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# Quantifying Great Lakes sea lamprey populations using an index of adults

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ABSTRACT

Effective control of aquatic invasive species requires knowledge of the population throughout the infested area. Lake-wide assessments of invasive sea lampreys (*Petromyzon marinus*) are used to assess their status in the Laurentian Great Lakes, informing fisheries managers and decision makers in the sea lamprey control program. Initially these assessments focused on an estimate of absolute abundance, but later switched to an estimate of relative abundance as an index. In this paper, we describe the recently developed index of sea lamprey abundance and the reasons for its use. Rather than trying to estimate spawning run sizes of all Great Lakes tributaries, the index instead estimates run sizes of a small subset of index streams. Streams chosen for the index had large spawning runs and a history of trapping operations that consistently yielded mark-recapture estimates. This change enabled the sea lamprey control program to abandon a previously used regression model that predicted run size on streams with no sea lamprey traps. Further research is needed to determine how strongly correlated the index is with actual patterns in the lake-wide population of adult sea lampreys.


## Introduction

Effective control of invasive species requires population-level knowledge throughout the infested area (Lodge et al., 2016, 2006). The most informative metrics are the same as those of interest in conserving threatened species: population size, number of mature individuals, abundance trends over time, and spatial distribution (IUCN, 2012). Such assessments can be particularly challenging for diadromous and potamodromous species because individuals may be difficult to sample at times other than during seasonal migrations. We explore these challenges and the state of the science in deriving an annual assessment of invasive sea lampreys (*Petromyzon marinus*) in the Laurentian Great Lakes.

Sea lampreys invaded the Great Lakes in the early 1900s and had replaced the top native predator, lake trout (*Salvelinus namaycush*), in the ecosystem by the 1950s (Hile, 1949; Hile et al., 1951a, 1951b; Smith and Tibbles, 1980). Control efforts and attempts to assess populations of sea lampreys began in the 1950s (Lawrie, 1970; Smith and Tibbles, 1980). These early efforts included trapping adult sea lampreys as they migrated up Great Lakes tributaries to spawn. The annual number of adult sea lampreys trapped continued as a means of assessment into the 1980s (Schuldt and Heinrich, 1982). By the late 1990s, the Great Lakes Fishery Commission began developing a process to derive lake-wide estimates of adult sea lamprey populations (Mullett et al., 2003).

Lake-wide assessments focused on adult sea lampreys, the most accessible life stage. Sea lampreys live their first 3–7 years as lar-

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vae burrowed in the bottom sediment of streams (Potter, 1980). The larval life stage is susceptible to chemical control (Applegate, 1950) and to sampling via electrofishing (Bergstedt and Genovese, 1994). However, the spatial extent of their distribution and the labor-intensive nature of sampling makes derivation of a lake-wide index of larval abundance cost inefficient (Hansen and Jones, 2008). In addition, larvae in any stream are a mix of age classes, age is not easily predicted, and age at transformation is not fixed (Dawson et al., 2021; Slade et al., 2003). Sea lampreys then transform into juveniles and migrate downstream to the lake in search of their first host to parasitize. This is the damaging life stage, most readily evidenced in victims of their attacks (either through mortality or wounds and scars) and of great interest to fisheries managers. However, the juvenile stage is the least susceptible to human capture (Young et al., 2003). Mark-recapture estimates have been attempted for recently metamorphosed and juvenile sea lampreys with mixed success (Bergstedt et al., 2003; Young et al., 2003). After 12–18 months in the lake, sea lampreys mature and migrate up streams to spawn and die. During this spawning migration, sea lampreys are susceptible to capture, especially at barriers where they concentrate in areas conducive to trapping.

The first attempt at generating lake-wide abundance estimates of sea lampreys, henceforth called the Mullett Method (Mullett et al., 2003), used a regression model that predicted spawning run size from drainage area and other metrics. The Mullett Method was used to assess the status of invasive sea lampreys in the Great Lakes and inform fisheries managers in the sea lamprey control program during 2000–2014. Specifically, the status of sea lamprey populations was determined by (1) comparing the three-year average adult abundance to a limit threshold (a "target" as defined by Treska et al., 2021) and (2) evaluating the five-year linear trend in abundance. The status of sea lampreys in each lake was used to gauge the performance of past control efforts and determine if and where additional control effort was needed in the future. For example, when the abundance of adult sea lampreys in Lake Erie was observed well above the limit threshold, the Great Lakes Fishery Commission responded by increasing control effort on Lake Erie tributaries in 2008 and 2009 (Newton et al., 2016). The Mullett Method has been cited in the peer-reviewed literature 59 times (www.webofknowledge.com, accessed 27 Jul 2020), on topics including alternative control strategies (Bergstedt and Twohey, 2007; Bravener and Twohey, 2016; Jones et al., 2003; Twohey et al., 2003), trapping performance (Bravener and McLaughlin, 2013; Holbrook et al., 2016), barrier removals (Jensen and Jones, 2018; Miehls et al., 2020), population dynamics (Dawson and Jones, 2009; Jones, 2007), parasite-host interactions (Bence et al., 2003; Madenjian et al., 2003), and status of native host fish populations (Brenden et al., 2010; Madenjian et al., 2004; Stapanian et al., 2010).

When conceived, the Mullett Method had two known shortcomings that were deemed tolerable: the unaccounted attraction of native lampreys (*Ichthyomyzon* spp. and *Lethenteron appendix*) and extrapolated stream estimates. The method took into account the influential presence of sea lamprey larvae in streams; they excrete pheromones that attract adult sea lampreys during their spawning migration (Sorensen and Vrieze, 2003). The attraction of larval sea lampreys was incorporated in the method via a negatively correlated surrogate, the stream-specific number of years since last lampricide treatment. However, the presence of native lampreys upstream of barriers to sea lamprey migration was not incorporated, although they also release a chemical cue attractive to migrating sea lampreys (Fine et al., 2004; Mullett et al., 2003; Sorensen and Vrieze, 2003). The second shortcoming was the extrapolation of predictions to unsampled streams with drainage areas beyond the sampled range. During deployment of the Mullett Method, other deficiencies (enumerated in the *Methods* section) became apparent, including one that caused large fluctuations in estimates unrelated to actual annual changes in sea lamprey abundance. In 2015, an alternative approach to quantifying trends in adult sea lamprey populations was adopted.

In this paper, we describe an index of adult sea lamprey abundance, henceforth called the Adult Index, currently in use as a status metric of sea lamprey populations of the Great Lakes. In the Methods section, we detail the derivation of the Adult Index and highlight weaknesses of the Mullett Method that were ameliorated by it. We organize the methods around key specifications in any survey design: objectives, target population, method of measurement, experimental unit, sample selection, and summary of data (Cochran, 1977). In the Discussion section, we expand on assumptions of the Adult Index and research directions that could address them.

## Methods

The purpose of annual assessments of adult sea lampreys was to quantify the population of each Great Lake such that trends could be tracked over time on a lake-wide scale. Because the focus is on relative (not absolute) abundance, the presence of systematic bias will not affect the performance of the estimates in their representation of temporal patterns. The target populations included all adult sea lampreys in each Great Lake in a given calendar year. In this section, we first discuss how adult sea lampreys were assessed at the stream scale, then address how streams were chosen for the Adult Index, and end with the culmination of estimates at the lake-wide scale.

### *Stream spawning run size*

Sea lampreys were trapped during their spring migration as they ascended Great Lakes tributaries to spawn. Mark-recapture estimates of spawning run size at release locations were used rather than trap catches alone, so improvements to (or experiments with) trapping operations could proceed without affecting lake-wide adult estimates. Otherwise, an index based on trap catches alone would be subject to variation due to annual changes in catchability.

Initial captures and recaptures typically occurred at a single trap location in each river. Sea lampreys were captured at the trap location, marked, and released downstream, with the intent of estimating the number of adults that passed the release location. Traps were checked almost daily (5–7 days per week). The proportion of captured sea lampreys marked and released was based on the expected number of recaptures (Table 1). For streams with historically large spawning runs and high estimated trap efficiencies (proportions trapped), the proportion marked was low. For streams with historically small spawning runs and moderate trap efficiencies, the proportion marked was high. A maximum was placed on the number marked per day to minimize handling stress and ensure marked sea lampreys were in good health after transport to the release location. No sea lampreys were marked and released during the final week of trapping.

These methods were largely unchanged since the Mullett Method, with one important exception. In 2017, the sea lamprey control program discontinued use of the modified Schaefer estimator (Mullett et al., 2003; Schaefer, 1951) in favor of the adjusted pooled Petersen estimator (Seber, 1982, 1970). The pooled Petersen estimator performs better than the Schaefer and other estimators in terms of accuracy and precision with large sample sizes and was more accurate than the Schaefer estimator with small sample sizes (Harper et al., 2018). Specifically, the Schaefer method under-

**Table 1**
Index streams for assessment of Great Lakes sea lampreys. Information includes lake, stream name, trapping location (Longitude, Latitude), distances (in km) from trapping location downstream to release location (Release) and lake (Lake), the proportion of captured sea lampreys that were marked and released (Marked), and the maximum number of sea lampreys marked per day (Daily cap, dashes indicate no upper limit). The proportion marked and released changed periodically, based on mean catch in recent years; those reported here were for the 2020 field season. Note that for the Echo River, the reported distance to the lake is actually the distance to the mouth of the Echo River, which empties into the St. Marys River.

| Lake | Stream | Longitude | Latitude | Release (km) | Lake (km) | Marked (%) | Daily cap |
|---|---|---|---|---|---|---|---|
| Superior | Middle River | −91.81 | 46.65 | 8.37 | 8.5 | 100 | 30 |
| Superior | Brule River | −91.60 | 46.70 | 10.14 | 10.3 | 100 | 30 |
| Superior | Bad River | −90.68 | 46.51 | 26.23 | 36.5 | 100 | 20 |
| Superior | Neebing River | −89.28 | 48.39 | 1.30 | 5.4 | 100 | – |
| Superior | Rock River | −86.92 | 46.46 | 0.13 | 0.1 | 50 | – |
| Superior | Tahquamenon River | −85.21 | 46.60 | 24.94 | 24.9 | 50 | 30 |
| Superior | Betsy River | −85.07 | 46.71 | 13.04 | 13.7 | 100 | 30 |
| Michigan | Peshtigo River | −87.75 | 45.05 | 17.38 | 20.1 | 10 | 60 |
| Michigan | St. Joseph River | −86.33 | 41.94 | 38.62 | 39.6 | 50 | 20 |
| Michigan | Manistique River | −86.25 | 45.97 | 2.12 | 2.4 | 10 | 60 |
| Michigan | Betsie River | −86.08 | 44.60 | 20.28 | 23.2 | 20 | 20 |
| Michigan | Big Manistee River | −85.94 | 44.26 | 28.00 | 51.8 | 100 | 20 |
| Michigan | Carp Lake Outlet | −84.83 | 45.75 | 0.24 | 0.5 | 10 | – |
| Huron | Cheboygan River | −84.48 | 45.64 | 1.77 | 2.7 | 10 | 50 |
| Huron | St. Marys River | −84.35 | 46.51 | 3.48 | 70.0 | 10 | – |
| Huron | Ocqueoc River | −84.11 | 45.48 | 5.79 | 6.1 | 10 | 50 |
| Huron | Echo River | −83.94 | 46.57 | 14.70 | 17.7 | 10 | – |
| Huron | East Au Gres River | −83.70 | 44.22 | 4.51 | 26.9 | 50 | 20 |
| Huron | Bridgeland Creek | −83.55 | 46.30 | 1.70 | 10.0 | 10 | – |
| Erie | Grand River | −80.94 | 41.76 | 13.52 | 50.5 | 100 | 20 |
| Erie | Little Otter Creek | −80.83 | 42.75 | 17.60 | 24.6 | 100 | – |
| Erie | Big Creek | −80.50 | 42.76 | 3.70 | 40.5 | 20 | – |
| Erie | Young's Creek | −80.26 | 42.76 | 0.25 | 0.4 | 100 | 25 |
| Erie | Cattaraugus Creek | −78.70 | 42.48 | 48.28 | 53.3 | 100 | 30 |
| Ontario | Humber River | −79.50 | 43.65 | 1.50 | 4.1 | 10 | – |
| Ontario | Duffins Creek | −79.06 | 43.85 | 2.80 | 6.5 | 50 | – |
| Ontario | Bowmanville Creek | −78.69 | 43.91 | 1.70 | 3.8 | 50 | 25 |
| Ontario | Sterling Creek | −76.65 | 43.32 | 6.12 | 8.5 | 100 | 20 |
| Ontario | Black River | −76.04 | 44.00 | 0.32 | 2.4 | 50 | 20 |

estimated population size when small numbers of animals were recaptured. Using the pooled Petersen estimator (with a modification by Chapman (1951)) allowed for more efficient field operations (no different weekly marks to keep track of) with fewer errors and more streamlined data management and estimation,

$$\tilde{N} = \frac{(M+1)(C+1)}{(R+1)} - 1$$

with variance

$$Var\left(\tilde{N}\right) = \frac{(C+1)(M+1)(C-R)(M-R)}{(R+1)^2(R+2)},$$

where $M$ is the total number marked, $C$ is the total number captured during the recapture period, and $R$ is the number of marked animals recaptured (Seber, 1970). Spawning run size at the release location was estimated using the pooled Petersen equation with two adjustments: (1) the subtraction of $R$ from $C$ to avoid double counting sea lampreys that ascended to the trapping location twice (Mullett et al., 2003) and (2) the addition of $P$, the number captured up to and including the first day of marking, to ensure captures made prior to the recapture period were counted,

$$\hat{N} = \frac{(M+1)(C-R+1)}{(R+1)} - 1 + P$$

with variance

$$Var\left(\hat{N}\right) = \frac{(C-R+1)(M+1)(C-2R)(M-R)}{(R+1)^2(R+2)}$$

Mark-recapture estimates were only calculated if at least three sea lampreys were recaptured ($R \geq 3$, Ricker, 1975).

In the event that no mark-recapture estimate was available from a given stream in a given year, an alternative estimate was used. For the Mullett Method, trap catch was divided by the historical mean trap efficiency at that trap (Mullett et al., 2003). Trap catch estimates performed well, but were complex; the trapping history of each stream had to be divided into periods of time (trapping periods) during which trap efficiencies were assumed constant.

If no trap catch was available for a given stream-year, then the Mullett Method used an estimate derived from a linear regression on drainage area (a surrogate for stream discharge), lake region, production potential (based on the stream's lampricide treatment history), the number of years since the stream was last treated (to represent the migratory pheromone signal from the building larval population), and year (a surrogate for basin-wide annual environmental effects; Mullett et al., 2003). The regression was originally intended to be applied only to streams without sea lamprey traps, as a way to scale up run size estimates on individual streams to a lake-wide population estimate. However, in practice, it was also applied to streams with intermittent trap operations (encompassing 40 streams during 1995–2014). This decision had serious unintended consequences, because for an individual stream, mark-recapture and drainage-regression run size estimates sometimes differed by an order of magnitude (estimates for 18 streams differed by factors <2, 18 streams by 2–10, 2 streams by 10–20, and 2 streams by factors >40; e.g., Fig. 1).

For the Adult Index, if no mark-recapture estimate was available, an estimate was derived from a lake-specific, weighted least squares, two-way analysis of variance (ANOVA) with main effects only (no interaction term). The response was the natural log of the mark-recapture estimate of the spawning run size at the release location ($Y = ln(\hat{N})$), and the independent categorical variables were stream and year. Responses were weighted by the inverse of the coefficient of variation squared ($1/CV^2 = \hat{N}^2/Var(\hat{N})$), such that run sizes estimated with greater precision were given more weight. The analysis was carried out

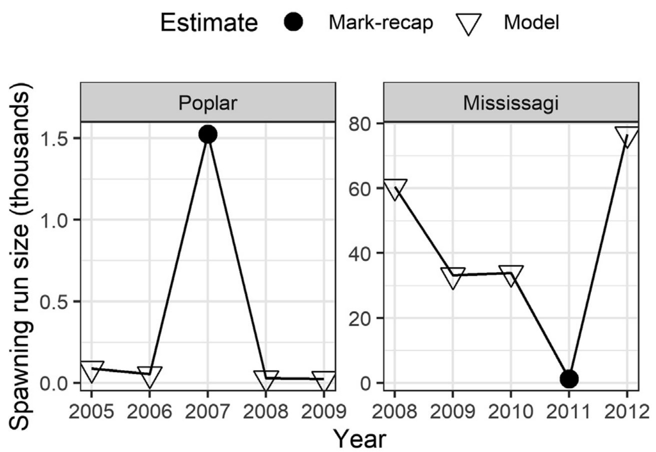


**Fig. 1.** Example of perturbations introduced to times series of sea lamprey spawning run size in Great Lakes tributaries by switching between estimates from mark-recapture studies and those from a drainage area-based linear regression. The Poplar River is a tributary of Lake Superior ($N46.69^{\circ}$, $W91.80^{\circ}$); the Mississagi River is a tributary of Lake Huron ($N46.17^{\circ}$, $W83.02^{\circ}$).

using R statistical software (R Core Team, 2018). Predicted values were calculated from the ANOVA on the back-transformed scale as

$$P = exp[\widehat{Y} + \widehat{\sigma}_Y^2/2] \ ,$$

with variance

$$Var(P) = exp(2\widehat{Y} + 2\widehat{\sigma}_Y^2) - exp(2\widehat{Y} + \widehat{\sigma}_Y^2)$$

where $\widehat{\sigma}_Y^2$ is the mean squared error from the ANOVA (Mood et al., 1974).

### Index streams

Rather than try to estimate spawning run sizes of sea lampreys in all Great Lakes tributaries, the Adult Index focused on a subset of index streams with a history of consistently yielding mark-recapture estimates. Streams with large spawning runs were targeted, but streams with smaller runs were also included if they provided better geographic coverage of the basin. Streams were ranked based on the median mark-recapture population estimates during 1995–2014 and the weighted proportion of years with mark-recapture estimates, with more weight given to recent estimates. The top ranking streams within each lake were selected, and additional streams were included to ensure adequate geographic coverage where possible. The sampled population thus included only adult sea lampreys that passed the release locations (downstream of the traps) in index streams of the Great Lakes.

As with any survey design, the resulting estimate requires the assumption that the sampled population is representative of the target population. In this case, sea lamprey spawning run sizes observed at index stream release locations are assumed to be representative of lake-wide patterns in adult sea lamprey abundance (Table 2). Year-to-year shifts in the proportion of adult sea lamprey moving into index streams could violate this assumption and be a source of observation variance in the Adult Index. Correlation analysis was used to quantify how well temporal patterns were represented by small subsets of streams. We used the Adult Index from years with no missing mark-recapture estimates as the benchmark temporal pattern for each lake (with a minimum sample size of 10 years). Then, for each lake, we took all possible subsets of two streams and calculated the Pearson correlation coefficient between the Adult Index and the sum of the mark-recapture estimates from the two subset streams. This approach was repeated for subset sizes of three and four streams.

**Table 2**
Summary of key assumptions required for the Adult Index to represent relative sea lamprey abundance in the Great Lakes, including the component and the average proportion of index streams affected by each assumption.

| Component | Proportion | Assumption |
|---|---|---|
| Survey design | 100% | Run size observed at index stream release locations representative of lake-wide patterns |
| Mark-recapture estimate of stream run size | 90% | Same capture probability of marked and unmarked fish |
| | | Random mixing of marked and unmarked fish |
| ANOVA estimate of stream run size | 10% | Annual changes in run size consistent among streams (no year*stream interaction) |
| | | Relative run sizes in stream consistent over time (no year*stream interaction) |

### Lake-wide total

Stream spawning run size estimates for sea lampreys in a given lake and year ($\widehat{N_i}$ and $P_i$, where $i$ represents index streams) were summed to calculate relative abundance on a lake-wide scale. The variance of the total ($T$) was calculated as the sum of the variances of the run size estimates, $Var(T) = \sum_i [Var(\widehat{N_i}) + Var(P_i)]$. This approach is similar for both the Mullett Method and the Adult Index, with a few important differences.

First, for the Mullett Method, the total was regarded as an estimate of absolute abundance, whereas for the Adult Index, the total was regarded as an estimate of relative abundance. This is an important distinction, as one of the shortcomings of the Mullett Method was the application of the drainage-regression to streams with drainage areas larger than those used to inform the regression. Extrapolations, especially on the log scale, are highly susceptible to error (Hahn, 1977). Setting aside the issue of streams with mixed estimate types (addressed in the *Index streams* section), the inclusion of drainage-regression estimates from unassessed streams in a lake-wide total would have only changed the scale of the total, but not its pattern over time.

Second, the Mullett Method totaled estimates for every lake year, regardless of the source of the estimates. The Adult Index was only calculated for a given lake and year if it had at least two index streams with mark-recapture estimates of spawning run sizes. This minimum requirement was chosen based on expert elicitation of sea lamprey managers who wished to reduce gaps while maintaining confidence in the lake-wide time series.

Third, for the Mullett Method, trap catch and drainage-regression estimates were recalculated every year, after new mark-recapture estimates and trap catches from the latest year of trapping were summarized. This resulted in an ever-changing time series of lake-wide estimates, which frustrated and confused fisheries managers and decision makers. For the Adult Index, although the ANOVA was re-fit every year as new data were added, historic estimates were left unchanged, unless some other change in the Adult Index was made. Although this was intended to contribute to a more stable time series, in practice, minor changes to the Adult Index occurred frequently, leading to an updated time series every 1–3 years. We expect this pattern to continue into the future. Given the length of the time series at this point (31–34 years), newly derived ANOVA estimates based on the addition of 1–3 years (<10%) of data would be little changed from historical estimates.

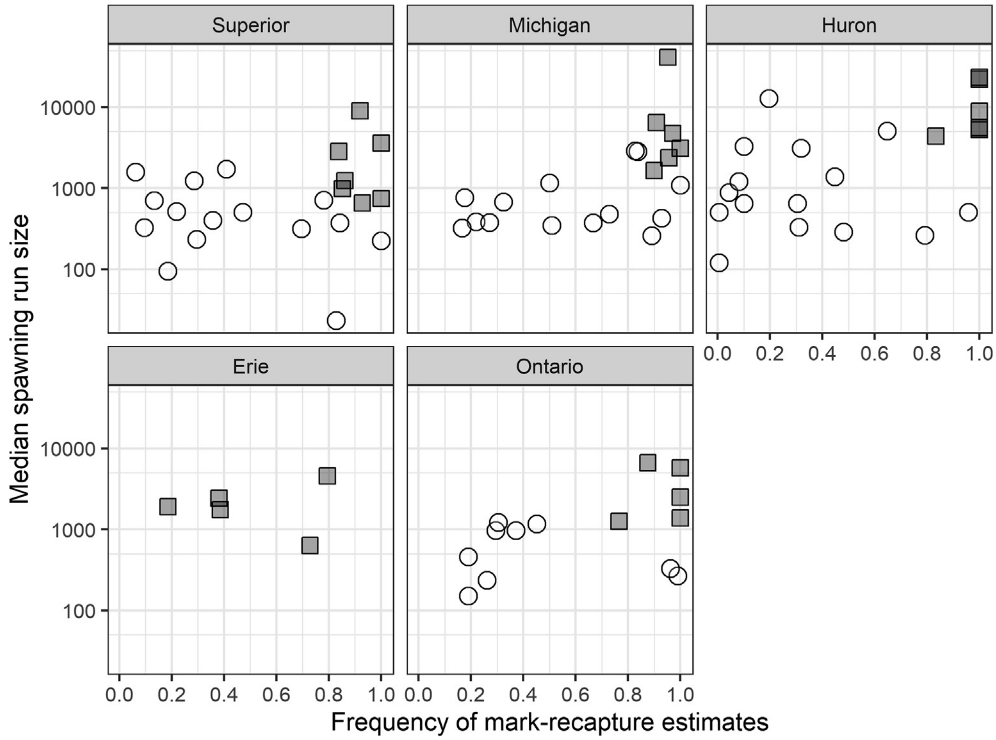


**Fig. 2.** Summary of trapping operations during 1995–2014, used to select index streams for assessment of adult sea lampreys in the Great Lakes. The 29 index streams (gray squares) were chosen for their large spawning run sizes and high frequency of mark-recapture estimates. The relative frequency of estimates was calculated as the mean proportion of years with a mark-recapture estimate, weighted by the number of years since 1994.

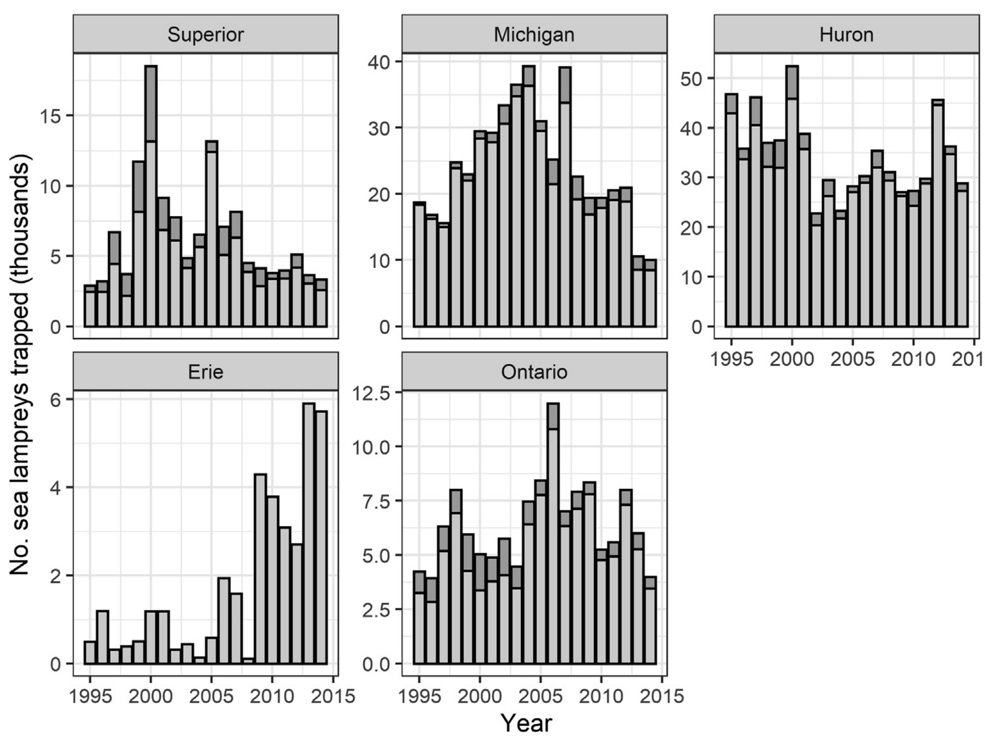


**Fig. 3.** Trap catch of adult sea lampreys during upstream spawning migration in the Great Lakes Basin, 1995–2014. Shading represents source stream: light gray for index streams, dark gray for non-index streams.

## Results

In this section, we first address the selection of index streams, then report results of the correlation analysis and the ANOVA, and end with the lake-wide estimates of relative abundance.

Of the 258 streams in the Mullett Method (Mullett et al., 2003), 82 had at least one mark-recapture estimate during 1995–2014. Most of these streams did not consistently yield mark-recapture estimates; fewer than nine streams in each lake had mark-recapture estimates at least 90% of the time (Fig. 2). Twenty-nine

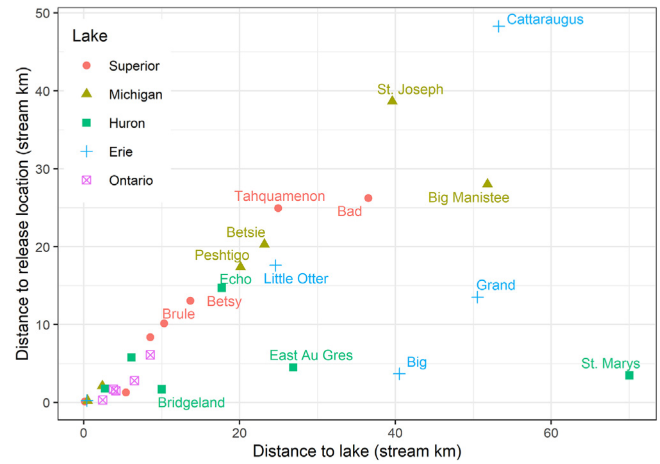


**Fig. 4.** Locations of sea lamprey traps in Great Lakes index streams expressed as distance upstream of the release location and the lake. Stream names are provided when trapping locations were ≥10 km from the release location or lake.

were selected as index streams to assess sea lamprey populations. Trapping ceased on 43 of the remaining 53 streams, with 10 continuing due to obligations with landowners and fisheries managers. Elimination of trapping locations on 43 Great Lakes tributaries reduced the number of streams trapped and simplified the annual field season for sea lamprey control agents, the U.S. Fish and Wildlife Service and Fisheries and Oceans Canada.

Four of five lakes had several streams that yielded mark-recapture estimates ≥ 75% of the time (Fig. 2). Lake Erie had only five streams with at least one mark-recapture estimate during 1995–2014, so all five were chosen as index streams. Three of those streams yielded mark-recapture estimates <50% of the time during 1995–2014. All trapped streams with a median spawning run size >5000 were selected as index streams for four lakes (Fig. 2). Lake Huron had two tributaries (both in Michigan) with large run sizes that did not consistently yield mark-recapture estimates: the Tittabawassee River with median run size 12,800 and mark-recapture estimates 20% of the time, and the Au Sable River with median run size 5,100 and mark-recapture estimates 65% of the time.

Because selection of index streams with large spawning run sizes was prioritized, the number of sea lampreys trapped for the Adult Index comprised the vast majority of the total catch of all streams included in the Mullett Method. During 2005–2014, an average of 70,000 sea lampreys were captured each year and an average of 92% (range 88–95%) of them were trapped in index streams (Fig. 3). Trapping locations in index streams varied in their distance from the lake (ranging from 0.1 to 70 km) and the release location (ranging from 0.1 to 48 km) for mark-recapture estimation (Fig. 4).

For the correlation analysis, four of the Great Lakes had at least 10 years with adult sea lamprey mark-recapture estimates in all index streams (Fig. 5). Benchmark temporal patterns were thus represented by 11 years in Lake Superior, 18 in Michigan, 22 in Huron, and 19 in Ontario. Lake Erie, with only three years of non-missing mark-recapture estimates, was excluded from the analysis. For Lakes Michigan, Huron, and Ontario a subset of only two streams was needed to yield a temporal pattern that was significantly correlated with the benchmark pattern in at least 75% of the subsets (Fig. 6). For Lake Superior, a subset of three streams was needed to achieve the same threshold.

Pooled Petersen mark-recapture estimates of spawning run sizes varied with stream and year. During 2010–2019, the

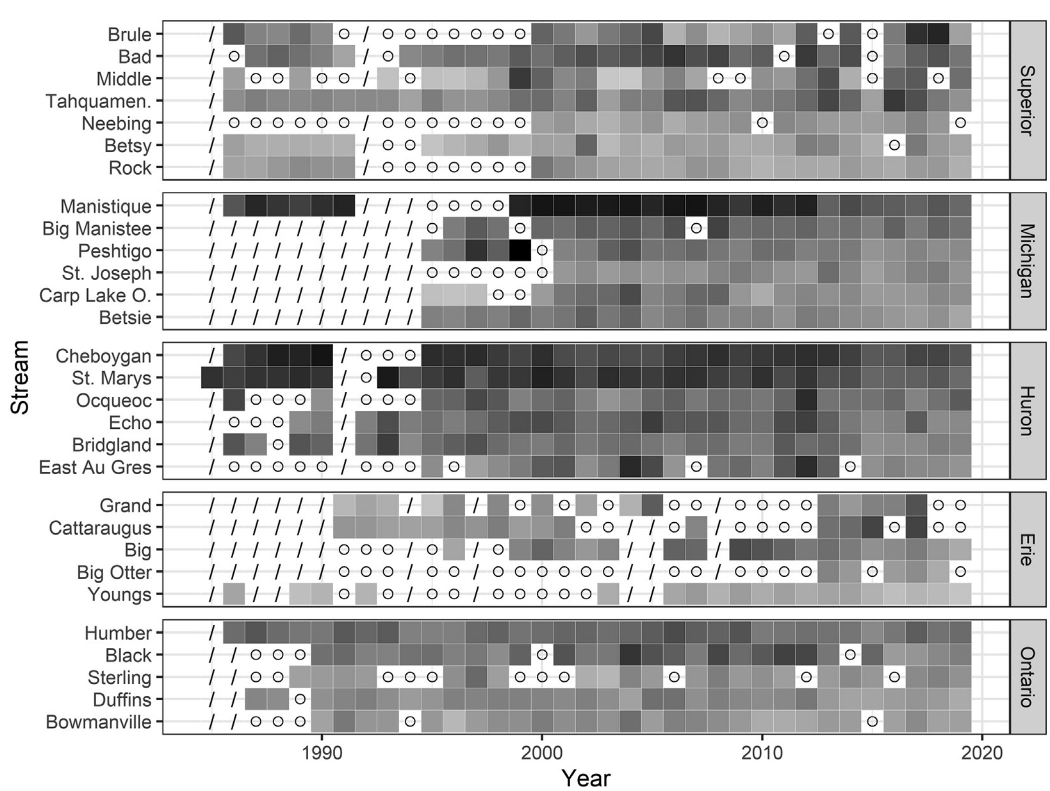


**Fig. 5.** Availability of mark-recapture estimates of sea lamprey spawning run size in Great Lakes index streams, 1985–2019. Darker shading represents stream-years with higher estimated run sizes at release locations. Symbols represent missing data, circles for stream-years with ANOVA estimates, and slashes for missing data in years with fewer than two mark-recapture estimates.

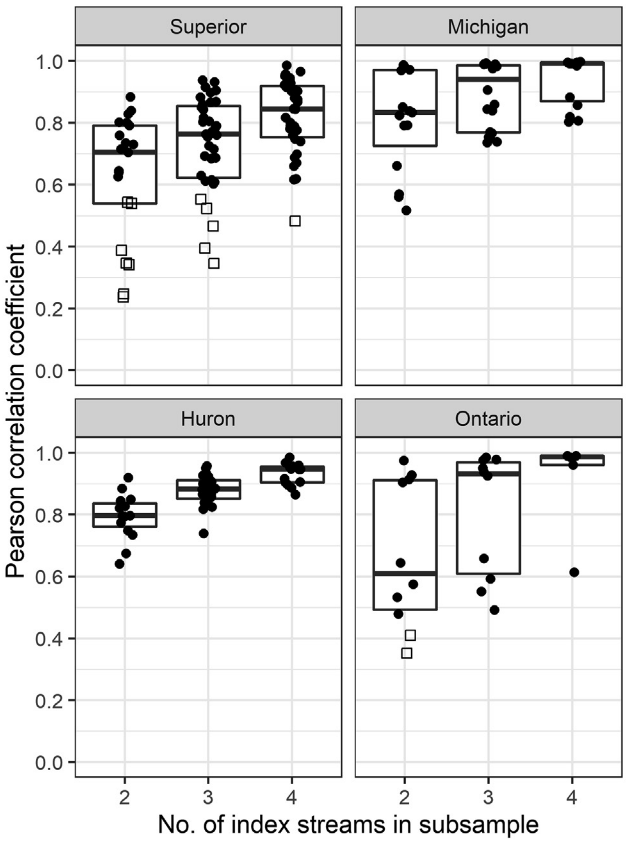


**Fig. 6.** Correlation of the Adult Index and the sum of the mark-recapture estimates from all possible subsets of streams, with subset sizes from two to four. Plot symbols represent significance of the correlation at the $\alpha = 0.05$ level: black circles significant, white squares insignificant. Boxes indicate the first, second, and third quartiles.

percentage of stream-years with mark-recapture estimates averaged 90% over all five Great Lakes (87% in Lake Superior, 100% in Michigan, 98% in Huron, 68% in Erie, and 92% in Ontario). The ANOVA was used to fill in the gaps for the 10% of stream-years missing mark-recapture estimates (Fig. 5). The ANOVA fit the data well with coefficients of determination ranging from $R^2$ = 78 to 94% (Table 3, Fig. 7). The median spawning run size estimate during 2015–2019 varied spatially, with relatively large and small run sizes in each lake (Fig. 8). Historic trap efficiencies of index streams varied widely, even within streams (Fig. 9).

Time series of mark-recapture spawning run size estimates, with ANOVA predictions filling in gaps, were combined to derive the lake-wide Adult Index (Fig. 10). Four lakes have had an annual estimate of adult sea lampreys every year since 1995. Lake Erie had several gaps corresponding to years in its time series (1994, 1997, 2004, 2005, and 2008) where fewer than two index streams yielded mark-recapture estimates (Fig. 2).

## Discussion

The Adult Index was designed to improve upon the Mullett Method in tracking trends in Great Lakes sea lamprey populations. One benefit of using indices rather than absolute abundance estimates is the removal of many potential biases by using the same sites in successive years (Greenwood et al., 1993). Quantifying the total number of adult sea lampreys in a Great Lake poses several challenges that the Mullett Method was unable to overcome: extrapolation to streams without barriers, extrapolation to streams with drainage areas larger than any stream trapped, and the assumption that estimated run size at the release location represents the entire spawning run of a stream (even when release locations were sometimes >10 km upstream of the stream mouth, Fig. 4). The application of the drainage-regression to intermittently trapped streams introduced large shifts in the lake-wide abundance time series, shifts caused by the estimation process itself not by underlying changes in sea lamprey abundance. These perturbations and their influence on the lake-wide estimates were a key factor in the decision to abandon the drainage-based regression and focus on index streams with a rich trapping history. This spared the program from having to (1) derive an appropriate drainage area for release locations, (2) arbitrarily define lake regions, (3) rely on a fixed categorization of production potential (which likely varies over time), (4) establish time periods during which trap efficiency was assumed constant, and (5) determine a treatment threshold for each stream that could be used to quantify the number of years since the stream was last treated with lampricide (often only a portion of a stream system was treated with lampricide in a given year). Instead, the Adult Index relies solely on stream-specific run size information.

Index streams were chosen from among those with historically successful trapping operations, which largely relied on portable traps at barriers. Increasing the number of permanent traps integrated with barriers to sea lamprey migration (Miehls et al., 2020), particularly in larger river systems that consistently recruit sea lamprey larvae, may be an effective approach to increasing the robustness of the index network. Improvements in trapping to consistently yield mark-recapture estimates should be prioritized on Lake Erie tributaries and two Lake Huron streams with large runs (Tittabawassee and Au Sable, previously mentioned). Plans are underway for trapping improvements on Cattaraugus Creek, and a new barrier integrated trap was recently constructed on the Grand River (both tributaries to Lake Erie). Extension of mark-recapture estimation to other streams with potentially large sea lamprey spawning runs requires advancements in the capture efficiency of traps not associated with barriers (e.g., via semiochemicals, Hume et al., 2020; Fissette et al., 2021). Such advancements would increase the number of candidates that could be considered to be index streams, possibly enabling a selection process that incorporates randomization.

The reduction in trapping operations caused by the switch to the Adult Index had minimal impact on the quantity and quality of information gathered on sea lamprey spawning runs, because

**Table 3**
Summary of two-way ANOVAs fitting the natural log of mark-recapture estimates as a function of stream and year effects, including the number of mark-recapture estimates, the number of index streams and years with corresponding $F$ values (all $P$ values were <0.0001), the residual degrees of freedom (Resid df), the residual standard error (Sigma), the coefficient of determination ($R^2$), and the number of ANOVA estimates used in the Adult Index.

| Lake | Years | No. M-R ests | No. streams | F stream | No. years | F year | Resid df | Sigma | $R^2$ % | No. ANOVA ests |
|---|---|---|---|---|---|---|---|---|---|---|
| Superior | 1986–2019 | 184 | 7 | 45.5 | 34 | 7.5 | 144 | 0.107 | 78 | 48 |
| Michigan | 1986–2019 | 140 | 6 | 191.5 | 31 | 6.9 | 104 | 0.110 | 92 | 16 |
| Huron | 1985–2019 | 174 | 6 | 125.3 | 34 | 4.0 | 135 | 0.139 | 85 | 25 |
| Erie | 1986–2019 | 74 | 5 | 90.7 | 32 | 7.4 | 38 | 0.057 | 94 | 54 |
| Ontario | 1986–2019 | 144 | 5 | 109.7 | 34 | 4.3 | 106 | 0.050 | 85 | 22 |

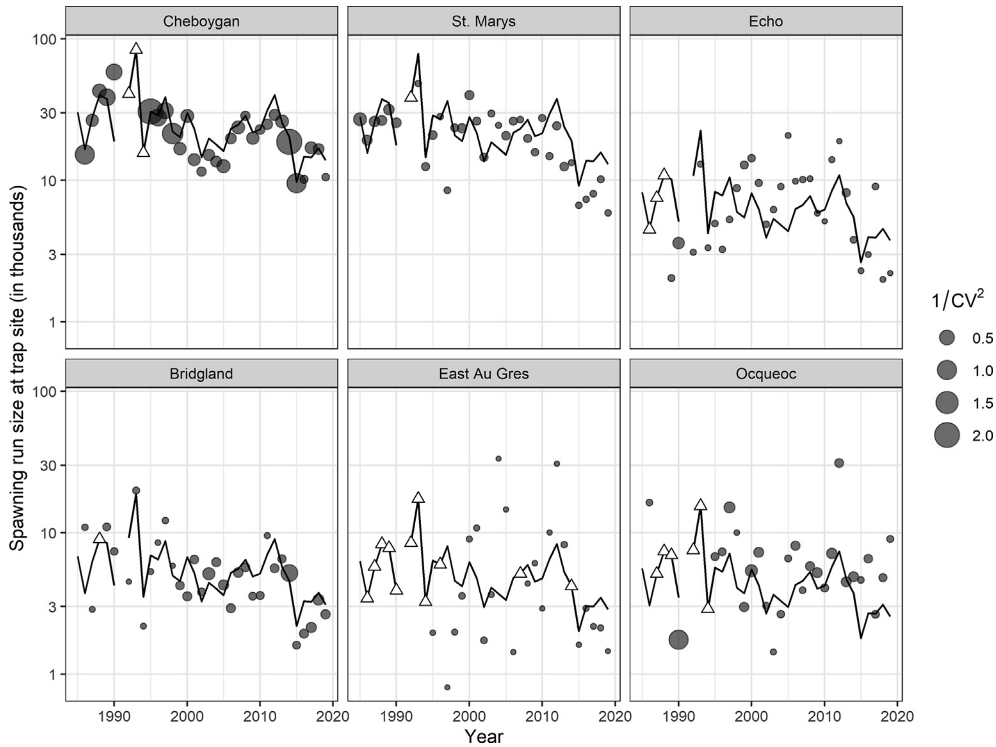


**Fig. 7.** Estimates of the spawning run size of sea lampreys at release locations in six index streams, all tributaries to Lake Huron. Gray circles represent mark-recapture estimates, with more precise estimates shown as larger circles (relative to $1/CV^2$). Lines represent predicted values from a two-way ANOVA on stream and year effects, weighted by the inverse of the squared coefficient of variation. White triangles represent ANOVA estimates that were combined with mark-recapture estimates to generate the Adult Index. Streams are ordered from highest (Cheboygan) to lowest (Ocqueoc) estimated stream effect.

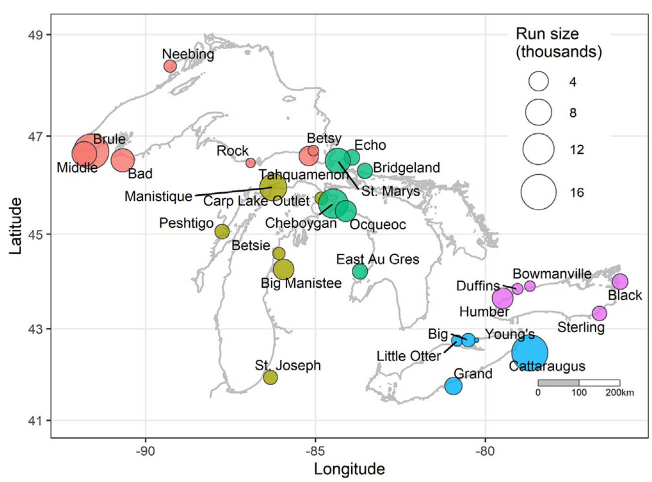


**Fig. 8.** Location of sea lamprey traps on 29 Great Lakes index streams. Symbol size varies with median size of sea lamprey spawning runs at release locations during 2015–2019. Colors are used to distinguish tributaries to different Great Lakes.

discontinued operations were on streams with smaller run sizes or irregularly produced mark-recapture estimates (Fig. 2). Nearly as many adult sea lampreys were trapped each year at fewer than half of the locations trapped for the Mullett Method, because the index focused on streams with large spawning runs. Reliance on a subset of streams means that any changes to those streams relative to unsampled streams will affect how well the Adult Index represents the lake-wide population of sea lampreys. This could occur if index streams were managed differently (e.g., in the frequency or intensity of lampricide applications or experimentation in diverting migrating sea lampreys toward or away from index streams; Hume et al., 2020).

Assessments that provide information on adult populations at higher spatial resolution could extend our understanding of their spawning migration. The Adult Index also misses smaller spatial scale changes in regions of the lake with no index streams. The Adult Index has been shown to vary with the spatial distribution of spawning run sizes in Lake Superior (Johnson et al., 2021). This spatial variation may be the reason why Lake Superior required more index streams than Lakes Michigan, Huron, and Ontario to generate an index of adult sea lamprey abundance highly correlated with the benchmark (Fig. 6). Johnson et al., 2021 also found the Lake Superior Adult Index to be highly correlated with winter ice cover, winter and spring precipitation, and sea lamprey size, reducing the power of the Adult Index to detect small changes in the sea lamprey population (Johnson et al., 2021) and highlighting the risk of interpreting the relative abundance time series in isolation. Incorporation of these biotic and abiotic effects could serve to improve the Adult Index in reflecting sea lamprey control actions.

During development of the Adult Index, the sea lamprey control program considered simply using trap catch and eliminating mark-recapture estimates. This would have further simplified field operations and would have avoided the release of sexually mature sea lampreys back into the system to reproduce. However, reliance on trap catch alone would have introduced too much variation in the Adult Index due to annual changes in trapping efficiency (Fig. 9; Wilberg et al., 2009). In addition, it would have inhibited the opportunity for further experiments with trapping operations, because subsequent improvements would have affected the Adult Index. Although the Adult Index is robust to changes in trapping operations and even trap locations within a stream, release locations must remain consistent over time, as that is the point at which the spawning run is estimated. Moving release locations upstream would decrease run size estimates, whereas moving them downstream would increase them. Release locations have

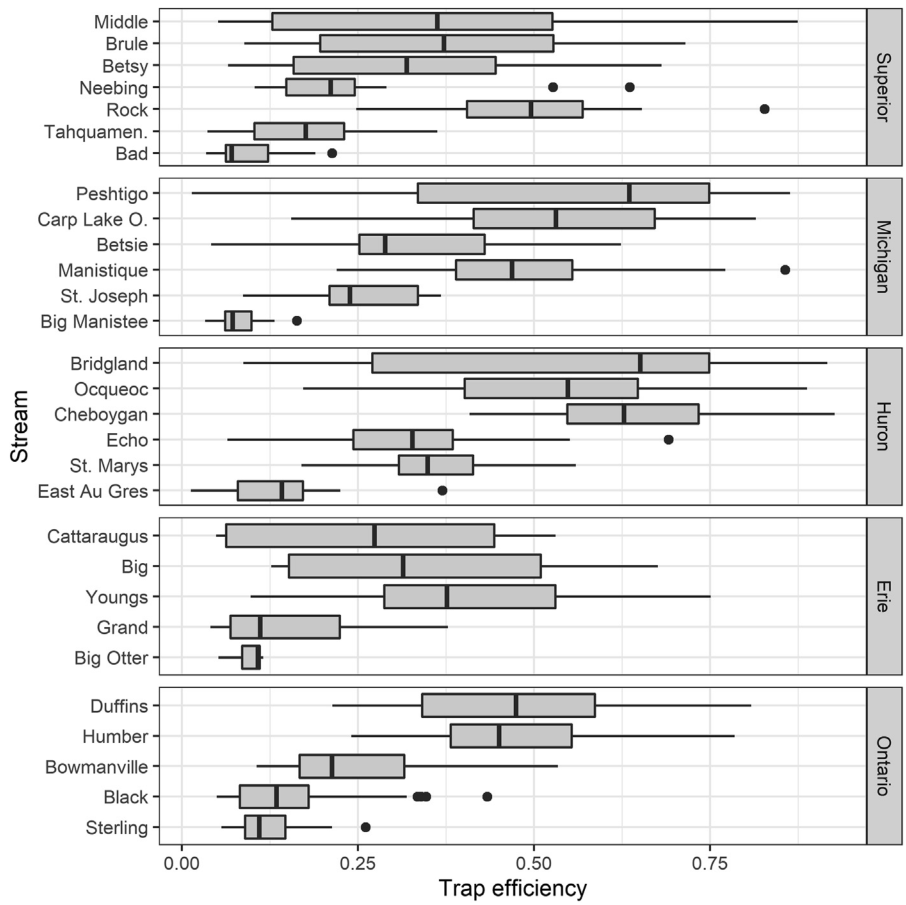


**Fig. 9.** Trap efficiencies of adult sea lampreys in 29 Great Lakes tributaries, 1985–2019. Trap efficiency was calculated as the total annual trap catch divided by the pooled Petersen mark-recapture estimate of spawning run size at the release location. Streams are ordered within each lake basin, by the variance of their annual trap efficiencies. Boxes represent quartiles with a vertical line at the median; whiskers extend to values within 1.5 times the interquartile range of a box; values beyond the whiskers are plotted individually.

been consistent over time in the majority of index streams, though in a few instances locations were moved substantial distances (Brule River release location moved downstream ~10 km in 2012 and Cattaraugus Creek release location moved downstream ~48 km in 2015). Future movements of a release locations would benefit from paired releases over several years to derive adjustment factors.

Valid mark-recapture estimates rely on several key assumptions. Most of these were met in estimating spawning run size at release locations in streams, including the same mortality of marked and unmarked fish (trap operations have achieved 90% recapture rates on occasion, suggesting handling mortality was not an issue); no loss of marks (fin clips remain clearly visible throughout the trapping season); identification of all marks (presumed to be highly accurate, especially since a single mark is used rather than distinct weekly marks); and negligible recruitment (Ricker, 1975). However, two assumptions were likely not met: same capture probability of marked and unmarked fish and random mixing of marked and unmarked fish (Table 2). Recent work has demonstrated that trap catchability of adult sea lampreys can vary with size (total length, Lewandoski et al., 2020) and sex (Johnson et al., 2020). Adult sea lampreys captured in traps exhibited consistent individual differences (in general activity, exploration, and boldness) from those captured via electrofishing (McLean and McLaughlin, 2018). If individual differences in size, sex, or behavior result in different vulnerability to traps, then a trapping bias may be introduced, because sea lampreys that were marked and released had already been captured in a trap once. This would lead to underestimation of spawning run size (Harper et al., 2018; Ricker, 1975; Zarnoch and Burkhart, 1980). Additionally, catchability can be higher for unmarked compared to marked individuals due to the positioning of sea lamprey assessment traps at locations downstream of barriers to upstream migration (allowing for multiple trap encounters by individual sea lamprey) and declining apparent survival late in the spawning run (Lewandoski et al., 2020). If once-captured sea lampreys were then trap-shy, overestimation could also result from trapping bias. Designing and deploying traps that target different behavioral traits would help address this bias. Mixing of marked and unmarked fish through the trapping period was encouraged by releasing new marked sea lampreys every day, such that marked and unmarked sea lampreys overlapped at the release location during a period of physiological advancement in their maturity.

The Adult Index is based on a conventional approach to modeling abundance over time, often referred to as *GLM standardization* in fisheries (Campbell, 2015; Carruthers et al., 2011; Payne, 2010) and *route regression* by bird researchers (Atkinson et al., 2006; Ter Braak et al., 1994). Abundance is modeled as a function of site and year effects, allowing for variation in abundance between sites and through time, respectively (Atkinson et al., 2006). Predictions in each year and site are summed across all sites, which is easier than extracting terms from the fitted model and calculating the indices analytically (Carruthers et al., 2011). Using this approach assumes that between-year changes are simi-

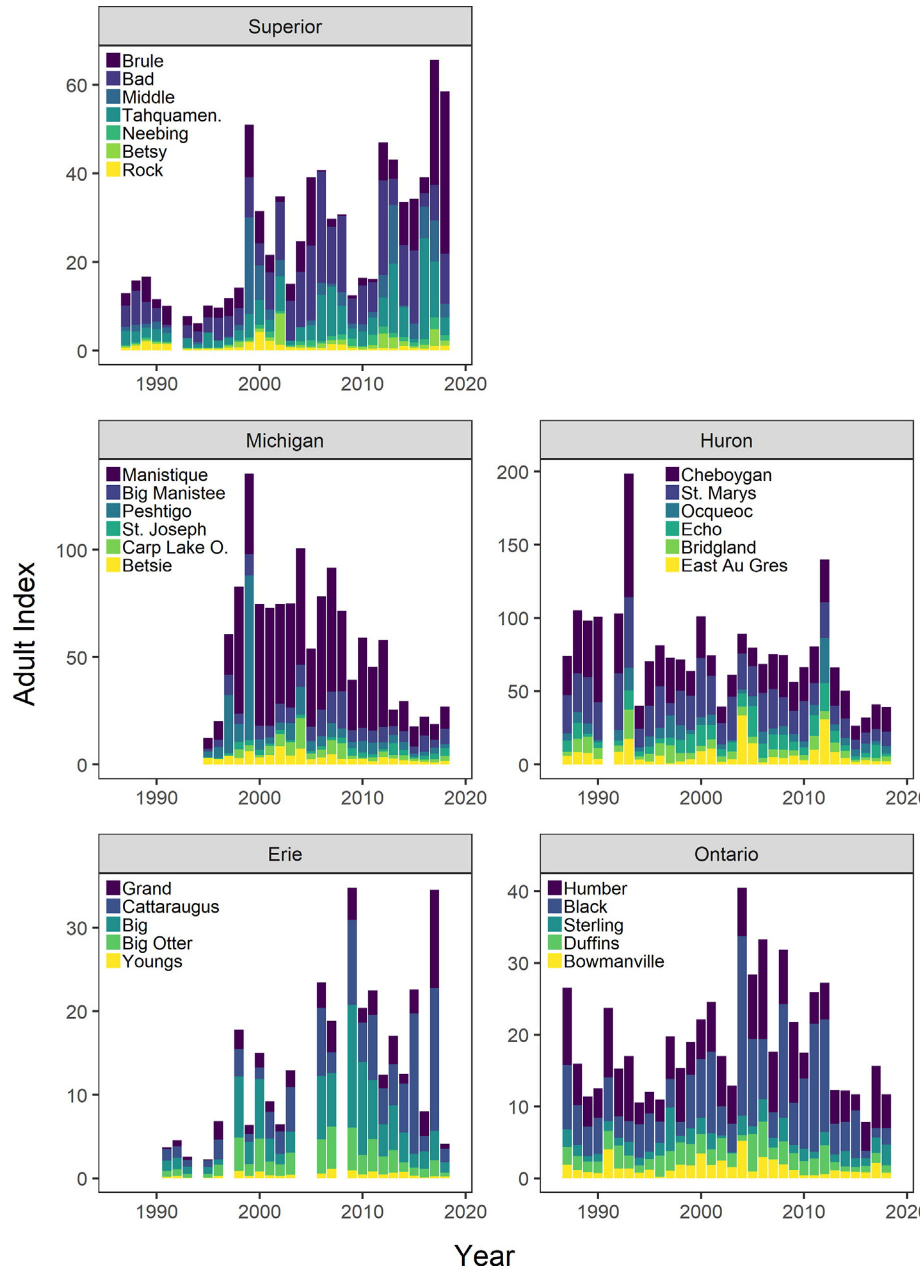


**Fig. 10.** Relative abundance of adult sea lampreys on the lake-wide scale as the sum of spawning run size estimates at release locations in Great Lakes index streams. Streams are ordered according to median mark-recapture run size estimate during 2015–2019.

lar across sites. In our case, this assumption is almost assuredly violated at the index stream scale, because different streams receive lampricide treatments in different years (e.g., Moore and Schleen, 1980), meaning ANOVA-derived run size estimates for streams with no mark-recapture estimate are likely biased. Failure to derive a mark-recapture estimate is caused by a low number of recaptures (<3), which is likely a non-random event. A reduced number of recaptures could occur in years with extremely high or low stream water levels or in streams with relatively small sea lamprey spawning runs or more challenging trap configurations. Atkinson et al. (2006) found that indices at broader spatial scales were relatively insensitive to missing data at individual sites. Payne (2010) derived a similar index of herring (*Clupea harengus*) larval abundance in the North Sea, which appeared to work well as an index of overall stock abundance. To avoid introducing large biases, Underhill and Prys-Jones (1994) recommended only using this approach when the missing counts compose no more than 15–20% of the total counts. This threshold was met for each of the Great Lakes, except for Lake Erie, which was missing 32% of its mark-recapture estimates during 2010–2019 (Fig. 5). Evaluation of this assumption would require replication of stream spawning run size estimates, which could be possible with the development of other methods of assessment. The Adult Index could be further improved by identifying sources of time-varying catchability (e.g., Johnson et al., 2021) and developing methods to standardize the Adult Index with respect to such sources.

The Adult Index must be strongly correlated with actual patterns in the lake-wide population of adult sea lampreys to serve the needs of fisheries managers. Our correlation analysis indicated that even as few as two to three index streams can theoretically represent lake-wide temporal patterns in the Great Lakes nearly as well as the Adult Index. Such representation is difficult to verify when sea lampreys are not effectively trapped in large streams without barriers and alternative methods of estimating lake-wide abundance of sea lampreys are not well established. Previous attempts to estimate lake-wide abundance by marking and releasing either transformers (recently metamorphosed larvae) or juveniles and recapturing them as adults has been met with mixed success (Bergstedt et al., 2003; Young et al., 2003). In addition, releasing transformers or juveniles to feed on valuable fish in the lakes may be negatively viewed by stakeholders and fisheries managers. An alternative index of transformers or juveniles that does not require their release has not yet been developed. Observed sea lamprey marks on lake trout and other host fishes could potentially be used to assess the sea lamprey population, but the relation has not been well described (e.g., Adams et al., 2020). Other promising assessment methods may be considered as alternatives to trapping sea lampreys, including assessing adults by conducting a genetic pedigree analysis of larval populations (Sard et al., 2020) and measuring environmental DNA shed by sea lampreys during their spawning migrations (Gingera et al., 2016). Broad ecosystem models that incorporate sea lampreys could also be used to validate abundance trends.

Although estimates of absolute abundance are generally preferred over estimates of relative abundance (Maunder and Piner, 2015), sampling challenges may limit options for estimating population size. Given the current state of sea lamprey trapping in the Great Lakes Basin (Bravener and McLaughlin, 2013; Holbrook et al., 2016; Miehls et al., 2020), an index of adult sea lamprey abundance may be the most promising for deriving population-level trends over time. Adoption of the Adult Index was the result of a beneficial process of critically evaluating past work and assumptions and striving for continuous improvements in the sea lamprey control program. Further research is needed to fully evaluate the assumptions required of the Adult Index, including (1) development of methods other than adult trapping to assess lake-wide patterns of sea lamprey abundance, (2) research into the biotic and abiotic effects on stream run size estimates, and (3) greater understanding of potential differences between trapped and untrapped adult sea lampreys. Investigations in these areas could lead to further improvements to population-level assessments of Great Lakes sea lamprey abundance.

## Declaration of Competing Interest

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

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