RECRUITMENT DYNAMICS OF GREAT LAKES SEA LAMPREY (*PETROMYZON MARINUS*) POPULATIONS AND IMPLICATIONS FOR INTEGRATED PEST MANAGEMENT

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ABSTRACT

RECRUITMENT DYNAMICS OF GREAT LAKES SEA LAMPREY (*PETROMYZON MARINUS*) POPULATIONS AND IMPLICATIONS FOR INTEGRATED PEST MANAGEMENT

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To determine whether the rate of sea lamprey (*Petromyzon marinus*) control in the Great Lakes is sufficient to achieve lasting benefits, we must understand sea lamprey recruitment and growth dynamics as the population is driven to low levels. The Great Lakes Fishery Commission (GLFC) wishes to reduce reliance on lampricides, and use alternative (adult) sea lamprey control methods that seek to reduce the number of spawners in order to decrease subsequent recruitment. However, management actions that aim to reduce reproductive success might not result in concomitant reductions in recruitment, for two reasons. First, populations may compensate for reduced spawning numbers through increased larval survival or growth. Second, density-independent factors that affect recruitment may vary among streams and years.

Sea lamprey stock-recruitment observed in streams across the Great Lakes basin indicated both compensation (density-dependent survival) and a large amount of density-independent recruitment variation. Lakes Superior and Michigan tributaries, streams with larger numbers of lamprey competitors, and streams regularly requiring lampricide treatment showed significantly higher recruitment, but year did not affect the observed recruitment pattern. Therefore, management models should account for differences in recruitment dynamics among sea lamprey-producing streams, but not common year effects.

Measuring recruitment in sea lamprey populations requires accurate assessments of larval sea lamprey age, so a standard protocol was developed for estimating the population age composition of larval sea lamprey using both length-frequency data and statolith data, which have both been used for age determination in sea lampreys. By establishing known-age populations in two contrasting streams and comparing the age determined by statolith interpretation to the known age, I was able to assess bias in this method of aging. When statolith data were bias-corrected and combined with length-frequency data in a statistical model to determine proportion-at-age in a sampled sea lamprey population, the precision of this estimate was substantially increased than when using only length-frequency data.

To evaluate control strategies, the GLFC has used models of sea lamprey population dynamics, but models can misinform managers if they fail to account properly for process error, measurement error, and model uncertainty. Since the effectiveness of adult control methods depends on the ability to overcome recruitment variation and the effectiveness of lampricide control depends on good stream selection, a sea lamprey population model that accounts for recruitment variation and larval assessment uncertainty was developed. This model simulates the existing control program for Lake Michigan and estimated the cost and effort at which adult control becomes a viable complement, or alternative to lampricide control. Assuming our current best estimates of adult control costs and efficacy, results suggest that increasing adult control efforts at the expense of lampricide use will result in an increased abundance of sea lamprey. Adult control measures must become less costly and more effective before using a combination of both control methods will compare favorably to using only lampricide control.

DEDICATION

I dedicate this dissertation to my family, who by reading this can finally understand what I have been doing all these years.

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INTRODUCTION

Sea lampreys (*Petromyzon marinus*) are parasitic pests that were a contributing factor in the collapse of lake trout (*Salvelinus namaycush*), whitefish (*Coregonus clupeaformis*), deepwater cisco (*Leucichthys johannae*) and blackfin cisco (*Coregonus nigripinnis*) populations in the Great Lakes during the 1940s and 1950s. Sea lamprey entered the Great Lakes from the Atlantic Ocean through a series of shipping canals that were built to connect the Upper Great Lakes with the Atlantic Ocean (Morman *et al.* 1980). Sea lampreys had invaded all of the Great Lakes by 1938, and by the early 1960s lake trout fishery harvests had declined to 2% of pre-invasion levels (Schneider *et al.* 1996). Management efforts began in the 1950s, and continue today to control sea lamprey populations throughout the Great Lakes.

The life cycle of the sea lamprey in the Great Lakes begins in lake tributaries where fertilized eggs hatch into small, wormlike larvae called ammocoetes which burrow into soft stream bottoms to feed on detritus for 3 to 6 years. After ammocoetes reach a certain size (~120 mm) they metamorphose into parasitic juveniles and migrate into the Great Lakes where they feed for 12 to 20 months. Maturing adults then migrate into streams to spawn, after which they die. The complete life cycle, from egg to adult, can take an average of 5 to 8 years to complete.

Juvenile sea lamprey do their damage by attaching to large fish with their suction-cup mouth and rasping a hole through the fish's scales and skin with their teeth so they can feed on its blood and body fluids. During its parasitic lifetime a single sea lamprey has been estimated to destroy 6.6 to 18.9 kg of hosts from May through September (Swink 2003). Bence *et al.* (2003) calculated values of 1.36, 1.32, and 0.75 for lake trout deaths per sea lamprey in lakes Superior, Huron, and Michigan, respectively. In the Great Lakes sea lampreys have no commercial value and other fish do not normally feed on them, so there are no natural population controls for sea lamprey. Due to destruction of valuable fish stocks and the adverse effect of sea lampreys on the ecological balance of fish species in the Great Lakes, the Great Lakes Fishery Commission (GLFC) was established in 1955 by a treaty between Canada and the United States. Their mission is to coordinate efforts to formulate and implement a program to eradicate or minimize sea lamprey populations in the Great Lakes (Pearce *et al.* 1980).

The sea lamprey control program uses several techniques to reduce abundance of sea lampreys during different stages of their life cycle. The primary technique involves applying a lampricide, 3-trifluoromethyl-4-nitrophenol, called TFM, to streams to kill ammocoetes while they are burrowed in the stream bottom. TFM is effective at killing ammocoetes, and its impact on other fish species, aquatic plants, invertebrates, and wildlife is minimal or of very short duration (Dahl *et al.* 1980). Lampricide treatments are believed, when effective, to remove between 95 and 99% of the ammocoetes from treated streams. Currently, about 250 Great Lakes tributaries are treated at regular intervals with lampricide, although the cost of TFM prohibits treating all streams that will produce parasitic sea lampreys each year (Steeves 2002). Through biological assessments and careful TFM use, the GLFC and its agents have successfully reduced sea lamprey populations in the Great Lakes by 90% from peak population levels. In 1995, the GLFC adopted an Integrated Pest Management Strategy, which included defining targets for control that optimize benefits, use of quantitative methods and systems approaches, and application of alternative methods of control (Christie and Goddard 2003).

Alternative methods of control have been used to target adult sea lampreys and include; 1) using barriers to prevent upstream migration during spawning; 2) sterilizing and releasing adult male lampreys; 3) and trapping adult lampreys during their spawning run. Newer barrier designs include velocity barriers that take advantage of the lampreys' poor swimming ability; electrical barriers that repel sea lampreys during the spawning run without risk to other fish or animals; and adjustable-crest barriers, which can be inflated during the spawning run and then deflated to allow other fish to pass during the rest of the year (Lavis *et al.* 2003). The sterile-male-release-technique has shown promise in larger streams such as the St. Marys River, where lampricide treatments and barriers are impractical (Schleen *et al.* 2003). Sea lamprey traps are also employed to catch adult lampreys during their upstream migration, and the use of pheromones to lure sea lampreys into traps is a relatively new alternative control method being investigated (Twohey *et al.* 2003*b*). Each of these alternative control techniques operates by reducing the effective size of the spawning population of sea lamprey in order to decrease subsequent recruitment, and thus are referred to here collectively as adult control methods.

These strategies are being considered as alternatives to the use of lampricides despite the obvious success of lampricides because of public concern about pesticide use and rising costs of TFM. Specifically, the GLFC wants to achieve 50% of control through adult control methods (GLFC 2001). However, the degree to which these adult control methods are effective will depend on the degree to which reductions in reproductive success consistently result in reduced recruitment. There are two reasons why reducing reproductive success might not result in concomitant reduction in recruitment. First, reducing the spawning population may result in lamprey populations compensating for this reduction with an increase in larval survival or growth rates. Second, density-independent factors affecting recruitment, such as winter severity may vary widely among streams and years leading to inconsistent patterns of recruitment relative to spawner numbers. Density-independent variation in lamprey recruitment poses a threat when using adult controls, because even at low spawner densities high recruitment events can result in larval densities that exceed acceptable levels.

Sea lamprey program managers using adult controls wish to reduce the spawning population to low levels and get a concomitant decrease in the level of recruitment. However, a stock-recruitment meta-analysis involving data from 49 stream-years, found evidence for significant compensation in Great Lakes sea lamprey populations and the existence of large recruitment events that occurred even when the number of spawning females was quite low (< 2 females per 100 m^2) (Jones *et al.* 2003). 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 under conditions that mimicked adult control methods that reduce spawners to a low level, as differences among streams may give us insight into how density-independent factors affect recruitment (Jones *et al.* 2003). The stock-recruitment data we currently have on Great Lakes sea lamprey consists of a few years of data on many streams, which makes it difficult to distinguish “stream” effects from “year” effects. Two factors that vary considerably among lamprey-producing streams and that are likely to influence recruitment are stream productivity and growing season length, and investigating factors such as these that may affect recruitment might help to determine when and where to apply adult controls. Analysis of a large sea lamprey stock-recruitment dataset can also be used to suggest to management a level of control on adult sea lamprey reproduction required to reasonably ensure success of adult control strategies.

Quantifying recruitment can be limiting due to error in larval age determination, because evaluating the recruitment of sea lamprey involves assessing the larval population in streams and separating the population into age classes. Identification of age classes through the inspection of length-frequency distributions is subjective, especially because there is often overlap in lengths between age classes. The error associated with this approach introduces uncertainty that is difficult to quantify into abundance at age 1 (i.e., recruitment) estimates and other analyses requiring estimation of the age composition of sea lamprey populations. Otoliths have been used to estimate age in teleosts, but lampreys do not have otoliths, having instead an analogous structure called a statolith. Statoliths are the only calcified structure found in lampreys, and when oriented properly and viewed under transmitted light, two types of bands appear as layers within the statoliths; the combination of the two corresponding bands has been shown to represent annual growth (Hollett 1998). However, of the techniques that have been used to prepare and evaluate age in sea lamprey statoliths, age determination of sea lamprey using statoliths has never been validated for more than one year, and the most accurate method has yet to be determined.

To develop a standard protocol for ammocoete age-assessment using both length-frequency and statolith data, requires the validation and improvement of both methods of age interpretation. Currently, age interpretation using length-frequency data is subjective; however Schnute and Fournier (1980) describe a statistical method for objectively estimating age composition from length-frequency data that assumes (1) a von Bertalanffy growth function and (2) that variance of length increases with age for larval sea lampreys. Fournier (1983) amended the approach to include partial age composition information, presumably obtained from a sample of fish from which a calcified structure was removed. To use statoliths as a method of aging larval sea lampreys it must be validated that the banding pattern can be repeatably visualized and represents the true age of the ammocoete over multiple years. Only by using mark-recapture studies or known-age fish can all age classes in a population be validated (Beamish and McFarlane 1983). This can most easily be accomplished by collecting statoliths over time from a single cohort of known age sea lamprey to determine which method of statolith evaluation more accurately estimates ammocoete age. Using a statistical method that combines length-frequency and statolith data to estimate age composition of sea lamprey populations would lead to more accurate estimates of recruitment, ammocoete growth rate, survival, and age at metamorphosis, which is very important life history information to the pursuance of sea lamprey control.

Models that have been used in the past to guide integrated management of sea lamprey and evaluate adult control strategies have not accounted for density-independent recruitment variation. Management models that did not explicitly incorporate density-independent recruitment variation substantially overestimated the benefits of adult lamprey control options that rely on reducing adult reproductive success (Jones *et al.* 2003). Current models also fail to include larval assessment uncertainty in short-term projections of juvenile sea lamprey populations to prioritize streams for lampricide control. Consequently, the estimates of abundance produced often do not accurately reflect actual lamprey abundance for a majority of streams (Steeves 2002). Models that guide the integrated management of sea lamprey are based partly on a synthesis of knowledge of sea lamprey demographics conducted during the 1980s. Components of management models, such as the recruitment, growth, survival, assessment, and abundance components need to be revised through data synthesized as part of the second Sea Lamprey International Symposium (SLIS) in 2000.

Accounting for density-independent recruitment variation, and uncertainty in larval growth and assessment in management models is important to facilitate a realistic comparison of the effectiveness of lampricide and adult control strategies. The use of models to explore the potential for hybrid strategies, where sea lampreys are controlled through a combination of lampricide and adult control, has been emphasized as a possible option, but has yet to be investigated. The use of adult control methods on larger streams is unlikely to eliminate the need for lampricide control; it is possible that simply reducing the frequency at which these streams need to be treated would be sufficient to justify the costs of adult control. Considerable savings may be achieved by directing adult control efforts at these rivers, but there are still many unanswered questions about the costs and efficacy of adult control. A more realistic sea lamprey population model that accounts for recruitment variation and assessment uncertainty, and allows for the evaluation of a range of sea lamprey control strategies is what is needed to estimate the cost and effort at which adult control becomes a viable complement or alternative to lampricide control.

Accurate estimation of the benefits of adult control strategies is essential for effective integrated management of sea lampreys. To address this issue this dissertation; in chapter 1 *i*) measures recruitment variation in lampreys at low spawning stock size in contrasting streams and investigates factors that may affect recruitment; in chapter 2 *ii*) creates "known-age" populations of larval sea lamprey to be used to validate age determination using statoliths and develops a standard protocol for ammocoete age assessment using length-frequency data and partial age composition data; and in chapter 3 *iii*) develops a realistic sea lamprey simulation model including current recruitment and assessment uncertainty and demographic information to assess the relative performance of sea lamprey management strategies.

Chapter 1

FACTORS AFFECTING RECRUITMENT DYNAMICS OF GREAT LAKES SEA LAMPREY POPULATIONS

Abstract

Knowledge of stock-recruitment dynamics is as important for control of pest species such as the sea lamprey (*Petromyzon marinus*) as it is for sustainable harvest management of exploited fish species. Sea lamprey stock-recruitment data combined from streams across the Great Lakes basin indicated both compensation (density-dependent survival) and a large amount of density-independent recruitment variation. A mixed-effects model tested factors that might affect recruitment variation, using a Great Lakes dataset comprising 90 stream-years. Lakes Superior and Michigan tributaries, streams with larger numbers of lamprey competitors, and streams regularly requiring lampricide treatment showed significantly higher recruitment. Year (as a random effect), alkalinity, and thermal stability did not affect the observed recruitment pattern. In four long-term study streams we observed significant differences among streams but not among years. Differences in recruitment were consistent with anecdotal evidence of quality of spawning and larval habitat among streams. Our findings indicate that management models need to account for differences in recruitment dynamics among sea lamprey-producing streams but not common year effects.

Introduction

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

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

Management actions that aim to reduce reproductive success might not result in concomitant reductions in recruitment, for two reasons. First, sea lamprey populations may compensate for reduced spawning numbers through increased larval survival or growth; in a stock-recruitment meta-analysis involving data from 49 stream-years, Jones *et al.* (2003) found evidence for significant compensation in Great Lakes sea lamprey populations. Second, density-independent factors that affect recruitment, such as winter severity, may vary among streams and years, and cause variations in recruitment that are unrelated to spawner numbers. Peterman *et al.* (1998) found that important environmental processes affecting variation in sockeye salmon survival rate from spawners to recruits operate at regional scales, rather than at the larger, ocean-basin scale. Sockeye salmon productivity within a region may therefore be driven by persistent changes in the environment rather than management actions such as enhancement or harvesting (Peterman *et al.* 1998). In their meta-analysis, Jones *et al.* (2003) found that density-independent recruitment variation was large and concluded that further research was needed to discriminate between “stream” effects and “year” effects. Density-independent variation in sea lamprey recruitment can limit the effectiveness of adult controls that reduce spawner abundance, because even at low spawner densities high recruitment events can produce larval densities that exceed acceptable levels. Deterministic sea lamprey management models that do not explicitly incorporate density-independent recruitment variation (e.g. Koonce *et al.* 1993) will substantially overestimate the benefits of adult sea lamprey control options that rely on reducing adult reproductive success (Jones *et al.* 2003).

This research differs from our earlier investigation of sea lamprey recruitment dynamics Jones *et al.* (2003) in five ways: (*i*) the number of stream-years of stock-recruitment data analyzed (90); (*ii*) the use of an objective, likelihood-based model, as opposed to subjective interpretation of length-frequency data, to separate age-1 recruits from other age-classes of sea lamprey; (*iii*) the assembly of data on stream characteristics analyzed to attempt to explain variation in recruitment patterns among streams; (*iv*) the establishment of four long-term study streams where we introduced spawners at a low level to mimic adult control reductions in spawner abundance, and measured the subsequent recruitment at age 1 over several years; and (*v*) an analysis of data from these four long-term study streams that aims to separate stream and year effects on sea lamprey recruitment dynamics.

Methods

We assembled data on spawning population size and on larval recruitment at age 1 in the following year from Jones *et al.* (2003), and from similar data collected subsequently, resulting in a database of 90 stream-years of sea lamprey stock-recruitment data (Figure 1). Spawner abundances were controlled by deliberately releasing adult sea lampreys above barriers in 55 cases, or spawning population abundance was estimated in 35 cases using a mark-recapture method applied to sea lampreys captured in adult assessment traps (Mullett *et al.* 2003). We estimated age-1 larval abundance using the same electrofishing survey technique in all streams, as described in Jones *et al.* (2003). Habitat was classified at randomly-spaced transects along the stream as Type I (fine sand and silt which is preferred by sea lampreys), Type II (coarser sand which is acceptable for sea lampreys), or Type III/IV (gravel, cobble, bedrock, exposed islands, all of which are unsuitable for sea lampreys. Using a backpack electrofisher we surveyed Type I plots at approximately half of the transects, and Type II plots were surveyed at about every eighth transect. Stock and recruitment were calculated from

$$S = \frac{\widetilde{S}}{H_w}, R = \frac{\widetilde{R}}{H_w} \tag{1),}$$

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

$$H_w = A_1 + \frac{\overline{D_{II}}}{\overline{D_I}} \cdot A_{II} \tag{2}$$

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

To determine the proportion of ammocoetes in our surveys that were age 1 we used a statistical method, similar to that described by Schnute and Fournier (1980) for objectively estimating age composition from length-frequency data (see chapter 2). This method was used because there is not consensus on the accuracy of statoliths for determining age composition of larval sea lampreys, and because we felt that the statistical methods would be preferable to a subjective determination of age composition from length-frequency data. The statistical method relies on an assumption about the growth dynamics of the fish stock of interest; we assumed larvae grew according to a von-Bertalanffy growth function and that individual variation in length increased linearly with age. We estimated age composition using maximum likelihood methods implemented in AD Model Builder (Otter Research 2000). We were able to determine proportion at age 1 using this model for nearly all stream-years that contained more than one age class of ammocoetes. In ten stream-years either only the age-1 class was present (five cases), or proportion at age 1 was determined subjectively by visual inspection of length-frequency plots, because the model did not converge to a solution (five cases). The estimated proportion at age 1 was multiplied by the total sea lamprey catch to estimate age-1 sea lamprey catch in each stream-year.

To learn how differences among streams might affect recruitment, we also collected data from four study streams (Figure 1) over a period of several years. We selected four streams that had previous years of sea lamprey stock-recruitment data: two warm, high-alkalinity streams in the Lake Ontario drainage (Port Britain and Grafton creeks -- 27 km apart) and two cold, low-alkalinity streams along the north shore of Lake Superior (Carp and Big Carp rivers-- 48 km apart). Three years of data from Port Britain and Grafton creeks (1999-2001) and four years from Carp (1997-2000) and Big Carp rivers (1998-2001) were available prior to this study. We wished to assess recruitment under conditions that mimicked adult control methods that reduce spawners to a low level, and further investigate how recruitment varies at very low spawner densities. Jones *et al.* (2003) stock-recruitment data indicated that no high recruitment events were observed at stock sizes of less than 0.5 spawning females·100 m^{-2}. In our study streams, by adding 10 pairs of spawners each year to each stream we kept stock size below 0.5 females·100 m^{-2}. We added only 10 adult male and 10 adult female sea lampreys above barriers in these streams for three years starting in 2002 (Carp and Big Carp rivers) or 2003 (Port Britain and Grafton creeks).

The mean age-1 density in each habitat type, the area of each habitat type and resulting abundance of age-1 larvae (i.e., recruitment) were computed for each stream-year. We fit the data to a Ricker stock-recruitment model of the form

$$R = \alpha \cdot S \cdot e^{-\beta \cdot S + \varepsilon} \tag{3}$$

which can be rewritten as a linear model

$$\ln\left(\frac{R}{S}\right) = \ln(\alpha) - \beta \cdot S + \varepsilon \tag{4}$$

where ln(R/S) is an index of survival to age 1 (effectively recruitment, in this study), S is the number of female spawners·100 m^{-2} of larval habitat, α describes average survival across stream-years when S is close to zero, β describes the degree to which survival falls as S increases, and ε is a normally distributed error term with mean zero and variance σ^2.

Jones *et al.* (2003) concluded that measurement error was a negligible component of the observed, overall error in ln(R/S), given the survey methods we used. To calculate an overall sea lamprey stock-recruitment relationship and to combine data from multiple streams in the stock-recruitment analysis, we assumed that all streams shared a common α term and that β depended 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.

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

$$\ln\left(\frac{R}{S}\right) = \ln(\alpha) + \nu + \chi + \delta + \lambda + \rho + b - \beta \cdot S + \varepsilon \qquad (5)$$

where b and ε are normally distributed with mean zero and variance σ^2.

α = Average survival across all streams when number of spawners is zero
ν = Lake effect
χ = Thermal stability effect
δ = Alkalinity effect
λ = Consistency of sea lamprey production effect
ρ = Competitor effect
b= Year effect (random)
β = Density dependence term
ε = Error term

Lake (Superior, Huron, Michigan, Ontario) was used as a surrogate for the effect of a stream's location. Thermal stability was included as a categorical variable, as stream temperatures were determined by sea lamprey control agents to either parallel air temperature (warm) or be more regulated by groundwater input (cold). In general, warm streams were those where summer water temperatures frequently exceeded 20°C. The thermal niche of larval sea lamprey is considered to be between 17.8 and 21.8 °C, and lab studies found maximal survival of exogenous feeding sea lamprey larvae reared at 21°C, and no survival at 23°C after a three-month period (Holmes and Lin 1994; Rodriguez-Muñoz *et al.* 2001). Alkalinity was used as a surrogate for stream productivity, and streams were classified as high if reported alkalinities were greater than 100 $mg \cdot L^{-1}$ $CaCO_3$ and low if they were below 100 $mg \cdot L^{-1}$ $CaCO_3$. The factor "consistency of sea lamprey production" refers to an *a priori* categorization of streams by sea lamprey control agents into regular or irregular sea lamprey producers. Regular producers are streams subjected to a reliable cycle of lampricide treatments (i.e., they have been treated every 3, 4, or 5 years, depending on the stream). Irregular producers are subjected to a less consistent cycle of treatment. The competitor effect was a categorical variable and was based on estimated numbers of native lampreys of all ages (*Ichthyomyzon spp.* or *Lampetra appendix*) and sea lampreys that were not age 1; i.e., all lampreys that were potential competitors to age-1 sea lamprey recruits. Categories were $<100 \cdot 100\ m^{-2}$ (few), between 100 and $299 \cdot 100\ m^{-2}$ (some), and >= 300 lamprey competitors$\cdot 100\ m^{-2}$ of larval habitat (many). The year of recruitment was included as a random factor, to account for year to year variability (Littell *et al.* 1996). The variance in the index of survival that can be attributed to the random effect was estimated using the Minimum Variance Quadratic Unbiased Estimators (MIVQUE) for estimating variance components and tested for significance using Restricted Maximum Likelihood (REML) in Statistica 7.0 (StatSoft, Inc. 2004), to see if year as a random effect should be included in the final model. All effects other than year were modeled as fixed effects.

We ran a separate analysis on the four long-term study streams established in this study (a total of 24 stream-years worth of observations) to test for the effect of stream and year on recruitment variation, using a mixed-effects model with stream as a fixed effect and year as a random effect, normally distributed with mean zero and variance σ^2.

Results

Doubling the size of the sea lamprey stock-recruitment database did not substantially alter the overall pattern described in an earlier study (Jones *et al.* 2003). Recruitment of sea lampreys was highly variable among streams, even after accounting for the effect of stock size (Figure 2*a*). The index of survival (ln(R/S) was lower at higher stock size, indicating the occurrence of compensation. As well, large recruitment events occurred even at stock sizes below 1·100 m^{-2}, although they were not observed at very low stock sizes (< 0.2 females·100 m^{-2}; Figure 2*b*). In our four long-term study streams we introduced spawners at low levels since 2002 (< 0.5 females·100 m^{-2}) to mimic adult control methods that reduce spawner abundance; recruitment was low (<50 age 1 larvae·100 m^{-2}) in all but one case (Figure 3).

The regression of ln(R/S) on S revealed a statistically significant, negative slope ($\beta = -0.1584$, SE = 0.0225, $p(\beta = 0) < 0.0001$, df =88; Figure 4), which provides statistical evidence of compensation. The amount of variance in the index of survival attributable to the random effect of year was close to zero ($\sigma_{year} = 0.0532$, $\sigma_{error} = 2.103$), and the variance component was not significantly different from zero (REML= 0.2030, p=0.48). Therefore, year was removed from the model and we tested the remaining fixed effects on survival. The resulting general linear model revealed significant effects of stock size, lake, consistency of sea lamprey production, and competitor abundance. Lake significantly affected survival (p=0.002, $F_{3,80}$=5.367), and Tukey HSD pair-wise comparisons indicated that streams tributary to Lakes Superior and Michigan experienced significantly higher survival than streams tributary to Lakes Huron and Ontario (Figure 5). Survival in streams with regular sea lamprey production was significantly higher than in those with irregular production (p=0.001, $F_{1,80}$=11.18, Regular producer LS mean=4.00, Irregular producer LS mean=2.86). The number of competitors significantly affected survival (p=0.002, $F_{2,80}$=6.602), but contrary to expectations, Tukey HSD pair-wise comparisons indicated significantly lower survival in streams with the fewest competitors (Figure 6).

The mixed model testing the effect of stream and accounting for year to year variability on the four long-term study streams revealed a significant effect of stream (p=0.0002, $F_{3,12}$=15.68) on survival. Tukey HSD pair-wise comparisons indicated Carp River had significantly higher and Port Britain Creek had significantly lower survival than the other streams (Figure 7). As with the larger dataset, the amount of variance in the index of survival attributable to the random effect of year was close to zero (σ_{year} = 0.0162, σ_{error} =1.005), and the variance component was not significantly different from zero (REML= 0.0705, p=0.89).

Discussion

When pest management includes tactics that aim to reduce the size of the reproducing population, it is valuable to know something about the relationship between stock and recruitment, just as it is for the management of exploited species.

Understanding the stock-recruitment relationship of a population will reduce uncertainties and risks related to management decisions not only about how to sustainably harvest a population, but how to effectively reduce the population of a harmful pest species. Density-independent variation in the survival of offspring can cause high or low recruitment from the same initial number of fertile, mature adults, which suggests that a better understanding of the factors causing this variation would be of use to managers, especially if those factors can be controlled or manipulated. Density-dependent, compensatory variation in survival can thwart efforts to control pests by targeting the adult stock, so an understanding of the power of a pest population to compensate is important to specifying the level of control necessary to overcome this compensatory power and reduce pest abundance over the long run.

In this study we provided further evidence of significant density-dependent compensation for sea lamprey populations in 37 streams in the Great Lakes basin. We also confirmed the presence of a large amount of density-independent recruitment variation (overall observed variance was 3.28), and showed that this variation can be partially explained by differences among streams, but not by coherent variation among years. Management models that are used to assess strategies for sea lamprey control aimed at adult sea lamprey should explicitly account for these stock-recruitment dynamics. Failure to do so will lead to optimistic assessments of the overall promise of such strategies (Jones *et al.* 2003) and potentially to sub-optimal decisions about where to target efforts to reduce adult numbers, as we discuss further below.

Many pest control techniques, such as the sterile male technique, were first developed to manage agricultural pests and achieved some success (Knipling 1955).

Early models of sterile insect release dynamics were simple algebraic models that assumed density-independent population regulation, so they predicted if the same numbers of sterile insects were released in each generation the percent decline in the pest population per generation would increase with time (Knipling 1955). However, many populations exhibit compensation at low population density, which can result in numbers rebounding after a release (Gould and Schliekelman 2004). Thus, the "increasing effect over time" predicted by the early models did not always occur, leading to failure of many pest eradication programs (Gould and Schliekelman 2004). Considerable financial resources have been invested in novel (mostly molecular) techniques designed to control pests, unfortunately the investment in population dynamics and population genetics research that is needed to assess, and potentially improve, the utility of the techniques has not been paralleled (Gould and Schliekelman 2004). Scott *et al.* (2002) found that different mechanisms of population regulation in mosquitoes that transmit malaria and dengue virus could lead to an unpredicted advantage for populations we are attempting to control through novel means, which could lead to disastrous results; only by gaining knowledge of their population regulation can we accurately begin to predict outcomes of proposed interventions.

The importance of density-dependent mechanisms for other vertebrate pest control strategies has also received recent attention. European rabbit (*Oryctolagus cuniculus*) populations were observed to exhibit strong compensatory increases in survival and recruitment when up to 80% of adult females were sterilized (Twigg and Williams 1999). Frederiksen *et al.* (2001) developed a population model for great cormorants (*Phalacrocorax carbo sinensis*) in northern Europe that demonstrated the limited effectiveness of culling operations due to observed density-dependent adult survival and maturation rates. They proposed that culling rates should be density-dependent themselves in order to stabilize future cormorant populations – that is, culling rates should decrease as cormorant densities decline. Brown and Walker (2004) developed a population model for carp (*Cyprinus carpio*) in Australia that included an empirical stock-recruitment relationship and used it to evaluate alternative strategies for carp control. Not surprisingly, they showed that the performance of "fishing down" strategies was sensitive to moderate variations in stock-recruitment parameters, and emphasized the importance of developing a larger empirical data set of stock and recruitment for carp, just as we have attempted to do for sea lampreys. Finally, Davis *et al.* (1999) emphasized the importance of recruitment variation by using a simple population model to demonstrate that the rate of introgression of inducible fatality or sterility transgenes into a population was underestimated if recruitment variation was not included in the model.

Our results can be used to specify a level of control on adult sea lamprey reproduction required to reasonably ensure success of adult control strategies. We did not observe large recruitment events (>200 age 1 larvae$\cdot$100m^{-2}) when spawner abundance were below 0.2 females$\cdot$100m^{-2} in either the full data set or the long-term study streams (Figs. 2, 3). When planning future adult control initiatives, such as trapping and/or sterile male release, sea lamprey managers should aim to reduce spawner abundance to this value or below to try and ensure low recruitment of sea lamprey populations.

Of the 35 cases in this study where natural spawning populations were estimated rather than intentionally introduced, over 80% had spawner abundances greater than 0.2 females·100 m^{-2} of larval habitat and over 50% had spawner abundances greater than 1 female·100 m^{-2}. To the extent that these streams are typical of sea lamprey producing streams in the Great Lakes, this implies that achieving the target abundance of 0.2 females·100 m^{-2} in approximately half of the streams will require trapping efficiencies (or reductions due to both trapping and sterile male releases) of 80% or greater. Currently in Great Lakes streams, sea lamprey trapping efficiencies range from 5% to 91% with a mean trapping efficiency of 39% (Gavin Christie, Great Lakes Fishery Commission, Ann Arbor, Michigan, personal communication). However, recent research has demonstrated that sea lamprey pheromones hold considerable promise as a tool to enhance trapping efficiency (Wagner *et al.* 2006, Johnson *et al.* 2006), which suggests that the targets implied by our recruitment research are achievable.

Our proposed target of 0.2 females·100 m^{-2} is a general reference point that could be applied to all streams, but an objective of this study was to determine whether we could explain density-independent variation in recruitment among our study streams, such that different streams might require different targets. We found that streams described by sea lamprey program staff as having a regular and predictable cycle of lampricide treatment experienced significantly higher survival than less predictable (irregular) streams. This result suggests that not only are these streams consistent sea lamprey producers, but they also tend to produce more recruits at a given stock size. We also found that streams in Lakes Superior and Michigan produced higher survival than streams from Lakes Huron or Ontario. Consistent with this finding, survival in our two

Lake Superior long-term study streams was higher than in the two Lake Ontario streams. This finding was in contrast to what we might have expected, because in general Lake Ontario sea lamprey streams tend to be warmer and more productive and require treatment with lampricide more frequently than streams on the upper Great Lakes. Finally, we found that survival was higher in streams where the number of competitors was greater, which again contradicted our predictions.

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

We did not attempt to quantify habitat supply in the streams included in this study. It is likely that not only the quality and quantity, but also the distribution of both spawning and larval habitat in a stream contributes to recruitment differences among streams. Spawning sea lampreys require gravel 1 to 5 centimeters in diameter for nest construction, with small amounts of sand available to which the eggs will adhere in the nest, while larval sea lamprey require soft bottom types to make their burrows (Applegate 1950). Because larvae are typically carried downstream in the current after hatching, suitable larval habitat must occur somewhere downstream of suitable spawning areas. One long-term study stream, the Carp River, had abundant amounts of clean gravel at the top of the reach with numerous patches of silt/sand bottom downstream. Another study stream, Port Britain Creek, has very limited areas of clean gravel with large closely-spaced cobble armored by sand for most of the stream length. We observed relatively high survival in the Carp River and low survival in Port Britain Creek (Figure 7), consistent with our hypothesis that habitat differences may explain recruitment variation.

An important next step in process-level research of sea lamprey recruitment variation will be to develop measures of habitat differences among streams that appear to explain recruitment variation. Baxter (1954) found that the stream gradient for sea lamprey streams in England was between 5 to 14.5 $m \cdot km^{-1}$, which allowed for good spawning habitat in the upper reaches and depositional areas for larval habitats downstream. Young *et al.* (1990) found that the presence/absence of sea lamprey ammocoetes within the Great Lakes was controlled, to a large degree, by substrate particle size. Alternative quantitative descriptions of habitat supply, that account for the juxtaposition of spawning and larval habitats on an ecologically meaningful scale (Derosier *et al.* 2007), should be included in future investigations of recruitment variation. If a measure of habitat supply can be shown to explain significant among-stream variation in recruitment after accounting for density-dependent (stock) effects, then this factor should be used to inform management. Streams with an abundance of good habitat would require greater reductions in spawner numbers to achieve target recruitment levels, on average, and thus would not be preferred candidates for adult control.

Both the full meta-analysis model (90 stream-years) and our four stream model revealed that the year of recruitment, specified as a random effect, was not a significant component of the overall variance in survival among observations (the estimate was essentially zero). Myers *et al.* (1997) looked at recruitment variation among populations of 19 species of fish from marine, marine-freshwater (anadromous) and freshwater habitat, and noted that recruitment patterns were correlated over time among nearby (<500 km apart) populations of marine fishes but only weakly and at short distances for freshwater species. Similar patterns of temporal covariation have been demonstrated for north Pacific stocks of sockeye (*Oncorynchus nerka*) and pink (*O. gorbuscha*) salmon within but not among broad regions such as the Fraser River and Bristol Bay (Peterman *et al.* 1998; Pyper *et al.* 2001). These studies suggest that moderate to large-scale, temporally variable environmental factors influence fish recruitment in marine systems, but are less important in freshwater systems. Our analysis of sea lamprey recruitment is consistent with this view – we found differences in temporal patterns of recruitment between streams as little as 27 and 48 km apart. In sea lampreys, where recruitment (as we have defined it here) takes place in individual streams, recruitment variation appears to be more strongly influenced by stream-specific factors, or by interactions between stream-specific factors and temporally varying environmental factors. From a management perspective this implies that simulation models of stream-level recruitment dynamics should treat interannual recruitment variation among streams as independent stochastic processes.

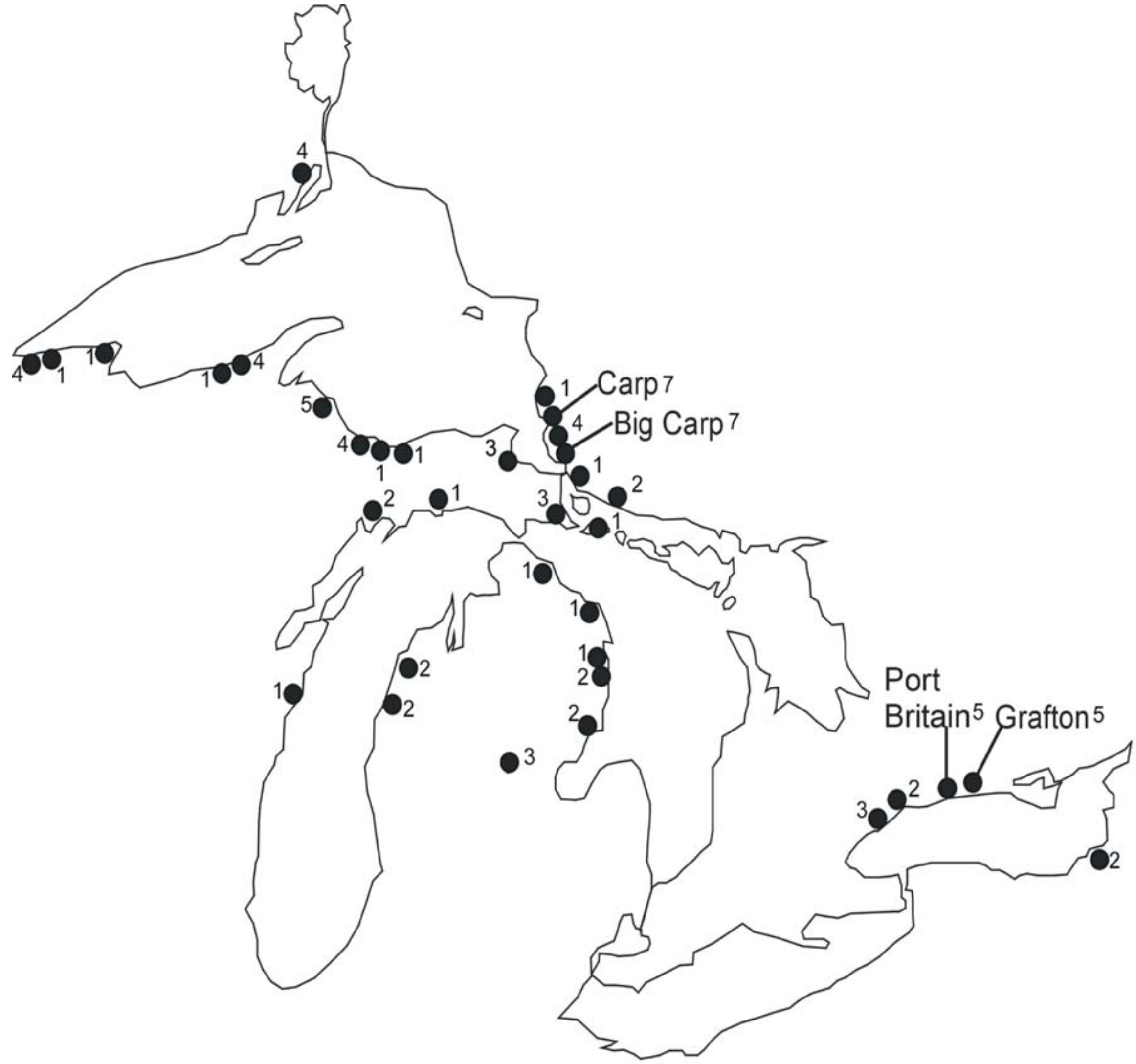

Figure 1. Location of streams from which we obtained sea lamprey stock-recruitment data. The four long-term study streams are highlighted with names. The numbers indicate the number of years of stock-recruitment data we have for each stream.

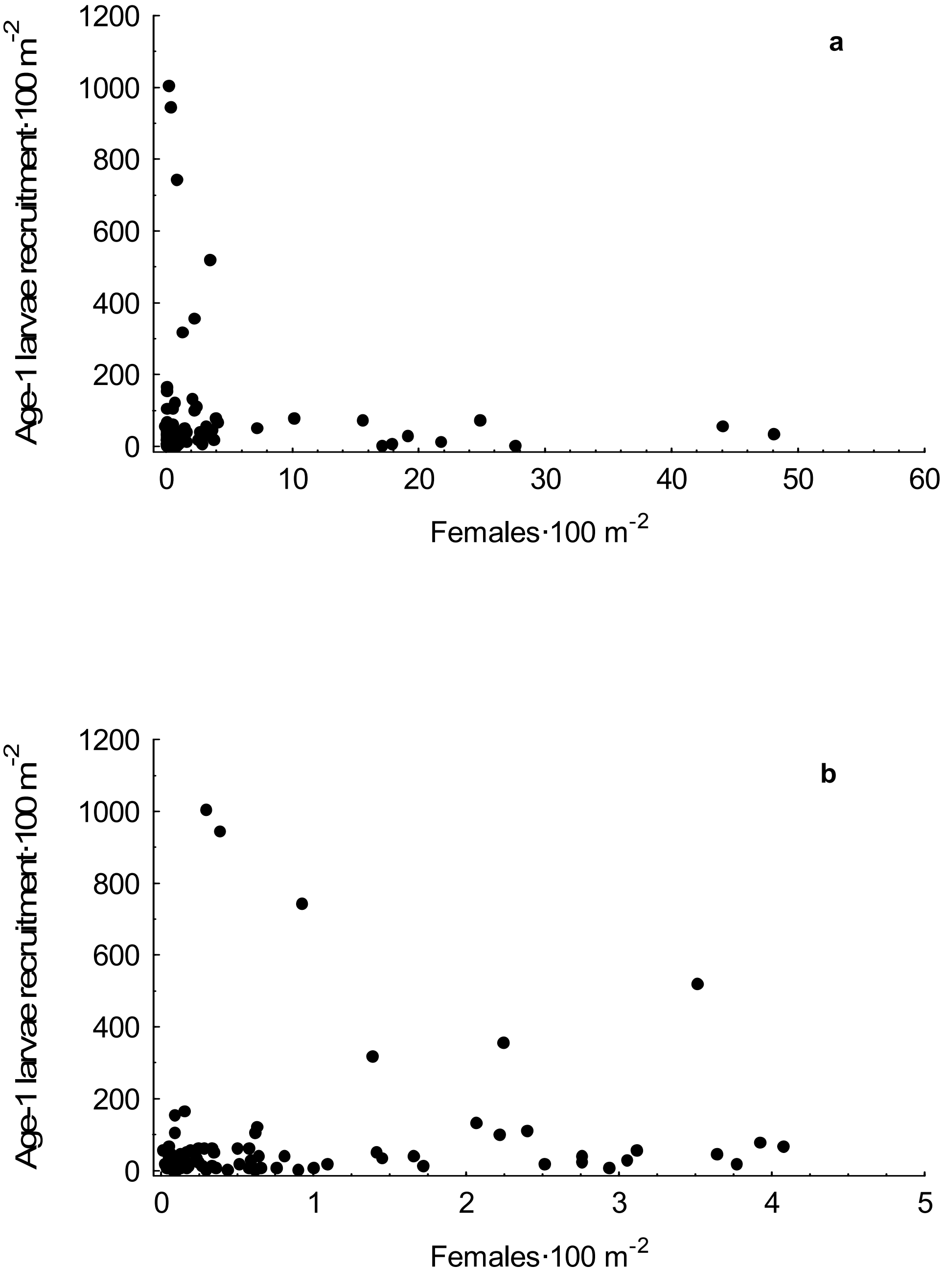

Figure 2. Females and yearling sea lamprey numbers are expressed as densities·100 m^{-2} of larval habitat (*a*) observed stock and recruitment for 90 stream-years and (*b*) includes only data when spawner densities were less than 5·100 m^{-2}.

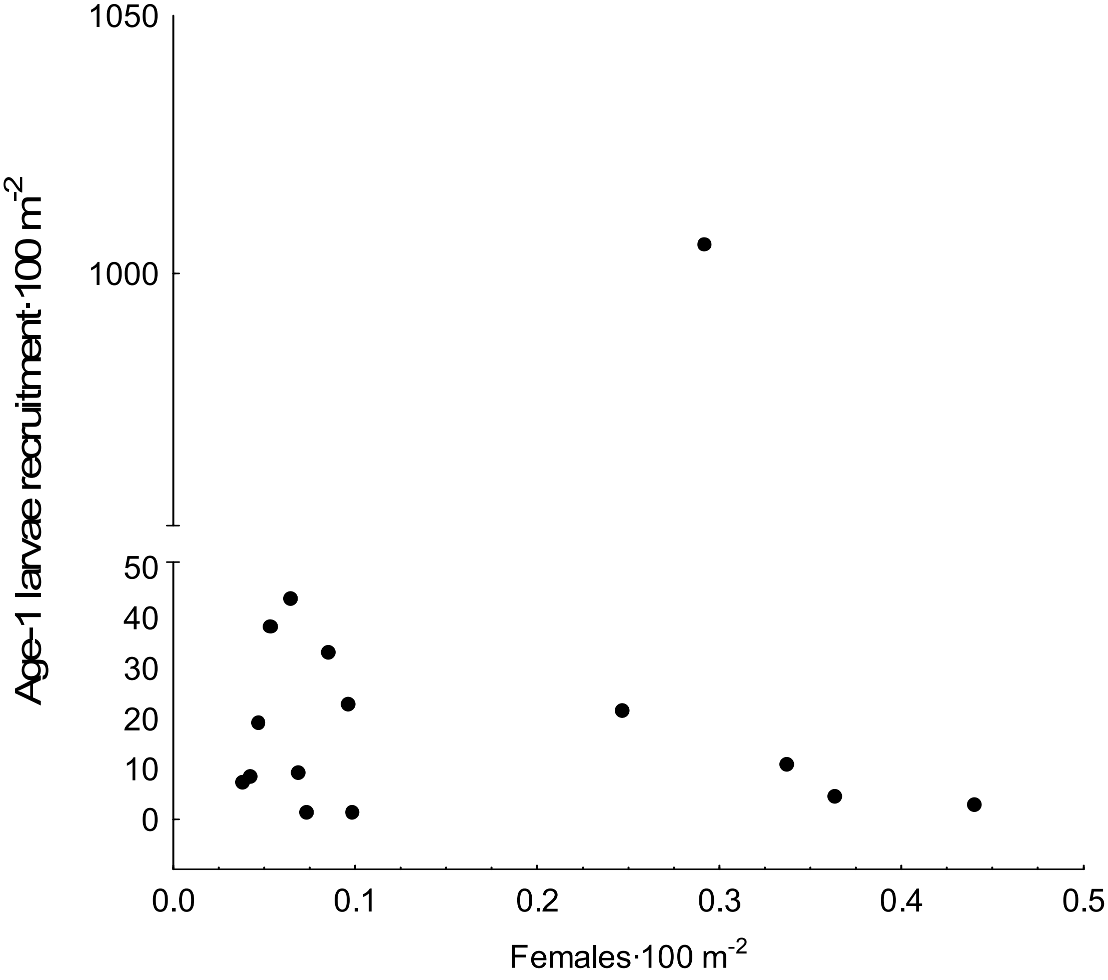

Figure 3. Observed sea lamprey stock and recruitment for the four long-term study streams (24 stream-years) when spawner densities were less than 0.5·100 m^{-2}.

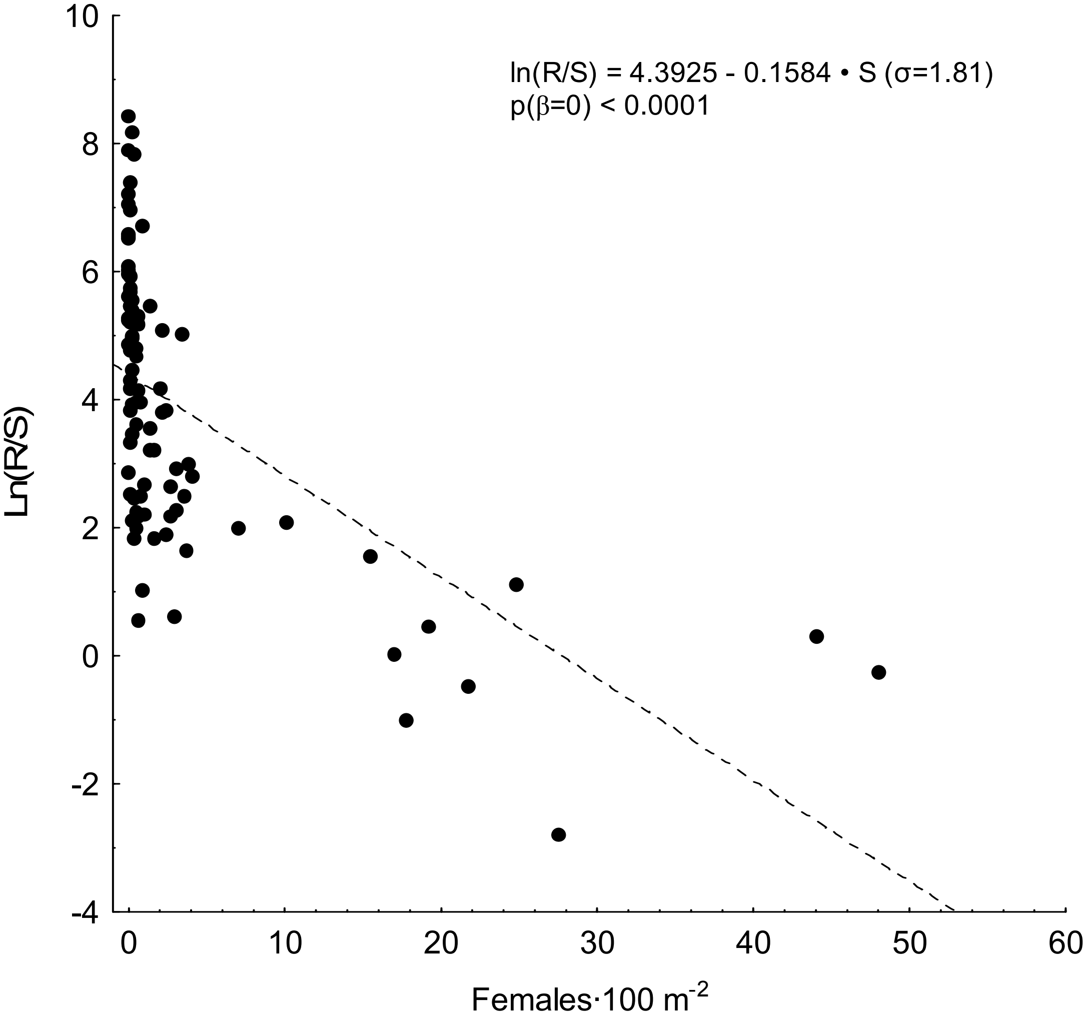

Figure 4. The linearized sea lamprey stock-recruitment relationship (ln(R/S) versus S) for the data plotted in Figure 2. Ln(R/S) is an index of sea lamprey survival to age 1. The regression line estimates are shown in the graph panel.

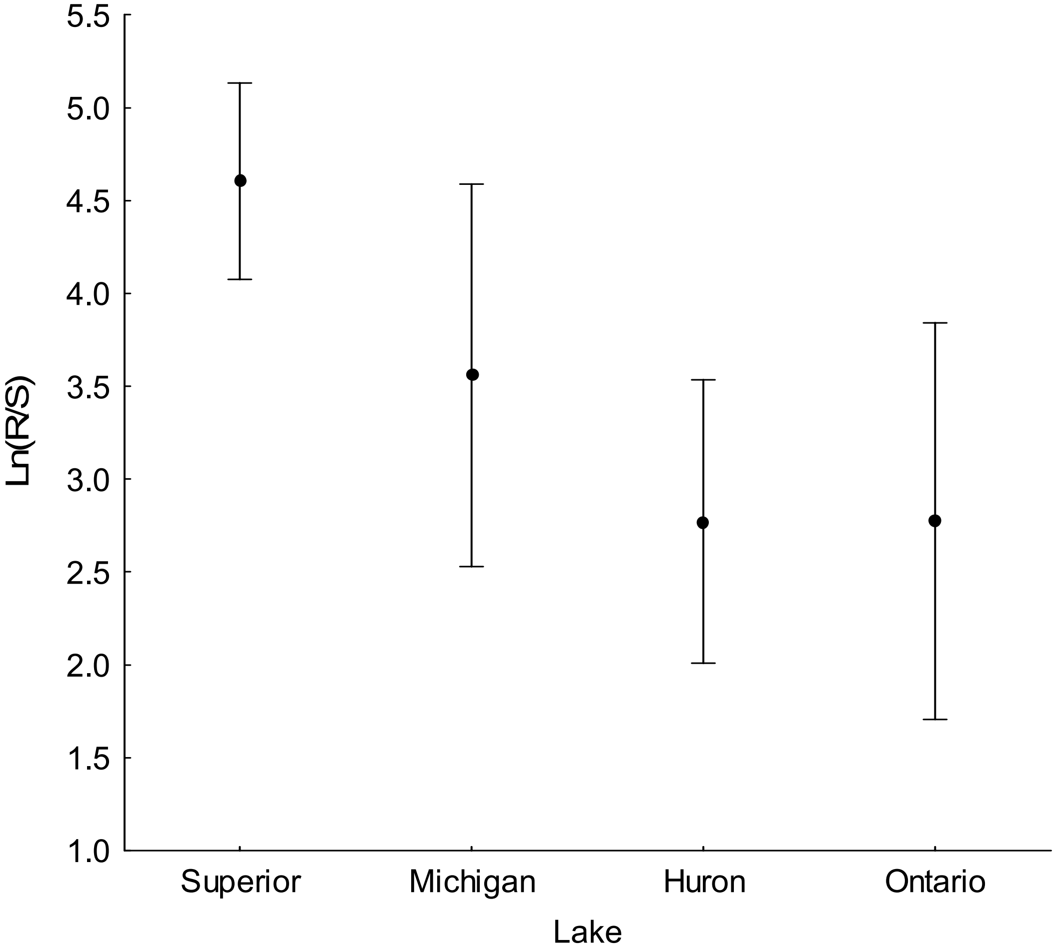

Figure 5. Least squares mean plot of ln(R/S) for age-1 sea lampreys versus lake from the general linear model on all available data (error bars represent 95% confidence intervals).

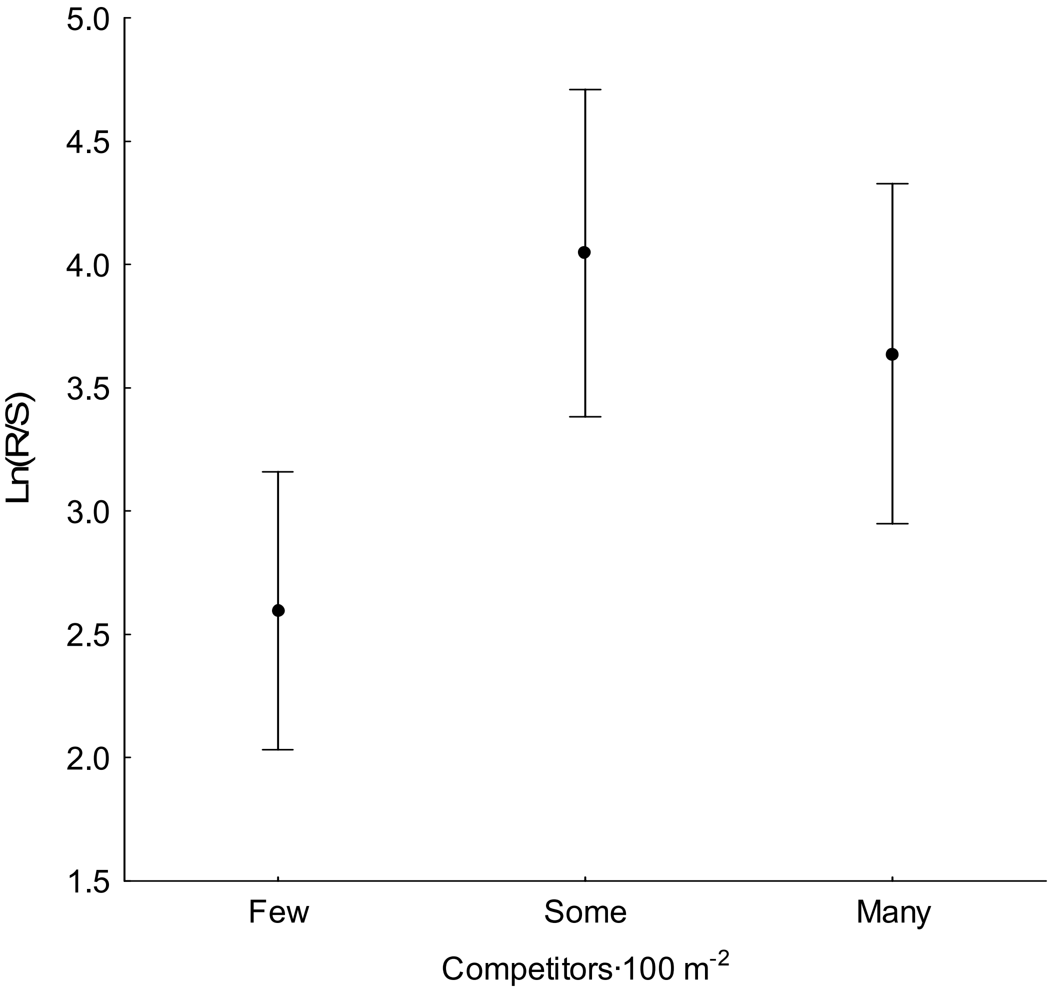

Figure 6. Least squares mean plot of ln(R/S) for age-1 sea lampreys versus competitors·100 m^{-2} of habitat from the general linear model on all available data (error bars represent 95% confidence intervals).

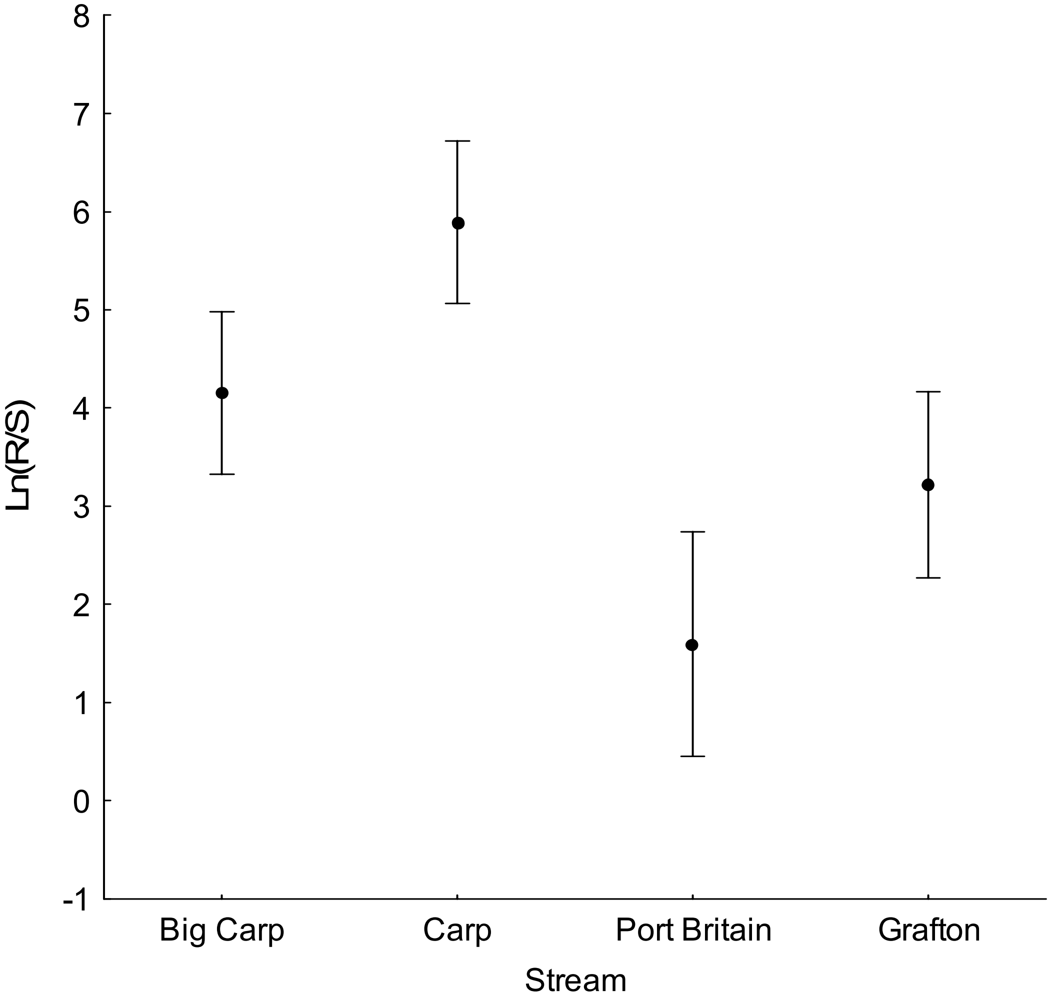

Figure 7. Least squares mean plot of ln(R/S) for age-1 sea lampreys versus stream from the mixed-effects model on the four long-term study streams (error bars represent 95% confidence intervals).

Chapter 2

DEVELOPMENT OF A STANDARD PROTOCOL TO IMPROVE ASSIGNMENT OF AGES TO LARVAL SEA LAMPREY POPULATIONS

Abstract

A standard protocol for more accurately determining larval sea lamprey (*Petromyzon marinus*) population age composition, provided it is not too costly, would be very valuable for sea lamprey control. Developing a standard method of age-assessment using both statolith and length-frequency data requires the validation and improvement of both methods of age interpretation. Identification of age classes through the inspection of length-frequency distributions is subjective, especially because there is often overlap in lengths between age classes. In this study, I evaluated a likelihood-based statistical model that estimated age composition from a large sample of length-frequency data and smaller sample of age composition information obtained from statoliths. Age determination of sea lampreys using statoliths has never been validated for more than one year, so I also established "known-age" populations in two contrasting streams by introducing a single cohort of sea lampreys and then compared the age determined by statolith interpretation to the known age using two different methods for statolith preparation and evaluation. Multiple independent age readings of sea lamprey statoliths indicated that the overall average percent error measuring bias was 33.0% for the Crystal Bond method and 27.3% for the Immersion Oil method. The statolith data were bias-corrected and combined with length-frequency data in the statistical model to determine proportion-at-age in a sampled sea lamprey population using all available information,

which resulted in a substantial increase in the precision of this estimate compared with using only information on length.

Introduction

Age, growth rate, and mortality rate are three of the most influential life history characteristics controlling the productivity of fish populations (Campana and Thorrold 2001). Measuring productivity and recruitment in sea lamprey (*Petromyzon marinus*) populations across the Great Lakes requires accurate assessments of larval sea lamprey age. Historically, aging of larval sea lamprey has relied on the use of length-frequency distributions. Jones *et al.* (2003) measured recruitment to age 1 by identifying age-1 individuals through inspection of length-frequency distributions. However, this method is subjective and there is often overlap in lengths between the age-1 group and older age classes, which introduces uncertainty into the estimation of the abundance of the age class (Potter 1980). The error associated with this approach introduces uncertainty that is difficult to quantify into estimates of abundance at age 1 (i.e., recruitment) and other analyses requiring estimation of the age composition of sea lamprey populations.

Statoliths, the analogous structure in lampreys to otoliths in teleosts, have been used for age determination in sea lampreys (Beamish and Medland 1988, Hollett 1998). Statoliths are the only calcified structure found in lampreys, and when oriented properly and viewed under transmitted light, two types of bands appear as layers within the statoliths; the combination of the two corresponding bands has been shown to represent annual growth (Volk 1986). However, this age determination method has never been validated for more than one year using a “known-age” population of ammocoetes. Also, statoliths from sea lamprey experiencing different ambient calcium ion concentrations display diversity in their reliability for estimating age when compared with length-frequency distributions (Barker *et al.* 1997). I wished to develop a protocol for more objectively determining age composition using length-frequency and statolith age information, which requires the validation and improvement of both methods of age interpretation.

Different methods have been employed for statolith preparation and evaluation to determine ages of larval lampreys (e.g., Volk 1986; Beamish and Medland 1988; Hollett 1998). Volk (1986) evaluated statolith banding patterns by balancing statoliths on their edges in immersion oil to view them from a posterior or lateral aspect (Immersion Oil method). Hollett (1998) evaluated statolith annuli by first storing statoliths in glycerin for a period of two weeks and then inserting them into a clear adhesive, which could be heated to reposition the statolith in the proper orientation (Crystal Bond method). Single-year validation of both methods has been completed using oxytetracycline marking of larvae (Beamish and Medland 1988 using Volk's (1986) Immersion Oil method), and animals undergoing metamorphosis (Hollett 1998 using the Crystal Bond method). These year-long studies concluded that a narrow dark band appeared beyond the region marked with oxytetracycline in larvae and animals undergoing metamorphosis. In accordance with criteria applied to the aging of teleost fishes, the narrow dark band on the statolith that formed during slow growth was taken as the annulus (Beamish and McFarlane 1983). However, Beamish and Medland (1988) and Hollett (1998) measured the precision, not the accuracy of the age they assigned to individual animals. Validation means proving a technique is accurate (Beamish and McFarlane 1983). We need to validate that the banding pattern can be repeatably visualized and represents the true age of the ammocoete over multiple years in contrasting environments, and also determine which method of statolith evaluation more accurately estimates ammocoete age. Only by using mark-recapture studies or known-age fish can all age classes in a population be validated (Beamish and McFarlane 1983).

The validation of statolith evaluation as an aging technique requires the examination of known-age sea lampreys from varying environments. Statolith growth and banding pattern have been found to be intimately associated with temperature, with annuli formation corresponding to sharp seasonal changes in growth (Medland and Beamish 1991). Barker *et al.* (1997) found that larval lamprey statoliths exhibited irregularities in size or presence from stream with alkalinities below 30 mg/L $CaCO_3$, which is most likely due to resorption of calcium from the statolith in animals from low-alkalinity environments. Beamish and Medland (1988) marked sea lamprey larvae from only one Great Lakes stream, a cold, low-alkalinity Lake Superior stream (Big Garlic River) and placed them in holding cages in their natal stream for one year. Hollett (1998) marked premetamorphic and metamorphic sea lamprey from four Great Lakes streams and placed them in laboratory tanks where all populations were reared in dechlorinated tap water, under temperatures that mimicked a warm Lake Ontario stream (Duffins Creek). To validate the use of statoliths as an aging method over multiple years in varying environments, statoliths could be collected over time from single cohorts of known-age sea lamprey in streams that contrast in temperature and alkalinity, but which both experience seasonal changes and have calcium ion levels that support statolith growth.

Using an objective, likelihood-based method in the development of a standard protocol for ammocoete age-assessment would be an important advance in sea lamprey management. Schnute and Fournier (1980) describe a statistical method for objectively estimating age composition from length-frequency data that relies on an assumption about the growth dynamics of the fish stock of interest. Fournier (1983) amended the approach to include partial age composition information, presumably obtained from a sample of fish from which a calcified structure was removed. When discerning age-classes of ammocoetes, obtaining age information from a subsample of the fish helps determine the number of age-classes present in the sample and avoid gross errors such as misaging all the fish by 1 year (Fournier 1983). Obtaining direct age information can also help adjust for errors, observed when using only length-frequency information, in parameter estimation of the von Bertalanffy growth equation, due to intrapopulation variability in growth parameters (Smith *et al.* 1997). Also, if bias in aging data can be quantified this error can be statistically removed from a set of age frequencies by using an aging error matrix (Richards *et al.* 1992). Combining length-frequency and age information to determine ammocoete ages makes the best use of the information contained in all the available data.

The objectives of this study were to create “known-age” populations of larval sea lamprey to be used to validate age determination using statoliths, and develop a standard protocol for larval sea lamprey (ammocoete) age assessment using length-frequency data and partial age composition data. To address these objectives, I first created a single year class of sea lamprey above barriers in two Michigan streams that contrast greatly in growing season length and alkalinity, as a tool to validate aging techniques. A sample of larval sea lampreys from the streams was collected each year and the reliability of current methods that use statoliths to accurately assess larval age was compared. Statolith data, which provided information on the growth dynamics of the fish stock, was bias-corrected and combined with length-frequency data to estimate age composition of the "known-age" streams and a stream with three age-classes of sea lamprey using an objective, likelihood-based statistical model. By using all available information to determine proportion-at-age we can try to increase the precision of ammocoete age assessments.

Methods

Bias and precision in "known-age" samples

I established "known-age" populations of sea lampreys in two streams by introducing 25 pairs of spawners above barriers. Big Garlic River, a cold, low-alkalinity (mean alkalinity = 52 mg/L $CaCO_3$) Lake Superior stream, received spawners in spring 2002, while Ogemaw Creek, a warmer, high-alkalinity (mean alkalinity = 175 mg/L $CaCO_3$) Lake Huron stream, received spawners in the spring of 2003 (Figure 1). Spawners were introduced in one year, and since populations were established above low-head barriers no other age classes of sea lamprey were present. Each stream was sampled by an AbP-2 backpack electroshocker, with the Big Garlic River sampled in the summer of 2003, 2004, 2005, and 2006 and Ogemaw Creek in 2004, 2005, and 2006. Soon after sampling, larvae that were identified as *Petromyzon marinus* were frozen and then weighed to the nearest milligram and measured to the nearest millimeter. Samples were kept frozen until 2006 when subsamples of larvae from each stream-year were randomly chosen for statolith evaluation.

Animals were prepared for statolith extraction by first cutting off the body posterior to the gills. Then under a dissecting microscope (10X) the head region was placed dorsal side up and sliced along the notochord from the anterior to the posterior of the animal. The otic capsules were located on either side of the notochord and were pierced with fine-tip forceps. The forceps were then used to grab material in which the statolith could be found, which was transferred to a Petri dish. An attempt was made to remove both right and left statoliths from each animal. The statoliths were cleaned using distilled water and allowed to dry. The statoliths were then prepared and evaluated based on either the Crystal Bond or the Immersion Oil method, to be described later.

Annuli were viewed most clearly when the statolith was oriented laterally by using both a dissecting microscope (75X) and transmitted light and a compound microscope (400X), however annuli could be seen more clearly at lower magnification. This is most likely due to the difficulty of using a compound microscope with a single plane of focus to evaluate the three-dimensional structure of a statolith (Hollett 1998). Annuli were counted by two readers; a light and a dark band were interpreted as comprising an annulus. Each reader aged each statolith twice. The bias of this statolith aging technique for Great Lakes sea lampreys was examined visually by age bias plots (Campana *et al.* 1995) and by comparing estimates of average percent error (APE). Age bias plots were constructed to compare the ages assigned by each reader to the true age. APE was calculated from:

$$100 \times \frac{1}{N} \sum_{j=1}^{N} \left(\frac{1}{R} \sum_{i=1}^{R} \frac{\left| X_{ij} - X_{j} \right|}{X_{ij}} \right) \qquad (1),$$

where N is the number of statoliths aged, R is the number of times each statolith was aged, X_{ij} is the ith age determination of the jth statolith, and X_j is the reference age (Beamish and Fournier 1981).

Most aging studies use the mean age observed by all readers for each structure as the reference age in APE calculations; in this study the true age is used as the reference age. However, I compared the APE using the mean age calculated by readers to get an estimate of precision, to that obtained when using the true age, which is an estimate of bias. This gives an indication of the influence of not knowing the true age on this measure of accuracy. I also plotted the length-frequency distributions for all sea lampreys sampled in each stream (across years) and compared this to the length versus true age distributions.

Comparing two methods of statolith evaluation

To compare two methods of statolith preparation and evaluation samples were kept frozen until 2005 when subsamples of larvae were randomly chosen from each stream-year (except 2006) for statolith evaluation by each method. "Known-age" fish only included ages 1-3 and I wished to avoid readers being able to limit their age interpretations to 3 or less. To that end, I added a sample of animals (N=31, mean length 86 mm) of unknown age, obtained from Bowmanville Creek, a Lake Ontario tributary, to the collection of statoliths to be interpreted. The Crystal Bond and Immersion Oil methods were evaluated by comparing the estimates of bias and precision in aging using the average percent error. The method observed to be the less biased and more precise was subsequently used to evaluate statoliths from the "known-age" streams in 2006 (*Bias* *and precision in "known-age" samples*) and when estimating the age distribution of sea lampreys in Grafton Creek in 2006 (*Applying a statistical model to estimate age distribution*).

The Crystal Bond method required that statoliths be transferred using a dissection pin to individual wells within a multiwell plate filled with glycerin, where they were stored for at least 9 days at room temperature. Hollett (1998) found that statoliths tended to disintegrate in glycerin after a period of 15 days. Because I was extracting statoliths from smaller animals than Hollett (1998), whose animals had a mean length of 115 mm, I was conservative by not allowing the statoliths to exceed 13 storage days in glycerin. After the storage period statoliths were removed from the wells by a pipette and placed on a microscope slide in a small amount of clear Crystal Bond ^{TM}(Aremco). Crystal Bond could be heated to allow for proper positioning of statoliths for clear visualization of annuli. Each statolith was assigned a random number that was written on the slide, and linked back to an animal after "blind" age-assessments were conducted by readers.

The Immersion Oil method required that statoliths be transferred using a dissection pin to random individual wells within a multiwell plate filled with immersion oil, where they were stored for at least 9 days, and no longer than 18 days at room temperature. Each well in which a statolith was immersed was assigned a random number, to link back to an animal after "blind" age-assessments were conducted by readers. After the storage period statoliths were removed from the wells by a pipette and placed on a depression microscope slide in a small amount of immersion oil. As found in Volk (1986), viscous immersion oil facilitated maneuvering of the statolith so that an optimum orientation could be achieved.

Applying a statistical model to estimate age distribution

To create a statistical model to estimate proportion of ages in a randomly sampled sea lamprey population I used a method similar to that described by Schnute and Fournier (1980) and Fournier (1983). The method requires structural assumptions about how the fish in the population grow and how individual fish vary in their growth rates. These two assumptions allow a prediction of the length composition of a mixed-age population, which can be compared to actual data. Using maximum likelihood methods, a set of growth and variation parameters that best fits the observed data can be obtained, and used to infer the age composition of the population. If we let u_i be the mean length of fish at age a_i, then if these means lie on a curve of the type proposed by von Bertalanffy, u_i is described by

$$u_i = L_\infty\left(1 - e^{-K(a_i - t_0)}\right) \qquad (2).$$

In this equation, L_∞ is the theoretical maximum length which fish approach as they grow older, K relates to the fraction by which the gap between current length and maximum length is reduced each year, and t_o is the age at which fish length extrapolates back to zero along the curve. Schnute and Fournier (1980) defined new parameters for von Bertalanffy growth that have greater biological meaning and numerical stability than the conventional parameters. They used the parameter set (L_1, L_M, k), which is much more appropriate to length-frequency analysis than (L_∞, K, t_o), with L_1 being the mean length of the youngest age class, L_M being the mean length of the oldest age class, and k being the distance between two successive mean lengths. Using these parameters u_i is described by

$$u_i = L_1 + (L_M - L_1)\frac{1-k^{t-1}}{1-k^{M-1}}; i = 1,\ldots,M. \quad (3),$$

with t being the age class and M being the maximum number of age classes (Schnute and Fournier 1980). I assumed for each age-class the lengths were normally distributed around their mean length and the standard deviations increased as a linear function of age-class. I estimated the most likely proportions at age using a multinomial log-likelihood function implemented in Ad Model Builder (Otter Research 2000). In chapter 1 I used this model to separate out the age-1 age-class from length-frequency data for the stock-recruitment streams.

I amended the statistical model (following Fournier 1983) to include partial age composition information. The observed proportion-at-age for a stream was determined through aging statoliths from a subsample of animals, and the bias observed in aging statoliths from "known-age" streams was corrected by using an aging error matrix to obtain the corrected proportion-at-age described by

$$p_a = \sum_{a'=1}^{A} C_{a,a'} \cdot p'_{a'} \quad (4),$$

where *p, p'* are the corrected and observed proportions-at-age, respectively, *C* is an aging error matrix, with rows *a* – true ages, and columns *a'* – observed ages, and A is the total number of ages. I added a second multinomial likelihood term to the objective function to use the corrected proportion-at-age in the model, which combined with length-frequency data, estimated the predicted proportion-at-age.

I tested the accuracy of the statistical model by estimating proportion-at-age for the two "known-age" populations when cohorts sampled from multiple years were combined into a single length-frequency plot. Sea lamprey sampled in 2003, 2004, 2005, and 2006 for the Big Garlic River, and 2004, 2005, and 2006 for Ogemaw Creek were combined into one length-frequency distribution for each stream. Using the statistical model I then estimated the proportion-at-age using only length-frequency information and compared the estimate with the "known" proportion-at age.

I also used these data to evaluate the statistical model when partial age-composition data were included. The aging error matrix I developed to adjust the bias in statolith aging was based on statoliths from both "known-age" streams evaluated in 2006 using the Immersion Oil method (my results showed this method to be the less biased and more precise on average). Results suggest that the direction of the aging bias was similar for both "known-age" streams, so data from both streams was used to develop the aging error matrix to correct the bias for both Ogemaw Creek and Big Garlic River. The statistical model estimated the most likely proportion-at-age given both length and age information, and I then compared the estimates with the "known" proportion-at-age.

I applied a similar method to estimate proportion-at-age using length-frequency and statolith data from one of our long-term study streams (see chapter 1). I used sea lampreys sampled from Grafton Creek in 2006 to compare proportion-at-age estimated by the statistical model when using just length information to that obtained using both length and age (statolith) information. Age information was obtained by taking a random sample of sea lampreys from the populations, removing their statoliths and aging them using the Immersion Oil method. Animals 25 mm or less were determined to be young-of-the-year, and since statoliths could not be evaluated for this population they were removed from this analysis. The Grafton Creek population only included ages 1-3 and I wished to avoid readers being able to limit their age interpretations to 3 or less. To that end, I added a sample of animals (N=5, mean length 110 mm) of unknown age, obtained from Ceville Creek, a Lake Michigan tributary, to the collection of Grafton Creek statoliths to be interpreted. Two readers aged each statolith two times and the average age of all readings was rounded to result in an age of 1, 2, or 3 for each statolith. Aging error was corrected using the aging error matrix based on statoliths from both "known-age" streams evaluated in 2006 using the Immersion Oil method. To evaluate the precision of the estimate, I derived approximate confidence limits from likelihood profiles. Using AD Model Builder the likelihood profiles are determined by calculating the conditional maximum of the likelihood function and then normalizing it so that it integrates to 1 (Otter Research 2000). I chose the 2.5th and 97.5th percentiles of the likelihood profile to represent 95% confidence limits.

Results

Bias and precision in "known-age" samples

Because I collected animals from each "known-age" stream in each year following spawner introduction I have lengths of the animals in each age class. The length-frequency distribution of animals from the Big Garlic River and Ogemaw Creek for all years combined indicated effectively no modal separation among age classes 2, 3, and 4 (Figure 2) and age classes 2 and 3 (Figure 3), respectively.

By 2006, we had sampled the cohort in the Big Garlic River at age-1, age-2, age-3, and age-4, and had sampled the cohort in Ogemaw Creek at age-1, age-2 and age-3. In 2006, I chose 98 statoliths at random from the entire collection to interpret using the Immersion Oil method (the less biased method). Animals whose statoliths were examined were a good representation of the sampled population for each stream-year (Tables 1 and 2). Overall APE was much larger for both readers when calculating APE based on the true age than when using the mean age, which indicates bias as well as imprecision in the interpretations (Table 3). Big Garlic animals that were age-1 were over-aged, with age-2 animals being slightly under-aged and animals older than age-2 being under-aged (Figure 4). Ogemaw Creek animals aged 1 and 2 were over-aged, with age-3 animals aged close to the true age by reader 1 and under-aged by reader 2 (Figure 4). Statolith interpretations differed from the true age between streams in a similar pattern as animals older than age 2 tended to be under-aged while animals aged 1 and 2 tended to be over-aged (Figure 4).

Comparing two methods of statolith evaluation

By 2005, we had sampled the cohort in the Big Garlic River at age-1, age-2, and age-3, and had sampled the cohort in Ogemaw Creek at age-1 and age-2. When removing statoliths from sea lamprey from our "known-age" populations, they were sometimes lost or broken in the extraction or mounting process. However, of the statoliths successfully extracted and mounted using the Crystal Bond method I chose 100 statoliths at random to interpret. I chose 52 statoliths at random to interpret using the Immersion Oil method. With a random sample some stream-years were over-represented, but animals whose statoliths were examined were a good representation of the sampled population for each stream-year present in 2005 (Tables 1 and 4).

Ages assigned by both readers using both evaluation methods differed from the true age in both streams. Overall APE was much larger for both readers when calculating

APE based on the true age than when using the mean age, which indicates larger bias than imprecision in the interpretations (Table 5). The bias in aging was higher using the Crystal Bond method, but when interpreting statoliths from Ogemaw Creek animals the Crystal Bond method was more precise. Both methods of statolith evaluation produced a similar pattern of how statolith interpretations differed from the true age between streams. Interpretations of statoliths from age-1 and age-2 animals from the Big Garlic River were less biased than those of the same age from Ogemaw Creek, while age-3 animals from the Big Garlic tended to be under-aged (Figure 5). Ogemaw Creek age 1 and 2 statoliths were over-aged by both readers (Figure 6).

Applying a statistical model to estimate age distribution

Because of the similarity observed in the direction of bias between the two streams the aging error matrix used data from both "known-age" streams to adjust bias in aging in the model for both "known-age" streams and Grafton Creek (Tables 6 and 7). The statistical model's estimate of proportion-at-age for the two "known-age" streams when age composition data were included was very similar to the true proportions-at-age. The model's ability to accurately estimate proportion-at-age was improved by adding bias-corrected age data to the Big Garlic River estimate (Table 8). However, the estimates of the proportion-at-age for Ogemaw Creek were actually closer to the true values when only the length-frequency data were included (Table 8).

Using only length information from the 2006 Grafton Creek population, our statistical model estimated over one-half of the population to be one-year-olds, and about one-fourth of the population to be two-year-olds, and the rest three-year-olds (Table 9,

Figure 7a). Statoliths were aged for a proportion of the population (N=30 statoliths, 19 sea lamprey aged), and the model estimates including bias-corrected age and length indicated that 40% of the animals were age-1, and age-2 and age-3 animals each made up 30% of the population (Table 9). With length and age information included, the model estimated proportion-at-age to consist of fewer age-1 animals and more age-3 animals compared to using length information only (Table 9, Figure 7b). Adding the statolith information substantially increased the precision of the model's estimate of the proportion-at-age-1, as evidenced by a comparison of likelihood profiles for the proportion-at-age-1 estimate, with and without age information included (Figure 8).

Discussion

Prior to this study, the interpretation of annuli formation on statoliths had only been demonstrated for a single year's growth. Using statoliths from "known-age" populations, readers observed that annuli are often difficult to visualize, resulting in a substantial bias in our age interpretations. Our estimates of APE for all age determinations using the Crystal Bond method (22.5-46.3%) and the Immersion Oil method (14.7-35.3%) were much higher than those reported by Beamish and Medland (1988) (2.8-5.2%) and Hollett (1998) (0.8-2.4%) for sea lampreys. However, their error rates were obtained by using mean age rather than true age as the reference age, which means they only assessed precision, not bias. Volk (1986) also reported a low incidence of error (i.e., high precision) in repeated sampling of the same statolith from sea lampreys. Our APE estimates based on mean age as the reference, using the Crystal Bond method (11-15.6%) or the Immersion Oil method (9.1-20.5%) are closer to those of

Beamish and Medland (1988) and Hollett (1998) but are still higher, suggesting lower overall precision in my study. However, the exclusion of statoliths for which age could not be assigned (Beamish and Medland 1988) or that were considered ambiguous (Volk 1986, Hollett 1998) may have resulted in higher estimated precision in those studies. I did not exclude statoliths whose interpretations were ambiguous from our analysis, but only excluded those that were unreadable (broken or burnt). The average percent error observed in this study was similar to those reported by Meeuwig and Bayer (2005) for Pacific lampreys (*Lampetra tridentata*) (16.7%) and western brook lampreys (*Lampetra richardsoni*) (33%) in a study in which precision in statolith aging was assessed and statoliths that were ambiguous or difficult to read were not excluded.

Both the Immersion Oil and Crystal Bond methods produced a similar pattern of how statolith interpretations differed from the true age between streams, with bias and precision similar on average between the two streams. I observed greater bias on average in age interpretations of statoliths from Ogemaw Creek, the warmer, high-alkalinity stream, and results suggests that statolith readers will tend to overestimate younger ages in fast-growing populations. Lower bias was observed in ages estimated by statoliths from the cold, low-alkalinity stream, and proportion-at-age estimates based on length-frequency information for ages 3 and 4 were far from the true proportion-at-age, but were considerably improved when age composition was included (Table 8). However, determining proportion-at-age for a population based on statolith interpretation for a sample of animals will be imprecise even if these estimates are unbiased or bias-corrected, particularly if the sample size is small. This may explain why, for Ogemaw Creek, proportion-at-age estimates based on length-frequency information were not improved when age composition data was included (Table 8). If, by chance, the sample of animals that are aged using statoliths deviates from the true age composition, addition of these data to the estimation model will not increase the accuracy of the proportion-at-age estimates. This would not be expected in the long run, however.

Model estimates of proportion-at-age for the Grafton Creek population revealed greater precision in the proportion-at-age-1 estimate using bias-corrected age and length. The estimate using all available information was more precise, with the 95% confidence interval much smaller than that obtained using length only (Figure 8). Addition of statolith age composition data would also affect estimates of other demographic parameters. For example estimates of the abundance of age-1 larvae for Grafton Creek in 2006 were 683 versus 470 when using only length versus using length and bias-corrected age information. Similarly, the estimated annual survival rate (minimum variance unbiased assuming selectivity is 1 for all ages) (Chapman and Robson 1960) increased from 0.618 to 0.661 when statolith data were included. In streams with greater numbers of sea lamprey these differences would be even larger. By including a direct aging method independent of size, we can analyze individual variability in the data, and our ability to investigate important life history parameters is greatly improved (Volk 1986). More precise age estimates will reduce the propagation of error through the assessment and management process (Morison *et al.* 2005).

The use of a calcified structure to provide age estimates is subject to error from two major sources: (1) error inherent in the structure itself, and (2) error in the process of interpreting its incremental structure (Campana 2001). Producing and preserving quality in statolith samples should decrease both types of errors. Study animals were frozen prior to statolith removal in this study, and statoliths were sometimes lost or broken in the extraction or mounting process. I chose to freeze animals, as it had been learned that statoliths would disintegrate when animals were preserved in formalin. However freezing animals for long periods dried out some samples, which made statolith extraction difficult and increased the brittleness of the statoliths. Another study investigating statolith microchemistry preserved sea lamprey in ethanol for up to one year and had no samples whose statoliths were difficult to extract or brittle, especially in contrast to their frozen samples (Carrol Hand, University of Windsor, Windsor, Ontario, personal communication). Methods of preserving animals for statolith evaluation and extraction should be compared to determine the method that results in the best quality samples over varying time periods; using animals collected from "known-age" streams would also determine if bias in aging differs with preservation method.

It is a more laborious process to include the growth dynamics of a population of fish by extracting and evaluating statoliths and correcting for bias in aging, than to simply interpret length-frequency distributions to determine proportion-at-age of a population, but the additional effort can result in substantially improved estimates. This study used an objective, likelihood-based model to estimate proportion-at-age, and determined that model estimates are more precise when including bias-corrected age and length information to estimate proportion-at-age. By including more data on age distribution besides length-frequency information, such as bias-corrected age information we are also more likely to approximate the true age distribution. Aging sea lamprey using length-frequency distributions requires large sample sizes, and older age-classes are often difficult to discriminate due to overlapping length distributions (Barker *et al.* 1997).

Barker *et al.* (1997) found that in low-alkalinity streams sea lamprey statoliths are diverse in size, banding patterns, and presence within and among populations, which emphasizes the importance of using length-frequency distributions in combination with statoliths aging to verify assigned ages. The current study improved both methods of sea lamprey aging by verifying statoliths as a method of aging with measured bias, and creating and testing an objective, likelihood based statistical model to estimate proportion-at-age using both length-frequency and age information.

To improve ammocoete age-assessments based on results of this study, a standard protocol for estimating age composition of sea lamprey in streams is suggested:

1. A random sample of sea lamprey (at least 100 animals) should be collected from throughout a stream.
2. All animals should be properly preserved (frozen or preserved in ethanol) then measured to the nearest millimeter, and a random subsample of sea lamprey (at least 25 animals) should be set aside for statolith extraction.
3. Statoliths should be extracted as described in the methods and prepared and evaluated using either the Immersion Oil or Crystal Bond method.
4. A length-frequency histogram should be prepared and the number of age-classes in a stream should be determined and included in the statistical model using length-frequency information and knowledge of the treatment history of the stream.
5. Using the length-frequency histogram, starting values for the statistical model parameters L_1, being the mean length of the youngest age class, and L_M, being the mean length of the oldest age class, should be determined

and included in the statistical model along with length-frequency information.

6. Observed proportion-at-age should be determined based on statolith evaluation and included in the statistical model. The appropriate aging error matrix created in this study should be included in the statistical model to correct the bias in statolith aging.
7. The statistical model should be used to estimate proportion-at-age based on the included information, and sensitivity of the model estimates to the starting values of L_1 and L_M should be explored. The resulting estimates can then be used as inputs to other modeling or assessment activities that contribute to the effective management of Great Lakes sea lampreys.

Table 1. Descriptive statistics of the sea lamprey in the entire sampled population of the "known-age" streams, N=number of sea lamprey.

			Total Length (mm)			
True age(years)	Year Collected	N	Mean	SE	Min	Max
			Big Garlic River			
1	2003	65	33	0.50	25	53
2	2004	177	57	0.74	36	86
3	2005	127	61	0.76	43	98
4	2006	81	84	1.21	65	107
			Ogemaw Creek			
1	2004	92	50	0.76	34	81
2	2005	99	90	1.00	69	119
3	2006	73	112	1.80	80	155

Table 2. Descriptive statistics of the sea lamprey from the "known-age" streams whose statoliths were examined in 2006, N=number of statoliths.

		Total Length (mm)			
True age(years)	N	Mean	SE	Min	Max
		Big Garlic River			
1	11	32	0.55	29	35
2	13	55	2.37	41	70
3	15	66	1.56	61	79
4	15	85	2.48	68	97
		Ogemaw Creek			
1	14	47	1.54	39	54
2	15	89	1.78	75	97
3	15	106	4.72	80	155

Table 3. Bias and precision of age estimates by two readers using statoliths from sea lampreys sampled from the "known-age" streams in 2006, N=number of statoliths.

	Bias			**Precision**	
Reader	APE	SE	N	APE	SE
			Big Garlic River		
1	31.6	5.8	54	11.6	1.97
2	29.9	4.2	54	16.6	2.65
			Ogemaw Creek		
1	34.5	6.6	44	20.5	3.12
2	30.7	5.0	44	18.0	2.47

Table 4. Descriptive statistics of the sea lamprey whose statoliths were examined in three rivers in 2005, N=number of statoliths.

Crystal Bond

		Total Length (mm)			
True age(years)	N	Mean	SE	Min	Max
			Big Garlic River		
1	4	31	1.25	28	34
2	13	55	2.58	36	67
3	20	63	2.20	50	92
			Ogemaw Creek		
1	15	55	2.84	43	81
2	26	93	2.11	71	119
			Bowmanville Creek		
N/A	22	89	2.08	67	117

Immersion Oil

		Total Length (mm)			
True age(years)	N	Mean	SE	Min	Max
			Big Garlic River		
1	6	32	0.31	31	33
2	12	65	2.11	53	77
3	8	67	7.34	43	98
			Ogemaw Creek		
1	9	52	1.88	40	57
2	8	83	2.36	78	98
			Bowmanville Creek		
N/A	9	83	3.51	65	94

Table 5. Bias and precision of the Crystal Bond and the Immersion Oil methods evaluated in 2005, N=number of statoliths.

Crystal Bond

	Bias			**Precision**	
Reader	APE	SE	N	APE	SE
			Big Garlic River		
1	25.2	3.42	37	15.6	2.03
2	22.5	3.58	37	15.3	2.13
			Ogemaw Creek		
1	37.8	6.94	41	13.0	1.94
2	46.3	7.54	41	11.0	1.69

Immersion Oil

	Bias			**Precision**	
Reader	APE	SE	N	APE	SE
			Big Garlic River		
1	16.7	3.73	26	12.2	3.01
2	14.7	3.93	26	9.1	2.57
			Ogemaw Creek		
1	35.3	8.85	17	17.7	3.19
2	25	8.3	17	16.0	2.35

Table 6. Aging error matrix used to remove bias from the observed proportion-at-age determined by statolith aging when three age-classes are present.

		Statolith Age		
		1	2	3
	1	0.59375	0.171429	0
True Age	2	0.1875	0.4	0.533333
	3	0.21875	0.428571	0.466667

Table 7. Aging error matrix used to remove bias from the observed proportion-at-age determined by statolith aging when four age-classes are present.

		Statolith Age			
		1	2	3	4
	1	0.59375	0.171429	0	0
True Age	2	0.1875	0.4	0.275862	0
	3	0.21875	0.428571	0.241379	0.5
	4	0	0	0.482759	0.5

Table 8. The true proportion-at-age and proportions-at-age estimated by the model for the two "known-age" streams from information only on length, and when using both bias-corrected age and length.

Age Class	True	Estimated by using length only	Estimated by using length and bias-corrected age
		Big Garlic River	
1	**0.145**	0.129	0.144
2	**0.393**	0.420	0.404
3	**0.282**	0.031	0.279
4	**0.180**	0.420	0.174
		Ogemaw Creek	
1	**0.349**	0.328	0.317
2	**0.375**	0.356	0.343
3	**0.276**	0.316	0.340

Table 9. Grafton Creek proportions-at-age determined by information only on length, only on bias-corrected age, and using both bias-corrected age and length (N=19 sea lamprey aged).

Age Class	Length only	Bias-corrected age only	Bias-corrected age and length
1	0.577	0.390	0.399
2	0.264	0.427	0.292
3	0.159	0.183	0.309

Figure 1. Location of streams in which I established “known-age” sea lamprey populations.

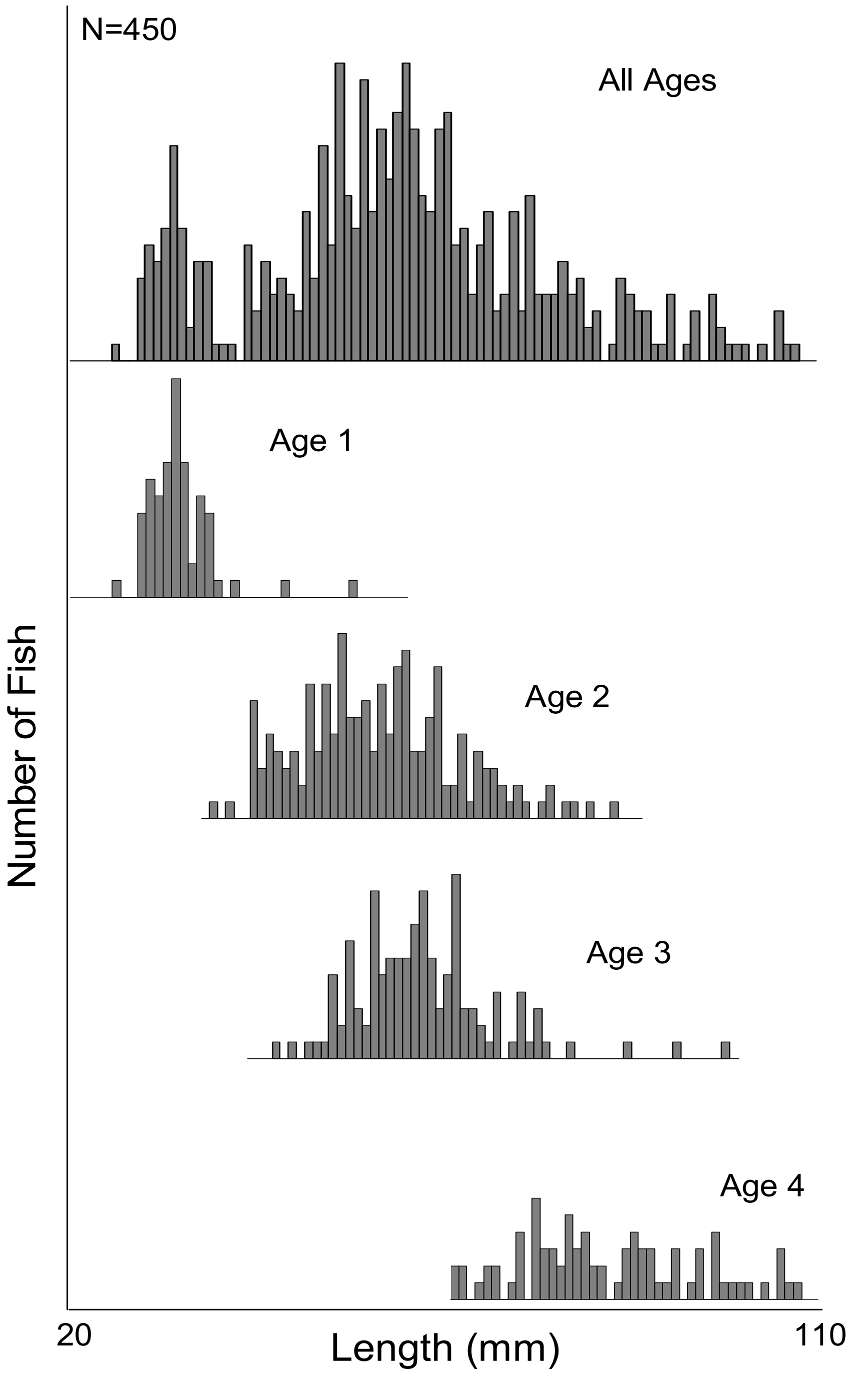

Figure 2. Length-frequency distributions for all ages combined and for ages 1, 2, 3 and 4 are shown for the Big Garlic River "known-age" sea lamprey population after four years of sampling. Sea lamprey lengths range from about 20 to 110 mm and N indicates the total number of sea lamprey sampled.

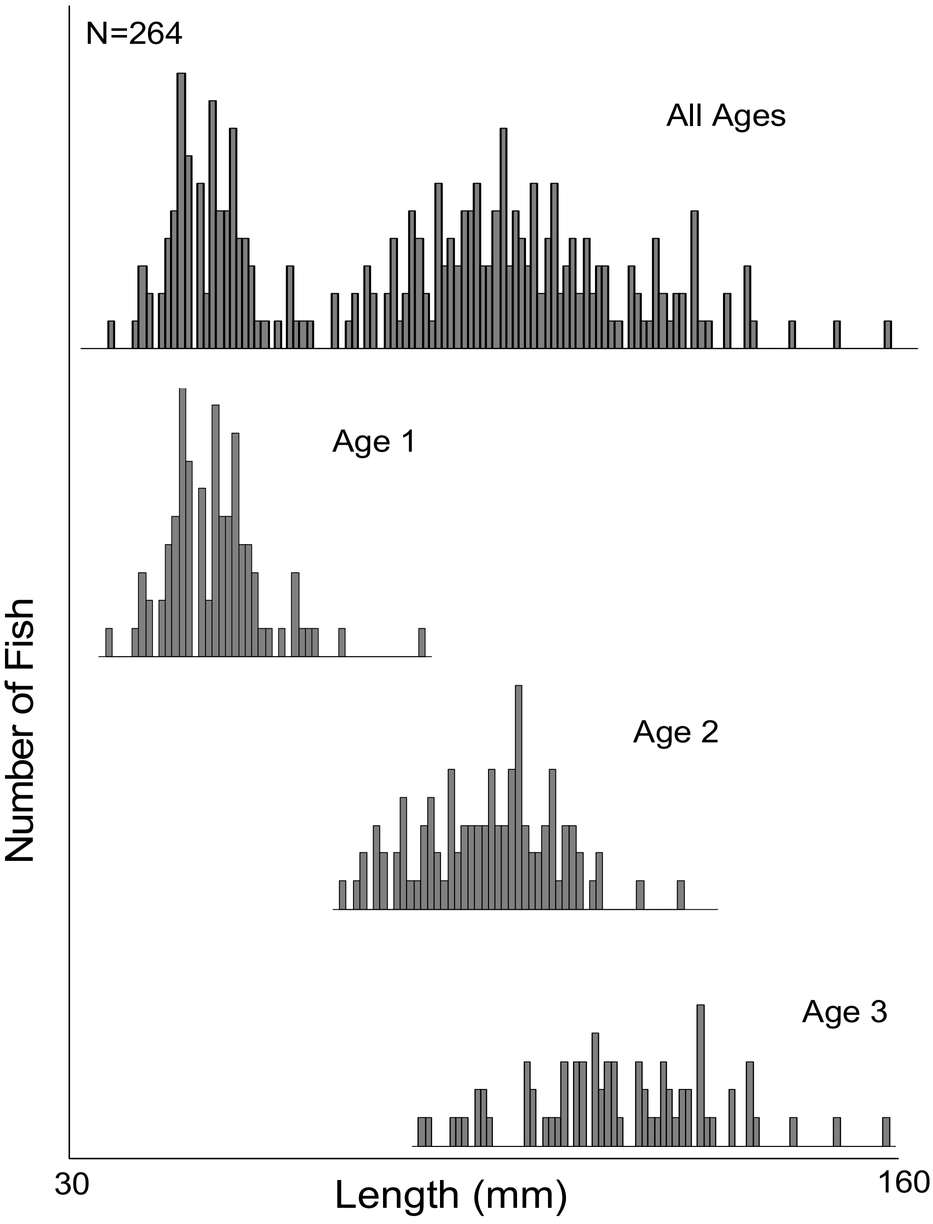

Figure 3. Length-frequency distributions for all ages combined and for ages 1, 2, and 3 are shown for the Ogemaw Creek "known-age" sea lamprey population after three years of sampling. Sea lamprey lengths range from about 30 to 160 mm and N indicates the total number of sea lamprey sampled.

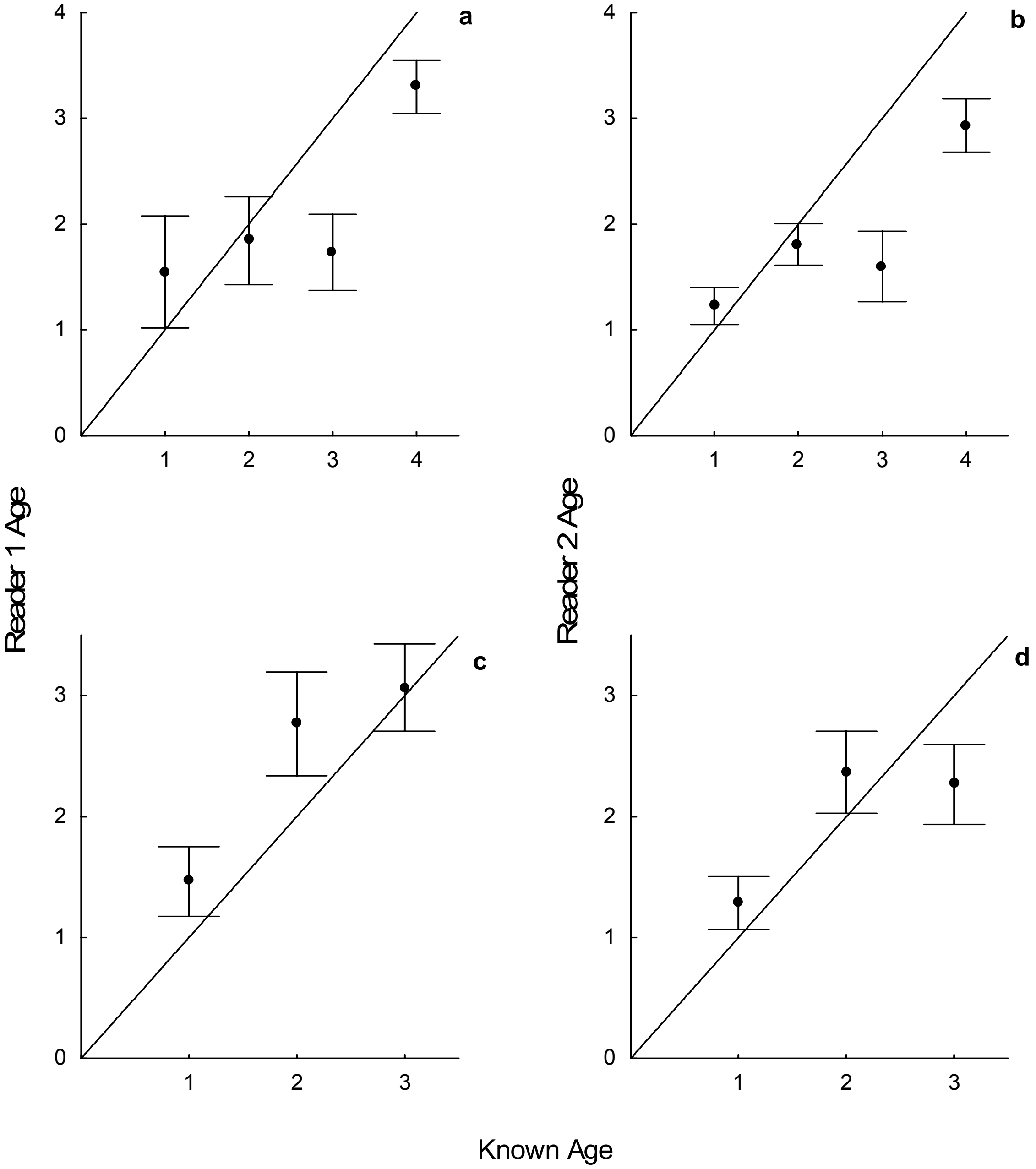

Figure 4. Age bias plots constructed from statoliths evaluated in 2007 from the two "known-age" streams that were aged by two readers. Panels a and b show the average age coded by each reader compared to the true age when evaluating the Big Garlic River population. Panels c and d show the average age coded by each reader compared to the true age when evaluating the Ogemaw Creek population. Error bars indicate 95% confidence intervals surrounding the mean age assigned by each reader to the true age.

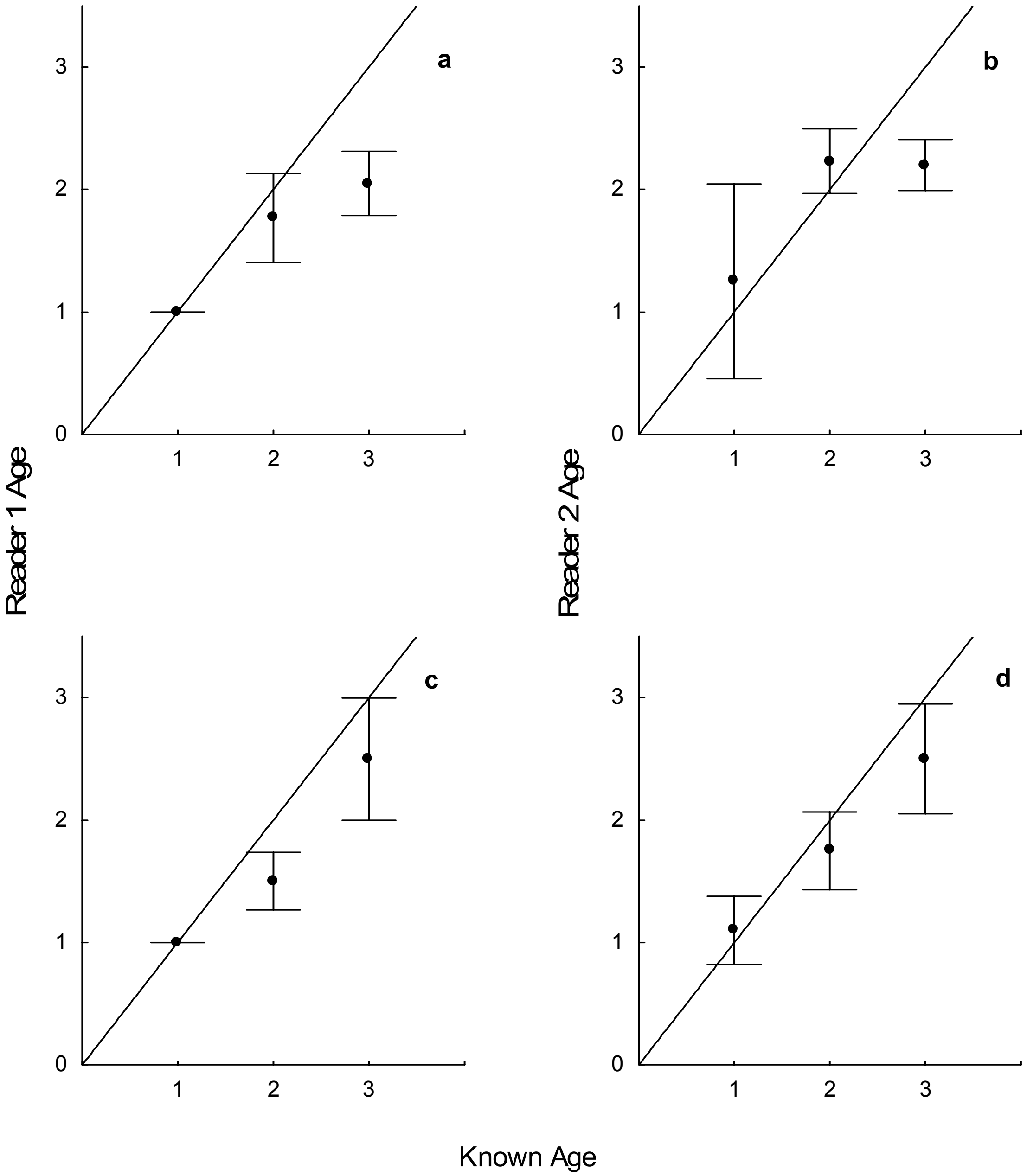

Figure 5. Age bias plots constructed from statoliths evaluated in 2005 from the Big Garlic River sea lamprey population that were aged by two readers. Panels a and b show the average age coded by each reader compared to the true age when using the Crystal Bond method. Panels c and d show the average age coded by each reader compared to the true age when using the Immersion Oil method. Error bars indicate 95% confidence intervals surrounding the mean age assigned by each reader to the true age.

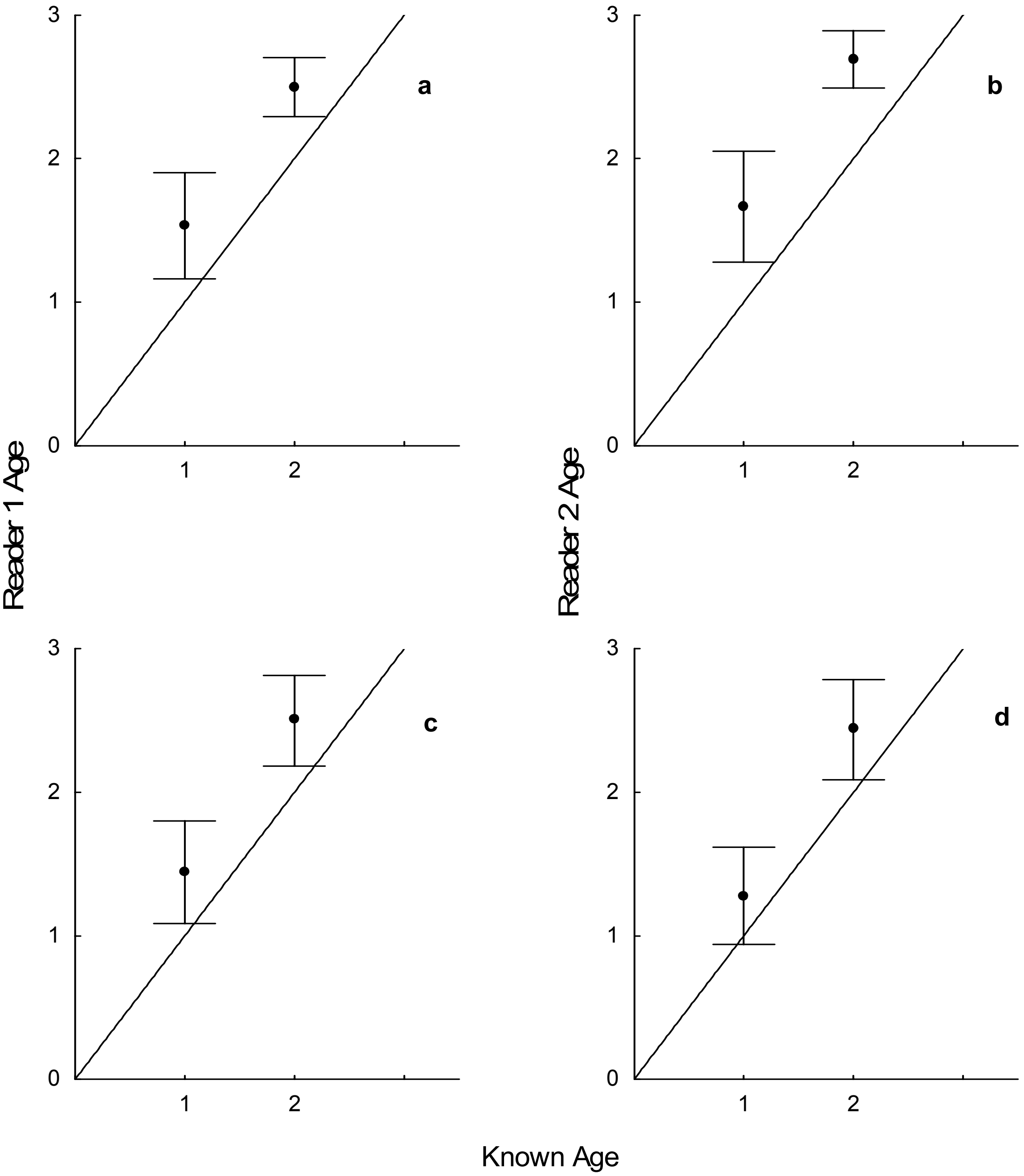

Figure 6. Age bias plots constructed from statoliths evaluated in 2005 from the Ogemaw Creek sea lamprey population that were aged by two readers. Panels a and b show the average age coded by each reader compared to the true age when using the Crystal Bond method. Panels c and d show the average age coded by each reader compared to the true age when using the Immersion Oil method. Error bars indicate 95% confidence intervals surrounding the mean age assigned by each reader to the true age.

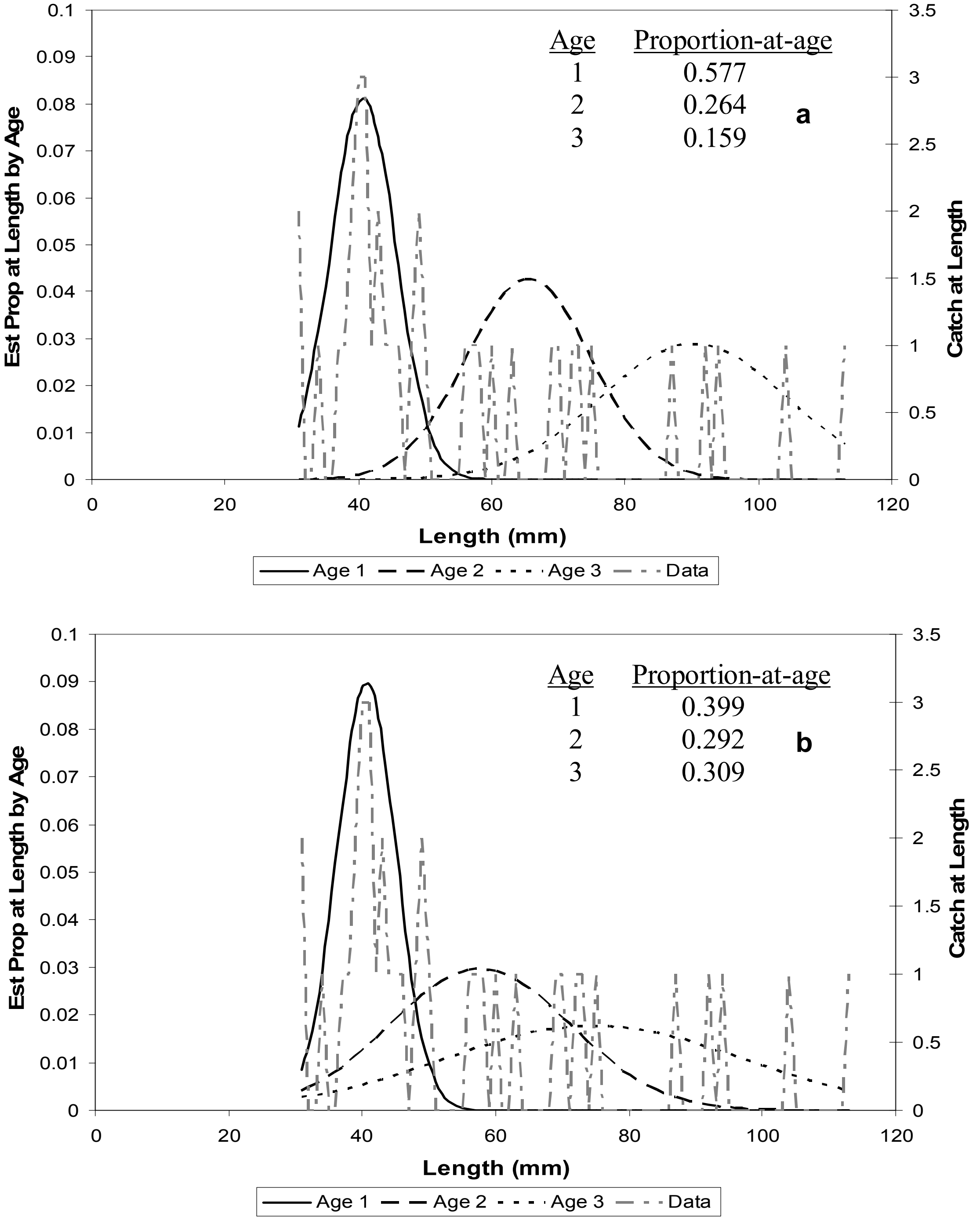

Figure 7. The actual length-frequency data for the Grafton Creek sea lamprey population is shown in gray with the approximate age-class distributions outputted by the model indicated as age 1, age 2, and age 3. Panel (a) shows the age-class distributions approximated by the model using only length information, and panel (b) shows approximations of the model using both length and bias-corrected age information. Proportions-at-age estimations are shown in the right-hand corner of each panel.

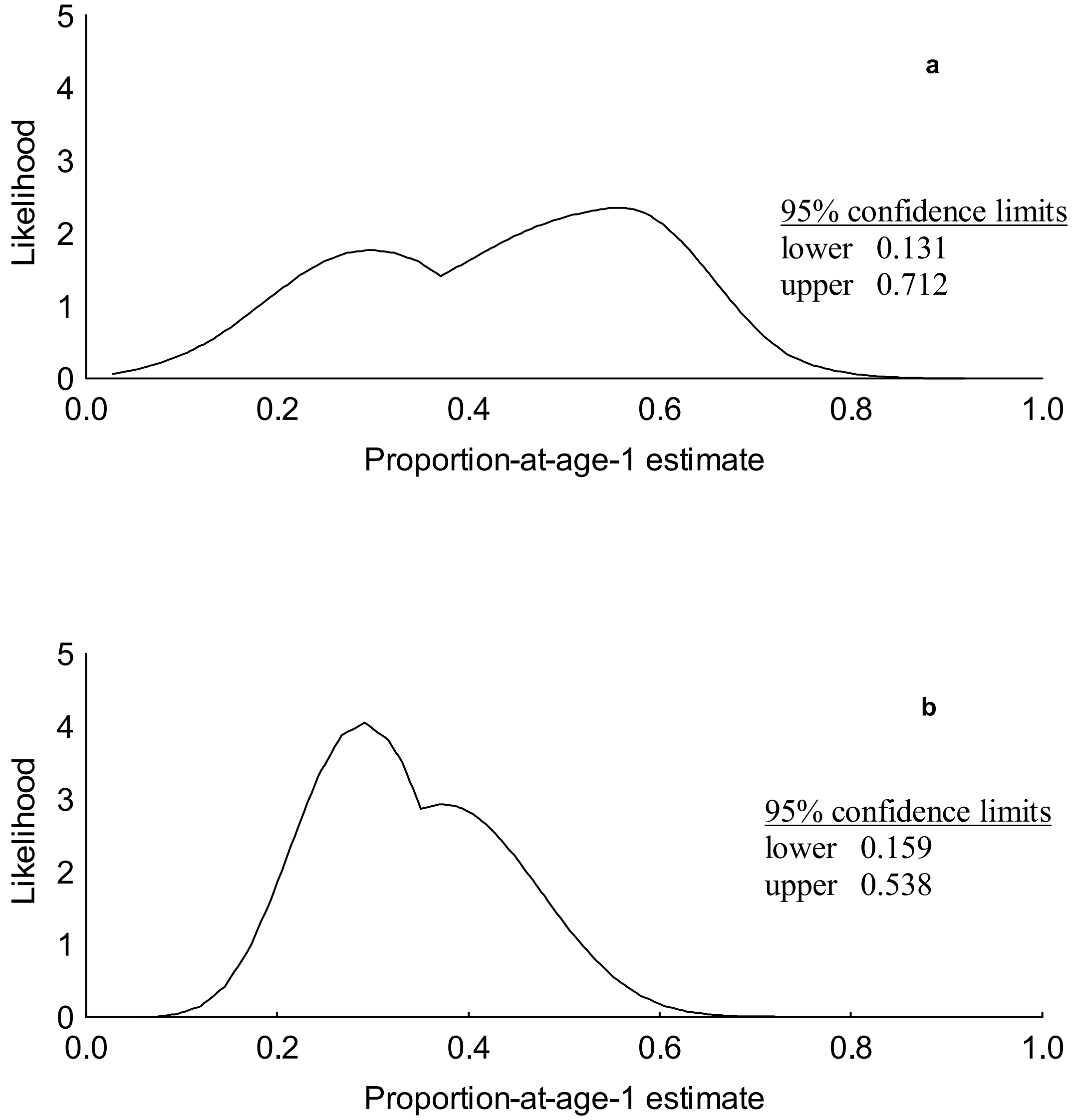

Figure 8. Likelihood profiles for the model estimates of proportion-at-age-1 for the Grafton Creek sea lamprey population when using a) only length information and b) when using both length and bias-corrected age information. 95% confidence limits for the estimates are shown in the lower right-hand corner of each panel.

Chapter 3

COMPARING SEA LAMPREY CONTROL STRATEGIES USING STOCHASTIC RECRUITMENT DYNAMICS AND ASSESSMENT UNCERTAINTY IN A SEA LAMPREY DECISION MODEL

Abstract

Incorporating density-independent recruitment variation and assessment uncertainty into sea lamprey (*Petromyzon marinus*) management models is important to facilitate a realistic comparison of the effectiveness of lampricide and adult (alternative) control strategies. Using recent data on recruitment and larval assessment uncertainty, a more realistic simulation model for an actual Great Lake was developed. This model simulates the existing sea lamprey control program for Lake Michigan and allows comparison of the effect of using only lampricide control to combinations of both lampricide and adult control methods (hybrid strategy). The sensitivity of the model to adult control costs and the effective proportion of spawners reduced by adult control was tested, using the current sea lamprey control budget for Lake Michigan. Assuming our best estimates of adult control costs and efficacy, results suggest that increasing adult control efforts at the expense of lampricide use will result in an increased abundance of sea lamprey. Adult control costs must be reduced and efficacy of adult control must be increased for a hybrid strategy to compare favorably to using only lampricide control. Sea lamprey pheromones may help reduce the proportion of effective spawners in each stream reach and decrease adult control costs, if pheromones can be inexpensively synthesized and applied. This modeling exercise was designed to effectively compare sea lamprey control strategies for the Great Lakes Fishery Commission which desires to

reduce reliance on lampricide control, and increase the role of adult control methods in controlling sea lamprey.

Introduction

The Great Lakes Fishery Commission (GLFC), in a recent mission statement, expressed the desire to achieve 50% of sea lamprey control (*Petromyzon marinus*) suppression with technologies alternative to lampricides, while reducing lampricide use by 20% (GLFC 2001). Extensive tests on the environmental safety of the two lampricides used by the Commission, TFM and Bayluscide, have revealed no long-term, detrimental effects to the ecosystem (Hubert 2003, Dawson 2003), and when effective, lampricide applications are believed to remove between 95 and 99% of the ammocoetes from treated streams (William Swink, U.S. Geological Survey, Hammond Bay Biological Station, unpublished data). Even though stream applications continue to be remarkably successful, public apprehension about pesticides and rapidly escalating lampricide costs compelled the Commission to find alternatives to lampricide control (GLFC 2001). Methods alternative to lampricide control use adult trapping (Mullett *et al.* 2003), barriers (Hunn and Youngs 1980, Lavis *et al.* 2003), and release of sterile males (Twohey *et al.* 2003*a*). Pheromones (Li *et al.* 2003, Sorensen and Vrieze 2003) also are being explored as a future alternative to lampricides. The available alternative methods all seek to reduce the number of adult spawners to decrease subsequent recruitment, and thus are referred to here as adult control methods.

The effectiveness of adult control methods depends on the ability to overcome recruitment variation; to reduce spawners to the point where few or no high recruitment events will occur. The relationship of sea lamprey spawning stock to the number of resulting recruits is highly variable at a wide range of spawning stock sizes, but high recruitment events (>200 age-1 larvae per $100m^2$) were not observed when spawner abundance was below 0.2 females per $100m^2$ (see chapter 1). Therefore, results suggest that adult control methods can be effective at trying to ensure low recruitment of sea lamprey populations if managers reduce spawner abundance to this value or below. However, we currently have very little information on the costs of adult control methods, and whether annual application of adult control methods on some streams could be cost-effective, or more effective at reducing the long-term adult sea lamprey population than lampricide use on some streams. Using a hybrid strategy in which lampricides are still used but at a substantially lower frequency on streams where adult control is applied, has been suggested as the majority of lampricide treatment expenditures each year are directed to a small number of large rivers (Brege 2003). Considerable savings may be achieved by directing adult control efforts at these rivers, but there are still many unanswered questions about the costs and efficacy of adult control.

The effectiveness of lampricide control depends on selecting the streams for treatment that will kill the most parasitic juveniles (transformers) per dollar spent. Since 1995 the GLFC has used a model, the Empiric Stream Treatment Ranking (ESTR) program (Christie *et al.* 2003), to rank stream reaches each year for lampricide treatment by using data from larval assessments to make short-term projections of the abundance of parasitic juveniles in each stream reach. This model fails to address the significant variability and uncertainty inherent in the stream ranking process (Hansen *et al.* 2003), uncertainty that is introduced through both measurement error (i.e., inaccurate estimates of larval habitat and abundance), and process error (i.e. inaccuracies in parameter estimates for growth rates and probability of metamorphosis) (Steeves 2002, Treble 2006). Consequently, there is concern about the accuracy of the estimates of abundance that it produces and thus the choice of streams for lampricide treatment (Steeves 2002).

To evaluate control strategies in the Great Lakes the GLFC has used models of sea lamprey population dynamics (Greig *et al.* 1992). Models are valuable tools for fisheries management but can misinform managers if they fail to account properly for process error, measurement error, and model uncertainty (Schnute and Richards 2001). For example, in the past, models used by the GLFC have not included density-independent recruitment variation (e.g. Koonce *et al.* 1993), a form of process error, when modeling sea lamprey population dynamics. Deterministic sea lamprey management models that do not explicitly incorporate density-independent recruitment variation will substantially overestimate the benefits of adult sea lamprey control options that rely on reducing adult reproductive success (Jones *et al.* 2003). A more realistic sea lamprey population model that accounts for recruitment variation and assessment uncertainty, and allows for the evaluation of a range of sea lamprey control strategies is what is needed to estimate the cost and effort at which adult control becomes a viable complement or alternative to lampricide control.

The objectives of this chapter were; (1) to develop a realistic model of sea lamprey population dynamics for a Great Lake (Lake Michigan) that allowed simulation of both lampricide and adult control; (2) to use this model to assess the relative performance of management strategies that differed in the allocation of control resources between lampricide control, which targets ammocoetes, and adult controls, which target adult sea lampreys; and (3) to determine the sensitivity of the results from objective 2 to alternative assumptions about adult control costs and the proportion of spawner reduction achieved by adult control.

Methods

Description of the model

A stochastic age-structured population model was used to forecast equilibrium parasitic sea lamprey abundance for Lake Michigan. The current model was derived from the whole-life cycle model previously described in Jones *et al.* (2003). The model is organized into several sub-model areas each described below, with definitions for all parameters provided in Tables 1 and 2. The complete set of sea lamprey-producing streams for Lake Michigan was explicitly represented in this model, following the data structure used in the ESTR database (Gavin Christie, Great Lakes Fishery Commission, Ann Arbor, MI, personal communication), which divides large streams into reaches for which independent lampricide treatment decisions can be made. Overall, the model is designed to forecast and compare the effect of different control strategies on the future abundance of parasitic sea lampreys in Lake Michigan.

Larval habitat

Each stream reach was characterized by its length, average width, and the area of two types of habitat suitable for larval sea lamprey production, all determined from habitat surveys. The total amount of larval habitat was then calculated from reach area and suitable habitat coverage

$$A_i = v_i \cdot w_i \cdot (p1_i + p2_i \cdot r_i) \tag{1}$$.

Type I habitat was defined as areas of fine sand and silt and is preferred by larval lampreys, while Type II habitat was defined as areas of coarser sand that is acceptable for larval lampreys. Type II habitat was weighted less heavily than Type I habitats based on observed differences in sea lamprey density in these two habitat types (Slade *et al.* 2003).

Sea lamprey life cycle simulation

Adult sea lamprey do not home to natal streams (Bergstedt and Seelye 1995), therefore spawning sea lampreys were allocated to stream reaches for spawning based on two rules: (1) the area of larval habitat in each reach, as streams with the greatest discharge have been found to accommodate the largest number of spawning-phase sea lampreys if other environmental factors are favorable (Mullett *et al.* 2003, Morman et al. 1980) and (2) the abundance of larvae in each reach, as lamprey have been shown to be attracted to a migratory pheromone released by stream-dwelling ammocoetes (Sorensen and Vrieze 2003). In all of the simulations used in this analysis, the two rules were given equal weight, and spawning sea lampreys were assumed to be positively related to both available larval habitat and larval abundance

$$S_i = S_A \cdot \frac{A_i}{\sum A_i} + S_P \cdot \frac{L_i}{\sum L_i} \tag{2}$$.

Spawners were divided into those that migrate based on the area of larval habitat

$$S_A = NA \cdot p_A \tag{3}$$,

and those that migrate based on the abundance of larvae in each reach

$$S_P = NA - S_A \tag{4}$$.

The estimate of larval habitat area combined with the density of spawning female sea lamprey was used to calculate recruitment of age-1 larvae following a stochastic Ricker stock-recruitment function

$$L_{i,1,t} = \alpha \cdot (S_{i,t} \cdot p^{f}) \cdot e^{-\beta \cdot \frac{(S_{i,t} \cdot p^{f})}{A_i} + \varepsilon_i^{r}} \quad (5).$$

The parameters for this relationship were estimated using data from 90 stream-years of sea lamprey stock-recruitment data (see chapter 1). We found empirical evidence of differences in this relationship for streams categorized *a priori* by sea lamprey control agents as regular (reg) or irregular (irr) sea lamprey producers (see chapter 1) and thus, used different *α and β* parameters for the two groups of streams (Table 1). Regular producers are streams subjected to a reliable cycle of lampricide treatments (i.e., they have been treated every 3, 4, or 5 years, depending on the stream). Irregular producers are subjected to a less consistent cycle of treatment. We also assumed that density-independent recruitment variation among streams was not correlated over time (no common “year effects”) based on our empirical analysis (see chapter 1). The empirical model related spawner numbers to age-1 abundance, so the number of age-0 sea lamprey from age-1 abundance was back-cast using an annual survival rate assumed constant among ages and stream reaches

$$L_{i,0,t} = \frac{L_{i,1,t}}{s_L} \quad (6).$$

The model was age-structured and growth of larval sea lamprey was calculated as

$$\overline{\ell}_{i,a} = a \cdot s\ell_i \cdot adg_i + \ell_0 \quad (7).$$

Season length and average daily growth estimates for each stream reach were obtained from the ESTR database. In addition, each cohort of larval sea lamprey was subdivided into a set of nine length bins, with the proportion of the cohort in each length bin characterized by a normal distribution with a fixed mean and coefficient of variation

$$\ell_{i,a,b} = \overline{\ell}_{i,a}(1 + cv_{\ell} \cdot d_b) \tag{8}$$

This change from the Jones *et al.* (2003) model was made to enable application of a length-dependent logistic model of metamorphosis, as is used in the ESTR system for forecasting future production of metamorphosing sea lampreys. The probability of metamorphosis depends on the length of the sea lamprey at the end of the previous year. The proportion of larvae from a given length bin to transform was calculated as

$$p_b^t = \frac{e^{\left(\beta_0 + \beta_1 \cdot \ell_{i,a,b}\right)}}{\left(1 + e^{\left(\beta_0 + \beta_1 \cdot \ell_{i,a,b}\right)}\right)} \tag{9}$$

The number of transformers estimated by the model in each reach was then calculated by

$$T_i = \sum_{a=1}^{6} (L_{i,a} \cdot p^b \cdot \sum_{b=1}^{9} p_b^t) \tag{10}$$

Application of sea lamprey control

A method analogous to the stream selection procedure utilized in the sea lamprey control program (Christie *et al.* 2003) was used to determine which stream reaches to treat in any given year of the simulation. Each year, stream reaches were ranked according to the number of transformers that would be removed from next year's parasitic population, per dollar of treatment cost. Stream reaches with large populations of large ammocoetes (i.e., those likely to metamorphose into parasites within a year) and modest treatment costs were ranked highest (Jones *et al.* 2003). If a reach was selected for TFM treatment, the entire larval population in that reach was reduced based on a reach-specific survival from chemical treatment

$$L_{i,t} = L_{i,t-1} \cdot s_c \tag{11}$$

Each year, reaches were treated in rank order, from highest to lowest, until the budget apportioned to lampricide control was utilized.

The number of parasites that enter the lake each year was calculated from the number of transformers last year that survived treatment in treated streams and the total number of transformers present in untreated streams

$$P_t = (\sum_{i=1}^{M} T_{i,t-1} \cdot s_{c\,i} + \sum_{j=M+1}^{N} T_{j,t-1}) \cdot s_T \tag{12}$$

The total number of spawners predicted in the lake next year is the number of parasites surviving the parasitic phase this year

$$NA_{t+1} = P_t \cdot s_j \tag{13}$$

The model included an additional source of parasitic sea lampreys, called the "untreatable pool" which was intended to represent production of sea lampreys from sources that are not presently vulnerable to lampricide control (e.g., lentic areas). Population dynamics (reproduction, larval growth and survival, etc.) in the untreatable pool followed the same rules as for the treatable stream reaches, as did the allocation of spawning sea lamprey to this compartment. The size (larval habitat area) of the untreatable pool was defined as a proportion of the overall area of larval habitat in the entire lake (10% was used in the current simulations).

Adult control was simulated by reducing the population of effective spawning females by a fixed percentage, relative to the predicted size of the spawning run in stream reaches

$$Momseff_{i,t} = (S_{i,t} \cdot p^{f})(1 - s_{r}) \qquad (14).$$

To be effective, controls directed at reducing sea lamprey spawning success would have to be applied annually because, unlike a lampricide treatment that affects all year classes of ammocoetes present in a reach at the time of treatment, an adult control action only affects a single year class (Jones *et al.* 2003).

Chemical control was applied over the entire infested length of a stream reach if a stream reach was selected for treatment (e.g., total stream area)

$$AS_{i} = v_{i} \cdot w_{i} \qquad (15).$$

For this reason, chemical control costs for the model were assumed to be a function of total stream reach area

$$C_{ci} = f_{ci} + u_{ci} \cdot AS_{i} \qquad (16).$$

Chemical control costs were obtained from recent data on lampricide costs for each stream reach. Linear regressions were performed on lampricide costs (C_{ci}) vs. total stream reach area (AS_{i}) to obtain values for fixed cost (f_{ci}) and unit cost (u_{ci}) per unit of stream reach area using Statistica 7.0 (StatSoft, Inc. 2004).

Adult control reduces the effective spawning population and attempts to reduce the total number of larvae produced by a stream reach; therefore adult control costs were assumed to be a function of larval habitat

$$C_{ai} = f_{ai} + u_{ai} \cdot A_i \qquad (17).$$

Adult control costs were obtained from recent data on barrier costs (average annual cost over 50 years) for a subsample of Lake Michigan streams. A linear regression was performed on barrier costs (C_{ai}) vs. larval habitat (A_i) to obtain values for fixed cost (f_{ai}) and unit cost (u_{ai}) per unit of larval habitat area using Statistica 7.0 (StatSoft, Inc. 2004).

Inclusion of uncertainty

Recruitment variation was added to the model using the ε_i^r term in the stock-recruitment equation (equation 9), based on the observed residual variation in ln(R/S) from my empirical analysis (see chapter 1).

For lampricide control, uncertainty in the stream reach selection process was simulated by adding an error term to the actual abundance of sea lamprey expected to transform and become parasites in the following year in each reach

$$Tobs_i = T_i + \varepsilon_i^T \qquad (18).$$

$$\varepsilon_i^T \sim \Gamma(0, cv_T)$$

The error was drawn independently for each stream reach from a gamma distribution with a CV of 1.71, which was derived from an analysis of uncertainty in the larval assessment procedures currently used to rank reaches (Steeves 2002). This mimicked the uncertainty in the larval assessment process that is used to rank reaches for TFM treatment.

Model calibration and simulations

The model was calibrated using recent observations of adult sea lamprey abundance and recent control expenditures, and by assuming that the adult sea lamprey population in Lake Michigan is roughly in equilibrium with recent control expenditures. The size of the untreatable pool was set to give plausible sea lamprey abundances at very high control expenditures. Then, I adjusted the survival rate of larval sea lampreys (the model was sensitive to this value and the true value is unknown) until the median forecasted adult sea lamprey abundance for long-term (100 year) simulations using a budget corresponding to recent control expenditures reasonably matched observed adult abundance for recent years.

All model simulations were run for 100 years to allow sea lamprey spawner abundance to reach an equilibrium state prior to the final years of the simulation when model estimates were evaluated. Each simulation was repeated 100 times to capture uncertainty due to density-independent recruitment variation and assessment error. The same sequence of random numbers was applied to each set of simulations, so that the differences among sets of simulations were not influenced by random variations among sets. For each set of simulations the median number of resulting spawners for each year over 100 simulations was recorded. The final outcome indicator was then the average of the median number of spawners for the final ten years of the simulation. Additionally, I recorded the number of times each of the ten largest streams were treated with lampricide in the 100-year cycle.

I assessed the performance of control strategies by varying the allocations of an overall control budget between lampricide and adult control. Management scenarios using only lampricide, only adult control, and a combination of both control methods were explored. Total cost of integrated sea lamprey management was the combined cost of chemical and adult control, not to exceed the current (2006) sea lamprey control budget for Lake Michigan which was $2.06 million dollars.

Initially, I considered an adult control strategy in which an 88% effective reduction of spawners was achieved, comparable to the adult control success achieved recently in the St. Mary’s River (Gavin Christie, Great Lakes Fishery Commission, Ann Arbor, Michigan, personal communication). To simulate increasing levels of adult control, I added streams (consisting of all the stream’s reaches) to the adult control program by starting with the largest (i.e., most expensive) stream first, and reducing the funds available for lampricide control by the costs of applying adult control to that stream. With an overall control budget of $2.06 million and adult control costs of $39500+ $0.06 · larval habitat area, applying adult control to the Muskegon River (largest stream in the Lake Michigan watershed, 2.67 million m^2 of larval habitat) reduces the budget available for lampricide control to $1.86 million ($2.06 million - $199,545 for Muskegon River adult control). Then I added the second largest stream and further reduced the lampricide budget accordingly. Adding a second stream (Manistique, 2.23 million m^2) further reduces the lampricide budget to $1.69 million.

My rationale for selecting the largest streams first was that these are the most expensive streams to treat with lampricide. If treatment frequency can be reduced on these streams the lampricide control costs may be much lower to achieve the same lake-wide level of chemical control. I continued this progressive addition of large streams to the adult control program for up to ten streams, and costs of adult control were increased according to the total larval habitat area affected.

I assessed the sensitivity of the performance of different adult control budgets to two key variables. First, I varied the percent reduction in spawners achieved in each stream by adult control. I successively increased the percent reduction of spawners by 2% from the initial value of 88% until reaching a point at which some adult control did better than lampricide control. Second, I varied the unit cost of adult control per m^2 of larval habitat. I successively decreased the unit cost of adult control by $0.01 from the initial value of $0.06 until I reached the point at which some adult control did better than lampricide control. Finally, I combined assumptions of reduced costs of adult control with a simultaneous increase in the percentage of spawners reduced, as described above, to find a point at which at least some adult control was equally effective as lampricide control alone in reducing spawning lamprey populations. I evaluated the performance of different strategies by comparing the long-term reductions of spawners achieved in the lake, and by comparing the number of times the ten largest streams were treated with lampricide.

To determine how sensitive the outcomes are to the stock-recruitment parameters, I evaluated the model results when applying adult control to a set of regular sea-lamprey producing streams compared to applying adult control to a set of irregular sea-lamprey producing streams of similar total area (and total cost of adult control). I looked for evidence to support the claim that regular sea lamprey-producing streams are less susceptible to adult control because they require greater reductions in spawner numbers, on average, to achieve target recruitment levels (see chapter 1). I evaluated whether four sets of regular sea lamprey-producing streams of similar total size and total cost to irregular sea lamprey-producing streams produced noticeably more spawners on average when adult control was applied in long-term simulations, and determined the frequency of lampricide applications in the ten largest streams.

Results

Visual inspection of the relationship between lampricide costs and stream reach area (Figure 1) suggested a different relationship for small and large streams, with unit costs increasing much more rapidly with area for smaller streams. Accordingly I divided the data into two groups of streams and fit separate regressions to each group (Figure 1, Table 2). After trying a range of cut-offs between small and large reaches, the best-fit regression lines occurred when small reaches (sm) were regarded as having a stream area of less than 400,000 m^2, with large reaches (lg) having a larger stream area. The best-fit line that described the fixed and unit costs of adult control based on larval habitat area, was the same for all stream reaches (Figure 2, Table 2). The fit of the adult control cost data to a regression line was poor (Adjusted R^2= 0.56). The fit of the lampricide control data to a regression line for small streams was good (Adjusted R^2=0.82), while the fit for large streams was poor (Adjusted R^2= 0.56) (Figures 1 and 2).

At the initial costs of adult control of \$39500 + \$0.06 · larval habitat, and an 88% spawner reduction, at no point did adult control perform better than lampricide control (Figure 3a). In fact, unit costs of adult control at this level of spawner reduction would have to be reduced to \$0.01 per m^2 of larval habitat to perform better than lampricide control (Figure 3b). In this case, if we treat the largest stream with adult control first, at a cost of \$39500 + \$0.01 · larval habitat, and use the rest of the budget for lampricide control, the median number of spawners in the lake can be reduced compared with using only lampricide control (Figure 3b).

Employing the costs of adult control of \$39500 + \$0.06 · larval habitat, the % reduction of spawners by adult control must be increased from 88% (Figure 4a) to 100% to do better than only using only lampricide control (Figure 4b). Under this scenario, I observed that by treating at least two of the largest streams with adult control, adult control does better or is almost equally as effective as only lampricide control in reducing the long-term number of spawners in the lake (Figure 4b).

By simultaneously increasing the % spawners reduced initially by adult control and decreasing the initial unit cost of adult control I found a few hybrid scenarios (using both adult and lampricide control) that perform better than using only lampricide control (Figure 5). By decreasing the unit cost of adult control by half (to \$0.03) and increasing the spawner reduction to 94%, which was achieved in the St. Mary's River in 2002, we can do better than using only lampricide control by treating two or six of the largest streams with adult control (Figure 5a). By increasing the spawner reduction to 96% and at a unit cost of \$0.04, we can treat the three largest streams with adult control and reduce the long-term number of spawners compared to using only lampricide control (Figure

5b). As the proportion of spawners reduced in each stream reach by adult control is increased, the frequency of lampricide treatments needed in the targeted stream reaches is reduced (Table 3).

When applying adult control to only regular sea-lamprey producing streams compared with applying adult control to only irregular sea-lamprey producing streams of similar total area and cost, results indicated that the number of spawners produced in long-term simulations was very similar between the stream types (Table 4). When adult control was applied to irregular streams the frequency of lampricide treatments on the seven largest regular sea lamprey-producing streams was higher in all cases (Table 4).

Discussion

Comparing the true effectiveness of adult controls to lampricide control requires the incorporation of density-independent recruitment variation and larval assessment uncertainty estimates, and is dependent on model parameters such as cost and effectiveness of adult control. Using my best estimates of adult control costs and the efficacy that can be achieved by adult control, results suggest that increasing adult control efforts at the expense of lampricide use will result in an increased abundance of sea lamprey. Results suggest that it would be unrealistic for adult control to compare favorably to lampricide control by either just reducing costs of adult control or just increasing the proportion of effective spawners that can be reduced by adult control. To compare favorably to lampricide control, adult controls costs must be minimized and the proportion of effective spawners that can be reduced by adult control must be increased. If this can be achieved, the treatment of a few large streams with adult control was observed to be an option for a successful hybrid strategy, in which lampricides are still used but at a substantially lower frequency on streams where adult control is applied (Table 3). Adult control on the two largest streams, assuming we can achieve a cost of \$39500 + 0.04 per m^2 of larval habitat costs \$0.275 million, while lampricide treatments currently cost over five times as much. Considerable savings may be achieved by directing adult control efforts at these streams, provided increased efficiency and reduced costs of adult control.

Sea lamprey pheromones hold considerable promise as a tool to enhance trapping efficiency (Wagner *et al.* 2006, Johnson *et al.* 2006), which suggests that the spawner reduction targets implied by these model results may be achievable. If chemical attractants could be inexpensively synthesized, then the proportion of effective spawners reduced by adult control could be increased at a reasonable cost (Li *et al.* 2003). The initial 88% effective reduction of spawners used in the model was based on adult control success achieved recently through trapping and sterile male release in the St. Mary's River, with recent reductions recorded at up to 94%. Trapping efficiency on Lake Michigan streams in 2005 ranged from 11-85% with an average trapping efficiency of 41%, on streams with no releases of sterile males. Besides the option of substantially increasing trapping efficiency through the use of pheromones in these streams, effective spawner reduction can still be achieved through other uses of pheromones. Recent modeling research found that rapid suppression of sea lamprey populations could be achieved by the combined application of the current level of trapping in the Great Lakes and release of pheromone-enhanced sterile males (Klassen *et al.* 2005).

When adult control was applied to only regular sea lamprey-producing streams and only irregular sea lamprey-producing streams of similar total size and total cost, similar numbers of spawners were produced in all cases. The Ricker alpha parameter, which describes average survival when spawner abundance is close to zero, of regular sea lamprey-producing streams is three times higher than that of irregular sea lamprey-producing streams (Table 1-log scale). Therefore, a regular sea lamprey-producing stream produces more recruits than an irregular sea lamprey-producing stream from the same size spawning population. This suggests that sea lamprey populations in irregular streams would be more vulnerable to all control measures, as the ability of the population to replace itself is reduced compared with regular streams. Results between adult control on regular and irregular sets of streams may be similar because treating irregular sea lamprey-producing streams with adult control could be very effective, but lampricide treatments must then be focused on productive streams (regular) less susceptible to lampricide control (Table 4), and thus the model estimates similar numbers of sea lampreys produced as in the regular stream sets. Treating regular sets of streams with adult control should be less effective, but lampricide treatments are applied, in this case at a more equal proportion on regular and irregular sea lamprey-producing streams, and since irregular streams are more susceptible to control measures the model estimates similar numbers of sea lampreys as produced in the irregular stream sets (Table 4). We do no better by applying adult control to those streams more susceptible to control efforts (irregular streams), due to the trade-off of applying lampricide control to streams less susceptible to control efforts (regular streams).

This model mimicked the sea lamprey control program for Lake Michigan and compared sea lamprey control strategies on the basis of cost in dollars and the long-term number of spawners produced. In this model, uncertainty in sea lamprey assessment procedures was characterized, and meta-analytic techniques were used to gather stock-recruitment data used in the life cycle simulation in an attempt to reduce the biological basis of uncertainty (Myers and Mertz 1998) and make the model more realistic. This model has, and should continue to be improved through input from sea lamprey managers, and can help in guiding sea lamprey managers in an integrated pest management program. But, ideally these results could provide the basis for the delineation of management experiments for individual streams (Jones *et al.* 2003) or for Lake Michigan as a whole. Experimenting with sea lamprey control strategies within an adaptive management framework on one of the five Great Lakes would provide greater understanding and the ultimate test of management strategies.

Table 1. Parameters, their assumed values, and state variables used in the sea lamprey population model.

Symbol	Definition	Assumed value
i	Reach	
a	Age	
b	Length bin(9) to hold each cohort of larval sea lamprey	
t	Year	
Habitat		
AS_i	Stream area	varies by reach
A_i	Larval habitat area	varies by reach
v_i	sea lamprey infested length of stream	varies by reach
w_i	mean width of stream	varies by reach
$p1_i$	proportion of type I larval habitat (preferred)	varies by reach
$p2_i$	proportion of type II larval habitat (acceptable)	varies by reach
r_i	index of type 2 habitat suitability, relative to type 1	0.38
Sea lamprey life cycle simulation		
NA_t	Number of spawners in lake	State variable
$S_{i,t}$	Spawning sea lamprey abundance	State variable
P_t	Number of parasites in lake	State variable, initially 100,000
$T_{i,a,t}$	Transformer abundance	State variable
$L_{i,a,t}$	Larval sea lamprey (ammocoete) abundance	State variable
a_0	initial age-0 larval density	1 per m^2
m_a	Age-specific probability of metamorphosis	0(2),.2(3),.4(4).7(5),1.(6)
p_A	proportion of spawners allocated by area	0.5
S_P	spawners to be allocated by area	50% of spawners in lake
S_A	spawners to be allocated by pheromone	50% of spawners in lake
α	Ricker model parameter	reg=4.815, irr=3.754
β	Ricker model parameter	reg=0.1616, irr=0.1473
s_L	annual survival during ammocoete phase	0.395

Table 1(continued).

s_{m}	survival during transformation phase	0.75
s_j	survival during parasitic (juvenile) phase	0.75
p^f	proportion of females	0.5
p^t	proportion of larvae transforming into parasites	varies
β_0	upper lakes logistic transformation curve parameter	0.1343101
β_1	upper lakes logistic transformation curve parameter	-19.22319
Growth		
$\ell_{i,a}$	larval length	varies by reach and age
$s\ell_i$	season length	varies by reach
adg_i	average daily growth	varies by reach
ℓ_o	initial length in millimeters	20
d_{b}	"distance" of length bin b from mean length	varies by bin
p^b	probability of being in a length bin	~(.04(1),.07(2),.12(3),.17(4),.20(5), .17(6),.12(7),.07(8),.04(9))
Uncertainty terms		
$\varepsilon^{\mathrm{r}}_i$	variance of process error in larval recruitment to age-1	reg=2.99, irr=3.24
ε^T	error on transformer abundance	$\sim \Gamma(0,1.71)$
cv_T	coefficient of variation of transformer abundance	1.71
cv_ℓ	coefficient of variation of length at age	0.33

Table 2. Parameters, their assumed values, and state variables used in applying sea lamprey control.

Symbol	Definition	Assumed value
C_{ci}	Cost of chemical control (dollars)	State variable
C_{ai}	Cost of adult control (dollars)	State variable
f_{ci}	fixed cost of chemical control (dollars)	sm=8000,lg=60000
u_{ci}	Unit cost of chemical control (dollars)	sm=0.52,lg=0.12
f_{ai}	fixed cost of adult control (dollars)	Initial=39500
u_{ai}	Unit cost of adult control (dollars)	Initial=0.06
s_c	survival from chemical treatment	varies by reach(<0.1)
s_r	reduction of effective female spawners by adult control	Initial=0.88
$Momseff_{i,t}$	Effective number of female spawners	varies

Table 3. Comparison of the number of times the ten largest streams were treated with lampricide under only lampricide control and when using different levels of adult control.

River Name	Larval habitat area (m^2)	Lampricide control only Times treated /100 year cycle	Adult control 88% spawner reduction \$0.04 unit cost Times treated /100 year cycle	Adult control 94% spawner reduction \$0.04 unit cost Times treated /100 year cycle	Adult control 96% spawner reduction \$0.04 unit cost Times treated /100 year cycle
Muskegon	2,667,426	22.45	6.37	4.01	3.03
Manistique	2,231,677	18.65	4.10	2.95	2.24
Pere Marquette	1,791,364	28.06	13.85	12.22	11.67
Big Manistee	1,600,131	26.6	14.66	13.31	12.8
St. Joseph	1,099,377	21.93	9.42	7.96	6.98
White	959,531	32.66	17.40	16.68	15.41
Ford	697,880	17.16	4.78	3.37	2.21
Cedar	579,338	24.52	10.91	9.77	8.62
Kalamazoo	527,311	24.60	11.17	9.74	8.6
Whitefish	435,059	23.94	11.26	9.40	8.51

Table 4. Detailed data on the comparison of treating four similar sets of regular sea lamprey-producing streams and irregular sea lamprey-producing streams with adult control.

Streams set	Area of larval habitat to which adult control was applied (m^2)	Cost of applying adult control (dollars)	Spawners produced when sea lamprey control was applied	Number of lampricide treatments on the seven largest regular streams in a 100-year cycle	Number of lampricide treatments on the three largest irregular streams in a 100-year cycle
Regular					
1	4,067,901	402,074	190,191	130.9	58.1
2	3,826,555	348,093	206,619	132.3	57.9
3	3,330,234	318,314	194,683	132.7	59.3
Irregular					
1	4,041,065	400,464	215,946	155.7	33.6
2	3,858,367	350,002	215,946	155.7	33.6
3	3,331,055	278,863	191,454	159.9	44.1

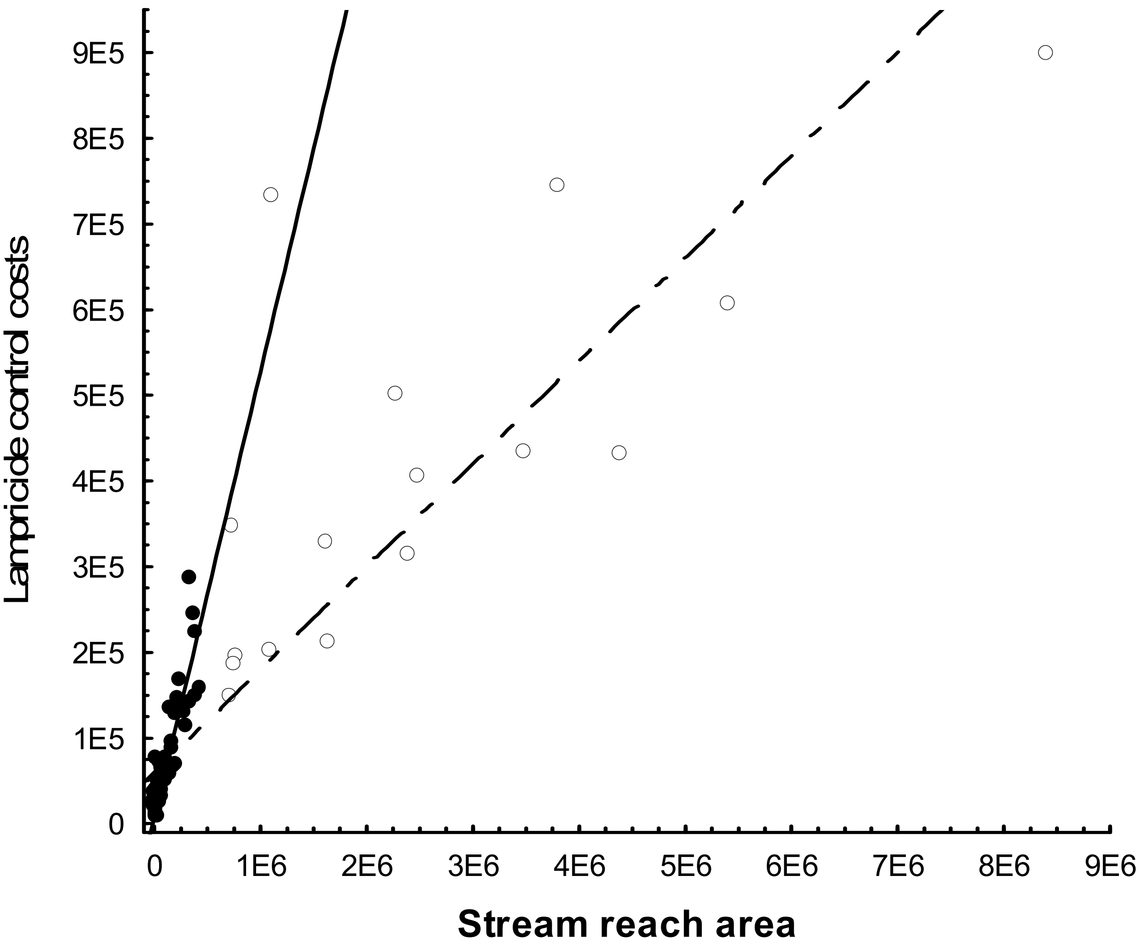

Figure 1. The regression of lampricide cost data for all streams in the model against the total stream reach area. The resulting line equations provide the cost structure inputted into the model of Total cost=fixed cost + unit cost · stream reach area. The fixed cost used in the model was adjusted to be slightly below the lowest lampricide control cost. Small stream reaches (<400,000m^2), illustrated by closed circles and the solid line, were found to follow a different linear relationship than large stream reaches (>400,000m^2), illustrated by open circles and the dashed line. The resulting line equations were 8000 + 0.52 · stream reach area and 60000 + 0.12 · stream reach area for small and large streams, respectively.

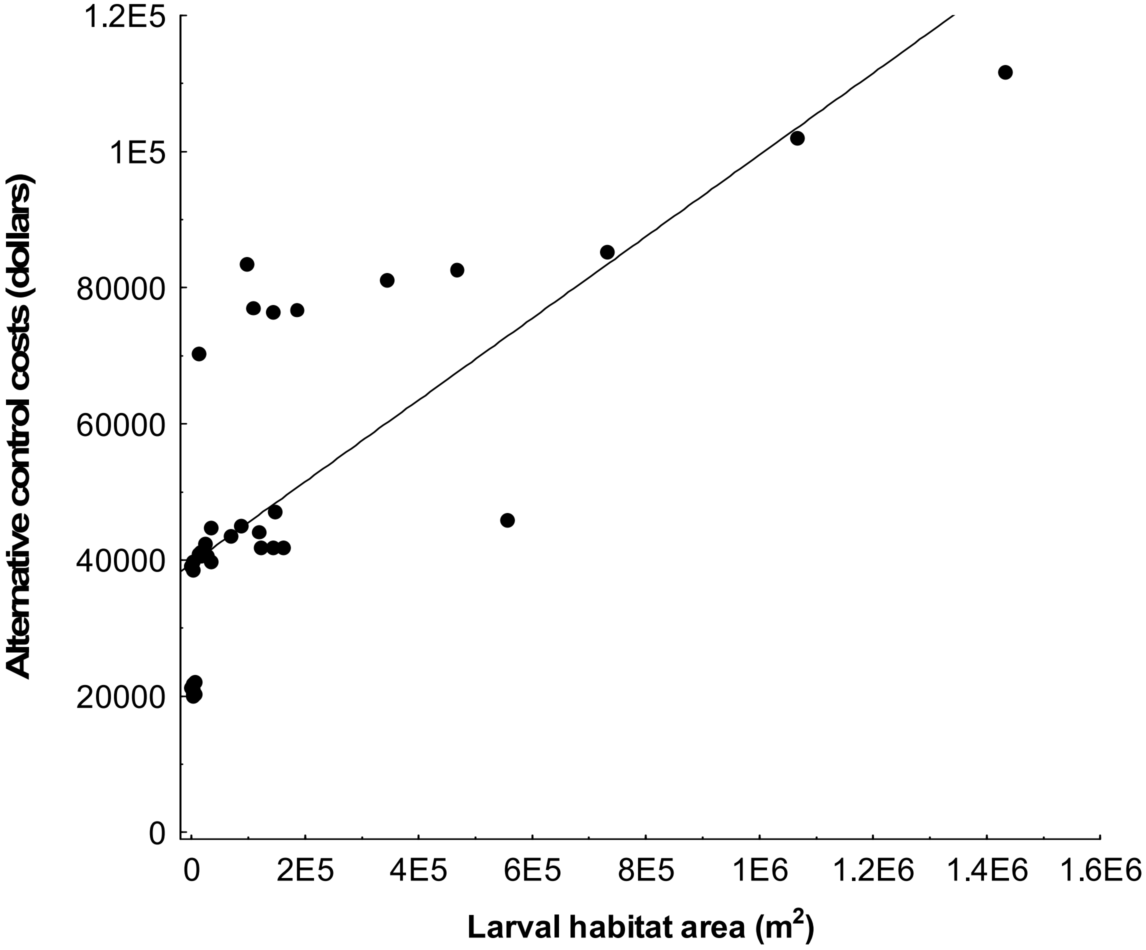

Figure 2. The regression of adult cost data for a subsample of streams in the model against the total larval habitat area. The resulting line equation provides the cost structure inputted into the model of total cost=fixed cost + unit cost · larval habitat area. The resulting line equation, illustrated by the solid line, was 39500 + 0.06 · larval habitat area.

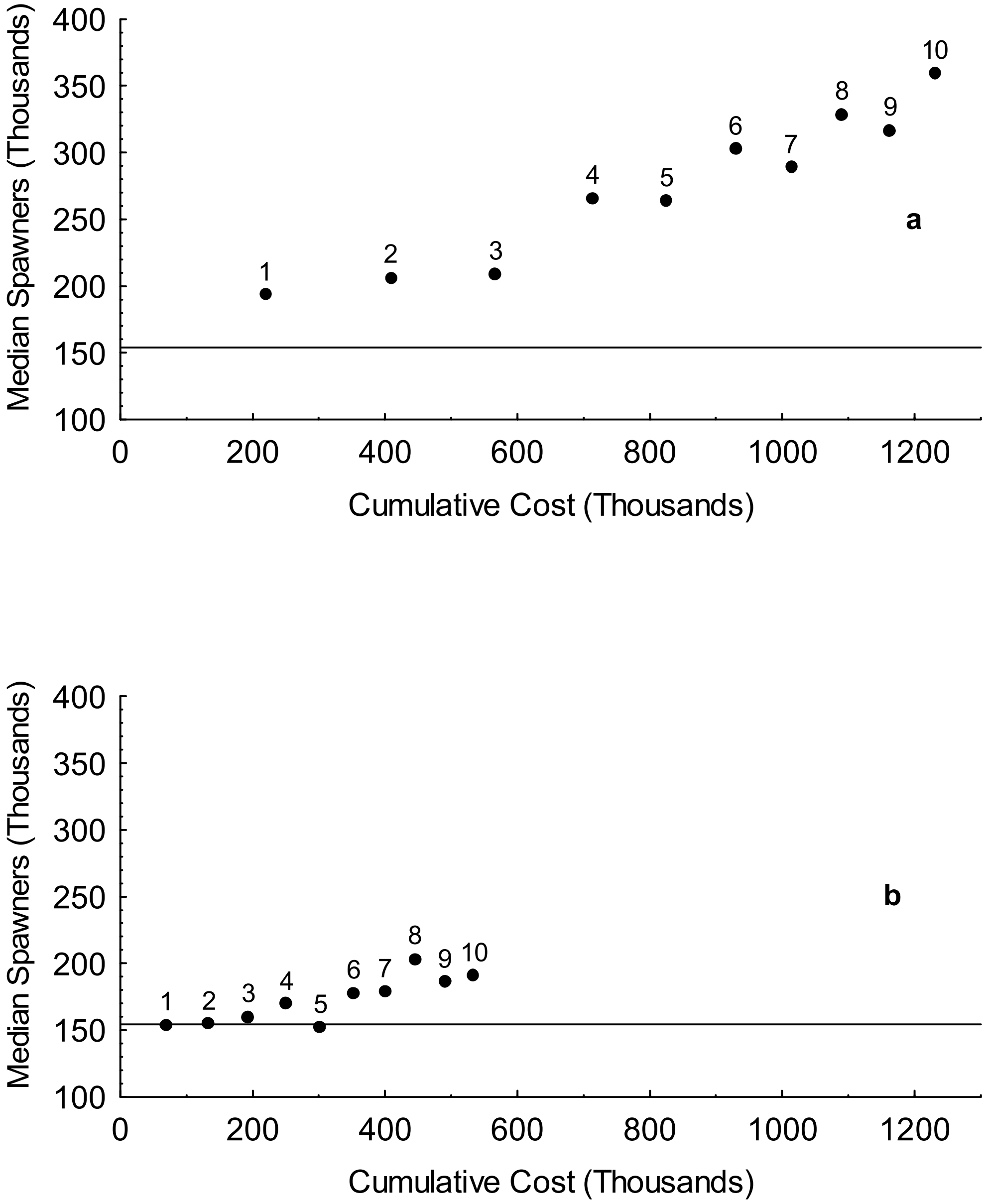

Figure 3. The median number of spawners produced versus the cumulative cost of adult control when using adult control costs and spawner reductions achieved by adult control of a) \$39500 + \$0.06 · larval habitat area and 88%; and b) \$39500 + \$0.01 · larval habitat area and 88%. The horizontal line in each graph represents the median number of spawners resulting from the application of only lampricide control. The number next to each point represents the number of streams treated by adult control; one to ten of the largest streams received adult control, added in order of decreasing size.

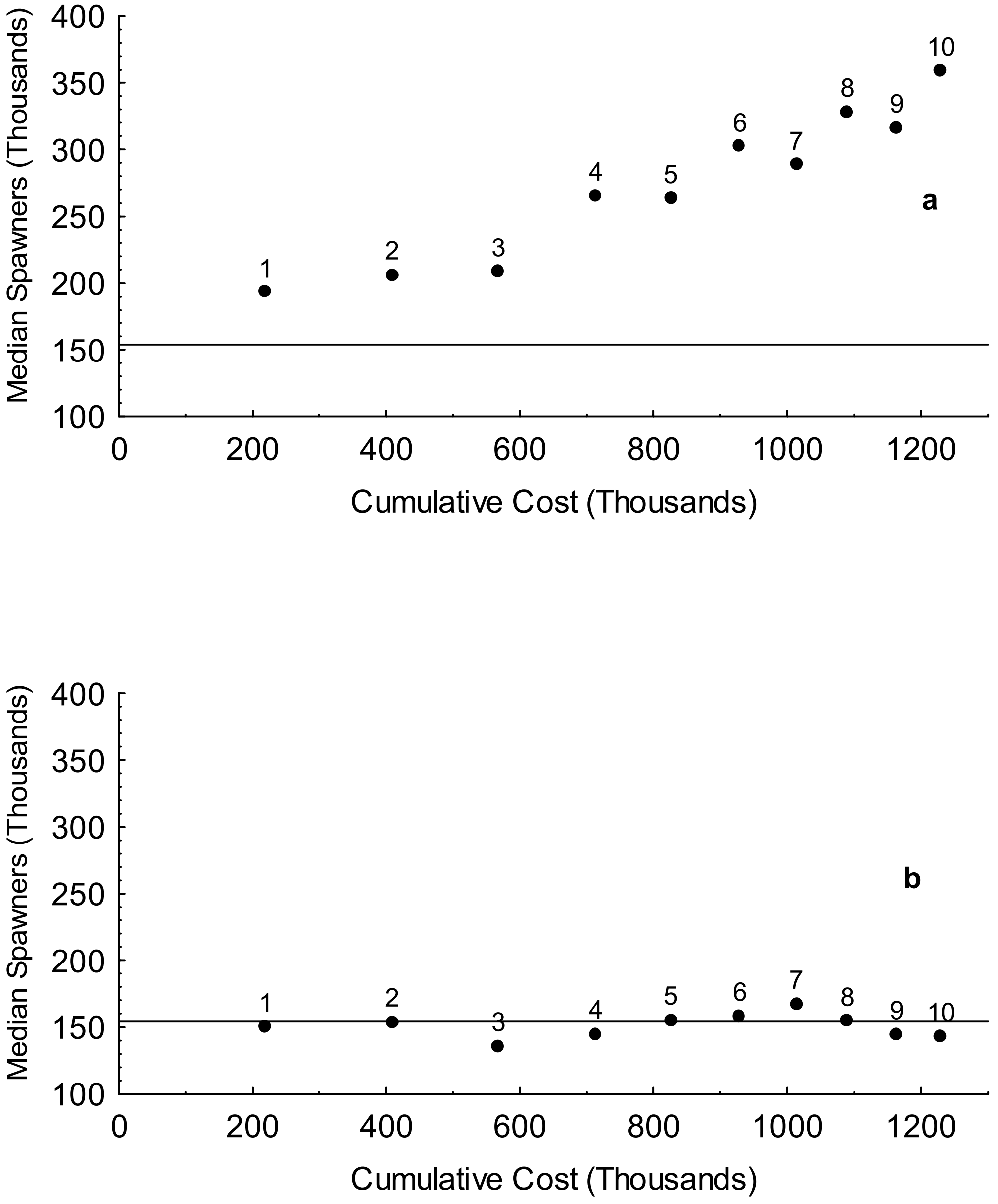

Figure 4. The median number of spawners produced versus the cumulative cost of adult control when using adult control costs and spawner reductions achieved by adult control of a) \$39500 + \$0.06 · larval habitat area and 88%; and b) \$39500 + \$0.06 · larval habitat area and 100%. The horizontal line represents the median number of spawners resulting from the application of only lampricide control. The number next to each point represents the number of streams treated by adult control; one to ten of the largest streams received adult control, added in order of decreasing size.

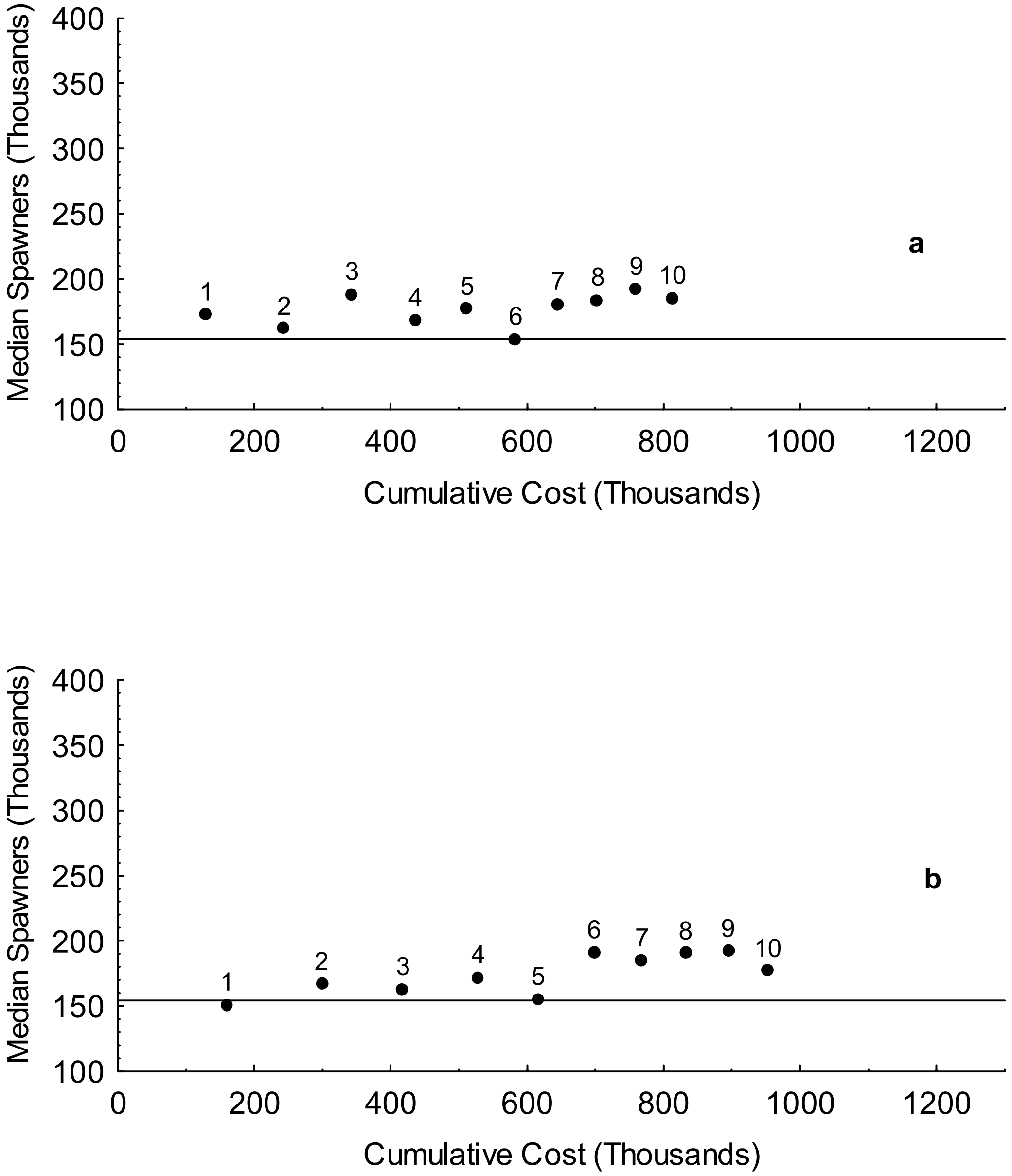

Figure 5. The median number of spawners produced versus the cumulative cost of adult control when using adult control costs and spawner reductions achieved by adult control of a) \$39500 + \$0.03 · larval habitat area and 94%; and b) \$39500 + \$0.04 · larval habitat area and 96%. The horizontal line in each graph represents the median number of spawners resulting from the application of only lampricide control. The number next to each point represents the number of streams treated by adult control; one to ten of the largest streams received adult control, added in order of decreasing size.

MANAGEMENT RECOMMENDATIONS

Observed sea lamprey stock-recruitment data for 90 stream-years (chapter 1) suggests to management a proposed adult (alternative) control target of 0.2 females$\cdot$100 m^{-2} of larval habitat in streams is required to reasonably ensure success of adult control strategies. Recruitment variation occurs at all spawner abundances, however, so there is no "ideal" reference point, but no high recruitment events were seen below 0.2 females$\cdot$100 m^{-2}, so this serves as a reasonable target. If this adult control target is to be achieved by trapping spawning-run sea lampreys then trapping efficiency must significantly increase from current levels across the basin. Since sea lamprey pheromones have been shown to effectively attract and capture sea lampreys in traps, thereby increasing trapping efficiency in field trials, pheromone strategies should be integrated into existing management techniques provided this can be done at a reasonable cost.

Using the simulation model research (chapter 3) as a guide, the best test of management strategies would be provided by designing management experiments and dovetailing this research with the design of the pheromone field trials to get at critical uncertainties concerning current adult control methods and adult control using pheromones. The simulation model results highlight that comparisons of different management strategies using combinations of lampricide and adult control depend critically on developing better estimates of the costs of adult control, and of determining the achievable levels of efficacy for adult control strategies. Management experiments and the pheromone field trials could be designed to answer questions from this dissertation, such as the magnitude of spawner reductions that could be achieved with existing adult control and pheromone-enhanced trapping, the level of age-1 recruitment that would be cost-effective to achieve with existing adult control and pheromone-enhanced trapping, and the true costs of adult control with and without pheromones. To answer these questions adult control managers on a stream would characterize and estimate the sea lamprey spawning run, trapping efficiency, larval habitat area controlled (i.e., area upstream of barrier or trap), recruitment-at-age-1 the following fall, and costs required to implement adult control. Many of these metrics are measured yearly by sea lamprey managers, so coordinating the estimate of all these measures in experimental streams should be feasible and contribute significantly to improving adult sea lamprey control.

The simulation model suggested we did no better by applying adult control to streams more susceptible to control efforts (lower survival of recruits), due to the trade-off of having to apply more lampricide control to streams less susceptible to control efforts; thus management experiments should focus adult control on the largest streams in the basin where lampricide costs are high and adult control may help reduce the frequency of treatments in these large steams and most likely reduce the amount of lampricide used basin-wide. Again, this presumes that the cost-effectiveness of adult control will be greater on these large streams due to economies of scale (i.e., fixed costs will not increase in proportion to stream size).

The objective, likelihood-based statistical model to estimate proportion-at-age (chapter 2) should be used by managers, as it is an improvement over subjectively assigning age-classes based on length-frequency data. Including information on the growth dynamics of populations by aging a subsample of animals using statoliths will further improve assessments. Accurate age-assessment is important to measure influential life history characteristics such as recruitment, growth rate, and mortality rate to improve our estimates of the productivity of sea lamprey populations and improve sea lamprey control, so the standard protocol outlined in chapter 2 should be implemented in the sea lamprey management program.

A fair comparison of control options should also consider the relative environmental costs of the control options as well as their benefits (McLaughlin *et al.* 2003). Social, environmental, and non-target costs and benefits should be a consideration when comparing sea lamprey control strategies, and not just costs and benefits in dollars. Pressure to use alternatives to lampricide control has increased due to public concern about pesticide use and rising costs of lampricides, however costs of adults control measures such as non-target effects of barriers and possible transmission of aquatic pathogens resulting from conducting the sterile-male-release technique should also be considered when comparing sea lamprey control strategies.

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