Estimating wounding of lake trout by sea lamprey in the upper Great Lakes: Allowing for changing size-specific patterns

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A B S T R A C T

A primary fishery concern in the Laurentian Great Lakes is mitigating the persistent negative impact of parasitic sea lamprey (Petromyzon marinus) on native lake trout (Salvelinus namaycush). Wounds observed on surviving lake trout are commonly used by managers to assess damages associated with sea lamprey predation. We estimated the relationship between wounding rates and lake trout size, and how this varied spatially and temporally. We built upon previously published work by fitting wounding rates as a logistic function of lake trout size. By using longer time series and data from three Great Lakes, our analysis harnessed substantially more contrast in host populations than previous work, and we also employed software advances for nonlinear mixed-effect models. Candidate models allowed logistic function parameters to be constant or to vary spatially, temporally, or both. Temporal effects were modeled as random walk processes. We also considered models that assumed either Poisson or negative binomial distributions for the number of wounds per fish at a given length. Models that allowed for both spatial and temporal effects in the shaping parameters and assumed a negative binomial wound distribution resulted in the best fit as indicated by Akaike’s Information Criterion. Wounding rate estimates from models selected for each lake in this analysis are contrasted with those of wounding rate models currently used as components of lake trout population assessments. Although model fit was improved substantially, differences in wounding rates estimates are modest and estimates follow very similar temporal trends. However, as time series of wound data continue to grow, models that incorporate temporal variability in parameter estimation are expected to be increasingly favored. This research provides managers with an updated tool to obtain more reliable estimates of sea lamprey wounding.

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Introduction

A primary Great Lakes fishery concern is the continued adverse effects of sea lamprey (Petromyzon marinus) on native lake trout (Salvelinus namaycush), and how to mitigate these effects (Irwin et al., 2012; Stewart et al., 2003). In the mid-twentieth century, each of the upper Great Lakes experienced rapid collapses in their lake trout populations. This is evidenced by sharp declines in annual commercial harvest of lake trout—dropping from 2.7 million to 0.18 million kilograms in Lake Huron (1935–1947), from 3.1 million to 0.16 million kilograms in Lake Michigan (1943–1949), and from 2.1 million to 0.23 million kilograms in Lake Superior (1950–1960) (Baldwin et al., 2009). Such sharp declines in lake trout populations are most often attributed to commercial fishing exploitation, predation by the invasive sea lamprey, and habitat degradation (Hansen, 1999). Although the magnitude of the contribution of each of these causes is often debated, the evidence for adverse effects of sea lamprey on lake trout is compelling (Bence et al., 2003). For example, lake trout total mortality has been shown to be positively related to wounding rates (Pycha, 1980), and Bergstedt and Schneider (1988) showed a positive correlation between the number of lake trout carcasses observed with fresh sea lamprey marks and the number of fresh wounds observed on live lake trout sampled in the same year in Lake Ontario. Since the implementation of the sea lamprey control program, sea lamprey abundances have been greatly reduced (Christie and Goddard, 2003; Smith and Tibbles, 1980). During this time, observed marking rates on sampled lake trout have decreased (Rutter and Bence, 2003), lake trout abundances have increased with the help of stocking (Hansen et al., 1995; Holey et al., 1995), and the age composition of lake trout populations has expanded to include older individuals (Hansen et al., 1995).

Prior to their spawning runs as adults in the spring, sea lampreys parasitize teleost fish for a single growing season (Bergstedt and Swink, 1995). The majority of sea lamprey growth occurs in the late summer and fall preceding the adult spawning migrations in the spring, and this is the period when most potentially lethal attacks on lake trout occur. Host fish that survive such attacks are left with easily observed marks called wounds. Wounds can be classified based upon their stage of healing (Ebener et al., 2006; King, 1980; King and Edsall, 1979). During spring, observed wounds that are in the earliest stages...
of healing are attributed to the most recent sea lamprey feeding season (Eshenroder and Koonce, 1984).

Owing to the difficulty in observing parasitic phase sea lamprey, wounds are essentially the only non-laboratory source of information about sea lamprey-host interactions (i.e., sea lamprey-induced mortality). Trends in wounding rates have been used by fishery managers to assess the success of the sea lamprey control program (Adams et al., 2003), and to help estimate lake trout mortality rates for use in catch-at-age models and for other purposes (Bence et al., 2003, 2011). One approach to analyze wound data involves reporting average wounding rates for each of several size classes of lake trout (Eshenroder and Koonce, 1984). This method, however, does not take advantage of the predictability of the increasing incidence of wounds with lake trout length, nor does it account for the biases associated with year-to-year variability in the size distributions of fish sampled within each length bin. Rutter and Bence (2003) addressed these concerns by modeling mean sea lamprey wounding rate as a continuous function of lake trout length using a logistic function (Fig. 1).

With no changes in host survival or size-selection of hosts by sea lamprey, the mean wounding rate would be expected to change proportionally across all sizes of lake trout in response to changes in sea lamprey and lake trout abundance. With other parameters fixed, such a change can be captured in the asymptotic wounding rate parameter of the logistic function (Bence et al., 2003). Due to annual actions by the sea lamprey control program, natural interannual variation in survival of sea lamprey larvae in streams, and the single parasitic feeding season of each cohort, interannual and spatial variation in the abundance of parasitic-phase sea lamprey is large. The asymptote parameter would be expected to show similar, larger interannual and spatial variation (Bence et al., 2003; Rutter and Bence, 2003). Bence et al. (2003) argued that selection for large lake trout over small ones was the primary reason why wounding rates increased with lake trout size before reaching an asymptote, although they acknowledged that differential survival did play some role. Foraging theory predicts that when desirable prey is scarce a predator will shift its feeding behavior to incorporate less desirable prey types (Pulliam, 1974), and several publications have hypothesized that sea lamprey may be responding in this way by increasing their relative selection for smaller lake trout when more desirable large lake trout are less abundant (Bence et al., 2003; Rutter, 2004; Rutter and Bence, 2003). In terms of the logistic relationship relating wounding rate and lake trout size, these changes in selectivity would be reflected in the parameters governing the inflection point (the shaping parameters, Fig. 1). Such changes might be expected to be gradual, as they would be tracking changes in the size distribution and abundance of the long-lived lake trout host.

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

Given the importance of wounding rates for Great Lakes fisheries management, we sought to improve these estimates. More specifically, one primary purpose of this research was to re-evaluate whether estimates should allow for temporal as well as spatial variation in the shape of the sea lamprey wounding versus size relationship. There are two basic reasons why we believed it was useful to explore this issue and expand upon the methods of Rutter and Bence (2003). First, the published application was limited to Lake Huron wounding data and a much shorter time-series than is now available. Management agencies, however, have been using variants of the model selected by Rutter and Bence (2003) to estimate sea lamprey mortality within stock-assessment models for other lakes and to the growing time series. To our knowledge a thorough evaluation of alternative variants allowing for spatial and temporal variation has not been conducted for the more extensive data to which the Rutter and Bence (2003) model has been applied. Second, advances in estimation software allowed us to explore technical approaches to estimation that were unavailable to Rutter and Bence (2003), and it is conceivable that these approaches would produce different estimates or influence whether a model allowing for temporal changes in the shape of the logistic function selection was selected. In particular we were able to model stochastic variations in parameters of the logistic model as random effects, and we were able to address evidence of overdispersion noted by Rutter and Bence (2003) by considering a negative binomial distribution for the number of wounds per fish of a given length in addition to the Poisson distribution they used. We include in our analyses a comparison between the wounding rate model

![Fig. 1. An example of the logistic model fit to lake trout wound data from southern Lake Huron (MH3456) in 1985 overlaid with observed data on wounds per fish. Observed wounds per fish were averaged for 20 mm length bins for visual clarity, although the model was fit to observed values from individual fish. From Eq. 1, \( \theta \) represents the asymptotic wounding rate, \( \beta \) corresponds to lake trout length at the inflection point, and \( \alpha \theta/4 \) is the slope of the function at the inflection point. The increased variability in the plotted data for larger fish likely resulted from smaller sample sizes for those size classes.](image-url)
currently used by fishery managers in Lake Huron lake trout population assessments and the model selected herein.

Methods

Wound data

We included wounding observations for individual lake trout within 1836 Treaty-ceded waters, which span much of the Michigan waters of Lakes Huron, Michigan, and Superior (Fig. 2). Data were available for years 1984 to 2010 for Lakes Huron and Michigan, and 1971 to 2010 for Lake Superior, for fish sampled during April-June primarily from agency surveys using gill nets. The sum of marks observed on individual fish classified as AI, AII and AIII were used as the number of wounds on each fish (King and Edsall, 1979). This is also consistent with the current practice of using spring and early summer wounding rates to estimate sea lamprey-induced mortality that occurred in the previous year in lake trout catch-at-age models (Bence et al., 2003). We restricted attention to treaty waters of these lakes because (a) data were readily available due to their ongoing use in lake trout assessments, and (b) sampling focused on lake trout is done during spring and early summer in all these lakes, allowing for a more consistent interpretation of marks left by sea lamprey on lake trout.

Recent methods of estimating sea lamprey-induced mortality in the upper Great Lakes have pooled data into larger spatial regions, and this practice was used in our analysis. These pooled areas represent combinations of either lake trout management units for Lake Superior (Hansen, 1996) or statistical districts for Lakes Michigan and Huron (Smith et al., 1961). Lake Huron data were pooled into three regions (MH1, MH2, and MH3456), Lake Michigan data into four regions (MM123, MM4, MM5, and MM678), and Lake Superior data into two regions (MI45 and MI67) (Fig. 2). Where these areas overlap with 1836 Treaty-ceded waters (all but MH3456), they correspond to the same areas used to summarize sea lamprey marking for treaty waters lake trout assessments. The MH3456 region matches the area used to summarize marking for an ongoing lake trout assessment in the southern part of Lake Huron (Sitar et al., 1999).

Model development

In general, sea lamprey wounding rates increase gradually as a function of lake trout length, eventually approaching an asymptote. Taking advantage of this observation, we followed Rutter and Bence (2003) and used the logistic function to describe how the expected number of wounds ($W(l)$) increased with lake trout length ($l$):

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

where $\theta$ describes the asymptotic wounding rate, $\beta$ corresponds to the length of lake trout at the inflection point, and $\alpha \theta/4$ is the slope at the inflection point (Fig. 1). In all cases, models were fit separately for each of the Great Lakes, with regional differences within lakes accounted for by model parameters. The asymptote parameter, $\theta$, varied over years and regions with a fixed-effect parameter estimated freely for each year and region combination for all models. We considered a range of models that varied in the extent to which the shaping parameters ($\alpha$ and $\beta$) of the logistic function varied spatially and temporally (Table 1). When the shaping parameters varied over time, the year effects were modeled as random walks. Details regarding random walks are described in the subsection “Models for spatial and temporal effects,” but in short, a random walk allows for gradual change over time by modeling interannual changes as process errors. When the shaping parameters varied spatially and over years, we considered models where the process errors either had different variances in different regions, or used a common (“lakewide”) variance. The different approaches used for the asymptote and shaping parameters reflect the different ways for which these parameters are expected to vary, as described in the Introduction.

Fig. 2. Lakes Huron, Michigan, and Superior with the regions used in this study specified. Region names and boundaries correspond to combinations of lake trout management units defined for Lake Superior (Hansen, 1996) or statistical districts (Smith et al., 1961) for the other lakes. For example, MM123 is the combined areas of the statistical districts MM1, MM2, and MM3. The shaded region is the state of Michigan.
Lastly, we fit all candidate models (Table 1) assuming either the Poisson distribution used by Rutter and Bence (2003), or a negative binomial distribution, for the expected number of wounds per fish of a given length. The negative binomial distribution allows the variance to increase as a function of the mean expected waiting time by incorporating an additional scaling parameter according to $\text{variance} = \mu + \mu^2/s$, where $\mu$ is the mean of the distribution and $s$ is the parameter that scales the variance-mean relationship. Large values of $s$ resemble a case where the mean is equal to the variance, and in such situations the Poisson distribution will be favored because it has one less parameter.

Models for spatial and temporal effects for shaping parameters

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

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

For our applications, $\gamma_t$ represents either $\log_e(\alpha)$ or $\log_e(\beta)$, which was either the value for the entire lake (“one random walk across years for all regions”) or for a single region (“region-specific random walks across years”). Eq. 2 can be rewritten as:

$$\gamma_t = \gamma + \sum_{t=1}^{t-1} \epsilon_t; \quad \epsilon_t \sim N\left(0, \sigma^2\right)$$ (3)

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

$$\gamma_{\alpha t} = g$$ (4)

$$\gamma_{\beta t} = \gamma$$ (5)

where $r$ and $t$ describe region and year of estimation, respectively, and $g$ represents an overall or regional baseline value. In the context of the text descriptions of Table 1, Eq. 4 corresponds to “constant across regions and years,” Eq. 5 to “region-effects, constant across years,” Eq. 6 to “one random walk across years for all regions” and Eq. 7 to “region-specific random walks across years.” When both spatial and temporal variation were allowed (Eq. 7), the variances for the process errors either varied uniquely among regions, (i.e., $\sigma_r^2$), or were the same for all regions (“lakewide $\sigma^2$”). Thus for example, model O used Eq. 6 for $\log_e(\alpha)$, Eq. 7 for $\log_e(\beta)$, and assumed the same process error variance across regions when applying Eq. 7.

Approach to estimation

We used the random effects module of AD Model Builder (ADMB) to estimate parameters by maximum likelihood (Fournier et al., 2012). We then used AIC for model comparison to choose the best model for each lake. It is important to discern fixed effects from random effects, as fixed effects are treated as parameters in AIC calculations. From the frequentist statistical inference perspective we used for estimation (for an introduction to this perspective for models including random effects see Pinheiro and Bates, 2000, Section 1.1), the fixed-effect parameters were the $\theta$s, the $g$s of Eqs. 4–7, and the $\sigma$s for any process errors influencing the $\alpha$s and $\beta$s. In contrast, the $\sigma$s should be viewed as random effects and not parameters. The general form of the log-likelihood that is maximized is:

$$\log L = \int f(X; \varphi, \delta) \rho(\delta) d\delta$$ (8)

where $X$ represents the data, $f()$ is the probability density (or mass) function for the data given the vector of parameters $\varphi$, and the

<table>
<thead>
<tr>
<th>Model</th>
<th>$\alpha$</th>
<th>$\beta$</th>
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<tbody>
<tr>
<td>A</td>
<td>Constant across regions and years</td>
<td>Constant across regions and years</td>
</tr>
<tr>
<td>B</td>
<td>Constant across regions and years</td>
<td>Region-effects, constant across years</td>
</tr>
<tr>
<td>C</td>
<td>Constant across regions and years</td>
<td>One random walk across years for all regions</td>
</tr>
<tr>
<td>D</td>
<td>Constant across regions and years</td>
<td>Region-specific random walks across years</td>
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<tr>
<td>E</td>
<td>Region-effects, constant across years</td>
<td>Region-specific $r$. w.'s across years (lakewide $\sigma^2$)</td>
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<tr>
<td>F</td>
<td>Region-effects, constant across years</td>
<td>Region-effects, constant across years</td>
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<tr>
<td>G</td>
<td>Region-effects, constant across years</td>
<td>One random walk across years for all regions</td>
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<td>H</td>
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<td>Region-specific random walks across years</td>
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<tr>
<td>I</td>
<td>Region-effects, constant across years</td>
<td>Region-specific r. w.'s across years (lakewide $\sigma^2$)</td>
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<tr>
<td>J</td>
<td>Region-effects, constant across years</td>
<td>Constant across regions and years</td>
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<tr>
<td>K</td>
<td>One random walk across years for all regions</td>
<td>Region-effects, constant across years</td>
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<tr>
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<tr>
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<td>One random walk across years for all regions</td>
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<td>O</td>
<td>One random walk across years for all regions</td>
<td>One random walk across years for all regions</td>
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<tr>
<td>P</td>
<td>Region-specific random walks across years</td>
<td>Region-specific r. w.'s across years (lakewide $\sigma^2$)</td>
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<tr>
<td>Q</td>
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<td>Region-specific r. w.'s across years (lakewide $\sigma^2$)</td>
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<td>S</td>
<td>Region-specific random walks across years</td>
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<td>T</td>
<td>Region-specific random walks across years</td>
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<tr>
<td>U</td>
<td>Region-specific $r$. w.'s across years (lakewide $\sigma^2$)</td>
<td>Region-specific $r$. w.'s across years (lakewide $\sigma^2$)</td>
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<tr>
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<tr>
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<td>Region-specific random walks across years</td>
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<tr>
<td>X</td>
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<td>Region-specific random walks across years</td>
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<tr>
<td>Y</td>
<td>Region-specific $r$. w.'s across years (lakewide $\sigma^2$)</td>
<td>Region-specific random walks across years</td>
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</table>

Table 1 Description of the $\alpha$ and $\beta$ parameters for the candidate set of models used in estimating sea lamprey wounding rates on lake trout. Random walk is abbreviated as “r. w.”
vector of random effects ($\delta$), and $p(\cdot)$ is the assumed probability density (or mass) function for the vector of random effects. The form of $f(\cdot)$ depended on whether a Poisson or negative binomial distribution was assumed. As shown in Eq. 8, during estimation the random effects were integrated out of the likelihood. In essence, the overall likelihood that was maximized was a weighted sum (or more accurately, integral) of the likelihood conditional on values for the random effects over all possible values of the random effects, with weights being the probability density for a given vector of random effects. ADMB integrates out random effects using the Laplace approximation. Predictions of random effects (loosely termed estimates) were those that maximized the term inside the integral of Eq. 8, with parameters fixed at their maximum likelihood estimates.

For purely technical reasons, we specify the $\gamma$s rather than the process error term as the effect that is integrated out (i.e., in Eq. 8, $\delta$ would be the vector of $\gamma$s). We did this because the conditional likelihood of data (i.e., $f(X|\phi, \delta)$), considered a year at a time, depends only on the $\gamma$ for that year. The full likelihood (Eq. 8) also involves the probability density for $\delta$. Although we have not directly expressed a density for the vector of $\gamma$s, this can be determined from the assumed normal distribution for $\varepsilon$ (Eq. 2), and the fact that each $\varepsilon$ can be expressed as a function of just two of the $\gamma$s:

$$\gamma_t = \gamma_{t-1} - \gamma_t$$  \hspace{1cm} (9)

This approach is computationally much less expensive and numerically more robust than directly integrating out the $\varepsilon$s (Fournier et al., 2012).

The likelihood function (Eq. 8) was said to be maximized when absolute values for gradients of less than 0.0001 for all parameters were achieved and the variance-covariance matrix was calculable. The model was thus said to have converged upon the best parameter estimates. Convergence was not achieved if during the model fitting process either of these conditions were not satisfied.

Results

Model selection

Results from AIC comparison showed that all negative binomial distribution models fit much better (typically hundreds of AIC units lower) than their respective Poisson distribution models for all 25 models differing in fixed effects parameters (Table 1). All further results will be presented from models fit using a negative binomial distribution.

AIC comparison shows that models that allowed for temporal and spatial variation in the shaping parameters resulted in the best fit (Table 2). All models that did not allow for such variation were greater than 40 AIC units worse than the best fitting model for each lake. The choice among models that either did or did not use a lakewide variance for the shaping parameters across regions varied between lakes. Model Y produced the best fit to the Lake Huron data and model X produced the best fit to both the Lake Michigan and Lake Superior data. Near-zero $\Delta$ AIC values suggest that more than one model is plausible for Lakes Huron and Superior. Convergence was not achieved for models N, S, and T for Lake Michigan wound data. However, for both Lakes Huron and Superior, models N, S, and T finished no better than third overall. Thus, we suspect that neither models N, S, nor T would have been the best model for Lake Michigan data, and that convergence was achieved for the best fitting model for Lake Michigan. We present estimated wounding rates and parameter estimates for only the models with the lowest AIC values for each respective lake, except when making explicit comparison with the status quo model of Rutter and Bence (2003). Even though several alternative models were plausible, we present only a single set of wounding rate estimates, rather than adopting a model averaging approach, because plausible alternative models made very similar predictions of these estimated quantities.

Patterns in estimated wounding rates

Differences in sea lamprey wounding between lakes and regions were examined by comparing estimated wounding rates from selected models for 500 mm and 650 mm lake trout across all years. Both of these sizes were generally well-represented in the data, with the major exception of MH1 prior to 1991 when lake trout rarely exceeded 650 mm. Temporal trends in wounding rates varied greatly, with differences between lakes being much greater than differences between regions within the same lake. In addition, wounding rates on 650 mm lake trout were generally much higher than on 500 mm lake trout (Fig. 3), and tended to vary absolutely more over time. The lower and more stable rates for 500 mm lake trout reflect (a) that this size was often substantially below the inflection point (and thus relatively un-impacted by changes in it), and (b) that while variations in the asymp-tote had the same percentage direct effect on 500 mm and 650 mm wounding rates, because the relative wounding was much lower for 500 mm lake trout, this translated into smaller absolute variations.

Wounding rates were high and variable in Lake Huron from 1984 to 1998 with wounding rates approaching 0.80 wounds per 650 mm fish estimated for MH2 in 1985 and 1995. Wounding rates in all regions of Lake Huron began to decline in the mid to late 1990s and have reached generally low and much less variable levels. Wounding rates on 500 and 650 mm lake trout in Lake Michigan were generally low for much of the entire time series in all regions, with the exception of northern Lake Michigan (MM123), where sea lamprey wounding began increasing for both sizes beginning in 2001. Wounding rates on 650 mm lake trout in northern Lake Michigan have since leveled off at around 0.35 for the past eight years, and are much higher than recent wounding rates in any of the other regions of Lake Michigan or Lake Huron. Estimates for Lake Superior have been much more temporally variable, especially at 650 mm. Yearly wounding rates were generally between 0.05 and 0.35 in MI45 and MI657 for much of the time series for 650 mm lake trout, but show a slightly increasing trend in both regions since 1994. Wounding rates on 500 mm lake trout have been very low since the mid-1990s in both MI45 and MI67.

Trends in parameter estimates

Overall, temporal variation in $\beta$ generally had more influence on the shape of the logistic function than did temporal variations in $\alpha$.

<table>
<thead>
<tr>
<th>Model</th>
<th>$\Delta$ AIC</th>
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<tbody>
<tr>
<td>Lake Huron</td>
<td>Lake Michigan</td>
</tr>
<tr>
<td>N</td>
<td>−122.6</td>
</tr>
<tr>
<td>O</td>
<td>−127.0</td>
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<tr>
<td>P</td>
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<tr>
<td>V</td>
<td>−71.2</td>
</tr>
<tr>
<td>W</td>
<td>−40.4</td>
</tr>
<tr>
<td>X</td>
<td>−2.4</td>
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<tr>
<td>Y</td>
<td>0.0</td>
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</table>
Changes in $\beta$ are also more easily interpretable in terms of a change in size-selection in that such changes represent an overall shift at what host size wounding rapidly increases with further increases in host size. Nonetheless, allowing for temporal variation in $\alpha$ led to substantial decreases in AIC (Table 2). Such large improvements in AIC associated with temporal variation in $\alpha$ are likely in part due to small improvements in model fit added up across very large amounts of data: 36,018 observations for Lake Huron, 37,123 for Lake Michigan, and 148,833 for Lake Superior. For these reasons we do not provide a figure with estimates of $\alpha$.

Estimates of the length of lake trout at the inflection point, $\beta$, showed great variation between lakes, and also between regions within the same lake (Fig. 4). In Lake Huron, distinct decreases in $\beta$ of nearly 100 mm occurred in both MH2 and MH3456 over the time series. Decreasing trends were also seen in MM123, MM4 and MM678 in Lake Michigan, with $\beta$ decreasing nearly 150 mm from 1992 to 2010 in MM4. Smaller decreases of about 50 mm were seen in MM123 and MM678. Estimates of $\beta$ were greatest in regions MM4, MM5 and MM678 of Lake Michigan, with values generally greater than 650 mm until the late 1990s. Temporal trends in Lake Superior were less distinct, as $\beta$ remained constant near 640 mm in MI45 and gradually increased from 580 mm to 640 mm from 1971 to 2010 in MI67. Interestingly, although models allowing temporal variation in $\beta$ were selected, variance estimates for the random walks for MM5 and MI45 were near-zero.

The asymptotic wounding rate parameter, $\theta$, also varied greatly between the lakes (Fig. 5). For Lakes Huron and Superior, trends in $\theta$ mimic those seen in estimated wounding rates on 650 mm lake trout (Fig. 3). In Lake Michigan, where $\beta$ estimates tended to be much higher than the other lakes for much of the time series, the relationship between 650 mm wounding rates and asymptotic wounding rates is not as tight. Due to high estimates for $\beta$ in Lake Michigan, especially earlier in the time series for MM4, asymptotic wounding rates were unlikely to be realized. An extreme example is seen in 1993 where the
asymptotic wounding rate in MM4 spiked to 0.97 wounds per fish, while the wounding rate on 780 mm lake trout (corresponding to the ninety-fifth percentile of lake trout lengths for fish sampled in MM4 in 1993) was only 0.65 wounds per fish. Thus, in Lake Michigan, the asymptote is often extrapolated beyond the range of the data (i.e., represents wounding rates on lake trout larger than those actually sampled).

Comparison with currently used wounding rate models

Sea lamprey wounding rate estimates were compared between wounding rate models currently used to provide estimates for lake trout assessments and those selected in this analysis. Currently, fishery managers use variants of the model selected by Rutter and Bence (2003), to estimate size-specific sea lamprey wounding rates. This corresponds to model B (Table 1) of this analysis, with a Poisson distribution assumed for the number of wounds per fish of a given length, and is further referred to as the Rutter model.

In general, the estimates of wounding rates from our new models and the Rutter model are surprisingly similar, and temporal trends track closely between the two models, even at the inflection point of the original model (Fig. 6). We expected (and verified) that differences in wounding rate estimates between the two models would be most apparent at lake trout lengths nearest the Rutter model inflection points, and for the years where our new model estimated the largest discrepancies in inflection points from those values. The large difference in AIC between the models is thus mostly attributable to differences near the inflection added up over a large number of observations. For MH2 and MH3456 there was a general tendency for our new model to estimate a lower wounding rate at the inflection point in the early years of the time series, and to estimate a higher wounding rate in the later years of the time series, in comparison with the Rutter model (Fig. 6). This pattern is consistent with the decline in \( \beta \) estimates from our new model over time for those areas (Fig. 4). While the differences are modest, relative to the overall magnitude of temporal changes in wounding, in MH3456 the Rutter model estimates correspond to a decline of 65% between the first five years and last five years of the time series compared to a 37% decline for the new model. Such a difference could potentially matter to fishery managers.

Discussion

Improved wounding rate estimates

A main objective of this research was to improve sea lamprey wounding rate estimates, whose primary application is in lake trout population assessments. Thus, it is of interest to examine the differences in sea lamprey wounding rates between wounding rate models currently used to provide estimates for lake trout assessments and those selected herein. Variants of the model selected by Rutter and...
Bence (2003) are currently used to estimate size-specific sea lamprey wounding rates for each of the lakes.

Initial inspection of wounding rates generated by both of the models reveals only small discrepancies between the estimates (Fig. 6). This finding was at first surprising, given the substantial improvement in model performance, as measured by AIC, by incorporating temporal and spatial variation in the shaping parameters. However, considering the large size of the wound dataset, such large improvements in model fit are reasonable despite apparently small differences in estimated values. This said, there are some non-trivial but modest changes in wounding estimates associated with changing from the Rutter to our new model. We limited the presentation of differences between our selected models and the Rutter model to Lake Huron because it was wounding data from this lake to which the Rutter model was originally fit and from which the only published results exist (it should be noted that in this comparison both models were fit to the full Lake Huron wound dataset). However, similar results were obtained when comparing models currently used by fishery managers and those selected in this analysis for Lakes Michigan and Superior, although the differences were larger for those lakes (C. Prichard, unpublished). The similarity in overall estimated patterns between our selected models and the Rutter model is a reassuring result, as it suggests that models currently used by fishery managers likely have performed an adequate job providing sea lamprey wounding estimates, especially for Lake Huron. However given the superior statistical performance of our new models and some non-trivial (although generally modest) differences in estimates we recommend that models that allow the inflection point to vary over time be adopted for management purposes.

Improved modeling framework

The approach used by Rutter and Bence (2003) differed from the true maximum likelihood approach. They found the combination of what we call parameters and random effects that maximized the term inside the integral of Eq. 8. From a Bayesian perspective, that term is proportional to the posterior density for the vector \( \phi, \delta \), hence these estimates are sometimes called highest posterior density estimates (HPD, Schnute, 1994) (they are also referred to as maximum penalized likelihood estimates). Rutter and Bence (2003) were not able to uniquely estimate the process error variances with HPD, a weakness that our analysis was able to overcome. Rutter and Bence (2003) obtained estimates for the \( \sigma \)'s, but only by carefully choosing starting values so that the estimates did not move toward zero or infinity. A second issue is that in comparing models that have a different number of random effects with AIC, using HPD as though it is likelihood may not be valid, and it is unclear what the number of parameters should be. Rutter and Bence (2003) treated each process error (i.e., the \( \sigma \)'s from our analysis) as a parameter. This overstated model complexity because these were not freely estimated parameters, and thus their analysis may have been biased against selecting for time-varying models. In contrast, we treated only process error variances and starting values of each random walk as parameters, and integrated out the \( \sigma \)'s.

Fig. 5. Asymptotic wounding rate (\( \theta \), Eq. 1) parameter estimates of models selected for each lake in this analysis. \( \theta \) estimates correspond to model Y for Lake Huron and model X for Lakes Michigan and Superior (Table 1). Asymptotic wounding rate parameters were not estimated for some unit-year combinations for Lake Michigan due to low sample size.
A possible explanation for the observance of overdispersion in each lake, as implied by the negative binomial models producing the best fits, is a difference in habitat use by lake trout and sea lamprey across lake trout sampling sites. If sea lamprey habitat and lake trout habitat differentially overlap among sampling sites then it is conceivable that lake trout sampled where they more frequently overlap with sea lamprey may exhibit a greater number of wounds than would be expected across all sampling sites. Another possible explanation for overdispersion may arise from differences in wounding between strains of stocked lake trout. It has long been observed that Seneca Lake origin strain lake trout generally have lower incidence of wounding than both wild and Great Lakes origin strains stocked in the Great Lakes (Schneider et al., 1996), and for this reason they have been stocked in increasing numbers in Lakes Huron and Michigan (Ebener, 1998). However, the spatial distribution of parasitic phase sea lamprey in the Great Lakes remains unknown. Relating wounding rates to sampling sites and lake trout strain was beyond the scope of this study, but warrants further investigation.

On another technical note, one might envision that a constant shape would correspond to models with constant shape parameters. This is not the case with our parameterization in which the slope at the inflection point depends upon both $\alpha$ and $\theta$. The asymptote varied, thus to maintain a constant shape $\alpha$ would also have to vary. Attempts to implement an alternative parameterization such that the slope itself was modeled as a parameter, rather than as a function of $\alpha$ and $\theta$, were met with failures to achieve convergence for models L and other more complex models. However, for the less complex models, AIC values were improved with slope modeled as an explicit parameter. Thus, this alternative approach has some potential if the convergence issues with the more complex models can be resolved.

**Potential causes for changes in wounding rates**

Generally, wounding rates are governed by two things, the first of which is the ratio of sea lamprey abundance to host abundance. Assuming an asymptotic functional response relating sea lamprey attack rates to host density, increases in host abundance in the asymptotic range would produce an overall decrease in wounding rates because the same number of attacks would be distributed among more hosts. Additionally, with host abundance held constant, overall marking rates would be expected to scale in direct proportion to the abundance of sea lamprey. In Lakes Michigan and Superior, general directional trends in wounding rates on lake trout (Fig. 3) appear to be closely linked to trends in lakewide estimates of spawning phase sea lamprey abundance (Sullivan and Adair, 2010). In Lake Huron, drastic decreases in wounding rates in the regions examined herein coincide with a gradual decrease in spawning phase sea lamprey abundance estimates. However, McLeod et al. (2011) found that overall wound probability increased 12.1% in Canadian waters of Lake Huron from 2000 to 2009. This suggests that wounding rates may be more influenced by the observed increases in lake trout abundance and the increases in larger and older lake trout observed in Michigan waters of Lake Huron (Caroffino and Lenart, 2011).

Second, wounding rates are affected by the size-selectivity of sea lamprey. Previous work has hypothesized that sea lamprey select for smaller lake trout when larger, more desirable, lake trout are scarcer (Bence et al., 2003; Rutter, 2004; Rutter and Bence, 2003), but as of yet no analyses have tested this directly. Changes in size-selection in response to varying prey abundances have been shown for a variety of predators including fishes (e.g., Sih and Christensen, 2001) but to our knowledge such relationships have not been shown for parasitic fish such as sea lamprey. A possible indicator of changes in size-selection of sea lamprey could be major shifts in the position of the inflection point of the logistic function relating sea lamprey wounding rate to lake trout size (Fig. 7). The three largest shifts in $\beta$ occurred in central and southern Lake Huron (MH2 and MH3456) and in Grand Traverse Bay (MM4). In all three regions $\beta$ decreased, suggesting the possibility of a shift in selectivity toward smaller lake trout. However, contrary to the expectation that a shift downward in the inflection point would indicate selectivity shifting toward smaller hosts associated with a decrease in larger lake trout, there is much evidence suggesting an overlap with sea lamprey may exhibit a greater number of wounds than would be expected across all sampling sites.
increase in abundance of large lake trout hosts in Lake Huron. For example, in the case of MH2, estimates of spawning stock biomass increased from near-zero levels in the early 1990s to levels more recently exceeding 200,000 pounds annually (2000–2008) (Caroffino and Lenart, 2011). In general, further research relating sea lamprey size selection to the abundance of different size classes of lake trout and other hosts, as well as other factors, is needed, especially given that some of our results suggest patterns diverging from earlier predictions.

Concluding remarks

Because the time series of wound data for each lake continue to grow, models that account for temporal variation become increasingly favored over models that do not. Factors that affect the relationship between sea lamprey wounding rates and lake trout length have been shown to change dramatically over time. Thus, allowing parameters to vary over time as random walks permits sharing of information over time, with data from the years nearest the year of estimation to have the most influence on estimated wounding for that year, reducing the influence of historic trends on the estimates for a specific year. However, drawbacks to this approach are increasing difficulty in achieving model convergence with the addition of successive years of data. We suggest further research be conducted to determine a model that incorporates flexibility in parameter estimates over time, while simplifying the models such that convergence is more easily achieved.

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