

Estimating Lake-wide Abundance of Spawning-phase Sea Lampreys (*Petromyzon marinus*) in the Great Lakes: Extrapolating from Sampled Streams Using Regression Models

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ABSTRACT. Lake-wide abundance of spawning-phase sea lampreys (*Petromyzon marinus*) can be used as one means to evaluate sea lamprey control efforts in the Great Lakes. Lake-wide abundance in each Great Lake was the sum of estimates for all streams thought to contribute substantial numbers of sea lampreys. A subset of these streams was sampled with traps and mark-recapture studies were conducted. When sea lampreys were captured in traps, but no mark-recapture study was conducted, abundance was estimated from a relation between trap catch and mark-recapture estimates observed in other years. In non-sampled streams, a regression model that used stream drainage area, geographic region, larval sea lamprey, production potential, the number of years since the last lampricide treatment, and spawning year was used to predict abundance of spawning-phase sea lampreys. The combination of estimates from sampled and non-sampled streams provided a 20-year time series of spawning-phase sea lamprey abundance estimates in the Great Lakes.

INDEX WORDS: Lake-wide abundance, sea lamprey, non-sampled streams, regression model.

INTRODUCTION

The abundance of parasitic-phase sea lampreys in the Laurentian Great Lakes is one indicator of whether the sea lamprey management program is achieving its objectives. Although the parasitic stage is the one that inflicts damage to fish, difficulties in sampling this stage led to the assessment of spawning-phase sea lampreys as a surrogate. Since 1980, traps have been the primary tool to monitor changes in spawning-phase sea lamprey populations

(Schuldt and Heinrich 1982, Heinrich *et al.* 2003). Spawning-phase sea lampreys were monitored in a subset of streams each year to assess lake-wide abundance. To use this information required development of a method to extrapolate information collected from sampled streams to an entire lake.

Stream discharge was considered to be an important factor influencing sea lamprey spawning runs in streams (Applegate 1950, Wigley 1959, Morman *et al.* 1980). Correlative tests carried out on 13 physical and chemical factors demonstrated a strong positive correlation ($r = 0.77$) between trap

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catches at electric weirs and stream discharge (Meyer 1985). Streams with the greatest discharge tended to accommodate the largest number of spawning-phase sea lampreys if other environmental factors required by sea lamprey larvae were favorable, such as soft substrate for burrowing larvae, tolerable water conditions, and sufficient oxygen concentrations (Morman *et al.* 1980). Moore and Schleen (1980) and Sorenson and Vrieze (2003) indicated that the presence of larval lampreys in streams was an important factor in predicting the number of spawning-phase sea lampreys that entered streams. The objective was to develop a comprehensive model using data from sampled streams to estimate abundance in non-sampled streams, and to sum the estimates from both sources to produce lake-wide estimates of spawning-phase sea lamprey abundance for each Great Lake.

METHODS

Measuring Abundance in Sampled Streams

Assessments of spawning-phase sea lampreys have been conducted with traps in a subset of tributaries since 1980 in Lake Superior, since 1977 in Lakes Michigan and Huron, since 1980 in Lake Erie, and since 1978 in Lake Ontario. Traps were used in streams with physical barriers that were known or believed to have spawning-phase sea lamprey present in them. Because trapping operations targeted streams with physical characteristics conducive to trapping (Schuldt and Heinrich 1982), sample sites were not randomly selected. Abundance estimates of spawning-phase sea lampreys were derived from mark-recapture studies conducted on a subset of the trapped streams during 1984 to 1999. Based on the relation between trap catch and mark-recapture estimates, abundance of spawning-phase sea lampreys was estimated for those streams with trap catch data but no mark-recapture information. Coefficients of variation (CV) were used to indicate the precision of the estimates.

Mark-recapture Estimates

Mark-recapture studies were typically conducted for 8 to 10 weeks using a single trap site in each river. A subset of the spawning-phase sea lampreys captured in the trap were given a week-specific mark in one or both of their dorsal fins with a v-notch tool similar to a hand-held paper punch. The rest of the lampreys were removed from the stream. Once marked, lampreys were transported down-

stream and released. Marked lampreys recaptured at the trap site were removed from the stream.

Abundance of spawning-phase sea lampreys was estimated from mark-recapture studies using an approach similar to the technique developed by Schaefer (1951). Schaefer marked fish at one site along their migration route and recovered them upstream at a different site. Because a single trap site was used instead of separate marking and recovery sites, Schaefer's estimate was modified by subtracting the total number of fish tagged,

$$N = \sum_{ij} \left(\frac{R_{ij} M_i C_j}{R_i R_j} \right) - \sum_i M_i, \quad (1)$$

where

- R_{ij} = number of fish tagged in the i th marking period which are recaptured in the j th recovery period,
- M_i = number of fish tagged in the i th marking period,
- C_j = number of fish caught and examined in the j th recovery period,
- R_i = total recaptures of fish tagged in the i th marking period, and
- R_j = total recaptures during the j th recovery period.

In Schaefer's (1951) study, with separate marking and recovery sites, each fish passed the recovery site only once. However, in this study, with a single trap site, marked lampreys passed the site twice, once when they were first captured for marking and again when they returned from the downstream release site. These marked lampreys were thus artificially added to the spawning population, and their number must be subtracted from the estimated total to avoid counting them twice. This adjustment can also be written as

$$N = \sum_{ij} N_{ij} = \sum_{ij} \left(\frac{R_{ij} M_i C'_j}{R_i R_j} \right), \quad (2)$$

where

- N_{ij} = estimated number of fish present in the i th marking period and the j th recovery period and
- C'_j = number of unmarked fish captured in the j th recovery period, i.e., $C_j - R_j$.

Based on this formula the variance of the abundance estimate was calculated from Chapman and Junge (1954),

$$\hat{\sigma}_N^2 = \sum_{ij} \left(\frac{N_{ij} \sum_j N_{ij} \sum_i N_{ij}}{M_i C'_j} \right). \quad (3)$$

The mark-recapture method of calculation used, even with the adjustment made to the Schaefer method, underestimated the population of spawning-phase sea lampreys because there was no estimate of the number of sea lampreys migrating past the trap site during the first period of marking. However, the bias in the estimate was negligible, because the assessments were designed to begin prior to the start of the spawning run and the trap catches during the first week were generally small.

Trap Catch Estimates

Although mark-recapture studies yielded the best estimates of spawning-phase sea lamprey populations, these could not be done in all streams in all years, and trap catch was a good indicator of stream abundance when trapping operations remained consistent among years. In years with trap catch data but no mark-recapture estimate, abundance of spawning-phase sea lampreys was estimated from a relation between trap catch and mark-recapture estimates observed in other years. Trap sampling efficiency, the proportion of the estimated population captured in traps, was assumed to be constant across all years for each stream. A ratio estimate of efficiency was used,

$$E_i = \frac{\sum_k t_{ik}}{\sum_k N_{ik}}, \quad (4)$$

where t_{ik} is the trap catch in stream i and year k , and index k includes only those years for which there were mark-recapture estimates. For each stream, the number of sea lampreys was estimated as the observed trap catch in that year divided by the trap efficiency,

$$N'_{ij} = \frac{t_{ij}}{E_i}, \quad (5)$$

where t_{ij} is the trap catch in stream i and year j , and index j includes only those years for which there was trap catch but no mark-recapture estimate.

Predicting Abundance in Non-sampled Streams

Independent Variables

A model was developed that used five independent variables to describe spawning-phase sea lam-

prey abundance in streams tributary to the Great Lakes: drainage area, geographic region, larval sea lamprey production potential, number of years since the last treatment, and spawning year. Three of these variables were categorical variables (region, production potential, and year) and two were continuous (drainage area, last treatment).

While stream discharge was preferred for the first variable, discharge data were only available as point-in-time measurements during lampricide treatments and only available for the years in which a stream was treated. Due to the scarcity of data and that these measurements did not adequately represent spring stream discharge, the relationship between discharge and drainage area (for streams in the model with data available) was examined, and a log transformation of drainage area was used for the first independent variable.

The second independent variable was geographic region within a lake. Given the size of the upper Great Lakes and observations from sampled streams, a regional difference was suspected in the allocation of spawning-phase sea lampreys among streams. Each of the upper Great Lakes (Superior, Michigan, and Huron) was divided into two geographic regions, and each stream was assigned to a region. Lake Superior was divided into east and west regions, and Lakes Michigan and Huron were divided into north and south regions (Fig. 1). To allow for a different relation between abundance and drainage area in each region, the interaction between geographic region and drainage area was included in the model.

The third and fourth independent variables accounted for the presence of larval sea lampreys in streams, an important factor in predicting the stream's abundance of spawning-phase sea lampreys (Moore and Schleen 1980, Sorenson and Vrieze 2003). The third variable was larval sea lamprey production potential, an assignment of streams to one of two categories based on their potential to produce larval sea lampreys. Streams that exhibited consistent and significant larval production and were treated regularly with TFM (3-trifluoromethyl-4-nitrophenol, at least once every 5 years) were classified as primary producers. Streams that exhibited significant, but sporadic, larval production and were treated irregularly with TFM (less frequently than once every 5 years) were classified as secondary producers. Streams that were not treated at least once during 1990 to 1999 were not included in the model. Abundance of spawning-phase sea lampreys in untreated streams was negligible, and it was assumed they made no



FIG. 1. Geographic regions in Lakes Superior, Michigan, and Huron in which streams were assigned for predicting abundance of spawning-phase sea lampreys.

contribution to spawning-phase sea lamprey population in the calculation of lake-wide estimates. The fourth variable was the number of years since the last TFM treatment in a stream. While larval sea lamprey production potential indicated the likelihood of a stream to produce consistent or sporadic populations, the years since last treatment accounted for the magnification of that effect for each additional year the stream remained untreated. The maximum value for this variable was set at 10 years to approximate a leveling off of this effect.

The fifth variable was spawning year, allowing for annual variability in the size of the lake-wide pool of spawning-phase sea lampreys.

Model Predictions

For all streams and years with abundance estimates available, i.e., sampled streams, a weighted least squares linear model was fit for each lake,

$$\ln(S_{ij}) = \beta_0 + \beta_1 \ln(D_i) + \beta_2 R_i + \beta_3 \ln(D_i)R_i + \beta_4 P_i + \beta_5 T_{ij} + Y_j + \varepsilon_{ij}, \quad (6)$$

where S_{ij} is the number of spawning-phase sea lampreys migrating up stream i in year j (from both mark-recapture and trap catch estimates), the β s are estimated parameters, D_i is the drainage area (in km^2), R_i is a dummy variable for region, P_i is a dummy variable for production potential (equal to zero for primary and one for secondary), T_{ij} is the number of years since the last treatment (set equal to 10 if the stream had not been treated in the past 10 years), Y_j is the year effect, and ε_{ij} is the normally distributed error with mean 0 and variance $\sigma^2 C_{ij}^2$ (C_{ij} is the coefficient of variation of S_{ij} , i.e., observations were weighted by the square of the inverse coefficient of variation). For Lake Superior, the region dummy variable, R , is equal to zero for

west and one for east; and for Lakes Michigan and Huron, R is equal to zero for north and one for south. Lakes Erie and Ontario were not divided into regions, so terms including R were not included in their models and β_2 and β_3 were not estimated. For Lakes Superior and Ontario, which had no secondary streams with spawning-phase abundance estimates, β_4 was fixed equal to $\ln(0.1) = -2.30$ for secondary stream predictions. This is based on the finding from data collected during 1950 to 1979 in 37 Lake Superior streams (28 primary, 9 secondary) showed that traps at weirs in secondary streams captured, on average, 10% of the lampreys per unit discharge as traps at weirs in primary streams. Therefore, model-predicted abundance estimates for secondary streams in Lake Superior and Ontario were adjusted to account for the reduced potential of these streams. For trap catch estimates, observations were weighted by a ratio estimate of the coefficient of variation of S_{ij} , based on mark-recapture population estimates and their variances in other years on the same stream,

$$C'_{i.} = \frac{\sum_k \hat{\sigma}_{N_{ik}}}{\sum_k N_{ik}}. \quad (7)$$

This approach assigns similar weights to trap catch estimates as to mark-recapture estimates.

The same model was used for predicting abundance in all five Great Lakes. Therefore, all variables and the interaction between region and the log transformation of drainage area were included in the model for each lake. A correction factor was applied when model estimates (\hat{L}_{ij}) were converted from the log scale back to original units,

$$\hat{S}_{ij} = e^{\hat{L}_{ij} + M/2}, \quad (8)$$

where M is the mean square error from the linear model (Hayes *et al.* 1995). The sum of the model predicted values for non-sampled streams and the estimates from sampled streams (mark-recapture and trap) was used to produce a lake-wide estimate of spawning-phase sea lampreys for each Great Lake.

RESULTS

Measuring Abundance in Sampled Streams

Data from assessments conducted in Great Lakes tributaries during 1977 to 1999 were used to calcu-

late 483 trap catch estimates and 409 mark-recapture estimates of spawning-phase sea lampreys (Table 1). The assessments were conducted annually on about 52 of the 258 streams included in the lake-specific models. Of the 258 streams in the models, 67% were defined as primary producers of sea lamprey larvae. More assessments were conducted in Lake Superior (an average of 17 streams per year for a total of 277 estimates), and fewer in Lake Erie (an average of three streams per year for a total of 48 estimates) than in the other lakes. Abundance estimates for spawning-phase sea lampreys were higher in Lake Huron streams (median 2,400 lampreys) and lower in Lake Superior (median 200) than in the other lakes. Estimates were most precise for Lakes Michigan and Huron (median CV 21% and 19%, respectively) and least precise for Lake Superior (median CV 35%).

Predicting Abundance in Non-sampled Streams

Individual models predicting spawning-phase abundance from the same independent variables were developed for each lake (Table 2, Fig. 2). Parameter estimates are given in Table 3 and Fig. 3, and observed versus predicted values are shown in Figure 4. Lake-wide abundance of spawning-phase sea lampreys was calculated for each Great Lake as far back as trap catch data existed (Fig. 5).

Drainage area was a significant predictor of spawning-phase sea lamprey abundance in all five lakes (Table 2). Drainage area was positively correlated with discharge in Lakes Superior, Michigan, Huron, and Ontario (Fig. 6, $r = 0.995, 0.984, 0.961$, and 0.969 , all $p < 0.05$). There were no correlation data for Lake Erie, but a similar relationship was assumed. Drainage area (Table 1) ranged from 12 to 10,938 km² in sampled streams and from 2 to 24,600 km² in non-sampled streams.

Geographic region was a significant predictor of spawning-phase sea lamprey abundance in Lakes Superior, Michigan, and Huron (Table 2). There was a significant interaction between drainage area and region in Lakes Superior and Huron. In the Lake Superior model, streams with drainage areas less than 5,500 km² yielded higher predicted numbers of lampreys in the west, and streams with drainage areas greater than 5,500 km² yielded higher predicted numbers of lampreys in the east. In the Lake Michigan model, northern streams yielded higher predictions than southern streams. In the Lake Huron model, predictions for northern streams

TABLE 1. Summary of spawning-phase sea lamprey assessments conducted on Great Lakes tributaries 1977 to 1999 and used in developing models to predict abundance in non-sampled streams.

| Lake | Assessment years | No. of streams | No. of primary streams | No. of secondary streams | Ave. no. of streams surveyed annually | No. of estimates | No. of mark and recap estimates | No. of trap catch estimates | Median estimate | Median CV | Median drainage area km ² | Range of drainage area km ² |
|----------|------------------|----------------|------------------------|--------------------------|---------------------------------------|------------------|---------------------------------|-----------------------------|-----------------|-----------|--------------------------------------|--|
| Superior | 1980–1999 | 72 | 54 | 18 | 17 | 277 | 133 | 144 | 214 | 35 | 192 | 20–2,270 |
| Michigan | 1977–1999 | 68 | 38 | 30 | 9 | 191 | 50 | 141 | 577 | 21 | 730 | 19–10,938 |
| Huron | 1977–1999 | 69 | 40 | 29 | 11 | 179 | 98 | 81 | 2,435 | 19 | 363 | 21–5,830 |
| Erie | 1980–1999 | 9 | 5 | 4 | 3 | 48 | 21 | 27 | 718 | 29 | 1,129 | 12–1,774 |
| Ontario | 1978–1999 | 40 | 37 | 3 | 12 | 197 | 107 | 90 | 709 | 27 | 118 | 28–4,827 |
| All | 1977–1999 | 258 | 174 | 84 | 52 | 892 | 409 | 483 | 653 | 23 | 285 | 12–10,938 |

TABLE 2. Summary of model predicting (log transformed) number of sea lamprey spawners for each lake. Years, number of observations (n), error degrees of freedom (df), mean square error (MSE), coefficient of determination (R²), and F and P values for each independent variable (log drainage area, region, log drainage by region interaction, production potential, years since last treatment and spawning year). Variables included in model after dropping terms ($\alpha = 0.05$, backwards elimination) have bold F and P values (main effects were not dropped if interaction was significant). Each independent variable has one degree of freedom, except year, for which the degrees of freedom are noted. Lakes Erie and Ontario were not divided into regions, and Lakes Superior and Ontario only had spawning-phase abundance estimates for primary producing streams.

| Lake | Error | | Drainage | | Region | | Interaction | | Potential | | Last trt | | Year | |
|---------------------|-------|-----|----------|----------------|---------------|-----------------|-------------|-----------------|-------------|-------------|--------------|-----------------|--------------|-----------------|
| Years | n | df | MSE | R ² | F | P | F | P | F | P | F | P | F | P |
| Superior 1980–99 | 277 | 253 | 0.0073 | 0.48 | 2.63 | 0.11 | 9.46 | <0.01 | 3.92 | 0.05 | — | — | 70.89 | <0.01 |
| Michigan 1977–99 | 191 | 163 | 0.0045 | 0.86 | 560.86 | <0.01 | 0.32 | 0.57 | 3.22 | 0.07 | 41.49 | <0.01 | 0.00 | 0.97 |
| Huron 1977–99 | 179 | 151 | 0.0055 | 0.82 | 250.38 | <0.01 | 0.01 | 0.94 | 4.70 | 0.03 | 7.99 | 0.01 | 0.03 | 0.86 |
| Erie 1980–99 | 48 | 25 | 0.0008 | 0.87 | 7.05 | 0.01 | — | — | — | — | 15.38 | <0.01 | 0.61 | 0.44 |
| Ontario 1978–99 | 197 | 173 | 0.0026 | 0.58 | 99.48 | <0.01 | — | — | — | — | 26.73 | <0.01 | 0.61 | 0.44 |
| | | | | | | | | | | | | | 4.85 | <0.01 |
| | | | | | | | | | | | | | 1.86 | 0.02 |

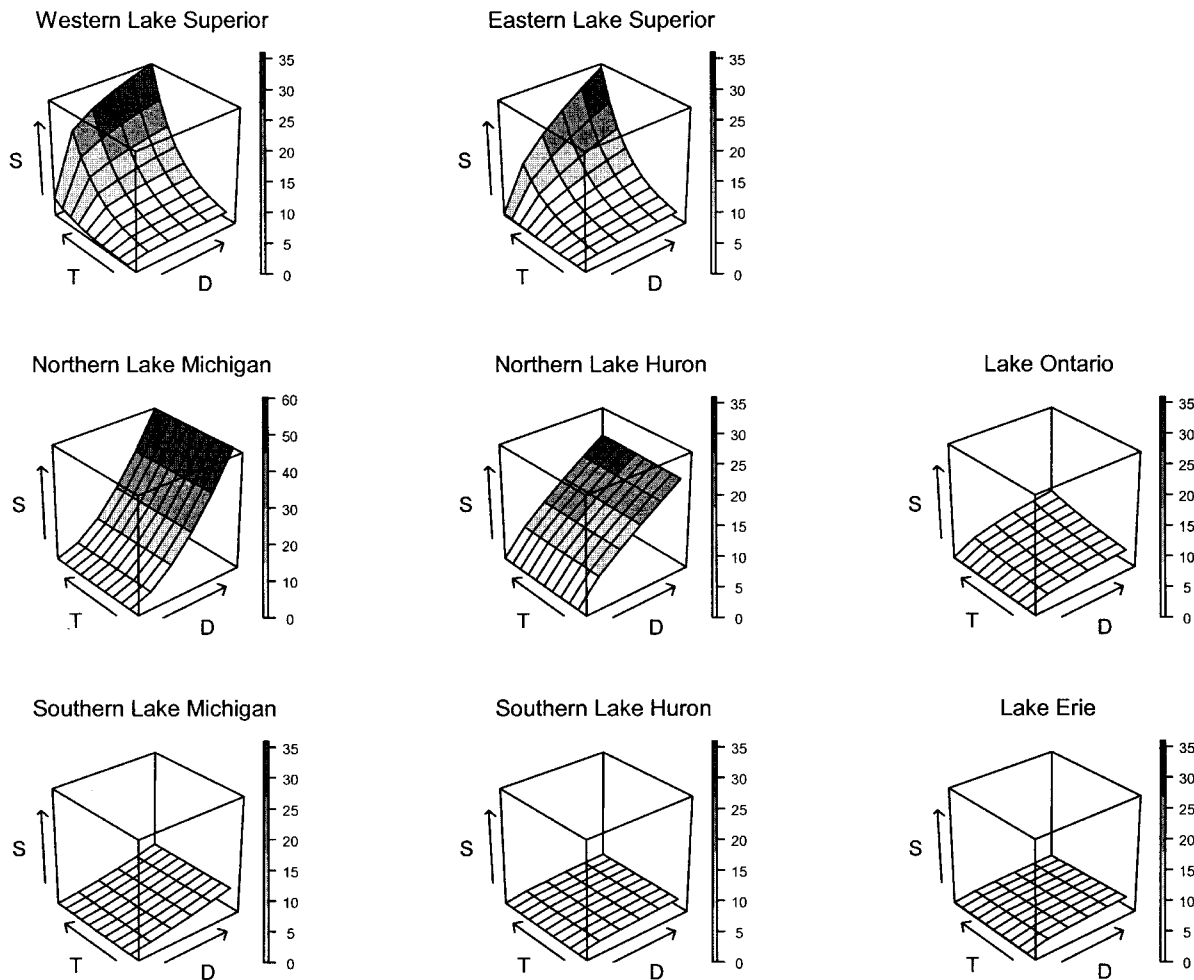


FIG. 2. Model predictions of abundance of spawning-phase sea lampreys for primary producing streams in 1999. Response surface predictions are a function of a 10 by 6 grid of T , from 1 to 10 years since last treatment, by D , drainage area from 2 to 5,000 km². The vertical scale, S , is in thousands of spawning-phase sea lampreys and ranges from 0 to 36,000 for all lakes and regions except for northern Lake Michigan, which ranges from 0 to 61,000.

TABLE 3. Parameter estimates (and standard errors) for models used to predict abundance of spawning-phase sea lampreys in the Great Lakes (year effects are displayed graphically in Fig. 3). The coefficient for production potential (β_4) was fixed equal to $\ln(0.1)$ for Lakes Superior and Ontario.

| Lake | Intercept β_0 | | Drainage β_1 | | Region β_2 | | Interaction β_3 | | Potential β_4 | | Treatment β_5 | |
|----------|------------------------|--------|-----------------------|--------|---------------------|--------|--------------------------|--------|------------------------|--------|------------------------|---------|
| Superior | 4.83 | (0.84) | 0.24 | (0.15) | -2.87 | (0.93) | 0.33 | (0.17) | -2.30 | — | 0.323 | (0.038) |
| Michigan | -3.62 | (0.51) | 1.66 | (0.07) | 0.93 | (1.63) | -0.38 | (0.21) | -2.81 | (0.44) | -0.001 | (0.034) |
| Huron | 3.46 | (0.33) | 0.79 | (0.05) | -0.07 | (0.91) | -0.28 | (0.13) | -2.02 | (0.72) | 0.004 | (0.021) |
| Erie | 5.15 | (0.94) | 0.38 | (0.14) | — | — | — | — | -1.06 | (0.27) | -0.049 | (0.063) |
| Ontario | 4.35 | (0.30) | 0.51 | (0.05) | — | — | — | — | -2.30 | — | 0.098 | (0.019) |

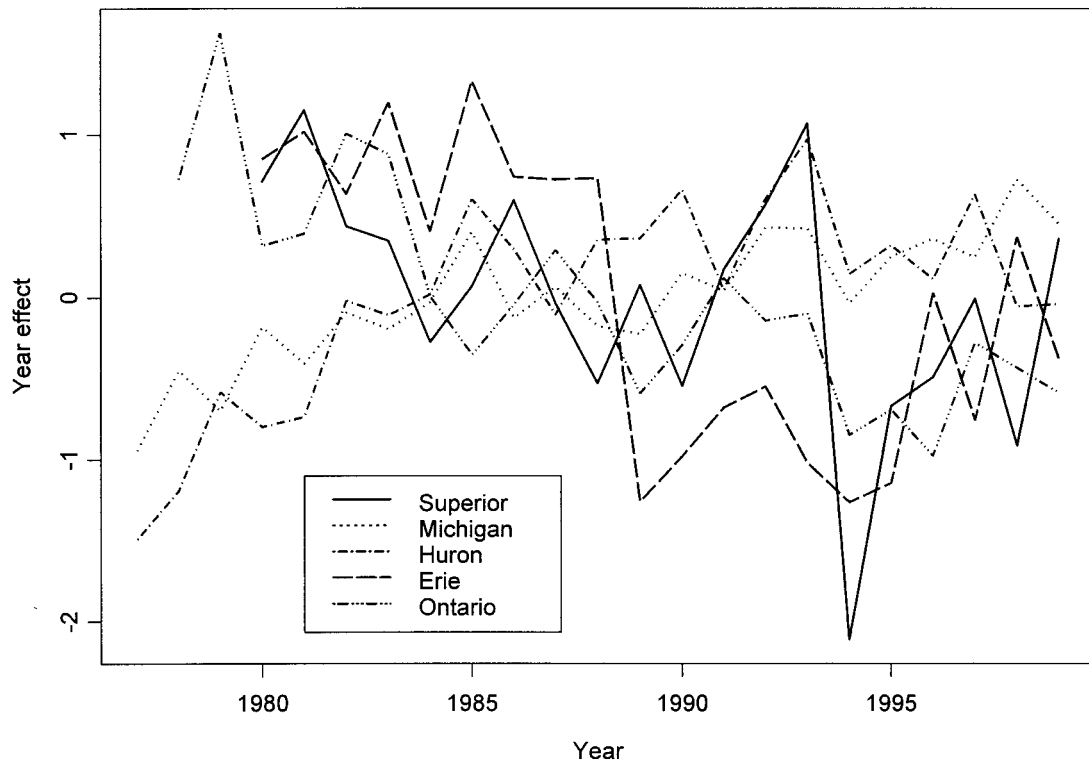


FIG. 3. Year effects for models used to predict abundance of spawning-phase sea lampreys in the Great Lakes.

were higher and increased more rapidly with increased drainage area than those for southern streams. Production potential was significant in predicting abundance of spawning-phase sea lampreys in Lakes Michigan, Huron, and Erie (Table 2). Production potential was not included in the models for Lakes Superior and Ontario because there were no secondary streams with spawning-phase abundance estimates in these two lakes. The number of years since treatment was significant only in Lakes Superior and Ontario, and year was significant in all five Great Lakes (Table 2).

DISCUSSION

Agencies have shifted in their initial focus of sea lamprey management in the Great Lakes from individual streams toward basin-wide management in recent years (Christie and Goddard 2003, Christie *et al.* 2003). This shift has paralleled the move by many natural resource agencies away from smaller-scale fisheries management toward larger watershed approaches (Toepfer *et al.* 2000). Estimating populations over large areas poses many challenges for sampling, and abundance-estimation techniques are

underdeveloped (Lewis *et al.* 1996, Toepfer *et al.* 2000). Hankin and Reeves (1988) recognized that time and budget limitations often rule out intensive sampling over large areas. While the literature on estimating abundance over large areas is relatively scarce, the common thread consists of sampling representative areas and extrapolating information to similar areas. Toepfer *et al.* (2000) was able to estimate abundance of stream fishes by sub-sampling a stream and extrapolating abundance estimates to the entire stream using habitat quality and geographic information systems technology. Lamouroux *et al.* (1999) demonstrated that it was possible to predict fish community characteristics from fluvial hydraulics.

Prior to the development of the model described in this paper, abundance of spawning-phase sea lampreys was estimated lake-wide in Lakes Michigan and Huron and in U.S. waters of Lake Superior from a simple linear regression that related stream discharge to spawning-phase abundance. During 1997, a panel of technical experts reviewed this linear regression approach and identified several limitations. Problems included assumption of direct proportionality between abundance and discharge;

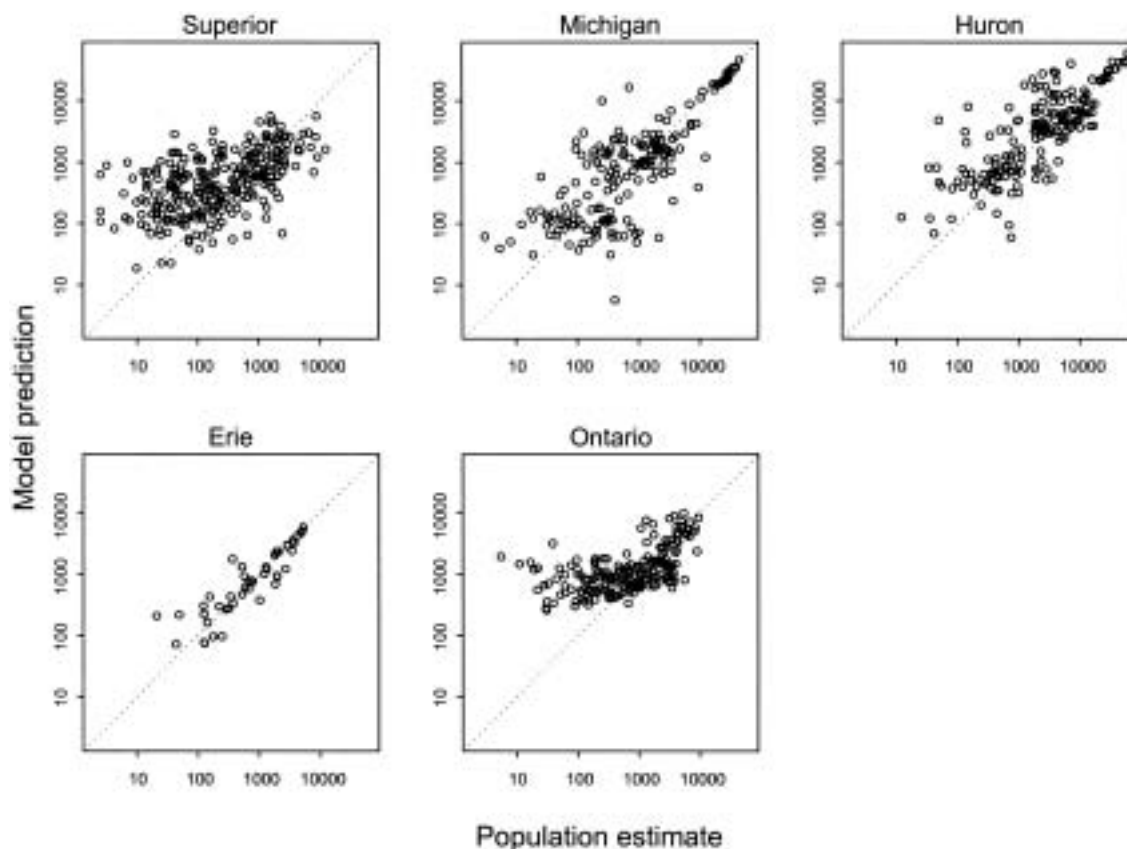


FIG. 4. Plot of estimated observed versus model-predicted spawning-phase sea lamprey abundance estimates for each Great Lake for years 1977 to 1999.

failing to account for heterogeneity of variance or severe non-normality of data; analyzing small data sets from individual years separately without taking into account any generality that applies across time or among lake regions; and, not accounting for potential effects of lampricide treatments.

The attempt to increase the predictive strength of the model brought some of the same concerns that Lamouroux *et al.* (1999) experienced regarding the numerous and diverse factors that potentially affect fish populations. Key factors that could be quantified or categorized to describe abundance of spawning-phase sea lampreys were used, but lack of, or inadequate data prevented testing all possible influences. The presence of native lampreys in sampled streams (Sorenson and Vrieze 2003), the effect power plants, and the plume effect from the stream discharge as it entered the lake were all potential factors that were not included in the model.

The revised model described in this paper esti-

mated abundance in all five lakes as far back as trap catch data existed. Sample size was increased by including abundance estimates calculated from trap catch. Hankin and Reeves (1988) demonstrated the ability to replace costly and time-consuming sampling methods with visual estimates. They demonstrated a strong positive correlation between diver counts (visual estimation) and the Moran-Zippen removal method abundance estimator (Seber 1982) for steelhead trout (*Salmo gairdneri*) and coho salmon (*Oncorhynchus kisutch*) in pools and riffles in a small Oregon stream. They believed the removal method generated estimates with very small errors and assumed them to be equal to the “true” numbers. Likewise, the mark-recapture estimates used were assumed to be the closest representation of the number of spawning-phase sea lampreys in a stream and were used as the benchmark. When trap catch estimates were compared to model-predicted estimates and to mark-recapture estimates, it was found that trap catch estimates explained 94% of

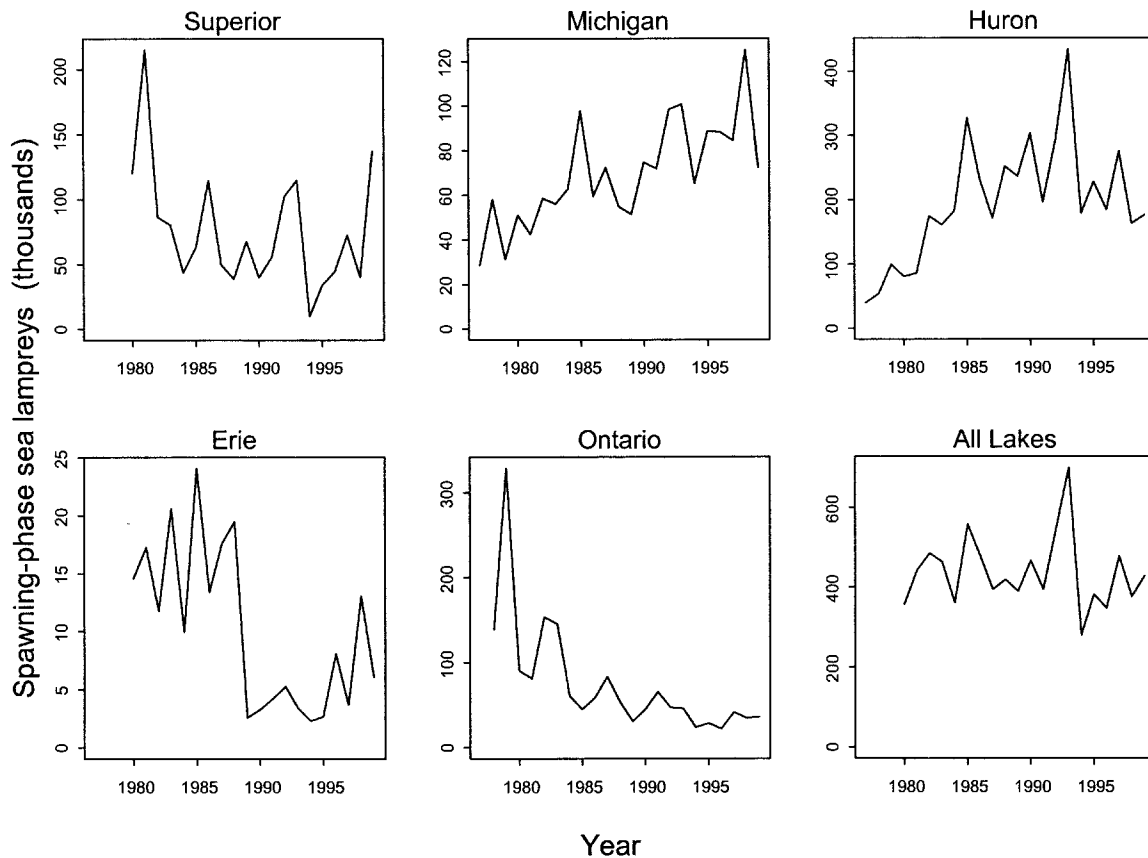


FIG. 5. Estimated abundance of spawning-phase sea lampreys in each Great Lake and all lakes combined during 1977 to 1999.

the variability in the mark-recapture estimates, while model predictions only explained 62%. This strong relation justified the assignment of similar weights to both trap catch and mark-recapture estimates in the model building process. By including abundance estimates from trap catch in the model, sample size was increased, more year-specific information was included, and more precise estimates than the model otherwise would have predicted were used for those streams.

The streams assessed in the models covered the range of stream drainage areas in a lake region. It was attempted to include the stream with the smallest drainage area, the largest drainage area, and about four to seven additional streams with drainage areas in between the smallest and largest for each geographic region in a lake. Trapping operations in streams with the smallest and middle range drainage areas have been successful. However, it was not possible to assess the streams with the largest drainage areas due to inadequate trap sites. Because of this, abundance estimates were

predicted based on extrapolations from the model for streams with drainage areas beyond the range of those used to build the model. Abundance extrapolations for these largest streams totaled 7% of the predicted abundance in Lake Superior, 2% in Michigan, 5% in Huron, and 3% in Ontario. The Nipigon River (Lake Superior) had a drainage area nearly seven times that of the largest Lake Superior stream with a stream abundance estimate. Lamouroux *et al.* (1999) experienced similar difficulty in validating his model in large rivers due to the difficulty of sampling fish in these systems. This has been an ongoing concern in the largest streams and remains a shortfall. Research and experimentation are needed to develop methods and technologies to assess spawning-phase lamprey abundance in these large streams.

The assumed effect of production potential in Lakes Superior and Ontario appeared reasonable. The coefficient β_4 was fixed equal to $\ln(0.1)$ for these lakes, based on the assumption that the spawning run in secondary streams was 10% of that

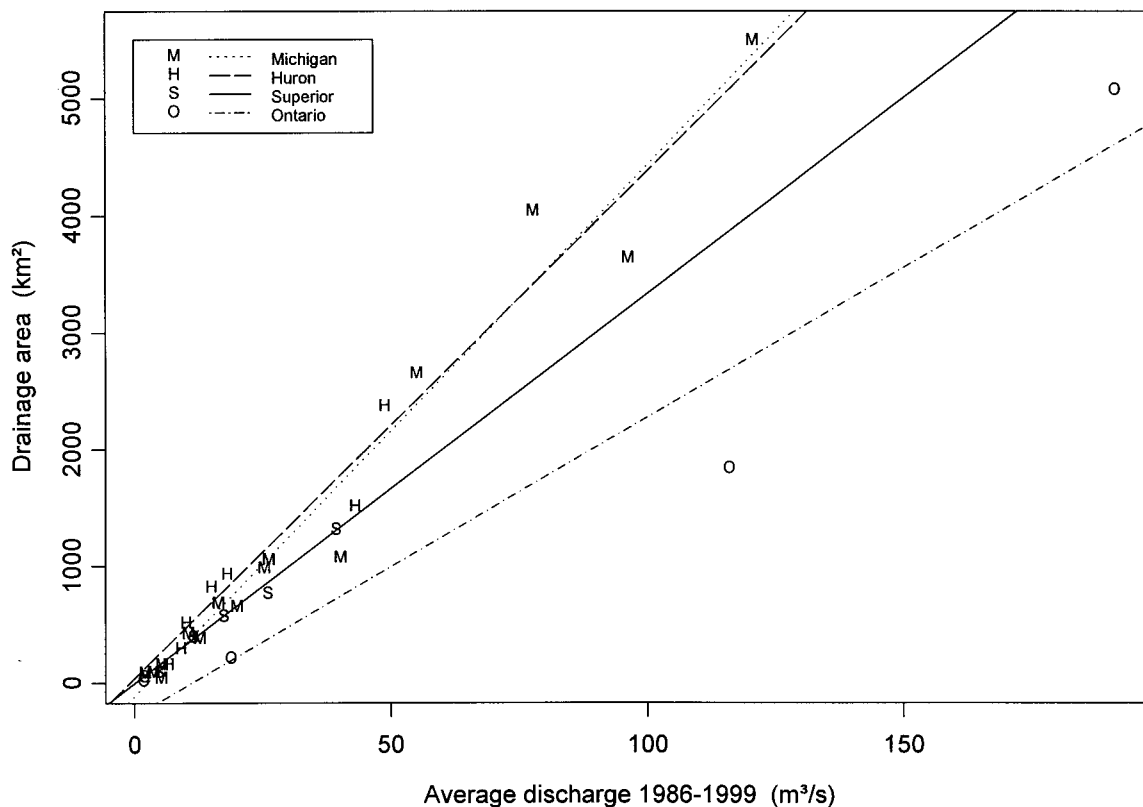


FIG. 6. Plot of drainage area (km^2) versus discharge (m^3/sec) from streams used in the models to predict abundance of spawning-phase sea lampreys in Lakes Superior, Michigan, Huron, and Ontario.

in primary streams of equal size. The estimated effects of production potential were 6% in Lake Michigan, 13% in Lake Huron, and 35% in Lake Erie. The weighted mean average effect of production potential for Lakes Michigan, Huron, and Erie was 10%. Still, the Lake Superior and Ontario models would be improved by sampling secondary streams.

Of the five lake models, Lake Superior and Lake Ontario demonstrated the weakest fit to the data. The coefficients of determination from the Lake Superior and Lake Ontario models were lower than the other three lakes. The observed versus predicted values indicated that the models for these two lakes tended to over-estimate the number of spawning-phase sea lampreys in streams with low mark-recapture estimates (Fig. 4). This could be related to the lack of secondary stream data in these models and the way primary and secondary streams are defined. The definition is based on treatment patterns and this may not sufficiently distinguish between

streams that were more or less productive in these two lakes.

One alternative method of assessment was to consider a whole lake method of estimating parasitic abundance and the possibility of integrating heterogeneous sources of data. Parasitic-phase mark-recapture studies have been conducted in Lake Huron (Bergstedt *et al.* 2003), and metamorphosing-phase mark-recapture studies began in 1998 and 1999 in Lake Superior. As results from these studies are analyzed, the reliability of the estimates from the different sources can be compared and integrated (Young *et al.* 2003) to design the optimum program to assess parasitic abundance, which may be used to measure the effectiveness of the sea lamprey management program. The addition of these data will undoubtedly provide additional information for assessing populations in the future and will add to the understanding of lake-wide populations of sea lampreys. However, data collected from parasitic-phase and metamorphosing-phase mark-recapture only dates back to the early 1990s,

and in only two lakes. These data lack the important historical information only available from the spawning-phase trap data: more than 20 years of data demonstrating trends through time of abundance of spawning-phase sea lampreys in each Great Lake (Heinrich *et al.* 2003, Lavis *et al.* 2003, Morse *et al.* 2003, Sullivan *et al.* 2003, Larson *et al.* 2003).

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