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Sea lamprey wounding in Canadian waters of Lake Huron from 2000 to 2009: Temporal changes differ among regions

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ABSTRACT

Lake Huron has undergone a number of substantial changes in recent years, including changes to management of the parasitic sea lamprey, *Petromyzon marinus*. While control strategies of lamprey involving lampricides have had some success, lamprey spawning in St. Marys River has been a major and persistent problem and has led to intensified treatment beginning in 1998. The objective of our study was to broadly examine lamprey spatial wounding dynamics of lake whitefish (*Coregonus clupeaformis*) and lake trout (*Salvelinus namaycush*) within the Canadian waters of Lake Huron from 2000 to 2009. Temporal trends were evident and these differed among regions (North Channel, northern Main Basin, southern Main Basin, northern Georgian Bay, and southern Georgian Bay). There was a monotonic annual increase in probability of wounding for both lake trout and lake whitefish in three of the five regions, with high increases seen in both northern and southern Georgian Bay. The increases in three of the five regions are unexpected given the ongoing treatment of St. Marys River.

Introduction

Lake Huron has undergone a number of recent major ecosystem changes, including the precipitous decline in abundance of the benthic macroinvertebrate *Diporeia* (Nalepa et al., 2007), the collapse of the offshore demersal fish community in 2006 (Riley et al., 2008), and the significant alteration in habitat use by offshore demersal fish (Riley and Adams, 2010). The direct and indirect effects of these changes on large-bodied piscivores have been substantial. *Diporeia* was a staple food source for lake whitefish (*Coregonus clupeaformis*) and its decline caused a significant decrease in whitefish condition and growth (Madenjian et al., 2006; McNickle et al., 2006; Rennie et al., 2009). For lake trout (*Salvelinus namaycush*), who were virtually extirpated from the lake in the 1960s due to sea lamprey (*Petromyzon marinus*) parasitism (Morse et al., 2003), a rehabilitation effort which has been in place since the 1970s (Eshenroder et al., 1995) appears to be succeeding (Morbey et al., 2008; Riley et al., 2007). However, despite increases in natural reproduction, lake trout underwent a 21% decline in energy density from 1995 to 2004 (Paterson et al., 2009) and showed a decline in growth and condition (He et al., 2008; He and Bence, 2007). Meanwhile, Chinook salmon (*Oncorhynchus tshawytscha*), a Pacific salmonid which has been stocked in Lake Huron since 1968, has shifted from a fishery that was once dependent entirely on stocking to one that is largely self-regulating (Johnson et al., 2010). In spite of these reproductive gains, there has been a decrease in growth and condition of Chinook salmon within Lake Huron in recent years (He et al., 2008).

In addition to these ecological changes, revisions have been made to the management of sea lamprey. Lampreys have exacted an enormous toll on lake whitefish and lake trout populations in Lake Huron since their initial invasion (Applegate, 1950). Conventional lamprey management has focused on chemical treatment of the larval stage of lampreys through the application of the lampricide TFM (3-trifluoromethyl-4-nitrophenol) to spawning tributaries. The success of TFM in Lake Huron has been limited however by the amount of spawning habitat in St. Marys River, whose discharge rate precludes cost-effective TFM treatment (Shen et al., 2003). By the late 1990s, St. Marys River was estimated to contribute 88% of adult parasitic phase sea lamprey to the lake (Schleen et al., 2003). Development in the mid-1990s of a granular lampricide Bayluscide® (2′,5-dichloro-4′-nitro-salicylanilide) made treatment of St. Marys River feasible, and application of Bayluscide® to the region has been on-going since 1998. Initial post-treatment assessment indicated a reduction in the larval population by 45% (Fodale et al., 2003). Within 5 years, treatment of St. Marys River was expected to reduce the abundance of parasitic phase lamprey in Lake Huron by 60% (Adams et al., 2003).

The effect of the St. Marys River treatment on lamprey-induced wounding of lake trout has been assessed for the Drummond Island Refuge. Declining lake trout wound occurrence indicated that the treatment was achieving success (Madenjian et al., 2008a). To our knowledge

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there has been no further assessment of wounding incidence on a broader geographical scale in Lake Huron, especially important in light of the suite of changes in the lake during the past decade. The objective of our study therefore was to examine changes in lamprey wounding rates during the period of 2000–2009 in Canadian waters of Lake Huron. We focused our analyses on lake trout, as done in similar studies (Rutter and Bence, 2003; Sitar et al., 1999), and on lake whitefish, a species of commercial importance that also is commonly parasitized by lamprey.

Methods

Data selection

Our study focused on the Canadian waters of Lake Huron for the period 2000–2009. Wounding data for lake trout and lake whitefish was extracted from commercial catch sampling data provided by the Ontario Ministry of Natural Resources (OMNR). This program is comprised of OMNR contract biologists who randomly sample a proportion of the commercial fishery catch throughout the year and record a variety of information including fish species, fork length, area of capture, and lamprey wounding details (e.g. Milne, 2003). Recording of lamprey-induced wounds on fish by the OMNR follows specific guidelines. Prior to 2003, the number of scars per fish, wounds per fish, wounds ≥ 25 mm, and wounds < 25 mm was recorded. From 2003 onward, the classification system of lamprey wounding was revised based on King and Edsall (1979). Under this system, lamprey wounds qualify as either a definite opening through skin with muscle visible (A-type), or a B-type where a lamprey attack occurred without penetration to muscle. The key uses a number system to indicate the level of healing (I–IV with I being fresh and IV being fully healed; King and Edsall, 1979). This system also provides estimates of wound size.

In our study, wounding data were condensed into binary occurrence data. This approach diverges from other studies that used the number of wounds per fish (Rutter and Bence, 2003; Sitar et al., 1999). However, the probability of wounding and mean wound number would both be substantially less than one, and therefore very similar in Lake Huron where fish having more than one wound are rare. For 2000–2002 data, all wounds ≥ 25 mm were assigned a value of "1"; as were all AI-AIII wounds ≥ 25 mm from the 2003–2009 data. These two classifications are considered equivalent as they both reflect the occurrence of recent lamprey attacks. Other lamprey marks (e.g. AIV and BI-BIV) and those records where no wounds were observed were assigned a value of "0". Observations where lamprey wounding data were not recorded were excluded from analyses.

As most of the OMNR commercial fisheries sampling occurs during the July–October period, data were pooled into this standardized time block to ensure sufficient sample sizes and statistical power to detect any changes that may have occurred over the study period. Additionally, using only AI–AIII wounds ≥ 25 captured the bulk of wounds suffered during the previous year. While pooling data in this way mixes wounds from the feeding season occurring at the time of capture and from those of the previous year, and prevents attributing wounds to specific year classes of lamprey (see Schneider et al., 1996), it is appropriate for assessing broad interannual trends in sea lamprey wounding levels.

Spatial autocorrelation

The finest spatial resolution available was the 5" × 5" (approximately 9.25 km × 6.62 km) grid system used by the OMNR for assessment purposes. The number of fish sampled varied widely among grids and years due to fluctuations in the intensity of fishing and monitoring. In order to obtain adequate sample sizes for spatial and temporal comparison, data from twelve assessment areas were used: two areas in each of the North Channel, northern Main Basin and southern Main Basin, and the remaining six in Georgian Bay. Spatial autocorrelation of wounding was used to determine how best to aggregate the twelve assessment areas. This was done separately for each species based on values of wounding frequency (the number of wounds divided by the total number of fish sampled) for each assessment area.

A spatial lattice arrangement was used to test for spatial autocorrelation. This allows irregularly distributed observations to be grouped into larger, arbitrary areas (Zuur et al., 2007). Distances between pairs of assessment areas were calculated as the shortest distances via water between the grids within each assessment area containing the greatest number of observations for lake trout and lake whitefish (referred to hereafter as observation centers; see Fig. 1). The matrix of pair-wise distances was converted to contiguity matrices (W) using an indicator function, $l(x)$:

$$I(x) = \begin{cases} 1 & if\ x\ is\ true \\ 0 & if\ x\ is\ not\ true \end{cases} \tag{1}$$

where the matrix W is of dimension 12-by-12 and its ijth element w_{ij} is given by

$$w_{ij}^{(k)} = w_{ij}(d_k, d_{k+1}) = I\left(d_k < d_{ij} \leq d_{k+1}\right) \tag{2}$$

In this equation, d_k are distances {0, 50, 100, 150, 200, 250, 300, 350 km} and indices i and j refer to the observation centers. An incremental distance of 50 km was chosen because it contained sufficient data to test for spatial autocorrelation.

Data on wound frequency were tested for spatial autocorrelation among assessment areas using Moran's I Coefficient (Zuur et al., 2007). Values generated by Moran's I Coefficient were converted to z-scores by taking the difference between the value given by Moran's and the value of the expected score divided by the standard deviation of the value given by Moran's. The expected value (E) is given by.

$E = -1/(n-1)$, where n is the number of observations (Zuur et al., 2007). Significant spatial autocorrelation of wounding frequency have z-scores > +1.96 (similarity) or < −1.96 (dissimilarity).

Models of probability of wounding

Probability of wounding was modeled using a generalized linear model (GLM) with a binomial error distribution and logit link function (i.e. logistic regression). We used two categorical variables (species and aggregated areas) and two covariates (fork length and year [adjusted so that 2000 = 0 and 2009 = 9]). Inclusion of fork length and species in the model was done because lampreys exhibit host-selectivity for larger fish over smaller fish (Schneider et al., 1996; Swink, 2003) and show host specificity (Christie and Kolenosky, 1980; Morse et al., 2003). The fully saturated model considered all explanatory variables, all two-way interactions, all four three-way interactions, and one four-way interaction. The form of the logistic regression function applied was

$$\begin{aligned} \log it(z) &= (1 + \exp[-z])^{-1} \\ z &= \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_1 x_2 + \cdots \end{aligned} \tag{3}$$

where the β_i represent the logistic coefficients while the x_i are the variables (or higher order transformation of variables) of interest. The effect of the interaction terms (i.e. x_1x_2) varied based upon the classification of the variable in question (categorical or continuous). For interaction terms between categorical variables (species and area), the term effectively meant that the intercept of the relationship varied for every combination of the two categorical variables. For interactions between categorical and continuous variables, the slope parameter for the continuous variable is allowed to vary among categories (i.e. different rates of change in probability of wounding as a function of increasing fork length for lake whitefish versus lake trout). For an interaction