GREAT LAKES FISHERY COMMISSION

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Integration of Sea Lamprey Functional Response Model and Lake Trout Stock Assessment Models for Lake Superior and Lake Huron

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Report of Progress - June 1997

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INTRODUCTION

The Great Lakes Fishery Commission, in order to help meet its defined goals of sea lamprey management (*Petromyzon marinus*), established a Management Protocol for the Integrated Management of Sea Lamprey (IMSL) in the Great Lakes Basin. This protocol establishes procedures for determining and setting optimal sea lamprey control targets for each of the five Great Lakes. A key component of IMSL is that it is an adaptive management protocol, and the protocol can be revised and improved as the understanding of sea lamprey dynamics are improved. In the following report we explore one area of sea lamprey and lake trout interactions, with a view toward improving some of the tools implemented by the IMSL protocol.

A portion of the IMSL protocol deals with the determination of sea lamprey-induced mortality on lean lake trout (*Salvelinus namaycush*), as well as other species, as a function of sea lamprey abundance. By determining the number of attacks on a given length class of lake trout, mortality can be determined by utilizing the probability of surviving a sea lamprey attack. These mortality rates are then used in setting management objectives. These mortality rates are determined by applying the IMSL functional response model, taking into account host (e.g., lake trout) and sea lamprey abundance. A functional response (Solomon 1949, Holling 1959) describes the relationship between prey density and the number of prey attacked per predator.

A second use of sea lamprey-induced mortality rates are in age-structured population dynamic models for lake trout. Currently, mortality rates are estimated using wounding data collected in lake trout assessments (Eshenroder and Koonce 1984), and are not functions of sea lamprey densities. By validating the sea lamprey attack model, an accurate functional response model can be integrated into lake trout catch-at-age models. This integration is important for two main reasons. First, observed sea lamprey wounding data are noisy and subject to observation error. Better estimates of sea lamprey-induced mortality could be obtained by integrating prior expectations based on an attack model and estimates of sea lamprey and lake trout abundance with the wounding data. Second, internal consistency in estimation will be enhanced. The IMSL protocol makes use of sea lamprey induced mortality rates that are produced by applying the functional response model to estimates of lake trout abundance. These lake trout abundance estimates come from lake trout models that themselves assume different levels of sea lamprey-induced mortality based on wounding data. Ultimately, a functional response model is required by the IMSL protocol for future forecasts, so it is not an option to rely solely on wounding data. Our approach will lead to internal consistency between the functional response model and its assumptions and overall patterns in observed wounding and other information on lake trout population dynamics.

This report focuses on work done in an attempt to validate the IMSL attack model. By comparing wounding data from Lake Superior and Lake Huron to the IMSL model, an effort has been made to calibrate the current IMSL model, as well as introduce an alternate model describing observed wounding rates. This information can then be used as a foundation for further work on the sea lamprey/lake trout functional response model, which in turn can strengthen sea lamprey control and lake trout restoration programs and procedures.

METHODS

Data for the study came from spring gill net surveys conducted by the Michigan Department of Natural Resources (Peck and Schorfhaar 1991, Johnson and VanAmberg 1995). The Lake Superior data cover statistical districts MI-3 to MI-7, from the years 1988 to 1995. Data used for Lake Huron are for the years 1984-1996, and consist of samples from districts MI-1 to MI-5. The Lake Superior data consist of 29,760 records of wounding on individual fish, while the Lake Huron data consist of 10,848 similar records. Data recorded included length of fish, district caught, year caught, and number of A1-A3 lamprey wounds observed (King 1980). Lake Huron fish were measured in millimeters, while the Lake Superior fish were measured in inches and converted to millimeters, and only fish greater then 432 mm in length were used in the analysis.

The data was first fit to the multi-species disc equation, predicting the number of attacks per prey class, presented in the IMSL Protocol Manual (Greig et al 1992). This model is represented by

$$A(l)_{prey} = \frac{S \times E(l) \times L}{1 + \sum_{prey} H \times E(l) \times N_l} \qquad \textbf{(1)}$$

where S is the length of feeding season, L the abundance of parasitic lamprey, H the mean attack duration and N_l the number of prey at length l. The function $E(l)$ is the effective search rate of sea lamprey as a function of prey length and is derived mechanistically as

$$E(l) = O \times S(l) \times R(l) \times P(l) \qquad \textbf{(2)}$$

where O is the habitat overlap, a function of prey type. Also, $S(l)$ is the search rate, $R(l)$ is the reactive area, and $P(l)$ is probability of attack, all functions of prey length.

The denominator of equation (1) is a constant over all prey lengths for a given area and year since the summation is over all prey types and prey lengths available to sea lamprey. Since S and L are also constant over prey length, equation (1) can be divided by N_l to determine the number of attacks per fish of length l, or $A(l) = \theta_I E(l)$, where θ_I is the IMSL specific constant described above. To convert attack rates to observed wounding rates, $A(l)$ can be multiplied by the probability of surviving a sea lamprey attack, $P_s(l)$, a function of prey length determined in laboratory experiments (Swink 1990). Therefore, predicted wounds-per-fish from the IMSL model can be expressed as $W_I(l) = P_s(l)\, \theta_I(l)\, E(l)$, with values for $P_s(l)$ given in table 1. The value of $E(l)$ can be calculated from the values of the parameters in Greig, et al., and leads to the expression for $W_I(l)$ given in equation (3). This form of the IMSL model can then be fit to the available data, estimating the constant θ_I to take in to account changing lake conditions, such as sea lamprey and lake trout population levels.

$$W_I(l) = \frac{\theta_I P_s(l)\ 1.39 \times 10^{-9}\ l^5}{62500 + l^2} \qquad \textbf{(3)}$$

Length	Probability of survival
< 432 mm	0 %
432-533 mm	35 %
533-635 mm	45 %
>635 mm	55 %

Table 1 Probability of surviving a sea lamprey attack (Swink 1990).

An alternative to the IMSL attack model is a three parameter logistic model (equation (4)). This model was chosen due the quality of fit to the given data, as opposed to a model based on mechanistic or biological processes. The parameter α describes the shape of the curve, while β transforms the curve along the length axis, while the asymptotic height of the logistic model is described by θ_L, and can be varied to take into account region and year effects. The θ_L parameter is equivalent to the marking rate of large fish in the system.

$$W_L(l) = \frac{\theta_L}{1 + e^{-\alpha(l-\beta)}} \quad \textbf{(4)}$$

All model fits reported here were obtained using maximum likelihood techniques. For a given prey length, there are multiple lake trout observations with varying number of observed wounds. The distribution of these wounds is assumed to be described by a Poisson distribution. The Poisson distribution has a single parameter, which corresponds to the average number of observed wounds-per-fish for a given size. This parameter can be varied as a function of length, and the best fit is achieved when the likelihood

$$\prod_i^n \frac{e^{-\mu(l_i)} \mu(l_i)^{w_i}}{w_i!} \quad \textbf{(5)}$$

is maximized, where n is the number of observations and w_i and l_i are the number of wounds on and the length of fish i, respectively. The function describing the mean as a function of length, $\mu(l)$, can be either of the models described above (equations (3) or (4)). Analysis and model fitting is simplified when the natural log of equation (5) is taken, resulting in a summation. The parameters of these models are adjusted to maximize equation (5) using the computer application Gauss' maximum likelihood package. Statistical and residual analysis were conducted using Mathematica.

Our analyses to date have treated all parameters equally, using standard numerical methods to search for the suite of parameter values that maximizes the likelihood. The models we have developed that incorporate effects due to both years and regions are time consuming to fit, even when using special purpose software and a multi-processing Unix computer. In the future we may want to build yet larger models as we add years and potentially combine analyses across lakes. We may also need to conduct simulations to assess uncertainty, which will further increase our computational needs. Fortunately, substantial increases in speed of fitting the models may be possible by adapting methods based on the generalized linear model. This is so because most of the parameters in these larger models (all region and year effects) enter multiplicatively (McCullagh and Nelder 1989). We are now exploring this possibility.

RESULTS

Using the maximum likelihood procedure, a value of θ_I was estimated by fitting the IMSL model to both the Lake Superior and Lake Huron data sets (table 2). Parameter estimates for the logistic model are in table 3. Models were fit over all years and districts.

	θ_I	Log-Likelihood
Lake Superior	0.4539 (.0112)	-6282.81
Lake Huron	0.9293(.0212)	-5569.96

Table 2: IMSL model parameter estimates, asymptotic standard errors in parentheses.

	α	β	θ_L	Log-Likelihood
Lake Superior	0.0210 (.0012)	629.813 (8.7804)	0.2436 (.0198)	-5655.71
Lake Huron	0.0205 (.0147)	584.990 (6.8964)	0.3451 (.0147)	-5094.13

Table 3: Logistic model parameter estimates, asymptotic standard errors in parentheses.

A full evaluation of model fit based on direct examination of residuals of the above models is not possible, given the noise in the data. Therefore, a moving average is used to smooth the data. Observations contained in four length bins to the left and four length bins to the right of a given length, as well as observations for that length, are used to obtain the average number of wounds-per-fish for a given length. The moving average is then plotted against the fitted model's predicted number of wounds only when four or more observations are used in computing the observed average number of wounds. Plots of the IMSL model predictions against the moving averages can be seen in figures 1 and 2, while a similar plot for the logistic model is shown in figures 3 and 4.

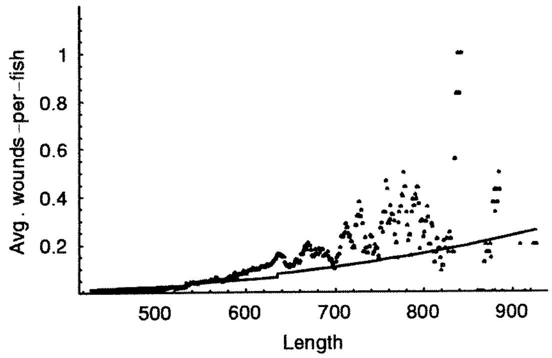

Figure 1: IMSL model, Lake Superior.

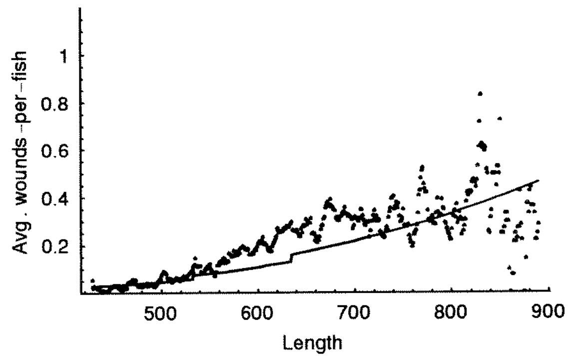

Figure 2: IMSL model, Lake Huron.

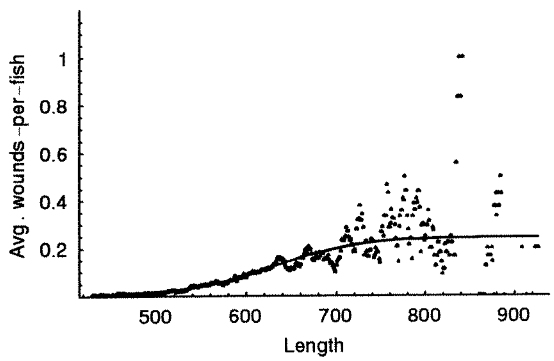

Figure 3: Logistic model, Lake Superior.

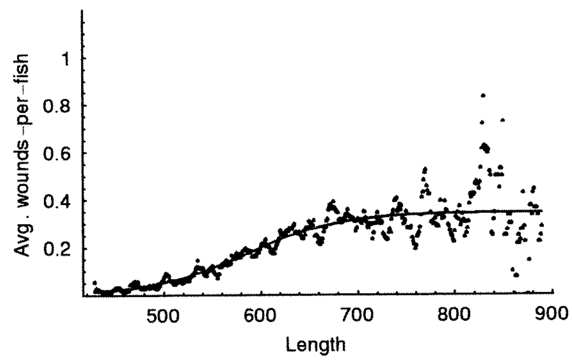

Figure 4: Logistic model, Lake Huron.

Avg with FN at level

The above models were fit to lake wide data sets regardless of year. Parameters that affect wounding rates, however, may not be constant over the years, or across regions. For example, lake trout and sea lamprey population abundances can fluctuate. In order to determine if these effects are present, moving averages of the data for a specific year or district are plotted against predicted values from the logistic model given in table 3.

Figure 5 shows the moving average of wounds per fish for 1994 in Lake Superior for all statistical districts. This plot shows mean wounding rates per fish across Lake Superior for this year to be less then the average for all years. A similar result is shown for statistical district MI-7, figure 6, where mean wounds-per-fish are greater then for all districts combined over all years. Similar trends can be shown for other year and districts in Lake Superior as well as Lake Huron.

We added year or region effects to the logistic model by estimating a value of θ_i for each year across all districts, and for each district across all years, as well as new values for α and β. Results with year effects can be seen in table 4 for Lake Superior, and in table 5 for Lake Huron. Region effects were also calculated, with the results for Lake Superior in table 6 and for Lake Huron in table 7.

Lake Superior Logistic Model	
θ	All districts
1988	0.0921 (.0141)
1989	0.4941 (.0540)
1990	0.3698 (.0416)
1991	0.3031 (.0354)
1992	0.2636 (.0355)
1993	0.2631 (.0324)
1994	0.1019 (.0181)
1995	0.1279 (.0181)
α	0.0214 (.0013)
β	633.17 (10.4173)
Log-likelihood	-5429.24

Table 4: Lake Superior logistic model with year effects.

Lake Huron Logistic Model	
θ	All districts
1984	0.0637 (.0104)
1985	0.5019 (.0307)
1986	0.2778 (.0258)
1987	0.3662 (.0311)
1988	0.2443 (.0258)
1989	0.3139 (.0301)
1990	0.4602 (.0361)
1991	0.3019 (.0345)
1992	0.3271 (.0297)
1993	0.5137 (.0501)
1994	0.4209 (.0384)
1995	0.4756 (.0460)
1996	0.3786 (.0382)
α	0.0200 (.0014)
β	586.70 (7.0570)
Log-likelihood	-4291.44

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Table 5: Lake Huron logistic model with year effects.

Lake Superior Logistic Model	
θ	All years
MI-3	0.2372 (.0239)
MI-4	0.2080 (.0188)
MI-5	0.1365 (.0133)
MI-6	0.2649 (.0244)
MI-7	0.3947 (.0380)
α	0.0220 (.0013)
β	618.28 (8.4583)
Log-likelihood	-5572.41

Table 6: Lake Superior logistic model with district effects.

Lake Huron Logistic Model	
θ	All years
MI-1	0.6069 (.0942)
MI-2	0.5284 (.0385)
MI-3	0.3959 (.0252)
MI-4	0.3237 (.0158)
MI-5	0.2590 (.0483)
α	0.0202 (.0013)
β	602.06 (7.5007)
Log-likelihood	-5060.31

Table 7: Lake Huron logistic model with district effects.

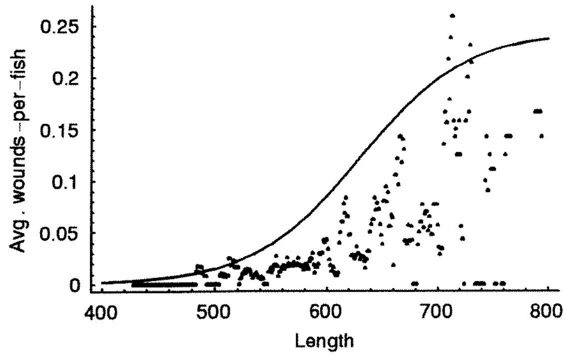

Figure 5: Lake Superior logistic model, fit to all years, compared to 1994 (all districts).

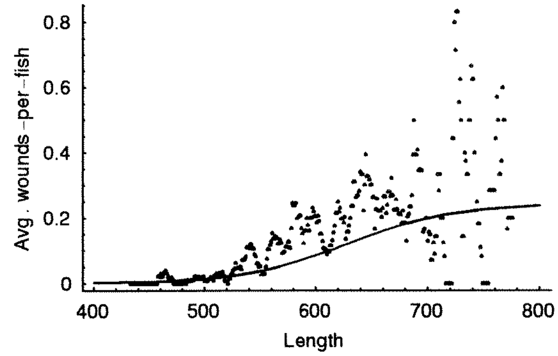

Figure 6: Lake Superior logistic model fit to all districts, compared to MI-7 (all years).

These results indicate marked changes in mean wounds-per-fish across time and areas. For example, attack rates in Northern Lake Huron, MI-1 and MI-2, are much greater then the rest of the lake, which is to be expected. Given the fluctuations in both year and district levels of wounding, a model incorporating both effects simultaneously was created. In this model, a value of θ_L was fit for each year and district, as well as new values for α and β. These results are listed in table 8 for Lake Superior and table 10 for Lake Huron. For comparison, year and region effects were added to the IMSL model, and a θ_I was estimated for each year and district. Results are in table 9 for Lake Superior, table 11 for Lake Huron. It should be noted that due to the large number of parameters, asymptotic standard errors for these models are unavailable, and we are exploring approaches for estimating them.

Lake Superior Logistic Model					
θ	MI-3	MI-4	MI-5	MI-6	MI-7
1988	0.1059	0.0628	0.0359	0.1801	0.1447
1989	0.2403	0.3907	0.4201	0.8098	0.6639
1990	0.2416	0.2235	0.2309	0.5415	0.8029
1991	0.3286	0.2096	0.1316	0.3603	0.5074
1992	0.7624	0.3045	0.1262	0.2210	-
1993	0.5694	0.3252	0.1158	0.1946	0.3416
1994	0.0928	0.1786	0.0692	0.0885	0.0553
1995	0.2251	0.1573	0.0386	0.0642	0.3286
α	0.0214				
β	627.20				
Log-Likelihood	-5254.57				

Table 8: Lake Superior logistic model with year and district effects.

Lake Superior IMSL Model					
θ	MI-1	MI-2	MI-3	MI-4	MI-5
1988	0.2501	0.1384	0.0822	0.4179	0.3701
1989	0.6287	0.8381	1.0407	2.0312	1.6715
1990	0.5344	0.4836	0.5811	1.3180	2.2077
1991	0.7971	0.4338	0.3063	0.8981	1.3306
1992	1.8451	0.7057	0.3025	0.5238	-
1993	1.4928	0.8402	0.3058	0.4830	0.9357
1994	0.2650	0.4869	0.1906	0.2371	0.1756
1995	0.5990	0.4002	0.1052	0.1591	0.8408
Log-likelihood	-5361.20				

Table 9: Lake Superior IMSL model with year and district effects.

Lake Huron Logistic Model					
θ	MI-1	MI-2	MI-3	MI-4	MI-5
1984	0.0931	0.0535	0.0646	0.0751	-
1985	1.4616	1.1957	0.5235	0.4173	-
1986	0.4319	0.6658	0.2420	0.2504	-
1987	0.1371	0.3381	0.5094	0.3959	-
1988	0.0073	0.2682	0.2894	0.2508	-
1989	1.1570	0.5844	0.3636	0.2675	-
1990	-	0.8257	0.4963	0.4455	-
1991	0.0011	0.3014	0.3388	0.3304	-
1992	0.0004	0.4886	0.5469	0.2849	-
1993	4.2341	0.5777	0.6338	0.4963	-
1994	0.3280	0.5331	0.3746	0.4533	-
1995	1.2987	0.9886	0.7744	0.2179	0.1811
1996	0.1920	0.3636	0.6791	0.4464	0.3294
α	0.0210				
β	601.84				
Log-likelihood	-4819.09				

Table 10: Lake Huron logistic model with year and district effects.

Lake Huron IMSL Model					
θ	MI-1	MI-2	MI-3	MI-4	MI-5
1984	0.2483	0.1541	0.2292	0.2685	-
1985	3.1689	3.5578	1.9572	1.4589	-
1986	0.8628	1.9986	0.8800	0.8723	-
1987	0.4126	1.1809	1.7786	1.4379	-
1988	0.0591	0.7482	0.9730	0.9191	-
1989	2.3308	1.9332	1.1304	0.9890	-
1990	-	2.6071	1.8442	1.5961	-
1991	0.0128	1.1224	1.1573	1.1042	-
1992	0.0038	1.6972	1.8723	0.9291	-
1993	7.7166	1.9315	2.1379	1.5872	-
1994	0.6424	2.0115	1.3478	1.5278	-
1995	3.2706	3.2575	2.5384	0.7459	0.6013
1996	0.3725	1.1905	2.3606	1.3882	1.1556
Log-likelihood	-4873.46				

Table 11: Lake Huron IMSL model with year and district effects.

Visual comparison of the IMSL model (figures 1 and 2) to the logistic model (figures 3 and 4) indicates a significantly better fit for the three parameter model described in equation (4). Improvements in the fit of a model were tested using a likelihood ratio statistic (Seber and Wild 1989), $2(L_{new} - L_{base})$, where L_{new} is the log-likelihood of the "improved model"with added parameters and L_{base} the log-likelihood of the baseline model you wish to compare the improved model to. The likelihood ratio statistic was compared with the Chi-square distribution on r degrees of freedom, where r equals the number of parameters in L_{new} minus the number of parameters in L_{base}. For Lake Superior, the logistic model fits significantly better then the IMSL model (LR=1254.2, P<.001), and this was also true for Lake Huron (LR=951.7, P<.001). It can therefore be concluded that the proposed logistic model has a significantly better fit than the IMSL model.

An examination of the residuals of observed average wounds-per-fish against the logistic model for Lake Superior, figure 7, shows that for length classes below 700 mm, the logistic model fits reasonably well. For length classes above 700 mm, the variance of the residuals increases as a function of length due to a decrease in sample size. The residuals for Lake Huron, figure 8, show a similar result of increasing variance with increasing length. Marking is generally more prevalent in Lake Huron, so there is less of a tendency for length classes to have zero observed wounds and hence the "horizontal line" of residuals seen in figure 7 is absent from figure 8. For both lakes, the magnitude of the residuals are skewed positively, as would be expected for the assumed Poisson distribution.

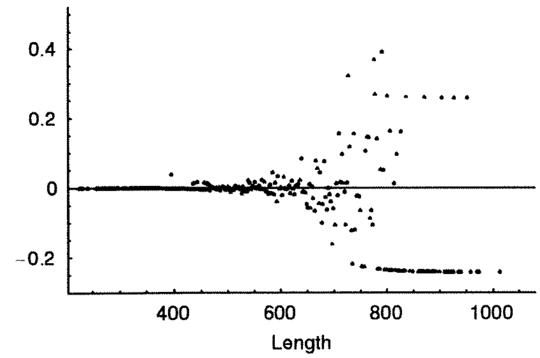

Figure 7: Lake Superior logistic model residual plot, all years and districts.

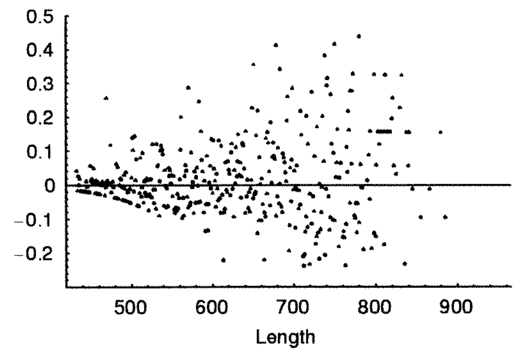

Figure 8: Lake Huron logistic model residual plot, all years and districts.

The addition of year and area effects to the model result in significant increases in log-likelihoods, and better fits. Figure 9 shows data from the year 1994 in Lake Superior, with a year specific value of θ_L from table 4. Compared to figure 5 above, the year specific logistic model fit is considerably better. Statistical evidence for a better fit comes from comparing the base logistic model to the year effect logistic model for Lake Superior (LR=452.9, P<.001) and Lake Huron (LR=345.4, P<.001). An example of the statistical district model results can be seen in figure 10, which contains the same data from MI-7 in Lake Superior used in figure 6, with logistic model parameters from table 6. This improvement in fit is again verified using the likelihood ratio statistic on Lake Superior (LR=166.6, P<.001) and Lake Huron (LR=67.7, P<.001).

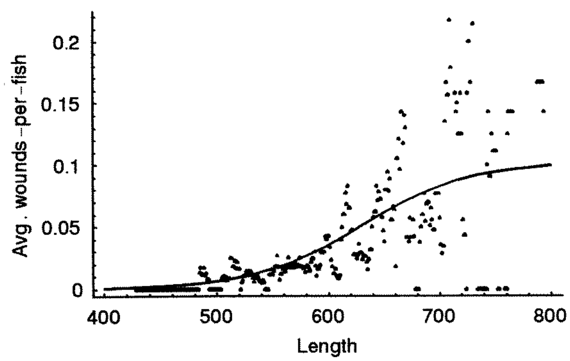

Figure 9: Lake Superior year specific logistic model for 1994 (all districts).

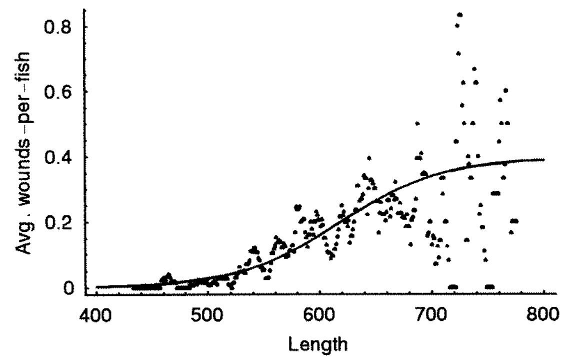

Figure 10: Lake Superior district specific model for MI-7 (all years).

Given the significant effects on fit from the year specific and statistical district specific models, it is reasonable to expect that a model considering the effects of years and regions simultaneously would further improve fit. For the Lake Superior wounding data, the joint model fit significantly better then the year (LR=349.3, P<.001) or district specific models (LR=635.7, P<.001). For Lake Huron we obtained similar results in comparison with the year-specific (LR=550.1, P<.001) and district-specific models (LR=550.1, P<.001). The IMSL model was also fit with a year and district specific model, but the year and district specific logistic model fit significantly better for both lake Superior (LR=213.26, P<.001) and Lake Huron (LR=108.74,

LR?

P<.001).

We found it difficult to observe trends in the residuals from the year and district specific model using millimeter length bins. As shown above, the smaller the sample size, the more difficult it is to analyze the residuals due an increase in the variance. When the wounding data is subdivided among year and districts, small sample sizes are common and an examination of the residuals on a year/district scale is not very helpful when analyzing the model for lack of fit.

Our approach to this difficulty was to (1) divide the raw wounding data into centimeter length bins, (2) calculate the average wounds-per-fish in the centimeter length bins, and (3) calculate a "centimeter residual" based on the length, in centimeters, of fish in a given length bin. These centimeter residuals were then plotted versus length, and to further reduce variation we also calculated the average (over years and districts) centimeter residual for each length bin and plotted these versus length. Results for Lake Superior are in figure 11. For lengths greater then 700 mm, small sample sizes are common, hence we restricted the analysis of residuals to fish smaller than this 700 mm cutoff, figure 12. Overall fit is generally good, although for the greater length bins fit is difficult to evaluate.

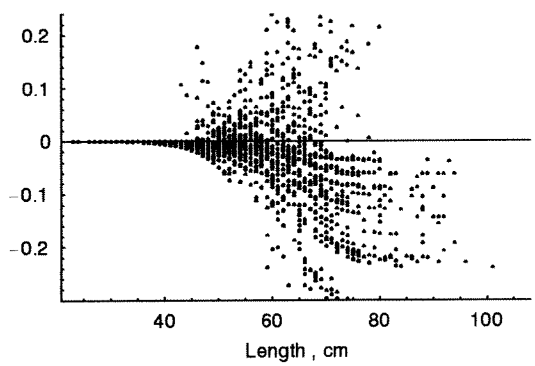

Figure 11: Lake Superior logistic model residual plot, using centimeter residuals, for year and district specific model.

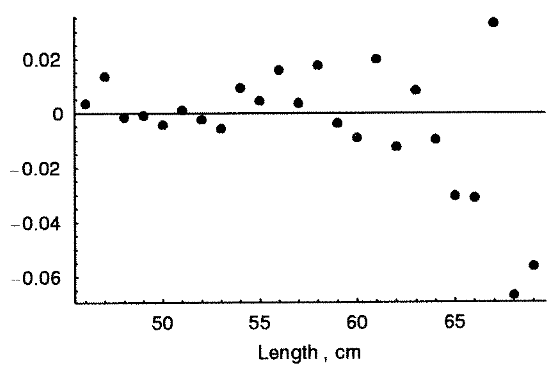

Figure 12: Lake Superior logistic model average (over years and districts) residual plot, using centimeter residuals, for year and district specific model.

The Lake Huron data set has approximately a third as many observations as the Lake Superior Data set. The centimeter residuals show patterns similar to those shown for Lake Superior (figure 13). The Lake Huron data includes observations from a wider range of length classes. When the subset of lengths less then 750 mm is examined, the average centimeter residual for a given length bin (figure 14) demonstrates an increasing variance in the residuals as length increases, but there is no trend of negative residuals as in the Lake Superior data. Hence the logistic model fit well for larger size classes when sufficient data to support an evaluation are available. The difference in absolute magnitude in residuals between the Lake Superior and Huron can be attributed to the smaller size of the Lake Huron data set.

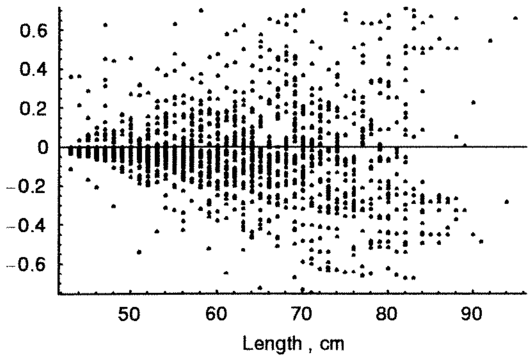

Figure 13: Lake Huron logistic model residual plot, using centimeter residuals, for year and district specific model.

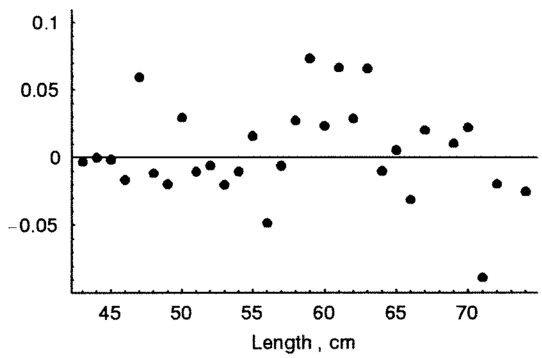

Figure 14: Lake Huron logistic model average (over years and districts) residual plot, using centimeter residuals, for year and district specific model.

We conclude that the three parameter logistic model, equation (4), fits the observed wounding data fairly well. The basis for our conclusion is in comparison with the IMSL model, the logistic model does a much better job of modeling how average wounds-per-fish increases with fish size for smaller fish. The logistic model also models the apparent leveling off of wounding rates for large length classes seen in the data, which is beyond the capabilities of the IMSL model. A comparison of the values of θ_L between Lakes Superior and Huron indicates that higher maximum wounding rates are occurring in Lake Huron, which is to be expected, given the contribution of the St. Mary's River and the larger sea lamprey population in Lake Huron. There are anomalously low values of θ_L for some years in northern Lake Huron. We suspect there are years when the number of observations of large lake trout are insufficient to estimate the true asymptote. We intend to explore these estimates further as we attempt to estimate uncertainty associated with these parameters.

ADDITIONAL ACTIVITIES RELATED TO MODEL BUILDING

We participated in a variety of activities in addition to building models and analyzing data as described above. These activities were designed both to provide us with additional information to aid in the work reported on here and to provide assistance to the Commission. We also report on activities that are not specifically part of this project, but for which this project provided important background information and knowledge. Michael Rutter attended the Sea Lamprey Marking Workshop (April 22-23, 1997, Lake Huron Biological Research Station). The purpose of the workshop was to learn about the consistency of how different individuals and agencies report sea lamprey wounds and to improve the consistency of this reporting. Our participation was important because our project relies critically on interpretation and validity of the wounding data. In an activity related to, but not part of this proposal, Jim Bence is participating as a member of the Panel reviewing the Commission's adult sea lamprey assessment program. His activities in the project reported on here provided important background information for that task. Michael Rutter also attended the plenary session of the Panel's initial meeting (May 28, 1997, Ann Arbor Michigan). Jim Bence worked together with Shawn Sitar (USFWS) and Gavin Christie (GLFC) to develop projections of lake trout mortality and how these would change in response to changes in sea lamprey control on the St. Mary's River. Jim Bence attended the Lake Huron Committee's annual meeting in Ann Arbor (March 18-19, 1997) at Gavin Christie's request to provide technical support and background for the Committee's deliberations on treatment strategies for the St Mary's River. Michael Rutter also attended the Lake Huron and Lake Superior Meetings, and the Sea Lamprey Research Workshop (February 12-13, 1997, Romulus) sponsored by the GLFC for informational purposes.

DISCUSSION

The IMSL sub model relating wounding rates to lake trout size (equation (1)) does not do a good job of predicting observed wounding rates, given the current values of model parameters. While we estimated more parameters for the logistic model then the IMSL model, three versus the one scaling parameter for the IMSL model, the IMSL model in fact has more potentially changeable "parameters". When the IMSL model is formulated, six different parameters are used in calculating effective search rate (equation (2)). Although some of these parameters could potentially be varied during fitting, choosing which parameters to manipulate would be difficult, and this would not guarantee a significantly better fit. Furthermore, the proposed logistic model allows for a more accurate prediction of wounding rates, and is more flexible across years, statistical districts, and lakes.

The area and year specific estimates provide a single measure for each place and time of the intensity of sea lamprey attacks. Together with the functions relating wounding rates to lake trout size (constant in shape over areas and years) and estimates of the probability of surviving an attack, these parameters can be used to generate values for sea lamprey induced mortality for use in lake trout models. As is, these estimates make use of more information and effectively reduce noise associated with sampling variability and small sample sizes, and are in a compact form. As a result they do allow estimates of sea lamprey-induced mortality, where this was not possible when estimates were based on raw wounding rates calculated for larger pooled size classes of lake trout (Sitar 1996). The parameter estimates describing wounding could potentially be improved further by smoothing changes in wounding rates either spatially or temporally.

In order to effectively model the dynamic relationship between sea lamprey and lake trout, it is important to understand the fluctuating levels in attack rates. The work presented above shows definite trends in attack rates over both time and area. The logistic model can also be used to predict attack rates if estimates of the probabilities of surviving an attack rate are used. The next step in creating a sea lamprey/lake trout functional response model is to find relationships between the values of θ_L and sea lamprey and lake population indices of abundance. For example, a cursory look at estimated levels of parasitic phase sea lamprey in Lake Superior and Lake Huron show the same trends over time as do table 4, the Lake Superior year specific model, and table 5, the Lake Huron year specific model. This is especially evident for Lake Huron in 1993, when a large increase in the parasitic sea lamprey population was estimated, and a similar year effect was estimated here (Gavin Christie, personal communication).

Future work on creating a valid functional response model for sea lamprey will be done by examining wounding data for years previous to 1988 in Lake Superior and 1984 in Lake Huron using the above techniques. Although some of the statistical districts used above have lake trout population estimates, further work will be needed to have a complete set of lake trout estimates. This information, combined with sea lamprey abundance estimates, will present the opportunity to see if observed wounding rate can be predicted by lake trout and sea lamprey population levels.

Once this relationship is established, a validated sea lamprey/lake trout functional response model will be obtainable. Sea lamprey-induced mortality rates can then be calculated as a function of sea lamprey and lake trout densities, allowing for more accurate estimates for use in lake trout and sea lamprey management. The functional response model will be useful in helping predict future levels of lake trout abundance given different levels of sea lamprey control, as well as offer a gauge for observing changes in sea lamprey attack patterns.

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