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Optimizing Larval Assessment to Support Sea Lamprey Control in the Great Lakes

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ABSTRACT. *Elements of the larval sea lamprey* (Petromyzon marinus) *assessment program that most strongly influence the chemical treatment program were analyzed, including selection of streams for larval surveys, allocation of sampling effort among stream reaches, allocation of sampling effort among habitat types, estimation of daily growth rates, and estimation of metamorphosis rates, to determine how uncertainty in each element influenced the stream selection program. First, the stream selection model based on current larval assessment sampling protocol significantly underestimated transforming sea lam-*

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prey abundance, transforming sea lampreys killed, and marginal costs per sea lamprey killed, compared to a protocol that included more years of data (especially for large streams). Second, larval density in streams varied significantly with Type-I habitat area, but not with total area or reach length. Third, the ratio of larval density between Type-I and Type-II habitat varied significantly among streams, and that the optimal allocation of sampling effort varied with the proportion of habitat types and variability of larval density within each habitat. Fourth, mean length varied significantly among streams and years. Last, size at metamorphosis varied more among years than within or among regions and that metamorphosis varied significantly among streams within regions. Study results indicate that: (1) the stream selection model should be used to identify streams with potentially high residual populations of larval sea lampreys; (2) larval sampling in Type-II habitat should be initiated in all streams by increasing sampling in Type-II habitat to 50% of the sampling effort in Type-I habitat; and (3) methods should be investigated to reduce uncertainty in estimates of sea lamprey production, with emphasis on those that reduce the uncertainty associated with larval length at the end of the growing season and those used to predict metamorphosis.

INDEX WORDS: *Sea lamprey, sampling, precision, larvae, growth, metamorphosis, Great Lakes.*

INTRODUCTION

Larval sea lamprey (*Petromyzon marinus*) population abundance is estimated in Great Lakes tributaries by sampling larval density and habitat in streams with sea lamprey populations (Slade *et al.* 2003). The results of these surveys are used to rank streams for chemical treatment through the use of a computer model, the Empiric Stream Treatment Ranking (ESTR) system. In the ESTR model, empirical data on larval density, size structure, and larval habitat area collected in year *t* are combined with estimates of daily growth from the survey date to the end of the growing season and rate of metamorphosis to forecast the abundance of transforming sea lampreys each stream will produce in year *t+1*. These forecasts are used to rank streams for chemical treatment based on the ratio of predicted numbers of larvae expected to metamorphose to the cost of treating streams with chemicals. Streams with the most favorable benefit-to-cost ratio are included in the treatment schedule for the following year (Christie *et al.* 2003).

Elements of the larval assessment program that most strongly influence the chemical treatment program include selection of streams for larval surveys, allocation of sampling effort among stream reaches, allocation of sampling effort between habitat types, estimation of daily growth rates, and estimation of metamorphosis rates. Each of these elements of the larval assessment program is estimated from sampling, and is therefore subject to uncertainty, so optimization of the sea lamprey control program in the Great Lakes should benefit from examination of the effect of uncertainty in the individual elements of the larval assessment program. The objective of this study was to analyze each of these elements of the larval assessment program, to determine how uncertainty in each element might influence the stream selection program.

SELECTING STREAMS FOR ASSESSMENT

The stream selection process for chemical treatment currently relies on larval assessment data from streams that were surveyed in the previous year. Large or productive streams may retain large residual populations of larval sea lampreys that survive chemical treatment even if treatment efficiency is high. Such streams are not considered for either assessment or re-treatment the following year unless direct evidence suggests that the previous treatment was ineffective. As a consequence, some streams may be omitted from consideration for chemical treatment even though a high residual sea lamprey population may make them cost effective to treat. In this analysis, the ESTR model was used to simulate transformer production in the Great Lakes, and to model the effect of including streams in the stream selection process that would not be included using the current larval assessment strategy.

Methods

The ESTR model was used to predict the number of metamorphosing sea lampreys (transformers) for each stream in which larval assessment surveys were conducted only in 2000 (1-year predictions; the current protocol) and for streams surveyed in 1998, 1999, and 2000 (3-year predictions; the simulated protocol). To estimate metamorphosed sea lamprey production using the simulated protocol, estimates of larval survival after a treatment (treatment efficiency), over-winter larval mortality, and larval growth were included in the ESTR model. Current model estimates were used for growth (stream-specific), and over-winter mortality (fixed at 20% for all streams). Two separate treatment efficiencies, 95% and 99% (W. D. Swink, U.S. Geological Survey, Millersburg, MI, 2001, personal communication,), were assumed to simulate the effects of variability in treatment efficiency on the estimates of production due to sea lampreys surviving chemical treatments. Four model outputs included: lists of streams ranked based on cost per transforming sea lamprey killed for 1-year and 3-year predictions at 95% and 99% treatment efficiency.

For each of the four model outputs, the total number of transformers produced from all sources, the total number of staff days required to treat all streams, the cost per transforming sea lamprey killed, and the total number of transformers that would survive treatment at the base treatment level (the 2001 base level of control effort; 4,370 staff days) were estimated. The cost per transforming sea lamprey killed was defined as the cost per sea lamprey killed at the base level of control effort. The number of transformers surviving treatment was calculated as the sum of the number of transformers in each untreated stream and the survivors from treated streams. Survivors from treated streams were determined by the treatment efficiency (95% or 99%). The total numbers of sea lampreys surviving were plotted against the cumulative staff days for each of the four simulations, to compare the two types of predictions for both levels of treatment efficiency. The list of streams that ranked for treatment was compared for each of the two prediction methods, and streams that ranked for treatment in 2001 that were not assessed for larval abundance in 2000 were identified.

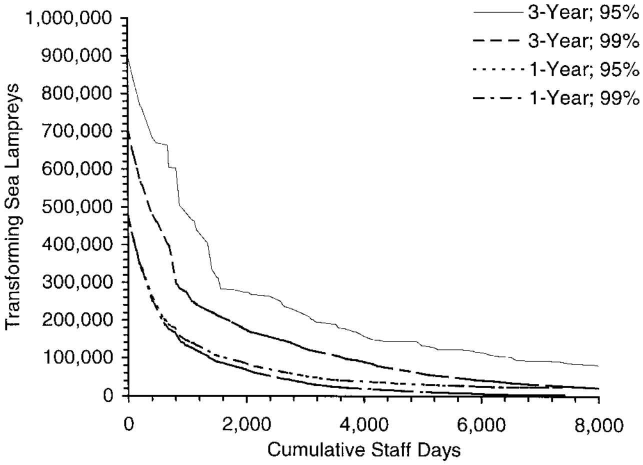

FIG. 1. Predicted production of transforming sea lampreys versus cumulative staff days of treatment effort for 3-year and 1-year ESTR model predictions at 95% and 99% levels of treatment efficiency in the Great Lakes.

Results

For all simulations, 3-year predictions suggested that more transforming sea lampreys were produced, more transforming sea lampreys were killed, and marginal costs per sea lamprey killed were lower than for 1-year predictions (Table 1, Fig. 1). The marginal cost per transforming sea lamprey killed was higher for 1-year predictions than 3-year predictions at both 95% and 99% treatment efficiency. The 3-year prediction lists identified 12 to 15 streams that would rank high enough to be treated in 2001, but were not surveyed for larval abundance in 2000 and consequently not included on the 1-year prediction list. Several of these streams were treated in 1999 or 2000 and the residual sea lampreys surviving treatment would not be considered for treatment in 2001 using the 1-year prediction list.

Discussion

Current methods may not be best for identifying the correct set of streams for treatment. Current

TABLE 1. Transformers produced, transformers surviving, and marginal cost per transformer killed for streams represented in 1-year and 3-year ESTR model predictions at 99% and 95% treatment efficiency and 2001 budget levels.

Prediction	Streams Modeled	Transformers Produced	Treatment Efficiency	Transformers Surviving	Marginal Cost/Kill
1-year	110	477,000	99%	17,000	$160
1-year	110	477,000	95%	35,000	$166
3-year	218	704,000	99%	76,000	$ 59
3-year	218	902,000	95%	176,000	$ 28

methods of ranking streams do not optimize the cost per transforming sea lamprey killed, and suppression of sea lampreys may not be optimized in the Great Lakes. Estimates of adult sea lamprey abundance in the Great Lakes for the year 2000 indicate that nearly 600,000 adults survived the parasitic phase and returned to tributaries to spawn (Klar and Schleen 2001). Schleen *et al.* (2003) estimated that 88% of the sea lampreys in Lake Huron during 1990–1995 were from the St. Marys River. If the contribution of sea lampreys to Lake Huron was similar in 2000, about 280,000 adults (0.88 × 318,000) were recruited to Lake Huron from the St. Marys River, which is not ranked for treatment using the ESTR model. Therefore, sources other than the St. Marys River accounted for over 300,000 adults in the Great Lakes in 2000. Based on 1-year predictions, regardless of treatment efficiency, fewer than 40,000 transforming sea lampreys should survive treatment and contribute to parasitic populations in the Great Lakes. This discrepancy between predicted and observed parasitic sea lamprey abundance suggests that major areas contributing sea lampreys to the Great Lakes are not currently being assessed on an annual basis (Slade *et al.* 2003). Further, the marginal cost per kill was 60–80% less based on 3-year predictions, and up to 15 streams would be ranked for treatment in 2001 that were not assessed for abundance in 2000. Christie *et al.* (2003) found that the marginal cost per sea lamprey killed during 1998–2000 declined faster with added treatment resources based on 1-year predictions, than when based on 3-year predictions.

The ESTR model should be used to identify streams where a potentially large residual larval population could remain after treatment. Sampling of such streams could subsequently be used to estimate treatment efficiency and to improve the model's predictive capability. However, the ESTR model should not be used to recommend streams for treatment without further validation. First, the ESTR model was developed to forecast transformer production one year after sampling was completed, not several years into the future. Consequently, the long-term accuracy of the ESTR model needs to be evaluated. Second, the results of analyses based on the ESTR model are subject to uncertainty. For example, the ESTR model includes a linear growth function (larval growth may be nonlinear), mortality rate and treatment efficiency are educated guesses, rate of metamorphosis varies greatly among streams (see below), and larval sea lamprey population estimates are assumed to be accurate. Consequently, the sensitivity of ESTR-model predictions to uncertainty in each of its components should be evaluated and included in estimates of uncertainty.

SAMPLING OF STREAM REACHES

Quantitative sampling protocols require that a minimum of 12 plots be sampled to collect at least 100 larval sea lampreys in each reach of a tributary, regardless of the larval density or amount of larval sea lamprey habitat in the reach. For purposes of sampling, stream habitat is classified according to its ability to support larval sea lampreys. Type-I habitat is preferred larval habitat that usually consists of sand, fine organic matter, and cover (detritus, aquatic vegetation), which is usually formed in areas of deposition. Type-II habitat is acceptable, but not preferred, larval habitat that usually consists of shifting sand, gravel, or rubble, and very little or no fine organic matter, but is soft enough for larvae to burrow into. Type-III habitat cannot be penetrated by larvae, so is unacceptable habitat, and usually consists of bedrock or hardpan clay, with rubble and coarse gravel. A consequence of the method for allocating sampling effort is that large reaches are surveyed with the same amount of effort as small reaches. If larval density is less variable in smaller stream reaches, less effort may be required to accurately describe overall abundance of larvae in these reaches. This sampling effort may then be reallocated to larger, more variable reaches. In this analysis, variability in larval density was related to Type-I habitat area, total area, or reach length.

Methods

Data collected during quantitative assessments in U.S. tributaries of Lakes Huron (34 streams and 58 reaches), Michigan (68 streams and 122 reaches), and Superior (26 streams and 35 reaches) during 1996 to 1999 was analyzed. For those tributaries that were sampled in multiple years, only the most recent data were analyzed. Field personnel collected larval sea lampreys from measured plots ranging from 5 m^2 to 15 m^2 of Type-I habitat using backpack electrofishing gear in streams that could be waded (< 0.8 m deep; Slade *et al.* 2003). Density was calculated as the number of sea lamprey larvae captured per square meter of Type-I habitat in a reach. Linear regression was used to quantify the

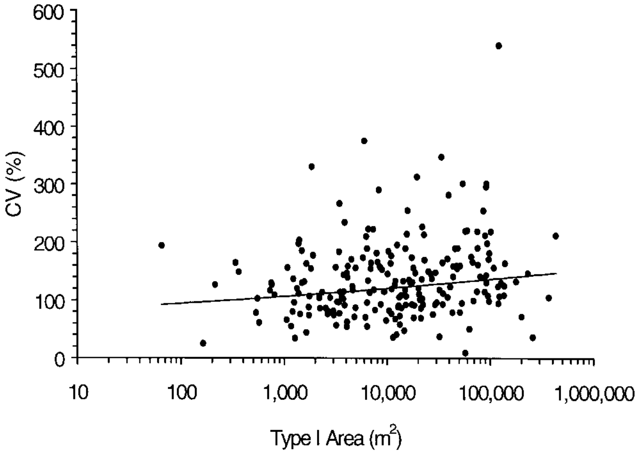

FIG. 2. Coefficient of variation (CV) of larval sea lamprey density versus area of Type I habitat area for U.S. tributaries of Lakes Huron, Michigan, and Superior during 1996 to 1999.

relation between the coefficient of variation of larval sea lamprey density and Type-I area (m^2), total area (m^2), and reach length (m). All variables were $\log_e$-transformed to normalize the residuals of the model.

Results

The coefficient of variation of larval density ($\log_e$ %) varied with Type-I habitat area ($\log_e$ m^2), but not with total area ($\log_e$ m^2) or reach length ($\log_e$ m) for U.S. tributaries of Lakes Huron, Michigan, and Superior during 1996 to 1999 (adjusted R^2 = 0.033, $F_{3, 210}$ = 3.440, P = 0.018). Variation in larval density was positively related to the amount of Type-I habitat area (Fig. 2; Coefficient = 0.109, SE = 0.037, t = 2.943; P = 0.004). However, variation in larval density was not related to the total area (Coefficient = 0.010, SE = 0.023, t = 0.430, P = 0.668) or reach length (Coefficient = –0.101, SE = 0.054, t = –1.866, P = 0.063).

Discussion

Variation in larval density increased as the amount of Type-I habitat area increased, which is supported by others who reported high density of larval sea lamprey in preferred habitat (Applegate 1950, Stauffer and Hansen 1958, Wigley 1959, Hardisty and Potter 1971, Manion and McLain 1971, Manion and Smith 1978, Morman *et al.* 1980, Potter 1980). However, only 3% of variability in larval density was explained by Type-I habitat area, total area, and reach length, so much of the variability remains unexplained. Further research is warranted to identify and quantify other factors that contribute to variation in larval sea lamprey density, before considering changes in sampling protocols.

SAMPLING OF LARVAL HABITATS

The current larval sea lamprey sampling protocol dictates that larvae are generally sampled only in Type-I habitat and assumes that larval density and variance in Type-II habitat is a constant proportion of larval density and variance in Type-I habitat (Slade *et al.* 2003). This assumed constant proportionality could have a large influence on estimates of larval abundance in streams with a predominance of Type-II habitat, yet a broad survey of the relationship between densities in these two habitats has not been conducted. In this analysis, larval sea lamprey density in Type-II and Type-I habitat was compared in a set of streams where larvae were sampled in both habitat types. The effect of reallocating sampling effort between habitat strata on sampling precision, and the effect of sampling effort on precision of abundance estimates was also examined.

Methods

Data from eight experimental streams selected in 1996 to evaluate the sterile-male release technique (Jones *et al.* 2003*;* Twohey *et al.* 2003) were used to evaluate larval density and sampling effort in Type-I and Type-II habitat (Stokely Creek and the Carp, Wolf, Rock, Big Garlic, Misery, and Middle rivers). Larval density and habitat amount were estimated using a modified quantitative assessment survey (QAS) protocol (Slade *et al.* 2003), in which both Type-I and Type-II habitat were sampled. Data collected from these streams in 2000, at which time four year-classes of larvae had been established, were analyzed. Data collected from the Goulais River in 1998, where sampling included Type-I and Type-II habitat, was also examined.

Ratio of Larval Density

The accuracy in estimated larval abundance in Type-II habitat that results from the use of a constant ratio of average larval density in Type-II and Type-I habitat was quantified. The current sampling protocol assumes that the average larval density in Type-II habitat is 27% of the average larval density in Type-I habitat. For each study stream, the larval abundance in Type-II habitat that was observed during stream surveys (observed abundance) was compared to the larval abundance predicted from the larval density in Type-I habitat (predicted abundance). Accuracy was calculated as the ratio of the observed abundance to the predicted abundance.

Allocation of Sampling Effort

The optimal allocation of effort among habitat strata for each study stream was determined using a non-parametric bootstrap procedure. The weighted mean density $\bar{y}_{st}$ (Rice 1995) is:

$$\bar{y}_{st} = \sum W_t \bar{y}_t \quad (1)$$

$$W_t = \frac{A_t}{A} \quad (2)$$

Where W_t is the weight assigned to habitat stratum t, $\bar{y}_t$ is the density in stratum t, A_t is the area in stratum t, and A is the total area of habitat used by larval sea lamprey. The standard error of the weighted mean stream density is:

$$s_{(\bar{y}_{st})} = \sqrt{\sum \frac{W_t^2 s_t^2}{n_t}} \quad (3)$$

Where s_t^2 is the density variance within stratum t, and n_t is the number of plots sampled in stratum t. Sampling effort was fixed at the observed range of the field data, from 38 to 105 plots per stream and then re-sampled the data 1,050 times, with replacement, for all combinations of n_1 and n_2, with the stipulation that each $n_t \geq 3$. The performance of each combination of n_1 and n_2 was assessed by averaging the coefficient of variation ($s_{(\bar{y}_{st})}/\bar{y}_{st}$) over all simulations. The optimal allocation of sampling effort was judged to be that combination of n_1 and n_2 that minimized the mean coefficient of variation.

Level of Optimal Sampling Effort

Simulation was used to determine the level of sampling effort that would achieve desired levels of sampling precision. A re-sampling approach was used to determine the performance of various sampling intensities relative to three target levels of precision, given the optimal allocation of sampling effort among habitat strata from the previous analysis. For each stream, the catch was simulated 150 times in each habitat stratum across a range of sampling intensities (n_t from 20 to 270). For each simulation, the mean density, $\bar{y}_{st}$, and the width of an approximate 95% confidence interval were determined:

$$CI = 2s_{(\bar{y}_{st})}t_q \quad (4)$$

The CI was compared to a specified level of d, the tolerable error of the mean. A simulation was deemed to be successful if $CI < d$ where the specified values of d were $\bar{y}_{st}$, $0.5 \times \bar{y}_{st}$, and $0.33 \times \bar{y}_{st}$. The performance of each level of sampling intensity was defined by the percentage of successful simulations.

Results

Ratio of Larval Density

The ratio of observed larval density in Type-II to Type-I habitat ranged from 0.16 to 0.77 among the eight study streams (Table 2). The mean observed density among streams differed greatly from the mean predicted density based on a fixed ratio of larval density between Type-I and Type-II. The fixed-ratio model overestimated larval abundance in three of eight streams (2 to 47%) and underestimated larval abundance in five of eight streams (12 to 44%).

Allocation of Sampling Effort

The optimal allocation of sampling effort among habitat strata is determined by W_t and s_t^2, and varies

TABLE 2. The mean density of larval sea lampreys (number/5-m^2) observed in Type-I and Type-II habitat in eight study streams in Lake Superior and estimated bias in the population estimate (ratio of observed population estimate to the predicted estimate assuming Type-II = 0.27 × Type-I density).

Stream	Type-I	Type-II	Type-II/ Type-I	1/Bias
Carp	32.9	14.9	0.45	0.74
Stokely	3.4	2.0	0.59	0.62
Wolf	21.3	5.6	0.26	1.02
Goulais	13.8	8.2	0.59	0.56
Rock	9.5	7.3	0.77	0.88
Garlic	20.3	4.0	0.20	1.11
Misery	27.1	4.3	0.16	1.47
Middle	15.9	9.3	0.58	0.65
Mean	18.0	7.0	0.45	0.88

among streams with the proportion of habitat types and the variability of larval density within each habitat. For these data, the mean proportion of Type-II habitat was usually much greater than Type-I habitat ($\bar{x}$ = 75%), but ranged from 22% to 93%. The variance of density within Type-I habitat was greater than the variance of density within Type-II habitat in all streams. The allocation among strata that minimized the coefficient of variation was variable, but suggested that more sampling effort should be allocated to Type-II habitat in most streams. In contrast, in the Rock River, where Type-I habitat was predominant, the coefficient of variation was minimized when more than 90% of sampling effort was applied to Type-I habitat.

In most cases, precision of larval density estimates improved by re-allocating sampling effort into Type-II habitat, with no change in total sampling effort. Sampling precision increased by 2% to 48% overall ($\bar{x}$ = 23%) as sampling increased in Type-II habitat (Fig. 3). For example, the coefficient of variation in the Goulais River decreased from 49% with n_1 = 35 and n_2 = 3 to 22% with n_1 = 8 and n_2 = 30. In contrast, in the Rock River, precision was maximized by sampling more Type-I habitat because of the predominance of Type-I habitat in that stream.

Optimal Sampling Effort

Current levels of sampling effort were sufficient to meet a precision target of $CI = \bar{y}_{st}$ in all but one stream, given the allocation of effort among habitat strata indicated by the previous analysis (Table 3). However, significantly greater sampling effort would be required to achieve higher levels of precision in most streams. For $CI = 0.5 \times \bar{y}_{st}$, sampling effort would need to be increased from the current mean of 58 samples to about 90 samples. For $CI = 0.33 \times \bar{y}_{st}$, mean sampling effort would need to be doubled over that required for $CI = 0.5 \times \bar{y}_{st}$.

Discussion

Using a fixed proportion of larval density in Type-I and Type-II habitat would not likely produce accurate estimates of larval sea lamprey abundance in most streams. The fixed-ratio model assumes no variance in larval density in Type-II habitat, but larval density varies substantially in Type-II habitat, which could lead to inaccurate estimates of larval abundance, especially in streams with large Type-II habitat area.

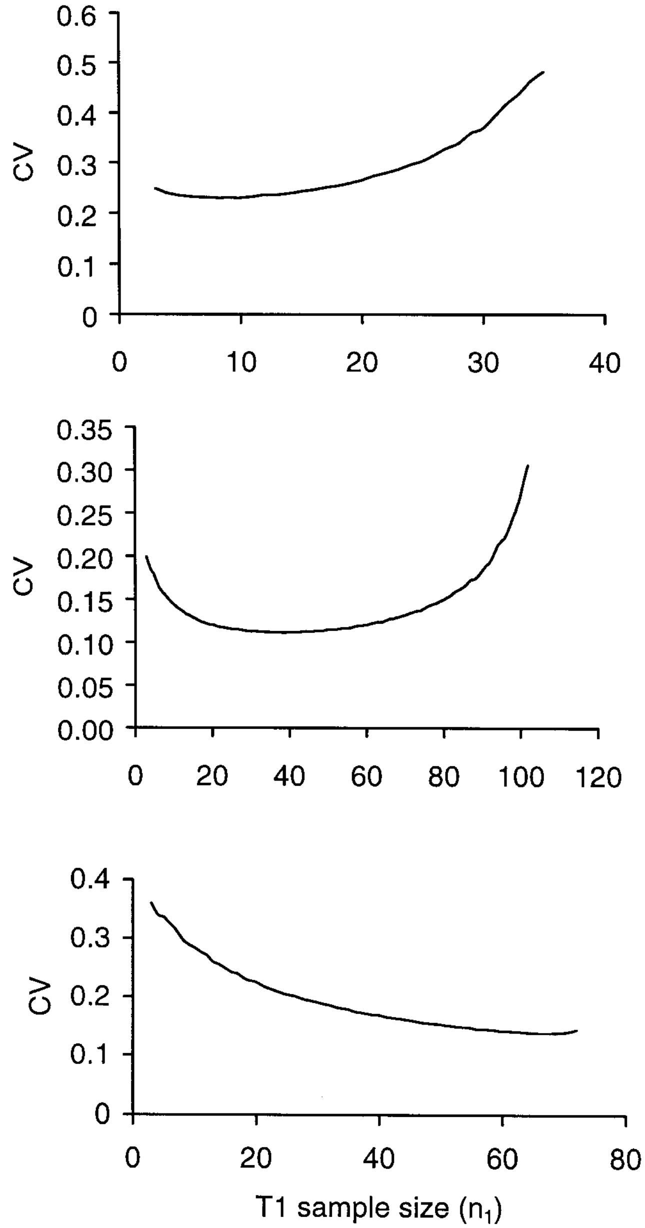

FIG. 3. Coefficient of variation versus number of samples (n_1) in Type-I habitat in the Goulais River (upper panel), Middle River (middle panel), and Rock River (lower panel).

Allocating sampling effort from Type-I habitat into Type-II habitat could increase the precision of larval sea lamprey density estimates. The optimal allocation of sampling effort between Type-I and Type-II habitat varied among streams depending on habitat composition and variability of larval density within each habitat. Therefore, the optimal alloca-

TABLE 3. Current number of samples and the number of samples required for three levels of precision (the width of the 95% confidence interval, expressed as a fraction of the mean $\bar{y}_{st}$) with 80% power in eight study streams in Lake Superior.

Stream	Current	$\bar{y}_{st}$	$0.5 \times \bar{y}_{st}$	$0.33 \times \bar{y}_{st}$
Carp	46	< 20	40	90
Stokely	60	40	130	> 270
Wolf	38	35	120	255
Goulais	38	40	135	270
Rock	75	< 20	75	165
Garlic	50	< 20	55	115
Misery	52	25	80	165
Middle	105	20	70	255
Mean	58	< 27	88	> 198

tion of sampling effort should be based on stream-specific estimates of the available habitat and sampling variance within each habitat.

Stream-specific estimates of sampling variance are not available for all streams, so an initial sampling design should consist of sampling Type-II habitat at ≥ 50% of the rate of Type-I habitat. This level of sampling effort would allow for some measure of the sampling variance in Type-II habitat in each stream, while maintaining the current level of sampling in Type-I habitat. Maintenance of the current level of sampling effort in Type-I habitat is critical for collecting a sample of larvae that adequately describes the size structure of the larval population in many streams and to avoid adversely affecting the time series of data collected under the current sampling protocol.

Decreasing the confidence interval of larval density estimates to one-half or one-third of the mean density would require substantial increases in sampling effort in most streams. Current sampling effort would need to be increased by 52% to increase precision of the larval density to 50% of the mean and by more than 240% to increase precision of the larval density estimate to 33% of the mean. Such levels of precision are probably not feasible with current larval sampling methods, given the large number of streams that must be surveyed each year to support the overall control program.

PREDICTING GROWTH RATES

Estimates of newly transformed sea lampreys produced in Great Lakes streams in year t+1 are based on estimates of the size structure of the larval population at the end of the growing season in year t. (Slade *et al.* 2003). However, sea lamprey larvae are collected from April to October in year t, requiring the end of season size structure to be estimated from the size structure at time of collection, using stream-specific growth rates. The degree to which growth varies among streams and within streams among years is not well understood. In this analysis, variability in mean length of the first cohort of larval sea lampreys established following chemical treatment was compared among streams and years to determine if these factors significantly affected estimated numbers of larval sea lampreys in Great Lakes streams. length-frequency distributions of larval sea lampreys collected by qualitative and quantitative sampling were also compared to see if stream- and year-specific growth could be accurately indexed using supplementary collections.

Methods

Variation in Growth Within and Among Streams

Historical stream survey data were reviewed to find suitable larval sea lamprey collections for analyzing variation in growth among and within streams. Criteria for inclusion in the analysis included: (1) the most recently recruited year class was easily identifiable in the collection when the stream was sampled following chemical treatment, (2) surveys for comparisons among streams occurred within 14 calendar days of one another, (3) surveys for comparisons among years occurred within the same two weeks each year, and (4) samples included 30 or more sea lampreys of the initial reestablished cohort.

For streams that had sufficient numbers of larval sea lampreys collected in the same years, analysis of variance (ANOVA) was used to partition the variance in mean length at the time of survey among streams and years. In Lake Ontario streams, larval collections were sufficient for analysis from four streams (Bronte Creek, Bowmanville Creek, Wilmot Creek, and Cobourg Brook) in four years (1981, 1984, 1987, and 1993). In Lake Superior streams, larval collections were sufficient for analysis from 4 streams (Gravel, Cypress, Wolf, and Neebing-McIntyre rivers) in 2 years (1991 and 1995). Because prediction of metamorphosis is linked to geographic region (see below), analysis of larval size of the same year class was restricted to streams within the same geographic area. For streams in Lake Ontario, Wilmot Creek was treated in 1993, so data were not available for this stream in that year. Variability in growth within and among streams was therefore analyzed for all four streams in 3 years (1981, 1984, and 1987) and for three streams (Bronte Creek, Bowmanville Creek, and Cobourg Brook) in all 4 years.

Qualitative Versus Quantitative Sampling

A quantitative assessment survey (QAS), modified for the study of compensatory mechanisms (Jones *et al.* 2003), was conducted during July 1999 on Lewis Creek, a tributary of Lake Champlain (N44°14″47′, W73°16″42′). A supplemental (qualitative) larval assessment was conducted during July 1999 on Lewis Creek using a 250 to 500 Volt DC electro-fisher. Qualitative sampling locations were contained within a 2.3-km reach, whereas QAS sampling locations encompassed the entire 6.0-km reach of Lewis Creek. The smaller reach was selected for qualitative sampling where high larval densities were found in previous sampling. Qualitative surveys were conducted by selectively sampling optimal sea lamprey habitat for a total sampling effort of three hours. Length-frequency histograms from qualitative and quantitative samples were compared to determine if qualitative and quantitative samples represented the population size frequency equally well.

Results

Variation in Growth Within and Among Streams

In Lake Ontario streams, sampled larvae were age-0 recruits from the year when sampling occurred. Mean larval length varied significantly among streams and years (Table 4). Significant interaction terms indicated that variability among streams was not consistent among years, though larvae were generally smallest in Wilmot Creek and largest in Bronte Creek and larvae were generally smaller in 1984 and 1993 than in 1981 or 1987 (Fig. 4).

TABLE 4. Analysis of variance of stream and year effects on length of larval sea lampreys at 1.5 years of age in Bronte Creek, Bowmanville Creek, Wilmot Creek, and Cobourg Brook, Lake Ontario in 1981, 1984, 1987, and 1993. Wilmot Creek was treated in 1993, so data were not available for this stream in that year.

Source	df	MS	F	P
Stream	2	623.94	20.02	< 0.01
Year	3	1,179.70	37.86	< 0.01
Stream × Year	6	434.95	13.96	< 0.01
Error	840	31.16		

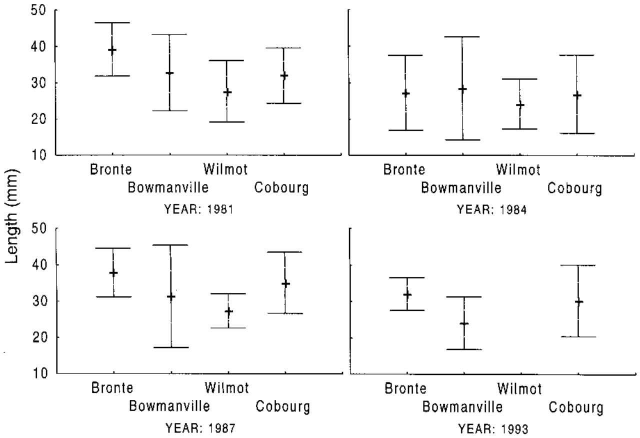

FIG. 4. Mean length of larval sea lampreys from Bronte Creek, Bowmanville Creek, Wilmot Creek, and Cobourg Brook, Lake Ontario in 1981, 1984, 1987, and 1993. The high-low-close symbols depict mean length ± 1.96 SE for each stream and year.

In Lake Superior streams, sampled larvae were age-1 recruits from the cohort recruited in the year prior to sampling. Mean larval length varied more among streams than among years (Table 5). A significant interaction term indicated that variability among streams was not consistent among years, though larvae were generally smallest in the Gravel River and largest in the Wolf and Neebing-McIntyre rivers (Fig. 5).

Qualitative Versus Quantitative Sampling

Qualitative sampling yielded a larger proportion of large larvae than QAS sampling, though total

TABLE 5. Analysis of variance of stream and year effects on length of larval sea lamprey at 1.5 years of age in the Gravel, Cypress, Wolf, and Neebing-McIntyre rivers, Lake Superior in 1991 and 1995.

Source	df	MS	F	P
Stream	3	5,902.08	130.65	< 0.01
Year	1	676.82	14.98	< 0.01
Stream × Year	3	206.92	4.58	< 0.01
Error	957	45.18		

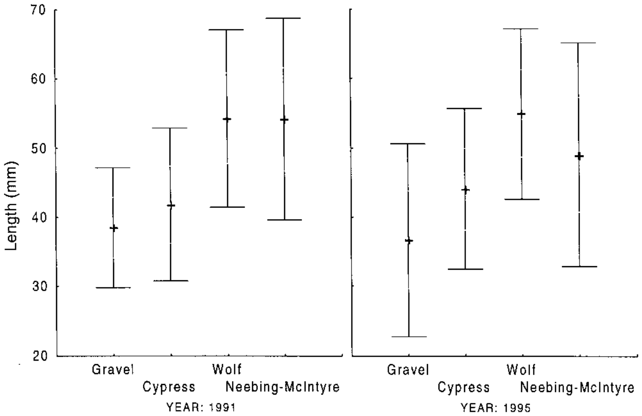

FIG. 5. Mean length of larval sea lampreys from the Gravel, Cypress, Wolf, and Neebing-McIntyre rivers, Lake Superior in 1991 and 1995. The high-low-close symbols depict mean length ± 1.96 SE for each stream and year.

numbers of larvae and sampling time were much less for qualitative than for QAS sampling. The length range of sampled larvae was similar between the two sampling techniques, though a higher proportion of large larvae were sampled by qualitative than by QAS sampling (Fig. 6). A larger number of larvae were obtained by QAS sampling (N = 856 larvae) than by qualitative sampling (N = 249 larvae), though QAS sampling time (two weeks of sampling) greatly exceeded qualitative sampling time (3 hours of sampling).

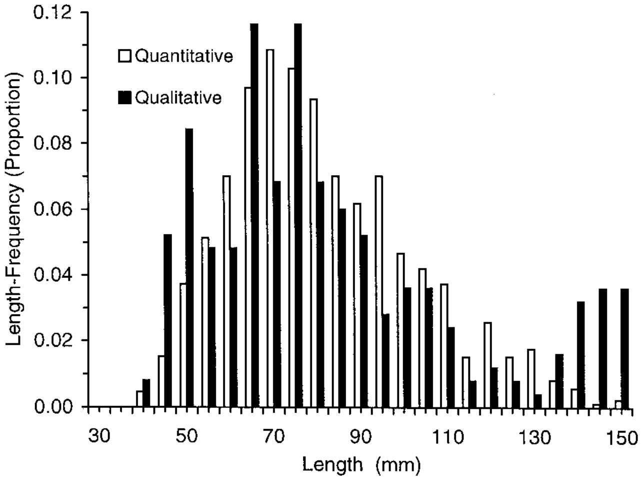

FIG. 6. Length-frequency of larval sea lampreys sampled with quantitative (N = 856) and qualitative (N = 249) sampling protocols in Lewis Creek, Lake Champlain, 1999.

Discussion

Larval sea lamprey growth varied significantly among streams and years, which is consistent with previous studies that indicate variability in larval growth likely derives from watershed characteristics, which define the productivity of each stream and contribute to variation in growth among streams (Purvis 1979, Potter 1980, Young *et al.* 1990), and annual environmental characteristics, such as temperature and precipitation, which contribute to variability in growth within streams (Manion and McLain 1971, Young *et al.* 1990). Larval density also influences larval growth rate both within and among streams (Manion and Smith 1978, Morman 1987, Jones *et al.* 2003), and partly depends on the number of adult sea lampreys that migrate into a stream, the number of adult sea lampreys that spawn, and the proportion of eggs that survive, each of which also varies annually among and within streams depending on watershed and environmental conditions. However, the streams used in this analysis were not selected randomly, so the findings may be an artifact of the streams selected. Further analysis of this subject is warranted, to confirm the findings of this study.

These analyses were based on comparisons of larval growth rates during their first two growing seasons, just as stream-specific growth rates used in the ESTR model are largely based on estimates of young larvae. However, accurate prediction of the number of sea lamprey expected to metamorphose requires forecasts of growth for larger, older larvae. Current methods, as well as the analysis presented here, implicitly assume that older larvae experience similar growth rates as the younger larvae for which growth data are more readily available. Growth rates may diminish as larvae become older, as is true for most fishes. Therefore, the assumption of age-independent growth rates should be evaluated through intensive growth studies of entire stream populations of larvae.

Growth rates used to estimate numbers of transforming sea lampreys in Great Lakes tributaries should be stream-specific, and year-specific information should be included when estimating numbers of transforming sea lampreys in some streams. Year-specific estimates of larval growth would reduce the uncertainty about the size structure of the larval population at the end of the growing season. For example, in Lake Ontario streams, annual variability in growth accounted for most of the observed differences in sea lamprey lengths collected from multiple streams in multiple years. In Lake Superior, annual variability in growth was not as significant as in Lake Ontario streams, perhaps because Lake Superior streams are typically larger than Lake Ontario streams or the growing season in Lake Superior is shorter than in Lake Ontario. Larger streams may buffer large annual variation in temperature and provide more stable habitats and food supplies, which positively influence growth (Morman 1987). A shorter growing season may reduce annual fluctuations in growth because annual variation in growing conditions is limited by the time available to cause a measurable effect. Regardless of the source or magnitude, annual variation in larval sea lamprey growth within streams contributes greatly to the observed size of larval sea lampreys at the end of the growing season, and consequently, to uncertainty around estimates of parasitic sea lamprey production.

To reduce the effects of uncertainty in growth estimates of parasitic sea lamprey production, larvae should be sampled in streams close to the end of the growing season. Sampling at the end of the growing season would provide explicit information on the size structure of the larval sea lamprey population, and thereby enable control agents to forego use of predictive growth models. The benefit of obtaining better information regarding the pre-metamorphic length of the larval population has to be weighed against the cost of late summer sampling in streams with the potential for chemical treatment the following year. The benefit of obtaining more accurate data on larval sea lamprey growth would be the decision to treat streams that contain more transforming sea lampreys *in lieu* of streams that contain fewer transforming sea lampreys.

Qualitative and quantitative sampling yielded similar length frequencies, though qualitative sampling produced a length-frequency with a greater proportion of large larvae than quantitative sampling. A higher proportion of large larvae in qualitative samples could have been caused by the higher voltage of electro-fishing equipment used, which may have a higher capture efficiency for larger size classes, or because the operator selected habitat that contained large larvae. Qualitative sampling may be useful for collecting a large sample of larvae with minimal effort (249 larvae captured in three hours of qualitative sampling, compared to 856 larvae captured in 2 weeks of QAS sampling), if sample locations are located throughout the stream and not restricted to one reach. Qualitative sampling may overestimate the abundance of transforming sea lampreys if sampling is restricted to a small portion of the stream that contains a high abundance of large larvae. Consequently, qualitative sampling needs to be further evaluated for estimating larval length-frequency.

PREDICTING METAMORPHOSIS

Estimates of metamorphosing sea lampreys produced in Great Lakes streams are used to rank streams for chemical treatment (Christie *et al.* 2003). Length-dependent logistic models are used to estimate the number of metamorphosed sea lampreys expected from Great Lakes tributaries, based on the estimated size structure of the larval population at the end of the growing season. These logistic models have been developed for 14 different geographical regions around the Great Lakes (Fig. 7). The appropriateness of regional models for predicting rates of metamorphosis of larval sea lampreys from streams in each region has never been evaluated. In this analysis, variability in transformation rates of larval sea lampreys among streams and regions was examined to determine if transformation rates were more homogeneous within regions than among regions. If transformation rates are more homogeneous within regions than among regions, regional transformation curves could be appropriately applied to all streams within a region. However, if transformation rates were more homogeneous among regions than within regions, alternative models would need to be developed.

Methods

Data on length and life stage (either larva or recently transformed sea lamprey) were available for 186 sea lamprey populations in Great Lakes streams during 1969 to 1996, where a population was defined as the animals present in an individual stream and year. For 80 populations, data for fewer than three recently metamorphosed animals were available, and were excluded from further analysis. For 106 populations, lengths of sea lampreys were adjusted to reflect the size structure of the population at the end of the previous growing season, based on the date of collection and assumed stream-specific growth rates for larvae and assuming no growth for recently transformed animals (Slade *et al.* 2003). A logistic regression model was then estimated to relate the probability of metamorphosis (p) to sea lamprey length in mm (L) for each population separately,

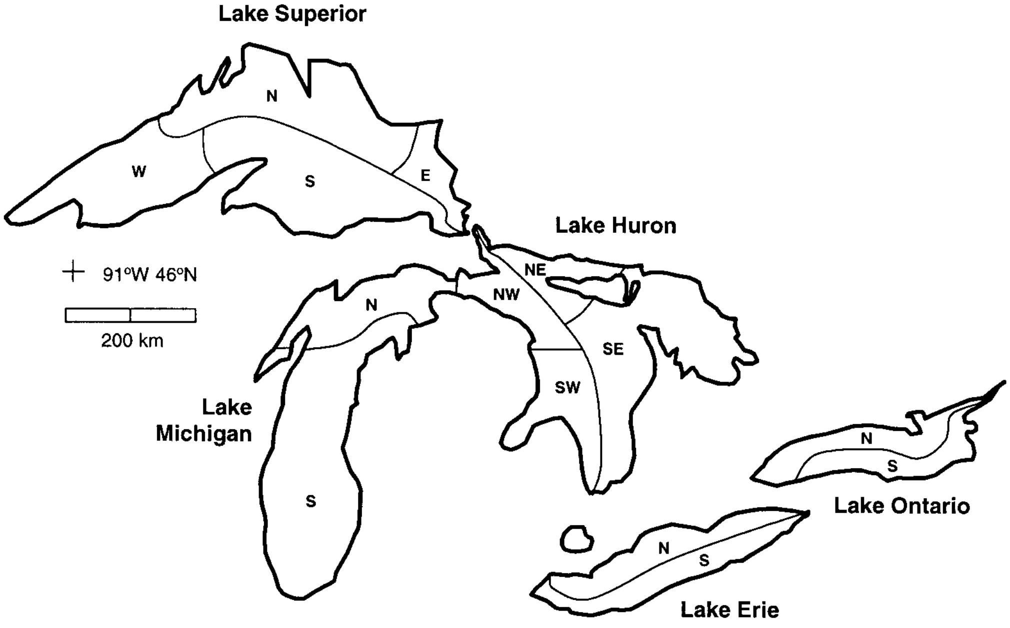

FIG. 7. Geographic regions used in developing models to predict metamorphosis of larval sea lampreys in Great Lakes streams.

$$p = \frac{e^{b_0 + b_1 L}}{(1 + e^{b_0 + b_1 L})} \tag{5}$$

Where b_0 and b_1 are estimated parameters. Only those populations for which the regressions converged were used in subsequent analyses. Logistic regression models failed to converge if: (1) all of the animals collected were larvae (no transformers were collected, so length at transformation could not be estimated); or (2) all of the animals shorter than length L were larvae and all of the animals longer than length L were transformers (lengths of larvae and transformers did not overlap, so several slopes were equally good predictors of length at transformation).

Relative variability among streams and regions in predicting metamorphosis was quantified. Four populations were selected with length-frequency distributions representative of the distributions observed among all populations. For each length-frequency distribution and each stream-specific logistic regression model, the proportion of larvae that would be expected to metamorphose the following year was estimated:

$$M = \frac{\sum \hat{p}_i n_i}{\sum n_i} \tag{6}$$

Where $\hat{p}_i$ is the estimated probability of metamorphosis for larval sea lamprey of length i and n_i is the number of larval sea lampreys of length i. Geographical patterns were examined within the variability of these predicted proportions among streams. To determine if different models should be used for streams in different regions, analysis of variance was used to determine if the predicted proportion of metamorphosed animals varied significantly among regions and streams. If significant differences were found among regions, the Tukey method was used to test pair-wise comparisons. Variance components analysis was used to quantify contributions to the variance in metamorphosis of region, stream (within region), and year (within stream).

Results

Only 79 of 106 populations had enough information on individual sea lamprey for logistic regression convergence (Table 6). From these 79 populations, 4 stream-years (Little Salmon River, 1982, Lake Ontario; Bad River, 1991, Lake Superior; Manistique River, 1989, Lake Michigan; and Chikanishing River, 1972, Lake Huron) had end-of-season length-frequency distributions that represented the range of length frequency distributions observed among all populations (Fig. 8).

TABLE 6. Number of streams, stream-years, and sea lampreys within regions of the Great Lakes used for predicting larval metamorphosis.

Lake	Region	Number		
		Streams	Stream-years	Lamprey
Superior	N	4	6	1,482
	E	4	9	1,611
	W	7	11	18,232
	S	6	7	7,885
Michigan	N	9	10	3,204
	S	5	8	6,864
Huron	NW	0	0	0
	SW	2	2	757
	NE	2	6	1,388
	SE	7	7	930
Erie	N	0	0	0
	S	2	2	621
Ontario	N	3	6	1,552
	S	4	5	2,558
Total		55	79	47,084

The estimated proportion of sea lamprey larvae that would metamorphose, based on the application of 79 logistic regression models, was similar among the four selected length-frequencies, so the results of one length frequency for the Manistique River are shown as an example. For all four length-frequencies, the predicted proportion of larvae that would metamorphose varied significantly among regions ($F_{11,\ 24} \geq 6$, $P \leq 0.001$) and among streams within regions ($F_{43,\ 24} \geq 2.1$, $P \leq 0.021$) (Fig. 9). However, for three of four length frequencies, only the two most extreme regions differed significantly in the predicted proportion of larvae that would metamorphose. For example, Ontario N had a higher predicted proportion of metamorphosing larvae than Michigan N, Superior N, Huron SE, and Superior S, and Michigan N had a lower predicted proportion of metamorphosing larvae than Huron SW, Ontario S, and Superior E.

For all four length-frequencies, variability in predicted metamorphosis was greater among years than among regions or streams (Table 7). For three of four length-frequencies, variability in predicted metamorphosis was greater among regions than among streams. Predicted metamorphosis for 15 streams with data from multiple years varied greatly among years (Fig. 10).

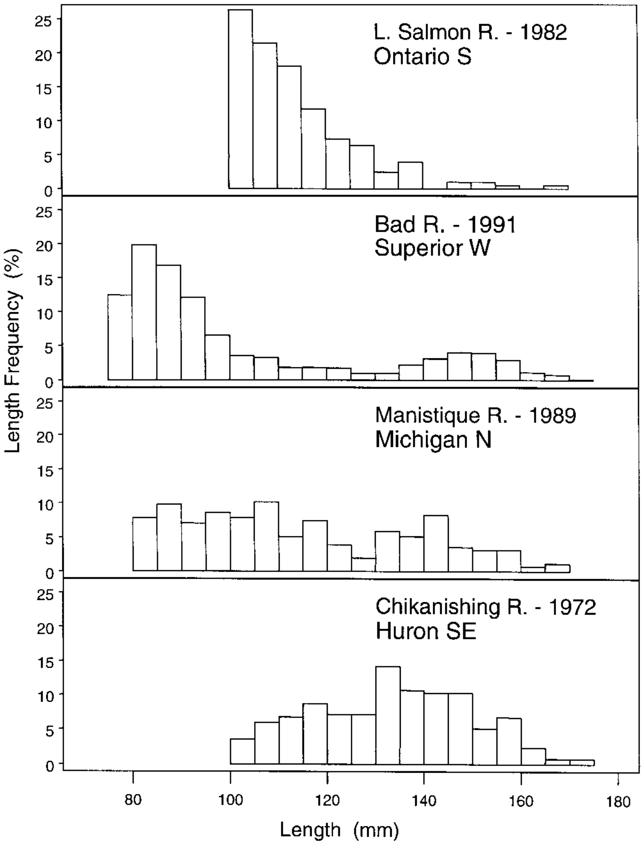

FIG. 8. Length-frequency of larval sea lamprey populations in the Little Salmon River, Lake Ontario, in 1982, the Bad River, Lake Superior, in 1991, the Manistique River, Lake Michigan, in 1989, and the Chikanashing River, Lake Huron, in 1972.

The rate of metamorphosis of larval sea lampreys did not vary consistently among years. More than one stream was occasionally sampled in the same pair of years, thereby permitting direct examination of year effects. Based on this subset of streams, models of larval metamorphosis developed from 1995 populations did not yield consistently higher or lower rates of metamorphosis than those from 1987 or 1991 populations (Table 8).

Discussion

Metamorphosis varied more among years than within or among regions and also varied significantly among streams within regions. Therefore, metamorphosis is not homogeneous within regions and regional metamorphosis models may not accurately estimate the number of larval sea lampreys that will transform. Furthermore, regions cannot be redefined to contain only streams with similar models for probability of metamorphosis, because rates

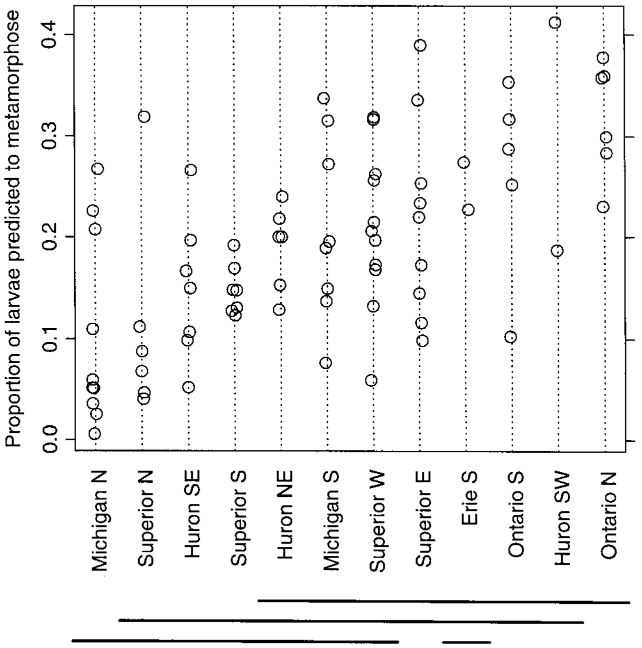

FIG. 9. Predicted metamorphosis from logistic regressions of 79 larval sea lamprey populations applied to the length-frequency distribution of larval sea lampreys in the Manistique River in 1989. Horizontal lines group regions with metamorphosis estimates that were not significantly different for three of four length-frequencies based on the results of Tukey multiple comparisons.

of metamorphosis overlapped greatly among the three upper Great Lakes. Finally, little information is available on rates of metamorphosis in tributaries to Lake Erie and western Lake Huron from which to develop models of metamorphosis.

The amount of variability in predicted metamorphosis that is caused by variation in estimates of larval growth needs to be further evaluated. Mean daily growth rate and time of sampling both affect the adjusted lengths that were used in the logistic regression model for each stream. The large among-year variation in growth rates reported in the previous section suggests that uncertainty about the

TABLE 7. Estimated variance components of the proportion of larvae predicted to metamorphose, based on logistic regressions of 79 sea lamprey populations applied to four length-frequency distributions for four populations.

	Variance component		
Population	Region	Stream	Year
Little Salmon River, 1982	0.0007	0.0011	0.0026
Bad River, 1991	0.0010	0.0002	0.0018
Manistique River, 1989	0.0026	0.0020	0.0054
Chikanishing River, 1972	0.0100	0.0084	0.0205

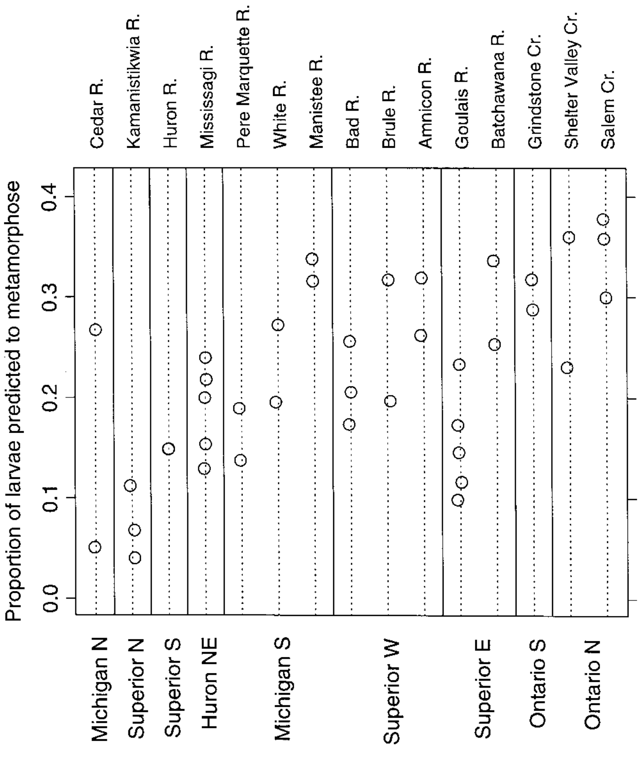

FIG. 10. Predicted metamorphosis of sea lampreys from 15 Great Lakes streams with observations in multiple years. Logistic regressions were applied to the length-frequency distribution of the Manistique River in 1989. Dotted lines connect annual predictions for individual streams and solid lines group streams by region.

TABLE 8. Effect of year on predicted rates of sea lamprey metamorphosis (proportion of larvae predicted to metamorphose) from four Great Lakes streams. Logistic regression was applied to the length-frequency distribution of the Manistique River in 1989. Dashes indicate that data were insufficient to fit models for those regions in those years.

Region	Stream	1987	1991	1995
Michigan – S	Pere Marquette	0.19	—	0.14
Michigan – S	White	0.20	—	0.27
Huron – NE	Mississagi	0.20	0.15	0.24
Superior – W	Bad	—	0.26	0.17

actual growth rate to apply to a specific stream and year may explain much of the otherwise unexplained variation in the logistic regression models shown here. If the larval growth rate were overestimated for a population, the logistic regression model would underestimate the proportion of metamorphosing larvae when applied to an accurate end-of-season length-frequency of another population. Estimates of year- and stream-specific growth rates or end-of-season length-frequencies would permit an evaluation of how uncertainty in estimated growth of larval sea lampreys influences estimates of the rate of metamorphosis.

In the face of variability in rates of metamorphosis among years, streams and regions, models should be refined to explain more of the apparent variability in rates of metamorphosis, or the stream treatment process should be made robust to variability in rates of metamorphosis. To refine the metamorphosis models, individual models could be developed for each stream, which would require sampling adequate numbers of sea lampreys during stream treatments. Stream treatments would need to occur in late summer or fall when metamorphosing animals are present during treatment and enough metamorphosing animals would need to be sampled from which to estimate a model. These two requirements may make stream-specific models of metamorphosis impractical, because fewer than half of the populations in this analysis (79 out of 186) had adequate samples of larval sea lampreys for estimating a logistic model.

Stream-specific models would only be useful for more than one year if annual variability in the rate of metamorphosis could be explained. To quantify factors that affect the proportion of larval sea lampreys that will metamorphose, transformation rates would need to be studied over several years in several streams. Many factors influence the rate of sea lamprey metamorphosis (Youson 2003), including stream-specific effects such as water temperature (Purvis 1980, Young *et al.* 1990, Holmes *et al.* 1994) and conductivity (Young *et al.* 1990), population-specific effects such as larval sea lamprey density (Manion and Smith 1978, Purvis 1980, Morman 1987), and larva-specific effects such as length (Manion and Smith 1978, Holmes *et al.* 1994), weight, lipid content, and condition factor (Potter *et al.* 1978, Holmes *et al.* 1994), and sex (Purvis 1979). Rates of metamorphosis differ between males and females for northern brook lamprey, *Ichthyomyzon fossor* (Purvis 1970) and least brook lamprey, *Lampetra aepyptera* (Docker and Beamish 1994), so may also differ for sea lampreys. Photoperiod (Holmes *et al.* 1994) and age (Manion and Smith 1978, Purvis 1979, Purvis 1980) do not seem to affect metamorphosis.

To make the stream treatment process robust to variability in metamorphic rates, models of metamorphosis could be eliminated altogether, and stream ranking could be based directly on larval production. Currently, streams are ranked based on transformer production to maximize the immediate benefit to the resource, because treating a stream that will produce 100 transformers will reduce damage in the lakes in the following year more than treating a stream with 10,000 larvae that will produce no transformers. However, when a stream is treated, larvae of all sizes and ages are affected, so treating a stream when the number of larvae predicted to metamorphose the following year is not particularly high may still effectively reduce sea lamprey production to the lake several years into the future. The long-term effect of this approach on the production of parasitic sea lampreys in the Great Lakes needs to be further evaluated, perhaps by modeling larval production under different scenarios of chemical treatment, as described above.

RECOMMENDATIONS

The 3-year prediction capability of ESTR should be used to identify streams with potentially high residual populations of larval sea lampreys and to schedule such streams for larval assessment. Two-year and 3-year ESTR model predictions should be compared to empirical estimates to improve the accuracy of the ESTR model through modification of input parameters.

Further research is needed to identify and quantify factors that contribute to variation in larval density. Variation in larval density increased as the amount of Type-I habitat area increased, but only 3% of variability in larval density was explained by Type-I habitat area, total area, and reach length. Therefore, much of the variability remains unexplained and needs to be further evaluated before changes in sampling are warranted.

Type-II larval habitat should be sampled in all streams at 50% of the rate of sampling of Type-I habitat, while maintaining current sampling effort in Type-I habitat. Coincident with increased sampling in Type-II habitat, population density and sampling variance should be quantified in Type-II habitat in each stream to determine how much density varies within and among streams. Sampling effort should be allocated optimally between Type-I and Type-II habitat, based on habitat area and sampling variance, when data are available. Costs of implementing this new sampling allocation should be weighed against the benefits of increased precision of resulting estimates.

Further study of methods that will reduce uncertainty in estimates of parasitic sea lamprey production is needed, especially to reduce uncertainty associated with estimates of larval length at the end of the growing season and rate of metamorphosis. Costs and benefits should be estimated for (1) refining growth and metamorphosis models and (2) sampling larvae at the end of the growing season for length frequency information. The effects of uncertainty in growth and metamorphic rates on the stream selection process should be quantified.

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