UNDERSTANDING
OBSERVED SEA LAMPREY MARKING RATES OF LAKE TROUT
IN THE GREAT LAKES

By

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ABSTRACT

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Sea lampreys (*Petromyzon marinus*), native to the north Atlantic Ocean, invaded the Laurentian Great Lakes in the early 1900s. By the mid-1900s native lake trout (*Salvelinus namaycush*) populations, that once supported commercial harvests of millions of pounds, were decimated, due in part to the sea lamprey invasion. In response to this decimation, a treaty was struck between Canada and the United States in 1954, creating the Great Lakes Fishery Commission (Commission), whose job it is to control sea lampreys. The Commission implemented a control program that greatly reduced Great Lakes sea lamprey populations.

Control continues on an annual basis; when control is relaxed, sea lampreys bounce right back, setting back fishery and ecosystem recovery by decades. Fishery managers and the Commission prioritize monitoring sea lamprey populations, to keep them in check, and to tailor and prioritize spending according to fishery needs on each lake. Annual indices of lake trout abundance, sea lamprey abundance, and sea lamprey-induced marking rates on lake trout are used to monitor success of past efforts and direct future efforts of sea lamprey control. A mark (or wound) on a host fish is an indication that a sea lamprey has attached to and potentially fed on host fish. Marking rates on lake trout are presumed to be largely driven by abundances of sea lampreys and lake trout. Occasionally, marking rates

increase when they are expected to decrease (or vice versa), leaving decision makers puzzled about the true status of sea lamprey control in the Great Lakes.

I investigated three possible reasons for these occasional inconsistencies in the status metrics: measurement error in each metric, survivor bias in marking rates, and alternative hosts. Inclusion of measurement error alone did not reproduce observed inconsistency rates, implying that a simple predator-prey model (a Type II functional response) lacked some important components. With survivor bias, the sea lamprey attack rate and sea lamprey-induced mortality rate were well indexed by Type A (piercing) marking rates if annual lethality rates were relatively constant. Other studies have demonstrated evidence of a relatively constant lethality rate, so survival bias is likely not a major contributor to observed inconsistencies. In Lake Ontario, sea lampreys exhibited a strong preference for lake trout, but switched to Chinook salmon when relative abundance of lake trout was low. Host switching impedes using a marking rate focused only on lake trout as an index of sea lamprey attacks.

I also developed stock-recruitment relations for sea lampreys. I used a lake-specific adult-to-adult stock recruitment model to quantify how lampricide treatment effort reduced sea lamprey recruitment.

This work eliminates measurement error as a primary cause of observed inconsistencies in sea lamprey status metrics and diminishes concern about survivor bias in Type A marking rates. Although I demonstrated that the presence of alternative hosts can affect sea lamprey-induced marking rates on lake trout, further research into this and other mechanisms contributing to variability in the status metrics is needed.

For my mother,
Theresa Uhrich Adams,
who embraced adventure,
dared to be different, and
told doubters to go jump in the lake.

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Thanks are due to many people who helped me along the way. **Mike Hansen** brought me into the family of Great Lakes fish researchers in 1994 when he hired me into what is now the US Geological Survey's Great Lakes Science Center. **Roger Bergstedt** introduced me to the sea lamprey control program in 1998. **Kasia Mullett** created the FishLamp Workgroup of the Great Lakes Fishery Commission in 2016 and nominated me to chair it. Questions posed by members of FishLamp inspired me to seek answers through an academic program. **Russ Strach** and **Kurt Newman** of the US Geological Survey and **Bob Lambe**, **Dale Burkett**, and **Mike Siefkes** of the Great Lakes Fishery Commission supported my leadership development and my pursuit of a PhD. **Mike Jones** agreed to be my advisor in 2017 and has been an outstanding mentor and friend, encouraging and challenging me every step of the way. The other members of my committee, **Jim Bence**, **Deb McCullough**, and **John Dettmers**, provided invaluable input through several engaging discussions. All my research relied on valuable fishery-independent lake trout and sea lamprey surveys conducted annually by state, provincial, tribal, and federal agencies around the Great Lakes. The ease with which I write that sentence belies the hardship behind the collection of such data by people dedicated to the resource. **Ted Treska** managed the Great Lakes Fishery Commission Sea Lamprey Database and helped me understand the nuances of the marking data. The Quantitative Fisheries Center provided office space and collegial camaraderie. Finally, I thank my husband, **John Heinrich**, for his unfailing support provided in equal parts tough coach and enthusiastic cheerleader.

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INTRODUCTION

Control of invasive sea lampreys (*Petromyzon marinus*) in the Laurentian Great Lakes was initiated in the 1960s in response to the decimation of native lake trout (*Salvelinus namaycush*) populations. Sea lamprey control is a critical part of the rehabilitation of lake trout, the preferred hosts of sea lampreys in the Great Lakes. Annual indices of lake trout abundance, sea lamprey abundance, and sea lamprey marking rates on lake trout are used to monitor success of past efforts and direct future efforts of the sea lamprey control program. Although the metrics are all inter-related, they don't always line up as expected, posing a challenge to decision makers. The goal of this dissertation is to investigate factors that might contribute to inconsistencies in the metrics: measurement error in status metrics, survival bias in the marking rate, and the effect of an alternative host. In addition, I estimated stock recruitment relations of Great Lakes sea lampreys.

0.1 Misalignment of predator-prey dynamics

Sea lamprey marking rates on lake trout are presumed to be largely driven by abundances of sea lampreys (the predator or parasite) and lake trout (the prey or host) in each lake. When lake trout abundance increases and sea lamprey abundance decreases, the marking rate (the predation or parasitism rate) is expected to decline. Conversely, when lake trout decline and sea lampreys increase, the marking rate is expected to increase. These metrics, however, occasionally change in ways that are inconsistent with expectations, leaving decision makers puzzled about the true status of sea lamprey control in the Great Lakes. In Chapter 1, I proposed and evaluated the hypothesis that actual Great Lakes lake trout and sea lamprey dynamics do vary as expected in a predator-prey model and that observed inconsistencies are simply a product of measurement error in the three status metrics (Figure 0.1).

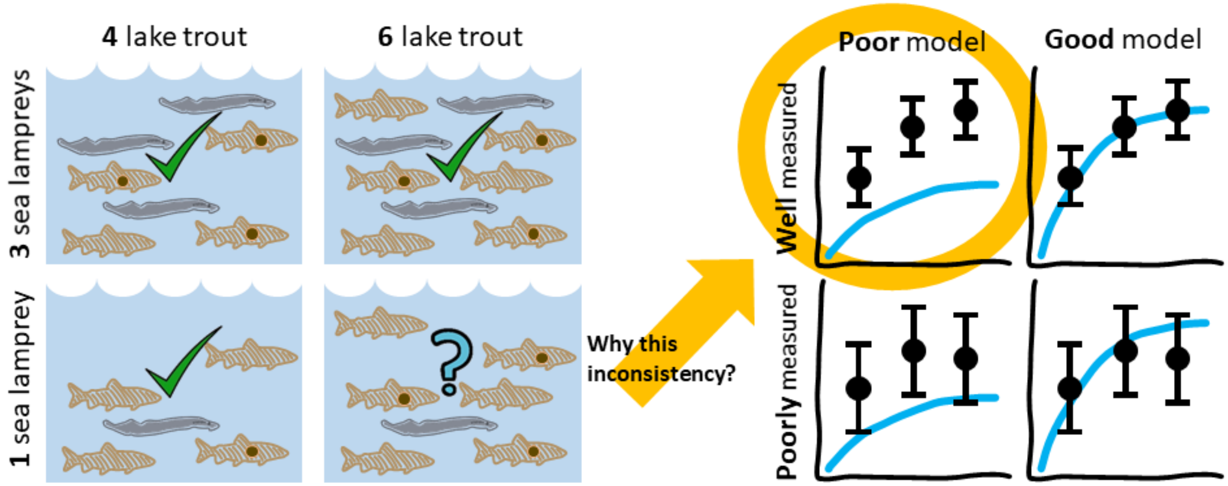

Figure 0.1. Determining the cause of inconsistencies in Great Lakes lake trout and sea lamprey dynamics: measurement error vs. model specification.

0.2 Marking rates

Assessments of lake trout and sea lampreys are key to models describing their population dynamics and host-parasite interactions and consequently to informing fishery management decisions. However, quantifying host mortality from sea lamprey marks observed on captured fish is challenging because only fish that have survived their injuries so far are observed. In fact, the group of most interest to fishery managers, those that died from sea lamprey attacks, is the group about which the least is known. Some hosts will have died before sampling takes place and are thus unobservable, and an unknown percentage of observed fish would have died from their wounds if they had not been sampled. In Chapter 2, I used simulation to determine how well observed Type A and B marking rates on lake trout index true attack and sea lamprey-induced mortality rates (Figure 0.2).

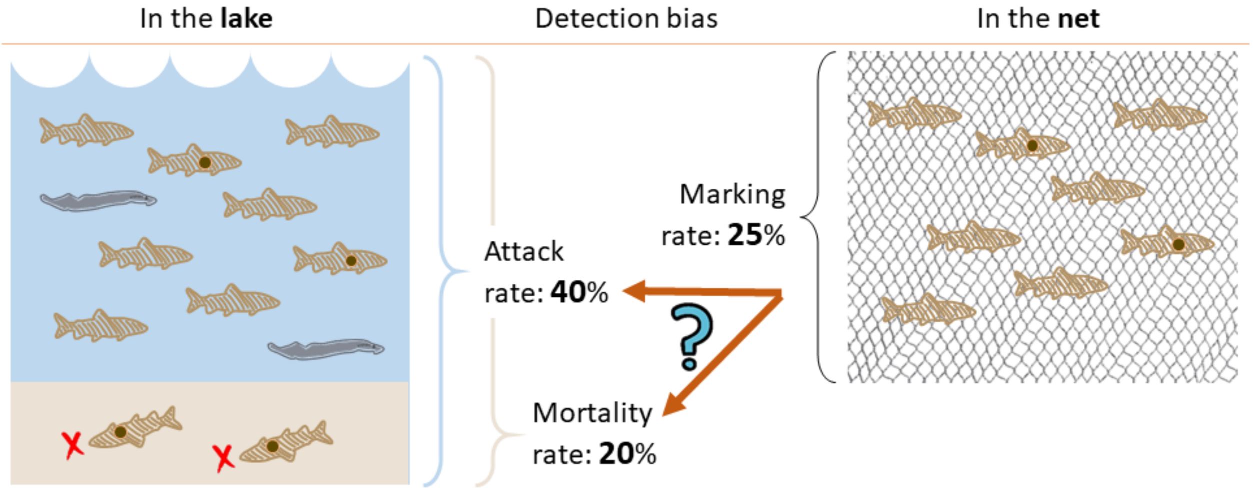

Figure 0.2. Detection bias in surveys of surviving lake trout, and the disconnect between observed marking rates and true attack and mortality rates.

0.3 Host switching

Lake trout are presumed to be the preferred hosts for invasive sea lampreys in the Great Lakes (Harvey et al., 2008; Pycha and King, 1975; Swink, 2003). But, juvenile sea lampreys attack many other Great Lakes species, especially large-bodied ones (Farmer and Beamish, 1973; Swink, 2003). Little is understood about how sea lamprey parasitism varies with host abundance (Bence et al., 2003; Koonce, 1987). Knowledge in this area would allow us to improve our estimates of host damage. In Chapter 3, I characterize sea lamprey preference for lake trout in Lake Ontario and determine if and when their preference switches to Chinook salmon based on field observations (Figure 0.3).

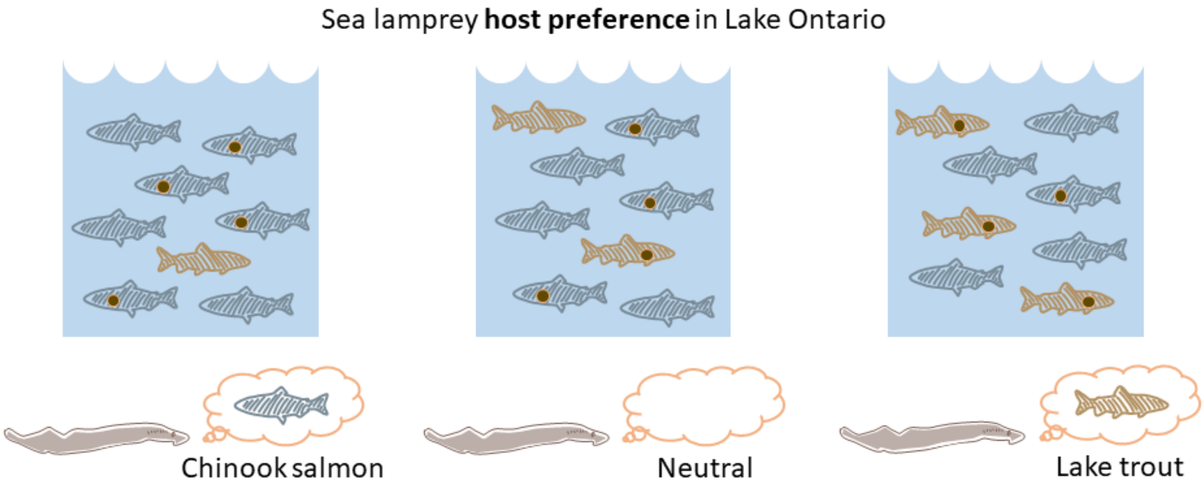

Figure 0.3. Host preference of sea lampreys in Lake Ontario faced only with the choice between lake trout and Chinook salmon.

0.4 Stock recruitment dynamics

To manage fisheries effectively, some understanding of recruitment dynamics and their dependence on stock size is key (Hilborn and Walters, 1992). Sustainable recruitment is critical to maintain fish populations and sustainable harvests (Zhao et al., 2013). Knowledge of recruitment dynamics is equally important to inform the control of invasive fishes, where recruitment overfishing (Hilborn and Walters, 1992) may be the goal (Dux et al., 2019; Weber et al., 2011). Stock-recruitment relations would be particularly helpful in exploring control options that target adult sea lampreys, to assess the effect of reductions in stock on recruitment (Jones, 2007; Jones et al., 2003, Jones and Adams, *In press*). In Chapter 4, I developed lake-wide stock-recruitment curves for Great Lakes sea lampreys, relating the number of spawning adults from one generation to the next (Myers et al., 1999). I incorporated proportional contributions from different cohorts of stock (those that matured 5, 6, and 7 years prior to recruitment), and two covariates: sea lamprey size as a surrogate for fecundity and lampricide quantity as a surrogate for anthropogenic mortality (Figure 0.4).

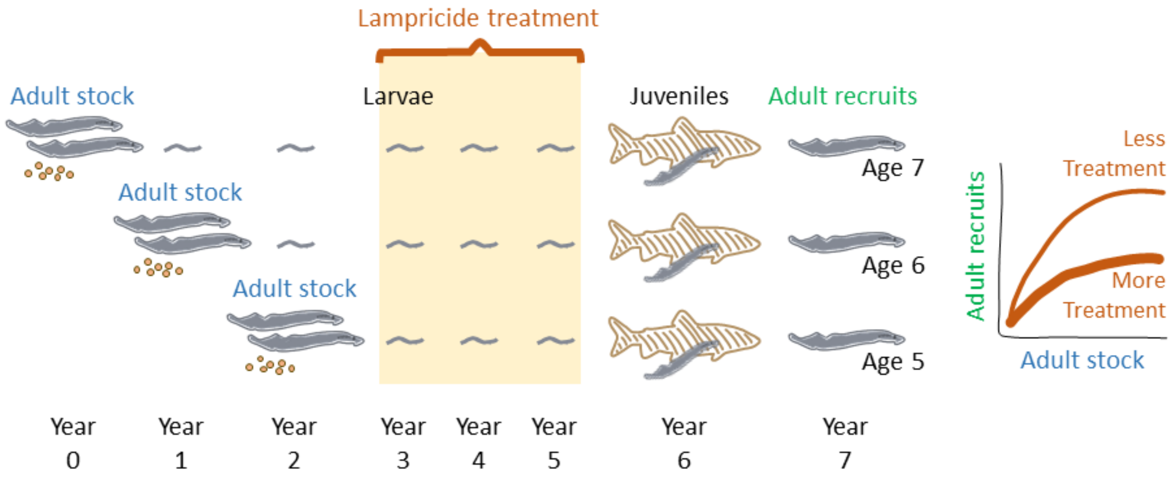

Figure 0.4. Adult-to-adult stock recruitment relation for Great Lakes sea lampreys, with proportional contributions from stock cohorts that matured 5, 6, and 7 years prior to recruitment, and effects of sea lamprey size as a surrogate for fecundity and lampricide quantity as a surrogate for anthropogenic mortality.

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CHAPTER 1

INVESTIGATING APPARENT MISALIGNMENT OF PREDATOR-PREY DYNAMICS: GREAT LAKES LAKE TROUT AND SEA LAMPREY

1.1 Introduction

Observed ecological metrics do not always align the way models suggest they should. The culprits are some combination of model error, process error, and measurement error, all of which can affect the accuracy and precision of models of ecological systems (Hoshino et al., 2014). Alignment is expected based on a model, either explicit or implicit, so one explanation for the lack of alignment could be that the chosen model is inappropriate (model error) or that covariates explaining annual variability have not been quantified (process error). Alignment also depends on how closely recorded metrics are to their true values (measurement error). I investigated the effects of measurement error, for which I had reasonable estimates, in a simulation of predator and prey dynamics.

The Great Lakes Fishery Commission (GLFC) has been charged with lake trout (*Salvelinus namaycush*) rehabilitation and sea lamprey (*Petromyzon marinus*) control since its formation in 1954 (Fetterolf, 1980). Annual indices of lake trout abundance, sea lamprey abundance, and sea lamprey marking rates on lake trout are used to monitor the success of past efforts and direct future efforts of the sea lamprey control program (www.glfc.org/status.php, 12 Jul 2019). Sea lamprey marking rates on lake trout are presumed to be largely driven by abundances of sea lampreys (the predator or parasite) and lake trout (the prey or host) in each lake. When lake trout abundance increases and sea lamprey abundance decreases, the marking rate (the predation or parasitism rate) is expected to decline. Conversely, when lake trout decline and sea lampreys increase, the marking rate is expected to increase. Occasionally, marking rates increase when they are expected to decrease (or vice versa), leaving decision makers puzzled about the true status of sea lamprey control in the Great Lakes.

I hypothesized that lake trout and sea lamprey dynamics vary just as predator-prey models suggest and that observed inconsistencies are simply a product of measurement error in the three status metrics. Measurement error has been shown to be an important source of uncertainty by others (Carpenter et al., 1994; Rosenberg and Restrepo, 1994; Schnute, 1991). Further, I investigated how measurement error in each metric contributed to the observed inconsistency rate, to determine if improved assessments would result in better aligned metrics. For each Great Lake, I fit a functional response relation to the lake trout and sea lamprey data. Then I carried out a simulation, assuming this relation to be the deterministic "truth" on a lake-wide basis (with no model error and no process error). Finally, I added the presumed current level of measurement error for all three metrics at once, and for each metric separately, and assessed their individual contributions to the resulting inconsistency rate.

1.2 Methods

1.2.1 Metrics

Lake trout relative abundance was assessed annually with fishery-independent gill net surveys. The relative abundance of large, lean lake trout (total length > 532 mm for Lakes Superior, Michigan, and Huron; age ≥ 5 years for Lake Erie; and total length > 431 mm for

Lake Ontario) was reported as catch per unit effort (fish/km/net night for Lakes Superior, Huron, and Ontario; fish/1000'/net night for Lake Michigan; and fish/lift for Lake Erie).

Sea lamprey abundance in each lake was assessed annually by trapping adults in selected index streams during their spawning migration. In each stream, a subset of captured sea lampreys was marked and released a short distance downstream of the traps. Numbers of marked, unmarked, and recaptured sea lampreys were used to give a pooled Petersen estimate of numbers approaching the traps (Seber, 1970). Petersen estimates in streams were then summed for a lake-wide adult index (Barber et al., *In preparation*), and the index was scaled up to a presumed lake-wide population level based on earlier work by Mullett et al. (2003).

Large, lean lake trout captured in gill net surveys were examined for evidence of sea lamprey attacks. Marks from sea lamprey attacks were categorized according to whether the skin was pierced, indicating sea lamprey feeding (type A marks), or intact (type B marks) and the extent of healing from fresh marks (stage 1) to well healed marks (stage 4) (Ebener et al., 2003; King, 1980). Great Lakes marking rates are typically summarized as the number of A1, A2, and A3 marks combined per 100 large lake trout, except for Lake Ontario, where they report the number of A1 marks per 100 large lake trout.

The three metrics were aligned to a common sea lamprey marking year. No alignment was necessary for lake trout abundance; lake trout surveys were assumed to reflect lake trout abundance in the year of sea lamprey marking. Adult sea lamprey abundance, measured in spring, was presumed to reflect abundance of juvenile sea lampreys in the previous year, when they were feeding on fish in the lake. Marking rates observed on lake trout collected in spring (as practiced on Lakes Superior and Huron) were presumed to reflect sea lamprey attacks in the previous year (Table 1.1). For example, in marking year 2000, lake trout abundances came from surveys in 2000; juvenile sea lamprey abundance came from surveys for adults in 2001; and marking rates came from surveys in 2000 for Lakes Michigan, Erie, and Ontario and in 2001 for Lakes Superior and Huron. Only those lake-years with estimates for all three metrics were included in the analysis.

Table 1.1. Metrics collected in each Great Lake at different times of year (column headers) were aligned to the same marking year (first two columns) prior to analysis.

Lake	Spring of marking year	Fall of marking year	Spring of marking year + 1
Superior	Lake trout CPE		Sea lamprey abundance Marking rate
Michigan		Lake trout CPE Marking rate	Sea lamprey abundance
Huron	Lake trout CPE		Sea lamprey abundance Marking rate
Erie		Lake trout CPE Marking rate	Sea lamprey abundance
Ontario		Lake trout CPE Marking rate	Sea lamprey abundance

All data were provided by the Great Lakes Fishery Commission; indices of lake trout abundance and marking rates were from the Sea Lamprey Wounding Database (Ted Treska, US Fish and Wildlife Service, personal communication). All analyses were conducted and figures produced with R (R Core Team, 2018) including packages ggplot2 (Wickham, 2016) and egg (Auguié, 2019).

1.2.2 Functional response

A Type II functional response model was fit to the parasite-host relation between sea lampreys and lake trout in the Great Lakes,

$$(1) \qquad A_i = \frac{\alpha_i D_i}{1 + \alpha_i \beta_i D_i} \ ,$$

where $A_i = M_i D_i / L_i$ represents an indexed attack rate on lake trout per sea lamprey per year in lake i, M_i is the number of sea lamprey marks per large lake trout, D_i is the index of large lake trout abundance (catch per unit effort, with different units of effort in each lake), L_i is the lake-wide abundance of sea lampreys, and α_i and β_i are parameters to be estimated (Figure 1.1).

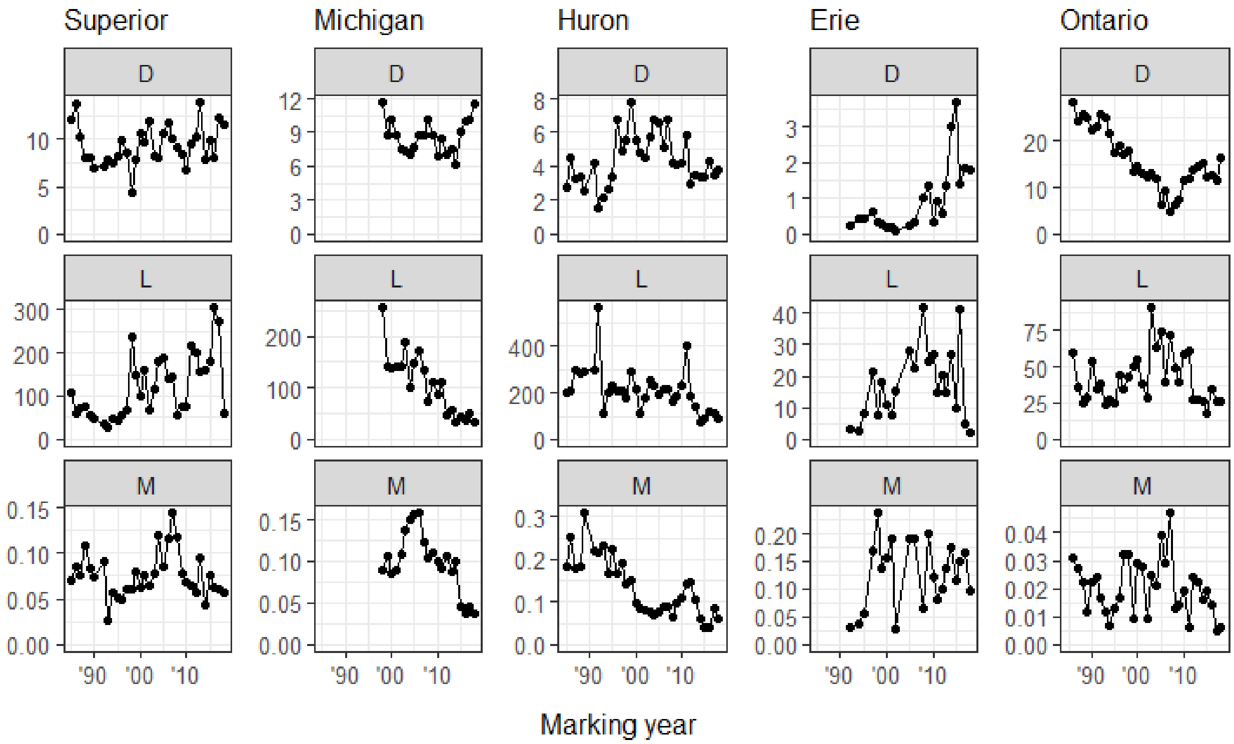

Figure 1.1. Metrics used to inform a functional response model of sea lamprey attacks on lake trout in the Great Lakes including lake trout catch per unit effort (D, in millions, in different units for each lake), sea lamprey abundance (L, in thousands), and marks per lake trout (M).

All three quantities in this relation are indices, which limit our ability to interpret the estimated parameters. If I had estimates of attacks per host, K, absolute abundance of lake trout, T, and absolute abundance of juvenile sea lampreys, L, I would write the functional response model for a single lake as

$$\frac{KT}{J} = \frac{eT}{1 + ehT},$$

where e is the effective search rate, and h is the handling time (Bence et al., 2003; Holling, 1959a). But, instead of actual attacks per host, I have an observed marking rate on hosts that survived being attacked, $M = sK$, where s is the survival of attacked lake trout. Instead of absolute abundance, I have an index of lake trout relative abundance, $D = qT$, where q is the catchability of lake trout. Instead of juvenile feeding sea lampreys, I have an estimate of adult sea lamprey abundance, $L = pJ$, where p is the survival of juveniles to the adult life stage. All three proportions (s, q, and p), are unknown, lake-specific, and assumed to be a constant over time. Rewriting the equation with these quantities, and solving for MD/L gives

$$\frac{MD}{L} = \frac{\left(\frac{se}{p}\right)D}{1 + \left(\frac{eh}{q}\right)D} = \frac{\left(\frac{se}{p}\right)D}{1 + \left(\frac{se}{p}\right)\left(\frac{ph}{sq}\right)D} .$$

Thus, the effective search rate is confounded with survival of both lake trout and sea lampreys, and the handling rate is confounded with both survivals as well as lake trout catchability. The estimated parameters, $\alpha = se/p$ and $\beta = ph/sq$ create plausible functional response relations for my simulation, but their units are essentially meaningless and are not comparable among lakes.

I used maximum likelihood to fit the model to all five lakes at once. I fit the model using the optim function of R (R Core Team, 2018), minimizing the negative log likelihood. The error was assumed to multiplicative and lognormal, and $\alpha_i = exp(\phi_i)$ and $\beta_i = exp(\eta_i)$ were constrained to be positive via parameter transformations,

$$log(A_i) = log\left(\frac{exp(\phi_i)D_i}{1 + exp(\phi_i)exp(\eta_i)D_i}\right) .$$

1.2.3 Measurement error

To judge the effect of measurement error on the observations, I started with a baseline estimate of the true measurement error in each metric.

For the lake trout abundance index, the baseline measurement error was approximated using the average coefficient of variation ($\overline{C}_D$) from a relation between lake trout density (selectivity corrected area weighted average catch per 64 m net) and associated standard errors estimated via mark-recapture (Sandstrom and Lester, 2009, Sandstrom, *In preparation*). Estimates were available from 10 Ontario lakes ranging in size from 217 to 3,008 ha with populations of large bodied lake trout (i.e., those often exceeding 450 mm in total length). The baseline measurement error for relative lake trout abundance was then modeled using a normal distribution with mean 0 and variance $(\overline{C}_D D)^2$.

For adult sea lamprey abundance, the baseline measurement error was approximated using an approach similar to that described for the lake trout abundance index, using the average coefficient of variation ($\overline{C}_I$) from a relation between adult sea lamprey indices and their standard errors. Annual adult sea lamprey indices were available from 148 lake-years. The annual index for each lake was the sum of pooled Petersen mark-recapture estimates (Barber et al., *In preparation*). The baseline measurement error for sea lamprey abundance was modeled using a normal distribution with mean 0 and variance $(\overline{C}_I L)^2$.

For marking rates, the baseline measurement error was also approximated by the coefficient of variation, after accounting for both sample variability and classification error. Sample variability was incorporated by taking 10 bootstrap samples of large lake trout within each of 140 lake-years, for a total of 1,400 bootstrap samples of lake trout. Each lake trout was associated with the number and class of marks that had been observed on it.

Classification error was incorporated by means of a transition matrix between known mark classifications and marks identified by fishery managers in a controlled workshop setting (Firkus et al., *In review*, Table 1.2). Each of 38 lake trout were examined by 13 to 20 individuals who recorded the number and class of marks. I used bootstrap resampling of mark classifications for each fish to create 1400 transition matrices that reflected variability in the classification process.

Table 1.2. Classification matrix of known sea lamprey marks (columns) on 38 lean lake trout versus observed marks (rows) identified by 13 to 20 fishery managers in a controlled workshop setting (Firkus et al., *In review*). Table numbers represent frequency of classifications by each person on each lake trout with known marking histories (Tyler Firkus, Michigan State University, unpublished data).

Observed	A1	A2	A3	A4	B1	B2	B3	B4	None	Total
A1	5	21	1	1	0	0	0	0	1	29
A2	3	53	5	3	0	0	0	5	1	70
A3	2	15	34	3	0	10	2	3	2	71
A4	0	4	5	8	0	3	4	9	4	37
B1	0	2	2	1	0	4	0	3	2	14
B2	0	9	1	1	0	13	2	4	1	31
B3	2	4	5	7	0	8	7	14	3	50
B4	1	3	2	18	0	0	5	31	33	93
None	1	10	0	73	0	0	0	67	162	313
Total	14	121	55	115	0	38	20	136	209	708

These bootstrapped transition matrices were then used to convert observed marks on bootstrapped lake trout to “true” marks using an iterative method following Kimura and Chikuni (1987) with code from Murta and Vendrell (2009). For each bootstrap sample, the "true" marking rate (sum of A1-A3 per lake trout for all lakes, except Ontario sum of A1 marks per lake trout) was calculated. For each lake-year, the standard error and coefficient of variation among the 10 bootstrap samples was calculated. The baseline measurement error for observed marking rate was then modeled using a normal distribution with mean 0 and variance $(\overline{C}_D M)^2$, where $\overline{C}_M$ is the average coefficient of variation from a relation between actual observed marking rates and associated standard errors.

1.2.4 Simulations

I used the estimated parameters of the functional response model as the assumed underlying deterministic relation and added the baseline measurement error to each component metric. To set up the deterministic relation, I generated assumed true (denoted by $'$) abundances of lake trout D'_{ij} and sea lampreys L'_{ij}, using random samples from lognormal distributions with sample sizes, means, standard deviations, and first order temporal autocorrelations based on observed sample statistics (Figure 1.2). Autocorrelations were estimated using the acf function of R (R Core Team, 2018), and time series of abundances were generated using the mvrnorm function of the R package MASS (Venables and Ripley, 2002). Simulated marking and attack rates were then calculated from these abundances and the functional response parameters,

$$M'_{ij} = \frac{L'_{ij}\hat{\alpha}}{1 + \hat{\alpha}\hat{\beta}D'_{ij}} ,$$

$$A'_{ij} = \frac{M'_{ij}D'_{ij}}{L'_{ij}} .$$

Finally, I added random noise from the baseline measurement error to each of the true metrics; resulting in simulated (denoted by *) metrics D^*_{ij}, M^*_{ij}, L^*_{ij}, and $A^*_{ij} = M^*_{ij}D^*_{ij}/L^*_{ij}$.

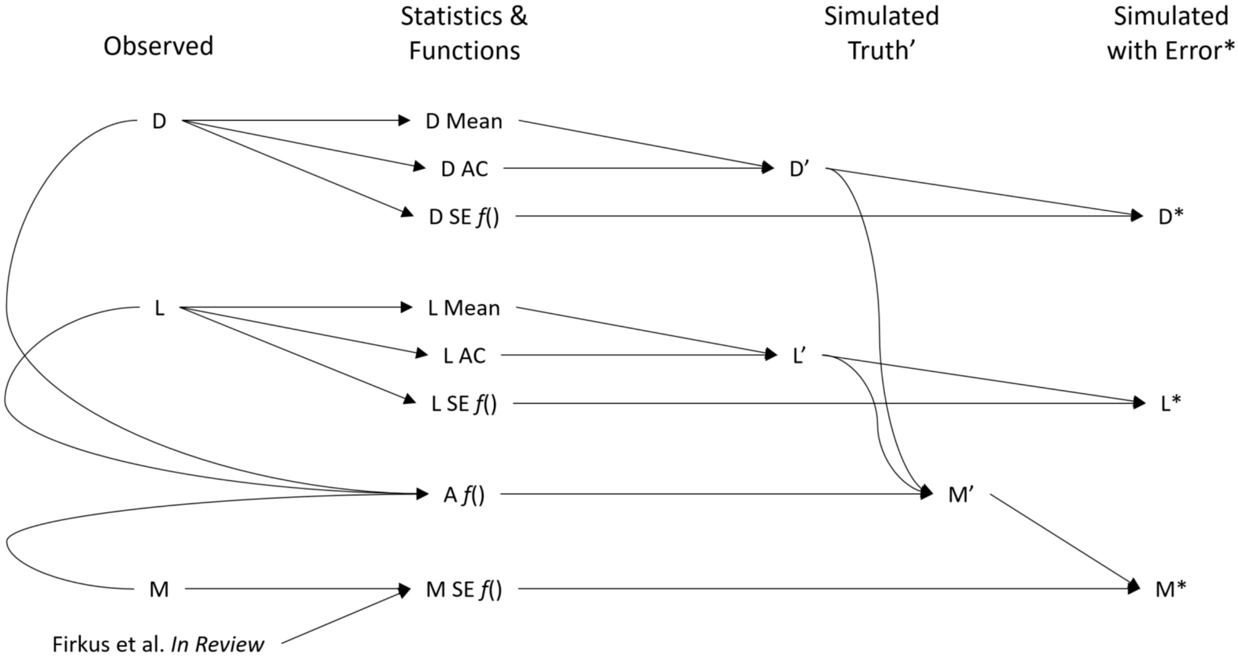

Figure 1.2. Diagram of single simulation of lake trout relative abundance, sea lamprey abundance, and sea lamprey marking rate on lake trout, using observed values (D, L, M, respectively) to generate simulated true values (D', L', M') and simulated values with measurement error (D^*, L^*, M^*). Abbreviations include AC for autocorrelation, SE for standard error, $f()$ for function, and A for sea lamprey attack rate on lake trout. The SE functions refer to estimated coefficients of variation ($\overline{C}_D$, $\overline{C}_L$, and $\overline{C}_M$); the attack rate function refers to equation (1) (Table 1.3).

I repeated this process 1,000 times and compared inconsistency rates of simulated data to those of actual observations. Inconsistency was defined as any observation from two consecutive years during which (1) lake trout abundance and marking rates increased while sea lamprey abundance declined or (2) lake trout abundance and marking rates declined while sea lamprey abundance increased. For each simulation, the inconsistency rate was quantified as the number of inconsistencies per pair of consecutive years for each lake, I_i^*. These were compared to inconsistency rates in observed metrics, I_i (Figure 1.3).

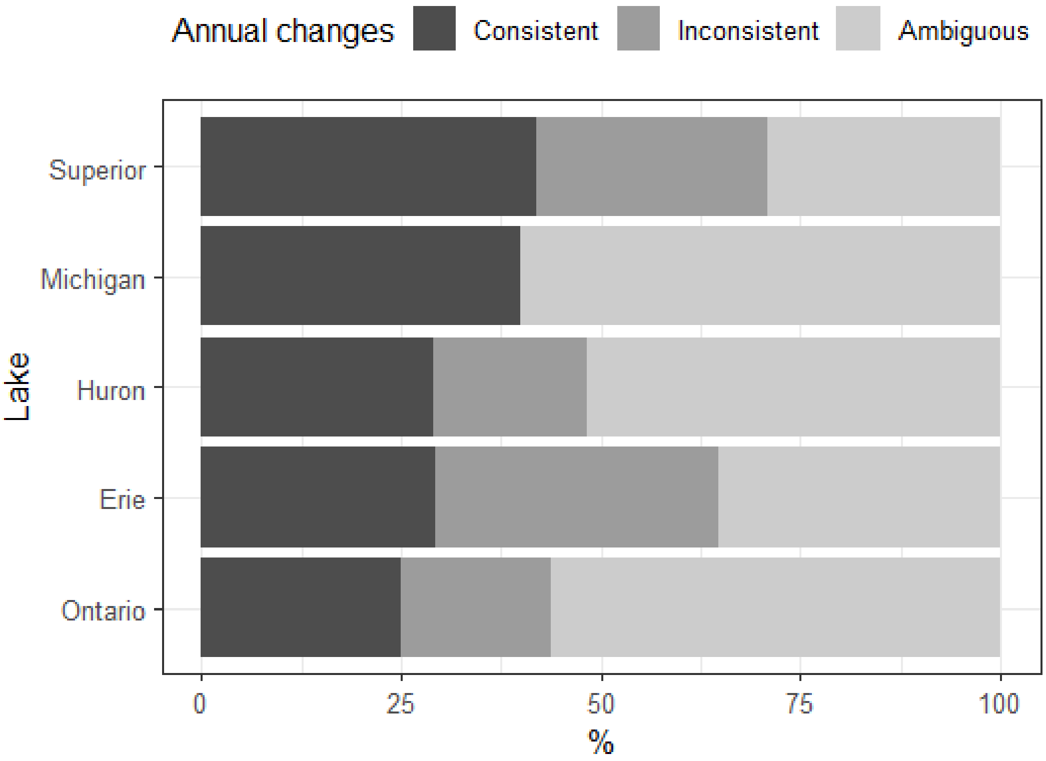

Figure 1.3. Percent composition of annual changes observed in 140 lake-years of lake trout and sea lamprey metrics in the Great Lakes. Marks are expected to increase with decreasing lake trout and increasing sea lampreys, and decrease with increasing lake trout and decreasing sea lampreys. When the expected change in marks is observed, the annual change is “consistent”. When the opposite change in marks is observed, the annual change is “inconsistent”. When lake trout and sea lampreys are both increasing or both decreasing, the annual change is “ambiguous”.

Finally, I repeated the simulation three more times, adding measurement error from just one component metric at a time to assess the contribution of each metric’s measurement error to the inconsistency rate.

1.3 Results

Estimates of all three status metrics (relative lake trout abundance, sea lamprey abundance, and sea lamprey marking rates on lake trout) were available for 137 lake-years (32 marking years for Lakes Superior, Huron, and Ontario; 20 marking years for Lake Michigan; and 21 marking years for Lake Erie; Table 1.1, Figure 1.1).

The Type II functional response model converged for all five lakes combined, with well-behaved curves for four lakes (Table 1.3). The attack rate for Lake Michigan rose rapidly from 0 to its maximum, remaining at that level for the entire range of observed lake trout CPEs (Figure 1.4).

Table 1.3. Estimated parameters from Type II functional response models relating lake trout relative abundance to sea lamprey attack rates in each Great Lake. Estimated parameters are not comparable across lakes. They are in different units (due to differences in recording lake trout relative abundance) and incorporate confounding effects of lake-specific lake trout survival, sea lamprey survival, and lake trout catchability.

Lake	Alpha	Beta
Superior	8.32e-07	1.87e-02
Michigan	1.43e-03	1.16e-01
Huron	1.39e-06	2.17e-01
Erie	8.65e-06	1.27e-05
Ontario	4.53e-07	2.58e-05

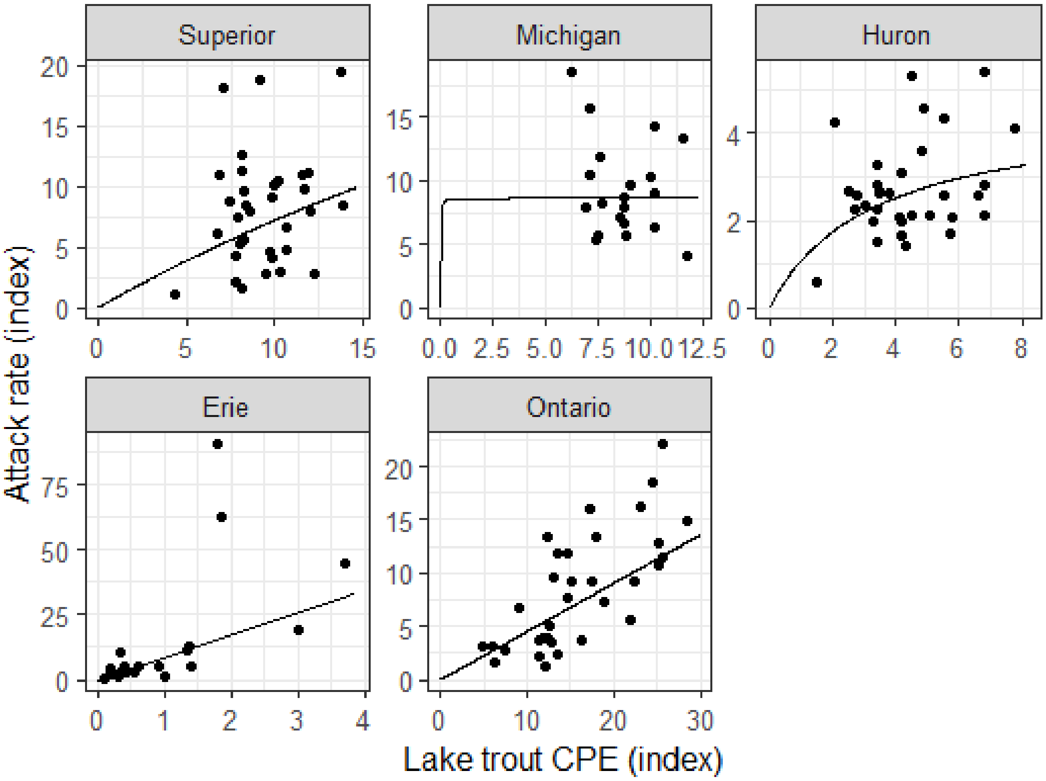

Figure 1.4. Sea lamprey attack rate (A, an index) as a function of the relative abundance of lake trout (D, in millions, in different units for each lake). Points represent observations; lines represent model predictions from a single Type II functional response model fit to all lakes simultaneously. Dashed lines show initial fit of different curves for Lakes Michigan and Huron; solid lines show final fit where Lakes Michigan and Huron share the same α parameter.

The average coefficient of variation was $\overline{C}_D = 0.233$ for lake trout density, $\overline{C}_L = 0.0700$ for adult sea lamprey abundance, and $\overline{C}_M = 0.392$ for marking rates (Figure 1.5).

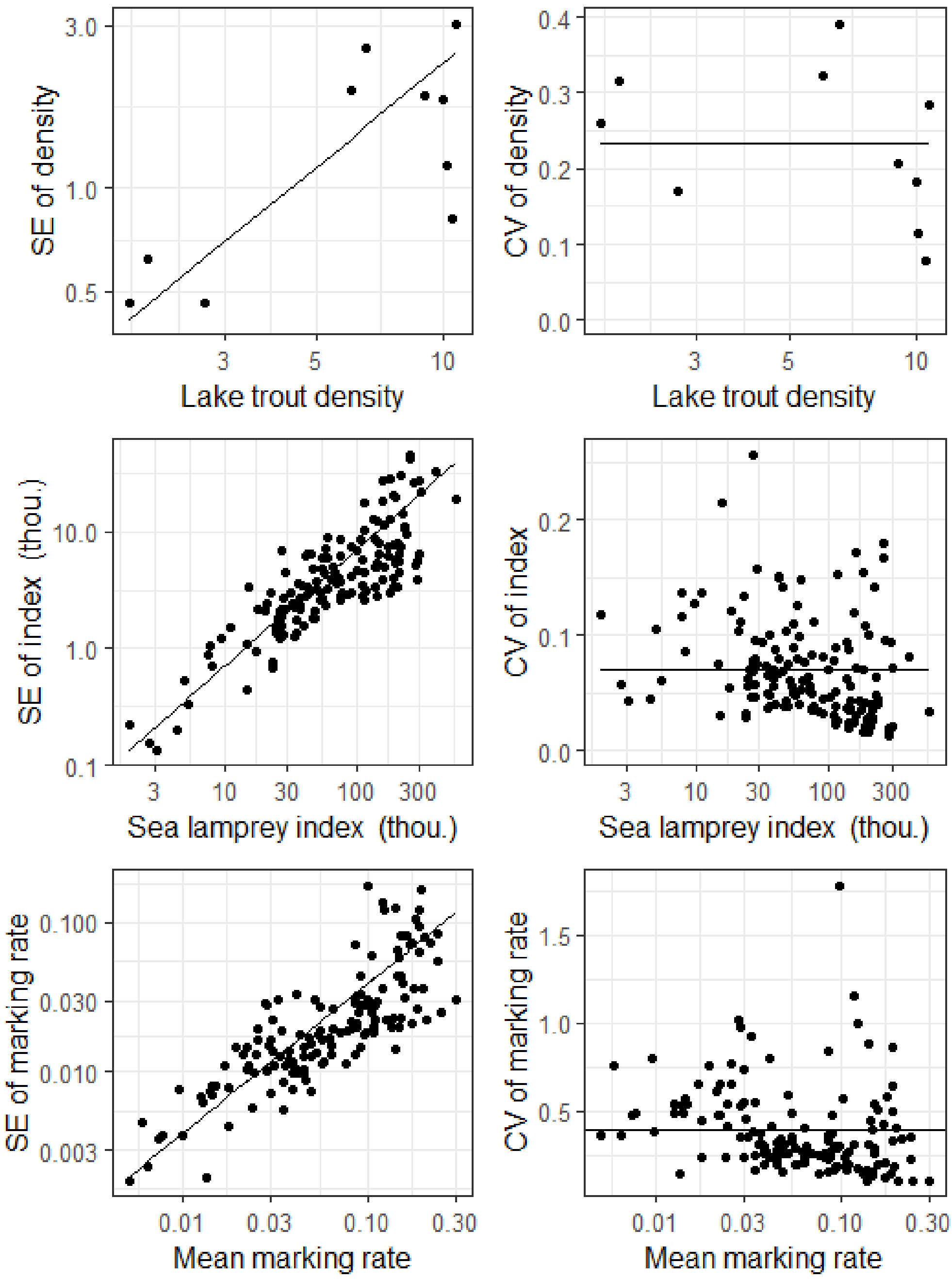

Figure 1.5. Relation between precision (standard errors and coefficients of variation) and means for lake trout density, an index of adult sea lamprey abundance, and marking rate. Points represent observations, lines represent fitted relations, which are used to generate measurement errors in the simulation model.

Sample statistics from observed data used to simulate time series of lake trout CPE and sea lamprey abundance are shown in Table 1.4. Simulated inconsistency rates were only similar to observed inconsistency rates in one lake, Michigan, which had no observed inconsistencies in 19 paired years (Table 1.5, Figure 1.6). Simulated inconsistency rates in the other lakes were well below observed values. Measurement error in marking rates consistently contributed the most to the average inconsistency rate from the simulations (Figure 1.7, Table 1.5).

Table 1.4. Sample size, mean, standard deviation (SD), and first order autocorrelation (AC) of lake trout CPE and sea lamprey abundance, all on the natural log scale, in each Great Lake. Prior to log transformation, lake trout relative abundance was expressed as the number (in millions) of large, lean lake trout captured (total length > 532 mm for Lakes Superior, Michigan, and Huron; age ≥ 5 years for Lake Erie; and total length > 431 mm for Lake Ontario) per unit effort (fish/km/net night for Lakes Superior, Huron, and Ontario; fish/1000'/net night for Lake Michigan; and fish/lift for Lake Erie). Prior to log transformation, sea lamprey abundance was expressed as the lake-wide number of adults (in thousands).

			Lake trout			Sea lamprey		
Lake	N	Years	Mean	SD	AC	Mean	SD	AC
Superior	33	1985-1990, 1992-2017	16.0	0.237	0.300	11.5	0.631	0.632
Michigan	21	1998-2017	16.0	0.172	0.357	11.4	0.627	0.665
Huron	33	1985-1989, 1991-2017	15.2	0.367	0.519	12.2	0.433	0.434
Erie	22	1992, 1994-1995, 1997-2002, 2005-2006, 2008-2017	13.3	1.013	0.705	9.5	0.866	0.331
Ontario	33	1986-2017	16.5	0.446	0.828	10.6	0.395	0.380

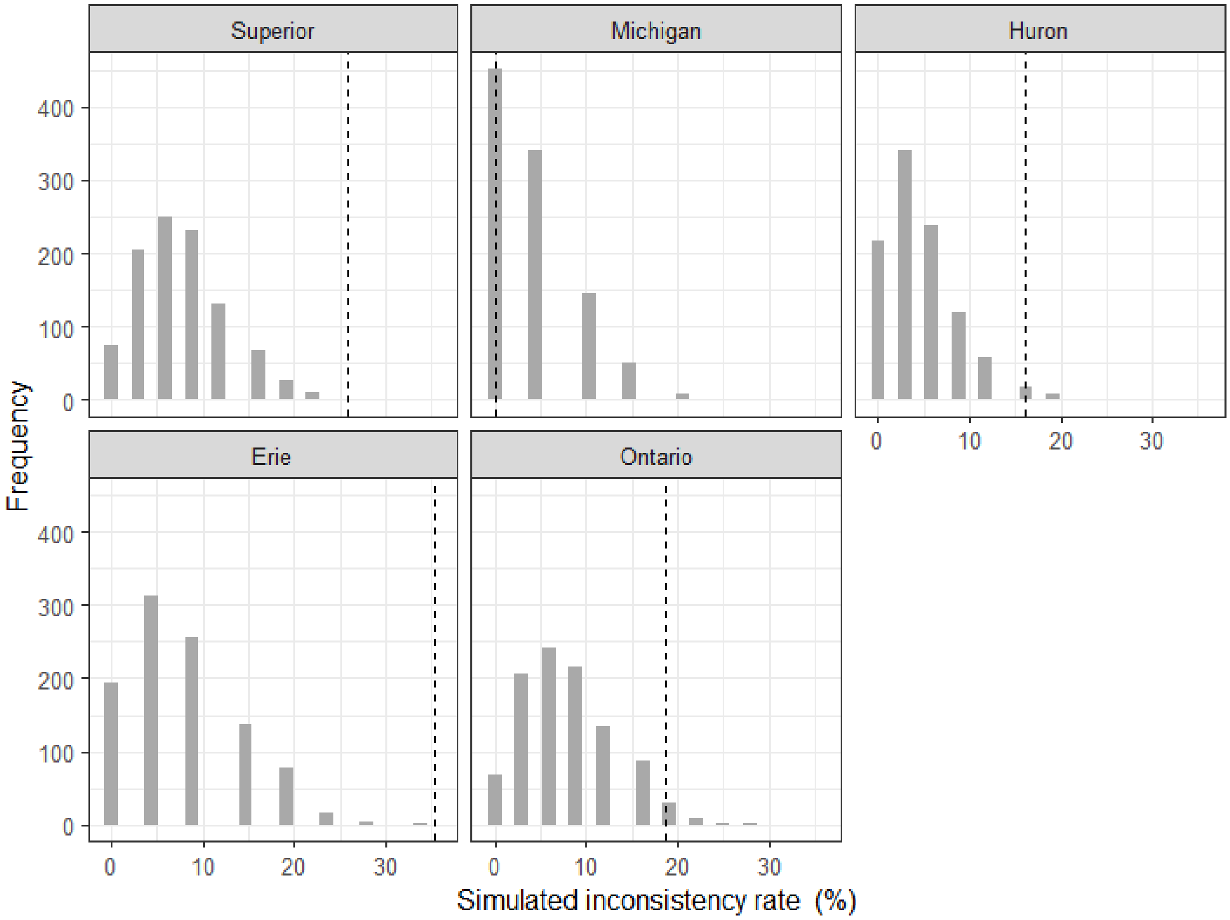

Figure 1.6. Distribution of inconsistency rates from 1,000 simulations with measurement error from all three metrics (lake trout, sea lampreys, and marking rates). Observed rates are denoted by vertical dashed lines.

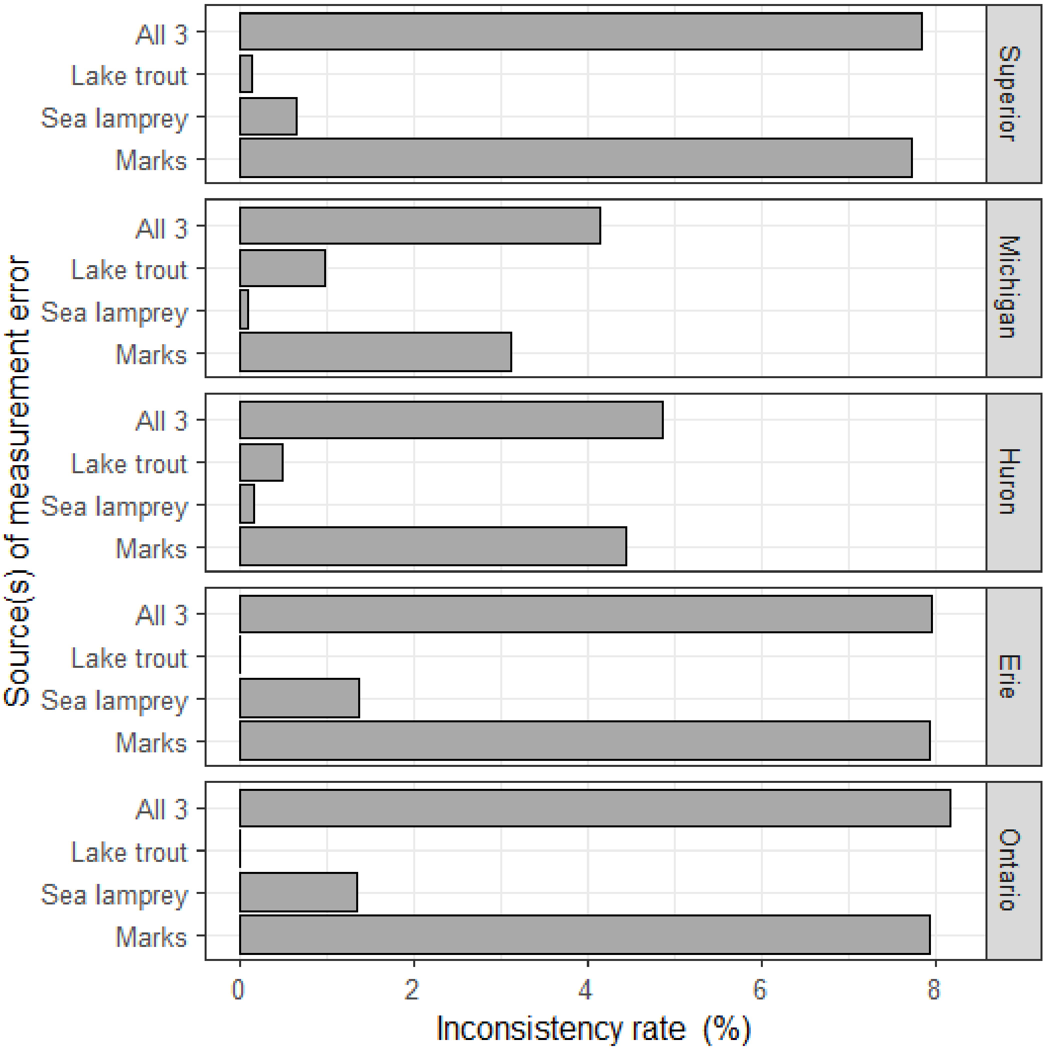

Figure 1.7. Inconsistency rate from simulated data with measurement error from all three metrics (all 3) and with measurement error from one metric at a time (lake trout, sea lampreys, and marks).

1.4 Discussion

Measurement error was not the primary cause of inconsistencies seen in sea lamprey predator-prey dynamics. Measurement error contributed far less to simulated inconsistency rates than expected, suggesting that inconsistencies are largely a result of model error. This could include environmental and population factors that may affect lake trout healing and lethality rates in response to sea lamprey attacks, factors that are currently ignored or assumed constant. I assumed constant non-sea lamprey-induced mortality of lake trout (fishing and natural mortality), constant mortality of juvenile sea lampreys, and constant lethality rate of lake trout attacked by sea lampreys, with negligible influence of sizes of juvenile sea lampreys and large lake trout. The model also assumed that sea lampreys only attacked lean lake trout and did so without regard to relative abundance and spatial distribution of lake trout stocks and strains, or other host species. Adams and Jones (2020) demonstrated that the abundance of an alternative host (Chinook salmon) affected the attack rate of sea lampreys on lake trout in Lake Ontario. Hoshino et al. (2014) found that ignoring spatial and stock structure can have a profound effect on bioeconomic fishery model error.

The measurement error I simulated for sea lamprey abundance is certainly underestimated. Although I am confident the error I simulated accurately reflects uncertainty in sea lamprey spawning run size in sampled streams, it does not capture any uncertainty in the factor used to scale up from relative to absolute abundance (Barber et al., *In preparation*). I gamed with increases in the sea lamprey measurement error to see how much simulated inconsistency rates were affected. Simulated inconsistency rates in Lakes Superior, Huron, and Ontario (22%, 18%, and 24% respectively) only approached observed rates when the coefficient of variation for sea lampreys was increased by two orders of magnitude ($100 \times C_L$).

The measurement error I simulated for lake trout may be slightly underestimated, because it was informed by gill net surveys conducted in lakes much smaller than the Great Lakes, with presumably reduced spatial variation and a smaller sampling fraction. Estimates of coefficients of variation from other studies on Great Lakes lake trout were larger than the estimate I used. Sitar et al. (1999) estimated a CV of 0.5 for lake trout CPE in southern Lake Huron in 1984-1994. Wilberg et al. (2003) estimated CVs for lake trout assessment survey CPE in Michigan management areas of Lake Superior ranging from 0.26 to 0.73 (mean 0.44) during 1984-1998. Wilberg et al. (2003) compared these CVs to those obtained from commercial fishing during 1929-1943 and found them to be comparable, so I do not expect the CVs to change over time.

The measurement error simulated for marking rates, which contributed the most to simulated inconsistency rates, should be represout that had known marking histories, including some lake trout with no marks (Firentative. I used mark misclassification information from a workshop conducted with lake trkus et al., *In review*). However, lake trout in that workshop were attacked by sea lampreys under controlled laboratory conditions (raceways held at 7.0-7.6°C), which could lead to different attack behavior and mark appearance than those resulting from attacks in the lake. The lake trout and sea lampreys all came from Lake Superior, which may also lead to differential healing and appearance of marks compared to other lakes. This may be particularly important for Lake Erie (with warmer temperatures).

My primary interest was not to define functional response models of sea lamprey predation. I just used them as plausible models to inform my investigation of inconsistencies. However, because few functional response models have been fit to sea lamprey data, they merit some discussion here.

The marking rate is not the same as a predation or parasitism rate that the functional response model is intended for (Holling, 1959a), although it is assumed to be related (Schneider et al., 1996, Adams et al., *In review*). Also, in Lake Erie, lake trout abundance and marking rates are summarized using different sub-populations of lake trout: those > 4 years for the abundance and those > 532 mm for the marking rate. The average length of an age-4 lean lake trout in eastern Lake Erie in 2017 (n = 17) was 640 mm (Coldwater Task Group, 2018), so the relative abundance metric is tracking a smaller number of larger lake trout than the marking rate.

My model allowed effective search rate and handling time to vary among lakes. Effective search rate depends on the reactive (ambush) area of an unattached sea lamprey, the probability that a sea lamprey attacks a lake trout when one is encountered, the distance swum by a lake trout during the attack season, and the overlap in lake trout and sea lamprey habitat (Bence et al., 2003). While the first component may be similar across the Great Lakes basin, the others likely vary. Handling time may be similar across the Great Lakes, if each lake has enough large lake trout as potential hosts. Catchability is not comparable among most lakes because of differences in how lake trout relative abundance was assessed.

Although I fit Type II functional response curves to attack rates based on theoretical assumptions (Bence et al., 2003), variability in the data did not support the choice of a non-linear Type II functional response over a linear Type I functional response. This was most evident in Lakes Erie and Ontario with their very small estimated β_i parameters. When the β_i in equation (1) is 0, the relation becomes linear, $A_i = \alpha_i D_i$. Using Akaike's Information Criterion (Burnham and Anderson, 2002), the linear Type I model had more support than the nonlinear Type II model. The Type I functional response curve is characteristic of predators that search for prey randomly at a constant rate, regardless of prey density (Holling, 1959b). In such cases, handling time is negligible or, at least, it does not interfere with searching for prey. A sea lamprey attached to and feeding on a lake trout may be simultaneously searching for its next host. And, if the host to which it is attached tends to aggregate, searching while attached may be more efficient than searching while unattached. Large lake trout, the preferred host of Great Lakes sea lampreys, aggregate on spawning grounds in autumn (Krueger and Ihssen, 1995), coinciding with the peak attack time of sea lampreys in the Great Lakes (Spangler et al., 1980; Swink, 2003). The more complex Type III functional response curve might also be appropriate (Stewart et al., 2003), but fitting such models requires predation data at both low and high prey densities, which are lacking for most of the Great Lakes (Figure 1.4).

My definition of the inconsistency rate aligns directly with the perspective of decision makers examining the estimated metrics each year, without reliance on a defined attack rate relation. A rate based on a presumed attack rate relation would be a bit more broadly defined, including situations that were not obviously inconsistent. An inconsistency rate based on the Type II functional response would be based on quantifying observations from two consecutive years during which (1) marking rates increased and

$$\frac{L_j}{L_{j+1}} > \frac{1 + \alpha\beta D_j}{1 + \alpha\beta D_{j+1}}$$

or (2) marking rates decreased and the inequality was reversed. For example, suppose relative abundance of lake trout in Lake Huron declined from D_1=5 to D_2=4 million, and abundance of sea lampreys was initially L_1=200,000. According to the definition I used, any decrease in the marking rate would be inconsistent if L_2 > 200,000. But according to the Type II functional response model, decreases in the marking rate would also be inconsistent if

$$L_2 > \frac{L_1(1+\hat{\alpha}\hat{\beta}D_2)}{1+\hat{\alpha}\hat{\beta}D_1} = 179{,}000 \ .$$

Lake Michigan was unique in having no inconsistencies observed during 1998-2017 (Table 1.5, Figure 1.3). Its low inconsistency rate was replicated in the simulation, with a modal rate of zero (Figure 1.6). Thus, Lake Michigan's low inconsistency rate was likely due to a combination of low sample size, low annual variability in lake trout abundance estimates, and high autocorrelation in sea lamprey abundance estimates, relative to the other lakes (Table 1.4).

Table 1.5. Observed number of inconsistencies (No. I) and inconsistency rates (IR, as percentages) from observed and simulated data.

		Observed		Simulated
Lake	Paired years	No. I	IR	IR
Superior	31	8	25.81	7.84
Michigan	20	0	0.00	4.14
Huron	31	5	16.13	4.86
Erie	17	6	35.29	7.95
Ontario	32	6	18.75	8.18

Efforts to reduce measurement error can be enticing, because they are often straightforward to implement (e.g., increasing sampling effort) and yield readily detectable results. Measurement error in lake trout and sea lamprey abundance estimates could be reduced by increased sampling effort, though an increase in sample size does not always reduce the effects of measurement error (Su and Peterman, 2012). Specifically, for sea lampreys, measurement error would be reduced by increasing the number of fin clipped sea lampreys recaptured, which could be achieved by clipping and releasing more adults or increasing trap capture efficiency. A better understanding of the relation between the sum of spawning run sizes in index streams and lake-wide adult sea lamprey abundance could allow us to estimate this error and perhaps reduce its influence. Measurement error in marking rates could be reduced by improved classification of marks, e.g., via the development of easily sampled protein biomarkers (Firkus et al., *In review*).

If measurement error is dwarfed by model error, as in this study, effort is better spent on improving the model. Several components could potentially reduce inconsistencies in the predator-prey metrics, including predictive relations of (1) lake trout survival of sea lamprey attacks (Adams et al., *In review*), (2) juvenile sea lamprey survival, (3) the presence of other host species (Adams and Jones, 2020), and (4) other potentially important covariates, e.g., sea lamprey size (Bence et al., 2003). Expanding lake-wide models to allow for varying effects at smaller spatial and temporal scales (Bence et al., 2003), could also help explain inconsistencies. For example, Rutter (2004) fit a multi-species functional response model for Lake Huron sea lampreys, with lake trout, lake whitefish (*Coregonus clupeaformis*), and Chinook salmon as potential hosts. His model was fit at a time when limited marking rate observations were available on alternative hosts, but now more data are available as many agencies regularly record marks on all species collected (Ted Treska, US Fish and Wildlife Service, personal communication). Rutter (2004) also found that some region-specific parameters outperformed lake-wide parameters. Carpenter et al. (1994) found that even with realistic measurement error, predator-prey models are difficult to identify correctly, specifically mentioning spatial variability as a significant source of error. However, increasing complexity introduces other uncertainties, which may or may not improve model performance. This is the well-established trade-off between bias and variance and the impetus behind information theoretic approaches that strive for parsimony (Burnham and Anderson, 2002; Guthery et al., 2005; Johnson and Omland, 2004; O'Neill, 1973).

Ecological metrics not aligned as expected cloud our interpretation of underlying relations. Investigating to understand causes of misalignment can yield insights that may be used to clarify points of confusion and potentially bring metrics into alignment. For misaligned Great Lakes lake trout and sea lamprey predator-prey dynamics, measurement error was initially suspected, but my investigation suggested model error was to blame instead. Armed with this information, fishery managers, sea lamprey control agents, and decision-makers can continue to scrutinize future inconsistencies for possible explanations rather than shrugging them off as an expected consequence of measurement error, and researchers can pursue new models to bring these metrics into alignment, e.g., via incorporation of spatially structured within-lake components or alternative hosts.

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CHAPTER 2

USING SIMULATION TO UNDERSTAND ANNUAL SEA LAMPREY MARKING RATES ON LAKE TROUT

2.1 Introduction

Control of invasive sea lampreys (*Petromyzon marinus*) in the Laurentian Great Lakes was initiated in the 1960s in response to the decimation of native lake trout (*Salvelinus namaycush*) populations. Sea lamprey control is a critical part of the rehabilitation of lake trout populations, the preferred hosts of sea lampreys in the Great Lakes. Assessments of lake trout and sea lampreys are key to models describing their population dynamics and host-parasite interactions and consequently to informing fishery management decisions. However, quantifying host mortality from sea lamprey marks observed on captured fish is challenging because only fish that have survived their injuries so far are observed. In fact, the group of most interest to fishery managers, those that died from sea lamprey attacks, is the group about which the least is known. Some hosts will have died before sampling takes place and are thus unobservable, and an unknown percentage of observed fish would have died from their wounds if they had not been sampled.

To assess lake trout rehabilitation, fishery independent gill net surveys are conducted annually by state, tribal, and federal agencies. Among other measurements, captured lake trout are examined for evidence of sea lamprey attacks. Marks from sea lamprey attacks are categorized according to whether the skin was pierced (Type A marks, indicating sea lamprey feeding) or intact (Type B marks) and the extent of healing from fresh marks (stage 1) to well healed marks (stage 4) (King, 1980; Ebener et al., 2003). Current practice in the Great Lakes is to report marking rates as the number of A1, A2, and A3 marks combined per 100 lake trout > 532 mm (Eshenroder and Koonce, 1984), except Lake Ontario which uses the number of A1 marks per 100 lake trout > 431 mm (Lantry et al., 2015). Time series of marking rates are used as an index of sea lamprey-induced mortality of lake trout (Sitar et al., 1999) and to assess the status of sea lamprey control in the Great Lakes (www.glfc.org/status, 27 Jun 2019), with lower marking rates indicating improved control.

Managers have focused their attention on pierced Type A marks, because they pose the greatest risk to lake trout and the greatest benefit to sea lampreys. However, because Type A marks are associated with potentially lethal attacks on lake trout (Swink, 2003), observed marking rates on survivors underestimate the actual average number of attacks per fish. This survivor detection bias could be corrected for, if the probability of death from a sea lamprey attack was known. However, the probability of death is unknown and likely to vary with factors such as host size and temperature (Swink, 2003). The need to adjust observed sea lamprey marking rates for the probability of survival has been discussed in the Great Lakes sea lamprey literature (see Bence et al., 2003 for a review). When an absolute attack rate is needed (e.g., when converting marking rates to mortality), the probability of survival has typically been assumed known and constant over time, although effects of host size have been taken into account (e.g., Sitar et al., 1999; Ebener et al., 2005).

The presence of detection bias in observing survivors of sea lamprey attacks has long been recognized in the interpretation of sea lamprey marks, and led to the convention of tracking only relatively fresh marks (A1–A3, Eshenroder and Koonce, 1984). The presence of the bias necessitated an assumption of a constant survival probability given a piercing attack (Eshenroder and Koonce, 1984), even though attack lethality was known to vary with water temperature and the ratio of host mass to sea lamprey mass (Farmer, 1980). Koonce and Locci-Hernandez (1989) later used the ratio of sizes to estimate attack lethality (with a survival threshold ≥ 40, i.e., a host with mass more than 40 times that of an attacking sea lamprey would survive an attack) in their sea lamprey management model. Both quantitative estimates of sea lamprey-induced mortality and the use of marking rates as indices of attack rates rely on an assumption of constant detection probability (Bence et al., 2003).

The influence of detection probability on observations is well understood in wildlife disease research, where the probability of detecting uninfected individuals is commonly higher than the probability of detecting infected ones (Heisey et al., 2006; Jennelle et al., 2007). Uncorrected disease prevalence data can lead investigators to report overestimates, underestimates, and exaggerated peaks in disease prevalence (Jennelle et al., 2007). Jennelle et al. (2007) conclude "observed variations in prevalence may be completely spurious artifacts of variation in detection probability, rather than changes in underlying disease dynamics."

The need for correcting detection bias in Type A marking rates may be avoided by focusing instead on non-pierced Type B marking rates. Type B marks are less lethal to lake trout (Swink, 2003), so they are less susceptible to survivor bias. Thus, observed Type B marking rates may be a better indicator of true sea lamprey attack rates and sea lamprey-induced mortality rates of lake trout. Why would a sea lamprey attach to a host without feeding?

Farmer (1980) hypothesized that lack of feeding is due to sea lampreys being satiated and that attachment is for energetic benefits of relying on hosts for locomotion. Sea lampreys gain about 25% of their body weight after just four days of feeding on large lake trout (leaving Type A marks), so satiation is certainly possible, but sea lampreys also gain some weight when they leave Type B marks, suggesting additional benefits beyond assisted locomotion (Tyler Firkus, Michigan State University, 16 Aug 2019, personal communication). Sea lampreys are poor swimmers compared to most teleosts and don't possess swim bladders, so they must expend energy just to maintain position in the water column (Beamish, 1974).

My objective was to determine how well observed Type A and B marking rates on lake trout index true attack rates and sea lamprey-induced mortality. I simulated sea lamprey attacks on lake trout and recorded the subsequent distribution of marks. The simulation enabled me to compare marking rates observed in surveys of surviving lake trout to underlying known attack rates and sea lamprey-induced mortality. A range of feasible sea lamprey attack rates, pierce rates, and lethality rates were simulated for several different size distributions of lake trout. Results were used to evaluate the performance of surveyed Type A and Type B marking rates as indices of attack rates and sea lamprey-induced mortality, under plausible assumptions about the attack process. I specifically addressed how variation in pierce and lethality rates might influence relationships between observed marking rates, actual attack rates, and lake trout mortality. In particular, I explored how correlated Type A and B marking rates were to (1) actual attack rates when pierce rates were held constant, (2) actual attack rates when lethality rates were held constant, (3) actual mortality rates when pierce rates were held constant, and (4) actual mortality rates when lethality rates were held constant.

2.2 Methods

Sea lamprey attacks were simulated for populations of lake trout, each defined by a length-frequency distribution. Lake trout were subjected to a single sea lamprey feeding season (June–December) with varying levels of sea lamprey attack rates, pierce rates, and lethality rates applied in monthly time steps (Table 2.1, Figure 2.1).

Table 2.1. Summary of terms used to describe sea lamprey attacks on lake trout. Only the first term, marking rate, is based on field observations; all other terms represent true rates unobservable in the field.

Term	Definition
Marking rate	Number of sea lamprey marks per lake trout based on observations of surviving lake trout
Attack rate	Number of sea lamprey attachments per lake trout
Pierce rate	Proportion of sea lamprey attacks that pierce the muscle wall (leaving a Type A mark)
Lethality rate	Proportion of sea lamprey-attacked lake trout that die as a result of the attack
Sea lamprey-induced mortality rate	Proportion of the lake trout population that is killed by sea lamprey attacks in a year

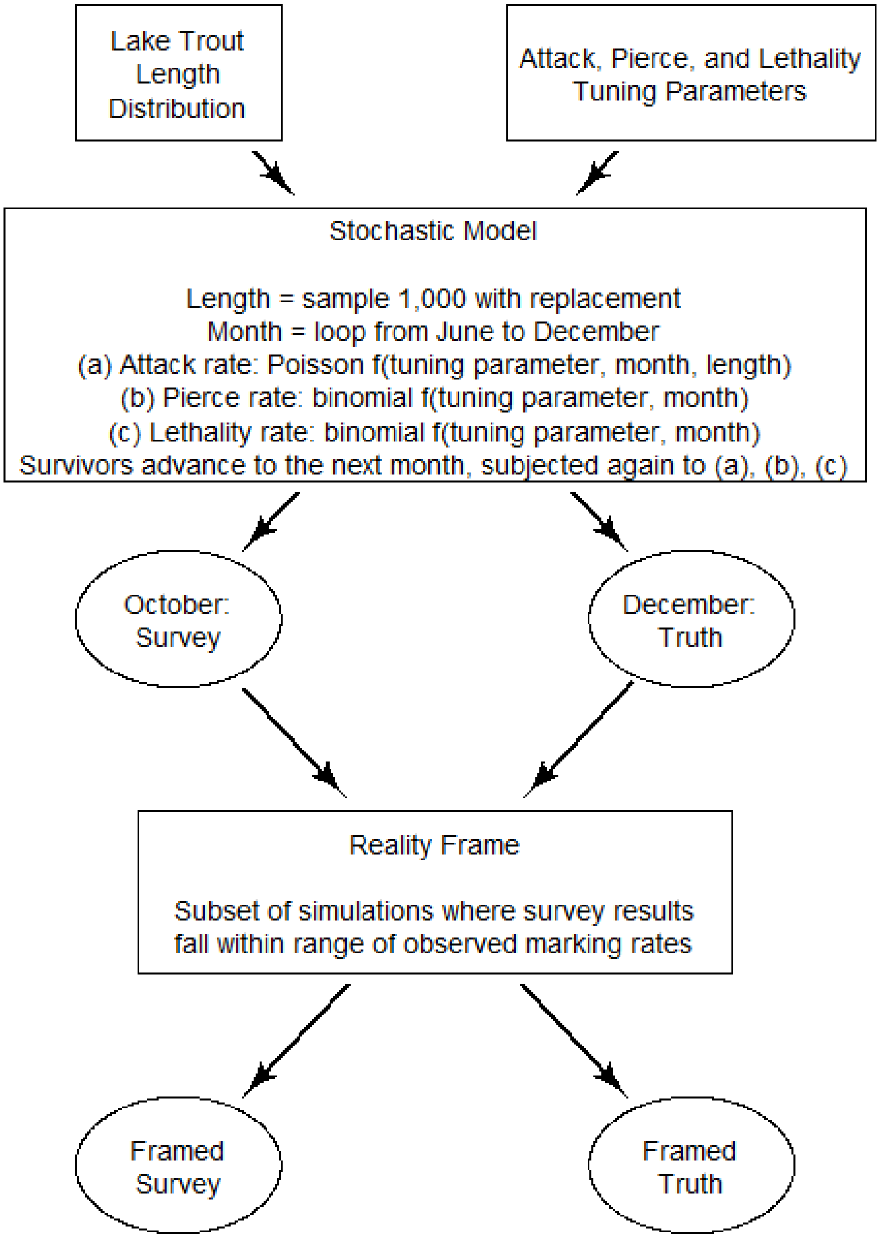

Figure 2.1. Simulation of sea lamprey attacks on a population of lake trout during a single feeding season in monthly time steps, June–December. Inputs are rectangles, outputs are ovals.

As described in detail below, sea lamprey attack rates, pierce rates, and lethality rates are set via “tuning parameters”. The tuning parameters are convenient surrogates for use in the simulation rather than explicitly modeling factors that might influence the attack, pierce, and lethality rates. Lack of prior information on appropriate levels for attack rates, pierce rates, and lethality rates necessitated that I explore a broad range of values in the simulation. All possible combinations of the three tuning parameters were included in the simulation, and a subset of plausible outputs were selected by constraining them to the range of marking rates observed during agency surveys in the Great Lakes.

All analyses were conducted and figures produced with R (R Core Team, 2018) including packages tidyverse (cran.r-project.org/package=tidyverse, Wickham and Grolemund, 2017), sp (Bivand et al., 2013; Pebesma and Bivand, 2005), rgeos (Bivand and Rundel, 2019), broom (cran.r-project.org/package=broom), and diagram (cran.r-project.org/package=diagram).

2.2.1 Lake trout

Gill net surveys provided information about lake trout size structure and sea lamprey marking in Lakes Superior, Huron, and Michigan over 10 years (2008–2017). Data were provided by the Great Lakes Fishery Commission (Ted Treska, US Fish and Wildlife Service, 6 Mar 2019, personal communication). In each survey, lake trout were measured to the nearest mm and examined for sea lamprey marks. Size distributions were resampled for the simulation and observed marking rates seen in the survey data were used to filter implausible results from the simulation output (see *Reality frame* section). Lake trout data from Lake Erie were too sparse to include. Lake Ontario was excluded from the analysis because of its unique way of tracking marking rates (using just the A1 marks).

For each simulation, 1,000 fish were sampled from a single lake-year's length-frequency distribution with replacement. Lake trout were assumed to be the same length (no growth) throughout the simulated marking period.

2.2.2 Attack rate

The simulated mean number of sea lamprey marks per lake trout was determined by month, lake trout size, and an attack rate tuning parameter. The relation to month was based on a three-parameter Gaussian curve (Figure 2.2) fit to observed sea lamprey attack rates on Lake Huron lake whitefish (*Coregonus clupeaformis*), age 3–5 years, during 1964–1967 (Spangler et al., 1980)

$$(1) \qquad W_1 = x \cdot exp\left[-0.5\left(\frac{D-z}{y}\right)^2\right]$$

where W_1 is the number of "fresh" (not healed) sea lamprey marks (A1–A3) per lake whitefish, D is the decimal month, x=0.189 is the maximum height of the curve, y=1.11 is a scale parameter relating to the width of the peak, and z=9.53 is the decimal month (mid-September) at which the peak occurs. The x, y, and z parameters were all estimated by nonlinear regression.

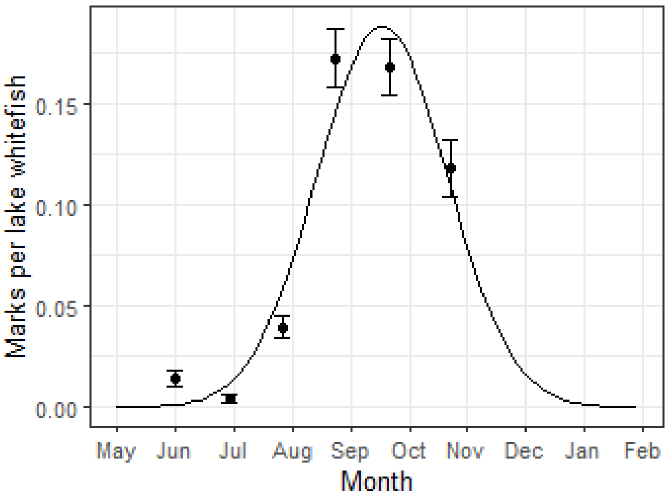

Figure 2.2. Number of fresh sea lamprey marks per lake whitefish age 3–5 years (19,179 lake whitefish) in the commercial catch at Burnt Island in northern Lake Huron from 1964 to 1967 (Spangler et al., 1980) with 95% confidence intervals. The line represents a three-parameter Gaussian fit.

The relation to size was based on a logistic relation of observed sea lamprey marks on Lake Huron lake trout,

$$(2) \qquad W_2 = \frac{\theta}{1 + exp[\alpha(\beta - L)]}$$

where W_2 is the mean number of marks per lake trout, L is lake trout total length (in mm), α=0.0231, β=567 (the mean of three regional βs for Lake Huron, ranging from 529 to 596), and θ=0.398 (the asymptotic marking rate, the mean of 52 region-year θs for Lake Huron in 1984–2000, ranging from 0.064 to 0.955, Rutter and Bence, 2003).

Note that these studies (Rutter and Bence, 2003; Spangler et al., 1980) were focused on *observed* marking rates, but I am using them to simulate plausible *actual* attack rates.

Equations (1) and (2) were combined into a single equation, replacing the product of their maxima ($x \cdot \theta$) with a single maximum, the attack rate tuning parameter, τ_1. The result is

W, the number of marks per simulated lake trout, which depends on the attack rate tuning parameter, month, and lake trout size,

$$W = W_1 \cdot W_2 = \frac{\tau_1 \cdot exp\left[-0.5\left(\frac{D - 9.53}{1.11}\right)^2\right]}{1 + exp[0.0231(567 - L)]}$$

Finally, marks were allocated to each lake trout (of a given size in a given month) using a Poisson distribution with mean and variance both equal to $\lambda = W$ (Bence et al., 2003; Eshenroder and Koonce, 1984).

2.2.3 Pierce rate

The probability an attacked lake trout is pierced by a sea lamprey (resulting in a Type A mark) was determined by the month, based on unpublished data from laboratory experiments described by Swink (2003). A locally weighted regression (loess) was fit to the proportion of pierced sea lamprey attacks on lake trout during June–December of 1983–1995 (Figure 2.3). This proportion was then scaled to have a maximum of one (by dividing the loess predictions by the monthly maximum, 0.856 in August) before multiplying it by a pierce rate tuning parameter, τ_2. This scaling results in a tuning parameter that represents the peak pierce rate in the sea lamprey feeding year. The scaled and tuned month-specific proportion of Type A marks was used as a binomial probability to determine whether each lake trout mark was Type A or Type B in a given month.

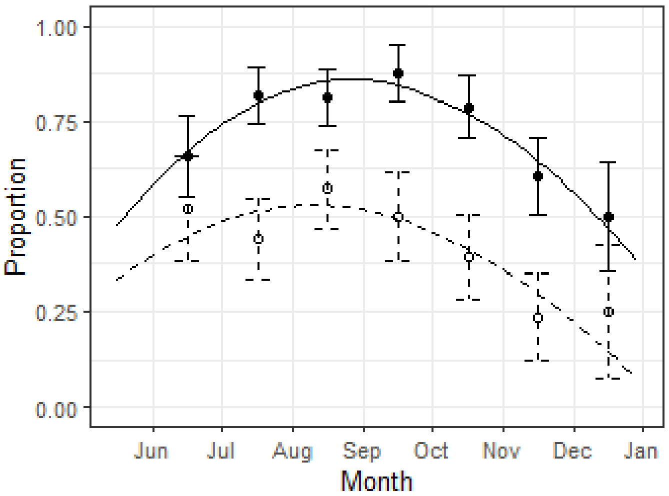

Figure 2.3. Monthly proportion of pierced sea lamprey attacks on lake trout (filled circles, 606 lake trout, Swink, 2003) and proportion of lake trout with Type A marks that died (open circles, 450 lake trout, Swink, 2003) with 95% confidence intervals. Lines represent fitted loess relations.

2.2.4 Lethality

The probability a pierced lake trout dies was determined by the month and the lethality tuning parameter. The relation to month was based on unpublished data described by Swink (2003) during which single sea lampreys were allowed to feed until they detached from the host or the host died (median attachment time 4.8 days, range 0.2 to 65.1 days). A locally weighted regression was fit to the lethal proportion of Type A (piercing) marks on Lake Huron lake trout during June–December of 1983–1995 (Figure 2.3). This proportion was then scaled to have a maximum of one (by dividing loess predictions by the monthly maximum, 0.529 in August) and multiplied by a lethality tuning parameter, τ_3. The scaled and tuned proportion was used as a binomial probability to determine the survival of each Type A marked lake trout in a given month. Type B marks were initially assumed to cause no mortality of lake trout (see also the *Lethality of B marks* section).

2.2.5 Simulation

Tuning parameters were set to a range of equally spaced values. The range of attack rate tuning parameters (0.05, 0.52) was selected to span from the minimum to twice the maximum of observed marking rates in the Great Lakes (Table 2.2), because observed marking rates are always less than true attack rates in the presence of sea lamprey-induced mortality. Pierce rate tuning parameters were set to range from the minimum observed pierce rate to one (0.27, 1.00). Lethality rate tuning parameters were set to range from very near zero to one (0.01, 1.00).

Table 2.2. Summary of lake trout data used in the simulation and as reality frame, including ranges of sample sizes, lengths (in mm), marking rates, and pierce rates during 2008–2017.

	Sample Size		Length		Marking Rate		Pierce Rate	
Lake	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.
Superior	776	2,353	533	1,130	0.10	0.25	0.27	0.65
Michigan	1,490	4,580	533	1,050	0.07	0.26	0.34	0.58
Huron	858	1,439	533	998	0.05	0.18	0.73	0.95

At the end of December, the true status and fate of every lake trout was tallied, $T_{..} = T_{us} + T_{ud} + T_{ms} + T_{md}$, where T_{ik} is the number of lake trout with $(i = m)$ or without $(i = u)$ marks that survived $(k = s)$ or died $(k = d)$, and the dot subscript $(i$ or $k = .)$ indicates summation over the corresponding index, e.g., the total number of survivors was $T_{.s} = \Sigma_i T_{is} = T_{us} + T_{ms}$. The number and type of marks was also known and tallied, $M_{..} = M_{as} + M_{ad} + M_{bs} + M_{bd}$, where M_{jk} is the number of Type A $(j = a)$ or B $(j = b)$ marks on dead or surviving (k) lake trout. Annual summary statistics were calculated for the true attack rate, $Q = M_{..}/T_{..}$; the true lethality rate, $1 - p = T_{md}/M_{..}$, where p is survival; their product, the true annual sea lamprey-induced mortality rate, $A_L = T_{md}/T_{..}$; and the true pierce rate, $M_{a.}/M_{..}$.

At the end of October, the number of surviving lake trout and their marks were tallied. This represents the information available from a fall lake trout gillnet survey, the current source of the marking rate metric for Lake Michigan. In Lakes Superior and Huron, spring gill net surveys are used to assess marks presumed to reflect attacks on lake trout the previous fall. The following annual summaries were calculated: the marking rates, $m_A = M'_{as}/T'_{.s}$ and $m_B = M'_{bs}/T'_{.s}$, and the surveyed pierce rate, $M'_{as}/M'_{.s}$, where apostrophes (′) indicate October tallies.

Simulations were run for all possible combinations of 33 lake-years of lake trout length-frequency distributions and 15 input values for each of the three tuning parameters, for a total of 111,375 ($= 33 \cdot 15 \cdot 15 \cdot 15$) simulations. I regard the 33 lake-years as replicate simulations incorporating variation in length frequency distributions, and stochasticity associated with the tuning parameters.

2.2.6 Reality frame

For simulation results to be informative, they must be framed within the bounds of reality. So, simulation results were discarded if they had surveyed marking rates outside the bounds of those observed on lake trout in the Great Lakes. This approach, termed pattern-oriented modeling, is useful for reducing uncertainty in model parameters (Grimm et al., 2005).

For each lake, annual observations of sea lamprey marking rates on lake trout > 532 mm were plotted in two-dimensional space, observed Type A marking rate vs. observed Type B marking rate. Only those based on at least 100 lake trout were included. Type A marks included all A1–A3 marks, and Type B marks included all B1-B4 marks. Ideally, all well healed marks (A4 and B4) would have been excluded, but healing stage was not consistently recorded for B marks, so all stages were included for them. The reality frame was defined as the convex hull of these points (i.e., the smallest polygon containing all points with no concavities) plus a buffer of 0.02 in both the Type A and Type B marking rates. Simulation results that fell on or within the reality frame of a lake were retained for further exploration and analysis.

2.2.7 Model rationale

Sea lamprey attack, pierce, and lethality rates each had a temporal pattern, peaking between August and September. This corresponds to the rapid growth of juvenile sea lampreys due largely to gonadal development and, to a lesser extent, higher temperatures occupied by lake trout then (Bergstedt and Swink, 1995; Farmer et al., 1977; Madenjian et al., 2003; Swink, 2003).

Observed sea lamprey marking rates on lake trout during 2008–2017 were used to frame simulation results. However, some components of the model were derived from species and times with different marking rates (attack rates on lake whitefish 1964–1967, pierce and lethality rates on lake trout 1983–1995). These model components only serve to capture seasonal patterns in rates, which are expected to be relatively consistent across host species and years. Magnitudes of rates are controlled by the tuning parameters, and filtering of plausible results using the reality frame.

2.2.8 Analysis

Throughout this paper, "simulated" refers to all results prior to reality framing, "framed" refers to the subset of results falling within the reality frame, and "observed" refers to information on lake trout captured in gillnet surveys. The distributions of framed attack, pierce, lethality, and mortality rates were explored for each lake.

Koonce (1982) derived a relation between the observed marking rate (m), the true attack rate (Q), and the lethality of an attack ($1-p$), $\exp(m) = 1 + \exp(Qp)[1 - \exp(-Q)]$. Assuming Type B marks are not lethal to hosts ($p_B = 1$), the relation simplifies to $\exp(m_B) = 1 + \exp(Q_B)[1 - \exp(-Q_B)] = \exp(Q_B)$. Thus, if the pierce rate is relatively constant and non-piercing attacks cause no host mortality, then observed Type B marking rates should be proportional Type A attack rates, $\exp(m_B) \propto \exp(Q_A)$.

Eshenroder and Koonce (1984) showed instantaneous mortality due to sea lamprey predation (Z_L) is proportional to marking rates, $Z_L = m(1-p)/p$. Thus, if lethality of a sea lamprey attack is relatively constant and non-piercing attacks cause no host mortality, then observed Type A marking rates could serve as an index of the true instantaneous mortality rates, $Z_L \propto m_A$. Furthermore, if pierce rates were roughly constant ($Q_A \propto Q_B$) and lethality rates were roughly constant ($Q_A \propto m_A$ and $Q_B \propto m_B$), then one would expect observed Type A and B marking rates to be highly correlated ($m_A \propto m_B$) and both would be tightly linked to both Type A attack rates and mortality.

In this study, I explored these relationships using the framed data. First I looked at how both Type A and B marking rates were correlated to Type A attack rates and lake trout mortality rates, when pierce rates were subsetted to narrow ranges (± 0.05). Second I looked at the same correlations when lethality rates were subsetted to narrow ranges (± 0.05).

A second series of 111,375 simulations were run to see if relations examined above were still strong even if Type B marks resulted in the death of some lake trout. The lethality of Type A marks was determined as previously described, and the lethality of Type B marks was set to 24% of the Type A lethality rate. This was the maximum monthly lethality rate of Type B marks relative to that of Type A marks observed by Swink (2003) (mean 8%, range 0–24%).

2.3 Results

Simulated marking rates covered the range of marking rates observed on lake trout captured in the Laurentian Great Lakes. The reality frames based on Type A and B marking rates observed during 2008–2017 varied among the three Great Lakes. Lakes Superior and Michigan had higher Type B marking rates than Lake Huron; Lakes Superior and Huron had a slightly broader range of Type A marking rates than Lake Michigan (Figure 2.4). All following results are limited to simulations within reality frames, unless explicitly stated otherwise.

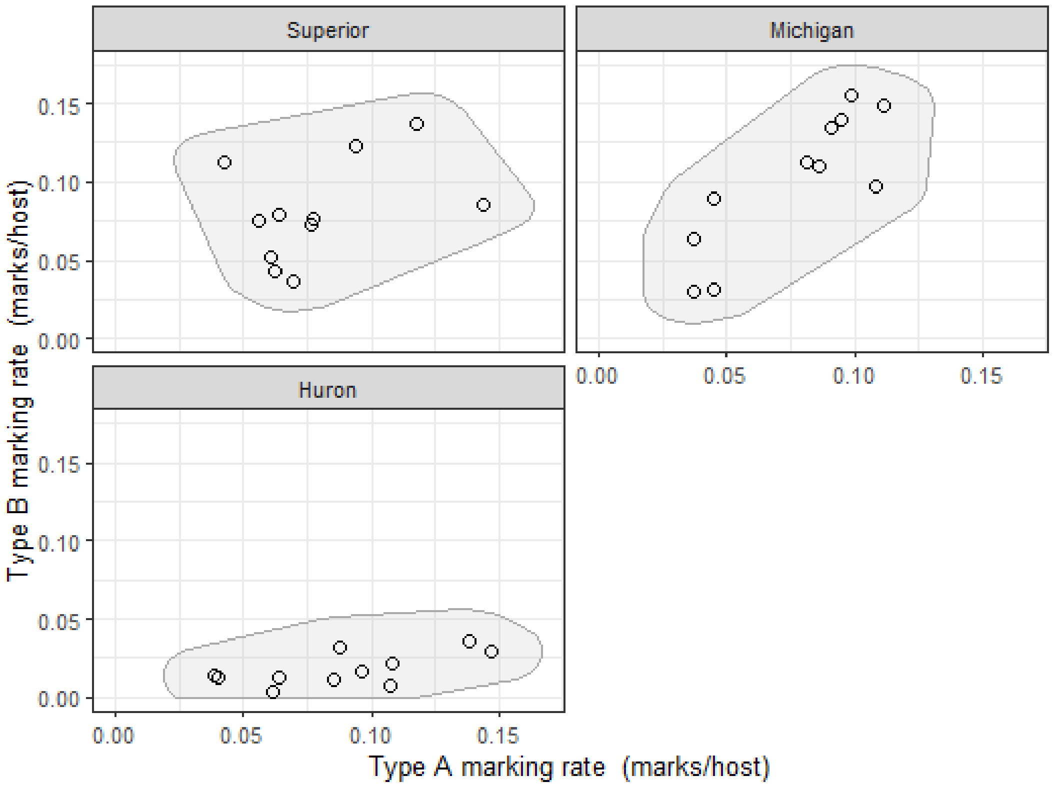

Figure 2.4. Sea lamprey marking rates (Type A and B) observed on lake trout captured during 2008–2017 and convex hulls with a buffer of 0.02 in direction of both Type A and Type B marking rates representing their reality frames.

Differences in lake reality frames led to different distributions of framed attack, pierce, lethality, and mortality rates among the lakes (Figure 2.5). The lower Type B marking rate on Lake Huron led to a noticeably higher pierce rate. Lake Huron also had a somewhat lower attack rate and a somewhat higher lethality rate, which in combination yielded a Type A marking rate similar to the other lakes. All three lakes had similar distributions of mortality rates.

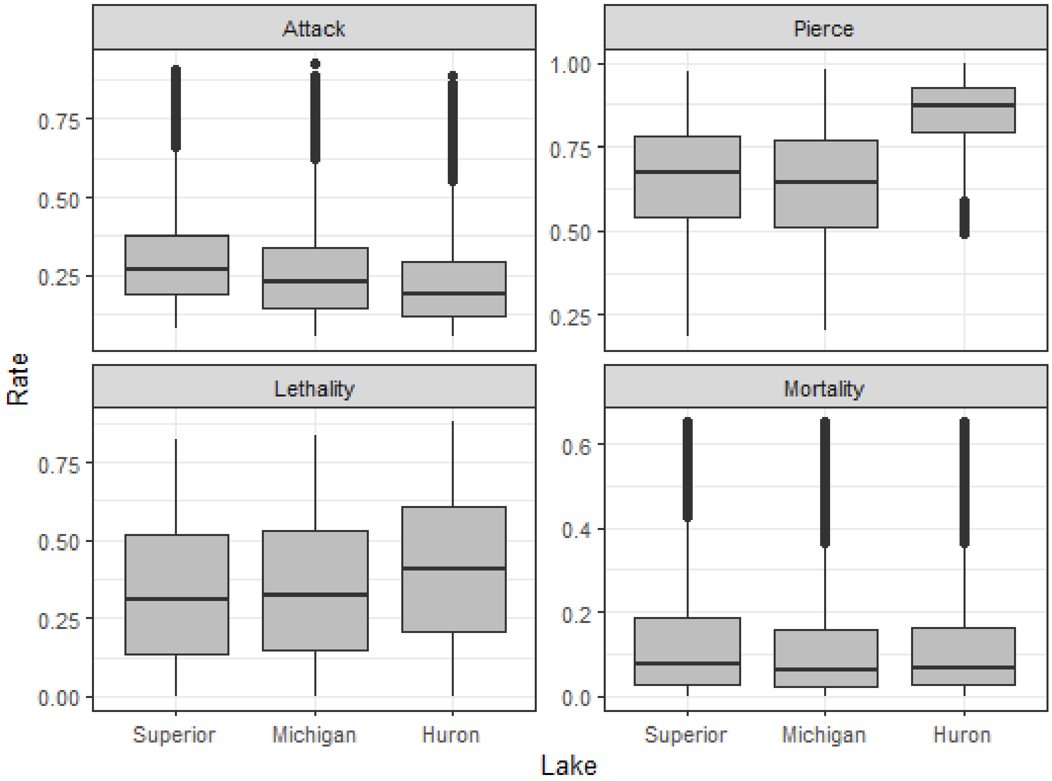

Figure 2.5. Distribution of framed attack, pierce, lethality, and annual mortality rates.

The framed Type B marking rate was more highly correlated with the Type A attack rate than with the framed Type A marking rate, when the pierce rate was held relatively constant (restricted to a range of ± 0.1, Figure 2.6). This is expected given that variations in lethality should not influence the relationship between Type B marking and attack rates. I also found that the framed Type A marking rate was more highly correlated with the Type A attack rate, when the lethality rate was held relatively constant (Figure 2.7). This reflects the fact that variation in the pierce rate does not alter the relationship between attacks that lead to piercing and later observation of survivors of those attacks.

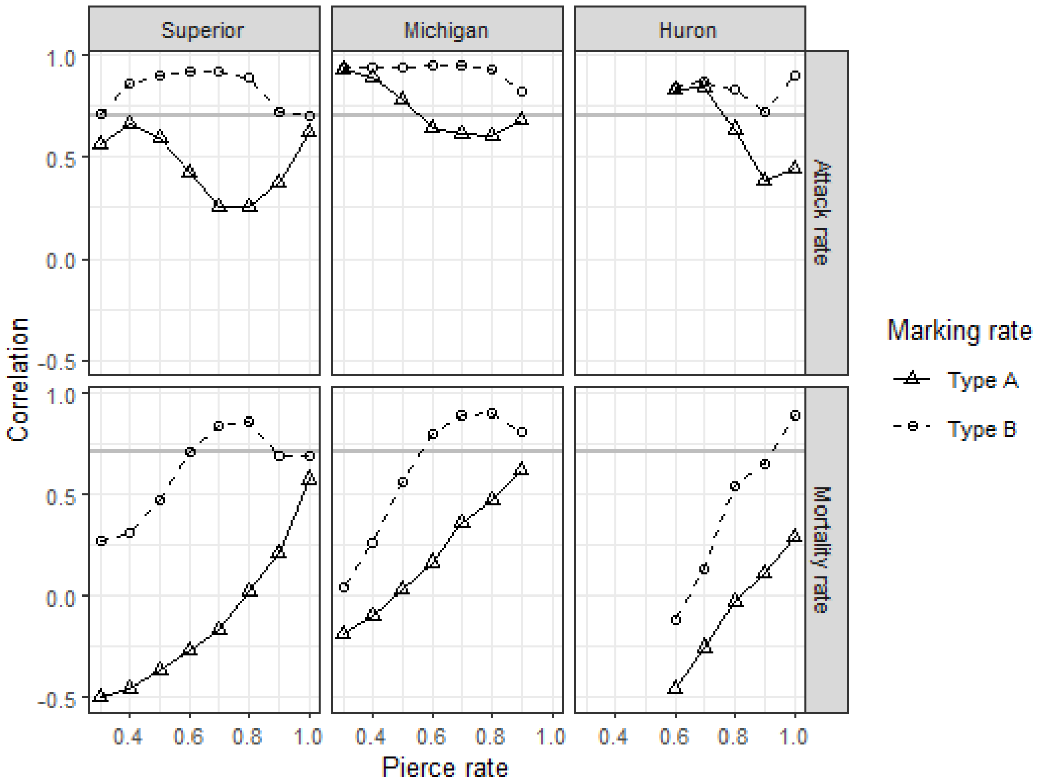

Figure 2.6. Correlation (r) between framed marking rates (both Type A and Type B separately) and Type A attack rates (first row) and instantaneous mortality rates (second row), for eight different pierce rates held relatively constant (restricted to the value on the x-axis ± 0.05). Correlations were only calculated when samples sizes were at least 100 (df ≥ 98). Points above the horizontal gray line indicate strong positive correlations, $r^2 > 50\%$.

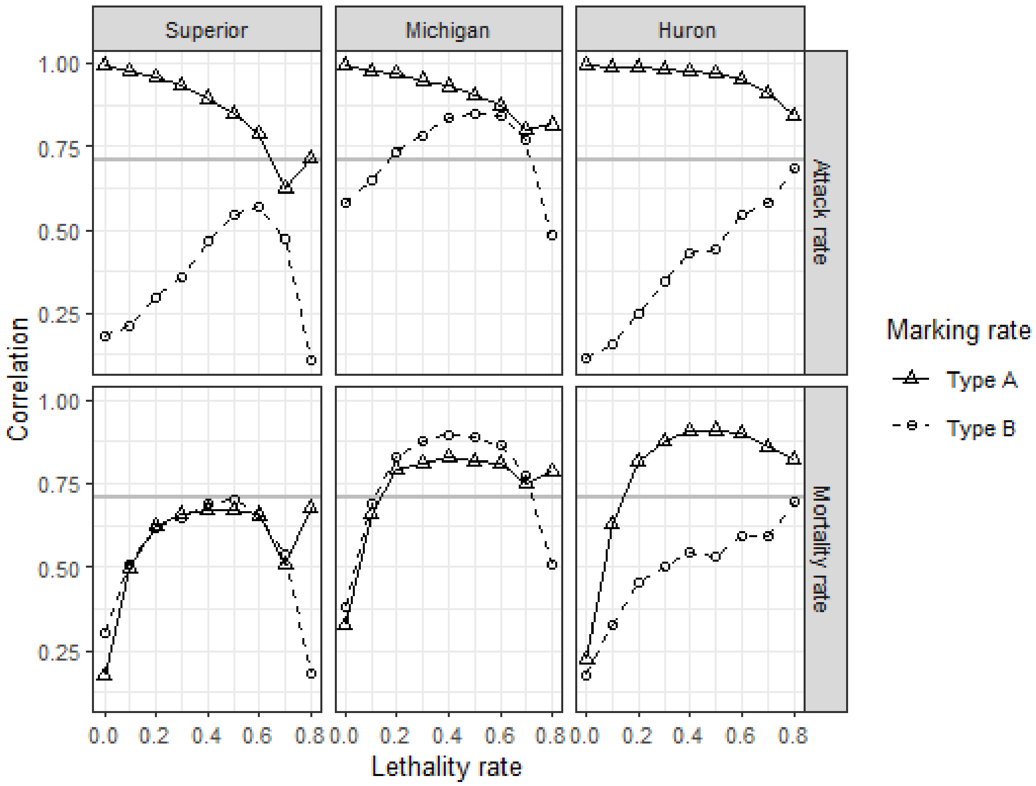

Figure 2.7. Correlation (r) between framed marking rates (both Type A and Type B separately) and Type A attack rates (first row) and instantaneous mortality rates (second row), for nine different lethality rates held relatively constant (restricted to the value on the x-axis ± 0.05). Correlations were only calculated when samples sizes were at least 100 ($df \geq 98$). Points above the horizontal gray line indicate strong positive correlations, $r^2 > 50\%$.

The framed Type B marking rate was more highly correlated with the instantaneous mortality rate than the framed Type A marking rate, when the pierce rate was held relatively constant (Figure 2.6). When the lethality rate was held relatively constant, the correlation of the framed marking rates and instantaneous mortality varied among lakes (Figure 2.7). For Lakes Superior and Michigan, both marking rates were similarly correlated with mortality; for Lake Huron, the framed Type A marking rate was more highly correlated with the instantaneous mortality rate than the framed Type B marking rate. In Lake Superior neither the Type A nor Type B marking rates were highly correlated with mortality for any lethality rates. In Lake Michigan, both marking rates were highly correlated with mortality for several lethality rates (Figures 2.7 and 2.8).

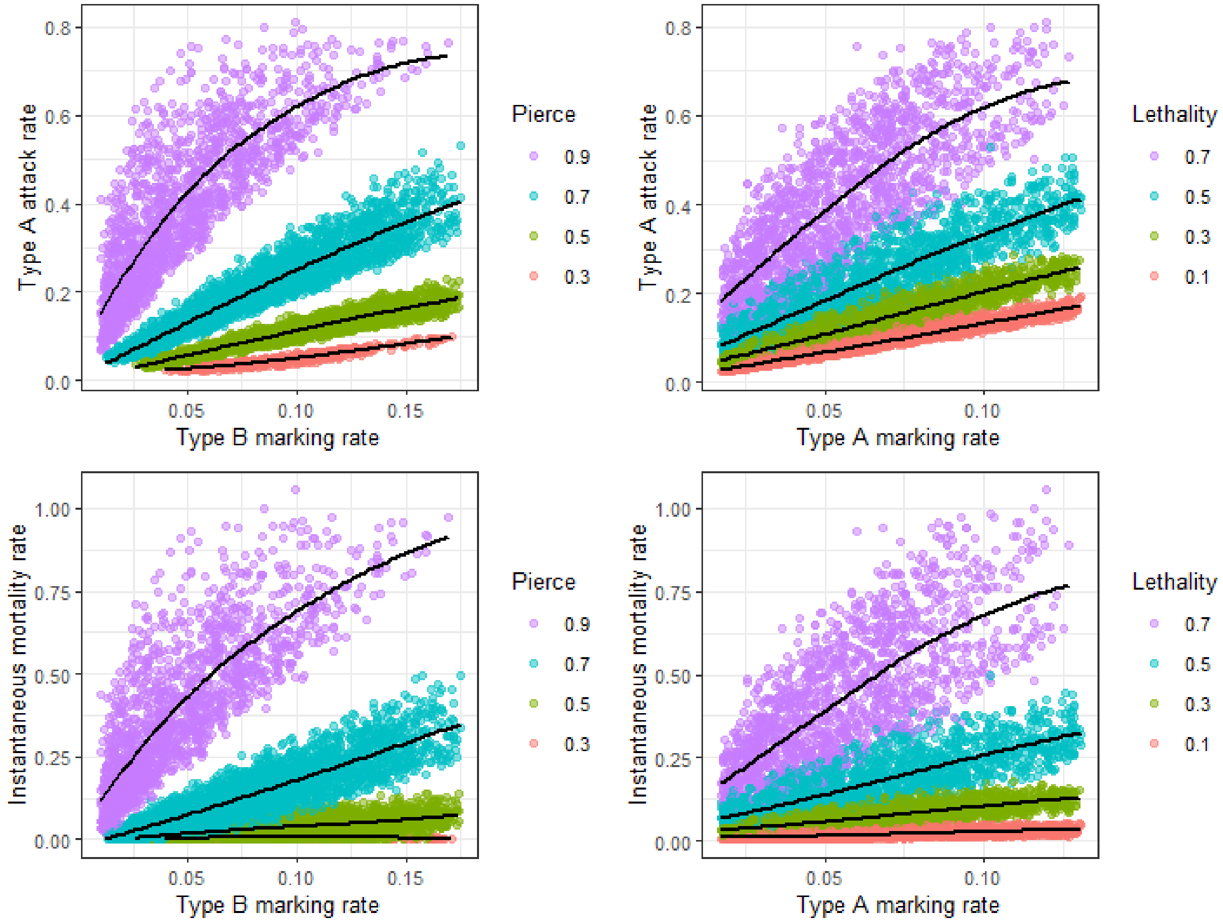

Figure 2.8. Relations between framed marking rates and Type A attack rates (top row) and instantaneous mortality rates (bottom row) in Lake Michigan simulations, for four different pierce rates (left column) and four different lethality rates (right column) held relatively constant (restricted to the value in the legend ± 0.05). Deviations in points of the same color reflect variation in length frequency distributions, stochasticity associated with tuning parameters, and different lethality (left column) or pierce (right column) rates.

The correlation between observed Type B marking rates and Type A attack rates held even in the presence of Type B lethality. Framed Type B marking rates explained more than 50% of the variation in Type A attack rates at pierce rates of 0.5–0.8 for Lake Superior, 0.4–0.9 for Lake Michigan, and 0.8 and 1.0 for Lake Huron. Framed Type A marking rates only explained more than 50% of the variation in Type A attack rates at pierce rates of 0.4, 0.5, and 0.9 for Lake Michigan and 0.8 for Lake Huron.

2.4 Discussion

Using observed sea lamprey marking rates on hosts as an index of attack or mortality rates requires the assumption that either the pierce rate or the lethality rate is relatively consistent from year to year. If both assumptions were true for upper Great Lakes lake trout, Type A and Type B marking rates over time would be highly correlated. They are significantly correlated for Lakes Michigan and Huron (r = 0.81 and 0.64, P = 0.004 and 0.046, respectively); but not for Lake Superior (r = 0.34, P = 0.333). So, for Lake Superior, at least one of the assumptions, and possibly both, are false.

Understanding whether the breakdown in the correlation between Type A and Type B marking in some cases is due to variable pierce rates or variable lethality has practical consequences. If lethality is constant but pierce rate varies then Type A marking rate would be a good index of both sea lamprey activity and mortality rates sea lampreys inflict on lake trout. If pierce rate is constant and lethality varied then it could be that neither Type A nor Type B can index mortality over years, whereas Type B could index sea lamprey activity. Which assumption has more support? Simulation results indicate that constant annual pierce and lethality rates are both capable of yielding the range of marking rates observed in the three Great Lakes during 2008–2017. There are two pieces of evidence that may support an assumption of relatively constant lethality. Schneider et al. (1996) found a linear relation between the log transformed number of Type A1 marks on lake trout and the log transformed density of dead lake trout in Lake Ontario, 1982–1992. Pycha (1980) found a linear relation between the percentage of lake trout with fresh sea lamprey marks and the log transformed instantaneous total mortality in Lake Superior during 1968–1978.

Estimating annual pierce rates in the field may be possible in the future as fish tagging technology continues to advance. Tags would have to (1) be small enough to be inserted into sea lampreys early in their juvenile life stage, (2) indicate whether a sea lamprey was attached to a host, and (3) detect whether a sea lamprey was feeding. Accelerometer tags could measure the activity level of each sea lamprey to tell whether it was swimming freely or attached to a host, however such tags are not yet small enough for use in Great Lakes sea lampreys (Broell et al., 2013; Gleiss et al., 2010). Feeding could be determined by a fish tag that monitors waste, digestive enzymes, or anorexigenic hormones such as cholecystokinin (Volkoff, 2016). I am not aware of any tags that currently have this capability. The combined knowledge of sea lamprey attachment and feeding would enable us to estimate annual pierce rates. Information from accelerometer tags alone could also be used to estimate the number of hosts a sea lamprey attaches to during its juvenile life stage and the timing and duration of the attachments. Little focus has been placed on the study and estimation of sea lamprey pierce rates. A greater understanding of factors influencing whether a sea lamprey feeds or simply hitches a ride when attached to a fish could inform estimates of fish damage (Bence et al., 2003; Irwin et al., 2012) and models of future control options (e.g., Thresher et al., 2018).

Estimates of lethality rates are critical components of models used to assess lake trout (Sitar et al., 1999) and guide sea lamprey control decisions (e.g., via economic injury levels, Irwin et al., 2012). Lethality rates are expected to vary with size distributions of hosts and sea lampreys (Swink, 2003), as well as temperature and host strain (Schneider et al., 1996). However, little information is available quantifying annual variability in lethality rates. Sea lamprey-induced mortality could be estimated in the field if sentinel lake trout were continuously monitored such that their fate at the end of each year was known (i.e., were they dead or alive) and cause of death could be determined. Annual lethality rates could then be derived from sea lamprey-induced mortality rates (Eshenroder and Koonce, 1984). Such an investigation would also yield estimates of the natural mortality of lake trout. However, identifying cause of death remotely or recovering dead lake trout from Great Lakes waters would be an expensive endeavor.

Median framed lethality rates ranged from P = 0.31 (Lake Superior) to 0.41 (Lake Huron), corresponding to a probability of survival ranging from 0.59 to 0.69. This agrees closely with estimate by Madenjian et al. (2008) of the probability of an adult lake trout surviving a sea lamprey attack in Lake Huron, 0.66. The conventional value of 0.55 used in modeling for lake trout 636 mm or longer (Sitar et al., 1999) fell within the interquartile range of simulated survival rates for each lake (P = 1 - lethality, Figure 2.5). The 0.43 laboratory estimate for lake trout 660 mm or longer (Swink, 2003) fell within the interquartile range of simulated survival rates for Lake Huron (0.39–0.80), but fell below the interquartile range for Lakes Superior (0.48–0.87) and Michigan (0.47–0.85). Laboratory experiments probably underestimate survival from sea lamprey attack due to stress from confinement (Bence et al., 2003).

The distribution of framed pierce rates was quite different for Lake Huron than the other two lakes. This was a result of the reality frame used for Lake Huron, and the low Type B marking rate observed during 2008–2017 (Figure 2.4). Lake Huron and Lake Michigan are the most similar of the Laurentian Great Lakes, connected by the 8 km wide Mackinac Straits (Barbiero et al., 2018), yet consistently higher pierce rates were observed in Lake Huron. Perhaps sea lampreys in Lake Huron use species of fish other than lake trout to attach to while satiated. This might be revealed by comparison of fish community marking rates. Or perhaps the discrepancy is the result of classification bias, a difference in the way people in Lake Huron are identifying marks relative to Lakes Superior and Michigan.

As with any model, several assumptions were required to carry out this simulation. Assuming lake trout did not grow during the simulation is justified given the short time frame (7 months) and the relatively slow growth of large lake trout. If lake trout growth had been incorporated in the model, it would have resulted in a slight but relatively consistent increase in marking rates from June through December, minimally affecting my results and conclusions. The exclusion of natural and fishing mortality of lake trout from the simulation is justified given the focus on sea lamprey-induced mortality. Assuming natural and fishing mortalities similarly affect medium to large size lake trout, their exclusion should not affect the results. Discrete monthly time steps made it possible to incorporate seasonally varying attack, pierce, and lethality rates. Shortening the time steps would have added to the complexity of the simulation without substantially improving its realism. Type B marks are difficult to detect in the field, especially if fish are not examined immediately upon removal from the water (Shawn Sitar, Michigan Department of Natural

Resources, personal communication). Thus there may be a detection bias for Type B marks that my simulation did not take into account.

Seasonal patterns in sea lamprey attacks may vary with host, year, and geographic region. The peak in observed sea lamprey marks that I used in my simulation (Figure 2.2) occurred after July for lake whitefish from northern Lake Huron (Spangler et al., 1980). However, the peak in observed marks occurred prior to July for Lake Superior lake trout in all collection years in the Bayfield area and one third of the collection years near Huron Islands (Jacobson, 1989). I reran the simulation using an attack rate relation (equation 1) with a peak in mid-June (z = 6.5), and the results were unchanged, indicating my simulation is not sensitive to the seasonal distribution of sea lamprey attacks.

Sea lamprey attacks were simulated on an unmarked lake trout population. This is equivalent to ignoring marks from previous marking seasons. Healing was not incorporated in the simulation because healing rates of sea lamprey marks are highly variable and difficult to predict with precision (Ebener et al., 2003; Nowicki, 2008). Given the short time frame of the simulation (7 months), assuming marks persisted (i.e., were always detectable) was reasonable (Ebener et al., 2003; Nowicki, 2008). The simulation assumes perfect classification of marks as Type A or Type B. Ebener et al. (2003) found marks identified as Type A were classified to a common standard 93% of the time and marks identified as Type B were classified to a common standard 81% of the time (their Table 1 with 49 sea lamprey marks identified by an average of 28 people each). Correct mark classification depends not only on the accuracy of the mark reader, but also the changing appearance of the mark itself. In a laboratory study on the healing of sea lamprey marks, known piercing marks looked like Type B marks in 7 of 19 lake trout and non-piercing marks looked like Type A marks in 11 of 21 lake trout after about 7 months of healing (Tyler Firkus, Michigan State University, 16 Feb 2018, personal communication).

Sizes of lake trout used in this simulation reflect actual size distributions in the Great Lakes and selectivities of gill nets used to sample them (Hansen et al., 1997). The gill net surveys referenced in this paper are generally designed to capture larger fish (Brenden et al., 2011; Bronte et al., 2007; Hansen et al., 1995; He et al., 2012). These larger lake trout are the ones targeted by sea lampreys. Because sea lampreys prefer to attack larger fish (Rutter and Bence, 2003), there was little loss of information by excluding smaller fish from the simulation. Throughout this paper, all marking statistics were summarized for the subset of lake trout > 532 mm, corresponding to current practice in assessing sea lamprey status in the Great Lakes.

Prichard and Bence (2013) found the negative binomial distribution was a better fit for sea lamprey attack rates than the Poisson distribution. However, their estimates of marking rates using the two distributions were similar. The Poisson distribution's need for one less parameter than the negative binomial is a critical advantage for this simulation.

Interpreting observed sea lamprey marking rates on Great Lakes lake trout is challenging. To use observed marking rates on lake trout as indices of true attack rates or sea lamprey-induced mortality, I must make assumptions about annual pierce or lethality rates. Given the difficulties and expense of estimating pierce and lethality rates in the field, modeling may be a more feasible way to learn more about these rates or bypass assumptions about them. Statistical catch at age models incorporate sea lamprey-induced mortality of lake trout externally calculated from observed marking rates and a size-based estimate of lethality, but do not account for annual changes in sea lamprey abundance (Sitar et al., 1999). I suggest the adult sea lamprey index (Barber et al., *In preparation*; Mullett et al., 2003) be incorporated in the statistical catch at age model, by way of a functional response relating sea lamprey feeding to lake trout abundance, if possible. Such an approach would require accounting for sea lamprey and lake trout abundance on the same spatial scale, which is challenging given several key differences between the two species, including seasonal movements, degree of stock mixing, and current methods of assessment (stream trapping and lake gill netting). Abundances of species other than lake trout may also need to be incorporated, because their role as alternative hosts for sea lampreys may influence lake trout marking rates (e.g., Adams and Jones, 2020; Moody et al., 2011). Rutter (2004) incorporated a multi-host species functional response for sea lampreys in an extension of a statistical catch at age model for Lake Huron lake trout (Sitar et al., 1999). Rutter (2004) had difficulty estimating handling time due to a lack of data on sea lamprey marks on alternative hosts; these data are now being collected for several species in the Great Lakes (Ted Treska, US Fish & Wildlife Service, 1 May 2019, personal communication). The process outlined by Rutter (2004) was complex enough that it was not adopted by Great Lakes fishery managers as standard practice for lake trout population assessments.

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CHAPTER 3

EVIDENCE OF HOST SWITCHING:
SEA LAMPREYS DISPROPORTIONATELY ATTACK CHINOOK SALMON WHEN LAKE TROUT ABUNDANCE IS LOW IN LAKE ONTARIO

3.1 Introduction

Lake trout (*Salvelinus namaycush*) are presumed to be the preferred hosts for invasive sea lampreys (*Petromyzon marinus*) in the Great Lakes (Harvey et al., 2008; Pycha and King, 1975; Swink, 2003). But, juvenile sea lampreys attack many other Great Lakes species, especially large-bodied ones (Farmer and Beamish, 1973; Swink, 2003), and population level impacts have been observed or hypothesized for several species: Chinook salmon (*Oncorhynchus tshawytscha*, McLeod et al., 2011), lake whitefish (*Coregonus clupeaformis*, Spangler et al., 1980; Ebener et al., 2010), burbot (*Lota lota*, Stapanian et al., 2006), and coregonines and suckers (*Coregonus* spp. and *Catostomus* spp., Harvey et al., 2008).

In spite of their pelagic habitat and fast swimming speeds, Chinook salmon are commonly attacked by sea lampreys. Most (62%) of the age-2 precocious Chinook salmon had sea lamprey-induced marks in Lake Huron in 1970 (Smith and Tibbles, 1980). Sea lamprey marking rates on Lake Huron Chinook salmon ranged from 0.14 to 0.33 marks per fish in 1988-1992 (Johnson et al., 1995). The abundance of juvenile sea lampreys was significantly positively correlated with Chinook salmon abundance in Lake Huron, suggesting that Chinook salmon could be an important component of the sea lamprey diet (Young et al., 1996).

Little is understood about how sea lamprey parasitism varies with host abundance (Bence et al., 2003; Koonce, 1987). Knowledge in this area would allow us to improve our estimates of host damage. Current estimates based on observed sea lamprey marking rates are subject to survivor bias (marks are only observed on hosts that survived attacks, Adams et al., *In review*) and from sampling bias (few host species other than lake trout are regularly surveyed on a lake-wide spatial scale). Although the focus of this study is predator-prey dynamics, I refer to sea lampreys as parasites (rather than predators) and lake trout and Chinook salmon as hosts (rather than prey).

The purpose of this study was to take the first step toward quantifying host preference of sea lampreys in the field. In this paper, the term preference is used to indicate sea lamprey attacks on hosts disproportionate to host relative abundance. To see a switch in preference in the field, feeding observations must be made over a wide range of relative abundances of hosts. That's why so many switching studies are carried out in the laboratory where the experimenter can control prey densities (Bayliss, 1982). I chose Lake Ontario as a case study, focusing on two host species: lake trout and Chinook salmon. Lake Ontario has a history of a relatively stable sea lamprey population, with variable lake trout abundance and increasing Chinook salmon abundance (Lantry et al., 2015). These conditions present a prime opportunity to observe host switching in sea lampreys, wherein sea lampreys switch their preference from lake trout to Chinook salmon below some threshold of the relative abundance of lake trout.

My objectives were to characterize the preference of sea lampreys for lake trout in Lake Ontario and determine if and when their preference switches to Chinook salmon based on field observations. Greater understanding of host preference may aid in efforts to control sea lampreys and manage their hosts in the Great Lakes (Stewart et al., 2003) as well as to inform conservation of sea lampreys in their native range (Maitland et al., 2015).

3.2 Methods

Evidence of host preference and host switching was explored using logistic regression models of sea lamprey parasitism on lake trout and Chinook salmon in Lake Ontario. Recall that I defined preference as sea lamprey attacks disproportionate to host relative abundance. The two key quantities are the proportion of hosts that are lake trout and the proportion of sea lamprey-induced marks that are on lake trout, assuming that lake trout and Chinook salmon are the only available hosts. The proportion of marks on lake trout was assumed to be a function of the proportion of hosts that were lake trout,

$$(1) \qquad ln\left(\frac{M_1}{1-M_1}\right) = \gamma_0 + \gamma_1\ ln\left(\frac{P_1}{1-P_1}\right),$$

where M_1 is the proportion of sea lamprey-induced marks on lake trout,

$$M_1 = \frac{S_1 O_1/E_1}{S_1 O_1/E_1 + S_2 O_2/E_2},$$

S_i is the estimated lake-wide abundance of species i ($i = 1$ for lake trout; $i = 2$ for Chinook salmon), O_i is the observed number of marks on E_i examined individuals of species i, $P_1 = S_1/\sum S_i$ is the proportion of host abundance that were lake trout, and γ_0 and γ_1 are parameters to be estimated. When fitting the logistic regression, the response was scaled to the total number of observed marks, $\sum O_i$, as the sample size. Because the scaled responses were not integers, the quasibinomial family was used in the general linear model rather than the usual binomial family. This is a natural log transformation of the simple ratio predation model (Murdoch, 1969) with the addition of a switching parameter, γ_1. If $\gamma_1 \neq 1$, there is evidence of a switch in host preference that depends on the proportion of hosts that were lake trout. If $\gamma_1 = 1$, there is no host switching, and preference over all host proportions is simply estimated by e^{γ_0} (equivalent to the constant c in the simple ratio predation model, Murdoch, 1969). If $\gamma_1 = 1$ and $\gamma_0 > 0$, then $M_1 > P_1$ and sea lampreys exhibit a preference for lake trout; if $\gamma_1 = 1$ and $\gamma_0 < 0$, then $M_1 < P_1$ and they exhibit a preference for Chinook salmon. Scatter plots of residuals from the full model were visually examined for qualitative evidence of patterns related to year, lake trout abundance, Chinook salmon abundance, adult sea lamprey relative abundance, and adult sea lamprey size.

Lake-wide abundance of hosts was estimated by two separate Lake Ontario statistical catch-at-age models (Table 3.1), one for lake trout (Brenden et al., 2011, Travis Brenden, Michigan State University, personal communication), and one for Chinook salmon (Kimberly Fitzpatrick, Cornell University, personal communication; estimates are preliminary and have not been endorsed by the Lake Ontario Committee or the Lake Ontario Technical Committee; data can be found in Connerton, 2019; Bishop et al., 2019; Connerton and Eckert, 2019; Lake, 2017; Prindle and Bishop, 2019; Sanderson et al., 2019; Yuille and Holden, 2017). Abundance of lake trout was calculated as the sum of age 3 and older fish (Brenden et al., 2011). Abundance of Chinook salmon was calculated as the sum of age 1 and older fish, corresponding to the spawning adults which were surveyed. For both species, the fish included in the abundance estimates are susceptible to sea lamprey predation.

Table 3.1. Lake trout relative abundance (expressed as the proportion of lake trout and Chinook salmon hosts) and lake trout and Chinook salmon parasitism rates (N = number of hosts observed, A1 = number of A1 or ‘‘fresh” sea lamprey-induced marks per host).

Year	Lake trout relative abundance	Lake trout N	Lake trout A1	Chinook salmon N	Chinook salmon A1
2000	0.516	993	0.023	646	0.000
2001	0.466	991	0.023	657	0.000
2002	0.391	909	0.008	624	0.002
2003	0.387	943	0.020	923	0.015
2004	0.398	891	0.018	744	0.009
2005	0.354	468	0.032	753	0.012
2006	0.316	609	0.025	630	0.006
2007	0.271	399	0.030	481	0.035
2008	0.252	554	0.016	669	0.016
2009	0.370	613	0.010	897	0.012
2010	0.414	785	0.015	719	0.000
2011	0.407	926	0.004	625	0.003
2012	0.402	871	0.025	574	0.003
2013	0.328	1122	0.017	584	0.003
2014	0.284	1268	0.010	675	0.006

Host parasitism rates were derived from observed sea lamprey marks on hosts. Host parasitism was estimated as the number of A1 marks per host > 431 mm, following current practice for Lake Ontario (Lantry et al., 2015; Larson et al., 2003). This rate is calculated as the total number of marks (including multiple marks on a single host) divided by the total number of fish examined for marks. The A1 classification indicates that the marks pierced the skin and are “fresh” or little healed (Ebener et al., 2003; King, 1980). For lake trout, observations of marks (Table 3.1) and measures of total length (Figure 3.1) came from two fishery independent gill net surveys: the Lake Ontario and Bay of Quinte fish community index gill netting survey conducted during June-September in Canada waters (Hoyle, 2018) and the lake trout assessment survey conducted during September-October in US waters (Lantry et al., 2018). For Chinook salmon, observations of marks and measures of total length came from the fall spawning migration up a fish ladder on Beaverdam Brook (a tributary of the Salmon River) into the New York State Department of Environmental Conservation Salmon River Fish Hatchery, Albion NY, (Prindle and Bishop, 2018).

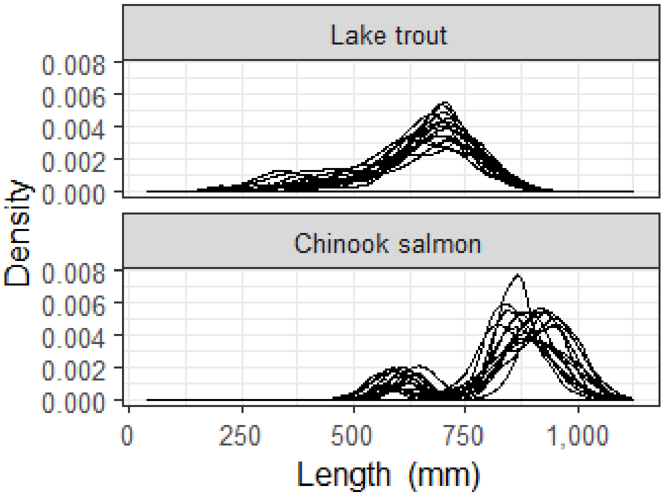

Figure 3.1. Annual length frequency distributions of lake trout and Chinook salmon captured in Lake Ontario 2000-2014. Each line represents a separate year.

The relative abundance of adult sea lampreys in Lake Ontario was assessed annually by mark-recapture studies in five index streams (Humber River, Duffins Creek, and Bowmanville River in Canada and Black and Sterling Rivers in the US) during their spawning migration (Mullett et al., 2003). The spawning migration occurs after sea lampreys spend 6-18 months in the lake feeding on fish as juveniles. The stream pooled Petersen estimates (Seber, 1970) were then summed for a lake-wide adult index (Barber et al., *In preparation*). Individual sea lampreys captured during these studies were weighed, and the median annual weight was used as an index of sea lamprey size in the exploration of model residuals.

Additional models were fit to the parasite-host data that accounted for the sizes of the two host species, because Great Lakes sea lampreys have a demonstrated preference for large fish (Bence et al., 2003; Farmer and Beamish, 1973; Rutter and Bence, 2003). Without accounting for host size, I expect that sea lamprey preference for lake trout will be underestimated, because Chinook salmon tend to be larger than lake trout in Lake Ontario (Figure 3.1).

Expected marking rates were modeled as a logistic function of host size (Rutter and Bence, 2003) for both host species combined (allowing marking rates to vary with host size regardless of species) and for each host species separately (allowing for species-specific size relations),

$$W = \frac{\theta}{1 + exp[-\alpha(L - \beta)]} ,$$

where W is the expected number of marks following a negative binomial distribution (Prichard and Bence, 2013), L is host length (in mm), θ is the asymptotic marking rate, β is the length of the host at the inflection point, and $\alpha\theta/4$ is the slope at the inflection point. Models were fit using maximum likelihood with the nlminb function of R (R Core Team, 2018). All three parameters were estimated in the natural log-transformed space to constrain them to be positive.

The expected proportion of sea lamprey-induced marks on lake trout based on the abundance and size distribution of the host species was calculated as

$$\tilde{P}_{1,\ size} = \frac{S_1 \widetilde{W}_{13}}{S_1 \widetilde{W}_{13} + S_2 \widetilde{W}_{23}}\ ,$$

$$\tilde{P}_{1,\ size+species} = \frac{S_1 \widetilde{W}_{11}}{S_1 \widetilde{W}_{11} + S_2 \widetilde{W}_{22}}\ ,$$

where $\widetilde{W}_{ig}$ is the annual mean predicted marking rate for species i calculated for group g of the data ($g = 1$ for lake trout alone, $g = 2$ for Chinook salmon alone, and $g = 3$ for both species combined). I then fit two additional parasitism models by replacing the P_1 in Model 1 with the expected proportions from asymptotic marking rates depending on host size alone (Model 2, $\tilde{P}_{1,\ size}$) and on host size and species (Model 3, $\tilde{P}_{1,\ size+species}$).

Finally, I fit two additional logistic regression models, where the independent variable of the relative abundance of lake trout, $ln[P_1/(1 - P_1)]$, was replaced by the absolute abundance of lake trout ($ln(S_1)$, Model 4) and by the absolute abundance of Chinook salmon ($ln(S_2)$, Model 5).

3.3 Results

Without taking host size into account (Model 1), the estimate for γ_1 was significantly different from 1 (5.54 with standard error 1.37), indicating a switch in host preference. Sea lampreys exhibited a preference for Chinook salmon when the combined abundance was $\leq$ 13% lake trout, switching to a preference for lake trout when combined abundance was $\geq$ 32% lake trout (γ_0 = 4.95 with standard error 1.30, Figure 3.2). The steepest increase in the proportion of marks on lake trout occurred when the combined abundance was 32.6% lake trout. No linear or nonlinear relations were evident in plots of the residuals from the full model versus year, lake trout abundance, Chinook salmon abundance, sea lamprey abundance, or sea lamprey size.

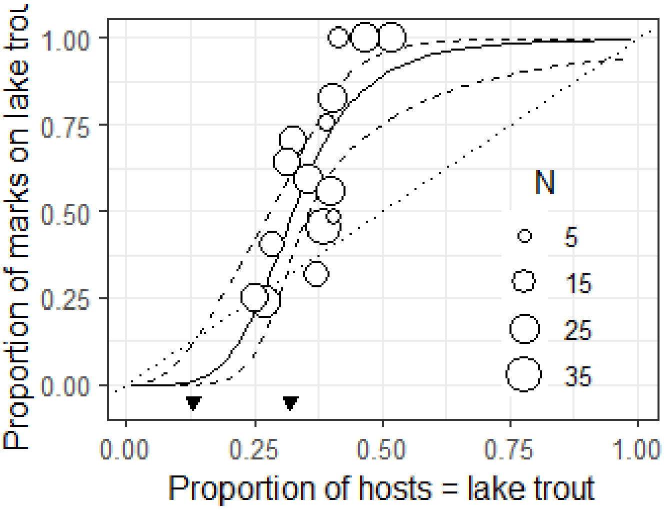

Figure 3.2. Relation between the proportion of hosts that were lake trout and the proportion of sea lamprey-induced marks that were on lake trout in Lake Ontario, assuming lake trout and Chinook salmon were the only available hosts. Symbols represent annual observations (2000-2014), symbol size represents number of hosts examined for marks, and lines represent predictions from Model 1 with 95% confidence intervals. The diagonal dotted line represents the null model, with no preference and no switching. The two triangles denote the switch points below which sea lampreys prefer Chinook salmon (left) and above which sea lampreys prefer lake trout (right).

Sea lamprey preference for lake trout was also evident when modeling marking rates as a function of host size (Figure 3.3). Marking rates on lake trout most steeply increased at a host length 132 mm shorter than that on Chinook salmon (Table 3.2). The asymptotic marking rate of lake trout was 1.4 times that of Chinook salmon. However, taking host size into account, either for both species together (Model 2, residual deviance 48.8) or each species separately (Model 3, 50.1) did not improve the fit achieved with Model 1 (residual deviance 47.4, $t = 3.82$, $P = 0.0021$, Figure 3.4), even with the inclusion of additional estimated parameters.

Table 3.2. Estimated parameters relating host length to sea lamprey-induced marking rate for both species combined and for lake trout and Chinook salmon separately.

Species	Alpha	Beta	Theta
Both	0.0200	587	0.0150
Lake trout	0.0207	383	0.0161
Chinook salmon	0.0197	718	0.0105

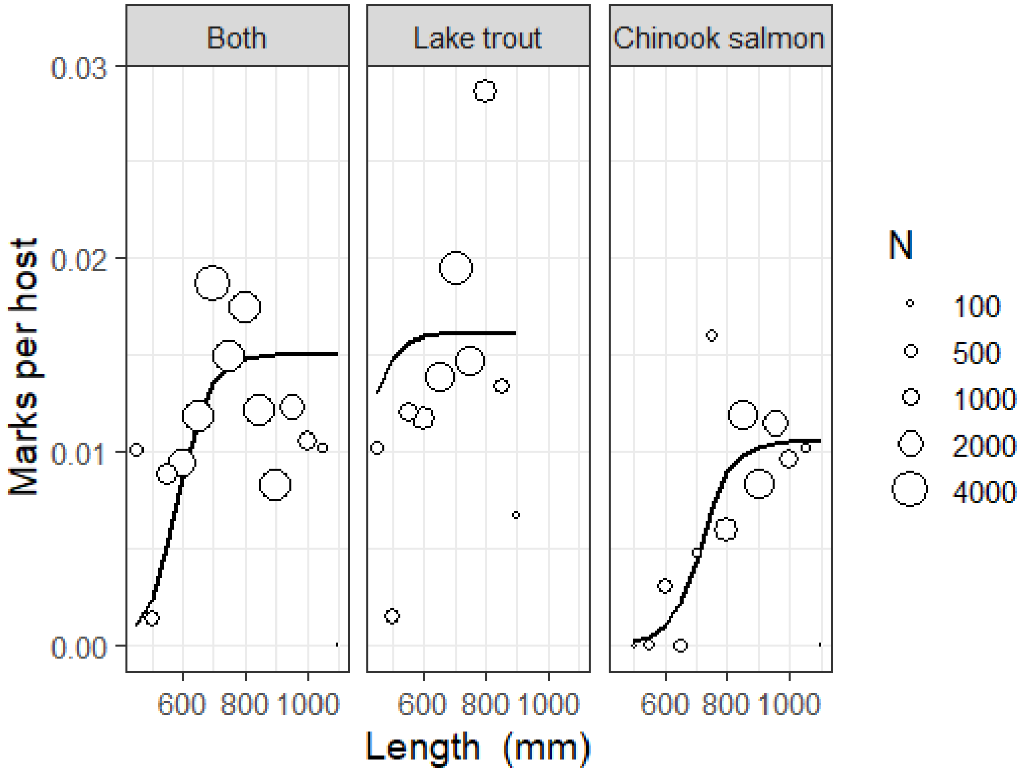

Figure 3.3. Sea lamprey-induced marking rate as a function of host size for just lake trout, just Chinook salmon, and both species combined in Lake Ontario 2000-2014. Symbols represent observed proportions for each 50 mm size group, symbol size represents the sample size, and lines represent predictions from the negative binomial model.

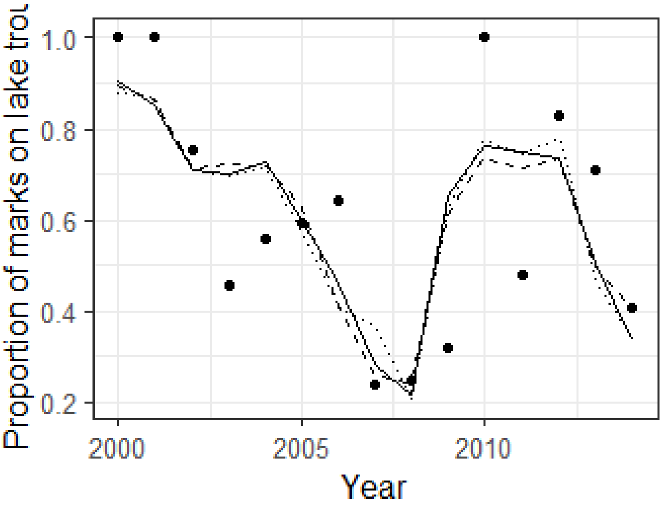

Figure 3.4. Proportion of sea lamprey-induced marks that were on lake trout (relative to Chinook salmon) over time in Lake Ontario 2000-2014. Points represent observations, lines represent predictions from three models based on (1) the proportion of hosts that were lake trout (solid), (2) the proportion of hosts that were lake trout and the size of the mixed hosts (dashed), and (3) the proportion of hosts that were lake trout and species-specific host size (dotted).

The proportion of marks on lake trout was also well explained by the absolute abundance of lake trout, with slightly less residual deviance (Model 4, residual deviance 47.3, t = 3.86, P = 0.0020, Figure 3.5) than by the proportional abundance of lake trout (Model 1). The estimate for γ_1 was 1.78 with standard error 0.43. Here, the γ_1 parameter loses its interpretation as a switching indicator, because this model depends on the abundance of only one host species. The estimate for γ_0 was 4.73 with standard error 1.22. The steepest increase in the proportion of marks on lake trout occurred when the absolute abundance of lake trout was 0.69 million fish.

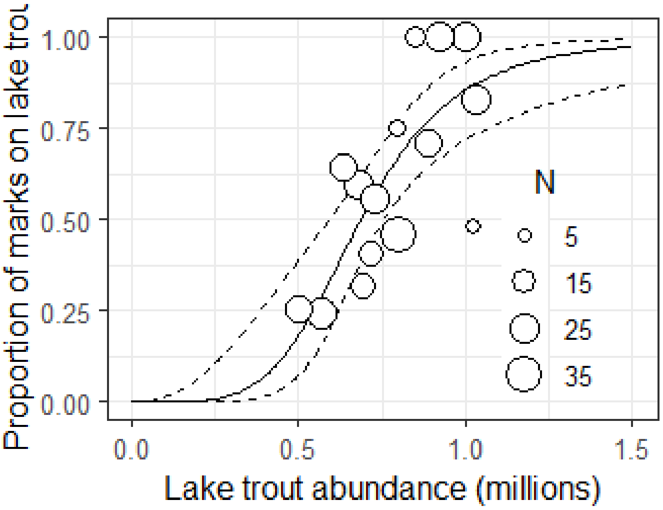

Figure 3.5. Relation between lake trout abundance and the proportion of sea lamprey-induced marks that were on lake trout (relative to Chinook salmon) in Lake Ontario. Symbols represent annual observations (2000-2014), symbol size represents number of hosts captured, and lines represent predictions from Model 1 with 95% confidence intervals.

In contrast, the absolute abundance of Chinook salmon was not a strong predictor of the proportion of marks on lake trout (Model 5, residual deviance 85.7, $t = -1.76$, $P = 0.10$).

3.4 Discussion

This study provides an example of a parasite with a strong host preference that switches when the relative and absolute abundance of the preferred prey is low. This is in contrast to the prediction by Murdoch (1969) that prey switching will not occur when the predator has strong prey preferences (Murdoch et al., 1975; Rubega and Inouye, 1994). In spite of their strong host preference in the Great Lakes, I consider the sea lamprey to be a generalist predator, attacking a wide range of fish species (Schoener, 1971). This varied diet is supported by studies of stable isotopes in Lake Superior (Harvey et al., 2008) and fatty acids in Lake Michigan (Happel et al., 2017). In the Atlantic, sea lamprey attacks have been documented on 54 host species (Silva et al., 2014). When prey abundance is high, most generalist predators feed on a single primary prey (Andersson and Erlinge, 1977). If that primary prey population declines, predators turn to less abundant alternatives (Angelstam et al., 1984). Switching behavior has been documented for several so-called generalist predators (Cornell, 1976; Murdoch, 1969; Patterson et al., 1998). Anecdotal evidence of host switching was observed in South Bay of Lake Huron when sea lamprey-induced marks on white suckers (*Catostomus commersonii*) coincided with the crash of the lake trout population in the 1950s (Coble, 1967).

Evidence for host-switching is based on the fit of the observed data to a switching model. For Lake Ontario during 2000-2014, Model 1 predicted that sea lampreys preferred lake trout in 11 of 15 years and exhibited no preference between lake trout and Chinook salmon the other four years (2006-2008 and 2014). None of the 15 years had a low enough proportion of hosts that were lake trout for Model 1 to predict sea lamprey preference for Chinook salmon. Thus, inferring that sea lampreys prefer attacking Chinook salmon if lake trout are relatively scarce is based on extrapolation beyond the range of data used to build the model. However, I did observe more marks on Chinook salmon than expected from their relative abundance in three years (2007-2009, the three points below the dotted line in Figure 3.2). These years likely correspond to more relatively small fish in the lake trout population, contributing to the rise in lake trout abundance after 2009 (Brian Lantry, US Geological Survey, personal communication.)

Switching to an alternative prey species makes sense for a number of reasons, most of which lead to an increase in feeding efficiency (Bayliss, 1982). According to optimal foraging theory, a predator chooses the prey that will give the maximum net benefit to the individual (Begg et al., 2003). The net benefit depends on handling time, nutritional value, and the abundance of alternative prey (Van Baalen et al., 2001).

Handling time incorporates the pursuit, capture, and digestion of prey (Fujii et al., 1986). Chinook salmon are much more active than lake trout, searching open water habitat for active pelagic prey (Stewart and Ibarra, 1991), which may make them more difficult for sea lampreys to pursue and attack. Although I found no laboratory studies of sea lampreys feeding on Chinook salmon, relatively low detachment rates (< 18%) have been observed for several species except for burbot (36%) and walleye (*Sander vitreus*, 75%) (Farmer and Beamish, 1973).

Switching to the most common prey species may be a consequence of the predator's searching behavior, e.g., the use of a search image of the locally most abundant prey species (May, 1977). A decrease in prey biomass results in an increase in the foraging costs of the preferred prey through increased search time (Krebs and Davies, 1987). Predators may forage in different patches, form prey search images, decrease prey handling time with experience, or increase searching efficiency within patches (Joern, 1988). Predators are more likely to detect prey if the prey are aggregated (Taylor, 1977). When prey are clumped, nearly double the number of predators have been observed switching to the alternative prey (Bayliss, 1982). If sea lampreys learn, their attack success rate might increase with successive attempts on a given species, as has been observed in the water boatman (*Notonecta glauca*, Hughes, 1979). A predator may also be more efficient at locating prey, if it concentrates on only one species (Bayliss, 1982).

Switching may also be the consequence of differences in energetic content of the prey. If the value of two prey types are quite different, I would expect the predator to specialize on the most valuable prey type and generalize when the latter is scarce (Hughes, 1979; Murdoch et al., 1975). The lipid content of lake trout was greater than that of Chinook salmon in Lake Ontario in 2013 (Mumby et al., 2018) and in Canadian waters of Lake Ontario during 1978-2008 (Neff et al., 2012). This higher energy content comes at the price of lower metabolic and digestion rates (Fall and Fiksen, 2020) for sea lampreys feeding at the lower water temperatures lake trout inhabit (to be discussed later). If lake trout were more profitable prey than Chinook salmon, then I might expect to see an effect on the size of the adult sea lampreys. In this case, the median weight of adult sea lampreys collected in Lake Ontario was not significantly correlated with the proportion of marks on lake trout (r=0.34, df=13, P=0.21). This supports the contention that prey preference is not necessarily reflected in comparative growth rates (Bayliss, 1982).

Building a switching model that depends on the relative abundance of the prey implies that the predator perceives the relative abundance of prey. The ability to do this depends on the extent to which the predator and prey species overlap spatially. The diversity of hosts attacked will reflect both their relative abundance and spatial distribution (Schoener, 1971). Sea lampreys captured in the open waters of Lake Superior fed primarily on lake trout, but those in Black Bay relied heavily on coregonines and suckers (Harvey et al., 2008). Laboratory preference studies focus on the active choice of predators when faced with more than one vulnerable prey species (e.g., Farmer and Beamish, 1973). Vulnerability of different species to sea lamprey attack in the field is largely unknown. If host populations were partitioned into vulnerable and invulnerable components, foraging arena theory asserts that the attack rates then depend on the exchange rates between the components (Ahrens et al., 2012). If recently metamorphosed sea lampreys (transformers) attack the first host fish they encounter upon exiting their natal stream, then host preference is less an active choice, and more the result of passive encounter probabilities and habitat overlap. For example, transformers are commonly observed attached to bloater (*Coregonus hoyi*) captured in bottom trawling in the Detour Channel of northern Lake Huron (Fleischer, 1993). Farmer and Beamish (1973) contended that sea lamprey preference in the Great Lakes depended largely on the ecological distribution of host species. Weitkamp et al. (2015) asserted that marking rates by western river (*Lampetra ayresii*) and Pacific (*Entosphenus tridentatus*) lampreys in the Columbia River estuary were influenced by the habitat selection of potential host species.

Lake trout and Chinook salmon occupy different habitats in Lake Ontario. Lake trout occupy the hypolimnion, near the bottom of the thermocline, and Chinook salmon occupy the metalimnion to maximize their growth rate potential in Lake Ontario (Mason et al., 1995). Chinook salmon feed almost exclusively on alewife in offshore pelagic areas; lake trout consume a broader mix of alewife (*Alosa pseudoharengus*) and other species, feeding on both pelagic and benthic prey in the hypolimnion (Mumby et al., 2018; Rand and Stewart, 1998). The fatty acid profiles of the two host species reflect this, indicating lake trout feed more on rainbow smelt (*Osmerus mordax*) and round gobies (*Neogobius melanostomus*) than Chinook salmon, which feed more on alewives (Happel et al., 2016).

The energy content of the host species likely changed during 2000-2104 due to changes in the composition of their prey: alewife condition increased, rainbow smelt abundance declined, and round goby biomass increased in Lake Ontario during 2000-2014 (Weidel et al., 2018). Sea lampreys are poorer swimmers than most teleosts and do not possess swim bladders, so they must expend energy just to maintain position in the water column (Beamish, 1974). Thus, it's energetically advantageous for free swimming juvenile sea lampreys to search for hosts near the lake bottom, where they are less likely to encounter Chinook salmon. However, sea lampreys that feed exclusively on hosts in the hypolimnnion have lower growth rates than those feeding on hosts in the thermocline as a result of thermal bioenergetics (Kitchell and Breck, 1980).

This lends theoretical support to the model based on lake trout abundance alone, regardless of Chinook salmon abundance (Model 4). Similar outcomes have been observed in other species. For example, the mollusk (*Lepsiella vinosa*) fed heavily on its preferred species, irrespective of the relative abundance of the alternative species (Bayliss, 1982), and coyotes (*Canis latrans*) only switched to an alternate prey when the absolute abundance of its preferred prey was low (Patterson et al., 1998). Merilaita and Ruxton (2009) suggested frequency-dependent predation should be common where predators face large temporal or spatial fluctuations of prey types. Further evidence from the field would require years of exceptionally high or low host abundance, where high absolute lake trout abundance could coincide with low relative lake trout abundance or vice versa. Otherwise choosing between these two models (Models 1 and 4) based on field observations alone is difficult, because the relative and absolute lake trout abundances were so highly correlated during 2000-2014 (r = 0.78, P = 0.0006, df = 13). If sea lampreys shift their distribution when lake trout become scarce, I should be able to observe this with acoustic telemetry (e.g., Holbrook et al., 2016) or archival tags (e.g., Bergstedt et al., 2012).

Sea lampreys spawning in Portuguese tributaries to the Atlantic Ocean use one of two different feeding strategies (Lança et al., 2013). Sea lampreys either tended to attack pelagic plankton feeders or benthic opportunist fish species. Lança et al. (2013) hypothesized that the feeding strategies were associated with different dispersion tactics. Sea lampreys that parasitize pelagic rather than demersal hosts enhance their dispersion but increase the risk of not returning to fresh water. The risk of not returning to a stream to spawn is presumably less in the more confined Great Lakes than in the Atlantic Ocean.

The presence of Chinook salmon as an alternative host for sea lampreys may serve as a buffer, benefiting both sea lampreys and lake trout when lake trout abundance is low. By concentrating attacks on the most common host, sea lampreys enable the rarer hosts to enjoy higher fitness via frequency-dependent natural selection (May, 1977). Thus, the presence of Chinook salmon in Lake Ontario may contribute to the persistence of lake trout in the system. A predator's switch to alternative prey relieves predation pressure when the prey densities are low, regardless of whether the alternative prey overlaps with the primary prey (Van Baalen et al., 2001). This persistence only arises if the predator switches between prey. However, the rapid increase in sea lamprey attacks on lake trout at abundance levels just above the switching point is an impediment to lake trout reproduction. Lake trout may then be caught in a "predator pit" (Walters, 1986) and maintained at low levels by sea lamprey parasitism in spite of lake trout restoration efforts.

Even low abundances of actively switching sea lampreys could maintain the lake trout at depressed levels.

Lake trout and Chinook salmon are not the only species attacked by sea lampreys in Lake Ontario. Boating anglers in US waters of Lake Ontario have also observed sea lampreys attached to brown trout (*Salmo trutta*), rainbow trout (*Oncorhynchus mykiss*), coho salmon (*Oncorhynchus kisutch*), and Atlantic salmon (*Salmo salar*) (in order of prevalence, Lantry et al., 2015; Lantry and Eckert, 2018). Sea lamprey marks have also been infrequently identified on other species collected in fishery-independent gill net surveys: northern pike (*Esox lucius*), walleye, burbot (*Lota lota*), and lake whitefish (Hoyle, 2018; Lantry et al., 2018). Thus the proportions of hosts and marks that I calculate from lake trout and Chinook salmon alone were biased low and introduced noise to the model, because the abundances of these other hosts and the prevalence of sea lamprey-induced marks on them has changed over time (Lantry et al., 2015). The host-switching that I detected had to have been strong enough to overcome this background noise. The preference of Great Lakes sea lampreys for lake trout surely contributed to my ability to detect the host-switching, because prey switching is less pronounced when no single species dominates the predator's diet (Hall-Scharf and Stallings, 2014; Van Leeuwen et al., 2013).

Different strains of lake trout in Lake Ontario were not distinguished in my analyses. The Seneca strain of lake trout (from Seneca Lake, NY) has dominated lake trout stocking in Lake Ontario since 1997 (Brenden et al., 2011), and has been recommended to be the majority of stocked lake trout in the future (Lantry et al., 2014). Most (55%) of the lake trout observed for sea lamprey marks in this study were not identified to strain. The most commonly recorded strain was Seneca (20% of the total, 44% of those identified to strain), with Superior strain a distant second (7% of the total, 15% of those identified to strain). Seneca strain lake trout tend to be caught in deeper colder water than other strains and have a lower chance of being attacked by sea lampreys and a higher chance of surviving if attacked (Lantry et al., 2015; Schneider et al., 1996). However, Senecas may be less adapted to conditions in Lake Ontario than previously thought (Brenden et al., 2011).

Using the observed sea lamprey marking rate as a measure of the true sea lamprey attack rate has a number of shortcomings, but the A1 marks (indicating recent piercing attacks) are believed to be the least affected by them. The classification of sea lamprey marks is subject to error, but the A1 marks are correctly classified most of the time (Ebener et al., 2003, their Table 1 with four A1 marks identified correctly by 67% of 30 people on average). However, the classification error associated with A1 marks exceeds that of A1-A3 marks combined, where the A2 and A3 marks are those that are partially healed (Adams and Jones, *In preparation*; Firkus et al., *In review*; Nowicki, 2008; Ebener et al., 2003). The observed marking rate is only a good index of the true attack rate if the annual lethality rate from sea lamprey attacks is relatively constant over time (Adams et al., *In review*). Fresh piercing marks (A1) should be less susceptible to survivor bias, because they may be observed on fatally wounded lake trout before the lake trout die. Survivor bias may be greater for Chinook salmon than lake trout, leading to underestimated marking rates, because host mortality increases with water temperature (Farmer et al., 1977). The A1 marking rate has also been shown to be correlated with recovery rates of dead lake trout in Lake Ontario (Bergstedt and Schneider, 1988). Finally, the use of A1 marks should also help reduce the age-based bias in the healing rates, caused by the contrast between the fast growing, young Chinook salmon and the slow growing, old lake trout in Lake Ontario. An additional complication when analyzing sea lamprey-induced marks on more than one host species is that the duration of the juvenile (parasitic) life stage of the sea lamprey may vary with host selection (Cline et al., 2014; Moody et al., 2011).

Alternative hosts are often blamed for confounding the reported sea lamprey marking rates on Great Lakes lake trout. This study confirms that suspicion in Lake Ontario, where the relative abundance of Chinook salmon affects the marking rate on lake trout. When I varied the proportion of hosts that were lake trout over the range observed (0.252 to 0.516) while holding the total abundance of hosts and the total number of marks on them constant, the resulting marking rate on lake trout ranged as much as 0.034 (Figure 3.6). Here, the lake trout marking rates are near their maximum when lake trout comprise at least 37% of the host abundance, but are reduced when the proportion of hosts that were lake trout declines below the Model 1 inflection point of 32.6% (in 2006-2008 and 2014).

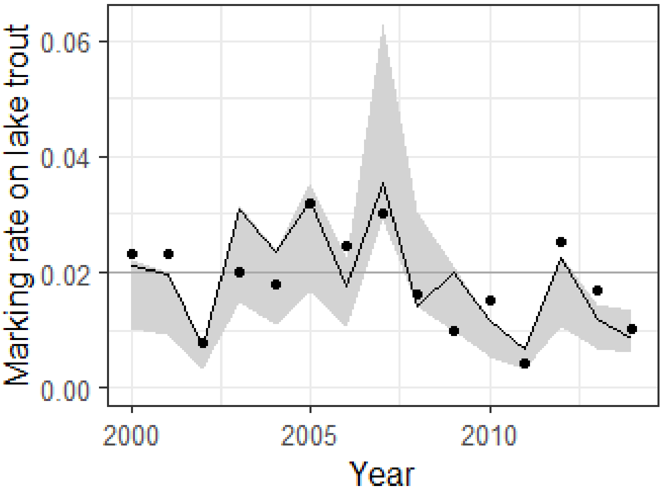

Figure 3.6. Model 1 predicted range of sea lamprey-induced marking rates on lake trout in Lake Ontario (shading) when the proportion of hosts that were lake trout (relative to Chinook salmon) varies over the range observed (0.252 to 0.516) while holding the total abundance of hosts and the total number of marks on them constant. Points represent observed marking rates; line represents predicted marking rates from Model 1 for observed proportional abundances.

I hope that the evidence from switching demonstrated in this study and the methods described will motivate further investigations into the host preference of sea lampreys. The effect of alternative hosts on lake trout marking rates is also suspected in other Great Lakes: siscowet lake trout in Lake Superior (Sitar et al., 2008), Chinook salmon in Lake Michigan, and Chinook salmon and lake whitefish in Lake Huron (Hansen et al., 2016). One impediment to such investigations is the lack of lake-wide absolute abundance estimates for the alternative hosts, which are necessary to calculate the proportional abundance relative to other hosts. Understanding the underlying causes of host switching could also be investigated via more complex models that incorporate spatial overlap and quantify host profitability to sea lampreys.

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CHAPTER 4

STOCK RECRUITMENT DYNAMICS OF GREAT LAKES SEA LAMPREYS

4.1 Introduction

To manage fisheries effectively, some understanding of recruitment dynamics and their dependence on stock size is key (Hilborn and Walters, 1992). Spawning recruitment is critical to maintain fish populations and sustainable harvests (Zhao et al., 2013). Knowledge of recruitment dynamics is equally important to inform the control of invasive fishes, where recruitment overfishing (Hilborn and Walters, 1992) may be the goal (Dux et al., 2019; Weber et al., 2011).

Invasive sea lampreys (*Petromyzon marinus*) have been the target of control measures in the Great Lakes since the formation of the Great Lakes Fishery Commission in 1955 (Fetterolf, 1980). Two primary methods of control have reduced Great Lakes sea lamprey populations to a fraction of their post-invasion peaks (Heinrich et al., 2003; Lawrie, 1970): lampricides that kill larvae and barriers that block upstream spawning migration of adults. Stock-recruitment relations would be particularly helpful in exploring control options that target adult sea lampreys, to assess the effect of reductions in stock on recruitment (Jones, 2007; Jones et al., 2003, Jones and Adams, *In press*).

I developed lake-wide stock-recruitment curves for Great Lakes sea lampreys, relating the number of spawning adults from one generation to the next (Myers et al., 1999). Young (2005) fit a similar model to Lake Huron sea lampreys, assuming an age at maturation of 6 years. I incorporated two covariates in the relations: sea lamprey size as a surrogate for fecundity and lampricide quantity as a surrogate for anthropogenic mortality.

I also incorporated proportional contributions from different cohorts of stock. Sea lampreys are semelparous with variable and difficult to measure age at maturity, which depends on the duration of the sedentary larval stage (Purvis, 1979) and the timing (spring or autumn) of metamorphosis to the parasitic juvenile stage. Structures typically used to age fish (scales, spines, and otoliths) are absent in sea lampreys, and statoliths (primitive otoliths) have not been found to be a good substitute (Barker et al., 1997; Potts et al., 2015), so estimates of sea lamprey ages typically depend on the analysis of larval length frequency distributions (Haeseker et al., 2003; Potter, 1980). I hoped that incorporation of stock from different spawning cohorts in the models would not only improve the fit, but also inform us of the typical age at maturation.

My primary objective was to develop stock-recruitment relations for Great Lakes sea lampreys. My secondary objective was to estimate the typical age composition of mature sea lampreys.

4.2 Methods

Sea lamprey stock-recruitment relations were estimated for all five Great Lakes at once, using the number of adults as both stock and recruits. Numbers in each lake were based on an annual index of adult abundance, the sum of mark-recapture population estimates (Mullett et al., 2003) from a subset of index streams, scaled up to a lake-wide estimate (Barber et al., *In preparation*). A Ricker stock-recruitment curve was fit (Ricker, 1975),

$$(1) \qquad R_{ij} = \alpha_j \sum_{k=5}^{7} (\rho_{kj}\ S_{i-k,j}\ e^{-\beta_j\ \rho_{kj}\ S_{i-k,j}})\ \epsilon_{ij}\ ,$$

where R_{ij} is the number of adults in year i and lake j (representing recruits) and S_{ij} is the number of adults in year i and lake j (representing stock from three different cohorts, 5, 6, and 7 years prior to recruitment). The 21 estimated parameters included α_j; β_j; ρ_{5j} and ρ_{6j}, the proportional contribution from stock 5 and 6 years prior to recruitment ($\rho_{7j} = 1 - \rho_{5j} - \rho_{6j}$); and σ^2, the variance of the lognormally distributed error ϵ with mean zero (on the log scale). This parameterization allows for contributions from mixed age classes while limiting the number of parameters estimated. The selected stock cohorts reflect the current presumed generation length of sea lampreys in the Great Lakes, corresponding to sea lamprey larval metamorphosis at age 3.5-5.5 years (Beamish and Medland, 1988; Young, 2005). Compensation was assumed to occur in the early stages of life, hence the incorporation of β_j with each contribution of the three stock cohorts to recruits.

Two additional predictors were considered for inclusion in the model: adult sea lamprey size and lampricide treatment effort. Adult sea lamprey size served as a surrogate for fecundity and was measured as the median individual weight of a subset of recaptured adults in each lake (in g). Treatment effort served as surrogate for anthropogenic mortality and was measured as the three-year average of TFM (3-Trifluormethyl-4-nitrophenol, Applegate et al., 1961) applied to larvae 2-4 years prior to recruitment to the adult life stage (in kg of active ingredient). Both predictors were centered and scaled by first subtracting their lake-specific means and then dividing by their lake-specific means (Figure 4.1). This standardization allowed me to fit a single stock-recruitment relation to all five lakes at once by placing covariate effects on a common unitless scale. The resulting coefficients correspond to the expected effect of a change relative to the mean. Each predictor was added to the base model one at a time,

$$(2) \qquad R_{ij} = \alpha_j \sum_{k=5}^{7} \left(\rho_{kj}\ S_{i-k,j}\ e^{-\beta_j\ \rho_{kj}\ S_{i-k,j}\ +\ \delta\ M_{i-k,j}} \right) \epsilon_{ij}\ ,$$

$$(3) \qquad R_{ij} = \alpha_j\ e^{\gamma\ E_{i,j}} \sum_{k=5}^{7} \left(\rho_{kj}\ S_{i-k,j}\ e^{-\beta_j\ \rho_{kj}\ S_{i-k,j}} \right) \epsilon_{ij}\ ,$$

$$(4) \qquad R_{ij} = \alpha_j\ e^{\gamma\ E_{i,j}} \sum_{k=5}^{7} \left(\rho_{kj}\ S_{i-k,j}\ e^{-\beta_j\ \rho_{kj}\ S_{i-k,j}\ +\ \delta\ M_{i-k,j}} \right) \epsilon_{ij}\ ,$$

where M_{ij} is the standardized adult sea lamprey mass for year i and lake j, E_{ij} is the standardized treatment effort for years i-2, i-3, and i-4 and lake j, and δ and γ are their estimated coefficients. Adult sea lamprey mass was incorporated separately for each stock cohort contribution, because it affects recruitment at the egg stage (Figure 4.2). Treatment effort was incorporated once for all cohorts combined, because it affects mixed age larvae prior to recruitment to the adult stage (Figure 4.2). Other model parameters are characteristic of the stock-recruitment model for adult sea lampreys of an average size and lampricide treatment effort at an average level, because when sea lamprey size is average, the additive $\delta M_{ij} = 0$ term drops out of the model, and when treatment effort is average, the $e^{\gamma E_{ij}} = 1$ multiplicative term drops out of the model.

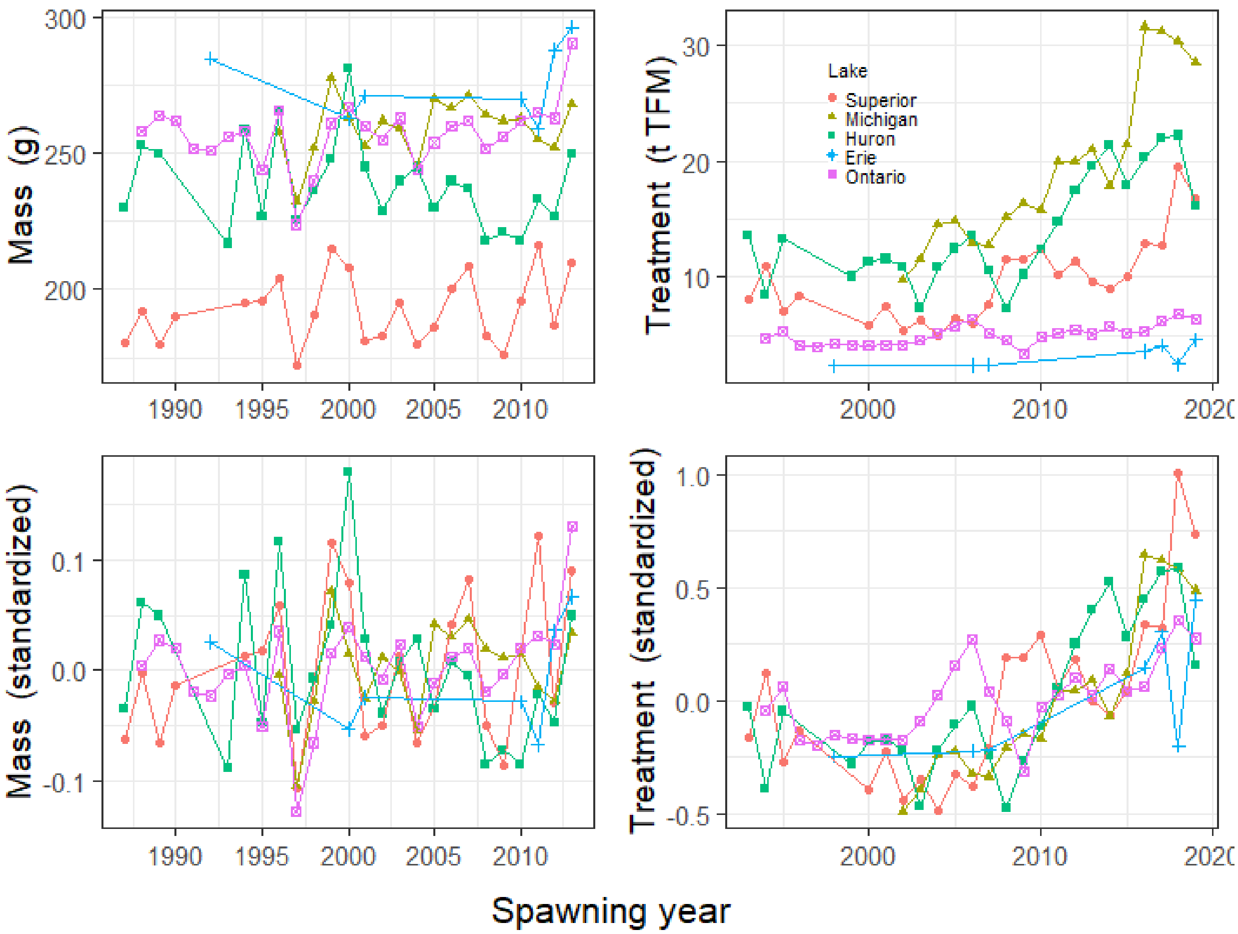

Figure 4.1. Median weight of individual adult sea lampreys recaptured in traps and mean lampricide treatment effort applied 2-4 years prior to recruitment (t of TFM active ingredient) 1993-2019. Top row is unscaled, bottom row is centered and scaled by the mean.

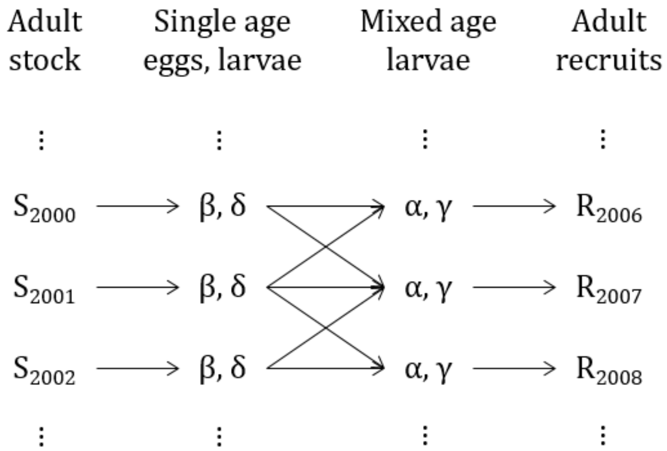

Figure 4.2. Conceptual diagram of Model 4 of sea lamprey stock-recruitment, relating adult stock in a few years to adult recruits 5-7 years later, with density dependence (β) and adult size effects (a surrogate for fecundity, δ) on individual cohorts of eggs and larvae and initial reproductive rate (α) and control effort effects (γ) on mixed cohorts of larvae.

Additional simplified versions of these four models were also considered. First, Great Lakes-wide (rather than lake-specific) proportions of stock cohorts were fit, leading to Models 5-8 with two (rather than 10) estimated proportions (Table 4.1). Second, stock was assumed to be composed of all three cohorts in equal proportions, leading to Models 9-12. Third, Great Lakes-wide α parameters were fit, leading to models 13-24.

Table 4.1. Number of parameters included in 20 Ricker stock-recruitment models for sea lampreys in the Great Lakes, and support for each model based on Akaike's information criterion. Proportional contribution from stock cohorts 5, 6, and 7 years prior to recruitment are denoted by p5, p6, and p7. The delta and gamma parameters represent coefficients for sea lamprey mass and lampricide treatment applied, respectively. The total number of parameters also includes σ^2. Level of empirical support based on ΔAIC: three asterisks for substantial support $\Delta AIC \leq 2$, one asterisk for considerably less support $2 < \Delta AIC \leq 7$, and no asterisks for essentially no support $\Delta AIC > 7$ (Burnham and Anderson, 2002).

Model	alpha	beta	p5	p6	p7	delta	gamma	No. Par.	delta AIC	Support
1	5	5	5	5	0	0	0	21	19.9	
2	5	5	5	5	0	1	0	22	17.8	
3	5	5	5	5	0	0	1	22	19.1	
4	5	5	5	5	0	1	1	23		
5	5	5	1	1	0	0	0	13	4.9	*
6	5	5	1	1	0	1	0	14	5.2	*
7	5	5	1	1	0	0	1	14	0.0	***
8	5	5	1	1	0	1	1	15	0.4	***
9	5	5	0	0	0	0	0	11	11.7	
10	5	5	0	0	0	1	0	12	12.5	
11	5	5	0	0	0	0	1	12	4.1	*
12	5	5	0	0	0	1	1	13	5.7	*
13	1	5	5	5	0	0	0	17	25.4	
14	1	5	5	5	0	1	0	18	21.2	
15	1	5	5	5	0	0	1	18	14.1	
16	1	5	5	5	0	1	1	19	16.1	
17	1	5	1	1	0	0	0	9	12.6	
18	1	5	1	1	0	1	0	10	12.2	
19	1	5	1	1	0	0	1	10	1.3	***
20	1	5	1	1	0	1	1	11	3.2	*
21	1	5	0	0	0	0	0	7	11.8	
22	1	5	0	0	0	1	0	8	11.1	
23	1	5	0	0	0	0	1	8	0.8	***
24	1	5	0	0	0	1	1	9	1.5	***

Models were compared using Akaike's Information Criterion (AIC). The best model was defined as that with the fewest parameters among those considered to have substantial support, $\Delta AIC \leq 2$ (Burnham and Anderson, 2002).

Models were fit via maximum likelihood using the optim function of R (R Core Team, 2018). Transformations were used to constrain parameters: $a_j = log(\alpha_j)$, $\alpha > 0$; $b_j = log(\beta_j)$, $\beta > 0$; $c_j = log(\rho_{5j}/(1 - \rho_{5j}))$, $0 < \rho_{5j} < 1$; $d_j = log(\tau_j/(1 - \tau_j))$ where τ_j is the proportion of $(1 - \rho_{5j})$ that metamorphoses at age 6, $\rho_{6j} = \tau_j * (1 - \rho_{5j})$, $0 < (\rho_{5j} + \rho_{6j}) < 1$. Asymptotic standard errors of parameter estimates were generated from the Hessian matrix. Finally, I visually inspected residual plots for evidence of serial autocorrelation (from one to seven years), trends over time, and unexplained patterns related to combined stock or predicted recruitment.

4.3 Results

Prior to model fitting, I expected stock-recruitment relations could be most reliably estimated for Lakes Superior, Michigan, and Huron with time series of at least 18 years and a range in stock sizes $>$ 0.6 orders of magnitude (Table 4.2). I was less certain whether covariates for sea lamprey size or lampricide treatment effort would be included in the best model. The ranges in sea lamprey sizes were $\leq$ 0.1 orders of magnitude for all lakes; the domain of lampricide treatment efforts ranged from 0.3 to 0.6 orders of magnitude.

Table 4.2. Summary of data available for fitting adult-to-adult stock-recruitment models to Great Lakes sea lampreys, including range and number of years, mean and domain of independent variables expressed as orders of magnitude (OOM, $log_{10}(Max/Min)$). Stock is the number of adult sea lampreys 5, 6, and 7 years prior to recruitment (in thousands), size is the median annual size of subsampled sea lampreys 5, 6, and 7 years prior to recruitment (in g), and treatment is the mean lampricide treatment effort applied 2-4 years prior to recruitment (in t of TFM active ingredient).

	Year			Stock		Size		Treatment	
Lake	Min	Max	No.	Avg	OOM	Avg	OOM	Avg	OOM
Superior	1993	2019	24	97	0.92	193	0.10	9.70	0.60
Michigan	2002	2019	18	122	1.04	259	0.08	19.17	0.51
Huron	1993	2019	24	214	0.70	238	0.11	13.99	0.48
Erie	1998	2019	7	15	1.13	278	0.10	3.20	0.28
Ontario	1994	2019	26	41	0.58	257	0.11	5.06	0.30

All five models with substantial support included a covariate for lampricide treatment effort and excluded lake-specific age composition, but they varied with respect to inclusion of a lake-specific α_j, a lake-generic age composition, and a covariate for sea lamprey size (Table 4.1). Among these, Model 23 with the fewest parameters (8) was defined as "best"; it included a covariate for lampricide treatment, a lake-generic α, and assumed contributions of 1/3 each from stock 5, 6, and 7 years prior to recruitment (Figure 4.3). All eight models with lake-specific age composition parameters had essentially no support. The most complex model (Model 4) did not converge, pushing the limits of the number of parameters that could be estimated from the data.

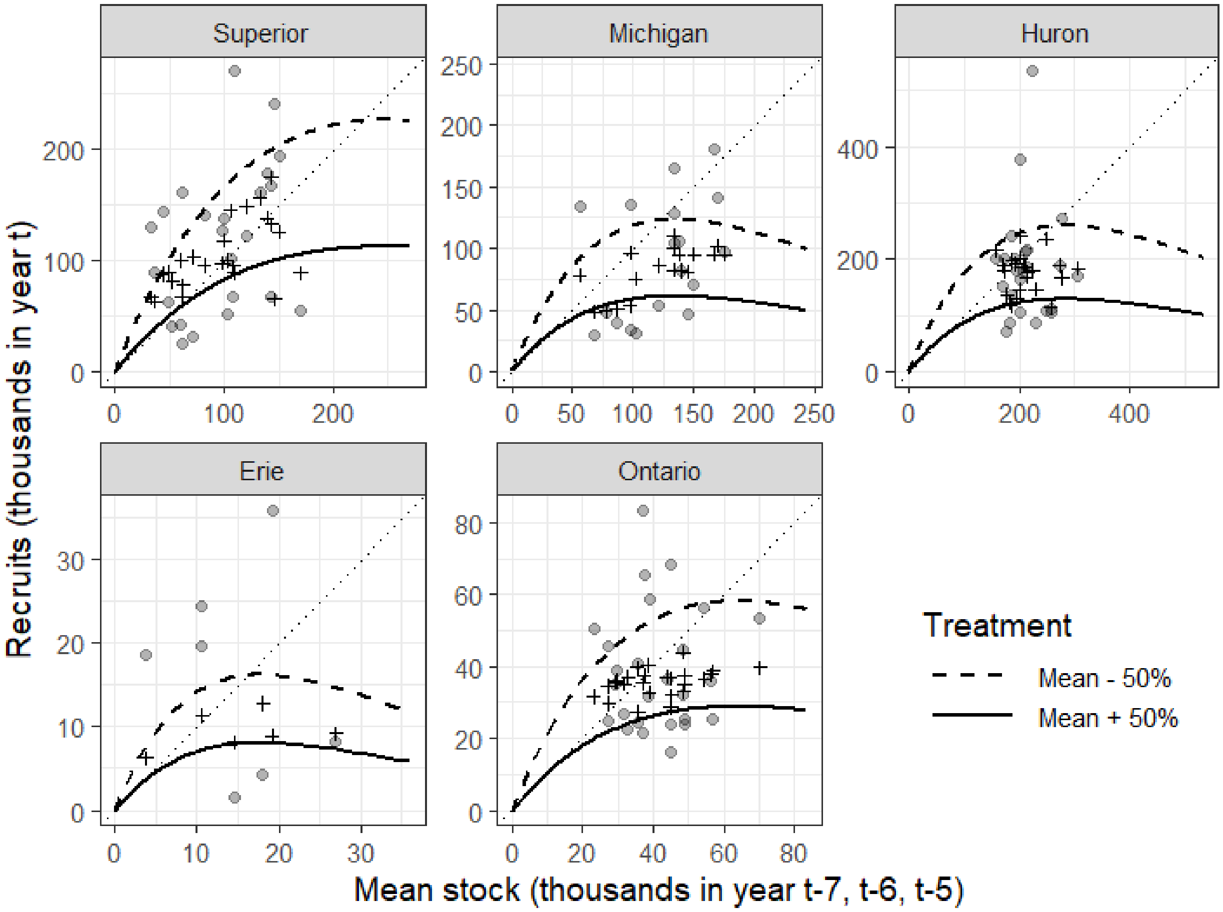

Figure 4.3. Adult-to-adult sea lamprey stock-recruitment relations in the Great Lakes. Symbols represent annual observations (circles) and predictions (plus signs). Symbols are plotted at the mean stock 5, 6, and 7 years prior to recruitment, but predictions (from Model 23) incorporate stock from each cohort separately. Curved lines represent the stock-recruitment relation of Model 23 with treatment effort 50% below ($E = -0.5$) and above ($E = 0.5$) average. Curves were drawn assuming equal contribution from each stock cohort. Model 23 uses a lake-generic α, lake-specific β_j, and a lake-generic γ for the treatment covariate. The diagonal dashed line represents the replacement line, above which recruits exceed stock.

Stock-recruitment parameters from Model 23 were well estimated for all lakes (Table 4.3, Figure 4.4). Estimated β_j parameters were similar for Lakes Superior, Michigan, and Ontario. Lake Erie had a significantly greater β_j than the other lakes and Lake Ontario had a significantly greater β_j than Lake Huron, indicating peak recruitment at lower numbers of combined stock (Figure 4.3). The β_j were significantly greater than zero for all lakes, indicating density dependent survival, consistent with previous work (Haeseker et al., 2003; Jones et al., 2003; Young, 2005). The equilibrium stock abundance with average lampricide treatment effort ($E = 0$) in each lake ranged from $ln(\alpha)/\beta$ = 3,300 in Lake Erie to 53,000 in Lake Huron.

Table 4.3. Parameter estimates for stock-recruitment Model 5, with 95% confidence intervals based on asymptotic standard errors.

Parameter	Lake	Estimate	Lower	Upper
Alpha	All	1.7518	1.16560	2.6329
Beta	Superior	0.0121	0.00447	0.0329
Beta	Michigan	0.0223	0.01347	0.0368
Beta	Huron	0.0106	0.00583	0.0193
Beta	Erie	0.1689	0.09112	0.3131
Beta	Ontario	0.0472	0.02450	0.0909
Gamma	All	-0.7003	-1.07327	-0.3273

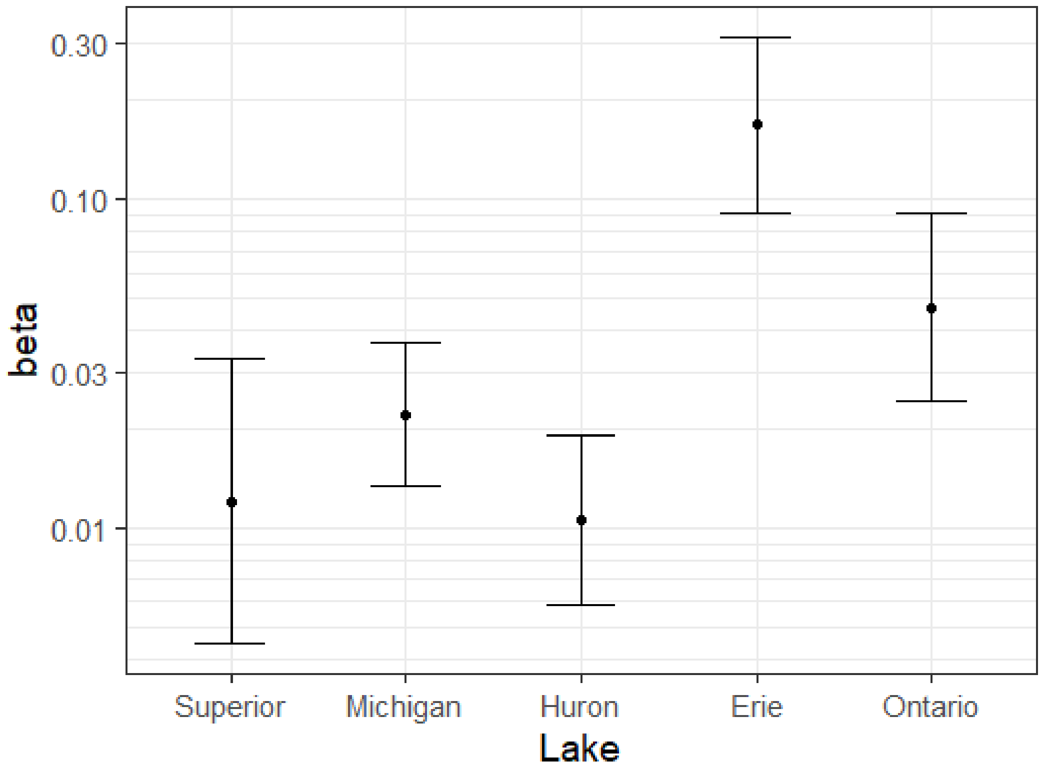

Figure 4.4. Estimated Ricker stock-recruitment β_j parameters for Great Lakes sea lampreys, with 95% confidence intervals based on asymptotic standard errors. Independent variables include stock from 5-7 years prior to recruitment and lampricide treatment effort 2-4 years prior to recruitment.

The coefficient for lampricide treatment effort was also well estimated. The γ parameter was negative, indicating a reduction in recruitment with an increase in treatment effort. For example, doubling the mean treatment effort ($E = 1$) results in a 50% reduction in recruitment ($e^{\gamma E} = e^{-0.7 \cdot 1} = 0.5$) with a 95% confidence interval of 34% to 72% (Table 4.3, Figure 4.3).

No lakes showed evidence of autocorrelation in residuals from their stock-recruitment models. Model residuals from three lakes exhibited significant trends over time, increasing in Lake Superior, decreasing in Lake Michigan, and increasing then decreasing in Lake Ontario (Figure 4.5). No pattern was evident in plots of residuals versus combined stock or predicted recruitment for any lake.

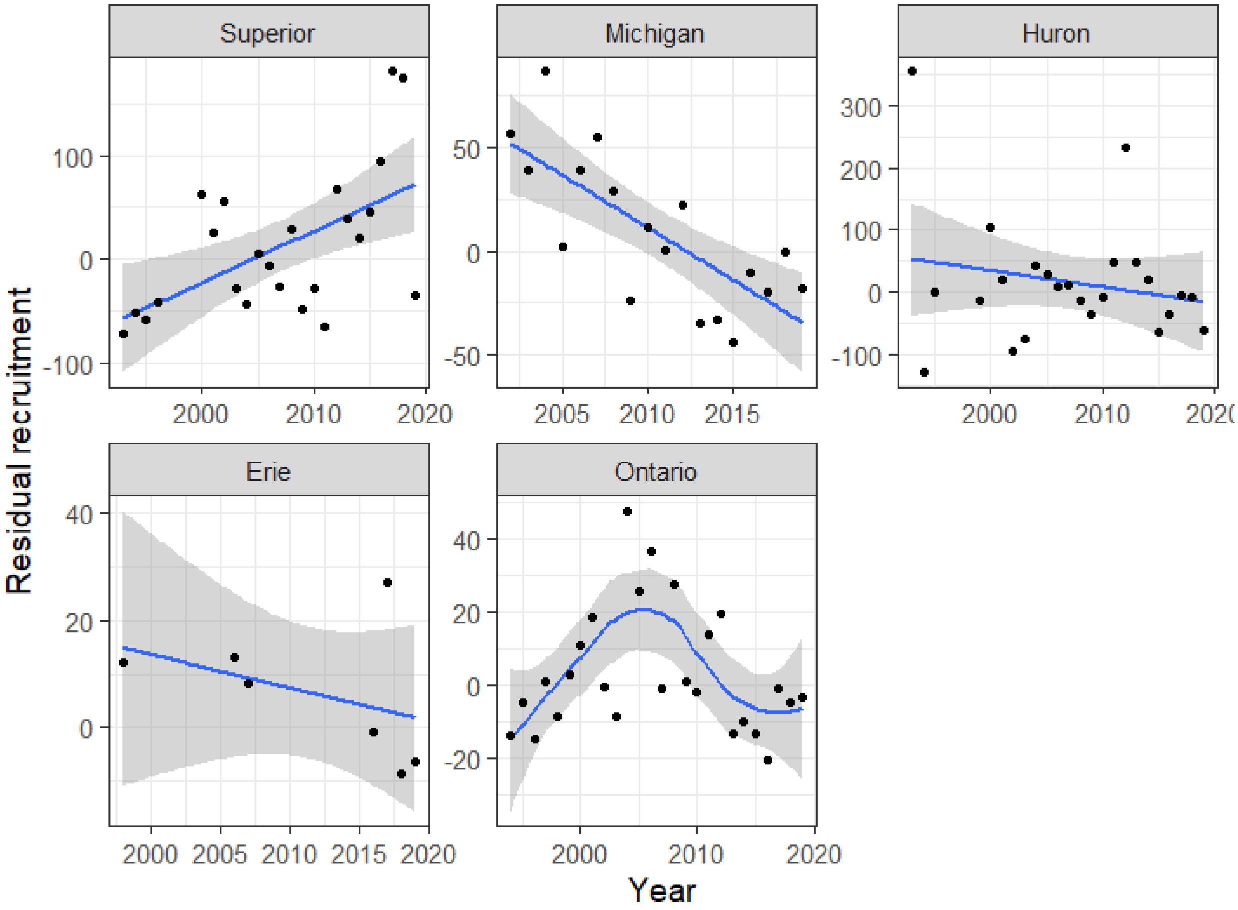

Figure 4.5. Temporal trends in residuals from adult-to-adult sea lamprey stock-recruitment models in the Great Lakes. Lines represent linear fits to all lakes except Ontario with a generalized additive model smoother. Shading represents the 95% confidence interval.

4.4 Discussion

I successfully developed stock-recruitment relations for Great Lakes sea lampreys, with three different cohorts of stocks, a single production parameter common to all five lakes, and a covariate for lampricide treatment effort. These are the only whole-lake sea lamprey stock-recruitment curves published other than those of Young (2005), which was for Lake Huron only, and Jones and Adams (*In press*). However, I was unable to use stock-recruitment models to estimate typical age composition of mature sea lampreys.

I had hoped to use stock-recruitment relations to inform our understanding of average age of maturation in Great Lakes sea lampreys. Knowledge of age at maturation would aid decision makers in efficiently planning for chemical control of larval sea lampreys in Great Lakes streams and improve models that inform those decisions (Howe et al., 2012; Jones et al., 2009; Robinson et al., 2013; Treble et al., 2008). Aging sea lampreys is difficult using statoliths or length-frequency distributions (Dawson et al., 2015), though recent genetic pedigree analysis of larval sea lampreys (Sard et al., 2020; Weise et al., 2019) may be extensible to adults if sequencing costs decline enough to allow for lake-wide sampling (Scott Miehls, US Geological Survey, personal communication). A younger age at maturation means increased productivity (Weaver et al., 2018) leading to an increased potential for recovery in threatened native populations, more lake trout wounding and more frequent treatments of rivers for invasive Great Lakes populations. However, models that estimated recruitment-at-age contributions did not outperform simpler models that assumed an uninformative fixed contribution of one third from each of three cohorts of stock.

I used Ricker stock-recruitment relations, because I anticipated overcompensation in Great Lakes sea lamprey populations. Overcompensation can be induced by predation on pre-recruits (Ricker, 1954), which is essentially what the sea lamprey control program does when it treats Great Lakes tributaries with lampricides, killing millions of larval sea lampreys. Whether native sea lamprey populations also exhibit overcompensation is unknown.

Ideally, I would have used only adult females as stock, but information on the sex of captured adults was not recorded consistently. In many years, sex was only recorded for adult sea lampreys that were recaptured, and in some years, equal numbers of males and females were selected for mark and release. Rather than rely on recorded sex ratios, I used the total estimated population (males and females) as stock in my models.

Lampricide treatment effort had a significant effect on sea lamprey recruitment in the Great Lakes, further testimony to the effectiveness of chemical control. My model suggests that decreasing treatment effort from 50% above to 50% below the mean level of TFM applied doubles the number of sea lampreys that recruit to spawn (Figure 4.3).

The maximum annual reproductive rate (α) is relatively constant within a species in the absence of anthropogenic mortality (Myers et al., 1999). The best model supported this finding, even while incorporating average anthropogenic mortality. Two models with substantial support included lake-specific α_j terms, suggesting that there may be underlying differences in the maximum annual reproductive rate of lake populations or the relative lampricide treatment effort applied to them, though not enough to overcome variability in the data. The estimated α was within the range of typical values estimated (1-7) for 30 different species by Myers et al. (1999). The maximum annual reproductive rate at average treatment levels was significantly less than that estimated by Young (2005) for Lake Huron 1959-2000: 3.95 with 95% confidence interval (2.90, 6.64). This is likely due to increases in lampricide treatment effort since 2000 (Figure 4.1).

The estimated β_j parameters reflect the capacity of the population, which is expected to vary among stocks (Hilborn and Walters, 1992). In this case, capacity tended to be greater in the lower lakes than the upper lakes, perhaps reflecting their greater productivity in general.

Stock-recruitment relations are susceptible to bias as a result of measurement error in the stock (Walters and Ludwig, 1981). If errors are large enough, recruitment may appear to be independent of stock, which did not occur in this study. While stream mark-recapture estimates that go into stock estimates are relatively precise (Adams and Jones, *In preparation*), there is unknown error associated with the factor used to scale up stream estimates to lake-wide populations (Barber et al., *In preparation*). If the domain of stocks is less than 0.6 orders of magnitude, as they are for Lake Ontario sea lampreys in this study, biases can be quite severe (Hilborn and Walters, 1992). Such bias tends to underestimate the response of recruitment to changes in stock.

The differing temporal patterns in recruitment for the lakes indicate that unexplained drivers are at the lake scale, not region-wide across the entire Great Lakes basin. Phytoplankton productivity in both Lakes Superior and Michigan has declined in recent years, so this does not explain the respective increase and decline in recruitment in those lakes (Fahnenstiel et al., 2016; Rowe et al., 2017). The patterns could be the result of changes in abundance or spatial distribution of host fish populations in the lakes, or smaller-scale environmental factors that may affect my ability to trap adult sea lampreys (Johnson et al., *In review*).

I had expected sea lamprey size to be an important covariate in the stock-recruitment relations, since fecundity increases with mass in most stocks (Walters, 1986). However, models that included sea lamprey size as a covariate failed to outperform simpler models without it, in contrast to the findings of Young (2005) for Lake Huron. Young (2005) included size information dating back to 1959 when adult sea lampreys trapped in Lake Huron were smaller than they are today, leading to a domain about three times that of this study. Variation in fecundity of Pacific salmon (Quinn and Bloomberg, 1992) is usually dwarfed by large annual fluctuations in juvenile survival (Waples, 2006). Sea lamprey sizes used (the median weight of a subset of recaptured adult sea lampreys) may be overestimated. The mass of these twice-trapped adults may represent a larger than normal segment of the population, because large adult sea lampreys exhibit reduced activity and spend more time in enclosures than small ones (McLean and McLaughlin, 2018). This bias should not have affected the results, since mass was standardized relative to the mean prior to inclusion in the model.

Pulses in the prevalence of small and large adult sea lampreys appeared to be synchronized across the Great Lakes, with the exception of Lake Erie (Figure 4.1). Excluding Erie, between lake correlations of sea lamprey size ranged from $r = 0.27$ (Superior and Huron) to 0.83 (Superior and Ontario). This apparent synchrony suggests that broader environmental or climatic changes that span the Great Lakes influence sea lamprey size. Similar conclusions have been found for recruitment dynamics in Great Lakes fishes, varying with water temperature, wind speed, and the North Atlantic Oscillation (Bunnell et al., 2017; Myers et al., 2015). Other studies of fish species outside of the Great Lakes have shown synchronicity in fish growth (Black, 2009; Jensen et al., 2011; Tao et al., 2018).

I believe these sea lamprey stock-recruitment models will be useful to fisheries managers with different objectives. In the Great Lakes and Lake Champlain (in New York, Vermont, and Quebec), they could be used to inform various recruitment overfishing strategies in the control of invasive sea lampreys. Jones and Adams (*In press*) have already used such an approach to investigate the possibility of sea lamprey eradication from the Great Lakes. In the Atlantic Ocean, the models could be used to inform restoration strategies in the conservation of native sea lampreys.

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