ESTIMATION OF SIZE-SPECIFIC SEA LAMPREY WOUNDING RATES ON LAKE
TROUT: SPATIAL AND TEMPORAL PATTERNS IN THE UPPER GREAT LAKES

By

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ABSTRACT

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The purpose of this research was first, to develop sea lamprey (*Petromyzon marinus*) wounding rate models for lake trout (*Salvelinus namaycush*) from each of the lakes within 1836 Treaty-ceded waters, and second, to explain how and why the length distributions of lake trout attacked by sea lamprey have differed spatially and over time. Despite substantial control efforts, the negative impacts of parasitic sea lamprey predation on native lake trout remain an important fisheries concern in the Great Lakes. In Chapter 1, I estimate wounding rates as a logistic function of lake trout length. A model comparison framework was used to develop unique wounding rate models for each of Lakes Huron, Michigan, and Superior. Models that assumed a negative binomial wound distribution and allowed for spatial and temporal effects in the shaping parameters were selected for each lake. Large spatial differences and temporal trends in sea lamprey size-selectivity were found. Chapter 2 attempts to explain spatial and temporal patterns in sea lamprey size-selectivity in a foraging theory context. Foraging theory predicts that in the scarcity of larger, more desirable prey, a predator will shift its feeding behavior by incorporating smaller, less desirable prey types. Wounding rate model parameter estimates were related to large lake trout abundance estimates to look for patterns consistent with foraging theory. Large lake trout abundance was a poor predictor of sea lamprey size-selectivity, but future research suggestions to examine the influence of alternative hosts and lake trout strain are described.

ACKNOWLEDGEMENTS

PREFACE

The work contained in Chapter 1 was written as a standalone document and has been submitted for publication to the *Journal of Great Lakes Research* as a co-authored paper by Carson G. Prichard and James R. Bence. It is presented here in essentially the same form as the submitted manuscript. For this reason, Chapter 1 is written in the first person plural narrative, although the thesis is singularly authored. All references are formatted in a style consistent with that journal.

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INTRODUCTION

History of Lake Trout and Sea Lamprey in the Upper Great Lakes

Prior to European colonization in the eighteenth and nineteenth centuries, lake trout (*Salvelinus namaycush*) were the dominant pelagic predator in the Great Lakes. Early in the twentieth century, large commercial fisheries supported by the diverse stocks of lake trout had developed on Lakes Huron, Michigan, and Superior. Each lake supported a massive commercial fishing industry with annual harvests exceeding 2 million kilograms dating back to the late 1800s (Hansen 1999). However, beginning in the late 1930s, lake trout populations in each lake collapsed – first in Lake Huron, second in Lake Michigan, and last in Lake Superior. This is evidenced by declines in annual commercial harvest – decreasing from 2.7 million to 0.18 million kilograms in Lake Huron (1935-1947), from 3.1 million to 0.16 million kilograms in Lake Michigan (1943-1949), and from 2.1 million to 0.23 million kilograms in Lake Superior (1950-1960) (Baldwin et al. 2009, Hansen 1999).   With each successive collapse, fishing effort shifted to areas where lake trout were still in abundance so that by the 1950s, after collapses in Lakes Huron and Michigan, the only commercial fisheries left for lake trout existed in Lake Superior (Hansen 1999). Lake trout populations in Lake Superior were so severely reduced that in 1962 both United States and Canadian governments imposed a general closure on lake trout fishing (Smith and Tibbles 1980). Lake trout commercial fisheries that had supported an annual combined average catch of 7 million kilograms in the 1940s had been reduced to nothing.

Sea lampreys (*Petromyzon marinus*), a parasitic fish native to the Atlantic Ocean, were first recorded in Lake Huron in 1937, Lake Michigan in 1936, and Lake Superior in 1946 (their observance in Lake Michigan prior to Lake Huron suggests they were present in Lake Huron

before 1937; Smith and Tibbles 1980). Assessing the extent to which sea lamprey mortality contributed to the collapse of lake trout in each lake is difficult due to the timing of their arrivals, and evidence of declining lake trout stocks in each lake is apparent several years before the establishment of significant abundances of sea lamprey. Total lake trout harvests remained at consistently high levels despite sharp increases in fishing effort and gear efficiency after World War II, prior to sea lamprey population explosions, implicating commercial fishing in early lake trout declines (Krueger and Ebener 2003). However, it is known that in the Great Lakes, lake trout serve as the principal host species (Bence et al. 2003, Harvey et al. 2008), and sea lamprey were abundant in all the Great Lakes by the 1950s. Although the extent to which commercial overfishing and sea lamprey predation contributed to these collapses is a source of much debate, it is generally accepted that each played a major role in the demise of lake trout (Hansen 1999).

Responding to the collapse of Great Lakes fisheries populations and the rapid expansion of sea lamprey populations, the U.S. and Canadian governments established the international Great Lakes Fishery Commission (GLFC) in 1955 with the following mandates:

(1)   *to develop coordinated programs of research on the Great Lakes, and, on the basis of the findings to recommend measures which will permit the maximum sustained productivity of stocks of fish of common concern; and,*

(2)   *to formulate and implement a program to eradicate or minimize sea lamprey populations in the Great Lakes.*

Initial control efforts to reduce spawning runs of sea lamprey were physical and electrical barriers installed in streams in order to restrict access of adult sea lamprey to spawning grounds. By 1960, 162 such barriers had been installed on tributaries to Lake Michigan and Lake Superior (Christie and Goddard 2003); however, the number of adults returning had not declined. Lamprey-specific toxicants discovered in the 1960s targeting the larval, stream-dwelling life stage proved most effective and their application reduced the return of spawning sea lampreys to 8% of peak abundances in Lake Superior tributaries by 1978 and showed similar success in Lakes Michigan and Huron (Smith and Tibbles 1980). More recently, releasing sterile males during the spawning period was implemented as an additional control technique (Twohey et al. 2003), although the use of sterile males as a control method have recently been scaled back.

Current Status of Lake Trout Populations

The status of lake trout rehabilitation differs greatly across the lakes. My analyses focus on 1836 Treaty-ceded waters and as such I do not address the statuses of Lakes Erie and Ontario here. Lake Superior lake trout populations are generally considered recovered. Wild, naturally reproducing populations of lake trout have been established lakewide (Hansen et al. 1995) such that stocking efforts have been largely reduced. Across Michigan waters of Lake Superior, modern lake trout abundances are at least as high as historic abundances (Wilberg et al. 2003). The restoration program of Lake Superior now focuses on limiting fishing mortality through total allowable catches to manage the predominantly wild fish stocks, as well as reducing the effects of sea lamprey induced mortality. Aside from natural mortality, sea lamprey mortality is the greatest mortality source affecting adult lake trout.

Only two small, naturally reproducing lake trout populations avoided collapse in Lake Huron – those of Iroquois Bay and Parry Sound (Berst and Spangler 1973). Stocking efforts were focused on offshore reefs in the mid-1980s where by the mid-1990s wild fry were observed (Desorcie and Bowen 2003). More recently, lakewide population collapses of alewife (*Alosa pseudoharengus)* in 2003-2004, as well as lake trout age-class expansion following reductions in sea lamprey abundances, have led to increased observances of basinwide wild recruitment of lake trout (Fitzsimons et al. 2010, He et al. 2012). Current management for lake trout in Lake Huron has focused on stocking strains that experience less sea lamprey predation (i.e., Seneca strain) and thus are better able to survive to reproductive age, as it appears that reproducing lake trout produce viable wild offspring.

Despite reductions in sea lamprey abundances and massive stocking efforts, lake trout rehabilitation efforts have been met with limited success in Lake Michigan. Natural recruitment has not been observed, and populations are reliant almost solely on stocked fish.

Research Goals

The impetus for sea lamprey control is improving the survival of fish populations targeted by management efforts through the reduction of sea lamprey populations (Christie and Goddard 2003). Although current control techniques have been effective in drastically reducing sea lamprey abundances, eradication is unfeasible (Christie et al. 2003). With this realization, the GLFC adopted an integrated pest management policy called the Integrated Management of Sea Lamprey (IMSL) (Davis et al. 1982). The goals defined by the IMSL are in terms of tolerable levels of sea lamprey abundance and reducing associated damages to levels

commensurate with fish community objectives established for Lakes Huron, Michigan and Superior (Desjardine et al. 1995, Eshenroder et al. 1995, Horns et al. 2003).

Accurate measure of the performance of sea lamprey control thus relies on an understanding of the damages caused by sea lamprey (Jones 2007). However, direct measurement of the numbers of fish killed by sea lampreys is difficult as victims tend to sink, are rarely observed, and are difficult to sample (Bergstedt and Schneider 1988). Early assessments of sea lamprey control focused only on estimates of adult lamprey abundances during spawning runs. More recently, methods have been developed to infer sea lamprey mortality rates based upon wounding rates observed on fish surviving sea lamprey attacks. Wound classification keys allow wounds observed on sampled fish to be assigned to a given sea lamprey feeding season, based on their stage of healing, with relatively high certainty (King and Edsall 1979, Ebener et al. 2006). In conjunction with lab estimates of the survivability of hosts to sea lamprey attacks (Swink 1990, Swink 2003, Madenjian et al. 2008), approaches to estimate sea lamprey mortality were developed (Sitar et al. 1999, Rutter and Bence 2003). Rutter and Bence (2003) successfully modeled sea lamprey wounding rates as a logistic function of lake trout length for wound data from Lake Huron, and fishery managers currently use variants of their model in statistical catch-at-age models to estimate lake trout population abundances and calculate acceptable harvest levels (Caroffino and Lenart 2011).

Given the importance of wounding rates for Great Lakes fishery management, I sought to improve these estimates and explain trends in the wounding rate versus host length relationship. In Chapter 1, several alternative parameterizations of the logistic shaped wounding model developed by Rutter and Bence (2003) were explored that allowed for varying degrees of spatial and temporal variability in the parameters that govern the shape of the function. I successfully

constructed unique wounding rate models for wound data from each of Lakes Huron, Michigan and Superior using an Akaike's Information Criterion model selection framework.

In my second chapter, I attempt to explain the trends in sea lamprey size-selection observed in Chapter 1. Foraging theory describes that in the scarceness of desirable prey a predator will shift its feeding behavior to include alternative less desirable prey (Pulliam 1976), yet the influence of host community composition on the distribution of sea lamprey attacks is largely unknown (Jones 2007). In this context, I hypothesized that sea lamprey would shift their feeding behavior to include smaller lake trout when large lake trout were lower in abundance. I used two approaches to examine the relationship between sea lamprey size selectivity and large lake trout abundance. First, I related inflection point estimates of the logistic wounding rate models selected in chapter one to large lake trout abundance estimates. A positive correlation would provide support for my hypothesis. Second, I modeled the position of the inflection point as a function of the abundance of large lake trout. An increasing function over the observed range of large lake trout abundances would also support my hypothesis. My analyses suggest that large lake trout abundance by itself is not a strong predictor of the trends observed in the size-selectivity of sea lamprey.

Despite the continued large investments in sea lamprey control, they remain a concern and the effects of the parasitic life stage on host fish need to be monitored into the future. As wounding rates are the key indicator of such effects, and the relationship between wounding rates and lake trout size has changed over time, continued refinement of our interpretation and assessment of wound data remains important (Krueger and Marsden 2007). Accordingly, the work herein makes substantial advances in the methodology for summarizing sea lamprey wounding data by applying recent advances in estimation software and computing efficiency. It

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also explains how the wounding rate versus lake trout size relationship has changed over time and serves as the baseline for addressing reasons for such changes. Although my initial hypothesis of why this relationship has changed over time was not confirmed, understanding the factors that influence sea lamprey host selection remains an important component of mitigating damages associated with sea lamprey attacks. Subsequent research should explore the extent to which length distributions and abundances of host species other than lake trout may affect sea lamprey size-selectivity. Further research in Lakes Huron and Michigan, where strains stocked have shown differential susceptibility to sea lamprey predation, should examine how strain-specific lake trout abundances and length distributions relate to sea lamprey size-selectivity, both for specific strains and across all lake trout.

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CHAPTER 1

ACCOUNTING FOR CHANGING PATTERNS OF SIZE-SPECIFIC WOUNDING OF LAKE
TROUT BY SEA LAMPREY IN THE UPPER GREAT LAKES

Abstract: A primary fishery concern in the Laurentian Great Lakes is mitigating the persistent

negative impact of parasitic sea lamprey (*Petromyzon marinus*) on native lake trout (*Salvelinus*

namaycush). Wounds observed on surviving lake trout are commonly used by managers to

assess damages associated with sea lamprey predation. We estimated the relationship between

wounding rates and lake trout size, and how this varied spatially and temporally. We built upon

previously published work by fitting wound rates as a logistic function of lake trout size. By

using longer time series and data from three Great Lakes, our analysis harnessed substantially

more contrast in host populations than previous work, and we also employed software advances

for nonlinear mixed-effect models. Candidate models allowed logistic function parameters to be

constant or to vary spatially, temporally, or both. Temporal effects were modeled as random

walk processes. We also considered models that assumed either Poisson or negative binomial

distributions for the number of wounds per fish at a given length. Models that allowed for both

spatial and temporal effects in the shaping parameters and assumed a negative binomial wound

distribution resulted in the best fit as indicated by Akaike's Information Criterion. This research

provides managers with a tool to obtain more reliable estimates of sea lamprey marking.

INTRODUCTION

A primary Great Lakes fishery concern is the continued adverse effects of sea lamprey (*Petromyzon marinus*) on native lake trout (*Salvelinus namaycush*), and how to mitigate these effects (Stewart et al. 2003, Irwin et al. accepted). In the mid-twentieth century, each of the upper Great Lakes experienced rapid collapses in their lake trout populations. This is evidenced by sharp declines in annual commercial harvest of lake trout – dropping from 2.7 million to 0.18 million kilograms in Lake Huron (1935-1947), from 3.1 million to 0.16 million kilograms in Lake Michigan (1943-1949), and from 2.1 million to 0.23 million kilograms in Lake Superior (1950-1960) (Baldwin et al. 2009). Such sharp declines in lake trout populations are most often attributed to commercial fishing exploitation, predation by the invasive sea lamprey, and habitat degradation (Hansen 1999). Although the magnitude of the contribution of each of these causes is often debated, the evidence for adverse effects of sea lamprey on lake trout is compelling (Bence et al. 2003). For example, lake trout total mortality has been shown to be positively related to wounding rates (Pycha 1980), and Bergstedt and Schneider (1988) showed a positive correlation between the number of lake trout carcasses observed with fresh sea lamprey marks and the number of fresh wounds observed on live lake trout sampled in the same year in Lake Ontario. Since the implementation of the sea lamprey control program, sea lamprey abundances have been greatly reduced (Smith and Tibbles 1980). During this time, observed marking rates on sampled lake trout have decreased (Rutter and Bence 2003), lake trout abundances have increased with the help of stocking (Hansen et al. 1995, Holey et al. 1995), and the age composition of lake trout populations has expanded to include older individuals (Hansen et al. 1995).

Prior to their spawning runs as adults in the spring, sea lampreys parasitize teleost fish for

a single growing season (Bergstedt and Swink 1995). The majority of sea lamprey growth

occurs in the late summer and fall preceding the adult spawning migrations in the spring, and this

is the period when most potentially lethal attacks on lake trout occur. Host fish that survive such

attacks are left with easily observed marks called wounds. Wounds can be classified based upon

their stage of healing (King and Edsall 1979, King 1980, Ebener et al. 2006). During spring,

observed wounds that are in the earliest stages of healing are attributed to the most recent sea

lamprey feeding season (Eshenroder and Koonce 1984).

Owing to the difficulty in observing parasitic phase sea lamprey, wounds are essentially

the only non-laboratory source of information about sea lamprey-host interactions (i.e., sea

lamprey-induced mortality). Trends in wounding rates have been used by fishery managers to

assess the success of the sea lamprey control program (Adams et al. 2003), and to help estimate

lake trout mortality rates for use in catch-at-age models and for other purposes (Bence et al.

2003, Bence et al. 2011). One approach to analyze wound data involves reporting average

wounding rates for each of several size classes of lake trout (Eshenroder and Koonce 1984).

This method, however, does not take advantage of the predictability of the increasing incidence

of wounds with lake trout length, nor does it account for the biases associated with year-to-year

variability in the size distributions of fish sampled within each length bin. Rutter and Bence

(2003) addressed these concerns by modeling mean sea lamprey wounding rate as a continuous

function of lake trout length using a logistic function (Figure 1.1).
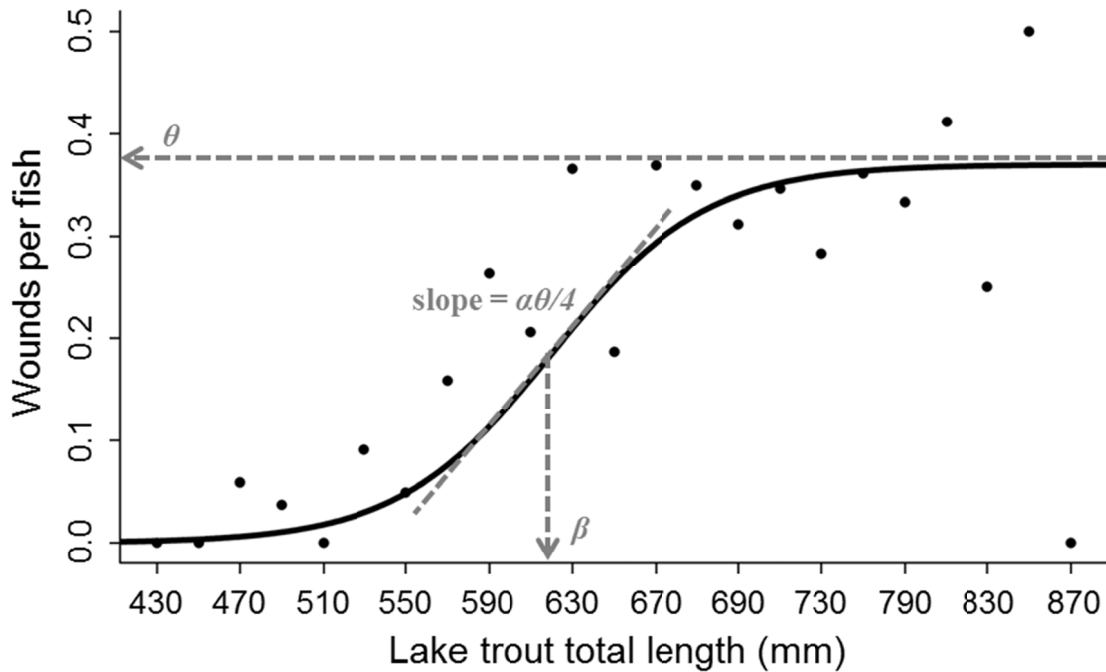
Figure 1.1: An example of the logistic model fit to lake trout wound data from southern Lake Huron (MH3456) in 1985 overlaid with observed data on wounds per fish. Observed wounds per fish were averaged for 20mm length bins for visual clarity, although the model was fit to observed values from individual fish. From eq. 1.1, θ represents the asymptotic wounding rate, β corresponds to lake trout length at the inflection point, and $\alpha\theta/4$ is the slope of the function at the inflection point. The increased variability in the plotted data for larger fish likely resulted from smaller sample sizes for those size classes.

With no changes in host survival or size-selection of hosts by sea lamprey, the mean wounding rate would be expected to change proportionally across all sizes of lake trout in response to changes in sea lamprey and lake trout abundance. With other parameters fixed, such a change can be captured in the asymptotic wounding rate parameter of the logistic function (Bence et al. 2003). Due to annual actions by the sea lamprey control program, natural interannual variation in survival of sea lamprey larvae in streams, and the single parasitic feeding season of each cohort, interannual and spatial variation in the abundance of parasitic-phase sea lamprey is large. The asymptote parameter would be expected to show similar larger interannual

and spatial variation (Bence et al. 2003, Rutter and Bence 2003). Bence et al. (2003) argued that selection for large lake trout over small ones was the primary reason why wounding rates increased with lake trout size before reaching an asymptote, although they acknowledged that differential survival did play some role. Furthermore, foraging theory predicts that when desirable prey is scarce a predator will shift its feeding behavior to incorporate less desirable prey types (Pulliam 1974). Following Bence et al. (2003) and Rutter and Bence (2003), we hypothesize that parasitic sea lamprey may be responding in this way by increasing their relative selection for smaller lake trout when more desirable large lake trout are less abundant. In terms of the logistic relationship relating wounding rate and lake trout size, these changes in selectivity would be reflected in the parameters governing the inflection point (the shaping parameters, Figure 1.1). Such changes might be expected to be gradual, as they would be tracking changes in the size distribution and abundance of the long-lived lake trout host.

Rutter and Bence (2003) fit the logistic wounding model to data from Lake Huron for 1984 to 2000. They considered a range of models that differed in how parameters varied spatially and temporally. Based upon Akaike's Information Criterion (AIC), they selected a model with a different inflection point for each region of Lake Huron that was constant over time, a slope at the inflection point that was the same for each region and also constant across all years, and with asymptotes estimated freely for each year-region combination. They attributed the spatial differences in the inflection point to adaptive changes in host selection. Their failure to find gradual temporal changes was viewed as somewhat puzzling, but possibly due to a lack of contrast in the data.

Given the importance of wounding rates for fishery management, we sought to improve these estimates. More specifically, the purpose of this research was to expand upon the methods

of Rutter and Bence for the following reasons. First, the published application was limited to Lake Huron wounding data. Management agencies, however, have been using variants of the model selected by Rutter and Bence for Lake Huron to estimate sea lamprey mortality within stock-assessment models for other lakes. To our knowledge, a thorough evaluation of alternative models allowing for spatial and temporal variation on these other lakes has not been conducted. We used model comparison to select – from a suite of candidate models – the model that best described sea lamprey wounding data on lake trout separately for each of Lakes Huron, Michigan and Superior. Second, advances in estimation software have made it possible to use random effects models that were not available to Rutter and Bence. Thus our approach is truly a maximum likelihood estimation approach for all models we consider. As a result, our model comparison using AIC is more appropriate than that done by Rutter and Bence. They used a method technically known as "highest posterior density" estimation, which has important drawbacks in comparison to true maximum likelihood estimation. These included the inability to freely and uniquely estimate variance parameters for process errors in the models allowing for temporal variation in the shaping parameters, and inappropriate AIC values that may have acted against selection of such models. These technical issues are further discussed in the Methods section. Third, Rutter and Bence assumed a Poisson distribution for the number of wounds per fish of a given length, but discussed some evidence of overdispersion. We explored the negative binomial distribution in addition to the Poisson distribution to see which distribution provided the best model fit. Lastly, many more data, with much more contrast in lake trout and sea lamprey abundance, were available for our analysis than were analyzed by Rutter and Bence.

METHODS

Wound Data

We included wounding observations for individual lake trout within 1836 Treaty-ceded waters, which span much of the Michigan waters of Lakes Huron, Michigan and Superior. Data were for years 1984 to 2010 for Lakes Huron and Michigan, and 1971 to 2010 for Lake Superior, for fish sampled during April-June primarily from agency surveys using gill nets. The sum of marks observed on individual fish classified as AI, AII and AIII were used as the number of wounds on each fish (King and Edsall 1979). This is also consistent with the current practice of using spring and early summer wounding rates to estimate sea lamprey-induced mortality that occurred in the previous year in lake trout catch-at-age models (Bence et al. 2003). We restricted attention to treaty waters of these lakes because (a) data were readily available due to their ongoing use in lake trout assessments, and (b) sampling focused on lake trout is done during spring and early summer in all these lakes, allowing for a more consistent interpretation of marks left by sea lamprey on lake trout.

Recent methods of estimating sea lamprey-induced mortality in the upper Great Lakes have pooled data into larger spatial regions, and this practice was used in our analysis. These pooled areas represent combinations of either lake trout management units for Lake Superior (Hansen 1996) or statistical districts for Lakes Michigan and Huron (Smith et al. 1961). Lake Huron data were pooled into three regions (MH1, MH2, and MH3456), Lake Michigan data into four regions (MM123, MM4, MM5, MM678), and Lake Superior data into two regions (MI45 and MI67) (Figure 1.2). Where these areas overlap with 1836 Treaty-ceded waters (all but MH3456), they correspond to the same areas used to summarize sea lamprey marking for treaty

water lake trout assessments. The MH3456 region matches the area used to summarize marking

for an ongoing lake trout assessment in the southern part of Lake Huron (e.g., Sitar et al. 1999).

Figure 1.2: Lakes Huron, Michigan and Superior with the regions used in this study specified.
Region names and boundaries correspond to combinations of lake trout management units
defined for Lake Superior (Hansen 1996) or statistical districts (Smith et al. 1961) for the
other lakes. For example, MM123 is the combined areas of the statistical districts MM1,
MM2, and MM3. The shaded region is the state of Michigan.

Model Development

In general, sea lamprey wounding rates increase gradually as a function of lake trout

length, eventually approaching an asymptote. Taking advantage of this observation, we followed

Rutter and Bence (2003) and used the logistic function to describe how expected number of wounds ($\overline{w}$) increased with lake trout length (*l*):

$$\overline{w}(l) = \frac{\theta}{\left(1 + \exp\left(-\alpha\left(1 - \beta\right)\right)\right)} \qquad (1.1)$$

where θ describes the asymptotic wounding rate, β corresponds to the length of lake trout at the inflection point, and $\alpha\theta/4$ is the slope at the inflection point (Figure 1.1). In all cases, models were fit separately for each of the Great Lakes, with regional differences within lakes accounted for by model parameters. The asymptote parameter, θ, varied over years and regions with a fixed-effect parameter estimated freely for each year and region combination for all models. We considered a range of models that varied in the extent to which the shaping parameters (α and β) of the logistic function varied spatially and temporally (Table 1.1). When the shaping parameters varied over time, the year effects were modeled as random walks. Details regarding random walks are described in the subsection "Models for spatial and temporal effects for shaping parameters", but in short, a random walk allows for gradual change over time by modeling interannual changes as process errors. When the shaping parameters varied spatially and over years, we considered models where the process errors either had different variances in different regions, or used a common ("lakewide") variance. The different approaches used for the asymptote and shaping parameters reflect the different ways for which these parameters are expected to vary, as described in the Introduction.

Lastly, we fit all candidate models (Table 1.1) assuming either the Poisson distribution, as used by Rutter and Bence (2003), or a negative binomial distribution for the expected number of wounds per fish of a given length. The negative binomial distribution allows the variance to

Table 1.1: Description of the α and β parameters for the candidate set of models used in estimating sea lamprey wounding rates on lake trout. Random walk is abbreviated as "r. w."

Model	α	β
A	Constant across regions and years	Constant across regions and years
B	Constant across regions and years	Region-effects, constant across years
C	Constant across regions and years	One r. w. across years for all regions
D	Constant across regions and years	Region-specific r. w.'s across years
E	Constant across regions and years	Region-specific r. w.'s across years (lakewide σ)
F	Region-effects, constant across years	Constant across regions and years
G	Region-effects, constant across years	Region-effects, constant across years
H	Region-effects, constant across years	One r. w. across years for all regions
I	Region-effects, constant across years	Region-specific r. w.'s across years
J	Region-effects, constant across years	Region-specific r. w.'s across years (lakewide σ)
K	One r. w. across years for all regions	Constant across regions and years
L	One r. w. across years for all regions	Region-effects, constant across years
M	One r. w. across years for all regions	One r. w. across years for all regions
N	One r. w. across years for all regions	Region-specific r. w.'s across years
O	One r. w. across years for all regions	Region-specific r. w.'s across years (lakewide σ)
P	Region-specific r. w.'s across years	Constant across regions and years
Q	Region-specific r. w.'s across years	Region-effects, constant across years
R	Region-specific r. w.'s across years	One r. w. across years for all regions
S	Region-specific r. w.'s across years	Region-specific r. w.'s across years
T	Region-specific r. w.'s across years	Region-specific r. w.'s across years (lakewide σ)
U	Region-specific r. w.'s across years (lakewide σ)	Constant across regions and years
V	Region-specific r. w.'s across years (lakewide σ)	Region-effects, constant across years
W	Region-specific r. w.'s across years (lakewide σ)	One r. w. across years for all regions
X	Region-specific r. w.'s across years (lakewide σ)	Region-specific r. w.'s across years
Y	Region-specific r. w.'s across years (lakewide σ)	Region-specific r. w.'s across years (lakewide σ)

increase as a function of the mean expected wounding rate by incorporating an additional scaling parameter according to *variance=m+m^2/s*, where *m* is the mean of the distribution and *s* is the parameter that scales the variance-mean relationship. Large values of *s* resemble a case where the mean is equal to the variance, and in such situations the Poisson distribution will be favored because it has one less parameter.

Models for spatial and temporal effects for shaping parameters

As indicated above, we used random walks to model interannual changes in the shaping parameters. A random walk allows for sharing of information over time and has a tendency toward gradual changes, without specifying an underlying mechanism. We used the Gaussian form of a random walk:

$$\gamma_t = \gamma_{t-1} + \varepsilon_t; \qquad \varepsilon_t \sim N\left(0, \sigma^2\right) \qquad\qquad (1.2)$$

For our applications, γ_t represents either $\log_e(\alpha)$ or $\log_e(\beta)$, which was either the value for the entire lake ("one random walk across years for all regions") or for a single region ("region-specific random walks across years"). Eq. 1.2 can be rewritten as:

$$\gamma_t = \gamma + \sum_{i=1}^{i=t} \varepsilon_i; \qquad \varepsilon_t \sim N\left(0, \sigma^2\right) \qquad\qquad (1.3)$$

which allows us to consider models with random walks as extensions of models without them. Thus the models we considered for $\log_e(\alpha)$ and $\log_e(\beta)$ were:

$$\gamma_{r,t} = g \qquad\qquad (1.4)$$

$$\gamma_{r,t} = g_r \qquad\qquad (1.5)$$

$$\gamma_{r,t} = g + \sum_{i=1}^{i=t} \varepsilon_i; \qquad \varepsilon_i \sim N\left(0, \sigma^2\right) \qquad\qquad (1.6)$$

$$\gamma_{r,t} = g_r + \sum_{i=1}^{i=t} \varepsilon_{r,i}; \qquad \varepsilon_i \sim N\left(0, \sigma_r^2\right) \text{ or } \varepsilon_i \sim N\left(0, \sigma^2\right) \qquad (1.7)$$

where *r* and *t* describe region and year of estimation, respectively. In the context of the text

descriptions of Table 1.1, eq. 1.4 corresponds to "constant across regions and years," eq. 1.5 to

"region-effects, constant across years", eq. 1.6 to "one random walk across years for all regions"

and eq. 1.7 to "region-specific random walks across years". When both spatial and temporal

variation were allowed (eq. 1.7), the variances for the process errors either varied uniquely

among regions, (i.e., σ_r^2), or were the same for all regions ("lakewide σ").

Approach to estimation

We used the random effects module of AD Model Builder (ADMB) to estimate

parameters by maximum likelihood (Fournier et al. 2012). We then used Akaike's Information

Criterion (AIC) for model comparison to choose the best model for each lake. It is important to

discern fixed effects from random effects, as fixed effects are treated as parameters in AIC

calculations. From the frequentist perspective we used for estimation, the fixed-effect

parameters were the θs, the *g*s of eqs. 1.4-1.7, and the σs for any process errors influencing the

αs and βs. In contrast, the εs should be viewed as random effects and not parameters. The

general form of the log-likelihood that is maximized is:

$$\text{LogL} = \int_{\delta} f(X|\varphi,\delta)p(\delta)d\delta \qquad\qquad (1.8)$$

where X represents the data, $f()$ is the probability density (or mass) function for the data given

the vector of parameters (φ), and the vector of random effects (δ), and $p()$ is the assumed

probability density (or mass) function for the vector of random effects. The form of $f()$ depended

on whether a Poisson or negative binomial distribution was assumed. As shown in eq. 1.8,

during estimation the random effects were integrated out of the likelihood. In essence, the

overall likelihood that was maximized was a weighted sum (or more accurately, integral) of the

likelihood conditional on values for the random effects over all possible values of the random

effects, with weights being the probability density for a given vector of random effects. ADMB integrates out random effects using the Laplace approximation. Predictions of random effects (loosely termed estimates) were those that maximized the term inside the integral of eq. 1.8, with parameters fixed at their maximum likelihood estimates.

For purely technical reasons, we specify the γs rather than the process error term as the effect that is integrated out (i.e., in eq. 1.8, δ would be the vector of γs). We did this because the conditional likelihood of data (i.e., $f(X|\varphi,\delta)$), considered a year at a time, depends only on the γ for that year. The full likelihood (eq. 1.8) also involves the probability density for δ. Although we have not directly expressed a density for the vector of γs, this can be determined from the assumed normal distribution for ε (eq. 1.2), and the fact that each ε can be expressed as a function of just two of the γs:

$$\varepsilon_t = \gamma_t - \gamma_{t-1} \qquad\qquad\qquad\qquad (1.9)$$

This approach is computationally much less expensive and numerically more robust than directly integrating out the εs (Fournier et al. 2012).

The likelihood function (eq. 1.8) was said to be maximized when absolute values for gradients of less than 1.0E-4 for all parameters were achieved and the variance-covariance matrix was calculable. The model was thus said to have converged upon the best parameter estimates. Convergence was not achieved if during the model fitting process either of these conditions were not satisfied.

The approach used by Rutter and Bence (2003) differed from the true maximum likelihood approach described above. They found the combination of what we call parameters and random effects that maximized the term inside the integral of eq. 1.8. From a Bayesian perspective, that term is proportional to the posterior density for the vector $\{\varphi,\delta\}$, hence these

estimates are sometimes called highest posterior density estimates (HPD, Schnute 1994) – they are also referred to as maximum penalized likelihood estimates. Rutter and Bence were not able to uniquely estimate the process error variances with HPD, a weakness that our analysis was able to overcome. Rutter and Bence obtained estimates for the σs, but only by carefully choosing starting values so that the estimates did not move toward zero or infinity. A second issue is that in comparing models that have a different number of random effects with AIC, using HPD as though it is likelihood may not be valid, and it is unclear what the number of parameters should be. Rutter and Bence treated each process error (i.e., the εs from our analysis) as a parameter. This overstated model complexity because these were not freely estimated parameters, and thus their analysis may have been biased against selecting for time-varying models. In contrast, we treated only process error variances and starting values of each random walk as parameters, and integrated out the εs.

RESULTS

Model Selection

Results from AIC comparison showed that all negative binomial distribution models fit much better (typically hundreds of AIC units lower) than their respective Poisson distribution models for all 25 models differing in fixed effects parameters (Table 1.1). All further results will be presented from models fit using a negative binomial distribution.

AIC comparison shows that models that allowed for temporal and spatial variation in the shaping parameters resulted in the best fit (Table 1.2). All models that did not allow for such variation were greater than 40 AIC units worse than the best fitting model for each lake. The choice among models that either did or did not use a lakewide variance for the shaping

Table 1.2: Akaike's Information Criterion (AIC) comparison for wounding models using the negative binomial distribution for wounding rate on lake trout of a given length. Δ AIC values are relative to the best fitting model for each lake, respectively. Model Y produced the best fit to the Lake Huron data and model X produced the best fit to both the Lake Michigan and Lake Superior data. Models A-M for each lake had much greater Δ AIC values and their results are not shown. Convergence was not achieved for models N, S and T for Lake Michigan.

Model	Δ AIC		
	Lake Huron	Lake Michigan	Lake Superior
N	-127.6	NA	-161.0
O	-127.0	-202.2	-160.2
P	-94.6	-76.9	-187.5
Q	-72.8	-56.5	-183.7
R	-44.4	-47.2	-98.0
S	-4.6	NA	-1.6
T	-3.2	NA	-3.2
U	-93.4	-73.1	-185.7
V	-71.2	-52.2	-181.7
W	-40.4	-44.3	-96.2
X	-2.4	**0.0**	**0.0**
Y	**0.0**	-6.1	-1.0

parameters across regions varied between lakes. Near-zero Δ AIC values suggest that more than one model is plausible for Lakes Huron and Superior. Convergence was not achieved for models N, S, and T for Lake Michigan wound data. However, for both Lakes Huron and Superior, models N, S, and T finished no better than third overall. Thus, we suspect that neither models N, S, nor T would not have been the best model for Lake Michigan data, and that convergence was achieved for the best fitting model for Lake Michigan. We present estimated wounding rates and parameter estimates for only the models with the lowest AIC values for each respective lake, except when making explicit comparison with the status quo model of Rutter and Bence (2003). Even though several alternative models were plausible, we present only a single set of wounding rate estimates, rather than adopting a model averaging approach, because plausible alternative models made very similar predictions of these estimated quantities.

Patterns in Estimated Wounding Rates

Differences in sea lamprey wounding between lakes and regions were examined by comparing estimated wounding rates from selected models for 500mm and 650mm lake trout across all years. Both of these sizes were generally well-represented in the data, with the major exception of MH1 prior to 1991 when lake trout rarely exceeded 650mm. Temporal trends in wounding rates varied greatly, with differences between lakes being much greater than differences between regions within the same lake. In addition, wounding rates on 650mm lake trout were generally much higher than on 500mm lake trout (Figure 1.3).

Wounding rates were high and variable in Lake Huron from 1984-1998 with wounding rates approaching 0.80 wounds per 650mm fish estimated for MH2 in 1985 and 1995. Wounding rates in all regions of Lake Huron began to decline in the mid to late 1990s and have reached generally low and much less variable levels.

Wounding rates on 500 and 650mm lake trout in Lake Michigan were generally low for much of the entire time series in all regions, with the exception of northern Lake Michigan (MM123), where sea lamprey wounding began increasing for both sizes beginning in 2001. Wounding rates on 650mm lake trout in northern Lake Michigan have since leveled off at around 0.35 for the past eight years, and are much higher than recent wounding rates in any of the other regions of Lake Michigan or Lake Huron. Estimates for Lake Superior have been much more temporally variable, especially at 650mm. Yearly wounding rates were generally between 0.05 and 0.35 in MI45 and MI67 for much of the time series for 650mm lake trout, but show a slightly increasing trend in both regions since 1994. Wounding rates on 500mm lake trout have been very low since the mid-1990s in both MI45 and MI67.
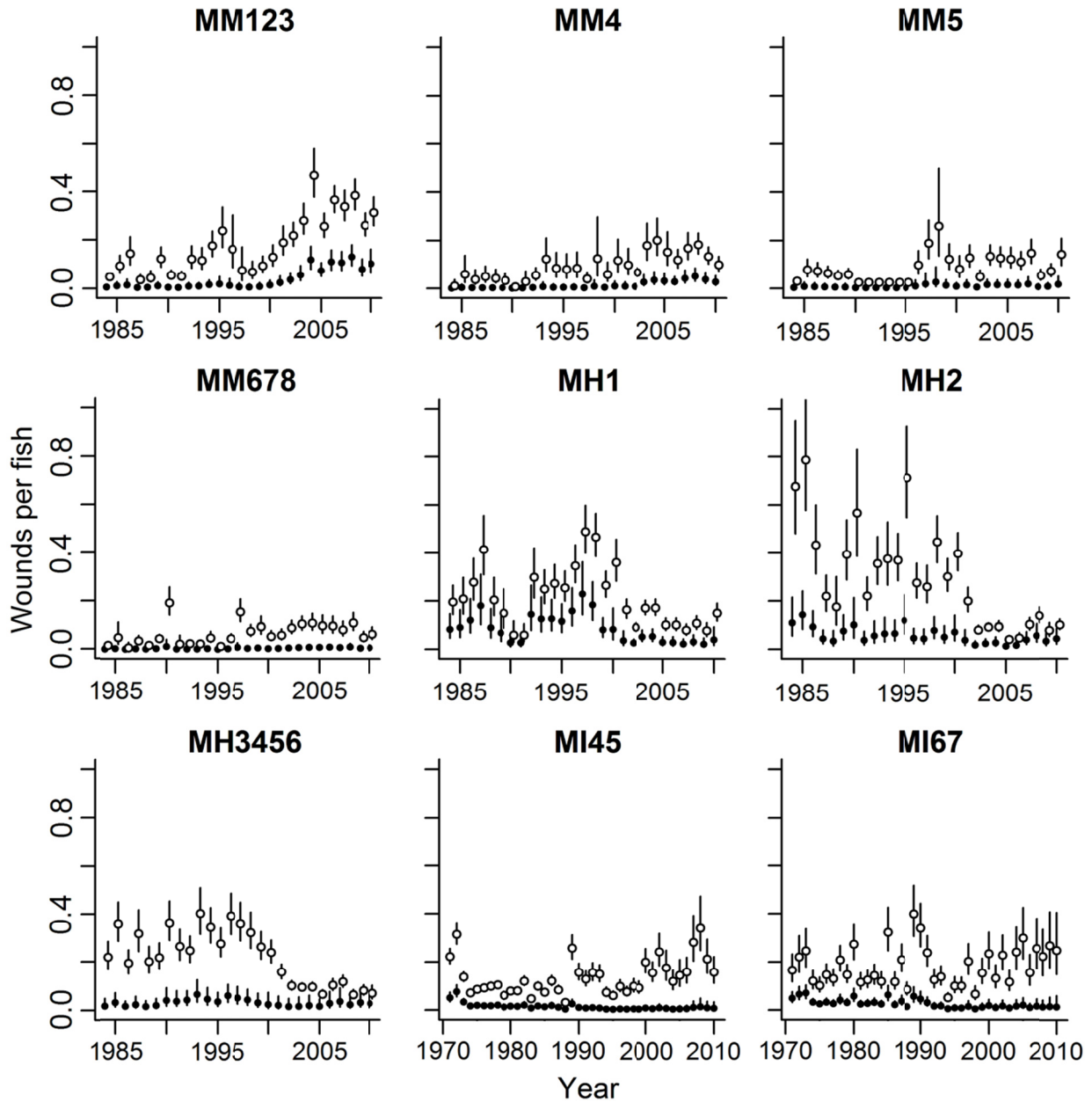
Figure 1.3: Wounding rate estimates for 500mm (solid circles) and 650mm (open circles) lake trout from each region analyzed in this study. Estimates correspond to model Y for Lake Huron and model X for Lakes Michigan and Superior (Table 1.1). Region abbreviations correspond to those described in Figure 1.2. Wounding rates were estimated on a $\log_e$ scale and values shown represent back-transformed estimates with error bars corresponding to estimates plus or minus one asymptotic standard error.

Trends in Parameter Estimates

Overall, temporal variation in β generally had more influence on the shape of the logistic function than did temporal variations in α over the observed range of estimated values for these parameters. Changes in β are also more interpretable in the context of our hypothesis in that the position of the inflection point is predicted to shift toward smaller lake trout lengths when preferred large lake trout become scarce. Nonetheless, allowing for temporal variation in α led to substantial decreases in AIC (Table 1.2). Such large improvements in AIC associated with temporal variation in α are likely in part due to small improvements in model fit added up across very large amounts of data: 36,018 observations for Lake Huron, 37,123 for Lake Michigan, and 148,833 for Lake Superior. For these reasons we do not provide a figure with estimates of α.

Estimates of the length of lake trout at the inflection point, β, showed great variation between lakes, and also between regions within the same lake (Figure 1.4). Estimates of β were greatest in regions MM4, MM5 and MM678 of Lake Michigan, with values generally greater than 650mm until the late 1990s. In Lake Huron, distinct decreases in β of nearly 100mm occurred in both MH2 and MH3456 over the time series. Decreasing trends were also seen in MM123, MM4 and MM678 in Lake Michigan, with β decreasing nearly 150mm from 1992 to 2010 in MM4. Smaller decreases of about 50mm were seen in MM123 and MM678. Temporal trends in Lake Superior were less distinct, as β remained constant near 640mm in MI45 and gradually increased from 580mm to 640mm from 1971 to 2010 in MI67. Interestingly, although models allowing temporal variation in β were selected, variance estimates for the random walks for MM5 and MI45 were near-zero.

The asymptotic wounding rate parameter, θ, also varied greatly between the lakes (Figure 1.5). For Lakes Huron and Superior, trends in θ mimic those seen in estimated wounding rates

on 650mm lake trout (Figure 1.3). In Lake Michigan, where β estimates tended to be much higher than the other lakes for much of the time series, the relationship between 650mm
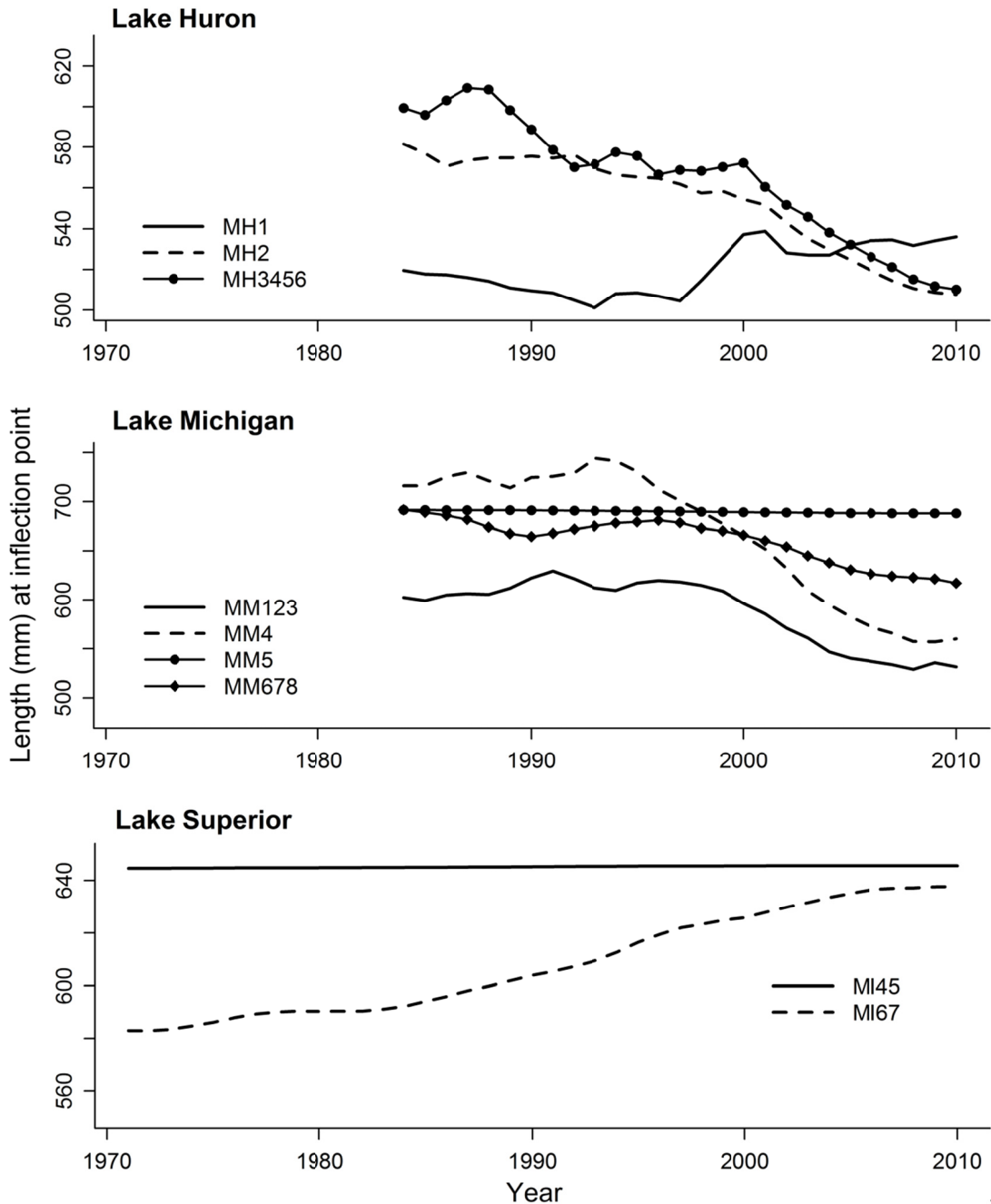
Figure 1.4: Lake trout length at which 50% of the asymptotic wounding rate was reached (β, eq. 1.1) for models selected for each lake in this analysis. β estimates correspond to model Y for Lake Huron and model X for Lakes Michigan and Superior (Table 1.1).
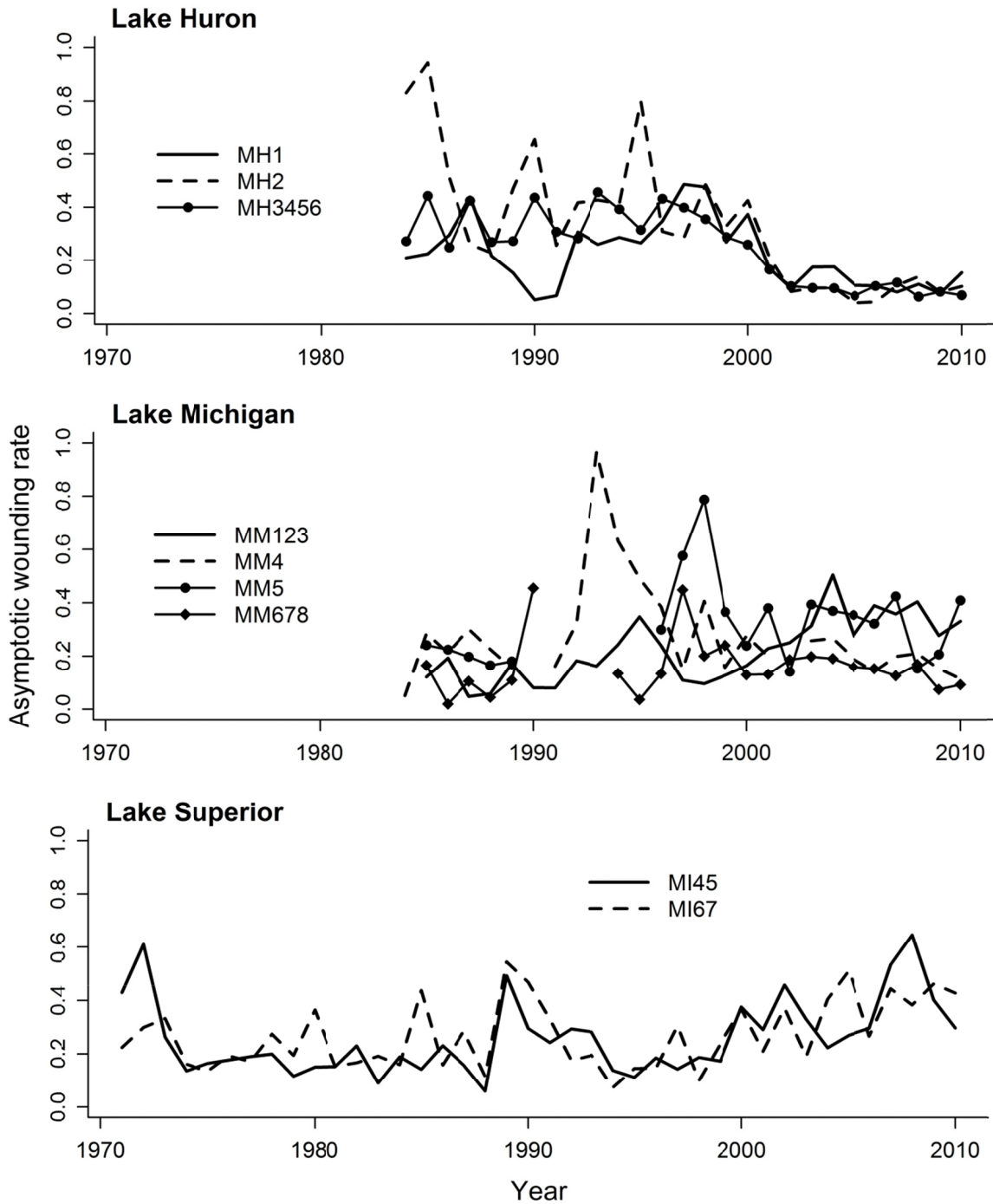
Figure 1.5: Asymptotic wounding rate (θ, eq. 1.1) parameter estimates of models selected for each lake in this analysis. θ estimates correspond to model Y for Lake Huron and model X for Lakes Michigan and Superior (Table 1.1). Asymptotic wounding rate parameters were not estimated for some unit-year combinations for Lake Michigan due to low sample size.

wounding rates and asymptotic wounding rates is not as tight. Due to high estimates for β in Lake Michigan, especially earlier in the time series for MM4, asymptotic wounding rates were unlikely to be realized. An extreme example is seen in 1993 where the asymptotic wounding rate in MM4 spiked to 0.97 wounds per fish, while the wounding rate on 780mm lake trout (corresponding to the ninety-fifth percentile of lake trout lengths for fish sampled in MM4 in 1993) was only 0.65 wounds per fish. Thus, in Lake Michigan, the asymptote is often extrapolated beyond the range of the data (i.e., represents wounding rates on lake trout larger than those actually sampled).

DISCUSSION

Generally, wounding rates are governed by two things, the first of which is the ratio of sea lamprey abundance to host abundance. Assuming an asymptotic functional response relating sea lamprey attack rates to host density, increases in host abundance in the asymptotic range would produce an overall decrease in wounding rates because the same number of attacks would be distributed among more hosts. Additionally, with host abundance held constant, overall marking rates would be expected to scale in direct proportion to the abundance of sea lamprey. In Lakes Michigan and Superior, general directional trends in wounding rates on lake trout (Figure 1.3) appear to be closely linked to trends in lakewide estimates of spawning phase sea lamprey abundance (Sullivan and Adair 2010). In Lake Huron, drastic decreases in wounding rates in the regions examined herein coincide with a gradual decrease in spawning phase sea lamprey abundance estimates, however, McLeod et al. (2011) found that overall wound probability increased 12.1% in Canadian waters of Lake Huron from 2000 to 2009. This suggests that wounding rates may be more influenced by the observed increases in lake trout

abundance and age-class expansion observed in Michigan waters of Lake Huron (Caroffino and

Lenart 2011).
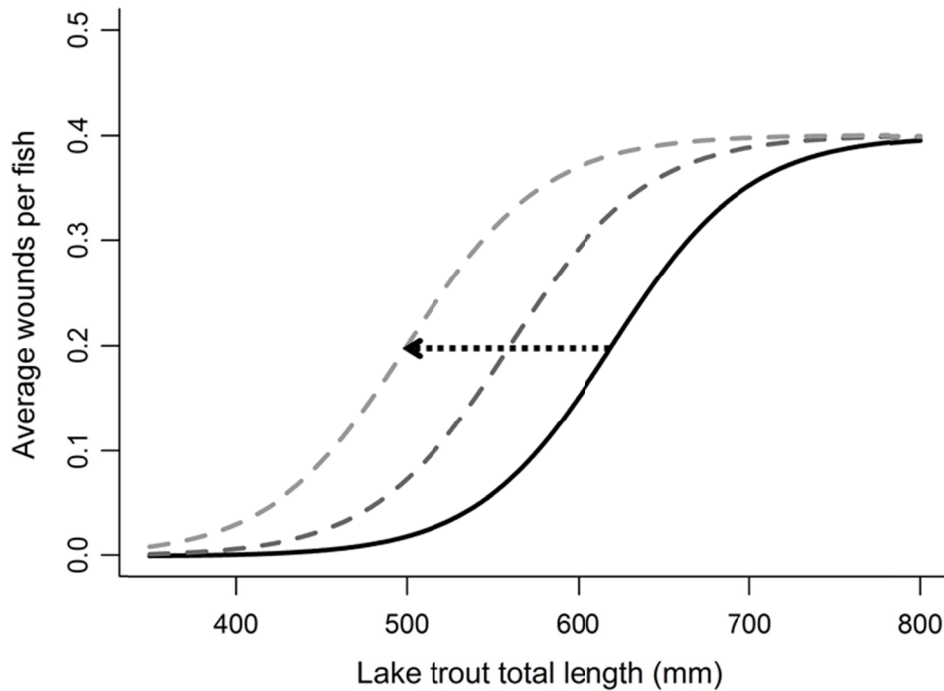
Figure 1.6: A visual example of how a change in the selectivity of sea lamprey for smaller lake
trout could result in a shift of the logistic function describing wounding rates versus lake
trout length. The shift from the solid curve to the dashed curves is the type of shift
hypothesized to occur in response to a decrease in the abundance of larger lake trout.

Second, wounding rates are affected by the size-selectivity of sea lamprey. We

hypothesized that sea lamprey select for smaller lake trout when larger, more desirable, lake trout

are scarcer. Changes in size-selection at varying prey abundances have been shown for other

fish species (e.g., Werner and Hall 1974) but to our knowledge such relationships have not been

shown for parasitic fish such as sea lamprey. A possible indicator of changes in size-selection of

sea lamprey could be major shifts in the position of the inflection point of the logistic function

relating sea lamprey wounding rate to lake trout size (Figure 1.6). If estimates of β and

abundance of large lake trout were positively correlated over the same time span, this would be consistent with optimal foraging theory.

Our results do not seem to support our initial hypothesis. The three largest shifts in β occurred in central and southern Lake Huron (MH2 and MH3456) and in Grand Traverse Bay (MM4). In all three regions β decreased, suggesting the possibility of a shift in selectivity toward smaller lake trout. However, there is much evidence suggesting the increase in abundance of large lake trout hosts in Lake Huron. For example, in the case of MH2, estimates of spawning stock biomass increased from near-zero levels in the early 1990's to levels more recently exceeding 200,000 pounds annually (2000-2008). Nevertheless, the size-selectivity of sea lamprey shifted to include smaller lake trout even though the abundance of large lake trout increased.

Further complicating the relationship between sea lamprey size-selectivity and large lake trout abundance are the dynamic abundances of alternative hosts. Although evidence does suggest that lake trout are the preferred host species of sea lamprey in the Great Lakes, as evidenced by higher proportions of attacks on lake trout relative to their proportion in survey catches compared other species (Harvey et al. 2008), population dynamics of alternative hosts likely have an impact on overall wounding rates across all species, thus impacting lake trout wounding rates.

In general, further research relating the temporal trends in the abundance of certain size classes of lake trout to sea lamprey size selection is needed. No analyses have been published that have documented changes in abundance of certain sizes of lake trout, per se. However, catch-per-effort (CPE) and biological data exist for these regions in support of lake trout assessments conducted regularly for 1836 Treaty-ceded waters. In a future manuscript we will

explore the nature of changes in size selection by sea lamprey and the connection between size selection and abundance of lake trout of certain sizes.

A possible explanation for the observance of overdispersion in each lake, as implied by the negative binomial models producing the best fits, is a difference in habitat use by lake trout and sea lamprey across lake trout sampling sites. If sea lamprey habitat and lake trout habitat differentially overlap among sampling sites then it is conceivable that lake trout sampled where they more frequently overlap with sea lamprey may exhibit a greater number of wounds than would be expected across all sampling sites. Another possible explanation for overdispersion may arise from differences in wounding between strains of stocked lake trout. It has long been observed that Seneca Lake origin strain lake trout generally have lower incidence of wounding than both wild and Great Lakes origin strains stocked in the Great Lakes (Schneider et al. 1996), and for this reason they have been stocked in increasing numbers in Lakes Huron and Michigan (Ebener 1998). However, the spatial distribution of parasitic phase sea lamprey in the Great Lakes remains unknown. Relating wounding rates to sampling sites and lake trout strain was beyond the scope of this study, but warrants further investigation.

On another technical note, one might envision that a constant shape would correspond to models with constant shape parameters. This is not the case with our parameterization in which the slope at the inflection point depends upon both α and β. The asymptote varied, thus to maintain a constant shape α would also have to vary. Attempts to implement an alternative parameterization such that the slope itself was modeled as a parameter, rather than as a function of α and β, were met with failures to achieve convergence for models L and more complex. However, for the less complex models (i.e., A through M), AIC values were improved with slope modeled as an explicit parameter.

Improved Wounding Rate Estimates

A main objective of this research was to improve sea lamprey wounding rate estimates. One use of these is in lake trout population assessments. Thus, it is of interest to examine the differences in sea lamprey wounding rates between wounding rate models currently used to provide estimates for lake trout assessment with those selected in the analysis. Currently, fishery managers use variants of the model selected by Rutter and Bence (2003), to estimate size-
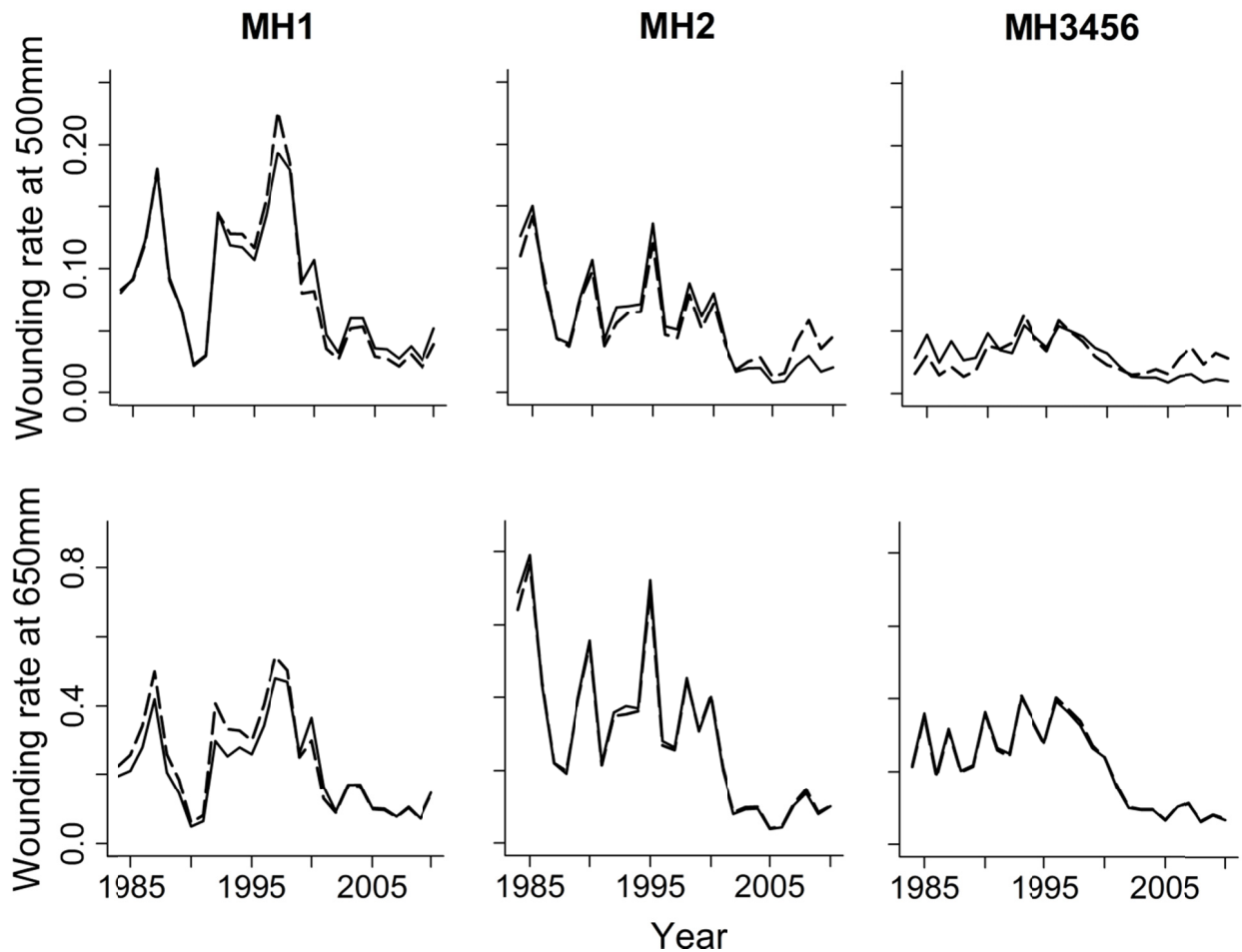
Figure 1.7: Wounding rate estimates for 500mm and 650mm fit to Lake Huron wound data. Region abbreviations correspond to those described in Figure 1.2. Estimates corresponding to the model selected by Rutter and Bence (2003) are given by the solid line and estimates corresponding to model Y (Table 1.1) are given by the dashed line.

specific sea lamprey wounding rates for each of the lakes. Their selection did not allow for

temporal variation in either of the shaping parameters, and only allowed spatial variation in the

position of the inflection point. This corresponds to model B (Table 1.1) of this analysis with a

Poisson distribution assumed for the number of wounds per fish of a given length, and is further

referred to as the Rutter model. To examine how the improvement in model fit affected model

predictions, wounding rate estimates were compared between the Rutter model and model Y

(Table 1.1), the model selected for Lake Huron in this analysis. We limited the examination of

differences to Lake Huron because it was wounding data from this lake to which the Rutter

model was originally fit.

Wounding rate estimates for 500mm and 650mm lake trout follow similar trends between

the Rutter model and model Y, but some key differences are apparent (Figure 1.7). Generally,

differences in estimated wounding rates between the two models on large (represented by

650mm) lake trout were minimal. However, in years 1992 to 1997, estimates for wounding rates

on 650mm lake trout were noticeably higher for the Rutter model. Although wounding rate

estimates for 500mm lake trout were generally low, they sometimes showed substantial percent

differences between the two models (MH2 and MH3456, 2006-2010).

Concluding Remarks

As the time series of wound data for each lake continue to grow, models that account for

temporal variation should become increasingly favored over models that do not. Factors that

affect the relationship between sea lamprey wounding rates and lake trout length have been

shown to change dramatically over time. Thus, allowing parameters to vary over time as random

walks permits sharing of information over time, with data from the years nearest the year of

estimation to have the most influence on estimated wounding for that year, reducing the influence of historic trends on the estimates for a specific year. However, a drawback to this approach is increasing difficulty in achieving model convergence with the addition of successive years of data. We suggest further research be conducted to determine a model that incorporates flexibility in parameter estimates over time, while simplifying the models such that convergence is more easily achieved.

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CHAPTER 2

SEA LAMPREY SIZE SELECTION OF LAKE TROUT IN A FORAGING THEORY
CONTEXT

Abstract: The observed number of marks per fish (wounding rate) on host fish that survive sea

lamprey (*Petromyzon marinus*) attacks has generally been higher on larger hosts in the Great

Lakes. A widely held belief is that this pattern largely reflects that sea lampreys are size-

selective and prefer to attack larger hosts. However, it remains unclear how a sea lamprey

discerns host size and makes subsequent choices to either attack or not attack a host. It has been

suggested, according to foraging theory, that sea lamprey may shift their feeding behavior to

include smaller, less desirable prey when larger, more desirable prey are less available. The

analyses of Chapter 1 revealed large differences in sea lamprey size-selectivity across lake trout

(*Salvelinus namaycush*) management units, as well as shifts in size-selectivity over time. The

purpose of this chapter is to examine how length distributions of sea lamprey wounding on lake

trout relate to annual abundance estimates of large lake trout. This was done by (1) relating the

shaping parameter estimates from Chapter 1 to large lake trout abundance estimates, and (2) by

refitting the wounding rate models from Chapter 1 to obtain new shaping parameter estimates,

where certain parameters of the logistic function relating sea lamprey predation to lake trout

length were assumed to be a function of the annual large lake trout abundance estimates. My

analyses suggest that large lake trout abundance, by itself, is not a strong predictor of spatial

differences and temporal trends of sea lamprey size-selectivity.

INTRODUCTION

Sea lamprey (*Petromyzon marinus*) attacks on host fish leave easily observable wounds on surviving fish, providing fishery managers with an important source of information useful in assessing the sea lamprey control program (Adams et al. 2003), and for estimating host mortality rates for use in population assessment models (Bence et al. 2003). In the Great Lakes, wounding rates on host fish that survive attacks have generally been higher on larger hosts (Berst and Wainio 1967, Pycha and King 1975). A series of lab studies of single sea lamprey attacks on hosts of alternative sizes have supported observations of sea lamprey size selection for larger hosts, as summarized by Swink (2003). That sea lamprey are size-selective is now a widely held belief, supported more recently by studies using field samples of marked lake trout from the Great Lakes.

Schneider et al. (1996) collected dead lake trout (*Salvelinus namaycush*) using bottom trawls in Lake Ontario and found that the vast majority of lake trout recovered bore sea lamprey wounds, and that 81% of AI marks (those in the most recent stage of healing and indicative of sea lamprey-induced mortality; King and Edsall 1979) observed on dead lake trout were on fish >600mm total length. In concurrent gillnet samples they found that length distributions of live, sea lamprey-marked lake trout did not differ significantly from length distributions of collected dead lake trout. Their results indicate plainly that sea lamprey preferentially attack larger lake trout hosts, and that previous observations of higher wounding rates on larger fish that survived attacks were not just the result of differential survivability between lake trout of different sizes.

Sitar (1996) used wounds observed on lake trout from spring gillnet surveys from 1984-1994 to estimate annual wounding rates for four large size bins for the Michigan waters of Lake Huron. He used the sum of AI, AII and AIII wounds as these are assumed to have come from

potentially lethal attacks from the previous fall lamprey feeding season. He found that in central

and southern Lake Huron, wounding rates increased significantly with length class of lake trout.

This works was expanded upon by Rutter and Bence (2003) who modeled mean Lake Huron sea

lamprey wounding rates as a continuous, logistic-shaped function of lake trout length (see Figure

1.1), taking advantage of the predictable way in which sea lamprey marking rates tend to

increase with host size. Based upon the model chosen in their model selection analysis, they

observed large interannual variability in the wounding rates observed on large lake trout between

northern, central and southern Lake Huron. They also found an increase in the length at which

50% of the asymptotic wounding rate (the wounding rate on large lake trout) was reached

moving from northern to southern Lake Huron (529mm in northern, 576mm in central, 596mm

in southern). They hypothesized that in northern Lake Huron, where large lake trout were at low

abundance during their years of analysis, sea lampreys may have been directing more attacks

towards smaller fish as a behavioral response. Such a hypothesis is consistent with foraging

theory (Pulliam 1976) which describes that a predator will shift its feeding behavior to include

smaller prey when larger prey become scarce.

In Chapter 1, the methods of Rutter and Bence (2003) were expanded upon to create

unique wounding rates models for Lakes Huron, Michigan and Superior, respectively. Models

that allowed for spatial and temporal variability in the shaping parameters – those governing the

position and slope of the inflection point of the logistic wounding rate function – were selected

as the best models for each lake based on model comparison. The position of the inflection point

showed great variation between lakes, and also between regions within the same lake. This

parameter is related to the size-selectivity of sea lamprey as it determines the size range over

which sea lamprey predation on lake trout occurs. If estimates of this parameter were positively

correlated with estimates of large lake trout abundances over time this would support the hypothesis that sea lamprey shift their feeding behavior according to foraging theory (Rutter and Bence 2003, Bence et al. 2003).

Although in Chapter 1 I discussed the density of large lake trout as one potential explanation for spatial and temporal variation in sea lamprey size-selectivity, no analyses were done that explicitly documented changes size-specific abundance or density of lake trout in the region and time-period wounding patterns were examined. Here, I use long time series of lake trout abundance estimates to examine the extent to which the annual abundances of large, desirable lake trout have changed, and how such changes may be related to the observed spatial and temporal differences in sea lamprey size-selectivity of lake trout. First, I compare trends in large lake trout abundance over time with the time-varying β parameter estimates from Chapter 1 to look for patterns consistent with foraging theory. Second, I develop wounding rate models for each region that allow β to vary as a function of large lake trout abundance and examine if this parameterization supports a foraging theory-type explanation of the observed temporal changes sea lamprey size-selectivity.

METHODS

Large Lake Trout Abundance Data

Lake trout assessments are regularly conducted for 1836 Treaty-ceded waters (Caroffino and Lenart 2011). The assessments produce yearly age-specific estimates of lake trout abundance. I used the most recent abundance estimates from stock assessment model runs for each of the following regions: MH1 and MH2 in Lake Huron, MM123, MM4, and MM5 in Lake Michigan, and MI5, MI6, and MI7 in Lake Superior (Figure 2.1). These provided estimates of

abundance for 1984-2010 for Lake Michigan. For Lake Superior, estimates started in 1975 (MI5 and MI7) or 1978 (MI6) and ended in 2008 (MI7) or 2010 (MI5 and MI6). In Lake Huron, assessment estimates started in different years depending on area, but were available for both areas starting in 1984 and ending in 2008 (MH2) or 2010 (MH1). These were used in conjunction with estimates of mean lake trout length-at-age to derive annual abundances of large lake trout.
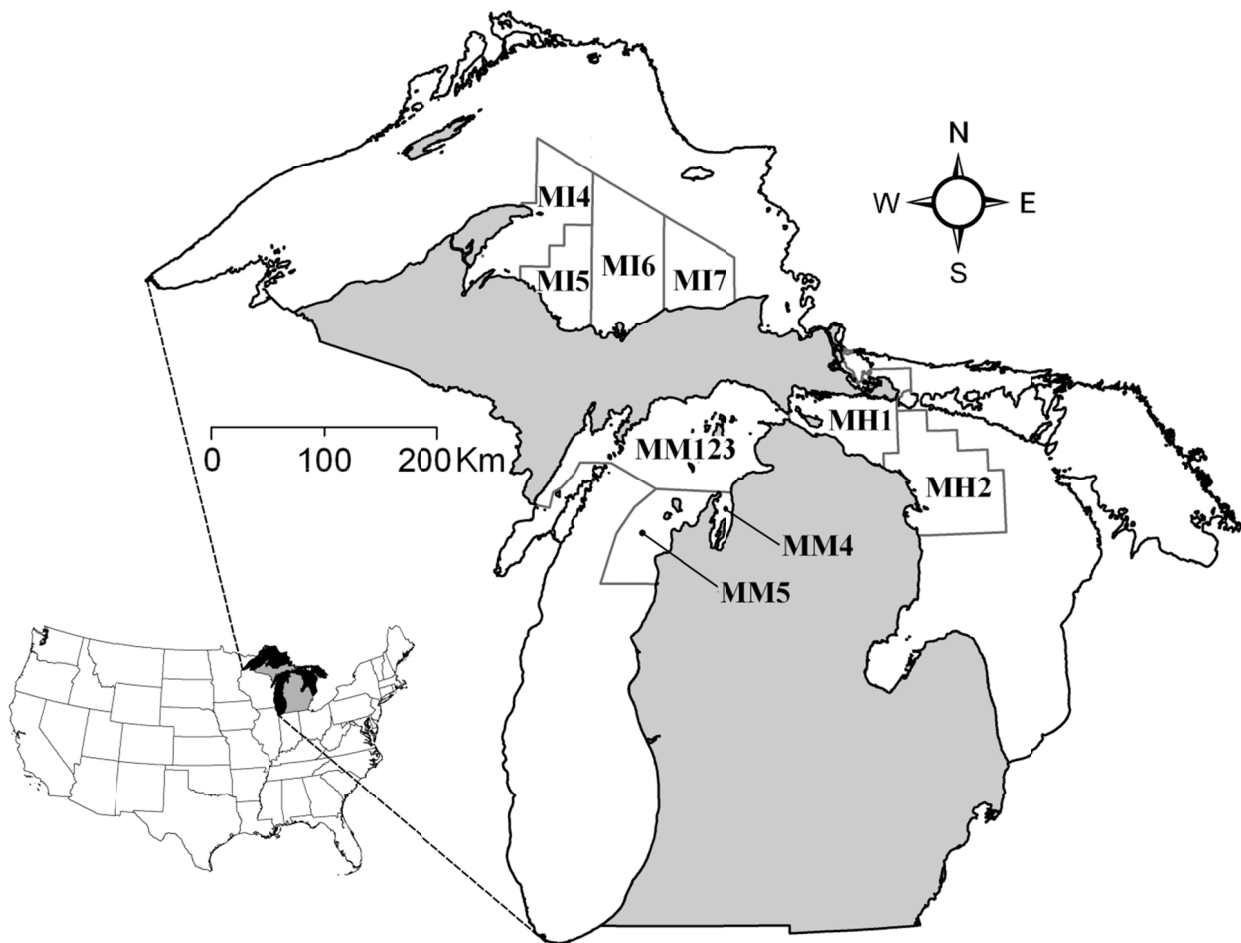

Figure 2.1: Lakes Huron, Michigan and Superior with the regions used in this study specified. Region names and boundaries correspond to lake trout management units defined for Lake Superior (Hansen 1996) or statistical districts (Smith et al. 1961) for the other lakes. MM123 is the combined areas of the statistical districts MM1, MM2, and MM3. The shaded region is the state of Michigan.

The methods used to obtain abundance estimates for large lake trout differed between the three lake basins based upon availability of size-at-age data. For Lakes Huron and Superior, mean length-at-age matrices from lake trout stock assessments (i.e., Caroffino and Lenart 2011) were used to determine which age classes for a given year constituted large hosts. For the Lake Huron estimates, length-at-age data from regions MH1 and MH2 for years 1975 to 2010 were fit to a von Bertalanffy growth model that accounted for time-varying growth according to He and Bence (2007), producing a matrix of mean length-at-age estimates for years 1976 to 2010. Growth model convergence was not achieved when the individual regions of Lake Huron were treated separately, so the data from regions MH1 and MH2 were combined resulting in a single matrix of mean lengths-at-age over time representative of the Michigan waters of Lake Huron. For the Lake Superior length-at-age estimates, the traditional von Bertalanffy growth model was fit to time blocks of data for each region corresponding to observed growth stanzas among years to decrease the chance of large annual variability in mean length-at-age estimates (S. Sitar, personal communication). We defined "large" for our analysis of Lakes Huron and Superior as fish within a cut-off age-class or older age-classes. The cut-off age was the age-class whose mean length-at-age was closest to 600mm. The length of 600mm was chosen based upon Swink (1991) who observed that sea lamprey avoid lake trout <600mm when larger fish are available. This length has also been previously used as the division comparing wounding rates between small and large hosts (e.g., Sitar et al. 2008). We chose to use a cut-off age to avoid situations where a poorly sampled older age might not be included in the large category because of chance variations. With such cut-off ages defined for each year for Lakes Huron and Superior, annual estimates of large lake trout abundance were calculated as the sum of age-specific abundance estimates starting at the cut-off age.

For Lake Michigan, von Bertalanffy estimates of mean length-at-age data were not readily available. Mean values of length for survey estimates of lake trout ages 4-7 from MM123 and MM5 (J. Jonas, unpublished data) show no obvious trends in lake trout growth among ages closest to 600mm. Age 5 lake trout were closest to 600mm across the time period examined, thus we assumed that age 5 and older lake trout were large for all years in MM123 and MM5. The findings of Madenjian and Desorcie (2010), who analyzed lake trout growth in the Northern Refuge of Lake Michigan between years 1991-1999 and 2000-2008, confirm that this is a reasonable assumption for MM123 (within which the refuge lies) and MM5 (which borders a portion of the refuge). They conducted a two-way analysis of variance, and found that time period had no significant effect on lake trout total length or weight. The interaction between lake trout age and time period also was not significant for total length or weight. Declines in mean length values for survey estimates of lake trout from MM4 (J. Jonas, unpublished data), however, suggest decreases in lake trout length-at-age in this region. Annual mean lengths were closest to 600mm for age-5 lake trout for much of the time series, but declined such that in years 1998 to 2010 age 6 was closest to 600mm. Accordingly, for MM4 we assumed age 5 and older fish were large for years 1984-1997, after which age 6 became the cutoff age.

Approaches to Examining Selectivity

We took two approaches to examining the relationship between large lake trout abundance estimates and sea lamprey size-selectivity. Both approaches rely on understanding the general relationship between sea lamprey wounding rates and host size. The logistic function is a three parameter model first used to describe the general relationship between sea lamprey

wounding rates versus lake trout length by Rutter and Bence (2003).   This model allows

wounding rates to increase gradually with host length and eventually approaches an asymptote.

The parameterization used by Rutter and Bence (2003), as well as Chapter 1 herein, is given by

equation 1.1, rewritten below:

$$\overline{w}(l) = \frac{\theta}{(1 + \exp(-\alpha(1-\beta)))}$$

where $\overline{w}$ is the average wounding rate of a fish of given length, l. Parameterized this way, θ

describes the wounding rate experienced by very large fish (the asymptotic wounding rate), $\alpha\theta/4$

is the slope at the inflection point, and β is the lake trout length at 50% of the asymptotic

wounding rate (Figure 1.1).

　　　With the first approach, we used estimates of β from Chapter 1 in which β was allowed to

follow a random walk process over time to account for potential temporal changes in sea

lamprey size selection of lake trout. These estimates, hereafter referred to as "time-varying βs,"

were plotted against large lake trout abundance estimates to observe any general patterns in the

relationship that might suggest evidence of size-selectivity. It should be noted that in Chapter 1,

unique vectors of time-varying βs were generated for each respective region analyzed with the

exception of Lake Superior. Due to the pooling of wound data in wounding rate models, in

chapter 1 time-varying β vectors were estimated for the combined regions of MI4 and MI5

(called MI45), and MI6 and MI7 (called MI67), rather than for the individual management units.

Thus, time-varying βs derived for the larger region MI45 were plotted against large lake trout

abundance estimates for MI5, and time-varying βs derived for the larger region MI67 were

plotted against large lake trout abundance estimates for MI6 and MI7, respectively.

In the second approach, wounding rate models were refit separately for each management

unit following the general approach used in Chapter 1 (see the section titled *Model

Development*). However, β was allowed to vary as a three-parameter quadratic function:

$$ln(\beta_t) = c + b * ln(N_t) + a * ln(N_t)^2 \hspace{4cm} (2.1)$$

where the N_ts are the year-specific large lake trout abundance estimates. In these respective

models the asymptote parameter, θ, varied freely over time with a fixed-effect parameter

estimated for each year, and only a single α was estimated for each model, which was held

constant over time. A negative binomial distribution was assumed for the number of wounds per

fish of a given length according to methods used in Chapter 1 (see *Model Development*). The

scaling parameter, s, was fixed at estimated values obtained in Chapter 1 to aid in model

convergence. The β estimates from this approach are henceforth referred to as "abundance-

varying βs."

RESULTS

Dynamics in Large Lake Trout Abundance

Large lake trout abundances varied greatly across the years examined for each

management unit. Patterns in large lake trout abundance appeared uncorrelated between lakes,

but appeared related within regions of the same lakes. General temporal trends in abundance

were very similar between the regions analyzed in Lake Huron (Figure 2.2). Age classes

representative of large lake trout were almost nonexistent in MH1 until the early 1990s, and were

at similarly low levels in MH2. Beginning in the early 1990s, large lake trout abundance

increased sharply in both regions, peaking in 2008 and 2004 in MH1 and MH2, respectively.

From years 1984-1989 to 2003-2008, average annual abundances of large lake trout increased

Lake Huron
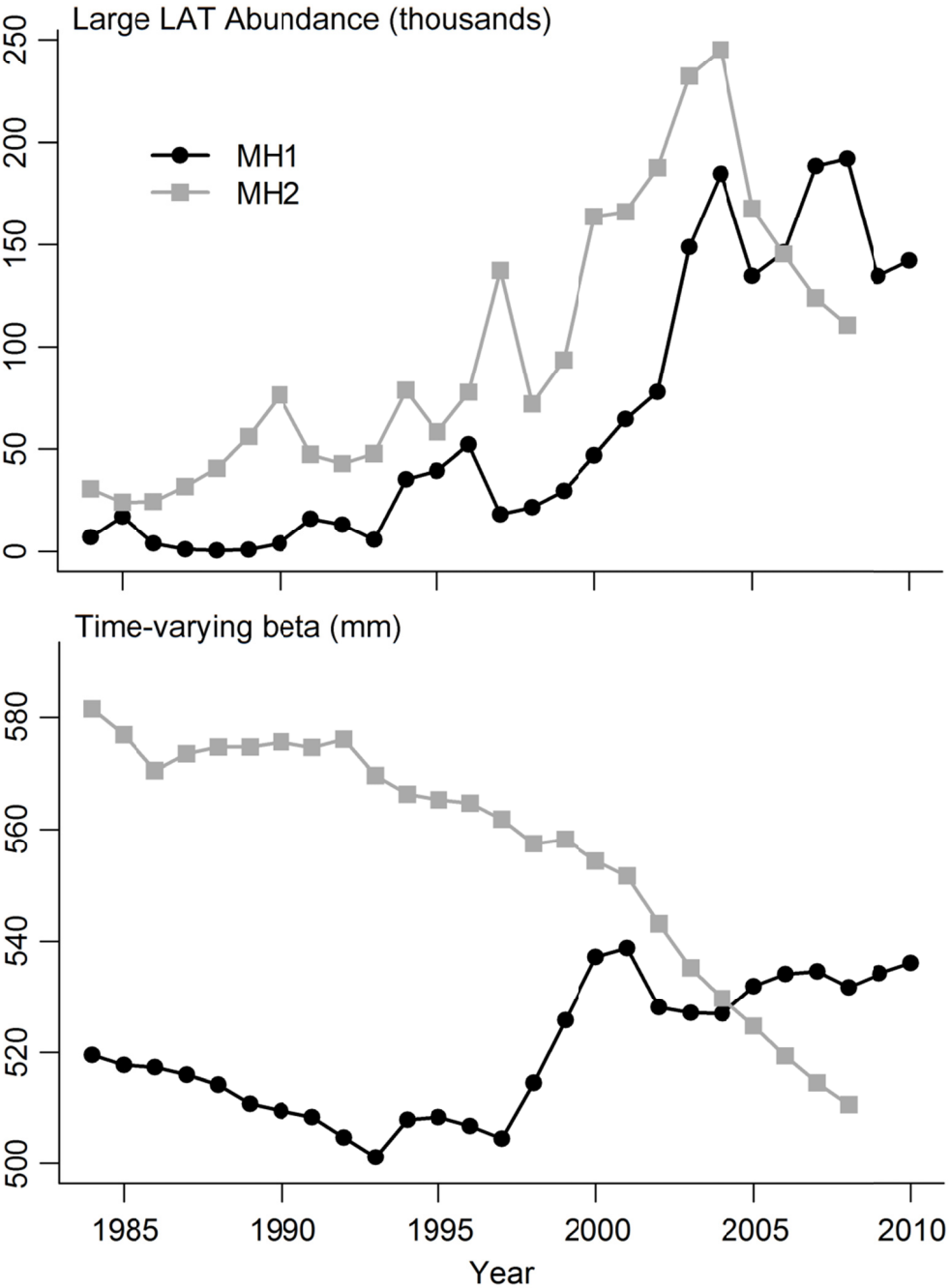
Figure 2.2: Estimates of large (>600mm) lake trout (LAT) abundance and time-varying β estimates for regions MH1 (1984-2010) and MH2 (1984-2008) in Lake Huron.
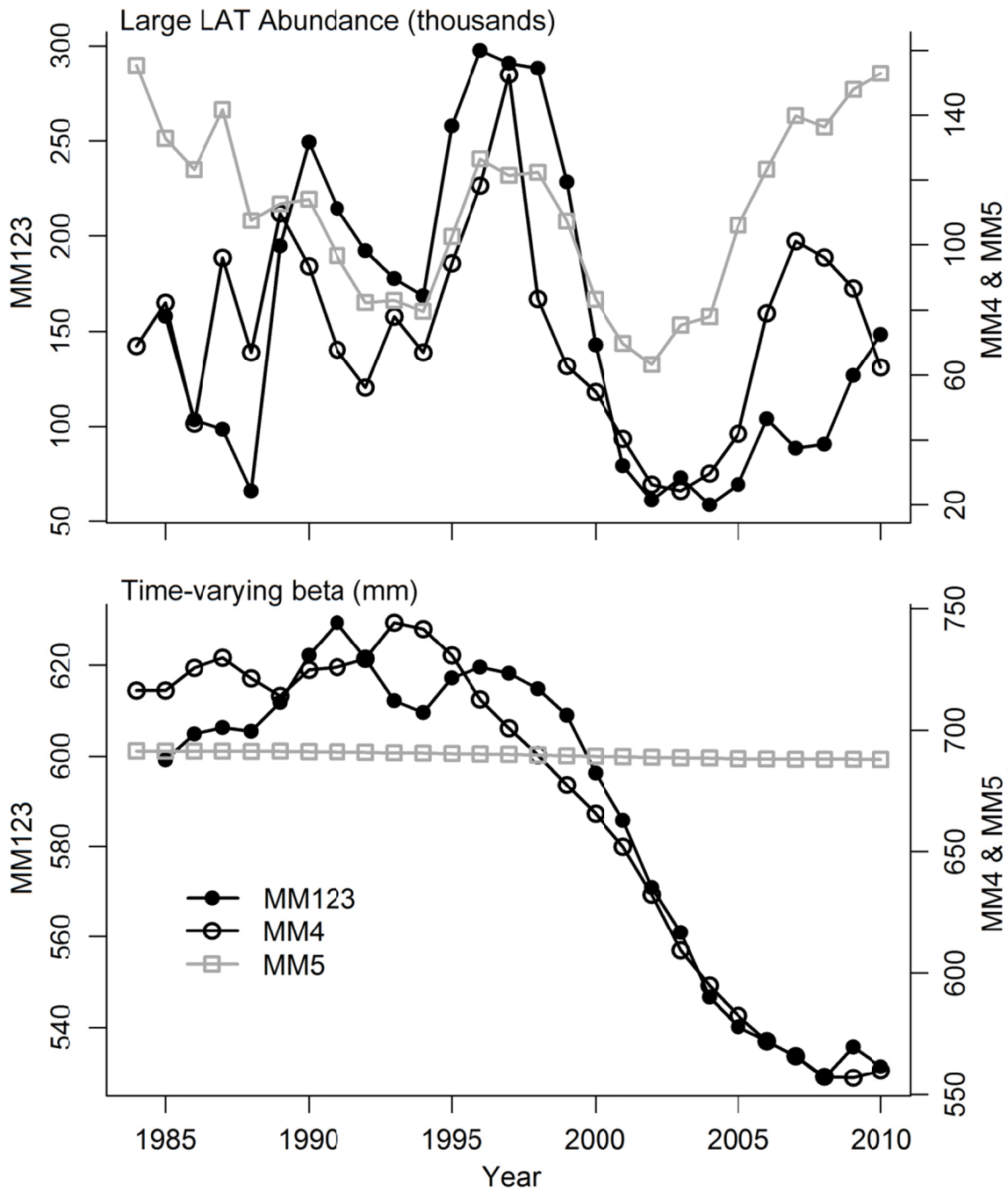
Figure 2.3: Estimates of large (>600mm) lake trout (LAT) abundance and time-varying β estimates for regions Lake Michigan regions MM123, MM4, and MM5 for years 1984-2010. The left y-axis corresponds to abundances and time-varying βs for MM123, and the right y-axis corresponds to estimates for MM4 and MM5.
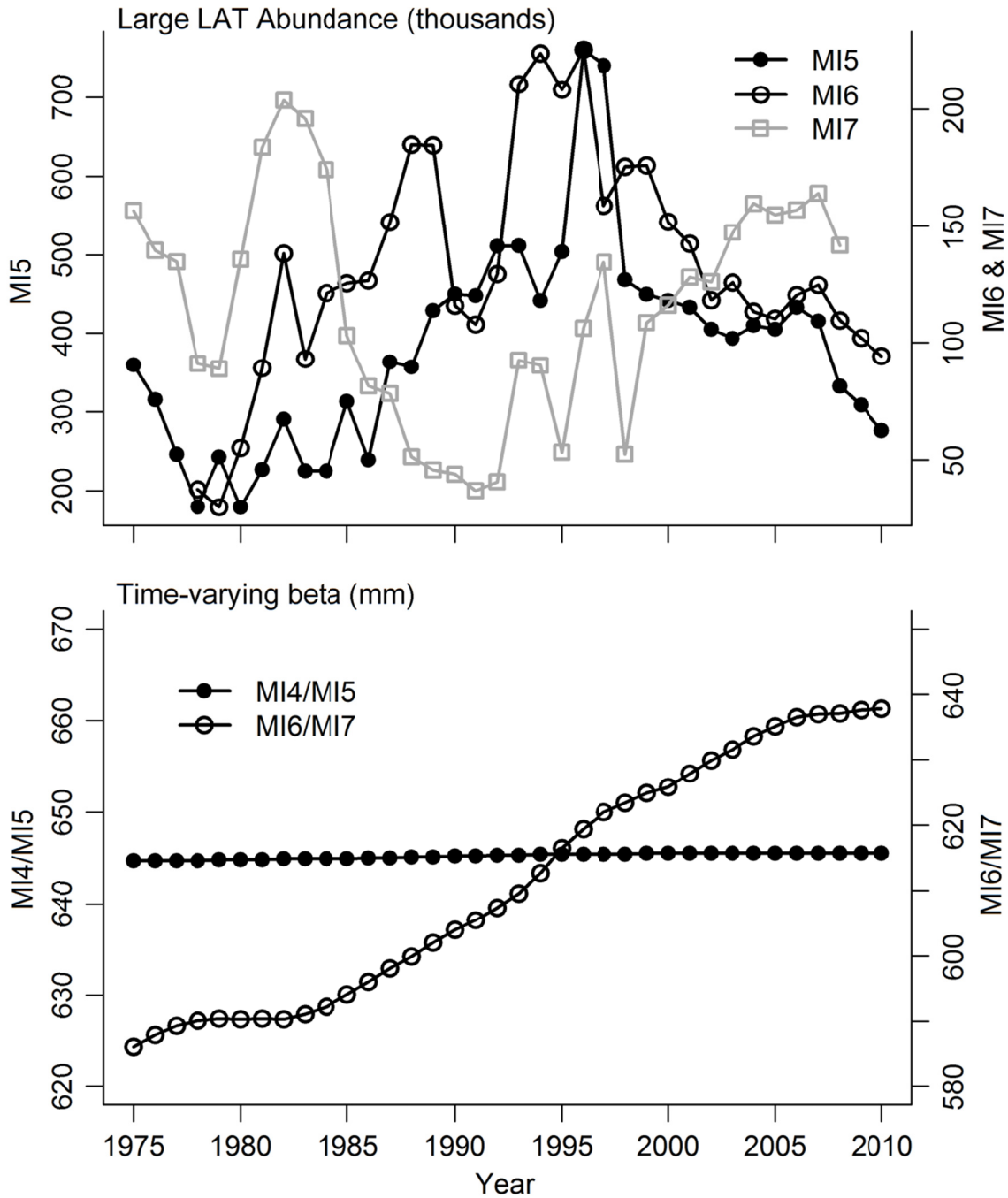
Figure 2.4: Estimates of large (>600mm) lake trout (LAT) abundance and time-varying β estimates for Lake Superior. For large LAT abundances, the left y-axis corresponds to MI5 and the right y-axis corresponds to MI6 and MI7. For time-varying β estimates, the left y-axis corresponds to the combined region MI4/MI5 and the right y-axis corresponds to the combined region MI6/MI7.

33-fold and 4.9-fold in MH1 and MH2, respectively. This is consistent with age-class expansions shown by He et al. (2012) who found that prior to 1997, age-5 and younger fish comprised at least 75% of annual spring gill-net survey catches in the main basin of Lake Huron, but by 2005 the proportion of age-5 and younger fish was only 13%.

In Lake Michigan, abundance estimates of large lake trout (Figure 2.3) showed roughly similar patterns among MM123, MM4, and MM5, especially after 1989. Among all regions, abundances decreased from 1990 to 1994, increased to peak (MM123 and MM4) or near-peak (MM5) abundances by the mid-1990s, decreased to time series-low abundances by the early 2000s, and have since generally increased through 2010. The most remarkable change in large lake trout abundance occurred in MM123 within which large lake trout abundance decreased from a peak of 298,000 in 1996 to 60,000 by 2002.

Trends in large lake trout abundances in Lake Superior (Figure 2.4) were similar between MI5 and MI6, but much different in MI7. Abundances generally increased in MI5 and MI6 beginning in 1978 to peak abundances in each region in 1996 and subsequently decreased 1996-2010. Abundances in MI7 peaked in 1982, sharply decreased 1982-1991, and have generally increased through 2008.

Coefficients of variation (CV) for total lake trout abundance estimates (i.e., the asymptotic standard error of the estimate divided by the estimate) from 2010 population assessment models (Figures 2.2-2.4) ranged from 1.5% to 6.1% for Lake Huron, 1.3% to 6.5% for Lake Michigan, and 7.4% to 24.8% for Lake Superior. These were reported with the statistical catch-at-age assessments used to assess lake trout abundance. Given the complexity of how "large lake trout" was defined it was not possible to quantitatively estimate uncertainty in these estimates. However, given the CVs of annual total large lake trout abundance, and that

typically hundreds of fish were measured and aged forming the basis for what proportion we deemed large, I believe the apparent trends seen in large lake trout abundances are largely real and not primarily estimation error. Furthermore, treating these estimates as known in subsequent analyses was reasonable because the uncertainty in the estimates was much less than the actual variability in large lake trout abundance.

Time-varying βs

The time-varying βs, as estimated in Chapter 1, were plotted against large lake trout abundances for each region analyzed (Figures 2.2-2.4). The largest shift was seen in MM4, where β remained relatively stable from 1984 to 1992, then decreased nearly 190mm from 1993 to 2010. Other large shifts were seen in MM123 (decreased 100mm, 1991-2008), MH2 (decreased 70mm, 1992-2010), and MI67 (increased 50mm, 1975-2010). Intermediate variability was seen in MH1, where β decreased slightly from 1984 to 1997 and then increased roughly 30mm by 2010. β estimates remained essentially constant across the time series for MI45 and MM5.

Because β determines the position of the logistic wounding curve with respect to lake trout total length, I expected the value of this parameter to increase or decrease with large lake trout levels. In general, however, temporal trends observed in time-varying β estimates did not track those of large lake trout abundances. Comparing the trends of large lake trout abundances and time-varying βs in figures 2-4, there is little evidence that the size-selectivity of sea lamprey varies with large lake trout abundances.

My hypothesis appears inconsistent with these observations in two ways. First, in adjacent regions with similar patterns in large lake trout abundances, sea lamprey size-selectivity

behaved differently. This is seen in Lake Huron where large lake trout abundances showed generally similar trends across the entire time series among MH1 and MH2, while the time-varying βs in each region exhibited dissimilar temporal patterns. Likewise, in Lake Superior, time-varying βs increased in the combined MI6/MI7 region across the entire time series, while they remained constant in the combined MI4/MI5 region; this is in contrast with the similarly trending large lake trout abundances among adjacent units MI5 and MI6. However, an exception was seen in Lake Michigan with MM123 and MM4 where similar temporal trends were observed in both time-varying βs and large lake trout abundance.

The second inconsistency with my foraging theory-type hypothesis is that in no region is the expected positive correlation between time-varying βs and large lake trout sustained across the entire series. Although there were some years during which changes in abundance were positively correlated with shifts in β, these instances appear coincidental, in no region is such a correlation sustained across the entire time series. In MH1, time-varying βs show no strong evidence of a positive correlation with large lake trout abundances. Contrary to my hypothesis, in MH2 where large lake trout abundances increased for most of the duration of the time series, time-varying β estimates decreased more than 60mm, suggesting that sea lamprey actually selected for smaller lake trout when larger, more desirable prey were becoming increasingly prevalent. In Lake Michigan, time-varying βs in MM5 were constant despite large fluctuations in large lake trout abundances, and although decreasing βs in both MM123 and MM4 were coincident with large declines in large lake trout abundances in the late 1990s and early 2000s, the correlation was not sustained throughout the rest of the time series. In Lake Superior, constant time-varying β estimates in MI4/MI5 and increasing estimates in MI6/MI7 do not

reflect the dynamically fluctuating large lake trout abundances seen in seen in MI5, MI6 and MI7 in a manner consistent with foraging theory.

Abundance-varying βs

Models that allowed β to vary as a quadratic function (eq. 2.1) of large lake trout abundance were successfully fit for each of the management units examined. The resulting abundance-varying β estimates are shown in Figure 2.5. In general, there does not appear to be a consistent relationship among regions relating the size-selectivity of sea lamprey to large lake trout abundance.

In Lake Huron, where adjacent units MH1 and MH2 had similarly trending patterns in large lake trout abundance (Figure 2.2), sea lamprey in MH1 selected larger hosts when large lake trout were more abundant, but in MH2 selected smaller hosts as large lake trout became more abundant. Results were similar among MM123 and MM4, with sea lamprey selecting for larger hosts at higher large lake trout abundances in MM123, while selecting for the largest hosts at intermediate abundances in MM4. Much the same as with the time-varying βs, sea lamprey size selectivity in MM5 changed little across the time series, despite dynamic large lake trout abundances. Sea lamprey size selection in regions MI5 and MI6 in Lake Superior appears consistent with foraging theory – increasing with respect to large lake trout abundance. However, in MI7, abundance-varying βs were negatively correlated with large lake trout abundance.
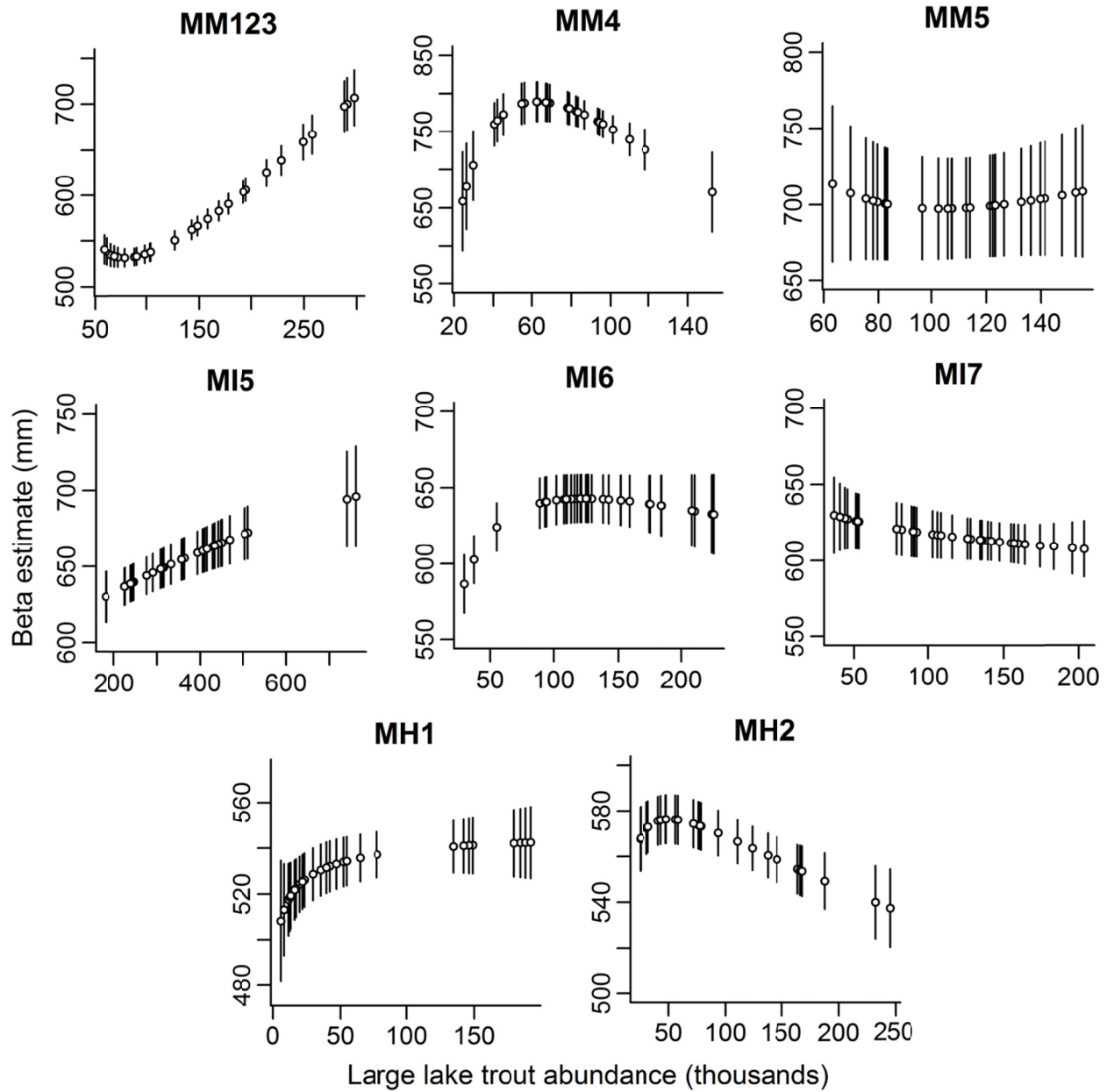
Figure 2.5: β estimates versus abundance of large lake trout for each management unit. Region abbreviations correspond to those described in Figure 1.2. Wounding rates were fit to the logistic wounding rate model (eq. 1.1), with β varying as a quadratic function of large lake trout abundance (eq. 2.1). Error bars represent one standard error.

DISCUSSION

Temporal changes in large lake trout abundances appear largely unrelated to the changes

in the size ranges of lake trout attacked by sea lamprey. Thus, the hypothesis proposed that sea lamprey will select for smaller, less optimal prey when large, more preferable prey are less abundant is not supported. The results are not likely due to the time series being too short in duration, as the shortest time series was 25 years (1984-2008, MH2). Additionally, these results are not an artifact of a narrow range of large lake trout abundances, as each region had a substantial contrast between maximum and minimum abundances.

A major assumption made for this analysis was that the size-selectivity of sea lamprey for lake trout would be independent of the length distributions and abundances of other host species. In this analysis, I expected spatial and temporal trends in large lake trout abundances alone to drive sea lamprey size selection. The failure find such a relationship indicates that sea lamprey may not conform to the expectations of foraging theory, but it could also be the case that the sea lamprey's desired prey type was not accurately defined.

Several studies have shown sea lamprey select for lake trout (Christie and Kolenosky 1980, Johnson and Anderson 1980, Morse et al. 2003, Harvey et al. 2008), but sea lamprey damages to other host species are often substantial. In Lake Huron, lake whitefish (*Coregonus clupeaformis*) are a major host species for parasitic sea lamprey. Mortality of lake whitefish is great enough that population assessments for 1836 Treaty-ceded waters of Lake Huron account for sea lamprey mortality when forecasting lake whitefish annual abundances (Caroffino and Lenart 2011). Similar to patterns observed on lake trout, sea lamprey wounding is generally greater on large lake whitefish (Ebener et al. 2010). Total biomass of lake whitefish in Lake Huron has followed generally similar trends among management units corresponding roughly to regions MH1 and MH2, and it is likely that length distributions of lake whitefish among these regions also followed similar trends. Consequently, lake whitefish dynamics do not explain the

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differences seen between MH1 and MH2 in the size-selectivity of sea lamprey for lake trout (Figure 2.2).

Unlike Lakes Huron and Michigan, a deepwater form of lake trout called siscowet lake trout inhabit Lake Superior. Siscowets are generally found in water greater than 80m (Bronte et al. 2003), deeper than water typically included in spring gillnet surveys for lake trout population assessments, and data on siscowets are not included in the wound data used in population models as fisheries tend to target lean lake trout (the morphotype also present in Lakes Huron and Michigan). Much less information exists on the population dynamics and ecology of siscowet than lean lake trout, although siscowets are now known to be the most abundant pelagic predator in Lake Superior (Bronte et al. 2003).

Sitar et al. (2008) compared differences in sea lamprey wounding rates between small (<600mm) and large (≥600mm) siscowets among three depth zones at sites within regions MI5 and MI6. They found that, similar to lean lake trout, wounding rates were significantly higher on large siscowets than on small siscowets. For large siscowets, they reported type A wounding rates of 0.831 in the shallow (<200m) zone, 1.385 in the deep (200-394m) zone, and 1.000 in the deepest (395-399m) zone. Comparing these to the 2006 asymptotic wounding rates (average wounding rates for large lake trout) for regions MI45 ($\theta = 0.296$) and MI67 ($\theta = 0.267$) as calculated for lean lake trout in Chapter 1 (Figure 1.5), siscowet wounding rates were much higher. Additionally, results of stable isotope ($\delta^{15}N$ and $\delta^{13}C$) analyses by Harvey et al. (2008) imply that sea lamprey actively select both the lean and siscowet forms of lake trout over other more abundant species in Lake Superior.

Given that sea lamprey prey heavily upon siscowets, and that siscowets are more much more abundant than lean lake trout in Lake Superior, if sea lamprey size-selection of hosts is

consistent with foraging theory it is likely to be influenced strongly by the population dynamics

and length distributions of siscowets. Abundance of siscowets has risen steadily as indicated by

increases in U.S. and Canadian commercial gillnet catch and effort data – from >20kg·km^{-1} in

the early 1950s to near 250 kg·km^{-1} by the late 1990s (Bronte et al. 2003). Mata (2009) reported

that siscowet abundance increases in the Michigan waters of Lake Superior likely leveled off

between 2000 and 2006. Interestingly, time-varying β estimates for MI67 increased across the

time series and appeared to level off in a pattern similar to that of siscowet lake trout abundances

(Figure 2.4). This does not necessarily support my proposed hypothesis, but it may at least be

consistent with foraging theory if siscowet hosts influence sea lamprey selectivity more than lean

lake trout, although it does not explain the constant size-selectivity seen in MI45 (Figure 2.4).

Evidence also strongly suggests that sea lamprey attack rates differ even among strains of

lake trout stocked in the Great Lakes. The Seneca strain of lake trout has been stocked in

varying amounts since 1985 in Lake Huron and 1995 in Lake Michigan. In Seneca Lake, New

York, from where this strain is derived, lake trout utilize deeper habitats than other strains

stocked in the Great Lakes, so the original motivation behind stocking this strain was in hopes

that these traits would increase the population diversity and promote lake trout rehabilitation

(Ebener 1998). Several studies have since shown that this strain of lake trout is less susceptible

to sea lamprey predation than other strains, and as a result Seneca strain lake trout are now the

predominant strain stocked in Lake Huron and a large component of lake trout stocked in Lake

Michigan (Figure 2.6).

The difference in sea lamprey attack rates between lake trout strains was first published

by Schneider et al. (1996) who conducted bottom trawls of Lake Ontario to recover dead lake

trout that had sank. They found that less than 1% of dead Seneca strain lake trout recovered
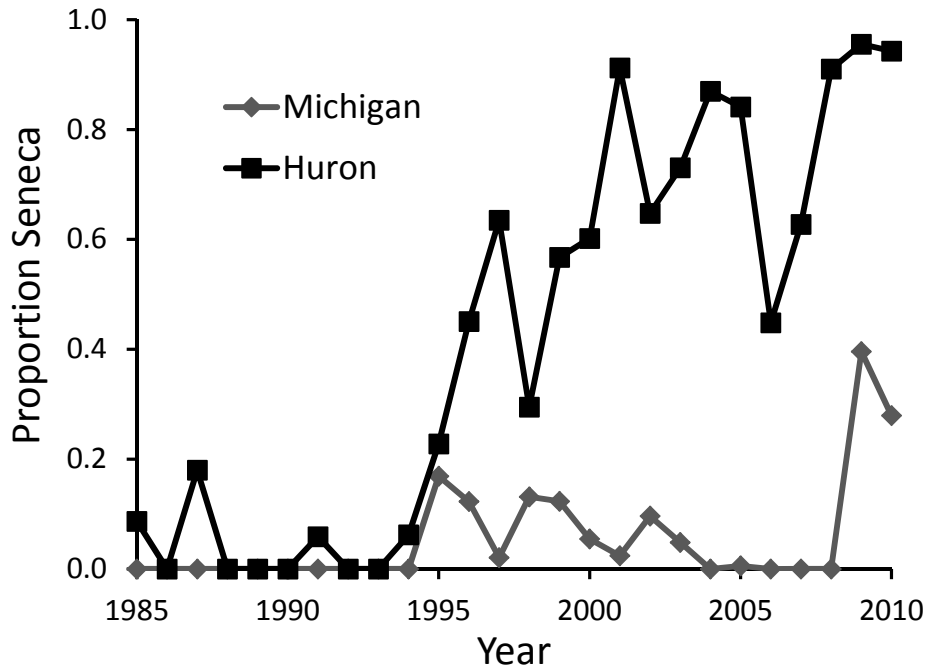
Figure 2.6: The proportion stocked lake trout that are Seneca strain from years 1985-2010. Prior to 1985, Seneca strain lake trout were not stocked in Lakes Huron and Michigan. Data correspond to combined totals of lake trout stocked in regions MH1 and MH2 for Lake Huron, and MM123, MM4, and MM5 for Lake Michigan. Data from the Great Lakes Fishing Stocking Database (http://www.glfc.org/fishstocking/).

could be attributed to sea lamprey, compared to 60% and 5% for Superior and Clearwater Lake strains, respectively. Lower wounding rates of Seneca strain lake trout have since been reported in Lake Huron (Eshenroder et al. 1995) and Lake Michigan (Bronte et al. 2007). However, McKee et al. (2004) found that Marquette strain lake trout survived better than Seneca strain in observations at Sheboygan Reef in Lake Michigan, but the higher survival occurred prior to age 3 before sea lamprey predation was a factor.

That Seneca strain lake trout are less vulnerable to sea lamprey predation presents a dilemma when relating size-selectivity of sea lamprey to abundances and length distributions of potential prey. Seneca strain lake trout are included in the spring gillnet lake trout surveys from which my wound data were obtained, and for my analyses, lake trout strain was not considered.

Specifically, if Seneca strain lake trout comprise a substantial portion of what I classified as "large" lake trout, my analysis may be inaccurately qualifying what a sea lamprey perceives as an available and desirable prey type.

Interestingly, the mechanism by which Seneca strain lake trout avoid sea lamprey attack more than other strains has not been established. Schneider et al. (1996) suggest two potential aspects of Seneca strain behavior that may contribute to different attack rates: (1) differential bathythermal distributions between strains, and (2) avoidance. They found that in gillnet surveys concurrent with their bottom trawls, Seneca strain lake trout were caught in deeper, colder water than both the Superior and Clearwater Lake strains. They reasoned that lower wounding rates on Seneca strain lake trout are potentially attributable to less habitat overlap with sea lamprey than other strains.

Bergstedt et al. (2003) used archival temperature tags to examine the extent to which differences in lake trout thermal habitat use could be attributed to lake trout strain in Lake Huron. Seneca strain lake trout generally occupied colder temperatures than other strains, with Seneca strain occupying significantly cooler temperatures from mid June to mid August during thermal stratification of the lake. A subsequent study in which Lake Huron lake trout were implanted with archival tags that recorded temperatures as well as depths was able to discern that the once again observed differences in thermal habitat use between Seneca and other strains of lake trout was attributable to deeper habitat use, and not simply differences in geographic distribution (Bergstedt et al. 2012). These two studies confirm that Seneca strain lake trout occupy colder, deeper water.

Evidence is lacking, however, that Seneca strain lake trout occupying deeper and colder habitat as the reason for lower wounding rates. Siscowet lake trout in Lake Superior occupy

much colder, deeper water than lean lake trout. Sitar et al. (2008) rarely found lean lake trout at depths >50m, however, siscowets were caught only in waters >40m, including depths nearing 400m. Siscowets were no less subjected to sea lamprey predation, suggesting that sea lamprey do occupy cold, deep habitats. Additionally, it is suspected that sea lamprey are endemic to the Seneca Lake, thus lake trout of this strain may have evolved an ability to avoid predation (Christie 1973, Ebener 1998).

Large lake trout abundance estimates for this analysis were derived from lake trout population assessments that rely on the sea lamprey wounding rate models currently used by fisheries biologists. As described in Chapter 1, such models do not allow for temporal variation in the shaping parameters of the logistic wounding rate function, and there is evidence of discrepancies in wounding rate estimates between these models and those selected for in Chapter 1 (Figure 1.7). Lake trout abundance estimates, however, were similar between lake trout population assessment model runs that incorporated sea lamprey mortalities estimated using either the currently used sea lamprey wounding rate models or those selected for in Chapter 1. For this reason I feel confident that the time-varying βs analysis is valid.

This work provides a baseline for understanding spatial differences and temporal trends seen in sea lamprey size selectivity. Although my analyses suggest that foraging theory does not explain the spatial differences and temporal changes observed in sea lamprey size-selectivity, large lake trout abundance alone, as defined in this analysis, may not accurately describe sea lamprey's preferred prey type. Further research is needed to understand the influence of alternative hosts. In Lake Superior, siscowet lake trout are clearly important, as are lake whitefish in Lake Huron, although there is strong evidence of other important hosts particularly in Lake Huron where substantial marking has been seen on a diversity of species (I. Tsehaye and

J. Bence, unpublished analyses). Other large salmonine hosts have also been important at certain times and locations (Bence et al. 2003, Morse et al. 2003). Additionally, a better understanding of the differences in sea lamprey selection between Seneca strain lake trout and other strains stocked in Lakes Huron and Michigan is needed. Archival tag studies of parasitic phase sea lamprey, such as those conducted for Lake Huron lake trout, would help determine the extent to which sea lamprey and Seneca strain lake trout habitat use overlaps. Furthermore, independent analysis of abundance of and sea lamprey wounding on Seneca and non-Seneca lake trout could help elucidate sea lamprey size selection dynamics. Such work is a challenge given that current lake trout assessment models and wound data do not distinguish lake trout strains, but moving in this direction could potentially improve assessments above and beyond providing better understanding of sea lamprey size-selection.

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