



## Spatial and temporal variation in marking rates and severity of sea lamprey attacks on salmonines in Lakes Michigan and Huron

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### ABSTRACT

The United States and Canada have invested substantial effort to control sea lamprey *Petromyzon marinus* in the Laurentian Great Lakes and to estimate their effects on lake trout *Salvelinus namaycush*, a native salmonine undergoing rehabilitation. However, sea lamprey also attack Pacific salmon *Oncorhynchus* spp. and brown trout *Salmo trutta*, which contribute to a fishery worth nearly \$7 billion USD annually. Marks on surviving hosts are used to assess damages caused by sea lamprey and success of control efforts. We examined spatial and temporal variation in marking rates, mark type, and stage of healing on lake trout, Chinook salmon *O. tshawytscha*, rainbow trout *O. mykiss*, coho salmon *O. kisutch*, and brown trout in Lakes Michigan and Huron. Mean marking rates were highest for lake trout, followed by brown trout, Chinook salmon, rainbow trout, and coho salmon in Lake Michigan, but were several times higher for Chinook salmon than for lake trout (all sizes) and small (533–635 mm) and medium (636–737 mm) rainbow trout in Lake Huron, particularly in summer. Chinook salmon had a lower proportion of healed marks relative to fresh marks compared to lake trout in both lakes, which may indicate differences in post-attack survival. Although lake trout may be the preferred sea lamprey host, Chinook salmon and other species are also suitable and available in Lake Michigan; and Chinook salmon may be a preferred host in Lake Huron. Accounting for alternate hosts could inform fisheries management and improve damage assessments of the sea lamprey control program.

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### Introduction

Sea lamprey *Petromyzon marinus* were one of the primary drivers of the collapse of lake trout *Salvelinus namaycush* in the Great Lakes (Lavis et al., 2003; Smith and Tibbles, 1980), where they continue to parasitize economically important salmonines. As a result, the federal governments of Canada and the United States have devoted substantial time and resources to control sea lamprey abundance and estimate their effects on host populations, especially economically important salmonines (Bence et al., 2003; Christie and Goddard, 2003). Because of the difficulty of directly observing sea lamprey feeding activity *in situ* and corresponding host mortality in large lakes, measurements of impacts on host species has largely been inferred from lethality of attacks based on laboratory experiments (e.g., Madenjian et al., 2008; Swink, 2003; 1991), combined with

trends in sea lamprey marking rates on surviving fish, sea lamprey population abundance, and host abundance (Adams et al., 2003; Larson et al., 2003; Sitar et al., 1999).

Sea lamprey spawn in tributaries containing clean gravel for nesting adjacent to off-channel nursery habitats with soft substrates, which frequently occur in northern Lake Michigan and Huron (Lavis et al., 2003; McLeod et al., 2011; Morman et al., 1980; Morse et al., 2003). Before sea lamprey spawn in the spring, they parasitize host fish for a single growing season (Bergstedt and Swink, 1995). Growth occurs primarily in late summer and fall, which is when most lethal attacks occur. Fish that survive attacks are left with marks, which are classified by the degree of muscle exposure and stage of healing (Ebener et al., 2006; King, 1980; King and Edsall, 1979). Marks observed in spring are usually in the earlier stages of healing, and can be attributed to the most recent sea lamprey feeding season from the previous fall (Eshenroder and Koonce, 1984).

Juvenile sea lamprey are difficult to quantify in nature, so mark numbers and types are the primary *in situ* measure of sea lamprey

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attacks and induced mortality. Control agents and fishery managers use trends in marking rates to assess the success of the sea lamprey control program (e.g., Adams et al., 2003) and to estimate host fish mortality in catch-at-age models and other purposes (e.g., Bence et al., 2011, 2003; Sitar et al., 1999; Truesdell and Bence, 2016). Most sea lamprey marking studies in the Great Lakes focus on lake trout, a native salmonine that once supported large-scale commercial fisheries (e.g., Baldwin et al., 2009; Hile, 1949; Hile et al., 1951) before populations collapsed from sea lamprey-induced mortality and over-exploitation (Smith, 1968; Smith and Tibbles, 1980; Wells and McLain, 1973). Since the 1950s, lake trout have been the focus of an international rehabilitation effort throughout the Great Lakes (e.g., Hansen, 1999; Kruger and Ebener, 2004; Muir et al., 2012). Lake trout total mortality has been shown to be positively related to marking rates (Pycha, 1980), and the number of lake trout carcasses with fresh sea lamprey marks has been positively correlated with marks in early stage of healing on live lake trout sampled the same year in Lake Ontario (Bergstedt and Schneider, 1988).

Sea lamprey also attack other salmonine hosts, including Pacific salmon (*Oncorhynchus* spp.) that contribute to a recreational sport fishery valued at nearly \$7 billion USD per year for local U.S. economies (American Sportfishing Association, 2008). Sea lamprey marking data on Pacific salmonines are limited due to low catch rates in bottom-set fishery-independent assessments designed to survey lake trout (Schneeberger et al., 1998), and a lack of sea lamprey marking data collected by most state and provincial creel programs. Therefore, the potential levels of sea lamprey parasitism and induced mortality on these alternative hosts have been largely overlooked (but see Bence et al., 2003; Morse et al., 2003).

Marking is only observed on fish that survive attacks; thus, lower marking rates on other salmonines could indicate either lower attack rate or higher sea lamprey-induced mortality (Adams et al., 2021; Bence et al. 2003). Relationships among sea lamprey abundance, lake trout abundance, and marking rates are highly variable and not always apparent (Adams et al., 2020; Madenjian et al., 2008). One mechanism that could contribute to such a disconnect is that sea lamprey attack alternative hosts with suitable abundance and large body size (Bence et al., 2003; Happel et al., 2017; Rutter, 2004; Rutter and Bence, 2003; Swink, 2003). This underscores the need for more information on marking on fish other than lake trout.

We sought to quantify sea lamprey marking rates on lake trout, Chinook salmon *Oncorhynchus tshawytscha*, rainbow trout (steelhead) *O. mykiss*, coho salmon *O. kisutch* and brown trout *Salmo trutta* captured by the sport fishery in Lakes Michigan and Huron during 2012–2018. Our objectives were to: 1) evaluate differences in marking rate and severity among species and between Lakes Michigan and Huron and 2) describe spatial and temporal variation in marking rates in Lakes Michigan and Huron. Although we originally hoped to do this for all salmonine species, analysis for this question was largely restricted to Chinook salmon and lake trout due to limitations in the data set, and for the same reason we did not evaluate spatial patterns within Lake Huron. Our third objective was to compare the distribution of mark healing stages in Chinook salmon and lake trout in both lakes as a potential indicator of sea lamprey-induced mortality. We expected marking rates would be highest for lake trout in both Lakes Michigan and Huron, given this species is believed to be a preferred host (e.g., Bence et al., 2003), but marking rate may vary among species and among spatial and temporal strata due to proximity to sea lamprey spawning habitat in northern recovery areas (Lavis et al., 2003; Morse et al., 2003) and seasonal peaks in attacks with timing potentially varying among years, areas and species (Jacobson, 1989; Spangler et al., 1980). We also expected no difference in the relative frequency of mark healing stages between lake

trout and Chinook salmon, or between the lakes, on the assumption that lethality of attacks and healing rates would be similar.

## Methods

Our study focused on Lake Michigan and U.S. waters of Lake Huron during 2012–2018 (Fig. 1). Sea lamprey marking data were obtained for lake trout, Chinook salmon, rainbow trout, coho salmon, and brown trout caught by sport fisheries during two seasons, spring (April–June) and summer (July–September), and subsequently sampled by trained biotechnicians as part of the broader Great Lakes Mass Marking Program (Bronte et al., 2012). This program is operated by the U.S. Fish and Wildlife Service and supports an annual coded-wire tagging and field recovery effort that involves all state and federal agencies that stock salmon and trout in the U.S. waters of the Great Lakes and its tributaries. Total length (nearest 1 mm), weight (nearest 0.1 kg), species, date, location, and sea lamprey mark data were recorded from all angler-caught salmon and trout that were sampled. Sampling fish from the sport fishery is currently the only way to collect data on most salmonines (except lake trout) across time and space in the Great Lakes, as fishery-independent surveys (Schneeberger et al., 1998) that target lake trout using bottom-set gill nets rarely encounter Pacific salmon that are mostly pelagic. Angler catches were surveyed at boat ramps and cleaning stations, fishing tournaments, and other areas with high angling volume to maximize recovery efficiency. Combined sampling effort was >300 field days each year, covered over 40 port cities across all U.S. state jurisdictions on Lakes Michigan and Huron, and was spread out over the spring and summer seasons. No recovery effort was expended in Ontario waters of Lake Huron. Recovery location for each fish was recorded as the port of landing and placed into a larger 10 × 10 min grid cell based on GPS coordinates.

Sea lamprey marks were classified according to King (1980) who recognized type-A and type-B marks, each with four stages of healing (I, II, III and IV). Type-A marks are those where the skin and muscle of the fish are penetrated, whereas type-B marks lack penetration. Stages I–IV indicate progressive stages of healing from none (stage I) to complete (stage IV). All field personnel were trained to use the standard dichotomous key for sea lamprey mark identification in the Great Lakes (Ebener et al., 2006). Slide marks or marks thought to be caused by the same individual sea lamprey (e.g., similar sized marks grouped together in proximity to one another) can be a source of variability in mark counts between observers (Ebener et al. 2003). Thus, in such instances field personnel were trained to follow guidance by Ebener et al. (2006) to record only the freshest mark, with type-A marks prioritized over type-B marks, and were instructed to photograph questionable marks for verification by a more experienced biologist. AI, AII, and AIII marks are considered to represent the most severe injury in various stages of healing and are thought to induce the lowest probability of survival (Ebener et al., 2003; Eshenroder and Koonce, 1984); therefore, we included these marks in our primary analysis of mean marking rates. However, we also examined patterns in type-B marks (stages I, II and III), which are not commonly published but may also affect hosts and potentially induce mortality, to ascertain whether they may be more meaningful than previously thought. Fully healed marks (AIV and BIV) may be years old and thus were not included in assessments of marking rates. However, all type-A and type-B marks were examined to determine the ratio of healed and fresh mark types in species where we observed high rates of marking.

To evaluate spatial patterns in sea lamprey marking, recovery locations were aggregated into larger regions (Fig. 1). We created four recovery regions in Lake Michigan and one in Lake Huron that

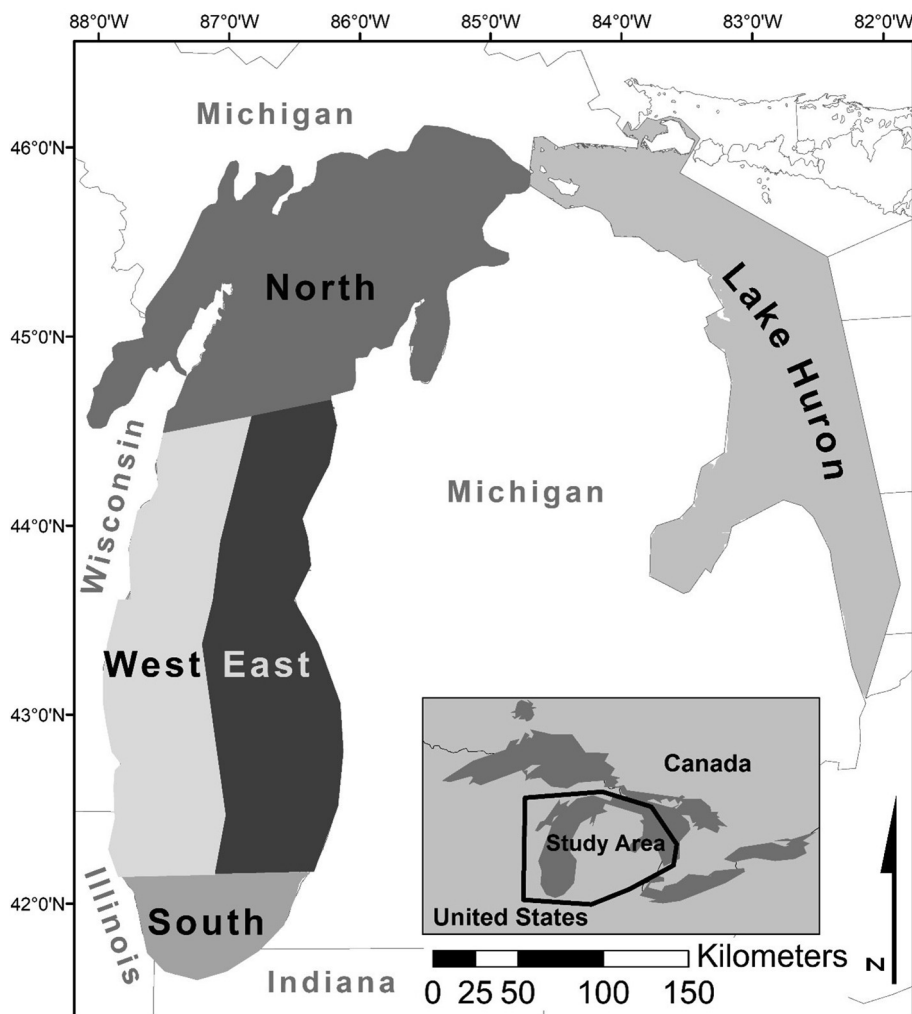


Fig. 1. Map of the study area with geographical fish recovery regions depicted.

were determined by tallying spatial concentrations of recovered fish among 10-minute grids nearest to the ports of landing, and then grouping grids into regions (North, South, East, and West) that were geographically meaningful for detecting spatial differences while retaining adequate sample sizes for analysis. Prior studies have suggested differences in sea lamprey marking on lake trout in northern compared to southern Lake Michigan (e.g., Kornis et al., 2019b; Lavis et al., 2003), and an east/west comparison was added because sample sizes were adequate to explore potential differences. Boundaries between regions were placed at natural breaks in the spatial distribution of samples (i.e., at locations where there were multiple 10-minute grid cells with zero samples). Sample sizes were not adequate for regional analysis within Lake Huron, but seasonal variation was examined as a potential factor in both lakes.

In general, sea lamprey marking rates increase gradually as a function of host length, eventually approaching an asymptote. Thus, several studies recommend evaluating sea lamprey marking rates by comparing logistic functions of marks versus body length among varying strata of interest (e.g., Prichard and Bence, 2013; Rutter and Bence, 2003). We initially attempted this approach, but found that logistic models failed to converge for rainbow trout, coho salmon and brown trout in both lakes. This was likely due to a low incidence of sea lamprey marks relative to the total number of fish examined (Table 1), and a relative scarcity of larger fish of these species in the samples, so that simultaneously estimating

the three parameters of the logistic function ( $\theta$  = asymptotic marking rate;  $\beta$  = inflection point in logistic model;  $\alpha$  = rate of increase in the curve; Rutter and Bence, 2003) was not possible.

To compare marking rates consistently among the five species, we instead handled the body size covariate by grouping fish into size classes commonly used in earlier studies of marking on lake trout (e.g., Eshenroder and Koonce, 1984). Three size classes, 533–635 mm, 636–737 mm, and > 737 mm total length (TL), were used and are referred to hereafter as ‘small’, ‘medium’, and ‘large’ fish, respectively. We analyzed data separately by size class (small, medium, and large), mark type (either A or B marks, using the combined count of stages I, II, and III for each type of mark), and lake (Lake Michigan or Huron). Marking rates for small fish provided an indication of the sizes at which marking rates begin to increase and stabilize. However, marking rates were low and likely in transition over the sizes included in the 533–635 mm size class, consistent with prior works (e.g., Pycha, 1980; Pycha and King, 1975). Thus, we focused only on larger fish (the 636–737 mm and > 737 mm classes), consistent with use of the asymptotic marking rate estimated by a logistic model as an index (e.g., Rutter and Bence, 2003) which is intended to standardize for effects of body size.

In our full models on the medium and large size classes, among-individual variation for each mark type and size class was treated as coming from a negative binomial distribution with a mean determined via a log-link function by region (used only for Lake

**Table 1**  
Mean type-A and type-B sea lamprey marking rates (marks/fish) with 95% confidence intervals about the mean for three size categories of salmonines caught by recreational anglers in Lakes Michigan and Huron during 2012–2018. Stage-IV wounds were not included in the analyses.

Species	Length Category (mm)	Lake Michigan					Lake Huron				
		N <sub>fish</sub>	Mark type	N <sub>marks</sub>	Mean	95% CI	N <sub>fish</sub>	Mark type	N <sub>marks</sub>	Mean	95% CI
Lake trout	533–635	6,169	A	47	0.008	0.006–0.010	1,217	A	23	0.019	0.012–0.030
			B	33	0.005	0.004–0.008		B	26	0.021	0.011–0.040
	636–737	6,957	A	195	0.028	0.024–0.033	1,551	A	51	0.034	0.025–0.046
			B	95	0.015	0.012–0.019		B	29	0.022	0.014–0.033
	>737	5,600	A	214	0.038	0.033–0.045	830	A	33	0.038	0.026–0.054
			B	169	0.032	0.026–0.039		B	14	0.017	0.010–0.029
Chinook salmon	533–635	4,302	A	16	0.004	0.002–0.006	180	A	20	0.111	0.066–0.187
			B	6	0.001	0.001–0.004		B	6	0.033	0.015–0.074
	636–737	7,809	A	54	0.007	0.005–0.009	231	A	21	0.095	0.058–0.156
			B	27	0.004	0.002–0.005		B	4	0.014	0.005–0.044
	>737	20,246	A	236	0.012	0.010–0.013	592	A	51	0.091	0.067–0.122
			B	147	0.007	0.006–0.009		B	14	0.026	0.016–0.043
Rainbow trout	533–635	2,872	A	5	0.002	0.001–0.004	244	A	2	0.008	0.002–0.033
			B	3	0.001	0.001–0.003		B	4	0.016	0.003–0.102
	636–737	4,091	A	20	0.005	0.003–0.008	181	A	1	0.006	0.001–0.039
			B	14	0.003	0.002–0.007		B	2	0.011	0.003–0.044
	>737	1,693	A	5	0.003	0.001–0.012	18	A	4	0.211	0.065–0.679
			B	6	0.004	0.001–0.011		B	1	0.053	0.007–0.381
Coho salmon	533–635	6,314	A	21	0.003	0.002–0.005	56	A	1	0.018	0.003–0.127
			B	16	0.003	0.001–0.005		B	0	0.000	–
	636–737	1,824	A	3	0.002	0.001–0.005	7	A	0	0.000	–
			B	5	0.003	0.001–0.007		B	0	0.000	–
	>737	163	A	0	0.000	–	1	A	0	0.000	–
			B	0	0.000	–		B	0	0.000	–
Brown trout	533–635	463	A	1	0.002	0.001–0.015	11	A	1	0.091	0.013–0.646
			B	1	0.002	0.001–0.015		B	0	0.000	–
	636–737	277	A	3	0.011	0.002–0.057	6	A	0	0.000	–
			B	2	0.007	0.002–0.029		B	0	0.000	–
	>737	110	A	3	0.027	0.005–0.140	0	A	0	0.000	–
			B	0	0.000	–		B	0	0.000	–

Michigan), season, and year (as a categorical variable). The approach can be viewed as an extension (because the negative binomial is not a member of the exponential family) of a generalized linear mixed effect model. We used a negative binomial distribution as our default distribution, rather than a Poisson distribution that has sometimes been used for marking data (e.g., Adams et al., 2021; Rutter and Bence, 2003), because marking data can be over-dispersed (Prichard and Bence, 2013), and when not accounted for overdispersion can influence inferences. The main effects of region, season, and year were fixed, and the full model allowed for a fixed interaction between season and region (for Lake Michigan), to allow for spatial differences in seasonality. Our full model also included a random interaction of year and region, which allowed for variations unique to each year and region that were assumed to come from a common probability distribution.

We treated the main effects of region and year as fixed, as we were interested in general patterns of marking rates in these specific places, and over these years. Our choice to treat the main effect of year as a fixed is consistent with treatment in other fisheries studies with similar objectives, and with recommendations for analyses when the number of categories (years) is low (Deroba and Bence, 2009; Harrison et al., 2018).

Our treatment of the interaction of year and region as random, regardless of the fact that both main effects were fixed, reflects a not uncommon approach in fishery models incorporating interactions with year (e.g., Campbell, 2015; Cooke, 1997; Deroba and Bence, 2009; Maunder and Punt, 2004). In this approach, the unique characteristics of a year and region combination are viewed as noise drawn from a common distribution. Because the interaction is random and influences the expected value for all observations in the year and region, its presence introduces correlation (non-independence) in the observations, after accounting for the influence of fixed effects (Samuels et al., 1991). The basic idea is

that complex non-independence can plausibly be approximated by such random interactions. Allowing random interaction between factors with fixed main effects contrasts with some classical presentations on mixed-effect models that state it does not make sense to treat interactions of two fixed-effects as random (e.g., Henderson, 1982). This classical perspective appears to stem from the view of random effects as arising from random selection of factor levels from a population. Our approach can be justified by an alternative view, that calling an effect random merely means that each effect in a batch of effects is treated as a realized value of a random variable from a common distribution (see Gelman (2005) and Gelman and Hill (2007) for more discussion about random effects).

Our first step in constructing models for inference was to focus on the random part of the model, and to decide whether to retain the random region-by-year interaction for the Lake Michigan models. To make this choice, we fit the full range models without the random interaction (i.e., all 10 possible models incorporating the various fixed effects as described in the Akaike Information Criterion (AIC) model comparisons below). For the most complex model (i.e., the model with the most estimated parameters) that converged, we then added in the random region-by-year interaction. If that model, with the random interaction, had a lower AIC than the corresponding model without the interaction, our approach was to proceed by fitting and comparing all models with the random effect (and not considering models without the random interaction further). Selection of the random part of a model, based on the most complex fixed-effect model and prior to evaluation of the fixed effects, is a procedure that has been recommended and is widely used in the mixed modeling literature (e.g., Deroba and Bence, 2009; Diggle et al., 1994; Ngo and Brand, 1997). As it turned out, in our study the most complex model with the random effect almost never had a lower AIC than the corresponding model with-

out the random effect. The lone exception was the model for type-B marks on large lake trout in Lake Michigan. For that exception, subsequent AIC comparisons and presented results included the random region-by-year interaction, whereas for all other models the subsequent AIC comparisons and presented results are for models without the random region-by-year interaction. We used AIC to compare models (within a lake, species, size class, and mark type) and identify cases where the explanatory factors helped describe patterns in marking rates (Bolker et al., 2009; Burnham and Anderson, 2002). We report estimated marking rates and their relationship to explanatory factors identified by the lowest AIC models, and to provide an overall summary of marking rates by lake, species, and size class. We also report marking rates for a null model that did not include season, region, or year effects. For Lake Michigan, the full suite of fixed effect models that were considered (for a species, size class, and mark type) included every possible combination of the fixed effects of year, region and season, and for models that included both region and season, we considered models with and without the interaction of region and season. We also considered a null model, where there were no effects of season, region, and year; thus there were 10 potential models in the candidate set (i.e., null, year, region, season, year + region, year + season, region + season, year + region + season, region + season + region:season, year + region + season + region:season). On Lake Huron, the only models we considered were a null model, a model with only season, a model with only year, and a model with both season and year (4 potential models in the candidate set). All models were fit by maximum likelihood using Template Model Builder (TMB), an R package designed for non-normal data and random effects, which requires problem-specific compiled (C++) model code (Kristensen et al., 2016).

The full suite of models could not always be fit due to sample size constraints. For Lake Michigan, if there were less than 10 total marks in a dataset being analyzed (i.e., on a given species and size class), or for Lake Huron, if there were less than 5 total marks, we did not attempt to evaluate the effects of year, season, or region. Instead, in these cases we fit only the null model with no effects, which produced a constant estimate of mean marking rate. The different criteria between lakes was because the Lake Michigan candidate models included region as well as year and season, and thus required a higher minimum number of mark observations. Although we had hoped to analyze temporal, seasonal, and spatial patterns for all five salmonine species, the number of observed marks only allowed an analysis for lake trout and Chinook salmon in both lakes, and for the medium size class of rainbow trout in Lake Michigan. In addition, if a level (or combination of levels for the region by season interaction) had no fish with marks, an unaltered model (i.e., without specifying a further constraint) could not be fit. This occurs because during the fitting process, once the predicted marking rate is very close to zero, changes in the parameters that determine the log-scale mean (the scale on which parameters are adjusted) have essentially no influence on predictions, which remain effectively zero, and convergence failure results because there is no unique set of parameters that maximizes the likelihood. When there were just a few such cases for a factor so that differences among levels were still meaningful (e.g., fish with no marks in one region but with adequate marks in the other regions), we constrained the model fit by fixing the parameters determining log-scale means for these combinations at values producing a low mean (log scale value of  $-19$ ). When there were too many such cases for a factor (defined as  $>2$  region by season combinations with no marks for including the interaction of region and season,  $>2$  years with no marks for including year, or  $>1$  region with no marks for including region), the corresponding factor was left out of the models we considered. Despite these steps, there still were cases where convergence failure occurred, most often

because no model using the negative binomial distribution converged. This appears to be due to marking rates being so low that the overdispersion parameter of the negative binomial distribution was not estimable (generally not distinguishable from zero). In these cases, a Poisson distribution was used instead (by setting the overdispersion parameter to zero), and an attempt was made to fit the full range of models.

We compared mean marking rates among species within a lake, and for the same species among lakes, by evaluating 95% confidence intervals around mean mark rate estimates from the models. We employed this approach, rather than a separate battery of statistical tests, because this approach is easily extended to allow us to make statistical comparisons of estimates obtained from models that included effects of region, year, and season. For example, we could compare the marking rates for a species for each region in Lake Michigan, based on Wald confidence intervals calculated for a model that included region, from the results presented in Electronic Supplementary Material (ESM) Tables S1 and S2. This approach permitted us to make general species comparisons (i.e., from results presented in Table 1) while also exploring the details under which species differences in marking occurred. Using 95% confidence intervals to infer statistical significance is imprecise, but is generally considered to be more conservative, at least for pairwise comparisons, than formal statistics by yielding a type I error rate that is less than  $\alpha = 0.05$  (e.g., Knol et al., 2011; Payton et al., 2003). For example, Knol et al. (2011) described that 83.4% to 93% confidence intervals would be required to obtain an  $\alpha = 0.05$  depending on the degree to which variances differed among effect estimates, and that a 95% confidence interval actually has a 0.0056 type I error probability if variances were equal.

We used two-sided Kolmogorov-Smirnov tests (Kolmogorov, 1933; Massey, 1951; Smirnov, 1939) to determine if the distributions in the number of marks per fish among mark-healing stages differed between length classes for Chinook salmon and lake trout in Lakes Michigan and Huron. The test was also used to evaluate differences in the distributions among mark-healing stages between lakes for Chinook salmon and lake trout, as well as differences in distributions among mark-healing stages between these species within each lake. We followed these analyses of distribution of marks among healing stages by specifically focusing on the proportion of marks in the earliest stage of healing (Stage I) relative to the total number of marks in stages I, II and III for each mark type (A and B), which may indicate host recovery potential. These proportions were calculated for Chinook salmon and lake trout in each year, and paired t-tests (Student, 1908) were used (with each year as a replicate) to evaluate differences in the proportion of marks that were Stage I (both type-A and type-B, analyzed separately) between Chinook salmon and lake trout in each lake. Data collected in 2012 were excluded from both lakes in the paired analysis due to low sample size in Lake Michigan and no sampling in Lake Huron that year. Analyses were conducted using Program R version 3.4.2 (R Core Team, 2013). Significance was determined at  $p < 0.05$  for all tests, and means  $\pm$  SE are presented unless otherwise noted.

## Results

### *Species and lake differences in mean marking rates*

We examined 74,015 angler-caught salmonines collected during 2012–2018 for sea lamprey marks. In Lake Michigan, 20,120 fish were 533–635 mm TL, 20,958 fish were 636–737 mm TL and 27,812 were  $>737$  mm TL (Table 1). In Lake Huron, 1708 fish were 533–635 mm TL, 1976 fish were 636–737 mm TL and 1441 were  $>737$  mm TL (Table 1). Non-overlapping 95% confidence intervals

were interpreted as indicating meaningful differences in comparing mean marking rates among species and lakes. Due to relatively low sample sizes, confidence intervals for brown trout encompassed mean marking rate estimates for all sizes and mark types of the other four species in Lake Michigan, and for small fish with type-A marks in Lake Huron (Table 1). Lake trout exhibited higher mean type-A marking rates in Lake Michigan compared to Chinook salmon, rainbow trout, and coho salmon for medium and large size classes (Table 1). Medium lake trout averaged 0.028 type-A marks per fish (0.024–0.033 CI) compared to upper 95% CI bounds of 0.005–0.009 for Chinook salmon, rainbow trout, and coho salmon. This was primarily driven by data from 2013 to 2015, when lake trout marking rates were highest. Confidence intervals for medium lake trout in North and East regions from 2016 to 2018 frequently overlapped with those of coho salmon, rainbow trout, and Chinook salmon (ESM Table S1). Large lake trout averaged 0.038 type-A marks per fish (0.033–0.045 CI) compared to upper CI bounds of 0.012–0.013 for Chinook salmon and rainbow trout (no model for large coho salmon), and this pattern was true in nearly all seasons, regions and years as most stratum-specific models were also non-overlapping (Appendix A). Type-A marking rates were negligible for the small size class and similar rates were observed among species, although the CI for small lake trout (0.006–0.010) were higher than the upper CI bounds for rainbow trout (0.004) and coho salmon (0.005).

Lake trout also exhibited higher mean type-B marking rates in Lake Michigan than Chinook salmon, rainbow trout, and coho salmon for medium (mean = 0.015 marks per fish; CI of 0.012–0.019 compared to upper CI bounds of 0.005–0.009 for the other three species) and large size classes (mean = 0.032, CI of 0.026–0.039 compared to upper CI bounds of 0.009–0.011 for Chinook salmon and rainbow trout [no model for large coho salmon]). Species differences in type-B marking for medium fish were driven by 2013–2015, when lake trout had relatively high marking rates; most confidence intervals among species overlapped from 2016 to 2018 (ESM Table S2). Species differences in type-B marking for large fish occurred during spring for most years (2012–2016) but confidence intervals overlapped during summer (ESM Table S2). Higher marking rates were observed for larger fish compared to small and medium fish in both lake trout and Chinook salmon, although some CIs had narrow overlap in size comparisons (Table 1). Marking rates were negligible on coho salmon and rainbow trout for all mark types and length classes in Lake Michigan (range of 0.00–0.005 mean marks per fish for all mark types).

In contrast to Lake Michigan, Chinook salmon exhibited higher mean type-A marking rates than lake trout and rainbow trout in Lake Huron for most size classes, with the exception of the contrast with large rainbow trout, which may be due to small sample size. Very few coho salmon ( $n = 64$ , with 56 of these in the small length class) and brown trout ( $n = 17$ ) were observed in Lake Huron, and thus mean mark rates were only reported for small fish, which had large confidence intervals. Small Chinook salmon averaged 0.111 type-A marks per fish (0.066–0.187 CI) compared to upper CI bounds of 0.030 and 0.033, for lake trout and rainbow trout, respectively. Medium Chinook salmon averaged 0.095 type-A marks (0.058–0.156 CI) compared to upper CI bounds of 0.046 and 0.039 for lake trout and rainbow trout, respectively. Large Chinook salmon averaged 0.091 type-A marks (0.067–0.122 CI), compared to an upper CI bound of 0.054 for lake trout. Mean type-A marking rate for large rainbow trout was 0.211, but was based on only 18 fish and thus had a large confidence interval (0.065–0.679) that overlapped with the CI for large Chinook salmon. Species differences in type-A marking rate in Lake Huron among medium fish were driven by summer marking patterns, as confidence intervals mostly overlapped among species for medium fish in spring (ESM Table S3). Type-B marking rate confidence intervals

overlapped for Chinook salmon, lake trout, and rainbow trout at all sizes.

Mean type-A and type-B marking rates were generally similar for lake trout of the same size class in Lake Michigan and Lake Huron, but were much higher for Chinook salmon (7.5–13.5 times higher for type-A and 3.5 times higher for type-B) in Lake Huron compared to Lake Michigan for both mark types and all size classes (Table 1). Type-A marking rates on Chinook salmon were higher in Lake Huron than in Lake Michigan for small (95% CI's of 0.066–0.187 and 0.002–0.006 in Lakes Huron and Michigan, respectively), medium (95% CI's of 0.058–0.156 and 0.005–0.009 in Lakes Huron and Michigan, respectively) and large size classes (95% CI's of 0.067–0.122 and 0.010–0.013 in Lakes Huron and Michigan, respectively). Differences among lakes for Chinook salmon type-A marking rates held for all stratum-specific models for large fish, but were driven by summer marking rates for medium fish (ESM Tables S1 and S3)). Type-B marking rates on Chinook salmon were also higher in Lake Huron than Lake Michigan for small and large fish, driven by spring patterns (ESM Tables S2 and S3), but confidence intervals overlapped for medium fish (Table 1). Large rainbow trout also appeared to have higher type-A marking rate in Lake Huron than Lake Michigan, with 95% confidence intervals overlapping for other sizes and mark types. Type-A and type-B marking rates were also higher on small lake trout in Lake Huron than in Lake Michigan, but 95% confidence intervals overlapped for medium and large lake trout. Mean marking rates of both mark types were also higher on the small size class in Lake Huron compared to Lake Michigan for all five species (Table 1), however 95% CIs were only non-overlapping for small lake trout and Chinook salmon.

#### *Temporal, seasonal, and spatial marking in Lake Michigan*

Our full model for Lake Michigan allowed for random variations unique to each region-by-year combination to influence marking rates, but we found no evidence for such random effects, with the one exception of type-B marks for large lake trout. For all other cases, once these random effects were dropped from the model, we formally assumed independence among observations within a given stratum (i.e., year, season, region). Our sampling design guards against spurious conclusions due to non-independence because samples were spread out through the seasons and geographically within regions, which may be one reason why we did not detect random effects. If observations within a region and season had been more similar than expected for independent observations after accounting for fixed effects, evidence in favor of the random effects should have been strong.

Regional and seasonal effects in marks were apparent for both lake trout and Chinook salmon in Lake Michigan. Models of type-A marks that included regional effects fit better (lower AIC) than alternatives for medium lake trout and large Chinook salmon in Lake Michigan. The best fit model for large lake trout only included a seasonal effect, while the best model for medium Chinook salmon was the null model (Table 2). The estimated mean type-A marking rate was lower for medium lake trout that were caught in eastern Lake Michigan than elsewhere in the lake. Year was also included in the best-fit model (and all competitive models within 10 AIC of the best-fit model; Table 2) for medium lake trout, and mean marking rate declined in all regions during 2012–2018 (Fig. 2). Type-A marking was higher in the spring than in summer for large lake trout as well as medium rainbow trout (Fig. 2). Only null models were fit for type-A marks for large rainbow trout as well as coho salmon and brown trout of both size classes because of sparse data (very few observed marks; Table 1). The Chinook salmon large fish model for type-A marks was more complex and included season, region, and year effects, although the null model

**Table 2**

Lowest AIC models ( $\Delta AIC < 10$ ) of type-A marks in Lake Michigan. Fig. 2 illustrates patterns that correspond with fixed parameters included in the lowest AIC models ( $\Delta AIC = 0$ ). Null models had no season (S), region (R), or year (Y) effects. AIC results are presented only for lake trout, Chinook salmon, and medium rainbow trout because only the null model was fit for other species or sizes, as too few marks were observed for those cases (see Methods).

Species	Length Category (mm)	Parameters	AIC	$\Delta AIC$
Lake trout	636–737	R + Y	1639.89	0.00
		S + R + Y	1641.63	1.73
		Y	1642.57	2.67
		S + Y	1643.35	3.46
		S + R + S * R + Y	1646.69	6.80
	>737	S	1754.47	0.00
		S + R	1758.32	3.85
		S + Y	1760.58	6.11
		S + R + Y	1762.48	8.01
		Null	629.72	0.00
		S	630.93	1.21
Chinook salmon	636–737	R	631.81	2.08
		S + R	633.73	4.01
		Y	635.12	5.40
		S + Y	636.15	6.43
		R + Y	639.15	9.42
	>737	S + R + Y	2510.42	0.00
		R + Y	2512.79	2.37
		Y	2514.83	4.41
		S + Y	2515.30	4.88
		S + R + S * R + Y	2515.41	4.99
		S + R	2517.65	7.23
Rainbow trout	636–737	R	2519.60	9.18
		S	229.57	0.00
		S + Y	232.04	2.47
		S + R	234.19	4.61
		S + R + Y	236.90	7.33
		Null	239.25	9.68

was best for medium fish, likely because of the overall low marking rate (Table 2). There was support for a seasonal effect on type-A marking rates for large Chinook salmon in Lake Michigan (Table 2) as the estimated seasonal difference was comparable to the differences among years and regions (Fig. 2). Type-A marking on large Chinook salmon was also estimated to be higher in eastern and northern Lake Michigan than other areas of the lake (Fig. 2). Type-A marking rate of large Chinook salmon was variable among years but showed no temporal trend (Fig. 2).

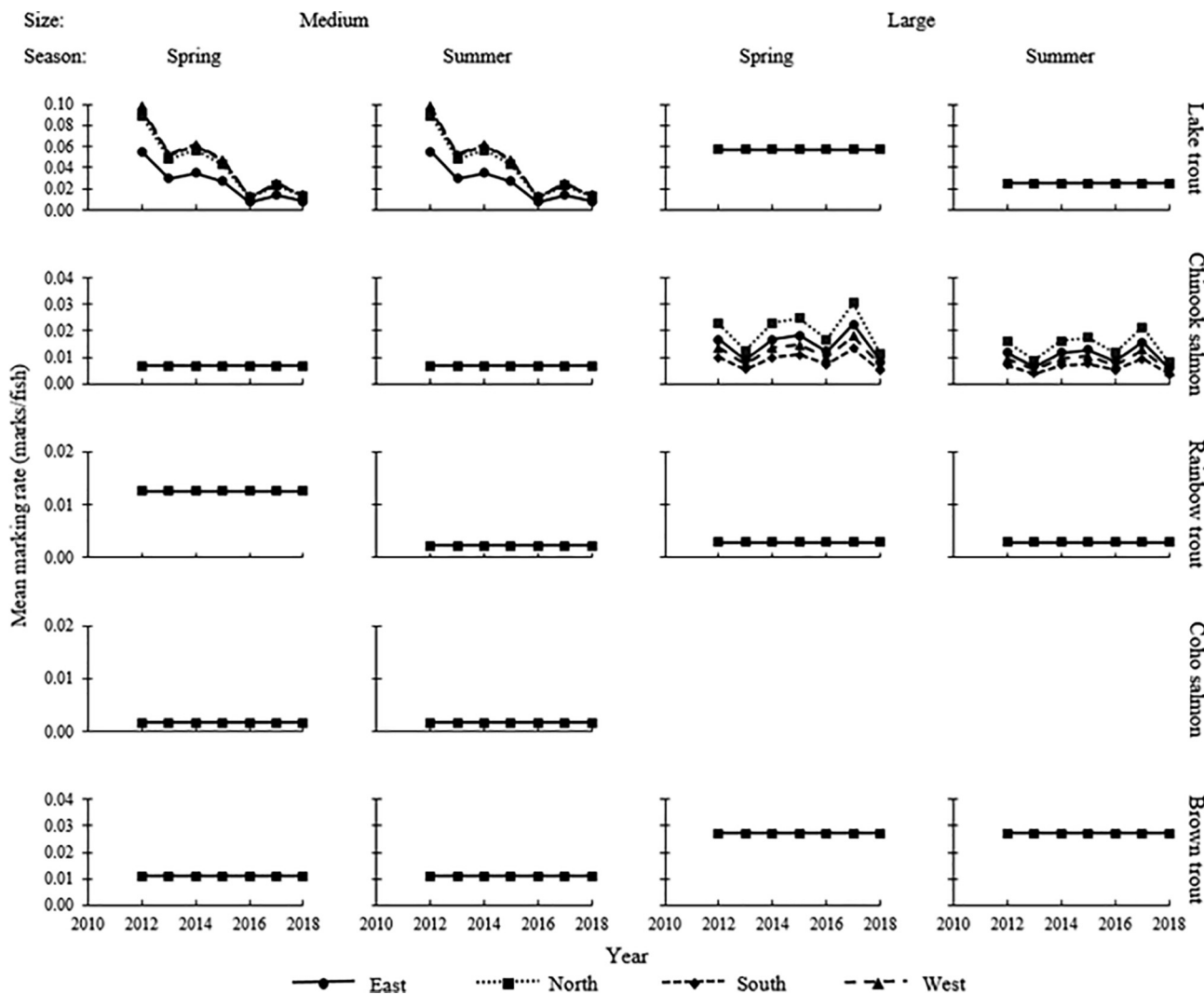
The lowest AIC models for type-B marks in Lake Michigan included some seasonal, regional, and year effects for lake trout and Chinook salmon. For medium rainbow trout the null model, with no effects of season, region, and year, was selected as best, whereas only the null model could be fit for large rainbow trout and both sizes of coho salmon and brown trout due to sparse data (low number of observed marks; Table 1). Type-B mark models that included seasonal effects were most parsimonious for large lake trout and both medium and large Chinook salmon in Lake Michigan (Table 3); the medium lake trout model only included a year effect. Both medium and large lake trout exhibited higher type-B marking rates from 2012 to 2015 than from 2016 to 2018, but only the large size of lake trout provided evidence for higher marking rates in spring than summer (Fig. 3). The model for type-B marks for large lake trout was the only one of our models to include a random interaction between region and year, suggesting some variation in regional effects over years (Table 3; Fig. 3). Medium and large Chinook salmon also had higher type-B marking rates in spring than summer (Fig. 3). The lowest AIC models for both Chinook salmon size classes also included regional effects: medium fish had higher type-B marking rates in the north and larger fish had higher type-B marking rates in the west than other areas, with regional differences more apparent for medium fish than for large fish.

#### Temporal and spatial marking in Lake Huron

Some seasonal and year effects were observed in Lake Huron for lake trout and Chinook salmon. Patterns were not evaluated for brown trout and coho salmon, and regional effects were not included in the models due to small sample sizes. The lowest AIC type-A marking models included a seasonal effect for medium lake trout and medium Chinook salmon, and a year effect for large lake trout. The null model (just an overall mean) was most parsimonious for large Chinook salmon; whereas, because of sparse data only the null model was fit for rainbow trout of both size classes (Table 4). For type-B marking models, a model with just a year effect was selected for medium lake trout, and a model with just a seasonal effect was selected for large Chinook salmon, with a null model selected for large lake trout and medium Chinook salmon. Only a null model could be fit for both sizes of rainbow trout due to sparse data (Table 5). Mean marking rate was higher in spring than summer for medium lake trout with type-A marks and large Chinook salmon with type-B marks, but was lower in spring than summer for medium Chinook salmon with type-A marks (Fig. 4). Mean type-A marking rate was lowest in 2016 and highest in 2017, followed by 2013 and 2014 for large lake trout in Lake Huron (Fig. 4). Similarly, mean type-B marking rate was lowest in 2016, but highest in 2013 and 2014 for medium lake trout in Lake Huron.

#### Distributions of fresh and healed mark types

Distributions of mark type did not significantly differ between medium and large length classes for Chinook salmon or lake trout with type-A or type-B marks in Lake Michigan or Lake Huron; small fish were not included in this analysis. Therefore, data were pooled over length classes for each species and subsequent analyses were conducted on fish >636 mm TL for each lake.



**Fig. 2.** Effects of season, region, and year on mean type-A marking rate (marks/fish) for medium (636–737 mm TL) and large (>737 mm TL) salmonines in Lake Michigan. Only stage I, II and III marks are included. Mean marking rate and confidence intervals are provided in ESM Table S1. Note that y-axis scales differ among species. Because of low overall numbers of marks, effects of season, region, and year were not evaluated for large rainbow trout, medium coho salmon, and both medium and large brown trout. The marking rate from the null model is provided for these cases for comparative purposes (see Methods). No type-A marks were observed on large coho salmon (see Table 1).

Distributions among mark-healing stages were not significantly different between Lake Michigan and Lake Huron for lake trout with type-A or type-B marks or for Chinook salmon with type-B marks, but significantly differed between lakes for Chinook salmon with type-A marks ( $D = 1, p = 0.03$ ). Chinook salmon in Lake Huron had 10-times the number of type-A marks than those in Lake Michigan (Fig. 5).

Distributions of marks among mark-healing stages did not significantly differ among Chinook salmon and lake trout for either mark type in Lake Huron or for type-B marks in Lake Michigan (Fig. 5). However, distributions of type-A marks were significantly different between the two species in Lake Michigan ( $D = 1, p = 0.03$ ). Type-A marked Chinook salmon in Lake Michigan had many fresh AI marks but few healed marks (AII, AIII and AIV), whereas lake trout had more healed marks, especially AIV, with fewer incidence of fresh AI marks (Fig. 5).

In Lake Michigan, the proportion of AI–AIII marks that were AI was significantly greater for Chinook salmon (61.4% on average) than for lake trout (31.1% average;  $t = 7.07, p = 0.0009$ ; Fig. 6). However, the proportion of BI–BIII marks that were BI was not statistically different between species (23.8% and 25.0% for Chinook salmon and lake trout, respectively;  $t = -0.17, p = 0.87$ ). This pat-

tern was similar for Lake Huron, where the proportion of AI–AIII marks that were AI was significantly greater for Chinook salmon (73.6% on average) than for lake trout (41.4% average;  $t = 3.67, p = 0.01$ ), but the proportion of BI–BIII marks that were BI was not statistically different between species (40.5% and 22.3% for Chinook salmon and lake trout, respectively;  $t = 0.87, p = 0.42$ ).

### Discussion

We quantified marking rates and severity of sea lamprey attacks on lake trout, Chinook salmon, rainbow trout, coho salmon, and brown trout in Lakes Michigan and Huron. We observed species-specific spatial and temporal patterns in sea lamprey attacks. Mean marking rates varied among species and lakes. Mean marking rates (type-A and type-B) were significantly higher for lake trout than for Chinook salmon, rainbow trout, and coho salmon in Lake Michigan. This was driven by 2013–2015 patterns for medium fish, but was true for large fish in most strata. By contrast, type-A marking rates were several times higher for Chinook salmon than for lake trout (all sizes) and small and medium rainbow trout in Lake Huron, particularly during summer. The relatively high incidence of marks that we observed on Chinook



**Table 3**

Lowest AIC models ( $\Delta AIC < 10$ ) of type-B marks in Lake Michigan. Fig. 3 illustrates patterns that correspond with fixed parameters included in the lowest AIC models ( $\Delta AIC = 0$ ). Null models had no season (S), region (R), or year (Y) effects. AIC results are presented only for lake trout, Chinook salmon, and medium rainbow trout because only the null model was fit for other species or sizes, as too few marks were observed for those cases (see Methods).

Species	Length Category (mm)	Parameters	AIC	$\Delta$ AIC		
Lake trout	636–737	Y	988.88	0.00		
		S + Y	990.16	1.28		
		R + Y	990.51	1.64		
		S + R + Y	990.79	1.91		
		S + R + S * R + Y	994.99	6.12		
	>737	S + Y	1391.12	0.00		
		S	1391.68	0.57		
		Y	1391.99	0.87		
		Null	1394.26	3.15		
		S + R + Y	1396.46	5.35		
		R + Y	1397.03	5.92		
		S + R	1397.17	6.05		
		R	1399.54	8.42		
		636–737	S + R	349.72	0.00	
				S + R + Y	354.42	4.70
				S	354.60	4.87
				Null	354.64	4.91
R + Y	355.51			5.79		
>737	R		357.24	7.52		
	S + R + S * R		358.88	9.16		
	S + R		1674.76	0.00		
	S		1675.09	0.34		
	R		1679.36	4.61		
	Null		1679.49	4.73		
Rainbow trout	636–737	Null	170.41	0.00		
		S	171.75	1.35		
		R	175.42	5.01		
		S + R	176.44	6.03		

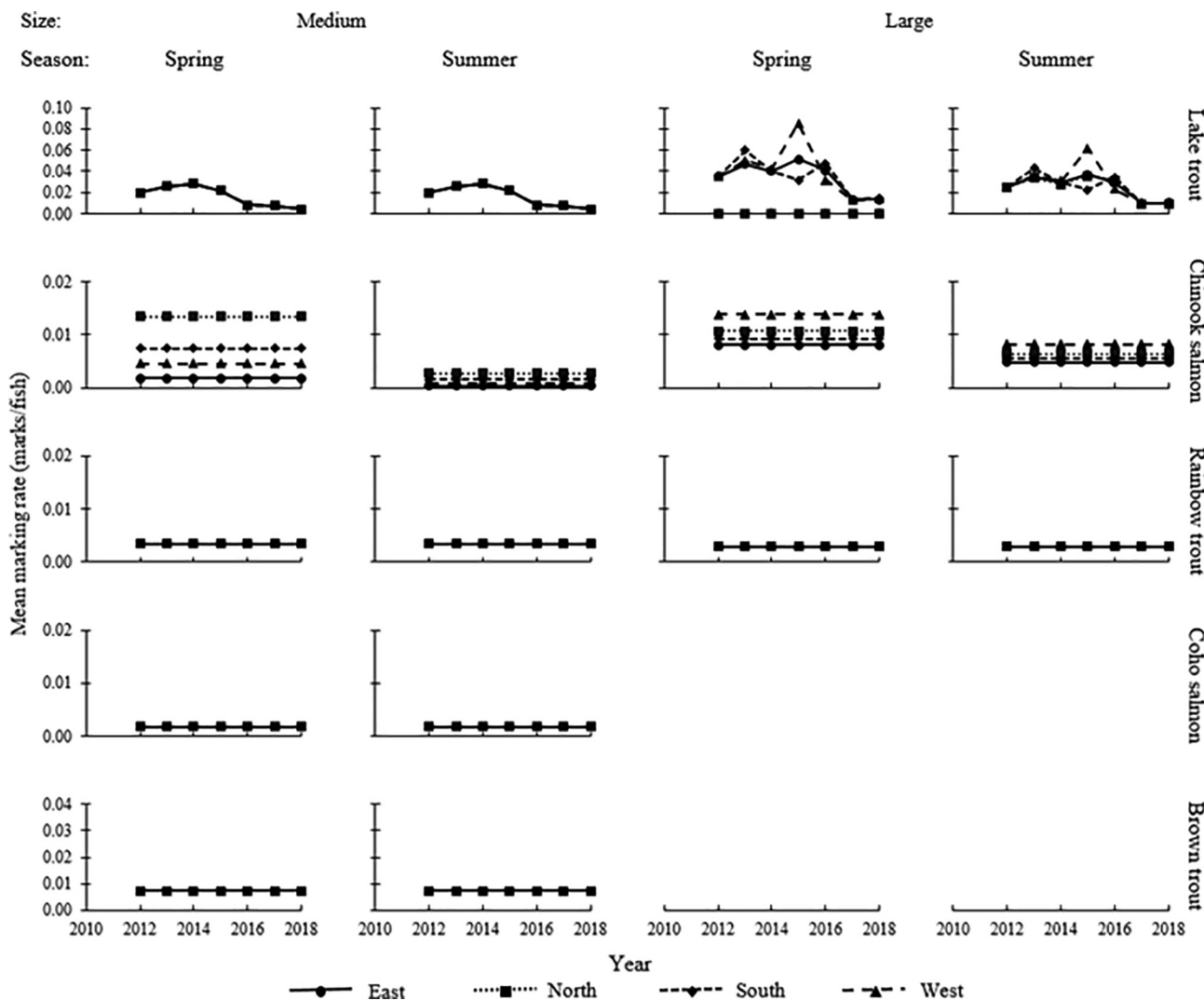
salmon in both lakes, rainbow trout in Lake Huron, and brown trout in Lake Michigan suggest that these species are sufficiently available and grow to sizes that are selected by sea lamprey. Chinook salmon are stocked throughout Lakes Michigan and Huron and grow to sizes that exceed 700 mm (Kornis et al., 2019a). In addition, Chinook salmon and brown trout migrate into rivers to spawn in the fall and rainbow trout aggregate near river mouths from fall through spring, increasing the probability of potential encounters with sea lamprey during the peak time of sea lamprey lethal attacks (Bence et al., 2003; Bergstedt and Schneider, 1988; Spangler et al., 1980). Our data suggest that, although lake trout may generally be the preferred sea lamprey host, Chinook salmon and other species such as brown trout are also suitable and available in Lake Michigan, and Chinook salmon may possibly be a preferred host in some areas of Lake Huron.

We expected marking rates would be highest for lake trout in both Lakes Michigan and Huron, given this species is believed to be a preferred host (e.g., Bence et al., 2003; Morse et al., 2003); but that host preference could change to alternative hosts if the availability of suitable-sized lake trout diminished (Lantry et al., 2015). In Lake Ontario, Adams and Jones (2021) observed that sea lamprey strongly preferred lake trout when their abundance comprised > 32% of potential host species, but that sea lamprey preference switched to Chinook salmon when lake trout abundance comprised < 13% of potential host species. Lantry et al. (2015) similarly noted higher attack rates on Chinook salmon and brown trout when attack rates on lake trout were reduced. In Lake Huron, Morse et al. (2003) observed higher marking rates for lake trout than similarly sized Chinook salmon, and Bence et al. (2003) reported that the marking rate of large Chinook salmon declined, but increased for lake trout, as lake trout abundance increased, suggesting that sea lamprey switched their host preference. Our findings in Lake Huron seem to contradict those of other studies on abundance-dependent host switching. Sea lamprey marking rates were higher on Chinook salmon than lake trout in

Lake Huron despite results from age-structured stock assessments that showed lake trout had roughly 3–5 times greater biomass than Chinook salmon in Lake Huron from 2004 to 2010 (He et al., 2015), with lake trout comprising over 70% of total piscivore biomass, compared to 13% for Chinook salmon, in 2010 (He et al., 2020). This disparity in biomass between the two species is even greater than it was when Morse et al. (2003) and Bence et al. (2003) reported higher marking rates on lake trout than Chinook salmon in Lake Huron.

Metrics that gauge the success of the sea lamprey control program (Adams et al., 2003), the incidence of attack and host mortality rates (Eshenroder et al., 1995; Sitar et al., 1999), and sea-lamprey-host models that inform the sea lamprey management program (Koonce et al., 1993; Larson et al., 2003) are predicated on accurate marking data and assume lake trout are the sea lamprey's primary host. Efficacy of the control program could be improved by taking into account alternative hosts that are heavily relied on in some times and places. The incidence of sea lamprey attacks on Chinook salmon and other salmonines are generally not taken into account, and thus not used to inform sea lamprey control strategies and outcomes.

Distribution of type-A marks showed a lower proportion of healed marks (AII and AIII) relative to fresh marks (AI) on Chinook salmon compared to lake trout, which may suggest a lower probability of survival for Chinook salmon than for lake trout. Alternatively, lower incidence of healed marks in Chinook salmon compared to lake trout may be attributed to differences in life histories between the two species. Chinook salmon in the Great Lakes have shorter lifespans (very few live beyond age 3 years) than lake trout (beyond 20 years), hence a potential alternative explanation is that they were simply not alive to be observed later after the marks had healed. If lifespan differences were the cause, however, differences in distribution of fresh and healed marks should have been observed in both type-A and type-B marks, and we detected no differences between the species in type-B marks. Given that



**Fig. 3.** Effects of season, region, and year on mean type-B marking rate (marks/fish) for medium (636–737 mm TL) and large (>737 mm TL) salmonines in Lake Michigan. Only stage I, II and III marks are included. Mean marking rate and confidence intervals are provided in ESM Table S2). Note that y-axis scales differ among species. Because of low overall numbers of marks, effects of season, region, and year were not evaluated for large rainbow trout, medium coho salmon, and medium brown trout. The marking rate from the null model for these cases is provided for comparative purposes (see Methods). No type-B marks were observed on large coho salmon or large brown trout (see Table 1).

**Table 4**

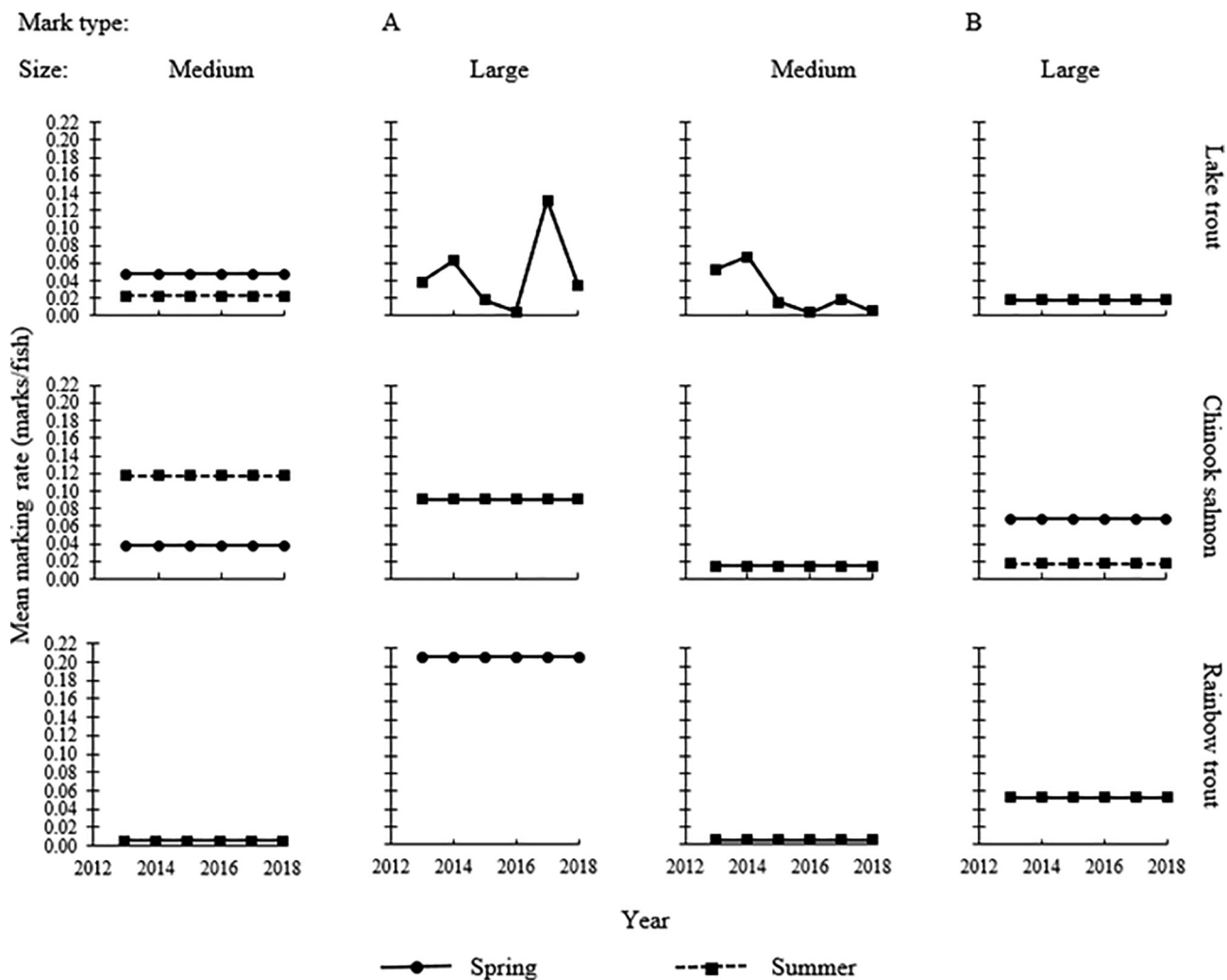
Lowest AIC models ( $\Delta AIC < 10$ ) of type-A marks in Lake Huron. Fig. 4 illustrates patterns that correspond with fixed parameters included in the lowest AIC models ( $\Delta AIC = 0$ ). Null models had no season (S) or year (Y) effects; data were insufficient to test for regional effects within Lake Huron. AIC results are presented only for lake trout and Chinook salmon because only the null model was fit for other species, as too few marks were observed for those cases (see Methods).

Species	Length Category (mm)	Parameters	AIC	$\Delta AIC$
Lake trout	636–737	S	441.39	0.00
		Y + S	442.25	0.86
		Y	444.10	2.70
		Null	445.19	3.80
		Y	274.21	0.00
Chinook salmon	636–737	Y + S	276.10	1.89
		S	138.08	0.00
		Null	139.12	1.04
		Y + S	142.25	4.18
	>737	Y	143.95	5.87
		Null	360.88	0.00
		S	362.54	1.66
		Y	364.31	3.42
		Y + S	366.30	5.42

**Table 5**

Lowest AIC models ( $\Delta AIC < 10$ ) of type-B marks in Lake Huron. Fig. 4 illustrates patterns that correspond with fixed parameters included in the lowest AIC models ( $\Delta AIC = 0$ ). Null models had no season (S) or year (Y) effects; data were insufficient to test for regional effects within Lake Huron. AIC results are presented only for lake trout and large Chinook salmon because only the null model was fit for other species or sizes, as too few marks were observed for those cases (see Methods).

Species	Length Category (mm)	Parameters	AIC	$\Delta$ AIC
Lake trout	636–737	Y	284.15	0.00
		Y + S	286.03	1.88
	>737	Null	155.33	0.00
		S	155.54	0.20
		Y + S	165.21	9.87
Chinook salmon	>737	S	138.85	0.00
		Null	143.34	4.49
		Y	147.73	8.87
		Y + S	165.21	9.87



**Fig. 4.** Effects of season and year on mean type-A and type-B marking rate (marks/fish) for medium (636–737 mm TL) and large (>737 mm TL) salmonines in Lake Huron. Only stage I, II and III marks are included. Mean marking rate and confidence intervals are provided in ESM Table S3. Because of low overall numbers of marks, effects of season, region, and year were not evaluated for rainbow trout and the marking rate from the null model for this species is provided for comparative purposes (see Methods). No marks were observed on coho salmon or brown trout (see Table 1).

one potential explanation for the mark type pattern difference for Chinook salmon versus lake trout is that attacks on Chinook salmon are more lethal, we believe further research on this topic is warranted. A higher Chinook salmon lethality rate than is suggested by the type AI–AIII marking rate could have important implications for our understanding of sea lamprey host usage and for Great Lakes fishery management.

In general, we observed higher sea lamprey marking rates for lake trout, Chinook salmon, and rainbow trout in Lake Huron than

in Lake Michigan, although lake trout and rainbow trout comparisons were only significant for select size classes. Marking rates were also substantially higher on small fish (533–635 mm TL) in Lake Huron than in Lake Michigan (although only significantly so for Chinook salmon and lake trout). This suggests that sea lamprey in Lake Huron utilize smaller fish as hosts than do sea lamprey in Lake Michigan, and this is consistent with Prichard and Bence’s (2013) estimated patterns of marking versus lake trout size for most lake regions and years. The higher marking rates in Lake

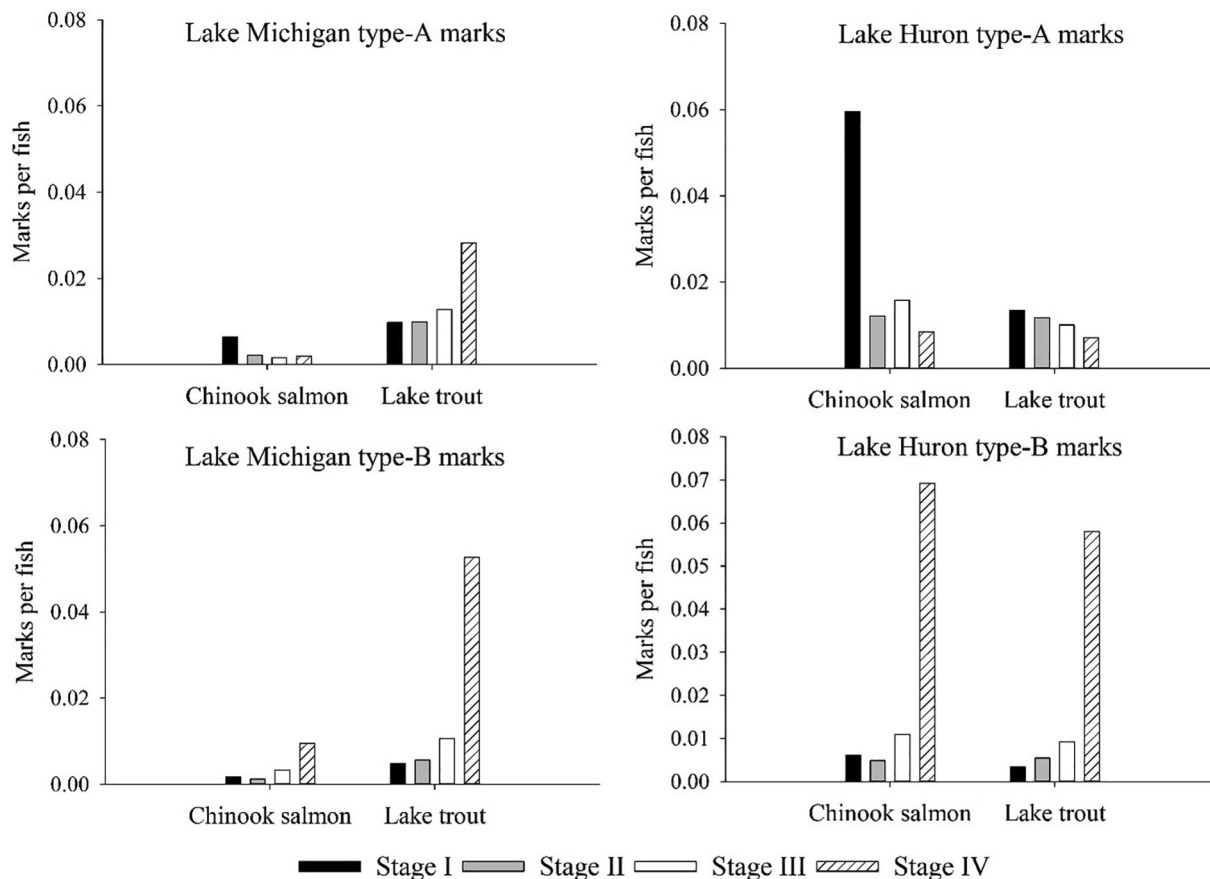


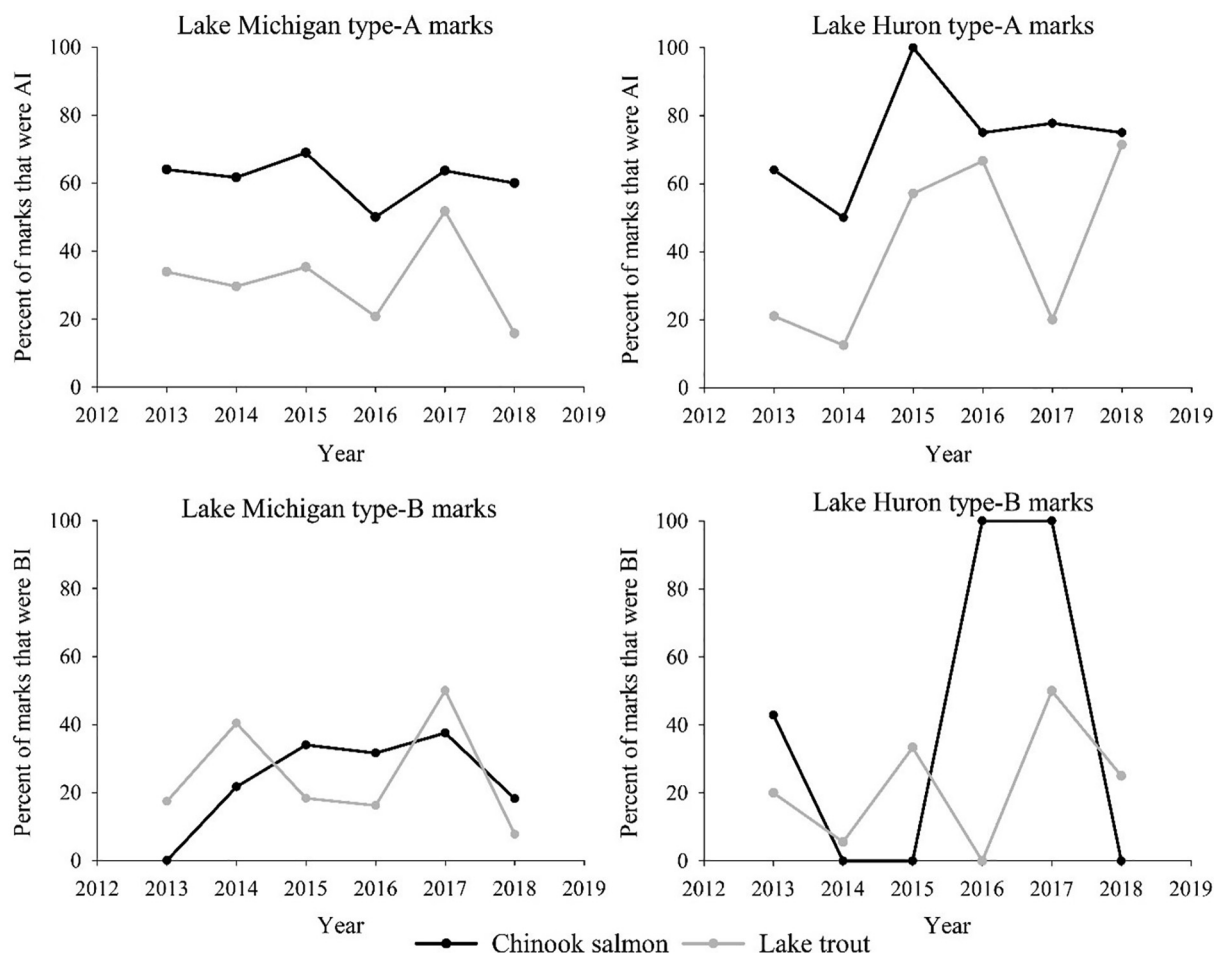
Fig. 5. Distribution of marks per fish among healing categories for Chinook salmon and lake trout with type-A and B sea lamprey marks in Lakes Michigan and Huron. Note that y-axes differ among plots.

Huron than Lake Michigan are consistent with higher sea lamprey-to-host ratio in Lake Huron than Lake Michigan, which may be attributed to higher abundances of sea lamprey, fewer hosts, or both. The index of adult sea lamprey abundance has been higher in Lake Huron than Lake Michigan in most years since about 2000, and was higher in Lake Huron during 2012–2018, covering all years sampled by our study (Lavis et al., 2003; Morse et al., 2003; Steeves and Barber, 2020). Sea lamprey abundance in Lake Huron is largely dependent on reproduction in the St. Mary’s, Garden, Spanish, Missasaugi, and Serpent rivers, which have been historically difficult to control (Morse et al., 2003; Schleen et al., 2003). Host abundance is more difficult to define because most available data are an aggregate of all sizes and thus do not account for size selectivity of sea lamprey. Nevertheless, total lake trout biomass estimates were similar in both Lakes Michigan and Huron (4–5 kt) from 2005 to 2010, but biomass of Chinook salmon was substantially higher in Lake Michigan (>10 kt) than Lake Huron (~1 kt) (Claramunt et al., 2019; He et al., 2015). Although these are lake wide comparisons that do not account for differential sea lamprey abundance within regions of each lake, they are consistent with a higher sea lamprey-to-host ratio in Lake Huron.

Our study suggests that Chinook salmon may currently be more vulnerable to attack than lake trout in Lake Huron. One hypothesis is that this potential vulnerability may be driven by high sea lamprey abundance in northern areas of both Lake Michigan and Lake Huron, where Chinook salmon stocked in Lake Huron commonly occur. More Chinook salmon were stocked in northwestern Lake Huron than elsewhere in the lake during our study than in previous years when Bence et al. (2003) and Morse et al. (2003) conducted their analyses. Hatchery-reared Chinook salmon stocked in north-

western Lake Huron move to northern Lake Michigan to feed (Clark et al., 2017; Kornis et al., 2019a), and both areas are known to have high sea lamprey abundance (Lavis et al., 2003; Morse et al., 2003; Schleen et al., 2003). Many of the fish that move to Lake Michigan later return to Lake Huron to spawn (Clark et al., 2017). Thus, the high rate of sea lamprey marking on Chinook salmon in Lake Huron could be due in part to sea lamprey attacks that occurred in Lake Michigan, or could be due to attacks that occur in northern Lake Huron during pre-spawn staging behavior. Either way, Chinook salmon recovered in Lake Huron have likely spent much of their lives in areas of lakes Michigan and Huron where encounters with sea lamprey are likely due to elevated sea lamprey abundance. Unfortunately, we could not fully evaluate the hypothesis that concentration of Chinook salmon in areas with high sea lamprey abundance (e.g., northern areas of both Lake Michigan and Lake Huron) explains the overall marking pattern because sample sizes were inadequate for a formal analysis of regional differences in marking within Lake Huron.

An alternative (but not mutually exclusive) hypothesis is that sea lamprey could take advantage of seasonal concentrations of Chinook salmon during late summer in Lake Huron as these fish stage to spawn. A greater proportion of the Chinook salmon we used in our analyses were captured in late summer in Lake Huron than was the case for Lake Michigan, and marking could increase through the summer. Due to the between lake migratory behavior, 53% and 68% of our observations on Chinook salmon 636–737 mm and >737 mm, respectively, occurred in August and September in Lake Huron, compared to 30% and 41% during August and September in Lake Michigan. However, we do not think seasonal concentrations of Chinook salmon was fully responsible for their elevated



**Fig. 6.** Percent of fresh marks (stage I) on Chinook salmon and lake trout with type-A and B sea lamprey marks in Lakes Michigan and Huron from 2013 to 2018. Percentages are relative to the total number of marks from stages I, II and III.

marking rates in Lake Huron compared to lake trout. Marking rates on Chinook salmon in Lake Huron were only higher in summer compared to spring for type-A marks in the 636–737 mm size class; type-A and type-B marking rates for other sizes classes of Chinook salmon were either similar for the two seasons or were higher in spring compared to summer. Moreover, season was not a component of the Lake Huron models for type-A marking rates on either large Chinook salmon or large lake trout.

Laboratory studies suggested that rainbow trout might be more resilient to mortality from sea lamprey attack than lake trout due to feeding efficiencies that enhanced their ability to meet increased energetic demands associated with being a host (Swink and Hanson, 1989). Rainbow trout may also have adapted to laboratory environments and feeding conditions better than lake trout, which may have contributed to lower rainbow trout mortality (Swink and Hanson, 1989). While these findings could suggest that Chinook salmon, which are congeners of rainbow trout, could also be resilient to mortality from sea lamprey attack, prey availability and feeding by lake trout and Chinook salmon vary substantially across the Great Lakes. Chinook salmon are obligatory pelagic foragers, and limited availability of alewife and rainbow smelt can limit their growth (Kornis et al., 2019a; Leonhardt et al., 2020). Lake trout have more diversified diets that can capitalize on both pelagic (e.g., alewife *Alosa pseudoharengus* and rainbow smelt *Osmerus mordax*) and benthic (e.g., round goby *Neogobius melanostomus* and sculpin *Cottus and Myoxocephalus* spp.) resources, which make them more resilient to forage base changes (Happel et al., 2018;

Kornis et al., 2020; Leonhardt et al., 2020; Luo et al., 2019). Given the higher growth rate and energetic demands of Chinook salmon, it is plausible that they may be more vulnerable to sea lamprey attacks and death if they cannot find enough forage to support their increased metabolic demands resulting from an attack. Chinook salmon maturation is known to be linked to energetic conditions experienced well in advance of spawning and requires a large energetic investment (e.g., Siegel et al., 2018). A lake trout attacked by a sea lamprey may reallocate energy from reproduction (Smith et al., 2016), whereas Chinook salmon may not have the capability to re-allocate resources and delay reproduction to a future year.

Inter-annual effects, when detected, generally showed a decline in mean marking rate over time, especially from 2014 to 2018 for lake trout. Declines in marking rates paralleled declines in abundance of sea lamprey due to increased control efforts (Steeves and Barber, 2020). Alternatively, this trend could also be indicative of sea lamprey switching to alternative hosts (Adams and Jones, 2021), or due to a type II functional response, where similar numbers of marks are spread over a larger number of hosts that could include fish smaller than 636 mm. However, given that the changes occurred in both Lake Huron and Lake Michigan over a period of relatively consistent lake trout abundance, we suspect the patterns do reflect success of the control program.

Spatial differences in marking rates were occasionally observed in Lake Michigan, but the patterns were inconsistent. Medium lake trout had less marking in eastern Lake Michigan than other regions, whereas large Chinook salmon had higher marking in eastern and

northern Lake Michigan than in southern and western regions. Sea lamprey densities are generally lower in southern Lake Michigan, and most of the unrestricted spawning tributaries are located in the eastern region (i.e., Michigan side; Lavis et al., 2003). Lake trout marking has been mainly higher in northern Lake Michigan than in other areas of the lake (Bronte et al., 2007; Kornis et al., 2019b; Lavis et al., 2003; Prichard and Bence, 2013). Chinook salmon are generally found in higher densities in southern Lake Michigan in the spring and follow alewife as they migrate north as temperatures warm during the summer (Clark et al., 2017; Kornis et al., 2019a). Thus, spatial patterns in marking could be attributable to differences in regional sea lamprey densities and movements of available sea lamprey hosts responding to seasonal environmental conditions. We generally observed higher marking rates during spring compared to summer. Most potentially lethal attacks on hosts are by rapidly growing sea lamprey in autumn (Bence et al., 2003; Bergstedt and Schneider, 1988; Spangler et al., 1980). In spring, large marks in stages of healing less than IV are believed to be from attacks from the same sea lamprey cohort responsible for lethal attacks the previous autumn (Eshenroder and Koonce, 1984). Densities and movement patterns of Chinook salmon may also help explain seasonal effects that were observed.

Variability in mark classification between observers may have affected our results. Prior studies have noted substantial variation among observers in mark classification, especially prior to the development of a standardized dichotomous key used by staff during this study (Ebener et al. 2003; 2006). Because of the broad spatial and temporal scales of our study (Lakes Michigan and Huron over a seven year period), use of multiple observers was unavoidable, as is often the case for evaluations of sea lamprey marks in the Great Lakes. However, we limited potential observer bias to the extent possible by providing identical training and frequent oversight to all observers and by mandating adherence to the same standard protocols for mark identification. The potential bias stemming from mark classification variability among observers was likely diluted by the customary lumping of AI–AIII marks and BI–BIII marks together into two groups. Errors in mark classification would have only affected these metrics when errors were made in distinguishing type-A from type-B marks based on the presence or absence of a pit in the host's flesh or in distinguishing fully healed marks (stage IV) from stages I–III. Given the relatively large differences between type-A and type-B marks, and fully healed compared to non-healed marks, we speculate that observer bias had only a modest effect on these lumped metrics. Observer variability in mark classification may have had a larger effect on our analysis of mark distribution among healing stages. However, we argue that any bias in mark classification among observers would have affected both Chinook salmon and lake trout equally and thus would be unlikely to influence our interpretation of the relative occurrence of healed mark types between the two species.

Our study illustrates that salmonines other than lake trout can be important sea lamprey hosts, and that spatial and temporal patterns can be complex and differ among species. Further research is needed to evaluate differences in lethal and sublethal responses to sea lamprey attacks among alternative hosts in the Great Lakes.

### Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jglr.2021.01.002>.

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