GREAT LAKES FISHERY COMMISSION

2007 Project Completion Report[1]

Sea lamprey population dynamics: updating demographic models and application to a novel control strategy

by:

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ABSTRACT:

Integrated management of sea lampreys requires the use of population models to compare the outcomes of a variety of management strategies. The reliability of decisions made based on population models is directly related to the accuracy of the parameters describing population processes contained within them. In an attempt to update current sea lamprey population models, we have estimated larval growth, recruitment, metamorphosis, and survival parameters using data from quantitative assessments carried out since 1995 as well as additional data collected to directly measure these demographic rates. We have found evidence that sea lamprey growth is non-linear, contrary to previous assumptions used in population models of sea lamprey growth. We have observed high levels of density-independent variation in sea lamprey recruitment, indicating that environmental factors may play a large role in determining year-class strength. We have also developed models of sea lamprey metamorphosis with higher predictive power than existing models. We were unable to generate accurate estimates of larval survival using quantitative assessment data, and recommend that surveys specifically designed to measure larval survival be used if an accurate measure is desired. We have developed an operating model of the entire sea lamprey management process, and included updated estimates of larval demographic rates generated through this study. We have used this model to evaluate the outcome a variety of sea lamprey management decisions. We have also used a variation of this model to explore the potential consequences of genetic manipulation for sea lamprey control, and determined that skewed sea lamprey sex ratios could increase the potential effectiveness of a genetic manipulation of sex determination. Our results also indicate that such a genetic manipulation could be maintained in the sea lamprey population indefinitely, increasing the risk of unintended and irreversible consequences. The operating model of sea lamprey management developed and refined through this study represents a powerful tool for examining the outcomes of management decisions, and our refinements of larval demographics have greatly improved the predictive power of this model.

PRESS RELEASE:

We have developed improved estimates of the population dynamics such as growth and survival of larval sea lampreys in to better understand how these processes influence the effectiveness of sea lamprey management actions. We have incorporated these estimates of larval population processes into a computer model that simulates the entire sea lamprey management process, including management actions such as assessment and chemical treatments as well as biological processes such as growth rates and spawning of adult sea lampreys. By creating a model that simulates all steps of sea lamprey management, we can evaluate potential outcomes of management decisions without actually implementing these decisions in the real world. For example, we have compared the number of parasitic sea lampreys we would expect in Lake Michigan under different methods of selecting streams for chemical treatment. We have also used a variation of this model to explore the consequences of a control strategy that genetically manipulates sex determination in sea lampreys. Such strategies are being developed for the control of common carp in Australia, and while the technology does not currently exist for sea lampreys, it may become a viable control option in the future. Our results show that introducing a gene that causes all offspring to be sons (the so-called “daughterless gene”) could result in a significant reduction in the number of parasitic sea lampreys in the Great Lakes. However, the gene would also become permanently established in the population, presenting a risk to native sea lampreys in the Atlantic Ocean and reducing the capacity of managers to mitigate any unintended consequences. Further research on the viability of genetic techniques for sea lamprey control is needed prior to implementing any strategy relying on genetic modification.

SUMMARY STATEMENT:

Overall we are satisfied with the outcomes of this research project. Under this and other GLFC grants, we have been able to successfully refine estimates of larval population dynamics and to increase understanding of spatial and temporal variation in these parameters. While some of these parameter estimates are the result of projects funded under other grants, there exists substantial overlap between the work done here and those other grants, and we have included the results of other projects here when relevant. A primary contribution of this project has been to use our improved parameter estimates to update a detailed sea lamprey management model, which has allowed us to use the model to explore a variety of questions that are of broad relevance to sea lamprey control. We have also developed a new model to evaluate the efficacy of a hypothetical genetic manipulation of sea lamprey populations. We have produced five manuscripts that are currently in various stages of preparation or review in peer-reviewed journals, and we anticipate the completion of several additional manuscripts in 2008 further demonstrating the utility of the sea lamprey population model developed in part as a result of this project.

The project objectives and outcomes are described below, and further information is included as Appendices.

Objectives and Outcomes:

1) Develop improved estimates of key parameters of sea lamprey population models that describe growth, recruitment, survival, and metamorphosis.

   Growth: We have re-analyzed growth data from past sea lamprey assessment surveys to determine whether a non-linear (von-Bertalanffy) growth model better describes the growth of larval sea lampreys as they approach metamorphosis. We have also examined data from Andrew Treble's research on metamorphosis and Heather Dawson's research on age determination for evidence of non-linear growth. These data do support the use of a non-linear growth model, which is described in more detail in Objective 3 and the associated Appendix.

   Recruitment: We synthesized all available sea lamprey stock-recruitment data as of 2005 and fitted these data to a modified Ricker stock-recruitment model that included environmental factors as well as stock size as predictors of recruitment. This analysis has been included in a manuscript submitted to Transactions of the American Fisheries Society, and is included here as Appendix 1.

   Survival: We have compiled data from quantitative larval surveys that occurred in successive years with no chemical treatments in between, estimated larval age compositions from these surveys using length-based methods, and attempted to estimate survival from age composition estimates. This analysis has been limited by the quality of data available, in that a small number of stream reaches were surveyed in successive years with sufficient numbers of individuals collected to facilitate accurate estimates of age composition and to allow cohorts to be tracked across more than one year. We have been able to generate some estimates of survival on a whole basin, lake, stream, and reach levels, although overall we believe that these estimates are of poor accuracy given the shortage of high-quality data available to conduct this analysis. We recommend that a study be designed specifically to measure larval survival in a variety of streams if an accurate estimate of larval survival is desired. Appendix 2 describes the methods and results of our survival analysis in more detail.

Metamorphosis: As a part of his Master's thesis research (defended successfully in May 2006), Andrew Treble developed new models to predict sea lamprey metamorphosis rates from biological (larval) and environmental (stream) data, and demonstrated that they have superior predictive power to existing models. A manuscript describing these models has been accepted, revised, and resubmitted to the Journal of Great Lakes Research, and is attached as Appendix 3.

2) Investigate factors that could potentially influence temporal and spatial variation in these parameters.

   As part of Heather Dawson's PhD dissertation research (defended successfully in December 2006), we have collected recruitment data from two Lake Superior and two Lake Ontario streams to assess temporal covariation among streams in recruitment and to explore stream-level influences on recruitment. We found little evidence of covariation among streams in temporal patterns of recruitment (year effects), in contrast to findings for other species. Our data also point to the hypothesis that larval and adult habitat quality varies among streams sufficiently to have a strong influence on recruitment rates. These findings are presented and discussed in the aforementioned Appendix 1.

   As part of Gretchen Anderson's Master thesis research (defended successfully in December 2006), we examined patterns of variation in larval growth and recruitment among sea lamprey producing streams, using over 50 years of historical assessment data. We sought to test the hypothesis that differences among streams in the regularity with which they require treatment with lampricides could be explained by differences in either recruitment or growth rates. We found that regularly producing streams had significantly higher rates of recruitment than irregular producers. We interpreted this finding as suggesting that regular producers always experience sufficient recruitment levels in the year immediately following treatment to ensure the need for subsequent treatment when the first post-treatment year-class reaches an average size at which the majority of larvae will enter metamorphosis. These findings are described in a manuscript that has been accepted with revisions, revised, and re-submitted to Transactions of the American Fisheries Society, and a draft of this manuscript is included here as Appendix 4.

3) Incorporate new parameter estimates into existing sea lamprey population models and apply the models to evaluate integrated control strategies.

   We have extensively revised our operating model of sea lamprey management (known as the MUSTR model) to incorporate findings from Objectives 1 and 2. The MUSTR model is a stochastic simulation model of sea lamprey population dynamics and control that operates at the spatial scale a single Great Lake, and has been parameterized to run for each of the five Great Lakes. We have used the model to understand trade-offs between assessment and control expenditures, investigate the effectiveness of different levels of alternative control vs. lampricide control, evaluate the effectiveness of alternative stream ranking algorithms, and to estimate Economic Injury Levels for sea lamprey in each of the Great Lakes. A manuscript describing the MUSTR model is currently being prepared for submission to the Canadian Journal of Fisheries and Aquatic Sciences, and we plan on submitting this manuscript by April 30, 2008. We have attached the abstract of this manuscript as Appendix 5, and other peer-reviewed publications describing the various ways in which it has been used will be submitted in 2008.

4) Evaluate the efficacy of a genetic manipulation option for sea lamprey control.

   Dr. Jones spent 6 months of his sabbatical in 2007 working with researchers at the CSIRO-MAR laboratory in Hobart, Tasmania. They developed a model to simulate genetic manipulation of sea lamprey sex determination, based on theoretical research on Australian carp population control conducted in Tasmania. Model results indicate that existing sex-ratio biases in Great Lakes sea lamprey populations would result in high effectiveness of a control strategy that relied upon genetic manipulation of sex determination, but would also result in the continued presence of the modified gene in the population at equilibrium levels, and thus increased risks of unintended consequences of genetic manipulations. A manuscript describing this model and discussing its results and implications for the future of sea lamprey control in the Great Lakes is attached as Appendix 6.

APPENDIX 1:

Factors affecting recruitment dynamics of Great Lakes sea lamprey (*Petromyzon marinus*) populations

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ABBREVIATED TITLE: Recruitment dynamics of Great Lakes sea lamprey

Abstract

Knowledge of stock-recruitment dynamics is as important for control of pest species such as the sea lamprey (*Petromyzon marinus*) as it is for sustainable harvest management of exploited fish species. Sea lamprey stock-recruitment data combined from streams across the Great Lakes basin into a Ricker stock-recruitment model indicated both compensation (density-dependent survival) and a large amount of density-independent recruitment variation. A mixed-effects model tested factors that might affect recruitment variation, using a Great Lakes dataset comprising 97 stream-years. Lakes Superior and Michigan tributaries, streams with larger numbers of lamprey competitors, and streams regularly requiring lampricide treatment showed significantly higher recruitment. Alkalinity and thermal stability did not affect the observed recruitment pattern among streams. In four long-term study streams we observed significant variation among streams with no evidence of a common pattern of variation among years, when stream and year were modeled as a fixed effect and random effect, respectively. Differences in recruitment among streams were consistent with evidence of quality of spawning and larval habitat among streams. Our findings suggest that management models should account for differences in recruitment dynamics among sea lamprey-producing streams, but not common year effects.

Index words: Stock-recruitment, population dynamics, sea lamprey, recruitment variation

Introduction

Stock-recruitment relationships are widely used in fishery management to inform decisions about sustainable harvest rates for exploited fish populations (c.f. Ricker 1975, Hilborn and Walters 1992). In contrast to this goal of sustaining economically valuable stocks to provide future benefits, the objective for pest species is to remove individuals from the population at a greater rate than they can be replaced. Although the management objective is quite different, understanding the stock-recruitment relationship is equally valuable, because it is the recruitment of the pest species as the population is driven to low levels that will determine whether the rate of control is sufficient to achieve lasting benefits. In this paper we present an empirical analysis of stock and recruitment in an important pest fish species, the Great Lakes sea lamprey (*Petromyzon marinus*), and discuss the implications of our findings for management of this species.

The sea lamprey is a parasitic fish that was a major factor in the collapse of lake trout, whitefish, and chub populations in the Great Lakes during the 1940s and 1950s (Smith and Tibbles 1980). Since the late 1950s, sea lamprey control has been achieved through the use of both chemical and non-chemical (alternative) control methods. Chemical methods have been the primary means of control, and involve the application of a lampricide, 4-nitro-3-(trifluoromethyl) phenol (TFM), to remove larvae from a stream before they become parasites (Smith and Tibbles 1980, Brege *et al.* 2003). When effective these methods are believed to remove between 95 and 99% of the ammocoetes from treated streams (W. Swink, U.S. Geological Survey, Hammond Bay Biological Station, unpublished data). Alternative methods of control use adult trapping (Mullett *et* *al.* 2003), barriers (Hunn and Youngs 1980, Lavis *et al.* 2003), and the release of sterile males (Twohey *et al.* 2003). Pheromones (Li *et al.* 2003, Sorensen and Vrieze 2003) are also being explored as a future alternative to lampricides. The Great Lakes Fishery Commission (GLFC) is seeking to increase their reliance on methods other than lampricides to achieve fishery goals in the Great Lakes (GLFC 2001). These alternative methods all seek to reduce the number of spawners in order to decrease subsequent recruitment, but are unlikely to achieve suppression levels near 100%. Consequently, the degree to which the alternatives are effective will depend on the recruitment dynamics of sea lamprey when spawner abundance is reduced to low levels.

Management actions that aim to reduce reproductive success might not result in concomitant reductions in recruitment, for two reasons. First, sea lamprey populations may compensate for reduced spawning numbers through increased larval survival or growth; in an earlier study we presented evidence for compensation in Great Lakes sea lamprey populations (Jones *et al.* 2003). Second, density-independent factors that affect recruitment, such as winter severity, may vary among streams and years, and cause variations in recruitment that are unrelated to spawner numbers – most notably high recruitment at low spawning stock size. Again we previously presented evidence for large density-independent recruitment variation in Great Lakes sea lampreys (Jones *et al.* 2003). We concluded in that study that further research into sea lamprey population dynamics is needed to discriminate between “stream” effects and “year” effects on recruitment variation. A better understanding of spatial and temporal variation in recruitment will inform pest management, for example by identifying types of streams (i.e., spatial effects) where recruitment tends to be higher than average at a given spawning stock size, and thus where higher rates of adult suppression may be needed.

In this paper we report on the findings of a follow-on study of sea lamprey recruitment dynamics in which we have nearly doubled the available data on stock and recruitment. We used these data, which now span ten years and 37 streams, together with data on stream characteristics to analyze variation in recruitment patterns among streams and years. Included in this data set are four long-term study streams where we introduced spawners above barriers at a low level to mimic alternative control reductions in spawner abundance, and measured the subsequent recruitment at age 1 over several years.

Methods

We assembled data on spawning population size and on larval recruitment at age 1 in the following year from Jones *et al.* (2003), and from similar data collected subsequently, resulting in a database of 97 stream-years of sea lamprey stock-recruitment data (Fig. 1). Spawner abundances were either controlled by deliberately releasing adult sea lampreys above barriers where no other sea lampreys were present (62 cases), or spawning population abundance was estimated (35 cases) using a mark-recapture method applied to sea lampreys captured in adult assessment traps (Mullett *et al.* 2003). We estimated age-1 larval abundance using the same electrofishing survey technique in all streams, as described in Jones *et al.* (2003). Habitat was classified at randomly-spaced transects as Type I (fine sand and silt which is preferred by larval sea lampreys), Type II (coarser sand which is acceptable for larval sea lampreys), or Type III/IV (gravel, cobble, bedrock, exposed islands, all of which are unsuitable for larval sea lampreys. Using a backpack electrofisher we surveyed Type I plots at approximately half of the transects, and Type II plots were surveyed at about every eighth transect. Transect widths averaged 4.7 m, and ranged from 1 m to 21.5 m. To combine data among streams, stock and recruitment were calculated as densities

$$(1) \qquad S = \frac{\tilde{S}}{H_w}, R = \frac{\tilde{R}}{H_w},$$

respectively, where $\tilde{S}$ is the total number of spawning females and $\tilde{R}$ is the total abundance of yearling larvae. H_w is the total amount of larval habitat in each stream. H_w was weighted by the relative suitability of Type I and Type II habitat

$$(2) \qquad H_w = A_I + \frac{\overline{D_{II}}}{\overline{\overline{D_I}}} \cdot A_{II}$$

where A is the area of habitat (m^2) and D is the density of yearlings in either Type I or Type II habitats. Type II habitat is weighted less heavily than Type I habitats based on sea lamprey density differences in the two habitats (Slade *et al.* 2003). Density of yearlings in Type II and Type I were determined for all streams and the ratio $\frac{\overline{D_{II}}}{\overline{\overline{D_I}}}$ used in habitat calculations was the average ratio of the densities across all streams in the data set. In this dataset the average across the streams was 0.381 (σ^2=0.180).

To determine the proportion of ammocoetes in our surveys that were age 1 we used a statistical method for objectively estimating age composition from length-frequency data (Schnute and Fournier 1980, Fournier 1983). This method was used because there is not consensus on the accuracy of statoliths for determining age composition of larval sea lampreys, and because we felt that the statistical methods would be preferable to a subjective determination of age composition from length-frequency data. The statistical method relies on an assumption about the growth dynamics of the fish stock of interest; we assumed larvae grew according to a von-Bertalanffy growth function and that individual variation in length increased linearly with age. We were able to determine proportion-at-age-1 using this model, produced in AD Model Builder (Version 6.0.2 of Otter Research 2000), for nearly all stream-years that contained more than one age class of ammocoetes. In ten stream-years either only the age-1 class was present (five cases), or proportion-at-age-1 was determined subjectively by visual inspection of length-frequency plots, because the model did not converge to a solution (five cases). In these five cases a cut-off length was selected for age-1 sea lampreys that corresponded roughly to the mid-point between the age 1 and age 2 modes of the length-frequency plot. Jones *et al.* (2003) showed that the results of the stock-recruitment analysis for a similar dataset were robust to moderate variations in these cutoff values. The estimated proportion-at-age-1 was multiplied by the total sea lamprey catch to estimate age-1 sea lamprey catch in each stream-year. Recruitment was calculated as

$$(3) \qquad \tilde{R} = \frac{C_{1,I}}{q} \cdot \frac{H_{I,T}}{H_{I,s}} + \frac{C_{1,II}}{q} \cdot \frac{H_{II,T}}{H_{II,s}},$$

where $C_{1,I\ or\ II}$ was the age-1 catch in Type I and II habitats, q was the electrofisher catchability, $H_{I\ or\ II,T}$ was the total Type I or II habitat area in the stream, and $H_{I\ or\ II,s}$ was the Type I or II habitat area surveyed. We assumed a fixed electrofisher catchability of 0.482 for all streams and habitat types (Steeves *et al.* 2003).

To learn more about temporal variation in recruitment, we collected data annually from four study streams (Fig. 1) over a period of 7 to 9 years. We selected four streams that had multiple years of sea lamprey stock-recruitment data from our earlier study: two high-alkalinity streams in the Lake Ontario drainage (Port Britain and Grafton creeks: 3

years) and two low-alkalinity streams along the north shore of Lake Superior (Carp and Big Carp rivers: 4 years). We continued monitoring recruitment on these four streams by adding only 10 adult male and 10 adult female sea lampreys above barriers in each stream for five years starting in 2002 (Carp and Big Carp) or four years starting in 2003 (Port Britain and Grafton). These introductions mimicked alternative control methods that reduced spawners to less than 1 spawning females/100 m^2 of larval habitat for Port Britain Creek and less than 0.5 spawning females/100 m^2 for the other three streams, a density below which we observed no high recruitment events in our earlier study.

To determine whether the presence/absence of sea lamprey ammocoetes within the Great Lakes was controlled by substrate particle size, we quantified habitat differences among study streams during the 2006 sampling season by further classifying Type III habitat (gravel, cobble, bedrock) as suitable for spawning (existence of gravel 1 to 5 centimeters in diameter for nest construction, with small amounts of sand available) or unsuitable (other streambed characteristics existed) (Applegate 1950). We further quantified the quality of suitable spawning areas by indicating the embeddedness of the substrate in suitable spawning areas using the embeddedness rating of Platts *et al.* (1983). We analyzed the relative suitability of habitat for spawning-phase and larval sea lampreys in the four study streams by separating each stream into four equal-length sections and evaluated the proportion of preferred larval habitat, acceptable larval habitat, spawning habitat, and unsuitable sea lamprey habitat in each section.

An aspect of habitat quality is the distribution of both spawning and larval habitat in a stream. Because larvae are typically carried downstream in the current after hatching, suitable larval habitat (silt/sand) must occur somewhere downstream of suitable spawning areas (medium-sized gravel with sand). The presence of good spawning habitat in the upper reaches and depositional areas for larval habitats downstream may be influenced by the gradient of a stream. Stream gradients for study sections of the four study streams were approximated using ArcGIS (Version 9.2 of Environmental Systems Research Institute, Inc. 2007).

We fit the data to a Ricker stock-recruitment model of the form

$$(4)\qquad R_{t+1} = \alpha \cdot S_t \cdot e^{-\beta \cdot S_t + \varepsilon_t}\ .$$

Visual inspection of the stock-recruitment data from this and other sea lamprey studies indicate a decline in recruitment at large stock sizes, consistent with the form of the Ricker stock-recruitment model. The Ricker model can be rewritten as a linear model

$$(5)\qquad \ln\left(\frac{R_{t+1}}{S_t}\right) = \ln(\alpha) - \beta \cdot S_t + \varepsilon_t$$

where *ln(R/S)* is an index of survival to age 1 (effectively recruitment, in this study), *S* is the number of female spawners/100 m^2 of larval habitat, α describes average survival across stream-years when S is close to zero, β describes the degree to which survival falls as S increases, and ε is a normally distributed error term with mean zero and variance σ_ε^2. We combined data from multiple streams in our stock-recruitment analysis by expressing S and R as densities, scaled to the amount of larval habitat (equations 1 and 2). We justified this approach by hypothesizing (as is generally believed by sea lamprey control biologists) that larval habitat rather than spawning habitat tends to limit recruitment in Great Lakes streams. To test for evidence of compensation we performed a regression of ln(R/S) on S to test whether the index of survival was higher at low stock sizes, indicated when $\hat{\beta}$ is significantly less than zero.

The linear form of the Ricker stock-recruitment function allowed us to use a general linear mixed-effects model (Littell *et al.* 1996) to assess other factors that might significantly affect recruitment. We tested each factor's main effect on recruitment, but did not test higher-order effects due to sample size limitations. The full model was

$$(6)\quad \ln\left(\frac{R_{t+1}}{S_t}\right)_{jklmnop} = \ln(\alpha) + \nu_j + \chi_k + \delta_l + \lambda_m + \rho_n + b_o + c_p - \beta \cdot S_t + \varepsilon_{jklmnop}$$

$j = 1,..,4$; $k = 1,2$; $l = 1,2$; $m = 1,2$, $n = 1,..,3$, $o = 1,..,9$, $p = 1,..,37$;
$b_o \sim N(0, \sigma_b^2)$, $c_p \sim N(0, \sigma_c^2)$, $\varepsilon_{jklmnop} \sim N(0, \sigma_\varepsilon^2)$

α = Average survival across all streams when number of spawners is zero
ν_j = Lake effect (1=Superior, 2=Michigan, 3=Huron 4=Ontario)
χ_k = Thermal stability effect (1=warm, 2=cold)
δ_l = Alkalinity effect (1=below 100 mg/L $CaCO_3$, 2=above 100 mg/L $CaCO_3$)
λ_m = Consistency of sea lamprey production effect (1=irregular, 2=regular)
ρ_n = Competitor effect (1=low, 2=moderate, 3=high)
b_o = Year effect (random) (ten years of data from 1997-2007, excluding 2002)
c_p = Stream effect (random) (37 streams)
β = Density dependence term
$\varepsilon_{jklmnop}$ = Error term

Lake was used as a surrogate for the effect of broad geographical differences in stream locations. Thermal stability was included as a categorical variable, as stream temperatures were determined, based on past and current data, by sea lamprey control agents to either parallel air temperature (warm) or be more regulated by groundwater input (cold). In general, warm streams were those where summer water temperatures frequently exceeded 20°C. The thermal niche of larval sea lamprey is considered to be between 17.8 and 21.8 °C, and lab studies found maximal survival of exogenous feeding sea lamprey larvae reared at 21°C, and no survival at 23°C after a three-month period (Holmes and Lin 1994; Rodriguez-Muñoz *et al.* 2001). Alkalinity was used as a surrogate for stream productivity, and streams were classified as above or below 100 mg/L $CaCO_3$ if reported average alkalinities from previous data were greater or less than the cutoff alkalinity value. The factor "consistency of sea lamprey production" refers to an *a priori* categorization of streams by sea lamprey control agents into regular or irregular sea lamprey producing streams. Regular producers are streams subjected to a reliable cycle of lampricide treatments (i.e., they have generally been treated every n years, where n can be 3, 4, or 5 for a particular stream). Irregular producers are subjected to a less consistent cycle of treatment. The competitor effect was a categorical variable and was based on estimated densities of native lampreys of all ages (*Ichthyomyzon spp.* or *Lampetra appendix*) and sea lampreys that were not age 1 in each stream-year; i.e., all lampreys that were potential competitors to age-1 sea lampreys. Categories were <100/100 m^2 (low), between 100 and 299/100 m^2 (moderate), and >= 300 lamprey competitors/100 m^2 of larval habitat (high).

The full model included the year of recruitment and stream as random factors, to account for year to year and stream to stream variability (Littell *et al.* 1996). All effects other than stream and year were modeled as fixed effects. To test whether the variance in the index of survival that can be attributed to the random effects was significant, and to see if year or stream as random effects should be included in the final model a Wald Z test was performed using SAS (Version 8 of the SAS System for Windows, Copyright 2000, SAS Institute Inc). Random effects that did not significantly contribute to the variance in the index of survival were removed from the full model. Corrected Akaike Information Criterion (AIC_C) values and strength of evidence ratios were generated using SAS and then used to rank potential models to determine which combination of fixed effects should be included in the best model (Burnham & Anderson 2002). Strength of evidence ratios are simply the ratio of the Akaike weights for any 2 models, and in this case we used the ratio of the best model (lowest AICc) to each other model, to indicate how much more likely one model in the pair is compared to the other (Burnham and Anderson 1998). All models whose AIC_C values exceed the best model by three or more or had strength of evidence ratios of greater than five were removed from further consideration, since this suggests there is considerably less statistical support for those models (Burnham & Anderson 2004).

We ran a separate analysis on the four long-term study streams established in this study (a total of 31 stream-years worth of observations) using the aforementioned approach, but the mixed-effects model tested only the effect of stream, here as a fixed effect, and year as a random effect on recruitment variation. The random effect and the residual variances were modeled as normally distributed with mean zero and variance σ_b^2 and $\sigma_\varepsilon^{\ 2}$, respectively.

Results

Doubling the size of the sea lamprey stock-recruitment database did not substantially alter the overall pattern described in an earlier study (Jones *et al.* 2003). Recruitment of sea lampreys was highly variable among streams, even after accounting for the effect of stock size (Fig. 2*a*). The regression of ln(R/S) on S revealed a statistically significant, negative slope ($\beta = -0.1593$, SE = 0.0226, $p(\beta = 0) < 0.0001$, df =95; Fig. 3), which provides statistical evidence of compensation. As well, large recruitment events (>400 age-1 larvae/100 m^2) occurred even at stock sizes below 1/100 m^2, although they were not observed at very low stock sizes (< 0.2 females/100 m^2; Fig.

2*b*). In our four long-term study streams where we introduced spawners at low levels since 2002 to mimic alternative control methods that reduce spawner abundance, recruitment was low (<400 age-1 larvae/100 m^2) in all cases (Fig. 4).

For the full dataset, the amount of variance in the index of survival attributable to the random effects was close to zero, with both stream (σ_c^2 = 0.600, SE = 0.422, p=0.0776) and year (σ_b^2 = 0.105, SE = 0.183, p=0.2825) not contributing significantly to the variance in the index of survival. Therefore, stream and year were removed from the model. The number of streams on which we had data for each year of the study is summarized in Table 1, with some years being underrepresented. Model selection on the remaining effects indicated there were no real differences between the AICc values for the full model and three reduced models (Table 2), so we tested for significance of fixed effects using the model with all fixed effects included. The resulting general linear model revealed significant effects of stock size, lake, consistency of sea lamprey production, and competitor density. These were also the effects that appeared in all four top models. Lake significantly affected survival (p=0.0003, $F_{3,87}$=7.111), and Tukey HSD pair-wise comparisons indicated that streams tributary to Lakes Superior and Michigan experienced significantly higher survival than streams tributary to Lakes Huron and Ontario (Fig. 5). Survival in streams with regular sea lamprey production was significantly higher than in those with irregular production (p=0.0007, $F_{1,87}$=12.38). The density of competitors significantly affected survival (p=0.0021, $F_{2,87}$=6.625), but contrary to expectations, Tukey HSD pair-wise comparisons indicated significantly lower survival in streams with the fewest competitors (Fig. 6). The thermal stability and alkalinity effects were not significant.

The mixed model testing the effect of stream and accounting for year to year variability on the four long-term study streams revealed a large effect of stream ($p<0.0001$, $F_{3,17}=34.71$) on survival. Tukey HSD pair-wise comparisons indicated Carp River had significantly higher survival than other streams, followed by the Big Carp River, Grafton Creek, and Port Britain Creek with significantly lower survival than the other streams (Fig. 7). The amount of variance in the index of survival attributable to the random effect of year ($\sigma_b^2 = 0.449$, SE=0.346, p=0.19) was not significantly different from zero.

Average competitor density across all years in the study streams was highest in streams with higher survival and lowest in streams with lower survival (Table 3). Temperature monitoring on the study streams during the summers (June-August) of 2003 and 2004 indicated that the stream with the highest survival had the lowest average summer temperature, while the stream with the lowest index of survival had the highest average summer temperature (Table 3). Stream gradients for the study sections of the four study streams did not correspond with the observed pattern of survival among the streams, but did fall within the range observed by Baxter (1954) (5-14.5 m/km) in English sea-lamprey producing streams (Table 3). Streams with higher survival had distributions of spawning and larval habitats that were most favorable to sea lamprey production (Fig. 8). Embeddedness of suitable spawning habitat was low (<5% of gravel surface covered by fine sediment) in 70% or more cases for all streams, with the exception of Port Britain, which had the lowest index of survival, where in 50% of the cases embeddedness was more pronounced (up to 25% of gravel surface covered by fine sediment).

Discussion

In our previous analysis of compensatory mechanisms in Great Lakes sea lamprey populations we used a simulation model to show that failure to account for compensation and large density-independent variation in recruitment will lead to optimistic assessments of the overall promise of pest control strategies that target spawning sea lampreys (Jones *et al.* 2003). This study has confirmed our earlier findings of significant density-dependent compensation and a large amount of density-independent recruitment variation for sea lamprey populations in the Great Lakes basin. For example, we observed recruitment varying by almost three orders of magnitude (2.5 vs 2084 age-1 larvae per 100 m^2) in streams with similar, low spawner numbers (0.3 females /100 m^2). Management models that are used to assess strategies for sea lamprey control aimed at adult sea lamprey need to explicitly account for these stock-recruitment dynamics.

We found that streams described by sea lamprey program staff as having a regular and predictable cycle of lampricide treatment experienced significantly higher survival than less predictable (irregular) streams. This result suggests that not only are these streams consistent sea lamprey producers, but they also tend to produce more recruits at a given stock size, which was also observed in another study measuring sea lamprey recruitment (G. A. Hansen, Michigan State University, personal communication). We also found that streams in Lakes Superior and Michigan produced higher survival than streams from Lakes Huron or Ontario. Consistent with this finding, survival in our two Lake Superior long-term study streams was higher than in the two Lake Ontario streams. This finding was in contrast to what we might have expected, because in general Lake

Ontario sea lamprey streams tend to be warmer and more productive and require treatment with lampricide more frequently than streams on the upper Great Lakes. Finally, we found that survival was higher in streams where the number of competitors was greater, which again contradicted our predictions.

We hypothesize that these results are the consequence of differences among streams in habitat quality. Our meta-analysis included streams from throughout the Great Lakes that were representative of sea lamprey population dynamics, but were not selected at random. Stream habitat quality for sea lampreys may, in general, be better in Lakes Superior and Michigan than in Lakes Huron and Ontario, or the streams included in this study may simply have had better habitat quality in the first two lakes. It seems plausible that streams classified as regular producers have better habitat, and similarly that streams with better habitat have larger populations of native lampreys (i.e., competitors).

We observed relatively high survival in the Carp River and low survival in Port Britain Creek, consistent with our hypothesis that habitat differences may explain recruitment variation. Of the four study streams, Carp River was the only one classified as a regular producer and age-1 larvae experienced the highest survival in this stream. Carp River also had the largest amount of spawning habitat in the upper reaches and the largest amount of preferred larval habitat in the lower reaches in comparison with the other study streams. Young *et al.* (1990) also found that the presence/absence of sea lamprey ammocoetes within the Great Lakes was controlled, to a large degree, by substrate particle size. Average competitor density across all years was higher in streams where higher survival and favorable habitat was observed and lowest where lower survival and unfavorable habitat existed.

An important next step in process-level research of sea lamprey recruitment variation will be to develop measures of habitat differences among streams, measures similar to those investigated in this study, that appear to explain recruitment variation. . Alternative quantitative descriptions of habitat supply, that account for the juxtaposition of spawning and larval habitats on an ecologically meaningful scale (Derosier *et al.* 2007), should be included in future investigations of recruitment variation. If a measure of habitat supply can be shown to explain significant among-stream variation in recruitment after accounting for density-dependent (stock) effects, then this factor should be used to inform management. Streams with an abundance of good habitat would require greater reductions in spawner numbers to achieve target recruitment levels, on average, and thus may not be preferred candidates for alternative control.

Both the full meta-analysis model (97 stream-years) and the study stream model (31 stream-years) revealed that the year of recruitment, specified as a random effect, was not a significant component of the overall variance in survival among observations. Myers *et al.* (1997) looked at recruitment variation among populations of 19 species of fish from marine, marine-freshwater (anadromous) and freshwater habitat, and noted that recruitment patterns were correlated over time among nearby (<500 km apart) populations of marine fishes but only weakly and at short distances for freshwater species. Similar patterns of temporal covariation have been demonstrated for north Pacific stocks of sockeye (*Oncorynchus nerka*) and pink (*Oncorynchus gorbuscha*) salmon within but not among broad regions such as the Fraser River and Bristol Bay (Peterman *et al.* 1998; Pyper *et al.* 2001). These studies suggest that moderate to large-scale, temporally variable environmental factors influence fish recruitment in marine systems, but are less important in freshwater systems. A significant effect of stream in the four-stream model, and the significance of several stream-level fixed effects in our full meta-analysis model indicates that in sea lampreys, where recruitment (as we have defined it here) takes place in individual streams, recruitment variation appears to be more strongly influenced by stream-specific factors, or by interactions between stream-specific factors and temporally varying environmental factors.

Our results can be used to specify a level of control on adult sea lamprey reproduction required to reasonably ensure success of alternative control strategies. We did not observe large recruitment events (>400 age 1 larvae/100 m^2) when spawner abundance was below 0.2 females/100 m^2 in either the full data set or the long-term study streams data set. When planning future alternative control initiatives, such as trapping and/or sterile male release, sea lamprey managers should aim to reduce spawner abundance to this value or below to try and ensure low recruitment of sea lamprey populations.

Of the 35 cases in this study where natural spawning populations were estimated rather than intentionally introduced, over 80% had spawner abundances greater than 0.2 females/100 m^2 of larval habitat and over 50% had spawner abundances greater than 1 female/100 m^2. To the extent that these streams are typical of sea lamprey producing streams in the Great Lakes, this implies that achieving the target abundance of 0.2 females/100 m^2 in approximately half of the streams will require trapping efficiencies (or reductions due to both trapping and sterile male releases) of 80% or greater. Currently in Great Lakes streams (2006 data), sea lamprey trapping efficiencies range from 7% to 91% with a mean trapping efficiency of 39% (G. C. Christie, Great Lakes Fishery

Commission, personal communication). However, recent research has demonstrated that sea lamprey pheromones hold considerable promise as a tool to enhance trapping efficiency (Wagner *et al.* 2006, Johnson *et al.* 2006), which may make the targets implied by our recruitment research more easily attainable.

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Table 1. The number of streams for which there is data in the years of the study.

Recruitment year	**Number of streams in full dataset**	**Number of streams in four-stream dataset**
1997	7	1
1998	17	2
1999	25	4
2000	25	4
2001	6	3
2003	2	2
2004	4	4
2005	4	4
2006	4	4
2007	3	3

Table 2. Top models from best-subsets model estimation to explain sea lamprey recruitment variation. The full model is indicated by an asterisk with the fixed effects spelled out.

Model parameters	**$\mathrm{AIC_C}$**	**Strength of evidence**
$\ln\left(\frac{R}{S}\right) = \ln(\alpha) + \nu_{S,H,M,O} + \delta_{b,a} + \lambda_{i,r} + \rho_{l,m,h} - \beta \cdot S + \varepsilon$	**345.7686**	**1.00**
$* \ln\left(\frac{R}{S}\right) = \ln(\alpha) + \nu_{S,H,M,O} + \chi_{w,c} + \delta_{b,a} + \lambda_{i,r} + \rho_{l,m,h} - \beta \cdot S + \varepsilon$ * (lake) + (thermal stability) + (alkalinity) + (sea lamprey production) + (competitor density)	**345.9195**	**1.078**
$\ln\left(\frac{R}{S}\right) = \ln(\alpha) + \nu_{S,H,M,O} + \lambda_{i,r} + \rho_{l,m,h} - \beta \cdot S + \varepsilon$	**347.9351**	**2.954**
$\ln\left(\frac{R}{S}\right) = \ln(\alpha) + \nu_{S,H,M,O} + \chi_{w,c} + \lambda_{i,r} + \rho_{l,m,h} - \beta \cdot S + \varepsilon$	**348.2819**	**3.514**

Table 3. Comparison of salient characteristics among the four study streams. Standard errors are shown in parentheses.

Stream	**Index of survival (Least square means)**	**Stream gradient (m/km)**	**Consistency of sea lamprey production**	**Average competitor density (competitors /100 m^2)**	**Average summer temperature during 2003-2004**
Carp	6.95	12.9	Regular	841.6 (204.4)	15.7 (0.147)
Big Carp	5.40	8.5	Irregular	842.6 (207.1)	17.2 (0.175)
Grafton	3.69	13.6	Irregular	540.9 (118.2)	16.7 (0.148)
Port Britain	2.01	7.9	Irregular	137.9 (60.9)	19.1 (0.148)

Figure Captions

Figure 1. Location of streams from which we obtained sea lamprey stock-recruitment data. The four long-term study streams are highlighted with names. The numbers indicate the number of years of stock-recruitment data we have for each stream.

Figure 2. Females and yearling sea lamprey numbers are expressed as densities/100 m^2 of larval habitat (*a*) observed stock and recruitment for 97 stream-years and (*b*) includes only data when spawner densities were less than 5/100 m^2.

Figure 3. The linearized sea lamprey stock-recruitment relationship (ln(R/S) versus S) for the data plotted in Fig. 2. Ln(R/S) is an index of sea lamprey survival to age 1. The regression line estimates are shown in the graph panel.

Figure 4. Observed sea lamprey stock and recruitment for the four long-term study streams when spawners were introduced at low levels (<1 females /100 m^2) to mimic alternative control (17 stream-years).

Figure 5. Least squares mean plot of ln(R/S) for age-1 sea lampreys versus lake from the general linear model on all available data (error bars represent 95% confidence intervals).

Figure 6. Least squares mean plot of ln(R/S) for age-1 sea lampreys versus competitors/100 m^2 of habitat from the general linear model on all available data (error bars represent 95% confidence intervals).

Figure 7. Least squares mean plot of ln(R/S) for age-1 sea lampreys versus stream from the mixed-effects model on the four long-term study streams (error bars represent 95% confidence intervals).

Figure 8. Sea lamprey habitat observed in the four long-term study streams, illustrated in four equal-length sections located from furthest upstream to furthest downstream for each stream.

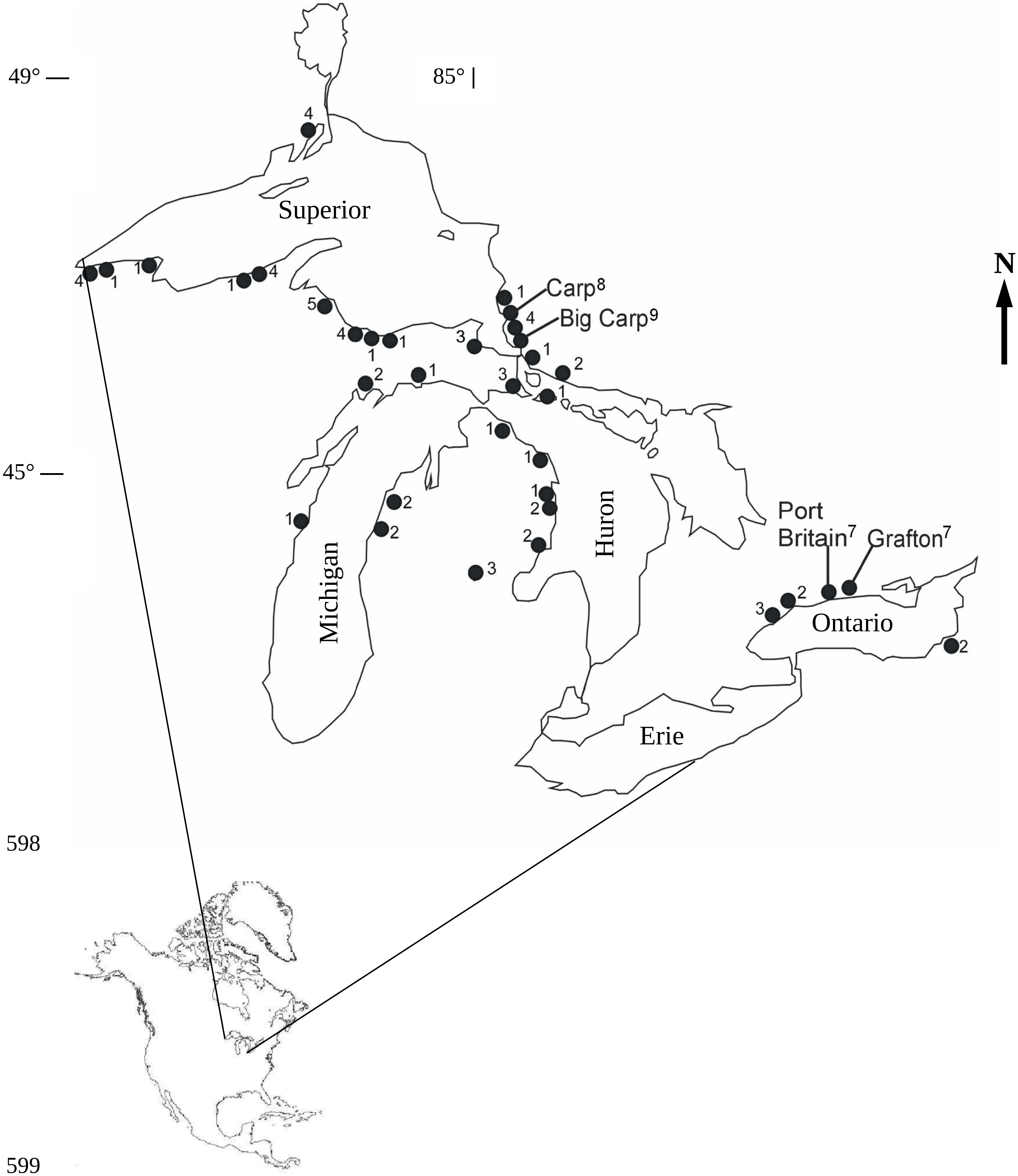

49° —
85° |
45° —
N
Superior
Michigan
Huron
Erie
Ontario
Carp⁸
Big Carp⁹
Port Britain⁷
Grafton⁷
4
4
1
1
1
4
5
4
1
1
3
2
1
1
4
1
2
3
1
1
1
1
2
2
2
1
2
3
2
3
2

Figure 1

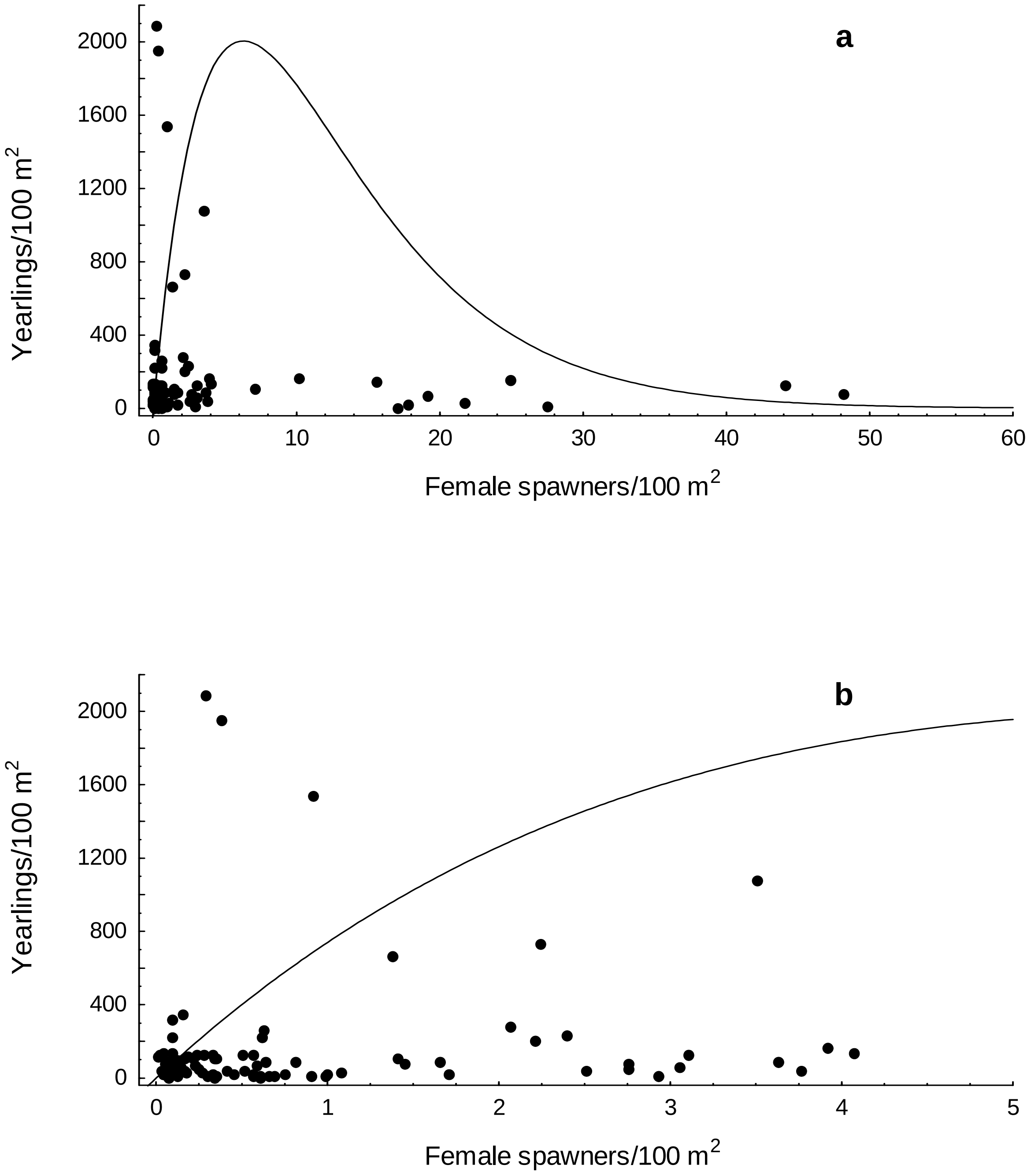

a
Yearlings/100 m2
2000
1600
1200
800
400
0
0
10
20
30
40
50
60
Female spawners/100 m2
b
Yearlings/100 m2
2000
1600
1200
800
400
0
0
1
2
3
4
5
Female spawners/100 m2

Figure 2

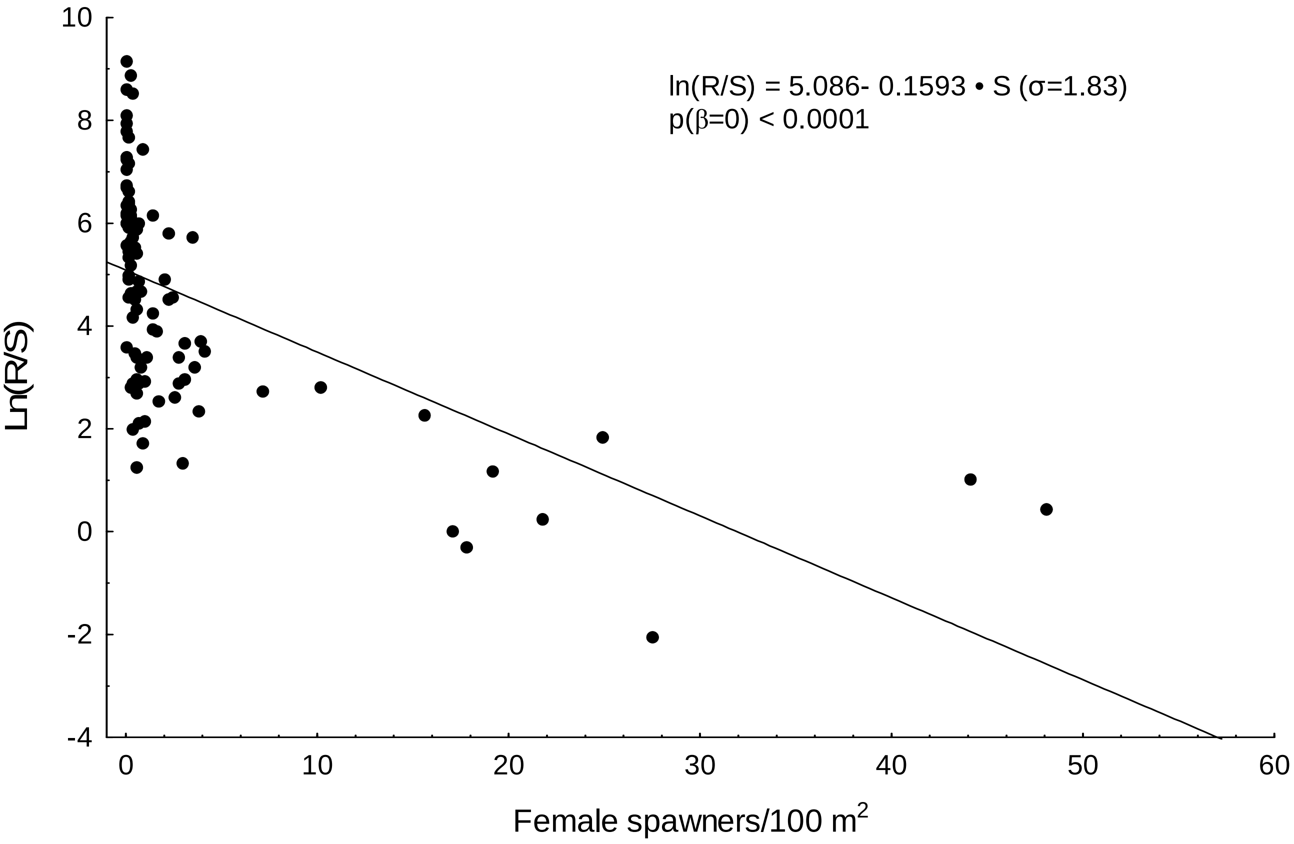

ln(R/S) = 5.086- 0.1593 • S (σ=1.83)
p(β=0) < 0.0001
Ln(R/S)
10
8
6
4
2
0
-2
-4
0
10
20
30
40
50
60
Female spawners/100 m2

Figure 3

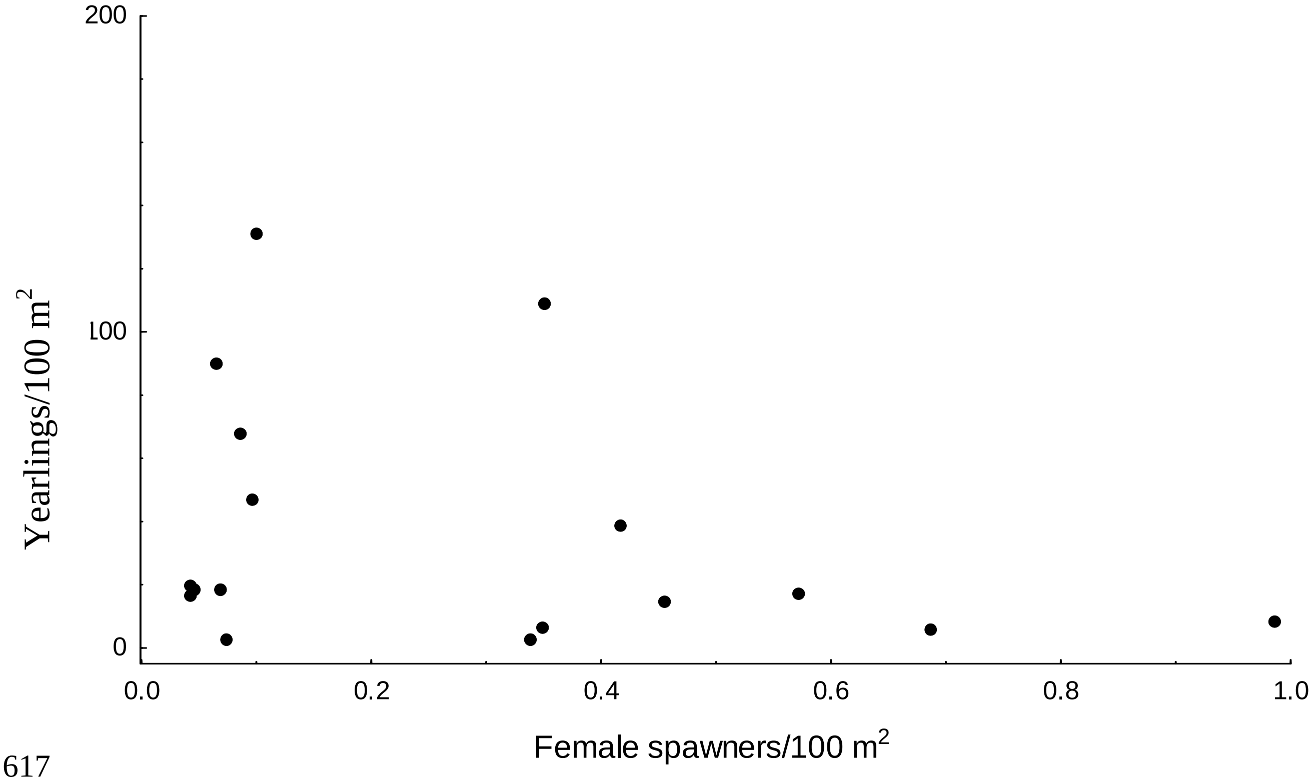

200
100
0
Yearlings/100 m^2
0.0
0.2
0.4
0.6
0.8
1.0
Female spawners/100 m^2

Figure 4

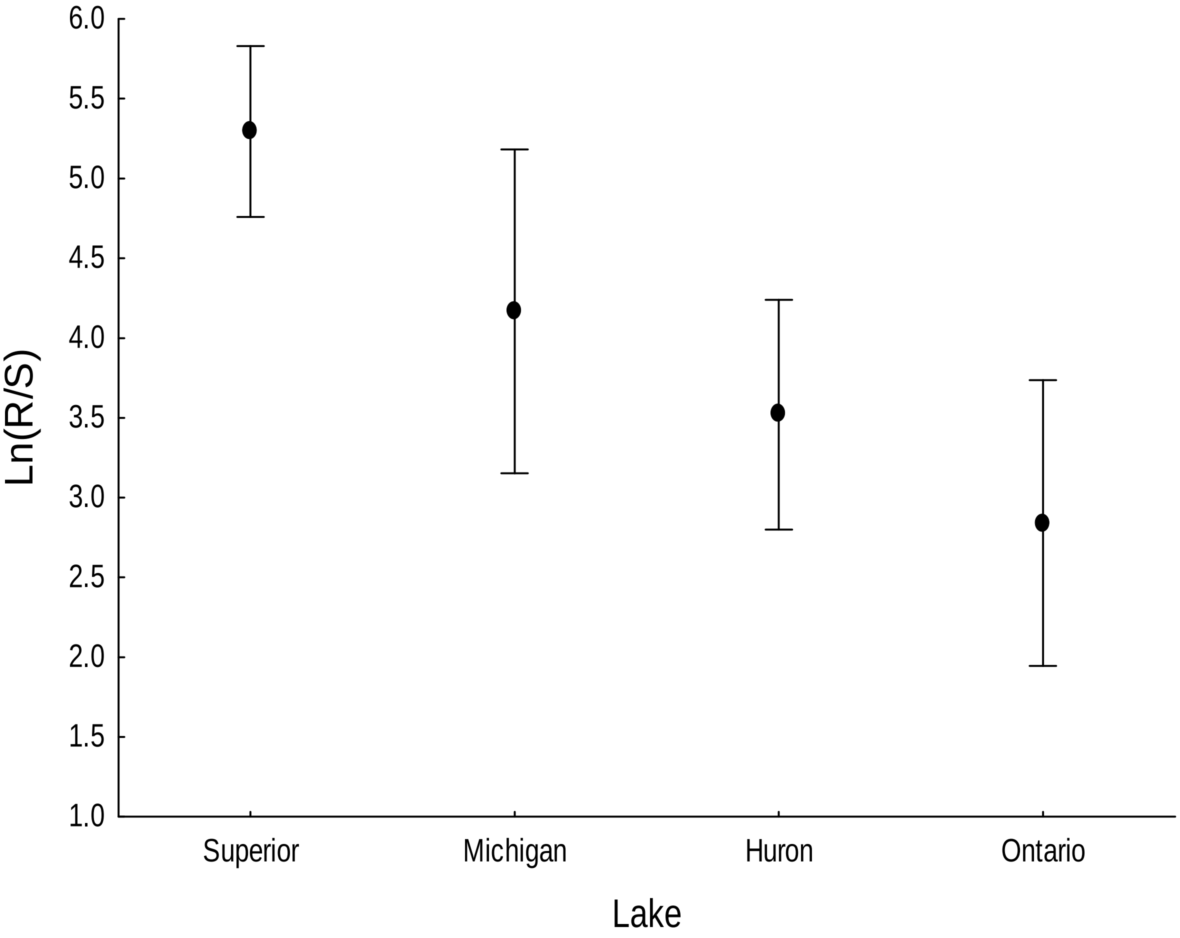
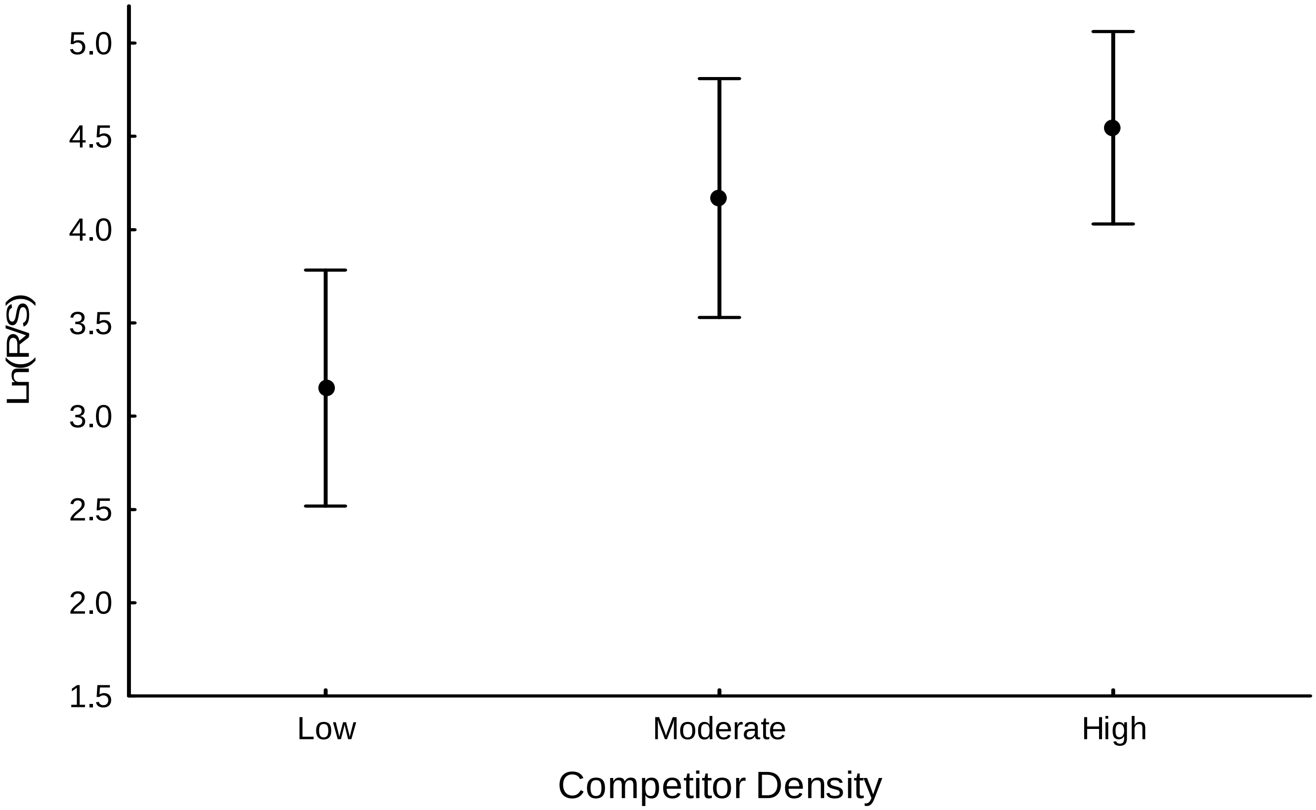

6.0
5.5
5.0
4.5
4.0
3.5
3.0
2.5
2.0
1.5
1.0
Ln(R/S)
Superior
Michigan
Huron
Ontario
Lake

Figure 5



5.0
4.5
4.0
3.5
3.0
2.5
2.0
1.5
Ln(R/S)
Low
Moderate
High
Competitor Density

Figure 6

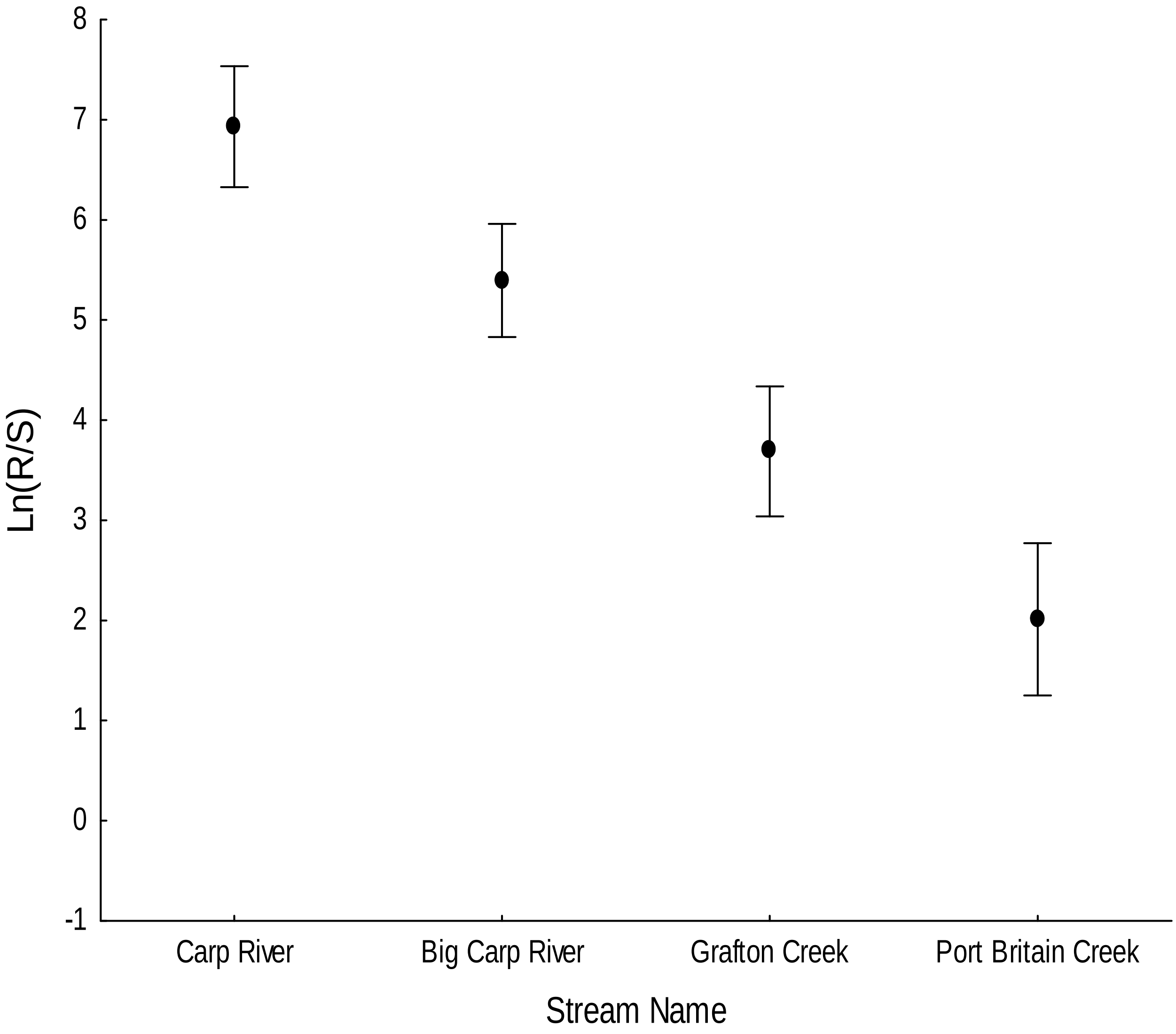

Ln(R/S)
8
7
6
5
4
3
2
1
0
-1
Carp River
Big Carp River
Grafton Creek
Port Britain Creek
Stream Name

Figure 7

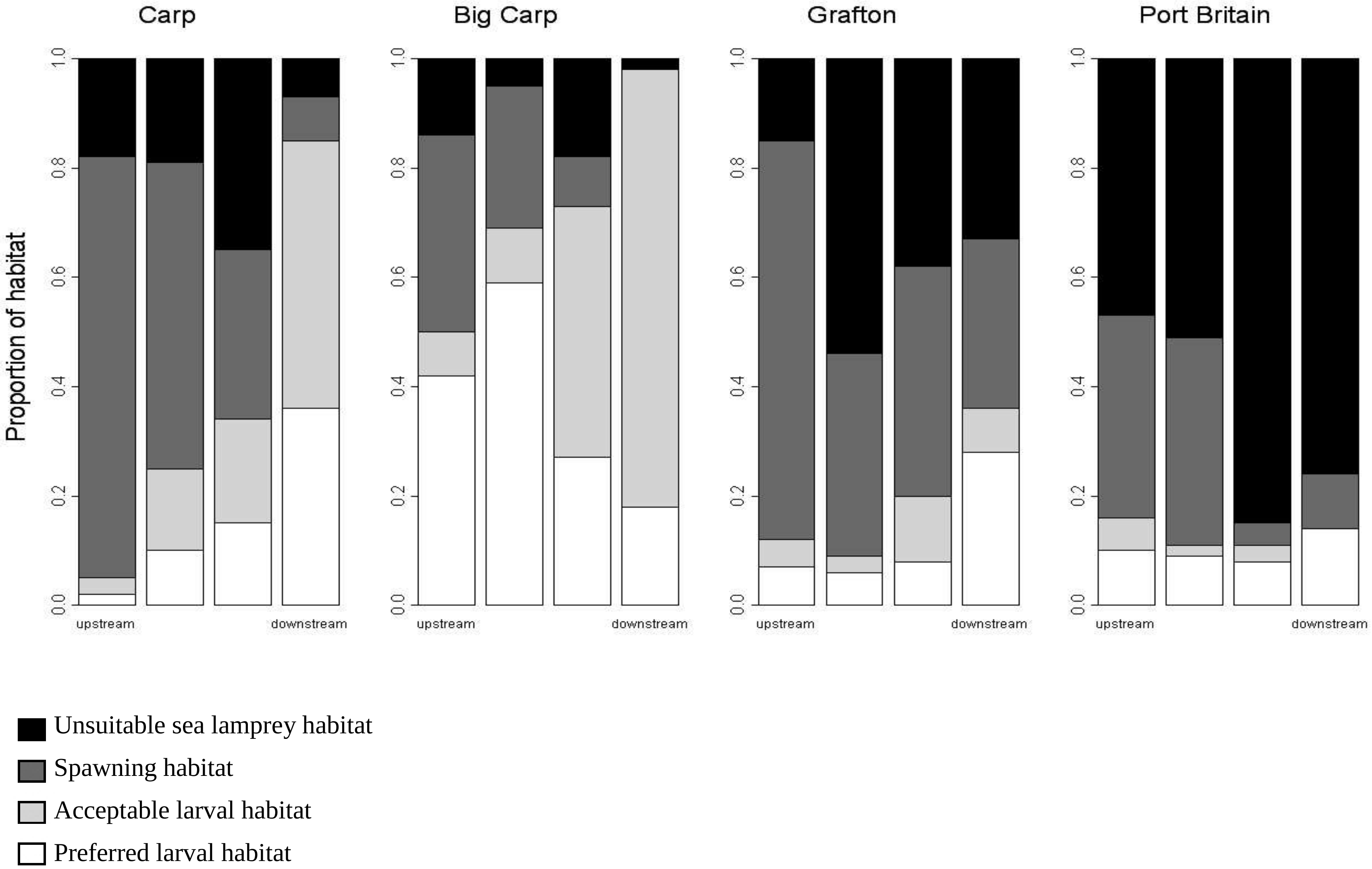

Carp
Big Carp
Grafton
Port Britain
Proportion of habitat
0.0
0.2
0.4
0.6
0.8
1.0
upstream
downstream
Unsuitable sea lamprey habitat
Spawning habitat
Acceptable larval habitat
Preferred larval habitat

Figure 8

APPENDIX 2

Estimation of larval sea lamprey survival using length-based age-assignment and catch-at-age analysis methods

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INTRODUCTION:

Since 1980 the Great Lakes Fishery Commission (GLFC) has utilized models designed to forecast the consequences of alternative sea lamprey management actions and to make informed choices regarding the allocation of treatment efforts on an annual basis as a part of the integrated management of sea lamprey (IMSL) management strategy (Greig and Meisner 1991; Christie and Goddard 2003). The reliability of decisions made based on population models is directly related to the accuracy of the parameters describing population processes contained within them. The parameters used in the population models developed in the 1980's and 1990's relied on very limited demographic information about sea lamprey populations. Since that time, the development and implementation of quantitative assessment techniques have yielded large amounts of larval sea lamprey abundance data that, combined with advances in methods for analyzing fisheries data (Quinn and Deriso 1999), could allow for a more accurate estimation of larval sea lamprey population rates. We have used all relevant quantitative assessment data to estimate larval sea lamprey survival rates across a variety of stream reaches, years, and larval ages. We believe that this comprehensive analysis of relevant data is likely to yield the most accurate estimate of larval survival possible given the current state of knowledge, and that improving our estimates of larval survival will lead to the improved reliability of model predictions and analyses used to guide decisions made by the GLFC.

OBJECTIVE:

Develop improved estimates of larval sea lamprey survival using all available quantitative survey data.

METHODS:

Data assembly

All quantitative assessment sampling (QAS) electrofishing surveys conducted from 1995-2006 were initially examined to determine their utility for this analysis. Surveys described in Jones et al. (2003), which are more intensive than QAS surveys and were designed to provide a precise measure of larval abundance, were also used considered for this analysis. Surveys were selected for this analysis if individuals were collected in two or more consecutive years on the same stream reach with no chemical treatment occurring in between. Surveys occurring on the same reach in consecutive years were assigned to the same "cycle", meaning a series of years throughout which age classes could be tracked. Multiple surveys from one year were used only if they occurred within 30 days of each other.

Electrofishing surveys do not capture all larval sea lampreys present in a surveyed plot, and probability of capture depends on the length of an individual, the density of individuals in the plot, the mean depth of the plot, and the conductivity of the stream (Steeves 2002). Some surveys identified as useful for this analysis did not have associated conductivity and/or depth values. For these surveys, we assembled all conductivity and depth values ever measured for each stream reach that was missing data. We then assigned conductivity and depth values to surveys from which they were missing by randomly drawing them from the distribution of values ever observed for that reach. Catch data from electrofishing surveys was then converted to abundance data using the catchability correction algorithm as described in Steeves (2002).

Age assignment

We used a statistical method for objectively estimating age composition from length-frequency data to assign ages to our estimates of larval abundances (Schnute and Fournier 1980). We used this method because it is difficult to distinguish reliably between multiple year-classes of larval sea lampreys based on length information alone (Potter 1980). The statistical method of age assignment relies on an assumption about the growth dynamics of the fish stock of interest; we assumed larvae grew according to a von-Bertalanffy growth function and that individual variation in length increased linearly with age. The model estimated proportions at age for each year in a given cycle simultaneously. If the model converged and successfully estimated proportions at age from a set of length-frequencies, these proportions were multiplied by the total catch and divided by the area surveyed to generate densities of the different age classes for a given stream reach across all years for which survey data were available.

Survival estimation
Survival was estimated using a catch-at-age analysis for each stream reach and cycle (Quinn and Deriso 1999). Densities of individual cohorts of larvae from each reach were tracked through multiple years, and survival was estimated using observed densities at age.

To conduct the catch-at-age analysis, several parameters were estimated. The density of larvae at age 1 (recruitment) for stream reach *j* and each year *y* ($D_{j,y,1}$) was assumed to vary around some mean recruitment level with multiplicative error:

$$D_{j,y,1} = \overline{D}_{j,1} * e^{\varepsilon_{j,y}};$$

where $\overline{D}_{j,1}$ and $\varepsilon_{j,y},...,\varepsilon_{j,y-1}$ were parameters estimated by the model, and $\sum_{y} \varepsilon_{j,y} = 0$.

Similarly, the density of larvae at year 1 of age a for stream j ($D_{j,1,a}$) was assumed to vary around a mean density level with multiplicative error:

$$D_{j,1,a} = \overline{D}'_{j,1} * e^{\delta_{j,a}};$$

where $\overline{D}'_{j,1}$ and $\delta_{j,2},...,\delta_{j,N_{ages}-1}$ were parameters estimated by the model, and $\sum_{a} \delta_{j,a} = 0$.

Densities at ages a+1 and years y+1 were estimated using the following equation:

$$D_{j,y+1,a+1} = D_{j,y,a} * S$$

where S is the survival parameter estimated by the model. We attempted to estimate a single survival rate for all stream reaches combined, as well as for each lake and for each reach separately. The model did not converge for the majority of reaches when all data were included. We then attempted to re-run the analysis using only stream reaches for which the model was generally able to converge. All parameters were estimated on the log scale. The log concentrated likelihood for the lognormal distribution was used as the objective function. A maximum gradient of <10 was considered a necessary criterion for model convergence. All age assignment and survival estimation was conducted using AD Model Builder (Version 6.0.2 of Otter Research 2000).

RESULTS:

Data Assembly
Data from 243 reaches and 685 stream-years was compiled for this analysis, and age composition estimates were attempted from length frequency information for a total of 308 cycles.

Age Assignment

Of the 308 cycles used as inputs for the age assignment model, proportions at age were successfully estimated for only 76 of these cycles, or approximately 25%. Comparison of data characteristics of cycles that worked to those that did not work in this step of the analysis did not reveal any common characteristics necessary for successful estimation of proportions at age (e.g., minimum number of individuals, minimum number of age classes, etc.).

Survival Estimation

When all data for which we were able to assign age compositions were included in the survival analysis and a common survival estimated for all lakes and stream reaches, the model did not converge on a single solution. When a separate survival rate was estimated for each lake, again, the model did not converge. When survival was estimated separately for reaches, the model was able to successfully estimate survival rates for 12 reaches, with estimates ranging from 0.11 to 0.75 (Table 1). Survival could not be estimated for any stream reaches from either Lake Erie or Lake Ontario. When a single survival estimate was attempted using only data from these reaches, the model did not converge.

DISCUSSION:

In this analysis, we used all quantitative sea lamprey assessment data available, and employed sophisticated statistical methods to generate densities at age, and subsequently survival estimates. We feel that our approach utilized the most extensive data available and the statistical methods most likely to produce accurate survival estimates. Despite these efforts, overall we feel that the survival estimates obtained from this analysis are not reliable enough to recommend updating existing models. The current Empirical Stream Treatment Ranking (ESTR) model assumes a survival estimate of 0.2, which was based on expert opinion and “best guesses” of lamprey managers (M. Kuc, Great Lakes Fishery Commission, personal communication). The reaches for which we were able to obtain estimates indicate that survival may vary substantially between reaches, and this best guess estimate may be more accurate for some reaches than for others. However, because we were able to estimate survival for only a small portion of the total number of infested reaches in the Great Lakes basin, we cannot draw reliable broad conclusions about larval survival, and do not feel any changes to the ESTR model are justified on the basis of this analysis.

Our analysis was constrained greatly by our inability to assign age composition to a large number of surveyed reaches. Assigning age compositions from length-frequency data requires large numbers of individuals. If a small number of individuals were captured in a given year or the separation between year classes was not sufficiently distinct to allow the model to distinguish between year classes, that year of data could not be used for further analysis. Often times the inadequacy of the data for one year would have a disproportionate effect, in that data from an entire cycle could be eliminated from further use if the year for which the model was unable to assign age information interrupted a set of consecutive years. Therefore, we recommend that future research focuses on reliably estimating age compositions of larval populations in order to improve our ability to estimate larval survival.

The small number of reaches and cycles for which we were able to generate a survival estimate indicates that the data in the majority of areas is insufficient for this type of analysis. We recommend that future attempts to estimate larval survival rely upon additional surveys specifically designed to estimate larval abundance across all age classes for multiple consecutive years uninterrupted by treatment. In the absence of a study specifically designed for this purpose, it is unlikely that reliable survival estimates will be generated.

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Table 1. Survival estimates (S) for all reaches for which the model converged on a solution.

Lake	Stream Number	Stream Name	Reach	S
Superior	10064	Sucker River	2	0.11
Superior	10122	Laughing Whitefish River	1	0.12
Superior	10295	Ontonagon River	5	0.20
Michigan	10023	Millecoquins River	4	0.54
Michigan	10046	Milakokia River	4	0.30
Michigan	10093	Sturgeon River	4	0.17
Michigan	10185	Baily Creek	1	0.57
Michigan	10467	Jordan River	3	0.29
Michigan	10562	Pere Marquette River	7	0.63
Huron	606	French River	2	0.45
Huron	10144	Cheboygan River	11	0.75
Huron	10144	Cheboygan River	13	0.21

APPENDIX 3:

DEVELOPMENT AND EVALUATION OF A NEW PREDICTIVE MODEL FOR METAMORPHOSIS OF GREAT LAKES LARVAL SEA LAMPREY (*PETROMYZON MARINUS*) POPULATIONS

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ABSTRACT

Accurate forecasts of the number of larval sea lamprey (*Petromyzon marinus*) within a stream that will enter into metamorphosis are critical to currently used methods for allocating lampricide treatments among streams in the Great Lakes basin. To improve our ability to predict metamorphosis we used a mark-recapture technique, involving the marking of individual larval lamprey with sequentially coded wire tags, to combine information regarding individual and stream level parameters collected in year *t*, with direct observations of metamorphic outcome of lamprey recaptured in year *t+1*. We used these data to fit predictive models of metamorphosis. The best model demonstrated excellent predictive capabilities and highlighted the importance of weight, age, larval density, stream temperature and geographic location in determining when individual lamprey are likely to transform. While this model was informative, it required data whose measures are not practical to obtain routinely during the larval sea lamprey assessment program. A second model, limited to data inputs that can be easily obtained, was developed and included length of larvae the fall prior to metamorphosis, stream latitude and longitude, drainage area, average larval density in type-2 habitat, and stream lamprey production category (a measure of the regularity with which treatments are required). This model accurately predicted metamorphosis 20% more often than current models of metamorphosis; however, we recommend further validation on an independent set of streams before adoption by the Great Lakes Fishery Commission for ranking streams.

INDEX WORDS: sea lamprey control, *Petromyzon marinus*, metamorphosis, predictive model

Introduction

The invasion of the Great Lakes by the parasitic sea lamprey (*Petromyzon marinus*) and the subsequent impacts on both fish populations and the ecosystem as a whole have been well documented (Smith & Tibbles 1980; Pearce *et al.* 1980; Christie and Goddard 2003). Since 1958, the lampricide 3-trifluoromethyl-4-nitrophenol (TFM) has been used by the Great Lakes Fishery Commission (GLFC) to reduce the abundance of sea lampreys in Great Lakes streams, resulting in a significant reduction in overall sea lamprey abundance in the Great Lakes (Smith & Tibbles 1980). Owing to the fact that the larval stage lasts several years (Manion & Smith 1978), it is neither necessary nor cost-effective to treat all sea lamprey producing streams with TFM every year. Effective lampricide control, therefore, requires choices to be made about which streams to treat each year. The logistics of the sea lamprey management program dictate that information for these choices be gathered one year prior to the anticipated year of stream treatment. Specifically, it is important to know what the sea lamprey production is in a given stream and what proportion of the sea lamprey population present is likely to undergo metamorphosis and enter the Great Lakes as parasitic-phase sea lampreys the following year. In this paper we develop an empirical model of metamorphosis and discuss why it might provide a preferred alternative to the current methods for predicting metamorphosis.

Methods used to select streams for treatment have changed considerably since the beginning of the lampricide program. Initially, subjective decisions about the treatment of streams were made based on the observed presence or absence of substantial numbers of large larvae during stream sampling. In 1982, the GLFC initiated a program of integrated sea lamprey management (IMSL), which among other things called for a more objective approach to balancing the benefits and costs of control alternatives (Sawyer 1980). Adoption of this approach led to the need for a more rigorous quantitative method to determine the sea lamprey population in streams and thus the potential benefit of stream-level control decisions. In 1995 the GLFC adopted a quantitative assessment survey (QAS) and stream ranking methodology, which combines survey data on larval density and habitat with predictive models of growth and metamorphosis to forecast the number of parasitic-stage lampreys that will leave a stream the following year. Streams are selected for lampricide treatment based on this estimate of parasitic escapement relative to the cost of stream treatment.

Metamorphosis in larval sea lampreys comprises a change in both physical form and behaviour; from blind, burrowing, filter-feeding ammocoetes to eyed, free-swimming juveniles that are predators on teleost fish (Youson 2003). The models that are presently used to forecast when metamorphosis is likely to occur were developed by collecting and measuring lengths of larvae and recently metamorphosed juveniles (transformers) during lampricide treatments. Estimates of stream-specific average daily growth were used to alter the length of sea lamprey larvae from the year of collection to their estimated length at the end of the previous year, while for transformers it was assumed that no growth in length would have occurred. This latter assumption was justified by research suggesting that larval sea lamprey enter a period of arrested somatic growth prior to entering into metamorphosis, instead directing energy intake to build up lipid reserves (Potter 1980; Holmes & Youson 1997). Logistic regression was then used to fit models to these data to forecast the length-dependent probability of metamorphosis in the following year. At present, two regional models are used to predict metamorphosis in the Great Lakes (Hansen *et al.* 2003); one for the upper lakes (Lakes Huron, Michigan, and Superior) and one for the lower lakes (Lakes

Ontario and Erie). Although these models were developed from the best data available at the time, the assumptions that growth is constant throughout the larval phase, that animals enter into an arrested growth phase prior to metamorphosis, and that length is the only critical factor in determining the onset of metamorphosis, contribute substantial uncertainty to our ability to select the most appropriate streams for treatment (Steeves 2002).

An independent review of the assessment and stream ranking process (Hansen *et al.* 2002) identified length-based probability of metamorphosis models as a major source of uncertainty that currently limits confidence in the selection of streams for treatment. Collections made at the time of lampricide treatment, as well as numerous field and laboratory studies, have documented that length at metamorphosis can be highly variable both among and within streams from year to year (Manion & Stauffer 1970; Purvis 1980; Morkert *et al.* 1998). Previous research has suggested that individual- and population-level variables such as sex, age and larval density, along with stream-level environmental parameters such as temperature, stream location, and water chemistry characteristics may affect growth and/or metabolism in such a way as to introduce variability over both space and time in rates of metamorphosis (Morman 1987; Murdoch *et al.* 1992; Rodriguez-Munoz *et al.* 2003). Near the end of the larval phase, somatic growth tends to decrease as metabolism shifts to the accumulation of lipids (Lowe *et al*. 1973; Youson *et al*. 1979). Potter (1980) documented an increase in lipid content of larval sea lampreys from approximately 4%, up to 14% prior to the onset of metamorphosis. This phase of reduced growth complicates the use of length as the sole predictor of metamorphosis, because two groups of lampreys in different stages of development may exist in a single length-class: those that recently attained that size, and those that attained their size earlier, and have shifted from somatic growth to the accumulation of lipids (for review, see Youson 2003).

Accurate measures of lipid content in fishes have until recently required lethal sampling, which eliminates the ability to observe the individual's metamorphic fate and thereby empirically establish the link between lipids and the onset of metamorphosis. Other models of metamorphosis have attempted to account for this stage of lipid accumulation by using various measures of condition (e.g., Fulton's condition factor = $\text{weight}/\text{length}^3 \times 10^6$) (Holmes *et al.* 1994; Henson *et al.* 2003). Unfortunately, there is often an inverse relationship between lipids and water content in fishes, and thus increases in lipid content are not necessarily reflected in proportional increases in mass or condition (Youson *et al.* 1993; Holmes & Youson 1994; Jonas *et al.* 1996). While hormonal and metabolic studies have illustrated the utility of condition factor in predicting metamorphosis in close proximity to the event (Youson 2003), these models have not performed well at predicting metamorphosis many months in advance, as is required to ranks streams for lampreicide treatment (Treble 2006).

The objective of this study was to develop a predictive model of metamorphosis in larval sea lampreys based on direct measurements of individual lamprey and stream-specific characteristics. Because previous research has emphasized the importance of lipid accumulation in preparing larvae for metamorphosis, this study incorporated direct, non-invasive estimates of lipid content in addition to other biotic and abiotic variables. By combining individual mark-recapture data with stream- and year-specific measures of temperature and water chemistry parameters, our goal is to explain some of the variation associated with metamorphosis in Great Lakes sea lamprey populations. Our overall objective was to improve our ability to predict metamorphosis and thus more accurately rank streams for lampricide treatment.

Methods

Our approach, following methods established by Hollett (1998), was to collect and individually mark large sea lamprey larvae from several Great Lakes streams where lampricide treatment was anticipated for the following year. Suitable streams were selected through consultation with both United States Fish and Wildlife Service (USFWS) and Department of Fisheries and Oceans Canada (DFO) sea lamprey biologists, who identified streams with abundant populations of large sea lamprey larvae (length>100mm) that would be likely candidates for a fall lampricide treatment the following year. Eight streams were selected from across the Great Lakes basin (Figure 1) that fit these criteria, as well as provide contrast in geographic location, water chemistry and larval densities.

INSERT FIGURE 1

In late summer of 2003, larval sea lampreys measuring >100 mm were collected from Bowmanville Creek, Little Sandy Creek, and Pancake River, using AbP-II DC backpack electrofishing gear (University of Wisconsin Engineering Technical Services, Madison, WI). Animals were anaesthetized using clove oil, measured for length (±1mm), weight (±0.01g), and scanned for total body electrical conductivity (TOBEC) using an EM-Scan Model SA-3000 Small Animal Body Composition Analyzer (EM-Scan Inc., Springfield, IL, 62704-5026). TOBEC provides a non-invasive index of lipid content based on the electrical impedance created when an individual is placed within a low-frequency electrical field (Piasecki *et al.* 1995; Scott et al. 2001; Treble 2006). Following the methodology described by Bergstedt *et al.* (1993), larval lampreys were injected with an individually identifiable coded wire tag (CWT; Northwest Marine Technology, Shaw Island, WA, USA) and released back into their natal stream. The same procedure was used in 2004 on larvae from Ceville Creek, Juniata Creek, Silver Creek, Root River and Crystal Creek. In both years, following the release of tagged larvae, temperature loggers (HOBO Water Temp Pro, Onset Computer Corporation, Pocasset, MA, USA) were installed within the release area and set to record water temperature every 4 hours.

The year following marking, streams were visited in late August to mid October during a scheduled lampricide treatment. Using long handled scap nets, crews collected dead and dying larval and metamorphosing sea lamprey throughout the study section of stream, from the uppermost point where marked animals were released, to the downstream limit of wadable water. Drift nets were also placed at suitable points throughout the study area to collect dead and dying animals as they drifted downstream with the lampricide block. After the treatment was completed, collections of lampreys were scanned for the presence of CWTs, using a Northwest Marine Coded Wire Tag V-Detector, and lampreys containing a CWT were measured for length and weight, and then frozen individually for transport back to the lab. A complete summary of marked and recaptured lamprey from the eight study streams is provided in Table 1.

INSERT TABLE 1

Averages of alkalinity, pH, and conductivity measurements were calculated from water chemistry records of both current and prior lampricide treatments. Temperature loggers were retrieved following treatments and the data downloaded. In two instances, loggers were lost, so temperature data from nearby streams were used as surrogates. On the Root River, temperature data from a logger installed in a tributary, Crystal Creek, was used, and on Little

Sandy Creek, data were obtained from two nearby streams and the average of the two daily temperature values was used (Fisheries & Oceans Canada, Sea Lamprey Control Centre, unpublished data).

Based on larval assessment and treatment data from the lamprey control program, estimates of the average larval density in type-1 (optimal) and type-2 (satisfactory) habitat (Dustin *et al.* 1989; Slade *et al.* 2003), along with the number of years since each stream was last treated, were added to the list of the variables examined. Streams were also categorized based on the regularity with which they are treated, and this was added as a categorical variable. Category one streams tend to have regular treatment intervals and consistent recruitment after treatment, whereas category three streams exhibit irregular treatment and lamprey production cycles; category two streams are intermediate between these two extremes (Anderson 2007). The geographic location of each stream mouth (latitude/longitude (decimal degrees)) and the size of its drainage area (ha) were obtained from the Sea Lamprey Control Centre's GIS database. A complete list of stream-level characteristics for each stream used in this study is presented in Table 2.

INSERT TABLE 2

Laboratory Methods

Tags were retrieved from recaptured lamprey by scanning larvae with a V-notch detector and continuously sectioning each tagged lamprey until the tag was found. Tags were cleaned, mounted between two magnetic brass pencils, and read using a stereoscopic dissecting microscope. Tag numbers, age, gender, and developmental stage of each recaptured animal were matched with measurements taken on the same individual when they were marked and released the previous year.

The age of recaptured lampreys was determined by extracting the statoliths following procedures described in Hollett (1998). Extracted statoliths were stored in a multiwell plate containing immersion oil for a period of 10-15 days, to improve the transparency and clarity of the annuli before being mounted to numerically coded slides using a small amount of Crystal Bond™ adhesive. Statoliths were aged by three people, using a compound microscope, without prior knowledge of the life stage, source stream, or previous age assignments. The interpreted ages were then compared, and statoliths where there was no agreement among readers (n=33) were removed from further analysis.

The sex of recaptured lampreys was determined following procedures described by Docker and Beamish (1994). Portions of recaptured lampreys were cross-sectioned while frozen and microscopically examined for the presence of ovaries. The remaining portion of the lamprey was fixed in a 10% formalin solution for later independent verification. Where the state of the specimen precluded the determination of sex (n=11), the animal was removed from the dataset. Estimates of pre-metamorphic lipid weight and percent body lipids were generated using empirical models developed specifically for larval sea lamprey (Treble 2006), that combine larval condition factor and TOBEC measurements (taken at the time of marking) to provide an estimate of lipid weight.

Data collected from temperature loggers were used to generate several possible explanatory temperature variables. For each stream, the number of days within a suitable temperature range for metamorphosis (9-25ºC) (Holmes & Youson 1998), the number of days within 2°C of the optimal temperature for metamorphosis (21ºC) (Holmes & Youson 1998), the average temperatures for each of the three months leading up to the onset of metamorphosis (April, May, June), and the overall mean annual temperature were calculated. A measure of the spring warming rate was also included, calculated as the average daily increase in water temperature, starting when streams reached the lower thermal limit of 9 ºC, and ending when the stream was within 2ºC of the suggested optimal temperature for metamorphosis (as some streams did not reach 21 ºC) (Holmes & Youson 1998).

Statistical Methods

We used a best-subsets multiple logistic regression technique (Statistica Version 7, StatSoft Inc.,Tulsa, OK, USA), with the developmental fate of individual sea lamprey (larvae versus transformer) as the dependent variable, to compare among models with different sets of independent variables. Corrected Akaike’s Information Criterion (AIC_C) values were used to compare models, as sample size relative to the number of possible parameters was low (Burnham & Anderson 2004). Because AIC_C values could only distinguish between models differing by more than a value of two, variance inflation factor (VIF) was used to remove models that contained highly correlated variables from the list of possible models. Model averaging was also used to develop a model that was a hybrid of the top models (Burnham & Anderson 2004). Given the large number of potential variables involved (N = 21), a Principal Components Analysis (PCA) was also performed to see if a less redundant, more parsimonious model would have improved predictive capabilities over the other models. The Kappa statistic (κ) (Cohen 1960) was used to select the final model, based on a confusion matrix (Manel *et al.* 2001). Parameters for the final model were then estimated using a mixed-effects generalized linear model with stream as a random effect.

Once the top model was selected, its ability to predict metamorphosis in larval sea lampreys was compared with that of two metamorphic models in common use, also using the Kappa statistic. These two models were: (1) the two-region length-based probability of metamorphosis model currently used by the GLFC in the empirical stream treatment ranking (ESTR) software (Christie *et al.* 2003); and (2) a minimum criteria (MC) model, which sets minimum thresholds for length, weight, and condition factor before metamorphosis is predicted to occur (Holmes & Youson 1994; Holmes *et al.* 1994; Hollett 1998; Henson *et al.* 2003). The number of correct transformer predictions, the number of correct predictions overall (of both larvae and tranformers) and the Kappa statistic were all used to compare the performance of each model relative to the other two.

Because one purpose of this study was to develop a model that could be used within the framework of the Great Lakes Fishery Commission's stream ranking process, a second model analysis was performed to develop a management-oriented model, following the same procedures as described above. In this analysis, the suite of variables used was limited to those that could be readily collected by field staff over the course of the field season. Additional stream-specific data were obtained from a similar mark-recapture study that was performed in 1995/1996 (Hollett 1998), allowing for the combination of these two data sets and providing an increase in both the number of streams and the overall number of observations with which to develop the management model.

Results

General Findings

Recaptured lampreys that entered into metamorphosis were significantly longer and heavier in the fall (at the time of marking) than those that did not (Table 3), with significant differences in the average size of both larvae and transformers from different streams. There was not a significant difference in size (either length or weight) between male and female larvae or transformers (Table 3). There was a significant trend for the growth of larvae to be greater in southern and eastern streams of the basin (r=-0.26, p<0.0001, N=212 for both latitude and longitude) and in streams with higher pH values (r=0.22, p<0.01, N=212). Of the eight temperature parameters explored in this analysis, only the average temperatures during May and June were significantly related to growth on the set of streams in this study (May: r=0.19, p<0.05; June: r=-17, p<0.05). Growth rates of category 1 and 2 streams, while not significantly different from one another, were significantly higher than growth rates from category 3 streams (one-way ANOVA, $F_{2,\ 209}$=6.035, p =.0030).

INSERT TABLE 3

Biological Model Analysis

The number of lampreys available for the development of the biological model analysis was reduced from the original 212 recaptures to 168, because reliable estimates of age or sex could not be determined for 44 larvae. The best-subsets model selection procedure, using the full suite of variables, produced a list of 29 potential models, all with AIC_C values differing by < 2 (Burnham & Anderson 2004). The use of principal components to identify independent variables did not improve model fit.

Since AIC_C values alone were not able to identify a single best model, the ability to correctly predict the occurrence of metamorphosis in individual lamprey and the kappa statistic were added to the selection criteria, resulting in the selection of a model that contained a measure of lamprey weight and age , as well as the stream-level effects of stream latitude, longitude, average larval density in type 2 habitat, and the number of days where the water temperature was between 19 and 23°C,. This model correctly predicted the fate of 92.9

% of the recaptured animals, and 82.2% of those that underwent metamorphosis (Table 4). The kappa statistic value for this model was 0.8126, which indicates nearly perfect agreement (Landis and Koch 1977).

INSERT TABLE 4

Model averaging was utilized to develop a hybrid model from the list of potential models, but the resulting composite model exhibited poor kappa values and could not consistently differentiate from streams with different rates of metamorphosis. The resulting Akaike weights, however, were useful in illustrating variables important to metamorphosis, in particular highlighting the importance of weight, age, stream longitude and drainage area measurements in the prediction of metamorphosis (Figure 2).

INSERT FIGURE 2

The variance estimate for the random effect of river was close to zero, and models that excluded river as a random effect had lower AIC_C values, leading us to conclude that the explicit inclusion of stream-level variables was able to account for the observed variability in metamorphic rates among streams (Table 5). As a result, the final model does not contain river as a random effect and should be applicable to streams outside of those used in model development.

INSERT TABLE 5

Management Oriented Model

The final biological model included variables (age, sex, time-integrated temperature) that are impractical to collect given the number of streams and lampreys that are sampled by the control agents each year. We conducted a second analysis, limiting the explanatory variables to those that could readily be obtained by management agencies. Since age or sex was not included in this analysis, the full dataset of 212 recaptured lampreys was used.

Supplementary water chemistry data from the lamprey control program allowed for the addition of mark-recapture data from Hollett (1998); which increased the number of streams in this analysis to 11 and brought the overall size of the dataset to 315 lampreys (214 larvae, 101 transformers).

INSERT TABLE 6

The results of the model selection procedure on the combined dataset produced four similar top models, only differing in their inclusion or omission of condition factor and stream conductivity (Table 6). While a model consisting of length, condition factor, and stream latitude, longitude, drainage area, and lamprey production category possessed the highest kappa value, the parameter estimate for condition factor was not significant, so a similar model without condition factor (the model ranked second based on kappa) was selected as the top model. This model was able to correctly predict the fate of individual larvae 87.6% of the time. Model averaging was not employed during the management model development, because only four very similar models were in consideration. Again, principal components did not improve model fit. As was the case with the biological model, the random effect of stream was not significant, showing that the inclusion of the stream-specific parameters accounted for inter-stream variability in metamorphic rate (Table 7).

INSERT TABLE 7

Comparison with other predictive models of metamorphosis

The two models developed in this study were much better at predicting which larvae would enter metamorphosis than the other two existing models (Table 8). A direct comparison of the management model with the biological model was not performed, as the datasets used to derive the two models differed in the both the number of variables and their sample size. Kappa values for the biological model indicated almost perfect agreement (Table 8A) while the management model exhibited substantial agreement (Table 8B) (Landis and Koch 1977). In contrast, the kappa values for the MC and ESTR models ranged only from slight to fair agreement when applied to either the biological or management model datasets. A stream-specific analysis of model output indicated that the management model provided equal or more accurate predictions of metamorphosis relative to the ESTR and MC models, on 8 of 11 streams.

INSERT TABLE 8

Discussion

Our results suggest that including additional variables within predictive models of metamorphosis can account for much of the variability observed in metamorphic rates of sea lamprey across the Great Lakes and greatly improve our ability to forecast parasitic sea lamprey production. The predictive accuracy of both the biological and management models was far superior to the length-based and condition-based models currently in use, for the streams used to develop our models. We recognize that this is not an ideal comparison because the data used to fit our models were also used to evaluate their accuracy. For this reason and others outlined below, we strongly recommend further efforts to test the accuracy of the new models relative to existing tools.

The biological model may not be practical for use within the existing sea lamprey control program, but it does point to factors that appear to influence the probability of metamorphosis in sea lamprey populations. Sea lamprey age was included in all of the top biological models, indicating that older larvae, independent of their length and weight, are more likely to enter metamorphosis. Weight was included in all but one of the top models, with estimated lipid weight replacing total weight in the one exceptional case. This result is consistent with the hypothesis that larvae must reach a certain mass and possess sufficient energy reserves prior to entering into metamorphosis (Holmes & Youson 1994). In contrast, our non-invasive estimates of larval lipid content only entered into two of the top biological models. Previous research has indicated that lipid accumulation is important to metamorphosis in sea lampreys, a phenomenon unique to sea lampreys (Holmes *et al.* 1999; for review, see Youson, 2003),) Our results suggest that either our non-invasive methods were not sufficiently accurate to discriminate important differences in actual lipid levels, or that this indicator is not evident in larvae sampled during the growing season prior to metamorphosis. To discriminate among these explanations, we recommend further investigation into non-invasive methods for determining lipid content of larval sea lampreys (Cox & Hartman 2005; Crossin & Hinch 2005).

Both the biological and management models included several stream-level variables that account for variation in the probability of metamorphosis among individual sea lampreys with similar lengths, weights and ages but from different streams. These included a stream temperature variable (biological model only), latitude and longitude, larval density in Type 2 habitat, drainage area (management model only) and stream category (management model only). Each of these factors represent environmental variables that could plausibly affect metamorphosis (temperature, regional edaphic factors, stream productivity, etc), but in general the direction of the observed effects was inconsistent either among models (e.g., larval density) or with *a priori* hypotheses. For example we observed a negative relationship between a stream temperature variable and probability of metamorphosis in the biological model, in contrast with previous studies (Holmes *et al.* 1994; Holmes & Youson 1997) which concluded that it is the rise in temperature in the spring that is the important cue, not the magnitude of the temperature increase. Because our analysis is limited to 9 (biological) or 11 (management) streams, and because the mechanisms underlying these environmental effects are not clear, it may be inappropriate to extrapolate our models that contain these variables to other streams without further validation and exploration of mechanisms.

We recommend that both existing and future models of metamorphosis be evaluated using individual-specific mark-recapture studies in the field before being affirmed as a basis for making lampricide treatment decisions. Recently, emphasis has been placed on evaluating larval assessment accuracy by conducting mark-recapture studies during lampricide treatments to estimate abundance (Hansen *et al.* 2003). In these evaluations, sea lamprey larvae are mass-marked by removing a piece of non-vascular tissue from the distal end of the caudal fin; consequently the physiological fate of individuals cannot be followed. Valuable additional information on metamorphosis could be obtained by modifying some of these mark-recapture studies to include measurements of individual lamprey and coded wire tag implantation at the time of marking, following the methods used for this study. In particular, selecting streams where the discrepancy in transformer estimates between different metamorphic models is the greatest may lead to a rapid improvement in our ability to develop models that more accurately predict metamorphosis.

Finally, the methods currently used by the GLFC to rank streams for lampricide treatment suffer from the fact that the models of metamorphosis being used, along with their underlying assumptions, have not been evaluated to assess how errors in their predictions might affect the stream ranking process. The uncertainty associated with both existing and new models should be integrated into a stream selection simulation analysis to compare the performance of alternative stream ranking protocols. We have conducted a preliminary analysis of this type which indicated that although stream ranking methods based on predictions of metamorphosis are optimal when the models are precise and accurate, other ranking methods may be more robust to the high degree of uncertainty that actually exists in these models (Steeves 2002; Treble 2006). Our results also suggest that a new metamorphic model that decreases uncertainty surrounding transformer forecasts could lead to a substantial improvement in our ability to control lamprey populations in the Great Lakes.

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Table Captions

Table 1. Number of marked and recaptured sea lamprey larvae by stream, including the year of marking and total numbers.

Table 2. Summary of stream-specific characteristics used in the development of the biological and management-based models.

Table 3. Results of Analysis of Variance (ANOVA) for differences in (A) length at the time of marking, (B) weight at the time of marking, between larval and metamorphosed sea lamprey from eight different streams.

Table 4. Model selection results for the biological model.

Table 5. Parameter estimates, standard errors, and p-values from a mixed model analysis for the biological model of metamorphosis selected as best (with the highest kappa statistic value and predictive accuracy), based on mark-recapture data (N=168) from eight streams.

Table 6. Model selection results for the management-based model.

Table 7. Parameter estimates, standard errors, and p-values from a mixed model analysis for the management model selected as best (with the highest kappa statistic value and predictive accuracy), based on combined mark-recapture data (N=315) from this study and Hollett (1998).

Table 8. Comparison of model predictions from the two models developed in this study with the two other common models of sea lamprey metamorphosis. Table A is based on the data collected in the mark-recapture study, minus animals where an accurate estimate of age was

not obtained. Table B is based on a combination of this mark-recapture data, plus that of Hollett (1998), but where the variables included in the model analysis were limited to those easily collected within the scope of the sea lamprey management program.

Table 1. Number of marked and recaptured sea lamprey larvae by stream, including the year of marking and total numbers.

Stream	Lake	Total Marked	Number Recaptured	Larvae	Trans-formers	Recapture Rate
Pancake River[1]	Superior	144	10	4	6	6.9%
Bowmanville Cr.[1]	Ontario	344	50	12	38	14.5%
Little Sandy Cr.[1]	Ontario	121	22	11	11	18.2%
Root River[2]	Huron	254	11	6	5	4.3%
Crystal Creek[2]	Huron	170	15	13	2	9.4%
Silver Creek[2]	Huron	182	40	37	3	22.0%
Juniata Creek[2]	Huron	168	37	34	3	22.0%
Ceville Creek[2]	Michigan	142	27	25	2	19.0%
Totals		**1525**	**212**	**143**	**70**	**13.9%**

[1] *denotes streams with larvae marked in 2003 and recaptured during lampricide treatments in 2004.*
[2] *denotes streams with larvae marked in 2004 and recaptured during lampricide treatments in 2005.*

Table 2. Summary of stream-specific characteristics used in the development of the biological and management-based models.

	Pancake R.	Root R.	Crystal Cr.	Silver Cr.	Juniata Cr.	Ceville Cr.	Bowmanville Cr.	Little Sandy Cr.	Gordon Cr.[*]	Oshawa Cr.[*]	Wilmot Cr.[*]
Lake Basin	Superior	Huron	Huron	Huron	Huron	Michigan	Ontario	Ontario	Huron	Ontario	Ontario
Stream Characteristics											
Drainage Area (ha)	11219	13132	1508	3097	2389	383	15964	4184	1500	12800	10800
Latitude (dd.dd°)	46.96	46.54	46.56	44.35	43.41	46.00	43.89	43.64	46.15	43.87	43.90
Longitude (dd.dd°)	84.66	84.21	84.24	83.49	83.49	84.36	78.66	76.17	83.89	78.82	78.60
Alkalinity[†]	15.30	21.62	22.27	140.10	203.28	197.57	202.40	50.55	41.60	230.10	216.30
Conductivity[†]	30	98	40	280	466	250	370	110	95	487	95
pH[†]	7.13	7.21	7.29	8.27	8.24	7.89	8.32	7.74	7.50	8.38	8.32
Stream-level Lamprey Characteristics											
Average Type-1 Density (#/m^2)[†]	2.66	1.36	2.60	23.59	0.22	6.63	6.98	6.27	0.28	3.15	2.83
Average Type-2 Density (#/m^2)[†]	0.76	1.24	5.33	12.92	0.08	1.67	2.43	5.20	0.02	2.35	0.37
Lamprey Production Category[†]	1	1	1	1	2	3	1	1	3	1	1
Last TFM Treatment (Years)[†]	6	6	2	5	7	5	3	3	4	3	3

[†] *Unpublished data, Sea Lamprey Control Centre, 1 Canal Drive, Sault Ste Marie, ON*

[*] *Streams added from Hollett (1998) for management model development*

Table 3. Results of Analysis of Variance (ANOVA) for differences in (A) length at the time of marking, (B) weight at the time of marking, between larval and metamorphosed sea lamprey from eight different streams.

(A) ANOVA Table (Dependent variable = Length)

Source	Effect	SS	DF	MS	F	Pr>F
Intercept	Fixed	1095034	1	1095034	3078.253	<0.0001
Stream	Random	4338	7	620	6.475	<0.0001
Larvae/Transformer	Fixed	6052	1	6052	63.230	<0.0001
Sex	Fixed	92	1	92	0.962	0.3282
Error		15123	158	96		

(B) ANOVA Table (Dependent variable = Weight)

Source	Effect	SS	DF	MS	F	Pr>F
Intercept	Fixed	551.522	1	551.522	549.791	<0.0001
Stream	Random	11.462	7	1.637	4.326	0.0002
Larvae/Transformer	Fixed	27.624	1	27.624	72.982	<0.0001
Sex	Fixed	0.518	1	0.518	1.368	0.2440
Error		59.804	158	0.379		

Table 4. Model selection results for the biological model.

Model Variables	df	AICc	Percent Overall Correct	Percent Larvae Correct	Percent Transformers Correct	Kappa Statistic
W / A / OT / Lat / Lon / T2	5	68.98	92.86%	96.75%	82.22%	0.8126
W / A / OT / pH / Lon / T2	5	68.30	92.26%	95.93%	82.22%	0.7984
W / A / OT / Con / Lon / T2	5	68.72	92.26%	95.93%	82.22%	0.7984
W / A / OT / pH / Lon / T1	6	68.78	92.26%	95.93%	82.22%	0.7984
W / A / Con / DA / Lon	5	68.96	92.26%	95.93%	82.22%	0.7984
W / A / MT / DA / Lon	6	68.37	92.26%	96.75%	80.00%	0.7955
W / A / Con / DA / LT	6	69.00	92.26%	96.75%	80.00%	0.7955
W / A / Lat / T2 / Cat	5	68.42	91.67%	95.12%	82.22%	0.7845
W / A / MT / DA / Lon / T1	7	68.67	91.67%	95.12%	82.22%	0.7845
W / A / DA / Lon / LT	6	68.52	91.67%	95.93%	80.00%	0.7814
W / A / OT / Con / Lon / T2 / Sx	5	68.54	91.67%	95.93%	80.00%	0.7814
W / A / Apr / May / DA / LT	6	68.76	91.67%	95.93%	80.00%	0.7814
W / A / Jun / DA / LT	6	68.87	91.67%	95.93%	80.00%	0.7814
W / A / OT / Alk / Lon / T1	5	68.92	91.67%	95.93%	80.00%	0.7814
W / A / SWT / DA / LT	5	68.96	91.67%	95.93%	80.00%	0.7814
W / A / DA / LT	4	67.07	91.67%	96.75%	77.78%	0.7782
W / A / Con / DA / Lon / LT	7	68.60	91.07%	95.12%	80.00%	0.7674
W / A / OT / Lat / Lon / T2 / Sx	6	68.61	91.07%	95.12%	80.00%	0.7674
W / A / ST / Lon / T1	6	68.67	91.07%	95.12%	80.00%	0.7674
W / A / DA / LT / ADG	6	69.04	91.07%	95.12%	80.00%	0.7674
W / A / OT / DA / LT	5	69.05	91.07%	95.12%	80.00%	0.7674
W / A / May / DA / LT	5	69.07	91.07%	95.12%	80.00%	0.7674
W / PLP / A / DA / LT	5	69.04	91.07%	95.93%	77.78%	0.7640
W / A / ST / Lon / T1 / Sx	6	68.52	90.48%	94.31%	80.00%	0.7537
W / A / MT / Lon / T1	6	68.94	90.48%	94.31%	80.00%	0.7537
W / A / OT / Lon / T1	5	68.11	90.48%	95.12%	77.78%	0.7501
W / A / DA / LT / Sx	5	69.05	90.48%	95.12%	77.78%	0.7501
PLW / A / DA / LT	5	69.01	89.29%	94.31%	75.56%	0.7189
W / A / pH / DA / Lon / LT	4	69.03	89.29%	94.31%	75.56%	0.7189

Where:

W=Weight (g)
A=Age (years)
Sx=Sex of lamprey
PLW=Predicted Lipid Weight (g)
PLP=Percent Lipid Percent (of wet body weight)(%)
Lat=Latitude (decimal degrees)
Lon=Longitude (decimal degrees)
DA=Stream drainage area (km^2)
Con=Conductivity (S/cm)
Alk=Alkalinity($CaCo_3$*/mg)*
pH=pH of stream (measure of acidity)
LT=years since last treatment

Cat=Stream Lamprey Production category
T1=Average larval density in Type-1 habitat
T2=Average larval density in Type-2 habitat
ADG=Avererage Daily Growth (mm)
ST=Suitable Temperature (between 9 and 25°C)
OT=Optimal Temperature (between 19 and 23°C)
MT=Mean Annual Temperature (°C)
Apr= Average stream temperature in April (°C)
May= Average stream temperature in May (°C)
Jun= Average stream temperature in June (°C)
SWT=Spring Warming Trend (slope of the line showing increase in temperature over time)

Table 5. Parameter estimates, standard errors, and p-values from a mixed model analysis for the biological model of metamorphosis selected as best (with the highest kappa statistic value and predictive accuracy), based on mark-recapture data (N=168) from eight streams.

Effect	**Parameter Estimate**	**Standard Error**	**p-value**
Fixed Effects:			
Intercept	39.49	17.67	0.025
Weight	4.76	1.03	<0.001
Age	3.05	0.96	0.002
# Days between 19 and 23°C	-0.16	0.06	0.008
Stream Latitude	1.27	0.49	0.010
Stream Longitude	-1.40	0.30	<0.001
Estimated Mean Larval Density in Type-2 Habitat	-0.39	0.16	0.013
	Variance Estimate	**Standard Error**	**p-value**
Random Effects:			
Stream	<0.0001	---	---

Table 6. Model selection results for the management-based model.

Model Variables	df	AICc	Percent Overall Correct	Percent Larvae Correct	Percent Transformers Correct	Kappa Statistic
L / CF / Lat / Lon / DA / T2 / Cat	8	182.44	87.94%	92.99%	77.23%	0.717
L / Lat / Lon / DA / T2 / Cat	7	182.66	87.62%	92.52%	77.23%	0.711
L / CF / Lat / Lon / DA / Con / T2 / Cat	9	184.12	87.30%	92.99%	75.25%	0.701
L / Lat / Lon / DA / Con / T2 / Cat	8	184.31	86.98%	92.06%	76.24%	0.696

Where:

L=Length (mm)
CF=Condition Factor
Lat=Latitude (decimal degrees)
Lon=Longitude (decimal degrees)
DA=Stream drainage area (*km*^{2})
Con=Conductivity (S/cm)
Cat=Stream Lamprey Production category
T2=Avererage larval density in Type-2 habitat

Table 7. Parameter estimates, standard errors, and p-values from a mixed model analysis for the management model selected as best (with the highest kappa statistic value and predictive accuracy), based on combined mark-recapture data (N=315) from this study and Hollett (1998).

Effect		**Parameter Estimate**	**Standard Error**	**p-value**
Fixed Effects:				
Intercept		-62.9748	16.3993	0.0001
Length		0.2125	0.0311	<0.0001
Latitude		3.8683	0.9445	<0.0001
Longitude		-1.7307	0.3771	<0.0001
Drainage Area		0.0004	0.0001	0.0001
Estimated Mean Larval Density in Type-2 Habitat		0.6541	0.2078	0.0016
Categorical Effects:				
Stream Production Category	(Category 1)	4.0551	1.6122	0.0119
	(Category 2)	-6.8757	1.9908	0.0006
	(Category 3)	1.0000	0.0000	---
Random Effects:		**Variance Estimate**	**Standard Error**	**p-value**
Stream		<0.0001	---	---

Table 8. Comparison of model predictions from the two models developed in this study with the two other common models of sea lamprey metamorphosis. Table A is based on the data collected in the mark-recapture study, minus animals where an accurate estimate of age was not obtained. Table B is based on a combination of this mark-recapture data, plus that of Hollett (1998), but where the variables included in the model analysis were limited to those easily collected within the scope of the sea lamprey management program.

	Model	Correct Larval Predictions	Correct Transformer Predictions	Correct Transformer Predictions (%)	Incorrect Predictions	Kappa Statistic
(A	***Full dataset (123 larvae / 45 transformers):***					
	Biological Model	119	37	82.2%	12	0.813
	ESTR	119	18	40.0%	31	0.439
	Minimum Criteria	122	4	8.9%	42	0.112
(B	***Expanded dataset (214 larvae / 101 transformers):***					
	Management Model	198	78	77.2%	48	0.711
	ESTR	201	57	56.4%	57	0.548
	Minimum Criteria	208	16	15.8%	91	0.164

Figure Captions

Figure 1. Location of the eight study streams selected for this study within the Great Lakes basin. * indicates the locations of streams added to the management model dataset from Hollett (1998).

Figure 2. Relative importance, based on Akaike weights, of predictor variables from the list of 26 top biological models for the prediction of metamorphosis. Age, with a weight of one, was the only predictor variable to be found in each one of the top models.

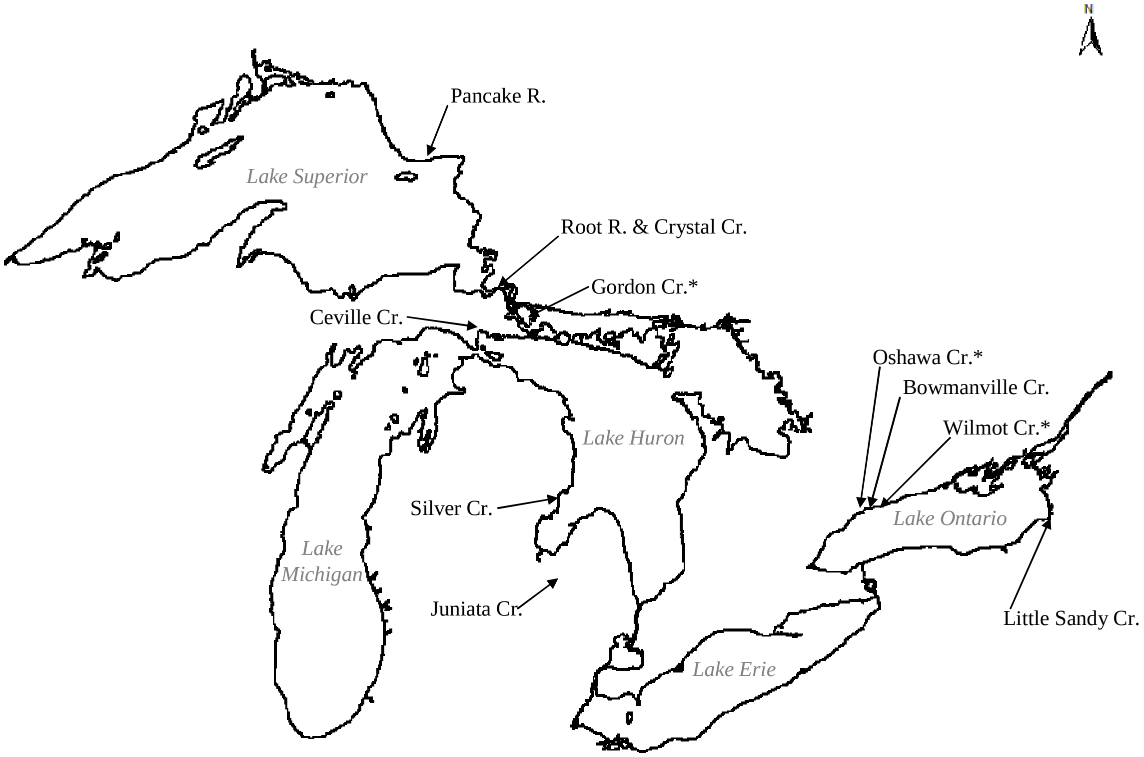

Figure 1. Location of the eight study streams selected for this study within the Great Lakes basin. Streams identified with an asterisk denote streams added to the management model dataset from Hollett (1998).

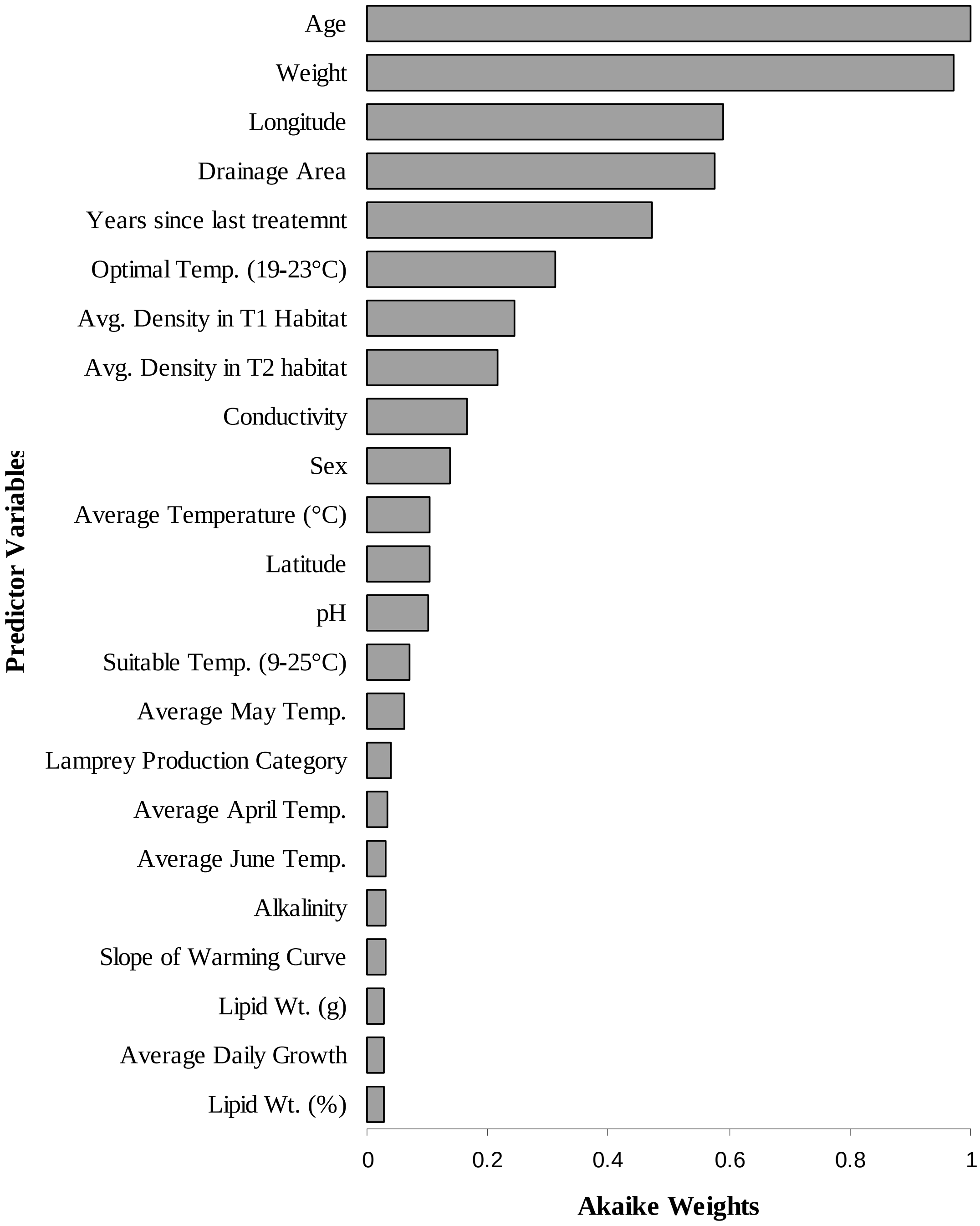

Figure 2. Relative importance, based on Akaike weights, of predictor variables from the list of 26 top biological models for the prediction of metamorphosis. Age, with a weight of one, was the only predictor variable to be found in each one of the top models.

APPENDIX 4

Variation in larval sea lamprey demographics among Great Lakes tributaries: A mixed-effects model analysis of historical survey data

by

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Running Title:

Larval sea lamprey demographics

Abstract

Understanding sources of variation in fish populations is valuable from both a management and an ecological perspective. If subsets of a population differ in demographic rates such as growth and recruitment, management practices should be tailored reflect these ecological differences. Great Lakes sea lampreys are controlled primarily by treating tributaries with lampricides that target the larval stage. The streams considered for chemical control have been divided into four categories based on their regularity of parasitic lamprey production inferred from the historic regularity of chemical treatments. This categorization was intended to direct future assessment efforts, but may also be a reflection of differences in early demographic rates. We analyzed assessment survey data collected from 1959 -2005 using mixed-effects models and variance components analyses to test for differences in recruitment and growth to age 1 among stream categories. Recruitment was twice as large in regularly treated streams than in irregularly treated streams, indicating that year class strength at age 1 is correlated to abundance at later life stages. We found no consistent differences in length at age 1 among categories of streams; however, Lake Superior streams that are treated irregularly also exhibit more annual variation in length at age 1 than streams that are treated regularly. The majority of variation in length at age 1 was due to within-year variation, although this type of variation was fairly consistent across stream types within each lake. Our results indicate that early life history differs among subsets of the Great Lakes sea lamprey population, and management practices should be modified to account for these differences. Mixed-effects models and variance components analyses are useful tools for analyzing large historical datasets for patterns of demographic variation within and among fish populations, whether the ultimate goal is to provide management advice for pest control, harvesting, or conservation.

Introduction

Many fish species show wide variation in demographic parameters among populations (e.g., Hutchings and Jones 1998; Shuter et al. 1998; Winemiller and Rose 1992), and nearly all populations exhibit such variation over time (Ricker 1954, Hilborn and Walters 1992). Both spatial and temporal variation in demographic parameters have implications for management. If not properly accounted for, this variability can cause high inter-annual variation in yield or catch rates in the case of desired fisheries, and high annual variation in control success in pest species such as sea lampreys (*Petromyzon marinus*). Across space, stocks with differing demographic characteristics have differential vulnerability to similar levels of exploitation (Shuter et al 1998; Hilborn et al. 2005; Purchase et al. 2005), while variation over time increases the need to devise management strategies that respond effectively or are robust to unplanned variations in abundance (e.g., Beddington and May 1977; Walters and Pearse 1996; Engen et al. 1997). Additionally, understanding the relationship between growth rates and later abundance and the identification of spatial and temporal patterns in recruitment variation have long been central goals of fisheries ecology (Ricker 1954; Anderson 1988). These implications suggest that studies which describe and increase mechanistic understanding of demographic variation in fish populations are valuable from both a managerial and ecological perspective.

Fish population dynamics are principally determined by the net effect of three demographic processes: recruitment, which for this discussion we define to include reproduction and early survival; growth; and mortality. Management strategies for exploited stocks can depend on which of these demographic processes have the greatest influence on spatial and temporal variation in abundance. For example, in lake trout populations, spatial variation in growth and mortality rates are thought to determine the differential vulnerability of populations to exploitation. Shuter et al. (1998) used an analysis of this variation to argue for different sustainable exploitation rates in lakes of differing size. In contrast, the dynamics of many other fish species are strongly influenced by the irregular occurrence of very large recruitment events. For example, large recruitment events in Lake Erie walleye (*Sander vitreus*) in 1984, 1988, and 2003 have overwhelmingly influenced yields in both commercial and recreational fisheries for this species (Thomas et al. 2007). As well, understanding spatial variation in recruitment dynamics helps managers to determine the degree to which models of recruitment developed for a subset of populations are suitable for application to other populations (Myers et al. 1997; Peterman et al. 1998).

Variation in recruitment and other demographic rates is also common among vertebrate pest species, and accounting for this variation can influence the effectiveness of control efforts on a variety of pests (e.g., European rabbits, *Oryctolagus cuniculus*, Twigg and Williams 1999; great cormorants, *Phalacrocorax carbo sinensis*, Frederiksen et al. 2001; carp, *Cyprinus carpio* L., Brown et al. 2005; and brushtail possums, *Trichosurus velpecula*, Ramsey 2005). Demographic variation is particularly important for the control of sea lampreys in the North American Great Lakes, where empirical research and modeling have shown that recruitment variation can have a large effect on the success of control tactics that target reproductive success (Jones et al. 2003). However, as in desired fish populations, the causes of variation in recruitment are often poorly understood.

In this paper we examine variability in indices of recruitment and growth to age 1 in sea lampreys in the Laurentian Great Lakes, and test whether these indices are associated with a key feature of management: the predictability of the need for chemical treatment of streams to control the pest population. Sea lampreys are invasive pests in the Great Lakes that parasitize other fishes during their juvenile stage. Larval sea lampreys (known as ammocoetes) are stream-dwelling filter feeders (Applegate 1950). Sea lampreys in the Great Lakes are controlled primarily through the periodic treatment of streams with the lampricide 3-triflouromethyl-4-nitrophenol (TFM), which kills from 95-100% of sea lampreys present in the stream at the time of treatment (Christie et al. 2003). Streams are not treated annually, because ammocoetes remain in their natal streams for several years before becoming parasitic. Ideally, the frequency of treatment should match the cycle of recolonization, growth, and maturation of sea lampreys following treatment events (hereafter referred to as “parasitic lamprey production”) in individual streams. However, spatial and temporal variability in demographic processes results in inconsistency in parasitic lamprey production, both within and among streams, and hinders the ability of managers to predict the timing of stream treatments that would optimally prevent the escapement of parasitic sea lampreys. This variability has necessitated the use of costly assessments of larval sea lamprey populations to aid the selection of streams for treatment (Slade et al. 2003). The goal of this study was to determine whether variation in early life demographic processes, specifically recruitment and growth, is able to account for this variation in parasitic lamprey production and thus treatment frequency.

Identification of the demographic processes responsible for variation in parasitic lamprey production within and among streams is of considerable practical interest. Recent studies have drawn attention to the uncertainty inherent in the current assessment methods that are used to select streams for lampricide treatment. In particular, these studies have demonstrated inaccuracies in estimates of parasitic lamprey abundance due to uncertainties in estimates of ammocoete abundance (Steeves et al. 2003), growth rates, and prediction of metamorphosis (Hansen et al 2003). It is doubtful that increases in assessment resources could fully resolve these uncertainties in the assessment and stream selection process (Hansen et al. 2003; Slade et al. 2003). A better understanding of the demographic processes that influence treatment cycles could point to more efficient assessment strategies that focus on these processes, and potentially provide a means to incorporate prior information on stream-specific demographic processes into the stream selection process.

In this study, we used data from historical surveys conducted between 1959 and 2005 to derive time series of recruitment and growth to age 1 for a number of sea lamprey producing streams. Our objective was to determine whether variation in treatment regularity among streams was correlated with measurable differences in recruitment or growth. We were interested in differences in both the mean and variance of recruitment and growth among streams, because either could affect treatment regularity. We hypothesized that streams with irregular treatment histories would have more variable demographic rates, and possibly lower mean rates. We developed mixed-effects statistical models and used variance components analysis to facilitate the use of these historical data sets for examination of this question, despite the fact that the data were not collected with this objective in mind. A secondary goal was to demonstrate the potential of this analysis strategy for opportunistic exploration of similar questions for other desirable and damaging fish species.

Methods

Study Area

Survey data used for these analyses were collected from throughout the Laurentian Great Lakes basin, excluding Lake Erie (Figure 1). Only two streams from the Lake Erie basin had more than one year of data that fit the timing criteria required for this analysis (described below). This paucity of data made the establishment of patterns in variation of population level processes among stream categories impossible. For the purposes of these analyses, we considered larval sea lampreys within different streams to be distinct populations. Parasitic sea lampreys mix as one population within the lake environment and do not home to natal streams (Bergstedt and Seelye 1995); however, mixing does not occur during the ammocoete phase, and growth and timing of metamorphosis are known to differ among streams (Hansen et al. 2003).

Stream Categorizations

Most lamprey-producing streams are treated on a 3-5 year cycle, but streams differ in the regularity with which large populations of transformers develop (Heinrich et al. 2003; Lavis et al. 2003; Morse et al. 2003). Some streams are highly regular in their cycles of parasitic lamprey production and need for treatment, while others vary widely. Previous authors have suggested that differences in recruitment, growth, and survival following lampricide treatments contribute to differences in treatment regularity (Heinrich et al. 2003; Lavis et al. 2003); however, these assertions have yet to be formally tested. Researchers and sea lamprey managers together have divided streams considered for chemical control into four categories based on their regularity of parasitic lamprey production inferred from the historic regularity of chemical treatments and from the expert opinion of assessment biologists who work on these streams. Category 1 streams are highly predictable in their parasitic lamprey production cycle and their treatment schedule. Category 2 streams are somewhat variable in their parasitic lamprey production cycle and treatment schedule, but show some signs of patterns in the length of time between treatments. Category 3 streams are highly variable in their production of sea lampreys and treatment schedule. Category 4 streams are streams in which sea lampreys have been found in the past, but do not currently support sea lamprey populations and are no longer treated. The location and category of each stream used in this analysis are presented in Figure 1.

Historical Survey Data

Over 30,000 larval sea lamprey assessment surveys were conducted between 1959 and 2005 by the United States Fish and Wildlife Service (USFWS) and the Department of Fisheries and Oceans, Canada (DFO). We obtained the results of subsets of these surveys determined by the timing criteria described below, and analyzed them separately for larval growth and recruitment. Several types of larval assessment surveys exist which are conducted for different purposes, and all types were initially obtained. Only age-1 individuals were used for these analyses, because age-1 ammocoetes are the first age class fully recruited to the electrofishing gear used to perform these surveys. To increase the likelihood of only age-1 and younger larvae being present in an assessment collection, surveys following fall lampricide treatments were used, since treatments that occur in the fall are more consistent than spring or summer treatments in their elimination of that year's recruits. Surveys that took place two years after fall treatments were selected for analysis, when the first year class with the potential to re-establish would be age 1. At the time of these surveys, the streams should have contained a maximum of two year classes (age 0 and age 1). However, some streams also contained residual sea lampreys that survived the lampricide treatment. We examined length-frequency histograms for each stream and year to determine which individuals were age 1 and should be included for further analysis. Distinguishing between age classes using length-frequency histograms can be difficult for older cohorts of sea lampreys, but generally the first two age classes are clearly separable (Potter 1980). Streams with two or more years of survey data that fit the timing criteria were included in this analysis. The number of streams (and individuals or stream years) by category and lake used for each component of this study are summarized in Table 1.

Mixed Model Analysis

The effect of stream category on recruitment and growth was analyzed using mixed effects models. In both the recruitment and growth models, for each categorical covariate with *n* levels, parameters were estimated for *n*-1 levels of the covariate, with the overall intercept value representing the first level of each factor.

Recruitment Analysis

Recruitment to age 1 was analyzed using a relative measurement of catch per unit effort (CPUE). To further standardize for effort, only so-called “index surveys” were used to calculate CPUE. Index surveys have been conducted at the same access points for many years with a relatively consistent level of sampling effort. A total of 900 surveys collected from 96 streams in 305 unique stream-years were used for this analysis. The CPUE value used for each stream-year was calculated by summing the total number of age-1 sea lampreys caught in all the surveys in a given stream-year and dividing the total catch by the total time spent electrofishing (meter time, in hours). Some surveys reported effort as “collecting time”, which is a measure of total time spent at a site rather than time spent electrofishing. These measures of collecting time were converted to meter time using a conversion factor of 1.595 units of collecting time for every 1.0 unit of meter time, developed by USFWS-Marquette sea lamprey control (M. Fodale, USFWS, Marquette, MI, unpublished data). Summary statistics of the data used for the recruitment analysis are shown in Table 2.

The recruitment analysis was conducted as a two-step process due to the large number of zeros present in the dataset. First, differences among stream categories in the probability of occurrence of an age-1 year class in the second year following a chemical treatment were analyzed using a binary response variable. Then, non-zero CPUE values were examined for differences in mean CPUE as well as variation in CPUE among stream categories.

Probability of Successful Recruitment

The objective of this analysis was to determine whether the probability of establishment of a cohort following the chemical treatment of a stream differed among stream categories. Streams with no age-1 sea lampreys collected two years following a fall treatment were assumed to have no recruitment, and recruitment was assumed to have occurred in streams with one or more age-1 sea lampreys collected. We modeled recruitment success using a generalized linear mixed effects model using the logit link function (Schall 1991; Venables and Dichmont 2004). The response variable (recruitment [Y]) was binary, equaling 1 if recruitment occurred and 0 if recruitment did not occur. The probability of successful recruitment in stream *j* and year *k* is defined as $\phi_{jk} = \Pr(Y_{jk} = 1)$. To test for differences among stream categories and lakes into which a stream flows in the probability of successful recruitment, stream category and lake were fitted as potential categorical fixed effects. To account for non-independence in recruitment data, sample year and stream were tested as potential categorical random effects. The full model is represented by:

$$\eta_{jklm} = \beta_0 + b_j + b_k + \beta_{1l} + \beta_{2m}, \qquad (1)$$

where

η_{jklm} = the logit of successful recruitment for stream *j* in year *k*, category *l* and lake *m*;

β_0 = the overall intercept;

b_j = the random effect of stream *j* on the intercept (*j* = 1,…,95) and $b_j \sim \mathrm{N}(0, \sigma_2^2)$;

b_k = the random effect of year *k* on the intercept (*k* = 1,…, 44) and $b_k \sim \mathrm{N}(0, \sigma_2^2)$;

β_{1l} = the fixed effect of stream category *l* (*l* = 1,…,4); and

β_{2m} = the fixed effect of lake *m* (*m* = 1,…,4).

All random effects were assumed to be normally distributed with a mean of zero and a variance estimated by the model. It was not possible to fit year and stream as random effects simultaneously, therefore the significance of each random effect was tested separately. After the model that best explained the probability of successful recruitment was selected, the logit of success for each level of a factor was converted to the probability of successful recruitment (ϕ) using the equation $\phi = \frac{1}{1+\exp(-\eta)}$ (Faraway 2006).

Analysis of Non-Zero Recruitment

Analysis of mean CPUE

The objective of this analysis was to determine if significant differences existed in mean CPUE among stream categories. All CPUE values > zero were modeled using linear mixed effects models. Due to non-normality of error terms, CPUE data were transformed using a quarter-root transformation prior to analysis, resulting in normally distributed residuals. As in the previous analysis, stream category and lake were included as potential categorical fixed effects and stream and year were included as potential random effects. The full model against which other models were tested was:

$$y_{jklm} = \beta_0 + b_j + b_k + \beta_{1l} + \beta_{2m} + \varepsilon_{jklm}, \quad (2)$$

where

y_{jklm} = the quarter-root transformed CPUE from stream *j*, year *k*, stream category *l*, and lake *m* (*N* = 255);

ε_{jklm} = the unexplained residual error, $\varepsilon_{jklm} \sim \mathrm{N}(0, \sigma^2)$, and the remaining variable definitions were the same as in model (1).

Analysis of variation in CPUE

The objective of this analysis was to determine if stream categories differed significantly in recruitment variation over time. After selecting the best model to describe mean CPUE (model 2), differences in variation of CPUE among categories were tested by modeling standard deviation ratios of the within group errors using variance covariates (Pinheiro and Bates 2000). The same fixed and random effects selected in the analysis of mean CPUE described above were used in this model. The error structure in the variance components model was represented by:

$$\varepsilon_l \sim \mathrm{N}(0, \sigma^2 \delta_l^2), \qquad (3)$$

where ε_l is the residual error for each sample from stream category *l* (*l* = 1,…,4), and δ_l is the variance parameter estimate for stream category *l*. To achieve identifiably of all parameters, restrictions must be placed on δ_l. The variance parameter of the first category was held constant at one ($\delta_1 = 1$), and the estimates of the other variance parameters represent the ratio between their standard deviations and the standard deviation of the first category (Pinheiro and Bates 2000).

Categories were determined to have significantly different levels of variation in CPUE if the model that estimated a separate variance component for each category resulted in a significantly better fit to the data than the model that estimated a constant level of variance for all stream categories. The relative fit of the two models to the data was assessed using a likelihood ratio test ($\alpha = 0.05$).

Growth Analysis

We used for this analysis a total of 2405 larval assessment surveys from 117 streams. A total of 60,149 age-1 larvae were collected in these surveys. All types of larval assessment surveys were used for the growth analysis, resulting in more surveys available for analysis than in the recruitment analyses. The data included in the growth analysis are summarized in Table 2.

Analysis of mean length at age 1

Our aim for this analysis was to determine if larval sea lampreys differed in mean length at age 1 among stream categories. We evaluated differences in mean length using general linear mixed effects models. Length data were $\log_e$ transformed to correct for non-normality and heteroscedasticity of residuals. When reporting results, estimates of back-transformed mean effect sizes were bias corrected (Beauchamp and Olsen 1973). The assessment surveys used for this analysis were conducted between May 1st and October 31st. The Julian day on which a survey was conducted (day of year, DOY) was included as a continuous fixed effect in all models to correct for differences in larval length due to different collection dates. DOY was centered around the mean survey DOY (Julian day 216.3) to avoid correlation among estimates of random slopes and intercepts (Pinheiro and Bates 2000). Stream category and the lake into which a stream flows were included as potential categorical fixed effects. Initially, all possible interactions among fixed effects were also included as fixed effects. However, the inclusion of category by lake and DOY by lake interactions caused models to not converge. Therefore, these interactions were not considered as potential fixed effects in model selection.

Because of the hierarchical nature of the data, nested random effects for the stream, reach, year, and survey from which individuals were collected were included in the model to account for the structure of the data and to correct for the lack of independence among individuals. Random slopes (representing the effect of each factor on the relationship between

DOY and length) and random intercepts were estimated for stream, year, and reach, and random intercepts were estimated for survey ID. The full model is represented by the equation:

$$y_{ijklmno} = \beta_0 + b_{j,1} + b_{jk,1} + b_{jkl,1} + b_{jklm} + (\beta_1 + b_{j,2} + b_{jk,2} + b_{jkl,2} + \beta_{2n}) DOY_i \\ + \beta_{3n} + \beta_{4o} + \varepsilon_{ijklmno}, \qquad (4)$$

where

$y_{ijklmno}$ = the log$_e$-transformed length of individual sea lamprey *i* (*i* = 1,…,60149);

β_0 = the overall mean length or intercept;

b_j = the random effect of stream *j* (*j* = 1,…,117), where $b_{j,1}$ is the random effect on the intercept and $b_{j,2}$ is the random effect on the slope, $b_{j,1} \sim \mathrm{N}(0, \sigma_1^2)$, $b_{j,2} \sim \mathrm{N}(0, \sigma_2^2)$;

b_{jk} = the random effect of year *k* within stream *j* (*k* = 1,...,N_j), where $b_{jk,1}$ is the random effect on the intercept and $b_{jk,2}$ is the random effect on the slope, $b_{jk,1} \sim \mathrm{N}(0, \sigma_3^2)$, $b_{jk,2} \sim \mathrm{N}(0, \sigma_4^2)$;

b_{jkl} = the random effect of reach *l* within year *k* and stream *j* (*l* = 1,…,N_{jk}), where $b_{jkl,1}$ is the random effect on the intercept and $b_{jkl,2}$ is the random effect on the slope, $b_{jkl,1} \sim \mathrm{N}(0, \sigma_5^2)$, $b_{jkl,2} \sim \mathrm{N}(0, \sigma_6^2)$;

b_{jklm} = the random effect on the intercept of survey ID *m* nested within reach *l*, year *k*, and stream *j* (*m* = 1,…,N_{jkl}), $b_{jklm} \sim \mathrm{N}(0, \sigma_7^2)$;

β_1 = the continuous fixed effect of being sampled on a given day of year for individual *i*, centered on the mean day of year;

β_{2n} = the fixed interaction effect of category *n* (*n* = 1,…,4) on the slope of the relationship between day of year and $\log_e$(length);

β_{3n} = the fixed effect of category *n* (*n* = 1,…,4);

β_{4o} = the fixed effect of lake *o* (*o* = 1,…,4); and

$\varepsilon_{ijklmno}$ = the unexplained residual error, $\varepsilon_{ijklmno} \sim \mathrm{N}(0,\sigma^2)$.

All random effects and error terms were assumed to be normally distributed with a mean of zero and a variance estimated by the model.

Analysis of variation in length at age 1

Our aim in this analysis was to test for different levels of variation in mean length at age 1 among stream categories and among lakes. Preliminary analysis showed that the relationship between stream category and variance in length at age 1 differed among lakes. In order to test for differences in variation, residual variances were estimated for each level of a stratification variable (Pinheiro and Bates 2000). To determine if the within group variance in length at age 1 differed significantly among lakes, variance parameters (∂_p) were estimated for each lake using stream and reach as random effects. To determine if within group variance in length at age 1 also differed among stream categories within lakes, variance parameters were then estimated for each category and lake combination, again including stream and reach as random effects. The error structure of these models is represented by:

$$\varepsilon_{ijklmno} \sim \mathrm{N}(0,\sigma^2\partial_p^2), \qquad (5)$$

where p = 1,…,N; and $\partial_1 = 1$. $\varepsilon_{ijklmno}$ is the residual error for each individual sea lamprey *i* from strata *p*, p is the stratification variable in which an individual was collected, either the lake or the stream category and lake combination, and ∂_p is the variance parameter estimate for variable *p*. The residual variance for each category and lake combination was calculated by multiplying the variance component estimate (∂^2) by the residual variance of the model.

We tested the significance of the variance components by testing the models with separate variance components against models with constant variance using likelihood ratio tests. If likelihood ratio tests were significant, indicating a better model fit when separate variance components were estimated for different strata, we used 95% confidence intervals on the variance parameter estimates for each stratum to determine which strata differed from one another in their variance estimates. For these variance models, the same fixed effects selected in the analysis of mean length at age 1 from model 4 were used, random slopes and intercepts were estimated for stream, and random intercepts were estimated for reach.

The variance component analysis that included stream and reach as random effects determined whether or not lakes, and categories within lakes, differed in their variances. These variances included both within- and among-year components. Both are important to sea lamprey managers, although the among-year variance is of most interest for this analysis. To determine the relative contribution of within- and among-year variance to the overall differences in variance observed among strata, an additional model was created that estimated random slopes and intercepts for each year in addition to the random effects estimated for stream and reach. Variance components were again estimated for each category and lake combination. Because of the inclusion of year as a random effect, the variance components estimated in this model included within-year variance only. The ∂^2 estimated for each stratification factor was multiplied by the residual variance of the model to estimate the within year variance for each category and lake combination, and compared to the estimate of the total residual variance obtained from the model in which only stream and reach were included as random effects.

Model Selection

The significance of random and fixed terms were evaluated using Akaike's information criterion (AIC), and effects were considered significant if their inclusion resulted in a decrease in AIC value of $\geq$2 (Burnham and Anderson 1998). Diagnostics of all selected models were examined to ensure no assumptions were violated. All modeling and statistical analyses were performed using R V.2.1.1 (R Core Development Team 2005).

Generalized Linear Mixed Models

For the analysis of the probability of successful recruitment, fixed effects were selected prior to random effects due to the inability of the model to converge with all fixed effects and random effects included. Models with only fixed effects were fitted using iteratively reweighted least squares, and the significance of individual fixed effects was evaluated using AIC. After the fixed effects structure was determined, the significance of stream and year as random effects was evaluated. For generalized linear mixed models, AIC values must be approximated because the $\log_e$-likelihood equation does not have a closed-form expression (Pinheiro and Bates 1995). To evaluate the significance of random effects, AIC values were approximated using the adaptive Gaussian quadrature (AGQ) approximation (Pinheiro and Bates 1995).

General Linear Mixed Models

Random effects were modeled with all possible fixed effects included for all models other than the probability of successful recruitment. Significance of individual random effects were evaluated using AIC values for individual models using the restricted maximum likelihood (REML) method of estimation of model fit (Pinheiro and Bates 2000). After determining the appropriate random effects structure for each model, significance of individual fixed effects were determined by sequentially removing fixed effects from the model and comparing AIC values. All tests for fixed effects were performed using the maximum likelihood (ML) method of estimation of model fit (Pinheiro and Bates 2000).

Results

Recruitment Analysis

The majority of streams and stream years included in the recruitment analysis were Category 1 and Lake Superior streams (Table 1 and Table 2). Category 1 streams are by definition treated more regularly than other stream categories, and Lake Superior streams have the longest treatment history of the Great Lakes. No Category 4 streams from Lake Huron or Lake Ontario were included in this analysis (Table 1). The percentage of failed recruitment was highest in Category 4 and Lake Superior streams, and lowest in Category 1 and l Lake Ontario streams, although streams from all categories and lakes other than Category 4 and Lake Ontario exhibited similar percentages of failed recruitment (Table 2). Raw mean recruitment was highest in Category 1 and Lake Ontario streams, and lowest in Category 4 and Lake Michigan streams (Table 2). The standard deviation of mean recruitment was large relative to the mean recruitment for all stream groupings.

Probability of Successful Recruitment

The probability of a successful recruitment event was best explained by a model including category as a fixed effect and year as a random effect (Table 3). Models with both year and stream as random effects could not be fit to the data due to insufficient sample number. Category 4 streams were half as likely to have successful recruitment events as any other type of stream, and categories 1-3 did not differ in their probability of a successful recruitment event

(Table 4, Figure 2). Streams from different lakes did not differ significantly in their probability of successful recruitment to age 1.

Analysis of Non-Zero Recruitment

Mean CPUE

Mean CPUE varied significantly among lakes and stream categories, and the model best explaining mean CPUE included no random effects (Table 5). Category 1 streams had the highest level of mean recruitment of any stream category, and Lake Ontario streams had the highest mean recruitment of any lake (Table 6). When held constant for lake, the mean recruitment level in category 1 streams was almost twice that of category 3 streams, and nearly five-fold that of category 4 streams (Figure 3). When held constant for category, the mean recruitment in Lake Ontario streams was more than twice that of streams in any other lake (Figure 4). While the best model explained significant differences in mean recruitment, it did not explain the majority of recruitment variation (Multiple $R^2 = 0.13$).

Variation in CPUE

Stream categories did not differ significantly in their variation in CPUE; the model allowing for different levels of variation for each category did not have greater support than the model with constant variance (Likelihood ratio = 3.3, DF = 3, p = 0.35).

Growth Analysis

Consistent with the breakdown of streams used for the recruitment analysis, the majority of streams and of individual sea lampreys included in the analysis of growth to age 1 were from Category 1 and Lake Superior streams due their more regular and longer treatment histories (Table 1 and Table 2). Raw mean length was highest in sea lampreys from Category 4 and Lake Ontario streams, and similar in the remainder of categories and lakes (Table 2). The standard deviation of length at age 1 was highest in Category 2, Lake Huron, and Lake Ontario streams, lowest in Category 4 streams, and similar in both Category 1 and 3 and Lake Superior and Michigan streams (Table 2).

Mean length at age 1

Mean length at age 1 was best explained by a model including stream, year, reach, and survey ID as random effects (Table 5). Random slopes and intercepts were estimated for stream and year, and random intercepts were estimated for reach and survey ID. DOY and lake were included in the model as fixed effects (Table 5). The standard deviation of $\log_e$ (length) at age 1 explained by each random effect is shown in Table 7.

Age-1 ammocoetes from Lake Ontario were on average 30% larger than those from Lake Superior (Table 6, Figure 5). Ammocoetes from Lakes Michigan and Huron did not differ significantly in their mean length at age 1 from Lake Superior sea lampreys (Table 6, Figure 5). The day that a survey was conducted positively influenced mean length at age 1 (Table 6).

Variation in length at age 1

Length at age 1 was better explained by the model with separate variance components for each lake than the model with no variance covariates (Likelihood ratio = 65.5, df = 3, $p<0.001$), and length at age 1 was more variable in sea lampreys from Lakes Superior and Michigan than from Lakes Huron and Ontario (Figure 6). Likewise, modeling separate variance components for category/lake combinations better explained variation in length at age 1 than modeling variance components for lake only (Likelihood ratio = 487.8, df = 10, $p<0.001$), indicating that variation in length at age 1 differed significantly among lakes and among categories within lakes. The relative variability in length at age 1 among stream categories differed among lakes, and all but one lake exhibited significant differences in variability of length at age 1 among categories.

In Lake Superior, sea lampreys from category 3 exhibited higher levels of variability in mean length at age 1 than sea lampreys from other types of streams (Figure 7a). The majority of variation in length at age 1 was due to within year variance, although among-year variance was also highest in category 3 streams (Figure 8a). In Lake Michigan and Lake Ontario, sea lampreys from category 1 streams were significantly more variable in length at age 1 than individuals from any other stream category (Figures 7b and 7c). In these two lakes, category 1 sea lampreys had the highest levels of both within- and among-year variance in length at age 1 (Figures 8b and 8c). Lake Huron sea lampreys showed no evidence of differences in overall variation in length at age 1 among stream categories (Figure 7d), although sea lampreys from category 3 streams did have higher among-year variance than any other category of streams in Lake Huron (Figure 8d).

Discussion

In this analysis, we demonstrated that differences in recruitment to age 1 were correlated with the regularity of parasitic lamprey production in Great Lakes tributaries. Streams with high recruitment to age 1 tended to have highly regular treatment cycles (Category 1 streams), and streams with a high propensity for failed recruitment to age 1 were no longer treated (Category 4 streams). Differences in growth rates were not generally associated with differences in chemical treatment regularity. Low variability in length at age 1 was associated with the regularity of chemical treatments in Lake Superior streams, although not in other lakes. Overall, successful recruitment to age 1 above a threshold level appeared to be more important than early larval growth in determining the regularity of parasitic lamprey production.

CPUE of age-1 ammocoetes was almost twice as high in Category 1 streams as in Category 3 streams, and nearly three times as high as in Category 4 streams. However, much variation in CPUE remained unexplained even by the best model, indicating that even within stream categories, recruitment varies widely. This variation could be due to actual variation in recruitment; sea lamprey recruitment can vary up to three orders of magnitude even with a constant number of spawning females (Jones et al. 2003). The high levels of unexplained variation could also be due to the imprecision of CPUE as an index of recruitment. Despite its imprecision, CPUE has been widely used as an index of population size in fisheries and is useful for comparative purposes (Hilborn and Walters 1992; Ney 1993). The variability in CPUE of age-1 sea lampreys did not differ among stream categories, contrary to our original hypothesis that regularly treated streams would have more consistent recruitment to age 1. These results indicate that a threshold size of age-1 ammocoetes may be necessary for a year class to persist in sufficient numbers to warrant treatment as the cohort approaches metamorphosis. Above this threshold level of recruitment, even high levels of variation do not appear to affect subsequent treatment regularities. However, below this threshold, normal variations in cohort survival and growth may result in an inconsistent need for chemical treatment.

The correlation between age-1 year class strength and future treatment regularity suggests, albeit indirectly, that variations in the size of an age-1 year class persist in subsequent years, a pattern that has been demonstrated in other fish populations (e.g., Campana 1996; Helle et al. 2000; Smith et al. 2005). Other researchers have emphasized the utility of sampling juvenile fishes in an attempt to index year-class strength of a cohort before they reach the age of management interest due to the importance of the larval stage in the determination of year-class strength (Rijnsdorp et al. 1985; Uphoff 1989; Sammons and Bettoli 1998). The correlation between our index of age-1 recruitment and treatment regularity also indicates that density-dependent processes affecting survival later in the ammocoete life stage are less important than early-life demographic rates.

Sea lampreys from different stream categories did not differ in their mean length at age 1, indicating that early differences in growth do not correspond to differences in parasitic lamprey production. Growth is thought to be related to survival in many larval fish species, with higher growth in the larval phase linked to higher survival and thus abundance at later stages (Anderson 1988). Fish generally experience extremely high mortality due to predation during their larval phase, and high growth rates early in life can greatly increase survival and thus future abundance by reducing the risk of predation (e.g.,Campana 1996; Bergenius et al. 2002; Jenkins and King 2006). Sea lamprey mortality is thought to be high in the egg phase and immediately following hatching, as ammocoetes disperse from nest sites to suitable larval habitats (Potter 1980). However, available evidence suggests that ammocoetes older than age 0 experience relatively low and uniform mortality throughout the remainder of the larval stage due to their propensity to burrow in sediments, thus avoiding predators (Potter 1980). Therefore, high growth rates may be less important in determining survival for larval sea lampreys than for other larval fish species.

Age-1 ammocoetes from Lake Ontario were significantly larger at age 1 than those from the upper lakes (Superior, Michigan, and Huron). Lower lakes sea lampreys are known to achieve larger sizes more quickly than upper lakes sea lampreys (Potter 1980; Hansen et al. 2003; Slade et al. 2003). We used mean length at age 1 as a surrogate for early larval growth, under the assumption that larger individuals must have grown faster in order to achieve that larger size. This assumption may not be correct, as larvae could emerge from nests at larger sizes or experience longer growing seasons in certain types of streams or in certain lake basins, allowing them to achieve larger sizes despite equivalent or even slower growth rates. Within-year growth of age-1 larvae was measured in our analysis through the relationship between the Julian day of sampling and the mean length of the larvae collected; however, this measure of growth was fairly crude, as collections from different streams and years were combined, and the range of dates sampled within a given stream and year were often too small to reliably predict growth rates. We found no significant interaction between stream category and Julian day of sampling, indicating that, at least with this crude measure of growth, within-year growth did not differ among stream categories. Within-year growth did differ among streams and years, as indicated by the random effects of stream and year on the relationship between day of sampling and length (random slope), as would be expected as a result of different growing conditions.

The relationship between variability in length at age 1 and stream category differed among lakes. In Lake Superior, sea lampreys from Category 3 streams exhibited the highest level of overall variability in length at age 1, while in the other lakes either no relationship existed between category and variability in length at age 1 (Lake Huron), or sea lampreys from Category 1 streams were the most variable in length at age 1 (Lakes Michigan and Ontario). In all lakes and categories, the majority of variation in length at age 1 was a result of within-year variation. Larvae of the same age in the same stream at the same time showed considerable variation in length, indicating the need for large sample sizes when conducting assessment surveys if a precise estimate of the size-structure of the stream population is desired. Despite accounting for the majority of residual variation, the level of within-year variation was fairly consistent among stream categories for a given lake, and the differences among categories in variation in length were due mainly to among-year differences. However, as with patterns in overall variation, only in Lake Superior were trends in among year growth consistent with our hypothesis that ammocoetes from irregularly treated streams would also experience more variable growth among years. In the other lakes, either ammocoetes from regularly treated streams exhibited the highest level of among-year variation in length at age 1, or no pattern in among-year variation existed.

The observed differences in variation in length at age 1 among lakes indicate that differences in early larval growth are not consistently correlated with differences in treatment regularity. However, in Lake Superior, streams with the highest levels of among-year variation in growth are the streams with irregular treatment histories. Lake Superior streams have been treated for the longest time period of any lake (Heinrich et al. 2003), and as a result more streams included in this analysis are from Lake Superior than any other lake. It is possible that as additional data become available from other lakes following more treatment cycles, similar patterns in growth may become apparent. Alternatively, differences in growth to age 1 may truly be more important in determining survival or age at metamorphosis in Lake Superior than in any other lake. Studies examining spatial variation in life history parameters of other species have demonstrated correlations between demographic rates of sub-populations on a regional scale, indicating that ecological processes may operate differently among regions (e.g., Peterman et al. 1998; Pyper et al. 2001), and these regional differences can have important management implications (Hilborn et al. 2005; Purchase et al. 2005).

The methods presented in this analysis would be useful in other systems where data have a hierarchical structure that must be accounted for using random effects, whether the ultimate goal is to provide management advice for pest control, harvesting, or conservation. Mixed-effects model analyses do not require assumptions about balanced data (Pinheiro and Bates 2000). Using mixed-effects models allowed us to observe patterns among stream categories and lakes using historical survey data despite the absence of data from some lake and category combinations (Table 1). Furthermore, the use of mixed models allowed us to parse out sources of variation in demographic rates that would be difficult to discern in the absence of such an approach. The standard deviation of CPUE of age 1 sea lampreys differed among categories and lakes, but the variance components analysis revealed no significant differences in variation of CPUE among categories or lakes. Similarly, the standard deviation of mean length was highest in Lakes Huron and Ontario, but the variance components analysis showed that when confounding factors such as day of sampling and stream were accounted for, length at age 1 varied least in these lakes. Determining spatial and temporal trends within populations such as those identified here can help better achieve management goals (Peterman et al. 1998; Pyper et al. 2001; Mueter et al. 2007) as well as increase ecological understanding.

Our results have practical implications for the sea lamprey assessment program. Because year class strength appears to be determined relatively early in the larval life cycle, assessment could be conducted several years before a stream might need to be treated, and the relative abundance of young larvae could serve as an indicator of the future transformer abundance on which managers could base treatment decisions. Additionally, the strong pattern observed of higher CPUE in regularly treated streams could allow for the identification of this threshold CPUE value to be used for management purposes. If such a threshold could be identified, streams could be surveyed one or two years following treatment to quantify recruitment to age 1, and if the threshold catch rate was observed, managers would schedule the stream for treatment some number of years later. Furthermore, our results indicate that because of their consistently high levels of recruitment, Category 1 streams could likely be selected for treatment with little to no assessment. Category 1 streams are composed of more reaches, on average, than streams of other categories, and the number of person-days required to survey a stream is directly related to its number of reaches. Reducing or eliminating assessment requirements on these types of streams could therefore reduce assessment costs substantially, allowing these resources to be used in other areas of sea lamprey management. This has in fact been the strategy recently adopted by the sea lamprey program with the introduction of so-called “expert judgment” streams, for which stream treatment decisions have been made in the absence of assessment data. Our analysis supports the continuation and expansion of this strategy to all Category 1 streams, and the increased use of historical larval assessment data in directing present day stream treatment decisions. Finally, the identification of demographic differences among stream types and among lakes provides a valuable first step towards identifying stream level characteristics that may influence which streams are regular producers, and further research should be focused on this area.

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Tables

Table 1. The sample size used for the growth (G) and recruitment (R) analyses of age-1 sea lampreys for each stream category and lake. For the growth analysis, sample size is represented by the number of streams and the number of individual sea lampreys (in parentheses). For the recruitment analysis, sample size is represented by the number of streams and the number of stream-years (in parentheses).

	Sample Size							
	Category 1		**Category 2**		**Category 3**		**Category 4**	
Lake	**G**	**R**	**G**	**R**	**G**	**R**	**G**	**R**
Superior	25	18	6	3	14	13	6	7
	(27,552)	(74)	(1,363)	(13)	(4,227)	(44)	(2,007)	(21)
Michigan	18	16	5	4	9	8	2	3
	(12,743)	(54)	(1,241)	(10)	(495)	(17)	(219)	(7)
Huron	11	9	7	5	5	6	0	0
	(4,844)	(26)	(2,151)	(16)	(1,388)	(13)	(0)	(0)
Ontario	3	1	3	2	2	1	0	0
	(1,171)	(4)	(403)	(4)	(345)	(2)	(0)	(0)

Table 2. Summary of data used for recruitment and growth analyses of age-1 sea lampreys, separated by both stream category and lake. The number of stream years (N_{SY}), percent of observations with zero recruitment, and CPUE mean and standard deviation are shown for recruitment data (mean and SD of CPUE were calculated from non-zero values only). The number of streams falling in each category (N_S), number of individual larvae collected from each category (N_i), and length mean and standard deviation are shown for growth data.

	Recruitment analysis				**Growth analysis**			
			CPUE (catch/hr)				**Length (mm)**	
Group	**N_{SY}**	**% zero**	**Mean**	**SD**	**N_S**	**N_I**	**Mean**	**SD**
Category 1	158	10.1	50.7	61.7	57	46310	44.5	12.1
Category 2	43	16.3	35.1	38.6	21	5158	44.5	13.9
Category 3	76	14.5	30.0	40.8	30	6455	42.8	12.1
Category 4	28	57.1	10.5	9.7	8	2226	51.0	10.0
Lake Superior	152	18.4	41.1	60.0	51	35149	44.5	11.5
Lake Michigan	88	14.8	34.0	30.8	34	14698	43.6	11.2
Lake Huron	55	16.4	43.5	51.6	23	8383	45.4	15.7
Lake Ontario	10	0.0	89.8	87.9	8	1919	50.0	15.0

Table 3. Model selection for the binary model of the probability of recruitment success of age-1 sea lampreys. Fixed effects were chosen prior to random effects. Candidate models are shown with the estimated number of parameters (K), the Akaike's information criterion (AIC) values, and the difference between the AIC value of a given model and that of the most parsimonious model (ΔAIC). AIC values for models including random effects were approximated using the adaptive Gaussian quadrature approximation.

Model	**Fixed effects**	**Random effects**	**K**	**AIC**	**Δ AIC**
1	Category	Year	5	248.0	0
2	Category	None	4	250.9	2.9
3	Category + Lake	None	7	253.4	5.4
4	Category	Stream	5	254.9	6.9
5	(Intercept)	None	1	274.1	26.1
6	Lake	None	4	276.0	18.0

Table 4. Fixed effects estimates for the most parsimonious binary model of recruitment success of age-1 sea lampreys. For this model, the intercept represents category 1 streams. The expected probability of successful recruitment for each category is also shown. A random year effect was also included in this model, and the error DF=301.

Parameter	Estimate	SE	z-value	p-value	p(success)
Intercept (Category 1)	2.36	0.37	6.39	<.001	0.91
Category 2	-0.50	0.54	-0.94	0.35	0.87
Category 3	-0.62	0.46	-1.34	0.18	0.85
Category 4	-2.60	0.52	-4.97	<.001	0.44

Table 5. Model selection for the models of mean recruitment (CPUE^1/4) and growth ($\log_e$[length]) of age-1 sea lampreys. The number of estimated parameters (K), AIC value, and the difference between the AIC value of a model and that of the most parsimonious model (ΔAIC) are shown for each model. AIC values were estimated using the REML method of model fit for random effect selection, and the ML method of model fit for fixed effect selection (see text for further explanation). In each model, random effects were selected first with all possible fixed effects included.

Model	Random effects	Fixed effects	K	AIC	Δ AIC
Recruitment model: random effects					
R1	None	Category+Lake	9	499.3	0.0
R2	Stream+Year	Category+Lake	11	508.4	9.1
R3	Stream	Category+Lake	10	511.2	11.9
R4	Year	Category+Lake	10	516.6	17.3
Recruitment model: fixed effects					
R5	None	Category+Lake	8	497.7	0.0
R6	None	Category	5	500.5	2.8
R7	None	Lake	5	518.7	21.0
R8	None	(Intercept)	1	520.7	23.0

Growth model: random effects

G1	Stream(I+S)[a]+Year(I+S)+Reach(I)+ID(I)	DOY+Category+Lake+Category*DOY	17	-79316.0	0.0
G2	Stream(I+S)+Year(I+S)+Reach(S+I)+ID(I)	DOY+Category+Lake+Category*DOY	18	-79313.0	3.0
G3	Stream(I+S)+Year(I+S)+Reach(I+S)	DOY+Category+Lake+Category*DOY	17	-72875.3	6440.7
G4	Stream(I+S)+Year(I+S)+Reach(I)	DOY+Category+Lake+Category*DOY	16	-72592.2	6723.7
G5	Stream(I+S)+Year(I+S)	DOY+Category+Lake+Category*DOY	15	-68616.5	10699.5
G6	Stream(I+S)+Year(I)	DOY+Category+Lake+Category*DOY	14	-63624.3	15691.7
G7	Stream(I)+Stream(S)	DOY+Category+Lake+Category*DOY	13	-47047.5	32268.5
G8	Stream(I)	DOY+Category+Lake+Category*DOY	12	-39910.6	39405.4
G9	None	DOY+Category+Lake+Category*DOY	11	-7883.1	71432.9

Growth model: fixed effects

G10	Stream(I+S)+Year(I+S)+Reach(I)+ID(I)	DOY+Lake	11	-79412.6	0.0
G11	Stream(I+S)+Year(I+S)+Reach(I)+ID(I)	DOY+Category+Lake	14	-79408.1	4.5
G12	Stream(I+S)+Year(I+S)+Reach(I)+ID(I)	DOY	8	-79403.7	8.9
G13	Stream(I+S)+Year(I+S)+Reach(I)+ID(I)	DOY+Category+Lake+Category*DOY	17	-79403.4	9.3
G14	Stream(I+S)+Year(I+S)+Reach(I)+ID(I)	DOY+Category	11	-79401.1	11.5

G15	Stream(I+S)+Year(I+S)+Reach(I)+ID(I)	DOY+Category+Category*DOY	14	-79396.2	16.4

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[a] In the growth model, random effects were estimated for the slope(S) and the intercept(I) of each level except survey ID

Table 6. Fixed effects estimates for each parameter included in the most parsimonious models of mean recruitment to age-1 and mean length at age-1 of larval sea lampreys. In the recruitment model, the intercept accounts for the effects of both category 1 and Lake Superior, and in the growth model, the intercept accounts for the effect of Lake Superior. Random intercepts for stream, year, reach, and survey, and random slopes for stream and year were also included in the growth model.

Parameter	Estimate	SE	DF	t-value	p-value
Recruitment model (CPUE^1/4)					
Intercept	2.41	0.07	248	35.07	<0.001
Category 2	-0.28	0.12	248	-2.35	0.02
Category 3	-0.38	0.10	248	-3.99	<0.001
Category 4	-0.73	0.19	248	-3.83	<0.001
Lake Michigan	-0.03	0.09	248	-0.28	0.78
Lake Huron	0.05	0.11	248	0.44	0.66
Lake Ontario	0.60	0.21	248	2.84	0.01
Growth model ($\log_e$[length])					
Intercept	3.74	0.02	57743	163.06	<0.001
DOY-216.3	3.91E-03	4.00E-04	57743	22.71	<0.001
Lake Michigan	4.37E-03	0.04	112	0.12	0.91
Lake Huron	0.04	0.04	112	0.98	0.33
Lake Ontario	0.26	0.07	112	3.85	<0.001

Table 7. Random effects and their standard deviation (with 95% confidence intervals) that were included in the final model of $\log_e$(length) at age-1 of larval sea lampreys. Fixed effects of day of year and lake were also included in this model.

Random effects			**95% CI**	
Level	**Term**	**SD**	**lower**	**upper**
Stream	Intercept	0.1414	0.1164	0.1717
	Slope	0.0009	0.0006	0.0015
Year	Intercept	0.1160	0.0998	0.1340
	Slope	0.0015	0.0012	0.0019
Reach	Intercept	0.0730	0.0623	0.0857
ID	Intercept	0.0787	0.0749	0.0826
	Residual	0.1190	0.1183	0.1197

Figure Captions

Figure 1. Locations and categories of all streams used for analyses of recruitment and growth to age 1.

Figure 2. Probability of successful (non-zero) recruitment of age-1 sea lampreys and 95% confidence intervals for each stream category as predicted by the binomial model of recruitment.

Figure 3. Mean CPUE of age-1 sea lampreys and 95% confidence intervals for each stream category as predicted by the linear model of recruitment when holding lake constant (values shown are for Lake Superior streams).

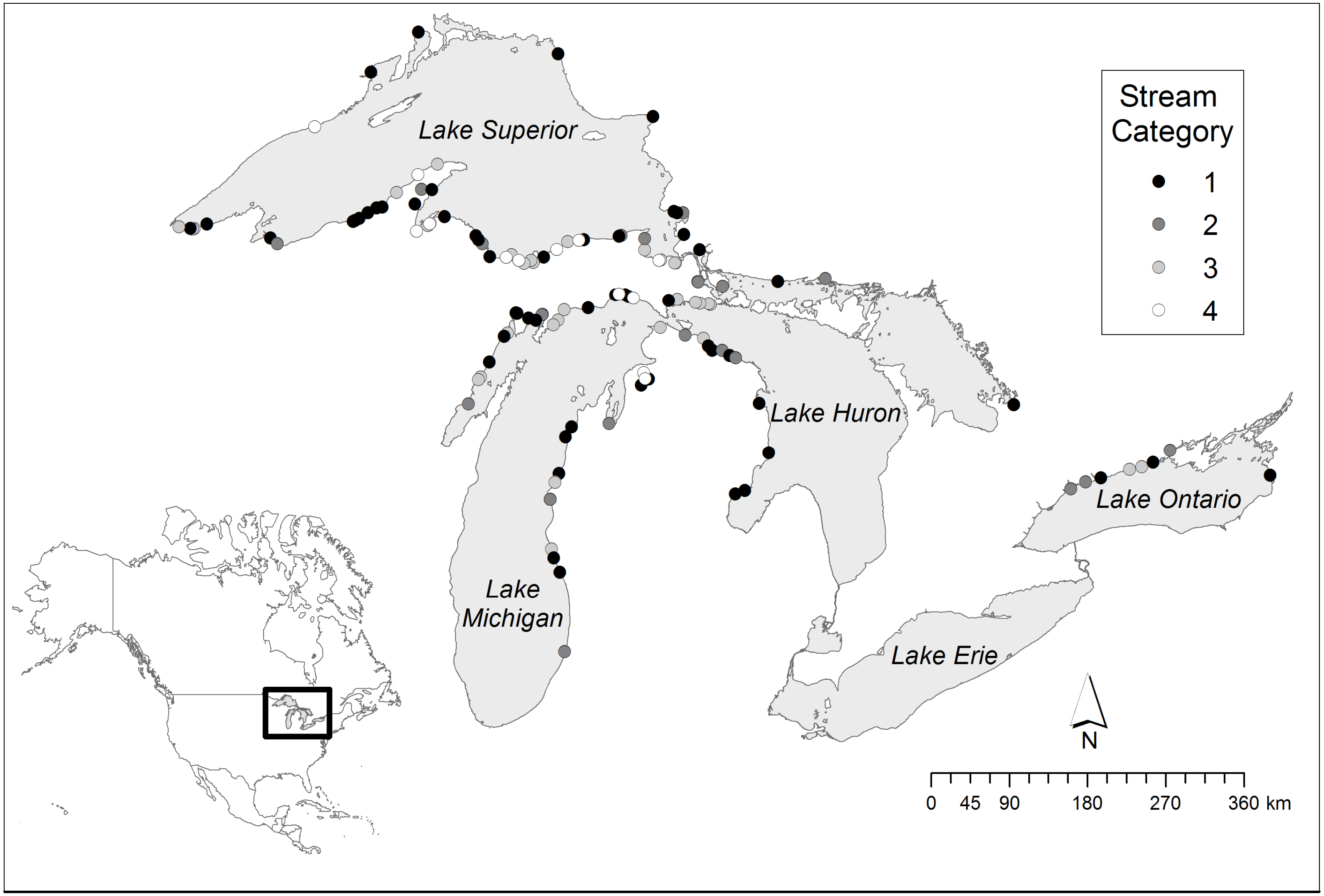
Figure 4. Mean CPUE of age-1 sea lampreys and 95% confidence intervals for each lake as predicted by the linear model of recruitment when holding category constant (values shown are for category 1 streams).

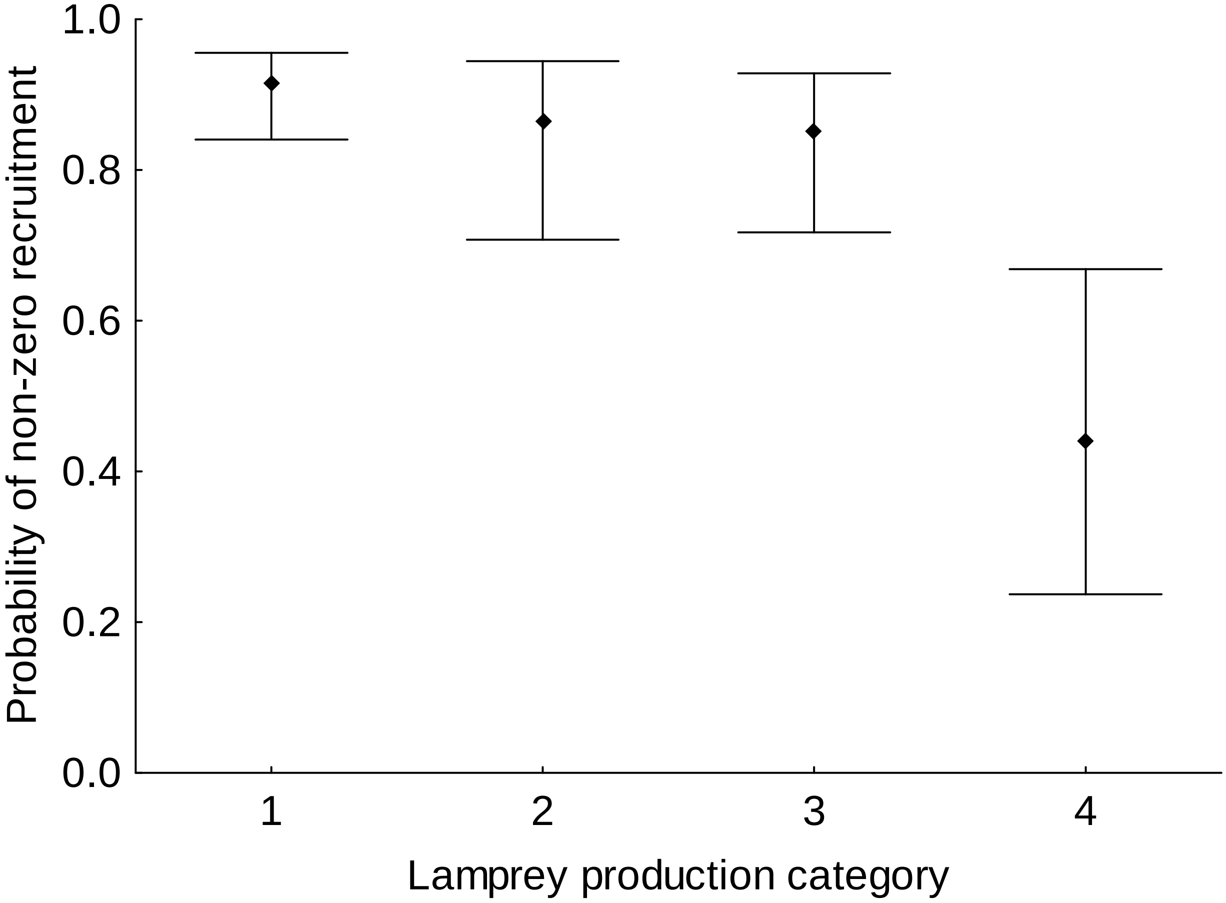
Figure 5. Mean length at age-1 of sea lampreys (bias-corrected) and 95% confidence intervals for each lake as predicted by the general linear mixed effects model of growth.

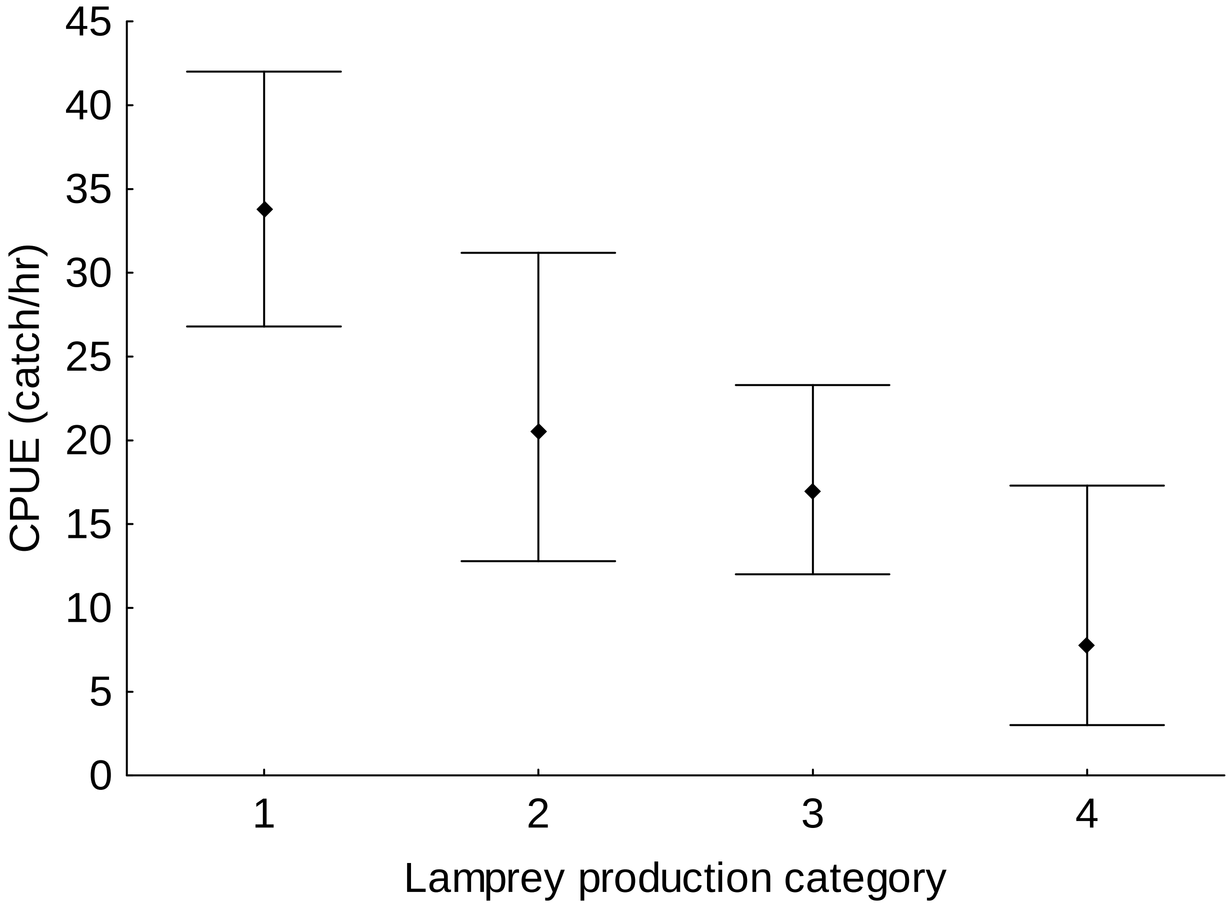
Figure 6. Variance component (δ) estimates of $\log_e$(length at age 1) of larval sea lampreys and 95% confidence intervals for each lake, with data from all categories combined. In order to fit the model, the variance component for Lake Superior was held constant at 1, and others estimated relative to it (see text).

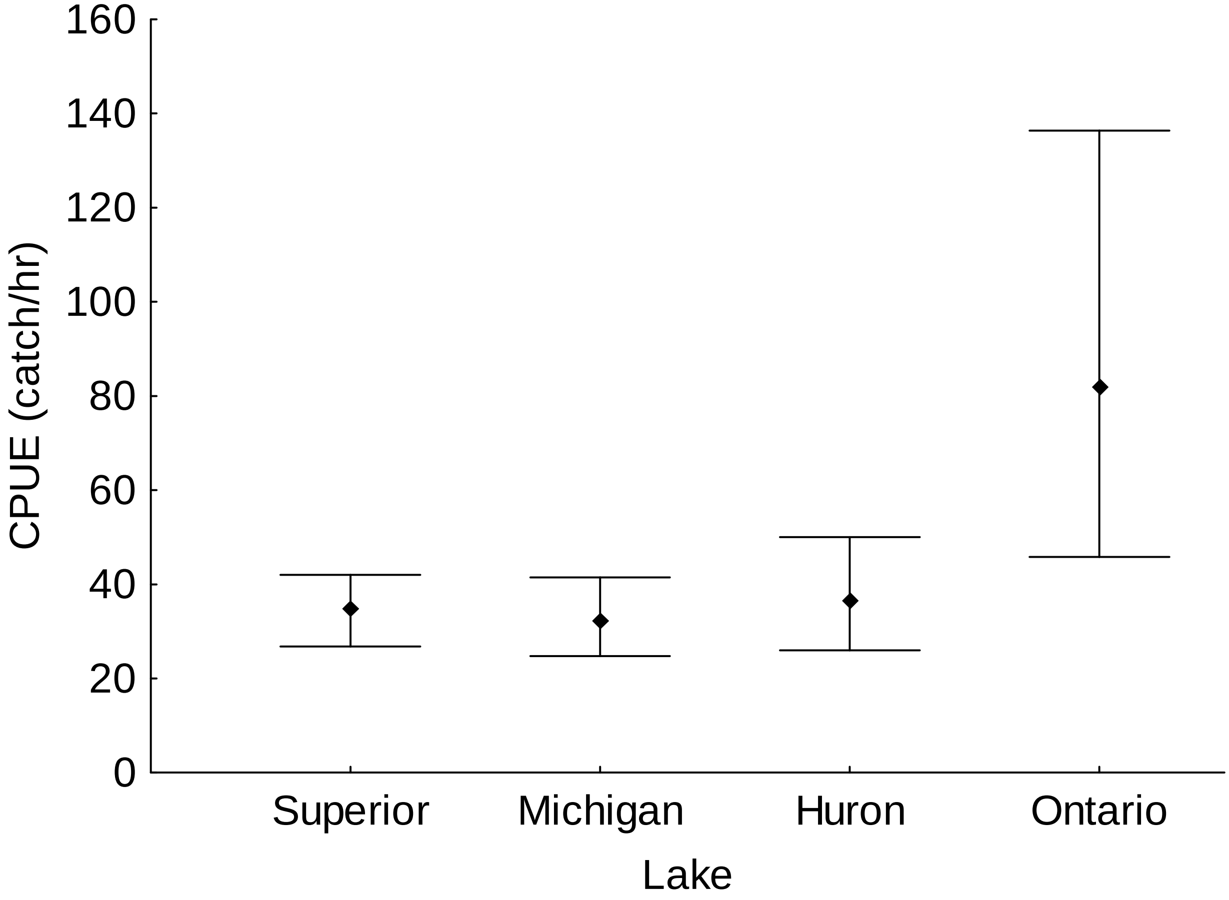
Figure 7. Variance component (δ) estimates of $\log_e$(length at age 1) of larval sea lampreys and 95% confidence intervals for each stream category in **a)** Lake Superior, **b)** Lake Michigan, **c)** Lake Ontario, and **d)** Lake Huron. In order to fit the model, the variance component of category 3 for Lake Superior was held constant at 1, and others estimated relative to it (see text).

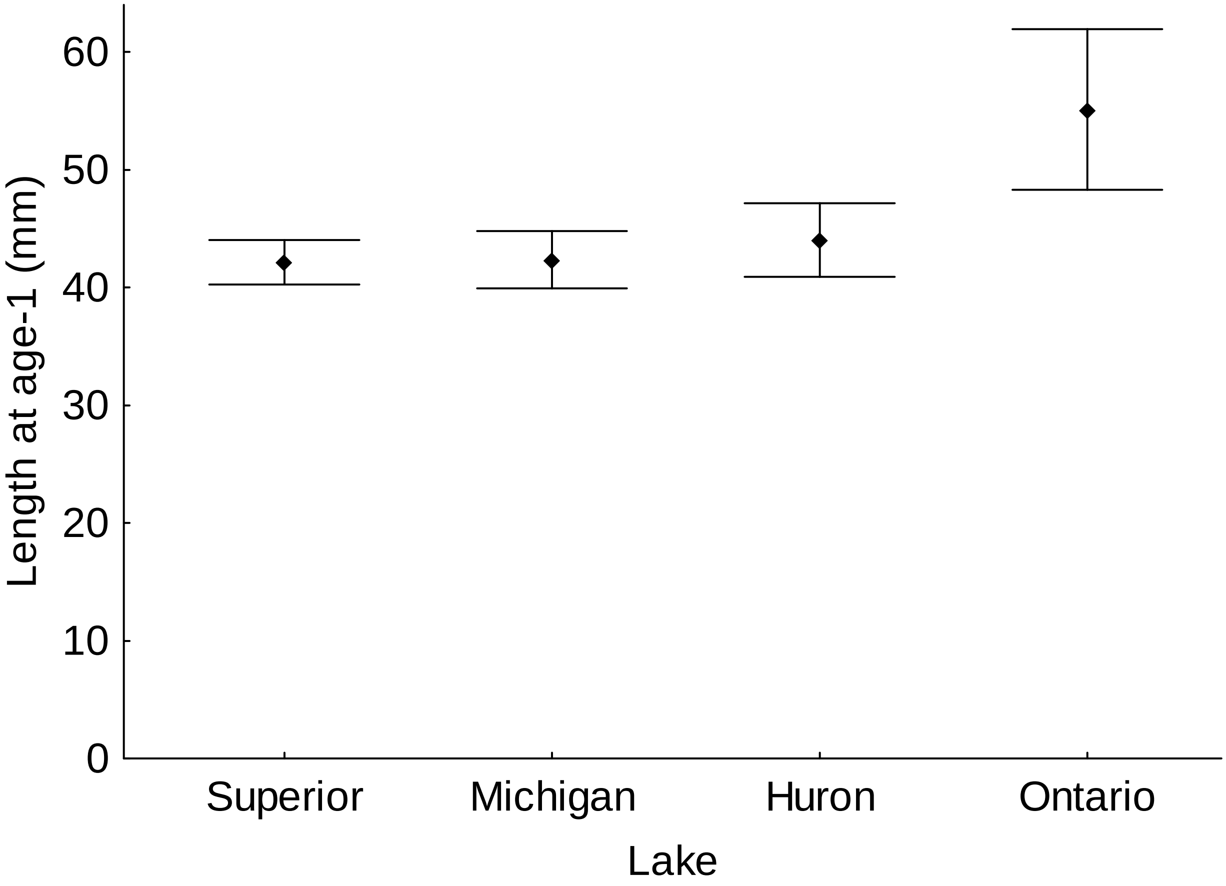
Figure 8. Residual variance attributable to within-year variance (light grey bars) and among-year variance (black bars) in $\log_e$(length at age 1) of larval sea lampreys for each stream category in **a)** Lake Superior, **b)** Lake Michigan, **c)** Lake Ontario, and **d)** Lake Huron

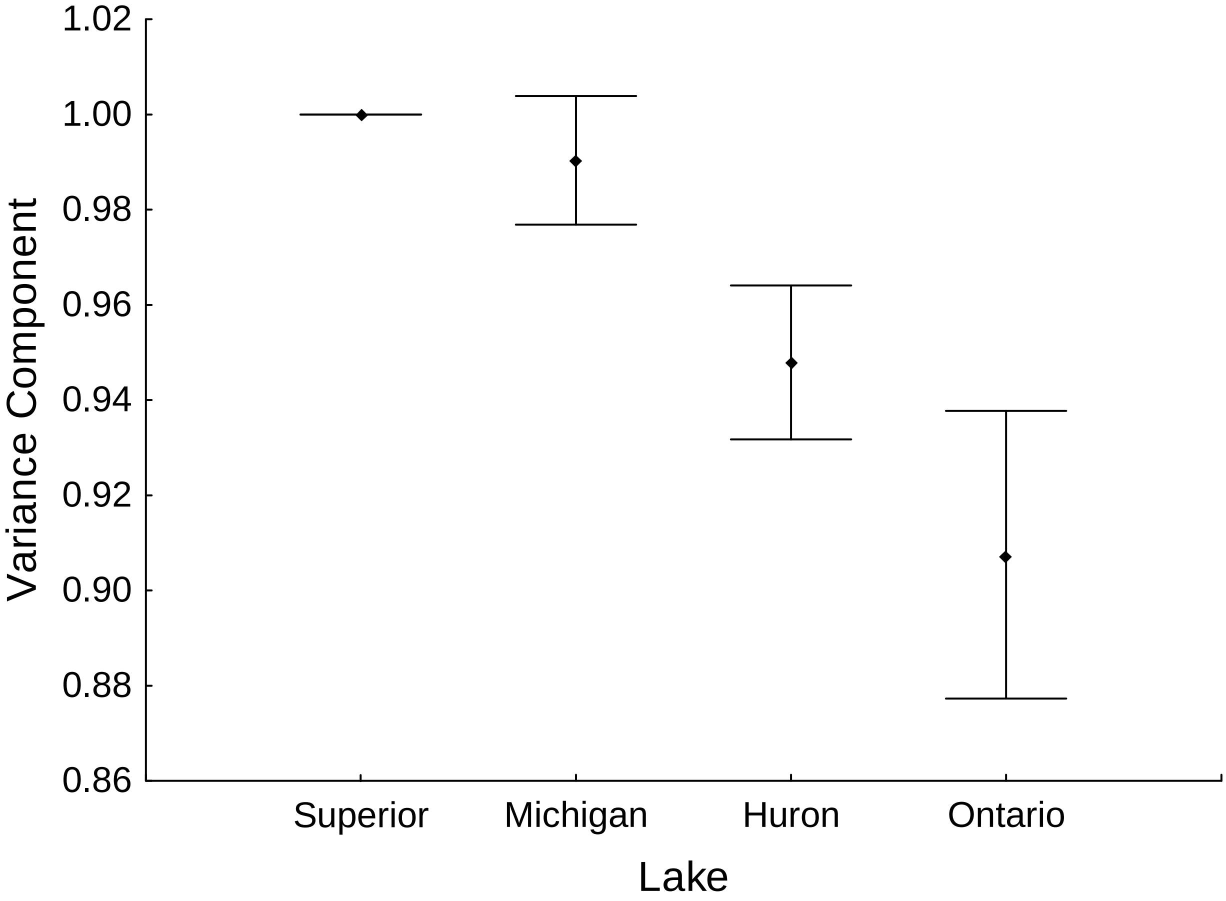

Lake Superior
Lake Michigan
Lake Huron
Lake Ontario
Lake Erie
Stream Category
● 1
● 2
● 3
○ 4
N
0
45
90
180
270
360 km

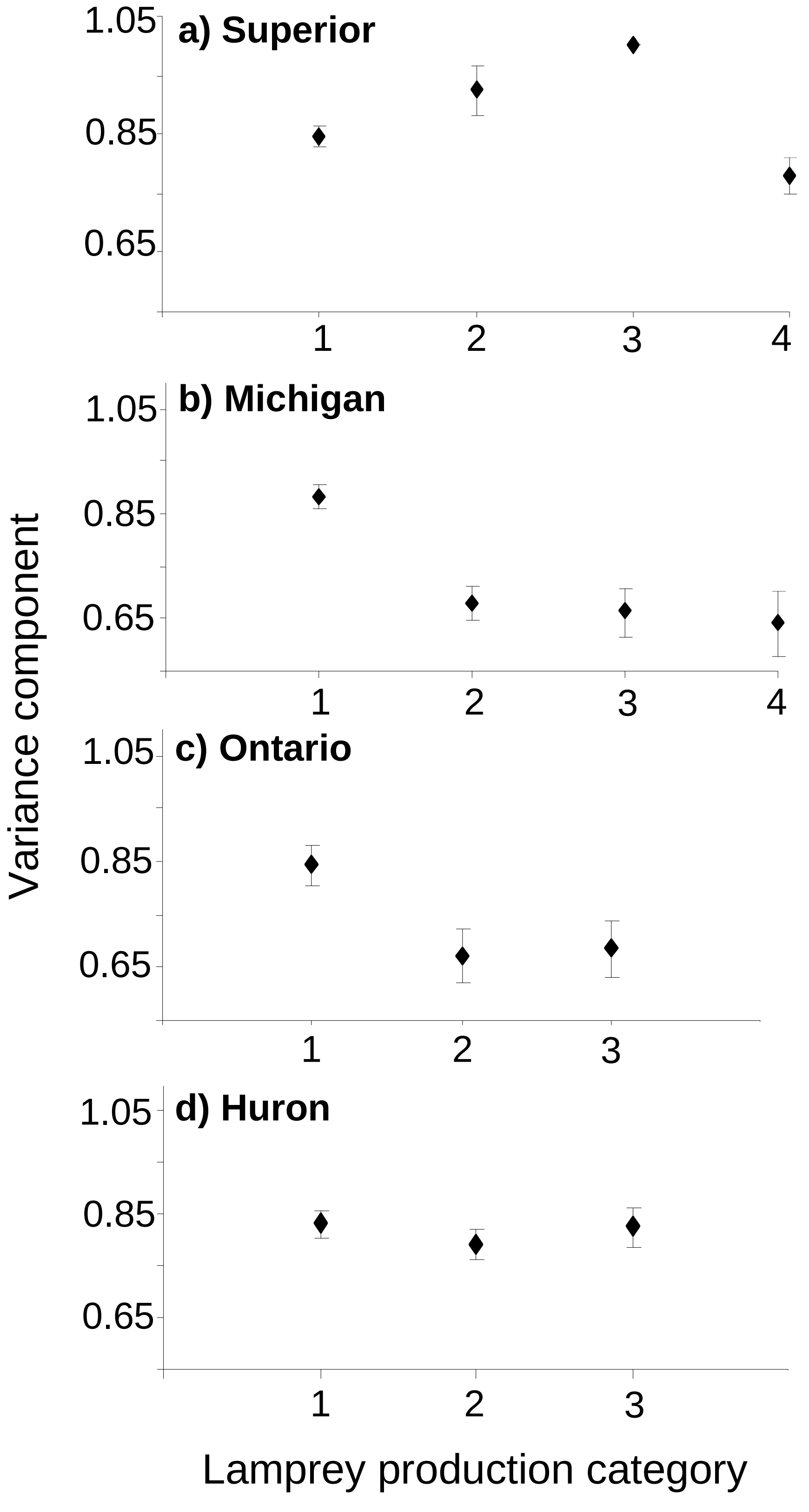

1.0
0.8
0.6
0.4
0.2
0.0
Probability of non-zero recruitment
1
2
3
4
Lamprey production category

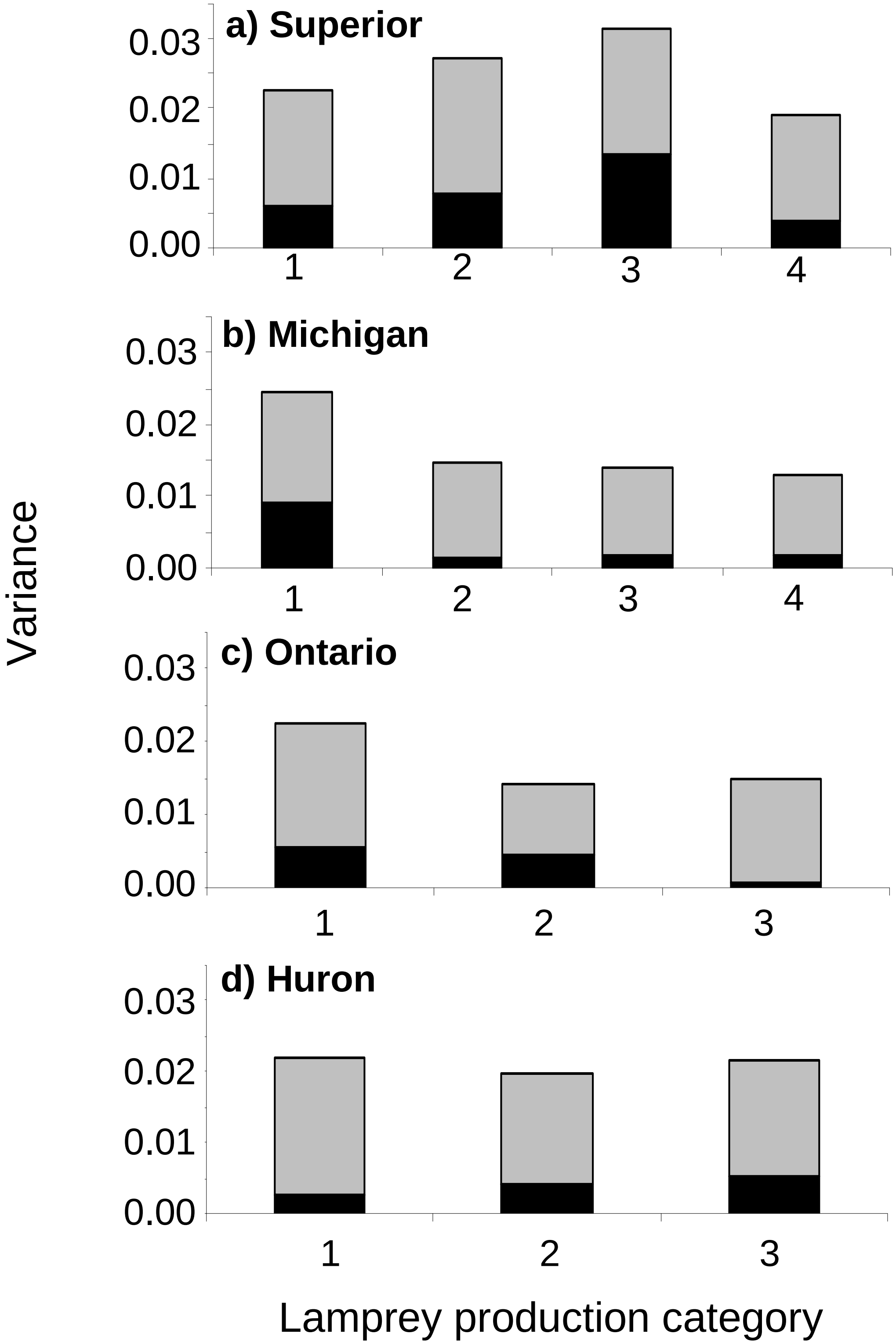

45
40
35
30
25
20
15
10
5
0
CPUE (catch/hr)
1
2
3
4
Lamprey production category


160
140
120
100
80
60
40
20
0
CPUE (catch/hr)
Superior
Michigan
Huron
Ontario
Lake


60
50
40
30
20
10
0
Length at age-1 (mm)
Superior
Michigan
Huron
Ontario
Lake


1.02
1.00
0.98
0.96
0.94
0.92
0.90
0.88
0.86
Variance Component
Superior
Michigan
Huron
Ontario
Lake


a) Superior
1.05
0.85
0.65
1
2
3
4
b) Michigan
1.05
0.85
0.65
1
2
3
4
c) Ontario
1.05
0.85
0.65
1
2
3
d) Huron
1.05
0.85
0.65
1
2
3
Variance component
Lamprey production category


a) Superior
0.03
0.02
0.01
0.00
1
2
3
4
b) Michigan
0.03
0.02
0.01
0.00
1
2
3
4
c) Ontario
0.03
0.02
0.01
0.00
1
2
3
d) Huron
0.03
0.02
0.01
0.00
1
2
3
Variance
Lamprey production category

APPENDIX 5:

An operating model for the integrated pest management of Great Lakes sea lampreys

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Abstract

Models of entire managed systems, known as operating models or management strategy evaluation (MSE) models, have been developed in recent years to account for uncertainty in all steps of fishery management. Here we describe and illustrate the use of an operating model of sea lamprey management in the Great Lakes. Control of sea lampreys is mainly achieved through the application of chemical lampricides that target stream-dwelling, non-parasitic larvae before they become parasites. The operating model described here simulates uncertainty in larval population dynamics, the accuracy of assessments used to direct chemical treatments to the appropriate streams, and the effectiveness of chemical control strategies. We illustrate the utility of this operating model by comparing the performance of stream selection strategies that either rely on assessments to direct chemical treatments, or eliminate the assessment process altogether. Our results indicate that similar numbers of parasitic sea lampreys are observed when resources allocated to treatment are increased by eliminating assessment and when assessment uncertainty is decreased to the minimal levels observed in field studies. These model results serve to illustrate the trade-off that exists between resources allocated to assessment and those allocated to control, and also demonstrate the importance of accounting for different types of uncertainty (i.e., assessment uncertainty) in an operating model. We outline a number of other potential uses of this operating model for sea lamprey pest management.

APPENDIX 6:

Biased sex ratios greatly enhance the efficacy of sex-ratio distorting genetic techniques to control invasive species

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One sentence summary: Intrinsic sex ratio biases can greatly increase the efficacy of sex-ratio distorting recombinant strategies for control of invasive species, suggesting a potentially powerful tool for permanent control of sea lampreys in the Great Lakes.

Abstract

Invasive species are one of the major threats to conservation of global biodiversity and motivate the search for effective pest control techniques. We demonstrate that a genetic construct that distorts a population's sex ratio can spread and strongly suppress a target pest population if the population naturally exhibits sex ratios that differ from 50:50. One such species is the sea lamprey (*Petromyzon marinus*), an iconic and extremely damaging invasive pest in the

North American Great Lakes which has female-biased sex ratios at low population sizes. Using a realistically parameterised model of the lamprey population, we show that a long-term and sustained reduction in pest numbers can result from a brief period of stocking "daughterless" carriers.

Body

Invasive species are a major threat to the conservation of biodiversity (*1*), have been conservatively estimated to cause hundreds of billions of dollars of damage globally (*2*), and once established are often uncontrollable at anything other than small scales. The need for more effective methods to mitigate the damage caused by invasive species has prompted research into recombinant technology as a means of reducing pest viability and fecundity (*3,4*). One such tactic is the introduction of a construct that causes genetic females to develop as functional males – the so-called "daughterless" strategy (*5*). Models indicate that such a strategy can be a powerful means of reducing pest populations (*6,7,8*) but the attractiveness of this and most other genetic approaches to pest control is constrained by the frequent requirement to stock large numbers of carriers with multiple copies of the construct for long periods (*7,8*), raising questions about logistical feasibility.

A critical assumption of models used to predict the efficacy of sex-ratio distorting recombinant tactics is that the sex ratio of the pest population in the absence of the recombinant strategy is 50:50. Violation of this assumption fundamentally alters the efficacy of a pest control program based on a sex-ratio distorting construct. Consider a pest population into which a number of genetically modified (GM) individuals have been introduced in a single generation, each of which is heterozygous at a single locus for a construct that causes all animals which inherit the construct to develop into functional males. Heterozygosity is not a critical assumption, but facilitates a simpler presentation of the theory because a construct that is only carried by phenotypic males will remain heterozygous in the population in future generations. Assume that the construct does not affect the fitness of GM adult males. Define p_t^1 as the proportion of male gametes carrying this construct in generation *t*. For heterozygous GM males, and assuming the construct does not affect fitness, the expected proportion of male gametes with the construct will be one-half of the proportion of adult males with the construct:

$$p_t^1 = 0.5 \cdot \frac{A_t^1}{A_t^1 + A_t^0} \qquad (1)$$

where *A* is the number of mature males, the superscript 1 denotes males carrying the construct, and the superscript 0 denotes the wild genotype (WT). Because all individuals carrying the construct are functional males, all gametes from females do not have the construct, and thus p_t^1 also equals the proportion of offspring carrying the construct, again assuming equal fitness of GM and WT genotypes. The number of GM and WT males in the next (*t+1*) generation is

$$\begin{aligned} A_{t+1}^1 &= G \cdot p_t^1 \\ A_{t+1}^0 &= G \cdot p_t^0 \cdot q \end{aligned} \qquad (2)$$

where *G* is a reproduction function that applies to all offspring, p^0 is the proportion of offspring without the construct (= 1-p^1), and *q* is the proportion of WT offspring that are males. Finally, to determine the fate of the introduced construct substitute equations (2) into (1) to get a difference equation for p_{t+1}^1 as a function of p_t^1

$$p_{t+1}^1 = 0.5 \cdot \frac{G \cdot p_t^1}{G\left[p_t^1 + p_t^0 q\right]} = 0.5 \cdot \frac{p_t^1}{p_t^1 + (1 - p_t^1)q} \qquad (3)$$

The fate of the construct over time (the ratio of p_{t+1}^1 to p_t^1) depends on p_t^1 and q. When q = 0.5 (i.e., equal WT sex ratios), $p_{t+1}^1 / p_t^1 < 1$ for all non-zero values of p_t^1, implying that, as expected, the construct disappears from the population in the absence of further introductions (Fig. 1). However, when $q < 0.5$ (WT sex ratio is female-biased) all non-zero values of p_t^1 move towards a non-zero equilibrium value. This equilibrium value is

$$p_{eq}^1 = \frac{0.5 - q}{1 - q} \qquad \text{for } q < 0.5 \qquad (4)$$

In wild populations where the natural sex ratio is biased towards females a daughterless construct not only persists, but is predicted to increase in frequency to a level determined by the magnitude of the bias toward females, even in the absence of repeated additions of GM males. The same would be true for a son-less construct in male-biased populations.

This effect could be used to permanently reduce the impacts of the sea lamprey (*Petromyzon marinus*) in the North American Great Lakes. After invading the upper Great Lakes in the 1930s, the sea lamprey destroyed commercial fisheries worth millions of dollars and fundamentally altered the lake ecosystems (*9*). Currently, sea lamprey populations are controlled by a joint U.S. and Canadian program based principally on biocidal treatment of spawning and nursery tributaries, at an annual cost exceeding $15 million. Sea lampreys show evidence of density-dependent sex ratios, shifting from a male bias at high, pre-management abundances to a female biased population at current, managed low abundances (*10*; for evidence of environmental sex determination in other lamprey species, see *11*). The effects of this female-bias on the performance of a daughterless control strategy were assessed by comparing a realistically modelled Great Lakes sea lamprey population experiencing ongoing chemical control (*12*) for an assumed 50:50 sex ratio with the currently observed ratio (35% male) (Figure 2). Under the equal sex ratio scenario, a 5% stocking rate of age 1 larval sea lampreys heterozygous for the construct at a single locus maintained for 10 years reduced adult female sea lamprey numbers by 20-25% within 50 years after stocking (Figure 2). In contrast, when the pre-treatment WT sex ratio was female biased, the adult female sea lamprey abundance was reduced by 44% by year 50, and 97% by year 200. This reduction occurs despite no further additions of GM males after year 10. Higher stocking rates, stocking for longer periods or release of carriers with higher copy number significantly increases the rate of population decline. Moreover, much lower stocking rates can be equally effective if age 1 GM sea lampreys are stocked into unoccupied habitats (i.e., above barriers to wild spawning sea lampreys) where their numbers will not be reduced by biocidal treatments prior to entering the lake.

We conclude that the demography of sea lampreys in the Great Lakes renders them vulnerable to cost-effective and logistically feasible control using a daughterless genetic strategy. It may be possible to contemplate for the first time a permanent solution to the sea lamprey problem. Nevertheless, we also note that this species' susceptibility to a daughterless strategy could increase the risk to native sea lamprey populations in the North Atlantic. To the extent that these populations also have naturally biased sex ratios, they would be vulnerable to immigration of carriers from the Great Lakes. Available data suggests the biased sex ratio of Great Lakes sea lamprey populations reflects population densities suppressed by current control actions; in Lake Champlain, where sea lamprey control has only recently been implemented the observed ratio in 2002/3 was 53% females (U.S.F.W.S., unpublished data). Balanced or male biased sex ratios in uncontrolled populations would limit the risk from escaped carriers. Nonetheless, a precautionary approach suggests stringent tests for species-specificity of the selected construct, close monitoring of the targeted population, nearby native sea lamprey populations and other lamprey species in the Great Lakes drainage, substantial efforts to prevent escapement of lampreys out of the Great Lakes, which could include a public awareness campaign about the risks of deliberately or accidentally transferring sea lamprey larvae (in bait buckets, for example), and ultimately the incorporation of a genetic “off switch” in the construct activated by release of a second set of carriers, should population rescue be required. Such an off switch could be based on, for example, Cre/lox recombination (*13*).

Sex ratios that naturally differ from equality are not unique to sea lampreys (*14,15*), and can be mediated by social factors, environmental factors, and population density (*14,16,17*). Further, skewed and environmentally influenced sex ratios have been observed in other taxa that include important pest species (*18-21*). Skewed sex ratios can dramatically increase the efficacy of a pest control program based on a gender manipulating construct for these species, to the extent that it may make possible long-term and substantial reductions in pests where control is now difficult or too costly. However, the increased risk of run-away selection for a gender distorting construct dictates that knowledge about the determinants of sex ratios and circumstances under which skewed ratios might be expected will be essential ingredients of risk assessments for these strategies.

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Supporting Online Material

www.sciencemag.org

Materials and Methods

Figure legends

Figure 1. Rates of change in the frequency of a sex-ratio distorting gene from one generation as a function of the current (non-zero) frequency, for wild genotype sex ratios of 35% males (dashed line), 50% males (solid line) and 65% males (dotted line). When the rate of change is equal to one (horizontal line) the gene frequency is at equilibrium (e.g., solid circle for the 35% males case). The equilibrium value is positive for all sex ratios with less than 50% males.

Figure 2. Changes in the adult female population and the frequency of the sex-ratio distorting gene for a simulated sea lamprey population. Blue lines correspond to the observed wild sex ratio of 35% males, red lines correspond to an equal proportion of males and females in the wild population. Individuals carrying the sex-ratio distorting gene were introduced for years 1-10 only at an effective stocking rate of 5% of the wild population. Model results represent a scenario in which chemical control is already being applied to the sea lamprey population (*10*) such that the overall population is at a low initial density and experiencing only weak compensation (density-dependent survival).

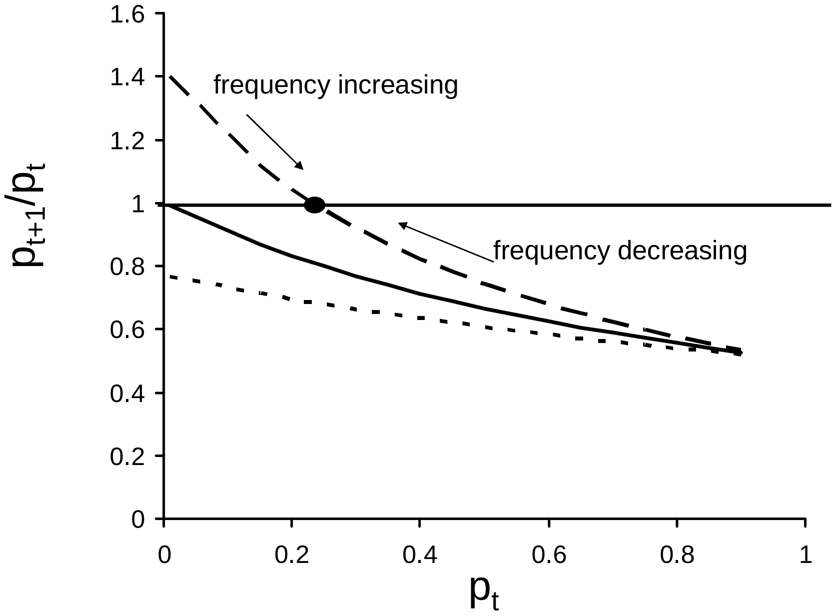
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
0
0.2
0.4
0.6
0.8
1
frequency increasing
frequency decreasing
p_{t+1}/p_t
p_t

Figure 1

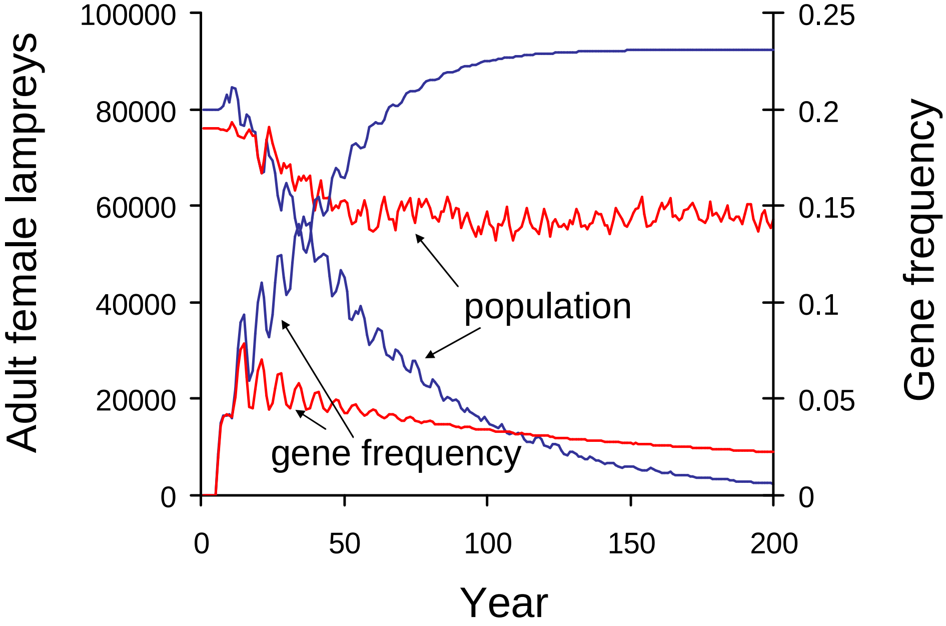
Adult female lampreys
Gene frequency
100000
80000
60000
40000
20000
0
0.25
0.2
0.15
0.1
0.05
0
0
50
100
150
200
Year
population
gene frequency

Figure 2

Supporting online material

Materials and Methods: Sea lamprey population model

The model simulated a stage/age structured population of sea lampreys in an individual Great Lake, with larvae ages 0-6, transformers (recently metamorphosed juveniles), parasites, and adults. Within each stage/age there were males and females. The males were also subdivided by the number of copies of the construct (i.e., the number of loci where the daughterless effect is expressed) they had. We allowed for up to eight copies of the construct to be present in a genetically modified male, although the simulation results presented here are for a single copy. We assumed that any sea lamprey containing at least one copy of the construct would be a phenotypic male; therefore by definition all females had a copy number of zero and all offspring with a copy number > 0 were classed as males. To simulate the effect of strategic distribution (stocking) of genetically modified (GM) larvae to enhance their survival, we also needed to separately track newly introduced GM individuals.

The number of sea lamprey larvae of sex k, copy number g, age a, in year t was given by:

$$\begin{aligned} N_{t+1,a+1}^{k,g} &= N_{t,a}^{k,g} \cdot s_N \cdot (1 - pm_a) \cdot (1 - m_{cl}) \\ G_{t+1,a+1}^{k,g} &= G_{t,a}^{k,g} \cdot s_G \cdot (1 - pm_a) \cdot (1 - m_{cG}) \end{aligned} \qquad (1)$$

where N,G refer to wild and stocked larvae, respectively,

k = 0 (males), 1 (females),

$g = 0\text{-}8$,

a = 0-6,

s_N , s_G are the annual (natural) survival rates of wild and stocked larvae respectively, both set at 0.395 for these simulations,

pm_a is the age-specific proportion of larvae that enter metamorphosis, set at 0.2, 0.5, 0.75 and 1.0 for ages 2-5 respectively, and

m_{cl}, m_{cG} are the proportions of non-metamorphosing wild and stocked larvae that are killed due to chemical control.

The number of transformers, parasites, and adults of sex k, copy number g, in year t were calculated from:

$$\begin{gathered} T_{t+1}^{k,g} = \sum_{a=2}^{6} N_{t,a}^{k,g} \cdot pm_a \cdot (1 - m_{ct}) \\ GT_{t+1}^{k,g} = \sum_{a=2}^{6} G_{t,a}^{k,g} \cdot pm_a \cdot (1 - m_{cGT}) \end{gathered} \tag{2}$$

$$P_{t+1}^{k,g} = (T_t^{k,g} + GT_t^{k,g}) \cdot s_T \tag{3}$$

$$A_t^{k,g} = P_t^{k,g} \cdot s_P \cdot (1 - m_r) \tag{4}$$

where T, GT refer to wild and stocked transformers respectively,

P, A refer to parasites and adults respectively,

m_{ct} , m_{cGT} are the proportions of metamorphosing wild and stocked larvae that are killed due to chemical control

s_T is the survival from transformer to parasite, set at 0.75,

s_P is the survival from parasite to adult, set at 0.75, and

m_r is the effective reduction in adults due to reproductive controls (set at zero for these simulations).

We modeled reproduction using a Ricker stock-recruitment function with log-normal process errors on recruitment and stock represented by the number of adult females:

$$N_{t,0}^{*} = \alpha \cdot A_t^{1,0} \cdot e^{-\beta \cdot A_t^{1,0} + \varepsilon_t} \tag{5}$$

where $N^{*}_{t,0}$ is the total number of age 0 larvae produced, regardless of sex or copy number,

$A_t^{1,0}$ is the number of adult female sea lamprey (sex = 1, copy number = 0),

α,β are Ricker structural parameters, set at $\alpha=469$ and $\beta=1.6 \times 10^{-6}$, and

ε_t is a process error term for recruitment $\sim N(0,\sigma_r^2)$, where $\sigma_r = 0.19$.

To allocate age zero larvae to sexes and copy numbers we needed to assign copy numbers to gametes. For the daughterless construct, all individuals with at least one copy of the construct are effectively males, so female gametes will necessarily have a copy number of 0, and the proportion of female gametes with copy number 0 ($p^{1,0}$) equals 1. To calculate the overall proportion of male gametes with copy numbers from 0 to 8 we used the binomial probability distribution function. We compute the probability of a male gamete with h copies of the construct deriving from a male adult lamprey with g copies and then sum that proportion, weighted by the relative abundance of male adult lamprey with g copies, over all cases where g ≥ h:

$$p^{0,h} = \sum_{g=h}^{8}\left[\frac{g!}{h!(g-h)!}\cdot 0.5^{h}\cdot 0.5^{(g-h)}\cdot\frac{A_t^{0,g}}{\sum_{g=0}^{8}A_t^{0,g}}\right] \qquad (6)$$

This calculation assumes that the loci containing the construct are not linked (i.e., they disassociate independently during meiosis) and that the construct is never homozygous at a locus. Because in our example the construct is only carried by phenotypic males, this latter assumption will necessarily be true. Finally, by assuming random mating, and noting that all female gametes have copy number 0, the proportion of offspring with copy number g will be

$$O^{g} = p^{0,g}\cdot p^{1,0} = p^{0,g} \qquad (7)$$

The number of age 0 larvae by sex and copy number is then:

$$\begin{aligned}
N_{t,0}^{1,g} &= N_{t,0}^{*} \cdot O^{0} \cdot \pi_{1} && g = 0 \\
N_{t,0}^{1,g} &= 0 && g > 0 \\
N_{t,0}^{0,g} &= N_{t,0}^{*} \cdot O^{0} \cdot \pi_{0} && g = 0 \\
N_{t,0}^{0,g} &= N_{t,0}^{*} \cdot O^{g} && g > 0
\end{aligned} \tag{8}$$

where π_1, π_0 are the expected proportions of females and males with copy number 0 in the population ($\pi_1 + \pi_0 = 1$).

The sex ratios of adult sea lampreys changed substantially from the pre-control (1950s) to the post-control (1980s) period (*1*), with a preponderance of males prior to control and a preponderance of females now. We assumed that this change in sex ratio was a compensatory response to changes in sea lamprey densities, and model the effect by allowing the proportion of males to increase linearly from 35% at an adult abundance of 150,000 to 65% at an adult abundance of 1,500,000. This approximates pre- and post-control abundances in one of the upper Great Lakes. Below 150,000 and above 1,500,000 the proportions were fixed at 35% and 65% respectively.

We calibrated the model by adjusting the stock-recruitment density-dependence parameter (β) to result in a population of roughly 1,000,000 adult sea lampreys in the absence of pest control, and then adjusted the larval survival rate (s_N) to result in a population size of roughly 150,000 adult sea lampreys in the presence of chemical control. These calibration values are representative of sea lamprey populations pre- and post- lampricide control in the upper Great Lakes. We used a more detailed, spatially explicit model of sea lamprey chemical control to estimate the annual mortality of larvae ($m_{cl} = 0.2$) and transformers ($m_{ct} = 0.46$) at the whole-lake scale due to lampricide application (*2*). A critical, but reasonable, assumption of our modeling strategy is that density-dependent mechanisms, represented by the β term of the stock-recruitment relationship, operate only weakly at the low population levels present in the Great Lakes today, due to the continued application of a lampricide control program which suppresses the population well below its carrying capacity.

References and Notes

1. M.L. Jones *et al. J. Great Lakes Res.* **29 (Suppl. 1)**, 113-129 (2003).
2. We assumed chemical control had a differential effect, at the population level, on larvae that entered metamorphosis and those that did not. Chemical control is directed towards those streams where the largest numbers of metamorphosing larvae are estimated to occur, relative to treatment costs. This means that lake-wide mortality of metamorphosing larvae will be substantially greater than that of typically smaller, non-metamorphosing larvae. Simulations of stream-level control using a spatially explicit model of sea lamprey control for Lake Michigan (M.L. Jones, unpublished data) resulted in an estimated 2.3-fold difference between larval and transformer mortality due to chemical control.