GREAT LAKES FISHERY COMMISSION

1982 Project Completion Report[1]

Lamprey Wounding Standardization

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LAMPREY WOUNDING STANDARDIZATION

CONVERSION OF ATTACK RATE TO WOUNDING RATE AND MORTALITY

The model developed for the Salmonid/Lamprey workshop (Koonce et al 1982) only calculated attack rates of lamprey on various species and the subsequent mortality. Assessment data for the Great Lakes, however, measures wounds in various stages of healing. To make the lamprey attack model in the workshop model compatible with assessment data, it is necessary to derive a relationship between attack rates and observed wounding rates. The following derivation is based on several assumptions:

1. The probabililty of death due to an attack is independent of any other attack or attack history;
2. Attacks are independent events; and
3. The distribution of attacks per fish is Poisson.

Little evidence is available to judge the validity of the first two assumptions. The third assumption appears consistent with available data (see Appendix 1) and various theoretical notions associated with similar host-parasitoid problems (cf. Smith 1968). The basic relationship between attack rate is thus

$$\exp(M)=1 + S*(1 - \exp(A)), \qquad (1)$$

where M is the average number of wounds per fish that occur in a year (coresponding to stages A1-A3), A is the mean number of attacks per fish during the year, and S is the mean survival of individuals in the population. Survival, of course, is a function of attack rate and the probability of surviving any single attack (p):

$$S = \exp(-A*(1-p)). \qquad (2)$$

Derivation of these relationships is given in more detail in Appendix 1.

Because equation 1 is non-linear, marking rates do not increase in proportion to attack rates (Fig. 1). The extent of deviation from a 1:1 ratio of marking to attack rates, however, is a function of the probability of surviving a single attack. This fundamental non-linearity between attack and wounding rates results in an apparently non-linear relationship between instantaneous mortality due to lamprey predation and marking rate (Fig. 2). An attack survival probability of 0.25, in fact, seems to have the same exponential form observed by Pycha (1980).

INTERPRETATION OF EXISTING DATA

Statistical Properties of Wound Data

One of the main concerns with existing wounding data is the adequacy of sample sizes to detect important changes in wounding rate. Assuming that wounds per fish is Poisson distributed, it is possible to calculate the sample size required to detect, at a specified significance level, a given change in wounding:

$$n = ((Za*sqr(2*Mc)+Zb*sqr(Mc+Mt))/(Mt-Mc))^2$$

where Za is the standard normal Z deviate for the desired alpha error (taken as 1.96 here, alpha/2 = 0.025), Zb is the Z deviate for the beta error (taken as 1.64 here, beta = 0.05), Mc is the observed wounding rate, and Mt is the wounding rate for a specified difference.

The sample size required to detect a specified change is clearly a function of the observed wounding rate. For a range of 50% to 200% change in wounding rate, low wounding rates require higher sample sizes than higher wounding rates (Fig. 3). As one might expect, this situation is reversed for fixed changes in wounding rate (Fig. 4). Because wounding rates are ultimately measures of the effectiveness of lamprey control, however, knowing the sample sizes necessary to detect changes in survival of Lake Trout might be more important. At low wounding rates, even a 5% decrease in survival can be detected with fewer than 100 animals in the assessment catch (Fig. 5). For higher wounding rates, larger sample sizes are required to detect the same per cent changes in survival, but, in general for survival changes greater than 10%, sample sizes of about 100 or less seem adequate. These assessments are based on an assumed probability of surviving an attack of 0.5. Because of the non-linear relationship between wounding rate and mortality, lower probabilities of survival will require even lower sample sizes.

Interpretation of Wounding and Lake Trout Assessment Data

To aid understanding of the population implications of observable wounding statistics, a steady-state version of the Salmonid/Lamprey Workshop Model was created. This steady-state model only examined the relationship among lamprey abundance, Lake Trout stocking, and typical assessment data. Two assessment statistics were of particular concern: catch per unit effort (CPUE) and mean length of the fish in the assessment catch. To emphasize the changes in mean length, a reference length was calculated from the difference between the average length in the catch and the length of age 5 Lake Trout (size at entry to assessment gear). Both indices show a pronounced negative association with wounding rates, but the actual values are very sensitive to other sources of mortality (Figs. 6 and 7). This model is documented in Appendix 2.

RECOMMENDATIONS

Based on these findings, the following recommendations seem appropriate to lamprey wounding standardization:

1. The best statistic to report would be the average number of wounds per fish or wounds per 100 fish;
2. The wound stages to be included should represent current year's wounds, certainly stages A1 to A2; and
3. Trends in effectiveness of Sea Lamprey control and Lake Trout rehabilitation may be apparent in both catch per

effort and mean size statistics from the assessment catch, but other sudden changes in mortality schedules of the Lake Trout may make interpretation difficult. Because of a basic symmetry in response of the model to reductions in lamprey abundance or increases in Lake Trout stocking, however, the relationship between wounding rate and either of these statistics is a good measure of the overall effectiveness of the program. These data should, therefore, be reported together with historical trend analysis.

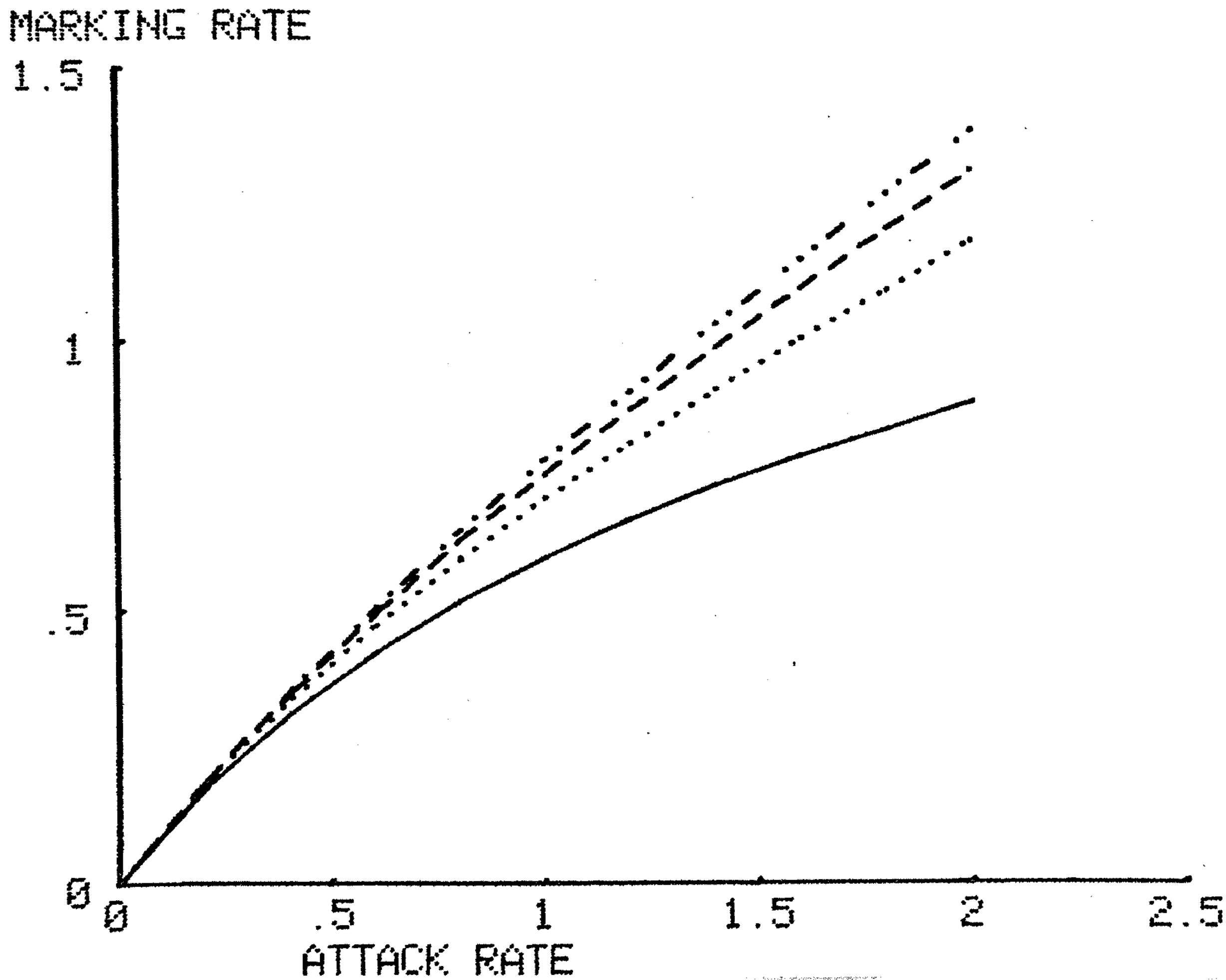

Fig. 1. Effects of various survival probabilities on the relationship between attack rate and observable marking rate. Solid line is for p = .25, dotted line is for p = .48, dashed line is for p = .57, and dashed-dotted line is for p = .62. The last three values represent the survival probabilities of 5, 6, and 8 year old Lake Trout as calculated in the Salmonid/Lamprey Workshop Model.

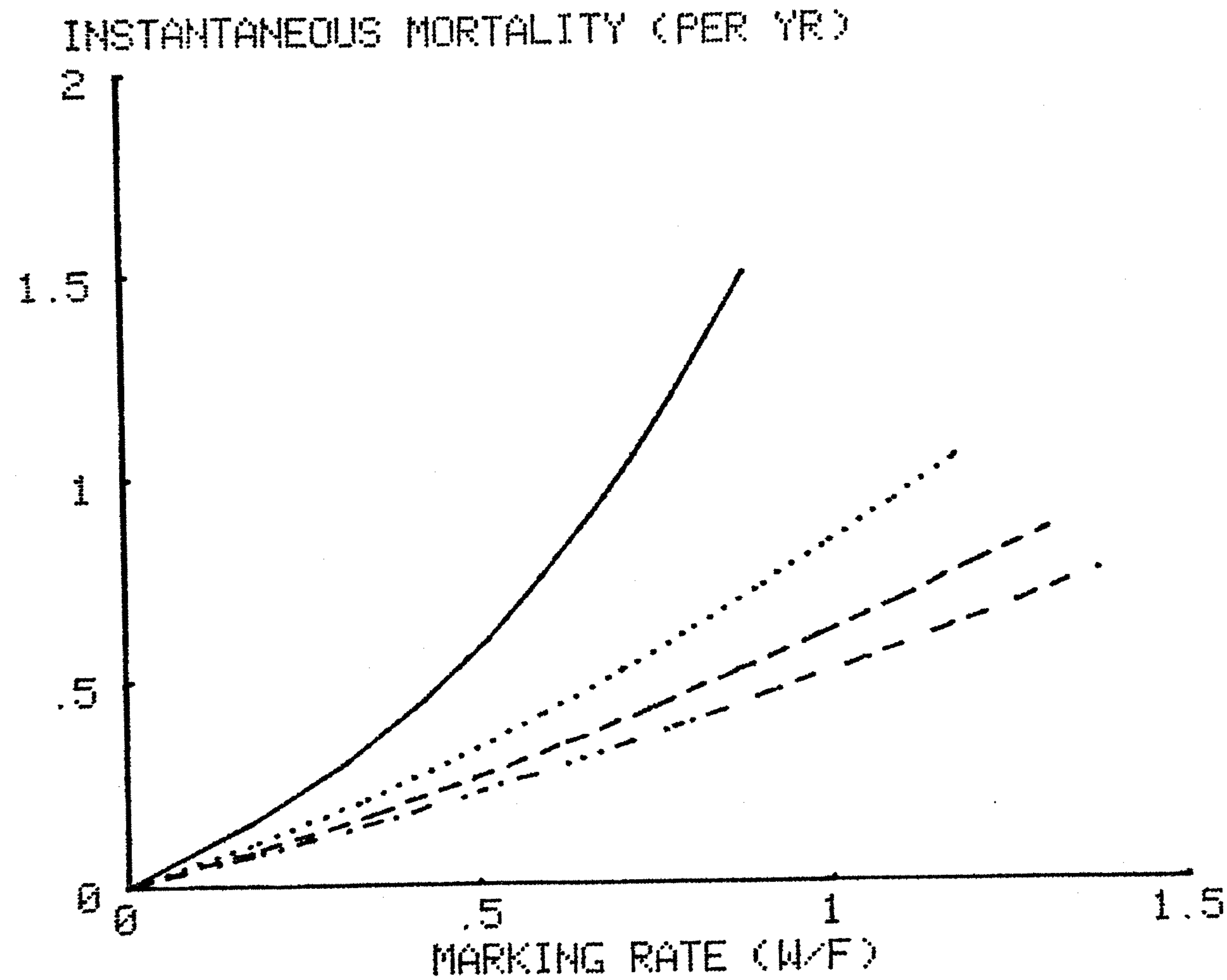

Fig. 2. Effects of various survival probabilities on the relationship between observable marking rate and instantaneous mortality. The lines for each survival probabililty are the same as for Fig. 1.

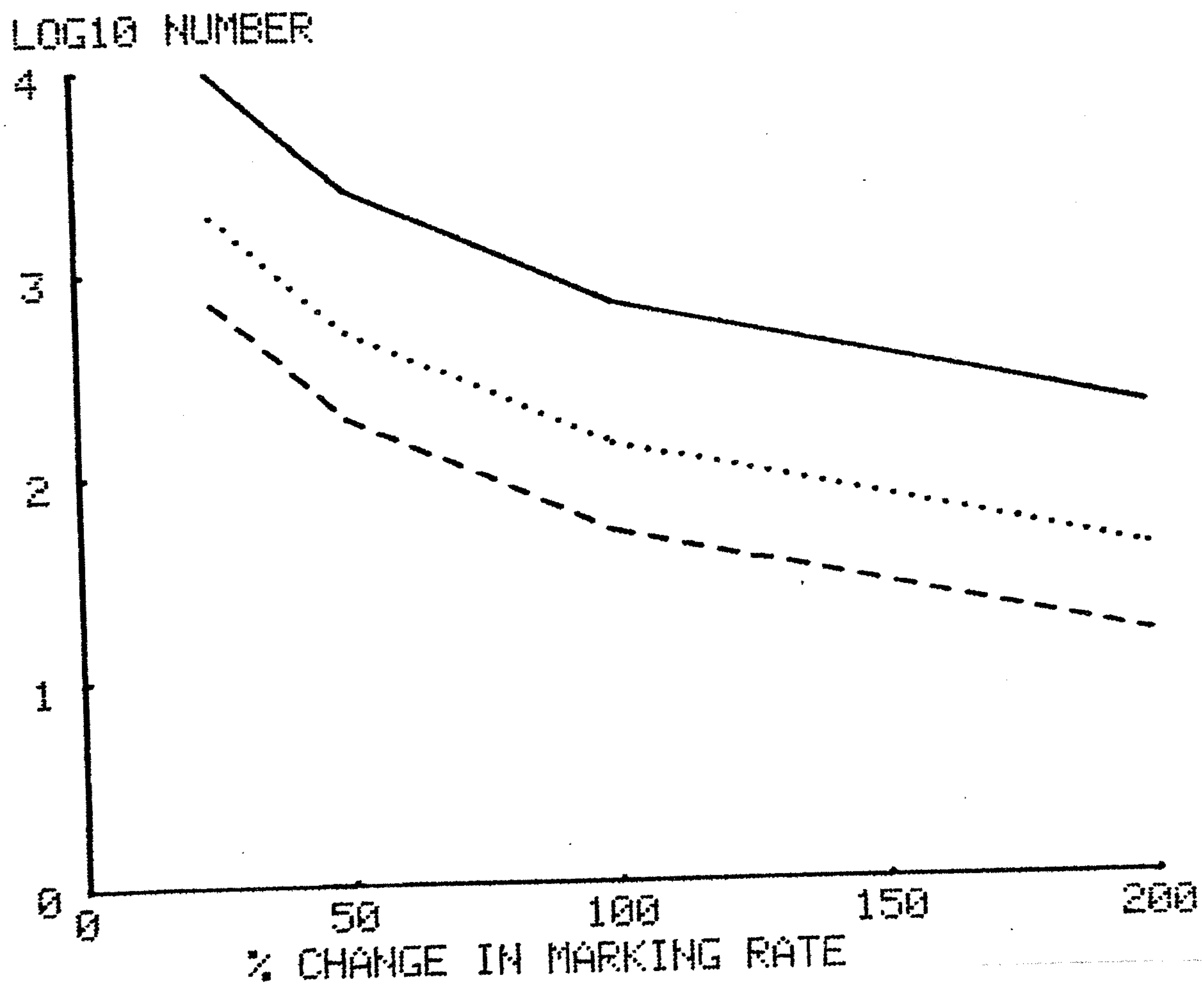

Fig. 3. Sample sizes required to detect various per cent changes in observed wounding rate. Solid line is for an observed wounding rate of 0.03, dotted line for 0.15, and dashed line for 0.40 wounds per fish.

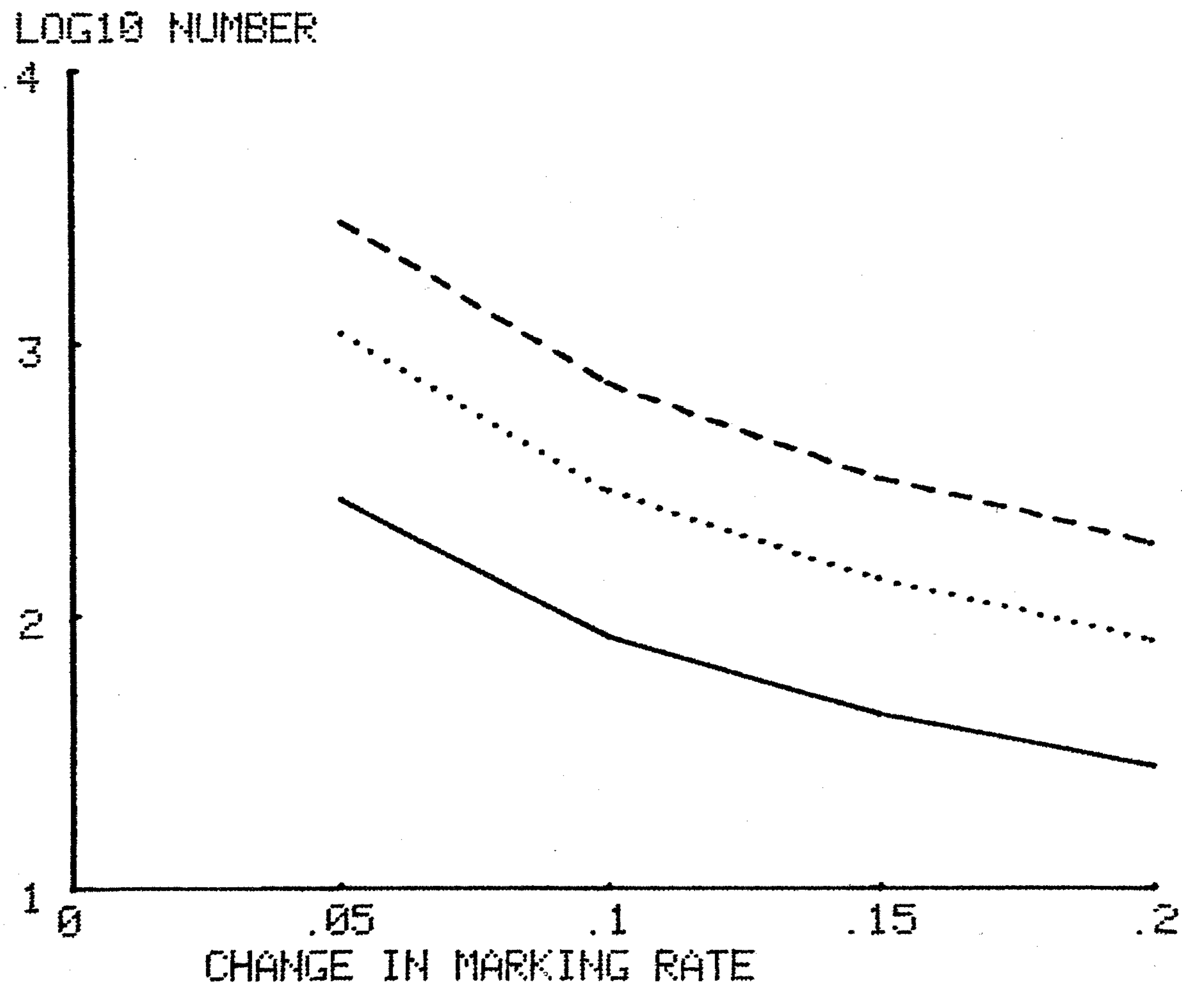

Fig. 4. Sample sizes required to detect various fixed changes in observed wounding rate. Lines for the three wounding rates are the same as in Fig. 3.

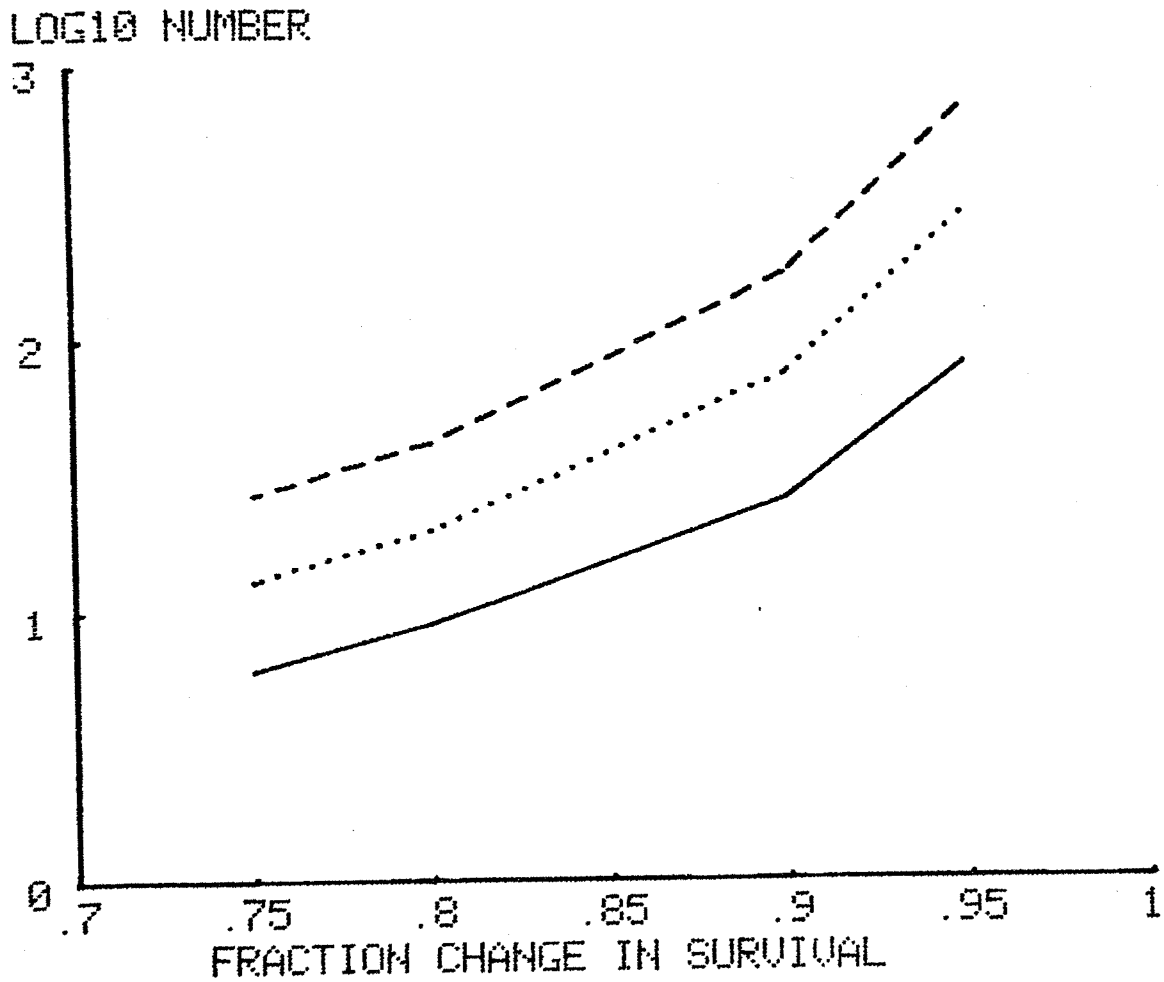

Fig. 5. Sample sizes required to detect various fractional changes in survival of the Lake Trout from lamprey predation. Lines for the three wounding rates are the same as in Fig. 3.

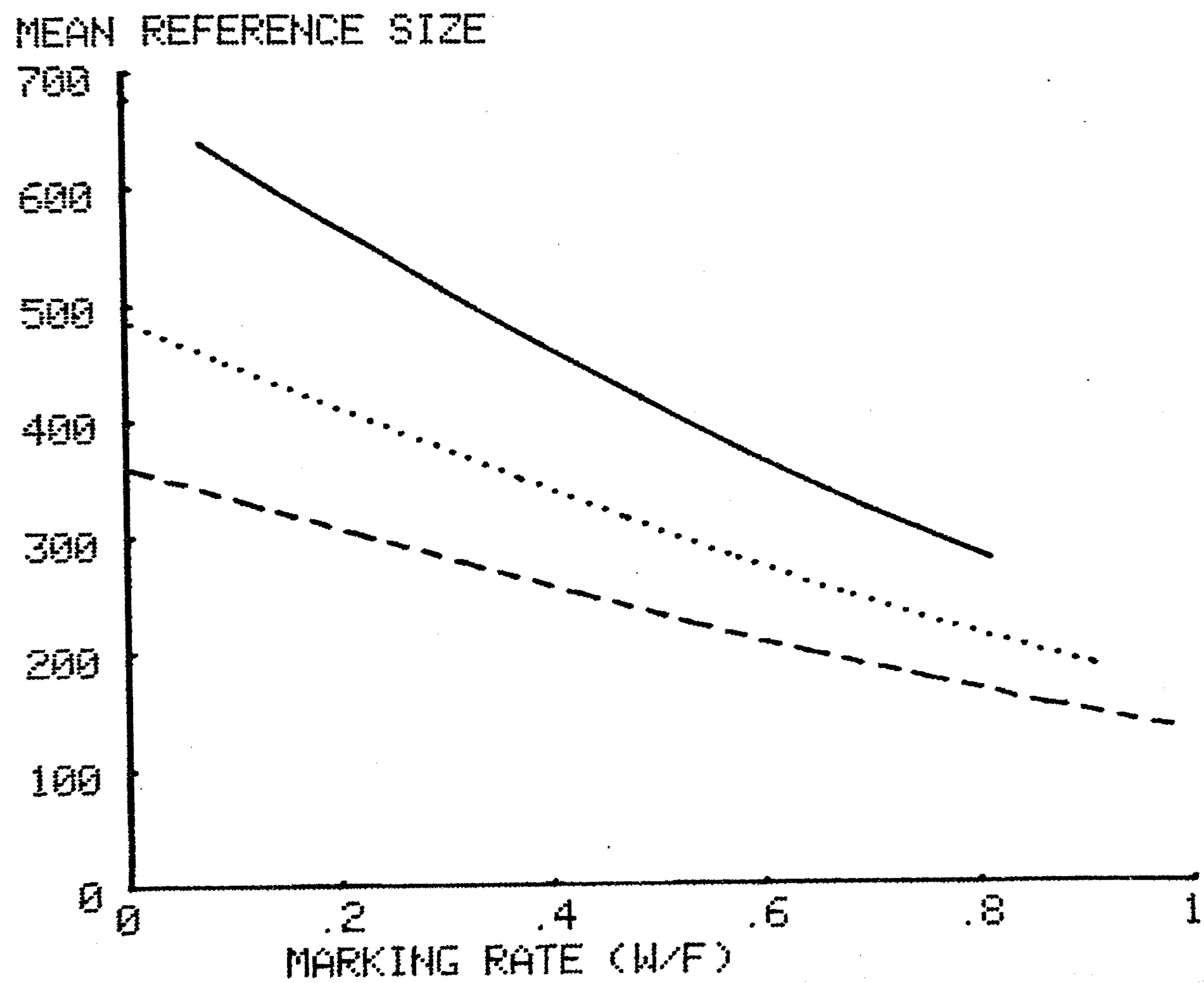

Fig. 6. The effects of various levels of fishing effort on the relationship between mean reference size and wounding rate. The solid line is for an effort of 0.3, dotted line for 0.5, and dashed line for 0.7 per yr.

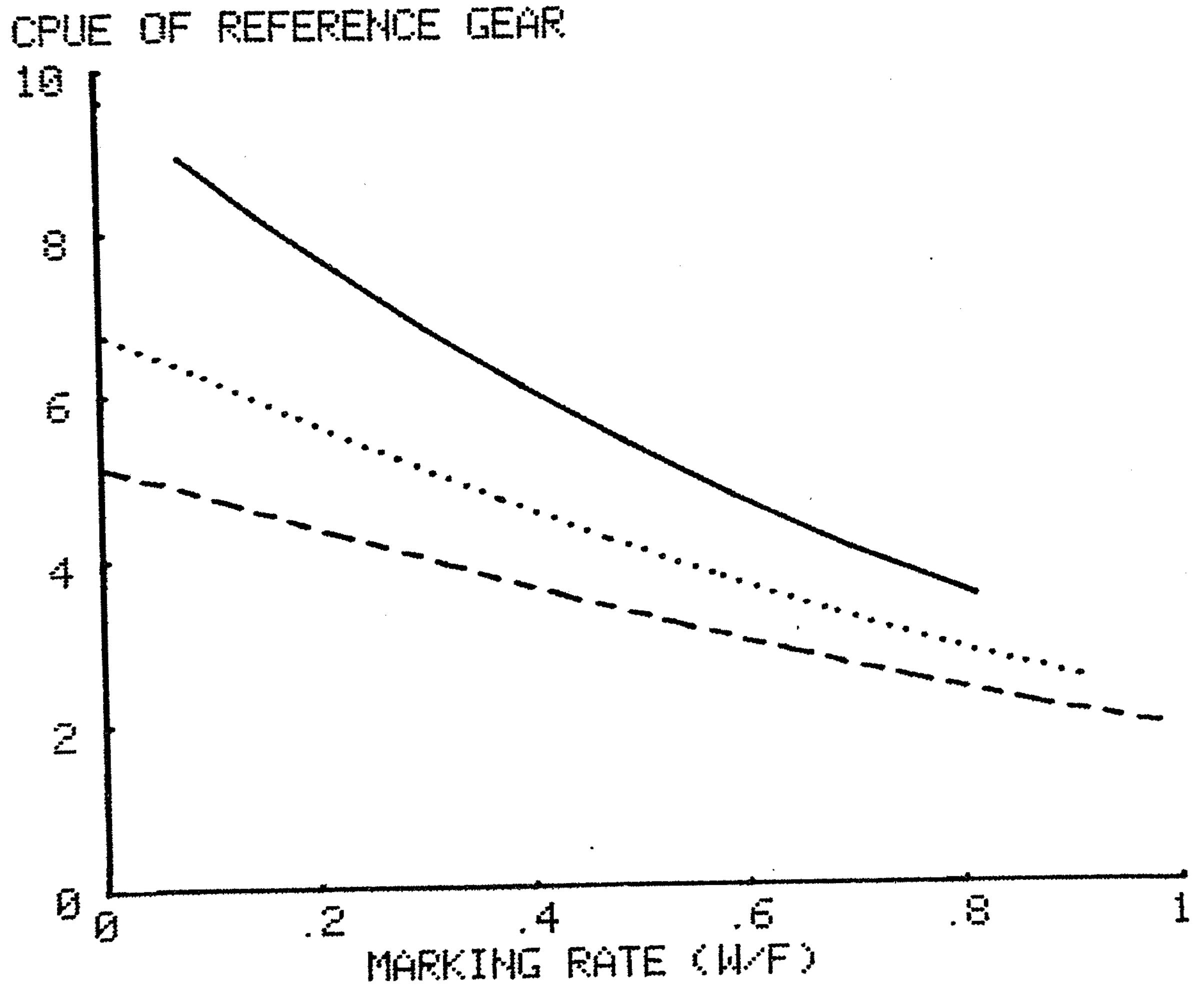

Fig. 7. The effects of various levels of fishing effort on the relationship between catch per unit of effort in assessment gear and the observed wounding rate. Lines for various effort levels are the same as in Fig. 6.

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Appendix 1. Relationship between Lamprey Wounding and Attack Rates.

If an attack by a lamprey has some likelihood of causing mortality, wounding rates that are estimated from samples of living animals will always be lower than the actual attack rates. In approaching similar problems in host-parasite interactions, it seems best to estimate the probability that an animal is not attacked (Smith 1968):

$$p = 1 - a/V,$$

where a is the effective search area of the parasite and V is the area (or volume) in which the host occurs with the parasite.

If there are N parasites searching independently, the probability that any single host is not parasitized is

$$p = (1 - a/V)*(1 - a/V)*...*(1 - a/V), \text{ or}$$

$$p = (1 - a/V)^n.$$

This equation is a binomial and when expanded will yield not only the probabililty of a host not being attacked, but also the probability that it is attacked once, twice, three times, and so on. If the probability of attack, a/V, is small and the number of parasites, N, is large, then the binomial may be approximated with a Poisson. The distribution of attacks per host would then be

$$p(i) = (q^i)*\exp(-q)/i!,$$

where q is the average number of attacks per host occuring in some short time and i is the category of number of attacks per host, and the probability of a host being unattacked would be

$$p(0) = \exp(-q).$$

To derive this model of the distribution of number of attacks per host, two key assumptions must be made

1. The probability parasite attack must be independent of any other attack; and
2. The time period for observation must be short enough to insure that the probabililty of attack is small.

It follows from this derivation that wounding frequencies should also be distributed as a Poisson, and these assumptions may be tested with appropriate data sets.

The Poisson wound frequency model may be tested in two ways. The first procedure is a Chi-Square goodness-of-fit test, and the second is a heterogeneity test based on the expected equality of mean and variance of any Poisson distributed random variable. In this work, I used two data sets to test the Poisson model: attack distributions from experiments on white suckers by Farmer and Beamish (1973) and Lake Trout wounding data from Cayuga Lake, New York (Eshenroder, personal communication). In the case of the white sucker data, the experimental protocol of eight suckers with eight lampreys yields a theoretical attack probability of 0.125. Such a high attack probability may be in violation of assumption 2, but as indicated in Table A1, the Poisson distribution for these data can not be rejected. In the second case, Lake Trout wounding data in Table A1 also can not be shown to be different from Poisson, especially when considering the more sensitive heterogeneity test. Given these results, therefore, the assumption of a Poisson model for multiple wounds or attacks does not seem unwarranted.

To extend this analysis to derive a relationship between attack rates and observed wounding rates requires some information on the probability of survival of attacks. As Walters et al (1980) observed, this is an area of some uncertainty. Based on the results of the Salmonid/Lamprey Workshop (Koonce et al 1982), however, two assumptions appear reasonable in the context wounding rates in the Great Lakes:

1. The probability of survival of an attack is independent of previous attacks; and
2. The probability of survival increases with the ratio of Lake Trout size to lamprey size.

With these assumptions and the frequency distribution of attacks given a mean number of attacks per host, the survival probability for a specific size of host is

$$s = \exp(-Q) + p*Q*\exp(-Q) + (p*Q)^2*\exp(-Q)/2 + \ldots$$

which may be rewritten as

$$s = \exp(-Q)*\exp(p*Q), \text{ or}$$

$$s = \exp(-Q*(1-p)),$$

where Q is the average attacks per host and p is the probability of surviving an attack.

The relationship between wounding rate and attack rate follows directly by calculating the frequency of unwounded hosts from the frequency of unattacked hosts weighted for attack mortalities:

$$\exp(m) = 1 + \exp(Q*p)*(1 - \exp(-Q)).$$

Table A1. Summary of tests of Poisson model of wound frequency distribution. Data for white sucker wounding are taken from Fig. 1. in Farmer and Beamish (1973), and the Cayuga Lake data are for various wound stages (King and Edsall 1979) for Lake Trout. Test statistics are either chi-square goodness-of-fit or heterogeneity. The heterogeneity statistic is the ratio of variance to mean times the degrees of freedom.

Data Source	OBSERVED WOUNDS PER FISH 0	1	2	3	4	Mean	STATISTICS Chi-Square	Heterogeneity
Farmer and Beamish	78	92	51	18	5	1.10	0.29 (p>.1)	222 (p>.1)
Cayuga Lake A1	270	80	9	0	-	0.27	1.49 (p>.1)	327 (p>.1)
A2	269	71	17	2	-	0.31	3.38 (p>.1)	396 (p>.1)
A3	259	84	11	5	-	0.34	7.89 (p>.05)	392 (p>.1)
A1-A3	798	235	37	7	-	0.31	2.99 (p>.1)	1126 (p>.1)

Appendix 2. Documentation of Steady-state Lamprey Wounding Model

Three kinds of statistics are obtained from assessment samples of Lake Trout in the Great Lakes: lamprey wounding frequency, average size, and catch per unit effort. Interpretation of lamprey wounding frequencies requires some understanding of the relationship of these statistics. As an aid to this understanding a steady-state Sea Lamprey/Lake Trout model was adapted from the Salmonid/Lamprey Workshop Model (Koonce et al 1982). Like the workshop model, the steady-state model assumes that lamprey attacks may be described with a multiple prey disc equation, but the steady-state model has simpler prey selection. Only Lake Trout are considered as prey, and probabilities of attack and mortality when attacked vary with age. To allow for alternative mortality sources, fishing effort may be changed and each age group has a characteristic catchabililty coefficient. Unlike the workshop model, each age group of Lake Trout has a different attack rate. Key parameters as a function of age are

Age	Size (mm)	p(i)	q(i)
1	1524	0.001	0.001
2	2692	0.001	0.005
3	4039	0.01	0.05
4	5080	0.8	0.5
5	5867	0.9	1.0
6	6477	0.9	1.0
7	6934	0.95	1.0
8	7290	1.0	1.0
9	7544	1.0	1.0
10	7874	1.0	1.0

where p(i) is the probability of attack given an encounter and q(i) is catchability (1/yr).

The probability of surviving an attack increases linearly with the size of Lake Trout as in the workshop model.

The model is set up for use with SIMCON. Instead of simulation through time, however, the model allows for the time variable, TI to increment lamprey abundance. For each level of lamprey abundance, the model performs a 15 year simulation to allow the Lake Trout abundance to reach a steady-state. The model is listed in Table A2, and the Z variables are defined in Table A3.

Table A2. Listing of the Steady-State Lamprey/Lake Trout Model.

```
18 FOR TIME = ZS TO NT
20  RESTORE : IF TI > 0 GOTO 100
99 LO = 500:LI = 10000
100  FOR JI = 0 TO 15
105  IF JI > 0 GOTO 1000
110 I1 = 1:I2 = 10:I3 = 5
120  FOR I = I1 TO I2: READ P(I): NEXT
130  FOR I = I1 TO I2: READ TL(I): NEXT
140  FOR I = I1 TO I2: READ Q(I): NEXT
150 Z = .6:S = 1E6
160 T(1) = S: FOR I = I1 + I1 TO I2:T(I) = T(I - 1) * Z: NEXT
170 L = LO + LI * TI
180 E = .7
190 M1 = 6E - 6:M3 = 3560:M4 = .292:M5 = 3.42200 NM = .2:K = 3.28E - 7
      :LZ = .33
210  FOR I = I1 TO I2:LC(I) = K * TL(I) * P(I):F(I) = E * Q(I)
      :SF(I) =  EXP ( - NM - F(I)):AH(I) = LC(I) * M1 * TL(I): NEXT
300  DATA        .001,.001,.01,.8,.9,.9,.95,1,1,1
310  DATA        1524,2692,4039,5080,5867,6477,6934,7290,7544,7874
320  DATA        .001,.005,.05,.5,1,1,1,1,1,1
1000  REM      START
2000 KK = 0: FOR I = I1 TO I2:KK = KK + AH(I) * T(I): NEXT
2100 KK = L / (1 + KK)
2200  FOR I = I1 TO I2:LA(I) = LZ  * LC(I) * KK:J1 = TL(I) / M3:J1 = J1 * M4
      * (J1 < M5) + (J1 >  = M5)
2250 SL(I) =  EXP (LA(I) * (J1 - 1)):LM(I) = LA(I) * (1 - J1)
2260 ZO =  EXP ( - LA(I))
2300 X = SL(I):XM = ZO / (X + (1 - X) * ZO):M(I) =  -  LOG (XM)
2400  NEXT
3000 T(I2) = T(I2) * SL(I2) * SF(I2) + T(I2 - I1) * SL(I2 - I1) * SF(I2 - I1)
3050 NS = TL(I2) * T(I2):NL = T(I2):NM = T(I2) * M(I2)
      :NA = LA(I2) * T(I2)
3100  FOR I = I2 - I1 TO I1 + I1 STEP  - I1:J = I - I1:T(I) = T(J) * SF(J) *
      SL(J)
3200  IF I >  = I3 THEN NS = NS + TL(I) * T(I):NL = NL + T(I):
      NM = NM + M(I) * T(I):NA = NA + LA(I) * T(I)
3300  NEXT :T(I1) = S
3500  IF NL <  = 0 THEN NL = 1
3600  NEXT JI
4000 Z(1,TI) = M(4):Z(2,TI) = M(5):Z(3,TI) = M(6):Z(4,TI) = M(7)
      :Z(5,TI) = M(8):Z(6,TI) = M(9):Z(7,TI) = M(10):Z(8,TI) =LM(5):Z(9,TI)
      = LM(7):Z(10,TI) = LM(9)
4010 Z(11,TI) = NS / NL:Z(12,TI) = NM / NL
4020 Z(13,TI) = LA(5):Z(14,TI) = LA(7):Z(15,TI) = LA(9)
4030 Z(16,TI) = L:Z(17,TI) = NL
4040 Z(18,TI) = NM:Z(19,TI) = NS / NL - TL(5):Z(20,TI) = NA / NL
5000  PRINT NA / NL;" ";NM / NL;" ";NS / NL
```

Table A3. Description of variables in Z array of the steady-state Lamprey/Lake Trout model.

Z variable	Description
1	Wound Frequency of 4 Year-Old Lake Trout
2	Wound Frequency of 5 Year-Old Lake Trout
3	Wound Frequency of 6 Year-Old Lake Trout
4	Wound Frequency of 7 Year-Old Lake Trout
5	Wound Frequency of 8 Year-Old Lake Trout
6	Wound Frequency of 9 Year-Old Lake Trout
7	Wound Frequency of 10 Year-Old Lake Trout
8	Instantaneous Lamprey Mortality 5 Year-Old Lake Trout
9	Instantaneous Lamprey Mortality 7 Year-Old Lake Trout
10	Instantaneous Lamprey Mortality 9 Year-Old Lake Trout
11	Average Size of Assessment Lake Trout
12	Mean Wound Frequency of of Assessment Lake Trout
13	Attack Frequency of 5 Year-Old Lake Trout
14	Attack Frequency of 7 Year-Old Lake Trout
15	Attack Frequency of 9 Year-Old Lake Trout
16	Lamprey Abundance
17	Abundance of Assessment Lake Trout
18	Total Number of Wounds
19	Reference Size of Assessment Lake Trout
20	Mean Attack Frequency of of Assessment Lake Trout