GREAT LAKES FISHERY COMMISSION
Research Completion Report *

QUANTIFIED LABORATORY ASSESSMENT OF LARVAL LAMPREY SUBSTRATE HABITAT SELECTION

by

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INTRODUCTION

The successful control of sea lamprey 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 control effort (Workshop for the Evaluation of Sea Lamprey Populations, WESLP; Johnson, 1987).

To meet this challenge, the determinants of larval lamprey habitat selection must be better defined to provide a framework for quantitative assessment of distribution and abundance. As populations decline, the effort expended in determining the distribution and abundance of shortly metamorphosing individuals increases. Further knowledge of habitat selection cues

may permit control agents to reduce survey efforts while maintaining or increasing the quality of information obtained. Such information can be used to quantitatively define habitat zones for spatially stratified population estimates. 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.

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). The physical substrate characteristics that promote burrowing have

never been identified and the potential importance of food particle distribution along with the possible effects of intraspecific and/or interspecific interference competition on ammocoete habitat selection have not been examined experimentally. Each of these aspects of life history has the potential to influence the local distribution and abundance of ammocoete populations in predictable ways but the relative importance of each remains unknown.

Study Design and Objectives

This study of ammocoete habitat selection determinants was undertaken to extend and quantify understanding of burrowing substrates with respect to mean grain size, porosity, permeability, and food particle distribution. Substrate porosity is directly proportional to the rate of gaseous diffusion while permeability is representative of susceptability of a substrate to direct water exchange. As such, they represent potential substrate properties that may act as selection cues. In addition, the relative effect of intra- and interspecific interference competition upon burrowing substrate selection was also explored. Due in part to previous research (eg. Malmqvist, 1980; Thomas, 1963; Reynolds and Casterlin, 1978; Potter et al., 1970), the effects of current velocity, temperature, and

oxygen tension were not included in this study. With respect to WESLP objectives, specific objectives of this work include:

1. Provision of a quantitative rationale of habitat stratification for population estimates.
2. Preliminary analysis of the importance of intra- and interspecific competition to habitat selection.
3. Preliminary analysis of the importance of food particle distribution and abundance to habitat selection.

METHODS

Test Species Collection and Holding Facilities

Burrowing substrate selection tests were conducted on larval sea lamprey (Petromyzon marinus) and larval North American brook lamprey (Lampetra appendix). 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 electro-samplers, 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 water which was aerated and recirculated through beds of dolomite and activated charcoal 7.7 times per hour. 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. 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 1 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 particle size distribution of substrates encountered in the field (Lee, 1989), the mix ratios for each are listed in table 2.

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 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 1 and 2.

In general, porosity was higher for ungraded laboratory substrates than for graded substrates (figure 1). Porosity of ungraded substrate groups was highest at the extremes of the mean grain diameter distribution

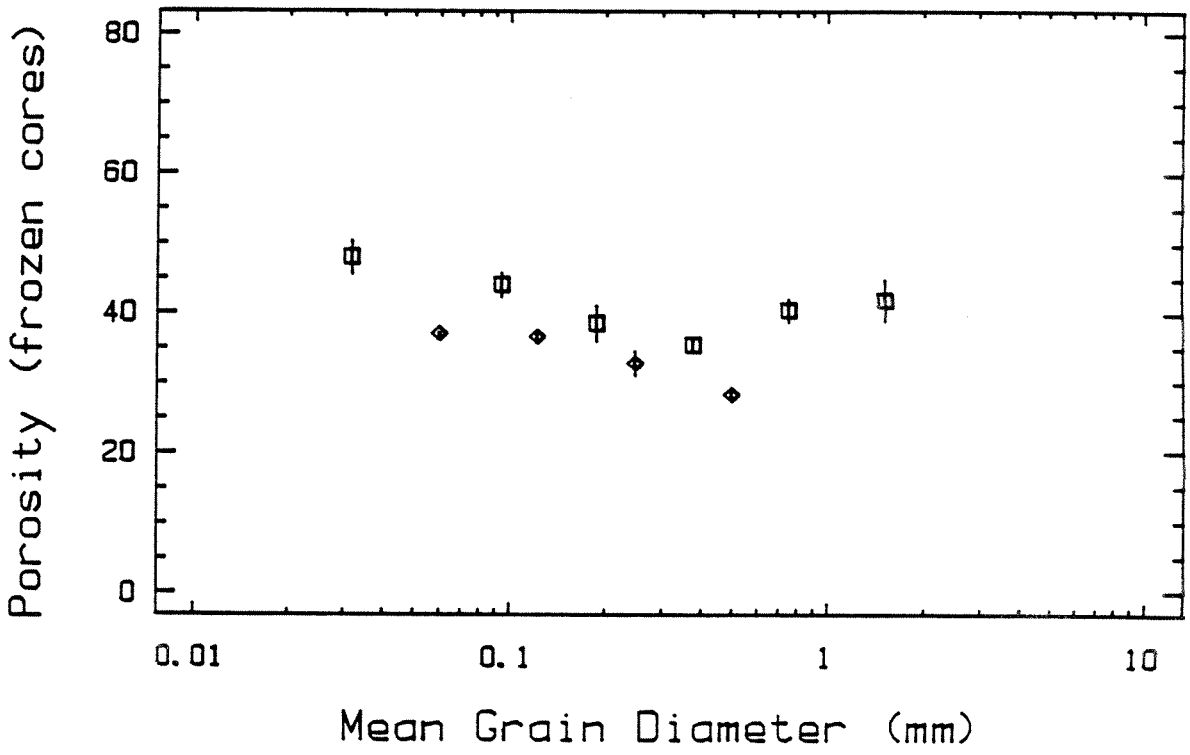
Table 1. Wentworth classification of laboratory substrates with mean (± se) values for porosity (P) and permeability (K).

"Common" Name	Grade Limits (mm)	Mean Diam. (mm)	P (% voids)	K (cm 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)

Table 2. Percentage composition of mixed sediments with weighted mean grain diameter along with mean (± se) values for porosity (P) and permeability (K).

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

Fig. 1: 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.


Porosity (frozen cores)
80
60
40
20
0
0.01
0.1
1
10
Mean Grain Diameter (mm)

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.

Within ungraded and graded laboratory substrates, permeability was multiplicatively related to group mean grain diameters (figure 2). 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 3). Because the test arenas only permitted testing of four substrates at a time,

Fig. 2: 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.

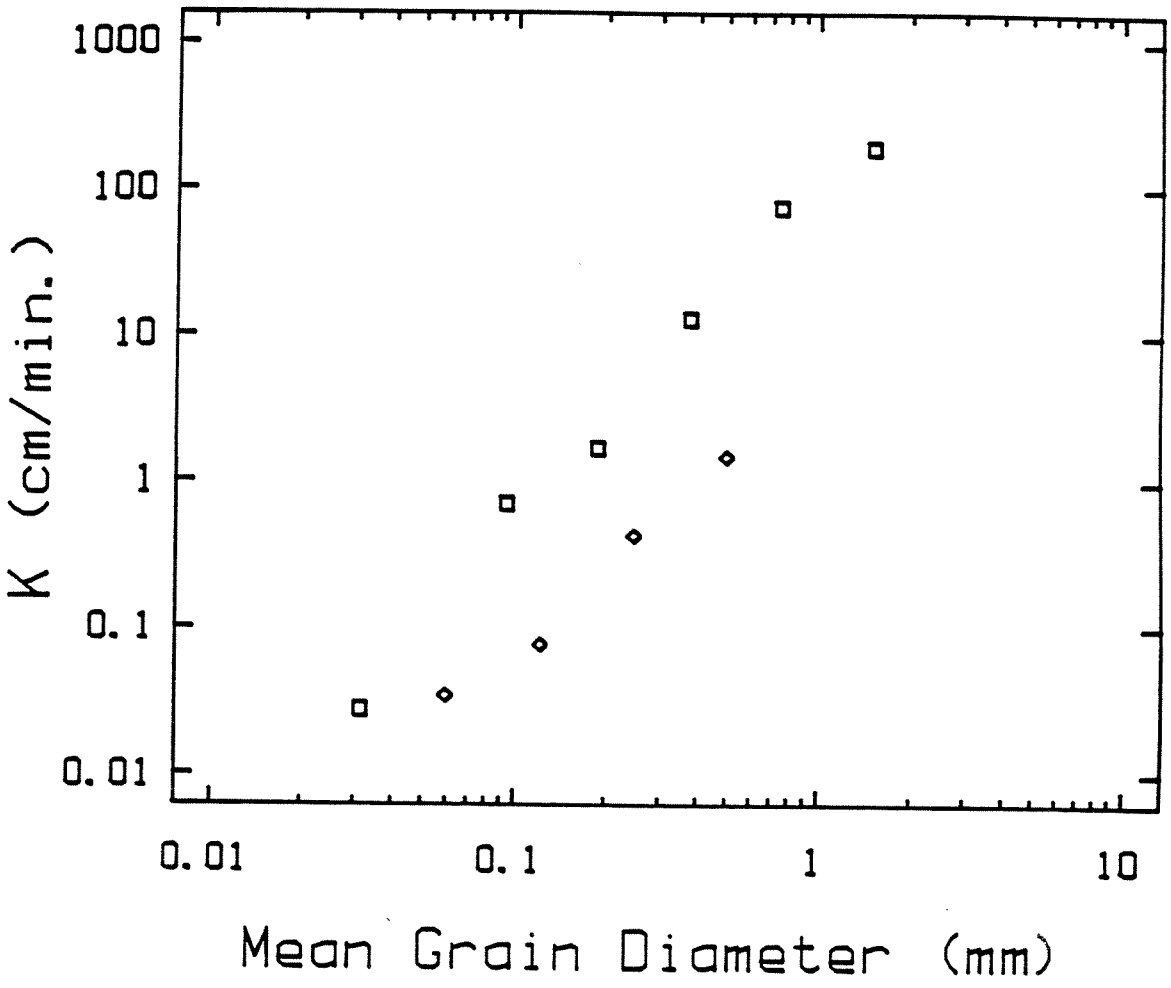
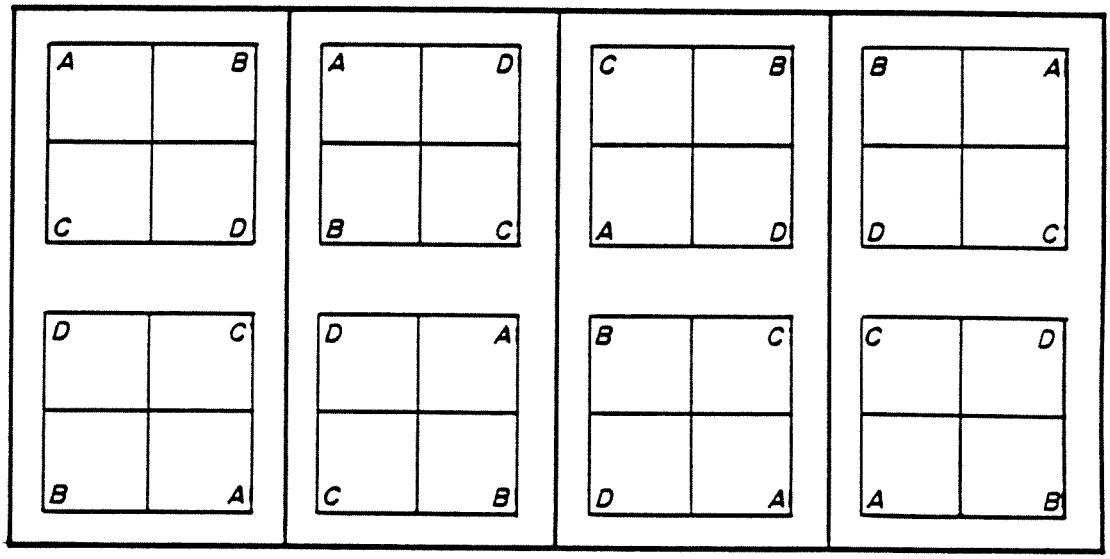
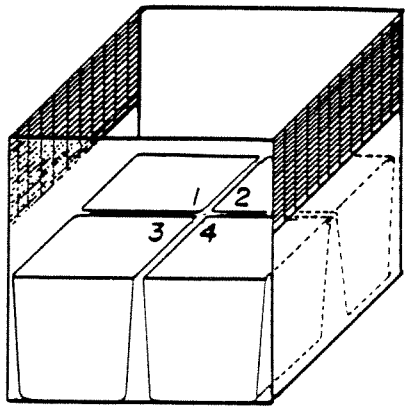

1000
100
10
1
0.1
0.01
K (cm/min.)
0.01
0.1
1
10
Mean Grain Diameter (mm)

Fig. 3: 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.


A B C D
A D B C
C B A D
B A D C
D C B A
D A C B
B C D A
C D A B


1
2
3
4

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 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. All experimental blocks are listed in

tables 3a-c by species, size class, density, and release pattern.

For a given experiment, ammocetes were released in the dark and allowed to burrow at leisure. 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.

Table 3. 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

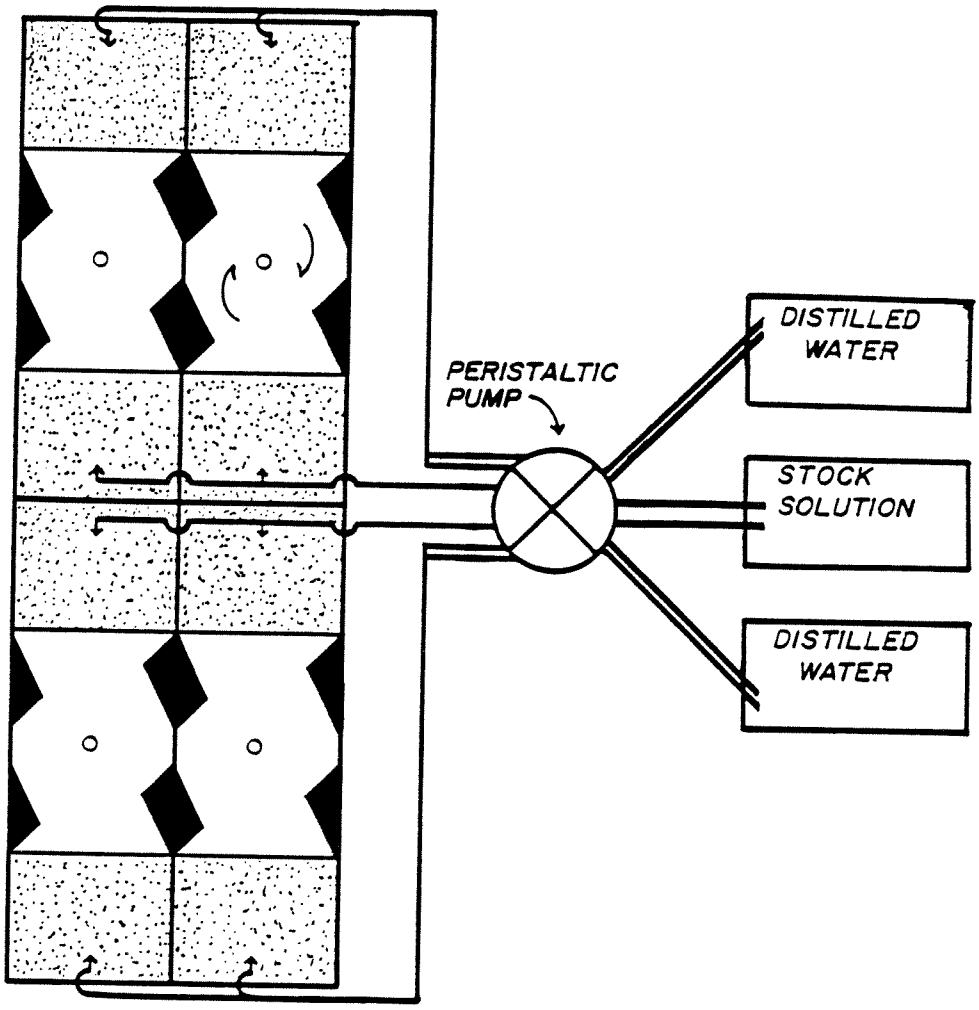
B.	Small *P. marinus*		Large *P. marinus*	
Density	Unstaggered Release	Staggered Release	Unstaggered Release	Staggered Release
4	X		X	
8	X	X	X	X
12	-	-	-	X

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

For 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. As shown in figure 4, the four individual two-place test chambers permitted the ammocetes a choice of burrowing where the water column contained an abundance of food particles vs. an area of zero food particle concentration. Using a peristaltic pump, solutions of distilled and yeast perfused water were pumped into opposing sides of a given test chamber at a rate of 7.8 ml per minute, draining towards a common center drain. Concentrations of yeast particles in the food chambers at the start of the experiments were $\approx$ 0.06 g/l.

Fig. 4: 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.


PERISTALTIC
PUMP
DISTILLED
WATER
STOCK
SOLUTION
DISTILLED
WATER

Ammocetes were sedated 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. Additional tests were run with an algae perfusion (Ankiestrodesmus falcatus.), a green alga listed by Hardisty and Potter (1977) as common in the gut of larval lamprey. The concentration of algal cells at the start of each experiment in terms of chlorophyll a ranged from 35 to 43 ug/l. The experimental blocking structure for all food/habitat selection experiments is listed in table 4 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 4. 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).

RESULTS

Summarized results of substrate preference and food related habitat selection experiments are presented below with basic frequency analyses and abstracted ANOVA results. The raw data are listed by experimental series in Appendix 3. 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 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 5 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 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

Table 5. Pooled percentages of ammocoetes occupying different burrowing substrates. Experimental series are identified by ammocoete size, species, density 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 5 continued on next page

Table 5 cont.

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

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 prostate 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 5, 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 6). 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 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.

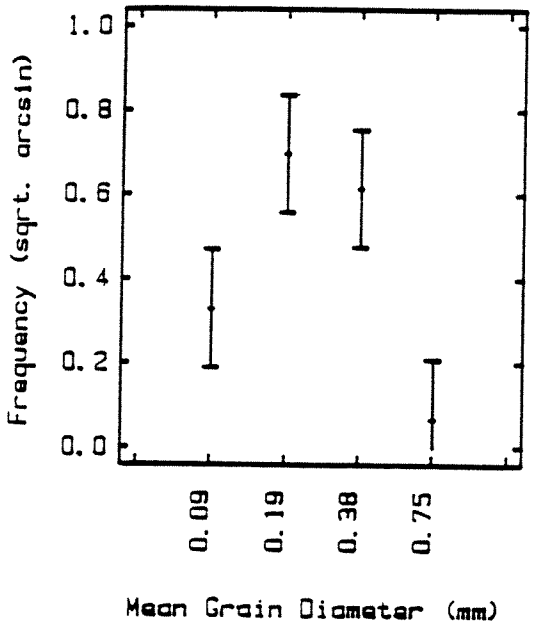
Figure 5 displays the resultant 95 percent confidence intervals for transformed frequencies of selection with respect to substrate type. Within a species there appears to be a shift in preference from fine to medium sands between small and large ammocetes (figure 5, a to c and b to d). Within the small size

Table 6. 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 / release pattern). [ns = not significant; *, **, ***, and **** represent significance at the 0.05, 0.01, 0.001, and 0.0001 levels respectively.]

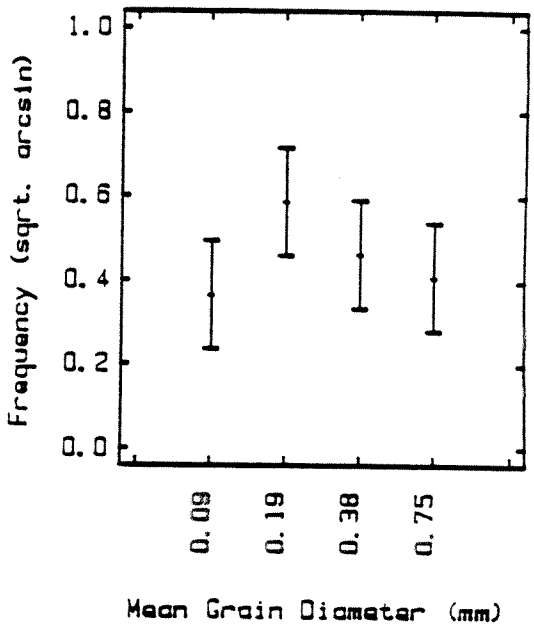
Experimental Series	Significance Level					
	Substrate only	Position only	Series only	Substrate x Position	Substrate x Series	Position x Series
Sm. L. appendix, pooling of D4ns with D8ns	****	ns	ns	ns	ns	ns
Lg. L. appendix, pooling of D4ns, D8ns, D12s, D4:4ns, and D8:8ns	****	ns	ns	ns	ns	ns
Sm. P. marinus,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

Fig. 5: 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.

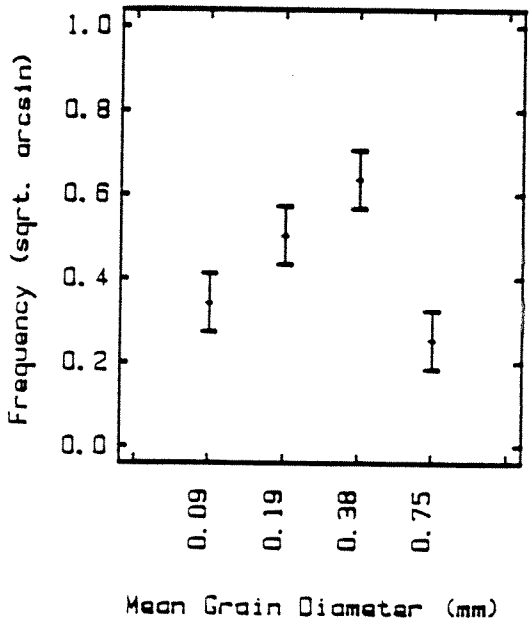
a) Small L. appendix



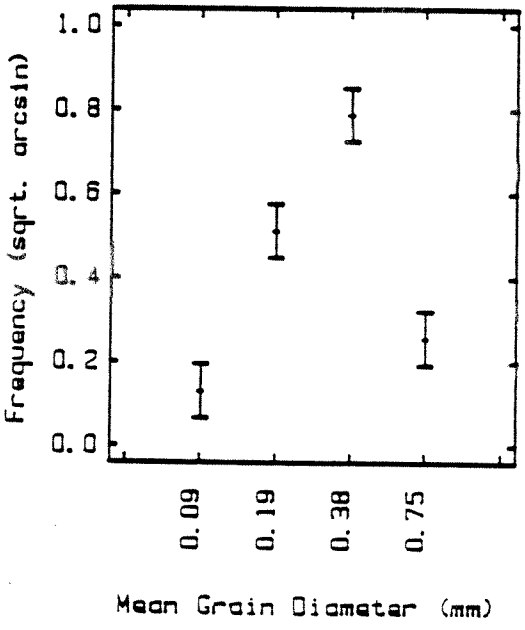
b) Small P. marinus



c) Large L. appendix



d) Large P. marinus



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

Table 8 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.

Table 7. 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

Table 8. 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

To specifically test for the effects of intraspecific competition on burrowing substrate selection, an ANOVA was run on all staggered release experiments (table 9). 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 effect 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 10 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

Table 9. 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 10. 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

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) was related to permeability (K) by the following model:

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

Ninety-five percent confidence intervals of mean branchial basket depth are plotted against permeability in figure 6 along with the regression line.

Frequency Analysis of Food/Habitat Preference Tests

Table 11 provides a summary of all food/habitat selection tests with reference to selection of habitats with food vs. 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

Fig. 6: 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.

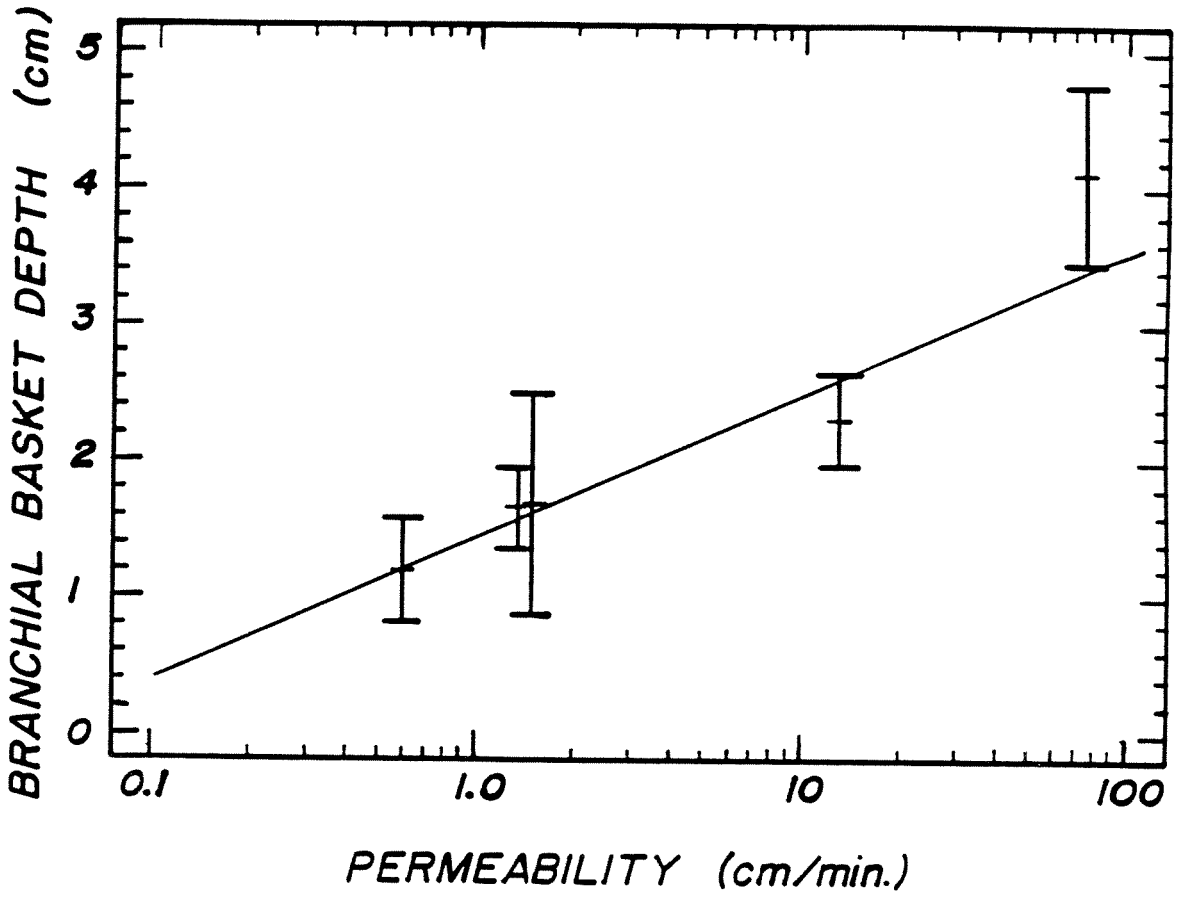

BRANCHIAL BASKET DEPTH (cm)
0
1
2
3
4
5
0.1
1.0
10
100
PERMEABILITY (cm/min.)

Table 11. Pooled percentages of ammocoetes occupying different burrowing substrates based on presence or absence of food. Experimental series are identified by ammocoete size, species, density 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

significantly positive effect on habitat selection while the presence of the green alga, Ankiestrodesmus falcatus, did not. The presence vs. 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.

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

Table 12 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 vs. no food was nonsignificant. With respect to food perfused vs. 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.

DISCUSSION

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

Table 12. 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 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.]

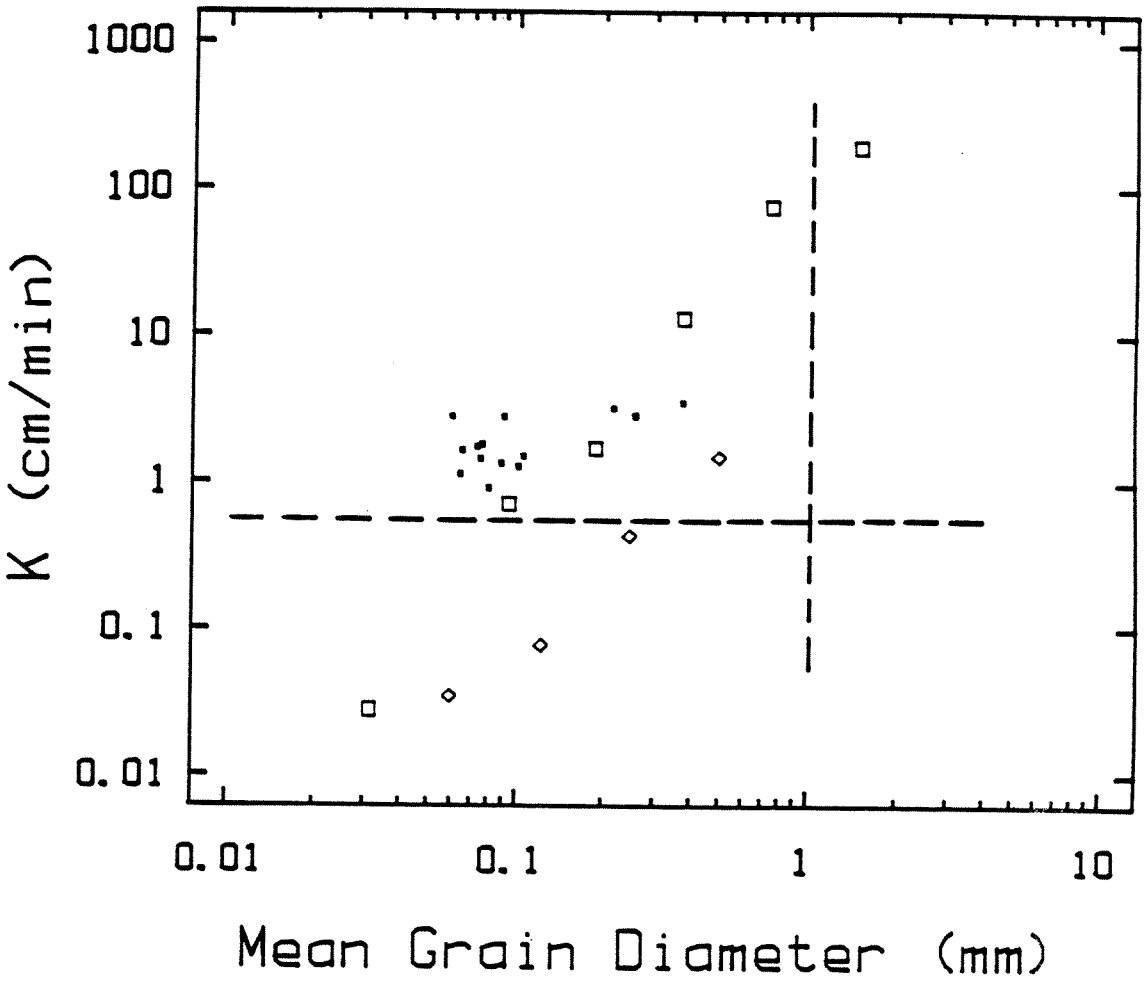
Experimental Series	Significance Level								
	Trtmnt only	Pos. only	Spp. only	Food Type	Trtmnt x Pos.	Trtmnt x Spp.	Trtmnt x Food	Pos. x Spp.	Pos. x Food
Yeast perfused vs. unperfused substrate selection tests	ns	**	ns	--	ns	ns	--	ns	--
Food perfused vs. unperfused water column selection tests	ns	ns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

tables 5 and 11. 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 vs. 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 7). 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 7, 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

Fig. 7: 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 occupied by lentic ammocetes (Lee, 1989).


1000
100
10
1
0.1
0.01
K (cm/min)
0.01
0.1
1
10
Mean Grain Diameter (mm)

occupied by lentic ammocetes (Lee, 1989). In support of this conclusion, Mallatt (1982) noted that larval P. marinus readily accepted diatomaceous earth with a mean grain diameter less than 0.015 mm.

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 select exhibited by lancelets, Branchiostoma lanc um. Webb and Theodor (1972) noted the gro f organic films on substrate partic could inc ease 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 sub ates 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. 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 Ankiestrodesmus 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 12).

Conclusions

Acting as delimiters of substrate "suitability", mean grain diameter and permeability are both determinants of larval lamprey habitat selection. While mean grain diameter and permeability set limits to substrate suitability, within these limits, the individual variation in substrate selection is high. There is no evidence for direct intra- or interspecific

competition for space in this study. Also, there is no evidence that food particle distribution or abundance exerts any influence on burrowing substrate selection. However, it should also be understood that potential competition for space and distribution of food particles may affect substrate habitat selection over longer time scales. Potential effects over extended time scales were not pursued in this study. An understanding of the bioenergetics of the ammocete stage is required to posit a reasonable framework for analysis of ammocete habitat selection over longer time scales.

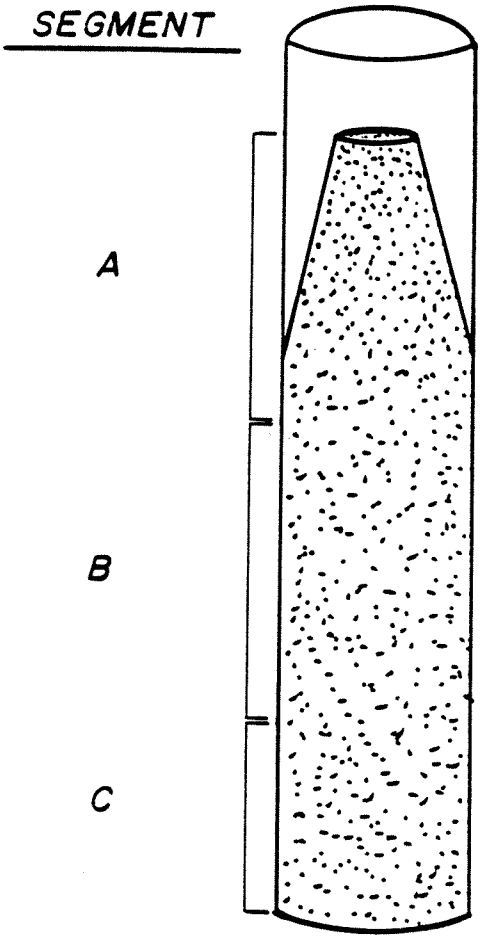
APPENDIX 1

Laboratory Measurement of Porosity

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. 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. 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 weight for the core when subtracted from the total wet

Fig. A1-1: Schematic profile of frozen sediment cores.



PROFILE OF FROZEN SEDIMENT CORES

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 vs. 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:

$$P_f = 14.59 + 1.739P_{uf}$$

where P_f = porosity of frozen cores

P_{uf} = porosity of unfrozen cores

with an R^2 of 76.9 percent. The ANOVA for the regression model is listed in table A1-1.

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

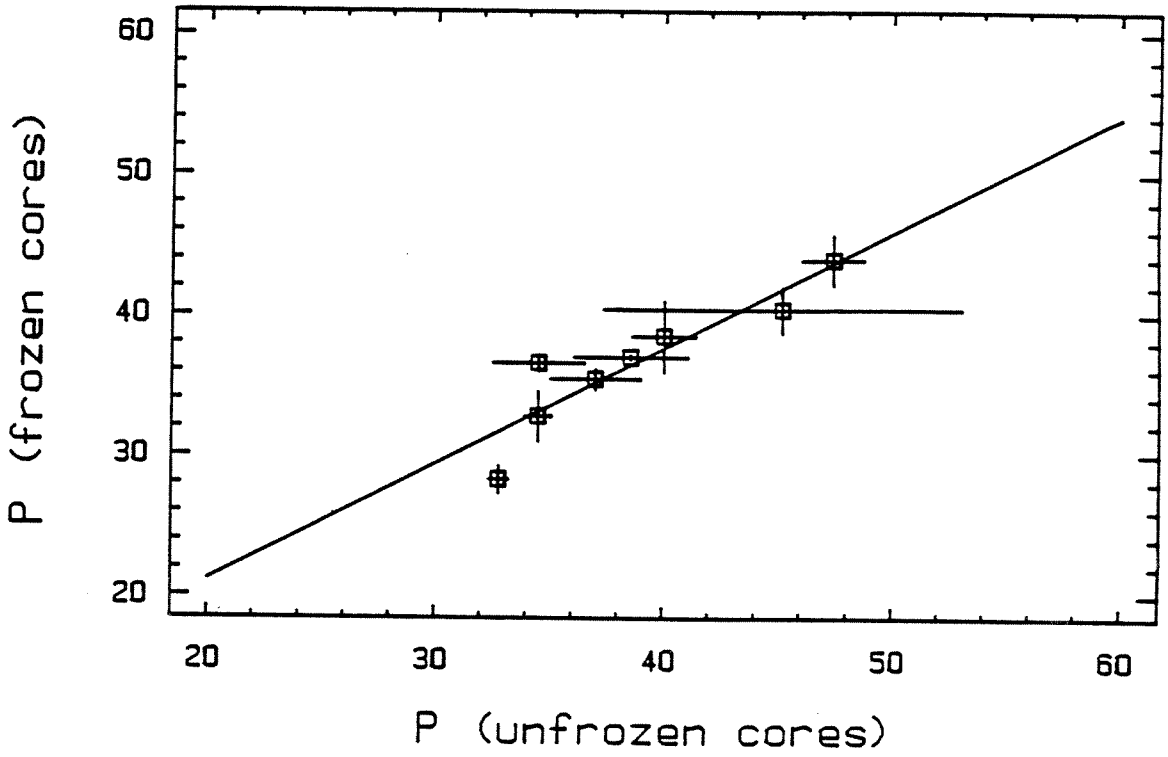

60
50
40
30
20
P (frozen cores)
20
30
40
50
60
P (unfrozen cores)

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	204.013	1	204.013	19.947	0.0043
Error	61.367	6	10.228		
Total	265.380	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).

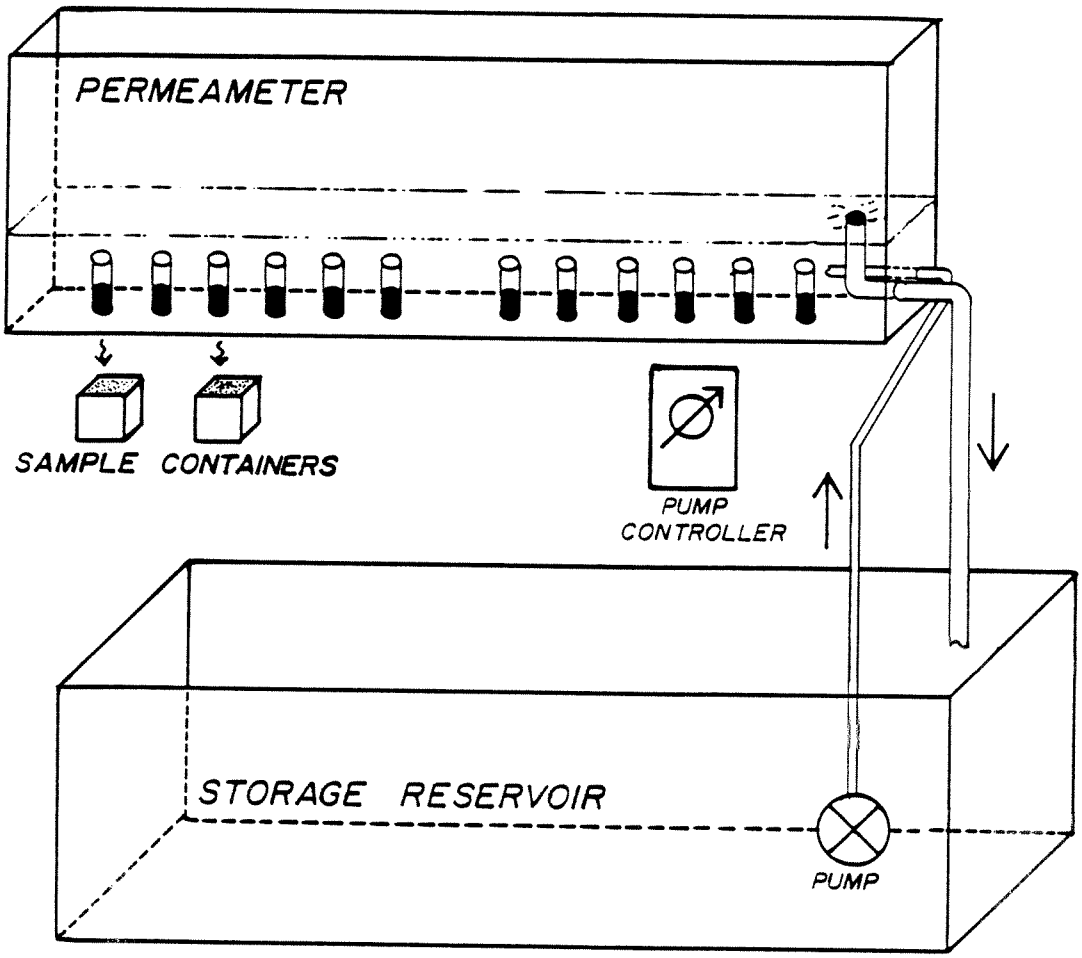
h = pressure head (cm).

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 ultrasonic sensor. The core tube, still containing the

Fig. 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.


PERMEAMETER
SAMPLE CONTAINERS
PUMP CONTROLLER
STORAGE RESERVOIR
PUMP

frozen sample, was then cut with a band saw using a 24 tpi 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 vs. unfrozen laboratory substrates was conducted (Figure A2-1). 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.

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

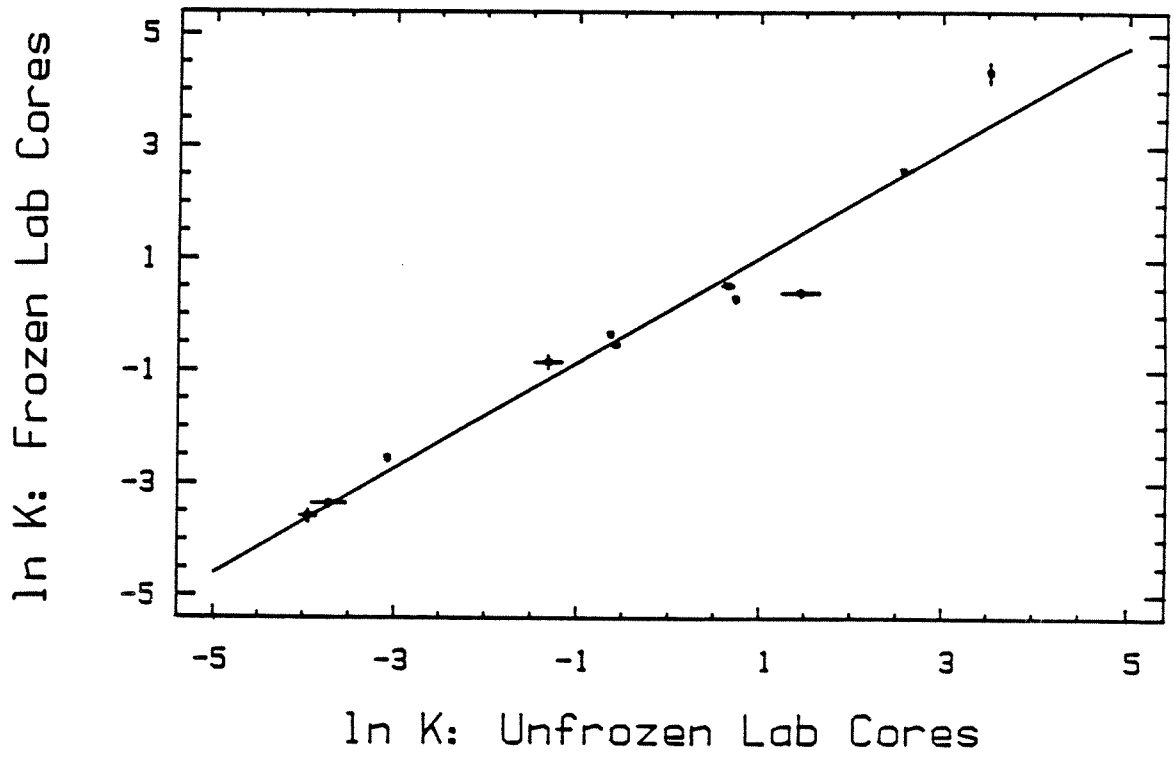

ln K: Frozen Lab Cores
5
3
1
-1
-3
-5
-5
-3
-1
1
3
5
ln K: Unfrozen Lab Cores

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. Raw larval lamprey habitat selection test data

The following data sets are organized by species, size, final density of individuals per test unit, and whether or not subgroups of individuals were release at the same time or staggered. As described in the text, substrate selection tests were conducted in twelve aquaria chilled to a temperature of 10.5 °C, with two four-place test units per aquarium. Four one liter freezette containers, each filled with a separate sediment type, were set into a given test unit in a square pattern. The position numbers for sediment containers are numbered from one to four, running left to right, starting in the upper left corner and ending in the lower right corner (see text figure 2). Sediment types in the following data sets are identified by mean grain diameter or mix label. Additional characteristics of each sediment type are listed in text tables 1 and 2. Food related habitat selection tests were run in two-place test units (see text figure 3) and substrate type was constant (0.3750 mm mean grain diameter) for all food related selection tests.

Ammocoetes were released into the test units in the dark and allowed to select a burrowing substrate at leisure. Duration of the tests ranged from four to six days. In the case of staggered releases, subgroups were released in the dark at 48 hour intervals. In all cases, ammocoetes would either burrow within two hours of release or remain unburrowed during the duration of the test. Only replicates where a minimum of 75 percent of all ammocoetes burrowed were included in the final statistical analysis (except in the case of small Petromyzon marinus with eight individuals per test unit/staggered release and small Lampetra appendix with four individuals per test unit/unstaggered release, where all replicates were included). Unused replicates are flagged with an asterisk next to the replicate number.

Test of <0.063 mm preferences, large Lampetra appendix, final density of eight per test unit, unstaggered release.

Replicate	Sediment Position	Sediment Type	Tot.
1	1	0.0315	0
	2	0.0938	4
	3	0.1875	1
	4	0.3750	1
2	4	0.0315	0
	3	0.0938	2
	2	0.1875	2
	1	0.3750	3
3	3	0.0315	0
	4	0.0938	2
	1	0.1875	3
	2	0.3750	3
4	2	0.0315	0
	1	0.0938	2
	4	0.1875	3
	3	0.3750	3
Pooled Distribution:		0.0315	0
		0.0938	10
		0.1875	9
		0.3750	10

Test of <0.063 mm preferences, large Petromyzon marinus, density of eight per test unit, unstaggered release.

Replicate	Sediment Position	Sediment Type	Tot.
1	1	0.0315	0
	2	0.0938	3
	3	0.1875	2
	4	0.3750	3
2	4	0.0315	0
	3	0.0938	2
	2	0.1875	3
	1	0.3750	3
3	2	0.0315	0
	4	0.0938	1
	1	0.1875	4
	3	0.3750	3
4	3	0.0315	0
	1	0.0938	0
	4	0.1875	5
	2	0.3750	3
Pooled Distribution:		0.0315	0
		0.0938	6
		0.1875	14
		0.3750	12

Test of 1.00 mm preferences, large Lampetra appendix, density of eight per test unit, unstaggered release.

Replicate	Sediment Position	Sediment Type	Tot.
1	2	0.1875	5
	1	0.3750	2
	4	0.7500	1
	3	1.5000	0
2	3	0.1875	4
	4	0.3750	2
	1	0.7500	2
	2	1.5000	0
3	1	0.1875	4
	4	0.3750	4
	3	0.7500	0
	2	1.5000	0
4	4	0.1875	4
	1	0.3750	3
	2	0.7500	1
	3	1.5000	0
Pooled Distribution:		0.1875	17
		0.3750	11
		0.7500	4
		1.5000	0

Test of 1.00 mm preferences, large Petromyzon marinus, density of eight per test unit, unstaggered release.

Replicate	Sediment Position	Sediment Type	Tot.
1	1	0.1875	0
	2	0.3750	5
	3	0.7500	1
	4	1.5000	0
2	4	0.1875	3
	3	0.3750	5
	2	0.7500	0
	1	1.5000	0
3	4	0.1875	4
	2	0.3750	2
	3	0.7500	2
	1	1.5000	0
4	1	0.1875	2
	3	0.3750	5
	2	0.7500	1
	4	1.5000	0
Pooled Distribution:		0.1875	9
		0.3750	17
		0.7500	4
		1.5000	0

Test of graded sediment mix preferences, large Lampetra appendix, final density of eight per test unit, unstaggered release.

Replicate	Position	Sediment mix	Tot.
1	1	A	0
	2	B	0
	3	C	0
	4	D	0
2	4	A	0
	3	B	0
	2	C	0
	1	D	0
3	1	A	0
	4	B	0
	2	C	0
	3	D	0

Large Petromyzon marinus, test of graded sediment preferences, final density of eight per test unit, unstaggered release.

Replicate	Position	Sediment mix	Tot.
1	4	A	0
	1	B	0
	3	C	0
	2	D	0
2	3	A	0
	2	B	0
	1	C	0
	4	D	0
3	2	A	0
	3	B	0
	4	C	0
	1	D	0

Pooled Distribution:		A	0
		B	0
		C	0
		D	0

Test of mix D preferences relative to 0.063 through 0.500 ungraded sediments, small Lampetra appendix, final density of eight per test unit, unstaggered release.

Replicate	Position	Sediment type	Tot.
1	1	D	0
	2	0.0938	3
	3	0.1875	1
	4	0.3750	4
2	4	D	1
	3	0.0938	3
	2	0.1875	2
	1	0.3750	2
3	4	D	0
	1	0.0938	2
	3	0.1875	4
	2	0.3750	2
4	1	D	0
	4	0.0938	3
	2	0.1875	3
	3	0.3750	2

Pooled Distribution:		
	D	1
	0.0938	11
	0.1875	10
	0.3750	10

Test of mix D preferences relative to 0.063 through 0.500 ungraded sediments, large Lampetra appendix, final density of eight per test unit, unstaggered release.

Replicate	Position	Sediment type	Tot.
1	1	D	3
	2	0.0938	2
	3	0.1875	1
	4	0.3750	2
2	4	D	2
	3	0.0938	2
	2	0.1875	1
	1	0.3750	3
3	4	D	0
	1	0.0938	3
	3	0.1875	5
	2	0.3750	0
4	1	D	0
	4	0.0938	1
	2	0.1875	4
	3	0.3750	3
Pooled Distribution:		D	5
		0.0938	8
		0.1875	11
		0.3750	8

Test of mix D preferences relative to 0.063 through 0.500 ungraded sediments, small Petromyzon marinus, final density of eight per test unit, unstaggered release.

Replicate	Position	Sediment type	Tot.
1	1	D	0
	2	0.0938	1
	3	0.1875	3
	4	0.3750	4
2	4	D	1
	3	0.0938	2
	2	0.1875	3
	1	0.3750	2
3	4	D	1
	3	0.0938	2
	1	0.1875	0
	2	0.3750	4
4	1	D	0
	2	0.0938	3
	4	0.1875	0
	3	0.3750	4

Pooled Distribution:		
	D	2
	0.0938	8
	0.1875	6
	0.3750	14

Small Petromyzon marinus, final density of four per test unit, unstaggered release.

Replicate	Sediment position	Sediment type	Tot.
1	3	0.0938	1
	2	0.1875	1
	1	0.3750	1
	4	0.7500	1
2	2	0.0938	1
	3	0.1875	0
	4	0.3750	2
	1	0.7500	1
3	2	0.0938	1
	1	0.1875	1
	4	0.3750	2
	3	0.7500	0
4	3	0.0938	0
	4	0.1875	1
	1	0.3750	2
	2	0.7500	1
5	1	0.0938	0
	2	0.1875	1
	3	0.3750	1
	4	0.7500	2
6	4	0.0938	1
	3	0.1875	0
	2	0.3750	1
	1	0.7500	2
7	1	0.0938	0
	4	0.1875	2
	2	0.3750	1
	3	0.7500	1
8	4	0.0938	1
	1	0.1875	1
	3	0.3750	0
	2	0.7500	2
Pooled Distribution:		0.0938	5
		0.1875	7
		0.3750	10
		0.7500	10

Small Petromyzon marinus, final density of eight per test unit unstaggered release.

Replicate	Sediment position	Sediment type	Tot.
1	3	0.0938	0
	2	0.1875	2
	1	0.3750	3
	4	0.7500	3
2	2	0.0938	3
	3	0.1875	3
	4	0.3750	0
	1	0.7500	2
3	2	0.0938	2
	1	0.1875	3
	4	0.3750	2
	3	0.7500	1
4	3	0.0938	2
	4	0.1875	2
	1	0.3750	1
	2	0.7500	2
5	1	0.0938	1
	2	0.1875	5
	3	0.3750	2
	4	0.7500	0
6	4	0.0938	1
	3	0.1875	4
	2	0.3750	1
	1	0.7500	2
7	1	0.0938	1
	4	0.1875	5
	2	0.3750	1
	3	0.7500	0
8	4	0.0938	2
	1	0.1875	2
	3	0.3750	2
	2	0.7500	2
Pooled Distribution:		0.0938	12
		0.1875	26
		0.3750	12
		0.7500	12

Large Petromyzon marinus, final density of four per test unit, unstaggered release.

Replicate	Sediment position	Sediment type	Tot.
1	1	0.0938	0
	2	0.1875	4
	3	0.3750	0
	4	0.7500	0
2	4	0.0938	0
	3	0.1875	1
	2	0.3750	3
	1	0.7500	0
3	1	0.0938	0
	4	0.1875	3
	2	0.3750	1
	3	0.7500	0
4	4	0.0938	0
	1	0.1875	1
	3	0.3750	3
	2	0.7500	0
5	3	0.0938	0
	2	0.1875	1
	1	0.3750	1
	4	0.7500	2
6	2	0.0938	0
	3	0.1875	1
	4	0.3750	2
	1	0.7500	1
7	2	0.0938	2
	1	0.1875	0
	4	0.3750	2
	3	0.7500	0
8	3	0.0938	1
	4	0.1875	0
	1	0.3750	3
	2	0.7500	0
Pooled Distribution:		0.0938	3
		0.1875	11
		0.3750	15
		0.7500	3

Large Petromyzon marinus, final density of eight per test unit, unstaggered release.

Replicate	Sediment position	Sediment type	Tot.
1	1	0.0938	0
	2	0.1875	5
	3	0.3750	3
	4	0.7500	0
2	4	0.0938	0
	3	0.1875	2
	2	0.3750	3
	1	0.7500	3
3	1	0.0938	0
	4	0.1875	3
	2	0.3750	4
	3	0.7500	1
4	4	0.0938	0
	1	0.1875	3
	3	0.3750	4
	2	0.7500	1
5	3	0.0938	0
	2	0.1875	3
	1	0.3750	3
	4	0.7500	2
6	2	0.0938	1
	3	0.1875	3
	4	0.3750	3
	1	0.7500	1
7	2	0.0938	2
	1	0.1875	2
	4	0.3750	2
	3	0.7500	2
8	3	0.0938	3
	4	0.1875	3
	1	0.3750	2
	2	0.7500	0
9	1	0.0938	0
	2	0.1875	2
	3	0.3750	4
	4	0.7500	2

Lg. Petromyzon marinus, D8, unstaggered release continued:

Replicate	Sediment position	Sediment type	Tot.
10	4	0.0938	0
	3	0.1875	3
	2	0.3750	3
	1	0.7500	2
11*	2	0.0938	0
	3	0.1875	2
	1	0.3750	4
	4	0.7500	0
12	3	0.0938	1
	2	0.1875	2
	4	0.3750	4
	1	0.7500	1
13*	1	0.0938	0
	4	0.1875	2
	3	0.3750	4
	2	0.7500	0
14	4	0.0938	0
	1	0.1875	3
	2	0.3750	1
	3	0.7500	5
15	2	0.0938	0
	1	0.1875	0
	4	0.3750	4
	3	0.7500	3
16	3	0.0938	0
	4	0.1875	2
	1	0.3750	3
	2	0.7500	2
Pooled Distribution: (Flagged replicates excluded)		0.0938	7
		0.1875	36
		0.3750	43
		0.7500	25

Small Petromyzon marinus, final density of eight per test unit, staggered release of two groups of four.

Replicate	Sediment Position	Sediment Type	Frequency Gp. 1	Gp. 2	Gp. 3	Tot.
1	3	0.0938	1	1	-	2
	2	0.1875	3	2	-	5
	1	0.3750	1	0	-	1
	4	0.7500	0	0	-	0
2	2	0.0938	0	0	-	0
	3	0.1875	1	1	-	2
	4	0.3750	1	0	-	1
	1	0.7500	2	3	-	5
3	2	0.0938	-	2	-	2
	1	0.1875	-	0	-	0
	4	0.3750	-	2	-	2
	3	0.7500	-	0	-	0
4	3	0.0938	0	1	-	1
	4	0.1875	1	0	-	1
	1	0.3750	0	3	-	3
	2	0.7500	0	0	-	0
Pooled Distribution:		0.0938	1	4	-	5
		0.1875	5	3	-	8
		0.3750	2	5	-	7
		0.7500	2	3	-	5

Large Petromyzon marinus, final density of eight per test unit, staggered release of two groups of four.

Replicate	Sediment Position	Sediment Type	Frequency Gp. 1	Gp. 2	Gp. 3	Tot.
1	1	0.0938	0	0	-	0
	2	0.1875	1	2	-	3
	3	0.3750	0	1	-	1
	4	0.7500	3	1	-	4
2	4	0.0938	0	0	-	0
	3	0.1875	2	1	-	3
	2	0.3750	2	3	-	5
	1	0.7500	0	0	-	0
3	1	0.0938	0	0	-	0
	4	0.1875	3	2	-	5
	2	0.3750	1	1	-	2
	3	0.7500	0	1	-	1
4	4	0.0938	1	1	-	2
	1	0.1875	1	1	-	2
	3	0.3750	2	2	-	4
	2	0.7500	0	0	-	0
5	3	0.0938	0	0	-	0
	2	0.1875	1	1	-	2
	1	0.3750	1	2	-	3
	4	0.7500	2	0	-	2
6	2	0.0938	2	1	-	3
	3	0.1875	0	2	-	2
	4	0.3750	1	0	-	1
	1	0.7500	1	0	-	1
7	2	0.0938	1	1	-	2
	1	0.1875	2	1	-	3
	4	0.3750	0	2	-	2
	3	0.7500	1	0	-	1
8	3	0.0938	0	1	-	1
	4	0.1875	0	0	-	0
	1	0.3750	3	3	-	6
	2	0.7500	1	0	-	1
9	1	0.0938	0	0	-	0
	2	0.1875	1	1	-	2
	3	0.3750	3	2	-	5
	4	0.7500	0	0	-	0

Lg. Petromyzon marinus, D8, staggered release continued:

Replicate	Sediment Position	Sediment Type	Frequency Gp. 1	Gp. 2	Gp. 3	Tot.
10	4	0.0938	0	0	-	0
	3	0.1875	1	2	-	3
	2	0.3750	2	1	-	3
	1	0.7500	1	0	-	1
Pooled Distribution:		0.0938	4	4	-	8
		0.1875	12	13	-	25
		0.3750	15	17	-	32
		0.7500	8	2	-	10

Large Petromyzon marinus, final density of twelve per test unit, staggered release of three groups of four.

Replicate	Sediment Position	Sediment Type	Frequency Gp. 1	Gp. 2	Gp. 3	Tot.
1	1	0.0938	0	0	0	0
	2	0.1875	1	1	0	2
	3	0.3750	2	2	4	8
	4	0.7500	1	1	0	2
2	4	0.0938	0	0	2	2
	3	0.1875	1	0	0	1
	2	0.3750	2	2	0	4
	1	0.7500	1	2	2	5
3*	1	0.0938	0	0	-	0
	4	0.1875	0	1	-	1
	2	0.3750	2	2	-	4
	3	0.7500	2	0	-	2
4	1	0.0938	0	1	1	2
	4	0.1875	0	1	1	2
	2	0.3750	2	2	1	5
	3	0.7500	2	0	1	3
5*	3	0.0938	0	0	-	0
	2	0.1875	1	2	-	3
	1	0.3750	3	2	-	5
	4	0.7500	0	0	-	0
6	2	0.0938	0	0	0	0
	3	0.1875	2	2	2	6
	4	0.3750	2	2	1	5
	1	0.7500	0	0	1	1
7	2	0.0938	0	1	0	1
	1	0.1875	0	0	0	0
	4	0.3750	2	2	4	8
	3	0.7500	1	0	0	1
8	3	0.0938	0	0	1	1
	4	0.1875	0	0	1	1
	1	0.3750	4	3	2	9
	2	0.7500	0	0	0	0
9	2	0.0938	0	0	1	1
	3	0.1875	3	1	0	4
	1	0.3750	0	1	1	2
	4	0.7500	0	1	0	1

Lg. Petromyzon marinus, D12, staggered releases continued:

Replicate	Sediment Position	Sediment Type	Frequency Gp. 1	Gp. 2	Gp. 3	Tot.
10	3	0.0938	0	0	0	0
	2	0.1875	0	1	0	1
	4	0.3750	2	2	1	5
	1	0.7500	1	0	1	2
11	1	0.0938	0	0	0	0
	4	0.1875	1	2	0	3
	3	0.3750	2	2	1	5
	2	0.7500	0	0	0	0
12	4	0.0938	1	0	0	1
	1	0.1875	1	2	0	3
	2	0.3750	2	2	4	8
	3	0.7500	0	0	0	0
13	2	0.0938	0	0	0	0
	1	0.1875	0	2	1	3
	4	0.3750	1	1	1	3
	3	0.7500	0	0	1	1
14	3	0.0938	0	1	0	1
	4	0.1875	1	0	2	3
	1	0.3750	2	3	2	7
	2	0.7500	0	0	0	0
Pooled Distribution: (Flagged replicates excluded)		0.0938	1	3	5	9
		0.1875	10	12	7	29
		0.3750	23	24	22	69
		0.7500	6	4	6	16

Small Lampetra appendix, final density of four per test unit, unstaggered release.

Replicate	Sediment position	Sediment type	Tot.
1	1	0.0938	1
	2	0.1875	0
	3	0.3750	3
	4	0.7500	0
2	4	0.0938	0
	3	0.1875	1
	2	0.3750	0
	1	0.7500	0
3	2	0.0938	0
	3	0.1875	2
	1	0.3750	2
	4	0.7500	0
4	3	0.0938	0
	2	0.1875	2
	4	0.3750	1
	1	0.7500	0
5	1	0.0938	1
	4	0.1875	1
	3	0.3750	0
	2	0.7500	0
6	4	0.0938	0
	1	0.1875	2
	2	0.3750	1
	3	0.7500	0
7	2	0.0938	0
	1	0.1875	1
	4	0.3750	2
	3	0.7500	0
8	3	0.0938	2
	4	0.1875	0
	1	0.3750	0
	2	0.7500	0
Pooled Distribution:		0.0938	4
		0.1875	9
		0.3750	9
		0.7500	0

Small Lampetra appendix, final density of eight per test unit, unstaggered release.

Replicate	Sediment position	Sediment type	Tot.
1	1	0.0938	0
	2	0.1875	4
	3	0.3750	4
	4	0.7500	0
2*	4	0.0938	0
	3	0.1875	1
	2	0.3750	0
	1	0.7500	1
3	1	0.0938	3
	4	0.1875	3
	2	0.3750	2
	3	0.7500	0
4	4	0.0938	1
	1	0.1875	2
	3	0.3750	4
	2	0.7500	0
5	3	0.0938	0
	2	0.1875	2
	1	0.3750	2
	4	0.7500	3
6	2	0.0938	1
	3	0.1875	3
	4	0.3750	4
	1	0.7500	0
7*	2	0.0938	1
	1	0.1875	1
	4	0.3750	3
	3	0.7500	0
8	3	0.0938	1
	4	0.1875	4
	1	0.3750	2
	2	0.7500	0
9	1	0.0938	0
	2	0.1875	3
	3	0.3750	4
	4	0.7500	0

Sm. Lampetra appendix, D8, unstaggered release continued:

10	4	0.0938	1
	3	0.1875	3
	2	0.3750	2
	1	0.7500	1
11	2	0.0938	1
	3	0.1875	2
	1	0.3750	4
	4	0.7500	1
12	3	0.0938	3
	2	0.1875	4
	4	0.3750	1
	1	0.7500	0
13	1	0.0938	0
	4	0.1875	6
	3	0.3750	2
	2	0.7500	0
14	4	0.0938	1
	1	0.1875	0
	2	0.3750	7
	3	0.7500	0
15	2	0.0938	1
	1	0.1875	4
	4	0.3750	2
	3	0.7500	0
16	3	0.0938	1
	4	0.1875	5
	1	0.3750	2
	2	0.7500	0

Pooled Distribution:	0.0938	14
(Flagged replicates excluded)	0.1875	45
	0.3750	42
	0.7500	5

Large Lampetra appendix, final density of four per test unit, unstaggered release.

Replicate	Sediment position	Sediment type	Tot.
1*	1	0.0938	0
	2	0.1875	0
	3	0.3750	2
	4	0.7500	1
2*	4	0.0938	0
	3	0.1875	1
	2	0.3750	2
	1	0.7500	0
3*	1	0.0938	3
	4	0.1875	0
	2	0.3750	0
	3	0.7500	0
4	4	0.0938	3
	1	0.1875	0
	3	0.3750	0
	2	0.7500	1
5	3	0.0938	1
	2	0.1875	1
	1	0.3750	0
	4	0.7500	2
6	2	0.0938	0
	3	0.1875	2
	4	0.3750	1
	1	0.7500	1
7	2	0.0938	0
	1	0.1875	2
	4	0.3750	1
	3	0.7500	1
8	3	0.0938	2
	4	0.1875	0
	1	0.3750	2
	2	0.7500	0
9	1	0.0938	0
	2	0.1875	0
	3	0.3750	2
	4	0.7500	2

Lg. Lampetra appendix, D4, unstaggered release continued:

Replicate	Sediment position	Sediment type	Tot.
10	4	0.0938	0
	3	0.1875	0
	2	0.3750	4
	1	0.7500	0
11	2	0.0938	0
	3	0.1875	2
	1	0.3750	2
	4	0.7500	0
12*	3	0.0938	1
	2	0.1875	2
	4	0.3750	0
	1	0.7500	0
13	1	0.0938	1
	4	0.1875	0
	3	0.3750	3
	2	0.7500	0
14	4	0.0938	2
	1	0.1875	2
	2	0.3750	0
	3	0.7500	0
15	2	0.0938	0
	1	0.1875	1
	4	0.3750	2
	3	0.7500	1
16	3	0.0938	0
	4	0.1875	2
	1	0.3750	2
	2	0.7500	0

Pooled Distribution:	0.0938	9
(Flagged replicates excluded)	0.1875	12
	0.3750	19
	0.7500	8

Large Lampetra appendix, final density of eight per test unit, unstaggered release.

Replicate	Sediment position	Sediment type	Tot.
1	1	0.0938	2
	2	0.1875	0
	3	0.3750	4
	4	0.7500	1
2	4	0.0938	3
	3	0.1875	3
	2	0.3750	1
	1	0.7500	0
3*	1	0.0938	3
	4	0.1875	0
	2	0.3750	1
	3	0.7500	0
4	4	0.0938	2
	1	0.1875	1
	3	0.3750	4
	2	0.7500	0
5	3	0.0938	6
	2	0.1875	2
	1	0.3750	0
	4	0.7500	0
6	2	0.0938	2
	3	0.1875	3
	4	0.3750	3
	1	0.7500	0
7	2	0.0938	0
	1	0.1875	0
	4	0.3750	3
	3	0.7500	4
8	3	0.0938	0
	4	0.1875	7
	1	0.3750	1
	2	0.7500	0
9*	1	0.0938	0
	2	0.1875	0
	3	0.3750	6
	4	0.7500	0

Lg. Lampetra appendix, D8, unstaggered release continued:

Replicate	Sediment position	Sediment type	Tot.
10	4	0.0938	0
	3	0.1875	0
	2	0.3750	3
	1	0.7500	4
11	2	0.0938	2
	3	0.1875	1
	1	0.3750	4
	4	0.7500	1
12	3	0.0938	3
	2	0.1875	0
	4	0.3750	4
	1	0.7500	1
13	1	0.0938	1
	4	0.1875	3
	3	0.3750	3
	2	0.7500	1
14	4	0.0938	3
	1	0.1875	1
	2	0.3750	2
	3	0.7500	2
15	2	0.0938	0
	1	0.1875	2
	4	0.3750	2
	3	0.7500	3
16	3	0.0938	0
	4	0.1875	4
	1	0.3750	3
	2	0.7500	1
Pooled Distribution: (Flagged replicates excluded)		0.0938	24
		0.1875	27
		0.3750	37
		0.7500	18

Large Lampetra appendix, final density of twelve per test unit, staggered release of three groups of four.

Replicate	Sediment Position	Sediment Type	Frequency Gp. 1	Gp. 2	Gp. 3	Tot.
1	1	0.0938	0	0	1	1
	2	0.1875	0	2	1	3
	3	0.3750	3	0	0	3
	4	0.7500	1	2	2	5
2	4	0.0938	0	0	2	2
	3	0.1875	1	2	0	3
	2	0.3750	1	2	2	5
	1	0.7500	2	0	0	2
3	1	0.0938	1	0	2	3
	4	0.1875	1	1	0	2
	2	0.3750	2	2	1	5
	3	0.7500	0	1	1	2
4	4	0.0938	0	2	1	3
	1	0.1875	0	1	0	1
	3	0.3750	4	1	2	7
	2	0.7500	0	0	1	1
5	3	0.0938	0	2	0	2
	2	0.1875	2	2	3	7
	1	0.3750	1	0	1	2
	4	0.7500	1	0	0	1
6	2	0.0938	2	2	2	6
	3	0.1875	0	0	0	0
	4	0.3750	2	1	2	5
	1	0.7500	0	1	0	1
7	2	0.0938	0	2	0	2
	1	0.1875	0	0	3	3
	4	0.3750	2	1	1	4
	3	0.7500	1	1	0	2
8	3	0.0938	1	1	2	4
	4	0.1875	1	0	1	2
	1	0.3750	2	1	1	4
	2	0.7500	0	2	0	2
9	1	0.0938	2	0	1	3
	2	0.1875	0	1	1	2
	3	0.3750	2	3	1	6
	4	0.7500	0	0	0	0

Large Lampetra appendix, D12, staggered release continued:

Replicate	Sediment Position	Sediment Type	Frequency Gp. 1	Gp. 2	Gp. 3	Tot.
10	4	0.0938	0	0	0	0
	3	0.1875	2	3	4	9
	2	0.3750	1	0	0	1
	1	0.7500	1	1	0	2
11	2	0.0938	0	1	1	2
	3	0.1875	2	1	2	5
	1	0.3750	2	2	1	5
	4	0.7500	0	0	0	0
12	3	0.0938	2	1	0	3
	2	0.1875	1	0	1	2
	4	0.3750	1	3	3	7
	1	0.7500	0	0	0	0
13	1	0.0938	0	1	1	2
	4	0.1875	3	1	0	4
	3	0.3750	1	2	1	4
	2	0.7500	0	0	0	0
14	4	0.0938	0	1	0	1
	1	0.1875	1	1	2	4
	2	0.3750	2	2	2	6
	3	0.7500	0	0	0	0
15	2	0.0938	0	2	1	3
	1	0.1875	1	1	1	3
	4	0.3750	1	1	1	3
	3	0.7500	2	0	1	3
16	3	0.0938	0	1	1	2
	4	0.1875	3	2	2	7
	1	0.3750	1	1	0	2
	2	0.7500	0	0	1	1
Pooled Distribution:		0.0938	8	16	15	39
		0.1875	18	18	21	57
		0.3750	28	22	19	69
		0.7500	8	8	6	22

Large Lampetra appendix and Petromyzon marinus, final density of four each per test unit, unstaggered release.

Replicate	Sediment Position	Sediment Type	L. appendix	P. marinus	Tot.
1	1	0.0938	0	0	0
	2	0.1875	2	3	5
	3	0.3750	2	1	3
	4	0.7500	0	0	0
2	4	0.0938	1	0	1
	3	0.1875	0	2	2
	2	0.3750	2	2	4
	1	0.7500	0	0	0
3	1	0.0938	0	0	0
	4	0.1875	2	1	3
	2	0.3750	2	3	5
	3	0.7500	0	0	0
4	4	0.0938	1	0	1
	1	0.1875	1	1	2
	3	0.3750	1	2	3
	2	0.7500	1	1	2
5	3	0.0938	0	0	0
	2	0.1875	4	0	4
	1	0.3750	0	3	3
	4	0.7500	0	1	1
6	2	0.0938	0	0	0
	3	0.1875	0	3	3
	4	0.3750	3	1	4
	1	0.7500	1	0	1
7	2	0.0938	1	0	1
	1	0.1875	0	0	0
	4	0.3750	2	4	6
	3	0.7500	1	0	1
8	3	0.0938	0	0	0
	4	0.1875	3	1	4
	1	0.3750	1	1	2
	2	0.7500	0	2	2
Pooled Distribution		0.0938	3	0	3
		0.1875	12	11	23
		0.3750	13	17	30
		0.7500	3	4	7

Large Lampetra appendix and Petromyzon marinus, final density of eight each per test unit, unstaggered release.

Replicate	Sediment Position	Sediment Type	L. appendix	P. marinus	Tot.
1	1	0.0938	1	0	1
	2	0.1875	2	3	5
	3	0.3750	5	5	10
	4	0.7500	0	0	0
2	4	0.0938	1	0	1
	3	0.1875	2	1	3
	2	0.3750	4	4	8
	1	0.7500	0	1	1
3	1	0.0938	3	0	3
	4	0.1875	1	4	5
	2	0.3750	2	3	5
	3	0.7500	2	1	3
4	3	0.0938	0	0	0
	2	0.1875	5	3	8
	1	0.3750	2	3	5
	4	0.7500	1	2	3
5	2	0.0938	0	0	0
	3	0.1875	2	4	6
	4	0.3750	3	3	6
	1	0.7500	0	1	1
6	2	0.0938	0	0	0
	1	0.1875	3	3	6
	4	0.3750	4	4	8
	3	0.7500	1	0	1
7	3	0.0938	1	0	1
	4	0.1875	4	3	7
	1	0.3750	2	5	7
	2	0.7500	1	0	1
Pooled Distribution		0.0938	6	0	6
		0.1875	19	21	40
		0.3750	22	27	49
		0.7500	5	5	10

Food/Habitat selection test, yeast perfused vs. un-perfused sediments, large Lampetra appendix, final density of eight per test unit, unstaggered release.

Replicate	Position	Treatment	Tot.
1	1	Y	2
	2	Y	1
	3	-	2
	4	-	2
2	1	-	1
	2	-	3
	3	Y	3
	4	Y	1
3	1	-	1
	2	Y	3
	3	Y	3
	4	-	1
4	1	Y	1
	2	-	1
	3	-	3
	4	Y	2
5	1	Y	1
	2	Y	1
	3	-	2
	4	-	4
6	1	-	1
	2	Y	5
	3	Y	1
	4	-	1
7	1	Y	0
	2	-	1
	3	-	3
	4	Y	3
8	1	Y	1
	2	-	2
	3	Y	2
	4	-	2
Pooled Distribution:		Y	30
		-	30

Food/Habitat selection test, yeast perfused vs. un-perfused sediments, large Petromyzon marinus, final density of eight per test unit, unstaggered release.

Replicate	Position	Treatment	Tot.
1	1	Y	3
	2	-	3
	3	Y	1
	4	-	1
2	1	-	1
	2	Y	3
	3	-	2
	4	Y	2
3	1	Y	2
	2	-	3
	3	-	2
	4	Y	0
4	1	-	0
	2	Y	1
	3	Y	4
	4	-	2
5	1	-	0
	2	-	1
	3	Y	2
	4	Y	3
6	1	-	1
	2	Y	1
	3	-	2
	4	Y	2
7	1	-	2
	2	Y	2
	3	Y	2
	4	-	1
8	1	Y	1
	2	-	1
	3	-	3
	4	Y	1
Pooled Distribution:		Y	30
		-	25

Food/Habitat selection test, yeast or algae perfused water vs. distilled water, Lampetra appendix or Petromyzon marinus, final density of eight per test chamber, unstaggered release.

Species	Replicate	Number/Treatment food	Number/Treatment no food
L. appendix	1	4	4
	2	6	2
(Food = yeast)	3	6	2
	4	5	3
	5	6	2
	6	3	5
	7	6	2
	8	2	6
	Total:	38	26
P. marinus	1	4	4
	2	5	3
(Food = yeast)	3	4	4
	4	3	5
	5	5	3
	6	1	7
	7	4	4
	8	3	5
	Total:	29	35
L. appendix	1	3	2
	2	2	2
(Food = algae)	3	4	4
	4	3	2
	5	2	6
	6	8	0
	Total:	22	16
	Grand Total:	89	77

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 of homogeneity of variance for substrate selection frequency (square root arcsin transformed) for individual experimental series subjected to model I ANOVA. [La = Lampetra appendix, Pm = Petromyzon marinus, ns = unstaggered release, s = staggered release.]

Species	Size	Density	Release Pattern	X^2_c	df	Signif. Level	variances homogenous?
La	Sm.	4	ns	105.80	3	<0.001	no
La	Sm.	8	ns	0.2580	3	0.9664	yes
La	Lg.	4	ns	1.2739	3	0.7451	yes
La	Lg.	8	ns	2.8654	3	0.4486	yes
La	Lg.	12	s	3.2604	3	0.4079	yes
Pm	Sm.	4	ns	0.0427	3	0.9790	yes
Pm	Sm.	8	ns	0.7934	3	0.8530	yes
Pm	Sm.	8	s	1.4892	3	0.6968	yes
Pm	Lg.	4	ns	2.5436	3	0.4817	yes
Pm	Lg.	8	ns	4.3795	3	0.2927	yes
Pm	Lg.	8	s	0.9487	3	0.8181	yes
Pm	Lg.	12	s	8.2451	3	0.0430	no
La/Pm	Lg.	4:4	ns	5.3038 101.17	3 3	0.1975 <0.001	yes no
La/Pm	Lg.	8:8	ns	0.9928 79.645	3 3	0.8082 <0.001	yes no

Table A4-2. 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	variances homogenous?
Test of variances among sediment type by experimental series						
La	Sm.	D4ns,D8ns	109.30	7	<0.001	no
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	no
Test of variances among sediment type only						
La	Sm.	D4ns,D8ns	11.172	3	0.0113	no
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	no
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	no
Pm	Sm/Lg	D4ns,D8ns,D8s,D12s, D4:4ns,D8:8ns	15.812	7	0.0276	no
Test of variances among sediment type by species						
La/Pm	Sm.	D4ns,D8ns,D8s	14.080	7	0.0498	no
La/Pm	Lg.	D4ns,D8ns,D8ns,D12s, D4:4ns,D8:8ns	21.720	7	0.0036	no
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	no
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 A4-3. 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.[illegible]0	7.909	0.0000
Substrate	5.4140	3	1.	17.280	0.0000
Position	0.2970	3	0.	0.948	0.4228
Exp. Series	0.0544	1	0.0[illegible]4	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 A4-4. 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 A4-5. 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	12.87[illegible]	7	1.8394	16.605	0.0000
Substrate	11.89[illegible]	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 A4-6. 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 A4-7. 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 A4-8. 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 A4-9. 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 A4-10. 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			

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