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

Gretchen J.A. Hansen *,1, Michael L. Jones 2

Quantitative Fisheries Center and Department of Fisheries and Wildlife, Michigan State University, 13 Natural Resources, East Lansing, MI 48912, USA

A R T I C L E   I N F O

Article history:
Received 25 August 2008
Accepted 27 July 2009

Communicated by J. Ellen Marsden

Index words:
Sea lamprey
Recruitment
Growth
Mixed-effects models
Variation

A B S T R A C T

Understanding variation in fish populations is valuable from both a management and an ecological perspective. Great Lakes sea lampreys are controlled primarily by treating tributaries with lampricides that target the larval stage. Great Lakes streams were 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 reflect differences in early demographics. We analyzed assessment data collected from 1959 to 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 as in irregularly treated streams, indicating that age-1 year-class strength is correlated with consistent chemical treatments. We found no differences in length at age 1 among stream categories; however, Lake Superior streams with irregular treatment histories exhibit more 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, which 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 populations, whether the ultimate goal is pest control, harvesting, or conservation.

© 2009 Elsevier Inc. All rights reserved.

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 variations 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). In addition, 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). The historical importance of variation in fish populations suggests 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 (Salvelinus namaycush) populations, spatial variation in growth and mortality rates is 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 lake trout 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

* Corresponding author. Tel.: +1 608 263 2465.
E-mail addresses: ghansen2@wisc.edu (G.J.A. Hansen), jonesml30@msu.edu (M.L. Jones).
1 Current address: Center for Limnology, University of Wisconsin-Madison, 680 N Park Street, Madison, WI 53706, USA
2 Tel.: +1 517 432 0465.
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 lamprocide 3-trifluoromethyl-4-nitrophenol (TFM), and successful treatments kill from 95% to 100% of sea lampreys present in the stream at the time of treatment (Smith and Tibbles, 1980; Christie et al., 2003; Heinrich et al., 2003). Streams are not treated annually, because ammocoetes remain in their natal streams for 3 to 7 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). However, as in desired fish populations, the causes of variation in recruitment are often poorly understood.

Survey data used for these analyses were collected from throughout the Laurentian Great Lakes basin, excluding Lake Erie (Fig. 1). Only two streams from the Lake Erie basin had more than 1 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 in population-level processes among stream categories impossible for this lake. 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 (i.e., they require chemical treatments at fixed intervals), while others vary widely. Previous authors have suggested that differences in recruitment, growth, and survival following lamprocide treatments contribute to differences in treatment regularity (Heinrich et al., 2003; Lavis et al., 2003); however, the relative role of each of these processes in determining treatment regularity is unknown. Researchers and sea lamprey managers 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. Stream treatment decisions are based on both the assessed abundance of stream-dwelling larval populations as well as the cost of treating a stream, and stream categories were developed based on the history of stream treatments. Survey data were not analyzed prior to categorizing streams.

The purpose of the four stream categories developed prior to this analysis was to guide future assessment efforts. Category 1 streams are highly predictable in their parasitic lamprey production cycle and their treatment schedule; that is, the same number of years consistently separates chemical treatments. The actual number of years between treatments varies among Category 1 streams, but is consistent within streams; that is, some are treated on a 3 year cycle while others are treated on a 4 or 5 year cycle. 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. For example, a Category 2 stream may have 4 years between some treatments and 3 years between others. Category 3 streams are highly variable in their production of sea lampreys and treatment schedule. For example, a Category 3 stream may have 4 years between some treatments and 10 years between...
others. 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 Fig. 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. Surveys that took place 2 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 (Table 1).

**Mixed model analysis**

Differences among stream categories in recruitment and growth to age-1 were analyzed using mixed-effects models. Mixed-effects models are statistical models that include both fixed and random effects. Mixed models can accommodate data that exist at multiple scales (i.e., multiple data points from the same stream or year) without violating assumptions of statistical independence (i.e.,

![Fig. 1. Locations and categories of all streams used for analyses of recruitment and growth to age 1.](image)

<table>
<thead>
<tr>
<th>Lake</th>
<th>Sample size</th>
<th>Category 1</th>
<th>Category 2</th>
<th>Category 3</th>
<th>Category 4</th>
</tr>
</thead>
<tbody>
<tr>
<td>Superior</td>
<td></td>
<td>G</td>
<td>R</td>
<td>G</td>
<td>R</td>
</tr>
<tr>
<td>Michigan</td>
<td></td>
<td>G</td>
<td>R</td>
<td>G</td>
<td>R</td>
</tr>
<tr>
<td>Huron</td>
<td></td>
<td>G</td>
<td>R</td>
<td>G</td>
<td>R</td>
</tr>
<tr>
<td>Ontario</td>
<td></td>
<td>G</td>
<td>R</td>
<td>G</td>
<td>R</td>
</tr>
</tbody>
</table>

For the growth analysis, sample size is represented by the number of streams and the number of individual sea lampreys (in parenthesis). For the recruitment analysis, sample size is represented by the number of streams and the number of stream-years (in parenthesis).
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 2 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 Dixon, 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 a and year b is defined as \( \phi_{ab} = \text{Pr}(Y_{ab} = 1) \). 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:

\[
\eta_{ab} = \beta_0 + \beta_a + \beta_b + \beta_{ac} + \beta_{bd},
\]

where all terms are defined in Table 3. All random effects were assumed to be normally distributed with a mean of 0 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 (\( \phi \)) using the equation \( \phi = \frac{1}{1 + \exp(-\eta)} \) (Faraway, 2006).

Table 2

<table>
<thead>
<tr>
<th>Group</th>
<th>Recruitment analysis</th>
<th>Growth analysis</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>N&lt;sub&gt;y&lt;/sub&gt;</td>
<td>% Zero</td>
</tr>
<tr>
<td>Category 1</td>
<td>158</td>
<td>10.1</td>
</tr>
<tr>
<td>Category 2</td>
<td>43</td>
<td>16.3</td>
</tr>
<tr>
<td>Category 3</td>
<td>76</td>
<td>14.5</td>
</tr>
<tr>
<td>Category 4</td>
<td>28</td>
<td>57.1</td>
</tr>
<tr>
<td>Lake Superior</td>
<td>152</td>
<td>18.4</td>
</tr>
<tr>
<td>Lake Michigan</td>
<td>88</td>
<td>14.8</td>
</tr>
<tr>
<td>Lake Huron</td>
<td>55</td>
<td>16.4</td>
</tr>
<tr>
<td>Lake Ontario</td>
<td>10</td>
<td>0.0</td>
</tr>
</tbody>
</table>

The number of stream-years (N<sub>y</sub>), percent of observations with zero recruitment, and CPUE mean and standard deviations 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<sub>c</sub>), number of individual larvae collected from each category (N<sub>i</sub>), and length mean and standard deviation are shown for growth data.
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 greater than 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:

\[ y_{abcd} = \beta_0 + b_a + b_b + \beta_1 + \beta_2 + \epsilon_{abcd} \]  

(2)

(Table 3).

Analysis of variation in CPUE

The objective of this analysis was to determine if stream categories differed in recruitment variation. After selecting the best model to describe mean CPUE (Eq. 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:

\[ \epsilon_{abcd} \sim N\left(0, \sigma^2_{abcd}\right) \]  

(3)

where \( \delta_c \) is the variance scaling parameter estimate for stream category \( c \). To achieve identifiability of all parameters, restrictions must be placed on \( \delta_c \). 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 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. The DOY was centered around the mean survey DOY (Julian day 216.3) to avoid correlation among estimates of random slopes and intercepts and to improve interpretability of results (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 differences among groups in the relationship between DOY and length) and random intercepts (representing differences among groups in mean length) were estimated for stream, year, and reach, and random intercepts were estimated for survey ID. The full model is represented by the equation:

\[ z_{cddefghi} = \beta_0 + \beta_1 + \beta_2 + b_3 + b_4 + b_{gh,1} + b_{gh,2} + b_{gh,3} + b_{gh,4} + b_{gh,5} + b_{gh,6} + b_{gh,7} + b_{gh,8} + \text{DOY}_v + \epsilon_{cddefghi}. \]  

(4)

where all terms are defined in Table 3.

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 (\( \delta_0 \)) were estimated for each lake using stream and reach as random effects. The error structure of this model is represented by (Table 3):

\[ cdegh \sim N\left(0, \sigma^2_{cdegh}\right). \]  

(5)

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 this model is represented by:

\[ cdefghi \sim N\left(0, \sigma^2_{cdefghi}\right). \]  

(6)

For both equations, \( \delta_1 = 1 \) (see Analysis of variation in CPUE for more details, and Table 3 for definitions of terms). The residual variance for each lake alone and for each category and lake combination was calculated by multiplying the variance component estimate (\( \sigma^2 \)) 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 $\hat{\sigma}^2$ 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 was evaluated using Akaike’s information criterion (AIC), and effects were considered significant if their inclusion resulted in a decrease in AIC value of $>2$ (Burnham and Anderson, 1998). Plots of residuals vs. fitted values, frequency histograms of residuals, normal QQ plots, and Cook’s distance plots of all selected models were visually examined to ensure that no assumptions were violated. All 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-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 was 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 was determined by sequentially removing fixed effects from the model and comparing AIC values. All tests for fixed effects were performed

![Diagram](image-url)
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 (Tables 1 and 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 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 stream category as a fixed effect and year as a random effect (Table 4). 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 5, Fig. 2a). Streams from different lakes did not differ significantly in their probability of successful recruitment to age 1.

Table 7

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate</th>
<th>SE</th>
<th>df</th>
<th>t-value</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Recruitment model</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intercept</td>
<td>2.41</td>
<td>0.07</td>
<td>248</td>
<td>35.07</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Category 2</td>
<td>-0.28</td>
<td>0.12</td>
<td>248</td>
<td>-2.35</td>
<td>0.02</td>
</tr>
<tr>
<td>Category 3</td>
<td>-0.38</td>
<td>0.10</td>
<td>248</td>
<td>-3.99</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Category 4</td>
<td>-0.73</td>
<td>0.19</td>
<td>248</td>
<td>-3.83</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Lake Michigan</td>
<td>-0.03</td>
<td>0.09</td>
<td>248</td>
<td>-0.84</td>
<td>0.41</td>
</tr>
<tr>
<td>Lake Huron</td>
<td>0.05</td>
<td>0.11</td>
<td>248</td>
<td>0.44</td>
<td>0.66</td>
</tr>
<tr>
<td>Lake Ontario</td>
<td>0.60</td>
<td>0.21</td>
<td>248</td>
<td>2.64</td>
<td>0.01</td>
</tr>
<tr>
<td>Growth model</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intercept</td>
<td>3.74</td>
<td>0.02</td>
<td>57743</td>
<td>163.06</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>DOY-216.3</td>
<td>3.91E-03</td>
<td>4000.0-04</td>
<td>57743</td>
<td>22.71</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Lake Michigan</td>
<td>4.37E-03</td>
<td>0.04</td>
<td>112</td>
<td>0.12</td>
<td>0.91</td>
</tr>
<tr>
<td>Lake Huron</td>
<td>0.04</td>
<td>0.04</td>
<td>112</td>
<td>0.98</td>
<td>0.33</td>
</tr>
<tr>
<td>Lake Ontario</td>
<td>0.26</td>
<td>0.07</td>
<td>112</td>
<td>3.85</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

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 effects of Lake Superior. Random intercepts, year, reach, and survey, and random slopes for stream and year were also included in the growth model.

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 6). 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 7). 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 (Fig. 2b). When held constant for category, the mean recruitment in Lake Ontario streams was more than twice that of streams in any other lake (Fig. 3a).

Table 6

<table>
<thead>
<tr>
<th>Model</th>
<th>Random effects</th>
<th>Fixed effects</th>
<th>K</th>
<th>AIC</th>
<th>ΔAIC</th>
</tr>
</thead>
<tbody>
<tr>
<td>Recruitment model:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>random effects</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>R1</td>
<td>None</td>
<td>Category + Lake</td>
<td>8</td>
<td>497.7</td>
<td>0.0</td>
</tr>
<tr>
<td>R2</td>
<td>Stream + Year</td>
<td>Category + Lake</td>
<td>10</td>
<td>508.4</td>
<td>10.7</td>
</tr>
<tr>
<td>R3</td>
<td>Stream</td>
<td>Category + Lake</td>
<td>9</td>
<td>511.2</td>
<td>13.5</td>
</tr>
<tr>
<td>R4</td>
<td>Year</td>
<td>Category + Lake</td>
<td>9</td>
<td>516.6</td>
<td>18.9</td>
</tr>
<tr>
<td>Recruitment model:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>fixed effects</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>R5</td>
<td>None</td>
<td>Category + Lake</td>
<td>8</td>
<td>497.7</td>
<td>0.0</td>
</tr>
<tr>
<td>R6</td>
<td>None</td>
<td>Category</td>
<td>5</td>
<td>500.5</td>
<td>2.8</td>
</tr>
<tr>
<td>R7</td>
<td>None</td>
<td>Lake</td>
<td>5</td>
<td>518.7</td>
<td>21.0</td>
</tr>
<tr>
<td>R8</td>
<td>None</td>
<td>(Intercept)</td>
<td>1</td>
<td>520.7</td>
<td>23.0</td>
</tr>
</tbody>
</table>

Growth model:        |                |               |     |      |      |

R9                     | None           | Category + Lake | 14 | 63.624 | 15.691 |
| G1                     | Stream(1+S) + Year(1+S) + Reach(1+S) + ID(1) | DOY + Category + Lake + Category*Doy | 17 | -79,316.0 | 0.0  |
| G2                     | Stream(1+S) + Year(1+S) + Reach(1+S) + ID(1) | DOY + Category + Lake + Category*Doy | 18 | -79,313.0 | 3.0  |
| G3                     | Stream(1+S) + Year(1+S) + Reach(1+S) | DOY + Category + Lake + Category*Doy | 17 | -72,875.3 | 6440.7 |
| G4                     | Stream(1+S) + Year(1+S) + Reach(1+S) | DOY + Category + Lake + Category*Doy | 16 | -72,992.2 | 627.7 |
| G5                     | Stream(1+S) + Year(1+S) | DOY + Category + Lake + Category*Doy | 15 | -68,615.2 | 10,699.5 |
| G6                     | Stream(1+S) + Year(1) | DOY + Category + Lake + Category*Doy | 14 | -63,624.3 | 15,691.7 |
| G7                     | Stream(1) + Stream(5) | DOY + Category + Lake + Category*Doy | 13 | -47,047.5 | 32,268.5 |
| G8                     | Stream(1) | DOY + Category + Lake + Category*Doy | 12 | -39,910.6 | 39,405.4 |
| G9                     | None           | DOY + Category + Lake + Category*Doy | 11 | -7833.1 | 71,432.9 |

Growth model: fixed effects

G10                    | Stream(1+S) + Year(1+S) + Reach(1+S) + ID(1) | DOY + Lake | 11 | -79,412.6 | 0.0  |
| G11                    | Stream(1+S) + Year(1+S) + Reach(1+S) + ID(1) | DOY + Category + Lake | 14 | -79,408.1 | 4.5  |
| G12                    | Stream(1+S) + Year(1+S) + Reach(1+S) | DOY | 8  | -79,403.7 | 8.9  |
| G13                    | Stream(1+S) + Year(1+S) + Reach(1+S) + ID(1) | DOY + Category + Lake + Category*Doy | 17 | -79,403.4 | 9.3  |
| G14                    | Stream(1+S) + Year(1+S) + Reach(1+S) + ID(1) | DOY + Category | 11 | -79,401.1 | 11.5 |
| G15                    | Stream(1+S) + Year(1+S) + Reach(1+S) | DOY + Category + Category*Doy | 14 | -79,396.2 | 16.4 |

The number of estimated parameters (K), AIC value, and the difference between the AIC value of a model and that of the most parsimonious (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.

* In the growth model, random effects were estimated for the slope (S) and the intercept (I) of each level except survey ID.
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 to their more regular and longer treatment histories (Tables 1 and 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 6). 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 6). The standard deviation of log$_e$(length) at age 1 explained by each random effect is shown in Table 8.

Age-1 ammocoetes from Lake Ontario were on average 30% larger than those from Lake Superior (Table 7, Fig. 3b). Ammocoetes from Lakes Michigan and Huron did not differ significantly in their mean length at age 1 from Lake Superior sea lampreys (Table 7, Fig. 3b). The day that a survey was conducted positively influenced mean length at age 1 (Table 7).

**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 (Fig. 4). 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 (Fig. 5a). The majority of variation in length at age 1 in Lake Superior streams was due to within-year variance, although among-year variance was also highest in Category 3 streams (Fig. 6a). 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 (Figs. 5b and c). In these two lakes, Category 1 sea lampreys had the highest levels of both within- and among-year variance in length at age 1 (Figs. 6b and c). Lake Huron sea lampreys showed no evidence of differences in overall variation in length at age 1 among stream categories (Fig. 5d), although sea lampreys from Category 3 streams did have slightly higher among-year variance than any other category of streams in Lake Huron (Fig. 6d).

**Discussion**

In this analysis, we demonstrated that differences in mean 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). The 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. The level of variation in recruitment among years did not correlate with differences in treatment regularity, contrary to our original hypothesis that regularly treated streams would have more consistent recruitment to age 1. Recruitment varies widely within categories of streams, as evidenced by the fact that the majority of variation in CPUE remained unexplained even by the best model. Sea lampreys from different stream categories did not differ in mean length at age 1. 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.

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; Bergennius 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 was 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 subpopulations 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, and avoid problems of non-independence associated with the use of traditional statistical methods on hierarchically structured data (Pinheiro and Bates, 2000; Wagner et al., 2006; Bolker et al., 2009). 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. Mean recruitment was highest in Category 1 streams, but variation did not differ among categories, indicating that a threshold number of age-1 ammocoetes may be necessary for a year class to persist in sufficient numbers to warrant treatment as the cohort approaches metamorphosis. Streams in which year-class strength exceeds this threshold level of recruitment are likely to require treatment on a regular schedule, even in the face of high levels of recruitment variation among streams and among years. However, below this threshold, normal variations in cohort survival and growth may result in an inconsistent need for chemical treatment. Exactly identifying the value of this threshold number is beyond the scope of this analysis, but our results indicate that it varies between lakes, and likely lies somewhere between 25 and 40 age-1 ammocoetes caught per hour of electrofishing time (Figs. 2b and 3a). Further research is required to more exactly identify a threshold suitable for management purposes, as a large amount of variation remains unexplained by our best model. 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 due to density-independent effects (Jones et al., 2003). The inclusion of environmental factors such as temperature, discharge, and other stream-specific variables could reduce the unexplained variance in our recruitment model; however, such variables were not available across the wide range of streams and years used in this analysis. 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 fact that this analysis was able to identify a pattern in recruitment to age 1 among stream categories in spite of the imprecision of CPUE as a metric of recruitment indicates that patterns might be stronger and variability would be lower if a more precise metric of recruitment were available. If a more precise threshold level of age-1 larvae could be identified, 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. Streams could be surveyed 1 or 2 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.

Of more immediate management importance is the observation that Category 1 streams consistently have higher recruitment to age 1 than other stream categories. Category 1 streams could likely be scheduled 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 quantitative 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.

Acknowledgments

This research was funded by the Great Lakes Fishery Commission, and additional financial support was provided for G.H. by a University Distinguished Fellowship from Michigan State University. We are indebted to the personnel of the United States Fish and Wildlife Service and the Department of Fisheries and Oceans, Canada, in particular Michael Fodale and Mike Steeves, for providing the data used for these analyses and for helping to interpret them. We thank Dr. Andrew McAdam for his assistance and insight regarding the statistical analyses. We thank Daniel Linden and Jared Myers for their guidance in the mapping of stream locations. We thank three anonymous reviewers for helpful comments on an earlier version of this manuscript. This is publication number 2009-17 of the Quantitative Fisheries Center at Michigan State University.

References
