0	0	0	0	0	0
2	$1.85x10^{-7}$	$1.85x10^{-7}$	$2.99x10^{-7}$	$1.54x10^{-7}$	$2.87x10^{-7}$	$2.42x10^{-7}$	$2.22x10^{-7}$	$2.03x10^{-7}$	$1.31x10^{-7}$	$1.29x10^{-7}$
3	$1.42x10^{-4}$	$1.42x10^{-4}$	$2.29x10^{-4}$	$1.18x10^{-4}$	$2.19x10^{-4}$	$1.85x10^{-4}$	$1.70x10^{-4}$	$1.55x10^{-4}$	$1.00x10^{-4}$	$9.89x10^{-5}$
4	$1.41x10^{-3}$	$1.41x10^{-3}$	$2.29x10^{-3}$	$1.18x10^{-3}$	$2.19x10^{-3}$	$1.85x10^{-3}$	$1.70x10^{-3}$	$1.55x10^{-3}$	$1.00x10^{-3}$	$9.87x10^{-4}$
5	$3.89x10^{-3}$	$3.89x10^{-3}$	$6.29x10^{-3}$	$3.24x10^{-3}$	$6.02x10^{-3}$	$5.09x10^{-3}$	$4.67x10^{-3}$	$4.26x10^{-3}$	$2.75x10^{-3}$	$2.72x10^{-3}$
6	$4.24x10^{-3}$	$4.24x10^{-3}$	$6.85x10^{-3}$	$3.53x10^{-3}$	$6.56x10^{-3}$	$5.54x10^{-3}$	$5.09x10^{-3}$	$4.64x10^{-3}$	$3.00x10^{-3}$	$2.96x10^{-3}$
7	$4.16x10^{-3}$	$4.16x10^{-3}$	$6.73x10^{-3}$	$3.46x10^{-3}$	$6.45x10^{-3}$	$5.45x10^{-3}$	$5.00x10^{-3}$	$4.56x10^{-3}$	$2.95x10^{-3}$	$2.91x10^{-3}$
8	$4.26x10^{-3}$	$4.26x10^{-3}$	$6.88x10^{-3}$	$3.54x10^{-3}$	$6.60x10^{-3}$	$5.57x10^{-3}$	$5.12x10^{-3}$	$4.67x10^{-3}$	$3.01x10^{-3}$	$2.97x10^{-3}$
9	$4.27x10^{-3}$	$4.27x10^{-3}$	$6.90x10^{-3}$	$3.55x10^{-3}$	$6.61x10^{-3}$	$5.58x10^{-3}$	$5.13x10^{-3}$	$4.68x10^{-3}$	$3.02x10^{-3}$	$2.98x10^{-3}$
10	$4.27x10^{-3}$	$4.27x10^{-3}$	$6.90x10^{-3}$	$3.55x10^{-3}$	$6.61x10^{-3}$	$5.58x10^{-3}$	$5.13x10^{-3}$	$4.68x10^{-3}$	$3.02x10^{-3}$	$2.98x10^{-3}$
11	$4.27x10^{-3}$	$4.27x10^{-3}$	$6.90x10^{-3}$	$3.55x10^{-3}$	$6.61x10^{-3}$	$5.58x10^{-3}$	$5.13x10^{-3}$	$4.68x10^{-3}$	$3.02x10^{-3}$	$2.98x10^{-3}$
12	$4.27x10^{-3}$	$4.27x10^{-3}$	$6.90x10^{-3}$	$3.55x10^{-3}$	$6.61x10^{-3}$	$5.58x10^{-3}$	$5.13x10^{-3}$	$4.68x10^{-3}$	$3.02x10^{-3}$	$2.98x10^{-3}$
13	$4.27x10^{-3}$	$4.27x10^{-3}$	$6.90x10^{-3}$	$3.55x10^{-3}$	$6.61x10^{-3}$	$5.58x10^{-3}$	$5.13x10^{-3}$	$4.68x10^{-3}$	$3.02x10^{-3}$	$2.98x10^{-3}$
14	$4.27x10^{-3}$	$4.27x10^{-3}$	$6.90x10^{-3}$	$3.55x10^{-3}$	$6.61x10^{-3}$	$5.58x10^{-3}$	$5.13x10^{-3}$	$4.68x10^{-3}$	$3.02x10^{-3}$	$2.98x10^{-3}$
15	$4.27x10^{-3}$	$4.27x10^{-3}$	$6.90x10^{-3}$	$3.55x10^{-3}$	$6.61x10^{-3}$	$5.58x10^{-3}$	$5.13x10^{-3}$	$4.68x10^{-3}$	$3.02x10^{-3}$	$2.98x10^{-3}$
16	$4.27x10^{-3}$	$4.27x10^{-3}$	$6.90x10^{-3}$	$3.55x10^{-3}$	$6.61x10^{-3}$	$5.58x10^{-3}$	$5.13x10^{-3}$	$4.68x10^{-3}$	$3.02x10^{-3}$	$2.98x10^{-3}$
17	$4.27x10^{-3}$	$4.27x10^{-3}$	$6.90x10^{-3}$	$3.55x10^{-3}$	$6.61x10^{-3}$	$5.58x10^{-3}$	$5.13x10^{-3}$	$4.68x10^{-3}$	$3.02x10^{-3}$	$2.98x10^{-3}$
18	$4.27x10^{-3}$	$4.27x10^{-3}$	$6.90x10^{-3}$	$3.55x10^{-3}$	$6.61x10^{-3}$	$5.58x10^{-3}$	$5.13x10^{-3}$	$4.68x10^{-3}$	$3.02x10^{-3}$	$2.98x10^{-3}$
19	$4.27x10^{-3}$	$4.27x10^{-3}$	$6.90x10^{-3}$	$3.55x10^{-3}$	$6.61x10^{-3}$	$5.58x10^{-3}$	$5.13x10^{-3}$	$4.68x10^{-3}$	$3.02x10^{-3}$	$2.98x10^{-3}$
20	$4.27x10^{-3}$	$4.27x10^{-3}$	$6.90x10^{-3}$	$3.55x10^{-3}$	$6.61x10^{-3}$	$5.58x10^{-3}$	$5.13x10^{-3}$	$4.68x10^{-3}$	$3.02x10^{-3}$	$2.98x10^{-3}$
>20	$4.27x10^{-3}$	$4.27x10^{-3}$	$6.90x10^{-3}$	$3.55x10^{-3}$	$6.61x10^{-3}$	$5.58x10^{-3}$	$5.13x10^{-3}$	$4.68x10^{-3}$	$3.02x10^{-3}$	$2.98x10^{-3}$

Table 43. Model estimates of instantaneous rates of commercial fishing mortality (year^{-1}) for lake trout in northern Lake Huron (MH-1).

	Year									
Age	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993
1	0	0	0	0	0	0	0	0	0	0
2	0.005	0.009	0.018	0.091	0.069	0.033	0.010	0.004	0.003	0.004
3	0.049	0.090	0.176	0.915	0.693	0.334	0.095	0.040	0.033	0.039
4	0.364	0.673	1.321	6.861	5.198	2.508	0.715	0.299	0.249	0.294
5	0.485	0.898	1.761	9.149	6.931	3.344	0.953	0.398	0.332	0.392
6	0.417	0.772	1.514	7.868	5.961	2.876	0.820	0.343	0.285	0.337
7	0.267	0.494	0.968	5.032	3.812	1.839	0.524	0.219	0.183	0.216
8	0.238	0.440	0.863	4.483	3.396	1.639	0.467	0.195	0.163	0.192
9	0.189	0.350	0.687	3.568	2.703	1.304	0.372	0.155	0.129	0.153
10	0.097	0.180	0.352	1.830	1.386	0.669	0.191	0.080	0.066	0.078
11	0.097	0.180	0.352	1.830	1.386	0.669	0.191	0.080	0.066	0.078
12	0.097	0.180	0.352	1.830	1.386	0.669	0.191	0.080	0.066	0.078
13	0.097	0.180	0.352	1.830	1.386	0.669	0.191	0.080	0.066	0.078
14	0.097	0.180	0.352	1.830	1.386	0.669	0.191	0.080	0.066	0.078
15	0.097	0.180	0.352	1.830	1.386	0.669	0.191	0.080	0.066	0.078
16	0.097	0.180	0.352	1.830	1.386	0.669	0.191	0.080	0.066	0.078
17	0.097	0.180	0.352	1.830	1.386	0.669	0.191	0.080	0.066	0.078
18	0.097	0.180	0.352	1.830	1.386	0.669	0.191	0.080	0.066	0.078
19	0.097	0.180	0.352	1.830	1.386	0.669	0.191	0.080	0.066	0.078
20	0.097	0.180	0.352	1.830	1.386	0.669	0.191	0.080	0.066	0.078
>20	0.097	0.180	0.352	1.830	1.386	0.669	0.191	0.080	0.066	0.078

Table 44. Model estimates of instantaneous rates of sea lamprey-induced mortality (year^{-1}) for lake trout in northern Lake Huron (MH-1).

	Year									
Age	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993
1	0	0	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0	0	0
3	0.200	0.193	0.361	0.141	0.122	0.140	0.035	0.240	0.248	0.093
4	0.156	0.163	0.319	0.120	0.097	0.093	0.015	0.207	0.235	0.053
5	0.425	0.348	0.576	0.253	0.254	0.382	0.140	0.409	0.311	0.298
6	0.987	0.733	1.106	0.540	0.588	0.988	0.415	0.827	0.488	0.814
7	0.820	0.600	0.886	0.507	0.532	0.808	0.426	0.674	0.581	0.681
8	1.503	1.036	1.427	0.941	1.009	1.543	0.914	1.133	1.036	1.342
9	1.525	1.054	1.427	0.985	1.049	1.565	0.974	1.147	1.115	1.372
10	1.525	1.054	1.427	0.985	1.049	1.565	0.974	1.147	1.115	1.372
11	1.534	1.050	1.370	1.060	1.114	1.573	1.094	1.130	1.295	1.405
12	1.592	1.108	1.428	1.118	1.171	1.631	1.151	1.187	1.353	1.463
13	1.592	1.108	1.428	1.118	1.171	1.631	1.151	1.187	1.353	1.463
14	1.592	1.108	1.428	1.118	1.171	1.631	1.151	1.187	1.353	1.463
15	1.592	1.108	1.428	1.118	1.171	1.631	1.151	1.187	1.353	1.463
16	1.592	1.108	1.428	1.118	1.171	1.631	1.151	1.187	1.353	1.463
17	1.592	1.108	1.428	1.118	1.171	1.631	1.151	1.187	1.353	1.463
18	1.592	1.108	1.428	1.118	1.171	1.631	1.151	1.187	1.353	1.463
19	1.592	1.108	1.428	1.118	1.171	1.631	1.151	1.187	1.353	1.463
20	1.592	1.108	1.428	1.118	1.171	1.631	1.151	1.187	1.353	1.463
>20	1.592	1.108	1.428	1.118	1.171	1.631	1.151	1.187	1.353	1.463

Table 45. Model estimates of number of lake trout deaths (x1000) due to natural mortality in northern Lake Huron (MH-1).

	Year									
Age	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993
1	66.538	238.253	458.751	233.496	314.071	320.326	275.112	470.387	418.139	319.684
2	73.937	19.079	68.040	126.547	65.081	89.024	91.828	79.073	135.242	120.186
3	33.102	27.119	6.226	17.766	35.065	21.150	34.549	33.647	29.048	53.296
4	0.004	0.010	0.008	0.002	0.003	0.007	0.005	0.011	0.010	0.008
5	10.109	2.211	2.388	0.242	0	0.006	0.491	2.632	6.946	6.262
6	3.591	2.748	0.339	0.062	0	0	0	0.136	1.017	2.522
7	2.716	0.880	0.476	0.011	0	0	0	0	0.044	0.394
8	0.289	0.705	0.172	0.027	0	0	0	0	0	0.014
9	0.027	0.051	0.116	0.009	0	0	0	0	0	0
10	0.003	0.005	0.010	0.010	0	0	0	0	0	0
11	0	0.001	0.001	0.001	0.001	0	0	0	0	0
12	0	0	0	0	0	0	0	0	0	0
13	0	0	0	0	0	0	0	0	0	0
14	0	0	0	0	0	0	0	0	0	0
15	0	0	0	0	0	0	0	0	0	0
16	0	0	0	0	0	0	0	0	0	0
17	0	0	0	0	0	0	0	0	0	0
18	0	0	0	0	0	0	0	0	0	0
19	0	0	0	0	0	0	0	0	0	0
20	0	0	0	0	0	0	0	0	0	0
>20	0	0	0	0	0	0	0	0	0	0
Total	190.316	291.062	536.526	378.173	414.221	430.514	401.985	585.887	590.446	502.365

Table 46. Model estimates of number of lake trout deaths (x1000) due to recreational fishing mortality in northern Lake Huron (MH-1).

	Year									
Age	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993
1	0	0	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0	0	0
3	0.027	0.022	0.008	0.012	0.045	0.023	0.034	0.030	0.017	0.031
4	0.074	0.141	0.134	0.004	0.021	0.076	0.100	0.198	0.116	0.105
5	0.365	0.080	0.139	0.007	0	0	0.021	0.104	0.177	0.158
6	0.148	0.113	0.023	0.002	0	0	0	0.006	0.030	0.073
7	0.112	0.036	0.032	0	0	0	0	0	0.001	0.011
8	0.012	0.030	0.012	0.001	0	0	0	0	0	0
9	0.001	0.002	0.008	0	0	0	0	0	0	0
10	0	0	0.001	0	0	0	0	0	0	0
11	0	0	0	0	0	0	0	0	0	0
12	0	0	0	0	0	0	0	0	0	0
13	0	0	0	0	0	0	0	0	0	0
14	0	0	0	0	0	0	0	0	0	0
15	0	0	0	0	0	0	0	0	0	0
16	0	0	0	0	0	0	0	0	0	0
17	0	0	0	0	0	0	0	0	0	0
18	0	0	0	0	0	0	0	0	0	0
19	0	0	0	0	0	0	0	0	0	0
20	0	0	0	0	0	0	0	0	0	0
>20	0	0	0	0	0	0	0	0	0	0
Total	0.740	0.425	0.356	0.028	0.066	0.099	0.156	0.339	0.341	0.378

Table 47. Model estimates of number of lake trout deaths (x1000) due to commercial fishing mortality in northern Lake Huron (MH-1).

	Year									
Age	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993
1	0	0	0	0	0	0	0	0	0	0
2	1.127	0.538	3.762	36.359	14.166	9.350	2.748	0.989	1.410	1.480
3	9.358	14.186	6.388	94.713	141.614	41.216	19.186	7.809	5.619	12.181
4	19.144	67.123	77.378	24.052	50.271	102.989	42.132	38.190	28.923	31.397
5	45.470	18.398	38.959	20.534	0.019	0.199	4.341	9.717	21.384	22.778
6	14.590	20.657	4.999	4.729	0.001	0	0.002	0.454	2.827	8.287
7	7.177	4.303	4.561	0.559	0.001	0	0	0	0.080	0.843
8	0.683	3.089	1.476	1.221	0.002	0	0	0	0	0.026
9	0.050	0.180	0.793	0.312	0.004	0	0	0	0	0
10	0.003	0.009	0.035	0.185	0.002	0	0	0	0	0
11	0	0.001	0.004	0.019	0.008	0	0	0	0	0
12	0	0	0	0.002	0.001	0	0	0	0	0
13	0	0	0	0	0	0	0	0	0	0
14	0	0	0	0	0	0	0	0	0	0
15	0	0	0	0	0	0	0	0	0	0
16	0	0	0	0	0	0	0	0	0	0
17	0	0	0	0	0	0	0	0	0	0
18	0	0	0	0	0	0	0	0	0	0
19	0	0	0	0	0	0	0	0	0	0
20	0	0	0	0	0	0	0	0	0	0
>20	0	0	0	0	0	0	0	0	0	0
Total	97.603	128.484	138.357	182.685	206.090	153.755	68.409	57.160	60.244	76.992

Table 48. Model estimates of number of lake trout deaths (x1000) due to sea lamprey-induced mortality in northern Lake Huron (MH-1).

	Year									
Age	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993
1	0	0	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0	0	0
3	38.562	30.564	13.093	14.639	25.010	17.251	7.088	47.098	41.917	28.730
4	8.217	16.287	18.698	0.419	0.937	3.813	0.869	26.524	27.329	5.610
5	39.791	7.128	12.734	0.569	0.001	0.023	0.640	9.969	20.058	17.292
6	34.528	19.601	3.652	0.325	0	0	0.001	1.097	4.828	20.007
7	22.053	5.229	4.174	0.056	0	0	0	0.001	0.254	2.661
8	4.320	7.278	2.441	0.256	0	0	0	0	0	0.182
9	0.406	0.542	1.648	0.086	0.002	0	0	0	0	0
10	0.044	0.055	0.141	0.100	0.001	0	0	0	0	0
11	0.005	0.006	0.015	0.011	0.007	0	0	0	0	0
12	0	0.001	0.002	0.001	0.001	0.001	0	0	0	0
13	0	0	0	0	0	0	0	0	0	0
14	0	0	0	0	0	0	0	0	0	0
15	0	0	0	0	0	0	0	0	0	0
16	0	0	0	0	0	0	0	0	0	0
17	0	0	0	0	0	0	0	0	0	0
18	0	0	0	0	0	0	0	0	0	0
19	0	0	0	0	0	0	0	0	0	0
20	0	0	0	0	0	0	0	0	0	0
>20	0	0	0	0	0	0	0	0	0	0
Total	147.927	86.691	56.599	16.463	25.959	21.088	8.598	84.688	94.387	74.482

Table 49. Model estimates of instantaneous rates of total mortality (year^{-1}) for lake trout in southern main basin Lake Huron (MH-3/4/5).

	Year									
Age	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993
1	0.666	0.666	0.666	0.666	0.666	0.666	0.666	0.666	0.666	0.666
2	0.322	0.424	0.369	0.363	0.348	0.365	0.432	0.432	0.391	0.562
3	0.186	0.317	0.236	0.250	0.221	0.257	0.325	0.308	0.278	0.413
4	0.192	0.411	0.283	0.339	0.272	0.331	0.441	0.337	0.348	0.382
5	0.251	0.519	0.434	0.486	0.404	0.387	0.612	0.374	0.431	0.436
6	0.259	0.534	0.469	0.533	0.440	0.385	0.641	0.377	0.436	0.468
7	0.265	0.537	0.470	0.586	0.458	0.396	0.645	0.409	0.418	0.509
8	0.275	0.542	0.474	0.637	0.477	0.412	0.654	0.446	0.402	0.548
9	0.279	0.543	0.473	0.664	0.485	0.421	0.656	0.468	0.391	0.569
10	0.283	0.545	0.473	0.687	0.492	0.429	0.658	0.485	0.383	0.587
11	0.287	0.546	0.473	0.712	0.500	0.437	0.660	0.503	0.374	0.606
12	0.286	0.546	0.473	0.706	0.498	0.435	0.660	0.499	0.376	0.602
13	0.284	0.545	0.474	0.695	0.495	0.431	0.659	0.490	0.381	0.593
14	0.287	0.546	0.473	0.712	0.500	0.437	0.660	0.504	0.374	0.607
15	0.283	0.545	0.474	0.686	0.492	0.428	0.659	0.483	0.384	0.586
16	0.290	0.547	0.472	0.727	0.504	0.442	0.661	0.515	0.368	0.618
17	0.290	0.547	0.472	0.727	0.504	0.442	0.661	0.515	0.368	0.618
18	0.290	0.547	0.472	0.727	0.504	0.442	0.661	0.515	0.368	0.618
19	0.290	0.547	0.472	0.727	0.504	0.442	0.661	0.515	0.368	0.618
20	0.290	0.547	0.472	0.727	0.504	0.442	0.661	0.515	0.368	0.618
>20	0.210	0.502	0.436	0.522	0.415	0.381	0.606	0.398	0.394	0.475

Table 50. Model estimates of instantaneous rates of total mortality ($year^{-1}$) for lake trout in central main basin Lake Huron (MH-2).

	Year									
Age	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993
1	0.666	0.666	0.666	0.666	0.666	0.666	0.666	0.666	0.666	0.666
2	0.318	0.319	0.319	0.319	0.319	0.319	0.319	0.319	0.319	0.320
3	0.376	0.369	0.242	0.180	0.289	0.207	0.187	0.228	0.335	0.373
4	0.369	0.335	0.228	0.164	0.284	0.217	0.198	0.233	0.348	0.429
5	0.491	0.343	0.273	0.229	0.369	0.350	0.309	0.326	0.426	0.512
6	0.536	0.346	0.340	0.302	0.410	0.458	0.352	0.405	0.472	0.540
7	0.505	0.340	0.349	0.309	0.391	0.453	0.324	0.399	0.454	0.502
8	0.482	0.341	0.371	0.326	0.393	0.460	0.338	0.399	0.457	0.499
9	0.465	0.343	0.400	0.351	0.400	0.481	0.354	0.411	0.466	0.497
10	0.468	0.345	0.396	0.351	0.409	0.475	0.379	0.395	0.458	0.471
11	0.462	0.339	0.393	0.346	0.389	0.473	0.331	0.406	0.452	0.472
12	0.470	0.347	0.398	0.353	0.417	0.476	0.400	0.390	0.461	0.471
13	0.465	0.342	0.395	0.349	0.400	0.475	0.359	0.400	0.456	0.472
14	0.475	0.351	0.401	0.357	0.434	0.478	0.441	0.381	0.467	0.470
15	0.475	0.351	0.401	0.357	0.434	0.478	0.441	0.381	0.467	0.470
16	0.475	0.351	0.401	0.357	0.434	0.478	0.441	0.381	0.467	0.470
17	0.475	0.351	0.401	0.357	0.434	0.478	0.441	0.381	0.467	0.470
18	0.475	0.351	0.401	0.357	0.434	0.478	0.441	0.381	0.467	0.470
19	0.475	0.351	0.401	0.357	0.434	0.478	0.441	0.381	0.467	0.470
20	0.475	0.351	0.401	0.357	0.434	0.478	0.441	0.381	0.467	0.470
>20	0.475	0.351	0.401	0.357	0.434	0.478	0.441	0.381	0.467	0.470

Table 51. Model estimates of instantaneous rates of total mortality ($year^{-1}$) for lake trout in northern main basin Lake Huron (MH-1).

	Year									
Age	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993
1	0.666	0.666	0.666	0.666	0.666	0.666	0.666	0.666	0.666	0.666
2	0.323	0.327	0.336	0.410	0.388	0.352	0.328	0.322	0.322	0.322
3	0.420	0.455	0.709	1.228	0.987	0.646	0.302	0.452	0.453	0.303
4	0.645	0.962	1.765	7.106	5.421	2.726	0.855	0.631	0.609	0.471
5	1.021	1.357	2.450	9.513	7.298	3.839	1.206	0.919	0.754	0.800
6	1.511	1.611	2.730	8.514	6.657	3.973	1.342	1.277	0.879	1.257
7	1.192	1.199	1.962	5.643	4.451	2.754	1.056	0.998	0.867	1.001
8	1.845	1.581	2.397	5.527	4.512	3.288	1.487	1.433	1.302	1.637
9	1.818	1.509	2.221	4.657	3.859	2.975	1.450	1.407	1.348	1.628
10	1.726	1.338	1.886	2.918	2.542	2.340	1.269	1.331	1.285	1.553
11	1.736	1.334	1.829	2.993	2.607	2.348	1.390	1.314	1.465	1.587
12	1.793	1.391	1.887	3.051	2.664	2.405	1.447	1.371	1.522	1.644
13	1.793	1.391	1.887	3.051	2.664	2.405	1.447	1.371	1.522	1.644
14	1.793	1.391	1.887	3.051	2.664	2.405	1.447	1.371	1.522	1.644
15	1.793	1.391	1.887	3.051	2.664	2.405	1.447	1.371	1.522	1.644
16	1.793	1.391	1.887	3.051	2.664	2.405	1.447	1.371	1.522	1.644
17	1.793	1.391	1.887	3.051	2.664	2.405	1.447	1.371	1.522	1.644
18	1.793	1.391	1.887	3.051	2.664	2.405	1.447	1.371	1.522	1.644
19	1.793	1.391	1.887	3.051	2.664	2.405	1.447	1.371	1.522	1.644
20	1.793	1.391	1.887	3.051	2.664	2.405	1.447	1.371	1.522	1.644
>20	1.793	1.391	1.887	3.051	2.664	2.405	1.447	1.371	1.522	1.644

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