Compensatory Mechanisms in Great Lakes Sea Lamprey Populations: Implications for Alternative Control Strategies

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ABSTRACT. *Compensatory mechanisms are demographic processes that tend to increase population growth rates at lower population density. These processes will tend to reduce the effectiveness of actions that use controls on reproductive success to suppress sea lamprey* (Petromyzon marinus), *an economically important pest in the Great Lakes. Historical evidence for compensatory mechanisms in sea lamprey populations was reviewed, and revealed: (1) strong evidence for shifts in sex ratios as sea lamprey abundance was reduced in the early years of the control program; (2) weak and equivocal evidence for increased growth rates of sea lamprey cohorts re-colonizing streams following a lampricide treatment; and (3) suggestions of other compensatory processes, such as earlier ages at metamorphosis, but with little empirical evidence. Larval size distribution data for cohorts in the first and second years following a lampricide treatment (26 pairs of cohorts in 20 streams) was analyzed and did not indicate a consistent pattern of more rapid growth of the first colonizing cohort (only 11 of 33 cases). To test for compensation between spawning and age-1 in sea lamprey populations, data were analyzed for 49 stream-years for which spawning female abundance was known and age-1 abundance was estimated in the following year. A fit of these data to a Ricker stock-recruitment function showed evidence for compensation, measured as reduced survival to age 1 at higher abundance of spawning females. More obvious, however, was a large amount of density-independent variation in survival, which tends to mask evidence for compensatory survival. The results were applied to a simple model that simulates sea lamprey populations and their con-*

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trol in a hypothetical lake. Control strategies that targeted reproductive success performed far less well than comparable strategies that targeted larval populations, because density-independent recruitment variation leads to occasional strong year classes even when spawner abundance is reduced to low levels through alternative control. It is concluded that further study of recruitment variation in lamprey populations is critical to rationalizing alternative controls that target reproductive success, and that recruitment variation needs to be incorporated into models used to evaluate sea lamprey control options.

INDEX WORDS: Stock-recruitment, sea lamprey, density dependence, population dynamics.

INTRODUCTION

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

A central challenge of most fishery management is to quantify the strength of compensatory mechanisms in exploited fish populations. As harvest rates increase and stocks become smaller, the resistance of a stock to over-exploitation is determined by the degree to which the population can compensate by altering vital rates in response to reduced population densities. When the objective is to manage a fish population for maximum sustainable harvest, managers seek to take advantage of compensatory mechanisms. In the case of sea lamprey control, where the objective is to reduce the size of the lamprey population to the minimum level economically achievable (Sawyer 1980, Koonce *et al.* 1993, Goddard and Christie 2003), managers face precisely the opposite challenge. They seek to overcome the compensatory capacity of lamprey populations so that the effectiveness of their control actions is not compromised by subsequent increases in the productivity of the residual population. In either case, knowledge of the extent to which compensation operates is a critical ingredient of well-informed decision-making.

Sea lamprey program managers have become particularly interested in compensatory mechanisms in recent years, because of a desire to reduce reliance on lampricides as the primary method of lamprey control (Great Lakes Fishery Commission 1992). Lampricide treatments are prescribed to remove large lamprey ammocetes from streams immediately before they metamorphose and emigrate from the streams to become parasites (Smith *et al.* 1974, Brege *et al.* 2003). Lampricide treatments, when effective, remove between 95 and 99% of the ammocetes from treated streams (William Swink, U.S. Geological Survey, Hammond Bay Biological Station, unpublished data). Because of the magnitude of mortality caused by lampricides, and because the action targets the life stage immediately prior to the parasitic stage, there is little potential for increased survival or growth of the residual lamprey to compensate for the control action. Alternative controls such as the release of sterilized males (Twohey *et al.* 2003a) and adult trapping (Mullett *et al.* 2003) target reproductive success, and may result in more modest reductions in the effective population size (a 3:1 ratio of sterilized to un-sterilized males produces only a 75% theoretical reduction in reproductive success). The degree to which these alternatives are effective will depend on the recruitment dynamics of lamprey. For example, if larval survival is enhanced by reductions in spawning stock size, the net effect of the alternative control on production of parasitic lamprey will be less than the immediate reduction in reproductive success.

To address current understanding of the importance of compensatory mechanisms and recruitment dynamics to sea lamprey management, this synthesis will cover three broad topics. First, previous evidence that compensatory mechanisms do operate in lamprey populations will be reviewed. The review will focus on three demographic responses that have been investigated in the past: changes in sex ratios, changes in larval growth rates, and changes in the size or age at metamorphosis. It will only consider evidence for compensation occurring during larval life stages, because compensation during the parasitic phase (such as

might result from shifts in host-parasite ratios with declining sea lamprey abundance) is not relevant to comparisons between lampricide and alternative controls. Second, new evidence for compensatory responses will be examined, as derived from routine larval survey data and ongoing research on lamprey stock-recruitment relationships. Third, a stochastic simulation model will be presented that incorporates current understanding of lamprey stock-recruitment dynamics and considers the implications for management, especially alternative control.

HISTORICAL EVIDENCE FOR COMPENSATORY MECHANISMS

Changes in Sex Ratio

The extent to which density-related changes in the proportion of females in a population will act as a compensatory mechanism will depend on the reproductive ecology of lamprey. If the supply of eggs (number of females) is correlated with the production of larvae and the supply of males does not limit recruitment, then a shift from a preponderance of males to a preponderance of females should, all else being equal, tend to compensate for a reduction in overall numbers of adults. Unlike the other compensatory responses discussed below, changes in sex ratios are only likely to affect subsequent generations, unless sea lamprey exhibit sex-related differences in larval survival, growth, or size at metamorphosis. There is no strong evidence of such differences.

A large shift in sex ratios of both adult and larval lamprey was observed in all three of the upper Great Lakes after the implementation of the sea lamprey control program during the 1960s (Purvis 1979, Heinrich *et al.* 1980). Prior to control, lamprey adult populations in all three lakes were predominantly male (Superior: 57 to 70%; Huron: 54 to 62%; Michigan: 64 to 70%) (Smith 1971). After the control program had successfully reduced the lamprey populations in these lakes to far below their pre-treatment levels (estimated reductions of 76 to 92% in Lake Superior) (Smith and Tibbles 1980), sex ratios shifted sharply to a predominance of females (Superior: 26 to 31% males; Huron: 31 to 39%; Michigan: 21 to 44%) (Purvis 1979). There is no evidence that the lampricide TFM is selectively toxic to male lamprey (Purvis 1979, National Research Council of Canada 1985), and observations on differences in duration of the larval period for males and females are equivocal (Manion and

Smith 1978). Therefore, it seems more likely that these shifts in sex ratio have resulted from a demographic response of the lamprey populations to reductions in their overall abundance than from a direct effect of sex-selective mortality due to lampricide treatments.

Beamish (1993) presented evidence for the existence of environmental sex determination in populations of southern brook lamprey (*Ichthyomyzon gagei*) and reported unpublished evidence for similar responses in least brook lamprey (*Lampetra aepyptera*). For both species he noted that the preponderance of males was positively correlated with larval density, although this was only the case for southern brook lamprey when conditions for larval growth were favorable. Under poor growth conditions, higher densities were associated with fewer males. Great Lakes sea lamprey populations also show evidence of environmental sex determination in the form of the frequent occurrence of relatively large larvae (> 100 mm) with incompletely differentiated gonads (Wicks *et al.* 1998). Because of the preponderance of these "intersex" larvae, and possibly because larval densities in Great Lakes streams remain low due to the control program, Wicks *et al.* (1988) were unable to detect an effect of larval density on sea lamprey sex ratios. Research into the fate of the intersex larvae is continuing (F.W.H. Beamish, University of Guelph, Guelph, Ontario, personal communication). However, current evidence suggests that the density changes likely to result from alternative controls are unlikely to cause large enough changes in sex ratio to give rise to substantial compensation.

Changes in Larval Growth Rates

Sea lamprey spend several years as suspension feeders, inhabiting the soft sediments of streams and feeding on organic detritus, algae, and bacteria (Moore and Beamish 1973, Sutton and Bowen 1994). Reductions in the densities of larvae occupying these habitats could reduce intraspecific competition for food and allow the remaining individuals to enjoy higher growth rates. Increased growth could, in turn, result in higher survival or earlier age at metamorphosis, both of which would have the effect of compensating for the initial reduction in density.

Considerable research has been conducted to assess the influence of density on growth of larval lamprey. Using laboratory aquaria and yeast solutions as food, Mallatt (1983) demonstrated reduced

growth of *Lampetra tridentata* larvae at higher densities over a range of densities from 3 to 100 larvae per m². Murdoch *et al.* (1992) obtained similar results in laboratory experiments with sea lamprey larvae, using densities ranging from 30 to 300 larvae per m². They also observed that growth rates varied widely among individual larvae exposed to the same density. Recent research on the details of ammocete feeding and digestion have indicated that lamprey feed very slowly but efficiently on organic detritus in streams, accumulating most of their energy during summer when temperatures are warm and food quality is high (Sutton and Bowen 1994, Yap and Bowen 2003). Interestingly, habitat type (Yap and Bowen 2003) and density (S.H. Bowen, Michigan Technological University, Houghton, MI, unpublished data) appeared to have relatively little influence on feeding rates, but did affect assimilation efficiency, leading to lower growth rates in poorer habitats and at higher densities.

Field studies have also shown an effect of density on larval growth. Morman (1987) placed sea lamprey in cages in five Michigan streams at two densities (25 and 75 larvae per m²) and monitored growth for 4½ years. Ammocete lengths were significantly greater in the low-density cages by the end of the study. Morman also reported substantially higher survival of ammocetes in the low density cages in two streams. Five animals were observed to enter metamorphosis in the low-density cages in these streams, while no metamorphosing animals were observed in the high-density cages.

The periodic treatment of infested streams with lampricide provides an opportunity to test for density effects on larval growth and production in a natural stream setting. The first year-class of larvae that colonizes a stream after treatment presumably experiences minimal inter-cohort competition, whereas subsequent cohorts face competition from prior cohorts. Purvis (1979) used length-frequency plots to compare the lengths of ammocete cohorts in Lake Superior and Michigan streams in successive years following a treatment. He concluded, "ammocetes of the first year class established after a chemical treatment grew faster than those of succeeding year classes." While this is evident for some of the eight streams he examined, the overall pattern is far from clear. In four cases (Bursaw, Deadhorse, Gratiot, Sullivan) there is no evidence for greater growth; in two cases (Hog Island, Little Garlic) the effect is minimal and unlikely to be statistically significant. On the other hand, Weise and Pajos (1998) present evidence for substantially

greater growth and production of the first larval cohort to colonize Salem Creek, a Lake Ontario tributary, following the 1989 treatment. Later in this report a related analysis of more recent data from post-treatment larval surveys is presented.

Changes in Age at Metamorphosis

Sea lamprey may also respond to lower abundance by shortening the duration of the larval period. This would operate as a compensatory mechanism by shortening the generation time of lamprey populations, thereby allowing population growth to be more rapid and necessitating more frequent stream treatments. This mechanism is closely related to the density-dependent growth effect because considerable evidence exists that the timing of metamorphosis is principally determined by ammocete growth (Youson 2003). Larvae begin metamorphosis after they reach 120 mm and have accumulated sufficient lipid reserves to survive the prolonged period of arrested growth associated with metamorphosis (Holmes and Youson 1996). Thus, evidence for density effects on ammocete growth rates is likely to imply earlier age-at-metamorphosis in addition to possible improvements in survival during the larval period.

Despite the potential importance of this compensatory mechanism, there is very little direct evidence that it has occurred in Great Lakes sea lamprey populations. Purvis (1979) noted that metamorphosing lamprey were consistently larger (longer) in post-treatment (residual) populations than in pre-treatment populations in the same stream, and suggested that this was evidence for density-related effects on growth and metamorphosis rates. However, reliable methods for determining the age of sea lamprey were not known at that time so there are no data on the age composition of these larvae. The increased size of the residual sea lamprey larvae could have resulted from greater growth rates following the treatment-induced population reduction or could also reflect size- or age-dependent differences in treatment mortality. Without age composition data, it is impossible to determine whether the increased size is indicative of potential changes in the duration of the larval stage.

The only published evidence that reduced density actually reduces the time to metamorphosis was a study by Mormon (1987). In his long-term cage experiments, Morman only observed metamorphosis in the low-density cages. His sample sizes were

very small, however (1 of 24 animals in one stream; 4 of 23 in a second stream). Preliminary data from recent investigations using statolith ageing (Beamish and Medland 1988) of ammocete populations in tributaries to Lake Champlain, before and after treatment, suggest the occurrence of earlier age-at-metamorphosis in reduced-density populations (Adam Zerrenner, University of Vermont, Burlington, VT, personal communication).

Although it seems plausible that density-related changes in ammocete growth rates could give rise to shifts in the age-at-metamorphosis, it is unclear whether the shifts will be large enough at the population level to lead to important demographic effects. Sea lamprey rarely enter metamorphosis before they reach 120 mm, and very few individuals over 180 mm have failed to metamorphose. It seems unlikely that density-related changes in growth would change by more than 1 year the time taken by a sea lamprey to reach 120 mm. As confidence in statolith ageing improves, it will be valuable to gather more data on the association between density and age-at-metamorphosis, to determine a plausible range for the shift. This empirical work should be combined with theoretical (modeling) investigations that examine the significance to sea lamprey control of density-dependent changes in growth and rates of metamorphosis.

NEW EVIDENCE

Methods

Post-treatment Surveys

Following the approach used by Purvis (1979) and Weise and Pajos (1998), evidence of density effects on larval lamprey growth was evaluated by comparing the average sizes reached by successive cohorts following treatment of a stream with lampricide. The first cohort colonizing a stream after a treatment should experience lower density than subsequent cohorts because no other potentially competing cohorts will be present. The working hypothesis was that the lower density would lead to mean lengths of ammocetes in the first cohort being greater than in later cohorts.

Data were obtained from surveys conducted by Department of Fisheries and Oceans Canada larval assessment crews during the period 1989 to 1996. On a number of occasions, they collected larvae from Ontario and New York streams in two consecutive years following a treatment. From these surveys data were extracted that met the following

criteria: (1) the dates upon which surveys occurred in successive years differed by no more than 20 days; (2) the observed length-frequency distribution in the second year enabled easy separation of the first and second cohorts (Fig. 1); and (3) enough larvae were collected in both years to allow precise determination of mean lengths for a cohort.

The first criterion ensured that differences in mean length among years would not be due to differences in the time of year of sampling (within-year growth effects). Because statoliths were not available to determine age for these samples, the second criterion was necessary to ensure that the mean size of the second cohort was not biased upward by erroneous assignment of older larvae from the first cohort to the second cohort. Application of this criterion limits the applicability of these results to streams where growth is relatively rapid and thus lengths at age 1 and 2 tend to show minimal overlap. A minimum sample size per cohort of 25 larvae was chosen to apply the third criterion. This sample size was selected to give power > 90% to detect a difference of 10 mm between cohorts at a significance level of 0.05, given a standard deviation of 10 mm. A difference of 10 mm between successive cohorts was judged to represent a minimum ecologically significant difference. Estimated standard deviations varied from 2 to 13 mm in these data sets and were less than 10 in 62 of 66 cases.

Applying these criteria yielded 26 survey data sets from 20 streams (Fig. 2). During fall surveys, age-0 ammocetes were large enough to be vulnerable to the sampling gear (backpack electrofishing units), while in spring and summer, age-1 ammocetes were the smallest individuals found in the surveys. Of the 26 data sets, 8 comprised age-0 ammocetes and 18 comprised age 1. To examine the hypothesis the mean length of ammocetes (age-0 or -1) in year t+1 (2nd cohort) was plotted against the mean length of ammocetes in year t (1st cohort) and the proportion of cases in which the points lay below the 1:1 line, implying a greater 1st cohort growth, was summarized.

Spawner-recruitment Data

In this meta-analysis data were combined from several sources (Fig. 2) where estimates of spawning sea lamprey abundance and of larval recruitment at age 1 in the following year were available. These data were used to estimate the parameters of a Ricker stock-recruitment relationship
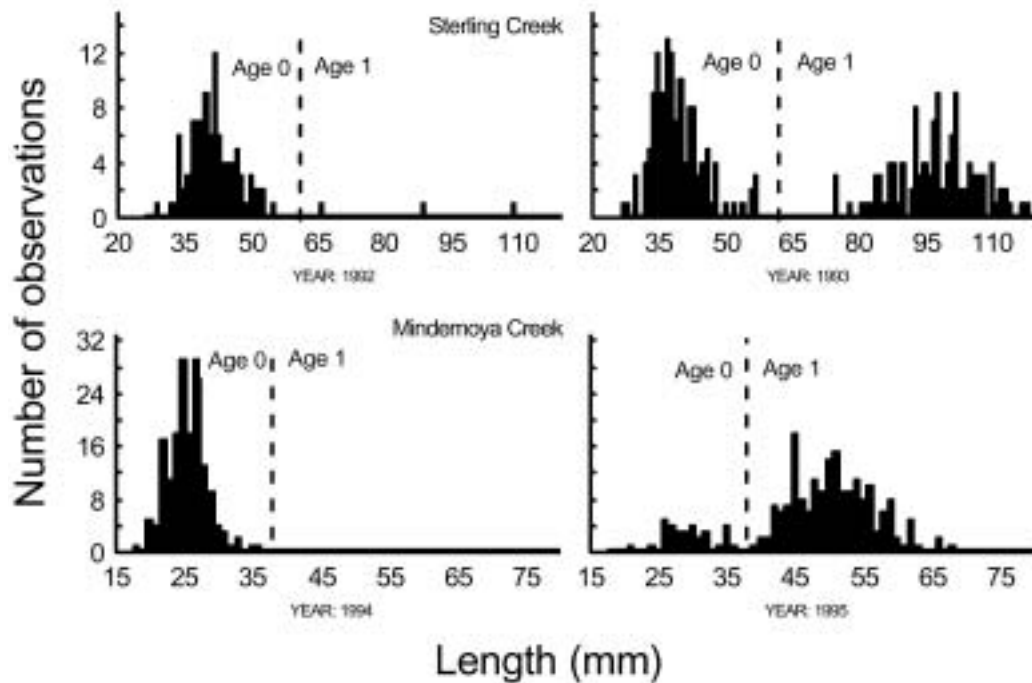
FIG. 1. *Examples of length-frequency plots for larval sea lamprey from two streams. The left panel shows the first year after treatment, and the right panel shows the second year. Sterling Creek is on Lake Ontario; Mindemoya Creek is on Lake Huron.*

$$R = \alpha S e^{-\beta S}, \qquad (1)$$

where R is recruitment, S is spawning female sea lamprey abundance, and α and β are the estimated parameters, and thereby test for the presence of compensation (density-dependent survival) between spawning and age 1. In contrast to most other stock-recruitment analyses (c.f. Hilborn and Walters 1992), data were combined from multiple spawning populations, under the assumption that a common stock-recruitment relationship exists among streams. As explained below, the stock (S) and recruitment (R) estimates are standardized to a common scale (numbers per unit area of larval habitat) which justifies the use of a common value for the parameter (β) that describes density dependence in the Ricker model. A common α parameter (related to density-independent survival) is also assumed, but the data are used to test whether differences in indices of stream productivity (based on temperature and alkalinity) explain some of the among-stream variability in α. These methods are roughly similar to those used by Myers and Mertz (1998) in their meta-analysis of stock-recruitment relationships among various fish taxa, although they assumed that the set of Ricker model parameters for different stocks in the same broad taxonomic group could be described by a distribution of parameters with a common mean and variance.

In the first study, which is part of a long-term study to evaluate the sterile-male-release technique (Twohey *et al.* 2003a), spawner abundances were controlled by deliberately releasing adult lamprey above barriers. Eight Lake Superior streams received controlled adult introductions in each of three years. Larval abundance at age 1 was estimated in each subsequent year. In 12 of the 24 cases, three sterile males were released above the barrier for every one fertile male. Based on empirical observations from earlier research (R. Bergstedt, U.S. Geological Survey, Hammond Bay Biological Station, unpublished data), it was assumed that the effective number of spawning females was reduced by 75% due to the addition of sterile males (the theoretical expectation if sterile males compete effectively with fertile males for mates).

In three other streams (one from Lake Huron and two from Lake Ontario), known numbers of adult
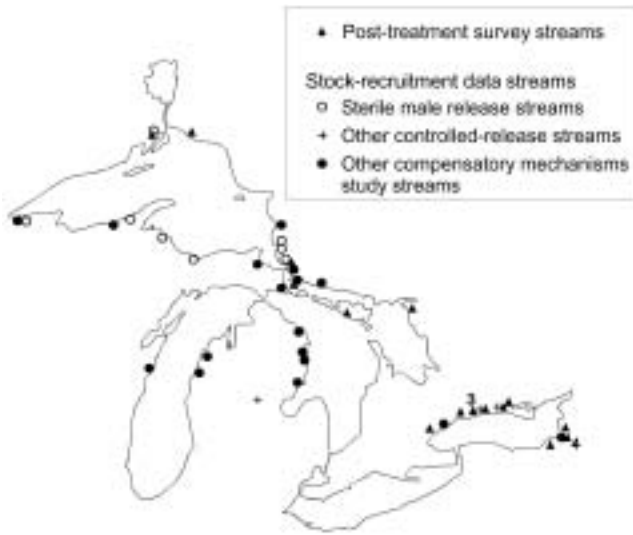
FIG. 2. *A map of the Great Lakes showing the location of streams from which data were collected for this study. For the post-treatment survey data (solid triangles), the numbers refer to cases where a single symbol represents more than one stream data set.*

male and female lamprey were introduced above barriers in two consecutive years and larval abundance was estimated in each subsequent year. No sterilized males were released into these streams. Finally, spawning population abundance was estimated using a mark-recapture method applied to lamprey captured in adult assessment traps (Mullett *et al.* 2003) in 26 additional stream-years, after which age-1 ammocete abundance was estimated the following year.

Age 1 larval abundance was estimated using the same technique in all streams. First, the entire accessible length of the stream upstream of the barrier was divided into randomly spaced transects. The number of transects varied among streams from 47 to 142. Along each transect, perpendicular to the direction of stream flow, the proportion of substrate that comprised each of four possible habitat types was measured. Types I (fine sand and silt, typically found in depositional areas of the stream) and II (coarser sand with very little organic matter evident) habitats are preferred and acceptable habitats for ammocetes, respectively, while Types III (gravel, cobble, bedrock, etc.) and IV (islands) are unsuitable. Mullett and Bergstedt (2003) provide detailed descriptions of these habitat types.

At approximately half of the transects in each stream, a randomly selected 5-m^2 plot of Type-I or -II habitat was surveyed using an AbP-2 backpack electroshocker, following a standardized larval assessment procedure (Slade *et al.* 2003). Type-I plots were preferentially selected when this type of habitat was present in the vicinity of the transect, although an effort was made to survey at least 12 Type-II habitat plots.

Visual inspection of length-frequency plots was used to determine the minimum and maximum lengths of yearling larvae for each stream-year. The yearling mode was always obvious from the length-frequency plots, but determination of the length cut-off between age-1 and age-2 ammocetes was frequently difficult. Because of this, the robustness of the results to use of alternative yearling length cut-offs was evaluated. Inspection of the length-frequency plots suggested a typical range of plausible cut-off lengths for age-1 ammocetes from 5 to 10 mm. Alternative estimates of yearling catches were generated by randomly varying the cut-off length ± 8 mm around our "best-guess" value for each stream-year. Then stock-recruitment parameters were estimated (see below) for each alternative yearling data set and the parameter estimates compared to those obtained from the best-guess cut-off value.

The mean yearling density in each habitat type was then computed from:

$$D_i = \frac{\sum_{j=1}^{p} C_{i,j}}{\sum_{j=1}^{p} Ap_{i,j}} \qquad (2)$$

where D is density of yearlings (number per m^2), C is number of yearlings caught, Ap is plot area (m^2), P is the number of plots, i is the habitat type index, and j is the plot index. Similarly, the area of habitat of each type was computed from:

$$A_i = \frac{\sum_{k=1}^{T} W_{i,k}}{\sum_{k=1}^{T} W_k} \cdot L \cdot \frac{\sum_{k=1}^{T} W_k}{T} = \frac{\sum_{k=1}^{T} W_{i,k}}{T} \cdot L, \qquad (3)$$

where A is the area of habitat (m^2), $W_{i,k}$ is the length of transect k that is Type i habitat (m), W_k is the total length of transect k (m), T is the number of transects, L is the length of the study area (m), and

k is the transect index. The abundance of yearling larvae (recruitment) in each stream-year is then:

$$\tilde{R} = \sum_{i=1}^{II} D_i \cdot A_i. \qquad (4)$$

Evidence for compensation was evaluated by fitting the data to a linear form of the Ricker stock-recruitment model:

$$\ln\left(\frac{R}{S}\right) = \ln(\alpha) - \beta \cdot S + \varepsilon, \qquad (5)$$

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

To carry out the among-stream meta-analysis, all streams are assumed to share a common α term and β is assumed to depend 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 intraspecific larval competition for rearing habitat. This allows the data from all stream-years to be used together to test for a β value significantly greater than zero by carrying out a linear regression of ln(R/S) on S, where

$$S = \frac{\tilde{S}}{H_w}, R = \frac{\tilde{R}}{H_w}, \qquad (6)$$

$\tilde{S}$ is the total number of spawning females, $\tilde{R}$ is the total number of yearlings, and H_w is the total amount of larval habitat in each stream.

Total larval habitat was computed from

$$H_W = A_I + \frac{\overline{D_{II}}}{\overline{D_I}} \cdot A_{II}. \qquad (7)$$

This index weights Type-II habitat less heavily than Type-I, based on the ratio of densities of yearling larvae in Type-II versus Type-I habitats, averaged over all streams and years. The relative density of larvae in the two types of habitat is presumably a reflection of the capacity of each habitat type for producing larvae, so this ratio provides an index of Type-II habitat suitability, relative to Type-I habitat.

An attempt was made to test the hypothesis that differences among streams included in this study explain some of the observed variability in the stock-recruitment relationship. The Ricker α value characterizes the productivity of the spawning population when abundance is low. Warm streams with high alkalinities might be expected to experience greater productivity, and thus larger α values, than cold streams with low alkalinity. Detailed temperature and alkalinity data were not available, but based on the expert opinion of sea lamprey program biologists, each stream was assigned to a cell in a 2×2 matrix of classes: "warm" or "cool" and "low" or "high" alkalinity. In general, warm streams were those where summer water temperatures frequently exceeded 20°C, while cool streams did not, and high-alkalinity streams were those typically exhibiting alkalinities in excess of 100 mg/L during past lampricide treatments. The regression of ln(R/S) on S was repeated, this time using a mixed model analysis of covariance, with the four categories of stream as random effects and S as the covariate. This allowed a test of the hypothesis that ln(α)—the regression intercept—is significantly different among the four stream classes.

RESULTS

Post-treatment Surveys

Lengths of age-0 and -1 ammocetes were not consistently greater in the first year following treatment (Fig. 3) as would be expected if density-dependent growth commonly led to higher growth rates of the first cohort. Age-0 ammocetes were larger on average in 4 of 8 cases and smaller in the other 4 cases. Age-1 ammocetes were larger in 7 of 18 cases, smaller in 8 cases, and not significantly different (error bars overlap the 1:1 line in Fig. 3) in 3 cases. Stream location (Lake Ontario versus Lake Huron or Lake Superior) also did not affect the results (Ontario: larger in 9 of 20 cases; Huron or Superior: larger in 2 of 6 cases).

Spawner-recruitment Data

Recruitment of yearling sea lamprey was highly variable among streams, even after accounting for the effect of adult stock size (Fig. 4a). The combined results from the 49 stream-years indicated that recruitment was reduced at very large adult stock sizes (> 15 adult females per 100 m² of larval rearing habitat), and that large recruitment events sometimes occurred even when the number of spawning females was quite low (< 2 females per
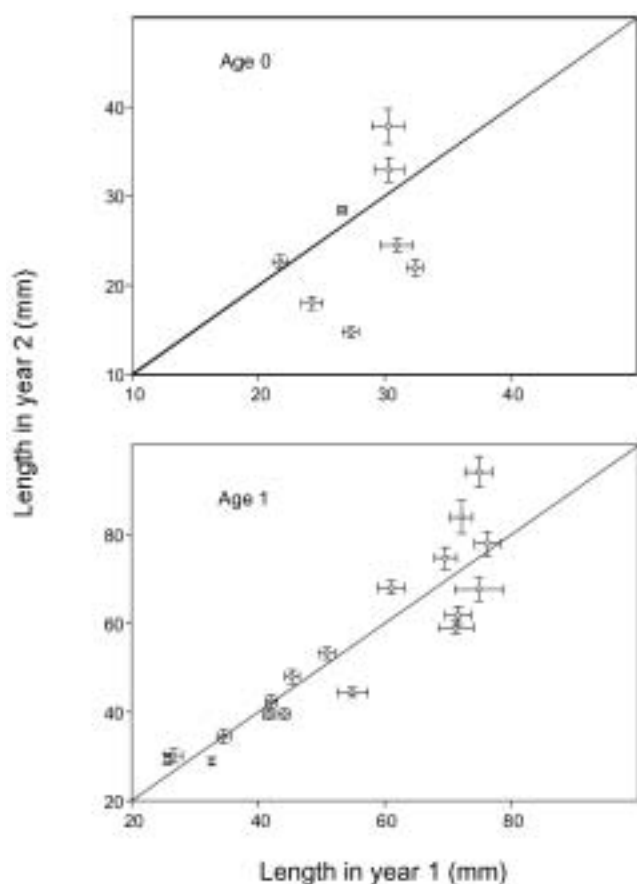
FIG. 3. *Mean lengths of larval sea lamprey collected in the first and second years following a lampricide treatment. The diagonal line represents equal lengths in years 1 and 2. The error bars indicate ± 2 standard errors from the mean.*

FIG. 4. *Observed stock and recruitment for 49 stream-years. Spawning female and yearling numbers are expressed as densities per 100 m² of larval habitat. The lower panel (b) only includes data for stream-years where densities of spawning females were less than 10 per 100 m².*

100 m²: Fig. 4b). At very low stock sizes (< 0.5 females per 100 m²) high recruitment events were not observed (Fig. 4b).

The recruitment data also showed evidence of compensation, measured as an index of density-dependent survival from spawning to age 1. The regression of ln(R/S) on S revealed a statistically significant negative slope (p < 0.0001, n = 49, β = 0.129, Fig. 5a). The slope estimate and its significance were strongly influenced by a small number of observations of very high densities of spawning females. When these observations were excluded (only densities of spawning females < 10 per m² are included in the regression), the point estimate of β was larger (β = 0.357), suggesting even stronger compensation, but it was no longer significantly different from zero (p = 0.062, n = 42, Fig. 5b). Density-independent variation in survival at lower

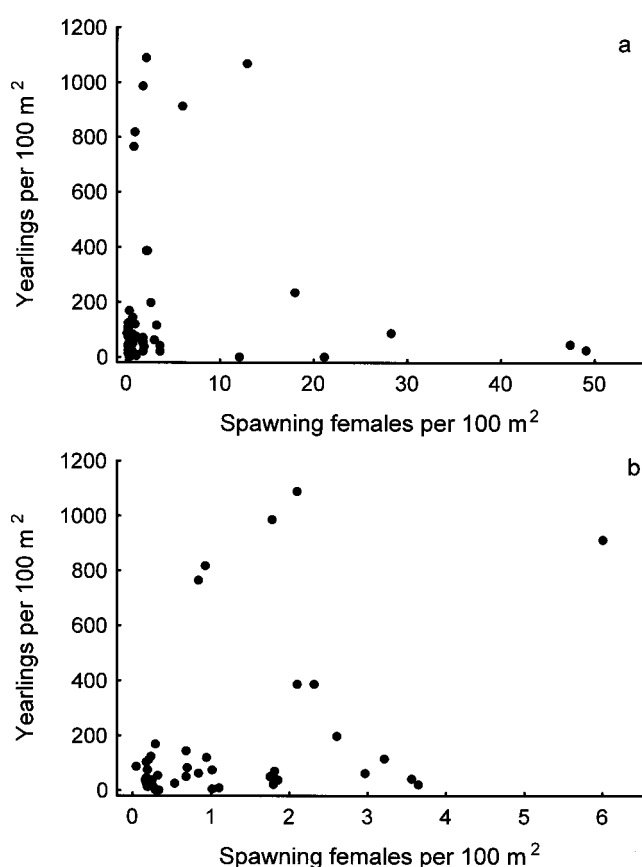densities of spawning females made it difficult to estimate the effect of compensation precisely. The parameter estimates were not sensitive to our assumed cut-off length for age-1 larvae. Variations of ± 8 mm in the cut-off resulted in variations of less than 0.5% and 1.2% in the α and β estimates, respectively. Finally, the analysis of covariance did not demonstrate a significant effect of stream type (alkalinity and temperature classes) on the regression intercept (p = 0.61, df = 3).

IMPLICATIONS OF RECRUITMENT VARIATION: A MODEL-BASED EVALUATION

Models that have been used in the past to guide integrated sea lamprey management have not accounted for recruitment variation (Greig *et al.* 1992, Koonce *et al.* 1993, Schleen *et al.* 2003). The re-
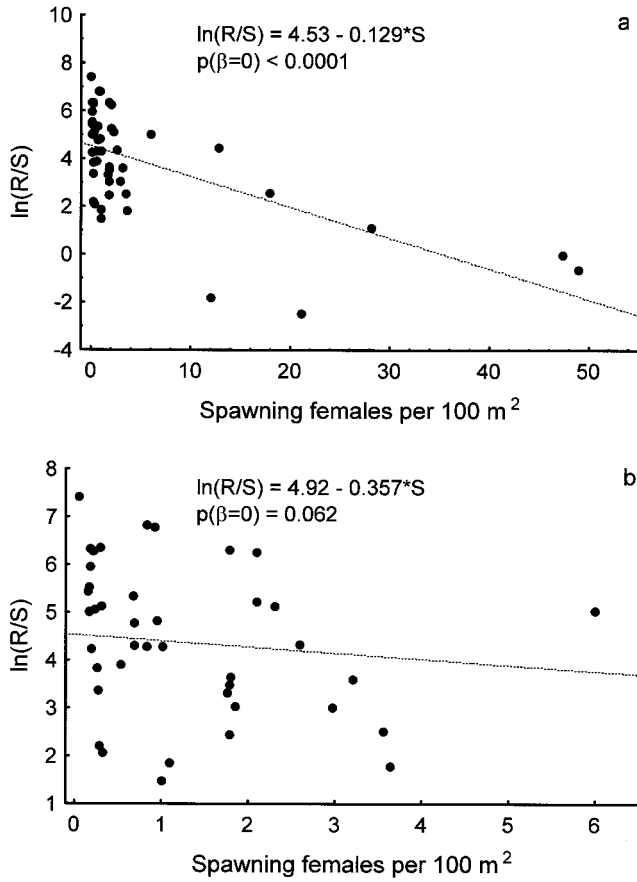
FIG. 5. *The linearized stock-recruitment relationship (ln(R/S) vs S) for the same data as plotted in Figure 3. The regression line for each panel was estimated using only the data presented in that panel.*

sults reported here suggest that such models may give a misleading impression of the efficacy of alternative control measures. The stock-recruitment data showed wide variability in the recruitment that results from any given stock size (Fig. 4). Compensatory responses will reduce the average effect on recruitment of a reduction in adult stock size, but even if compensation is weak or absent, in any given year the recruitment could depart substantially from this average. This can lead to significant risk of an unsuccessful control action (a larger recruitment than would be expected, on average, given the control action). To examine the ramifications of these results for sea lamprey control strategies a simple but realistic model of a controlled sea lamprey population was developed.

The model simulated the dynamics of a sea lamprey population in a lake with 10 tributary streams

utilized by lamprey for spawning and larval rearing. The purpose of the simulations was to compare the performance of lampricide control strategies that target larval populations to alternative strategies, such as sterile-male releases, that target reproductive success. A single parasitic population was modeled and it was assumed that adult lamprey do not home to natal streams (Bergstedt and Seelye 1995). The allocation of spawners to streams was assumed to be proportional to the relative abundance of ammocetes in each of the ten streams, which is consistent with the view that lamprey are attracted to streams for spawning by the presence of a migratory pheromone released by stream-dwelling ammocetes (Sorensen and Vrieze 2003). Recruitment of age-0 larvae was forecasted from a stock-recruitment relationship (see below). Larvae remain in the stream until they either die (natural mortality) or metamorphose and enter the parasite population. Larvae that metamorphose in year t become parasites in year t+1 and return as spawners in year t+2. The model equations are as follows, where *i* and *j* refer to stream and age class, respectively (other symbols and their assumed values are described in Table 1):

$$S_{i,t} = P_t \cdot \frac{\sum\limits_{j} l_{i,j,t}}{\sum\limits_{i,j} l_{i,j,t}} \cdot s_p \cdot p_f \qquad (8)$$

$$l_{i,0,t} = \alpha \cdot S_{i,t} \cdot e^{-\beta \cdot \frac{S_{i,t}}{H_i} + \varepsilon_{i,t}} \qquad (9)$$

$$l_{i,j,t+1} = l_{i,j-1,t} \cdot s_l \cdot (1 - m_j) \qquad (10)$$

$$P_{t+1} = \sum_{i,j} (l_{i,j,t} \cdot m_j) \cdot s_m \qquad (11)$$

Lampricide control was simulated by removing a fixed proportion of the entire larval population from any stream that is selected for treatment. A method analogous to the stream selection procedure utilized in the sea lamprey control program (Christie *et al.* 2003) was used to determine which streams to treat in any given year of the simulation. Each year, potential treatments in all ten streams were ranked according to the number of metamorphosing ammocetes that would be removed from next year's parasitic population, per dollar of treatment cost. Streams with large populations of older ammocetes

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

Symbol	Definition	Assumed value
S	Spawning lamprey abundance	State variable
P	Parasitic lamprey abundance	State variable, initially 25,000
l	Larval lamprey (ammocete) abundance	State variable
H	Larval habitat area	30,000 m^2
s_p	survival during parasitic phase	0.75
p_f	proportion females	0.5
α	Ricker model parameter	4.53
β	Ricker model parameter	0.129
σ^2	Variance of process error in recruitment	3.03 or 1.51 (see text)
s_l	annual survival during ammocete phase	0.3
m	age-specific probability of metamorphosis	0(2),.2(3),.4(4),.7(5),1.(6)
s_m	survival during year of metamorphosis	0.75

and modest treatment costs were ranked highest. Each year, streams were treated in rank order, from highest to lowest, until a pre-specified control budget was completely utilized. This is the optimal control strategy for maximizing the suppression of parasitic lamprey given a fixed budget. For simplicity, perfect knowledge of stream ammocete abundance was assumed, as was a fixed treatment effectiveness (proportion of ammocetes killed by the treatment) of 90%.

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

Recruitment variation was added to the model using the $\varepsilon_{i,t}$ term in the stock-recruitment equation. The observed variance in ln(R/S) (Fig. 5) was used to obtain an empirical estimate of recruitment variability. However, this variability includes sources of error that should not be included in the simulations. The observed variance of ln(R/S) has three components:

$$\text{var}(\varepsilon_{i,t}) = \sigma_{P_{i,t}}^2 + \sigma_{S_i}^2 + \sigma_M^2 \qquad (12)$$

where P refers to process error (interannual variation in recruitment in an individual stream), S refers to stream effects (variations in recruitment due to differences among streams in the relationship between stock and recruitment), and M refers to measurement error associated with empirical estimates of recruitment. Only the process error should be included in the model, because the other two are not related to the true uncertainty about the recruitment that will result from a given adult stock size in an individual stream. The regression analysis yielded an estimate for var($\varepsilon_{i,t}$) of 3.03.

The measurement error was estimated from the age 1 assessment data. Recall that recruitment was estimated from:

$$\hat{R} = A\left[\overline{D_I}\,\overline{p}_I + \overline{D_{II}}\,\overline{p}_{II}\right] \qquad (13)$$

where A is the total area of the stream (m^2), p is the estimated proportion of Type-I or -II habitat, and D is the estimated density in each habitat type (number per m^2). Assuming that A is measured without error, the variance of R can be computed from

$$\text{var}(\hat{R}) = A^2\left[\sum_{i=1}^{II}\left(D_i^2\,\text{var}(p_i) + p_i^2\,\text{var}(D_i)\right)\right] \qquad (14)$$

Measurement error in R was assumed to be log-normally distributed. According to (Law and Kelton 1982) we can compute σ_M^2 for a log-normal distribution from

$$\sigma_M^2 = \ln(CV^2 + 1) \qquad (15)$$

where *CV* is the coefficient of variation of the recruitment estimate

$$\left(\frac{\sqrt{\text{var}(\hat{R})}}{\hat{R}} \right).$$

The average *CV* for the 49 stream-years in our data set was 0.22, which yields a value for σ_M^2 of 0.047. From this analysis it was concluded that measurement error was a negligible component of the observed, overall error in ln(R/S).

The ANCOVA results indicated that addition of the two "stream" factors (temperature and alkalinity) did not explain any of the observed recruitment variation. This could be interpreted as indicating that σ_S^2 is also negligible, but it is more likely that the factors included in the analysis are poor indicators of among-stream differences in the mechanisms governing larval recruitment. In the absence of alternative estimates of stream effects, simulations were run for two cases—one where σ_S^2 is assumed to be zero and a second where it is assumed to be 1.52 (that half of the observed recruitment variation is due to unexplained stream effects).

Simulation results were compared for four scenarios: lampricide control and alternative control, with and without recruitment variation. Because the stock-recruitment parameters were estimated from log-transformed data, it was necessary to correct the recruitment estimates for back-transformation bias when recruitment variation was set to zero and the untransformed Ricker model was applied. Trial simulations using the conventional bias-correction method and no lamprey control yielded higher parasitic abundance in the deterministic case (no variation around the estimated stock-recruitment model) than in the stochastic case. This may occur because the Ricker model is non-linear and the effect on the population trajectories of the relatively frequent low recruitments in the stochastic case is greater than the effect of the relatively infrequent very high recruitments, even though on average recruitment is the same. To provide a reasonable basis for comparison the bias correction was adjusted downward for the deterministic case until the forecasted trajectory, in the absence of control, matched the average trajectory for the stochastic case. In other words, population trajectories were compared for simulations where, in the absence of any control, the results would be the same. In this way the performance of lampricide and alternative control options was compared, as was the effect on performance of the interaction of recruitment variation with each option.

Each simulation began with an uncontrolled lamprey population, and simulated lamprey control over a 50-year period, beginning control in the fourth year of the simulation. The predicted average number of parasites in years 35 to 50 was used as a measure of performance. Treatment costs for each stream and the overall budget were set such that one stream could be treated each year in the lampricide control scenarios.

Simulation Results

The lampricide control option without recruitment variation resulted in a 93% reduction in lake-wide parasitic sea lamprey abundance, relative to a no-control scenario (Table 2). To achieve a comparable effect on parasitic abundance using alternative control requires a 70% reduction in reproduction in all streams, compared to the uncontrolled population (Table 2). When recruitment variation was included, the average parasitic abundance was reduced even further (to 99%) for the lampricide control option (Table 2). In contrast, the performance of the alternative control option was considerably worse with recruitment variation included (85% reduction in parasitic abundance, Table 2, Fig. 6). With recruitment variation, average parasitic sea lamprey abundance was more than ten
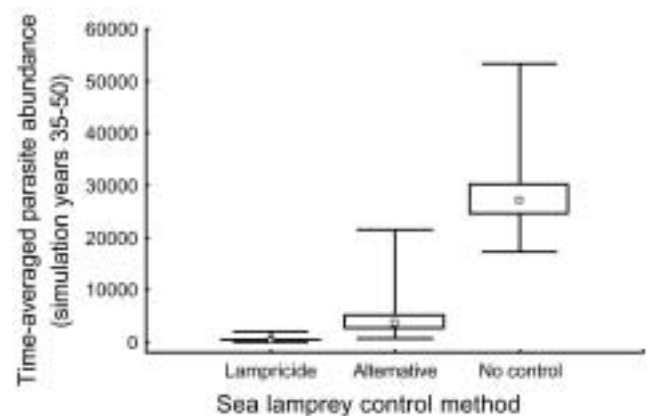
FIG. 6. A comparison of simulation results for lampricide control, alternative control, and no control, with the process error variance set at 3.03. The open square represents the median for 1,000 simulations, the box shows the interquartile range, and the whiskers show the maximum and minimum.

TABLE 2. **Results of simulations showing the effect of including process uncertainty in the stock-recruitment relationship. Results are shown for process error variances of 3.30 and 1.51, which reflect assumptions that all or half of the variation observed around the stock-recruitment relationship was due to process uncertainty, respectively. For the lampricide option, one stream was treated each year, with 90% effectiveness. For the alternative option, reproduction was reduced by 70% in all streams, each year.**

Management option description	Variance	Mean[1]	SD[2]	% Reduction[3]
No Control	3.03	27,425	4,700	0
Lampricide	0	1,820	0	0.93
Lampricide	3.03	361	205	0.99
Alternative	0	1,675	0	0.94
Alternative	3.03	4,080	2,085	0.85
No Control	1.51	23,000	2,900	0
Lampricide	0	826	0	0.96
Lampricide	1.51	281	131	0.99
Alternative	0	667	0	0.97
Alternative	1.51	1,849	826	0.92

[1] mean of time-averaged parasitic abundance in simulation years 35–50 for 1,000 simulations
[2] standard deviation of same
[3] computed from {(no control mean—option mean) / (no control mean)}

times as great if alternative control was used instead of lampricide control, for management options that had equivalent performance characteristics in the absence of recruitment variation. The results were similar, although the differences between the two control options were not as great, when process error variance was assumed to be only 50% of the estimate obtained from the stock-recruitment data.

DISCUSSION

This synthesis was motivated by a practical concern, expressed by sea lamprey program managers, that compensatory mechanisms might reduce the effectiveness of alternative control strategies, particularly those that operate by reducing the reproductive success of lamprey populations. Neither the review of historical evidence nor the analyses of recent data suggest a strong, repeatable influence of density-dependent compensatory mechanisms on sea lamprey populations. This was especially true within the range of sea lamprey abundance levels observed since the implementation of a basin-wide sea lamprey control program in the Great Lakes. The only striking, consistent compensatory response was the shift in sex ratios that occurred when control was initiated on each of the Great Lakes, and this shift was only clear when controlled populations were compared to pre-control populations.

Previous research (Purvis 1979, Weise and Pajos 1998) has led others to conclude that density-dependent growth of larval sea lamprey occurs when a new cohort of larvae colonize a stream after treatment. However, the analysis of larval growth yielded equivocal results. In general, similar or lower growth rates were observed in the first colonizing cohort after a treatment equally as often as increased growth (Fig. 3). This suggests that other factors that vary from year to year, such as weather and timing of hatch, may be at least as important as ammocete density in controlling cohort mean lengths. Further, these factors are equally likely to lead to increased or decreased growth of the first cohort relative to those that follow, implying that even the cases where first cohort growth was apparently greater could be explained by factors other than density.

The stock-recruitment analysis revealed evidence of compensation but its magnitude was obscured by the large amount of density-independent variation in recruitment. For example, the best-fit stock-recruitment parameter estimates imply that decreasing density of spawning females from 2 per 100 m^2 to 0.5 per 100 m^2 would result, on average, in an increase in recruits per spawning female (R/S) from 326 to 396. Assuming a normally distributed error

for ln(R/S) the regression variance estimate implies that 67% of the R/S values would lie between 13 and 409 at a density of 2 spawning females per 100 m^2. Density-independent variation will be responsible for far more of the interannual variation in sea lamprey recruitment in streams than density dependent variation.

The absence of evidence for strong compensatory effects does not imply, however, that control strategies that aim to reduce sea lamprey reproductive success will offer effective alternatives to a lampricide-based control method. Density-independent recruitment variation may mask density-dependent effects, but it also leads to the lack of a consistent, repeatable demographic response in a particular stream to a reduction in the effective number of spawning lamprey. The simulation results illustrate this effect. When recruitment variation was added to the model, the performance of the alternative control strategy declined substantially. Even though the reproductive output was reduced by 70% in all streams, recruitment variation led to occasional large year-classes of larval sea lamprey in some streams. Unlike a lampricide control strategy, the alternative strategy does not allow a response to such events because the contol actions are taken before recruitment occurs.

In contrast, the lampricide control strategy actually appeared to benefit from the addition of recruitment variation. This occurred because recruitment variation leads to differences among streams in the abundance of larvae. Only one stream can be treated each year, and if that one stream contains a disproportionately large fraction of the lake-wide larval population, its selection for treatment will lead to a greater overall effect than if all streams have similar populations. Because the lampricide strategy is based on selection of streams after recruitment occurs, recruitment variation actually makes this strategy more effective.

The lampricide forecasts in the simulations are optimistic compared to what might be expected for a real situation because of two simplifying assumptions. First it was assumed that there were no uncontrollable sources of parasitic lamprey in the lake. However, larvae that colonize untreatable lentic habitats or marginal streams that are never cost-effective to treat will result in persistent residual populations not represented in these simulations. Perhaps more important is the assumption of perfect knowledge of larval abundance in each stream. The larval assessment methods used to select streams for treatment are neither precise nor ac-

curate (Christie *et al.* 2003, Hansen *et al.* 2003, Slade *et al.* 2003), so the actual treatment program is probably less effective than would be possible with perfect knowledge. This assumption may lead to overestimates of the merits of lampricide control relative to alternative control and thus warrants further exploration.

Implications for Alternative Control Strategies

The simulation results indicate that, despite the lack of strong compensatory responses, the effectiveness of alternative controls may be seriously compromised by density-independent variation in recruitment. The simulation results presented here could represent a lake-wide sterile-male-release program with 2.3 sterile males released for every one non-sterilized male. Sterile-male-releases and other alternative controls would have to achieve much larger reductions in the effective spawning population size at reasonable cost to compare favorably to lampricide control. Using the parameters in the simulations reported here as an example, a lake-wide sterile:fertile male ratio of 5.5:1 would be necessary to achieve a result comparable to that obtained using a 90% effective lampricide treatment on one stream per year.

Despite this result, alternative controls may have an important role to play on individual streams where lampricide treatment is very costly. The St. Marys River is an obvious example, and is currently the primary object of the sterile male release program (Schleen *et al.* 2003, Twohey *et al.* 2003a). As well, Brege *et al.* (2003) pointed out that the majority of lampricide treatment expenditures each year are directed to a small number of large rivers. It is possible that considerable savings could be achieved by directing alternative control effort at these rivers, even if the consequence would only be to reduce the frequency of lampricide treatments. This possibility warrants further investigation using modeling tools like the one presented here.

Control strategies that target reproductive success may still prove to be valuable, large-scale alternatives to lampricide control for two reasons. First, the development of more effective techniques for trapping adult lampreys, particularly through the use of chemical attractants (Li *et al.* 2003, Sorensen and Vrieze 2003, Twohey *et al.* 2003b), may make it possible to achieve the large reductions in effective spawners that the simulations presented here suggest will be necessary, and

at a reasonable cost. Second, pressure to use alternatives to lampricide control or low-head barriers to avoid non-target effects may increase to the point where selective trapping or sterile-male releases offer the only socially acceptable alternatives. A fair comparison of control options should consider the relative environmental costs of the options as well as their benefits (McLaughlin *et al.* 2003).

Significance to IMSL Procedures

The modeling tools that have been developed for use by the Great Lakes Fishery Commission to determine lampricide treatment schedules (Christie *et al.* 2003) and evaluate alternative control strategies (Goddard and Christie 2003) do not currently incorporate uncertainty. Density-independent recruitment variation has been shown to be one source of uncertainty that can be of considerable importance when alternatives are being considered. We recommend that this uncertainty be incorporated into IMSL management tools before they are used for future planning. We also support the suggestion of Christie *et al.* (2003) that other key sources of uncertainty be identified and incorporated into these management tools.

Priority Areas for Further Research

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

in this study could be considered for continued monitoring in this context.

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

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

Finally, more theoretical work is needed to determine the limits to the potential of alternative control strategies. The simulation model presented in this synthesis illustrates the kind of tool that could be used. We suggest a strategy in which simple models, such as the one presented herein, are used first to explore possible management options. Then promising options are applied to more realistic

models such as the IMSL tools (Greig *et al.* 1992). These tools could then be used to define management experiments for individual streams or even for whole-lake systems that provide the ultimate test of management strategies. The sea lamprey control program provides an unusually rich and promising area for the kind of adaptive management approach suggested by this scenario.

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