GREAT LAKES FISHERY COMMISSION

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# Genetic Variation Among Sea Lamprey (*Petromyzon marinus*) Ammocoetes from Lake Michigan and Lake Huron

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# GENETIC VARIATION AMONG SEA LAMPREY (PETROMYZON MARINUS) AMMOCOETES FROM LAKE MICHIGAN AND LAKE HURON.

## I. VARIATION WITHIN AND AMONG DRAINAGES AND VARIATION AMONG YEARCLASSES

## II. POPULATION STRUCTURE

BY

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# Genetic Variation Among Sea Lamprey (*Petromyzon marinus*) Ammocoetes From Lake Michigan and Lake Huron. I. Variation Within and Among Drainages and Variation Among Yearclasses

## Abstract

Allelic variation in sea lamprey (Petromyzon marinus) ammocoetes from Lake Huron and Lake Michigan drainages was studied by starch gel electrophoresis. Previously untried enzyme systems were examined in sea lamprey ammocoetes. No new polymorphic enzyme systems were found. Allelic frequencies of sequential yearclasses of ammocoetes from two tributaries to Lake Michigan appeared constant. This result suggests that allelic frequencies of ammocoetes in a drainage are temporally stable. Variation in the allelic frequencies of ammocoetes samples was greater within drainages than among drainages. This result has bearing on the use of allelic frequencies for identification of sea lamprey populations. Allelic variation observed among ammocoete samples from different drainages may not reflect differences among populations because variation among drainages is confounded by variation within drainages. More than one sample ammocoetes should be taken from each drainage in future electrophoretic studies of sea lamprey population genetics so that effects of variation within drainages is minimized.

## Introduction

Three recent studies have shown that electrophoretic investigations of genetic variation in sea lamprey (Petromyzon marinus) may be useful in the identification of sea lamprey stocks. Krueger (1980) found differences in the allelic frequencies of ammocoetes (larval sea lamprey) from the Lake Superior, Oneida Lake, Lake Champlain, and Bay of Fundy drainages. Krueger and Spangler (1981) studied allelic variation in sea lamprey ammocoetes from drainages in the Lake Superior basin and concluded that sea lamprey in Lake Superior may be subdivided into five discrete stocks. Krueger and Spangler (1981) speculate that the pattern of genetic variation that they observed in Lake Superior is temporally stable. Brussard et al. (1981) found evidence for three genetically distinct groups of sea lamprey in eastern North America.

In each of these studies a single sample of ammocoetes was generally used to estimate the allelic frequencies for all of the ammocoetes in a drainage. These studies share the implicit assumption that allelic variation among ammocoete samples from different locations in the same drainage is negligible when compared to the variation between drainages.

The purpose of the present study was to test the

assumption that allelic variation among samples of sea lamprey ammocoetes from the same drainage is small. The results have bearing on the interpretation of previous electrophoretic studies and the design of future ones. The second purpose of the present study was to compare the allelic frequencies of different yearclasses of ammocoetes in the same drainage. This effort represents an initial attempt to test the hypothesis of temporal stability in the allelic frequencies of sea lamprey.

## Materials and Methods

### General

Ammocoetes were collected during 1982 from tributaries of the upper Great Lakes by electroshocking or by application of the lampricide TFM (3-trifluoromethyl-4-nitrophenol) as described by Smith et al. (1974). Ammocoetes collected at each location were frozen as quickly as possible, transported to the laboratory and stored at -20 $^{o}$ C until they were analyzed.

Variation in the expression of enzyme loci was studied by horizontal starch gel electrophoresis as described by May et al. (1979). Four polymorphic enzyme loci described by Krueger (1980) were used in this study: AGP, alpha-glycerophosphate dehydrogenase, E.C. 1.1.1.8; MDH-1, malate dehydrogenase, E.C. 1.1.1.37; PGI-2, phosphoglucose isomerase, E.C. 5.3.1.8; PGM-1, phosphoglucomutase, E.C. 2.7.5.1. The nomenclature for enzymes and enzyme loci used here is that of Krueger (1980) and Allendorf and Utter (1979). Buffer systems, sample preparation, and enzyme stains used were the same as those described by Krueger (1980) except that a tris-citrate buffer system described by Siciliano and Shaw (1976) was used for AGP and PGI-2 because it improved the resolution of these enzymes. Data recorded for each specimen included an identification number, length

to the nearest millimeter, and the genotypes at polymorphic enzyme loci.

Enzyme Screening

Enzyme systems that had not been previously examined were screened for polymorphic expression in sea lamprey ammocoetes. The activity and resolution of the following enzymes were examined in a preliminary screening: acid phosphatase, E.C. 3.1.3.2; alpha-galactosidase, E.C. 3.2.1.22; alpha-mannosidase, E.C. 3.2.1.24; beta-glucosidase, E.C. 3.2.1.21; beta-glucuronidase, E.C. 3.2.1.31; glutamate-pyruvate-transaminase, E.C. 2.6.1.2; glycerate-2-dehydrogenase, E.C. 1.1.1.29; nucleoside phosphorylase, E.C. 2.4.2.1; 2,3-phosphoglycerate mutase, E.C. 5.4.2.1. Recipes for enzyme stains were taken from Siciliano and Shaw (1976). Each stain was tested on four buffer systems: Ridgway and Clayton-Tretiak buffer systems described by Krueger (1980) and the tris-citrate and tris-versene-borate systems described by Siciliano and Shaw (1976).

Five enzymes (alpha-mannosidase, beta-glucosidase, beta-glucuronidase, and glutamate-pyruvate-transaminase on the tris-versene-borate buffer system; acid phosphatase on the Clayton-Tretiak buffer system) showed good activity and good resolution. The banding patterns for each of these

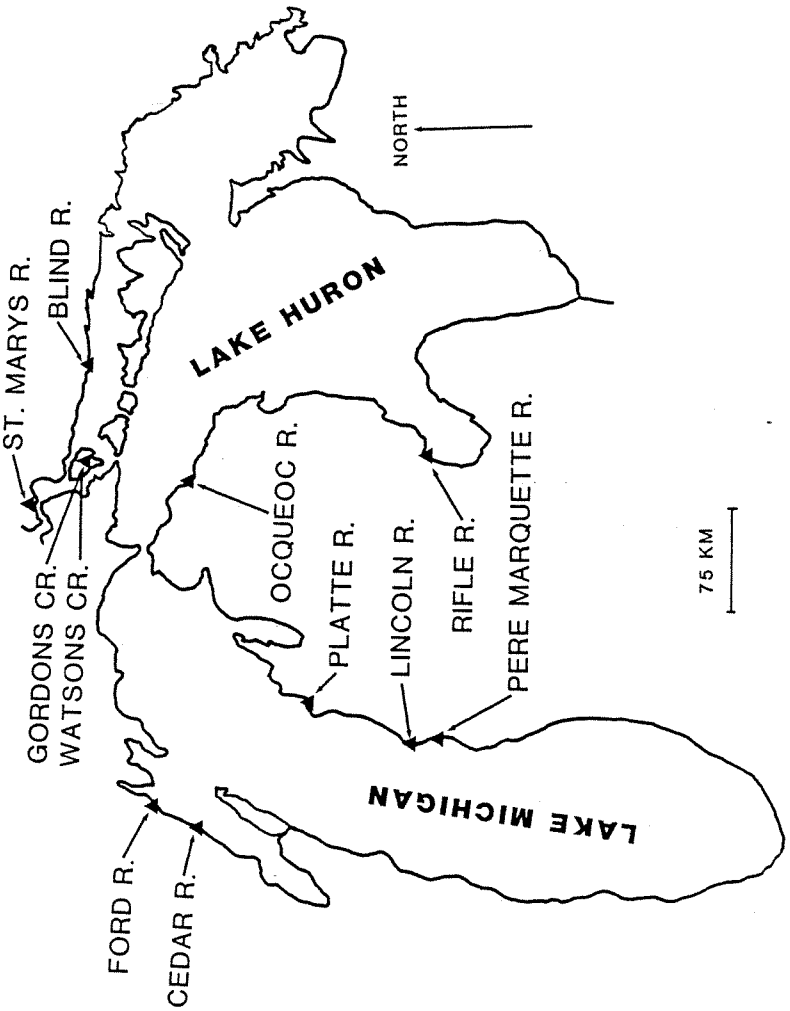
enzymes were examined in a total of 200 ammocoetes from several Lake Superior and Lake Michigan drainages.

Variation Within and Among Drainages

The total variance in the allelic frequencies of samples from a lake was partitioned into within and between drainage components by a hierarchical analysis of variance as described by Wright (1978, pp. 86-89) using the computer program BIOSYS-1 (Swofford and Selander 1981). Ammocoete samples from four locations in each of four Lake Michigan drainages (Platte River, Lincoln River, Pere Marquette River, Cedar River) and from two locations in each of six Lake Huron drainages (Ocqueoc River, Rifle River, Watsons Creek, Gordons Creek, Blind River, St. Marys River) were used (Figure 1). The data for each lake were analyzed separately.

Sample sizes were balanced so that calculation of variance components would be simplified (Sokal and Rohlf 1981, pp. 293). After electrophoresis, data for 35 ammocoetes were selected from the total for each of the Lake Michigan locations and data for 50 ammocoetes were selected from the total for each of the Lake Huron sampling locations. This was done by excluding all individuals for which the genotype at one or more loci could not be determined and then sampling randomly until either 35 or 50

Figure 1. Drainages from which ammocoetes were collected.


NORTH
LAKE HURON
ST. MARYS R.
BLIND R.
GORDONS CR.
WATSONS CR.
OCQUEOC R.
PLATTE R.
LINCOLN R.
RIFLE R.
PERE MARQUETTE R.
75 KM
LAKE MICHIGAN
FORD R.
CEDAR R.

individuals remained.

Genotypic frequencies for each sample were tested for conformance to Hardy-Weinberg equilibrium values by an exact test (Haldane 1954) as described by Elston and Forthofer (1977). Allelic frequencies of samples that were collected at different locations in the same drainage were tested for heterogeneity using log likelihood ratios and contingency tables (Sokal and Rohlf 1981, pp. 731-747). Frequencies of the rare alleles PGI-2(90) and PGI-2(122) were combined before testing for heterogeneity. Probability values smaller than or equal to 0.05 were required for rejection of the null hypothesis of allelic homogeneity in all statistical tests.

## Allelic Variation Among Yearclasses

Ammocoetes from different yearclasses were identified in two Lake Michigan drainages by analysis of length-frequency distributions. Manion and Smith (1978) showed that the modal lengths of the 0, I, and II ageclasses could be inferred from the length-frequency distribution of ammocoetes captured at the same location. This characteristic can be used to identify individuals in the first three ageclasses if growth rates are good and judgement is exercised conservatively.

A large number of ammocoetes were collected from

different locations on two Lake Michigan drainages. Samples were taken from three locations on the Ford River and two locations on the Pere Marquette River (Figure 1). Collections from the Pere Marquette River were made during June 28-29, 1982 before individuals from the 1982 yearclass were large enough to be collected. A successful sea lamprey control treatment (Smith et al. 1974) had been carried out in the Pere Marquette River during July 24-28, 1979 after the sea lamprey had spawned (spawning in the Pere Marquette River is usually over by late June). Thus, only the 1980 and 1981 yearclasses were present in large numbers in the collections from the Pere Marquette River.

The Ford River was subjected to a sea lamprey control treatment on May 31, 1980 before spawning was completed for that year. Collections from the Ford River were made during November 4-5, 1982. Individuals from the 1982 yearclass were large enough to be collected at that time. Thus, only the 1980, 1981, and 1982 yearclasses contributed significantly to the samples from the Ford River.

The modes of the length-frequency distributions were well separated in all collections. Samples of ammocoetes from each yearclass were obtained by choosing individuals whose lengths were near the modal value for that yearclass (Figure 2 and Figure 3). The 99% confidence intervals for the length-frequency distributions of different yearclasses

Figure 2. Length-frequency distributions for ammocoetes collected from two locations on the Pere Marquette River. The distributions for all of the ammocoetes collected at a location are given as open histograms. The distributions for the ammocoetes selected from each year-class are given as shaded histograms. I = 1981 year-class, II = 1982 year-class.

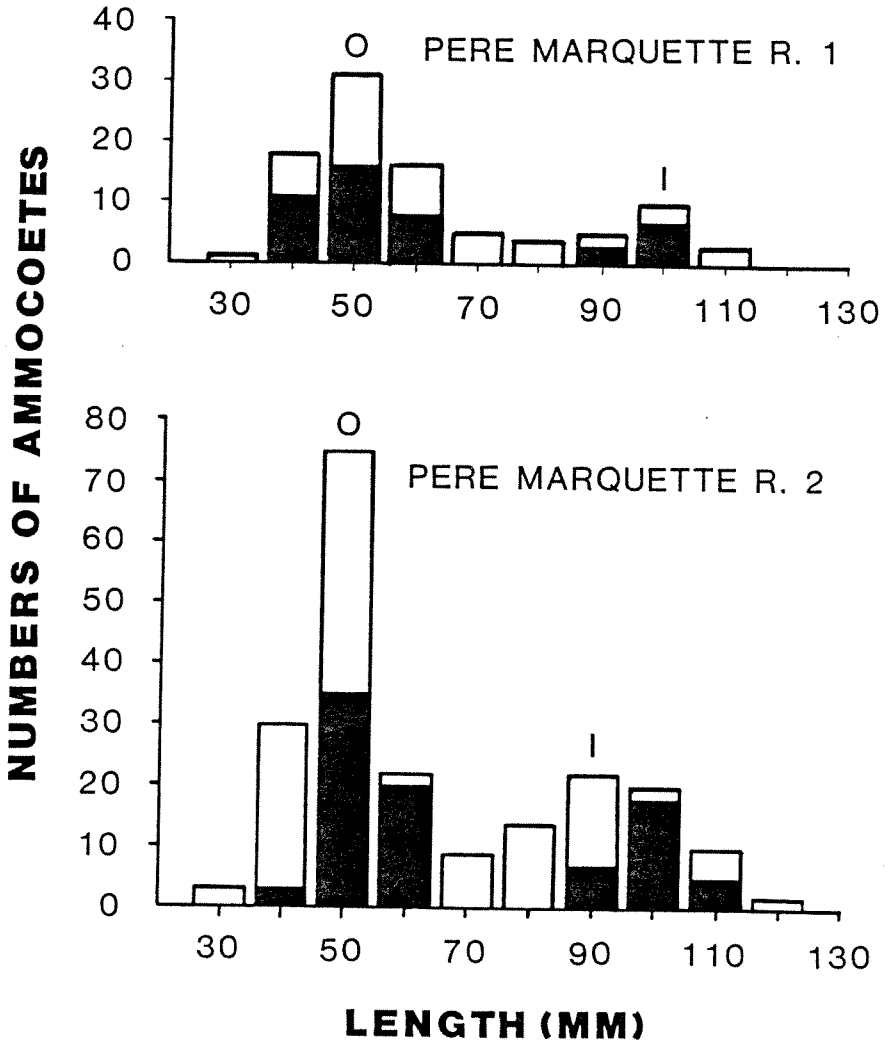
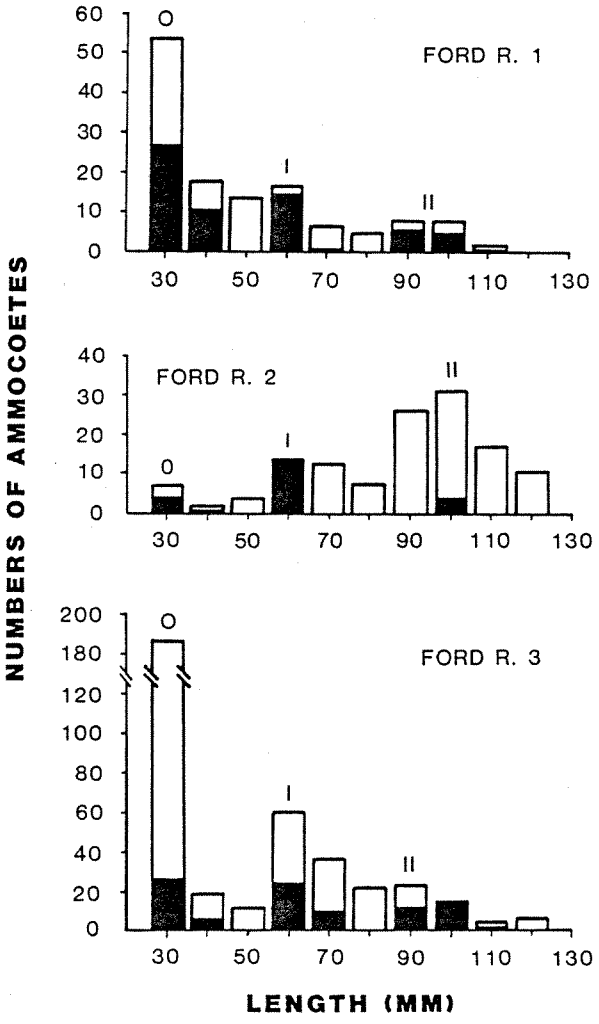

NUMBERS OF AMMOCOETES
40
30
20
10
0
O
PERE MARQUETTE R. 1
I
30
50
70
90
110
130
80
70
60
50
40
30
20
10
0
O
PERE MARQUETTE R. 2
I
30
50
70
90
110
130
LENGTH (MM)

Figure 3. Length-frequency distributions for ammocoetes collected from three locations on the Ford River. The distributions for all the ammocoetes collected at a location are given as open histograms. The distributions for ammocoetes selected from each year-class are given as shaded histograms. 0 = 1982 year-class, I = 1981 year-class, II = 1980 year-class.


NUMBERS OF AMMOCOETES
FORD R. 1
FORD R. 2
FORD R. 3
O
I
II
LENGTH (MM)

from the same location did not overlap.

Genotypic frequencies of each yearclass at each sampling location were tested for conformance to Hardy-Weinberg equilibrium values as already described. Allelic frequencies were tested for heterogeneity using log likelihood ratios and contingency tables as described by Fienberg (1980, pp. 27-51, 95-97). Allelic frequencies were arrayed in three dimensional contingency tables (ageclasses X sampling locations X alleles) and tested for heterogeneity among yearclasses within sampling sites and among sampling sites within yearclasses. If no differences were found among yearclasses within sampling locations then yearclasses were pooled so that heterogeneity among sampling locations for the drainage as a whole could be assessed. Similarly, if no differences were found among sampling locations within yearclasses, then sampling locations were pooled and tested for heterogeneity. The test for allelic heterogeneity among yearclasses of ammocoetes from the same drainage was a test of the temporal stability hypothesis.

# Results

## Enzyme Screening

No polymorphisms were detected in the enzymes that were screened during this study. The rest of this report deals with variation in the four polymorphic enzymes described previously (AGP, MDH-1, PGI-2, and PGM-1).

## Variation Within and Among Drainages

Genotypic frequencies (Table 1) conformed to Hardy-Weinberg equilibrium values less often than expected on the basis of chance. Genotypic frequencies of Lake Michigan samples differed significantly from Hardy-Weinberg values in 4 out of 64 (6%) of the total comparisons: Platte River 1, AGP; Lincoln River 1, AGP; Lincoln River 4, PGM-1; Pere Marquette River 4, PGM-1. An F-statistic, calculated from the observed and expected frequencies of heterozygotes in samples as described by Nei (1977), can be used to describe the departure of a genotypic distribution from Hardy-Weinberg values. Positive values of the statistic indicate heterozygote deficiencies, negative values indicate heterozygote excesses and a value of zero indicates perfect conformance to Hardy-Weinberg equilibrium values. Values of the F-statistic for the cases listed above were -0.429, 0.352, -0.429, and -0.373, respectively.

Table 1. Genotypic and allelic frequencies for samples used in the hierarchical analysis.

| | AGP | | | | | MDH-1 | | | | | PGI-2 | | | | | | | | PGM-1 | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Genotypes | | | Alleles | | Genotypes | | | Alleles | | Genotypes | | | | | Alleles | | | Genotypes | | | Alleles | |
| Sample | 100/ 100 | 100/ 146 | 146/ 146 | 100 | 146 | -100/ -100 | -100/ -165 | -165/ -165 | -100 | -165 | 90/ 100 | 90/ 122 | 100/ 100 | 100/ 122 | 122/ 122 | 90 | 100 | 122 | 100/ 100 | 100/ 148 | 148/ 148 | 100 | 148 |
| Lake Michigan (N = 35 for all samples) | | | | | | | | | | | | | | | | | | | | | | | |
| Platte River | | | | | | | | | | | | | | | | | | | | | | | |
| 1 | 9 | 24 | 2 | 0.60 | 0.40 | 29 | 5 | 1 | 0.90 | 0.10 | 0 | 0 | 33 | 2 | 0 | 0.00 | 0.97 | 0.03 | 5 | 21 | 9 | 0.44 | 0.56 |
| 2 | 8 | 19 | 8 | 0.50 | 0.50 | 28 | 7 | 0 | 0.90 | 0.10 | 0 | 0 | 32 | 3 | 0 | 0.00 | 0.96 | 0.04 | 16 | 15 | 4 | 0.67 | 0.33 |
| 3 | 20 | 14 | 1 | 0.77 | 0.23 | 16 | 18 | 1 | 0.71 | 0.29 | 10 | 0 | 23 | 2 | 0 | 0.14 | 0.83 | 0.03 | 16 | 18 | 1 | 0.71 | 0.29 |
| 4 | 14 | 19 | 2 | 0.67 | 0.33 | 19 | 16 | 0 | 0.77 | 0.23 | 0 | 0 | 35 | 0 | 0 | 0.00 | 1.00 | 0.00 | 5 | 19 | 11 | 0.41 | 0.59 |
| Lincoln River | | | | | | | | | | | | | | | | | | | | | | | |
| 1 | 9 | 11 | 15 | 0.41 | 0.59 | 31 | 4 | 0 | 0.94 | 0.06 | 0 | 0 | 34 | 1 | 0 | 0.00 | 0.99 | 0.01 | 8 | 19 | 8 | 0.50 | 0.50 |
| 2 | 8 | 23 | 4 | 0.56 | 0.44 | 30 | 5 | 0 | 0.93 | 0.07 | 8 | 0 | 24 | 3 | 0 | 0.12 | 0.84 | 0.04 | 13 | 16 | 6 | 0.60 | 0.40 |
| 3 | 0 | 18 | 17 | 0.26 | 0.74 | 0 | 35 | 0 | 1.00 | 0.00 | 0 | 0 | 35 | 0 | 0 | 0.00 | 1.00 | 0.00 | 11 | 17 | 7 | 0.56 | 0.44 |
| 4 | 7 | 18 | 10 | 0.46 | 0.54 | 27 | 8 | 0 | 0.89 | 0.11 | 1 | 0 | 33 | 1 | 0 | 0.01 | 0.97 | 0.02 | 9 | 24 | 2 | 0.60 | 0.40 |
| Pere Marquette River | | | | | | | | | | | | | | | | | | | | | | | |
| 1 | 10 | 19 | 6 | 0.56 | 0.44 | 31 | 3 | 1 | 0.93 | 0.07 | 0 | 0 | 35 | 0 | 0 | 0.00 | 1.00 | 0.00 | 21 | 11 | 3 | 0.76 | 0.24 |
| 2 | 8 | 20 | 7 | 0.51 | 0.49 | 27 | 6 | 2 | 0.86 | 0.14 | 0 | 0 | 34 | 1 | 0 | 0.00 | 0.99 | 0.01 | 11 | 14 | 10 | 0.51 | 0.49 |
| 3 | 21 | 12 | 2 | 0.77 | 0.23 | 23 | 12 | 0 | 0.83 | 0.17 | 0 | 0 | 35 | 0 | 0 | 0.00 | 1.00 | 0.00 | 7 | 17 | 11 | 0.44 | 0.56 |
| 4 | 21 | 14 | 0 | 0.80 | 0.20 | 19 | 16 | 0 | 0.77 | 0.23 | 0 | 0 | 35 | 0 | 0 | 0.00 | 1.00 | 0.00 | 16 | 19 | 0 | 0.73 | 0.27 |
| Cedar River | | | | | | | | | | | | | | | | | | | | | | | |
| 1 | 17 | 11 | 7 | 0.64 | 0.36 | 24 | 10 | 1 | 0.83 | 0.17 | 0 | 0 | 35 | 0 | 0 | 0.00 | 1.00 | 0.00 | 14 | 18 | 3 | 0.66 | 0.34 |
| 2 | 7 | 15 | 13 | 0.41 | 0.59 | 18 | 16 | 1 | 0.74 | 0.26 | 2 | 0 | 30 | 3 | 0 | 0.03 | 0.93 | 0.04 | 18 | 15 | 2 | 0.73 | 0.27 |
| 3 | 10 | 16 | 9 | 0.51 | 0.49 | 21 | 14 | 0 | 0.80 | 0.20 | 2 | 0 | 31 | 2 | 0 | 0.03 | 0.94 | 0.03 | 11 | 21 | 3 | 0.61 | 0.39 |
| 4 | 8 | 21 | 6 | 0.53 | 0.47 | 26 | 9 | 0 | 0.87 | 0.13 | 0 | 0 | 33 | 2 | 0 | 0.00 | 0.97 | 0.03 | 15 | 16 | 4 | 0.66 | 0.34 |

Table 1. (Continued)

Lake Huron (N = 50 for all samples)

| | | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Ocqueoc River | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1 | 8 | 35 | 7 | 0.51 | 0.49 | 32 | 15 | 3 | 0.79 | 0.21 | 0 | 1 | 43 | 6 | 0 | 0.01 | 0.92 | 0.07 | 24 | 23 | 3 | 0.71 | 0.29 |
| 2 | 12 | 22 | 16 | 0.46 | 0.54 | 34 | 12 | 4 | 0.80 | 0.20 | 3 | 0 | 46 | 1 | 0 | 0.03 | 0.96 | 0.01 | 28 | 19 | 3 | 0.75 | 0.25 |
| Rifle River | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1 | 5 | 25 | 20 | 0.35 | 0.65 | 49 | 1 | 0 | 0.99 | 0.01 | 3 | 0 | 14 | 33 | 0 | 0.03 | 0.64 | 0.33 | 15 | 2 | 33 | 0.32 | 0.68 |
| 2 | 13 | 24 | 13 | 0.50 | 0.50 | 38 | 10 | 2 | 0.86 | 0.14 | 1 | 0 | 46 | 3 | 0 | 0.01 | 0.96 | 0.03 | 23 | 20 | 7 | 0.66 | 0.34 |
| Watsons Creek | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1 | 14 | 24 | 12 | 0.52 | 0.48 | 37 | 11 | 2 | 0.85 | 0.15 | 2 | 0 | 48 | 0 | 0 | 0.02 | 0.98 | 0.00 | 27 | 22 | 1 | 0.76 | 0.24 |
| 2 | 8 | 30 | 12 | 0.46 | 0.54 | 43 | 7 | 0 | 0.93 | 0.07 | 1 | 0 | 49 | 0 | 0 | 0.01 | 0.99 | 0.00 | 15 | 32 | 3 | 0.62 | 0.38 |
| Gordons Creek | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1 | 6 | 23 | 21 | 0.35 | 0.65 | 29 | 21 | 0 | 0.79 | 0.21 | 0 | 0 | 43 | 7 | 0 | 0.00 | 0.93 | 0.07 | 14 | 32 | 4 | 0.60 | 0.40 |
| 2 | 31 | 10 | 9 | 0.72 | 0.28 | 37 | 13 | 0 | 0.87 | 0.13 | 0 | 0 | 50 | 0 | 0 | 0.00 | 1.00 | 0.00 | 24 | 23 | 3 | 0.71 | 0.29 |
| Blind River | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1 | 9 | 21 | 20 | 0.39 | 0.61 | 41 | 9 | 0 | 0.91 | 0.09 | 0 | 0 | 31 | 18 | 1 | 0.00 | 0.80 | 0.20 | 24 | 20 | 6 | 0.68 | 0.32 |
| 2 | 12 | 28 | 10 | 0.52 | 0.48 | 45 | 5 | 0 | 0.95 | 0.05 | 0 | 0 | 34 | 15 | 1 | 0.00 | 0.83 | 0.17 | 21 | 23 | 6 | 0.65 | 0.35 |
| St. Marys River | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1 | 12 | 24 | 14 | 0.48 | 0.52 | 37 | 11 | 2 | 0.85 | 0.15 | 0 | 0 | 50 | 0 | 0 | 0.00 | 1.00 | 0.00 | 21 | 26 | 3 | 0.68 | 0.32 |
| 2 | 15 | 27 | 8 | 0.57 | 0.43 | 31 | 17 | 2 | 0.79 | 0.21 | 0 | 0 | 44 | 6 | 0 | 0.00 | 0.94 | 0.06 | 22 | 24 | 4 | 0.68 | 0.32 |

Genotypic frequencies of Lake Huron samples differed significantly from Hardy-Weinberg equilibrium values in 6 out of 48 (13%) of the total comparisons: Ocqueoc River 1, AGP; Rifle River 1, PGI-2 and PGM-1; Watsons Creek 2, PGM-1; Gordons Creek 1, PGM-1; Gordons Creek 2, AGP. Values of the F-statistic were: -0.401, -0.498, 0.908, -0.358, -0.333, and 0.504, respectively.

Significant differences in allelic frequencies among sampling locations in the same drainage were common. There were significant differences among sampling locations at one or more loci in all drainages except for the Blind and Ocqueoc rivers (Lake Huron).

Variation among samples of ammocoetes from the same drainage was larger than the variation among drainages (Table 2). Negative variance components with small absolute value were obtained in some cases. Following the discussion by Searle (1971, pp. 406-408), negative values were taken as evidence that the true variance component is zero. The variance within and among drainages can be expressed as proportions of the total variance (Sokal and Rohlf 1981, pp. 283). The weighted average of the variation in allelic frequencies within Lake Michigan drainages was 84% of the total variation. The weighted average of the variation within Lake Huron drainages was 100% of the total.

Table 2. Variance components for sampling locations within drainages, and drainages within lakes. The total variance is the sum of the two components. Percentage of total variance is given in parentheses. Negative variance components were taken to be zero. The values for individual loci were weighted by p(1-p) (where p is the frequecy of the most common allele) and then averaged to give the overall values.

| Locus | Locations Within Drainages | | Drainages Within Lakes | | Total |
|---|---|---|---|---|---|
| Lake Michigan | | | | | |
| AGP | 0.023 | (68%) | 0.011 | (32%) | 0.034 |
| MDH-1 | 0.0057 | (67%) | 0.0029 | (33%) | 0.0086 |
| PGI-2 | 0.0044 | (100%) | -0.00060 | (0%) | 0.0038 |
| PGM-1 | 0.020 | (100%) | -0.0030 | (0%) | 0.017 |
| overall | 0.053 | (84%) | 0.010 | (16%) | 0.063 |
| Lake Huron | | | | | |
| AGP | 0.027 | (100%) | -0.013 | (0%) | 0.014 |
| MDH-1 | 0.0036 | (58%) | 0.0026 | (42%) | 0.0062 |
| PGI-2 | 0.017 | (88%) | 0.0023 | (12%) | 0.019 |
| PGM-1 | 0.021 | (100%) | -0.00091 | (0%) | 0.020 |
| overall | 0.068 | (100%) | -0.0090 | (0%) | 0.059 |

## Allelic Variation Among Yearclasses

Allelic heterogeneity (Table 3 and Table 4) was detected among yearclasses within sampling locations in the Pere Marquette River (MDH-1) and the Ford River (AGP). Allelic heterogeneity among sampling locations within yearclasses was detected in the Pere Marquette River (AGP and MDH-1) and the Ford River (AGP and MDH-1). Additionally, there was evidence for a three-way interaction between yearclasses, sampling locations and alleles in the Pere Marquette River (MDH-1) and the Ford River (AGP).

There were six cases in which no significant differences were detected among yearclasses within sampling locations. Yearclasses were combined in these cases so that allelic heterogeneity among locations for entire drainages could be evaluated. Significant differences were detected among sampling locations for the Pere Marquette River (AGP) and for the Ford River (MDH-1).

There were four cases in which no significant differences among sampling locations within yearclasses were noted. In these cases, sampling locations were combined so that heterogeneity among yearclasses could be evaluated for entire drainages. No significant differences among yearclasses within drainages were detected.

Table 3. Genotypic frequencies, allelic frequencies and sample sizes for samples used in yearclass comparisons. O = 1982 yearclass, I = 1981 yearclass, II = 1980 yearclass. Two locations were sampled on the Pere Marquette River and three locations were sampled on the Ford River. The sampling locations within each drainage are numbered consecutively.

| | AGP | | | | | | MDH-1 | | | | | | PGI-2 | | | | | | | PGM-1 | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Genotypes | | | Alleles | | | Genotypes | | | Alleles | | | Genotypes | | | Alleles | | | | Genotypes | | | Alleles | |
| Sample | N | 100/ 100 | 100/ 146 | 146/ 146 | 100 | 146 | N | -100/ -100 | -100/ -165 | -165/ -165 | -100 | -165 | N | 90/ 100 | 100/ 100 | 100/ 122 | 90 | 100 | 122 | N | 100/ 100 | 100/ 148 | 148/ 148 | 100 | 148 |
| Pere Marquette River | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1-I | 35 | 14 | 16 | 5 | 0.63 | 0.37 | 35 | 29 | 5 | 1 | 0.90 | 0.10 | 35 | 0 | 35 | 0 | 0.00 | 1.00 | 0.00 | 35 | 17 | 15 | 3 | 0.70 | 0.30 |
| 1-II | 10 | 6 | 3 | 1 | 0.75 | 0.25 | 10 | 7 | 1 | 2 | 0.75 | 0.25 | 10 | 0 | 10 | 0 | 0.00 | 1.00 | 0.00 | 10 | 6 | 4 | 0 | 0.80 | 0.20 |
| 2-I | 54 | 11 | 27 | 16 | 0.45 | 0.55 | 58 | 33 | 18 | 7 | 0.72 | 0.28 | 58 | 0 | 55 | 3 | 0.00 | 0.97 | 0.03 | 57 | 22 | 28 | 7 | 0.63 | 0.37 |
| 2-II | 30 | 8 | 18 | 4 | 0.57 | 0.43 | 30 | 25 | 5 | 0 | 0.92 | 0.08 | 30 | 0 | 30 | 0 | 0.00 | 1.00 | 0.00 | 30 | 12 | 13 | 5 | 0.62 | 0.38 |
| Ford River | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1-0 | 15 | 5 | 8 | 2 | 0.60 | 0.40 | 38 | 29 | 7 | 2 | 0.86 | 0.14 | 38 | 2 | 34 | 2 | 0.02 | 0.95 | 0.03 | 38 | 17 | 16 | 5 | 0.66 | 0.34 |
| 1-I | 16 | 3 | 9 | 4 | 0.47 | 0.53 | 16 | 10 | 5 | 1 | 0.78 | 0.22 | 16 | 1 | 14 | 1 | 0.03 | 0.94 | 0.03 | 16 | 5 | 8 | 3 | 0.56 | 0.44 |
| 1-II | 12 | 2 | 8 | 2 | 0.50 | 0.50 | 12 | 9 | 3 | 0 | 0.87 | 0.13 | 12 | 1 | 10 | 1 | 0.04 | 0.93 | 0.03 | 12 | 1 | 9 | 2 | 0.46 | 0.54 |
| 2-0 | 2 | 1 | 0 | 1 | 0.50 | 0.50 | 6 | 4 | 2 | 0 | 1.00 | 0.00 | 6 | 0 | 6 | 0 | 0.00 | 0.83 | 0.17 | 6 | 1 | 1 | 4 | 0.25 | 0.75 |
| 2-I | 14 | 7 | 7 | 0 | 0.75 | 0.25 | 14 | 14 | 0 | 0 | 1.00 | 0.00 | 14 | 0 | 14 | 0 | 0.00 | 1.00 | 0.00 | 14 | 4 | 8 | 2 | 0.57 | 0.43 |
| 2-II | 4 | 0 | 1 | 3 | 0.13 | 0.87 | 4 | 3 | 1 | 0 | 0.88 | 0.12 | 4 | 0 | 4 | 0 | 0.00 | 1.00 | 0.00 | 4 | 0 | 3 | 1 | 0.38 | 0.62 |
| 3-0 | 14 | 8 | 4 | 2 | 0.71 | 0.29 | 32 | 22 | 8 | 2 | 0.81 | 0.19 | 32 | 2 | 29 | 1 | 0.03 | 0.95 | 0.02 | 31 | 12 | 14 | 5 | 0.61 | 0.39 |
| 3-I | 33 | 6 | 16 | 11 | 0.42 | 0.58 | 34 | 19 | 13 | 2 | 0.75 | 0.25 | 34 | 3 | 29 | 2 | 0.04 | 0.93 | 0.03 | 34 | 14 | 16 | 4 | 0.65 | 0.35 |
| 3-II | 29 | 10 | 13 | 6 | 0.57 | 0.43 | 29 | 22 | 6 | 1 | 0.86 | 0.14 | 29 | 0 | 2 | 27 | 0.03 | 0.97 | 0.00 | 29 | 11 | 16 | 2 | 0.65 | 0.35 |

Table 4: Allelic heterogeneity among ammocoetes from the Ford and Pere Marquette rivers. The model that was fit to the data is indicated by "+". Model 1 specifies the null hypothesis (no differences among yearclasses within sampling locations and no differences among sampling locations within yearclasses). Model 2 specifies differences among locations within yearclasses. Model 3 specifies differences among yearclasses within locations, differences among locations within yearclasses and a three-way interaction between yearclasses, locations and alleles.

| Locus | Model 1 | Model 2 | Model 3 |
|---|---|---|---|
| Ford River | | | |
| AGP | | | + |
| MDH-1 | | + | |
| PGI-2 | + | | |
| PGM-1 | + | | |
| Pere Marquette River | | | |
| AGP | | + | |
| MDH-1 | | | + |
| PGI-2 | + | | |
| PGM-2 | + | | |

# Discussion

## Variation Within and Among Drainages

F-statistics for the genotypic distributions that did not conform to Hardy-Weinberg expectations were of large absolute value (> 0.3), indicating substantial deviation from expected values. F-statistics were not consistently positive or consistently negative, indicating that both heterozygote deficiencies and excesses were common.

A Wahlund effect, due to the mixing of yearclasses with different allelic frequencies, probably accounts for the genotypic distributions with positive fixation indices (heterozygote deficiencies). A Wahlund effect is a deficiency of heterozygotes in a sample that occurs when the sample is made up of a mixture of groups that have different allelic frequencies (Hartl 1980, pp. 191-195). A single sample of ammocoetes may contain three or more yearclasses, depending on when the drainage was last subjected to a sea lamprey control treatment and the rate at which the drainage is recolonized by sea lamprey. If the yearclasses in a sample of ammocoetes have different allelic frequencies then a Wahlund effect is expected. The genetic variation observed in the present study among yearclasses in the Pere Marquette and Ford rivers supports this hypothesis.

Robertson (1965) showed that heterozygote excesses will

result when the number of spawners is low because of differences in allelic frequencies that arise by chance between the parental sexes. This phenomenon probably accounts for the genotypic distributions with negative fixation indices (heterozygote excesses). Results of the present study support this hypothesis. Allelic frequencies of ammocoete samples from the same yearclass differed among sampling locations in the Ford and Pere Marquette rivers. The differences among ammocoete collections probably reflect differences in the allelic frequencies of spawning groups at different locations in the drainage. Differences in the allelic frequencies of the spawning groups in a drainage will arise if the number of spawners in some of the groups is small (see discussion below). If spawner abundance is low (due to ongoing sea lamprey control) or spawning habitat is widely scattered then the ammocoetes at a single location may be the progeny of few adults. The number of successful spawners will be further reduced by differences in spawning success, differences in survival among sib-groups, unbalanced sex ratios and polygyny (Hanson and Manion 1978, pp. 11).

Factors affecting Hardy-Weinberg equilibrium in ammocoete samples probably interact. A Wahlund effect may be counteracted in a sample by heterozygote excesses due to allelic frequency differences between the parental sexes.

The explanations for deviation from Hardy-Weinberg equilibrium, though disparate, lead to the same inference that the size of local spawning groups may often be small.

Field observations support the hypothesis that the number of sea lamprey in spawning groups is often small. Catches of spawning run sea lamprey by electric weirs on index streams in the Lake Superior basin show that small runs of spawning sea lamprey are common, particularly since the advent of sea lamprey control (Smith el al. 1974).

The Pere Marquette River illustrates the possibility that spawning groups may be of small size. The Pere Marquette River is a large dendritic drainage with many miles of suitable spawning habitat that consistently support high levels of ammocoete production. The abundance and distribution of spawning habitat probably limits the number of spawning adults that utilize any particular spawning site. During June 9-25, 1971 (sea lamprey spawning season) U. S. Fish and Wildlife Service personnel spent 48 hours examining 124 miles of sea lamprey spawning habitat along the Pere Marquette River. No spawning sea lamprey and only 17 nests were observed. During May 4 - June 22, 1973 46 hours were spent examining spawning habitat along 107 miles of stream. No spawning adults and only 9 nests were observed (Unpublished data, U.S.F.W.S., Ludington, MI). Sea lamprey spawn in the daytime over a period of weeks

(Applegate 1950) and would have been observed if present in large numbers.

Brussard et al. (1981), Krueger (1980), and Krueger and Spangler (1981) report that the genotypic frequencies of ammocoete samples differed from Hardy-Weinberg equilibrium values in 4 out of 60, 0 out of 19, and 3 out of 72 cases, respectively. In the present study 10 out of 112 cases differed from Hardy-Weinberg values. These proportions do not differ significantly by a chi-square test. A tendency to diverge from Hardy-Weinberg equilibrium values may be characteristic of the genotypic distributions of ammocoete samples. This characteristic may have gone undetected in previous studies because relatively few samples were used.

Allelic variation among locations within drainages was larger than the variation among drainages. Variance in allelic frequencies among samples of ammocoetes from different locations in the same drainage was probably also due to small numbers of spawning adults. Variance in the allelic frequencies of local spawning groups of size n drawn from a large spawning run to a drainage is the binomial variance of sampling means $pq/2n$ where p and q are allelic frequencies (Falconer 1981, pp. 49). Variance is inversely proportional to the size of the spawning groups so that the variance in allelic frequencies of spawning groups will increase as the size of the spawning groups decrease.

Variance among ammocoete collections probably reflects the variance in the allelic frequencies of small spawning groups. The frequent failure of genotypic frequencies to conform to Hardy-Weinberg equilibrium values, the variance in the allelic frequencies of collections from different locations in the same drainage, and field observations suggest that the ammocoetes at a sampling location are often the progeny of a small number of spawners.

Results of this study show that single samples are inadequate for characterizing allelic frequencies of ammocoetes in drainages of the Lake Huron and Lake Michigan basins. Future electrophoretic investigations of stock structure in these lakes should use samples of ammocoetes collected from two or more locations in each drainage. Previous studies (Brussard et al. 1981; Krueger 1980; Krueger and Spangler 1981;) in which single samples of ammocoetes were used to estimate the allelic frequencies for entire drainages should be reexamined in light of these results.

## Genetic Variation Among Yearclasses

Allelic frequencies of sequential yearclasses of ammocoetes were constant in two Lake Michigan drainages. The results were consistent with the hypothesis that the Ford and Pere Marquette rivers are associated with a

population or populations that maintain constant allelic frequencies from one year to the next.

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# Genetic Variation Among Sea Lamprey (*Petromyzon marinus*) Ammocoetes From Lake Michigan and Lake Huron.

## II. Population Structure

## Abstract

Genetic variation in sea lamprey (Petromyzon marinus) ammocoetes from tributaries of Lake Michigan and Lake Huron was examined by starch gel electrophoresis. Significant differences in allelic frequencies were detected among drainages in both lakes but cluster analysis of genetic distances provided no evidence that sea lamprey in Lake Huron or Lake Michigan were subdivided into separate populations. Results of this study contrast with results of a previous one in which evidence for distinct populations of sea lamprey in Lake Superior was obtained.

## Introduction

Identification of constituent populations can lead to more effective management of a fishery resource. For this reason, population identification has become common in connection with the management of fishery resources (e.g. Thorpe and Mitchell 1981; Casselman et al. 1981; Goodier 1981). Fish populations can be identified by a variety of methods but the analysis of electrophoretically detectable enzyme polymorphisms has proven to be a particularly useful tool for this purpose (Ihssen et al. 1981).

The management and control of the predatory sea lamprey (Petromyzon marinus) in the Great Lakes could be improved if populations of sea lamprey were identified. Sea lamprey are controlled primarily by application of the selective toxicants TFM (3-trifluoromethyl-4-nitrophenol) and Bayer-73 (2',5-dichloro-4'-nitrosalicylanilide) to streams that contain sea lamprey ammocoetes (larva). In general, a stream is treated with toxicant if it contains large ammocoetes that will soon transform into the predatory adult form, enter the lake and begin to feed (Smith et al. 1974). Krueger and Spangler (1981) suggest that sea lamprey control might be improved by simultaneously treating all of the spawning streams associated with a population rather than treating the streams on an individual basis.

The Great Lakes Fishery Commission has recently adopted an Integrated Pest Management (IPM) policy for sea lamprey control in the Great Lakes (Sawyer 1980). The IPM approach requires frequent estimates of lamprey abundance so that management effectiveness can be continuously evaluated. Relative abundance of spawning sea lamprey can be estimated from the numbers of sea lamprey caught in assessment traps that are set in spawning streams (Smith et al. 1974). It is not clear, however, to what geographical unit the estimates of abundance should be applied. If populations were identified and associated with spawning streams, then abundance estimates could be associated with sea lamprey that occupy a particular section of a lake.

In this paper, electrophoretic evidence for populations of sea lamprey in Lake Michigan and Lake Huron is presented and discussed. Electrophoretic variation in sea lamprey has received considerable attention (Thomas and McCrimmon 1964; Wilson et al. 1964; Uthe et al. 1966; Uthe and Tsuyuki 1967; Horowitz and Whitt 1972; Krueger 1980; Brussard et al. 1981; Krueger and Spangler 1981; Jacobson 1983) but the question of sea lamprey populations in Lake Michigan and Lake Huron has not previously been investigated.

Jacobson (1983) has shown that single samples of ammocoetes from drainages are inadequate for identifying populations in sea lamprey that inhabit Lake Michigan and

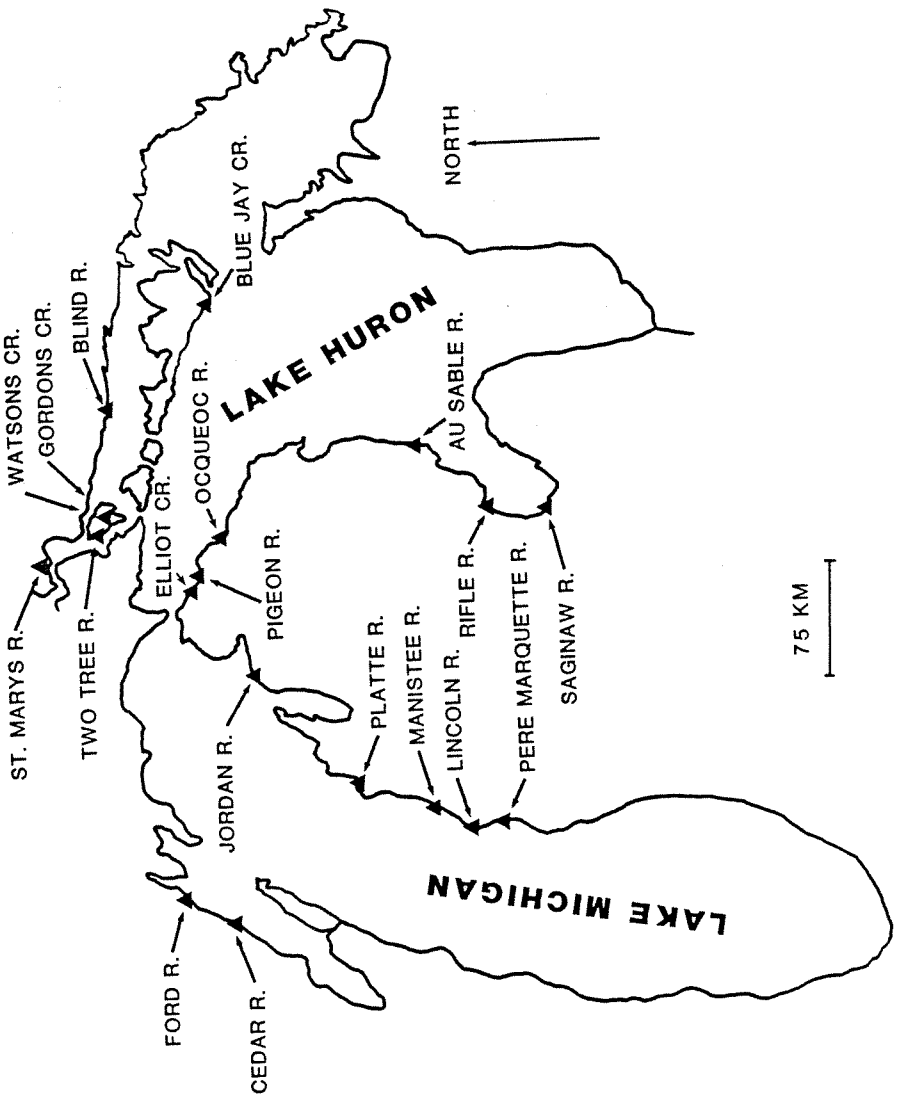
Lake Huron because of allelic variation within drainages. The present study is unique in that multiple samples were collected from drainages so that the effects of variation within drainages could be minimized.

## Materials and Methods

Sea lamprey ammocoetes were collected during May - November, 1982 from seven drainages in the Lake Michigan basin and twelve drainages in the Lake Huron basin (Figure 1). Two or more samples were taken from most drainages and all of the ammocoetes in a sample were collected at the same location. Collection procedures, treatment of samples, and electrophoretic methods were described by Jacobson (1983). Four polymorphic enzyme loci were used: AGP, alpha-glycerophosphate dehydrogenase, E. C. 1.1.1.8; MDH-1, malate dehydrogenase, E. C. 1.1.1.37; PGI-2, phosphoglucose isomerase, E. C. 5.3.1.8; PGM-1, phosphoglucomutase, E. C. 2.7.5.1. The nomenclature described by Allendorf and Utter (1979) is used in this report for enzymes, enzyme loci, and alleles.

Genotypic frequencies of each sample were tested for conformance to Hardy-Weinberg equilibrium values by an exact test (Haldane 1954) according to the methods described by Elston and Forthofer (1977). Allelic frequencies of ammocoete samples from different locations in the same drainage were tested for heterogeneity by a chi-square test. Data for different locations in the same drainage were pooled and the allelic frequencies of ammocoetes from different drainages were tested for heterogeneity.

Figure 1. Drainages in the Lake Michigan and Lake Huron basins from which ammocoetes were collectecd.


NORTH
LAKE HURON
LAKE MICHIGAN
WATSONS CR.
GORDONS CR.
BLIND R.
BLUE JAY CR.
OCQUEOC R.
ELLIOT CR.
TWO TREE R.
ST. MARYS R.
PIGEON R.
JORDAN R.
PLATTE R.
MANISTEE R.
LINCOLN R.
RIFLE R.
AU SABLE R.
PERE MARQUETTE R.
SAGINAW R.
FORD R.
CEDAR R.
75 KM

Probability values smaller than or equal to 0.05 were required for rejection of the null hypothesis in all statistical tests. F-statistics (Wright 1965) were calculated from the observed and expected numbers of heterozygotes by the method of Nei (1977) and from the variance of allelic frequencies by the method of Wright (1978, pp. 86-89). The chord distance of Cavalli-Sforza and Edwards (1967) was used as a measure of genetic distance between drainages within lakes. Cluster analysis of the genetic distance measures was used to examine the patterns of allelic variation within lakes (Ihssen et al. 1981). An unweighted pair-group algorithm with arithmetic averaging was used for cluster analysis (Sneath and Sokal 1973). The computer program BIOSYS-1 (Swofford and Selander 1981) was used for data analysis.

## Results and Discussion

Genotypic frequencies of ammocoete samples (Table 1 and Table 2) conformed to Hardy-Weinberg equilibrium values less often than expected on the basis of chance. Genotypic frequencies of ammocoetes from the Lake Michigan basin differed significantly from Hardy-Weinberg values in 10 of 96 (10%) comparisons: Jordan R. 1, AGP; Platte R. 1, AGP; Lincoln R. 2, AGP; Lincoln R. 3, AGP; Lincoln R. 4, PGM-1; Pere Marquette R. 1, MDH-1; Pere Marquette R. 2, MDH-1; Pere Marquette R. 4, PGM-1; Cedar R. 2, AGP; Cedar R. 4, PGM-1. Genotypic frequencies in the Lake Huron data differed from Hardy-Weinberg values in 5 of 80 (6%) comparisons: Elliot Cr., MDH-1; Ocqueoc R. 1, AGP; Rifle R. 1, PGI-2 and PGM-1; Gordons Cr. 2, AGP. Reasons for the frequent departure from Hardy-Weinberg equilibrium values are discussed by Jacobson (1983).

Allelic frequencies of ammocoete samples collected at different locations in the same drainage were heterogeneous. There were significant differences at one or more loci among locations in all of the Lake Michigan tributaries and in all but three of the Lake Huron tributaries (Au Sable River, Saginaw River, and the Blind River). Allelic frequencies of ammocoetes from different drainages in the same lake differed as well. Significant differences among drainages

Table 1. Genotypic frequencies, allelic frequencies and sample sizes for ammocoete samples from tributaries to Lake Michigan.

| | AGP | | | | | | MDH-1 | | | | | | PGI-2 | | | | | | | | | PGM-1 | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Genotypes | | | Alleles | | | Genotypes | | | Allelles | | | Genotypes | | | | | Alleles | | | | Genotypes | | | Alleles | |
| Sample | N | 100/ 100 | 100/ 146 | 146/ 146 | 100 | 146 | N | -100/ -100 | -100/ -165 | -165/ -165 | -100 | -165 | N | 90/ 90 | 90/ 100 | 90/ 122 | 100/ 100 | 100/ 122 | 90 | 100 | 122 | N | 100/ 100 | 100/ 148 | 148/ 148 | 100 | 148 |
| Jordan R. | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1 | 52 | 20 | 25 | 7 | 0.63 | 0.37 | 53 | 42 | 11 | 0 | 0.90 | 0.10 | 53 | 0 | 0 | 0 | 50 | 3 | 0.00 | 0.97 | 0.03 | 53 | 15 | 30 | 8 | 0.57 | 0.43 |
| 2 | 46 | 17 | 29 | 0 | 0.68 | 0.32 | 60 | 36 | 24 | 0 | 0.80 | 0.20 | 60 | 0 | 0 | 0 | 52 | 8 | 0.00 | 0.93 | 0.07 | 60 | 25 | 26 | 9 | 0.63 | 0.37 |
| Platte R. | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1 | 40 | 12 | 26 | 2 | 0.63 | 0.37 | 40 | 33 | 6 | 1 | 0.90 | 0.10 | 40 | 0 | 0 | 0 | 38 | 2 | 0.00 | 0.97 | 0.03 | 40 | 6 | 24 | 10 | 0.45 | 0.55 |
| 2 | 37 | 8 | 21 | 8 | 0.50 | 0.50 | 38 | 30 | 8 | 0 | 0.90 | 0.10 | 38 | 0 | 0 | 0 | 34 | 4 | 0.00 | 0.95 | 0.05 | 38 | 17 | 16 | 5 | 0.66 | 0.34 |
| 3 | 39 | 21 | 16 | 2 | 0.74 | 0.26 | 39 | 20 | 18 | 1 | 0.74 | 0.26 | 38 | 0 | 11 | 0 | 25 | 2 | 0.14 | 0.83 | 0.03 | 39 | 16 | 22 | 1 | 0.69 | 0.31 |
| 4 | 40 | 16 | 22 | 2 | 0.67 | 0.33 | 40 | 23 | 17 | 0 | 0.79 | 0.21 | 40 | 0 | 0 | 0 | 40 | 0 | 0.00 | 1.00 | 0.00 | 40 | 5 | 21 | 14 | 0.39 | 0.61 |
| Big Manistee R. | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1 | 26 | 14 | 12 | 0 | 0.77 | 0.23 | 28 | 14 | 14 | 0 | 0.75 | 0.25 | 28 | 0 | 3 | 0 | 23 | 2 | 0.05 | 0.91 | 0.04 | 28 | 22 | 5 | 1 | 0.88 | 0.12 |
| 2 | 60 | 22 | 29 | 9 | 0.61 | 0.39 | 60 | 42 | 15 | 3 | 0.82 | 0.18 | 60 | 0 | 2 | 0 | 56 | 2 | 0.02 | 0.97 | 0.01 | 60 | 31 | 25 | 4 | 0.72 | 0.28 |
| Lincoln R. | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1 | 47 | 10 | 20 | 17 | 0.43 | 0.57 | 48 | 43 | 5 | 0 | 0.95 | 0.05 | 48 | 0 | 0 | 0 | 46 | 2 | 0.00 | 0.98 | 0.02 | 48 | 9 | 29 | 10 | 0.49 | 0.51 |
| 2 | 59 | 14 | 39 | 6 | 0.57 | 0.43 | 59 | 48 | 11 | 0 | 0.91 | 0.09 | 59 | 0 | 12 | 0 | 43 | 4 | 0.10 | 0.86 | 0.04 | 59 | 25 | 26 | 8 | 0.64 | 0.36 |
| 3 | 57 | 0 | 30 | 27 | 0.26 | 0.74 | 57 | 57 | 0 | 0 | 1.00 | 0.00 | 57 | 0 | 0 | 0 | 57 | 0 | 0.00 | 1.00 | 0.00 | 57 | 18 | 26 | 13 | 0.54 | 0.46 |
| 4 | 57 | 13 | 27 | 17 | 0.47 | 0.53 | 57 | 44 | 13 | 0 | 0.89 | 0.11 | 57 | 0 | 1 | 1 | 53 | 2 | 0.02 | 0.95 | 0.03 | 57 | 17 | 37 | 3 | 0.62 | 0.38 |
| Pere Marquette R. | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1 | 55 | 20 | 27 | 8 | 0.61 | 0.39 | 55 | 45 | 7 | 3 | 0.88 | 0.12 | 55 | 0 | 0 | 0 | 55 | 0 | 0.00 | 1.00 | 0.00 | 55 | 30 | 22 | 3 | 0.74 | 0.26 |
| 2 | 118 | 27 | 68 | 23 | 0.52 | 0.48 | 122 | 87 | 28 | 7 | 0.83 | 0.17 | 122 | 0 | 2 | 0 | 116 | 4 | 0.01 | 0.97 | 0.02 | 121 | 46 | 59 | 16 | 0.62 | 0.38 |
| 3 | 57 | 35 | 19 | 3 | 0.78 | 0.22 | 57 | 40 | 17 | 0 | 0.85 | 0.15 | 57 | 0 | 0 | 0 | 57 | 0 | 0.00 | 1.00 | 0.00 | 57 | 13 | 28 | 16 | 0.47 | 0.53 |
| 4 | 56 | 33 | 23 | 0 | 0.80 | 0.20 | 57 | 34 | 23 | 0 | 0.80 | 0.20 | 57 | 0 | 0 | 0 | 57 | 0 | 0.00 | 1.00 | 0.00 | 57 | 29 | 28 | 0 | 0.75 | 0.25 |
| Ford R. | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1 | 76 | 28 | 35 | 13 | 0.60 | 0.40 | 106 | 77 | 25 | 4 | 0.84 | 0.16 | 106 | 1 | 6 | 0 | 94 | 5 | 0.04 | 0.94 | 0.02 | 105 | 30 | 55 | 20 | 0.55 | 0.45 |
| 2 | 61 | 14 | 30 | 17 | 0.47 | 0.53 | 66 | 55 | 11 | 0 | 0.92 | 0.08 | 66 | 0 | 0 | 0 | 64 | 2 | 0.00 | 0.99 | 0.01 | 66 | 7 | 40 | 19 | 0.41 | 0.59 |
| 3 | 122 | 32 | 61 | 29 | 0.51 | 0.49 | 146 | 102 | 38 | 6 | 0.83 | 0.17 | 146 | 0 | 11 | 0 | 131 | 4 | 0.04 | 0.95 | 0.01 | 145 | 62 | 67 | 16 | 0.66 | 0.34 |
| Cedar R. | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1 | 61 | 26 | 25 | 10 | 0.63 | 0.37 | 61 | 39 | 19 | 3 | 0.79 | 0.21 | 61 | 0 | 0 | 0 | 61 | 0 | 0.00 | 1.00 | 0.00 | 61 | 25 | 30 | 6 | 0.66 | 0.34 |
| 2 | 26 | 13 | 7 | 6 | 0.64 | 0.36 | 58 | 52 | 6 | 0 | 0.95 | 0.05 | 58 | 0 | 0 | 0 | 58 | 0 | 0.00 | 1.00 | 0.00 | 58 | 21 | 31 | 6 | 0.63 | 0.37 |
| 3 | 48 | 9 | 22 | 17 | 0.42 | 0.58 | 60 | 33 | 25 | 2 | 0.76 | 0.24 | 60 | 0 | 6 | 0 | 49 | 5 | 0.05 | 0.91 | 0.04 | 60 | 28 | 29 | 3 | 0.71 | 0.29 |
| 4 | 69 | 21 | 31 | 17 | 0.53 | 0.47 | 74 | 44 | 29 | 1 | 0.79 | 0.21 | 74 | 0 | 2 | 0 | 69 | 3 | 0.01 | 0.97 | 0.02 | 74 | 27 | 42 | 5 | 0.65 | 0.35 |
| 5 | 35 | 8 | 21 | 6 | 0.53 | 0.47 | 55 | 39 | 14 | 2 | 0.84 | 0.16 | 55 | 0 | 1 | 0 | 51 | 3 | 0.01 | 0.96 | 0.03 | 55 | 27 | 22 | 6 | 0.69 | 0.31 |

Table 2. Genotypic frequencies, allelic frequencies and sample sizes for ammocoete samples from tributaries to Lake Huron.

| | AGP | | | | | | MDH-1 | | | | | | PGI-2 | | | | | | | | | | PGM-1 | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Genotypes | | | Alleles | | | Genotypes | | | Alleles | | | Genotypes | | | | | | Alleles | | | | Genotypes | | | Alleles | |
| Sample | N | 100/ 100 | 100/ 146 | 146/ 146 | 100 | 146 | N | -100/ -100 | -100/ -165 | -165/ -165 | -100 | -165 | N | 90/ 90 | 90/ 100 | 90/ 122 | 100/ 100 | 100/ 122 | 122/ 122 | 90 | 100 | 122 | N | 100/ 100 | 100/ 148 | 148/ 148 | 100 | 148 |
| Pigeon R. | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1 | 58 | 34 | 22 | 2 | 0.78 | 0.22 | 58 | 32 | 21 | 5 | 0.73 | 0.27 | 58 | 0 | 0 | 0 | 58 | 0 | 0 | 0.00 | 1.00 | 0.00 | 58 | 24 | 30 | 4 | 0.67 | 0.33 |
| Elliot Cr. | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1 | 41 | 7 | 27 | 7 | 0.50 | 0.50 | 60 | 40 | 13 | 7 | 0.78 | 0.22 | 60 | 1 | 2 | 0 | 55 | 2 | 0 | 0.03 | 0.95 | 0.02 | 60 | 23 | 26 | 11 | 0.60 | 0.40 |
| Ocqueoc R. | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1 | 58 | 9 | 41 | 8 | 0.51 | 0.49 | 59 | 38 | 17 | 4 | 0.79 | 0.21 | 59 | 0 | 0 | 1 | 48 | 9 | 1 | 0.01 | 0.89 | 0.10 | 59 | 29 | 27 | 3 | 0.72 | 0.28 |
| 2 | 59 | 12 | 24 | 23 | 0.41 | 0.59 | 60 | 38 | 15 | 7 | 0.76 | 0.24 | 60 | 0 | 3 | 0 | 56 | 1 | 0 | 0.02 | 0.97 | 0.01 | 60 | 33 | 24 | 3 | 0.75 | 0.25 |
| Au Sable R. | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1 | 23 | 5 | 13 | 5 | 0.50 | 0.50 | 23 | 17 | 5 | 1 | 0.85 | 0.15 | 23 | 0 | 2 | 0 | 21 | 0 | 0 | 0.04 | 0.96 | 0.00 | 23 | 9 | 13 | 1 | 0.67 | 0.33 |
| 2 | 61 | 22 | 31 | 8 | 0.61 | 0.39 | 61 | 42 | 18 | 1 | 0.84 | 0.16 | 61 | 0 | 3 | 1 | 53 | 4 | 0 | 0.03 | 0.93 | 0.04 | 61 | 28 | 26 | 7 | 0.67 | 0.33 |
| Rifle R. | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1 | 51 | 5 | 26 | 20 | 0.35 | 0.65 | 51 | 50 | 1 | 0 | 0.99 | 0.01 | 51 | 0 | 3 | 0 | 14 | 34 | 0 | 0.03 | 0.64 | 0.33 | 51 | 15 | 2 | 34 | 0.31 | 0.69 |
| 2 | 51 | 14 | 24 | 13 | 0.51 | 0.49 | 51 | 38 | 11 | 2 | 0.85 | 0.15 | 51 | 0 | 1 | 0 | 47 | 3 | 0 | 0.01 | 0.96 | 0.03 | 51 | 23 | 21 | 7 | 0.66 | 0.34 |
| Two Tree R. | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1 | 59 | 23 | 27 | 9 | 0.62 | 0.38 | 60 | 54 | 6 | 0 | 0.95 | 0.05 | 60 | 0 | 8 | 0 | 52 | 0 | 0 | 0.07 | 0.93 | 0.00 | 60 | 25 | 28 | 7 | 0.65 | 0.35 |
| Watsons Cr. | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1 | 59 | 18 | 27 | 14 | 0.53 | 0.47 | 59 | 42 | 15 | 2 | 0.84 | 0.16 | 58 | 0 | 2 | 0 | 56 | 0 | 0 | 0.02 | 0.98 | 0.00 | 59 | 34 | 24 | 1 | 0.78 | 0.22 |
| 2 | 58 | 10 | 33 | 15 | 0.46 | 0.54 | 58 | 50 | 8 | 0 | 0.93 | 0.07 | 58 | 0 | 1 | 0 | 57 | 0 | 0 | 0.01 | 0.99 | 0.00 | 58 | 22 | 33 | 3 | 0.66 | 0.34 |
| Gordons Cr. | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1 | 55 | 6 | 27 | 22 | 0.36 | 0.64 | 55 | 32 | 23 | 0 | 0.79 | 0.21 | 55 | 0 | 0 | 0 | 45 | 10 | 0 | 0.00 | 0.91 | 0.09 | 55 | 17 | 32 | 6 | 0.60 | 0.40 |
| 2 | 58 | 38 | 10 | 10 | 0.74 | 0.26 | 59 | 45 | 14 | 0 | 0.88 | 0.12 | 59 | 0 | 0 | 0 | 59 | 0 | 0 | 0.00 | 1.00 | 0.00 | 59 | 26 | 29 | 4 | 0.69 | 0.31 |

Table 2. (Continued)

| | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Blind R. | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1 | 50 | 9 | 21 | 20 | 0.39 | 0.61 | 57 | 46 | 11 | 0 | 0.90 | 0.10 | 57 | 0 | 0 | 0 | 35 | 21 | 1 | 0.00 | 0.80 | 0.20 | 57 | 27 | 23 | 7 | 0.67 | 0.33 |
| 2 | 58 | 13 | 33 | 12 | 0.51 | 0.49 | 58 | 52 | 6 | 0 | 0.95 | 0.05 | 58 | 0 | 0 | 0 | 40 | 17 | 1 | 0.00 | 0.84 | 0.16 | 58 | 25 | 25 | 8 | 0.65 | 0.35 |
| Blue Jay Cr. | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1 | 58 | 27 | 26 | 5 | 0.69 | 0.31 | 58 | 33 | 23 | 2 | 0.77 | 0.23 | 58 | 0 | 15 | 0 | 43 | 0 | 0 | 0.13 | 0.87 | 0.00 | 58 | 23 | 24 | 11 | 0.60 | 0.40 |
| 2 | 36 | 7 | 14 | 15 | 0.39 | 0.61 | 47 | 35 | 11 | 1 | 0.86 | 0.14 | 59 | 0 | 0 | 0 | 42 | 17 | 0 | 0.00 | 0.86 | 0.14 | 59 | 19 | 33 | 7 | 0.60 | 0.40 |
| St. Marys R. | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1 | 58 | 18 | 26 | 14 | 0.53 | 0.47 | 60 | 44 | 14 | 2 | 0.85 | 0.15 | 60 | 0 | 0 | 0 | 60 | 0 | 0 | 0.00 | 1.00 | 0.00 | 60 | 26 | 31 | 3 | 0.69 | 0.31 |
| 2 | 59 | 16 | 33 | 10 | 0.55 | 0.45 | 59 | 37 | 20 | 2 | 0.80 | 0.20 | 59 | 0 | 2 | 0 | 51 | 6 | 0 | 0.02 | 0.93 | 0.05 | 59 | 24 | 30 | 5 | 0.66 | 0.34 |
| Saginaw R. | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1 | 16 | 3 | 10 | 3 | 0.50 | 0.50 | 16 | 10 | 5 | 1 | 0.78 | 0.22 | 16 | 0 | 0 | 0 | 16 | 0 | 0 | 0.00 | 1.00 | 0.00 | 16 | 5 | 9 | 2 | 0.59 | 0.41 |
| 2 | 12 | 4 | 5 | 3 | 0.54 | 0.46 | 12 | 9 | 2 | 1 | 0.83 | 0.17 | 12 | 0 | 1 | 0 | 11 | 0 | 0 | 0.04 | 0.96 | 0.00 | 12 | 7 | 5 | 0 | 0.79 | 0.21 |
| 3 | 3 | 1 | 0 | 2 | 0.33 | 0.67 | 3 | 1 | 2 | 0 | 0.67 | 0.33 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0.00 | 1.00 | 0.00 | 3 | 1 | 2 | 0 | 0.67 | 0.33 |
| 4 | 3 | 1 | 1 | 1 | 0.50 | 0.50 | 3 | 3 | 0 | 0 | 1.00 | 0.00 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0.00 | 1.00 | 0.00 | 3 | 1 | 2 | 0 | 0.67 | 0.33 |
| 5 | 8 | 4 | 3 | 1 | 0.69 | 0.31 | 8 | 6 | 2 | 0 | 0.88 | 0.12 | 8 | 0 | 0 | 0 | 8 | 0 | 0 | 0.00 | 1.00 | 0.00 | 8 | 5 | 2 | 1 | 0.75 | 0.25 |

were detected at each locus for both lakes.

There was no electrophoretic evidence that sea lamprey in Lake Michigan or Lake Huron were subdivided into populations since drainages near one another geographically were generally not grouped together by cluster analysis (Figure 2 and Figure 3). The Ford and Cedar rivers (Green Bay, Lake Michigan) clustered together but this should not be regarded as evidence for population subdivision since the probability of a single such occurrence is high on the basis of chance alone. Differences that were observed in the allelic frequencies of ammocoete samples from different drainages did not appear to reflect underlying population structure. These results were consistent with the results of mark-recapture studies of parasitic-phase sea lamprey in Lake Michigan and Lake Huron (Smith and Elliot 1953; Applegate and Smith 1951; Moore et al. 1974) which document extensive movement in parasitic phase sea lamprey in Lake Michigan and Lake Huron. Sea lamprey from different natal drainages may mix in the lake to such an extent that discrete populations cannot exist.

$F_{DL}$ values ($F_{DL}$ is an F-statistic that measures the genetic differentiation of ammocoetes in drainages relative to the total population in the lake basin) that were obtained for Lake Huron were larger than the values obtained for Lake Michigan (Table 3). This result suggests

Figure 2. Cluster analysis for sea lamprey ammocoetes from drainages in the Lake Michigan basin.

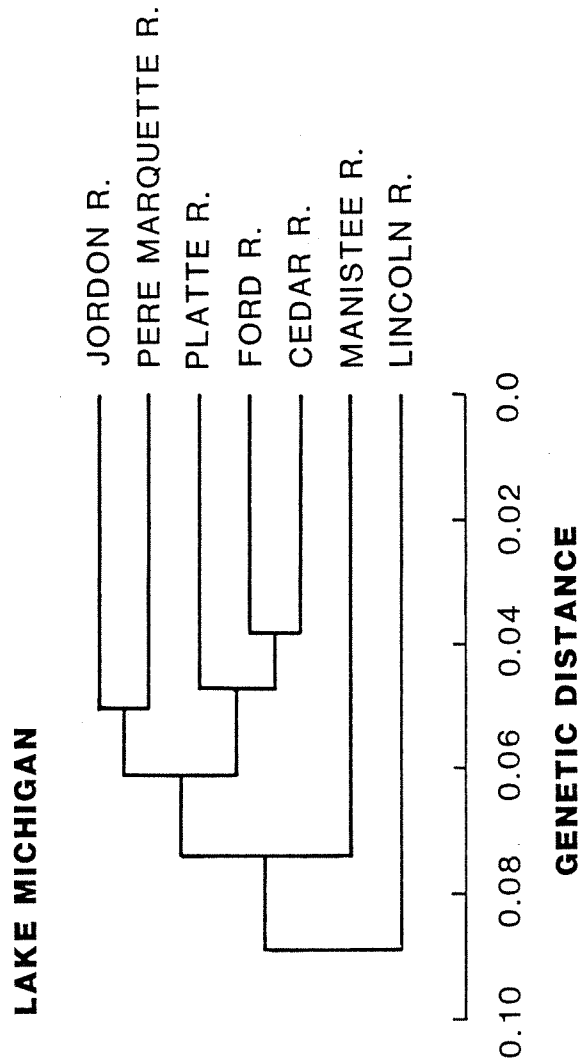
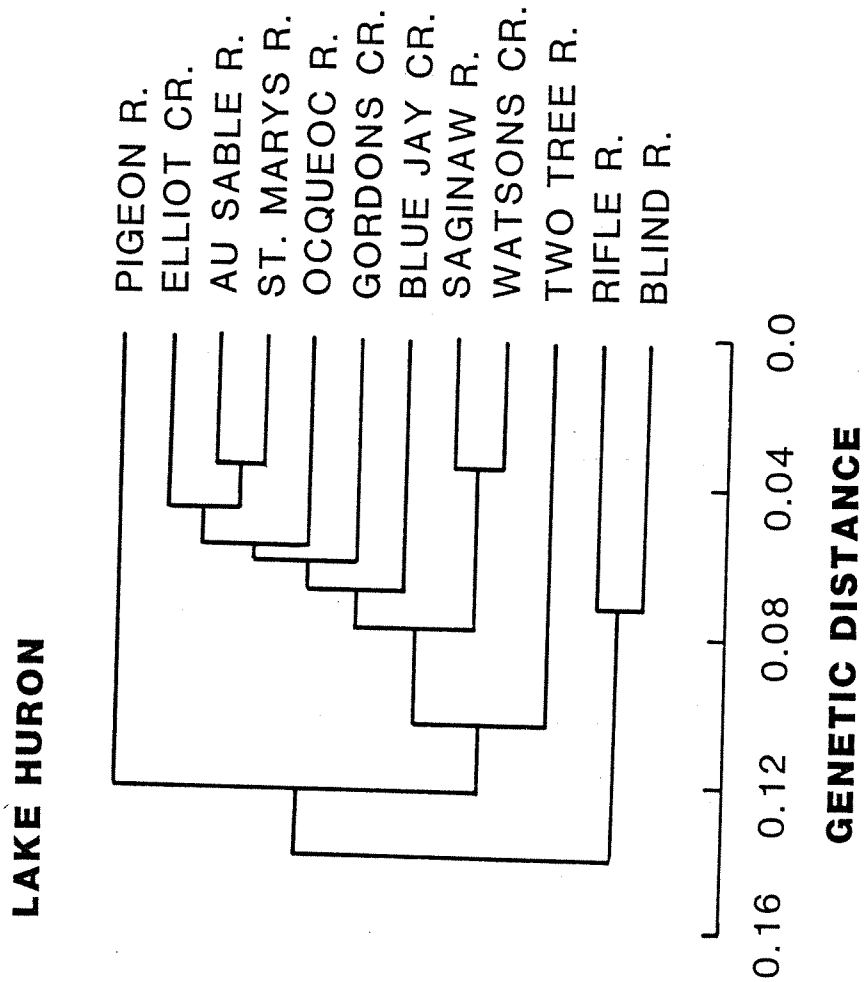

LAKE MICHIGAN
JORDON R.
PERE MARQUETTE R.
PLATTE R.
FORD R.
CEDAR R.
MANISTEE R.
LINCOLN R.
0.10
0.08
0.06
0.04
0.02
0.0
GENETIC DISTANCE

Figure 3. Cluster analysis for sea lamprey ammocoetes collected from drainages in the Lake Huron basin.


LAKE HURON
PIGEON R.
ELLIOT CR.
AU SABLE R.
ST. MARYS R.
OCQUEOC R.
GORDONS CR.
BLUE JAY CR.
SAGINAW R.
WATSONS CR.
TWO TREE R.
RIFLE R.
BLIND R.
0.16
0.12
0.08
0.04
0.0
GENETIC DISTANCE

that ammocoetes in tributaries of Lake Huron were genetically differentiated to a greater extent than ammocoetes in tributaries of Lake Michigan. This hypothesis must be made cautiously, however, because the difference between the values for the two lakes was small and may not be significant.

$F_{ID}$ values (an F-statistic that measures the genetic differentiation of individual ammocoetes relative to the total population in the drainage) were negative for all loci in the data for both lakes with the exception of MDH-1 for Lake Michigan. $F_{IL}$ values (an F-statistic that measures the genetic differentiation of individual ammocoetes relative to the the total population in the lake basin) were negative for all loci in the Lake Michigan data and positive for all loci in the Lake Huron data. Negative values of $F_{ID}$ and $F_{IL}$ indicate excess heterozygosity in drainages and lakes, respectively. Positive values indicate heterozygote deficiencies.

Negative $F_{ID}$ values may be due to small spawning groups (Jacobson 1983). The difference in sign between the $F_{IL}$ values for Lake Michigan and Lake Huron were due to greater excesses of heterozygotes (larger negative $F_{ID}$ values) in ammocoete samples from Lake Michigan and less apparent genetic differentiation (smaller $F_{DL}$ values) among ammocoetes from drainages in the Lake Michigan basin.

Table 3. F-statistics for ammocoetes from tributaries to Lake Michigan and Lake Huron. $F_{ID}$ for individuals relative to drainages, $F_{DL}$ for drainages relative to lakes, and $F_{IL}$ for individuals relative to lakes. Values for loci were weighted before averaging by p(1-p) where p is the frequency of the most common allele.

| | Locus | $F_{ID}$* | $F_{DL}$* | $F_{IL}$* | $F_{DL}$** |
|---|---|---|---|---|---|
| Lake Michigan | | | | | |
| | AGP | -.060 | .026 | -.032 | .023 |
| | MDH-1 | -.042 | .012 | -.029 | .009 |
| | PGI-2 | -.022 | .007 | -.015 | .004 |
| | PGM-1 | -.055 | .022 | -.032 | .019 |
| | mean | -.052 | .020 | -.030 | .017 |
| Lake Huron | | | | | |
| | AGP | -.004 | .032 | .028 | .025 |
| | MDH-1 | .073 | .031 | .102 | .025 |
| | PGI-2 | -.063 | .062 | .003 | .057 |
| | PGM-1 | -.018 | .018 | .000 | .012 |
| | mean | .001 | .030 | .031 | .024 |

*By the method of Nei (1977)

**By the method of Wright (1978)

This is easy to see if one recalls that $(1 - F_{IL}) = (1 - F_{ID})(1 - F_{DL})$. This analysis suggests that the factors that encourage small spawning groups and heterozygote excesses may be more important in the Lake Michigan basin than in the Lake Huron basin.

The results of this study contrast markedly with those obtained by Krueger and Spangler (1981) for sea lamprey from Lake Superior. $F_{ID}$ values for ammocoetes from Lake Superior were positive. Krueger and Spangler (1981) obtained evidence from a cluster analysis of genetic distances that sea lamprey in Lake Superior were subdivided into separate populations.

$F_{DL}$ values for sea lamprey from Lake Michigan and Lake Huron were smaller than the value for sea lamprey from Lake Superior. The average value of $F_{DL}$ obtained by Krueger and Spangler (1981) from the variance of allelic frequencies among drainages was 0.04. Average $F_{DL}$ values obtained by the same method for Lake Michigan and Lake Huron were 0.017 and 0.024, respectively. Jacobson (1983) reports that the total variance in the allelic frequencies of ammocoete samples from Lake Michigan and Lake Huron was due mostly to variation among sampling localities within drainages. It is likely that the $F_{DL}$ value reported by Krueger and Spangler (1981) is inflated because the estimate of the variance among drainages that they used

for calculations contained a substantial component due to variation within drainages. In the present study most of the drainages were sampled repeatedly so that the effects of variation within drainages could be minimized. Nevertheless, it is probable that the values of $F_{DL}$ obtained for Lake Huron and Lake Michigan were also inflated. The fact that $F_{DL}$ values reported for Lake Superior, Lake Michigan, and Lake Huron were small and the probability that those values were inflated suggests that the true $F_{DL}$ values were near zero and that there was little genetic differentiation among drainages in sea lamprey of the upper Great Lakes.

An alternative explanation for the differences between the results for Lake Huron, Lake Michigan, and Lake Superior is that differences exist in the ecology of sea lamprey among the upper Great Lakes. Factors that affect the movement of sea lamprey, such as ship traffic and the types of prey fishes (reviewed by Morman et al. 1980), may differ among the lakes sufficiently to account for the genetic differences observed. Future studies should be directed towards investigating these possibilities.

Additional information from mark-recapture studies of sea lamprey in the Great Lakes would be helpful in evaluating the possible existence of discrete populations. Mark-recapture studies would be particularly useful if

ammocoetes were marked in their natal streams by microtag or by the methods described by Schoonord and Maitland (1983) and then recovered as adults in spawning streams. A project of this sort is currently underway. Lamprey control agents are studying dispersal in adult lamprey by marking transforming sea lamprey in tributaries to Oneida Lake for recapture as spawning adults (J. J. Tibbles, personal communication). It is possible that discrete but genetically undifferentiated populations of sea lamprey exist in Lake Huron and Lake Michigan that were not detected by this electrophoretic analysis. Mark-recapture studies using ammocoetes and spawning adults could be used to investigate this possibility.

Ammocoetes have been used as sample material in all of the population investigations to date. Allendorf and Phelps (1981) discuss a problem inherent in using samples of fry to study the population genetics of anadromous species. Tests for allelic heterogeneity among samples of ammocoetes can be thought of as tests for heterogeneity among the spawning groups that produced the ammocoetes. It is the allelic variation among spawners that is of interest, ammocoetes are sampled only because they are convenient. If the number of ammocoetes in a sample is larger than the number of spawners that produced the ammocoetes, then the degrees of freedom used in the test are inflated and the probability of

rejecting the null hypothesis of allelic homogeneity is inflated as well. This problem probably accounts for a substantial amount of the allelic heterogeneity observed among ammocoete samples in this as well as previous studies. Samples of adults from spawning runs should be used in future electrophoretic studies of sea lamprey population genetics.

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