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Research Completion Report *

THE EFFECT OF ENVIRONMENTAL VARIABLES ON THE POPULATION DYNAMICS OF SEA LAMPREY, *Petromyzon marinus*

by

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ABSTRACT

Hypotheses concerning the influence of environmental factors on population characteristics of sea lamprey (*Petromyzon marinus*) were tested using data collected by sea lamprey control and natural resources agencies. Discriminant analysis was used to classify 57 Great Lakes tributaries as positive or negative with respect to presence of sea lamprey ammocoetes. Eleven habitat (physical stream characteristics) and chemical (productivity related) variables were used as descriptors. Classification success was ~80% for both calibration and test data sets. Canonical variate analysis suggested that substrate size characteristics were most important in determining ammocoete presence/absence. Streams with ammocoetes had a higher proportion of sand and silt and a lower proportion of large particle sizes than streams without lamprey. As well, multiple regression of substrate size characteristics on catch-per-unit-effort (CPUE) was significant, suggesting that between stream differences in CPUE can be explained largely by the proportion of preferred particle size. Step-wise regression indicated that variation in growth rate between streams could best be explained by stream productivity characteristics (e.g. conductivity). We suggest that a transformation rate regression based on stream productivity could be developed because of the previously observed correlation between growth and metamorphosing lamprey.

The change in biological parameters (length, weight, sex ratio) of spawning phase lamprey was examined using time series analysis (1977 - 1987). Data indicated that these biological parameters remained relatively constant in the period following the implementation of control measures. We suggest that, considering the response of lamprey biological parameters to the initiation of control, the lamprey population may be in a steady state.

Spawning run capture data was not significantly correlated with discharge among Lake Ontario tributaries. These data do not support the hypothesis of lake wide allocation of spawning lamprey based on discharge. However, we did observe a significant relationship between spawners captured and discharge among Canadian tributaries of L. Ontario. Our results suggest that either the sample size of streams is not large enough to adequately discribe the relationshop between the abundance of spawning lamprey and discharge or that allocation of spawners to streams may occur in smaller geographical areas than the whole lake.

TABLE OF CONTENTS

INTRODUCTION

Reports of significant mortality to native fish stocks induced by parasitic sea lamprey (Petromyzon marinus) in the St. Laurence Great Lakes have appeared since the 1940's (history summarized by Smith and Tibbles 1980). The Great Lakes Fisheries Convention Act was signed in 1954 by the governments of Canada and the United States to resolve problems facing the fishery, including the effects from sea lamprey. In 1956, the Great Lakes Fishery Commission (GLFC) developed a sea lamprey control program in order to minimize the recruitment of parasitic lamprey to the lake populations. Hypotheses and results of research into the biology and control of sea lamprey were synthesized at a workshop in 1979 (Sea Lamprey International Symposium - Can. J. Fish. Aquat. Sci. 37). The principles of integrated pest management (IPM) were presented at that workshop (Sawyer 1980), expanded (Davis and Manion 1982; Eshenroder 1986) and were intended as a framework within which activities of the GLFC could be managed and assessed.

Systems models are incorporated in the IPM process so that the complexities of understanding and managing ecosystems can be accomplished rationally and quantitatively (Sawyer 1980). This principle resulted in the development of a systems model for the Great Lakes fishery community created through the adaptive management process (Spangler and Jacobson 1985 and subsequently modified by Koonce 1987). As with most systems models, the development of the IMSL (Intergrated Management of Sea Lamprey) model is an iterative process. Consequently, systems models are revised as the understanding of community relationships become more precise. This process enables the model to become more useful in the management process.

The IMSL model development included most aspects of sea lamprey life history, even though not all of these aspects had been well documented. As a result, some of the relationships were based on limited data, restricted by geographical constaints. Where no work had been done (e.g. ammocoete habitat suitability index HSI), relationships were based on control agent experience. The purpose of this study was to contribute to the knowledge of sea lamprey life history by quantitatively assessing some of the poorly documented relationships.

We assumed that the variation in physical/chemical environmental factors would affect sea lamprey throughout the Great Lakes basin in a similiar manner. In that context, we examined the relationship between physical/chemical factors and:

1) ammocoete presence/absence in streams
2) ammocoete relative abundance
3) ammocoete growth
4) spawning run abundance

In addition, we examined changes in spawning lamprey size and sex ratio in relation to lamprey abundance. These relationships have been examined previously to varying extents. However, we attempted to strengthen hypotheses and explore universality by extending our scope to steams and lakes in all of the Great Lakes basin.

MATERIALS & METHODS

1) Environmental factors influencing the presence of ammocoetes.

To determine if physical/chemical characteristics of streams could be used to classify Great Lakes streams as to their ability (or inability) to support sea lamprey ammocoetes, we used data from 57 tributaries of Lakes Superior (11), Huron (20), Erie (7), and Ontario (19). These streams had been previously assessed for lamprey presence - absence, substrate characteristics and water quality. Streams with obvious barriers to lamprey populations (i.e. streams that dried up in summer, or streams with dams or waterfalls that prevent spawning migration) were excluded from this analysis.

The Sea Lamprey Control Centre (SLCC, Sault Ste. Marie, ON.) visually classified the stream bottom at each sampling station into 6 substrate classes (Table 1). The mean of each substrate class was calculated from all stations in a stream. Because frequently treated streams were regularly surveyed between chemical treatments (3-5 y) and streams not treated were surveyed less frequently, data from one to three surveys were averaged to obtain values for bottom composition. Survey stations were not randomly selected but were biased towards areas in the stream perceived to most likely be occupied by lamprey (D. Cuddy pers. comm., Sault Ste. Marie). Consequently, our variables are an average for the "optimal habitat" in each stream.

We obtained average daily discharge measurements and stream temperatures for 42 streams from Water Survey Canada (1975; 1983; 1984; 1986). Water quality data and water temperatures for the remaining 15 streams were obtained from the Ontario Ministry of the Environment's stream water quality survey (Table 1). Discharge was calculated as the mean daily discharge over 3 y. Stream water temperature and water chemistry variables were calculated as the mean of approximately monthly samples over 1 to 3 y.

All analyses were performed using the micro-computer version 4.0 of Systat (Wilkinson 1988). Discriminant analysis was used to determine the influence of the 11 physical/chemical stream characteristics on occurrence of sea lamprey ammocoetes. The presence or absence of ammocoetes from survey records acted as the grouping variable and the 11 physical/chemical characteristics were the descriptors. Prior to analysis, data were transformed to normalize the distribution and stabilize the variance. The arcsin, square root transformation was used to normalize variables expressed as "percent" and log (x+1) transformation was used with all other data (Legendre and Legendre 1983). Streams were randomly separated into calibration (51 streams) and test data sets (6 streams). The canonical variate was calculated using the calibration data set and the robustness of the canonical variate was tested by using it to predict lamprey occurrence in the 6 streams of the test data set.

2) Environmental factors influencing the relative abundance of ammocoetes.

We used regression analysis to examine the relationship between relative abundance of sea lamprey ammocoetes and environmental variables. We selected 23 streams which had recent catch-per-unit-effort (CPUE) data, estimates of bottom composition and water chemistry data (see previous section for details on the methods used for water chemistry data collection). The average CPUE (number of lamprey captured per hour) was calculated from electrofishing and granular Bayluside (Bayer 73) population surveys. The method of collection used (i.e. electro-fishing vs. Bayer) was determined by stream size and survey conditions. Although these two collection methodologies have not been calibrated or compared, we assumed the most efficient technique was used on each stream. The stream characteristics used as descriptors in the discriminant analysis from the previous section (Table 1) were used as independent variables in a step-wise multiple regression with CPUE as the dependent variable. The criteria for variable coefficients of alpha = 0.05 to enter or be removed from the model was established a priori. A multiple linear regression was estimated following variable selection in the step-wise regression procedure (Wilkinson 1988). Residuals were plotted against estimated values and used in a box plot and probability plots in order to examine deviations from regression analysis assumptions.

3) Environmental factors influencing size of ammocoetes.

The objective of this analysis was to identify environmental factors influencing larval growth in Great Lakes tributaries. Few larval sea lamprey populations have been aged (Volk 1986; Medland and Beamish 1987; Beamish and Medland 1988) using techniques other than inspection of length-frequency histograms, because of the time required to process and analyze statoliths, and because of the constraints in the technique. For example, there is uncertainty whether an annulus is formed during transformation (T. Medland pers. comm., Univ. of Guelph). Some populations (Tahquamenon R.) do not form statoliths, and there is some suspicion that more than one annulus may be formed within a year. We used maximum likelihood statistical procedures (MacDonald and Pitcher 1979; MacDonald 1987) for estimating age-group parameters from size-frequency data.

To set constraints for our approach to analyzing larval sea lamprey size distribution data, we first plotted size at age (Figure 1) for known age (Manion and McLain 1971; Medland and Beamish 1987; Beamish and Medland 1988) larval lamprey populations. We found that when larvae were <110 mm, growth at age was generally linear. Growth rate of animals >110 mm decreased, resulting in the overlap of length frequencies of older age classes. Next, we used the maximum likelihood analysis (MIX, Ichthus Data Systems) on aged populations (Figure 2) where data had been provided (see sources above). For the Bent Creek population (Medland and Beamish 1987) the mean lengths, certainly for the first four age groups, were as expected. The proportion of the youngest age group, however, was lower than what one would expect, perhaps a result of sampling bias (small larvae not adequately sampled) or unequal recruitment among years.

From our analysis, it became clear that adequate interpretation of size distributions was only possible prior to the onset of asymptotic growth. As a result, we confined our analysis to that portion of the distribution where animals were <110 mm (generally < age IV). With these constraints, our analysis coincided with size at age assigned for three of five aged populations (from Medland and Beamish 1987; Beamish and Medland 1988), the exceptions being the Big Garlic River and Lynde Creek (where we underestimated the number of age classes by one). While we have hypotheses to explain these differences, it is sufficient to recognize the consistency among the aged populations and our length-frequency analysis.

Survey and/or chemical treatment collections of larval sea lamprey were selected for 17 streams which had a strong data base for environmental factors. Age class I and II were statistically defined using MIX analysis. Mean length for age class II was adjusted for a standard age of 24 months by weighting the length against annual growth between age class I and II (Table 2). Age class II was selected for comparison because it is well represented in electrofishing surveys and chemical treatments, and schedules for chemical treatments in Lake Ontario tributaries are established when the predominant age class in the streams is age II. Although none of the ammocoetes used in the MIX analysis were aged by examination of statoliths, we were confident of the number of age classes in each stream because of the robustness of the length frequency analysis and because the number of potential spawning runs between treatments was known.

The mean size of year class II was used as the dependant variable in a step-wise regression with the environmental variables of sections 1 and 2 (Table 1). Data were re-analyzed following variable selection in step-wise regression in order to estimate regression coefficients. Residuals were examined for deviations from regresion analysis assumptions.

MIX analysis was used to statistically describe year classes of larval and transforming sea lampreys from four tributaries of Lake Ontario in accordance with the criteria established above. All samples used in this analysis were from stream treatment collections. Statolith aging of transformers from Salem Creek and Chipewa River indicate transformation occurs from age II+ to IV+. However, non-random selection of specimens and small sample sizes (N=15) precluded partitioning mean length proportions and variances of length frequency histograms based on aged specimens. We were unable to separate year classes of transformers with confidence using MIX, therefore we assumed (probably erroneously) that all transformers were from one age class. Transformation rate was calculated as the ratio of the number of transformers to number of animals >110 mm.

4) Influence of environmental variables on the size of sea lamprey spawning runs.

The objective of this analysis was to further examine the apparent relationship between the abundance of spawning run sea lamprey and stream discharge. There has not been a sufficient number of spawning run population estimates to test this hypothesis in any of the Great Lakes with the exception of L. Superior (Daugerty et al. 1987; Meyer 1984). However, 12 streams in L. Ontario were trapped regularly during the period 1986-88 (Daugerty et al. 1987, 1989; Dustin et al. 1988) using both dam and portable traps.

A positive relationship between discharge and the size of the sea lamprey spawning run would imply that larger steams have proportionately larger runs than smaller streams. We examined the hypothesis of lake-wide allocation of spawning lamprey with the regression of the mean number of lamprey trapped during 1986-88 against the mean discharge recorded by SLCC during spring (May-June) treatments.

The capture statistics used in this study could be misleading if trap effectiveness was significantly different between trapping techniques or if capture statistics did not accurately reflect population abundance estimates (from mark-recapture studies). We calculated trap effectiveness (i.e. # of lamprey captured * population estimate $^{-1}$) for all streams with population estimates reported by GLFC (Daugerty et al. 1987, 1989; Dustin et al. 1988). Dam traps had greater trapping effectiveness than portable traps by a factor of approximately 2.2 (Table 7). We adjusted the portable trap catch statistics in our data set to reflect this difference. As well, the correlation between the capture statistics and population estimates was significant ($P < 0.05$, $R > 0.9$) for both trapping techniques. Consequently, we were confident that the capture statistics, adjusted for trapping technique, were an accurate reflection of the spawning run populations.

The correlation between SLCC discharge data and those streams continuously monitored by Water Survey Canada was significant. Therefore, we assumed that SLCC discharge data accurately reflected relative stream size.

5) Are size and sex ratio influenced by population abundance?

SLCC in Sault Ste. Marie, ON. and Marquette, MI. annually trap sea lamprey spawning runs to monitor sea lamprey abundance and condition. We examined data collected from 1978 to 1987. The relative abundance in Lakes Superior, Huron and Ontario was determined from the sum of animals captured each year in one or more index stations. Streams were used if they were consistently trapped (at least 9 of the 10 year study period) and if the same trapping methodology was maintained throughout the study period. Three streams from L. Superior (Big Garlic, Rock and Tahquamenon), two from L. Ontario (Bowmanville and Wilmot) and one from L. Huron (Thessalon) were selected. We are aware that there are factors that affect capture statistics but it is beyond the scope of this report for these factors to be considered.

The control agents retained a sub-sample of the animals captured for further biological studies from throughout the run. The length, weight, and sex ratio were reported in the GLFC annual reports. We calculated a weighted average based on the number of animals captured in the index streams for length, weight and sex ratio.

We used multivariate regression procedures (Wilkinson 1988) to examine the relationship between sea lamprey relative abundance with size and sex ratio. For each lake we calculated the multivariate regression of logged length, weight and sex ratio against the log of relative abundance. We examined the residuals for deviation from regression analysis assumptions.

RESULTS & DISCUSSION

1) Environmental factors influencing the presence of ammocoetes.

The discriminant analysis successfully classified 82% of the 52 streams in the calibration data set for sea lamprey presence (Table 3). The rate of successful classification was similar between streams with and without lampreys (84% vs 80%). The canonical variate was able to successfully predict all streams without lampreys and two of three streams with lampreys in the test data set (Table 3). Of the five streams that produce ammocoetes and were misclassified in the calibration data set, four (Boyne R., Little Pic R., Wanapetei R. and Oakville Cr.) were inconsistent or low producers of lamprey, and were treated less frequently. These streams may represent only marginal habitat. The Ausable River was misclassified as having lamprey. Lamprey production in this stream may be adversely affected since the lower part of this stream has been channelized, a process which usually eliminates depositional areas and produces very homogeneous habitat (Hynes 1970; Chapman and Knudsen 1980). Streams that had sea lamprey ammocoetes had significantly greater flow, a higher proportion of sand and silt, a lower proportion of bedrock, rubble and clay, as well as lower conductivity than streams without ammocoetes (Figure 3). Discharge, conductivity, bedrock, clay and silt also had the highest standardized canonical coefficients (Table 4) among variables that were significantly different between streams with and without ammocoetes. However, discharge and silt were positively correlated ($P < 0.01$) and were most likely acting as one variable in our discriminant analysis. Thus, the coefficient for the effect described by discharge and silt may have been split between the two variables (Bock 1975). Although the proportion of gravel was not significantly different between streams with and without ammocoetes, it had a large canonical coefficient suggesting that it was important to the analysis because it was acting to suppress within group variance. The relatively high canonical coefficient of conductivity may have been an artifact as we were unable to include a proportionate number of negative streams from northern Ontario, an area which typically has low conductivity in streams.

Our analysis suggests that between stream differences in lamprey occurrence is largely a function of particle size or variables correlated with particle size. Four of the five variables that had the highest canonical coefficients were substrate size variables and discharge. These results are similar to previous studies of lamprey (Malmqvist 1980) and fish occurrence (e.g. Binns and Eiserman 1979; Layer et al. 1987) in that relatively few variables (3-9) in these studies were required to explain a significant proportion of occurrence or biomass variation. Our results suggest that larval sea lamprey occurrence in the Great Lakes streams of our study can be explained in large part by the presence of suitable burrowing habitat (silt and sand) and the absence of difficult burrowing habitat (bedrock, rubble and clay).

2) Environmental factors influencing the relative abundance of ammocoetes.

The stream variables retained by step-wise regression included discharge and gravel (Table 5). The multiple-regression model using discharge and gravel to predict CPUE was significant ($P < 0.01$). However, examination of residual plots identified Shelter Valley Creek as an outlier because its CPUE was disproportionately higher than other streams in this study. With Shelter Valley Creek excluded from the analysis, the variance explained by the regression model was again significant ($R^2 = 0.524, P = 0.001$). Both discharge and gravel had positive standardized regression coefficients (Table 5), suggesting that streams with greater flow and more gravel had higher lamprey CPUE. However, discharge was positively correlated with sand and silt, and negatively correlated with rubble and clay suggesting that discharge is integrating the variation explained by most of the substrate variables. To test this hypothesis, we re-analyzed the data using the six substrate variables to predict CPUE. The variance explained by this model was significant ($R^2 = 0.540, P = 0.024$), suggesting that substrate type alone can explain as much variance as the discharge - gravel model.

It is unlikely that discharge is the cause of sea lamprey abundance variation. However, discharge is an excellent predictor variable for lamprey abundance in this study because it is usually correlated with variables previously suggested (Potter et al. 1986; Malmqvist 1980) to be important in determining lamprey abundance (e.g. substrate particle size, the amount of organic material in the substrate, chlorophyll "a" and substrate stability). Our conclusion is similar to those of Malmqvist (1980) and Thomas (1962, 1963) who suggested that most of the significant factors affecting lamprey abundance are due to gradient. As well, Hynes (1970) and Vannote et al. (1980) suggest that biological communities are largely regulated by fluvial geomorphic processes. Therefore, it is likely that between stream differences in lamprey populations is a function of stream size, gradient and local geology.

3) Environmental factors influencing size of ammocoetes.

Adjusted mean lengths of year class II

ammocoetes ranged from 44 mm to 131 mm in the 17 streams used in this analysis. The stepwise regression using the environmental variables to explain size variance indicated that only conductivity was significant. Linear regression using conductivity to predict ammocoete size (Figure 4) was significant ($R^2 = 0.624$, $P < 0.001$), suggesting growth was dependent on stream productivity (as reflected by stream conductivity).

Although conductivity was not significant in explaining the relative abundance of ammocoetes among streams (Table 5), it was the only variable we found to be significant in explaining differences in size among streams. Lamprey from hardwater streams (i.e. high conductivity) grew more quickly than lamprey from softwater streams, which are considered to be less productive (Ryder 1965).

Economic injury to salmonids induced by sea lamprey occurs only after larval lamprey "transform" to the parasitic phase of the life cycle and migrate to the lake environment. Although there are no definitive data indicating the factors controlling the metamorphic process in lamprey (Youson 1980), transformation of sea lamprey rarely occurs before an individual reaches 120 mm in length (Potter 1980). Given the strong observed correlation between ammocoete length at age and transformation, our results suggest that an empirical relationship describing transformation could be derived based on an adequate representation of stream productivity.

The range of transformation rates was from 17.35% to 50.50% (mean = 29.5%) of ammocoetes greater than 110 mm (Table 6). The oldest age classes in these populations ranged from II+ to III+. The transformation rates calculated here should be viewed with some skepticism since we are unable to determine either the number of age classes of ammocoetes and transformers >110 mm or their proportions of the collections. Verification of transformation rates will require statolith aging of random samples of ammocoete and transformation collections, as well as a thorough evaluation of the aging technique.

4) Influence of environmental variables on the size of sea lamprey spawning runs.

The regression of spawning run capture data against stream discharge was not significant ($R^2 = 0.095$, $P = 0.329$) for L. Ontario tributaries (Figure 5). These data do not support the hypothesis of lake-wide allocation of prespawning lamprey based on stream discharge. However, we observed a significant relationship between spawning run capture and discharge among the Canadian tributaries of L. Ontario ($R^2 = 0.80$, $P = 0.007$, Figure 6). The apparent absence of a relationship between capture data and discharge among L. Ontario tributaries is not consistent with Daughery et al. (1987) who observed a significant linear relationship for L. Superior tributaries. Meyer (1984) reported a significant correlation between electrical barrier capture data and discharge but not between assessment trap captures and discharge.

We re-examined the data presented in Daugherty et al. (1987) in an attempt to find an explanation for the contradictory results (Figure 7). Our analysis differed in that we used regression with a constant. The results of the two studies were similar (Table 8). However, we were concerned that the distribution of points along the discharge axis was unevenly distributed. Data were concentrated in two clouds of points at either end of the discharge axis with most of the data coming from smaller streams. We suggest that paucity of data from intermediate sized streams and the large variation in spawning run abundance among larger streams weakens the conclusion of linearity. The three points associated with larger streams were identified by regression diagnostics as having unusually large residuals (violating the assumption of stable variance along the discharge axis), influence (Cook's D statistic) or both (Figure 8). We re-analyzed the data excluding the largest 3 streams. Even though the remaining 10 streams (76% of the original data) spanned almost an order of magnitude in discharge ($0.4\ m^3{*}sec^{-1}$ to $3.4\ m^3{*}sec^{-1}$) we found no linear relationship between spawning run abundance and discharge ($R^2 = 0.14$, $P = 0.29$).

We were able to correct most of the problems with unstable variance and the unbalance selection of streams along the discharge axis by using a log transformation of the population estimates and discharge. The log transformation compressed the axes which stabilized the variance and reduces the influence of the larger streams. The fit of this model was significant but the percent of variance explained was less than the origninal analysis. As well, the use of log transformations to fit the model indicates that there is not a simple linear relationship between discharge and the size of spawning runs. A log-log transformation suggests a curvilinear relationship between spawning run abundance and discharge (Sokal and Rolf 1981), which is not immediately evident from Figure 7.

The hypothesis that spawning run abundance increases with stream discharge is intuitively appealing. However, our results from L. Ontario are not consistent with this hypothesis. We suggest that an experiment with adequate replication in all sizes of streams is needed before any conclusions can be made regarding the relationship of spawning run sizes and abundances. The significant regression observed when the L. Ontario data was restricted to the Canadian tributaries suggests that stream size may be important in geographical areas smaller than the whole of L. Ontario. It is possible that lamprey may be in localized areas (e.g. based on the distribution of salmonids within the lake) prior to the spawning run. Consequently, lamprey could select streams (proportional to discharge) from those in their immediate vicinity.

The proportion of pre-spawning lamprey allocated to a stream in the spawning phase sub model of IMSL (Spangler and Jacobson 1985 is determined by the function:

$$\text{Proportion Allocated} = 0.5*(SQ*TQ^{\cdot -1}) + 0.5*(SD*TD^{\cdot -1})$$

where SQ is stream discharge, TQ is total discharge to the lake, SD is stream abundance of ammocoetes and TD is total ammocoete abundance. This allocation protocol suggests that pre-spawning lamprey are attracted by streams with large discharge and/or by streams with large populations of ammocetes. Our analysis indicates that there is not strong evidence to support lake-wide allocation based on discharge in L. Ontario. Moore and Schleen (1980) and Teeter (1980) present data that support the hypothesis that spawning lamprey are attracted by an unknown pheromone released by ammocetes. However, the largest spawning run in L. Ontario among streams trapped by sea lamprey control agents occurs in the Humber R. where there are few, if any, ammocetes. As well, large runs occur in streams (e.g. Shelter Valley Creek) where ammocoete populations have been reduced by the construction of low head barrier dams and other obstructions. The lack of ammocete population estimates in streams concurrent with estimates of spawning-run abundance precludes any test of interaction between the two factors in the spawning run allocation function.

We do not refute the intuitive appeal of the two relationships utilized by the spawning phase sub model of IMSL. However, given the importance of these relationships to the predictions and outputs of this submodel, we suggest that it is imperative that further studies are conducted and directed at clarifying the apparent contradictions.

5) Are size and sex ratio influenced by population abundance?

i) Lake Superior.

The number of lamprey captured each year ranged from 469 to 1357. Our data set did not contain a sufficient number of years to statistically test for trends (Legendre and Legendre 1983). However, the number of animals captured was variable but appeared to have declined through the study period (Figure 9). Length, weight and sex ratio remained relatively stable through this period (Table 9) and exhibited no apparent trend. Consequently, the multivariate regression of size and sex ratio variables versus relative abundance was not significant ($F = 1.113$, $P = 0.426$).

ii) Lake Ontario.

Annual capture rate in the two index streams varied by an order of magnitude during the study period (Table 9). No monotonic trend is evident from the data suggesting that relative abundance varied greatly during the study period. Length and weight remained relatively stable during this period, varying by less than 6% of the mean. Sex ratio varied more as the proportion of males captured ranged from 46.5% to 63.6%. The multivariate regression of biological characteristics versus capture rate was not significant (F=3.13, P=0.11). However, there was a significant relationship between the log sex ratio and log capture ($R^2=0.59$, P=0.009). This may be a spurious observation since the multivariate regression was not significant.

iii) Lake Huron.

Capture rate at the Thessalon R. varied from 230 to 4566 during the study period. The pattern of capture was similar to the L. Ontario index streams in that capture rate varied greatly but showed no linear trend through the study period. As well, length and weight remained relatively stable during the study (Table 9). The sex ratio varied greatly with the proportion of males ranging from 36% to 62%. The multivariate regression of the biological characteristics and capture rate was significant (F=6.26, P=0.038). This relationship can largely be attributed to the significant relationship between the log of sex ratio and log capture rate ($R^2=0.74$, P=0.003).

The factors that influence length and weight include intra-specific competition, availability of suitable hosts and water temperature (Heinrich et al. 1980; Kitchell 1980) among other environmental factors. Our observations suggest that the size of lamprey has remained relatively stable during the period from 1978-87. These data are consistent with Heinrich et al. (1980) who observed a period of increasing pre-spawning lamprey size that occurred after chemical control of ammocoetes and fish stock rehabilitation was initiated. Lamprey size appeared to peak and remain relatively stable. Our data suggest the main factors influencing within lake lamprey size variation (i.e. lamprey abundance and salmonid availability) are at levels that do not appear to affect lamprey size.

The factors that affect pre-spawning lamprey sex ratio are more ambiguous than those affecting lamprey size. Periods of large lamprey populations have been correlated with a preponderance of males in the population (Heinrich et al. 1980). However, sex differentiation of brook lamprey occurs during the ammocoete stage and may be affected by a number of factors, including larval density. If the same mechanism applies to sea lamprey, large male populations would result from streams with high densities of ammocoetes. High pre-spawning lamprey abundance could also result from increases in ammocoete abundance. Thus, sex ratio and pre-spawning lamprey capture abundance may fluctuate together, mediated by chemical control cycles.

In conclusion, there were no significant relationship between lamprey size and capture abundance in Lakes Superior, Huron and Ontario. However, variation in sex ratio were correlated with changes in capture rates from index streams in Lakes Huron and Ontario. We speculated that density dependent factors during larval development affected sex ratio and relative abundance. Parasitic populations are likely low enough in relation to salmonid availability to maintain stability in lamprey size.

GENERAL DISCUSSION

While there have been reviews of techniques, summaries of life history data (Johnson 1987), and scientific workshops (Sea Lamprey International Symposium 1979), a number of identified hypotheses (Walters et al. 1980) have remained untested. These hypotheses, often originating from uncorroborated assumptions (outlined earlier), formed the focal point for our analysis. Our results have been directed solely at the life history of the sea lamprey and have ignored, by and large, their relation to the fishery of the Great Lakes. The data originated from pre-treatment assessments of ammocoete abundance and the presence of transformers, or assessments of spawning phase adults in tributaries, all designed to direct efforts to control sea lamprey populations. As a consequence, data collection was not designed for the purpose for which it was used and our assessment must be viewed with these constraints in mind.

The intrinsic ability of sea lamprey to disperse and increase in abundance has been recognized (e.g. Pearce et al. 1980; Morman et al. 1980; Smith and Tibbles 1980). However, it was uncertain (Walters et al. 1980) whether stream habitat limited lamprey colonization and production, or whether prey abundance at high lamprey densities imposed population regulation. Our discriminant analysis suggests that substrate properties are effective in describing the presence/absence of ammocoetes. Consequently, regional dispersion may well have been limited by availability of suitable habitat. Further, for those streams in which lamprey exist, substrate characteristics explained a significant portion of the variation in catch per unit effort. While we recognize that between stream differences in lamprey abundance are likely a result of fluvial geomorphic processes (Hynes 1970; Vannote et al. 1980), we feel these differences can be adequately described by differences in stream gradient or substrate.

Density and temperature have been suggested as dominant factors in regulating growth and transformation of larval sea lampreys (Purvis 1980). Our results suggest that stream productivity as reflected by conductivity (or alkalinity) is related to growth of ammocoetes in situ. Ryder and Pesendorfer (1988) suggested that chemical differences among streams are extremely important as determinants of their productivity. However, it is likely that space limitations (strongly influenced by stream gradient) combined with trophodynamic processes (temperature and nutrient sources may operate in concert in the Great Lakes) dominate growth and ultimately transformation in Great Lakes sea lamprey populations.

Although the relation between discharge and abundance (Meyer 1984; Daugerty et al. 1987) and the attraction of adults to streams containing ammocoetes have been suggested (Moore and Schleen 1980), factors influencing the size of spawning populations has received only limited attention. Although our analysis provides limited support for this hypothesis, it also identifies the strong need for additional research in order to clarify this relationship. Further, we are uncertain how this relationship would apply to streams which do not support lamprey populations. We submit that properties unique to streams, particularly gradient as it affects discharge and habitat, bear a considerable influence on all aspects of sea lamprey life history.

Sea lamprey are expected to grow more quickly and the proportion of females increase when populations are reduced (Heinrich et al. 1980). We did not observe a response of lamprey size to variation in pre-spawning lamprey abundance but did observe a significant correlation of abundance with sex ratio in two of the three lakes examined. The examination of these properties of sea lamprey populations is possibly inappropriate in the absence of adequate characterization of prey, therefore we attribute limited significance to these results. However, we feel that our result may reflect a steady - state in the balance of lamprey to salmonids in the Great Lakes.

The modelling of sea lamprey population dynamics and lamprey-salmonid interactions is one of several facets in the implimentation of IMSL by the GLFC (Davis and Manion 1982). Its purpose should be to bring together the current understanding of population biology and pinpoint information gaps that will lead to a more effective lamprey control program. Although it was not the original purpose of this study, we have identified some areas in which the IMSL systems model might be improved. For example, the current ammocoete sub-model uses an untested qualitative habitat suitability index and does not incoporate any function that describes variation in rates of transformation between streams. Our analyses suggest that the distribution and possibly the relative abundance of ammocoetes are affected by variables describing substrate size. We also identified stream productivity variables as important predictors of size at age and suggest the same variables could be used to predict rate of transformation. As well, we identified potential weakness of the spawner allocation function used in the IMSL system. Additional work is required to describe the relationship of stream discharge with the size of spawning runs as well as other factors infuencing the allocation of spawners to streams.

Our analyses also identify serious information gaps concerning sea lamprey population dynamics. Very few ammocoete population or density estimates have been published from tributaries of the Great Lakes. There is little understanding on how variation in physical, chemical and biological factors or various control stategies affect growth, survival, and transformation of ammocoetes. At present, there is no mechanism to predict or evaluate the number of animals entering the parasitic population. As well, additional research is required to make accurate assessments of the mortality (or economic loss) induced by the parasitic population on the fish community of the Great Lakes. Thus, there is little quantitative information to make decisions regarding optimal allocation of current sea lamprey control measures or how alternative control stategies will affect sea lamprey population dynamics. Further quantitative population biology research is imperative to the successful implimentation of IMSL and ultimately to future improvements in lamprey control and program assessment.

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TABLE 1. Range of values of variables used in discriminant analysis of presence/absence data.

VARIABLE	**MEAN**	**MAX**	**MIN**	**SIGNIFICANCE**
Bedrock	0.110	0.735	0.000	$P<0.05$
Rubble	0.281	0.735	0.000	$P<0.05$
Gravel	0.381	0.774	0.000	$P<0.05$
Sand	0.551	0.984	0.201	$P<0.05$
Silt	0.522	0.920	0.000	$P<0.05$
Clay	0.355	0.645	0.000	$P<0.05$
Discharge	2.005	5.810	0.171	$P<0.05$
Temperature	2.442	2.970	2.054	$P<0.05$
Conductivity	5.780	7.155	3.829	$P<0.05$
Dissolved Oxygen	2.420	2.565	2.175	$P>0.05$
Suspended Sediments	3.031	5.069	0.531	$P>0.05$

TABLE 2. Mean Length of Age Class II larval sea lamprey from selected streams.

Stream Name	Year	Age (mo)	Mean Length (mm)	L1-L2 (mm)	Correction Factor	Length at 24 mo. (mm)
Chippewa R. (MI)						
-Upper	1987	29.0	109.84	29.20	-12.71	97.67
-Lower	1987	29.0	148.99	42.79	-17.83	131.16
Batchewana R.	1983	26.5	61.80	23.58	-4.91	56.89
	1980	26.5	62.75	24.43	-5.09	57.66
Black R.	1987	26.0	110.29	39.71	-6.62	103.67
Bowmanville Cr.	1985	22.5	107.42	57.90	+7.24	114.66
-Soper Br.	1985	22.5	84.87	48.60	+6.08	90.95
Bronte Cr.	1982	27.0	103.53	35.70	-8.93	94.60
	1980	22.5	88.93	46.90	+5.86	94.79
	1977	22.5	88.06	48.73	+6.09	94.15
	1974	22.5	85.16	45.59	+5.70	90.86
Credit R.	1987	22.5	118.74	62.51	+7.81	126.55
Duffin Cr.	1980	27.0	118.54	41.81	-10.45	108.09
Farewell Cr.	1985	22.5	97.85	55.03	+6.88	104.73
Garden R.	1984	23.5	64.21	29.65	+1.24	65.45
	1979	27.5	76.93	29.11	-8.49	68.44
	1970	25.0	68.93	30.07	-2.51	66.42
Goulais R.	1988	26.0	70.98	24.03	-4.01	66.97
Grindstone Cr.	1984	23.5	62.07	24.66	+1.03	63.10
	1982	22.5	58.82	29.29	+3.66	62.48
Kaministiquia	1986	25.0	86.40	46.31	-3.86	82.54
Lynde Cr.	1984	22.5	90.41	46.81	+5.85	96.26
	1983	23.0	94.84	53.18	+4.43	99.27
	1983	27.0	117.48	42.29	-10.57	106.91
Michipicoten R.	1986	24.5	59.53	27.18	-1.13	58.40
	1982	25.5	71.37	29.80	-3.73	67.64
	1979	25.5	68.80	34.19	-4.27	64.53
Mississagi R.	1987	24.5	51.83	15.76	-1.97	49.86
	1983	24.5	58.84	23.88	-1.00	57.84
Muskoka R.	1987	23.5	55.99	20.31	+0.85	56.84
Nipigon R.	1984	25.5	50.40	17.52	-2.19	48.21
	1979	24.5	45.62	19.96	-0.83	44.79

Stream Name	Year	Age (mo)	Mean Length (mm)	L1-L2 (mm)	Correction Factor	Length at 24 mo. (mm)
Salem Cr.	1985	27.0	82.02	31.88	-7.97	74.05
	1985	22.5	70.23	34.67	+4.33	74.56
	1984	27.0	89.13	30.53	-7.63	81.50
Sand Cr.	1987	28.0	105.33	29.02	-9.67	95.66
	1978	25.0	95.77	51.00	-4.25	91.52
Shelter Valley Cr.	1982	27.0	96.35	43.77	-10.94	85.41
	1981	23.0	74.08	30.20	+1.26	75.34
	1974	22.5	74.24	37.82	+4.73	78.97
Silver Cr.	1979	23.5	68.74	35.37	+1.47	70.21
	1976	24.0	94.37	50.49	0.00	94.37
	1972	23.0	68.14	34.01	+2.83	71.54
Skinner Cr.	1983	23.0	69.84	32.95	+2.75	72.59
	1978	28.5	85.82	28.30	-10.61	75.21
Spanish R.	1981	25.5	83.12	29.62	-3.70	79.42
St. Marys R.	1984	24.0	47.05	14.03	0.00	47.05
	1980	25.0	42.66	15.87	-1.32	41.34
	1975	26.0	51.21	12.50	-2.08	49.13
Wanapitei R.	1987	23.5	68.02	34.14	+1.42	69.44
Wilmot Cr.	1983	24.0	84.19	51.57	0.00	84.19
	1982	27.0	98.44	35.81	-8.95	89.49
White R.	1988	25.5	59.22	19.40	-2.43	56.79

TABLE 3. Classification success of discriminant analysis using (a) calibration data and (b) test data.

A.

	Absent	Present
Correctly Classified	17	26
Misclassified	4	5
Total	21	31

B.

	Absent	Present
Correctly Classified	3	2
Misclassified	0	1
Total	3	3

TABLE 4. Standardized canonical coefficients of variables used in discriminant analysis.

Variable	Canonical Coefficient
Bedrock	-0.48
Rubble	-0.04
Gravel	0.94
Sand	0.04
Silt	0.36
Clay	-0.39
Discharge	0.81
Dissolved Oxygen	0.07
Conductivity	-0.55
Temperature	0.10
Suspended Sediments	0.38

TABLE 5. Coefficients and regression ANOVA of CPUE vs. habitat variables.

VARIABLE	COEFFICIENT	STANDARDIZED	P
Constant	0.77	0.00	0.825
Discharge	0.08	0.49	0.013
Gravel	5.81	0.80	0.001

ANOVA

SOURCE	S.S.	DF	M.S.	F-RATIO	P
Regression	1485	2	743	10.48	0.001
Residual	1351	19	71		

TABLE 6. Transformation rates of age classes >110 mm from four Lake Ontario tributaries.

STREAM	AGE OF POPULATION >110 mm	TRANSFORMATION RATE (%)
Duffin Creek	2+	27.7
Farewell Creek	2+	17.4
Salem Creek	3+	22.5
Shelter Valley Creek	3+	50.5
Mean		29.5

TABLE 7. Comparison of trap effectivenes (# of animals captured/ # in spawning run estimate) and the correlation between the number captured and spawning run estimates for dam and portable traps.

Trap Type	n	Effectiveness	r
Portable	15	0.29	0.93
Dam	14	0.65	0.96

TABLE 8. Comparison of regression statistics from the analysis of GLFC (1986) and the reanalysis of the data in this study.

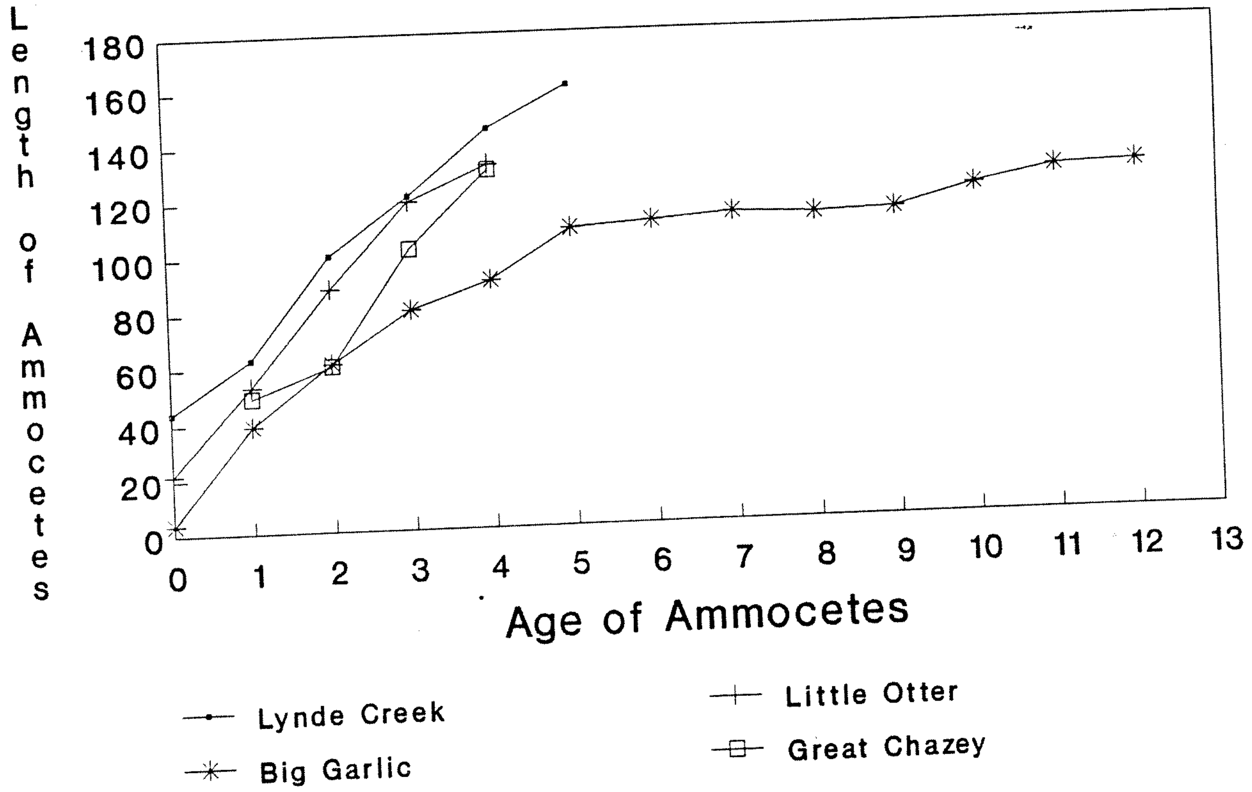
Analysis	Constant	Coeffecient	R^2	p
GLFC (1986)	na	0.73	0.67	<0.001
This study	-122	11.10	0.56	0.003

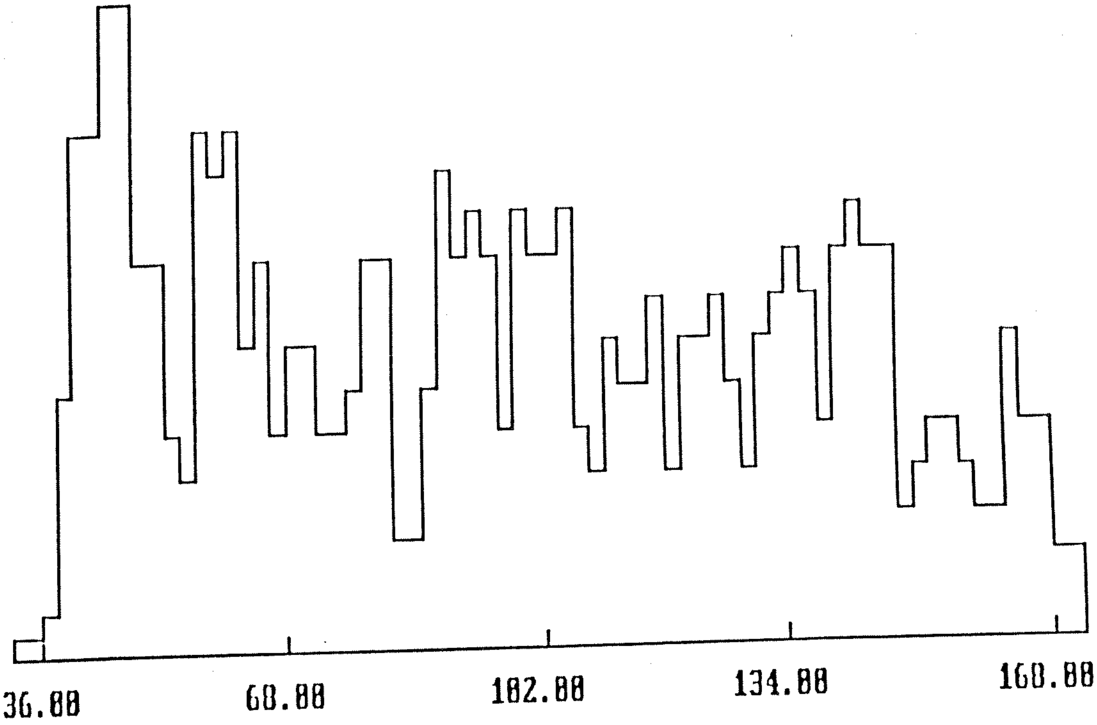
TABLE 9. Range in size, sex ratio and # captured observed at index stations in L. Superior, Huron and Ontario.

	L. SUPERIOR				**L. HURON**				**L. ONTARIO**			
	#Captured	**Length**	**Weight**	**% Males**	**#Captured**	**Length**	**Weight**	**% Males**	**#Captured**	**Length**	**Weight**	**% Males**
Min	469	410	158	30	230	450	182	36	77	465	235	46
Max	1357	430	179	41	4566	492	249	62	774	498	270	64
Mean	987	422	168	36	1320	472	231	50	344	482	254	58
S.D.	320	7.8	8.3	4.0	1452	14.2	21.1	9.5	242	11.1	13.2	5.8

FIGURE 1. Length at age for ammocoetes collected in 4 Great Lakes tributaries (data from Beamish and Medland 1988; Manion and Smith 1978)

FIGURE 2. Maximum likelihood analysis of brook lamprey collected from Bent Creek (Medland and Beamish 1987)

Length of Ammocetes
180
160
140
120
100
80
60
40
20
0
0
1
2
3
4
5
6
7
8
9
10
11
12
13
Age of Ammocetes
Lynde Creek
Big Garlic
Little Otter
Great Chazey


36.00
60.00
102.00
134.00
160.00

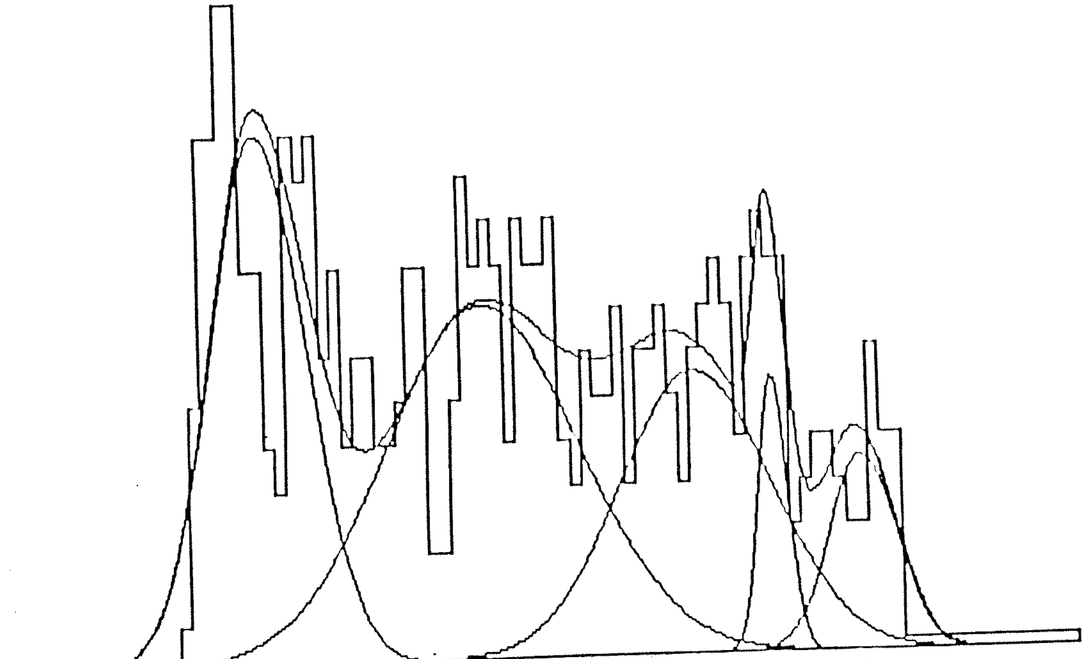


FIGURE 3. Frequency polygon of discriminant analysis scores from 52 streams. Stippled area represents the streams misclassified.

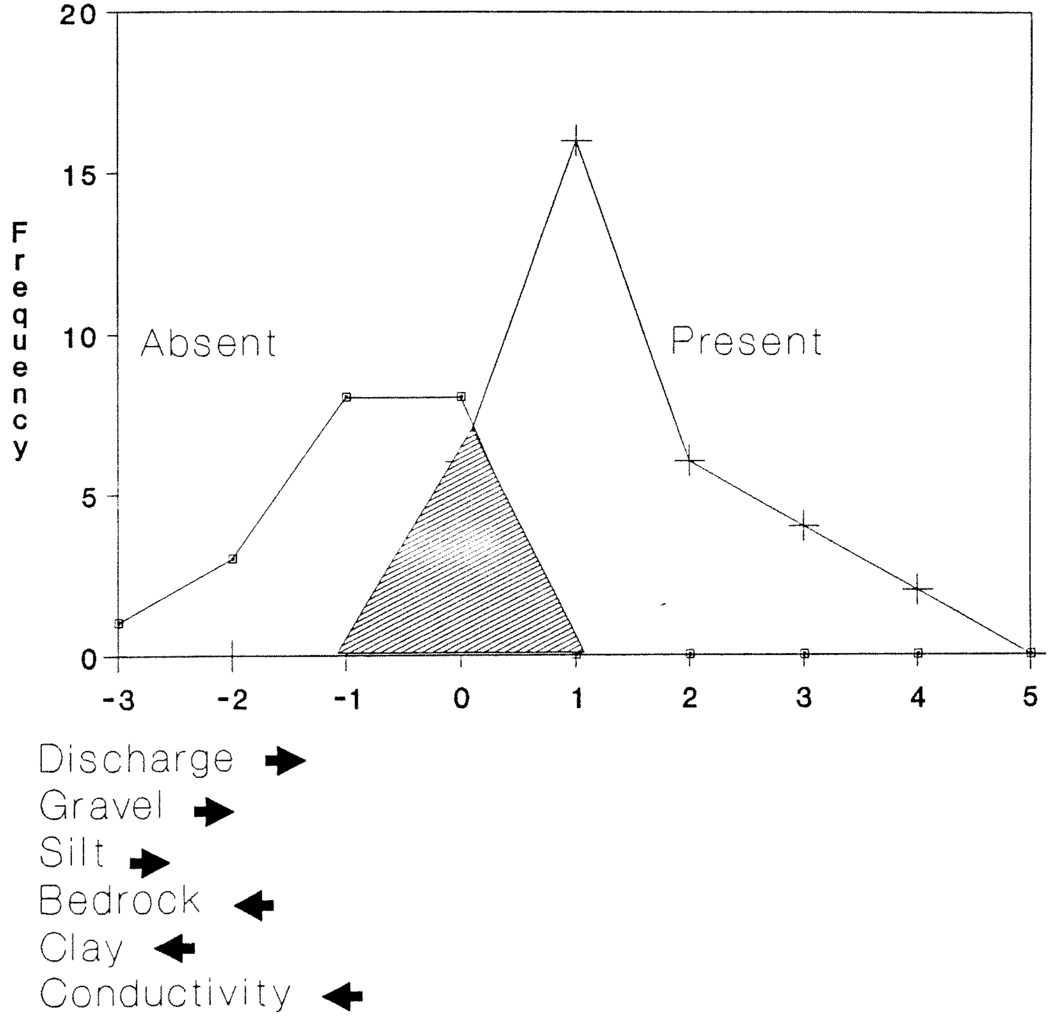
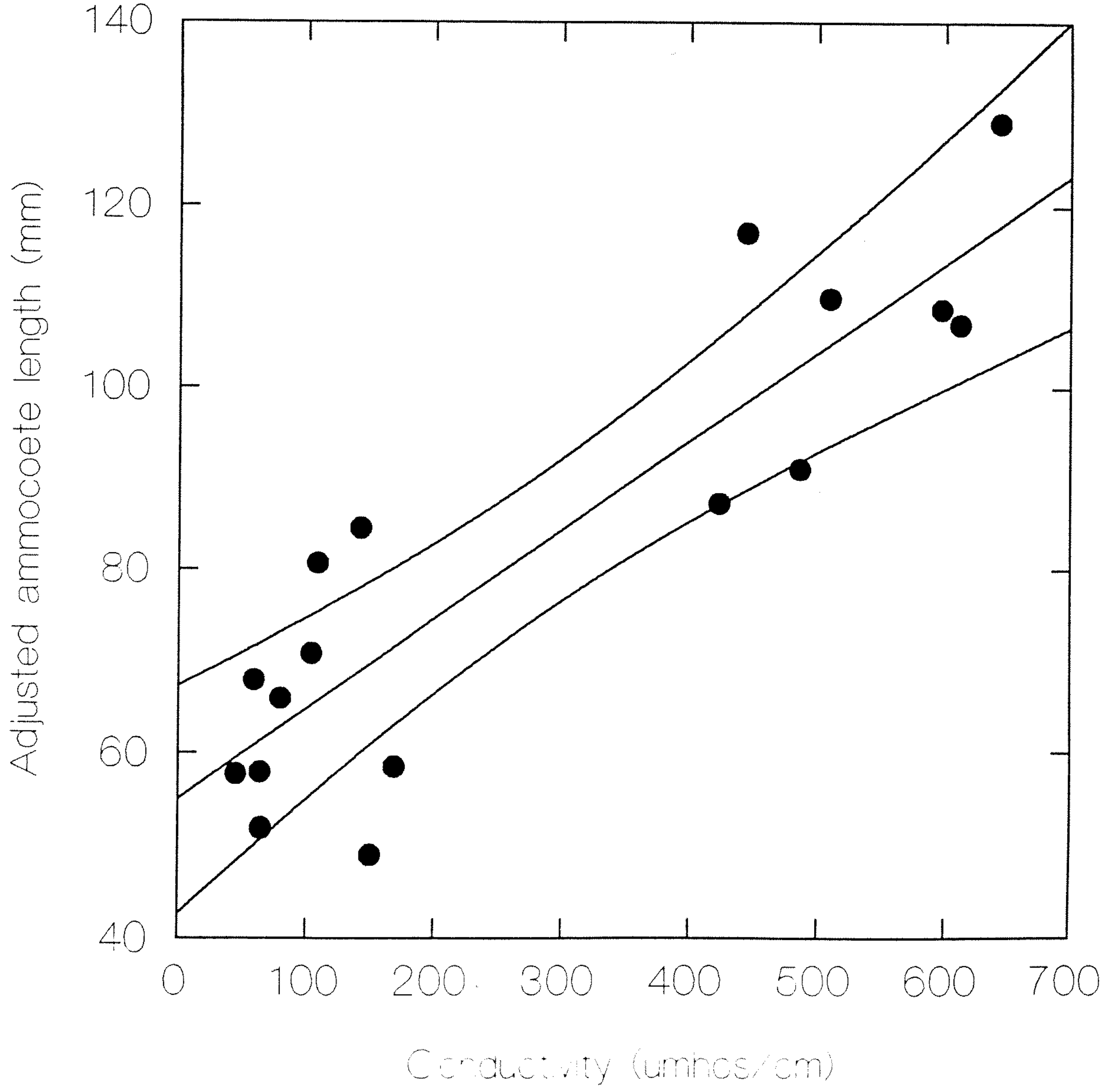

Frequency
20
15
10
5
0
-3
-2
-1
0
1
2
3
4
5
Absent
Present
Discharge ➡
Gravel ➡
Silt ➡
Bedrock ⬅
Clay ⬅
Conductivity ⬅

FIGURE 4. Regression of length of ammocoetes adjusted to 24 months versus conductivity ($N=17$; $R^2=0.624$; $P<0.001$)



Adjusted ammocoete length (mm)
140
120
100
80
60
40
0
100
200
300
400
500
600
700
Conductivity (umhos/cm)

FIGURE 5. Mean annual capture of pre-spawning lamprey versus discharge for 12 L. Ontario streams

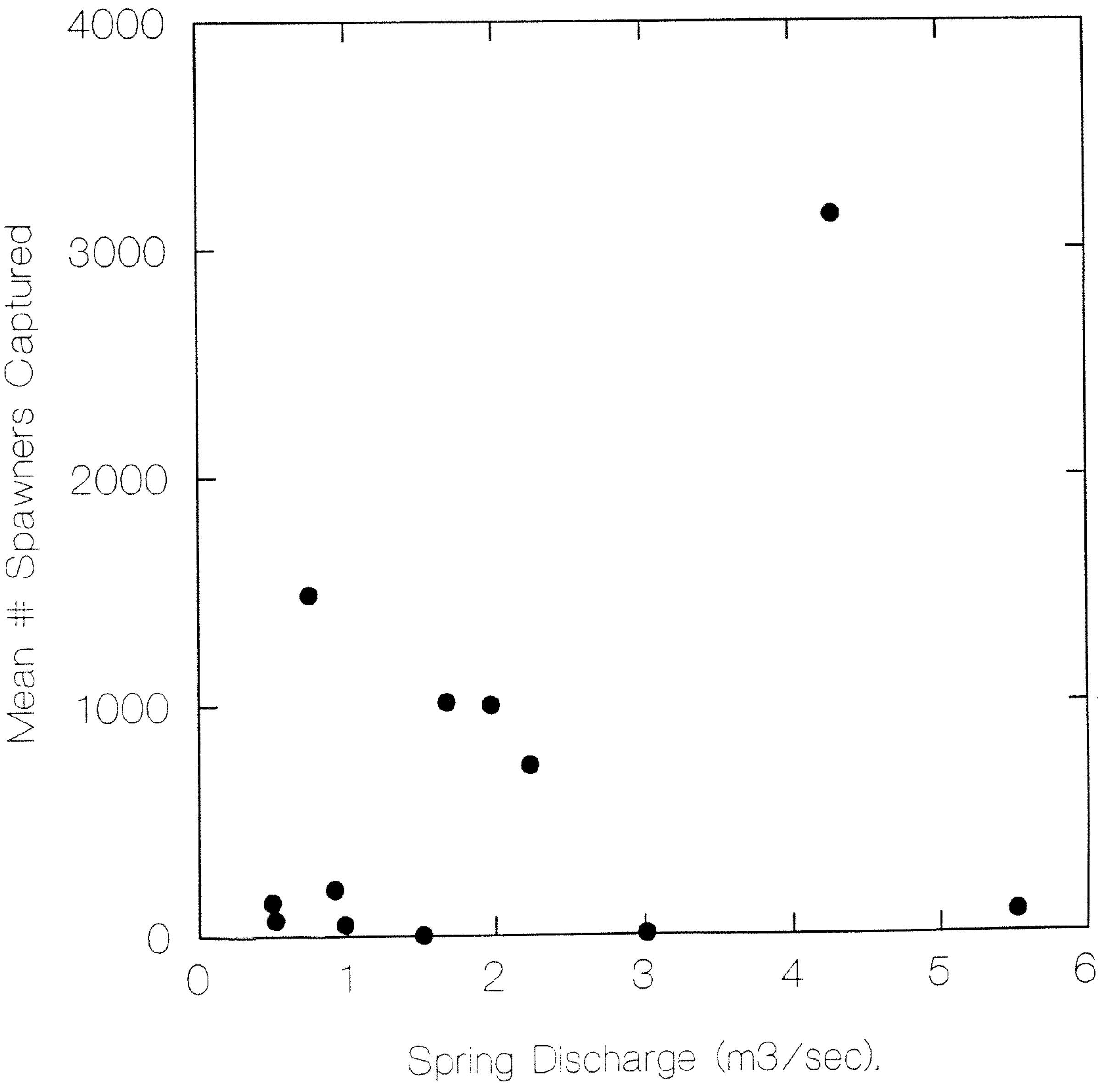

4000
3000
2000
1000
0
Mean # Spawners Captured
0
1
2
3
4
5
6
Spring Discharge (m3/sec).

FIGURE 6. Mean annual capture of pre-spawning lamprey versus discharge for Canadian streams in L. Ontario

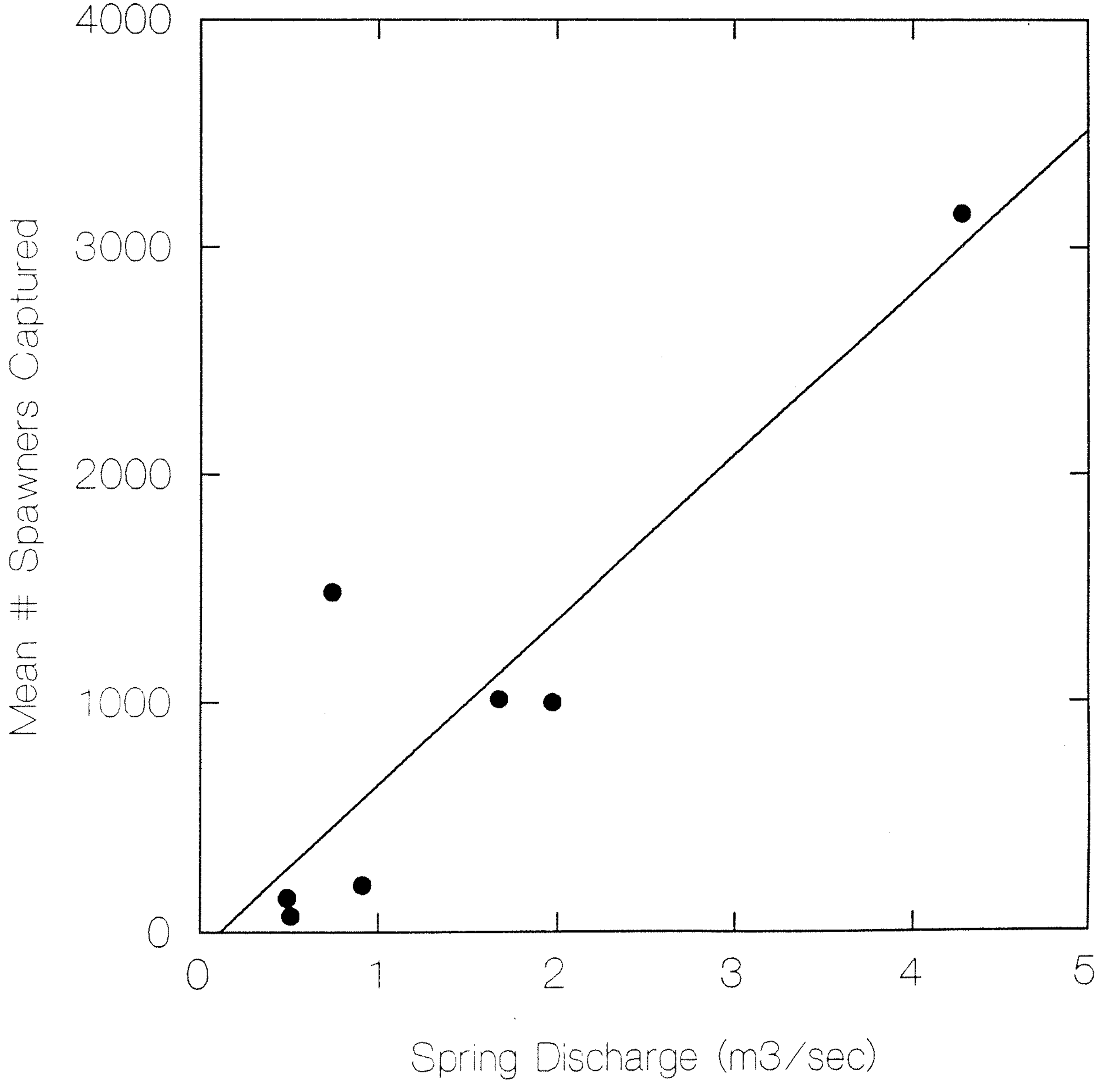
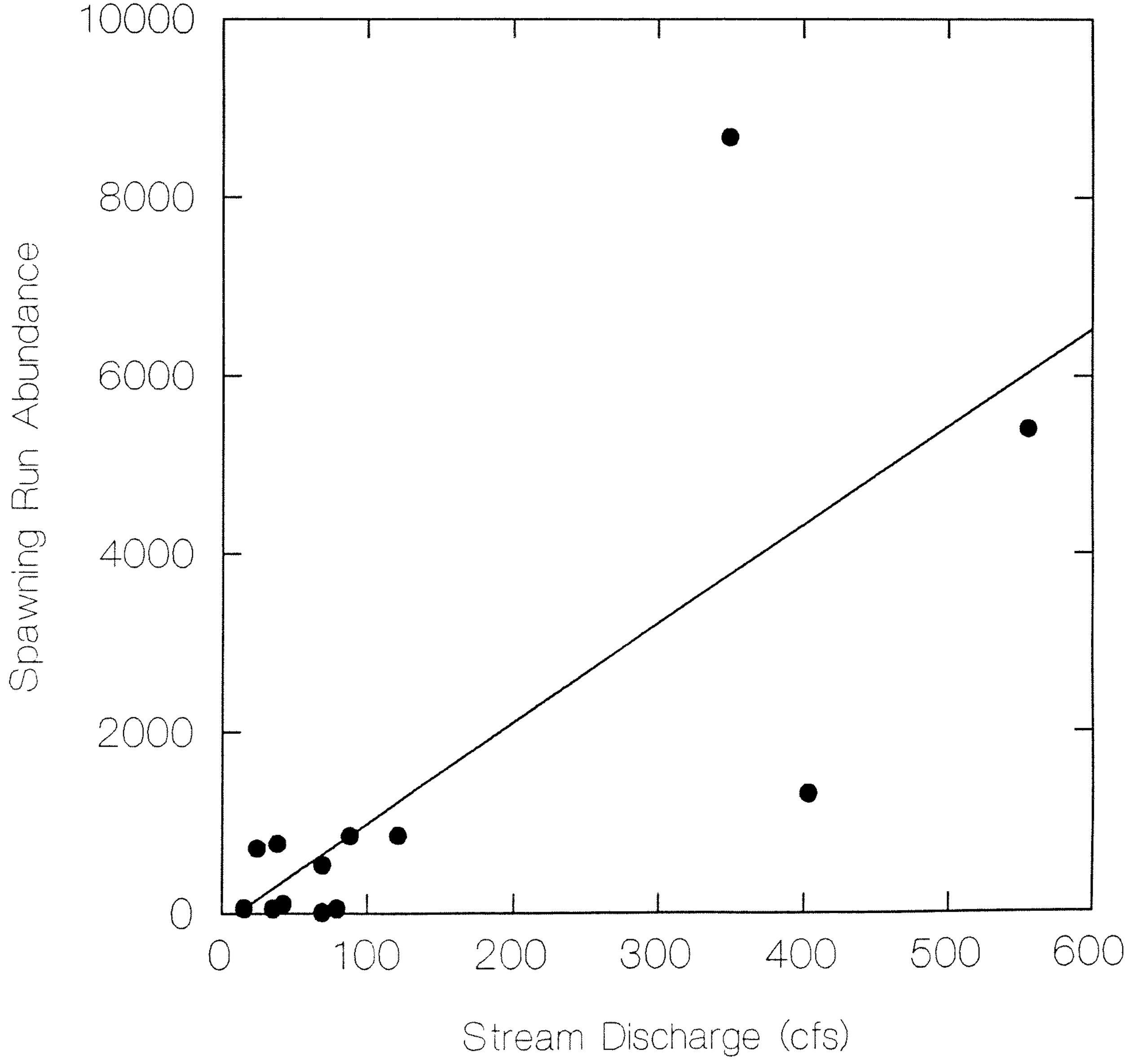
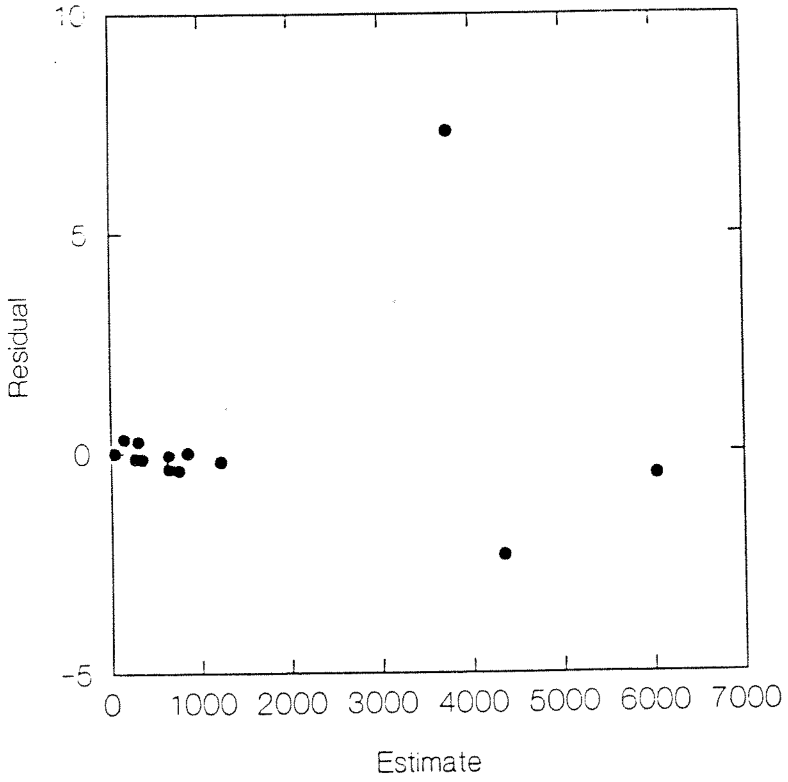

4000
3000
2000
1000
0
Mean # Spawners Captured
0
1
2
3
4
5
Spring Discharge (m3/sec)

FIGURE 7. Abundance of pre-spawning lamprey versus discharge from L. Superior streams (from Daugherty et al. 1987)



Spawning Run Abundance
10000
8000
6000
4000
2000
0
0
100
200
300
400
500
600
Stream Discharge (cfs)

FIGURE 8. Plots of (a) residuals versus estimates and (b) Cook's D versus estimates from regression of spawning run abundance and stream discharge in L. Superior (from Daugherty et al. 1987)


10
5
0
-5
Residual
0
1000
2000
3000
4000
5000
6000
7000
Estimate

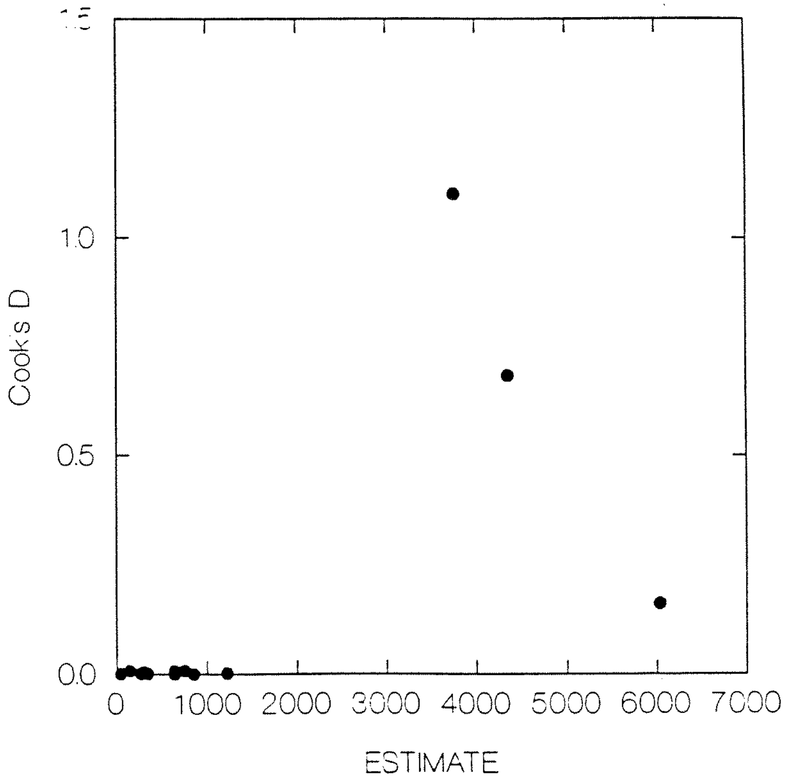
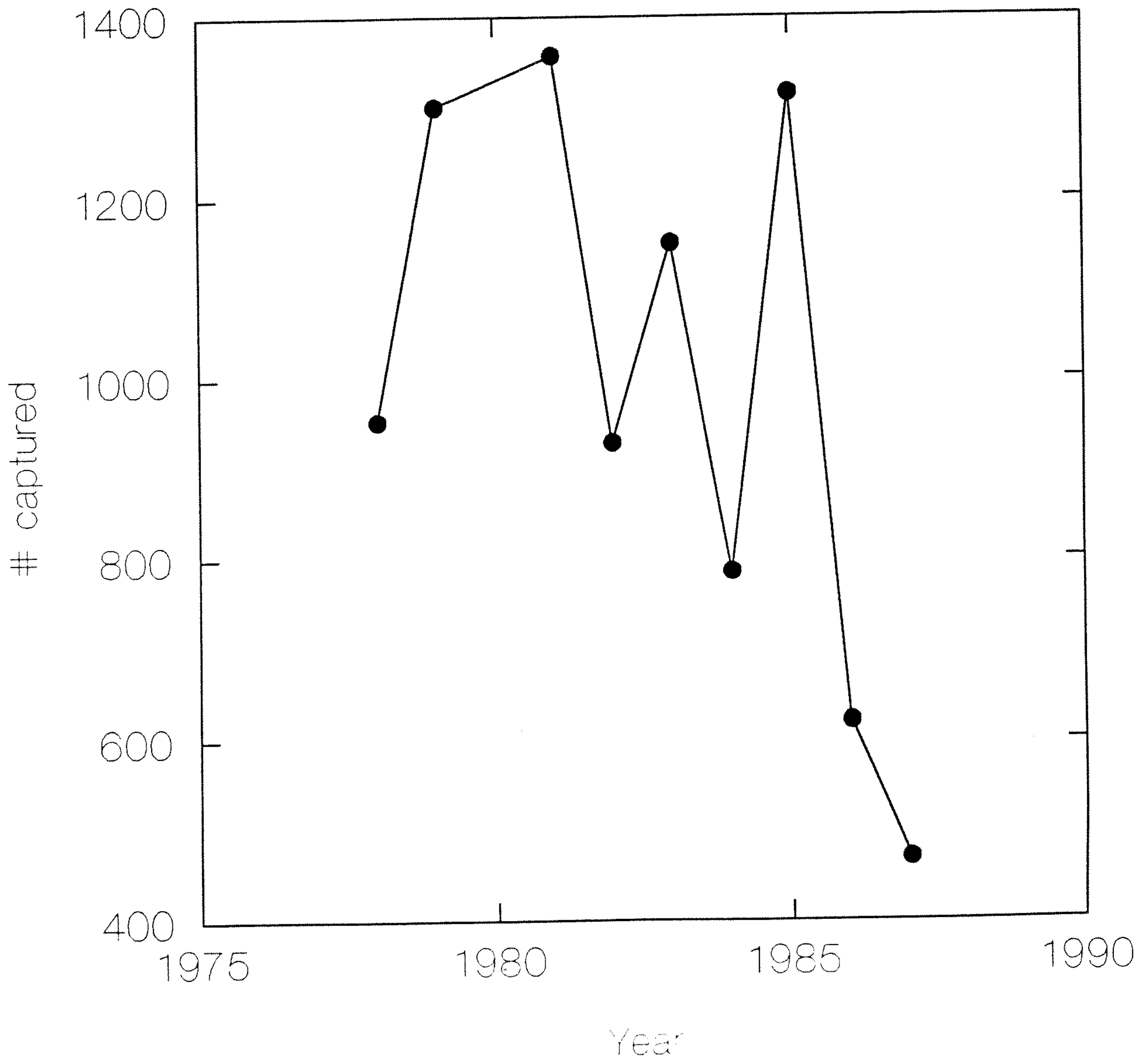

1.5
1.0
0.5
0.0
Cook's D
0
1000
2000
3000
4000
5000
6000
7000
ESTIMATE

FIGURE 9. Change in number of pre-spawning lamprey captured at L. Ontario index streams from 1978-1987



1400
1200
1000
800
600
400
captured
1975
1980
1985
1990
Year

FIGURE 10. Regression of log % males versus log capture of pre-spawning lamprey at index streams from L. Ontario

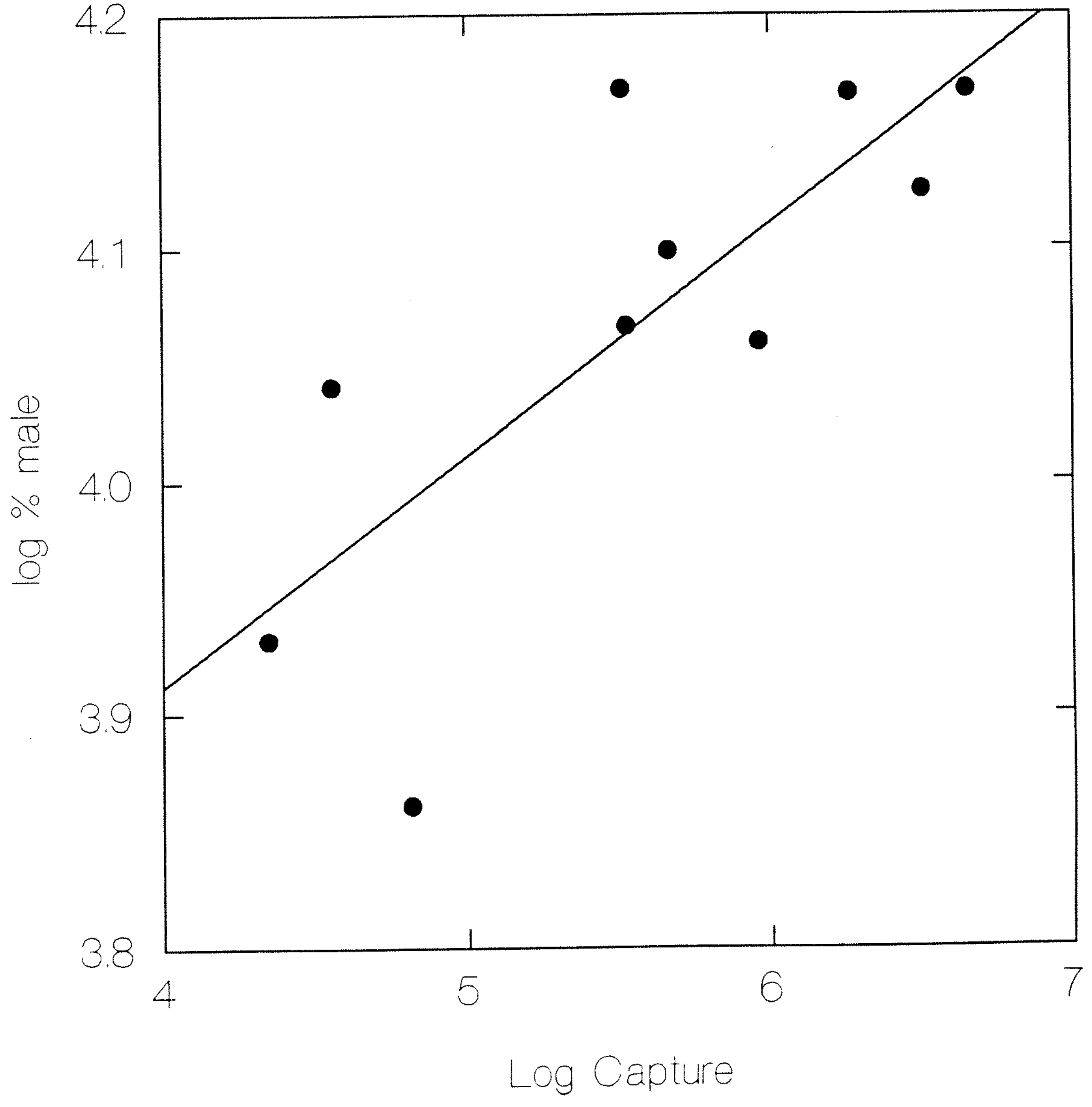
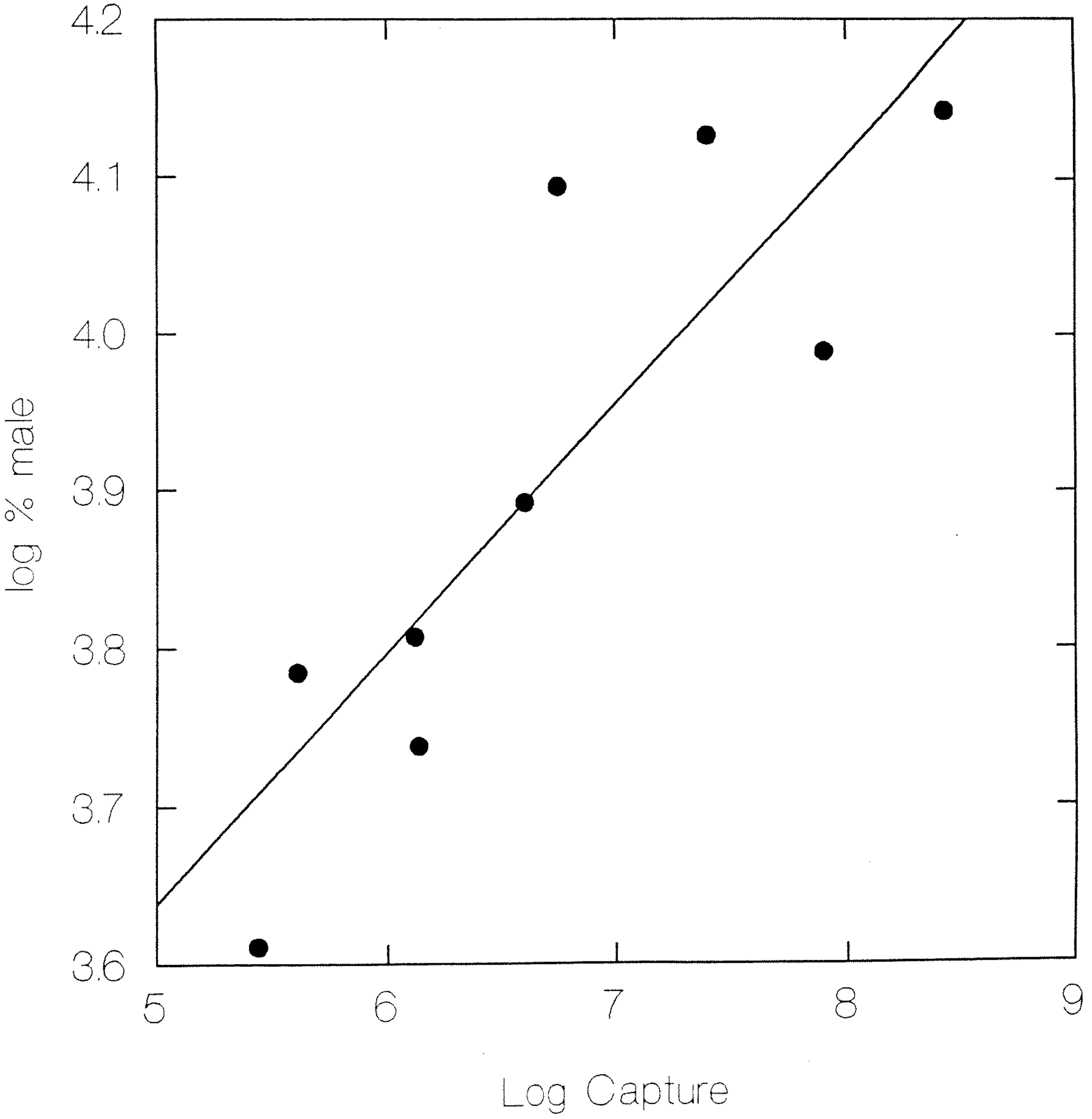

4.2
4.1
4.0
3.9
3.8
log % male
4
5
6
7
Log Capture

FIGURE 11. Regression of log % males versus log capture of pre-spawning lamprey at index streams from L. Huron


4.2
4.1
4.0
3.9
3.8
3.7
3.6
log % male
5
6
7
8
9
Log Capture