GREAT LAKES FISHERY COMMISSION
Research Completion Report *

OCCURRENCE, RELATIVE ABUNDANCE AND SIZE OF LANDLOCKED SEA LAMPREY (PETROMYZON MARINUS) AMMOCOETES IN RELATION TO STREAM CHARACTERISTICS IN THE GREAT LAKES.

by

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The effect of 14 environmental variables on the occurrence of sea lamprey (Petromyzon marinus) ammocoetes was examined in 73 tributaries of the Great Lakes. We successfully classified 86% of streams without lamprey and 90.5% of streams with ammocoete populations using discriminant analysis. 80% of streams in a test data set were also successfully classified. The classification success was largely determined by differences in stream substrate characteristics based on the magnitude of canonical coefficients and contribution to the multivariate F-statistic. Streams with ammocoetes had significantly ($p<.10$) higher proportion of sand and a lower proportion of bedrock and clay than streams without ammocoetes. CPUE of ammocoetes collected with electro-fishing gear was also significantly related ($p=.004$) to the proportion of rubble, gravel and clay. As well, we observed a significant ($p<.01$) positive relationship between conductivity and temperature with size of 2^+ ammocoetes. Results indicate that it should be possible to develop predictions for the number of metamorphosing ammocoetes based upon differences in stream characteristics.

INTRODUCTION

The sea lamprey (Petromyzon marinus) is of considerable economic importance to the Great Lakes because it parasitizes salmonids and other game species resulting in significant mortality (Smith and Tibbles 1980; Moore and Lychwick 1980). The Great Lakes fishery is an important natural resource and has been valued at over $1.4 billion (Talhelm 1986). Resource managers are concerned that, despite current control measures, sea lamprey contribute to salmonid mortality (Pycha 1980; Bergstedt and Schneider 1988) such that a significant proportion of the fish that otherwise would be available to sport and commercial exploitation are removed. At present, lamprey populations are controlled primarily by killing their ammocoetes (ie. the immature, stream-resident life stage) before metamorphosis to the juvenile, parasitic phase (lake-resident). Chemical control is achieved through the application of the larvicide, 3-trifluromethyl-4-nitrophenol (TFM) to Great Lake tributaries with resident ammocoete populations (Torblaa and Westman 1980).

Sea lamprey have readily adapted to the Great Lakes from the anadromous form of the species common to the Atlantic Ocean. However, sea lamprey ammocoetes have been reported from less than 7.5% of Great Lakes tributaries (Morman et al. 1980) despite the widespread distribution of adults throughout the lakes. Hardisty and Potter (1971), Potter (1980), and Morman et al. (1980) have shown that, within a stream, distribution of ammocoetes is largely determined by the availability of of burrowing habitat, ambient water quality and physical barriers to spawning sea lamprey. Morman et al. (1980) and Purvis (1979) have shown that density and metamorphosis vary considerably among streams in the Great Lakes. As well, Potter (1980) has reported that the onset of metamorphosis is dependent on size and growth of ammocoetes. While we know that only 433 streams produce sea lamprey ammocoetes and that considerable differences exist in abundance and transformation rates, the environmental factors that cause these differences among streams in the Great Lakes Basin have not been identified. Consequently, we first determined if the distribution (presence/absence) of sea lamprey ammocoetes among Great Lakes tributaries could be described as a function of physical and chemical habitat variables using classification analysis. Next, we examined the relationship between a surrogate of abundance (catch per unit effort - CPUE) and growth (size of ammocoetes at age 2^+) with physical and chemical habitat variables of streams from L. Superior to L. Ontario.

MATERIALS AND METHODS

1) Presence/absence of ammocoetes in Great Lakes tributaries.

Data from streams historically surveyed by the Sea Lamprey Control Centres of the Great Lakes Fishery Commission (GLFC) were used to determine if physical/chemical characteristics of streams could be used to classify streams as suitable for sea lamprey ammocoetes. We selected 73 tributaries of Lakes Superior, Michigan, Huron, Erie and Ontario that had been previously surveyed for lamprey presence, substrate composition and water chemistry (Table 1). Streams with obvious barriers to spawning sea lamprey (ie. streams that dried up in summer or had dams or waterfalls that prevented spawning migrations) were excluded from this analysis.

Lamprey survey crews visually classified the stream bottom composition at each sampling station. Six substrate classes were used in streams found along the Canadian and New York shores and seven classes along the remaining U.S. shoreline. We arbitrarily combined two classes "boulder" and "rubble" from U.S. data in order to harmonize the two data sets (Table 1). The average of each substrate class was calculated from all stations in a stream. Data from 1-3 surveys were averaged to obtain values for stream bottom composition because streams frequently treated with TFM (3-5 year treatment rotation) were regularly surveyed between chemical treatments and untreated streams were surveyed less frequently. Survey stations were not randomly selected by the survey crews but were areas which historically supported sea lamprey ammocoetes. Therefore, the stations used were biased towards stream sections

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perceived as "optimal" ammocoete habitat.

Discharge data were obtained from published annual reports of Water Survey of Canada (WSC 1983, 1984, 1986) and the U.S. Geological Survey (USGS 1985, 1986, 1987). Discharge was calculated as the average daily discharge over a 3 y period.

Stream water temperatures and water chemistry data (Table 1) were acquired from published reports of WSC (1975), USGS (1985, 1986, 1987) and the Ontario Ministry of the Environment (OMOE) stream water quality survey. The yearly average of approximately monthly water chemistry samples was calculated for each stream.

Statistical analyses were performed using a micro-computer version of Systat 4.0 (Wilkinson 1988). Discriminant analysis (Bock 1975) was used to determine the ability of the 14 physical and chemical stream characteristics (descriptor variables) to classify streams as to whether ammocoetes were present or absent (grouping variable). Prior to analysis, the data set was randomly separated into a calibration data set (63 streams) and a test data set (10 streams). The canonical variate was calculated using the calibration data set and its predictive ability assessed with the test data set.

2) <u>Relative Abundance of Ammocoetes</u>

Streams with known sea lamprey populations are regularly sampled using electro-fishing gear to determine distribution and population structure within streams. We calculated the catch per unit effort (CPUE) as the number of ammocoetes collected per person hour of effort from 16 Canadian tributaries of Lakes Superior, Huron, and Ontario. Mean log CPUE was calculated as the average CPUE from 2 to 10 sampling stations on each stream. We used stepwise regression to develop models to estimate mean log CPUE for each stream from our suite of environmental variables. Residuals were examined for deviations from regression model assumptions. Because electro-fishing for ammocoetes was designed to establish distribution, bias may result from using this data to reflect abundance. However, no alternative exists to compare differences in abundance among streams.

3) Size of Ammocoetes at age 2^+

We used regression analysis to examine the relationship between physical and chemical variables and ammocoete size. We selected 17 streams that had both environmental data and relatively large collections of ammocoetes. Year classes were assigned using a maximum likelihood method (Mix 2.3) to analyse length frequency distributions (see MacDonald and Pitcher 1979; MacDonald 1987). We then estimated the mean length of year class (YC) 2^+ ammocoetes. No attempt was made to verify ages by analyzing statolith banding (Beamish and Medland 1988). However, we were confident in the aging technique because we knew the number of years between chemical treatments and we assumed a low survival rate following these treatments. We did not consider young-of-the-year because they are small, difficult to collect and are poorly represented in most samples. Older year classes were excluded because the degree of overlap between length frequency distributions was such that individual year classes could not be reliably separated.

Step-wise regression was used to assess the physical or chemical variables most important in determining differences in ammocoete length between streams. Residuals of the regression analysis were examined to assess deviations from regression analysis assumptions.

RESULTS

Presence/absence of ammocoetes in Great Lakes tributaries

The classification success of the discriminant analysis model for the calibration data set was 86% for streams without lamprey and 90.5% for streams with lamprey (Table 2a). Eight of ten streams in the test data were correctly classified by the canonical variate (Table 2b) with similar classification success among the present and absent groups. The multivariate test statistic (Wilks Lambda) was significant (F=3.602; DF=14, 48; p<.001), indicating that the classification success was not spurious.

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The magnitude of the standardized canonical coefficients (absolute value) are generally used to determine the relative importance of descriptor variables used in discriminant analysis (Legendre and Legendre 1983). However, the stability of these coefficients and the ease of interpretation is reduced when there is a high degree of correlation among the descriptor variables (Bock 1975; Campbell and Atchley 1981). In our data set, there was considerable correlation among the 14 variables used to classify lamprey streams (Bartlett chi-square = 583.31, DF=91, p<.001). Examination of the significant correlation coefficients (Bonferroni adjusted probabilities) suggested correlation among the substrate size variables and discharge, productivity related variables (i.e. alkalinity, conductivity and total phosphorus) and between turbidity and suspended sediments.

Wilkinson (1975) outlines four criteria for determining the importance of variables in canonical variate analysis:

i) the magnitude of the univariate F-tests,

ii) the magnitude of the standardized canonical coefficients,

iii) the contribution of each variable to the multivariate F-statistic, and

iv) multivariate and univariate confidence intervals for linear contrasts between groups.

In our study, iv) reduces to the significance of the T-test or ANOVA because we had only 1 D.F. for groups.

Table 3 contrasts the relative importance of the stream characteristics using these four criteria. In the univariate case, 10 of the 14 variables were significantly different between streams with and without sea lamprey ammocoetes. Total phosphorus, conductivity,and bedrock had the largest univariate F-statistics. When viewed univariately, these 3 stream attributes are the most valid response variables (Wilkinson 1975). However, bedrock, sand, and clay had the greatest standardized canonical coefficients indicating that they contributed most to the discrimination between streams with and without ammocoetes. Finally, bedrock had the largest reduction in the multivariate F-statistic which further supports the importance of substrate variables in the classification of streams.

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The interpretation of the discriminant analysis was complicated by the extent of correlation among the stream characteristics. Ammocoetes are clearly less likely to occur in streams with larger average substrate size than in streams with smaller average particle size (Fig 1). Our analysis indicates the presence/absence of sea lamprey ammocoetes within the Great Lakes is controlled, to a large degree, by substrate particle size.

Relative Abundance

The average CPUE among the 16 streams used in this study ranged from <0.1 ammocoetes.h^{-1} to 180 ammocoetes.h^{-1}. The step-wise regression between CPUE and relative abundance retained rubble, gravel, clay and total phosphorus. These variables were significantly related to CPUE (R^2=.65, p=.004) and were defined by the equation:

1) log CPUE = 3.89-0.66*rubble+0.49*gravel-1.59*clay

Rubble and gravel had the largest standardized coefficients which indicates that they were the most important variables in the regression (Table 4). In addition, the coefficients of these variables were negative which indicates that the low relative abundance occurred in streams with a higher proportion of difficult burrowing habitat like rubble and clay. On the other hand, gravel had a positive relation to relative abundance. This suggests that streams with higher relative abundance of ammocoetes had a larger proportion of gravel.

Size of ammocoetes at age 2^+

The average length of YC 2^+ ammocoetes in the 17 streams ranged from 57 mm to 126 mm. Of the 14 stream characteristics used to explain the variation in ammocoete lengths, only conductivity and temperature were retained by step-wise multiple regression. Ammocoete length was related to temperature and conductivity (n=17, R^2=.83, p<.001) and was defined by the equation:

1) Length = 31.70 + (0.09* Conductivity) + (2.60* Temperature)

Conductivity had a larger standardized regression coefficient than temperature (Table 5). Therefore, we concluded that conductivity was more important in explaining between stream differences in ammocoete length. As stream conductivity increased, the length of 2+ ammocoetes also increased (Fig 2). Conductivity in the linear regression model explained 69% of variation in ammocoete length.

DISCUSSION

Only 433 of the 5747 tributaries of the Great Lakes have collection records for sea lamprey ammocoetes (Morman et al. 1980). In our data set, streams without ammocoetes had larger average substrate particle size and, apparently, an insufficient proportion of sand-silt habitat to maintain an ammocoete population, given current populations of parasitic-phase lamprey. Conversely, streams with sea lamprey ammocoetes had lower proportions of bedrock and rubble and higher proportions of sand substrate. Our results are the first to suggest that availability of optimal stream substrate size may be an important factor limiting the distribution of landlocked sea lamprey ammocoetes within the Great Lakes. Further, our conclusions are similar to previous studies that have cited substrate particle size as an important variable influencing the occurrence and abundance of ammocoetes of several species of lamprey within a stream (Thomas 1962; Hardisty and Potter 1971; Malmqvist 1980; Potter et al. 1986). We have also demonstrated a significant relationship between substrate conditions and relative abundance (CPUE) of ammocoetes from 16 streams used in this analysis. While we have concern about the validity of the catch per effort data, the general relationship between the quality of burrowing habitat and ammocoete abundance is logical in light of the factors that determine presence/absence of ammocoetes.

The link between ammocoete population densities and stream habitat could enable the development of predictive relationships for abundances of ammocoete populations akin to the morphoedaphic index for fish yield (Ryder 1982). Relationships such as those developed here could permit the estimation of sea lamprey ammocoete populations in a lake-wide perspective. Variables other than substrate size, such as water depth, current velocity and the concentration of organic material in the substrate have been identified (Potter et al. 1986; Malmqvist 1980) as important factors influencing the abundance of ammocoetes. Quantitative assessment of any of these variables in all tributary systems of the Great Lakes with lamprey populations would be prohibitively expensive. However, many stream characteristics are similar in that most are a function of stream channel gradient and local geology (Baxter 1957; Hardisty & Potter 1971; Malmqvist 1980). Gradient will determine the depositional and erosional areas, water depth and velocity while local geology will influence the origin and size of particles in the stream. The simplest method of developing predictive relationships for ammocoete populations might result from using gradient profiles as a "surrogate variable" for the suite of environmental variables now used to describe optimal ammocoete habitat.

Our results also indicate that conductivity and temperature were significantly related to ammocoete size, and by extension, growth in established stream populations. Streams with higher conductivity (hardwater streams) were associated with larger 2^{+}

ammocoetes. Lamprey ammocoetes feed by filtering algae and detritus (Hardisty and Potter 1971). In general, hardwater streams have greater primary production than softwater streams (Ryder 1965; Ryder and Pesendorfer 1988; Hynes 1970). As well, conductivity was correlated with total P and alkalinity in our data set. Therefore, the amount of food available to lamprey should be greater in hardwater streams and should result in faster growth rates. We also found larger ammocoetes in streams with higher average temperatures, which we would generally expect from poikilotherms operating within their thermal tolerances. Our results confirm that growth of ammocoetes in Great Lakes tributaries are at least in part influenced by temperature (Purvis 1979; Purvis 1980). Because faster growing ammocoetes metamorphose to the parasitic phase more quickly (Potter 1980), differences in conductivity and temperature are likely to influence growth and metamorphosis of ammocoetes throughout the Great Lakes.

We submit that our results be accepted with caution largely because several critical variables (CPUE, substrate variables) were measured semi-quantitatively. Nevertheless, it is evident that differences in substrate among streams are important in determining first, whether streams are colonized by sea lamprey and second, the relative abundance of ammocoetes. In established populations, the size of 2^+ ammocoetes was related to temperature and conductivity. Thus, production of ammocoetes among streams can be modelled using few environmental attributes. Accurate predictions of the number of metamorphosing ammocoetes entering the Great Lakes will be a critical element in future attempts at modelling the sea lamprey - salmonid interactions under varying sea lamprey control strategies.

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TABLE 1 Treatment means of stream characteristics (variables from 73 streams in 5 Great Lakes) used in discriminant analysis.

VARIABLE	ABSENT	PRESENT
Bedrock (%)	7.13	0.88
Rubble (%)	11.53	6.69
Gravel (%)	12.65	16.05
Sand (%)	29.53	39.75
Silt (%)	23.39	24.40
Clay (%)	15.45	10.23
Discharge (m^3/s)	6.54	40.11
Temp (°C)	11.08	10.46
Alkalinity (mg/L)	159.11	125.58
Conductivity (uS/m@25°C)	571.22	339.03
Dissolved O_2 (mg/L)	10.13	10.45
Total P (mg/L)	0.12	.06
Seston (mg/L)	42.34	26.01
Turbitity (FTU)	21.05	11.45

TABLE 2: **Classification of streams for the presence or absence of sea lamprey ammocoetes as determined by discriminant analysis using data from A) the calibration data set and B) the test data set.**

A CALIBRATION DATA SET

	Predicted		
Group	Absent	Present	Total
Absent	18	3	21
Present	4	38	42
Total	22	41	63

B TEST DATA

	Predicted		
Group	Absent	Present	Total
Absent	4	1	5
Present	1	4	5
Total	5	5	10

TABLE 3 Univariate F-statistics, standardized canonical coefficients, canonical loadings and contributions to the multi-variate F statistic for stream characteristics used in discriminant analysis

Variable	F-ratio	St. Coeff	Loading	MV-F
Bedrock	9.408	1.390	0.383	3.082
Rubble	3.492	0.804	0.233	3.780
Gravel	1.029	0.340	-0.127	3.934
Sand	4.063	1.572	-0.252	3.762
Silt	0.088	0.611	-0.037	3.879
Clay	4.848	1.281	0.275	3.412
Discharge	6.513	-0.399	-0.319	3.517
Temp	0.983	0.039	0.124	3.956
Alkalinity	2.852	-0.197	0.211	3.897
Conductivity	11.075	0.865	0.416	3.266
Dissolved O_2	1.440	0.041	-0.150	3.955
Total P	11.089	0.221	0.416	3.905
Seston	3.509	-0.943	0.234	3.183
Turbidity	3.905	0.300	0.247	3.837

TABLE 4 **Regression coefficients, standardized coefficients of stream characteristics retained by step-wise regression of CPUE and the habitat.**

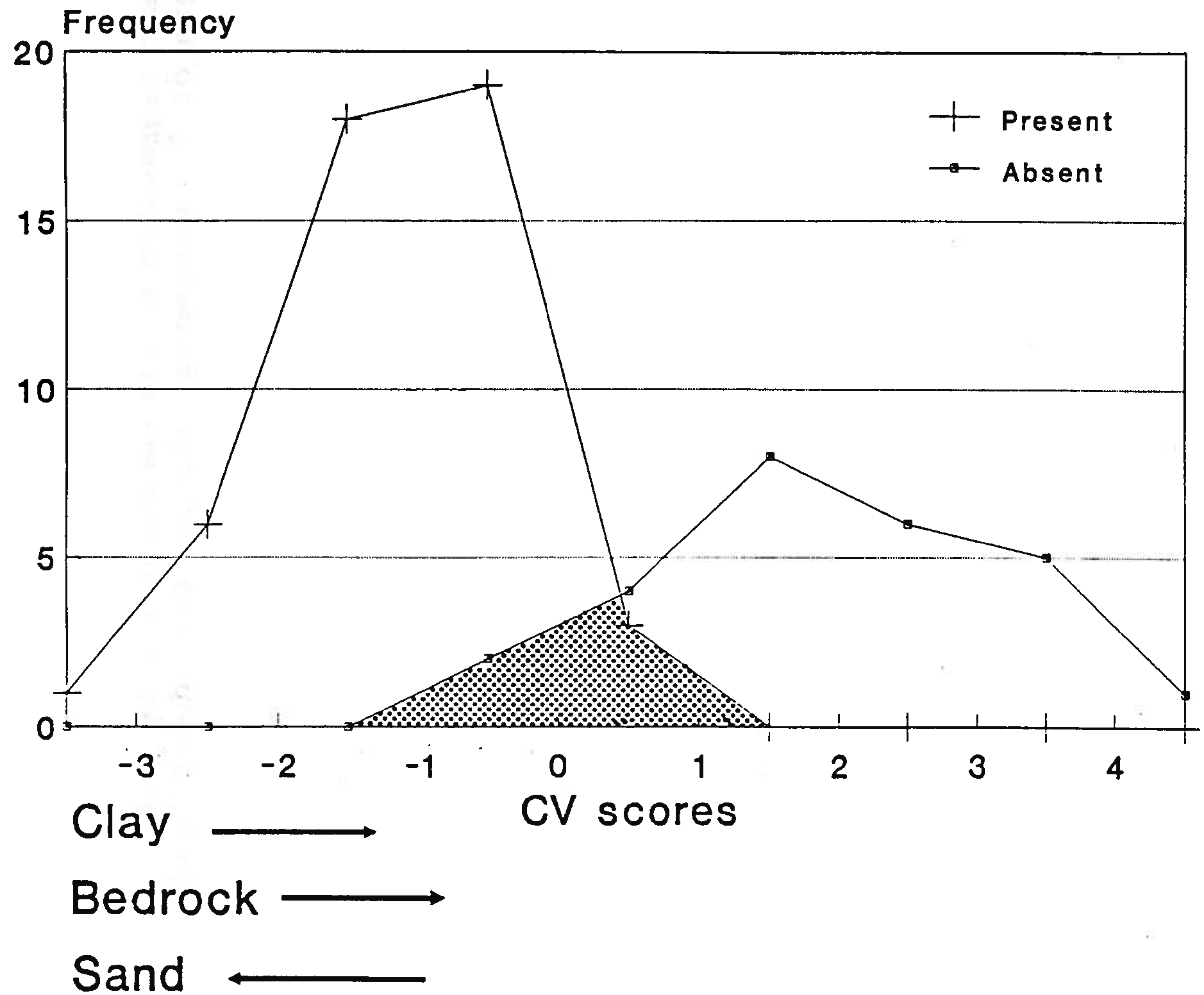
Variable	Coefficient	S.E.	Standardized Coefficient	P
Constant	3.89	1.01	0.00	0.00
Rubble	-0.66	0.27	-0.45	0.03
Gravel	0.49	0.23	0.42	0.05
Clay	-1.59	0.60	-0.49	0.02

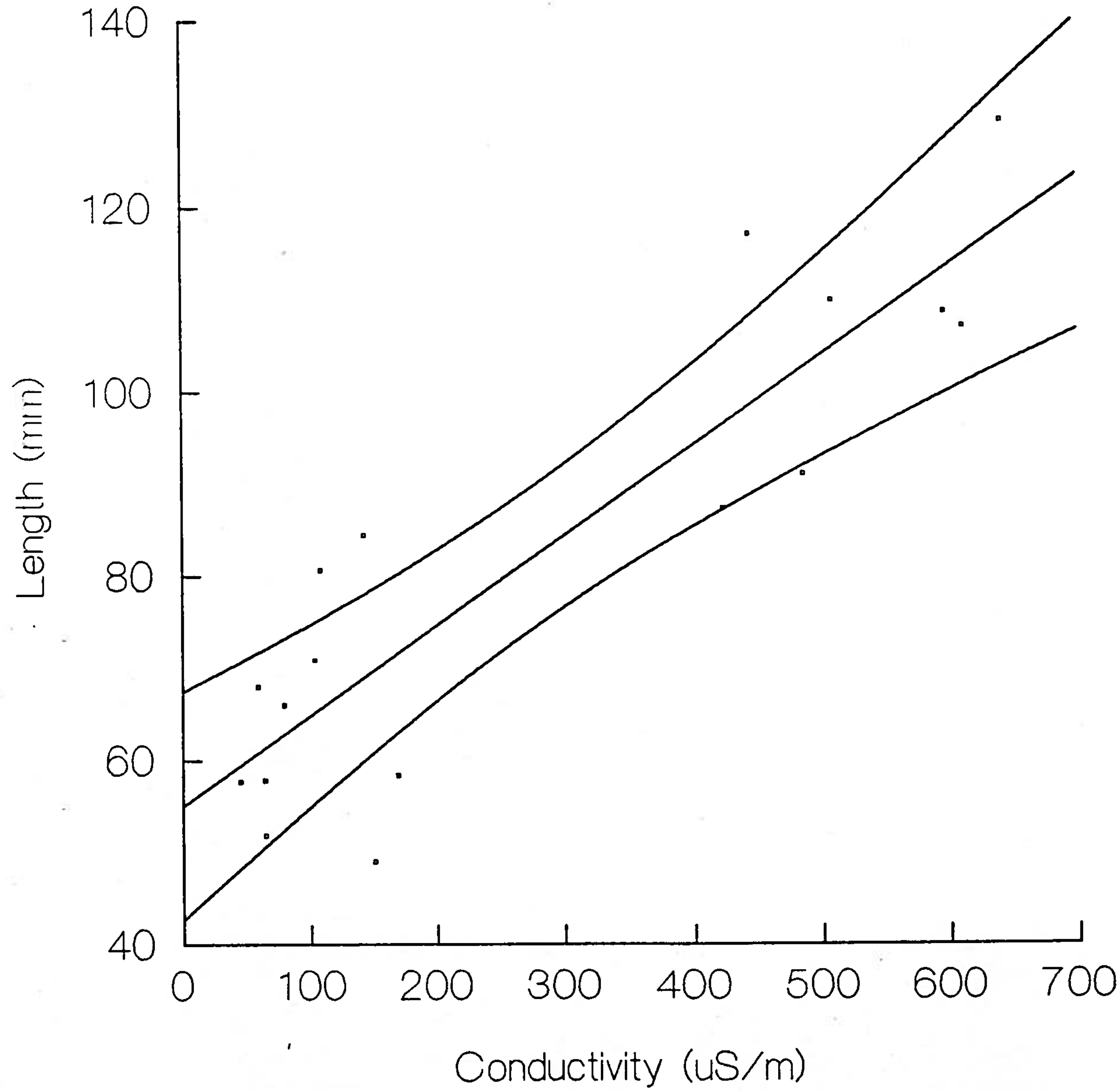
TABLE 5 **Regression coefficients, standardized coefficients and prob. of variables retained by step-wise regression of size of 2^{+} ammocoetes and habitat variables.**

Variable	Coefficient	S.E.	Standardized Coefficient	P
Constant	31.70	13.06	0.00	0.029
Conductivity	0.09	0.01	0.83	0.001
Temperature	2.59	1.37	0.21	0.080

Figure 1. Frequency polygon of canonical variate scores from 63 streams with and without sea lamprey ammocoetes. The stippled area represents the region of misclassification. The arrows represent the correlation between important discriminating variables and the canonical variate.

Figure 2. Linear regression of stream conductivity and length of 2^+ ammocoetes with 95% confidence bands.


Frequency
20
15
10
5
0
Present
Absent
-3
-2
-1
0
1
2
3
4
CV scores
Clay
Bedrock
Sand


Length (mm)
140
120
100
80
60
40
0
100
200
300
400
500
600
700
Conductivity (uS/m)