THE UNIVERSITY OF MANITOBA

A BIOCHEMICAL GENETIC STUDY OF ZOOGEOGRAPHY OF LAKE WHITEFISH, *COREGONUS CLUPEAFORMIS*, IN WESTERN CANADA IN RELATION TO THEIR POSSIBLE SURVIVAL IN A NAHANNI GLACIAL REFUGIUM

by

CHRISTOPHER JOHN FOOTE

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ABSTRACT

Lake whitefish, Coregonus clupeaformis, populations from across western Canada were studied in reference to their isolation and subsequent dispersal from separate glacial refugia. Frequencies of alleles of the genes governing electrophoretic phenotypes of glycerol-3-phosphate dehydrogenase (G-3-PDH), heart-type lactate dehydrogenase (LDH) and isocitrate dehydrogenase (IDH) proved useful for characterizing populations. Hemoglobin electrophoretic phenotypes and modal gillraker numbers for each population were useful in discerning differences among large groups of populations.

Three biochemically distinct population groups of lake whitefish were found in western Canada and it is suggested that the most plausible hypothesis to account for the genetic integrity and geographical distribution of these groups is that they have separate origins in glacial refugia. Selection did not appear to account for the present genetic distinctions between the groups. It has been shown previously that lake whitefish probably survived the Wisconsin glaciation in both the Bering and Mississippi-Missouri glacial refugia. Recent geological evidence and the results of the present study regarding the distribution

of populations of one of the groups favour isolation and dispersal from an additional refugium in the area of the present Nahanni National Park, N.W.T. Lake whitefish, apparently derived from a Bering refuge stock, occupy habitats in the Yukon, Alsek, upper Liard and Peel River systems. Movement out of the Yukon River system appears to have been aided by temporary headwater exchanges. It is also probable that lake whitefish dispersed from the Bering refugium along the Arctic coast. Populations apparently derived from a Nahanni refugium stock now seem to occupy habitats in the Fraser, Peace, Athabasca, Tetcela and lower Liard River watersheds. The most plausible dispersal route for the ancestral populations was via waterways in an ice free corridor which probably existed along the eastern foothills of the Rocky Mountains during late Wisconsin glaciation. Most of the populations of the plains of western Canada are probably derived from a Mississippi-Missouri refugium stock. Dispersal appears to have been via connections of the large glacial lakes which occupied a large proportion of the plains during deglaciation.

Contact of the different refugial forms appears to have led to introgression in some cases but, in general, most populations remain genetically distinct even in the absence of physical barriers to gene flow.

This thesis is dedicated to my mother,

Margaret Lillian (Peggy) Bruce

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INTRODUCTION

The amino acid sequence of a given enzyme appears to evolve at approximately the same rate irrespective of the organism in which it occurs (Kimura and Ohta 1974, Sarich 1977, Wilson et al. 1977). The rates vary among different classes of proteins, depending on their functional complexity (Kimura and Ohta 1974, Sarich 1977, Wilson et al. 1977). For example, Sarich (1977) pointed out that in apparently all organisms plasma proteins and various other secreted proteins undergo amino acid substitution at a ten times greater rate than intracellular enzymes involved in complex metabolic pathways such as glycolysis. The discovery that within any given class of proteins the rate of amino acid substitution appears to be nearly solely dependent on time is proving useful in the fields of paleontology, anthropology, and systematic biology (Wilson et al. 1977). These studies are complicated by the effects of population bottlenecks whereby alleles may be lost due to a combination of founder effect and genetic drift, leading to an inaccurate estimation of the time elapsed since the separation of different populations (Chakraborty and Nei 1977). On the other hand, allele losses arising from population bottlenecks can be useful in distinguishing populations. For example, Avise and Selander

(1972) used genetic differences they concluded to be caused by genetic drift to show that there was little interbreeding between the surface and cave-dwelling fish species of the genus Astyanax. Therefore both the occurrence of new substitutions (i.e., new alleles) and the loss of alleles in separated populations can prove useful in measuring the integrity of these stocks if contact is ever re-established.

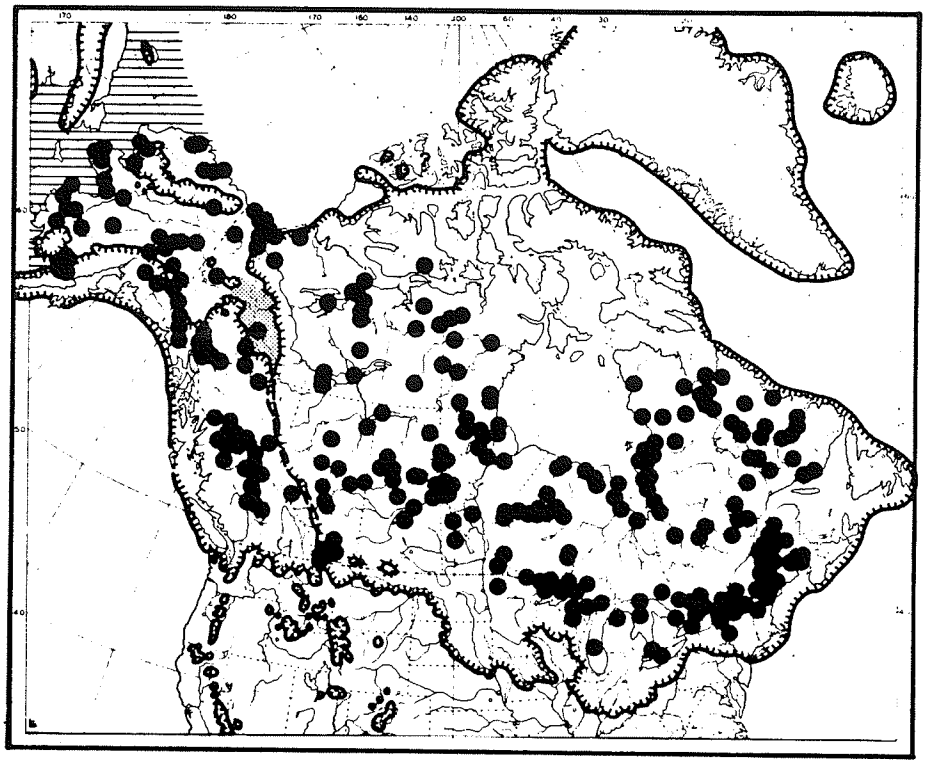
Fish populations separated by the effects of pleistocene glaciation often show biochemical divergence (Lindsey et al. 1970, Avise and Selander 1972, Avise and Smith 1974, Franzin and Clayton 1977, Bodaly and Lindsey 1977, Wiseman et al. 1978, Lynch and Vyse 1979, Ryman et al. 1979). These biochemical differences can be used to establish probable areas of population survival during glaciation and to outline the extent of dispersal and intergradation since deglaciation.

Lake whitefish, Coregonus clupeaformis, exhibit considerable and continuous morphological variability over their range in North America and it is mainly for this reason that the species is referred to as a 'complex' by McPhail and Lindsey (1970). Some of this morphological plasticity has been attributed to the isolation of populations in separate refugia during the time when the Wisconsin ice sheets covered most of Canada (Lindsey et al. 1970). These refugial populations were probably separated for at least 50,000 years.

Deglaciation allowed the dispersal of these separate stocks from their respective refugia to nearly all of Canada (Fig. 1). The lake whitefish populations of western Canada were considered by McPhail and Lindsey (1970) to have dispersed from two discrete refugia: the Bering (unglaciated parts of the Yukon and Alaska) and Mississippi-Missouri (unglaciated northern sections of the watersheds of these rivers). Recently, Ford (1976) discovered evidence for the existence of at least one glacial lake during the Wisconsin glaciation in Nahanni National Park, Northwest Territories, which may have also served as a refuge for lake whitefish populations.

The distribution of lake whitefish in western Canada, with special reference to glacial refugia, was studied biochemically by Franzin and Clayton (1977). They concluded that lake whitefish populations had dispersed from the Mississippi-Missouri and Bering refugia and mixed throughout most of western Canada. In contrast, populations in the upper Liard, Alsek and Yukon River watersheds were apparently derived solely from the Bering population. This distinction was postulated to be preserved by physical barriers such as the Liard canyon which prevented gene flow from the Mississippi-Missouri populations from reaching the Bering populations. Dispersal from the Bering refugium has probably occurred via the upper Liard River system (Franzin and Clayton 1977), the

Figure 1. Distribution of native lake whitefish populations in North America in relation to the maximum extent of Wisconsin glaciation (from Lindsey et al. 1970).



Peel River system (Bodaly and Lindsey 1977) and movement along the Arctic coast (McPhail and Lindsey 1970). One population on the headwaters of the Flat River, a tributary to the Nahanni River, was found to be genetically distinct from all other lake whitefish populations sampled (Franzin and Clayton 1977). It is now suggested that the existence of this population supports the idea that lake whitefish may also have survived Wisconsin glaciation in a Nahanni refugium.

The purpose of this study was to investigate the apparent dispersal of lake whitefish out of the Bering refugium and their subsequent primary zones of contact with other stocks of lake whitefish derived from populations which survived glaciation in other refugia.

Possible primary zones of contact are examined from across western Canada with special emphasis on the Liard River system where populations which may have survived in a Nahanni refugium would also be expected to come in contact with fish dispersing from the Bering and Mississippi-Missouri refugia.

METHODS

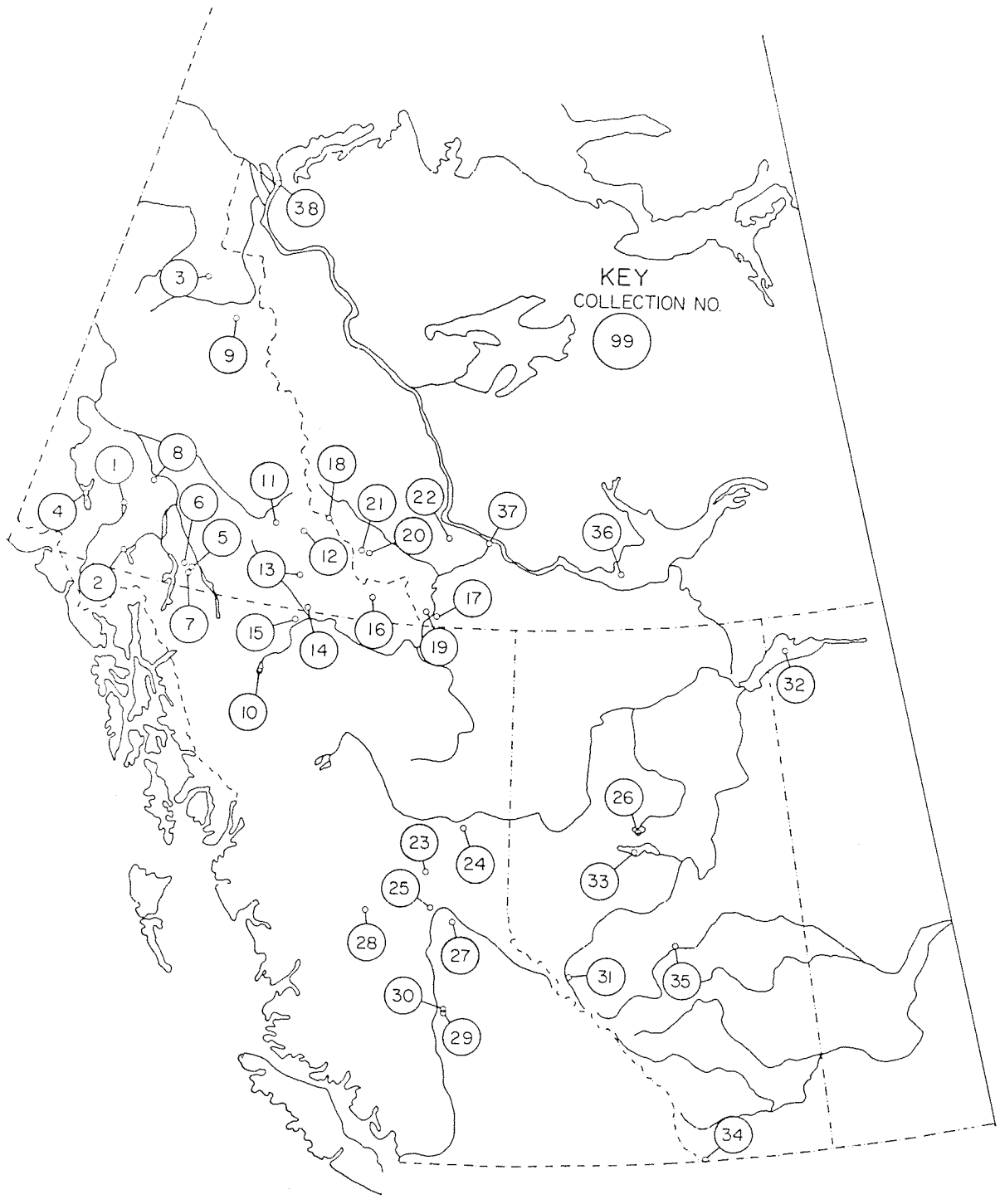
Collection of Lake Whitefish

Lake whitefish were collected from 38 locations from across western and northwestern Canada (Fig. 2) using experimental gill nets (two types: both 38.1 m long and 2.1 m deep with panels in order of either 2.54, 5.08, 7.62, 3.81 and 6.35 cm or 3.81, 7.62, 11.48, 5.08 and 10.02 cm stretched mesh monofilament nylon) over the period of 1970 to 1978. Fish carcasses were either iced or frozen directly after capture, and within four days, stored at -40C until required for further analysis. Hemoglobin samples from lake whitefish were taken, stored and shipped to our laboratory in Winnipeg following the methods outlined by Lindsey et al. (1970). Electrophoresis was performed within 7 days of collection.

Biochemical Analysis

Chemicals used in this study are abbreviated as follows: nicotinamide-adenine dinucleotide phosphate (NADP), N,N-bis-(2-hydroxyethyl)-glycine (Bicine), phenazine methosulphate (PMS) and 2;2'-di-p-nitrophenyl-5,5'-diphenyl-3-3- (3,3'-dimethoxy-4,4'-biphenylene)-ditetrazolium chloride (Nitro BT, NBT).

Figure 2. Collection sites for lake whitefish populations from western Canada. Numbers on map correspond to those of Table 2.


KEY
COLLECTION NO.
99
38
3
9
1
8
4
6
11
18
21
22
37
5
20
36
12
2
13
17
7
15
16
19
14
32
10
26
23
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29
34

Phenotypes for four isozyme systems were visualized following the semi-micro electrophoresis method of Tsuyuki et al. (1966a). The enzyme or protein examined, tissue sampled and exact methods of electrophoresis are given in Table 1.

The nomenclature for the genetic basis of LDH, IDH and G-3-PDH follows the system proposed by Bailey et al. (1976) for the duplicated salmonid LDH loci. LDH isozyme nomenclature (Franzin and Clayton 1977) and IDH isozyme nomenclature (Bodaly 1977) have previously been presented in this form. The G-3-PDH isozyme designations of Clayton et al. (1973) are converted to the format proposed by Bailey et al. (1976) in this study (see Results; G-3-PDH).

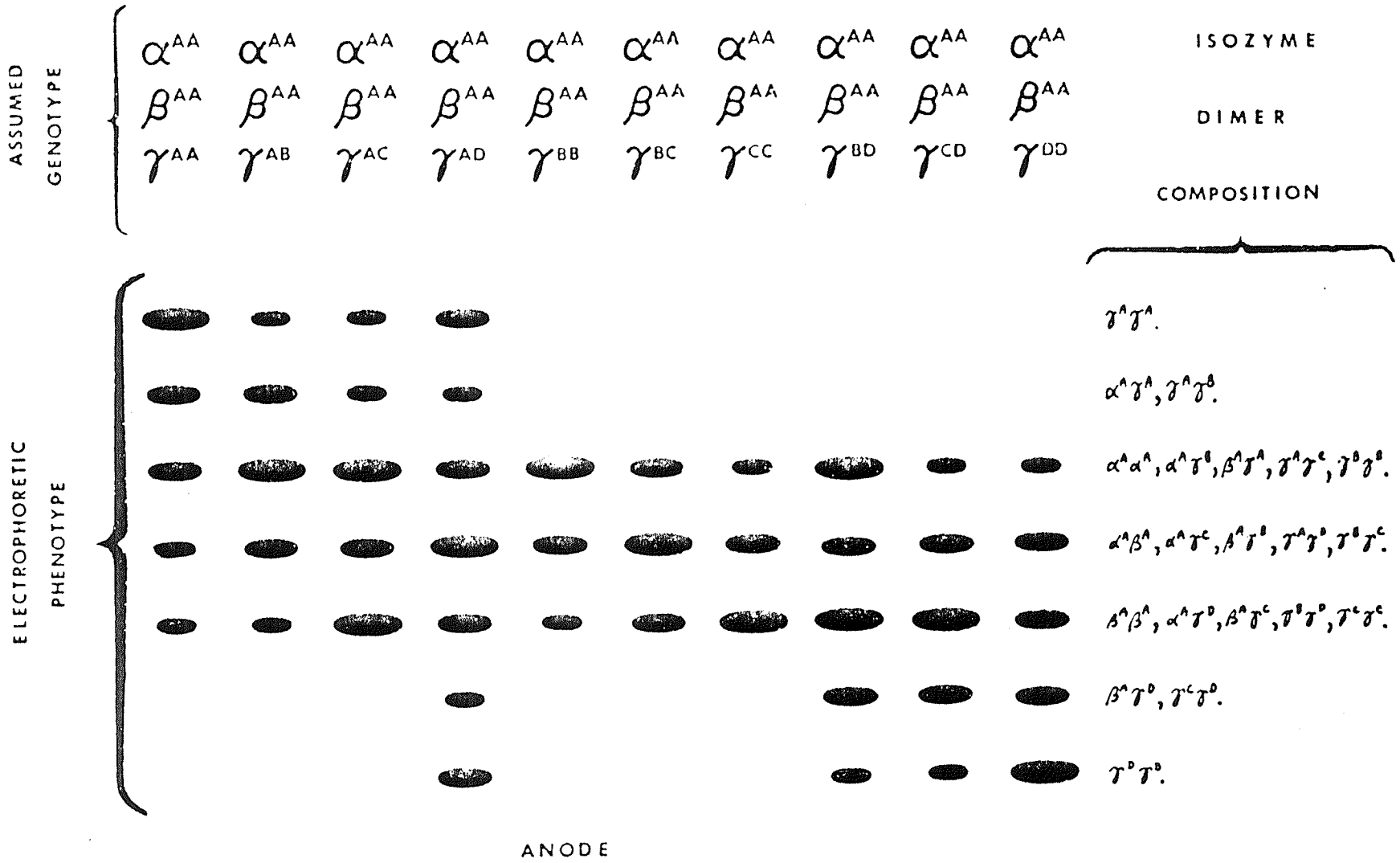
The genotype corresponding to the electrophoretic phenotype of each fish was derived from the established genetic models for LDH (Clayton and Franzin 1970) and G-3-PDH Clayton et al. (1973). The IDH genotypes were inferred from a genetic model presented in Bodaly (1977) (Fig. 3). This involves three loci, two monomorphic and one polymorphic with four alleles. Bodaly (1977) considered IDH (supernatant NADP form) in lake whitefish to function as a dimer. There is some doubt as to whether the IDH isozymes in lake whitefish are the products of two or three loci. Allendorf and Utter (1973) concluded the IDH (supernatant NADP form) isozymes in

Table 1. The isozyme systems analysed, tissues sampled and exact electrophoretic methods used in the study of lake whitefish populations from across western Canada.

Enzyme or Protein	EC No.	Locus Abbreviation	Tissues	Electrophoretic Methods
Glycerol-3-phosphate dehydrogenase (G-3-PDH)	1.1.1.8	g-3-pdh	white muscle	Clayton et al. (1973)
Lactate dehydrogenase Heart-type (LDH)	1.1.1.27	ldhH	red muscle	Clayton and Franzin (1970)
Isocitrate dehydrogenase (IDH) (NADP supernatant form)	1.1.1.42	idh	liver	Bodaly (1977)[1]
Hemoglobin			red blood cells	Lindsey et al. (1970)

[1] Liver tissue was ground with a teflon grinder with 2 volumes of 300 mg/L NADP in 0.25 M sucrose. Samples were centrifuged for 20 minutes at 25,000 g and 1°C. Buffer solutions and concentration of starch were the same as those noted in Clayton and Franzin (1970) except that NADP at 100 mg/l was added to the starch buffer, as was 3-mercapto, 1,2-propanediol (at a level of 5×10^{-3}M). The following stain solution was used: 0.15 m Bicine pH 8.5 (Na OH): 80.0 ml, sodium isocitrate monohydrate: 120 mg, $MgCl_2$ 6 H_2O: 40 mg, NADP (30 mg/ml): 0.8 ml, NBT (10 mg/ml): 1.6 ml, PMS (5 mg/ml): 0.48 ml.

Figure 3. Assumed genotype and subunit composition for isocitrate dehydrogenase (supernatant NADP form) electrophoretic phenotypes (from Bodaly 1977).


ASSUMED GENOTYPE
ELECTROPHORETIC PHENOTYPE
ISOZYME DIMER COMPOSITION
ANODE
α^{AA} β^{AA} γ^{AA}
α^{AA} β^{AA} γ^{AB}
α^{AA} β^{AA} γ^{AC}
α^{AA} β^{AA} γ^{AD}
α^{AA} β^{AA} γ^{BB}
α^{AA} β^{AA} γ^{BC}
α^{AA} β^{AA} γ^{CC}
α^{AA} β^{AA} γ^{BD}
α^{AA} β^{AA} γ^{CD}
α^{AA} β^{AA} γ^{DD}
$\gamma^{A}\gamma^{A}$.
$\alpha^{A}\gamma^{A}$, $\gamma^{A}\gamma^{B}$.
$\alpha^{A}\alpha^{A}$, $\alpha^{A}\gamma^{B}$, $\beta^{A}\gamma^{A}$, $\gamma^{A}\gamma^{C}$, $\gamma^{B}\gamma^{B}$.
$\alpha^{A}\beta^{A}$, $\alpha^{A}\gamma^{C}$, $\beta^{A}\gamma^{B}$, $\gamma^{A}\gamma^{D}$, $\gamma^{B}\gamma^{C}$.
$\beta^{A}\beta^{A}$, $\alpha^{A}\gamma^{D}$, $\beta^{A}\gamma^{C}$, $\gamma^{B}\gamma^{D}$, $\gamma^{C}\gamma^{C}$.
$\beta^{A}\gamma^{D}$, $\gamma^{C}\gamma^{D}$.
$\gamma^{D}\gamma^{D}$.

rainbow trout, Salmo gairdneri, a species in the same family as lake whitefish, were the products of two loci, one monomorphic and the other with four alleles.

Hemoglobin electrophoretic phenotypes were scored as either 'fast' or 'slow' depending on their mobility in the anodal direction on the starch gel. Lindsey et al. (1970) previously used this obvious distinction to characterize lake whitefish populations. The 'slow' class corresponds to the 'type B' figured by Tsuyuki et al. (1966b).

Previously unknown isozyme patterns of G-3-PDH were discovered in the present study. Clayton et al. (1973) demonstrated that the isozyme products of different G-3-PDH loci could be differentiated on the basis of their resistance to thermal denaturation. Samples containing the new isozyme patterns were electrophoresed concurrently with control samples, whose probable genetic base had been determined by breeding experiments. Before staining, the gel containing both the new isozyme patterns and the control was placed in a 50^{o}C hot water bath for 10 minutes. The isozymes were then stained and the relative amount denaturation noted between the new isozymes and those of known genetic base.

A large proportion of the electrophoretic data used in this study have been presented in the following publications: Franzin and Clayton (1977), Bodaly and Lindsey (1977), Bodaly (1977) and Franzin (1974). In addition, all of these authors have kindly donated additional unpublished data for use

in this thesis. The source(s) of the electrophoretic information for each population examined is given in Table 2.

Division of the Liard and Peace River Systems Into Upper and Lower Portions

For the purposes of present study the Liard River watershed is divided into upper and lower portions in the region of the Grand Canyon of the Liard (see Fig. 14). Rapids in this region were considered by McPhail and Lindsey (1970) to prevent upstream dispersal of fish species. The exact line for the division of the Liard River system is taken here to be where the Deer River (see Fig. 14) joins the Liard River. Rapids in this area (Devil's Portage) have been identified as the most impenetrable of those of the Grand Canyon of the Liard (J. Irvine, pers. comm.). The Peace River Canyon, near Hudson Hope, B.C., is used to divide the Peace River system into upper and lower portions for similar reasons.

Table 2. Gene frequencies ($ldh\text{-}A^A$ ($ldh\text{-}A^B$ = 1 - $ldh\text{-}A^A$), $g\text{-}3\text{-}pdh\text{-}A^A$ ($g\text{-}3\text{-}pdh\text{-}A^B$ = 1 - g-3-pdh A^A) $g\text{-}3\text{-}pdh\text{-}B^A$,B,C, and D and $idh\text{-}A^A$,B,C and D) hemoglobin 'Fast' class frequencies, sample size, and geographic data for 38 collections of lake whitefish. Also the number of lake whitefish sampled for gillraker counts (No) from the Liard and Tetcela River watersheds is included. The source(s) of electrophoretic data used in this study are listed as follows: A=the present study; B=Franzin and Clayton (1977); C=Franzin (1974); D=Bodaly (1977); E=Bodaly and Lindsey (1977 F=Franzin (unpubl. data); G=Bodaly (unpubl. data); H=Clayton and Lindsey (unpubl. data); and I=Clayton (unpubl. data). Only the 'low raker' lake whitefish forms (Bodaly 1977) of Little Teslin, Squanga and Dezadeash Lakes were considered in this study.

Location	Lat. (°)	Long. (°)	Elev. (m)	ldh-A A	ldh-A N	g-3-pdh (α) A	g-3-pdh (β) A	g-3-pdh B	g-3-pdh C	g-3-pdh D	g-3-pdh N	idh A	idh B	idh C	idh D	idh N	Hemoglobin 'Fast'	Hemoglobin N	Source of Data	No.
Alsek System																				
1. Aishihik L.	61.50	137.25	918	0.000	-[a]	0.000	0.000	0.000	0.815	0.185	62	0.000	0.250	0.750	0.000	22	0.000	31	B,C,D,G,	
2. Dezadeash L.	60.50	137.00	705	0.000	63	0.080	0.000	0.000	0.500	0.500	101	0.070	0.210	0.720	0.000	89	0.000	28	A,D,G	
Yukon System																				
3. Davis L.	66.18	136.42	382	0.000	93	0.489	0.000	0.000	1.000	0.000	92	0.000	0.154	0.846	0.000	52	--		E,I	
4. Kluane L.	61.17	138.50	784	0.000	--	0.000	0.000	0.000	0.357	0.647	14	0.020	0.250	0.730	0.000	26	--		B,C,D,G	
5. Little Teslin L.	60.48	133.48	765	0.000	--	0.190	0.000	0.000	0.310	0.690	72	0.119	0.176	0.704	0.000	70	0.000	7	A,B,G	
6. McClintock L.	60.58	133.43	765	0.000	--	0.050	0.000	0.000	0.733	0.267	30	0.040	0.170	0.780	0.000	23	--		B,F,D,G	
7. Squanga L.	60.47	133.63	792	0.000	58	0.220	0.000	0.000	0.340	0.660	123	0.020	0.050	0.930	0.000	29	0.000	37	A,B,C,D,G	
8. Tatchun L.	62.28	136.12	459	0.000	--	0.000	0.000	0.000	0.481	0.519	26	0.057	0.016	0.926	0.000	61	0.000	64	A,B,C,F	
Peel System																				
9. Margaret L.	65.35	134.50	491	0.000	29	0.034	0.000	0.000	0.635	0.362	29	0.000	0.018	0.982	0.000	28	--		D,E,I	
Upper Liard System																				
10. Dease L.	58.70	130.03	754	0.000	34	0.013	0.000	0.000	0.663	0.338	40	0.275	0.213	0.513	0.000	40	0.000	38	A	30
11. Finlayson L.	61.72	130.67	960	0.000	4	0.000	0.000	0.000	0.600	0.400	5	0.000	0.000	1.000	0.000	4	0.000	3	A	2
12. Frances L.	61.25	129.30	777	0.000	29	0.011	0.000	0.000	0.831	0.169	59	--	--	--	--		--		B,C	
13. Simpson L.	60.72	129.23	688	0.000	27	0.000	0.000	0.000	0.778	0.222	27	0.241	0.148	0.611	0.000	27	0.000	10	A	26
14. Watson L.	60.10	128.80	682	0.000	27	0.000	0.000	0.000	0.478	0.022	23	0.067	0.017	0.517	0.000	30	0.000	12	A,B,C	
15. Wheeler L.	59.68	129.17	688	0.000	54	0.000	0.000	0.000	0.951	0.049	51	0.000	0.390	0.610	0.000	30	--		G	19
16. Toobally L.	60.38	126.20	688	0.649	63	0.000	0.021	0.000	0.686	0.293	70	0.031	0.031	0.439	0.000	65	0.833	42	A	30
Lower Liard System																				
17. Bovie L.	60.18	122.95	324	1.000	9	0.000	0.000	0.000	0.581	0.419	9	0.000	0.000	1.000	0.000	9	--		A	9
18. Divide L.	61.95	128.23	1295	0.814	24	0.000	0.000	0.000	1.000	0.000	21	0.000	0.044	0.956	0.000	23	0.000	25	A,B,C	
19. Fisherman L.	60.83	123.78	373	1.000	43	0.000	0.000	0.000	0.581	0.419	43	0.000	0.000	1.000	0.000	43	0.214	28	A	30
20. McLeod L.	61.38	126.50	688	1.000	3	0.000	0.000	0.000	0.833	0.167	3	0.000	0.000	1.000	0.000	3			A	3
21. Seaplane L.	61.42	126.83	688	1.00	35	0.000	0.000	0.000	1.000	0.000	35	0.000	0.000	1.000	0.000	34			A	30
Tetcela System																				
22. Little Doctor L.	60.83	123.23	221	0.865	25	0.000	0.000	0.000	0.192	0.808	24	0.000	0.000	1.000	0.000	26			A	26
Upper Peace System																				
23. McLeod L.	54.92	122.42	680	0.805	36	0.000	0.000	0.000	0.743	0.257	37	0.000	0.000	1.000	0.000	36		30	A	
24. Moberly L.	55.82	121.75	694	0.908	71	0.000	0.000	0.000	0.535	0.465	71	0.000	0.000	1.000	0.000	27		28	A,B,C	
25. Summit L.	54.28	122.67	706	0.990	48	0.000	0.000	0.000	0.792	0.208	48	--	--	--	--				B,C	
Lower Peace System																				
26. Utikuma L.	55.90	115.40	645	--		0.000	0.014	0.000	0.480	0.507	74	--	--	--	--				H	
Fraser System																				
27. Aleza L.	54.12	122.07	610	1.000	20	0.000	0.000	0.000	0.450	0.550	20	0.000	0.000	1.000	0.000	19	--		A,H	
28. Fraser L.	54.09	124.75	670	0.550	9	0.000	0.000	0.000	0.560	0.440	9	0.000	0.000	1.000	0.000	9	0.556	9	A,F	
29. Lac la Hache	51.82	121.50	808	0.674	83	0.000	0.000	0.000	0.300	0.700	80	0.000	0.000	1.000	0.000	39	0.971	35	A,B,C	
30. Williams L.	52.12	122.08	567	0.136	22	0.000	0.000	0.000	0.591	0.409	22	0.000	0.000	1.000	0.000	21	0.375	8	A,B,D,F	
Athabasca System																				
31. Talbot L.	53.08	118.00	1001	0.886	48	0.000	0.000	0.000	0.740	0.260	48	0.000	0.000	1.000	0.000	41	1.000	10	A,B,C	
32. Athabasca L.	59.42	110.00	213	0.825	63	0.024	0.000	0.397	0.183	0.420	63	0.000	0.017	0.833	0.150	30			A,B,C	
33. Lesser Slave L.	55.40	115.30	577	--		0.007	0.000	0.033	0.289	0.678	76	--	--	--	--				H	
South Saskatchewan System																				
34. Waterton L.	49.05	113.90	1279	0.800	20	0.000	0.000	0.625	0.025	0.350	20	0.000	0.000	1.000	0.000	22	1.000	19	A,B,C	
North Saskatchewan System																				
35. Wabamun L.	53.53	114.58	725	0.983	55	0.000	0.000	0.046	0.630	0.324	54	0.000	0.021	0.978	0.000	47	0.000	37	A,B,C	
Mackenzie System																				
36. Great Slave L.	62.00	114.00	158	0.896	24	0.000	0.000	0.364	0.272	0.364	22	0.000	0.056	0.889	0.056	54	.539	26	A,B,C	
37. Liard and Mackenzie River Junction	61.85	121.30	130	0.409	11	0.091	0.000	0.364	0.409	0.227	11	0.000	0.100	0.800	0.100	10	--		A	
38. Mackenzie Delta	68.35	133.77	0	0.200	37	0.27	0.000	0.070	0.410	0.530	35	0.125	0.167	0.708	0.000	36	--		A,E,I	
Totals					1167						1654					1125		527		

[a] Franzin and Clayton (1977) considered Yukon and Alsek River system populations homozygous for $ldh\text{-}A^B$ after probability of finding another allele dropped to below 5%.

Determination of Fish Species Composition of Liard River Study Lakes

The species composition of the Liard study lakes was determined by setting gillnets in a variety of environments; usually two strung together set perpendicularly from shore, another series of two set on the bottom in open water and at least one floater set in open water. In addition, sections of the shoreline were fished with a seine to attempt to determine the smaller fish species present.

Gillraker Counts

The first left gill arch was removed from each individual in a subsample (usually 30 when possible) of lake whitefish from all populations sampled along the Liard River system. The gillrakers were counted with the aid of a microscope. All rakers with a boney rudiment were included. The modal count (the one occurring the most frequently) was determined for each population. In cases where two adjacent counts occurred in the same frequency the lower value was chosen. Each population was checked for a possible bi-modality in gillraker numbers.

Statistical Analysis

The phenotypes for LDH, G-3-PDH and IDH for each population considered were compared using the χ^2 test to their Castle-Hardy-Weinberg equilibrium expected values. The test was performed only if each class had an expected value of greater than 5.

Populations of lake whitefish, represented by 10 or more specimens, were genetically compared using Nei's (1972) standard measure of genetic identity:

$$I_{xy} = \frac{\sum x_i \, y_i}{(\sum x_i^2 \sum y_i^2)^{\frac{1}{2}}}$$

where x and y are the frequencies of the i^{th} allele in populations x and y and the summation is over all alleles and all loci compared. In this study 15 alleles at seven different loci were considered. Populations which share identical alleles in the identical frequencies have a similarity value of 1. Populations which share no alleles would have a similarity value of 0. Nei's index of similarity is used here simply as a comparison of the genetic similarities among the populations. The genetic similarities were not, as is commonly done, used to calculate a genetic distance which can then be used to estimate the time elapsed since the isolation of different stocks.

The isozyme systems used in the present study were chosen because they had either previously been shown to aid in the differentiation of populations or had been inferred to do so on the basis of preliminary analysis. This non-random selection of isozyme systems invalidates the measure of genetic distance between populations. A packaged computer programme (CLUSTAN, prepared by D. Wishart, University College, London) was used to cluster the Nei genetic similarity values. The actual clustering was done using the 'procedure hierarchy' group average method. This is equivalent to the unweighted pair-group arithmetic average clustering method presented in Sneath and Sokal (1973).

RESULTS

Biochemical Analysis

Glycerol-3-phosphate dehydrogenase. Clayton et al. (1973) proposed a genetic model for the electrophoretic phenotypes of lake whitefish G-3-PDH and confirmed it with breeding experiments. G-3-PDH phenotypes observed in lake whitefish from across western Canada were concluded to be the products of two loci, one with two and the other with three alleles. In the present study, two new phenotypes were discovered in the population from Toobally L. (16) (16 - the population number, referred to in all figures and tables). The simplest explanation to account for the new phenotypes is the occurrence of a new allele at one of the extant loci. Lake whitefish G-3-PDH B isozymes were shown to be more resistant to thermal denaturation than G-3-PDH A isozymes (Clayton et al. 1973). The new isozymes were similar to G-3-PDH B isozymes in their resistance to thermal denaturation and on this basis, are interpreted as representing an allele at the locus designated G-3-PDHb by Clayton et al. (1973).

In accord with the nomenclature suggestions of Bailey et al. (1976), the replicated salmonid loci will be represented by a greek letter and the different alleles by letters of the English alphabet. The nomenclature of Clayton et al. (1973)

has been modified so that the former G-3-PDHa locus becomes g-3-pdhα and the G-3-PDHb locus is now designated as g-3-pdhβ. The G-3-PDHa alleles, G-3-PDHa^1 and G-3-PDHa^2 are now g-3-pdhα^A and g-3-pdhα^B, respectively. The new allele discovered at the G-3-PDHb locus is designated g-3-pdhβ^A as its isozyme products migrated the least towards the anode as compared to the other alleles of this locus (Fig. 4). The three other G-3-PDHb alleles, G-3-PDHb^1, G-3-PDHb^2 and G-3-PDHb^3 are thus designated g-3-pdhβ^B, g-3-pdhβ^C and g-3-pdhβ^D, respectively. The new isozyme patterns and their probable genetic base are shown in Fig. 4 in comparison to other isozyme patterns for G-3-PDH previously found in western Canadian populations of lake whitefish. In addition, isozymes attributed to the g-3-pdhβ^E allele, found only in lake whitefish populations from eastern North America, are included for comparison (Fig. 4).

Franzin and Clayton (1977) showed the distribution of alleles of the g-3-pdhβ locus to be disjunct in lake whitefish populations from across western Canada (Fig. 5). No populations from the Fraser, upper Peace, upper Liard, Alsek and Yukon River drainages expressed the g-3-pdhβ^B allele. Bodaly and Lindsey (1977) also failed to find this allele in a population (9) from the Peel River system. The additional populations included in the present study from these watersheds,

Figure 4. The two new G-3-PDH isozyme patterns, their probable genotype (g-3-pdhβ^{A}) and subunit composition, presented in comparison with other G-3-PDH isozyme patterns, the genetics of which have been confirmed with breeding experiments. One of the G-3-PDH isozyme patterns (g-3-pdhβ^{E}) unique to eastern North American populations is included for comparisons.

Lake whitefish white muscle G-3-PDH phenotypes

(polymorphism at *g-3-pdhα* & *g-3-pdhß* loci)

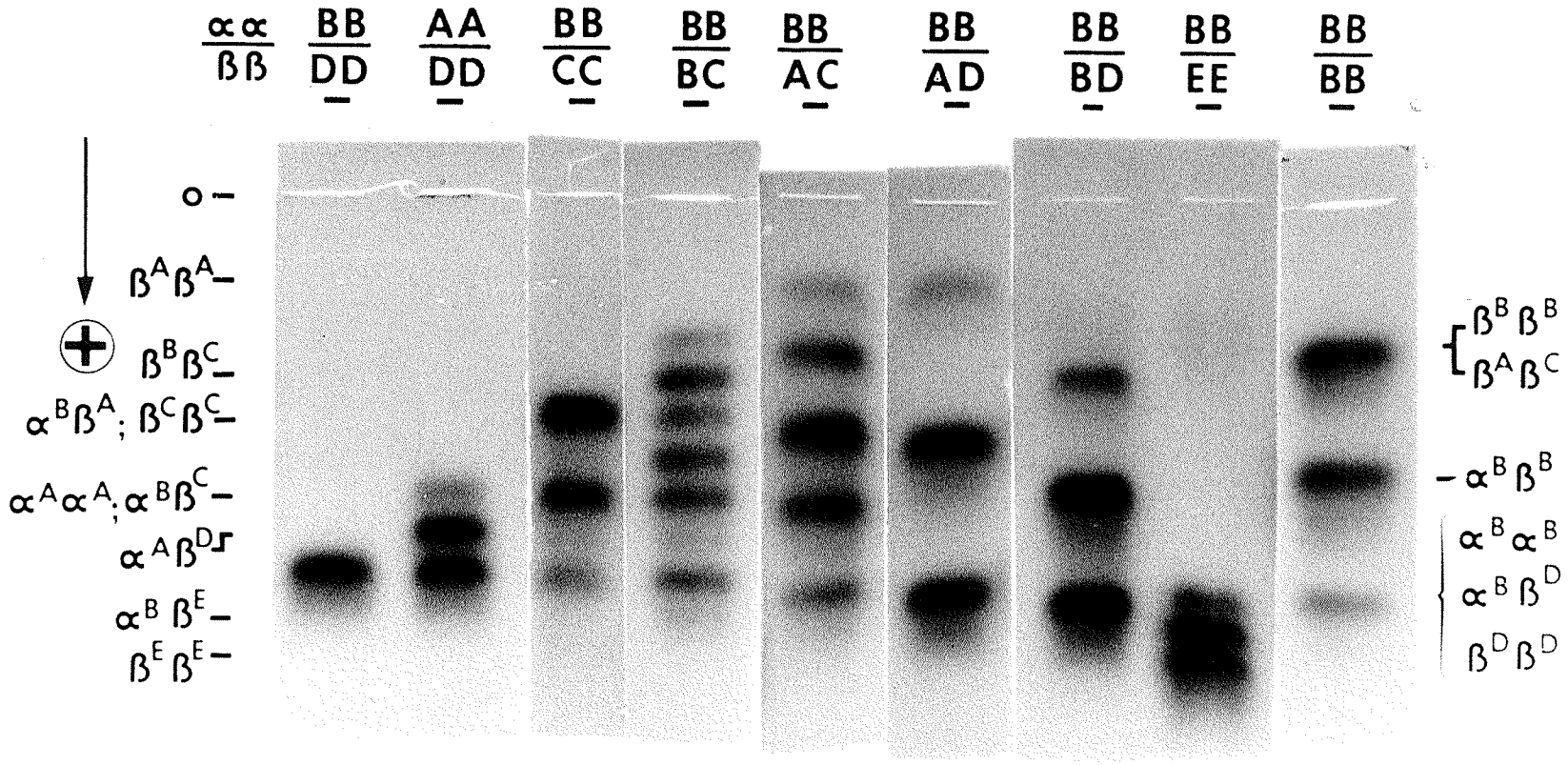
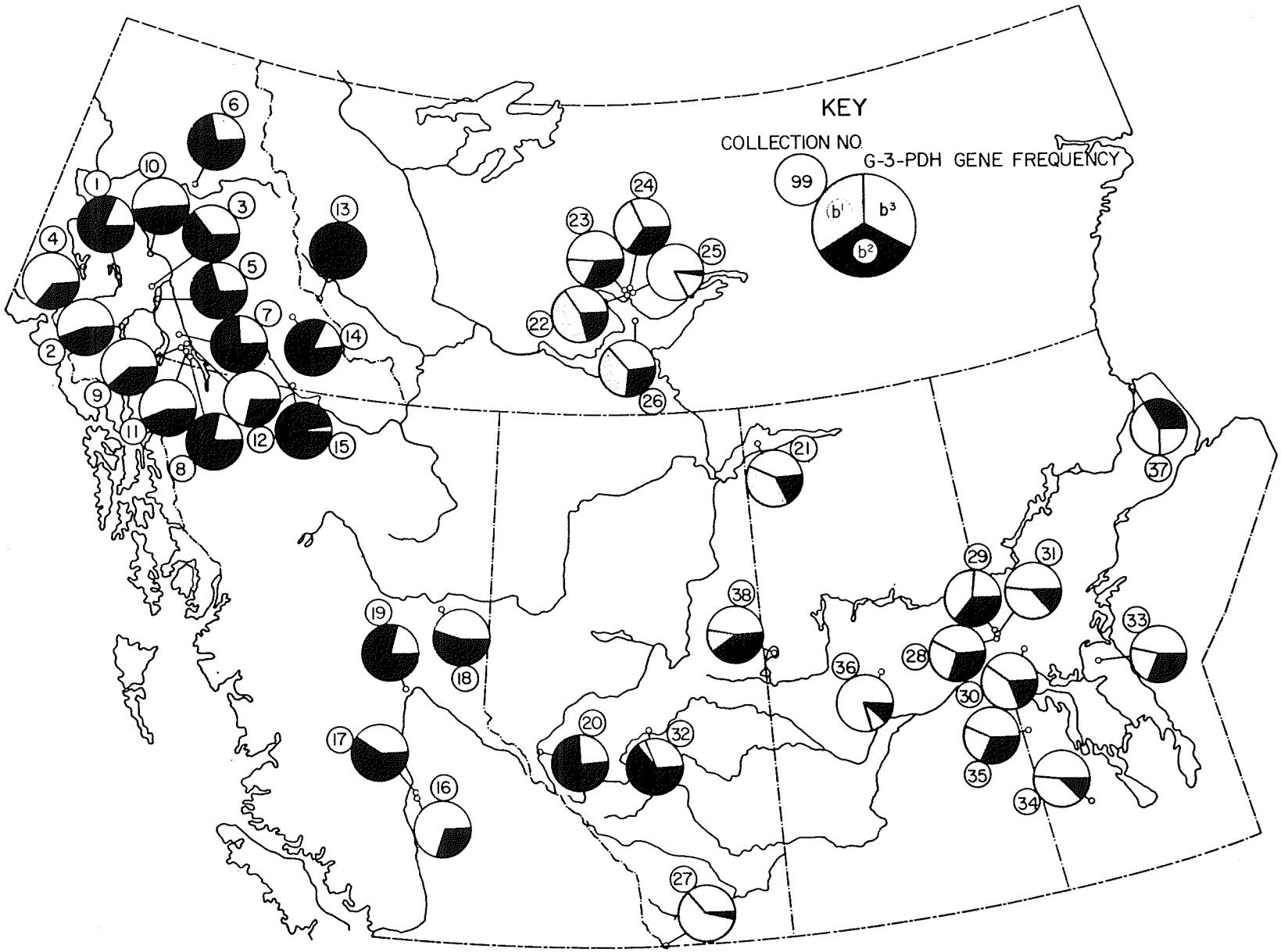


Figure 5. Frequencies of L-glycerol-3-phosphate dehydrogenase (g-3-pdhβ) alleles in lake whitefish populations from across western Canada (from Franzin and Clayton 1977). The nomenclature of G-3-PDHb^1, G-3-PDHb^2, and G-3-PDHb^3 is converted to g-3-pdhβ^B, g-3-pdhβ^C and g-3-pdhβ^D, respectively, in the present study.


KEY
COLLECTION NO.
99
G-3-PDH GENE FREQUENCY
b¹
b²
b³
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
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as well as from the lakes of the lower Liard (17-21) and Tetcela (22) River watersheds also did not express the g-3-pdhβ^B allele (Fig. 6). In populations from the Mackenzie delta (38), Utikuma L. (26), Lesser Slave L. (33) and Wabamun L. (35) g-3-phdβ^B was present in very low frequencies (Fig. 6, Table 2). In most other populations considered in the present study (Fig. 6) and previously (Franzin and Clayton 1977) (Fig. 5) the g-3-pdhβ^B allele occurred in frequencies comparable to those of g-3-pdhβ^C and g-3-pdhβ^D, with exception of the Waterton L. (34) population where g-3-pdhβ^B occurred in by far the highest frequency.

Franzin and Clayton (1977) found both g-3-pdhα^A and g-3-pdhα^B to be present in at least some populations from all the watersheds sampled, with the exception of the upper Peace[1] and Fraser River watersheds where the g-3-pdhα^A allele was apprently absent in all populations sampled. The distribution of g-3-pdhα alleles is not amenable to the graphical type of presentation as used for the g-3-pdhβ alleles due to the usual very low frequency of g-3-pdhα^A when it does occur. The frequency of g-3-pdhα^A is given for each population (Table 2) and the distribution of this allele in lake whitefish populations from across western Canada can be examined by noting in which watersheds it was found to

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[1] The reported (Franzin and Clayton 1977) occurrence of g-3-pdhα^A in the Moberly L. (24) and Wabamun L. (35) lake whitefish populations were the products of clerical error (J. W. Clayton, pers. comm.).

Figure 6. Frequencies of L-glycerol-3-phosphate dehydrogenase (g-3-pdh-β) alleles in the 38 lake whitefish populations, from across western Canada, specifically considered in the present study.

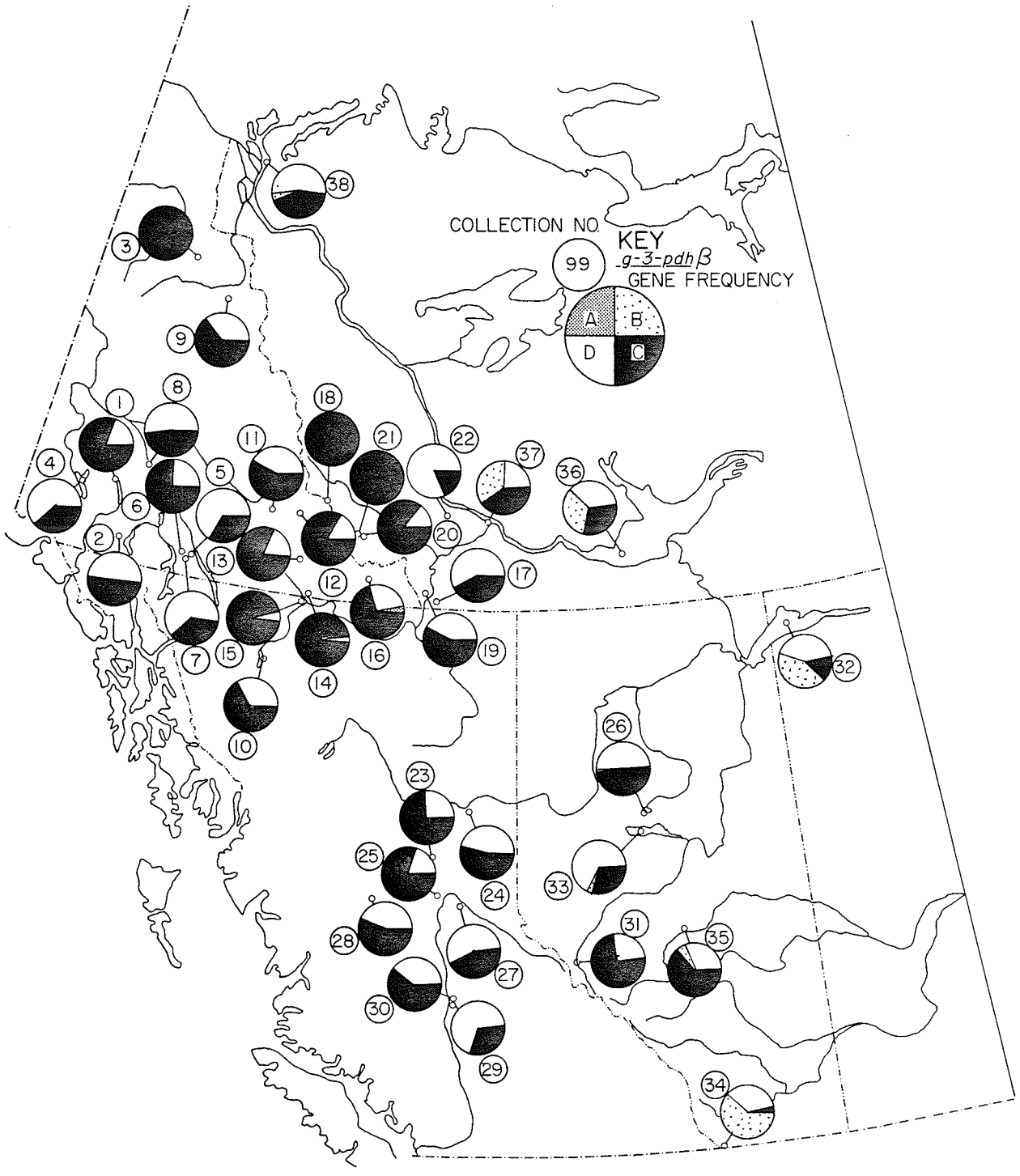
COLLECTION NO.
99
KEY
g-3-pdh β
GENE FREQUENCY
A
B
D
C
1
2
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Table 3. Lake whitefish L-glycerol-3-phosphate dehydrogenase (G-3-PDH-B) observed and expected (Castle-Hardy-Weinberg equilibrium) numbers of phenotypes per population. χ^2 values were not calculated where the expected values were less than 5. Significance at the 0.05 level is indicated by *.

Location	BB	BC	BD	CC	CD	DD	AC	AD	χ^2_m
Alsek System									
1. Aishihik L.	0(0.00)	0(0.00)	0(0.00)	41(41.18)	19(18.70)	2(2.12)	0(0.00)	0(0.00)	
2. Dezadeash L.				23(24.75)	54(50.49)	24(25.76)			0.60
Yukon System									
3. Davis L.				92(92.00)	0(0.00)	0(0.00)			
4. Kluane L.				1(1.78)	8(6.43)	5(5.79)			
5. Little Teslin L.				10(6.72)	24(30.56)	38(34.72)			3.32*
6. McClintock L.				18(16.12)	8(11.74)	4(2.14)			
7. Squanga L.				20(13.97)	43(54.96)	60(54.07)			5.86*
8. Tatchun L.				8(6.02)	9(12.98)	9(7.00)			2.44
Peel System									
9. Margaret L.				13(11.80)	11(13.40)	5(3.80)			
Upper Liard System									
10. Dease L.				16(17.56)	21(17.89)	3(4.55)			
11. Finlayson L.				2(1.56)	1(1.88)	1(0.56)			
12. Frances L.				43(40.53)	12(16.57)	4(1.69)			
13. Simpson L.				16(16.34)	10(9.32)	1(1.33)			

cont'd

Table 3 cont'd.

Location	BB	BC	BD	CC	CD	DD	AC	AD	$\chi^2_{(1)}$
14. Watson L.	0(0.00)	0(0.00)	0(0.00)	22(22.00)	1(0.00)	0(0.00)	0(0.00)	0(0.00)	
15. Wheeler L.				46(46.12)	5(4.75)	0(0.12)			
16. Toobally L.				32(33.19)	30(28.11)	5(6.00)	2(2.06)	1(0.44)	
Lower Liard System									
17. Bovie L.				2(1.78)	4(4.44)	3(2.78)	0(0.00)	0(0.00)	
18. Divide L.				22(22.00)	0(0.00)	0(0.00)			
19. Fisherman L.				14(14.53)	22(20.93)	7(7.53)			0.11
20. McLeod L.				2(1.99)	1(0.83)	0(0.08)			
21. Seaplane L.				35(35.00)	0(0.00)	0(0.00)			
Tetcela River System									
22. Little Doctor L.				1(0.96)	8(8.08)	17(16.96)			
Upper Peace System									
23. McLeod L.				21(20.43)	13(14.13)	3(2.44)			
24. Moberly L.				20(20.32)	36(35.33)	15(15.35)			0.03
25. Summit L.				30(30.11)	16(15.82)	2(2.08)			
Lower Peace System									
26. Utikuma L.	0(0.01)	1(1.60)	1(1.01)	13(17.05)	44(36.02)	15(19.02)			
Fraser System									
27. Aleza L.	0(0.00)	0(0.00)	0(0.00)	5(4.05)	8(9.90)	7(6.05)			
28. Fraser L.				4(2.82)	2(4.44)	3(1.74)			
29. Lac la Hache				5(7.20)	38(33.60)	37(39.20)			1.11
30. Williams L.				9(7.68)	8(10.64)	5(3.68)			1.4

cont'd

Table 3 cont'd.

Location	BB	BC	BD	CC	CD	DD	AC	AD	$\chi^2_{(1)}$
Athabasca System									
31. Talbot L.	0(0.00)	0(0.00)	0(0.00)	28(26.29)	15(18.47)	5(3.25)	0(0.00)	0(0.00)	1.7
32. Athabasca L.	8(9.93)	11(9.15)	23(21.01)	0(2.11)	12(9.68)	9(11.11)			
33. Lesser Slave L.	0(0.08)	1(1.45)	4(3.39)	7(6.35)	29(29.78)	35(34.94)			
South Saskatchewan System									
34. Waterton L.	7(7.81)	1(0.63)	10(8.75)	0(0.01)	0(0.35)	2(2.45)			
North Saskatchewan System									
35. Wabamun L.	1(1.14)	2(3.13)	1(1.61)	23(21.43)	20(22.05)	7(5.67)			
Mackenzie System									
36. Great Slave L.	4(2.92)	4(4.36)	4(5.83)	2(1.63)	4(4.36)	4(2.92)			
37. Laird River Mouth	1(1.46)	4(3.28)	2(1.82)	1(1.84)	3(2.04)	0(0.57)			
38. Mackenzie Delta	0(0.34)	2(2.03)	2(2.64)	6(6.08)	14(15.08)	11(10.28)			

occur. The g-3-pdhα^B allele was expressed in a relatively high frequency in every population sampled while the g-3-pdhα^A allele was either absent or present at a low frequency (Table 2). Only in the population from Davis L. (3) did the g-3-pdhα^A allele occur in a frequency similar to that of g-3-pdhα^B. The g-3-pdhα^A allele was not found in the lake populations of the lower Liard (17-21), Tetcela (22), upper Peace (23-25), and Fraser (27-29) River systems. It was also not expressed in the populations considered in this study from the North (35) and South (34) Saskatchewan River systems but Franzin and Clayton (1977) did note its occurrence in lake whitefish populations from further east in the same watershed. The frequency of g-3-pdhα^A was usually higher in lake whitefish populations from the Yukon River watershed than it was in populations from any other watershed (Table 2). Only the two river populations, the Liard River mouth (37) and the Mackenzie delta (38) expressed the g-3-pdhα^A allele in frequencies comparable to most of the Yukon River populations.

The number of lake whitefish in each phenotypic class of G-3-PDHβ as well as the Castle-Hardy-Weinberg expectations are presented in Table 3. Nine populations were tested for their agreement to the predicted equilibrium and, of these, only two populations, Little Teslin L. (5) and Squanga L. (7), were found to differ significantly from the expected

equilibrium. Qualitatively, all other populations considered with the exception of Utikuma L. (26), were in good agreement with the predicted equilibrium values. The number of lake whitefish in some of the phenotypic classes of G-3-PDHα was often extremely low and therefore the observed and expected results have not been presented. In a few of the Yukon River system populations, Davis L. (3), Little Teslin L. (5) and Squanga L.(7), the numbers of lake whitefish examined were so high as to allow tests for deviations from the predicted equilibrium values. Only the Squanga L. (7) population differed significantly. All the populations which differed significantly from the predicted equilibrium values for either phenotypic class group, G-3-PDHα and G-3-PDHβ were ones which were found to occur with a 'high gillraker' form of lake whitefish. The reasons for these deviations were unclear (Bodaly 1977).

Heart-type lactate dehydrogenase. Three electrophoretically distinguishable phenotypes of heart-type lactate dehydrogenase (LDH) were found in lake whitefish populations from western Canada. Clayton and Franzin (1970) used breeding experiments to demonstrate that these were the products of one polymorphic locus with two alleles and one invariant

locus. Franzin and Clayton (1977) studied the distribution and frequencies of these alleles in populations from across western Canada (Fig. 7). In the Yukon, Alsek, and upper Liard River drainages only $\underline{ldhH\alpha}^{B}$ was found, while both $\underline{ldhH\alpha}^{A}$ and $\underline{ldhH\alpha}^{B}$ were found in all other lake whitefish populations.

Thirty-six of the populations considered in the present study were analysed for heart-type LDH and the frequency of the $\underline{ldhH\alpha}^{A}$ allele for each population is given in Table 2. Only $\underline{ldhH\alpha}^{B}$ was found in lake whitefish populations from the Alsek (1,2), Yukon (3-8), and Peel (9) River systems (Fig. 8). It was also the only allele expressed in six of the seven populations (10-15) sampled from the upper Liard watershed. Both $\underline{ldhH\alpha}^{A}$ and $\underline{ldhH\alpha}^{B}$ occurred in the lake whitefish population from Toobally L. (16) (Fig. 8). The five lake whitefish populations (17-21) from lakes in the lower Liard River drainage all expressed very high frequencies of the $\underline{ldhH\alpha}^{A}$ allele. In fact, four of these populations appear to be homozygous for this allele, although the significance of this observation must be qualified by the fact that two of these populations (17,20) were represented by very small sample sizes (Table 2). The two river populations sampled, from the Liard River mouth (37) and the Mackenzie delta (38), displayed relatively high frequencies of $\underline{ldhH\alpha}^{B}$ in comparison to other populations in which both alleles

Figure 7. Frequencies of heart-type lactate dehydrogenase (*ldhH-α*) alleles in lake whitefish populations from across western Canada (from Franzin and Clayton 1977).

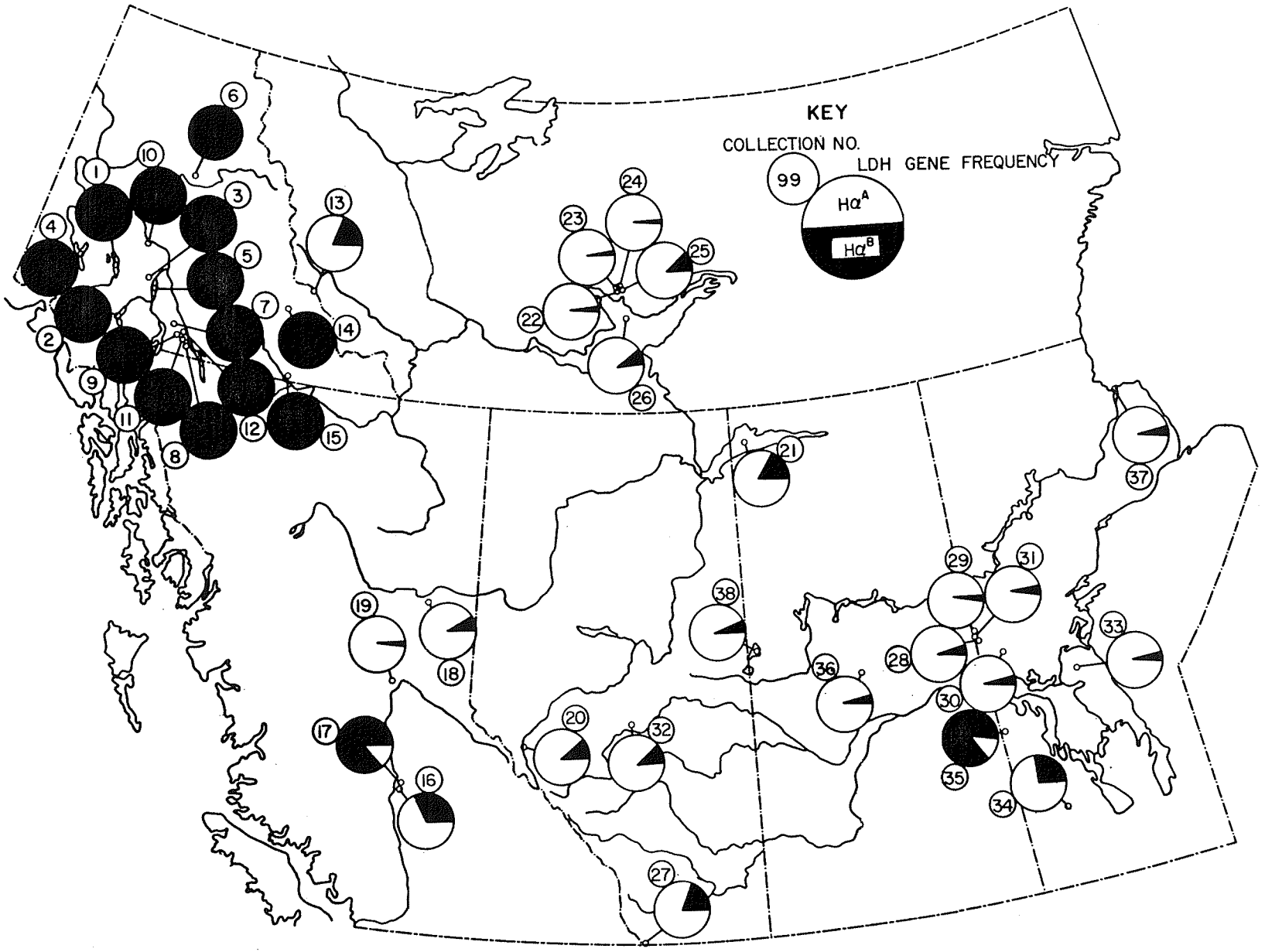
KEY
COLLECTION NO.
99
LDH GENE FREQUENCY
Hα^A
Hα^B
1
2
3
4
5
6
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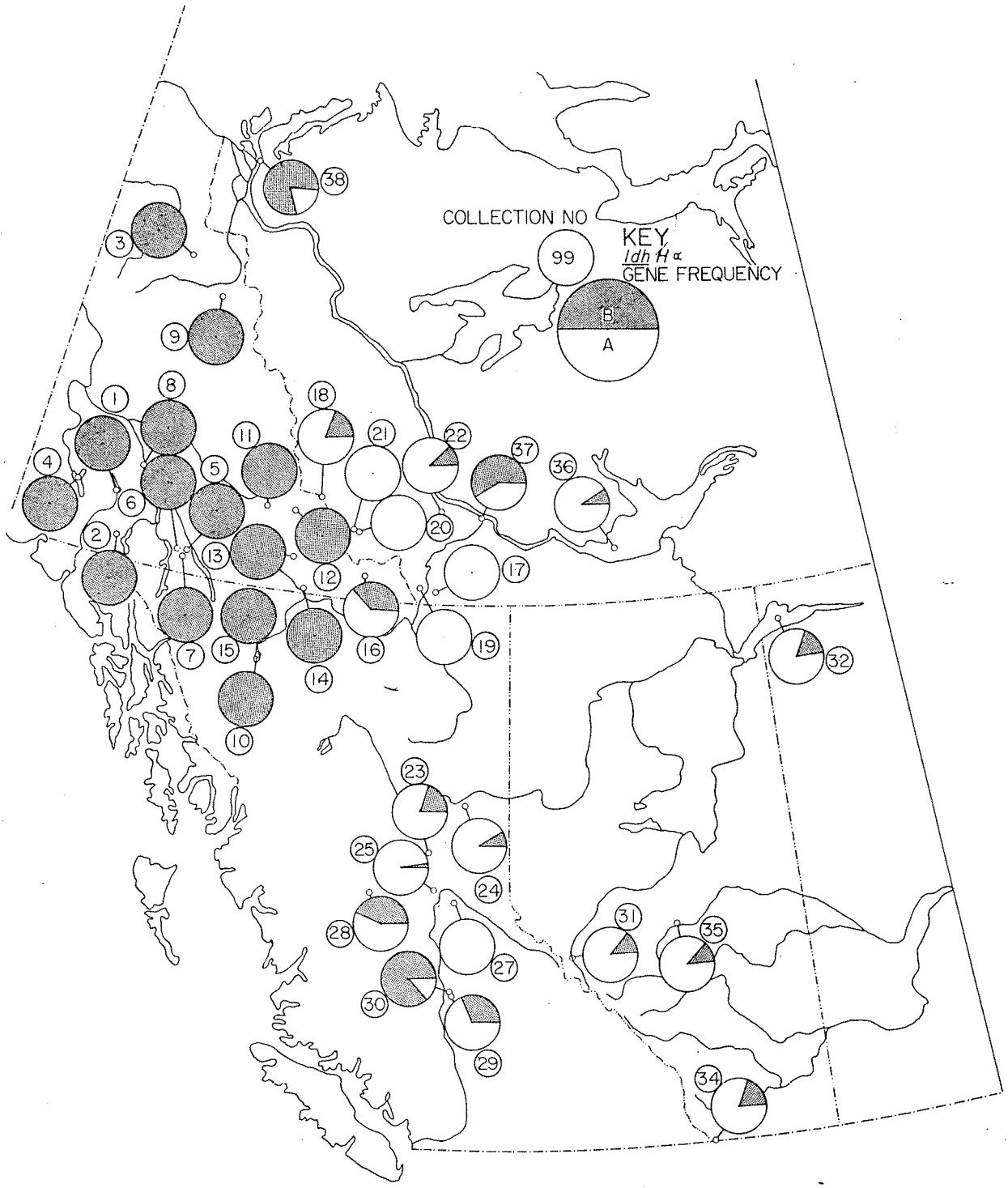
Figure 8. Frequencies of heart-type lactate dehydrogenase (*ldhH-A*) alleles in 36 lake whitefish populations, from across western Canada, specifically considered in this study.


COLLECTION NO
99
KEY
ldh H α
GENE FREQUENCY
B
A
1
2
3
4
5
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9
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11
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occurred (Figs. 7 and 8). The sample of lake whitefish from Aleza L. (27) was homozygous for $\underline{ldhH\alpha}^{A}$. All other populations investigated had both alleles present although the $\underline{ldhH\alpha}^{B}$ was often found in low frequencies (Fig. 8).

The number of lake whitefish of each phenotypic class of heart-type LDH as well as the Castle-Hardy-Weinberg expectations are given for all populations in Table 4 except for those of the Yukon and Alsek River systems which were all homozygous for $\underline{ldhH\alpha}^{B}$. Of the two populations with expected classes large enough to conduct χ^2 tests for equilibrium, the Toobally L. (16) population did not differ significantly from the predicted equlibrium while the population from Lac la Hache (29) did. Franzin (1974) considered that the sampling of different subpopulations in Lac la Hache may have led to the observed deviation from the expected values. Qualitatively, most of the other populations appear to be in good agreement with the Castle-Hardy-Weinberg expected values.

Isocitrate dehydrogenase. Bodaly (1977) surveyed lake whitefish populations from twelve lakes in the Yukon and Alsek River drainages for phenotypic differences in isocitrate dehydrogenase (IDH). These results, along with preliminary results from other parts of western Canada (J. W. Clayton and A. H. Kristofferson, unpublished data), indicated that

Table 4. Lake whitefish heart-type lactate dehydrogenase (LDH∝) observed and expected (Castle-Hardy-Weinberg equilibrium) numbers of phenotypes per population. All populations from the Alsek and Yukon River watersheds are not included as all were homozygous for *ldhH∝*^{B}. χ^2 values were not calculated where the expected values were less than 5. Significance at the 0.05 level is indicated by *.

Location	AA	AB	BB	$\chi^2_{(1)}$
Peel System				
9. Margaret L.	0 (0.00)	0 (0.00)	29 (29.00)	
Upper Liard System				
10. Dease L.			34 (34.00)	
11. Finlayson L.			4 (4.00)	
12. Frances L.			29 (29.00)	
13. Simpson L.			27 (27.00)	
14. Watson L.			10 (27.00)	
15. Wheeler L.			59 (59.00)	
16. Toobally L.	27 (25.23)	26 (29.20)	10 (8.39)	0.76
Lower Liard System				
17. Bovie L.	9 (9.00)	0 (0.00)	0 (0.00)	
18. Divide L.	17 (15.84)	5 (7.31)	2 (0.84)	
19. Fisherman L.	43 (43.00)	0 (0.00)	0 (0.00)	
20. McLeod L.	3 (3.00)	0 (0.00)	0 (0.00)	
21. Seaplane L.	35 (35.00)	0 (0.00)	0 (0.00)	

cont'd

Table 4. cont'd.

Location	AA	AB	BB	$\chi^2_{(1)}$
22. Little Doctor L.	20 (19.36)	4 (5.28)	1 (0.36)	
Peace System				
23. McLeod L.	26 (23.36)	6 (11.28)	4 (1.36)	
24. Moberly L.	29 (58.54)	11 (11.86)	1 (0.60)	
25. Summit L.	47 (47.04)	1 (0.95)	0 (0.00)	
Fraser System				
27. Aleza L.	20 (20.00)	0 (0.00)	0 (0.00)	
28. Fraser L.	3 (2.78)	4 (4.45)	2 (1.78)	
29. Lac la Hache	45 (39.8)	25 (35.3)	13 (7.8)	7.2*
30. Williams L.	2 (0.41)	2 (5.17)	18 (16.42)	
Athabasca System				
31. Talbot L.	38 (37.68)	9 (9.70)	1 (0.62)	
32. Athabasca L.	43 (42.88)	18 (18.19)	2 (1.93)	
South Saskatchewan System				
34. Waterton L.	12 (12.80)	8 (6.40)	0 (0.80)	
35. Wabamun L.	44 (42.79)	9 (11.45)	2 (0.77)	
Mackenzie System				
36. Great Slave L.	19 (19.27)	5 (4.47)	0 (0.26)	
37. Liard River Mouth	3 (1.84)	3 (5.32)	5 (3.84)	
38. Mackenzie Delta	1 (1.52)	13 (11.84)	23 (23.52)	

$idh\gamma^{A}$ was absent from watersheds outside of the Yukon and that $idh\gamma^{D}$ was absent from the lakes in Alsek, Yukon, Peel, and upper Liard River systems, though probably present in most other western Canadian lake whitefish populations.

Thirty-four lake whitefish populations were examined for IDH (Fig. 9) and the respective allele frequencies for each population are given in Table 2. The distribution of alleles at the $idh\gamma$ locus is very disjunct across western Canada (Fig. 9). The $idh\gamma^{C}$ allele was found to occur in all populations and was the only allele found in lake populations from the lower Liard (17-21) excluding Divide L. (18), Tetcela (22), Fraser (27-30), upper Peace (23-24), upper Athabasca (31) and South Saskatchewan (34) River systems (Fig. 9). The Finlayson L. population (11) in the upper Liard River system was also apparently fixed for this allele but this observation must be qualified by the very small sample of fish available from this population (Table 2). The $idh\gamma^{B}$ allele was also expressed in populations over a wide geographical range, occurring in all populations except those already noted to be homozygous for $idh\gamma^{C}$. The $idh\gamma^{B}$ allele was found in all Manitoban lake whitefish populations so far examined (J. W. Clayton and A. H. Kristofferson, unpublished data). The $idh\gamma^{A}$ allele was found in most populations of the Alsek (2), Yukon (4-8), and upper Liard River (10, 13, 14 and 16) watersheds (Fig. 9). It was absent in all lake whitefish populations from outside these

Figure 9. Frequencies of isocitrate dehydrogenase (NADP, supernatant form) (idhγ) alleles from the 34 lake whitefish populations examined from across western Canada for this enzyme.

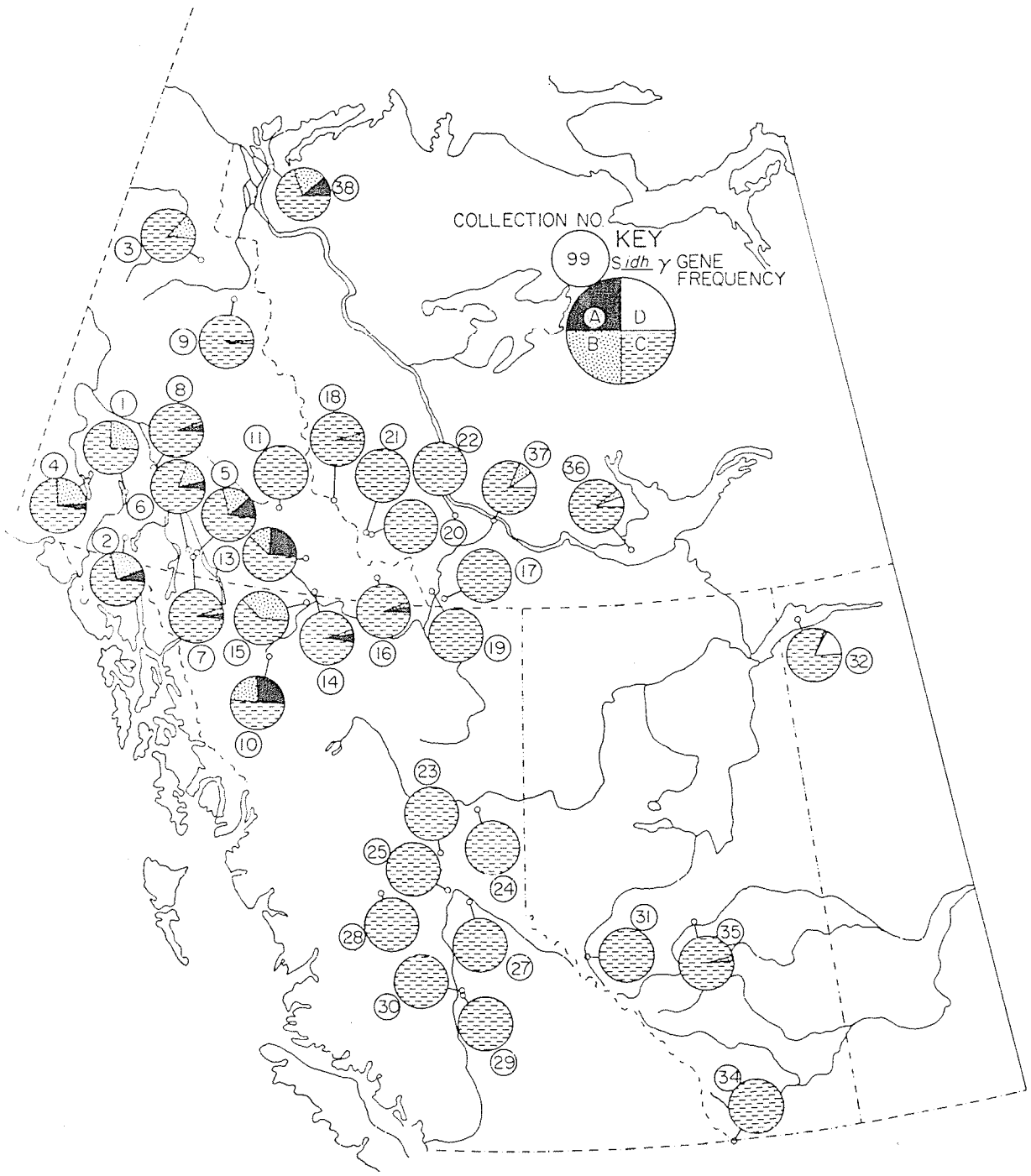
COLLECTION NO.
KEY
99
Sidh γ GENE FREQUENCY
A
B
C
D
1
2
3
4
5
6
7
8
9
10
11
13
14
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Table 5. Lake whitefish isocitrate dehydrogenase (NADP, supernatant form) (IDH7) observed and expected (Castle-Hardy-Weinberg equilibrium) phenotypes per population. χ^2 values were not calculated where the expected classes were less than 5. Significance at the 0.05 level is indicated by *.

Location	AA	AB	AC	AD	BB	BC	CC	BD	CD	DD	χ^2_{df}
Alsek System											
1. Aishihik L.	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	0 (1.38)	11 (8.25)	11 (12.38)	0 (0.00)	0 (0.00)	0 (0.00)	
2. Dezadeash L.	0 (0.44)	0 (2.62)	13 (8.97)		4 (3.93)	29 (26.91)	43 (46.14)				
Yukon System											
3. Davis L.	0 (0.00)	0 (0.00)	0 (0.00)		1 (1.23)	14 (13.55)	37 (37.22)				
4. Kluane L.	0 (0.01)	0 (0.25)	1 (0.72)		1 (1.63)	11 (9.50)	13 (13.89)				
5. Little Teslin L.	0 (0.91)	2 (2.86)	14 (11.28)		2 (2.24)	19 (17.72)	33 (34.99)				
6. McClintock L.	0 (0.05)	0 (0.35)	2 (1.59)		1 (0.70)	6 (6.27)	14 (14.09)				
7. Squanga L.	0 (0.01)	0 (0.06)	1 (1.08)		0 (0.07)	3 (2.70)	25 (25.08)				
8. Tatchun L.	0 (0.20)	0 (0.12)	7 (6.49)		0 (0.16)	2 (1.85)	52 (52.33)				
Peel System											
9. Margaret L.	0 (0.00)	0 (0.00)	0 (0.00)		0 (0.01)	1 (0.99)	27 (27.01)				

cont'd

Table 5. cont'd

Location	AA	AB	AC	AD	BB	BC	CC	BD	CD	DD	χ^2_a
Upper Liard System											
10. Dease L.	0 (3.025)	7 (4.69)	15 (11.286)	0 (0.00)	1 (1.82)	8 (8.74)	9 (10.52)	0 (0.00)	0 (0.00)	0 (0.00)	
11. Finalyson L.	0 (0.00)	0 (0.00)	0 (0.00)		0 (0.00)	0 (0.00)	4 (4.00)				
13. Simpson L.	0 (1.56)	0 (1.43)	18 (7.95)		0 (0.59)	8 (4.88)	6 (10.08)				
14. Watson L.	0 (0.13)	0 (0.07)	4 (3.67)		0 (0.01)	1 (0.92)	25 (25.21)				
15. Wheeler L.	0 (0.00)	0 (0.00)	0 (0.00)		10 (8.41)	23 (26.19)	22 (20.40)				0.84
16. Toobally L.	0 (0.06)	0 (0.12)	4 (3.75)		0 (0.06)	4 (3.75)	57 (57.24)				
Lower Liard System											
17. Bovie L.	0 (0.00)	0 (0.00)	0 (0.00)		0 (0.00)	0 (0.00)	9 (9.00)				
18. Divide L.	0 (0.00)	0 (0.00)	0 (0.00)		0 (0.04)	2 (1.91)	21 (21.04)				
19. Fisherman L.	0 (0.00)	0 (0.00)	0 (0.00)		0 (0.00)	0 (0.00)	43 (43.00)				
20. McLeod L.							3 (3.00)				
21. Seaplane L.							35 (35.00)				
22. Little Doctor L.							26 (26.00)				

cont'd

Table 5. cont'd

Location	AA	AB	AC	AD	BB	BC	CC	BD	CD	DD	$\chi^2_{(1)}$
Upper Peace System											
23. McLeod L.	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	36 (36.00)	0 (0.00)	0 (0.00)	0 (0.00)	
24. Moberly L.							27 (27.00)				
Fraser System											
27. Aleza L.							19 (19.00)				
28. Fraser L.							9 (9.00)				
29. Lac la Hache							39 (39.00)				
30. Williams L.							22 (22.00)				
Athabasca System											
31. Talbot L.							42 (42.00)				
32. Athabasca L.					0 (0.00)	1 (0.83)	21 (20.82)	0 (0.13)	7 (6.67)	1 (0.53)	
South Saskatchewan System											
34. Waterton L.					0 (0.00)	0 (0.00)	22 (22.00)	0 (0.00)	0 (0.00)	0 (0.00)	
North Saskatchewan System											
35. Wabamun L.					0 (0.02)	2 (1.96)	45 (45.02)				
Mackenzie System											
36. Great Slave L.					1 (0.17)	4 (5.38)	43 (42.68)	0 (0.34)	6 (5.38)	0 (0.17)	

cont'd

Table 5.cont'd

Location	AA	AB	AC	AD	BB	BC	CC	BD	CD	DD	$\chi^2_{(0)}$
37. Liard River Mouth	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	2 (1.60)	6 (6.40)	0 (0.20)	2 (1.60)	0 (0.10)	
38. Mackenzie delta	0 (0.56)	1 (1.50)	8 (6.37)		1 (1.00)	9 (8.51)	17 (18.05)	0 (0.00)	0 (0.00)	0 (0.00)	

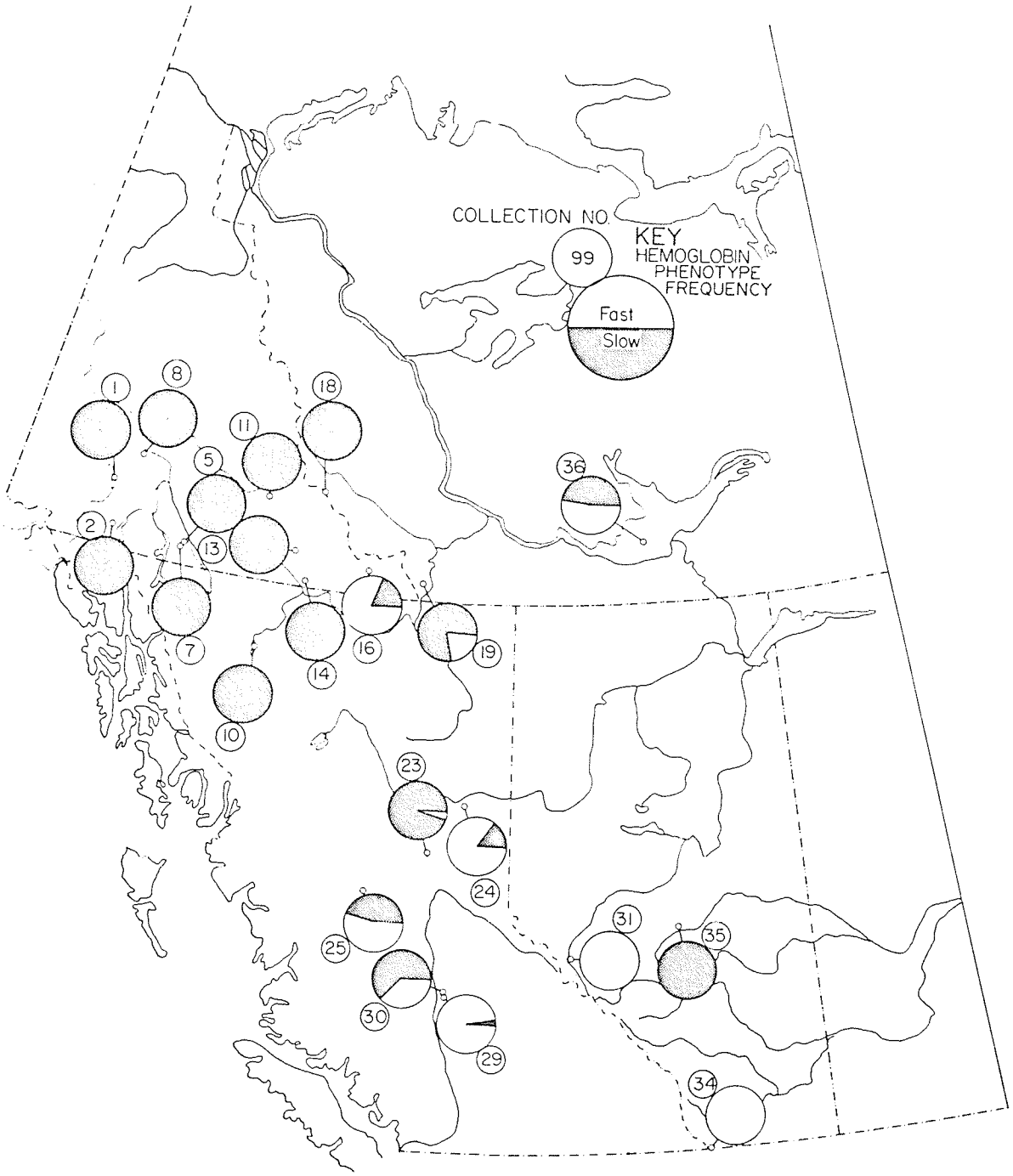
systems but present in a relatively high frequency in the Mackenzie River delta population (38). The $idh\gamma^{D}$ allele was found to occur only in the Liard River mouth (37), Great Slave L. (36) and L. Athabasca (32) populations considered in this study (Fig. 9). This allele is also present in Manitoba populations (J. W. Clayton and A. H. Kristofferson, unpublished data). The ranges of the $idh\gamma^{A}$ and $idh\gamma^{D}$ alleles were never found to overlap (Fig. 9).

The number of lake whitefish of each phenotypic class of IDH as well as the Castle-Hardy-Weinberg expectations are given for each population in Table 5. Only in the population from Wheeler L. (15) were the classes large enough to conduct a χ^2 test for equilibrium. In this case the agreement between the observed and expected numbers was satisfactory and it may be seen (Table 5) that there is qualitative agreement with the Castle-Hardy-Weinberg expectations in most other populations.

Hemoglobin polymorphism. The distribution of electrophoretic classes of lake whitefish hemoglobin was shown to be different in populations sampled from across western Canada (Lindsey et al. 1970). Populations from the Yukon showed only the slow class while all others generally expressed the fast as well as the slow class.

Hemoglobin samples were obtained from 21 of the lake whitefish populations considered in this study and the frequency of occurrence of each class per population is shown in Fig. 10. In a total of 167 lake whitefish (Table 2) from five populations (1, 2, 5, 7 and 8) from the Yukon and Alsek River system only the slow class was expressed (Fig. 10). Four of the populations (10, 11, 13 and 14) of the upper Liard River watershed also displayed only the slow class while the Toobally L. (16) population showed a high frequency of the fast class. Both classes were found in some populations from the lower Liard (19), Mackenzie (36), Fraser (28-30) and Peace (23-24) River systems. Populations from the Athabasca (31) and South Saskatchewan (34) River systems appeared fixed for the fast class, while, in contrast, only the slow class of hemoglobin was found in the single population (35) considered from the North Saskatchewan River watershed. Both classes were found in other populations from further east in this river system (Franzin 1974). The significance of the findings is limited by the small sample size in several populations (Table 2). Although there is great variability in the frequency of occurrence of the two classes of hemoglobin between populations, there is no evident geographic trend (Fig. 10).

Figure 10. Frequencies of the 'fast' and 'slow' classes of hemoglobin in 21 lake whitefish populations from across western Canada.


COLLECTION NO.
KEY
HEMOGLOBIN PHENOTYPE FREQUENCY
99
Fast
Slow
1
8
18
11
5
36
2
13
7
16
19
14
10
23
24
25
31
35
30
29
34

Geographic Pattern of Modal Gillraker Counts in the Liard River Watershed

In general, lake whitefish populations from the Yukon and Alaska are known to exhibit the lowest modal gillraker counts (20-26 gillrakers) while higher modal counts (25-33 gillrakers) (Fig. 11) have been found across the rest of North America (Lindsey et al. 1970). Populations from central British Columbia are characterized by consistently high modal counts (Fig. 11).

The modal gillraker counts for all the Liard River watershed lake whitefish populations (10-21) examined in the present study, along with one population (22) from the Tetcela River system, are shown in Fig. 12. The number of lake whitefish examined in each population is given in Table 2. No bimodal distributions of gillraker counts were found in any of these populations and in most populations the individual gillraker counts ranged from three below to three above the modal count. The modal gillraker number varied greatly over the whole Liard River system (24-33 gillrakers) and the variability was greater among the upper Liard populations (10-16) (24-33 gillrakers) than among the lower Liard populations (17-21) (26-31 gillrakers). No cline was found in the modal gillraker number of populations along the Liard River. Only the upper Liard River watershed contains populations with modal counts in the range (20-26 gillrakers) known for

Figure 11. Modal gillraker counts in lake whitefish populations from across North America (from Lindsey et al. 1970).

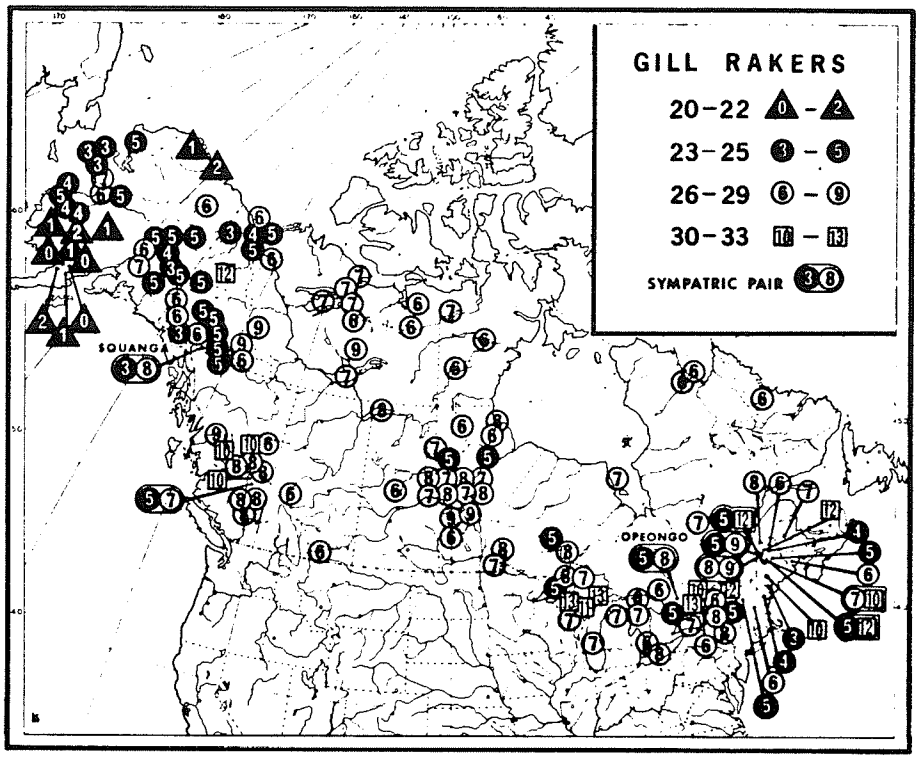
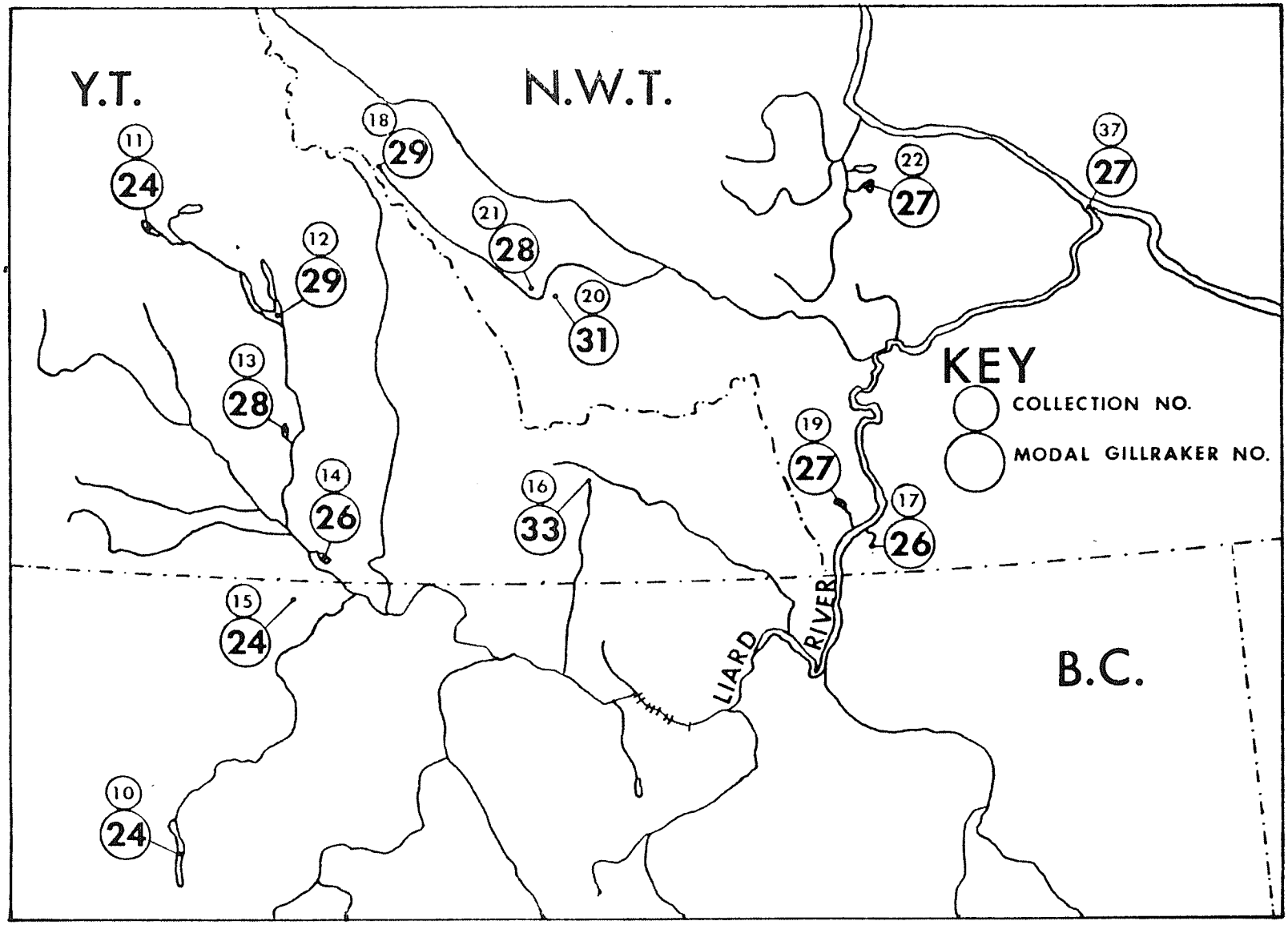

GILL RAKERS
20–22 0 – 2
23–25 3 – 5
26–29 6 – 9
30–33 10 – 13
SYMPATRIC PAIR 3 8
SQUANGA
OPEONGO

Figure 12. Modal gillraker counts in lake whitefish populations sampled from the Liard and Tetcela River watersheds.


Y.T.
N.W.T.
B.C.
KEY
COLLECTION NO.
MODAL GILLRAKER NO.
LIARD RIVER
11
24
18
29
21
28
22
27
37
27
12
29
20
31
13
28
19
27
14
26
16
33
17
26
15
24
10
24

Yukon and Alaskan populations (Lindsey et al. 1970). The remaining populations of the upper Liard and all those of the lower Liard and Tetcela River watersheds have modal counts (25-33 gillrakers) similar to those found across the rest of North America.

Distribution of Fish Species Within the Liard River Watershed in Relation to Their Possible Recent Zoogeographic Origins

Twenty-nine fish species are known to occur within the Liard River system; of these 27 have been found in the lower and 14 in the upper Liard River watershed (Table 6). These species are grouped (Table 6) on the basis of the refugia they are thought to have survived in during Wisconsin glaciation (see McPhail and Lindsey 1970). In addition, certain species forms in the Liard River watershed, which have been considered in other studies (McAllister and Lindsey 1961, McPhail 1963, McPhail and Lindsey 1970, Khan and Qadri 1971, Lindsey and Franzin 1972, Franzin and Clayton 1977, and Lynch and Vyse (1979) to represent dispersal from a particular refugium, are indicated as follows: MT = Mississippi-Missouri refugium type; BT = Bering refugium type; and PT = Pacific refugium type.

The fish fauna of the lower Liard River watershed appears to represent a mixture of species derived from all three known western North American refugia (Table 6). Eleven species are present which are thought to have survived only in the Mississippi-Missouri refugium. The ninespine stickleback, Pungitius pungitius, which is believed to have survived in both the Mississippi-Missouri and Bering refugia, is represented in the upper Mackenzie River watershed by its Mississippi form (McPhail 1963). Three species present in the lower Liard River system are thought to have survived only in the Bering refugium (Table 6). In addition, the Bering forms of two species thought to have occupied multiple refugia, round whitefish, Prosopium cylindraceum (McPhail and Lindsey 1970) and Arctic grayling, Thymallus arcticus (Lynch and Vyse 1979), are now thought to be in the lower Liard River system. In contrast, the Pacific form of the Dolly Varden, Salvelinus malma, a species thought to have survived also in the Bering refugium, occurs throughout the Liard River system (McPhail and Lindsey 1970). The probable specific origins of the remaining species in the lower Liard River system have yet to be determined. It seems clear that the fish fauna of the lakes of the lower Liard and Tetcela River watersheds (Table 6) reflect inputs from each of the western North American glacial refugia.

Table 6. Known fish species composition of the lower and upper Liard River systems presented in relation to glacial refugia they are thought to have dispersed from (McPhail and Lindsey 1970). In addition, forms previously identified (footnote to reference in top right corner) as representing dispersal from a particular refugium are included and identified as follows: MT=Mississippi-Missouri refugium type; BT=Bering refugium type; PT=Pacific refugium type. All species distributions from McPhail and Lindsey (1970) unless otherwise noted in bottom corner.

Lower Liard System	Catostomus commersoni	Coregonus artedii	Cottus ricei	Culea inconstans	Hiodon alosoides	Notropis atherinoides	Notropis hudsonius	Percopsis omiscomaycush	Pfrille neogaea	Platygobio gracilis	Stizostedion vitreum	Prosopium williamsoni	Rhinichthys cataractae	Couesius plumbeus	Coregonus clupeaformis	Esox lucius	Prosopium cylindraceum	Pungitius pungitius	Salvelinus namaycush	Thymallus arcticus	Catostomus catostomus	Cottus cognatus	Lota lota	Prosopium coulteri	Salmo gairdneri	Salvelinus malma	Coregonus autumnalis	Coregonus sardinella	Stenodus leucichthys
	Mississippi-Missouri Refugium Only											Mississippi-Missouri&Pacific Refugium			Bering and Mississippi-Missouri Refugium						Bering, Pacific & Mississippi-Missouri Refugium				Bering & Pacific Refugium		Bering Only		
	MT[7]	MT[7]	MT[7]	MT[3]	MT[7]	MT[7]	MT[7]	MT[7]	MT[7]	MT[7]	MT[7]	X	X	MT[7]	X	X	BT[7]	MT[6]	X	BT[4,7]	X	X	X			PT[7]	BT[7]	BT[7]	BT[7]
Bovie L.	Xm										Xm				Xm														
Divide L.															Xl		Xl			Xl						Xl			
Fisherman L.	X						X	X			X				X	X						X	X						
McLeod L.															Xw								Xw						
Seaplane L.															X	X						X							
Little Doctor L.	X	Xnm						X			X				X	X		X	Xr		X	Xnm				Xr			Xr
Upper Liard System												X	X	MT[7]	BT[1]	BT[7]	BT[7]		BT[2]	BT[4,7]	BT[7]	BT[5]	BT[7]	BT[3]	X	PT[7]			
Dease L.												X			X	X	X		X	Xr	X	X	Xnm	X		X			
Finlayson L.															X		X		X	X		X	X						
Frances L.														X	Xl		Xl		Xl	Xl	Xl	X	Xl						
Simpson L.												X			X	X	X		X	X	Xl	X	X	X		Xr			
Toobally L.												X			X	X	X		X	X		X	X						
Watson L.															Xl	X			Xl	Xl	Xl								
Wheeler L.															Xl	Xl			Xl	Xl									

1 = Franzin and Clayton (1977), 2 = Khan and Qadri (1971), 3 = Lindsey and Franzin (1972), 4 = Lynch and Vyse (1979), 5 = McAllister and Lindsey (1961), 6 = McPhail (1963), 7 = McPhail and Lindsey (1970).

i = J. Irvine, pers. comm., l = Lindsey et al. (1980), m = McKinnon and Hnytka (1979), nm = National Museum collections, r = reported by locals, sc = Scott and Crossman (1973), s = Stein et al. (1973), w = R. W. Wickstrom, pers. comm.

The fish fauna of the upper Liard River watershed may also represent a mixture of species derived from all three known western North American refugia (Table 6). None of the 11 species thought to have survived solely in the Mississippi-Missouri refugia nor the Mississippi form of the ninespine stickleback, which occur in the lower Liard River system have been found in the upper Liard River system. Three species thought to be derived only from the Bering refugium are absent from the upper Liard River watershed (Table 6). Of the 14 species known to be present in the Upper Liard River system, only the lake chub, Couesius plumbeus, is considered to be derived from the Mississippi-Missouri refugium (McPhail and Lindsey 1970) (Table 6). Nine of the others have been identified as being represented only by their Bering form and one other, the Dolly Varden, is considered derived from the Pacific refugium (Table 6). The glacial refugia of the remaining three species forms have yet to be identified but it is interesting to note that they all shared the Pacific refugium and no other refugium as a common place of survival.

Genetic Comparisons Among Western Canadian Lake Whitefish Populations

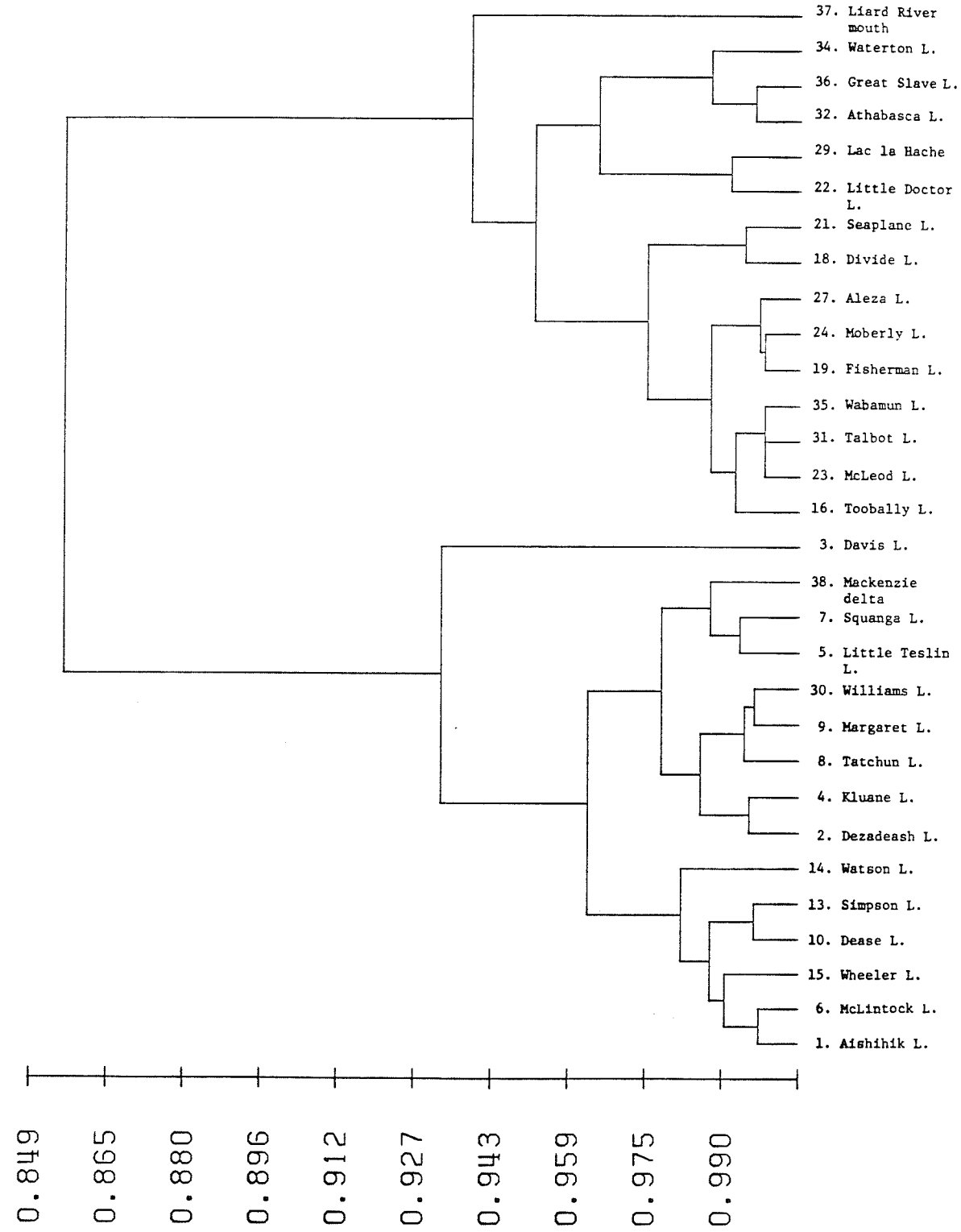
The gene frequencies inferred from LDH, G-3-PDH and IDH zymograms for each population (Sample size greater than 10) were used to calculate the genetic similarities (Nei 1972) of the populations. The genetic similarity data were clustered using a method equivalent to the unweighted pair-group arithmetic average method (Sneath and Sokal 1973) (Fig. 13). The cophenetic correlation coefficient, the measure of the degree of similarity between the relationships described in the matrix of genetic similarity values (Table 7) and those described in the resulting dendrogram (Fig. 13), was 0.848. Sneath and Sokal (1973) considered agreement above the level of 0.8 to indicate an adequate representation of the original scores in the dendrogram.

The dendrogram derived from the genetic similarities (Fig. 13) divides the lake whitefish populations of western Canada into two broad groups. One group (the Yukon group) consists principally of populations from the Yukon, Alsek, Peel and upper Liard River watersheds, while the other (the non-Yukon group) is represented by populations from the lower Liard, Tetcela, Mackenzie, Peace, Fraser, Athabasca and North and South Saskatchewan River systems. Three populations are exceptional in that they are closely grouped with populations distant in a geographic sense. The Mackenzie delta (38)

Table 7. Matrix of Nei genetic similarity comparisons between lake whitefish populations represented by 10 or more specimens.

	Lake Population Numbers																														
	1	2	3	4	5	6	7	8	9	10	13	14	15	16	18	19	21	22	23	24	27	29	30	31	32	34	35	36	37	38
1. Aishihik L.																														
2. Dezadeash L.	0.982																													
3. Davis L.	0.955	0.929																												
4. Kluane L.	0.966	0.996	0.893																											
5. Little Teslin L.	0.950	0.962	0.903	0.993																										
6. McClintock L.	0.978	0.990	0.957	0.976	0.966																									
7. Squanga L.	0.950	0.987	0.915	0.986	0.994	0.967																								
8. Tatchun L.	0.978	0.993	0.917	0.990	0.984	0.986	0.989																							
9. Margaret L.	0.987	0.988	0.944	0.978	0.970	0.994	0.980	0.996																						
10. Dease L.	0.986	0.987	0.928	0.975	0.967	0.988	0.953	0.974	0.974																					
13. Simpson L.	0.993	0.981	0.943	0.964	0.954	0.993	0.946	0.974	0.980	0.997																				
14. Watson L.	0.990	0.959	0.962	0.935	0.920	0.988	0.930	0.963	0.982	0.967	0.984																			
15. Wheeler L.	0.994	0.962	0.953	0.941	0.922	0.986	0.915	0.946	0.963	0.978	0.986	0.982																		
16. Toobally L.	0.923	0.915	0.875	0.904	0.890	0.926	0.901	0.925	0.932	0.905	0.914	0.923	0.903																	
18. Divide L.	0.886	0.817	0.858	0.825	0.804	0.881	0.820	0.856	0.878	0.853	0.873	0.901	0.880	0.982																
19. Fisherman L.	0.826	0.828	0.775	0.824	0.810	0.832	0.824	0.843	0.845	0.809	0.816	0.825	0.801	0.979	0.968															
21. Seaplane L.	0.836	0.798	0.811	0.776	0.756	0.833	0.774	0.810	0.832	0.802	0.823	0.854	0.829	0.969	0.995	0.975														
22. Little Doctor L.	0.809	0.850	0.734	0.863	0.856	0.825	0.866	0.866	0.849	0.810	0.802	0.790	0.767	0.951	0.899	0.975	0.902													
23. McLeod L.	0.887	0.873	0.844	0.861	0.846	0.889	0.861	0.886	0.896	0.863	0.875	0.892	0.867	0.996	0.990	0.990	0.986	0.952												
24. Moberly L.	0.848	0.854	0.793	0.852	0.839	0.855	0.853	0.869	0.869	0.833	0.838	0.844	0.820	0.985	0.965	0.998	0.968	0.982	0.992											
27. Aleza L.	0.814	0.828	0.755	0.830	0.819	0.823	0.832	0.844	0.840	0.803	0.805	0.807	0.783	0.971	0.948	0.997	0.956	0.988	0.981	0.998										
29. Lac la Hache	0.875	0.907	0.805	0.915	0.907	0.889	0.917	0.922	0.910	0.872	0.868	0.859	0.836	0.974	0.920	0.971	0.911	0.992	0.966	0.983	0.980									
30. Williams L.	0.979	0.988	0.928	0.977	0.967	0.987	0.979	0.995	0.997	0.967	0.972	0.974	0.953	0.955	0.903	0.883	0.864	0.888	0.925	0.905	0.880	0.940								
31. Talbot L.	0.866	0.852	0.824	0.841	0.825	0.869	0.841	0.866	0.876	0.842	0.855	0.872	0.847	0.991	0.989	0.994	0.989	0.953	0.999	0.993	0.985	0.962	0.908							
32. Athabasca L.	0.830	0.854	0.764	0.859	0.849	0.841	0.856	0.865	0.856	0.828	0.824	0.816	0.799	0.955	0.918	0.967	0.917	0.972	0.955	0.972	0.973	0.971	0.891	0.956						
34. Waterton L.	0.805	0.831	0.737	0.838	0.828	0.817	0.840	0.848	0.838	0.798	0.796	0.793	0.769	0.928	0.886	0.939	0.885	0.950	0.927	0.945	0.946	0.950	0.872	0.927	0.989					
35. Wabamun L.	0.864	0.858	0.815	0.851	0.836	0.868	0.850	0.871	0.877	0.844	0.853	0.865	0.842	0.991	0.981	0.997	0.981	0.966	0.998	0.997	0.991	0.972	0.910	0.999	0.969	0.949				
36. Great Slave L.	0.827	0.842	0.763	0.844	0.831	0.835	0.840	0.853	0.848	0.819	0.819	0.817	0.799	0.963	0.936	0.979	0.939	0.972	0.968	0.982	0.982	0.970	0.885	0.970	0.997	0.987	0.980			
37. Liard River Mouth	0.944	0.949	0.899	0.942	0.933	0.951	0.939	0.844	0.954	0.935	0.937	0.934	0.924	0.968	0.929	0.922	0.902	0.917	0.949	0.937	0.919	0.951	0.967	0.938	0.960	0.949	0.945	0.934		
38. Mackenzie Delta	0.957	0.986	0.930	0.980	0.989	0.971	0.986	0.978	0.971	0.967	0.958	0.934	0.933	0.934	0.869	0.869	0.830	0.892	0.900	0.892	0.872	0.935	0.975	0.884	0.897	0.874	0.899	0.885	0.966	

Figure 13. Dendrogram of clustered Nei's genetic similarity values (Nei 1972). The cophenetic correlation coefficient is 0.848.


37. Liard River mouth
34. Waterton L.
36. Great Slave L.
32. Athabasca L.
29. Lac la Hache
22. Little Doctor L.
21. Seaplane L.
18. Divide L.
27. Aleza L.
24. Moberly L.
19. Fisherman L.
35. Wabamun L.
31. Talbot L.
23. McLeod L.
16. Toobally L.
3. Davis L.
38. Mackenzie delta
7. Squanga L.
5. Little Teslin L.
30. Williams L.
9. Margaret L.
8. Tatchun L.
4. Kluane L.
2. Dezadeash L.
14. Watson L.
13. Simpson L.
10. Dease L.
15. Wheeler L.
6. McLintock L.
1. Aishihik L.
0.849
0.865
0.880
0.896
0.912
0.927
0.943
0.959
0.975
0.990

and William L. (30) populations are placed within the Yukon group and the Toobally L. (16) population is placed within the non-Yukon group.

The Yukon group can be considered as consisting of three major sub-groups formed by subdivisions at genetic similarities equal to and less than 0.963 (Fig. 13). The Davis L. (3) population is genetically the most dissimilar of all the Yukon group populations. The next subdivision separates some populations of the Alsek (1), Yukon (6) and upper Liard (10, 13-15) River systems from others of the Alsek (2) and Yukon (4-5, 7-8) River systems, along with the single populations from the Peel (9), Mackenzie (38) and Fraser (30) River systems (Fig. 13).

The non-Yukon group can also be examined in terms of three sub-groups formed by subdivisions at genetic similarities equal to or less than 0.952 (Fig. 13). The Liard River mouth (37) population is genetically the most dissimilar of all of the non-Yukon group populations. The next subdivision separates all the populations considered from the lower Liard (18-19, 21), Peace (23-24), and North Saskatchewan (35) River systems, along with single populations of the Fraser (27), Athabasca (31) and upper Liard (16) River systems from single populations of the Mackenzie (36), Tetcela (22), Fraser (29), Athabasca (32) and South Saskatchewan (34) River systems (Fig. 13).

Examination of the matrix of genetic similarities (Table 7) reveals that certain relationships are obscured in the dendrogram. In particular, the three populations, Toobally L. (16), Williams L. (30) and Mackenzie delta (38), noted for their placement in a group separate from other populations from the same watershed, all show higher genetic similarities to populations of their own watershed than is expressed in the dendrogram (Fig. 13). For example, the genetic similarity between the Mackenzie delta (38) and Liard River mouth (37) populations is 0.966 (Table 7) but it is depicted in the dendrogram as 0.857 (Fig. 13). Similarly, the Toobally L. (16) and all the populations of the Yukon group are genetically similar around the level of 0.9 (Table 7) while these genetic relationships are expressed as being lower, 0.857, in the dendrogram (Fig. 13). Two populations of the non-Yukon group, Little Doctor L. (22) and Lac la Hache (29) are depicted in the dendrogram as being genetically more similar to populations from Great Slave L. (36), C. Athabasca (32) and Waterton L. (34) than they are to the populations from the Peace (23-24), lower Liard (18, 19, 21), Fraser (27), upper Athabasca (31) and North Saskatchewan (35) River systems. These two populations (22 and 29) have higher genetic affinities (Table 7) to all of these latter populations, except Divide L. (18) and Seaplane L. (21), than they do to any of the populations (32, 34, 36) they are grouped with.

The Liard River system appears to be populated by three relatively distinct population groups. All the upper Liard River populations (10, 13, 14, 15) except Toobally L. (16) are grouped with populations from the Yukon, while Toobally L. (16) and the lower Liard populations (18, 19, 21, 37) are grouped with populations from other parts of western Canada (Fig. 13). The lower Liard lake populations (18, 19, 21) show higher genetic similarities to geographically distant populations in central British Columbia (23, 24, 27, 29) and Alberta (31, 34, 35) than they do to the population from the Liard River (37) which is in close proximity (Fig. 13). The three distinct groups are then; the upper Liard lake populations (excluding Toobally L), the lower Liard lake populations (including Toobally L. (16) of the upper Liard), and the lower Liard River population.

DISCUSSION

Genetic Comparison of the Liard River System Lake Whitefish Populations With Others From Western Canada

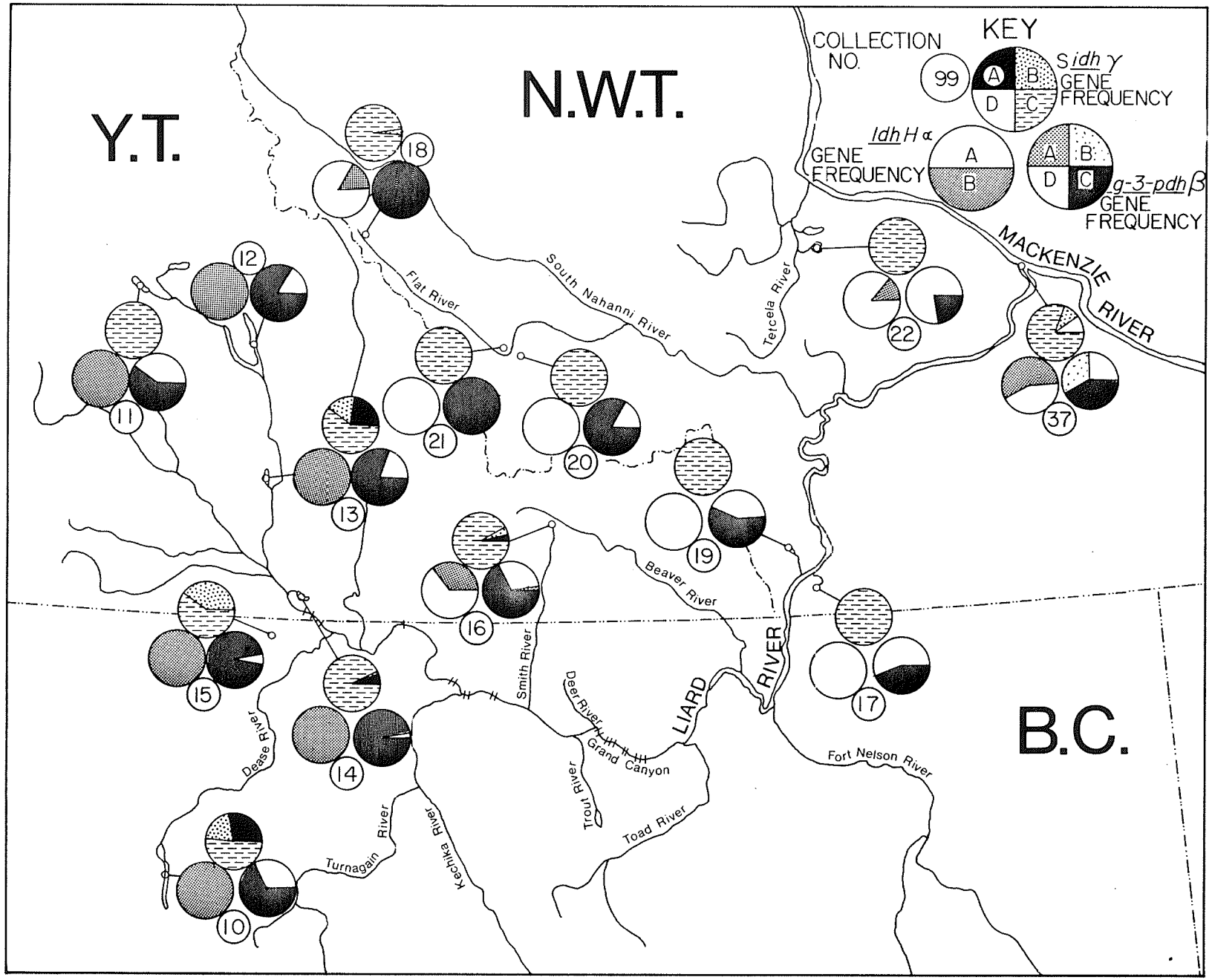
Nei's genetic index of similarity (Nei 1972) compares the frequencies of the same alleles in different populations. The more similar the frequencies the higher is the genetic similarity between the populations. It does not, however, differentiate the case where an allele is absent in one population and present in a low frequency in another population from the case where the allele is present in both populations with the magnitude of the difference in allele frequencies being the same as in the first case. This point is very important in relation to the present study, for it will be shown that many of the populations which are only partially differentiated when only the allele frequencies are considered, appear totally distinct when their respective allele compositions are compared. The purpose of this section, then, is to compare the three lake whitefish groups from the Liard River system to populations occurring in other watersheds in western Canada by examining their genetic similarities, with special reference to their allele composition among the polymorphic loci studied.

The upper Liard (10-15) lake whitefish populations (excluding Toobally L. (16)) show greater similarities to populations from the Alsek (1, 2), Yukon (3-8) and Peel (9) River systems than to any populations from outside these systems in their allelic constitution at the g-3-pdhα, g-3-pdhbβ, ldhHα and idhγ loci (Figs. 6, 8 and 9, Table 2). The ldhHα^{A} (Fig. 8), g-3-pdhβ^{B} (Fig. 6) and idhγ^{D} (Fig. 9) alleles are absent in all of these populations, while at least one of them occurs in all other populations sampled from across western Canada. In addition, the idhγ^{A} allele is present in most populations from the upper Liard, Yukon and Alsek River systems (Fig. 9). This allele has been observed only in the Mackenzie delta (38) population among populations from outside these river systems. The g-3-pdhα^{A} allele was noted by Franzin and Clayton (1977) to occur in lake whitefish populations from across western Canada with populations from the Yukon usually expressing the highest frequencies. This allele was also discovered in two populations from the upper Liard (10, 12) and in the Margaret L. (9) population of the Peel River system (Table 2). The similarity of the upper Liard (excluding Toobally L.), Alsek, Yukon and Peel River system populations in allele composition was also evident in the comparisons of allele frequencies (Fig. 13). The genetic similarity displayed by populations from all of these systems had previously been noted by

Franzin and Clayton (1977), Bodaly (1977) and Bodaly and Lindsey (1977).

The occurrence of alleles at the g-3-pdhβ, idhγ and ldhHα loci is quite variable among the Toobally L. (16) and lower Liard (17-21) lake populations (Fig. 14). The ldhHα^{B} and g-3-pdhβ^{D} alleles are apparently absent in some populations while present in others. Both of these alleles were found in almost every other population sampled from western Canada (Figs. 5, 6, 7, and 8). The g-3-pdhβ^{A} allele was found only in the Toobally L. (16) lake whitefish population (Fig. 6) and probably represents a new mutation. Most of the lower Liard lake populations (17, 19-21) appear to be homozygous for idhγ^{C} but the idhγ^{B} allele occurs in a low frequency in the Divide L. (18) population (Fig. 9). The idhγ^{A} and idhγ^{B} alleles occur in the Toobally L. (16) population of the upper Liard drainage, in addition to idhγ^{C} (Fig. 9). The idhγ^{A} allele is usually restricted to lake whitefish populations from the Yukon, Alsek and upper Liard River systems in which the ldhα^{A} allele is absent (Fig. 14). The Toobally (16) and lower Liard lake populations (17-21) are similar to each other in that the ldhHα^{A} allele is always present while the g-3-pdhβ^{B}, g-3-pdhα^{A} (Table 2) and idhγ^{D} (Fig. 14) alleles are always absent. This similarity in allele distribution differentiates the Toobally and lower

Figure 14. Frequencies of L-glycerol-3-phosphate dehydrogenase (g-3-pdhβ), heart-type lactate dehydrogenase (ldhHα) and isocitrate dehydrogenase (idhγ) alleles from lake whitefish populations sampled in the Liard and Tetcela River watersheds. The location of the Grand Canyon and the major tributaries of the Liard River are also shown.


Y.T.
N.W.T.
B.C.
KEY
COLLECTION NO.
99
S idh γ GENE FREQUENCY
A
B
C
D
Idh H α GENE FREQUENCY
g-3-pdh β GENE FREQUENCY
MACKENZIE RIVER
Flat River
South Nahanni River
Tetcela River
Beaver River
Smith River
Deer River
LIARD RIVER
Grand Canyon
Fort Nelson River
Trout River
Toad River
Kechika River
Turnagain River
Dease River
10
11
12
13
14
15
16
17
18
19
20
21
22
37

Liard lake whitefish populations from the populations of the upper Liard (10-15), Alsek (1,2), Yukon (3-8) and Peel (9) River systems in which the idhHα^{A} allele is always missing (Fig. 8) and the g-3-pdhα^{A} allele is often found (Table 2). It also differentiates these populations from the sample taken directly from the lower Liard River (37) in which the g-3-pdhβ^{B}, idhγ^{D} (Fig. 14) and g-3-pdhα^{A} (Table 2) alleles all occur in relatively high frequencies.

The lake whitefish populations sampled from the Tetcela (22), upper Peace (23-25), and Fraser (27-30) River systems, as well as the Talbot L. (31) population from the Athabasca River system, are similar to the Toobally (16) and lower Liard lake populations (17-21) in that ldhHα^{A} (Fig. 8) is always present, while g-3-pdhβ^{B} (Fig. 7), g-3-pdhα^{A} (Table 2) and idhγ^{D} (Fig. 9) are always absent. The Tetcela (22), upper Peace (24, 25) and Fraser (27-30) River system populations and the population from Talbot L. (31) all appear to be homozygous for idhγ^{C}, as do most of the lower Liard lake populations (17, 19-21) (Fig. 9).

Populations which show genetic similarities to the Toobally and lower Liard lake populations in terms of the presence and absence of alleles occur both north and south of the Liard River system. For example, the Little Doctor L. (22) lake whitefish population from north of the Liard River system has, among the loci examined, a similar distribution of alleles to most of populations sampled from the upper

Peace)23-25), Fraser (28-30) and Athabasca (31) River systems, which are south of the Liard River system (Figs. 6, 8, and 9, Table 2). Similarly, the Aleza L. (27) population of the Fraser River system shares the same alleles, at the loci examined, with lower Liard populations from Bovie L. (17), Fisherman L. (19) and Macleod L. (21). All of these populations are differentiated from all other populations studied in Alberta, Saskatchewan and Manitoba, as well as from the populations sampled in the Great Slave L. (36) region, by the absence of g-3-pdhβ^{B}; an allele which is present all of the latter populations in relatively high frequencies (Figs. 5 and 6). The idhγ^{D} (Fig. 9) and g-3-pdhα^{A} (Table 2) alleles which are absent in populations from the Fraser (27-30), upper Peace (23, 24) and Tetcela (22) River systems populations, as well as from Toobally L. (16) and lower Liard lakes (17-21) populations, occur in some of the populations from the Prairies and Great Slave L. region. All of the alleles, among the set of loci examined, which are found in all the latter populations also occur in the Liard River mouth (37) population. In particular, these include g-3-pdhα^{A} (Table 2), g-3-pdhβ^{B} (Figs. 5 and 6), idhγ^{B} and idhγ^{D} (Fig. 9). The frequencies of ldhHα^{B} and g-3-pdhα^{A} (Table 2) in the lower Liard River mouth (37) population are relatively high compared to the Prairie and Great Slave L. region lake whitefish populations.

The separation of lake whitefish populations from central British Columbia (23, 24, 27, 29, 30), Talbot L. (31), Toobally L. (16), Little Doctor L. (22) and the lower Liard lakes (18, 19, 21) from the populations from the Liard River mouth (37), Great Slave L. 36), L. Athabasca (32), Wabamum L. (35) and Waterton L. (34) which is apparent when the allele distribution is considered, but it is not as apparent when the allele frequencies are compared in the Nei calculation (Fig. 13). Part of this lack of separation is apparently due to the minor effect the low frequency occurrences of idhγ^{B}, idhγ^{D} and g-3-pdhα^{A} have on reducing the genetic similarity values between populations because these alleles when present seldom occur at frequencies greater than 0.15 (Table 2). In contrast, fluctuations between populations in the frequencies of ldhHα^{B}, g-3-pdhβ^{C} and g-3-pdhβ^{D} (Figs. 6 and 8) make large contributions to the reduction of genetic similarity yet they do not seem to be supported by any external evidence that would suggest these differences have great biological significance. These large fluctuations in allele frequencies within a group probably obscure some of the smaller differences between the groups which are caused by the presence of an allele occurring only in low frequencies. One of the 'flaws' in the dendrogram (Fig. 14) is the placement of the Little Doctor L. (22) and Lac la Hache (29) populations in a cluster with the Waterton L. (34), L. Athabaska (32) and Great Slave L. (36) populations, which they both differ from in at least the presence of

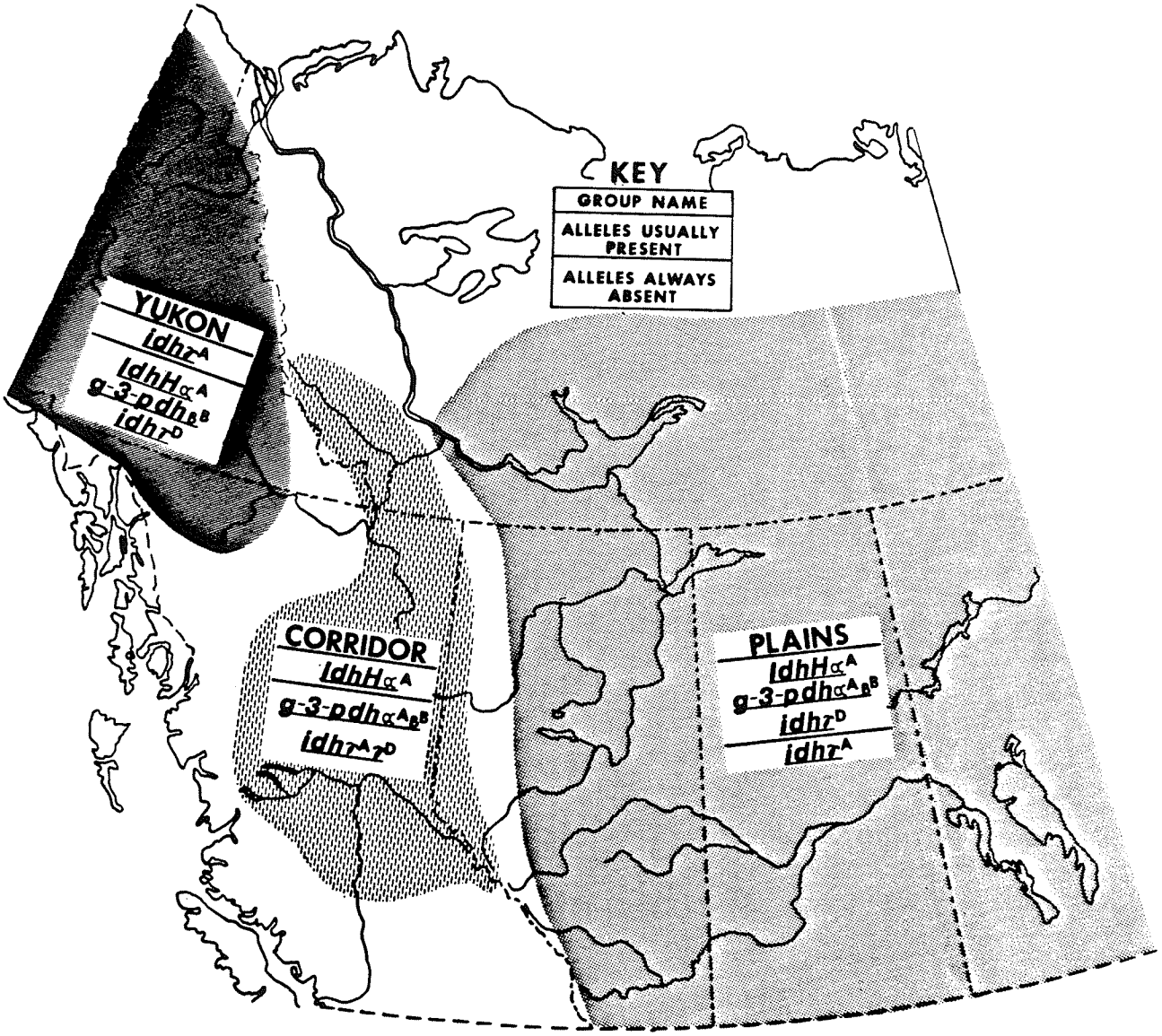
g-3-pdhβ^B (Fig. 6). It was noted in the Results that the Lac la Hache (29) and Little Doctor L. (22) populations actually share higher genetic similarities with most of the other populations from central British Columbia (23, 24, 27) and the lower Liard (19) watershed than they do with any of the populations they are clustered with (Table 7). This relationship is obscured in the dendrogram because of the low similarity these two populations share with the Divide L. (18) and Seaplane L. (21) populations. This relatively low genetic similarity is produced by the great difference in the frequency of g-3-pdhβ^C among the populations (Fig. 6). The frequency of g-3-pdhβ^C is very variable among lake whitefish populations from across western Canada (Figs. 5 and 6). Genetic similarity differences produced by fluctuations in the frequency of an allele common to all populations are considered in this study to be less important in distinguishing population groups than the frequencies of alleles which show disjunct geographic distributions. Another 'misplacement', based on allele composition, is the grouping of the Wabamum L. (35) population, in which g-3-pdhβ^B was found, in with populations (16, 18, 19, 21, 23, 24) in which this allele is absent (Fig. 6). The high genetic similarity displayed among these populations is apparently due to the very low frequency of g-3-pdhβ^B in the Wabamun L. (35) population. The genetic similarity values (Table 7) are clearly reproduced in the dendrogram (Fig. 13). The lower

Liard River mouth (37) population also does not express as high a genetic affinity to the Great Slave L. (36), Athabasca (32) and Waterton L. (34) populations in the comparison of allele frequencies as it does in the comparison of allele distribution. These differences are apparently caused by the relatively high frequency of $\underline{ldhH\alpha}^{B}$ in the Liard River mouth (37) lake whitefish population. Two populations which have low frequencies of $\underline{ldhH\alpha}^{A}$ from the Mackenzie delta (38) and Williams L. (30) are grouped with the Yukon (3-8), Alsek (1, 2), Peel (9) and upper Liard (10, 13-15) River system populations on the basis of allele frequency comparisons (Fig. 14). The $\underline{ldhH\alpha}^{A}$ allele has never been found in the hundreds of lake whitefish examined from the Yukon, Alsek and Peel River systems, nor has it been found in most of the upper Liard populations sampled (Fig. 8). Another allele, $\underline{g\text{-}3\text{-}pdh\beta}^{B}$, which has never been found in over 500 lake whitefish examined from the Yukon, Alsek, Peel and upper Liard River system populations, occurs at a low frequency in the Mackenzie delta (38) population. This allele is normally restricted to lake whitefish populations from the plains of western Canada (Figs. 5 and 6). As noted in the Results, the Williams L. (30) and Mackenzie delta (38) populations express higher genetic similarities to populations from their own watershed than is depicted in the dendrogram (Fig. 13). It can be seen that certain populations are more similar to other populations when allele frequency comparisons are considered than they are when

allele distributions are considered. Possible reasons for the distinctive allele frequencies observed in these 'misplaced' populations will be discussed later.

The consideration of the allele distribution, among the loci examined, as well as the genetic similarity values, points to the existence of three genetically distinct groups of lake whitefish in western Canada, corresponding basically to the three population groups observed in the Liard River watershed. These groups, which will now be named, are made up of the following populations: 1) Yukon population group; all populations of the Alsek (1,2), Yukon (3-8), Peel (9) and upper Liard (10-15) (Excluding Toobally L. (16)) River systems, 2) Corridor population group; all populations from the Fraser (27-30), upper Peace (23-25) and Tetcela (22) River systems, along with Talbot L. (31) of the Athabasca River system and all the lake populations of the lower Liard (17-21) River system, 3) Plains population group; all the populations of the North and South Saskatchewan River systems, including those from Waterton (34) and Wabamum L.(35) populations considered in this study, all populations from the Churchill River system, all populations in the region of Great Slave L. (36), including those from the Liard River mouth (37) and L. Athabasca (32). The distinctive allele composition, as well as the geographic distribution of each group is shown in Fig. 15. The Mackenzie delta (38) and Toobally L. (16) populations are not included within any group because they

Figure 15. The distribution and characteristic allele composition, among the g-3-pdhβ, ldhHα and idhγ loci examined, of the 'Yukon', 'Corridor', and 'Plains' populations. The blank areas correspond to unknown lake whitefish population types or areas where the lake whitefish populations possess alleles characteristic of more than one group.


KEY
GROUP NAME
ALLELES USUALLY PRESENT
ALLELES ALWAYS ABSENT
YUKON
$Idhr^{A}$
$IdhH\alpha^{A}$
$g\text{-}3\text{-}pdh_{B}^{B}$
$Idhr^{D}$
CORRIDOR
$IdhH\alpha^{A}$
$g\text{-}3\text{-}pdh\alpha^{A}{}_{B}^{B}$
$Idhr^{A}r^{D}$
PLAINS
$IdhH\alpha^{A}$
$g\text{-}3\text{-}pdh\alpha^{A}{}_{B}^{B}$
$Idhr^{D}$
$Idhr^{A}$

possess alleles characteristic of more than one group. The Toobally L. (16) population possesses the ldhHα^{A} allele, but not the g-3-pdhβ^{B} allele which characterizes a Corridor population, but it also possesses the idhγ^{A} allele, a character of the Yukon populations (Fig. 15). The Mackenzie delta population expresses the ldhHα^{A} and g-3-pdhβ^{B} alleles, characteristic of a Plains population in combination with the idhγ^{A} allele, a Yukon population character (Fig. 15).

The distinction of the Corridor lake whitefish populations from the Plains lake whitefish populations is dependent on the absence of alleles in the Corridor populations which are present in the Plains group populations (Fig. 15). The question is, what is the probability that these alleles are actually absent and have not just been missed due to sampling error? To answer this, two assumptions must be made: 1) lake populations of a river system are derived from the same refugial stock of lake whitefish, 2) that the allele compositions of the populations, among the loci examined, are characteristic of these refugial stocks and not the recent results of selection or other stochastic processes. The distribution and frequencies of alleles of the ldhHα, g-3-pdhα and g-3-pdhβ loci in lake whitefish populations were considered by Franzin and Clayton (1977) to identify lake whitefish with specific refugia and not to be the recent products of selection,

thereby supporting the latter assumption. The possible effects of selection on the distributions of alleles from all the loci examined will be discussed later but it is important both for the consideration of this and other discussions that the distinction of each group be demonstrated. In the lower Liard lake (17-21) populations 111 lake whitefish were examined for polymorphism in G-3-PDH and 113 for IDH. The g-3-pdhα^A and g-3-pdhβ^B alleles were absent in all the lake whitefish examined (Table 2, Fig. 6) and there is a 95% probability (using binomial tables, Mainland et al. 1956) that in repeated samples of this size from these lakes less than five lake whitefish would be found to possess either of these alleles. Similarly, the idhγ^A and idhγ^D alleles were also absent in all lake whitefish examined from the lower Liard lakes. In repeated samples of 113 fish there is a 95% probability that less than five fish expressing either of these alleles would ever be found. The upper Peace and Fraser River systems were probably colonized at the same time by the same refugial populations of lake whitefish (Lindsey et al. 1970), therefore, under the assumption given, populations from these two systems can be grouped. In total, 287 lake whitefish were examined for G-3-PDH and 152 for IDH. The g-3-pdhα^A and g-3-pdhβ^B alleles were absent in all these lake whitefish (Fig. 6, Table 2) and there is a 95% probability that in repeated sampling of the same number of lake whitefish from these populations that fewer than three would be found to

possess either of these alleles. The $\underline{idh\gamma}^{A}$ and $\underline{idh\gamma}^{D}$ alleles were absent from all lake whitefish populations of the upper Peace (23, 24) and Fraser (27-30) systems (Fig. 9) and there is a 95% probability that in repeated sampling of these populations fewer than four lake whitefish out of 152 would express this allele. Therefore, while it is not possible to rule out the occurrence of any of these four alleles which are characteristic of other population groups, in the Fraser and upper Peace River system populations and in the lower Liard lake populations, it has been demonstrated that if any of these alleles do occur, they do so in very low frequencies which would still distinguish these populations from the others of western Canada. The Plains group populations are characterized, for the most part, by the presence of certain alleles (Fig. 15) and therefore it is not necessary to measure the probability for the occurrence of any allele. The Yukon group populations are characterized by the presence, in many cases, of the $\underline{g\text{-}3\text{-}pdh\alpha}^{A}$ and $\underline{idh\gamma}^{A}$ alleles and the absence of $\underline{idh\gamma}^{D}$, $\underline{ldhH\alpha}^{A}$ and $\underline{g\text{-}3\text{-}pdh\beta}^{B}$ (Fig. 15). Franzin and Clayton (1977) concluded that the populations of the Yukon and Alsek River drainages were homozygous for $\underline{ldhH\alpha}^{B}$ when the probability of finding another allele at this locus dropped below 5%. Three hundred and seventy-five lake whitefish from the Yukon and Alsek River systems were analysed for IDH. In repeated samples of this size there

is a 95% probability that the idhγ^{D} allele, never observed in these populations, would occur in fewer than two fish. In this study 521 lake whitefish from the Yukon and Alsek River watersheds were examined for G-3-PDH. In repeated samples of the same size there is a 95% probability that fewer than two fish would be found possessing the g-3-pdhβ^{B} allele. As in the case of the Corridor population, if the alleles, whose absence is characteristic of the Yukon populations, do occur in these populations, they do so in extremely low frequencies.

In general, the characterization of the populations by their absence of alleles, as well as by the presence of certain alleles, is supported by their absence in very large samples of lake whitefish from different drainages.

Selection of Alleles as a Possible Explanation for the Occurrence of the Three Genetic Groups of Lake Whitefish

Selection has been suggested to be responsible for the latitudinal clines observed in enzyme allele frequencies in the fathead minnow, Pimephales promelas, (Merritt 1972), and in the sucker, Catostomus clarki, (Koehn and Rasmussen 1967). In both studies temperature was considered to be a major selective factor. If the frequencies and distributions of the enzyme alleles examined in the present study are the products of selection, then the three lake whitefish population groups may represent differential selection for certain alleles within each of the areas they occupy. The allele composition similarity between populations within a group would then represent similar selection and not necessarily imply a common heritage for the populations. If, on the other hand, selection does not account for the allele composition differences between the groups or similarities within the groups, then the allele composition may function as a genetic marker of a common heritage for populations within each group. The purpose of this section is to determine whether the distributions and frequencies of the alleles studied agree with either a selection or non-selection hypothesis.

The breaks in the distributions of alleles, whose presence or absence is a characteristic of one of the population groups, occur in the same general region. It appears unlikely that alleles of different enzymes would be affected in the same way and in the exact same areas by selection. But if selection does account for such distinct and overlapping breaks in the distributions of different alleles, then clines in allele frequencies should be expected from regions where the alleles are selected for to where they are selected against. The idhβ alleles, though very disjunct in their distribution (Fig. 9) show no obvious clines in frequencies between areas where they are present and absent. In fact the $idh\beta^{B}$ allele which is very rare in the Corridor group is found in most populations of the Yukon and Plains groups which occur on either side of it (Fig. 9).

All the data of Franzin and Clayton (1977) were combined with the results of the present investigation to yield sample sizes of populations examined at the ldhH∝, g-3-pdh∝ , and g-3-pdhβ loci large enough to allow a test of each population group for clinal variation in the frequencies of alleles from these loci. To ensure some accuracy in the estimate of the respective allele frequencies only populations represented by 14 or more lake whitefish were chosen. The frequencies of the following alleles, $ldhH\alpha^{B}$, $g\text{-}3\text{-}pdh\alpha^{A}$, $g\text{-}3\text{-}pdh\beta^{B}$ and $g\text{-}3\text{-}pdh\beta^{C}$ were correlated with the longitude, latitude and

elevation of the lakes in which they are resident. The simple correlation coefficients for these variables are shown in Tables 8A, B, C and D for; A) when all the data are taken together, B) when the Yukon group populations are considered alone, C) when the Corridor populations are considered alone and D) when the Plains populations are considered alone. This breakdown into the identified population groups is thought to be justified because if selection is producing clines they should still be evident within the group. The Toobally L. (16) and Mackenzie delta (38) populations are not considered in the separate group analysis because they share characters of more than one group, as discussed earlier. It is immediately evident that virtually all of the significant correlations found when all the data are considered together are removed when the groups are considered separately. Most of the correlation found initially appears to be the result of the mixing of at least partially discrete population groups. Other than the interrelationships of longitude, latitude and elevation, only three significant correlations remain when the population groups are considered separately; in the Yukon group g-3-pdhα^{A} is positively correlated with latitude, in the Corridor group g-3-pdhβ^{C} is positively correlated with elevation and in the Plains group g-3-pdhβ^{C} is negatively correlated with g-3-pdhβ^{B}. The reason for the latter is obvious; as the frequency of one allele at a locus varies other alleles at the same locus inevitably vary.

Table 8(A). Simple correlation coefficients for all lake whitefish collections of 14 or greater. Significance at 5%* = 0.285, at 1%** = 0.360, N = 50, df = 48.

Variable		1	2	3	4	5	6	7
Latitude	1	1.000						
Longitude	2	0.614 **	1.000					
Elevation	3	-0.250	0.448 **	1.000				
g-3-pdhα^A	4	0.444 **	0.374 **	-0.095	1.000			
g-3-pdhβ^B	5	-0.339 *	-0.772 **	-0.404 **	-0.198	1.000		
g-3-pdhβ^C	6	0.325 *	0.613 **	0.447 **	0.133	-0.678 **	1.000	
ldhHα^B	7	0.427 **	0.741 **	0.359 *	0.414 **	-0.523 **	0.433 **	1.000

Table 8(B). Simple correlation coefficients for Yukon group lake whitefish populations represented by 14 or more specimens. Significance at 5%* = 0.433, at 1%** = 0.549, N = 19, df = 17.

Variable		1	2	3	4	5	6	7
Latitude	1	1.000						
Longitude	2	0.449*	1.000					
Elevation	3	-0.696**	-0.110	1.000				
g-3-pdhα^A	4	0.497*	0.252	-0.407	1.000			
g-3-pdhβ^B	5	0.0	0.0	0.0	0.0	1.000		
g-3-pdhβ^C	6	0.189	-0.413	0.217	-0.036	0.0	1.000	
ldhHα^B	7	0.0	0.0	0.0	0.0	0.0	0.0	1.000

Table 8(C). Simple correlation coefficients for Corridor group lake whitefish populations represented by 14 or more specimens. Significance at 5%* = 0.602, at 1%** = 0.735, N = 11, df = 9.

	Variance	1	2	3	4	5	6	7
Latitude	1	1.000						
Longitude	2	0.781 **	1.000					
Elevation	3	-0.125	0.121	1.000				
g-3-pdhα^A	4	0.0	0.0	0.0	1.000			
g-3-pdhβ^B	5	0.0	0.0	0.0	0.0	1.000		
g-3-pdhβ^C	6	0.293	0.484	0.615 *	0.0	0.0	1.000	
ldhHα^B	7	-0.451	-0.147	0.019	0.0	0.0	-0.148	1.000

Table 8(D). Simple correlation coefficients for Plains group lake whitefish populations represented by 14 or more specimens. Significance at 5%* = 0.468, at 1%** = 0.590, N = 18, df = 16.

	Variance	1	2	3	4	5	6	7
Latitude	1	1.000						
Longitude	2	0.478 *	1.000					
Elevation	3	-0.703 **	0.214	1.000				
g-3-pdhα^A	4	0.211	-0.273	-0.392	1.000			
g-3-pdhβ^B	5	0.102	-0.152	0.080	0.132	1.000		
g-3-pdhβ^C	6	0.021	0.073	-0.064	-0.177	-0.474 *	1.000	
ldhHα^B	7	-0.341	-0.148	0.433	0.186	-0.135	-0.016	1.000

Selection does not appear to be responsible for the first two correlations, because similar relationships with the same alleles over latitude are not found within the other population groups (Tables 8 B, C, D). Snedecor and Cochran (1973) pointed out that extreme values in more than one character could lead to significant correlations. Franzin and Clayton (1977) found a non-significant negative relation between g-3-pdhα^{A} and latitude in their Yukon group (this did not include the upper Liard watershed populations or those from Davis and Margaret lakes). The difference found in this study appears to be due to the inclusion of the Davis L. (3) population which is both the furthest north of all Yukon group populations and shows by far the highest frequency of g-3-pdhα^{A} ever found (Table 2). Other than this extreme value value no apparent cline exists for g-3-pdhα^{A} in the Yukon populations. The Divide L. (18) population occurs at the highest elevation of any known lake whitefish population in Canada. It also is apparently homozygous for g-3-pdhβ^{B}, but in this case a weak cline appears to exist even when the Divide L. (18) population is not considered. The reasons for this cline are not clear but it does not account for the differences among the groups as some of the Corridor populations occur at similar altitudes as some Plains populations yet still display different alleles at the g-3-pdhβ locus. As was noted, no similar cline occurs within the other groups.

The important thing to note from the analysis on the separate population groups is that there are no correlations of any of the alleles with longitude (Table 8 B, C, D). Since the population groups are split longitudinally from one another (Fig. 15), then clines in allele frequencies should have been apparent along this axis if selection was producing the genetic differences observed between the groups.

In conclusion, the overlapping of the areas of occurrence and non-occurrence of alleles from different enzymes, along with only one apparent cline possibly caused by the selection of alleles, suggests that selection does not account for the overall genetic differences observed between the population groups. Therefore the similarity in allele distribution shown within each of the population groups probably represents a common ancestry at some point in time. The common alleles within each group act as a label by which to measure the migration and intergradation of each of the three ancestral forms.

The Distribution of Hemoglobin Classes in Relation to the Three Population Groups of Lake Whitefish

The distribution of the fast hemoglobin class overlaps that of $\underline{ldhH\alpha}^{A}$ (Figs. 8 and 10) and thus appears to support the separation of the Yukon group populations from the others of western Canada. The fast phenotypic class is absent in all Yukon populations and present in most Corridor and Plains populations.

There are no apparent geographic clines (Fig. 10) in the frequencies of the two hemoglobin classes, suggesting that selection is not responsible for the overall distribution of the two phenotypes. This is supported by the fact that the break in the distribution of one of the hemoglobin classes occurs in the same region noted for the disjunct distributions of the $\underline{idh\gamma}^{A}$ (Fig. 9), $\underline{ldhH\alpha}^{A}$ (Fig. 8), and $\underline{g\text{-}3\text{-}pdh\alpha}^{A}$ (Table 2) alleles, for which there were also no indications of selection. Franzin (1974) and Lindsey et al. (1970) also arrived at this conclusion but noted that the extreme frequency fluctuations between closely situated populations may reflect some form of selection not yet accounted for.

The Range of Modal Gillraker Numbers in Relation to the Different Population Groups

Gillraker counts have long been used in classifying different coregonid species (for example, see Scott and Crossman 1973). Svardson (1970) concluded that the number of gillrakers is a heritable character subject to selection. Bodaly (1979) found a striking relationship between the diet and number of gillrakers in three Yukon lakes which support sympatric populations of lake whitefish; 'high raker' fish are mainly planktonic feeders while the 'low raker' form utilizes the benthic resource to a much greater degree. Based on the high genetic similarity exhibited between the high and low raker forms of lake whitefish, Bodaly (1977) concluded that the high raker form evolved from the low raker form since the Yukon populations of lake whitefish became isolated from the rest of those of western Canada. Therefore, with selection it is apparently possible to produce high gillraker forms of Yukon lake whitefish populations. The corollary to this is that the present gillraker numbers exhibited by the Yukon populations and all other populations for that matter, may be the result of selection. Therefore, while gillraker numbers may be a heritable character, the possible effects of selection weaken their use as genetic markers for populations derived from a common ancestral stock.

In broad terms, the modal gillraker numbers support the distinctions of the three population groups. Corridor populations from Little Doctor (22) and lakes in the lower Liard drainage (17-21) have modal gillraker counts (26-31 gillrakers) (Fig. 12) similar to those from central British Columbia (26-30 gillrakers) (Fig. 11). Lindsey et al. (1970) earlier noted the distinction of the central British Columbia lake whitefish populations from those from the rest of Canada based on this character. The Plains populations exhibit a lower, narrower range of modal counts (25-29 gillrakers) than those of the Corridor populations, while the Yukon populations show the lowest modal counts (23-29 gillrakers), though their range is quite large (Figs. 11 and 12).

In summary, the modal gillraker counts provide a measure of support for the division of the lake whitefish populations of western Canada into three groups.

The Amount of Gene Flow Between the Different Population Groups of Lake Whitefish

Franzin and Clayton (1977) considered the lake whitefish populations of the Yukon, Alsek and upper Liard River systems to be derived from stocks which survived Wisconsin glaciation solely in the Bering refugium and the populations from the rest of western Canada were said to be derived from both of the Bering and Mississippi refugia forms. The populations from central British Columbia were suggested to be derived from the mixing of the Bering refugium form with an 'early wave' of the Mississippi refugium form which lacked g-3-pdhℓ^{B}. These conclusions were based on the distributions of alleles and the results of correlation analysis. The absence of certain alleles in the Yukon populations which are present in other populations has already been noted (Figs. 6, 8 and 9). Franzin and Clayton (1977) also found that many of the correlations of allele frequencies to physical factors such as longitude, latitude and elevation of each population were removed when the populations were broken into Yukon (all populations of the Yukon and Alsek R. drainages) and non-Yukon groups (all other populations, including those of the upper Liard River system and central British Columbia) and these authors concluded that many of the original correlations were the product of the lumping of at least two partially discrete population groups. The correlations within the non-Yukon group

indicated decreasing clines from west to east in the frequencies of $\underline{\text{ldhH}\alpha}^{b}$ and $\underline{\text{g-3-pdh}\beta}^{C}$ and an increasing cline in the frequency of $\underline{\text{g-3-pdh}\beta}^{B}$. These results were taken to indicate that $\underline{\text{ldhH}\alpha}^{B}$ and probably $\underline{\text{g-3-pdh}\beta}^{C}$ were originally present only in populations which survived glaciation in the Bering refugium and $\underline{\text{g-3-pdh}\beta}^{B}$ was present only in populations which survived in the Mississippi refugium. The apparent cline in the frequencies of these alleles in lake whitefish populations from across the plains of western Canada was considered the result of the mixing of these two forms (Franzin and Clayton 1977). The only apparent barriers to gene flow were considered to be physical, such as the Liard and Peace River Canyons (Franzin and Clayton 1977). The purpose of this section is to examine the amount of gene flow between the three western Canadian population groups and to relate this to the conclusions of Franzin and Clayton (1977).

The correlations of the different allele frequencies with longitude found by Franzin and Clayton (1977) are not apparent when the populations are separated into the three groups (Table 8 B, C, D). There appear to be no broad clines in any allele frequencies across either the Plains or Corridor population groups (Figs. 5, 6, 7, 8 and 9). The correlations found by Franzin and Clayton (1977) in their non-Yukon group appear to be the result of the lumping together of populations

from the three discrete population groups identified in this study. Their non-Yukon group consisted of Yukon group populations from the upper Liard River system and Corridor populations from central British Columbia, as well as the populations from the Plains group. Considering allele frequencies then, there is no evidence to suggest massive introgression across western Canada of populations dispersing from separate refugia. This lack of introgression is supported by the distribution of the idhγ^{A} allele (Fig. 9) which would be expected to be found in lake whitefish populations from across western Canada in the case of complete introgression, and by the disjunction in the distributions of the idhγ^{B} (Fig. 9) and g-3-pdhα^{A} (Fig. 15, Table 2) alleles across western Canada.

Only two populations in the present study can be identified as 'hybrids' between population groups on the basis of the presence of alleles or allele combinations which are characteristic of more than one group. These are the Toobally L. (16) and Mackenzie delta (38) populations. The Toobally L. (16) population has the idhγ^{A} allele found almost exclusively in Yukon group populations (Fig. 9) and the combination of the presence of ldhHα^{A} and absence of g-3-pdhβ^{B} alleles characteristic of Corridor populations (Fig. 15). The ldhHα^{B} allele also occurs in a higher frequency than found in most non-Yukon populations (Fig. 8). The agreement of the heart-type LDH

phenotypes with Castle-Hardy-Weinberg expectations (Table 4), the unimodal distribution of gillrakers in the population and the occurrence of the $\underline{ldhH\alpha}^{A}$ and $\underline{idh\gamma}^{A}$ alleles in two different individual fish indicates that extensive intermixing of the populations has occurred. The high $\underline{ldhH\alpha}^{A}$ frequency indicates that the major portion of the genetic composition of the population has come from the Corridor populations. The Mackenzie delta (38) population also has the $\underline{idh\gamma}^{A}$ allele characteristic of the Yukon populations (Fig. 9) and the combination of $\underline{g\text{-}3\text{-}pdh\beta}^{B}$ and $\underline{ldhH\alpha}^{A}$ alleles characteristic of the Plains populations (Fig. 15). The actual interbreeding of the population groups is indicated by the presence of the $\underline{idh\gamma}^{A}$ allele in individual fish which also possessed $\underline{ldhH\alpha}^{A}$ or $\underline{g\text{-}3\text{-}pdh\beta}^{B}$ alleles. The major proportion of the genetic component of this population appears to be derived from Yukon populations, as inferred by the high frequencies of $\underline{ldhH\alpha}^{B}$, $\underline{idh\gamma}^{A}$ and $\underline{g\text{-}3\text{-}pdh\alpha}^{A}$ (Table 2, Figs. 7 and 9) and the low frequency of $\underline{g\text{-}3\text{-}pdh\beta}^{B}$ (Fig. 6). It should be noted that gene flow from the Corridor group into this population may have occurred but cannot be identified due to the lack of any known allele which occurs widespread in the Corridor populations but not in the Plains population. A mixing of Plains and Corridor populations would show the same genetic components as the Plains population, though the

frequency of g-3-pdhβ^B would be epxected to be lower. However, a demonstrated mixing of Plains and Yukon populations, as is seen in the Mackenzie delta, also produces a lowered g-3-pdhβ^B frequency so that a Corridor population component could exist and not be identified.

In addition to the two populations identified as 'hybrids' on the basis of allele composition, six populations express frequencies of either the ldhHα^B or g-3-pdhβ^B allele which may reflect intermixing of stocks derived from separate population groups. Caution must be exercised in interpreting allele frequency data because random fluctuations as well as intermixing of different stocks, can produce varied allele frequencies. For example, Avise and Smith (1974) discovered relatively large frequency fluctuations in alleles among even closely situated and related populations of the bluegill sunfish, Lepomis macrochirus. Three populations, Williams L. (30), Fraser L. (28) and the Liard River mouth (37) express relatively high frequencies of ldhHα^B (Fig. 8) suggesting possible gene flow from the Yukon populations. In the case of the Williams L. (30) and Fraser L. (28) populations there appears to be no obvious dispersal route for the Yukon populations into these lakes which would avoid the other populations (27, 29) of the Fraser River system or the populations (23-25) of the upper Peace River system, which express ldhHα^B in frequencies similar to other non-Yukon group populations (Figs. 7 and 8). The idhβ^A (Fig. 9) and g-3-pdhα^A (Table 2) alleles, commonly found in Yukon group

populations (Fig. 15), are absent from all the populations considered in the upper Peace and Fraser River systems, also indicating that intermixing with stocks derived from the Yukon populations has not taken place. The high amount of variability in the frequency of $\underline{ldhH\alpha}^{B}$ in the central British Columbia populations is probably attributable to random fluctuations among the populations and not to 'hybridization' between Corridor and Yukon group populations. The Liard River mouth (37) is the only other population to show a relatively high frequency of $\underline{ldhH\alpha}^{B}$. The Liard River mouth (37) population differs from the Fraser L. (28) and Williams L. (30) populations in that it occurs in a river system in which Yukon group populations also occur. Yukon group populations are found in the upper Liard and Peel River drainages (Fig. 15) and as indicated by the genetic mixing of stocks derived from the Yukon and Plains population groups in the Mackenzie delta (38), gene flow from the Yukon populations has spread into at least the lower Mackenzie River system. In addition to expressing the $\underline{ldhH\alpha}^{B}$ allele in a relatively high frequency (Fig. 8), the Liard River mouth population also displays a relatively high frequency of $\underline{g\text{-}3\text{-}pdh\alpha}^{A}$ (Table 2) for a non-Yukon group population. In fact, the only non-Yukon population to express a higher frequency of the $\underline{g\text{-}3\text{-}pdh\alpha}^{A}$ allele is the one from the Mackenzie delta (38) (Table 2), which was identified as a 'hybrid' on the basis of allele composition as well as by the frequencies of

certain alleles. Therefore, on the basis of the proximity of the Liard River mouth (37) population to Yukon group populations and on the elevated frequencies of two alleles, indicative of Yukon population input, it appears likely that this population is derived from the intermixing of stocks from at least the Yukon and Plains population groups. The absence of the idhγ^{A} allele, a genetic marker for the Yukon populations (Fig. 9) could be due to the small sample of lake whitefish (11 fish) available from this locality.

Three Plains group populations, Utikuma L. (26), Lesser Slave L. (33) and Wabamun L. (35) all express the g-3-pdhβ^{B} allele in the lowest frequencies found in all the Plains populations (Figs. 5 and 6). These populations all lie in close proximity to Corridor populations, in which the g-3-pdhβ^{B} allele is absent. As discussed, there is no known allele which occurs throughout the Corridor populations which does not also occur in the Plains group populations, so intermixing between the groups can only be identified by allele frequencies which are intermediate to those found in the more central populations from each group. The fact that three of the populations (26, 33, 35) in closest contact with the Corridor populations all show very low frequencies of g-3-pdhβ^{B} suggests that these frequencies are more likely the product of the introgression of the two forms than they are to be the products of random fluctuations in allele frequencies within the three lakes. Two of the

populations, Utikuma L. (26) and Lesser Slave L. (33) are intermediate genetically and physically to Corridor and Plains group lake whitefish populations of the Peace and Athabasca River systems, respectively. The low frequencies of g-3-pdhβ^{B} in all these populations (26, 33, 35) suggests that the major genetic input into these populations has come from the Corridor population group.

Overall, a relatively limited amount of introgression appears to have occurred among the population groups. Physical barriers to gene flow as postulated by Franzin and Clayton (1977), do not appear to account for the maintenance of the genetic distinctions of the different population groups. For example, in the Liard River system the rapids of the Grand Canyon (Fig. 14) appear to prevent the upstream dispersal of at least 14 species of fish (Table 6). Corridor populations of lake whitefish have at some point in time either surmounted these rapids or by-passed them to gain entrance into the upper Liard River system, as shown by the occurrence of a 'hybrid' population of Corridor and Yukon group origins, in Toobally L. (16). Therefore, as long as there is no further blockage to fish migration in portions of the upper Liard River upstream of the canyon, gene flow from the Corridor populations should be able to physically reach the pure Yukon group populations in the upper reaches of the Liard River. In any case, the rapids of the Grand Canyon or further upstream in the Liard River probably do not present a major barrier to fishes dispersing

downstream and gene flow derived from Yukon populations should therefore be able to come in contact with the Corridor populations of Fisherman L. (19) and Bovie L. (17), which appear topographically to be open to fish invasion. Gene flow from Yukon as well as Plains populations has apparently produced the present Liard River mouth (37) and Mackenzie delta (38) populations yet gene flow from neither group appears to have been incorporated into the lake populations of lake whitefish along the lower Liard and Tetcela River systems (Fig. 14). The fish species composition of these lakes (Table 6) indicates successful invasion has come from the Pacific, Bering and Mississippi-Missouri refugia, suggesting that if the Yukon and Plains populations are derived from stocks which survived Wisconsin glaciation in the Bering and Mississippi-Missouri refugia respectively, as postulated by Lindsey, et al. (1970) and Franzin and Clayton (1977), then these lake whitefish populations should also have been able to invade these lakes.

In the broad overview, complete introgression of all the forms appears physically possible everywhere except for in the Yukon, Alsek, Peel, upper Peace and Fraser River systems and possibly the upper Liard River system, where obstructions in the river or separate watersheds prevent fish dispersal. Outside of these systems, though, little introgression of the three forms has occurred. For example, Great Slave L. is

physically open to the invasion of lake whitefish derived from all three population groups but the genetic evidence suggests that only pure Plains group populations occupy it and the surrounding lakes (Figs. 5, 6, 7, 8 and 9). Similarly, in the region of contact of the Plains and Corridor populations in Alberta, lakes (24, 31, 32) situated on the same river systems and apparently physically open to invasion harbour pure populations from only one of the groups. As discussed, some introgression does appear to have occurred in lakes (26, 33, 35) intermediate to the pure populations but it has not resulted in the complete introgression of the forms where physically possible (Fig. 6).

In summary, overall the three population groups remain distinct even in the absence of physical barriers to prevent invasion of lake whitefish from other population groups. A limited amount of introgression appears to occur in the zones of contact of the three groups.

Possible Modes of Origin of the Corridor Group Populations

In western Canada there appear to be three distinct forms of lake whitefish (Fig. 15) with limited interbreeding occurring among them. The Yukon and Plains populations are equivalent to the forms identified by Franzin and Clayton (1977) as having solely Bering refuge and Bering-Mississippi refugia origins, respectively. In light of the discovery of a third intermediate population group, there is no evidence to support the vast intermixing between Bering and Mississippi forms previously thought to have occurred in the western Canadian plains. Therefore excluding the populations identified as being 'hybrids', the Plains populations are probably derived solely from stocks which survived Wisconsin glaciation in the Mississippi refugium. The purpose of this section is to examine the possible modes of origin of the intermediate group; the Corridor populations.

If it is assumed that all of the Corridor populations are derived from the same ancestral population, then there are basically only three ways in which the Corridor group could have been formed. The three possible origins of the Corridor group thus are: introgression of the Yukon and Plains forms to create, in time, a third distinct group, the sympatric evolution within one of the other population groups of the original Corridor population and finally the allopatric evolution caused by the isolation of the original Corridor population from other lake whitefish populations.

The assumption of a common ancestry for all the Corridor populations is the simplest explanation to account for overall similarity in allele composition among the Corridor populations, in the absence of selection. The same alleles, at the loci examined, were expressed in one of the most northerly Corridor lake whitefish populations, Little Doctor L. (22) as were found in the most southerly Corridor populations (29,30). A parallel similarity exists between the Aleza L. (27) population of the Fraser River system and three lake whitefish populations (17, 19, 20) examined from the lower Liard River system.

Svardson (1970) attributed the evolution of some of the many closely related coregonid species in Sweden to the introgression of some of the populations of originally allopatric species which occupied Sweden following deglaciation. It was suggested that a coregonid species formed by the introgression of populations of two separate species would show intermediate gillraker numbers to the parental species. Svardson (1970) also recommended the development of other systems of marker genes to further study the phenomenon. The modal gillraker numbers of the Corridor populations are not intermediate to those of the Yukon and Plains lake whitefish populations, tending overall to be even slightly higher than the Plains populations (Figs. 11 and 12). Consideration of the enzyme allele composition of the Corridor lake whitefish populations also does not support formation of the group by introgression. Corridor populations expressed fewer alleles

at the seven loci examined than either the Yukon or Plains populations (Table 2). A mixture of the latter two forms would probably produce a form with more alleles than either parental form, due to the fact that the Yukon and Plains lake whitefish populations each have unique alleles.

Sympatric evolution of the Corridor populations is also unlikely because all three groups have been defined both on their genetic homogeneity as well as by their geographic integrity within plausible migration limiting boundaries. This is especially true for the Yukon group. Corridor lake whitefish populations possess the $\underline{ldhH\alpha^{A}}$ allele and fast hemoglobin phenotype which are absent from all the Yukon lake whitefish populations. There is a slim possibility that the Corridor populations evolved sympatrically from the Plains group populations, for the Corridor populations do not express any alleles not found in the Plains populations. To explain the geographical integrity of the two forms and the fact that they never apparently occur sympatrically without apparently hybridizing, this hypothesis would require that one form or the other then displaced the other one depending on the locality, which seems unlikely. Overall then, it does not appear that the Corridor populations evolved sympatrically from either of the other lake whitefish population groups.

In summary, it does not appear as if the Corridor populations evolved sympatrically from one of the other population groups nor is there any evidence to suggest that the Corridor populations were formed by the introgression of the Plains and Yukon lake whitefish populations. Allopatric evolution requires geographic isolation of the different stocks for relatively long periods of time. The following section presents evidence for the exitence of at least two areas of possible refuge and thus isolation for lake whitefish populations during the Wisconsin glaciation.

Possible Allopatric Origins of the Corridor Group Populations

The Yukon and Plains populations are probably derived from stocks which survived Wisconsin glaciation in the Bering and Mississippi refugia, respectively. The Corridor populations are probably also derived from a stock isolated in a separate refugium during glaciation. Lindsey et al. (1970) considered the central British Columbia lake whitefish populations and thus the Corridor populations, to be derived from a stock which survived glaciation in the Missouri River system. Lindsey et al. (1970) found no evidence to suggest that lake whitefish survived glaciation in a Pacific refugium. The discovery by Ford (1976) of evidence for the existence of a glacial lake in the Mackenzie Mountains during the Wisconsin ice age provides another possible refugium for the ancestors of the Corridor populations. Glacial Lake Tetcela was formed by the blockage of the Nahanni River by the Laurentide ice sheet. It occupied the lower portions of the Nahanni River and the upper portions of the Tetcela River (see Fig. 14 for the location of these rivers) (Ford 1976). A much larger glacial lake, Lake Nahanni, extended further up the Nahanni River possibly during the early Wisconsin but more likely during the much earlier Illinoian glaciation (Ford 1976). As major portions of both lakes occupied what is presently Nahanni National Park, this area will be referred to as the Nahanni