

GREAT LAKES FISHERY COMMISSION

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Observability of Lake Trout Mortality  
Due to Attacks by Sea Lamprey

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RESEARCH COMPLETION REPORT

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DUE TO ATTACKS BY SEA LAMPREY

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## ABSTRACT

The issue addressed here is the reliability of lake trout marking data as indicators of mortality due to sea lamprey attacks. For Lake Superior, two problems challenge existing modeling studies and laboratory experiments: seasonal variability of marking rates and some questions about the variability of attack lethality with size of lake trout. We find that patterns of Fall/Spring variation in marking are not inconsistent with models of the attack process, but they do imply variation in either attack intervals or attack lethality for parasitic phase sea lamprey after they have achieved maximum body size. Concerning the second problem, we find that, contrary to existing assumptions, probability of death due to attack does not decline to zero with size of lake trout.

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## INTRODUCTION

Since the collapse of Lake Trout populations of the upper Great Lakes, control of sea lamprey has been a dominant concern in Great Lakes resource management (Fetterolf, 1980). Throughout the control program, marking data on various host species have been important indicators of the lamprey problem. Starting in the late 1940's, many management agencies collected and reported marking data, but standard procedures for classifying marks (King and Edsall 1979) and reporting data (Eshenroder and Koonce 1984) have been proposed only recently.

Interpretation of marking has always been problematical. At best, marking data are indications of the ratio of the abundance of host species and sea lamprey. Many factors influence reliable interpretations of the data. Sources of uncertainty include observational error, temporal and spatial variation of lake trout abundance, and variation in abundance of alternate prey species. These, coupled with a basic uncertainty about the best marking statistic to use (i.e. fresh wounds, Eshenroder and Koonce 1984, or accumulated scars, e.g. Spangler et al 1980) inhibit the use of marking data to evaluate the effectiveness and efficiency of the control program.

Although the interpretation of marking is problematical, sea lamprey are pests in the Great Lakes. Sea lamprey have been observed to attack and kill a wide variety of prey species. In the Great Lakes, they have shown a preference for lake trout. Lawrie (1970) argued that sea lamprey were the primary causes of the decline of lake trout populations in the upper Great Lakes

and, following Fry (1953), were almost certainly the cause of the extirpation of lake trout in Lakes Huron and Michigan. Christie (1974) noted, along with Budd et al (1969), that sea lamprey prefer the largest fish. In the case of Lake Ontario, which had coexisting lake trout and sea lamprey populations, Christie (1974) argued that by reducing the abundance of large lake trout, overexploitation led to increased attacks on less resistant, smaller individuals in lake trout population; thereby increasing the contribution of lamprey predation to lake trout mortality.

Several modeling studies have addressed sea lamprey/lake trout interactions and the uncertainties surrounding interpretation of marking data. Walters et al (1980) argued on the basis of modeling studies that lake trout rehabilitation would require modification of both fishing mortality and lamprey abundance with stocking accelerating the rate of recovery. Based on this work, two models were developed in Adaptive Environmental Assessment and Management Workshops (Holling 1978). The first of these (Koonce et al 1982) confronted several issues concerning effects of sea lamprey on salmonid communities, and the second (Spangler and Jacobson 1985) focused on integrated pest management strategies for sea lamprey control.

These models share some common assumptions. First, the models assumed that sea lamprey searched randomly with a preference for largest fish. To accommodate a combined effect of variation in abundance and size of fish within a fish community, attack rates were assumed to obey a multispecies disc equation (see equation 1 below). Using this formulation, alternative prey

species could buffer attack rates on lake trout as a function of relative abundance of various prey species. Based on the work of Farmer and Beamish (1973), the models assumed that probability of attacks were independent and that the distribution of attacks per host was approximately Poisson (see Eshenroder and Koonce 1984 for more detail on the justification for this assumption). Survival of attack by sea lamprey was also assumed to be size dependent. Following Farmer (1980), survival was assumed to decrease with ratio of lake trout to lamprey size. For lake trout greater than 40 times the weight of a parasitic lamprey, Farmer (1980) argued that lake trout would survive blood loss-- supporting Christie's (1974) contention that sea lamprey are primarily parasites on larger lake trout.

Estimation of duration of attack proved to be very uncertain. Early studies (e.g. Parker and Lennon 1956) indicated that feeding intervals generally decreased with lamprey size. Farmer (1980) attributes this variability to the ratio of lake trout to lamprey size, but for large lake trout duration of attack could be anything from 48 hours to 3 months and be consistent with available data. Given such a wide range of observed feeding intervals, the actual abundance ratio of prey to sea lamprey is not easy to estimate from observed marking rates.

Recognition of this basic ambiguity of marking data was not a novel finding from these modeling efforts. Although Smith et al (1974) argued that marking data were correlated with catches of spawning phase sea lamprey at barrier dams in Lake Superior, generalizations are certainly not possible between lakes. Pycha

(1980), for example, reports a positive correlation between wounding rates of lake trout and estimates of their total instantaneous mortality, but Youngs (1980) failed to find any association for inland lake data. One of the justifications for developing the models, therefore, was to provide a way to explore the effects of various factors on lake trout rehabilitation and its observability.

In general, however, the models predict faster rehabilitation than seems to be actually occurring. Lawrie (1970) also noted that recovery of lake trout populations in Lake Superior was slower than expected; both suggesting the possibility of a flaw in understanding of lake trout-sea lamprey interactions. An implicit assumption in building models is that any ambiguities in interpretation of marking data originate with incomplete characterization of size composition and abundance of affected lake trout populations and of the "buffering" effect of other species. Given data on the abundance and size distribution of prey and lethality of attacks by sea lamprey, the problem of observing sea lamprey attacks is thus contained--leaving only issues of statistical inference to be solved. These inconsistencies with observations in Lake Superior, however, suggest that part of the poor predictions of the models for that lake may rest with incorrect understanding the lethality of lamprey attacks.

Procedures for standardizing reports of marking data emphasize the use of incidence of fresh wounds in fall samples of lake trout greater than 53 cm in length (Eshenroder and Koonce

1984). Such statistics more closely match the assumptions of the models discussed above than do statistics at other times of the year or at a more disaggregated spatial scale. Pycha and King (1975), however, report substantial seasonal variation in percentage of lake trout wounded in Lake Superior samples. In most cases, spring marking rates are much higher than fall rates. The elevated spring rates are clearly not caused by overlap of successive lamprey cohorts because there is no evidence of change in size of wounds in fall and spring collections. Furthermore, the data summarized by Pycha and King (1975) also show variation between marking rates in Wisconsin and Michigan waters of Lake Superior. Although the spatial variations in marking rates could be accommodated by increasing the spatial resolution of the models, assumptions of a constant, size-specific probability of surviving lamprey attack does not appear consistent with these observations.

Based on field observations (e.g. Christie 1974) and laboratory studies (e.g. Farmer 1980), the models assume that the probability of mortality due to a lamprey attack decreases with the biomass ratio of lake trout to lamprey. In general, Pycha and King (1975) report that percentage wounded increases with size. These results coupled with the analysis of instantaneous mortality (Pycha 1980) imply that the probability of surviving a lamprey attack does not decrease with size and may, in fact, increase with size. More recent analysis of size dependent mortality of lake trout in Wisconsin waters of Lake Superior also suggest that some factor is leading to increased mortality with



size. That these changes of mortality with size occur in refuges as well as areas open to fishing suggests that the factor is related to lamprey predation (Selgeby, personal communication).

Another puzzling inconsistency with model assumptions appears in comparisons of plots of percentage wounded versus size for various years. In most cases, results are similar to the data reported in Pycha and King (1975), but occasionally, percentage wounded increases to a maximum at an intermediate size and then declines for the largest lake trout in the sample (Fig. 1a). Although no detailed analysis of this phenomenon exists, it can not easily be dismissed as statistical artifact. Small sample sizes of the largest lake trout do result in overlapping confidence regions (Fig. 1b), but these occasional inconsistencies taken with the others above cast some doubt on the credibility of the assumptions used in the models. Furthermore, if mortality due to lamprey attack did not decline with size, recovery of lake trout populations might be much slower than expected. The purpose of this paper, therefore, is to show that existing models can be reconciled with these observations from Lake Superior.

## MODELING METHODS

### Queueing Model for Lamprey Attack

The purpose of this model is to determine the effects of dynamics of seasonal growth and attack characteristics of sea lamprey on the observable statistics for marking and lake trout mortality. Two problems are thus addressed. First, we can

determine the limitations of using annual average, spring, or fall marking rates as indicators of a seasonally varying process. Second, we can relate lamprey induced mortality and observed wounding rates directly to the attack process. To meet its objectives, we designed the model to simulate behavior of individual lamprey at daily intervals over a 1-year period. We assumed that lamprey and their lake trout prey occupied a very large volume in which the distribution of lamprey and lake trout were random. We fixed the initial ratio of lamprey and lake trout, and the units of abundance were thus relative to these initial ratios. To simplify computation, we finally assumed that only one size class of lake trout was present. We based the model on two other models. We used the attack and handling characteristics derived for the IPM model (Spangler and Jacobson 1985), which relied on Farmer's (1980) model of time to death as a function of daily blood loss. To model growth of lamprey, we used a bioenergetic model (Kitchell and Breck 1980) previously applied to lamprey growth in Lake Superior.

These independently derived models were not completely compatible. Using Farmer's (1980) estimates of handling times and consumption rates with Kitchell and Breck's (1980) bioenergetics of growth led to extreme overestimates of seasonal growth. Although this incompatibility might be nothing more than differences in parameter estimation, it is also possible that the sea lamprey may have significant refractory periods following an attack event. Because we were unable to pursue these possibilities with available data, we simply modified the

conversion efficiencies in Kitchell and Breck (1980) to produce reasonable growth of lamprey in the queueing model. A more serious parameter estimation problem arose in calculating average handling time per attack. Farmer's (1980) model of time to death is valid only when the ratio of lake trout to lamprey biomass is greater than 0.025. If a lamprey is too small to kill a lake trout by the criteria established in Farmer (1980), the length of attachment could be indefinite. Parker and Lennon (1956) did not observe duration of feeding greater than 11 days. King and Edsall (1979), however, reported single feeding attachments lasting 3 months. Given this range of possible handling times for non-fatal attacks, maximum duration of attacks could not be fixed. Instead, we arbitrarily set maximum handling time to 3 months.

The IPM model recognized two classes of lamprey attacks; fatal, i.e. those that would result in mortality if the time to death were less than the maximum handling time, and non-fatal, attacks terminated before death of the host. In various studies (Parker and Lennon 1956, and Farmer 1980), lamprey have been observed to terminate an attack after a few hours to days. These non-lethal attacks were the only attacks considered non-fatal in the IPM model. In the queueing model, however, non-fatal attacks consisted of both these non-lethal attacks and fatal attacks that would require longer duration of attack than allowed by the convention of a maximum handling time. A curious result of these distinctions is that ongoing attacks could constitute a significant fraction of the observed marking statistics. The

marking statistic was assumed to be a wound in an A1 to A3 stage of healing according to the wound staging classification proposed by King and Edsall (1979). Healing times were assumed to be temperature dependent. Thus the observed marking statistic included ongoing attacks and wounds of survived attacks occurring within a temperature varying interval of the past.

## RESULTS AND DISCUSSION

The discussion above raises three types of inconsistencies between models and observation of lake trout marking in Lake Superior: spatial variability in marking rates, seasonal variability in marking rates, and factors affecting survival of lamprey attack. Of these three, the last two are more important to resolve. It is simply not possible to describe spatial pattern dynamics of lamprey and prey with sufficient precision to justify detailed spatial modeling. Given the variability in wound classifications by trained observers (Eshenroder and Koonce 1984), it is also difficult to determine the extent of observer bias in the regional variations of reported marking rates. Clarifying the other two inconsistencies, however, is central to any model of lake trout-sea lamprey interaction, and the remainder of the paper will be devoted to these issues.

### Seasonal Variation in Lamprey Attack Characteristics

Growth of sea lamprey during a year complicates the interpretation of seasonal variability in marking data. In Lake Superior, transformers enter the lake during the fall (Smith et al 1974), but do not appear on lake trout until the following

spring or early summer. They reach maximum length (305 to 610 mm) by the end of November. Prior to spawning in late spring weight loss has been observed. Over the approximately 12 month interval in which sea lamprey feed on lake trout, therefore, they increase in weight by an order of magnitude, and most of this growth occurs during a relatively short time in the fall (Kitchell and Breck 1980). Of the models discussed above, only the IPM model (Spangler and Jacobson 1985) attempted to represent seasonal variability in size of lamprey. Nevertheless, all the models essentially treat mortality due to lamprey attacks as an average annual phenomenon. To explore the limitations of this approach, we used the queueing model of lamprey attack.

#### Results of Queueing Model Simulations

The main issue addressed by the queueing model of lamprey attacks was the variation in Fall/Spring marking rates. Using the relationship posed by Farmer (1980), we first assumed that probability of survival of an attack was a function of the ratio of lake trout size to lamprey size. Starting with first lamprey attacks on lake trout in June, therefore, survival probabilities decrease with growth of the lamprey and reach a minimum value in late October or early November. With this assumption, marking rates show a slight increase from October to May (Fig. 2), but this increase is certainly not as much as observed by Pycha and King (1975). One possible way to increase the difference between October and May observations of marking rates was to assume that survival probabilities increased as the lamprey neared maximum size. Such an hypothesis is consistent with both decreased

consumption rates by lamprey at maximum body size or increased survival of lake trout over winter due to decreased activity. This assumption results in 3 to 4 fold increases in May versus October marking rates (Fig. 3).

A secondary issue concerned the proportion of observed marks due to ongoing attacks. This issue arises from substantial uncertainty about the average duration of a sea lamprey attack. The results in Fig. 3 illustrate the information value of estimates of this proportion. To obtain large differences in October and May marking rates, we assumed that the fraction of lethal attacks decreased as lamprey approached their maximum body size. The effect of this assumption was to decrease the average handling time. As a result, the proportion of observed marks due to ongoing attacks dropped from about 80% in October to 20% in May (Fig. 3). In Fig. 2, using the alternative assumption, this proportion remained near the 80% level during the entire simulation.

The effect of handling time variation on proportion of marks due to current attacks does not vary with the ratio of lake trout to sea lamprey. The functional form of attacks per prey in the queueing model is

$$A = T * p * a * L / (1 + \sum h * p * a * N_i) \quad (1)$$

where  $p * a$  is the effective search rate,  $h$  is the average handling time,  $T$  is the time interval over which attacks are observed,  $L$  is the lamprey abundance, and  $N$  is lake trout abundance. Due to the characteristics of this problem,

$$\sum h * a * p * N_i \gg 1,$$

and equation 1 may be simplified to:

$$A \cong T*L/(h*N) \quad (2)$$

Attack rates and, depending upon survival, marking rates are thus dependent upon two ratios:  $T/h$ , the observation interval to average handling time, and  $L/N$  the predator to prey ratio. These two ratios act to confound each other in current parameter estimation schemes. However, if data were available for ongoing attacks, the absolute ratio of current attachments and an estimated proportion of observed marks due to current attachments could resolve these confounding effects.

#### Discussion and Tentative Conclusions from Queueing Model

We developed the queueing model to see if observations of seasonal variability of marking rates were inconsistent with models of the process of sea lamprey attack used in the AEAM workshop models. These models simulate marking rates for one time observation period during the year. As with Eshenroder and Koonce (1984), the models attempt to predict fall marking statistics. Existence of only one size class of sea lamprey in the fall is the primary justification for this preference. In Lake Superior, however, Spring marking rates are much higher than fall, and there is no evidence that Spring marks are generated by large and small size groups of sea lamprey. In recent years, therefore, only Spring data have been reported for the lake. Results of the queueing model simulations imply that arbitrary selection of observation interval should not invalidate the models. Difficulties do arise, however, in parameter estimation.

Structurally, the basic attack model seems sound. Using it

to describe annual or subannual variability in marking rates, however, forces different interpretations of the parameters. Application to seasonal variability, for example, means that handling time and lethality of attack change with growth of the sea lamprey. These two parameters are themselves averages for a given population of parasitic phase sea lamprey, but they can be characterized on an "instantaneous" basis from their underlying seasonal dynamics. In contrast, observable marking statistics always have a finite observation interval imposed by healing time and duration of ongoing attacks. In applications to annual variability of marking statistics, interpretations of marking statistics change less than do characteristics of lamprey seasonal dynamics. In fact, the finite nature of the observation interval of marking statistics imposes constraints on model parameters representing basic attributes of sea lamprey (e.g. size, handling time, lethality of attack to various sized hosts, preference for various sized prey, etc.). Unfortunately, the model's flexibility is also its chief weakness. As was demonstrated in Figs. 2 and 3, it can accommodate a wide range of conflicting hypotheses as assumptions.

Although there are probably other functional descriptions of lamprey attack that could produce similar behavior, the extensions of the AEAM models used in the queueing model do provide some insights. First, the Fall/Spring differences in marking rates must involve variations in survival of attack. Several hypotheses are consistent with observed variation, but they do imply different proportions of observable marks due to



ongoing attacks as well as differences in the fraction of lake trout of various sizes experiencing ongoing attacks. These data are not now available, but future research along these lines could contribute to the testing of several implicit hypotheses. Second, annual Spring or Fall statistical summaries are equally usable for the models. In any application, however, the models must be calibrated with estimates of total mortality of prey by size or age categories. Fortunately, statistical summaries (e.g. Pycha 1980) are readily available for this purpose. With constraints on total mortality, it is possible to calculate survival probabilities from either Fall or Spring marking data.

#### Variation in Survival of Sea Lamprey Attack

##### Problems with Observations of Attack Survival

Above, we argued that reconciliation of model and seasonal changes in observed marking rates required changes in assumptions about the lethality of sea lamprey attacks. Understanding of lamprey feeding behavior in situ, however, is poor. Much of the data which support various hypotheses regarding sea lamprey attacks are based on laboratory studies. From Parker and Lennon's (1956) experiments to those summarized by Farmer (1980), the standard protocol has been to confine small fish (generally less than 50 cm) with variable numbers and size of sea lamprey in aquaria. Mortality and other characteristics of sea lamprey attacks on larger lake trout had to be inferred from observations of marking rates (e.g. Budd et al 1969; and Christie 1974). Questions about such matters as the average duration of attack on

large lake trout or their probability of surviving an attack can not be resolved with this mix of background data. Nevertheless, as we discussed above, there is substantial reason to believe that lethality of attacks for large lake trout is much higher than previously hypothesized. The main support for this argument is set of recent analyses by Selgeby (personal communication) and (Fig. 1a and 1b).

In general, model predictions are inconsistent with these observations. The IPM model (Spangler et al, in preparation), for example, relies on Farmer's (1980) characterization of lethality of sea lamprey attacks. A fixed percentage of all feeding attacks by sea lamprey are assumed to be non-lethal (10% to 25%). For the remainder, time to death is calculated after Farmer (1980; Fig. 4). If time to death were greater than a defined maximum, then the probability of survival is assigned a value of 1.0. Otherwise, handling time for a lethal attack is the time to death. The consequence of these assumptions is that the probability of surviving an attack is constant to some size, which is determined by the ratio of lake trout to lamprey weight, and jumps to a maximum value for all larger prey. Fig. 4 summarizes consequences of this assumption for marking statistics and lake trout mortality. It is clear that these results are not consistent with the observations by Selgeby or the results in Figs. 1a and 1b.

Assuming for the moment that these observations are not statistical artifacts, two kinds of errors could cause these inconsistencies. First, derivation of attack characteristics,

including probability of survival, from Farmer's (1980) experiments could be incorrect. Secondly, the basic assumption that lethality of attack somehow decreases with lake trout size could also be wrong. Each of these possibilities must be considered in more detail.

#### Evaluation of Alternative Models of Attack Lethality

In the IPM model, sea lamprey are either in a non-lethal or a lethal attack mode. Laboratory observations of sea lamprey behavior, however, are different. According to data reported by Parker and Lennon (1956, Table 7), sea lamprey spend less than 30% of the parasitic phase attached to prey. Their statistics show that the average feeding interval is 27 hours with an attack probability of 0.22 per day, or, on average, one attack every 4.5 days. Of course, these data are for small prey (less than 30 cm). Although they are not inconsistent with Farmer's (1980) analyses, they do raise the possibility that satiation or some other factor leads to a finite attack interval independent of prey size. The structure of the IPM parasitic phase submodel could accommodate this distinction, but handling time would then be an interval of both duration of feeding attack and subsequent refractory period. The distinction between lethal and non-lethal attacks, however, would not be consistent nor would constant survival probability be consistent with these observations of the feeding behavior of sea lamprey.

To evaluate effects of alternative assumptions about feeding behavior on model performance requires a different description of the lethality of an attack. The primary assumption necessary to

implement Parker and Lennon's (1956) observations is that the duration of a feeding attack is a random variable. We could also assume that the refractory period was a random variable, but the effect of a refractory period is on the total number of attacks made by a lamprey during its parasitic phase and not on the lethality of these attacks. We will, therefore, limit the analysis to the feeding attack interval. Calculation of the probability of survival of an attack requires specification of the probability density function of the feeding interval and specification of the time to death of various sized prey. With these data, we can estimate the probability that an attack interval will not include the time to death for a particular size of prey, and we then define this probability as the probability of survival. For convenience, we assume that duration of attack has a Poisson distribution. The probability density function of feeding interval is thus

$$f[x;\mu] = (\mu^x e^{-\mu})/x! \quad (3)$$

where  $\mu$  is average duration of an attack.

The relation between lethality of attack and size of lake trout depends on the duration of the feeding interval. Several examples are contrasted in Fig. 5 with the assumption now used in the IPM model. Even with this modification, however, the variation of mortality and mark statistics with size (Fig. 6) do not approach those in Fig. 1. In fact, the only way for marking statistics to show the pattern in Fig. 1a. is for probability of survival to exhibit a dome shaped dependence on size; i.e. both

large and small lake trout should have lower survival probability than intermediate sized lake trout. Three possible mechanisms could produce a this relation: changes in survival due to multiple attacks, increased likelihood that sea lamprey attack location changes to more vulnerable spots (gills, abdomen, etc.) on larger lake trout, or behavioral differences among lake trout that leave the oldest animals more vulnerable to lamprey attack. Superficially all three are consistent with Selgeby's observations, but only the first is consistent with the observations in Fig. 1.

The phenomenon in Fig. 1 clearly occurs sporadically (Pycha and King 1975). Because the frequency of multiple attacks varies with abundance of lake trout, temporal variations in abundance of the largest lake trout could lead to the periodic nature of the low marking of these fish. The other two mechanisms would result in constant patterns of decreased marking of largest fish. Where observed, however, frequencies of multiple marks per fish have been consistent with the assumption that the lethality of an attack is independent of any other attack (Eshenroder and Koonce 1984).

Analysis of multiple marking data usually assume a Poisson distribution for attacks per fish and marks per fish (e.g. Spangler et al 1980; and Eshenroder and Koonce 1984). Farmer and Beamish (1973) have shown that sea lamprey do not preferentially attack fish with other sea lamprey attached. The consistency between observations and expectations of these multiple attack models, therefore, tend to invalidate the multiple attack

hypothesis described above. Nevertheless, multiple marks can be created in two ways: multiple simultaneous attacks and multiple sequential attacks. Because a fresh wound remains in the A1 to A3 wound phase of King and Edsall (1980) for as long as 3 months, multiple sequential attacks could be relatively important. Thus there is an ambiguity. The probability of surviving attacks may be independent for multiple sequential attacks, but not for multiple simultaneous attacks.

To illustrate this ambiguity in a simple way, we assume that size specific probability of surviving an attack will decline as the fraction of multiple simultaneous attacks increase:

$$P_i = P_{s_i} * P_1 / (1 - P_0), \quad (4)$$

where  $P_{s_i}$  is the survival probability of size group  $i$  (as in Fig. 5) and  $P_1$  and  $P_0$  are expected frequencies of one and zero attacks derived from equation 3. This formula implies that more than one attack during a handling period will kill a host. Of course, observed marking statistics result from attacks over an interval of a few to several handling periods, and observers actually measure a mixture of simultaneous and sequential multiple attacks.

Using a Monte-Carlo simulation, we explored the effects of increasing attack rate on deviation from expected frequencies of multiple marks on lake trout greater than 40 times the size of attacking sea lamprey. According to Farmer (1980), these lake trout should be able to survive blood loss during a feeding interval for a sea lamprey. The simulation allowed for a

variable length period over which marks would accumulate (an observation period). We assumed that all lake trout attacked more than once by sea lamprey during an attack interval died and allowed attack rates to be set by the ratio of initial lake trout and sea lamprey abundance. We began each simulation with 1000 lake trout. Varying the length of the observation period from 1 to 6 attack intervals, deviation from expected frequencies is statistically significant only at very high lamprey to lake trout ratios (Table 1).

Conditions necessary to produce decreased marking of largest lake trout, therefore, include the dome shaped survival versus size relation discussed above and a high ratio of sea lamprey to large lake trout. Even in situations where sea lamprey are 4 times as abundant as the largest lake trout, however, multiple simultaneous attacks can not create a pattern of % wounded vs size (Fig. 7) similar to Fig. 1. Buffering effect due to the abundance of smaller lake trout could obscure the expected relationship, and a population state different from that used in Fig. 7 might duplicate the observations in Fig. 1. Setting aside this buffer effect, the maximum number of attacks possible during a handling interval is set by the ratio of lamprey to lake trout. Assuming the correction for multiple simultaneous attacks in equation 4 is determined by this maximum attack probability, decrease in marking of largest lake trout occur (Fig. 8). Unfortunately, the assumptions required to produce the similarity of Figs. 1 and 8 are not reasonable.

Two factors compromise these results. First, to produce a

large enough increase in lethality of attacks due to multiple simultaneous attacks requires the direction of nearly all attacks toward the largest lake trout. Such a requirement is inconsistent with observed marking trends of smaller lake trout. Second, the results in Fig. 8 indicate that instantaneous mortality of the largest lake trout should increase sharply from the next lowest size category. Such abrupt changes in survival versus size plots are not observed (Selgeby, personal communication). In view of these difficulties in reconciling the model with observations in Fig. 1, the possibility exists that these trends are sampling artifacts.

#### Observability of Lethality of Sea Lamprey Attacks

The overlap of 95% confidence intervals in Fig. 1b indicate that the decrease in marking of the largest lake trout is not statistically significant. Of course, it is also clear that the trend of increasing marking over the 45 to 64 cm size range also is not statistically significant. The question is whether these are just problems of small sample size. As discussed above, the assumptions required to get Fig. 8 are not reasonable. Although the possibility of finding a combination of reasonable assumptions and population state can not be eliminated, there is no evidence that the occurrence of the phenomenon is associated with changes in abundance of lake trout or their age structure. For example, the phenomenon occurred in the Spring statistics from Michigan waters of Lake Superior in 1962, 1963, 1966, and 1970. Examination of catch per unit effort data from these same samples (Pycha and King 1975, Table 6) reveals a complete absence



of any relation that would support reasoning for increased mortality due to multiple simultaneous attacks. Because we are unable to show consistency between characteristics of this phenomenon and any of the mechanisms that we have proposed to account for it, we must conclude that at least the decline in marking occasionally seen for largest lake trout is a sampling artifact.

Despite resolving some questions about the lethality of sea lamprey attacks, we have no evidence that lethality decreases with size for large lake trout. Due to the limitations of laboratory experimentation and availability of experimental animals, attack lethality of large sea lamprey on large lake trout is rarely observed. There is some evidence, however, that the probability of surviving an attack does have some upper limit that is independent of body size. Attack location can affect lethality. Survival of attacks in the gill region or of attacks in which the body cavity is punctured is low (Seeley, personal communication). Farmer (1980) reported evidence that sea lamprey prefer attachment locations below the lateral line between the head and caudal peduncle. Incidental collection of dead lake trout in bottom trawls from Lake Ontario revealed a single ventral wound as the likely cause of death (Bergstedt 1985). With a preference for areas with thinner musculature, it seems reasonable to suspect that some fraction of attacks will result in a wound from which not even large lake trout can recover, and the lethality of these wounds is not necessarily related to ability to replace blood loss during feeding of sea lamprey.

This possibility coupled with Selgeby's (personal communication) observation of increasing mortality with size implies that large lake trout do not escape mortality due to lamprey attacks, and the models should be modified accordingly.

## CONCLUSIONS

Evaluation of the effectiveness of an integrated sea lamprey control program requires observability of lake trout mortality due to lamprey predation. Based on the reconciliations of various discrepancies in the theory and interpretation of marking data, it now seems possible to develop a framework for analysis of joint lake trout rehabilitation and sea lamprey control programs. We base this optimism on the resolution of three major issues:

1. Inconsistency of the relation between marking statistics and the lamprey component of total lake trout mortality as exemplified in the differences reported for Lake Superior (Pycha 1980) and Lake Cayuga (Youngs 1980);
2. The limitations imposed by seasonal variations in lake trout marking statistics on identification and estimation of the relation between lake trout mortality and sea lamprey predation; and
3. Inconsistencies between understanding of the behavior, physiology, and lethality of lamprey feeding on lake trout (e.g. Farmer 1980) and both the slower than expected recovery of lake trout in Lake Superior (Lawrie 1970) and more recent indications that mortality due to lamprey predation may increase with lake trout size.

In this paper, we have shown that resolution of these issues is possible by examining consequences of models based on competing hypotheses or can be resolved with specific, new observations.

Probability of survival of an attack by sea lamprey is the central uncertainty for all of these issues. It is clearly a function of size of lake trout and attacking lamprey, and it may also vary with some abiotic environmental variables (temperature or water quality measures like pH, alkalinity, hardness, etc.). In spite of the possible sources of variation, however, it is possible to estimate probability of survival. In Lake Superior, for example, Pycha (1980) reported estimates of instantaneous mortality of lake trout aged 7 to 9 over the period 1966 to 1978. Adopting the recommendations of Eshenroder and Koonce (1984), reanalysis of Pycha's (1980) and more recent data yields an estimate of 0.14 for the probability of surviving a single lamprey attack (Fig. 9). The association between mortality and marks per fish in Fig. 9 accounts for 90% of overall variability of mortality during the period of observation, and the intercept implies a natural mortality rate of  $0.18 \text{ yr}^{-1}$  (Koonce and Pycha MS).

Assuming a 7 year old lake trout is about 69 cm in length and 3.3 kg in weight, time to death by Farmer's criteria due to an attack by a 200g lamprey would be about 20 days. Using the relationship in equation 3 and assuming that 10% of attacks will be lethal due to attack location alone, an overall survival probability of 0.14 would require an average attack interval of 25 to 30 days. From the queueing model, this attack interval

indicates that over 35% of the marks are ongoing attacks-- implying a relatively high lamprey to lake trout abundance ratio.

Although a series of assumptions are required for this estimation scheme, it illustrates what can now be accomplished. As availability of data compel the analysis to move from age or size specific mortality and marking data to more aggregated summaries, however, the observability deteriorates. In Fig. 10, for example, marks per fish decline as lake trout abundance, as indicated by catch per unit effort of fish 51 cm and greater in length, increases. This association accounts for only 16% of the variability in marking. Catch per unit effort of 7 year old fish only could improve the association. Alternatively, lamprey abundance may also vary substantially during this period. The data from Cayuga Lake (Youngs 1980) represent an extreme in aggregation. Total mortality and marks per fish are mean values for all fish over 4 years of age. Mean probability of survival for a wide size range of fish will vary significantly with the size composition of the population. Separating the effects of variation in relative abundance from other sources of variation (e.g. lamprey abundance and fishing effort) is difficult. Nevertheless, Youngs (1980) observations of little apparent association between mortality and marking, despite a high mean of 0.53 marks per fish, implies either that probability of survival is higher in Cayuga Lake than in Lake Superior or that the average duration of an attack is significantly shorter. In either case, the proportion of marks due to ongoing attacks would be important information to resolve this matter further.

Resolving the other two issues also required fundamental rethinking of the factors determining attack lethality. The main finding concerns generalization of the decline in lethality of an attack with size that had been observed in laboratory experiments (e.g. Parker and Lennon 1956; and Farmer 1980). To make the implications of field observations consistent with these physiological data required an assumption of some minimum level of attack lethality. Variation in lethality due to attack location seemed a reasonable explanation for this requirement, and some recent field observations lend credibility to the assumption (Bergstedt 1985). The models used in the IPM model, therefore, are structurally sound, and with better parameter estimation schemes, a derivative of the IPM model could serve as a tool with which to explore future integrated management schemes for sea lamprey.

Despite correcting some problems with models of the attack process, several remain. These problems will inhibit further application of the model. The first is observational error. It is possible (Swanson, personal communication), that the differences in marking rates reported from Wisconsin and Michigan waters of Lake Superior are due to different interpretations of a wound. Although the recent proposal to standardize fresh marks as wounds in healing stages A1 to A3 (Eshenroder and Koonce, 1984), substantial variation in interpretation will continue to persist. Future applications of the models must deal explicitly with sources of observational error. The second problem concerns data reporting and aggregation of statistics. Clearly, size

specific mortality and marking data are required for optimal estimation. Implications of relying on more aggregated statistics need to be explored. Finally, fraction of marks due to ongoing attacks has emerged as an important source of information to test some of the implications of the models and explanations of inconsistencies.

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Table 1. Summary of significance probabilities for various combinations of probability of attack during an interval and number of attack intervals. Data are derived from the results of a Monte-Carlo simulation of observed and expected frequencies of multiple attacks under the condition that multiple simultaneous attacks in any attack interval were fatal.

PROBABILITY OF ATTACK	ATTACK INTERVALS PER OBSERVATION PERIOD		
	1	3	6
.01	.24	.22	.34
.05	.70	.96	.66
.10	.97	.99	.50
.20	>.99	>.99	>.99

## FIGURE LEGENDS

Fig. 1. Wounding rates versus size for lake trout in Lake Superior. Panel A contains data from statistical districts in Michigan for 1977. Panel B summarizes data for the Apostle Island area of Wisconsin waters for 1977; included are the 95% confidence intervals on the % wounded statistic.

Fig. 2. Results of 12 month (July to June) simulation of queueing model with probability of surviving an attack assumed to be constant. The ten curves are plotted on a scale of zero to a maximum value. Curves and maximum values are 1--lamprey size (170 g); 2--fraction blood loss per day (.5); 3--average duration of new attacks (90 days); 4--abundance of lake trout (2000); 5--mean size of lake trout (2500 g); 6--wound healing time (100 days); 7--fraction of marks due to ongoing attacks (1); 8--observed marks per fish (.5); 9--lake temperature (14 C); and 10--mean handling time of ongoing attacks (100 days).

Fig. 3. Results of 12 month (July to June) simulation of queueing model with probability of surviving an attack decreasing with sea lamprey size. Curves and maximum values are the same as Fig. 2.

Fig. 4. Relation between three factors (probability of surviving attack,  $P_s$ ; lake trout instantaneous mortality due to attacks by sea lamprey,  $Z$ ; and fraction wounded,  $W$ ) and size of lake trout,  $L$ . Curves shown are derived from the IPM model (Spangler and Jacobson 1985).

Fig. 5. Survival probability versus size for three levels of mean duration of attack ( $h=10, 20, 30$  days). Also included for reference is the curve assumed in the IPM model.

Fig. 6. Implications of the relation between size and survival probability (assuming mean duration of attack is 10 days) for variation of mortality ( $Z_L$ ) and fraction wounded ( $W$ ).

Fig. 7. Implications of the relation between size and survival probability (assuming mean duration of attack is 10 days) for variation of mortality ( $Z_L$ ) and fraction wounded ( $W$ ), but with the assumption that multiple simultaneous attacks are lethal. Frequency of multiple simultaneous attacks is a function of attack frequency.

Fig. 8. Implications of the relation between size and survival probability (assuming mean duration of attack is 10 days) for variation of mortality ( $Z_L$ ) and fraction wounded ( $W$ ), but with the assumption that multiple simultaneous attacks are lethal. Frequency of multiple simultaneous attacks is a function of the ratio of lake trout to sea lamprey by size.

Fig. 9. Relation between wounds per fish and instantaneous mortality of lake trout for Lake Superior from 1966 to 1984.

Fig. 10. Relation between catch per unit effort and wounds per fish of lake trout for Lake Superior from 1966 to 1978 (data after Pycha 1980).

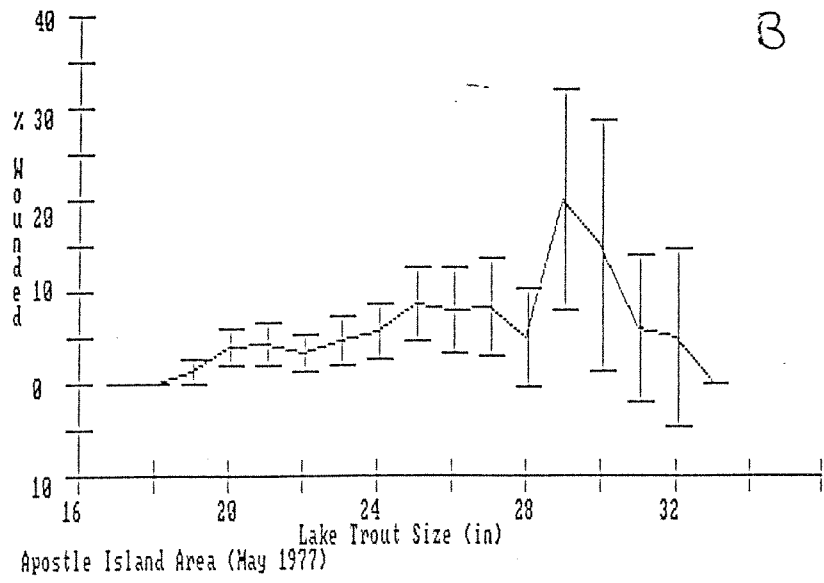
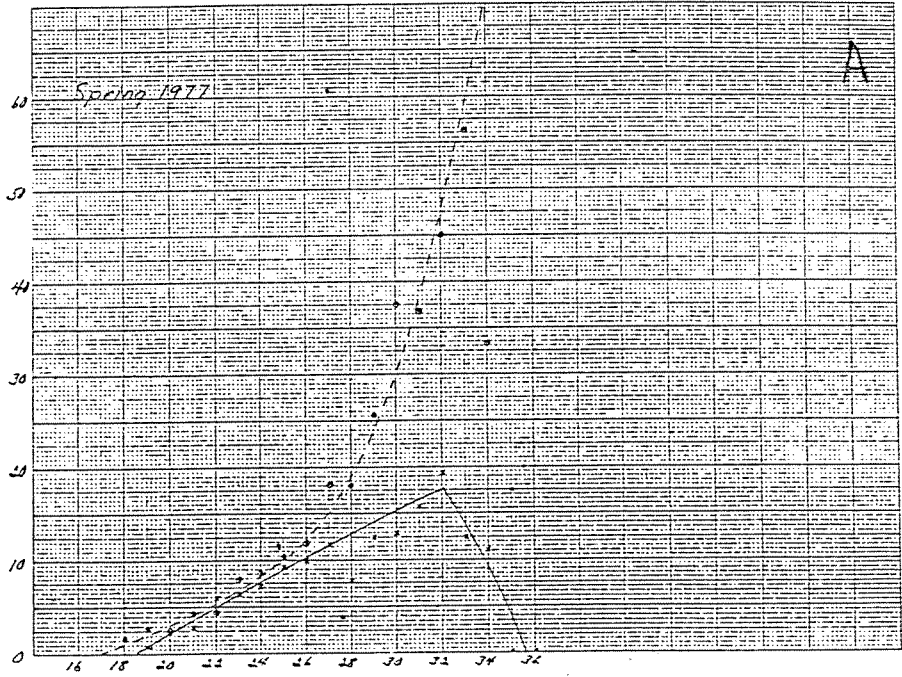


Fig. 1

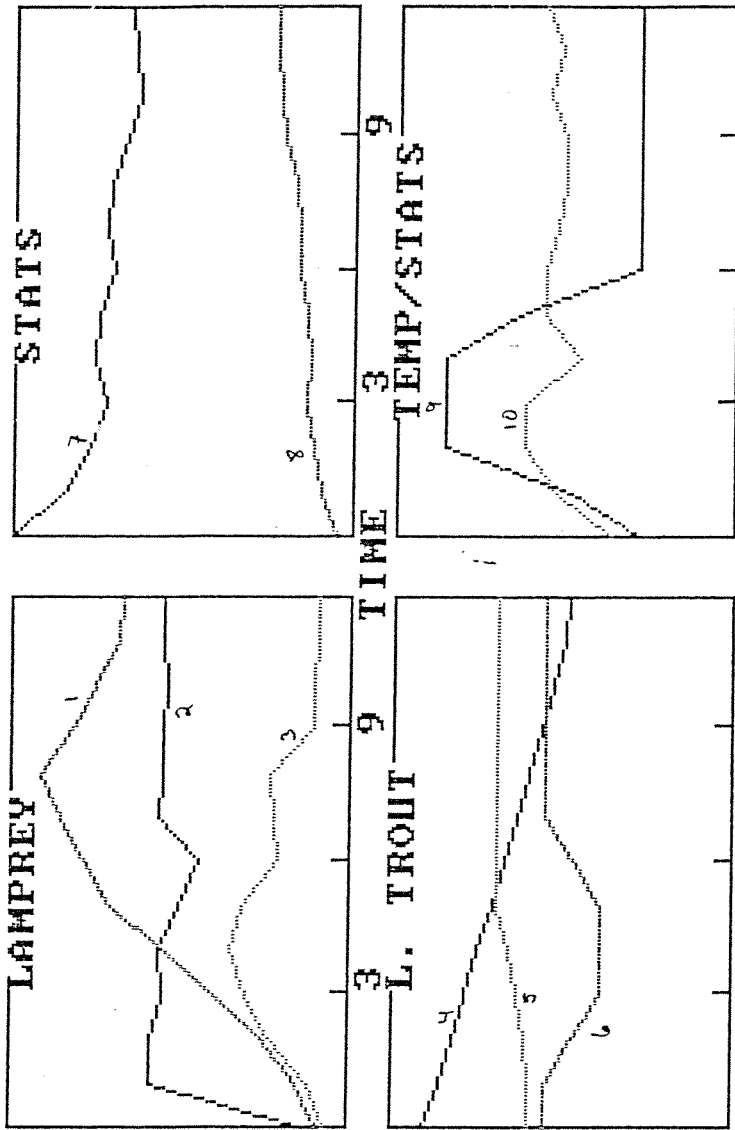


Fig. 2

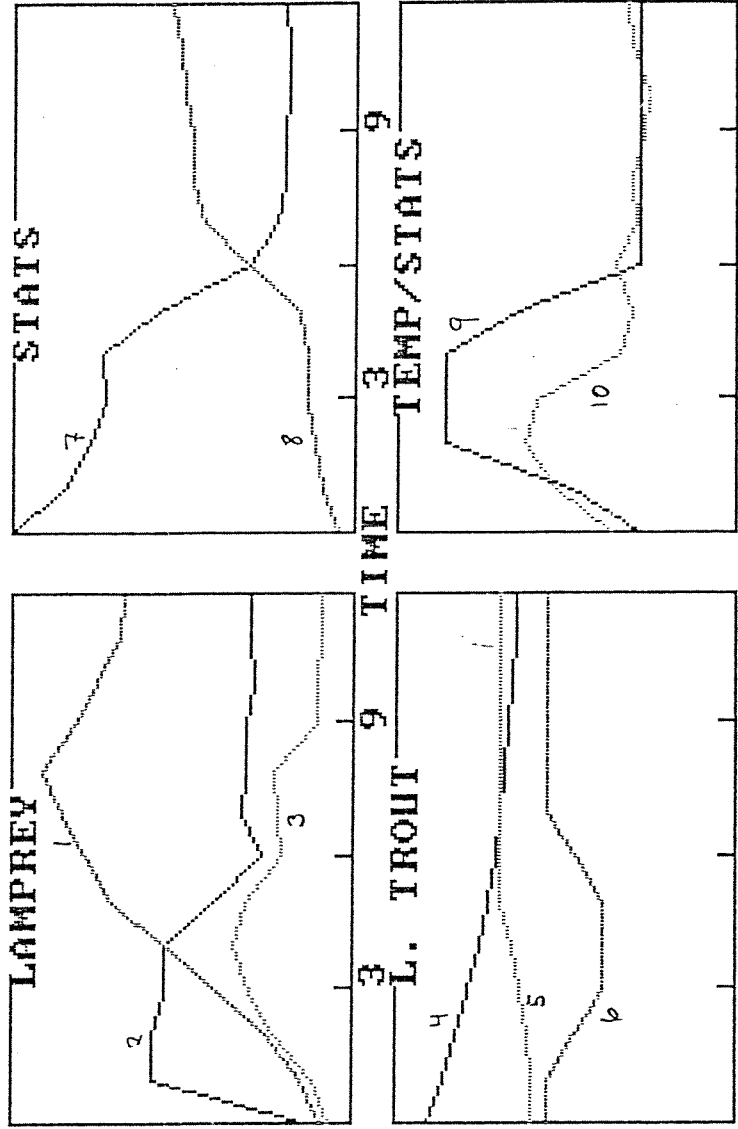
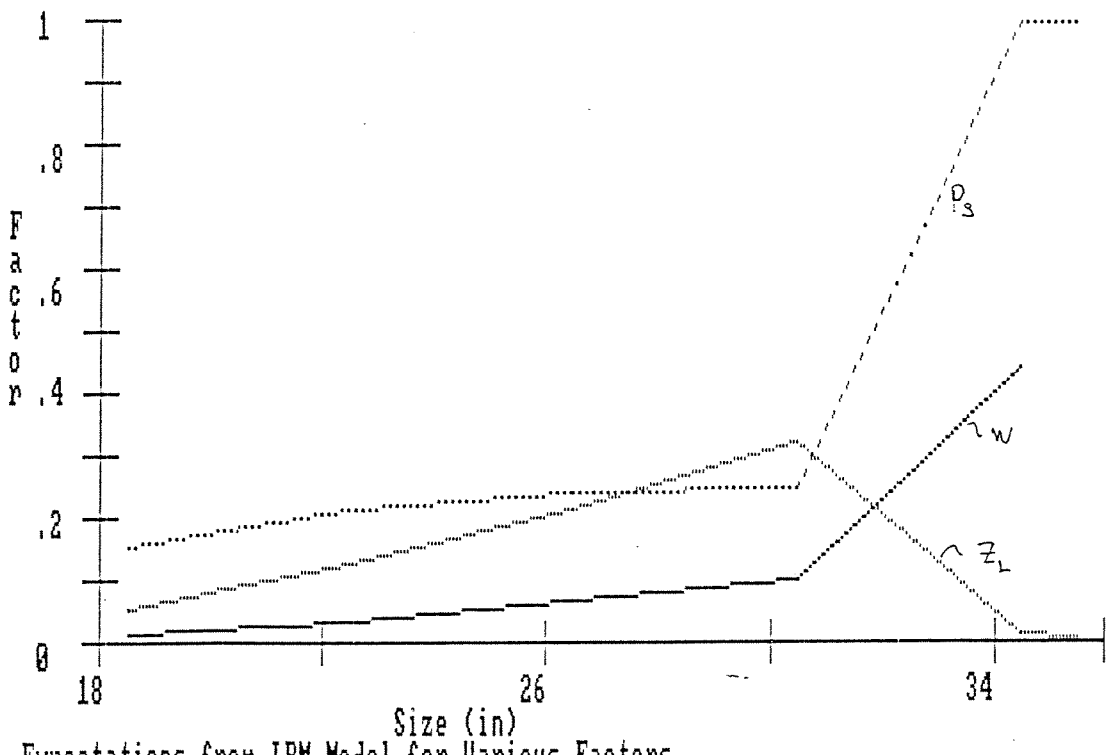
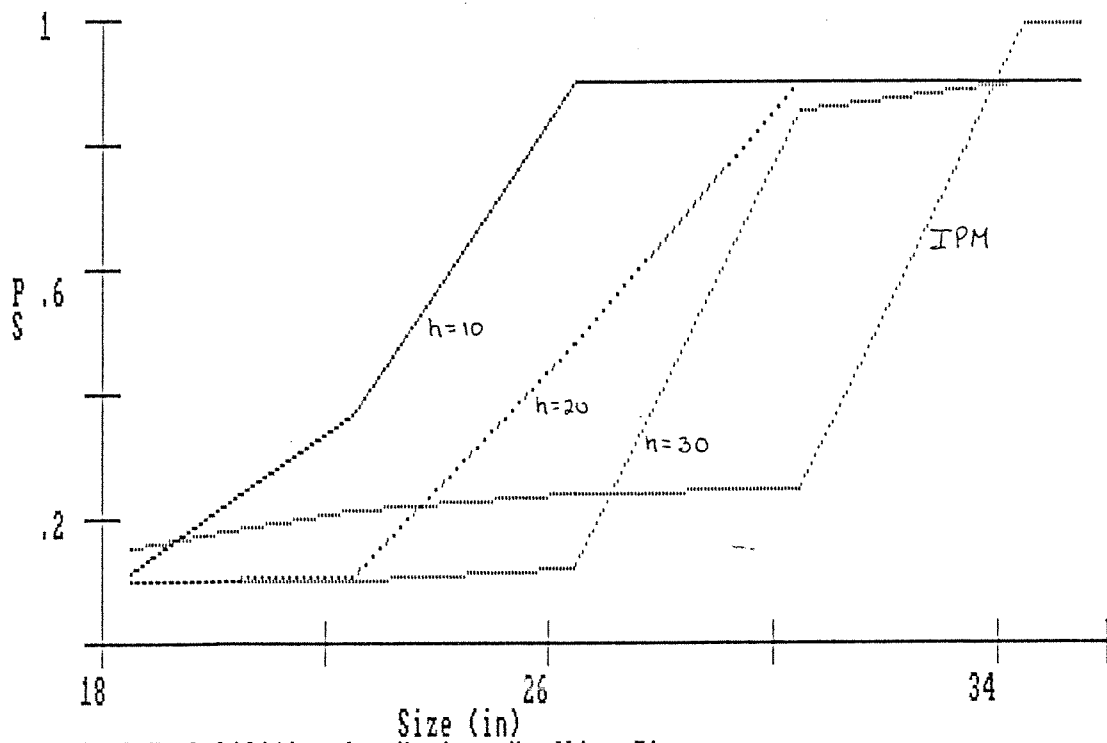


Fig. 3



Expectations from IPM Model for Various Factors

Fig. 4



Survival Probabilities for Various Handling Times

Fig. 5



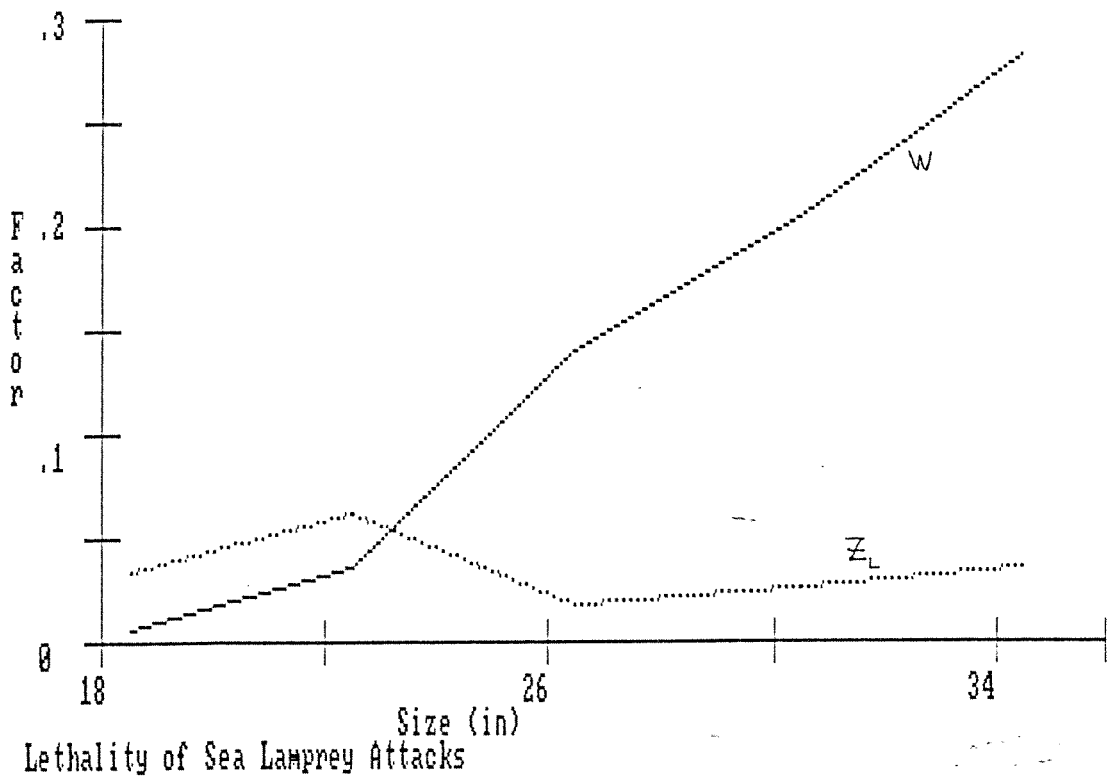
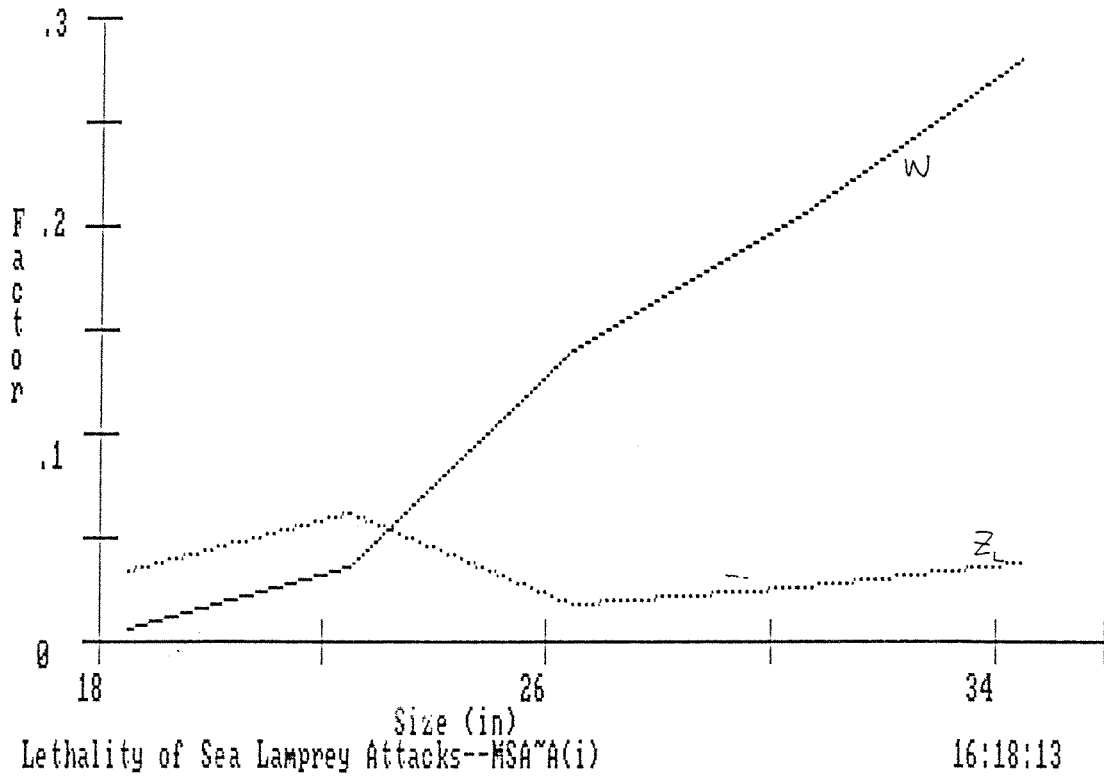
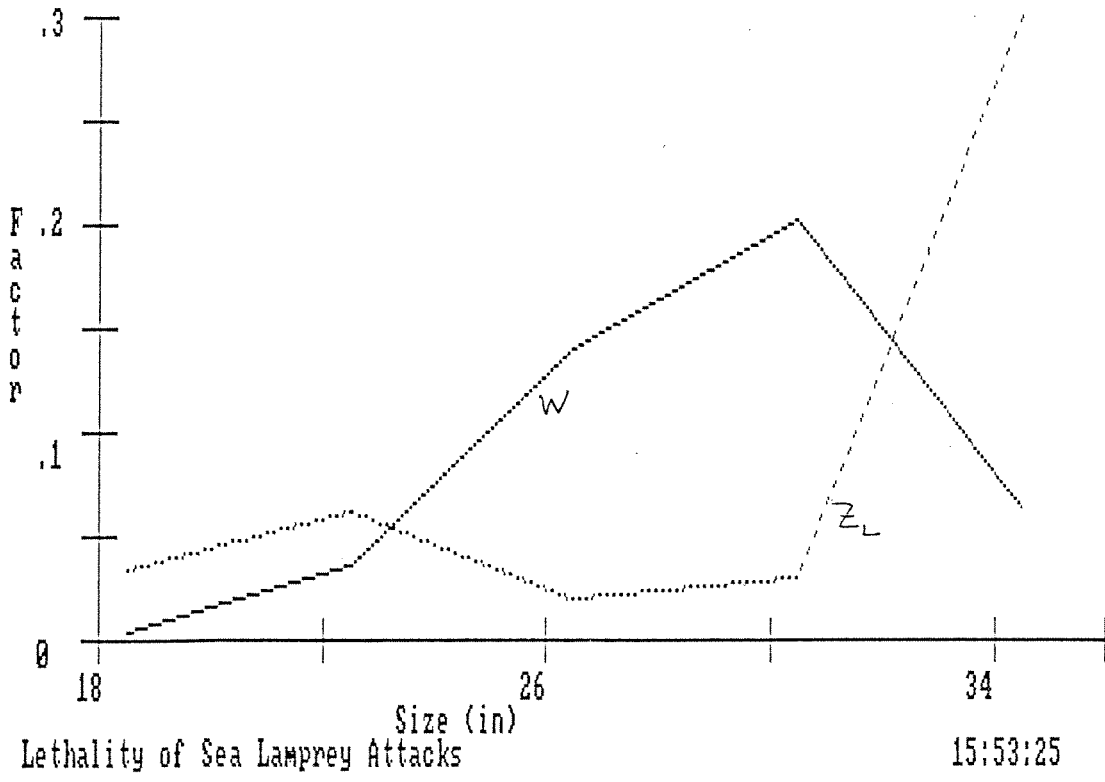


Fig. 6



7

Fig. 7



Lethality of Sea Lamprey Attacks

15:53:25

Fig. 8

# LAKE SUPERIOR-MICHIGAN

Weighted Marks for Lake Trout > 25

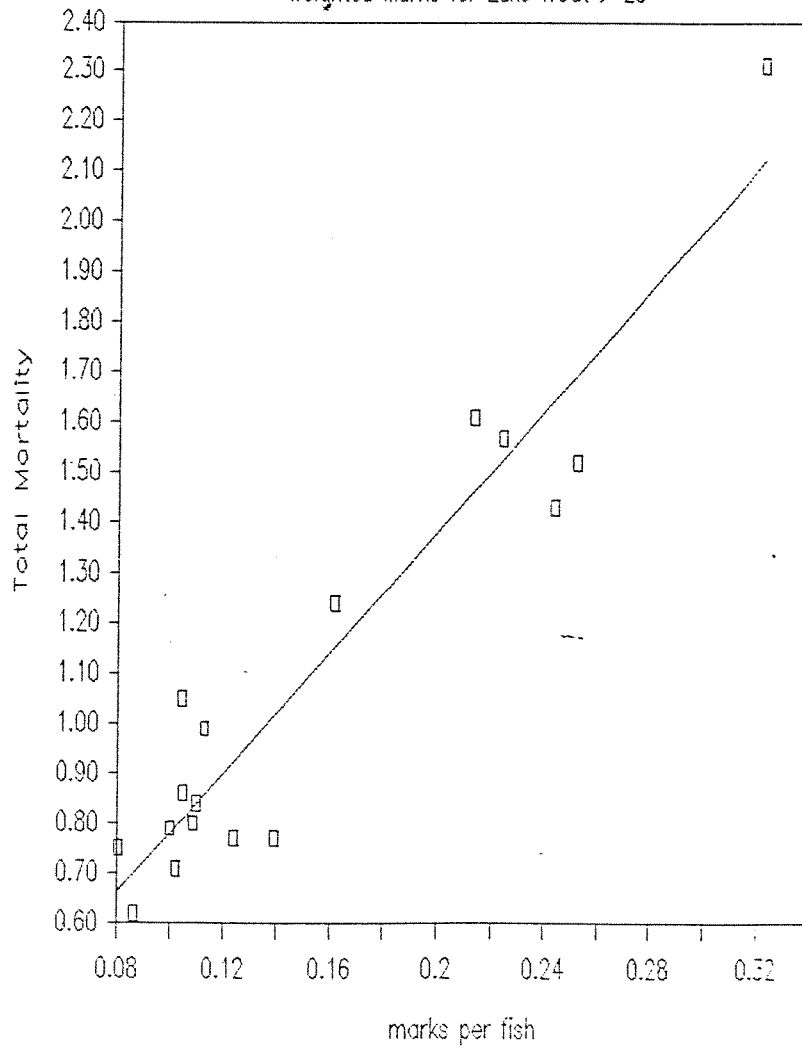


Fig. 9

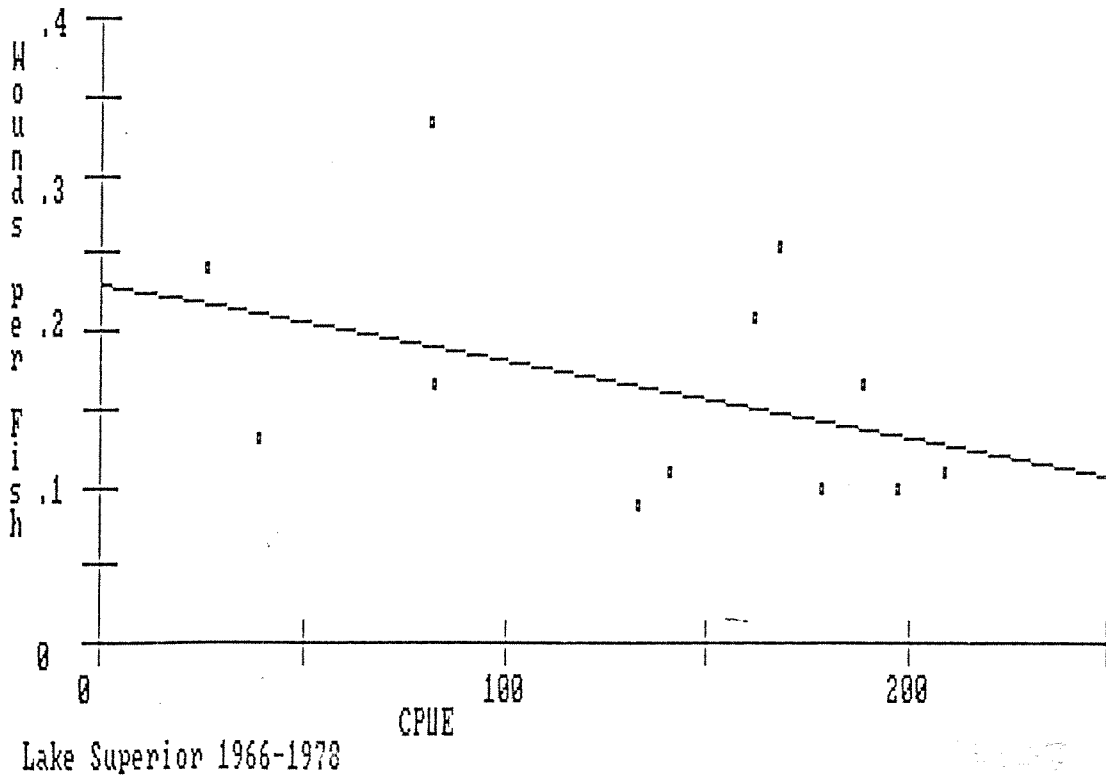


Fig. 10