GREAT LAKES FISHERY COMMISSION

1986 Project Completion Report¹

Application of the Results of Adaptive Environmental Assessment Methodology Workshops Sponsored by the Great Lakes Fishery Commission to the Development and Practice of Multispecies Fishery Management

by:

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INTRODUCTION

Summary of Project Goals and Proposed Products

The goal of this project was to apply the results of two AEAM workshops (Koonce, et al. 1982 and Spangler and Jacobson 1985) to address the issue of realistic trade-offs between sea lamprey control and lake trout management in Lake Superior. More recently, the Great Lakes Fishery Commission has referred to this trade-off as Integrated Management of Sea Lamprey (IMSL). Two specific goals were first to improve the technical credibility of the workshop models and second to reexamine their applicability to policy development.

The work plan focused on collaborative analysis of models and their role in policy formulation. In the first year, I proposed a series of "mini-workshops" to address the observability of lamprey induced mortality in lake trout populations of Lake Superior. Improvements of workshop models required review of this central problem, and the major product was to be a report on the status of this problem and its theoretical implications. Assuming progress on this problem, the second year's work plan focused on improvements in the socio-economic factors of the workshop models. By further consultation with agency personnel, I wanted to produce a version of the workshop models that would support analysis of The major product of the second year was to be a policy options. documented software package for a specific application application of relevance to current lamprey control policy questions.

Research Accomplishments

The work was funded for a two year period (4/1/84 to 3/31/86). As proposed, the activities have been collaborative (Table 1). The problem of observability of effects of sea lamprey on lake trout was indeed the central technical issue impeding application of workshop models. The observability problem is affected by two uncertainties: abundance of sea lamprey and lethality of attack.

A major difficulty with evaluation of the effectiveness of control of sea lamprey has been the absence of a reliable indicator of abundance of sea lamprey. Marking statistics on lake trout, whitefish, or other species have been the only indicators reported continuously. Interpretation of these marking statistics, therefore, is the central technical issue in understanding the interrelations of sea lamprey control and lake trout rehabilitation. For this reason, credibility of the workshop models depended on resolving some of this uncertainty and

Table 1. Summary of activities during the first two years' research

12/5/84 Atte to Tech 12/7/84 resu mana	Fall Anal 1984 data prep inte	10/10/84 Atte to Labo 10/12/84 popu	8/5/84 Atter to Techn 8/10/84 preli	7/15/84 Analysis to compilat 8/4/84 Superior	7/11/85 Meet new wound	6/10/84 Mini-w to improv 6/16/84 models	4/1/84 Revie to prepa 6/1/84 meet	2/1/84 Spec sprii supe	DATE
Attend meeting of Lake Superior Technical Committee and present results of analysis of new models; ways to use of models in lake trout management plan also explored	Analysis of new models and wounding data for Lake Superior and preparation of a report on the interpretation of lamprey marking statistics	Attend WESLP meetings at Hammond Bay Laboratory and discuss sea lamprey population estimation and lethality of attack	Attend meeting with Lake Superior Technical Committee to report preliminary findings and to explore the developing lake trout management plan	Analysis of new attack models and compilation of marking data for Lake Superior	Meeting with Lawry to explore new models and to seek multiple wounding data for Lake Superior	Mini-workshop with Pycha on improvements of lamprey wounding models	Review of AEAM workshop models and preparation of computer aids for June meeting'	2/1/84 Special meeting with Pycha to set up Work plan for spring work schedule for Lake Spring 1984 Superior lamprey study	DESCRIPTION OF ACTIVITY
Report	Report	Information exchange	Information exchange	Improved attack and marking models	Information exchange	Queuing model and multiple attack model	IBM-PC versions of workshop models	Work plan for Spring 1984	PRODUCT
<u> </u>	198 Mar 198	8/8 tc 8/8	Sum 198	5/7 to 5/8	3/1 t 3/2	Win 198	2/2	1/2 1/3	DAT

Table 1. Summary of activities during the first two years' research (continued)

March 1986	Fall 1985	8/4/85 to 8/8/85	Summer 1985	5/7/85 to 5/8/85	3/19/85 to 3/20/85	Winter 1985	2/20/85	1/2/85 to 1/3/85	DATE
Presentation at Plenary Session of the Council of Lake Committees meeting, 19 March 1986, on status of AEAM workshop models and lake trout mortality in Lake Superior	Review of possible applications of IPM to sea lamprey control and modifications of existing workshop models	Attend Workshop to Evaluate Sea Lamprey Populations; development of alternative control models with Jester	Consolidation of criticisms of interim results and preparation of two manuscripts for publication	Presentation to Annual Meeting of Great Lakes Fishery Commission on progress in estimation of lake trout mortality due to sea lamprey	Presentation of report on estimation of lamprey induced mortality in lake trout populations	Analysis of the lethality of sea lamprey attack and exploration of limits of measurement error	Meeting with Eshenroder in Ann Arbor to prepare for reports to Lake Committees and Commissioners	Attend meeting of parasitic phase subcommittee of WESLP at the Lamprey Control Center	DATE DESCRIPTION OF ACTIVITY PRODUCT
Report	Preliminaries to implementing policy version of models	Information exchange and simplified control model	Manuscripts	Report presentation	Report presentation	Report	Information Exchange	Information exchange	PRODUCT

updating them accordingly. The first year's collaborative activities thus focused on the problem of observing lethality of attack by sea lamprey.

The collaboration with Dr. Richard L. Pycha, USFWS, and other members of the Lake Superior Technical Committee was fruitful. Early on, we identified several possible inconsistencies between assumptions in the workshop models and observed patterns of seasonal variation in marking, variation in marking with size, and age-specific mortality rates of lake trout. The results of this collaborative effort were documented in two manuscripts (Koonce and Pycha, MSa, Appendix A; and Koonce and Pycha, MSb, Appendix B), and they are currently receiving peer review through the Secretariat of the Great Lakes Fishery Commission. A key finding was that the lethality of attack may not decline to zero with size of lake trout as assumed in the workshop models. Furthermore, combining the description of the attack process in the models with marking data for Lake Superior, it is possible to estimate the relative abundance of sea lamprey in the entire lake or defined regions of the lake.

One of the original goals of the AEAM workshops was to develop simulation models to aid policy decisions by the sea lamprey control agents and the fishery management agencies. second Ste. St. Marie workshop, in fact, explicitly focused on opportunities to apply principles of integrated pest management (Spangler and Jacobson 1985). Justification for research on the technical issues of estimating and modeling attack lethality for sea lamprey depends ultimately on the continued need for this policy application. During the course of this project, three other initiatives of the Great Lakes Fishery Commission, have not only confirmed the need for policy analysis tools, but have provided a new context for their development.

In the past, there was no explicit linkage of sea lamprey control efforts and fishery management initiatives. In part, this separation was due to the obvious need to reduce sea lamprey abundance to as low a level as possible, but recent emphasis on efficiency and effectiveness of the control program by an internal audit and by the adoption of a strategic plan for integrated management of sea lamprey by the Great Lakes Fishery Commission has led to a reevaluation of the linkages. The first of the new initiatives of the Great Lakes Fishery Commission relevant to this research, therefore, is the explicit consideration of a policy statement on an approach to implement integrated pest management of sea lamprey. Clearly, some kind of analysis tool will be required to explore trade-offs of various policy options involved in integrated pest management, and the product of this research effort continues to address this need.

The two other initiatives providing a context for this policy application are the formal Lake Trout Management Plans for each of the Great Lakes and the convening of the Workshop to Evaluate Sea Lamprey Populations (WESLP). Participation in these efforts has been part of the activities of this project (Table 1). Much of the work of the Lake Superior Technical Committee during 1984 was devoted to the formulation of a fishery management plan. sessions provided an opportunity to review parts of the workshop models for the continued relevance to current fishery management problems in Lake Superior, and I have now incorporated this perspective into a new policy version of the workshop models that I demonstrated at the March 1986 meeting of the Council of Lake Committees.

Similarly, WESLP, which was organized by the sea lamprey control agents and research personnel, provided a context for review of the models from the view of the control program. collaboration with Doug Jester, I examined the possible simplification of the control models, and we explored alternative scenarios for organizing the control effort on a lake-wide basis. More importantly, workshop participants developed proposals for systematically evaluating sea lamprey populations and effectiveness of the control program. These proposals for each of the lakes addressed such issues as linkage to fishery management plans, designation of ecological zones for sea lamprey control, and data and analysis requirements to evaluate effectiveness of control.

As a consequence of these initiatives, the need for a specific policy gaming tool was less important than a full evaluation of the technical issues linking lake trout management and sea lamprey control. To examine the consequences of the findings reported in Koonce and Pycha (MSa), an updated version of the IPM Workshop Model (Spangler and Jacobson 1985) was created. This version of the workshop models, IMSL, is the final product of the current research, and I will provide its documentation in this report.

RESULTS OF RESEARCH

Progress toward Estimating Sea Lamprey Impacts on Lake Trout

BACKGROUND. The central question in the first phase of this project was whether lamprey induced mortality could be observed in the traditional, lake trout assessment data. Pycha (1980) showed a clear association between wounding and total lake trout mortality in Lake Superior, but, finding no association between

mortality and wounding in Cayuga Lake, Youngs (1980) raised questions about the interpretation of wounding data in the Great Lakes. The approach in the IPM Workshop Model (Spangler and Jacobson 1985) followed the work of Farmer (1980) and assumed that lethality of attack should decrease with increasing size of lake trout. Although this assumption did not resolve the inconsistency between the work of Pycha and Youngs, it did provide a context for understanding the shift between parasitic and predatory effects of sea lamprey on lake trout populations. That such a shift could occur seemed apparent in Lake Superior given the seasonal variation in wounding reported by Pycha and King (1975).

Before reviewing research related to observability of lamprey induced mortality, it is first necessary to review some of the formal descriptions of the attack process that were derived for the workshop models (Koonce et al. 1982 and Spangler and Jacobson 1985). As justified in Eshenroder and Koonce (1984), the preferred mark statistic is marks per 100 fish. The reason is that instantaneous mortality due to sea lamprey predation is a linear function of mean marks per fish:

$$Z_{T_i} = M(1 - p)/p \tag{1}$$

where p is the probability of surviving an attack and M is the mean marks per fish. If fishing mortality is constant or negligible, p may be estimated from the slope of a regression of total instantaneous mortality versus marks per fish:

$$Z_{rp} = c + [(1 - p)/p]*M$$
 (2)

where c is natural mortality (or natural mortality plus fishing mortality if fishing mortality is constant and high relative to natural mortality).

Attack rates of sea lamprey vary with size of prey. Simulation models developed in the AEAM workshops represented this variation as a multi-prey disc equation (e.g. Koonce et al 1982). Koonce and Pycha (MSa, Appendix A) modified this basic description of prey selectivity to represent attacks per prey size group over the time period during which a healing wound would be classified in Stages Al to A3:

$$A_{i} = H*q_{i}*L/[1 + \sum_{i}(h*q_{i}*N_{i})]$$
 (3)

where q_i is a selectivity coefficient, N_i is the density of the

ith size group, h is the mean duration of an attack, L is the density of sea lamprey, and H is the mean healing time of a wound. Because sea lamprey spend little time searching for prey,

$$\sum_{i} h * q_i * N_i >> 1$$
, and

equation 3 is approximated by:

$$A_{i} = H*q_{i}*L/(\sum_{i} h*q_{i}N_{i})$$
 (4)

Using a simplification of equation 4, I obtain:

$$\sum_{i} A_{i} = H*L/(\overline{h}*N_{WS})$$
 (5)

where \overline{h} is the mean handling time and $N_{WS} = \sum_i q_i N_i / \sum_i q_i$, which is a weighted total lake trout abundance. Assuming that the mean duration of attack is constant with size, equation 5 implies that total attacks should be proportional to density of sea lamprey, but inversely proportional to density of lake trout. Furthermore, because marks per fish is directly proportional to attack rate (Eshenroder and Koonce 1984), average marking rates will also express these relations:

$$\overline{M} = H*L/(p*\overline{h}*N_{WS}), \qquad (6)$$

where p is the mean probability of surviving an attack and \overline{M} is the mean marking rate for various size groups of lake trout.

A consequence of these relations is that lamprey abundance and lethality of attack could be estimated from lake trout assessment data. Using these equations, Koonce and Pycha (MSb, Appendix B) suggest a simple protocol to estimate both relative abundance of parasitic phase sea lamprey in Lake Superior and the lethality of an attack. Data required for this protocol include estimates of total mortality of the largest fish in assessment catches (estimated from the descending limb of the catch curve--cf. Pycha 1980), catch per effort by size group, and marks per fish by these same size groups and by age. The protocol for estimation of lethality of attack is to fit equation 2 to the total mortality and mean weighted marks per fish by a least squares procedure, where marks per fish are weighted for representation in the assessment catch:

Weighted
$$M = [\sum_{i} (CPE_{i} * M_{i})] / [\sum_{i} CPE_{i}]$$

The protocol for estimating relative abundance of parasitic phase sea lamprey also uses weighted marks per fish and total catch per effort, but over as wide a size range as possible (functionally lake trout 17 inches and larger in Lake Superior). Relying on equation 6, this protocol requires:

- Regression of weighted marks per fish versus 1/CPE for 1. all sizes showing marks;
- Use regression parameters in 1 to estimate the expected 2. marks per fish from observed CPE for each year in the data set; and
- Estimate relative abundance of parasitic phase sea lamprey by dividing observed marks per fish in 2 by the expected marks per fish.

SEASONAL VARIATION IN MARKING. In general, Pycha and King (1975) observed that Spring marking rates were higher than Fall rates in Lake Superior. Pycha (personal communication) never observed small marks (<25 mm) in Spring and concluded that, at least in Lake Superior, Spring marking was not confounded by overlapping cohorts of parasitic phase sea lamprey. The workshop models did not address seasonal variation in marking explicitly. Therefore. a different modeling approach was needed to explore the implications of seasonal variation in marking to the formal description of attacks. The result of this work was a queuing model of sea lamprey attack (Koonce and Pycha MSa, Appendix A).

The queuing model viewed sea lamprey as servers of lake trout of a single size category. Combining bioenergetics descriptions from Kitchell and Breck (1980) and Farmer (1980), the model portrayed the growth and attack characteristics of 100 lampreys for 2000 lake trout. Results of this modeling effort indicated that only varying attack lethality (Fig. 1) could produce the kind of Fall-Spring variation in marking observed in Lake Superior.

ABUNDANCE OF SEA LAMPREY. As discussed above, equation 6 implies that estimates of relative abundance of sea lamprey may be derived from lake trout assessment data. Koonce and Pycha (MSb, Appendix B) reported results of an application to Lake Superior. For Michigan waters (Fig. 2), the association between marking and 1/CPE is not significant; accounting for less than 1% of the variability in marking rates. Wisconsin and Minnesota have only marginally better associations (Koonce and Pycha MSb). Using the protocol to estimate relative abundance of parasitic phase sea lamprey, sea lamprey abundance seems to be generally declining over the period 1958 to 1984, with peaks in 1958-1969 and around 1972, Fig. 3. Comparing this pattern of abundance with the runs recorded at six electric weirs operated in Michigan waters reveals a significant correlation that accounts for about 50% of the variability in weir catches (Fig. 4). This agreement is also

QUEUING MODEL RESULTS

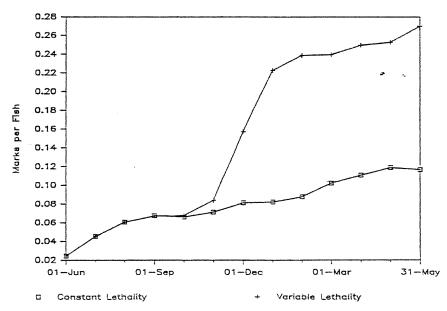


Fig. 1. Seasonal patterns of marking predicted by Queuing Model for constant and variable lethality of attack (After Koonce and Pycha, MSa, Appendix A).

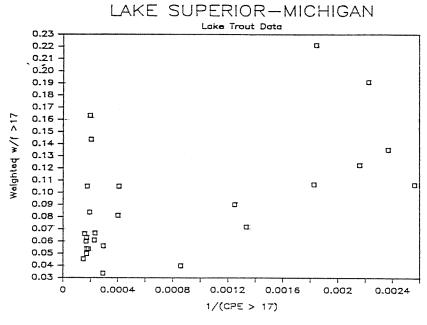
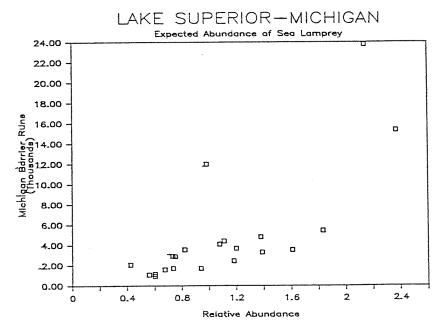


Fig. 2. Correlation of weighted marks per fish and 1/CPE for lake trout 17 inches and longer in Michigan waters of Lake Superior. Coefficient of Determination is 0.0055.

LAKE SUPERIOR-MICHIGAN Expected Sea Lamprey Abundance 2:60 2.40 2.20 2.00 1.80 Relative Abundance 1.60 1,40 1.20 1.00 0.80 D.60 -0.40 0.20 0.00-58 62 66 70 74 78 82

Changes in estimated relative abundance of parasitic phase sea lamprey in Lake Superior waters of Michigan over the period 1958-1984.



Association of estimated relative abundance of sea lamprey with runs at electric weirs (barrier dams) at 6 rivers on the Michigan shoreline of Lake Superior from 1958-1978. Coefficient of Determination is 0.50.

surprising given all of the possible sources of error and changing size structure of the lake trout population over this period.

Combining the estimated relative abundance of sea lamprey for Michigan, Wisconsin, and Minnesota reveals an even more interesting pattern (Fig 5). The basic synchronization of these patterns suggest that the peak in 1972 was not isolated to Michigan waters. Although there is some indication that from 1974 to 1978 Minnesota experienced higher lamprey abundance that the other jurisdictions, the data do not suggest local infestations, but more detailed studies would be required to test this possibility more thoroughly.

LETHALITY OF ATTACK. Application of equation 1 to data from Michigan waters of Lake Superior revealed a highly significant association between marking and total mortality of lake trout 25 inches and longer (Fig 6). The analysis implied an instantaneous natural mortality of 0.18 per year and an average probability of surviving attack of only 0.14. As encouraging as this result is, there are two types of problems. First, the high lethality of attack is not believable. Although various methods of estimating lake trout mortality produced similar results, such high lethality did not seem consistent with high scarring rates observed in Lake Superior and elsewhere. Furthermore the low value of the intercept (0.18) in Fig. 6 indicated that fishing mortality did not contribute significantly to the variability in lake trout mortality during the 1966 to 1982 period. This result also appeared suspect to various individuals who provided criticism of our earlier work. These questions coupled with the still unresolved differences between Pycha (1980) and Youngs (1980), led to a fundamental reevaluation of the estimation procedure.

Use of catch curves to estimate mortality requires a number of assumptions. Although Pycha (1980) corrected catch per effort for each age by the relative strength of the cohorts, the procedure still requires an equivalence of historical and contemporary schedules of mortality with age. Fig. 7 illustrates the consequences of failure to meet this assumption. Here I assume that lake trout mortality abruptly increases in year 0. Using relative abundance of ages 5 to 10 to estimate total mortality, it is clear that 6 years is required before the estimate of total mortality adjusts to the increase. The estimates of probability of surviving lamprey attack change similarly.

Given this problem, it is not clear that the data in Fig. 6 are reasonable. Assuming that lamprey abundance changed gradually overtime, Figs. 8 and 9 show that significant associations between

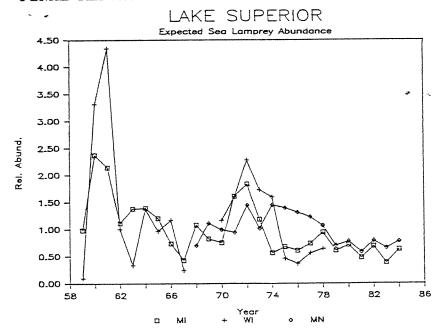


Fig. 5. Patterns of estimated relative abundance of sea lamprey in waters of Michigan, Wisconsin, and Minnesota for the period 1958 to 1984.

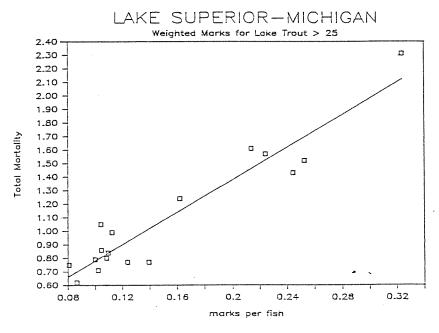


Fig. 6. Relation between total instantaneous mortality and mean marks per fish, weighted by CPE for lake trout 25 inches in length and larger. Data are for Michigan waters of Lake Superior and are drawn from Pycha (1980) and Pycha (personal communication). Intercept of regression is 0.18, slope is 5.99, and coefficient of determination is 0.90.

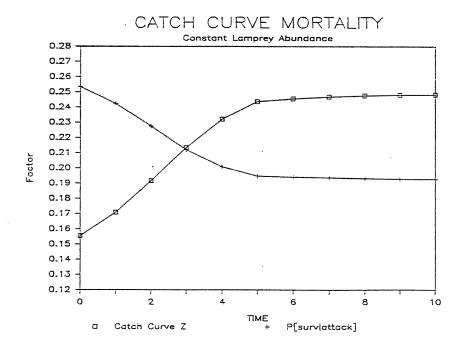


Fig. 7. Variation in total mortality estimate from catch curve data for age 5 to 10 lake trout. Simulated conditions have lake trout mortality increasing from 0.15 to 0.25 in year 0 and remaining constant thereafter.

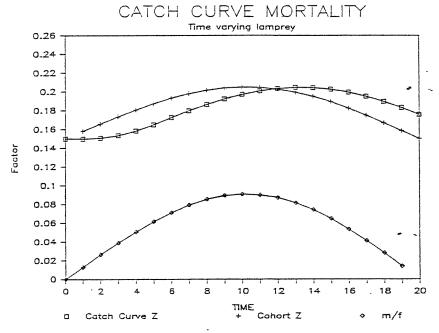


Fig. 8. Comparison of total mortality estimates from catch curve and cohort data. Smoothly changing marking reveals the assumed lamprey dynamics in the example.

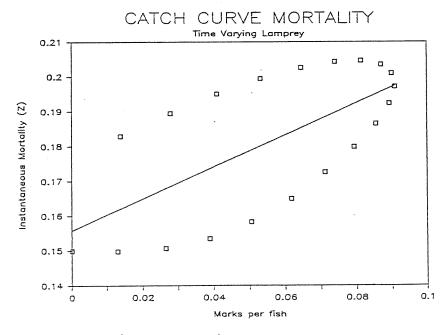


Fig. 9. Correlation analysis of catch curve mortality versus marking for the data in Fig. 8. Estimated and true values of probability of survival were 0.69 and 0.8 and estimated and true values of natural mortality were 0.16 and 0.15.

marking and total mortality can be obtained. In Fig. 8, the total mortality estimated from catch curve data lags behind the true cohort mortality, which is in phase with marking as expected. The resulting correlation (Fig. 9) is quite good and reproduces the assumed non-lamprey mortality and attack lethality. Randomly varying lamprey abundance, however, produces serious errors in the estimates of the true parameters (Figs. 10 and 11).

True variation of lamprey from 1966 to 1982 is between these two extremes. Figs. 12 and 13 show the same analysis for the pattern of abundance of sea lamprey in Michigan waters of Lake Superior for the period 1966 to 1982 suggested by Koonce and Pycha (MSb). Despite the obvious mismatch between assumptions and estimation of total mortality from catch curve data, the estimates of lethality of attack and natural mortality are close to the true values used in the simulation. In these analyses, however, it is clear that the estimate of total mortality should be derived from cohort data.

In theory, total mortality estimates from cohort data have many advantages. The critical assumption to use this approach, however, is that catchability remains constant from year to year. This requirement goes beyond gear selectivity, and the extreme variability of catchability in Lake Superior was a principal reason for preferring the catch curve method (Pycha, personal communication). Figs. 14 to 16 summarize the relation between total mortality and marking for lake trout age 7 to 9 in Michigan waters of Lake Superior for the years 1968-78 during which it was possible to reconstruct cohorts. The following table summarizes some of the important information:

Age	Attack Survival Probability	Intercept Fishing and Natural Mortality	R	_
7	0.44	0.44	0.20	
8	0.36	0.18	0.58	
9	0.20	0.16	0.57	

Because none of the correlations is statistically significant, it is difficult to draw major conclusions from these results. Nevertheless, some tentative conclusions are possible. Pycha's and Selgeby's (personal communication) contention that lake trout mortality due to attacks by sea lamprey does not decline with size receives support. In fact, survival seems to decrease with size. Secondly, the maximum attack survival probabilities for

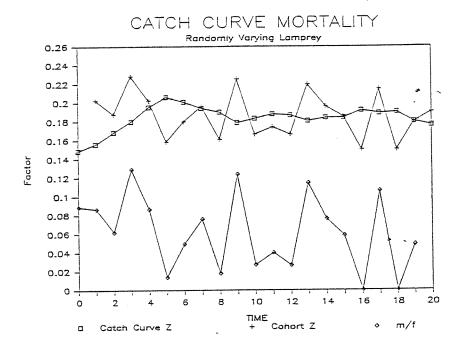


Fig. 10. Comparison of total mortality estimates from catch curve and cohort data. Assumed lamprey dynamics in the example random variations over the same range as in Fig. 8.

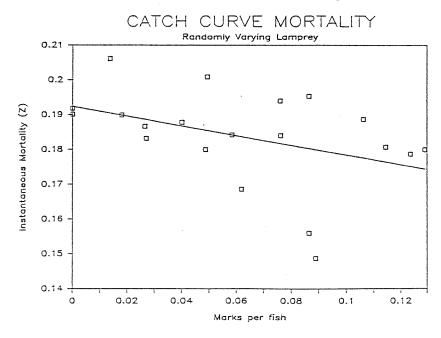


Fig. 11. Correlation analysis of catch curve mortality versus marking for the data in Fig. 10. Estimated and true values of probability of survival were 1.16 and 0.8 and estimated and true values of natural mortality were 0.19 and 0.15.

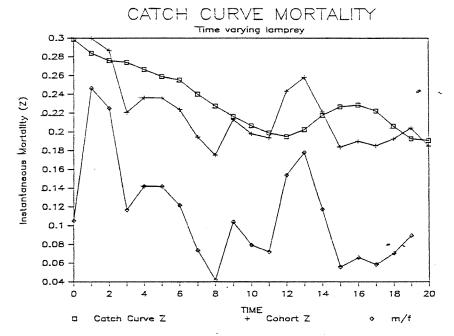


Fig. 12. Comparison of total mortality estimates from catch curve and cohort data. Lamprey dynamics in this example were assumed to follow the relative abundance pattern estimated by Koonce and Pycha (MSb) for 1966-82 in Michigan waters of Lake Superior.

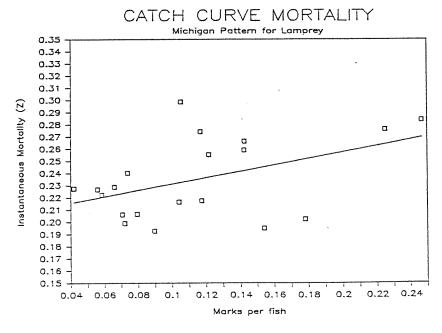


Fig. 13. Correlation analysis of catch curve mortality versus marking for the data in Fig. 12. Estimated and true values of probability of survival were 0.79 and 0.8 and estimated and true values of natural mortality were 0.18 and 0.15.

MARKING RATES VS PALOHEIMO MORTALITY

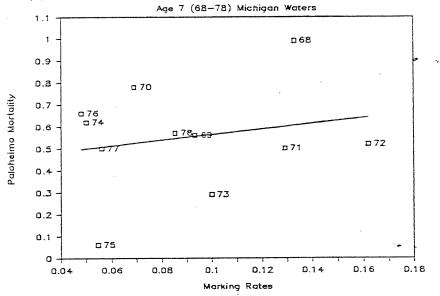


Fig. 14. Correlation of cohort mortality versus marking for age 7 lake trout in Michigan waters of Lake Superior over the period 1968-78.



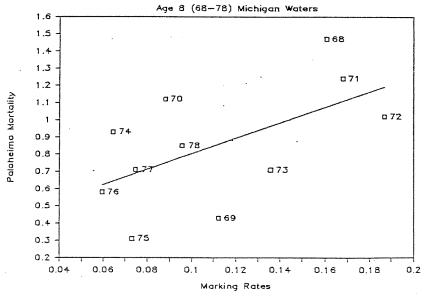


Fig. 15. Correlation of cohort mortality versus marking for age 8 lake trout in Michigan waters of Lake Superior over the period 1968-78.

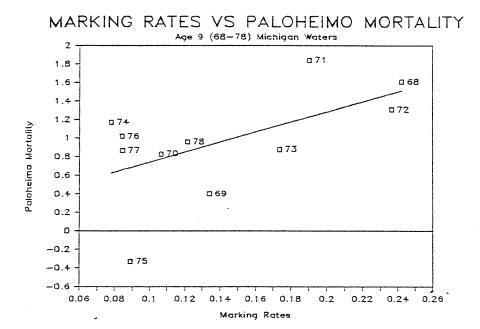


Fig. 16. Correlation of cohort mortality versus marking for age 9 lake trout in Michigan waters of Lake Superior over the period 1968-78.

lake trout in Lake Superior seem to be in the range of 0.14 to 0.44. I believe these results tend to invalidate the descriptions of attack lethality in the workshop models. The corrections suggested in Koonce and Pycha (MSa) seem to be appropriate.

Formulation of an IMSL Analysis Model

BACKGROUND. I derived the current version of IMSL from the Integrated Pest Management Workshop Model (Spangler and Jacobson 1985). Modifications included revision of the description of attack lethality in the parasitic phase submodel, revision of lake trout growth in the lake trout submodel, and correction of structural errors in the ammocete submodel. The full listing of IMSL is in Appendix C. As with the other workshop models, IMSL requires merger with a version of SIMCON. In this case, code and SIMCON version are compatible with BASICA for an IBM PC or similar computer.

Concerning attack lethality, the workshop models (Koonce et al 1982; and Spanger and Jacobson 1985) assumed that probability of surviving an attack increased to 1.0 as the ratio of lake trout to lamprey weight approached 40:1. Growth of parasitic phase lamprey was assumed to occur over two seasons. Both of these assumptions were modified in IMSL. Average size of parasitic phase lamprey became a function of host density:

$$P9=QR*P8/(P8+PQ)$$
,

where QR is the maximum mean size (0.2 kg), PQ a constant, and

$$P8 = PN(I)*PY*QN(I)/{1 + PN(I)*PY*QN(I)},$$

where PY is the mean handling time (10 days), QN(I) is density of prey I, and PN(I) is the effective search rate for prey I. Attack survival depended on the ratio of sea lamprey to lake trout size, but was limited to a maximum value:

$$QB_i = QMAX*(1 - PR^2 / (PR^2 + QA)),$$

where QMAX is the maximum attack survival probability, PR is the ratio of sea lamprey weight to prey weight of age i, and QA is a constant.

Growth of lake trout in Spangler and Jacobson (1985) was exponential at all ages. Retaining the same dependence of growth

rate on stock density and Walford description of growth, I modified IMSL to treat growth of lake trout for two different age groups:

1) Age 3 and Under:

$$w_k = 0.20 - 0.1*10^{-4}*SS$$

 $r = 3.00 - 0.15*10^{-4}*SS$

2) Age 4 and over:

$$w_k = 1.3 - 0.5*10^{-4}*SS$$

 $r = 0.9 - 0.15*10^{-4}*SS$

where r is the growth rate coefficient and w_k the intercept coefficient in the Walford plot, and SS is the stock density in metric tons. The only other modification of the lake trout submodel was to assume that scars disappeared at a rate of 10% per year.

The Ammocete and Transformer Submodel in Spanger and Jacobson (1985) had a persistent structural error. Inability to find this error resulted in a much simplified description of ammocete dynamics in Appendix D of Spangler and Jacobson (1985). The structural error appeared to be in line 5630 of the original code. This code incorrectly updated ammocete density following treatment and resulted in maximum densities—requiring continual treatment. The following code replaced line 5360:

where CFT(I,K) is the proportion of habitat K treated in $I\underline{th}$ year following the last chemical treatment.

RESULTS. To illustrate the usefulness of IMSL, I would like to address two issues: the wounding/scarring ratios at high lethality and the evaluation of trade-offs between lamprey control and fisheries management.

As discussed above, a criticism of the estimates of high lethality of attack by sea lamprey is that it seems inconsistent

with high scarring rates. Fig. 17 illustrates the relationship between scarring and marking assuming a mean attack lethality of 0.75. The simulation began assuming that lake trout were unmarked, and I assumed that scars would disappear at a rate of 10 percent per year. Under these conditions, marks stabilized at about .02 marks per fish, but scars had not yet equilibrated at 0.2 scars per fish. Thus high scarring is not inconsistent with high lethality of attack.

Because the lake trout management plans provide specific goals for rehabilitation, the model can evaluate the relative contributions of various actions to the achievement of the goal. The original models provided many possible trade-offs, and I will focus on three as an example. Assuming that sea lamprey control is primarily constrained by budget, I will represent lamprey control trade-off by the detection threshold used to decide on treatment of a stream; as detection threshold increases there is a short term savings on chemical. The primary trade-offs in fishery management are stocking and fishery regulation. Figs. 18 and 19 summarize two indicators of the following trade-offs:

Policy	Detection Threshold	Stocking (millions)	Fishing Mortality
Baseline	0.001	1.0	0.4
CLRED	0.005	1.0	0.4
STRED	0.001	0.5	0.4

The stocking and baseline policies have the same effect on marking rates (Fig. 18), but decreased stocking causes lake trout biomass to decline (Fig. 19). In contrast, decreasing lamprey control causes dramatic increases in marking and a moderate drop in lake trout biomass.

CONCLUSION

Pursuit of Integrated Management of Sea Lamprey will require some type of computer aid to facilitate the analysis of policy options. The Adaptive Environmental Assessment and Management Workshops provided a demonstration of the feasibility of developing such aids, and I believe that subsequent work has enhanced the technical credibility of the models. What is needed now is a case study to attempt a trial implementation of IMSL. This will require a policy statement by the GLFC and application of this model to a specific lake. Ideally, the application should be for one of the lower lakes, e.g. Lake Erie or Lake Ontario, where tests of the model will be more stringent.

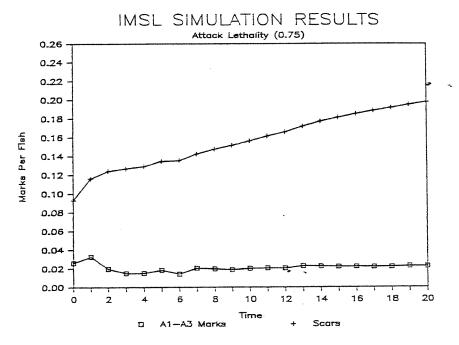


Fig. 17. Dynamics of scarring and marking for age 10 lake trout simulated by the simulation model IMSL.

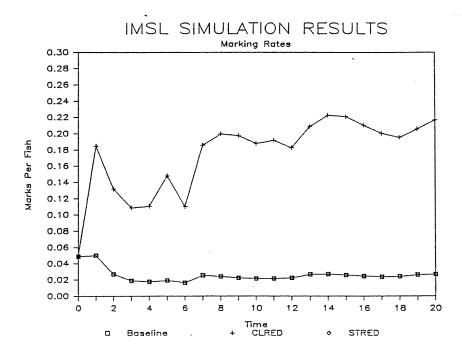


Fig. 18. Dynamics of marking simulated by IMSL for three different policies. Details of policies are in text.

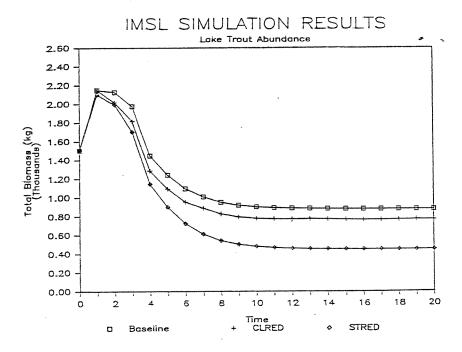


Fig. 19. Dynamics of lake trout biomass simulated by IMSL for three different policies. Details of policies are in text.

LITERATURE CITED

- Farmer, G. J. 1980. Biology and physiology of feeding in adult lampreys. Can. J. Fish. Aquat. Sci., 37: 1751-1761.
- Eshenroder, R. L. and J. F. Koonce. 1984. Recommendations for standardizing the reporting of sea lamprey marking data. Great Lakes Fish. Comm., Spec. Publ. 84-1. 21p.
- Kitchell, J. F. and J. E. Breck. 1980. Bioenergetics model and
 foraging hypothesis for sea lamprey (Petromyzon marinus).
 Can. J. Fish. Aquat. Sci. 37: 2159-2168.
- Koonce, J. F., L. A. Greig, B. A. Henderson, D. B. Jester, C. K. Minns, and G. R. Spangler. 1982. A review of the adaptive management workshop addressing salmonid/lamprey management in the Great Lakes. Great Lakes Fish. Comm., Spec. Publ. 82-2. 57p.
- Koonce, J. F. and R. L. Pycha. MSa. Observability of lake trout mortality due to attacks by sea lamprey.
- Koonce, J. F. and R. L. Pycha. MSb. A simple protocol to estimate relative abundance of sea lamprey from lake trout assessment data in Lake Superior.
- King, L. E. and T. A. Edsall. 1979. Illustrated field guide for the classification of sea lamprey attack marks on Great Lakes lake trout. Great Lakes Fish. Comm., Spec. Publ. 79-1. 41p.
- Pycha, R. L. 1980. Changes in mortality of lake trout (Salvelinus namaycush) in Michigan waters of Lake Superior in relation to sea lamprey (Petromyzon marinus) predation. 1968-1978. Can. J. Fish. Aquat. Sci., 37: 2063-2073.
- Pycha, R. L. and G. R. King. 1975. Changes in the lake trout population of southern Lake Superior in relation to the fishery, the sea lamprey, and stocking, 1950-70. Great Lakes. Fish. Comm. Tech. Rept. 28. 34p.
- Spangler, G. R. and L. D. Jacobson [eds.]. 1985. A workshop concerning the application of integrated pest management (IPM) to sea lamprey control in the Great Lakes. Great Lakes Fish. Comm. Spec. Publ. 85-2. 97 p.

- Pycha, R. L. 1980. Changes in mortality of lake trout
 (Salvelinus namaycush) in Michigan waters of Lake Superior in
 relation to sea lamprey (Petromyzon marinus) predation.
 1968-1978. Can. J. Fish. Aquat. Sci., 37: 2063-2073.
- Youngs, W. D. 1980. Estimate of lamprey-induced mortality in a lake trout (Salvelinus namaycush) population. Can. J. Fish. Aquat. Sci. 37: 2151-2158.