Understanding sea lamprey abundances in the Great Lakes prior to broad implementation of sea lamprey control

Kelly F. Robinson a,⁎, Scott M. Miehls b, Michael J. Siefkes c

aMichigan State University, Department of Fisheries and Wildlife, Quantitative Fisheries Center, 480 Wilson Road, 2B Natural Resources Building, East Lansing, MI 48824 USA
bU.S. Geological Survey, Great Lakes Science Center, Hammond Bay Biological Station, 11188 Ray Road, Millersburg, MI 49759, USA
cGreat Lakes Fishery Commission, 2200 Commonwealth Blvd. Suite 100, Ann Arbor, MI 48105, USA

A R T I C L E   I N F O
Article history:
Received 31 July 2020
Accepted 5 April 2021
Available online xxxx
Communicated by Mike Steeves

Keywords:
Sea lamprey
Petromyzon marinus
Lampricide
Fisheries management
Historical catch data

A B S T R A C T
Control of invasive sea lamprey in the Great Lakes with a selective pesticide (lampricide) that targeted larval sea lamprey began in the late 1950’s and continues to be one of the main methods for control. Although the Great Lakes Fishery Commission, which was formed with the mandate of controlling sea lamprey, often expresses the success of the sea lamprey control program in terms of percent reduction from lake-wide pre-lampricide control adult sea lamprey abundances, there remains a large amount of uncertainty surrounding these estimates. In this study, we gathered historical data on adult sea lamprey captures from trapping efforts from the mid-1950’s through the late 1970’s to better understand pre-control abundance. We used this information to estimate lake-wide population abundances of adult sea lamprey using a weighted linear regression that includes environmental and lampricide treatment predictor variables. We varied trampling efficiency for early trapping data to evaluate the uncertainty in abundance estimates. Pre-control adult sea lamprey abundances in all lakes were much greater than current population sizes, but estimates were quite sensitive to trampling efficiency. In Lake Superior, declines in abundance aligned with increases in control efforts, but in other lakes, declines were occurring prior to the onset of lampricide application, perhaps because of a loss of prey. We suggest that previous estimates of pre-control adult sea lamprey abundance may have been underestimated unless trampling efficiency was greater than what is currently achieved in the basin.

© 2021 The Authors. Published by Elsevier B.V. on behalf of International Association for Great Lakes Research. The contribution to this work by the United States Geological Survey (USGS) author was provided as part of the USGS authors official duties as an employee of the United States Government, and this contribution is a work of the United States Government. In accordance with 17 U.S.C. 105, no copyright protection is available for such works under U.S. Law and the CC BY license shall therefore not apply to the USGS authors contribution to the work. This is an open access article under the CC BY license [http://creativecommons.org/licenses/by/4.0/].

Introduction

The sea lamprey (Petromyzon marinus) invaded the Great Lakes upstream of Niagara Falls in the early 20th century and was a major contributor to devastating ecological changes and fishery collapses in the upper Great Lakes (Coble et al., 1990; Smith and Tibbles, 1980). Although the status of the sea lamprey as indigenous to Lake Ontario is debated (Bryan et al., 2005; Eshenroder, 2014, 2009; Waldman et al., 2004), sea lamprey populations in Lake Ontario increased in the early-to-mid 20th century causing similar impacts on the ecosystem and fishery to those experienced in the upper Great Lakes (Marsden and Siefkes, 2019). Consequently, the Great Lakes Fishery Commission (GLFC) was formed in 1955 with a primary mandate to formulate and implement a sea lamprey control program across the Great Lakes basin to enable ecosystem and fishery rehabilitation (GLFC, 1954). During the late 1950’s, a selective pesticide (lampricide) that targeted larval sea lamprey in their natal streams was developed and widespread application in Great Lakes tributaries quickly began (Howell et al., 1980). This lampricide, 3-trifluoromethyl-4-nitrophenol (TFM), and another identified in the 1960’s, 2,5-dichloro-4-nitrosa licylalanilide (niclosamide or Bayluscide®), were found to be highly successful and are still in use today to keep sea lamprey populations suppressed across the Great Lakes (Siefkes, 2017).

⁎ Corresponding author.
E-mail address: kfrobins@msu.edu (K.F. Robinson).

https://doi.org/10.1016/j.jglr.2021.04.002
0380-1330/© 2021 The Authors. Published by Elsevier B.V. on behalf of International Association for Great Lakes Research. The contribution to this work by the United States Geological Survey (USGS) author was provided as part of the USGS authors official duties as an employee of the United States Government, and this contribution is a work of the United States Government. In accordance with 17 U.S.C. 105, no copyright protection is available for such works under U.S. Law and the CC BY license shall therefore not apply to the USGS authors contribution to the work. This is an open access article under the CC BY license [http://creativecommons.org/licenses/by/4.0/].

Please cite this article as: K.F. Robinson, S.M. Miehls and M.J. Siefkes, Understanding sea lamprey abundances in the Great Lakes prior to broad implementation of sea lamprey control, Journal of Great Lakes Research, https://doi.org/10.1016/j.jglr.2021.04.002
The sea lamprey control program annually evaluates the effects of control efforts on sea lamprey populations by comparing an annual index of adult sea lamprey abundance (Adams et al., This issue) to a specific index target (Treska et al., This issue) for each lake. Counts of sea lamprey marks on lake trout (Salvelinus namaycush) are collected by management agencies for each lake and compared to a target marking rate as another measure of the effects of the control program (Treska et al., This issue). These metrics are useful for tracking the status of sea lamprey populations and marking rates on lake trout relative to targets, as well as trends over time, however, data are limited or simply missing prior to 1980 (GLFC, 2020a), making assessment of sea lamprey populations and the effects of early control program efforts challenging. Nevertheless, the success of the sea lamprey control program is often expressed as a percent reduction from pre-lampricide control (hereafter, “pre-control”) population levels (90% reduction; GLFC, 2020b) without a clear understanding as to how pre-control population estimates (GLFC, 2020a) were generated or the veracity of the estimates.

Early sea lamprey control efforts from 1940 to 1960 included efforts to block migrating adult sea lamprey from spawning sites with mechanical and electrical barriers, although these tactics were deemed ineffective and were discontinued during the 1960’s (Christie and Goddard, 2003; Humm and Youngs, 1980). Nevertheless, these barriers usually had associated traps to capture and remove migrating adults (Siefkes et al., 2013) and consequently provided useful pre-control assessment data that could be used to estimate spawning run size in the associated tributary (Lawrie, 1970; Smith and Tibbles, 1980). Heinrich et al. (2003) used the trap catch data from Lake Superior to generate pre-control adult sea lamprey population estimates for the entire lake, but the exact methods used to generate these estimates were not presented. To date, pre-control adult population estimates for the other lakes and the methods for calculating the pre-control population estimates used by the GLFC remain unpublished.

Given that reductions from pre-control adult population levels are often cited as a measure of sea lamprey control program success (GLFC, 2020a), generating these estimates in a way that is transparent and allows for full understanding of the uncertainty around these estimates is important. Here we explore the available data for each of the Great Lakes and attempt to generate pre-control adult population estimates for each lake where possible, noting the uncertainties and caveats for each lake.

Methods

Data sources

We collected trap data from various sources beginning in 1953 in Lakes Superior and Huron and 1955 in Lake Michigan. These data were gathered from peer-reviewed publications (Heinrich et al., 1980; Smith and Tibbles, 1980), reports and proceedings of meetings, including annual reports from the GLFC (Johnson, 1987; GLFC, 1957), and records from sea lamprey control personnel from the United States Fish and Wildlife Service (USFWS) and Fisheries and Oceans Canada (DFO). Data generally described the annual number of adult sea lamprey captured in traps on individual streams, the type of trap or barrier (e.g., electric weir), and occasionally notes describing anomalies in the catches (e.g., in one year, collections ceased early in the season because the dip netter was hospitalized with formaldehyde poisoning; Heinrich et al., 1980). Data were also gathered for Lakes Ontario and Erie, but these data were quite sparse prior to 1980 and therefore not useful for the modeling exercise. Trapping data used for Lakes Superior, Michigan, and Huron were obtained from sea lamprey control program records (DFO, Sea Lamprey Control Centre, Sault Ste Marie, Ontario, Canada; USFWS, Marquette Biological Station, Marquette, Michigan, USA) and are available as electronic supplementary material (ESM Tables S1–S3).

Adult sea lamprey population estimation

We used the methods of Mullett et al. (2003) to estimate population size of adult sea lamprey in Lakes Superior, Michigan, and Huron from the early 1950’s through 2014. Previously, data used for this method began in 1977. For 1953–1976, in streams where trap data were available, we estimated the abundance of sea lamprey in the stream by dividing the number of captured individuals by an assumed trapping efficiency. As we could not find data indicating trapping efficiency for the early years of trapping (i.e., 1953–1976), we chose not to vary trapping efficiency year-to-year or stream-by-stream in the model, although we suspected that these efficiencies were likely variable across time and space. We instead used three different trapping efficiencies (20%, 40%, and 66%) for these early years to evaluate the sensitivity of lake-wide abundance estimates to this variable. We chose 66% to replicate the population estimation procedure described in Heinrich et al. (2003) for sea lamprey in Lake Superior. Heinrich chose this value based on mark-recapture estimates from seven sea lamprey barriers with permanent traps on Lake Superior in the 1990’s. We chose to use 40% trapping efficiency (TE) because estimated efficiencies in recent years average about 40% (Steeves and Barber, 2020). In addition, because efficiency of trapping efforts early during sea lamprey control were possibly quite low (e.g., Smith and Tibbles [1980] noted that early weirs were inefficient and allowed large numbers of adult sea lamprey upstream), we also chose to estimate population size with a 20% efficiency—half of the current average. After 1976, mark-recapture data were used to estimate trapping efficiencies for streams and years with trapping data, as described in Mullett et al. (2003) and Heinrich et al. (2003). Therefore, there was only one stream-specific abundance estimated per year after 1976.

In streams without trapping data, we duplicated the linear model described in Mullett et al. (2003) to estimate adult sea lamprey abundance. We chose this model, rather than the newer approach of Adams et al. (This issue), which uses a subset of 5–7 index streams, because most of the index streams were not trapped during early control efforts. The model from Mullett et al. (2003) allowed us to make use of all available data. This model was a weighted linear regression, with environmental and lampricide treatment predictor variables, that estimated the natural log of the population of sea lamprey in a given stream:

\[
\ln(S_j) = \beta_0 + \beta_1 \ln(D_j) + \beta_2 R_i + \beta_3 \ln(D_j)R_i + \beta_4 P_i + \beta_5 T_j + Y_j + \epsilon_{ij}
\]

where \(S_j\) is the estimate of adult sea lamprey in stream \(j\) in year \(j\), \(D_j\) is the drainage area, \(R_i\) is the region (equal to 1 for north or east regions, 0 otherwise), \(P_i\) is the production potential of stream \(i\) (equal to 0 for a primary producer and 1 for a secondary), \(T_j\) is the years since the last lampricide treatment, \(Y_j\) is the year effect, and \(\epsilon_{ij}\) is the error term (Mullett et al., 2003). The error term is normally distributed with mean = 0 and variance = \(\sigma^2C_j\), where \(C_j\) is the coefficient of variation of the estimate of stream abundance (\(S_j\)). Observations for which a coefficient of variation of the stream abundance were available were used for the error structure, in that the variance was weighted by the square of the inverse of the coefficient of variation (Mullett et al., 2003). However, in some instances, the older trapping data (those collected prior to 1977) were collected from streams in which no mark-recapture estimates, and therefore no estimates of the coefficient of variation were available across the time series. In these cases, we used the lake-wide median
value of the square of the inverse of the coefficient of variation for the lake in question as the weight for the variance in the linear model. In addition, in Lake Superior, a variable to denote sterile male release study streams was included in the linear model.

The linear model required data on the time since the last lampricide treatment (\(T_r\)) for each stream but did not allow for \(T_r\) to be greater than 10, representing 10 years since last treatment. For data prior to 1977, we used the lampricide treatment history from Johnson’s history of sea lamprey control, which is an unpublished historical document written in 1985 and made available to the authors by C. Brant (GLFC, pers. comm., July 2020). If no treatment occurred on a stream, this variable was set to 10, even if time since last treatment was greater than 10 years. Although there were likely treatments listed in this database that targeted only a portion of a stream, our decision rule was to include any listed treatment as a full treatment, as data to the contrary were not available. We believe that this was the most conservative approach for this modeling effort.

If there were no data to fit the model for a given year (e.g., no trap or mark-recapture estimates), that year was excluded from the model predictions. Data were unavailable for 1977–1979 for Lake Superior and 1961–1963 and 1966–1976 for Lake Michigan. In addition, previous population estimates for the St. Marys River were calculated from a separate procedure by sea lamprey experts, 1977–1985. There were no data for the St. Marys River prior to this time frame, so we decided to omit the St. Marys River completely from our estimates of population abundance in Lake Huron, as we could not estimate abundance prior to 1977.

Lake-wide population estimates for adult sea lamprey were calculated as the sum of the estimates from trap data, mark-recapture, and model estimates for all streams in the system. To evaluate the effect of stream-specific trapping data prior to 1977, we also conducted a leave-one-out procedure for population estimates. In this procedure, we sequentially removed the trapping data from one stream at a time, instead estimating the abundance in that stream with the population model. In this way, we could evaluate the influence of early trapping data on lake-wide population estimates. Although data were not available to extend the estimates of population size back in time for Lakes Ontario and Erie, lake-wide population estimates from the beginning of the available time series (1978 for Lake Ontario and 1980 for Lake Erie) were calculated for these lakes. Finally, we calculated five-year running averages for each lake to account for the potential annual variability in estimates associated with lampricide treatment schedules.

**Results**

We were able to recover trap catch data and lampricide treatment schedules from various sources around the Great Lakes. Trap catch data for the three upper lakes, as well as Lake Ontario, were variable in terms of the length of the time series among streams (ESM Tables S1–S4). In general, the trap catch data for the upper Great Lakes declined in catch over time, whereas the data for Lake Ontario are more variable, with older data only coming from two streams that were sampled via dip net (ESM Table S4). Our efforts did not return any trap catch data for Lake Erie that were not already available in the data used by the Sea Lamprey Control Program for the Mullett et al. (2003) model. Prior to 1977, annual trap catch data were available for 8–39% of Lake Superior streams, 6–44% of Lake Michigan streams, and 1–13% of Lake Huron streams (ESM Table S5). In addition, lampricide treatment began in 1958 in Lake Superior (11% of streams treated), 1960 in Lake Michigan (7% of streams treated) and Huron (4% of streams treated), 1971 in Lake Ontario (47% of streams treated), and 1980 in Lake Erie (3% of streams treated; Fig. 1).

Lake-wide pre-control adult sea lamprey population estimates were affected by the assumed efficiency of the traps used during this time period (Fig. 1). Peak sea lamprey abundance occurred in 1961 in Lake Superior and ranged from almost 777,000 with an assumed efficiency (TE) of 66% to greater than 2.56 million with a 20% trapping efficiency (Fig. 1; ESM Table S6). In Lakes Michigan and Huron, the greatest abundance was in 1955, which was the first year of available data for Lake Michigan for our model. Peak abundance ranged from about 421,000 (TE = 66%) to over 1.39 million (TE = 20%) in Lake Michigan and from about 1 million (TE = 66%) to over 3.3 million (TE = 20%) in Lake Huron in 1955 (Fig. 1, ESM Table S6). In addition, the timing of the implementation of lampricide treatment coincided with a large decline in sea lamprey abundance in Lake Superior, but declines in abundance in Lakes Michigan and Huron began prior to the implementation of lampricide treatment (Fig. 1). Data from Lakes Erie and Ontario were sparse and the first year of available data for our model was 1978 for Lake Ontario and 1980 for Lake Erie (Fig. 1; ESM Table S6). Estimates for Lakes Erie and Ontario were more variable and did not appear to always coincide with lampricide treatment efforts. The five-year running averages of population size for each lake (ESM Fig. S1) show similar trends in abundance through time, as compared to the trends from our annual estimates (Fig. 1).

The results of the leave-one-out procedure showed that there were some streams whose data prior to 1977 could affect estimates of lake-wide population size in Lakes Superior, Michigan, and Huron, with pre-control abundances in some years changing greatly when these streams were removed (Fig. 2; ESM Tables S7–S9). In Lake Superior, the effects of this procedure are most obvious for estimates in 1960. The omission of Bad River trapping data increased estimates in 1960 by 73% (almost 1.5 million lampreys greater), whereas the omission of Brule River trapping data led to a decrease of almost 48% (1.28 million fewer; Fig. 2; ESM Table S7). In Lake Michigan, population estimates in 1956 and 1964 were most affected. In 1956, abundance estimates were 28% greater (383,483 lampreys greater) when trapping data from the Taconico River were omitted and 21% lower when the Cedar River trapping data were removed (282,485 fewer; Fig. 2; ESM Table S8). In 1964, the population estimate was twice as large when the Pere Marquette was removed as compared to using trapping data from all streams (632,708 greater). In Lake Huron, the removal of trapping data from three different streams led to increased population estimates in three different years: the Briggland in 1953 (58%; 1.05 million greater), the Koshkawong in 1955 (29%; 965,054 greater), and the Koshkawong and the Sturgeon in 1956 (141%; 2.1 million greater for each; Fig. 2; ESM Table S9).

**Discussion**

Our attempt to summarize and model lake-wide pre-control adult sea lamprey abundance highlights the data limitations and uncertainties surrounding early population estimates, but our results can provide an important tool for understanding and communicating what sea lamprey control means in the Great Lakes. The limited data available from pre-control years present difficulties for conducting a true assessment of the impact of lampricide control. However, stream-specific catches and the modeling presented here provide a sense of sea lamprey production potential prior to human intervention with treatment and when sea lamprey prey resources, such as lake trout, were plentiful. Because stream- and year-specific mark-recapture data that could be used to estimate capture efficiencies were lacking, we present a range of possible population estimates resulting from variable capture efficiencies (range: 20%–66%). Heinrich et al. (2003) suggested 66% capture efficiency during previous attempts to estimate Lake
Fig. 1. Estimates of lake-wide adult sea lamprey abundance in Lakes A) Superior (1953–2014), B) Michigan (1955–2014), C) Huron (1953–2014), D) Erie (1980–2014), and E) Ontario (1978–2014). Abundance was estimated assuming a trapping efficiency (TE) of 20, 40, and 66% for data collected prior to 1977. Trapping efficiency for the time period 1977–2014 was calculated based on stream specific mark-recapture estimates. Therefore, there is only one estimate of sea lamprey abundance for each lake during this later time period. Dotted grey line depicts the cumulative proportion of streams treated with lampricide for a given lake.
Superior pre-control abundances, and though early electric weirs (the predominant capture tool used in Lake Superior during early control efforts) can operate with high efficiency (as documented recently by Johnson et al., 2016), we believe that estimate to be high when applied to all streams. Less than seven percent of conventional sea lamprey traps operated between 1987 and the present have achieved a capture efficiency equal to or greater than 66% with a range from less than 10% to greater than 80% (USFWS, Marquette Biological Station, Marquette, Michigan USA, unpublished data; DFO, Sea Lamprey Control Centre, Sault Ste. Marie, Ontario, Canada, unpublished data). Hence we presented a wide range of TE to further highlight the potential variability and uncertainty around pre-control abundances. Given recent capture efficiencies, the previous estimates of pre-control abundance were likely conservative.

The model predicted considerably larger lake-wide pre-control adult sea lamprey abundances than previous work (Heinrich et al., 2003) when the lower trapping efficiencies were applied and is relatively sensitive to this parameter. The model used for this exercise (Mullett et al., 2003) has produced higher than expected estimates compared to mark-recapture based estimates when previously used for lake-wide abundance prediction for Lakes Superior and Ontario, potentially because of the inclusion of secondary streams in these lakes. In addition, this model has been shown to produce large fluctuations among years in estimates of adult sea lamprey as compared to more recent mark-recapture estimates based on index streams (Adams et al., This issue), a phenomenon observed when our leave-one-out analysis was conducted. Nevertheless, we believe that the estimates produced from our modeling efforts provide more clarity in the differences in adult sea lamprey abundance at the time of their greatest recorded abundance and after the implementation of control efforts and loss of their prey base.
Limited pre-control adult sea lamprey abundance data also create challenges for identifying the actual peak abundance or potential sea lamprey abundance prior to the implementation of control. In Lakes Michigan and Huron, abundance appears to already have been in decline when data collection began, and Lake Superior abundance was still increasing when lampricide treatments began. However, the estimates we present represent the peak abundances for Lakes Michigan and Huron or had those populations already declined from some higher peak? Would abundance have continued to increase in Lake Superior or did 1961 represent the peak given that prey resources (including both siscowet and lean morphotypes of lake trout) were declining from sea lamprey predation and overfishing? The collapse of lake trout in Lakes Michigan and Huron has been attributed primarily to sea lamprey predation (Coble et al., 1990), and the observed early decline in sea lamprey abundance resulted from a lack of prey (Lawrie, 1970), so it is reasonable that sea lamprey abundance could have been considerably higher when prey availability was not a limiting factor. In Lake Superior the collapse of lake trout was likely driven by a combination of sea lamprey predation and overfishing (Coble et al., 1990) and paired with the initiation of lampricide control during the late 1950s might explain the sudden and dramatic decline in sea lamprey abundance observed between 1961 and 1962. Here the modeling approach developed by Mullett et al. (2003) allowed us to estimate what adult sea lamprey abundances may have been during pre-control years and compare to current day abundance estimates.

For the upper three Great Lakes, success of the sea lamprey control program is also evident in continued low adult sea lamprey abundance in recent years (Steeves and Barber, 2020) even with increased lake trout populations resulting from stocking (Michigan and Huron) or natural reproduction (Superior; He et al., 2012; Muir et al., 2013; Modeling Subcommittee Technical Fisheries Committee, 2020). Sea lamprey are still present in the lakes, their food supply has been replenished, and with pollution abatement measures over the past 60 years many additional miles of potential larval rearing habitat are now available (Pratt, T., Great Lakes Laboratory for Fisheries and Aquatic Science, pers. comm., 2020), yet the sea lamprey population remains low. In some systems, invaders will crash back down to a new lower equilibrium state and remain there (Strayer et al., 2017). However, the potential for sea lamprey populations to rebound can be seen in the historic data as well as the modeling presented here, regardless of which trapping efficiency estimate is applied. At times the sea lamprey control program has experimented with reductions in the application of lampricide (either application process or concentration) and in those instances sea lamprey numbers began to increase (Sullivan et al., This issue). In addition, recent modeling efforts evaluating the effects of barrier removals in the Great Lakes have indicated that increasing spawning habitat without increased lampricide application will lead to much greater abundances of sea lamprey. The collapse of lake trout in Lakes Michigan and Huron has been attributed primarily to sea lamprey predation (Coble et al., 1990), and the observed early decline in sea lamprey abundance resulted from a lack of prey (Lawrie, 1970), so it is reasonable that sea lamprey abundance could have been considerably higher when prey availability was not a limiting factor. In Lake Superior the collapse of lake trout was likely driven by a combination of sea lamprey predation and overfishing (Coble et al., 1990) and paired with the initiation of lampricide control during the late 1950s might explain the sudden and dramatic decline in sea lamprey abundance observed between 1961 and 1962. Here the modeling approach developed by Mullett et al. (2003) allowed us to estimate what adult sea lamprey abundances may have been during pre-control years and compare to current day abundance estimates.

For the upper three Great Lakes, success of the sea lamprey control program is also evident in continued low adult sea lamprey abundance in recent years (Steeves and Barber, 2020) even with increased lake trout populations resulting from stocking (Michigan and Huron) or natural reproduction (Superior; He et al., 2012; Muir et al., 2013; Modeling Subcommittee Technical Fisheries Committee, 2020). Sea lamprey are still present in the lakes, their food supply has been replenished, and with pollution abatement measures over the past 60 years many additional miles of potential larval rearing habitat are now available (Pratt, T., Great Lakes Laboratory for Fisheries and Aquatic Science, pers. comm., 2020), yet the sea lamprey population remains low. In some systems, invaders will crash back down to a new lower equilibrium state and remain there (Strayer et al., 2017). However, the potential for sea lamprey populations to rebound can be seen in the historic data as well as the modeling presented here, regardless of which trapping efficiency estimate is applied. At times the sea lamprey control program has experimented with reductions in the application of lampricide (either application process or concentration) and in those instances sea lamprey numbers began to increase (Sullivan et al., This issue). In addition, recent modeling efforts evaluating the effects of barrier removals in the Great Lakes have indicated that increasing spawning habitat without increased lampricide application will lead to much greater abundances of sea lamprey (Jensen and Jones, 2018; Lin and Robinson, 2019). Here we show, despite great uncertainty around lake-wide pre-control adult sea lamprey abundance estimates, sea lamprey production potential is great, and control is necessary if the goal of limiting sea lamprey-induced mortality on host species remains a fisheries management priority.

In Lake Erie the impact of sea lamprey control in the last 20 years is less evident. Specifically, present-day abundance estimates exceed historic estimates. Lampricide applications began in Lake Erie during the mid-1980s and by the late 1980s there was a noticeable decrease in lake-wide adult sea lamprey abundance (Sullivan et al., 2003). However, by 2000 the population had surpassed pre-control levels. This lack of response to control efforts observed in adult abundance estimates may simply be the result of highly variable data. Gaps in the time series of trap data on Lake Erie, limited streams with trapping operations, and inconsistent mark-recapture estimates, make estimation of adult sea lamprey abundance more difficult for this lake. Alternatively, habitat restoration has expanded the spawning and larval habitat opportunities for sea lamprey in Lake Erie and may be driving the observed increase in abundance. When sea lamprey control efforts began in the 1980s, 9 tributaries were considered consistent producers requiring continuous treatment (Sullivan et al., 2003). As environmental clean-up efforts improved water quality around the Lake Erie watershed (e.g., Hartig et al., 2007), more sea lamprey habitat has become available (Grunder et al., This issue). During 2013–2018 an additional 12 tributaries were determined to contain larval sea lamprey populations requiring lampricide treatment. Additionally, during this timeframe sea lamprey larvae and out-migrating juveniles were collected from the St. Clair River suggesting it as a potential source of sea lamprey production (Barber et al., 2015; Grunder et al., 2021; Hinderer et al., 2016). Given the size of the St. Clair River, its production potential could dwarf all other tributaries to Lake Erie and only a fraction of the potential larval habitat could be treated during a given year (Grunder et al., This issue).

Unfortunately, conventional trap catch data were unavailable for Lake Ontario prior to 1979. The 1979 population spike observed in the model results is likely the result of those limited data. Sea lamprey control began in Lake Ontario in 1971, and the population has been stable since continuous trap catch records have been available starting in 1980. Mullett et al. (2003) noted that the models for Lakes Superior and Ontario tended to overestimate the abundance of adult sea lamprey in streams where the population estimates from mark-recapture data were low. Prior to 1985, there were no data available for mark-recapture estimates and very little data on trap catches (as shown in Fig. 1E). Therefore, the large change in abundance estimates 1978–1980 could be an artifact of using trap catch data from only two streams, the Grindstone and Little Salmon rivers, which showed a fairly large change in catch among those years.

The GLFC uses lake-wide adult sea lamprey abundance estimates from the pre- versus post-lampricide eras when communicating to the public, to managers, and to policy makers to illustrate sea lamprey damage potential in the Great Lakes and thus justify the continuation of sea lamprey control. Lawrie (1970) described sea lamprey control as an “ongoing social service that will require continued evaluation to determine if the return warrants the investment.” Here we present the raw data upon which many of the pre-control versus post-control comparisons are based, along with the caveats and uncertainties that should be considered. Previous attempts to estimate the impact of sea lamprey control (Heinrich et al., 2003) assumed a trapping efficiency considerably higher than current trapping efficiency rates. If trapping efforts were not as effective as previously assumed these previous assessments were likely conservative; and, as we present here, sea lamprey abundances may have been considerably higher prior to the implementation of lampricide control.

Conclusion

Adult sea lamprey populations in the Great Lakes have been controlled through application of lampricides and use of barriers to upstream migration during spawning runs. Data from early trapping efforts on streams in the upper Great Lakes indicated that populations were likely much larger prior to lampricide control, but exact methods for any previous estimates of pre-control abundances were unavailable. We found sea lamprey populations likely were much larger prior to implementation of lampricide control, but that population estimates were very sensitive to the assumed trapping efficiency for data collected prior to the onset of control. Sea lamprey populations in some lakes appeared to be declining.
prior to implementation of lampricide control, likely because of a coincident loss of their preferred prey, lake trout. However, we note that sea lamprey abundance remains at a fraction of our estimates of historical abundance, despite the rehabilitation of lake trout populations in the upper Great Lakes, likely because of continued sea lamprey control efforts in the Great Lakes basin.

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.

Acknowledgments

We thank G. Bravener, P. Hrodey, and S. Lewandoski for providing trapping and control information, J. Adams for review of an early version of this manuscript, J. Barber for providing code and data for the original adult abundance model, H. Lin for discussions regarding analysis, and J. Robinson for helpful suggestions for analysis and R code. We also thank T. Steeves, N. Johnson, and two anonymous reviewers for helpful comments on this manuscript. This work was supported by the USDA National Institute of Food and Agriculture, Hatch project 1012487. Use of trade, firm, or product names is for descriptive purposes only and is not an endorsement by the U.S. Government. This is publication no. 2021-07 of the Quantitative Fisheries Center.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jglr.2021.04.002.

References

Adams, J.V, Barber, JM., Bravener, G.A., Lewandoski, S.A. (this issue). Quantifying Great Lakes sea lamprey populations using an index of adults. J. Great Lakes Res. (this issue)

Barber, J., Bravener, G., and Adams, J. V., 2015. Estimating Lake Erie juvenile abundance and assessing survival of migrating juveniles in the St. Clair - Detroit River System. Great Lakes Fishery Commission Completion Report, Ann Arbor, Michigan, USA. http://www.glfc.org/pubs/pdf/research/reports/Barber_2015_0603.pdf, July 30, 2020.

Bryan, M.B., Zalinski, D., Fileck, K.B., Libants, S., L., W., Scribner, K.T., 2005. Patterns of invasion and colonization of sea lamprey (Petromyzon marinus) in North America as revealed by microsatellite genotypes. Mol. Ecol. 14, 3757–3773.

Christie, G.L., Goddard, C.J., 2003. Sea lamprey international symposium (SLS II), advances in the integrated management of sea lampreys in the Great Lakes. J. Great Lakes Res. 29 (Suppl 1), 1–14.

Coble, D.W., Bruesewitz, K., Fratt, T.W., Scheiter, J.W., 1990. Lake trout, sea lamprey, and overfishing in the upper Great Lakes: a review and reanalysis. Trans. Am. Fish. Soc. 119, 985–995.

Eshenroder, R.L., 2009. Comment: mitochondrial DNA analysis indicates sea lamprey are indigenous to Lake Ontario. Trans. Am. Fish. Soc. 138, 1178–1189.

Hun, J.B., Youngs, W.D., 1980. Role of physical barriers in the control of sea lamprey (Petromyzon marinus) as related to lamprey abundance, prey abundance, and sea lamprey control. Can. J. Fish. Aquat. Sci. 37, 1811–1817.

Hinderer, J.L.M., Adams, J., Bennion, D., Jubar, A., Neave, F., Faust, M., Siefkes, M., 2016. Have water quality changes in the Huron-Erie Corridor contributed to increases in Lake Erie sea lamprey populations? Great Lakes Fishery Commission Completion Report, August 17, 2016. Ann Arbor, Michigan USA, http://www.glfc.org/pubs/pdf/research/reports/2014_HIN_76005.htm.

Howell, J.H., Lech, J.J., Allen, J.L., 1980. Development of sea lamprey (Petromyzon marinus) larvae. Can. J. Fish. Aquat. Sci. 37, 2103–2107.

Hun, J.B., Youngs, W.D., 1980. Role of physical barriers in the control of sea lamprey (Petromyzon marinus). Can. J. Fish. Aquat. Sci. 37, 2118–2122.

Jensen, A.J., Jones, M.L., 2018. Forecasting the response of Great Lakes Sea lamprey (Petromyzon marinus) to barrier removals. Can. J. Fish. Aquat. Sci. 75, 1415–1420.

Johnson, B.G.H. (ed.), 1887. Evaluation of sea lamprey populations in the Great Lakes: Background papers and Proceedings of the August 1985 Workshop. Great Lakes Fishery Commission, Special Publication 87–2, Ann Arbor, Michigan, USA. Johnson, B.G.H., Mils, S.M., O’Connell, D.M., 2001. Changes in biological characteristics of Lake Superior whitefish (Coregonus clupeaformis) in response to sea lamprey (Petromyzon marinus) as related to lamprey abundance, prey abundance, and sea lamprey control. Can. J. Fish. Aquat. Sci. 58, 2001–2013.

K.F. Robinson, S.M. Miehls and M.J. Siefkes Journal of Great Lakes Research xxx (xxxx) xxx

Lawnie, A.H., 1970. The sea lamprey in the Great Lakes. Trans. Am. Fish. Soc. 99, 415–425.

Lin, H.Y., Robinson, K.F., 2019. How do migratory fish populations respond to barrier removal in spawning and nursery grounds? Theor. Ecol. 12, 379–390. https://doi.org/10.1007/s12080-018-0405-0.

Maridens, R., Siefkes, M.J., 2019. Control of invasive sea lamprey in the Great Lakes, Lake Champlain and Finger Lakes of New York, in: Dockrill, M.F. (Ed.), Lampreys: biology, conservation, and control. Vol. 2. Fish and Fisheries Series 38, Springer, New York, New York, USA, 411–479.

Modeling Subcommittee, Technical Fisheries Committee. 2020. Technical Fisheries Committee Administrative Report 2020: Status of Lake Trout and Lake Whitefish populations in the 1836 Treaty-Ceded Waters of Lakes Superior, Huron and Michigan, with Recommended Yield and Effort Levels for 2020. https://www.greatlakesmollusks.org/documents/dm2020status-Stocks_Final_699576_7.pdf.

Muir, A.M., Krueger, C.C., Hansen, M.J., 2013. Re-establishing lake trout in the Laurentian Great Lakes: past, present, and future. In: Taylor, W.W. (ed) Great Lakes fisheries policy & management: a binational perspective. Michigan State University Press, East Lansing, pp 533–588.

Muelle, K.A., Heinrich, J.W., Adams, J.V., Young, R.J., Henson, M.P., McDonald, R.B., Pedoja, M.W., 2003. Estimating lake-wide abundance of spawning-phase sea lampreys (Petromyzon marinus) in the Great Lakes: extrapolating from sampled streams using regression models, J. Great Lakes Res. 29 (Suppl 1), 240–252.

Siefkes, M.J., 2017. Use of physiological knowledge to control the invasive sea lamprey (Petromyzon marinus) in the Laurentian Great Lakes. Conserv. Physiol. 5 (1) 0031. https://doi.org/10.1093/conphys/cox031.

Siefkes, M.J., Steeves, T.B., Sullivan, W.P., Towevo, M.B., Li, W., 2013. Sea lamprey control: past, present, and future. In: Taylor, W.W. (Ed.), Great Lakes fisheries policy & management: a binational perspective. Michigan State University Press, East Lansing, Michigan, USA, pp. 651–704.

Smith, B.R., Tible, P.J., 1980. Lake sea lamprey (Petromyzon marinus) in Lkns Huron, Michigan, and Superior: history of invasion and control, 1936–78. Can. J. Fish. Aquat. Sci. 37, 1780–1801.

Steeves, M., Barber, J., 2020. Sea lamprey control in the Great Lakes 2019. Annual report to the Great Lakes Fishery Commission, Great Lakes Fishery Commission, Ann Arbor, Michigan, USA. http://www.glfc.org/pubs/pdf/slc/p LupAnnualReports/ANNUAL_REPORT_2019.pdf.

Strayer, D.L., A’Donantio, C., Essl, F., Fowler, M.S., Geist, J., Hilt, S., Jöhnk, K., Jöhnk, K., Jones, C.G., Lambin, X., Zlatka, A.W., Pergl, J., Pyšek, P., Robertson, P., von Schmalensee, M., Stefansson, R.A., Wright, J., Jeschke, J.M., 2017. Boom-bust dynamics in biological invasions: towards an improved application of the concept. Ecol. Lett. 20, 1337–1350.

Sullivan, W.P., Christie, G.C., Cornelius, F.C., Fodale, M.F., Johnson, D.A., Koonce, J.F., Larson, G.L., McDonald, R.B., Muelle, K.A., Murray, C.C., Ryan, P.A., 2003. The sea lamprey in Lake Erie: a case history. J. Great Lakes Res. 29 (Suppl 1), 615–636.

Sullivan W.P., Burkett D.P., Boogaard M.A., Criger L.A., Freiburger C.E., Hubert T.D., Leinster K.G., Morrison B.J., Nowicki S.M., Robertson S.N.P., Rowlinson A.C., Scovil C.K, Sullivan, T.B., (this issue). Advances in the use of lampricide to control sea lampreys in the Laurentian Great Lakes, 2000–2019. J. Great Lakes Res. (this issue).

Treska, T.J., Eben, M.P., Christie, G.C., Adams, J.V., Siefkes, M.J. (this issue). A case study of setting threshold suppression targets for sea lamprey in the Great Lakes. J. Great Lakes Res. (this issue).

Waldman, J.R., Grunwald, C., Roy, N.K., Virgin, I., 2004. Mitochondrial DNA analysis indicates sea lampreys are indigenous to Lake Ontario. Trans. Am. Fish. Soc. 133, 950–960.