This is to certify that the

dissertation entitled

PROXIMATE DETERMINANTS OF LARVAL LAMPREY HABITAT SELECTION

presented by

Douglas S. Lee

has been accepted towards fulfillment
of the requirements for

Ph.D. degree in Zoology

William E Cooper
Major professor

Date 08 March 1989

PROXIMATE DETERMINANTS OF LARVAL LAMPREY HABITAT SELECTION

By

Douglas S. Lee

A DISSERTATION

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Department of Zoology

1989

ABSTRACT

PROXIMATE DETERMINANTS OF LARVAL LAMPREY HABITAT SELECTION

By

Douglas S. Lee

The sea lamprey continues to threaten the native lake trout and whitefish assemblage of the Laurentian Great Lakes. Larval sea lamprey are the focus of chemical control in tributary streams and nearshore areas. The existence of lentic larval lamprey populations composed of native lamprey (Lampetra appendix and Ichthyomyzon spp.) and the sea lamprey (Petromyzon marinus) has been recognized since late 1950; however, little formal research has been conducted on what determines their local distribution and abundance. Larval lamprey distribution was assessed with SCUBA and a manned submersible off the mouth of the Chippewa River (Lake Superior, Ontario, Canada) in tandem with laboratory analyses of habitat selection cues. Tested cues included burrowing substrate characters, (particle size distribution, porosity, and permeability), food particle distribution, and density-dependent interactions. The effect of substrate characters, seasonal thermal regime, and food particle distribution in the substrate and at the sediment/water interface on larval habitat selection were also assessed in the field. Based on laboratory results, substrate

particle size distribution and permeability set limits to the "suitability" of a substrate. Sediments characterized by particle diameters exceeding 1.00 mm were avoided by larval P. marinus and L. appendix. Permeability sets a lower limit to substrate suitability through relative resistance to interstitial water exchange. Neither food particle distribution and abundance or ammocete density exert any effect on habitat selection. Given suitable burrowing substrate, the distribution of lentic ammocetes is a function of currents and temperature. Wind driven vertical circulation cells set up zones of well irrigated substrates which are preferentially selected by ammocetes. Substrates in waters exceeding 19 °C are avoided, prompting a down-slope and offshore habitat shift over the course of the summer. Shallow areas avoided by lentic ammocetes with increasing temperatures correspond to annual Bayer 73 treatment locations. The effectiveness of Bayer 73 as a lampricide is reduced below 15 °C so treatments are usually conducted in late August or September. During these months, temperatures at depth can meet or exceed 19 °C. Timing of control treatments should occur when the water temperature lies between the two limits.

ACKNOWLEDGMENTS

As major professor, Bill Cooper has my deepest thanks and appreciation for generating an independent yet supportive environment in which to pursue this research. Drs. D. J. Hall, D. O. Straney, and F. W. H. Beamish each provided timely insights and unique guidance for which I am deeply appreciative. For their assistance in the field, I wish to extend thanks to Jerry Weise (CDFO) and Chris Sierzputowski who provided yeoman surface support for diving operations and collection of ammocetes. The ship and crew of the R/V Seward Johnson also have my thanks for their assistance in all submersible operations. Robert Tusting (HBOI) and Don Allen (USFWS) deserve thanks for all elements of adapting larval lamprey electrosampling techniques to manned submersibles. In the laboratory, Steve Mero proved himself invaluable as an assistant. Paul Groll deserves special thanks for his friendship, assistance in various computer programming tasks, and willingness to assist in the field whenever possible.

Hellin and Pentti Saarinen deserve especial thanks for their friendship and graciously allowing me use of

the Whispering Pines Resort facilities during the last two field seasons. Lastly, to my wife Mary Beth who provided support and love throughout the program, my deepest love and appreciation for putting up with me during the ups and downs of research.

This work was supported by the M.S.U. Foundation, the Max and Victoria Dreyfus Foundation, the National Undersea Research Center at the University of Connecticut, and the Great Lakes Fishery Commission.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

The successful control of sea lamprey (Petromyzon marinus) in the Great Lakes has been built in part upon general knowledge of the distribution and abundance of larval sea lamprey in nursery streams (Weise and Rugen, 1987). Based on this information, effective stream control with TFM (3-triflouromethyl-4-nitrophenol) has been established over the past 30 years. Estimates of stream ammocete abundance in the Lake Superior watershed currently range from 7 to 12 percent of pre-treatment levels (Torblaa and Westman, 1980; Moore and Schleen, 1980). With this success has come the necessity for increased rigor in the estimation of ammocete distribution and abundance. This demand for quantification is predicated by the need to evaluate the effectiveness of control measures with respect to further control efforts (Workshop for the Evaluation of Sea Lamprey Populations, WESLP; Johnson, 1987).

To meet this challenge, the determinants of larval lamprey habitat selection must be identified. Such knowledge provides a framework for quantitative

assessment of distribution and abundance. As populations decline, the effort expended in determining the distribution and abundance of pre-metamorphic individuals increases. Knowledge of habitat selection cues may permit control agents to reduce survey efforts while maintaining or increasing the quality of information obtained. Of obvious value for surveying streams with small but persistent populations, knowledge of habitat selection cues should also provide a predictive framework for quantitative sampling and treatment of lentic and large river populations.

While adult sea lamprey spawn in streams, control efforts on the larval stage may be compromised by lentic populations of ammocetes considered to originate from stream populations. The extent to which these individuals pose a threat remains a subject of conjecture within sea lamprey control circles. That large river populations such as those in the St. Mary's and St. Clair rivers may represent a threat to control efforts is well known within resource management circles. Less well known are the difficulties that have been encountered in assessing the distribution and abundance of larval sea lamprey populations in lentic areas and large rivers. Many of the difficulties are related to the sheer size of the system. Information

that acts to quantitatively reduce the "effective" size of the system will also reduce the difficulty of assessment.

Ammocetes exhibit selective patchiness in distribution and abundance, a prerequisite for postulation of stereotypic habitat selection. The absence of well defined determinants of habitat selection prevents a priori application of habitat selection models. Wiens (1976) aptly pointed out that "patchiness of an environment is organism-defined, and must be considered in terms of the perceptions of the organism". Precisely what defines a patch and cues selection by ammocetes however, is not clear.

Factors associated with the distribution and abundance of ammocetes in streams include bottom particle size, current velocity, temperature, and oxygen tensions (Malmqvist, 1980; Potter, 1980; Reynolds and Casterlin, 1978; Potter et al., 1970). Other factors that may affect local distribution and abundance include food particle concentration, and competition for space (both intra- and interspecific) though neither of these have been pursued experimentally. None of these factors have been studied with respect to the distribution and abundance of lentic ammocete populations.

Consequently, the overall goal of the research presented herein is to identify and understand the specific determinants of lentic larval lamprey habitat selection.

Present Understanding

Sea lamprey in the upper Great Lakes complete their life cycle entirely in freshwater. In the spring, adults ascend local streams and spawn in gravel and cobble beds. The sedentary young burrow into the substrate where they filter feed on algae and detritus. After 5 to 18 years as larvae (Manion and Smith, 1978), ammocetes undergo metamorphosis to the adult stage. Adults move into the lake where they feed on salmonids and other suitable fish species for approximately 18 months until sexual maturation. Native lamprey species in the Great Lakes watershed include the non-parasitic American brook lamprey (Lampetra appendix), and three species of Ichthyomyzon, two of which are parasitic but feed primarily in rivers and bays. The larval portion of the life history of all species is similar.

With respect to burrowing substrate selection, our present understanding has been derived from qualitative stream habitat descriptions and crude measures of grain size distribution and consolidation. Descriptions of

preferred burrowing substrates for larval Petromyzon marinus include "sand and mud" (Gage, 1928), "soft bottoms of silt and silt-sand", "mucky bottoms" (Applegate, 1950), "sand-silt bottoms covered with detritus", and "most abundant where 90 percent of sand particle were less than 0.50 mm" (Manion and McLain, 1971). Characterization of substrates as sand, silt, mud, etc. have generally been made without reference to a grade scale.

All descriptions of substrate selection concur that burrowing occurs where stream flow is "low", "sluggish", or "meandering". Following the lead of Baxter (1957), Thomas (1963) attempted to quantify characteristics of habitats in terms of stream flow and bed stability. Based on measures of current speed and bed consolidation with a "home-made" penetrometer, Thomas proposed maximum stream flow and sediment compaction limits of 62 cm/sec and 2,224 g compactness for larval P. marinus, and 79 cm/sec with 2,691 g compactness for larval L. appendix.

Malmqvist (1980) conducted the most complete field analysis of ammocete distribution relative to habitat characters, using discriminant analysis to relate density of larval brook lamprey (Lampetra planeri) to particle size distribution, median particle size, degree

of insolation, depth, presence of macrophytes, chlorophyll, organic content, and current velocity. Highly significant positive correlations ($P < 0.01$) were found with sediment particles in the 0.5 - 1.0 mm and 1.0 - 2.0 mm diameter size classes with a negative correlation to current velocity. Significant positive correlations ($P < 0.05$) were found with sediment particle diameters of 0.125 to 0.250 mm and median grain diameter while negative correlations were found with grain diameters exceeding 2.0 mm and sediment chlorophyll content. All other correlations were nonsignificant.

A single laboratory experiment of substrate selection, based on grain size distribution, was conducted at the Hammond Bay Biological Station (Great Lakes Fishery Commission, 1962). Three sediment types ranked as "pea-size gravel, silt, and clay" were tested in pairwise fashion against a fourth type, "sand." In the cases of "sand-gravel" and "sand-silt" comparisons, "sand" was selected by 89.9 and 76.7 percent of larval sea lamprey respectively. In the case of the "sand-clay" comparison, the "clay" substrate was avoided entirely. The sediment categories used were defined only as "common bottom types"; with no reference to a

grade scale. Further experimentation to identify substrate selection cues was not conducted.

Reynolds and Casterlin (1978) tested the thermoregulatory behavior of larval sea lamprey. Cold-acclimated (1 °C) ammocetes were allowed to acclimate at a temperature of choice in a linear temperature gradient of 0 to 32 °C prior to individual testing. Initially avoiding temperatures exceeding 10 to 12 °C, ammocetes displayed a distinct median temperature preferendum of 14.0 ± 2.06 °C (mean ± sd). The range of selected temperatures was 10 to 19 °C. The incipient lethal temperature for larval P. marinus ranges from 28 to 31.5 °C depending upon initial acclimation temperature (range: 5 - 25 °C; Potter and Beamish, 1974).

Larval mountain brook lamprey, Ichthyomyzon hubbsi exhibited tolerance of oxygen tensions as low as 7, 12, and 16 mm Hg at 5, 15.5, and 22.5 °C respectively (Potter et al., 1970). Ammocetes typically extended the oral hood out of the substrate whenever interstitial oxygen concentrations were low. Potter (1980) concluded that ammocetes would emerge and seek more favorable habitats whenever oxygen tensions dropped to lethal levels in overlying waters.

It is generally agreed that filter feeding of larval lamprey has a negligible effect on the abundance and distribution of food particles (Moore and Beamish, 1973; Malmqvist and Brönmark, 1981; Mallatt, 1982). As a result, food resource competition is unlikely. It is possible that ammocetes may select habitats on the basis of food particle concentrations. However the negative correlation of chlorophyll concentration and lack of correlation of substrate organic content with ammocete density noted by Malmqvist (1980) suggests otherwise.

While food resource competition is unlikely, resource competition for substrate type and/or interference competition for space is possible. Morman (1987) demonstrated density dependence in growth of caged larval sea lamprey in five Michigan streams. Mallatt (1983) noted density dependence of growth in laboratory populations of Pacific lamprey (Lampetra tridentata) and attributed it to the production of growth inhibiting substances rather than direct competition for space.

Study Design and Objectives

This study of ammocete habitat selection was undertaken to distinguish and quantify larval lamprey

patch selection cues. The scope of the problem required a flexible research strategy. Results of preliminary field research were used to refine working hypotheses which in turn were formally tested in the laboratory. Results of refined hypotheses tested in the laboratory were then readdressed in the field along with additional working hypotheses. To clarify the operational rationale used in the study, I have preserved the interactive nature of the research in the discussion section. Consequently, the methods and results are presented in chronological order.

Field research in 1985/86 was designed to determine the gross distribution and abundance of lentic ammocete populations and provide quantitative data with which to refine the initial working hypotheses of habitat selection. The following working hypotheses of habitat selection were addressed:

1. The distribution and abundance of lentic ammocete populations is a simple function of selecting the first habitat encountered upon entering lentic habitats (eg. null selection hypothesis).

2. The distribution and abundance of lentic ammocete populations is a function of substrate suitability.

3. The distribution and abundance of lentic ammocete populations is a function of the thermal environment.

4. The distribution and abundance of lentic ammocete populations is a function of dissolved oxygen concentrations.

Laboratory analysis of burrowing substrate selection in 1987/88 was designed to identify specific substrate properties conducive to selection and to test the effect of competition on substrate selection. In addition, the effect on substrate selection of food particle distribution in the substrate and water column was examined. Results of the laboratory analysis were then compared with fine scaled measures lentic ammocete distribution and abundance in light of substrate particle size distribution, permeability, inferred hydrodynamics, temperature, and food particle distribution.

STUDY SITE

Located in Canadian waters of southeastern Lake Superior, the Batchawana Bay study site (figure 1) was selected on the basis of early research on lentic populations in the bay and a perennial lentic ammocete population associated with the Chippewa River (Thomas, 1961; unpub. data, Sault Ste. Marie Sea Lamprey Control

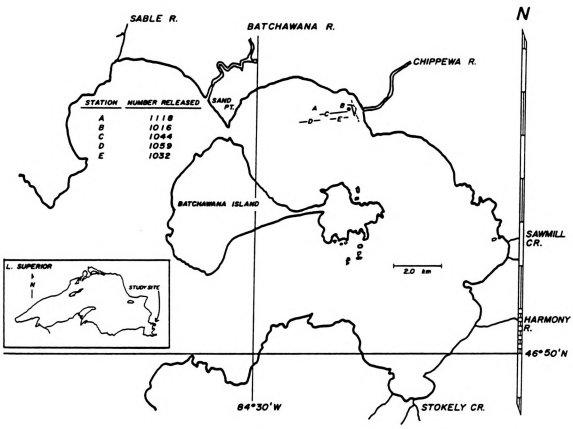


Figure 1. Map of greater Batchawana Bay, Lake Superior and details of 1985/86 study site. Depths of release points range from 24 m for points B and E to 30 m for points A and D. Solid lines around and through release points denote submersible transects while the dashed line delineates the leading edge of the alluvial fan. The solid circle denotes the position of the cross factor study patches. Perennial populations of lentic ammocetes are found off the Sable, Batchawana, and Chippewa Rivers and Stokely Creek.

Centre). An alluvial fan (depth 1.5 m) extends approximately 500 m from the mouth of the Chippewa River. The depth abruptly increases to 11 m at the edge of the fan (delta drop-off), descending to a depth of 33 m over 3 km distance thereafter. Ammocetes are known to populate the drop-off based on annual sampling with Bayer 73 (a 5 percent coating 2',5-dichloro-4'-nitrosalicylanilide on silica grains). The extent to which they inhabit deeper areas is not known.

METHODS

1985/86 Preliminary Field Research

Submersible and SCUBA based research during 1985/86 was designed to provide baseline data on the distribution and abundance of lentic ammocetes with respect to depth, distance from the alluvial fan, temperature, oxygen concentration, and sediment particle size distribution. A basin-wide mark/recapture study was conducted in 1985 to determine the density and distribution of lentic populations in the deep portions of Batchawana Bay. In 1986, field research involved experimental separation of substrate <u>versus</u> thermal acclimation as determinants of lentic habitat selection.

1985 Field Methods

Over 5000 marked ammocetes were released in a five die pattern at depths greater than 22 m on 11 and 12 July, two weeks prior to the arrival of the submersible. Another 1300 marked ammocetes were released along the delta drop-off on 24 July. The release sites and number of lamprey are shown in figure 1. To avoid releasing larval sea lamprey in an uncontrolled situation, Lampetra appendix were used in response to concerns expressed by control personnel. Ecologically, this substitution was justified on the basis of similarity in stream habitat selection and broadly overlapping larval distributions of both species (Morman, 1979). In lentic populations associated with streams feeding Batchawana Bay, both species are found in proportions matching those of the presumptive parent stream (unpub. data, Sault Ste. Marie Sea Lamprey Control Centre).

Ammocetes were collected from regional streams with backpack electrosamplers and prior to mark and release were held in outdoor troughs (12-14 °C) at the Sea Lamprey Control Centre (Canada Dept. of Fisheries and Oceans) in Sault Ste. Marie, Ontario. Equipment limitations at the Centre prevented the ammocetes from being kept at a constant 6-8 °C, the temperature of the

deeper portions of the study site during summer stratification. Six groups were marked differently with a subcutaneous injection of latex pigment suspended in Carbopol 960 (Hansen, 1972). On 11/12 July, each group of ammocetes was transported to the bottom in a 225 l plastic bag using SCUBA and released 2 m above the bottom. Each release point was identified by a subsurface sonar target 3 m above the bottom and a surface buoy. The majority of individuals initiated burrowing within 5 m of the release point.

To estimate the handling mortality of marked ammocetes in relation to depth and density, six groups of larval L. appendix were caged at 10 m with another six groups at 23 m two weeks before the main study. Two 0.186 m^2 cages at each depth contained 21, 42, and 63 ammocetes in a size range similar to that in lentic populations measured off the Chippewa River.

Sediment samples were taken with a ponar dredge, frozen, and later evaluated for particle size distribution by the Soils Testing Laboratory at Michigan State University using standard hydrometric methods (ASTM Designation D422-63; Segun Yerokun, Aug./85, pers. comm.). Two Ryan J-180 bathythermographs, one at 21 m and the other at 9.1 m, were deployed on 19 June 1985

and recovered 77 days later on 4 September 1985. Resultant strip charts were digitized and daily median temperature and range were calculated.

To sample ammocete populations in deep water, a submersible mounted electrosampling system was developed (Lee and Tusting, 1987), representing the first application of electrosampling technology to submersibles. The electrode array sampled an area of 0.46 m^2 and covered a 76 cm swath when used in continuous transects. The array was attached to the submersible's manipulator arm and tied into a sampling pump system. Ammocetes shocked from the sediments were videotaped and sucked into one of 12 sample buckets. When calibrated in the lab for field conditions of 10 °C and conductivity of 100 uS cm^{-1}, the system exhibited an overall efficiency of 59.5 ± 6.5 percent (X ± sd) in eliciting emergence of ammocetes.

Upon arrival of the submersible on 25 July 1985, a 500 m transect was conducted along the delta drop-off at the 12 m isobath. An additional 200 m transect orthogonal to the north terminus of the baseline transect was also completed. In deeper waters, 980 m^2 were electrosampled in three transects with particular effort at release points C, D, and E (figure 1). At

random points along the transects, water samples were taken through the hull and O_2 concentration was measured with a YSI oxygen meter. Lack of time prevented transects through release points A and B.

On 26 and 29 July, 1985, Sea Lamprey Control personnel treated the delta drop-off zone with Bayer 73. Treatment plots ranging in depth from 1.5 to 13 m and 0 to 60 m from the edge of the alluvial fan were lined out on the surface with buoys and measuring lines. Bayer 73 was applied at a rate of 248 kg per hectare at the surface and allowed to sink to the bottom. Distressed and dying ammocetes swimming to the surface were netted at the surface. In addition, control personnel conducted a Bayer 73 treatment at Sand Point approximately 3.5 km due west of the experimental site on 30 July.

1986 Field Methods

Based on 1985 results, a 2^2 factorial field analysis of thermal acclimation and substrate particle size distribution as determinants of lentic habitat selection was conducted. Four patches (3 m x 3 m) at a depth of 20.5 m were lined out with PVC frames. Lined out from north to south, the distance between adjacent

patches was 7.5 m. A total of 1 m^3 of washed sand (0.25 mm mean diameter) was added to modify two of the patches (0.5 m^3 each, see table 1). The location of this experiment relative to the 1985 study area is shown in figure 1.

On one modified and one unmodified patch, 500+ treatment specific marked L. appendix were held in situ for four weeks in 1.0 m^3 cages starting 11 June. To prevent premature escape of marked ammocetes and disturbance of ammocetes during cage retrieval the cages had recessed trap doors. Consequently, 8-9 cm of washed sand was used above the trap doors as temporary burrowing substrate. Twenty-four hours before all ammocetes were released, two non-acclimation treatment cages were placed on the remaining patches. To maintain homogeneity in handling of ammocetes (except holding period), the same cage protocol was used.

On 9 July, the trap doors on all cages were opened and ammocetes along with the cage substrate were released into the center 1 m^2 of each patch. All ammocetes reburrowed into the sediment within 20 minutes and the cages were lifted from the bottom. On 22 July 1986, three 0.46 m^2 samples were collected from each patch with the submersible electrosampler. Samples I

Table 1. Number of ammocetes released and recovered along with patch substrate particle size distribution for 1986 habitat modification/thermal acclimation experiment off the mouth of the Chippewa River.

Treatment	Number Released	Percent sand/silt/clay	Recoveries I	II	III
Unmodified & Unacclimated	505	35.6/51.7/12.7	2	38	0
Unmodified & Acclimated	531	32.6/51.7/15.7	1	11	1
Modified & Unacclimated	515	87.0/ 4.3/ 8.7	1	9	2
Modified & Acclimated	503	79.6/11.7/ 8.7	0	5	6

and III in all patches were taken at opposing corners while sample II was taken in the center of each patch at the release point.

1987/88 Laboratory and Field Research

Laboratory and field research in 1987/88 was designed to pinpoint the determinants of larval lamprey habitat selection. To identify and separate specific substrate selection cues, burrowing substrate selection of larval lamprey was tested in the laboratory. In addition to classification of substrate by particle size distribution, substrates were classified by porosity and permeability. Porosity is directly proportional to the rate of gaseous diffusion through a porous media. Permeability is indicative of the susceptibility of a porous media to a direct exchange of fluid. Additional tests were conducted to examine the effect of differing levels of intra- and interspecific density, and food particle distribution on habitat selection. Lentic ammocete distribution and abundance with respect to complementary environmental measures were then contrasted with laboratory results.

C

p

wi

fr

ref

Each

deio

thro

times

deion

strea

1987/88 Laboratory Methods

Test Species Collection and Holding Facilities

Burrowing substrate selection tests were conducted on larval sea lamprey and larval American brook lamprey. Sea lamprey ammocetes were collected from the Great Chazy River in New York with the assistance of USFWS personnel from Vermont and from various streams in the lower peninsula of Michigan by USFWS personnel based at Ludington, Michigan. Control personnel from Ludington also provided L. appendix ammocetes collected from various lower peninsula streams in Michigan. Additional larval L. appendix were collected from East Davignon Creek in Ontario with the assistance of control personnel based at Sault Ste. Marie, Ontario. Retrieved with backpack electrosamplers, ammocetes ranged in size from 40 to 170 mm total length.

Ammocetes were held in the laboratory in refrigerated stream units 2.08 m long and 0.56 m wide. Each stream contained approximately 500 liters of deionized tap water which was aerated and recirculated through beds of dolomite and activated charcoal 7.7 times per hour to control ammonium concentrations. With deionization, total dissolved solids in the laboratory streams matched that of Batchawana Bay ($\approx$ 100 uS cm^{-1}).

The temperature was kept constant at 10.0 ± 0.5 °C and a daily 12 on/12 off lighting cycle was maintained throughout the study.

Ordered by size in 20 mm increments, ammocetes were held in the stream units in 29.2 x 17.8 x 33.0 cm (LWH) polyethylene containers screened with 18 mesh polypropylene. Each holding container was filled with washed sand with a particle diameter size range of 0.063 to 1.00 mm to a depth of 11.5 cm. The total density of ammocetes per container never exceeded 70 g per container for individuals over 120 mm long and was normally less than 35 g per container for individuals under 120 mm. Each stream unit held a maximum of 9 holding containers.

Ammocetes in each stream were fed a maintenance ration of 100 g dry yeast per stream every four days (Mallatt, 1983). Each stream was drained and cleaned once every month on average. At this time, ammocetes were transferred to clean holding containers with new sand and placed in the cleaned stream with pre-chilled deionized water. Used sand was rinsed and dried in a drying oven at 65 - 70 °C then recycled for use during the next cleaning period.

Burrowing Substrate Classification

Initial classification of substrate groups by grain diameter was chosen as a familiar point of departure for further classification based on porosity and permeability. The Wentworth grade scale was used to facilitate limited comparison of laboratory results with prior qualitative field descriptions of selected habitats. Burrowing substrates were created by sifting unwashed silica and mixed riverine sands through a set of nested sieves with a motorized sieve shaker. After sieving, each substrate group was rinsed to remove clinging silt/clay particles and organic material.

Using a particle diameter of 63 microns as the threshold point between sand and silt (Wentworth, 1922; Taylor, 1948), test substrates were ordered by a 2x geometric progression starting with sand particles retained on a 63 micron mesh sieve. Particles passing this mesh were classified as silt/clay. No effort to further subdivide the silt/clay class was made. The resultant substrate groups are listed in table 2 by "common" name, grade limits, and mean grain diameter. In addition to the substrate groups above, a set of four mixed substrates composed of differing percentages of particle size groups was created. Designed to match the

Table 2. Wentworth classification of laboratory substrates with mean (± se) values for porosity (P) and permeability (K).

"Common" Name	Grade Limits (mm)	Mean Diam. (mm)	Porosity (P: % voids)	Permeability (K: ml min^{-1})
Silt/Clay	≤0.063	0.0315	47.9 (2.34)	0.028 (0.003)
Very fine sand	0.063-0.125	0.0938	43.9 (1.76)	0.587 (0.022)
Fine sand	0.125-0.250	0.1875	38.5 (2.54)	1.331 (0.074)
Medium sand	0.250-0.500	0.3750	35.4 (0.75)	12.94 (0.467)
Coarse sand	0.500-1.000	0.7500	40.4 (1.61)	75.08 (14.93)
Very coarse sand	1.000-2.000	1.5000	41.7 (2.97)	191.3 (5.56)

particle size distribution of substrates encountered in the field in 1985, the mix ratios for each are listed in table 3.

Porosity of all laboratory substrates, defined as the ratio of the volume of space between sediment particles to total sample volume, was measured using the protocol and formulas outlined in appendix 1. Substrate permeability, in terms of centimeters of water flow per minute, was measured in a constant low head permeameter at 25.5 ± 0.5 °C. Specific operation of the permeameter and a detailed discussion of permeability calculations employed may be found in appendix 2. Porosity and permeability values are included for all substrates listed in tables 2 and 3.

In general, porosity was higher for ungraded laboratory substrates than for graded substrates (figure 2). Porosity of ungraded substrate groups was highest at the extremes of the mean grain diameter distribution and lowest for medium sands (0.375 mm mean diameter), ranging between 35 and 48 percent. Porosity of graded substrate groups decreased with increasing mean grain diameter, ranging between 28 and 37 percent.

Table 3. Percentage composition of mixed sediments with weighted mean grain diameter along with mean (± se) values for porosity (P), percent mass water (PMW), density of saturation, and permeability (K).

Mix	Percent Composition		Mean Diam. (mm)	Porosity (P: % voids)	Permeability (K: ml min^{-1})
A	70%	≤0.063	0.0596	36.9	0.035
	20%	0.063-0.125		(0.16)	(0.002)
	10%	0.125-0.250			
B	30%	≤0.063	0.1216	36.5	0.077
	40%	0.063-0.125		(0.63)	(0.005)
	20%	0.125-0.250			
	10%	0.250-0.500			
C	10%	≤0.063	0.2469	32.7	0.429
	20%	0.063-0.125		(1.79)	(0.054)
	40%	0.125-0.250			
	20%	0.250-0.500			
	10%	0.500-1.000			
D	10%	0.063-0.125	0.4969	28.2	1.482
	20%	0.125-0.250		(0.98)	(0.010)
	40%	0.250-0.500			
	20%	0.500-1.000			
	10%	1.000-2.000			

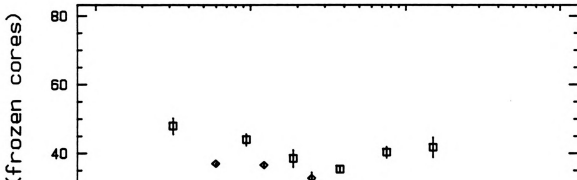


Figure 2. Mean porosity (± sd) in relation to mean grain diameter for laboratory substrates. Squares correspond to ungraded Wentworth substrates while diamonds correspond to graded substrate mixes. All porosity values were determined from frozen cores.

Within ungraded and graded laboratory substrates, permeability was linearly related to group mean grain diameters (figure 3). Permeability ranged between 0.02 and 200 cm min^{-1} for ungraded substrates and 0.03 to 1.5 cm min^{-1} for graded substrates. For a given mean grain diameter, permeability was higher for ungraded than graded substrates.

Sediment Selection Experiments with Tests for Interference Competition Effects

All substrate selection studies were conducted in twelve 100 l aquaria set in a refrigerated water bath. In each aquarium, two four-place test arenas measuring 22.2 cm by 22.2 cm by 35.6 cm (LWH) were placed at opposite ends. Tested in groups of four, different substrates in square 0.98 liter polyethylene containers were distributed among groups of four test aquaria in a preset pattern such that each test arena received a full complement of test substrates and each substrate was distributed equally among all positions in the test arenas (figure 4). Because the test arenas only permitted testing of four substrates at a time, preliminary analysis of substrate selection at both ends of the Wentworth scaled sediment distribution were conducted to identify and bracket the preferred substrate classes. After selection experiments on

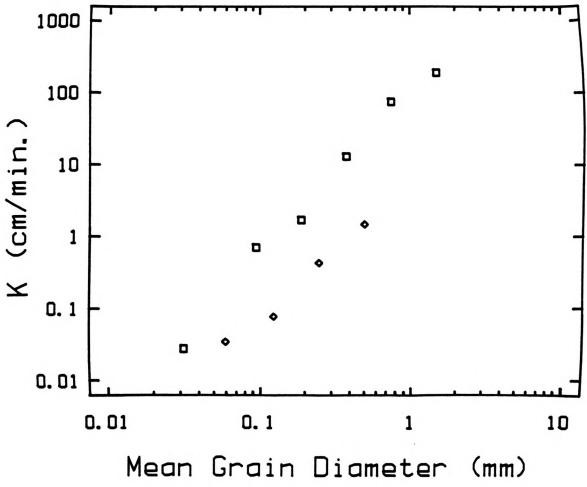


Figure 3. Mean permeability with respect to mean grain diameter for laboratory substrates. Squares correspond to ungraded Wentworth substrates while diamonds correspond to graded substrate mixes. All permeability values were determined from frozen cores.

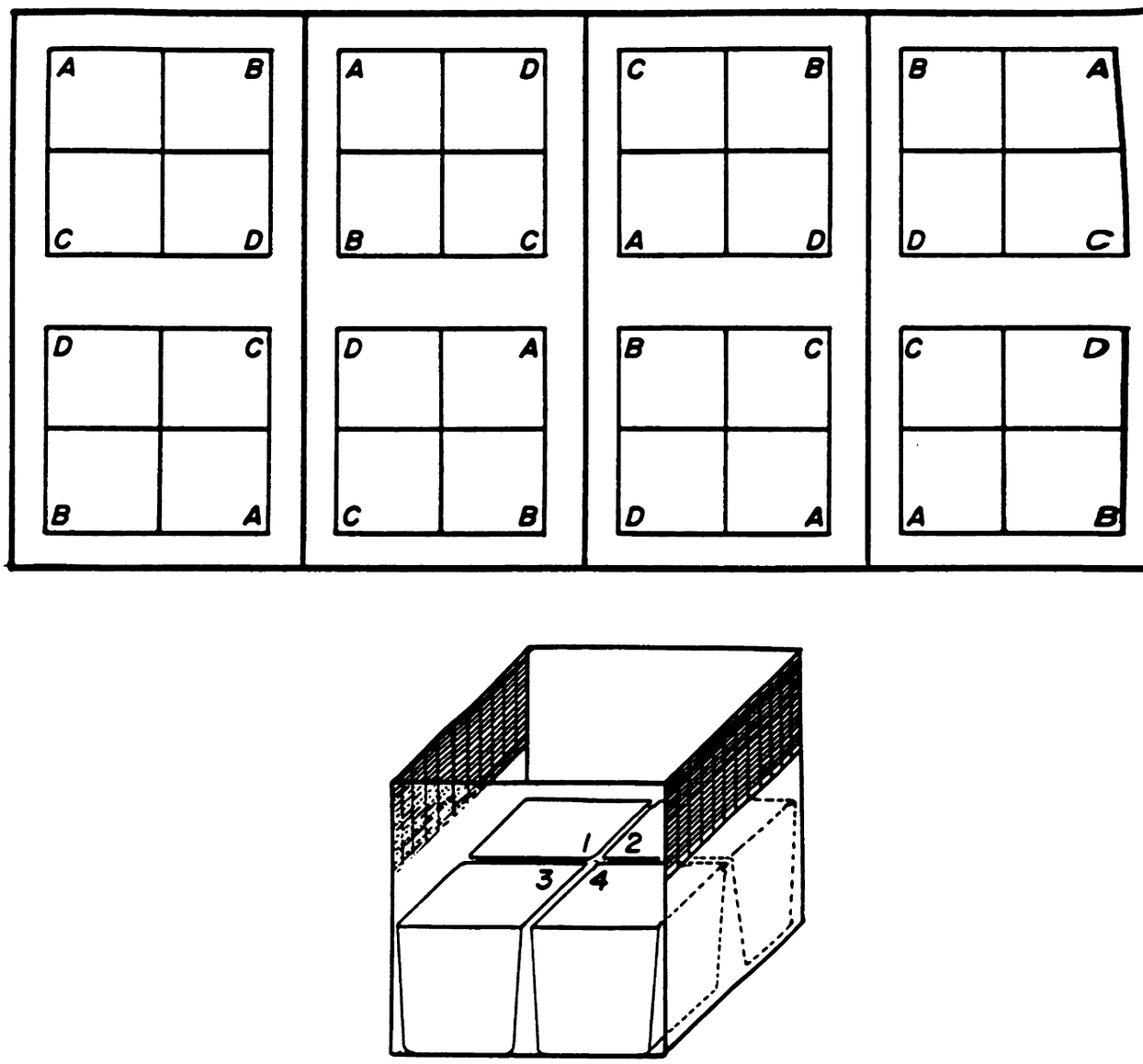


Figure 4. Schematic representation of substrate distribution among test arenas and oblique view of a test arena. Letters A through D correspond to different substrate types. Each substrate tested in a given series occupies each position in a test arena twice. An air stone is positioned between each test arena in an aquarium and circulates water through the side meshes of the test arenas.

Wentworth scaled substrates were completed, selection experiments on graded substrates (mixes A - D) were conducted.

Separate substrate selection tests were performed on small (40 to 79 mm TL) and large (120+ mm TL) ammocetes of both species. To evaluate the effect of intraspecific competition within a size class, series of unstaggered and staggered releases of ammocetes at different densities were conducted. The results of unstaggered releases of ammocetes at a low density of 4 per test arena and a high density of 8 per test arena were contrasted with the staggered releases of two and three groups of four per test arena. The short-term importance of intraspecific competition for space was assessed by comparison of substrate selection patterns between different release/density treatments. To evaluate interspecific competition effects on substrate selection within a given size class, the results of simultaneous releases of 4 L. appendix with 4 P. marinus were contrasted with the substrate preferences exhibited individually by both species at densities of 4 and 8 per test arena. Experimental blocks are listed in table 4 by species, size class, density, and release pattern.

Table 4. Blocking structure for experimental analysis of larval lamprey substrate habitat selection and evaluation of intra- and interspecific competition effects.

A.	Small *L. appendix*		Large *L. appendix*	
Density	Unstaggered Release	Staggered Release	Unstaggered Release	Staggered Release
4	X		X	
8	X	-	X	-
12	-	-	-	X

B.	Small *P. marinus*		Large *P. marinus*	
Density	Unstaggered Release	Staggered Release	Unstaggered Release	Staggered Release
4	X		X	
8	X	X	X	X
12	-	-	-	X

C.	Large *L. appendix* : Large *P. marinus*	
Density	Unstaggered Release	Staggered Release
4:4	X	-
8:8	X	-

For a given experiment, ammocetes were released in the dark and allowed to burrow. All tests ranged in duration from 4 to 6 days and staggered groups were released at 48 hour intervals. Each experimental run was conducted at a constant temperature of 10 ± 0.5 °C and the maintenance feeding schedule was sustained throughout the course of all experiments. At the end of a given experiment series, each test arena was dismantled and the number of ammocetes in each substrate container was recorded by sediment type and container position. Burrow depth for individual ammocetes, defined as the difference between the midpoint of the branchial basket and substrate surface, were recorded in a subset of test arenas.

Food Related Habitat Selection Experiments

A different set of habitat selection experiments were conducted to test the effect of food particle distribution on burrowing behavior. These tests were broken down into two categories to analyze the effect of food particle distribution in sediments versus that of food particle distribution in the water column.

For the sediment/food particle distribution experiments, a constant sediment size of 0.375 mm mean

grain diameter (range: 0.25 to 0.50 mm) was used in all four positions of the test arenas. Two of the four positions in each test arena were injected with 20 ml of a 100 g/l yeast perfusion. The pattern of perfused versus unperfused sediments across all replicates insured equal distribution of treatments over all positions in the test arenas. Ammocetes of both species were released individually in unstaggered groups of 8 and allowed to come to distributional equilibrium in accordance with the test arena protocol detailed above.

To test the effect of food particle distribution in the water column as opposed to sediments, a different test apparatus was used. Shown in figure 5, the four individual two-place test chambers permitted the ammocetes a choice of burrowing where the water column contained an abundance of food particles versus an area of zero food particle concentration. Solutions of distilled and yeast perfused water were pumped into opposing sides of the test unit at a rate of 7.8 ml per minute, draining towards a common center drain. Additional tests were run with an algae perfusion (Ankistrodesmus falcatus.), a green alga common in the gut of larval lamprey (Hardisty and Potter, 1977). Concentrations of yeast in the food chambers at the

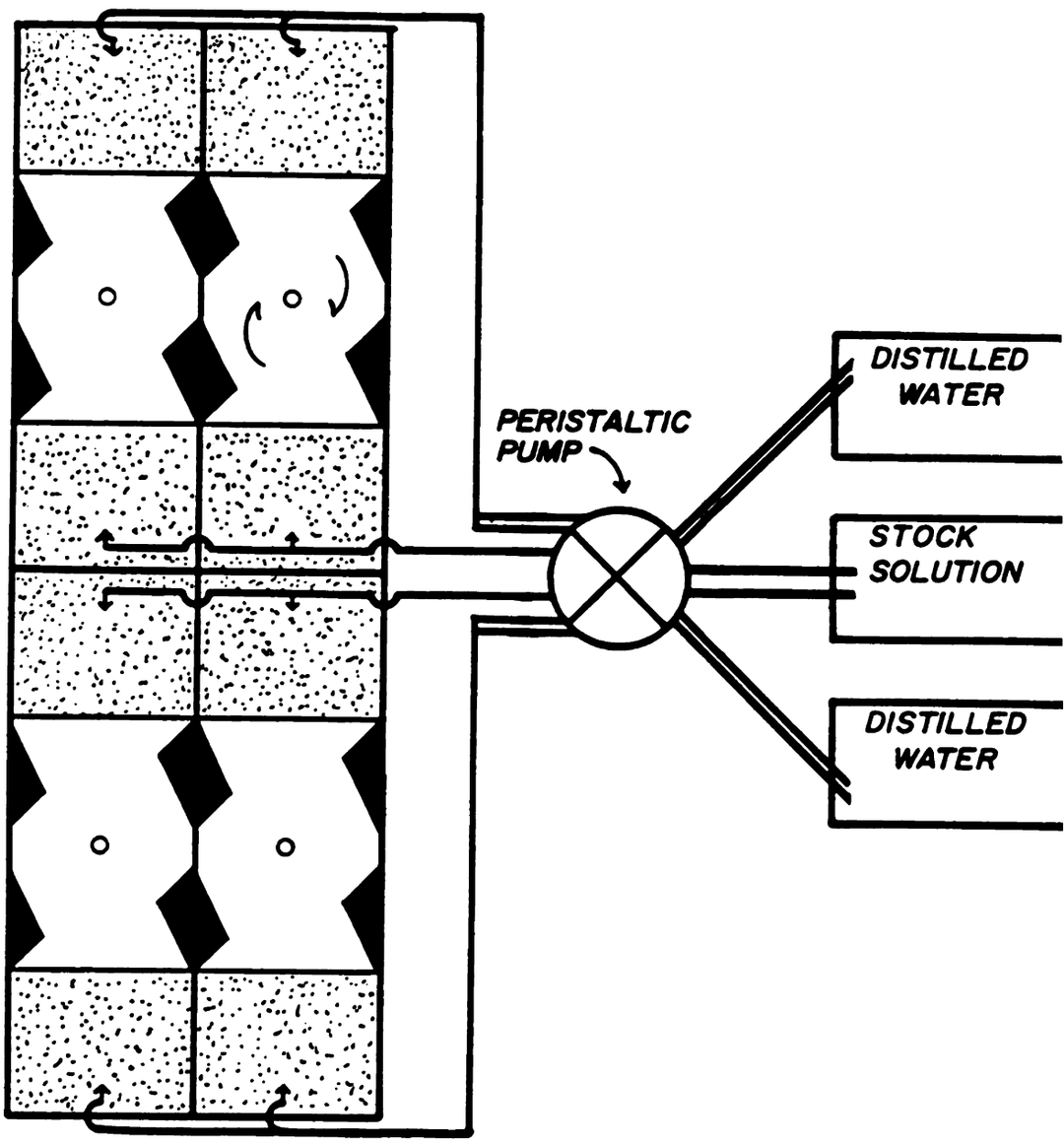


Figure 5. Schematic representation of food/habitat selection test apparatus. A food particle stock solution is pumped through separate lines to the inner ends of four separate test chambers while distilled water is pumped through another set of lines to the outer end of each test chamber. The flow rate was set to 7.8 ml $min.^{-1}$ for each line and controlled with a peristaltic pump. In use, opposing flows from each end of a test chamber run towards a center drain.

start of the experiments were ≈ 0.06 g/l. for yeast and 35 to 43 ug chl a./l for Ankistrodesmus.

Ammocetes were lightly sedated (MS-222: 3-aminobenzoic acid ethyl ether) and released in the dark at the center of each test chamber and allowed to make their choice upon recovery from the anesthetic. Tests were run overnight and counts of ammocetes burrowed in both sides of the test chamber were recorded. The experimental blocking structure for all food/habitat selection experiments is listed in table 5 by species, category, and food type.

Statistical Analyses

Frequency data from each experimental series was initially tested for departure from random substrate selection using a replicated G-test with William's correction (Sokal and Rohlf, 1981). This approach permitted separate testing of substrate selection and homogeneity of replicates. When the total number of ammocetes tested in an experimental series was less than 33, results of the G-test were compared with the likelihood ratio test, an exact probability test.

Table 5. Blocking structure for experimental analysis of food/habitat selection. All releases were unstaggered and sediment type remained constant across all experiments (mean grain diameter 0.375 mm, range 0.250 - 0.500 mm).

	L. appendix		P. marinus	
Food	Substrate	Water	Substrate	Water
Yeast Perfusion	X	X	X	X
Algae Perfusion	-	X	-	-

Further analyses of substrate preferences were conducted with multifactor model I ANOVA's to test for effects of position in the test arenas, differences in substrate preferences between species and size classes, and effects of intra- and interspecific interference competition. Unplanned multiple comparisons among means for a given analysis were conducted with the T-method when variances were homogenous (Sokal and Rohlf, 1981) and the Games and Howell method when variances were heterogenous (Games and Howell, 1976)(see Appendix 4).

1987/88 Field Methods

An underwater transect was used as a reference frame for fine scaled field measures of substrate grain size distribution and associated properties, food particle distribution, and temperature regime off the mouth of the Chippewa River. Using SCUBA, I lined out an initial transect extending perpendicularly from the upper edge of the alluvial fan along the bottom with 90 m of nylon cord on 21 May 1987. The transect endpoints were anchored with concrete blocks and identified at the surface with buoys. Between the endpoints, the transect line was anchored with PVC stakes every 10 m.

Thirty reference stations were defined along the transect at 3 m intervals with indelible ink marks on the line and twist-tied aluminum labels. The transect was further extended on 25 July 1987, with the addition of three buoyed stations at 120, 200, and 320 m from the edge of the alluvial fan along the same heading.

At each station, depth was measured with an electronic depth sensor (ORCA Industries) with 25 cm accuracy and the bed slope was gauged within ± 1.0° with an inclinometer. This information was used to fix the horizontal distance of each station from the edge of the alluvial fan using right triangle geometry in tandem with the known station positions along the transect line.

To track the formation and downslope movement of the thermocline over the course of the summer, three Ryan J-180 bathythermographs were deployed along the transect at stations 10, 16, and 24 at depths/distances of 10/25.3, 12.2/43.1, 13.7/67.0 m respectively. The station 10 bathythermograph was anchored on the bottom with a concrete block on 24 May 1987 while the others were similarly placed on 13 June 1987. The thermal sensors were set within 25 cm of the sediment/water

interface. Resultant strip charts were digitized and daily median temperature and range were calculated for each station

To characterize the sediment particle size distribution along the transect, 0.98 liter sediment grabs at 1.3 m depth increments were made by hand on 24 May using SCUBA. Sand, silt, and clay fractions were separated using standard hydrometric methods (ASTM Designation D422-63) at the M.S.U. Soils Testing Laboratory. In addition, to characterize substrate porosity, permeability, and substrate food particle distribution over space and time, three 2.54 cm diameter cores exceeding 8 cm in length were taken by hand according to the schedule outlined in table 6 using SCUBA. Core samples were slowly frozen in the core tube to limit disruption of the sediment fabric (Rutledge and Fleeger, 1988).

Two of the replicate cores for a given station and date were used in the determination of porosity and permeability while the remaining core was saved to analyze sediment food particle distribution and abundance. Kept in the dark, the frozen cores were processed in the laboratory within six months of collection. Lenz and Fritsche (1980) verified

Table 6. Summer 1987 sediment core sampling schedule. Stations 31-33 not set up until mid July. Missing values on 21 August due to unsafe diving conditions.

Station	Depth (m)	Distance (m)	Date			
			7/03	7/26	8/21	9/22
1	1.8	0.0	•	•	•	•
2	3.4	2.6	•	•	•	•
3	4.9	5.2	•	•	•	•
4	6.4	7.8	•	•	•	•
5	7.3	10.6	•	•	•	•
8	8.8	19.4	•	•	•	•
10	10.1	25.3	•	•	•	•
12	11.0	31.2	•	•	•	•
16	12.2	43.1	•	•	•	•
20	13.1	55.1	•	•	•	•
24	13.7	67.0	•	•	•	•
29	14.9	81.9	•	•	•	•
31	17.0	130		•		•
32	19.0	200		•		•
33	22.8	320		•		•

negligible degradation chlorophyll in frozen samples stored up to six months at -20° C.

Food particle distribution and abundance were monitored in the substrate and at the sediment/water interface throughout the summer. The temporal distribution and abundance of organic material and chlorophyll a in the sediments were estimated from replicate cores collected as described above. Using a vacuum sampling system (figure 6), two 1140 ml water samples were collected from the water column within 1.0 cm of the sediment/water interface at a given station. The sampling schedule by date and location is listed in table 7. A detailed discussion of field and laboratory processing of substrate and water column samples is included in appendix 3.

The distribution and abundance of lentic ammocetes along the transect was assessed using a trap tray method modified from Thomas (1961). A total of 30 trap trays were built from plastic children's sandboxes (75 x 75 x 18 cm LWH). Each trap tray was fitted with a continuous aluminum flange riveted to the inner edge of the box and protruding 5 cm above the lip. A 1.0 cm hole was drilled into one corner of the tray for use as a TFM injection port. Sampling an area of 0.5625 m^2 each,

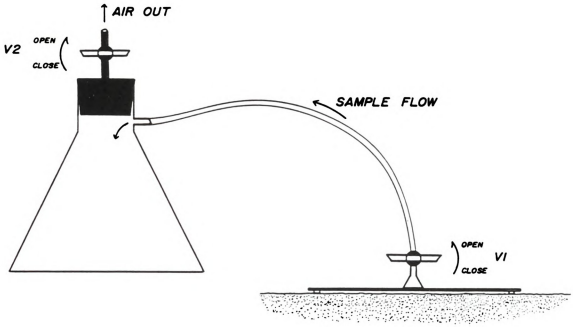


Figure 6. Schematic representation of diver operated water sampler. In use, the plexiglass sampling plate was slowly set over the sampling point without disrupting the substrate. A 1140 ml sample from the layer of water within 1.0 cm of the sediment/water interface (SWI) was taken by slowly opening the stopcock (V1) at the plexiglass sampling plate and allowing the partial vacuum created in the submerged flask to suck in part of the water sample. After equalization of pressure in the vacuum flask, the rest of the sample was taken by slowly opening of the flask stopcock (V2) and bleeding off residual air. The volume of water covered by the plexiglass plate was 1.5 times as great as that held in the flask to insure that the sample came from the SWI as opposed to shallower strata.

Table 7. Summer 1987 water sampling schedule. Stations 31-33 not set up until mid-July. Missing values for 21 August due to unsafe diving conditions.

Station	Depth (m)	Distance (m)	Date			
			7/05	7/27-28	8/21	9/18-19
1	1.8	0.0	•	•	•	•
2	3.4	2.6	•	•	•	•
4	6.4	7.8	•	•	•	•
9	9.8	22.3	•	•	•	•
17	12.2	46.1	•	•	•	•
29	14.9	81.9	•	•	•	•
31	17.0	130		•		•
32	19.0	200		•		•
33	22.8	320		•		•

trap trays were used in groups of three. Trapping effort was extended over space and time according to the schedule outlined in table 8.

Trap trays were placed on the bottom with the aluminum flange imbedded in the sediment acting both as an anchor and an impediment to lateral burrowing of ammocetes. A concentrated solution of TFM was then introduced through the injection port with a 25 ml syringe. The amount of TFM injected was scaled to provide a final concentration of 9.5 ppm active ingredient within the volume enclosed by the trap tray.

Ammocete movement patterns with respect to changes in abiotic and biotic factors over space and time were assessed with a mark/recapture study. A total of 1046 larval L. appendix were collected on 20 May from East Davignon Cr., Sault Ste. Marie, Ontario. Separated into two groups, 522 received a ventral subcutaneous mark while the remaining 524 received a dorsal mark. The marks were different from marks used in previous years. The water temperature was 10 °C when the ammocetes were collected. During marking and prior to lentic release, ammocetes were held in 7 °C water. On 23 May, the ventral marked ammocetes were released at station 10 (10 m depth, 25.3 m from edge of alluvial

Table 8. Temporal distribution of sampling effort by 5+ station blocks and distance from edge of alluvial fan.

Station Block	Distance (m)	Area Sampled (m^2)	
		June/July	Aug./Sep.
1 - 5+	0.0 - 13.5	9.00	5.63
6 - 10+	13.5 - 28.5	6.19	10.69
11 - 15+	28.5 - 43.1	8.44	11.25
16 - 20+	43.1 - 57.9	8.44	7.31
21 - 25+	57.9 - 73.0	6.75	5.06
26 - 30	73.0 - 84.7	6.75	9.56
31	130	3.38	3.38
32	200	3.38	3.38
33	320	0.00	3.38

fan) while the dorsal marked ammocetes were released at station 24 (13.7 m depth, 64 m from edge of alluvial fan). The temperature at both stations was 9 °C during release.

Ammocetes were transported to the release points in sealed 24 liter containers using SCUBA and released from individual containers by removal of the cover with immediate inversion of the container and placement on the substrate. Inverted containers were not removed until all ammocetes burrowed (within 5 minutes). Ammocetes were released at station 24 in a five die pattern within a 1 m square while dorsal marked ammocetes were released in a four die pattern within the same amount of area. On 24 September 1987, the marked ammocete release points were sampled with 8 trap trays in a modified "X" pattern to measure the final density and the local pattern of dispersal at each point.

To couple results of laboratory substrate selection experiments with probable conditions encountered by ammocetes released in 1985, six substrate cores were taken at each of the 1985 release points on 31 July 1988 using their LORAN C coordinates. Frozen at -20 °C as per 1987 methods, permeability was measured in three

cores from each station using the procedures outlined in appendix 2.

RESULTS

1985 Field Results

Daily median, minimum, and maximum temperatures at 9.1 and 21 m in 1985 are shown in figure 7. Median temperature at 9.1 m increased gradually to a maximum of 19.5 °C on 18 August while temperatures at 21 m remained relatively constant. Daily temperature variation was greater at 9.1 m than 21 m, exceeding 4 °C in conjunction with passing weather disturbances. The thermocline (10 ± 1 °C) set up by 4 July at 11.6 m and progressively descended to a depth of 17 m by 31 July.

The size distribution of sediment particles relative to depth, distance from the edge of the alluvial fan, and interdiction of the thermocline with the bottom is shown in figure 8. The sediment particle size distribution along the delta drop-off zone is characterized by a large sand fraction. The silt/clay content of the substrate increases with increasing depth and distance from the alluvial fan.

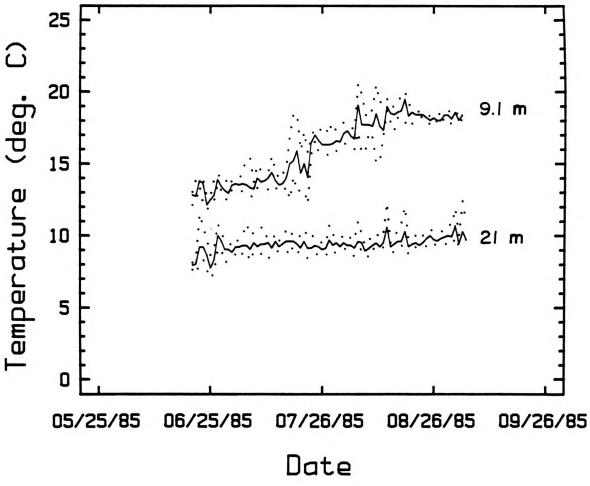


Figure 7. Daily median, minimum, and maximum temperatures at 9.1 and 21 m during summer 1985.

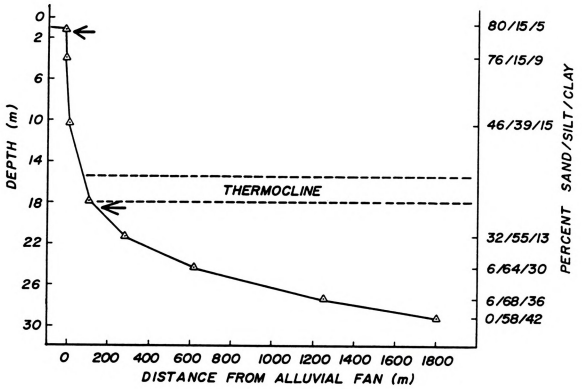


Figure 8. Composite relationship between depth, substrate particle size distribution, distance from the edge of the alluvial fan, and final depth of the thermocline. The measured distribution of lentic ammocetes relative to all factors is delimited by the arrows.

Results of the handling mortality study were confounded by the loss of some individuals during loading of the cages on the bottom but of those individuals successfully transferred, 100 percent survived. As a check, cage sediments were carefully sifted for dead individuals upon retrieval. No evidence of dead individuals was found.

Although problems with the suction system tied into the electrosampler array precluded collection of ammocetes with the submersible in 1985, emergent ammocetes were recorded visually during transects. A total of 69 ammocetes were located over approximately 116 m^2 within 50 m of the edge of the alluvial fan in an area of known distribution based on annual Bayer 73 treatments. Five additional ammocetes were located at depths of 15.2 to 19.2 m, ranging approximately 50 to 170 m from the edge of the alluvial fan. No marked or unmarked ammocetes were located with the submersible in deeper portions of the study site at or near release points C, B, or E. Sampled water was saturated with oxygen at all depths.

A total of 4,216 ammocetes were recovered during the 26 July Bayer 73 treatment of 20,130 m^2 surface area

along the delta drop-off in depths ranging from 1.8 to 13 m. Of those recovered, 113 were recaptures of shallow released ammocetes. Also recaptured were 4 individuals from release point A, 4 from release point E, and 1 each from release points B and C. Three days later, an additional 10,065 m^2 of surface area bracketing the above area was treated with Bayer 73 and an additional individual from release point C was recovered along with 430 unmarked ammocetes. Total bottom area treated (31,596 m^2) was estimated by calculating the hypotenuse of a triangle formed by the surface widths of the treatment areas and change in depth, multiplied by the length of the treatment areas. The percent species composition of captured ammocetes was 19.5 P. marinus, 80.4 L. appendix, and 0.1 I. spp.

The Bayer 73 treatment at Sand Point, approximately 3.5 km due west of the experimental area, on 30 July resulted in the recovery of another lamprey from release point A. In addition, during stream collections of ammocetes in May 1986, 1 ammocete from release point C was recovered in Sawmill Creek over 8 km from the study site and 1 each from release points C and E were recovered in Stokely Creek over 12 km from the site.

1986 Field Results

Results of the cross factor study of sediment particle size distribution versus thermal acclimation of ammocetes are shown in table 1. The greatest number of ammocetes were collected from the unmodified, unacclimated patch (40), while similar numbers (11 - 13) were collected in the other three patches. Only subsamples I and III were used in the model II ANOVA (table 9) because all samples taken in the middle of a patch were biased with respect to habitat modification by sand used as a burrowing substrate within release cages. Small sample sizes contributed to a mean square with a large error. There were no statistically significant differences.

1987/88 Laboratory Results

Summarized results of substrate preference and food related habitat selection experiments are presented below with basic frequency analyses and abstracted ANOVA results. Appendix 4 contains results of tests for homogeneity of variance for both single experimental series and pooled data sets along with full ANOVA tables for all pooled analyses. Results of a stepwise linear

Table 9. Model II ANOVA for 1986 habitat modification/thermal acclimation experiment off the mouth of the Chippewa R.

Source of Variation	df	SS	MS	F	P
Habitat modification	1	3.12	3.12	0.609	0.505
Acclimation	1	1.12	1.12	0.218	0.308
Interaction	1	1.13	1.13	0.220	0.309
Error	4	20.50	5.13		
Total	7	25.87			

regression analysis of mean burrowing depth with respect to substrate permeability, porosity, and ammocete weight follows the summarized results of burrowing substrate selection tests.

Frequency Analysis of Substrate Preferences

Table 10 provides a summary of all substrate preference/competition series with reference to tested substrates. Neither large L. appendix or P. marinus selected silt/clay or very coarse sand substrates (0.0315 and 1.5 mm mean grain diameter respectively). In each case, the data departed significantly from uniform or random substrate selection and the replicates were statistically homogenous. Consequently, all subsequent tests using the Wentworth scaled substrates were limited to very fine through coarse sands (0.0938 through 0.75 mm mean group grain diameters).

With respect to statistical departure from random substrate selection and homogeneity of replicates, results of substrate preference tests for very fine through coarse sands were varied across experimental series. Generally, for L. appendix and P. marinus released allopatrically, fine and medium sands were preferred over very fine and coarse sands. This

Table 10. Pooled percentages of ammocetes occupying different burrowing substrates. Experimental series are identified by ammocete size, species, density (D) per test arena, release pattern, and number of replicates. Subgroups for all staggered releases are listed in sequence vertically. To indicate departure from random selection of substrates, significance levels for the likelihood ratio test (LRT; when $n \leq 32$) and G-test for pooled data (G_{wp}; Williams correction) are included. The significance level of G_{het} provides an index of homogeneity among replicates within an experimental series.

Experimental Series	Mean Group Grain Diameter						Signif. Level		
	0.0315	0.0938	0.1875	0.3750	0.7500	1.500	LRT	G_{wp}	G_{het}
Large L. appendix, D8, unstaggered, 4 replicates	0.0	34.5	31.0	34.5	--	--	.0016	<.001	.9340
Large P. marinus, D8, unstaggered, 4 replicates	0.0	18.8	43.8	37.5	--	--	<.001	<.001	.7446
Large L. appendix, D8, unstaggered, 4 replicates	--	--	53.1	34.4	12.5	0.0	<.001	<.001	.9129
Large P. marinus, D8, unstaggered, 4 replicates	--	--	30.0	56.7	13.3	0.0	<.001	<.001	.3910
Small L. appendix, D4, unstaggered, 8 replicates	--	15.6	21.9	31.3	31.3	--	.0033	.0029	.4480
Small L. appendix, D8, unstaggered, 16 replicates	--	13.3	41.6	39.8	5.3	--	-	<.001	.0958
Large L. appendix, D4, unstaggered, 16 replicates	--	21.7	25.0	38.3	15.0	--	-	.1569	.0056
Large L. appendix, D8, unstaggered, 16 replicates	--	23.3	23.3	37.9	15.5	--	-	.0770	<.001
Large L. appendix, D12, staggered, 16 replicates	-- -- --	12.9 25.0 24.6	29.0 28.1 34.4	45.2 34.4 31.1	12.9 12.5 9.8	-- -- --	-	<.001	.0070
Small P. marinus, D4, unstaggered, 8 replicates	--	15.6	21.9	31.3	31.3	--	.5180	.5157	.6851
Small P. marinus, D8, unstaggered, 8 replicates	--	19.4	41.9	19.4	19.4	--	-	.0411	.4455

Table 10 continued on next page

Table 10 (cont'd).

Experimental Series	Mean Group Grain Diameter						Signif. Level		
	0.0315	0.0938	0.1875	0.3750	0.7500	1.500	LRT	G_{wp}	G_{het}
Small P. marinus, D8, staggered, 4 replicates	-- --	10.0 26.7	50.0 20.0	20.0 33.3	20.0 20.0	-- --	.8295	.7979	.0043
Large P. marinus, D4, unstaggered, 8 replicates	--	9.4	34.4	46.9	9.4	--	.0037	.0040	.0341
Large P. marinus, D8, unstaggered, 16 replicates	--	5.7	32.5	41.5	20.3	--	-	<.001	.2841
Large P. marinus, D8, staggered, 10 replicates	-- --	10.3 11.1	30.8 36.1	38.5 47.2	20.5 5.6	-- --	-	<.001	.0220
Large P. marinus, D12, staggered, 14 replicates	-- -- --	2.1 6.0 10.0	22.9 30.0 14.0	58.3 56.0 44.0	16.7 8.0 12.0	-- -- --	-	<.001	.0393
Large L. appendix: P. marinus, D4:4, unstaggered, 8 replicates	-- --	9.7 0.0	38.7 34.4	41.9 53.1	9.7 12.5	-- --	.0081 <.001	.0071 <.001	.0924 .4517
Large L. appendix: P. marinus, D8:8 unstaggered, 7 replicates	-- --	11.5 0.0	36.5 39.6	42.3 50.9	9.6 9.4	-- --	- -	<.001 <.001	.3589 .9452
Experimental series	--	mix A	mix B	mix C	mix D	--	LRT	G_{wp}	G_{het}
Large L. appendix: D8, unstaggered, 3 replicates	--	0.0	0.0	0.0	0.0	--	-	-	-
Large P. marinus: D8, unstaggered, 3 replicates	--	0.0	0.0	0.0	0.0	--	-	-	-
Experimental series	--	0.0938	0.1875	0.3750	mix D	--	LRT	G_{wp}	G_{het}
Small L. appendix: D8, unstaggered, 4 replicates	--	34.4	31.3	31.3	3.1	--	.0109	.0096	.6980
Large L. appendix: D8, unstaggered, 4 replicates	--	25.0	34.4	25.0	15.6		.5399	.5267	.0375
Small P. marinus: D8, unstaggered, 4 replicates	--	26.7	20.0	46.7	6.7	--	.0180	.0182	.2081

preference was statistically significant for eight of twelve series. However, replicates were statistically homogenous in only five of twelve series. For large L. appendix and P. marinus released sympatrically, both species exhibited significant departure from uniform substrate selection at densities of four and eight each per test arena. In both series, the replicates were statistically homogenous.

In preference tests of graded substrate mixes A through D, none were selected by either species. Ammocetes attempted to burrow in all mixes but quickly emerged or gave up and lay prostrate on the bottom for the duration of the experiment. Based on the similarity in permeability between fine sands (0.1875 mm mean grain diameter) and substrate mix D, additional preference tests were conducted between mix D and very fine through medium sands. Small L. appendix and P. marinus exhibited significant rejection of mix D. Replicates for both species were statistically homogenous. Large L. appendix also exhibited reduced usage of mix D, but the departure from uniform substrate selection was not significant. Replicates for large L. appendix were statistically heterogenous.

Multifactor Model I ANOVA's of Substrate Preference Test Blocking Factors

Due to the similarity of results among experimental series within a given species and size class in table 10, frequency data were pooled by species and size for the model I ANOVA's. Proportional use data for very fine through coarse sands from all replicates were subjected to a square-root arcsin transformation prior to analysis (Sokal and Rohlf, 1981). Within given experimental series and pooled data sets, variances in frequency among substrates were generally homogenous. Exceptions were attributable to lower preferences for very fine and coarse sands resulting in lower variance at the extremes of the tested substrate distribution (appendix 4).

To verify the apparent uniformity of substrate preferences across all test arena densities, ANOVA's on test series pooled across test densities by species and size class were conducted (table 11). With the exception of small P. marinus, the effect of substrate type on habitat selection was highly significant. Treatment effects of substrate position in the test arenas and density of ammocetes were nonsignificant. Only in the case of large P. marinus pooled over all

Table 11. Results of multifactor model I ANOVA'S for pooling of experimental series by species and size. Frequency of specific substrate selection (square root arcsin transformed) analyzed with respect to substrate type, substrate position in test arena, and experimental series (eg. density [D]/ release pattern). [ns = not significant; *, **, ***, and **** represent significance at the 0.05, 0.01, 0.001, and 0.0001 levels respectively.]

Experimental Series	Significance Level					
	Substrate only	Position only	Series only	Substrate x Position	Substrate x Series	Position x Series
Sm. L. appendix, pooling of D4ns with D8ns	****	ns	ns	ns	ns	ns
Lg. L. appendix, pooling of D4ns, D8ns, D12s, D4:4ns, and D8:8ns	****	ns	ns	ns	ns	ns
Sm. P. marinus, pooling of D4ns, D8ns, and D8s	ns	ns	ns	ns	ns	ns
Lg. P. marinus, pooling of D4ns, D8ns, D8s, D12s, D4:4ns, and D8:8ns	****	ns	ns	ns	*	ns

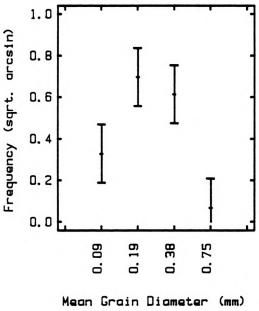
densities was a significant interaction noted between substrate type and density of ammocete release. No interaction effects between substrate type and position nor position and density of ammocetes released were significant.

Figure 9 displays the resultant 95 percent confidence intervals for transformed frequencies of selection with respect to substrate type. Within a species there appears to be a shift in preference from fine to medium sands between small and large ammocetes (figure 9, a to c and b to d). Within the small size class, selectivity for substrates was higher for larval L. appendix than for larval P. marinus. Within the large size class, selectivity appears to be highest for larval P. marinus with a marked preference for medium sands and avoidance of very fine sands in comparison to larval L. appendix.

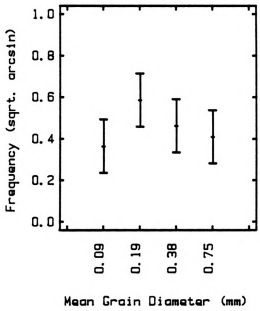
Results of an ANOVA to test for intraspecific differences in burrowing substrate selection within both species by size are shown in table 12. With respect to both species, substrate type was a highly significant factor in burrowing habitat selection. Position in the test arena was significant only for L. appendix. There was a clear interaction effect between substrate type

Figure 9. Ninety-five percent confidence intervals for mean values of test substrate selection frequency (square-root arcsin transformed) by species and size class. Mean grain diameters of 0.09, 0.19, 0.38, and 0.75 mm correspond to ungraded test substrates of very fine through coarse sands.

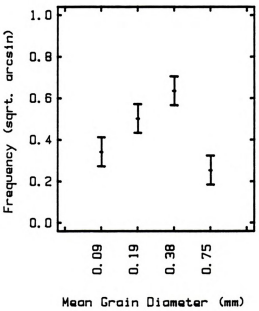
9a) Small L. appendix



9b) Small P. marinus



9c) Large L. appendix



9d) Large P. marinus

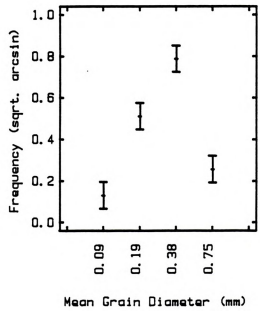


Table 12. Results of multifactor model I ANOVA'S for size specific differences in substrate preferences. Frequency of specific substrate selection (square root arcsin transformed) analyzed with respect to substrate type, substrate position in test arena, and size class (eg. small vs. large). [ns = not significant; *, **, ***, and **** represent significance at the 0.05, 0.01, 0.001, and 0.0001 levels respectively.]

Experimental Series	Significance Level					
	Substrate only	Position only	Size only	Substrate x Position	Substrate x Size	Position x Size
Small vs. large *L. appendix*, pooled over all series	****	*	ns	ns	*	ns
Small vs. large *P. marinus*, pooled over all series	****	ns	ns	*	****	ns

and ammocete size class. Interaction effects between substrate type and position in the test arena or position and ammocete size were nonsignificant.

Table 13 shows the results of an ANOVA to test for differences in burrowing substrate selection between species in the same size class. With respect to treatment effects, only substrate type was significant. There was a significant interaction effect between substrate type and species. No significant interaction effects between substrate type and position in the test arena nor position and species was detected.

To specifically test for the effects of intraspecific competition on burrowing substrate selection, an ANOVA was run on all staggered release experiments (table 14). With the exception of small P. marinus, substrate type again exerted a highly significant effect on burrowing habitat selection. Treatment effects of position in the test arena and the release group number were not significant. There was no significant interaction effects between substrate type and release group with the exception of large P. marinus at a density of 8 ammocetes per test arena. There were no significant interaction effects between substrate and position nor position and release group.

Table 13. Results of multifactor model I ANOVA'S to identify species differences in substrate preferences within a given size class. Frequency of specific substrate selection (square root arcsin transformed) analyzed with respect to substrate type, substrate position in test arena, and species. [ns = not significant; *, **, ***, and **** represent significance at the 0.05, 0.01, 0.001, and 0.0001 levels respectively.]

Experimental Series	Significance Level					
	Substrate only	Position only	Spp. only	Substrate x Position	Substrate x Spp.	Position x Spp.
Sm. L. appendix vs. P. marinus, pooled over all series	****	ns	ns	ns	**	ns
Lg. L. appendix vs. P. marinus, pooled over all series	****	ns	ns	ns	****	ns

Table 14. Results of multifactor model I ANOVA'S for testing of intraspecific competition effects on substrate selection. Frequency of specific substrate selection (square root arcsin transformed) analyzed with respect to substrate type, substrate position in test arena, and staggered release groups. [ns = not significant; *, **, ***, and **** represent significance at the 0.05, 0.01, 0.001, and 0.0001 levels respectively.]

Experimental Series	Significance Level					
	Substrate only	Pos. only	Rel. Grp. only	Substrate x Position	Substrate x Rel. Grp.	Position x Rel. Grp.
Large L. appendix, D12, 3 staggered release groups	****	ns	ns	ns	ns	ns
Small P. marinus, D8s, 2 staggered release groups	ns	ns	ns	ns	ns	ns
Large P. marinus, D8s, 2 staggered release groups	****	ns	ns	*	ns	ns
Large P. marinus, D12s, 3 staggered release groups	****	ns	ns	ns	ns	ns

Table 15 contains the results of ANOVA's to test for the effect of interspecific competition on burrowing habitat selection. With respect to treatment effects, only substrate type was highly significant. With respect to interaction effects, including substrate type versus the presence or absence of the competing species, no interaction effects were significant.

Stepwise Linear Regression Analysis of Burrow Depths

One hundred and twenty-four observations of branchial basket depth in substrate mix D and very fine through coarse sands were subjected to back-stepped multiple regression analysis. Independent variables tested in the model were substrate porosity, permeability (natural log transform), and individual ammocete weight. At a significance threshold of 0.05, only permeability was included in the final model ($\alpha \leq 0.001$). With an R^2 of 30.12 percent, branchial basket depth (D: cm) was related to permeability (K: cm min^{-1}) by the following model:

$$D = 1.4159 + 0.4655(\ln K)$$

The regression slope and intercept were significant at the $\alpha = 0.0001$ level. Ninety-five percent confidence

Table 15. Results of multifactor model I ANOVA'S for testing of interspecific competition effects on substrate selection. Frequency of specific substrate selection (square root arcsin transformed) analyzed with respect to substrate type, substrate position in test arena, and presence/absence of competing species. [ns = not significant; *, **, ***, and **** represent significance at the 0.05, 0.01, 0.001, and 0.0001 levels respectively.]

Experimental Series	Significance Level					
	Substrate only	Pos. only	Compt. only	Substrate x Position	Substrate x Comp.	Position x Comp.
Large L. appendix, with and without P. marinus	****	ns	ns	ns	ns	ns
Large P. marinus, with and without L. appendix	****	ns	ns	ns	ns	ns

intervals of mean branchial basket depth are plotted against permeability in figure 10 along with the regression line.

Frequency Analysis of Food/Habitat Preference Tests

Table 16 provides a summary of all food/habitat selection tests with reference to selection of habitats with food versus those without. For large L. appendix and P. marinus, the presence of food particles in the substrate did not have a significant effect on habitat selection. Replicates were statistically homogenous for both species. Results of habitat selection tests based on the presence or absence of food particles in the water column were more equivocal. For large L. appendix, the presence of yeast particles had a significantly positive effect on habitat selection while the presence of the green alga, A. falcatus, did not. The presence versus absence of yeast did not have a significant effect on habitat selection exhibited by large P. marinus. Replicates were statistically homogenous for both species when a yeast perfusion was used but heterogenous in the case of large L. appendix and green alga perfusion.

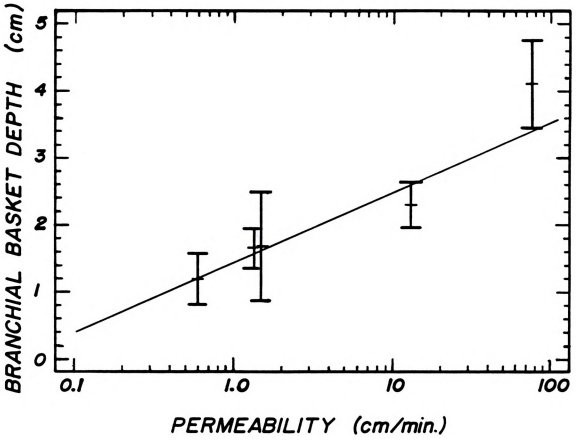


Figure 10. Ninety-five percent confidence intervals for mean branchial basket depth of ammocetes with respect to substrate permeability. The regression line for corresponds to that calculated for a regression through all data points.

Table 16. Pooled percentages of ammocetes occupying different burrowing substrates based on presence or absence of food. Experimental series are identified by ammocete size, species, density (D) per test arena, release pattern, food type (yeast or algae perfusion), and number of replicates. To indicate departure from random selection of substrates, signifcance levels of G-tests for pooled data with Williams correction (G_{wp}) and heterogeneity across replicates (G_{het}) are included.

Experimental Series	Treatment Level		Signif. Level	
	no food	food	G_{wp}	G_{het}
Substrate based food/ habitat selection:				
Large L. appendix: D8, unstaggered, yeast, 8 replicates	50.0	50.0	0.8544	0.4690
Large P. marinus: D8, unstaggered, yeast, 8 replicates	45.5	54.5	0.5036	0.4933
Water column based food/hab. selection:				
Large L. appendix: D8, unstaggered, yeast, 8 replicates	40.6	59.4	0.0464	0.4233
Large L. appendix: D8, unstaggered, algae, 6 replicates	42.1	57.9	0.4140	0.0278
Large P. marinus: D8, unstaggered, yeast, 8 replicates	54.7	45.3	0.4815	0.4877

Multifactor Model I ANOVA'a of Food/Habitat Preference Test Blocking Factors

Table 17 contains the results of ANOVA's testing the effect of food particle distribution on habitat selection pooled by species, but separated by substrate versus water column experiments. In both sets of experiments, the treatment effect of food versus no food was nonsignificant. With respect to food perfused versus unperfused substrate tests, position in the test arena was significant. This was not the case for water column tests. There were no significant interaction effects between any of the main treatments.

1987 Field Results

Daily median, minimum, and maximum temperatures at stations 10, 16, and 24 (10, 12.2, and 13.8 m depth respectively) are shown in figure 11a-c. Daily temperature variation was greatest from mid-June through late August, exceeding 8 °C at all stations on several occasions. At each station, temperature increased gradually, peaking in mid to late August, and decreasing thereafter.

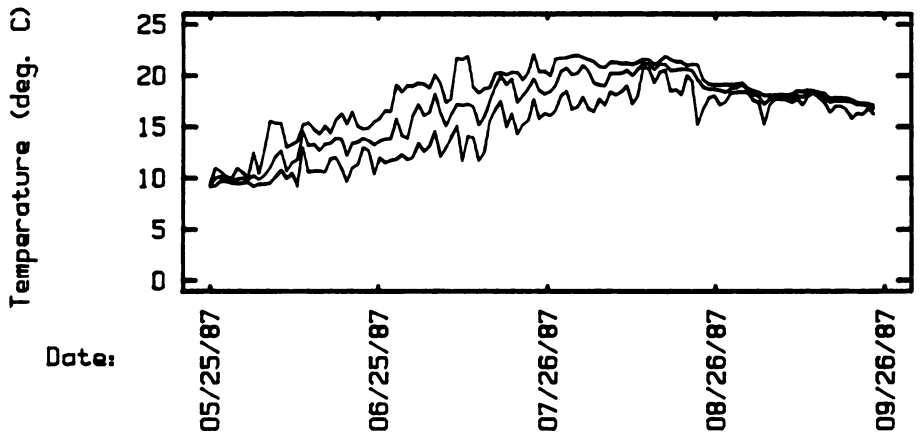
The fine scale distribution of substrate particles relative to distance from the edge of the alluvial fan

Table 17. Results of multifactor model I ANOVA's to test the effect of food particle distribution on habitat selection. Frequency of selection for food perfused vs. unperfused habitats (square root arcsin transformed) analyzed with respect to treatment (food vs. no food), substrate position in test arena, species, and food type (yeast vs. algae). [ns = not significant; *, **, ***, and **** represent significance at the 0.05, 0.01, 0.001, and 0.0001 levels respectively.]

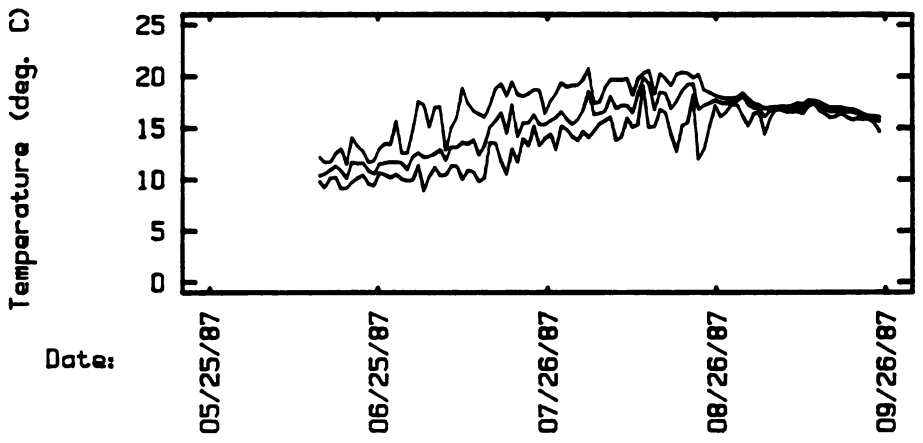
Experimental Series	Significance Level								
	Trtmnt only	Pos. only	Spp. only	Food Type	Trtmnt x Pos.	Trtmnt x Spp.	Trtmnt x Food	Pos. x Spp.	Pos. x Food
Yeast perfused vs. unperfused substrate selection tests	ns	**	ns	--	ns	ns	--	ns	--
Food perfused vs. unperfused water column selection tests	ns	ns	ns	ns	ns	ns	ns	ns	ns

Figure 11. Daily median, minimum and maximum temperatures at stations 10, 16, and 24 (10, 12.2, and 13.8 m depths) during summer 1987.

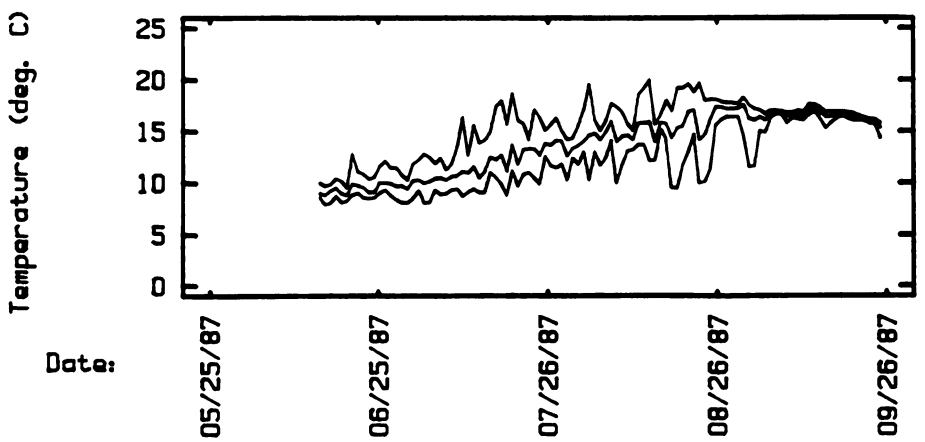
11a) Station 10: 10 meters



11b) Station 16: 12.2 meters



11c) Station 24: 13.8 meters



is shown in figure 12. As in 1985, the leading edge of the alluvial fan is characterized by a sand fraction exceeding 80 percent which generally declines with increasing distance from the alluvial fan. The fine scale measurement of particle size distribution also reveals a localized minima of sand grains with a matching maxima of silt/clays.

Substrate permeability in the top 4 cm of substrate, initially high along the leading face of the alluvial fan, rapidly declines with an isolated increase at station 10 corresponding to the local minima of sand particles (figure 13). Permeability again declines with increasing depth to a local minima at a distance of 82 m from the edge of the alluvial fan. Beyond 82 m from the edge of the alluvial fan, permeability ranges between 1 to 2 cm min^{-1}.

Substrate porosity follows a different pattern from that of permeability. In the upper 4 cm of the substrate, porosity is lowest at the upper edge of the alluvial fan, rapidly increasing to a local maxima along the face and lower edge of the alluvial fan (figure 14). This area corresponds to an active slumping zone where the slope is at its maximum angle of repose (30-35°). A local minima in porosity at station 10 corresponds to

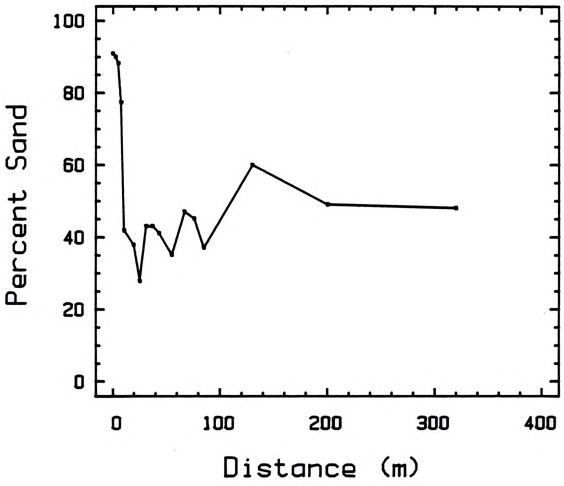


Figure 12. Percent sand composition of substrate with respect to distance from the edge of the alluvial fan during summer 1987.

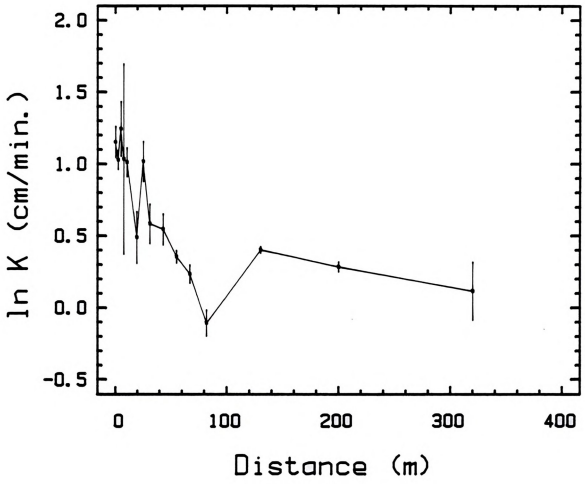


Figure 13. Profile of mean substrate permeability (± sd) with respect to distance from the edge of the alluvial fan during summer 1987. All permeability values were determined from frozen cores.

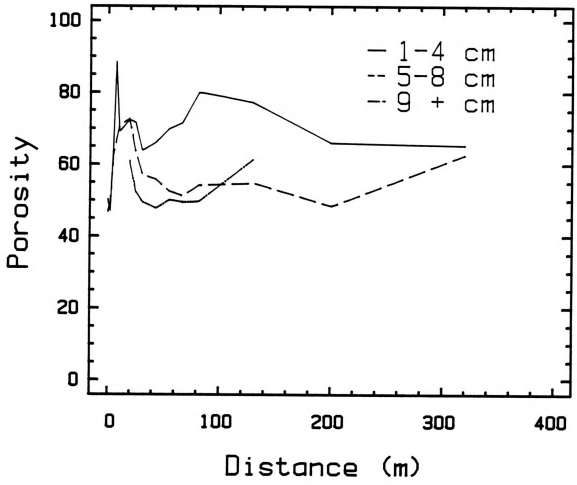


Figure 14. Porosity at 4 cm depth intervals in the substrate with respect to distance from the edge of the alluvial fan during summer 1987. All porosity values were determined from frozen cores.

the local minima of sand particles in figure 12. After station 10, at 22 m from the edge of the alluvial fan, porosity again increases to a local maxima at 82 m, corresponding to a local minima in permeability and maxima in sand fraction. Beyond 82 m from the edge of the alluvial fan, porosity in the upper 4 cm decreases gradually with increasing depth and distance.

At substrate depths exceeding 4 cm, porosity reaches a local maxima in the area between the active slump zone and station 10. From a local minima ranging between 40 to 65 m from the edge of the alluvial fan, porosity at substrate depths greater than 4 cm remains more or less constant at a value of 50 to 60 percent.

Food particle distribution in the top 4 cm of the substrate based on chlorophyll a concentration is shown in figure 15. In general, the concentration of chlorophyll is lowest at the upper edge of the alluvial fan increasing to a local maxima at a distance of 15 to 25 m and tapers off thereafter. Over the course of the summer, peak chlorophyll concentrations decreased from a high of 7.5 to a low of 3.6 ug/g within 20 m from the edge of the alluvial fan. The ratio between chlorophyll a and pheophytin a generally decreases with increasing depth and distance from the edge of the alluvial fan

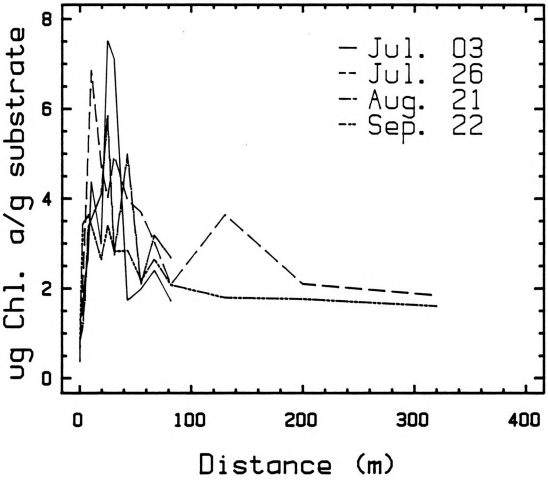


Figure 15. Chlorophyll a in the top 4 cm of the substrate with respect to time and distance from the edge of the alluvial fan during summer 1987.

(figure 16). A localized temporal progression of declining index values, centered at a distance of 22 m from the alluvial fan, corresponds to the local minima of sand particles in figure 12.

In terms of chlorophyll a concentrations, the food particle distribution at the sediment/water interface follows the same general trend as that in the substrate (figure 17). The chlorophyll/pheophytin ratio at the sediment/water interface also exhibits a general decrease with increasing depth and distance from the edge of the alluvial fan (figure 18). In contrast to the distribution of chlorophyll a, the distribution of organic particles less than 180 um exhibits a local minima at a distance of 22 m from the edge of the alluvial fan (figure 19) except in late September. This region corresponds to the local minima of sand particles in figure 12.

Trap tray effort levels pooled by 11 m distance increments and time (early *versus* late summer) are listed in table 8. The average density of unmarked ammocetes *versus* distance from the edge of the alluvial fan is plotted in figure 20. In general, density decreases with increasing distance from the edge of the alluvial fan to a local minima at 45 m distance. Beyond

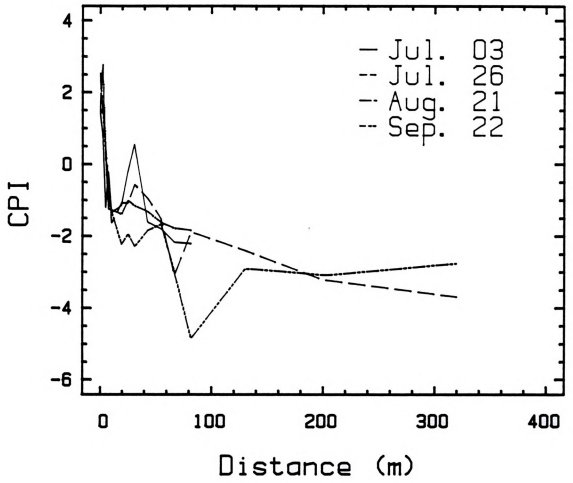


Figure 16. Chlorophyll/pheophytin index (CPI) values in the top 4 cm of the substrate with respect to time and distance from the edge of the alluvial fan during summer 1987. Index values are calculated as the natural log of the ratio of chlorophyll to pheophytin concentrations. An index value above zero reflects a greater proportion of chlorophyll while values below zero reflect a larger proportion of pheophytin.

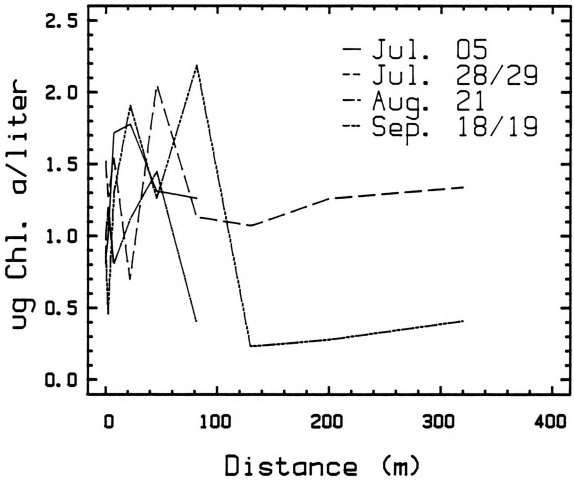


Figure 17. Chlorophyll a concentrations at the sediment/water interface with respect to time and distance from the edge of the alluvial fan during summer 1987.

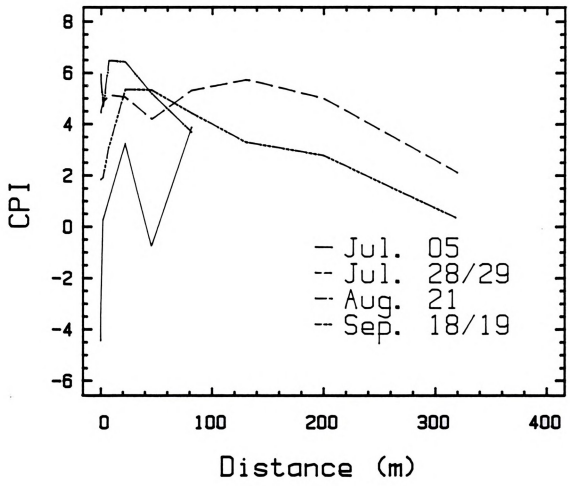


Figure 18. Chlorophyll/pheophytin index (CPI) values at the sediment/water interface with respect to time and distance from the edge of the alluvial fan during summer 1987.

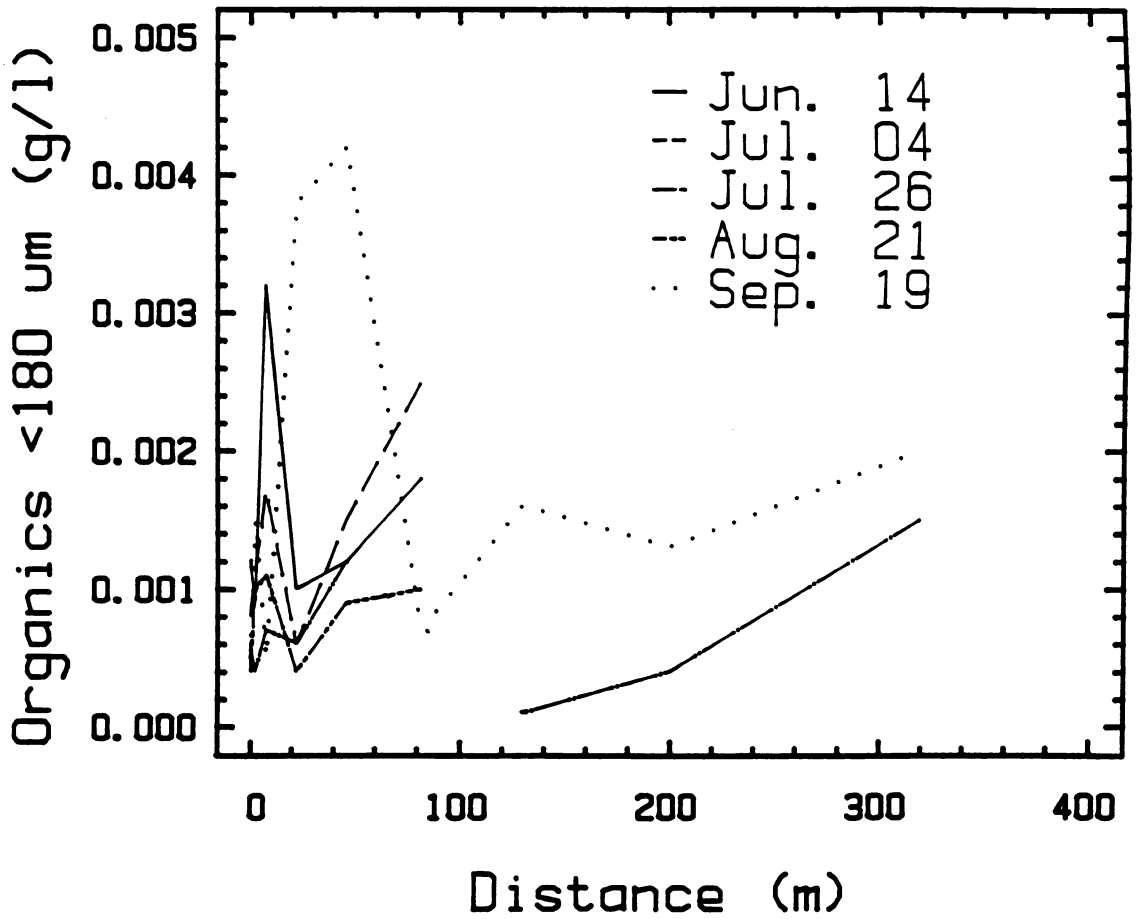


Figure 19. Distribution of particulate organic carbon (POM, diam. ≤ 180 um) at the sediment/water interface with respect to time and distance during summer 1987. Sample from station 29 on July 26 was fouled with sediment during sampling and discarded.

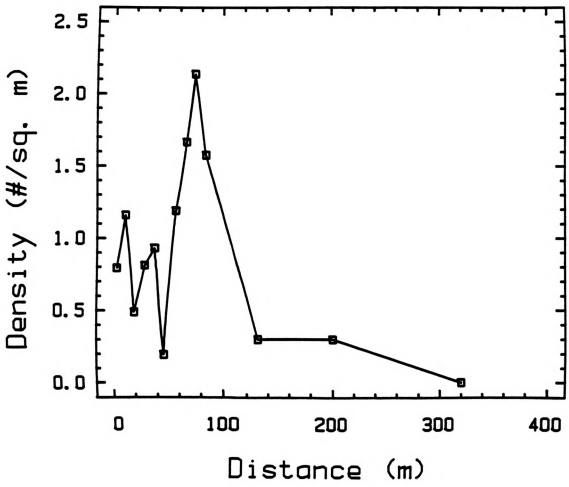


Figure 20. Average density of ammocetes with respect to distance from the edge of the alluvial fan during summer 1987.

45 m from the alluvial fan, density increases to a local maxima at a distance of 78 m. Ranging from 20 to 82 m from the edge of the alluvial fan, the distribution of ammocetes corresponds to that of the sand particle distribution in figure 12.

Figure 21 shows the time and pattern of marked ammocete recaptures along with the final densities and local dispersal patterns at marked ammocete release points. In contrast to initial densities of 520+ ammocetes m^{-2}, final densities at stations 10 and 24 were 6.7 and 13.8 m^{-2} respectively. Immigrants from station 10, captured over the course of the summer, were caught in deeper waters during late summer. Immigrants from station 24, captured over the course of the summer, were caught in both shallower and deeper waters in early summer.

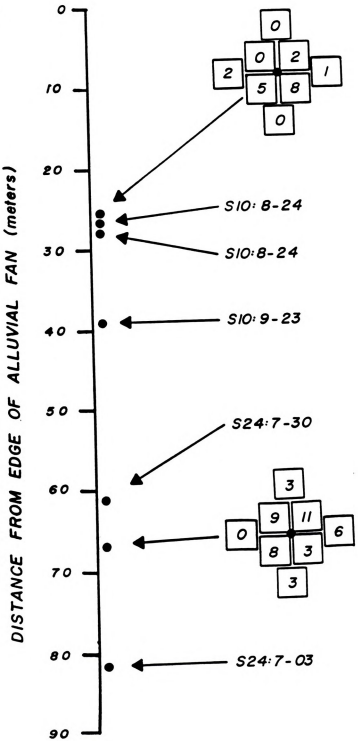
DISCUSSION

Local Distribution and Abundance

Based on recaptures of marked shallow released ammocetes from the Bayer 73 treatments in 1985, a total of 53,044 ammocetes resided within the treatment area with a 95 percent confidence interval of $43,469 \leq N \leq$

Figure 21. Recovery map of marked ammocetes released at stations 10 and 24 during summer 1987. Stations 10 and 24 were sampled on 23 September with eight sample trays arranged in the illustrated pattern. Each square represents one tray (0.5625 m^2) and the number of marked ammocetes recovered. Migrants from the release points are identified by release point, date, and location of recovery.

Figure 21


DISTANCE FROM EDGE OF ALLUVIAL FAN (meters)
0
10
20
30
40
50
60
70
80
90
0
0 2
2 5 8 1
0
S10: 8-24
S10: 8-24
S10: 9-23
S24: 7-30
3
0 9 11 6
8 3
3
S24: 7-03

62,619 (Chapman, 1951; Ricker, 1978). This estimate suggests an average density of 1.68 ± 0.32 ammocetes per m^2 bottom area of which 19.5 percent were larval sea lamprey. An average density estimate of 0.997 ammocetes per m^2 obtained from the submersible transect data corrected for electrosampler efficiency yields a total estimate of 31,490 ammocetes within 50 m of the edge of the alluvial fan. From a distance of 50 to 200 m from the edge of the alluvial fan, an average density estimate of 0.108 ammocetes per m^2 within and below the thermocline was obtained with the submersible.

The magnitude of 1987 density estimates compares favorably with those of 1985. The density of ammocetes within 55 m of the edge of the alluvial fan ranged between 1.2 and 0.2 individuals per m^2 based on 1987 trap tray results (figure 20). This area corresponds to the area sampled in 1985 with the submersible and Bayer 73. Within 30 m of the edge of the alluvial fan, the area normally subjected to annual Bayer 73 treatments, densities ranged between 0.5 and 1.2 individuals per m^2. The higher densities of ammocetes (1.2 to 2.2 per m^2) between 55 and 87 m from the edge of the alluvial fan were not detected in 1985. However, comparable depths sampled by the submersible in 1985 were located 300 m to the north of the 1987 transect.

Analysis of Habitat Selection Determinants

1985/86 Preliminary Analysis

The distribution of ammocetes off the mouth of the Chippewa River appears to be limited to a zone parallel to the leading edge of the alluvial fan based on the Bayer 73 treatment records and the submersible work in 1985. As per working hypothesis 1, this is where one would expect to find them if they simply drift out of the river during seasonal flooding and select the first substrate they encounter (figures 8, 12). This area is an active deposition zone for large particles, containing an abundance of leaves, sticks, and occasional branches.

The tendency for ammocetes to settle out in these areas has given rise to the argument within sea lamprey control circles, that lentic ammocetes do not actively select habitats. However, the absence of marked and unmarked ammocetes in the deep portions of the study site with the subsequent occupation of shallow, high gradient habitats by marked ammocetes released in deep water suggests otherwise. The dramatic distances (from 1 to 12+ km) that deep released ammocetes traversed to reach such habitats underscores this conclusion.

With respect to environmental correlates of lentic ammocete distribution and abundance, marked and unmarked ammocetes selected areas characterized by sandy substrates and temperatures greater than 10 °C in concordance with working hypotheses 2 and 3. As water was in equilibrium with atmospheric oxygen concentration at all depths, rejection of deepwater habitats based on low oxygen tensions (working hypothesis 4) can be dismissed.

Deep portions of the study site are characterized by sand fractions less than 10 percent while areas where ammocetes were found had sand fractions greater than 35 percent with correspondingly low clay fractions (figure 8). Malmqvist (1980) noted that sediments with a relatively larger fraction of fine sand particles (0.125 - 0.25 mm diameter) contained significantly higher densities of larval brook lamprey (Lampetra planeri) in a Swedish stream. The same general preference has been qualitatively noted for all lamprey species in the Great Lakes basin (Applegate, 1950; Manion and McLain, 1971). Consequently, rejection of deepwater habitats may have been mediated by substrate type and/or unidentified substrate property.

The general distribution of ammocetes along the slope also suggests that thermal preferences played a role in rejection of deepwater habitats. The deep released marked ammocetes were not acclimated to the thermal environment of the release points, which may have affected their survival and behavior. However, the results of the handling mortality study do not support the hypothesis of increased mortality below the thermocline. Consequently, marked ammocetes may have rejected deepwater release points on the basis of non-acclimation or potentially, on the basis of thermal habitat selection driven in part by recent thermal history.

The cross factor study of substrate particle size distribution versus thermal acclimation in 1986 was designed to test the relative importance and interaction of both factors. Based on the results, neither factor appears to play a significant role in terms of habitat selection. While care was taken to insure that the experimental patches were located below the thermocline, they were inadvertently located in an area characterized by sand fractions exceeding 32 percent. As a result, the quality of the substrate treatment portion of the experiment is suspect.

A decline in density within each patch is to be expected given the high initial release densities (1000 individuals m^{-2} initially, 55 individuals m^{-2} after cage removal) but the high densities used here to insure sampling success may have led to over-dispersal upon release. Adverse density-dependent effects could have promoted excessive emigration directly through competitive interactions or indirectly through a build up of metabolic products.

Although not measured in 1985/86, the distribution and quality of chlorophyll in surface sediments and the water column, which in turn reflects the distribution and abundance of autochonous particles within the size range filtered by larval lamprey, has been shown to be inversely related to depth and distance from the shore (Stevenson and Stoermer, 1981; Moll and Brahce, 1986; Nalepa and Quigley, 1987). This relation suggests that larval lamprey distribution in lentic areas could also be related to local patterns of food abundance and quality. Furthermore, the strong differential in water density over a short distance resulting from the interdiction of the thermocline with the bed slope suggests that food particles could be concentrated close to the bottom and above the thermocline in depths

ranging from 9 to 17 m depending upon the depth of the thermocline.

1985/86 Working Conclusions

The results of the cross factor study while not conclusive due to small sample sizes (potentially related to over-dispersal) and a reduced treatment differential for substrates, suggests that other factors may influence lentic habitat selection. These include substrate properties unidentified and/or uncontrolled in the 1986 experimental design, density-dependence in burrowing substrate selection, local food particle distribution, and thermal habitat selection driven in part by trends in the photo-period or recent thermal history. Taking each as working hypotheses, laboratory and field research in 1987/88 was designed to clarify the importance of each factor.

1987/88 Analysis

In the laboratory, ammocetes exhibited a highly variable response to substrate type as witnessed by the significance of G_{het} for experimental series listed in tables 10 and 16. Based on the model I ANOVA's, the variability among replicates in a series was not related

to treatment or interaction effects. The same variability was shown in the regression model of branchial basket depth versus permeability, where the R^2 value was only 30.12 percent. Consequently, though selective preferences were expressed on average, it is clear that "suitability" of a burrowing substrate is broadly defined on an individual basis .

The laboratory results indicate that both mean grain diameter and permeability set limits to burrowing substrate suitability. Mean grain diameter set an upper limit to substrate suitability while permeability defined the lower limit (figure 22). Very coarse sands (1.0 - 2.0 mm diam.) were rejected by all test subjects while permeability set the lower limit through its relationship to burrow depth, presumably in relation to resistance to respiratory currents.

There is no evidence that mean grain diameter per se sets a lower limit to substrate suitability based on 1987 field measures of permeability with respect to mean grain diameter (figure 22, small squares). Even though silt/clays and sand/silt/clay mixes were rejected in the laboratory, substrates in the field with mean grain diameters and similar particle size distributions were occupied by ammocetes. It should be noted however, that

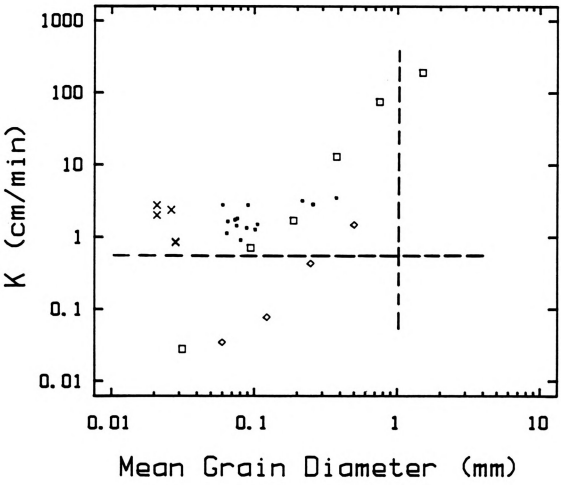


Figure 22. Permeability of field and laboratory substrates with respect to mean grain diameter and threshold values of permeability and maximum mean grain diameter. Large squares and diamonds correspond to Wentworth scaled and mixed laboratory substrates respectively. Small squares correspond to mean values of substrates along the summer 1987 while the "x" symbols correspond to mean values measured for substrates at 1985 deepwater release points.

deepwater release points with even smaller mean particle diameters were rejected in 1985, though permeabilities measured in 1988 exceeded the threshold value (figure 22, x symbols). Thus substrates with mean particle diameters below 0.06 mm may be rejected though permeabilities surpass the threshold value. However, larval P. marinus readily accepted diatomaceous earth with a mean grain diameter less than 0.015 mm (Mallatt 1982).

These results illustrate the importance of the substrate fabric or lattice to properties such as permeability. Webb (1975) clearly defined the effect of substrate consolidation on permeability and related this to substrate selection exhibited by lancelets, Branchiostoma lanceolatum. Webb and Theodor (1972) noted that the growth of organic films on substrate particles could increase permeability by 70 percent. Laboratory substrates in this study were well consolidated in comparison to field substrates and devoid of any organic films. Consequently, the relationship between mean grain diameter and permeability in the laboratory substrates differs from that exhibited by substrates in the field.

In support of the qualitative conclusions reached by Mallatt (1983) and Morman (1987), laboratory analysis

of substrate selection did not provide evidence for direct density-dependent interactions between ammocetes. While crowding may affect the suitability of a substrate over time as per Mallatt's hypothesis, there is no short-term effect on burrowing substrate selection.

The results of laboratory analyses of habitat selection based on local food particle distribution in the water column and substrate, indicate that the latter is also not a determinant of ammocete distribution and abundance. Comparison of the 1987 distribution of lentic ammocetes with the distribution and quality of food particles in the substrate supports this conjecture. Concentrations of food particles in the substrate were highest throughout the summer within 60 m of the alluvial fan while quality was highest within 30 m (figures 15, 16). In contrast, the average density of ammocetes increased with increasing distance from the edge of the alluvial fan to a local maxima at 80 m (figure 20).

Results of the laboratory tests of food particle distribution in the water column on habitat selection were more equivocal. While larval P. marinus did not exhibit selection for yeast perfused waters in the frequency analysis, larval L. appendix did (α = 0.0464,

table 16). However, larval L. appendix did not exhibit selection for waters perfused with A. falcatus. When pooled together across species and food types in multifactor model I ANOVA's, there was no indication of significant habitat selection with respect to treatment or interaction effects (table 17).

Comparisons of the 1987 distribution of lentic ammocetes with that of food particles at the sediment/water interface are equally equivocal. Concentrations of food particles in terms of chlorophyll a are generally higher within 60 m of the alluvial fan, decreasing with increasing distance thereafter with the exception of late September (figure 17). This pattern is similar to that for substrate chlorophyll concentrations. However, concentrations of food particles in terms of particulate organic matter (POM) peak at the base of the alluvial fan, show an average local minima at a distance of 25 m, and then increase with increasing distance thereafter, again with the exception of late September (figure 19). This pattern roughly matches that of the average distribution and abundance of ammocetes in figure 20.

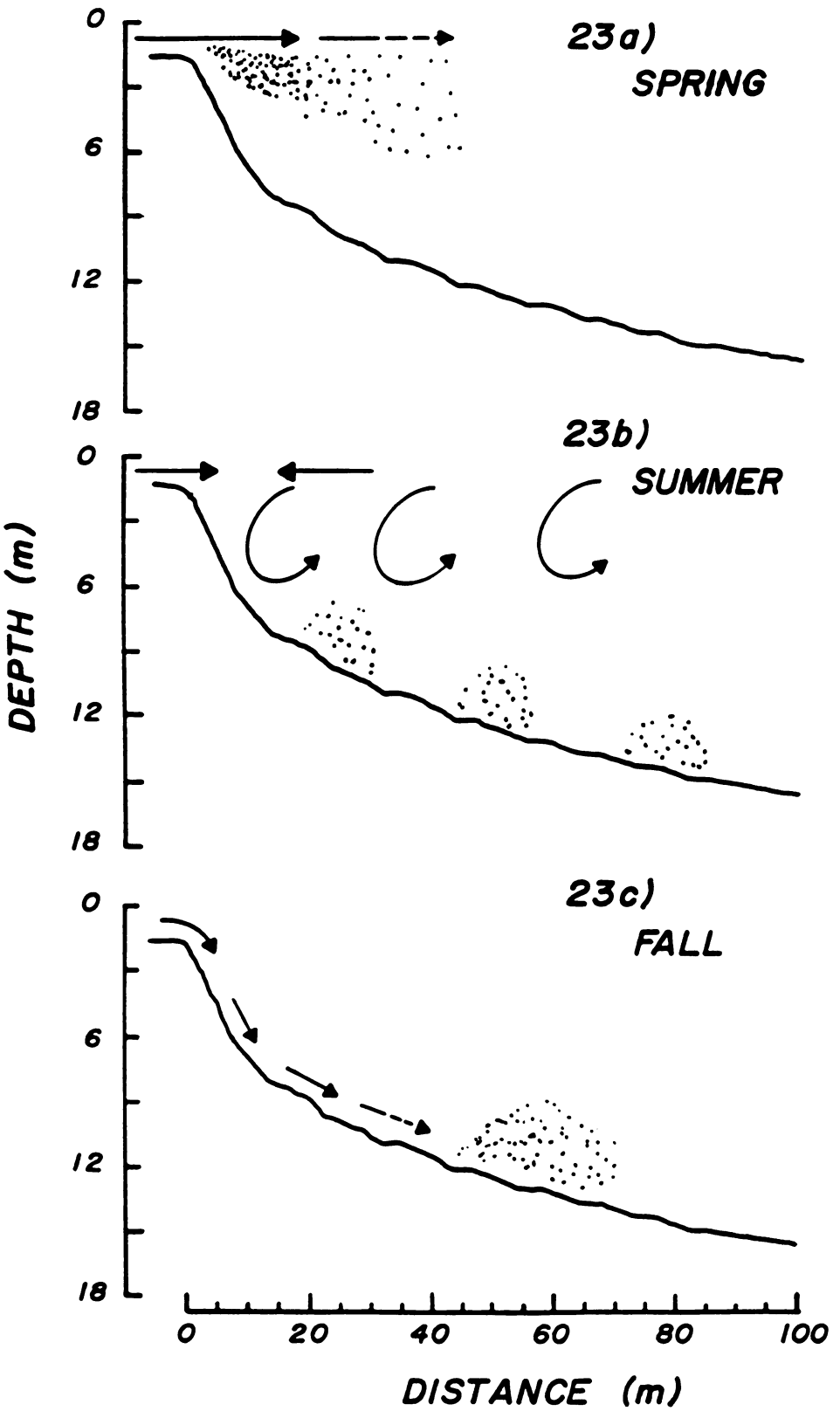
If the overall results of the food/habitat selection experiments in the laboratory are taken at

face value, the rough correlation between average ammocete distribution and POM is either coincidental or evidence of a physical process affecting both in a similar fashion. The best single explanation revolves around local current patterns. The simplest model depends only upon the interaction of wind driven surface currents with river discharge.

The substrate particle size distribution in figure 12 indicates the presence of a hydrodynamic wall at the confluence of bay waters with the outfall of the Chippewa River. Southwest and westerly winds predominate in the spring and summer, setting up wind driven surface currents orthogonal to the face of the alluvial fan (figure 23b). This process leads to a strong deposition zone for fine organic and inorganic particles at a depth of 10 m and distance of 25 m from the upper edge of the alluvial fan.

On the bay side of the hydrodynamic wall, finer organic and inorganic particles are then picked up by wind-driven vertical circulation cells and swept out to secondary deposition zones, 55 and 82 m from the edge of the alluvial fan. Empirical support for this model is found in the relationship between daily temperature variation measured at stations 10, 16, and 24 with local

Figure 23. Schematic representation of current regimes at the edge of the alluvial fan off the mouth of the Chippewa River in spring, summer, and fall.


23a)
SPRING
23b)
SUMMER
23c)
FALL
DEPTH (m)
0
6
12
18
0
20
40
60
80
100
DISTANCE (m)

meteorological conditions at Sault Ste. Marie, Ontario, 35 km south of the study site (Meteorological Summaries, Environment Canada).

To test this supposition, average wind speed and direction along with degrees of wind shift over 24 and 48 hour periods were used as blocking factors in a series of one-way ANOVA's of daily temperature range at depth. The significance levels for each analysis are listed in table 18. Individual significance levels for average wind speed, direction, and degrees of wind shift over 24 hours increase with increasing depth and distance from the edge of the alluvial fan. In contrast, the significance level for degrees of wind shift over 48 hours decreases with increasing depth and distance.

As shown in figures 24 - 26, maximum daily temperature ranges at station 24 were correlated to winds southwest to westerly, high, and steady. Maximum daily temperature ranges at station 10 were correlated with variable winds over a 48 hour period (figure 27). Station 24 is the farthest temperature station from the hydrodynamic wall and thus most likely to reflect the effects of vertical circulation cells alone. Station 10, being the shallowest and closest temperature station

Table 18. Significance levels for one-way ANOVA's of daily temperature range at stations 10, 16, and 24 with respect to average wind direction, speed, and wind shifts.

	ANOVA Significance Level (α)		
Blocking Factor	Sta. 10	Sta. 16	Sta. 24
Average Wind Direction	0.893	0.223	0.011
Average Wind Speed	0.663	0.150	0.007
Wind Shift over 24 hrs.	0.750	0.174	0.058
Wind Shift over 48 hrs.	0.053	0.225	0.674

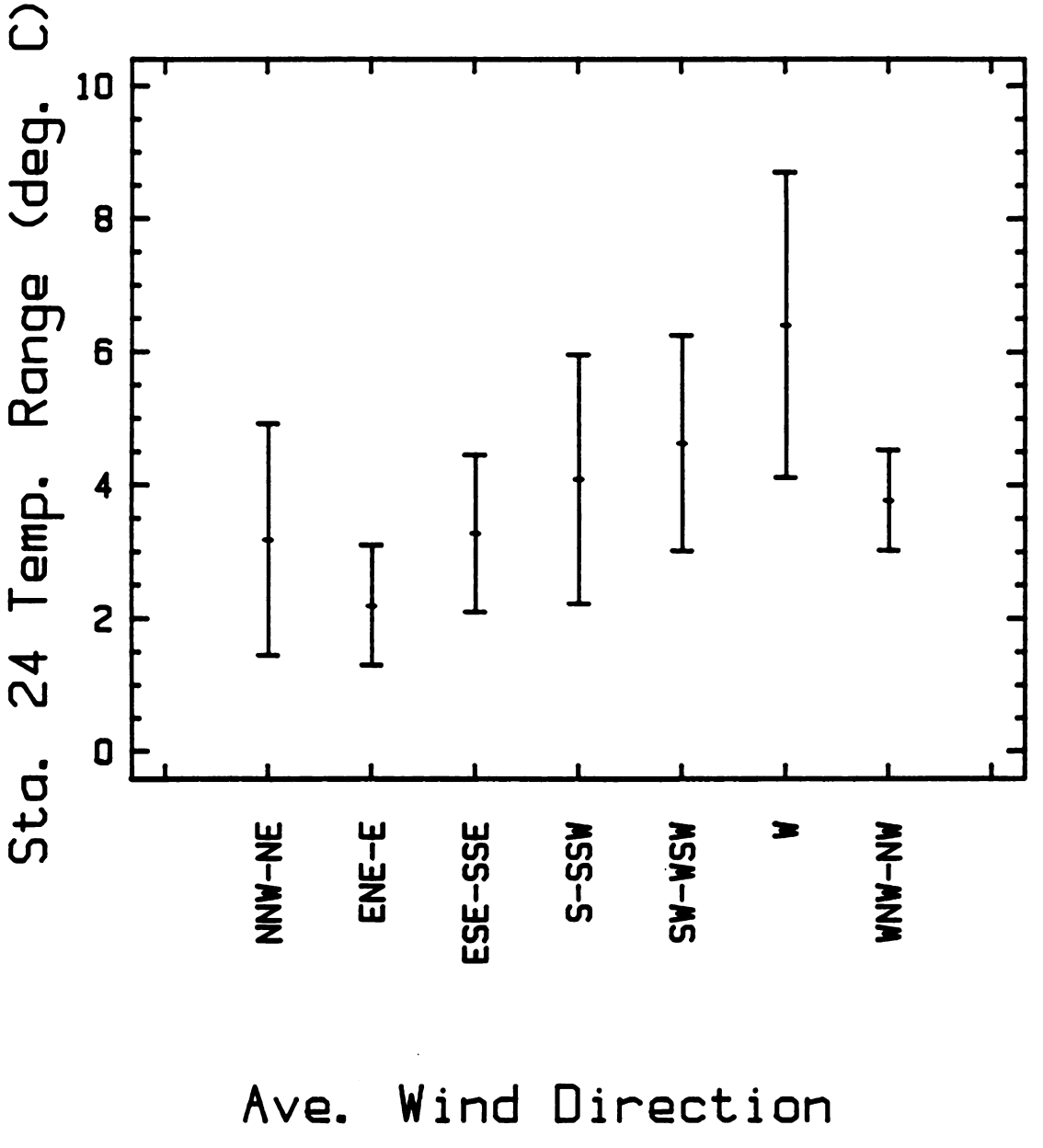


Figure 24. Ninety-five percent confidence intervals of daily temperature range at station 24 with respect to average wind direction during summer 1987.

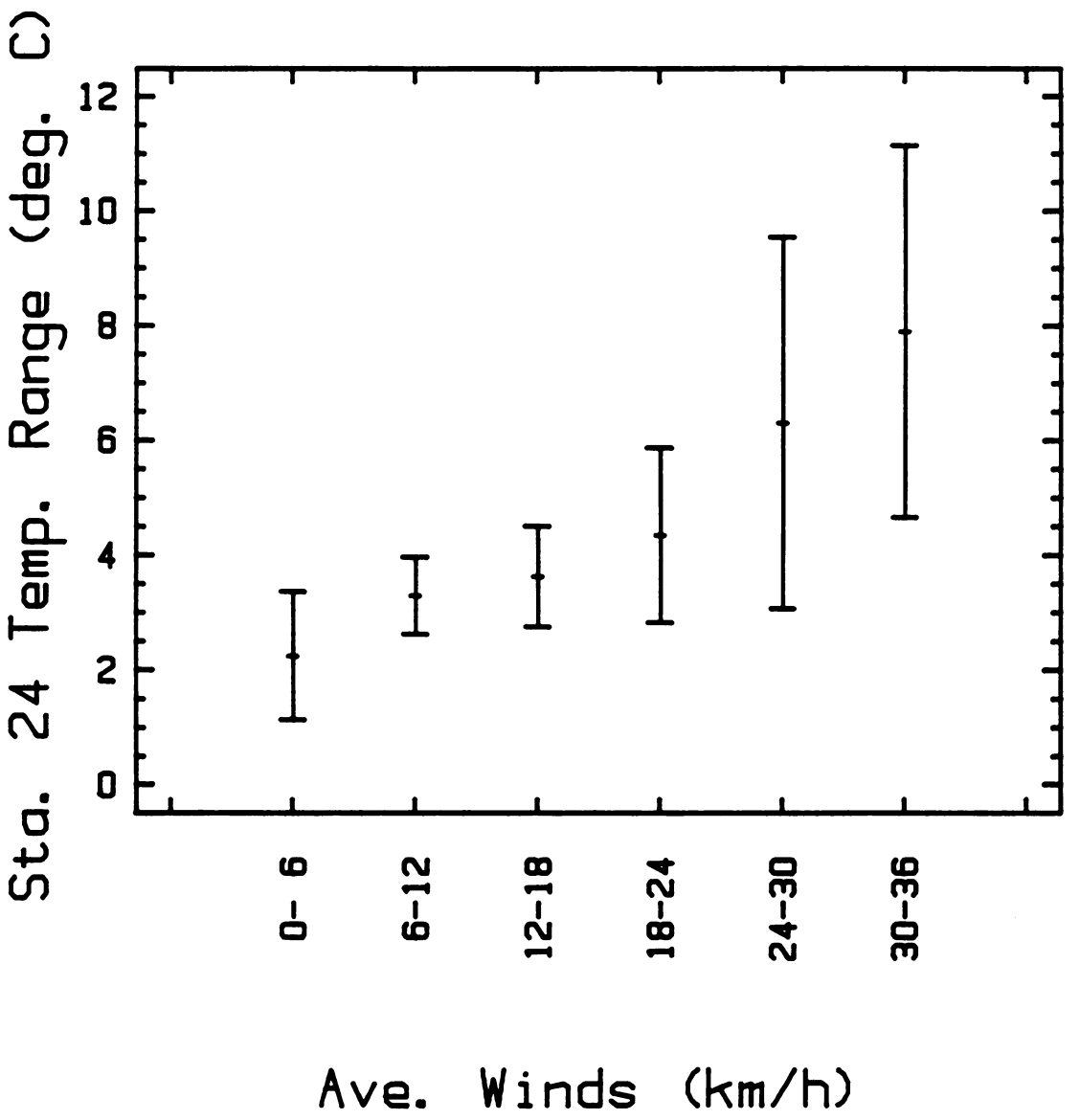


Figure 25. Ninety-five percent confidence intervals of daily temperature range at station 24 with respect to average wind speed during summer 1987.

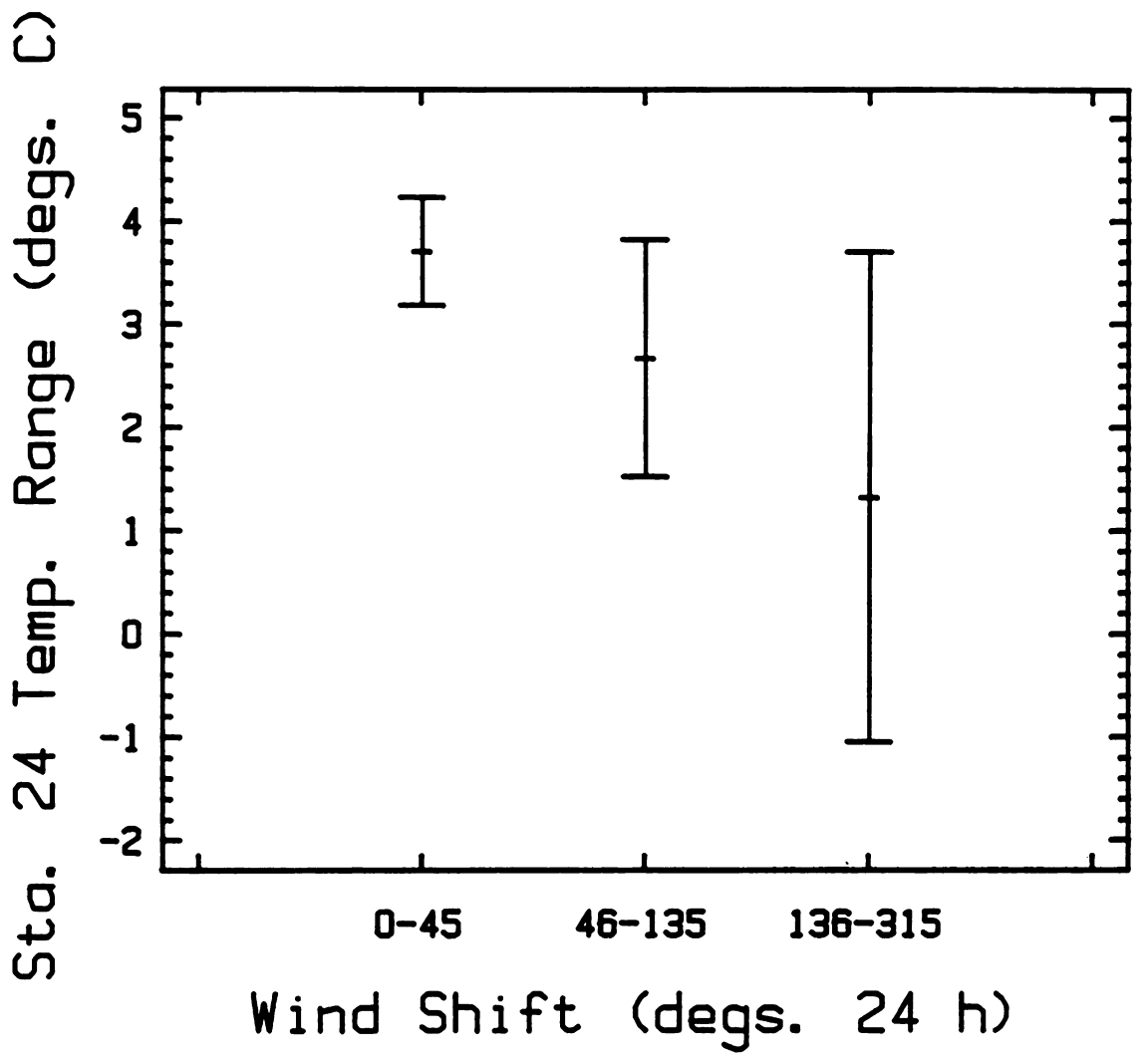


Figure 26. Ninety-five percent confidence intervals of daily temperature range at station 24 during summer 1987 with respect to degrees of wind shift over 24 hours.

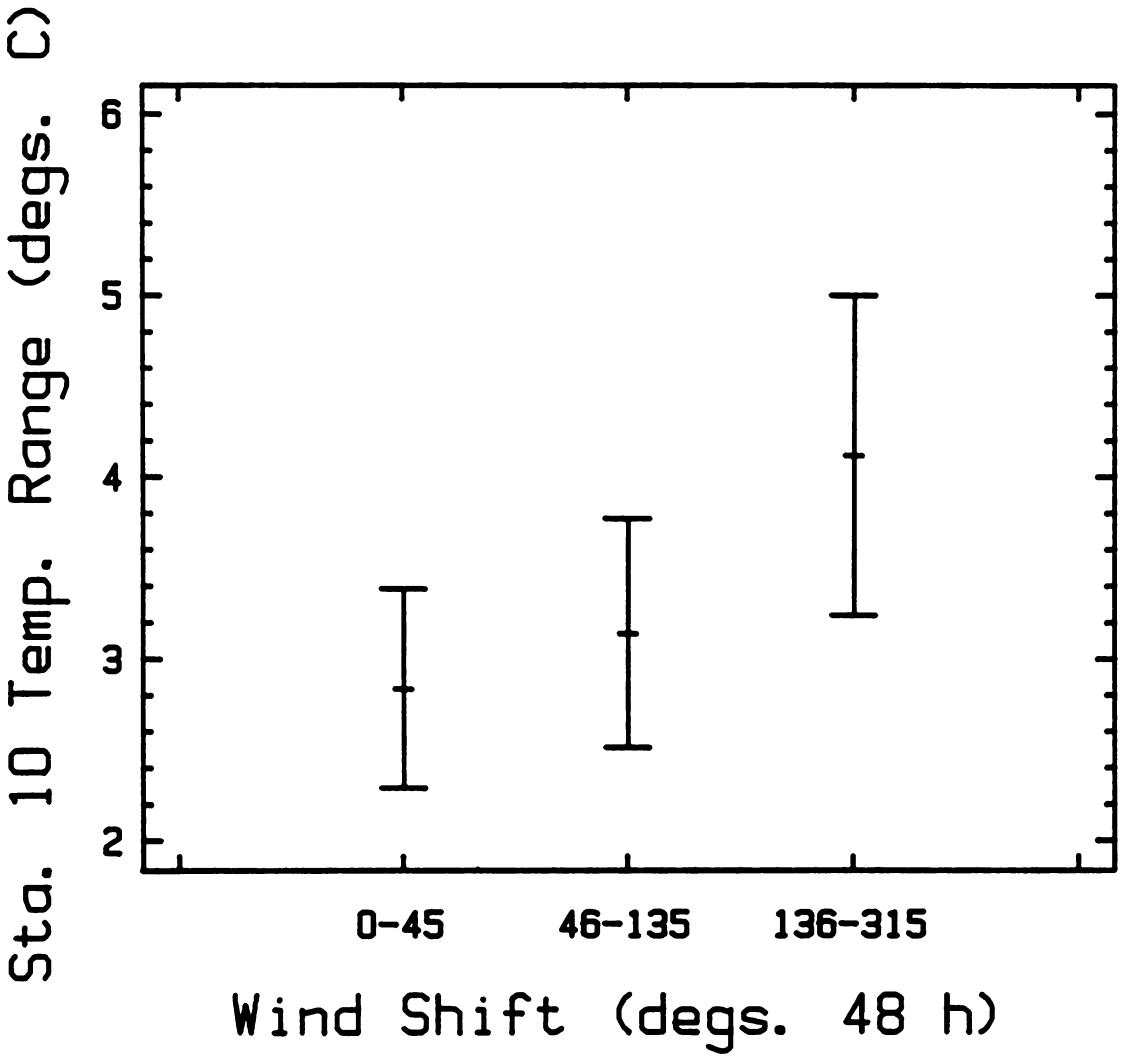


Figure 27. Ninety-five percent confidence intervals of daily temperature range at station 10 during summer 1987 with respect to degrees of wind shift over 48 hours.

to the hydrodynamic wall, is most likely to reflect temperature variations due to turbulent mixing of bay and river waters and the effects of shifting weather patterns.

Based on empirical relationships between fetch, wave height, wave length, and depth, sufficient vertical oscillation of the water mass to transport unconsolidated silts, clay, and fine organic particles can be generated to a depth of 15 m at the study site. With an average fetch of 5 km from the west, the theoretical maximum wave height at the study site is 0.75 m (Hutchinson, 1957). Wave heights at the edge of the alluvial fan approached this value many times in association with westerly winds (pers. obs.). Empirically, the ratio between wave height and length ranges from 1:10 to 1:100 (Wetzel, 1975). Local minima of sand fraction are spaced an average of 32 m apart (figure 12). Assuming they represent the spacing of vertical circulation cells as per figure 23b, the resultant wave height:length ratio of 1:42 falls within the middle of the range. If the amplitude of vertical oscillation cells is halved for each depth increase of the local depth divided by nine (Wetzel, 1975), then the vertical oscillation at depth is approximated by the following equation:

$$O_d = e^{[(-6.2383d)/(hL)]}$$

Where: O_d = vertical oscillation at depth d (m)

d = local depth (m)

h = wave height (m)

L = wave length (m)

At station 24 with a depth of 13.8 m and assuming a wave height of 0.75 m with a length of 32 m, the vertical oscillation of the water column at the substrate/water interface should be approximately 2.8 cm.

The rough correlation of substrate sand fraction between 25 and 82 m from the edge of the alluvial fan in figure 12 with that of average ammocete distribution in figure 20 may be explained with the model in figure 23. As the vertical circulation cells sweep across the bottom, they irrigate the substrate. Those areas characterized by an increasing sand fraction with increasing distance from the edge of the alluvial fan match locations subjected to sweeping from vertical circulation cell currents. These areas also match local maxima of ammocete density.

Webb (1975) noted the importance of similar currents driven by surface pressure waves in crest and ripple substrate formations and related them to the

local distribution of amphioxus. Station 10 corresponds to a slack current region based on figure 23, while station 24 corresponds to an active current region. Of the marked animals released at stations 10 and 24, twice as many remained at station 24 through the summer.

The model outlined in figure 23 also provides an explanation for the shift in POM distribution from summer to fall. In September, prevailing winds shift from the northwest to northeast and the temperature of the river drops significantly below that of the bay. This leads to the creation of a shallow current of river water flowing over the bottom (figure 23c). In the field, this current was quite strong, moving not only fine particles across the bottom but also small twigs and leaves within 40 m of the alluvial fan (pers. obs.). Beyond 70 m, the current was not as noticeable.

Evidence for temporal shifts in ammocete distribution and abundance in response to the local thermal habitat was also obtained from summer 1987 data. Early <u>versus</u> late summer distribution and abundance of ammocetes is shown in figure 28. In early summer (June/July), ammocete density within 60 m of the edge of the alluvial decreased with increasing distance. Ammocetes within 40 m of the edge of the alluvial fan

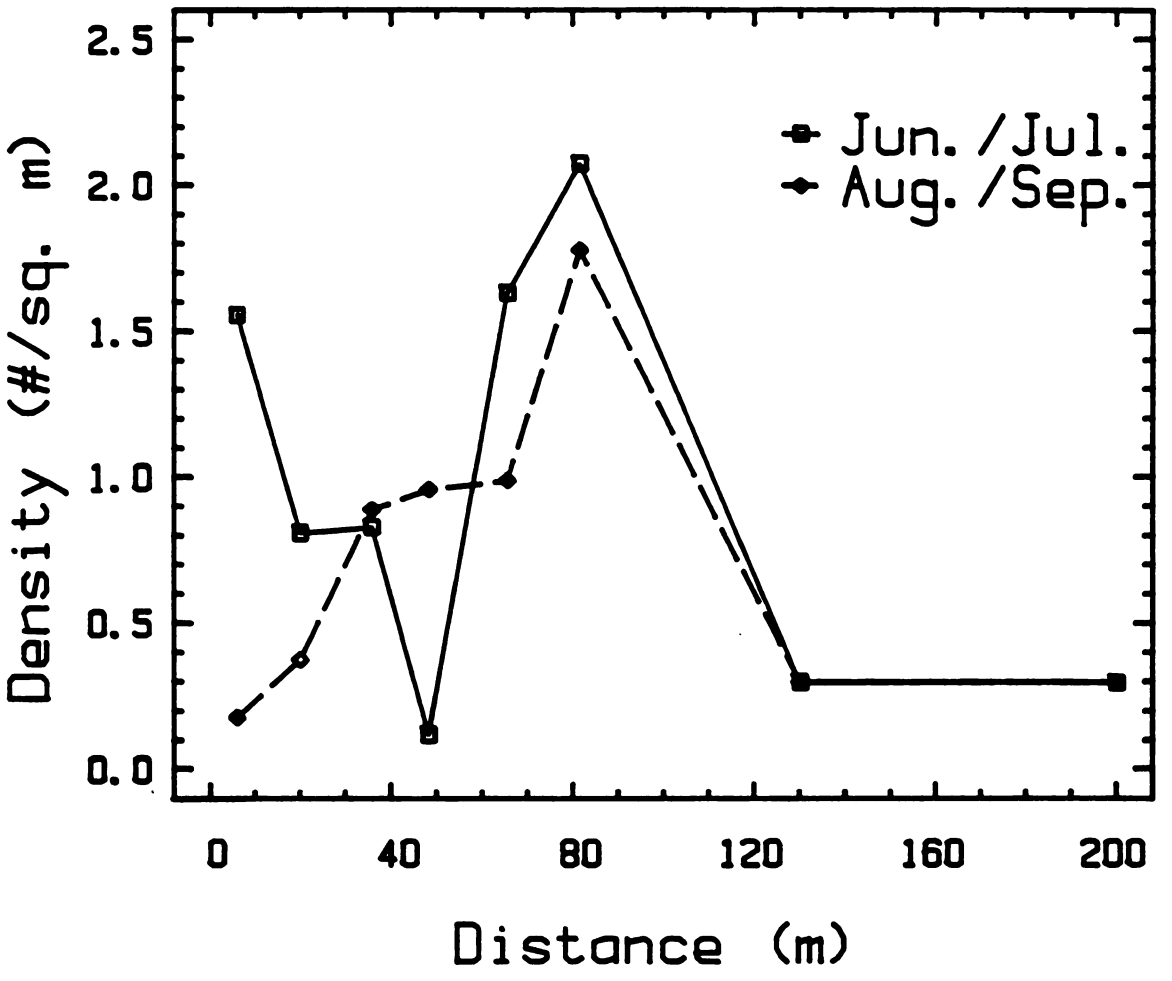


Figure 28. Early vs. late summer distribution and abundance of ammocetes with respect to distance from the edge of the alluvial fan during summer 1987.

moved to deeper waters further offshore between early and late summer. An analysis of covariance for differences among slopes was significant at the α = 0.005 level. Ammocetes located beyond 60 m from the edge of the alluvial fan did not demonstrate temporal shifts in distribution and abundance.

To track average changes in temperature with respect to depth and distance from the edge of the alluvial fan, daily median temperatures at stations 10, 16, and 24 were subjected to third degree polynomial smoothing and plotted together (figure 29). Smoothed temperatures from 9.1 and 21 m depths in 1985 were included for reference. From this a series of temperature isoclines, including that of the thermocline and the median thermal preferendum, were derived (figure 30).

Based on figure 30 and diving observations, the thermocline set up by 14 June at an average depth of 12.2 m and progressively descended to a depth of 18 m by 31 July. By early August, median temperatures had reached 17 °C at a depth of 12.2 m and distance of 43 m from the edge of the alluvial fan. The 14 °C isocline tracks the downslope movement of the thermal preferendum measured by Reynolds and Casterlin (1978). By early

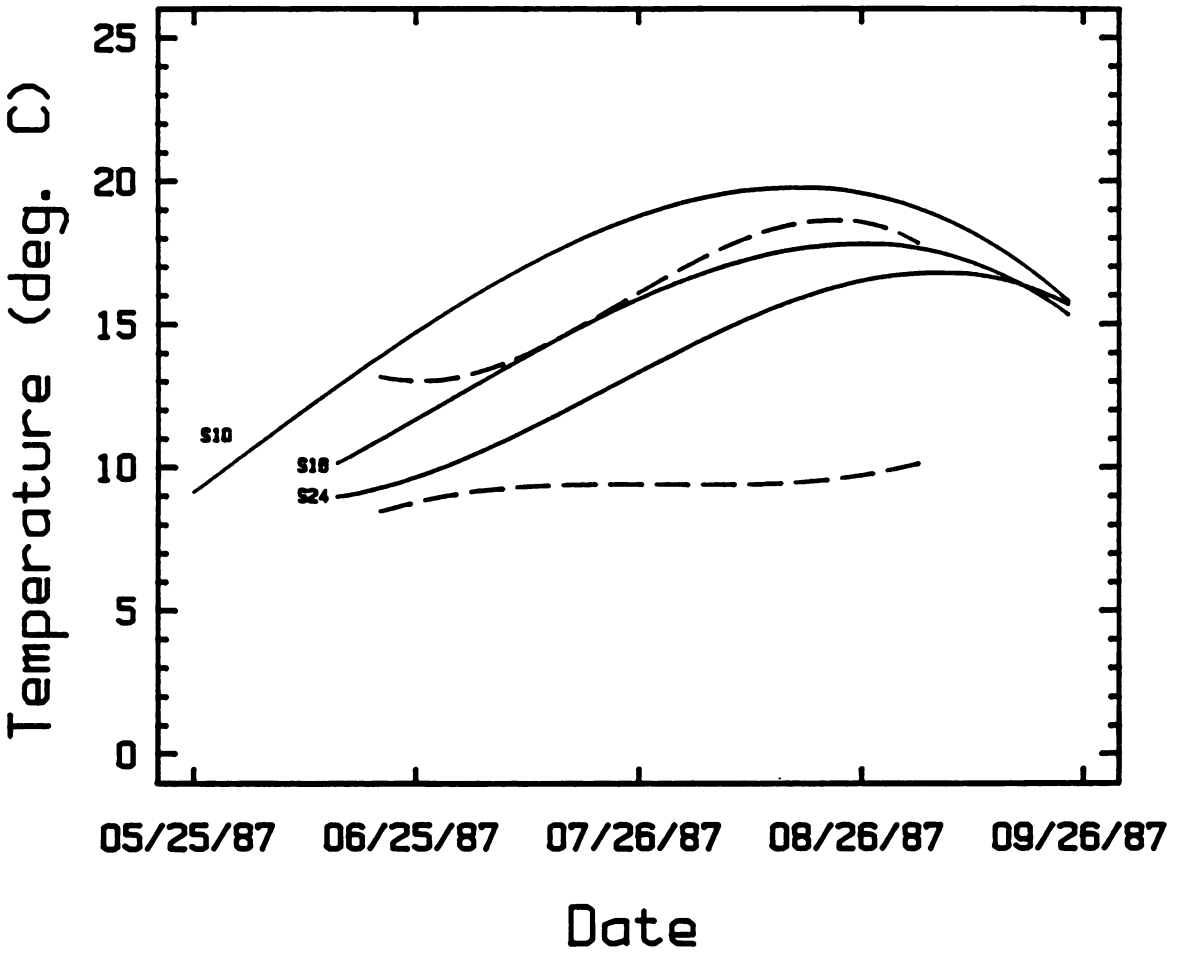


Figure 29. Polynomially smoothed daily median temperatures at stations 10, 16, and 24 during summer 1987 (solid lines) and at 9.1 and 21 m depths from summer 1985 (dashed lines).

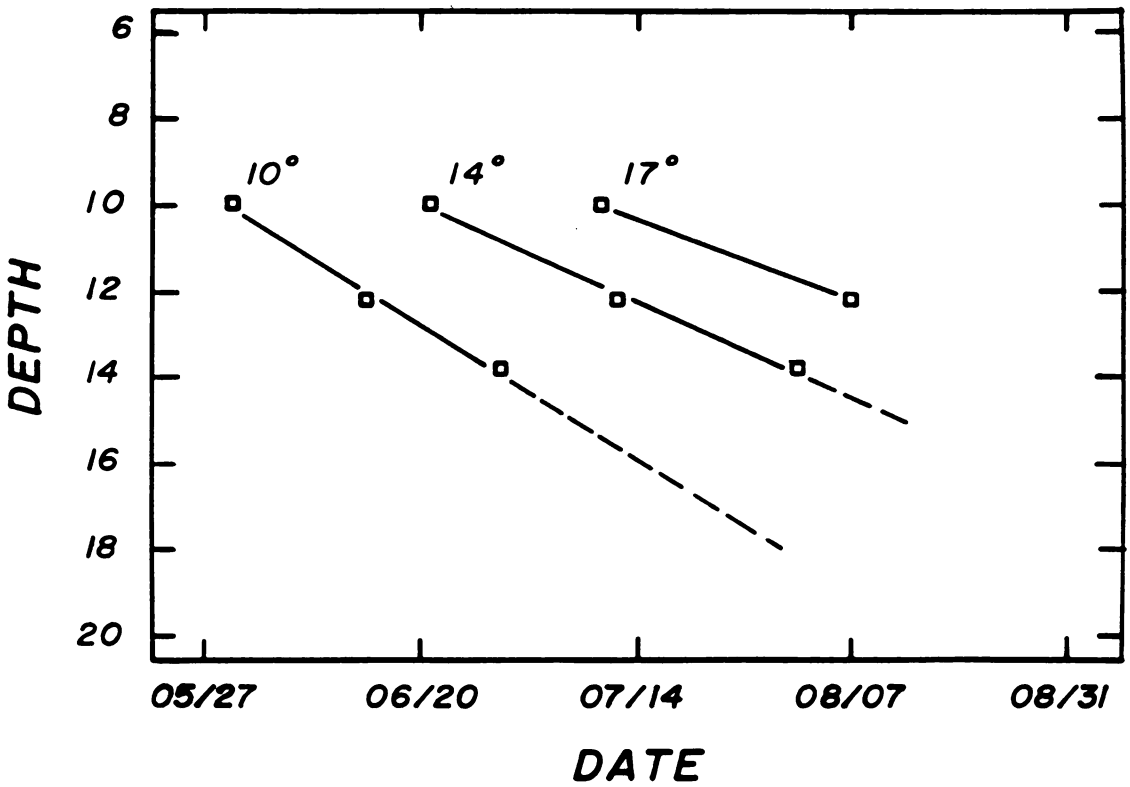


Figure 30. Derived temperature isoclines with respect to depth and date during summer 1987. The 10 °C temperature isocline tracks the downslope movement of the thermocline after 14 June.

August, median temperatures of 14 °C intersected the bottom at a depth of 14 m and a distance of 70+ m from the edge of the alluvial fan while temperatures within 20 m of the edge of the alluvial fan exceeded 19 °C.

The dramatic shift in ammocete abundance within 20 m of the edge of the alluvial fan corresponds to median temperatures exceeding 19 °C. This matches the upper limit of voluntarily selected temperatures noted by Reynolds and Casterlin. The general pattern of ammocete movement within 40 m of the edge of the alluvial fan corresponds to that expected if ammocetes were roughly tracking the upper end of the thermal preferendum. The same pattern was observed in the marked ammocetes released at station 10 where the pattern of dispersal at the release point was biased towards deeper waters and migrants were caught at increasing depths over the course of the summer.

Conclusions

Acting as delimiters of substrate "suitability", mean grain diameter and permeability are both determinants of larval lamprey habitat selection. The failure of the 1986 cross-factor study to reflect a substrate treatment effect is attributable to both

modified and unmodified patches meeting the "suitability" limits. Whether mean grain diameter sets a lower limit to substrate suitability remains unclear but the ready acceptance of diatomaceous earth as a burrowing substrate noted by Mallatt (1982) argues against the proposition. While mean grain diameter and permeability set limits to substrate suitability, within these limits, the individual variation in substrate selection is high.

The local thermal regime also drives larval lamprey habitat selection based in part on the recent thermal history of the individual. Demonstrated in the field by the shift to cooler waters with temperatures exceeding the upper end of the thermal preferendum, the same mechanism may also explain the rejection of 1985 deepwater release points by marked ammocetes. Though cold-acclimated ammocetes in Reynolds and Casterlin's work initially avoided temperatures of 10 - 12 °C, they gravitated towards the 14 °C preference point within a week once aware of the availability of warmer temperatures.

The vertical circulation cell/current model may also explain the selection against deepwater release points in 1985 and 1986. At depths of 21 m, the total

vertical oscillation available to irrigate the substrate under the assumption of wave heights of 0.75 m with a length of 32 m is only 4.3 mm. Consequently, the exchange rate for interstitial waters may be too low to adequately refresh interstitial water and/or remove metabolic wastes.

Given that the substrates off the mouth of the Chippewa River meet the suitability limits set by mean grain diameter and permeability, the pattern of ammocete distribution and abundance can be explained by the interaction of local temperature changes, inferred hydrodynamics and annual Bayer 73 treatments. As represented in figure 23a, warmer river water discharge flows over the cooler bay waters. In the process, velocity drops and particulates settle out according to density. Ammocetes moving into the lentic area at this time also settle out with decreasing stream velocity. The average and early summer distribution of ammocetes within 60 m of the edge of the alluvial fan in figures 20 and 28 supports this conjecture.

Prevailing westerly winds in late spring through mid summer as shown in figure 23b lead to the establishment of a hydrodynamic wall and resultant vertical circulation cells. With the establishment of

zones of preferential substrate irrigation, local ammocete distribution shifts in favor of well irrigated substrates. When annual Bayer 73 treatments within 30 m of the edge of the alluvial fan are conducted before local temperatures prompt movement further offshore as shown in figure 28, most ammocetes are killed. However, if treatments are conducted in late August or September

(as is frequently the case), many ammocetes move out of the treatment area in response to temperature. This process leads to the locally high density of ammocetes between 60 and 87 m from the edge of the alluvial fan.

The implications for sea lamprey control in lentic areas are clear. There is a time window for Bayer 73 treatments that must be met to insure successful treatment. Treated too early, water temperatures may not be high enough for efficient use of Bayer 73. Treated too late, when water temperatures have risen to the point where ammocetes migrate to deeper waters, the results will be equally unsatisfactory.

While this research has defined proximate determinants of habitat selection (eg. those that act over short time periods), ultimate determinants such as the individual assessment of energetic return over long

time spans have not been addressed. Before strong statements about ultimate determinants of habitat selection can be made, a better understanding of the energetic requirements for growth of ammocetes is required. This information in tandem with the understanding of the proximate determinants of habitat selection provided here is needed to create a null model of habitat selection against which ultimate determinants of habitat selection can be addressed.

APPENDICES

APPENDIX 1

Laboratory Measurement of Porosity

Assuming complete saturation of sediments, and a density of 1.00 g/ml for water, substrate porosity was calculated as the difference between wet and dry weight of the core segment divided by the volume of core segment. Cores were extruded by hand from the core tubes while frozen and cut into 4 cm segments with a nichrome wire heated with an electrical current. Slow freezing of sediment cores causes some deformation of the substrate lattice as the outer edges of the core freeze at a slightly faster rate. This acts to force the central portions of the core upwards (figure A1-1). Consequently, estimation of the actual volume of the substrate segment was required to correct for "excess" water surrounding the sediment core.

As shown below, this correction was achieved in two steps. First, the actual volume of the substrate and interstitial water was roughly estimated by a first order model based on the geometry of a conic segment. The difference between this volume and the cylindrical volume of the core segment yielded a corrected total

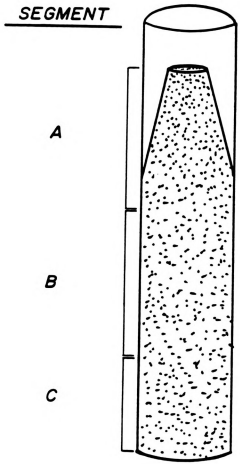


Figure A1-1. Schematic profile of frozen sediment cores.

weight for the core when subtracted from the total wet weight of the core. The difference between the dry weight of the core and the corrected wet weight provided a volume for the voids. The total volume of the core segment was then calculated by dividing the dry weight of the core segment by the density of quartz sands (2.65 g/ml; Holtz and Kovacs, 1981) and adding the substrate volume to voids volume.

$$P = (V_v)/(V_t)'$$

$$\text{when } V_v = [W_t - (V_t - V_c)] - W_d$$

$$\text{and } V_t' = (W_d/2.65) + V_v$$

where V_v = estimated volume of voids

V_t = cylindrical volume of total core segment

V_c = conic segment volume estimate

V_t' = corrected total volume of core segment

W_t = wet weight of cylindrical core segment

W_d = dry weight of core segment

Considering the deformation of the sediment lattice during freezing, the nature of the relationship between porosity calculated from frozen core segments versus unfrozen cores needs to be ascertained. Because unfrozen cores could not be sectioned, comparisons were

made between whole frozen and unfrozen cores of laboratory substrates. Shown in figure A1-2, the relationship between mean porosity for frozen and unfrozen cores is described by the following equation:

$$P_f = 4.702 + 0.823P_{uf}$$

where P_f = porosity of frozen cores

P_{uf} = porosity of unfrozen cores

with an R^2 of 83.0 percent. The ANOVA for the regression model is listed in table A1-1.

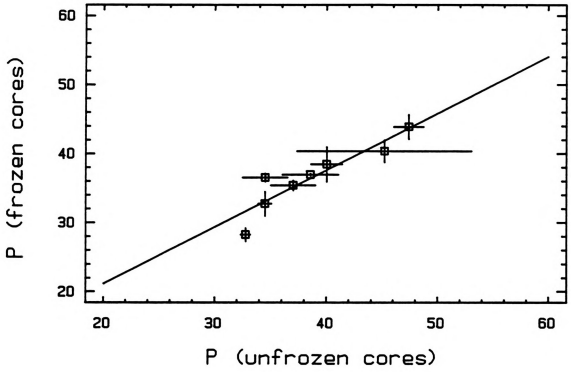


Figure A1-2. Linear regression through mean porosity values of frozen and unfrozen cores. Error bars for each mean are included.

Table A1-1. ANOVA of linear regression model through mean porosity values from frozen and unfrozen laboratory substrates.

Source	SS	df	MS	F-ratio	Signif.
Model	130.894	1	130.894	29.229	0.0017
Error	26.869	6	4.478		
Total	157.763	7			

APPENDIX 2

Laboratory Measurement of Permeability

Permeability of the top four centimeters of laboratory and field substrates was measured in a 12-place, low head permeameter (figure A2-1) at 25.0 ± 0.5° C. A constant head of 5 cm was maintained by pumping water to the permeameter from the storage reservoir and allowing the excess to drain back to the reservoir. Permeability (K) was calculated using Darcy's law for flow through a porous media (Holtz and Kovacs, 1981):

$$K = (QL)/(hAt)$$

where K = the coefficient of permeability (cm/min.).

Q = volume of water (cm^3) drained through core over time t.

L = length of sediment core (cm).

h = pressure head (cm).

A = cross sectional area of sediment core (cm^2).

t = time (min.)

While still frozen, the sediment/water interface was delineated in the core tube with a commercial

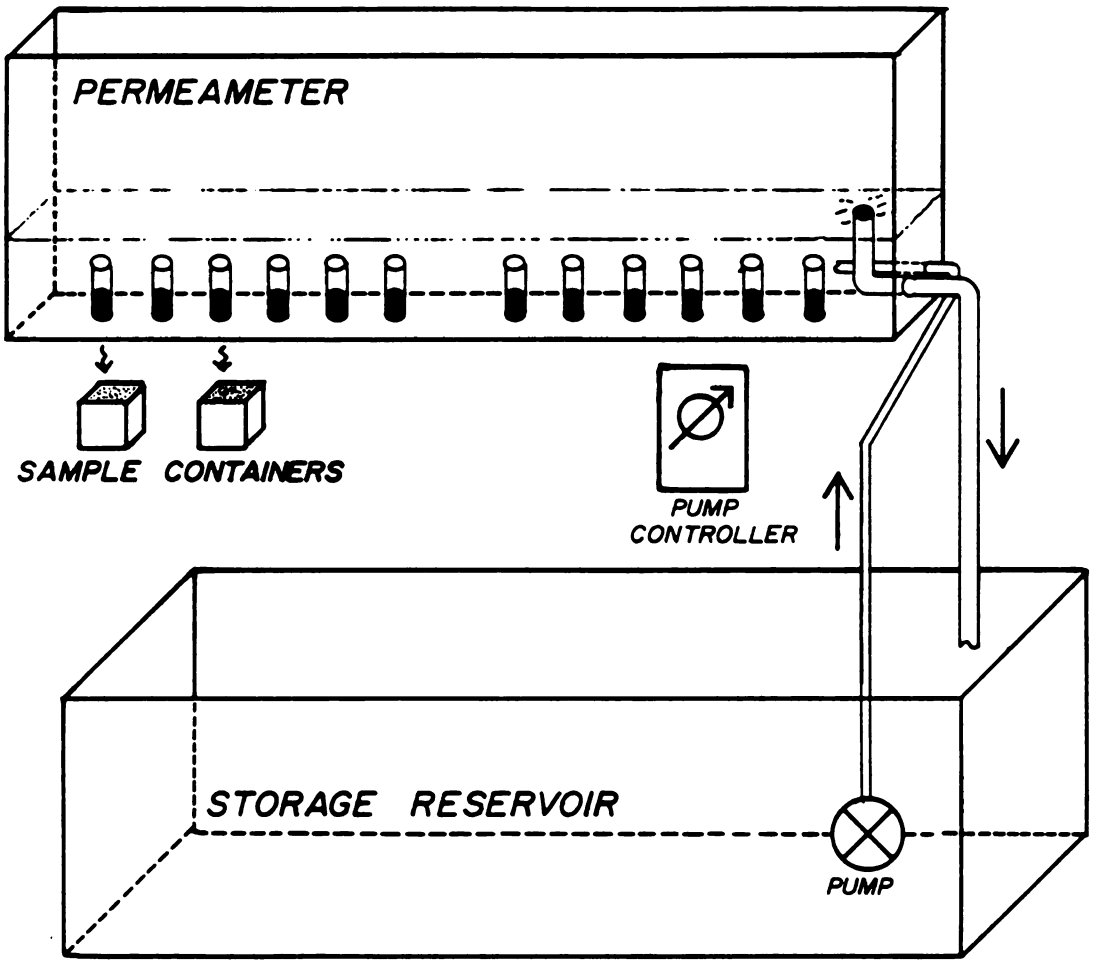


Figure A2-1. Schematic representation of the constant head permeameter. Constant head is maintained with a low velocity pump and overflow stand-pipe set to the desired head.

ultrasonic sensor. The core tube, still containing the frozen sample, was then cut with a band saw using a 24 teeth per inch blade. The core tube and sample was then sectioned again 4 cm down from the sediment/water interface with the band saw. The 4 cm segment (still frozen) and sandwiched by two 2.54 cm female slip/slip PVC fittings was then fitted into the permeameter. The frozen segment were then allowed to thaw in the permeameter and come to thermal equilibrium with the permeameter for 12 to 16 hours before measurement of permeability.

The core segments were supported in the permeameter on 2.64 cm diameter aluminum screens (18 mesh) and loss of substrate was prevented by a single layer of tissue cut from KimWipes$^{(tm)}$ between the bottom of the core segment and the aluminum retaining screen. Porosity of the aluminum/tissue support (both before and after use with a substrate sample) was greater by two orders of magnitude than through the cores themselves.

In operation, five timed runs for each substrate core were conducted. The run-specific K's for a given core were then exponentially regressed against the run number to obtain an estimate of substrate permeability free of any artifacts created by shifting substrate lattices or clogging of the aluminum/tissue support. To

assess the effect of freezing on substrate permeability, a linear regression of permeability values for the natural log of frozen versus unfrozen laboratory substrates was conducted (Figure A2-2). The ANOVA for the regression model is shown in table A2-1.

Described by the relationship:

$$\ln K_f = 0.0911 + 0.9370(\ln K_{uf})$$

where K_f = permeability of frozen cores

K_{uf} = permeability of unfrozen cores

the R^2 of the regression was 95.72. Based on a standard error of 0.0660 for the slope, the relationship between frozen and unfrozen values was 1:1.

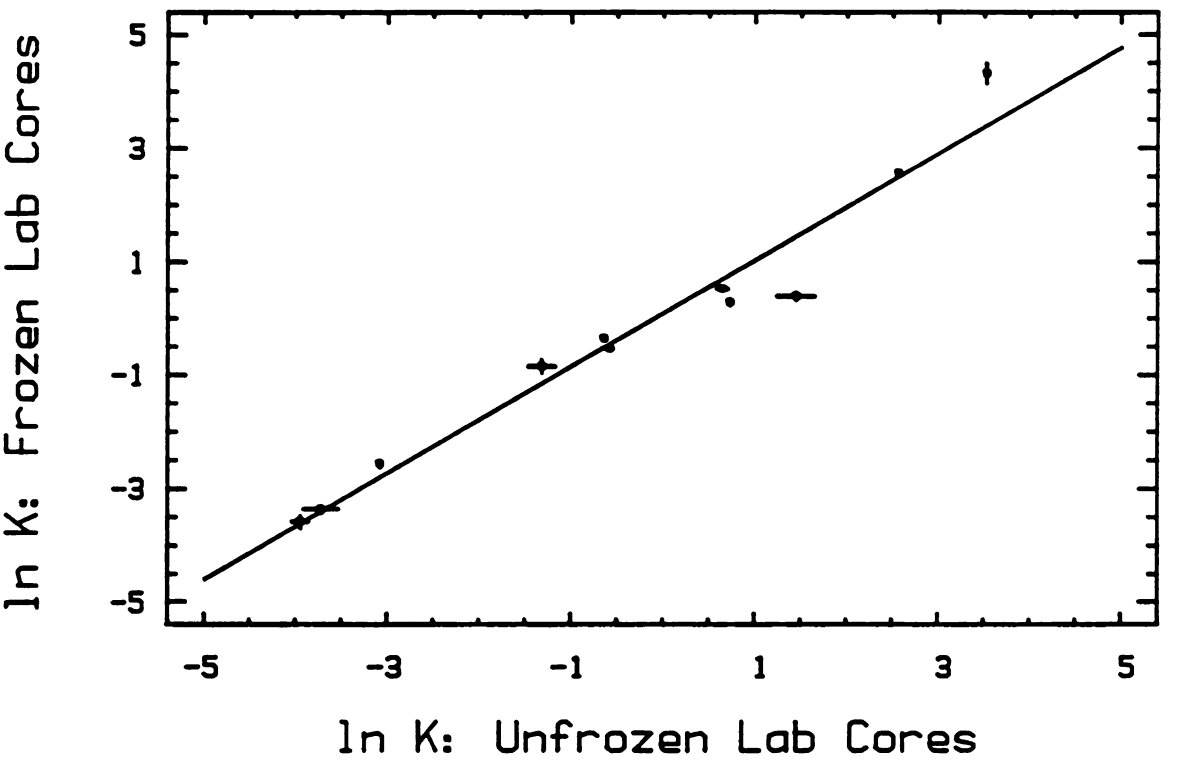


Figure A2-2. Linear regression through mean ln permeability values of frozen and unfrozen cores. Error bars for each mean are included.

Table A2-1. ANOVA of linear regression model through mean permeability values from frozen and unfrozen laboratory substrates.

Source	SS	df	MS	F-ratio	Signif.
Model	54.238	1	54.238	201.44	0.0000
Error	2.423	9	0.269		
Total	56.661	10			

APPENDIX 3

Analysis of Food Particle Distribution and Abundance: Processing of Sediment Cores and Water Samples.

Chlorophyll a concentrations were determined fluorometrically while gross organic content was estimated by the difference between dry weight and rehydrated weight after ignition at 500° C. The field preparation and subsequent laboratory analyses for sediment cores and water samples are reviewed separately below. Prior to all fluorometric analyses of chlorophyll concentration, calibration curves were generated from florescence values for 0.5x serial dilutions of a stock solution (299 ug chl. a/l).

Sediment Cores

Sediment cores were extruded from the core tube while still frozen and cut at 1 cm intervals using a nichrome wire heated with an electrical current (Nalepa and Quigley, 1987). Subsamples of each depth segment (approx. 2.5 cm^3 each) were placed in clean, pre-ashed and weighed glass scintillation vials. Photosynthetic pigments were extracted in the dark with 15.7 ml of 100%

ethanol for 36 hours at -20° C. Assuming an average water content of 50% by volume, samples were treated as if extracted with 17 ml's of 92% ethanol.

After extraction, the samples were centrifuged at 1000 rpm for 8 minutes and the supernatant was pipetted to 15 ml polyethylene centrifuge tubes. Florescence of the supernatant before and after acidification with HCl (final molarity of 0.003; Holm-Hansen, 1978), was measured in the dark with a Turner Model 100 Fluorometer using standard excitation and emission filters for chlorophyll measurement. Chlorophyll a and Pheophytin a concentrations were calculated using the formulas of Strickland and Parsons (1968). Mean values for the acid ratio and fluorometric conversion factor were obtained from the serial dilutions.

Remaining sediments and extract in each scintillation vial were air dried under a fume hood then transferred to a convection oven for 24 hours at 60° C to remove residual moisture. Samples were ashed at 500° C for 1.5 hours, cooled in a desiccator, rehydrated, and then redried at 60° C prior to reweighing. Inorganic and organic substrate components were calculated from resultant values for each sample.

Water Samples

Of the replicate 1140 ml water samples collected at specific stations on a given day, one was analyzed for gross organic content above and below a threshold point of 180 um (near the upper limit of ingestible particle size; Mallatt, 1981) while the other was analyzed for chlorophyll concentration above and below the 180 um partition. Particle size partitioning was completed by prefiltering each water sample through a 180 um sieve and back-washing material retained on the sieve into a new container.

To determine the organic content of each partition for a given sample, individual partitions were vacuum filtered onto preweighed and ashed Gelman A/E glass fiber discs in the field and allowed to dry in an air-tight desiccator. Resultant samples were stored in the desiccator until processed in the lab within 6 days of collection. In the lab, organic content of each sample partition was estimated through standard analysis of ash-free dry weight.

Water sample partitions for chlorophyll analysis were also separately filtered out on Gelman G/E glass fiber discs but were immediately frozen at -20° C. In the laboratory, the samples were extracted with 10 mls

of 90% ethanol for 36 hours in polyethylene centrifuge tubes. During extraction, the centrifuge tubes were violently agitated to break up the filter disc. After extraction, the samples were spun in a centrifuge at 2500 rpm for 10 minutes. Florescence of the supernatant was measured as above for sediment chlorophyll samples.

Additional considerations on fluorometric determination of chlorophyll a concentrations

Small sample sizes required the use of an efficient extraction solvent and fluorometric estimation of pigment concentrations. Ethanol was selected over acetone and methanol based on the superior extraction performance of alcoholic solvents and relative safety of ethanol (Nusch, 1980). Fluorometric analysis of photosynthetic pigments in lacustrine samples can be confounded by the overlap of the pheophytin a emission band with that of chlorophyll a after acidification (Marker, et al.). While Coveney (1982) developed a technique based on the differential acid reaction kinetics of chlorophylls a and b to correct for this error, the technique was built around acetone as the extraction solvent.

The U/A ratio can indicate when chlorophyll b interference is particularly disruptive. In 90% ethanol

in the absence of chlorophyll b, the U/A ratio for pure chlorophyll a ranges from a value of 1.00 for completely degraded pigment to 2.05 for undegraded pigment. U/A ratios for field values were always within these limits, ranging from 1.24 to 2.02 (mean: 1.69, standard deviation: 0.159).

APPENDIX 4

Detailed Statistics of Burrowing Substrate Analyses

The following nine tables contain the results of all tests of homogeneity and pooled model I ANOVA's. Each corresponds to the abstracted results presented in the main text. The last column of table A4-1 indicates whether or not the results of the ANOVA were verified based on multiple comparisons of means with the T-method or Games and Howell's method depending upon the homogeneity of variances.

Table A4-1. Bartlett's test for homogeneity of variance for pooled experimental series subjected to model I ANOVA. [La = Lampetra appendix, Pm = Petromyzon marinus, ns = unstaggered release, s = staggered release.]

Species	Size	Density and Release Patterns	X^2_c	df	Signif. Level	ANOVA results representative
Test of variances among sediment type by experimental series						
La	Sm.	D4ns,D8ns	109.30	7	<0.001	yes
La	Lg.	D4ns,D8ns,D12s, D4:4ns,D8:8ns	27.992	19	0.0866	yes
Pm	Sm.	D4ns,D8ns,D8s	17.735	11	0.0904	yes
Pm	Lg.	D4ns,D8ns,D8s,D12s D4:4ns,D8:8ns	201.17	23	<0.001	yes
Test of variances among sediment type only						
La	Sm.	D4ns,D8ns	11.172	3	0.0113	yes
La	Lg.	D4ns,D8ns,D12s, D4:4ns,D8:8ns	6.2648	3	0.0996	yes
Pm	Sm.	D4ns,D8ns,D8s	2.8774	3	0.4473	yes
Pm	Lg.	D4ns,D8ns,D8s, D12s,D4:4ns,D8:8ns	14.024	3	0.0036	yes
Test of variances among sediment type by ammocoete size class						
La	Sm/Lg	D4ns,D8ns,D12s, D4:4ns,D8:8ns	18.150	7	0.0120	yes
Pm	Sm/Lg	D4ns,D8ns,D8s,D12s, D4:4ns,D8:8ns	15.812	7	0.0276	yes
Test of variances among sediment type by species						
La/Pm	Sm.	D4ns,D8ns,D8s	14.080	7	0.0498	yes
La/Pm	Lg.	D4ns,D8ns,D8ns,D12s, D4:4ns,D8:8ns	21.720	7	0.0036	yes
Test of variances among sediment type with/without other spp.						
La	Lg.	D4ns,D8ns,D12s vs. D4:4ns,D8:8ns	10.295	7	0.2215	yes
Pm	Lg.	D4ns,D8ns,D8s,D12s vs. D4:4ns,D8:8ns	188.25	7	<0.001	yes
Tests of variances among food/habitat selection tests						
La/Pm	Lg.	Yeast perfused vs. unperfused sediments	0.1852	1	0.7458	yes
La/Pm	Lg.	Food perfused vs unperfused water column	2.5405	3	0.4820	yes

Table A4-2. Multifactor model I ANOVA's for pooled Lampetra appendix; selection frequency (square root arcsin transformed) analyzed by substrate type, position in test arena, and experimental series (density/release pattern).

Small Lampetra appendix, pooled D4ns, D8ns

Source of Variation	SS	df	MS	F-ratio	Signif. Level
Main Effects	5.7820	7	0.8260	7.909	0.0000
Substrate	5.4140	3	1.8047	17.280	0.0000
Position	0.2970	3	0.0990	0.948	0.4228
Exp. Series	0.0544	1	0.0544	0.521	0.4808
Interactions	1.3561	15	0.0904	0.866	0.6038
Substrate x Position	0.3805	9	0.0423	0.405	0.9281
Substrate x Exp. Series	0.1879	3	0.0626	0.600	0.6176
Position x Exp. Series	0.8081	3	0.2694	2.579	0.0611
Residual	6.7885	65	0.1044		
Total	13.9266	87			

Large Lampetra appendix, pooled D4ns, D8ns, D12s, D4:4ns, D8:8ns

Main Effects	8.5568	10	0.8557	7.591	0.0000
Substrate	7.7643	3	2.5881	22.961	0.0000
Position	0.8077	3	0.2692	2.388	0.0689
Exp. Series	0.0456	4	0.0114	0.101	0.9820
Interactions	3.7941	33	0.1150	1.020	0.4418
Substrate x Position	0.7123	9	0.0791	0.702	0.7069
Substrate x Exp. Series	1.0638	12	0.0887	0.786	0.6644
Position x Exp. Series	2.1254	12	0.1771	1.571	0.0987
Residual	35.168	312	0.1127		
Total	47.519	355			

Table A4-3. Multifactor model I ANOVA's for pooled Petromyzon marinus; selection frequency (square root arcsin transformed) analyzed by substrate type, position in test arena, and experimental series (density/release pattern).

Small Petromyzon marinus, pooled D4ns, D8ns, D8s

Source of Variation	SS	df	MS	F-ratio	Signif. Level
Main Effects	1.1577	8	0.1447	1.534	0.1639
Substrate	0.5933	3	0.1978	3.097	0.1098
Position	0.4428	3	0.1476	1.565	0.2069
Exp. Series	0.0804	2	0.0402	0.426	0.6548
Interactions	2.5110	21	0.1196	1.268	0.2323
Substrate x Position	1.1170	9	0.1241	1.316	0.2473
Substrate x Exp. Series	0.7191	6	0.1199	1.271	0.2839
Position x Exp. Series	0.5341	6	0.0890	0.944	0.4706
Residual	5.8481	62	0.0943		
Total	9.5168	91			

Large Petromyzon marinus, D4ns, D8ns, D8s, D12s, D4:4ns, D8:8ns

Main Effects	23.8654	11	2.1696	22.579	0.0000
Substrate	23.5941	3	7.8647	81.849	0.0000
Position	0.1259	3	0.0420	0.437	0.7269
Exp. Series	0.0989	5	0.0198	0.206	0.9599
Interactions	6.0537	39	0.1552	1.615	0.0144
Substrate x Position	1.5091	9	0.1677	1.745	0.0781
Substrate x Exp. Series	2.8991	15	0.1933	2.011	0.0142
Position x Exp. Series	1.7630	15	0.1175	1.223	0.2523
Residual	30.844	321	0.0961		
Total	60.764	371			

Table A4-4. Multifactor model I ANOVA's for pooled Lampetra appendix and pooled Petromyzon marinus. Substrate selection frequency (square root arcsin transformed) analyzed by substrate type, position in test arena, and size class (small or large).

Large/Small Lampetra appendix, pooled D4ns, D8ns, D12s, D4:4ns, D8:8ns

Source of Variation	SS	df	MS	F-ratio	Signif. Level
Main Effects	12.8759	7	1.8394	16.605	0.0000
Substrate	11.8972	3	3.9657	35.800	0.0000
Position	1.0213	3	0.3404	3.073	0.0276
Size Class	0.0031	1	0.0031	0.028	0.8683
Interactions	1.9370	15	0.1291	1.166	0.2958
Substrate x Position	0.5709	9	0.0634	0.573	0.8197
Substrate x Size Class	1.2481	3	0.4160	3.756	0.0110
Position x Size Class	0.0779	3	0.0260	0.234	0.8724
Residual	46.636	421	0.1108		
Total	61.449	443			

Lg./Sm. Petromyzon marinus, pooled D4ns, D8ns, D8s, D12s, D4:4ns, D8:8ns

Main Effects	21.0485	7	3.0069	30.397	0.0000
Substrate	20.7683	3	6.9226	69.981	0.0000
Position	0.0975	3	0.0325	0.329	0.8048
Size Class	0.0852	1	0.0852	0.861	0.3638
Interactions	5.6922	15	0.3795	3.836	0.0000
Substrate x Position	1.8117	9	0.2013	2.035	0.0342
Substrate x Size Class	3.5409	3	1.1803	11.932	0.0000
Position x Size Class	0.5138	3	0.1713	1.731	0.1598
Residual	43.625	441	0.0989		
Total	70.366	463			

Table A4-5. Multifactor model I ANOVA's for contrast of Lampetra appendix and Petromyzon marinus within a size class; selection frequency (square root arcsin transformed) analyzed by substrate type, position in test arena, and species.

Pooled Small Lampetra appendix vs. Petromyzon marinus

Source of Variation	SS	df	MS	F-ratio	Signif. Level
Main Effects	4.4714	7	0.6388	6.341	0.0000
Substrate	4.3479	3	1.4493	14.388	0.0000
Position	0.0588	3	0.0196	0.195	0.9000
Species	0.0375	1	0.0375	0.372	0.5491
Interactions	3.1945	15	0.2130	2.114	0.0117
Substrate x Position	0.8253	9	0.9150	0.908	0.5195
Substrate x Species	1.6000	3	0.5333	5.295	0.0017
Position x Species	0.6654	3	0.2218	2.202	0.0900
Residual	15.815	157	0.1007		
Total	23.481	179			

Pooled Large Lampetra appendix vs. Petromyzon marinus

Main Effects	29.0990	7	4.1570	38.946	0.0000
Substrate	28.2944	3	9.4315	88.361	0.0000
Position	0.7883	3	0.2628	2.462	0.0615
Species	0.0252	1	0.0252	0.236	0.6322
Interactions	3.9584	15	0.2640	2.472	0.0015
Substrate x Position	0.7544	9	0.0838	0.785	0.6301
Substrate x Species	3.0026	3	1.0009	9.377	0.0000
Position x Species	0.1914	3	0.0638	0.598	0.6166
Residual	75.250	705	0.1067		
Total	108.308	727			

Table A4-6. Analysis of intraspecific competition effects on substrate selection by Petromyzon marinus and Lampetra appendix. Model I ANOVA of substrate selection frequency (square root arcsin transformed) with respect to substrate type, position, and release group.

Source of Variation	SS	df	MS	F-ratio	Signif. Level
Large Lampetra appendix, D12, staggered release of three groups of four					
Main Effects	4.8884	8	0.6111	5.250	0.0000
Substrate	4.5221	3	1.5074	12.950	0.0000
Position	0.3613	3	0.1204	1.035	0.3788
Release Group	0.0050	2	0.0025	0.022	0.9787
Interactions	2.2715	21	0.1082	0.929	0.5541
Substrate x Position	0.6040	9	0.0671	0.577	0.8150
Substrate x Release Group	1.0648	6	0.1775	1.525	0.1731
Position x Release Group	0.6028	6	0.1005	0.863	0.5235
Residual	18.856	162	0.1164		
Total	26.016	191			
Small Petromyzon marinus, D8, staggered release of two groups of four					
Main Effects	0.6650	7	0.0950	0.418	0.8752
Substrate	0.6055	3	0.2018	0.889	0.4709
Position	0.1026	3	0.0342	0.151	0.9275
Release Group	0.0121	1	0.0121	0.053	0.8231
Interactions	1.5493	6	0.2582	1.137	0.03913
Substrate x Release Group	1.0850	3	0.3617	1.593	0.2357
Position x Release Group	0.5539	3	0.1846	0.813	0.5077
Residual	3.1739	14	0.2271		
Total	5.3936	27			
Large Petromyzon marinus, D8, staggered release of two groups of four					
Main Effects	3.8083	7	0.5440	6.187	0.0000
Substrate	3.0483	3	1.0161	11.554	0.0000
Position	0.2844	3	0.0948	1.078	0.3658
Release Group	0.0000	1	0.0000	0.000	1.0000
Interactions	2.2391	15	0.1594	1.813	0.0551
Substrate x Position	1.7638	9	0.1960	2.228	0.0330
Substrate x Release Group	0.3293	3	0.1098	1.248	0.3008
Position x Release Group	0.2431	3	0.0810	0.921	0.4364
Residual	5.0126	57	0.0879		
Total	11.2123	79			
Large Petromyzon marinus, D12, staggered release of three groups of four					
Main Effects	13.1909	8	1.6489	13.451	0.0000
Substrate	12.1175	3	4.0392	32.950	0.0000
Position	0.6822	3	0.2274	1.855	0.1412
Release Group	0.0067	2	0.0034	0.027	0.9730
Interactions	2.1196	21	0.1009	0.823	0.6864
Substrate x Position	1.0074	9	0.1119	0.913	0.5166
Substrate x Release Group	0.5479	6	0.0913	0.745	0.6146
Position x Release Group	0.5806	6	0.0968	0.789	0.5800
Residual	13.975	114	0.1226		
Total	29.285	143			

Table A4-7. Contrast of substrate selection between species released individually vs. together. Model I ANOVA of frequency (square root arcsin transformed) with respect to substrate (very fine through coarse sands), position, release group.

Large Lampetra appendix, pooled D4ns, D8ns, D12s versus large Lampetra appendix, pooled D4:4ns, D8:8ns.

Source of Variation	SS	df	MS	F-ratio	Signif. Level
Main Effects	8.5130	7	1.2161	10.926	0.0000
Substrate	7.7643	3	2.5881	23.252	0.0000
Position	0.8077	3	0.2692	2.419	0.0661
Presence of Pm	0.0017	1	0.0017	0.016	0.9019
Interactions	1.9413	15	0.1294	1.163	0.2996
Substrate x Position	0.7056	9	0.0784	0.704	0.7049
Substrate x Presence of Pm	0.4797	3	0.1599	1.437	0.2319
Position x Presence of Pm	0.7105	3	0.2368	2.128	0.0965
Residual	37.065	333	0.1113		
Total	47.519	355			

Large Petromyzon marinus, pooled D4ns, D8ns, D8s, D12s versus large Petromyzon marinus, pooled D4:4ns, D8:8ns.

Main Effects	23.7676	7	3.3954	33.992	0.0000
Substrate	23.5941	3	7.8647	78.737	0.0000
Position	0.1259	3	0.0420	0.420	0.7387
Presence of La	0.0010	1	0.0010	0.010	0.9199
Interactions	2.1357	15	0.1424	1.425	0.1326
Substrate x Position	1.5121	9	0.1680	1.682	0.0919
Substrate x Presence of La	0.4604	3	0.1535	1.536	0.2048
Position x Presence of La	0.1125	3	0.0375	0.375	0.7708
Residual	34.860	349	0.0999		
Total	60.764	371			

Table A4-8. Results of multifactor model I ANOVA on the effect of sedimentary food particle distribution on substrate selection. Frequency of specific substrate selection (square root arcsin transformed) analyzed with respect to treatment (yeast perfused or unperfused substrate), substrate position in test arena, and species.

Source of Variation	SS	df	MS	F-ratio	Signif. Level
Main Effects	0.5080	5	0.1016	2.978	0.0196
Treatment	0.0073	1	0.0073	0.215	0.6495
Position	0.4990	3	0.1663	4.877	0.0047
Species	0.0016	1	0.0016	0.046	0.8332
Interactions	0.1017	7	0.0145	0.426	0.8817
Treatment x Position	0.0603	3	0.0201	0.589	0.6249
Treatment x Species	0.0130	1	0.0130	0.381	0.5463
Position x Species	0.0358	3	0.0119	0.350	0.7892
Residual	1.7396	51	0.0341		
Total	2.3492	63			

Table A4-9. Results of multifactor model I ANOVA on the effect of food particle distribution in the water column on substrate selection. Frequency of specific substrate selection (square root arcsin transformed) analyzed with respect to treatment (yeast perfused or unperfused substrate), substrate position in test arena, food type (yeast or algae suspensions), and species.

Source of Variation	SS	df	MS	F-ratio	Signif. Level
Main Effects	0.1175	4	0.0294	0.446	0.7748
Treatment	0.1005	1	0.1005	1.524	0.2255
Position	0.0103	1	0.0103	0.155	0.7000
Food Type	0.0000	1	0.0000	0.000	1.0000
Species	0.0000	1	0.0000	0.000	1.0000
Interactions	0.2883	5	0.0577	0.874	0.5085
Treatment x Species	0.1828	1	0.0187	2.773	0.1051
Treatment x Position	0.0000	1	0.0000	0.000	1.0000
Treatment x Food Type	0.0002	1	0.0002	0.002	0.9613
Position x Food Type	0.0187	1	0.0187	0.283	0.6038
Position x Species	0.0007	1	0.0007	0.010	0.9224
Residual	2.2420	34	0.0659		
Total	2.6479	43			

LITERATURE CITED

LITERATURE CITED

American Society for Testing and Materials. 1985. Standard methods for particle size analysis of soils. Designation D422-63, Ann. Book of ASTM Standards, Vol. 04.08:116-126.

Applegate, V. C. 1950. Natural history of the sea lamprey, Petromyzon marinus, in Michigan. Spec. Sci. Rep. U.S. Fish. Wildl. Serv. 55:1-237.

Applegate, V. C. and Brynildson, C. L. 1951. Downstream movement of recently transformed sea lamprey, Petromyzon marinus, in the Carp Lake River, Michigan. Trans. Amer. Fish. Soc. 81:275-290.

Baxter, E. W. 1957. Lamprey distribution in streams and rivers. Letter to Nature, June 3, 1957. Biology Dept., Guys Hospital Medical School, London, S.E.1.

Chapman, D. G. 1951. Some properties of the hypergeometric distribution with applications to zoological sample censuses. Univ. Calif. Publ. Stat. 1:131-160.

Coveney, M. F. 1982. Elimination of chlorophyll b interference in the fluorometric determination of chlorophyll a and phaeopigment a. Arch. Hydrobiol. Beih. Ergebn. Limnol. 16:77-90.

Dodge, D. P. 1965. An electric trawl designed for capture of lamprey ammocetes/Estimates of population densities of sea lamprey ammocetes in certain bays of Lake Superior, 1964. Fish. Res. Bd. Can., Ann. Rep. of the London, Ont. Biol. Stat., 1964-1965, Appendices 35/36.

Gage, S. H. 1928. The lampreys of New York State - life history and economics. Biological survey of the Oswega River System. N.Y. State Conserv. Dep. Ann. Rep. 17:158-191.

Games, P. A. and J. F. Howell. 1976. Pairwise multiple comparison procedures with un-equal N's and/or variances: A Monte Carlo study. J. Educ. Stat. 1:113-125.

Great Lakes Fishery Commission. 1962. Annual report of the Great Lakes Fishery Commission, 1962. Great Lakes Fisheries Laboratory, Ann Arbor, Michigan. 57p.

Hansen, L. H. 1972. An evaluation of selected marks and tags for marking recently metamorphosed sea lamprey. Prog. Fish-Cult. 34:70-75.

Hansen, M. J. and Hayne D. W. 1962. Sea lamprey larvae in Ogontz Bay and Ogontz River, Michigan. J. Wildl. Manage. 26:237-247.

Hardisty, M. W., and I. C. Potter. 1977. Diets and culture of lampreys. In Rechcigl, M. (ed.). CRC handbook series in nutrition and food; Section G: Diets, culture media, and food supplements. Vol. 2. CRC Press, Cleveland, Ohio, 462p.

Holm-Hansen, O. 1978. Chlorophyll a determination: improvement in methodology. Oikos. 30:438-447.

Holtz, R. D. and W. D. Kovacs. 1981. An introduction to geotechnical engineering. Prentice-Hall, Englewood Cliffs, New Jersey. 733p.

Hutchinson, G. E. 1957. A treatise on limnology. I. geography, physics, and chemistry. John Wiley and Sons, New York, 1015p.

Johnson, B. G. H. (ed.) 1987. Evaluation of sea lamprey populations in the Great Lakes: Background papers and proceedings of the August 1985 Workshop. Great Lakes Fish. Comm. Spec. Publ. 87-2.

Lee, D. S. and Tusting, R. F. 1987. Development and use of an electrosampling device for submersible operations. In Proc. ROV '87 Conf., pp. 89-93. Marine Technology Society, San Diego Sect.

Lenz, J. and P. Fritsche. 1980. The estimation of chlorophyll a in water samples: a comparative study on retention in a glass-fibre and membrane filter and on the reliability of two storage methods. Arch. Hydrobiol. Beih. Ergebn. Limnol. 14:46-51.

Mallatt, J. 1981. The suspension feeding mechanism of the larval lamprey Petromyzon marinus. J. Zool. Lond. 194:103-142.

Mallatt, J. 1982. Pumping rates and particle retention efficiencies of the larval lamprey, an unusual suspension feeder. Biol. Bull. 163:197-210.

Mallatt, J. 1983. Laboratory growth of larval lampreys (Lampetra (Entosphenus) tridentata Richardson at different food concentrations and animal densities. J. Fish. Biol. 22:293-301.

Malmqvist, B. 1980. Habitat selection of larval brook lampreys (Lampetra planeri Bloch) in a south Swedish stream. Oecologia 45:35-38.

Malmqvist, B. and C. Brönmark. 1981. Filter feeding in larval Lampetra planeri: effects of size, temperature and particle concentration. Oikos 38:40-46.

Manion, P. J. and A. L. McLain. 1971. Biology of larval sea lampreys (Petromyzon marinus) of the 1960 year class, isolated in the Big Garlic River, Michigan, 1960-1965. Great Lakes Fish. Comm. Tech. Rep. 16:35p.

Manion, P. J. and Smith, B. R. 1978. Biology of larval and metamorphosing sea lamprey, Petromyzon marinus, of the 1960 year class in the Big Garlic River, Michigan, Part II, 1966-1972. Tech. Rep. Great Lakes Fish. Comm. 30:35p.

Marker, A. F. H., E. A. Nusch, H. Rai, and B. Riemann. 1980. The measurement of photosynthetic pigments in freshwaters and standardization of methods: Conclusions and recommendations. Arch. Hydrobiol. Beih. Ergebn. Limnol. 14:91-106.

Moll, R. and Brahce, M. 1986. Seasonal and spatial distribution of bacteria, chlorophyll, and nutrients in nearshore Lake Michigan. J. Great Lakes Res. 12:52-62.

Moore, H. H. and L. P. Schleen. 1980. Changes in spawning runs of sea lamprey (Petromyzon marinus) in selected streams of Lake Superior after chemical control. Can. J. Fish. Aquat. Sci. 37:1851-1860.

Moore, J. W. and F. W. H. Beamish. 1973. Food of larval sea lamprey (Petromyzon marinus) and American brook lamprey (Lampetra appendix). J. Fish. Res. Board Can. 30:7-15.

Morman, R. H. 1979. Distribution and ecology of lampreys in the Lower Peninsula of Michigan, 1957-75. Tech. Rep. Great Lakes Fish. Comm. 33:59p.

Morman, R. H. 1987. Relationship of density to growth and metamorphosis of caged larval sea lampreys, Petromyzon marinus Linnaeus, in Michigan streams. J. Fish. Biol. 30:173-181.

Nalepa, T. F. and Quigley, M. A. 1987. Distribution of photosynthetic pigments in nearshore sediments of Lake Michigan. J. Great Lakes Res. 13:37-42.

Nusch, E. A. 1980. Comparison of different methods for chlorophyll and phaeopigment determination. Arch. Hydrobiol. Beih. Ergebn. Limnol. 14:14-36.

Potter, I. C. 1980. Ecology of larval and metamorphosing lampreys. Can. J. Fish. Aquat. Sci. 37:1641-1657.

Potter, I. C. and F. W. H. Beamish. 1974. Lethal temperatures in ammocetes of four species of lampreys. Acta Zool. 56:85-91.

Potter, I. C., Hill, B. J., and Gentleman, S. 1970. Survival and behavior of ammocetes at low oxygen tensions. J. Exp. Biol. 53:59-73.

Reynolds, W. W. and Casterlin, M. E. 1978. Behavioral thermoregulation of ammocete larvae of the sea lamprey (Petromyzon marinus) in an electronic shuttlebox. Hydrobiologia 61:145-147.

Ricker, W. E. 1978. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Bd. Can. 191:382p.

Rutledge, P. A. and J. W. Fleeger. 1988. Laboratory studies on core sampling with application to subtidal meio-benthos collection. Limnol. Oceanogr. 33:274-280.

Sokal, R. R. and F. J. Rohlf. 1981. Biometry. W. H. Freeman and Co., New York. 859p.

Stevenson, R. J. and Stoermer, E. F. 1981. Quantitative differences between benthic algal communities along a depth gradient in Lake Michigan. J. Phycol. 17:29-36.

Strickland, J. D. H. and T. R. Parsons. 1968. A practical handbook of sea water analysis. Fish. Res. Bd. Can. Bull. 167:1-311.

Taylor, D. W. 1948. Fundamentals of soil mechanics. John Wiley and Sons, Inc., New York, 700p.

Thomas, M. L. H. 1961. The distribution of sea lamprey ammocetes in the lake of eight rivers draining into the Canadian waters of Lake Superior. Fish. Res. Bd. Can. Manuscript Rep. Ser. 710:30p.

Thomas, M. L. H. 1963. Studies on the biology of ammocetes in streams. Fish. Res. Bd. Can. Rep. 742:143p.

Tibbles, J. J. and Dodge, D. P. 1963. Estimates of population density of sea lamprey ammocetes in Batchawana Bay, Lake Superior, 1963. Ann. Rep. Great Lakes Fish. Comm. 1963- 1964, Appendix 9.

Torblaa, R. L. and Westman, R. W. 1980. Ecological impacts of lampricide treatments on sea lamprey (Petromyzon marinus) ammocetes and metamorphosed individuals. Can. J. Fish. Aquat. Sci. 37:1835-1850.

Wagner, W. C. and Stauffer, T. M. 1962a. Sea lamprey larvae in lentic environments. Trans. Amer. Fish. Soc. 91:384-387.

Wagner, W. C. and Stauffer, T. M. 1962b. The population of sea lamprey larvae in East Bay, Alger County, Michigan. Pap. Mich. Acad. Sci., Arts and Lett. 47:235-245.

Webb, J. E. 1975. The distribution of amphioxus. Symp. zool. Soc. Lond. No. 36:179-212.

Webb. J. E. and Theodor, J. 1972. Wave-induced circulation in submerged sands. J. Mar. Biol. Ass. U.K. 52:903-914.

Weise, J. G. and P. C. Rugen. 1987. Evaluation of methods and population studies of larval phase sea lamprey in: Johnson, B. G. H. (ed.) 1987. Evaluation of sea lamprey populations in the Great Lakes: Background papers and proceedings of the August 1985 Workshop. Great Lakes Fish. Comm. Spec. Publ. 87-2.

Wentworth, C. K. 1922. A scale of grade and class terms for clastic sediments. J. Geol. 30:377-392.

Wetzel, R. G. 1975. Limnology. W. B. Saunders. Philadelphia, Pa., 743p.

Wiens, J. A. 1976. Population responses to patchy environments. Ann. Rev. Ecol. Syst. 7:81-120.