A Biochemical Genetic Study of Wisconsin Lake Herring (*Coregonus artedii*)

by

Laverne Cleveland

Wisconsin Cooperative Fishery Research Unit

A Thesis

submitted in partial fulfillment of
the requirements for the degree of

MASTER OF SCIENCE

College of Natural Resources

UNIVERSITY OF WISCONSIN

Stevens Point, Wisconsin

March 1982

APPROVED BY THE GRADUATE COMMITTEE

Professor of Fisheries and Advisor

Professor of Fisheries

Professor of Biology

Associate Professor of Biology

Date of Thesis Presentation _____

Typed by _____

ABSTRACT

Genetic and phenotypic variation among Wisconsin populations of lake herring (*Coregonus artedii*) found in Sunset Lake, Pallette Lake, Green Lake, and Lac Courte Oreilles were assessed by vertical starch gel electrophoresis and comparison of meristic traits. Each lake had natural lake herring populations except Sunset Lake in which the population was established by transplant from Pallette Lake in 1961.

Electrophoretic analysis of the enzymes lactate and malate dehydrogenase indicated that gene expression for the enzymes was monomorphic and uniform among the populations. Glycerol-3-phosphate dehydrogenase was monomorphic and uniform in the Sunset and Pallette Lake populations, but polymorphic in Green Lake and Lac Courte Oreilles.

Comparison of fork length/pectoral fin length, fork length/ventral to anal fin distance, fork length/pectoral fin to ventral fin distance, fork length/dorsal fin to adipose fin distance, fork length/internaral width, and fork length/head length in Pallette and Sunset Lakes indicated that a large amount of variation existed between the populations. All of the ratios had significantly different means except fork length/pectoral fin length and fork length/dorsal fin to adipose fin distance.

To estimate the relative influence of genetic and environmental factors on trait variation in Pallette Lake it was assumed that, due to inbreeding, the genetic variance

in the Sunset Lake population was essentially zero. Under this assumption variance partitioning indicated that heredity was responsible for trait variation in Pallette Lake. The relation between lake herring growth and an index of lake productivity indicated that the environment influences growth rates.

ACKNOWLEDGEMENTS

I gratefully thank Dr. Henry Booke, for his excellent supervision, encouragement, and review of the manuscript. Appreciation is extended to Drs. D. Coble, F. Copes, and D. Post for assistance and review of the manuscript.

I thank R. Jesien and M. Imhof, for their assistance, and special thanks is extended to my wife Jean for typing, and her understanding and patience.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

There is extensive morphological and meristic variation within and among species in the subfamily Coregoninae, the whitefishes (family Salmonidae). It is typical for populations of the same species from different lakes to vary in shape, size, rate of growth, and morphometric and meristic characters. So variable and wide ranging is Coregonus artedii, the lake herring, that McPhail and Lindsay (1970) referred to it as the "C. artedii complex", a species group. The whitefishes are presently the most perplexing of all Canadian freshwater fishes to the taxonomist (Woodger, 1976). Morphological and meristic variation in Coregonine fishes has made it difficult to distinguish species by traditional measurements.

Fish proteins have been shown to be less variable than some meristic characters (Lindsey et al., 1970). Hence, considerable attention has been directed during the past decade toward the use of electrophoretic analysis of fish protein molecules for obtaining information about protein structure and genetic relatedness within and among populations (Clayton and Gee, 1969; Loch, 1974; Bailey et al., 1976).

The objectives of this study were to assess genetic variation among populations of lake herring (Coregonus artedii) found in four Wisconsin lakes—Lac Courte Oreilles (Sawyer County), Pallette Lake (Vilas County), Green Lake (Green Lake County), and Sunset Lake (Portage County); to

determine the relation between lake herring growth and lake productivity; and to assess the relative influence of genetic and environmental factors on variation within the species.

The lakes were chosen because of their geographical isolation from each other which assured non-mixing of the gene pools of their respective lake herring populations. Also, the lake herring population of Sunset Lake was established by transplant from Pallette Lake in 1961. Thus, the data from traits which did not change between the Pallette and Sunset Lake populations could be pooled and used as a control in comparisons with Lac Courte Oreilles and Green Lake.

MATERIALS AND METHODS

One hundred and nine lake herring were captured in Green Lake on October 22 and 23, 1974. The fish were taken at depths of 18 - 60m with a 62mm mesh gill net. One hundred and five specimens were collected in Pallette Lake during the spawning season on November 19, 1974. These fish were captured in 0.31 - 0.92m of water with a 23 x 1m, 6 x 6 mm mesh straight seine. Lake herring were collected in Sunset Lake during the spawning season on November 17 and 18, 1975; 51 specimens were collected in 0.61 - 1.2m of water, with a 230-volt electroshocker, and 14 were captured in 50mm mesh and 1 in 72mm mesh multifilament nylon gill nets. One hundred and twenty-six lake herring were collected from the north shore of Lac Courte Oreilles during the spawning sea-

son on November 21, 1975. The fish were captured with a 19.5mm mesh bag seine in 0.31 to 0.92m of water. The number of fish electrophoretically examined from Green Lake, Pallette Lake, Sunset Lake, and Lac Courte Oreilles were 102, 105, 66 and 79, respectively.

To help prevent loss of enzyme activity, all specimens were packed on ice immediately after capture and were later stored at 0 to -4 C (32 to 24.8 F).

Samples of red and white muscle tissue were taken from the left side of each frozen fish along the lateral line (red muscle) and from the region anterior to the dorsal fin just above the lateral line (white muscle). The samples were homogenized in ice chilled distilled water with a teflon and glass tissue grinder. The ratio of tissue to water was 1g:3ml. The extracts were centrifuged at 20,000g at 0 C (32 F) for 45 minutes. The clear supernatant was then decanted and stored at 0 to -4 C (32 to 24.8 F) for later vertical starch gel electrophoresis.

Analysis of lake herring specimens for lactate dehydrogenase (LDH = L-lactate:NAD oxidoreductase) was carried out, in general, by the methods of Bailey et al. (1976). Starch gels were 13.4% gels in 0.0013M citric acid, adjusted to pH 8.2 with tris[1] (Clayton and Gee, 1969). The electrode buffer was 0.04M citric acid, adjusted to pH 8.5 with tris. Electro-

---

[1]Tris-(hydroxymethyl)-aminomethane (2-amino-2-hydroxymethyl)-1-3-propanediol). Aldrich Chemical Company, Inc.

phoresis was conducted at 4 - 5 C (39.4 - 41 F) with 210 - 220 volts for 14 - 15 hours. The LDH bands were made visible by slicing the gels into two layers and placing each layer in 100 ml of staining solution for 15 - 20 minutes, at room temperature in the dark. The staining solution contained 20 mg nicotinamide-adenine-dinucleotide, 15 ml Nitro BT[2], 10 mg phenazine methosulphate, 10 ml of 2M lithium lactate of pH 7.0 and 90 ml of 0.15M diethanolamine adjusted to pH 9.0 with HCl (Clayton and Gee, 1969). The gels were then washed in distilled water and stored in the dark in methanol, acetic acid, and water (5:1:5 by volume).

Analysis of malate dehydrogenase (MDH = L-malate:NAD oxidoreductase) was carried out in the same manner except that the gel buffer was adjusted to pH 5.5 with N(-3-aminopropyl)-morpholine (Clayton and Tretiak, 1972). Also, 10 ml of 2M malic acid adjusted to pH 7.0 with NaOH was substituted in the staining solution for lithium lactate, and the staining time was increased to 1 - 2 hours.

Analysis of glycerol-3-phosphate dehydrogenase (G-3-PD = L-glycerol-3-phosphate:NAD oxidoreductase) was the same as that for LDH except that 10 ml of 2M-glycerol phosphate was substituted in the staining solution for lithium lactate, and the staining time was increased to 1 - 2 hours.

Electrophoretic banding patterns were characterized for LDH and MDH. Each G-3-PD electropherogram was scored

---

[2]Nitro Blue Tetrazolium, (2,2' -D-p-nitrophenyl-5,5' diphenylene) ditetrazolium Chloride), Sigma Chemical Co., St. Louis, MO.

according to the genetic model of Clayton et al. (1973). Genotypes were assigned to the electrophoretic phenotypes of G-3-PD on the basis of the number of bands present, staining intensity of the bands, and relative mobilities of the bands. Band mobility was determined primarily by the subunit composition of the isozymes. The mobility of the A2A2 isozyme was greater than the A1A1. The B3B3 isozyme was more mobile than the B2B2 which was more mobile than the B1B1 isozyme (Figures 1 and 2). After scoring, the phenotype frequencies of G-3-PD were tested for Castle-Hardy-Weinberg equilibrium (chi-square) by use of the equation

$$(B1+B2+B3)^2 = B1^2 + 2B1B2 + B2^2 + 2B1B3 + 2B2B3 + B3^2$$

(Li, 1976). The Castle-Hardy-Weinberg equilibrium principle assumes that in randomly mating populations, in the absence of selection, mutation, or migration, the expected distribution of phenotypes is determined by the random combination of the total number of alleles (Utter et al. 1974).

The following measurements were made on 50 preserved specimens from both Pallette and Sunset Lakes: pectoral fin to ventral fin distance, ventral fin to anal fin distance, and dorsal fin to adipose fin distance (Koelz, 1929); pectoral fin length, fork length, and head length (Hubbs and Lagler, 1964); and internaral width (Svärdson, 1959). Ventral fin to anal fin distance, pectoral fin length, and fork length were measured for 50 specimens from Green Lake and 48 from Lac Courte Oreilles. To adjust for the differences

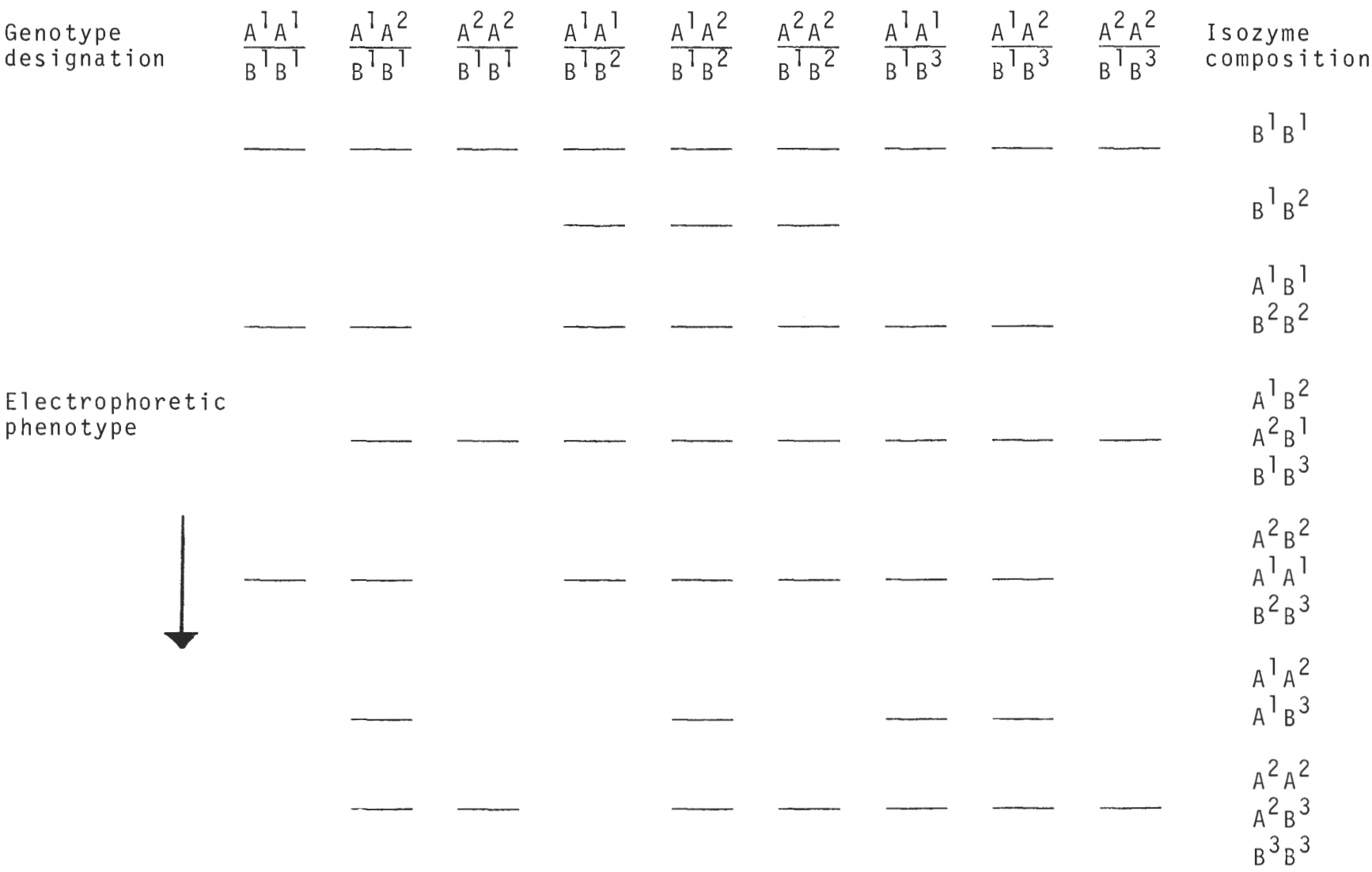

Figure 1. Diagram of lake herring G-3-PD genotypes that contain B^1 subunit showing assumed composition of the isozymes (Clayton et. al., 1973) Arrow indicates direction of migration.

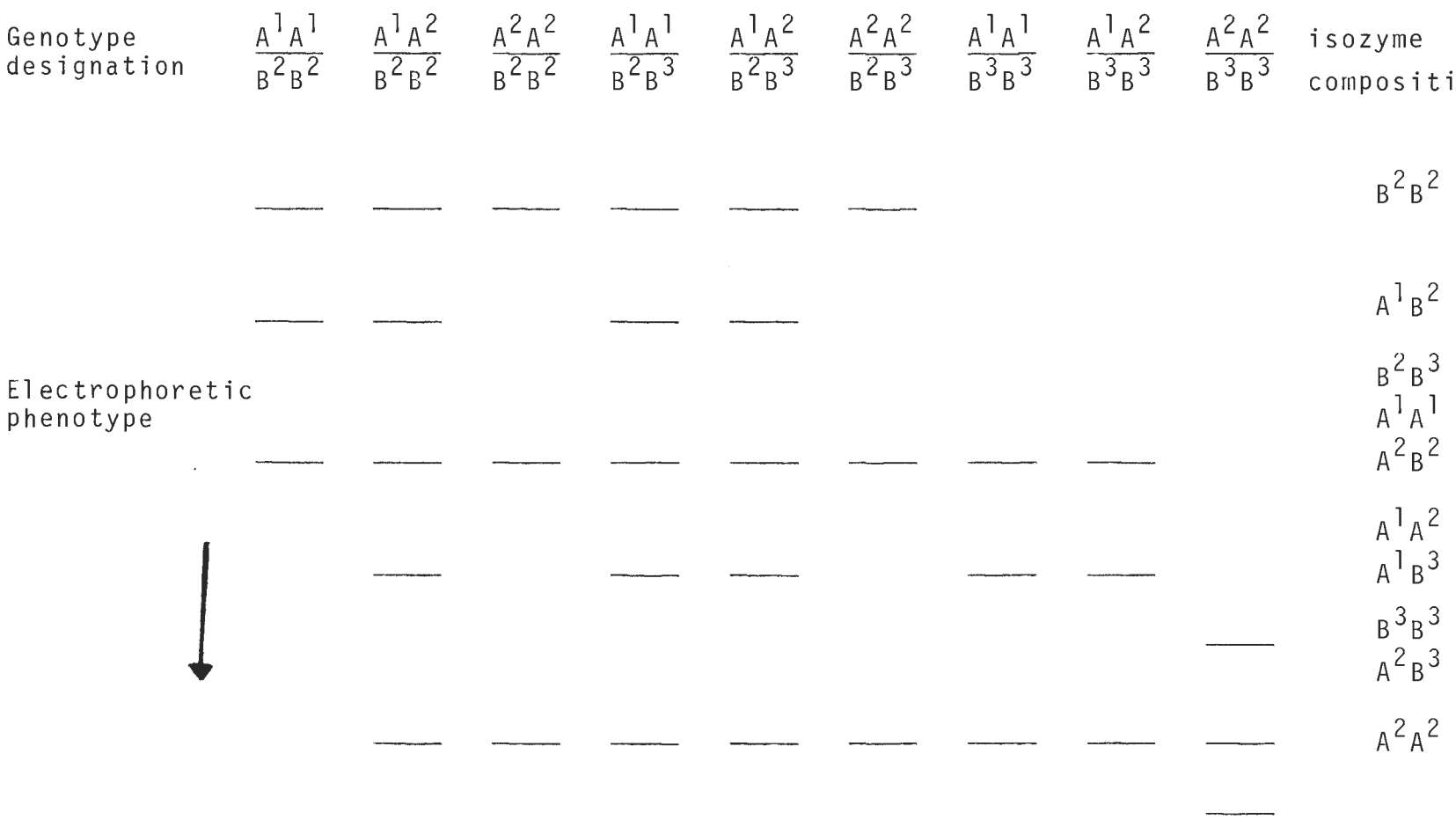

Figure 2. Diagram of lake herring G-3-PD genotypes that lack the B^1 subunit showing assumed subunit composition of the isozymes (Clayton et al., 1973). Arrow indicates direction of migration.

in trait measurements due to the overall size of the fish, each measurement was converted to a function of fork length. This was accomplished by dividing each measurement into the fork length of the fish (Appendix A).

A t-test and a two tailed F-test were used to compare the means and variances (Snedecor, 1965) of the trait ratios in Pallette and Sunset Lakes. When one cannot assume that the variances of two independent samples are equal, the standard t is replaced by the quantity

$$t = \frac{\bar{X}_1 - \bar{X}_2}{\sqrt{\frac{S_1^2}{n_1} + \frac{S_2^2}{n_2}}}$$

and the corresponding degrees of freedom becomes

$$df = \frac{(n_1-1)(n_2-1)(1+C)^2}{(n_1-1)C^2+(n_2-1)} \quad \text{where} \quad C = \frac{n_1 S_2^2}{n_2 S_1^2}.$$

Mean fork length/pectoral fin lengths ratios of fish from Pallette and Sunset Lakes were not significantly different, therefore the values were pooled and compared to Green Lake and Lac Courte Oreilles by one-way analysis of variance followed by a multiple means comparison test (Snedecor, 1965). The variances of the ratios of fork length/ventral fin to anal fin distance, fork length/pectoral fin to ventral fin distance, fork length/internaral width, and fork length/ head length in Pallette and Sunset Lakes were partitioned by the method outlined by Falconer (1960). Variance of the traits

in Pallette Lake was partitioned by use of the equation

$$V_P = V_G + V_E$$

where V_P is the phenotypic variance, V_G is the genetic contribution to phenotypic variance, and V_E is the environmental contribution to the phenotypic variance (Falconer, 1960).

Speciemens were aged by standard techniques (Lagler, 1956). Scales for age determination were removed from the dorso-lateral region of 36 fish from Pallette Lake, 39 fish from Green Lake, and 34 from Lac Courte Oreilles. Each annulus and the scale margin was considered as one year growth for fish from each lake. Total length at annulus formation was back calculated for fish from Green Lake (Ricker, 1975). Age and growth data for 71 fish from Sunset Lake were obtained from Jesien (1977). All scale readings except those in Sunset Lake were verified by Mark Imhof, a fellow graduate student. Mean total lengths were plotted against age to show differences in growth rates among the four populations.

The Morphoedaphic Index (MI) (Ryder, 1965) was calculated for the four lakes (Table 1). Total dissolved solids were estimated by multiplying the known conductivity by 0.55 (Standard Methods, 14th ed.), and mean depth was calculated from the area and volume of the lakes. The MI for each lake was compared with the mean total length of 3-year-old fish from each population to determine the relation between fish growth and lake productivity.

Table 1. Geographical location and physiochemical description of Sunset Lake, Green Lake, Lac Courte Oreilles, and Pallette Lake.

Lake	Location Description	Maximum Depth (m)	Mean Depth (m)	Area (ha)[a/]	Volume (m^3)	Shorline (km)	Conductivity unhos/cm	MI[b/]
Sunset Lake	Portage Co., WI Sec. 22, T-24-N R-10-E	17	10	26	2.6×10^6	2.0	273	4.6
Green Lake	Green Lake Co., WI T-15, 16 N R-12-13-E	70	31	2,865	8.882×10^8	34	363	2.0
Lac Courte Oreilles	Sawyer Co., WI T-39, 40 N R-8, 9 W	27	10	2,040	2.04×10^8	41	102	2.0
Pallette Lake	Vilas Co., WI Sec. 3, T-4-N R-7-E	20	10	70	7.0×10^6	3.5	26	0.5

a/ 1 ha = 2.47 acres

b/ $MI = \frac{\text{Total dissolved solids}}{\text{mean depth (feet)}} = \frac{\text{Conductivity} \times 0.55}{\text{mean depth (feet)}}$

RESULTS

Because the full complement of LDH isozymes was not present in either red or white muscle of lake herring, analysis for LDH was not useful in distinguishing phenotypes. Electrophoretic analysis of lake herring red muscle tissue for isozymes of LDH showed only one electrophoretic phenotype for each population (Figure 3). After electrophoresis for 14-15 hours the number and relative mobilities of bands for LDH were found to be uniform among the four populations. White muscle also contained one set of LDH isozymes but only the 5 bands located at the cathodal region were present.

Electrophoretic analysis of white muscle tissue for isozymes of MDH showed one electrophoretic phenotype for each population (Figure 4). The electrophoretic mobility of MDH isozymes from lake herring muscle was similar to that of lake whitefish (C. clupeaformis) (Figure 4). Attempts to analyze lake herring red muscle tissue for isozymes of MDH resulted in poor electrophoretic separation and staining, thus, analysis was limited to white muscle tissue.

The G-3-PD system in lake herring white muscle was polymorphic for the populations in Lac Courte Oreilles and Green Lake. The $A^1A^1B^1B^2$, $A^1A^1B^1B^3$, $A^1A^1B^2B^3$, $A^1A^1B^3B^3$, $A^1A^2B^1B^2$, $A^1A^2B^1B^3$, $A^1A^2B^3B^3$, $A^1A^2B^2B^2$, $A^1A^2B^2B^3$, $A^1A^2B^1B^1$, $A^2A^2B^1B^2$, $A^2A^2B^2B^2$, $A^2A^2B^2B^3$, and $A^2A^2B^1B^3$ G-3-PD genotypes were observed in Lac Courte Oreilles (Figure 5: $A^1A^1B^1B^3$, $A^1A^1B^3B^3$, $A^1A^2B^1B^2$, and $A^2A^2B^1B^3$ not shown). The $A^1A^1B^1B^3$,

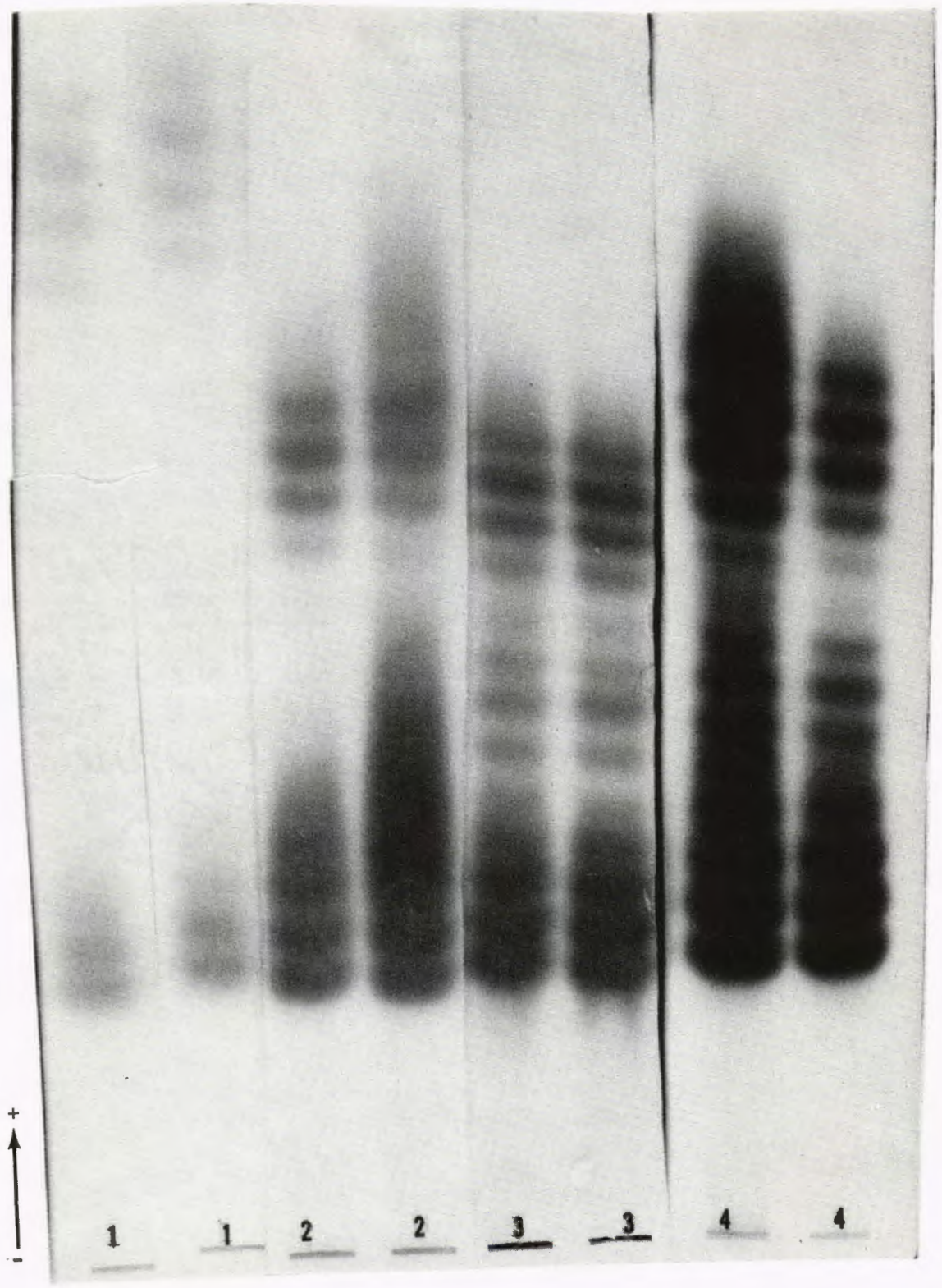

Figure 3. LDH phenotypes of lake herring red muscle. 1) Pallette Lake, 15 hours; 2) Sunset Lake, 14 hours; 3) Lac Courte Oreilles, 14 hours; and 4) Green Lake, 14 hours.

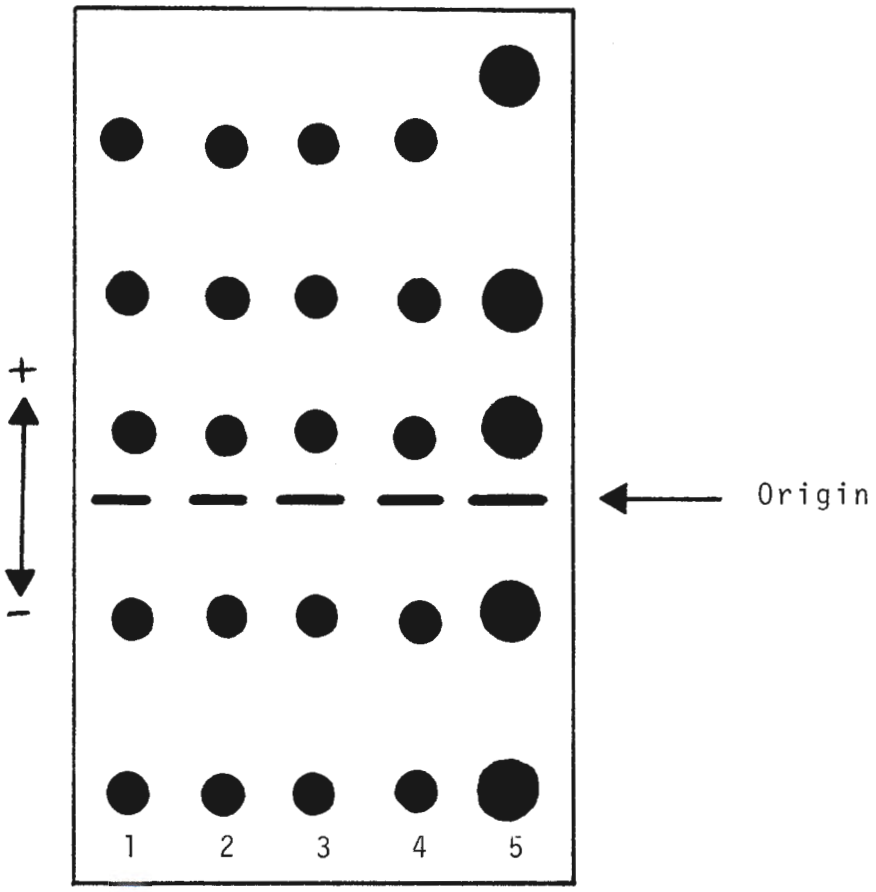

Figure 4. MDH electrophoretic phenotypes of lake herring and whitefish white muscle. 1) Pallette Lake; 2) Sunset Lake; 3) Lac Courte Oreilles; 4) Green Lake; 5) Lake whitefish from Lake Michigan.

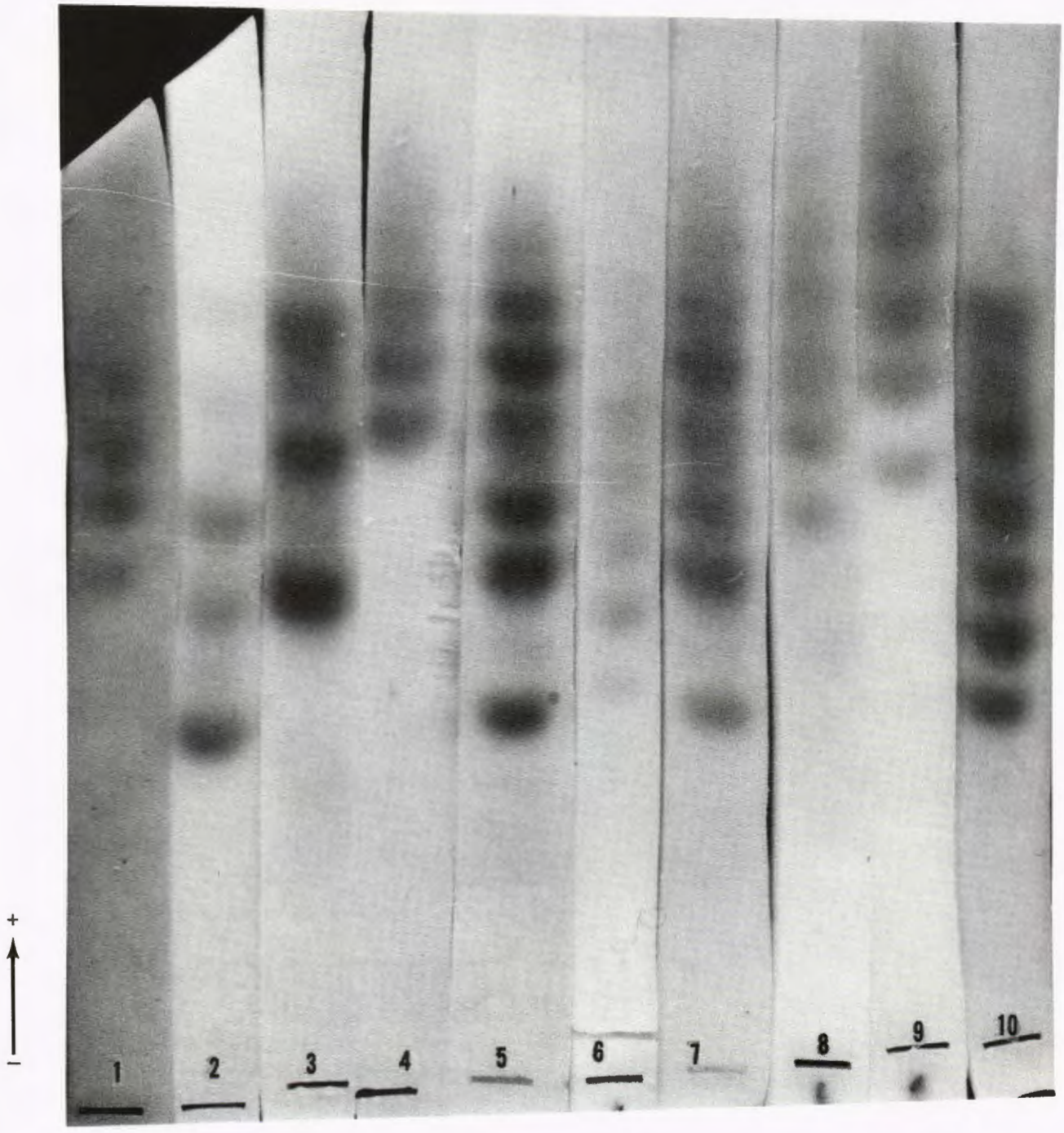

Figure 5. G-3-PD genotypes of lake herring white muscle in Lac Courte Oreilles.

1) $A^1A^1B^2B^3$: 2) $A^2A^2B^2B^2$; 3) $A^2A^2B^2B^3$; 4) $A^1A^2B^3B^3$; 5) $A^1A^2B^1B^1$; 6) $A^1A^2B^2B^3$; 7) $A^1A^2B^1B^3$; 8) $A^1A^2B^2B^2$; 9) $A^1A^1B^1B^2$; and 10) $A^2A^2B^1B^2$.

$A^1A^1B^1B^1$, $A^1A^1B^3B^3$, $A^1A^2B^1B^3$, $A^1A^2B^1B^1$, $A^1A^2B^3B^3$, $A^2A^2B^1B^1$, $A^2A^2B^1B^3$ and $A^2A^2B^3B^3$ G-3-PD genotypes were present in Green Lake (Figure 6: $A^1A^1B^1B^3$, $A^1A^1B^1B^1$, $A^1A^1B^3B^3$, and $A^2A^2B^3B^3$ not shown). Only the $A^2A^2B^1B^1$ genotype was observed in Pallette and Sunset Lakes (Figure 6, Electropherogram 1). The various A allele isozymes were not scored because they were difficult to distinguish on the electropherograms. Many of them had similar mobilities. However, the B allele isozymes were easily distinguished and their frequencies for G-3-PD indicated that each population was different except those in Pallette and Sunset Lakes. The G-3-PD B alleles (Table 2A) and their genotype frequencies (Table 2B) were significantly different ($p \leq 0.001$) for each population except those in Pallette and Sunset Lakes, which were identical. Banding patterns for G-3-PD were comparable to those obtained by Clayton et al. (1973) for lake herring and lake whitefish.

Castle-Hardy-Weinberg equilibrium was found for the Lac Courte Oreilles ($p \geq 0.68$) and Green Lake ($p \geq 0.99$) populations (Table 3). Castle-Hardy-Weinberg equilibrium could not be calculated for Pallette and Sunset Lakes since the populations were monomorphic for the B1 allele.

A high degree of variation in fork length/meristic trait existed among the Pallette and Sunset Lake populations. All trait ratios had significantly different ($p \leq 0.05$) means except fork length/pectoral fin length and fork length/dorsal to adipose fin distance (Table 4). The mean of fork length/pectoral fin length ratios of fish pooled from

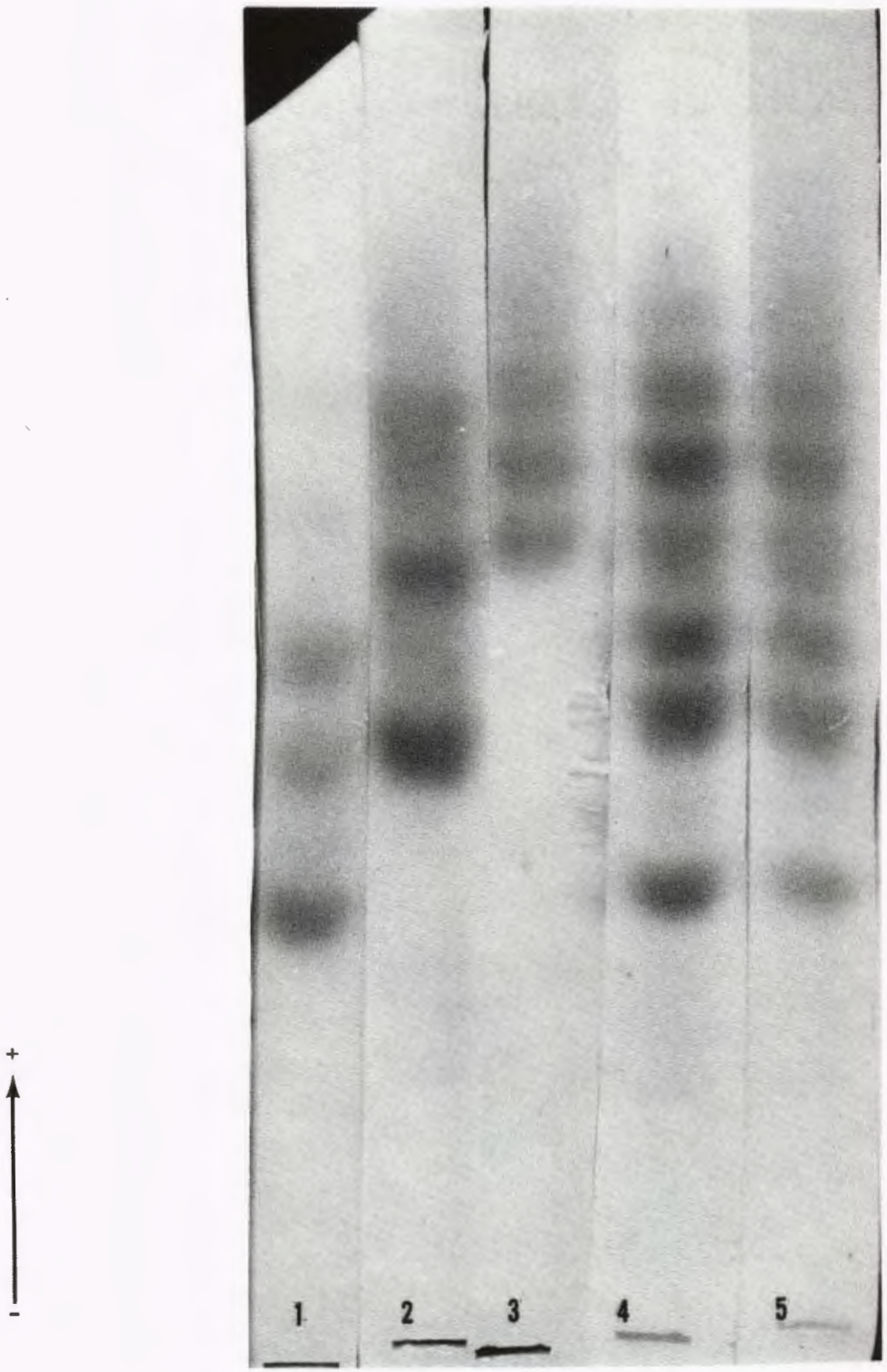

Figure 6. G-3-PD genotypes of lake herring white muscle in Green Lake.

1) $A^1A^2B^1B^1$: 2) $A^2A^2B^1B^3$; 3) $A^1A^2B^3B^3$; 4) $A^1A^2B^1B^1$; and 5) $A^1A^2B^1B^3$. Only electropherogram 1 was observed in Pallette and Sunset Lakes.

Table 2. Chi-square comparison of (A) G-3-PD B^X alleles, and (B) G-3-PD genotype frequencies among lakes (X^2 = chi-square value, df = degrees of freedom)

		Green Lake vs Lac Courte Oreilles	Pallette Lake vs Lac Courte Oreilles	Sunset Lake vs Lac Courte Oreilles	Pallette Lake vs Green Lake	Sunset Lake vs Green Lake	Sunset Lake vs Pallette Lake
A.	X^2	87.5[a/]	180.8[a/]	125.8[a/]	85.2[a/]	56.2[a/]	0
	df	2	2	2	2	2	2
B.	X^2	86.7[b/]	155.8[b/]	116.9[b/]	79.3[b/]	54.4[b/]	0
	df	5	5	5	5	5	5

a/ Allelic frequencies significantly different $P \leq 0.001$.

b/ Genotype frequencies significantly different $P \leq 0.001$.

Table 3. Chi-square comparison of the observed and expected Castle-Hardy-Weinberg genotype frequencies for the G-3-PD B alleles (O = observed number, e = expected Castle-Hardy-Weinberg number).

		B^1B^1	B^1B^2	B^2B^2	B^1B^3	B^2B^3	B^3B^3	Total	Chi-Square
Lac Courte Oreilles	o	7	23	8	19	15	4	76	3.17[a/]
	e	10.3	19.8	9.6	15.4	14.9	5.8		
Green Lake	o	46	0	0	43	0	13	102	0.34[b/]
	e	44.5	0	0	45.5	0	11.6		

a/ $p \geq 0.68$, df = 5

b/ $p \geq 0.99$, df = 5

Table 4. Comparison of means of meristic trait ratios[a/] for fish from Sunset and Pallette Lakes.

Trait Ratios	Sunset Lake	Pallette Lake	Degrees of Freedom
fork length/ pectoral fin length	6.5 ±0.4	6.6 ±0.7	75
fork length/ventral to anal distance	3.8 ±0.1	3.9[b/] ±0.3	68
fork length/pectoral to ventral distance	3.4 ±0.2	3.5[b/] ±0.3	69
fork length/dorsal to adipose distance	2.8 ±0.11	2.8 ±0.23	70
fork length/ internaral width	34.3 ±2.4	36.7[c/] ±4.2	78
fork length/ head length	5.3 ±0.2	4.7[c/] ±0.4	65

a/ Values shown are mean ± standard deviations of ratios that were obtained by dividing fork length (mm) by individual trait measurements (mm) (n=50 for each trait).

b/ Mean significantly different from Sunset Lake ($p \leq 0.05$).

c/ Mean significantly different from Sunset Lake ($p \leq 0.01$).

Pallette and Sunset Lakes was not significantly different from that for fish from Green Lake, but differed significantly ($p \leq 0.01$) for fish in Lac Courte Oreilles. The ratio of fork length/pectoral fin length was also different between Lac Courte Oreilles and Green Lake (Table 5). The variances of all trait ratios in Pallette and Sunset Lakes were significantly different ($p \leq 0.05$) (Table 6).

Partitioning of the variance (Falconer, 1960) to determine the influence of genetic and environmental factors on trait variation indicated the following heritability values for the various traits in the Pallette Lake population: Fork length/ventral fin to anal fin distance, 82%; fork length/pectoral fin to ventral fin distance, 77%; fork length/internaral width, 67%; and fork length/head length, 86% (Table 7).

The oldest lake herring aged in Green Lake, Sunset Lake, Pallette Lake, and Lac Courte Oreilles were 8, 8, 5, and 3 years old, respectively. Age 3 fish from Sunset Lake were the longest followed in order by age 3 fish from Pallette Lake, Green Lake, and Lac Courte Oreilles (Figure 7).

Lake productivity as determined by the morphoedaphic index was highest in Sunset Lake followed in order by Green Lake and Lac Courte Oreilles, and lowest in Pallette Lake. In general, mean total length of age 3 fish was positively related to lake productivity (Figure 8).

Table 5. Comparison of the ratios of fork length/pectoral fin length[a/] from the pooled Pallette-Sunset Lake Control, Lac Courte Oreilles, and Green Lake populations.

Trait Ratio and Sample Size (n)	Pooled Pallette-Sunset Control	Lac Courte Oreilles	Green Lake
Fork length/ pectoral fin length	6.5	6.9[b/]	6.4[c/]
	±0.6	±0.6	±0.7
n	100	48	50

a/ Values shown are means ± standard deviations of ratios that were obtained by dividing the fork length (mm) of individual fish by its pectoral fin length (mm).

b/ Mean significantly different from control ($p \leq 0.01$).

c/ Mean significantly different from Lac Courte Oreilles but not from control ($p \leq 0.01$).

Table 6. Comparison of variances of meristic trait ratios[a/] for fish from Sunset and Pallette Lakes.

Trait Ratios	Sunset Lake	Pallette Lake	Degrees of Freedom
Fork length/ pectoral fin length	0.14	1.48[b/]	49,49
Fork length/ventral to anal distance	0.02	0.11[b/]	49,49
Fork length/pectoral to ventral distance	0.03	0.13[b/]	49,49
Fork length/dorsal to adipose distance	0.01	0.05[b/]	49,49
fork length/ internaral width	5.6	17.3[b/]	49,49
Fork length/ head length	0.02	0.14[b/]	49,49

a/ Ratios were obtained by dividing fork length (mm) by individual trait measurements (mm) (n=50 for each trait).

b/ Variance significantly different from Sunset Lake ($p \leq 0.05$).

Table 7. Partitioned variances[a/] of meristic trait ratios for fish from Sunset and Pallette Lakes.

Population	Variance Components	Observed Variances: Fork length/ Ventral to anal distance	Fork length/ Pectoral to ventral distance	Fork length/ Internaral width	Fork length/ Head length
Outbred (Pallette)	$V_P=V_G+V_E$[b/]	0.11	0.13	17.30	0.14
Inbred (Sunset, Assuming $V_G=0$)	V_E	0.02	0.03	5.64	0.02
Difference	V_G	0.09	0.10	11.65	0.12
Heritability	V_G/V_P	0.82	0.77	0.67	0.86

a/ Variances were estimated from ratios that were obtained by dividing form length (mm) by individual trait measurements (mm) (n=50 for each trait).

b/ V_P = Variance of phenotypes
V_G = Variance of genotypes
V_E = Environmental variance

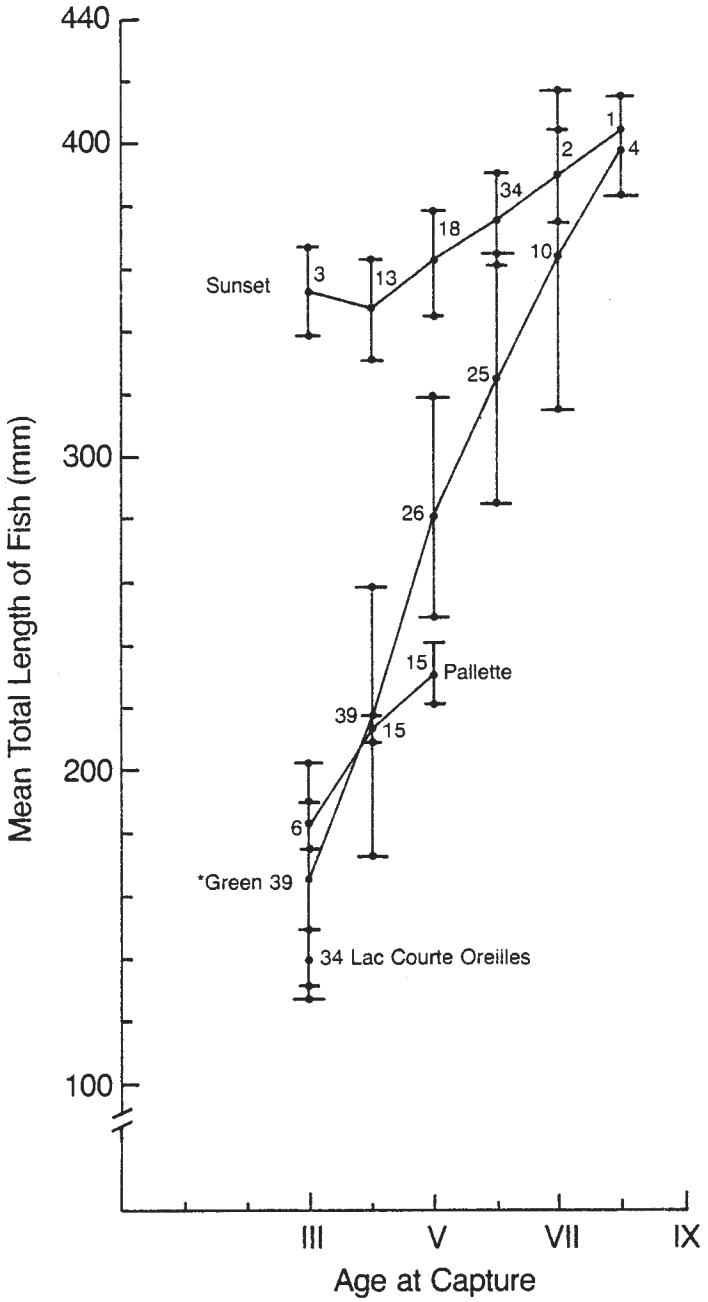

Figure 7. Mean total length vs age at capture of lake herring from each population. Numbers beside points indicate the sample size aged and the vertical lines are standard deviation of points. Fish were caught during October and November.

*Total length at annulus formation was back calculated for fish in Green Lake.

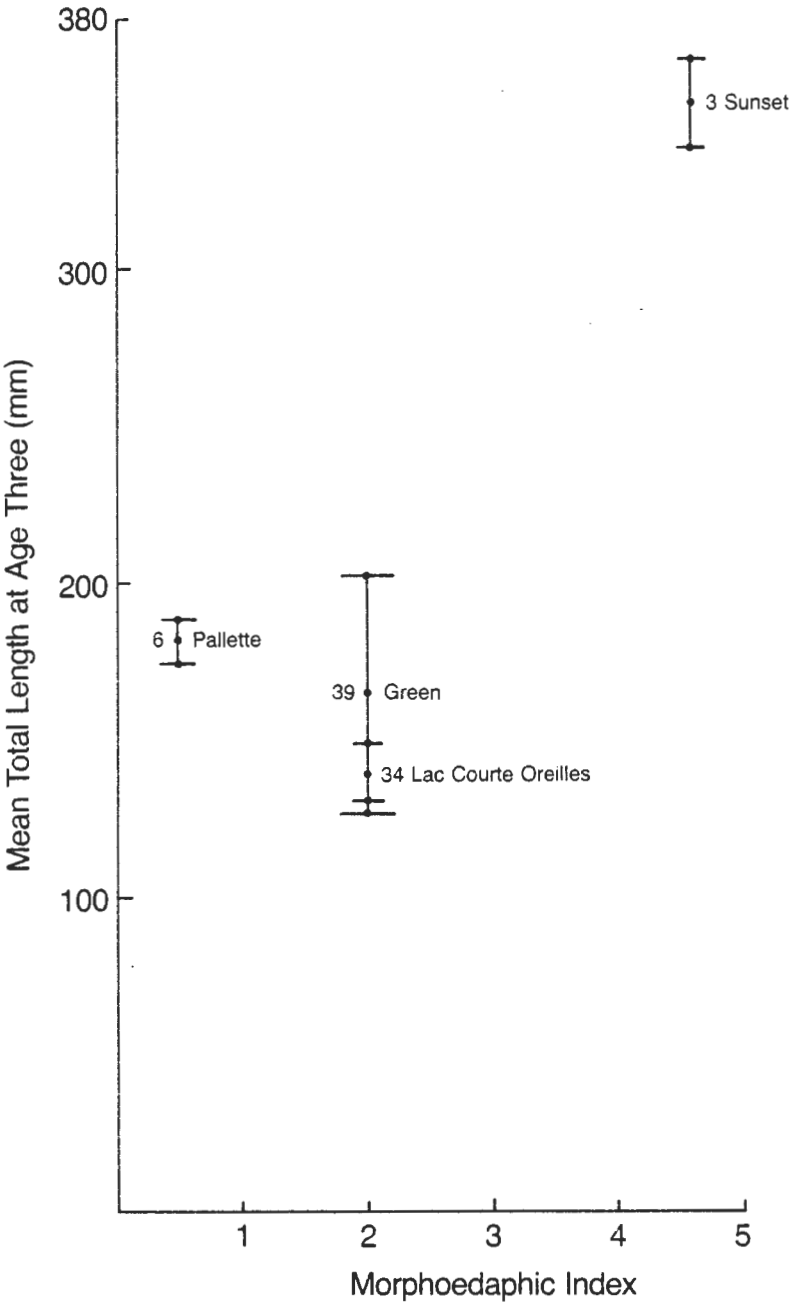

Figure 8. Mean total length of lake herring at age 3 vs morphoedaphic index. Numbers beside points are sample sizes that were aged and vertical lines are standard deviation of points.

*Total length at annulus formation was back calculated for fish in Green Lake.

DISCUSSION

Geographic isolation of the lake herring populations had no recent effect on the genes responsible for LDH and MDH production in muscle. Although gene expression for the LDH and MDH enzymes was uniform and monomorphic for each population of lake herring, LDH has been shown to be polymorphic in other salmonids (Bouch and Ball, 1968; Williscroft and Tsuyuki, 1970; Northcote et al. 1970; Bailey et al. 1976), and in lake whitefish (Clayton and Franzin, 1970).

The presence of the single $A^2A^2B^1B^1$ genotype for G-3-PD in Pallette and Sunset Lakes suggest that the populations have either evolved to the homozygotic state for the enzyme or that the other possible genotypes have been selected against or never existed in the Pallette population. The higher frequencies for the B^1 allele compared to B^2 and B^3 alleles indicated that there may have been selection for B^1 alleles in each population (Table 8). Castle-Hardy-Weinberg equilibrium assumes that individuals of different genotypes make equal contributions to the next generation. However, if the proportion of surviving individuals differs from genotype to genotype, the zygotic frequencies may not fit Castle-Hardy-Weinberg expectations, and gene frequencies may not remain constant from generation to generation. Thus, selection against certain genotypes may suppress or eliminate alleles from populations.

The similarity of the allele and genotype frequencies for G-3-PD in Pallette and Sunset Lake implies that the

Table 8. Observed B allele frequencies (p, q, and r) for G-3-PD in Green Lake, Lac Courte Oreilles, Pallette Lake, and Sunset Lake.

Locations	Alleles			
	B_1	B_2	B_3	TOTAL
Green Lake	135 p = 0.661	0 q = 0	69 r = 0.338	204
Lac Courte Oreilles	56 p = 0.368	54 q = 0.355	42 r = 0.276	152
Pallette Lake	210 p = 1	0 q = 0	0 r = 0	210
Sunset Lake	132 p = 1	0 q = 0	0 r = 0	132

transfer of lake herring from Pallette to Sunset Lake in 1961 had no effect on the gene pool. However, a change in gene frequencies between the populations may not be evident after only 15 years since the process of change by mutation may require a much longer period of time. But, the absence of the B^2 allele in Green Lake and the B^2 and B^3 allele in Pallette and Sunset Lakes indicate that the G-3-PD system in Wisconsin lake herring may be evolving in a manner that favors homozygosity of G-3-PD.

Similarity of variation in the ratios of fork length/pectoral fin length and fork length/dorsal fin to adipose fin distance reinforces the genetic data from Pallette and Sunset Lakes, where no differences were also observed for isozymes of LDH, MDH, and G-3-PD. When compared to the pooled Pallette and Sunset control population, the Lac Courte Oreilles population showed more variation than did the Green Lake population and was significantly different for both pectoral fin length ratio and isozymes of G-3-PD. The Green Lake population differed only for isozymes of G-3-PD.

An outbred population is a large, randomly mating, population that exhibits characteristics typical of the entire gene pool of the species. An inbred population, as was assumed in Sunset Lake, could be due to restriction in lake size or area, and thus matings would occur between relatives. New gene frequencies are established in small inbreeding populations that depart from the gene frequencies observed in an

outbred gene pool. Inbreeding rapidly increases homozygosity in a population, and produces individuals with identical genotypes (Strickberger, 1968). In partitioning the variances of trait ratios of fish from Pallette Lake, it was assumed that, due to inbreeding, the genotype variance for the subpopulation in Sunset Lake was essentially zero. Hence, measurement of the phenotypic variance of fish from Sunset Lake provided an estimate of the environmental variance. An estimate of the genetic variance of the Pallette Lake population was obtained by subtracting the estimated environmental variance from the phenotypic variance measured in the outbred mother population in Pallette Lake. Following the assumption that the genotypic variance in the Sunset Lake population was zero, the variance partitioning results indicated that heredity is responsible for a higher percentage of variation in Pallette Lake fish than environmental factors. The genotypic variance estimates for the Pallette Lake population are probably too low because the genotypic variance in Sunset Lake is likely not zero. Similar heritability values have been reported for white spotting and butterfat content in cattle, and thickness of back fat in pigs (In: Falconer, 1960).

In the more productive Sunset Lake, fish grew to a greater size at respective ages up to age six. Apparently growth conditions were better in Sunset Lake than in Pallette Lake which allowed the greater expression of the genetic potential of Sunset-Pallette stock for growth.

Although the data allowed comparison of growth rates among the four lakes, sample sizes for some ages were small. Additional sampling would provide more confidence in comparison of growth among the lakes. The relation between growth and index of lake productivity indicated that the environment influences growth rates. This indication is consistent with the variance partitioning results from Pallette and Sunset Lakes, which also indicated that the environment affects morphology.

In conclusion, with the exception of the populations in Pallette and Sunset Lakes which, in general, were the same, the biochmeical and meristics results indicated that each population was different. Three enzyme systems in lake herring from Sunset Lake have remained genetically unchanged from those of the mother population in Pallette Lake for 15 years. These results suggest that lake herring may be transferred from one environment to another for short periods of time without gentic change occurring. Further studies, including the return of a sample of Sunset Lake herring to Pallette Lake to determine if the growth rate normally exhibited there is attained, the transferring of other lake herring to different environments, and analysis of other enzyme systems would be helpful for confirming this conclusion. Analysis of other enzyme systems for lake herring populations in Wisconsin lakes would also be beneficial in determining

the extent of genetic variation within and among the populations.

REFERENCES

Bailey, G. S., H. Tsuyuki, and A. C. Wilson. 1976. The number of genes for lactate dehydrogenase in salmonid fishes. J. Fish. Res. Board Can. 33:760-767.

Bouck, G. R., and R. C. Ball. 1968. Comparative electrophoretic patterns for lactate dehydrogenase in three species of trout. J. Fish. Res. Board Can. 25:1323-1331.

Clayton, J. W., and J. H. Gee. 1969. Lactate dehydrogenase isozymes in longnose and blacknose dace (Rhinichthys cataratae and R. atratulus) and the hybrid. J. Fish. Res. Board Can. 26:3047-3053.

Clayton, J. W., and W. G. Franzin. 1970. Genetics of multiple lactate dehydrogenase in muscle tissue of lake whitefish (Coregonus clupeaformis). J. Fish. Res. Board Can. 27:1115-1121.

Clayton, J. W., D. N. Tretiak, and A. H. Kooyman. 1971. Genetics of multiple malate dehydrogenase in skeletal muscle of Walleye (Stizostedion vitreum). J. Fish. Res. Board Can. 28:1005-1008.

Clayton, J. W., and D. N. Tretiak. 1972. Amine-citrate buffers for p^H control in starch gel electrophoresis. J. Fish. Res. Board Can. 29:1169-1172.

Clayton, J. W., W. G. Franzin, and D. N. Tretiak. 1973. Genetics of glycerol-3-phosphate dehydrogenase isozymes in white muscle of lake whitefish (Coregonus clupeaformis). J. Fish. Res. Board Can. 30:187-193.

Falconer, D. S. 1960. Introduction to Quantitative Genetics. The Ronald Press Company, New York. 365 p.

Hubbs, C. L., and K. F. Lagler. 1964. Fishes of the Great Lakes region. University of Michigan Press, Ann Arbor, Michigan. 213 p.

Jesien, R. V. 1977. The contribution of stocked trout to the sport fishery of three small Wisconisn lakes. M.S. Thesis. University of Wisconsin-Stevens Point. 124 pp.

Lagler, K. F. 1956. Freshwater fishery biology. 2nd ed. Wm. C. Brown Co., Dubuque, Iowa. 421 p.

Li, C. C. 1976. First Course in Population Genetics. Boxwood Press, Pacific Grove, California. 631 p.

Lindsey, C. C., J. W. Clayton, and W. G. Franzin. 1970. Zoogeographic problems and protein variation in the Coregonus clupeaformis whitefish species complex. p. 127-146. In C. C. Lindsey and C. S. Wood (ed.) The biology of coregonid fishes. University Manitoba Press, Winnipeg, Manitoba.

Loch, J. S. 1974. Phenotypic variation in the lake whitefish Coregonus clupeaformis, induced by introduction into a new environment. J. Fish. Res. Board Can. 31:55-62.

McPhail, J. D., and C. C. Lindsey. 1970. Freshwater fishes of Northern Canada and Alaska. Fish. Res. Board Can. Bull. 173. 381 p.

Northcote, T. G., S. N. Williscroft, and H. Tsuyuki. 1970. Meristic and lactate dehydrogenase genotype differences in stream populations of rainbow trout below and above a waterfall. J. Fish. Res. Board Can. 27:1987-1995.

Richer, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish Res. Board. Can. No. 191, 382 pp.

Ryder, R. A. 1965. A method for estimating the potential fish production of north-temperate lakes. Trans. Am. Fish. Soc. 94(3):214-218.

Snedecor, W. G. 1965. Statistical Methods. Iowa State University Press. Ames, Iowa. 534pp.

Strickberger, M. W. 1968. Genetics. The MacMillan Company, New York. Collier-MacMillian Limited, London. 868 pp.

Svärdson, G. 1950. The Coregonid problem II. Morphology of two Coregonid species in different environments. Rep. Inst. Freshwater Res. Drottningholm. 31:151-162.

Thorne, C. J. R., L. I. Grossman, and N. O. Kaplan. 1963. Starch gel electrophoresis of malate dehydrogenase. Biochem. Biophys. Acta. 73:193-203.

Utter, F. M., H. O. Hodgins, and F. W. Allendorf. 1974. Biochemical genetic studies of fishes: potentialities and limitations. In D. C. Malins and J. R. Sargent (ed.) Biochemical and biophysical perspectives in marine biology. Vol. 1. Academic Press, New York.

Williscroft, S. N., and H. Tsuyuki. 1970. Lactate dehydrogenase systems of rainbow trout--evidence of polymorphism in liver and additional subunits in gills. J. Fish. Res. Board Can. 27:1563-1567.

Woodger, C. D. 1976. Morphological variation as induced by environment in Coregonids. Env. Biol. Fish. 1(1):101-105.

APPENDIX A

Meristic[1/] traits (mm) of lake herring from each study area.

Sunset Lake

Serial Number	Pectoral Fin Length	Ventral to Anal Distance	Pectoral to Ventral Distance	Dorsal to Adipose Distance	Fork Length	Internaral Width	Head Length
33	50(6.4)	83(3.9)	93(3.5)	116(2.8)	322	10 (32.2)	61(5.3)
49	51(6.3)	85(3.8)	95(3.4)	115(2.8)	325	10 (32.5)	62(5.3)
50	53(6.1)	85(3.8)	92(3.5)	118(2.8)	327	9 (36.3)	61(5.4)
8	50(6.8)	83(4.0)	100(3.4)	134(2.5)	339	9 (37.6)	62(5.4)
6	51(6.3)	85(3.8)	91(3.5)	113(2.8)	322	11 (29.3)	61(5.3)
19	56(6.1)	91(3.7)	101(3.4)	121(2.8)	343	9 (38.1)	62(5.5)
3	50(6.4)	85(3.8)	100(3.2)	117(2.8)	322	9 (35.7)	60(5.4)
61	49(6.6)	85(3.8)	101(3.2)	113(2.8)	324	10 (32.4)	61(5.3)
34	50(6.6)	90(3.7)	98(3.4)	118(2.8)	333	10 (33.3)	63(5.2)
54	55(6.0)	88(3.7)	99(3.3)	119(2.8)	331	11 (30.0)	61(5.4)
20	51(6.5)	92(3.6)	92(3.6)	120(2.8)	330	9 (36.7)	65(5.0)
51	50(6.6)	88(3.7)	93(3.5)	110(3.0)	329	10 (32.9)	62(5.3)
11	48(6.4)	79(3.9)	89(3.5)	112(2.8)	310	9 (34.4)	62(5.3)
60	49(6.7)	86(3.8)	94(3.5)	116(2.8)	328	9 (36.4)	61(5.3)
35	50(6.4)	80(4.0)	104(3.1)	115(2.8)	322	9 (35.8)	61(5.3)
31	52(6.6)	91(3.8)	98(3.5)	125(2.8)	346	11 (31.4)	65(5.3)
44	55(6.1)	90(3.8)	98(3.4)	116(2.9)	338	10 (33.8)	64(5.3)

APPENDIX A CONTINUED

Serial Number	Pectoral Fin Length	Ventral to Anal Distance	Pectoral to Ventral Distance	Dorsal to Adipose Distance	Fork Length	Internaral Width	Head Length
32	49(6.9)	89(3.8)	108(3.1)	122(2.8)	342	10 (34.2)	68(5.0)
13	55(6.0)	84(3.9)	103(3.2)	114(2.9)	331	10 (33.1)	65(5.1)
22	54(6.0)	86(3.8)	114(2.9)	113(2.9)	329	9 (36.5)	62(5.3)
30	51(6.6)	92(3.6)	96(3.5)	116(2.9)	339	9 (37.6)	63(5.4)
29	57(6.1)	89(3.9)	106(3.3)	128(2.7)	348	10 (34.8)	64(5.4)
65	51(6.3)	80(4.0)	96(3.3)	119(2.6)	320	11 (29.0)	61(5.2)
18	58(5.7)	77(4.3)	98(3.4)	117(2.8)	334	9 (37.1)	62(5.4)
4	45(6.9)	80(3.8)	94(3.3)	109(2.8)	311	10 (31.1)	60(5.1)
7	46(7.1)	92(3.5)	99(3.3)	115(2.8)	331	9 (36.7)	60(5.5)
36	48(6.7)	83(3.8)	93(3.4)	116(2.7)	322	11 (29.2)	63(5.1)
25	59(5.6)	90(3.7)	95(3.5)	119(2.8)	335	9 (37.2)	64(5.2)
14	53(6.1)	91(3.6)	96(3.4)	115(2.8)	328	10 (32.8)	61(5.3)
9	56(6.0)	95(3.5)	97(3.4)	113(2.9)	336	10 (33.6)	64(5.2)
2	42(7.1)	82(3.6)	90(3.3)	110(2.7)	302	9 (33.5)	57(5.2)
10	49(6.4)	84(3.7)	97(3.2)	118(2.6)	318	9 (35.3)	59(5.3)
13	46(6.7)	82(3.7)	103(3.0)	114(2.7)	311	10 (31.1)	59(5.2)
53	52(6.3)	81(4.0)	92(3.5)	118(2.7)	329	9 (36.5)	64(5.1)
1	48(6.5)	81(3.8)	91(3.4)	115(2.7)	314	9 (34.8)	59(5.3)
12	49(6.8)	86(3.8)	99(3.3)	124(2.6)	334	10 (33.4)	60(5.5)
29	46(7.5)	89(3.9)	106(3.2)	128(2.7)	348	9 (38.6)	65(5.3)
69	51(6.5)	85(3.9)	92(3.6)	117(2.8)	334	10 (33.4)	63(5.5)
16	50(6.8)	95(3.6)	109(3.1)	124(2.7)	344	10 (34.4)	65(5.2)
67	50(6.4)	82(3.8)	87(3.6)	122(2.6)	319	9 (35.4)	59(5.4)

APPENDIX A CONTINUED

Serial Number	Pectoral Fin Length	Ventral to Anal Distance	Pectoral to Ventral Distance	Dorsal to Adipose Distance	Fork Length	Internaral Width	Head Length
21	48(6.7)	87(3.7)	90(3.6)	120(2.7)	324	9 (36.0)	63(5.1)
28	44(7.0)	79(3.9)	99(3.1)	114(2.7)	311	9 (34.5)	66(4.7)
24	52(6.3)	87(3.7)	100(3.3)	117(2.8)	328	10 (32.8)	62(5.2)
26	47(7.0)	87(3.7)	100(3.3)	115(2.8)	330	9 (36.6)	63(5.2)
17	50(6.4)	82(3.9)	93(3.4)	118(2.7)	321	9 (35.6)	63(5.0)
23	52(6.7)	97(3.6)	100(3.5)	121(2.9)	353	11 (32.0)	66(5.3)
27	45(6.6)	80(3.7)	85(3.5)	111(2.7)	300	9 (33.3)	58(5.1)
5	48(6.7)	85(3.8)	103(3.1)	120(2.7)	325	9 (36.1)	61(5.3)
68	54(6.3)	91(3.7)	100(3.4)	120(2.8)	345	10 (34.5)	66(5.2)
57	53(6.4)	91(3.7)	98(3.7)	105(3.2)	344	10 (34.4)	65(5.2)
			Pallette				
85	25(6.4)	42(3.3)	48(3.3)	58(2.7)	160	4 (40.0)	33(4.8)
74	23(8.5)	49(4.0)	55(3.5)	66(2.9)	196	5 (39.2)	40(4.9)
26	32(6.1)	51(3.8)	56(3.5)	70(2.8)	196	6 (32.6)	41(4.7)
88	24(6.7)	41(3.9)	46(3.5)	59(2.7)	163	4 (40.7)	34(4.7)
104	30(7.2)	52(4.1)	67(3.2)	76(2.8)	216	6 (36.0)	45(4.8)
80	30(6.5)	54(3.6)	56(3.5)	67(2.9)	197	4 (49.2)	41(4.8)
4	27(6.6)	43(4.1)	55(3.2)	63(2.8)	180	5 (36.0)	40(4.5)
61	31(6.0)	47(4.0)	36(5.2)	65(2.8)	188	5 (37.6)	40(4.7)
63	28(7.5)	49(4.3)	57(3.7)	64(3.2)	211	5 (42.2)	39(5.4)
89	31(6.8)	56(3.7)	58(3.6)	75(2.8)	211	6 (35.1)	45(4.6)
96	33(6.9)	56(4.0)	65(3.5)	82(2.7)	228	6 (38.0)	46(4.9)

APPENDIX A CONTINUED

Serial Number	Pectoral Fin Length	Ventral to Anal Distance	Pectoral to Ventral Distance	Dorsal to Adipose Distance	Fork Length	Internaral Width	Head Length
86	24(6.9)	44(3.7)	47(3.5)	63(2.6)	167	5 (33.4)	36(4.6)
94	29(7.3)	49(4.3)	58(3.6)	75(2.8)	214	5 (42.9)	45(4.7)
102	26(7.3)	53(3.6)	57(3.3)	68(2.8)	192	5 (38.4)	39(4.9)
32	32(5.8)	50(3.7)	53(3.5)	68(2.7)	188	5 (37.6)	41(4.5)
76	33(6.7)	53(4.1)	61(3.6)	71(3.1)	222	6 (37.0)	46(4.8)
101	32(6.0)	50(3.8)	54(3.5)	68(2.8)	192	6 (32.0)	44(4.3)
84	30(6.9)	55(3.8)	61(3.4)	74(2.8)	209	5 (41.8)	44(4.7)
2	33(5.7)	48(3.9)	55(3.4)	62(3.0)	191	6 (31.8)	42(4.5)
97	27(6.9)	48(3.9)	50(3.7)	69(2.7)	188	5 (37.6)	41(4.5)
99	32(6.1)	49(4.0)	58(3.4)	70(2.8)	198	6 (33.0)	42(4.7)
43	39(5.5)	56(3.8)	61(3.5)	72(3.0)	217	6 (36.1)	43(5.0)
35	25(7.5)	48(3.9)	55(3.4)	66(2.8)	189	6 (31.5)	42(4.5)
73	27(7.0)	49(3.8)	58(3.2)	64(2.9)	191	5 (38.2)	41(4.6)
45	24(6.8)	42(3.9)	45(3.6)	62(2.6)	164	5 (32.8)	32(5.1)
64	31(3.9)	57(2.1)	60(2.0)	79(1.5)	121	5 (24.2)	48(2.5)
65	30(6.4)	49(3.9)	51(3.7)	66(2.9)	193	5 (38.6)	42(4.5)
3	24(6.8)	43(3.8)	48(3.4)	61(2.6)	164	4 (41.0)	35(4.6)
83	29(6.4)	48(3.9)	53(3.5)	66(2.8)	188	6 (31.3)	40(4.7)
14	24(6.7)	38(4.2)	47(3.4)	60(2.6)	161	4 (40.2)	31(5.1)
105	30(6.4)	45(4.3)	48(4.0)	65(2.9)	194	5 (38.8)	42(4.6)
5	26(7.2)	49(3.8)	54(3.4)	65(2.8)	188	5 (37.6)	40(4.7)
103	23(6.7)	43(3.6)	45(3.4)	60(2.5)	155	4 (38.7)	34(4.5)
90	33(5.6)	50(3.7)	58(3.2)	66(2.8)	188	6 (31.3)	42(4.4)

APPENDIX A CONTINUED

Serial Number	Pectoral Fin Length	Ventral to Anal Distance	Pectoral to Ventral Distance	Dorsal to Adipose Distance	Fork Length	Internaral Width	Head Length
82	30(6.9)	51(4.0)	62(3.3)	72(2.8)	207	6 (34.5)	43(4.8)
78	30(7.0)	56(3.7)	61(3.4)	70(3.0)	212	5 (42.4)	44(4.8)
24	35(6.3)	55(4.0)	62(3.5)	79(2.7)	221	6 (36.8)	46(4.8)
25	28(6.9)	47(4.1)	54(3.5)	63(3.0)	194	6 (32.3)	40(4.8)
62	26(7.5)	44(4.4)	59(3.3)	74(2.6)	195	5 (39.0)	40(4.8)
98	34(5.8)	49(4.0)	57(3.4)	71(2.8)	199	6 (33.1)	43(4.6)
36	31(6.7)	52(4.0)	63(3.3)	73(2.8)	210	6 (35.0)	45(4.6)
34	30(6.9)	55(3.8)	61(3.4)	70(2.9)	209	5 (41.8)	44(4.7)
87	33(5.9)	46(4.2)	57(3.4)	70(2.7)	195	6 (32.5)	41(4.7)
95	32(6.0)	50(3.9)	55(3.5)	70(2.7)	195	5 (39.0)	42(4.6)
77	31(6.2)	49(3.9)	55(3.5)	68(2.8)	194	5 (38.8)	41(4.7)
75	24(7.2)	47(3.7)	51(3.4)	59(2.9)	174	5 (34.8)	34(5.1)
31	32(6.6)	53(4.0)	56(3.8)	72(2.9)	214	6 (35.6)	43(4.9)
79	31(6.0)	46(4.1)	52(3.6)	73(2.5)	189	5 (37.8)	31(4.6)
100	30(6.3)	48(3.9)	54(3.5)	65(2.9)	189	5 (37.8)	43(4.3)
81	28(6.7)	44(4.2)	54(3.4)	62(3.0)	188	6 (31.3)	39(4.8)
			Green Lake				
59	61(5.7)	82(4.2)			349		
84	55(5.4)	66(4.5)			301		
83	54(6.1)	81(4.0)			330		
69	53(6.1)	76(4.2)			325		
58	45(7.2)	86(3.7)			325		

APPENDIX A CONTINUED

Serial Number	Pectoral Fin Length	Ventral to Anal Distance	Fork Length
45	53(6.8)	96(3.7)	364
60	52(6.1)	80(4.0)	320
65	53(6.0)	82(3.8)	318
71	56(6.6)	99)3.7)	375
77	54(7.0)	93(4.0)	381
64	56(5.8)	79(4.1)	328
52	58(6.6)	98(3.9)	385
50	52(6.1)	83(3.8)	319
101	25(6.1)	34(4.5)	153
100	29(4.4)	41(3.1)	130
103	28(6.1)	42(4.0)	172
93	32(6.5)	52(4.0)	210
97	28(6.1)	32(5.3)	171
105	29(5.6)	38(4.3)	165
104	25(6.0)	32(4.6)	150
107	28(5.8)	40(4.1)	165
106	27(6.2)	37(4.5)	170
80	53(6.1)	74(4.3)	324
82	50(6.6)	77(4.2)	330
73	44(6.7)	78(3.8)	297
57	55(6.4)	78(4.5)	355
75	52(6.2)	84(3.8)	325
95	35(6.2)	54(4.0)	220

APPENDIX A CONTINUED

Serial Number	Pectoral Fin Length	Ventral to Anal Distance	Fork Length
62	50(6.6)	79(4.1)	331
70	60(6.6)	98(4.0)	399
74	60(5.9)	88(4.0)	357
66	55(5.8)	77(4.2)	324
44	52(8.7)	82(5.5)	455
49	57(6.4)	91(4.0)	365
54	54(7.3)	100(3.9)	395
43	53(6.4)	85(4.0)	340
72	55(7.2)	84(4.7)	397
47	61(6.3)	96(4.0)	386
51	52(7.3)	97(3.9)	381
85	54(5.9)	75(4.2)	320
76	56(6.3)	93(3.8)	356
81	55(6.3)	83(4.2)	350
61	59(5.9)	94(3.7)	351
53	59(6.0)	90(3.9)	355
87	28(6.4)	41(4.3)	180
86	24(7.3)	42(4.1)	176
90	26(6.9)	35(5.1)	180
89	27(6.9)	42(4.4)	187
91	24(7.6)	40(4.5)	183
56	55(7.0)	87(4.4)	387

APPENDIX A CONTINUED

Serial Number	Pectoral Fin Length	Ventral to Anal Distance	Fork Length
	Lac Courte Oreilles		
43	19(6.5)	30(4.1)	125
44	21(6.8)	33(4.3)	143
41	17(7.5)	29(4.4)	128
45	20(6.8)	33(4.1)	136
42	19(6.3)	32(3.7)	121
63	18(7.0)	29(4.3)	126
64	17(7.0)	27(4.4)	120
65	17(7.0)	27(4.4)	120
62	18(7.5)	30(4.5)	135
61	17(7.6)	33(3.9)	130
51	20(6.7)	32(4.1)	134
15	19(6.6)	29(4.3)	127
13	21(6.8)	34(4.2)	144
11	17(7.5)	31(4.1)	129
28	20(6.8)	28(4.8)	136
27	20(6.7)	30(4.4)	134
30	19(6.5)	31(4.0)	125
29	20(7.0)	32(4.4)	141
38	18(6.9)	31(4.0)	125
39	20(7.2)	35(4.1)	144
37	21(6.6)	32(4.3)	140

APPENDIX A CONTINUED

Serial Number	Pectoral Fin Length	Ventral to Anal Distance	Fork Length
71	21(6.3)	31(4.2)	133
40	19(6.7)	32(4.0)	128
36	20(6.3)	28(4.5)	127
53	20(6.5)	30(4.3)	130
54	18(7.1)	25(5.1)	129
55	19(6.4)	29(4.2)	122
31	20(6.9)	35(3.9)	138
33	21(6.7)	37(3.8)	142
34	23(6.3)	32(4.5)	145
32	19(7.0)	30(4.4)	134
47	22(6.1)	34(4.0)	136
49	17(7.2)	29(4.2)	124
50	19(6.6)	33(3.8)	127
46	22(6.5)	30(4.8)	145
48	20(6.2)	29(4.3)	125
66	19(6.7)	31(4.1)	129
76	21(6.4)	31(4.3)	135
68	17(7.8)	30(4.4)	133
69	22(6.5)	31(4.6)	143
70	21(7.0)	33(4.4)	148
58	17(7.4)	30(4.2)	126
57	17(9.8)	29(5.7)	168
60	19(6.7)	33(3.9)	129

APPENDIX A CONTINUED

Serial Number	Pectoral Fin Length	Ventral to Anal Distance	Fork Length
59	19(6.8)	30(4.3)	130
56	20(6.3)	30(4.3)	126
14	17(7.4)	30(4.2)	126
12	19(6.6)	28(4.5)	126

1/ Numbers in parentheses are ratios obtained by dividing each trait into the fork length of the fish.

APPENDIX B

Age (years), total length (mm), and scale dimensions (mm) of fish from Pallette Lake, Lac Courte Oreilles, and Green Lake.

PALLETTE LAKE

Fish ID Number	Age of Fish	Total Length of Fish	Length of Scale Radius	Distance (mm) From Focus to Annulus						
				I	II	III	IV	V	VI	VII
14	III	176	100	42	81					
88	III	181	100	50	72					
4	III	195	110	50	95					
75	III	186	90	45	60					
45	III	178	74	30	61					
3	III	181	125	41	60					
80	IV	219	125	40	80	110				
102	IV	210	112	40	65	83				
97	IV	210	80	30	56	68				
90	IV	208	85	29	55	78				
83	IV	210	60	25	45	55				
79	IV	210	90	25	50	75				

PALLETTE LAKE (CONT'D)

Fish ID Number	Age of Fish	Total Length of Fish	Length of Scale Radius	Distance (mm) From Focus to Annulus						
				I	II	III	IV	V	VI	VII
81	IV	210	109	40	65	85				
32	IV	210	170	80	110	140				
35	IV	210	75	30	55	70				
74	IV	216	93	40	60	85				
77	IV	215	100	32	65	90				
73	IV	213	95	35	70	85				
99	IV	220	81	28	50	70				
2	IV	214	80	40	65	72				
98	IV	221	95	35	73	85				
65	V	216	122	30	69	95	118			
26	V	216	90	30	55	78	85			
95	V	216	84	20	50	69	80			
87	V	219	115	40	65	90	110			
82	V	229	158	60	100	120	142			

PALLETTE LAKE (CONT'D)

Fish ID Number	Age of Fish	Total Length of Fish	Length of Scale Radius	Distance (mm) From Focus to Annulus						
				I	II	III	IV	V	VI	VII
96	V	250	136	35	73	95	125			
84	V	231	120	35	84	95	115			
34	V	230	97	40	50	70	94			
36	V	233	130	45	90	110	123			
104	V	235	136	60	90	115	130			
89	V	230	111	35	76	94	108			
78	V	234	170	70	115	146	160			
64	V	241	137	49	78	110	130			
76	V	243	104	30	60	80	98			
43	V	238	141	50	91	120	130			

LAC COURTE OREILLES

Fish ID Number	Age of Fish (years)	Total Length of Fish (mm)	Length of Scale Radius (mm)	Distance (mm) From Focus to Annulus						
				I	II	III	IV	V	VI	VII
62	III	135	68	40	60					
27	III	144	78	30	60					
39	III	154	63	35	50					
29	III	141	.80	35	65					
37	III	140	95	50	80					
46	III	155	81	35	60					
61	III	140	81	40	68					
31	III	148	71	43	65					
32	III	146	72	30	55					
53	III	140	78	40	65					
45	III	146	93	45	75					
44	III	153	70	40	60					
51	III	144	69	45	61					
28	III	146	86	47	75					
35	III	145	89	30	70					

LAC COURTE OREILLES (CONT'D)

Fish ID Number	Age of Fish (years)	Total Length of Fish (mm)	Length of Scale Radius (mm)	Distance (mm) From Focus to Annulus						
				I	II	III	IV	V	VI	VII
34	III	155	73	40	60					
30	III	125	56	35	50					
36	III	127	80	35	50					
40	III	128	82	40	74					
38	III	125	91	42	85					
71	III	133	80	42	70					
55	III	130	77	35	67					
64	III	130	95	52	85					
65	III	130	59	25	50					
48	III	135	86	36	70					
50	III	137	80	40	72					
66	III	139	69	30	57					
49	III	135	70	25	60					
54	III	139	68	35	60					
41	III	138	71	35	67					
42	III	131	52	25	48					

LAC COURTE OREILLES (CONT'D)

Fish ID Number	Age of Fish (years)	Total Length of Fish (mm)	Length of Scale Radius (mm)	Distance (mm) From Focus to Annulus I	II	III	IV	V	VI	VII
63	III	136	92	40	83					
33	III	152	72	25	60					
47	III	149	100	45	80					

GREEN LAKE

Fish ID Number	Age of Fish (years)	Total Length of Fish (mm)	Length of Scale Radius (mm)	Distance (mm) From Focus to Annulus I	II	III	IV	V	VI	VII
97	IV	136	60	15	34	57				
104	IV	165	56	12	30	42				
101	IV	172	45	17	26	40				
90	IV	181	75	22	40	70				
87	IV	198	52	15	35	45				
105	IV	184	85	26	49	80				
107	IV	185	47	12	22	40				
106	IV	186	58	17	29	47				
103	IV	190	55	11	22	40				
93	IV	231	65	10	24	50				
98	IV	210	75	17	37	70				

GREEN LAKE (CON'D)

Fish ID Number	Age of Fish (years)	Total Length of Fish (mm)	Length of Scale Radius (mm)	Distance (mm) From Focus to Annulus						
				I	II	III	IV	V	VI	VII
86	IV	200	70	25	40	67				
100	IV	204	73	25	40	67				
95	V	246	67	17	36	55	62			
78	VI	332	135	18	32	40	105	125		
62	VI	370	110	22	48	65	80	95		
84	VI	332	115	24	50	65	80	94		
66	VI	355	115	19	43	65	88	103		
65	VI	355	130	40	60	79	92	120		
10	VI	356	143	35	78	95	120	130		
85	VI	360	135	30	60	85	104	119		
50	VI	356	157	50	82	105	115	142		
64	VI	365	126	22	45	89	100	116		
80	VI	363	155	22	47	83	102	135		
82	VI	368	95	22	56	70	80	89		
69	VI	363	141	23	40	80	110	130		
81	VI	390	119	18	50	67	81	108		
61	VI	385	144	28	63	89	110	130		
72	VI	376	141	25	60	80	100	120		
57	VII	395	187	40	90	115	140	170	184	
53	VII	390	140	20	63	82	100	116	135	

GREEN LAKE (CONT'D)

Fish ID Number	Age of Fish (years)	Total Length of Fish (mm)	Length of Scale Radius (mm)	Distance (mm) From Focus to Annulus						
				I	II	III	IV	V	VI	VII
59	VII	390	166	45	74	90	106	120	150	
51	VII	415	180	25	48	70	90	108	120	
49	VII	405	141	36	60	80	100	119	133	
71	VII	410	105	20	52	65	80	90	97	
45	VIII	416	170	20	34	60	90	120	140	155
47	VIII	426	170	19	40	84	110	130	148	159
70	VIII	441	158	26	62	92	105	125	135	147
54	VIII	445	155	25	38	55	80	100	120	143

APPENDIX C

Age (years) and total length (mm) of fish from Sunset Lake

AGE OF FISH	TOTAL LENGTH OF FISH
III	341
III	350
III	368
IV	315
IV	349
IV	352
IV	353
IV	352
IV	360
IV	362
IV	364
IV	365
IV	365
IV	349
IV	328
IV	330
V	354
V	355
V	355
V	365
V	367
V	370
V	372
V	375
V	376
V	376
V	385
V	386
V	328
V	335
V	360
V	360
V	371
V	333
VI	368
VI	370
VI	371
VI	374
VI	375
VI	364
VI	372
VI	375
VI	375
VI	382
VI	382
VI	382
VI	387
VI	390
VI	392
VI	394
VI	395
VI	395
VI	395
VI	398
VI	398
VI	400
VI	348
VI	354
VI	358
VI	359
VI	360
VI	362
VI	363
VI	364
VI	365
VI	365
VI	365
VI	368
VII	380
VII	400
VIII	405