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

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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. A better understanding of spatial and temporal variation in recruitment of pest populations may inform managers on where and when to effectively apply different control methods. 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. We evaluated the use of a mixed-effects model to look at common year effects and stream-level variables that could affect productivity and growing season length, with the objective of identifying factors that may explain this density-independent variation in recruitment. After selecting the “best model”, we tested factors that might affect recruitment variation, using a Great Lakes dataset comprising 97 stream-years. Lake Superior tributaries, streams with larger numbers of lamprey competitors, and streams regularly requiring lampricide treatment showed significantly higher recruitment. Alkalinity and thermal regulation did not affect the observed recruitment pattern among streams. In four long-term study streams we observed significant variation among streams, tested as a fixed effect, but no evidence suggested a common pattern of variation among years. 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.

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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. This is because changes to recruitment of a pest species as the population is driven to low levels 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 of 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 (Salvelinus namaycush), lake whitefish (Coregonus clupeaformis), and deepwater cisco (Coregonus sp.) 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 chemical and non-chemical 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 larvae (ammocoetes) from treated streams (W. Swink, U.S. Geological Survey, Hammond Bay Biological Station, unpublished data). Adult control methods consist of adult trapping (Mullett et al., 2003), barriers (Hunn and Youngs, 1980; Lavis et al., 2003) to the upstream movement of migrating adults, and the release of sterile adult males (Twehey et al., 2003). The exploitation of sea lamprey pheromones (Li et al., 2003; Sorensen and Vrieze, 2003) to the upstream movement of migrating adults, and the release of sterile adult males (Twehey et al., 2003). The exploitation of sea lamprey pheromones (Li et al., 2003; Sorensen and Vrieze, 2003) is also being explored, as adult sea lampreys rely on two types of pheromones to complete their life cycle; the larvae release a pheromone that aids migratory adults in identifying suitable spawning grounds, and sexually mature adults release pheromones that attract the opposite sex (Teeter, 1980). The Great Lakes Fishery Commission (GLFC) is seeking to increase their reliance on methods other than lampricides to achieve fish community goals in the Great Lakes (GLFC, 2001). These adult control methods all seek to reduce the number of spawners in order to
decrease subsequent recruitment, but are unlikely to achieve total suppression. Consequently, the degree to which adult control is 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; an earlier study (Jones et al., 2003) provided evidence for compensation in Great Lakes sea lamprey populations. 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. Evidence was presented by Jones et al. (2003) for large density-independent recruitment variation in Great Lakes sea lampreys. That study concluded that further research into sea lamprey population dynamics was needed to discriminate between “stream” effects and “year” effects on recruitment variation. For example, identifying types of streams (i.e., spatial or stream effects) where recruitment tends to be higher than average at a given spawning stock size helps pest managers determine where higher rates of adult suppression may be needed. A better understanding of spatial and temporal variation in recruitment may inform managers on where and when to effectively apply different control methods.

In this paper we report on the findings of a follow-up study to Jones et al. (2003) of sea lamprey recruitment dynamics in which we have nearly doubled the available data on stock and recruitment. We used these data, together with data on stream characteristics to analyze variation in recruitment patterns among streams and years. Included in this dataset are four streams in which we introduced spawners annually at particularly low levels to mimic adult control reductions in spawner abundance, and measured the subsequent yearling recruitment over a period of several years.

**Methods**

We assembled data on spawning population size and on yearling recruitment 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. Data were collected between 1997 and 2007 from 37 streams located across the Great Lakes basin (Table 1, 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 yearling abundance using the same electrofishing survey technique in all.

### Table 1

<table>
<thead>
<tr>
<th>Recruitment year</th>
<th>Number of streams in full dataset</th>
<th>Number of streams in four-stream dataset</th>
</tr>
</thead>
<tbody>
<tr>
<td>1997</td>
<td>7</td>
<td>1</td>
</tr>
<tr>
<td>1998</td>
<td>17</td>
<td>2</td>
</tr>
<tr>
<td>1999</td>
<td>25</td>
<td>4</td>
</tr>
<tr>
<td>2000</td>
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<td>4</td>
</tr>
<tr>
<td>2001</td>
<td>6</td>
<td>3</td>
</tr>
<tr>
<td>2002</td>
<td>2</td>
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</tr>
<tr>
<td>2003</td>
<td>4</td>
<td>4</td>
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<td>2004</td>
<td>4</td>
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<td>2005</td>
<td>4</td>
<td>4</td>
</tr>
<tr>
<td>2006</td>
<td>4</td>
<td>4</td>
</tr>
<tr>
<td>2007</td>
<td>3</td>
<td>3</td>
</tr>
</tbody>
</table>

**Fig. 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.
streams, as described in Jones et al. (2003). Larval habitat was classified along randomly-spaced transects as proportions of 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 electrofishing we surveyed plots of up to 5 m² of Type I habitat at approximately half of the transects, and similar plots of Type II habitat were surveyed at about every eighth transect. In this study, transect widths averaged 4.7 m, and ranged from 1 to 21.5 m.

To determine the proportion of ammocoetes that were yearlings in our surveys 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 no 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. We assumed larvae grew according to a von-Bertalanffy growth function and that individual variation in length was linearly related to age 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 (Dawson, 2007). 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 latter five cases a cutoff length was selected for yearlings that corresponded roughly to the mid-point between the presumed age 1 and age 2 modes of the length-frequency plot. The results of the Jones et al. (2003) 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 from the larval survey to estimate yearling catch in each stream-year.

We calculated recruitment as

\[ \tilde{R} = \frac{C_{II}}{q} H_{II} T + \frac{C_{I\,I}}{q} H_{I} T, \]

where \( C_{I\,I} \) or \( q \) was the yearling catch in Type I and II habitats, \( q \) was the electrofishe catchability, \( H_{I\,I} \) or \( H_{I} \) was the total Type I or II habitat area in the stream, and \( H_{I\,I} \) or \( H_{I} \) was the Type I or II habitat area surveyed. We assumed a fixed electrofisher catchability of 0.482 for all streams and habitat types (Steves et al., 2003).

Larval habitat was calculated in each stream, and was weighted by the relative suitability of Type I and Type II habitats

\[ H_{w} = A_{I} + \frac{D_{I}}{D_{II}} A_{II}, \]

where \( A \) is the estimated area of each type of habitat (m²) in the stream and \( D_{I} \) is the density of yearlings in either Type I or Type II habitats; \( D_{II} = A_{II} \). 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 was determined for all streams and the ratio \( D_{II}/D_{I} \) used in habitat calculations was the average ratio of the densities across all streams in the dataset. In this dataset the average ratio across the streams was 0.381 (s² = 0.180).

To combine data among streams, stock and recruitment were calculated as densities

\[ S = \frac{\tilde{S}}{H_{w}}, \quad R = \frac{\tilde{R}}{H_{w}}, \]

respectively, where \( \tilde{S} \) is the total number of spawning females released or estimated by mark/recapture and \( \tilde{R} \) is the total abundance of yearling larvae estimated by backpack electrofishing.

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 wished to observe recruitment in contrasting sets of streams and these streams differed in average water temperature and alkalinity, which is often used as a surrogate for stream productivity. 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 four or five years starting in 2002 (Carp and Big Carp, respectively) or four years starting in 2003 (Port Britain and Grafton). These introductions mimicked adult control methods that reduced spawners to less than 1 spawning female/100 m² of larval habitat for Port Britain Creek and less than 0.5 spawning females/100 m² for the other three streams. Jones et al. (2003) observed no high recruitment events when spawning density was below 0.5 spawning females/100 m².

We wished to evaluate whether differences in recruitment among these four streams were consistent with hypotheses about the influence of physical habitat, thereby pointing towards formal hypothesis testing in a future study. Consequently, the spatial distribution of spawning and larval habitat was quantified by separating each stream into four equal-length sections and estimating the proportion of preferred (Type I), acceptable (Type II) larval habitat, spawning habitat, and unsuitable habitat in each section. Data on larval habitat was collected during larval surveys performed each year for each stream, as described above. During 2006 we further classified Type III and IV habitats as suitable for spawning (existance of gravel 1 to 5 cm in diameter for nest construction, with small amounts of sand available) or unsuitable for spawning (other streambed characteristics existed) (Applegate, 1950). We quantified the quality of suitable spawning areas by assessing the embeddedness of the substrate in suitable spawning areas using the embeddedness rating of Platts et al. (1983). The more embedded the substrate the less available that substrate is to sea lampreys constructing nests. We then compared the amount and distribution of preferred and acceptable larval habitat, spawning habitat, and unacceptable sea lamprey habitat and the embeddedness rating for each stream with the observed variation in recruitment.

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

\[ R_{t+1} = \alpha \cdot S_{t} \cdot e^{-\beta \cdot S_{t}} + \epsilon, \]

Visual inspection of the stock–recruitment data from this and other sea lamprey studies indicates 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

\[ \ln \left( \frac{R_{t+1}}{S_{t}} \right) = \ln(\alpha) - \beta \cdot S_{t} + \epsilon, \]

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 m² of larval habitat, \( \alpha \) describes average survival across stream–years when \( S \) is zero, \( \beta \) describes the degree to which survival falls as \( S \) increases, and \( \epsilon \) is a normally distributed error term with mean zero and variance \( \sigma^{2} \). 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 (Eq. (3)). 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 \( \beta \cdot S \) 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

$$\ln\left(\frac{R}{S}\right)_k = \ln(\alpha) + v_j + \chi_k + \delta_l + \lambda_m + \rho_n + b_o + c_p - \beta \alpha$$

$$j = 1, \ldots, 4; k = 1, 2; l = 1, 2; m = 1, 2, n = 1, \ldots, 9, \alpha = 1, \ldots, 37; b_o \sim N(0, \sigma_b^2), c_p \sim N(0, \sigma_c^2). \quad \epsilon_{ijklmnop} \sim N(0, \sigma_\epsilon^2)$$

$$\lambda_m = \text{Consistency of sea lamprey production effect (1 = irregular (i), 2 = regular (t))}.$$  
$$\rho_n = \text{Competitor effect (1 = low (l), 2 = moderate (m), 3 = high (h))}.$$  
$$b_o = \text{Year effect (random) (ten years of data from 1997–2007, excluding 2002).}$$  
$$c_p = \text{Stream effect (random) (37 streams).}$$  
$$\beta = \text{Density dependence term.}$$  
$$\epsilon_{ijklmnop} = \text{Error term.}$$

Lake was used as a surrogate for the effect of broad geographical differences in stream locations. Thermal regulation 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 (air) or be more regulated by groundwater input (groundwater). In general, those streams regulated by air temperature 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 alkalinitities 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., consistent cycle of treatment. The competitor effect was a categorical variable, and was selected as the best model (lowest AIC$_C$) 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 exceeded the best model by three or more had strength of evidence ratios of greater than five were removed from further consideration, since this suggests that there is considerably less statistical support for those models (Burnham and Anderson, 2004). F tests and Tukey–Kramer a-posteriori tests were used in the top-ranked models to further explore the significance of explanatory variables.

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 models being evaluated tested only the effect of stream, here as a fixed effect, or tested the effect of stream as a fixed effect, and the effect of year as a random effect on recruitment. We chose to use stream as a fixed effect in this instance because we were specifically interested in contrasts among this group of four streams. The random effect and the residual variances were modeled as normally distributed with mean zero and variance $\sigma_y^2$ and $\sigma^2$, respectively.

### Results

Doubling the size of the sea lamprey stock–recruitment database (Table 1) 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. 2a). As well, large recruitment events ($>$400 yearlings/100 m$^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. 2b). The regression of $\ln(R/S)$ on $S$ revealed a statistically significant, negative slope ($\beta = -0.1593$, SE = 0.0226, $r^2 = 0.34$, $p$ ($\beta = 0$) $<$ 0.0001, df = 95; Fig. 2c), which provides statistical evidence of compensation. In our four long-term study streams, where since 2002 we introduced spawners at low levels, recruitment was low (<400 yearlings/100 m$^2$) in all cases (Fig. 2d).

For the full dataset, we determined that stream and year as random effects should be removed from the model (Table 2). Model selection on the remaining effects indicated support for the full model and three reduced models (Table 2). All other reduced models had AIC$_C$ values at least three units greater than the top model. Because the model with all fixed effects included was not significantly worse than the more parsimonious model ($<$3 AIC units difference) we used SAS (Version 8 of the SAS System for Windows, Copyright 2000, SAS Institute Inc.) to

### Table 3

Results from model selection procedures to find the best model to explain sea lamprey recruitment variation among the four long-term study streams.

<table>
<thead>
<tr>
<th>Model parameters AIC$_C$</th>
<th>Strength of evidence</th>
</tr>
</thead>
<tbody>
<tr>
<td>ln(R/S) = ln(a) + (C$_0$ - 5 + e)</td>
<td>95.95</td>
</tr>
<tr>
<td>ln(R/S) = ln(a) + b$_1$ + b$_n$ - (5 + e)</td>
<td>102.45</td>
</tr>
</tbody>
</table>

The model indicated by an asterisk includes stream as a fixed effect and was selected as the “best model”. See text for explanation of model variables.
test for significance of fixed effects using this model. 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 ($p = 0.0003, F_{1,87} = 7.111$), and a Tukey-Kramer test indicated that streams tributary to Lake Superior experienced significantly higher survival than streams tributary to Lakes Huron and Ontario (Fig. 3a). Survival in streams with regular sea lamprey production was significantly higher than in streams 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. A Tukey-Kramer test indicated significantly lower survival in streams with low competitor density than in streams with high competitor density (Fig. 3b). The thermal regulation and alkalinity effects were not significant.

For the long-term study streams dataset, we determined that year as a random effect should be removed from the model (Table 3). The general linear model testing the effect of stream revealed a large effect of stream ($p < 0.0001, F_{3,26} = 21.82$) on survival. A Tukey-Kramer test performed on the model with the random effect of year excluded indicated that 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. 3c).

Average competitor density across all years in the four long-term study streams was highest in streams with higher survival and lowest in streams with lower survival (Table 4). Temperature monitoring on the four study streams during the summers (June–August) of 2003 and 2004 indicated that the stream with the highest index of survival had the lowest average summer temperature, while the stream with the lowest survival had the highest average summer temperature (Table 4). Streams with higher survival had distributions of spawning and larval habitats that were most favorable to sea lamprey production (Fig. 4). 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) (Table 4).

### Table 4

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

<table>
<thead>
<tr>
<th>Stream</th>
<th>Index of survival (Least square means)</th>
<th>Percentage of cases where embeddedness of spawning habitat was low</th>
<th>Consistency of sea lamprey production</th>
<th>Average competitor density (competitors/100 m²)</th>
<th>Average summer temperature during 2003–2004</th>
</tr>
</thead>
<tbody>
<tr>
<td>Carp</td>
<td>6.87</td>
<td>69.6</td>
<td>Regular</td>
<td>8416 (204.4)</td>
<td>15.7 (0.147)</td>
</tr>
<tr>
<td>Big Carp</td>
<td>5.27</td>
<td>76.4</td>
<td>Irregular</td>
<td>8426 (207.1)</td>
<td>17.2 (0.175)</td>
</tr>
<tr>
<td>Grafton</td>
<td>3.68</td>
<td>71.9</td>
<td>Irregular</td>
<td>540.9 (118.2)</td>
<td>16.7 (0.148)</td>
</tr>
<tr>
<td>Port Britain</td>
<td>2.08</td>
<td>49.7</td>
<td>Irregular</td>
<td>137.9 (60.9)</td>
<td>19.1 (0.148)</td>
</tr>
</tbody>
</table>

Standard errors are shown in parentheses.

**Discussion**

In a previous analysis, Jones et al. (2003) 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. This study has confirmed the findings of Jones et al. (2003) 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 versus 2084 yearlings/100 m²) in streams with similar, low spawner numbers (0.3 females/100 m²). 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. This was also observed in another study measuring sea lamprey recruitment (G. J. A. Hansen, Michigan State University, personal communication). We also found that larval in streams from Lake Superior had higher survival than those 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. However, if summer temperatures in a stream fall outside the thermal
niche of larval sea lamprey (17.8–21.8 °C as determined by Holmes and Lin (1994)) then recruitment is likely to be affected. Only in Port Britain Creek did the 2003–2004 average daily summer temperature exceed 21.8 °C (Table 4) on more than one occasion, consistent with the observation of relatively low survival in this stream. 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-producing streams in the basin, but were not selected at random. Stream habitat quality for sea lampreys may, in general, be better in Lake Superior than in Lakes Huron and Ontario, or the streams included in this study may simply have had better habitat quality in Lake Superior. 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).

Observing recruitment in four intensively sampled streams allowed us to look more closely at factors that may affect recruitment. 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 yearling larvae experienced the highest survival in this stream (Table 4). Carp River 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 (Fig. 4). Young et al. (1990) found that the presence/absence of sea lamprey ammocoetes within the Great Lakes was controlled, to a large degree, by substrate particle size. Port Britain Creek had a substantially lower proportion of spawning habitat with un-embedded substrate (Table 4). 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. Stream gradients for the study sections of the four study streams (Environmental Systems Research Institute, Inc., 2007) 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.

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 (Oncorhynchus nerka) and pink (Oncorhynchus 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. We saw 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. This 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 adult control strategies. We did not observe large recruitment events (~400 yearlings/100 m²) when spawner abundance was below 0.2 females/100 m² in either the full dataset or the long-term study stream dataset. When planning future adult 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 in 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 m² of larval habitat and over 50% had spawner abundances greater than 1 female/100 m². 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 m² 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.

Our findings suggest that 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 adult control.

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