THE UNIVERSITY OF MANITOBA

Ecology and Morphology of Sympatric and Allopatric Populations of Mountain Whitefish, *Prosopium williamsoni*, and Round Whitefish, *P. cylindraceum* in Lakes in Western Canada.

by

Brent Richard Guinn

A THESIS

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ECOLOGY AND MORPHOLOGY OF SYMPATRIC AND ALLOPATRIC POPULATIONS OF MOUNTAIN WHITEFISH, PROSOPIUM WILLIAMSONI, AND ROUND WHITEFISH, P. CYLINDRACEUM IN LAKES IN WESTERN CANADA

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A thesis submitted to the Faculty of Graduate Studies of the University of Manitoba in partial fulfillment of the requirements of the degree of

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Abstract

Diet analysis conducted on round whitefish (Prosopium cylindraceum) and mountain whitefish (P. williamsoni) from the one lake in which they are found in equal abundance indicated that there were diet differences between species and between different sizes of each species. Counts of six body parts taken on round whitefish differed between allopatric and sympatric lakes after accounting for environmental differences between lakes. This convergent character displacement was assumed to be a result of competition for food. There was no indication of hybridization between these species.

Analysis of occurrence, distribution and abundance data of coregonids in western Canada suggests that mountain whitefish colonized lower Liard River lakes before lake whitefish (Coregonus clupeaformis) and round whitefish had access to the area. Round whitefish probably did not disperse farther south because of the presence of northward dispersing mountain whitefish. Mountain whitefish are able to colonize lakes that contain round whitefish because of their ability to make use of streams tributary to such lakes. Mountain whitefish apparently never become abundant in lakes previously colonized by round and lake whitefish.

ACKNOWLEDGMENTS

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Character displacement in round whitefish (*Prosopium cylindraceum*) populations in sympatry with mountain whitefish (*P. williamsoni*) in western Canada.

Chapter 1

Abstract

Character displacement of 11 body counts and 1 body measurement was investigated in allopatric and sympatric lake populations of round whitefish (Prosopium cylindraceum) and mountain whitefish (P. williamsoni) from western Canada. The effects of 7 environmental variables on these counts and measurements was measured using all possible subset regression. Analysis of covariance entering significant environmental variables and individual counts or measurements was used to test for differences between allopatic and sympatric populations. If the R^2 from regression analysis was low, t-tests were used to investigate the differences. The counts and measurements were also used to check for hybridization between these two species.

Six counts from round whitefish showed convergent character displacement. The ecological significance of a decrease in caudal peduncle scale count in sympatry was unknown. Decrease in anal fin rays and vertebrae in sympatry are assumed to be related to a more pelagic existance. Increases in upper limb gill rakers, lower limb gill rakers and total gill rakers in sympatry are assumed to represent a shift away from a strictly benthic diet.

There was no indication of hybridization but mean pyloric caeca counts for round whitefish in 3 lakes were lower than that reported for all other western, Bering refugium derived populations.

INTRODUCTION

Character displacement is considered divergent when morphological, physiological and behavioral differences between species are accentuated in sympatry (Brown and Wilson 1956; Grant 1972) and convergent when differences are lessened in sympatry (MacArthur and Levins 1967; Cody 1969; Grant 1972). Divergent character displacement has been documented in a variety of organisms, including: skates (Raja) (McEachren and Marten 1977), suckers (Catostomus) (Dunham et al. 1979), sticklebacks (Gasterosteus) (McPhail 1969; Bell 1976), skinks (Typhlosaurus) (Huey et al. 1974; Huey and Pianka 1974), snails (Hydrobia) (Fenchel 1975; Fenchel and Kofoed 1976), frogs (Pseudacris) (Fouquette 1975), toads (Bufo) (Blair 1974), fruit flies (Drosophila) (Wasserman and Koepfer 1978), grasshoppers (Warramba) (Atchly 1978), damselflies (Calapteryx) (Waage 1975, 1979), and fossil trilobites (Phacops) (Eldredge 1974) and snails (Poecilozonites) (Schindel and Gould 1977).

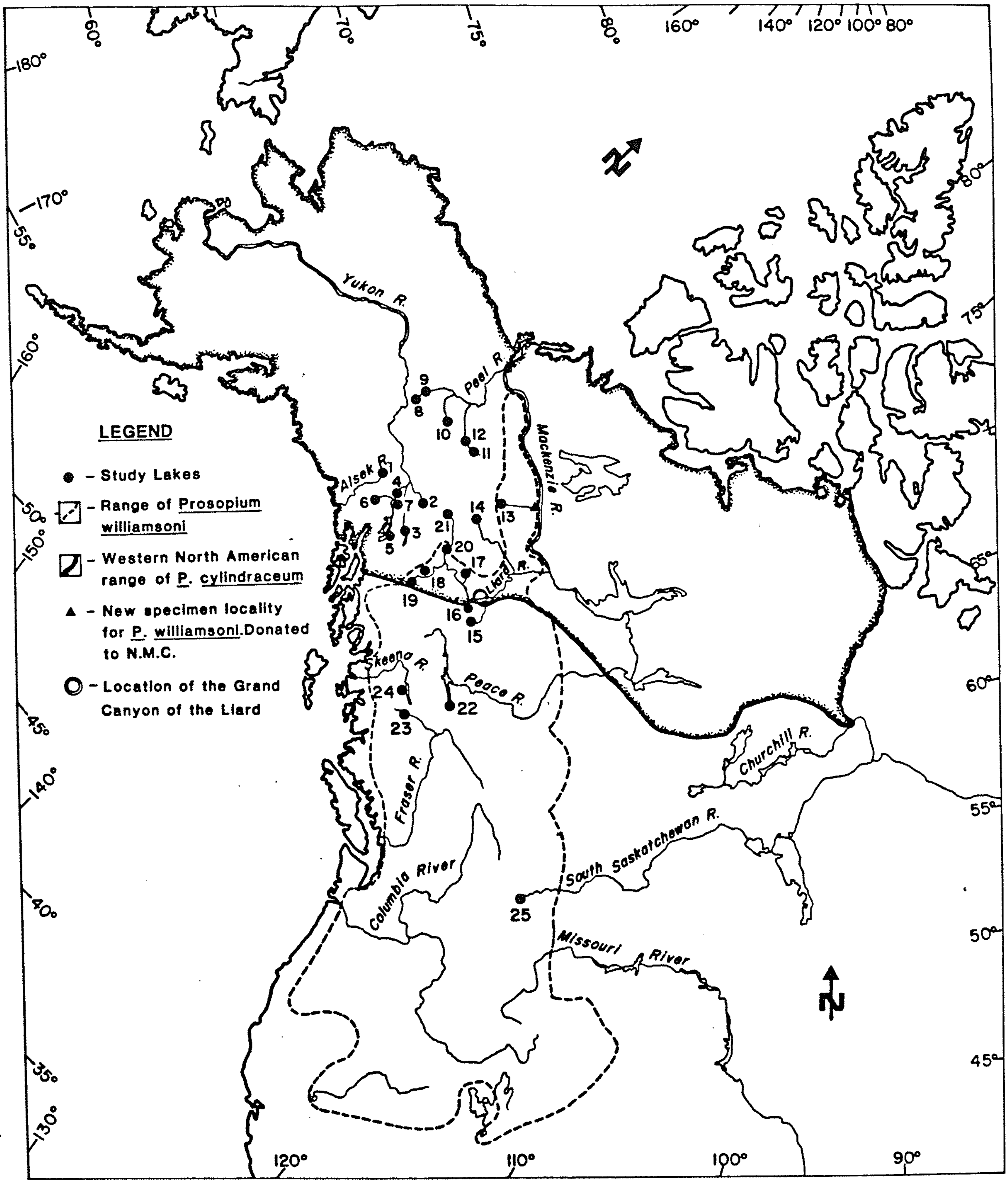
Convergent character displacement has been documented in bunting (Passerina) calls (Emlen et al. 1975) and in displays of meadowlarks (Sternella) (Rohwer 1972).

With the exception of Dunham et al. (1979) most studies have disregarded the possible effect of environment on character variation between areas of sympatry and allopatry. Environmental effects can be separated using multiple regression techniques (Dunham et al. 1979). Differences observed between means of a character from allopatric and sympatric areas, after environmental variables are accounted for, imply that character displacement has occurred. The purpose of this study was to determine, using related statistical techniques, whether character displacement has occurred between the closely related mountain whitefish, Prosopium *williamsoni* (Girard) and round whitefish, *P. cylindraceum* (Pallas) in a relatively narrow range of overlap in western Canada. McPhail and Lindsey (1970) suggested that their almost mutually exclusive ranges indicated that competition may limit the dispersal of each. Competition is assumed to be one of the causes of character displacement.

Collections during the summer of 1978 for this project and specimens obtained from British Columbia Hydro, the Freshwater Institute, FWI (Winnipeg, Manitoba), and information from the National Museum of Canada (NMC) indicate that the range of overlap includes most of the Liard River drainage and probably most of the streams that drain into the west side of the Mackenzie River (Fig. 1). This is based on collections of mountain whitefish in the Dahadinni River and in Dal Lake (13) by Dr. C. C. Lindsey. These specimens were identified by the author and have been deposited in the NMC.

Distribution records of Western Canadian round whitefish and mountain whitefish indicate that they probably survived in different ice free refugia during the last ice age and have only recently occurred sympatrically (Guinn 1982). Thus allopatric areas have the original (control) character state while sympatric areas have the most recent (experimental) character state, providing an ideal experiment for study of character displacement. The large areas of allopatry enable one to study the character states in a wide variety of environmental combinations, thereby reducing the probability that observed differences between allopatry and sympatry are due to some unmeasured environmental variable.

Figure 1. Study lakes and distribution of mountain whitefish and western North American round whitefish. Study lakes listed in Table 1. (Range of *Prosopium cylindraceum* from Scott and Crossman [1973]; range of *P. williamsoni* based on Scott and Crossman [1973] but northern range is modified by more recent collections described in text.)


LEGEND
● - Study Lakes
- Range of Prosopium williamsoni
- Western North American range of P. cylindraceum
▲ - New specimen locality for P. williamsoni. Donated to N.M.C.
◎ - Location of the Grand Canyon of the Liard
Yukon R.
Peel R.
Mackenzie R.
Alsek R.
Liard R.
Skeena R.
Peace R.
Fraser R.
Columbia River
South Saskatchewan R.
Churchill R.
Missouri River
N
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
120°
110°
100°
90°
60°
55°
50°
45°
180°
170°
160°
150°
140°
130°
160°
140°
120°
100°
80°
75°
70°
65°
60°
55°
50°
45°
40°
35°

METHODS

Although behavioural characters such as discriminatory ability (Wasserman and Koepfer 1978; Waage 1979) have been shown to exhibit character displacement, and are probably among the first characters to do so, these variables could not be examined in the field. Therefore, to get an adequate sample of overall variability in a character state, morphological characters were examined. This has the benefit that sample size can be increased by examining museum collections.

Specimens were obtained from various lakes in Western Canada (Table 1) using gill nets. The number following a lake name mentioned in the text corresponds to its location in Fig. 1. A total of 396 round whitefish from 19 lakes and 181 mountain whitefish from 11 lakes were examined. Mountain whitefish from Toobally (17), Dease (19) and Simpson (20) lakes were not included in any analysis because the sample sizes were too small (n=1 or 2). Both preserved and frozen fish were used in the analysis.

Ten counts were taken on the left side of the fish whenever possible. Caudal Peduncle Scale count (CPS) was the number of complete rows of scales around the narrowest part of the caudal peduncle (Hubbs and Lagler 1967). If a large scale covered two rows then only one row was counted. When counting Dorsal Fin Rays (D), all rudimentary rays in front of the fin were included. Sometimes dissection was necessary to reveal the smallest rudimentary rays. The last two rays of the fin were counted as one (Hubbs and Lagler 1967). Anal Fin Rays (A), Pectoral Fin Rays (P1), Pelvic Fin Rays (P2), Lateral Line Scales (LLS), Vertebrae (V) (counted from x-rays), gill raker counts including lower limb (LGR), upper limb (UGR) and total count (TGR) were counted following the methods of Hubbs and Lagler (1967). Pyloric

Caeca (PC) were counted by removing them to eliminate double counts. Gill raker length was measured using dial calipers under a dissecting microscope and was considered the straight line distance from the tip of the raker to the anterior angle of junction with the arch. The longest gill raker on the lateral side of the first arch on the left side was measured. All gill raker lengths were measured on arches that had been preserved in 10% formalin, rinsed with water, and then stored in 70% isopropyl alcohol. Standard length of each specimen was measured to the nearest mm as described by Hubbs and Lagler (1967). Measurements were made on frozen (those identified as being stored at FWI, Table 1) and formalin preserved specimens (all other specimens). An experiment was conducted that measured the effects of formalin on standard length of dead, non-preserved fish (Appendix 1). A mean species shrinkage value of 2.0% was found for mountain whitefish and 2.4% for round whitefish. Standard lengths of frozen specimens were corrected using these shrinkage values. Some fish lengths were adjusted using lake specific mean shrinkage values (e.g., Waterton Lake [25] mountain whitefish).

In order to make comparisons of gill raker length between specimens of different adjusted standard lengths,the lines obtained from linear regression analysis of gill raker length against adjusted standard length, were used to adjust all gill raker lengths to a common standard length (Appendix 2). The standard length of 230 mm was chosen as the common length of comparison because it was contained in all but one sample, Dal Lake (13) mountain whitefish. This sample was eliminated from this analysis because of this. For one lake, Aishihik (1), no linear relationship was found, so the gill raker length was not adjusted. The range of standard lengths in this sample included the common length.

The environmental variables chosen to study the effect of environment on morphology were: latitude , longitude, elevation, mean July temperature (MJT), taken from nearby weather stations or from climatic maps, surface area of water in lake, maximum known depth of lake (Zmax), and toatal dissolved solids (T.D.S.) (Table 1). The first four variables were chosen because they represent a climatic component of the environment to which meristic counts of fish often show responses (Lindsey and Harrington 1972). Surface area was included because it has been found to be correlated with the number of species in lakes (Barbour and Brown 1974). T.D.S. has been shown to be indicative of the general level of productivity of some British Columbia lakes (Northcote and Larkin 1956). Much of the environmental data is taken from other sources (identified in Table 1). Some values of T.D.S. were estimated from a line calculated using linear regression of the concentration of $CaCO_3$ (hardness) versus T.D.S. of 26 Yukon lakes (Appendix 3), because T.D.S. had not been obtained for some of these lakes but hardness had been recorded. The r^2 for the line was 0.88 and the slope was significantly different from 0 ($P < 0.0005$). The equation for the line was:

$$\text{T.D.S. (mg L}^{-1}\text{)} = 0.9908\ [CaCO_3](\text{mg L}^{-1}) + 21.8\ (\text{mg L}^{-1}).$$

The T.D.S. value for Teslin (3) was estimated by examining values given by Lindsey et al. (1981) for neighbouring lakes of similar size. A value two times larger than this value was also used in initial analyses to see if there would be any significant change in the conclusions. No values of Zmax or T.D.S. were known or estimated for Laberge (4) or McLeod (22) lakes. Neither T.D.S. nor hardness have been measured in Chapman Lake (11).

Table 1. Environmental data and whitefish (Prosopium and Coregonus) distribution for some lakes in western Canada.

Location	Lat. (°)	Long. (°)	Elev. (m)	MJT* (°C)	Area (km²)	Zmax (m)	TDS (mg L⁻¹)	Whitefish Species Present* MWF	RWF	LWF	PWF	LC	BWF
Alsek System													
1. Aishihik L.	61.50	137.25	915	11.9	151.0	120.0^A	100^A		$X^{J,K}$	X^A			
Yukon System													
2. Quiet L.	61.20	133.08	802	14.2	53	$>100.0^A$	80^A		X^J	X^A	X^A	X^A	X^A
3. Teslin L.	60.20	132.70	682	13.4	337.3	214.0^A	80^A		X^K	X^A		X^A	X^A
4. L. Laberge	61.00	135.05	628	14.2	213.6	-	-		X^K	X^A		X^A	
5. Atlin L.	59.50	133.75	668	11.9	588.7	283.0^A	81^A		X^K	X^A		X^A	
6. Kusawa L.	60.50	136.21	671	12.8	142.7	16.8^A	40^A		X^K	X^A		X^A	
7. Chadburn L.	60.70	134.95	655	14.2	1.8	42.5^A	910^A		X^K		X^A		
Peel System													
8. North Fork Pass L.	64.63	138.38	1144	13.3	0.2	3.6^A	-		X^K				
9. Chapman L.	64.85	138.35	990	13.3	1.1	12.0^A	60^A		X^K				
10. Elliott L.	64.48	135.57	990	13.3	1.1	22.0^A	140^A		X^K		X^H		
11. Bonnet Plume L.	64.30	132.00	1082	12.5	3.7	12.0^A	158^G		X^K				
12. Pinguicula L.	64.83	133.42	777	12.8	1.1	12.2^A	327^G		X^K				
Redstone System													
13. Dal L.	63.10	126.50	840	14.2	1.3	27.0^E	183^G	X^L	X^J				
Liard System													
14. Divide L.	61.95	128.23	1295	13.9	0.2	10.4^A	225^G		X^K	X^A			
15. Summit L.	58.83	124.67	1219	14.2	0.3	25.0^D	160^B	$X^{J,L}$					
16. Muncho L.	59.02	125.67	817	14.2	15.1	110.0^B	195^B	$X^{J,L}$					
17. Toobally L.	60.38	126.20	688	12.1	12.4	50.0^D	210^D	X^L	$X^{J,L}$	X^D			
18. Simmons L.	59.18	129.78	945	13.1	2.1	48.0^D	45^B	X^L	X^L				
19. Dease L.	58.70	130.00	754	12.8	178.8	115.0^D	195^B	X^L	$X^{J,L}$	X^D	$X^{A,D}$		
20. Simpson L.	60.72	129.23	688	14.2	20.5	55.0^A	190^A	X^L	X^J	$X^{A,D}$	X^D		
21. Finlayson L.	61.72	130.67	960	14.2	19.9	16.8^D	230^A		X^J	$X^{A,D}$			
Peace System													
22. McLeod L.	54.92	122.42	680	14.4	12.6	-	-	X^J		X^D			
Fraser System													
23. Fraser L.	54.09	124.75	640	14.4	54.6	30.5^B	100^B	X^K		X^K			
Skeena System													
24. Babine L.	54.80	126.00	712	12.7	445.0	207.3^F	63^F	X^K		X^F	X^I		
Saskatchewan System													
25. Waterton L.	49.02	113.50	1278	13.9	9.4	135.3^C	64^C	$X^{J,K}$		X^K	X^H		

Sources:
A. Lindsey et al. 1981; Teslin L. TDS estimated from their map of TDS.
B. British Columbia Min. Envt. (pers. comm.).
C. Anderson and Green 1976.
D. This study.
E. Lindsey unpublished data.
F. Stockner and Shortreed 1978.
G. TDS values estimated from hardness -- Appendix 3.
H. Lindsey and Franzin 1972.
I. McCart 1965.

Location of Specimens:
J. University of Manitoba, Dept. Zoology Fish Collection.
K. Freshwater Institute, Winnipeg.
L. National Museum of Canada.

*MWF=Prosopium williamsoni, RWF=P. cylindraceum, LWF=Coregonus clupeaformis, PWF=P. coulteri, LC=C. sardinella, BWF=C. nasus. MJT=mean July temperature.

STATISTICAL ANALYSIS

Means, their 95% confidence intervals, and ranges were established for each count and for standardized gill raker lengths from each sample. Discriminant function analysis was used to determine if the two species could be separated on the basis of morphological characters. This also served as a method of checking for hybrids. This was conducted using BMDP7M (Dixon and Brown 1979).

To establish the amount of variation in dependent variables (counts and gill raker length) that was explained by the independent (environmental) variables, all possible subset regression was employed using BMDP3R (Dixon and Brown 1979). This regression technique was run on each dependent variable, separately, because of unequal sample sizes of the variables. The analysis was carried out separately for each species.

Two major analyses were run on each species; one using 7 and the other using 5 environmental variables because of the missing environmental data.

If the effects of environment were significant ($R^2 \geq 0.10$, $P \leq 0.05$) it was necessary to eliminate these effects to establish whether there were differences in the dependent variables from allopatry to sympatry, apart from those due to environment. This was done using analysis of covariance (ANCOVA) available in BMDP1V (Dixon and Brown 1979).

In this procedure, independent variables that contributed significantly to the R^2 of the regression analysis were used as covariates. The range of these covariates must overlap between the groups being tested to eliminate the need for extrapolation (Cochran 1957). Another assumption in covariance analysis is that the slopes of the lines in each group should be parallel. BMDP1V gave the ranges of the covariates and also tested for equality of these slopes.

Any variables that were found to have an R^2 <0.10 were considered to be not sufficiently affected by this array of environmental variables to invalidate a t-test. A t-test was used to establish if the means of the dependent variables differed significantly between sympatric and allopatric populations. Additional t-tests were run on those variables with an R^2 between 0.20 and 0.10. ANCOVA could not be used for the mountain whitefish samples because there are only two sympatric samples with more than two specimens. Because of this, only those dependent variables with low R^2's were analysed further. In these cases the difference in means was tested with a t-test.

RESULTS

Ranges and means, and their 95% confidence limits,for each count and measurement are illustrated in Figures 2A-L. Mountain whitefish tended to have more pectoral fin rays than round whitefish (Fig. 2D). No other fin ray count showed consistent species differences (Fig. 2A-C).

There was no consistent difference in pyloric caeca count between species (Fig. 2E), but it should be noted that round whitefish populations from Chadburn (7), Bonnet Plume (8), and Dal (13) lakes have mean counts lower than that reported by McPhail and Lindsey (1970) for other western populations of round whitefish. On this character they resemble eastern North American populations.

Mountain whitefish populations always had lower mean vertebral counts than round whitefish (Fig. 2F), although overlap in ranges was occasionally found. One round whitefish from Finlayson Lake (21) had 59 vertebrae, while at the other extreme, one round whitefish from Aishihik Lake (1) was excluded from the vertebrae analysis because it had 68 vertebrae. This is the highest recorded count for this species by either Scott and Crossman (1973) or McPhail and Lindsey (1970).

Mountain whitefish generally had fewer LLS than round whitefish (Fig. 2G), although there was sometimes overlap in ranges.

The range of the CPS of the two species overlapped in only one instance, in which a mountain whitefish from Waterton (25) had 23 scales (Fig. 2H).

Mountain whitefish tended to have more gill rakers in both the upper and lower limbs than did round whitefish (Fig. 2I, J). Confidence intervals never overlapped in LGR or TGR (Fig. 2K). Ranges overlapped somewhat in LGR and TGR with more overlap in UGR.

Figure 2. Ranges,and means (longest horizontal bar) and their 95% confidence intervals (boxes), of various counts and measurements of round (closed boxes) and mountain whitefish (open boxes). "S" represents sympatric lakes

2-A. Dorsal fin rays

2-B. Anal fin rays

2-C. Pelvic fin rays

2-D. Pectoral fin rays

2-E. Pyloric caeca count

2-F. Vertebrae

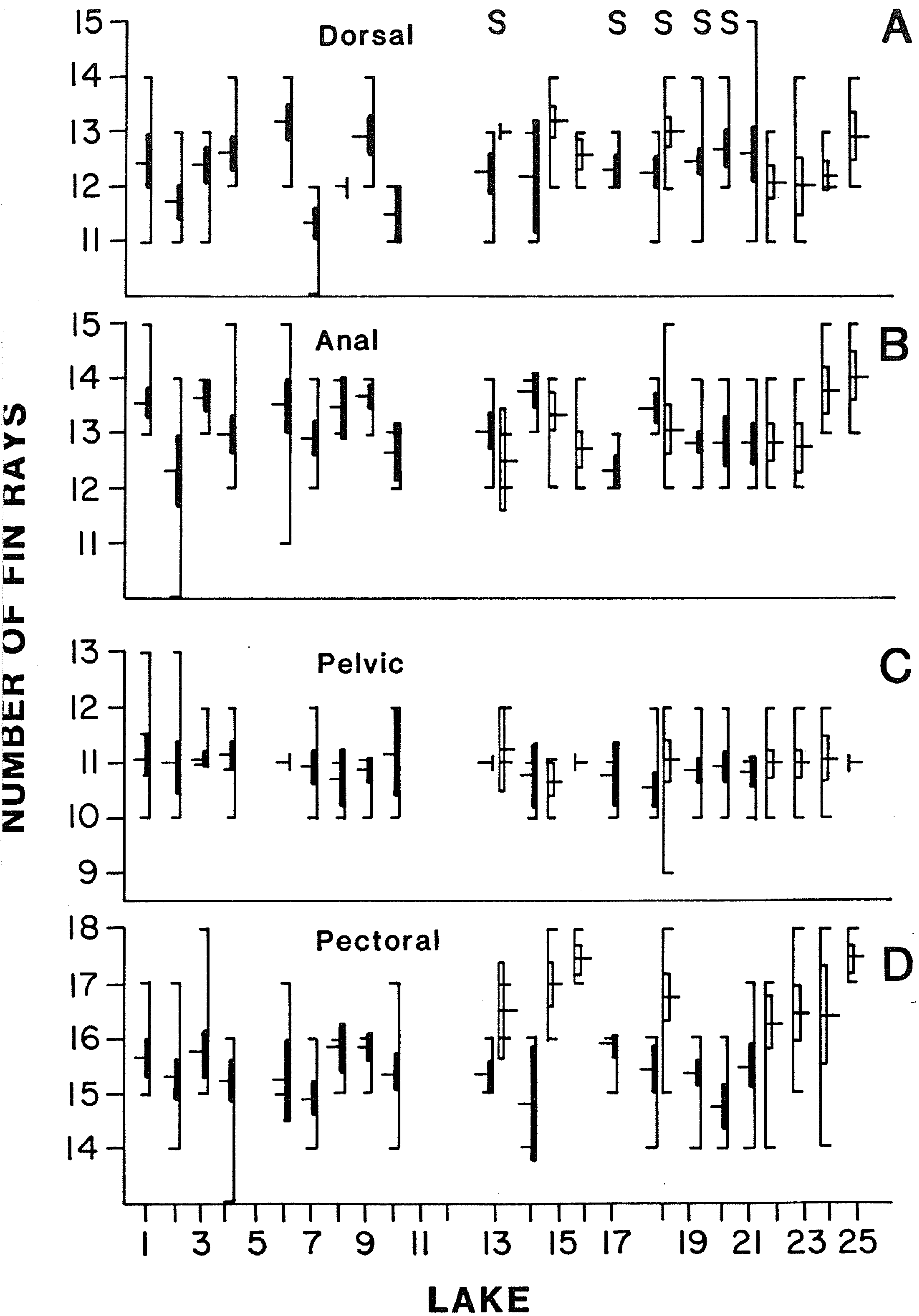
2-G. Lateral line scales

2-H. Caudal peduncle scale count

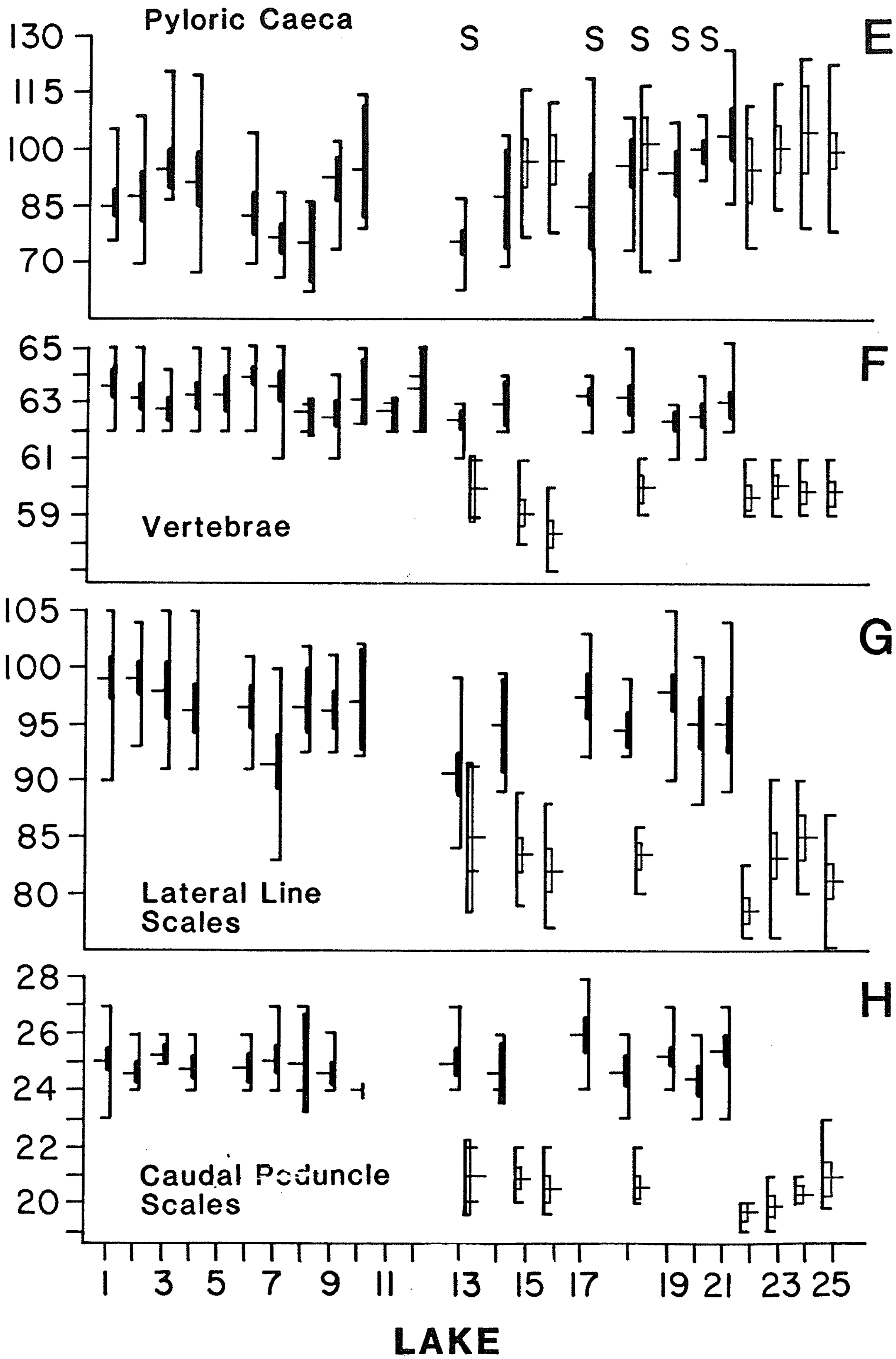
2-I. Lower limb gill rakers

2-K. Total gill raker count

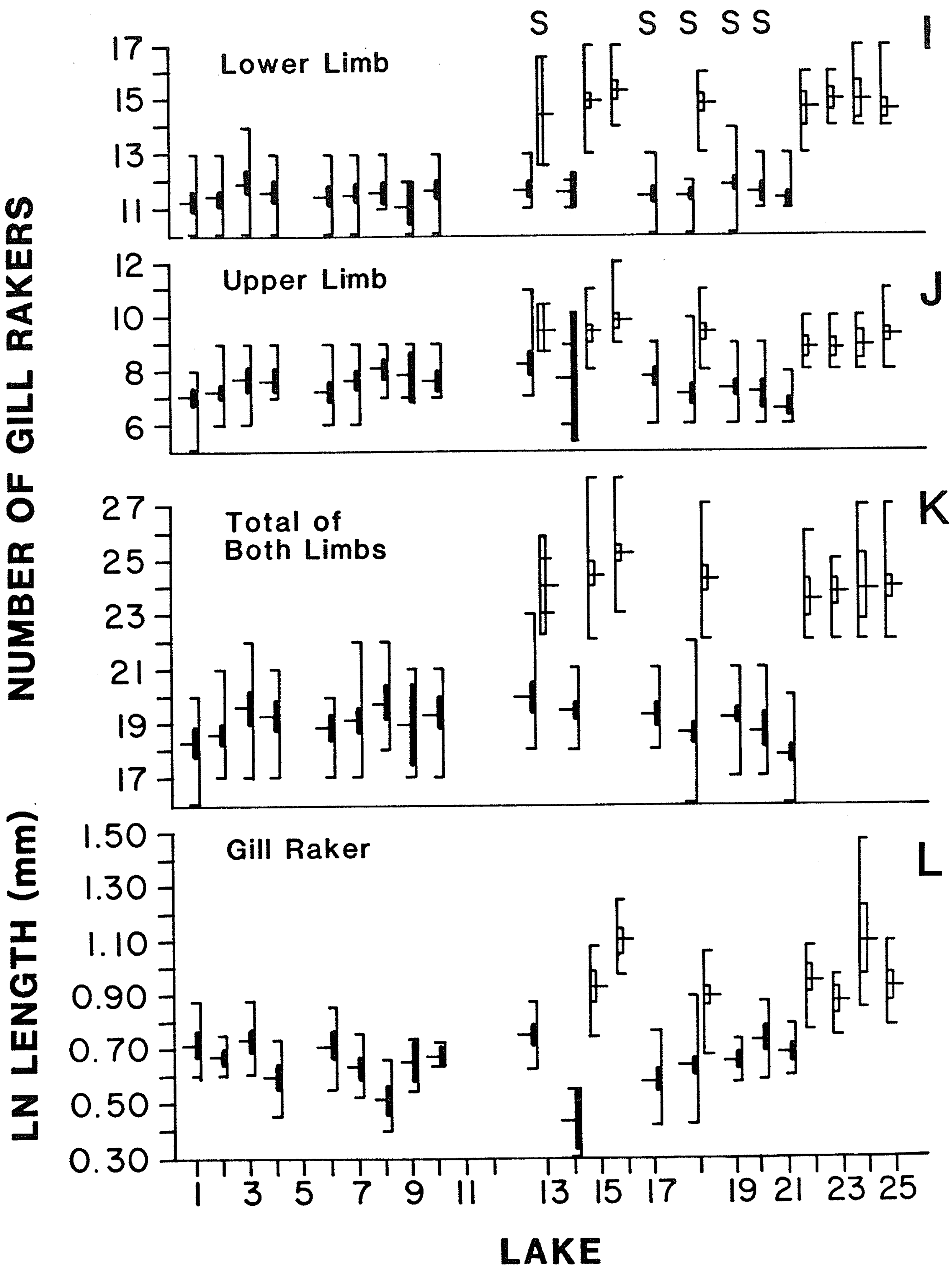
2-L. Gill raker length



NUMBER OF FIN RAYS
Dorsal
A
S
S S S S
15
14
13
12
11
Anal
B
15
14
13
12
11
Pelvic
C
13
12
11
10
9
Pectoral
D
18
17
16
15
14
1 3 5 7 9 11 13 15 17 19 21 23 25
LAKE



Pyloric Caeca
E
S S S S S
130
115
100
85
70
F
65
63
61
59
Vertebrae
G
105
100
95
90
85
80
Lateral Line Scales
H
28
26
24
22
20
Caudal Peduncle Scales
1 3 5 7 9 11 13 15 17 19 21 23 25
LAKE



S S S S S
Lower Limb
I
17
15
13
11
Upper Limb
J
12
10
8
6
Total of Both Limbs
K
27
25
23
21
19
17
Gill Raker
L
1.50
1.30
1.10
0.90
0.70
0.50
0.30
NUMBER OF GILL RAKERS
LN LENGTH (mm)
1 3 5 7 9 11 13 15 17 19 21 23 25
LAKE

The means of TGR for round whitefish from these lakes all fall within the range of counts given by McPhail and Lindsey (1970) for western populations.

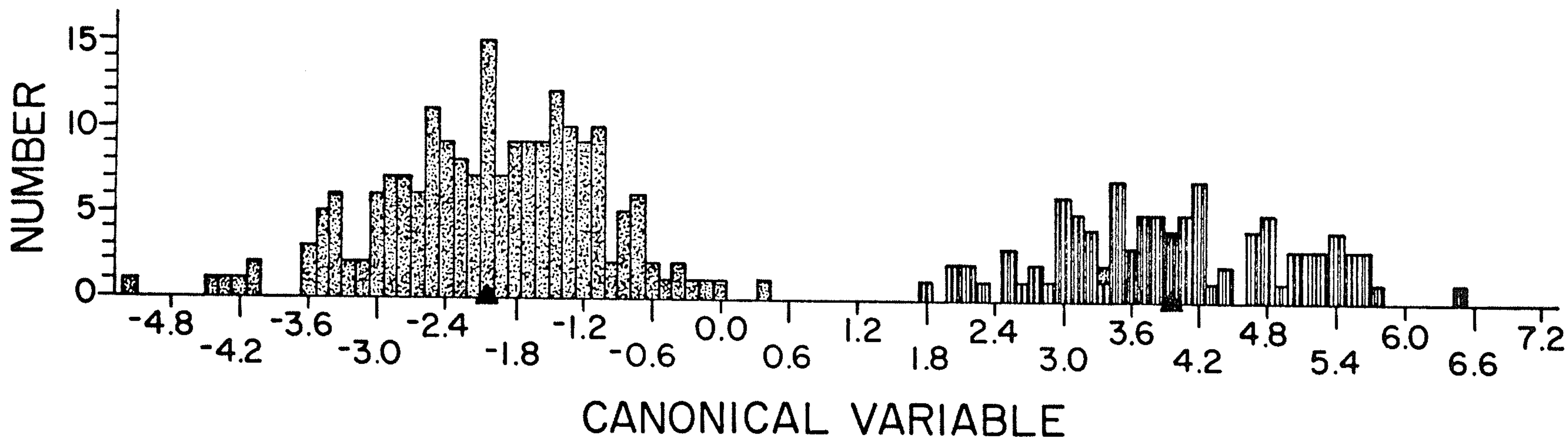
Mountain whitefish always had longer mean gill raker lengths than did round whitefish; there was no overlap of confidence intervals (Fig. 2L).

Specimens were placed into two groups on the basis of CPS; those with a count ≤ 22 were identified as mountain whitefish, while those with a count >22 were identified as round whitefish. Using discriminant function analysis and either LGR or V, specimens were correctly classified into these groups 96.7 and 97.5% of the time, respectively. Using LGR, V and LLS 100% of the mountain whitefish and 99.5% of the round whitefish were correctly classified. Histograms of the canonical variables from this run showed that the one fish initially identified as a round whitefish by CPS was definitely a mountain whiteifsh (Fig. 3) (Wilks' lambda=0.1114; df=3,1,295). The counts for the following variables did not contribute to the separation of the two species: A, P2, PC, UGR and TGR. The latter two counts do differ significantly between the species but their contribution is minimal after their correlation with LGR is removed.

There was no evidence of hybridization. The canonical variable histogram shows two distinct groups with no points in the intermediate area (Fig. 3).

All possible subset regression using latitude, longitude, elevation, MJT and area as independent variables and each of 12 dependent morphological variables yielded the values given in Table 2 and 3 for mountain and round whitefish, respectively. Little of the variation in the dependent variables of round whitefish was explained by these 5 environmental variables. The highest R^2 was 14.7% for that of LLS. Eight of the values for R^2 were $<9.9\%$. The R^2 values were considerably higher for mountain whitefish. The highest value was that of 37.6% for GRL. Only 5 R^2's were $<9.9\%$.

Figure 3. Canonical variable histogram of round whitefish (stippling) and mountain whitefish (vertical stripes) using LGR, V and LLS. (Group means indicated by a triangle).



NUMBER
15
10
5
0
-4.8
-4.2
-3.6
-3.0
-2.4
-1.8
-1.2
-0.6
0.0
0.6
1.2
1.8
2.4
3.0
3.6
4.2
4.8
5.4
6.0
6.6
7.2
CANONICAL VARIABLE

Table 2. All possible subset regression results for mountain whitefish using 5 environmental variables. Those variables contributing to R^2 are indicated by a '+'.

Y	# of Cases	Latitude	Longitude	Elevation	$\bar{x}$ July Temperature	Area	R^2
D	101	+		+			0.338
A	99	+		+		+	0.352
P2	101			+			0.027[1,2]
P1	101			+			0.117[1]
PC	103				+		0.041[1,2]
V	101	+	+				0.143[1]
LLS	101		+	+		+	0.189[1]
CPS	101			+			0.217
LGR	181	+					0.030[1,2]
UGR	181	+	+				0.097[1]
TGR	181	+					0.055[1,2]
GRL	114	+	+	+	+	+	0.376

[1]Denotes R^2 low enough to make interpretations from t test meaningful.

[2]Denotes R^2 too low for these environmental variables to be considered as covariates.