GREAT LAKES FISHERY COMMISSION
Research Completion Report *

EVALUATION OF MODELS FOR INTEGRATED MANAGEMENT OF SEA LAMPREY

by

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FINAL REPORT

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1 OVERVIEW

This report is submitted in completion of a research contract between the Great Lakes Fishery Commission and Case Western Reserve University, "Evaluation of Models for Integrated Management of Sea Lamprey." The objective of this project was to evaluate error properties of the Lake Ontario Decision Support System and to establish error bounds on target levels of control of sea lamprey in Lake Ontario. This work was a component of the work of the Sea Lamprey Task Group, which was chaired by Dr. Charles. K. Minns and Dr. Joseph. F. Koonce under the auspices of the Board of Technical Experts of the Great Lake Fishery Commission. During term of this project, the task group with the aid of Mr. Gavin Christie (IMSL Specialist of the Great Lakes Fishery Commission) upgraded the Lake Ontario Decision Support System to an IMSL Decision Support System (Koonce and Locci-Hernandez 1989).

The goal of the Sea Lamprey Task Group was to evaluate models and data for the integrated management of sea lamprey in Lake Ontario. To that end, the task group and the IMSL Specialist organized a series workshops to examine model predictions and observations of ammocoete dynamics. The work reported here supported these initiatives. The report is divided into two parts. Part 1 (Section 2) deals with application of models to evaluation of policy options for the implementation of integrated management of sea lamprey (IMSL). Part 2 (Section 3) is the presentation of a model of the regulation of abundance and distribution of ammocoetes in a stream. This model was developed for the ammocoete workshop of the task group.

2 POLICY OPTIONS FOR IMSL

2.1 Introduction

Policy for control of sea lamprey in the Great Lakes has changed in the last 10 years. The original objective of sea lamprey control was eradication. Combinations of electrical weirs, barrier dams, and chemical control characterized a control program oriented to suppress lamprey abundance to the limit of available technology and budget. As the impossibility of eradication became apparent, however, new issues arose. Questions of judging or improving program effectiveness, allocation of control resources among lakes, and justification of budget moved to the forefront. In an attempt to develop quantitative goals for the control program, the Great Lakes Fishery Commission changed the philosophical basis of the program from eradication to coexistence. According to Eshenroder (personal communication), the pivotal transition came in 1982:

> "In 1982 the Great Lakes Fishery Commission adopted a policy document that outlined a new concept as a basis for conducting the sea lamprey control program in the Great Lakes. This document, <u>A Strategic Plan for</u>

Integrated Management of Sea Lamprey in the Great Lakes (IMSL), established goals and strategies for converting the conventional control program into an operation employing many features of integrated-pest-management (IPM)."

The IMSL plan drew upon the IPM concepts that Sawyer (1980) reviewed at the Sea Lamprey International Symposium. The distinguishing feature of the IPM approach is its attempt to minimize the damage inflicted by a pest according to an optimal trade-off of ecological, social, and economic constraints. Two key concepts emphasized by Sawyer (1980) were integrated control and economic injury level. Drawing on these concepts, the GLFC saw IMSL a way to relate sea lamprey control to fishery objectives, to develop and implement new control methods, and to set an economically justified level of control. The economic injury level was this economic threshold for control. If pest abundance is greater than this threshold, more control would be required. The concept of economic injury level as the target level of control, therefore, could contribute both to a rationalization of budget and to decisions about allocation of control resources between lakes.

In spite of the conceptual appeal of an integrated pest management framework, IMSL has not advanced to an operational stage. The barriers to implementation of IMSL have been both technical and institutional. The most important technical problem was the absence of quantifiable measures of the effectiveness of control of sea lamprey. Direct measures of sea lamprey damage were not available, and indirect measures from marking statistics were not sufficient to estimate fish mortality due to lamprey attacks. More importantly, quantification of ammocoete abundance and production of transformers has not advanced to the level required to predict the effects of control on numbers of transformers entering a lake.

These technical barriers were worsened by some key institutional impediments. For example, there were until recently no fish community goals for any of the Great Lakes. Unlike agricultural integrated pest management, fisheries are not concerned with a single crop. Without these community goals, acceptable levels of damage can not be established. In addition, the GLFC itself had neither proposed criteria for allocating control resources nor set up a structure to coordinate policy options among control agents and fishery managers.

The complexity of many of the issues involved in the implementation of IMSL, led the Board of Technical Experts to commission a series of workshops and research projects. The IMSL Decision Support System, in fact, is the culmination of the efforts to measure effectiveness of control and to integrate it with fishery management. Koonce and Locci-Hernandez (1989) document the history of this effort. Use of models in IMSL, however, has not met with universal acceptance. From early on, models of salmonid/lamprey interactions attempted to bridge gaps in quantification of stages of sea lamprey life history, and they brought together a lot of untested speculations and assumptions (cf. Walters et al 1980; Koonce et al 1982; and Spangler and Jacobson 1985). The scientific status of these models was thus suspect. While the validity of the models and their improvement is an important and on-going activity, the role of the models aiding policy formulation has steadily expanded. The use of models to examine consequences of policy choices is irreplaceable. The veracity of model predictions will always be tested against experience, but predictions of future behavior of a system necessarily requires a model of system dynamics.

2.2 Application of IMSL Decision Support System to Estimation of Target Levels of Control of Sea Lamprey

The IMSL Decision Support System is a network of databases and models. The system is arranged in three components: a database management system, a problem specification system, and a simulation/analysis system. Within the simulation/analysis component are model and trade-off analysis modules. Simulations can be used to explore the consequences of various policy options as illustrated in Koonce and Locci-Hernandez (1989) or simulation output can itself be analyzed to calculate optimal policies. The analysis presented in this section is an example of this use of the IMSL Decision Support System. The estimation of economic injury level discussed here, in fact, replaces a trade-off analysis spreadsheet in the decision support system. The purpose of this application is to show the relation between economic injury level and target level for control; including the effects of uncertainty.

2.2.1 Cost Analysis of IMSL

The purpose of analysis of the costs of IMSL is to establish a basis for choice of level of control of sea lamprey. This choice assumes implicitly that extirpation of sea lamprey is not feasible and that managers of the fisheries resources of the Great Lakes could accept some minimum, residual population of sea lamprey. Although choices of this type are not exclusively economic, theory of economic optimization does provide a structure within which to examine the trade-offs to achieve a target abundance of sea lamprey.

The theory of the firm seems appropriate in this case (e.g. Thompson, 1973, or Cohen and Cyert, 1975). This theory is a formal representation of the trade-offs of the costs of production (or control of sea lamprey in this case) against either the profit to the firm or the damage associated with production. The theory provides for optimization of the trade-off on the basis marginal net costs; either maximizing net profit or minimizing net costs of damage and production for a unit increment of production. The first case would be a marginal profit optimization and the second would be a marginal damage optimization. Either approach will yield the same optimal production level. In the case of sea lamprey control, however, the marginal damage optimization seems more appropriate.

To cast IMSL as a marginal damage optimization problem requires specification of the costs of management and the damage caused by parasitic phase sea lamprey. Unfortunately, the institutional characteristics of IMSL defy a strict representation as a "firm" and some approximations are necessary. Costs of IMSL, for example, are distributed over several agencies and programs. The Great Lakes Fishery Commission funds control of sea lamprey. Fishery management cost accounting is more complex. Each state or provincial agency has responsibility for managing fisheries within its jurisdictional waters of the Great Lakes. The costs of this activity may include some costs associated with stocking programs, but the U.S. Fish and Wildlife Service also funds major portions of the overall lake trout stocking program in the Great Lakes. Even the accounting for sea lamprey control in the Great Lakes Fishery Commission is complicated by the combinations of control options (chemical treatment, barrier dam construction, sterile male introduction, etc.) that could be possible within a given budget constraint.

Calculation of damage costs are also problematical for IMSL. Damage of sea lamprey is certainly clear enough: mortality of lake trout and other salmonids. The value of animals killed by sea lamprey, however, can not be estimated directly. The usual approach in this case is to develop a non-market economic analysis of fisheries and thereby establish a "value" of each fish (e.g. Talhelm, 1988). As is illustrated below, value of fish is a key factor influencing optimal levels of control and thus target levels of parasitic phase sea lamprey. Nevertheless, there is no alternative to this non-market approach to assessment of damage associated with sea lamprey in the Great Lakes.

Applying the theory of the firm to IMSL thus requires a number of simplifying assumptions. These assumptions concern sea lamprey control, fisheries management, and damage. Within these groups, they are as follows:

*Sea Lamprey Control

1) Chemical control (TFM application) is the primary mode of control. Costs of maintaining existing barrier dams are included as part of the fixed costs of chemical control.
2) Variable costs of control are assumed to be proportional to amount of TFM applied.
3) Effectiveness of TFM application is calculated from steady-state model simulations. These implicitly

assume a fixed rotation and stream selection procedure that is dependent upon the annual budget available for control of sea lamprey in Lake Ontario.

*Fishery Management:

1) Fishery management costs are all fixed costs except for stocking.
2) Variable stocking costs are proportional to number of yearlings (or yearling equivalents) stocked per year.
3) Fishery management costs are thus proportional to stocking necessary to maintain a specified number of adult lake trout.
4) The goal of fishery management is to keep total lake trout mortality to 0.5 per year (instantaneous basis).

*Costs due to Damage:

1) Damage assessment is limited to lake trout.
2) Costs of damage are proportional to the number of lake trout killed by sea lamprey per year.

The object of a marginal damage analysis is to minimize the costs of integrated management of sea lamprey. Total cost is the sum of management costs and damage:

$$C_T = C_S + C_C + D \tag{1}$$

where C_T is the total cost, C_S is the cost of stocking and fishery management, C_C is the cost of sea lamprey control, and D is the cost of damage due to parasitic phase sea lamprey.

As assumed above, damage cost is proportional to number of lake trout killed by parasitic phase sea lamprey:

$$D = \frac{Z_L}{Z} \cdot (1 - e^{-Z}) \cdot N^* \cdot V \tag{2}$$

where Z is total mortality, which is assumed to be fixed by fishery policy, N^* is the desired abundance of adult lake trout, and V is the value of each lake trout. Instantaneous mortality of lake trout due to sea lamprey attack is assumed to follow a disc equation as specified in the IMSL DSS Simulation Model (Koonce and Locci-Hernandez, 1989):

$$Z_L = \frac{T \cdot a \cdot L^*}{1 + a \cdot h \cdot N^*} \cdot (1 - p) \tag{3}$$

where T is the duration of the attack season, a is a coefficient for effective search rate of sea lamprey, h is the mean duration of an attack, and p is the probability of surviving an attack. Abundance of parasitic phase sea lamprey at steady state with a sea lamprey control regimen is assumed to be a function of TFM application:

$$L^* = L_{\min} + \alpha \cdot e^{-\beta * F} \tag{4}$$

The constants α, β, and L_{min} are estimated from simulated steady-state pairs of TFM, F, and steady-state abundance of sea lamprey, L^*.

Costs of control and fishery management are simpler to express. Control costs are

$$C_C = g_0 + g_1 \cdot F \tag{5}$$

where g_0 and g_1 are fixed and variable cost coefficients respectively. Similarly, fishery management costs are

$$C_S = f_0 + f_1 \cdot S^* \tag{6}$$

where f_0 is the sum of fixed costs for stocking and fishery management, f_1 is the variable cost coefficient of stocking, and S^* is the steady state stocking rate necessary to obtain a steady state abundance of N^*. Assuming that the analysis is limited to the stocking domain for which allowable harvest of lake trout is greater than zero, C_S is constant for a given level of N^*. As TFM application changes, the trade-off is for harvest mortality:

$$Z_F = Z - Z_L - Z_m \tag{7}$$

where Z_F is the allowable fishing mortality and Z_m is non-predatory, natural mortality.

2.2.2 Economic Optimization

Calculation of optimal control of sea lamprey requires finding the minimum of equation 1 as a function of TFM application. Solving the first derivative of 1 at zero provides the optimal TFM application:

$$\frac{dC_T}{dF} = \frac{dC_S}{dF} + \frac{dC_C}{dF} + \frac{dD}{dF} \tag{8}$$

Because the derivative of all constant or fixed costs is zero, equation 8 with substitutions from equations 2, 3, 4, and 5 becomes:

$$\frac{dC_T}{dF} = g_1 - \alpha \cdot \beta \cdot V \cdot \frac{(1-e^{-Z}) \cdot N^*}{Z} \cdot \frac{(1-p) \cdot T \cdot a}{1 + a \cdot h \cdot N^*} \cdot e^{-\beta \cdot F} \tag{9}$$

Solving 9 at zero, the optimal TFM application is thus

$$\hat{F} = -\frac{1}{\beta} \cdot \ln\left\{ \frac{e_1 \cdot Z \cdot (1 + a \cdot h \cdot N^*)}{\alpha \cdot \beta \cdot V \cdot (1 - e^{-Z}) \cdot N^* \cdot (1-p) \cdot T \cdot a} \right\} \tag{10}$$

Finally, substituting $\hat{F}$ into equation 4 provides an estimate of the economic injury level of sea lamprey:

$$\hat{L}^* = L_{\min} + \alpha \cdot e^{-\beta * \hat{F}} \tag{11}$$

Reliance on equations 10 and 11 to calculate optimal TFM application and residual abundance of sea lamprey requires an understanding of the dependence of these optimal levels on parameter values. This understanding requires simplification of equation 10, which by rearranging terms, becomes:

$$\hat{F} = -\frac{1}{\beta} \cdot \ln\left\{\frac{g_1}{V} \cdot \frac{1 + a \cdot h \cdot N^*}{T \cdot a} \cdot \frac{Z}{1 - e^{-Z}} \cdot \frac{1}{\alpha \cdot \beta} \cdot \frac{1}{N^* \cdot (1 - p)}\right\} \tag{12}$$

At high densities of lake trout, sea lamprey are not limited by prey availability and their attack rates depend only upon handling time:

$$\frac{1 + a \cdot h \cdot N^*}{T \cdot a} \approx \frac{a \cdot h \cdot N^*}{T \cdot a} = \frac{h \cdot N^*}{T} \tag{13}$$

Substituting equation 13 into equation 12 and simplifying, therefore, optimal TFM application is

$$\hat{F} \approx -\frac{1}{\beta} \cdot \ln\left\{\frac{g_1}{V} \cdot \frac{h}{T} \cdot \frac{Z}{1 - e^{-Z}} \cdot \frac{1}{\alpha \cdot \beta} \cdot \frac{1}{(1 - p)}\right\} \tag{14}$$

2.2.3 Summary of Important Factors

Equations 10 and 11 provide a means of calculating optimal control of sea lamprey from basic characteristics of IMSL. Using the Lake Ontario version of the IMSL Decision Support System (Koonce and Locci-Hernandez 1989), we derived a set of parameters for equation 14 (Table 1). We obtained coefficients for equation 4 from a regression of simulated pairs of TFM application rate and average abundance of sea lamprey. Assuming constrained budget with a stream selection strategy that maximized the benefit to cost ratio for treatment, average lamprey abundance was calculated for years 16 to 20 of simulated time following adoption of the control strategy. Other parameter values (p and Z) were taken directly from the IMSL DSS model. We assumed the same value of lake trout (V) as used by Eshenroder et al (1987). Finally, we estimated values of h and T such that their ratio would produce an average of 10 sea lamprey attacks during a year. We could not use the values in Koonce and Locci-Hernandez (1989) because of the simplified fish community assumed in this model, but the IMSL DSS model does predict about 10 lake trout attacks per year.

Table 1. Parameter values used to evaluate equation 14. All parameters were taken from Koonce and Locci-Hernandez (1989) except as noted in the text.

Parameter	Value	Units
L_{min}	25,000	Number
g_1	0.15	$/kg
α	257,000	Number
β	4.2E-7	1/kg
h	.05	yr
p	.25	unitless
T	.5	yr
V	12	$
Z	.5	1/yr

The parameters in Table 1 have variable effects on optimal rates of application of TFM. Table 2 lists standardized ranges of optimal TFM and economic injury level obtained by subjecting each of the parameters in equation 14 to a 10% increase or decrease. All ranges are standardized to the value of $\hat{F}$ or $\hat{L}^*$ obtained from the parameter values in Table 1. Optimal TFM is most sensitive to variation of β, which is the effectiveness of TFM application, and least sensitive to L_{min}, which is the lowest abundance level of parasitic phase sea lamprey obtainable by treatment. All other parameters except Z and p affect optimal TFM application equally. Nearly the same pattern of sensitivity appears for the economic injury level of sea lamprey. The main exception is that equation 11 is more sensitive to variation in L_{min} and least sensitive to variation in α.

Table 2. Sensitivity of optimal TFM application and economic injury level of sea lamprey to parameters in equation 14. The sensitivity is the absolute value of the range of values of $\hat{F}$ or $\hat{L}^*$ associated with a 10% increase or decrease of a parameter.

Parameter	$\hat{F}$ Range	$\hat{L}^*$ Range
L_{min}	0	0.166
Z	0.012	0.008
p	0.017	0.011
g_1	0.051	0.034
α	0.051	0
h	0.051	0.034
T	0.051	0.034
V	0.051	0.034
β	0.150	0.034

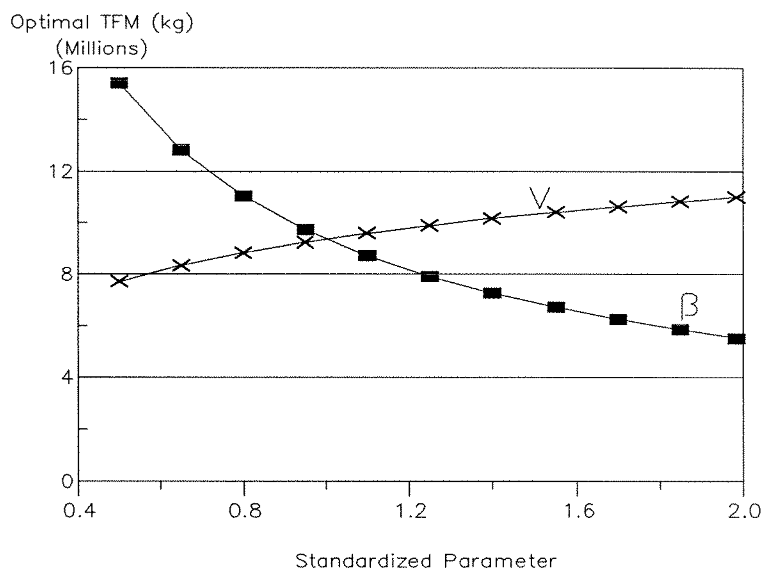
Through the analysis of trade-off options in sea lamprey control, stocking, and fishery management, this economic optimization procedure does provide a basis for establishing optimal target levels of control for a lake. For Lake Ontario, parameters in Table 1 suggest:

$\hat{F}$ = 9,400,000 kg/yr (mean annual average) and

$\hat{L}^*$ = 30,000 parasitic phase sea lamprey.

Uncertainty about parameter values does affect confidence in these values, and, in the next section, we discuss ways of deriving confidence intervals for these estimators. Nevertheless, the sensitivity analysis provides enough evidence to focus on two parameters in particular, β and V.

Fig. 2.2.1. Comparison of the relations between standardized parameter values of V, β, and optimal TFM application rate.



Of the parameters to which $\hat{F}$ is equally sensitive, V (value of a lake trout) is the most uncertain. The ratio of mean duration of attack and duration of attack season is well bounded by experimental and theoretical studies (e.g. Farmer, 1980, and Kitchell and Breck, 1980). The variable cost coefficient for sea lamprey control, g_1, could be measured more precisely through rigorous cost accounting, but is also well bounded by known quantities: budget for sea lamprey control and total annual application of TFM. Two of the regression parameters for equation 4 are also important, but the slope term, β is the most sensitive term influencing $\hat{F}$. Thus V and β emerge as the primary candidates for critical parameters. Further emphasizing their importance is substantial ambiguity concerning methods with which to estimate them. Estimates of β are totally dependent upon assumptions about the efficiency of sea lamprey control, and to some degree these assumptions are matters for policy choices. The determination of non-market value of lake trout is extremely problematical. A value of $12 per lake trout is certainly conservative, and higher values could justify even more control (Fig. 2.2.1)

2.3 Error Characteristics of Target Levels of Control

2.3.1 Sources of Error and Error Propagation

Our treatment of economic optimization of integrated management of sea lamprey has focused mainly on TFM application. The direct concern, however, is the abundance of parasitic phase sea lamprey and establishing a basis for choosing a target level of control. An important part of any such decision is the effect of errors on the target value. Given some information about errors and error propagation in the calculation of target level, the choice should ideally be of an interval for target level of control. Unfortunately, there are no standard statistical procedures to estimate confidence intervals for target level. The main difficulty is that the models underlying the analysis are overdetermined, and their parameters have not been uniformly obtained through regression. Instead, we develop an approximate confidence interval by analyzing error propagation in the calculation of optimal target level of control.

Error propagates in one or more of three ways. These three basic types of error are structural error of model, sampling error, and process error, which is associated with random variation in natural systems. Because structural errors introduce systematic bias of predictions, they affect target levels rather than confidence intervals. Only sampling and process error, therefore, require analysis to estimate confidence intervals on target levels of control.

Uncertainty of model predictions ultimately arises from model calibration. Estimation of parameters in Table 1 was not the result of a rigorous data fitting procedure. Instead, derivation of these parameter values was a mixture incorporation of parameters from the IMSL Simulation Model (Koonce and Locci-Hernandez 1989) and from analysis of its predictions.

IMSL Model Evaluation

Calibration of the IMSL Simulation Model for Lake Ontario required estimates of several parameters as well as use of parameters derived for earlier models (Koonce et al 1982 and Spangler and Jacobson 1985). The parameters or sets of parameters, which were explicitly calibrated for Lake Ontario, are presented in Table 3 along with the data sets used for calibration.

Because this calibration procedure is so complex and the completeness of data sources is so varied, explicit characterization of error propagation is difficult if not impossible. On a more heuristic level, however, this model calibration shares common elements with all sampling and inference procedures. To wit, all parameters are drawn from distributions with their own means and variances. Fitting thus entails selecting a set of parameters that minimizes deviation from observations. For the IMSL Simulation Model, marking statistics and estimated carcass densities were observations for calibration. Obviously, no unique combination of parameters emerges from this process. Parameter values are constrained, but ultimately, error propagation and uncertainty of model predictions are issues arising from interaction of the parameters. This feature of the calibration procedure is accessible to more formal analysis.

Table 3. Summary of the contribution of selected parameters and variables to calibration of the IMSL Simulation model.

Parameter(s) and Variables	Role in Model Calibration	Data Sets Used
Annual Stocking Levels by Species	Estimation of Yearling Equivalents added by stocking. IMSL Model focused on lake trout, coho salmon, and chinook salmon.	Historical stocking data and estimation of stocking mortality
Natural Mortality of lake trout and juvenile salmon	Establish minimum, non-predatory, non-fishing mortality levels for lake trout and non-spawning cohos and chinooks.	Estimated on basis of experience and consistency with other lake trout populations
Historical Fishing Mortality	Determine historical pattern of fishing mortality by species and by age.	Estimated from historical catches and estimated abundance of species.
Total Mortality Rates	Bounds of total mortality by age and species are necessary to constrain model calibration	Estimated variously from catch curves and CPUE for tagged animals
Habitat Overlap Coefficient	Established the season overlap of lamprey habitat with potential prey species	Assumed correspondence between lake trout habitat and sea lamprey. Others estimated on basis of similarity to lake trout distribution.
Lethality of Attack by Sea Lamprey	Object of calibration. Varied to fit observed marking and carcass density patterns.	Marking Data (esp. A1 marks per fish) and estimates of lake wide carcass abundance.
Growth Rate Parameters for all species	Established growth rate parameters for lake trout, coho, chinook, and sea lamprey. Sea lamprey size was a function of consumption rate.	Size at age data by species. Estimation of minimum age for transformation of ammocoetes.
Ammocoete Habitat by Stream	Flow rate and habitat area were necessary to allocate spawners and to determine density of ammocoetes	DFO data on treatment history of streams
Sea Lamprey Control History by Stream	Quantity of TFM applied and area treated by stream for each year of treatment	DFO data on treatment history of streams
Physical Variables for Lake Ontario	Needed to specify volume of lamprey habitat and seasonal temperature pattern.	Various reports

2.3.2 Monte-Carlo Experiments and Results

To understand the effects of parameter uncertainty on predictions of target levels of control requires estimation of their confidence intervals. Accordingly, we chose to apply Monte-Carlo sampling techniques to explore the sampling distributions of $\hat{F}$ and $\hat{L}^*$. The goal of this analysis was to estimate 95% confidence intervals on each of the variables as a function of various levels of parameter uncertainty. With a Monte-Carlo procedure, therefore, we could calculate the mean and standard deviation of the variables that were required for estimation of confidence intervals.

The Monte-Carlo procedure was a simple repetitive evaluation of equations 11 and 14. For each evaluation, parameters in Table 1 were randomly drawn from Normal distributions. Means were obtained from Table 2 and all parameters were assumed to have the same coefficient of variation (ratio of standard deviation to mean). The Standard Deviation of each distribution was thus calculated from the product of its mean and the constant coefficient of variation. Assuming a value of the coefficient of variation, the sampling procedure was repeated 1,000 times. For each set of 1,000 samples of parameters, a mean and standard deviation of $\hat{F}$ and $\hat{L}^*$ were obtained. Confidence intervals were calculated as:

$$\overline{X} \pm 1.96 \cdot S \tag{15}$$

where $\overline{X}$ is the mean and S is the standard deviation of each variable.

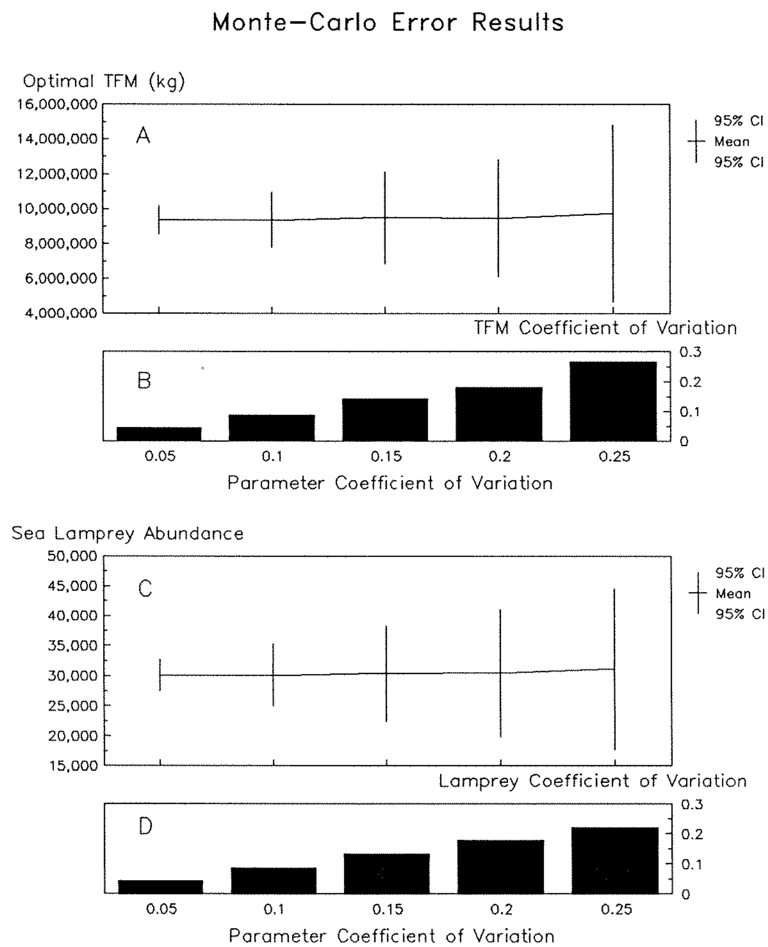


Fig. 2.3.1. Estimated dependence of 95% confidence intervals of $\hat{F}$ and $\hat{L}^*$ on various levels of error in estimates of parameters listed in Table 1. Error levels are specified by coefficient of variation assumed for the parameter set. Panels B and C show the coefficients of variation for $\hat{F}$ and $\hat{L}^*$ respectively as a function input parameter error. Coefficient of variation is the ratio of standard deviation to mean.

As they should, confidence intervals for $\hat{F}$ and $\hat{L}^*$ increase with increasing parameter error (Fig. 2.3.1). Input coefficient of variation generally resulted in lower coefficient of variation for target levels of control (Fig. 2.3.1, panels B and D). Optimal TFM application, however, showed a slight tendency for instability to error. Its coefficient of variation seemed to be greater than the input coefficient of variation for parameters in equation 14 for values greater than 0.2. Again, this emphasizes the greater sensitivity of $\hat{F}$ than $\hat{L}^*$ to error.

2.3.3 Error Bounds on Target Levels of Control

The Monte-Carlo experiments are insufficient to determine error levels for $\hat{F}$ and $\hat{L}^*$. Required first is a way of estimating the coefficient of variation of parameters in Table 1. As discussed above, a heuristic approach to this dilemma is to invoke an analogy to simpler parameter estimation problems. The goal of this approach is to establish a relation between some measure of adequacy of model calibration and the coefficient of variation of model parameters. To this end, consider parameter uncertainty in simple, linear regression:

$$Y = b_0 + b_1 \cdot X$$

From an analysis of variance perspective, the Coefficient of Determination is the ratio of "explained" variation to total variation of a random variable:

$$R^2 = \frac{\text{Regression Sum of Squares}}{\text{Total Sum of Squares}}$$

The notion of explanation here is that some proportion of the variability of a random variable is associated with variation in another, i.e. a set of dependent and independent variables. The remaining, or "unexplained," variation is due to some combination of sampling error or random noise, which is estimated as:

$$S_{ey}^2 = \frac{n-1}{n-2} \cdot S_y^2 \cdot (1-R^2)$$

where n is the sample size and S_y^2 is the variance of the dependent variable, Y. The estimate of the slope and its standard error are

$$b_1 = \frac{S_y}{S_x} \cdot \sqrt{R^2}$$

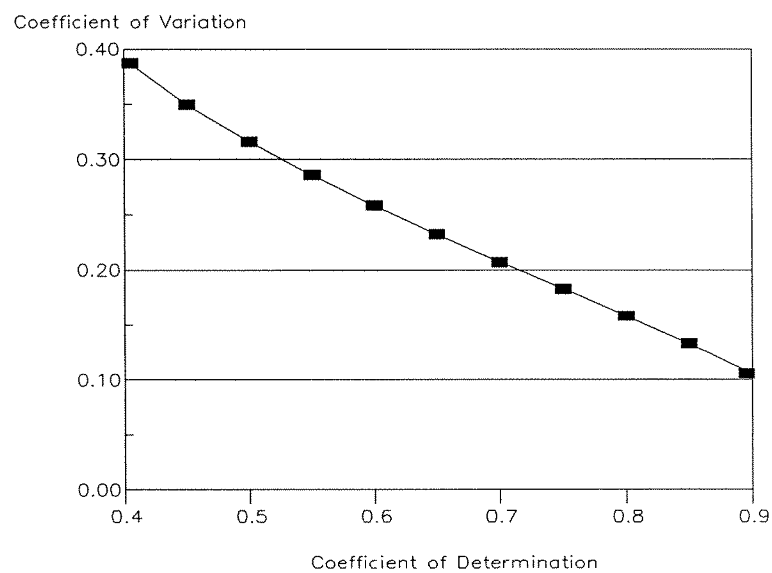
$$S_{b_1} = \sqrt{\frac{S_{ey}^2}{S_x^2 \cdot (n-1)}}$$

where S_x^2 is the variance of the independent variable X and the other terms are as defined above. The coefficient of variation of the slope term is thus

$$\frac{S_{b_1}}{b_1} = \sqrt{\frac{1-R^2}{R^2 \cdot (n-2)}} \tag{16}$$

Fig. 2.3.2 illustrates the dependence of the coefficient of variation of the slope term on R^2. Extension of this argument to multiple correlation and multiple regression is simple. R^2 is the measure of the extent to which any model accounts for the variation in observed data, and equation 16 would apply equally well to the mean coefficient of variation of the parameters if the model were equally sensitive to all parameters. In the case of equations 11 and 14, mean coefficient of variation would be weighted by some measure of the sensitivity of the model to each parameter, but the implications would remain the same.

Fig. 2.3.2. Expected association of coefficient of variation and coefficient of determination after equation 16.

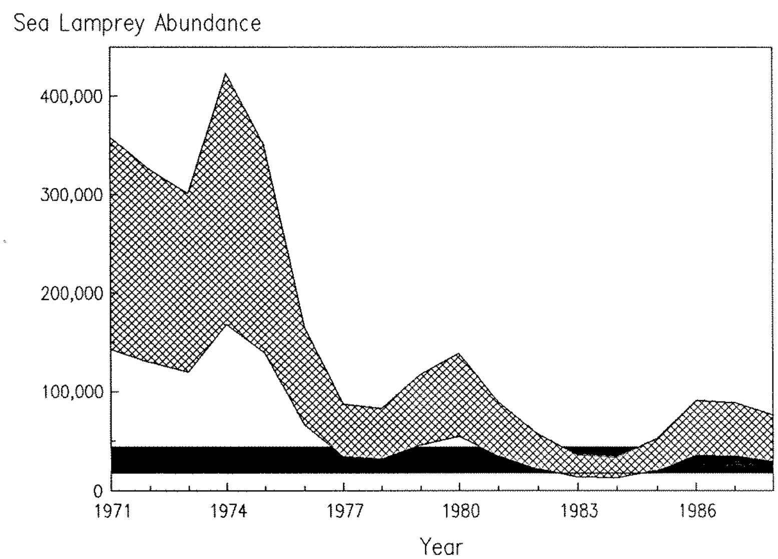


This heuristic argument has produced a relation between the coefficient of variation of model parameters and a measure of model fit, R^2. Unfortunately, the IMSL Simulation Model was not calibrated by regression, and no overall measure of fit is available. However, Koonce et al. (MS) have tested model predictions of lake trout abundance with observed assessment catch statistics. This correlation yields an R^2 of 0.77. Fit to marking data is not as good, and in general, correlation coefficients for ecological data rarely exceeds 0.8 with relatively small sample sizes. A conservative approach, therefore, is to assume that R^2 for the IMSL Simulation is 0.6. From Fig. 2.3.2, we would thus obtain a coefficient of variation of 0.25 for model parameters. Confidence intervals for target levels of control would thus be

$\hat{F}$ = 9.73 (4.66, 14.8) million kg; and

$\hat{L}^*$ = 31,000 (17,100; 44,600).

Fig 2.3.3. Comparison of 95% Confidence Intervals for historical reconstruction of abundance of spawning phase sea lamprey and the economic injury level of abundance of parasitic phase sea lamprey.



The control program for sea lamprey has moved toward these target levels of control. Assuming that model predictions have a 25% coefficient of variation, the 95% confidence interval for historical abundance of sea lamprey has generally overlapped the target interval (Fig. 2.3.3). Similarly, the historical rate of TFM application has been within the 95% confidence interval for the optimal rate in several years (Fig. 2.3.4). Treatment cycles for Lake Ontario, however, often fall below the optimal interval. Average historical application rates have been below the mean optimal level and the recent trends have been at the lower bound of the 95% confidence level. The implication is that treatment of Lake Ontario is suboptimal. The actual situation may be much worse. The optimal TFM application rate derives from very optimistic assumptions about the effectiveness of treatment. The most important assumption is that method used to select streams for treatment is itself optimal for cost effectiveness. If actual treatment schedules fall below this standard, current control levels could fail to reach the lower bound of optimal TFM application rate.

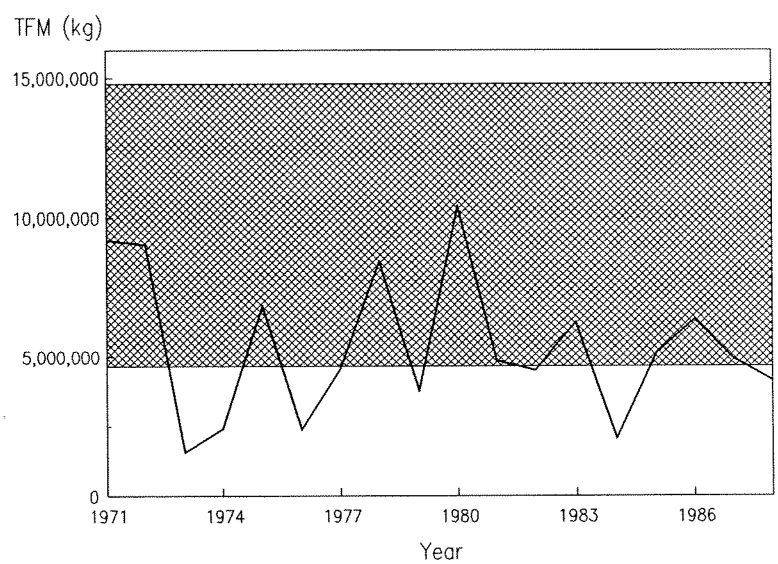


Fig. 2.3.4. Comparison of 95% Confidence Interval for optimal TFM application rate with the historical application rate for Lake Ontario streams

2.4 Future Initiatives and Research Needs

The goals of IMSL are agreement on target levels of control, coordination of stocking and harvest regulation, allocation of control resources, and justification of budget for control of sea lamprey. Implementation of IMSL thus requires rationalization of trade-offs in control of sea lamprey and in fisheries management. Through a cost analysis of IMSL, we have shown that this rationalization is feasible, that uncertainty is boundable, and that incremental adjustments to policy can be directional. For example, the clear implication of this analysis is that control of sea lamprey in Lake Ontario is sub-optimal. The major weakness of this analysis, however, is that the rationalization of trade-offs is only loosely tied to operational levels of management. Two key parameters in Table 1, treatment effectiveness and value of lake trout, illustrate this problem of operational ambiguity.

More than market factors determine the value of a lake trout. Ryder and Edwards (1985) have argued that lake trout is an important indicator of ecosystem integrity of oligotrophic portions of the Great Lakes. Restoration of lake trout, in this context, has more than a utilitarian motive. Restoration and preservation of the ecosystems of the Great Lakes are goals in a more comprehensive social commitment to an ethical standard of stewardship for natural resources. In seeking economic surrogates for this mix of market and non-market components of value of lake trout, willingness to postpone or deny harvest is as necessary as "willingness to pay" as a measure of value. In operational terms, fishery managers set a "value" on lake trout through their decision about maximum total mortality. Table 3 shows one possible relation between maximum total mortality and value of lake trout. High values of Z^* imply that maximizing harvest of lake trout is the primary goal of management. The value in this case is a function of either willingness to pay for fishing opportunity by a recreational fishery or some direct market value if the harvest is allocated to a commercial fishery. Decisions to restrict harvest imply that some higher value is at stake. Data in Table 3 are only suggestive. Certainly more research is required to quantify this effect, but such an operational linkage results in more stringent targets of control for sea lamprey as total mortality goals for lake trout decrease.

Table 3. Possible relation among total mortality of lake trout, value of lake trout, and target levels of control.

Z^*	Value	$\hat{F}$ (kg TFM)	$\hat{L}^*$
0.20	$37	12,400,000	26,400
0.25	$29	11,800,000	26,800
0.30	$24	11,200,000	27,300
0.35	$19	10,700,000	27,900
0.40	$16	10,200,000	28,600
0.45	$14	9,800,000	29,300
0.50	$12	9,400,000	30,000

IMSL Model Evaluation

Like the difficulties in evaluating the value of a lake trout, the wide array of possible control options are difficult to translate into a measure of effectiveness of control for sea lamprey. These options fall into three categories: techniques, tactics, and strategies of control. Control techniques determine the efficiency of the chemical treatment of a stream. Because chemical control must balance efficiency of killing ammocoetes against risk of killing non-target animals, the scope for improvement is mainly limited to finding new and better methods of chemical control. Control tactics are more open. The main tactical decision is the choice of a set of streams or stream reaches to treat. Decision rules influence these choices, but unforeseen circumstances often alter treatment schedules. Nevertheless, this tactical decision is a major determinant of the effectiveness of treatment (cf. Jones et al 1987). Finally, strategies of control affect the mix of control options (e.g. barrier dams, sterile male program, and decision rules for stream treatment selection). This category offers the greatest potential to alter effectiveness. Barrier dam construction, for example, reduces the area required for treatment and thus increases the proportion of total ammocoete habitat that is treatable per unit of TFM. The variety and hierarchical nature of these options resist simple summary or quantification in terms of effectiveness. Methods of forecasting the consequences of various control options are required to understand variation in effectiveness. The IMSL Decision Support System offers a method for these evaluations, but it or similar tools need to be extended to all of the Great Lakes.

In addition to operational ambiguity, institutional factors also impede consensus building for target levels of control. The multi-jurisdictional responsibilities for management of Great Lakes ecosystems means that no agency has lead responsibility or authority. No one is in charge. With diffused responsibility, management by consensus results in two levels of problems: Great Lakes basin and individual lake. At a lake level, there is no tradition of joint consideration of fishery policy and management of sea lamprey control. Recent attempts to develop goals for management of the fish community of each of the Great Lakes have encountered this problem. Without an explicit IMSL context for the rationalization of the management goals, natural bias and differences in problem perception will haunt attempts to develop a common approach with agencies having quite different jurisdictional responsibilities. At a basin-wide level, the institutional structure is simpler with the Great Lakes Fishery Commission serving as a coordinating body, but the problems are more difficult. Without an explicit rationalization for IMSL initiatives, the GLFC will continue to have difficulties in allocating resources for sea lamprey control among lakes and in determining the budget requirements necessary to achieve fish community goals derived for each of the lakes. Setting a value for lake trout is difficult, but determining the relative value of rehabilitation of different lakes is nearly impossible without an operational policy for IMSL.

Improvements in the management of sea lamprey in the Great Lakes requires development and implementation of an operational framework for IMSL. Because consensus building is central to the reality of fishery management, this framework must foster rational analysis of policy options. The work reported here has established the feasibility of setting target levels of control of sea lamprey through evaluation of various trade-offs in management policies. This approach, however, is not yet sufficient for operational implementation on a basin-wide level. The impediments are in part conceptual and in part institutional. To address them, we recommend the following:

1) **Additional analysis of value of lake trout and effectiveness of control of sea lamprey**. Setting target levels of control requires work on two conceptual problems: valuation of lake trout and further evaluation of the effectiveness of control. In particular, both tactics and strategies of sea lamprey control must be explicitly related to a measure of effectiveness. Trade-off analysis of fishery management policy and sea

lamprey control must include explicit consideration of control options. Only by considering trade-offs in treatment schedules or mix of control strategies can variation in control intensity be related to control activity.

2) **Development of a rationalized scheme to allocate resources for control of sea lamprey among the Great Lakes**. Allocation of control resources is the ultimate responsibility of the Great Lakes Fishery Commission. At present, no such scheme exists. Failure to develop such a scheme will result in substantial conflicts if control resources are insufficient to meet target levels of control in each lake.

3) **Initiate an accounting system for sea lamprey control that will provide an accurate relation between control costs and effectiveness of control**. Setting target levels of control for each lake simplifies the process of justifying budget levels necessary for the Great Lakes Fishery Commission to control sea lamprey. Budget rationalization, however, implies the need for a detailed accounting of the components of the cost of control. Without such an assessment, the cost-efficiency of control activities will be difficult to determine. The

target levels of control calculated for Lake Ontario in this work derived from very crude assumptions about control costs. Future work must improve these estimates.

3 AMMOCOETE HABITAT ISSUES

3.1 Introduction

Quantification of the dynamics of larval sea lamprey in streams has been a persistent technical barrier to IMSL. For this reason, the Sea Lamprey Task Group of BOTE selected larval assessment as its primary area of activity. The task group planned a series of workshops and special studies to improve estimation of abundance of ammocoetes and transformers and of critical life history parameters. By more fully exploiting existing data sets, this work would also help in the evaluation of the IMSL Simulation Model for Lake Ontario. As indicated in Table 3, the larval data had not been used in model calibration, and they offered an independent way to test the model and to improve it as necessary. The task group chose to pursue this task in a series of workshops with one workshop explicitly focusing on the interaction of key life history parameters and stream habitat.

As an aid to workshop participants, the following model was developed to describe the behavior of ammocoetes in a complex habitat structure. The model was designed to be open to manipulation of key assumptions about factors regulating ammocoete behavior and abundance. The model included treatment mortality and sampling components with which to simulate actual treatment and survey activity. In this form, the model served three purposes: 1) it could be an aid to workshop participants; 2) it could aid understanding of survey design and error properties; and 3) it could help guide the way to incorporation of better indices of habitat suitability into the stream inventory data base of the IMSL Decision Support System.

3.2 Model Documentation[1]

3.2.1 Overview

The Ammocoete Distribution Model, STRMSIM.BAS, is a simulation model written in QBasic version 4.5. The purpose of this model is to explore the effects of treatment on the abundance, distribution, and age (size) structure of ammocoetes in a given stream.

The model divides the hypothetical stream into twenty cells of equal area. This number can be changed to suit a particular stream. Five substrate types are assumed to exist in the stream. These types are differentiated in terms of particle size: fine sand-silt, sand-silt, muck (silt-detritus), coarse sand, and

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1 Program documentation prepared by Ms. Paola Ferreri, Department of Biology, Case Western Reserve University as part of her M.S. Thesis.

gravel. The ammocoetes are grouped into three size categories: less than or equal to 80 mm, greater than 80 mm but less than 125 mm, and greater than 125 mm.

3.2.2 The Program

The program has two distinct parts: an initialization and a simulation.

Initialization

The initialization part of the program begins by calculating the amount of each substrate present in each cell. Presently, this calculation is:

$$ca(i,j) = ca(i,j) \cdot 1800$$

where $ca(i,j)$ is the percentage of cell i that is of a given substrate type, and 1800 is the total area of cell i in meters squared. This calculation will be modified to accommodate the use of stream characteristics to determine the amount of substrate per cell.

The initialization also sets up the hatch distribution probability and the transformer distribution probability. These probabilities are assigned by cells and describe the fraction of hatchlings and transformers that will enter a given cell. This section of the program also sets up the ammocoete substrate preference by size. The preference is a probability that an ammocoete of a given size will enter a given substrate in any cell.

The population structure of the ammocoetes present in the stream before the simulation begins is also set up. This initialization assumes a high density with smaller animals. In addition, all initial variable and constant values are set up in this section of the program.

Simulation

The simulation part of the program consists of an annual time loop (Fig. 3.2.1). The variable *treat* designates the treatment decision and is either 0 for no treatment or 1 for treatment. The number of years between treatments (i.e. the treatment cycle) can be changed to accommodate the cycles of different streams. Mortality due to treatment is also updated at this time.

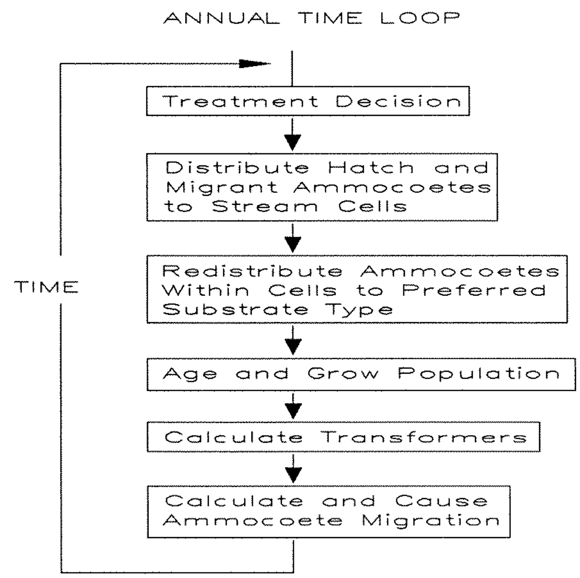


Fig. 3.2.1. Logical flow of model.

3.2.3 Assumptions and Equations

Distribution of Ammocoetes to Stream Cells

The second step in the annual time loop is to distribute the hatch and the migrant ammocoetes by age into the stream cells. The number of transformers in cell i is also calculated at this time using:

$$trans(i) = ptrans(i) \cdot ttrans$$

where $ptrans(i)$ is the transformer distribution probability for cell i, and $ttrans$ is the total number of transformers produced by the stream in the previous year.

The hatch distribution probability, $hdp(i)$, is used to distribute the hatch into each cell:

$$newtotal = hatch \cdot hdp(i)$$

where $newtotal$ is the new total number of age k ammocoetes in cell i, and $hatch$ is the total number of age 0 ammocoetes. The mean size $xbar$ of these ammocoetes is set to a constant age 0 length.

To determine the new total number of age k ammocoetes, for ages 1 to 6+, the total number of age k ammocoetes present in the cell is summed across substrate types. The cumulative sizes are also summed. Then, the total number of migrants to cell i of age k and their cumulative sizes are added to the age k pool in cell i:

$$newtotal = newtotal + m(i,k)$$

$$xbar = xbar + \{m(i,k) \cdot mx(i,k)\}$$

where $m(i,k)$ is the total number of migrants to cell i of age k, and $mx(i,k)$ is the mean size of migrants from cell i of age k. The new mean size of the age k group in cell i is determined by dividing the cumulative size by the total number of ammocoetes in the group.

The $m(i,k)$ and $mx(i,k)$ arrays are set to 0 in preparation for the next year calculations.

Distribution of Ammocoetes to Substrate Within Cells

Once the hatch and migrant ammocoetes have been distributed to cells throughout the stream, the ammocoetes have to be redistributed within the cells into preferred substrate type. This step is accomplished by first determining the size category the age k ammocoetes of cell i are in using $xbar$. The size categories are <= 80 mm, 80<size<125 mm, and >= 125 mm. The ammocoetes that choose substrate j are:

$nm(i,j,k) = newtotal \cdot pref(isize,j)$

where $nm(i,j,k)$ are the non-migrant ammocoetes in cell i, substrate j, of age k, and $pref(isize,j)$ is the substrate preference by size array. The new mean size of these ammocoetes is set equal to $xbar$ which was calculated above.

Mortality and Growth

The next step in the annual time loop is to induce mortality and growth. It is assumed that growth rate is higher at low densities and lower at high densities. Natural mortality is assumed to be higher at high densities. Treatment mortality is age rather than density dependent, therefore it is assigned at the outset of the program.

Since both mortality and growth are density dependent, the density of ammocoetes in a given substrate type must be determined:

$$ammden = ammden + nm(i,j,k)$$

where $ammden$ is the total number of ammocoetes (added across all ages) in substrate j of cell i. This number is then divided by the area in which the substrate is available within the cell. Using this total, which is in units of individuals/meter squared, substrate specific growth and mortality parameters can be set up.

For growth, the parameters are:

$$wk = wkmax \cdot \left(1 - \frac{ammden}{ammden + kwk}\right)$$

and

$$\rho = rhomax \cdot \left(1 - \frac{ammden}{ammden + krho}\right)$$

where wk is the substrate specific y-intercept on a growth vs density curve, $wkmax$ is the maximum y-intercept on a growth vs time curve, kwk is a constant (threshold in the growth vs density curve), ρ is the substrate specific slope of the growth vs density curve, $rhomax$ is the maximum slope of the growth vs time curve, and $krho$ is a constant (threshold in the growth vs density curve).

The mortality parameter is:

$$zm = zmmin + zmmax \cdot \frac{ammden^2}{ammden^2 + kzm}$$

where zm is the substrate specific natural mortality, $zmmin$ is the minimum natural mortality, $zmmax$ is the maximum natural mortality, and kzm is a constant (threshold value in the mortality vs density curve).

The total number of ammocoetes in a given substrate type is:

$$nm(i,j,k) = nm(i,j,k) \cdot e^{-zm-ztm(k)}$$

where $ztm(k)$ is the mortality of age k due to treatment.

The mean size of these ammocoetes is:

$$nmx(i,j,k) = wk + (\rho \cdot nmx(i,j,k))$$

where $nmx(i,j,k)$ is the mean size of the ammocoetes in cell i, substrate j, of age k.

Transformer Production

The model assumes that transformers leave the system, thus they are not added to the number of migrant animals. It is also assumed that a minimum size of 125 mm is required for transformation to occur. Finally, it is assumed that the probability of transforming increases with increasing size.

The first step in calculating transformer production is to determine if the mean size of the animal is greater than 125 mm. Then, the difference in size is determined and squared. Thus, the probability of transformation is:

$$ptrans = ptmax \cdot \frac{sizdif}{sizdif + kpt}$$

where $ptmax$ is the maximum probability of transforming, $sizdif$ is the squared difference between the actual mean size and 125 mm, and kpt is a constant (threshold in a probability of transformation vs size curve).

The total number of transformers is:

$$ttrans = ttrans + \{nm(i,j,k) \cdot ptrans\}$$

Multiplying the total number of ammocoetes ($nm(i,j,k)$) by 1 minus the probability of transforming determines the number of ammocoetes that remain in cell i, substrate j, of age k.

Aging the Population

The ammocoetes that survive and do not transform are aged for the next time step. The age 5 ammocoetes of cell i and substrate j are added to the age 6+ group of the corresponding cell and substrate. The mean size of the new age 6+ group is determined by adding the mean sizes of the two old groups and dividing by the total number of animals in the new group. The rest of the age groups are simply assigned to the corresponding older age in a step wise fashion; for example, the age 4 become age 5, age 3 become age 4, and so on. Each group takes with it its corresponding mean size.

Migration

The model assumes that the probability of migration increases with size and density. It also assumes that the probability of moving downstream is much greater than moving upstream. This assumption can be easily changed to accommodate streams that have suitable habitat both up and downstream. Presently, migration begins at the top cell and proceeds by age and by cell.

The probability of migration is:

$$pmig = cpm(k) + pmax(k) \cdot \frac{ammden^{pmn}}{ammden^{pmn} + kpm(k)^{pmn}}$$

where $cpm(k)$ is the minimum probability of migration at age k, $pmax(k)$ is the maximum probability of migration at age k, $ammden$ is the ammocoete density in a given substrate within a cell, $kpm(k)$ is a constant, and pmn is the exponent used to give the curve desired shape.

The number of migrants is the product of the total number of ammocoetes in the cell and the probability of migration:

$$nummig = pmig \cdot nm(i,j,k)$$

where $nummig$ is the number of migrant ammocoetes summed over substrate types. Thus, the total number of migrants from cell i of age k is:

$$m(i,k) = m(i,k) + nummig$$

where $m(i,k)$ is the number of migrants from cell i of age k.

The number of ammocoetes that do not migrate from cell i, substrate j, of age k ($nm(i,j,k)$) is the product of the total number in that area before migration and 1 minus the probability of migrating.

The cumulative size of the migrant ammocoetes from cell i of age k is calculated as:

$$mx(i,k) = mx(i,k) + \{nmx(i,j,k) \cdot nummig\}$$

where $nmx(i,j,k)$ is the average size of the ammocoetes in cell i, substrate j, of age k. The average size of the migrants is calculated by dividing the cumulative size by the total number of migrants from cell i of age k.

Migration starts at the top cell and proceeds by age down the stream. For cells 19 through 2, migration is calculated as:

$$m(i+1,k) = m(i+1,k) + \{m(i,k) \cdot pmu\}$$

$$m(i-1,k) = m(i-1,k) + \{m(i,k) \cdot pmd\}$$

where $m(i+1,k)$ is the number of migrants of age k moving to the cell above cell i, pmu is the probability of moving upstream, $m(i-1,k)$ is the number of migrants of age k moving from cell i to the cell below, and pmd is the probability of moving downstream. The number still needing to migrate from cell i is:

$$m(i,k) = m(i,k) \cdot \{1 - pmu - pmd\}$$

The equations for calculating the mean sizes of the migrants follow the same format.

Migration from the top cell occurs only downstream. While migration from the bottom cell occurs both up and downstream, only those ammocoetes moving upstream are accounted for. The ammocoetes moving downstream from the bottom cell are considered to have left the system.

3.2.4 Directory of Variables

Legend:
- * = value updated in model
- ! = value read in as data by model
- u = unitless

Table 1: General Variables

Variable	Description	Value	Units
age0len	Length at age 0	20	mm
ammden	Ammocoete density in a particular substrate within a cell	*	ind/sq.m
avgabund(k)	Average abundance of age group within particular substrate in a cell	*	u
avgsize(k)	Average size of age group within particular substrate in cell	*	mm
ca(i,j)	Substrate area by cell	!	sq. m
hatch	Number of hatchlings for the year (age 0)	100000	u
hdp(i)	Hatch distribution rule	!	u
i	Cell index	counter	u
initnum	Initial number of ammocoetes in the stream. (initialization)	15000	u
isize	Size category (< 80mm, 80 < size >125mm, >125mm)	*	mm
j	Substrate index	counter	u
k	Age index	counter	u
l(k)	Length at age	!	mm

Table 1 (continued)

Variable	Description	Value	Units
newtotal	Total number of ammocoetes in a cell after migration and hatch are added	*	u
nsize	Counter	*	u
pref(sz,j)	Substrate preference by size	!	u
treat	Decision to treat in a given year (1 = treat, 0 = no treatment)	*	u
xbar	Mean length of ammocoetes age k	*	mm

Table 2: Growth Variables

Variable	Description	Value	Units
krho	Constant in equation determining substrate specific slope accounting for density effects	100	ind/sq.m
kwk	Constant in equation determining substrate specific y-int accounting for density effects	100	ind/sq.m
rho	Substrate specific slope on growth vs density curve	*	u
rhomax	Maximum slope of the growth vs time curve	0.55	u
wk	Substrate specific y-intercept on growth vs density curve	*	mm
wkmax	Maximum y-intercept on a growth vs time curve	74	mm

Table 3: Mortality Variables

Variable	Description	Value	Units
kzm	Constant in equation determining substrate specific natural mortality accounting for density	100	ind/sq.m
zm	Natural mortality particular to density within given substrate	*	1/yr
zmmax	Maximum natural mortality	0.4	1/yr
zmmin	Minimum natural mortality	0.2	1/yr
ztm(k)	Maximum treatment mortality by age	*	1/yr
ztmax(k)	Maximum treatment mortality by age	!	1/yr

Table 4: Transformation Variables

Variable	Description	Value	Units
avgtrans	Average number of transformers per cell	*	u
kpt	Constant in determining probability of transformation as a function of size	25	mm
mintransize	Minimum size required for transformation	125	mm
ptmax	Maximum probability of transformation	1	u
ptrans	Probability of transformation as a function of size	*	u
ptrans(i)	Distribution probability of transformers into cell i	!	u
sizdif	Difference between mintransize and size of ammocoetes	*	mm
trans(i)	Number of transformers in cell i	*	u
ttrans	Total number of transformers in stream	*	u

Table 5: Migration Variables

Variable	Description	Value	Units
cpm(k)	Minimum migration probability by age	!	u
kpm(k)	Constant in migration function accounting for density by age	!	ind/sq.m
m(i,k)	Migrant ammocoetes by cell and age	*	u
mx(i,k)	Mean size of corresponding migrant ammocoetes	*	mm
nm(i,j,k)	Non-migrant ammocoetes by cell, substrate, age	*	u
nmx(i,j,k)	Mean size of corresponding non-migrant ammocoetes	*	mm
nummig	Intermediate variable used to sum the number migrating over substrate types.	*	u
pmax(k)	Maximum migration probability by age	!	u
pmd	Probability of downstream migration	0.2	u
pmig	Probability of migration due to density effects	*	u
pmn	Exponent in migration function	3	u
pmu	Probability of upstream migration	0.05	u

3.3 Application of Model to Sampling Issues

Due to changing priorities of the Sea Lamprey Task Group, the main use of the model has been to understand effects of habitat structure on ammocoete dynamics. This work has focused on the problem of obtaining an index of usable habitat area for ammocoetes from basic hydraulic characteristics of a stream and constitutes the subject for on-going research of the task group. Nevertheless, the model has proven useful to understanding the implications of trends in treatment collection data, which were examined during an Ammocoete Workshop held in Saulte Ste. Marie, Ontario, in February, 1989.

Examination of aggregated data for treatment collections of ammocoetes for Lake Ontario streams was puzzling. Trends clearly indicated that ammocoete densities were recovering within the treatment cycle for all 49 streams that were treated for lamprey control. Wilmot Creek (Fig. 3.3.1) illustrated this trend. Population survey data revealed the possibility of even higher densities after prolonged treatment, but changing definitions of effort used to calculate catch per unit effort made these data less reliable.

Two issues stood out in these patterns. First was the apparent recovery of ammocoete densities to their pre-treatment levels within a treatment cycle. Second was the implications of these patterns to production of transformers. Fig. 3.3.2 and

Fig. 3.3.1. Patterns of treatment collection and population surveys obtained for Wilmot Creek, Ontario.

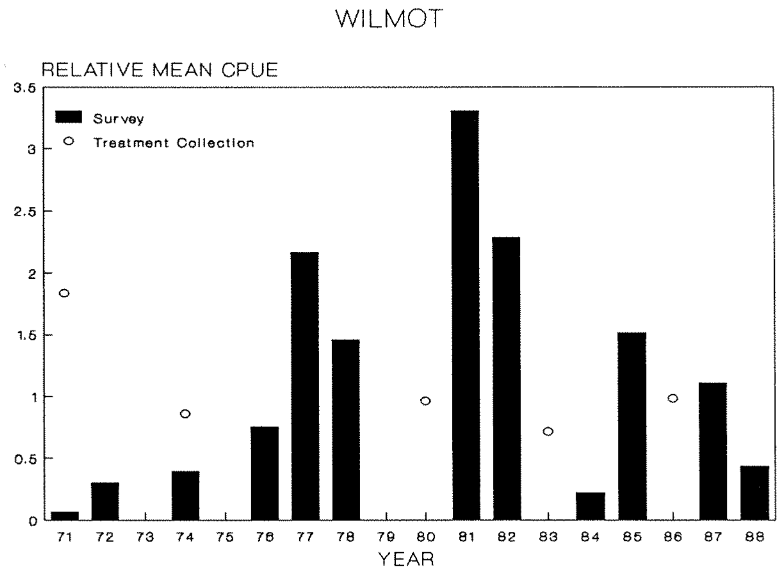


Fig. 3.3.3 address the first issue. Approach to pre-treatment ammocoete densities during a three-year treatment cycle is possible given a fast recovery rate (Fig. 3.3.2). Random variability imposed on slower recovery could also show this rebound of ammocoete density (Fig. 3.3.3). In either case, the model implies that treatment collection data could show no effect of treatment (see Fig. 3.3.3 expected trend of treatment collections). For Lake Ontario, the implication is that even at low adult densities ammocoete densities are fully recovering from treatment within the average three-year treatment cycle. Assuming that transformation does not occur before age 3, the effect of this recovery on production of transformers is minimal (Fig. 3.3.4), but if treatment cycles were to lengthen due to reduced budget, transformer production could rise substantially.

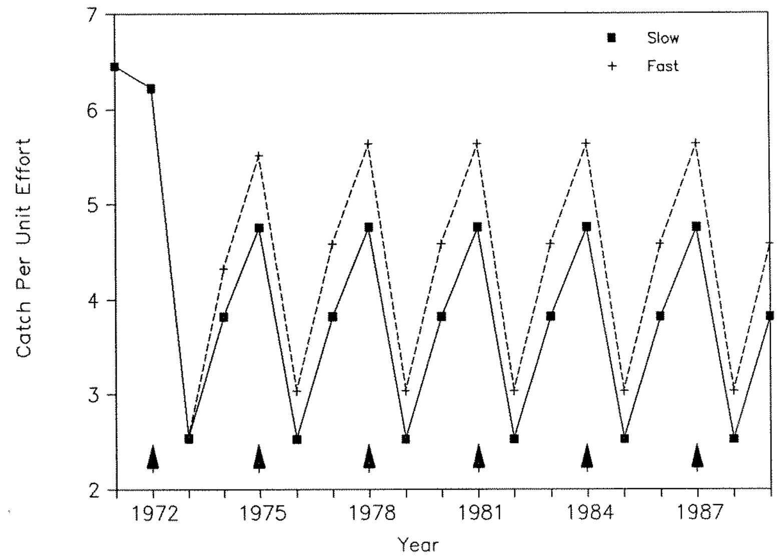


Fig. 3.3.2. Summary of expected trends of ammocoete densities for slow and rapid re-colonization assuming a three-year treatment cycle. Treatment collections would occur at times marked by arrows.

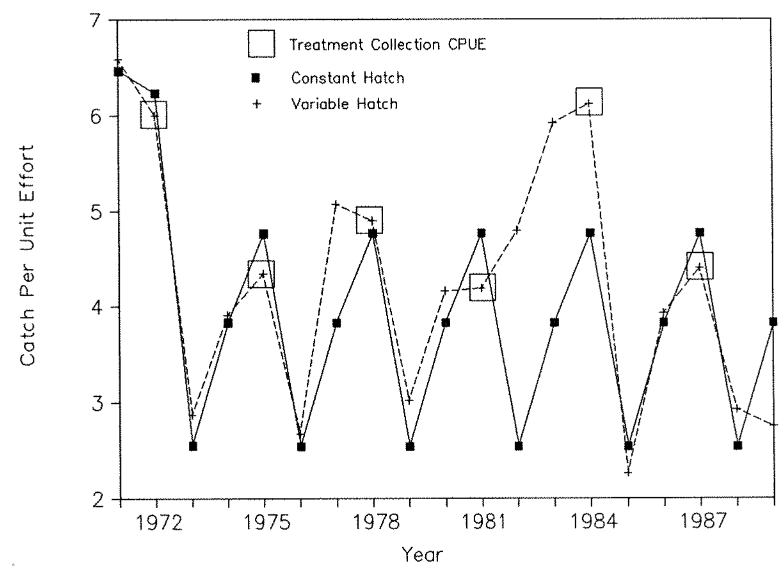
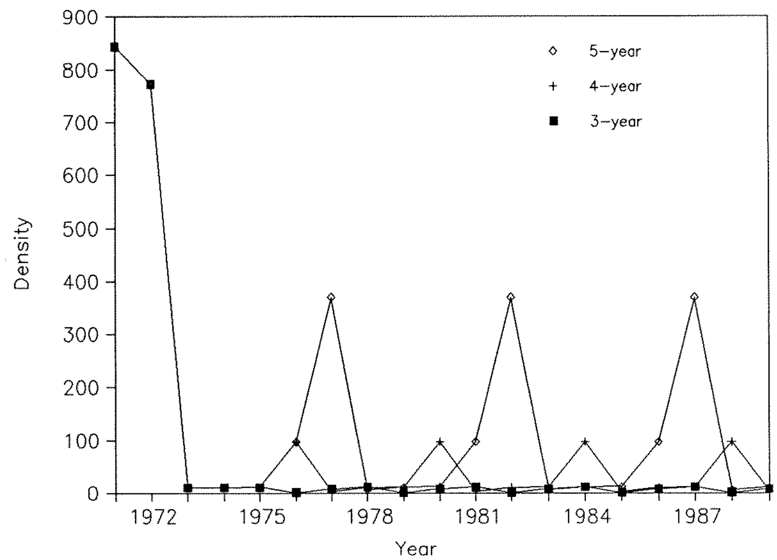


Fig. 3.3.3. Summary of the effects of random variation of hatch on expected trends of ammocoete densities for a three-year treatment cycle. Expected pattern of treatment collections is indicated by the pattern of large markers.

Fig. 3.3.4. Predicted effects of variation in treatment cycle on transformer densities.



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