Great Lakes Fishery Commission

Project Completion Report*

Compensatory Mechanisms in Great Lakes Sea Lamprey Populations: An Integrated Program of Research and Assessment

By

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Preface

This completion report summarizes the findings of two components of a larger study to investigate evidence for compensatory mechanisms in Great Lakes sea lamprey populations. Here we report on (1) a meta-analysis of evidence of compensation obtained from an extensive survey of recruitment in lamprey-producing streams distributed throughout the Great Lakes basin, and a modeling study of the implications of these findings; and (2) an intensive examination of early life history processes in lamprey during their first year of life, with a focus on potential implications for density dependence. The two other components of the study have been summarized in other completion reports. Kelso and O'Connor (November, 2001) report on an intensive investigation of sea lamprey reproductive success in two Lake Ontario tributary streams. Beamish and Griffiths (February 2001) summarize the final component of a study to examine the lability of sex determination in larval lamprey, and particularly the influence of larval density on sex determination.

Part 1
Stock and recruitment in Great Lakes sea lamprey populations: evidence for compensation, recruitment variation, and implications for alternative control.

(Note: this section of our completion report is excerpted from a manuscript currently being revised for the Sea Lamprey International Symposium II Proceedings. We wish to acknowledge the substantial contribution of that manuscript's co-authors to this study: Roger Bergstedt – USGS; Michael Twohey, Michael Fodale, Jeff Slade – USFWS; Doug Cuddy – DFO)

Compensatory mechanisms refer to demographic processes in animal populations that tend to regulate the abundance of those populations (McFadden 1977). Specifically, compensatory mechanisms operate by reducing birth rates or increasing death rates when population density increases. In fishery management, compensatory mechanisms are frequently described using a stock-recruitment relationship, which characterizes the extent to which recruitment of fish per spawning adult (i.e., an effective birth rate) increases as the size of the spawning population becomes smaller. In this synthesis we examine the evidence for compensatory mechanisms in Great Lakes sea lamprey populations and explore the management implications of alternative hypotheses about the sea lamprey stock-recruitment relationship.

A central challenge of most fishery management is to quantify the strength of compensatory mechanisms in exploited fish populations. As harvest rates increase and stocks become smaller, the resistance of a stock to over-exploitation is determined by the degree to which the population can *compensate* by increasing vital rates in response to reduced population densities. When the objective is to manage a fish population for maximum sustainable harvest, managers seek to take advantage of compensatory mechanisms. In the case of sea lamprey control, where the objective is to reduce the size of the lamprey population to the minimum level economically achievable (Koonce et al. 1993), managers face precisely the opposite challenge. They seek to overcome the compensatory capacity of lamprey populations so that the effectiveness of their control actions is not compromised by subsequent increases in the productivity of the residual population. In either case, however, knowledge of whether and to what extent compensation operates is a critical ingredient of well-informed decision-making.

Sea lamprey program managers have become particularly interested in compensatory mechanisms in recent years, because of a desire to reduce reliance on lampricides as the primary method of lamprey control (Great Lakes Fishery Commission 1992). Lampricide treatments are prescribed to remove large lamprey ammocoetes from streams immediately before they metamorphose and emigrate from the streams to become parasites (Brege SLIS II). Lampricide treatments are believed, when effective, to remove between 95 and 99% of the ammocoetes from treated streams. Because of the magnitude of the mortality caused by lampricides, and because the action targets the life stage immediately prior to the parasitic stage, there is very little scope for a demographic response (i.e., increased survival) of the residual lamprey to compensate for the control action. Alternative controls such as the release of sterilized males (Twohey SLIS II) and adult trapping, on the other hand, target reproductive success, and may result in more modest reductions in the effective population size (e.g., a 3:1 ratio of sterilized to un-sterilized males produces only a 75% theoretical reduction in reproductive success). The degree to which these alternatives are effective will depend on the recruitment dynamics of lamprey. If larval survival is enhanced by reductions in spawning stock size, for example, the net effect of the alternative control on production of parasitic lamprey may be limited.

To explore the potential consequences of compensation in lamprey populations we combined data from several studies (Figure 1) in a form of meta-analysis whose purpose was to determine the nature of the stock-recruitment relationship in Great Lakes lamprey populations. Each of the studies provided data on spawning populations and of larval recruitment at age 1. We fit the data to a Ricker stock-recruitment relationship and tested for the presence of compensation (density-dependent survival) between spawning and age 1. In contrast to other stock-recruitment analyses, we are combining data from multiple spawning populations, which necessitates the implicit assumption of a common stock-recruitment relationship among streams.

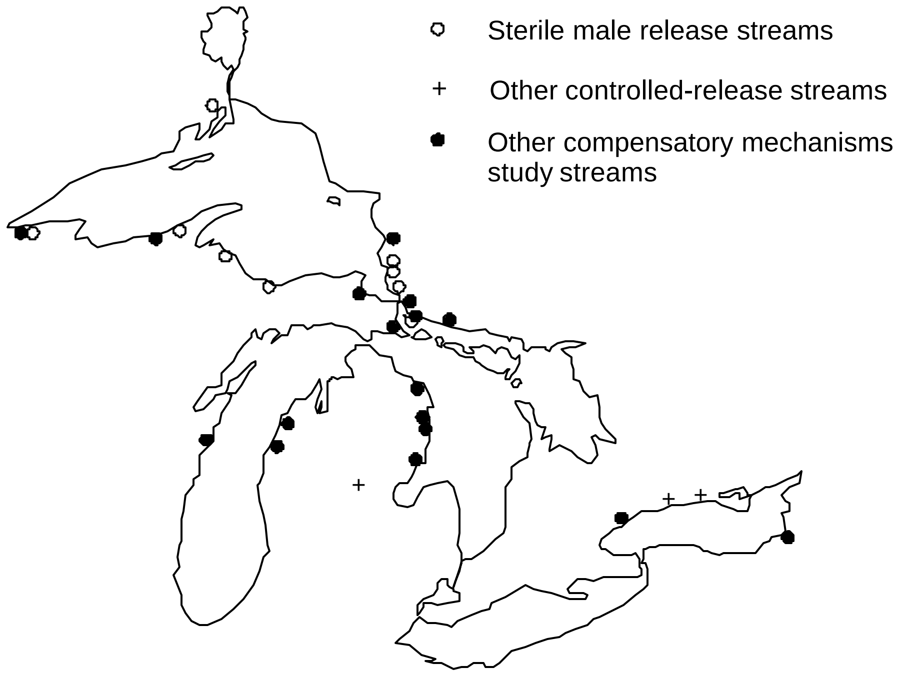

Figure 1. Location of streams from which we obtained stock-recruitment data.

Methods

In the first study, which is part of a long-term study to evaluate the Sterile Male Release Technique (Twohey SLIS II), spawner abundance was controlled by deliberately releasing adult lamprey above barriers. Eight Lake Superior streams received controlled adult introductions in each of three years. Larval abundance at age 1 was estimated in each subsequent year. In 12 of 24 cases, three sterile males were released above the barrier for every one fertile male. Based on the results of earlier research and additional data collected during this study (R. Bergstedt, unpublished data), we assume that the effective number of spawning females was reduced by 75% due to the addition of sterile males (the theoretical expectation if sterile males compete effectively with fertile males for mates).

In three other streams (one Lake Huron, two Lake Ontario), known numbers of adult male and female lamprey were introduced above barriers, without sterile males, for two years, and larval abundance was estimated in the following year. Finally, spawning population sizes were estimated using a mark-recapture method applied to lamprey captured in adult assessment traps (Mullett SLIS II) in 26 additional stream-years after which age 1 ammocoete abundances were estimated the following year.

We estimated age 1 larval abundance using the same technique in all streams. First, the entire accessible length of the stream upstream of the barrier was divided into between 47 and 142 randomly spaced transects, where the average distance between transects was equal to the accessible stream length divided by the number of transects used. Along each transect, perpendicular to the direction of stream flow, we measured the proportion of substrate that comprised each of four possible habitat types. Type I and II habitats are preferred and acceptable habitats for ammocoetes, respectively, while Type III and IV are unsuitable.

At between 26 and 79 of the transects in a stream we collected larvae from a randomly selected, 5 m^2 plot of Type I or II habitat using an AbP-2 backpack electroshocker, following a standardized larval assessment procedure (Slade SLIS II). Type I plots were preferentially selected when this type of habitat was present in the vicinity of the transect, although an effort was made to survey at least 12 Type II habitat plots on each stream.

We did not collect statoliths for all the larvae we sampled, so we relied upon inspection of length-frequency plots to determine the minimum and maximum lengths of yearling larvae for each stream-year. The yearling mode was always obvious from the length-frequency plots, but determination of the cut-off between age 1 and age 2 ammocoetes was frequently difficult. This step may therefore introduce error into our estimates of yearling densities. The mean yearling density in each habitat type was then computed from:

$$D_i = \frac{\sum_{j=1}^{P} C_{i,j}}{\sum_{j=1}^{P} Ap_{i,j}}$$

where D is density of yearlings, C is catch of yearlings, Ap is plot area, P is the number of plots, i is the habitat type index and j is the plot index. Similarly, we computed the area of habitat of each type from:

$$A_i = \frac{\sum_{k=1}^{T} W_{i,k}}{\sum_{k=1}^{T} W_k} \cdot L \cdot \frac{\sum_{k=1}^{T} W_k}{T} = \frac{\sum_{k=1}^{T} W_{i,k}}{T} \cdot L$$

where A is the area of habitat (m^2), $W_{i,k}$ is the length of transect k that is Type i habitat, W_k is the total length of transect k, T is the number of transects, L is the length of the study area and k is the transect index. The abundance of yearling larvae (i.e., recruitment) in each stream-year is then:

$$R = \sum_{i=I}^{II} D_i \cdot A_i$$

We tested for evidence of compensation by fitting the data to a Ricker stock-recruitment model of the form:

$$R = a \cdot S \cdot e^{-b \cdot S + e}$$

which can be re-written as a linear model:

$$\ln\left(\frac{R}{S}\right) = \ln(a) - b \cdot S + e$$

where R is recruitment (yearlings), S is adult stock, α describes survival when S is small, β describes the degree to which survival falls as S increases, and ε is a normally distributed error term. Since β indicates the degree to which survival is density dependent, an estimate of β that is greater than zero indicates the presence of compensation.

To carry out this among-stream meta-analysis, we assume that all streams share a common α term and that β depends on the availability of larval habitat in each stream, such that if S is expressed in adults per unit of larval habitat, β will also have a common value for all streams, determined by intra-specific larval competition for rearing habitat. We can therefore test for a β value significantly greater than zero by carrying out a linear regression of ln(R/S) on S/H, where H is the amount of larval habitat in each stream, using the data from all stream-years together.

We computed total larval habitat from

$$H_W = A_I + \frac{\overline{D_{II}}}{\overline{D_I}} \cdot A_{II}$$

This index weights Type II habitat less heavily than Type I, based on the ratio of densities of yearling larvae in Type II versus Type I habitats, averaged over all streams and years. The density ratio serves as an index of Type II habitat suitability, relative to Type I habitat.

Results

Recruitment of yearling sea lamprey was highly variable among streams, even after accounting for the effect of adult stock size (Figure 2a).

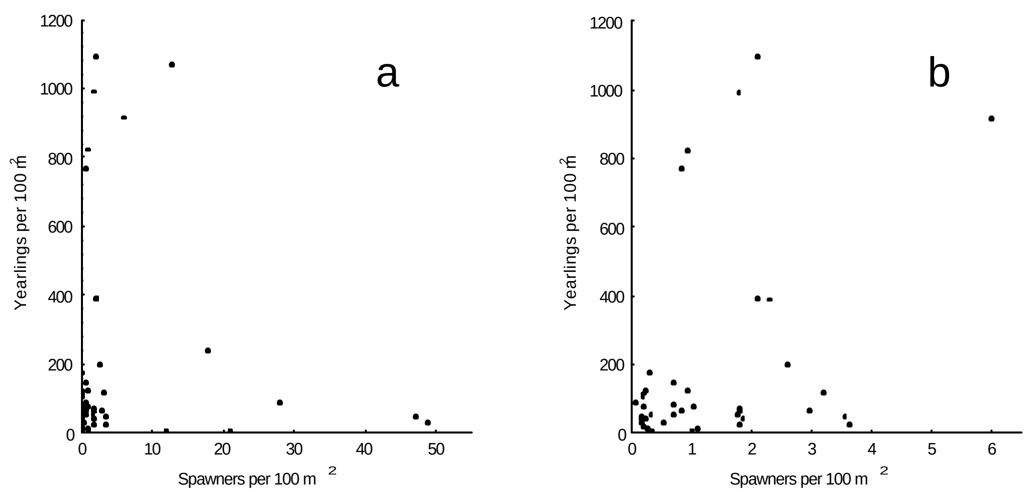

Figure 2. Observed stock and recruitment for 49 stream-years. Spawner and yearling numbers are expressed as densities per 100 m^2 of larval habitat. The right panel (b) only includes data from stream-years where spawner densities were less than 10 per 100 m^2

The combined results from the 49 stream-years indicate that recruitment is reduced at very large adult stock sizes (adult females per 100 m^2 of larval rearing habitat), and that large recruitment events occur frequently even when the number of spawning females is quite low (< 2 females per 100 m^2: Figure 2b). Inspection of the pattern of recruitment at very low stock sizes (< 0.5 females per 100 m^2) suggests a possibility of reduced frequency of high recruitment events (Figure 2b).

The recruitment data also show evidence of compensation, measured as density dependent survival from spawning to age 1. The regression of ln(R/S) vs S revealed a statistically significant, negative slope (ß = 0.129, p(ß =0)<0.0001, df=47, Figure 3a).

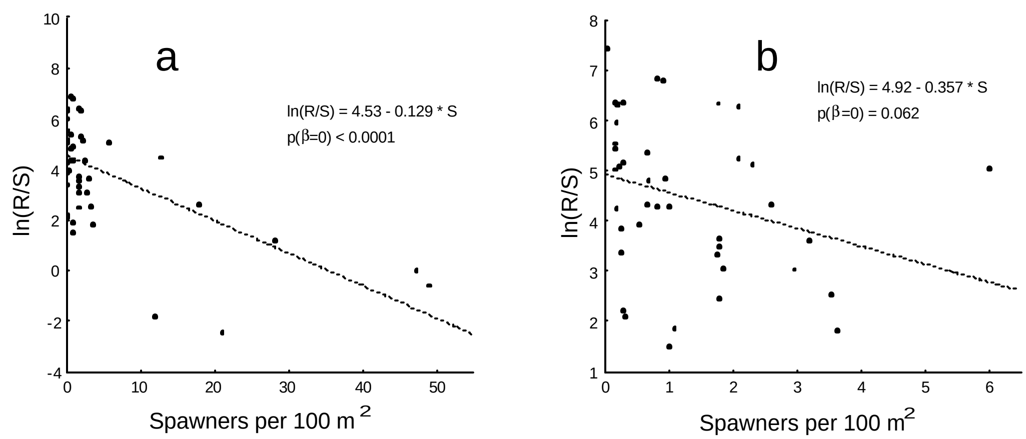

Figure 3. The linearized stock-recruitment relationship (ln(R/S) vs S) for the same data as plotted in Figure 2. The regression line for each panel was estimated using only the data presented in the corresponding panel.

The significant negative slope is influenced by a small number of observations of very high spawner densities, however. When these observations are excluded (i.e., only spawner densities < 10 per m^2 are included), the point estimate of ß is larger (ß = 0.357) but it is no longer significantly different from zero (p(ß=0) = 0.062, df=40, Figure 3b). Even at low densities of spawners, the data suggest that compensatory effects are present, but the large amount of density independent recruitment variation obscures the effect.

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For example, the regression estimate (ß = 0.357) at low spawner densities implies a 43% increase in survival with a unit decrease in spawner densities. By contrast the observed variability about the stock-recruitment relationship (σ^2 = 3.03) suggests much greater density independent variation (e.g., the data shown in Figure 3b suggests that variation in *ln(R/S)* of two units at a given density should not be unexpected – this variation implies approximately a ten-fold variation in survival).

Management Implications

We have presented evidence for large, density-independent variability in recruitment rates of larval lampreys. This variability may mask density-dependent effects, but it also leads to the lack of a consistent, repeatable demographic response of the lamprey population in a particular stream to a reduction in the effective number of spawning lamprey in that stream. Regardless of the strength of the compensatory responses that operate, this implies that in any given year larval recruitment could depart substantially from a long-term average value. This leads, in effect, to a significant *risk* of an unsuccessful control action.

To date, models that have been used to guide integrated sea lamprey management have not accounted for recruitment variation (Koonce et al. 1993, Schleen SLIS II). Our findings suggest that such models will yield a misleading impression of the efficacy of alternative control measures. To formally illustrate the ramifications of our results, and to make the case for including recruitment variation in management models in the future, we present a simple but realistic model of a controlled sea lamprey population.

The model simulates the dynamics of a sea lamprey population in a lake with 10 tributary streams utilized by lamprey for spawning and larval rearing. The purpose of the simulations will be to compare the performance of control strategies that target larval populations (lampricide controls) to that for strategies, such as sterile male releases, that target reproductive success. We model a single parasitic population and assume that adult lamprey do not home to natal streams (Bergstedt and Seelye 1995). The allocation of spawners to streams is assumed to be proportional to the relative abundance of ammocoetes in each of the ten streams, which is consistent with the view that lamprey are attracted to streams for spawning by the presence of a migratory pheromone released by stream-dwelling ammocoetes (Sorenson and Vrieze SLIS II). Recruitment of age 0 larvae is determined from a stock-recruitment relationship (see below). Larvae then remain in the stream until they either die (natural mortality) or metamorphose, at which time they enter the parasite population. Larvae that metamorphose in year t become parasites in year t+1 and return as spawners in year t+2. The model equations are as follows (symbols and their assumed values are described in Table 1):

$$S_{i,t} = P_t \cdot \frac{\sum_j l_{i,j,t}}{\sum_{i,j} l_{i,j,t}} \cdot s_p \cdot p_f$$

$$l_{i,0,t} = a \cdot S_{i,t} \cdot e^{-b \cdot S_{i,t} + e}$$

$$l_{i,j,t+1} = l_{i,j-1,t} \cdot s_l \cdot (1 - m_j)$$

$$P_{t+1} = \sum_{i,j} (l_{i,j,t} \cdot m_j) \cdot s_m$$

Table 1. Parameters, their assumed values, and state variables used in the lamprey model. For the age-specific probability of metamorphosis, values are presented for each ammocoete age group (associated ages in parentheses).

Symbol	Definition	Assumed value
S	Spawning lamprey abundance	State variable
P	Parasitic lamprey abundance	State variable, initially 13,600
l	Larval lamprey (ammocoete) abundance	State variable
s_p	survival during parasitic phase	0.75/yr
p_f	proportion females	0.5
a	Ricker model parameter	4.53
ß	Ricker model parameter	0.129
e	Process error in recruitment	1.7
s_l	annual survival during ammocoete phase	0.3
m	age-specific probability of metamorphosis	0(2),.2(3),.4(4),.7(5),1.(6)
s_m	survival during year of metamorphosis	0.75

We simulate lampricide control by removing a fixed proportion of the entire larval population from any stream that is selected for treatment. We use a method analogous to the GLFC stream selection procedure to determine which streams to treat in any given year of the simulation. Each year, all ten streams are ranked according to the number of metamorphosing ammocoetes that would be removed from next year's parasitic population by treatment, per dollar of treatment cost. Streams with large populations of older ammocoetes and modest treatment costs will be ranked highest. Each year, streams are treated in rank order, from highest to lowest, until a pre-specified control budget is completely utilized. This is the optimal control strategy for maximizing the suppression of parasitic lamprey given a fixed budget. For simplicity, we assume perfect knowledge of stream ammocoete abundance, and a fixed treatment effectiveness (proportion of ammocoetes killed by the treatment) of 90%.

We simulate alternative control by reducing the abundance of spawning lamprey by a fixed proportion in all streams. While a mixture of lampricide and alternative control is more likely to occur in operational situations, the objective of this analysis is to compare the performance of the two control strategies under conditions of recruitment variation consistent with those observed in our stock-recruitment dataset. If all control funds were directed at reducing lamprey spawning success, it is likely that control would have to be applied in all streams in all years because, unlike a lampricide treatment that affects all year classes of ammocoetes present in a stream at the time of treatment, an alternative control action only affects a single year class.

To compare lampricide control to alternative control, it would be best to simulate the level of control that would be possible if the same budget were applied exclusively to alternative control. Unfortunately, alternative control programs such as sterile male releases have not yet become operational on the Great Lakes, the only exception being the St Marys River (Schleen SLIS II). Thus it is difficult to know how much alternative control is possible within the constraints of a fixed annual budget. Instead, we have used our model to determine the amount of alternative control that would be necessary to achieve a comparable level of suppression of parasitic abundance in the lake, *in the absence of recruitment variation*, to that achieved using the lampricide control technique.

Then we compare the performance of the two control strategies in the presence of recruitment variation.

Incorporating recruitment variation

We can use the results of our stock-recruitment study to obtain an empirical estimate of recruitment variability. The observed error on ln(R/S) shown in Figure 3 included sources of error that should not be included in our simulations, however. First, there is measurement error in the observed recruitment. Second, there is variability due to "stream effects", differences among streams in the true stock-recruitment relationship. The remaining variability is stream-specific process error – density independent variability in recruitment due to processes not accounted for by the stock-recruitment model (e.g., inter-annual variations in winter severity and its effect on survival of age 0 ammocoetes). Only this process error should be included in our model, because the other two are not related to the true uncertainty about the recruitment that will result from a given adult stock size in an individual stream.

The process error in the stock-recruitment relationship is given by:

$$s_P^2 = s_T^2 - s_S^2 - s_M^2$$

where s_T^2 = the variance about the stock-recruitment relationship shown in Figure 3, s_S^2 is the variance due to stream effects and s_M^2 is measurement error. Our regression analysis yielded an estimate for s_T^2 of 3.03.

We can estimate the measurement error from the age 1 assessment data. Recall that recruitment was estimated from:

$$\hat{R} = A\left[\overline{D}_I\,\overline{p}_I + \overline{D}_{II}\,\overline{p}_{II}\right]$$

where A is the total area of the stream, p is the estimated proportion of type I or II habitat D is the estimated density in each habitat type. Assuming that A is measured without error, the variance of R can be computed from

$$\mathrm{var}(\hat{R}) = A^2\left[\sum_{i=I}^{II}\left(D_i^2\,\mathrm{var}(p_i) + p_i^2\,\mathrm{var}(D_i)\right)\right]$$

We further assume that the measurement error in R is log-normally distributed. According to Law and Kelton (1982) we can compute s_M^2 for a log-normal distribution from

$$s_M^2 = \ln(CV^2 + 1)$$

where CV is the coefficient of variation of the recruitment estimate ($\frac{\sqrt{\mathrm{var}(\hat{R})}}{\hat{R}}$). The average CV for the 49 stream-years in our data set was 0.22, which implies a value of s_M^2 of 0.047. We conclude from this analysis that measurement error is a negligible component of the observed, overall error in ln(R/S).

As part of our stock-recruitment study, we hypothesized that two factors likely to contribute to differences in the stock-recruitment relationship among streams would be temperature and alkalinity. As a result, we classified each stream in our study as being "warm" or "cool" and as having "low" or "high" alkalinity. Warm streams were those where summer water temperatures frequently exceeded 20°C, while cool streams did not, usually as a result of substantial groundwater inputs to the latter group. We used an alkalinity cut-off of 100 mg/L to distinguish high and low alkalinity streams. We repeated the regression of ln(R/S) on S, this time using a mixed model analysis of covariance, with alkalinity and temperature classes as random effects and S as the covariate. The results indicated that addition of the two "stream" factors did not explain any of the observed recruitment variation. This result suggests that s_S^2 is negligible, but we suspect it is more likely that the factors we included in our analysis are poor indicators of among-stream differences in the mechanisms governing larval recruitment. We present modeling results below for two cases – one where s_S^2 is zero and one for $s_S^2 = s_T^2/2$ (i.e., that half of the observed recruitment variation is due to unexplained stream effects).

Simulation Results

We used the model to simulate lamprey control over 50 years, beginning control in the fourth year of the simulation. We used the predicted average number of parasites in years 35-50 as our measure of performance. We set the treatment costs for each stream and the overall budget such that one stream could be treated each year in the lampricide control scenarios. Under these conditions, and with recruitment variation set to zero, a 90% treatment effectiveness led to a 99% reduction in parasitic lamprey abundance in the lake by year 35 (Table 2, Figure 4a).

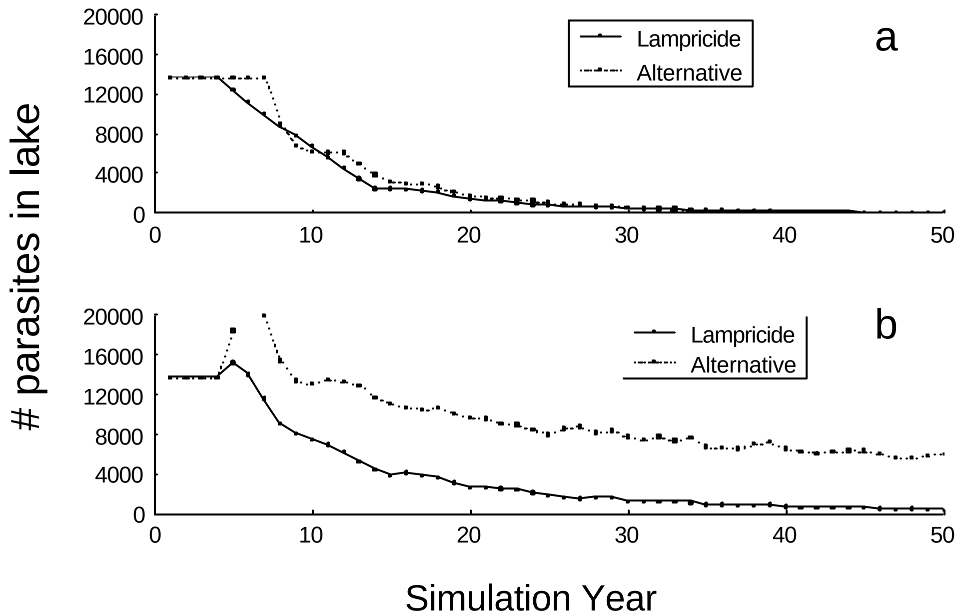

Figure 4. Simulated abundances of parasitic lamprey over 50 years with lampricide (90% reduction, one stream per year) and alternative (67% reduction, all streams each year) control strategies applied. Top panel: recruitment process error variance = 0; Bottom panel: recruitment process error variance = 3.03.

This is an optimistic projection for a real system, and reflects the simplifying assumptions that there are no uncontrollable sources of parasitic lamprey in the lake and that we have perfect knowledge of larval abundance in each stream. In the absence of recruitment variation, an alternative control policy that reduces reproductive success by 67% in all streams, each year, results in a similar outcome (Table 2, Figure 4a).

When recruitment variation is added to the model, the performance of the lampricide option, reported as the average of 100 stochastic simulations, declines very little (97% instead of 99% control – Table 2, Figure 4b). In contrast, the performance of alternative strategy is substantially poorer (68% versus 99% - Table 2, Figure 4b). In addition, the variability in the outcomes for the alternative control strategy is quite large (Table 2, Figure 5) implying a risk of outcomes substantially worse (or better) than the average.

Table 3. Results of simulations showing the effect of adding process uncertainty to the stock-recruitment relationship on the performance of lampricide and alternative control policies.

Policy Description	Process Error Variance	Simulation Results Mean	SD	% Reduction
No control	0	13600	0	0.000
Lampricide (90%, one stream per year)	0	129	0	0.991
Alternative (67%, all streams each year)	0	137	0	0.990
No control	3.03	19750	1834	0.000
Lampricide (90%, one stream per year)	3.03	578	355	0.971
Alternative (67%, all streams each year)	3.03	6275	1617	0.682
No control	1.51	18781	1914	0.000
Lampricide (90%, one stream per year)	1.51	299	151	0.984
Alternative (67%, all streams each year)	1.51	2681	856	0.857

Mean refers to average # parasites in year 35-50
SD refers to standard deviation of same
% Reduction compares policy mean to no control population
100 simulations for each policy with non-zero process error variance

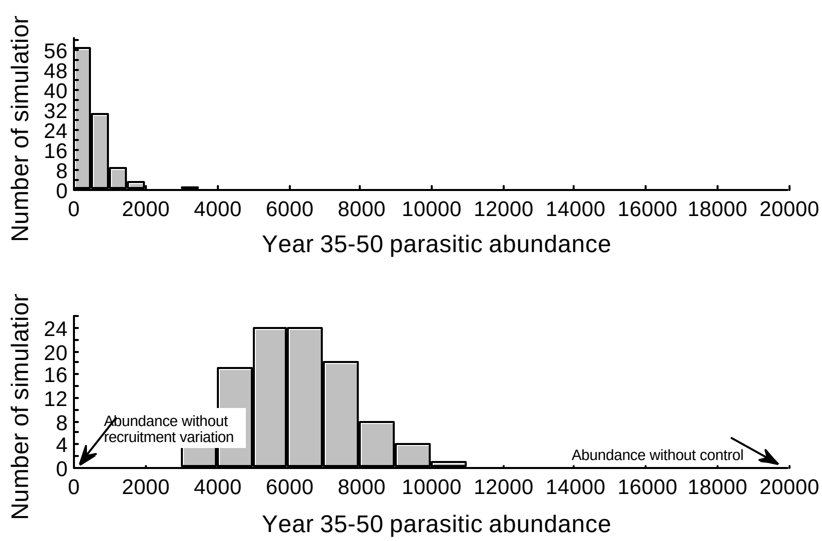

Figure 5. Frequency of simulations with different levels of eventual parasitic abundance (average of years 35-50). The results are for 100 simulations with recruitment process error as the only stochastic component. Top panel: lampricide control (90% reduction, one stream per year); Bottom panel: alternative control (67% reduction, all streams each year).

Reducing the assumed process uncertainty by one half (to remove possible stream effects) yields a much smaller difference between the performance of the alternative control strategy with and without process uncertainty included (86% versus 99% - Table 2). Nevertheless, the alternative control policy results in a parasite population that is nearly 10 times greater than the population resulting from the lampricide policy that compares favorably when process uncertainty is ignored.

Discussion

Our simulation results indicate that the effectiveness of alternative controls may be seriously compromised by density-independent variation in recruitment. The simulation results presented here could represent a lake-wide sterile male release program with two sterile males release for every one non-sterilized male. To compare favorably to lampricide control, alternative controls would have able to achieve much larger reductions in the effective spawning population size at reasonable cost. For example, with the process error variance set at 3.03, a sterile:fertile male ratio of 7.5:1 is necessary to achieve a result comparable to that obtained using a 90% effective lampricide treatment.

This result suggests that controls on reproductive success may be of limited value as a whole-lake alternative to lampricide control. On the other hand, these methods may have an important role to play on individual streams where lampricide treatment is very costly. The St. Marys River is an obvious example, and is currently the primary object of the sterile male release program (Schleen SLIS II). As well, Brege (SLIS II) pointed out that the majority of lampricide treatment expenditures each year are directed to a small number of large rivers. It is possible that considerable savings could be achieved by directing alternative control effort at these rivers, even if the consequence would only be to reduce the frequency of lampricide treatments. This possibility warrants further investigation using modeling tools like the one presented here.

Control strategies that target reproductive success may still prove to be valuable, large-scale alternatives to lampricide control, despite the results we have presented here, for two reasons. First, the development of more effective techniques for trapping adult lampreys, particularly through the use of chemical attractants may make it possible to achieve the large reductions in effective spawners that our simulations suggest will be necessary, at reasonable cost. Second, pressure to use alternatives to lampricide control or low-head barriers to avoid non-target effects may increase to the point where selective trapping or sterile male releases offer the only socially acceptable alternatives. A fair comparison of control options should consider the relative environmental costs of the options as well as their benefits.

Significance to IMSL procedures

The modeling tools that have been developed for use by the Great Lakes Fishery Commission to determine lampricide treatment schedules and evaluate alternative control strategies do not currently incorporate uncertainty. We have shown that density-independent recruitment variation is one source of uncertainty that can be of considerable importance when alternatives are being considered. We recommend that this uncertainty be incorporated into IMSL management tools before they are used for future planning. Other key sources of uncertainty should also be identified and incorporated into these management tools.

Priority areas for further research

Our stock-recruitment analysis relies on a critical assumption that the populations included in the analysis share a common stock-recruitment relationship. This assumption was made necessary by the lack of stock and recruitment time series data for individual streams. Collecting these data simultaneously from many streams was seen as the only practical way to quickly assemble the data sets necessary to test for compensation. We attempted to account for among-stream differences by introducing stream thermal stability and alkalinity as factors affecting stock productivity, but our preliminary results suggest that these factors provide little explanatory power. It seems unlikely that differences among streams are inconsequential, given the wide range of environmental conditions present in Great Lakes streams containing lamprey populations. As a result, we suggest that priority should be given to establishing long term stock-recruitment data sets for a number of Great Lakes streams that provide good contrast in environmental conditions, and where spawner abundance and recruitment can be readily measured.

Several of the streams included in this study could be considered for continued monitoring in this context.

It would also be valuable to better understand the mechanisms that are responsible for density independent recruitment variation. The establishment of streams for long-term monitoring of recruitment will enable us to separate "stream effects" from true interannual variation, but process-level research is needed to understand more about what causes recruitment variation. Knowledge of the relevant mechanisms, might help to determine when and where to apply alternative controls. For example, preliminary results from two Lake Ontario streams included in our study suggest that spawning success may be influenced by the energetic condition of adults when they enter rivers to spawn (Lisa O'Connor, Department of Fisheries and Oceans, Sault Ste. Marie, Ontario, personal communication). If adult body condition results from environmental conditions in the lake where the adults fed as parasites, and poor condition implies reduced recruitment (via reduced spawning success), it might be possible to direct sterile male releases to lakes where adult condition is already expected to be poor, based on surveys of parasitic lamprey.

Our ability to estimate recruitment depends on accurate assignment of ages to ammocoetes collected from our study streams. In this study we used length-frequency data to develop stream-specific age-length keys. In many cases determination of the length cut-off between age 1 and older ammocoetes was very difficult. Assigning ages to older ammocoetes based on length measurements is virtually impossible. Statolith interpretation has been proposed as an alternative to length-based methods (Beamish and Medland 1988), but little has been done to validate the method. Deliberate introductions of single year-classes of lamprey above barriers could be used to create known-age populations of ammocoetes, which could in turn be used to validate statolith-based methods of age assignment. In addition, and because statolith-based assessments are costly, we should examine the potential of methods that combine length data with partial statolith information (e.g., Fournier 1983).

Finally, more theoretical work is needed to determine the limits to the potential of alternative control strategies. The simulation model presented in this synthesis illustrates the kind of tool that could be used. We suggest a strategy in which simple models such as the one presented herein are used first to explore possible management options. Then promising options are applied to more realistic models such as the IMSL tools. These tools could then be used to define management experiments for individual streams or even for whole-lake systems that provide the ultimate test of management strategies. The sea lamprey control program provides unusually rich and promising area for kind of adaptive management approach suggested by this scenario.

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Part 2
Early life history of sea lamprey larvae: emergence, dispersal and effects of density on movement

(Note: this section of our completion report is based on the Masters thesis recently completed by Amy Derosier at Michigan State University (December 2001) – a complete copy of the thesis is available from the authors).

Due to increasing costs of TFM and public concerns about using chemicals in streams, the Great Lakes Fishery Commission wants to reduce the reliance on chemical controls (Strategic Vision of the Great Lakes Fishery Commission, 1992 and 2001). To do this, managers will need to rely more heavily on alternative control methods such as: increased trapping, continued use of barriers, and the sterile male release program. These alternative control methods may not be as effective as chemical control. Chemical controls target the larval stage of sea lamprey, whereas the alternative control methods target reproduction. This difference in targeted life stages may compromise effective alternative control. Chemical controls reduce the population just before the parasitic life stage, while with alternative control methods there are many life stages between when the population is reduced and when they become parasites, allowing time for compensatory mechanisms to play out.

Compensatory mechanisms are density-dependent demographic responses that effectively increase population growth at low densities and decrease population growth at high densities. There is evidence to suggest that compensatory mechanisms exist in sea lamprey populations (Smith, 1971; Purvis, 1979; Heinrich et al., 1980; Morman, 1987; Murdoch et al., 1992), yet the evidence is far from conclusive (Jones et al., in review). To effectively control sea lamprey populations using alternative control methods, managers need to determine at what life stages compensatory mechanisms exist and their magnitude. If sea lamprey populations are not able or only slightly able to compensate, the effectiveness of the alternative control methods may not be compromised. But if compensatory mechanisms are strong, control efforts using alternative methods may not decrease the population sufficiently to justify the decision. To determine the potential effectiveness of these alternative control methods more information is needed on the demographics of sea lamprey particularly during reproduction and larval life stages.

The early life stages of fish are generally thought to heavily influence recruitment (Cushing, 1996; Wootton, 1990). Hjort (1914) proposed that the greatest mortality occurs during the early life of fish and coined this the critical period. Sea lamprey fecundity is estimated to be high, producing between 55,000 and 69,000 eggs per female (Manion and Hanson, 1980). However, typical age-1 and older larval densities are reported to be around 2 per m^2 (Jones et al., in review), suggesting that mortality is high during the first year of life.

Little is known of the first year of life of the sea lamprey (age-0). Sea lamprey at this stage are small (4-20 mm in length, 1-2 mm in width) and hence difficult to sample. The embryological development has been fully described (Piavis, 1961), as have some aspects of the emergence stage. Because of the lack of information on age-0 sea lamprey and the apparent importance of the first year of life in determining recruitment in fish, we chose to explore three aspects of age-0 sea lamprey ecology. We expanded on the description of emergence that was reported by Applegate (1950) and Manion and McLain (1971), by following emergence from 10 nests in each of two streams. We investigated age-0 sea lamprey dispersal or distributions during the first growing season, which has not been done in the past, using field and microsatellite methods. We also examined movements of larvae after settlement in relation to density and temperature/season in the laboratory.

1 Sea lamprey emergence from nests.

Recent authors suggest that the greatest mortality in fishes occurs during transitions (Benoît and Pepin, 1999), such as hatching, emergence, and the shift from endogenous (yolk) to exogenous (active) feeding (Lasker, 1981; Diana, 1995). The timing and pattern of emergence will influence the conditions that larvae experience before and during their first feeding. The timing of emergence also determines the length of the first growing season (Elliott and Hurley, 1998) and thus the size that age-0 fish reach before entering their first winter. Hence, emergence can be a key stage in a fish species' life history and knowledge of this stage may provide insight into processes affecting early larval survival.

Although sea lamprey emergence from nests has been previously investigated, a full description of this stage is lacking. Applegate (1950) followed only 3 nests from fertilization to emergence, and reported the number of larvae emerging each day. Emergence occurred 19 to 20 days after fertilization. Applegate (1950) also provided a histogram of lengths for one nest (222 individuals, average length = 8.54 mm). Manion and McLain (1971) monitored 48 nests but only reported the average (22 days) and the maximum (34 days) number of days it took for prolarvae to emerge. These authors did not describe the duration (Elliott, 1984; Snucins et al., 1992) or the diel pattern (Field-Dodgson, 1988; Kempinger, 1988) of sea lamprey emergence.

The objectives for this component of our study was to: (1) describe emergence relative to spawning activity; (2) examine the diel pattern of emergence; (3) compare the numbers and size (lengths) of prolarvae produced in individual nests and between streams; (4) quantify the duration of the emergence period; and (5) determine if emergence timing can be predicted using cumulative degree days (CDD).

To address these objectives, we conducted a field study, a laboratory experiment, and a secondary analysis of published data. Twenty nests, in the Trout and Black Mallard Rivers (ten in each), were monitored from construction to prolarval emergence. Eggs were raised in the laboratory until prolarvae burrowed into a sand substrate (similar to Piavis, 1960), to test whether prolarvae burrow at the same time as prolarvae emerge from nests. To supplement these two components, data from Applegate (1950) and Piavis (1961) were reanalyzed to calculate degree days.

Results / Discussion

The patterns of emergence for sea lamprey are similar to those of other species (Field-Dodgson, 1988; Johnston, 1997). Emergence occurs predominately during the darkest hours of the night (1200 – 0300 h) and declines sharply after 0300 h (Figure 1). Studies sampling drift or movements of young-of-the-year stream fishes have also reported increased drift around midnight and a decline towards dawn. (Brown and Armstrong, 1985; Bennett and Ross, 1995; Johnston, 1997). The overall duration of the emergence period is short, on average it took 8 to 14 days for 80% of prolarvae to emerge; Applegate (1950) reported duration's of 3 to 4 days. This difference is likely due to water temperature variations.

The numbers of emergent prolarvae varied greatly from nest to nest and stream to stream (Table 1). The Trout River produced 5,569 prolarvae per female seen, on average and the Black Mallard River produced 604 prolarvae per nest, on average. No correlation was evident between the numbers of females present and the numbers of prolarvae produced (Figure 2). Applegate (1950) collected only 222 – 622 prolarvae from individual nests. Manion (1968) dismantled 19 nests before emergence and reported 1,763 to 10,545 prolarvae per nest. He also noted that on average, a single nest (one pair of spawners) produced 3,240 prolarvae and a double nest (two pairs of spawners) produced 7,531 prolarvae. It is possible that the numbers of prolarvae collected in our study are under-estimates because prolarvae may have drifted around the mouth of the drift nets. Although Applegate (1950) constructed enclosed raceways around nests to collect all emerging prolarvae, his numbers may also be under-estimates.

Table 1. Total number of prolarvae collected in each nest for each stream, the total number of prolarvae collected by stream, the mean number of prolarvae collected per nest, and the standard deviation of prolarvae collected per nest.

Nest	Black Mallard River	Trout River
1	87	346
2	267	14,880
3	201	1,316
4	535	12,015
5	1,900	1,044
6	164	14,632
7	109	3,986
8	768	11,093
9	666	3,516
10	1,340	20,713
Total	6,037	83,541
Mean	604	8,354
Std Dev	600	7,190

The raceways may have changed the water flow to the nest and perhaps increased nest mortality. Regardless, the numbers of prolarvae produced in nests and streams varied greatly, but can be large. Variations in nesting success may in part explain the large amount of density independent variation in recruitment success observed by Jones et al. (in review).

In addition to producing more prolarvae, the Trout River prolarvae are on average larger (8.65 mm, range 4.69 – 12.80 mm) than those in the Black Mallard River (7.96 mm, range 4.86 – 12.45 mm) (Figure 3) and they emerged later (Trout River: 370 CDD; Black Mallard: 290 CDD) (Table 2). Water temperatures between the two streams are relatively similar and hence this seems unlikely to be the reason for these differences.

Table 2. Mean cumulative degree days (± standard deviation) and days (range) from fertilization to the beginning, peak, and end of prolarval emergence (or burrowing) for all study components.

		Field Studies			**Laboratory Studies**	
		Black Mallard River	**Trout River**	**Applegate's Data**	**Laboratory Exp.**	**Piavis's Lab Exp.**
CDD	Start	254 ± 24	318 ± 37	--	--	--
	Peak	290 ± 17	370 ± 47	303 ± 3	267 ± 12	248 ± 41
	End	338 ± 28	432 ± 53	--	--	--
Days	Start	23 (18-26)	22 (18-25)			
	Peak	26 (23-28)	31 (26-39)	20 (19-20)	24 (22-28)	22 (17-33)
	End	29 (23-35)	36 (28-41)			

The size of a female will influence the size of the offspring produced (Benoit and Pepin, 1999; Kamler, 1992; Elliott and Hurley, 1998) and their survival (Diana, 1995). There were more adults in the Trout River possibly allowing only the larger females to spawn and hence providing a higher survival to the Trout River eggs and prolarvae. Larger eggs tend to have longer developmental periods in fishes (Ware, 1975; Economou, 1991). Furthermore, the rate of yolk absorption tends to be high in small eggs and lower in larger eggs (Kamler, 1992). Consequently, prolarvae in the Black Mallard River perhaps absorbed their yolk and had to emerge earlier to begin exogenous feeding. In contrast, the Trout River prolarvae possibly had more yolk reserves due to larger eggs and hence had higher survival and a longer development time. This variation in recruitment of emerging prolarvae suggests that knowledge about the linkage between the condition of parents (O'connor and Kelso, in review) and egg size to the timing of emergence may provide more insight into larval recruitment.

With the addition of the secondary analysis, our evidence suggests that cumulative degree days to emergence are greater in the field than in the laboratory (Table 2, Figure 4). The Black Mallard and Trout River's cumulative degree days to emergence were higher than in our laboratory study and Piavis' study (1961). It took more degree days to reach peak emergence in the field, when temperature fluctuated, than in the laboratory, when it was held constant. Traditionally, emergence is estimated to occur about 22 days after fertilization (Piavis, 1961). Yet in the field emergence began 18 to 26 days, peaked 23 to 39 days, and ended 23 to 41 days after fertilization (Table 2), suggesting that laboratory results are generally under-estimates of what is happening in the field.

The results presented herein could be used to estimate the optimal timing for TFM treatments. While in the nests, eggs and prolarvae are less vulnerable to TFM. If managers want to target an additional year-class it may be wise to wait to treat until 36 days or at least 400 CDD after the spawning period. For some costly-to-treat streams, it would be useful and more cost effective to know when the majority of prolarvae have emerged so that an extra year-class can be targeted, thereby increasing the time interval between costly treatments. Unfortunately, to apply these results knowledge of the timing of spawning is needed; spawning surveys are uncommon on lamprey producing streams. On the other hand, many rivers have adult traps on them, and if the relationship between the numbers of adults collected in traps and the timing of spawning were available, this emergence work could be used more broadly to better target optimal treatment times.

2 Dispersal of age-0 sea lamprey during their first growing season

Dispersal of larval fish away from spawning habitat seems likely to be a critical process in determining the habitat conditions and level of intra-specific competition (Howard, 1960) experienced by young-of-the-year (age-0) fish and thus their survival rates. Densities are generally at a maximum at this stage and fish are at their smallest and most vulnerable size. If dispersal is passive, age-0 fish may be found in sub-optimal habitats and may clump together (Robinson et al., 1998). If dispersal is active, individuals may become more evenly spaced (Robinson et al., 1998) or may continue dispersing to find optimal habitats. Competition may be a driving factor in determining recruitment if dispersal is limited. Yet, physical transport processes may be more important if dispersal is wide or unlimited (Economou, 1991). Of course a combination of these may be more likely. However, as dispersal distances increase so does the risk of not finding suitable habitat (Economou, 1991), becoming prey, and depleting energy reserves (Kamler, 1992). Understanding the extent to which fish disperse can provide valuable insight into recruitment processes.

Densities of age-0 ammocoetes have also not been documented, despite routine stream assessments by the Sea Lamprey Control Program. Because of their small size, age-0 ammocoetes are not collected or reported. Our emergence work showed that recruitment was variable but could be very high. The potential for large numbers of prolarvae to emerge over a concentrated period of time suggests that high densities could be prevalent if dispersal is limited and habitat is limited. This overcrowding could potentially affect their feeding rates (Yap and Bowen, in review), growth rates (shown in age 1+: Morman, 1987; Murdoch et al., 1992; Weise and Pajos, 1998), and movements, and hence survival.

Because age-0 sea lampreys are not often sampled, methods and sampling designs are not documented. We expected age-0 ammocoetes to be difficult to find and clumped when found. Adaptive sampling is an innovative approach to compensate for the potentially inefficient sampling of rare and clustered populations (Thompson, 1992; Thompson and Seber, 1996). Adaptive sampling allows for the flexibility to increase sampling intensity in areas that have the object of interest, in this case age-0 ammocoetes.

The objectives for this study component were to: (1) document densities of age-0 ammocoetes; (2) determine if age-0 ammocoetes cluster close to nests of origin or if they disperse widely; (3) look for evidence in the field of density affects on growth of age-0 ammocoetes; and (4) determine the efficiency of adaptive sampling for estimating densities of age-0 ammocoetes.

Study design

To address these objectives, we needed to be able to associate ammocoetes collected in the stream with a specific source nest. This could be accomplished by restricting nests to a few widely separated locations or by marking prolarvae to uniquely identify their nest of origin. We tried to restrict spawning areas by installing cages in streams and introducing adults into them. However, this was unsuccessful – adults escaped and no nesting occurred within these cages. Tagging prolarvae is not practical because of their size (4.5 – 12 mm). Therefore, we chose to introduce small numbers of adults above barriers in two streams which otherwise were not accessible to sea lamprey. We then identified two nests in each stream that were isolated and conducted surveys to estimate age-0 densities at a range of distances downstream of nests. We collected samples on three occasions from July to October, approximately every three weeks. To further enhance our ability to associate ammocoetes with source nests we also collected DNA samples from adults and larvae and used microsatellite methods to assign larvae to parents and determine siblings.

Downstream from each nest three sampling zones were created. The first sampling zone was considered near the nest and started at the nest and extended downstream 50 m. The next zone extended from 55 to 155 m downstream of a nest and was called the middle zone. The third zone included habitats between 160 m and 310 m downstream from the nest, and was called the far zone. A 5 m buffer between each zone was not sampled. Catches of ammocoetes were compared between zones to determine dispersal. If ammocoetes were principally collected in the near zone then they were considered to be limited dispersers. If ammocoetes were commonly found in the far zone, they were considered widely dispersed.

We used a backpack gold-mining dredge (Keene Equipment, CO) to sample 25 x 25 cm^2 patches of type 1 (fine, depositional sediments) habitat to collect age-0 ammocoetes. Initially six random plots were sampled. Following the adaptive sampling approach, if an age-0 ammocoetes was collected in a random plot, additional neighborhood plots were sampled. The neighborhood samples in this study consisted of one additional plot upstream and downstream of the random plot. During the first sampling event, neighborhood plots were sampled until no age-0 ammocoetes were collected; hence the number of neighborhood plots could consist of more than two additional plots. This was changed to only one neighborhood plot upstream and downstream during the second and third sampling event because of time constraints.

Results / Discussion

Fine-scale densities of age-0 ammocoetes can be very high (384 / m^2), although average densities were low, 4 and 10 ammocoetes per m^2 in Ogemaw Creek and the Carp River, respectively. Age-0 ammocoetes were relatively rare, they were found in only 74 of the 313 plots that were sampled in both streams (Figure 5). Densities reported here are not much higher than those seen for older ammocoetes. Other authors report densities of age-1 and older ammocoetes in the field between 0 and 10 per m^2 (Manion and McLain, 1971, Jones et al., in review), most yearling densities range between 0 and 2 per m^2 (Jones et al., in review). Given the large numbers of ammocoetes expected to emerge from nests (range 87 – 20,713 prolarvae per nest, as reported in the emergence component) and the relatively small amount of habitat, we expected high densities to be prevalent. Yet these results suggest that age-0 ammocoetes are generally found in low densities. Due to the study design used, i.e. introducing low numbers of spawning adults, the densities reported here may be lower than in naturally occurring populations however.

We estimated the overall abundance of age-0 ammocoetes by multiplying the average density below nests by the amount of larval habitat (type 1 = fine, depositional sediments). In Ogemaw Creek, estimated abundance's are relatively low (Table 3). This could be due to low nesting success as seen in the Black Mallard River in the emergence component, or it could be due to early mortality of recently emerged larvae, wide dispersal, gear efficiency, or a combination of all four. Abundance estimates in the Carp River (Table 3) are relatively high during the first two sampling events and suggest high nesting success as was seen in the Trout River in the emergence component. However, by the last sampling event, the abundance estimate drops sharply suggesting either mortality later in the season or continuing dispersal.

Table 3. Estimated abundance of age-0 ammocoetes in each stream reach below nests for each sample event.

Stream	Nest	Event 1	Event 2	Event 3
Ogemaw Creek	1	106	318	265
	2	466	689	813
Carp River	1	4,166	3,986	772
	2	643	3,517	105

Both the field and microsatellite data suggest that age-0 ammocoetes do not clump near nests but disperse widely. There were no significant differences in age-0 ammocoete densities between zones or between sample events (Two-way ANOVA: Zones – $F_{2,27}$=0.47, p=0.63; Event – $F_{2,27}$=1.66, p=0.21; interaction – $F_{4,27}$=0.45, p=0.77) (Figure 6 and 7). By the second sampling event siblings were 820 m apart and by the third sampling event 874 m apart. This is a minimum estimate of dispersal distance because our study area only extended 974 m downstream of the upstream nest. However, these distances are based on low confidences (30 out of 42 larvae have been assigned to parents with less than 60% confidence using six loci: SLGA210F / Kim210R, FGT3, Spl120, SLGA38F / 3SLGA38R, GISE5, GISB15) of parental assignment and must be interpreted cautiously. Manion and McLain (1971) suggested that age-0 ammocoetes initially remained close to spawning areas and then generally scattered. In their study, adults were introduced into stream reaches that were separated by either falls or installed dams. The most downstream reach did not receive any adults. Ammocoetes were not found in the most downstream reach until the next spring. The reach above the most downstream reach was 1.3 km long, suggesting that ammocoetes dispersed less than that during their first growing season. Hardisty (1961) suggested that age-0 ammocoetes are dependent on heavy rains to help them disperse; however we do not believe this to be the case and present evidence in the movement and density experiments component that ammocoetes disperse readily early in the first growing season.

Ogemaw Creek ammocoetes were larger than those in the Carp River and also grew more between sampling events. In Ogemaw Creek the average length of ammocoetes during the second sampling event was 12.69 mm and 17.21 mm in the third sampling event (sample event 1 was not recorded). In the Carp River, ammocoetes averaged 11.40, 13.54, and 15.59 mm in length during the first, second, and third sampling event, respectively. There were significant length differences between streams during the second sampling event ($F_{1,96}$=7.04, p<0.05) but not during the last sampling event ($F_{1,21}$=3.32, p=0.08); however only 5 ammocoetes were collected in the Carp River at this time. The Carp River had much higher densities than were found in Ogemaw Creek. The scatter plot of length by density (Figure 8) does show a slight downward trend as densities increase in the Carp River. Increasing density affects growth rates of older ammocoetes (Murdoch et al., 1992; Mallatt, 1983; Morman, 1987) over longer periods of time. However, these differences in our study streams are just as likely due to cooler water temperatures in the Carp River and a shorter growing season because of its more northerly location.

The catch data do not follow a Poisson distribution (χ^2 = 181.86, df=2, p<0.05), suggesting that age-0 ammocoetes are not distributed randomly but are aggregated. Yet the adaptive cluster sampling design did not decrease the variance of the density estimates more so than a simple random design. Efficiency values are calculated as the ratio of the adaptive cluster sample (acs) variance and the simple random sample (srs) variance. These values ranged from 0.29 to 10.03 (Table 4) however most were 1 or greater; those values < 1 indicate that the acs design was more efficient. This inefficiency of the adaptive design is likely due to age-0 ammocoetes not aggregating to the extent expected. They were not found in high concentrations; in Ogemaw Creek the maximum number collected in a plot was five and in the Carp River, a maximum of 23 were collected in a plot. Therefore, a simple random sampling design is sufficient for estimating densities of age-0 ammocoetes. However, one advantage to the adaptive cluster design is the increased number of animals collected (Thompson, 1992). The neighborhood samples in the Carp River had a higher catch per unit effort (0 – 3.12) than did the random sample plots (0.12 – 0.95); in Ogemaw Creek the catch per unit efforts between the neighborhood and random plots were essentially the same. Hence, if individuals are needed for other parameters of interest, this design can be very effective.

Table 4. Efficiency values for Ogemaw Creek and the Carp River by zone and sampling event.

		Event 1			Event 2			Event 3		
Stream	Nest	A	B	C	A	B	C	A	B	C
Ogemaw	1	--	--	1.00	1.00	--	1.00	1.00	0.56	--
	2	1.00	1.00	1.00	0.63	--	1.00	1.00	0.29	1.00
Carp	1	1.00	0.33	0.38	10.03	0.91	1.00	1.00	--	1.00
	2	1.00	--	4.00	4.00	1.00	0.93	--	--	1.00

The dredge was an effective device to sample the early age-0 ammocoetes and generally did not kill them. However, processing the dredge material was time consuming and the technique is fairly destructive to the habitat. For these reasons, we do not suggest using this method as a sole means for sampling age-0 ammocoetes. Age-0 ammocoetes are susceptible to the traditional AbP-2 electrofishing method by late summer (mid to late August). With fine mesh paddles, electrofishing is a relatively effective way of sampling these small fish. Hence, we suggest using the dredge method to capture the early age-0 ammocoetes for intense research activities and the AbP-2 electrofisher for routine assessments.

3 The effects of density on the movements of sea lamprey larvae in the laboratory

The relation between growth and density of sea lamprey ammocoetes is density dependent in aquaria and cages (Mallatt, 1983; Morman, 1987; Murdoch et al., 1992). However, field observations are inconclusive as to the presence or degree of density effects on growth (Jones et al., 2001). These contrary conclusions may be due to the limitations of the enclosure experiments, as they do not allow for dispersal. Dispersal may be an important mechanism in lessening the demographic effects of density. To date, no studies have investigated ammocoete dispersal and its relationship to density.

We examined the following questions: 1) do ammocoetes move / disperse at any density; 2) does density of ammocoetes affect their likelihood of moving; and 3) are there seasonal differences in movement. We conducted trials using age-1 and older ammocoetes (age 1+) but concentrated on age-0 ammocoetes. Densities are highest during the first year of life and hence may be subjected to greater density effects than later stages. In addition, this early life stage often determines population size in fishes (Trippel and Chambers, 1997).

Experimental Design

Dispersal may be hard to discern from mortality (Le Cren, 1973). Studies in natural systems often can only report the difference in numbers of animals from one time period to the next and generally label this as mortality. Tagging methods can be used to monitor dispersal in the field, however age-0 ammocoetes are too small to use these techniques. In laboratory aquarium experiments, only mortality can be assessed due to the constrained environment.

Therefore, an experimental design was required to monitor movements of individual animals or small groups of animals and to be able to manipulate densities. Because of the difficulties of conducting this in the field, we designed a laboratory study (adapted from Fonseca and Hart, 1996) that:

1. allowed for movement of ammocoetes,
2. simulated natural stream conditions,
3. and allowed easy monitoring of movement by creating source areas with ammocoetes and unoccupied sink areas.

Ammocoetes were placed in replicate artificial streams at three randomly assigned densities: 5, 15, and 30 per experimental unit, equivalent to 80, 240, and 480 ammocoetes per m^2 respectively. The two lower densities are similar to those used in previously published growth and density studies (Mallatt, 1983; Morman, 1987; Murdoch et al., 1992). We conducted thirty replicates for each density of age-0 ammocoetes between August and September 2000. These two time periods were chosen to examine summer and fall seasonal effects. Fifteen replicates were completed for each density of age-1+ ammocoetes from July to September. Fewer trials using age-1+ ammocoetes were conducted because of the emphasis on age-0 ammocoetes, and hence seasonal effects were not tested.

Results / Discussion

Approximately a quarter (20 - 25 %) of ammocoetes moved out of the source tray in July and August, regardless of density (Kruskil-Wallis: age-0: $p>0.8$, $n=33$; age-1+:

p>0/9, n=45). The average percent of age-0 ammocoetes that moved out of the source tray (±SE) was 27.3 ± 7.8 % in the low-density trials, 20.6 ± 4.8 % in the medium-density trials, and 26.4 ± 5.4 % in the high-density trials (Figure 9). These results suggest that density-independent dispersal predominates when temperatures are warm, regardless of age. Other fishes also have high drift or movement rates soon after emergence (Atlantic salmon, white sucker, and sea lamprey: Johnston, 1997; multiple species: Copp and Cellot, 1988; Brown and Armstrong, 1985). These results suggest a possible mechanism for the wide dispersal observed in the dispersal component of our study. The dispersal process may assist in moving ammocoetes away from nests to discourage clumping.

Our data suggest that dispersal differs with water temperatures and possibly season. The average percent of age-0 ammocoetes that moved out of the source tray (±SE) in September was 4.2 ± 1.9 % in low-density trials, 6.3 ± 2.5 % in medium-density trials, and 10.7 ± 2.6 % in high-density trials. Movements were lower in cooler temperatures (Figure 10) and were significantly different between densities (age-0: p=0.03, n=57) (Figure 9). Because temperature and lighting were not controlled in the experiments, temperature is presumed to be an indicator for seasonal changes, although other factors, such as day length and barometric pressure, may confound these results. Kerans et al. (2000) found that the caddisfly larvae *Hydropsyche slossonae* (fifth instar) exhibited density-independent dispersal in the fall, and density-dependent dispersal in the spring. This caddisfly pupates in late spring and being heaviest at this time do not disperse as frequently. Age-0 ammocoetes showed the opposite pattern in that, dispersal seemed to be controlled by density-independent processes in warm temperatures (e.g. summer) and density-dependent processes in cooler temperatures (e.g. fall). Observations of age-1+ ammocoetes in warm temperatures were similar. Similar to *H. slossonae*, ammocoete movements were greater when density-independent dispersal predominated. Life cycle characteristics may also explain ammocoetes tendency for density-dependent dispersal in cooler temperatures (e.g. September).

Early winter is suggested to be a critical time for fish as they seek to build up energy reserves to assist in overwinter survival at a time when food supply is limited. Yap and Bowen (2001, in review) reported that the northern brook lampreys available food and assimilation efficiency declined from May through August, but increased briefly in September. Cunjak (1988) examined brown and brook trout energy stores over winter and found that in early winter (November – December), both lipid and serum protein levels decreased rapidly, even though food supply was sufficient. Gardiner and Geddes (1980) reported similar results in Atlantic salmon from October to December. The amount of fat or energy stored in tissues before the early winter period may determine the overwinter survival of fish. These observations suggest that when food is more limiting, ammocoete dispersal may be more sensitive to density.

Body size is a major factor in determining overwinter survival, especially for young-of-the-year fish because they are at their smallest size (Shuter and Post, 1990). Because sea lampreys hatch in mid- to late-summer and grow relatively slowly, the fall may be a crucial time for ammocoetes to feed. As previously mentioned, growth is affected by density when ammocoetes (age-1+) are confined to tanks or cages (Mallatt, 1983; Morman, 1987; Murdoch et al., 1992). Mallett (1983) found that even at high food concentrations, increasing density inhibited ammocoete growth, and suggested that ammocoetes might release “some growth-inhibiting compound into the surrounding sediments”. The density-related-dispersal behavior shown in our experiments may increase or enhance survival by allowing ammocoetes to more efficiently feed before winter by finding lower densities of ammocoetes. Such dispersal may also provide decreased interactions between ammocoetes during winter; these interactions could increase activity levels and consequently deplete energy reserves faster, as shown in pumpkinseeds (Bernard and Fox, 1997).

The average densities of age-0 ammocoetes reported in the dispersal component (5 to 10 per m^2) are low compared to the low density used in these experiments (80 per m^2). Densities were reported as high as 384 per m^2 (dispersal component), but infrequently. It is possible that the process of density-independent dispersal early in the season and ammocoetes ability to disperse widely, allow individuals to establish low densities such that density-dependent dispersal is not very prevalent. The densities reported in the dispersal component from streams where the spawning population size was kept very low may be much lower than is seen in streams open to adult migrations, however.

Of the ammocoetes that moved, 83.1% were not found in any sink tray during the August trials and were assumed to have been lost down the drain. In September, only 30.1% of ammocoetes that moved were not found. In the low density trials, ammocoetes were found only in the first sink tray. Whereas, in the medium and high density trials, ammocoetes were found in all sink trays but in decreasing numbers with increasing distance away from the source tray (Table 5). Although this was the trend, the numbers of ammocoetes found in sink trays were not significantly different from each other within each density treatment (August: $p>0.3$, $n=99$; September: $p>0.3$, $n=171$).

A limitation of our experiments is the use of sub-optimal habitat (sand) in the source and sink trays. It is possible that larvae may be able to withstand higher densities in more optimal habitats (type 1 = fine, depositional sediments). However, because of the short time period (1 night) over which we saw ammocoete movement and Mallett's (1983) observations of decreased growth even with high food concentrations, it seems unlikely that more optimal habitat would have had any major effect to change these results.

Table 5. Number of age-0 ammocoetes that moved out of source trays and where they settled for each density and month.

Month	Density	Number of trials	Total individuals used	Number moved	Destination			
					Sink tray 1	Sink tray 2	Sink tray 3	Missing
August	Low	11	55	15	1	0	0	14
	Medium	11	165	34	3	0	2	29
	High	11	330	87	7	5	5	70
September	Low	19	95	4	1	0	0	3
	Medium	19	285	18	5	3	3	7
	High	19	570	61	18	16	12	15
Summary (August + September)	Low	30	150	19	2	0	0	17
	Medium	30	450	52	8	3	5	36
	High	30	900	148	25	21	17	85

The results of this study suggest that the ability to gain body mass, and possibly the accumulation of lipids, as water temperatures decline may be an important factor in overwinter survival. We propose that larvae move more at high densities because they do not grow freely, and furthermore suggest that this growth and hence accumulation of fats, i.e. lipids, determines survival. If proven, percent lipids in age-0 ammocoetes in the fall could provide a key variable in determining recruitment for that year-class. Further work is needed to test this hypothesis.

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Figures

Figure 1. Box plot of the percent of emergent prolarvae collected during set 1 (2100-2400 h), set 2 (2400-0300 h), and set 3 (after 0300 h). The whiskers show the minimum and maximum values, the box depicts the 25 and 75 % quartiles, and the dash the median.

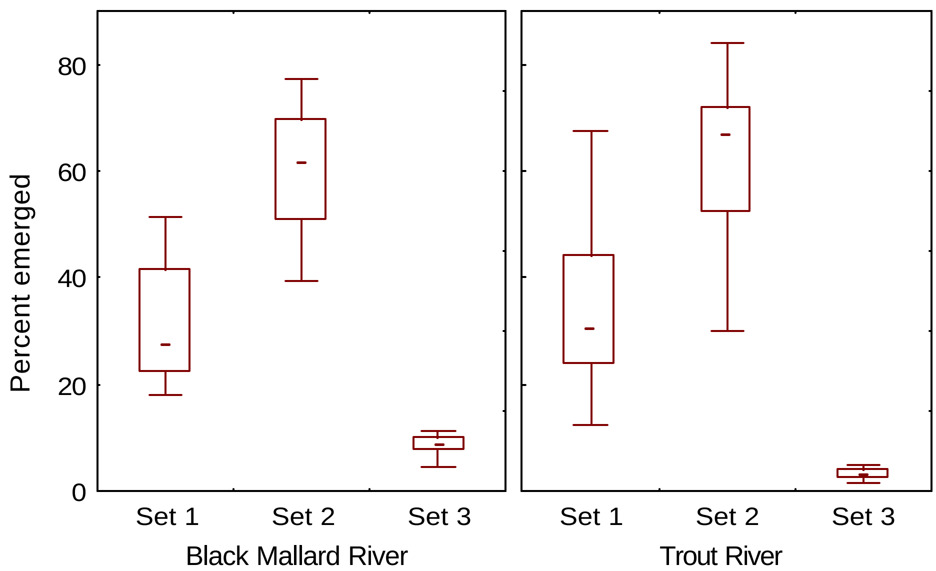


Figure 2. Scatterplot of the number of prolarvae produced vs. the number of spawners seen on nests in the Trout River, no spawners were seen on nests in the Black Mallard River.

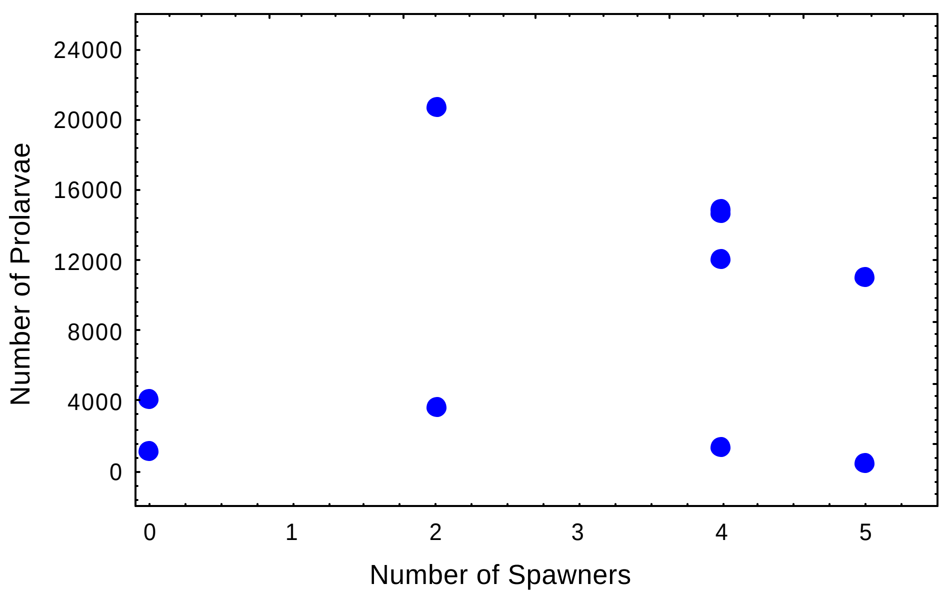
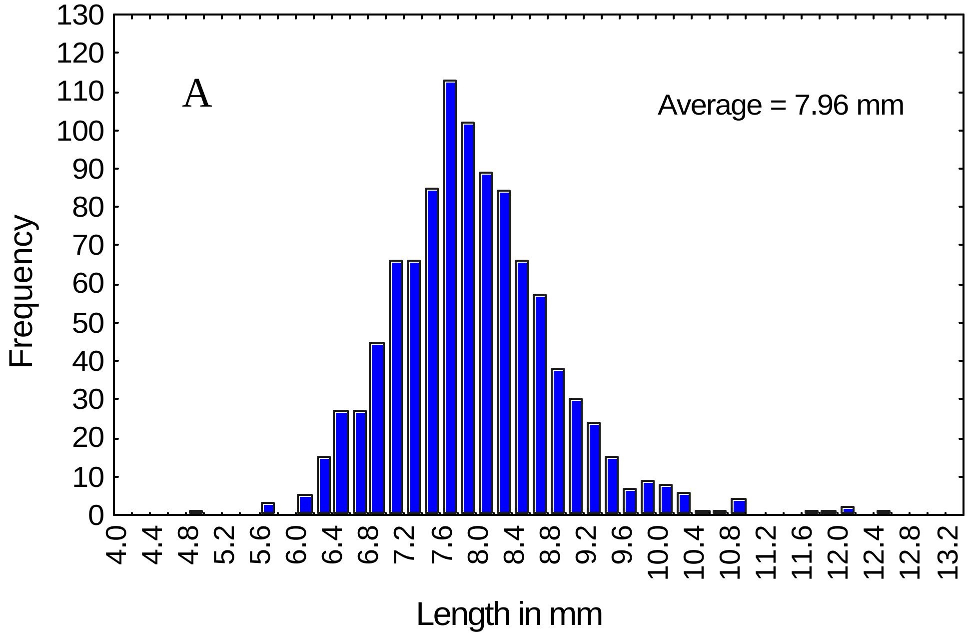


Figure 3. Distribution of lengths for emerging prolarvae for each stream, the Black Mallard River (A) and the Trout River (B).



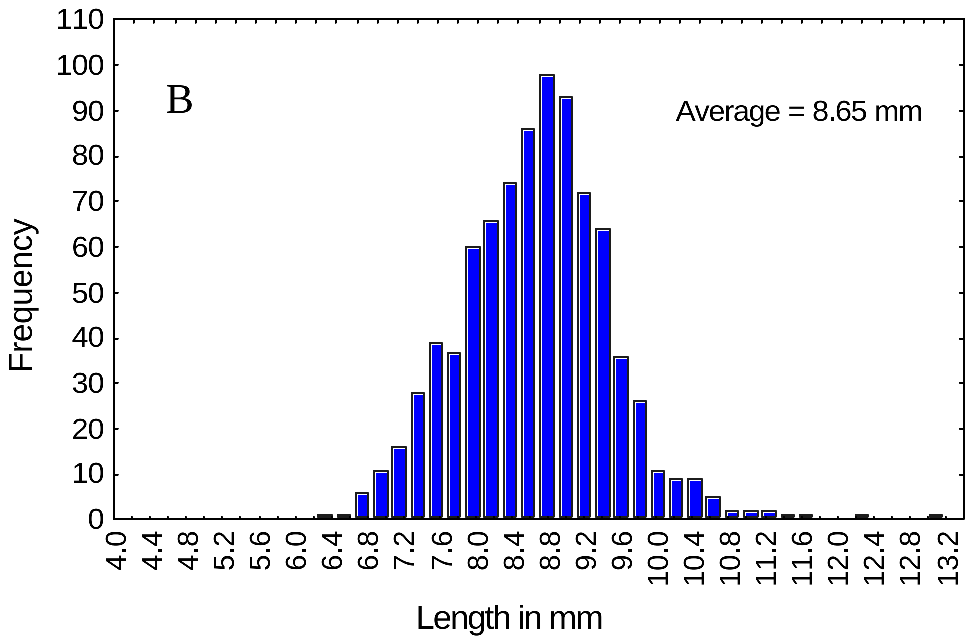


Figure 4. Boxplot of cumulative degree days for the peak of prolarval emergence for each study component, the line is the mean, the box represents the standard deviation, and the whiskers are the minimum and maximum values.

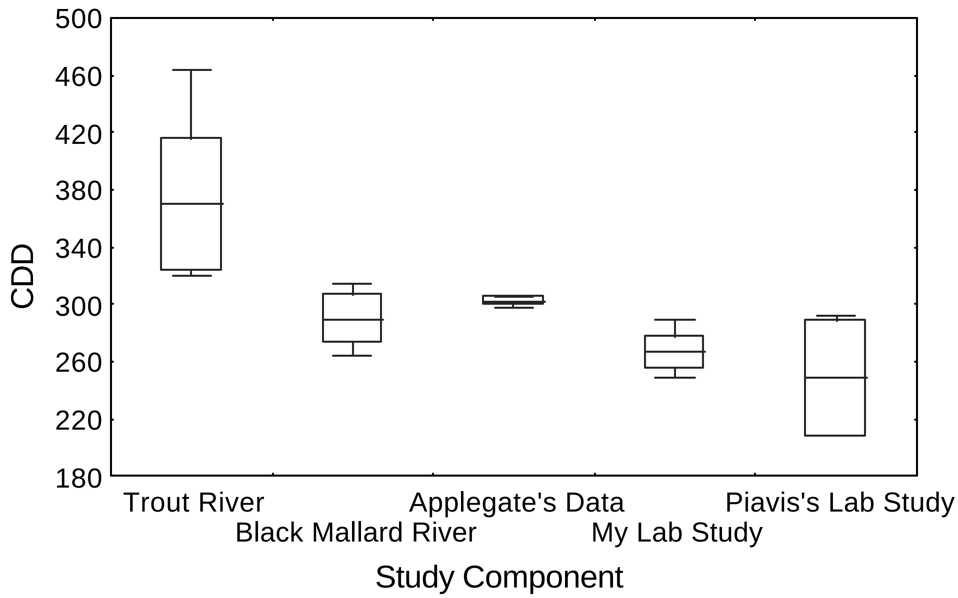
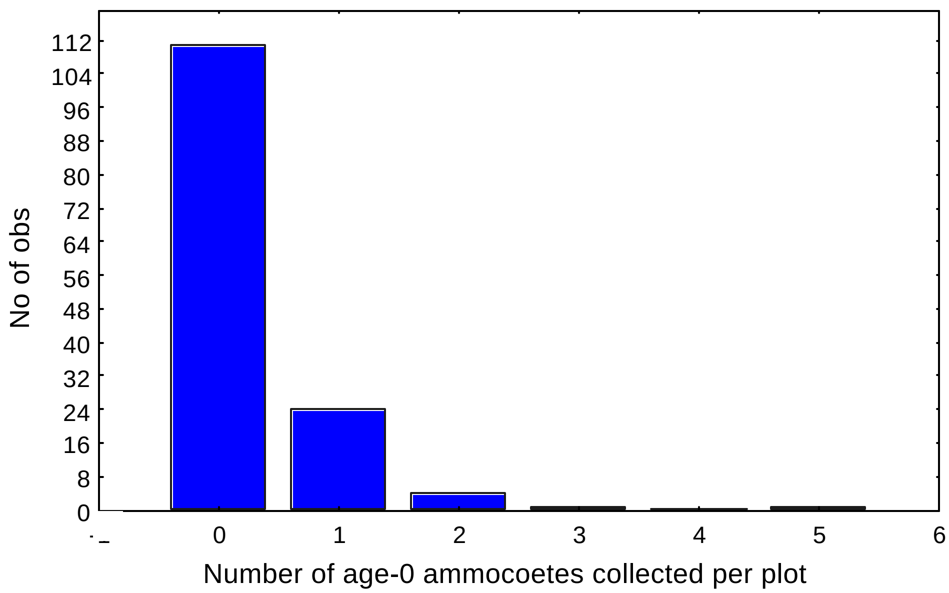


Figure 5. Histograms of the number of age-0 ammocoetes collected per plot in Ogemaw Creek (A) and the Carp River (B).

A.



B.

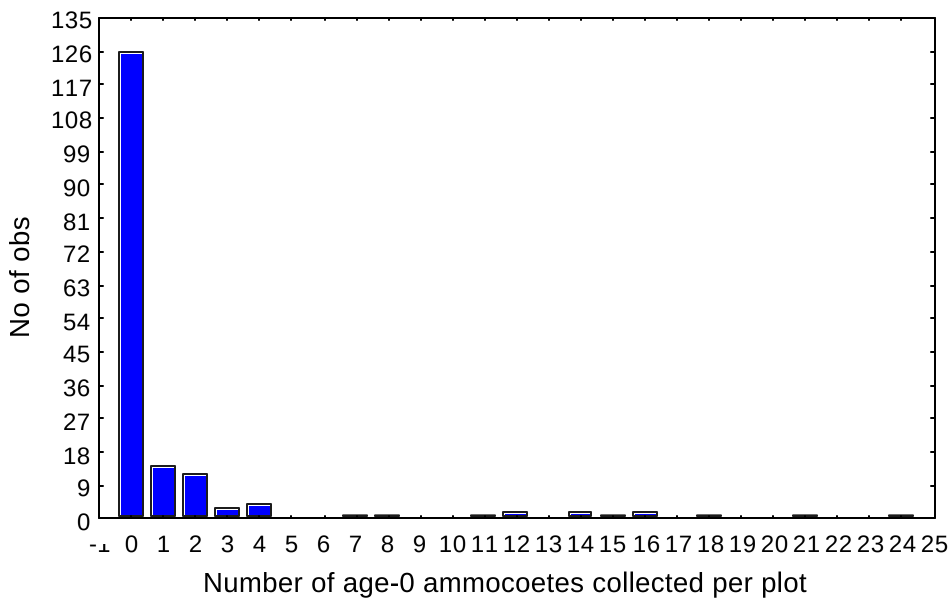


Figure 6. Box plots of the mean densities of age-0 ammocoetes per m^2 by zone for Ogemaw Creek (white boxes) and the Carp River (shaded boxes). The box represents the 25^{th} and 75^{th} quartile, the line the mediam and the whiskers the minmum and maximum.

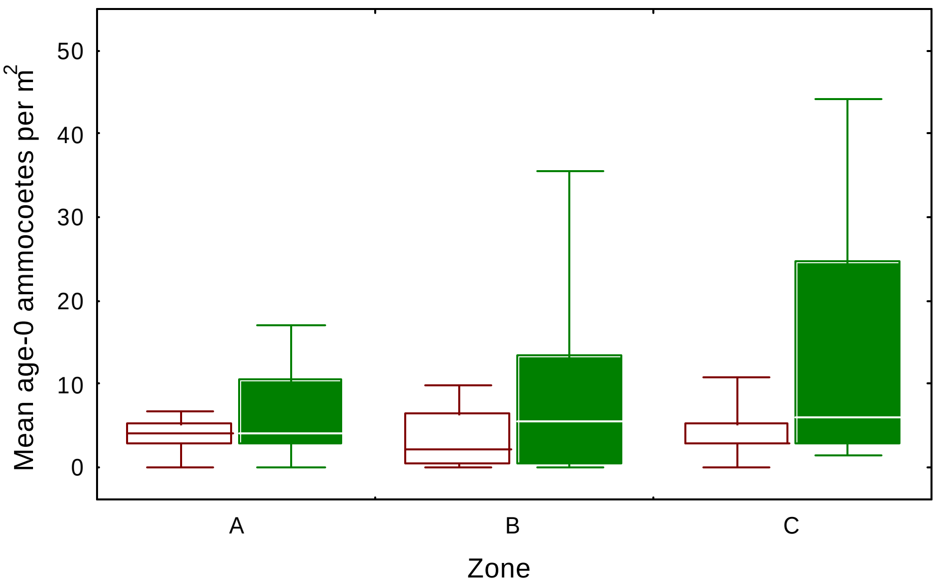


Figure 7. Box plots of the mean densities of age-0 ammocoetes per m^2 by sample event for Ogemaw Creek (white boxes) and the Carp River (shaded boxes). The box represents the 25^{th} and 75^{th} quartile, the line the mediam and the whiskers the minmum and maximum.

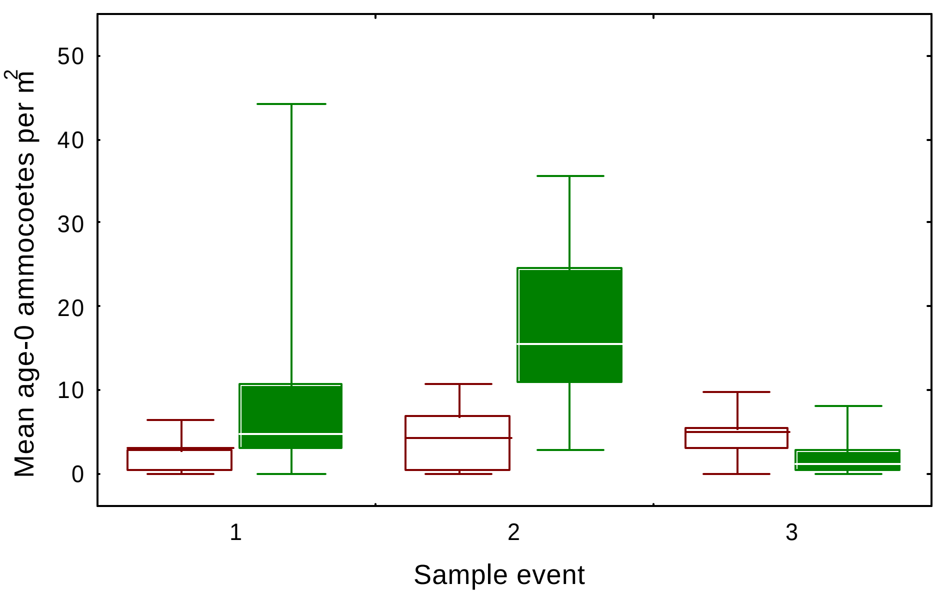
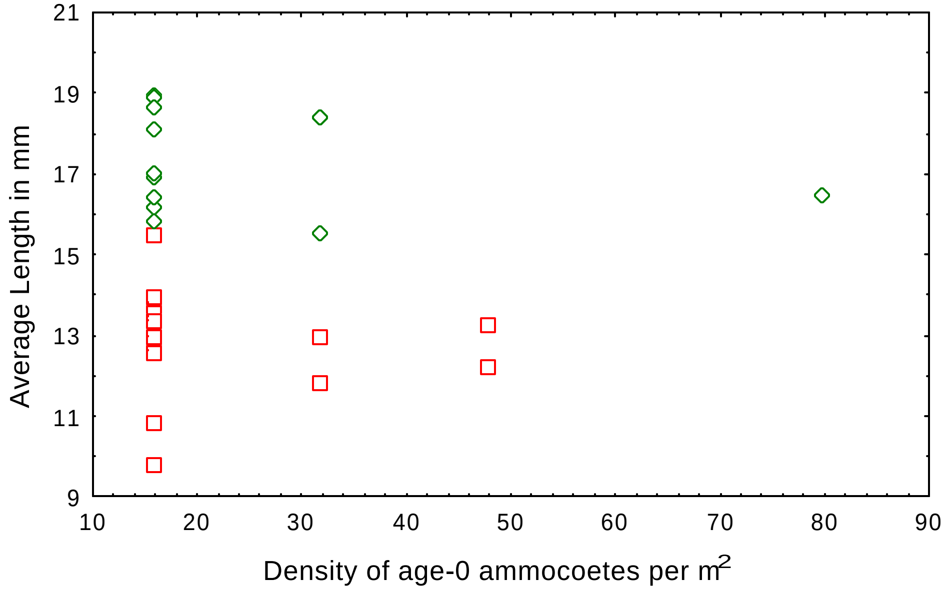


Figure 8. Scatterplot of average age-0 ammocoete lengths in mm in relation to the density of the habitat patch in Ogemaw Creek (A) and the Carp River (B). The circles represent ammocoetes during the first sampling event, the squares the second sampling event, and the diamonds the third sampling event.

A.



B.

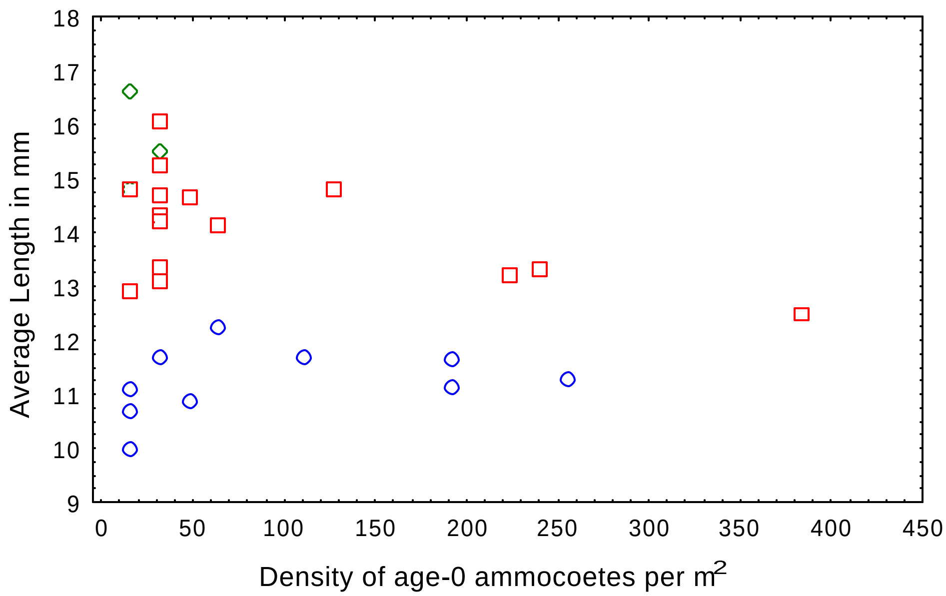


Figure 9. Average percent of age-0 ammocoetes that moved out of the source tray in August (n=11) and September (n=19) for each density. Error bars represent ± 1 standard error.

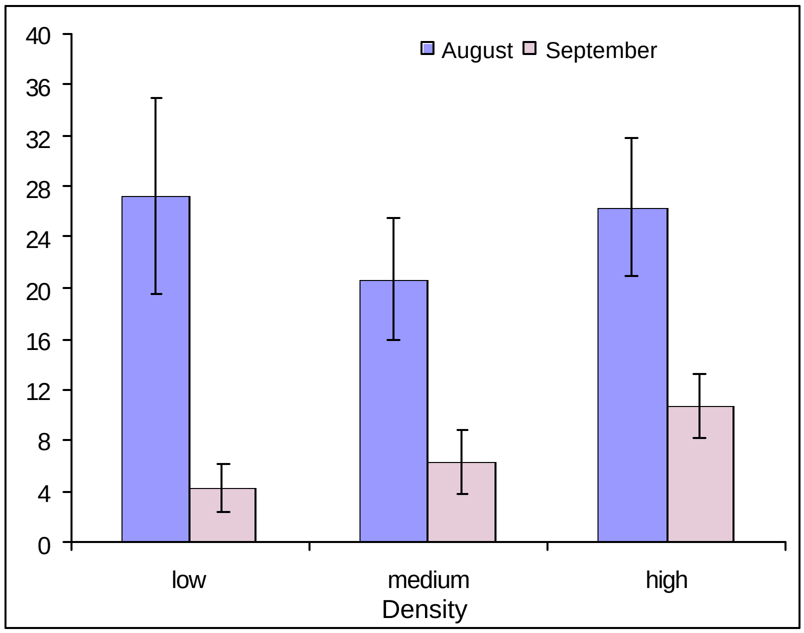
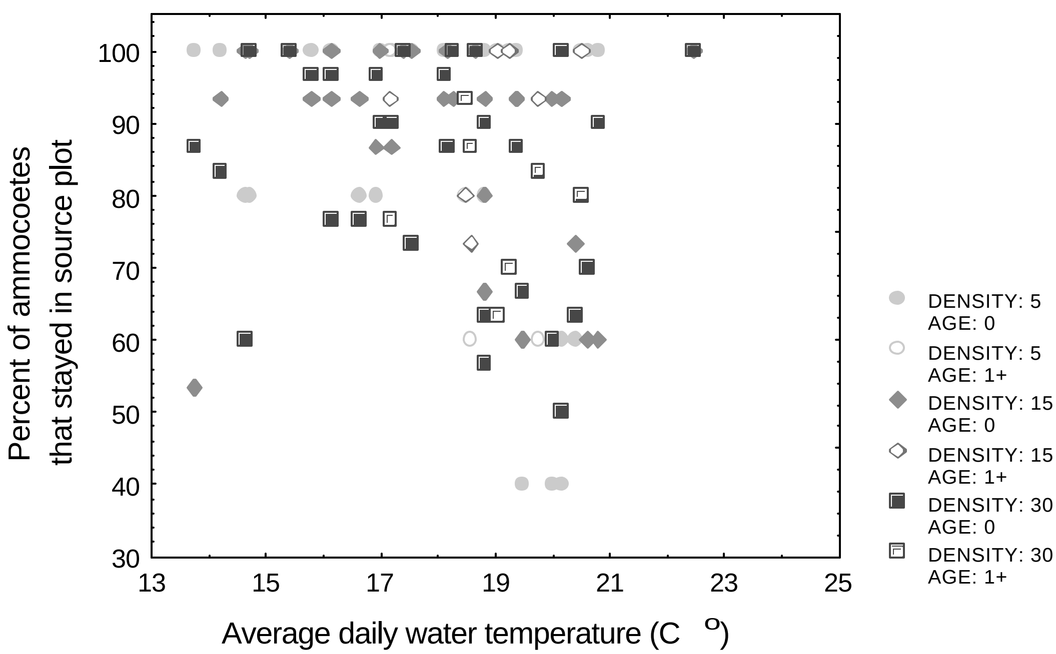


Figure 10. Percent of ammocoetes that did not move out of source tray versus average daily water temperature for all densities and ages.



Compensatory Mechanisms in Great Lakes Sea Lamprey Populations:

An Integrated Program of Research and Assessment

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Completion Report for the Sea Lamprey Compensatory Mechanisms Project

The Streams

Grafton Creek (also called Barnum House Creek), approximately 12 km east of Cobourg, Ontario, had a Sea Lamprey Control Centre (SLCC) low-head barrier installed in 1987 and was last treated with 3-triflouromethyl-4-nitrophenol (TFM) above the barrier in May, 1988. Since this time, there have been no recorded incidents of sea lamprey passage over the barrier. Grafton Creek is divided into two sections: a lower section of approximately 4.5 km from the SLCC barrier to a small (low-head type) barrier in the Conservation Area and an upper section of approximately 4.2 km. The historical distribution of sea lampreys in the upper section was separated from a previously un-colonized portion of the stream by an old milldam. This structure was destroyed by a flood event in the early 1990's. Consequently, we installed a (temporary) low head barrier to prevent introduced adults from reaching new habitat and to reduce the requirements of the post study treatment program.

The second stream, Port Britain Creek, is located approximately 8 km west of Port Hope, Ontario. A SLCC low-head barrier was built in 1989, and the entire stream (9.6 km) was treated with TFM in May of 1991. There have been no recorded breaches of the barrier by sea lampreys since this treatment. On Port Britain Creek, we reduced the amount of stream available to the sea lampreys to 3.2 km by the construction of a (temporary) low head barrier at the HWY 401 bridge. This barrier reduced the available spawning habitat and the amount of stream that will require treatment at the completion of this project. The lower section of stream is also divided approximately in half at 1.5 km by the CN train bridge which has a drop of about 1 m in the summer months. Temperature data loggers are installed in both streams to monitor daily conditions.

Salem Creek, located 15 km west of Brighton, Ontario, was added to the project in the spring of 1999, for one year. This is an open system, providing sea lampreys with approximately 2.8 km of stream before reaching a 2 m high barrier. There are currently four beaver dams on the stream, providing 'natural' sections. The majority of the spawning habitat occurs within 1.5 km of the stream mouth, and a large beaver dam (1.3 m) at 2116 m from the stream mouth is likely a sea lamprey impediment. For these reasons, the majority of the spawning surveys were confined to the area of stream within 1500 m from the estuary. One temperature data logger was installed in Salem Creek to monitor daily conditions.

Adult additions

1998

Grafton Creek, the stream receiving the low-density addition of adults (see research proposal), received 106 males and 100 females in the upper portion of the stream on May 2, 1998[1]. The lampreys were taken from traps on both the Humber River (80%) and Duffins Creek (20%). For both sexes, all were measured (± 1 mm) and 60% of the animals were weighed (± 1 g) and tagged with an individually numbered cantilever zip tag, and all received a distinctive v-notch clip to differentiate between streams and sexes.

Adult sea lampreys for Port Britain Creek, the stream receiving the high-density addition of adults[2], were brought from the trap on the Humber River on May 4, 5, and 6. Because of an initial mortality, we counted our total introduction of sea lampreys as those animals surviving on May 9. Thus we introduced a population of 259 males, (147 tagged, 57%) and 231 females, (151 tagged, 65%). The sea lampreys were introduced at the 'top end' of the stream and were again marked with a distinctive v-notch clip to differentiate between streams and sexes.

1999

Sea lampreys were transported to Grafton Creek from the Humber River on May 6. The number of adults remained the same as in 1998. An initial mortality between May 6 and May 7 resulted in a final introduction of 178 sea lampreys for 1999. All sea lampreys were sorted by sex and tagged with a distinctive v-notch denoting the sex of the animal and the stream of introduction. In addition, approximately 50% of the sea lampreys were tagged using an individually numbered polyethylene streamer tag (PST); thus, 85 males (46 PST tagged, 54%) and 93 females (46 PST tagged, 49%) were introduced. As well as the PST tags, 10 female sea lampreys received an individually pulse-coded ATS radio transmitter.

In 1999, the number of sea lampreys introduced into Port Britain Creek was reduced to match that of Grafton Creek (100 per sex). Adult sea lampreys were transported from the Humber River and Duffins Creek on May 7. An initial mortality of three male sea lampreys reduced the total number introduced to 201. Approximately 50% of the sea lampreys were tagged with PST tags, and 10 females received individually pulse-coded ATS radio transmitters, for an introduction of 102 females (50 PST tags, 49%) and 99 males (50 PST tags, 51%). Due to

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[1] This number approximates the estimate of the number of spawners required to yield age-1 larval densities of 5/m^2 (0.017 spawning females/m2 of larval habitat, 100000 eggs/female, 0.01 survival to age-0, 0.4 survival to age-1). This number approximated the minimum number of additions (130) called for in the Sterile Male Release Technique (SMRT) protocol (Twohey et al. 200x).

[2]The number of adult spawners added is estimated to yield age-1 larval densities of approximately 13/m^2 using parameters in footnote 1.

predation of female sea lampreys with radio transmitters, two more were added on May 13, bringing the total number of females introduced to 104. On May 20, a tagged male (from Port Britain Creek) was re-released into the stream and on May 26, 10 male sea lampreys, marked with fin v-notches and PST tagged, were released to into the stream to provide marked animals for an abundance estimate. The total number of males introduced in 1999 was 110, for a stream total of 214 sea lampreys.

2000

On May 10, 2000, adult sea lampreys were introduced into both Port Britain and Grafton creeks. The introduction locations remained the same as in 1998 and 1999, at the upper temporary barriers in both streams. A total of 50 females and 51 males were released in Port Britain (total 101) and 44 females and 58 males in Grafton Creek (total 102). The numbers released were approximately the same in both streams and about half the number of adult sea lampreys released in 1999. Adults were collected in both the Humber and Duffins Creek traps. All animals were measured (± 1 mm), and 50% were weighed (± 1 g). All adults were marked with unique fin clips denoting the stream of release, sex, and all adults were tagged with an individually numbered PST tag.

2001

Adult sea lampreys were not introduced to either Port Britain or Grafton creek in 2001.

Nesting Observations

In 1998 and 1999 all of the streams were walked on a regular basis by trained observed who looked for evidence of live animals, evidence of nesting and later, presence of sea lamprey carcasses. All 'sea lamprey like' depressions, those areas in riffles, mixed gravel, pebbles and small boulders that appeared cleaned and disturbed, were sampled for the presence of sea lamprey eggs (whether adults were seen on the nest or not). Any nest found to contain sea lamprey eggs was marked with a visible numbered marker. A site map was drawn to show the nest location in the stream, and the eggs were later staged according to Piavis' (1971) embryology key. For any adult sea lampreys located on a nest, the sex of the lamprey and the presence of any individual tag numbers were noted. In order not to disturb the spawning pairs (where located), the nests were marked and then sampled within 24 hrs (after the sea lampreys had left the nest) to determine if egg deposition had occurred.

1998

In Grafton Creek, the first sea lamprey nest containing eggs was found on May 18 and the last new nest confirmed nest was located on June 22, however using Piavis' 1971 embryological key determined the nest was approximately six days old (approximate spawning date June17). A total of 20 nests with eggs were located in the stream during the spawning period (Figure 1). In addition to the nests with eggs, a total of 64 nests that did not contain sea lamprey eggs were found and sampled, for a total of 84 nests. Thus, 76% of the nests found in 1998 were not used by spawning sea lampreys for egg deposition. Only one pair of spawning sea lampreys was observed on a nest (June 11) that was later found to contain sea lamprey eggs. In total, 14 (nine males, four females, one unknown sex) live sea lampreys were observed; 11 were involved in nest building behaviour (two females, seven males, one pair) and three were swimming or resting (no nest associated with the individual).

In Port Britain Creek, the first nest with eggs was located on May 18 and the last on June 22; however, using Piavis' 1971 embryological key, this nest was found to be approximately four days old (approximate spawning date of June 18). A total of 20 nests were located during the spawning period. Two of the nests contained a second spawning, the first on May 23 and the second on May 28, for a total of 22 spawning events by sea lampreys in the stream in 1998 (Figure 2). In addition to the nests with eggs, 63 nests without egg deposition were located, for a total of 85 sea lamprey nests. Overall, 75% of the nests located did not contain sea lampreys eggs in 1998. A total of 94 (20 male, 20 female, remainder sex not determined) live sea lampreys were seen. Only nine paired sea lampreys and one male were observed on nests later found to contain sea lamprey eggs. Only one nest located without egg deposition was observed with a sea lamprey, in this case a lone female. Additionally, 74 sea lampreys were observed either swimming or resting during the spawning period. The number of nests and the dates found for Grafton and Port Britain Creeks are summarized in Figure 3.

1999

The first nest in Grafton Creek was located on May 29 and the last was constructed on June 17. A total of 57 nests with eggs were located during the spawning period. Multiple nest use was common in 1999. In total, 45 (79%) were used only once, seven (12%) a second, three (5%) for a third spawning and two (4%) for a fourth spawning. A total of 76 spawning events were confirmed during the spawning period (Figure 4). Sea lampreys were observed in 54 of the 76 nests (71%) in a variety of pairings. Monogamous spawning parings were observed on 17 (31%), polygamous (one male, two females) on 11 (20%), single males 15(28%), single females seven (13%), multiple females (three) with one male on two (4%), two females on one (2%) and one nest with two males and two females (2%). Of the 55 females observed on nests with eggs, 41 (87%) were observed on one nest, four (9%) on two and two (4%) on three separate nests during the spawning period. For the 47 males, 35 (88%) were located on one nest, four (10%) on two, and one (3%) on four nests. In addition to the nests with eggs, a total of 60 nests without egg deposition were sampled, for a total of 136 nests during the spawning period.

The first sea lamprey nest with eggs was located in Port Britain Creek on May 26 and the last was found on June 5, for a total of five nests. A second spawning event was confirmed in one nest, brining the total spawning events to six (Figure 5). A total of eight nests without egg deposition were located in the stream during the spawning period, bringing the total number of nests to 14. Only three (one male, one female, one unidentified) live sea lampreys were seen in 1999, though none were involved in either nesting or spawning.

Salem Creek was followed for nesting observations at the same time as both Port Britain and Grafton Creeks. The first nest with eggs was located in Salem Creek on May 23 and the last on June 12. A total of 18 nests with eggs were located and one nest was used for a second spawning, for a total of 19 nesting events (Figure 6). Throughout the spawning season, 11 nests without egg deposition were located, for a total of 30 nests. Twenty-three live sea lampreys were seen during the spawning period. The time of nesting on all three streams is compared in Figure 7.

2000

Nest surveys were conducted on June 18 – 21 and June 26, 27, 2000. High water and cooler temperatures occurred in both streams in 2000. No nests were located in Port Britain Creek, though high water (bank damaged indicated flows of at least 1 m above normal levels), may have obliterated any signs of nesting. The recovery of one1 young of the year larvae, (see larval section), indicates that successful spawning did occur in 2000.

In Grafton Creek, a total of nine nests were located on June 20. Sea lampreys were found on three nests and egg samples from the remaining nests indicated spawning had occurred within two days of nest discovery. A total of 12 sea lampreys were located in 2001, 2 pairs, 5 males and 1 female. Spawning occurred later in 2000 in Grafton Creek, compared to 1998 and 1999 when spawning was completed by approximately June 17. Again, effects from high water were evident in Grafton Creek. Nests were re-examined on June 26, 27. Only five nests were located and surveys took place in conditions of higher water and greater turbidity. The presence of young of the year larvae, (see larval section), again confirmed that successful spawning had taken place.

Table 1: Summary of spring sea lamprey observations for Grafton, Port Britain and Salem creeks for 1998, 1999, 2000.

	Grafton Creek			Port Britain Creek			Salem Creek
	1998	1999	2000	1998	1999	2000	1999
Number of adults released	206	178	102	490	214	101	67[6]
Total mortality (live release)	61	18[5]	1	106	18[5]	N/A	3
Estimated at spawning	112	133	N/A	375	N/A	N/A	36
Number of nests with eggs	20	76[2]	9	22[1]	6[3]	0	19[4]
Total number of nests	84	136	8	85	14	4	30
Number of live sighting	14	143	12	94	3	0	23
Nests (eggs)/estimated adult	0.179	0.571	0.088	0.059	0.031	0.040	0.528

[1]20 nests found; two confirmed 'double spawns'
[2]57 nests found; 45 (one spawn), seven (two spawns), three (three spawns), two (four spawns)
[3]5 nests found, one confirmed 'double spawn'
[4]18 nests found; one confirmed 'double spawn'
[5] carcasses recovered in stream and 12 radio tagged animals 'removed' in Port Britain and two in Grafton, carcasses not recovered
[6]Schnabel Population Estimate for Salem Creek

Population Estimates at Spawning

In 1998, Port Britain and Grafton creeks had the population of adults remaining at the time of spawning estimated both by the direct counts of those that emigrated, were removed by predators and those that died prior to spawning and through the use of a Petersen mark/recapture abundance estimate. For the Petersen mark/recapture estimates, large sections of the streams were electrofished, and any sea lampreys collected were measured, weighed, re-marked and re-released. The recapture of marked animals when spawning began was used to estimate the abundance remaining at the time of spawning.

In 1999, an additional stream, Salem Creek, was added to the study as an open system to complement Port Britain and Grafton creeks, where the total number of adults introduced was known. In order to estimate the number of animals in Salem Creek, two portable traps were placed in the stream and a Schnabel population estimate was calculated to estimate the size of the sea lamprey population during the spawning migration.

The use of the direct counts for those that emigrated, were attacked by predators, and those that died prior to spawning, were applied to all three streams during the spawning period in 1999. A Petersen mark/recapture estimate was also undertaken in all three streams at the time of spawning using electrofishing as a method of capturing adults for re-marking purposes. In Port Britain Creek, no adult lampreys were captured, though the entire stream was eventually electrofished. As a result, 10 male sea lampreys (marked) were added on May26. Portable traps were added to both Port Britain and Grafton creeks in 1999 in an effort to mark more lampreys in a less stressful manner. The traps fished for approximately 15 days in Grafton and eight days in Port Britain Creek.

Direct Estimates of Numbers Remaining at Spawning

Pre-spawning Mortality:

1998

In Grafton Creek, we began to find carcasses on May 13, almost two weeks after our initial introduction of adults (Figure 1). A peak in sea lamprey mortality occurred on May 18, coinciding with the discovery of the first confirmed sea lamprey nest. The carcass discovery rate fell sharply after this point but continued to occur throughout the spawning period. The last carcass was found on June 20, a male found in a pool, but the carcass was decomposed. A total of 61 (32 male, 28 female, one unidentified) carcasses were found in 1998.

In Port Britain Creek, observations made after the adult introduction followed a similar pattern to that of Grafton Creek. After an initial mortality at the time of introduction, the first carcass was discovered on May 15 (Figure 2). The first confirmed sea lamprey nest was located on May 18, and a peak in mortality occurred on May 20. The carcass discovery rate continued to fall after this point but continued through the spawning period. The last carcass was found on June 9, and our last nest was found on June 22. A total of 106 (51 male, 52 female and 3 unidentified) were found in 1998.

In 1998, mortality may have been related to the cantilever-zip tag that was used on the sea lampreys as the proportion of tagged lampreys found was significantly greater than those not tagged for both Port Britain and Grafton creeks (χ^2, $p<0.05$). The ratio of male and female mortalities was the same (1:1) for both tagged and untagged lampreys. The proportion of carcasses collected with tags indicated a total mortality rate of 29% in Port Britain Creek and 41% in Grafton Creek. For the lampreys without tags, the rates are 10 and 13% for the same streams. Carcasses, with and without tags, were collected over the 51 days of the study period.

1999

In Grafton Creek in 1999, mortality occurred throughout the spawning period and was not associated with the nesting period as in 1998. A total of eight carcasses (five female, three males) were found in the streams and an additional six females and two males were captured. Four females were removed from nests and two were captured in the stream. One male was collected beside a nest and the second was swimming in the stream. Three additional females thought to be dead were not recovered. The use of radio telemetry indicated three radio signals in inaccessible locations: under the temporary dam, and two in deep undercut banks. It is unknown if the females perished in these locations or if the tags became entangled and pulled off. The first carcass was recovered on June 3 and the last on June 12. The relationship between mortality and nest counts is shown in Figure 4.

Few carcasses were recovered in Port Britain Creek in 1999. A total of six carcasses, five females and one male, were located during the spawning period. The first carcass was located on May 12 and the last on May 25. Mortality did not follow the timing of nest construction, as in 1998 (Figure 5).

In Salem Creek, three carcasses were located during the daily stream walks. One female and two males were collected in the stream during the spawning period in 1999 (Figure 6).

In 1999, mortality did not appear to be related to either the timing of nesting as in 1998, nor did it appear to be tag related for any of the 3 streams. The use of the PST tag was continued in 2000 as a result of the decreased mortality in 1999.

2000

One carcass was recovered in Grafton Creek on June 19, while no carcasses were recovered in Port Britain Creek. Few stream walks (six) were conducted during the time of spawning in 2000 in either stream due to high water and poor visibility.

Predation:

Predation occurred in 1998 and 1999 in both Port Britain and Grafton creeks. Predation was determined in 1998 through the recovery of carcasses in the stream. A total of three sea lampreys were recovered in Port Britain and two in Grafton in 1998.

In 1999, the addition of the radio-telemetry component of the study indicated, at least in Port Britain Creek, that predation may have had a greater effect on spawning sea lamprey populations than previously observed. Based on the radio-telemetry information, predation rates on Port Britain Creek were high, with 11 of the 12 radio-tagged females (92%) removed from the stream by May 26. In eight cases, the transmitter was located on the stream bank with the wiring harness chewed through and the carcasses were not recovered, and for three other sea lampreys, the radio transmitter was tracked to an animal den and neither the tag nor the carcass was recovered. One additional radio tag was recovered in the stream, without the sea lamprey, so was not known how the tag became dislodged. The use of direct counts of carcasses would have lead to an underestimation of predation, as only one carcass was recovered in 1999. Thus, it is possible that predation may have been higher than expected in Port Britain Creek in 1999, as sea lampreys that were removed from the stream would not have been detected.

Predation also occurred in Grafton Creek in 1999. Only two radio tagged animals were removed from the stream, the first was removed six days after the introduction and the second 17 days later. Also, a bird may have attacked one sea lamprey, as it was found on shore, alive, during one of the daily stream surveys. Only one carcass exhibiting signs of predation was found in 1999, so, again, predation rates may have been underestimated through the use of recovered carcasses alone.

Emigration:

Emigration occurred in both Port Britain and Grafton creeks in both years. In 1998, the total emigration, as measured by the return of marked animals to a stream with a sea lamprey trap, was 19 individuals. Both Grafton and Port Britain Creek sea lamprey traps captured a total of four animals, while Cobourg Brook, the central stream, recovered 11. Due to problems with records kept by the trap contractor (the same individual operated all three traps), the stream of origin could not be determined for any of the recovered sea lampreys. While it is likely that the sea lampreys in Port Britain and Grafton creeks were introduced to those streams, this can not be determined for certain. In total, approximately 3% of the 696 sea lampreys released in 1998 were recovered in a sea lamprey trap at a barrier.

In 1999, three sea lampreys were recovered during the trapping season. In Port Britain Creek, two sea lampreys (one male, one female), from this stream were recovered on May 19. One male sea lamprey, released into Grafton Creek, was recovered in the Grafton trap on June 14. Using these captures, the emigration rate for 1999 was approximately 1% for both streams.

In 2000, one male sea lamprey released in Grafton Creek was recovered in the Port Britain Creek low-head barrier dam trap. No Port Britain Creek animals were recovered in barrier traps in 2000, thus the known emigration for Grafton Creek was 1% of the total adults released.

Population estimates, post-introduction

1998

To estimate the number of sea lampreys in the stream, we electrofished a portion of the creek and used a distinctive mark, a fin clip made with pinking shears, for any captured lampreys. On May 12 in Grafton Creek, eight sea lampreys were marked and released and on May 13, 27 sea lampreys were marked and released in Port Britain Creek. The recovery rates among carcasses were four and seven individuals, respectfully. Population estimates from the mark/recapture study for adults remaining at the time of spawning are summarized in Table 2.

1999

In 1999, two methods were used to capture and mark sea lampreys to estimate the population of remaining sea lampreys in the stream during the spawning season. As in 1998, large sections of the streams were electrofished and in 1999 we also used portable assessment traps (PAT).

Electrofishing on Port Britain Creek was conducted May 21, 22, 23, and covered the entire length of the stream. No sea lampreys were recovered using this technique, though the electrofisher settings were the same as in 1998. Grafton Creek was electrofished on May 21 and one sea lamprey was retrieved. Six additional sea lampreys were captured by hand and tagged on May 21 for population estimation.

Two portable traps were set in Port Britain Creek, the first on May 22, above the second train bridge, and the second on May 24, below the first train bridge. The upper trap was moved approximately 200 m further upstream on May 27, to a location where sea lampreys had spawned in 1998. The traps fished continuously until May 30, a total of eight days. No sea lampreys were caught in either trap during this time. As no sea lampreys had been marked for the second population estimate, 10 male sea lampreys (new) were marked and released into the stream on May 26. Over the spawning season, no marked sea lampreys were recovered; thus no mark/recapture abundance estimate is available for Port Britain Creek in 1999.

One PAT was set in Grafton Creek on May 22. One sea lamprey was captured in the trap on May 23 and the trap was relocated approximately 300 m downstream on May 27. The trap was removed on June 6, after fishing for 15 days and capturing a total of 15 sea lamprey, including three recaptures. Using the electrofishing technique and the PAT, a total of 19 sea lampreys were marked, and, over the course of the spawning season, a total of 20 marked sea lampreys were recaptured. The estimated spawning population remaining in the stream is in Table 2.

Salem Creek is an open system, without a Sea Lamprey Control Center low-head barrier or trapping device in the stream. In order to estimate the population of sea lampreys during the initial migration into the stream, prior to the spawning season, two PAT's were set, the first at approximately 700 m from the stream mouth and the second at approximately 2000 m from the stream mouth. The traps were set on May 5 and removed on May 22. During the 17 days the traps were operated, a total of 96 adult sea lampreys were captured including 40 recaptures. The sea lampreys were measured and tagged with an individual PST tag, but not sexed, as we were not confident in our ability to determine sex. A Schnabel population estimate was calculated, with 67 sea lampreys estimated during the initial spawning migration. On May 23, Salem Creek was electrofished, resulting in three sea lampreys captured and, on May 27, three additional animals were marked for a population estimate at the time of spawning. The results of the Salem Creek population estimates are summarized in Table 2.

Table 2: Petersen population estimates, and known sea lamprey removals (mortality, predation, emigration):

	Potential (introduced-known removals)		Petersen Estimate (95% Confidence Limits)		Difference	
Grafton Creek:	1998	1999	1998	1999	1998	1999
All sea lampreys:	139(206 –61)	159 (178-18)	112 (53-236)	133 (83-211)	27	26
All males:	74 (106 – 32)	80 (85 - 5)	55 (21– 121)	74 (38-150)	19	6
All females:	72(100 – 28)	82 (93 – 13)	50 (20-111)	63 (37-111)	22	19
Port Britain Creek:						
All sea lampreys:	380(490-106)	194 (214-18)	375 (203-699)	N/A*	5	N/A*
All males:	208 (259–51)	108 (110-1)	156 (69 – 343)	N/A*	52	N/A*
All females:	179 (231–52)	86 (104-17)	180 (85 – 381)	N/A*	-1	N/A*
	Schnabel Estimate		Petersen Estimate			
Salem Creek:	1998	1999	1998	1999	1998	1999
All sea lampreys		67		36 (13-71)		31

*Populations estimates could not be calculated as no marked sea lampreys were recovered

Sea lamprey carcass sampling

1998

Of the total (842) sea lampreys transported to the two streams, 318 died. 169 carcasses were frozen at the time of death: 30 from Grafton Creek and 139 from Port Britain Creek. All carcasses were checked for the presence of a tag number, electrofishing clip, sex, and reproductive status. Only one sea lamprey was labeled in the field as spawned, but upon dissection that was not the case (very small female). One sea lamprey was a small, almost undifferentiated male and it was not kept for further analysis.

Of the collected carcasses, 79 sea lampreys were re-weighed and a length taken and 78 (49 from Port Britain and 29 from Grafton) were saved for lipid and caloric analysis. For these sea lampreys, the gonads were removed and weighed separately, and for all females, five egg sub-samples were weighed, counted and used to estimate fecundity. Two of the animals from Port Britain Creek were incorrectly marked as females (1%). One died at release and the second was found later. No animals from Grafton Creek were known to be incorrectly sexed. The ratio of male to female carcasses was approximately 1:1 both creeks. In both locations we found sea lampreys whose sex was indeterminate as only the head portion was found (predation).

1999

Of the 431 adult sea lamprey transported to Port Britain and Grafton creeks between May 6 and May 7, a total of 89 died by the time the spawning season was completed. The total includes the 14 radio tagged female sea lampreys removed by predators, where the carcasses were not recovered and one recovered carcass (mutilated by a predator), that was not saved for analysis. A total of 74 carcasses were kept and frozen for further chemical analysis, 57 from Grafton Creek and 17 from Port Britain Creek.

In addition, three carcasses (two males, one female) collected in Salem Creek were also kept for analysis. All sea lampreys collected were checked for an individual tag number, a second mark for population estimation, sex and reproductive condition. In 1999, none of the sea lampreys collected were found incorrectly marked for sex. All preserved (frozen) sea lampreys were dissected and the fecundity of females was estimated using the same methodology as in 1998. The sex ratios for the carcasses found in the stream for Grafton Creek were roughly equal (62% female, 38% male, n=8), but not in Port Britain Creek (83% female, 17% male, n=6).

Table 3: Summary of mortality for Grafton, Port Britain and Salem Creeks:

	Grafton Creek		Port Britain Creek		Salem Creek
	1998	1999	1998	1999	1999
Mortality (from live release[1])	61	18[2]	106	18[3]	N/A
Sea lamprey kept for analysis	29	57	49	17	3
Total number of females	28 (46%)	11(69%)	52 (49%)	17(94%)	1 (33%)
Total number of males	32 (52%)	5(31%)	51(48%)	1 (59%)	2 (67%)
Indeterminate sex	2	0	3	0	0

[1]from all sea lamprey released into the stream, including known predation, but excluding the mortality that occurred in the first three days post-release.
[2]Grafton Creek: 16 carcasses were collected and two radio-transmittered sea lampreys died without carcass recovery
[3]Port Britain Creek: six carcasses were collected and 12 radio-transmittered sea lamprey died without carcass recovery

SMRT survey results for Grafton and Port Britain

Habitat Observations

Tables 4, 5, and 6 provide 1997 to 2001 estimates of the percentage of habitat surveyed and the amounts scaled to the streams during the fall SMRT sampling. Between 1997 and 1999, while the amount of Type I and Type II larval habitats was different between years, the changes were relatively small from year to year (Tables 5, 6). In 2000, the amount of Type I habitat estimated as available in Grafton Creek was approximately one half that in 1999, while the amount of Type II was relatively stable. In Port Britain Creek, the estimated amount of Type I habitat was reduced by more than seven times the estimated amount in 1999 and Type II was reduced to about the 1998 levels. In 2000, numerous flooding events occurred, as recorded by measurements at the permanent sea lamprey low-head barriers. In total, the lower traps were inoperable for approximately 13 days in each stream due to high water conditions. The floodwater conditions likely removed/redistributed some of the available Type I habitat in both streams compared to previous years. In 2001, following the fall flood events of 2000, low water conditions occurred throughout most of the Great Lakes region. Water levels in Port Britain and Grafton creeks were some of the lowest observed in approximately 20 years (Ganaraska River and Lower Trent Conservation Authorities, personal communications). Though the water levels were lower than in the past during the summer, by fall the mean stream widths were approximately the same as in the pervious survey years. Type I and Type II habitat amounts appeared to be more consistent with pre 2000 surveys.

Table 7 summarizes the number and area of Type I and Type II plots surveyed in both streams from 1998 to 2001. Both the number of Type I plots and the total Type I area electrofished increased in 2001 for both streams, while the number of plots and total area of Type II habitat electrofished was consistent with past surveys for 2001.

Table 4: Comparison of stream length, width, and area, 1997 to 2001.

	Stream Length (m)	Mean Stream Width (m)	Total Area (m^2)
Grafton Creek			
1997[1]	9289	3.6	33440
1998[2]	9716	3.4	32743
1999[3]	8408	3.5	29428
2000[3]	8190	3.8	31099
2001[3]	8070	3.5	27842
Port Britain Creek			
1997	3200	5.1	16320
1998	3200	5.2	16672
1999	3229	5.1	16328
2000	3242	5.3	17150
2001	3200	5.2	16640

[1]length excludes the distance from Stn. 13 to Stn. 21 – width measured every 50 m
[2]includes entire stream length up to transect 105, and average width for all transects sampled
[3]length excluded approximately 1 km of the upper tributary, as the creek was less than 1m wide and 3cm deep in the fall.

Table 5: Comparison of % habitat type in SMRT surveys

Year	% Type 1	% Type 2	% Type 3	% Type 4
Grafton Creek				
1997[1]	8.4	17.1	74.5	N/A
1998	4.4	20.5	73.7	1.4
1999	5.2	15.1	77.0	2.7
2000	2.5	13.4	78.7	5.5
2001	4.9	19.1	71.1	4.9
Port Britain Creek				
1997[1]	3.8	14.2	82	N/A
1998	6.7	4.5	87.6	1.2
1999	5.8	7.0	86.4	0.8
2000	0.7	5.1	92.8	1.4
2001	8.2	5.6	85.2	0.89

[1]measured every 50 m – not measured between Stn. 13 and 21

Table 6: Total area of habitat types in different years, calculated using Table 5 % habitat estimates.

Stream/Survey Year	Type 1 Habitat (m^2)	Type 2 Habitat (m^2)	Type 3 Habitat (m^2)	Type 4 Habitat (m^2)
Grafton Creek				
1997	2809	5718	24913	-
1998	1441	6712	24132	458
1999	1526	4442	22657	803
2000	764	4169	24461	1704
2001	1375	5321	19787	1359
Port Britain Creek				
1997	620	2317	13382	-
1998	1117	750	14605	200
1999	943	1152	14109	124
2000	122	866	15919	244
2001	1357	957	14177	149

Table 7: Habitat sampled in Fall SMRT surveys

	Grafton Creek				Port Britain Creek			
	1998	1999	2000	2001	1998	1999	2000	2001
Transects sampled	100[1]	98[2]	105	105	100[1]	99[2]	108	100
Type 1 plots electrofished	13	17	15	23	26	15	13	32
Type 2 plots electrofished	25	15	24	24	11	11	19	15
Type 1 plots with larvae	9	13	13	18	6	5	1	14
Type 2 plots with larvae	19	10	16	19	1	3	8	4
Area of type 1 plots	33.9 m^2	43.5 m^2	35 m^2	51.5 m^2	72.4 m^2	36.5 m^2	39 m^2	75 m^2
Area of type 2 plots	82.5 m^2	45.5 m^2	53 m^2	59 m^2	22.7 m^2	22.0 m^2	58.5 m^2	27 m^2

[1]of the 100 targeted transects, 3 in each stream could not be electrofished due to deep water. At one additional transect in Grafton Creek, habitat data was not recorded.

[2] of the 100 targeted transects, 2 on Grafton Creek and 1 on Port Britain Creek were too close together to sample according to the SMRT Protocol.

Larval Lamprey Sampling

The number of lamprey larvae electrofished in both streams from 1998 to 2001 using the Sterile Male Release Technique (SMRT) survey protocol (Twohey *et al.* 200x) are summarized in Table 8. Both *Petromyzon marinus* and *Lampetra appendix* larvae have been collected in all years in Grafton Creek, while only *P. marinus* have been collected in Port Britain Creek while using the SMRT protocol. In 2001, three *L. appendix* larvae were identified in the collections made for the coded-wire tag marking and release during the summer of 2001. The abundance of adult sea lampreys introduced into each stream along with the subsequent larval year class densities, based on the SMRT population estimates, are summarized in Table 9 for each year of the study. While the density estimates for young-of-the-year (YOY) larvae are considered unreliable, as electrofisher efficiency for YOY's is low, the estimates have been included in the summary table to allow for year class comparisons throughout the duration of the project. The population estimates reported are not corrected for electrofisher sampling efficiency, and are thus an underestimation of true larval lamprey density.

1998 Observations

No larval sea lampreys, either age-0 or older, were captured in the SMRT survey of Grafton creek (their presence in Grafton is confirmed by dredge sampling - see below) (Table 11). The SMRT survey found only age-0 sea lampreys in Port Britain Creek (Table 9).

No American brook lampreys, (*L. appendix*), were collected in Port Britain. Both age-0 and age 1+ *L. appendix* were collected in the SMRT survey in Grafton Creek. Age-0 *L. appendix* densities in the stream are greater than $3/m^2$ and age 1+ densities are over $2/m^2$. *L. appendix* were not evenly distributed in Grafton. Densities on the order of 20-25 per m^2 were found at plots sampled at 2282 m, 2404 m, and 2729 m. These plots are all downstream of the crossing at Barnum House road south of Highway 2. Other sample plot densities did not exceed 4.8 per m^2. Between Barnum House Road and Highway 401, little larval habitat was found (only 2 sites electrofished) and only 1 *L. appendix* was captured. *L. appendix* were found between the north-side of Highway 401 up to the temporary barrier location as well as in the eastern split of Grafton Creek to approximately 7000 m. Given that the available habitat above 7000m did not meet the criteria for electrofishing utilizing the SMRT protocol, it is unknown whether *L. appendix* inhabit the area, though it is probably that populations exist in these pockets.

1999 Observations

During the SMRT survey of Grafton Creek, both *P. marinus* and *L. appendix* YOY's were collected, though lower numbers of *L. appendix* YOY's were collected than in 1998 (seven vs. 124). YOY electrofishing estimates are considered unreliable, so these numbers were not included in the total larval estimates for 1999. The densities of *L. appendix* in Grafton Creek are higher for both Type I (2.85/m^2 vs. 0.28/m^2) and Type II (1.16/m^2 vs. 0.22/m^2) habitats than densities of *P. marinus*. The maximum density of *L. appendix* in 1999 was 14 /m^2, compared with 25/m^2 in 1998. The maximum density of *P. marinus* was 3.0/m^2 in Type II habitat compared with the maximum of 1.3/m^2 in Type I habitat. For both species, the maximum density in Type I habitat was 14/m^2 and 10/m^2 in Type II habitat. The distribution for *P. marinus* in 1999 occurred from 465 m above the SLCC low head barrier to 6154 m, thus they inhabit almost all of Grafton Creek.

In Port Britain Creek, only age 1 *P. marinus* were collected in the 1999 SMRT survey. YOY's were found during separate sampling events, confirming nesting success. The maximum larval densities found in 1999 were 3.5/m^2 in Type I habitat and 1.0/m^2 in Type II habitats. The distribution for year 1 larval *P. marinus* ranged from 245 m above the SLCC low head barrier to 2685 m. In 1998, the distribution ranged from 977 m to 2915 m above the SLCC barrier.

Salem Creek was not surveyed in 1999 for either larval abundance or habitat distribution. Larval lamprey surveys were not completed in Salem Creek until 2001, when a Quantitative Assessment Survey (QAS) was conducted in June. The total larval abundance (corrected for electrofisher efficiency using ESTR) was 46,096, of which approximately 15,846 are expected to be the product of the 1999 sea lamprey spawning population (19 successful nests).

2000

In 2000, in both streams, all lampreys were measured and weighed (± 0.001 g) in the field, and those larger than 50 mm were injected with a coded-wire tag. All larval lampreys were marked with a tail clip and released at the location of capture. This was done in order to mark individual sea lampreys for larval growth and movement studies as well as to continue the mark-recapture work started in the summer of 2000 (see Mark/Recapture section).

SMRT surveys were conducted in both Port Britain and Grafton Creeks in the fall of 2000. YOY's were collected in both streams, indicating that successful spawning had occurred. In Port Britain Creek, a total of 63 *P. marinus* larvae were collected during the surveys. The maximum densities in Type I larval habitat were 4/m^2 and 1.2/m^2 in Type II habitat. The larval distribution ranged from 30 m above the low-head barrier to 3000 m in the stream. Large larval sea lampreys were prevalent in Port Britain Creek, with 45 of the lampreys collected greater than

100 mm in length. Two larval sea lampreys appeared to have begun transformation and were removed from the stream. These lampreys were frozen and saved for future statolith aging.

In Grafton Creek, both sea lampreys and American brook lampreys were found in 2000. Maximum densities for sea lampreys reached $6/m^2$, while the maximum for American brook lampreys was $12/m^2$, for Type I habitat. In Type II habitat, the maximum density for larval sea lampreys was $2.7/m^2$, while for brook lampreys the maximum was $11/m^2$. A total of 78 sea lampreys and 171 brook lampreys were collected in the stream. Sea lampreys in Grafton Creek were found through most of the stream, ranging from 267m above the low-head barrier to 5934m.

2001

2001 was the final year for SMRT surveys for Port Britain and Grafton creeks. Both streams were surveyed in the fall of 2001. No YOY's were collected in either stream indicating that a breach of the low-head sea lamprey barrier was unlikely to have occurred in either stream. In Port Britain Creek, a total of 56 larval sea lampreys were collected, including 6 tagged lampreys. The majority of the sea lampreys (46) were greater than 100 mm in length, though none of the lampreys collected appeared to be undergoing metamorphosis. The maximum density of larval lamprey in both Type I and Type II habitat was $2.7/m^2$. Densities during the fall survey appeared lower than in previous years. The larval distribution ranged from 783 m above the low-head barrier to 3166 m in the stream. Confirmation of larval sea lampreys in habitat closer to the low-head barrier was made, though the sites were not a part of the SMRT survey and as such were not included in the population estimates.

In Grafton Creek, both sea lamprey and American brook lamprey larvae were again captured in the stream during the SMRT survey. A total of 100 larval sea lampreys and 232 American brook lampreys were collected. Six of the sea lampreys and five of the American brook lampreys were recaptures. The maximum density for the sea lamprey larvae were $4/m^2$, while the American brook lamprey reached densities of $17/m^2$ in Type I habitat. In Type II habitat, densities of larval sea lampreys were similar to those of 2000, at $2.6/m^2$, while for American brook lampreys, the density was lower at $3.2/m^2$. Sea lamprey larvae were again smaller than those collected in Port Britain Creek. Of the 100 sea lampreys collected, only 11 were larger than 100 mm and none appeared to be entering metamorphosis. Sea lamprey larvae were distributed throughout the stream, from 7m above the low-head barrier to 6502m upstream.

Table 8: Number of lampreys, *Petromyzon marinus* and *Lampetra appendix*, electrofished in Type I and Type II habitats, 1998 to 2001.

	Grafton Creek				Port Britain Creek			
	1998	1999	2000	2001	1998	1999	2000	2001
Petromyzon marinus Type I	0	12	44	56	14	11	40	40
Petromyzon marinus Type II	0	10	34	44	3	4	23	16
Lampetra appendix Type I	107	116	122	170	0	0	0	0
Lampetra appendix Type II	227	49	59	62	0	0	0	0
Total lampreys collected Type I	107	128	156	226	14	11	40	40
Total lampreys collected Type II	227	59	93	106	3	4	23	16

Table 9 a: Summary of fall 1998 to 2000 SMRT surveys estimates for Grafton Creek; population estimates are not corrected using either the standard 0.48 correction factor or the logistic model.

	1998			1999		
# *P. marinus* spawners	100 females/106 males			93 females/85 males		
# females/m^2 TI habitat	0.070			0.061		
Larval lamprey densities	Estimated total number	Type 1 habitat density (/m2)	Type 2 habitat density (/m2)	Estimated total number	Type 1 habitat density (/m2)	Type 2 habitat density (/m2)
YOY *P. marinus* larvae	0	0	0	101	0.02	0.01
Age 1+ *P. marinus* larvae	0	0	0	1405	0.28	0.22
Age 1+ *L. appendix* larvae	25568	3.45	3.07	9502	2.85	1.16
All age 1 + larval lamprey	25568	3.45	3.07	10907	3.13	1.38

YOY's were not collected in the SMRT sampling for 1998. Dredge sampling confirmed that successful spawning had occurred. As an effective technique for sampling YOY using electrofishing has not been established, only the age 1+ densities are considered a true estimate. YOY 'estimates' are included for interest only.

	2000			2001		
# *P. marinus* spawners	44 females/58 males			No Adults Introduced		
# females/m^2 TI habitat	0.058					
Larval lamprey densities	Estimated total number	Type 1 habitat density (/m2)	Type 2 habitat density (/m2)	Estimated total number	Type 1 habitat density (/m2)	Type 2 habitat density (/m2)
YOY *P. marinus* larvae	56	0.01	0.01	0	0	0
Age 1+ *P. marinus* larvae	3635	1.26	0.64	5463	1.09	0.75
Age 1+ *L. appendix* larvae	787	3.2	1.11	10129	3.30	1.05
All age 1 + larval lamprey	11321	4.83	1.83	16735	4.56	1.97

Table 9 b: Summary of fall 1998 to 2000 SMRT surveys estimates for Port Britain Creek; population estimates are not corrected using either the standard 0.48 correction factor or the logistic model.

	1998			1999		
# *P. marinus* spawners added	231 females/259 males			104 females/110 males		
# females/m² TI larval habitat	0.207			0.110		
Larval lamprey densities	Estimated total number	Type 1 habitat density (/m2)	type 2 habitat density (/m2)	Estimated total number	Type 1 habitat density (/m2)	Type 2 habitat density (/m2)
YOY *P. marinus* larvae	426	0.19	0.13	0	0	0
Age 1+ *P. marinus* larvae	0	0	0	284	0.30	0.18
Age 1+ *L. appendix* larvae	0	0	0	0	0	0
All age 1 + larval lamprey	426	0.19	0.13	494	0.30	0.18

As an effective technique for sampling YOY using electrofishing has not been established, only the age 1+ densities are considered a true estimate. YOY 'estimates' are included for interest only. No YOY *P. marinus* larvae were captured in a SMRT plot in 1999. Additional electrofishing confirmed that successful spawning had occurred in Port Britain Creek.

	2000			2001		
# *P. marinus* spawners added	50 females/51 males			No Adults Introduced		
# females/m² TI larval habitat	0.410[1]					
Larval lamprey densities	Estimated total number	Type 1 habitat density (/m2)	Type 2 habitat density (/m2)	Estimated total number	Type 1 habitat density (/m2)	Type 2 habitat density (/m2)
YOY *P. marinus* larvae	10	0.01	0.00	0	0	0
Age 1+ *P. marinus* larvae	465	1.03	0.39	1301	0.53	0.60
Age 1+ *L. appendix* larvae	0	0	0	3	0.001	0.001
All age 1 + larval lamprey	465	1.03	0.39	1304	0.53	0.60

1. The ratio of females/m² TI larval habitat is large in Port Britain Creek in 2000, due to the small amount of Type I larval habitat estimated during the SMRT surveys. Only 122 m² of Type I habitat was estimated compared to 943 m² in 1999.

Coded Wire Marking:

Larval Sea Lamprey Tagging 2000

In 2000, individually numbered coded wire tags were applied to larval sea lampreys greater than 50 mm long in Port Britain and Grafton creeks. Port Britain Creek was electrofished for larval sea lampreys August 22 to 24, 2000. A total of 185 larval sea lampreys were tagged with CWT and marked with a tail clip. One transforming larval sea lamprey was collected during the survey of the stream and retained for statolith aging. Of the total larvae collected, 135 were larger than 100 mm in length at the time of tagging.

In Grafton Creek, larval surveys were conducted from August 24 to 28, 2000. Both *L. appendix* and *P. marinus* larvae were collected during this period. A total of 250 larval sea lampreys were collected and those larger than 50 mm (n=148) were coded wire tagged and tail clipped prior to release. Very few large sea lamprey larvae were captured in Grafton Creek, with only seven of the larvae greater than 95mm in length. In addition to the sea lampreys, 575 larval *L. appendix* were collected and marked with a tail clip prior to release.

During the fall SMRT surveys, marked lampreys were collected in both Port Britain and Grafton creeks. Petersen mark/recapture estimates were calculated based on the return of marked larval sea lampreys compared to the catch. Table 10 compares the Petersen mark/recapture and SMRT abundance estimates for 2000. Data was not corrected for electrofisher efficiency for either estimate.

Larval Tagging 2001

In 2001, coded wire tags were again used to individually mark sea lampreys greater than 50 mm in length in both Grafton and Port Britain creeks. In addition to the coded wire tags, Visible Implant Fluorescent Elastomer (VIE) dye was used to mark the sea lampreys. Port Britain Creek was divided into two sections for the dye marking, while Grafton Creek was divided into five. The dye was added to the study in order to visibly mark the sea lampreys by section of the stream in which they were captured. This also provided an easier method of determining which sea lampreys should contain a coded wire tag (in the case of ambiguous mark or lost tag). All sea lampreys collected in both streams were measured (± 1 mm) and weighed (± 0.001 g), marked with a tail clip and where longer than 50 mm, both a coded-wire tag and a VIE mark.

In Port Britain Creek, larval surveys were conducted from July 9 to 12. A total of 195 sea lampreys were collected and 190 were marked and returned to the stream. The majority of the sea lampreys collected (N=135) were larger than 100 mm, however, none of the sea lampreys collected appeared to be entering metamorphosis. A total of 20 sea lampreys were recaptured from the 2000 marking period. In addition to the sea lampreys, 3 American brook lampreys were also collected in the stream. While American brook lampreys have been collected in the headwaters of the stream in previous surveys, this marks the first collection of *L. appendix* in the lower reaches of the stream during the Compensatory Mechanisms project.

In Grafton Creek, larval surveys were conducted over two time periods. The first, May 29 to June 3, covered the majority of the stream, while the survey from July 12 to 14, completed the remaining sections. A total of 761 sea lamprey larvae were collected during the survey periods, including 15 that had been marked in the previous year. Two of the sea lampreys were retained for coded-wire tag removal. Only 15 of the sea lampreys collected were larger than 100 mm and none appeared to have begun the process of metamorphosis. In addition to the sea lampreys, 919

L. appendix larvae were also collected and marked with a tail clip. Forty-two of *L. appendix* were marked with a tail clip from 2000.

During the spring/summer larval surveys, lampreys marked in the 2000 surveys were collected. Petersen mark/recapture estimates were calculated based on the return of marked larval lampreys and over all catch for the spring sampling period. These are compared with the fall SMRT abundance estimates for 2001 in Table 10. In addition to the SMRT and Petersen abundance estimates, the SMRT data has been corrected for electrofisher efficiency using the ESTR model by the SLCC. The ESTR abundance estimate (for sea lampreys only) has also been included in Table 10, with the separation between transformer and larval sea lampreys.

Table 10. Summary of Petersen mark/recapture abundance estimates for Port Britain and Grafton creeks compared to the SMRT abundance estimates. Neither estimate is corrected for electrofisher efficiency.

	Grafton Creek			Port Britain Creek	
	P. marinus	*L. appendix*	All Larvae	All *P. marinus*	> 100 mm
2000					
Total Collected	250	575	825	190	134
Total Tagged	148	575	723	185	134
SMRT Estimate	3635	7087	11321	465	351
Petersen Estimate	3924	6192	10739	627	388
(95% C. L.)	(1418–7718)	(3846-9829)	(6846-16658)	(404 – 962)	(241 – 616)
2001					
Total Collected	761	919	1680	195	135
Total Tagged	521	919	1440	190	135
SMRT Estimate	5463	10129	16735	1301	1084
Petersen Estimate – spring (95% C. L.)	10668 (6626-16933)	15982 (11896-21431)	20984 (16260-27050)	2277 (1499-3431)	1166 (767-1756)
P. marinus only:	Transformers	Ammocoetes		Transformers	Ammocoetes
ESTR Estimate	152	8614		2100	2873

Dredge pump technique: summary of 1998 fall stream collections

Dredge pump sampling was undertaken, in part, to evaluate this technique for age-0 sea lamprey sampling. Sampling was not random. We choose upstream areas in each stream near adult addition sites and nest sites, we selectively chose habitats to sample, and sometimes we also chose not to dredge sites where preliminary electrofishing indicated no larval sea lampreys.

For all samples, electrofishing was carried out for 22.5 seconds in 0.25 m^2 plots. In Grafton, plastic liners and mesh were laid down to delineate a 0.25 m^2 square plot and to prevent escape of larvae. The plots were then electrofished and the number of larvae seen by the electrofisher was recorded. Single larvae may have been seen and counted more than once, inflating the estimate of the number of larvae drawn out of the sediments by electrofishing. The larvae returned to the sediments and re-burrowed. Dredging of the plot was then done. In Port Britain, the first two plots were sampled in the same way. Thereafter, plots of 0.25 m^2 were marked out with metal stakes and electrofished. Caught larvae were then held in buckets while the plastic liner and mesh was then laid out in the area electrofished. The caught larvae were marked with a tail fin clip, returned to the plot, and the plot was then dredged to determine the efficiency with which marked larvae were caught again by dredging.

In both streams, frequency distributions are similar for electrofishing versus dredging (Table 11). Summing all plots within Grafton Creek, electrofishing versus dredging yielded 17 versus 18 larvae. For two of the 17 plots, the number of lamprey (both species) seen during electrofishing exceeded the number caught dredging by one and in one plot, the electrofishing sightings exceeded the dredge catch by two. In five other plots one larvae was caught dredging, while none were seen during the electrofishing.

Table 11: Comparison of dredge and electrofishing catches

	Grafton Creek (*P. marinus* and *L. appendix*)				**Port Britain (*P. marinus*)**	
		Dredge Frequency				
Catch	Electrofishing frequency	*L. appendix*	*P. marinus*	Both species	Electrofishing frequency	Dredge frequency
0	10	11	11	7	7	6
1	3	3	5	7	4	3
2	2	1	1	1	1	2
3	0	2	0	0	0	1
4	0	0	0	1	1	0
5	2	0	0	1	0	0
6	0	0	0	0	0	0
7	0	0	0	0	0	0
8	0	0	0	0	0	1
Total	**17**	**11**	**7**	**18**	**10**	**18**

Dredging appeared to be less effective in capturing the larger age 1+ larvae due to the depth to which we sampled (<6 cm). In one Grafton plot all five electrofishing sightings were noted to be > 7 cm but only two of these age 1+ larvae were recaptured in the dredge. In another plot it was also noted that five larvae sited during the electrofishing were larger on average than the five captured in the dredge sample. Although the majority of larvae captured in dredge (15 of 18) were age-0, the size of larvae sited in electrofishing was generally not noted. Subtracting the five known sightings of age 1+ larvae from the total electrofishing sightings yields 12 as a maximum number of age-0 sightings. Thus, for age-0 larvae, the density estimate by electrofishing relative to dredge pumping is a maximum of 12/15, or 80%.

In Port Britain all larvae caught by electrofishing or dredging were age-0 sea lampreys. 10 larvae were caught electrofishing versus 18 by dredge. Thus the density estimate for electrofishing is 10/18, or 56%, of the density estimate made using samples from the dredge pump. However, this may be an underestimate because one plot was likely electrofished for less than 22.5 seconds and at that site eight lampreys were dredged and only four were electrofished.

Mark-recapture results indicate that 11 out of 12 marked age-0 larvae (and possibly 12 of 12) were recaptured in the dredge (Table 12). In all plots for which we used mark-recapture methods, all captured larvae were returned to the plot before dredging. Summing across plots, 11 of the 19 dredge captures were re-marks. The ratio 11/19, or 58%, provides another estimate of the relative difference in density estimates for age-0 larvae via electrofishing versus dredge pumping.

Table 12: Combined *P. marinus* and *L. appendix* age-0 mark-recapture results for dredge pump samples

Creek	Plot #	# captured and marked	dredge captures	Dredge recaptures	marks/recaps	marks/total dredge capture
Grafton	13	2	2	1[1]	0.5	0.5
Port Britain	3	1	1	1	1	1
Port Britain[2]	5	4	8	4	1	0.5
Port Britain	7	1	1	1	1	1
Port Britain	8	1	2	1	1	0.5
Port Britain	9	2	3	2	1	0.66
Port Britain	10	1	2	1	1	0.5
Total		**12**	**19**	**11**	**0.93**	**0.42**
Plot mean					**0.92**	**0.66**

[1]May have been 2 recaptures for this plot.
[2]Electrofishing in this plot may have been less than 22.5 s.

Size of sea lamprey larvae

Throughout the duration of the Compensatory Mechanisms project, the larval sea lampreys collected in Port Britain Creek during the sampling periods have been larger than those collected in Grafton Creek. The larger size has remained consistent throughout the first three years of larval sampling, 1998 to 2000. In 2001, while the sea lampreys collected in Port Britain Creek are larger, visual separation of the year classes became too difficult. At age 1, the sea lampreys in Port Britain are significantly larger in both length (mm) ($p<0.05$, N=36) and weight (g), ($p<0.05$, N=36), 1999 SMRT survey data. This continues through the age-2 year class in

2000. In Figure 8, the length frequency histograms for 2000 show the difference in length at 'age' for Port Britain and Grafton creeks. The age assignments are based on a visual observation of the modal distribution and overlaps in lengths between age classes are known to occur. These appear to be the best representations of the potential age classes within the streams. The histogram also provides a visual reference for the increase in larval populations in Grafton Creek in 1999, based on the increased number of nests with eggs in 1999 (see nesting success section), and the lower spawning success in Port Britain Creek for the same year. The Salem Creek length frequency histogram for 2001 has also been included, with the larval length collected in 2001 using QAS sampling. Larval size appears to be closer to that of the Grafton Creek larval populations. The age-2 year class is the product of the adult sea lamprey population followed for nesting success in 1999.

Summary and conclusions

1998

- Mark-recapture estimates of adult sea lamprey abundance correspond reasonably well with the number introduced less the total number of lamprey carcasses.
- The number of sea lamprey nests in each stream is similar, even though a higher number of adult sea lampreys were introduced into Port Britain Creek than Grafton.
- Age-0 sea lamprey were found in both streams in the fall after the spring introductions
- A multi-age class population of *L. appendix* exists in Grafton Creek but no native lampreys were collected from Port Britain.
- Our dredge technique recaptured nearly all the age-0 larvae caught by electrofishing. The age-0 density estimate yielded by electrofishing is estimated to be in the order of 50-80% of the dredge pump estimate.

1999

- Adult mortality was lower in both creeks in 1999
- A population estimation immediately prior to spawning was made for Grafton and Salem Creeks, but not Port Britain Creek
- Nesting success in Grafton Creek was much greater in 1999 than in 1998 (76 vs. 20 nesting events)
- Both male and female sea lampreys were found on multiple nests
- Age-0 sea lamprey were found in both streams in the fall after the spring introductions

- A multi-age class population of *L. appendix* exists in Grafton Creek but no native lampreys were found in Port Britain Creek

2000

- Flood water conditions occurred in both streams during the spawning period
- Spawning was later in Grafton Creek in 2000 than in previous years, most likely due to the cooler water temperatures
- Successful spawning occurred in both streams as evidenced through the collection of YOY's in both streams
- Larval sea lampreys are larger in Port Britain Creek than in Grafton, as the number of larvae greater than 100 mm was 135 compared to seven during the CWT application
- Transformation of sea lampreys to the parasitic phase has begun in Port Britain Creek; three transformers were collected and retained for aging, while several other were beginning to develop eye-spots. The population in Port Britain Creek remains low at this time (uncorrected estimate of 465 sea lampreys)
- Of the sea lampreys collected in Port Britain Creek, only 19 met the criteria described by Youson *et al.* (1993) of length >120 mm, weight > 3.0 g, and Fulton's Condition factor (W/L^3) of > 1.50. One of the metamorphosing sea lampreys did not meet either the length or weight criteria.

2001

- Adult sea lampreys were not introduced into either stream in 2001
- Low water conditions occurred in both streams throughout the summer which may have affected larval lamprey survival
- No YOY sea lampreys were collected in either stream in 2001, indicating that a breach of low-head barrier was unlikely to have occurred in either stream
- Sea lampreys with coded wire tags were recaptured in both streams during the larval surveys – age and growth information will be collected from these individuals
- *L. appendix* larvae were collected in both streams in 2001 for the first time
- Larval sea lampreys are larger in Port Britain Creek than in Grafton Creek, though the population is lower. The majority of the sea lampreys collected in Port Britain Creek (at both sampling periods) are larger than 100 mm (N= 181) compared with Grafton Creek (N=26).
- No metamorphosing sea lampreys were collected in Port Britain Creek in 2001, in either sampling period. While 64 of sea lampreys collected during the coded-wire tagging sampling

period appeared to be developing eye-spots, none appeared to transforming when collected during the fall surveys. Of the sea lampreys collected in the fall of 2001, 22 met the criteria described by Youson *et al.* (1993) as ready to undergo transformation.

- The marked lampreys remaining in the streams will be useful for population estimates, growth and development of larval lampreys in differing stream conditions, and movement throughout the stream.

Summary

Adult sea lampreys were introduced into 2 similar Lake Ontario tributaries between 1998 and 2000. Adults were introduced in equal sex ratios (1:1), in all years of the study and for two years at the same adult density in Grafton Creek and in varying densities for the remaining years/streams. During the intensive adult population and subsequent nesting surveys of 1998 and 1999, it was found that the adult population at the time of spawning was lower than the numbers introduced. The adult sea lamprey populations were reduced in both years through emigration, predation, and pre-spawning mortality. Predators (raccoon and mink), were found to be responsible for the removal of a large number of adult sea lampreys in Port Britain Creek in 1999. It is possible that predators may play a larger role in the reduction of adults in the streams at the time of the spawning migration than had previously been reported. Nesting success varied both between streams and among years, though at the lower adult sea lamprey abundance, nesting success was higher (Grafton Creek). This was also the case in Salem Creek, a 'wild migration' of sea lampreys, in the third tributary added to the project in 1999. In 2000, nesting occurred almost 1 month later in the streams, likely the result of cooler water temperatures and adverse water conditions (flood events) during the spawning season. The first nests in Grafton Creek were located June 20, while spawning in the previous years had been completed by approximately June 17.

Larval sea lamprey development was followed throughout the four years of the project, 1998 to 2001. Successful spawning was confirmed in each of the streams in all three years of adult additions through larval sea lamprey sampling. The resulting larval population strength follows the nesting success of the adult sea lampreys introduced into the streams. An increase in larval production occurred in Grafton Creek in 1999, following the increased nesting success of the introduced adults, while at the same time, a reduction in the number of larvae occurred in Port Britain Creek. Overall, the age-1 larval sea lampreys in Port Britain Creek were significantly larger in both length (mm) ($p<0.05$, N=36) and weight (g) ($p<0.05$, N=36), compared to those collected in Grafton Creek, 1999 SMRT sampling. The first transformers were collected in Port

Britain Creek in 2000, while those in Grafton Creek do not currently appear large enough to begin the metamorphosing process.

Coded-wire tagged sea lampreys have been released in both Port Britain and Grafton creeks. These sea lampreys can be used in studies of growth and movement within the stream basin over time, as well as information regarding age at length using the statolith aging technique. Samples should be collected, with documented collection sites, prior to the proposed stream treatments of 2002.

References

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Figure 1: Daily number of carcasses located and nests with eggs found in Grafton Creek, 1998.

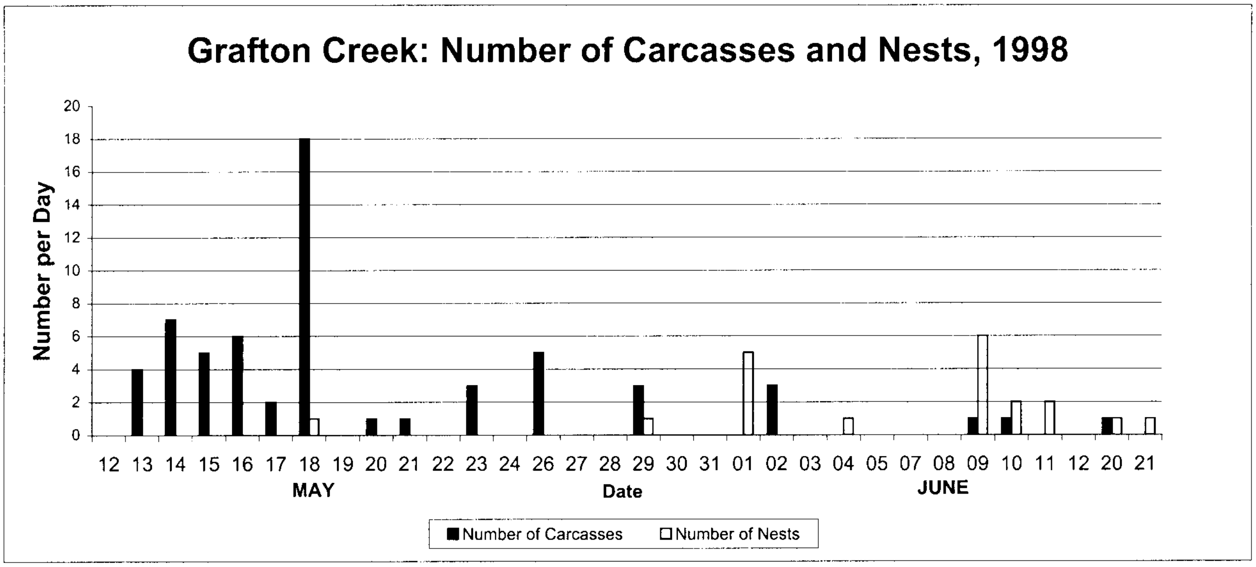


Figure 2: Daily number of carcasses located and nests with eggs found in Port Britain Creek, 1998.

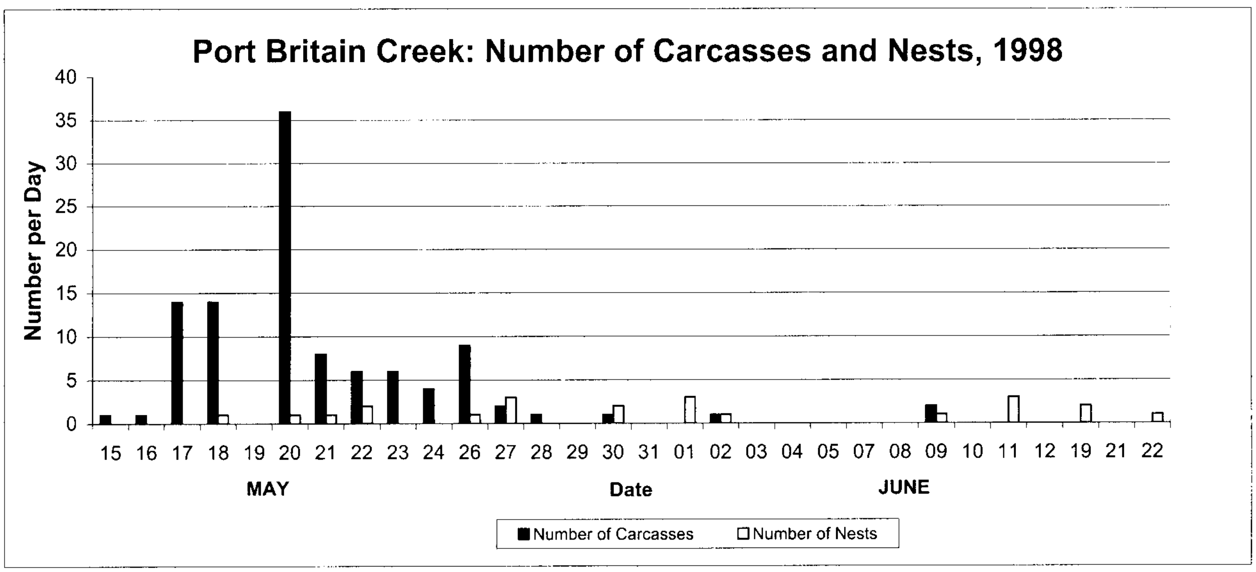


Figure 3: Daily number of nests with eggs found in Grafton and Port Britain creeks, 1998.

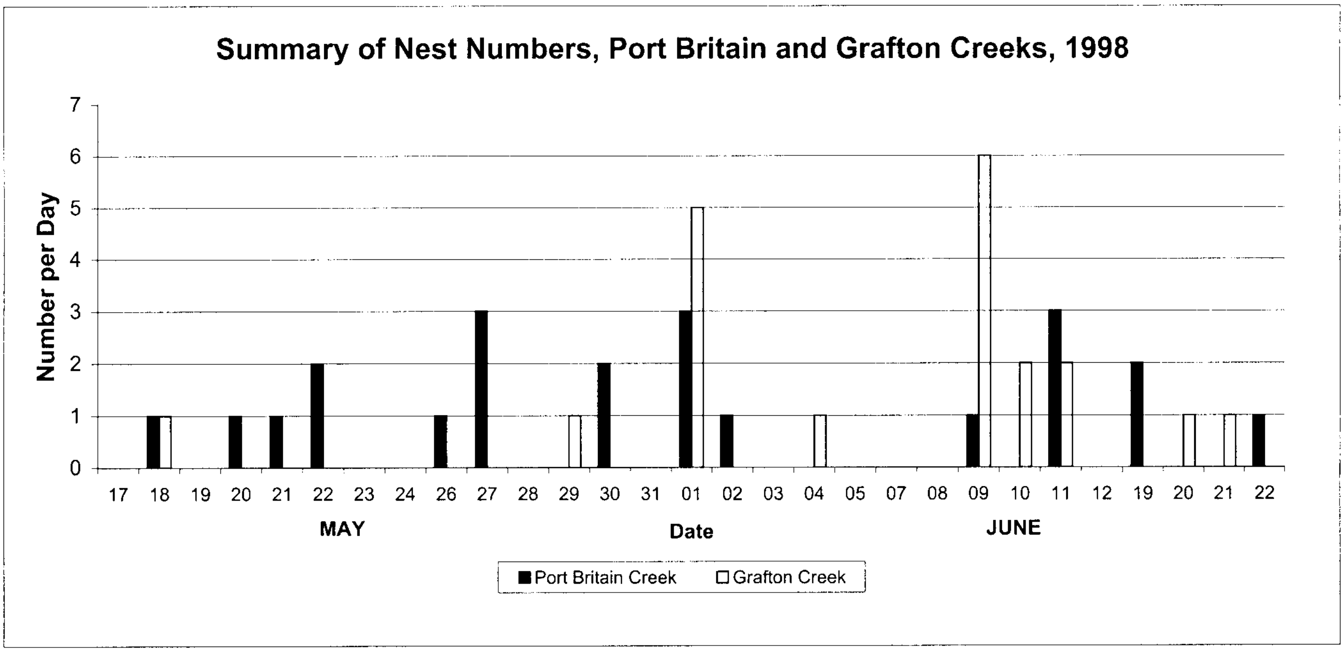


Figure 4: Daily number of carcasses and nests with eggs found in Grafton Creek, 1999.

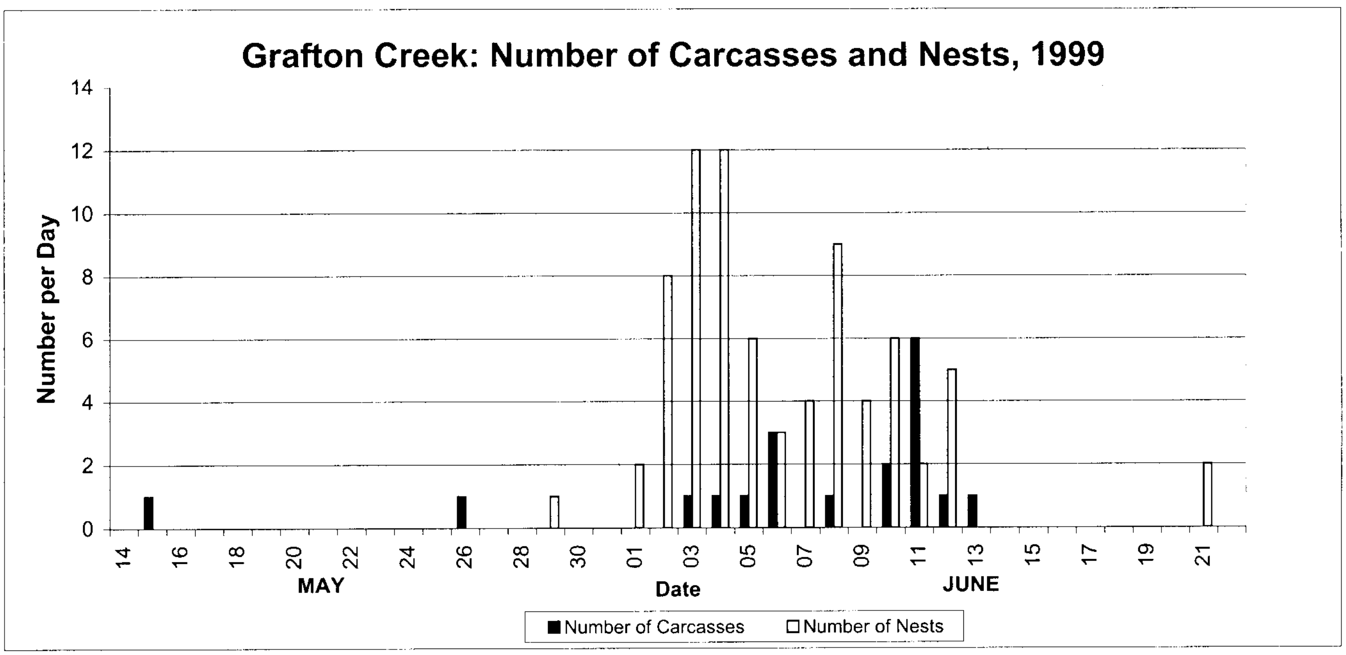


Figure 5: Daily number of carcasses and nests with eggs found in Port Britain Creek, 1999.

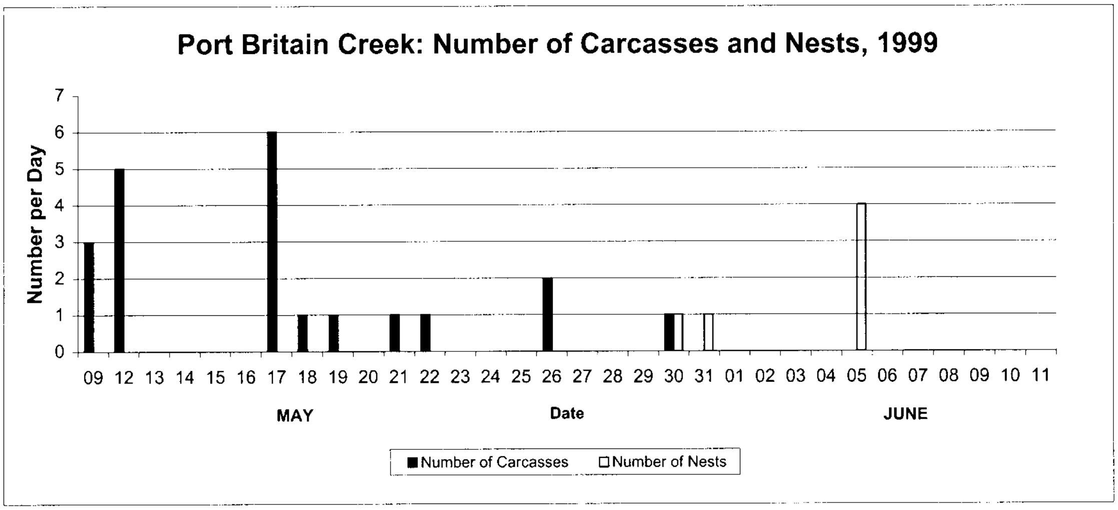


Figure 6: Daily number of carcasses and nests with eggs found in Salem Creek, 1999.

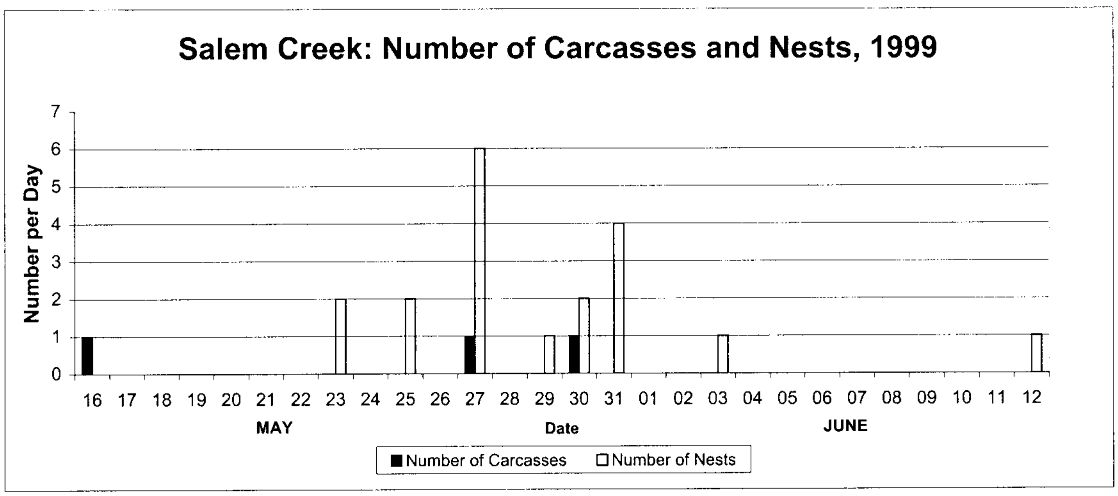


Figure 7: Daily number of nests with eggs found in Grafton, Port Britain, and Salem creeks, 1999.

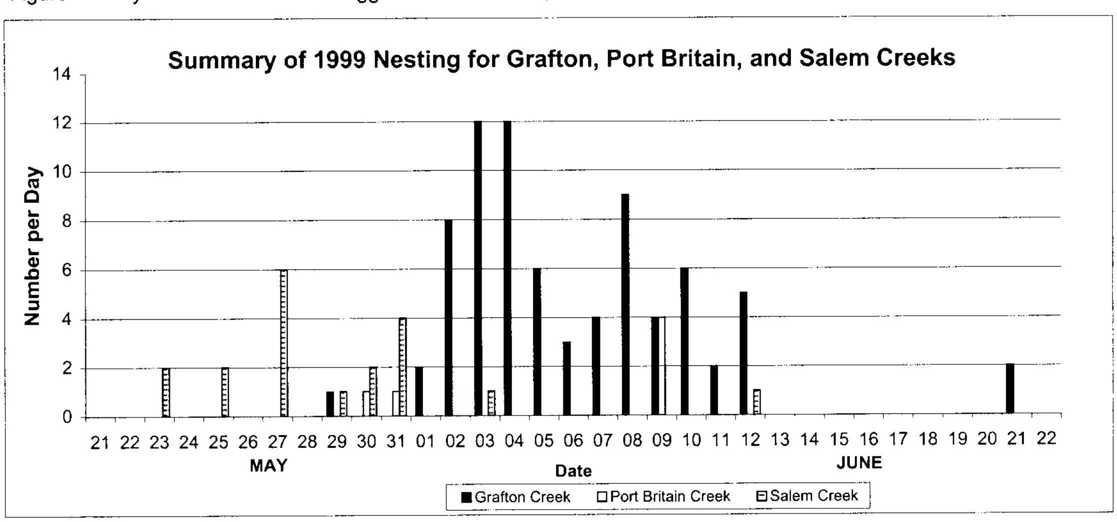
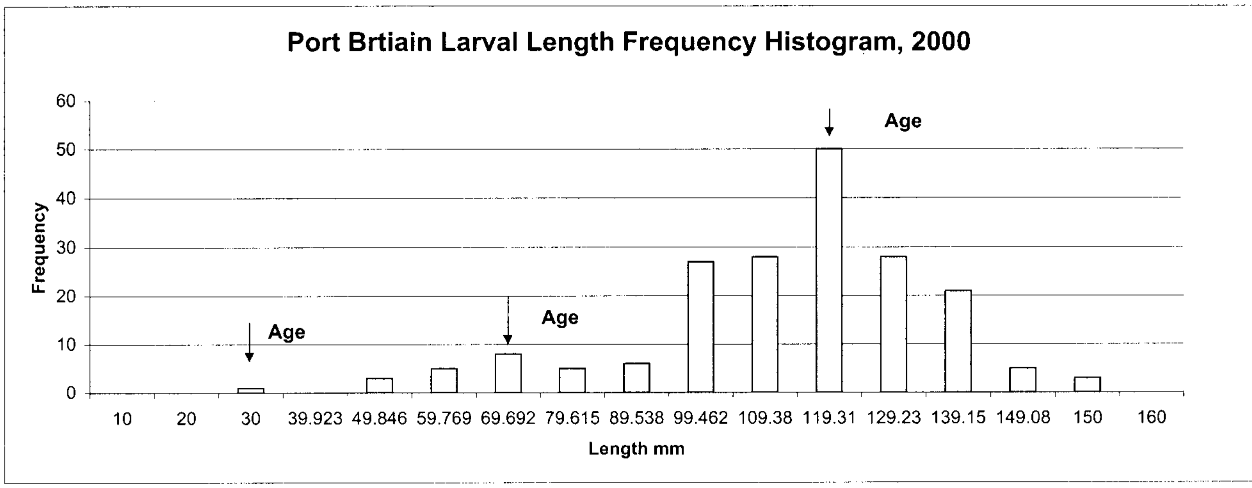
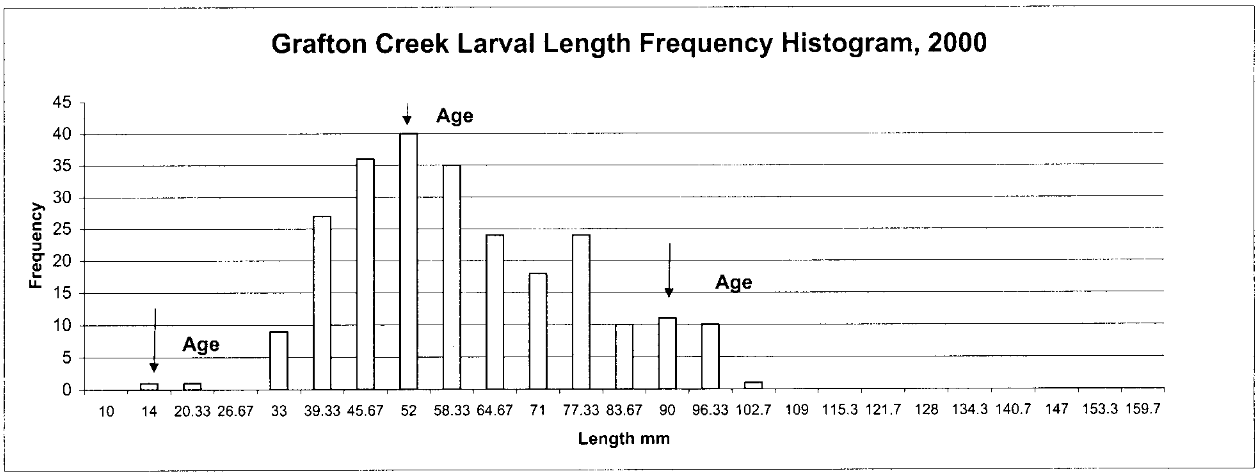
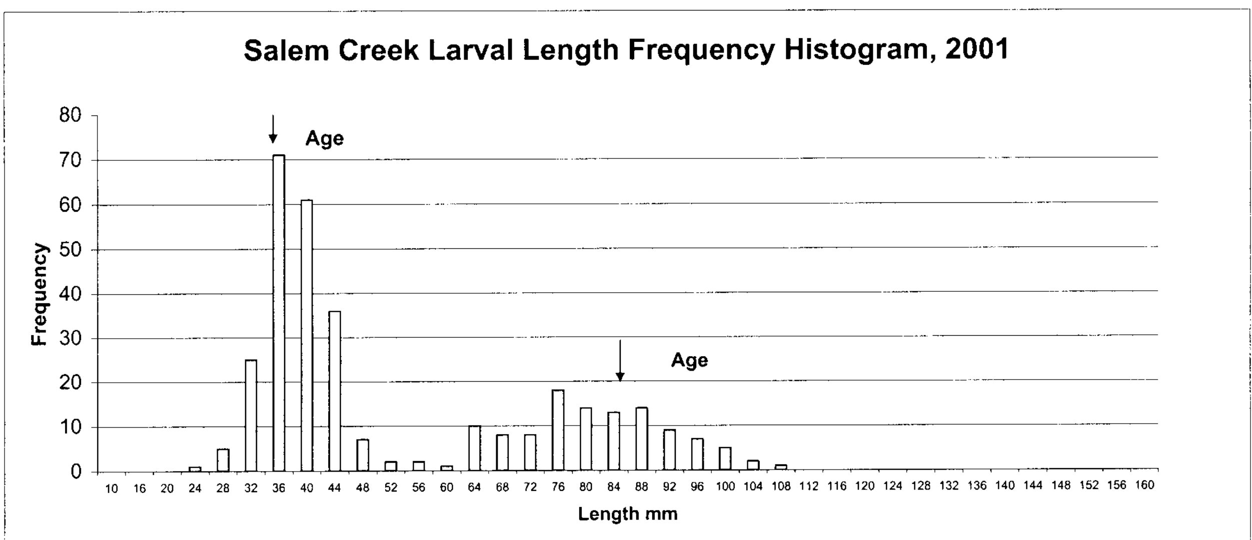


Figure 8: Length frequency histograms for Port Britain, Grafton, and Salem creeks, comparing the size at age for the streams.







GREAT LAKES FISHERY COMMISSION

2001 Project Completion Report[1]

Compensatory Mechanisms in Sea Lamprey

by:

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[1]Project completion reports of Commission-sponsored research are made available to the Commission's Cooperators in the interest of rapid dissemination of information that may be useful in Great Lakes fishery management, research, or administration. The reader should be aware that project completion reports have not been through a peer review process and that sponsorship of the project by the Commission does not necessarily imply that the findings or conclusions are endorsed by the Commission.

PROGRESS REPORT

Compensatory Mechanisms in Sea Lamprey

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February 2001

Our research program on compensatory mechanisms in sea lamprey larvae has focused on three aspects: growth rates, mortality rates, and sexual lability. We have previously reported on our research examining the response of larval growth, size-at-metamorphosis, age-at- metamorphosis, and mortality to a reduction in density and environmental factors. Most of these results are now in print. Furthermore, many aspects of our work on sexual liability are also now in print. The last component of our research program - effect of larval density on the sex and fecundity of lamprey larvae - is reported herein.

Project Hypothesis: Larval density affects the sex and fecundity of lamprey larvae:

Fish gonads like those of other vertebrates develop from an undifferentiated mass of primordial germ cells into either ovaries or testes. Gonochoristic gonads exhibit two patterns of differentiation: a) from an undifferentiated gonad directly into a testis or ovary; and b) from an undifferentiated gonad into an ovarian-like organ that subsequently may change into a testis. In the latter case, the gonad may possess both female and male sex cells for a time; a condition sometimes referred to as intersex.

In landlocked sea lamprey, sex was thought to be determined when larvae reached a total length of about 100 mm. Prior to this, the gonad consists only of germ cells or contains both oocytes and germ cells. We have observed numerous sea lamprey larvae beyond 100 mm from streams throughout the Great Lakes basin and tributary to the Northwest Atlantic Ocean with undifferentiated gonads as well as marked deviations in patterns of gonadogenesis. We use the term 'atypical' to describe those gonads displaying significant deviations in gonadogenesis. The frequent occurrence of atypical gonads suggests these observations are not anomalies.

Environmental sex determination has been reported in lampreys with larval density, growth rate, temperature and pH suggested as controlling factors. Density-dependent sex determination of landlocked sea lamprey has been suggested for the change in the sex ratio following chemical control in the Great Lakes.

Our initial experiments followed gonadal development of individual large sea lamprey larvae (> 100 mm) with typical and atypical gonads through to their definitive sex using a specially developed, non-lethal, biopsy technique which permitted sequential sampling of individual larvae. All larvae were injected with coded wire tags, allowing individual recognition. Concurrently we examined the influence of hormones on sexual differentiation of landlocked sea lamprey and the effects of larval density on endogenous hormones.

Subsets of biopsied sea lamprey larvae were sampled at intervals up to 52 weeks following surgery. Over this period there was a significant increase in the number of presumptive testes over that at the outset of the study. This was a result of presumptive testis development from atypical gonads, oocyte atresia and sex reversals. A companion study clearly showed gonadal biopsy itself did not affect gonadal development. Results of this study suggested that sex may change in as little time as 8 weeks and that it remains labile throughout the larval period.

In another experiment we extended our study of gonadal lability beyond the larval period to include that from early metamorphosis through to the juvenile or parasitic period some 10 months later, again using the non-lethal gonadal biopsy technique. In this study none of the metamorphosing lamprey initially biopsied had atypical gonads. No sex reversals were observed in either the biopsy or sham groups through to the juvenile period when lampreys were actively feeding on teleost fishes. Oocyte numbers did not change over the course of the study in ovaries but oocyte diameter increased. This study indicated that once metamorphosis commences, sex was differentiated and no longer labile.

We have some evidence that the potentially feminizing hormone, 15-hydroxyprogesterone, is produced by the gonads of larvae and juveniles. No synthesis of potentially masculinizing androgens was apparent, nor did larval gonads appear to metabolize androgen substrate. The earlier observation that environmental stimuli are associated with larvae masculinization has prompted the suggestion that sea lamprey gonads may differentiate into ovaries by default and into testes via an environmental synthesis. Larvae about to metamorphose and metamorphosing and transformed lampreys metabolized an androgen precursor and produced steroids possibly used in gonad development and/or metamorphosis.

Our latest experiments examined the effect larval density on gonadogenesis in sea lamprey. In our initial experiment, 88 large larvae from the Harris River were biopsied to determine their sex. Each animal was micro-tagged so that it could be identified at the end of the experiment. These animals were randomly distributed into 28 tanks: 22 tanks with 1 larva, 2 tanks with 7 larvae, 2 tanks with 11 larvae and 2 small tanks with 12 larvae, which simulated densities of 4, 11, 25 and 40 animals m^{-2}. The estimated density of larvae in the Harris River was 9.4 animals m^{-2}. After 14 weeks, the larvae in all tanks were killed and re-sexed. Of the 72 larvae that survived the experiment period and did not lose their microtag, 43 larvae (59.7%) showed no change in sex. Density had no effect on sex. Overall, 22 larvae showed a shift towards femaleness (an increase in oocyte density and a decrease in germ cell density) with 11 larvae becoming females. In contrast, only 7 larvae showed a shift towards maleness (a decrease in oocyte density and an increase in germ cell density), with 3 animals becoming males.

Our second experiment this past summer used a greater density of larvae to examine the effect of larval density on gonadogenesis as well as examining the effect of odour on larval gonadogenesis. Chemical cues likely are the primary form of communication among lamprey larvae. Dr. P.W. Sorensen has shown that lamprey odour can elicit behavioral responses in lamprey at concentrations in the order of 10-100 pg/L.

In this experiment, 48 large larvae from the Bighead River were marked with elastomer and biopsied. After recovering from the surgery, 3 potential male larvae were placed in each of 6 tanks, 3 potential female larvae with placed in each of 6 tanks and 3 potential female or intersex larvae were placed in each of

6 tanks. The sex assigned to each larva was based on observations on biopsied gonads. Eighteen non-biopsied larvae then were added to each of the six tanks with the 3 female biopsied larvae (high-density treatment), while six non-biopsied larvae were added to each of the tanks with the 3 female or intersex biopsied larvae (median-density treatment). No additional larvae were added to the six tanks with the 3 male biopsied larvae (low-density treatment). Each tank contained about 40L of non-chlorinated water, with a flow rate of 0.5 to 1.0 L/min. This design specifically tested whether males under low densities would transform toward femaleness, while females under high densities would transform toward maleness.

To examine the influence of larval odour on gonadogenesis, 18 large larvae from the Bighead River were biopsied to determine their sex. One animal was placed in each of 18 small re-circulating aquaria (12 females and 6 males). Water from each of the 18 tanks was siphoned into one small aquarium at a rate of 0.1 to 0.2 L/min (single flow-through design). The low-density treatment tanks provided the water to the small aquaria with the male larvae. The median and high-density treatment tanks provided the water to the small aquaria with the female larvae. A single, biopsied larva thus was exposed to lamprey odour at one of three concentrations for a 20-week period. Water from 6 tanks was collected and preserved to determine the concentration of lamprey odour.Dr. P.W. Sorenson,University of Minnesota has kindly offered to analysize the water for the concentration of sea lamprey odour. The results of these analyses are not likely to be available before April 2001.

After 20 weeks, the biopsied larvae in the tanks and the aquaria were killed and sectioned to determine their sex. As in the previous experiment, larval density had no effect on sex determination. Shifts toward maleness and femaleness did not depend on larval density. Interestingly, larvae began to metamorphosis starting in early September. We noted that the proportion of larvae metamorphosing by the end of October was also not dependent on larval density, as 17-22% of the larvae in the different treatments metamorphosed.

Experiments thus in 1999 and 2000 both showed that up to 40% of large larvae (greater than 115 mm in length) undergoes a shift in gender as indicated by the density of oocytes and germ cells. Shifts towards femaleness dominated in these experiments, but the shifts in sex were not dependent on larval densities over a range of 4 to 81 larvae per square metre. Once the odour concentrations from the tanks have been determined, we may better be able to associate the laboratory densities with larval densities in streams.

Refereed journal publications resulting from this research

Published or in press:

Beamish,F.W.H. and L.A. Barker. (in press). Gonadal development in sea lampreys from the larval
to the juvenile period:observations through gonadal biopsies. J.Great lakes Res.

Griffiths,R.W. , F.W.H. Beamish, Morrison, B.J., and L.A. Barker. 2001. Factors affecting growth rates and size-at-metamorphosis of larval sea lamprey in lampricide-treated streams. Trans. Amer. Fish. Soc. (in press).

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Barker, L.A. and F.W.H. Beamish. 2000. Gonadogenesis in landlocked and anadromous forms of the sea lamprey, Petromyzon marinus. Environmental Biology of Fishes 59: 229-234.

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Barker, L.A., B.J. Morrison, B.J. Wicks and F.W.H. Beamish. 1998. Potential fecundity of landlocked sea lamprey larvae, Petromyzon marinus, with typical and atypical gonads. Copeia 1998 (4): 1070-1075.

Wicks,B.J.,L.A. Barker.B.J. Morrison,and F.W.H. Beamish.1998. Gonadal variation in Great Lakes
sea lamprey (Petromyzon marinus) larvae. J.Great lakes Res. 24:962-968.